UNIVERZITA PALACKÉHO V OLOMOUCI
PŘÍRODOVĚDECKÁ FAKULTA

Fylogeneze, klasifikace a diverzita Elateriformia (Insecta: Coleoptera) se zaměřením na čeleď Elateridae a tribus Drilini

HABILITAČNÍ PRÁCE
Obor: Zoologie

RNDr. Robin Kundrata, Ph.D.
Katedra zoologie PřF UP v Olomouci

Olomouc 2019

Prohlašuji, že jsem předloženou habilitační práci vypracoval samostatně s použitím řádně citovaných literárních zdrojů.

V Olomouci dne 1. 3. 2019

RNDr. Robin Kundrata, Ph.D.

Obsah

1. Úvod

Hmyz je nejpočetnější a nejdiverzifikovanější skupinou živočichů a pravděpodobně tvoří více než polovinu globální biodiverzity (Foottit & Adler 2009, Stork *et al.* 2015). Odhady počtu druhů hmyzu se dlouhodobě liší napříč studiemi, dnes však převládají hodnoty kolem šesti milionů (Novotný *et al.* 2002, Basset *et al.* 2012, Stork *et al.* 2015, Larsen *et al.* 2017). Naprostá většina hmyzí rozmanitosti je soustředěna do skupiny Holometabola, kam patří linie s proměnou dokonalou - tedy ty, u nichž hraje v ontogenezi zásadní roli stádium kukly. Zde patří také čtyři největší řády hmyzu, jenž překonaly v počtu dosud popsaných druhů hranici 100 000, a to Coleoptera (brouci), Hymenoptera (blanokřídlí), Diptera (dvoukřídlí) a Lepidoptera (motýli) (Grimaldi & Engel 2005).

Řád Coleoptera je dlouhodobě považovaný za druhově nejbohatší a evolučně nejúspěšnější skupinu živočichů na Zemi (Farrell 1998, Grove & Stork 2000, Hunt *et al.* 2007, Ślipiński *et al.* 2011). Předpokládáme, že takovou diverzitu pravděpodobně umožnila přeměna předních křídel ve sklerotizované krovky, které v koadaptaci s pterothoraxem a abdomenem kryjí metathorakální a abdominální spirakuly (vyústění dýchací soustavy na povrchu těla), čímž zabraňují ztrátám vody (Cloudsley-Thompson 1965, Lawrence & Britton 1991). Tato adaptace, umožňující skrytý způsob života, spolu se schopností disperze pomocí aktivního letu jsou další klíčové faktory, které umožnily broukům osídlit téměř všechny dostupné ekologické niky (Grimaldi & Engel 2005). Obrovská diverzita řádu Coleoptera také pravděpodobně úzce souvisí se vznikem angiospermních rostlin a jejich diverzifikací v období druhohorní křídy, přestože dnešní studie opakovaně potvrdily, že většina hlavních linií Coleoptera již existovala dávno před vznikem a následnou dominancí angiospermních rostlin (Farrell 1998, Hunt *et al.* 2007, Wang *et al.* 2013, Ahrens *et al.* 2014, Zhang *et al.* 2018).

Přestože některé recentní studie naznačují, že diverzita dosud nepopsaných, zejména parazitoidních, skupin Hymenoptera může převyšovat celkový počet druhů Coleoptera (např. Forbes *et al.* 2018), brouci s přehledem drží první místo v počtu formálně popsaných druhů. Coleoptera totiž tvoří čtvrtinu veškeré popsané biodiverzity - z přibližně 1,5 milionu dosud popsaných druhů organismů jich 390 000 patří právě mezi brouky (Hammond 1992, Costello *et al.* 2012, Bocák *et al.* 2014), přičemž další řády v pořadí, t.j. blanokřídlí, dvoukřídlí i motýli, obsahují každý asi 150 000 popsaných druhů (Grimaldi & Engel 2005, Foottit & Adler 2009). I pokud vezmeme v úvahu pouze ty střídmější odhady celkového počtu druhů brouků (přibližně 1,5 milionu; Stork *et al.* 2015), naprostá většina diverzity tohoto řádu stále zůstává neobjevena a čeká na formální popis. Není proto žádným překvapením, že ročně jsou popisovány stovky nových druhů brouků ze všech zoogeografických regionů včetně entomologicky nejvíce probádaných oblastí, jako je například Evropa (Fontaine *et al.* 2012). Přestože dnes stále převládají menší či středně rozsáhlé taxonomické revize, výjimkou již nejsou ani studie popisující stovku nových druhů v jediné publikaci (Riedel *et al.* 2013, 2014), a to zejména z tropických oblastí, kde je předpokládána nejvyšší biodiverzita (McKenna & Farrell 2006).

Rapidní nárůst počtu nově objevených linií brouků a tím i neustále se zvětšující znalosti o jejich morfologické diverzitě se logicky promítají do klasifikace tohoto řádu, která od éry prvních systematiků prošla dramatickými změnami (Lawrence *et al.* 1995b, Lawrence 2016a). Nesčetné systematicky a fylogeneticky zaměřené práce založené jak na morfologických (Crowson 1955; Lawrence & Newton 1982, 1995; Lawrence *et al.* 2011), tak i na molekulárních datech (Hunt *et al.* 2007, Bocák *et al.* 2014, McKenna *et al.* 2015, Zhang *et al.* 2018), zaznamenaly obrovský pokrok ve studiu fylogeneze a vyšší klasifikace Coleoptera, přestože některé otázky i po mnoha letech výzkumu zůstávají ne zcela uspokojivě zodpovězeny. Rovněž klasifikace na úrovni čeledí a níže je v mnoha skupinách dosud neustálená a často zastaralá, částečně kvůli nedostatečně prozkoumané diverzitě dané linie, problematické interpretaci morfologických znaků (např. problémy s homoplastickými znaky), obtížně přístupnému typovému materiálu či nedostatku odborníků. Znalost fylogenetických vztahů mezi jednotlivými skupinami a tím i vytvoření přirozené klasifikace jsou však důležitým stavebním kamenem pro následný výzkum evolučně zajímavých linií, důležitých hospodářských škůdců a ochranářsky významných taxonů.

V předložené habilitační práci se zabývám fylogenetickými vztahy, evolucí, systematikou, klasifikací a diverzitou vybraných linií v rámci série Elateriformia, a to na třech taxonomických úrovních. Habilitační práce je vypracována jako obecný přehled řešené problematiky a do širšího kontextu zasazený komentář k souboru 13 původních vědeckých prací (**Přílohy 1–13**), z nichž 12 bylo publikováno v mezinárodních impaktovaných vědeckých časopisech a jedna byla nedávno přijata. V první části popisuji fylogenezi, historický vývoj klasifikace a diverzitu série Elateriformia, což je morfologicky i ekologicky výrazně heterogenní skupina přibližně 43 500 popsaných druhů řazených do pěti nadčeledí. Zástupci těchto linií osídlili suchozemské i vodní prostředí, často jsou ovlivněni neotenií a dokázali vyvinout řadu úspěšných antipredačních strategií včetně bioluminiscence, mimikry a silně sklerotizovaného těla v kombinaci s tzv. klikacím mechanismem. V této části tak shrnuji veškeré dosavadní znalosti o této evolučně zajímavé skupině, včetně objasnění fylogenetické pozice starobylé čeledi Artematopodidae, pro vědu zcela nové unikátní čeledi Iberobaeniidae a také enigmatické skupiny Podabrocephalinae, o jejímž postavení v systému se mezi vědci donedávna vedly spory. Tato témata jsou pak detailněji rozebrána v **Přílohách 1–4**.

V druhé části práce se zabývám fylogenezí a historickým vývojem morfologicky heterogenní a klasifikačně neustálené čeledi kovaříkovitých (Elateridae), která se svými přibližně 10 000 popsanými druhy tvoří podstatnou část diverzity série Elateriformia a patří do ní i významní zemědělští škůdci. Současně diskutuji paralelní evoluci některých fenotypových znaků, které bývaly v minulosti často používány pro klasifikaci Elateridae, přestože se ukázaly jako homoplastické. Dále se také zabývám testováním monofylie podčeledí Agrypninae a Pityobiinae, okolnostmi popisu nové podčeledi Parablacinae z Australasijské zoogeografické oblasti, fylogenetickou pozicí převážně tropických Tetralobinae, mezi něž patří vůbec největší kovaříkovití brouci světa, a také molekulární fylogenezí a supraspecifickou klasifikací podčeledi Cardiophorinae. Tato témata jsou předmětem **Příloh 5–7**.

V třetí části mé práce popisuji fylogenezi a historický vývoj klasifikace tribu Drilini, který v minulosti tvořil vlastní čeleď, ale dnes je řazen mezi kovaříkovité brouky. Tato linie je velmi zajímavá z evolučního hlediska, neboť patří mezi neotenické skupiny, u nichž samci jsou plně vyvinutí a letuschopní, kdežto samice svým vzhledem připomínají larvy a jsou zcela bezkřídlé. Dravé larvy se živí suchozemskými plži, a proto jsou vhodným modelem pro studium interakcí mezi predátorem a kořistí. Kromě toho se v práci zabývám historickým vznikem a diverzifikací této skupiny v oblasti Středozemního moře s ohledem na geologickou minulost regionu, dále pak diverzitou a datováním vzniku jednotlivých linií Drilini v oblasti tropické Afriky, a také evolucí morfologických znaků souvisejících s přechodem od silně sklerotizovaného po měkké tělo. Tato témata jsou podrobně rozepsána v **Přílohách 8–13**.

Přílohy v této habilitační práci jsou reprezentativním výběrem mé dosavadní publikační činnosti na téma „Fylogeneze, klasifikace a diverzita Elateriformia (Insecta: Coleoptera) se zaměřením na čeleď Elateridae a tribus Drilini”, přičemž v samotném textu jsou zmíněny též výsledky z některých dalších mnou publikovaných prací na výše zmíněné téma, které však netvoří přímou součást této habilitační práce.

2. Fylogeneze, klasifikace a diverzita Elateriformia

(Přílohy 1–4)

2.1. Pozice Elateriformia v systému Coleoptera

Řád Coleoptera se dělí na čtyři nestejně velké podřády obsahující více než 180 čeledí (Lawrence & Newton 1995, Bocák *et al.* 2014, McKenna *et al.* 2015). Archostemata a Myxophaga obsahují dohromady pouze přes 130 popsaných druhů a spolu s Adephaga zahrnují přibližně pouhých 15 % celkové diverzity řádu (Bocák *et al.* 2014). Druhově nejbohatší podřád Polyphaga se dále dělí na 17 nadčeledí rozdělených do sedmi sérií, t.j. Staphyliniformia, Scarabaeiformia, Scirtiformia, Elateriformia, Derodontiformia, Bostrichiformia a Cucujiformia (Lawrence & Newton 1995, Bouchard *et al.* 2011, Bocák *et al.* 2014, Lawrence 2016a, Kusý *et al.* 2018a). Série Elateriformia dnes obsahuje pět nadčeledí (Rhinorhipoidea, Dascilloidea, Byrhoidea, Buprestoidea a Elateroidea), které však dohromady nejsou definovány žádnou unikátní synapomorfií, což mimochodem také přispělo k poměrně chaotické a v průběhu historie často se měnící klasifikaci skupiny (Beutel *et al.* 2016). Elateriformia jsou morfologicky i ekologicky extrémně heterogenní skupinou obsahující mimo jiné silně sklerotizované linie s přítomností tzv. klikacího mechanismu (např. Elateridae, Eucnemidae a další), linie s měkkým tělem a častou přítomností mimikry, bioluminiscence a neotenie (např. Lampyridae, Cantharidae, Lycidae a další), vyklenuté mechožravé zástupce Byrrhidae, herbivorní krasce (Buprestidae) a povětšinou s vodním prostředím spojené dryopoidní skupiny. Tato série v dřívějších klasifikacích zahrnovala i čeledi dnešních Scirtiformia, tehdy souhrnně nazývané buď jako Eucinetoidea (Lawrence & Newton 1982) nebo Scirtotidea (Lawrence & Newton 1995). Moderní molekulární studie však dokázaly, že scirtiformní linie nejen že netvoří monofyletickou skupinu, ale že patří mezi vůbec nejstarší klády v evoluci Coleoptera (Hunt *et al.* 2007, Bocák *et al.* 2014, McKenna *et al.* 2015, Zhang *et al.* 2018, Cai *et al.* 2019). Lawrence & Newton (1982) zahrnuli do jejich široce pojaté definice Elateriformia také nadčeleď Scarabaeoidea (roháčovití, chrobákovití, vrubounovití a další), která má však ve většině klasifikací svou vlastní sérii a ani moderní molekulární analýzy nepotvrdily jejich sesterský vztah s Elateriformia (Bocák *et al.* 2014, Kundrata *et al.* 2014a, McKenna *et al.* 2015, Timmermans *et al.* 2016, Zhang *et al.* 2018). Výsledky molekulárně založených studií jsou zde v rozporu s doposud nejrozsáhlejší analýzou morfologických znaků Coleoptera (Lawrence *et al.* 2011), která opět indikovala blízké fylogenetické vztahy mezi Elateriformia a Scarabaeiformia. Dle nejnovějších hypotéz jsou Elateriformia buď sesterskou skupinou k Bostrichiformia (Hunt *et al.* 2007, Bocák *et al.* 2014), části Bostrichiformia (Kundrata *et al.* 2014a), Bostrichiformia + Cucujiformia (McKenna *et al.* 2015), nebo Polyphaga bez Scirtiformia a Derodontidae (Zhang *et al.* 2018). Doposud nevyjasněný je též vztah Elateriformia k druhově nepočetné čeledi Nosodendridae. Tato čeleď se v některých analýzách objevuje v blízkosti Elateriformia (Kundrata *et al.* 2014a, McKenna *et al.* 2015), ale její skutečná pozice v systému zůstává nejasná (Kusý *et al.* 2018a).

2.2. Fylogeneze a klasifikace Elateriformia

Série Elateriformia prošla od svého uvedení až po dnešek velmi dlouhou a komplikovanou řadou více či méně zásadních změn. Její definice se mnohokrát měnila a některé klasifikační problémy nejsou vyřešeny dodnes (Beutel *et al.* 2016, Kundrata *et al.* 2017b [**Příloha 3**]). Sérii Elateriformia poprvé představil Crowson (1960), jenž původně vycházel z definice bývalých Dascilliformia (Crowson 1955), které redefinoval odstraněním Eucinetoidea (dnešní Scirotidea) a přesunem Dascilloidea do Scarabaeiformia. Původní série tedy obsahovala nadčeledi Rhipiceroidea (čeledi Rhipiceridae, Callirhipidae), Byrrhoidea (Byrrhidae), Dryopoidea (Artematopodidae a skupiny vázané převážně na vodní prostředí: Dryopidae, Psephenidae, Ptilodactylidae, Heteroceridae, Limnichidae, Chelonariidae, Elmidae), Buprestoidea (Buprestidae), Elateroidea (skupiny se silně sklerotizovaným tělem: Elateridae, Cebrionidae, Throscidae, Cerophytidae, Eucnemidae, Perothopidae) a Cantharoidea (Brachypsectridae a skupiny se slabě sklerotizovaným tělem: Karumiidae, Cantharidae, Lampyridae, Lycidae, Omalisidae, Drilidae, Phengodidae, Telegeusidae) (Crowson 1960). Crowson (1971) redefinoval Dascilloidea, kam spolu s Dascillidae zařadil i Rhipiceridae (dříve v Rhipiceroidea) a Karumiidae (dříve v Cantharoidea). Později Crowson (1972) redefinoval také Cantharoidea. Přesunul zde rod *Cneoglossa* Guérin-Menéville z Dascillidae a vytvořil pro něj vlastní čeleď Cneoglossidae. Pro rod *Plastocerus* Schaum, který byl dříve zařazen v Elateroidea, vytvořil v Cantharoidea čeleď Plastoceridae, a některé rody dříve řazené v čeledích Lampyridae, Cantharidae a Drilidae spojil do další nové čeledi Omethidae s třemi podčeleděmi. O rok později Crowson (1973) zavedl v rámci Elateriformia novou nadčeleď Artematopoidea, do které zařadil tři čeledi, které byly dříve řazeny do Dryopoidea (Artematopodidae, tehdy chybně psané jako Artematopidae), Rhipiceroidea

(Callirhipidae) a Cantharoidea (Brachypsectridae). Hlavac (1975) poté redefinoval tuto nadčeleď a vyjmul z ní Callirhipidae, přičemž zde naopak zařadil Cerophytidae. Kasap & Crowson (1975) poukázali na fakt, že Brachypsectridae jsou spíše příbuzní Cantharoidea (kam byli skutečně dříve řazeni) než Artematopoidea. V rámci Dryopoidea také zavedli čeledi Eulichadidae a Lutrochidae, jejíž zástupci byli do té doby klasifikováni v čeledích Ptilodactylidae a Limnichidae (Crowson 1955, 1960). Crowson (1978) poté diskutoval pravděpodobné fylogenetické vztahy v rámci Dryopoidea.

Lawrence & Newton (1982) ve svém souhrnném díle o evoluci a klasifikaci řádu Coleoptera oddefinovali Elateriformia v dosud nejširším pojetí. Přetáhli sem opět Eucinetoidea (čeledi Eucinetidae, Clambidae a Scirtidae) a navíc zde zařadili i celé Scarabaeoidea. V rámci série Elateriformia pak poukázali na blízký fylogenetický vztah mezi Byrrhoidea a Buprestoidea a dále také na základě podobné morfologie larev i dospělců navrhli monofylii Artematopoidea + Elateroidea + Cantharoidea. Lawrence (1988) popsal monotypickou čeleď Rhinorhipidae a zkoumal její postavení v rámci Elateriformia pomocí analýzy morfologických znaků. Ve svém díle opět redefinoval sérii Elateriformia, přičemž Buprestoidea a část Dryopoidea včetně Dryopidae přesunul do Byrrhoidea, pro zbývající čeledi Dryopoidea použil název Psephenoidea, a také vytvořil jednu velkou nadčeleď Elateroidea *sensu lato* pro všechny čeledi dříve řazené do Artematopoidea, Elateroidea a Cantharoidea. Série Elateriformia tedy tentokrát obsahovala čtyři nadčeledi - Dascilloidea (čeledi Dascillidae a Rhipiceridae), Byrrhoidea (Buprestidae, Byrrhidae, Dryopidae, Lutrochidae, Elmidae, Heteroceridae, Limnichidae), Psephenoidea (Psephenidae, Callirhipidae, Eulichadidae, Cneoglossidae, Ptlodactylidae, Chelonariidae) a Elateroidea (Rhinorhipidae, Artematopodidae, Elateridae (+ Cebrionidae), Eucnemidae, Throscidae, Cerophytidae, Brachypsectridae, Plastoceridae, Drilidae, Omalisidae, Lycidae, Phengodidae, Telegeusidae, Lampyridae, Omethidae, Cantharidae). Lawrence & Britton (1991) opět vyčlenili Buprestidae do samostatné nadčeledi Buprestoidea a spojili Byrrhoidea a Psephenoidea do jediné skupiny.

Beutel (1995) analyzoval morfologické larvální znaky napříč skupinami klasifikovanými v Elateriformia a potvrdil monofylii široce definovaných Elateroidea (tedy včetně bývalých Artematopoidea a Cantharoidea). Naopak ale poukázal na to, že ani Dryopoidea *sensu* Crowson (1955, 1960) či Dryopoidea a Psephenoidea *sensu* Lawrence (1988) nejsou přirozené taxony. Namísto toho čeledi řazené do těchto skupin tvořily čtyři samostatné klády. Lawrence *et al.* (1995a) opět redefinovali limity Elateriformia, když zde zařadili také Scirtoidea (= Eucinetoidea) včetně nově popsané čeledi Decliniidae. Ani jedna z jejich analýz nepodpořila dříve definované taxony Byrrhoidea, Dryopoidea a Psephenoidea. Lawrence & Newton (1995) ve svém přehledovém díle věnovaném biologii, fylogenezi a klasifikaci Coleoptera členili Elateriformia do pěti nadčeledí - Scirtoidea, Dascilloidea, Buprestoidea, Byrrhoidea (včetně Dyropoidea a Psephenoidea) a Elateroidea. Dvě monotypické čeledi, Podabrocephalidae (Indie) a Rhinorhipidae (Austrálie), jejichž pozice v systému byla dlouhodobě neustálená, byly klasifikovány jako Elateriformia *incertae sedis*. Costa *et al.* (1999) provedli kladistickou morfologickou analýzu zástupců Byrrhoidea *sensu* Lawrence & Newton (1995). Výsledky zpochybnily monofylii Ptilodactylidae, Elmidae a Limnichidae, přičemž čeledi Eulichadidae a Callirhipidae byly vyřazeny z Byrrhoidea jako Elateriformia *incertae sedis*. Pozdější autoři však tyto výsledky neakceptovali a v hlavním souhrnném díle o řádu Coleoptera, Handbook of Zoology (Beutel & Leschen 2005), tak byla použita klasifikace dle Lawrence & Newtona (1995).

Nástup moderních molekulárních metod znamenal mimo jiné další možnosti testování fylogenetických vztahů mezi jednotlivmi skupinami v rámci Elateriformia. Sagegami-Oba *et al.* (2007b) zkoumali evoluci aposematismu a bioluminiscence u elateroidních skupin na základě sekvencí jaderného markeru 18S. Elateroidea v jejich analýzách netvořili monofylum, pravděpodobně kvůli použití pouze jediného markeru. Bocáková *et al.* (2007) zkoumali evoluci bioluminiscence a neotenie v rámci Elateriformia, přičemž použili dva jaderné a dva mitochondriální markery. Do té doby se předpokládalo, že jak měkkotělé cantharoidní skupiny, tak i silně sklerotizované linie s klikacím mechanismem tvoří monofyla uvnitř široce definovaných Elateroidea, avšak tato studie přinesla velmi zajímavou informaci o jejich vzájemné nemonofyletičnosti. Elateridae tvořili spolu s většinou měkkotělých cantharoidních skupin terminální linie, zatímco zbytek silně sklerotizovaných skupin spolu s několika cantharoidními liniemi tvořil bazální klády. Elateridae konzistentně tvořili klád s měkkotělými čeleděmi Drilidae, Omalisidae, Phengodidae a Rhagophthalmidae. Buprestoidea okupovali pozici uvnitř části byrrhoidních skupin. Hunt *et al.* (2007) zkoumali fylogenezi celého řádu Coleoptera na základě analýz tří genů, přičemž prokázali monofylii Elateriformia a všech nadčeledí kromě Byrrhoidea, kdy Byrrhidae a zbytek (= Dryopoidea *sensu* Crowson) tvořili samostatné větve. Jimi publikovaná topologie potvrdila výsledky předchozí práce ohledně nemonofyletičnosti cantharoidních skupin v rámci Elateroidea.

Druhý díl Handbook of Zoology přinesl několik změn v klasifikaci Elateriformia (Lawrence *et al.* 2010a). Rhinorhipidae byli bez komentáře vyjmuti z *incertae sedis* a vráceni do Elateroidea, kdežto Cydistinae (dříve v Dascillidae nebo Phengodidae), *Neocrowsonia* Kistner & Abdel-Galil (Throscidae) a několik linií světluškovitých (Lampyridae) byli naopak do Elateriformia *incertae sedis* nově zařazeni. Lawrence *et al.* (2011) publikovali dosud poslední velkou fylogenezi Coleoptera založenou výhradně na morfologických znacích. Ve své práci analyzovali kombinaci znaků larválních stádií i dospělců a dospěli k podobnému výsledku jako studie z 80. let (Lawrence & Newton 1982, Lawrence 1988). Jejich výsledná topologie je však v příkrém rozporu s výsledky dnešních molekulárních studií. Uvnitř Elateriformia se opět objevili Scarabaeoidea, sesterští k Dascillidae. Klád Rhipiceridae + Rhinorhipidae byl sesterský ke zbytku Elateriformia, čímž se Dascilloidea (t.j. Dascillidae a Rhipiceridae) stali nemonofyletickou skupinou. Byrrhoidea byli rozděleni na dvě skupiny, přičemž první navíc obsahovala Buprestidae a druhá odpovídala Psephenoidea *sensu* Lawrence (1988). Artematopodidae tvořili větev sesterskou ke zbytku Elateroidea a Podabrocephalidae byli sesterští ke kládu měkkotělých skupin odpovídajícímu historické nadčeledi Cantharoidea. Zřejmý rozpor mezi výsledky této studie a všemi dosavadními molekulárně-fylogenetickými analýzami poukázal na zřejmé limity kódování morfologických znaků u Elateriformia v důsledku mnohonásobného vzniku měkkotělých neotenních skupin a s tím spojeným paralelním vznikem korelovaných morfologických modifikací, které tak vytvářejí falešný fylogenetický signál (Bocáková *et al.* 2007, Kundrata & Bocák 2011a, Kundrata *et al.* 2014a, Bocák *et al.* 2018).

Kundrata & Bocák (2011a) zkoumali fylogenetické vztahy uvnitř Elateroidea na základě čtyř molekulárních markerů a zrušili měkkotělou čeleď Drilidae, když ji přesunuli do Elateridae a klasifikovali ji jako tribus v podčeledi Agrypninae. Tato studie také potvrdila blízkou příbuznost silně sklerotizovaných Elateridae s měkkotělými čeleděmi Omalisidae, Phengodidae a Rhagophthalmidae. Timmermans & Vogler (2012) zkoumali vztahy mezi jednotlivými klády Elateriformia za pomoci mitochondriálních genomů, avšak jejich analýzy nepřinesly jednoznačné výsledky. Stromy z různých analýz vykazovaly odlišné topologie, ale nadčeleď Byrrhoidea nebyla nikdy monofyletická. Kundrata *et al.* (2013) [**Příloha 1**] zkoumali fylogenetickou pozici menší čeledi Artematopodidae, která byla na základě morfologických znaků larev i dospělců dříve řazena v Dascilloidea, Dryopoidea, Artematopoidea i Elateroidea. Přestože některé novější morfologicky zaměřené práce považovaly Artematopodidae za jeden z bazálních taxonů v Elateroidea, dosavadní výsledky nebyly zcela jednoznačné a chyběla k tomu robustní fylogenetická hypotéza založená na jiných než morfologických datech. Sagegami-Oba *et al.* (2007b) sice ve své studii použili jeden gen jednoho druhu rodu *Eurypogon* Motschulsky, ale jejich výsledná topologie zasadila Artematopodidae do statisticky nepodpořeného kládu obsahujícího některé z byrrhoidních linií a Buprestoidea, což byl pravděpodobně artefakt analýzy. Kundrata *et al.* (2013)

[**Příloha 1**] se rozhodli tento dlouhodobý problém vyřešit, přičemž osekvenovali čtyři standardně používané geny pro tři japonské druhy rodu *Eurypogon* a potvrdili pozici Artematopodidae na bázi Elateroidea, ať už jako samostatné větve nebo v jednom kládu s měkkotělými čeleděmi Omethidae a Telegeusidae. Výsledky této studie pak byly potvrzeny v celé řadě následujících molekulárně-fylogenetických analýz. Bocák *et al.* (2014) dali dohromady čtyřgenový datový soubor o téměř 8500 zástupcích celého řádu Coleoptera. Jejich analýza potvrdila monofylii Elateriformia s Dascilloidea sesterskými ke zbytku skupiny, a s Buprestoidea uvnitř Byrrhoidea. Čeledi Artematopodidae, Omethidae a Telegeusidae opět tvořily bazální skupiny v Elateroidea, a Elateridae tvořili klád s měkkotělými čeleděmi Omalisidae, Phengodidae a Rhagophthalmidae.

Kundrata *et al.* (2014a) publikovali dosud nejobsáhlejší molekulární fylogenezi Elateroidea a jako první zařadili do analýz i zástupce čeledi Cerophytidae. Pro své analýzy použili datový soubor, který obsahoval dva jaderné a dva mitochondriální geny pro 513 zástupců Elateriformia (sampling zaměřený především na Elateroidea), z čehož přibližně 300 bylo nově sekvenovaných. Zastoupeny byly všechny hlavní linie Elateroidea kromě čeledí Brachypsectridae, Plastoceridae a Rhinorhipidae, které však dohromady tvoří pouze 0,03 % druhové rozmanitosti skupiny. Autoři potvrdili Dascilloidea jako sesterský klád ke zbytku skupiny a Buprestoidea uvnitř Byrrhoidea, avšak různě koncipované analýzy poukázaly na nejednotnou bazální topologii včetně nedořešeného postavení čeledi Byrrhidae (samostatná linie mimo Dryopoidea versus Byrrhoidea *sensu* Lawrence & Newton 1995). Elateroidní linie byly neformálně rozděleny na druhově méně početné bazální skupiny a tzv. vyšší Elateroidea, zahrnující statisticky vysoce podpořený terminální klád s nejvyšší druhovou diverzitou skupiny. Bazální skupiny zahrnovaly klád Artematopodidae + Telegeusidae + Omethidae, a dále tři samostatné klády tvořené silně sklerotizovanými Eucnemidae, Throscidae a Cerophytidae. Jelikož Telegeusidae konstantně vycházeli uvnitř Omethidae, kteří byli v analýzách reprezentováni všemi třemi podčeleděmi, autoři je zařadili jako čtvrtou podčeleď v rámci Omethidae. Vyšší Elateroidea zahrnovali klády Lycidae, Lampyridae + Cantharidae, Elateridae a Phengodidae + Rhagophthalmidae + Omalisidae. Blízká příbuznost Elateridae s většinou měkkotělých cantharoidních skupin tak byla statisticky robustně podpořena na dosud nejvyšším počtu analyzovaných druhů tohoto kládu. Tyto výsledky byly následně potvrzeny re-analýzou výše zmíněného datového souboru s přidáním dalších systematicky důležitých cantharoidních taxonů (Kundrata *et al.* 2015b [**Příloha 9**]).

McKenna *et al.* (2015) publikovali v té době nejrobustnější molekulární fylogenezi Coleoptera, když zkoumali příbuznost téměř 400 druhů reprezentujících 172 čeledí na základě analýz osmi jaderných genů. Tito autoři poprvé zařadili do molekulárně-fylogenetické analýzy zástupce druhově nepříliš početné čeledi Brachypsectridae, která byla dříve klasifikována v Cantharoidea, Artematopoidea i Elateroidea *sensu stricto* (viz Beutel *et al.* 2016). Výsledky veskrze potvrdily předchozí hypotézy o vyšší klasifikaci skupiny, avšak Buprestoidea nebyli uvnitř Byrrhoidea ale pouze jejich sesterskou skupinou, a topologie vyšších Elateroidea se lišila od většiny ostatních prací. Brachypsectridae však byli zcela jasně součástí bazálních linií Elateroidea, ať už jako sesterská skupina ke kládu obsahujícímu Eucnemidae, Throscidae a Cerophytidae, nebo k celým vyšším Elateroidea. Poprvé sekvenovaní Podabrocephalidae a Cneoglossidae zapadli do kládu s Ptilodactylidae, které tím učinili nemonofyletickou skupinou.

Bocák *et al.* (2016) [**Příloha 2**] publikovali objev nové čeledi Iberobaeniidae z Iberského poloostrova a zkoumali její fylogenetické vztahy pomocí analýzy dvou odlišných datových souborů, z nichž jeden obsahoval čtyřgenovou matici použitou v Kundrata *et al.* (2014a) a druhý byl složen ze dvou jaderných a 13 protein-kódujících mitochondriálních genů. Objev této nové čeledi byl významný z mnoha důvodů, z nichž uvádím alespoň tři nejdůležitější. V 21. století bylo popsáno pouze 11 z celkového počtu přibližně 180 čeledí brouků (počty se mírně liší dle různých klasifikací), ale v naprosté většině se jednalo o již známé linie, které byly na úroveň čeledi povýšeny pouze na základě fylogenetických analýz (např. Robertson *et al.* 2015). Objev naprosto nové a do té doby neznámé linie brouků je tedy poměrně dosti unikátní záležitostí. Druhým důvodem, proč je takový objev významný, je oblast výskytu této čeledi. Z 36 čeledí, které byly popsány po roce 1950, jen jedna jediná pocházela z Evropy, a to Crowsoniellidae (viz Bocák *et al.* 2016, Supplementary Text [**Příloha 2**]). Iberobaeniidae pocházejí z jihu Iberského poloostrova, a přestože obsahují poměrně malé zástupce, je s podivem, že na jednom z entomologicky nejvíce prozkoumaném území světa nebyli do té doby nikdy hlášeni. Třetím důvodem je pak fakt, že zástupci této čeledi jsou neoteničtí (t.j. zachovávají si larvální znaky v dospělosti) a každý objev takové linie nám může pomoci objasnit vznik a evoluci tohoto fenoménu v rámci Elateriformia. Fylogenetické analýzy přesvědčivě zařadili Iberobaeniidae do vyšších Elateroidea jako sesterskou skupinu čeledi Lycidae a molekulární datování ukázalo, že tato reliktní linie vznikla pravděpodobně již ve spodní juře v období druhohor. Tento objev také zdůraznil význam Iberského refugia a celkově Mediteránní oblasti jako horkého místa biodiverzity (Myers *et al.* 2000).

Timmermans *et al.* (2016) zkoumali fylogenetické vztahy uvnitř Coleoptera na základě mitochondriálních genomů. Autoři samozřejmě zařadili do analýz daleko menší počet zástupců Elateriformia než studie věnované přímo této sérii, a tak zde chyběly některé fylogeneticky důležité skupiny. Byla však potvrzena monofylie Elateriformia, Buprestoidea, Elateroidea a Dryopoidea, přičemž Byrrhidae tvořili jeden klád s Dascillidae. V druhém vydání prvního dílu Handbook of Zoology opět došlo k několika změnám v klasifikaci Elateriformia (Lawrence 2016a). Autor sice nereflektoval dřívější změny v klasifikaci Elateroidea (Drilidae, Telegeusidae), ale naopak bez komentáře zařadil Podabrocephalidae jako podčeleď Ptilodactylidae a z Elateriformia *incertae sedis* vyjmul všechny taxony s výjimkou Cydistinae.

Jelikož problematika monofylie, definice a limitů Elateroidea se zdála být až na několik menších výjimek víceméně vyřešena, Kundrata *et al.* (2017b) [**Příloha 3**] se ve své studii zaměřili na analýzu fylogenetických vztahů v systematicky problematické linii Byrrhoidea + Buprestoidea. Jedná se o doposud nejrobustnější datový soubor Elateriformia, obsahující 210 zástupců Byrrhoidea, 89 zástupců Buprestoidea, 160 zástupců Elateroidea a sedm zástupců Dascilloidea. Autoři zahrnuli do analýz naprostou většinu recentních čeledí Elateriformia, pro které použili kombinaci čtyř genů běžně používaných pro studium fylogeneze Coleoptera, čímž umožnili propojení nově generovaných dat s již dříve publikovanými sekvencemi. Přes značné úsilí věnované analytické části práce se nepodařilo zcela uspokojivě vysvětlit vztahy ve skupině a získat statisticky podpořenou základní topologii kládu Byrrhoidea + Buprestoidea. Dascilloidea byli opět sesterskou skupinou kládu zahrnujícího Byrrhoidea (s Buprestoidea uvnitř) a Elateroidea. Fylogenetické vztahy v rámci kládu Byrrhoidea + Buprestoidea nebyly přesvědčivě vyřešeny na základě stávajícího datového souboru a nešlo tedy určit, jak přesně se jednotlivé bazální klády v rámci evoluce skupiny odštěpovaly. Přestože nebylo jasné, jak jsou si jednotlivé klády příbuzné, na základě provedeného setu analýz lze konzistentně pozorovat přítomnost čtyř hlavních kládů, a to Byrrhidae, Dryopidae + Lutrochidae, Buprestoidea, a kládu obsahujícího zbývající byrrhoidní skupiny. Žádná analýza nepodporovala dřívější hypotézy o monofylii jakkoliv definovaných Byrrhoidea, Dryopoidea či Psephenoidea. Většina čeledí vyšla monofyletická, pouze Limnichidae nebyli monofyletičtí ve většině analýz, a Psephenidae a Ptilodactylidae nebyli monofyletičtí v žádné z provedených analýz. Autoři poukázali na fakt, že přestože se jedná o největší datový soubor pro tuto skupinu brouků, výsledky nejenže některé otázky nedokázaly zodpovědět, ale navíc i některé další otázky přinesly. Studie nejspíše ukázala limity klasicky používané kombinace genů a nutnost vytvořit ještě robustnější datový soubor za použití jiných markerů jako jsou mitogenomy či transkriptomy. Je ovšem nutno dodat, že vztahy mezi jednotlivými bazálními liniemi kládu Byrrhoidea + Buprestoidea se doposud nepodařilo s jistotou vyřešit nejen ve studiích obsahujících kombinaci jaderných a mitochondriálních genů (Bocáková *et al.* 2007, Bocák *et al.* 2014, Kundrata *et al.* 2014a, Kundrata *et al.* 2017b [**Příloha 3**]), ale i v těch využívající morfologii (Lawrence *et al.* 1995a, 2011; Costa *et al.* 1999), jaderné protein-kódující geny (McKenna *et al.* 2015) či mitochondriální genomy (Timmermans & Vogler 2012, Timmermans *et al.* 2016).

Bocák *et al.* (2018) poprvé sekvenovali typový taxon čeledi Plastoceridae a potvrdili některé dřívější hypotézy o začlenění této skupiny do čeledi Elateridae. Zhang *et al.* (2018) zkoumali molekulární fylogenezi Coleoptera založenou na analýze 95 protein-kódujících genů, a potvrdili Dascilloidea jako sesterskou skupinu k ostatním elateriformním liniím, přičemž Buprestoidea byli sesterskou skupinou k Byrrhoidea + Elateroidea, a Byrrhidae sesteršti k dryopoidním skupinám. Kusý *et al.* (2018a) poprvé sekvenovali zástupce Rhinorhipidae a na základě široké škály provedených analýz vytvořili pro tuto enigmatickou skupinu vlastní nadčeleď. Rhinorhipidae vycházeli v analýzách buď jako jedna z bazálních linií Polyphaga nebo jako sesterská skupina Elateriformia. S ohledem na morfologii a další aspekty autoři preferovali druhou variantu a umístili tak Rhinorhipoidea do série Elateriformia. V další studii Kusý *et al.* (2018b) na základě výsledků z genomového sekvenování potvrdili dřívější hypotézy o zařazení některých měkkotělých linií do Elateridae a nově zde klasifikovali také zástupce Omalisidae.

Výše uvedený text názorně demonstruje dlouhý a komplikovaný vývoj klasifikace Elateriformia, která dodnes prochází neustálými změnami a očividně stále ještě není kompletně vyřešená. Fylogenetické vztahy v rámci této série jsou tak i nadále výzvou pro moderní systematiky. Následující podkapitoly budou věnovány přehledu diverzity jednotlivých recentních čeledí Elateriformia včetně jejich fylogeneze, klasifikace, distribuce a biologie.

2.3. Přehled diverzity Rhinorhipoidea, Dascilloidea a Buprestoidea

Nadčeleď Rhinorhipoidea, obsahující jedinou čeleď Rhinorhipidae pro jediný druh rodu *Rhinorhipus* z Austrálie, byla ustanovena teprve nedávno (Kusý *et al.* 2018a). Autoři poprvé analyzovali molekulární data pro tuto linii a dospěli k závěru, že Rhinorhipidae jsou pravděpodobně sesterskou skupinou Elateriformia, čímž vyvrátili hypotézy o pozici Rhinorhipidae uvnitř Elateroidea (Lawrence 1988, Lawrence *et al.* 2010a).

Základy moderní definice Dascilloidea položil Crowson (1971), jenž do této skupiny kromě Dascillidae zařadil také Rhipiceridae a Karumiidae. Posledně jmenovaní jsou dnes považováni pouze za podčeleď Dascillidae (Lawrence & Newton 1995, Lawrence 2016b). Monofylii Dascilloidea dokazují nejen morfologická, ale i molekulární data (Crowson 1971, Kundrata *et al.* 2017b [**Příloha 3**]). Dascillidae se vyskytují ve všech zoogeografických regionech, ale největší zastoupení mají na severní polokouli. Celkem asi 100 popsaných druhů je rozděleno do šesti rodů v podčeledi Dascillinae a pěti rodů v Karumiinae (Jin *et al.* 2013b). Ti se vyskytují v aridních oblastech a jsou pravděpodobně vázáni na termity. Narozdíl od zbytku nadčeledi mají poněkud měkčí tělo a jsou různě morfologicky modifikovaní, včetně např. značně zkrácených krovek (Lawrence 2016b). Do Karumiinae byli dříve řazeni i enigmatičtí Cydistinae, avšak ti jsou dnes klasifikováni jako Elateriformia *incertae sedis* (Lawrence *et al.* 2010b, Lawrence 2016a). Rhipiceridae jsou parazitoidy imaturních stádií cikád. Zahrnují přibližně 85 popsaných druhů klasifikovaných v osmi rodech a dvou podčeledích, Rhipicerinae a Sandalinae, známých ze všech zoogeografických regionů (Jin *et al.* 2013a, Lawrence 2016b).

Nadčeleď Buprestoidea dnes obsahuje téměř 15 000 popsaných druhů, vyskytujících se ve všech zoogeografických oblastech světa (Bellamy & Volkovitsh 2016). Zahrnovala jedinou čeleď Buprestidae (Crowson 1955), avšak dnes jsou jako čeleď klasifikováni i Schizopodidae, jenž dříve bývali pouze jednou z podčeledí Buprestidae (Lawrence 2016a). Buprestidae se dnes tedy dělí na šest podčeledí: Julodinae, Polycestinae, Galbellinae, Chrysochroinae, Buprestinae a Agrilinae (Bouchard *et al.* 2011). Ačkoliv mnohé z publikovaných studií ukazují na blízkou příbuznost nadčeledi Buprestoidea s byrrhoidnii liniemi (např. Lawrence 1988, Lawrence *et al.* 2011, Kundrata *et al.* 2017b [**Příloha 3**]), její přesné postavení zatím zůstává i nadále předmětem spekulací.

2.4. Přehled diverzity Byrrhoidea

Nadčeleď Byrrhoidea dnes sdružuje bývalé Byrrhoidea, Dryopoidea a Psephenoidea různých autorů, a obsahuje téměř 4500 popsaných druhů řazených do 12 čeledí ze všech zoogeografických regionů (Lawrence & Newton 1995, Bocák *et al.* 2014, Lawrence 2016a). Otázka monofylie této nadčeledi není dosud úspěšně vyřešena (Kundrata *et al.* 2017b [**Příloha 3**]). Mnozí zástupci byrrhoidních linií jsou alespoň v některém stádiu ontogeneze spjati s vodním prostředím a patří mezi akvatické či příbřežní brouky (Jäch & Balke 2008, Short 2018). Neustálená topologie této skupiny brání podrobnější evolučně orientované studii zaměřené na vznik akvatických a semi-akvatických linií.

Byrrhidae obsahují přibližně 500 druhů ve 40 rodech klasifikovaných do tří podčeledí: Byrrhinae, Amphicryptinae a Syncalyptinae (Maier *et al.* 2016). Zástupci této čeledi jsou rozšířeni zejména ve vyšších zeměpisných šířkách a vyskytují se v chladnějších habitatech, kde se většinou živí mechy, lišejníky a řasami. Přestože není sporu o monofylii této čeledi, otázkou zůstává, zda tvoří samostatnou vývojovou linii v rámci Elateriformia, či zda je příbuzná Buprestoidea a dryopoidním liniím (Lawrence 1988, Lawrence *et al.* 2011, Timmermans & Vogler 2012, Kundrata *et al.* 2017b [**Příloha 3**]).

Elmidae jsou kosmopolitní skupinou, jejíž zástupci (larvy i dospělci) žijí většinou v tekoucích vodách. Tato čeleď obsahuje přibližně 1500 druhů ve 150 rodech zařazených do podčeledí Elminae a Larainae (Jäch *et al.* 2016). Monofylie ani jedné z těchto podčeledí však nebyla prokázána v molekulárně-fylogenetických studiích (Kodada *et al.* 2016a, Kundrata *et al.* 2017b [**Příloha 3**]). Jäch *et al.* (2016) vyčlenili bývalý africký tribus řazený do Elminae a zavedli pro něj samostatnou čeleď Protelmidae, avšak tato zatím nebyla kvůli chybějící fylogenetické analýze zcela akceptována (Short 2018). Fylogenetické studie nejsou jednotné ve výběru sesterské skupiny Elmidae, ale některé molekulární analýzy naznačují jejich blízký vztah s hlavním jádrem Ptilodactylidae (Timmermans & Vogler 2012, Kundrata *et al.* 2017b [**Příloha 3**]).

Dryopidae jsou téměř kosmopolitní čeledí obsahující přes 30 rodů a téměř 300 druhů (Kodada *et al.* 2016b). Většina zástupců má terestrické larvy, ale naprostá většina dospělců žije ve vodním prostředí (Jäch & Balke 2008). Přestože dosud nebyla publikována studie věnovaná fylogenetickým vztahům v rámci této čeledi, prvotní výsledky šířeji pojatých studií obsahujících větší počet dryopidních zástupců naznačují, že morfologicky mírně odlišný rod *Ceradryops* Hinton je sesterský zbytku skupiny, která se dále dělí na suchozemský a vodní subklád (Kodada *et al.* 2016b, Kundrata *et al.* 2017b [**Příloha 3**]).

Lutrochidae jsou malou americkou čeledí obsahující přes 20 popsaných akvatických či semi-akvatických druhů, patřících do jediného rodu. Diverzita této skupiny je však mnohem větší a v nejbližší době budou popsány další rody a druhy (Maier 2016). Lutrochidae jsou sesterskou skupinou Dryopidae, což je podpořeno jak morfologickými znaky, tak i recentními molekulárně-fylogenetickými analýzami (Bocák *et al.* 2014, McKenna *et al.* 2015, Kundrata *et al.* 2017b [**Příloha 3**]).

Limnichidae obsahují necelých 400 popsaných semi-akvatických či příbřežních druhů ze všech zoogeografických regionů (Jäch & Balke 2008). V současnosti se dělí na čtyři podčeledi, t.j. Limnichinae, Cephalobyrrhinae, Thaumastodinae a Hyphalinae (Hernando & Ribera 2016). Pravděpodobnou sesterskou skupinou k Limnichidae jsou Heteroceridae. Jejich blízký vztah je podpořen nejen podobnou morfologií jejich dospělců i larev (Crowson 1978, Beutel 1995), ale i molekulární fylogenezí (McKenna *et al.* 2015, Timmermans *et al.* 2016). Monofylie Limnichidae však zůstává diskutabilní (Crowson 1978, Costa *et al.* 1999, Kundrata *et al.* 2017b [**Příloha 3**]).

Heteroceridae jsou malá kosmopolitní skupina brouků, do které je řazeno kolem 300 druhů klasifikovaných ve dvou podčeledích: Heterocerinae a Elythomerinae (Vanin *et al.* 2016). Zástupci této čeledi obývají břehy vod. Recentní molekulárně-fylogenetické studie naznačují blízké vztahy mezi Heteroceridae, Limnichidae a Chelonariidae (McKenna *et al.* 2015, Kundrata *et al.* 2017b [**Příloha 3**]).

Psephenidae obsahují přibližně 300 druhů ze všech zoogeografických regionů, řazených do pěti podčeledí: Afroeubriinae, Eubrianacinae, Eubriinae, Psepheninae a Psephenoidinae (Lee *et al.* 2007, 2016). Tato skupina obsahuje zástupce, kteří mají striktně akvatické larvy a terestrické dospělce; kukla může být buď terestrická (většina) nebo akvatická (Psephenoidinae). Fylogenetická pozice a monofylie Psephenidae zůstávají nevyřešené. Přestože Lee *et al.* (2007) definoval několik morfologických synapomorfií podporujících monofylii Psephenidae, tato čeleď pravděpodobně monofyletická není (Kundrata *et al.* 2014a, 2017b [**Příloha 3**], 2019 [**Příloha 4**]). McKenna *et al.* (2015) sice potvrdili monofylii Psepheninae + Eubrianacinae, avšak Kundrata *et al.* (2017b) [**Příloha 3**], kteří zahrnuli do svých analýz více zástupců z Eubriinae a Eubrianacinae, neměli ani v jedné topologii tyto dvě skupiny ve společném kládu. Pro potvrzení monofylie skupiny je tedy potřeba analyzovat datový soubor se zastoupením všech byrrhoidních linií a podčeledí Psephenidae.

Cneoglossidae jsou monogenerickou čeledí obsahující devět druhů z Neotropické oblasti (Costa *et al.* 1999). Crowson (1972) sice považoval tuto skupinu za součást Cantharoidea, avšak další morfologicky založené studie dávaly Cneoglossidae do příbuzenství s Psephenidae (např. Lawrence *et al.* 1995a, 2011; Costa *et al.* 1999). McKenna *et al.* (2015) poukázal na možný příbuzenský vztah Cneoglossidae a Ptilodactylidae.

Ptilodactylidae obsahují přes 500 popsaných druhů v 35 rodech, které jsou klasifikovány v pěti podčeledích: Ptilodactylinae, Anchytarsinae, Araeopidiinae, Aploglossinae a Cladotominae (Lawrence 2016c, Kundrata *et al.* 2019 [**Příloha 4**]). Stribling (1987) ve své dizertační práci částečně revidoval tuto kosmopolitní skupinu a navrhnul novou klasifikaci, ale ta zůstala nepublikována a Ptilodactylidae jsou tak i nadále čeledí, která je v rámci Byrrhoidea nejméně taxonomicky prozkoumaná a nutně potřebuje revidovat klasifikaci. Dlouhodobě nezodpovězenou otázkou je i monofylie skupiny, která bývá často zpochybňována (Lawrence & Newton 1982, Beutel 1995, Costa *et al.* 1999). Cladotominae tvoří samostatnou linii mimo ostatní Ptilodactylidae v morfologických i molekulárních studiích, a pravděpodobně čekají na formální ustanovení nové čeledi (Beutel 1995, Costa *et al.* 1999, Bocáková *et al.* 2007, Hunt *et al.* 2007, Bocák *et al.* 2014, Kundrata *et al.* 2014a, 2017b [**Příloha 3**], 2019 [**Příloha 4**]). Araeopidiinae dosud nebyli sekvenováni, ale morfologicky zaměřené studie opakovaně prokázaly jejich samostatné postavení mimo Ptilodactylidae (Beutel 1995, Lawrence *et al.* 1995a). Ptilodactylinae a Anchytarsinae tvoří pravděpodobně jádro pravých Ptilodactylidae (Beutel 1995, Costa *et al.* 1999, Lawrence *et al.* 2011, Kundrata *et al.* 2014a, 2017b [**Příloha 3**], 2019 [**Příloha 4**]). McKenna *et al.* (2015) zahrnul do své analýzy pouze zástupce Ptilodactylinae a Anchytarsinae, které našel v jednom kládu s Cneoglossidae a Podabrocephalidae. To pravděpodobně vedlo Lawrence (2016a) k tomu, že zařadil Podabrocephalinae do Ptilodactylidae jako další podčeleď (nikoli však Cneoglossidae). Kundrata *et al.* (2019) [**Příloha 4**] analyzovali dostupné sekvence pro Ptilodactylidae včetně Podabrocephalinae a zaměřili se také na morfologii těchto taxonů. Jejich výsledky ukázaly, že *Podabrocephalus* Pic je pouze morfologicky modifikovaný zástupce podčeledi Ptilodactylinae. Autoři také identifikovali dosud nepopsaný rod, který morfologicky nepatří do žádné z dosud známých podčeledí. Bude potřeba rozsáhlejší analýza s použitím většího množství zástupců z dalších, dosud nesekvenovaných podčeledí. Nutnost taxonomické revize dokládá například fakt, že v rámci Ptilodactylidae jsou stále klasifikovány druhy, které patří do naprosto odlišných nadčeledí (Kundrata & Jäch 2017).

Chelonariidae jsou terestrickou skupinou obsahující přibližně 300 druhů ve třech rodech, které se vyskytují zejména v tropických oblastech s výjimkou Afriky (Beutel & Leschen 2016). Jejich fylogenetická pozice v rámci Byrrhoidea zůstává nevyjasněna, ale tři recentní studie založené na odlišných datech i analýzách nastínily blízký vztah Chelonariidae k Limnichidae a Heteroceridae (Timmermans & Vogler 2012, McKenna *et al.* 2015, Kundrata *et al.* 2017b [**Příloha 3**]).

Eulichadidae obsahují dva popsané rody, z nichž *Eulichas* Jacobson (přes 40 druhů) se vyskytuje v Asii a monotypický *Stenocolus* LeConte v americké Kalifornii. Larvy jsou akvatické, kdežto dospělci terestričtí (Jäch & Balke 2008). Jejich pozice zůstává nevyřešena, jisté je však to, že nejsou příbuzní čeledi Callirhipidae, což navrhovalo několik dřívějších studií (Lawrence & Newton 1982, Lawrence 1988, Costa *et al.* 1999).

Callirhipidae obsahují 175 popsaných druhů řazených do sedmi rodů, které se vyskytují ve všech regionech s výjimkou tropické Afriky, Madagaskaru a Nového Zélandu (Hájek 2011). Tato skupina byla dříve součástí nadčeledí Rhipiceroidea a Artematopoidea, avšak dnes s určitostí víme, že patří do Byrrhoidea, přestože její pozice v rámci byrrhoidního komplexu není zcela vyjasněna (McKenna *et al.* 2015, Kundrata *et al.* 2017b [**Příloha 3**]).

2.5. Přehled diverzity Elateroidea

Nadčeleď Elateroidea s přibližně 24 000 popsanými druhy řazených do 13 čeledí tvoří největší část diverzity série Elateriformia a je jednou z největších skupin Polyphaga (Lawrence & Newton 1995; Kundrata & Bocák 2011a; Bocák *et al.* 2014, 2016 [**Příloha 2**], 2018; Kundrata *et al.* 2014a). Skupina je definována několika larválními i adultními znaky, ale některé z nich se vyskytují i u jiných skupin Elateriformia (Lawrence & Newton 1982). Elateroidea jsou velmi zajímavou linií z evolučního hlediska, především díky přítomnosti evolučních adaptací jako jsou klikací mechanismus, aposematické zbarvení, bioluminiscence, a neotenie (Bocáková *et al.* 2007).

Klikací mechanismus je zajímavou antipredační strategií u elateroidních skupin se silně sklerotizovaným tělem, které byly dříve řazeny v původní nadčeledi Elateroidea (Crowson 1955). Tento vymršťovací aparát je na ventrální straně prvního a druhého hrudního článku a sestává z prosternálního výběžku zapadajícího do mesoventrální jamky. Při prudkém pohybu prosternálního výběžku směrem do jamky se brouk dokáže vymrštit do vzduchu, což může sloužit k jeho návratu do správné pozice či jako únik před predátorem (Evans 1972, 1973; Costa *et al.* 2010). Přestože Vahtera *et al.* (2009) považují vícenásobný vznik tohoto mechanismu za nepravděpodobný díky jeho relativně složité stavbě, dnešní molekulární studie konzistentně potvrzují nemonofyletičnost silně sklerotizovaných skupin v rámci Elateroidea (např. Bocáková *et al.* 2007, Kundrata & Bocák 2011a, Kundrata *et al.* 2014a).

Aposematické zbarvení a bioluminiscence jsou doménou zejména slabě sklerotizovaných linií v rámci Elateroidea, t.j. skupin dříve klasifikovaných v Cantharoidea. Měkké tělo a ztráta únikových reakcí u těchto skupin pravděpodobně souvisí s modifikací jejich ontogenetického procesu v důsledku neotenie (Bocák *et al.* 2008). Zástupci těchto linií většinou nepatří mezi nejefektivnější letce a jelikož nemají silně sklerotizované tělo jako předchozí skupiny, bez přítomnosti nějaké další antipredační strategie by se stávali snadnou kořistí predátorů. V několika více či méně příbuzných elateroidních liniích se tak vyvinuly nejedlé druhy, které tuto vlastnost varovně signalizují predátorům pomocí barevných aposematických vzorů či schopnosti emitovat světlo (Branham & Wenzel 2001, Bocáková *et al.* 2007, Sagegami-Oba *et al.* 2007b, Eisner *et al.* 2008, Martin *et al.* 2017, Fallon *et al.* 2018, Motyka *et al.* 2018). Bioluminiscence, tedy jev, při němž dochází za přítomnosti enzymu luciferázy k oxidaci luciferinu za vzniku studeného světla (Shimomura 2012, Wilson & Hastings 2013), hraje u elateroidních skupin důležitou roli v komunikaci s okolím, ať už při hledání sexuálního partnera či kořisti, nebo při varovné signalizaci predátorům (Lloyd 1978, 1984; Oba 2009). Je zajímavé, že u brouků se bioluminiscence vyskytuje téměř výhradně u Elateroidea (Viviani & Bechara 1997, Branham & Wenzel 2001, Oba 2009), kde se několikanásobně vyvinula u čeledí Lampyridae, Phengodidae, Rhagophthalmidae a Elateridae (Bocáková *et al.* 2007, Sagegami-Oba *et al.* 2007b, Kundrata *et al.* 2014a, Martin *et al.* 2017, Fallon *et al.* 2018). Akumulace bioluminiscentních linií v rámci Elateroidea je vysvětlována sdílenou evolucí genu pro luciferázu (Oba 2009 a citace uvnitř). Gen kódující luciferázu je totiž homologický s genem pro syntetázu mastných kyselin, jenž se vyskytuje u zástupců, kteří schopnost bioluminiscence nemají. Na základě toho, že luciferáza vykazuje jistou syntetickou aktivitu ve vztahu k mastným kyselinám, se dá předpokládat, že se původní gen pro syntetázu mastných kyselin u některých linií v rámci Elateroidea přiblížil genu pro luciferázu do té míry, že zde došlo k paralelnímu vzniku světlo emitujících linií (Oba *et al.* 2003, Oba 2009, Day *et al.* 2009).

Dalším evolučně velmi zajímavým jevem vyskytujícím se v Elateroidea je přítomnost neotenických linií (Cicero 1988, Bocák *et al.* 2008). Neotenie je jedním z heterochronických procesů, což jsou jevy, při nichž se v evoluci adultní znaky u potomka objevují během ontogeneze později nebo dříve než u jeho předka. Při neotenii pak během ontogeneze dochází ke zpomalení růstu určitých morfologických struktur, aniž by současně docházelo ke zpomalení rychlosti pohlavního dospívání (Gould 1977). V důsledku tohoto jevu pak může docházet k nekompletní metamorfóze, kdy si některé linie v Elateroidea zachovávají i v dospělosti larvální znaky (Crowson 1972, Cicero 1988, Bocáková *et al.* 2007, Kobieluszová & Kundrata 2015, Kundrata *et al.* 2015a [**Příloha 10**]). Neotenie se u některých živočichů vyskytuje jako fakultativní evoluční adaptace na neustále se měnící podmínky prostředí (Gould 1977), avšak u Elateroidea se jedná o naprosto obligátní strategii, která se v evoluci skupiny vyvinula opakovaně a s různým či naopak podobným stupněm morfologické modifikace u zcela nepříbuzných linií (Bocáková *et al.* 2007, Bocák *et al.* 2008, Boček *et al.* 2018). Bocák *et al.* (2008) předpokládali, že prvním projevem modifikace ontogenetického procesu může být pravděpodobně již redukce sklerotizace těla, což bylo později potvrzeno ve studii věnované graduálnímu vzniku měkkého těla a neotenie u kovaříkovitých brouků (Kundrata & Bocák v tisku) [**Příloha 13**]. Morfologické modifikace elateroidních zástupců tak reprezentují kontinuum od měkkého těla přes formy s larviformním abdomenem, abdomenem i thoraxem, brachypterií či úplnou redukcí křídel až po kompletně larviformní samice (Bocák *et al.* 2008, 2018; Bocák & Brlík 2008; Mášek *et al.* 2015; Kundrata *et al.* 2015a [**Příloha 10**]). Neotenie vznikla několikanásobně nejen v celé nadčeledi Elateroidea (Bocáková *et al.* 2007, Sagegami-Oba *et al.* 2007b, Kundrata & Bocák 2011a, Kundrata *et al.* 2014a), ale také v čeledích Elateridae, Lycidae a Lampyridae (Kundrata & Bocák 2011a; Bocák *et al.* 2008, 2018; Kusý *et al.* 2018b). Tento jev ovlivňuje zejména samice a je rozšířený u Omethidae (Telegeusinae), Iberobaeniidae, Lycidae, Lampyridae, Phengodidae, Rhagophthalmidae a Elateridae (Omalisinae, Cebrionini, Drilini). Neotenní linie, přestože jsou mnohdy poměrně starobylé, jsou druhově chudší ve srovnání s jejich nemodifikovanými příbuznými. To může souviset s jejich omezenou schopností disperze v důsledku morfologických modifikací a jejich přežívání v dlouhodobě stabilních habitatech jako jsou např. pleistocénní refugia (Malohlava & Bocák 2010, Bocák *et al.* 2016 [**Příloha 2**], Boček *et al.* 2018). Redukce vagility u neotenních elateroidních linií v kombinaci s fragmentací jejich populací může vést ovšem také k vyšší míře speciace (Ikeda *et al.* 2012), což z těchto skupin dělá vhodné modelové taxony pro studium evoluce speciačních procesů (Bocák *et al.* 2008, Kundrata *et al.* 2015a [**Příloha 10**], Bray & Bocák 2016).

Klasifikace nadčeledi Elateroidea prošla v průběhu své historie mnohými změnami a přestože je dnes ve srovnání s byrrhoidním komplexem relativně ustálenější, stále se objevují studie aktualizující stávající systém (Bocáková *et al.* 2007; Kundrata & Bocák 2011a; Kundrata *et al.* 2014a; Bocák *et al.* 2016, 2018; Kusý *et al.* 2018a, 2018b). Dnešní široký koncept nadčeledi formálně vytvořil až Lawrence (1988) spojením dřívějších Elateroidea *sensu stricto*, Cantharoidea a Artematopoidea, přestože blízké příbuznosti těchto skupin si autoři všimli již dříve (Crowson 1955, Lawrence & Newton 1982). Původní Elateroidea obsahovali pouze skupiny se silně sklerotizovaným tělem a přítomností klikacího mechanismu, do Cantharoidea zase byly řazeny pouze měkkotělé skupiny s častým výskytem morfologických modifikací způsobených neotenií (Crowson 1972) a do Artematopoidea se řadili zejména Artematopodidae a Brachypsectridae, kteří se svou morfologií vymykali oběma předchozím nadčeledím. I po spojení do jediné nadčeledi však byly silně sklerotizované a měkkotělé skupiny považovány za monofyletické, což se také odrazilo na obsahu tehdejších fylogenetických analýz, když měli autoři tendenci zkoumat silně i slabě sklerotizované linie odděleně (Calder *et al.* 1993, Muona 1995, Branham & Wenzel 2003, Lawrence *et al.* 2007, Stanger-Hall *et al.* 2007). Bocáková *et al.* (2007), Sagegami-Oba *et al.* (2007b) a Hunt *et al.* (2007) později prokázali, že ani bývalí Cantharoidea a ani Elateroidea *sensu stricto* netvoří monofyla. Další molekulárně-fylogenetické studie na ně navázaly, potvrdily tyto závěry a napomohly k formování klasifikace Elateroidea až do současného stavu (Kundrata & Bocák 2011a; Kundrata *et al.* 2013 [**Příloha 1**], 2014a, 2015b [**Příloha 9**]; Bocák *et al.* 2016 [**Příloha 2**], 2018; Kusý *et al.* 2018a, 2018b). Následující přehled čeledí Elateroidea tak reflektuje všechny podstatné recentní změny.

Artematopodidae obsahují přibližně 70 popsaných druhů řazených do osmi rodů ve třech podčeledích: Artematopodinae, Allopogoniinae a Electribiinae (Hörnschemeyer 1998, Kundrata *et al.* 2013 [**Příloha 1**], Gimmel & Bocáková 2015). Tato čeleď má disjunktivní distribuci a je známa z Nového světa, východní Asie a Itálie. Asijské druhy byly donedávna známy pouze ze Sibiře, Dálného východu, Japonska a Taiwanu, ale Kundrata *et al.* (2013) [**Příloha 1**] popsali první dva zástupce této skupiny z pevninské Číny. Diverzita Artematopodidae je však mnohem větší a mnoho dosud nepopsaných druhů z různých oblastí stále čeká na formální deskripci (Kundrata, nepublikovaná data). Artematopodidae jsou dnes považováni za jednu z nejstarších bazálních linií Elateroidea (Kundrata *et al.* 2014a, McKenna *et al.* 2015, Bocák *et al.* 2016 [**Příloha 2**], Kusý *et al.* 2018a), což dokládají i nálezy druhohorních fosilií (Cai *et al.* 2015). Přestože v minulosti byla tato skupina dávána do příbuzenství s Brachypsectridae a Callirhipidae (Crowson 1973), dnešní molekulárně-fylogenetické studie tuto hypotézu striktně odmítají a dávají Artematopodidae do jednoho kládu spolu s Omethidae (např. Kundrata *et al.* 2013 [**Příloha 1**], 2014; McKenna *et al.* 2015).

Omethidae jsou malá čeleď s měkkotělými zástupci, jejíž definice se v poslední době několikrát měnila. Crowson (1972) do této skupiny zařadil tři podčeledi na základě rodů, které do té doby patřily do Cantharidae, Lampyridae a Drilidae. Omethinae obsahují osm druhů v pěti rodech a vyskytují se v severní Americe a Japonsku, Matheteinae čítají tři druhy ve dvou rodech a vyskytují se pouze na západě USA, a Driloniinae jsou monogenerická skupina s 22 popsanými druhy z jižní, jihovýchodní a východní Asie (Ramsdale 2010a). Kundrata *et al.* (2014a) na základě molekulární fylogeneze převedli do Omethidae do té doby samostatnou čeleď Telegeusidae. Ta obsahuje 10 druhů ve třech rodech známých z Ameriky, a byla dříve spíše považována za skupinu blízkou další americké čeledi Phengodidae. Samci Telegeusinae mají silně zkrácené krovky a samice jsou neznámé, proto se předpokládá, že jsou neotenické a nelétavé. Zaragoza-Caballero & Zurita-García (2015) provedli morfologickou analýzu čeledi Phengodidae a převedli jednu její podčeleď, Penicillophorinae s šesti druhy v pěti rodech, do Telegeusidae. Jelikož jsou Telegeusidae dnes podčeledí Omethidae, Penicilliophoridae se stali tribem v této skupině. V této čeledi také můžeme očekávat popisy mnoha nových druhů, a to jak z Asie, tak zejména z Ameriky (Ivie 2002, Ramsdale 2010a).

Eucnemidae jsou kosmopolitní čeledí, zahrnující přibližně 1500 popsaných druhů řazených do devíti podčeledí: Perothopinae, Phyllocerinae, Pseudomeninae, Palaeoxeninae, Phlegonidae, Anischiinae, Melasinae, Eucneminae a Macraulacinae (Muona 2010). Larvy Eucnemidae se dělí na dvě skupiny dle ekologie; některé jsou v zemi, ale většina žije ve dřevě. Dospělci mají silně sklerotizované tělo a většina z nich má funkční klikací mechanismus, proto byla tato skupina spolu s Elateridae, Throscidae a Cerophytidae vždy řazena do původně definovaných Elateroidea (Crowson 1955). Pozice Anischiinae nebyla dlouho úplně jasná a tato skupina byla klasifikována také v Elateridae a Cerophytidae (Lawrence & Newton 1995). Analýza Lawrence *et al.* (2007) však dokázala její postavení v Eucnemidae, což bylo následně potvrzeno i v dalších studiích s větším zastoupením elateroidních skupin (např. Kundrata *et al.* 2014a). Dříve sem byly řazeny i rody, které dnes patří do Elateridae: Thylacosterninae a Subprotelaterinae (Lawrence & Newton 1995, Costa *et al.* 2010, Kundrata & Bocák 2011a, Kundrata *et al.* 2014a). Eucnemidae jsou v naprosté většině molekulárních analýz nacházeni jako jedna z bazálních radiací Elateroidea (Kundrata & Bocák 2011a; Bocák *et al.* 2014, 2016 [**Příloha 2**]; Kundrata *et al.* 2014a; McKenna *et al.* 2015; Kusý *et al.* 2018a). Zatím nebyla provedena robustní fylogenetická analýza celé čeledi, a podle kvalifikovaných odhadů je zatím popsána pouze polovina všech druhů (Muona 2010).

Throscidae jsou další ze silně sklerotizovaných bazálních linií Elateroidea s vyvinutým klikacím mechanismem. Tato kosmopolitní skupina obsahuje většinou drobné zástupce řazené do 150 druhů v pěti rodech (Muona *et al.* 2010). Dříve sem byly řazeny i rody, které dnes patří do Elateridae: Lissominae a Thylacosterninae (Kundrata & Bocák 2011a; Kundrata *et al.* 2014a, 2016 [**Příloha 5**], 2018a [**Příloha 6**]). Fylogenetická pozice morfologicky modifikovaného afrického rodu *Neocrowsonia* zůstává neobjasněna (Lawrence *et al.* 2010b).

Cerophytidae obsahují také silně sklerotizované zástupce s klikacím mechanismem. Tato čeleď patřila do původních Elateroidea a dnes je považována za jednu z bazálních větví Elateroidea (Costa *et al.* 2003, Kundrata *et al.* 2014a, McKenna *et al.* 2015). Seznam recentních i fosilních taxonů spadajících do Cerophytidae publikovali Kundrata & Jäch (2017), přičemž tato skupina dnes obsahuje 23 druhů řazených do čtyř rodů. Největší diverzita je v Neotropické oblasti, ale čtyři druhy jsou známy i z oblasti Holarktické. Monotypický rod *Afrocerophytum* Costa, Vanin & Rosa byl objeven teprve nedávno a je rozšířen v tropických deštných lesích západní a střední Afriky (Costa *et al.* 2014, Šormová & Kundrata 2017).

Brachypsectridae byli dříve řazeni v Cantharoidea a Artematopoidea, ale dnešní studie umístily tuto lini mezi bazální větve Elateroidea, většinou jako sesterskou skupinu k vyšším Elateroidea *sensu* Kundrata *et al.* (2014) (McKenna *et al.* 2015, Kusý *et al.* 2018a). Dospělci mají středně sklerotizované tělo, nemají funkční klikací aparát a celkově jsou morfologicky mezistupněm mezi silně a slabě sklerotizovanými liniemi. Costa *et al.* (2006) revidovali tehdy monogenerickou čeleď Brachypsectridae s čtyřmi popsanými druhy z Ameriky, jižní Indie a Singapuru, a jedním druhem z Austrálie známým pouze v larválním stádiu. Hájek (2010) popsal první palearktický druh této čeledi z Íránu. Kolega C. Makris objevil na Kypru torzo samice dosud nepopsaného druhu rodu *Brachypsectra*, kterou mi poslal na detailní studium. Později se nám podařilo v terénu objevit i larvu tohoto druhu a v muzejních sbírkách další palearktický materiál, což vyústilo v popis nového druhu z Turecka (Petrželková *et al.* 2017), což významně rozšířilo dosud známou distribuci této linie. Nepoškozeného dospělce kyperského druhu se doposud nepodařilo odchytit, proto zůstává i nadále nepopsaný. Kovalev & Kirejtshuk (2016) popsali dva druhy enigmatického a morfologicky poměrně odlišného nového rodu *Asiopsectra* z Íránu a Tádžikistánu, čímž redefinovali limity celé čeledi.

Čeleď Iberobaeniidae byla objevena teprve nedávno a obsahuje velmi malé měkkotělé zástupce z jižní části Iberského poloostrova (Bocák *et al.* 2016 [**Příloha 2**]). Původně byly popsány pouze dva druhy, pro něž byli známí dospělci, a jeden nepopsaný druh byl znám pouze na základě larválního stádia. Kundrata *et al.* (2017a) popsali třetí druh této čeledi dle dospělců sbíraných na místě, kde byly dříve nalezeny výše zmíněné nepopsané larvy, a přidali informace o biologii a ekologii skupiny, mapu rozšíření a identifikační klíč. Iberobaeniidae jsou ve všech analýzách sesterskou skupinou Lycidae, což dokazují i morfologické znaky (Bocák *et al.* 2016 [**Příloha 2**], 2018). Samice této skupiny jsou neznámé, ale předpokládáme, že jsou neotenické a žijí kryptickým způsobem života podobně jako larvy.

Lycidae jsou kosmopolitní měkkotělou čeledí, obsahující přibližně 4500 popsaných druhů řazených do sedmi podčeledí: Lycinae, Libnetinae, Leptolycinae, Dictyopterinae, Lyropaeinae a Dexorinae (Bocák & Bocáková 2008, 2010; Mášek *et al.* 2018). Největší diverzita leží v tropických oblastech. Dosavadní klasifikace založené na morfologických znacích jsou zpochybňovány molekulárně-fylogenetickými studiemi (např. Bocák *et al.* 2008, Sklenářová *et al.* 2013, Boček & Bocák 2017, Mášek *et al.* 2018). Lycidae obsahují několik neotenických linií, které vznikly několikanásobně, a z nichž některé obsahují tzv. trilobitní larvy, které jsou morfologicky k nerozeznání od larev a jsou daleko větší než samci (Mášek *et al.* 2015). Dřívější autoři předpokládali blízký příbuzenský vztah Lycidae s Cantharidae a Lampyridae, což však recentní studie většinou nepodporují. Po objevu Iberobaeniidae všechny dosavadní analýzy ukazují, že Lycidae jsou sesterskou skupinou právě k této drobné reliktní linii (Bocák *et al.* 2016 [**Příloha 2**], 2018).

Cantharidae jsou další větší kosmopolitní čeledí, jejíž zástupci mají pouze slabě sklerotizované tělo. Je popsáno více než 5000 druhů, které jsou klasifikovány do podčeledí Cantharinae, Malthininae, Silinae, Dysmorphocerinae a Chauliognathinae (Ramsdale 2010b). Některé linie mají výrazně zkrácené krovky, jiné jsou zajímavé chemickou obranou či aposematickým zbarvením (např. Machado & Araújo 2001, Ramsdale 2010b). Cantharidae se v recentních studiích objevují buď v jednom kládu s Lampyridae (Bocák *et al.* 2014, 2018; Kundrata *et al.* 2014a) nebo jako sesterská skupina ke kládu obsahujícímu Elateridae (včetně Omalisidae), Phengodidae, Rhagophthalmidae a Lampyridae (McKenna *et al.* 2015, Bocák *et al.* 2016 [**Příloha 2**], Kusý *et al.* 2018a).

Lampyridae obsahují přibližně 2000 popsaných druhů řazených do šesti podčeledí: Lampyrinae, Psilocladinae, Pterotinae, Luciolinae, Photurinae a Ototretinae (Lawrence 2016a). Pozice Pterotinae a Ototretinae uvnitř Lampyridae byla sice zpochybněna morfologickou analýzou (Branham & Wenzel 2001) a tyto taxony byly přesunuty do Elateriformia *incertae sedis* (Lawrence *et al.* 2010b), avšak nejnovější studie je vrátily zpět do Lampyridae (Janišová & Bocáková 2013, Kundrata *et al.* 2014a, Martin *et al.* 2017). Nevyřešené však zůstávají vztahy Lampyridae a kládu Phengodidae + Rhagophthamidae (např. Kundrata *et al.* 2014a, Kusý *et al.* 2018a). Zástupci čeledi Lampyridae jsou známí svou schopností bioluminiscence; emitovat světlo dokážou všechny dosud známé larvy a většina dospělců (Branham & Wenzel 2001). V této skupině je také poměrně častá neotenie, která ovlivňuje zejména morfologii samic, které jsou často brachypterní, apterní či téměř larviformní (Cicero 1988).

Phengodidae jsou malou americkou čeledí obsahující přibližně 270 popsaných druhů řazených do podčeledí Phengodinae a Mastinocerinae (Zaragoza-Caballero & Pérez Hernández 2014, Zaragoza-Caballero & Zurita-García 2015). Donedávna zde byla klasifikována i podčeleď Penicillophorinae, avšak tu Zaragoza-Caballero & Zurita-García (2015) na základě morfologicky zaměřené fylogenetické analýzy přesunuli do Telegeusidae. Tito autoři také zpochybnili monofylii obou podčeledí Phengodidae. Některé dřívější studie řadily do Phengodidae také rod *Cydistus* Bourgeois z Asie, avšak tento rod je nyní řazen do Elateriformia *incertae sedis* (Lawrence *et al.* 2010b). Samci této skupiny mají sice často zkrácené krovky, ale jsou plně letuschopní, kdežto samice jsou larviformní a živí se v hrabance mnohonožkami (Costa & Zaragoza-Caballero 2010). Všechny larvy a samice a také někteří samci jsou schopni bioluminiscence (Viviani & Bechara 1997). Phengodidae tvoří jeden, většinou statisticky dobře podpořený, klád s Rhagophthalmidae, kteří bývali v minulosti dokonce klasifikováni jako podčeleď Phengodidae (Bocáková *et al.* 2007; Kundrata & Bocák 2011a; Kundrata *et al.* 2013 [**Příloha 1**], 2014a, 2017b [**Příloha 3**]; Bocák *et al.* 2014, 2016 [**Příloha 2**], 2018; McKenna *et al.* 2015, Kusý *et al.* 2018a).

Rhagophthalmidae obsahují přibližně 60 druhů převážně z jižní, východní a jihovýchodní Asie (Kundrata & Bocák 2011b), ale limity této skupiny nejsou ještě dostatečně ustálené (Janišová & Bocáková 2013, Kawashima *et al.* 2010). Rhagophthalmidae někdy bývali řazeni jako podčeleď uvnitř Phengodidae nebo Lampyridae, avšak dnes jsou považováni za samostatnou čeleď sesterskou k Phengodidae (Kundrata *et al.* 2014a). Larvy, samice a někteří dospělci dokážou emitovat světlo. Samice jsou buď kompletně či neúplně larviformní (Kawashima *et al.* 2010).

Elateridae jsou kosmopolitní a druhově nejbohatší čeledí Elateriformia (Costa *et al.* 2010; Kundrata & Bocák 2011a; Kundrata *et al.* 2016 [**Příloha 5**], 2018a [**Příloha 6**]). Většina zástupců této skupiny je na první pohled dosti uniformní; larvy jsou typickými drátovci a dospělci se vyznačují silně sklerotizovaným, kompaktním tělem s plně funkčním klikacím mechanismem (Costa *et al.* 2010). Existují zde ale morfologicky modifikované linie, které dříve byly klasifikovány mimo Elateridae, např. v měkkotělých Cantharoidea, a často tvořily samostatné čeledi. Cebrionini zde byli zařazeni již dříve (Lawrence 1988), avšak Drilini, Plastocerinae a Omalisinae teprve nedávno (Kundrata & Bocák 2011a, Bocák *et al.* 2018, Kusý *et al.* 2018a). Bocák *et al.* (2018) a Kundrata & Bocák (v tisku) [**Příloha 13**] detailně zkoumali přechod od silně sklerotizovaného na měkké tělo a evoluci vybraných morfologických znaků v důsledku graduálně se zvyšující míry neotenie u vybraných linií Elateridae. Fylogeneze, klasifikace a diverzita této čeledi bude detailně rozebrána v další části této práce.

2.6. Elateriformia *Incertae sedis*

Některé taxony v rámci Elateriformia dříve byly či nadále zůstávají klasifikačně problematické. Několik skupin bylo proto zařazeno do Elateriformia *incertae sedis* anebo provizorně klasifikováno v některé z morfologicky podobných čeledí. Tyto enigmatické taxony byly většinou detailně morfologicky prostudovány, ale kvůli nejasně interpretovatelné morfologii a množství homoplastických znaků uvnitř Elateriformia nemohly být s jistotou zařazeny do žádné skupiny.

Lawrence & Newton (1995) klasifikovali v Elateriformia *incertae sedis* monotypické skupiny Rhinorhipidae a Podabrocephalidae. Lawrence *et al.* (2010a) později přesunuli bez komentáře Rhinorhipidae do Elateroidea, a Kusý *et al.* (2018a) pro ně dokonce zřídili samostatnou nadčeleď Rhinorhipoidea na základě molekulární fylogeneze. Lawrence *et al.* (2010b) zařadili do Elateriformia *incertae sedis* Podabrocephalidae, Cydistinae, *Neocrowsonia*, Ototretinae, Pterotinae, *Harmatelia* Walker a *Stenocladius* Fairmaire. Poslední čtyři taxony byly původně vyjmuty z Lampyridae po morfologické analýze Branhama & Wenzela (2001), ale po čase tam byly opět vráceny na základě molekulární fylogeneze (Sagegami-Oba *et al.* 2007b, Kundrata *et al.* 2014a, Martin *et al.* 2017). Podabrocephalidae byli později přesunuti do Ptilodactylidae; původně jako samostatná podčeleď (Lawrence 2016a) a poté na základě kombinace molekulární fylogeneze a morfologie jako součást podčeledi Ptilodactylinae (Kundrata *et al.* 2019 [**Příloha 4**]). Monotypický termitofilní rod *Neocrowsonia* byl původně řazen do čeledi Throscidae. Přestože modifikovaná morfologie tohoto rodu znesnadňuje jeho správné taxonomické zařazení, s velkou pravděpodobností jde o zástupce některé ze silně sklerotizovaných elateroidních linií (Lawrence & Newton 1995, Lawrence *et al.* 2010b). V dnešní době jsou tedy jediným taxonem s nevyřešenou fylogenetickou pozicí Cydistinae. Tato monogenerická skupina je reprezentována sedmi druhy z oblasti Levantu, Malé Asie a Íránu (Wittmer 1944, 1979). Dřívější autoři ji nejprve porovnávali s Phengodidae a Cantharidae, později ji zařadili do Drilidae (Olivier 1910, Wittmer 1944). Crowson (1955) uvedl, že *Cydistus* je mezistupněm mezi Phengodidae a Karumiidae, a od té doby bývá tento rod klasifikován buď v jedné nebo druhé skupině. Jelikož se nám nedávno podařilo sehnat jedince rodu *Cydistus* vhodné pro extrakci DNA, momentálně s mezinárodním týmem odborníků pracujeme na objasnění fylogenetické pozice tohoto dlouhodobě klasifikačně problematického taxonu.

3. Fylogeneze, klasifikace a diverzita Elateridae

(Přílohy 5–7)

3.1. Monofylie a fylogenetická pozice Elateridae

Elateridae jsou zdaleka největší čeledí v rámci Elateriformia a devátou největší čeledí Coleoptera, co se týče počtu popsaných druhů. Přes 10 000 druhů ze všech zoogeografických regionů je dnes řazeno do přibližně 500 rodů a 19 podčeledí (Costa *et al.* 2010; Kundrata & Bocák 2011a; Kundrata *et al.* 2016 [**Příloha 5**], 2018a [**Příloha 6**]; Kusý *et al.* 2018a). Externí morfologie většiny zástupců Elateridae je až extrémně homogenní a naprostá většina dospělců je tak na první pohled dobře rozeznatelná díky podlouhlému tvaru těla, velkému a dobře pohyblivému prothoraxu, štítu s protaženými zadními rohy, většinou pilovitým tykadlům a přítomnosti funkčního klikacího mechanismu. Dospělci jsou fytofágní a většinou se vyskytují na vegetaci či pod kůrou stromů. Silně sklerotizované typické larvy, tzv. drátovci, jsou buď predátoři nebo fytofágové a najdeme je většinou v hnijícím dřevě, půdě či hrabance. Celý ontogenetický vývoj trvá v průměru okolo dvou let (Costa *et al.* 2010).

Zástupci několika linií Elateridae jsou schopni emitovat světlo. Bioluminiscence u této skupiny byla donedávna výhradní doménou amerických linií. Nejznámější takovou skupinou je bezesporu tribus Pyrophorini, který obsahuje asi 200 druhů z Neotropické oblasti a Oceánie. U této skupiny byla prokázána bioluminiscence u vajíček, larev, kukel i dospělců (Costa 1982, Costa *et al.* 2010). Dospělci mají většinou pár luminiscenčních orgánů umístěných na bázi štítu, přičemž na prvním abdominálním segmentu mají ještě jeden přídavný, který je však aktivován pouze při letu. Zajímavostí jsou larvy rodu *Pyrearinus* Costa, které žijí ve starších hnízdech termitů a pomocí bioluminiscence se snaží přilákat okolo letící hmyz, kterým se živí. Dalšími americkými skupinami, které obsahují zástupce schopné bioluminiscence, jsou Thylacosterninae a Campyloxeninae. Thylacosterninae obsahují asi 20 druhů, z nichž však pouze jeden dokáže emitovat světlo. Podčeleď Campyloxeninae obsahuje pouze dva druhy, z nichž bioluminiscence je schopný opět pouze jeden. Ani u jednoho ze dvou výše zmíněných světlo emitujících druhů neznáme imaturní stádia (Costa 1984, Costa *et al.* 2010). V roce 2019 čínští autoři publikovali mitochondriální genom prvního zástupce čeledi Elateridae z asijského kontinentu, který je schopen bioluminiscence (He *et al.* 2019). Momentálně pracujeme na jeho detailním popisu a na základě molekulárních dat se snažíme zjistit jeho pozici v rámci Elateridae a tím i pochopit vznik a evoluci bioluminiscence v této čeledi.

Dřívější autoři předpokládali blízkou příbuznost Elateridae s dalšími silně sklerotizovanými liniemi s klikacím mechanismem (viz původní koncept Elateroidea *sensu* Crowson 1955) (Lawrence 1988; Calder *et al.* 1993; Lawrence *et al.* 1995a, 2011; Lawrence & Newton 1995; Muona 1995). Monofylie Elateridae však byla již v minulosti často diskutována, většinou ve spojení s dřívější čeledí Cebrionidae (např. Lawrence 1988). Hned první molekulární studie poukázaly na to, že některé měkkotělé skupiny, donedávna řazené do Cantharoidea, jsou blízce příbuzné Elateridae, kdežto ostatní silně sklerotizované linie s klikacím mechanismem netvoří s Elateridae jeden klád (Bocáková *et al.* 2007, Sagegami-Oba *et al.* 2007b, Hunt *et al.* 2007). Následující molekulárně-fylogenetické studie tak postupně do Elateridae zařadily bývalé cantharoidní čeledi Drilidae (Kundrata & Bocák 2011a), Plastoceridae (Bocák *et al.* 2018) a Omalisidae (Kusý *et al.* 2018a). Anischiinae, kteří někdy bývali také řazeni do Elaterinae, byli potvrzeni jako součást Eucnemidae (Lawrence *et al.* 2007). Naopak skupiny Cebrionini, Lissominae a Thylacosterninae, které byly mnohdy vyčleňovány z definice Elateridae, jsou dnes na základě molekulárních studií součástí této čeledi (Kundrata & Bocák 2011a; Kundrata *et al.* 2016 [**Příloha 5**], 2018a [**Příloha 6**]). Otázkou tedy zůstává pouze pozice dvou malých enigmatických skupin - Eudicronychinae a Subprotelaterinae (Lawrence & Newton 1995, Costa *et al.* 2010). Co se týče první skupiny, výsledky molekulární fylogeneze založené na poměrně rozsáhlém materiálu by měly být brzy publikovány (Kundrata, nepublikovná data), avšak zástupce druhé skupiny vhodné pro izolaci DNA se doposud nepodařilo získat.

3.2. Fylogeneze a klasifikace Elateridae

Názory na fylogenetické vztahy mezi jednotlivými liniemi Elateridae a s tím související supraspecifickou klasifikaci čeledi nejsou jednotné od prvotní definice skupiny až po současnost (např. Candèze 1857, Schwarz 1906, Fleutiaux 1947, Calder 1996, Costa *et al.* 2010). První autoři se zaměřili výhradně na morfologii dospělců, dle které usuzovali na vzájemné vztahy mezi jimi definovanými vyššími taxonomickými jednotkami v rámci Elateridae. Lacordaire (1857) a Candèze (1857) původně rozdělili Elateridae do osmi tribů (Agrypnides, Mélanactides, Hémirhipides, Chalcolépidiides, Oxynoptérides, Tetralobides, Elatérides vrais a Campylides), a už prvně jmenovaný autor zmínil složitost práce na tvorbě klasifikace této čeledi. Později Candèze (1891) provedl revizi své klasifikace a zvedl počet tribů na 27. Schwarz (1906, 1907) vytvořil katalog všech druhů čeledi Elateridae a klasifikoval je do 28 tribů (Agrypnini, Octocryptini, Hemirhipini, Chalcolepidiini, Oxynopterini, Tetralobini, Dicrepidiini, Eudactylini, Monocrepidiini, Elaterini, Physorrhinini, Pomachiliini, Hypnoidini, Cardiophorini, Melanotini, Athouni, Pyrophorini, Ludiini, Crepidomenini, Hemicrepidiini, Allotriini, Dimitini, Hypodesiini, Cardiorhinini, Steatoderini, Adrastini, Lepturoidini a Physodactylini). Hyslop (1917) jako první použil larvální znaky pro konstrukci klasifikace Elateridae a na základě toho definoval čtyři podčeledi, z čehož dvě ponechal bez tribů a dvě větší rozdělil na sedm (Pyrophorinae) a šest (Elaterinae) tribů. Schenkling (1925, 1927) ve svém doposud nejobsáhlejším světovém katalogu rozdělil Elateridae do 29 podčeledí, z nichž většina víceméně korespondovala s dřívějšími Schwarzovými triby. Fleutiaux (1947) revidoval faunu Francouzské Indočíny a vytvořil identifikační klíč k 23 tamějším podčeledím včetně Anischiinae.

Crowson (1961) upozornil na fakt, že téměř všechny dosavadní studie používají pro klasifikaci čeledi tytéž znaky, t.j. tvar přední části hlavy, maxilárních palpů, tykadel, pronotosternálních švů, prosterna, mesoventrální jamky, kyčelních jamek, krytů zadních kyčlí, tarsů a drápků. Crowson se snažil najít nové znaky na křídelní žilnatině a stejně jako před ním i Hyslop na larvách, a následně rozdělil Elateridae do šesti podčeledí. Ôhira (1962) v revizi japonské fauny zdvojnásobil tento počet podčeledí a také vytvořil schéma předpokládaných fylogenetických vztahů v rámci Elateridae, z čehož později vycházel i Kishii (1987). Gurjeva (1974) detailně zkoumala znaky na thoraxu napříč skupinami v Elateridae a přišla s novou klasifikací, která čítala 10 podčeledí. Dolin (1975) následně provedl detailní výzkum křídelní žilnatiny u všech skupin Elateridae a potvrdil dřívější klasifikaci Gurjevy. Později také vytvořil schéma fylogeneze Elateridae, zahrnující všechny jím dříve definované skupiny (Dolin 1978). Stibick (1979) kompletně překopal dosavadní klasifikace a na základě larválních i adultních znaků vytvořil novou, když definoval 12 podčeledí, 37 tribů a 20 podtribů. Jeho klasifikace však veskrze nebyla pozdějšími autory akceptována. Lawrence (1988) zařadil mezi Elateridae bývalou čeleď Cebrionidae, jejíž zástupci mají mírně odlišnou morfologii, pravděpodobně v důsledku neotenie. Samice v této skupině jsou totiž fyzogastrické, nelétavé, a mají zkrácená tykadla a krovky. Calder *et al.* (1993) revidovali podčeleď Lissominae, přičemž na základě kladistické analýzy kombinovaných larválních a adultních znaků zkoumali fylogenetické vztahy uvnitř Elateridae. Jejich výsledky ukázaly Cebrioninae jako sesterskou skupinu k ostatním Elateridae a poukázaly na nejasné postavení Thylacosterninae. Lawrence & Newton (1995) shrnuli dosavadní poznatky o skupině a inspirováni předchozí prací, klasifikovali v Elateridae 15 podčeledí, přičemž další tři (Anischiinae, Eudicronychinae a Subprotelaterinae) ponechali jako Elateridae *incertae sedis*. Australskou faunu později klasifikoval Calder (1996), americkou Johnson (2002), palearktickou Cate *et al.* (2007) a africkou Girard (2017). Costa *et al.* (2010) v Handbook of Zoology shrnuli veškeré dosavadní znalosti o Elateridae, které rozdělili do 17 podčeledí: Agrypninae, Campyloxeninae, Cardiophorinae, Cebrioninae, Denticollinae, Elaterinae, Eudicronychinae, Hemiopinae, Lissominae, Morostomatinae, Negastriinae, Oxynopterinae, Physodactylinae, Pityobiinae, Semiotinae, Subprotelaterinae a Thylacosterninae.

První molekulárně založené studie poukazovaly na blízký vztah Elateridae s původně cantharoidní měkkotělou čeledí Drilidae, avšak nízký počet analyzovaných zástupců těchto linií neumožňoval vyvození nějakých detailnějších závěrů (Bocáková *et al.* 2007, Hunt *et al.* 2007, Timmermans *et al.* 2010). Kundrata & Bocák (2011a) proto analyzovali dataset čítající 210 zástupců Elateriformia včetně přibližně 80 zástupců Elateridae a 10 zástupců Drilidae. Výsledné topologie ukázaly, že Cebrioninae jsou pouze terminální linií podčeledi Elaterinae a Drilidae tvoří součást podčeledi Agrypninae. Nástup molekulárních metod tedy přinesl revoluci ve vnímání Elateridae, kteří přestali být extrémně homogenní skupinou. Další výhoda molekulárně-fylogenetických metod tkvěla v tom, že autoři konečně mohli vyřešit dlouho přetrvávající klasifikační problémy, které se nedařilo objasnit za použití samotné morfologie, často kvůli přítomnosti homoplastických znaků v nepříbuzných skupinách. Takto například Lawrence *et al.* (2007) dokázali, že Anischiinae nepatří mezi Elateridae, ale měli by být klasifikováni v Eucnemidae.

Kundrata *et al.* (2016) [**Příloha 5**] vytvořili robustní čtyřgenovou molekulární fylogenezi Elateridae na základě datového souboru o počtu 148 zástupců Elateridae a 30 zástupců outgroup. Primárním cílem studie bylo testovat monofylii podčeledi Pityobiinae *sensu* Calder (1996), která zahrnovala dva americké rody a několik rodů z Austrálie a Nového Zélandu. Již předchozí autoři si všimli rozdílné morfologie amerických a australasijských skupin, avšak chyběla fylogenetická hypotéza, která by potvrdila či vyvrátila monofylii skupiny. Jelikož jak americký rod *Pityobius* LeConte, tak i skupina australasijských rodů tvořili samostatné nepříbuzné větve, autoři byli nuceni popsat a definovat novou podčeleď, kterou nazvali Parablacinae dle typového rodu *Parablax* Schwarz. Výsledky dále ukázaly sesterský vztah Elaterinae ke zbytku Elateridae, monofylii Elaterinae, Agrypninae, Cardiophorinae, Negastriinae, a též kládu Lissominae a Thylacosterninae, přičemž posledně jmenovaná skupina tvořila pouze terminální větev uvnitř Lissominae. Velmi diverzifikovaný klád obsahující Morostomatinae, Dendrometrinae (včetně bývalých podčeledí Hypnoidinae, Diminae, Oxynopterinae a Semiotinae), Cardiophorinae a Negastriinae sice nebyl statisticky podpořený, ale podobnou topologii publikovali již Sagegami-Oba *et al.* (2007a) na základě zcela odlišně koncipovaného datového souboru. Práce potvrdila pozice Drilini v Agrypninae a Cebrionini v Elaterinae. Další důležitou studii publikovali Bocák *et al.* (2018), kteří poprvé sekvenovali typový druh rodu *Plastocerus,* aby testovali jeho pozici v Elateroidea. Autoři se totiž dlouhou dobu přeli o tom, zda tento rod patří do vlastní čeledi Plastoceridae či do Elateridae (např. Crowson 1972, Platia & Németh 2011). Výsledky molekulární fylogeneze jasně určily postavení rodu *Plastocerus* Schaum uvnitř Elateridae, kde pro něj autoři vytvořili podčeleď Plastocerinae.

Dlouhodobým klasifikačním problémem bylo postavení Tetralobinae. Tato skupina obsahuje několik rodů z tropické Afriky, Asie a Australské oblasti (Kubaczková & Kundrata 2017). Zástupci této skupiny patří mezi vůbec největší Elateridae světa (délka až 8 cm) a jejich larvy nepřipomínají klasické elateridní drátovce (Costa *et al.* 1994, 2010). Jelikož mají dospělci na křídelní žilnatině tzv. anální buňku a na bázi drápku několik dlouhých set, což jsou znaky běžně používané pro definici podčeledi Agrypninae, byli Tetralobinae některými autory řazeni právě sem (např. Stibick 1979, Calder 1996, Costa *et al.* 2010). Kundrata *et al.* (2018a) [**Příloha 6**] poprvé zkoumali postavení Tetralobinae za použití molekulárních markerů. Do analýz zařadili zástupce tří rodů ze všech zoogeografických oblastí a jejich výsledky jasně ukázaly, že Tetralobinae rozhodně do Agrypninae nepatří. Namísto toho je tato skupina pravděpodobně sesterská ke všem ostatním kovaříkům, což podporuje i odlišný typ larvy a některé morfologické znaky dospělců (Kundrata *et al.* 2018a) [**Příloha 6**]. Tato studie potvrdila, že dřívější klasifikace, založené na z velké části homoplastických morfologických znacích, nejsou přirozené. Proto je velmi důležité spojit znalosti morfologie a ekologie skupiny s molekulární fylogenezí a podívat se tak na problemtiku příbuzenských vztahů v rámci Elateridae komplexněji. Výsledky této studie poukázaly na fakt, že i v dalších skupinách bude třeba použít tzv. integrativní taxonomii pro odhalení potenciálních homoplastických znaků, které jsou zcela nevhodné pro tvorbu klasifikace. To se přesně potvrdilo i v následující studii, která byla věnovaná molekulární fylogenezi uvnitř podčeledi Cardiophorinae (Douglas *et al.* 2018 [**Příloha 7**]). Poslední důležitou změnou v klasifikaci čeledi je zařazení bývalé měkkotělé cantharoidní čeledi Omalisidae do Elateridae (Kusý *et al.* 2018b). Omalisidae byli v mnoha předchozích publikovaných analýzách poblíž nebo dokonce uvnitř Elateridae, a jejich zařazení do této čeledi (jako podčeleď Omalisinae) je tedy logickým vyústěním. Jelikož s nástupem éry genomového sekvenování přicházejí nové možnosti testovat fylogenetické vztahy uvnitř Elateroidea i Elateridae, můžeme v následujících letech očekávat další změny.

3.3. Přehled diverzity Elateridae

Jak je patrné z předchozí podkapitoly, obrovská druhová diverzita ve spojení s uniformní morfologií většiny zástupců Elateridae je překážkou v konstrukci přirozené klasifikace. Dosud neexistuje koncenzus supraspecifické klasifikace, který by uznávala naprostá většina autorit v oboru. Stejně tak je tomu i s rodovou a druhovou klasifikací, kdy se někdy názory autorů diametrálně odlišují. Hyslop (1921) publikoval katalog rodových jmen v Elateridae, který následně doplnil Arnett (1955) o později popsané rody. Od té doby byla ustanovena spousta dalších rodů a podrodů, avšak moderní katalog reflektující nejnovější klasifikaci a změny na úrovni rodových jmen za posledních více než 60 let stále chybí. Spolu s mezinárodním týmem kolegů jsme se rozhodli tento nedostatek napravit a právě máme v recenzním řízení první část tohoto katalogu, která pokrývá rodová jména v prvních deseti podčeledích, včetně ustanovení nových rodů, nových taxonomických kombinací a vysvětlení spousty dlouhodobě neřešených nomenklatorických problémů, které částečně způsobovaly chaotickou klasifikaci (Kundrata *et al.* nepublikovaná data). Jelikož na projektu spolupracují přední odborníci na Elateridae spolu s členy ICZN (The International Commission on Zoological Nomenclature), třídílný katalog by se měl stát široce akceptovanou základní literaturou pro všechny budoucí systematické entomology zabývající se (nejen) nadčeledí Elateroidea.

Bohužel také neexistuje žádný globální druhový katalog, a proto se musíme spoléhat na více či méně aktuální katalogy zahrnující různě velké regiony světa. Jedním z nejobsáhlejších děl je určitě Katalog palearktických brouků, v němž jsou obsaženi i Elateridae (Cate *et al.* 2007). Seznam australských druhů zpracoval Calder (1996) a africké druhy shrnul Girard (2017). Katalog Elateridae Nového světa by potřeboval aktualizaci (Blackwelder 1944), a druhový seznam kovaříků Orientální oblasti, která je jednou z druhově nejbohatších oblastí světa, naprosto chybí. Stejně jako geograficky orientované katalogy jsou důležité i ty, které jsou zaměřené taxonomicky. V poslední době byly například zpracovány komentované katalogy pro Selatosomini (Schimmel *et al.* 2015, 2016), Tetralobinae (Kubaczková & Kundrata 2017), Cardiophorinae (Douglas 2017), Dimini (Kundrata *et al.* 2018b), Senodoniini (Kundrata *et al.* 2018c). Následující přehled obsahuje souhrn informací o klasifikaci a diverzitě jednotlivých podčeledí Elateridae.

Agrypninae tvoří přibližně čtvrtinu veškeré druhové rozmanitosti Elateridae a jsou tak druhou největší podčeledí této čeledi. Vyskytují se ve všech zoogeografických regionech a momentálně se dělí do devíti tribů: Agrypnini, Anaissini, Euplinthini, Drilini, Hemirhipini, Oophorini, Platycrepidiini, Pseudomelanactini a Pyrophorini. Tato podčeleď vznikla spojením Agrypninae *sensu* Hayek (1973) s Pyrophorinae, Drilidae, Hemirhpinae a Monocrepidiinae (=Oophorinae) (Costa *et al.* 2010, Kundrata & Bocák 2011a). Tribus Drilini obsahuje měkkotělé samce a larviformní neotenní samice. Larvy zástupců této skupiny predují plže. Pyrophorini obsahují zástupce schopné bioluminiscence. Molekulární analýzy (Kundrata & Bocák 2011a; Kundrata *et al.* 2016 [**Příloha 5**], 2018a [**Příloha 6**]) sice robustně potvrzují monofylii podčeledi Agrypninae, ale současně naznačují, že bude nezbytná důkladná revize její tribální klasifikace.

Campyloxeninae byli dříve řazeni do Agrypninae z důvodu přítomnosti luminiscenčních orgánů na prothoraxu (Lawrence & Newton 1995). Dnes zde patří dva monotypické rody, z nichž pouze jeden je schopný bioluminiscence (Costa *et al.* 2010, Arias-Bohart 2015). Larvy této podčeledi jsou neznámé.

Cardiophorinae obsahují přibližně 1100 popsaných druhů řazených do 38 rodů (Douglas 2017, Douglas *et al.* 2018 [**Příloha 7**]). Dospělci se většinou vyznačují srdčitým štítkem, typickým tvarem prothoraxu a křídelní žilnatinou, která je však částečně sdílená s Negastriinae. Larvy se vyznačují též specifickou morfologií; jsou to predátoři a žijí většinou v půdě nebo ve dřevě (Douglas 2017). Douglas (2011) poprvé testoval monofylii a fylogenetické vztahy uvnitř skupiny za použití morfologicky zaměřené analýzy, a později revidoval rodovou klasifikaci (Douglas 2017). Recentní molekulární fylogeneze Cardiophorinae (Douglas *et al.* 2018 [**Příloha 7**] a Kundrata et al., nepublikovaná data) poukazují na fakt, že některé dlouhou dobu používané morfologické znaky jsou pro klasifikaci skupiny zcela nevhodné a že rodová diverzita této čeledi je daleko větší, než se očekávalo. Analýzy též odhalily přítomnost kládu obsahujícího zejména rody s gondwanským rozšířením, jenž je také definován unikátní morfologií v rámci podčeledi (Douglas *et al.* 2018 [**Příloha 7**]).

Dendrometrinae (= Denticollinae) patří díky přibližně 1700 popsaným druhům mezi největší podčeledi Elateridae, avšak limity této skupiny se v každé klasifikaci dost podstatně liší (Kundrata & Bocák 2011). Některé ze zde zařazených tribů jsou totiž mnohými autory považovány za samostatné podčeledi (Costa *et al.* 2010). Molekulární fylogeneze většinou ukazují Dendrometrinae skutečně jako nemonofyletickou skupinu (Kundrata *et al.* 2016 [**Příloha 5**], 2018a [**Příloha 6**]; Bocák *et al.* 2018). Momentálně jsou zde řazeny triby

Crepidomenini, Dendrometrini, Dimini, Hypnoidini, Oxynopterini, Pleonomini, Prosternini, Selatosomini, Semiotini a Senodoniini (Kundrata *et al.* 2018a) [**Příloha 6**]. Někteří zástupci působí jako škůdci zemědělských plodin (Costa *et al.* 2010). Aktualizované druhové katalogy jsou známé pro Selatosomini (Schimmel *et al.* 2015, 2016), Dimini (Kundrata *et al.* 2018b) a Senodoniini (Kundrata *et al.* 2018c).

Elaterinae jsou druhově nejpočetnější podčeledí Elateridae. Bylo popsáno přibližně 200 rodů a 3500 druhů ze všech zoogeografických regionů (Costa *et al.* 2010, Kundrata & Bocák 2011a). Podčeleď je řazena do 12 tribů: Agriotini, Ampedini, Aplastini, Cebrionini, Dicrepidiini, Elaterini, Megapenthini, Melanotini, Odontonychini, Physorhinini, Pomachiliini, Synaptini (Kundrata *et al.* 2018a [**Příloha 6**]). Většina předchozích studií (např. Lawrence & Newton 1995, Costa *et al.* 2010) považovala Cebrionini za samostatnou podčeleď obsahující rody původně řazené v čeledi Cebrionidae a v tribu Aplastini *sensu* Stibick (1979). Kundrata & Bocák (2011a) však dokázali, že Aplastini nejsou příbuzní Cebrionini, a že obě skupiny jsou pouze terminálními liniemi v Elaterinae. Do této podčeledi jsou řazeni nejvýznamnější zemědělští škůdci v rámci Elateridae (např. Furlan *et al.* 2017). Publikovaná i dosud nepublikovaná data naznačují, že tribální klasifikace podčeledi Elaterinae je pouze uměle vytvořená a bude potřeba zásadní revize stávající klasifikace (Kundrata *et al.* 2016 [**Příloha 5**], 2018a [**Příloha 6**], nepublikovaná data).

Eudicronychinae byli dříve pod názvem Dicronychidae samostatnou čeledí v Elateroidea, a někteří autoři je za samostatnou čeleď považují dodnes (např. Girard 2011, 2017). Tato skupina se vyznačuje dosti unikátní morfologií samčích pohlavních orgánů a pretarsálních drápků. Několik desítek převážně afrických druhů je řazeno do tří nebo čtyř rodů (Costa *et al.* 2010, Girard 2011). Larvy této skupiny jsou neznámé. Molekulární fylogeneze skupiny by měla odhalit fylogenetickou pozici Eudicronychinae v rámci Elateroidea (Kundrata *et al.*, nepublikovaná data).

Hemiopinae obsahují několik rodů příbuzných asijskému rodu *Hemiops* Laporte. Limity skupiny zůstávají nejasné a v budoucích pracích bude potřeba také detailně prostudovat vztah Hemiopinae a Oestodinae (Stibick 1979, Kundrata *et al.* 2016 [**Příloha 5**], 2018a [**Příloha 6**]). Larvy této skupiny jsou taktéž neznámé (Costa *et al.* 2010).

Lissominae Laporte, 1835 byli dříve klasifikováni jako samostatná čeleď či podčeleď v Throscidae (např. Burakowski 1973). Dnes se dělí na dva triby, Lissomini a Protelaterini, které obsahují několik rodů řazených do přibližně 150 druhů ze všech zoogeografických oblastí (Calder *et al.* 1993, Costa *et al.* 2010). Tribus Oestodini, který zde byl dříve též řazen, byl na základě molekulární fylogeneze (Kundrata *et al.* 2016 [**Příloha 5**]) vyjmut z Lissominae a je pravděpodobně příbuzný s Hemiopinae. Otázka monofylie a definice skupiny je však stále otevřená, protože některé analýzy naznačují, že jednou z terminálních linií v Lissominae jsou rody běžně řazené do Thylacosterninae (Kundrata *et al.* 2016 [**Příloha 5**], 2018a [**Příloha 6**]; Bocák *et al.* 2018).

Morostomatinae je malá enigmatická skupina madagaskarských kovaříků. Její zástupci byli dříve řazeni do různých skupin a monofylie této podčeledi i nadále zůstává otázkou (Dolin 2000, Costa *et al.* 2010). Molekulární studie naznačují, že tato skupina je jednou z terminálních linií spolu s Agrypninae, Dendrometrinae, Cardiophorinae a Negastriinae (Kundrata *et al.* 2014, 2016 [**Příloha 5**], 2018a [**Příloha 6**]).

Negastriinae obsahují většinou velmi malé druhy vázané na břehy tekoucích vod. Skupina se dělí na triby Negastriini a Quasimusini a obsahuje přibližně 500 popsaných druhů (Schimmel & Tarnawski 2009, Kundrata & Bocák 2011a). Negastriinae sdílejí některé morfologické znaky s Cardiophorinae (Douglas 2011, 2017) a molekulární studie jejich příbuznost většinou potvrzují (Kundrata *et al.* 2016 [**Příloha 5**], Douglas *et al.* 2018 [**Příloha 7**], Bocák *et al.* 2018).

Oestodinae je malá podčeleď obsahující dva severoamerické rody (Johnson 2002, Kundrata *et al.* 2016 [**Příloha 5**]). Dříve byla tato skupina součástí Lissominae, avšak dnes je považována za sesterskou skupinu Hemiopinae (Stibick 1979; Kundrata *et al.* 2016 [**Příloha 5**], 2018a [**Příloha 6**]).

Omalisinae byli ještě donedávna považováni za samostatnou čeleď. Dříve byli klasifikováni v Cantharoidea, kde byli dáváni do blízkosti Lycidae či Drilidae (Crowson 1972). Definice této skupiny prošla nedávno razantními změnami. Omalisinae momentálně obsahují 27 druhů v šesti rodech (Bocák & Brlík 2008; Kundrata & Bocák 2011a; Kundrata *et al.* 2015b [**Příloha 9**], 2018d; Boček *et al.* 2018). Zástupci této podčeledi se vyskytují v oblasti Středozemního moře, v Malé Asii a na Kavkaze (Boček *et al.* 2018; Kundrata *et al.* 2018d). Samci mají měkké tělo, ale jsou letuschopní, samice jsou brachypterní a larvy predují mnohonožky (Bocák & Brlík 2008). Fylogenetická pozice Omalisinae v rámci Elateridae zůstává nevyřešena (Kusý *et al.* 2018b), ale nedávné molekulární studie zaznamenaly pokrok v otázce fylogenetických vztahů uvnitř skupiny (Kundrata *et al.* 2015b [**Příloha 9**], Boček *et al.* 2018).

Podčeleď Parablacinae byla vytvořena pro 22 druhů v sedmi rodech z Austrálie a Nového Zélandu (Kundrata *et al.* 2016 [**Příloha 5**]). Rody dnes patřící do této skupiny byly dříve řazeny do Pityobiinae, s výjimkou rodu *Ophidius* Candèze (Elaterinae) (Calder 1996, Costa *et al.* 2010). Arias-Bohart & Elgueta (2015) poukázali na blízkou příbuznost rodů řazených v Parablacinae s jihoamerickou faunou, což svědčí o tzv. gondwanském rozšíření této starobylé skupiny.

Physodactylinae byla skupina navzájem nepříbuzných rodů, jejichž zástupci sdíleli srpovité mandibuly a hrabavé zadní končetiny (Costa *et al.* 2010). Rosa (2014) provedla revizi této skupiny a ponechala zde pouze dva jihoamerické rody, z nichž ani jeden však dosud nebyl sekvenován a jejich larvy jsou neznámé.

Podčeleď Pityobiinae zahrnovala rod *Pityobius* LeConte ze severní Ameriky, *Tibionema* Solier z jižní Ameriky a několik rodů z Austrálie a Nového Zélandu, které dnes tvoří podčeleď Parablacinae (Kundrata *et al.* 2016 [**Příloha 5**]). Již předchozí autoři si všimli rozdílné morfologie amerických a australasijských skupin, avšak chyběla fylogenetická hypotéza, která by nastínila skutečné vztahy mezi těmito liniemi. Kundrata *et al.* (2016) [**Příloha 5**]) dokázali, že *Pityobius* není příbuzný s dnešními Parablacinae. *Tibionema* je sice morfologicky odlišná od rodu *Pityobius*, avšak momentálně zůstává v této podčeledi, dokud se její pozice neobjasní. Stibick (1979) zde umístil také rod *Pectocera* Hope, ale ten je dnes součástí tribu Oxynopterini v Dendrometrinae (Costa *et al.* 2010, Kundrata & Bocák 2011a).

Subprotelaterinae je monogenerická asijská podčeleď, jejíž fylogenetické vztahy zůstávají nevyřešeny. Tato skupina byla dříve klasifikována v Eucnemidae či Elateridae *incertae sedis* (Lawrence & Newton 1995, Costa *et al.* 2010).

Tetralobinae patří mezi největší kovaříky světa. Tato skupina je známá zejména z Afriky, ale vyskytuje se i v Austrálii a v menší míře v Asii (Costa *et al.* 1994, 2010). Bylo popsáno 78 druhů v sedmi rodech, řazených do tribů Tetralobini a Piezophyllini (Kubaczková & Kundrata 2017). Larvy této skupiny jsou odlišné od většiny ostatních Elateridae; jsou měkké, fyzogastrické a chlupaté, a pravděpodobně se živí termity (Costa *et al.* 1994). Dříve byli Tetralobinae řazeni do Agrypninae (Stibick 1979; Costa *et al.* 1994, 2010), avšak recentní molekulárně-fylogenetická hypotéza ukazuje Tetralobinae jako sesterskou skupinu ostatních linií Elateridae (Kundrata *et al.* 2018a) [**Příloha 6**].

Thylacosterninae byli v minulosti řazeni mezi Eucnemidae či Throscidae (např. Crowson 1961). Dnes zde patří asi 45 druhů z jižní Ameriky, Afriky, Asie a Austrálie (Vahtera *et al.* 2009). Jeden druh je schopen bioluminiscence, avšak u ostatních tato nebyla nikdy pozorována (Costa *et al.* 2010). Molekulární studie naznačují, že by Thylacosterninae mohli být ve skutečnosti součástí podčeledi Lissominae (Kundrata *et al.* 2016 [**Příloha 5**], 2018a [**Příloha 6**]; Bocák *et al.* 2018).

4. Fylogeneze, klasifikace a diverzita Drilini

(Přílohy 8–13)

4.1. Monofylie a fylogenetická pozice Drilini

Drilini je malá měkkotělá skupina obsahující přibližně 150 druhů, jenž byla dříve považována za samostatnou čeleď v rámci Cantharoidea (např. Wittmer 1944, Crowson 1972). Vznik této linie je datován do období pozdního eocénu, přibližně před 35,5 miliony lety (Kundrata & Bocák v tisku [**Příloha 13**]). Zatímco dospělí samci mají plně vyvinuté krovky a zadní křídla, samice jsou bezkřídlé a téměř kompletně larviformní (např. Crowson 1972, Kobieluszová & Kundrata 2015). Larvy jsou měkké, dle stádia ontogeneze chlupaté či téměř lysé, a jsou predátory suchozemských plžů (Baalbergen *et al.* 2014 [**Příloha 8**], Šormová *et al.* 2018 [**Příloha 12**]). Většina diverzity je známa z Palearktické a Afrotropické oblasti, ale několik druhů se vyskytuje také v jižní a jihovýchodní Asii (Kundrata & Bocák 2017 [**Příloha 11**], Kundrata & Šormová 2018, Kundrata & Bocák v tisku [**Příloha 13**]).

Čeleď Drilidae dlouhou dobu sloužila jako taxon, kam se řadily převážně rody, které morfologicky nezapadaly do ostatních čeledí Cantharoidea. Wittmer (1944) ve svém katalogu uváděl 35 rodů z různých zoogeografických oblastí, avšak Crowson (1972) později výrazně redukoval definici skupiny. Bocák *et al.* (2010) v Handbook of Zoology uváděli pouze šest rodů, z nichž tři byly později na základě molekulární fylogeneze převedeny do Omalisidae (dnes Elateridae: Omalisinae) (Kundrata & Bocák 2011a, Kundrata *et al.* 2015b [**Příloha 9**]). Ve skupině tak zůstaly pouze rody *Drilus* Olivier, *Malacogaster* Bassi a *Selasia* Laporte, které byly nedávno doplněny o dalších 11 rodů, zejména z tropické Afriky (Kundrata & Bocák 2017 [**Příloha 11**], Kundrata & Bocák v tisku [**Příloha 13**]). Monofylie takto revidovaného tribu Drilini byla potvrzena v posledně jmenované studii. Hlavní morfologické znaky definující dospělé samce Drilini jsou měkké, slabě sklerotizované tělo, jedenáctičlánková tykadla, bidentátní mandibuly, krátký pedicel, který je vždy kratší než třetí tykadlový článek, zkrácený čtvrtý tarsální segment, který má na spodní straně membranózní lalok, pretarsální drápek se setami na bázi a výrazně zakřivený falus s preapikálním hákem. Hlavními znaky dospělých samic jsou larvální vzhled, malé oči, bidentátní mandibuly, tykadla s 8–12 články, nepřítomnost křídel, ovipositor s krátkými styly a bursa copulatrix bez viditelných skleritů (Kundrata & Bocák v tisku [**Příloha 13**]).

Bocáková *et al.* (2007) poprvé zkoumali evoluci neotenie u Elateroidea pomocí molekulárních markerů, přičemž zjistili blízkou příbuznost Drilidae s Elateridae. Jejich datový soubor však obsahoval jenom několik zástupců čeledi Elateridae a jednoho zástupce rodu *Drilus*. Kundrata & Bocák (2011a) se ve své studii přímo zaměřili na testování fylogenetické pozice Drilidae. Autoři zjistili, že tato skupina je pouze terminální větví uvnitř Elateridae, a proto ji klasifikovali jako tribus Drilini v podčeledi Agrypninae. Pozice Drilini v Elateridae byla poté potvrzena mnoha dalšími molekulárně-fylogenetickými studiemi (např. Bocák *et al.* 2014, 2016 [**Příloha 2**]; Kundrata *et al.* 2014a, 2015b [**Příloha 9**], 2016 [**Příloha 5**], 2018a [**Příloha 6**]; McKenna *et al.* 2015; Amaral *et al.* 2016; Timmermans *et al.* 2016; Martin *et al.* 2017; Kusý *et al.* 2018a, 2018b).

4.2. Fylogeneze a klasifikace Drilini

Fylogenetické vztahy uvnitř Drilini donedávna zůstávaly neprostudovány, mimo jiné pravděpodobně také proto, že nikdo často pořádně netušil, co vlastně do této skupiny zrovna patří. Historie klasifikace Drilini je totiž plná až převratných změn, které z různých důvodů mnohdy nebyly plně akceptovány ještě dlouho po jejich publikování. Od konce 19. století až do poloviny 20. století zde byla klasifikována spousta navzájem si zcela nepříbuzných linií, které však spojovalo měkké tělo, typicky „podivný habitus" a často silně pilovitá až hřebenitá tykadla, a které nešlo zařadit mezi tehdy definované ostatní skupiny Malacodermata a později Cantharoidea. Olivier (1910) uvedl ve svém katalogu Drilidae 20 rodů a později Wittmer (1944) dokonce 35 rodů. Zástupci Drilidae tehdy pocházeli téměř z celého světa, převážně z Afriky, Evropy a tropické Asie, ale také například z Nového světa.

Crowson (1972) ve své revizi tehdejší nadčeledi Cantharoidea drasticky zredukoval počet rodů patřících do Drilidae. Uvedl, že do této skupiny by měly být zařazeny pouze „rody *Drilus*, *Malacogaster*, *Selasia* a snad i některé další malé a málo známé rody, které ale osobně nestudoval" (Crowson 1972: 51). Provizorně zde zařadil i rod *Pseudeuanoma*, který dříve patřil do čeledi Omalisidae. Většinu rodů pak převedl do Lampyridae, Phengodidae, Omethidae a Lycidae, avšak některé taxony z Wittmerova katalogu ve své práci nezmínil, a nebylo tedy patrné, kam by měly být zařazeny. Kazantsev (2007) zařadil do Drilidae rod *Pachytarsus* Motschulsky, ale jelikož se s největší pravděpodobností jedná o zástupce čeledi Lampyridae (Kundrata, nepublikovaná data), pozdější autoři toto zařazení neakceptovali. Bocák (2007) v Katalogu palearktických brouků uvedl v čeledi Drilidae šest rodů, když zde dodatečně zařadil drobný monotypický rod *Paradrilus* a také *Euanoma* z důvodu jeho podobnosti s rodem *Pseudeuanoma* (Kundrata & Bocák 2007, Bocák *et al.* 2010). Přestože rod *Thilmanus* Gemminger byl prokazatelně součástí čeledi Omalisidae (Bocák & Brlík 2008), Kazantsev (2010, 2011) jej klasifikoval v Drilidae jako součást podčeledi Thilmaninae, kterou dělil na triby Thilmanini a Euanomini.

Kundrata & Bocák (2011a) v molekulárně-fylogenetické studii zaměřené na pozici Drilidae zjistili, že *Drilus* a *Selasia* jsou pouze terminální větví uvnitř podčeledi Agrypninae v Elateridae. Autoři tedy čeleď reklasifikovali jako tribus Drilini. Rod *Pseudeuanoma* však tvořil klád s rodem *Omalisus* Geoffroy, a proto byl i s morfologicky podobným rodem *Euanoma* přesunut do čeledi Omalisidae (oba rody jsou dnes mimochodem synonymizovány; Boček *et al.* 2018). V další publikaci Kundrata & Bocák (2011b) detailně zkoumali morfologii rodu *Pseudothilmanus* Pic, který byl naposledy zmiňován právě ve Wittmerově katalogu, a klasifikovali jej v čeledi Rhagophthalmidae. Stejně tak Jeng (2012) studoval rod *Rhipidiomorphus* Pic a zařadil jej do byrrhoidní čeledi Psephenidae. Kundrata *et al.* (2014a) poté analyzovali příbuzenské vztahy v rámci Elateroidea a nově zařadili do datového souboru také zástupce rodu *Malacogaster*, který zapadl do kládu s rody *Drilus* a *Selasia*.

Problematickým rodem stále zůstával *Paradrilus* z jihu Iberského poloostrova, jehož jediný druh byl známý pouze z historických sbírek a naprosto chyběl čerstvý materiál vhodný pro izolaci DNA. Jelikož se však poprvé za posledních přibližně 100 let podařilo několik jedinců v terénu odchytit, Kundrata *et al.* (2015b) [**Příloha 9**] dostali příležitost testovat pozici tohoto rodu na základě molekulárně-fylogenetické analýzy. Rod *Paradrilus* vytvořil samostatnou větev v rámci čeledi Omalisidae, což také potvrdilo detailní studium jeho morfologie. Kundrata *et al.* (2015b) [**Příloha 9**] do Omalisidae vrátili rod *Thilmanus* (Thilmaninae), který tam byl řazen již dříve (Bocák & Brlík 2008). Jeho pozice v Omalisidae byla později potvrzena i na základě výsledků molekulární fylogeneze (Boček *et al.* 2018). Drilini tak poté obsahovali pouze tři „klasické" rody *Drilus*, *Malacogaster* a *Selasia*, které sdílejí podobnou morfologii. Kundrata & Bocák (2017) [**Příloha 11**] nedávno popsali pět nových rodů z tropické Afriky a v blízké době přibude dalších pět afrických a jeden palearktický rod (Kundrata & Bocák v tisku [**Příloha 13**]).

Kundrata & Bocák (v tisku) [**Příloha 13**] poprvé podrobně zkoumali fylogenetické vztahy mezi jednotlivými liniemi v rámci celého tribu Drilini, když sekvenovali 66 jedinců reprezentujících 44 druhů, patřících do všech známých rodů. Jejich výsledky naznačily, že studovaná skupina vznikla pravděpodobně v tropické Africe a až později se dostala do Palearktické a Orientální oblasti. Každopádně tak mizí obvyklé vnímání Drilini jako víceméně palearktické skupiny, protože veškerá data poukazují na vznik a největší diverzitu skupiny právě v oblasti tropické Afriky. Drilini jsou rozděleni do pěti hlavních kládů, které vznikly krátce po vzniku celé skupiny v pozdním eocénu. Tři bazální klády obsahují šest výhradně afrických rodů a rod *Selasia*, který má taktéž největší diverzitu v tropické Africe, ale některé druhy zasahují přes Sokotru, Arabský poloostrov, Himaláje a Indický subkontinent až do severního Thajska (Trllová & Kundrata 2015, Kundrata & Šormová 2018). Čtvrtý klád obsahuje velikostně velmi drobné druhy z pralesů západní a střední Afriky, rozdělené do čtyř rodů (Kundrata & Bocák 2017 [**Příloha 11**], Kundrata 2018). Výhradně palearktické rody, včetně *Drilus* a *Malacogaster*, tvoří pátý klád. Jelikož některé z analýz naznačily, že rod *Drilus* by nemusel být monofyletický, bude třeba více materiálu a následných analýz k testování fylogenetických vztahů uvnitř palearktických linií, zejména k vyjasnění pozice rodů *Drilus* a *Malacogaster*. Detailní výzkum morfologie antennálních sensil taktéž poukazuje na blízký vztah těchto dvou rodů (Faucheux & Kundrata 2017).

Kundrata & Bocák (v tisku) [**Příloha 13**] však nezkoumali pouze vznik, fylogenezi a biogeografii Drilini. Studie také dokumentovala postupnou evoluci morfologických znaků spojených s přechodem ze silně sklerotizovaného těla k měkkotělosti v důsledku neotenie. Takovým způsobem modifikovaných linií je v čeledi Elateridae několik, včetně Plastocerinae, Omalisinae, Cebrionini a Drilini (Kundrata & Bocák 2011a, Bocák *et al.* 2018, Kusý *et al.* 2018b). Přestože jsou morfologické změny nejlépe pozorovatelné u samic, neotenie do jisté míry ovlivňuje i samce. Když Kundrata & Bocák (2011a) zařadili Drilini s měkkotělými samci, larviformními samicemi a drátovcům nepodobnými larvami do čeledi Elateridae, která byla po většinu své existence známá morfologickou homogenitou svých silně sklerotizovaných a klikacím mechanismem opatřených zástupců, pro většinu vědců to byl šok a někteří to zprvu odmítali přijmout (viz např. Lawrence 2016a). Kundrata & Bocák (v tisku) [**Příloha 13**] však podávají jasný důkaz o postupných změnách spojených s přechodem ze silně sklerotizovaného těla po měkkotělý „cantharoidní” vzhled, zejména v postupném zeslabení kutikuly a redukcích částí ústního ústrojí, thoraxu a abdomenu. Nejpatrnější změny jsou vidět na thoraxu a abdomenu. Typický silně sklerotizovaný zástupce čeledi Elateridae má dobře vyvinutý prosternální výběžek, mesoventrální jamku a mesoventrální výběžek, přičemž abdomen je kompaktní a skládá se z pěti ventritů (t.j. viditelných sternitů), z čehož první čtyři jsou srostlé. Je nutno poznamenat, že žádní Drilini nemají funkční klikací aparát a jejich abdomen je rozvolněnější, skládající se z nejméně sedmi ventritů. Zástupci prvních dvou bazálních kládů Drilini však mají sice redukované, ale viditelně prodloužené prosternální a mesoventrální výběžky, namísto mesoventrální jamky mají více či méně hlubokou depresi a jejich abdomen je poměrně kompaktní a sestává ze sedmi ventritů, z čehož první čtyři jsou srostlé. Třetí klád, včetně rodu *Selasia*, má podobnou strukturu thoraxu jako dvě předchozí skupiny, ale abdomen je rozvolněný, bez srostlých ventritů. Terminální klády Drilini pak mají ještě více redukovaný thorax, většinou bez výběžků na prosternu a mesoventritu, a jejich abdomen je ještě více rozvolněný a sestává dokonce z osmi ventritů. Tato studie tak podává svědectví o graduálním charakteru morfologických změn v důsledku modifikací ontogenetického vývoje.

4.3. Přehled diverzity Drilini

Pro naprostou většinu druhů v rámci Drilini známe pouze dospělé samce, jelikož je lze odchytit tradičními entomologickými metodami jako je smyk, sklep či lov na světlo. Samice a larvy, které většinu života stráví v ulitách plžů, není tak snadné nalézt, zvláště když sběr ulit plžů není pro většinu entomologů či amatérských sběratelů zcela obvyklým způsobem odchytu brouků. Samice a larvy jsou známé jen pro devět druhů rodu *Drilus* a dva druhy rodu *Malacogaster*, přičemž všechny tyto druhy se vyskytují výhradně v Evropě a severní Africe (Kobieluszová & Kundrata 2015, Kundrata *et al.* 2015a [**Příloha 10**], Faucheux *et al.* 2016). Sporadicky publikované nálezy afrických larev a samic jsou problematické, jelikož nelze s určitostí říct, kterému druhu či dokonce rodu patří.

O ontogenetickém vývoji Drilini se toho dosud mnoho neví, ale je zřejmé, že každý instar mladé pohyblivé larvy spořádá jednoho plže, v jehož ulitě se poté svleče a aktivně si vyhledá další potravu. O počtu instarů se dosud vedou spory a je pravděpodobné, že se to bude lišit u různých linií (Baalbergen *et al.* 2014 [**Příloha 8**], 2016; Šormová *et al.* 2018 [**Příloha 12**]). Aktivní larvální instary se na podzim mění v málo pohyblivý typ larvy, tzv. pseudoupu, a v tomto stádiu přezimují v ulitě své poslední oběti, než se na jaře opět změní v aktivní typ larvy. Tento koloběh se opakuje nejméně dva roky (Baalbergen *et al.* 2016). Baalbergen *et al.* (2014) [**Příloha 8**] zkoumali vztah predátor-kořist na několika druzích rodu *Drilus* na Krétě. Většina tamních druhů má na svém jídelníčku plže rodu *Albinaria* Vest z čeledi Clausilidae. Míra specializace na tento rod se však druh od druhu liší, takže lze rozeznat fakultativní i obligátní specialisty na tento rod. Autoři také zkoumali predaci v závislosti na geografii a zjistili, že na místech s největší akumulací plžů se průměrná míra predace pohybuje okolo 20 %, ale může být i daleko vyšší (viz také Welter-Schultes 2000). To znamená, že nejméně každá pátá ulita nese stopy po predaci larvou rodu *Drilus*. Studie také poskytla prvotní data pro budoucí evolučně-ekologické studie zaměřené na koevoluci predačních i obranných strategií v systému predátor-kořist.

Naprostá většina druhů tribu Drilini je nedostatečně taxonomicky zpracována. Popisy morfologických znaků, založené téměř bez výjimky na omezeném počtu jedinců, jsou většinou zcela nedostatečné a neposkytují relevantní informace o inter- a intraspecifické variabilitě. Stejně tak informace o distribuci jednotlivých druhů jsou často útržkovité a velmi vágní. Z důvodu chybějících alfa-taxonmických revizí a s tím souvisejících identifikačních klíčů nelze spoustu druhů spolehlivě určit bez studia typového materiálu. Typové exempláře jsou však mnohdy ztraceny a pokud ne, tak jsou roztroušeny po celé řadě evropských a afrických institucí. I přes recentní snahy o změnu (Kobieluszová & Kundrata 2015, Trllová & Kundrata 2015, Kundrata *et al.* 2015a [**Příloha 10**], Kundrata & Bocák 2017 [**Příloha 11**], Šormová *et al.* (2018) [**Příloha 12**]) tak taxonomie Drilini zůstává poměrně nepřehledná. Kompletní revize skupiny na alfa-taxonomické úrovni by znamenala důležitý krok pro poznání její celkové diverzity a také pro detailnější prozkoumání příbuzenských vztahů mezi jednotlivými liniemi.

Rod *Drilus* obsahuje 45 popsaných a přibližně 15 nepopsaných druhů z Palearktické oblasti od Iberského poloostrova po Írán (Kundrata & Bocák v tisku [**Příloha 13**], Kundrata, nepublikovaná data). Afrotropické druhy popsané v tomto rodu jsou momentálně revidovány a ani jeden reálně nepatří do rodu *Drilus* (Kundrata, nepublikovaná data). Většina druhů se vyskytuje v oblasti Středozemního moře a Malé Asie, přičemž kvůli omezené vagilitě samic zde tvoří množství endemických druhů vázaných na poměrně malé území. Pouze dva druhy rodu *Drilus* pronikly na sever od Alp, a to *D. concolor* Ahrens a *D. flavescens* (Geoffroy). Tyto druhy jsou známy téměř z celé Evropy včetně České republiky, přesto však patří mezi poměrně vzácně sbírané taxony. Alfa-taxonomické studie zahrnující rod *Drilus* byly publikovány pro Iberský poloostrov a Baleárské ostrovy (Bahillo de la Puebla & López Colón 2005), Levant (Kundrata *et al.* 2014b, Petrželková & Kundrata 2015), Malou Asii (Kobieluszová & Kundrata 2015), Krétu (Kundrata *et al.* 2015a) [**Příloha 10**] a Kypr (Šormová *et al.* 2018) [**Příloha 12**]. Většina prací je zaměřených na dospělé samce, avšak v poslední době se autoři zaměřili také na imaturní stádia a larviformní samice (např. Baalbergen *et al.* 2014 [**Příloha 8**], Faucheux *et al.* 2016, Šormová *et al.* 2018 [**Příloha 12**]). Kobieluszová & Kundrata (2015) studovali morfologii tykadel samic Drilini na základě publikovaných dat a veškerých dostupných jedinců z muzejních sbírek a zjistili, že tykadla jsou u této skupiny značně variabilním znakem. Počet tykadlových článků se neliší jen mezi samotnými druhy rodu *Drilus*, ale mnohdy i v rámci populace jednoho druhu. Kundrata *et al.*

(2015a) [**Příloha 10**]) zkoumali diverzitu krétských druhů rodu *Drilus* za použití integrativní taxonomie, přičemž na základě vybraných úseků DNA dokázali přiřadit u tří druhů larvy, samice a samce. Na tuto studii poté navázali Šormová *et al.* (2018) [**Příloha 12**], kteří obdobným způsobem zkoumali diverzitu této skupiny na Kypru, přičemž revidovali veškeré tamější druhy a pro některé z nich poprvé popsali imaturní stádia a samice.

Kundrata *et al.* (2015a) [**Příloha 10**]) a Šormová *et al.* (2018) [**Příloha 12**] také vytvořili dosud nejobsáhlejší molekulární fylogenezi rodu *Drilus*. Autoři v první studii navazovali na ekologicko-evoluční práci Baalbergen *et al.* (2014) [**Příloha 8**], a proto se zaměřili zejména na druhy rodu *Drilus* z oblasti Jónských ostrovů, Peloponésu a Kréty. Analýza dvou mitochondriálních markerů ukázala, že tyto druhy nejsou monofyletickou skupinou, neboť jeden druh z Peloponésu (*Drilus* sp. E) vytvořil spolu s druhem z Iberského poloostrova jednu z bazálních linií rodu *Drilus*, zatímco všechny ostatní řecké druhy tvořily statisticky robustně podpořený terminální klád. Molekulární fylogeneze zde byla v souladu nejen s morfologií, ale i s ekologií studovaných druhů, neboť *Drilus* sp. E, stejně jako jeho příbuzný druh z Iberského poloostrova, je predátorem větších plžů z čeledi Achatinidae, kdežto naprostá většina ostatních řeckých druhů je více či méně specializována na daleko menší zástupce čeledi Clausilidae. Autoři také zjistili, že diverzita rodu *Drilus* v oblasti jižního Řecka úzce souvisí s geologickou historií regionu, kdy vždy po částečné fragmentaci pevniny docházelo ke speciačním událostem. Tento jev byl nejlépe zdokumentovaný na druzích Kréty, kde dnešní distribuce tamějších druhů přibližně kopíruje rozmístění dřívějších tzv. paleoostrovů, které zůstaly zachovány z původní plochy ostrova v období zvýšené hladiny Středozemního moře. Šormová *et al.* (2018) [**Příloha 12**] se zaměřili na diverzitu a fylogenetické vztahy v rámci rodu *Drilus* z Kypru, přičemž z výsledků analýz tří molekulárních markerů a studie morfologie veškerého dostupného materiálu došli k závěru, že kyperská fauna má blízký vztah jak k oblasti Řecka, tak také k Malé Asii a Levantu.

Rod *Malacogaster* obsahuje 11 popsaných druhů z oblasti severní Afriky, Španělska a Itálie. Taxonomická situace tohoto rodu je chaotická a naprostá většina materiálu v muzejních sbírkách je neurčená nebo určená chybně (Kundrata, nepublikovaná data). Dospělí samci tohoto rodu mají většinou poměrně výrazně zkrácené krovky, červený štít a černé krovky. Nedávná studie odhalila, že pravděpodobně proto byly ještě donedávna v rodu *Malacogaster* chybně klasifikovány i některé takto zbarvené druhy rodu *Drilus* (Kundrata *et al.* 2014b). Molekulární fylogeneze i alfa-taxonomická revize rodu *Malacogaster* je v přípravě (Kundrata, nepublikovaná data).

Rod *Selasia* tradičně obsahoval druhy se silně hřebenitými tykadly z tropické Afriky, Arabského poloostrova, Sokotry, Himalájí a Orientální oblasti (Wittmer 1944, Geisthardt 2007). Jelikož dřívější autoři studovali morfologii tropických linií Drilini pouze velmi povrchně, řadili všechny druhy do rodu *Selasia*, čímž se tento stal druhově nejpočetnějším rodem v rámci Drilini. Momentálně obsahuje 64 popsaných druhů, ale je zřejmé, že některé z nich budou dříve či později převedeny do jiných, nejspíše pro vědu nových, rodů (Kundrata & Bocák v tisku [**Příloha 13**]). Až dnešní výzkum totiž pomalu odhaluje, jaká netušená morfologická i genetická diverzita tribu Drilini leží v oblasti tropické Afriky. Kundrata & Bocák (2017) [**Příloha 11**] studovali diverzitu tribu Drilini z kamerunských deštných lesů, přičemž objevili pro vědu zcela neznámých 17 druhů této skupiny, které zařadili do pěti nových rodů včetně jednoho podrodu. Tato studie jasně prokázala důležitost tropických deštných lesů západní a střední Afriky jako horkého místa biodiverzity. Kamerunské pralesy jsou také místem s největší sympatrickou diverzitou suchozemských plžů na zeměkouli (De Winter & Gittenberger 1998). Kundrata & Bocák (2017) [**Příloha 11**] tedy předpokládali, že jelikož tamější linie Drilini mají přebytek potravy, žijí v klimaticky dlouhodobě stabilním regionu a navíc všichni dostupní zástupci byli sbíráni pouze na několika málo lokalitách, v budoucnosti můžeme z tropické Afriky očekávat objevy desítek pro vědu dosud neznámých druhů či dokonce rodů této skupiny. To také následně potvrdily objevy dalších, do té doby neznámých, rodů a druhů afrických Drilini (Kundrata 2018, Kundrata & Bocák v tisku [**Příloha 13**]). Detailní znalost diverzity a rozšíření jednotlivých linií v rámci tribu Drilini nám může pomoci pochopit vznik a evoluci neotenie a s tím souvisejících morfologických modifikací uvnitř dříve poměrně homogenní skupiny kovaříkovitých brouků. Bude potřeba také detailního studia imaturních stádií a samic z tropických linií, včetně jejich vazby na tamější suchozemské plže, neboť ty mohou být klíčové pro pochopení evoluce vztahu predátor-kořist v této zajímavé linii brouků.

5. Závěr

Z výše uvedeného přehledu vývoje našich znalostí o fylogenezi, systematice, klasifikaci a diverzitě Elateriformia, Elateridae a Drilini jasně vyplývá, že s nástupem molekulárních metod došlo v této oblasti k mnohdy převratným a zčásti překvapivým objevům a zjištěním. Mnohé, velmi často dlouhodobě přetrvávající, problémy byly úspěšně vyřešeny, jako například systematická pozice některých morfologicky ne zcela jednoznačně zařaditelných taxonů jako jsou Drilini (Kundrata & Bocák 2011), Artematopodidae (Kundrata *et al.* 2013) [**Příloha 1**], *Paradrilus* (Kundrata *et al.* 2015b) [**Příloha 9**], Tetralobinae (Kundrata *et al.* 2018a) [**Příloha 6**] či Podabrocephalinae (Kundrata *et al.* 2019) [**Příloha 4**]. Některé otázky však dosud zůstávají nezodpovězeny. V rámci Elateriformia stále neznáme fylogenetické vztahy mezi hlavními skupinami a neznámé zůstávají také vztahy mezi většinou linií v komplexu Byrrhoidea-Buprestoidea (Kundrata *et al.* 2017b) [**Příloha 3**]. Dlouhodobě nevyjasněnou otázkou je též pozice enigmatického rodu *Cydistus*, jehož vědci nedokážou na základě morfologických znaků zařadit ani do nadčeledi (Lawrence *et al.* 2010b). V rámci Elateridae zůstává neobjasněna bazální radiace skupiny a také pozice několika menších, dosud nesekvenovaných skupin, jako například Eudicronychinae, Subprotelaterinae a Physodactylinae (Kundrata *et al.* 2018a) [**Příloha 6**]. Jak napovídají dosavadní molekulárně-fylogenetické studie zaměřené na čeleď Elateridae, bude potřeba důkladná revize stávající interní klasifikace jednotlivých podčeledí (Kundrata *et al.* 2016 [**Příloha 5**], 2018a [**Příloha 6**]; Douglas *et al.* 2018 [**Příloha 7**]). Co se týče Drilini, hlavním problémem zůstává naše omezená znalost diverzity této skupiny. Vždyť teprve nedávno byla identifikována naprostá většina dosud známých rodů tohoto tribu (Kundrata & Bocák 2017 [**Příloha 11**], Kundrata & Bocák v tisku [**Příloha 13**]) a také poprvé objeven druh z jihovýchodní Asie, čímž se podstatně rozšířila známá oblast výskytu Drilini směrem na východ (Kundrata & Šormová 2018). Zařazení linií z Orientálního regionu do molekulární fylogeneze nám může pomoci objasnit historické procesy vedoucí k dnešní distribuci skupiny. Rychlý nástup nové generace sekvenování přináší možnost využití například genomových či transkriptomových dat pro řešení fylogenetických problémů v rámci Elateriformia (Kusý *et al.* 2018a, 2018b). V blízké budoucnosti tak můžeme očekávat vyřešení mnoha dosud nezodpovězených otázek týkajících se fylogeneze a systematiky této evolučně a ekologicky zajímavé skupiny brouků.

6. Seznam použité literatury

Ahrens, D., Schwarzer, J. & Vogler, A.P. (2014) The evolution of scarab beetles tracks the sequential rise of angiosperms and mammals. *Proceedings of the Royal Society B - Biological Sciences*, 281: 20141470.

Amaral D.T., Mitani, Y., Ohmiya, Y. & Viviani, V.R. (2016) Organization and comparative analysis of the mitochondrial genomes of bioluminescent Elateroidea (Coleoptera: Polyphaga). *Gene*, 586: 254–262.

Arias-Bohart, E.T. (2015) *Malalcahuello ocaresi* gen. & sp. n. (Elateridae, Campyloxeninae). *ZooKeys*, 508: 1–13.

Arias-Bohart, E.T. & Elgueta, M. (2015) Description of *Sharon* gen. nov. for the Chilean species *Asaphes amoenus* Philippi, 1861 (Coleoptera: Elateridae). *European Journal of Taxonomy*, 142: 1–15.

Arnett, R.H. (1955) Supplement and corrections to J. A. Hyslop's genotypes of the Elaterid beetles of the world. *Proceedings of the United States National Museum*, 103: 599–619.

Baalbergen, E., Helwerda, R., Schelfhorst, R., Castillo Cajas, R.F., van Moorsel, C.H.M., Kundrata, R., Welter-Schultes, F.W., Giokas, S. & Schilthuizen, M. (2014) Predator-prey interactions between shell-boring beetle larvae and rock-dwelling land snails. *PLoS ONE*, 9: e100366.

Baalbergen, E., Schelfhorst, R. & Schilthuizen, M. (2016) *Drilus* larvae in the Netherlands (Coleoptera: Elateridae: Drilini). *Entomologische Berichten*, 76: 165–173.

Bahillo de la Puebla, P. & López Colón, J.I. (2005) Los Drilidae Lacordaire, 1857 de la Península Ibérica e Islas Baleares (Coleoptera). *Boletín de la Sociedad Entomológica Aragonesa*, 37: 119–128.

Basset, Y., Čížek, L., Cuénoud, P., Didham, R.K., Guilhaumon, F., Missa, O., Novotný, V., Ødegaard, F., Roslin, T., Schmidl, J., Tishechkin, A.K., Winchester, N.N., Roubik, D.W., Aberlenc, H.-P., Bail, J., Barrios, H., Bridle, J.R., Castaño-Meneses, G., Corbara, B., Curletti, G., Duarte da Rocha, W., De Bakker, D., Delabie, J.H.C., Dejean, A., Fagan, L.L., Floren, A., Kitching, R.L., Medianero, E., Miller, S.E., Gama de Oliveira, E., Orivel, J., Pollet, M., Rapp, M., Ribeiro, S.P., Roisin, Y., Schmidt, J.B., Sørensen, L. & Leponce, M. (2012) Arthropod diversity in a tropical forest. *Science*, 338: 1481–1484.

Bellamy, C.L. & Volkovitsh, M.G. (2016) Buprestoidea Crowson, 1955. In: Beutel, R.G. & Leschen, R.A.B (Eds), Handbook of zoology, Arthropoda: Insecta, 2nd edition; Coleoptera, beetles, Volume 1: Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Walter de Gruyter, Berlin/New York, pp. 543–552.

Beutel, R.G. (1995) Phylogenetic analysis of Elateriformia (Coleoptera: Polyphaga) based on larval characters. *Journal of Zoological Systematics and Evolutionary Research*, 33: 145–171.

Beutel, R.G. & Leschen, R.A.B. (2005) Classification. In: Beutel, R.G. & Leschen, R.A.B (Eds), Handbook of zoology, Arthropoda: Insecta, 2nd edition; Coleoptera, beetles, Volume 1: Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Walter de Gruyter, Berlin/New York, pp. 11–16.

Beutel, R.G. & Leschen, R.A.B. (2016) Chelonariidae Blanchard, 1845. In: Beutel, R.G. & Leschen, R.A.B (Eds), Handbook of zoology, Arthropoda: Insecta, 2nd edition; Coleoptera, beetles, Volume 1: Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Walter de Gruyter, Berlin/New York, pp. 639–644.

Beutel, R.G., Leschen, R.A.B., Bocák, L. & Bocáková, M. (2016) Elateriformia Crowson, 1960. In: Beutel, R.G. & Leschen, R.A.B (Eds), Handbook of zoology, Arthropoda: Insecta, 2nd edition; Coleoptera, beetles, Volume 1: Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Walter de Gruyter, Berlin/New York, pp. 527–530.

Blackwelder, R.E. (1944) Checklist of the Coleopterous insects of Mexico, Central America, the West Indies, and South America. Part 2. *Bulletin of the U.S. National Museum*, 185: 189–341.

Bocák, L. (2007) Drilidae. In: Löbl, I. & Smetana, A. (Eds), Catalogue of Palaearctic Coleoptera. Vol. 4. Apollo Books, Stenstrup, pp. 209–210.

Bocák, L. & Bocáková, M. (2008) Phylogeny and classification of the family Lycidae (Insecta: Coleoptera). *Annales Zoologici*, 58: 695–720.

Bocák, L. & Bocáková, L. (2010) Lycidae Laporte, 1836. In: Leschen, R.A.B., Beutel, R.G. & Lawrence, J.F. (Eds), Handbook of zoology, Arthropoda: Insecta; Coleoptera, beetles, Volume 2: Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter de Gruyter, Berlin, pp. 114–123.

Bocák, L. & Brlík, M. (2008) Revision of the family Omalisidae (Coleoptera, Elateroidea). *Insect Systematics & Evolution*, 46: 189–212.

Bocák, L., Barton, C., Crampton-Platt, A., Chesters, D., Ahrens, D. & Vogler, A.P. (2014) Building the Coleoptera tree-of-life for >8000 species: composition of public DNA data and fit with Linnaean classification. *Systematic Entomology*, 39: 97–110.

Bocák, L., Bocáková, M., Hunt, T. & Vogler, A.P. (2008) Multiple ancient origins of neoteny in Lycidae (Coleoptera): consequences for ecology and macroevolution. *Proceedings of the Royal Society B - Biological Sciences*, 275: 2015–2023.

Bocák, L., Branham, M.A. & Kundrata, R. (2010) Family Drilidae Blanchard, 1845. In: Leschen, R.A.B., Beutel, R.G. & Lawrence, J.F. (Eds), Handbook of zoology, Arthropoda: Insecta; Coleoptera, beetles, Volume 2: Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter de Gruyter, Berlin, pp. 104–110.

Bocák, L., Kundrata, R., Andújar Fernández, C. & Vogler, A.P. (2016) The discovery of Iberobaeniidae (Coleoptera: Elateroidea), a new family of beetles from Spain, with immatures detected by environmental DNA sequencing. *Proceedings of the Royal Society B - Biological Sciences*, 283: 20152350.

Bocák, L., Motyka, M., Boček, M. & Bocáková, M. (2018) Incomplete sclerotization and phylogeny: The phylogenetic classification of *Plastocerus* (Coleoptera: Elateroidea). *PLoS ONE*, 13: e0194026.

Bocáková, M., Bocák, L., Hunt, T., Teraväinen, M. & Vogler, A.P. (2007) Molecular phylogenetics of Elateriformia (Coleoptera): evolution of bioluminescence and neoteny. *Cladistics*, 23: 477–496.

Boček, M. & Bocák, L. (2017) The comparison of molecular and morphology-based phylogenies of trichaline net-winged beetles (Coleoptera: Lycidae: Metriorrhynchini) with description of a new subgenus. *PeerJ*, 5: e3963.

Boček, M., Fancello, L., Motyka, M., Bocáková, M. & Bocák, L. (2018) The molecular phylogeny of Omalisidae (Coleoptera) defines the family limits and demonstrates low dispersal propensity and ancient vicariance patterns. *Systematic Entomology*, 43: 250–261.

Bouchard, P., Bousquet, Y., Davies, A. E., Alonso-Zarazaga, M.A., Lawrence, J.F., Lyal, C.H.C., Newton, A.F., Reid, C.A.M., Schmitt, M., Ślipiński, A. & Smith, A.B.T. (2011) Family-group names in Coleoptera (Insecta). *ZooKeys*, 88: 1–972.

Branham, M.A. & Wenzel, J.W. (2001) The evolution of bioluminescence in cantharoids (Coleoptera: Elateroidea). *Florida Entomologist*, 84: 565–583.

Branham, M.A. & Wenzel, J.W. (2003) The evolution of photic behavior and the evolution of sexual communication in fireflies (Coleoptera: Lampyridae). *Cladistics*, 84: 565–586.

Bray, T.C. & Bocák, L. (2016) Slowly dispersing neotenic beetles can speciate on a penny coin and generate space-limited diversity in the tropical mountains. *Scientific Reports*, 6: 33579.

Burakowski, B. (1973) Immature stages and biology of *Drapetes biguttatus* (Piller) (Coleoptera, Lissomidae). *Annales Zoologici*, 30: 335–347.

Cai, C.Y., Lawrence, J.F., Ślipiński, A. & Huang, D.Y. (2015) Jurassic artematopodid beetles and their implications for the early evolution of Artematopodidae (Coleoptera). *Systematic Entomology*, 40: 779–788.

Cai, C.Y., Lawrence, J.F., Yamamoto, S., Leschen, R.A.B., Newton, A.F., Ślipiński, A., Yin, Z., Huang, D.Y. & Engel, M.S. (2019) Basal polyphagan beetles in mid-Cretaceous amber from Myanmar: biogeographic implications and long-term morphological stasis. *Proceedings of the Royal Society B - Biological Sciences*, doi: 10.1098/rspb.2018.2175.

Calder, A.A. (1996) Click beetles: Genera of the Australian Elateridae (Coleoptera). Monographs on invertebrate taxonomy, Vol. 2. CSIRO Publishing, Victoria, Australia, 401 pp.

Calder, A.A., Lawrence, J.F. & Trueman, J.W.H. (1993) *Austrelater*, gen. nov. (Coleoptera: Elateridae), with a description of the larva and comments on elaterid relationships. *Invertebrate Taxonomy*, 7: 1349–1394.

Candèze, E.C.A. (1857) Monographie des Élatérides. Tome premier. *Mémoires de la Société Royale des Sciences de Liège*, 12: 1–400.

Candèze, E.C.A. (1891) Catalogue méthodique des Élatérides connus en 1890. H. Vaillant-Carmanne, Liége, 246 pp.

Cate, P.C., Sánchez-Ruiz, A., Löbl, I. & Smetana, A. (2007) Elateridae. In: Löbl, I. & Smetana, A. (Eds), Catalogue of Palaearctic Coleoptera. Vol. 4. Apollo Books, Stenstrup, pp. 89–209.

Cicero, J.M. (1988) Ontophylogenetics of cantharoid larviforms (Coleoptera: Cantharoidea). *The Coleopterists Bulletin*, 42: 105–151.

Cloudsley-Thompson, J.L. (1965) On the function of the subelytral cavity in desert Tenebrionidae (Col.). *Entomologist’s Monthly Magazine*, 100: 148–151.

Costa, C. (1982) *Pyrearinus termitilluminans*, sp.n., with description of the immature stages (Coleoptera, Elateridae, Pyrophorini). *Revista Brasileira de Zoologia*, 1: 23–30.

Costa, C. (1984) Note on the bioluminescence of *Balgus schnusei* (Heller, 1974) (Trixagidae, Coleoptera). *Revista Brasileira de Entomologia*, 28: 397–398.

Costa, C. & Zaragoza-Caballero, S. (2010) Phengodidae LeConte, 1861. In: Leschen, R.A.B., Beutel, R.G. & Lawrence, J.F. (Eds), Handbook of zoology, Arthropoda: Insecta; Coleoptera, beetles, Volume 2: Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter de Gruyter, Berlin, pp. 126–135.

Costa, C., Lawrence, J.F. & Rosa, S.P. (2010) Elateridae Leach, 1815. In: Leschen, R.A.B., Beutel, R.G. & Lawrence, J.F. (Eds), Handbook of zoology, Arthropoda: Insecta; Coleoptera, beetles, Volume 2: Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter de Gruyter, Berlin, pp. 75–103.

Costa, C., Vanin, S.A. & Casari-Chen, S.A. (1994) Cladistic analysis and systematics of the Tetralobini *sensu* Stibick, 1979 (Coleoptera, Elateridae, Pyrophorinae). *Arquivos de Zoologia*, 32: 111–157.

Costa, C., Vanin, S.A. & Ide, S. (1999) Systematics and bionomics of Cneoglossidae with a cladistic analysis of Byrrhoidea *sensu* Lawrence & Newton (1995) (Coleoptera, Elateriformia). *Arquivos de Zoologia*, 3: 231–300.

Costa, C., Vanin, S.A., Lawrence, J.F. & Ide, S. (2003) Systematics and cladistic analysis of Cerophytidae (Elateroidea: Coleoptera). *Systematic Entomology*, 28: 375–407.

Costa, C., Vanin, S.A., Lawrence, J.F., Ide, S. & Branham, M. (2006) Review of the family Brachypsectridae (Coleoptera: Elateroidea). *Annals of the Entomological Society of America*, 99: 409–432.

Costa, C., Vanin, S.A. & Rosa, S.P. (2014) Description of a new genus and species of Cerophytidae (Coleoptera: Elateroidea) from Africa with a cladistic analysis of the family. *Zootaxa*, 3878: 248–260.

Costello, M.J., Wilson, S. & Houlding, B. (2012) Predicting total global species richness using rates of species description and estimates of taxonomic effort. *Systematic Biology*, 61: 871–883.

Crowson, R.A. (1955) The natural classification of the families of Coleoptera. Nathaniel Lloyd, Co., Ltd., London, 187 pp.

Crowson, R.A. (1960) The phylogeny of Coleoptera. *Annual Review of Entomology*, 5: 111–134.

Crowson, R.A. (1961) On some new characters of classificatory importance in adults of Elateridae (Coleoptera). *Entomologist's Monthly Magazine*, 96: 158–161.

Crowson, R.A. (1971) Observations on the superfamily Dascilloidea (Coleoptera: Polyphaga), with the inclusion of Karumiidae and Rhipiceridae. *Zoological Journal of the Linnean Society*, 50: 11–19.

Crowson, R.A. (1972) A review of the classification of Cantharoidea (Coleoptera), with the definition of two new families: Cneoglossidae and Omethidae. *Revista de la Universidad de Madrid*, 21: 35–71.

Crowson, R.A. (1973) On a new superfamily Artematopoidea of polyphagan beetles, with the definition of two new fossil genera from the Baltic amber. *Journal of Natural History*, 7: 225–238.

Crowson, R.A. (1978) Problems of phylogenetic relationships in Dryopoidea (Coleoptera). *Entomologica Germanica*, 4: 250–257.

Day, J.C., Goodall, T.I. & Bailey, M.J. (2009) The evolution of the adenylate-forming protein family in beetles: Multiple luciferase gene paralogues in fireflies and glow-worms. *Molecular Phylogenetics and Evolution*, 50: 93–101.

Dolin, V.G. (1975) Wing venation in click-beetles (Coleptera, Elateridae) and its significance in the taxonomy of the family. *Zoologicheskii Zhurnal*, 54: 1618–1633.

Dolin, V.G. (1978) Phylogeny of click beetles (Coleoptera: Elateridae). *Vestnik Zoologii*, 3: 3–12.

Dolin, V.G. (2000) Znachenie lichinochnykh priznakov i zhilkovaniya krylev v sistematike Elateroidea (Coleoptera). Doklad na pyat’desyat vtorom ezhegodnom chtenii pamyati N A Kholodkskogo 1 aprelya 1999 g. Zoologicheskii Institut, St-Petersburg, 49 pp.

Douglas, H. (2011) Phylogenetic relationships of Elateridae inferred from adult morphology, with special reference to the position of Cardiophorinae. *Zootaxa*, 2900: 1–45.

Douglas, H. (2017) World reclassification of the Cardiophorinae (Coleoptera, Elateridae), based on phylogenetic analyses of morphological characters. *ZooKeys*, 655: 1–130.

Douglas, H., Kundrata, R., Janošíková, D. & Bocák, L (2018) Molecular and morphological evidence for new genera in the click-beetle subfamily Cardiophorinae (Coleoptera: Elateridae). *Entomological Science*, 21: 292–305.

Eisner, T., Schroeder, F.C., Snyder, N., Grant, J.B., Aneshansley, D.J., Utterback, D., Meinwald, J. & Eisner, M. (2008) Defensive chemistry of lycid beetles and of mimetic cerambycid beetles that feed on them. *Chemoecology*, 18: 109–119.

Evans, M.E.G. (1972) The jump of the click beetle (Coleoptera, Elateridae) - a preliminary study. *Journal of Zoology*, 167: 319–336.

Evans, M.E.G. (1973) The jump of the click beetle (Coleoptera: Elateridae) - energetics and mechanics. *Journal of Zoology*, 169: 181–194.

Fallon, T.R., Lower, S.E., Chang, C.H., Bessho-Uehara, M., Martin, G.J., Bewick, A.J., Behringer, M., Debat, H.J., Wong, I., Day, J.C., Suvorov, A., Silva, C.J., Stanger-Hall, K.F., Hall, D.W., Schmitz, R.J., Nelson, D.R., Lewis, S.M., Shigenobu, S., Bybee, S.M., Larracuente, A.M., Oba, Y. & Weng, J.K. (2018) Firefly genomes illuminate parallel origins of bioluminescence in beetles. *Elife*, 7: e36495.

Farrell, B.D. (1998) "Inordinate fondness" explained: Why are there so many beetles? *Science*, 281: 555–559.

Faucheux, M.J. & Kundrata, R. (2017) Comparative antennal morphology of male Drilini with special reference to the sensilla (Coleoptera: Elateridae: Agrypninae). *Zoologischer Anzeiger*, 266: 105–119.

Faucheux, M.J., Beaulieu, G. & Agnas, M. (2016) Deux espèces marocaines de Drilini (Coleoptera: Elateridae: Agrypninae): *Drilus mauritanicus* Lucas 1849 et *Malacogaster passerinii* Bassi 1833: Morphologie larvaire et imaginale, écologie générale. *Bulletin de la Société des sciences naturelles de l'Ouest de la France (N.S.),* 38: 1–58.

Fleutiaux, E. (1947) Révision des Élaterides (Coléoptères) de l´Indo-Chine Française. Première partie. *Notes d´Entomologie Chinoise*, 11: 233–420.

Fontaine, B., van Achterberg, K., Alonso-Zarazaga, M.A., Araujo, R., Asche, M., Aspöck, H., Aspöck, U., Audisio, P., Aukema, B., Bailly, N., Balsamo, M., Bank, R.A., Belfiore, C., Bogdanowicz, W., Boxshall, G., Burckhardt, D., Chylarecki, P., Deharveng, L., Dubois, A., Enghoff, H., Fochetti, R., Fontaine, C., Gargominy, O., Lopez, M.S., Goujet, D., Harvey, M., Heller, K.G., van Helsdingen, P., Hoch, H., De Jong, Y., Karsholt, O., Los, W., Magowski, W., Massard, J.A., McInnes, S.J., Mendes, L.F., Mey, E., Michelsen, V., Minelli, A., Nafria, J.M., van Nieukerken, E.J., Pape, T., De Prins, W., Ramos, M., Ricci, C., Roselaar, C., Rota, E., Segers, H., Timm, T., van Tol, J. & Bouchet, P. (2012) New species in the Old World: Europe as a frontier in biodiversity exploration, a test bed for 21st century taxonomy. *PLoS ONE*, 7: e36881.

Foottit R.G. & Adler P.H. (2009) Insect biodiversity: science and society. Wiley-Blackwell, Chichester, United Kingdom, 632 pp.

Forbes, A.A., Bagley, R.K., Beer, M.A., Hippee, A.C. & Widmayer, H.A. (2018) Quantifying the unquantifiable: why Hymenoptera - not Coleoptera - is the most speciose animal order. *BMC Ecology*, 18: 221.

Furlan, L., Contiero, B., Chiarini, F., Colauzzi, M., Sartori, E., Benvegnù, I., Fracasso, F. & Giandon, P. (2017) Risk assessment of maize damage by wireworms (Coleoptera: Elateridae) as the first step in implementing IPM and in reducing the environmental impact of soil insecticides. *Environmental Science and Pollution Research*, 24: 236–251.

Geisthardt, M. (2007) Remarks on some African *Selasia*-species and description of new species (Coleoptera: Drilidae). *Mitteilungen des Internationalen Entomologischen Vereins*, 32: 27–43.

Gimmel, M.L. & Bocáková, M. (2015) A new extant species of *Electribius* Crowson from Honduras (Coleoptera: Elateroidea: Artematopodidae). *Zootaxa*, 3926: 296–300.

Girard, C. (2011) Sept nouvelles espèces afrotropicales du genre *Eudicronychus* Méquignon, 1931 (Coleoptera, Eudicronychidae). *Bulletin de la Société entomologique de France*, 116: 135–146.

Girard, C. (2017) Catalogue commenté des Coléoptères Elateridae d´Afrique subsaharienne (Cardiophorinae exclus). *Société entomologique de France*, 10: 1–404.

Gould, S.J. (1977) Ontogeny and phylogeny. Harvard University Press, Cambridge, Massachusetts, 501 pp.

Grimaldi, D. & Engel, M.S. (2005) Evolution of the insects. Cambridge University Press, New York/Cambridge, 755 pp.

Grove, S.J. & Stork, N.E. (2000) An inordinate fondness for beetles. *Invertebrate Taxonomy*, 14: 733–739.

Gurjeva, E.L. (1974) Thoracic structure of click beetles (Coleoptera, Elateridae) and the significance of the structural characters for the system of the family. *Entomological Review*, 53: 67–79.

Hájek, J. (2010) *Brachypsectra kadleci* sp. nov. from western Iran - the first Palaearctic member of the family Brachypsectridae (Insecta: Coleoptera: Elateriformia). *Annales Zoologici*, 60: 29–33.

Hájek, J. (2011) World catalogue of the family Callirhipidae (Coleoptera: Elateriformia), with nomenclatural notes. *Zootaxa*, 2914: 1–66.

Hammond, P. (1992) Species Inventory. In: Groombridge, B. (Ed.), Global Biodiversity. Springer, Dordrecht, pp. 17–39.

Hayek, C.M.F. von (1973) A reclassification of the subfamily Agrypninae (Coleoptera: Elateridae). *Bulletin of the British Museum (Natural History), Entomology*, Supplement 20: 1−309.

He, J., Bi, X., Dong, Z., Liu, G., Zhao, R., Wang, W. & Li, X. (2019) The mitochondrial genome of the first luminous click-beetle (Coleoptera: Elateridae) recorded in Asia. *Mitochondrial DNA Part B,* 4: 565–567.

Hernando, C. & Ribera, I. (2016) Limnichidae Erichson, 1846. In: Beutel, R.G. & Leschen, R.A.B (Eds), Handbook of zoology, Arthropoda: Insecta, 2nd edition; Coleoptera, beetles, Volume 1: Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Walter de Gruyter, Berlin/New York, pp. 605–612.

Hlavac, T.F. (1975) The prothorax of Coleoptera (except Bostrichiformia - Cucujiformia). *Bulletin of the Museum of Comparative Zoology*, 147: 137–183.

Hörnschemeyer, T. (1998) New species of *Electribius* Crowson 1973 (Coleoptera: Artematopodidae) from Baltic amber. *Paläontologische Zeitschrift,* 72: 299–306.

Hunt, T., Bergsten, J., Levkaničová, Z., Papadopoulou, A., St. John, O., Wild, R., Hammond, P.M., Ahrens, D., Balke, M., Caterino, M.S., Gómez-Zurita, J., Ribera, I., Barraclough, T.G., Bocáková, M., Bocák, L. & Vogler, A.P. (2007) A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. *Science*, 318: 1913–1916.

Hyslop, J.A. (1917) The phylogeny of the Elateridae based on larval characters. *Annals of the Entomological Society of America*, 10: 241–263.

Hyslop, J.A. (1921) Genotypes of the Elaterid beetles of the world. *Proceedings of the United States National Museum,* 58: 621–673.

Ikeda, H., Nishikawa, M. & Sota, T. (2012) Loss of flight promotes beetle diversification. *Nature Communications,* 3: 1–7.

Ivie, M.A. (2002) The transfer of *Pseudokarumia* Pic from Dascillidae (Karumiinae) to Telegeusidae, with a key to World genera of Telegusidae. *The Coleopterists Bulletin*, 56, 582–584.

Jäch, M.A. & Balke, M. (2008) Global diversity of water beetles (Coleoptera) in freshwater. *Hydrobiologia,* 595: 419–442.

Jäch, M.A., Kodada, J., Brojer, M., Shepard, W.D. & Čiampor, F. (2016) Coleoptera: Elmidae and Protelmidae. World Catalogue of Insects, vol. 14. Brill, Leiden, 318 pp.

Janišová, K. & Bocáková, M. (2013) Revision of the subfamily Ototretinae (Coleoptera: Lampyridae). *Zoologischer Anzeiger,* 252: 1–19.

Jeng, M.L. (2012) Re-classification of *Rhipidiomorphus malaccanus* Pic, a long-neglected genus and species of Psephenoidinae (Coleoptera: Psephenidae). *Zootaxa*, 3180: 66–68.

Jin, Z., Escalona, H.E., Ślipiński, A. & Pang, H. (2013a) Phylogeny and Classification of Rhipicerinae (Coleoptera: Rhipiceridae) with a review of the Australian taxa. *Annales Zoologici*, 63: 275–317.

Jin, Z., Ślipiński, A. & Pang, H. (2013b) Genera of Dascillinae (Coleoptera: Dascillidae) with a review of the Asian species of *Dascillus* Latreille, *Petalon* Schonherr and *Sinocaulus* Fairmaire. *Annales Zoologici*, 63: 551–652.

Johnson, P.J. (2002) Elateridae Leach 1815. In: Arnett, R.H., Thomas, M.C., Skelley, P.E. & Frank, J.H. (Eds), American Beetles, Vol. 2. CRC, Boca Raton, Florida, pp. 160–173.

Kasap, H. & Crowson, R.A. (1975) A comparative anatomical study of Elateriformia and Dascilloidea (Coleoptera). *Transactions of the Royal Entomological Society of London*, 126: 441–495.

Kawashima, I., Lawrence, J.F. & Branham, M.A. (2010) Rhagophthalmidae Olivier, 1907. In: Leschen, R.A.B., Beutel, R.G. & Lawrence, J.F. (Eds), Handbook of zoology, Arthropoda: Insecta; Coleoptera, beetles, Volume 2: Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter de Gruyter, Berlin, pp. 135–140.

Kazantsev, S.V. (2007) Comparative morphology of the genus *Euanoma* Reitter, 1889 (Coleoptera: Drilidae). *Russian Entomological Journal*, 16: 439–449.

Kazantsev, S.V. (2010) New taxa of Omalisidae, Drilidae and Omethidae, with a note on systematic position of Thilmaninae (Coleoptera). *Russian Entomological Journal*, 19: 51–60.

Kazantsev, S.V. (2011) An annotated checklist of Cantharoidea (Coleoptera) of Russia and adjacent territories. *Russian Entomological Journal*, 20: 387–410.

Kishii, T. (1987) A taxonomic study of the Japanese Elateridae (Coleoptera), with the keys to the subfamilies, tribes and genera. T. Kishii, Kyoto, 262 pp.

Kobieluszová, L. & Kundrata, R. (2015) Taxonomic review of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) from Asia Minor, with descriptions of seven new species and comments on the female antennal morphology in Drilini. *Zootaxa*, 4012: 78–96.

Kodada, J., Jäch, M.A. & Čiampor, F. (2016a) Elmidae Curtis, 1830. In: Beutel, R.G. & Leschen, R.A.B (Eds), Handbook of zoology, Arthropoda: Insecta, 2nd edition;

Coleoptera, beetles, Volume 1: Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Walter de Gruyter, Berlin/New York, pp. 561–589.

Kodada, J., Jäch, M.A. & Čiampor, F. (2016b) Dryopidae Bilberg, 1820 (1817). In: Beutel, R.G. & Leschen, R.A.B (Eds), Handbook of zoology, Arthropoda: Insecta, 2nd edition; Coleoptera, beetles, Volume 1: Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Walter de Gruyter, Berlin/New York, pp. 590–602.

Kovalev, A.V. & Kirejtshuk, A.G. (2016) *Asiopsectra* gen. n., a second genus of the family Brachypsectridae (Coleoptera, Elateroidea) from the Palaearctic Region. *Insect Systematics & Evolution*, 47: 195–208.

Kubaczková, M. & Kundrata, R. (2017) Annotated catalogue of the click-beetle subfamily Tetralobinae (Coleoptera: Elateridae). *Zootaxa*, 4323: 151–184.

Kundrata, R. (2018) New minute Drilini species significantly extend the distributions of *Lolosia* and *Microselasia* (Coleoptera: Elateridae: Agrypninae) in tropical Africa. *Acta Entomologica Musei Nationalis Pragae*, 58: 531–538.

Kundrata, R. & Bocák, L. (2007) A revision of *Euanoma* and *Pseudeuanoma* (Coleoptera: Drilidae). *Annales Zoologici*, 57: 427–441.

Kundrata, R. & Bocák, L. (2011a) The phylogeny and limits of Elateridae (Insecta, Coleoptera): is there a common tendency of click beetles to soft-bodiedness and neoteny? *Zoologica Scripta*, 40: 364–378.

Kundrata, R. & Bocák, L. (2011b) Redescription and relationships of *Pseudothilmanus* Pic (Coleoptera: Rhagophthalmidae) – a long-term neglected glow-worm beetle genus from the Himalayas. *Zootaxa*, 2794: 57–62.

Kundrata, R. & Bocák, L. (2017) Taxonomic review of Drilini (Elateridae: Agrypninae) in Cameroon reveals high morphological diversity, including the discovery of five new genera. *Insect Systematics & Evolution*, 48: 441–492.

Kundrata, R. & Bocák, L. (v tisku) Molecular phylogeny reveals the gradual evolutionary transition to soft-bodiedness in click-beetles and identifies Sub-Saharan Africa as a cradle of diversity for Drilini (Coleoptera: Elateridae). *Zoological Journal of the Linnean Society*.

Kundrata, R. & Jäch, M.A. (2017) *Ptilodactyla crenatostriata* Redtenbacher, 1868 (Coleoptera: Ptilodactylidae) transferred to *Phytocerum* Costa, Vanin, Lawrence & Ide, 2003 (Coleoptera: Cerophytidae). *Zootaxa*, 4324: 371–377.

Kundrata, R. & Šormová, E. (2018) *Platiana cechovskyi* sp. nov. from Malaysia, a remarkable new member of Dimini (Elateridae: Dendrometrinae) with strongly serrate antennae. *Zootaxa*, 4524: 132–138.

Kundrata, R., Baalbergen, E., Bocák, L. & Schilthuizen, M. (2015a) The origin and diversity of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) in Crete based on mitochondrial phylogeny. *Systematics and Biodiversity*, 13: 52–75.

Kundrata, R., Baena, M. & Bocák, L. (2015b) Classification of Omalisidae based on molecular data and morphology, with description of Paradrilinae subfam. nov. (Coleoptera: Elateroidea). *Zootaxa*, 3915: 413–422.

Kundrata, R., Baena, M. & Bocák, L. (2017a) *Iberobaenia andujari* sp. nov., the third species of Iberobaeniidae (Coleoptera: Elateroidea) from southern Spain. *Annales Zoologici*, 67: 121–129.

Kundrata, R., Bocáková, M. & Bocák, L. (2013) The phylogenetic position of Artematopodidae (Coleoptera: Elateroidea), with description of the first two *Eurypogon* species from China. *Contributions to Zoology*, 82: 199–208.

Kundrata, R., Bocáková, M. & Bocák, L. (2014a) The comprehensive phylogeny of the superfamily Elateroidea (Coleoptera: Elateriformia). *Molecular Phylogenetics and Evolution*, 76: 162–171.

Kundrata, R., Gunter, N.L., Douglas, H. & Bocák, L. (2016) Next step toward a molecular phylogeny of click-beetles (Coleoptera: Elateridae): redefinition of Pityobiinae, with a description of a new subfamily, Parablacinae, from the Australasian Region. *Austral Entomology*, 55: 291–302.

Kundrata, R., Gunter, N.L., Janošíková, D. & Bocák, L. (2018a) Molecular evidence for the subfamilial status of Tetralobinae (Coleoptera: Elateridae), with comments on parallel evolution of some phenotypic characters. *Arthropod Systematics & Phylogeny*, 76: 137–145.

Kundrata, R., Ivie, M.A. & Bocák, L. (2019) *Podabrocephalus* Pic is the morphologically modified lineage of Ptilodactylinae (Coleoptera: Elateriformia: Ptilodactylidae). *Insect Systematics & Evolution*, doi: 10.1163/1876312X-00002190.

Kundrata, R., Jäch, M.A. & Bocák, L. (2017b) Molecular phylogeny of the Byrrhoidea-Buprestoidea complex (Coleoptera, Elateriformia). *Zoologica Scripta*, 46: 150–164.

Kundrata, R., Kobieluszová, L. & Bocák, L. (2014b) A review of Drilini (Coleoptera: Elateridae: Agrypninae) of the Northern Levant, with description of a new species from Syria and a key to Levantine species. *Zootaxa*, 3755: 457–469.

Kundrata, R., Mušálková, M. & Kubaczková, M. (2018b) Annotated catalogue of the click-beetle tribe Dimini (Coleoptera: Elateridae: Dendrometrinae). *Zootaxa*, 4412: 1–75.

Kundrata, R., Mušálková, M. & Prosvirov, A.S. (2018c) Annotated catalogue of the click-beetle tribe Senodoniini (Coleoptera: Elateridae: Dendrometrinae). *Zootaxa,* 4532: 273–287.

Kundrata, R., Šormová, E. & Kakiopoulos, G. (2018d) Revisiting the diversity of *Euanoma* Reitter, 1889 (Coleoptera: Omalisidae), with descriptions of four new species from Turkey. *Annales Zoologici*, 68: 357–373.

Kusý, D., Motyka, M., Andújar, C., Boček, M., Mášek, M., Sklenářová, K., Kokas, F., Bocáková, M., Vogler, A.P. & Bocák, L. (2018a) Genome sequencing of *Rhinorhipus* Lawrence exposes an early branch of the Coleoptera. *Frontiers in Zoology,* 15: 21.

Kusý, D., Motyka, M., Boček, M., Vogler, A.P. & Bocák, L. (2018b) Genome sequences identify three families of Coleoptera as morphologically derived click beetles (Elateridae). *Scientific Reports,* 8: 17084.

Lacordaire, J.T. (1857) Histoire naturelle des Insectes. Genera des Coléoptères ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes. Tome quatrième. Librairie Encyclopédique de Roret, Paris, 579 pp.

Larsen, B.B., Miller, E.C., Rhodes, M.K. & Wiens, J.J. (2017) Inordinate fondness multiplied and redistributed: the number of species on Earth and the new Pie of Life. *The Quarterly Review of Biology,* 92: 229–265.

Lawrence, J.F. (1988) Rhinorhipidae, a new beetle family from Australia, with comments on the phylogeny of the Elateriformia. *Invertebrate Taxonomy*, 2: 1–53.

Lawrence, J.F. (2016a) Classification (families & subfamilies). In: Beutel, R.G. & Leschen, R.A.B (Eds), Handbook of zoology, Arthropoda: Insecta, 2nd edition; Coleoptera, beetles, Volume 1: Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Walter de Gruyter, Berlin/New York, pp. 13–22.

Lawrence, J.F. (2016b) Dascilloidea Guérin-Méneville, 1843. In: Beutel, R.G. & Leschen, R.A.B (Eds), Handbook of zoology, Arthropoda: Insecta, 2nd edition; Coleoptera, beetles, Volume 1: Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Walter de Gruyter, Berlin/New York, pp. 531–542.

Lawrence, J.F. (2016c) Ptilodactylidae Laporte, 1836. In: Beutel, R.G. & Leschen, R.A.B (Eds), Handbook of zoology, Arthropoda: Insecta, 2nd edition; Coleoptera, beetles, Volume 1: Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Walter de Gruyter, Berlin/New York, pp. 632–639.

Lawrence, J.F. & Britton, E.B. (1991) Coleoptera (beetles). In: CSIRO (Ed.), The insects of Australia. A textbook for students and research workers. 2nd Edition. Volumes 1–2. Melbourne University Press, Carlton, Victoria, pp. 543–683.

Lawrence, J.F. & Newton, A.F. (1982) Evolution and classification of beetles. *Annual Review of Ecology and Systematics,* 13: 261–290.

Lawrence, J.F. & Newton, A.F. (1995) Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). In: Pakaluk, J. & Ślipiński, A. (Eds), Biology, phylogeny, and classification of Coleoptera. Papers celebrating the 80th birthday of Roy A. Crowson, Volumes 1–2. Muzeum i Instytut Zoologii PAN, Warszawa, pp. 779–1083.

Lawrence, J.F., Beutel, R.G., Leschen, R.A.B. & Ślipiński, A. (2010a) Changes in classification and list of families and subfamilies. In: Leschen, R.A.B., Beutel, R.G. & Lawrence, J.F. (Eds), Handbook of zoology, Arthropoda: Insecta; Coleoptera, beetles, Volume 2: Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim. Walter de Gruyter, Berlin, pp. 1–7.

Lawrence, J.F., Kawashima, I. & Branham, M.A. (2010b) Elateriformia *Incertae sedis*. In: Leschen, R.A.B., Beutel, R.G. & Lawrence, J.F. (Eds), Handbook of zoology, Arthropoda: Insecta; Coleoptera, beetles, Volume 2: Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim. Walter de Gruyter, Berlin, pp. 162–177.

Lawrence, J.F., Muona, J., Teräväinen, M., Ståhls, G. & Vahtera, V. (2007) *Anischia, Perothops* and the phylogeny of Elateroidea (Coleoptera: Elateriformia). *Insect Systematics & Evolution,* 38: 205–239.

Lawrence, J.F., Nikitsky, N.B. & Kirejtshuk, A.G. (1995a) Phylogenetic position of Decliniidae (Coleoptera: Scirtoidea) and comments on the classification of Elateriformia (*sensu lato*). In: Pakaluk, J. & Ślipiński, A. (Eds), Biology, phylogeny, and classification of Coleoptera. Papers celebrating the 80th birthday of Roy A. Crowson. Volumes 1–2. Muzeum i Instytut Zoologii PAN, Warszawa, pp. 375–410

Lawrence, J.F., Ślipiński, A. & Pakaluk, J. (1995b) From Latreille to Crowson: a history of the higher-level classification of beetles. In: Pakaluk, J. & Ślipiński, A. (Eds), Biology, phylogeny, and classification of Coleoptera. Papers celebrating the 80th birthday of Roy A. Crowson. Volumes 1–2. Muzeum i Instytut Zoologii PAN, Warszawa, pp. 87–154.

Lawrence, J.F., Ślipiński, A., Seago, A.E., Thayer, M.K., Newton, A.F. & Marvaldi, A.E. (2011) Phylogeny of the Coleoptera based on morphological characters of adults and larvae. *Annales Zoologici*, 61: 1–217.

Lee, C.F., Jäch, M.A. & Beutel, R.G. (2016) Psephenidae Lacordaire, 1854. In: Beutel, R.G. & Leschen, R.A.B (Eds), Handbook of zoology, Arthropoda: Insecta, 2nd edition; Coleoptera, beetles, Volume 1: Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Walter de Gruyter, Berlin/New York, pp. 615–628.

Lee, C.F., Satô, M., Shepard, W.D. & Jäch, M.A. (2007) Phylogeny of Psephenidae (Coleoptera: Byrrhoidea) based on larval, pupal and adult characters. *Systematic Entomology*, 32: 502–538.

Lloyd, J.E. (1978) Insect bioluminescence. In: Herring, P.J. (Ed.), Bioluminescence in action. Academy Press, New York, pp. 241–272.

Lloyd, J.E. (1984) Occurrence of aggressive mimicry in fireflies. *The Florida Entomologist*, 67: 368–376.

Machado, V. & Araújo, A.M. (2001) The aggregation of *Chauliognathus* species (Coleoptera, Cantharidae) and its possible role for coexistence and mimicry. *Iheringia, Série Zoologia*, 91: 29–32.

Maier, C.A. (2016) Phylogeny, ecology, and taxonomic revision of the Travertine Beetles (Coleoptera: Lutrochidae). PhD thesis, University of Kansas, Kansas, 332 pp.

Maier, C.A., Lawrence, J.F. & Leschen, R.A.B. (2016) Byrrhidae Latreille, 1804. In: Beutel, R.G. & Leschen, R.A.B (Eds), Handbook of zoology, Arthropoda: Insecta, 2nd edition; Coleoptera, beetles, Volume 1: Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Walter de Gruyter, Berlin/New York, pp. 554–561.

Malohlava, V. & Bocák, L. (2010) Evidence of extreme habitat stability in a Southeast Asian biodiversity hotspot based on the evolutionary analysis of neotenic net-winged beetles. *Molecular Ecology*, 19: 4800–4811.

Martin, G.J., Branham, M.A., Whiting, M.F. & Bybee, S.M. (2017) Total evidence phylogeny and the evolution of adult bioluminescence in fireflies (Coleoptera: Lampyridae). *Molecular Phylogenetics and Evolution*, 107: 564–575.

Mášek, M., Motyka, M., Kusý, D., Boček, M., Li, Y. & Bocák, L. (2018) Molecular phylogeny, diversity and zoogeography of net-winged beetles (Coleoptera: Lycidae). *Insects*, 9: 154.

Mášek, M., Palata, V., Bray, T.C. & Bocák, L. (2015) Molecular phylogeny reveals high diversity and geographic structure in Asian neotenic net-winged beetles *Platerodrilus* (Coleoptera: Lycidae). *PLoS ONE*, 10: e0123855.

McKenna, D.D. & Farrell, B.D. (2006) Tropical forests are both evolutionary cradles and museums of leaf beetle diversity. *Proceedings of the National Academy of Sciences of The United States of America*, 103: 10947–10951.

McKenna, D.D., Wild, A.L., Kanda, K., Bellamy, C.L., Beutel, R.G., Caterino, M.S., Farnum, C.W., Hawks, D.C., Ivie, M.A., Jameson, M.L., Leschen, R.A.B., Marvaldi, A.E., McHugh, J.V., Newton, A.F., Robertson, J.A., Thayer, M.K., Whiting, M.F., Lawrence, J.F., Ślipiński, A., Maddison, D.R. & Farrell, B.D. (2015) The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Systematic Entomology*, 40: 835–880.

Motyka, M., Kampová, L. & Bocák, L. (2018) Phylogeny and evolution of Müllerian mimicry in aposematic *Dilophotes*: evidence for advergence and size-constraints in evolution of mimetic sexual dimorphism. *Scientific Reports*, 8: 3744.

Muona, J. (1995) The phylogeny of Elateroidea (Coleoptera), or which tree is the best today? *Cladistics*, 11: 317–341.

Muona, J. (2010) Eucnemidae Eschscholtz, 1829. In: Leschen, R.A.B., Beutel, R.G. & Lawrence, J.F. (Eds), Handbook of zoology, Arthropoda: Insecta; Coleoptera, beetles, Volume 2: Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter de Gruyter, Berlin, pp. 61–69.

Muona, J., Lawrence, J.F. & Ślipiński, A. (2010) Throscidae Laporte, 1840. In: Leschen, R.A.B., Beutel, R.G. & Lawrence, J.F. (Eds), Handbook of zoology, Arthropoda: Insecta; Coleoptera, beetles, Volume 2: Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter de Gruyter, Berlin, pp. 69–74.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403: 853–858.

Novotný, V., Basset, Y., Miller, S.E., Weiblen G.D., Bremer, B., Čížek, L. & Drozd, P. (2002) Low host specificity of herbivorous insects in a tropical forest. *Nature*, 416: 841–844.

Oba, Y. (2009) On the origin of beetle luminescence. In: Meyer-Rochow, V.B. (Ed.), Bioluminescence in focus - A collection of illuminating essays. Research Signpost, Kerala, pp. 277–290.

Oba, Y., Ojika, M. & Inouye, S. (2003) Firefly luciferase is a bifunctional enzyme: ATP-dependent monooxygenase and a long chain fatty acyl-CoA synthetase. *FEBS Letters*, 540: 251–254.

Ôhira, H. (1962) Morphological and taxonomic study on the larvae of Elateridae in Japan (Coleoptera). H. Ôhira, Okazaki, 179 pp.

Olivier, E. (1910) Rhagophthalmidae, Drilidae. In: Schenkling, S. (Ed.), Coleopterorum Catalogus, Pars 10. W. Junk, Berlin, pp. 1–10.

Petrželková, I., Makris, C. & Kundrata, R. (2017) The genus *Brachypsectra* LeConte, 1874 (Coleoptera: Brachypsectridae) in the Palaearctic Region. *European Journal of Taxonomy*, 276: 1–14.

Platia, G. & Németh, T. (2011) On some Palearctic click-beetles deposited in the Hungarian Natural History Museum (Coleoptera Elateridae). *Annales Historico-Naturales Musei Nationali Hungarici*, 103: 65–106.

Ramsdale, A.S. (2010a) Omethidae LeConte, 1861. In: Leschen, R.A.B., Beutel, R.G. & Lawrence, J.F. (Eds), Handbook of zoology, Arthropoda: Insecta; Coleoptera, beetles, Volume 2: Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter de Gruyter, Berlin, pp. 149–153.

Ramsdale, A.S. (2010b) Cantharidae Imhoff, 1856. In: Leschen, R.A.B., Beutel, R.G. & Lawrence, J.F. (Eds), Handbook of zoology, Arthropoda: Insecta; Coleoptera, beetles, Volume 2: Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter de Gruyter, Berlin, pp. 153–162.

Riedel, A., Sagata, K., Surbakti, S., Tänzler, R. & Balke, M. (2013) One hundred and one new species of *Trigonopterus* weevils from New Guinea. *ZooKeys*, 280: 1–150.

Riedel, A., Tänzler, R., Balke, M., Rahmadi, C. & Suhardjono, Y.R. (2014) Ninety-eight new species of *Trigonopterus* weevils from Sundaland and the Lesser Sunda Islands. *ZooKeys*, 467: 1–162.

Robertson, J.A., Ślipiński, A., Moulton, M., Shockley, F.W., Giorgi, A., Lord, N.P., McKenna, D.D., Tomaszewska, W., Forrester, J., Miller, K.B., Whiting, M.F. & McHugh, J.V. (2015) Phylogeny and classification of Cucujoidea and the recognition of a new superfamily Coccinelloidea (Coleoptera: Cucujiformia). *Systematic Entomology*, 40: 745–778.

Rosa, S.P. (2014) Phylogenetic analysis and taxonomic revision of Physodactylinae (Coleoptera, Elateridae). *Papéis avulsos de zoologia, São Paulo*, 54: 217–292.

Sagegami-Oba, R., Oba, Y. & Ôhira, H. (2007a) Phylogenetic relationships of click beetles (Coleoptera: Elateridae) inferred from 28S ribosomal DNA: Insights into the evolution of bioluminescence in Elateridae. *Molecular Phylogenetics and Evolution*, 42: 410–421.

Sagegami-Oba, R., Takahashi, N. & Oba, Y. (2007b) The evolutionary process of bioluminiscence and aposematism in cantharoid beetles (Coleoptera: Elateroidea) inferred by the analysis of 18S ribosomal DNA. *Gene*, 400: 104–113.

Schenkling, S. (1925) Fam. Elateridae I. Coleopterorum Catalogus, pars 80. W. Junk, Berlin, pp. 1–263.

Schenkling, S. (1927) Fam. Elateridae II. Coleopterorum Catalogus, pars 88. W. Junk, Berlin, pp. 265–636.

Schimmel, R. & Tarnawski, D. (2009) Monograph of the tribe Quasimusini (Insecta: Coleoptera, Elateridae, Negastriinae). *Polish Taxonomical Monographs*, 17: 1–169 pp.

Schimmel, R., Tarnawski, D., Han, T. & Platia, G. (2015) MonograSaph of the new tribe Selatosomini from China (Elateridae: Denticollinae). Part I: Genera *Pristilophus* Latreille, 1834 stat. nov., *Selatosomus* Stephens, 1830, *Warchalowskia* (Tarnawski, 1995) stat. nov., and *Sinophotistus* gen. nov. *Polish Entomological Monographs*, 11: 1–328.

Schimmel, R., Tarnawski, D., Han, T. & Platia, G. (2016) Monograph of the new tribe Selatosomini from China (Elateridae: Denticollinae). Part II: Genera *Mosotalesus* Kishii, 1977, *Sinophotistus* Schimmel, Tarnawski, Han & Platia, 2015, *Costalicus* Schimmel & Tarnawski, 2016, and *Sinopristilopus* gen. nov. *Polish Entomological Monographs*, 12: 1–280.

Schwarz, O. (1906) Coleoptera. Fam. Elateridae. In: Wytsman, P.A. (Ed.), Genera Insectorum. Vol. VII. Fascicules 46A, 46B. P. Wytsman, Bruxelles, pp. 1–112, 113–224.

Schwarz, O. (1907) Coleoptera. Fam. Elateridae. In: Wytsman, P.A. (Ed.), Genera Insectorum. Vol. VII. Fascicule 46C. P. Wytsman, Bruxelles, pp. 225–370.

Shimomura, O. (2012) Bioluminescence. Chemical principles and methods. World Scientific, Singapore, 496 pp.

Short, A.E.Z. (2018) Systematics of aquatic beetles (Coleoptera): current state and future directions. *Systematic Entomology*, 43: 1–18.

Sklenářová, K., Chesters, D. & Bocák, L. (2013) Phylogeography of poorly dispersing net-winged beetles: A role of drifting India in the origin of Afrotropical and Oriental fauna. *PLoS ONE*, 8: e67957.

Ślipiński, A., Leschen, R.A.B. & Lawrence, J.F. (2011) Order Coleoptera Linnaeus, 1758. In: Zhang, Z.Q. (Ed.), Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. *Zootaxa*, 3148: 203–208.

Stanger-Hall, K.F., Lloyd, J.E. & Hillis, D.M. (2007) Phylogeny of North American fireflies (Coleoptera: Lampyridae): Implications for the evolution of light signals. *Molecular Phylogenetics and Evolution*, 45: 33–49.

Stork, N.E., McBroom, J., Gely, C. & Hamilton, A.J. (2015) New approaches narrow global species estimates for beetles, insects, and terrestrial arthropods. *Proceedings of the National Academy of Sciences of the United States of America*, 112: 7519–7523.

Stibick, J.N.L. (1979) Classification of the Elateridae (Coleoptera). Relationships and classification of the subfamilies and tribes. *Pacific Insects*, 20: 145–186.

Stribling, J.B. (1986) World generic revision of Ptilodactylidae (Coleoptera: Dryopoidea). PhD Thesis, Ohio State University, Columbus, 200 pp.

Šormová, E. & Kundrata, R. (2017) *Afrocerophytum vix* Costa, Vanin et Rosa, 2014 (Elateroidea: Cerophytidae) newly recorded from Ghana. *Folia Entomologica Hungarica*, 78: 35–38.

Šormová, E., Kramp, K. & Kundrata, R. (2018) Diversity and phylogenetic relationships of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) in Cyprus. *Zoologischer Anzeiger*, 275: 1–12.

Timmermans, M.J.T.N. & Vogler, A.P. (2012) Phylogenetically informative rearrangements in mitochondrial genomes of Coleoptera, and monophyly of aquatic elateriform beetles (Dryopoidea). *Molecular Phylogenetics and Evolution*, 63: 299–304.

Timmermans, M.J.T.N., Barton, C., Haran, J., Ahrens, D., Culverwell, C. L., Ollikainen, A., Dodsworth, S., Foster, P.G., Bocák, L. & Vogler, A.P. (2016) Family-level sampling of mitochondrial genomes in Coleoptera: compositional heterogeneity and phylogenetics. *Genome Biology and Evolution*, 8: 161–175.

Timmermans, M.J., Dodsworth, S., Culverwell, C.L., Bocák, L., Ahrens, D., Littlewood, D.T., Pons, J. & Vogler, A.P. (2010) Why barcode? High-throughput multiplex sequencing of mitochondrial genomes for molecular systematics. *Nucleic Acids Research*, 38: e197.

Trllová, Š. & Kundrata, R. (2015) A review of the genus *Selasia* (Elateridae: Agrypninae: Drilini) in the Palaearctic Region. *Zootaxa*, 3920: 563–571.

Vahtera, V., Muona, J. & Lawrence, J.F. (2009) Phylogeny of the Thylacosterninae (Coleoptera, Elateridae). *Cladistics*, 25: 147–160.

Vanin, S.A., Costa, C., Ide, S. & Beutel, R.G. (2016) Heteroceridae MacLeay, 1825. In: Beutel, R.G. & Leschen, R.A.B (Eds), Handbook of zoology, Arthropoda: Insecta, 2nd edition; Coleoptera, beetles, Volume 1: Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Walter de Gruyter, Berlin/New York, pp. 612–615.

Viviani, V.R. & Bechara, E.J. (1997) Bioluminescence and biological aspects of Brazilian railroad-worms (Coleoptera: Phengodidae). *Annals of Entomological Society of America*, 90: 389–398.

Wang, B., Zhang, H. & Jarzembowski, E.A. (2013) Early Cretaceous angiosperms and beetle evolution. *Frontiers in Plant Science*, 4: 360.

Welter-Schultes, F.W. (2000) The pattern of geographical and altitudinal variation in the land snail *Albinaria idaea* from Crete (Gastropoda: Clausiliidae). *Biological Journal of the Linnean Society*, 71: 237–250.

Wilson, T. & Hastings, J.W. (2013) Bioluminescence - Living lights, lights for living. Harvard University Press, Cambridge, 185 pp.

Wittmer, W. (1944) Catalogue des Drilidae E. Oliv. (Coleoptera - Malacodermata). *Revista de la Sociedad Entomológica Argentina*, 12: 203–221.

Wittmer, W. (1979) 64. Beitrag zur Kenntnis der palaearktischen Cantharidae, Phengodidae und Malachiidae (Col.). *Entomologica Basiliensia*, 4: 327–346.

Zaragoza-Caballero, S. & Pérez Hernández, C.X. (2014) Sinopsis de la familia Phengodidae (Coleoptera): trenecitos, bigotudos, glow-worms, railroad-worms o besouros trem de ferro. Instituto de Biología, Universidad Nacional Autónoma de México, México, D.F., 128 pp.

Zaragoza-Caballero, S. & Zurita-García, M.L. (2015) A preliminary study on the phylogeny of the family Phengodidae (Insecta: Coleoptera). *Zootaxa*, 3947: 527–542.

Zhang, S.-Q., Che, L.-H., Li, Y., Liang, D., Pang, H., Ślipiński A. & Zhang, P. (2018) Evolutionary history of Coleoptera revealed by extensive sampling of genes and species. *Nature Communications*, 9: 205.

7. Seznam příloh

[Příloha 1]
Kundrata, R.*, Bocáková, M. & Bocák, L. (2013) The phylogenetic position of Artematopodidae (Coleoptera: Elateroidea), with description of the first two *Eurypogon* species from China. *Contributions to Zoology*, 82: 199–208.
[IF 2,029; 6 citací na WoS; celkem 7 citací bez autorových autocitací]
[autorský podíl: 33 %]

[Příloha 2]
Bocák, L.*, **Kundrata, R.**, Andújar Fernández, C. & Vogler, A.P. (2016) The discovery of Iberobaeniidae (Coleoptera: Elateroidea), a new family of beetles from Spain, with immatures detected by environmental DNA sequencing. *Proceedings of the Royal Society B - Biological Sciences*, 283: 20152350.
[IF 4,940; 20 citací na WoS; celkem 16 citací bez autorových autocitací]
[autorský podíl: 35 %]

[Příloha 3]
Kundrata, R.*, Jäch, M.A. & Bocák, L. (2017) Molecular phylogeny of the Byrrhoidea-Buprestoidea complex (Coleoptera, Elateriformia). *Zoologica Scripta*, 46: 150–164.
[IF 3,057; 6 citací na WoS; celkem 7 citací bez autorových autocitací]
[autorský podíl: 40 %]

[Příloha 4]
Kundrata, R.*, Ivie, M.A. & Bocák, L. (2019) *Podabrocephalus* Pic is the morphologically modified lineage of Ptilodactylinae (Coleoptera: Elateriformia: Ptilodactylidae). *Insect Systematics & Evolution*, doi: 10.1163/1876312X-00002190.
[IF 0,763; ještě není na WoS; celkem 1 citace bez autorových autocitací]
[autorský podíl: 40 %]

[Příloha 5]
Kundrata, R.*, Gunter, N.L., Douglas, H. & Bocák, L. (2016) Next step toward a molecular phylogeny of click-beetles (Coleoptera: Elateridae): redefinition of Pityobiinae, with a

description of a new subfamily, Parablacinae, from the Australasian Region. *Austral Entomology*, 55: 291–302.
[IF 1,341; 18 citací na WoS; celkem 5 citací bez autorových autocitací]
[autorský podíl: 45 %]

[Příloha 6]
Kundrata, R.*, Gunter, N.L., **Janošíková, D.** & Bocák, L. (2018) Molecular evidence for the subfamilial status of Tetralobinae (Coleoptera: Elateridae), with comments on parallel evolution of some phenotypic characters. *Arthropod Systematics & Phylogeny*, 76: 137–145.
[IF 1,703; 5 citací na WoS]
[autorský podíl: 45 %]

[Příloha 7]
Douglas, H., **Kundrata, R.***, **Janošíková, D.** & Bocák, L. (2018) Molecular and morphological evidence for new genera in the click-beetle subfamily Cardiophorinae (Coleoptera: Elateridae). *Entomological Science*, 21: 292–305.
[IF 1,069; 2 citace na WoS]
[autorský podíl: 35 %]

[Příloha 8]
Baalbergen, E., Helwerda, R., Schelfhorst, R., Castillo Cajas, R.F., van Moorsel, C.H.M., **Kundrata, R.**, Welter-Schultes, F.W., Giokas, S. & Schilthuizen, M.* (2014) Predator-prey interactions between shell-boring beetle larvae and rock-dwelling land snails. *PLoS ONE*, 9: e100366.
[IF 3,234; 14 citací na WoS; celkem 7 citací bez autorových autocitací]
[autorský podíl: 12 %]

[Příloha 9]
Kundrata, R., Baena, M. & Bocák, L.* (2015) Classification of Omalisidae based on molecular data and morphology, with description of Paradrilinae subfam. nov. (Coleoptera: Elateroidea). *Zootaxa*, 3915: 413–422.
[IF 0,994; 7 citací na WoS; celkem 4 citace bez autorových autocitací]
[autorský podíl: 40 %]

[Příloha 10]

Kundrata, R.*, Baalbergen, E., Bocák, L. & Schilthuizen, M. (2015) The origin and diversity of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) in Crete based on mitochondrial phylogeny. *Systematics and Biodiversity*, 13: 52–75.

[IF 1,985; 10 citací na WoS; celkem 6 citací bez autorových autocitací]

[autorský podíl: 30 %]

[Příloha 11]

Kundrata, R.* & Bocák, L. (2017) Taxonomic review of Drilini (Elateridae: Agrypninae) in Cameroon reveals high morphological diversity, including the discovery of five new genera. *Insect Systematics & Evolution*, 48: 441–492.

[IF 0,763; 8 citací na WoS; celkem 2 citace bez autorových autocitací]

[autorský podíl: 50 %]

[Příloha 12]

Šormová, E., Kramp, K. & **Kundrata, R.*** (2018) Diversity and phylogenetic relationships of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) in Cyprus. *Zoologischer Anzeiger*, 275: 1–12.

[IF 1,345; 2 citace na WoS; celkem 1 citace bez autorových autocitací]

[autorský podíl: 45 %]

[Příloha 13]

Kundrata, R.* & Bocák, L. (v tisku) Molecular phylogeny reveals the gradual evolutionary transition to soft-bodiedness in click-beetles and identifies Sub-Saharan Africa as a cradle of diversity for Drilini (Coleoptera: Elateridae). *Zoological Journal of the Linnean Society*.

[IF 2,685]

[autorský podíl: 50 %]

Poznámky: tučně = autor a jeho studenti; * = korespondující autor

U všech publikací, ve kterých jsem uveden jako korespondující autor, jsem analyzoval veškerá data (kromě Přílohy 11, v níž byla studována pouze alfa-taxonomie, a Přílohy 12, kde se na analýzách částečně podílela má studentka), napsal první verzi rukopisu, submitoval rukopis a komunikoval s editory. Ve třech případech, kdy nejsem korespondující autor, je připojeno prohlášení korespondujícího autora o mém podílu na publikaci (za Přílohou 13).

8. Přílohy

Příloha 1

Kundrata, R., Bocáková, M. & Bocák, L. (2013) The phylogenetic position of Artematopodidae (Coleoptera: Elateroidea), with description of the first two *Eurypogon* species from China. *Contributions to Zoology*, 82: 199–208.
[IF 2,029; 6 citací na WoS; celkem 7 citací bez autorových autocitací]
[korespondující autor; autorský podíl: 33 %]

Contributions to Zoology, 82 (4) 199-208 (2013)

The phylogenetic position of Artematopodidae (Coleoptera: Elateroidea), with description of the first two *Eurypogon* species from China

Robin Kundrata[1,3], Milada Bocakova[2], Ladislav Bocak[1]
[1] Department of Zoology, Faculty of Science, Palacky University, 17. listopadu 50, 779 00, Olomouc, Czech Republic
[2] Department of Biology, Pedagogical Faculty, Palacky University, Purkrabska 2, 771 40, Olomouc, Czech Republic
[3] E-mail: robin.kundrata@upol.cz

Key words: mtDNA, rDNA, diversity, Elateriformia, new species, Palaearctic Region, phylogeny, taxonomy

Abstract

The Artematopodidae is a species-poor beetle family with contentious relationships to byrrhoid and elateroid families. Recent molecular phylogenetic analyses brought ambiguous results based on a single sequenced species. We investigated the taxonomic placement of Artematopodidae within Elateriformia using ribosomal (18S, 28S) and mitochondrial (*rrnL*, *cox1*) molecular markers and three artematopodid species. Our analyses placed Artematopodidae close to Omethidae+Telegeusidae in a basal position of broadly defined Elateroidea. Additionally, we described the first artematopodid species from China – *Eurypogon jaechi* sp. nov. and *E. heishuiensis* sp. nov. These species are reported from mountains of Yunnan and can be easily distinguished from their Palaearctic congeners by their large bodies and metallic green elytra. They differ from each other by the shape of the pronotum, puncturation of the head and pronotum, the relative lengths of the antennomeres 3-5, and the morphology of the female genitalia. With respect to our findings, we discussed the phylogeny, diversity and distribution of the family Artematopodidae.

Contents

Introduction

The Artematopodidae is a species-poor beetle lineage currently classified in Elateroidea (Bouchard *et al.*, 2011). Altogether 66 extant species are placed in eight genera; six species were described from amber fossils (Hörnschemeyer, 1998; Lawrence, 2010). Artematopodids are characterized by the presence of paired carinae on the prosternum, connate abdominal ventrites, and an interlocking tongue-like process on the internal part of the elytral apex (Lawrence, 1995). Three subfamilies are recognized: Artematopodinae, which consist of Artematopodini, Ctesibiini and Macropogonini, monogeneric Allopogoniinae, and Electribiinae (Lawrence, 2005; Table S3).

The relationships of the Artematopodidae were contentious since their description by Lacordaire (1857) and even recent studies did not provide a robust phylogenetic hypothesis (Lawrence, 1995). The Artematopodidae were originally treated as a subgroup of the Dascillidae (*e.g.* Horn, 1880; Pic, 1914), mainly because of the similar general appearance and the presence of membranous lamellae on the ventral parts of the tarsomeres. Forbes (1926) placed them with Cerophytidae and Brachypsectridae among the basal Elateriformia. Using larval characters, Böving and Craighead (1931) classified them under the name Eurypogonidae into the Dryopoidea. Crowson (1955) formally followed their concept, but discussed the conflicting signal from adult morphology which suggests relationships to elateroid lineages. Later, he erected the superfamily Artematopoidea for the Artematopodidae, Brachypsectridae and Callirhipidae and discussed the relationships of the Artematopoidea with the Elateroidea and Cantharoidea (Crowson, 1973). Lawrence and Newton (1982) separated the Callirhipidae from the Artematopodidae. Lawrence (1988) merged the Artematopoidea, Elateroidea and Cantharoidea into a single broadly defined Elateroidea and inferred the Artematopodidae in variable positions: as sister to the Elateroidea *sensu stricto* (Crowson, 1955) + Brachypsectridae, sister to the Elateroidea *sensu stricto* + Brachypsectridae + some dryopoid lineages,

Table 1. The list of newly sequenced taxa with GenBank accession and voucher numbers.

Family	Genus/Species	Geographical origin	Markers				Specimen voucher
			18S rDNA	28S rDNA	16S mtDNA	COI mtDNA	
Artematopodidae	*Eurypogon japonicus*	Japan, Nara Pref.	KF294761	KF294767	KF294755	KF294774	UPOL RK0091
Artematopodidae	*Eurypogon hisamatsui*	Japan, Tokushima Pref.	KF294762	KF294768	KF294756	KF294775	UPOL RK0128
Artematopodidae	*Eurypogon brevipennis*	Japan, Nagano Pref.	KF294763	KF294769	KF294757	KF294776	UPOL 001335
Omethidae	*Drilonius* sp. b	India, Kunchappanai	KF294764	KF294770	KF294758	KF294777	UPOL 001273
Omethidae	*Drilonius* sp. c	Philippines, Mindanao	KF294765	KF294771	KF294759	KF294778	UPOL RK0134
Throscidae	*Trixagus meybohmi*	Czech Republic, Moravia	KF294766	KF294772	KF294760	KF294779	UPOL RK0139

or as a basal lineage of the Elateroidea. Beutel (1995) analyzed larval characters and found artematopodids regularly in monophyletic Elateroidea *sensu* Lawrence (1988) either close to the Elateridae, Cebrionidae and Cantharidae, or sister to the remaining Elateroidea. Lawrence *et al*. (1995) combined larval and adult characters and artematopodids either occupied a basal position in Elateroidea, were sister to the Elateroidea *sensu stricto*, formed a basal lineage in a clade containing the Elateroidea and several unrelated lineages, or were in an unresolved position within Elateriformia. The latest morphology-based phylogeny of Coleoptera (Lawrence *et al*., 2011) found Artematopodidae to be the basalmost lineage of Elateroidea.

No artematopodids were included in most molecular phylogenetic studies (Bocakova *et al*., 2007; Hunt *et al*., 2007; McKenna and Farrell, 2009; Kundrata and Bocak, 2011). Only Sagegami-Oba *et al*. (2007) used the artematopodid genus *Eurypogon* in their dataset of 18S rDNA sequences and placed *Eurypogon japonicus* as a sister to the Heteroceridae in a wider clade of several byrrhoid families and Buprestidae. In the latest molecular phylogeny of the Coleoptera, Bocak *et al*. (2013) analyzed over 8000 terminals and Artematopodidae formed one of the basal lineages in Elateroidea, however, only two ribosomal loci (18S and 28S rDNA) represented *Eurypogon japonicus* in the five-marker dataset. Although the placement of the Artematopodidae in the Elateroidea is widely accepted (Cooper, 1991; Lawrence and Newton, 1995; Young, 2002; Lawrence, 2010; Bouchard *et al*., 2011), an underlying phylogenetic hypothesis is absent.

In this study, we expand available complete four-marker data by newly sequenced representatives of basal elateroid lineages and three *Eurypogon* species to investigate the position of Artematopodidae within the elateriform series, and we describe two *Eurypogon* species, which represent the first record of the family in China.

Material and methods

Molecular dataset and laboratory procedures

The dataset contained 158 terminals. The newly sequenced 18S rDNA (~1900 bp), 28S rDNA (~700 bp), *rrnL* mtDNA (~600 bp), and *cox1* mtDNA (723 bp) fragments were produced for three *Eurypogon* species (Artematopodidae), two species of *Drilonius* Kiesenwetter (Omethidae) and *Trixagus meybohmi* Leseigneur, 2005 (Throscidae; Table 1). Total DNA was extracted using the Wizard SV96 Purification System (Promega Corp., Madison, WI, USA). Further laboratory procedures, sequencing and primers were reported by Kundrata and Bocak (2011). The newly obtained data were merged with the dascilloid, byrrhoid and elateroid sequences used in recent molecular phylogenic studies of Elateroidea (Kundrata and Bocak, 2011; Table S1). *Dascillus cervinus* Linnaeus, 1758 (Dascillidae) as a member of basal Elateroidea (Bocak *et al*., 2013) was used as an outgroup. Only taxa with a complete set of four DNA markers were included in the dataset. GenBank accession numbers of sequences are listed in Tables 1 and S1. The classification follows Bouchard *et al*. (2011), with modifications made by Kundrata and Bocak (2011; for Elateridae and Omalisidae) and Janisova and Bocakova (2013; for Lampyridae: Ototretinae).

Sequence handling, alignment and phylogenetic analyses

Sequences were edited using Sequencher 4.7 (Gene Codes Corp., Ann Arbor, MI, USA). Protein-coding *cox1* sequences containing no indels were aligned by ClustalX 1.81 under default settings (Thompson *et al*., 1997). Additionally, for the alignment of rDNA and *rrnL* mtDNA sequences we used either ClustalX or BlastAlign, which omits parts of the length variable loops when reliable alignment cannot be inferred (Belshaw and Katzourakis, 2005). The concatenated datasets were analyzed under parsimony (MP), maximum likelihood (ML) and Bayesian algorithms. The MP analyses were carried out using TNT 1.0 (Goloboff *et al*. 2003, 2008) with gaps treated as missing characters. The most parsimonious trees were found 50times and the bootstrap values were calculated from 1000 pseudoreplicates. Consensus trees were inferred from PAUP* 4.03b10 (Swofford, 2002). For ML and Bayesian analyses, the datasets were partitioned by genes and codon positions, yielding a total of six partitions. The Bayesian analyses were performed with Mr. Bayes 3.1.2 (Huelsenbeck and Ronquist, 2001). Four chains were run for 40.10^6 generations, with trees sampled every 1,000 generations. The stationarity was detected in Tracer 1.5 (Rambaut and Drummond, 2007). For each analysis, the first 15% of trees were discarded as burn-in. The posterior probabilities were determined from the remaining trees. The ML analyses were conducted using RAxML 7.3.1 (Stamatakis, 2006) via the CIPRES web server (www.phylo.org; Miller *et al*., 2010). Branch supports were calculated using the rapid bootstrap algorithm (Stamatakis *et al*., 2008) with 1000 bootstrap iterations under the GTRCAT model.

Morphological taxonomy

The morphological study was based on adult semaphoronts. Genitalia were dissected, cleared in 10% aqueous solution of potassium hydroxide, dyed by chlorazol black and photographed using a digital camera mounted on a stereoscopic microscope. The following measurements were taken: BL-body length, measured from the fore margin of the head to the elytral apex; EL-elytral length; WHe-width of head including eyes; WH-width at humeri; PL-pronotal length at midline; PWA-pronotum width at anterior angles; PWP-pronotum width at posterior angles; Edist-minimum interocular distance in the frontal part of the cranium; Ediam-maximum eye diameter in lateral view; LV-length of valvifer; LC-length of coxit. A forward slash (/) separates different lines on a label. The species descriptions follow in general the recommendations of Ratcliffe (2013) and the morphological terminology follows those of Sakai (1982) and Lawrence (2010). The type material is deposited in the Naturhistorisches Museum Wien in Austria (NHMW).

Results

The 158-taxa concatenated BlastAlign and ClustalX datasets contained 4675 and 4330 homologous positions with 31.1 and 39.6% parsimony-informative characters, respectively. The numbers of homologous positions and constant, variable parsimony-informative and parsimony-uninformative characters for total matrices and individual markers shows the Table S2. The *rrnL* and *cox1* mtDNA fragments contained considerably higher percentage of parsimony-informative characters than 18S and 28S rDNA. Base frequencies showed high AT levels in mitochondrial DNA (Table S2). The maximum uncorrected pairwise distances among investigated taxa varied between 8.9% for 18S rDNA and 35.0% for *cox1* mtDNA (Table S2).

The phylogenetic analyses of data in the present constellation recovered Elateroidea *sensu* Lawrence and Newton (1995; *i.e.*, including Artematopodidae) as a monophylum (Fig. 1). The concept of Elateroidea was supported by bootstrap values (BS) of 58-68% in ML analyses, less than 50% in MP analyses, and 74-88% posterior probabilities (PP) in Bayesian analyses (Fig. 1). The Byrrhoidea was strongly supported in ML and Bayesian analyses of ClustalX alignment and weakly supported or paraphyletic in the remaining analyses. Artematopodidae were recovered in a basal position of the broadly defined Elateroidea; they formed an independent lineage in ML analysis of BlastAlign alignment (Fig. 1B; less than 50% BS) or they were sister to Omethidae + Telegeusidae in all remaining analyses (Fig. 1A; 58 and 100% PP in Bayesian analyses of BlastAlign and ClustalX alignments, respectively, 97% BS in ML analysis of ClustalX alignment, and less than 50% BS in MP analyses). Elateroidea *minus* Artematopodidae + (Omethidae + Telegeusidae) obtained strong support in analyses of BlastAlign alignment (84% BS, 100% PP) and low to moderate support in analyses of ClustalW alignment (Fig. 1). Throscidae and Eucnemidae formed either independent lineages (4 analyses, Fig. 1B) or a single clade (2 analyses, Fig. 1A). The strongly supported clade consisting of two subclades Lycidae + Lampyridae + Cantharidae and Omalisidae + Phengodidae + Rhagophthalmidae + Elateridae was found in all analyses. All analyses recovered elateroid families monophyletic, only Bayesian analysis of BlastAlign alignment showed paraphyletic Elateridae including a clade Omalisidae + Phengodidae + Rhagophthalmidae (less than 50% BS). All families but Omalisidae (<50-92% BS, 99-100% PP) and Elateridae (<50-75% BS, 94%

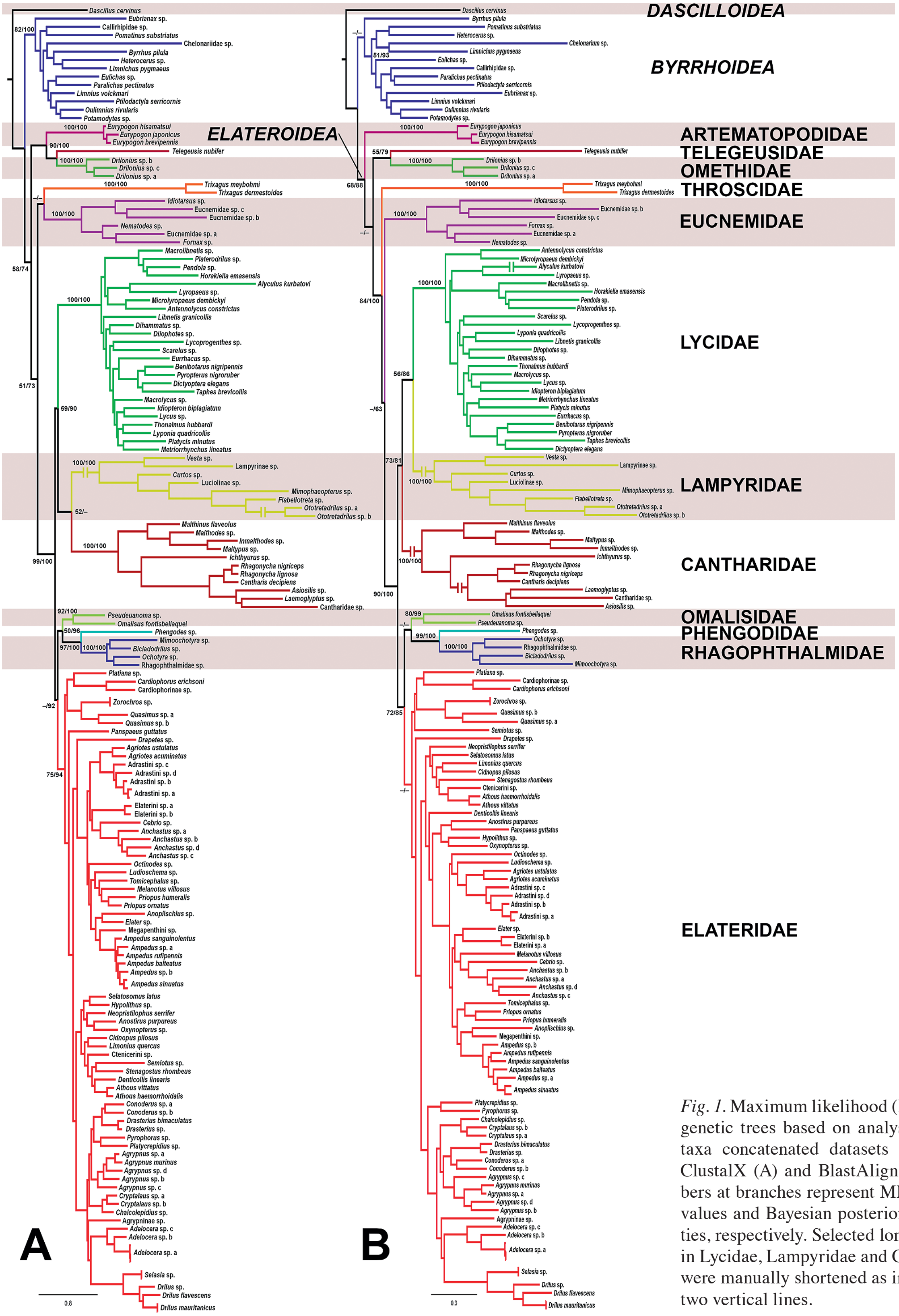


Fig. 1. Maximum likelihood (ML) phylogenetic trees based on analyses of 158-taxa concatenated datasets aligned by ClustalX (A) and BlastAlign (B). Numbers at branches represent ML bootstrap values and Bayesian posterior probabilities, respectively. Selected long branches in Lycidae, Lampyridae and Cantharidae were manually shortened as indicated by two vertical lines.

PP) obtained strong support in all analyses (92-100% BS, 100% PP). Among Artematopodidae, the sistergroup relationship between *Eurypogon hisamatsui* Sakai, 1982 and *E. brevipennis* Sakai, 1982 obtained strong support in 4 analyses. In ML and Bayesian analyses of BlastAlign alignment, *E. hisamatsui* was found sister to *E. japonicus* Sakai, 1982 (65% BS and 99% PP, respectively).

Discussion

The phylogenetic position of Artematopodidae

In this study, we combined ribosomal and mitochondrial DNA data to investigate the position of Artematopodidae. According to our analyses, Artematopodidae were never recovered near byrrhoid lineages as suggested by Sagegami-Oba *et al*. (2007; Fig. 1). The position of the Callirhipidae as a part of the Byrrhoidea and distant from Artematopodidae rejects Crowson's Artematopoidea (Crowson, 1973). The results placed artematopodids as a part of deep radiation of elateroid lineages in concordance with some recently published morphological and molecular analyses (*e.g.* Lawrence *et al*., 2011; Bocak *et al*., 2013; Fig. 1). Lawrence *et al*. (2011) recovered Artematopodidae as the basamost elateroid lineage and Bocak *et al*. (2013) inferred artematopodids as a sister to Elateroidea *minus* Telegeusidae and Omethidae. The basal position of Artematopodidae is also indicated by the fact that several species of Macropogonini feed on mosses (Lawrence, 2010). In our study, five out of six analyses revealed heretofore unknown sistergroup relationships of Artematopodidae and Omethidae + Telegeusidae (Fig. 1A). Only one analysis showed Artematopodidae sister to the remaining Elateroidea, but this topology was weakly supported (Fig. 1B). The Elateroidea except the three above mentioned basal lineages showed consistent support across the recent molecular analyses (Bocakova *et al*., 2007; Kundrata & Bocak, 2011; this study; Fig. 1). On the other hand, although we can consider the placement of Artematopodidae in the basal radiation of the Elateroidea as well supported, their relationships to Omethidae and Telegeusidae remain unresolved (Bocak *et al*., 2013; this study; Fig. 1). The Brachypsectridae (supposed as the close relatives of Artematopodidae by *e.g*., Crowson, 1973) fixed for the DNA isolation and more data for Omethidae and Telegeusidae are needed for better understanding of the relationships among the basal elateroid lineages.

The zoogeography and diversity of the Asian Artematopodidae

Currently, eight extant artematopodid genera are defined (Lawrence, 2010; Table S3). *Artematopus* Perty is the most diverse genus (44 species), three genera contain 2-11 species, and four genera are monotypic. The artematopodids have the highest diversity in the New World (all genera and most species; Table S3), with *Macropogon* Motschulsky and *Eurypogon* distributed additionally in the Palaearctic Region. Three species of *Macropogon* occur in the Russian Far East, one *Eurypogon* species is known from southern Europe and seven *Eurypogon* species are distributed in East Asia (Sakai, 1982; Hörnschemeyer, 1998; this study). *Eurypogon* had contained only Nearctic species until Sakai (1982) described four species from Japan and one from Taiwan (Table S4), but no species was recorded from continental Asia. Here, we described two *Eurypogon* species from the geographically very distant area in Yunnan (Fig. 3; for the species descriptions see the Appendix). Hörnschemeyer (1998) considered the pattern of Artematopodidae distribution as relict. The distant isolated ranges of Chinese and Japanese species of *Eurypogon* suggest much more extensive distribution of this genus in the past. Of course, we cannot exclude further records of these rare beetles from further localities in China, but all *Eurypogon* occur in a low number of species in small isolated ranges across the World and they have not been reported from large regions between the known ranges (Tables S3 and S4).

Acknowledgements

We are grateful to Manfred Jäch (NHMW) who kindly provided us with the material of newly described species. This study was supported by following grants: GAČR P506/11/1757 (LB), internal grant of Faculty of Science, UP Olomouc (LB, RK), and EU-SYNTHESYS BE-TAF 2193 (RK). We also thank two anonymous reviewers for critical comments on an earlier version of the manuscript.

References

Belshaw R, Katzourakis A. 2005. BlastAlign: a program that uses blast to align problematic nucleotide sequences. *Bioinformatics* 21: 122-123.

Beutel R. 1995. Phylogenetic analysis of Elateriformia (Coleoptera: Polyphaga) based on larval characters. *Journal of Zoological Systematics and Evolutionary Research* 33: 145-171.

Bocak L, Barton C, Crampton-Platt A, Chesters D, Ahrens D, Vogler AP. 2013. Building the Coleoptera tree-of-life for >8000 species: composition of public DNA data and fit with Linnaean classification. *Systematic Entomology*. doi: 10.1111/syen.12037.

Bocakova M, Bocak L, Hunt T, Vogler AP. 2007. Molecular phylogenetics of Elateriformia (Coleoptera): evolution of bioluminescence and neoteny. *Cladistics* 23: 477-496.

Bouchard P, Bousquet Y, Davies AE, Alonso-Zarazaga MA, Lawrence JF, Lyal CHC, Newton AF, Reid CAM, Schmitt M, Ślipiński SA, Smith ABT. 2011. Family-Group names in Coleoptera (Insecta). *ZooKeys* 88: 1-972.

Böving AG, Craighead FC. 1931. An illustrated synopsis of the principal larval forms of the order Coleoptera. *Entomologica Americana* 1: 1-351.

Cooper KW. 1991. Artematopodidae (Elateroidea). Pp. 407-409 in: Stehr FW, ed., *Immature Insects*. Volume 2. Dubuque, Iowa: Kendall/Hunt Publishing Company.

Crowson RA. 1955. *The natural classification of the families of Coleoptera*. London: Nathaniel Lloyd & Co., Ltd.

Crowson RA. 1973. On a new superfamily Artematopoidea of polyphagan betles, with the definition of two new fossil genera from the Baltic amber. *Journal of Natural History* 7: 225-238.

Forbes WTM. 1926. The wing folding patterns of the Coleoptera. *Journal of the New York Entomological Society* 34: 1-139.

Goloboff PA, Farris JS, Nixon KC. 2003. TNT: Tree analysis using new technology. www.zmuc.dk/public/phylogeny/tnt.

Goloboff PA, Farris JS, Nixon KC. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774-786.

Horn GH. 1880. Synopsis of the Dascyllidae of the United States. *Transactions of the American Entomological Society* 8: 76-114.

Hörnschemeyer T. 1998. New species of *Electribius* Crowson 1973 (Coleoptera: Artematopodidae) from Baltic amber. *Paläontologische Zeitschrift* 72: 299-306.

Huelsenbeck JP, Ronquist F. 2001. MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754-755.

Hunt T, Bergsten J, Levkanicova Z, Papadopoulou A, St-John O, Wild R, Hammond PM, Ahrens D, Balke M, Caterino MS, Gómez-Zurita J, Ribera I, Barraclough TG, Bocakova M, Bocak L, Vogler AP. 2007. A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. *Science* 318: 1913-1916.

Janisova K, Bocakova M. 2013. Revision of the subfamily Ototretinae (Coleoptera: Lampyridae). *Zoologischer Anzeiger* 252: 1-19.

Kundrata R, Bocak L. 2011. The phylogeny and limits of Elateridae (Insecta, Coleoptera): is there a common tendency of click beetles to soft-bodiedness and neoteny? *Zoologica Scripta* 40: 364-378.

Lacordaire T. 1857. *Histoire Naturelle des Insectes. Genera des Coléoptères*. Tome IV. Librairie Encyclopédique de Roret, Paris.

Lawrence JF. 1988. Rhinorhipidae, a new beetle family from Australia, with comments on the phylogeny of the Elateriformia. *Invertebrate Taxonomy* 2: 1-53.

Lawrence JF. 1995. *Electribius* Crowson: alive and well in Mesoamerica, with notes on *Ctesibius* Champion and the classification of Artematopodidae. Pp. 411-431 in: Pakaluk J, Ślipiński SA, eds, *Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson*. Warszawa, Poland: Muzeum i Instytut Zoologii Polska Akademia Nauk.

Lawrence JF. 2005. *Brevipogon*, a new genus of North American Artematopodidae (Coleoptera), with a key to world genera. *The Coleopterists Bulletin* 59: 223-236.

Lawrence JF. 2010. 4.2. Artematopodidae Lacordaire, 1857. Pp. 42-47 in: Leschen RAB, Beutel RG, Lawrence JF, vol. eds, *Coleoptera, Beetles; Volume 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)*. In: Kristensen NP, Beutel RG, eds, *Handbook of Zoology, Arthropoda: Insecta*. Berlin/New York: Walter de Gruyter GmbH & Co. KG.

Lawrence JF, Newton AF. 1982. Evolution and classification of beetles. *Annual Review of Ecology and Systematics* 13: 261-290.

Lawrence JF, Newton AF. 1995. Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). Pp. 779-1006 in: Pakaluk J, Ślipiński SA, eds, *Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson*. Warszawa, Poland: Muzeum i Instytut Zoologii Polska Akademia Nauk.

Lawrence JF, Nikitsky NB, Kirejtshuk AG. 1995. Phylogenetic position of Decliniidae (Coleoptera: Scirtoidea) and comments on the classification of Elateriformia (sensu lato). Pp. 375-410. In: Pakaluk J, Ślipiński SA, eds, *Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson*. Warszawa, Poland: Muzeum i Instytut Zoologii Polska Akademia Nauk.

Lawrence JF, Ślipiński SA, Seago AE, Thayer MK, Newton AF, Marvaldi AE. 2011. Phylogeny of the Coleoptera based on morphological characters of adults and larvae. *Annales Zoologici* 61: 1-217.

Leseigneur L. 2005. Description de *Trixagus meybohmi* n. sp. et note sur la morphologie des *Trixagus* du groupe carinifrons (Coleoptera, Throscidae). *Bulletin de la Société entomologique de France* 110: 89-96.

McKenna DD, Farrell BD. 2009. Beetles (Coleoptera). Pp. 278-289 in: Hedges SB, Kumar S, eds, *The Timetree of Life*. New York: Oxford University Press.

Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Pp. 1-8 in: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 Nov. 2010, New Orleans, LA.

Pic M. 1914. Dascillidae, Helodidae, Eucinetidae. In: Schenkling S, ed., *Coleopterorum Catalogus*. Pars 58. Berlin, W. Junk, 65 pp.

Rambaut A, Drummond AJ. 2007. Tracer version 1.5. Institute of Evolutionary Biology University of Edinburgh, Edinburgh.

Ratcliffe, BC. 2013. Best writing and curatorial practices for describing a new species of beetle: A primer. The Coleopterists Bulletin 67: 107-113.

Sagegami-Oba R, Takahashi N, Oba Y. 2007. The evolutionary process of bioluminescence and aposematism in cantharoid beetles (Coleoptera: Elateroidea) inferred by the analysis of 18S ribosomal DNA. *Gene* 400: 104-113.

Sakai M. 1982. Occurence of the genus *Eurypogon* Motschulsky in Japan and Taiwan (Coleoptera: Artematopidae). *Transactions of the Shikoku Entomological Society* 16: 51-61.

Stamatakis A. 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688-2690.

Stamatakis A, Hoover P, Rougemont J. 2008. A Rapid Bootstrap Algorithm for the RAxML Web Servers. *Systematic Biology* 57: 758-771.

Swofford DL. 2002. PAUP*: Phylogenetic Analysis Using Parsimony (*and other Methods), v.4.0b10. Sinauer Associates, Sunderland, MA.

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG. 1997. The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Research 25: 4876-4882.

Young DK. 2002. Artematopodidae Lacordaire 1857. Pp. 146-147. In: Arnett RH, Thomas MC, Skelley PE, Frank JH, eds, *American Beetles. Volume 2: Polyphaga: Scarabaeoidea through Curculionoidea*. Boca Raton, Florida, USA, CRC Press LLC.

Received: 26 June 2013
Revised and accepted: 5 November 2013
Published online: 20 December 2013
Editor: H. de Jong

On-line Supplementary Information

Table S1. The list of previously published sequences used in the dataset (Bocakova *et al*., 2007; Kundrata and Bocak 2011).
Table S2. Numbers of characters, base frequencies and maximum uncorrected pairwise distances.
Table S3. List of artematopodid genera, with geographical distributions.
Table S4. List of described species of the genus *Eurypogon* Motschulsky, with geographical distributions.

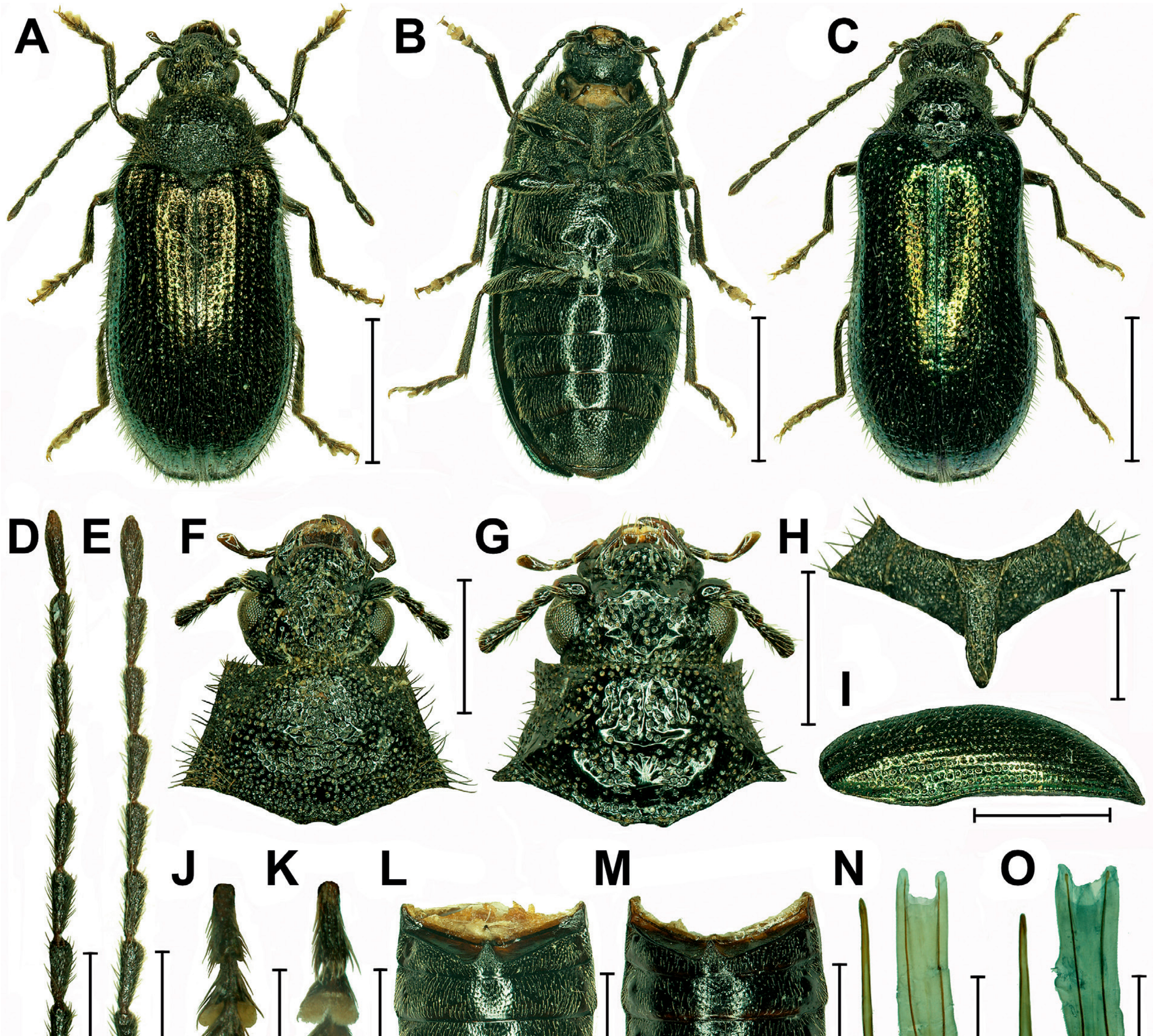


Fig. 2. Habitus of *Eurypogon* spp.: (A) *E. jaechi* sp. nov., dorsal habitus, (B) ventral habitus, (C) *E. heishuiensis* sp. nov., dorsal habitus; antenna: (D) *E. jaechi* sp. nov., (E) *E. heishuiensis* sp. nov.; pronotum: (F) *E. jaechi* sp. nov., (G) *E. heishuiensis* sp. nov.; *E. jaechi* sp. nov.: (H) prosternum, (I) elytron, dorsolaterally, (J) tarsomeres, dorsally, (K) ventrally; abdominal ventrites: (L) *E. jaechi* sp. nov., (M) *E. heishuiensis* sp. nov.; spiculum ventrale and valvifer with coxites: (N) *E. jaechi* sp. nov., (O) *E. heishuiensis* sp. nov. Scale bars: 2 mm (Figs 2-4, 10, 13-14), 1 mm (Figs 5-8, 15-16), 0.5 mm (Figs 9, 11-12).

Appendix

Systematics

Eurypogon Motschulsky, 1859

Diagnosis. Within Macropogonini, *Eurypogon* can be easily distinguished from *Macropogon* by subequal antennomeres 4 and 5 which are each considerably longer than antennomere 3 (in *Macroprogon* antennomere 5 is 2.5 times longer than antennomere 4 which is subequal to antennomere 3), basal pro- and mesotarsomeres without ctenidium and larva without distinct paired urogomphi on the 9th abdominal tergite (Crowson, 1973; Lawrence, 2005). The East Palaearctic *Eurypogon* species were described in detail by Sakai (1982).

Eurypogon jaechi sp. nov.
Fig. 2A-B, D, F, H-L, N

Type material. Holotype, 1 female, "China Yunnan, 1.-19.VII. / HEISHUI, 35 km N Lijiang / 27° 13'N 100° 19'E / E. Jendek leg. 1992" (NHMW).

Diagnosis. *Eurypogon jaechi* sp. nov. and *E. heishuiensis* sp. nov. are the only known artematopodids from continental Asia and can be easily distinguished from their Japanese and Taiwanese congeners by larger body and metallic green coloration of elytra (species from Japan and Taiwan are uniformly black). *E. jaechi* sp. nov. differs from similar *E. heishuiensis* sp. nov. by the following characters: dull metallic elytral coloration, slightly wider body (Fig. 2A, C), pronotum with less concave sides and less prominent hind angles, larger and denser punctures on head and pronotum (Fig. 2F-G), different relative lengths of antennomeres 3-5 (Fig. 2D-E), less prominent elevations near lateral sides of abdomen (Fig. 2L-M), and higher valvifer/coxit length ratio (Fig. 2N-O).

Description. Female. Body 6.1 mm long, 2.7 times as long as wide at humeri (Fig. 2A-B). Body coloration grey to black; elytra metallic dark green, moderately shiny; legs dark brown, tarsal lamellae yellow. Entire body densely covered by suberect or erect pubescence. Head deflexed (*i.e*., there is a deflexion point between frons and clypeus; anterior part of cranium is declined), cranium irregularly covered with large punctures; punctures circular to oval, sparser and variable in size on clypeus, interstices smooth, narrow, up to width of puncture diameter on clypeus; anterior clypeal margin slightly convex (Fig. 2F). Eyes protuberant; interocular distance 2.0 times eye diameter in dorsal view. Maxillary palpi almost 2 times longer than labial palpi, apical palpomere slender, widest at apex (Fig. 2F). Antennae 11-segmented, reaching second third of elytral length, covered by suberect hairs; antennomere 1 pear-shaped, antennomeres 2-3 simple, their combined lengths slightly longer than length of antennomere 4; antennomeres 4-10 slightly serrate, subequal in length, apical antennomere simple (Fig. 2D). Pronotum pentagonal, moderately convex, anterior edge simple, almost straight, lateral margins moderately straight, posterior margin evenly rounded, slightly sinuate in middle part. Anterior angles almost rectangular; posterior angles acute (Fig. 2F); surface with large, ovoid, moderately deep punctures, with smooth, very narrow interstices; shiny, covered by erected, long setae, mainly at margins. Prosternum transverse, with paired longitudinal ridges in front of coxae, continuing as sides of prosternal process; prosternal process overlapping mesoventrite (Fig. 2B, H). Scutellum flat, triangle-shaped. Elytra moderately shiny, sinuate behind humeri, widest at third fourth, finely and deeply punctate with distinct puncture rows (Fig. 2A, I); covered by suberect pubescence; elytral margins strenghtened, particularly apically. Legs slender, femora widest mesally, tibiae elongate, bearing spurs apically. Tarsomeres 2-4 ventrally with deeply bifid lamellae; lamella of tarsomere 3 largest; penultimate tarsomere shortest, ultimate tarsomere slender, longest; claws slightly curved (Fig. 2J, K). Abdomen short, well-sclerotized, finely and moderately deeply punctate, with suberect pubescence. All ventrites connate, each ventrite with a circular smooth elevation near lateral edges (Fig. 2L). Spiculum ventrale long, slender (Fig. 2N). Female genitalia with long and slender valvifer; valvifer 2.5 times longer than coxit (Fig. 2N).

Measurements. BL 6.1 mm, EL 4.7 mm, WHe 1.1 mm, WHum 2.2 mm, PL 1.1 mm, PWA 1.2 mm, PWP 1.9 mm, Edist 0.8 mm, Ediam 0.4 mm, LV 1.4 mm, LC 0.6 mm.

Distribution. This species is known only from the type locality in Yunnan, China (Fig. 3).

Etymology. The species is dedicated to Manfred Jäch (NHMW) who provided us with the type material.

Eurypogon heishuiensis sp. nov.
Fig. 2C, E, G, M, O

Type material. Holotype, 1 female, "China Yunnan, 1.-19.VII. / HEISHUI, 35 km N Lijiang / 27° 13'N 100° 19'E / E. Jendek leg. 1992" (NHMW).

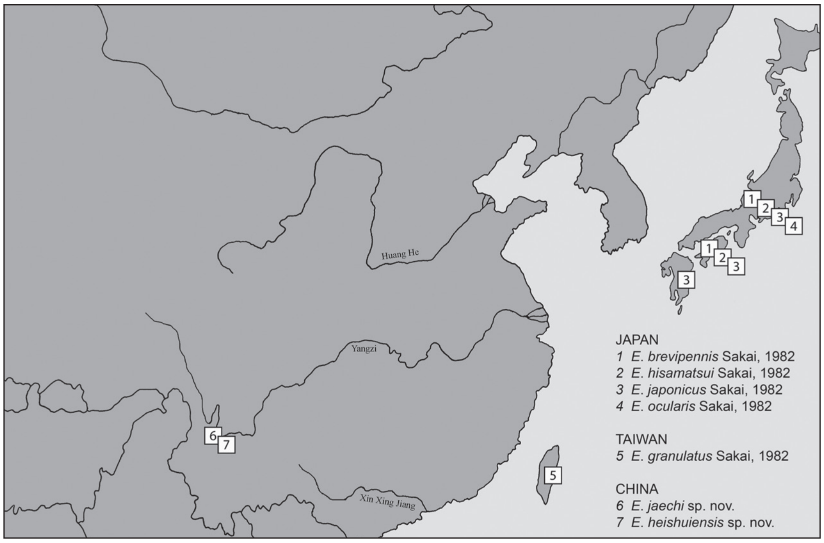


Fig. 3. The distribution of the genus *Eurypogon* in East Palaearctic Region.

Diagnosis. *E. heishuiensis* sp. nov. differs from *E. jaechi* sp. nov. by more metallic elytral coloration, narrower body (Fig. 2A, C), more concave pronotal sides and more prominent pronotal hind angles, smaller and sparser punctures on head and pronotum (Fig. 2F-G), different relative lengths of antennomeres 3-5 (Fig. 2D-E), more prominent elevations near lateral sides of abdomen (Fig. 2L-M), and lower valvifer/coxit length ratio (Fig. 2N-O).

Description. Body 6.1 mm long, 2.9 times as long as wide at humeri (Fig. 2C). Body coloration grey to black; elytra strongly metallic green, shiny; legs dark brown, tarsal lamellae yellow. Head irregularly and sparsely covered with moderately large punctures. Eyes protuberant; interocular distance 1.9 times eye diameter. Antennae with antennomere 1 pear-shaped, antennomeres 2-3 simple, minute, their combined lengths subequal to length of antennomere 4; antennomeres 4-10 slightly serrate; antennomere 5 slightly longer than antennomere 4; antennomeres 6-10 slightly shorter than antennomere 5, subequal in length; apical antennomere simple (Fig. 2E). Pronotum with anterior edge almost straight, lateral margins slightly concave, posterior margin evenly rounded, slightly sinuate in middle part. Anterior angles deflexed, almost rectangular; posterior angles acute (Fig. 2G); surface of disc shiny, with moderately large, ovoid punctures. Elytra shiny, finely and deeply punctate with distinct puncture rows (Fig. 2C). Abdominal ventrites with apparent circular smooth elevation near lateral edges (Fig. 2M). Spiculum ventrale moderately long, slender (Fig. 2O; valvifer 2.0 times longer than coxit (Fig. 2O).

Measurements. BL 6.1 mm, EL 4.7 mm, WHe 1.2 mm, WHum 2.1 mm, PL 1.0 mm, PWA 1.2 mm, PWP 1.8 mm, Edist 0.8 mm, Ediam 0.4 mm, LV 1.2 mm, LC 0.6 mm.

Distribution. This species is known only from the type locality in Yunnan, China (Fig. 3).

Etymology. The species name *heishuiensis* refers to the type locality of the species.

Table S1. The list of previously published sequences used in the dataset (Bocakova *et al*., 2007; Kundrata and Bocak 2011).

				Markers			
Superfamily/Family	Subfamily	Genus/Species	Geographic origin	18S rDNA	28S rDNA	16S mtDNA	COI mtDNA
DASCILLOIDEA							
Dascillidae	Dascillinae	*Dascillus cervinus*	United Kingdom	AY745558	DQ198700	DQ198621	DQ198543
BYRRHOIDEA							
Byrrhidae	Byrrhinae	*Byrrhus pilula*	United Kingdom	AF427604	DQ198705	DQ198625	DQ198548
Limnichidae	Limnichinae	*Limnichus pygmaeus*	United Kingdom	AF451923	DQ198719	DQ198631	DQ198554
Chelonariidae		*Chelonarium* sp.	Indonesia	DQ100488	DQ198724	DQ198635	DQ198558
Heteroceridae		*Heterocerus* sp.	Slovakia	AF451928	DQ198718	DQ198630	DQ198553
Dryopidae		*Pomatinus substriatus*	United Kingdom	AF451924	DQ198708	DQ198626	DQ198549
Psephenidae	Eubrianacinae	*Eubrianax* sp.	Indonesia	DQ100485	DQ198721	DQ198632	DQ198555
Elmidae	Elminae	*Limnius volckmari*	Spain	AF451914	DQ198712	DQ198627	DQ198550
Elmidae	Elminae	*Oulimnius rivularis*	Portugal	AF451913	DQ198714	DQ198628	DQ198551
Elmidae	Larainae	*Potamodytes* sp.	South Africa	AF451912	DQ198715	DQ198629	DQ198552
Callirhipidae		gen. sp.	Malaysia	DQ100490	DQ198726	DQ198637	DQ198560
Ptilodactylidae	Ptilodactylinae	*Ptilodactyla serricornis*	Japan	AF451932	DQ198723	DQ198634	DQ198557
Ptilodactylidae	Cladotominae	*Paralichas pectinatus*	Japan	DQ100486	DQ198722	DQ198633	DQ198556
Eulichadidae		*Eulichas* sp.	Malaysia	DQ100489	DQ198725	DQ198636	DQ198559
ELATEROIDEA							
Telegeusidae		*Telegeusis nubifer*	USA	DQ100503	DQ198751	DQ198660	DQ198582
Omethidae	Driloniinae	*Drilonius* sp. a	Indonesia	DQ100502	DQ198750	DQ198659	DQ198581
Throscidae		*Trixagus dermestoides*	United Kingdom	AF451950	DQ198747	DQ198656	DQ198578
Eucnemidae		gen. sp. a	Indonesia	HQ333807	HQ333902	HQ333716	HQ333988
Eucnemidae		gen. sp. b	Indonesia	HQ333829	HQ333923	HQ333736	HQ334009

Eucnemidae		gen. sp. c	Indonesia	HQ333830	HQ333924	HQ333737	HQ334010
Eucnemidae	Macraulacinae	*Fornax* sp.	Bolivia	DQ100492	DQ198729	DQ198640	DQ198562
Eucnemidae	Macraulacinae	*Nematodes* sp.	Bolivia	DQ100495	DQ198731	DQ198642	DQ198564
Eucnemidae	Eucneminae	*Idiotarsus* sp.	Bolivia	DQ100493	DQ198730	DQ198641	DQ198563
Lycidae	Libnetinae	*Libnetis granicollis*	Japan	DQ181107	DQ181181	DQ181033	DQ181255
Lycidae	Dictyopterinae	*Lycoprogenthes* sp.	Indonesia	DQ181070	DQ181144	DQ180996	DQ181218
Lycidae	Dictyopterinae	*Taphes brevicollis*	Laos	DQ181098	DQ181172	DQ181024	DQ181246
Lycidae	Dictyopterinae	*Dictyoptera elegans*	Japan	DQ181073	DQ181147	DQ180999	DQ181221
Lycidae	Dictyopterinae	*Benibotarus nigripennis*	Japan	DQ181075	DQ181149	DQ181001	DQ181223
Lycidae	Dictyopterinae	*Pyropterus nigroruber*	Japan	DQ181077	DQ181151	DQ181003	DQ181225
Lycidae	Lyropaeinae	*Alyculus kurbatovi*	Indonesia	DQ181072	DQ181146	DQ180998	DQ181220
Lycidae	Lyropaeinae	*Lyropaeus* sp.	Malaysia	DQ181042	DQ181116	DQ180968	DQ181190
Lycidae	Lyropaeinae	*Antennolycus constrictus*	Malaysia	DQ181051	DQ181125	DQ180977	DQ181199
Lycidae	Lyropaeinae	*Microlyrop. dembickyi*	Indonesia	DQ181071	DQ181145	DQ180997	DQ181219
Lycidae	Lyropaeinae	*Platerodrilus* sp.	Malaysia	DQ181037	DQ181111	DQ180963	DQ181185
Lycidae	Lyropaeinae	*Macrolibnetis* sp.	Malaysia	DQ181050	DQ181124	DQ180976	DQ181198
Lycidae	Lyropaeinae	*Pendola* sp.	Indonesia	DQ181058	DQ181132	DQ180984	DQ181206
Lycidae	Lyropaeinae	*Horakiella emasensis*	Malaysia	DQ181110	DQ181184	DQ181036	DQ181258
Lycidae	Ateliinae	*Dilophotes* sp.	Malaysia	DQ181066	DQ181140	DQ180992	DQ181214
Lycidae	Ateliinae	*Scarelus* sp.	Malaysia	DQ181085	DQ181159	DQ181011	DQ181233
Lycidae	Lycinae	*Dihammatus* sp.	Malaysia	DQ181043	DQ181117	DQ180969	DQ181191
Lycidae	Lycinae	*Eurrhacus* sp.	Ecuador	DQ181056	DQ181130	DQ180982	DQ181204
Lycidae	Lycinae	*Macrolycus* sp	China	DQ181049	DQ181123	DQ180975	DQ181197
Lycidae	Lycinae	*Thonalmus hubbardi*	Montserrat	DQ181094	DQ181168	DQ181020	DQ181242
Lycidae	Lycinae	*Lyponia quadricollis*	Korea	DQ181101	DQ181175	DQ181027	DQ181249
Lycidae	Lycinae	*Lycus* sp.	South Africa	DQ181039	DQ181113	DQ180965	DQ181187

Lycidae	Lycinae	*Idiopteron biplagiatum*	Ecuador	DQ181057	DQ181131	DQ180983	DQ181205
Lycidae	Lycinae	*Metriorrhynchus lineatus*	Malaysia	DQ181040	DQ181114	DQ180966	DQ181188
Lycidae	Lycinae	*Platycis minutus*	Czech Republic	DQ181069	DQ181143	DQ180995	DQ181217
Lampyridae	Lampyrinae	*Vesta* sp.	Indonesia	DQ100511	DQ198760	DQ198669	DQ198592
Lampyridae	Lampyrinae	gen. sp.	Indonesia	DQ100509	DQ198759	DQ198667	DQ198590
Lampyridae	Luciolinae	*Curtos* sp.	Indonesia	DQ100513	DQ198761	DQ198671	DQ198594
Lampyridae	Luciolinae	gen. sp.	Indonesia	DQ100514	DQ198762	DQ198672	DQ198595
Lampyridae	Ototretinae	*Mimophaeopterus* sp.	Indonesia	DQ100521	DQ198764	DQ198679	DQ198602
Lampyridae	Ototretinae	*Flabellotreta* sp.	Indonesia	DQ100520	DQ198763	DQ198678	DQ198601
Lampyridae	Ototretinae	*Ototretadrilus* sp. a	India	DQ100524	DQ198765	DQ198682	DQ198605
Lampyridae	Ototretinae	*Ototretadrilus* sp. b	India	DQ100525	DQ198766	DQ198683	DQ198606
Cantharidae	Malthininae	*Malthinus flaveolus*	United Kingdom	AF451938	DQ198775	DQ198692	DQ198615
Cantharidae	Malthininae	*Malthodes* sp.	France	DQ100532	DQ198776	DQ198693	DQ198616
Cantharidae	Malthininae	*Maltypus* sp.	Indonesia	DQ100533	DQ198777	DQ198694	DQ198617
Cantharidae	Malthininae	*Inmalthodes* sp.	Indonesia	DQ100534	DQ198778	DQ198695	DQ198618
Cantharidae	Chauliognathinae	*Ichthyurus* sp.	Indonesia	DQ100531	DQ198774	DQ198691	DQ198614
Cantharidae	Cantharinae	*Cantharis decipiens*	Czech Republic	DQ100526	DQ198768	DQ198685	DQ198608
Cantharidae	Cantharinae	*Rhagonycha lignosa*	United Kingdom	AF451939	DQ198770	DQ198687	DQ198610
Cantharidae	Cantharinae	*Rhagonycha nigriceps*	France	DQ100527	DQ198769	DQ198686	DQ198609
Cantharidae	Silinae	*Asiosilis* sp.	Indonesia	DQ100530	DQ198773	DQ198690	DQ198613
Cantharidae	Silinae	*Laemoglyptus* sp.	Indonesia	DQ100528	DQ198771	DQ198688	DQ198611
Cantharidae		gen. sp.	Indonesia	DQ100529	DQ198772	DQ198689	DQ198612
Omalisidae		*Omalisus fontisbellaquei*	Czech Republic	AF451948	DQ198749	DQ198658	DQ198580
Omalisidae		*Pseudeuanoma* sp.	Greece	HQ333832	KF294773	HQ333738	HQ334011
Phengodidae	Phengodinae	*Phengodes* sp.	USA	DQ100504	DQ198752	DQ198661	DQ198583
Rhagophthalmidae		*Bicladodrilus* sp.	China	DQ100507	DQ198755	DQ198664	DQ198586

Rhagophthalmidae		*Mimoochotyra* sp.	Malaysia	DQ100505	DQ198753	DQ198662	DQ198584
Rhagophthalmidae		*Ochotyra* sp.	India	DQ100508	DQ198756	DQ198665	DQ198587
Rhagophthalmidae		gen. sp.	Indonesia	DQ100506	DQ198754	DQ198663	DQ198585
Elateridae	Agrypninae	*Agrypnus* sp. a	Japan	HQ333757	HQ333852	HQ333676	HQ333941
Elateridae	Agrypninae	*Agrypnus* sp. b	Indonesia	HQ333783	HQ333878	HQ333697	HQ333965
Elateridae	Agrypninae	*Agrypnus* sp. c	Japan	HQ333810	HQ333905	HQ333719	HQ333991
Elateridae	Agrypninae	*Agrypnus* sp. d	Indonesia	HQ333820	HQ333915	HQ333727	HQ334000
Elateridae	Agrypninae	*Adelocera* sp. a	Japan	HQ333772	HQ333867	HQ333689	HQ333955
Elateridae	Agrypninae	*Adelocera* sp. a	Japan	HQ333778	HQ333873	HQ333694	HQ333961
Elateridae	Agrypninae	*Adelocera* sp. a	Japan	HQ333817	HQ333912	HQ333724	HQ333997
Elateridae	Agrypninae	*Adelocera* sp. b	Indonesia	HQ333806	HQ333901	HQ333715	HQ333987
Elateridae	Agrypninae	*Adelocera* sp. c	Malaysia	HQ333818	HQ333913	HQ333725	HQ333998
Elateridae	Agrypninae	*Conoderus* sp. a	Panama	HQ333746	HQ333841	HQ333665	HQ333931
Elateridae	Agrypninae	*Conoderus* sp. b	Panama	HQ333747	HQ333842	HQ333666	HQ333932
Elateridae	Agrypninae	*Drasterius bimaculatus*	Slovakia	HQ333793	HQ333888	HQ333704	HQ333975
Elateridae	Agrypninae	*Drasterius* sp.	Morocco	HQ333816	HQ333911	HQ333723	HQ333996
Elateridae	Agrypninae	gen. sp.	Malaysia	HQ333798	HQ333893	HQ333708	HQ333980
Elateridae	Agrypninae	*Platycrepidius* sp.	Panama	HQ333748	HQ333843	HQ333667	HQ333933
Elateridae	Agrypninae	*Pyrophorus* sp.	Panama	HQ333751	HQ333846	HQ333670	HQ333936
Elateridae	Agrypninae	*Chalcolepidius* sp.	Panama	HQ333752	HQ333847	HQ333671	HQ333937
Elateridae	Agrypninae	*Cryptalaus* sp. a	Japan	HQ333768	HQ333863	HQ333685	HQ333951
Elateridae	Agrypninae	*Cryptalaus* sp. b	Malaysia	HQ333834	HQ333926	HQ333740	HQ334014
Elateridae	Agrypninae	*Selasia* sp.	SouthAfrica	HQ333824	HQ333919	HQ333731	HQ334004
Elateridae	Agrypninae	*Selasia* sp.	SouthAfrica	HQ333825	HQ333920	HQ333732	HQ334005
Elateridae	Agrypninae	*Drilus* sp.	Greece	HQ333826	HQ333921	HQ333733	HQ334006
Elateridae	Agrypninae	*Drilus mauritanicus*	Spain	HQ333836	HQ333927	HQ333742	HQ334015

Elateridae	Agrypninae	*Drilus mauritanicus*	Spain	HQ333837	HQ333928	HQ333743	HQ334016
Elateridae	Agrypninae	*Agrypnus murinus*	Slovakia	AF451943	DQ198735	DQ198645	DQ198567
Elateridae	Agrypninae	*Drilus flavescens*	Malta	DQ100501	DQ198748	DQ198657	DQ198579
Elateridae	Cardiophorinae	gen. sp.	Namibia	AF451942	DQ198739	DQ198649	DQ198571
Elateridae	Cardiophorinae	*Cardiophorus erichsoni*	Slovakia	HQ333790	HQ333885	HQ333701	HQ333972
Elateridae	Denticollinae	*Athous vittatus*	Czech Republic	HQ333755	HQ333850	HQ333674	HQ333939
Elateridae	Denticollinae	*Limonius quercus*	Czech Republic	HQ333775	HQ333870	HQ333692	HQ333958
Elateridae	Denticollinae	*Cidnopus pilosus*	Slovakia	HQ333792	HQ333887	HQ333703	HQ333974
Elateridae	Denticollinae	*Anostirus purpureus*	Slovakia	HQ333761	HQ333856	HQ333679	HQ333945
Elateridae	Denticollinae	*Neopristilophus serrifer*	Japan	HQ333765	HQ333860	HQ333682	HQ333948
Elateridae	Denticollinae	*Selatosomus gravidus*	Czech Republic	HQ333774	HQ333869	HQ333691	HQ333957
Elateridae	Denticollinae	gen. sp.	Japan	HQ333787	HQ333882	HQ333700	HQ333969
Elateridae	Denticollinae	*Platiana* sp.	Indonesia	HQ333782	HQ333877	HQ333696	HQ333964
Elateridae	Denticollinae	*Hypolithus* sp.	Japan	HQ333795	HQ333890	HQ333705	HQ333977
Elateridae	Denticollinae	*Semiotus* sp.	Chile	HQ333799	HQ333894	HQ333709	HQ333981
Elateridae	Denticollinae	*Oxynopterus* sp.	Philippines	HQ333800	HQ333895	HQ333710	HQ333982
Elateridae	Denticollinae	*Panspaeus guttatus*	United Kingdom	DQ100499	DQ198742	DQ198652	DQ198574
Elateridae	Denticollinae	*Stenagostus rhombeus*	United Kingdom	AF451945	DQ198744	DQ198653	DQ198576
Elateridae	Denticollinae	*Denticollis linearis*	Czech Republic	DQ100498	DQ198741	DQ198651	DQ198573
Elateridae	Denticollinae	*Athous haemorrhoidalis*	United Kingdom	AF451944	DQ198738	DQ198648	DQ198570
Elateridae	Elaterinae	*Octinodes* sp.	Panama	HQ333749	HQ333844	HQ333668	HQ333934
Elateridae	Elaterinae	*Elater* sp.	Japan	HQ333766	HQ333861	HQ333683	HQ333949
Elateridae	Elaterinae	*Tomicephalus* sp.	Panama	HQ333750	HQ333845	HQ333669	HQ333935
Elateridae	Elaterinae	Elaterini gen. sp. a	Indonesia	HQ333773	HQ333868	HQ333690	HQ333956
Elateridae	Elaterinae	Elaterini gen. sp. b	Indonesia	HQ333819	HQ333914	HQ333726	HQ333999
Elateridae	Elaterinae	*Ludioschema* sp.	Japan	HQ333777	HQ333872	HQ333693	HQ333960

Elateridae	Elaterinae	*Anoplischius* sp.	Panama	HQ333745	HQ333840	HQ333664	HQ333930
Elateridae	Elaterinae	*Ampedus* sp. a	Japan	HQ333758	HQ333853	HQ333677	HQ333942
Elateridae	Elaterinae	*Ampedus sanguinolentus*	Slovakia	HQ333760	HQ333855	HQ333678	HQ333944
Elateridae	Elaterinae	*Ampedus rufipennis*	Slovakia	HQ333762	HQ333857	HQ333680	HQ333946
Elateridae	Elaterinae	*Ampedus* sp. b	Japan	HQ333771	HQ333866	HQ333688	HQ333954
Elateridae	Elaterinae	*Ampedus sinuatus*	Slovakia	HQ333791	HQ333886	HQ333702	HQ333973
Elateridae	Elaterinae	*Ampedus sinuatus*	Czech Republic	HQ333822	HQ333917	HQ333729	HQ334002
Elateridae	Elaterinae	*Agriotes acuminatus*	Czech Republic	HQ333756	HQ333851	HQ333675	HQ333940
Elateridae	Elaterinae	*Agriotes ustulatus*	Czech Republic	HQ333786	HQ333881	HQ333699	HQ333968
Elateridae	Elaterinae	Megapenthini gen. sp.	Japan	HQ333767	HQ333862	HQ333684	HQ333950
Elateridae	Elaterinae	Adrastini gen. sp. a	Japan	HQ333769	HQ333864	HQ333686	HQ333952
Elateridae	Elaterinae	Adrastini gen. sp. a	Japan	HQ333770	HQ333865	HQ333687	HQ333953
Elateridae	Elaterinae	Adrastini gen. sp. b	Japan	HQ333779	HQ333874	HQ333695	HQ333962
Elateridae	Elaterinae	Adrastini gen. sp. c	Malaysia	HQ333801	HQ333896	HQ333711	HQ333983
Elateridae	Elaterinae	Adrastini gen. sp. d	Malaysia	HQ333812	HQ333907	HQ333720	HQ333993
Elateridae	Elaterinae	*Melanotus villosus*	Czech Republic	HQ333754	HQ333849	HQ333673	HQ333938
Elateridae	Elaterinae	*Priopus ornatus*	Laos	HQ333785	HQ333880	HQ333698	HQ333967
Elateridae	Elaterinae	*Priopus humeralis*	Indonesia	HQ333821	HQ333916	HQ333728	HQ334001
Elateridae	Elaterinae	*Anchastus* sp. a	Indonesia	HQ333804	HQ333899	HQ333714	HQ333986
Elateridae	Elaterinae	*Anchastus* sp. b	Indonesia	HQ333809	HQ333904	HQ333718	HQ333990
Elateridae	Elaterinae	*Anchastus* sp. c	Indonesia	HQ333813	HQ333908	HQ333721	HQ333994
Elateridae	Elaterinae	*Anchastus* sp. d	Indonesia	HQ333814	HQ333909	HQ333722	HQ333995
Elateridae	Elaterinae	*Cebrio* sp.	Spain	DQ100497	DQ198740	DQ198650	DQ198572
Elateridae	Elaterinae	*Ampedus balteatus*	United Kingdom	AF427605	DQ198736	DQ198646	DQ198568
Elateridae	Lissominae	*Drapetes* sp.	Czech Republic	HQ333828	HQ333922	HQ333735	HQ334008
Elateridae	Negastriinae	*Zorochros* sp.	Malaysia	HQ333796	HQ333891	HQ333706	HQ333978

Elateridae	Negastriinae	*Zorochros* sp.	Malaysia	HQ333797	HQ333892	HQ333707	HQ333979
Elateridae	Negastriinae	*Quasimus* sp. a	Malaysia	HQ333802	HQ333897	HQ333712	HQ333984
Elateridae	Negastriinae	*Quasimus* sp. b	Malaysia	HQ333803	HQ333898	HQ333713	HQ333985

References for Table S1

Bocakova M, Bocak L, Hunt T, Vogler AP. 2007. Molecular phylogenetics of Elateriformia (Coleoptera): evolution of bioluminescence and neoteny. *Cladistics* 23: 477–496.

Kundrata R, Bocak L. 2011. The phylogeny and limits of Elateridae (Insecta, Coleoptera): is there a common tendency of click beetles to soft-bodiedness and neoteny? *Zoologica Scripta* 40: 364–378.

Table S2. Numbers of characters, base frequencies and maximum uncorrected pairwise distances. * *cox1* mtDNA aligned only by ClustalX..

Alignment/ Partition	Number of characters	Constant characters	Variable uninformative	Parsimony informative	Base frequencies (%) A	C	G	T	Max. uncorrec. pairw. dist. (%)
BlastAlign									
Total dataset	4675	2781	441	1453	27.17	21.08	24.38	27.38	15.41
18S rDNA	2186	1587	163	436	24.03	24.44	27.94	23.59	08.90
28S rDNA	1001	635	128	238	25.49	23.46	30.93	20.12	16.74
rrnl mtDNA	765	334	104	327	32.28	09.73	17.13	40.87	26.58
cox1 mtDNA*	723	225	046	452	33.25	17.86	14.51	34.39	35.00
ClustalX									
Total dataset	4330	2245	372	1713	27.12	20.99	24.37	27.53	19.07
18S rDNA	2130	1449	160	521	23.94	24.52	27.97	23.57	12.40
28S rDNA	910	396	123	391	25.33	23.57	30.97	20.13	30.47
rrnl mtDNA	567	175	43	349	32.18	09.47	17.01	41.33	32.28
cox1 mtDNA*	723	225	046	452	33.25	17.86	14.51	34.39	35.00

Table S3. The list of the artematopodid genera, with geographical distribution.

Subfamily Tribe	Genus	Nr. of species	Recent species	Fossil species	Geographical distribution
Artematopodinae Lacordaire, 1857					
Artematopodini Lacordaire, 1857					
	Artematopus Perty, 1830	44	44	0	South and Central America (from Bolivia to Nicaragua)
	Carcinognathus Kirsch, 1873	1	1	0	Peru
	Protartematopus Crowson, 1973	1	0	1	–
Ctesibiini Crowson, 1973					
	Brevipogon Lawrence, 2005	1	1	0	USA
	Ctesibius Champion, 1897	1	1	0	Mexico
Macropogonini LeConte, 1861					
	Eurypogon Motschulsky, 1859	11	11	0	USA, Canada, Italy, China, Taiwan, Japan
	Macropogon Motschulsky, 1845	7	7	0	USA, Canada, Eastern Siberia, Far East
Allopogoniinae Crowson, 1973					
	Allopogonia Cockerell, 1906	1	1	0	USA
Electribiinae Crowson, 1975					
	Electribius Crowson, 1973	6	2	4	Salvador, Mexico
*Incertae sedis**					
Electrapatini Cobos, 1963					
	Electrapate Iablokoff-Khnzorian, 1962	1	0	1	–

* – The genus *Electrapate* Iablokoff-Khnzorian was placed in Artematopodidae by Lawrence (2010) without mentioning a reason, although previous authors classified this taxon in Buprestoidea (*e.g.*, Bellamy, 1995; Bouchard *et al*., 2011).

References for Table S3

Bellamy CL. 1995. Buprestidae (Coleoptera) from Amber deposits: A brief review and family switch. *The Coleopterists Bulletin* 49: 175–177.

Bouchard P, Bousquet Y, Davies AE, Alonso-Zarazaga MA, Lawrence JF, Lyal CHC, Newton AF, Reid CAM, Schmitt M, Ślipiński SA, Smith ABT. 2011. Family-Group names in Coleoptera (Insecta). *ZooKeys* 88: 1–972.

Champion GC. 1897. Elateridae-Dascillidae. *Biologia Centrali-Americana. Insecta. Coleoptera. Vol. 3*. Part 1: 258–662.

Cobos A. 1963. Comentarios críticos sobre algunos Sternoxia fósiles del ámbar del Báltico recientemente descritos (Coleoptera). *Eos* 39: 345–355.

Cockerell TDA. 1906. Preoccupied generic names of Coleoptera. *Entomological News and Proceedings of the Entomological Section Academy of Natural Sciences* 17: 240–244.

Crowson RA. 1973. On a new superfamily Artematopoidea of polyphagan betles, with the definition of two new fossil genera from the Baltic amber. *Journal of Natural History* 7: 225–238.

Crowson RA. 1975. The evolutionary history of Coleoptera, as documented by fossil and comparitive evidence. In: *Atti del 10. Congresso nazionale italiano di entomologia*. Sassari, Italia, 20-25 Maggio 1974. Firenze, Coppini: 47–90.

Iablokoff-Khnzorian SM. 1962. Representatives of Sternoxia (Coleoptera) from the Baltic amber. Family Throscidae Bach, 1849 (Trixagidae *sensu* Crowson). *Paleontologicheskiy Zhurnal* 3: 81–89.

Kirsch T. 1873. Beiträge zur Kenntnis der Peruanischen Käferfauna auf Dr. Abendroths's Sammlungen basirt (Zweites Stück). *Berliner Entomologische Zeitschrift* 17:339–418.

Lacordaire T. 1857. *Histoire Naturelle des Insectes. Genera des Coléoptères. Tome IV*. Librairie Encyclopédique de Roret, Paris, 597 pp.

Lawrence JF. 2010. 4.2. Artematopodidae Lacordaire, 1857. Pp. 42–47. In: Leschen RAB, Beutel RG, Lawrence JF, vol. eds, *Coleoptera, Beetles; Volume 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)*. In: Kristensen NP, Beutel RG, eds, *Handbook of Zoology, Arthropoda: Insecta*. Berlin/New York, Walter de Gruyter GmbH & Co. KG, 786 pp.

Motschulsky V. 1845. Remarques sur la collection de coléoptères Russes de Victor de Motschulsky. *Bulletin de la Société Impériale des Naturalistes de Moscou* 18: 1–127.

Motschulsky V. 1859. Coléoptères nouveaux de la Californie. *Bulletin de la Société Impériale des Naturalistes de Moscou* 32: 357–410.

Lawrence JF. 2005. *Brevipogon*, a new genus of North American Artematopodidae (Coleoptera), with a key to world genera. *The Coleopterists Bulletin* 59: 223–236.

LeConte JL. 1861. *Classification of the Coleoptera of North America*. Part 1. Smithsonian Miscellaneous Collections, Washington, 285 pp.

Perty M. 1830. Delectus Animalium Articulatorum. In: Spix JB, Martius CEP, eds, *Reise in Brasilien auf Befehl S.M. Maximilian Joseph I., Königs von Bayern in den Jahren 1817–1820*. Munich, 385 pp.

Table S4. The list of described species of the genus *Eurypogon* Motschulsky, with geographical distribution.

Spp. of *Eurypogon* Motschulsky, 1859	Geographical distribution
Nearctic Region	
E. californicus Horn, 1880	USA, Canada
E. harrisi (Westwood, 1862)	USA
E. niger (Melsheimer, 1846)	USA, Canada
Palaearctic Region	
E. cribratus (Hampe, 1866)	Italy
E. brevipennis Sakai, 1982	Japan (Honshu, Shikoku)
E. hisamatsui Sakai, 1982	Japan (Honshu, Shikoku)
E. japonicus Sakai, 1982	Japan (Honshu, Shikoku, Kyushu)
E. ocularis Sakai, 1982	Japan (Honshu)
E. granulatus Sakai, 1982	Taiwan
E. jaechi sp. nov.	China (Yunnan)
E. heishuiensis sp. nov.	China (Yunnan)

References for Table S4

Hampe C. 1866. Beschreibung einiger neuen Käfer. *Berliner Entomologische Zeitschrift* 10: 373–375.

Horn GH. 1880. Synopsis of the Dascyllidae of the United States. *Transactions of the American Entomological Society* 7: 76–115.

Melsheimer FE. 1846. Descriptions of new species of Coleoptera of the United States. *Proceedings of the Academy of Natural Sciences of Philadelphia* 2: 302–318.

Motschulsky V. 1859. Coléoptères nouveaux de la Californie. *Bulletin de la Société Impériale des Naturalistes de Moscou* 32: 357–410.

Sakai M. 1982. Occurence of the genus *Eurypogon* Motschulsky in Japan and Taiwan (Coleoptera: Artematopidae). *Transactions of the Shikoku Entomological Society* 16: 51–61.

Westwood M. 1862. Description du genre *Sclerodes*, Coléoptère appartenant à la tribu des Cébrionites. *Revue et Magazin de Zoologie pure et appliquée* 2: 373–375.

Příloha 2

Bocák, L., **Kundrata, R.**, Andújar Fernández, C. & Vogler, A.P. (2016) The discovery of Iberobaeniidae (Coleoptera: Elateroidea), a new family of beetles from Spain, with immatures detected by environmental DNA sequencing. *Proceedings of the Royal Society B - Biological Sciences*, 283: 20152350.
[IF 4,940; 20 citací na WoS; celkem 16 citací bez autorových autocitací]
[autorský podíl: 35 %]

PROCEEDINGS B

rspb.royalsocietypublishing.org

Research

Cite this article: Bocak L, Kundrata R, Fernández CA, Vogler AP. 2016 The discovery of Iberobaeniidae (Coleoptera: Elateroidea): a new family of beetles from Spain, with immatures detected by environmental DNA sequencing. *Proc. R. Soc. B* **283**: 20152350.
http://dx.doi.org/10.1098/rspb.2015.2350

Received: 30 September 2015
Accepted: 11 April 2016

Subject Areas:
evolution, taxonomy and systematics, ecology

Keywords:
biodiversity, endemism, mitogenomes, soil arthropods, molecular phylogeny, neoteny

Author for correspondence:
L. Bocak
e-mail: ladislav.bocak@upol.cz

Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2015.2350 or via http://rspb.royalsocietypublishing.org.

THE ROYAL SOCIETY
PUBLISHING

The discovery of Iberobaeniidae (Coleoptera: Elateroidea): a new family of beetles from Spain, with immatures detected by environmental DNA sequencing

L. Bocak[1,2], R. Kundrata[1], C. Andújar Fernández[2,3] and A. P. Vogler[2,3]

[1]Department of Zoology, Faculty of Science, Palacky University, 17 listopadu 50, Olomouc 771 46, Czech Republic
[2]Department of Life Science, Natural History Museum, Cromwell Road, London SW75BD, UK
[3]Department of Life Science, Silwood Park Campus, Imperial College London, Ascot SL5 7BD, UK

The ongoing exploration of biodiversity and the implementation of new molecular tools continue to unveil hitherto unknown lineages. Here, we report the discovery of three species of neotenic beetles for which we propose the new family Iberobaeniidae. Complete mitochondrial genomes and rRNA genes recovered Iberobaeniidae as a deep branch in Elateroidea, as sister to Lycidae (net-winged beetles). Two species of the new genus *Iberobaenia*, *Iberobaenia minuta* sp. nov. and *Iberobaenia lencinai* sp. nov. were found in the adult stage. In a separate incidence, a related sequence was identified in bulk samples of soil invertebrates subjected to shotgun sequencing and mitogenome assembly, which was traced to a larval voucher specimen of a third species of *Iberobaenia*. *Iberobaenia* shows characters shared with other elateroid neotenic lineages, including soft-bodiedness, the hypognathous head, reduced mouthparts with reduced labial palpomeres, and extremely small-bodied males without strengthening structures due to miniaturization. Molecular dating shows that Iberobaeniidae represents an ancient relict lineage originating in the Lower Jurassic, which possibly indicates a long history of neoteny, usually considered to be evolutionarily short-lived. The apparent endemism of Iberobaeniidae in the Mediterranean region highlights the importance of this biodiversity hotspot and the need for further species exploration even in the well-studied European continent.

1. Introduction

In the beetles (Coleoptera), the most diverse order of insects, several thousand new species are described every year. Yet new high-level taxa are rarely discovered and most of the main lineages had already been described by the end of the nineteenth century. Altogether, 36 of the 179 extant families were proposed since 1950. Most of them have been elevated to the status of family as their divergent phylogenetic position became clear, whereas only a few were based on newly discovered specimens (see the electronic supplementary material). Not surprisingly, only one of the newly described families (Crowsoniellidae Iablokoff-Khnzorian, 1983) was collected in Europe, which can be considered the best-explored region worldwide. Here, three decades after the last discovery of a beetle family in Europe, we report a unique new lineage within the superfamily Elateroidea from Spain, for which we propose the taxonomic rank of family.

Despite the proverbial evolutionary success of the beetles [1], evident from enormous species richness and great morphological and ecological diversification, some lineages of Coleoptera are very species-poor. This includes some groups that are fairly common in the fossil record, such as the Archostemata, which today consists of approximately 40 species grouped in four highly divergent families. Other ancient, but species-poor and rare lineages are exemplified by the families Aspidytidae, Meruidae, Crowsoniellidae, Jurodidae, Decliniidae, Lymexylidae, Rhinorhipidae and others, all represented by one or a few species only, which mostly occur in unique habitats or exhibit localized distributions [2]. Similarly, the Elateroidea (click beetles, fireflies, soldier beetles and allies) includes several deep routed families such as Omethidae including Telegeusinae, Omalisidae, Plastoceridae, Brachypsectridae and Rhagophthalmidae, which are species-poor (less than 100 known species worldwide, each) and generally rare in ecosystems (e.g. [3]). These groups, with few exceptions, exhibit females that are neotenic (retaining juvenile traits) to various degrees, and are either completely larviform, show a metamorphosed head but with the rest of the body larviform, or retain larval traits only in the abdomen. Soft-bodiedness and loosely connected abdominal sclerites resembling larval morphology possibly represent an initial stage of ontogenetic modifications [4]. Owing to the morphological similarities, families with these characteristics were traditionally grouped into a separate superfamily of soft-bodied lineages, the Cantharoidea ([5]; figure 1*b*) or as a monophylum within Elateroidea [7]. However, molecular data have shown the polyphyly of soft-bodied lineages, indicating the parallel evolution of soft-bodiedness and neoteny ([8], figure 1*b*–*c*).

Recently, when searching for neotenics for DNA analyses in the Iberian Peninsula, we encountered a series of elateroid specimens that could not be assigned to any known family. Independently, metagenomic sequencing of assemblages of beetles from soil biodiversity surveys in southern Spain recovered several partial and complete mitochondrial genome sequences that formed deep independent lineages in Elateroidea [9]. These sequences, obtained from mixtures of adult and larval specimens, indicated the existence of evolutionarily divergent taxa in the soil samples, which, however, could not be identified any further based on morphological characters. DNA sequences enabled us to link the adult males with the independently obtained metagenomic samples. Extensive phylogenetic analyses combined with the thorough study of adult and larval morphology confirmed the presence of a new family of Elateroidea. These findings confirm the Mediterranean basin as a reservoir of ancient lineages and a hotspot of diversity [10,11].

2. Material and methods

A total of 11 adult male specimens from several localities in the Murcia and Jaén provinces of southern Spain were studied. DNA from one specimen was extracted and deposited in the collection of Palacky University, Olomouc (UPOL) and the larvae and dry mounted specimens were deposited in the collections of the Natural History Museum, London (BMNH) and the collections of J. L. Lencina (JLC), A. Allen (AAC) and M. Baena (MBC). The full addresses of collections are given in authors' affiliations.

(a) Molecular phylogenetics

(i) Four-marker dataset

Existing sequences for the four most widely used mtDNA (*cox1* and *rrnL*) and nuclear (*SSU* and *LSU* rRNA) genes were compiled for the taxonomically most extensive dataset of Elateroidea to date (557 taxa, approx. 5300 bp), representing the main elateroid lineages and outgroup taxa [8,12]. Sequence data for two representatives of the newly discovered taxon were added to this matrix, generating two versions of the four-marker dataset: (i) *v1* a chimeraical terminal was assembled from the sequences of *cox1*, *SSU* and *LSU* for an adult specimen, sequenced using procedures reported by Bocakova *et al.* [13] (GenBank accession nos. KT339296–98; electronic supplementary material, table S1), and *rrnL* sequence for the larval specimen BMNH1042541 of Andújar *et al.* [14] obtained from a full mitogenome sequence (see Mitogenome dataset paragraph); and (ii) *v2* two terminals were added including an adult (fragments as listed above) and the larva (*cox1* and *rrnL* sequences of [14]). Sequences were edited using SEQUENCHER 4.9 (Gene Codes Corp., Ann Arbor, MI, USA). The length invariable *cox1* sequences were aligned using TRANSALIGN [15] and the rRNA fragments using default parameters of MAFFT 7.2 [16] and BLASTALIGN 1.2 [17].

Maximum-likelihood (ML) phylogenetic analyses using RAxML 7.3.1 [18,19] were conducted on the CIPRES web server to analyse individual gene alignments for *SSU*, *LSU* and *cox1* and the four-marker concatenated dataset (*SSU*, *LSU*, *rrnL* and *cox1*), the latter partitioned by genes and by codon positions. All analyses were duplicated, with the ribosomal genes aligned using either MAFFT (Q-INS-I algorithm [16]) or BLASTALIGN. All ML tree searches were performed using 100 replicates for the best tree under a GTR+G+I model proposed by JMODELTEST2 [20], with bootstrap values calculated using the rapid algorithm [21] with 1000 bootstrap iterations under the GTRCAT model.

(ii) Mitogenome dataset

The full mitogenome sequence of the larval specimen BMNH1042541 was re-sequenced (accession number KT825140; [14] for details) to complement the partial mitogenome available from Andújar *et al.* [9]. Additional mitochondrial genomes were retrieved from GenBank (electronic supplementary material, table S2), and the 13 protein coding genes (PCGs) were extracted using GENEIOUS and individually aligned with TRANSALIGN. *SSU* and *LSU* rRNA sequences were retrieved from GenBank for the same species or, in a few cases, for the same genus (electronic supplementary material, table S3). The rRNA fragments were aligned using MAFFT (Q-INS-I algorithm) and concatenated with the PCGs. The final mitogenome dataset (mtDNA, *SSU*, and *LSU* genes; 64 taxa) additionally included the sequences obtained from the adult specimen. This dataset was used for phylogenetic inference using ML, as described above. Analyses were repeated applying: (i) a 3-partition scheme (*SSU*+*LSU*+mtDNA); (ii) an 8-partition scheme (six partitions by plus/minus strand and 1st, 2nd and 3rd codon position+*SSU*+*LSU*); (iii) a 15-partition scheme (partitions by genes); and (iv) a 38-partition scheme (partitions by gene and by codon position). Bayesian analyses on the concatenated matrix were performed using BEAST v. 1.81 [22] to estimate a phylogenetic tree and ages of diversification simultaneously. The best ML tree was used as a starting tree. Analyses were repeated using the four partition schemes as before, applying a GTR+G+I substitution model as above and an uncorrelated lognormal clock to each partition [23]. Polyphaga were designated as sister to the remaining clades [24–26]. A Yule speciation prior was applied and analyses were run for 150 million generations sampling one tree every 5000 generations. Consensus trees were estimated with TREEANNOTATOR [22] discarding the required fraction as a burn-in after checking the ESS of the tree likelihood and ensuring that values had reached a plateau in TRACER v. 1.6 (http://beast.bio.ed.ac.uk/Tracer).

Fossils relevant to the origin of Elateriformia and Scarabaeiformia [27,28] were used as calibration priors. The earliest fossils of Elateriformia date back to the Hettangian and Sinemurian deposits (190.8–201 Ma; Elateridae, *Elaterophanes* [29]) and the fossil of Scarabaeiformia to the Jurassic Formation of Switzerland (196.5–201.6 Ma; *Aphodiites* [30]). We applied a lognormal distribution as recommended for fossil calibration [31] with a minimum age hard bound at 190.8 Ma and with a 95% range of 190.8–228.5 Ma (offset: 190.8; log(mean): 0.01; log(s.d.): 2.2) as a prior for the node

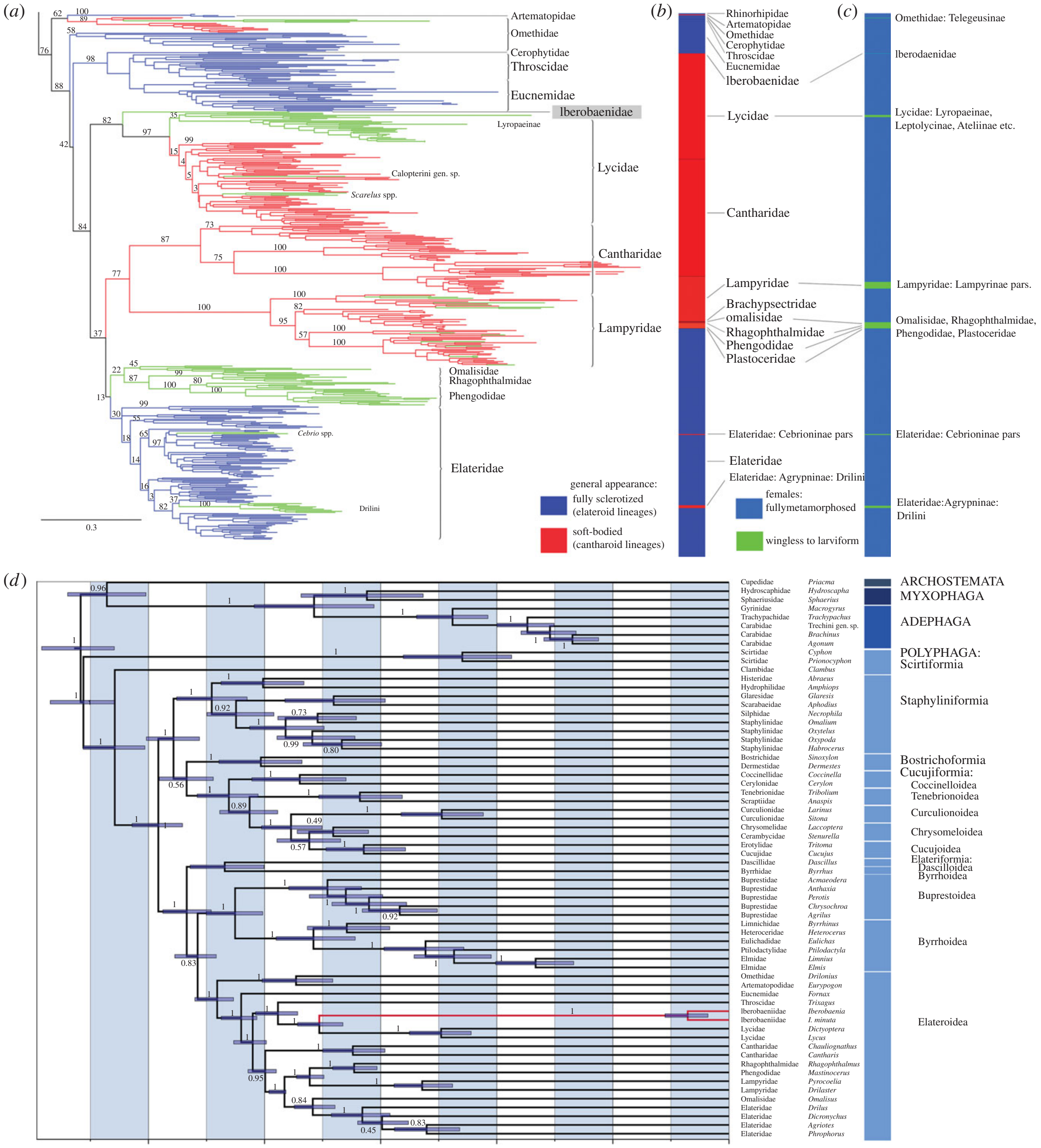


Figure 1. (*a*) Phylogenetic hypothesis of Elateroidea inferred from the four-gene BlastAlign dataset using maximum-likelihood optimality criterion. *Iberobaenia* represented by a four-gene chimera. (*b*) Relative species diversity of soft-bodied and completely sclerotized elateroid lineages. (*c*) Phylogenetic position and relative species diversity of neotenic and completely metamorphosing lineages. The numbers of species are taken from Bocak *et al.* [2,6]. (*d*) Maximum clade credibility ultrametric tree resulting from the Bayesian analysis of 13 mtDNA genes, *LSU* and *SSU* rRNA in the program Beast (8-partitions applied). (Online version in colour.)

representing the split of Elateridae from other Elateroidea and a log-normal distribution with a minimum age hard bound at 196 Ma and a 95% range of 196–233 Ma (offset: 196; log(mean): 0.01; log(s.d.): 2.2) for the split between Scarabaeoidea and Staphylinoidea.

3. Results

(a) Molecular phylogenetic relationships of Iberobaenia

The well-resolved tree produced by the analyses of the four-marker dataset showed the clade of Omalisidae, Phengodidae, Rhagophthalmidae and Elateridae, deeply rooted Lycidae in an independent position and the newly discovered individuals were placed as the sister group of Lycidae with 62–85% bootstrap support (figure 1*a*, electronic supplementary material, figure S3). The relationships inferred from single-gene matrices varied, but the new lineage was never placed within any clade representing the existing families. When Lycidae were excluded, the new taxon was recovered as the sister to elaterid subfamilies Thylacosterninae + Lissominae, which have been difficult to place in molecular analyses (although placed in Elateridae based on morphology) and

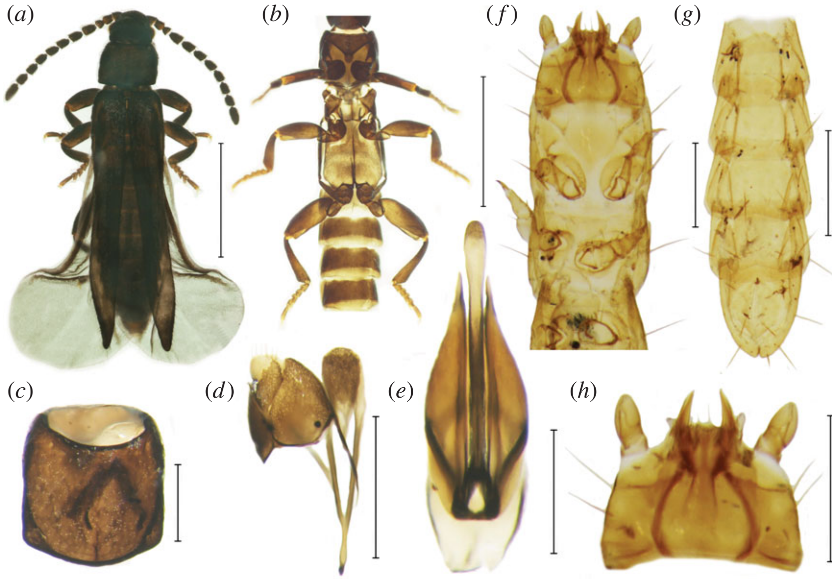


Figure 2. Morphology of *Iberobaenia minuta* sp. nov. (*a–e*, adult) and *Iberobaenia* sp. (*f–h*, larva). (*a*) General appearance, (*b*) thorax ventrally, (*c*) pronotum, (*d*) terminal abdominal segments, (*e*) male genitalia, (*f*) thorax and head ventrally, (*g*) abdomen ventrally, (*h*) head ventrally. Scale bars: 1.0 mm (*a,b*), 0.5 mm (*g*), 0.25 mm (*c–f,h*). (Online version in colour.)

have a tendency to group with Lycidae using rRNA markers (e.g. [25]). The ML analyses of the mitogenome dataset recovered *Iberobaenia* in a clade containing besides Lycidae also *Mastinocerus* (Phengodidae) and Throscidae (electronic supplementary material, figure S4).

The mitogenome sequence (GenBank accession number KT339298) had a perfect match (100% similarity) with the *cox1* of the sequence from the same larval specimen (voucher BMNH 1042541). A second larval specimen (BMNH 1042563) differed by 1 of the 651 bp of the *cox1* gene (GenBank accession numbers AB123456–7). Both specimens were 92% similar to the adult specimen from Jaén, indicating they are different species, but closely related. The mitogenome showed a gene order unique among the Coleoptera, as gene rearrangement affected several PCGs, tRNAs and the control region [14]. This rearrangement explained the failure of the PCR amplifying the *rrnL–nad1* region using primers 16Sa and ND1A. Combined with 62 other mitogenomes of Elateriformia (14 697 positions), the analyses of two rRNA genes and 13 PCGs resulted in the well-supported sister relationship of *Iberobaenia* and Lycidae for the Bayesian analyses in BEAST (posterior probability of 1 with any data partitioning scheme applied; figure 1*d*). The calibration analyses with BEAST dated the split between these two lineages to the Jurassic at 170.7–176.6 Ma depending on the partitioning scheme (146.5–194.8, maximum 95% highest posterior density (HPD)). The ML analyses of the mitogenome dataset recovered the clade (Throscidae (Lycidae(*Mastinocerus*, *Iberobaenia*))) (electronic supplementary material, figure S4*a*). As the ML analyses of the mitogenome dataset merged *Mastinocerus* and *Iberobaenia* (electronic supplementary material, figure S4*a*), we constrained such topology in an additional dating analysis with eight partitions and parameters as above. The similarly deep split of *Iberobaenia* and its sister groups was inferred at 171.0 Ma (149.7–190.3, 95% HPD).

(b) Morphology and taxonomy

Iberobaenia **gen. nov.**

Type species: *Iberobaenia minuta* **sp. nov.**

Diagnosis. *Iberobaenia* are small-bodied beetles (1.9–2.5 mm) and similar to *Thilmanus* Gemminger, 1869 and *Paradrilus* Kiesenwetter, 1865 (Omalisidae) in general appearance (figure 2*a*), but have a hypognathous head and two-segmented labial palpi (electronic supplementary material, figure S1*c*). The prosternum is slightly transverse (figure 1*b*), with apical processes directed upwards, the pronotum and elytra do not bear any ridges or costae and the pronotum has rounded lateral margins (figure 1*c*). Legs are short, robust and non-compressed (figure 1*b*). The phallus is trilobate with slender pointed apexes of parameres; its phallobase is plate-like and v-shaped (figure 1*e*). All similar small-bodied neotenic beetles in Lycidae have developed apparent pronotal lateral edges, costae or at least papillae on the elytra, have a very short prosternum with two diverging processes at the apex, and compressed legs [32]. The full description is available in the electronic supplementary material.

The larva of *Iberobaenia* has two-segmented antennae with a finger-like process at the apex of the terminal antennomere similar to net-winged beetles (figure 1*h*; [33]). The larval mandibles of *Iberobaenia* are in opposite position, short, robust and with a sucking groove (figure 1*f,h*). Conversely, the larvae of Lycidae have slender, divergent mandibles consisting of two blades. The terminal abdominal segment of *Iberobaenia* is rounded with a deep notch (figure 1*g*); all net-winged beetle larvae have fixed urogomphi with variable length.

Etymology. The name *Iberobaenia* is derived from 'Iberia' referring to geographical origin of the taxon and in honour of M. Baena, the collector of the type species. Gender: feminine.

Iberobaenia minuta **sp. nov.**

Type material. Holotype, male. SPAIN. Sierra de la Pandera, Valdepeñas de Jaén, 9.vi.2012, M. Baena leg. (UPOL). Paratypes, 2 males, same data (UPOL, MBC).

Diagnosis. *Iberobaenia minuta* is very similar to *I. lencinai* in size and general appearance, however, they differ in the more transverse prosternum in *I. lencinai* sp. nov. and in the male genitalia (electronic supplementary material, figure S1*a,b*).

Description. Male adult as in the diagnosis of the genus *Iberobaenia* and description of *I. minuta* in the electronic supplementary material.

Etymology. The specific epithet refers to the very small body of the male.

Iberobaenia lencinai **sp. nov.**

Material studied. Holotype, male. SPAIN, Molina de Segura, El Rellano, P. E. "Vicente Blanes", 15.iv–1.vi.2009, J. L. Lencina leg. (JLC). Paratypes: see the electronic supplementary material.

Diagnosis. See the differential diagnosis under *I. minuta* sp. nov. and description in the electronic supplementary material.

Etymology. The species name is a patronym in honour of the collector J. L. Lencina.

Iberobaenia sp.

Material studied. Larva, SPAIN, Camino Viejo a la Ermita, Sierra de Cabra, 37.481117N, 4.388536 W, 970 m, 6.xii.2012, grassland, C. Andújar & P. Arribas leg.; larva, SPAIN, Ermita Nta. Sra. de la Sierra, Sierra de Cabra, 37.490527N, 4.381292 W, 1145 m, 6.xii.2012, C. Andújar & P. Arribas leg. (BMNH).

(c) Iberobaeniidae fam. nov.

The phylogenetic relationships, ancient divergence and morphology justified the establishment of a new taxon at the rank of family and we thus define monogeneric Iberobaeniidae **fam. nov.** The diagnosis of the family is the same as that of the genus *Iberobaenia* **gen. nov.**

4. Discussion

(a) Relationships and morphological traits of Iberobaeniidae

The trees inferred from the four-marker dataset consistently supported *Iberobaenia* as a sister group to the Lycidae (figure 1*a*, electronic supplementary material, figure S3). The same relationships were recovered by the BEAST analysis of the mitogenome data (figure 1*d*) and the morphology of adult males and larvae supports this hypothesis. The only analyses inconsistent with this placement were obtained after removing the Lycidae, which grouped Iberobaeniidae with the elaterid subfamily Lissominae in the four-marker dataset, and in the ML analysis of the rRNA/mtDNA with (Lycidae(*Mastinocerus*, *Iberobaenia*)) clade (electronic supplementary material, figure S4). However, these spurious relationships are a problem associated with the other sequences, not with *Iberobaenia*. Lissominae has a tendency to group with Lycidae [25], and close relatives of *Mastinocerus* (e.g. *Rhagophthalmus*) were never found with Lycidae in all previous analyses [8,13,25]. No morphological character of Lissominae or *Mastinocerus* supports a close relationship to Lycidae and *Iberobaenia*. Iberobaeniidae share the trilobate phallus and mouthparts adapted for sucking liquids with other Elateroidea [3,33]. Adult *Iberobaenia* differs from Lycidae by the filiform male antennae with a long antennomere 2, the absence of the sharp lateral edge and strengthening structures in the pronotum, the elytra without costae or tubercles, and the uncompressed legs (figure 1*a*,*b*). Yet, some characters are shared between both families, such as the v-shaped phallobase that is similar to those in some Lyropaeini [34] and the short prosternum with two apical processes (although these are directed upwards; figure 1*b*). Females are absent in our sample and we suppose that they remain larviform or at least incompletely metamorphosed when sexually mature, with a short lifespan and cryptic lifestyle. Lycidae contain several lineages with completely larviform females and small-bodied males, although in many cases (e.g. *Alyculus* Kazantsev, 1999, *Antennolycus* Bocakova & Bocak, 1999) the supposedly neotenic females have never been encountered, similarly to the Iberobaeniidae. The larvae of *Iberobaenia* differ from Lycidae in the uncompressed body, mandibles in opposing positions and able to bite (unlike Lycidae exhibiting mandibles with closely positioned bases and divergent tips that are not able to bite), fully sclerotized cranium and absent urogomphi (figure 1*f*–*h*). Both families share two-segmented larval antennae with a unique dorsal slender peg of the apical antennomere (figure 2*h*). The two-blade mandibles remain a synapomorphy of Lycidae, to the exclusion of Iberobaeniidae. All diagnostic morphological characters of Iberobaeniidae are summarized in the electronic supplementary material.

Iberobaenia males resemble various neotenic small-bodied elateroid genera (e.g. *Antennolycus*, *Paradrilus*, *Thilmanus*), including taxa with vestigial or absent elytra (*Alyculus*, *Cautires apterus* [2,6]). Additional morphological traits shared among neotenic elateroid lineages are found in the mouthparts, including a rounded, small mouth opening (electronic supplementary material, figure S1*c*), vestigial mandibles, reduced maxillae and labium and a lowered number of palpomeres, as these have been found in *Iberobaenia*. Our phylogenetic analyses confirm that shared morphological traits encountered in neotenic elateroids developed independently multiple times (figure 1*c*). Convergences in these traits have to be seen in the context of miniaturization of males, i.e. sexually linked body size differentiation [34,35] and hypothesized to be a result of the K- and r-strategy of the respective sexes [4]. Miniaturization is linked to the absence of the pronotal carinae and elytral costae as strengthening structures. Similarly, the patterns of four or nine longitudinal elytral costae are widespread in Elateroidea (e.g. Omalisidae, Lycidae, Omethidae) and the substantial reduction of costae is characteristic for neotenic forms with an extremely small body [32,36].

(b) Evolutionary biology and distribution

The split between Iberobaeniidae and Lycidae was dated with elateriform and scarabaeiform fossils [27–29], using a conservative approach by applying minimum ages to the stem clades of these taxa. The time-calibrated phylogeny placed the radiation of most families of Elateroidea to the Jurassic and the origin of Iberobaeniidae at 170.7–176.6 Ma depending on partitioning scheme (figure 1*d*). The inferred dates agree with the supposed early origins of beetle families proposed by Hunt *et al.* [37] and Misof *et al.* [24], but the age of Elateroidea (approx. 217 Ma) is slightly older than those inferred by McKenna *et al.* [25]. Their dating of Elateroidea was based on click beetles in the Karatau deposits (152 Ma) when Elateridae were already a diversified lineage (greater than 100 species; [38]), and in agreement with our date for the origin of Elateridae. Despite these differences, either dating approach infers Iberobaeniidae as a very ancient lineage. This supports the taxonomic rank of family.

The deep separation of Iberobaeniidae and the shallow separation of the two species of *Iberobaenia* near the tip make it impossible to date the origin of neotenic development along the terminal branch with any degree of precision. However, neotenic lineages in Lycidae and other early branches of Elateroidea (Omalisidae, Phengodidae, Rhagophthalmidae) are placed deeply in the tree and have undergone diversification, albeit at a low rate [4]. Thus, the Iberobaeniidae may represent another example of an ancient neotenic lineage, despite being species-poor. Equally, various neotenic lineages of Lycidae and Omalisidae exhibit high endemism and relict occurrence [4,36], as found in Iberobaeniidae. Neotenic females are apterous and short-lived during the adult stage, and thus due to their limited dispersal, population persistence is predicted to require geological and climatic stability [35,39]. Additionally, the discovery of a new beetle family in Europe, only the second since the nineteenth century, emphasizes the need for the protection of natural habitats and, in combination with the high level of threat from human activities, justifies the designation of the western Mediterranean as a biodiversity hotspot [11]. Further morphological and palaeontological studies are needed for understanding of the evolutionary history of neotenic lineages.

Finally, novel molecular tools provide new approaches for recognizing these divergent lineages. Most neotenic lineages of Lycidae, Omalisidae and also Iberobaeniidae have been collected either by sweeping the lowest strata of the vegetation or by sifting ([6,32]; M. Baena and M. Geiser 2012, personal communication). This presumably targets the males during short mating flights, while we detected the larvae in the deep soil that presumably identifies their main ecological affinities. Assemblages of soil arthropods composed of different life stages and usually minute individuals constitute a huge challenge for taxonomists. Therefore, both knowledge of deep soil species diversity as well as life history of many known taxa remains incomplete. Shotgun sequencing of bulk specimen samples, followed by assembly of mitochondrial genomes and phylogenetic analysis against a set of reference sequences [9,40], now provides a new approach to search for these undiscovered lineages, for a more complete knowledge of the major branches of the tree of life and for the identification of regions of exceptional high phylogenetic diversity.

Data accessibility. The DNA sequences reported in this article can be accessed in GenBank under accessions KT339296–98 and KT825140.

Authors' contributions. L.B. and A.P.V. participated in the study design, R.K. and C.A.F. carried out the molecular laboratory work and data analyses, all authors contributed to the draft of the manuscript and discussed results. All authors gave final approval for publication.

Competing interests. We have no competing interests.

Funding. The study was funded by the IGA and GACR projects (PrF02015-018, 506/11/1757 to L.B. and R.K.), Leverhulme Trust (F/00696/P to A.P.V. and L.B.) and the NHM Biodiversity Initiative.

Acknowledgements. The authors are obliged to J. L. Lencina and M. Baena for collecting and providing specimens of Iberobaenia and to R. Bilkova for technical assistance.

References

1. Farrell BD. 1998 'Inordinate Fondness' explained: why are there so many beetles? *Science* **281**, 555–559. (doi:10.1126/science.281.5376.555)
2. Bocak L, Barton C, Crampton-Platt A, Chesters D, Ahrens D, Vogler AP. 2014*a* Building the Coleoptera tree-of-life for >8000 species: composition of public DNA data and fit with Linnaean classification. *Syst. Entomol.* **39**, 97–110. (doi:10.1111/syen.12037)
3. Leschen RAB, Beutel RG, Lawrence JF (eds). 2010 Coleoptera, beetles; volume 2: morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). In *Handbook of zoology, Arthropoda: Insecta* (eds NP Kristensen, RG Beutel), 786 pp. Berlin, Germany: Walter de Gruyter GmbH & Co. KG.
4. Bocak L, Bocakova M, Hunt T, Vogler AP. 2008 Multiple ancient origins of neoteny in Lycidae (Coleoptera): consequences for ecology and macroevolution. *Proc. R. Soc. B* **275**, 2015–2023. (doi:10.1098/rspb.2008.0476)
5. Crowson RA. 1960 The phylogeny of Coleoptera. *Annu. Rev. Entomol.* **5**, 111–134. (doi:10.1146/annurev.en.05.010160.000551)
6. Bocak L, Grebennikov VV, Sklenarova K. 2014 *Cautires apterus*, a new species and the first record of wingless male Lycidae (Coleoptera) discovered in the North Pare Mountains, Tanzania. *Ann. Zool.* **64**, 1–7. (doi:10.3161/000345414X680500)
7. Lawrence JF. 1988 Rhinorhipidae, a new beetle family from Australia, with comments on the phylogeny of the Elateriformia. *Invertebr. Taxon.* **2**, 1–53. (doi:10.1071/IT9880001)
8. Kundrata R, Bocakova M, Bocak L. 2014 The comprehensive phylogeny of the superfamily Elateroidea (Coleoptera: Elateriformia). *Mol. Phylogenet. Evol.* **76**, 162–171. (doi:10.1016/j.ympev.2014.03.012)
9. Andújar C, Arribas P, Ruzicka F, Crampton-Platt A, Timmermans MJTN, Vogler AP. 2015 Phylogenetic community ecology of soil biodiversity using mitochondrial metagenomics. *Mol. Ecol.* **24**, 3603–3617. (doi:10.1111/mec.13195)
10. Hewitt GM. 1999 Post-glacial re-colonization of European biota. *Biol. J. Linn. Soc.* **68**, 87–112. (doi:10.1111/j.1095-8312.1999.tb01160.x)
11. Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000 Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858. (doi:10.1038/35002501)
12. Kundrata R, Baena M, Bocak L. 2015 Classification of Omalisidae based on molecular data and morphology, with description of Paradrilinae subfam. nov. (Coleoptera: Elateroidea). *Zootaxa* **3915**, 413–422. (doi:10.11646/zootaxa.3915.3.6)
13. Bocakova M, Bocak L, Hunt T, Vogler AP. 2007 Molecular phylogenetics of Elateriformia (Coleoptera): evolution of bioluminescence and neoteny. *Cladistics* **23**, 477–496. (doi:10.1111/j.1096-0031.2007.00164.x)
14. Andújar C, Arribas P, Linard B, Kundrata R, Bocak L, Vogler AP. In press. The mitochondrial genome of *Iberobaenia* (Coleoptera: Iberobaeniidae): first rearrangement of protein coding genes in the beetles. *Mitochondr. DNA*.
15. Bininda-Emonds ORP. 2005 transAlign: using amino acids to facilitate the multiple alignment of protein-coding DNA sequences. *BMC Bioinformatics* **6**, 156. (doi:10.1186/1471-2105-6-156)
16. Katoh K, Misawa K, Kuma K, Miyata T. 2002 MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Res.* **30**, 3059–3066. (doi:10.1093/nar/gkf436)
17. Belshaw R, Katzourakis A. 2005 BlastAlign: a program that uses blast to align problematic nucleotide sequences. *Bioinformatics* **21**, 122–123. (doi:10.1093/bioinformatics/bth459)
18. Stamatakis A. 2006 RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22**, 2688–2690. (doi:10.1093/bioinformatics/btl446)
19. Miller MA, Pfeiffer W, Schwartz T. 2010 Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In *Proc. of the Gateway Computing Environments Workshop* (GCE), New Orleans, LA, USA, pp. 1–8.
20. Darriba D, Taboada GL, Doallo R, Posada D. 2012 jModelTest 2: more models, new heuristics and parallel computing. *Nat. Methods* **9**, 772. (doi:10.1038/nmeth.2109)
21. Stamatakis A, Hoover P, Rougemont J. 2008 A rapid bootstrap algorithm for the RAxML web servers. *Syst. Biol.* **57**, 758–771. (doi:10.1080/10635150802429642)
22. Drummond AJ, Suchard MA, Xie D, Rambaut A. 2012 Bayesian phylogenetics with BEAUti and the

BEAST 1.7. *Mol. Biol. Evol*. **29**, 1969 – 1973. (doi:10.1093/molbev/mss075)

23. Andújar C, Serrano J, Gómez-Zurita J. 2012 Winding up the molecular clock in the genus *Carabus* (Coleoptera: Carabidae): assessment of methodological decisions on rate and node age estimation. *BMC Evol. Biol*. **12**, 40. (doi:10.1186/1471-2148-12-40)
24. Misof B *et al.* 2014 Phylogenomics resolves the timing and pattern of insect evolution. *Science* **346**, 763 – 767. (doi:10.1126/science.1257570)
25. McKenna DD *et al.* 2015 The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Syst. Entomol*. **40**, 835 – 880. (doi:10.1111/syen.12132)
26. Timmermans MJTN *et al.* 2016 Family-level sampling of mitochondrial genomes in Coleoptera: compositional heterogeneity and phylogenetics. *Genome Biol. Evol*. **8**, 161 – 175. (doi:10.1093/gbe/evv241)
27. Rasnitsyn AP, Quicke DLJ (eds). 2002 *History of insects*, 517 pp. Dordrecht, The Netherlands: Kluwer Academic Publisher.
28. Behrensmeyer AK, Turner A. 2015 Taxonomic occurrences of Elateriformia and Scarabaeiformia recorded in the Paleobiology Database Fossilworks. See http://fossilworks.org.
29. Whalley PES. 1985 The systematics and palaeogeography of the Lower Jurassic insects of Dorset, England. *Bull. Br. Mus. Nat. Hist*. **39**, 107 – 189.
30. Heer O. 1865 *Die Urwelt der Schweiz*, 622 pp. Zürich, Switzerland: Friedrich Schulthess.
31. Ho, SYW, Phillips MJ. 2009 Accounting for calibration uncertainty in phylogenetic estimation of evolutionary divergence times. *Syst. Biol*. **58**, 367 – 380. (doi:10.1093/sysbio/syp035)
32. Bocak L, Bocakova M. 2008 Phylogeny and classification of the family Lycidae (Insecta: Coleoptera). *Ann. Zool*. **58**, 695 – 720. (doi:10.3161/000345408X396639)
33. Bocak L, Matsuda K. 2003 Review of the immature stages of the family Lycidae (Insecta: Coleoptera). *J. Nat. Hist*. **37**, 1463 – 1507. (doi:10.1080/00222930210125362)
34. Masek M, Ivie MA, Palata V, Bocak L. 2014 Molecular phylogeny and classification of Lyropaeini (Coleoptera: Lycidae) with description of larvae and new species of *Lyropaeus*. *Raffles Bull. Zool*. **62**, 136 – 145.
35. Masek M, Palata V, Bray TC, Bocak L. 2015 Molecular phylogeny reveals high diversity, geographic structure and limited ranges in neotenic net-winged beetles *Platerodrilus* (Coleoptera: Lycidae). *PLoS ONE* **10**, e0123855. (doi:10.1371/journal.pone.0123855)
36. Bocak L, Brlik M. 2008 Revision of the family Omalisidae (Coleoptera, Elateroidea). *Insect Syst. Evol*. **39**, 189 – 212. (doi:10.1163/187631208788784101)
37. Hunt T *et al.* 2007 A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. *Science* **318**, 1913 – 1916. (doi:10.1126/science.1146954)
38. Doludenko MP, Ponomarenko AG, Sakulina GV. 1990 *La géologie du gisement unique de la faune et de la flore du jurassique supérieur d'Aulié* (*Karatau, Kazakhstan du Sud*), 24 pp. Moscow, Russia: Academie des Sciences de l'URSS, Inst. Géologique.
39. Malohlava V, Bocak L. 2010 Evidence of extreme habitat stability in a Southeast Asian biodiversity hotspot based on the evolutionary analysis of neotenic net-winged beetles. *Mol. Ecol*. **19**, 4800 – 4811. (doi:10.1111/j.1365-294X.2010.04850.x)
40. Crampton-Platt A, Timmermans MJTN, Gimmel ML, Narayanan Kutty S, Cockerill TD, Vun Khen C, Vogler AP. 2015 Soup to tree: the phylogeny of beetles inferred by mitochondrial metagenomics of a Bornean rainforest sample. *Mol. Biol. Evol*. **32**, 2302 – 2316. (doi:10.1093/molbev/msv111)

The list of Supplementary materials

Supplementary methods (1) Table S1. The list of taxa and GenBank accession numbers for the four-gene dataset. (2) The list of taxa and GenBank accession numbers for the *LSU*, *SSU*, and mitochondrial dataset. (3)Table S3. Primers and PCR settings.

Supplementary texts. (1) The list of beetle families proposed after 1950. (2) The list of family-group names mentioned in the text with taxonomic authorities and the year of the description given. (3) Morphological descriptions of the genus *Iberobaenia* and species placed in the genus. (4) An overview of the synapomorphies of Elateroidea identified in Iberobaeniidae, the shared characters of the cantharoid clade (the characters for both assemblages as identified by Lawrence *et al.* 2011), and the unique diagnostic characters of the clade Iberobaeniidae + Lycidae and unique diagnostic characters for Iberobaeniidae.

Figure S1. Morphology of *Iberobaenia lencinai* **sp. nov**. and *I. minuta* **sp. nov.**

Figure S2. Structure of the mitochondrial genome of *Iberobaenia* sp. and *Tribolium castaneum* (from Andújar et al. 2016).

Figure S3. Phylogenetic hypothesis of Elateroidea inferred from the four-gene BlastAlign dataset using maximum likelihood optimality criterion. *Iberobaenia* represented by *I. minuta* **sp. nov.** (adult, *LSU*, *SSU* rRNA, *cox1* mtDNA) and *Iberobaenia* sp. (larva, *rrnL* and *cox1* mtDNA).

Figure S4. Phylogenetic hypothesis of Elateroidea inferred from the *LSU*, *SSU* and 13 mtDNA protein coding gene dataset using the maximum likelihood optimality criterion.

Table S1. The list of taxa and GenBank accession numbers for the four-gene dataset.

			Markers				
Superfamily/family	Subfamily	Genus/Species	18S	28S	*rrnL*	*cox1*	Specimen voucher
SCIRTOIDEA							
Decliniidae		*Declinia versicolor*	AY745556	AJ862791	N	N	BMNH 693609
Eucinetidae		*Eucinetus* sp.	AF427609	DQ198697	N	DQ198541	BMNH 679351
Eucinetidae		*Eucinetus haemorrhoidalis*	KF625496	KF626097	KF625806	KF625198	UPOL 001319
Scirtidae		*Cyphon hilaris*	AF201419	DQ198698	DQ198620	DQ198542	BMNH 679123
Scirtidae		*Scirtes hemisphericus*	AF451937	DQ198699	N	N	BMNH 679275
Clambidae		*Clambus pubescens*	EF362951	N	AM884186	DQ155704	BMNH 673260
Clambidae		gen. sp.	KF625497	KF626105	KF625804	KF625196	UPOL 001320
Scirtidae		gen. sp.	KF625505	KF626106	KF625813	KF625206	UPOL 001321
Scirtidae		gen. sp.	KF625498	KF626098	KF625807	KF625199	UPOL RK0147
Scirtidae		gen. sp.	KF625499	KF626099	N	KF625200	UPOL RK0159
Scirtidae		*Scirtes* sp.	KF625500	KF626100	KF625808	KF625201	UPOL RK0160
Scirtidae		*Cyphon* sp.	KF625501	KF626101	KF625809	KF625202	UPOL RK0161
Scirtidae		gen. sp.	KF625502	KF626102	KF625810	KF625203	UPOL RK0162
Scirtidae		gen. sp.	KF625504	KF626104	KF625812	KF625205	UPOL RK0165
Scirtidae		gen. sp.	KF625512	KF626113	KF625819	KF625212	UPOL RK0166
Scirtidae		gen. sp.	KF625513	KF626114	N	KF625213	UPOL RK0167
Scirtidae		*Prionocyphon sexmaculatus*	KF625516	KF626117	KF625822	KF625216	UPOL RK0170
HYDROPHILOIDEA							
Sphaeritidae		*Sphaerites glabratus*	AJ810728	DQ202650	AM287077	DQ222001	BMNH 679280
Hydrophilidae	Georissinae	*Georissus crenulatus*	AY745584	DQ202637	DQ202580	DQ221983	BMNH 679200
Hydrophilidae	Sphaeridiinae	*Cercyon ustulatus*	AM287129	N	AM287071	AM287093	-
Hydrophilidae	Chaetarthriinae	*Anacaena globulus*	AM287125	N	AM287064	AM287086	-
Hydrophilidae	Hydrophilinae	*Hydrobius fuscipes*	AJ810720	N	AM287070	AM287092	-
STAPHYLINOIDEA							
Staphylinidae	Pseudopsinae	*Pseudopsis sulcata*	AY745630	DQ202651	DQ202587	DQ221990	BMNH 679246
Staphylinidae	Scaphidiinae	*Scaphidium quadrimaculatum*	AY745631	DQ202643	DQ202582	DQ221985	BMNH 679234
Staphylinidae	Oxytelinae	*Bledius femoralis*	AY745627	DQ202681	DQ202608	DQ222015	BMNH 679369
Silphidae	Silphinae	*Thanatophilus rugosus*	EF213790	EF213811	AB285546	AB606434	BMNH 673311
Silphidae	Silphinae	*Oiceoptoma thoracicum*	AJ810736	AB285581	AB285549	AB606436	-
Leiodidae	Cholevinae	*Catops picipes*	AJ810734	N	FM209287	FM209288	-
Leiodidae	Cholevinae	*Nargus velox*	AJ810735	N	GU356766	HQ164624	BMNH 833811
Hydraenidae	Ochthebiinae	*Ochthebius melanescens*	AJ810732	AJ810767	N	HE970900	MNCN AI344
Hydraenidae	Ochthebiinae	*Ochthebius minimus*	AJ810731	DQ202624	FM209291	FM209292	BMNH 679120
SCARABAEOIDEA							

Scarabaeidae	Scarabaeinae	*Cheironitis hoplosternus*	AY821528	AY131781	AY131597	AY131940	BMNH 679878
Scarabaeidae	Scarabaeinae	*Onthophagus crinitis*	AY821535	AY131759	AY131574	AY131924	BMNH 679858
Scarabaeidae	Aphodiinae	*Australammoecius occidentalis*	EF487639	AY132457	EF487822	EF656781	BMNH 703639
Scarabaeidae	Aphodiinae	*Podotenus storeyi*	EF487648	AY132494	EF487788	AY132432	BMNH 703575
Scarabaeidae	Melolonthinae	*Lepidiota stradbrokensis*	EF487696	EU084209	EF487881	EF487763	BMNH 671319
Scarabaeidae	Dynastinae	gen. sp.	EF487663	AY132488	EF487817	AY132397	BMNH 703635
Scarabaeidae	Cetoniinae	*Oxythyrea cinctella*	EF487653	EU084149	EF487962	EF487733	BMNH 678461
Scarabaeidae	Melolonthinae	*Holotrichia seticollis*	EF487687	DQ524596	DQ680877	DQ524528	BMNH 677874
Scarabaeidae	Sericinae	*Omaloplia nigromarginata*	EF487705	EU084255	EF487791	EF487770	BMNH 747063
Scarabaeidae	Sericinae	*Serica brunnea*	EF487712	EU084263	EF487872	EF487776	BMNH 703005
Scarabaeidae	Sericinae	*Gynaecoserica variipennis*	EF487683	EU084189	EF487968	EF487752	BMNH 678396
BUPRESTOIDEA							
Buprestidae	Agrilinae	*Agrilus* sp.	AF451934	DQ198701	DQ198622	DQ198544	UPOL 001047
Buprestidae	Buprestinae	*Anthaxia hungarica*	DQ100484	DQ198702	DQ198623	DQ198545	UPOL 000M24
Buprestidae	Julodinae	gen. sp.	AF451935	DQ198703	DQ198624	DQ198546	BMNH 679324
Buprestidae	Agrilinae	*Trachys minutus*	AF451936	DQ198704	N	DQ198547	BMNH 679281
BYRRHOIDEA							
Byrrhidae	Byrrhinae	*Byrrhus pilula*	AF427604	DQ198705	DQ198625	DQ198548	BMNH 679172
Byrrhidae	Syncalyptinae	*Chaetophora spinosa*	AF451929	DQ198706	N	N	BMNH 679203
Byrrhidae	Syncalyptinae	*Curimopsis setigera*	AF451930	DQ198707	N	N	BMNH 679204
Dryopidae		*Dryops algiricus*	AF451926	N	AJ862734	N	BMNH 693620
Dryopidae		*Pomatinus substriatus*	AF451924	DQ198708	DQ198626	DQ198549	BMNH 693616
Elmidae	Elminae	*Elmis maugetti*	AF451916	DQ198709	N	N	BMNH 693612
Elmidae	Elminae	*Homalosolus hospitalis*	AF451921	DQ198710	N	N	BMNH 693626
Elmidae	Elminae	*Limnius volckmari*	AF451914	DQ198712	DQ198627	DQ198550	BMNH 679263
Elmidae	Elminae	*Macronychus quadrituberculatus*	AF451920	DQ198713	EF209458	EF209578	BMNH 693611
Elmidae	Elminae	*Oulimnius rivularis*	AF451913	DQ198714	DQ198628	DQ198551	BMNH 679264
Elmidae	Elminae	*Limnius perrisi*	AF451915	DQ198711	AJ862736	AJ862800	BMNH 693613
Elmidae	Elminae	*Stenelmis canaliculata*	AF451919	DQ198716	N	N	BMNH 693614
Elmidae	Larainae	*Potamophilus acuminatus*	AF451911	N	EF209464	EF209584	EC_E07
Elmidae	Larainae	*Potamodytes* sp.	AF451912	DQ198715	DQ198629	DQ198552	BMNH 679360
Heteroceridae	Heterocerinae	*Augyles maritimus*	AF451927	DQ198717	N	N	BMNH 693618
Heteroceridae	Heterocerinae	*Heterocerus* sp.	AF451928	DQ198718	Q198630	DQ198553	UPOL 001048
Limnichidae	Limnichinae	*Limnichus pygmaeus*	AF451923	DQ198719	DQ198631	DQ198554	BMNH 679196
Limnichidae	-	gen. sp.	KF625495	KF626096	KF625805	KF625197	UPOL 001318
Psephenidae	-	gen. sp.	KF625503	KF626103	KF625811	KF625204	UPOL RK0163
Psephenidae	Eubrianacinae	*Eubrianax edwardsi*	AF451933	DQ198720	N	N	BMNH 679347
Psephenidae	Eubrianacinae	*Eubrianax* sp.	DQ100485	DQ198721	DQ198632	DQ198555	UPOL 000M33
Psephenidae		gen. sp.	KF625514	KF626115	KF625820	KF625214	UPOL RK0168

Psephenidae		gen. sp.	KF625515	KF626116	KF625821	KF625215	UPOL RK0169
Chelonariidae		gen. sp.	KF625508	KF626109	KF625816	KF625209	UPOL 001323
Chelonariidae		gen. sp.	KF625509	KF626110	KF625817	KF625210	UPOL 001324
Chelonariidae		gen. sp.	DQ100488	DQ198724	DQ198635	DQ198558	UPOL 000M06
Eulichadidae		*Eulichas* sp.	DQ100489	DQ198725	DQ198636	DQ198559	UPOL 000M22
Callirhipidae		*Horatocera nipponica*	KF625510	KF626111	N	N	UPOL 001248
Callirhipidae		gen. sp.	KF625511	KF626112	KF625818	KF625211	UPOL 001249
Callirhipidae		gen. sp.	DQ100490	DQ198726	DQ198637	DQ198560	UPOL 000M23
Ptilodactylidae	Cladotominae	*Paralichas pectinatus*	DQ100486	DQ198722	DQ198633	DQ198556	UPOL 000M41
Ptilodactylidae	Ptilodactylinae	*Ptilodactyla serricornis*	AF451932	DQ198723	DQ198634	DQ198557	BMNH 693606
Ptilodactylidae		gen. sp.	KF625517	KF626118	KF625823	KF625222	UPOL RK0131
Ptilodactylidae		gen. sp.	KF625518	KF626119	KF625824	KF625217	UPOL RK0149
Ptilodactylidae		gen. sp.	KF625519	KF626120	N	KF625218	UPOL RK0150
Ptilodactylidae		gen. sp.	KF625520	KF626121	KF625825	KF625219	UPOL RK0151
Ptilodactylidae		gen. sp.	KF625521	KF626122	KF625826	KF625220	UPOL RK0152
Ptilodactylidae		gen. sp.	KF625522	KF626123	KF625827	KF625221	UPOL RK0153
ELATEROIDEA							
Artematopodidae	Artematopodinae	*Eurypogon brevipennis*	KF294763	KF294769	KF294757	KF294776	UPOL 001335
Artematopodidae	Artematopodinae	*Eurypogon japonicus*	KF294761	KF294767	KF294755	KF294774	UPOL RK0091
Artematopodidae	Artematopodinae	*Eurypogon hisamatsui*	KF294762	KF294768	KF294756	KF294775	UPOL RK0128
Omethidae	Telegeusinae	*Telegeusis nubifer*	DQ100503	DQ198751	DQ198660	DQ198582	UPOL 000321
Omethidae	Telegeusinae	gen. sp.	KF625531	KF626132	N	KF625231	UPOL RK0360
Omethidae	Telegeusinae	gen. sp.	N	KF626318	N	KF625425	UPOL 001345
Omethidae	Driloniinae	*Drilonius* sp.	DQ100502	DQ198750	DQ198659	DQ198581	UPOL 000M26
Omethidae	Driloniinae	*Drilonius* sp.	KF294764	KF294770	KF294758	KF294777	UPOL 001273
Omethidae	Driloniinae	*Drilonius* sp.	KF294765	KF294771	KF294759	KF294778	UPOL RK0134
Omethidae	Driloniinae	*Drilonius striatulus*	KF625527	KF626128	KF625830	KF625227	UPOL 001272
Omethidae	Driloniinae	*Drilonius* sp.	KF625528	KF626129	KF625831	KF625228	UPOL 001274
Omethidae	Driloniinae	*Drilonius* sp.	KF625523	KF626124	KF625832	KF625223	UPOL RK0132
Omethidae	Driloniinae	*Drilonius* sp.	KF625524	KF626125	KF625833	KF625224	UPOL RK0135
Omethidae	Driloniinae	*Drilonius* sp.	KF625525	KF626126	KF625834	KF625225	UPOL RK0136
Omethidae	Driloniinae	*Drilonius* sp.	KF625526	KF626127	KF625835	KF625226	UPOL RK0362
Omethidae	Omethinae	*Troglomethes leechi*	KF625529	KF626130	KF625828	KF625229	UPOL 001340
Omethidae	Matheteinae	*Ginglymocladus* sp.	KF625530	KF626131	KF625829	KF625230	UPOL 001341
Cerophytidae		*Cerophytum elateroides*	KF625714	KF626302	KF626002	KF625407	UPOL RK0129
Throscidae		*Trixagus meybohmi*	KF294766	KF294772	KF294760	KF294779	UPOL RK0139
Throscidae		*Trixagus dermestoides*	AF451950	DQ198747	DQ198656	DQ198578	BMNH 679235
Throscidae		gen. sp.	KF625543	KF626143	KF625842	KF625243	UPOL 001326
Throscidae		gen. sp.	KF625544	KF626144	N	KF625244	UPOL 001327

Throscidae		gen. sp.	KF625532	KF626133	N	KF625232	UPOL RK0137
Throscidae		gen. sp.	KF625533	KF626134	KF625836	KF625233	UPOL RK0138
Throscidae		gen. sp.	KF625534	KF626135	N	KF625234	UPOL RK0140
Throscidae		gen. sp.	KF625535	KF626136	KF625837	KF625235	UPOL RK0141
Throscidae		gen. sp.	KF625536	KF626137	KF625838	KF625236	UPOL RK0175
Throscidae		gen. sp.	KF625537	KF626138	N	KF625237	UPOL RK0330
Throscidae		gen. sp.	KF625538	N	N	KF625238	UPOL RK0331
Throscidae		gen. sp.	KF625539	KF626139	KF625839	KF625239	UPOL RK0333
Throscidae		gen. sp.	KF625540	KF626140	N	KF625240	UPOL RK0336
Throscidae		gen. sp.	KF625541	KF626141	KF625840	KF625241	UPOL RK0337
Throscidae		gen. sp.	KF625542	KF626142	KF625841	KF625242	UPOL RK0338
Throscidae		gen. sp.	HQ333838	N	KF625844	HQ334017	UPOL RK0086
Eucnemidae	Anischiinae	*Anischia kuscheli*	KF625545	KF626145	KF625845	KF625246	UPOL RK0119
Eucnemidae	Anischiinae	*Anischia bicolor*	KF625546	KF626146	KF625846	KF625247	UPOL RK0120
Eucnemidae	Eucneminae	*Idiotarsus* sp.	DQ100493	DQ198730	DQ198641	DQ198563	BMNH 703097
Eucnemidae	Macraulacinae	gen. sp.	KF625578	KF626178	KF625873	KF625276	UPOL 001233
Eucnemidae	Macraulacinae	gen. sp.	KF625553	KF626152	KF625852	KF625253	UPOL RK0126
Eucnemidae	Macraulacinae	gen. sp.	KF625580	KF626180	KF625875	KF625278	UPOL 001235
Eucnemidae	Macraulacinae	gen. sp.	KF625583	KF626184	KF625879	KF625282	UPOL 001330
Eucnemidae	Macraulacinae	*Nematodes* sp.	DQ100495	DQ198731	DQ198642	DQ198564	BMNH 703107
Eucnemidae	Macraulacinae	*Fornax* sp.	DQ100492	DQ198729	DQ198640	DQ198562	BMNH 703106
Eucnemidae	Melasinae	*Entomophthalmus americanus*	DQ100491	DQ198727	DQ198638	N	BMNH 703104
Eucnemidae	Melasinae	*Protofarsus* sp.	DQ100496	DQ198732	N	DQ198565	BMNH 703095
Eucnemidae	Melasinae	*Arrhipis* sp.	N	DQ198745	DQ198654	DQ198577	BMNH 703101
Eucnemidae	Melasinae	*Microrhagus* sp.	KF625569	KF626169	KF625866	KF625270	UPOL 001223
Eucnemidae	Melasinae	*Micorhagus pygmaeus*	KF625570	KF626170	KF625867	KF625271	UPOL 001224
Eucnemidae	Melasinae	*Isorhipis marmottani*	N	KF626183	KF625878	KF625281	UPOL 001329
Eucnemidae	Melasinae	*Melasis buprestoides*	KF625558	KF626158	KF625858	KF625259	UPOL RK0344
Eucnemidae		gen. sp.	HQ333807	HQ333902	HQ333716	HQ333988	UPOL RK0054
Eucnemidae		gen. sp.	HQ333829	HQ333923	HQ333736	HQ334009	UPOL RK0076
Eucnemidae		gen. sp.	HQ333830	HQ333924	HQ333737	HQ334010	UPOL RK0077
Eucnemidae		gen. sp.	HQ333831	HQ333925	KF625843	KF625245	UPOL RK0078
Eucnemidae		gen. sp.	KF625571	KF626171	KF625868	KF625272	UPOL 001225
Eucnemidae		gen. sp.	KF625572	KF626172	KF625869	KF625273	UPOL 001226
Eucnemidae		gen. sp.	KF625573	KF626173	KF625870	KF625274	UPOL 001227
Eucnemidae		gen. sp.	KF625574	KF626174	N	N	UPOL 001228
Eucnemidae		gen. sp.	KF625575	KF626175	KF625871	N	UPOL 001229
Eucnemidae		gen. sp.	KF625576	KF626176	KF625872	KF625275	UPOL 001230
Eucnemidae		gen. sp.	KF625577	KF626177	N	N	UPOL 001231

Eucnemidae		gen. sp.	KF625579	KF626179	KF625874	KF625277	UPOL 001234
Eucnemidae		gen. sp.	KF625581	KF626181	KF625876	KF625279	UPOL 001236
Eucnemidae		gen. sp.	KF625582	KF626182	KF625877	KF625280	UPOL 001328
Eucnemidae		gen. sp.	KF625584	KF626185	N	KF625283	UPOL 001331
Eucnemidae		gen. sp.	KF625585	KF626186	KF625880	KF625284	UPOL 001332
Eucnemidae		gen. sp.	KF625586	KF626187	KF625881	KF625285	UPOL 001333
Eucnemidae		gen. sp.	N	KF626188	N	KF625286	UPOL 001334
Eucnemidae		gen. sp.	KF625547	KF626147	KF625847	KF625248	UPOL RK0121
Eucnemidae		gen. sp.	KF625548	KF626148	KF625848	KF625249	UPOL RK0122
Eucnemidae		gen. sp.	KF625549	KF626149	KF625849	KF625250	UPOL RK0123
Eucnemidae		gen. sp.	KF625550	KF626150	KF625850	KF625251	UPOL RK0124
Eucnemidae		gen. sp.	KF625552	KF626151	KF625851	KF625252	UPOL RK0125
Eucnemidae		gen. sp.	KF625551	KF626153	KF625853	KF625254	UPOL RK0171
Eucnemidae		gen. sp.	KF625554	KF626154	KF625854	KF625255	UPOL RK0303
Eucnemidae		gen. sp.	KF625555	KF626155	KF625855	KF625256	UPOL RK0340
Eucnemidae		gen. sp.	KF625556	KF626156	KF625856	KF625257	UPOL RK0341
Eucnemidae		gen. sp.	KF625557	KF626157	KF625857	KF625258	UPOL RK0343
Eucnemidae		gen. sp.	KF625559	KF626159	KF625859	KF625260	UPOL RK0345
Eucnemidae		gen. sp.	KF625560	KF626160	KF625860	KF625261	UPOL RK0346
Eucnemidae		gen. sp.	KF625561	KF626161	KF625861	KF625262	UPOL RK0347
Eucnemidae		gen. sp.	KF625562	KF626162	N	KF625263	UPOL RK0348
Eucnemidae		gen. sp.	KF625563	KF626163	N	KF625264	UPOL RK0349
Eucnemidae		gen. sp.	KF625564	KF626164	KF625862	KF625265	UPOL RK0350
Eucnemidae		gen. sp.	KF625565	KF626165	KF625863	KF625266	UPOL RK0351
Eucnemidae		gen. sp.	KF625566	KF626166	KF625864	KF625267	UPOL RK0355
Eucnemidae		gen. sp.	KF625567	KF626167	N	KF625268	UPOL RK0356
Eucnemidae		gen. sp.	KF625568	KF626168	KF625865	KF625269	UPOL RK0357
Iberobaeniidae		*Iberobaenia minuta* sp. nov.	KT339296	KT339297	N	KT339298	UPOL RK0790
Lycidae	Libnetinae	*Libnetis* sp.	DQ181038	DQ181112	DQ180964	DQ181186	UPOL 000L02
Lycidae	Libnetinae	*Libnetis* sp.	DQ181104	DQ181178	DQ181030	DQ181252	UPOL 001002
Lycidae	Libnetinae	*Libnetis* sp.	DQ181105	DQ181179	DQ181031	DQ181253	UPOL 001008
Lycidae	Libnetinae	*Libnetis granicollis*	DQ181107	DQ181181	DQ181033	DQ181255	UPOL 001012
Lycidae	Dictyopterinae	*Lycoprogenthes* sp.	DQ181070	DQ181144	DQ180996	DQ181218	UPOL 000358
Lycidae	Dictyopterinae	*Lycoprogenthes* sp.	DQ181095	DQ181169	DQ181021	DQ181243	UPOL 000801
Lycidae	Dictyopterinae	*Lycoprogenthes* sp.	DQ181096	DQ181170	DQ181022	DQ181244	UPOL 000802
Lycidae	Dictyopterinae	*Taphes brevicollis*	DQ181098	DQ181172	DQ181024	DQ181246	UPOL 000812
Lycidae	Dictyopterinae	*Dictyoptera elegans*	DQ181073	DQ181147	DQ180999	DQ181221	UPOL 000570
Lycidae	Dictyopterinae	*Dictyoptera speciosa*	DQ181074	DQ181148	DQ181000	DQ181222	UPOL 000571
Lycidae	Dictyopterinae	*Benibotarus nigripennis*	DQ181075	DQ181149	DQ181001	DQ181223	UPOL 000572

Lycidae	Dictyopterinae	*Benibotarus spinicoxis*	DQ181076	DQ181150	DQ181002	DQ181224	UPOL 000573
Lycidae	Dictyopterinae	*Pyropterus nigroruber*	DQ181077	DQ181151	DQ181003	DQ181225	UPOL 000574
Lycidae	Dictyopterinae	*Dictyoptera* sp.	KF625686	KF626272	KF625976	KF625385	UPOL 001275
Lycidae	Dictyopterinae	*Dictyoptera aurora*	KF625687	KF626273	KF625977	KF625386	UPOL 001276
Lycidae	Dictyopterinae	*Pyropterus nigroruber*	KF625688	KF626274	KF625978	KF625387	UPOL 001277
Lycidae	Dictyopterinae	Dictyopterini gen. sp.	KF625689	KF626275	KF625979	KF625388	UPOL 001278
Lycidae	Dictyopterinae	Dictyopterini gen. sp.	KF625690	KF626276	KF625980	KF625389	UPOL 001280
Lycidae	Dictyopterinae	Dictyopterini gen. sp.	KF625691	KF626277	KF625981	KF625390	UPOL 001282
Lycidae	Dictyopterinae	Dictyopterini gen. sp.	KF625692	KF626278	KF625982	KF625391	UPOL 001283
Lycidae	Dictyopterinae	*Lopheros* sp.	KF625693	KF626279	N	N	UPOL 001284
Lycidae	Dictyopterinae	*Benibotarus taygetanus*	KF625694	KF626280	KF625983	KF625392	UPOL 001285
Lycidae	Dictyopterinae	*Benibotarus* sp.	KF625698	KF626284	KF625987	KF625396	UPOL 001367
Lycidae	Dictyopterinae	*Helcophorus* sp.	KF625699	KF626285	KF625988	KF625397	UPOL 001369
Lycidae	Lyropaeinae	*Alyculus kurbatovi*	DQ181072	DQ181146	DQ180998	DQ181220	UPOL 000543
Lycidae	Lyropaeinae	*Lyropaeus* sp.	DQ181042	DQ181116	DQ180968	DQ181190	UPOL 000L11
Lycidae	Lyropaeinae	*Lyropaeus* sp.	DQ181087	DQ181161	DQ181013	DQ181235	UPOL 000584
Lycidae	Lyropaeinae	*Lyropaeus* sp.	DQ181088	DQ181162	DQ181014	DQ181236	UPOL 000585
Lycidae	Lyropaeinae	*Antennolycus constrictus*	DQ181051	DQ181125	DQ180977	DQ181199	UPOL 000L22
Lycidae	Lyropaeinae	*Microlyropaeus dembickyi*	DQ181071	DQ181145	DQ180997	DQ181219	UPOL 000542
Lycidae	Lyropaeinae	*Platerodrilus* sp.	DQ181037	DQ181111	DQ180963	DQ181185	UPOL 000L01
Lycidae	Lyropaeinae	*Platerodrilus* sp.	DQ181091	DQ181165	DQ181017	DQ181239	UPOL 000588
Lycidae	Lyropaeinae	Platerodrilini gen. sp.	DQ181089	DQ181163	DQ181015	DQ181237	UPOL 000586
Lycidae	Lyropaeinae	Platerodrilini gen. sp.	DQ181090	DQ181164	DQ181016	DQ181238	UPOL 000587
Lycidae	Lyropaeinae	*Macrolibnetis* sp.	DQ181050	DQ181124	DQ180976	DQ181198	UPOL 000L21
Lycidae	Lyropaeinae	*Pendola* sp.	DQ181058	DQ181132	DQ180984	DQ181206	UPOL 000M45
Lycidae	Lyropaeinae	*Horakiella emasensis*	DQ181110	DQ181184	DQ181036	DQ181258	UPOL 001043
Lycidae	Lyropaeinae	Platerodrilini gen. sp.	KF625700	KF626286	KF625989	KF625398	UPOL 001371
Lycidae	Lyropaeinae	Platerodrilini gen. sp.	KF625701	KF626287	KF625990	KF625399	UPOL 001372
Lycidae	Lyropaeinae	Platerodrilini gen. sp.	KF625702	KF626288	KF625991	KF625400	UPOL 001373
Lycidae	Lyropaeinae	Platerodrilini gen. sp.	KF625703	KF626289	KF625992	KF625401	UPOL 001374
Lycidae	Lyropaeinae	Platerodrilini gen. sp.	KF625704	KF626290	KF625993	KF625402	UPOL 001376
Lycidae	Lyropaeinae	Platerodrilini gen. sp.	KF625705	KF626291	KF625994	N	UPOL 001377
Lycidae	Lyropaeinae	Platerodrilini gen. sp.	KF625706	KF626292	KF625995	N	UPOL 001378
Lycidae	Lyropaeinae	Platerodrilini gen. sp.	KF625707	KF626293	KF625996	KF625403	UPOL 001379
Lycidae	Lyropaeinae	*Platerodrilus* sp.	KF625708	KF626294	KF625997	KF625404	UPOL 001380
Lycidae	Lyropaeinae	Platerodrilini gen. sp.	KF625709	KF626295	KF625998	N	UPOL 001382
Lycidae	Lyropaeinae	Platerodrilini gen. sp.	KF625710	KF626296	N	N	UPOL 001384
Lycidae	Lyropaeinae	Platerodrilini gen. sp.	KF625711	KF626297	KF625999	KF625405	UPOL 001385
Lycidae	Lyropaeinae	Platerodrilini gen. sp.	KF625712	KF626298	KF626000	N	UPOL 001387

Lycidae	Lyropaeinae	Platerodrilini gen. sp.	KF625713	KF626299	KF626001	KF625406	UPOL 001388
Lycidae	Ateliinae	*Dilophotes* sp.	DQ181066	DQ181140	DQ180992	DQ181214	UPOL 000244
Lycidae	Ateliinae	*Scarelus* sp.	DQ181046	DQ181120	DQ180972	DQ181194	UPOL 000L15
Lycidae	Ateliinae	*Scarelus* sp.	DQ181085	DQ181159	DQ181011	DQ181233	UPOL 000582
Lycidae	Ateliinae	*Scarelus* sp.	DQ181086	DQ181160	DQ181012	DQ181234	UPOL 000583
Lycidae	Lycinae	*Dihammatus* sp.	DQ181043	DQ181117	DQ180969	DQ181191	UPOL 000L12
Lycidae	Lycinae	*Dihammatus* sp.	DQ181103	DQ181177	DQ181029	DQ181251	UPOL 001001
Lycidae	Lycinae	*Dihammatus* sp.	DQ181106	DQ181180	DQ181032	DQ181254	UPOL 001009
Lycidae	Lycinae	*Dihammatus* sp.	DQ181108	DQ181182	DQ181034	DQ181256	UPOL 001017
Lycidae	Lycinae	*Eurrhacus* sp.	DQ181056	DQ181130	DQ180982	DQ181204	UPOL 000M43
Lycidae	Lycinae	*Conderis signicollis*	DQ181062	DQ181136	DQ180988	DQ181210	UPOL 000194
Lycidae	Lycinae	*Conderis rufohumeralis*	DQ181084	DQ181158	DQ181010	DQ181232	UPOL 000581
Lycidae	Lycinae	*Conderis* sp.	DQ350139	DQ350138	DQ350141	DQ350140	UPOL 000M42
Lycidae	Lycinae	*Plateros* sp.	DQ181044	DQ181118	DQ180970	DQ181192	UPOL 000L13
Lycidae	Lycinae	*Plateros* sp.	DQ181059	DQ181133	DQ180985	DQ181207	UPOL 000031
Lycidae	Lycinae	*Plateros* sp.	DQ181065	DQ181139	DQ180991	DQ181213	UPOL 000243
Lycidae	Lycinae	*Plateros* sp.	DQ181067	DQ181141	DQ180993	DQ181215	UPOL 000303
Lycidae	Lycinae	*Plateros* sp.	DQ181109	DQ181183	DQ181035	DQ181257	UPOL 001031
Lycidae	Lycinae	*Macrolycus* sp.	DQ181049	DQ181123	DQ180975	DQ181197	UPOL 000L18
Lycidae	Lycinae	*Macrolycus* sp.	DQ181102	DQ181176	DQ181028	DQ181250	UPOL 000828
Lycidae	Lycinae	*Thonalmus sinuaticostis*	DQ181093	DQ181167	DQ181019	DQ181241	UPOL 000594
Lycidae	Lycinae	*Thonalmus hubbardi*	DQ181094	DQ181168	DQ181020	DQ181242	UPOL 000595
Lycidae	Lycinae	*Lyponia nigrohumeralis*	DQ181048	DQ181122	DQ180974	DQ181196	UPOL 000L17
Lycidae	Lycinae	*Lyponia delicatula*	DQ181099	DQ181173	DQ181025	DQ181247	UPOL 000815
Lycidae	Lycinae	*Lyponia* sp.	DQ181100	DQ181174	DQ181026	DQ181248	UPOL 000816
Lycidae	Lycinae	*Lyponia quadricollis*	DQ181101	DQ181175	DQ181027	DQ181249	UPOL 000817
Lycidae	Lycinae	*Lycus* sp.	DQ181039	DQ181113	DQ180965	DQ181187	UPOL 000L03
Lycidae	Lycinae	*Lycostomus* sp.	DQ181055	DQ181129	DQ180981	DQ181203	UPOL 000L27
Lycidae	Lycinae	*Calopteron* sp.	DQ181053	DQ181127	DQ180979	DQ181201	UPOL 000L25
Lycidae	Lycinae	*Idiopteron biplagiatum*	DQ181057	DQ181131	DQ180983	DQ181205	UPOL 000M44
Lycidae	Lycinae	gen. sp.	DQ181092	DQ181166	DQ181018	DQ181240	UPOL 000592
Lycidae	Lycinae	*Metapteron* sp.	AF451946	DQ198757	N	DQ198588	BMNH 679218
Lycidae	Lycinae	*Cautires* sp.	DQ181045	DQ181119	DQ180971	DQ181193	UPOL 000L14
Lycidae	Lycinae	*Cautires* sp.	DQ181041	DQ181115	DQ180967	DQ181189	UPOL 000L06
Lycidae	Lycinae	*Metriorrhynchus lineatus*	DQ181040	DQ181114	DQ180966	DQ181188	UPOL 000L05
Lycidae	Lycinae	*Microtrichalus* sp.	DQ181052	DQ181126	DQ180978	DQ181200	UPOL 000L23
Lycidae	Lycinae	*Leptotrichalus* sp.	DQ181064	DQ181138	DQ180990	DQ181212	UPOL 000208
Lycidae	Lycinae	*Calochromus* sp.	DQ181047	DQ181121	DQ180973	DQ181195	UPOL 000L16
Lycidae	Lycinae	*Calochromus* sp.	DQ181060	DQ181134	DQ180986	DQ181208	UPOL 000033

Lycidae	Lycinae	*Calochromus* sp.	DQ181068	DQ181142	DQ180994	DQ181216	UPOL 000347
Lycidae	Lycinae	*Platycis minutus*	DQ181069	DQ181143	DQ180995	DQ181217	UPOL 000348
Lycidae	Lycinae	*Platycis nasutus*	DQ181079	DQ181153	DQ181005	DQ181227	UPOL 000576
Lycidae	Lycinae	*Konoplatycis otome*	DQ181078	DQ181152	DQ181004	DQ181226	UPOL 000575
Lycidae	Lycinae	*Lopheros* sp.	DQ181080	DQ181154	DQ181006	DQ181228	UPOL 000577
Lycidae	Lycinae	*Lopheros* sp.	DQ181081	DQ181155	DQ181007	DQ181229	UPOL 000578
Lycidae	Lycinae	*Eropterus nothus*	DQ181082	DQ181156	DQ181008	DQ181230	UPOL 000579
Lycidae	Lycinae	*Eropterus* sp.	DQ181083	DQ181157	DQ181009	DQ181231	UPOL 000580
Lycidae	Lycinae	*Flagrax* sp.	DQ181054	DQ181128	DQ180980	DQ181202	UPOL 000L26
Lycidae	Lycinae	*Plateros* sp.	KF625685	KF626271	KF625975	KF625384	UPOL RK0377
Lycidae	Lycinae	*Platycis cosnardi*	KF625695	KF626281	KF625984	KF625393	UPOL 001286
Lycidae	Lycinae	*Platycis* sp.	KF625696	KF626282	KF625985	KF625394	UPOL 001365
Lycidae	Lycinae	*Platycis* sp.	KF625697	KF626283	KF625986	KF625395	UPOL 001366
Lampyridae	Lampyrinae	gen. sp.	DQ100509	DQ198759	DQ198667	DQ198590	UPOL 000M19
Lampyridae	Lampyrinae	gen. sp.	DQ100510	N	DQ198668	DQ198591	UPOL 000M04
Lampyridae	Lampyrinae	*Vesta* sp.	DQ100511	DQ198760	DQ198669	DQ198592	UPOL 000M17
Lampyridae	Cyphonocerinae	*Cyphonocerus ruficollis*	DQ100512	N	DQ198670	DQ198593	UPOL 000191
Lampyridae	Luciolinae	*Curtos* sp.	DQ100513	DQ198761	DQ198671	DQ198594	UPOL 000M16
Lampyridae	Luciolinae	gen. sp.	DQ100514	DQ198762	DQ198672	DQ198595	UPOL 000M03
Lampyridae	Luciolinae	*Bourgeoisia* sp.	DQ100515	N	DQ198673	DQ198596	UPOL 000M07
Lampyridae	Luciolinae	gen. sp.	DQ100516	N	DQ198674	DQ198597	UPOL 000M18
Lampyridae	Ototretinae	gen. sp.	DQ100518	N	DQ198676	DQ198599	UPOL 000M38
Lampyridae	Ototretinae	*Flabellotreta obscuricollis*	DQ100519	N	DQ198677	DQ198600	UPOL 000M05
Lampyridae	Ototretinae	*Flabellotreta* sp.	DQ100520	DQ198763	DQ198678	DQ198601	UPOL 000M34
Lampyridae	Ototretinae	gen. sp.	DQ100521	DQ198764	DQ198679	DQ198602	UPOL 000M37
Lampyridae	Ototretinae	*Drilaster borneensis subvittatus*	DQ100522	N	DQ198680	DQ198603	UPOL 000M39
Lampyridae	Ototretinae	gen. sp.	DQ100523	N	DQ198681	DQ198604	UPOL 000M32
Lampyridae	Ototretinae	*Lamellipalpus pacholatkoi*	KF625664	KF626254	KF625955	KF625363	UPOL RK0379
Lampyridae	Ototretinae	gen. sp.	DQ100524	N	DQ198682	DQ198605	UPOL 000156
Lampyridae		gen. sp.	KF625636	N	KF625928	KF625335	UPOL RK0087
Lampyridae		gen. sp.	KF625637	KF626238	N	KF625336	UPOL RK0089
Lampyridae		gen. sp.	KF625638	KF626239	KF625929	KF625337	UPOL RK0093
Lampyridae		gen. sp.	KF625639	N	KF625930	KF625338	UPOL RK0095
Lampyridae		gen. sp.	KF625640	KF626240	KF625931	KF625339	UPOL RK0096
Lampyridae		gen. sp.	KF625641	KF626241	KF625932	KF625340	UPOL RK0097
Lampyridae		gen. sp.	KF625642	N	KF625933	KF625341	UPOL RK0098
Lampyridae		gen. sp.	KF625643	KF626242	KF625934	KF625342	UPOL RK0099
Lampyridae		gen. sp.	KF625644	KF626243	KF625935	KF625343	UPOL RK0101
Lampyridae		gen. sp.	KF625645	N	KF625936	KF625344	UPOL RK0102

Lampyridae		gen. sp.	KF625646	N	KF625937	KF625345	UPOL RK0103
Lampyridae		gen. sp.	KF625647	N	KF625938	KF625346	UPOL RK0104
Lampyridae		gen. sp.	KF625648	KF626244	KF625939	KF625347	UPOL RK0106
Lampyridae		gen. sp.	KF625649	KF626245	KF625940	KF625348	UPOL RK0107
Lampyridae		gen. sp.	KF625650	KF626246	KF625941	KF625349	UPOL RK0108
Lampyridae		gen. sp.	KF625651	N	KF625942	KF625350	UPOL RK0109
Lampyridae		gen. sp.	KF625652	KF626247	KF625943	KF625351	UPOL RK0110
Lampyridae		gen. sp.	KF625653	KF626248	KF625944	KF625352	UPOL RK0111
Lampyridae		gen. sp.	KF625654	N	KF625945	KF625353	UPOL RK0112
Lampyridae		gen. sp.	KF625655	N	KF625946	KF625354	UPOL RK0113
Lampyridae		gen. sp.	KF625656	KF626249	KF625947	KF625355	UPOL RK0118
Lampyridae		gen. sp.	KF625657	KF626250	KF625948	KF625356	UPOL RK0173
Lampyridae		gen. sp.	KF625658	N	KF625949	KF625357	UPOL RK0372
Lampyridae		gen. sp.	KF625659	N	KF625950	KF625358	UPOL RK0373
Lampyridae		gen. sp.	KF625660	KF626251	KF625951	KF625359	UPOL RK0374
Lampyridae		gen. sp.	KF625661	KF626252	KF625952	KF625360	UPOL RK0375
Lampyridae		gen. sp.	KF625662	N	KF625953	KF625361	UPOL RK0376
Lampyridae		gen. sp.	KF625663	KF626253	KF625954	KF625362	UPOL RK0378
Lampyridae		gen. sp.	KF625665	KF626255	KF625956	KF625364	UPOL RK0380
Lampyridae		gen. sp.	KF625666	KF626256	KF625957	KF625365	UPOL RK0381
Lampyridae		gen. sp.	KF625667	N	KF625958	KF625366	UPOL RK0382
Lampyridae		gen. sp.	KF625668	KF626257	KF625959	KF625367	UPOL RK0383
Lampyridae		gen. sp.	KF625669	KF626258	KF625960	KF625368	UPOL RK0384
Lampyridae		gen. sp.	KF625670	KF626259	KF625961	KF625369	UPOL RK0385
Lampyridae		gen. sp.	KF625671	KF626260	KF625962	KF625370	UPOL RK0386
Lampyridae		gen. sp.	KF625672	KF626261	KF625963	KF625371	UPOL RK0387
Lampyridae		gen. sp.	KF625673	N	KF625964	KF625372	UPOL RK0388
Lampyridae		gen. sp.	KF625674	N	KF625965	KF625373	UPOL RK0389
Lampyridae		gen. sp.	KF625675	KF626262	KF625966	KF625374	UPOL RK0390
Lampyridae		gen. sp.	KF625676	KF626263	KF625967	KF625375	UPOL RK0391
Lampyridae		gen. sp.	KF625677	KF626264	KF625968	KF625376	UPOL RK0392
Lampyridae		gen. sp.	KF625678	KF626265	KF625969	KF625377	UPOL RK0393
Lampyridae		gen. sp.	KF625679	KF626266	KF625970	KF625378	UPOL RK0394
Lampyridae		gen. sp.	KF625680	KF626267	KF625971	KF625379	UPOL RK0395
Lampyridae		gen. sp.	KF625681	KF626268	KF625972	KF625380	UPOL RK0396
Lampyridae		gen. sp.	KF625682	N	KF625973	KF625381	UPOL RK0397
Lampyridae		gen. sp.	KF625683	KF626269	KF625974	KF625382	UPOL RK0398
Lampyridae		gen. sp.	KF625684	KF626270	N	KF625383	UPOL RK0399
Cantharidae	Cantharinae	*Cantharis rufa*	N	DQ198767	DQ198684	DQ198607	BMNH 703089

Cantharidae	Cantharinae	gen. sp.	DQ100526	DQ198768	DQ198685	DQ198608	UPOL 000M14
Cantharidae	Cantharinae	*Rhagonycha nigriceps*	DQ100527	DQ198769	DQ198686	DQ198609	UPOL 000M15
Cantharidae	Cantharinae	*Rhagonycha lignosa*	AF451939	DQ198770	DQ198687	DQ198610	BMNH 679176
Cantharidae	Cantharinae	gen. sp.	KF625614	KF626216	KF625906	KF625313	UPOL 001300
Cantharidae	Cantharinae	*Athemus* sp.	KF625615	KF626217	KF625907	KF625314	UPOL 001301
Cantharidae	Cantharinae	*Themus* sp.	KF625616	KF626218	KF625908	KF625315	UPOL 001302
Cantharidae	Cantharinae	*Prothemus* sp.	KF625617	KF626219	KF625909	KF625316	UPOL 001303
Cantharidae	Cantharinae	*Habronychus* sp.	KF625625	KF626227	KF625917	KF625324	UPOL 001311
Cantharidae	Cantharinae	*Cratosilis sicula*	KF625587	KF626189	KF625882	KF625287	UPOL RK0094
Cantharidae	Cantharinae	*Athemellus insulsus*	KF625620	KF626222	KF625912	KF625319	UPOL 001306
Cantharidae	Cantharinae	*Cantharis rustica*	AF451940	N	EU301849	DQ156062	BMNH 676948
Cantharidae	Cantharinae	*Podabrus temporalis*	KF625621	KF626223	KF625913	KF625320	UPOL 001307
Cantharidae	Cantharinae	*Rhagonycha* sp.	KF625628	KF626230	KF625920	KF625327	UPOL 001314
Cantharidae	Cantharinae	gen. sp.	KF625629	KF626231	KF625921	KF625328	UPOL 001315
Cantharidae	Cantharinae	*Cantharis* sp.	KF625631	KF626233	KF625923	KF625330	UPOL 001317
Cantharidae	Cantharinae	*Lycocerus* sp.	KF625591	KF626193	KF625886	KF625291	UPOL RK0176
Cantharidae	Chauliognathinae	*Chauliognathus opacus*	HM156710	HM156702	FJ613418	FJ613418	BT0055
Cantharidae	Chauliognathinae	*Ichthyurus* sp.	DQ100531	DQ198774	DQ198691	DQ198614	UPOL 000M12
Cantharidae	Chauliognathinae	*Chauliognathus* sp.	KF625600	KF626202	KF625892	KF625300	UPOL 001250
Cantharidae	Chauliognathinae	*Ichthyurus* sp.	KF625605	KF626207	KF625897	KF625304	UPOL 001291
Cantharidae	Chauliognathinae	gen. sp.	KF625612	KF626214	KF625904	KF625311	UPOL 001298
Cantharidae	Chauliognathinae	*Chauliognathus* sp.	KF625613	KF626215	KF625905	KF625312	UPOL 001299
Cantharidae	Chauliognathinae	*Microichthyurus* sp.	KF625619	KF626221	KF625911	KF625318	UPOL 001305
Cantharidae	Chauliognathinae	*Trypherus mutilatus*	KF625622	KF626224	KF625914	KF625321	UPOL 001308
Cantharidae	Chauliognathinae	gen. sp.	KF625623	KF626225	KF625915	KF625322	UPOL 001309
Cantharidae	Chauliognathinae	gen. sp.	KF625634	KF626236	KF625926	KF625333	UPOL 001393
Cantharidae	Chauliognathinae	gen. sp.	KF625635	KF626237	KF625927	KF625334	UPOL 001394
Cantharidae	Chauliognathinae	gen. sp.	KF625589	KF626191	KF625884	KF625289	UPOL RK0155
Cantharidae	Chauliognathinae	gen. sp.	KF625592	KF626194	N	KF625292	UPOL RK0177
Cantharidae	Chauliognathinae	gen. sp.	KF625594	KF626196	KF625888	KF625294	UPOL RK0179
Cantharidae	Chauliognathinae	gen. sp.	KF625599	KF626201	N	KF625299	UPOL RK0200
Cantharidae	Malthininae	*Malthodes* sp.	DQ100532	DQ198776	DQ198693	DQ198616	UPOL 000M20
Cantharidae	Malthininae	gen. sp.	DQ100533	DQ198777	DQ198694	DQ198617	UPOL 000M21
Cantharidae	Malthininae	*Inmalthodes* sp.	DQ100534	DQ198778	DQ198695	DQ198618	UPOL 000M27
Cantharidae	Malthininae	gen. sp.	KF625602	KF626204	KF625894	KF625302	UPOL 001288
Cantharidae	Malthininae	*Inmalthodes* sp.	KF625603	KF626205	KF625895	KF625303	UPOL 001289
Cantharidae	Malthininae	*Inmalthodes* sp.	KF625604	KF626206	KF625896	N	UPOL 001290
Cantharidae	Malthininae	gen. sp.	KF625624	KF626226	KF625916	KF625323	UPOL 001310
Cantharidae	Malthininae	gen. sp.	KF625626	KF626228	KF625918	KF625325	UPOL 001312

Cantharidae	Malthininae	*Malthinus* sp.	KF625627	KF626229	KF625919	KF625326	UPOL 001313
Cantharidae	Malthininae	gen. sp.	KF625630	KF626232	KF625922	KF625329	UPOL 001316
Cantharidae	Malthininae	gen. sp.	KF625590	KF626192	KF625885	KF625290	UPOL RK0157
Cantharidae	Malthininae	gen. sp.	KF625593	KF626195	KF625887	KF625293	UPOL RK0178
Cantharidae	Malthininae	gen. sp.	KF625595	KF626197	KF625889	KF625295	UPOL RK0180
Cantharidae	Malthininae	*Malthinus* sp.	KF625596	KF626198	KF625890	KF625296	UPOL RK0181
Cantharidae	Silinae	*Laemoglyptus* sp.	DQ100528	DQ198771	DQ198688	DQ198611	UPOL 000M10
Cantharidae	Silinae	*Asiosilis* sp.	DQ100530	DQ198773	DQ198690	DQ198613	UPOL 000M13
Cantharidae	Silinae	*Laemoglyptus* sp.	KF625601	KF626203	KF625893	KF625301	UPOL 001287
Cantharidae	Silinae	gen. sp.	KF625606	KF626208	KF625898	KF625305	UPOL 001292
Cantharidae	Silinae	gen. sp.	KF625607	KF626209	KF625899	KF625306	UPOL 001293
Cantharidae	Silinae	gen. sp.	KF625608	KF626210	KF625900	KF625307	UPOL 001294
Cantharidae	Silinae	gen. sp.	KF625609	KF626211	KF625901	KF625308	UPOL 001295
Cantharidae	Silinae	gen. sp.	KF625610	KF626212	KF625902	KF625309	UPOL 001296
Cantharidae	Silinae	gen. sp.	KF625588	KF626190	KF625883	KF625288	UPOL RK0154
Cantharidae	Silinae	gen. sp.	KF625597	KF626199	N	KF625297	UPOL RK0182
Cantharidae	gen. sp.	gen. sp.	KF625611	KF626213	KF625903	KF625310	UPOL 001297
Cantharidae	gen. sp.	gen. sp.	DQ100529	DQ198772	DQ198689	DQ198612	UPOL 000M11
Cantharidae	gen. sp.	*Micropodabrus* sp.	KF625618	KF626220	KF625910	KF625317	UPOL 001304
Cantharidae	gen. sp.	gen. sp.	KF625632	KF626234	KF625924	KF625331	UPOL 001391
Cantharidae	gen. sp.	gen. sp.	KF625633	KF626235	KF625925	KF625332	UPOL 001392
Cantharidae	gen. sp.	gen. sp.	KF625598	KF626200	KF625891	KF625298	UPOL RK0199
Omalisidae	Omalisinae	*Omalisus sanguinipennis*	HQ333835	N	HQ333741	N	UPOL RK0083
Omalisidae	Omalisinae	*Omalisus fontisbellaquei*	AF451948	DQ198749	DQ198658	DQ198580	UPOL 000377
Omalisidae	Omalisinae	*Phaeopterus unicolor*	N	N	N	KJ909286	UPOL RK0092
Omalisidae	Thilmaninae	*Pseudeuanoma* sp.	HQ333832	KF626300	HQ333738	HQ334011	UPOL RK0079
Omalisidae	Thilmaninae	*Pseudeuanoma* sp.	HQ333833	KF626301	N	HQ334012	UPOL RK0080
Omalisidae	Paradrilinae	*Paradrilus opacus*	KJ909284	KJ909285	N	KJ909287	UPOL RK0626
Rhagophthalmidae		gen. sp.	KF625717	KF626305	KF626005	KF625410	UPOL 001359
Rhagophthalmidae		gen. sp.	KF625718	N	KF626006	KF625411	UPOL 001363
Rhagophthalmidae		gen. sp.	KF625715	KF626303	KF626003	KF625408	UPOL RK0088
Rhagophthalmidae		gen. sp.	KF625716	KF626304	KF626004	KF625409	UPOL RK0370
Rhagophthalmidae		*Mimoochotyra* sp.	DQ100505	DQ198753	DQ198662	DQ198584	UPOL 000M30
Rhagophthalmidae		gen. sp.	DQ100506	DQ198754	DQ198663	DQ198585	UPOL 000M31
Rhagophthalmidae		*Bicladodrilus* sp.	DQ100507	DQ198755	DQ198664	DQ198586	UPOL 000M35
Rhagophthalmidae		*Rhagophthalmus* sp.	DQ100508	DQ198756	DQ198665	DQ198587	UPOL 000155
Rhagophthalmidae		*Rhagophthalmus ohbai*	AB298864	N	NC_010964	NC_010964	71225
Phengodidae	Phengodinae	*Phengodes* sp.	DQ100504	DQ198752	DQ198661	DQ198583	UPOL 000M29
Phengodidae	Phengodinae	*Phengodes* sp.	KF625725	KF626312	KF626011	KF625418	UPOL 001238

Phengodidae	Phengodinae	*Phengodes* sp.	KF625726	KF626313	KF626012	KF625419	UPOL 001241
Phengodidae	Phengodinae	*Phengodes* sp.	KF625723	KF626310	KF626009	KF625416	UPOL RK0366
Phengodidae		gen. sp.	KF625727	KF626314	KF626013	KF625420	UPOL 001243
Phengodidae		gen. sp.	KF625728	KF626315	KF626014	KF625421	UPOL 001245
Phengodidae		gen. sp.	KF625729	KF626316	KF626015	KF625422	UPOL 001246
Phengodidae		gen. sp.	KF625730	KF626317	KF626016	KF625423	UPOL 001247
Phengodidae		gen. sp.	KF625731	N	KF626017	KF625424	UPOL 001343
Phengodidae		gen. sp.	KF625732	KF626319	N	KF625426	UPOL 001346
Phengodidae		gen. sp.	KF625733	N	KF626018	KF625427	UPOL 001348
Phengodidae		gen. sp.	KF625734	N	N	KF625428	UPOL 001349
Phengodidae		gen. sp.	KF625735	N	KF626019	KF625429	UPOL 001350
Phengodidae		gen. sp.	KF625736	KF626320	KF626020	KF625430	UPOL 001351
Phengodidae		gen. sp.	KF625737	N	KF626021	N	UPOL 001353
Phengodidae		gen. sp.	KF625738	N	KF626022	KF625431	UPOL 001354
Phengodidae		gen. sp.	KF625719	KF626306	KF626007	KF625412	UPOL RK0361
Phengodidae		gen. sp.	KF625720	KF626307	N	KF625413	UPOL RK0363
Phengodidae		gen. sp.	KF625721	KF626308	KF626008	KF625414	UPOL RK0364
Phengodidae		gen. sp.	KF625722	KF626309	N	KF625415	UPOL RK0365
Phengodidae		gen. sp.	KF625724	KF626311	KF626010	KF625417	UPOL RK0368
Elateridae	Agrypninae	*Adelocera* sp.	HQ333794	HQ333889	KF626035	HQ333976	UPOL RK0041
Elateridae	Agrypninae	*Adelocera* sp.	HQ333815	HQ333910	KF626033	KF625439	UPOL RK0062
Elateridae	Agrypninae	*Lacon* sp.	HQ333789	HQ333884	KF626036	HQ333971	UPOL RK0036
Elateridae	Agrypninae	*Pyrophorus* sp.	HQ333753	HQ333848	HQ333672	KF625435	UPOL 001423
Elateridae	Agrypninae	*Tetrigus cyprius*	KF625744	KF626327	KF626032	KF625438	UPOL RK0228
Elateridae	Agrypninae	*Cryptalaus* sp.	HQ333781	HQ333876	KF626034	N	UPOL RK0028
Elateridae	Agrypninae	*Pyrophorus* sp.	KF625742	KF626325	KF626030	KF625436	UPOL RK0213
Elateridae	Agrypninae	*Chalcolepidius* sp.	KF625743	KF626326	KF626031	KF625437	UPOL RK0219
Elateridae	Agrypninae	*Drilus concolor*	HQ333827	KF626322	HQ333734	HQ334007	UPOL RK0074
Elateridae	Agrypninae	*Malacogaster passerinii*	KF625741	KF626321	KF626029	KF625432	UPOL RK0369
Elateridae	Agrypninae	*Selasia* sp.	KF625739	KF626323	KF626027	KF625433	UPOL RK0158
Elateridae	Agrypninae	*Selasia* sp.	KF625740	KF626324	KF626028	KF625434	UPOL RK0172
Elateridae	Agrypninae	Anaissini gen. sp.	KF625761	KF626341	KF626055	KF625452	UPOL RK0301
Elateridae	Agrypninae	*Agrypnus murinus*	AF451943	DQ198735	DQ198645	DQ198567	UPOL 001049
Elateridae	Agrypninae	*Agrypnus* sp.	HQ333757	HQ333852	HQ333676	HQ333941	UPOL RK0004
Elateridae	Agrypninae	*Agrypnus* sp.	HQ333783	HQ333878	HQ333697	HQ333965	UPOL RK0030
Elateridae	Agrypninae	*Agrypnus* sp.	HQ333810	HQ333905	HQ333719	HQ333991	UPOL RK0057
Elateridae	Agrypninae	*Agrypnus* sp.	HQ333820	HQ333915	HQ333727	HQ334000	UPOL RK0067
Elateridae	Agrypninae	*Adelocera* sp.	HQ333778	HQ333873	HQ333694	HQ333961	UPOL RK0025
Elateridae	Agrypninae	*Adelocera* sp.	HQ333806	HQ333901	HQ333715	HQ333987	UPOL RK0053

Elateridae	Agrypninae	*Adelocera* sp.	HQ333817	HQ333912	HQ333724	HQ333997	UPOL RK0064
Elateridae	Agrypninae	*Adelocera* sp.	HQ333818	HQ333913	HQ333725	HQ333998	UPOL RK0065
Elateridae	Agrypninae	*Conoderus* sp.	HQ333746	HQ333841	HQ333665	HQ333931	UPOL 001416
Elateridae	Agrypninae	*Conoderus* sp	HQ333747	HQ333842	HQ333666	HQ333932	UPOL 001417
Elateridae	Agrypninae	*Drasterius bimaculatus*	HQ333793	HQ333888	HQ333704	HQ333975	UPOL RK0040
Elateridae	Agrypninae	*Drasterius* sp.	HQ333816	HQ333911	HQ333723	HQ333996	UPOL RK0063
Elateridae	Agrypninae	gen. sp.	HQ333798	HQ333893	HQ333708	HQ333980	UPOL RK0045
Elateridae	Agrypninae	*Platycrepidius* sp.	HQ333748	HQ333843	HQ333667	HQ333933	UPOL 001418
Elateridae	Agrypninae	*Pyrophorus* sp.	HQ333751	HQ333846	HQ333670	HQ333936	UPOL 001421
Elateridae	Agrypninae	*Chalcolepidius* sp.	HQ333752	HQ333847	HQ333671	HQ333937	UPOL 001422
Elateridae	Agrypninae	*Cryptalaus* sp.	HQ333768	HQ333863	HQ333685	HQ333951	UPOL RK0015
Elateridae	Agrypninae	*Cryptalaus* sp.	HQ333834	HQ333926	HQ333740	HQ334014	UPOL RK0082
Elateridae	Agrypninae	*Selasia* sp.	HQ333824	HQ333919	HQ333731	HQ334004	UPOL RK0071
Elateridae	Agrypninae	*Drilus flavescens*	DQ100501	DQ198748	DQ198657	DQ198579	UPOL 001046
Elateridae	Agrypninae	*Drilus* sp.	HQ333826	HQ333921	HQ333733	HQ334006	UPOL RK0073
Elateridae	Agrypninae	*Drilus* sp.	N	N	HQ333739	HQ334013	UPOL RK0081
Elateridae	Agrypninae	*Drilus mauritanicus*	HQ333837	HQ333928	HQ333743	HQ334016	UPOL RK0085
Elateridae	Cardiophorinae	*Cardiophorus erichsoni*	HQ333790	HQ333885	HQ333701	HQ333972	UPOL RK0037
Elateridae	Cardiophorinae	gen. sp.	HQ333823	HQ333918	HQ333730	HQ334003	UPOL RK0070
Elateridae	Cardiophorinae	gen. sp.	AF451942	DQ198739	DQ198649	DQ198571	BMNH 679341
Elateridae	Cardiophorinae	*Dicronychus rubripes*	HQ333764	HQ333859	KF626023	HQ333947	UPOL RK0011
Elateridae	Cardiophorinae	*Dicronychus cinereus*	HQ333776	HQ333871	KF626024	HQ333959	UPOL RK0023
Elateridae	Cardiophorinae	gen. sp.	HQ333784	HQ333879	KF626025	HQ333966	UPOL RK0031
Elateridae	Cardiophorinae	gen. sp.	HQ333788	HQ333883	KF626026	HQ333970	UPOL RK0035
Elateridae	Dendrometrinae	*Athous vittatus*	HQ333755	HQ333850	HQ333674	HQ333939	UPOL RK0002
Elateridae	Dendrometrinae	*Pheletes quercus*	HQ333775	HQ333870	HQ333692	HQ333958	UPOL RK0022
Elateridae	Dendrometrinae	*Cidnopus pilosus*	HQ333792	HQ333887	HQ333703	HQ333974	UPOL RK0039
Elateridae	Dendrometrinae	*Anostirus purpureus*	HQ333761	HQ333856	HQ333679	HQ333945	UPOL RK0008
Elateridae	Dendrometrinae	*Neopristilophus serrifer*	HQ333765	HQ333860	HQ333682	HQ333948	UPOL RK0012
Elateridae	Dendrometrinae	*Selatosomus latus*	HQ333774	HQ333869	HQ333691	HQ333957	UPOL RK0021
Elateridae	Dendrometrinae	gen. sp.	HQ333787	HQ333882	HQ333700	HQ333969	UPOL RK0034
Elateridae	Dendrometrinae	*Platiana* sp.	HQ333782	HQ333877	HQ333696	HQ333964	UPOL RK0029
Elateridae	Dendrometrinae	*Hypolithus* sp.	HQ333795	HQ333890	HQ333705	HQ333977	UPOL RK0042
Elateridae	Dendrometrinae	*Semiotus* sp.	HQ333799	HQ333894	HQ333709	HQ333981	UPOL RK0046
Elateridae	Dendrometrinae	*Oxynopterus* sp.	HQ333800	HQ333895	HQ333710	HQ333982	UPOL RK0047
Elateridae	Dendrometrinae	*Aplotarsus incanus*	N	DQ198737	DQ198647	DQ198569	BMNH703088
Elateridae	Dendrometrinae	*Athous haemorrhoidalis*	AF451944	DQ198738	DQ198648	DQ198570	BMNH 679174
Elateridae	Dendrometrinae	*Denticollis linearis*	DQ100498	DQ198741	DQ198651	DQ198573	UPOL 000M25
Elateridae	Dendrometrinae	*Panspaeus guttatus*	DQ100499	DQ198742	DQ198652	DQ198574	BMNH 703090

Elateridae	Dendrometrinae	*Stenagostus rhombeus*	AF451945	DQ198744	DQ198653	DQ198576	BMNH 679144
Elateridae	Dendrometrinae	*Denticollis* sp.	HQ333759	HQ333854	KF626041	HQ333943	UPOL RK0006
Elateridae	Dendrometrinae	*Nothodes parvulus*	HQ333763	HQ333858	HQ333681	KF625443	UPOL RK0010
Elateridae	Dendrometrinae	gen. sp.	KF625751	KF626338	KF626053	KF625451	UPOL RK0251
Elateridae	Dendrometrinae	*Hemicrepidius hirtus*	KF625754	KF626340	KF626054	KF625448	UPOL RK0297
Elateridae	-	gen. sp.	KF625762	KF626346	KF626057	N	UPOL 001237
Elateridae	Elaterinae	*Octinodes* sp.	HQ333749	HQ333844	HQ333668	HQ333934	UPOL 001419
Elateridae	Elaterinae	*Elater* sp.	HQ333766	HQ333861	HQ333683	HQ333949	UPOL RK0013
Elateridae	Elaterinae	*Tomicephalus* sp.	HQ333750	HQ333845	HQ333669	HQ333935	UPOL 001420
Elateridae	Elaterinae	gen. sp.	HQ333773	HQ333868	HQ333690	HQ333956	UPOL RK0020
Elateridae	Elaterinae	gen. sp.	HQ333819	HQ333914	HQ333726	HQ333999	UPOL RK0066
Elateridae	Elaterinae	*Ludioschema* sp.	HQ333777	HQ333872	HQ333693	HQ333960	UPOL RK0024
Elateridae	Elaterinae	*Ludioschema* sp.	HQ333808	HQ333903	HQ333717	HQ333989	UPOL RK0055
Elateridae	Elaterinae	*Anoplischius* sp.	HQ333745	HQ333840	HQ333664	HQ333930	UPOL 001415
Elateridae	Elaterinae	*Ampedus* sp.	HQ333758	HQ333853	HQ333677	HQ333942	UPOL RK0005
Elateridae	Elaterinae	*Ampedus sanguinolentus*	HQ333760	HQ333855	HQ333678	HQ333944	UPOL RK0007
Elateridae	Elaterinae	*Ampedus rufipennis*	HQ333762	HQ333857	HQ333680	HQ333946	UPOL RK0009
Elateridae	Elaterinae	*Ampedus* sp.	HQ333771	HQ333866	HQ333688	HQ333954	UPOL RK0018
Elateridae	Elaterinae	*Ampedus sinuatus*	HQ333791	HQ333886	HQ333702	HQ333973	UPOL RK0038
Elateridae	Elaterinae	*Ampedus* sp.	HQ333822	HQ333917	HQ333729	HQ334002	UPOL RK0069
Elateridae	Elaterinae	*Ampedus balteatus*	AF427605	DQ198736	DQ198646	DQ198568	BMNH 679173
Elateridae	Elaterinae	*Agriotes acuminatus*	HQ333756	HQ333851	HQ333675	HQ333940	UPOL RK0003
Elateridae	Elaterinae	*Agriotes ustulatus*	HQ333786	HQ333881	HQ333699	HQ333968	UPOL RK0033
Elateridae	Elaterinae	*Agriotes lineatus*	N	DQ198733	DQ198643	DQ198566	BMNH 703086
Elateridae	Elaterinae	*Cebrio* sp.	DQ100497	DQ198740	DQ198650	DQ198572	BMNH 679376
Elateridae	Elaterinae	gen. sp.	HQ333767	HQ333862	HQ333684	HQ333950	UPOL RK0014
Elateridae	Elaterinae	gen. sp.	HQ333769	HQ333864	HQ333686	HQ333952	UPOL RK0016
Elateridae	Elaterinae	gen. sp.	HQ333770	HQ333865	HQ333687	HQ333953	UPOL RK0017
Elateridae	Elaterinae	gen. sp.	HQ333801	HQ333896	HQ333711	HQ333983	UPOL RK0048
Elateridae	Elaterinae	gen. sp.	HQ333812	HQ333907	HQ333720	HQ333993	UPOL RK0059
Elateridae	Elaterinae	*Melanotus villosus*	HQ333754	HQ333849	HQ333673	HQ333938	UPOL RK0001
Elateridae	Elaterinae	*Priopus ornatus*	HQ333785	HQ333880	HQ333698	HQ333967	UPOL RK0032
Elateridae	Elaterinae	*Priopus humeralis*	HQ333821	HQ333916	HQ333728	HQ334001	UPOL RK0068
Elateridae	Elaterinae	*Anchastus* sp.	HQ333804	HQ333899	HQ333714	HQ333986	UPOL RK0051
Elateridae	Elaterinae	*Anchastus* sp.	HQ333809	HQ333904	HQ333718	HQ333990	UPOL RK0056
Elateridae	Elaterinae	*Anchastus* sp.	HQ333813	HQ333908	HQ333721	HQ333994	UPOL RK0060
Elateridae	Elaterinae	*Anchastus* sp.	HQ333814	HQ333909	HQ333722	HQ333995	UPOL RK0061
Elateridae	Elaterinae	*Mulsanteus* sp.	HQ333744	HQ333839	KF626037	HQ333929	UPOL 001414
Elateridae	Elaterinae	*Agriotes obscurus*	HQ333805	HQ333900	KF626039	KF625441	UPOL RK0052

Elateridae	Elaterinae	Adrastini gen. sp.	HQ333780	HQ333875	KF626038	HQ333963	UPOL RK0027
Elateridae	Elaterinae	*Cebrio* sp.	KF625745	KF626329	KF626040	KF625440	UPOL RK0142
Elateridae	Elaterinae	*Octinodes* sp.	KF625746	KF626328	N	KF625442	UPOL RK0306
Elateridae	Elaterinae	gen. sp.	KF625752	KF626337	KF626052	KF625449	UPOL RK0203
Elateridae	Elaterinae	Physorhinini gen. sp.	KF625758	KF626334	KF626056	KF625453	UPOL RK0310
Elateridae	Elaterinae	gen. sp.	KF625755	KF626339	KF626046	KF625455	UPOL RK0400
Elateridae	Elaterinae	gen. sp.	KF625757	KF626343	KF626048	KF625457	UPOL RK0404
Elateridae	Elaterinae	gen. sp.	KF625759	KF626344	KF626049	KF625458	UPOL RK0406
Elateridae	Elaterinae	Agriotini gen. sp.	KF625763	KF626345	N	KF625459	UPOL 001413
Elateridae	Hemiopinae	gen. sp.	KF625756	KF626342	KF626047	KF625456	UPOL RK0403
Elateridae	Lissominae	*Drapetes mordelloides*	HQ333828	HQ333922	HQ333735	HQ334008	UPOL RK0075
Elateridae	Lissominae	gen. sp.	KF625747	KF626330	KF626042	KF625444	UPOL RK0334
Elateridae	Lissominae	gen. sp.	KF625748	KF626331	KF626043	KF625445	UPOL RK0335
Elateridae	Lissominae	gen. sp.	KF625749	KF626332	KF626044	KF625446	UPOL RK0353
Elateridae	Lissominae	gen. sp.	KF625750	KF626333	KF626045	KF625447	UPOL RK0354
Elateridae	Lissominae	gen. sp.	KF625760	KF626336	KF626051	KF625450	UPOL RK0174
Elateridae	Morostomatinae	*Diplophoenicus* sp.	KF625753	KF626335	KF626050	KF625454	UPOL RK0145
Elateridae	Negastriinae	*Zorochros* sp.	HQ333796	HQ333891	HQ333706	HQ333978	UPOL RK0043
Elateridae	Negastriinae	*Quasimus* sp.	HQ333802	HQ333897	HQ333712	HQ333984	UPOL RK0049
Elateridae	Negastriinae	*Quasimus* sp.	HQ333803	HQ333898	HQ333713	HQ333985	UPOL RK0050
Elateridae	Negastriinae	gen. sp.	HQ333811	HQ333906	N	HQ333992	UPOL RK0058
Elateridae	Thylacosterninae	*Balgus* sp.	DQ100500	DQ198746	DQ198655	N	BMNH 669202
Elateridae	Thylacosterninae	*Pterotarsus bimaculatus*	N	DQ198743	N	DQ198575	BMNH 703093

Table S3. The list of taxa included in the *SSU*, *LSU* rRNA and mitochondrial protein coding genes dataset.

				Mitochondrial genomes		*LSU* rRNA (28S)	*SSU* rRNA (18S)
Suborder/Series	Superfamily	Family	Genus	GenBank #	Voucher #		
Archostemata		Cupedidae	*Priacma*	JX412806	BMNH 842702	GU591995	EU797411
Myxophaga		Sphaeriusidae	*Sphaerius*	EU877950	BT0074	GU591993	EU797414
		Hydroscaphidae	*Hydroscapha*	AM493667	-	n.a.	AF012525
Adephaga	Gyrinoidea	Gyrinidae	*Macrogyrus*	FJ859901	-	n.a.	AJ318664
	Caraboidea	Trachypachidae	*Trachypachus*	EU877954	-	n.a.	EU797418
		Carabidae	Trechini gen. sp.	HQ232802	-	n.a.	GU556140
		Carabidae	*Agonum*	JX412835	BMNH 832916	FJ173098	AF002775
		Carabidae	*Brachinus*	JX412826	BMNH 844234	GQ503347	JN170213
Polyphaga							
Scirtiformia	Scirtoidea	Scirtidae	*Prionocyphon*	JX412728	BMNH 842693	KF626117	KF625516
		Scirtidae	*Cyphon*	EU877949	BT0012	DQ198698	AF201419
		Clambidae	*Clambus*	JX412725	BMNH 840362	KF626105	EU797403
Staphyliniformia	Staphylinoidea	Staphylinidae	*Omalium*	JX412759	BMNH 844244	EF213819	JN619067
		Staphylinidae	*Oxypoda*	JX412751	BMNH 844246	KC132598	JN619024
		Staphylinidae	*Oxytelus*	JX412796	BMNH 844247	JX878729	JN619332
		Staphylinidae	*Habrocerus*	JX412795	BMNH 844248	KJ844961	AY745613
		Silphidae	*Necrophila*	GU176343	-	KJ845066	AY745606
	Hydrophiloidea	Hydrophilidae	*Amphiops*	JX412726	BMNH 838127	KJ845086	AM287129
	Histeroidea	Histeridae	*Abraeus*	JX313690	BMNH844242	KJ844924	AY028338
	Scarabaeoidea	Scarabaeidae	*Aphodius*	JX412729	BMNH 843252	EF656701	EF487600
		Glaresidae	*Glaresis*	JX412819	BMNH 843266	JN969219	JN969154
Bostrichiformia	Bostrichoidea	Bostrichidae	*Sinoxylon*	JX412742	BMNH 838164	DQ202653	AY748107
		Dermestidae	*Dermestes*	JX313683	BMNH 835562	EF213923	EF213893
Cucujiformia	Cucujoidea	Cucujidae	*Cucujus*	GU176341	-	AY310660	AF423767
		Erotylidae	*Tritoma*	HQ232822	-	DQ202652	AY748163
	Tenebrionoidea	Tenebrionidae	*Tribolium*	NC003081	-	HM156703	HM156711
		Scraptiidae	*Anaspis*	JX412814	BMNH 840490	DQ202632	AY748208
	Coccinelloidea	Cerylonidae	*Cerylon*	HQ232821	-	EU145661	EF209832

		Coccinellidae	*Coccinella*	JQ321839	-	DQ202668	AY748147
	Chrysomeloidea	Cerambycidae	*Stenurella*	JX220998	BMNH 704360	AJ841662	AJ841533
		Chrysomelidae	*Laccoptera*	JX412753	BMNH 838107	AJ841638	AJ841509
	Curculionoidea	Curculionidae	*Sitona*	JN163948	-	FJ867710	AF250087
		Curculionidae	*Larinus*	JN163952	-	HQ883541	AJ850013
Elateriformia	Dascilloidea	Dascillidae	*Dascillus*	JQ034414	-	AJ862777	AJ810748
	Buprestoidea	Buprestidae	*Agrilus*	JX412786	BMNH 833027	KM364165	KM364043
		Buprestidae	*Acmaeodera*	JX412781	BMNH 838158	KM364226	KM364099
		Buprestidae	*Anthaxia*	JX412831	BMNH 840209	KM364242	KM364110
		Buprestidae	*Perotis*	JX412762	BMNH 840447	KM364265	KM364128
		Buprestidae	*Chrysochroa*	EU826485	-	KM364261	KM364165
	Byrrhoidea	Byrrhidae	*Byrrhus*	JQ034419	-	DQ198705	AF427604
		Heteroceridae	*Heterocerus*	HQ232811	-	AJ862773	AF451928
		Eulichadidae	*Eulichas*	HQ232812	-	DQ198725	DQ100489
		Elmidae	*Limnius*	JX412747	BMNH 843148	DQ198712	AF451914
		Elmidae	*Elmis*	JX412821	BMNH 843150	AJ862764	AF451916
		Ptilodactylidae	*Ptilodactyla*	JX412727	BMNH 840214	AJ862776	AF451932
		Limnichidae	*Byrrhinus*	JX412827	BMNH 838097	DQ198719	AF451923
	Elateroidea	Artematopodidae	*Eurypogon*	JX412809	BMNH 842698	KF294769	KF294763
		Omethidae	*Drilonius*	JX412822	BMNH 840464	KF626126	KF625525
		Throscidae	*Trixagus*	JX412793	BMNH 840455	KF294772	KF294766
		Eucnemidae	*Fornax*	JX412858	BMNH 899821	DQ198729	DQ100492
		Lampyridae	*Pyrocoelia*	AF452048	-	DQ198759	AB298846
		Lampyridae	*Drilaster*	HQ232816	-	DQ198764	AB298853
		Cantharidae	*Chauliognathus*	FJ613418	-	HM156702	HM156710
		Cantharidae	*Cantharis*	HQ232817	-	KF626233	KF625631
		Iberobaeniidae	*Iberobaenia* sp.	KT339298	BMNH 1042541	n.a.	n.a.
		Iberobaeniidae	*Iberobaenia minuta*	KT339298	UPOL RK0790	KT339297	KT339296
		Lycidae	*Dictyoptera*	JX412733	BMNH 844238	KF626273	KF625687
		Lycidae	*Lycus*	HQ232814	-	DQ181113	DQ181039
		Phengodidae	*Mastinocerus*	JX412758	BMNH 900076	KF626313	KF625726
		Rhagophthalmidae	*Rhagophthalmus*	AB267275	-	n.a.	DQ100508

Omalisidae	*Omalisus*	JX412744	BMNH 840456	DQ198749	AF451948
Elateridae	*Drilus*	HQ232815	BMNH 840459	HQ333921	HQ333826
Elateridae	*Pyrophorus*	EF398270	-	HQ333848	HQ333753
Elateridae	*Agriotes*	JX412737	BMNH 842673	DQ198734	HQ333805
Elateridae	*Dicronychus*	JX412848	BMNH 844235	HQ333871	HQ333776

Table S2. Primers used for PCR amplifications* of the studied genes

Gene	Code	-mer	Sequence (5' >> 3')
18S rRNA	fragment A		
	18S 5'	24	GACAACCTGGTTGATCCTGCCAGT
		18S b5.0 19	TAACCGCAACAACTTTAAT
	fragment B		
	18S ai	22	CCTGAGAAACGGCTACCACATC
	18S b2.5	20	TCTTTGGCAAATGCTTTCGC
	fragment C		
	18S a1.0	20	GGTGAAATTCTTGGACCGTC
	18S bi	20	GAGTCTCGTTCGTTATCGGA
	fragment D		
	18S a2.0	19	ATGGTTGCAAAGCTGAAAC
	18S 3'I	24	CACCTACGGAAACCTTGTTACGAC
28S rRNA	28S ff	20	TTACACACTCCTTAGCGGAT
	28S dd	19	GGGACCCGTCTTGAAACAC
rrnL mtDNA			
	16a	20	CGCCTGTTTAACAAAAACAT
	16b	22	CCGGTCTGAACTCAGATCATGT
cox1 mtDNA			
	JerM	23	CAACAYYTATTTTGRTTYTTTGG
	Pat	25	TCCATTGCACTAATCTGCCATATTA
	Marilyn	21	TCATAAGTTCAGTATCATTG

* PCR was performed using 0.5-0.6 U Taq polymerase, 1 mM $MgCl_2$, 50 mM each dNTP, 0.2 mM primer, and typically 0.03 mg of template in 50 ml reaction volume. Cycle conditions were generally 2 min at 94^{o}C, 30-60 sec at 94^{o}C, 30-60 sec at 45-52^{o}C (depending on the melting temperatures of primer pairs used), 1-2 min at 72^{o}C (repeated for 30-40 cycles), and 10 min at 72^{o}C. ABI technology was used for DNA sequencing and sequences were edited using Sequencher 4.0.5 software (Gene Codes Corp.).

Supplementary Text. The list of beetle families proposed after 1950 with taxonomic authorities and the year of description given.

JURODIDAE Ponomarenko, 1985
CROWSONIELLIDAE Iablokoff-Khnzorian, 1983
TORRIDINCOLIDAE Steffan, 1964
MERUIDAE Spangler and Steiner, 2005
ASPIDYTIDAE Ribera, Beutel, Balke and Vogler, 2002
BELOHINIDAE Paulian, 1959
DIPHYLLOSTOMATIDAE Holloway, 1972
DECLINIIDAE Nikitsky, Lawrence, Kirejtshuk and Gratshev, 1994
LUTROCHIDAE Kasap and Crowson, 1975
RHINORHIPIDAE Lawrence, 1988
PLASTOCERIDAE Crowson, 1972
CHAETOSOMATIDAE Crowson, 1952
METAXINIDAE Kolibáč, 2004
PHYCOSECIDAE Crowson, 1952
MAURONISCIDAE Majer, 1995
BOGANIIDAE Sen Gupta and Crowson, 1966
PROTOCUCUJIDAE Crowson, 1954
HOBARTIIDAE Sen Gupta and Crowson, 1966
AGAPYTHIDAE Sen Gupta and Crowson, 1969
PRIASILPHIDAE Crowson, 1973
MYRABOLIIDAE Lawrence and Britton, 1991
CAVOGNATHIDAE Sen Gupta and Crowson, 1966
LAMINGTONIIDAE Sen Gupta and Crowson, 1969
PROPALTICIDAE Crowson, 1952
TASMOSALPINGIDAE Lawrence and Britton, 1991
MURMIDIIDAE Robertson et al., 2015
TEREDIDAE Robertson et al., 2015
EUXESTIDAE Robertson et al., 2015
ANAMORPHIDAE Robertson et al., 2015
EUPSILOBIIDAE Robertson et al., 2015
MYCETAEIDAE Robertson et al., 2015
CYCLAXYRIDAE Gimmel, Leschen and Ślipiński, 2009
AKALYPTOISCHIIDAE Lord, Hartley, Lawrence, McHugh and Miller, 2010
ARCHEOCRYPTICIDAE Kaszab, 1964
CHALCODRYIDAE Watt, 1974
CARIDAE Thompson, 1992

REFERENCES FOR AUTHORSHIP AND DATE OF PUBLICATION FOR FAMILIES DESCRIBED SINCE 1950

Crowson RA (1952) The classifcation of the families of British Coleoptera. The Entomologist's Monthly Magazine 88: 64–72, 109–132.

Crowson RA (1972) A review of the classification of Cantharoidea (Coleoptera), with the definition of two new families, Cneoglossidae and Omethidae. Revista de la Universidad de Madrid. Estudios de Entomologia 21 (82): 35–77.

Holloway BA (1972) Thee systematic position of the genus Diphyllostoma Fall (Coleoptera: Scarabaeoidea). New Zealand Journal of Science 15 (1): 31–38.

Crowson RA (1973) Further observations on Phloeostichidae and Cavognathidae, with definitions of new genera from Australia and New Zealand. The Coleopterists Bulletin 27 (2): 54–62.

Gimmel ML, Leschen RAB, Ślipiński SA (2009) Review of the New Zealand endemic family Cyclaxyridae, new family (Coleoptera: Polyphaga). Acta Entomologica Musei Nationalis Pragae 49 (2): 511–528.

Iablokoff-Khnzorian SM (1983) Notes sur la phylogénie des Cucujoidea et le classement géné- ral des coléoptères. Deutsche Entomologische Zeitschrift (Neue Folge) 30 (1/3): 45–68.

Kasap H, Crowson RA (1975) A comparative anatomical study of Elateriformia and Dascilloidea (Coleoptera). Transactions of the Royal Entomological Society of London 126: 441–495.

Kaszab Z (1964) Thee zoological results of Gy. Topál's collectings in South Argentina. 13. Coleoptera - Tenebrionidae. Annales Historico-Naturales Musei Nationalis Hungarici (Pars Zoologica) 56: 353–387.

Kolibáč J (2004) Metaxinidae fam. n., a new family of Cleroidea (Coleoptera). Entomologica Basiliensia 26: 239–268.

Lawrence JF (1988) Rhinorhipidae, a new beetle family from Australia, with comments on the phylogeny of the Elateriformia. Invertebrate Taxonomy 2 (1): 1–53.

Lawrence JF, Britton EB (1991) Coleoptera (beetles) [pp. 543–683]. The insects of Australia A textbook for students and research workers Second edition Volume II. Melbourne University Press, Melbourne, Australia, vi + 543–1137.

Lord NP, Hartley CS, Lawrence JV, McHugh MFW, Miller KB (2010) Phylogenetic analysis of the minute brown scavenger beetles (Coleoptera: Latridiidae), and recognition of a new beetle family, Akalyptoischiidae fam.n. (Coleoptera: Cucujoidea). Systematic Entomology 35 (4): 753–763.

Majer K (1995) A review of the classification of the Melyridae and related families (Coleoptera, Cleroidea). Entomologica Basiliensia 17 [1994]: 319–390.

Nikitsky NB, Lawrence JF, Kirejtshuk AG, Gratshev WG (1994) A new beetle family, Decliniidae fam. n., from the Russian Far East and its taxonomic relationships (Coleoptera Polyphaga). Novoe semeystvo zhestkokrylykh Decliniidae fam. n. s Dalnego Vostoka Rossii i ego taksonomicheskie sbyazi (Coleoptera Polyphaga). Russian Entomological Journal 2 (5/6): 3–10.

Paulian R (1959) Un nouveau Coléoptère scarabéide de Madagascar, type d'une nouvelle sous-famille. Le Naturaliste Malgache 10 [1958] (1/2): 39–46.

Ponomarenko AG (1969b) Cretaceous insects from Labrador. 4. A new family of beetles (Coleoptera: Archostemata). Psyche 76 (3): 306–310.

Ribera I, Beutel RG, Balke M, Vogler AP (2002) Discovery of Aspidytidae, a new family of aquatic Coleoptera. Proceedings of the Royal Society of London / Biological Sciences (Series B) 269 (1507): 2351–2356.

Robertson, JA, Slipinski, A, Moulton, M. Shockley, FW, Giorgi, A, Lord, NP, Mckenna, DD, Tomaszewska, W, Forrester, J, Miller, KB, Whiting, MF, Mchugh, JV (2015) Phylogeny and classification of Cucujoidea and the recognition of a new superfamily Coccinelloidea (Coleoptera: Cucujiformia). Systematic Entomology 40(4): 745-778.

Sen Gupta T, Crowson RA (1966) A new family of cucujoid beetles, based on six Australian and one New Zealand genera. The Annals and Magazine of Natural History (13) 9 (97/99):61–85.

Sen Gupta T, Crowson RA (1969b) Further observations on the family Boganiidae, with definition of two new families Cavognathidae and Phloeostichidae. Journal of Natural History 3 (4): 571–590.

Spangler PJ, Steiner WE, Jr. (2005) A new aquatic beetle family, Meruidae, from Venezuela (Coleoptera: Adephaga). Systematic Entomology 30 (3): 339–357.

Steffan AW (1964) Torridincolidae, coleopterorum nova familia e regione aethiopica. Entomologische Zeitschrift 74 (17): 193–200.

Thompson RT (1992) Observations on the morphology and classification of weevils (Coleoptera, Curculionoidea) with a key to major groups. Journal of Natural History 26 (4): 835–891.

Watt JC (1974) Chalcodryidae: a new family of heteromerous beetles (Coleoptera: Tenebrionoidea). Journal of the Royal Society of New Zealand 4 (1): 19–38.

Supplementary Text. The list of family-group names mentioned in the text with taxonomic authorities and the year of the description given

ELATERIDAE Leach, 1815
PLASTOCERIDAE Crowson, 1972
DRILINI Blanchard, 1845
OMALISIDAE Lacordaire, 1857
LYCIDAE Laporte, 1836
TELEGEUSINAE Leng, 1920
PHENGODIDAE LeConte, 1861
RHAGOPHTHALMIDAE Olivier, 1907
LAMPYRIDAE Rafinesque, 1815
OMETHIDAE LeConte, 1861
CANTHARIDAE Imhoff, 1856

REFERENCES FOR TAXONOMIC AUTHORITIES AND THE YEAR OF THE DESCRIPTION OF THE FAMILY-GROUP NAMES

Blanchard CÉ (1845a) Histoire naturelle des insectes leurs moeurs, leurs métamorphoses et leur classification ou traité élémentaire d'entomologie. Tome premier. F. Savy, Paris, v + 398 pp., pls. 1–10. Tome second. F. Savy, Paris, 524 pp., pls. 11–20.

Crowson RA (1972) A review of the classification of Cantharoidea (Coleoptera), with the definition of two new families, Cneoglossidae and Omethidae. Revista de la Universidad de Madrid. Estudios de Entomologia 21 (82): 35–77.

Lacordaire JT (1857) Histoire naturelle des insectes. Genera des Coléoptères ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes. Tome quatrième contenant les familles des buprestides, throscides, eucnémides, élatérides, cébrionides, cérophytides, rhipicérides, dascyllides, malacodermes, clérides, lyméxylones, cupésides, ptiniores, bostrichides et cissides. Librairie Encyclopédique de Roret, Paris, 579 pp.

Laporte [=Castelnau] FLNC, de (1836) Études entomologiques, ou descriptions d'insectes nouveaux et observations sur la synonymie [continued]. Revue Entomologique 4: 5–60, table.

Leach WE (1815) Entomology [pp. 57–172]. In: Brewster D (Ed). Brewster's Edinburgh Encyclopedia. Volume IX [part I]. W. Blackwood, J. Waugh, etc., Edinburgh, 764 pp.

LeConte JL (1861) Classification of the Coleoptera of North America. Part I. [pp. 1–208]. Smithsonian Miscellaneous Collections 3 (No. 136): xxiv + 214 pp.

Leng CW (1920) Catalogue of the Coleoptera of America, North of Mexico. John D. Sherman, Jr., Mount Vernon, New York, x + 470 pp.

Olivier E (1907) 53me fascicule. Coleoptera. Fam. Lampyridae. In: Wytsman PA (Ed) Genera Insectorum. Vol. VIII. Verteneuil & Desmet, Bruxelles, 74 pp. + 3 pls.

Rafinesque CS (1815) Analyse de la nature ou tableau de l'univers et des corps organisés. C. S. Rafinesque, Palermo, 224 pp.

Imhoff L (1856) Versuch einer Einführung in das Studium der Koleoptern. L. Imhoff ["auf Kosten des Verfassers"], Basel, xxxi + [2] + 118 + [2] + 272 + [25] pp. + 25 pls.

Supplementary text. Morphological descriptions of the genus *Iberobaenia* and species placed in the genus

Iberobaenia gen. nov.

Type species. *Iberobaenia minuta* sp. nov.

Differential diagnosis. The genus *Iberobaenia* is the only genus placed in Iberobaeniidae and it differs from other elateroid genera in the diagnostic characters used for the definition of the family Iberobaeniidae fam. nov. as described in the main text and supplementary materials.

Iberobaenia minuta sp. nov.

Type material. Holotype, male. SPAIN. Jaén, Sierra de la Pandera, Valdepeñas de Jaén, 9. Jun 2012, M. Baena leg. (UPOL). Paratypes, 2 males. The same locality data (UPOL, MBC).

Diagnosis. *Iberobaenia minuta* sp. nov. is very similar to *I. lencinai* in size and general appearance, however these species differ in the shape of the prosternum (more transverse in *I. lencinai* sp. nov.) and in the shape of male genitalia (Fig. 1B, E). *Iberobaenia lencinai* has more slender body (Figs 2A, S1A).

Description. Adult, male. Body very slender, 2.3–2.5 mm long, about 4.5 as long as wide at humeri, slightly dorso-ventrally flattened, but slightly more convex below, parallel-sided (Fig. 1); whole body weakly sclerotized, cuticle on elytra and abdomen very soft, flexible; dark brown to black, only tarsi and bases of trochanters testaceous. Surface mat, finely punctured, with sparse, long, decumbent vestiture.

Head small, slightly narrower than anterior margin of prothorax; slightly longer than wide behind eyes, apparently narrowed and prolonged anteriorly, cranium fully exposed from prothorax, hypognathous, with well developed but tiny mouthparts; without antennal sockets and any groove, surface of cranium mat, with fine microstructure. Tentorium vestigial, corpotentorial bridge absent. Eyes lateral, quite small, only slightly protuberant, more or less circular, eye diameter distinctly smaller than frontal interocular distance. Antennal insertions exposed, located frontally, antennal cavities rounded, separated by bridge about 0.6 width of maximum diameter of antennal cavity, Antennae with 11 antennomeres, round in cross section (Fig. 1A). Scape robust, parallel-sided, slightly asymmetrical; pedicel almost parallel-sided, cylindrical, robust, its length about half of antennomere 3, rounded apically; antennomere 3 cup-shaped, shorter than pedicel, narrowly attached to preceding antennomere, gradually widened to apex; antennomere 4 twice longer than antennomere 3, slender at base, gradually widened to basal fourth then almost parallel-sided, cylindrical; antennomeres 5–9 sub-equal, gradually shortened, the basal part always slender, forming short, slender tube at base of subterminal antennomeres (Fig. 2A), terminal antennomere oval, 1.7 times longer than antennomere 10, with similar slender basal part as preceding antennomeres. All antennomeres with moderately dense, erect pubescence. Fronto-clypeal suture absent; anterior edge of frontoclypeus concave, mouth cavity rounded with slightly longer fronto-posterior axis, labrum plate-shaped, without any internal processes, transverse, fully sclerotized, widely rounded apically, without any long setae, only short sparse pubescence present at frontal margin, hypopharynx long, relatively slender, well sclerotized, without any lateral processes, with robust sclerotized suboesophaginal ring. Mandibles slender apically, robust at base, slightly curved; incisor edge simple, without any teeth. Maxilla with reduced cardo and stipes, galea and lacinia absent, palpifer transverse, vestigial; maxillary palpi four-segmented, palpomere 1 transverse, palpomere 2 long, apical palpomere short, with slender apical process (Fig. S1C). Labium small, short and wide, reduced to double-ring in which palpi are attached, without ligula, no setae present in apical part of mentum, labial palpi tiny, two-segmented, apical palpomere slender, pointed at apex.

Prothorax about as wide as elytra in humeral part, flat, pronotum width 1.16–1.18 times length, pronotal disc flat, without any carinae forming pronotal areolae or longitudinal keel; disc mat, finely structured, with more apparent punctures at frontal and posterior corners (Fig. 1C). Anterior margin of prothorax widely concave, anterior angles unapparent, posterior angles well marked, obtuse; posterior edge simple, widely convex, lateral margins rounded. Prosternum projected before anterior margin of pronotum (visible in lateral view), relatively robust, about 0.3 times long transverse, pentagonal, with flat, rather short and widely rounded prosternal process, two slender internal processes present subapically at posterior part of prosternum (Fig. 1B), these processes directed upwards. Procoxal cavities widely open, prothoracic trochantins triangular in general shape, plate-like, well-sclerotized, with slender process attached to coxae, prothoracic trochantins bare, without any setae. Scutellum flat, small, parallel-sided, shallowly emarginate apically, sparsely pubescent. Mesoventrite flat, slightly wider than long, transverse, frontal margin straight, weakly sclerotized, with very short longitudinal keel in posterior part, disc mat, finely structured, with punctures at frontal and posterior corners, coxae attached in deep excavations laterally; mesotrochantins slender, small, only slightly curved, without any setae, attached to mesothoracic costae in middle of frontal coxal margin (Fig. 1B) with longitudinal keel. Metaventrite long, large, with longitudinal keel reaching approximately to mid of mesothoracic coxae, slender pleural parts connected to metaventrite with membrane, sparse setae present only in posterior two thirds of metaventrite (Fig. 1B). Metendosternite reduced, small, with simple, slender stalk, lateral arms absent (Figs 1B, S1E). Elytra only weakly sclerotized, sometimes shorter than abdomen, very slender, tapering to apex, without pleurae, flat (Fig. S1D), no longitudinal elytral costae present, some punctures at humeri arranged in lines (apparent when elytron observed at angle); apexes separately rounded, dark colored (Fig. S1D). Hind winds fully developed, relatively wide, about 2.3 times longer than wide in widest part, slightly surpassing apex of elytra even when folded (Figs 1A, S1A), apical field of the hind wing about one third of wing length, praecosta, costa and subcosta merged, very short, reaching less than one third of length of frontal margin, most of frontal margin strengthened by radia running from wing base to two third of wing length, radial cell vestigial, open due to absence of cross vein r_3 closing radial cell in related families, vestiges of radial cell present, but much weaker than radia RA, cross vein r_4 absent, wide triangular area between RA and MP_{1+2} membranous, without any clear strengthening structures, RP vestigial, extremely short, R-M loop vestigial, very slender and short; only MP3 and MP4 present, unconnected with MP_{1+2}, only single cubital vein merged at base with median vein complex, basal part of hind wing narrow, anal lobe absent, as well as anal and cubital veins; apical part of wing without distinct veins, even transverse or oblique linear sclerites absent, only pigmented oblique patch present in apical part of hind wing (Fig. S1G).

Legs slender, very weakly compressed (Fig. 1B). Coxae separated, located in open prothoracic cavities, all coxae only slightly elongate, robust; trochanters slender, obliquely attached to femora, femora robust, about three times longer than wide in middle part, with membranous area reaching deeply in femur, in case of hind coxae membrane reaching almost mid of coxal length; tibiae slender basally, widest at apex, slightly compressed, densely pubescent especially in apical part, with pair of spines apically, tarsi with five tarsomeres in all legs, tarsomeres 1–4 subequal, only tarsomere 4 with pulvilla, tarsomere 5 slender, long (Fig. 1B); claws simple.

Abdomen with eight visible, very weakly sclerotized sclerites, all sclerites small, none of them connate, all free and connected with extensive non-pigmented membranes, basal ventrite partly membranous in middle part, without any intercoxal process or longitudinal carinae, terminal male ventrite very narrow, with long, well sclerotized lateral rods, these merge in Y-shaped structure in apical fifth, terminal tergite partly membranous, with long sparse setae, subapical tergite with very slender lateral rods attached to basal part of terminal sternite, apical margin v-shaped, short median longitudinal keel present at anterior margin (Figs 1D, S1F). Male genitalia symmetrical, trilobate type, with relatively short phallobase, its length less than one third of male genitalia length, phallobase plate-like, v-shaped, without bent margins, only with inconspicuous longitudinal keel; parameres relatively long (Figs 1E, S1B); firmly connected with basal part of phallus, widest at basal two fifths, apices of parameres simple, without any thorns or membranous parts; phallus slender, fully sclerotized, very wide, triangular at base, parallel-sided in most of its length, gradually widened in apical fifth and widely rounded apically, widely open in apical third of its length; internal sac inconspicuous, membranous.

Measurements. Body length 2.3–2.5 mm, width at humeri 0.5 mm, width of pronotum 0.47–0.50 mm, length of pronotum 0.40–0.43 mm, frontal eye distance 0.26–0.27 mm, maximum eye diameter 0.12–0.13 mm, length of phallus 0.78 mm.

Adult, female. Unknown.

Iberobaenia lencinai **sp. nov.**

Material studied. Holotype, male. SPAIN, Molina de Segura (MU), pitfall trap TC VB 03/1, El Rellano P. E. "Vicente Blanes", 15. Apr – 1. Jun 2009, J. L. Lencina leg. Paratypes. male, E. Molina de Segura (MU), TC VB 06/2, El Rellano P. E. "Vicente Blanes", 15. Apr – 1. Jun 2009, J. L. Lencina leg.; male, E. Jumilla (MU), Sierra del Carche, TIV C2-, 15. – 30. Jun 2007, Lencina & Gallego leg.; male, Jumilla (MU), Sierra del Carche, TC C5 38°25'N, 1°19'W, 1278 m, 2. Apr. – 25. Jun 2011, J. L. Lencina leg.; male, E. Jumilla (MU), Diapiro de la Rosa, TC DR1, 29. Apr – 18. Jun 2010, J. L. Lencina leg.; 3 males, E. Jumilla (MU), Diapiro de la Rosa, TC DR3, 29. Apr – 18. Jun 2010, J. L. Lencina leg. (JLC, UPOL, A. Allen Collection).

Diagnosis. *Iberobaenia lencinai* sp. nov. differs from *I. minuta* sp. nov. in a smaller body, more transverse pronotum (Fig. S1A) and prosternum, and in the shape of male genitalia (Fig. S1B).

Description. Adult, male. Body very slender, 6.4 times longer than wide at humeri, 1.9–2.3 mm long, elytra slender, weakly dorso-ventrally flattened, parallel-sided (Fig. S1A); dark brown to black, tarsi lighter. Surface finely punctured, with sparse, moderately long vestiture. Head small, prolonged anteriorly, slightly narrower than prothorax. Eyes small; antennomeres as in Fig. S1A; mandibles slender, slightly curved; maxillary palpi four-segmented; labial palpi tiny, two-segmented. Pronotum flat, 1.26–1.28 times as wide as long (Fig. S1A). Prosternum transverse, with very short and widely rounded prosternal process bearing two upward directed internal processes in posterior part. Scutellum small, shallowly emarginate apically. Elytra weakly sclerotized, very slender, tapering to apex (Fig. S1A). Legs slender; coxae slightly elongate; trochanters slender, obliquely attached to femora; femora robust; tibiae with pair of spines apically; tarsomeres 1–4 robust, subequal, tarsomere 4 with pulvilla, tarsomere 5 slender, longest; claws simple. Abdomen long, slender. Male genitalia with long phallus, slender, gradually slightly widened apically; parameres long, with sharp apices; phallobase plate-like, v-shaped (Fig. S1B).

Remark. The characters not mentioned in the description above are the same in both species of *Iberobaenia* available in adults.

Etymology. The species name is a patronym in honor of the collector of the type series, J. L. Lencina (Murcia, Spain).

Measurements. Body length 1.9–2.3 mm, width at humeri 0.4 mm, width of pronotum 0.37–0.43 mm, length of pronotum 0.29–0.34 mm, frontal eye distance 0.19–0.23 mm, maximum eye diameter 0.10–0.11 mm, length of phallus 0.56 mm.

Iberobaenia sp.

Material studied. Larvae. Spain, Voucher BMNH 1042563, Camino Viejo a la Ermita, Cabra, Sierra de Cabra, Córdoba (SP), 37.481117N, 4.388536W, 970 m, 6. Dec. 2012, grassland, C. Andújar & P. Arribas leg.; Spain, Voucher BMNH 1042541: Ermita Nta. Sra. de la Sierra, Cabra, Sierra de Cabra, Córdoba (SP), 37.490527N, 4.381292W, 1145 m, 6. Dec. 2012, *Pinus halepensis* forest, C. Andújar & P. Arribas leg. (BMNH).

Diagnosis. Body cylindrical (Figs 3K–L), lateral part of cranium fully sclerotized, stemmata absent, antennae 2-segmented (Fig. 3M), apical antennomere membranous apically, with finger-like dorsal sclerotized peg, mandibles robust, triangular in shape and in opposite position; tergites without processes, terminal abdominal segment widely rounded with deep narrow notch apically. The net-winged beetle larvae share with *Iberobaenia* the unique shape of the terminal antennomere, but differ in the split mandibles which are not able to chew and are used for sucking in an open position. Additionally, all Lycidae have at least short fixed urogomphi (Bocak & Matsuda 2003).

Description. Larva. Body campodeiform, cylindrical, sub-parallel in whole length, weakly sclerotized; sclerites large, intersegmental and pleural membranes reduced.

Head prognathous, wide, relatively large, only partly retracted into pronotum; dorso-ventrally flattened, transverse. Stemmata absent. Frons, clypeus and labrum fused; sutures absent. Lateral part of cranium fully sclerotized. Antennae 2-segmented, with large basal articulatory membrane, fully exposed, antennomere 1 strongly transverse, ring-like, simple in shape; antennomere 2 cylindrical, with membranous apex; sclerotized part with dorsal peg (Fig. 1H). Mandibles robust, falciform, triangular in shape, without mola; bases distant and mandibles able to bite; with sucking groove. Mouthparts very tiny, forming maxillolabial complex, without lateral movability of maxilla. Maxillae with 3-segmented slender and short palpi. Labium reduced, consisting from single sclerite and bearing 2-segmented labial palpi, ligula absent.

Thorax cylindrical with slightly convex tergum. General shape of all thoracic segments similar, parallel-sided, prothorax more sclerotized and slightly wider than meso-, metathorax and abdominal segments. Thoracic terga consisting of one large undivided plate; prosternum triangular, well-developed, meso and metasternum smaller, weakly sclerotized and pigmented. Lateral portions of thoracic segments with unclear, weakly sclerotized sclerites, Legs 5-segmented, fairly short and robust, coxa ring-like large, femora and tibiae fairly short; pretarsus simple, slender (Fig. 1F).

Abdomen 10-segmented, with uniform segments 1–8. Tergites consisting of single median plate, all sclerites weakly sclerotized, without any processes, bearing only long setae; segment 9 widely rounded at apex, with deep notch at apex; segment 10 forms short pygopodium (Fig. 1G).

Supplementary Text. An overview of the synapomorphies of Elateroidea and the shared characters of the cantharoid clade (both as identified by Lawrence *et al.* 2011) and the diagnostic characters of the clade Iberobaeniidae + Lycidae and of the family Iberobaeniidae fam. nov.

The diagnostic characters of the superfamily Elateroidea, which were identified in Iberobaeniidae:

1. Adult corpotentorial bridge incomplete or absent
2. The apical field of the hind wing without distinct veins, only with transverse patches which are not obvious veinal remnants (Fig. S1G).
3. Larval labral tormae absent.
4. Larval maxillolabial complex present (Fig. 1H).
5. Larval stipes more than 2 times as long as wide.
6. Larval maxillary articulating area absent.
7. Larval oral cavity blocked (evolved due to liquid feeding) (Fig. 1H).
8. Larval tentorial bridge absent.

***The diagnostic characters shared by Iberobaeniidae and other soft-bodied Elateroidea as defined by Lawrence* et al. *2011* (i.e. a grouping corresponding with the historical concept of Cantharoidea; these lineages represent a polyphyletic assemblage according to all recent DNA-based studies):**

1. Adult procoxal cavities reduced (Fig. 2B).

2. Lateral portion of the adult prosternum in the front of the procoxal cavity or procoxal base less than 0.5 times as long as mid length of the cavity or coxal base at that point (Fig. 2B).

3. Anterior edge of the adult scutellar shield not or only slightly or gradually elevated (Fig. 2A).

4. Adult mesotrochantin glabrous (Fig. 2B).

5. Adult mesocoxal cavities secondarily reduced, not or only barely impressed (Fig. 2B).

6. Adult mesoventral and metaventral processes distinctly separated from one another or absent (Fig. 2B).

7. The anterior process of the metendosternite at least as long as wide (Figs 2B).

8. Eight male abdominal ventrites (sternites 2–9).

9. Male sternite 8 ventrally not concealed by sternite 7.

Note. The morphological diagnostic characters referring to females cannot be evaluated as female of *Iberobaenia* remains unknown.

Unique characters shared by the clade Lycidae + Iberobainiidae and characters discriminating these families

	Iberobaeniidae	Lycidae
ADULT		
Adult antennae	filiform	compressed, serrate
Adult trochanters with femoral attachment	strongly oblique (Fig. 1B)	moderately oblique
Lateral margin of the pronotum	rounded, with inconspicuous edge	with sharp edge
Terminal sternite	compact, spoon-like	with sclerotized rods (Fig. 1D)
LARVA		
Larval antennae	2-segmented (Fig. 1H)	2-segmented
Fingers-shaped terminal process of the larval antennomere 2	present	present or modified in multi-process type in Lyropaeinae
Larval mandibles	compact (Fig. 1H)	each mandible split in two blades
Larval mandibles	in opposite position, able to bite (Fig. 1H)	divergent, unable to bite
Cranium (larvae)	compact	laterally with membrane

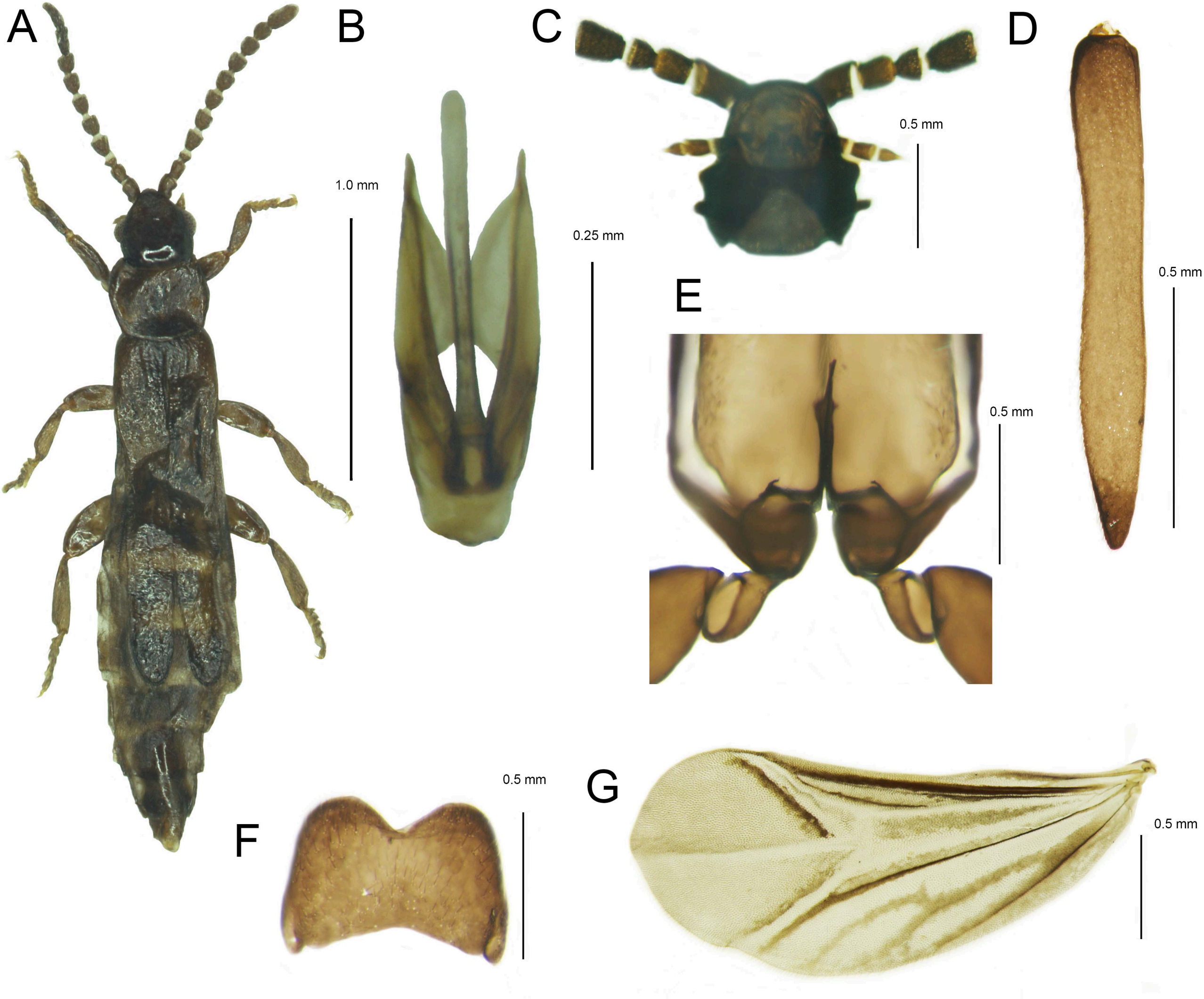


Figure S1. Morphology of *Iberobaenia lencinai* sp. nov. A–general appearance, B–male genitalia. *Iberobaenia minuta* sp. nov. C–head ventrally, D–elytron, E–metafurca and coxae, F–abdominal sternum, G–wing.

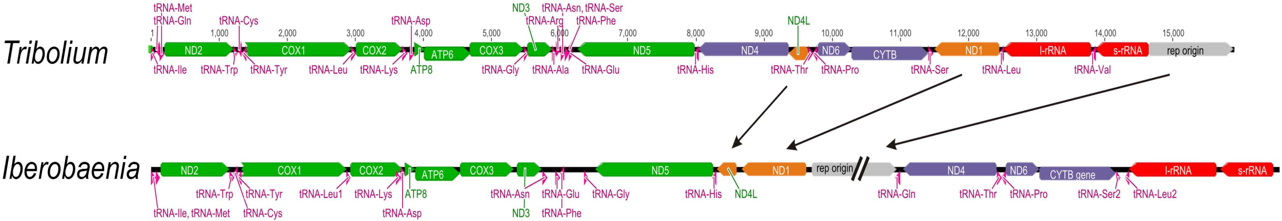


Figure S2. Structure of the mitochondrial genome of *Iberobaenia* sp. and *Tribolium castaneum* (from Andújar et al. submitted).

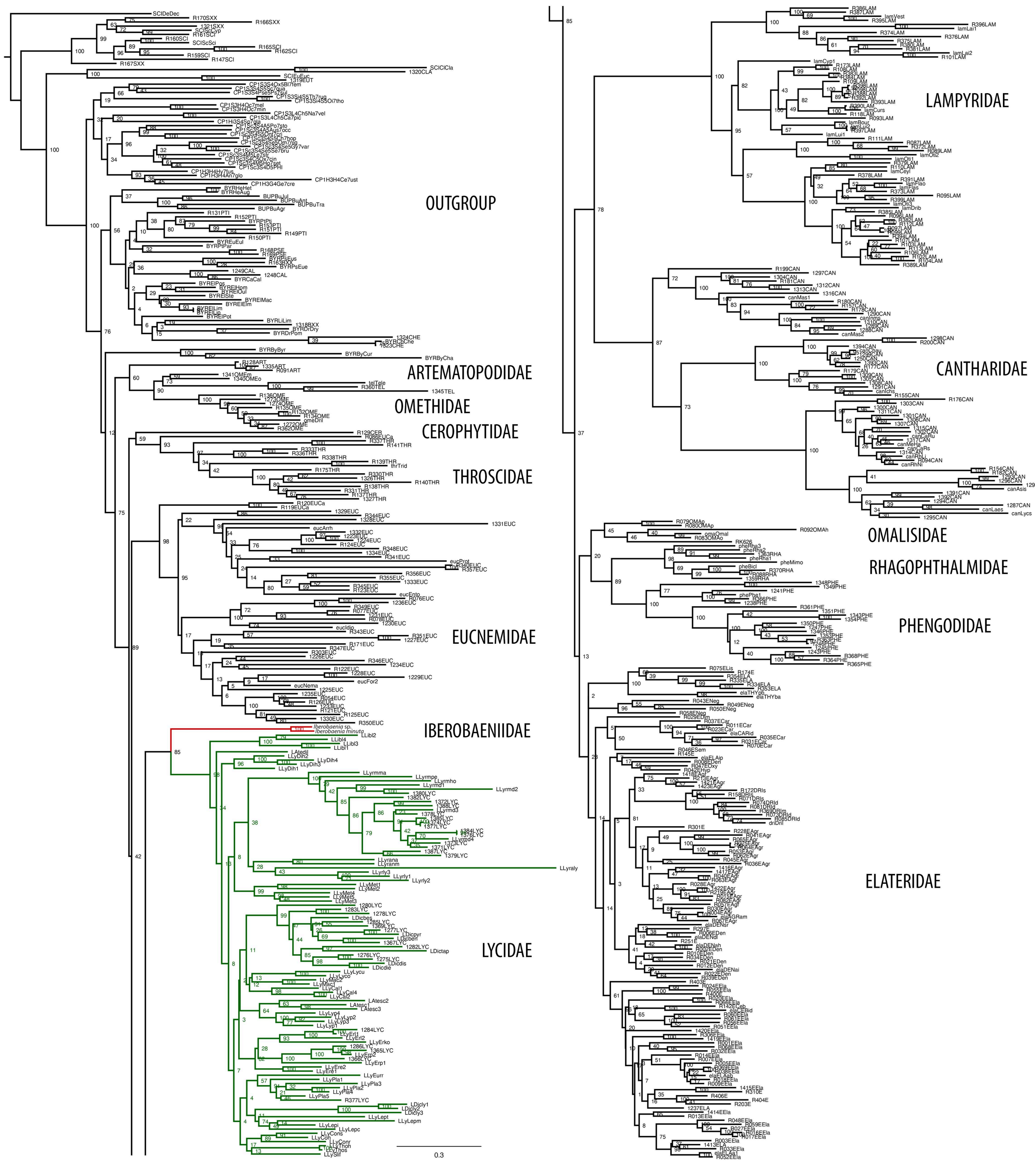


Figure S3 Phylogenetic hypothesis of Elateroidea inferred from the four-gene BlastAlign dataset using the maximum likelihood optimality criterion. Iberobaeniidae represented by *I. minuta* (adult, *LSU*, *SSU* rRNA, cox1 mtDNA) and *Iberobaenia* sp. (larva, *rrnL* and *cox1* mtDNA).

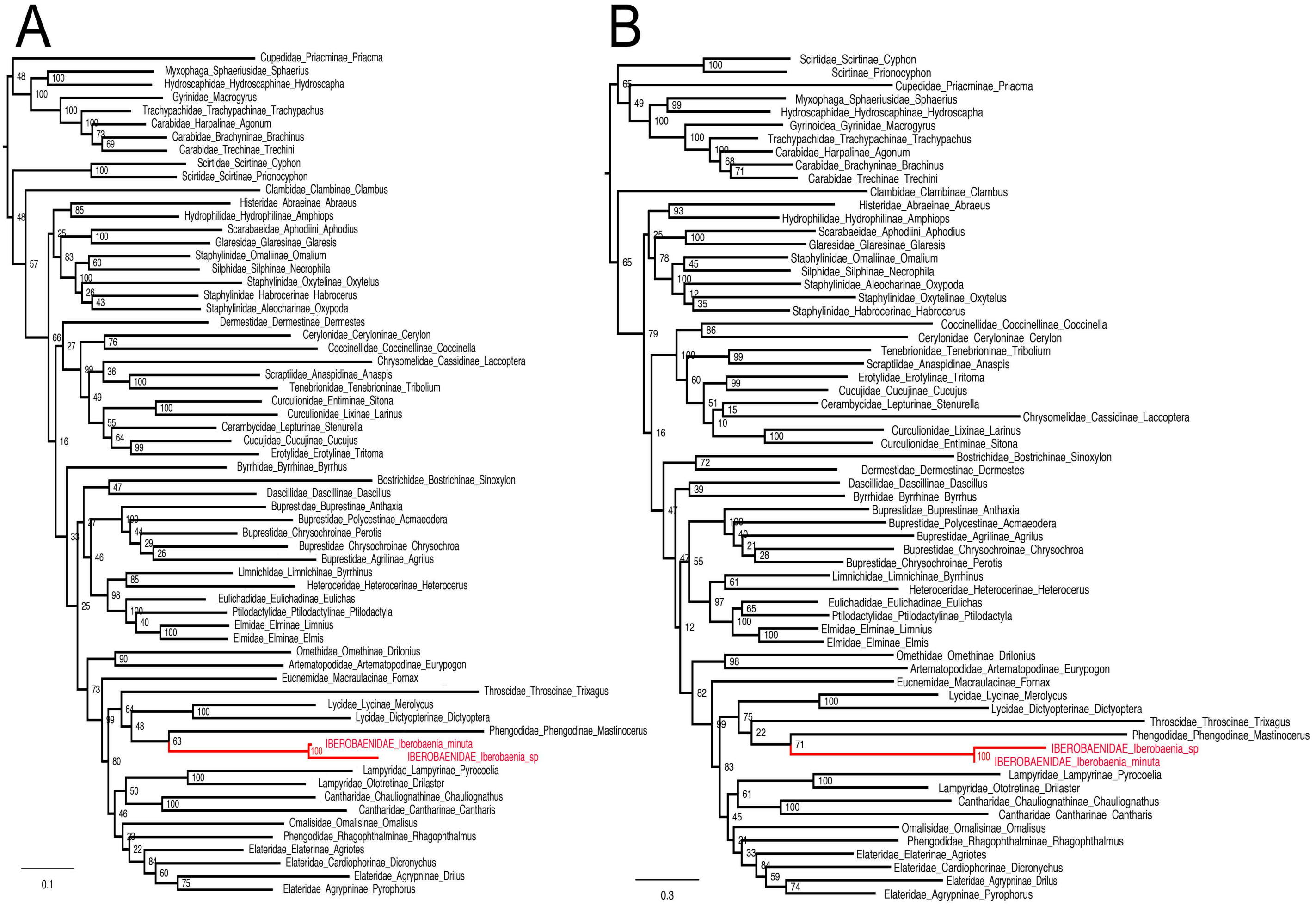


Figure S4. Phylogenetic hypothesis of Elateroidea inferred from the LSU, SSU and 13 mtDNA protein coding gene dataset using the maximum likelihood optimality criterion. (A) 3 partitions, (B) 38 partitions. The topology inferred from analyses set to 3, 8 and 15 partitions were similar. For partition details see Methods.

Příloha 3

Kundrata, R., Jäch, M.A. & Bocák, L. (2017) Molecular phylogeny of the Byrrhoidea-Buprestoidea complex (Coleoptera, Elateriformia). *Zoologica Scripta*, 46: 150–164.
[IF 3,057; 6 citací na WoS; celkem 7 citací bez autorových autocitací]
[korespondující autor; autorský podíl: 40 %]

Zoologica Scripta

Molecular phylogeny of the Byrrhoidea–Buprestoidea complex (Coleoptera, Elateriformia)

Robin Kundrata, Manfred A. Jäch & Ladislav Bocak

Submitted: 22 February 2016
Accepted: 26 May 2016
doi:10.1111/zsc.12196

Kundrata, R., Jäch, M. A. & Bocak, L. (2016). Molecular phylogeny of the Byrrhoidea–Buprestoidea complex (Coleoptera, Elateriformia). — *Zoologica Scripta*, *46*, 150–164.

The superfamilies of Elateriformia have been in a state of flux since their establishment. The recent classifications recognize Dascilloidea, Buprestoidea, Byrrhoidea and Elateroidea. The most problematic part of the elateriform phylogeny is the monophyly of Byrrhoidea and the relationships of its families. To investigate these issues, we merged more than 500 newly produced sequences of 18S rRNA, 28S rRNA, *rrnL* mtDNA and *cox1* mtDNA for 140 elateriform taxa with data from GenBank. We assembled an all-taxa (488 terminals) and a pruned data set, which included taxa with full fragment representation (251 terminals); both were aligned in various programs and analysed using maximum-likelihood criterion and Bayesian inference. Most analyses recovered monophyletic superfamilies and broadly similar relationships; however, we obtained limited statistical support for the backbone of trees. Dascilloidea were sister to the remaining Elateriformia, and Elateroidea were sister to the clade of byrrhoid lineages including Buprestoidea. This clade mostly consisted of four major lineages, that is (i) Byrrhidae, (ii) Dryopidae + Lutrochidae, (iii) Buprestoidea (Schizopodidae sister to Buprestidae) and (iv) a clade formed by the remaining byrrhoid families. Buprestoidea and byrrhoid lineages, with the exception of Byrrhidae and Dryopidae + Lutrochidae, were usually merged into a single clade. Most byrrhoid families were recovered as monophyletic. Callirhipidae and Eulichadidae formed independent terminal lineages within the Byrrhoidea–Buprestoidea clade. Paraphyletic Limnichidae were found in a clade with Heteroceridae and often also with Chelonariidae. Psephenidae, represented by Eubriinae and Eubrianacinae, never formed a monophylum. Ptilodactylidae were monophyletic only when *Paralichas* (Cladotominae) was excluded. Elmidae regularly formed a clade with a bulk of Ptilodactylidae; however, elmid subfamilies (Elminae and Larainae) were not recovered. Despite the densest sampling of Byrrhoidea diversity up to date, the results are not statistically supported and resolved only a limited number of relationships. Furthermore, questions arose which should be considered in the future studies on byrrhoid phylogeny.

Corresponding author: *Robin Kundrata, Department of Zoology, Faculty of Science, Palacky University, 17. listopadu 50, 779 00 Olomouc, Czech Republic. E-mail: robin.kundrata@upol.cz*
Robin Kundrata, Department of Zoology, Faculty of Science, Palacky University, 17. listopadu 50, 779 00 Olomouc, Czech Republic. E-mail: robin.kundrata@upol.cz
Manfred A. Jäch, Naturhistorisches Museum Wien, Burgring 7, A-1010 Wien, Austria. E-mail: manfred.jaech@nhm-wien.ac.at
Ladislav Bocak, Department of Zoology, Faculty of Science, Palacky University, 17. listopadu 50, 779 00 Olomouc, Czech Republic. E-mail: ladislav.bocak@upol.cz

Introduction

The series Elateriformia contains over 42 500 species placed within 34 families and represents more than 10% of beetle diversity (Beutel & Leschen 2005; Bocak *et al.* 2014; Table S1). The limits of this series stabilized when scirtoid lineages were excluded (Hunt *et al.* 2007; Lawrence *et al.* 2011) and several DNA-based studies convincingly demonstrated the monophyly of the current concept of Elateriformia consisting of Dascilloidea, Buprestoidea, Byrrhoidea and Elateroidea (Bocakova *et al.* 2007; Kundrata & Bocak 2011; Kundrata *et al.* 2014; McKenna *et al.* 2015). At present, the weakest part of the elateriform phylogeny is the monophyly of Byrrhoidea and the relationships of families as they are currently delimited (Beutel & Leschen 2005). In contrast with other elateriform superfamilies, current Byrrhoidea remain poorly studied and they were previously only included in whole-order phylogenies (Hunt *et al.* 2007; Bocak *et al.* 2014; McKenna *et al.* 2015) and as an outgroup in analyses of related elateriform lineages (Kundrata *et al.* 2014). Only a single analysis, based on a limited number of the mitochondrial genomes, focused on Byrrhoidea (Timmermans & Vogler 2012). The acute problem of all previous studies of byrrhoid and buprestoid lineages was the inclusion of a low number of taxa with high fragment representation in analyses (33 spp., Bocakova *et al.* 2007; 18 spp., Hunt *et al.* 2007; 16 spp., Timmermans & Vogler 2012; 22 spp., McKenna *et al.* 2015).

The latest formal classifications follow the wide concept of Byrrhoidea (Lawrence & Newton 1995; Beutel & Leschen 2005), but the support for monophyly remains contentious and the constituent families have been variously grouped in earlier studies (Fig. 1, Table S2). Crowson (1955, 1960) split the byrrhoid families into three lineages represented by Byrrhoidea, Dryopoidea and Rhipiceroidea. Later, Rhipiceroidea were dissolved by the transfer of Rhipiceridae to Dascilloidea (Crowson 1971) and Callirhipidae to the newly introduced Artematopoidea (Crowson 1973). Lawrence (1988) merged byrrhoid families and Buprestoidea into the widely defined Byrrhoidea (incl. Buprestidae and a part of Dryopoidea) and along with these he proposed Psephenoidea (= another part of Dryopoidea). Lawrence & Newton (1995) established the current wide concept of Byrrhoidea (incl. Dryopoidea) and the independent Buprestoidea. However, a recent morphological phylogenetic analysis provided no support for such an arrangement (Lawrence *et al.* 2011). Morphology of the byrrhoid lineages is very diverse (Fig. 2C–J) and some characters might be affected by similar life history strategies in putatively unrelated lineages, eventually by miniaturization (Grebennikov & Beutel 2002).

Recent morphological and molecular phylogenetic analyses found the byrrhoid families to be either a monophyletic or a paraphyletic assemblage in a close relationship to Elateroidea (Beutel 1995; Lawrence *et al.* 1995, 2011; Bocak *et al.* 2014; Kundrata *et al.* 2014; McKenna *et al.* 2015; Timmermans *et al.* 2016) and confirmed close affinities between byrrhoids and Buprestoidea, but without their reciprocal monophyly being demonstrated. Buprestidae were recovered either as a sister group or as a terminal lineage within Byrrhoidea (Crowson 1982; Lawrence 1988; Costa *et al.* 1999; Bocakova *et al.* 2007; Lawrence *et al.* 2011; Timmermans & Vogler 2012; Bocak *et al.* 2014; Kundrata *et al.* 2014; McKenna *et al.* 2015). The monophyly of current Byrrhoidea (i.e. Byrrhidae + Dryopoidea) and/or Dryopoidea was seriously questioned (e.g. Lawrence 1988; Timmermans & Vogler 2012).

Fourteen families are included in the latest concept of Byrrhoidea (Beutel & Leschen 2005; Jäch *et al.* 2016). This group contains various ecologically specialized terrestrial, riparian and aquatic lineages. Among the predominantly aquatic ones, there are true water beetles (Elmidae) and false water beetles (Eulichadidae, Psephenidae) (Jäch 1998; Beutel & Leschen 2005). The diversity of life strategies and miniaturization are factors, which affect morphological evolution, and therefore, molecular data are used here to provide an insight into the evolution of these lineages.

We present the most extensive four-marker DNA data set for byrrhoid lineages with over 500 new sequences compiled with data available from Genbank (e.g. F. Čiampor & I. Ribera, unpublished data; Bocakova *et al.* 2007; Kundrata *et al.* 2014). This data set represents 210 byrrhoid taxa, that is about 5.5% of the superfamily's species diversity. The aims of this study are (i) to investigate the phylogenetic position of the byrrhoid–buprestoid complex within Elateriformia, (ii) to study internal relationships within the byrrhoid–buprestoid clade, c) to test monophyly of the families and (iii) to assess the suitability of commonly used genes to resolve the Byrrhoidea phylogeny.

Materials and methods

Taxon sampling and laboratory procedures

The previously published data were expanded by 140 specimens belonging to Byrrhoidea (99 spec.) and the outgroup lineages (Scirtoidea, five spec., Dascilloidea, three spec., Buprestoidea, 33 spec.; Table S3). Specimens were fixed in 96% alcohol and subsequently stored in −20°C. Whole-genomic DNA was extracted using Wizard SV96 Purification System kit (Promega Corp., Madison, WI, USA) following standard protocols. The voucher specimens are deposited in the collection of the Laboratory of Molecular Systematics, UP Olomouc (Table S3). The PCR and cycle sequencing conditions followed Bocakova *et al.* (2007) and Kundrata & Bocak (2011); the details are listed in Table S4. Four molecular markers were amplified: 18S rRNA (~1830 bp; 139 terminals), the D2 loop of 28S rRNA (~640 bp; 125 terminals) and the fragments of *rrnL* (~520 bp; 115 terminals) and *cox1-3′* mtDNA (723 bp; 136 terminals). PCR products were purified using PCRμ96 plates (Millipore Corp., Bedford, MA, USA) and sequenced by the ABI 3130 Genetic Analyzer using Big Dye Terminator 1.1 Cycle Sequencing kit. GenBank accession numbers of the newly produced sequences are listed in Table S3.

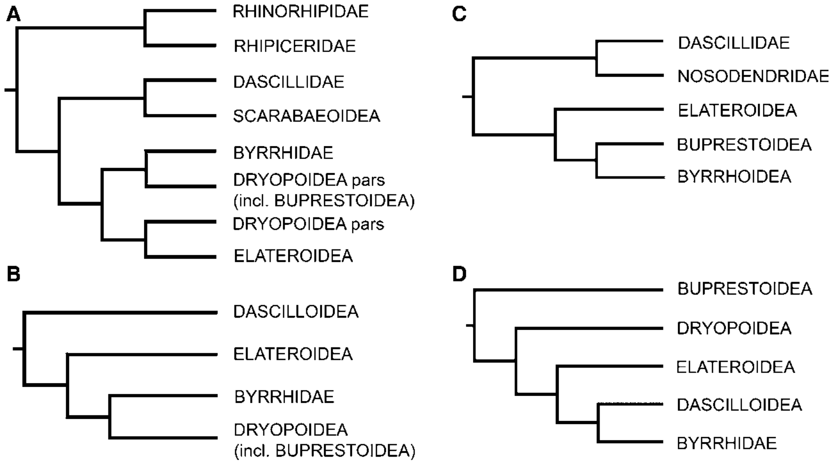


Fig. 1 Overview of the previous hypotheses on the Elateriformia phylogeny. —A. Lawrence *et al.* (2011): analysis of morphological characters; —B. Bocak *et al.* (2014): analysis of combined rRNA and mtDNA; —C. McKenna *et al.* (2015): analysis of combined rRNA and NPC genes; —D. Timmermans *et al.* (2016): analysis of mitochondrial genomes.

Data set assembling and alignment methods

Sequences were edited using GENEIOUS 7.1.7 (Biomatters Ltd.; www.geneious.com). We merged newly produced data with the Elateriformia sequences deposited in GenBank (Table S3; F. Čiampor & I. Ribera, unpublished; Bocakova *et al.* 2007; Hunt *et al.* 2007; Bocak *et al.* 2008, 2016; King *et al.* 2011; Kundrata & Bocak 2011; Kundrata *et al.* 2014; Evans *et al.* 2015). The data set included Byrrhoidea (11 of 14 extant families, 210 specimens) and representatives of other Elateriformia (Dascilloidea: two families, seven specimens; Elateroidea: 13 families, 160 specimens; Buprestoidea: two families, 89 specimens; Table S3). The Scirtoidea (four families, 22 terminals) represents non-elateriform outgroup (Hunt *et al.* 2007; Bocak *et al.* 2014). We assembled the all-taxa data set containing terminals for which at least two markers were available (except *Emmita serricornis* (Escalera, 1913) for which only *cox1* mtDNA was available; 488 specimens) and the pruned data set with terminals represented by all four fragments (except several taxonomically important lineages, which were kept despite incomplete marker representation: e.g. Dascillidae: *Emmita* Escalera, Schizopodidae, some Byrrhidae, *Lutrochus* Erichson, *Ceradryops* Hinton, Limnichidae: *Cephalobyrrhus* Pic, some Psephenidae: Eubriinae; 251 specimens, Table S3).

Length invariable protein-coding *cox1* sequences were aligned by Mafft 7.157 (default parameters; Katoh *et al.* 2002; Katoh & Standley 2013) and checked by amino acid translation. Length variable sequences were aligned separately using MAFFT and MUSCLE 3.7 (Edgar 2004) under the default parameters. Alignments were manually edited where apparent misalignments were observed. Pruned data sets were aligned using BLASTALIGN 1.2 (Belshaw & Katzourakis 2005), which omits parts of the length variable regions when reliable alignment cannot be inferred. The edited Mafft alignment omitting all positions with indels was analysed to test the impact of the alignment methods on topology. Alternatively, we aligned 18S, 28S and *rrnL* sequences using the MAFFT Q-INS-I algorithm considering the RNA secondary structure (Katoh & Toh 2008). The impact of the variable 3rd codon position in the *cox1* fragment was tested by the analysis of a 1st and 2nd position data set. The distant position of the psephenid subfamilies Eubriinae and Eubrianacinae was tested using the 236-taxa data set aligned by Mafft. In this analysis, sister groups to both Eubriinae and Eubrianacinae identified by previous analyses were removed (Eulichadidae, seven taxa; Callirhipidae, six taxa; Ptilodactylidae: *Paralichas pectinatus* (Kiesenwetter, 1874) and Limnichidae: *Cephalobyrrhus* sp.; Figs 2 and S3).

NeighbourNet networks and substitution saturation test

The phylogenetic networks calculated in SPLITSTREE 4.13.1 (Huson & Bryant 2006) were used to visualize the signal content in the data set. We used the NEIGHBOURNET algorithm (Bryant & Moulton 2004) and uncorrected p-distances to generate NeighbourNet graphs. If these graphs have tree-like structures (i.e. more distinct split patterns), there is more signal-like information than contradicting evidence in the corresponding alignment. On the other hand, star-like graphs and cobweb structures indicate the lack of phylogenetic signal and conflicting signal, respectively. The NeighbourNet networks were calculated for each gene separately, with 18S sequences divided into two fragments of the same length to minimize the effect of the sequence length on the estimation of distances between the taxa (see Gunter *et al.* 2014). To examine the split decomposition pattern in the concatenated data set, we used the

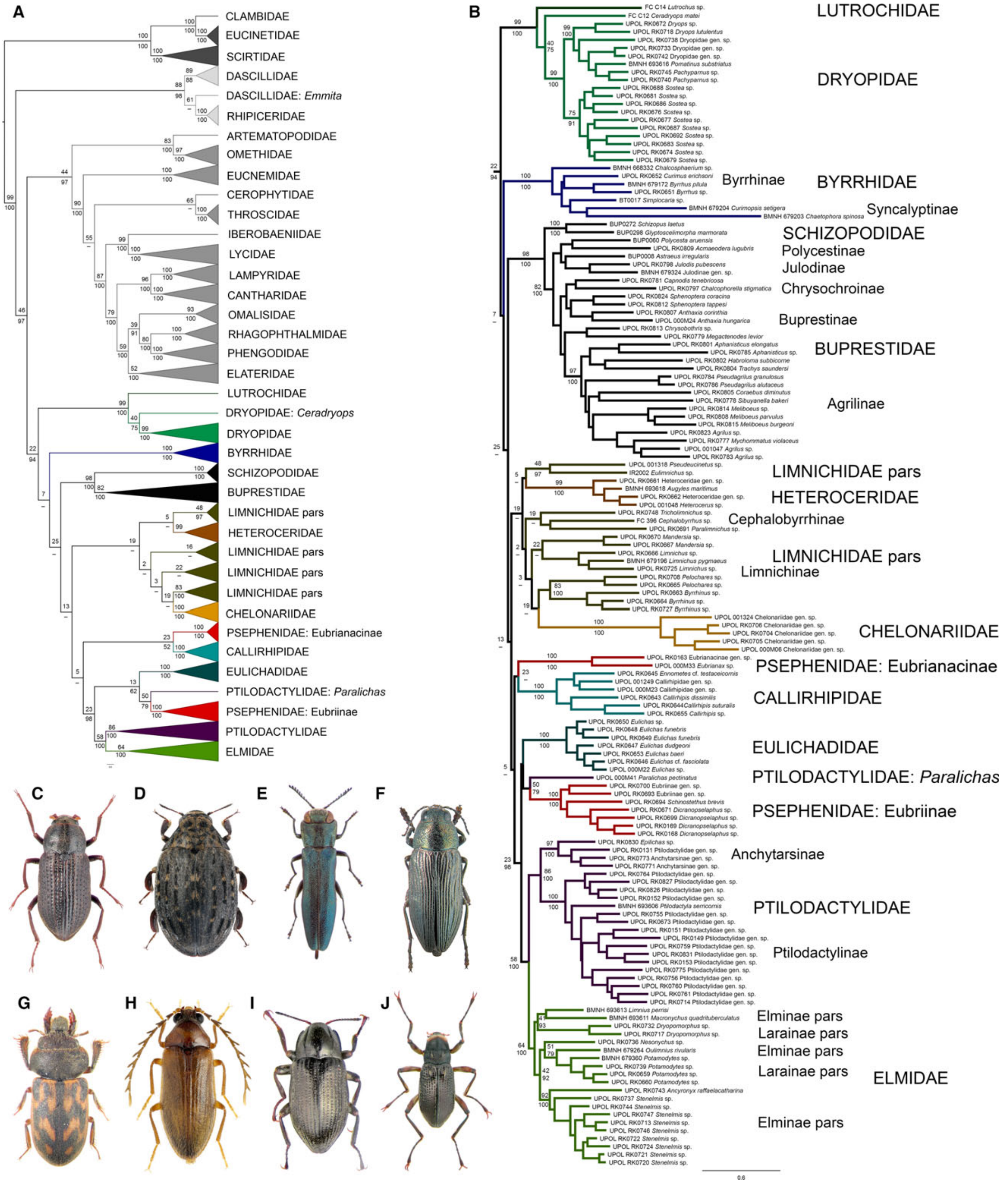


Fig. 2 —A. Phylogenetic hypothesis for the Elateriformia based on the RAxML maximum-likelihood analysis of 251 taxa represented by four fragments (18S and 28S rDNA, *rrnL* and *cox1* mtDNA) and aligned in Mafft. Branches are collapsed. —B. The same tree, but uncollapsed and with only the Byrrhoidea-Buprestoidea complex kept. Numbers at the branches are likelihood and bayesian frequencies, respectively. (C–J) Habitus images of various byrrhoid and buprestoid taxa. —C. *Helichus ussuriensis* Lafer (Dryopidae). —D. *Byrrhus pilula* (L.) (Byrrhidae). —E. *Agrilus laticornis* (Illiger) (Buprestidae). —F. *Buprestis haemorrhoidalis* Herbst (Buprestidae). —G. *Heterocerus parallelus* Gebler (Heteroceridae). —H. *Pseudoepilichas niponicus* (Lewis) (Ptilodactylidae). —I. *Limnius volckmari* (Panzer) (Elmidae). —J. *Macronychus quadrituberculatus* Müller (Elmidae).

reduced Mafft alignments (209 taxa for Elateriformia, 116 taxa for Byrrhoidea + Buprestoidea) to avoid the effect of the missing data on the resulting network.

To test the presence of the phylogenetic signal in our data, we performed an entropy-based Xia's nucleotide substitution saturation test (Xia *et al.* 2003) implemented in DAMBE 5.6.14 (Xia & Lemey 2009; Xia 2013) for each non-coding gene and each position of the protein-coding *cox1*. This test is based on the Iss (index of substitution saturation) statistic compared to Iss.c (critical substitution saturation index, assuming either a symmetrical or extremely asymmetrical tree topology). For this method, if Iss is significantly lower than Iss.c, the sequences have experienced little substitution saturation. Similarly, if Iss is higher than Iss.c, the sequences have experienced high level of saturation and have limited use in the phylogenetic reconstruction (Xia & Lemey 2009). We estimated the empirical proportion of invariant sites from the data and used 10 000 replicates on both all sites and fully resolved sites to perform the analyses.

Model selection, phylogenetic analyses and rogue taxa identification

The best-fit partitioning schemes and partition-specific substitution models were tested using a greedy algorithm in PARTITIONFINDER 1.1.1 (Lanfear *et al.* 2012) under Bayesian (BIC) and corrected Akaike information criteria (AICc). We identified six partitions (18S, 28S, *rrnL* and three *cox1* codon positions) as the optimal scheme, with nucleotide substitution model GTR+I+G for most partitions and SYM+I+G for 28S rRNA or both 18S and 28S rRNAs (Table S5). In cases, when AICc and BIC suggested different model schemes, we ran two analyses, each with one of the suggested model schemes. The resulting trees did not differ in topology so we further discuss only the results of analyses using the preferred AICc model schemes.

Maximum-likelihood (ML) analyses were conducted using RAXML 8.1.24 (Stamatakis 2006) via the CIPRES Web server (www.phylo.org; Miller *et al.* 2010). We applied the GTR+I+G model and the partitioning scheme of six partitions as defined by PartitionFinder. Branch supports were calculated using the RAPID BOOTSTRAP algorithm (Stamatakis *et al.* 2008) with 1000 bootstrap replicates.

Data sets of 251 taxa and those with rogue taxa and taxa with incomplete fragment representation excluded were additionally analysed under Bayesian inference (BI) using MRBAYES 3.1.2 (Huelsenbeck & Ronquist 2001) via the CIPRES web server (Miller *et al.* 2010), with the partitioning schemes and nucleotide substitution models as identified in PartitionFinder. Four chains were run for 4×10^7 generations using the Markov chain Monte Carlo method and stationary phase and convergence were detected in TRACER 1.5 (Rambaut & Drummond 2007). The 10% generations were discarded as burn-in, and a 50% majority-rule consensus was constructed to determine the posterior probabilities (PP) from the remaining trees.

We used the ROGUENAROK algorithm to search for rogue taxa (Aberer *et al.* 2012; http://exelixis-lab.org/roguenarok.html). The RAxML-inferred bootstrap trees from the 251-taxa data sets aligned by Mafft and Muscle were used as input, with the majority-rule consensus threshold, optimizing support and using the maximum drop set size = 1. Rogue taxa with a raw improvement (i.e. the fraction of overall improvement in bootstrap values across the tree when the taxa of a particular drop set are removed) of at least 0.1 (Table S7) together with taxa with incomplete fragment representation were excluded from data sets and newly assembled matrices of 208 (Muscle) and 209 taxa (Mafft) were re-aligned.

Results

Data set/alignment parameters

The four gene 488-taxa data sets comprised 5210 (Mafft), 5536 (Muscle) and 4972 (BlastAlign) homologous positions. Pruned data sets (251 taxa) included 4749 (Mafft), 4914 (Muscle) and 4704 (BlastAlign) homologous positions. Numbers of constant, variable and parsimony informative characters in various data sets are summarized in Table S6. Nucleotide composition was almost unbiased in the nuclear genes (18S: A = 24.1, C = 24.4, T = 23.7, G = 27.9; 28S: A = 25.3, C = 23.5, T = 20.2, G = 31.0), whereas the mitochondrial genes showed a higher AT content (*rrnL*: A = 32.9, C = 9.4, T = 40.6, G = 17.0; *cox1*: A = 32.2, C = 17.4, T = 35.6, G = 14.8).

Molecular phylogeny analyses

Most analyses recovered broadly similar relationships; however, we obtained limited statistical support along the backbone of the trees (Figs 2 and S3). The ML phylogenetic trees obtained from the 251 and 488-taxa data sets are shown in Figs 2 and S3, respectively, and the recovery of selected clades is given in Tables 1 and 2.

Dascilloidea were sister to the remaining elateriform lineages in majority of analyses and their monophyly was well supported in all analyses. However, the interrelationships within Dascillidae were equivocal and varied in different analyses. Dascillinae and Karumiinae were often a paraphyletic assemblage due to the unexpected position of *Emmita* (only *cox1* sequence available) in a clade with Rhipiceridae (Figs 2 and S3). Elateroidea were sister to the clade consisting of byrrhoid lineages and Buprestoidea (Figs 2 and S3). Their monophyly was recovered (although with low support) except for three analyses when Dascilloidea were inferred within the elateroid clade (Table 1).

Table 1 Recovery of selected clades with bootstrap support in maximum-likelihood (ML) and posterior probabilities in Bayesian (BI) analyses from different alignments of full-data (488 taxa) and pruned data sets (208–251 taxa)

Analysis/data set/alignment	DAS	ELA	BUP	BUP +BYR^{95}	BUP +BYR^{-BD}	BYR^{95}	DRY	BYR^{88}	PSE^{88}	BYR^{-BD}	Dryopid clade	Het + Lim + Chel	Het + Lim	Ptilod^{-Par} + Elmid	Eubriinae + *Paralichas*
ML 488 MAFFT	M (91)	M (34)	M (98)	M (23)	M (43)	P	P	P	P	M (25)	M (97)	P	M (30)	M (21)	M (45)
ML 488 MUSCLE	M (84)	M (38)	M (99)	M (21)	M (31)	P	P	P	P	M (21)	M (98)	P	M (16)	M (38)	P
ML 251 MAFFT	M (88)	M (44)	M (98)	M (22)	M (25)	P	P	P	P	M (13)	M (99)	M (19)	P^{1}	M (58)	M (50)
ML 251 MUSCLE	M (85)	M (56)	M (99)	M (17)	M (31)	P	P	P	P	M (27)	M (96)	M (20)	M (25)	M (49)	M (27)
BI 251 MAFFT	M (98)	M (97)	M (100)	M (94)	Unres.^{2}	P	P	P	P	Unres.^{2}	M (100)	P	Unres.	M (100)	M (79)
BI 251 MUSCLE	M (100)	M (93)	M (100)	M (80)	M (100)	P	P	P	P	P^{3}	M (100)	M (51)	Unres.	M (100)	M (99)
ML 209 MAFFT	M (97)	M (54)	M (100)	M (49)	M (27)	P	P	P	P	P^{3}	–	M (32)	M (44)	M (34)	M (58)
ML 208 MUSCLE	M (100)	M (41)	M (100)	M (20)	M (17)	P	P	P	P	M (16)	–	M (36)	P	M (49)	–
BI 209 MAFFT	M (100)	P^{4}	M (100)	P	P^{2}	P	P	P	P	P^{2,3}	–	P	M (100)	M (100)	M (94)
BI 208 MUSCLE	M (100)	M (97)	M (100)	M (95)	P	P	P	P	P	P	–	P	M (100)	M (97)	–
ML 251 MAFFT Q-INS-I	M (85)	P^{4}	M (99)	P	P	P	P	P	P	M (29)	M (99)	M (21)	P^{1}	M (46)	M (54)
ML 251 MAFFT 3RD_OUT	M (86)	M (39)	M (95)	M (23)	M (19)	P	P	P	P	P^{3}	M (100)	M (22)	M (28)	M (43)	M (58)
ML 251 MAFFT GAPS_OUT	M (75)	M (38)	M (98)	M (16)	P	M (5)	P	P	P	P	M (85)	M (12)	P	M (31)	P
ML 251 BLASTALIGN	M (82)	P^{4}	M (98)	M (21)	M (42)	P	P	P	P	M (30)	M (95)	M (28)	P^{1}	M (22)	M (27)

M, monophylum; P, paraphylum; unres., unresolved; DAS, Dascilloidea *sensu* (Lawrence & Newton 1995); ELA, Elateroidea *sensu* (Lawrence 1988); BUP, Buprestoidea *sensu* (Lawrence & Newton 1995); BYR95, Byrrhoidea *sensu* (Lawrence & Newton 1995); DRY, Dryopoidea (*sensu* different authors, e.g. Crowson 1960; Lawrence & Newton 1982); BYR-BD, Byrrhoidea *sensu* (Lawrence & Newton 1995) minus Byrrhidae, Dryopidae and Lutrochidae; BYR88, Byrrhoidea *sensu* (Lawrence 1988); PSE, Psephenoidea *sensu* (Lawrence 1988); Dryopid clade, Dryopidae incl. *Ceradryops* Hinton + Lutrochidae; Het, Heteroceridae; Lim, Limnichidae; Chel, Chelonariidae; Ptilod-Par, Ptilodactylidae minus *Paralichas* White; Elmid, Elmidae.

[1] Heteroceridae + Limnichidae pars.

[2] Chelonariidae outside of the group

[3] Buprestoidea within the group

[4] Dascilloidea within Elateroidea

Table 2 Recovery of selected elateriform families and subfamilies with bootstrap support in maximum-likelihood (ML) and posterior probabilities in Bayesian (BI) analyses from different alignments of full-data and pruned data sets

Analysis/data set/ alignment	Bupre	Schizo	Byrrh	B:Byrr	B:Sync	Dryo[1]	Chelon	Hetero	Limni	Callirh	Pseph[2]	P:Eubr	Eulich	Ptilod[3]	Elmid	E:Elmi	E:Lara[4]
ML 488 MAFFT	M (98)	M (99)	M (100)	P	M (39)	M (99)	M (100)	M (96)	P	M (99)	P	M (100)	M (100)	M (74)	M (41)	P	M (75)
ML 488 MUSCLE	M (51)	M (99)	M (100)	P	P	M (98)	M (100)	M (90)	P	M (100)	P	M (100)	M (100)	M (77)	M (56)	P	M (56)
ML 251 MAFFT	M (82)	M (100)	M (100)	P	M (81)	M (99)	M (100)	M (99)	P	M (100)	P	M (100)	M (100)	M (86)	M (64)	P	M (99)
ML 251 MUSCLE	M (75)	M (100)	M (100)	P	M (65)	M (98)	M (100)	M (98)	P	M (99)	P	M (100)	M (100)	M (90)	M (66)	P	M (99)
BI 251 MAFFT	M (100)	M (100)	M (100)	P	M (81)	M (100)	M (100)	M (100)	P	M (100)	P	M (100)	M (100)	M (100)	M (100)	P	M (100)
BI 251 MUSCLE	M (98)	M (100)	M (100)	P	M (79)	M (100)	M (100)	M (100)	P	M (100)	P	M (100)	M (100)	M (100)	M (100)	P	M (100)
ML 209 MAFFT	M (100)	–	M (100)	–	–	M (100)	M (100)	M (100)	M (27)	M (100)	P	M (100)	M (100)	M (85)	M (56)	P	M (99)
ML 208 MUSCLE	M (100)	–	M (100)	–	–	M (100)	M (100)	M (100)	M (42)	M (100)	P	M (100)	M (100)	M (89)	M (69)	P	M (96)
BI 209 MAFFT	M (100)	–	M (100)	–	–	M (100)	M (100)	M (100)	P	M (100)	P	M (100)	M (100)	M (100)	M (100)	P	M (100)
BI 208 MUSCLE	M (100)	–	M (100)	–	–	M (100)	M (100)	M (100)	M (86)	M (100)	P	M (100)	M (100)	M (100)	M (100)	P	M (100)
ML 251 MAFFT Q-INS-I	M (85)	M (100)	M (100)	P	M (67)	M (100)	M (100)	M (98)	P	M (100)	P	M (100)	M (100)	M (87)	M (59)	P	M (98)
ML 251 MAFFT 3RD_OUT	M (81)	M (99)	M (100)	P	M (77)	M (96)	M (100)	M (97)	M (17)	M (100)	P	M (100)	M (100)	M (81)	M (66)	P	M (100)
ML 251 MAFFT GAPS_OUT	M (85)	M (98)	M (100)	P	M (92)	M (98)	M (100)	M (98)	M (13)	M (99)	P	M (100)	M (100)	M (81)	M (39)	P	M (95)
ML 251 BLASTALIGN	M (85)	M (99)	M (100)	P	M (52)	M (99)	M (100)	M (98)	P	M (98)	P	M (100)	M (100)	M (84)	M (74)	P	M (99)

M, monophylum; P, paraphylum; Bupre, Buprestidae; Schizo, Schizopodidae; Byrrh, Byrrhidae; B:Byrr, Byrrhinae; B:Sync, Syncalyptinae; Dryo, Dryopidae; Chelon, Chelonariidae; Hetero, Heteroceridae; Limni, Limnichidae; Callirh, Callirhipidae; Pseph, Psephenidae; P:Eubr, Eubriinae; Eulich, Eulichadidae; Elmid, Elmidae; E:Elmi, Elminae; E:Lara, Larainae.

[1] excl. *Ceradryops* Hinton.

[2] Eubriinae + Eubrianacinae.

[3] excl. *Paralichas* White.

[4] excl. *Dryopomorphus* Hinton.

The superfamilies Byrrhoidea and Buprestoidea were not recovered as reciprocal monophyla. Buprestoidea, although regularly a monophylum, were found among byrrhoid lineages. The combined Byrrhoidea + Buprestoidea mostly consisted of four major lineages, that is (i) Byrrhidae, (ii) Dryopidae + Lutrochidae (referred further as the 'dryopid clade'), (iii) Buprestoidea (Schizopodidae sister to Buprestidae) and (iv) the clade formed by the remaining byrrhoid families (Figs 2 and S3). The interrelationships within the Byrrhoidea + Buprestoidea lineage were equivocal and not well supported; however, the position of Buprestoidea was inferred usually in a clade with byrrhoid lineages except Byrrhidae and dryopid clade (Figs 2 and S3; Table 1).

Byrrhidae were monophyletic in all analyses, mostly with well-supported monophyletic Syncalyptinae inside the paraphyletic Byrrhinae (Table 2). Syncalyptinae were consistently recovered as a sister to *Simplocaria* Stephens, and *Byrrhus* L. formed a clade with *Curimus* Erichson.

Dryopoidea (i.e. Byrrhoidea minus Byrrhidae) were always recovered as a paraphylum, similarly to the Byrrhoidea and Psephenoidea *sensu* Lawrence (1988). Lutrochidae and Dryopidae formed a well-supported clade (85–100% BS, 100% PP; Table 1). Monophyletic Dryopidae including *Ceradryops* (always sister to remaining dryopids) obtained BS 40–72% and PP 75–99% values; Dryopidae without *Ceradryops* obtained higher support (96–100% BS, 100% PP; Table 2).

The clade of Heteroceridae + Limnichidae + Chelonariidae was found in most analyses, often as sister to the remaining byrrhoid (or byrrhoid–buprestoid) lineages except the dryopid clade and Byrrhidae (Fig. 2, Table 1). Within this clade, Limnichidae were often paraphyletic due to Chelonariidae being in the terminal position and/or *Cephalobyrrhus*, *Eulimnichus* Casey, *Paralimnichus* Delève and *Pseudeucinetus* Heller (either some or all of them) being sister to Heteroceridae (Fig. 2, Tables 1 and 2). In some cases, *Cephalobyrrhus* was recovered in a clade with Callirhipidae and Psephenidae: Eubrianacinae. When Chelonariidae did not form a clade with Limnichidae and Heteroceridae, they either occupied one of the basal positions in Elateriformia phylogeny (some Bayesian analyses; Table 1) or were placed in various positions within the clade containing Buprestoidea and byrrhoid lineages except Byrrhidae and the dryopid clade (Fig. S3). Callirhipidae and Eulichadidae formed independent and highly supported lineages, the former always in a deeper position than the latter (Figs 2 and S3; Table 2).

Psephenidae (represented in our analyses by Eubriinae and Eubrianacinae) never formed a monophylum; Eubriinae were constantly recovered in a clade with *Paralichas* White (Ptilodactylidae: Cladotominae) (with variable support; Table 2), and Eubrianacinae were sister either to Eulichadidae (45–62% BS, 98–100% PP; most analyses of Muscle alignments) or Callirhipidae (<23% BS, 52–65% PP; Figs 2 and S3). When all possible sister groups of Eubriinae and Eubrianacinae (i.e. Callirhipidae, Eulichadidae, *Paralichas* and *Cephalobyrrhus*) were removed to test their impact on the psephenid non-monophyly, Eubriinae were sister to Heteroceridae, and Eubrianacinae were sister to Chelonariidae (both weakly supported).

Ptilodactylidae were never monophyletic, with *Paralichas* (Cladotominae) in a distant position to the remaining ptilodactylids. Ptilodactylinae + Anchytarsinae consistently formed a terminal clade with Elmidae (Figs 2 and S3; Table 1). Elmidae were monophyletic, with maximal support from BI (100% PP) and lower support from ML analyses (<74% BS). Both Elminae and Larainae were paraphyletic and with unstable positions; the latter subfamily was monophyletic and well supported when *Dryopomorphus* was excluded (Table 2). *Macronychus*, *Limnius* and *Dryopomorphus* formed a clade sister to the remaining Elmidae in most analyses, but always with low support (Fig. 2).

Rogue taxa, NeighbourNet networks and saturation test

We identified 18 rogue taxa in the pruned data sets aligned by Mafft and Muscle (Table S7). Raw improvement and relative bipartition information criterion values are given in Table S7. The analyses of data sets with removed rogue taxa resulted in broadly similar tree topologies as the original analyses (Tables 1 and 2); however, in three of four analyses, Limnichidae were monophyletic unlike the all-taxa analyses (Table 2).

Split networks, which represent incompatible and ambiguous signals in the data sets, were calculated for each gene fragment as well as for the concatenated 116-taxa (Byrrhoidea + Buprestoidea) and 209-taxa (Elateriformia) matrices aligned in Mafft. Using the NeighbourNet algorithm and uncorrected p-distances in Splitstree, we obtained graphs with indistinct internal and long terminal branches for both analysed matrices and to various extents for all genes included (Figs S1 and S2). The presence of the star-like graphs with internal net-like structures without distinct split patterns indicate the limited and conflicting phylogenetic signal.

The substitution saturation index values for all gene fragments and the 1st and 2nd codon positions in *cox1* were significantly lower than the critical values in analyses on fully resolved sites for both symmetrical and extremely asymmetrical topologies. The substantial to very high levels of saturation was present in the non-coding genes in analyses performed on all sites. The 3rd codon positions in *cox1* were highly saturated in all analyses. The detailed results of the saturation tests are provided in Table S8.

Discussion

Main lineages of Elateriformia

The monophyly of Elateriformia after the exclusion of Scirtiformia is widely accepted (Bocak *et al.* 2014), and the only taxon unexpectedly recovered in recent studies in the Elateriformia clade is Nosodendridae (McKenna & Farrell 2009; Kundrata *et al.* 2014; McKenna *et al.* 2015). Due to the incomplete fragment representation for the available Nosodendridae, we could not address this problem. We regularly found Dascilloidea as sister to the remaining Elateriformia, and Elateroidea as sister to the Byrrhoidea–Buprestoidea clade, which is in agreement with recent studies (Bocak *et al.* 2014; Kundrata *et al.* 2014; McKenna *et al.* 2015). Unlike the morphological analysis by Lawrence *et al.* (2011), in which Dascillidae were sister to Scarabaeoidea and Rhipiceridae formed a clade with Rhinorhipidae, we recovered Dascilloidea (Dascillidae + Rhipiceridae) as a monophylum with high support (Fig. 2; Table 1). Better sampling will be needed for the inference of lower-level relationships within Dascilloidea (Fig. S3).

Position of the Buprestoidea clade

The close relationships of Buprestoidea and Dryopoidea have been proposed by several authors based on similar morphology (Crowson 1955, 1982; Kasap & Crowson 1975; Lawrence 1988; Lawrence *et al.* 2011). Conversely, the independent position of Buprestoidea has been supported by some DNA analyses, mostly by studies based on mitogenomes (Timmermans & Vogler 2012; Timmermans *et al.* 2016) and a combined eight-gene Coleoptera data set of rRNA and nuclear protein-coding genes (NPC, McKenna *et al.* 2015). In contrast with these, the analyses of the combination of rRNA and mtDNA recovered Buprestoidea as a terminal branch within the broadly defined Byrrhoidea (Caterino *et al.* 2005; Bocakova *et al.* 2007; Bocak *et al.* 2014; Kundrata *et al.* 2014). Herein, having similar markers in our data sets, we constantly recovered a similar topology placing Buprestoidea within the paraphyletic Byrrhoidea. Expanded sampling for both Buprestoidea and Byrrhoidea did not improve the robustness of the deep branches of the tree and the topology remains weakly supported. The superfamily Buprestoidea is formed by two families, Buprestidae and Schizopodidae (e.g. Nelson & Bellamy 1991), the latter always considered as sister to the remaining lineages (Lawrence & Newton 1982; Bellamy & Volkovitsh 2005). This relationship was based on morphology (Nelson & Bellamy 1991; Lawrence *et al.* 2011) and is confirmed by recent molecular phylogenies (Evans *et al.* 2015; McKenna *et al.* 2015; this study; Fig. S3, Table 1). Almost all buprestid subfamilies are nonmonophyletic (Fig. S3) as reported by Evans *et al.* (2015) who analysed a different data set.

Family level relationships within Byrrhoidea

The families currently placed in Byrrhoidea (Lawrence & Newton 1995; Lawrence *et al.* 2011; Table S1) were historically split into several superfamilies (Table S2), and still, there is no consensus on the classification and limits of the lineage (Fig. 1). Originally, Byrrhoidea included only a single family Byrrhidae, whereas the remaining families were placed in Dryopoidea (Crowson 1955; Lawrence & Newton 1982). Lawrence (1988) expanded the Byrrhoidea by including Buprestidae, Dryopidae, Lutrochidae, Elmidae, Limnichidae and Heteroceridae and proposed a new superfamily, Psephenoidea, for the remaining dryopoid families. The current concept of Byrrhoidea (i.e. Byrrhidae + Dryopoidea) was established by Lawrence & Newton (1995) and has been followed by most recent authors (e.g. Beutel & Leschen 2005; Löbl & Smetana 2006).

However, neither of the previously defined superfamilies get any support from our analyses, similar to the results of the morphology-based phylogenies (e.g. Kasap & Crowson 1975; Crowson 1978; Beutel 1995; Lawrence *et al.* 1995; Costa *et al.* 1999). Dryopoidea was monophyletic in Hunt *et al.* (2007), but with negligible support and only limited taxon sampling, similarly to that found in the analyses of mitogenomes (Timmermans & Vogler 2012; Timmermans *et al.* 2016). However, there were no representatives of Dryopidae and Lutrochidae, which do not cluster with the remaining dryopoids in our analyses (Figs 2 and S3; Table 1). Byrrhoidea *sensu* Lawrence & Newton (1995) was monophyletic only in the study by McKenna *et al.* (2015), but again with a very low support. Additionally, the recent support for Byrrhoidea and Psephenoidea *sensu* Lawrence (1988) is limited to the morphological analysis by Lawrence *et al.* (2011). Despite the generally low support for the basal splits, we identified several consistently recovered relationships, which are discussed in the following section.

Overview of the families of Byrrhoidea

Byrrhidae are morphologically different in several aspects from the remaining lineages in the superfamily (for details see Crowson 1955, 1978; Kasap & Crowson 1975; Lawrence & Newton 1982; Lawrence 1991; Beutel 1995). Most of the DNA-based studies published to date confirmed the independent position of Byrrhidae, with various lineages (incl. Dryopoidea) proposed as potential sister groups. Herein, Byrrhidae regularly represented one of the deepest splits of the Byrrhoidea–Buprestoidea clade along with the dryopid clade (i.e. Dryopidae + Lutrochidae) (Figs 2 and S3).

Dryopidae were placed in relationships to Lutrochidae, Limnichidae and Heteroceridae (Crowson 1978; Lawrence & Newton 1982; Lawrence 1988; Lawrence *et al.* 1995; Costa *et al.* 1999). A sister-group relationship of Dryopidae and Lutrochidae was hypothesized in many morphological studies and confirmed by the recent DNA-based analyses, in which these families regularly occupied one of the deep positions within the Byrrhoidea–Buprestoidea clade (present study, Bocak *et al.* 2014; McKenna *et al.* 2015; Figs 2 and S3; Table 1). Additionally, such relationships are supported by morphology as Lutrochidae and some Dryopidae share the free abdominal sternite 5 and functional ventral longitudinal muscles in sternite 4 (Crowson 1978; Lawrence & Newton 1982). Within Dryopidae, *Ceradryops* differs morphologically from other dryopids and its placement has been questioned (Kodada *et al.* 2016b). *Ceradryops* was regularly recovered as sister to the remaining Dryopidae in the current analyses (Figs 2 and S3). Dryopidae obtained substantially higher support when *Ceradryops* was excluded (Table 2); however, this might have been affected by the incomplete fragment representation for *Ceradryops* (Table S3). We found two major clades within Dryopidae, the first represented by the aquatic genera and the second by the terrestrial *Sostea* Pascoe (Figs 2 and S3), which is in agreement with Kodada *et al.* (2016b).

The systematic position of the highly specialized terrestrial Chelonariidae remains unclear (Beutel & Leschen 2005). This family appeared in variable relationships in the Dryopoidea phylogenies including the molecular analyses (Bocakova *et al.* 2007; Hunt *et al.* 2007; Bocak *et al.* 2014; Kundrata *et al.* 2014). We did not find any support for the close relationship between Chelonariidae and Ptilodactylidae as proposed by Lawrence (1988) and Costa *et al.* (1999). Instead, we found Chelonariidae in some analyses in a clade with Limnichidae and Heteroceridae, similarly to Timmermans & Vogler (2012) and McKenna *et al.* (2015). These three studies are based on different sets of markers.

The relationship between Limnichidae and Heteroceridae was suggested in morphology-based studies (Crowson 1978; Beutel 1995; Lawrence *et al.* 1995), and later by the analyses of ribosomal and mitochondrial markers (Bocakova *et al.* 2007), a set of two ribosomal and six NPC genes (McKenna *et al.* 2015), and mitogenomes (Timmermans *et al.* 2016). Our analyses confirm these relationships (Figs 2 and S3; Table 1). The monophyly of Limnichidae was challenged by morphological (e.g. Hinton 1939; Crowson 1978; Beutel 1995; Costa *et al.* 1999) and recent molecular studies (present study, Bocak *et al.* 2014; Fig. 2; Table 2). The current analyses inferred Limnichidae (including Limnichinae, Cephalobyrrhinae and Thaumastodinae) as paraphyletic with Chelonariidae in a terminal position (Fig. 2; Tables 1 and 2) and/or with several limnichid genera (*Pseudeucinetus*, *Eulimnichus*, eventually *Paralimnichus*) found in a sister relationship to Heteroceridae (Figs 2 and S3). The uncertainties in the delimitation of Limnichidae persist, and more data are needed for definitive conclusions (Hernando & Ribera 2005).

Callirhipidae is a monophyletic family with an uncertain position in the Elateriformia classification in the past. We found Callirhipidae as one of the terminal lineages [although with unstable positions in different analyses, similarly as in McKenna *et al.* (2015)] within the Byrrhoidea–Buprestoidea clade, and the historical concepts of Rhipiceroidea (Crowson 1955), widely defined Artematopoidea (Crowson 1973) and proposed relationships with Eulichadidae as Elateriformia *incertae sedis* (Costa *et al.* 1999) are rejected. This finding agrees with the majority of recent DNA-based studies (Hunt *et al.* 2007; Timmermans & Vogler 2012; Bocak *et al.* 2014; McKenna *et al.* 2015).

Eulichadidae is another family with a controversial phylogenetic placement in the past (Kasap & Crowson 1975). Based on the metendosternite and wing morphology, Eulichadidae were hypothesized to be related to Callirhipidae (Forbes 1926; Lawrence & Newton 1982; Lawrence 1988; Costa *et al.* 1999); however, molecular studies showed their affinities to Ptilodactylidae, Psephenidae and Elmidae (either all or some of them; Hunt *et al.* 2007; Bocak *et al.* 2014; Kundrata *et al.* 2014; McKenna *et al.* 2015; this study; Fig. 2) or Eulichadidae formed a clade with Ptilodactylidae and Elmidae if Psephenidae were missing in the analysis (Timmermans & Vogler 2012; Timmermans *et al.* 2016).

Psephenidae were thought to be related to Cneoglossidae based on the morphology (Lawrence 1988; Lawrence *et al.* 1995, 2011; Costa *et al.* 1999), but this is contradicted by the recent molecular study of McKenna *et al.* (2015), which as the first included Cneoglossidae. Beutel (1995) mentioned the resemblance of psephenid and elmid larvae; however, this might have been based on homoplasies evolved due to similar ecology and habitats as no DNA-based support has been found for such relationships. In molecular studies, Psephenidae were recovered in a clade with Eulichadidae (Bocakova *et al.* 2007; Hunt *et al.* 2007; Bocak *et al.* 2014) or Eulichadidae + Elmidae (McKenna *et al.* 2015). Unfortunately, no Psephenidae were included in the study of an Elateriformia phylogeny based on the mitogenomes by Timmermans & Vogler (2012). The monophyly of Psephenidae was recovered by Lee *et al.* (2007), who defined several morphological apomorphies for the family, but their outgroup contained only three representatives of Elmidae and Cneoglossidae. Here, we found Psephenidae (represented by Eubriinae and Eubrianacinae; Table S3) to be non-monophyletic, forming two distantly related lineages, similar to that found in Kundrata *et al.* (2014). In all other previous DNA-based studies, Psephenidae were only represented by Eubrianacinae (Bocakova *et al.* 2007; Hunt *et al.* 2007; Bocak *et al.* 2014) or Eubrianacinae and Psepheninae (McKenna *et al.* 2015). Eubriinae were related to *Paralichas*, both often in a clade with

Eulichadidae, whereas Eubrianacinae formed a clade with either Callirhipidae (most cases) or Eulichadidae (Figs 2 and S3). We additionally tested the monophyly of Psephenidae by analysis of a data set where sister groups to both Eubriinae and Eubrianacinae identified by previous analyses were removed (i.e. Eulichadidae, Callirhipidae, *Paralichas pectinatus* and *Cephalobyrrhus*). Surprisingly, neither analysis recovered Psephenidae as monophyletic. Due to the unstable tree topology, we refrain from any formal changes in the classification, although some psephenid subfamilies were treated as independent families by previous authors (see Brown 1991 and Lee *et al.* 2007 for more details). The phylogeny of Psephenidae should be revisited with representatives of all five currently recognized subfamilies.

The mitogenome-based relationship of Elmidae and Ptilodactylidae (Timmermans & Vogler 2012) was confirmed here (Figs 2 and S3; Table 1). Elmidae contain two morphologically and ecologically different subfamilies, Elminae and Larainae (Lawrence & Newton 1995; but see Jäch *et al.* 2016). Although several authors hypothesized that both subfamilies are only distantly related (e.g. Beutel 1995; Costa *et al.* 1999), we confirm the predominant concept of Elmidae (Lawrence & Newton 1995), similar to McKenna *et al.* (2015). The investigation of the intrafamilial relationship is beyond the scope of our study, but it is worth pointing out that neither Elminae nor Larainae seem to be monophyletic (see also Kodada et al. 2016a). *Dryopomorphus* (Larainae) forms a separate lineage within deep splits in the tree (Figs 2 and S3; Table 2), which was suggested by Crowson (1978) and Kodada *et al.* (2016a).

Ptilodactylidae is one of the most taxonomically overlooked beetle families, and its classification remains chaotic (Lawrence 2005). Monophyly of Ptilodactylidae was disputed by several authors (e.g. Lawrence & Newton 1982; Beutel 1995; Lawrence *et al.* 1995; Costa *et al.* 1999). Currently, there are several morphologically different lineages classified in the family (Stribling 1986; Lawrence & Stribling 1992). Ptilodactylinae and Anchytarsinae formed a monophylum in the morphology-based analyses (Beutel 1995; Lawrence *et al.* 2011), which was confirmed by the current analyses (Figs 2 and S3). McKenna *et al.* (2015) sampled only one representative for each Ptilodactylinae and Anchytarsinae and found Ptilodactylinae sister to Podabrocephalidae, and Anchytarsinae sister to Cneoglossidae, together forming a clade. Araeopidiinae, when present in analyses, never formed a monophylum with any of the ptilodactylid lineages (Beutel 1995; Lawrence *et al.* 1995). Similarly, Cladotominae were recovered outside the bulk of Ptilodactylidae by both morphological and molecular studies (Beutel 1995; Bocakova *et al.* 2007; Hunt *et al.* 2007; Bocak *et al.* 2014; Kundrata *et al.* 2014), or sister to Chelonariidae or Callirhipidae within paraphyletic Ptilodactylidae (Costa *et al.* 1999; Hunt *et al.* 2007; respectively). We found the cladotomine genus *Paralichas* in a clade with Psephenidae: Eubriinae in most analyses, always only distantly related to the remaining Ptilodactylidae (Figs 2 and S3; Tables 1 and 2). The Cladotominae status remains open and can be solved only when all morphologically distinct ptilodactylid lineages are included in the data set.

The families of Byrrhoidea, which have not been included in this study, that is Cneoglossidae (one genus, eight species), Podabrocephalidae (one species) and Protelmidae (four genera, six species), represent only a small fraction of the total byrrhoid diversity. Cneoglossidae were hypothesized to be related to Psephenidae based on the morphology by many authors (see, e.g. Costa *et al.* 1999; Lawrence *et al.* 2011), but McKenna *et al.* (2015) found it embedded within Ptilodactylidae along with Podabrocephalidae. The close relationship between Podabrocephalidae and Ptilodactylidae is in agreement with previous hypothesis (e.g. Lawrence *et al.* 2010; but not with Lawrence *et al.* 2011). Protelmidae were until recently regarded as a tribe of Elmidae, with which it is probably not closely related (Jäch *et al.* 2016).

Suitability of the mtDNA/rRNA molecular markers

The RNA and mtDNA markers (here 18S and 28S rRNA, *rrnL* and *cox1* mtDNA) are commonly used for phylogeny reconstruction. Whereas ribosomal genes have been used for the investigation of the basal relationships, mitochondrial genes are more suitable for the lower taxonomic levels. These markers were used for studies dealing with the whole order (Hunt *et al.* 2007; Bocak *et al.* 2014), superfamilies (Dytiscoidea, Balke *et al.* 2005; Bostrichoidea, Bell & Phillips 2012; Cleroidea, Bocakova *et al.* 2012, 2016; Cucujoidea, Robertson *et al.* 2015; McElrath *et al.* 2015; Buprestoidea, Evans *et al.* 2015; Elateroidea, Bocakova *et al.* 2007; Kundrata *et al.* 2014; Tenebrionoidea, Gunter *et al.* 2014; Curculionoidea, Gunter *et al.* 2016) and the lower taxonomic ranks such as families, subfamilies, tribes and genera. Additionally, numerous sequences in publicly available databases (Bocak *et al.* 2014) simplify a compilation of outgroups for individual analyses.

Despite wide usage, the signal provided is limited in some cases, for example Tenebrionoidea (Gunter *et al.* 2014; Kergoat *et al.* 2014), Bostrichoidea (Bell & Phillips 2012) or Curculionoidea (Gunter *et al.* 2016). We identified conflicting support for the basal splits within Elateriformia as well as for the byrrhoid–buprestoid lineages. The NeighbourNet networks calculated in Splitstree revealed conflict in the phylogenetic signal within all genes (Figs S1 and S2). It means that the increased taxon sampling will probably not help resolve the deep elateriform and byrrhoid phylogeny and that further markers are needed. The recovery of some generally accepted lineages within Elateroidea in the Elateriformia was independent from alignment algorithm, but instability was observed in numerous parts of the tree (Figs 2 and S3).

Conclusions

Despite a large amount of data and the densest sampling of Byrrhoidea diversity up to date, the results solved a limited number of relationships and posed further questions that should be considered in the future. Further markers, such as NPC genes (McKenna *et al.* 2015), mitogenomes (Timmermans *et al.* 2016) or transcriptomes (Misof *et al.* 2014), should provide new testable hypotheses for the Byrrhoidea–Buprestoidea complex. The problems with low robustness of the Byrrhoidea phylogeny are not limited to the analyses of ribosomal and mitochondrial genes (Bocakova *et al.* 2007; Hunt *et al.* 2007; McKenna & Farrell 2009; Bocak *et al.* 2014; Kundrata *et al.* 2014; this study), ribosomal and NPC genes (McKenna *et al.* 2015) or mitochondrial genomes (Timmermans & Vogler 2012; Timmermans *et al.* 2016) but also to those based on morphological characters (Crowson 1978; Lawrence *et al.* 1995, 2011; Costa *et al.* 1999). Therefore, searching for the consensual signal from various analyses and accumulation of independent data is needed to resolve further clades in the higher phylogeny of Byrrhoidea and investigate processes leading to the evolution of the water and riparian lifestyles.

Acknowledgements

We thank I. Ribera, C. Hernandes (Barcelona, Spain; Limnichidae), V. Kubáň (Prague, Czech Republic; Buprestidae) and J. Hájek (Prague, Czech Republic; Callirhipidae) for the identification of samples. The following colleagues provided us with the specimens for DNA isolation: M. Bednařík, R. Gabriš, E. Jendek, V. Kubáň, Y. Li, Z. Lucbauer and D. Windsor. We thank G. Oatley (University of Otago, New Zealand) for critical reading of the manuscript and K. Makarov (Moscow, Russia) for a kind permission to use his photographs. We gratefully acknowledge funding from the Czech Science Foundation (P506/11/1757, LB) and the internal grant (IGA) from the Faculty of Science, Palacky University, Olomouc.

References

Aberer, A. J., Krompass, D. & Stamatakis, A. (2012). Pruning rogue taxa improves phylogenetic accuracy: an efficient algorithm and webservice. *Systematic Biology*, *62*, 162–166.

Balke, M., Ribera, I. & Beutel, R. G. (2005). The systematic position of Aspidytidae, the diversification of Dytiscoidea (Coleoptera, Adephaga) and the phylogenetic signal of third codon positions. *Journal of Zoological Systematics and Evolutionary Research*, *43*, 223–242.

Bell, K. L. & Phillips, T. K. (2012). Molecular systematics and evolution of the Ptinidae (Coleoptera: Bostrichoidea) and related families. *Zoological Journal of the Linnean Society*, *165*, 88–108.

Bellamy, C. L. & Volkovitsh, M. G. (2005). Buprestoidea Crowson, 1955. In R. G. Beutel & R. A. B. Leschen (Volume Eds) *Coleoptera*, *Beetles; Volume 1: Morphology and Systematics* (*Archostemata*, *Adephaga*, *Myxophaga*, *Polyphaga partim*). In N. P. Kristensen & R. G. Beutel (Eds) *Handbook of Zoology*, *Arthropoda: Insecta* (pp. 461–468). Berlin/New York: Walter de Gruyter.

Belshaw, R. & Katzourakis, A. (2005). BlastAlign: a program that uses blast to align problematic nucleotide sequences. *Bioinformatics*, *21*, 122–123.

Beutel, R. G. (1995). Phylogenetic analysis of Elateriformia (Coleoptera: Polyphaga) based on larval characters. *Journal of Zoological Systematics and Evolutionary Research*, *33*, 145–171.

Beutel, R. G. & Leschen, R. A. B. (2005). Elateriformia Crowson, 1960. Introduction, Phylogeny (Table 1). In R. G. Beutel & R. A. B. Leschen (Volume Eds) *Coleoptera*, *Beetles; Volume 1: Morphology and Systematics* (*Archostemata*, *Adephaga*, *Myxophaga*, *Polyphaga partim*). In N. P. Kristensen & R. G. Beutel (Eds) *Handbook of Zoology*, *Arthropoda: Insecta* (pp. 427–429). Berlin/New York: Walter de Gruyter.

Bocak, L., Bocakova, M., Hunt, T. & Vogler, A. P. (2008). Multiple ancient origins of neoteny in Lycidae (Coleoptera): consequences for ecology and macroevolution. *Proceedings of the Royal Society B*, *275*, 2015–2023.

Bocak, L., Barton, C., Crampton-Platt, A., Chesters, D., Ahrens, D. & Vogler, A. P. (2014). Building the Coleoptera tree-of-life for >8000 species: composition of public DNA data and fit with Linnaean classification. *Systematic Entomology*, *39*, 97–110.

Bocak, L., Kundrata, R., Andújar Fernández, C. & Vogler, A. P. (2016). The discovery of Iberobaeniidae (Coleoptera: Elateroidea), a new family of beetles from Spain, with immatures detected by environmental DNA sequencing. *Proceedings of the Royal Society B: Biological Sciences*, *283*, 20152350.

Bocakova, M., Bocak, L., Hunt, T., Teraväinen, M. & Vogler, A. P. (2007). Molecular phylogenetics of Elateriformia (Coleoptera): evolution of bioluminescence and neoteny. *Cladistics*, *23*, 477–496.

Bocakova, M., Constantin, R. & Bocak, L. (2012). Molecular phylogenetics of the melyrid lineage (Coleoptera: Cleroidea). *Cladistics*, *28*, 117–129.

Bocakova, M., Bocak, L., Gimmel, M. L., Motyka, M. & Vogler, A. P. (2016). Aposematism and mimicry in soft-bodied beetles of the superfamily Cleroidea (Insecta). *Zoologica Scripta*, *45*, 9–21.

Brown, H. P. (1991). Psephenidae (Dryopoidea) (including Eubriidae, Psephenoididae). In F. W. Stehr (Ed.) *Immature Insects, Volume 2* (pp. 395–397). Dubuque, IA: Kendall/Hunt Publishing.

Bryant, D. & Moulton, V. (2004). Neighbor-net: an agglomerative method for the construction of phylogenetic networks. *Molecular Biology and Evolution*, *21*, 255–265.

Caterino, M. S., Hunt, T. & Vogler, A. P. (2005). On the constitution and phylogeny of Staphyliniformia (Insecta: Coleoptera). *Molecular Phylogenetics and Evolution*, *34*, 655–672.

Costa, C., Vanin, S. A. & Ide, S. (1999). Systematics and bionomics of Cneoglossidae with a cladistic analysis of Byrrhoidea *sensu* Lawrence & Newton (1995) (Coleoptera, Elateriformia). *Arquivos de Zoologia*, *35*, 231–300.

Crowson, R. A. (1955). *The natural classification of the families of Coleoptera*. London: Nathaniel Lloyd.

Crowson, R. A. (1960). The phylogeny of Coleoptera. *Annual Review of Entomology*, *5*, 111–134.

Crowson, R. A. (1971). Observations on the superfamily Dascilloidea (Coleoptera: Polyphaga), with the inclusion of Karumiidae and Rhipiceridae. *Zoological Journal of the Linnean Society*, *50*, 11–19.

Crowson, R. A. (1973). On a new superfamily Artematopoidea of polyphagan betles, with the definition of two new fossil genera from the Baltic amber. *Journal of Natural History*, *7*, 225–238.

Crowson, R. A. (1978). Problems of phylogenetic relationships in Dryopoidea (Coleoptera). *Entomologica Germanica*, *4*, 250–257.

Crowson, R. A. (1982). On the dryopoid affinities of Buprestidae. *Coleopterists Bulletin*, *36*, 22–25.

Edgar, R. C. (2004). MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, *32*, 1792–1797.

Evans, A. M., McKenna, D. D., Bellamy, C. L. & Farrell, B. D. (2015). Large-scale molecular phylogeny of metallic wood-boring beetles (Coleoptera: Buprestoidea) provides new insights into relationships and reveals multiple evolutionary origins of the larval leaf-mining habit. *Systematic Entomology*, *40*, 385–400.

Forbes, W. T. M. (1926). The wing folding patterns of the Coleoptera. *Journal of the New York Entomological Society*, *34*, 42–68. 91–139

Grebennikov, V. V. & Beutel, R. G. (2002). Morphology of the minute larva of *Ptinella tenella*, with special reference to effects of miniaturisation and the systematic position of Ptiliidae (Coleoptera: Staphylinoidea). *Arthropod Structure & Development*, *31*, 157–172.

Gunter, N. L., Levkanicova, Z., Weir, T. H., Ślipiński, A., Cameron, S. L. & Bocak, L. (2014). Towards a phylogeny of the Tenebrionoidea (Coleoptera). *Molecular Phylogenetics and Evolution*, *79*, 305–312.

Gunter, N. L., Oberprieler, R. G. & Cameron, S. L. (2016). Molecular phylogenetics of Australian weevils (Coleoptera: Curculionoidea): exploring relationships in a hyperdiverse lineage through comparison of independent analyses. *Austral Entomology*, *55*, 217–233.

Hernando, C. & Ribera, I. (2005). 18.5. Limnichidae Erichson, 1846. In R. G. Beutel & R. A. B. Leschen (Volume Eds) *Coleoptera, Beetles; Volume 1: Morphology and Systematics* (*Archostemata*, *Adephaga*, *Myxophaga*, *Polyphaga partim*). In N. P. Kristensen & R. G. Beutel (Eds) *Handbook of Zoology*, *Arthropoda: Insecta* (pp. 512–518). Berlin/New York: Walter de Gruyter.

Hinton, H. E. (1939). An inquiry into the natural classification of the Dryopoidea, based partly on a study of their internal anatomy (Col.). *Transactions of the Royal Entomological Society of London*, *89*, 133–184.

Huelsenbeck, J. P. & Ronquist, F. (2001). MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, *17*, 754–755.

Hunt, T., Bergsten, J., Levkanicova, Z., Papadopoulou, A., St. John, O., Wild, R., Hammond, P. M., Ahrens, D., Balke, M., Caterino, M. S., Gómez-Zurita, J., Ribera, I., Barraclough, T. G., Bocakova, M., Bocak, L. & Vogler, A. P. (2007). A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. *Science*, *318*, 1913–1916.

Huson, D. H. & Bryant, D. (2006). Application of phylogenetic networks in evolutionary studies. *Molecular Biology and Evolution*, *23*, 254–267.

Jäch, M. A. (1998). Annotated check list of aquatic and riparian/littoral beetle families of the world (Coleoptera). In M. A. Jäch & L. Ji (Eds) *Water Beetles of China*, vol. II. pp. 25–42. Wien: Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein.

Jäch, M. A., Kodada, J., Brojer, M., Shepard, W. D. & Čiampor, F. (2016). *Coleoptera: Elmidae and Protelmidae. World Catalogue of Insects*, vol. 14. Leiden: Brill.

Kasap, H. & Crowson, R. A. (1975). A comparative anatomical study of Elateriformia and Dascilloidea (Coleoptera). *Transactions of the Royal Entomological Society*, *126*, 441–495.

Katoh, K. & Standley, D. M. (2013). MAFFT multiple sequence alignment software Version 7: improvements in performance and usability. *Molecular Biology and Evolution*, *30*, 772–780.

Katoh, K. & Toh, H. (2008). Improved accuracy of multiple ncRNA alignment by incorporating structural information into a MAFFT-based framework. *BMC Bioinformatics*, *9*, 212.

Katoh, K., Misawa, K., Kuma, K. & Miyata, T. (2002). MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research*, *30*, 3059–3066.

Kergoat, G. J., Soldati, L., Clamens, A.-L., Jourdan, H., Jabbour-Zahab, R., Genson, G., Bouchard, P. & Condamine, F. L. (2014). Higher level molecular phylogeny of darkling beetles (Coleoptera: Tenebrionidae). *Systematic Entomology*, *39*, 486–499.

King, J. G., Starr, J. R. & Lago, P. K. (2011). Molecular data resolves relationships within Heteroceridae (Coleoptera: Dryopoidea). *Systematic Entomology*, *36*, 435–445.

Kodada, J., Jäch, M. A. & Čiampor, F. (2016a). Elmidae Curtis, 1830. In R. G. Beutel & R. A. B. Leschen (Volume Eds) *Coleoptera, Beetles; Volume 1: Morphology and Systematics* (*Archostemata*, *Adephaga*, *Myxophaga*, *Polyphaga partim*). In N. P. Kristensen & R. G. Beutel (Eds) *Handbook of Zoology*, *Arthropoda: Insecta*, 2nd edn (pp. 561–589). Berlin/New York: Walter de Gruyter.

Kodada, J., Jäch, M. A. & Čiampor, F. (2016b). Dryopidae Bilberg, 1820 (1817). In R. G. Beutel & R. A. B. Leschen (Volume Eds) *Coleoptera*, *Beetles; Volume 1: Morphology and Systematics* (*Archostemata*, *Adephaga*, *Myxophaga*, *Polyphaga partim*). In N. P. Kristensen & R. G. Beutel (Eds) *Handbook of Zoology*, *Arthropoda: Insecta*, 2nd edn (pp. 590–602). Berlin/New York: Walter de Gruyter.

Kundrata, R. & Bocak, L. (2011). The phylogeny and limits of Elateridae (Insecta, Coleoptera): is there a common tendency of click beetles to soft-bodiedness and neoteny? *Zoologica Scripta*, *40*, 364–378.

Kundrata, R., Bocakova, M. & Bocak, L. (2014). The comprehensive phylogeny of the superfamily Elateroidea (Coleoptera: Elateriformia). *Molecular Phylogenetics and Evolution*, *76*, 162–171.

Lanfear, R., Calcott, B., Ho, S. Y. W. & Guindon, S. (2012). PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, *29*, 1695–1701.

Lawrence, J. F. (1988). Rhinorhipidae, a new beetle family from Australia, with comments on the phylogeny of the Elateriformia. *Invertebrate Taxonomy*, *2*, 1–53.

Lawrence, J. F. (1991). Byrrhidae (Byrrhoidea). In F. W. Stehr (Ed.) *Immature Insects*, Volume *2* (pp. 384–386). Iowa, Dubuque: Kendall/Hunt Publishing.

Lawrence, J. F. (2005) Ptilodactylidae Laporte, 1836. In R. G. Beutel & R. A. B. Leschen (Volume Eds) *Coleoptera, Beetles; Volume 1: Morphology and Systematics* (*Archostemata*, *Adephaga*, *Myxophaga*, *Polyphaga partim*). In N. P. Kristensen & R. G. Beutel (Eds) *Handbook of Zoology*, *Arthropoda: Insecta* (pp. 536–542). Berlin/New York: Walter de Gruyter.

Lawrence, J. F. & Newton, A. F. (1982). Evolution and classification of beetles. *Annual Review of Ecology and Systematics*, *13*, 261–290.

Lawrence, J. F. & Newton, A. F. (1995). Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). In J. Pakaluk & S. A. Slipinski (Eds) *Biology*, *Phylogeny*, *and Classification of Coleoptera. Papers Celebrating the 80th Birthday of Roy A. Crowson*. Volumes *1–2* (pp. 779–1083). Warszawa: Muzeum i Instytut Zoologii PAN.

Lawrence, J. F. & Stribling, J. B. (1992). A new genus of Ptilodactylidae (Coleoptera: Elateriformia) from North Queensland, with description of the presumed larva. *Journal of the Australian Entomological Society*, *31*, 19–27.

Lawrence, J. F., Nikitsky, N. B. & Kirejtshuk, A. G. (1995). Phylogenetic position of Decliniidae (Coleoptera: Scirtoidea) and comments on the classification of Elateriformia (sensu lato). In J. Pakaluk & S. A. Slipinski (Eds) *Biology*, *Phylogeny*, *and Classification of Coleoptera. Papers Celebrating the 80th Birthday of Roy A. Crowson*. Volumes 1–2 (pp. 375–410). Warszawa: Muzeum i Instytut Zoologii PAN.

Lawrence, J. F., Kawashima, I. & Branham, M. A. (2010) Elateriformia *Incertae sedis*. In R. A. B. Leschen, R. G. Beutel & J. F. Lawrence (Volume Eds) *Coleoptera*, *Beetles; Volume 1: Morphology and Systematics* (*Archostemata*, *Adephaga*, *Myxophaga*, *Polyphaga partim*). In N. P. Kristensen & R. G. Beutel (Eds) *Handbook of Zoology*, *Arthropoda: Insecta* (pp. 162–177). Berlin/New York: Walter de Gruyter.

Lawrence, J. F., Ślipiński, S. A., Seago, A. E., Thayer, M. K., Newton, A. F. & Marvaldi, A. E. (2011). Phylogeny of the Coleoptera based on morphological characters of adults and larvae. *Annales Zoologici*, *61*, 1–217.

Lee, C.-F., Satô, M., Shepard, W. D. & Jäch, M. A. (2007). Phylogeny of Psephenidae (Coleoptera: Byrrhoidea) based on larval, pupal and adult characters. *Systematic Entomology*, *32*, 502–538.

Löbl, I. & Smetana, A. (Eds) (2006). *Catalogue of Palaearctic Coleoptera*, *Volume 3. Scarabaeoidea*, *Scirtoidea*, *Dascilloidea*, *Buprestoidea*, *Byrrhoidea*. Stenstrup, Denmark: Apollo Books.

McElrath, T. C., Robertson, J. A., Thomas, M. C., Osborne, J., Miller, K. B., McHugh, J. V. & Whiting, M. F. (2015). A molecular phylogenetic study of Cucujidae s.l. (Coleoptera: Cucujoidea). *Systematic Entomology*, *40*, 705–718.

McKenna, D. D. & Farrell, B. D. (2009). Beetles (Coleoptera). In S. B. Hedges & S. Kumar (Eds) *The Timetree of Life* (pp. 278–289). New York: Oxford University Press.

McKenna, D. D., Wild, A. L., Kanda, K., Bellamy, C. L., Beutel, R. G., Caterino, M. S., Farnum, C. W., Hawks, D. C., Ivie, M. A., Jameson, M. L., Leschen, R. A. B., Marvaldi, A. E., McHugh, J. V., Newton, A. F., Robertson, J. A., Thayer, M. K., Whiting, M. F., Lawrence, J. F., Ślipiński, A., Maddison, D. R. & Farrell, B. D. (2015). The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Systematic Entomology*, *40*, 835–880.

Miller, M. A., Pfeiffer, W. & Schwartz, T. (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 Nov. 2010 (pp. 1–8). New Orleans, LA.

Misof, B., Liu, S., Meusemann, K., Peters, R. S., Donath, A., Mayer, C., Frandsen, P. B., Ware, J., Flouri, T., Beutel, R. G., Niehuis, O., Petersen, M., Izquierdo-Carrasco, F., Wappler, T., Rust, J., Aberer, A. J., Aspöck, U., Aspöck, H., Bartel, D., Blanke, A., Berger, S., Bohm, A., Buckley, T. R., Calcott, B., Chen, J., Friedrich, F., Fukui, M., Fujita, M., Greve, C., Grobe, P., Gu, S., Huang, Y., Jermiin, L. S., Kawahara, A. Y., Krogmann, L., Kubiak, M., Lanfear, R., Letsch, H., Li, Y., Li, Z., Li, J., Lu, H., Machida, R., Mashimo, Y., Kapli, P., McKenna, D. D., Meng, G. & Nakagaki, Y., Navarrete-Heredia, J. L., Ott, M., Ou, Y., Pass, G., Podsiadlowski, L., Pohl, H., Reumont, B. M., von Schutte, K., Sekiya, K., Shimizu, S., Slipinski, A., Stamatakis, A., Song, W., Su, X., Szucsich, N. U., Tan, M., Tan, X., Tang, M., Tang, J., Timelthaler, G., Tomizuka, S., Trautwein, M., Tong, X., Uchifune, T., Walzl, M. G., Wiegmann, B. M., Wilbrandt, J., Wipfler, B., Wong, T. K., Wu, Q., Wu, G., Xie, Y., Yang, S., Yang, Q., Yeates, D. K., Yoshizawa, K., Zhang, Q., Zhang, R., Zhang, W., Zhang, Y., Zhao, J., Zhou, C., Zhou, L., Ziesmann, T., Zou, S., Li, Y., Xu, X., Zhang, Y., Yang, H., Wang, J., Wang, J., Kjer, K. M. & Zhou, X. (2014). Phylogenomics resolves the timing and pattern of insect evolution. *Science*, *346*, 763–767.

Nelson, G. H. & Bellamy, C. L. (1991). A revision and phylogenetic re-evaluation of the family Schizopodidae (Coleoptera: Buprestoidea). *Journal of Natural History*, *25*, 985–1026.

Rambaut, A. & Drummond, A. J. (2007). *Tracer 1.5*. Edinburgh: Institute of Evolutionary Biology University of Edinburgh. Available at http://beast.bio.ed.ac.uk/Tracer.

Robertson, J. A., Ślipiński, A., Moulton, M., Shockley, F. W., Giorgi, A., Lord, N. P., Mckenna, D. D., Tomaszewska, W., Forrester, J., Miller, K. B., Whiting, M. F. & McHugh, J. V. (2015). Phylogeny and classification of Cucujoidea and the recognition of a new superfamily Coccinelloidea (Coleoptera: Cucujiformia). *Systematic Entomology*, *40*, 745–778.

Stamatakis, A. (2006). RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, *22*, 2688–2690.

Stamatakis, A., Hoover, P. & Rougemont, J. (2008). A rapid bootstrap algorithm for the RAxML web servers. *Systematic Biology*, *57*, 758–771.

Stribling, J. B. (1986). World generic revision of Ptilodactylidae (Coleoptera: Dryopoidea). Columbus: Ohio State University (PhD Thesis).

Timmermans, M. J. T. N. & Vogler, A. P. (2012). Phylogenetically informative rearrangements in mitochondrial genomes of Coleoptera, and monophyly of aquatic elateriform beetles (Dryopoidea). *Molecular Phylogenetics and Evolution*, *63*, 299–304.

Timmermans, M. J. T. N., Barton, C., Haran, J., Ahrens, D., Culverwell, C. L., Ollikainen, A., Dodsworth, S., Foster, P. G., Bocak, L. & Vogler, A. P. (2016). Family-level sampling of mitochondrial genomes in Coleoptera: compositional heterogeneity and phylogenetics. *Genome Biology and Evolution*, *8*, 161–175.

Xia, X. (2013). DAMBE 5: a comprehensive software package for data analysis in molecular biology and evolution. *Molecular Biology and Evolution*, *30*, 1720–1728.

Xia, X. & Lemey, P. (2009). Assessing substitution saturation with DAMBE. In P. Lemey, M. Salemi & A.-M. Vandamme (Eds) *The Phylogenetic Handbook: A Practical Approach to DNA and Protein Phylogeny*, 2nd edn (pp. 615–630). Cambridge: Cambridge University Press.

Xia, X., Xie, Z., Salemi, M., Chen, L. & Wang, Y. (2003). An index of substitution saturation and its application. *Molecular Phylogenetics and Evolution*, *26*, 1–7.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. NeighbourNets showing conflicting splits for the concatenated 209-taxa Mafft alignment (A) and for each gene separately – 28S rRNA (B), 18S rRNA (divided into two parts; C, D), *rrnL* mtDNA (E), and *cox1* mtDNA (F).

Fig. S2. NeighbourNets showing conflicting splits for the concatenated 116-taxa Mafft alignment of Buprestoidea + Byrrhoidea (A) and for each gene separately – 28S rRNA (B), 18S rRNA (divided into two parts; C, D), *rrnL* mtDNA (E), and *cox1* mtDNA (F).

Fig. S3. Maximum-likelihood phylogenetic tree for Elateriformia based on the RAxML analysis of the 488-taxa data set aligned in Mafft.

Table S1. List of families and superfamilies currently included in Elateriformia.

Table S2. The historical overview of the classifications of the byrrhoid lineages.

Table S3. List of 488 terminals used in the analyses, with voucher and GenBank accession numbers.

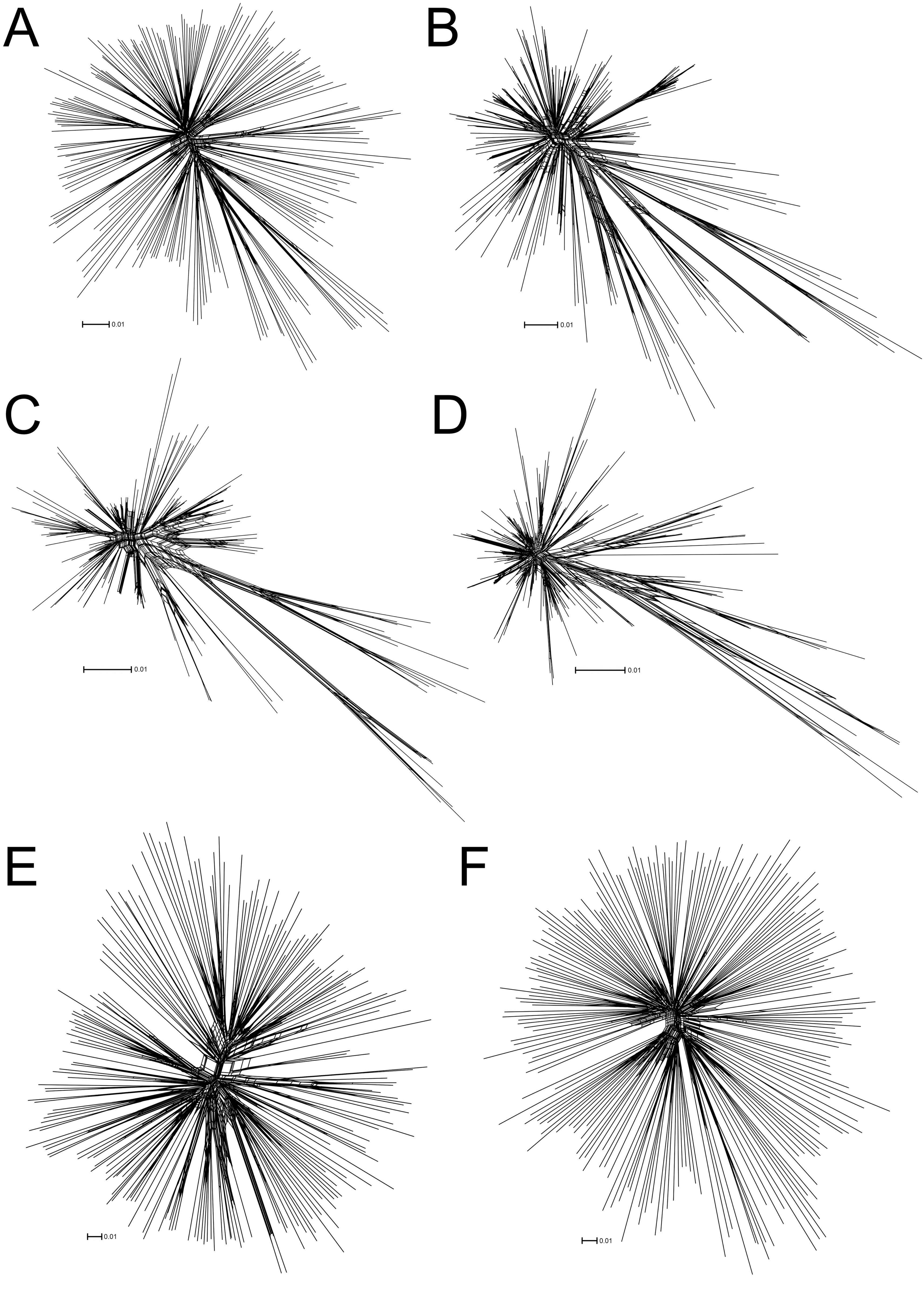
Table S4. Primers used for the PCR amplifications of the studied genes.

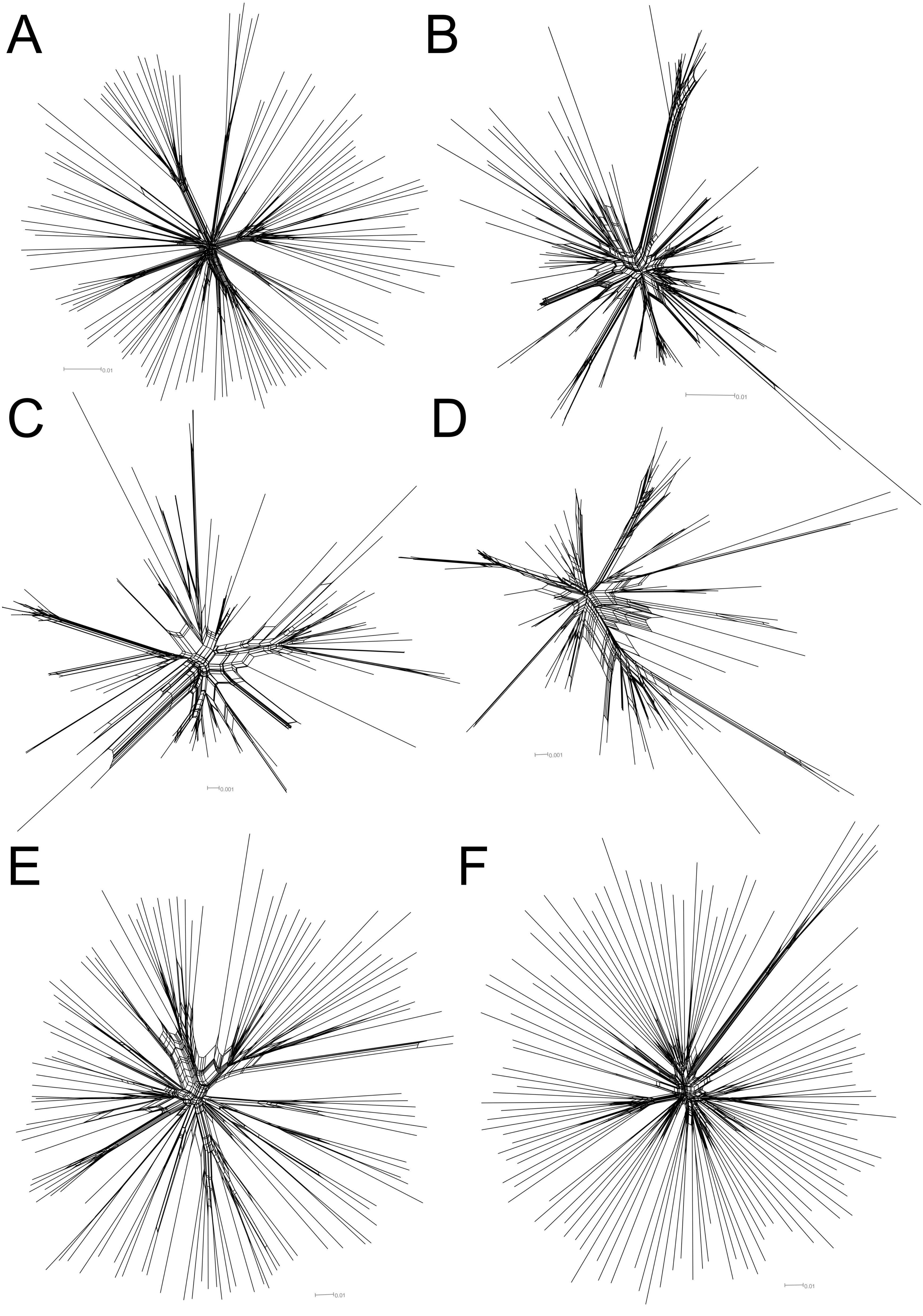
Table S5. Summary of the PartitionFinder results.

Table S6. Numbers and types of characters in the analysed data sets.

Table S7. Summary of the RogueNaRok results from the RAxML-inferred bootstrap trees (251 taxa aligned by Mafft and Muscle algorithms).

Table S8. Results of the Xia's nucleotide substitution saturation test in DAMBE, based on simulations with 32 operational taxonomic units (10 000 replicates).


A
0.01
B
0.01
C
0.01
D
0.01
E
0.01
F
0.01


A
0.01
B
0.01
C
0.001
D
0.001
E
0.01
F
0.01

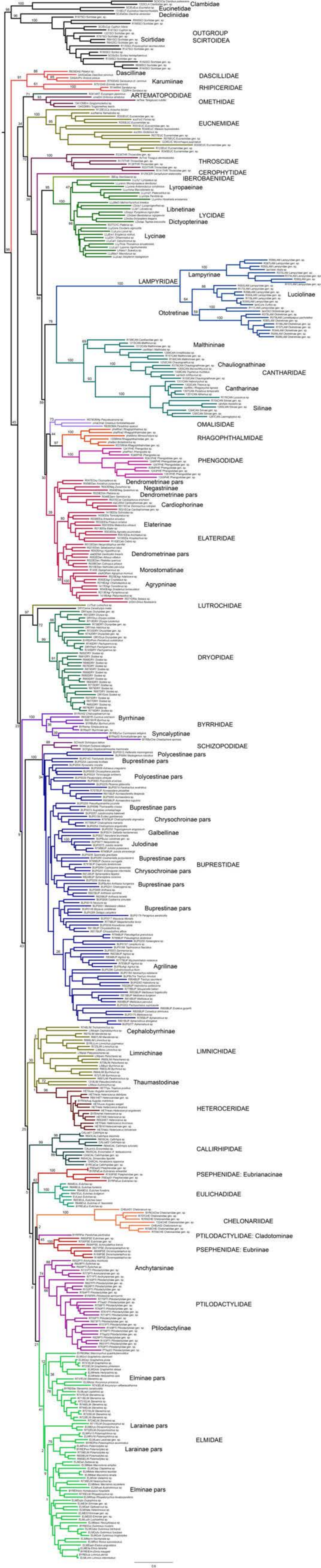

Clambidae
Eucinetidae
Decliniidae
OUTGROUP SCIRTOIDEA
Scirtidae
DASCILLIDAE
Dascillinae
Karumiinae
RHIPICERIDAE
ARTEMATOPODIDAE
OMETHIDAE
EUCNEMIDAE
THROSCIDAE
CEROPHYTIDAE
IBEROBAENIIDAE
Lyropaeinae
Libnetinae
LYCIDAE
Dictyopterinae
Lycinae
LAMPYRIDAE
Lampyrinae
Luciolinae
Ototretinae
Malthininae
Chauliognathinae
CANTHARIDAE
Cantharinae
Silinae
OMALISIDAE
RHAGOPHTHALMIDAE
PHENGODIDAE
Dendrometrinae pars
Negastriinae
Dendrometrinae pars
Cardiophorinae
Elaterinae
ELATERIDAE
Dendrometrinae pars
Morostomatinae
Agrypninae
LUTROCHIDAE
DRYOPIDAE
Byrrhinae
BYRRHIDAE
Syncalyptinae
SCHIZOPODIDAE
Polycestinae pars
Buprestinae pars
Polycestinae pars
Buprestinae pars
Chrysochroinae pars
Galbellinae
Julodinae
Buprestinae pars
BUPRESTIDAE
Chrysochroinae pars
Buprestinae pars
Buprestinae pars
Agrilinae
Cephalobyrrhinae
Limnichinae
LIMNICHIDAE
Thaumastodinae
HETEROCERIDAE
CALLIRHIPIDAE
PSEPHENIDAE: Eubrianacinae
EULICHADIDAE
CHELONARIIDAE
PTILODACTYLIDAE: Cladotominae
PSEPHENIDAE: Eubriinae
Anchytarsinae
PTILODACTYLIDAE
Ptilodactylinae
Elminae pars
Larainae pars
ELMIDAE
Larainae pars
Elminae pars
0.5

Table S1. List of families and superfamilies currently included in Elateriformia.

Elateroidea Leach, 1815	Byrrhoidea Latreille, 1804	Buprestoidea Leach, 1815	Dascilloidea Guérin-Méneville, 1843
extant			
Artematopodidae Lacordaire, 1857	Byrrhidae Latreille, 1804	Buprestidae Leach, 1815	Dascillidae Guérin-Méneville, 1843
Brachypsectridae LeConte & Horn, 1883	Callirhipidae Emden, 1924	Schizopodidae LeConte, 1859	Rhipiceridae Latreille, 1834
Cantharidae Imhoff, 1856	Chelonariidae Blanchard, 1845		
Cerophytidae Latreille, 1834	Cneoglossidae Champion, 1897		
Elateridae Leach, 1815	Dryopidae Billberg, 1820		
Eucnemidae Eschscholtz, 1829	Elmidae Curtis, 1830		
Iberobaeniidae Bocak et al. 2016	Eulichadidae Crowson, 1973		
Lampyridae Rafinesque, 1815	Heteroceridae MacLeay, 1825		
Lycidae Laporte, 1836	Limnichidae Erichson, 1846		
Omalisidae Lacordaire, 1857	Lutrochidae Kasap & Crowson, 1975		
Omethidae LeConte, 1861	Podabrocephalidae Pic, 1930		
Phengodidae LeConte, 1861	Protelmidae Jeannel, 1851		
Plastoceridae Crowson, 1972	Psephenidae Lacordaire, 1854		
Rhagophthalmidae Olivier, 1907	Ptilodactylidae Laporte, 1836		
Rhinorhipidae Lawrence, 1988			
Throscidae Laporte, 1840			
extinct			
Berendtmiridae Winkler, 1987	Lasiosynidae Kirejtshuk et al. 2010		
Lebanophytidae Kirejtshuk, 2013			
Praelateriidae Dolin, 1973			

Table S2. The historical overview of the classifications of the byrrhoid lineages. * - families not included in the current Byrrhoidea.

Crowson (1960)

Byrrhoidea	Byrrhidae
Dryopoidea	Dryopidae, Elmidae, Psephenidae, Limnichidae (incl. Lutrochidae), Heteroceridae, Chelonariidae, Ptilodactylidae (incl. Cneoglossidae and Eulichadidae), Artematopodidae*
Rhipiceroidea	Rhipiceridae*, Callirhipidae

Crowson (1981)

Byrrhoidea	Byrrhidae
Dryopoidea	Dryopidae, Elmidae, Psephenidae, Limnichidae, Lutrochidae, Heteroceridae, Chelonariidae, Ptilodactylidae, Eulichadidae
Artematopoidea	Artematopodidae*, Brachypsectridae*, Callirhipidae
Cantharoidea	Cneoglossidae, part of elateroid families*

Lawrence & Newton (1982)

Byrrhoidea	Byrrhidae
Dryopoidea	Dryopidae, Elmidae, Psephenidae, Limnichidae, Lutrochidae, Heteroceridae, Chelonariidae, Ptilodactylidae, Eulichadidae, Callirhipidae
Cantharoidea	Cneoglossidae, part of elateroid families*

Lawrence (1988)

Byrrhoidea	Byrrhidae, Buprestidae*, Dryopidae, Lutrochidae, Elmidae, Limnichidae, Heteroceridae
Psephenoidea	Psephenidae, Ptilodactylidae, Cneoglossidae, Chelonariidae, Eulichadidae, Callirhipidae

Lawrence & Newton (1995), Leschen & Beutel (2005)

Byrrhoidea	Byrrhidae, Dryopidae, Lutrochidae, Elmidae, Limnichidae, Heteroceridae, Psephenidae, Ptilodactylidae, Cneoglossidae, Chelonariidae, Eulichadidae, Callirhipidae
Incertae sedis	Podabrocephalidae, Rhinorhipidae*

Costa et al. (1999)

Byrrhoidea	Byrrhidae, Dryopidae, Lutrochidae, Elmidae, Limnichidae, Heteroceridae, Psephenidae, Ptilodactylidae, Cneoglossidae, Chelonariidae
Incertae sedis	Eulichadidae, Callirhipidae

Table S3. List of 488 terminals used in the analyses, with voucher and GenBank accession numbers. The sequences with KX accession number were produced in the current study.The chimeric taxa are marked with an asterisk (*).

				Markers						
Superfamily/family	Subfamily	Genus/Species	Geographic origin	18S	28S	*rrnL*	*cox1*	Specimen voucher	Matrix voucher	Source
SCIRTOIDEA										
Clambidae		*Clambus pubescens*	United Kingdom	EF362951	N	AM884186	DQ155704	BMNH 673260	SCIClCla	Hunt et al. 2007
Clambidae		gen. sp.	Indonesia	KF625497	KF626105	KF625804	KF625196	UPOL 001320	1320CLA	Kundrata et al. 2014
Decliniidae		*Declinia versicolor*	Japan	AY745556	AJ862791	N	N	295520	SCIDeDec	Bocakova et al. 2007
Eucinetidae		*Eucinetus haemorrhoidalis*	Czech Republic	KF625496	KF626097	KF625806	KF625198	UPOL 001319	1319EUT	Kundrata et al. 2014
Eucinetidae		*Eucinetus* sp.	USA	AF427609	AJ862793	AJ862756	AJ862822	APV–2001	SCIEuEuc	Bocakova et al. 2007
Scirtidae		*Prionocyphon sexmaculatus*	Japan	KF625516	KF626117	KF625822	KF625216	UPOL RK0170	R170SCI	Kundrata et al. 2014
Scirtidae		*Scirtes hemisphaericus*	United Kingdom	AF451937	DQ198699	DQ202592	DQ221997	BMNH 679275	SCIScSci	Bocakova et al. 2007
Scirtidae		*Scirtes* sp.	Japan	KF625500	KF626100	KF625808	KF625201	UPOL RK0160	R160SCI	Kundrata et al. 2014
Scirtidae		*Cyphon hilaris*	United Kingdom	AF201419	DQ198698	DQ198620	DQ198542	BMNH 679123	SCIScCyp	Bocakova et al. 2007
Scirtidae		*Cyphon* sp.	Cameroon	KF625501	KF626101	KF625809	KF625202	UPOL RK0161	R161SCI	Kundrata et al. 2014
Scirtidae		gen. sp.	Malaysia	KF625505	KF626106	KF625813	KF625206	UPOL 001321	1321SCI	Kundrata et al. 2014
Scirtidae		gen. sp.	Ethiopia	KF625498	KF626098	KF625807	KF625199	UPOL RK0147	R147SCI	Kundrata et al. 2014
Scirtidae		gen. sp.	Cameroon	KF625499	KF626099	N	KF625200	UPOL RK0159	R159SCI	Kundrata et al. 2014
Scirtidae		gen. sp.	Indonesia	KF625502	KF626102	KF625810	KF625203	UPOL RK0162	R162SCI	Kundrata et al. 2014
Scirtidae		gen. sp.	Philippines	KF625504	KF626104	KF625812	KF625205	UPOL RK0165	R165SCI	Kundrata et al. 2014
Scirtidae		gen. sp.	Indonesia	KF625512	KF626113	KF625819	KF625212	UPOL RK0166	R166SCI	Kundrata et al. 2014
Scirtidae		gen. sp.	Japan	KF625513	KF626114	N	KF625213	UPOL RK0167	R167SCI	Kundrata et al. 2014
indet.		gen. sp.	Cameroon	KX092896	KX093035	KX092644	KX092758	UPOL RK0641	R641SCI	present study
indet.		gen. sp.	Cameroon	KX092897	KX093036	KX092645	KX092759	UPOL RK0642	R642SCI	present study
indet.		gen. sp.	Cameroon	KX092898	KX093037	N	KX092762	UPOL RK0767	R767SCI	present study
indet.		gen. sp.	Japan	KX092894	KX093033	N	KX092760	UPOL RK0695	R695SCI	present study
indet.		gen. sp.	Indonesia	KX092895	KX093034	KX092643	KX092761	UPOL RK0698	R698SCI	present study
DASCILLOIDEA										
Dascillidae	Dascillinae	*Dascillus cervinus*	United Kingdom	AY745558	DQ198700	DQ198621	DQ198543	BMNH 679199	DASDaDas	Bocakova et al. 2007
Dascillidae	Dascillinae	*Petalon* sp.	Laos	KX092899	N	KX092646	KX092763	UPOL RK0639	R639DAS	present study
Dascillidae	Karumiinae	*Anorus piceus*	USA	KM364159	KM364302	N	N	MSC1281	DASAnPic	Evans et al. 2014
Dascillidae	Karumiinae	*Genecerus* cf. *cervinus*	Oman	KX092900	KX093038	KX092647	KX092764	UPOL RK0793	R793DAS	present study
Dascillidae	Karumiinae	*Emmita serricornis*	Morocco	N	N	N	KX092765	UPOL RK0791	R791DAS	present study
Rhipiceridae	Sandalinae	*Sandalus* sp.	South Africa	KF625506	KF626108	KF625814	KF625208	UPOL RK0144	R144RHI	Kundrata et al. 2014
Rhipiceridae	Sandalinae	*Sandalus* sp.	Zambia	KF625507	KF626107	KF625815	KF625207	UPOL 001322	1322RHI	Kundrata et al. 2014
BUPRESTOIDEA										
Schizopodidae	Schizopodinae	*Dystaxia elegans*	USA	KM364155	KM364299	N	KM364417	BUP0025	SCHdyst	Evans et al. 2014
Schizopodidae	Schizopodinae	*Glyptoscelimorpha marmorata*	USA	KM364156	KM364300	N	KM364418	BUP0298	SCHglyp	Evans et al. 2014
Schizopodidae	Schizopodinae	*Schizopus laetus*	USA	KM364083	KM364209	N	KM364343	BUP0272	SCHschl	Evans et al. 2014
Buprestidae	Agrilinae	*Agrilus* sp.	UK/Czech Rep.	AF451934	DQ198701	DQ198622	DQ198544	UPOL 001047	BUPBuAgr	Bocakova et al. 2007
Buprestidae	Agrilinae	*Trachys minutus*	Russia	AF451936	DQ198704	N	DQ198547	BMNH 679281	BUPBuTra	Bocakova et al. 2007
Buprestidae	Agrilinae	*Paragrilus aeraticollis*	Costa Rica	KM364075	KM364199	N	KM364333	BUP0179	BUP0179	Evans et al. 2014
Buprestidae	Agrilinae	*Aphanisticus* sp.	–	KM364048	KM364171	N	KM364311	BUP0277	BUP0277	Evans et al. 2014
Buprestidae	Agrilinae	*Cylindromorphus filum*	–	KM364053	KM364176	N	KM364316	BUP0286	BUP0286	Evans et al. 2014
Buprestidae	Agrilinae	*Meliboeus* sp.	Armenia	KM364068	KM364191	N	KM364327	BUP0175	BUP0175	Evans et al. 2014
Buprestidae	Agrilinae	*Taphrocerus fasciatus*	Costa Rica	KM364080	KM364205	N	KM364339	BUP0188	BUP0188	Evans et al. 2014
Buprestidae	Agrilinae	*Leiopleura* sp.	Costa Rica	KM364064	KM364187	N	KM364324	BUP0197	BUP0197	Evans et al. 2014
Buprestidae	Agrilinae	*Hylaeogena* sp.	Costa Rica	KM364061	KM364184	N	KM364321	BUP0200	BUP0200	Evans et al. 2014
Buprestidae	Agrilinae	*Pachyschelus cupricauda*	Costa Rica	KM364071	KM364194	N	KM364329	BUP0202	BUP0202	Evans et al. 2014
Buprestidae	Agrilinae	*Habroloma* sp.	–	KM364060	KM364183	N	KM364320	BUP0282	BUP0282	Evans et al. 2014
Buprestidae	Agrilinae	*Neotrachys estebana*	Costa Rica	KM364069	KM364192	N	KM364328	BUP0184	BUP0184	Evans et al. 2014
Buprestidae	Agrilinae	*Germarica* sp.	Australia	KM364056	KM364179	N	KM364317	BUP0003	BUP0003	Evans et al. 2014
Buprestidae	Agrilinae	*Mychommatus violaceus*	Cameroon	KX092902	KX093039	KX092648	KX092767	UPOL RK0777	R777BUP	present study
Buprestidae	Agrilinae	*Sibuyanella bakeri*	Philippines	KX092903	KX093040	KX092649	KX092768	UPOL RK0778	R778BUP	present study

Buprestidae	Agrilinae	*Agrilus* sp.	Cameroon	KX092904	KX093041	KX092650	KX092769	UPOL RK0783	R783BUP	present study
Buprestidae	Agrilinae	*Pseudagrilus granulosus*	Ethiopia	KX092907	KX093043	KX092652	KX092772	UPOL RK0784	R784BUP	present study
Buprestidae	Agrilinae	*Aphanisticus* sp.	Cameroon	KX092908	KX093044	KX092653	KX092773	UPOL RK0785	R785BUP	present study
Buprestidae	Agrilinae	*Pseudagrilus alutaceus*	Ethiopia	KX092909	KX093045	KX092654	KX092774	UPOL RK0786	R786BUP	present study
Buprestidae	Agrilinae	*Aphanisticus elongatus*	Italy	KX092914	KX093048	KX092657	KX092779	UPOL RK0801	R801BUP	present study
Buprestidae	Agrilinae	*Habroloma subbicorne*	China	KX092915	KX093049	KX092658	KX092780	UPOL RK0802	R802BUP	present study
Buprestidae	Agrilinae	*Meliboeus fulgidicollis*	Turkey	KX092916	KX093050	KX092659	KX092781	UPOL RK0803	R803BUP	present study
Buprestidae	Agrilinae	*Trachys saundersi*	China	KX092917	KX093051	KX092660	KX092782	UPOL RK0804	R804BUP	present study
Buprestidae	Agrilinae	*Coraebus diminutus*	China	KX092923	KX093057	KX092666	KX092788	UPOL RK0805	R805BUP	present study
Buprestidae	Agrilinae	*Agrilus* sp.	China	KX092918	KX093052	KX092661	KX092783	UPOL RK0806	R806BUP	present study
Buprestidae	Agrilinae	*Meliboeus parvulus*	Turkey	KX092929	KX093063	KX092672	KX092794	UPOL RK0808	R808BUP	present study
Buprestidae	Agrilinae	*Meliboeus* sp.	Ethiopia	KX092930	KX093064	KX092673	KX092795	UPOL RK0814	R814BUP	present study
Buprestidae	Agrilinae	*Meliboeus burgeoni*	Cameroon	KX092931	KX093065	KX092674	KX092796	UPOL RK0815	R815BUP	present study
Buprestidae	Agrilinae	*Agrilus* sp.	China	KX092932	KX093066	KX092675	KX092797	UPOL RK0823	R823BUP	present study
Buprestidae	Agrilinae	*Endelus gyoerfii*	China	KX092913	KX093047	N	KX092778	UPOL RK0800	R800BUP	present study
Buprestidae	Buprestinae	*Anthaxia hungarica*	France	DQ100484	DQ198702	DQ198623	DQ198545	UPOL 000M24	BUPBuAnt	Bocakova et al. 2007
Buprestidae	Buprestinae	*Anthaxia* sp.	South Africa	KM364089	KM364216	N	KM364350	BUP0088	BUP0088	Evans et al. 2014
Buprestidae	Buprestinae	*Chrysobothris* sp.	Malaysia	KX092926	KX093060	KX092669	KX092791	UPOL RK0813	R813BUP	present study
Buprestidae	Buprestinae	*Anthaxia corinthia*	Cyprus	KX092919	KX093053	KX092662	KX092784	UPOL RK0807	R807BUP	present study
Buprestidae	Buprestinae	*Anthaxia tenella*	Greece	KX092933	KX093067	N	KX092798	UPOL RK0825	R825BUP	present study
Buprestidae	Buprestinae	*Bilyaxia cordillerae*	Chile	KM364087	KM364213	N	KM364347	BUP0148	BUP0148	Evans et al. 2014
Buprestidae	Buprestinae	*Chalcogenia* sp.	South Africa	KM364095	KM364222	N	KM364356	BUP0241	BUP0241	Evans et al. 2014
Buprestidae	Buprestinae	*Pseudhyperantha jucunda*	Malaysia	KM364129	KM364266	N	KM364391	BUP0300	BUP0300	Evans et al. 2014
Buprestidae	Buprestinae	*Trachykele blondeli*	USA	KM364117	KM364249	N	KM364379	BUP0143	BUP0143	Evans et al. 2014
Buprestidae	Buprestinae	*Knowltonia calida*	USA	KM364096	KM364223	N	KM364357	BUP0039	BUP0039	Evans et al. 2014
Buprestidae	Buprestinae	*Coomaniella purpurascens*	Thailand	KM364099	KM364226	N	KM364360	BUP0290	BUP0290	Evans et al. 2014
Buprestidae	Buprestinae	*Anilara* sp.	Australia	KM364086	KM364212	N	KM364346	BUP0209	BUP0209	Evans et al. 2014
Buprestidae	Buprestinae	*Selagis caloptera*	Australia	KM364111	KM364243	N	KM364373	BUP0289	BUP0289	Evans et al. 2014
Buprestidae	Buprestinae	*Neocuris* sp.	Australia	KM364109	KM364240	N	KM364371	BUP0019	BUP0019	Evans et al. 2014
Buprestidae	Buprestinae	*Julodimorpha bakewelli*	Australia	KM364103	KM364233	N	KM364365	BUP0257	BUP0257	Evans et al. 2014
Buprestidae	Buprestinae	*Maoraxia littoralis*	Australia	KM364104	KM364234	N	KM364366	BUP0017	BUP0017	Evans et al. 2014
Buprestidae	Buprestinae	*Melobasis vittatus*	Australia	KM364106	KM364236	N	KM364368	BUP0001	BUP0001	Evans et al. 2014
Buprestidae	Buprestinae	*Spectralia gracilipes*	USA	KM364113	KM364245	N	KM364375	BUP0206	BUP0206	Evans et al. 2014
Buprestidae	Buprestinae	*Castiarina simulata*	Australia	KM364094	KM364221	N	KM364355	BUP0006	BUP0006	Evans et al. 2014
Buprestidae	Buprestinae	*Lasionota bivittata*	Chile	KM364100	KM364227	N	KM364361	BUP0254	BUP0254	Evans et al. 2014
Buprestidae	Buprestinae	*Augrabies schotiaphaga*	South Africa	KM364091	KM364218	N	KM364352	BUP0073	BUP0073	Evans et al. 2014
Buprestidae	Buprestinae	*Thomasettia crassa*	South Africa	KM364115	KM364247	N	KM364377	BUP0086	BUP0086	Evans et al. 2014
Buprestidae	Buprestinae	*Trigonogenium angulosum*	Chile	KM364119	KM364251	N	KM364381	BUP0250	BUP0250	Evans et al. 2014
Buprestidae	Buprestinae	*Megactenodes levior*	Cameroon	KX092921	KX093055	KX092664	KX092786	UPOL RK0779	R779BUP	present study
Buprestidae	Buprestinae	*Chrysobothris affinis*	Slovakia	KX092927	KX093061	KX092670	KX092792	UPOL RK0817	R817BUP	present study
Buprestidae	Chrysochroinae	*Chalcophora mariana*	Slovakia	KX092901	N	N	KX092766	UPOL RK0776	R776BUP	present study
Buprestidae	Chrysochroinae	*Chalcophora angulicollis*	USA	KM364122	KM364255	N	KM364384	BUP0054	BUP0054	Evans et al. 2014
Buprestidae	Chrysochroinae	*Cyphosoma lawsoniae*	Spain	KM364123	KM364257	N	KM364385	BUP0264	BUP0264	Evans et al. 2014
Buprestidae	Chrysochroinae	*Ectinogonia intermedia*	Chile	KM364124	KM364258	N	KM364386	BUP0251	BUP0251	Evans et al. 2014
Buprestidae	Chrysochroinae	*Evides gambiensis*	South Africa	KM364127	KM364262	N	KM364389	BUP0139	BUP0139	Evans et al. 2014
Buprestidae	Chrysochroinae	*Nanularia brunneata*	USA	KM364128	KM364265	N	KM364390	BUP0027	BUP0027	Evans et al. 2014
Buprestidae	Chrysochroinae	*Dicerca corrugata*	China	KX092912	N	KX092656	KX092777	UPOL RK0799	R799BUP	present study
Buprestidae	Chrysochroinae	*Sphenoptera tappesi*	Turkey	KX092925	KX093059	KX092668	KX092790	UPOL RK0812	R812BUP	present study
Buprestidae	Chrysochroinae	*Sphenoptera coracina*	Turkey	KX092928	KX093062	KX092671	KX092793	UPOL RK0824	R824BUP	present study
Buprestidae	Chrysochroinae	*Capnodis tenebricosa*	Greece	KX092920	KX093054	KX092663	KX092785	UPOL RK0781	R781BUP	present study
Buprestidae	Chrysochroinae	*Chalcophorella stigmatica*	Turkey	KX092922	KX093056	KX092665	KX092787	UPOL RK0797	R797BUP	present study
Buprestidae	Galbellinae	*Galbella hantamensis*	South Africa	KM364132	KM364269	N	KM364393	BUP0074	BUP0074	Evans et al. 2014
Buprestidae	Julodinae	gen. sp.	South Africa	AF451935	DQ198703	DQ198624	DQ198546	BMNH 679324	BUPBuJul	Bocakova et al. 2007
Buprestidae	Julodinae	*Julodis recenta*	South Africa	KM364133	KM364272	N	KM364396	BUP0075	BUP0075	Evans et al. 2014
Buprestidae	Julodinae	*Neojulodis* sp.	South Africa	KM364134	KM364274	N	KM364398	BUP0077	BUP0077	Evans et al. 2014
Buprestidae	Julodinae	*Julodis ehrenbergii*	Greece	KX092906	KX093042	N	KX092771	UPOL RK0780	R780BUP	present study

Buprestidae	Julodinae	*Julodis pubescens*	Greece, Crete	KX092911	KX093046	KX092655	KX092776	UPOL RK0798	R798BUP	present study
Buprestidae	Polycestinae	*Acmaeodera* sp.	South Africa	KM364138	KM364281	N	KM364403	BUP0093	BUP0093	Evans et al. 2014
Buprestidae	Polycestinae	*Astraeus irregularis*	Australia	KM364139	KM364283	N	KM364404	BUP0008	BUP0008	Evans et al. 2014
Buprestidae	Polycestinae	*Helferella manningensis*	Australia	KM364141	KM364285	N	KM364406	BUP0012	BUP0012	Evans et al. 2014
Buprestidae	Polycestinae	*Mastogenius robustus*	USA	KM364143	KM364287	N	KM364408	BUP0064	BUP0064	Evans et al. 2014
Buprestidae	Polycestinae	*Paratrachys australius*	Australia	KM364146	KM364290	N	KM364410	BUP0014	BUP0014	Evans et al. 2014
Buprestidae	Polycestinae	*Polycesta aruensis*	USA	KM364149	KM364293	N	KM364413	BUP0060	BUP0060	Evans et al. 2014
Buprestidae	Polycestinae	*Ptosima gibbicollis*	USA	KM364150	KM364294	N	KM364414	BUP0205	BUP0205	Evans et al. 2014
Buprestidae	Polycestinae	*Chrysophana placida*	USA	KM364140	KM364284	N	KM364405	BUP0058	BUP0058	Evans et al. 2014
Buprestidae	Polycestinae	*Thrincopyge ambiens*	USA	KM364151	KM364295	N	KM364415	BUP0024	BUP0024	Evans et al. 2014
Buprestidae	Polycestinae	*Paratyndaris olneyae*	USA	KM364148	KM364292	N	KM364412	BUP0029	BUP0029	Evans et al. 2014
Buprestidae	Polycestinae	*Xyroscelis crocata*	Australia	KM364154	KM364298	N	KM364416	BUP0004	BUP0004	Evans et al. 2014
Buprestidae	Polycestinae	*Acmaeodera pilosellae*	Greece	KX092910	N	N	KX092775	UPOL RK0787	R787BUP	present study
Buprestidae	Polycestinae	*Acmaeodera lugubris*	Spain	KX092924	KX093058	KX092667	KX092789	UPOL RK0809	R809BUP	present study
Buprestidae	Polycestinae	*Acmaeoderella despecta*	Cyprus	KX092905	N	KX092651	KX092770	UPOL RK0811	R811BUP	present study
ELATEROIDEA										
Artematopodidae	Artematopodinae	*Eurypogon japonicus*	Japan	KF294761	KF294767	KF294755	KF294774	UPOL RK0091	R091ART	Kundrata et al. 2013
Omethidae	Telegeusinae	*Telegeusis nubifer*	USA	DQ100503	DQ198751	DQ198660	DQ198582	UPOL 000321	telTele	Bocakova et al. 2007
Omethidae	Driloniinae	*Drilonius striatulus*	Japan	KF625527	KF626128	KF625830	KF625227	UPOL 001272	omeDril	Kundrata et al. 2014
Omethidae	Omethinae	*Troglomethes leechi*	USA	KF625529	KF626130	KF625828	KF625229	UPOL 001340	1340OMEo	Kundrata et al. 2014
Omethidae	Matheteinae	*Ginglymocladus* sp.	USA	KF625530	KF626131	KF625829	KF625230	UPOL 001341	1341OMEm	Kundrata et al. 2014
Cerophytidae		*Cerophytum elateroides*	Slovakia	KF625714	KF626302	KF626002	KF625407	UPOL RK0129	R129CER	Kundrata et al. 2014
Throscidae		*Trixagus dermestoides*	United Kingdom	AF451950	DQ198747	DQ198656	DQ198578	BMNH 679235	thrTrid	Bocakova et al. 2007
Throscidae		gen. sp.	Indonesia	KF625533	KF626134	KF625836	KF625233	UPOL RK0138	R138THR	Kundrata et al. 2014
Throscidae		gen. sp.	Japan	KF625535	KF626136	KF625837	KF625235	UPOL RK0141	R141THR	Kundrata et al. 2014
Throscidae		gen. sp.	Cameroon	KF625536	KF626137	KF625838	KF625236	UPOL RK0175	R175THR	Kundrata et al. 2014
Throscidae		gen. sp.	Indonesia	KF625541	KF626141	KF625840	KF625241	UPOL RK0337	R337THR	Kundrata et al. 2014
Throscidae		gen. sp.	Malaysia	KF625542	KF626142	KF625841	KF625242	UPOL RK0338	R338THR	Kundrata et al. 2014
Eucnemidae	Anischiinae	*Anischia bicolor*	New Caledonia	KF625546	KF626146	KF625846	KF625247	UPOL RK0120	R120EUCa	Kundrata et al. 2014
Eucnemidae	Eucneminae	*Idiotarsus* sp.	Bolivia	DQ100493	DQ198730	DQ198641	DQ198563	BMNH 703097	eucIdio	Kundrata et al. 2014
Eucnemidae	Eucneminae	gen. sp.	Indonesia	HQ333829	HQ333923	HQ333736	HQ334009	UPOL RK0076	R076EUC	Kundrata Bocak 2011
Eucnemidae	Eucneminae	gen. sp.	Indonesia	HQ333830	HQ333924	HQ333737	HQ334010	UPOL RK0077	R077EUC	Kundrata Bocak 2011
Eucnemidae	Macraulacinae	*Fornax* sp.	Bolivia	DQ100492	DQ198729	DQ198640	DQ198562	BMNH 703106	eucFor2	Kundrata et al. 2014
Eucnemidae	Macraulacinae	*Nematodes* sp.	Bolivia	DQ100495	DQ198731	DQ198642	DQ198564	BMNH 703107	eucNema	Kundrata et al. 2014
Eucnemidae	Macraulacinae	gen. sp.	Japan	KF625564	KF626164	KF625862	KF625265	UPOL RK0350	R350EUC	Kundrata et al. 2014
Eucnemidae	Melasinae	*Melasis buprestoides*	Greece	KF625558	KF626158	KF625858	KF625259	UPOL RK0344	R344EUC	Kundrata et al. 2014
Eucnemidae	Melasinae	*Micorhagus pygmaeus*	Czech Republic	KF625570	KF626170	KF625867	KF625271	UPOL 001224	1224EUC	Kundrata et al. 2014
Eucnemidae	Melasinae	gen. sp.	Philippines	KF625559	KF626159	KF625859	KF625260	UPOL RK0345	R345EUC	Kundrata et al. 2014
Eucnemidae	Melasinae	gen. sp.	Indonesia	KF625549	KF626149	KF625849	KF625250	UPOL RK0123	R123EUC	Kundrata et al. 2014
Eucnemidae	Melasinae	gen. sp.	Japan	KF625565	KF626165	KF625863	KF625266	UPOL RK0351	R351EUC	Kundrata et al. 2014
Eucnemidae	Melasinae	gen. sp.	Cameroon	KF625566	KF626166	KF625864	KF625267	UPOL RK0355	R355EUC	Kundrata et al. 2014
Eucnemidae	indet.	gen. sp.	Panama	KF625554	KF626154	KF625854	KF625255	UPOL RK0303	R303EUC	Kundrata et al. 2014
Iberobaeniidae		*Iberobaenia* sp.	Spain	KT339296	KT339297	KT825140	KT339298	UPOL RK0790*	IBEsp	Bocak et al. 2016
Lycidae	Libnetinae	*Libnetis* sp.	Malaysia	DQ181038	DQ181112	DQ180964	DQ181186	UPOL 000L02	LLibl1	Bocak et al. 2008
Lycidae	Dictyopterinae	*Lycoprogenthes* sp.	Indonesia	DQ181070	DQ181144	DQ180996	DQ181218	UPOL 000358	LDicly1	Bocak et al. 2008
Lycidae	Dictyopterinae	*Taphes brevicollis*	Laos	DQ181098	DQ181172	DQ181024	DQ181246	UPOL 000812	LDictap	Bocak et al. 2008
Lycidae	Dictyopterinae	*Dictyoptera elegans*	Japan	DQ181073	DQ181147	DQ180999	DQ181221	UPOL 000570	LDicdie	Bocak et al. 2008
Lycidae	Dictyopterinae	*Benibotarus nigripennis*	Japan	DQ181075	DQ181149	DQ181001	DQ181223	UPOL 000572	LDicben	Bocak et al. 2008
Lycidae	Dictyopterinae	*Pyropterus nigroruber*	Japan	DQ181077	DQ181151	DQ181003	DQ181225	UPOL 000574	LDicpyr	Bocak et al. 2008
Lycidae	Lyropaeinae	*Lyropaeus* sp.	Malaysia	DQ181042	DQ181116	DQ180968	DQ181190	UPOL 000L11	LLyrly1	Bocak et al. 2008
Lycidae	Lyropaeinae	*Antennolycus constrictus*	Malaysia	DQ181051	DQ181125	DQ180977	DQ181199	UPOL 000L22	LLyrana	Bocak et al. 2008
Lycidae	Lyropaeinae	*Microlyropaeus dembickyi*	Indonesia	DQ181071	DQ181145	DQ180997	DQ181219	UPOL 000542	LLyranm	Bocak et al. 2008
Lycidae	Lyropaeinae	*Platerodrilus* sp.	Malaysia	DQ181037	DQ181111	DQ180963	DQ181185	UPOL 000L01	LLyrmd1	Bocak et al. 2008
Lycidae	Lyropaeinae	*Macrolibnetis* sp.	Malaysia	DQ181050	DQ181124	DQ180976	DQ181198	UPOL 000L21	LLyrmma	Bocak et al. 2008
Lycidae	Lyropaeinae	*Pendola* sp.	Indonesia	DQ181058	DQ181132	DQ180984	DQ181206	UPOL 000M45	LLyrmpe	Bocak et al. 2008
Lycidae	Lyropaeinae	*Horakiella emasensis*	Malaysia	DQ181110	DQ181184	DQ181036	DQ181258	UPOL 001043	LLyrmho	Bocak et al. 2008

Lycidae	Ateliinae	*Scarelus* sp.	Malaysia	DQ181046	DQ181120	DQ180972	DQ181194		UPOL 000L15	LAtesc1	Bocak et al. 2008
Lycidae	Lycinae	*Dihammatus* sp.	Malaysia	DQ181043	DQ181117	DQ180969	DQ181191		UPOL 000L12	LLyDih1	Bocak et al. 2008
Lycidae	Lycinae	*Conderis signicollis*	Malaysia	DQ181062	DQ181136	DQ180988	DQ181210		UPOL 000194	LLyCons	Bocak et al. 2008
Lycidae	Lycinae	*Plateros* sp.	French Guyana	KF625685	KF626271	KF625975	KF625384		UPOL RK0377	R377LYC	Kundrata et al. 2014
Lycidae	Lycinae	*Macrolycus* sp.	China	DQ181049	DQ181123	DQ180975	DQ181197		UPOL 000L18	LLyMac1	Bocak et al. 2008
Lycidae	Lycinae	*Thonalmus sinuaticostis*	Montserrat	DQ181093	DQ181167	DQ181019	DQ181241		UPOL 000594	LLyThos	Bocak et al. 2008
Lycidae	Lycinae	*Lyponia nigrohumeralis*	China	DQ181048	DQ181122	DQ180974	DQ181196		UPOL 000L17	LLyLyp1	Bocak et al. 2008
Lycidae	Lycinae	*Lycus* sp.	South Africa	DQ181039	DQ181113	DQ180965	DQ181187		UPOL 000L03	LLyLycu	Bocak et al. 2008
Lycidae	Lycinae	*Idiopteron biplagiatum*	Ecuador	DQ181057	DQ181131	DQ180983	DQ181205		UPOL 000M44	LLyLepi	Bocak et al. 2008
Lycidae	Lycinae	*Metriorrhynchus lineatus*	Malaysia	DQ181040	DQ181114	DQ180966	DQ181188		UPOL 000L05	LLyMet3	Bocak et al. 2008
Lycidae	Lycinae	*Calochromus* sp.	China	DQ181047	DQ181121	DQ180973	DQ181195		UPOL 000L16	LlyCal1	Bocak et al. 2008
Lycidae	Lycinae	*Eropterus nothus*	Japan	DQ181082	DQ181156	DQ181008	DQ181230		UPOL 000579	LLyEre1	Bocak et al. 2008
Lampyridae	Lampyrinae	*Vesta* sp.	Indonesia	DQ100511	DQ198760	DQ198669	DQ198592		UPOL 000M17	lamVest	Bocakova et al. 2007
Lampyridae	Luciolinae	*Curtos* sp.	Indonesia	DQ100513	DQ198761	DQ198671	DQ198594		UPOL 000M16	lamCurs	Bocakova et al. 2007
Lampyridae	Ototretinae	gen. sp.	Indonesia	DQ100521	DQ198764	DQ198679	DQ198602		UPOL 000M37	lamOti2	Bocakova et al. 2007
Lampyridae	Ototretinae	*Lamellipalpus pacholatkoi*	India	KF625664	KF626254	KF625955	KF625363		UPOL RK0379	R379LAM	Kundrata et al. 2014
Lampyridae		gen. sp.	South Africa	KF625638	KF626239	KF625929	KF625337		UPOL RK0093	R093LAM	Kundrata et al. 2014
Lampyridae		gen. sp.	Indonesia	KF625640	KF626240	KF625931	KF625339		UPOL RK0096	R096LAM	Kundrata et al. 2014
Lampyridae		gen. sp.	Philippines	KF625643	KF626242	KF625934	KF625342		UPOL RK0099	R099LAM	Kundrata et al. 2014
Lampyridae		gen. sp.	Malaysia	KF625644	KF626243	KF625935	KF625343		UPOL RK0101	R101LAM	Kundrata et al. 2014
Lampyridae		gen. sp.	Indonesia	KF625648	KF626244	KF625939	KF625347		UPOL RK0106	R106LAM	Kundrata et al. 2014
Lampyridae		gen. sp.	Indonesia	KF625649	KF626245	KF625940	KF625348		UPOL RK0107	R107LAM	Kundrata et al. 2014
Lampyridae		gen. sp.	Malaysia	KF625653	KF626248	KF625944	KF625352		UPOL RK0111	R111LAM	Kundrata et al. 2014
Lampyridae		gen. sp.	Indonesia	KF625656	KF626249	KF625947	KF625355		UPOL RK0118	R118LAM	Kundrata et al. 2014
Lampyridae		gen. sp.	Cameroon	KF625657	KF626250	KF625948	KF625356		UPOL RK0173	R173LAM	Kundrata et al. 2014
Lampyridae		gen. sp.	French Guyana	KF625660	KF626251	KF625951	KF625359		UPOL RK0374	R374LAM	Kundrata et al. 2014
Lampyridae		gen. sp.	French Guyana	KF625661	KF626252	KF625952	KF625360		UPOL RK0375	R375LAM	Kundrata et al. 2014
Lampyridae		gen. sp.	Japan	KF625663	KF626253	KF625954	KF625362		UPOL RK0378	R378LAM	Kundrata et al. 2014
Lampyridae		gen. sp.	South Africa	KF625665	KF626255	KF625956	KF625364		UPOL RK0380	R380LAM	Kundrata et al. 2014
Lampyridae		gen. sp.	Philippines	KF625670	KF626259	KF625961	KF625369		UPOL RK0385	R385LAM	Kundrata et al. 2014
Lampyridae		gen. sp.	Panama	KF625671	KF626260	KF625962	KF625370		UPOL RK0386	R386LAM	Kundrata et al. 2014
Lampyridae		gen. sp.	Panama	KF625672	KF626261	KF625963	KF625371		UPOL RK0387	R387LAM	Kundrata et al. 2014
Lampyridae		gen. sp.	Indonesia	KF625675	KF626262	KF625966	KF625374		UPOL RK0390	R390LAM	Kundrata et al. 2014
Lampyridae		gen. sp.	Indonesia	KF625678	KF626265	KF625969	KF625377		UPOL RK0393	R393LAM	Kundrata et al. 2014
Lampyridae		gen. sp.	Indonesia	KF625679	KF626266	KF625970	KF625378		UPOL RK0394	R394LAM	Kundrata et al. 2014
Lampyridae		gen. sp.	Indonesia	KF625680	KF626267	KF625971	KF625379		UPOL RK0395	R395LAM	Kundrata et al. 2014
Lampyridae		gen. sp.	Malaysia	KF625683	KF626269	KF625974	KF625382		UPOL RK0398	R398LAM	Kundrata et al. 2014
Cantharidae	indet.	gen. sp.	Papua New Guinea	KF625598	KF626200	KF625891	KF625298		UPOL RK0199	R199CAN	Kundrata et al. 2014
Cantharidae	Cantharinae	*Rhagonycha lignosa*	United Kingdom	AF451939	DQ198770	DQ198687	DQ198610		BMNH 679176	canRhLi	Bocakova et al. 2007
Cantharidae	Cantharinae	*Athemus* sp.	USA	KF625615	KF626217	KF625907	KF625314		UPOL 001301	1301CAN	Kundrata et al. 2014
Cantharidae	Cantharinae	*Themus* sp.	Japan	KF625616	KF626218	KF625908	KF625315		UPOL 001302	1302CAN	Kundrata et al. 2014
Cantharidae	Cantharinae	*Podabrus temporalis*	Japan	KF625621	KF626223	KF625913	KF625320		UPOL 001307	1307CAN	Kundrata et al. 2014
Cantharidae	Cantharinae	*Habronychus* sp.	Japan	KF625625	KF626227	KF625917	KF625324		UPOL 001311	1311CAN	Kundrata et al. 2014
Cantharidae	Cantharinae	*Lycocerus* sp.	Laos	KF625591	KF626193	KF625886	KF625291		UPOL RK0176	R176CAN	Kundrata et al. 2014
Cantharidae	Silinae	*Laemoglyptus* sp.	Indonesia	KF625601	KF626203	KF625893	KF625301		UPOL 001287	1287CAN	Kundrata et al. 2014
Cantharidae	Silinae	*Asiosilis* sp.	Indonesia	DQ100530	DQ198773	DQ198690	DQ198613		UPOL 000M13	canAsis	Bocakova et al. 2007
Cantharidae	Silinae	gen. sp.	Indonesia	KF625607	KF626209	KF625899	KF625306		UPOL 001293	1293CAN	Kundrata et al. 2014
Cantharidae	Silinae	gen. sp.	Indonesia	KF625608	KF626210	KF625900	KF625307		UPOL 001294	1294CAN	Kundrata et al. 2014
Cantharidae	Silinae	gen. sp.	Indonesia	KF625609	KF626211	KF625901	KF625308		UPOL 001295	1295CAN	Kundrata et al. 2014
Cantharidae	Silinae	gen. sp.	Ethiopia	KF625588	KF626190	KF625883	KF625288		UPOL RK0154	R154CAN	Kundrata et al. 2014
Cantharidae	Chauliognathinae	*Chauliognathus* sp.	USA	KF625600	KF626202	KF625892	KF625300		UPOL 001250	1250CAN	Kundrata et al. 2014
Cantharidae	Chauliognathinae	*Ichthyurus* sp.	Indonesia	DQ100531	DQ198774	DQ198691	DQ198614		UPOL 000M12	canIchs	Bocakova et al. 2007
Cantharidae	Chauliognathinae	*Microichthyurus* sp.	Japan	KF625619	KF626221	KF625911	KF625318		UPOL 001305	1305CAN	Kundrata et al. 2014
Cantharidae	Chauliognathinae	*Trypherus mutilatus*	Japan	KF625622	KF626224	KF625914	KF625321		UPOL 001308	1308CAN	Kundrata et al. 2014
Cantharidae	Chauliognathinae	gen. sp.	Ethiopia	KF625589	KF626191	KF625884	KF625289		UPOL RK0155	R155CAN	Kundrata et al. 2014
Cantharidae	Chauliognathinae	gen. sp.	Philippines	KF625594	KF626196	KF625888	KF625294		UPOL RK0179	R179CAN	Kundrata et al. 2014

Cantharidae	Malthininae	*Malthinus* sp.	Czech Republic	KF625627	KF626229	KF625919	KF625326	UPOL 001313	1313CAN	Kundrata et al. 2014
Cantharidae	Malthininae	*Malthodes* sp.	France	DQ100532	DQ198776	DQ198693	DQ198616	UPOL 000M20	canMas1	Bocakova et al. 2007
Cantharidae	Malthininae	*Inmalthodes* sp.	Indonesia	KF625603	KF626205	KF625895	KF625303	UPOL 001289	1289CAN	Kundrata et al. 2014
Cantharidae	Malthininae	gen. sp.	Japan	KF625626	KF626228	KF625918	KF625325	UPOL 001312	1312CAN	Kundrata et al. 2014
Cantharidae	Malthininae	gen. sp.	Ethiopia	KF625590	KF626192	KF625885	KF625290	UPOL RK0157	R157CAN	Kundrata et al. 2014
Cantharidae	Malthininae	gen. sp.	Cameroon	KF625595	KF626197	KF625889	KF625295	UPOL RK0180	R180CAN	Kundrata et al. 2014
Omalisidae	Thilmaninae	*Pseudeuanoma* sp.	Greece	HQ333832	KF626300	HQ333738	HQ334011	UPOL RK0079	R079OMAp	Kundrata Bocak 2011
Omalisidae	Omalisinae	*Omalisus fontisbellaquei*	Czech Republic	AF451948	DQ198749	DQ198658	DQ198580	UPOL 000377	omaOmal	Bocakova et al. 2007
Omalisidae	Paradrilinae	*Paradrilus opacus*	Spain	KJ909284	KJ909285	N	KJ909287	UPOL RK0626	R626OMA	Kundrata et al. 2015
Rhagophthalmidae		*Rhagophthalmus* sp.	India	DQ100508	DQ198756	DQ198665	DQ198587	UPOL 000155	pheRha1	Bocakova et al. 2007
Rhagophthalmidae		*Mimoochotyra* sp.	Malaysia	DQ100505	DQ198753	DQ198662	DQ198584	UPOL 000M30	pheMimo	Bocakova et al. 2007
Rhagophthalmidae		*Bicladodrilus* sp.	China	DQ100507	DQ198755	DQ198664	DQ198586	UPOL 000M35	pheBicl	Bocakova et al. 2007
Rhagophthalmidae		gen. sp.	Indonesia	KF625717	KF626305	KF626005	KF625410	UPOL 001359	1359PHE	Kundrata et al. 2014
Rhagophthalmidae		gen. sp.	Thailand	KF625716	KF626304	KF626004	KF625409	UPOL RK0370	R370RHA	Kundrata et al. 2014
Rhagophthalmidae		gen. sp.	Indonesia	DQ100506	DQ198754	DQ198663	DQ198585	UPOL 000M31	pheRha2	Bocakova et al. 2007
Phengodidae		*Phengodes* sp.	USA	DQ100504	DQ198752	DQ198661	DQ198583	UPOL 000M29	phePhe1	Bocakova et al. 2007
Phengodidae		*Phengodes* sp.	Panama	KF625726	KF626313	KF626012	KF625419	UPOL 001241	1241PHE	Kundrata et al. 2014
Phengodidae		gen. sp.	Panama	KF625723	KF626310	KF626009	KF625416	UPOL RK0366	R366PHE	Kundrata et al. 2014
Phengodidae		gen. sp.	Belize	KF625719	KF626306	KF626007	KF625412	UPOL RK0361	R361PHE	Kundrata et al. 2014
Phengodidae		gen. sp.	Panama	KF625721	KF626308	KF626008	KF625414	UPOL RK0364	R364PHE	Kundrata et al. 2014
Phengodidae		gen. sp.	Panama	KF625727	KF626314	KF626013	KF625420	UPOL 001243	1243PHE	Kundrata et al. 2014
Phengodidae		gen. sp.	Panama	KF625728	KF626315	KF626014	KF625421	UPOL 001245	1245PHE	Kundrata et al. 2014
Phengodidae		gen. sp.	Panama	KF625729	KF626316	KF626015	KF625422	UPOL 001246	1246PHE	Kundrata et al. 2014
Phengodidae		gen. sp.	Panama	KF625730	KF626317	KF626016	KF625423	UPOL 001247	1247PHE	Kundrata et al. 2014
Phengodidae		gen. sp.	Panama	KF625736	KF626320	KF626020	KF625430	UPOL 001351	1351PHE	Kundrata et al. 2014
Elateridae	Agrypninae	*Agrypnus murinus*	Slovakia	AF451943	DQ198735	DQ198645	DQ198567	UPOL 001049	elaAGRam	Bocakova et al. 2007
Elateridae	Agrypninae	*Adelocera* sp.	Japan	HQ333778	HQ333873	HQ333694	HQ333961	UPOL RK0025	R025EAgr	Kundrata Bocak 2011
Elateridae	Agrypninae	*Conoderus* sp	Panama	HQ333747	HQ333842	HQ333666	HQ333932	UPOL 001417	1417EAgr	Kundrata Bocak 2011
Elateridae	Agrypninae	*Drasterius bimaculatus*	Slovakia	HQ333793	HQ333888	HQ333704	HQ333975	UPOL RK0040	R040EAgr	Kundrata Bocak 2011
Elateridae	Agrypninae	*Platycrepidius* sp.	Panama	HQ333748	HQ333843	HQ333667	HQ333933	UPOL 001418	1418EAgr	Kundrata Bocak 2011
Elateridae	Agrypninae	*Pyrophorus* sp.	French Guyana	KF625742	KF626325	KF626030	KF625436	UPOL RK0213	R213EAgr	Kundrata et al. 2014
Elateridae	Agrypninae	*Chalcolepidius* sp.	French Guyana	KF625743	KF626326	KF626031	KF625437	UPOL RK0219	R219EAgr	Kundrata et al. 2014
Elateridae	Agrypninae	*Cryptalaus* sp.	Malaysia	HQ333834	HQ333926	HQ333740	HQ334014	UPOL RK0082	R082EAgr	Kundrata Bocak 2011
Elateridae	Agrypninae	*Selasia* sp.	South Africa	HQ333824	HQ333919	HQ333731	HQ334004	UPOL RK0071	R071DRIs	Kundrata Bocak 2011
Elateridae	Agrypninae	*Drilus flavescens*	Malta	DQ100501	DQ198748	DQ198657	DQ198579	UPOL 001046	driDril	Bocakova et al. 2007
Elateridae	Cardiophorinae	*Dicronychus rubripes*	Slovakia	HQ333764	HQ333859	KF626023	HQ333947	UPOL RK0011	R011ECar	Kundrata Bocak 2011
Elateridae	Cardiophorinae	gen. sp.	Indonesia	HQ333784	HQ333879	KF626025	HQ333966	UPOL RK0031	R031ECar	Kundrata Bocak 2011
Elateridae	Cardiophorinae	*Cardiophorus erichsoni*	Slovakia	HQ333790	HQ333885	HQ333701	HQ333972	UPOL RK0037	R037ECar	Kundrata Bocak 2011
Elateridae	Cardiophorinae	gen. sp.	Namibia	AF451942	DQ198739	DQ198649	DQ198571	BMNH 679341	elaCARid	Bocakova et al. 2007
Elateridae	Dendrometrinae	*Nothodes parvulus*	Slovakia	HQ333763	HQ333858	HQ333681	KF625443	UPOL RK0010	R010EDen	Kundrata Bocak 2011
Elateridae	Dendrometrinae	*Athous vittatus*	Czech Republic	HQ333755	HQ333850	HQ333674	HQ333939	UPOL RK0002	R002EDen	Kundrata Bocak 2011
Elateridae	Dendrometrinae	*Pheletes quercus*	Czech Republic	HQ333775	HQ333870	HQ333692	HQ333958	UPOL RK0022	R022EDen	Kundrata Bocak 2011
Elateridae	Dendrometrinae	*Cidnopus pilosus*	Slovakia	HQ333792	HQ333887	HQ333703	HQ333974	UPOL RK0039	R039EDen	Kundrata Bocak 2011
Elateridae	Dendrometrinae	*Anostirus purpureus*	Slovakia	HQ333761	HQ333856	HQ333679	HQ333945	UPOL RK0008	R008EDen	Kundrata Bocak 2011
Elateridae	Dendrometrinae	*Neopristilophus serrifer*	Japan	HQ333765	HQ333860	HQ333682	HQ333948	UPOL RK0012	R012EDen	Kundrata Bocak 2011
Elateridae	Dendrometrinae	*Selatosomus latus*	Czech Republic	HQ333774	HQ333869	HQ333691	HQ333957	UPOL RK0021	R021EDen	Kundrata Bocak 2011
Elateridae	Dendrometrinae	*Platiana* sp.	Indonesia	HQ333782	HQ333877	HQ333696	HQ333964	UPOL RK0029	R029EDim	Kundrata Bocak 2011
Elateridae	Dendrometrinae	*Hypolithus* sp.	Japan	HQ333795	HQ333890	HQ333705	HQ333977	UPOL RK0042	R042EHyp	Kundrata Bocak 2011
Elateridae	Dendrometrinae	*Semiotus* sp.	Chile	HQ333799	HQ333894	HQ333709	HQ333981	UPOL RK0046	R046ESem	Kundrata Bocak 2011
Elateridae	Dendrometrinae	*Oxynopterus* sp.	Philippines	HQ333800	HQ333895	HQ333710	HQ333982	UPOL RK0047	R047EOxy	Kundrata Bocak 2011
Elateridae	Dendrometrinae	*Denticollis linearis*	Czech Republic	DQ100498	DQ198741	DQ198651	DQ198573	UPOL 000M25	elaDENdl	Bocakova et al. 2007
Elateridae	Elaterinae	*Cebrio* sp.	Italy	KF625745	KF626329	KF626040	KF625440	UPOL RK0142	R142ECeb	Kundrata et al. 2014
Elateridae	Elaterinae	*Octinodes* sp.	Panama	HQ333749	HQ333844	HQ333668	HQ333934	UPOL 001419	1419EEla	Kundrata Bocak 2011
Elateridae	Elaterinae	*Elater* sp.	Japan	HQ333766	HQ333861	HQ333683	HQ333949	UPOL RK0013	R013EEla	Kundrata Bocak 2011
Elateridae	Elaterinae	*Tomicephalus* sp.	Panama	HQ333750	HQ333845	HQ333669	HQ333935	UPOL 001420	1420EEla	Kundrata Bocak 2011
Elateridae	Elaterinae	*Anoplischius* sp.	Panama	HQ333745	HQ333840	HQ333664	HQ333930	UPOL 001415	1415EEla	Kundrata Bocak 2011

Elateridae	Elaterinae	*Ampedus sinuatus*	Slovakia	HQ333791	HQ333886	HQ333702	HQ333973	UPOL RK0038	R038EEla	Kundrata Bocak 2011
Elateridae	Elaterinae	*Agriotes acuminatus*	Czech Republic	HQ333756	HQ333851	HQ333675	HQ333940	UPOL RK0003	R003EEla	Kundrata Bocak 2011
Elateridae	Elaterinae	*Melanotus villosus*	Czech Republic	HQ333754	HQ333849	HQ333673	HQ333938	UPOL RK0001	R001EEla	Kundrata Bocak 2011
Elateridae	Elaterinae	*Priopus ornatus*	Laos	HQ333785	HQ333880	HQ333698	HQ333967	UPOL RK0032	R032EEla	Kundrata Bocak 2011
Elateridae	Elaterinae	*Anchastus* sp.	Indonesia	HQ333804	HQ333899	HQ333714	HQ333986	UPOL RK0051	R051EEla	Kundrata Bocak 2011
Elateridae	Morostomatinae	*Diplophoenicus* sp.	Madagascar	KF625753	KF626335	KF626050	KF625454	UPOL RK0145	R145E	Kundrata et al. 2014
Elateridae	Negastriinae	*Zorochros* sp.	Malaysia	HQ333796	HQ333891	HQ333706	HQ333978	UPOL RK0043	R043ENeg	Kundrata Bocak 2011
Elateridae	Negastriinae	*Quasimus* sp.	Malaysia	HQ333802	HQ333897	HQ333712	HQ333984	UPOL RK0049	R049ENeg	Kundrata Bocak 2011

BYRRHOIDEA

Byrrhidae	Byrrhinae	*Byrrhus pilula*	United Kingdom	AF427604	DQ198705	DQ198625	DQ198548	BMNH 679172	BYRByByr	Bocakova et al. 2007
Byrrhidae	Byrrhinae	*Byrrhus* sp.	France	KX092934	KX093068	N	KX092799	UPOL RK0651	R651BYR	present study
Byrrhidae	Byrrhinae	*Curimus erichsoni*	Czech Republic	KX092935	KX093069	KX092676	KX092800	UPOL RK0652	R652BYR	present study
Byrrhidae	Byrrhinae	gen. sp.	–	EF209486	N	EF209426	EF209546	FC_C11	BYRsp01	Ciampor & Ribera
Byrrhidae	Byrrhinae	*Simplocaria* sp.	–	KM364160	KM364303	N	N	BT0017	BYRsimp	Evans et al. 2014
Byrrhidae		*Chalcosphaerium* sp.	–	EF214158	N	EF214030	EF214233	BMNH 668332	BYRch02	Hunt et al. 2007
Byrrhidae	Syncalyptinae	*Chaetophora spinosa*	United Kingdom	AF451929	DQ198706	N	N	BMNH 679203	BYRByCha	Bocakova et al. 2007
Byrrhidae	Syncalyptinae	*Curimopsis setigera*	United Kingdom	AF451930	DQ198707	N	N	BMNH 679204	BYRByCur	Bocakova et al. 2007
Byrrhidae	Syncalyptinae	gen. sp.	–	EF209488	N	EF209428	EF209548	FC_F01	BYRsp02	Ciampor & Ribera
Callirhipidae		*Callirhipis* sp.	–	KM364162	KM364305	N	N	CO129	CALca01	Evans et al. 2014
Callirhipidae		*Calliriphis* sp.	–	EF209489	N	EF209429	EF209549	FC_222	CALca02	Ciampor & Ribera
Callirhipidae		*Callirhipis dissimilis*	Malaysia	KX092944	KX093078	KX092685	KX092809	UPOL RK0643	R643CAL	present study
Callirhipidae		*Callirhipis suturalis*	Malaysia	KX092942	KX093076	KX092683	KX092807	UPOL RK0644	R644CAL	present study
Callirhipidae		*Callirhipis* sp.	Indonesia	KX092943	KX093077	KX092684	KX092808	UPOL RK0655	R655CAL	present study
Callirhipidae		*Ennometes* sp.	–	EF209490	N	EF209430	EF209550	FC_223	CALenno	Ciampor & Ribera
Callirhipidae		*Ennometes* cf. *testaceicornis*	Malaysia	KX092946	KX093080	KX092686	KX092810	UPOL RK0645	R645CAL	present study
Callirhipidae		*Horatocera nipponica*	Japan	KF625510	KF626111	N	N	UPOL 001248	1248CAL	Kundrata et al. 2014
Callirhipidae		*Simianides laportei*	Panama	KX092945	KX093079	N	N	UPOL RK0654	R654CAL	present study
Callirhipidae		gen. sp.	Malaysia	DQ100490	DQ198726	DQ198637	DQ198560	UPOL 000M23	BYRCaCal	Bocakova et al. 2007
Callirhipidae		gen. sp.	Malaysia	KF625511	KF626112	KF625818	KF625211	UPOL 001249	1249CAL	Kundrata et al. 2014
Chelonariidae		*Chelonarium* sp.	–	EF209493	N	EF209433	EF209553	FC_E16	CHEch01	Ciampor & Ribera
Chelonariidae		*Chelonarium* sp.	–	EF209492	N	EF209432	EF209552	FC_A19	CHEch02	Ciampor & Ribera
Chelonariidae		gen. sp.	Indonesia	DQ100488	DQ198724	DQ198635	DQ198558	UPOL 000M06	BYRChChe	Bocakova et al. 2007
Chelonariidae		gen. sp.	Indonesia	KF625509	KF626110	KF625817	KF625210	UPOL 001324	1324CHE	Kundrata et al. 2014
Chelonariidae		gen. sp.	China	KX092996	KX093124	KX092731	KX092857	UPOL RK0704	R704CHE	present study
Chelonariidae		gen. sp.	China	KX092997	KX093125	KX092732	KX092858	UPOL RK0705	R705CHE	present study
Chelonariidae		gen. sp.	China	KX092998	KX093126	KX092733	KX092859	UPOL RK0706	R706CHE	present study
Chelonariidae		gen. sp.	Malaysia	KX092999	KX093127	N	KX092860	UPOL RK0707	R707CHE	present study
Dryopidae	*incertae sedis*	*Ceradryops matei*	–	EF209494	N	EF209434	EF209554	FC_C12	DRYCema	Ciampor & Ribera
Dryopidae		gen. sp.	–	EF209497	N	EF209437	EF209557	FC_D17	DRYDrys	Ciampor & Ribera
Dryopidae		*Dryops costae*	–	EF209496	N	EF209436	EF209556	FC_B14	DRYDryc	Ciampor & Ribera
Dryopidae		*Pomatinus substriatus*	United Kingdom	AF451924	DQ198708	DQ198626	DQ198549	BMNH 693616	BYRDrPom	Bocakova et al. 2007
Dryopidae		gen. sp.	–	EF209495	N	EF209435	EF209555	FC_E02	DRYspec	Ciampor & Ribera
Dryopidae		*Helichus* sp.	–	EF209498	N	EF209438	EF209558	FC_B20	DRYHeli	Ciampor & Ribera
Dryopidae		*Pachyparnus* sp.	–	EF209499	N	EF209439	EF209559	FC_A17	DRYPach	Ciampor & Ribera
Dryopidae		*Sostea* sp.	–	EF209500	N	EF209440	EF209560	FC_405	DRYSost	Ciampor & Ribera
Dryopidae		*Dryops* sp.	Madagascar	KX092971	KX093101	KX092709	KX092835	UPOL RK0672	R672DRY	present study
Dryopidae		*Sostea* sp.	Cambodia	KX092983	KX093112	KX092721	KX092846	UPOL RK0674	R674DRY	present study
Dryopidae		*Sostea* sp.	Malaysia	KX092984	KX093113	KX092722	N	UPOL RK0675	R675DRY	present study
Dryopidae		*Sostea* sp.	Malaysia	KX092989	KX093118	KX092725	KX092851	UPOL RK0676	R676DRY	present study
Dryopidae		*Sostea* sp.	Malaysia	KX092985	KX093114	KX092723	KX092847	UPOL RK0677	R677DRY	present study
Dryopidae		*Sostea* sp.	Indonesia	KX092986	KX093115	N	KX092848	UPOL RK0678	R678DRY	present study
Dryopidae		*Sostea* sp.	Indonesia	KX092987	KX093116	KX092724	KX092849	UPOL RK0679	R679DRY	present study
Dryopidae		*Sostea* sp.	Indonesia	KX092988	KX093117	N	KX092850	UPOL RK0680	R680DRY	present study
Dryopidae		*Sostea* sp.	Indonesia	KX092977	KX093107	KX092715	KX092841	UPOL RK0681	R681DRY	present study

Dryopidae		*Sostea* sp.	Indonesia	KX092978	KX093108	KX092716	N	UPOL RK0682	R682DRY	present study
Dryopidae		*Sostea* sp.	Indonesia	KX092980	KX093110	KX092718	KX092843	UPOL RK0683	R683DRY	present study
Dryopidae		*Sostea* sp.	Indonesia	KX092981	N	KX092719	KX092844	UPOL RK0685	R685DRY	present study
Dryopidae		*Sostea* sp.	Indonesia	KX092982	KX093111	KX092720	KX092845	UPOL RK0686	R686DRY	present study
Dryopidae		*Sostea* sp.	Philippines	KX092990	KX093119	KX092726	KX092852	UPOL RK0687	R687DRY	present study
Dryopidae		*Sostea* sp.	Philippines	KX092992	KX093120	KX092728	KX092854	UPOL RK0688	R688DRY	present study
Dryopidae		*Sostea* sp.	Philippines	KX092991	N	KX092727	KX092853	UPOL RK0689	R689DRY	present study
Dryopidae		*Sostea* sp.	China	KX092979	KX093109	KX092717	KX092842	UPOL RK0692	R692DRY	present study
Dryopidae		*Sostea* sp.	Malaysia	KX092993	KX093121	N	KX092855	UPOL RK0715	R715DRY	present study
Dryopidae		*Sostea* sp.	Malaysia	KX092994	KX093122	KX092729	N	UPOL RK0716	R716DRY	present study
Dryopidae		*Dryops lutulentus*	France	KX092976	KX093106	KX092714	KX092840	UPOL RK0718	R718DRY	present study
Dryopidae		gen. sp.	Indonesia	KX092972	KX093102	KX092710	KX092836	UPOL RK0733	R733DRY	present study
Dryopidae		gen. sp. (nov.)	Cameroon	KX092995	KX093123	KX092730	KX092856	UPOL RK0738	R738DRY	present study
Dryopidae		*Pachyparnus* sp.	Indonesia	KX092973	KX093103	KX092711	KX092837	UPOL RK0740	R740DRY	present study
Dryopidae		gen. sp.	Indonesia	KX092974	KX093104	KX092712	KX092838	UPOL RK0742	R742DRY	present study
Dryopidae		*Pachyparnus* sp.	Malaysia	KX092975	KX093105	KX092713	KX092839	UPOL RK0745	R745DRY	present study
Elmidae	Elminae	*Ancyronyx procerus*	–	DQ266489	N	DQ266478	DQ266500	MNCN-FC-B05	ELMAnpr	Ciampor & Ribera
Elmidae	Elminae	*Austrolimnius* sp.	–	EF209503	N	EF209443	EF209563	FC_E14	ELMAust	Ciampor & Ribera
Elmidae	Elminae	*Cleptelmis* sp.	–	EF209504	N	EF209444	N	FC_E13	ELMClep	Ciampor & Ribera
Elmidae	Elminae	*Dupophilus* sp.	–	EF209506	N	EF209446	EF209566	FC_D04	ELMDupo	Ciampor & Ribera
Elmidae	Elminae	*Elmis latreillei*	–	EF209509	N	EF209449	EF209569	FC_A13	ELMElla	Ciampor & Ribera
Elmidae	Elminae	*Elmis maugetii*	Slovakia	AF451916	DQ198709	N	N	BMNH 693612	BYRElElm	Bocakova et al. 2007
Elmidae	Elminae	*Esolus angustatus*	–	EF209510	N	EF209450	EF209570	FC_B12	ELMEsan	Ciampor & Ribera
Elmidae	Elminae	*Graphelmis clermonti*	–	DQ266483	N	DQ266473	DQ266494	MNCN-FC-D14	ELMGrcl	Ciampor & Ribera
Elmidae	Elminae	*Graphelmis obesa*	–	DQ266481	N	DQ266471	DQ266492	MNCN-FC-D16	ELMGrob	Ciampor & Ribera
Elmidae	Elminae	*Graphelmis picea*	–	DQ266482	N	DQ266472	DQ266493	MNCN-FC-B09	ELMGrpi	Ciampor & Ribera
Elmidae	Elminae	*Hedyselmis* sp.	–	EU311733	N	EU311732	EU311731	FC2008	ELMHeds	Ciampor & C.-Z.
Elmidae	Elminae	*Hedyselmis opis*	–	DQ005517	N	DQ005519	DQ005515	-	ELMHedo	Ciampor & Ribera
Elmidae	Elminae	*Heterlimnius* sp.	–	EF209511	N	EF209451	EF209571	FC_D18	ELMHete	Ciampor & Ribera
Elmidae	Elminae	*Homalosolus hospitalis*	Malaysia	AF451921	DQ198710	N	N	BMNH 693626	BYRElHom	Bocakova et al. 2007
Elmidae	Elminae	*Leptelmis* sp.	–	EF209513	N	EF209453	EF209573	FC_A10	ELMLept	Ciampor & Ribera
Elmidae	Elminae	*Limnius intermedius*	–	DQ266485	N	DQ266475		MNCN-FC-B10	ELMLimn	Ciampor & Ribera
Elmidae	Elminae	*Limnius perrisi*	–	AF451915	AJ862767	AJ862736	AJ862800	BMNH 693613	BYRElLip	Bocakova et al. 2007
Elmidae	Elminae	*Luchoelmis* sp.	–	EF209515	N	EF209455	EF209575	FC_D19	ELMLuch	Ciampor & Ribera
Elmidae	Elminae	*Macrelmis leonilae*	Mexico	JQ292972	N	N	JQ479013	MZFC Macle–1l	ELMMele	Curiel-Alvarez & M.
Elmidae	Elminae	*Macrelmis scutellaris*	Mexico	JQ292977	N	N	JQ479018	MZFC Macsc–1l	ELMMesc	Curiel-Alvarez & M.
Elmidae	Elminae	*Macrelmis striata*	Mexico	JQ292969	N	N	JQ479010	MZFC Macst–1a	ELMMest	Curiel-Alvarez & M.
Elmidae	Elminae	*Macronevia simplex*	–	EF209516	N	EF209456	EF209576	FC_A02	ELMMasi	Ciampor & Ribera
Elmidae	Elminae	*Macronychus quadrituberculatus*	Hungary	AF451920	DQ198713	EF209458	EF209578	BMNH 693611	BYRElMac	Ciampor & Ribera
Elmidae	Elminae	*Neocylloepus* sp.	–	EF209519	N	EF209459	EF209579	FC_E01	ELMNeoc	Ciampor & Ribera
Elmidae	Elminae	*Normandia* sp.	–	EF209520	N	EF209460	EF209580	FC_B08	ELMNorm	Ciampor & Ribera
Elmidae	Elminae	*Optioservus* sp.	–	EF209521	N	EF209461	EF209581	FC_E12	ELMOpti	Ciampor & Ribera
Elmidae	Elminae	*Oulimnius rivularis*	Portugal	AF451913	DQ198714	DQ198628	DQ198551	BMNH 679264	BYRElOul	Bocakova et al. 2007
Elmidae	Elminae	*Oulimnius bertrandi*	Spain	GU935698	N	GU935677	GU935722	FZ313	ELMOube	Ciampor & Kodada
Elmidae	Elminae	*Oulimnius fuscipes*	Morocco	GU935702	N	GU935680	GU935726	FZ126	ELMOufu	Ciampor & Kodada
Elmidae	Elminae	*Oulimnius troglodytes*	Portugal	GU935703	N	GU935682	GU935729	FZ114	ELMOutr	Ciampor & Kodada
Elmidae	Elminae	*Rhopalonychus levatorponderis*	–	DQ266488	N	DQ266477	DQ266499	MNCN-FC-B01	ELMRhop	Ciampor & Ribera
Elmidae	Elminae	*Riolus subviolaceus*	–	EF209525	N	EF209465	EF209585	FC_B07	ELMRiol	Ciampor & Ribera
Elmidae	Elminae	*Stenelmis canaliculata*	France	AF451919	DQ198716	N	N	BMNH 693614	BYRElSte	Bocakova et al. 2007
Elmidae	Elminae	*Vietelmis* sp.	–	EF209527	N	EF209467	EF209587	FC_A03	ELMViet	Ciampor & Ribera
Elmidae	Elminae	*Zaitzevia* sp.	–	EF209528	N	EF209468	EF209588	FC_E08	ELMZait	Ciampor & Ribera
Elmidae	Elminae	*Stenelmis* sp.	China	KX093003	KX093131	N	KX092864	UPOL RK0713	R713ELM	present study
Elmidae	Elminae	*Stenelmis* sp.	Malaysia	KX093004	KX093132	KX092737	KX092865	UPOL RK0720	R720ELM	present study
Elmidae	Elminae	*Stenelmis* sp.	Malaysia	KX093005	KX093133	N	KX092866	UPOL RK0721	R721ELM	present study
Elmidae	Elminae	*Stenelmis* sp.	Malaysia	KX093006	KX093134	N	KX092867	UPOL RK0722	R722ELM	present study
Elmidae	Elminae	*Graphelmis philemoni*	Malaysia	KX093007	N	KX092738	KX092868	UPOL RK0723	R723ELM	present study

Elmidae	Elminae	*Stenelmis* sp.	Malaysia	KX093008	KX093135	EF209466	KX092869		UPOL RK0724/FC19*	R724ELM	present study
Elmidae	Elminae	*Stenelmis* sp.	Laos	KX093009	KX093136	KX092739	KX092870		UPOL RK0731	R731ELM	present study
Elmidae	Elminae	*Rhopalonychus* sp.	Indonesia	KX093011	N	N	KX092872		UPOL RK0735	R735ELM	present study
Elmidae	Elminae	*Nesonychus* sp.	Indonesia	KX093012	KX093138	KX092741	KX092873		UPOL RK0736	R736ELM	present study
Elmidae	Elminae	*Stenelmis* sp.	Indonesia	KX093013	KX093139	N	KX092874		UPOL RK0737	R737ELM	present study
Elmidae	Elminae	*Graphelmis* sp.	Indonesia	KX093015	N	KX092743	KX092876		UPOL RK0741	R741ELM	present study
Elmidae	Elminae	*Ancyronyx raffaelacatharina*	Indonesia	KX093016	KX093141	KX092744	KX092877		UPOL RK0743	R743ELM	present study
Elmidae	Elminae	*Stenelmis* sp.	Indonesia	KX093017	KX093142	N	KX092878		UPOL RK0744	R744ELM	present study
Elmidae	Elminae	*Stenelmis* sp.	Malaysia	KX093018	KX093143	KX092745	KX092879		UPOL RK0746	R746ELM	present study
Elmidae	Elminae	*Stenelmis* sp.	Malaysia	KX093019	KX093144	N	KX092880		UPOL RK0747	R747ELM	present study
Elmidae	Elminae	Elminae sp.	–	EF209508	N	EF209448	EF209568		FC_E04	ELME04	Ciampor & Ribera
Elmidae	Elminae	Elminae sp.	–	EF209507	N	EF209447	EF209567		FC_E03	ELME03	Ciampor & Ribera
Elmidae	Elminae	Elminae sp.	–	EF209514	N	EF209454	EF209574		FC_D20	ELMD20	Ciampor & Ribera
Elmidae	Larainae	*Dryopomorphus* sp.	–	EF209505	N	EF209445	EF209565		FC_C16	ELMDryo	Ciampor & Ribera
Elmidae	Larainae	*Dryopomorphus* sp.	Indonesia	KX093010	KX093137	KX092740	KX092871		UPOL RK0732	R732ELM	present study
Elmidae	Larainae	*Dryopomorphus* sp.	Malaysia	KX093000	KX093128	KX092734	KX092861		UPOL RK0717	R717ELM	present study
Elmidae	Larainae	*Potamodytes* sp.	South Africa	AF451912	DQ198715	DQ198629	DQ198552		BMNH 679360	BYRElPos	Bocakova et al. 2007
Elmidae	Larainae	*Potamodytes* sp.	–	EF209522	N	EF209462	EF209582		FC_D01	ELMPotm	Ciampor & Ribera
Elmidae	Larainae	*Potamodytes* sp.	Madagascar	KX093001	KX093129	KX092735	KX092862		UPOL RK0659	R659ELM	present study
Elmidae	Larainae	*Potamodytes* sp.	Madagascar	KX093002	KX093130	KX092736	KX092863		UPOL RK0660	R660ELM	present study
Elmidae	Larainae	*Potamodytes* sp.	Zambia	KX093014	KX093140	KX092742	KX092875		UPOL RK0739	R739ELM	present study
Elmidae	Larainae	*Potamophilus acuminatus*	–	AF451911	N	EF209464	EF209584		EC_E07	BYRElPot	Ciampor & Ribera
Elmidae	Larainae	Larainae sp.	–	EF209512	N	EF209452	EF209572		FC_E15	ELMLars	Ciampor & Ribera
Elmidae	Larainae	*Potamophilinus* sp.	–	EF209523	N	EF209463	EF209583		FC_C13	ELMPo13	Ciampor & Ribera
Elmidae	Larainae	*Potamophilinus* sp.	–	DQ266490	N	DQ266479	DQ266501		MNCNFCA16	ELMPo16	Ciampor & Ribera
Eulichadidae		*Eulichas* sp.	Malaysia	DQ100489	DQ198725	DQ198636	DQ198559		UPOL 000M22	BYREuEul	Bocakova et al. 2007
Eulichadidae		*Eulichas* sp.	–	EF209529	N	EF209469	EF209589		FC_E06	EULeuli	Ciampor & Ribera
Eulichadidae		*Eulichas* cf. *fasciolata*	Malaysia	KX092937	KX093071	KX092678	KX092802		UPOL RK0646	R646EUL	present study
Eulichadidae		*Eulichas dudgeoni*	China	KX092936	KX093070	KX092677	KX092801		UPOL RK0647	R647EUL	present study
Eulichadidae		*Eulichas funebris*	China	KX092938	KX093072	KX092679	KX092803		UPOL RK0648	R648EUL	present study
Eulichadidae		*Eulichas funebris*	China	KX092939	KX093073	KX092680	KX092804		UPOL RK0649	R649EUL	present study
Eulichadidae		*Eulichas* sp.	China	KX092941	KX093075	KX092682	KX092806		UPOL RK0650	R650EUL	present study
Eulichadidae		*Eulichas baeri*	Philippines	KX092940	KX093074	KX092681	KX092805		UPOL RK0653	R653EUL	present study
Heteroceridae	Heterocerinae	gen. sp.	Indonesia	KX093031	KX093156	KX092756	KX092892		UPOL RK0661	R661HET	present study
Heteroceridae	Heterocerinae	gen. sp.	Malaysia	KX093032	KX093157	KX092757	KX092893		UPOL RK0662	R662HET	present study
Heteroceridae	Heterocerinae	*Augyles maritimus*	Morocco	AF451927	DQ198717	N	N		BMNH 693618	BYRHeAug	Bocakova et al. 2007
Heteroceridae	Heterocerinae	*Augyles auromicans*	USA	N	HQ446916	HQ605027	N		UMIC:K8	HETAuau	King et al. 2011
Heteroceridae	Heterocerinae	*Augyles weigeli*	India	N	HQ446917	HQ629786	N		UMIC:K59	HETAuwe	King et al. 2011
Heteroceridae	Heterocerinae	*Heterocerus* sp.	Slovakia	AF451928	DQ198718	DQ198630	DQ198553		UPOL 001048*	BYRHeHet	Bocakova et al. 2007
Heteroceridae	Heterocerinae	*Heterocerus* sp.	–	EF209532	N	EF209472	EF209592		FC_F06	HETH06	Ciampor & Ribera
Heteroceridae	Heterocerinae	*Heterocerus angolensis*	Namibia	N	HQ446914	HQ629795	N		UMIC:K54	HETHean	King et al. 2011
Heteroceridae	Heterocerinae	*Heterocerus boliviensis*	Bolívia	N	HQ446896	HQ629791	N		UMIC:K75	HETHebo	King et al. 2011
Heteroceridae	Heterocerinae	*Heterocerus brunneus*	USA	N	HQ446892	HQ629787	N		UMIC:K11	HETHebr	King et al. 2011
Heteroceridae	Heterocerinae	*Heterocerus debilipes*	Australia	N	HQ446913	HQ629796	N		UMIC:K64	HETHede	King et al. 2011
Heteroceridae	Heterocerinae	*Heterocerus texanus*	USA	N	HQ446900	HQ629793	N		UMIC:K6	HETHete	King et al. 2011
Heteroceridae	Heterocerinae	*Tropicus pusillus*	USA	N	HQ446883	HQ629797	N		UMIC:K5	HETTrpu	King et al. 2011
Heteroceridae	Heterocerinae	gen. sp.	–	EF209530	N	EF209470	EF209590		FC_B18	HETB18	Ciampor & Ribera
Limnichidae	Cephalobyrrhinae	*Cephalobyrrhus* sp.	–	EF209534	N	EF209474	EF209594		FC_396	LIMceph	Ciampor & Ribera
Limnichidae	Thaumastodinae	*Pseudeucinetus* sp.	Malaysia	KF625495	KF626096	KF625805	KF625197		UPOL 001318	1318LIM	Kundrata et al. 2014
Limnichidae	Limnichinae	*Limnichus pygmaeus*	United Kingdom	AF451923	DQ198719	DQ198631	DQ198554		BMNH 679196	BYRLiLim	Bocakova et al. 2007
Limnichidae	Limnichinae	*Limnichus* sp.	–	EF209535	N	EF209475	EF209595		FC_290	LIMlims	Ciampor & Ribera
Limnichidae	Limnichinae	*Limnichus* sp.	Indonesia	KX093022	KX093147	KX092748	KX092883		UPOL RK0666	R666LIM	present study
Limnichidae	Limnichinae	*Limnichus* sp.	Malaysia	KX093025	KX093150	KX092751	KX092886		UPOL RK0725	R725LIM	present study
Limnichidae	Limnichinae	*Eulimnichus* sp.	–	AF451922	HQ634240	N	N		IR2002/979750*	LIMeuli	Ribera et al.
Limnichidae	Limnichinae	*Platypelochares* sp.	–	EF209538	N	EF209478	EF209598		FC_D15	LIMplat	Ciampor & Ribera
Limnichidae	Limnichinae	*Byrrhinus* sp.	–	EF209533	N	EF209473	EF209593		FC_E05	LIMbyrr	Ciampor & Ribera

Limnichidae	Limnichinae	*Pelochares* sp.	–	EF209537	N	EF209477	EF209597	FC_444	LIMpelo	Ciampor & Ribera
Limnichidae	Limnichinae	*Pelochares* sp.	China	KX093024	KX093149	KX092750	KX092885	UPOL RK0708	R708LIM	present study
Limnichidae	Limnichinae	*Pelochares* sp.	Indonesia	KX093023	KX093148	KX092749	KX092884	UPOL RK0665	R665LIM	present study
Limnichidae	Limnichinae	*Byrrhinus* sp.	Cameroon	KX093021	KX093146	KX092747	KX092882	UPOL RK0663	R663LIM	present study
Limnichidae	Limnichinae	*Byrrhinus* sp.	Indonesia	KX093028	KX093153	KX092753	KX092889	UPOL RK0664	R664LIM	present study
Limnichidae	Limnichinae	*Byrrhinus* sp.	Malaysia	KX093027	KX093152	KX092752	KX092888	UPOL RK0727	R727LIM	present study
Limnichidae	Limnichinae	*Mandersia* sp.	Indonesia	KX093029	KX093154	KX092754	KX092890	UPOL RK0667	R667LIM	present study
Limnichidae	Limnichinae	*Mandersia* sp.	China	KX093030	KX093155	KX092755	KX092891	UPOL RK0670	R670LIM	present study
Limnichidae	Limnichinae	*Tricholimnichus* sp.	Malaysia	KX093026	KX093151	N	KX092887	UPOL RK0748	R748LIM	present study
Limnichidae	Limnichinae	*Paralimnichus* sp.	Philippines	KX093020	KX093145	KX092746	KX092881	UPOL RK0691	R691LIM	present study
Lutrochidae		*Lutrochus* sp.	–	EF209539	HQ634239	EF209479	EF209599	FC_C14/JK–2011*	LUTlutr	Ciampor & Ribera
Psephenidae	Eubrianacinae	*Eubrianax edwardsii*	USA	AF451933	DQ198720	N	N	BMNH 679347	BYRPsEue	Bocakova et al. 2007
Psephenidae	Eubrianacinae	*Eubrianax* sp.	Indonesia	DQ100485	DQ198721	DQ198632	DQ198555	UPOL 000M33	BYRPsEus	Bocakova et al. 2007
Psephenidae	Eubrianacinae	gen. sp.	Cambodia	KF625503	KF626103	KF625811	KF625204	UPOL RK0163	R163PSE	Kundrata et al. 2014
Psephenidae	-	gen. sp.	–	EF209540	N	EF209480	EF209600	FC_B16	PSEsp01	Ciampor & Ribera
Psephenidae	-	gen. sp.	–	EF209541	N	EF209481	EF209601	FC_B17	PSEsp02	Ciampor & Ribera
Psephenidae	Eubriinae	*Dicranopselaphus* sp.	Malaysia	KF625514	KF626115	KF625820	KF625214	UPOL RK0168	R168PSE	Kundrata et al. 2014
Psephenidae	Eubriinae	*Dicranopselaphus* sp.	Indonesia	KF625515	KF626116	KF625821	KF625215	UPOL RK0169	R169PSE	Kundrata et al. 2014
Psephenidae	Eubriinae	*Dicranopselaphus* sp.	China	KX092951	KX093082	KX092691	KX092811	UPOL RK0671	R671PSE	present study
Psephenidae	Eubriinae	*Dicranopselaphus* sp.	Indonesia	KX092949	N	KX092689	KX092812	UPOL RK0699	R699PSE	present study
Psephenidae	Eubriinae	gen. sp.	Indonesia	KX092947	N	KX092687	KX092813	UPOL RK0693	R693PSE	present study
Psephenidae	Eubriinae	*Schinostethus brevis*	Japan	KX092950	KX093081	KX092690	KX092814	UPOL RK0694	R694PSE	present study
Psephenidae	Eubriinae	gen. sp.	Indonesia	KX092948	N	KX092688	KX092815	UPOL RK0700	R700PSE	present study
Ptilodactylidae	Cladotominae	*Paralichas pectinatus*	Japan	DQ100486	DQ198722	DQ198633	DQ198556	UPOL 000M41	BYRPtPar	Bocakova et al. 2007
Ptilodactylidae	Anchytarsinae	gen. sp.	Cameroon	KX092963	KX093094	KX092702	KX092827	UPOL RK0773	R773PTI	present study
Ptilodactylidae	Anchytarsinae	*Epilichas* sp.	Japan	KX092967	KX093098	KX092705	KX092831	UPOL RK0829	R829PTI	present study
Ptilodactylidae	Anchytarsinae	*Epilichas* sp.	Japan	KX092968	KX093099	KX092706	KX092832	UPOL RK0830	R830PTI	present study
Ptilodactylidae	Anchytarsinae	*Anchycteis monticola*	Japan	KX092970	N	KX092708	KX092834	UPOL RK0832	R832PTI	present study
Ptilodactylidae	Ptilodactylinae	*Ptilodactyla serricornis*	Japan	AF451931	DQ198723	DQ198634	DQ198557	BMNH 693606	BYRPtPti	Bocakova et al. 2007
Ptilodactylidae	Ptilodactylinae	*Ptilodactyla* sp.	China	KX092954	KX093085	KX092694	KX092818	UPOL RK0673	R673PTI	present study
Ptilodactylidae	Ptilodactylinae	*Ptilodactyla* sp.	China	KX092956	KX093087	KX092696	KX092820	UPOL RK0756	R756PTI	present study
Ptilodactylidae	Ptilodactylinae	*Ptilodactyla* sp.	Japan	KX092969	KX093100	KX092707	KX092833	UPOL RK0831	R831PTI	present study
Ptilodactylidae	Ptilodactylinae	gen. sp.	Indonesia	KF625518	KF626119	KF625824	KF625217	UPOL RK0149	R149PTI	Kundrata et al. 2014
Ptilodactylidae	Ptilodactylinae	gen. sp.	Indonesia	KF625520	KF626121	KF625825	KF625219	UPOL RK0151	R151PTI	Kundrata et al. 2014
Ptilodactylidae	Ptilodactylinae	gen. sp.	Indonesia	KF625522	KF626123	KF625827	KF625221	UPOL RK0153	R153PTI	Kundrata et al. 2014
Ptilodactylidae	Ptilodactylinae	gen. sp.	–	EF209542	N	EF209482	EF209602	FC_E18	PTIsp01	Ciampor & Ribera
Ptilodactylidae	Ptilodactylinae	gen. sp.	–	EF209543	N	EF209483	EF209603	FC_E19	PTIsp02	Ciampor & Ribera
Ptilodactylidae	Ptilodactylinae	gen. sp.	–	EF209544	N	EF209484	EF209604	FC_E20	PTIsp03	Ciampor & Ribera
Ptilodactylidae	Ptilodactylinae	gen. sp.	Malaysia	KX092953	KX093084	KX092693	KX092817	UPOL RK0714	R714PTI	present study
Ptilodactylidae	Ptilodactylinae	gen. sp.	China	KX092955	KX093086	KX092695	KX092819	UPOL RK0755	R755PTI	present study
Ptilodactylidae	Ptilodactylinae	gen. sp.	Malaysia	KX092957	KX093088	KX092697	KX092821	UPOL RK0759	R759PTI	present study
Ptilodactylidae	Ptilodactylinae	gen. sp.	Indonesia	KX092958	KX093089	KX092698	KX092822	UPOL RK0760	R760PTI	present study
Ptilodactylidae	Ptilodactylinae	gen. sp.	Malaysia	KX092959	KX093090	KX092699	KX092823	UPOL RK0761	R761PTI	present study
Ptilodactylidae	Ptilodactylinae	gen. sp.	Malaysia	KX092960	KX093091	N	KX092824	UPOL RK0763	R763PTI	present study
Ptilodactylidae	Ptilodactylinae	gen. sp.	Cameroon	KX092952	KX093083	KX092692	KX092816	UPOL RK0775	R775PTI	present study
Ptilodactylidae	Ptilodactylinae	gen. sp.	Philippines	KX092966	KX093097	N	KX092830	UPOL RK0828	R828PTI	present study
Ptilodactylidae	-	gen. sp.	Cameroon	KX092962	KX093093	KX092701	KX092826	UPOL RK0771	R771PTI	present study
Ptilodactylidae	-	gen. sp.	Madagascar	KF625517	KF626118	KF625823	KF625222	UPOL RK0131	R131PTI	Kundrata et al. 2014
Ptilodactylidae	-	gen. sp.	Indonesia	KF625519	KF626120	N	KF625218	UPOL RK0150	R150PTI	Kundrata et al. 2014
Ptilodactylidae	-	gen. sp.	Indonesia	KF625521	KF626122	KF625826	KF625220	UPOL RK0152	R152PTI	Kundrata et al. 2014
Ptilodactylidae	-	gen. sp.	Malaysia	KX092961	KX093092	KX092700	KX092825	UPOL RK0764	R764PTI	present study
Ptilodactylidae	-	gen. sp.	Philippines	KX092964	KX093095	KX092703	KX092828	UPOL RK0826	R826PTI	present study
Ptilodactylidae	-	gen. sp.	Philippines	KX092965	KX093096	KX092704	KX092829	UPOL RK0827	R827PTI	present study

Table S4. Primers used for the PCR amplifications* of the studied genes.

Gene	Code	-mer	Sequence (5’ >> 3’)
18S rRNA	fragment A		
	18S 5'	24	GACAACCTGGTTGATCCTGCCAGT
	18S b5.0	19	TAACCGCAACAACTTTAAT
	fragment B		
	18S ai	22	CCTGAGAAACGGCTACCACATC
	18S b2.5.1	22	CGTTTTTGGCAAATGCTTTCGC
	fragment C		
	18S a1.0.1	20	GGTGAAATTCTTGGATCGTC
	18S bi	20	GAGTCTCGTTCGTTATCGGA
	fragment D		
	18S a2.0	19	ATGGTTGCAAAGCTGAAAC
	18S 3'Irk1	20	TACGACTTTTACTTCCTCTA
28S rRNA	28S ff	20	TTACACACTCCTTAGCGGAT
	28S dd	19	GGGACCCGTCTTGAAACAC
rrnL mtDNA	16a	20	CGCCTGTTTAACAAAAACAT
	16b	22	CCGGTCTGAACTCAGATCATGT
	ND1-A	27	GGTCCCTTACGAATTTGAATATATCCT
cox1 mtDNA	S-Pat	21	GCACTAWTCTGCCATATTAGA
	S-Jerry	23	CAACATYTATTYTGATTYTTTGG

* PCR conditions included an initial denaturation step of 1–2 min at 94–96°C, followed by 40 cycles as follows: 30–60 sec at 94°C, 30–60 sec at 41–50°C (depending on the melting temperatures of primer pairs used), 1–2 min at 72°C, and a final step of 10 min at 72°C. ABI technology was used for the DNA sequencing.

Table S5. Summary of the PartitionFinder results. Settings: branchlengths = linked, models of evolution = mrbayes, search algorithm = greedy. Q-INS-i - dataset aligned by the Q-INS-i algorithm in Mafft; gaps_out - all positions with at least one gap character discarded; 3rd_out - the third codon positions in the *cox1* sequences discarded. * - Partition scheme in PartitionFinder format = (Gene1_pos1) (Gene2_pos1) (Gene3_pos1) (Gene4_pos1) (Gene4_pos2) (Gene4_pos3).

Dataset (taxa/aln)	Criterion	AICc (BIC)	lnL	#parameters	#subsets*	Best Model
488/Mafft	AICc	531572.65503	-264494.43724	1035	6	GTR+I+G, SYM+I+G (28S)
488/Mafft	BIC	537846.75134	-264494.43724	1035	6	GTR+I+G, SYM+I+G (28S)
488/Muscle	AICc	542099.34686	-269776.39343	1035	6	GTR+I+G, SYM+I+G (28S)
488/Muscle	BIC	548473.48032	-269776.39343	1035	6	GTR+I+G, SYM+I+G (28S)
251/Mafft	AICc	322420.57255	-160574.02201	561	6	GTR+I+G, SYM+I+G (28S)
251/Mafft	BIC	326021.82413	-160635.04857	561	6	GTR+I+G, SYM+I+G (28S)
251/Muscle	AICc	324694.00390	-161786.00195	561	6	GTR+I+G, SYM+I+G (28S)
251/Muscle	BIC	328330.14950	-161793.61840	558	6	GTR+I+G, SYM+I+G (18S, 28S)
209/Mafft	AICc	284023.72908	-141481.47985	477	6	GTR+I+G, SYM+I+G (28S)
209/Mafft	BIC	287001.09352	-141481.47985	477	6	GTR+I+G, SYM+I+G (28S)
208/Muscle	AICc	284044.77581	-141496.37256	475	6	GTR+I+G, SYM+I+G (28S)
208/Muscle	BIC	287017.85153	-141503.25102	472	6	GTR+I+G, SYM+I+G (18S, 28S)
251/Mafft Q-INS-i	AICc	318998.25647	-158864.80684	561	6	GTR+I+G, SYM+I+G (28S)
251/Mafft Q-INS-i	BIC	322484.35840	-158873.69096	558	6	GTR+I+G, SYM+I+G (18S, 28S)
251/Mafft gaps_out	AICc	236155.27966	-117406.51688	561	6	GTR+I+G, SYM+I+G (28S)
251/Mafft gaps_out	BIC	239370.06209	-117414.29001	558	6	GTR+I+G, SYM+I+G (18S, 28S)
251/Mafft 3rd_out	AICc	226036.19490	-112391.51165	550	5	GTR+I+G, SYM+I+G (28S)
251/Mafft 3rd_out	BIC	229410.50818	-112391.51165	550	5	GTR+I+G, SYM+I+G (28S)
251/BlastAlign	AICc	277325.33948	-138025.55144	561	6	GTR+I+G, SYM+I+G (28S)
251/BlastAlign	BIC	280781.58322	-138031.52060	558	6	GTR+I+G, SYM+I+G (18S, 28S)

Table S6. Numbers and types of characters in the analyzed datasets. * - *cox1* mtDNA aligned only by Mafft; 3rd_out - the third codon positions in the *cox1* sequences discarded; gaps_out - all positions with at least one gap character discarded.

Number of taxa/ Alignment type	Characters total	18S rRNA	28S rRNA	*rrnL* mtDNA	*cox1* mtDNA*	constant	variable	parsimony informative
488/Mafft	5210	2495	1352	640	723	1904	2873	2235
488/Muscle	5536	2668	1460	685	723	1928	3288	2460
251/Mafft	4749	2324	1112	590	723	2133	2381	1860
251/Muscle	4914	2382	1180	629	723	2121	2654	1969
251/BlastAlign	4704	2182	1030	769	723	2182	2082	1579
251/Mafft Q-INS-i	4862	2398	1118	623	723	2212	2339	1809
251/Mafft 3rd_out	4508	2324	1112	590	482	2133	2140	1619
251/Mafft gaps_out	3425	1729	576	397	723	1918	1507	1250
209/Mafft	4744	2320	1111	590	723	2185	2318	1830
208/Muscle	4908	2377	1180	628	723	2183	2586	1926

Table S7. Summary of the RogueNaRok results from the RAxML-inferred bootstrap trees (251 taxa aligned by Mafft and Muscle algorithms). Maximum dropset size = 1. Raw improvement = overall fraction of improvement in bootstrap values. RIBC = relative bipartition information criterion.

Voucher	Family	Genus/Species	raw improvement	RBIC
251-taxa Mafft alignment				
R748LIM	Limnichidae	*Tricholimnichus* sp.	1.107143	0.677971
R001EEla	Elateridae	*Melanotus villosus*	0.843254	0.645429
R021EDen	Elateridae	*Selatosomus latus*	0.691468	0.648217
BYRElMac	Elmidae	*Macronychus 4-tuberculatus*	0.605159	0.650658
R013EEla	Elateridae	*Elater* sp.	0.603175	0.653090
R025EAgr	Elateridae	*Adelocera* sp.	0.595238	0.655490
LLyrmd1	Lycidae	*Platerodrilus* sp.	0.591270	0.660246
LLyThos	Lycidae	*Thonalmus sinuaticostis*	0.588294	0.657862
LIMceph	Limnichidae	*Cephalobyrrhus* sp.	0.566468	0.662530
R805BUP	Buprestidae	*Coraebus diminutus*	0.548611	0.680676
R674DRY	Dryopidae	*Sostea* sp.	0.526786	0.664655
R691LIM	Limnichidae	*Paralimnichus* sp.	0.515873	0.666735
R791DAS	Dascillidae	*Emmita serricornis*	0.237103	0.668635
R091ART	Artematopodidae	*Eurypogon japonicus*	0.234127	0.667679
LLibl1	Lycidae	*Libnetis* sp.	0.164683	0.670931
R686DRY	Dryopidae	*Sostea* sp.	0.145833	0.669223
LDicly1	Lycidae	*Lycoprogenthes* sp.	0.138889	0.669783
R377LYC	Lycidae	*Plateros* sp.	0.120040	0.670267
251-taxa Muscle alignment				
R129CER	Cerophytidae	*Cerophytum elateroides*	1.614087	0.647777
1415EEla	Elateridae	*Anoplischius* sp.	1.143849	0.652390
R686DRY	Dryopidae	*Sostea* sp.	0.721230	0.655298
R377LYC	Lycidae	*Plateros* sp.	0.710317	0.668031
R082EAgr	Elateridae	*Cryptalaus* sp.	0.637897	0.657870
LAtesc1	Lycidae	*Scarelus* sp.	0.624008	0.660386
LLibl1	Lycidae	*Libnetis* sp.	0.593254	0.665167
LDicly1	Lycidae	*Lycoprogenthes* sp.	0.592262	0.662774
LLyrmd1	Lycidae	*Platerodrilus* sp.	0.590278	0.670411
BYRPtPar	Ptilodactylidae	*Paralichas pectinatus*	0.565476	0.672691
LIMceph	Limnichidae	*Cephalobyrrhus* sp.	0.564484	0.674967
BYRElLip	Elmidae	*Limnius perrisi*	0.553571	0.684200
R025EAgr	Elateridae	*Adelocera* sp.	0.342262	0.677699
R791DAS	Dascillidae	*Emmita serricornis*	0.335317	0.676319
R145E	Elateridae	*Diplophoenicus* sp.	0.301587	0.678915
1247PHE	Phengodidae	gen. sp.	0.238095	0.679876
R691LIM	Limnichidae	*Paralimnichus* sp.	0.129960	0.680400
telTele	Omethidae	*Telegeusis nubifer*	0.106151	0.680828

Table S8. Results of the Xia's nucleotide substitution saturation test in DAMBE, based on simulations with 32 operational taxonomic units (10 000 replicates). Iss - index of substitution saturation; Iss.c^S - critical value for symmetrical tree topology; Iss.c^A - critical value for extremely assymetrical tree topology; T - T value; DF - degrees of freedom; P^S, P^A - probability that Iss is significantly different from the critical value (Iss.c^S or Iss.c^A, respectively); Pinv - proportion of invariable sites.

Marker/codon pos.	Iss	Iss.c^S	T	DF	P^S	Iss.c^A	T	DF	P^A	Pinv
All sites										
18S rRNA	0.813	0.796	0.332	1753	0.740	0.529	5.616	1753	0,000	0.245
28S rRNA	1.425	0.755	8.749	937	0.000	0.456	12.661	937	0.000	0.157
rrnL mtDNA	0.679	0.711	0.525	560	0.600	0.383	4.776	560	0.000	0.049
cox1 mtDNA/1st	0.250	0.683	11.441	226	0.000	0.360	2.902	226	0.004	0.057
cox1 mtDNA/2nd	0.116	0.683	22.525	205	0.000	0.360	9.668	205	0.000	0.145
cox1 mtDNA/3rd	0.699	0.683	0.578	240	0.564	0.360	12.546	240	0.000	0.000
Fully resolved sites										
18S rRNA	0.054	0.764	94.058	960	0.000	0.473	55.404	960	0.000	0.245
28S rRNA	0.079	0.692	38.439	342	0.000	0.363	17.833	342	0.000	0.157
rrnL mtDNA	0.243	0.689	12.373	194	0.000	0.373	3.615	194	0.000	0.049
cox1 mtDNA/1st	0.226	0.689	11.679	195	0.000	0.372	3.678	195	0.000	0.057
cox1 mtDNA/2nd	0.088	0.689	26.627	177	0.000	0.372	12.589	177	0.000	0.145
cox1 mtDNA/3rd	0.700	0.689	0.384	207	0.702	0.372	11.451	207	0.000	0.000

Příloha 4

Kundrata, R., Ivie, M.A. & Bocák, L. (2019) *Podabrocephalus* Pic is the morphologically modified lineage of Ptilodactylinae (Coleoptera: Elateriformia: Ptilodactylidae). *Insect Systematics & Evolution*, doi: 10.1163/1876312X-00002190 [publikováno online, čeká na zařazení do čísla].
[IF 0,763; ještě není na WoS; celkem 1 citace bez autorových autocitací]
[korespondující autor; autorský podíl: 40 %]

BRILL Insect Systematics & Evolution (2018) DOI 10.1163/1876312X-00002190 brill.com/ise

Podabrocephalus Pic is the morphologically modified lineage of Ptilodactylinae (Coleoptera: Elateriformia: Ptilodactylidae)

Robin Kundrata[a],*, Michael A. Ivie[b] and Ladislav Bocak[a]

[a]Department of Zoology, Faculty of Science, Palacky University, 17. listopadu 50,
771 46, Olomouc, Czech Republic
[b]Montana Entomology Collection, Montana State University, Bozeman, MT 59717, USA
*Corresponding author, e-mail: robin.kundrata@upol.cz

Abstract

A molecular phylogeny of Ptilodactylidae shows that *Podabrocephalus* Pic, 1913, the type genus of Podabrocephalidae Pic, 1930 is closely related to *Ptilodactyla* Illiger, 1807 and other genera of Ptilodactylinae. Consequently, Podabrocephalidae Pic, 1930 **syn. n.** is proposed as a junior synonym of Ptilodactylidae Laporte, 1836. Earlier authors used the highly modified morphology of the male to justify a high rank for *Podabrocephalus*. The molecular phylogeny of Ptilodactylidae further indicates that *Paralichas* White, 1859 (Cladotominae) does not form a monophylum with remaining ptilodactylids. Ptilodactylinae and an undescribed lineage from Indonesia are sister to the broadly delimited Anchytarsinae. Within Ptilodactylinae, *Pherocladus* Fairmaire, 1881 is sister to a clade formed by *Ptilodactyla* spp. and *Podabrocephalus*. We remove *Falsotherius* Pic, 1913 from Ptilodactylinae to Ptilodactylidae incertae sedis, and return *Daemon* Laporte, 1836 from Ptilodactylinae to Anchytarsinae. Cross validation of morphology- and DNA-based phylogenies is needed for interpreting phylogenetic inference in morphologically modified lineages.

Keywords

Byrrhoidea; classification; molecular phylogeny; morphology; Oriental Region

Introduction

The enigmatic *Podabrocephalus* Pic, 1913 from southern India has an obscure history. The genus was originally based on a single damaged specimen without an explicit family placement and compared only with the cantharid *Chauliognathus* Hentz, 1830 (Pic 1913). In the Zoological Record (Sharp 1916), *Podabrocephalus* was placed in the Malacodermidae, at that time an amalgamation of the cantharids, lampyrids, lycids, melyrids and other distantly related elateroid and cleroid lineages sharing a soft-bodied morphology. This was the first explicit familial placement of this morphologically distinct beetle. Later, Pic (1930) claimed he had described it in the Cantharidae, but felt it

DOI 10.1163/1876312X-00002190

was closer to Drilidae, and proposed a separate family Podabrocephalidae. His description is a short paragraph at the end of a paper on other topics. This taxon seemingly languished for the next several decades, and was later treated by Wittmer (1969), who discussed the placement a few dozen of Pic's Cantharidae names. Unfortunately, this paper has been mostly overlooked, leading to the continued misplacement of the taxon (e.g., Lawrence & Newton 1995). Apparently unaware of Pic's 1930 paper erecting a family for the genus, Wittmer (1969), citing advice from Crowson, in litteris, suggested that *Podabrocephalus* might be related to Ptilodactylidae. Stribling (1986) treated this genus as *incertae sedis* in his generic revision of Ptilodactylidae, and Lawrence & Newton (1995) and Lawrence et al. (2010) classified it as Podabrocephalidae under Elateriformia incertae sedis. Bouchard et al. (2011) placed Podabrocephalidae in Byrrhoidea. Lawrence et al. (2011) provided a phylogenetic hypothesis for Coleoptera based on morphological characters and found *Podabrocephalus* within Elateroidea as a sister to all soft-bodied lineages (i.e., former Cantharoidea). McKenna et al. (2015) used molecular markers to reveal the phylogenetic relationships within Coleoptera and found *Podabrocephalus* sister to *Ptilodactyla* Illiger, 1807, both forming a clade with *Anchycteis* Horn, 1880 + *Cneoglossa* Guérin-Méneville, 1849 (Cneoglossidae). Probably, based on these results, Lawrence (2016a, b) classified *Podabrocephalus* in Ptilodactylidae using the subfamily Podabrocephalinae Pic, 1930, in fact a new status but not explicitly designated as such. A time-line of *Podabrocephalus* placement is summarized in Table 1.

There are numerous beetle families and their relationships are mostly well understood (Hunt et al. 2007; McKenna et al. 2015). A few, such as Podabrocephalidae, are cited in various classifications, but their detailed positions have remained unclear. In this study, we merge the *Podabrocephalus* sequences published by McKenna et al. (2015) with other sequences of the Ptilodactylidae and their relatives used in the molecular phylogeny of Byrrhoidea by Kundrata et al. (2017). We infer the molecular phylogeny of Ptilodactylidae to determine the position of *Podabrocephalus* within the

Table 1. Time-line of familial placement of *Podabrocephalus* Pic, 1913.

Year	Author(s)	Placement of *Podabrocephalus* Pic, 1913
1913	Pic	not formally placed, compared with Cantharidae
1916	Sharp	Malacodermidae
1930	Pic	Podabrocephalidae, close to Drilidae
1969	Wittmer	Ptilodactylidae
1986	Stribling	incertae sedis [unpublished study]
1995	Lawrence & Newton	Podabrocephalidae in Elateriformia incertae sedis
1999	Lawrence et al.	Podabrocephalidae in Elateriformia incertae sedis
2002	Ivie	Podabrocephalidae
2010	Lawrence et al.	Podabrocephalidae in Elateriformia incertae sedis
2011	Lawrence et al.	Podabrocephalidae in Elateroidea, sister to "Cantharoidea"
2011	Bouchard et al.	Podabrocephalidae in Byrrhoidea
2015	McKenna et al.	Ptilodactylidae (*Podabrocephalus*+*Ptilodactyla*) + (*Anchycteis*+*Cneoglossa*)
2016	Lawrence	Ptilodactylidae: Podabrocephalinae

family and question the validity of recognizing *Podabrocephalus* at the family-group level. Additionally, we discuss the parallel evolution of some characters repeatedly leading to a mistakenly high rank for the morphologically modified soft-bodied lineages.

Material and Methods

Dataset, alignment and phylogenetic methods

To test the phylogenetic placement of *Podabrocephalus*, we used the sequences of this genus and available Ptilodactylidae deposited in GenBank (Table 2; Bocakova et al. 2007; Kundrata et al. 2014, 2017; McKenna et al. 2015). The outgroup selection and markers used for the phylogenetic analyses were based on the molecular phylogeny of Byrrhoidea by Kundrata et al. (2017). The representatives of Callirhipidae, Eulichadidae, Psephenidae, and Elmidae were used as outgroups, and the trees were rooted with *Anthaxia corinthia* Reiche & Saulcy, 1856 (Buprestidae). Fragments of two nuclear (18S rRNA, 28S rRNA) and two mitochondrial (*rrnL* mtDNA, *cox1* mtDNA) genes were used for the phylogenetic analyses. Our dataset contained 38 terminals; 32 of them were represented by all four markers (Table 2). Mitochondrial markers were not available for *Podabrocephalus* (McKenna et al. 2015). The sequences were aligned using Mafft (default parameters; Katoh et al. 2002; Katoh & Standley 2013) and Muscle (default parameters; Edgar 2004) algorithms in Geneious 7.1.7 (Kearse et al. 2012; http://www.geneious.com). Alignment of the length invariable protein-coding *cox1* sequences was checked by amino acid translation. The best-fit partitioning schemes and partition-specific substitution models were tested in PartitionFinder 1.1.1 (greedy algorithm; Lanfear et al. 2012) using the corrected Akaike information criterion.

Maximum likelihood (ML) analysis was conducted using RAxML 8.2.10 (Stamatakis 2006) on the CIPRES web server (www.phylo.org; Miller et al. 2010). We applied the GTR+I+G model and the partitioning scheme by genes and codon positions as defined by PartitionFinder. The confidence of the branches of the best ML tree was assessed based on 1000 thorough bootstrap replicates (BS). Bayesian inference (BI) analysis was performed in MrBayes 3.2.6 (Huelsenbeck & Ronquist 2001) via the CIPRES portal (Miller et al. 2010), with partitioning schemes and nucleotide substitution models identified in PartitionFinder. Four chains as described in the MrBayes manual were run for $4x10^7$ generations using the Markov chain Monte Carlo method. Stationary phase and convergence were detected in Tracer 1.5 (Rambaut & Drummond 2007) and the first $8x10^6$ of generations were discarded as burn-in. The majority-rule consensus tree was constructed to determine the posterior probabilities (PP) from the remaining trees. The resulting trees were visualized and edited in FigTree 1.3.1 (Rambaut 2009).

Morphology

Both type and non-type material of Ptilodactylidae from the following collections was morphologically examined for the purpose of this study: the Muséum National d'histoire Naturelle, Paris, France (MNHN), the Natural History Museum, London,

Table 2. List of 38 terminals used in the analyses, with voucher and GenBank accession numbers. B2007: Bocakova et al. (2007), K2014: Kundrata et al. (2014), K2017: Kundrata et al. (2017), M2015: McKenna et al. (2015); * - re-determination of this specimen was not possible, data taken from GenBank.

	Markers								
Superfamily/family	Subfamily	Genus/Species	Geographic origin	18S	28S	*rrnL*	*cox1*	Specimen voucher	Source
Buprestidae	Buprestinae	*Anthaxia corinthia*	Cyprus	KX092919	KX093053	KX092662	KX092784	UPOL RK0807	K2017
Callirhipidae		*Callirhipis* sp.	Indonesia	KX092943	KX093077	KX092684	KX092808	UPOL RK0655	K2017
Eulichadidae		*Eulichas funebris*	China	KX092938	KX093072	KX092679	KX092803	UPOL RK0648	K2017
Psephenidae	Eubrianacinae	gen. sp.	Cambodia	KF625503	KF626103	KF625811	KF625204	UPOL RK0163	K2014
Psephenidae	Eubriinae	*Dicranopselaphus* sp.	Malaysia	KF625514	KF626115	KF625820	KF625214	UPOL RK0168	K2014
Psephenidae	Eubriinae	*Schinostethus brevis*	Japan	KX092950	KX093081	KX092690	KX092814	UPOL RK0694	K2017
Elmidae	Elminae	*Nesonychus* sp.	Indonesia	KX093012	KX093138	KX092741	KX092873	UPOL RK0736	K2017
Elmidae	Elminae	*Stenelmis* sp.	Malaysia	KX093004	KX093132	KX092737	KX092865	UPOL RK0720	K2017
Elmidae	Larainae	*Dryopomorphus* sp.	Indonesia	KX093010	KX093137	KX092740	KX092871	UPOL RK0732	K2017
Elmidae	Larainae	*Potamodytes* sp.	Madagascar	KX093001	KX093129	KX092735	KX092862	UPOL RK0659	K2017
Ptilodactylidae	Cladotominae	*Paralichas pectinatus*	Japan	DQ100486	DQ198722	DQ198633	DQ198556	UPOL 000M41	B2007
Ptilodactylidae	Anchytarsinae	*Epilichas* sp.	Japan	KX092967	KX093098	KX092705	KX092831	UPOL RK0829	K2017
Ptilodactylidae	Anchytarsinae	*Epilichas* sp.	Japan	KX092968	KX093099	KX092706	KX092832	UPOL RK0830	K2017
Ptilodactylidae	Anchytarsinae	*Anchycteis monticola*	Japan	KX092970	N	KX092708	KX092834	UPOL RK0832	K2017
Ptilodactylidae	Anchytarsinae	gen. sp.	Cameroon	KX092963	KX093094	KX092702	KX092827	UPOL RK0773	K2017
Ptilodactylidae	Anchytarsinae	gen. sp.	Cameroon	KX092962	KX093093	KX092701	KX092826	UPOL RK0771	K2017
Ptilodactylidae	Anchytarsinae	*Daemon* cf. *vittatus*	Madagascar	KF625517	KF626118	KF625823	KF625222	UPOL RK0131	K2014
Ptilodactylidae	-	gen. sp.	Indonesia	KF625519	KF626120	N	KF625218	UPOL RK0150	K2014
Ptilodactylidae	Ptilodactylinae	*Pherocladus* sp.	Indonesia	KF625521	KF626122	KF625826	KF625220	UPOL RK0152	K2014
Ptilodactylidae	Ptilodactylinae	*Pherocladus* sp.	Malaysia	KX092961	KX093092	KX092700	KX092825	UPOL RK0764	K2017
Ptilodactylidae	Ptilodactylinae	*Pherocladus* sp.	Philippines	KX092964	KX093095	KX092703	KX092828	UPOL RK0826	K2017
Ptilodactylidae	Ptilodactylinae	*Pherocladus* sp.	Philippines	KX092965	KX093096	KX092704	KX092829	UPOL RK0827	K2017
Ptilodactylidae	Ptilodactylinae	*Podabrocephalus* sp.	India	KP419237	KP419593	N	N	MSC1355	M2015

Ptilodactylidae	Ptilodactylinae	*Ptilodactyla* sp.*	Japan	N	DQ198723	DQ198634	DQ198557	BMNH 693606	B2007
Ptilodactylidae	Ptilodactylinae	*Ptilodactyla* sp.	China	KX092954	KX093085	KX092694	KX092818	UPOL RK0673	K2017
Ptilodactylidae	Ptilodactylinae	*Ptilodactyla* sp.	China	KX092956	KX093087	KX092696	KX092820	UPOL RK0756	K2017
Ptilodactylidae	Ptilodactylinae	*Ptilodactyla* sp.	Japan	KX092969	KX093100	KX092707	KX092833	UPOL RK0831	K2017
Ptilodactylidae	Ptilodactylinae	*Ptilodactyla* sp.	Indonesia	KF625518	KF626119	KF625824	KF625217	UPOL RK0149	K2014
Ptilodactylidae	Ptilodactylinae	*Ptilodactyla* sp.	Indonesia	KF625520	KF626121	KF625825	KF625219	UPOL RK0151	K2014
Ptilodactylidae	Ptilodactylinae	*Ptilodactyla* sp.	Indonesia	KF625522	KF626123	KF625827	KF625221	UPOL RK0153	K2014
Ptilodactylidae	Ptilodactylinae	*Ptilodactyla* sp.	Malaysia	KX092953	KX093084	KX092693	KX092817	UPOL RK0714	K2017
Ptilodactylidae	Ptilodactylinae	*Ptilodactyla* sp.	China	KX092955	KX093086	KX092695	KX092819	UPOL RK0755	K2017
Ptilodactylidae	Ptilodactylinae	*Ptilodactyla* sp.	Malaysia	KX092957	KX093088	KX092697	KX092821	UPOL RK0759	K2017
Ptilodactylidae	Ptilodactylinae	*Ptilodactyla* sp.	Indonesia	KX092958	KX093089	KX092698	KX092822	UPOL RK0760	K2017
Ptilodactylidae	Ptilodactylinae	*Ptilodactyla* sp.	Malaysia	KX092959	KX093090	KX092699	KX092823	UPOL RK0761	K2017
Ptilodactylidae	Ptilodactylinae	*Ptilodactyla* sp.	Malaysia	KX092960	KX093091	N	KX092824	UPOL RK0763	K2017
Ptilodactylidae	Ptilodactylinae	*Ptilodactyla* sp.	Cameroon	KX092952	KX093083	KX092692	KX092816	UPOL RK0775	K2017
Ptilodactylidae	Ptilodactylinae	*Ptilodactyla* sp.	Philippines	KX092966	KX093097	N	KX092830	UPOL RK0828	K2017

United Kingdom (BMNH), the Naturhistorisches Museum, Vienna, Austria (NHMW), the Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany (SDEI), the collection of author MAI (MAIC, Bozeman, Montana, USA), and the voucher collection of the Laboratory of Molecular Systematics, Palacky University, Olomouc, Czech Republic. Morphological study of *Podabrocephalus* was based on the holotype of *Podabrocephalus sinuaticollis* Pic, 1913 and one additional specimen of that species from the BMNH, as well as 15 specimens of a still undescribed species from MAIC, including the specimen used by McKenna et al. (2015) (MAI, unpublished information).

Results

Dataset/Alignment parameters

The 38-taxa Mafft alignment included 3808 homologous positions (1872, 670, 543, and 723 positions for 18S, 28S, *rrnL*, and *cox1*, respectively), from which 2866 were conserved, 896 variable, and 653 parsimony-informative. The Muscle alignment included 3817 homologous positions (1866, 671, 557, and 723 positions for 18S, 28S, *rrnL*, and *cox1*, respectively), from which 2883 were conserved, 902 variable, and 649 parsimony-informative.

Both ML and BI analyses from Mafft and Muscle alignments yielded similar relationships and support for major clades (Fig. 1). The relationships within outgroup taxa varied to some extent, but Psephenidae (Eubriinae and Eubrianacinae) were never monophyletic, and Elmidae were regularly recovered as sister to the bulk of Ptilodactylidae. Ptilodactylidae were split between *Paralichas* White, 1859 (Cladotominae), which was among outgroups in a distant position to the remaining ptilodactylids. The Ptilodactylidae clade, i.e., Ptilodactylidae without *Paralichas*, was moderately to strongly supported in all analyses (86–94% BS, 100% PP). The clade containing *Epilichas* White, 1859, *Anchycteis* Horn, 1880, *Daemon* Laporte, 1836, and a still undescribed genus from Cameroon (= Anchytarsinae in further text) was moderately to strongly supported, and was recovered as a sister to the clade containing Ptilodactylinae, including *Podabrocephalus*, and a genus from Sumatra (RK0150; Fig. 1). *Podabrocephalus* was recovered nested within Ptilodactylinae and the clade obtained strong support in all analyses (98–99% BS, 100% PP). *Pherocladus* Fairmaire, 1881 was always recovered as sister to the *Ptilodactyla* clade, i.e., *Ptilodactyla* including *Podabrocephalus*. The monophyly of the *Ptilodactyla* clade did not obtain reasonable support in the ML analyses. However, no alternative topology was indicated by any analysis. The internal topology of the clade was variable; however, species BMNH 693606 from Japan was always recovered as sister to the remaining species (Fig. 1). *Podabrocephalus* is nested within the clade of the current broadly defined *Ptilodactyla* (Fig. 1). The immediate sister-relationships of *Podabrocephalus* obtained low bootstrap support, probably due to the presence of only 18S and 28S markers for this taxon in the dataset. However, robust support was inferred in the molecular analysis for the placement of *Podabrocephalus* within Ptilodactylinae.

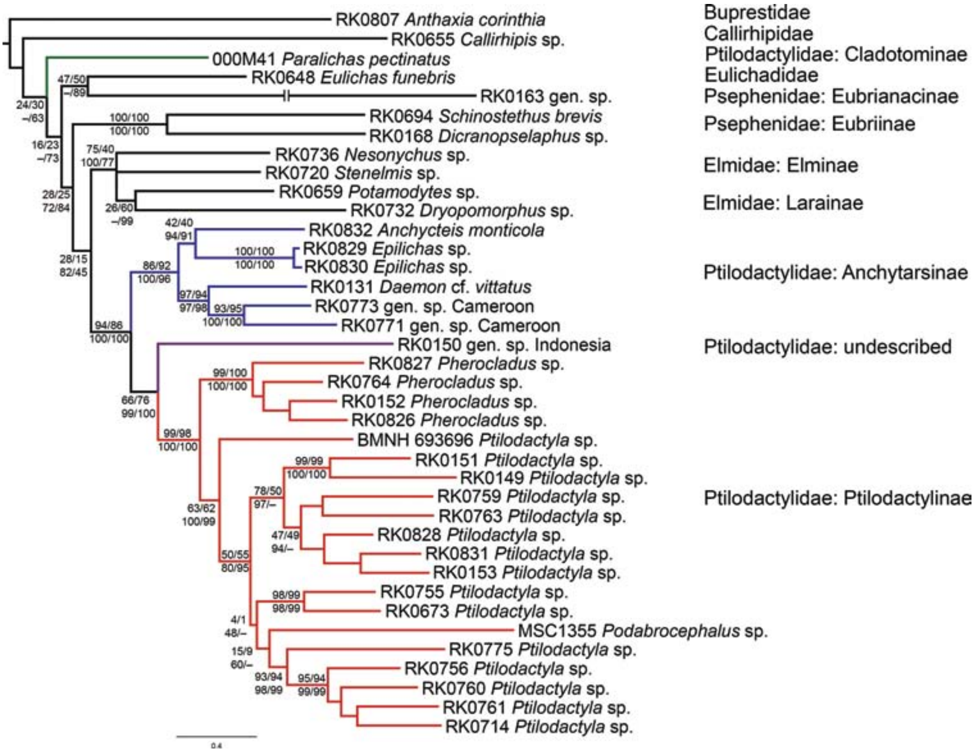


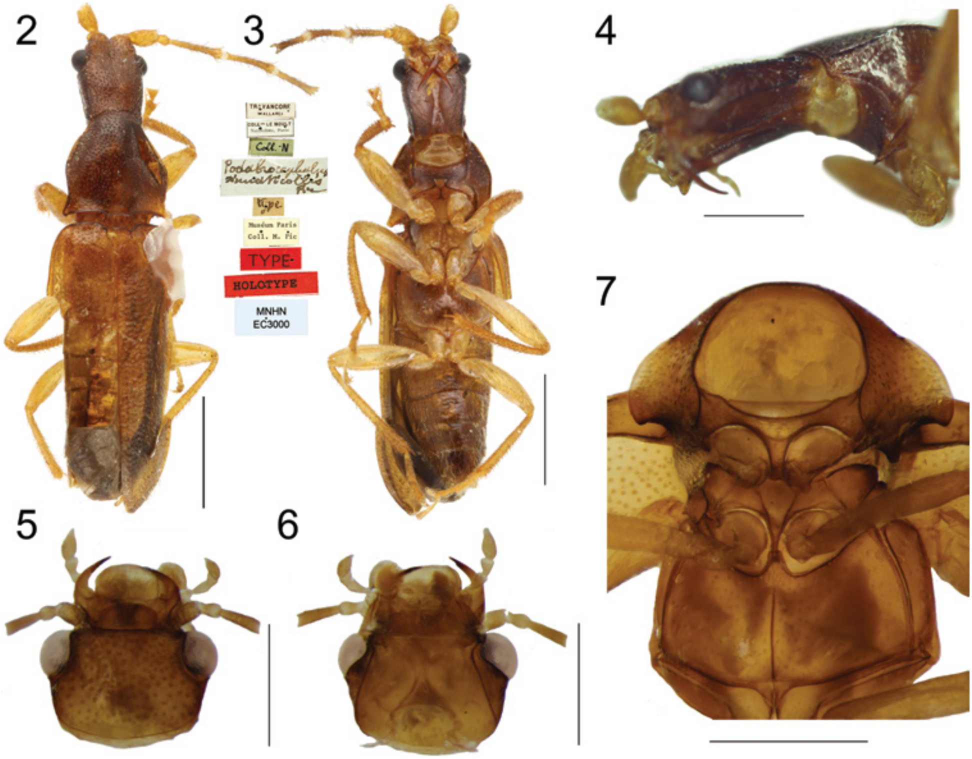
Fig. 1. Phylogenetic hypothesis for Ptilodactylidae inferred from the ML analysis of the Mafft alignment. Numbers at the branches indicate bootstrap values for ML analyses of the Mafft and Muscle alignments, and posterior probabilities for BI analyses of the Mafft and Muscle alignments, respectively.

Systematics

Family Ptilodactylidae Laporte, 1836
Subfamily Ptilodactylinae Laporte, 1836
Ptilodactylidae Laporte, 1836: 21.
Type genus: *Ptilodactyla* Illiger, 1807: 342.
=Podabrocephalidae Pic, 1930, **syn. n.**
Podabrocephalidae Pic, 1930: 314.
Type genus: *Podabrocephalus* Pic, 1913: 118.

Diagnosis, redescription and composition of the subfamily Ptilodactylinae

Diagnosis. Eyes strongly protuberant (Figs. 3–6); antennal insertions widely separated; subantennal groove absent; antenna 11-segmented; gular sutures narrowly separated (Figs. 3, 6); cervical sclerites present. Pronotum wider than long, widest posteriorly, narrowed anteriorly (Fig. 2); procoxal cavities slightly transverse, internally open (Figs. 3, 7); protrochantin not exposed, concealed by posterolateral extension of prosternum which meet hypomeral projection. Elytra without scutellary striole; epipleuron complete.



Figs. 2–7. Ptilodactylinae. *Podabrocephalus sinuaticollis* Pic, 1913, holotype. (2) habitus, dorsally; (3) habitus, ventrally; (4) prosternal process, laterally. *Ptilodactyla* sp. (5) head, dorsally; (6) head, ventrally; (7) thorax, ventrally. Scale bars = 1.0 mm (Figs. 2–3), 0.5 mm (Figs. 4–7). Credit for Figs. 2–3: A. Mantilleri (MNHN).

Mesocoxal cavities narrowly separated, open laterally (Figs. 3, 7). Metacoxae contiguous or narrowly separated. Hind wing with elongate radial cell; cross-vein r3 very short; wedge cell absent. Tibial spurs double on all pairs of legs. Tarsi pseudotetramerous, tarsomere III lobate ventrally, tarsomere IV reduced, pretarsal claws toothed or bifid. Abdomen with five ventrites, basal three connate.

Redescription. Adult (Figs. 2–8). Body medium-sized, 3–7 mm long, rarely longer. Head subquadrate, declined (most genera; Figs. 5–6) or elongate, not declined (*Podabrocephalus*; Figs. 2–4, 8); frontal region declined apically to strongly deflexed and vertical only at apex. Eyes entire, strongly protuberant, finely facetted (Figs. 3–6). Antennal insertions widely separated; subantennal groove absent. Antenna 11-segmented; male antenna with articulated rami on antennomeres 4–10 (most genera) or filiform (*Podabrocephalus*; Figs. 2–3, 8), female antenna filiform to serrate; labrum subquadrate (most genera) or more transverse (*Podabrocephalus*). Gular sutures narrowly separated (Figs. 3, 6). Cervical sclerites present. Mandible relatively short, broad, bidentate, with prostheca (most genera; Figs. 5–6) or long, falcate, unidentate, pointing posteroventrally, without prostheca (*Podabrocephalus*; Figs. 3–4, 8). Maxilla with distinct acute galea and lacinia forming spore brush (most genera) or with only a single apical lobe (*Podabrocephalus*), terminal maxillary palpomere variously shaped,

Fig. 8. *Podabrocephalus* sp.; habitus, laterally.

sometimes sexually dimorphic. Labium with simple ligula, terminal labial palpomere variously shaped. Pronotum wider than long, widest posteriorly, narrowed anteriorly, lateral carinae incomplete anteriorly (most genera) or complete (*Podabrocephalus*; Figs. 4, 8), anterior angles not produced, posterior angles not produced (most genera) or produced posterolaterally (*Podabrocephalus*; Figs. 2, 8), posterior margin distinctly sinuate, crenulate (most genera) or simple (*Podabrocephalus*, *Chelonariomorphus*). Prosternal process complete (most genera; Fig. 7) or incomplete, strongly produced ventrally (*Podabrocephalus*; Figs. 3–4, 8). Procoxal cavities slightly transverse, contiguous or narrowly separated, internally open. Protrochantin not exposed, concealed by posterolateral extension of prosternum which meet hypomeral projection. Scutellar shield abruptly elevated, with anterior margin simple, notched or crenulate. Elytra 1.5–2.3 times as long as wide, irregularly punctate, without scutellary striole; epipleuron complete. Mesoventrite shallowly depressed medially, anteriorly on same plane as metaventrite. Mesocoxal cavities narrowly separated, open laterally. Metaventrite with discrimen moderately to very long. Metacoxae contiguous or narrowly separated. Hind wing with radial cell elongate, with inner posterobasal angle acute, cross-vein r3 very short, wedge cell absent. Leg long, slender; tibial spurs double on all pairs of legs; tarsi pseudotetramerous, tarsomere III lobate ventrally, tarsomere IV reduced; pretarsal claws toothed or bifid. Abdomen with five ventrites, basal three connate; ventrite 1 without (*Podabrocephalus*) or with slender intercoxal process (most genera); ventrite 5 more or less emarginate. Functional spiracles on segment VIII absent. Aedeagus trilobate, phallobase without struts, paramere and phallus of different shapes. Ovipositor long, gonocoxites not divided, gonostyli absent.

Composition. Ptilodactylinae as here defined corresponds mostly with the Ptilodactylini or Ptilodactylinae of Pic (1914), Crowson (1955), Stribling (1986, unpublished dissertation, summarized by Ivie [2002]) and the most recent summary by

Chatzimanolis et al. (2012). With the changes proposed here, the subfamily contains eight genera and about 400 described species: *Ptilodactyla* Illiger, 1807 (about 370 spp.); *Chelonariomorphus* Pic, 1916 (1 sp.); *Lachnodactyla* Champion, 1897 (4 spp.); *Lomechon* (1 sp.); *Microdrupeus* (1 sp.); *Pherocladus* Fairmaire, 1881 (9 spp.); *Podabrocephalus* (1 sp.); *Stirophora* Champion, 1897 (= *Chaetodactyla* Champion, 1897) (2 spp.).

The genus *Daemon*, placed in Ptilodactylinae by Stribling (1986) and Chatzimanolis et al. (2012), is here moved to Anchytarsinae based on the results of molecular phylogeny (Fig. 1). Such placement was already proposed by Lawrence & Newton (1995), and it is additionally supported by the morphology (e.g., visible protrochantins and simple claws in *Daemon* spp.). *Falsotherius* Pic, 1913, although classified in Ptilodactylinae by Stribling (1986), Lawrence & Newton (1995) and Chatzimanolis et al. (2012), does not fit the definition of this subfamily as it has partly visible protrochantins (concealed in Ptilodactylinae), lobate tarsomere II (simple in Ptilodactylinae), and simple claws (toothed or bifid in Ptilodactylinae). Because this genus cannot be placed to any other existing ptilodactylid subfamily, we place *Falsotherius* in Ptilodactylidae incertae sedis until the family revision is carried out.

Genus *Podabrocephalus* Pic, 1913
Podabrocephalus Pic, 1913: 118.

Type species. *Podabrocephalus sinuaticollis* Pic, 1913; by monotypy.

Type locality. India: Travancore: Wallardi.

Diagnosis. Members of the genus *Podabrocephalus* share particular characters with some non-ptilodactyline lineages, such as the prolonged head with *Octoglossa* (which has also longer mandibles than most other ptilodactylids) or the transverse labrum and complete lateral pronotal margins with Cladotominae, but it can be clearly recognized by the characters typical for the Ptilodactylinae, i.e., concealed protrochantins, pseudotetramerous tarsi, and toothed claws. Within Ptilodactylinae, *Podabrocephalus* can be recognized by its less sclerotized, subparallel-sided, more elongate body (Figs. 2–3, 8), elongate head, long, narrow, falcate mandibles (Figs. 4, 8), reduced maxilla, pronotal posterior angles strongly produced posterolaterally (Figs. 2–3, 8), lateral pronotal carinae complete (Figs. 4, 8), and prosternal process strongly produced ventrally (Figs. 3–4, 8). Female and immature stages are unknown.

Composition. Only *P. sinuaticollis* Pic, 1913 is described.

Discussion

Monophyly, phylogeny and classification of Ptilodactylidae

The monophyly of Ptilodactylidae has been questioned in many studies (e.g., Beutel 1995, Lawrence et al. 1995; Costa et al. 1999; Kundrata et al. 2017) and the current results corroborate the hypothesis on the non-monophyly of this family (Fig. 1).

Cladotominae, represented here only by *Paralichas*, are inferred as not related to remaining ptilodactylids and more data is needed for their well-supported placement. Their position outside the Ptilodactylidae has already been suggested using morphology and molecular data (Beutel 1995; Bocakova et al. 2007; Kundrata et al. 2017). Cladotominae are characterized by the strongly transverse labrum, inflated pronotal disc, complete pronotal lateral carinae, reduced wedge cell, absence of gonostyli, and the distinctive larva with a spiracular siphon.

The here provided molecular phylogeny shows the monophyly of Anchytarsinae + a yet undescribed lineage + Ptilodactylinae. However, many lineages are not yet represented in our molecular dataset. For instance, a majority of described genera of both subfamilies are missing, and all *Ptilodactyla* studied were Old World species, although this very heterogeneous group contains hundreds of species in the New World. The close relationship of Anchytarsinae and Ptilodactylinae was suggested previously by both morphology (Costa et al. 1999; Lawrence et al. 2011) and DNA studies (McKenna et al. 2015; Kundrata et al. 2017). In our study, Anchytarsinae were represented by *Anchycteis*, *Daemon*, *Epilichas* and two unidentified Afrotropical taxa, and their monophyly was well supported (Fig. 1). Stribling (1986) created a tribe within Ptilodactylinae for *Daemon* and an undescribed African genus. The latter is most probably congeneric with the RK0771 and RK0773 from Cameroon in our study. *Daemon* was placed in Anchytarsinae by Lawrence & Newton (1995), but it was returned to the Ptilodactylinae by Chatzimanolis et al. (2012). Here, we recover a relationship of *Daemon* and the undescribed African genus with *Epilichas* and *Anchycteis* (Fig. 1), and we combine this well-supported clade as Anchytarsinae sensu lato. Further investigation is needed to determine whether morphological synapomorphies exist for this group.

Another undescribed ptilodactylid lineage is represented here by a male specimen from Indonesia: Sumatra coded as RK0150. We keep this lineage as undescribed until more material is available for more detailed morphological investigation.

Podabrocephalus was consistently recovered within *Ptilodactyla* despite the morphological divergence (Fig. 1). The genus differs from "typical" Ptilodactylinae in the general appearance, weaker sclerotization, the prolonged head, strongly produced pronotal posterior angles, and straight base of the pronotum (a character shared with *Chelonariomorphus* only). The configuration of the protrochantins, tarsi, genitalia and claws are characters supporting *Podabrocephalus* placement in Ptilodactylinae sensu stricto. Based on the current results, we synonymize the family Podabrocephalidae Pic, 1930 **syn. n.** with the Ptilodactylidae Laporte, 1836. We recovered *Podabrocephalus* within the widely defined *Ptilodactyla*, but the genus has been used as a collective taxon for morphologically diverse taxa and is in a need of taxonomic revision.

Parallel evolution of morphological modifications in soft-bodied lineages

The monophyly and morphology-based relationships among the majority of beetle families have been mostly confirmed by molecular analyses (Hunt et al. 2007; Bocak et al. 2014; McKenna et al. 2015). Unlike many other groups, conflicting relationships were recovered for the incompletely sclerotized beetle lineages. Lawrence et al. (2011) recovered *Podabrocephalus* in the Elateroidea as a sister to a "clade" of soft-bodied lineages using a formal morphological phylogenetic analysis. The close relationship of *Ptilodactyla* and *Podabrocephalus* was recovered by McKenna et al. (2015), but both taxa were represented only by a single terminal and *Podabrocephalus* was kept as a representative of the monotypic subfamily Podabrocephalinae (Lawrence et al. 2016a). Our molecular analysis places *Podabrocephalus* within the widely defined *Ptilodactyla* of the Ptilodactylinae (Fig. 1).

Molecular analyses of Elateroidea that include taxonomic groups defined by the soft-bodied adults repeatedly recovered them as a polyphyletic assemblage of independently rooted clades related to Artematopodidae (Omethidae and Telegeusidae) or Elateridae (Phengodidae, Rhagophthalmidae, Omalisidae), deeply rooted in the Elateroidea tree (Cantharidae, Lycidae and Lampyridae; Bocakova et al. 2007; Kundrata et al. 2014; McKenna et al. 2015), or even forming a terminal lineage within Elateridae (Drilidae; Kundrata & Bocak 2011). This conflict in molecular and morphological signal is, therefore, commonly encountered in beetles with what has been called the "malacoderm facies".

Podabrocephalus was originally compared with Cantharidae (Pic 1913) or Drilidae (Pic 1930) and conversely, the position of *Podabrocephalus* within Ptilodactylinae is now robustly inferred from molecular data (Fig. 1). This taxon becomes a further example of an inappropriately high rank for a morphologically modified elateriform lineage. The female of *Podabrocephalus* remains unknown and we cannot exclude that it is wingless. Until the female is collected the question on the level of modification of *Podabrocephalus* females remains open.

The adult male of *Podabrocephalus sinuaticollis* differs from other Ptilodactylinae in numerous characters, but in contrast with the soft-bodied elateroids, with which it was formerly associated, it is quite well sclerotized and does not substantially differ in this trait from other *Ptilodactyla* sensu lato. The male differs in having a long head, specifically a long occipital region, long sickle-shaped mandibles, pronotal posterior angles strongly produced, promesothoracic interlocking mechanism absent, prosternal process incomplete and strongly produced ventrally, and a shorter and narrower abdomen without co-adapted abdominal and elytral margins (Figs. 2–4, 8). Some of these modifications, e.g., non-coadapted margins of elytra and abdomen, resemble those of soft-bodied elateroid lineages. Similarly, the modified shape of the cranium is a variable character and modifications are common in some elateroid beetles, e.g. the males of *Dexoris* Waterhouse, 1878 and *Lyropaeus* Waterhouse, 1878 (Bocak & Bocakova 2008). The absent promesothoracic interlocking mechanism is characteristic for weakly sclerotized click beetles (Elateridae), e.g., Agrypninae: Drilini (Kundrata & Bocak 2017) and Elaterinae: Cebrionini (Kundrata & Bocak 2011). Similarly, the close co-adaptation of pro- and mesothorax was lost in males of the modified dermestid *Thylodrias contractus* Motschulsky, 1839 (Lawrence & Ślipiński 2010). The long, sickle-shaped mandibles are characteristic for *Podabrocephalus* and unknown from other Ptilodactylidae. We know only a single case when a taxon with modified morphology differs from its close relatives in the long, slender mandibles, i.e., *Platerodrilus* Pic, 1921 (Lycidae: Lyropaeinae: Platerodrilini; Masek & Bocak 2014). The function of the prosternal process and long mandibles remains unknown.

The modified morphology provided a false morphological signal and based on the morphological divergence an inappropriately high rank was assigned to *Podabrocephalus*. These cases are common and the relationship of *Podabrocephalus* with other Ptilodactylinae genera demonstrates the importance of cross-validation of the morphological and molecular signal.

Acknowledgements

We are very obliged to A. Mantilleri (MNHN) for allowing us to use the photograph of the holotype of *Podabrocephalus sinuaticollis* Pic, 1913, to Patrice Bouchard, Anthony Downes, and Harald Schillhammer for language assistance regarding nuances of Pic and Wittmer literature, and to Isidor Plonski (NHMW) for help with obtaining literature. The short-term stays of RK in the Naturhistorisches Museum, Wien, Austria (AT-TAF 6821), the Muséum national d'Histoire naturelle, Paris, France (FR-TAF 6701), and the Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany (DE-TAF 7085) were funded by the EU-SYNTHESYS grants. This support as well as the help from M. Jäch, I. Plonski (NHMW), O. Montreuil, A. Mantilleri (MNHN), S. Blank, T. Schmitt and K. Kramp (SDEI) is gratefully acknowledged. MAI was supported by US-NSF Grant # 0531768 to Brian Farrell, and thanks David Maddison, Duane McKenna, and Kaniyarikkal Divakaran Prathapan. This is a contribution of the Montana Agricultural Experiment Station.

References

Beutel, R.G. (1995) Phylogenetic analysis of Elateriformia (Coleoptera: Polyphaga) based on larval characters. *Journal of Zoological Systematics and Evolutionary Research* **33**: 145–171.

Bocak, L., Barton, C., Crampton-Platt, A., Chesters, D., Ahrens, D. & Vogler, A.P. (2014) Building the Coleoptera tree-of-life for >8000 species: composition of public DNA data and fit with Linnaean classification. *Systematic Entomology* **39**: 97–110.

Bocak, L. & Bocakova, M. (2008) Phylogeny and classification of the family Lycidae (Insecta: Coleoptera). *Annales Zoologici* **58**: 695–720.

Bocakova, M., Bocak, L., Hunt, T., Teraväinen, M. & Vogler, A.P. (2007) Molecular phylogenetics of Elateriformia (Coleoptera): evolution of bioluminescence and neoteny. *Cladistics* **23**: 477–496.

Bouchard, P., Bousquet, Y., Davies, A.E., Alonso-Zarazaga, M.A., Lawrence, J.F., Lyal, C.H.C., Newton, A.F., Reid, C.A.M., Schmitt, M., Ślipiński, S.A. & Smith, A.B.T. (2011) Family-group names in Coleoptera (Insecta). *ZooKeys* **88**: 1–972.

Costa, C., Vanin, S.A. & Ide, S. (1999) Systematics and bionomics of Cneoglossidae with a cladistic analysis of Byrrhoidea sensu Lawrence & Newton (1995) (Coleoptera, Elateriformia). *Arquivos de Zoologia* **35**: 231–300.

Crowson, R. (1955) The natural classification of the families of Coleoptera. Nathaniel Lloyd, London: 187 pp.

Chatzimanolis, S., Cashion, M.E., Engel, M.S. & Falin, Z.H. (2012) A new genus of Ptilodactylidae (Coleoptera: Byrrhoidea) in mid-Cretaceous amber from Myanmar (Burma). *Geodiversitas* **34**: 569–574.

Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* **32**: 1792–1797.

Huelsenbeck, J.P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**: 754–755.

Hunt, T., Bergsten, J., Levkanicova, Z., Papadopoulou, A., St. John, O., Wild, R., Hammond, P.M., Ahrens, D., Balke, M., Caterino, M.S., Gómez-Zurita, J., Ribera, I., Barraclough, T.G., Bocakova, M., Bocak, L. & Vogler, A.P. (2007) A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. *Science* **318**: 1913–1916.

Illiger, J.K.W. (1807) Vorschlag zur Aufnahme im Fabricischen Systeme fehlende Käfergattungen. *Magazin für Insektenkunde* **6**: 318–349.

Ivie, M.A. (2002) Family 49. Ptilodactylidae. In: Thomas, M.C., Arnett, R.H, Skelley, P.E. & Frank, J.H. (eds.) American Beetles, Volume 2, Polyphaga: Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, Florida: pp. 135–138.

Katoh, K., Misawa, K., Kuma, K. & Miyata, T. (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* **30**: 3059–3066.

Katoh, K. & Standley, D.M. (2013) MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability. *Molecular Biology and Evolution* **30**: 772–780.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Mentjies, P. & Drummond, A. (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* **28**: 1647–1649.

Kundrata, R. & Bocak, L. (2011) The phylogeny and limits of Elateridae (Insecta, Coleoptera): is there a common tendency of click beetles to soft-bodiedness and neoteny? *Zoologica Scripta* **40**: 364–378.

Kundrata, R. & Bocak, L. (2017) Taxonomic review of Drilini (Elateridae: Agrypninae) in Cameroon reveals high morphological diversity, including the discovery of five new genera. *Insect Systematics & Evolution* **48**: 441–492.

Kundrata, R., Bocakova, M. & Bocak, L. (2014) The comprehensive phylogeny of the superfamily Elateroidea (Coleoptera: Elateriformia). *Molecular Phylogenetics and Evolution* **76**: 162–171.

Kundrata, R., Jäch, M.A. & Bocak, L. (2017) Molecular phylogeny of the Byrrhoidea-Buprestoidea complex (Coleoptera, Elateriformia). *Zoologica Scripta* **46**: 150–164.

Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* **29**: 1695–1701.

Laporte, F.L. (1836) Études entomologiques, ou descriptions d'insectes nouveaux, et observations sur la synonymie. *Revue Entomologique* **4**: 5–60.

Lawrence, J.F. (2016a) Classification (families & subfamilies). In: Beutel, R.G. & Leschen, R.A.B. (volume eds.), Coleoptera, Beetles; Volume 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), 2nd Edition. In: Kristensen, N.P. & Beutel, R.G. (eds.), Handbook of Zoology, Arthropoda: Insecta. Walter de Gruyter, Berlin/Boston: pp. 13–22.

Lawrence, J.F. (2016b) Ptilodactylidae Laporte, 1836. In: Beutel, R.G. & Leschen, R.A.B. (volume eds.), Coleoptera, Beetles; Volume 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), 2nd Edition. In: Kristensen, N.P. & Beutel, R.G. (eds.), Handbook of Zoology, Arthropoda: Insecta. Walter de Gruyter, Berlin/Boston: pp. 632–639.

Lawrence, J.F., Kawashima, I. & Branham, M.A. (2010) Elateriformia Incertae sedis. In: Leschen, R.A.B., Beutel, R.G. & Lawrence, J.F. (volume eds.) Coleoptera, Beetles; Volume 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). In: Kristensen, N.P. & Beutel, R.G. (eds.) Handbook of Zoology, Arthropoda: Insecta. Walter de Gruyter, Berlin/New York: pp. 162–177.

Lawrence, J.F. & Newton, A.F. (1995) Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). In: Pakaluk, J. & Ślipiński, S.A. (eds.) Biology, Phylogeny, and Classification of Coleoptera. Papers Celebrating the 80th Birthday of Roy A. Crowson, Volumes **1–2**. Muzeum i Instytut Zoologii PAN, Warszawa: pp. 779–1083.

Lawrence, J.F., Nikitsky, N.B. & Kirejtshuk, A.G. (1995) Phylogenetic position of Decliniidae (Coleoptera: Scirtoidea) and comments on the classification of Elateriformia (sensu lato). In: Pakaluk, J. & Ślipiński, S.A. (eds.) Biology, Phylogeny, and Classification of Coleoptera. Papers Celebrating the 80th Birthday of Roy A. Crowson, Volumes 1–2. Muzeum i Instytut Zoologii PAN, Warszawa: pp. 375–410.

Lawrence, J.F. & Ślipiński, A. (2010) Dermestidae Latreille, 1804. In: Leschen, R.A.B., Beutel, R.G. & Lawrence, J.F. (volume eds.) Coleoptera, Beetles; Volume 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). In: Kristensen, N.P. & Beutel, R.G. (eds.) Handbook of Zoology, Arthropoda: Insecta. Walter de Gruyter, Berlin/New York: pp. 198–206.

Lawrence, J.F., Ślipiński, A., Seago, A.E., Thayer, M.K., Newton, A.F. & Marvaldi, A.E. (2011) Phylogeny of the Coleoptera based on morphological characters of adults and larvae. *Annales Zoologici* **61**: 1–217.

Masek, M. & Bocak, L. (2014) The taxonomy and diversity of *Platerodrilus* (Coleoptera, Lycidae) inferred from molecular data and morphology of adults and larvae. *ZooKeys* **426**: 29–63.

McKenna, D.D., Wild, A.L., Kanda, K., Bellamy, C.L., Beutel, R.G., Caterino, M.S., Farnum, C.W., Hawks, D.C., Ivie, M.A., Jameson, M.L., Leschen, R.A.B., Marvaldi, A.E., McHugh, J.V., Newton, A.F., Robertson, J.A., Thayer, M.K., Whiting, M.F., Lawrence, J.F., Ślipiński, A., Maddison, D.R. & Farrell, B.D. (2015) The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Systematic Entomology* **40**: 835–880.

Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010. LA, New Orleans: pp. 1–8.

Pic, M. (1913) Un curieux genre de Coléoptères des Indes. *L'Echange* **29**: 117–118.

Pic, M. (1914) Pars 58. Dascillidae, Helodidae, Eucinetidae. In: Schenkling, S. (ed.), Coleopterorum Catalogus. W. Junk, Berlin: 65 pp.

Pic, M. (1930) Contribution a l'étude de Coléoptères malacodermes (2e article). II. - Quelques données générales sur la systématique et cas particuliers. *Annales de la Société entomologique de France* **99**: 311–314.

Rambaut, A. (2009) FigTree 1.3.1. Available at http://tree.bio.ed.ac.uk/software/figtree/.

Rambaut, A. & Drummond, A.J. (2007) Tracer 1.5. Institute of Evolutionary Biology University of Edinburgh, Edinburgh. Available at http://beast.bio.ed.ac.uk/Tracer.

Sharp, D. (1916) Insecta. *Zoological Record* [for the year 1914] **51**: 1–342.

Stamatakis, A. (2006) RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22**: 2688–2690.

Stribling, J.B. (1986) World generic revision of Ptilodactylidae (Coleoptera: Dryopoidea). PhD Thesis, Ohio State University, Columbus: 200 pp.

Wittmer, W. (1969) Synonymische und systematische Notizen über Coleopteren. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* **42**: 126–134.

Příloha 5

Kundrata, R., Gunter, N.L., Douglas, H. & Bocák, L. (2016) Next step toward a molecular phylogeny of click-beetles (Coleoptera: Elateridae): redefinition of Pityobiinae, with a description of a new subfamily, Parablacinae, from the Australasian Region. *Austral Entomology*, 55: 291–302.
[IF 1,341; 18 citací na WoS; celkem 5 citací bez autorových autocitací]
[korespondující autor; autorský podíl: 45 %]

Austral Entomology

Austral Entomology (2016) **55**, 291–302

Next step toward a molecular phylogeny of click-beetles (Coleoptera: Elateridae): redefinition of Pityobiinae, with a description of a new subfamily Parablacinae from the Australasian Region

Robin Kundrata,[1]* Nicole L Gunter,[1,2] Hume Douglas[3] and Ladislav Bocak[1]

[1]*Department of Zoology, Faculty of Science, Palacky University, Olomouc 771 46, Czech Republic.*
[2]*CSIRO National Research Collections Australia, Canberra, ACT 2601, Australia.*
[3]*Canadian National Collection of Insects, Arachnids and Nematodes, Agriculture and Agri-Food Canada, 960 Carling Avenue, Ottawa, ON K1A 0C6, Canada.*

Abstract Elateridae represents one of the largest families within Coleoptera, yet their interrelationships remain under-investigated. Molecular data are missing for most lineages, especially for the species-poor suprageneric taxa. In this study, we investigated the limits and phylogenetic position of Pityobiinae *sensu* Calder (1996), a group of several small genera from the New World and Australasia, using maximum likelihood and Bayesian inference methods. We merged new sequence data with those deposited in GenBank, producing a final matrix of 178 terminal taxa and covering the main click-beetle subfamilies. The resulting topologies showed Elaterinae as sister to remaining click-beetle lineages, and Agrypninae as sister to the Morostomatinae + Dendrometrinae + Cardiophorinae + Negastriinae clade. Members of Hemiopinae, Lissominae, Thylacosterninae and Pityobiinae formed basal lineages within Elateridae – Elaterinae. We found Lissominae to be polyphyletic, including Thylacosterninae as a terminal lineage and with Oestodini forming an independent lineage outside that clade. Therefore, the subfamily Oestodinae stat. nov. was reinstated for the North American genera *Oestodes* LeConte and *Bladus* LeConte. The Australian genera *Dicteniophorus* Candèze, *Drymelater* Calder and *Stichotomus* Candèze were transferred from Dendrometrinae to Elaterinae. Pityobiinae was recovered as two distant lineages in all analyses and correspondingly the subfamily is reduced to contain only the North American *Pityobius* LeConte and tentatively the South American *Tibionema* Solier, for which we have no DNA sequences. Additionally, we propose Parablacinae subfam. nov. for the remaining former pityobiine genera from Australia and New Zealand. The new subfamily includes *Parablax* Schwarz, *Metablax* Candèze, *Wynarka* Calder, *Xuthelater* Calder, *Tasmanelater* Calder, *Parasaphes* Candèze and also *Ophidius* Candèze, which is transferred here from Elaterinae. We failed to find universally diagnostic synapomorphies in adult morphology for Parablacinae, a common problem in elaterid taxonomy. Future research, including a comprehensive phylogeny of the subfamily and re-examination of the morphology of its species is crucial to understanding the limits and classification of this lineage.

Key words Australia, classification, Lissominae, New Zealand, Oestodinae.

INTRODUCTION

The Elateridae (commonly known as click-beetles) with ca. 10 000 described species are among the richest families in Coleoptera (Costa *et al*. 2010; Bocak *et al*. 2014). Despite their worldwide distribution and great popularity among both professional and amateur entomologists, click-beetle classification is chaotic and in a state of flux (Dolin 1975; Calder *et al*. 1993; Johnson 2002; Kundrata & Bocak 2011). The family contains several large, widely accepted and cosmopolitan subfamilies such as Elaterinae, Agrypninae, Dendrometrinae, Cardiophorinae and Negastriinae. On the other hand, many species-poor lineages have unstable taxonomic positions and their ranks, limits and hypothesised relationships vary greatly depending on different authors' classifications (e.g. Cebrioninae, Diminae, Eudicronychinae, Lissominae, Oxynopterinae, Thylacosterninae) (Hyslop 1917; Fleutiaux 1947; Crowson 1961; Gur'yeva 1974; Dolin 1975; Stibick 1979; Lawrence & Newton 1995; Calder 1996; Johnson 2002; Costa *et al*. 2010; Kundrata & Bocak 2011).

One such small group with unclear composition and position is Pityobiinae (Calder 1992; Fig. 1). Hyslop (1917) created the tribe Pityobiini within Pyrophorinae (=Agrypninae) for a single North American genus *Pityobius* LeConte. His conclusions were based primarily on larval characters. Crowson (1961) also included the endemic New Zealand genus *Metablax* Candèze in Pityobiinae based on similarities of larval morphology with that of *Pityobius*, and

---

*robin.kundrata@upol.cz

Early View version of record published on 23 November 2015.

doi:10.1111/aen.12185

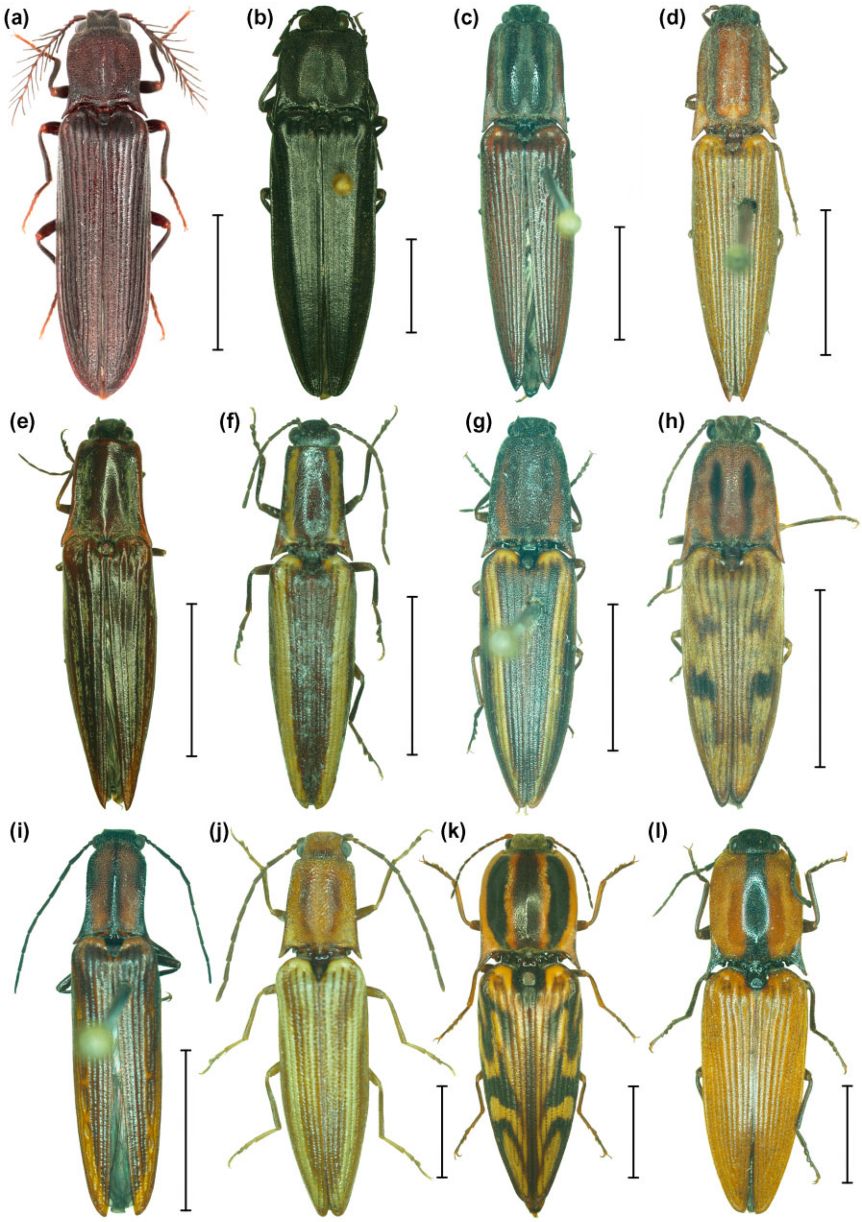


Fig. 1. Pityobiinae. (a) *Pityobius anguinus* LeConte, 1853 (author's collection), (b) *Tibionema abdominalis* Guérin-Méneville, 1838 (HNHM). Parablacinae subfam. nov. (c) *Parablax quinquesulcatus* (Blackburn, 1900) (ANIC), (d) *Metablax trisulcatus* Schwarz, 1903 (holotype; synonym of *P. quinquesulactus*) (SDEI), (e) *M. acutipennis* (White, 1846) (ANIC), (f) *M. cinctiger* (White, 1846) (HNHM), (g) *Wynarka sylvestre* Calder, 1986 (paratype) (ANIC), (h) *Xuthelater moppiensis* Calder, 1996 (paratype) (ANIC), (i) *Tasmanelater pelionensis* Calder, 1996 (paratype) (ANIC), (j) *Parasaphes elegans* Candéze, 1882 (ANIC), (k) *Ophidius histrio* (Boisduval, 1835) (ANIC), (l) *O. elegans* Candéze, 1863 (ANIC). Scales: 2 mm (j), 5 mm (c–i, k–l), 10 mm (a–b).

Gur'yeva (1974) confirmed this relationship based on the adult thoracic morphology. Dolin (1975) added the Australian *Parablax* Schwarz and South American *Tibionema* Solier to the subfamily due to similarities in wing venation and listed several larval and adult characters to define Pityobiinae. However, Calder (1976) transferred *Metablax* from Pityobiinae to Campsosterninae (=Oxynopterinae). Stibick (1979) redefined Pityobiinae to contain three tribes – Pityobiini (*Pityobius*), Rostricephalini (*Rostricephalus* Fleutiaux) and Pectocerini (*Pectocera* Hope, *Ceroleptus* Fleutiaux, *Julodischema* Thompson). Stibick's (1979) classification was not accepted by subsequent authors including Ulrich (1988), who studied the larval morphology of Pityobiinae and recognised two tribes – Pityobiini (*Pityobius*, *Metablax* pars and unassociated species from Australia and South Africa) and Tibionemini (*Tibionema*, *Metablax* pars). Calder (1992) re-examined pityobiine genera and included the following in the subfamily: *Pityobius*, *Tibionema*, *Parablax*, *Metablax*, *Parasaphes* Candèze and *Wynarka* Calder. Most recently, Calder (1996) added his newly described genera *Tasmanelater* Calder and *Xuthelater* Calder to the subfamily, bringing the number of included genera to eight (Fig. 1; Table S4). This concept of Pityobiinae was adopted by Costa *et al*. (2010) in the *Handbook of Zoology* and is considered here to be Pityobiinae as currently defined.

The classification, phylogenetic position and relationships of these eight genera have always been problematic, and various authors studying the morphology of both adults and larvae have produced different hypotheses. *Pityobius* was considered either sister to Pyrophorini (=Agrypninae), close to Dendrometrinae or sister to a clade representing the remaining Elateridae, Eucnemidae and Throscidae (Hyslop 1917; Ulrich 1988; Douglas 2011; respectively). *Tibionema* and *Parasaphes* were classified in Hemicrepidiini/ae, *Parablax* and *Wynarka* in

Crepidomeninae and *Metablax* either in Crepidomeninae or Campsosternini/ae (Schwarz 1906, 1907; Schenkling 1927; Neboiss 1956; Calder 1976, 1986; Stibick 1979). Stibick (1979) assumed a close relationship between Pityobiinae and Oxynopterinae, together sister to Pyrophorinae (=Agrypninae). In a morphology-based phylogeny, *Pityobius* + *Metablax* were sister to Agrypninae (Calder *et al*. 1993). Johnson (2002), followed by Kundrata and Bocak (2011), treated pityobiines as a tribe within widely defined Dendrometrinae. However, these hypotheses were based only on morphological concepts and none of Calder's (1996) eight pityobiine genera have ever been included in a molecular phylogenetic analysis. Sagegami-Oba *et al*. (2007) included *Pectocera* in Pityobiinae in their analysis based on the Stibick's (1979) classification; however, this genus belongs in subfamily Oxynopterinae (Costa *et al*. 2010).

In this study, we analyse the expanded elaterid DNA data set, emphasising pityobiines and their relatives. The main aims of this study are to (1) test the monophyly and limits of Pityobiinae *sensu* Calder (1996) compared with previous taxonomic concepts, (2) reveal the phylogenetic positions of pityobiine genera included in the analysis, and (3) translate our results into the formal taxonomic classification of Elateridae.

MATERIALS AND METHODS

Taxon sampling, morphology and laboratory methods

The current Elateridae data set contains taxa analysed by Kundrata *et al*. (2014) and the additional 28 click-beetle species from the different zoogeographical regions (Table 1), which were poorly represented in the previous studies. The data set contains for the first time the genera of Pityobiinae *sensu* Calder (1992, 1996). We sampled specimens from four of eight pityobiine genera, including *Pityobius* (type genus and species), *Metablax*, *Parablax* and *Wynarka*. We also sequenced *Pectocera* Hope, which was classified in Pityobiinae by Stibick (1979) and Kishii (1987) but is currently included within Oxynopterinae. The subfamilial classification of Elateridae follows that of Costa *et al*. (2010), with changes proposed by Kundrata and Bocak (2011), and Bouchard *et al*. (2011). The morphological terminology follows Calder (1996) but is modified as in Douglas (2011). The type and determined non-type specimens of Pityobiinae used to re-examine some morphological characters were loaned from the Hungarian Natural History Museum, Budapest, Hungary (HNHM); Australian National Insect Collection CSIRO, Canberra, Australia (ANIC); and Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany (SDEI).

The material was fixed in 96% alcohol in the field and subsequently stored at –20°C. Voucher specimens are deposited at ANIC (Australia) and the Laboratory of Molecular Systematics (Palacky University, Olomouc) (Table 1). DNA was extracted using DNeasy Blood & Tissue kit (Qiagen, Hilden, Germany) following standard protocols. The PCR amplification and sequencing were carried out in two laboratories. Australian specimens were processed in the ANIC molecular systematics laboratory following the procedures described in detail by Gunter *et al*. (2013). The remaining specimens were amplified and sequenced in the Laboratory of Molecular Systematics, UP Olomouc as in Bocakova *et al*. (2007) and Kundrata and Bocak (2011). Four molecular markers were amplified – 18S rRNA (SSU; either whole ~1900 bp or partial ~950 bp fragment) and partial fragments of 28S rRNA (LSU; ~650 bp), *rrnL* mtDNA (~530 bp), and cytochrome c oxidase subunit I mtDNA (*cox1*; 723 bp). GenBank accession and voucher numbers for new sequences are listed in Table 1.

Data set assembling, alignment procedures and phylogenetic analyses

Sequences were edited using Geneious 7.1.7 (Biomatters Ltd; http://www.geneious.com). We merged newly produced data with 120 Elateridae sequences from Kundrata *et al*. (2014; Table S1). Rhagophthalmidae (nine taxa) and Phengodidae (21 taxa) were used as out-groups (Kundrata & Bocak 2011; Amaral *et al*. 2014; Kundrata *et al*. 2014). The matrix consisted of 178 terminal taxa. All but four taxa included at least three fragments (Table 1; Table S1). Fragments were aligned separately using Mafft's default parameters (Katoh *et al*. 2002) in Geneious software and BlastAlign 1.2 (Belshaw & Katzourakis 2005). The protein-coding *cox1* sequences containing no indels were aligned only by Mafft and subsequently checked by amino acid translation. The individual gene alignments produced by Mafft were checked for the apparent misalignments and subsequently concatenated. The program PartitionFinder (Lanfear *et al*. 2012) was used to select best-fit partitioning schemes and molecular evolution models for the analyses.

The BlastAlign and Mafft alignments were analysed under maximum likelihood (ML) approach using RAxML 7.3.1 (Stamatakis 2006) as implemented in CIPRES portal (http://www.phylo.org; Miller *et al*. 2010). Bootstrap values (BS) were calculated using the Rapid Bootstrap algorithm (Stamatakis *et al*. 2008) with 1000 replications under the GTRCAT model. Additionally, we analysed our data under Bayesian inference (BI) using Mr. Bayes 3.1.2 (Huelsenbeck & Ronquist 2001) on the CIPRES web server (Miller *et al*. 2010). Four chains were run for 40×10^6 generations using the Markov chain Monte Carlo (MCMC) method, with trees sampled every 1000 generations. The stationary phase was detected in Tracer 1.5 (Rambaut & Drummond 2007). For each analysis, the first 15% of trees were discarded as burn-in and the posterior probabilities (PP) were determined from the remaining trees. The consensus trees were inferred from PAUP* 4.03b10 (Swofford 2002). The resulting trees were visualised and edited in FigTree 1.3.1 (Rambaut 2009).

RESULTS

Alignment parameters

The aligned 178-taxa data sets included 4379 (BlastAlign) and 4025 (Mafft) homologous positions. Numbers of constant,

Table 1 The list of newly produced sequences of Elateridae with Genbank and voucher numbers

Subfamily	Genus/Species	Geographic origin	Markers				
			18S	28S	*rrnL*	*cox1*	Specimen voucher
Agrypninae	*Agrypnus* sp.	Australia	KT460125	KT460144	KT460118	KT460170	COL027
Agrypninae	*Conoderus* sp.	Australia	KT460126	KT460147	KT460119	KT460174	COL031
Agrypninae	*Heteroderes* sp.	Australia	KT460127	KT460145	KT460120	KT460185	COL096
Agrypninae	*Pseudaeolus* sp.	Australia	KT460128	KT460146	N	KT460186	COL113
Agrypninae	*Aphileus* sp.	Australia	KT460123	KT460142	KT460122	KT460166	COL022
Agrypninae	*Paracalais* sp.	Australia	KT460124	KT460143	KT460121	KT460184	COL076
Cardiophorinae	*Paracardiophorus* sp.	Australia	KT460140	KT460148	KT460116	KT460177	COL049
Cardiophorinae	*Cardiotarsus* sp.	Australia	KT460139	KT460149	KT460117	KT460181	COL055
Dendrometrinae	*Crepidomenus* sp.	Australia	KT460137	KT460151	KT460112	KT460169	COL026
Dendrometrinae	*Glypheus* sp.	Australia	KT460136	KT460150	KT460110	KT460167	COL024
Dendrometrinae	*Microdesmes* sp.	Australia	KT460138	KT460153	KT460113	KT460175	COL047
Dendrometrinae	*Litotelater* sp.	Australia	N	KT460152	KT460111	KT460187	COL1036
Dendrometrinae	*Pectocera jianxiana*	China	KT447368	KT447374	KT447365	KT447379	UPOL RK0562
Elaterinae	*Dicteniophorus* sp.	Australia	KT460130	KT460157	KT460102	KT460171	COL028
Elaterinae	*Drymelater* sp.	Australia	KT460132	KT460156	KT460104	KT460180	COL052
Elaterinae	*Stichotomus* sp.	Australia	KT460131	KT460155	KT460103	KT460172	COL029
Elaterinae	*Ascesis* sp.	Australia	KT460133	KT460154	KT460101	KT460168	COL025
Elaterinae	*Glyphochilus* sp.	Australia	N	KT460163	KT460114	KT460179	COL051
Elaterinae	*Melanoxanthus* sp.	Australia	N	KT460158	KT460106	KT460176	COL048
Elaterinae	*Megapenthes* sp.	Australia	KT460129	KT460159	KT460105	KT460183	COL057
Lissominae	*Lissomus* sp.	Trinidad & Tobago	KT447371	KT447376	KT447367	KT447381	UPOL RK0795
Lissominae	*Austrelater* sp.	Australia	KT460141	KT460164	KT460115	KT460173	COL030
Oestodinae stat. nov.	*Oestodes tenuicollis*	Canada	KT447370	KT447375	KT447366	KT447380	UPOL RK0796
Parablacinae subfam. nov.	*Parablax* sp.	Australia	KT460135	KT460162	KT460108	KT460182	COL056
Parablacinae subfam. nov.	*Wynarka* sp.	Australia	N	KT460161	KT460107	KT460178	COL050
Parablacinae subfam. nov.	*Ophidius* sp.	Australia	KT460134	KT460160	KT460109	KT460165	COL021
Parablacinae subfam. nov.	*Metablax acutipennis*	New Zealand	KT447372	KT447373	KT447363	KT447377	UPOL RK0870
Pityobiinae	*Pityobius anguinus*	Canada	KT447369	N	KT447364	KT447378	UPOL RK0794

variable uninformative and parsimony informative characters for the analysed data sets are listed in Table S2. The final matrix contained 169 sequences of 18S rRNA, 168 of 28S rRNA, 169 of *rrnL* mtDNA and 174 of *cox1* mtDNA. Maximum uncorrected pairwise distances within Elateridae varied from 4.4% in 18S to 26.0% in *cox1* in the Mafft alignment (only full-length sequences included). PartitionFinder selected six partitions (18S, 28S, *rrnL* and three *cox1* codon positions) as the optimal scheme, with nucleotide substitution model GTR+I + G for the mitochondrial genes/codon positions and SYM+I + G for the nuclear markers.

Phylogenetic inference

The BlastAlign and Mafft alignments analysed under ML criterion and Bayesian inference produced similar topologies and identified well-supported monophyletic subfamilies Agrypninae, Elaterinae, Cardiophorinae and Negastriinae (Table 2; Fig. 2). Elaterinae (excluding *Ophidius* Candèze and including *Dicteniophorus* Candèze, *Drymelater* Calder and *Stichotomus* Candèze) were always a sister lineage to the remaining Elateridae. Dendrometrinae (excluding Pityobiinae) were placed in an unresolved polytomy with *Diplophoenicus* Candèze (Morostomatinae) by BI analysis of Mafft alignment; in the remaining analyses they were paraphyletic and formed either three or four lineages within a poorly supported clade with Morostomatinae, Cardiophorinae and Negastriinae (Fig. 2). The Cardiophorinae + Negastriinae clade was supported by ML and BI analyses of Mafft alignment; in analyses of BlastAlign alignment, Cardiophorinae formed a clade with Dendrometrinae pars (Semiotini, Dimini) and Negastriinae. Morostomatinae were inferred to be either sister to Dendrometrinae + Cardiophorinae + Negastriinae (ML analyses; Fig. 2), sister to Dendrometrinae, or as a terminal lineage within Dendrometrinae. Lissominae was always polyphyletic (Table 2; also in partial analyses, results not shown), and included Thylacosterninae, whereas *Oestodes* LeConte (Oestodini) was sister to either Elateridae − Elaterinae (BI from BlastAlign), *Pityobius* (Pityobiinae; BI from Mafft) or *Hemiops* Laporte (Hemiopinae, both ML analyses), and distant from the remaining lissomines (Fig. 2). Lissominae (excl. Oestodini) + Thylacosterninae clade was supported by high BS and PP values (Table 2). The position of *Panspoeus guttatus* Sharp, 1877 was not resolved, occurring in different positions in various trees either as an independent lineage (ML from Mafft alignment; Fig. 2), within Dendrometrinae (ML and BI from BlastAlign) or sister to Cardiophorinae + Negastriinae (BI from Mafft). Pityobiinae was polyphyletic in all partial and all-data analyses (Table 2; Fig. 2; Table S3). *Pityobius* was always placed as an independent lineage within deep elaterid splits and its detailed position varied between analyses; it was sister either to Lissominae + Thylacosterninae (both ML analyses; 53–60% BS), *Oestodes* (BI from Mafft; 84% PP) or *Hemiops* (BI from BlastAlign; 77% PP) (Table S3). The remaining pityobiine genera, *Parablax*, *Metablax* and *Wynarka*, always formed a robust clade with *Ophidius* (Table 2; Fig. 2). *Pectocera* was recovered as sister to *Oxynopterus* Hope (Dendrometrinae) far from any Pityobiinae in all analyses. *Crepidomenus* Erichson was found nested in a clade of *Hypolithus* Eschscholtz (Hypnoidini) + *Glypheus* Candèze + *Microdesmes* Candèze + *Litotelater* Calder within Dendrometrinae (Fig. 2).

DISCUSSION

The phylogeny of Elateridae

Current taxonomic and phylogenetic concepts of Elateridae are unstable with subfamilial and tribal limits varying substantially among specialists (for a review see Costa *et al*. 2010). Establishing a stable higher classification and natural groupings based on morphological synapomorphies is problematic. Most morphological characters used to define several subfamilies and tribes are also present in unrelated lineages, thereby confusing their definitions (e.g. Hyslop 1917; Gur'yeva 1974; Dolin 1975; Douglas 2011). The most striking example is the similarity of adults of the widespread and species-rich Elaterinae and Dendrometrinae (Calder 1996; Costa *et al*. 2010), although larvae from the two subfamilies are readily

Table 2 Recovery of selected clades with bootstrap support in maximum likelihood (ML) and posterior probabilities in Bayesian (BI) analyses from BlastAlign and Mafft alignments of the 178-taxa data set

Selected clade	BlastAlign	BlastAlign	Mafft	Mafft
Type of alignment and analysis	ML	BI	ML	BI
Agrypninae	M(95)	M(100)	M(98)	M(100)
Elaterinae†	M(91)	M(100)	M(95)	M(100)
Cardiophorinae	M(100)	M(100)	M(100)	M(100)
Negastriinae	M(86)	M(63)	M(95)	M(100)
Dendrometrinae (excl. Pityobiinae)	P	P	P	M
Lissominae	P	P	P	P
Lissominae (excluding Oestodini; including Thylacosterninae)	M(100)	M(100)	M(99)	M(100)
Pityobiinae *sensu* Calder (1996)	P	P	P	P
Parablax + *Wynarka* + *Metablax* + *Ophidius*	M(98)	M(100)	M(99)	M(100)

Only values above 50% are shown. The subfamilial classification follows that of Kundrata and Bocak (2011). †Excluding *Ophidius* and including *Dicteniophorus*, *Drymelater* and *Stichotomus*.

M, monophylum; P, paraphylum.

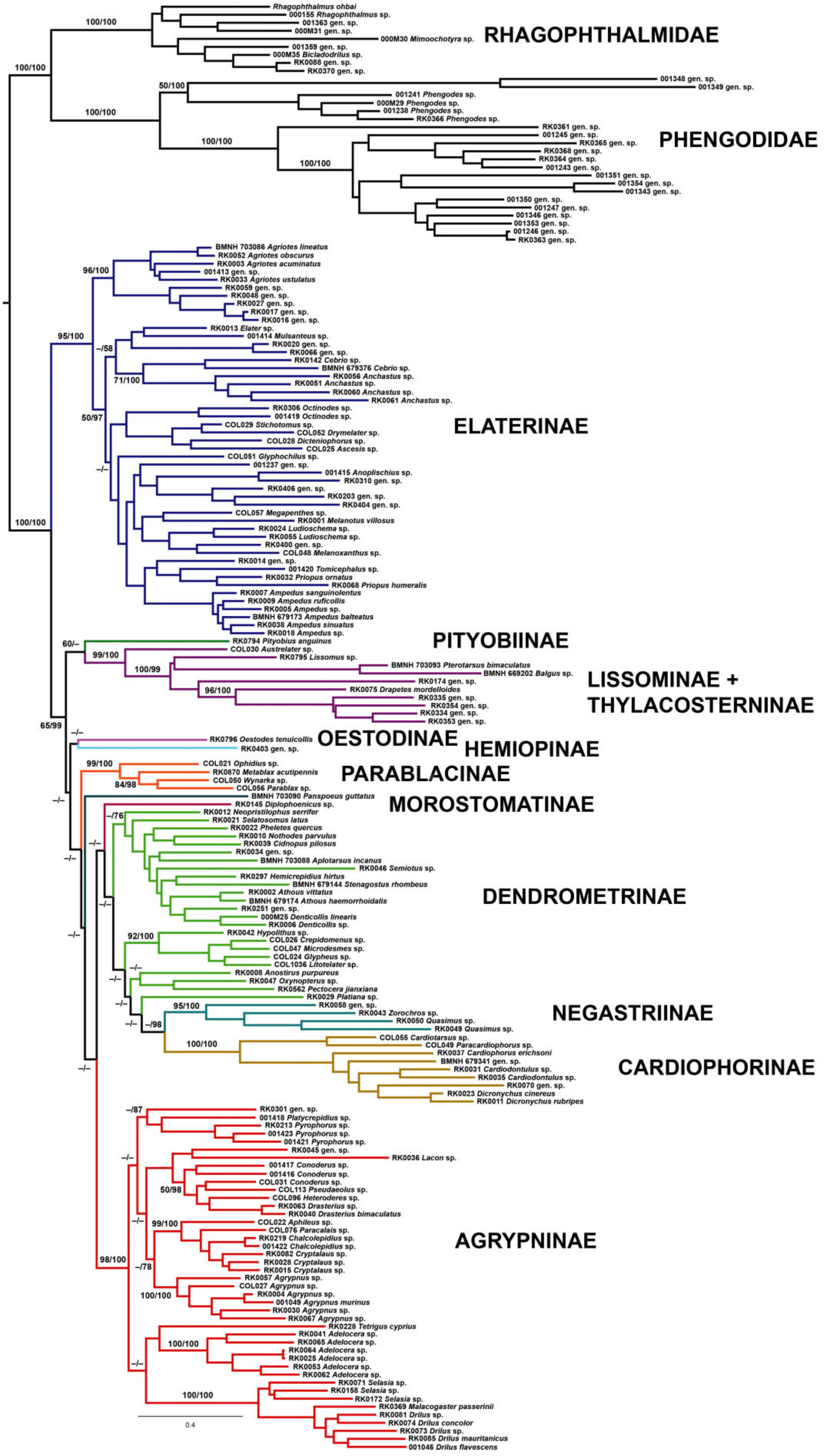

100/100
Rhagophthalmus ohbai
000155 Rhagophthalmus sp.
001363 gen. sp.
000M31 gen. sp.
000M30 Mimoochotyra sp.
RHAGOPHTHALMIDAE
001359 gen. sp.
000M35 Bicladodrilus sp.
RK0088 gen. sp.
RK0370 gen. sp.
100/100
001348 gen. sp.
50/100
001349 gen. sp.
001241 Phengodes sp.
000M29 Phengodes sp.
001238 Phengodes sp.
100/100
RK0366 Phengodes sp.
RK0361 gen. sp.
001245 gen. sp.
RK0365 gen. sp.
PHENGODIDAE
100/100
RK0368 gen. sp.
RK0364 gen. sp.
100/100
001243 gen. sp.
001351 gen. sp.
001354 gen. sp.
001343 gen. sp.
001350 gen. sp.
001247 gen. sp.
001346 gen. sp.
001353 gen. sp.
001246 gen. sp.
RK0363 gen. sp.
BMNH 703086 Agriotes lineatus
RK0052 Agriotes obscurus
RK0003 Agriotes acuminatus
96/100
001413 gen. sp.
RK0033 Agriotes ustulatus
RK0059 gen. sp.
RK0048 gen. sp.
RK0027 gen. sp.
RK0017 gen. sp.
RK0016 gen. sp.
RK0013 Elater sp.
95/100
001414 Mulsanteus sp.
–/58
RK0020 gen. sp.
RK0066 gen. sp.
RK0142 Cebrio sp.
BMNH 679376 Cebrio sp.
RK0056 Anchastus sp.
71/100
RK0051 Anchastus sp.
RK0060 Anchastus sp.
RK0061 Anchastus sp.
RK0306 Octinodes sp.
001419 Octinodes sp.
50/97
COL029 Stichotomus sp.
ELATERINAE
COL052 Drymelater sp.
COL028 Dicteniophorus sp.
COL025 Ascesis sp.
COL051 Glyphochilus sp.
–/–
001237 gen. sp.
001415 Anoplischius sp.
RK0310 gen. sp.
RK0406 gen. sp.
RK0203 gen. sp.
RK0404 gen. sp.
COL057 Megapenthes sp.
100/100
RK0001 Melanotus villosus
RK0024 Ludioschema sp.
RK0055 Ludioschema sp.
RK0400 gen. sp.
COL048 Melanoxanthus sp.
RK0014 gen. sp.
001420 Tomicephalus sp.
RK0032 Priopus ornatus
RK0068 Priopus humeralis
RK0007 Ampedus sanguinolentus
RK0009 Ampedus ruficollis
RK0005 Ampedus sp.
BMNH 679173 Ampedus balteatus
RK0038 Ampedus sinuatus
RK0018 Ampedus sp.
PITYOBIINAE
60/–
RK0794 Pityobius anguinus
COL030 Austrelater sp.
99/100
RK0795 Lissomus sp.
100/99
BMNH 703093 Pterotarsus bimaculatus
BMNH 669202 Balgus sp.
LISSOMINAE +
RK0174 gen. sp.
96/100
RK0075 Drapetes mordelloides
RK0335 gen. sp.
THYLACOSTERNINAE
RK0354 gen. sp.
RK0334 gen. sp.
65/99
RK0353 gen. sp.
–/–
RK0796 Oestodes tenuicollis
OESTODINAE
HEMIOPINAE
RK0403 gen. sp.
99/100
COL021 Ophidius sp.
RK0870 Metablax acutipennis
PARABLACINAE
84/98
COL050 Wynarka sp.
COL056 Parablax sp.
–/–
BMNH 703090 Panspoeus guttatus
MOROSTOMATINAE
RK0145 Diplophoenicus sp.
–/76
RK0012 Neopristilophus serrifer
RK0021 Selatosomus latus
RK0022 Pheletes quercus
RK0010 Nothodes parvulus
–/–
RK0039 Cidnopus pilosus
–/–
RK0034 gen. sp.
BMNH 703088 Aplotarsus incanus
RK0046 Semiotus sp.
RK0297 Hemicrepidius hirtus
BMNH 679144 Stenagostus rhombeus
–/–
RK0002 Athous vittatus
DENDROMETRINAE
BMNH 679174 Athous haemorrhoidalis
RK0251 gen. sp.
000M25 Denticollis linearis
RK0006 Denticollis sp.
–/–
92/100
RK0042 Hypolithus sp.
COL026 Crepidomenus sp.
COL047 Microdesmes sp.
COL024 Glypheus sp.
COL1036 Litotelater sp.
–/–
RK0008 Anostirus purpureus
–/–
RK0047 Oxynopterus sp.
RK0562 Pectocera jianxiana
–/–
RK0029 Platiana sp.
95/100
RK0058 gen. sp.
NEGASTRIINAE
RK0043 Zorochros sp.
–/–
–/98
RK0050 Quasimus sp.
RK0049 Quasimus sp.
COL055 Cardiotarsus sp.
100/100
COL049 Paracardiophorus sp.
RK0037 Cardiophorus erichsoni
BMNH 679341 gen. sp.
CARDIOPHORINAE
–/–
RK0031 Cardiodontulus sp.
RK0035 Cardiodontulus sp.
RK0070 gen. sp.
RK0023 Dicronychus cinereus
RK0011 Dicronychus rubripes
–/87
RK0301 gen. sp.
001418 Platycrepidius sp.
RK0213 Pyrophorus sp.
001423 Pyrophorus sp.
001421 Pyrophorus sp.
RK0045 gen. sp.
–/–
RK0036 Lacon sp.
001417 Conoderus sp.
001416 Conoderus sp.
COL031 Conoderus sp.
50/98
COL113 Pseudaeolus sp.
COL096 Heteroderes sp.
RK0063 Drasterius sp.
RK0040 Drasterius bimaculatus
–/–
99/100
COL022 Aphileus sp.
COL076 Paracalais sp.
RK0219 Chalcolepidius sp.
AGRYPNINAE
001422 Chalcolepidius sp.
RK0082 Cryptalaus sp.
98/100
RK0028 Cryptalaus sp.
–/78
RK0015 Cryptalaus sp.
RK0057 Agrypnus sp.
COL027 Agrypnus sp.
100/100
RK0004 Agrypnus sp.
001049 Agrypnus murinus
RK0030 Agrypnus sp.
RK0067 Agrypnus sp.
RK0228 Tetrigus cyprius
RK0041 Adelocera sp.
100/100
RK0065 Adelocera sp.
RK0064 Adelocera sp.
RK0025 Adelocera sp.
–/–
RK0053 Adelocera sp.
RK0062 Adelocera sp.
RK0071 Selasia sp.
RK0158 Selasia sp.
100/100
RK0172 Selasia sp.
RK0369 Malacogaster passerinii
RK0081 Drilus sp.
0.4
RK0074 Drilus concolor
RK0073 Drilus sp.
RK0085 Drilus mauritanicus
001046 Drilus flavescens

Fig. 2. The maximum likelihood phylogenetic tree for 178 terminals including 148 Elateridae and 30 out-group taxa, resulting from the RAxML analysis of concatenated Mafft alignment of four molecular markers (18S rRNA, 28S rRNA, *rrnL* mtDNA and *cox1* mtDNA). Values at selected branches indicate bootstrap support and Bayesian posterior probabilities, respectively. Only values above 50% are shown.

distinguished (Stibick 1979). With recent advances in molecular techniques, several studies have begun to reveal the click-beetle interrelationships (Sagegami-Oba *et al*. 2007; Kundrata & Bocak 2011), but sequenced species still represent less than 2% of known elaterid diversity (Bocak *et al*. 2014). A comprehensive elaterid phylogeny is beyond the scope of this study, yet the results here provide some additional insights into elaterid relationships.

The support for basal branches was not sufficient to infer all subfamilial interrelationships, but our results largely agreed with Sagegami-Oba *et al*. (2007). They inferred Elaterinae as sister to the remaining lineages, and Agrypninae as sister to the clade containing Dendrometrinae (including Hypnoidinae, Oxynopterinae and Diminae) and Cardiophorinae + Negastriinae (for comparison, see Fig. 2). Furthermore, we included members of Lissominae, Thylacosterninae, Morostomatinae, Hemiopinae and Pityobiinae, which were unavailable in that study. The positions of early-branching clades in Elateridae – Elaterinae (i.e. Hemiopinae, both subclades of polyphyletic Pityobiinae, Lissominae: Oestodini, remaining Lissominae including Thylacosterninae, and *Panspoeus guttatus*) were recovered with very low support and were unstable across different analyses in our study. However, strong support was found for monophyletic Agrypninae, Elaterinae (including some former dendrometrine genera; for more details see discussion below), Cardiophorinae and Negastriinae (Fig. 2; Table 2). On the other hand, the hypotheses of monophyly can be rejected for several other subfamilies. The clade containing most Lissominae included Thylacosterninae as a terminal lineage, while the lissomine tribe Oestodini formed a distant independent lineage. The close relationship of Lissominae and Thylacosterninae has already been found by recent studies (Calder *et al*. 1993; Lawrence *et al*. 2007; Kundrata & Bocak 2011) and several adult and larval morphological characters suggest the distant position of Oestodini (Hyslop 1917; Crowson 1961; Lawrence & Arias 2009). Pityobiinae never formed a monophylum in our study, with *Pityobius* always distant from the Australasian genera (Calder 1996). The widely defined Dendrometrinae (Johnson 2002; Sagegami-Oba *et al*. 2007; Costa *et al*. 2010; Kundrata & Bocak 2011) was found to be non-monophyletic, which is in accordance with Douglas (2011) and Kundrata *et al*. (2014). Morostomatinae (represented by *Diplophoenicus*) was always found near dendrometrines, but their detailed phylogenetic position remains unclear.

A continuing problematic issue is the position of *Panspoeus guttatus* (Cate 2007). In molecular analyses, *Panspoeus* Sharp was inferred either as one of the basal elaterid splits, sister to Negastriinae or Negastriinae + Cardiophorinae, or embedded within Dendrometrinae pars (Kundrata & Bocak 2011; Kundrata *et al*. 2014; this study). Some have hypothesised that Cardiophorinae (alone or with either Negastriinae or Negastriinae and Dimini) were the basal-most lineage in Elateridae (Hyslop 1917; Ôhira 1962; Stibick 1979; Kundrata & Bocak 2011; Kundrata *et al*. 2014). However, our results along with those of Sagegami-Oba *et al*. (2007) constantly recovered Cardiophorinae as nested deeply within a clade containing also Dendrometrinae and Negastriinae (Fig. 2). A sister group relationship between Cardiophorinae and Negastriinae was reported by Stibick (1979), Sagegami-Oba *et al*. (2007) and Douglas (2011). Yet this needs further investigation because some results are equivocal and other taxa (e.g. Dimini) were often repeatedly found to be closely related to them (Kundrata & Bocak 2011; Kundrata *et al*. 2014; this study).

Taxonomic conclusions

Elaterinae

Although Elaterinae and Dendrometrinae are clearly separated from one another in most taxonomic studies on Elateridae, including this one (see e.g. Dolin 1978 and Sagegami-Oba *et al*. 2007; Fig. 2), no reliable synapomorphies based on adult morphology have been proposed even for the apparently monophyletic Elaterinae (Calder 1996; Costa *et al*. 2010). The boundaries of these subfamilies are vague and many genera have been classified in both subfamilies at different times (see e.g. Dolin 1975; Calder 1996). This is also the case for the Australian genera *Dicteniophorus* and *Drymelater* (=*Agonischius* Candèze), which were classified in Ludiinae (=Elaterinae) (Neboiss 1956) and then transferred to Dendrometrinae based on hind wing venation (Calder 1996). These genera are morphologically similar to *Ascesis* Candèze (Elaterinae) and *Stichotomus* (Dendrometrinae) (Calder 1996). Based on our results, all four of these genera form a clade that clearly belongs to the Elaterinae (Fig. 2). Thus, we herein transfer genera *Dicteniophorus* Candèze, 1863, *Drymelater* Calder, 1996 and *Stichotomus* Candèze, 1863 from Dendrometrinae to Elaterinae.

Dendrometrinae sensu lato

The concept and limits of Dendrometrinae vary among authors and the current, widely defined subfamily contains several tribes that are often classified as independent subfamilies e.g. Dimini/ae, Hypnoidini/ae, Oxynopterini/ae, Semiotini/ae and Pityobiini/ae (Costa *et al*. 2010; Kundrata & Bocak 2011). We found strong support for the non-monophyly of Dendrometrinae *sensu lato* (Table 2; Fig. 2) similar to Douglas (2011), Kundrata and Bocak (2011) and Kundrata *et al*. (2014). In general, we also recovered support for the subfamilial ranking of several lineages currently considered as tribes within Dendrometrinae *sensu lato*. All sequenced genera of Pityobiini were always recovered in distant positions to the Dendrometrinae and their classification is discussed in the section below. In the analyses of molecular data sets, Dimini were inferred either as sister to the remaining Dendrometrinae (Sagegami-Oba *et al*. 2007) or outside of Dendrometrinae in close relationships to Cardiophorinae and/or Negastriinae (Kundrata & Bocak 2011; Kundrata *et al*. 2014; this study; Fig. 2). We regularly found *Hypolithus* (Hypnoidini), Oxynopterini, *Anostirus* Thomson and the Australian genera *Crepidomenus*, *Glypheus*, *Microdesmes* and *Litotelater* (and in some cases Semiotini) outside of core Dendrometrinae, but their positions still remain unclear. However, it is important to note that the lineages, which were inferred to occupy alternating phylogenetic positions, were only represented by a few species here and thus, potential taxonomic changes should be avoided until more representative sampling is included in molecular analyses.

Lissominae/Thylacosterninae

The subfamily Lissominae *sensu lato* (e.g. Calder *et al*. 1993; Lawrence & Newton 1995) includes also the Oestodinae of Gur'yeva (1974) and Dolin (1975) and is subdivided into the tribes Oestodini, Lissomini and Protelaterini (Costa *et al*. 2010). This current grouping is not supported by any known reliable adult morphological characters. The Oestodini was consistently found to be a sister group to the remaining lissomines by Calder *et al*. (1993). Douglas (2011) found *Oestodes* to be only distantly related to *Lissomus* Dalman in his morphology-based phylogeny. Our molecular results did not resolve the phylogenetic position of *Oestodes*, and although varying in position between analyses, it was never close to the remaining Lissominae (Fig. 2). The distant position of Oestodini is supported also by several morphological characters, such as e.g. simple retinaculum, lack of the specialised tergal spines (in larvae), frontal region gradually declined at midline, base of pronotum with paired sublateral incisions and simple tarsomeres (in adults) (Lawrence & Arias 2009). Based on these results, we propose to reinstate the independent subfamily Oestodinae Hyslop, 1917 stat. nov. for the North American genera *Oestodes* and *Bladus* LeConte (formerly Lissominae: Oestodini; Johnson 2002, Lawrence & Arias 2009). A more resolved position of this lineage within Elateridae needs further study; however, two analyses here inferred the close relationships between *Oestodes* and *Hemiops* as proposed by Stibick (1979).

A close relationship between Lissominae and Thylacosterninae was suggested by several authors (Calder *et al*. 1993; Kundrata & Bocak 2011); however, none have proposed synonymisation. We found Thylacosterninae to be embedded within Lissominae in all topologies; however, taxon sampling was insufficient to draw firm taxonomic conclusions about this subfamily. The additional Thylacosterninae (mainly the type genus *Thylacosternus* Bonvouloir), *Protelater* Sharp, *Sphaenelater* Schwarz and several other genera need to be studied to inform strong insights into thylacosternine/lissomine/oestodine relationships.

The monophyly, phylogeny and limits of Pityobiinae

The Pityobiinae as currently defined (Dolin 1975; Calder 1992, 1996; Costa *et al*. 2010) contains the North American *Pityobius*, the South American *Tibionema* and several small genera from Australia and New Zealand (Fig. 1). This subfamily has been a shifting assemblage of genera, at one time assigned to Agrypninae (*Pityobius*), Dendrometrinae (as Athoinae; *Pityobius*), Campsosterninae (*Metablax*), Crepidomeninae (*Parablax*, *Wynarka*, *Metablax*, *Tibionema*) and Hemicrepidiinae (*Parasaphes*, *Tibionema*) (Calder 1976; Ulrich 1988; and references therein). There have been three main hypotheses about the position of Pityobiinae: as sister to Agrypninae (Hyslop 1917; Dolin 1978; Calder *et al*. 1993); as sister to Oxynopterinae in a clade containing also Agrypninae (Stibick 1979); and in Dendrometrinae (Ulrich 1988; Johnson 2002; Kundrata & Bocak 2011). Moreover, Stibick (1979) treated some oxynopterine genera (e.g. *Pectocera*) as Pityobiinae (Table S4). Dolin (1978) also supposed close relationships between Oxynopterinae, Agrypninae and Pityobiinae.

The current study found Pityobiinae to be non-monophyletic; instead, the genera always formed two lineages in deeper splits within Elateridae − Elaterinae and were distant from both Agrypninae and Dendrometrinae including Oxynopterini (Fig. 2; Table 2). Based on our results, Stibick's three-tribe concept of Pityobiinae, including Pityobiini, Rostricephalini and Pectocerini, was rejected. *Pectocera* (Pectocerini) is clearly a part of Oxynopterini as already proposed by various authors (e.g. Fleutiaux 1947; Ôhira 1962; Dolin 1975); *Rostricephalus* (Rostricephalini) also belongs in Oxynopterini (Costa *et al*. 2010). Our findings indicate that the Pityobiinae *sensu* Calder (1996) needs redefinition. Calder (1992) questioned pityobiine monophyly, and indeed, our results agree that *Pityobius* is distant from the Australasian genera (Fig. 2). Ulrich (1988) and Calder (1992) summarised the unique morphological characters of *Pityobius*, such as tridentate mandibles and a ridged denticulate subnasale (in larvae) and the structures of tarsomeres and female genitalia (in adults), respectively. The position of *Tibionema* has long been controversial (see Ulrich 1988). However, due to extensive homoplasy of adult elaterid morphology (e.g. Calder 1996; Douglas 2011), we cannot resolve its phylogenetic placement until fresh specimens are available for DNA isolation, leaving *Tibionema* tentatively in Pityobiinae as proposed by Dolin (1975). The occurrence of the subfamily Pityobiinae in the Afrotropical Region based on four unidentified larval specimens as proposed by Ulrich (1988) is also dubious.

Regardless of the analytical method, our results provide strong support for the monophyly of the Australian/New Zealand genera *Parablax*, *Wynarka*, *Metablax* and *Ophidius* (Fig. 2; Table 2). All these taxa have been at some point placed within Crepidomeninae (now in Dendrometrinae; e.g. Schwarz 1906; Neboiss 1956; Calder 1986), but more recently the first three genera were classified in Pityobiinae, whereas

Ophidius was placed in Elaterinae (Calder 1992, 1996). Both of these phylogenetic hypotheses are rejected based on the results of our analyses. We recovered *Crepidomenus* within the Dendrometrinae + Cardiophorinae + Negastriinae clade, precluding a relationship of the Australasian genera with Crepidomeninae. Additionally, *Pityobius* was always recovered as distant from the Australasian pityobiines. We propose here a new click-beetle subfamily Parablacinae Kundrata, Gunter, Douglas & Bocak, subfam. nov. for *Parablax*, *Metablax*, *Wynarka* (all transferred here from Pityobiinae) and *Ophidius* (transferred from Elaterinae). The Australian genera *Xuthelater*, *Tasmanelater* and *Parasaphes*, which are all currently classified in Pityobiinae, are also proposed to belong to the new subfamily because they share similar morphology and geographical affinities with the above-mentioned genera (Calder 1992, 1996).

Parablacinae Kundrata, Gunter, Douglas & Bocak, subfam. nov.

Type genus. *Parablax* Schwarz, 1906. Neue Elateriden aus Australien. Deutsche Entomologische Zeitschrift 1906(ii): 353–369 [Date published 10 September 1906] [368].

Diagnosis

At present, no adult or larval morphological synapomorphies are known for this group. Included taxa differ e.g. in head, prothoracic carinae, scutellum, suture between meso- and metaventrite, hind wing venation and female genitalia (Calder 1992, 1996). The most evident characteristics, such as frontoclypeal region produced forwards to cover labrum, scutellum without well-defined anterior margin and wing apex with one anterior and one posterior field sclerotisations, are not present in all included taxa. Adults of the Parablacinae subfam. nov. can be recognised by the following characters in combination: both maxillary and labial palpi securiform, antennae with 11 antennomeres, with sensory elements on antennomeres 4–11, pronotum longer than wide, with hind angles divergent, prosternal spine longer than the diameter of procoxae, tarsomeres 1–3 or 1–4 with apico-ventral filamentous pads, and simple tarsal claws (Calder 1976, 1992, 1996). The thorough re-examination of the morphology of the group may reveal some characters that would define this subfamily.

Description

Adults. Body 7–29 mm long, elongate to oblong, clothed with semidecumbent setae; body yellow–brown to black, in some cases with yellow stripes along elytra (*Parasaphes*, *Wynarka*, some *Parablax*, some *Metablax*) or black markings (*Tasmanelater*, *Xuthelater*, *Ophidius*).

Frons convex in most genera (flattened in *Xuthelater*). Frontoclypeal region produced forwards, partially concealing labrum (except in *Ophidius* where frontoclypeal region is gradually sloping to labral base). Supra-antennal carinae at midline convergent to absent (in *Tasmanelater*). Mandibles bidentate (unidentate in *Xuthelater*). Labrum wider than long, partly covered by frontoclypeal region in dorsal view (most genera) or not (*Ophidius*). Maxillary and labial palpi securiform. Antennae slender, with 11 antennomeres, subserrate to serrate from antennomere 4, sensory elements present on antennomeres 4–11.

Prothorax longer than wide; pronotum with sides entirely (most genera) or not entirely (*Wynarka*) carinate, carina visible in dorsal view (directed ventrally on anterior half in *Wynarka* and *Ophidius*); pronotal hind angles with one dorsal carina in most genera (absent in *Tasmanelater*), divergent. Anterior prosternal lobe covering ventral mouthparts when head is retracted. Prosternal process longer than procoxal diameter. Scutellum with anterior margin obtuse to rounded, gradually sloping downwards to prescutum (most genera, *Metablax approximans* species-group) or with anterior margin sharply angulate and steeply declivous to prescutum (*Ophidius*, *Metablax acutipennis* species-group). Mesocoxal cavities open to mesepimeron and mesanepisternum. Suture between mesoventrite and metaventrite distinct (obsolete in *Metablax brouni* Sharp, 1877). Hind wing with short radial cell; vein CuA_1 present; anal cell present (absent in *Parasaphes*); apical field occupying less than 0.2 times total wing length; apex either with one (*Tasmanelater*), two (most genera) or three (*Ophidius*) sclerotisations. Tarsomeres 1–4 (1–3 in *Metablax* and *Parasaphes*) with filamentous pads apico-ventrally. Tarsal claws simple, without basal setae. Male genitalia with parameres each with sharp subapical lateral expansion, apex more or less sclerotised. Female genitalia with ovipositor occupying 0.5–1.0 times abdomen length; coxites with styli attached subapically (absent in *Metablax approximans* species-group); vagina with sclerotised structures (absent in *Xuthelater* and *Ophidius*), anteriorly enlarged (moderately in *Xuthelater*); colleterial glands well developed, hemispherical (*Ophidius*) to pedunculate with elongate apex; bursa copulatrix divided into two parts, anterior section sac-like, with sclerotised spines (without spines in *Tasmanelater*); posterior section with sclerotised spermatheca: one in most *Parablax*, *Tasmanelater*, *Xuthelater*, two in *Parasaphes*, *Wynarka*, *Metablax*, *Ophidius*, absent in *Parablax nunden* species-group, all with elongate spermathecal gland duct leading to multilobed spermathecal gland (Calder 1976, 1992, 1996; summarised herein).

Larvae. Body up to 35 mm long, robust, flattened, yellow–brown to reddish-black. Head flattened, nasale tridentate, postmentum triangular, galea two-segmented, mandibles unidentate. Prothorax subequal in length to meso- and metathorax combined, presternal area triangular. Abdominal segment 9 with large caudal notch, anterior margin of sternite 9 with transverse carina (absent in some *Metablax*). Larvae are known only for *Metablax*, *Wynarka* and *Parasaphes* (Hudson 1934; Calder 1976, 1996). For more detailed descriptions of *Metablax acutipennis* (White, 1846) and some unassociated species from New Zealand and Australia, see Ulrich (1988).

Genera and species included

Altogether, 22 species in 7 genera are included in Parablacinae subfam. nov.: *Parablax* (9 spp.), *Metablax* (5), *Parasaphes* (1), *Tasmanelater* (1), *Wynarka* (1), *Xuthelater* (1), and *Ophidius* (4) (Fig. 1; see Table S5 for the species list).

Distribution

Australia (including Tasmania), New Zealand.

Etymology

The name Parablacinae is derived from the type genus *Parablax* (prefix -para and the Greek word blax, -akos [= dull]; Brown 1954).

Remarks

All genera of Parablacinae subfam. nov., but *Ophidius*, were recently classified together in Pityobiinae (e.g. Calder 1992; Costa *et al*. 2010) because of similarities in the frons (Calder 1992). *Ophidius* is the most morphologically distinct genus in the lineage and its sister position to the others is supported also by Bayesian and ML analyses of the Mafft alignment (Fig. 2). A relationship between *Parablax*, *Metablax* (either one of them or both) and *Ophidius* was proposed by several authors (Candèze 1863; Schwarz 1907; Schenkling 1927; Neboiss 1956) who added these genera to their concept of Crepidomenini (at different taxonomic ranks from subtribe to subfamily). However, the group also included some very distantly related genera (*Anaissus* Candèze, *Crepicardus* Candèze, *Crepidomenus*, *Paracrepidomenus* Schwarz) so the morphological affinities proposed to link the genera are not reliable. Another question is the monophyly of genus *Metablax*, which was challenged by Ulrich (1988); however, with only limited material included in our analyses, we do not propose any suprageneric ranks within the lineage until further taxon sampling is conducted. The addition of sequences from the other Australian genera and species-groups (including more *Metablax* from New Zealand), plus re-examining their adult and larval morphologies is needed to understand the phylogeny of Parablacinae, subfam. nov. and improve its classification.

Conclusion

Here we present an updated molecular phylogeny of the Elateridae. Our primary goal was not to discuss the intrafamilial relationships of click-beetles. Instead, we used molecular markers to investigate the limits and position of the small and taxonomically unstable subfamily Pityobiinae. Yet, our results provide interesting insights into the phylogeny of the family. In most topologies, Elaterinae were sister to the remaining Elateridae, and Agrypninae were sister to Morostomatinae + Dendrometrinae + Cardiophorinae + Negastriinae, which is consistent with the molecular phylogeny of Sagegami-Oba *et al*. (2007). Several taxonomic changes were proposed to stabilise the group and reflect evolutionary history: the genera *Dicteniophorus*, *Drymelater* and *Stichotomus* were transferred from Dendrometrinae to Elaterinae and *Oestodes* and *Bladus* were removed from Lissominae and reinstated as subfamily Oestodinae stat. nov. We did not propose other taxonomic changes to Dendrometrinae because some lineages (e.g. Ctenicerini, Semiotini, Oxynopterini, Dimini, Hypnoidini) are poorly represented and need investigation. The Lissominae (excluding Oestodinae) were found to be rendered paraphyletic by the Thylacosterninae; however, improved taxon sampling is needed before taxonomic changes are made. The most problematic issues in reconstructing the Elateridae phylogeny were the short internal branches with unresolved deeper splits (Fig. 2) and limited taxon sampling (Bocak *et al*. 2014). Undoubtedly, future studies with more taxa will prompt improvements to the classification of click-beetles.

The most recent taxonomic concepts of the subfamily Pityobiinae (*sensu* Dolin 1975; Stibick 1979; Calder 1996) were never recovered as monophyletic regardless of which method we used. Instead, our results always returned *Pityobius* as distant to the Australasian members of the subfamily. Here we proposed reducing Pityobiinae to only *Pityobius* and *Tibionema*. However, including *Tibionema* is dubious and may change after its DNA is made available. We proposed erecting Parablacinae subfam. nov. for the remaining Australasian genera formerly included in Pityobiinae (*Parablax*, *Metablax*, *Wynarka*, *Tasmanelater*, *Xuthelater*, *Parasaphes*) plus *Ophidius*, which was transferred from Elaterinae. We failed to find any synapomorphy or morphological diagnosis that would uniquely define this group, but a thorough morphological re-examination of all species may change this. Additionally, the DNA data for Australian Parablacinae not yet sequenced are crucial to understanding its phylogeny. Given that even the large and robust subfamilies, including the Elaterinae, evade definition by adult morphological synapomorphies (despite strong molecular support), we propose that the new subfamily is warranted. The description of this new subfamily is a step towards resolving taxonomical stability in the Elateridae.

ACKNOWLEDGEMENTS

We thank S. Laplante (CNCI, Canada), R. Leschen (New Zealand), B. C. Schmidt (CNCI, Canada) and P. de Tonnancour (Terrasse-Vaudreuil, Canada) for donating fresh specimens for the DNA isolation; J. Lawrence (CSIRO, Australia) for comments on the manuscript; A. Ślipiński (CSIRO, Australia) and G. Platia (Gatteo, Italy) for helping find literature; T. A. Weir (CSIRO, Australia) for help with the material identification; and A. Ślipiński, C. Lemann (CSIRO, Australia), O. Merkl, T. Németh (HNHM, Hungary) and S. M. Blank (SDEI, Germany) for the specimen loan. We gratefully acknowledge funding from GAČR P506/11/1757 (LB), the ESF and the Ministry of Education of the Czech Republic CZ.1.07/2.3.00/30.0004 (NG), the IGA project from the Palacky University (RK) and the EU-SYNTHESYS grant FR-TAF 4665 (RK). The authors declare no conflict of interest.

REFERENCES

Amaral DT, Arnoldi FGC, Rosa SP & Viviani VR. 2014. Molecular phylogeny of Neotropical bioluminescent beetles (Coleoptera: Elateroidea) in southern and central Brazil. *Luminescence: The Journal of Biological and Chemical Luminescence* **29**, 412–422.

Belshaw R & Katzourakis A. 2005. BlastAlign: a program that uses blast to align problematic nucleotide sequences. *Bioinformatics (Oxford, England)* **21**, 122–123.

Bocak L, Barton C, Crampton-Platt A, Chesters D, Ahrens D & Vogler AP. 2014. Building the Coleoptera tree-of-life for >8000 species: composition of public DNA data and fit with Linnaean classification. *Systematic Entomology* **39**, 97–110.

Bocakova M, Bocak L, Hunt T, Teraväinen M & Vogler AP. 2007. Molecular phylogenetics of Elateriformia (Coleoptera): evolution of bioluminescence and neoteny. *Cladistics: The International Journal of the Willi Hennig Society* **23**, 477–496.

Bouchard P, Bousquet Y, Davies AE *et al*. 2011. Family-group names in Coleoptera (Insecta). *Zookeys* **88**, 1–972.

Brown RW. 1954. *Composition of scientific words: a manual of methods and a lexicon of materials for the practice of logotechnics*. Published by the author, Baltimore, Md, 882 pp.

Calder AA. 1976. The New Zealand genus *Metablax* (Coleoptera: Elateridae) and its relationship to the Campsosterninae. *New Zealand Journal of Zoology* **3**, 313–325.

Calder AA. 1986. Classification, relationships and distribution of the Crepidomeninae (Coleoptera: Elateridae). *Australian Journal of Zoology, Supplementary Series* **122**, 1–222.

Calder AA. 1992. Notes on *Parablax* Schwarz and the subfamily Pityobiinae with description of *Parablax ossa* sp. n. from Tasmania (Coleoptera: Elateridae). *Journal of the Australian Entomological Society* **31**, 143–158.

Calder AA. 1996. *Click-beetles: Genera of the Australian Elateridae (Coleoptera)*, Vol. 2, *Monographs on invertebrate taxonomy*, CSIRO Publishing, Collingwood, Vic., Australia. x + 401 pp.

Calder AA, Lawrence JF & Trueman JWH. 1993. *Austrelater*, gen. nov. (Coleoptera: Elateridae), with a description of the larva and comments on elaterid relationships. *Invertebrate Taxonomy* **7**, 1349–1394.

Candèze E. 1863. Monographie des Élatérides, vol. 4. *Memoires de la Société Royale des Sciences de Liége* **17**, 1–534.

Cate PG. 2007. Family Elateridae. In: *Catalogue of Palaearctic Coleoptera*, Vol. 4, *Elateroidea – Derodontoidea – Bostrichoidea – Lymexyloidea – Cleroidea – Cucujoidea* (eds I Löbl & A Smetana), pp. 89–209. Apollo Books, Stenstrup, Denmark.

Costa C, Lawrence JF & Rosa SP. 2010. Elateridae Leach, 1815. In: *Handbook of Zoology, Volume IV* (eds NP Kristensen, RG Beutel), *Part 38, Volume 2: Coleoptera, Polyphaga, part* (eds RAB Leschen, RG Beutel & JF Lawrence), pp. 75–103. Walter de Gruyter, New York, NY, USA, and Berlin, Germany.

Crowson RA. 1961. On some new characters of classificatory importance in adults of Elateridae (Coleoptera). *Entomologist's Monthly Magazine* **96**, 158–161.

Dolin VG. 1975. Wing venation in click-beetles and its significance for the taxonomy of the family. *Zoologicheskii Zhurnal* **54**, 1618–1633.

Dolin VG. 1978. Phylogeny of click-beetles (Coleoptera: Elateridae). *Vestnik Zoologii* **3**, 3–12.

Douglas H. 2011. Phylogenetic relationships of Elateridae inferred from adult morphology, with special reference to the position of Cardiophorinae. *Zootaxa* **2900**, 1–45.

Fleutiaux E. 1947. Révision des Élatérides (Coléoptères) de l'Indo-Chine Française. *Notes d'Entomologie Chinoise* **11**, 233–420.

Gunter NL, Leavengood JM, Bartlett JS, Chapman EG & Cameron SL. 2013. A molecular phylogeny of the checkered beetles and a description of Epiclininae a new subfamily (Coleoptera: Cleroidea: Cleridae). *Systematic Entomology* **38**, 626–636.

Gur'yeva YL. 1974. Thoracic structure of click-beetles (Coleoptera, Elateridae) and the significance of the structural characters for the system of the family. *Entomologicheskoye Obozreniye* **53**, 96–113.

Hudson GV. 1934. *New Zealand beetles and their larvae: an elementary introduction to the study of our native Coleoptera*. Ferguson & Osborne, Wellington, 236 pp.

Huelsenbeck JP & Ronquist F. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics (Oxford, England)* **17**, 754–755.

Hyslop JA. 1917. The phylogeny of the Elateridae based on larval characters. *Annals of the Entomological Society of America* **10**, 241–263.

Johnson PJ. 2002. Elateridae Leach 1815. In: *American Beetles*, Vol. 2, *Polyphaga: Scarabaeoidea through Curculionoidea* (eds RH Arnett, MC Thomas, PE Skelley & JH Frank), pp. 160–173. CRC Press, Boca Raton, FL, USA.

Katoh K, Misawa K, Kuma K & Miyata T. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* **30**, 3059–3066.

Kishii T. 1987. *A taxonomic study of the Japanese Elateridae (Coleoptera), with the keys to the subfamilies, tribes and genera*. T. Kishii, Kyoto, 262 pp.

Kundrata R & Bocak L. 2011. The phylogeny and limits of Elateridae (Insecta, Coleoptera): is there a common tendency of click-beetles to soft-bodiedness and neoteny? *Zoologica Scripta* **40**, 364–378.

Kundrata R, Bocakova M & Bocak L. 2014. The comprehensive phylogeny of the superfamily Elateroidea (Coleoptera: Elateriformia). *Molecular Phylogenetics and Evolution* **76**, 162–171.

Lanfear R, Calcott B, Ho SYW & Guindon S. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* **29**, 1695–1701.

Lawrence JF & Arias ET. 2009. *Valdivelater*, a new genus of Protelaterini (Elateridae: Lissominae) from the forests of central and southern Chile. *Annales Zoologici* **59**, 319–328.

Lawrence JF & Newton AF. 1995. Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). In: *Biology, Phylogeny, and Classification of Coleoptera. Papers Celebrating the 80th Birthday of Roy A. Crowson*, Vol. 1–2 (eds J Pakaluk & SA Ślipiński), pp. 779–1083. Muzeum i Instytut Zoologii PAN, Warszawa, Poland.

Lawrence JF, Muona J, Teräväinen M, Ståhls G & Vahtera V. 2007. *Anischia*, *Perothops* and the phylogeny of Elateroidea (Coleoptera: Elateriformia). *Insect Systematics & Evolution* **38**, 205–239.

Miller MA, Pfeiffer W & Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 Nov. 2010, pp. 1–8. New Orleans, LA, USA.

Neboiss A. 1956. A check list of Australian Elateridae (Coleoptera). *Memoirs of the National Museum of Victoria* **22**, 1–75.

Ôhira H. 1962. *Morphological and taxonomic study on the larvae of Elateridae in Japan (Coleoptera)*. H. Ôhira, Okazaki, 179 p.

Rambaut A. 2009. FigTree 1.3.1. [Accessed 03 Sept 2014.] Available at http://tree.bio.ed.ac.uk/software/figtree/.

Rambaut A & Drummond AJ. 2007. Tracer 1.5. Institute of Evolutionary Biology University of Edinburgh, Edinburgh. [Accessed 03 Sept 2014.] Available at http://beast.bio.ed.ac.uk/Tracer.

Sagegami-Oba R, Oba Y & Ôhira H. 2007. Phylogenetic relationships of click-beetles (Coleoptera: Elateridae) inferred from 28S ribosomal DNA: insights into the evolution of bioluminescence in Elateridae. *Molecular Phylogenetics and Evolution* **42**, 410–421.

Schenkling S. 1927. Elateridae II. In: *Coleopterorum Catalogus, auspiciis et auxilio W. Junk, Pars 88*, pp. 264–636. W. Junk, Berlin, Germany.

Schwarz O. 1906. Neue Elateriden aus Australien. *Deutsche Entomologische Zeitschrift* **1906**, 353–369.

Schwarz O. 1907. *Genera Insectorum. Fasc. 46A–C. Coleoptera, fam. Elateridae*. P. Wytsman, Brussels, Belgium.

Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics (Oxford, England)* **22**, 2688–2690.

Stamatakis A, Hoover P & Rougemont J. 2008. A Rapid Bootstrap Algorithm for the RAxML Web Servers. *Systematic Biology* **57**, 758–771.

Stibick JNL. 1979. Classification of the Elateridae (Coleoptera). Relationships and classification of the subfamilies and tribes. *Pacific Insects* **20**, 145–186.

Swofford DL. 2002. PAUP*: Phylogenetic Analysis Using Parsimony (*and other Methods), v.4.0b10. Sinauer Associates, Sunderland, MA, USA.

Ulrich GW. 1988. The phylogeny of the Pityobiinae based upon larval morphology (Elateridae: Coleoptera). PhD Dissertation. University of California, Berkeley, USA. 169 pp.

Accepted for publication 15 October 2015.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1 Sequences downloaded from GenBank and used in this study, with GenBank and voucher numbers.

Table S2 Numbers and types of characters in the analysed data sets.

Table S3 The position of *Pityobius* LeConte in partial- and full-data analyses.

Table S4 The overview of the classifications of Pityobiinae.

Table S5 Checklist of genera and species included in Parablacinae subfam. nov., with their geographical distributions.

Table S1. Sequences downloaded from the GenBank and used in this study, with GenBank and voucher numbers.

				Markers				
Family	Subfamily	Genus/Species	Geographic origin	18S	28S	*rrnL*	*cox1*	Specimen voucher
Rhagophthalmidae		*Rhagophthalmus ohbai*	Japan	AB298864	N	NC_010964	NC_010964	71225
Rhagophthalmidae		*Rhagophthalmus* sp.	India	DQ100508	DQ198756	DQ198665	DQ198587	UPOL 000155
Rhagophthalmidae		*Mimoochotyra* sp.	Malaysia	DQ100505	DQ198753	DQ198662	DQ198584	UPOL 000M30
Rhagophthalmidae		*Bicladodrilus* sp.	China	DQ100507	DQ198755	DQ198664	DQ198586	UPOL 000M35
Rhagophthalmidae		indet.	Indonesia	DQ100506	DQ198754	DQ198663	DQ198585	UPOL 000M31
Rhagophthalmidae		indet.	Indonesia	KF625717	KF626305	KF626005	KF625410	UPOL 001359
Rhagophthalmidae		indet.	Indonesia	KF625718	N	KF626006	KF625411	UPOL 001363
Rhagophthalmidae		indet.	Thailand	KF625715	KF626303	KF626003	KF625408	UPOL RK0088
Rhagophthalmidae		indet.	Thailand	KF625716	KF626304	KF626004	KF625409	UPOL RK0370
Phengodidae		*Phengodes* sp.	USA	DQ100504	DQ198752	DQ198661	DQ198583	UPOL 000M29
Phengodidae		*Phengodes* sp.	Panama	KF625725	KF626312	KF626011	KF625418	UPOL 001238
Phengodidae		*Phengodes* sp.	Panama	KF625726	KF626313	KF626012	KF625419	UPOL 001241
Phengodidae		*Phengodes* sp.	Panama	KF625723	KF626310	KF626009	KF625416	UPOL RK0366
Phengodidae		indet.	Panama	KF625727	KF626314	KF626013	KF625420	UPOL 001243
Phengodidae		indet.	Panama	KF625728	KF626315	KF626014	KF625421	UPOL 001245
Phengodidae		indet.	Panama	KF625729	KF626316	KF626015	KF625422	UPOL 001246
Phengodidae		indet.	Panama	KF625730	KF626317	KF626016	KF625423	UPOL 001247
Phengodidae		indet.	Panama	KF625731	N	KF626017	KF625424	UPOL 001343
Phengodidae		indet.	Panama	KF625732	KF626319	N	KF625426	UPOL 001346
Phengodidae		indet.	Panama	KF625733	N	KF626018	KF625427	UPOL 001348
Phengodidae		indet.	Panama	KF625734	N	N	KF625428	UPOL 001349
Phengodidae		indet.	Panama	KF625735	N	KF626019	KF625429	UPOL 001350
Phengodidae		indet.	Panama	KF625736	KF626320	KF626020	KF625430	UPOL 001351
Phengodidae		indet.	Panama	KF625737	N	KF626021	N	UPOL 001353
Phengodidae		indet.	Panama	KF625738	N	KF626022	KF625431	UPOL 001354
Phengodidae		indet.	Belize	KF625719	KF626306	KF626007	KF625412	UPOL RK0361
Phengodidae		indet.	Panama	KF625720	KF626307	N	KF625413	UPOL RK0363
Phengodidae		indet.	Panama	KF625721	KF626308	KF626008	KF625414	UPOL RK0364
Phengodidae		indet.	Panama	KF625722	KF626309	N	KF625415	UPOL RK0365
Phengodidae		indet.	Panama	KF625724	KF626311	KF626010	KF625417	UPOL RK0368
Elateridae	Agrypninae	*Agrypnus murinus*	Slovakia	AF451943	DQ198735	DQ198645	DQ198567	UPOL 001049
Elateridae	Agrypninae	*Agrypnus* sp.	Japan	HQ333757	HQ333852	HQ333676	HQ333941	UPOL RK0004
Elateridae	Agrypninae	*Agrypnus* sp.	Indonesia	HQ333783	HQ333878	HQ333697	HQ333965	UPOL RK0030
Elateridae	Agrypninae	*Agrypnus* sp.	Japan	HQ333810	HQ333905	HQ333719	HQ333991	UPOL RK0057
Elateridae	Agrypninae	*Agrypnus* sp.	Indonesia	HQ333820	HQ333915	HQ333727	HQ334000	UPOL RK0067
Elateridae	Agrypninae	*Adelocera* sp.	Japan	HQ333778	HQ333873	HQ333694	HQ333961	UPOL RK0025
Elateridae	Agrypninae	*Adelocera* sp.	Indonesia	HQ333806	HQ333901	HQ333715	HQ333987	UPOL RK0053
Elateridae	Agrypninae	*Adelocera* sp.	Japan	HQ333817	HQ333912	HQ333724	HQ333997	UPOL RK0064
Elateridae	Agrypninae	*Adelocera* sp.	Malaysia	HQ333818	HQ333913	HQ333725	HQ333998	UPOL RK0065
Elateridae	Agrypninae	*Adelocera* sp.	Indonesia	HQ333794	HQ333889	KF626035	HQ333976	UPOL RK0041
Elateridae	Agrypninae	*Adelocera* sp.	Indonesia	HQ333815	HQ333910	KF626033	KF625439	UPOL RK0062
Elateridae	Agrypninae	*Lacon* sp.	Indonesia	HQ333789	HQ333884	KF626036	HQ333971	UPOL RK0036
Elateridae	Agrypninae	*Conoderus* sp.	Panama	HQ333746	HQ333841	HQ333665	HQ333931	UPOL 001416

Elateridae	Agrypninae	*Conoderus* sp	Panama	HQ333747	HQ333842	HQ333666	HQ333932	UPOL 001417
Elateridae	Agrypninae	*Drasterius bimaculatus*	Slovakia	HQ333793	HQ333888	HQ333704	HQ333975	UPOL RK0040
Elateridae	Agrypninae	*Drasterius* sp.	Morocco	HQ333816	HQ333911	HQ333723	HQ333996	UPOL RK0063
Elateridae	Agrypninae	indet.	Malaysia	HQ333798	HQ333893	HQ333708	HQ333980	UPOL RK0045
Elateridae	Agrypninae	*Platycrepidius* sp.	Panama	HQ333748	HQ333843	HQ333667	HQ333933	UPOL 001418
Elateridae	Agrypninae	Anaissini	Panama	KF625761	KF626341	KF626055	KF625452	UPOL RK0301
Elateridae	Agrypninae	*Pyrophorus* sp.	Panama	HQ333751	HQ333846	HQ333670	HQ333936	UPOL 001421
Elateridae	Agrypninae	*Pyrophorus* sp.	Panama	HQ333753	HQ333848	HQ333672	KF625435	UPOL 001423
Elateridae	Agrypninae	*Pyrophorus* sp.	French Guyana	KF625742	KF626325	KF626030	KF625436	UPOL RK0213
Elateridae	Agrypninae	*Tetrigus cyprius*	Greece	KF625744	KF626327	KF626032	KF625438	UPOL RK0228
Elateridae	Agrypninae	*Cryptalaus* sp.	Indonesia	HQ333781	HQ333876	KF626034	N	UPOL RK0028
Elateridae	Agrypninae	*Chalcolepidius* sp.	French Guyana	KF625743	KF626326	KF626031	KF625437	UPOL RK0219
Elateridae	Agrypninae	*Chalcolepidius* sp.	Panama	HQ333752	HQ333847	HQ333671	HQ333937	UPOL 001422
Elateridae	Agrypninae	*Cryptalaus* sp.	Japan	HQ333768	HQ333863	HQ333685	HQ333951	UPOL RK0015
Elateridae	Agrypninae	*Cryptalaus* sp.	Malaysia	HQ333834	HQ333926	HQ333740	HQ334014	UPOL RK0082
Elateridae	Agrypninae	*Drilus concolor*	Hungary	HQ333827	KF626322	HQ333734	HQ334007	UPOL RK0074
Elateridae	Agrypninae	*Malacogaster passerinii*	Italy	KF625741	KF626321	KF626029	KF625432	UPOL RK0369
Elateridae	Agrypninae	*Selasia* sp.	Ethiopia	KF625739	KF626323	KF626027	KF625433	UPOL RK0158
Elateridae	Agrypninae	*Selasia* sp.	Cameroon	KF625740	KF626324	KF626028	KF625434	UPOL RK0172
Elateridae	Agrypninae	*Selasia* sp.	South Africa	HQ333824	HQ333919	HQ333731	HQ334004	UPOL RK0071
Elateridae	Agrypninae	*Drilus flavescens*	Malta	DQ100501	DQ198748	DQ198657	DQ198579	UPOL 001046
Elateridae	Agrypninae	*Drilus* sp.	Greece	HQ333826	HQ333921	HQ333733	HQ334006	UPOL RK0073
Elateridae	Agrypninae	*Drilus* sp.	Turkey	N	N	HQ333739	HQ334013	UPOL RK0081
Elateridae	Agrypninae	*Drilus mauritanicus*	Spain	HQ333837	HQ333928	HQ333743	HQ334016	UPOL RK0085
Elateridae	Cardiophorinae	*Cardiophorus erichsoni*	Slovakia	HQ333790	HQ333885	HQ333701	HQ333972	UPOL RK0037
Elateridae	Cardiophorinae	indet.	Morocco	HQ333823	HQ333918	HQ333730	HQ334003	UPOL RK0070
Elateridae	Cardiophorinae	indet.	Namibia	AF451942	DQ198739	DQ198649	DQ198571	BMNH 679341
Elateridae	Cardiophorinae	*Dicronychus rubripes*	Slovakia	HQ333764	HQ333859	KF626023	HQ333947	UPOL RK0011
Elateridae	Cardiophorinae	*Dicronychus cinereus*	Czech Republic	HQ333776	HQ333871	KF626024	HQ333959	UPOL RK0023
Elateridae	Cardiophorinae	indet.	Indonesia	HQ333784	HQ333879	KF626025	HQ333966	UPOL RK0031
Elateridae	Cardiophorinae	indet.	Indonesia	HQ333788	HQ333883	KF626026	HQ333970	UPOL RK0035
Elateridae	Dendrometrinae	*Denticollis* sp.	Japan	HQ333759	HQ333854	KF626041	HQ333943	UPOL RK0006
Elateridae	Dendrometrinae	*Nothodes parvulus*	Slovakia	HQ333763	HQ333858	HQ333681	KF625443	UPOL RK0010
Elateridae	Dendrometrinae	indet.	Czech Republic	KF625751	KF626338	KF626053	KF625451	UPOL RK0251
Elateridae	Dendrometrinae	*Hemicrepidius hirtus*	Bulgaria	KF625754	KF626340	KF626054	KF625448	UPOL RK0297
Elateridae	Dendrometrinae	*Athous vittatus*	Czech Republic	HQ333755	HQ333850	HQ333674	HQ333939	UPOL RK0002
Elateridae	Dendrometrinae	*Pheletes quercus*	Czech Republic	HQ333775	HQ333870	HQ333692	HQ333958	UPOL RK0022
Elateridae	Dendrometrinae	*Cidnopus pilosus*	Slovakia	HQ333792	HQ333887	HQ333703	HQ333974	UPOL RK0039
Elateridae	Dendrometrinae	*Anostirus purpureus*	Slovakia	HQ333761	HQ333856	HQ333679	HQ333945	UPOL RK0008
Elateridae	Dendrometrinae	*Neopristilophus serrifer*	Japan	HQ333765	HQ333860	HQ333682	HQ333948	UPOL RK0012
Elateridae	Dendrometrinae	*Selatosomus latus*	Czech Republic	HQ333774	HQ333869	HQ333691	HQ333957	UPOL RK0021
Elateridae	Dendrometrinae	Ctenicerini indet.	Japan	HQ333787	HQ333882	HQ333700	HQ333969	UPOL RK0034
Elateridae	Dendrometrinae	*Platiana* sp.	Indonesia	HQ333782	HQ333877	HQ333696	HQ333964	UPOL RK0029
Elateridae	Dendrometrinae	*Hypolithus* sp.	Japan	HQ333795	HQ333890	HQ333705	HQ333977	UPOL RK0042
Elateridae	Dendrometrinae	*Semiotus* sp.	Chile	HQ333799	HQ333894	HQ333709	HQ333981	UPOL RK0046
Elateridae	Dendrometrinae	*Oxynopterus* sp.	Philippines	HQ333800	HQ333895	HQ333710	HQ333982	UPOL RK0047
Elateridae	Dendrometrinae	*Aplotarsus incanus*	United Kingdom	N	DQ198737	DQ198647	DQ198569	BMNH703088
Elateridae	Dendrometrinae	*Athous haemorrhoidalis*	United Kingdom	AF451944	DQ198738	DQ198648	DQ198570	BMNH 679174
Elateridae	Dendrometrinae	*Denticollis linearis*	Czech Republic	DQ100498	DQ198741	DQ198651	DQ198573	UPOL 000M25

Elateridae	Dendrometrinae	*Panspoeus guttatus*	United Kingdom	DQ100499	DQ198742	DQ198652	DQ198574	BMNH 703090
Elateridae	Dendrometrinae	*Stenagostus rhombeus*	United Kingdom	AF451945	DQ198744	DQ198653	DQ198576	BMNH 679144
Elateridae	Elaterinae	indet.	Zambia	KF625762	KF626346	KF626057	N	UPOL 001237
Elateridae	Elaterinae	*Mulsanteus* sp.	Panama	HQ333744	HQ333839	KF626037	HQ333929	UPOL 001414
Elateridae	Elaterinae	Adrastini indet.	Japan	HQ333780	HQ333875	KF626038	HQ333963	UPOL RK0027
Elateridae	Elaterinae	*Octinodes* sp.	Panama	HQ333749	HQ333844	HQ333668	HQ333934	UPOL 001419
Elateridae	Elaterinae	*Octinodes* sp.	Panama	KF625746	KF626328	N	KF625442	UPOL RK0306
Elateridae	Elaterinae	indet.	French Guyana	KF625752	KF626337	KF626052	KF625449	UPOL RK0203
Elateridae	Elaterinae	Physorhinini	Panama	KF625758	KF626334	KF626056	KF625453	UPOL RK0310
Elateridae	Elaterinae	indet.	New Caledonia	KF625755	KF626339	KF626046	KF625455	UPOL RK0400
Elateridae	Elaterinae	indet.	Ethiopia	KF625757	KF626343	KF626048	KF625457	UPOL RK0404
Elateridae	Elaterinae	indet.	Ethiopia	KF625759	KF626344	KF626049	KF625458	UPOL RK0406
Elateridae	Elaterinae	Agriotini	Panama	KF625763	KF626345	N	KF625459	UPOL 001413
Elateridae	Elaterinae	*Elater* sp.	Japan	HQ333766	HQ333861	HQ333683	HQ333949	UPOL RK0013
Elateridae	Elaterinae	*Tomicephalus* sp.	Panama	HQ333750	HQ333845	HQ333669	HQ333935	UPOL 001420
Elateridae	Elaterinae	indet.	Indonesia	HQ333773	HQ333868	HQ333690	HQ333956	UPOL RK0020
Elateridae	Elaterinae	indet.	Indonesia	HQ333819	HQ333914	HQ333726	HQ333999	UPOL RK0066
Elateridae	Elaterinae	*Ludioschema* sp.	Japan	HQ333777	HQ333872	HQ333693	HQ333960	UPOL RK0024
Elateridae	Elaterinae	*Ludioschema* sp.	Indonesia	HQ333808	HQ333903	HQ333717	HQ333989	UPOL RK0055
Elateridae	Elaterinae	*Anoplischius* sp.	Panama	HQ333745	HQ333840	HQ333664	HQ333930	UPOL 001415
Elateridae	Elaterinae	*Ampedus* sp.	Japan	HQ333758	HQ333853	HQ333677	HQ333942	UPOL RK0005
Elateridae	Elaterinae	*Ampedus sanguinolentus*	Slovakia	HQ333760	HQ333855	HQ333678	HQ333944	UPOL RK0007
Elateridae	Elaterinae	*Ampedus rufipennis*	Slovakia	HQ333762	HQ333857	HQ333680	HQ333946	UPOL RK0009
Elateridae	Elaterinae	*Ampedus* sp.	Japan	HQ333771	HQ333866	HQ333688	HQ333954	UPOL RK0018
Elateridae	Elaterinae	*Ampedus sinuatus*	Slovakia	HQ333791	HQ333886	HQ333702	HQ333973	UPOL RK0038
Elateridae	Elaterinae	*Ampedus balteatus*	United Kingdom	AF427605	DQ198736	DQ198646	DQ198568	BMNH 679173
Elateridae	Elaterinae	*Agriotes acuminatus*	Czech Republic	HQ333756	HQ333851	HQ333675	HQ333940	UPOL RK0003
Elateridae	Elaterinae	*Agriotes ustulatus*	Czech Republic	HQ333786	HQ333881	HQ333699	HQ333968	UPOL RK0033
Elateridae	Elaterinae	*Agriotes obscurus*	Czech Republic	HQ333805	HQ333900	KF626039	KF625441	UPOL RK0052
Elateridae	Elaterinae	*Agriotes lineatus*	United Kingdom	N	DQ198733	DQ198643	DQ198566	BMNH 703086
Elateridae	Elaterinae	*Cebrio* sp.	Italy	KF625745	KF626329	KF626040	KF625440	UPOL RK0142
Elateridae	Elaterinae	*Cebrio* sp.	Spain	DQ100497	DQ198740	DQ198650	DQ198572	BMNH 679376
Elateridae	Elaterinae	Megapenthini indet.	Japan	HQ333767	HQ333862	HQ333684	HQ333950	UPOL RK0014
Elateridae	Elaterinae	Adrastini indet.	Japan	HQ333769	HQ333864	HQ333686	HQ333952	UPOL RK0016
Elateridae	Elaterinae	Adrastini indet.	Japan	HQ333770	HQ333865	HQ333687	HQ333953	UPOL RK0017
Elateridae	Elaterinae	Adrsatini indet.	Malaysia	HQ333801	HQ333896	HQ333711	HQ333983	UPOL RK0048
Elateridae	Elaterinae	Adrastini indet.	Malaysia	HQ333812	HQ333907	HQ333720	HQ333993	UPOL RK0059
Elateridae	Elaterinae	*Melanotus villosus*	Czech Republic	HQ333754	HQ333849	HQ333673	HQ333938	UPOL RK0001
Elateridae	Elaterinae	*Priopus ornatus*	Laos	HQ333785	HQ333880	HQ333698	HQ333967	UPOL RK0032
Elateridae	Elaterinae	*Priopus humeralis*	Indonesia	HQ333821	HQ333916	HQ333728	HQ334001	UPOL RK0068
Elateridae	Elaterinae	*Anchastus* sp.	Indonesia	HQ333804	HQ333899	HQ333714	HQ333986	UPOL RK0051
Elateridae	Elaterinae	*Anchastus* sp.	Indonesia	HQ333809	HQ333904	HQ333718	HQ333990	UPOL RK0056
Elateridae	Elaterinae	*Anchastus* sp.	Indonesia	HQ333813	HQ333908	HQ333721	HQ333994	UPOL RK0060
Elateridae	Elaterinae	*Anchastus* sp.	Indonesia	HQ333814	HQ333909	HQ333722	HQ333995	UPOL RK0061
Elateridae	Hemiopinae	indet.	Indonesia	KF625756	KF626342	KF626047	KF625456	UPOL RK0403
Elateridae	Lissominae	*Drapetes mordelloides*	Czech Republic	HQ333828	HQ333922	HQ333735	HQ334008	UPOL RK0075
Elateridae	Lissominae	indet.	Cameroon	KF625747	KF626330	KF626042	KF625444	UPOL RK0334
Elateridae	Lissominae	indet.	Cameroon	KF625748	KF626331	KF626043	KF625445	UPOL RK0335
Elateridae	Lissominae	indet.	Cameroon	KF625749	KF626332	KF626044	KF625446	UPOL RK0353

Elateridae	Lissominae	indet.	Cameroon	KF625750	KF626333	KF626045	KF625447	UPOL RK0354
Elateridae	Lissominae	indet.	Cameroon	KF625760	KF626336	KF626051	KF625450	UPOL RK0174
Elateridae	Morostomatinae	*Diplophoenicus* sp.	Madagascar	KF625753	KF626335	KF626050	KF625454	UPOL RK0145
Elateridae	Negastriinae	*Zorochros* sp.	Malaysia	HQ333796	HQ333891	HQ333706	HQ333978	UPOL RK0043
Elateridae	Negastriinae	*Quasimus* sp.	Malaysia	HQ333802	HQ333897	HQ333712	HQ333984	UPOL RK0049
Elateridae	Negastriinae	*Quasimus* sp.	Malaysia	HQ333803	HQ333898	HQ333713	HQ333985	UPOL RK0050
Elateridae	Negastriinae	indet.	Malaysia	HQ333811	HQ333906	N	HQ333992	UPOL RK0058
Elateridae	Thylacosterninae	*Balgus* sp.	Bolivia	DQ100500	DQ198746	DQ198655	N	BMNH 669202
Elateridae	Thylacosterninae	*Pterotarsus bimaculatus*	Bolivia	N	DQ198743	N	DQ198575	BMNH 703093

Table S2. Numbers and types of characters in the analysed datasets; * = *cox1* mtDNA aligned only by Mafft.

Alignment type	Characters total	18S	28S	*rrnL*	*cox1* *	constant	variable uninformative	parsimony informative
BlastAlign	4379	2034	873	749	723	3005	318	1056
Mafft	4025	1962	770	570	723	2670	253	1102

Table S3. The position of *Pityobius* LeConte in partial and full-data analyses. *Lissominae minus Oestodini, including Thylacosterninae.

Dataset	Alignment method	Analysis method	Topology	Support (BS or PP)
Partial datasets				
18S rRNA	Mafft	ML	(*Pityobius*(Lissominae*))	56% BS
16S mtDNA	Mafft	ML	(*Oestodes*(*Balgus*+*Pityobius*))	8%; 21% BS
cox1 mtDNA	Mafft	ML	(*Pityobius*(Agrypninae pars)	1% BS
Complete datasets				
	Mafft	ML	(*Pityobius*(Lissominae*))	60% BS
	BlastAlign	ML	(*Pityobius*(Lissominae*))	53% BS
	Mafft	BI	(*Pityobius*+*Oestodes*)	84% PP
	BlastAlign	BI	(*Pityobius*+*Hemiops*)	77% PP

Table S4. An overview of the classifications of Pityobiinae. *–genera not treated in Calder (1996), **–genera transferred here to Parablacinae subfam.nov.

Genus	Hyslop 1917	Crowson 1961	Gur'yeva 1974	Dolin 1975	Stibick 1979	Calder 1992	Calder 1996	this study
Pityobius LeConte	yes	yes	yes	yes	yes	yes	yes*	yes
Tibionema Solier	no	no	no	yes	no	yes	yes*	yes
Parablax Schwarz	no	no	no	yes	no	yes	yes	no**
Metablax Candèze	no	yes	yes	yes	no	yes	yes	no**
Parasaphes Candèze	no	no	no	no	no	yes	yes	no**
Wynarka Calder	-	-	-	-	-	yes	yes	no**
Tasmanelater Calder	-	-	-	-	-	-	yes	no**
Xuthelater Calder	-	-	-	-	-	-	yes	no**
Pectocera Hope	no	no	no	no	yes	no	no	no
Ceroleptus Fleutiaux	-	no	no	no	yes	no	no	no
Julodischema Thompson	no	no	no	no	yes	no	no	no
Rostricephalus Fleutiaux	-	no	no	no	yes	no	no	no

Table S5. Checklist of genera and species included in Parablacinae subfam. nov., with their geographical distributions.

Parablax Schwarz, 1906 [Australia; *P. nunden* species-group: Tasmania]
P. quinquesulcatus species-group
P. quinquesulcatus (Blackburn, 1900) [type species]
P. ingwa species-group
P. ingwa Calder, 1986
P. markrah Calder, 1986
P. moorda species-group
P. moorda Calder, 1986
P. rumaiy Calder, 1986
P. nunden species-group
P. nunden Calder, 1986
P. ooliekirra Calder, 1986
P. ossa Calder, 1992
P. padmuri Calder, 1986

Metablax Candèze, 1869 [New Zealand]
M. acutipennis species-group
M. acutipennis (White, 1846) [type species]
M. brouni Sharp, 1877
M. approximans species-group
M. approximans (White, 1846)
M. cinctiger (White, 1846)
M. gourlayi Calder, 1976

Wynarka Calder, 1986 [Australia]
W. sylvestre Calder, 1986 [type species]

Parasaphes Candèze, 1882 [Australia]
P. elegans Candèze, 1882 [type species]

Tasmanelater Calder, 1996 [Australia: Tasmania]
T. pelionensis Calder, 1996 [type species]

Xuthelater Calder, 1996 [Australia]
X. moppiensis Calder, 1996 [type species]

Ophidius Candèze, 1863 [Australia]
O. dracunculus Candèze, 1863
O. elegans Candèze, 1863 [type species]
O. histrio (Boisduval, 1835)
O. vericulatus Neboiss, 1975

Příloha 6

Kundrata, R., Gunter, N.L., Janošíková, D. & Bocák, L. (2018) Molecular evidence for the subfamilial status of Tetralobinae (Coleoptera: Elateridae), with comments on parallel evolution of some phenotypic characters. *Arthropod Systematics & Phylogeny*, 76: 137–145.
[IF 1,703; 5 citací na WoS]
[korespondující autor; autorský podíl: 45 %]

ARTHROPOD SYSTEMATICS
& PHYLOGENY

76 (1): 137–145
14.5.2018

SENCKENBERG

Molecular evidence for the subfamilial status of Tetralobinae (Coleoptera: Elateridae), with comments on parallel evolution of some phenotypic characters

Robin Kundrata*,[1], Nicole L. Gunter[1,2], Dominika Janosikova[1] &
Ladislav Bocak[1]

[1] Department of Zoology, Faculty of Science, Palacky University, 17. listopadu 50, 771 46 Olomouc, Czech Republic; Robin Kundrata [robin.kundrata@upol.cz]; Ladislav Bocak [ladislav.bocak@upol.cz] — [2] The Cleveland Museum of Natural History, 1 Wade Oval Drive, Cleveland, 44106, Ohio, USA; Nicole L. Gunter [ngunter@cmnh.org] — * Corresponding author

Accepted 14.ii.2018.

Editors in charge: Brian Wiegmann & Klaus-Dieter Klass

Abstract. Tetralobinae is a distinct click-beetle lineage containing 78 species in seven genera. Adults are large-bodied, and larvae live in termite nests and are grub-like unlike typical elaterid wireworms. Their taxonomic position in the Elateridae has been unstable and they were treated either as a separate elaterid subfamily or a tribe within Agrypninae. Here, we provide the first molecular investigation of Tetralobinae to test their phylogenetic position using two nuclear and two mitochondrial molecular markers from three total taxa, one from each of the following genera: *Tetralobus* Lepeletier & Audinet-Serville, *Sinelater* Laurent, and *Pseudotetralobus* Schwarz. Two different datasets were analyzed, Elateridae (181 terminals) and Elateroidea (451 terminals), both composed by the earlier published datasets supplemented with the newly produced tetralobine sequences. The results suggest that Tetralobinae is the sister lineage to the remaining Elateridae and that warrants the subfamilial status instead of an subordinate position in the Agrypninae. *Pseudotetralobus* (Australia) was sister to the *Tetralobus* (Africa) + *Sinelater* (China) consistent with previously published morphological analysis. Additionally, we discuss the homoplastic phenotypic characters which were used for building the earlier click-beetle classification, and which indicated the relationships between Tetralobinae and Agrypninae.

Key words. Agrypninae, classification, click-beetles, diversity, morphology, phylogeny.

1. Introduction

Elateridae (click-beetles) are an easily recognizable, widespread, and species-rich beetle family, however, their suprageneric classification is notoriously unstable (e.g., Schwarz 1906; Fleutiaux 1947; Dolin 1975; Stibick 1979; Johnson 2002; Costa et al. 2010; Douglas 2011; Kundrata et al. 2016). Many lineages, especially species poor groups delimited by a single or a limited number of unique characters, were given variable taxonomic ranks in previous classification schemes. Such is the case of Tetralobinae, a small group of distinctive, large-bodied click-beetles from the tropical Africa, eastern Asia and Australia which have been classified either as a separate subfamily or a tribe within Agrypninae. Currently, this lineage contains 78 species in seven genera, i.e., *Neotetralobus* Girard, 1987, *Paratetralobus* Laurent, 1964a, *Pseudalaus* Laurent, 1967, *Pseudotetralobus* Schwarz, 1902, *Sinelater* Laurent, 1967, *Tetralobus* Lepeletier & Audinet-Serville, 1828 (all Tetralobini), and *Piezophyllus* Hope, 1842 (Piezophyllini) (Laurent 1967; Costa et al. 1994; Kubaczkova & Kundrata 2017).

The taxonomic status and position of Tetralobinae in the Elateridae classification has been controversial since the establishment of the taxon. Early authors suggested the close relationships between Tetralobinae and Oxynopterinae, based mainly on the large body and flabellate antennae (Hope 1842; Lacordaire 1857; Candéze 1857; Hyslop 1917). Tetralobinae were long considered as a distinct subfamily by many students of Elateridae

Table 1. Tetralobinae representatives used in this study, with GenBank and voucher numbers. * data taken from Gunter et al. (2016).

		Markers				
Genus/Species	**Geographic origin**	**18S**	**28S**	***rrnL***	***cox1***	**Specimen voucher**
Pseudotetralobus cf. *australasiae*	Australia, Queensland, Tregole N.P.	MF507002	KF802025*	KF801694*	KF801862*	COL075
Sinelater perroti	China, Guangdong, Dadongshan	MF507001	MF507004	MF506987	MF507013	UPOL RK0878
Tetralobus cf. *curticollis*	Central Afr. Rep., 70 km NW Mbaiki	MF507000	MF507003	MF506986	MF507012	UPOL RK0877

(e.g., Fleutiaux 1919, 1947; Schenkling 1925; Neboiss 1956, 1961; Van Zwaluwenburg 1959; Laurent 1964a, b,c,d, 1965a,b, 1967, 1968; Girard 1971, 1979, 1987; Gur'yeva 1974, Hayek 1974; Dolin 1975) and only Dolin (1978) discussed their position within Elateridae, suggesting the close relationships of Tetralobinae and Diminae. Based on the basal setae on claws in adults and mandibles without teeth in larvae, Stibick (1979) classified Tetralobinae as a tribe within Pyrophorinae (now Agrypninae), which he placed close to Oxynopterinae and Pityobiinae. Stibick's concept was followed by e.g., Calder (1990, 1996), Costa et al. (1992, 1994, 2010), Girard (2003), Girard et al. (2007), Bouchard et al. (2011), and Rosa et al. (2015), but some authors still recognized Tetralobinae as a separate subfamily (Gur'yeva 1974; Dolin 1975; Lawrence & Newton 1995; Suzuki 2002; Cate 2007; Girard 2016). Calder et al. (1993) analyzed both larval and adult morphological characters of Elateridae and recovered the only tetralobine genus sampled in the analysis, *Pseudotetralobus*, either as a sister to the bulk of Elateridae (except *Cebrio* Olivier, 1790 and *Cussolenis* Fleutiaux, 1918) or to Elateridae minus *Cebrio*, *Cussolenis*, *Semiotus* Eschscholtz, 1829, and Lissominae. Douglas (2011) used adult morphological data to reconstruct a phylogeny of Elateridae, and recovered *Tetralobus* in various positions in the Elateridae topology, mostly as a sister to Agrypninae, however without statistical support. All phylogenetic hypotheses on the position of Tetralobinae to date have relied exclusively on morphological data and only included a single species in analyses. Furthermore, no tetralobines were sampled in recent DNA-based phylogenetic analyses of Elateridae (Sagegami-Oba et al. 2007; Kundrata & Bocak 2011; Han et al. 2016; Kundrata et al. 2016). Our study presents the first molecular data to investigate the position of three tetralobine genera, i.e., *Tetralobus*, *Sinelater* and *Pseudotetralobus*, within Elateridae, necessary to compare previous classifications and morphology-based hypotheses.

2. Material and methods

2.1. Taxon sampling, morphology and laboratory procedures

To test the phylogenetic placement of Tetralobinae, we sequenced the representatives of *Tetralobus* cf. *curticollis* from Central African Republic, *Sinelater perroti* (Fleutiaux, 1940) from China (type species of *Sinelater*) and *Pseudotetralobus* cf. *australasiae* from Australia (Table 1; Figs. 2–4), and combined the data with the Elateroidea and Elateridae datasets used in Kundrata et al. (2014, 2016). The subfamilial classification of Elateroidea follows that of Kundrata et al. (2014), and the suprageneric classification of Elateridae (Table 2) follows that of Costa et al. (2010), with changes proposed by Kundrata & Bocak (2011), Bouchard et al. (2011), and Kundrata et al. (2016). The morphological terminology follows Costa et al. (1994, 2010) and Calder (1996). The type and identified non-type specimens of Tetralobinae used for the morphological examination, as well as other Elateridae used for the comparison with Tetralobinae, were studied in the collections of the Koninklijk Museum voor Midden-Afrika, Tervuren (RMCA), the Museum National d'Histoire Naturelle, Paris, France (MNHN), the Natural History Museum, Budapest, Hungary (HNHM), the Naturhistorisches Museum, Vienna, Austria (NHMW), the Australian National Insect Collection CSIRO, Canberra, Australia (ANIC), and the Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany (SDEI). Altogether we examined the material belonging to 60 out of 78 species of Tetralobinae, including the type material of the type species for all genera but *Pseudotetralobus*, for which the type material has been probably destroyed (Kubaczkova & Kundrata 2017). Details of the species examined are available in the Electronic Supplement (Table S1).

Specimens were fixed in 96% alcohol and stored at –20ºC. Whole-genomic DNA was extracted using DNeasy Blood & Tissue kit (Qiagen, Hilden, Germany) following standard protocols. The PCR amplification and sequencing were carried out in two laboratories. *Pseudotetralobus* cf. *australasiae* was processed in the molecular systematics laboratory of the ANIC, Canberra, Australia following the procedures described by Gunter et al. (2013). *Sinelater* and *Tetralobus* spp. were amplified and sequenced in the Laboratory of Molecular Systematics, UP Olomouc as described in Bocakova et al. (2007) and Kundrata & Bocak (2011). Four molecular markers were amplified: 18S rRNA (~1000 bp), the D2 loop of 28S rRNA (~640 bp), and the fragments of *rrnL* (~530 bp), and *cox1-3'* mtDNA (723 bp). The 28S, *rrnL*, and *cox1* sequences of *Pseudotetralobus* cf. *australasiae* were published as outgroup data in a study of Scarabaeoidea (Gunter et al. 2016). Here, we added the fragment of 18S rRNA gene sequenced from the same voucher specimen to supplement our four-gene matrix. GenBank accession numbers for the Tetralobinae sequences as well as the voucher numbers are listed in Table 1. Voucher specimens are deposited at the ANIC (*Pseudotetralobus*) and the Laboratory of Molecular Systematics, Palacky University, Olomouc (*Sinelater*, *Tetralobus*).

2.2. Dataset assembling, alignment methods and phylogenetic analyses

We used two different datasets (i.e., within the family and superfamily) to explore the phylogenetic position of Tetralobinae. When all elateroid families are included, the alignment is complicated by differences in loop length of 18S and 28S (i.e., short loops are characteristic in Elateridae (Bocakova et al. 2007; Kundrata et al. 2014) and long loops in some other families, e.g., Lampyridae and Eucnemidae), thus support values within the family-only analysis may be more reliable. To compare analyses based on different alignments, first, we merged Tetralobinae sequences with the complete Elateridae dataset by Kundrata et al. (2016). This dataset contained 181 terminals (including 151 Elateridae), with Phengodidae and Rhagophthalmidae used as an outgroup. As a second analysis, we added Tetralobinae sequences to the most comprehensive Elateroidea dataset to date by Kundrata et al. (2014). This dataset contained 451 terminals (including 114 Elateridae, all taxa represented by all four markers), and members of Scirtoidea were used as an outgroup. Newly produced sequences were edited using Geneious 7.1.7 (http://www.geneious.com; Kearse et al. 2012). Sequences were aligned separately using default parameters in Mafft algorithm (Katoh et al. 2002; Katoh & Standley 2013) as implemented in Geneious software. Alignment of the length invariable protein-coding *cox1* sequences was checked by amino acid translation. The best-fit partitioning schemes and partition-specific substitution models were tested in PartitionFinder 1.1.1 (greedy algorithm; Lanfear et al. 2012) using the corrected Akaike information criterion.

Both Elateridae and Elateroidea alignments were analyzed by the Maximum likelihood (ML) criterion using RAxML 8.2.10 (Stamatakis 2006) via the CIPRES web server (www.phylo.org; Miller et al. 2010). We applied the GTR+I+G model and the partitioning scheme as defined by PartitionFinder. Branch supports were calculated using the Rapid Bootstrap algorithm (Stamatakis et al. 2008) with 1000 bootstrap replicates. Bootstrap values (BV) ≥ 70% were considered as moderate support whereas BV ≥ 90% indicated strong support for a node. The Elateridae dataset was further analyzed under the Bayesian inference (BI) using MrBayes 3.2.6 (Huelsenbeck & Ronquist 2001) on the CIPRES portal (Miller et al. 2010), with the partitioning schemes and nucleotide substitution models as identified in PartitionFinder. Four chains were run for 4×10^7 generations using the Markov chain Monte Carlo method. Stationary phase and convergence were detected in Tracer 1.5 (Rambaut & Drummond 2007) and the first 20% of generations were discarded as burn-in. The 50% majority-rule consensus was constructed to determine the posterior probabilities (PP) from the remaining trees. Posterior probabilities ≥ 95% indicates significant statistical support (Felsenstein 2004). The resulting trees were visualized and edited in FigTree 1.3.1 (Rambaut 2009).

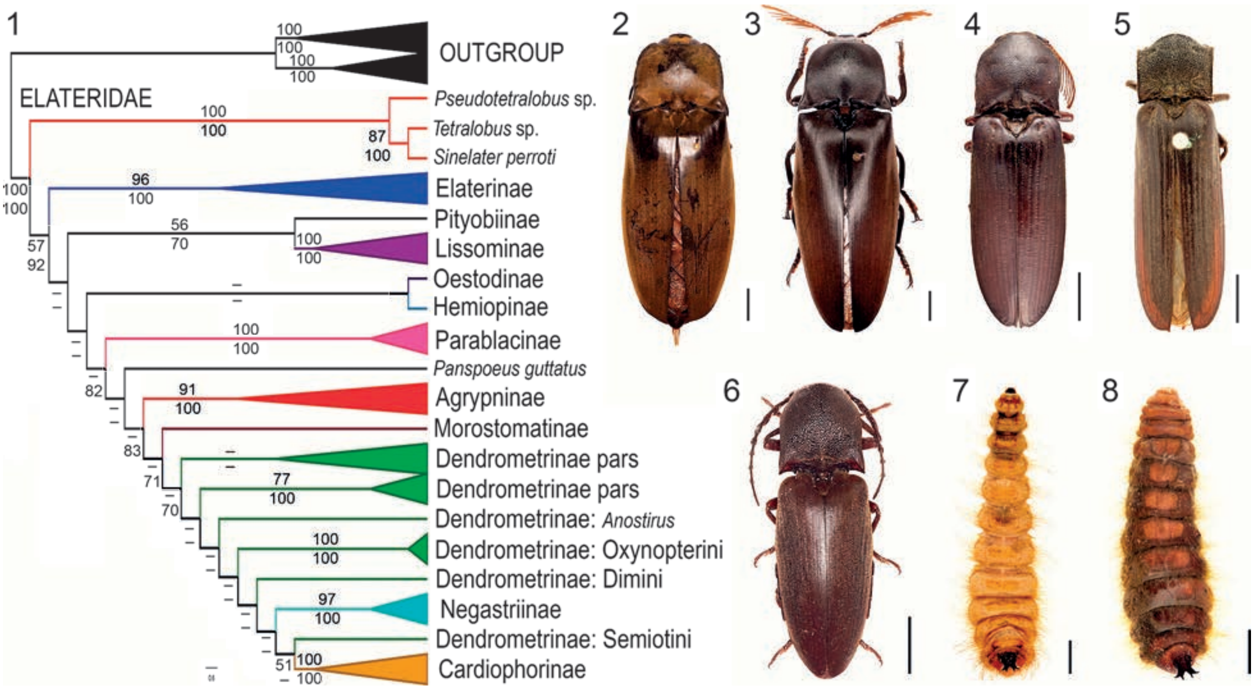
3. Results

3.1. Dataset/Alignment parameters

The Elateridae alignment contained 181 terminals and included 4021 homologous positions (1964, 770, 564, and 723 positions for 18S, 28S, *rrnL*, and *cox1*, respectively), from which 2585 were conserved, 1365 variable, and 1117 parsimony informative. The nucleotide composition of the markers used in our study was as follows: 18S: A = 23.8, C = 24.7, T = 23.4, G = 28.1; 28S: A = 25.2, C = 23.9, T = 19.8, G = 31.2; *rrnL*: A = 31.4, C = 9.7, T = 41.4, G = 17.5; *cox1*: A = 32.9, C = 18.1, T = 34.3, G = 14.6. The Elateroidea alignment contained 451 terminals and included 5285 homologous positions (2569, 1386, 607, and 723 positions for 18S, 28S, *rrnL*, and *cox1*, respectively), from which 1953 were conserved, 3010 variable, and 2471 parsimony informative. PartitionFinder identified six partitions (all genes and codon positions in *cox1*) as the optimal scheme. The nucleotide substitution model GTR+I+G was selected for all partitions.

3.2. Phylogenetic analyses

The position of Tetralobinae within Elateridae was investigated using the 181-taxa dataset. The collapsed ML phylogenetic tree with the Elateridae subfamilies (except for Tetralobinae) and with statistical support values from both ML and BI analyses is shown in Fig. 1; the full-resolution tree is given in Fig. S1. The ML and BI analyses of the Elateridae dataset yielded very similar tree topologies. In both analyses, Elateridae were monophyletic, and Tetralobinae sister to all remaining elaterid lineages. Tetralobinae were monophyletic (100% BV, 100% PP), and *Pseudotetralobus* was sister to *Tetralobus* + *Sinelater*; the latter clade was moderately to strongly supported (Figs. 1, S1). To test the effect of alignment on the recovered position of Tetralobinae within the Elateridae, we additionally used the 451-taxa dataset. Tree topology yielded by the ML analysis recovered Elateridae monophyletic but statistically unsupported. Tetralobinae were monophyletic (100% BV), and recovered in an unsupported clade with Lissominae and Cardiophorinae within deep Elateridae splits, far from Agrypninae (Fig. S2). Since this dataset contained more distant outgroups which generally causes problems with ambiguous alignment of length variable sequences, we do not further discuss the exact position of Tetralobinae inferred from the Elateroidea dataset.



Figs. 1–8. 1: Phylogenetic hypothesis for Elateridae, resulting from the ML analysis of concatenated Mafft alignment of four molecular markers (18S rRNA, 28S rRNA, *rrnL* mtDNA and *cox1* mtDNA). Upper and lower values at branches indicate ML bootstrap support and Bayesian posterior probabilities, respectively. Only values above 50% are shown. **2**: *Tetralobus* sp., Central African Republic, sequenced specimen RK0877 (UPOL). **3**: *Sinelater perroti* (Fleutiaux, 1940), China, sequenced specimen RK0878 (UPOL). **4**: *Pseudotetralobus* cf. *australasiae*, Australia, sequenced specimen COL075 (ANIC). **5**: *Pseudotetralobus capucinus*, Australia (RBINS). **6**: *Piezophyllus benitensis* Fleutiaux, 1902, Central African Republic (UPOL). **7**: *Pseudotetralobus* sp., larva, Australia (ANIC). **8**: *Pseudotetralobus* cf. *murrayi*, larva, Australia (ANIC). Scale bars: 5 mm.

3.3. Taxonomy

Tetralobinae Laporte, 1840, status revised

Tétralobites Laporte, 1840: 230; Tetralobitae: Blanchard (1853: 84); Tétralobides: Candèze (1857: 365); Tetralobidae: Quedenfeldt (1886: 28); Tetralobinae: Fleutiaux (1919: 32); Tetralobini: Schwarz (1906: 57).
= Phyllophoridae Hope, 1842: 73.

Type genus. *Tetralobus* Lepeletier & Audinet-Serville, 1828.

Subfamilial diagnosis. Adult (Figs. 2–6). Body 15–80 mm long, moderately to strongly elongate, convex, clothed with sparse to dense setae. ***Head***: frontoclypeal region produced forward, anterior part of frons excavated and forming thick projecting pad, nasale high (narrow in *Paratetralobus*); mandible unidentate, robust, with tuft of setae located in dorso-lateral pit; terminal maxillary palpus slightly securiform to oblong-ovate, with apex truncate to rounded; antenna with 11 antennomeres (12 in males of *Pseudotetralobus* and *Tetralobus* subgenus *Dodecamerus* Laurent), antennomeres II–III simple, short, transverse; remaining antennomeres except ultimate one serrate (Piezophyllini, females of Tetralobini) or flabellate (males of Tetralobini) from antennomere IV. ***Thorax***: pronotum moderately convex in most species, strongly convex in *Neotetralobus*, often with median longitudinal depression; with well developed tubercle postero-medially in front of scutellum, turned upwards in Piezophyllini; lateral carina complete in most Tetralobini, incomplete posteriorly in *Neotetralobus*, incomplete anteriorly in Piezophyllini; prosternum anteriorly produced forwards to form short chin piece, prosternal process more or less horizontal. Scutellar shield subtriangular, longer than wide. Mesoventral cavity declivitous in most species, vertical in *Pseudalaus*. Mesoventrite and metaventrite medially separated by distinct suture. Metaventrite with anterior margin simple in Tetralobini or elevated, V-shaped in Piezophyllini; metanepisternum large, wide, forming about 1/4 of the metaventrite width in Tetralobini, relatively longer and much narrower in Piezophyllini. Metacoxal plate reaching epipleura, not distinctly narrowed laterally in most species (in some *Tetralobus* spp. plate with tooth in basal third, then slightly narrowed laterally). Elytra subovate to strongly elongate and subparallel-sided in some *Tetralobus* and *Pseudotetralobus* spp., often with 10 weakly developed punctate striae, striae and/or punctures inconspicuous, incomplete or obsolete in some species of Tetralobini; apices not dehiscent in most Tetralobini, slightly dehiscent with short spines in some Tetralobini, or distinctly dehiscent in Piezophyllini; epipleura narrowly open distally or widely open in *Sinelater*. Hind wings well developed; apical field 0.1–0.2 × total wing length; radial cell usually conspicuously elongate, cross-vein r3 long, horizontal; wedge cell absent. Leg moderately long; tibia with (Tetralobini) or without apical spurs (Piezophyllini);

tarsomeres I–IV apico-ventrally conspicuously lobed ("spongiose pads" of Calder 1996); tarsal claws simple, basally covered with setae of different numbers, positions, and lengths; empodium bisetose or multisetose in some *Tetralobus* and *Pseudotetralobus* spp. ***Male terminalia***: sternite VIII reduced, transverse, emarginate apico-medially; tergite X in males reduced, fused to tergite IX. Aedeagus trilobate, symmetrical; median lobe partly membranous, sheath-like; parameres apically simple or slightly lobate (distinctly lobate in Piezophyllini), margins of parameres simple or with tooth in *Pseudalaus* and *Sinelater*, phallobase U-shaped. ***Female terminalia***: sternite VIII usually longer than wide, V-shaped, with spiculum ventrale. Gonocoxite with short subapical stylus; internal tract with omega-like sclerite in all Tetralobini, without sclerite in all Piezophyllini. For more details see Costa et al. (1994). — **Larva** (Figs. 7, 8). Body broad, grub-like, weakly sclerotized, densely covered with long hairs; head prognathous, phragmotic, heavily sclerotized, covered with foliaceous and bristle-like setae, stemmata absent (*Pseudotetralobus*) or present (*Tetralobus*), epicranial stem short, frontal arms absent, nasale tridentate, mandible falcate, unidentate, basally and laterally covered with foliaceous setae, cardo elongate; abdomen physogastric, posterior part of segment VIII with chitinized plates (probably glandular openings). Only larvae of several species of *Tetralobus* and *Pseudotetralobus* (Tetralobini) have been known. Pupal cocoons have been reported for species of both genera. For more details see Costa et al. (1992) and Girard et al. (2007).

Tribal characteristics. Within Tetralobinae, Tetralobini differ from Piezophyllini in the flabellate antennae in males (serrate in Piezophyllini), lateral pronotal carina complete anteriorly (incomplete in Piezophyllini), anterior margin of metaventrite simple (elevated, V-shaped in Piezophyllini), wide metanepisternum (narrow in Piezophyllini), basal median tubercle on pronotum more or less horizontal (distinctly turned upwards in Piezophyllini), presence of tibial spurs (absent in Piezophyllini), not or only slightly dehiscent elytral apices (distinctly dehiscent in Piezophyllini), and parameres apically simple or slightly lobate (distinctly lobate in Piezophyllini) (see Costa et al. 1994 for more details).

Taxa included. Tribe Tetralobini: genera *Neotetralobus* Girard, 1987 (1 sp.), *Paratetralobus* Laurent, 1964a (1 sp.), *Pseudalaus* Laurent, 1967 (2 spp.), *Pseudotetralobus* Schwarz, 1902 (16 spp.), *Sinelater* Laurent, 1967 (1 sp.), *Tetralobus* Lepeletier & Audinet-Serville, 1828 (52 spp.). — Tribe Piezophyllini: genus *Piezophyllus* Hope, 1842 (5 spp.). For more details and a complete species list see the catalogue by Kubaczkova & Kundrata (2017).

Distribution. Afrotropical region including Madagascar (*Neotetralobus*, *Paratetralobus*, *Pseudalaus*, *Tetralobus* pars, *Piezophyllus* pars), East Palaearctic and/or Oriental regions (*Sinelater*, *Tetralobus* pars, *Piezophyllus* pars), Australian region including New Guinea and the Maluku Islands (*Pseudotetralobus*).

Biology. Adults have been collected mainly at light in various habitats from the semi-arid grasslands to tropical rainforests. The larvae were often associated with termite nests. They are predaceous, most probably feeding on the termites and have been collected from the decaying wood, termite infested logs, and the termite mounds (Froggatt 1917; Calder 1990, 1996; Costa et al. 1992; Girard et al. 2007; Costa & Vanin 2010). Jamal (1994) reported *Tetralobus* as a pest on the *Acacia* (gum arabic) trees in Sudan.

4. Discussion

In this study, we examined the phylogenetic position of Tetralobinae using four molecular markers. Our results, as well as the previous morphology-based analyses (Calder et al. 1993; Douglas 2011), suggest that Tetralobinae are an independent lineage that warrants its subfamilial status (Table 2). They are recovered as a sister to all remaining click-beetle groups (Figs. 1, S1). Their placement within Elateridae is unambiguous given their strong morphological affinities including an exposed labrum, projecting hind pronotal angles, a clicking mechanism including a long prosternum and a mesoventral cavity, well developed metacoxal plates, and connate four basal ventrites (Calder 1996). The results of our Elateroidea analysis (Fig. S2) also confirm the placement of Tetralobinae within Elateridae. Additionally, our results clearly demonstrate that previous hypotheses on the Tetralobinae relationships were false, based mainly on the misinterpretation of homoplastic morphological characters.

Based on the presence of flabellate antennae in Tetralobinae and Oxynopterinae, early authors (e.g., Lacordaire 1857) hypothesized close relationships between these two groups. This hypothesis was generally accepted and these taxa were long placed next to each other in the Elateridae systems (e.g., Schwarz 1906; Schenkling 1925; Girard 1971). Oxynopterinae, currently classified by most authors as a tribe in Dendrometrinae (Costa et al. 2010), are placed within the Dendrometrinae + Negastriinae + Cardiophorinae clade (Sagegami-Oba et al. 2007; Kundrata et al. 2016; this study; Figs. 1, S1), and differ from Tetralobinae in many aspects e.g., the different frontal region of head, relatively longer falcate mandibles without pits with setae, only antennomere II short and simple (not II and III), relatively wider scutellum, tarsi without ventral lobes, and claws without basal setae.

Stibick (1979) suggested the suprageneric classification of Elateridae and placed Tetralobinae as a tribe within Pyrophorinae (= Agrypninae), lowering both tetralobine tribes to a subtribe level. In his "phylogenetic

Table 2. An updated suprageneric classification of extant Elateridae.

- **Agrypninae Candèze, 1857**
  - Agrypnini Candèze, 1857
  - Anaissini Golbach, 1984
  - Euplinthini Costa, 1975
    - Cleidecostina Johnson, 2002
    - Compsoplinthina Costa, 1975
    - Euplinthina Costa, 1975
  - Drilini Blanchard, 1845
  - Hemirhipini Candèze, 1857
    - Hemirhipina Candèze, 1857
    - Tetrigusina Schimmel & Tarnawski, 2012
  - Oophorini Gistel, 1848
  - Platycrepidiini Costa & Casari-Chen, 1993
  - Pseudomelanactini Arnett, 1967
  - Pyrophorini Candèze, 1863
    - Hapsodrilina Costa, 1975
    - Nyctophyxina Costa, 1975
    - Pyrophorina Candèze, 1863
- **Campyloxeninae Costa, 1975**
- **Cardiophorinae Candèze, 1859**
- **Dendrometrinae Gistel, 1848**
  - Crepidomenini Candèze, 1863
  - Dendrometrini Gistel, 1848
    - Dendrometrina Gistel, 1848
    - Denticollina Stein & Weise, 1877
    - Hemicrepidiina Champion, 1896
  - Dimini Candèze, 1863
  - Hypnoidini Schwarz, 1906
  - Oxynopterini Candèze, 1857
  - Pleonomini Semenov & Pjatakova, 1936
  - Prosternini Gistel, 1856
  - Selatosomini Schimmel, Tarnawski, Han & Platia, 2015
    - Mosotalesina Schimmel, Tarnawski, Han & Platia, 2015
    - Selatosomina Schimmel, Tarnawski, Han & Platia, 2015
  - Semiotini Jakobson, 1913
  - Senodoniini Schenkling, 1927
- **Elaterinae Leach, 1815**
  - Agriotini Laporte, 1840
    - Agriotina Laporte, 1840
    - Cardiorhinina Candèze, 1863
  - Ampedini Gistel, 1848
  - Aplastini Stibick, 1979
  - Cebrionini Latreille, 1802
  - Dicrepidiini Thomson, 1858
  - Elaterini Leach, 1815
  - Megapenthini Gurjeva, 1973
  - Melanotini Candèze, 1859
  - Odontonychini Girard, 1973
  - Physorhinini Candèze, 1859
  - Pomachiliini Candèze, 1859
  - Synaptini Gistel, 1856
- **Eudicronychinae Girard, 1971**
- **Hemiopinae Fleutiaux, 1941**
- **Lissominae Laporte, 1835**
  - Lissomini Laporte, 1835
  - Protelaterini Schwarz, 1902
- **Morostomatinae Dolin, 2000**
- **Negastriinae Nakane & Kishii, 1956**
  - Negastriini Nakane & Kishii, 1956
  - Quasimusini Schimmel & Tarnawski, 2009
    - Loebliquasimusina Schimmel & Tarnawski, 2009
    - Quasimusina Schimmel & Tarnawski, 2009
    - Striatoquasimusina Schimmel & Tarnawski, 2009
    - Wittmeroquasimusina Schimmel & Tarnawski, 2009
- **Oestodinae Hyslop, 1917**
- **Parablacinae Kundrata, Gunter, Douglas & Bocak, 2016**
- **Physodactylinae Lacordaire, 1857**
- **Plastocerinae Crowson, 1972**
- **Pityobiinae Hyslop, 1917**
- **Subprotelaterinae Fleutiaux, 1920**
- **Tetralobinae Laporte, 1840**
  - Piezophyllini Laurent, 1967
  - Tetralobini Laporte, 1840
- **Thylacosterninae Fleutiaux, 1920**

chart", he highlighted the basal setae on claws in adults and mandibles without teeth in larvae as characters supporting his widely defined Pyrophorinae. Calder (1990, 1998) mentioned basal setae on claws and the absence of the wedge cell in the hind wing venation as an evidence for proposed relationships. Costa et al. (2010) also listed the two above-mentioned characters, together with a combination of a triangular postmentum, simple mandibles without retinaculum, and lightly sclerotized segments with a notched abdominal tergum IX for larvae as synapomorphies for Agrypninae including Tetralobinae.

The morphological support for Agrypninae + Tetralobinae is questionable if these character states are homoplastic. Agrypninae is defined by having at least one basally located seta on claws. However, this character is known also from the distantly related click-beetle lineages including Morostomatinae, some Dendrometrinae (e.g., *Beliophorus* Eschscholtz, 1829) and Cardiophorinae (*Tropidiplus* Fleutiaux, 1903). Furthermore, some agrypnine taxa (*Danosoma* Thomson, 1859, *Octocryptus* Candèze, 1892) do not have setae on claws. Similarly, the absence of wedge cell in the hind wing venation of Agrypninae and Cardiophorinae was considered to be an important diagnostic character e.g., by Hyslop (1917) and Crowson (1961). However, Dolin (1975) showed that this is a very unstable character present also in some Elaterinae and Dendrometrinae, and subsequent authors also reported the missing wedge cell in Negastriinae, Subprotelaterinae, *Oestodes* Leconte, 1853 (Oestodinae), and *Drapetes* Dejean, 1821 (Lissominae) (Calder 1996; Costa et al. 2010; Douglas 2011). Additionally, the 12-segmented male antennae of some Agrypninae (Hemirhipini) and Tetralobinae are known in several unrelated elaterid lineages, e.g., *Diplophoenicus* Candèze, 1895 (Morostomatinae), *Wardulupicola* Calder, 1996 (Dendrometrinae) and some Elaterinae (Odontonychini, Eudicronychini, *Euthysanius* Leconte, 1853). Regarding larvae, only mandibles without teeth on inner egde can be regarded as a synapomorphy for Agrypninae and Tetralobinae. However, the latter group contains a specialized termitophilous physogastric larvae quite distinct from typical agrypnine larvae. As larval stages of many elaterids are unknown (Stibick 1979; Costa et al. 2010), we cannot exclude the possibility that also some other, yet undescribed, elaterid larvae possess unidentate mandibles. Therefore, there is no unambiguous morphological support for the close relationships between Agrypninae and Tetralobinae.

In previous phylogenetic analyses based on the combination of adult and larval morphological characters, Calder et al. (1993) found *Pseudotetralobus* always unrelated to Agrypninae. Douglas (2011) analyzed only adult characters and recovered *Tetralobus* either as an unrelated taxon or a sister to Agrypninae, but neither relationships obtained sufficient statistical support. However, both studies focused on different classification issues in the Elateridae (Lissominae and Cardiophorinae, respectively), and taxon sampling was limited. Here, our results demonstrate that Tetralobinae is not closely related to

Agrypninae, and the Agrypninae minus Tetralobinae obtained strong statistical support (> 90% BV in ML analyses, 100% PP in BI analyses; Figs. 1, S1, S2). The independent positions of Agrypninae and Tetralobinae are further supported by several unique phenotypic traits in the latter: the anterior part of frons excavated and forms a thick projecting pad, mandibles with tuft of setae located in a dorso-lateral pit, metacoxal plates meeting epipleura, the epipleura distally open, radial cell in the hind wing elongate, with the long cross-vein r3, lobed tarsomeres I – IV, male genitalia with the partly membranous median lobe, which looks like a sheath, female genitalia with the omega-like sclerite in genital tract, and physogastric larva which constructs pupal cocoons. Furthermore, many Tetralobini exhibit unique characters such as 12-segmented flabellate male antennae, almost smooth elytra, and multisetose empodium. The conspicuously widened metanepisternum in Tetralobini and metaventrite with the elevated, V-shaped anterior margin in Piezophyllini are also unique for this subfamily (Costa et al. 1994). These characters define some small clades but do not contribute to the phylogenetic inference at deeper levels.

Molecular data provide independent source of information for phylogenetic inference. Neither source of data can be considered superior but the commonly identified conflict should be closely investigated. When some morphological traits indicate conflicting topologies, it is worth to study such characters in detail and identify if these characters are stable within the group and if the same character states are present also in other lineages. Multiple origin of some characters in unrelated click-beetles might indicate their homoplastic origin and if they are used for definition of higher taxa they might produce misleading classifications. The detailed history of elaterid classification was summarized by Costa et al. (2010). Within the clicking elateroids, the homology of multiple characters, both larval and adult, was questioned by Muona (1995) and Calder et al. (1993). For example, elaterid lineages such as Agrypninae: Drilini and Elaterinae: Cebrionini, which are both morphologically affected by the incomplete metamorphosis of females, were long considered to be separate families (see Kundrata & Bocak 2011). Additionally, many elaterid lineages have been defined only be plesiomorphic characters which do not provide an evidence for monophyly although they might be used as diagnostic characters. Numerous taxa were placed in various tribes and subfamilies in alternative classifications (Costa et al. 2010). Recent molecular studies show that some morphological characters, e.g., the shapes of frontoclypeal region, scutellum and tarsal claws, commonly used for the definitions of supraspecific taxa should be re-evaluated and new diagnostic characters (if available at all) should be defined (Kundrata et al. 2016; Douglas et al. 2018).

This study is a further step towards the natural classification of Elateridae and shows that the generally accepted affiliation of Agrypninae and Tetralobinae was based on the homoplastic characters such as the absence of wedge cell in the hind wings and the presence of setae on claws. The exact position of Tetralobinae in the Elateridae phylogeny remains uncertain as no analysis to date recovers a well resolved and supported topology (Calder et al. 1993; Douglas 2011; this study). Tetralobinae are usually found among the deepest splits of Elateridae, and our study suggests their sister position to all remaining click-beetle lineages (Figs. 1, S1). Improved taxon and gene sampling should be used in future research to resolve the position of Tetralobinae and to investigate the internal relationships within the group.

5. Acknowledgements

We are very obliged to J. Halada (Czech Republic) and Y. Li (Guangzhou, China) for the fresh specimens of *Tetralobus* and *Sinelater*, respectively, and to A. Prosvirov (Moscow, Russia), I. Plonski (Vienna, Austria) and H. Douglas (Ottawa, Canada) for their help with literature. The short-term stays of RK in the Koninklijk Musem voor Midden-Afrika, Tervuren, Belgium (BE-TAF 6078), the Museum National d'Histoire Naturelle, Paris, France (FR-TAF 6701), the Naturhistorisches Museum Wien, Austria (AT-TAF 6821), and the Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany (DE-TAF 7085) were funded by the EU-SYNTHESYS grants. Support from D. VandenSpiegel (RMCA), M. Jäch (NHMW), A. Mantilleri (MNHN) and S. Blank (SDEI) is gratefully acknowledged. J. Constant, C. Locatelli (RBINS), C. Lemann (ANIC), T. Németh (HNHM), M. Motyka (UPOL, Czech Republic), and R. Wherely (Cleveland, Ohio, USA) kindly provided us with the photographs of Tetralobinae. This study was supported by the internal grant of the Faculty of Science UP (IGA_PrF_2017_023; RK, DJ), and was co-financed by the European Social Fund and the state budget of the Czech Republic (POST-UP a reg. c. CZ.1.07/2.3.00/30.0004; LB, NG).

6. References

Blanchard C.E. 1853. Description des insectes. Pp. 1 – 422 in: Hombros J., Jacquinot H. (eds), Voyage au Pole Sud et dans l'Océanie sur les corvettes l'Astrolabe et la Zélée; exécuté par ordre du Roi pendant les années 1837 – 1838 – 1839 – 1840, sous le commandement de M J Dumont d'Urville, Capitaine de vaisseau; publié par ordre du gouvernement, sous la direction supérieure de M Jacquinot, Capitaine de vaisseau, commandant de la Zélée Zoologie par MM Hombron et Jacquinot Tome quatrième. – Gide & J. Baudry, Paris.

Bocakova M., Bocak L., Hunt T., Teraväinen M., Vogler A.P. 2007. Molecular phylogenetics of Elateriformia (Coleoptera): evolution of bioluminescence and neoteny. – Cladistics **23**: 477 – 496.

Bouchard P., Bousquet Y., Davies A.E., Alonso-Zarazaga M.A., Lawrence J.F., Lyal C.H.C., Newton A.F., Reid C.A.M., Schmitt M., Ślipiński S.A., Smith A.B.T. 2011. Family-group names in Coleoptera (Insecta). – ZooKeys **88**: 1 – 972.

Calder A.A. 1990. *Anthracalaus australis* Fleutiaux, a little-known Australian elaterid (Coleoptera: Elateridae), with a key to related genera. – Invertebrate Taxonomy **3**: 551 – 563.

Calder A.A. 1996. Click Beetles: Genera of the Australian Elateridae (Coleoptera). Monographs on invertebrate taxonomy. Vol. 2. – CSIRO Publishing, Victoria, Australia. 401 pp.

Calder A.A. 1998. Coleoptera: Elateroidea. Pp. 1 – 248 in: Wells A. (ed.), Zoological Catalogue of Australia. Vol. 29.6. – CSIRO Publishing, Melbourne, Australia.

Calder A.A., Lawrence J.F., Trueman J.W.H. 1993. *Austrelater*, gen. nov. (Coleoptera: Elateridae), with a description of the larva and comments on elaterid relationships. – Invertebrate Taxonomy **7**: 1349 – 1394.

Candèze E.C.A. 1857. Monographie des Élatérides. Tome premier. – Mémoires de la Société Royale des Sciences de Liège **12**: 1 – 400.

Cate P. 2007. Elateridae. Pp. 89 – 209 in: Löbl I., Smetana A. (eds), Catalogue of Palaearctic Coleoptera. Vol. 4. – Apollo Books, Stenstrup, Denmark.

Costa C., Casari-Chen S.A., Vanin S.A. 1992. On the larvae of Tetralobini (Coleoptera, Elateridae). – Revista Brasileira de Entomologia **36**: 879 – 888.

Costa C., Lawrence J.F., Rosa S.P. 2010. Elateridae Leach, 1815. Pp. 75 – 103 in: Leschen R.A.B., Beutel R.G., Lawrence J.F. (volume eds), Coleoptera, Beetles; Volume 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim); in: Kristensen N.P., Beutel R.G. (eds), Handbook of Zoology, Arthropoda: Insecta. – Walter de Gruyter GmbH & Co. KG, Berlin/New York.

Costa C., Vanin S.A. 2010. Coleoptera larval fauna associated with termite nests (Isoptera) with emphasis on the “Bioluminescent Termite Nests“ from Central Brazil. – Psyche **2010**: 1 – 12.

Costa C., Vanin S.A., Casari-Chen S.A. 1994. Cladistic analysis and systematics of the Tetralobini sensu Stibick, 1979 (Coleoptera, Elateridae, Pyrophorinae). – Arquivos de Zoologia **32**: 111 – 157.

Crowson R.A. 1961. On some new characters of classificatory importance in adults of Elateridae (Coleoptera). – Entomologist’s Monthly Magazine **96**: 158 – 161.

Dolin V.G. 1975. Wing venation in click beetles and its significance for the taxonomy of the family. – Zoologicheskii Zhurnal **54**: 1618 – 1633.

Dolin V.G. 1978. Phylogeny of click beetles (Coleoptera: Elateridae). – Vestnik Zoologii **3**: 3 – 12.

Douglas H. 2011. Phylogenetic relationships of Elateridae inferred from adult morphology, with special reference to the position of Cardiophorinae. – Zootaxa **2900**: 1 – 45.

Douglas H., Kundrata R., Janosikova D., Bocak L. 2018. Molecular and morphological evidence for new genera in the click-beetle subfamily Cardiophorinae (Coleoptera: Elateridae). – Entomological Science, in press: doi:10.1111/ens.12306.

Felsenstein J. 2004. Inferring Phylogenies. – Sinauer Associates, Inc., Sunderland, MA, USA. 664 pp.

Fleutiaux E. 1919. Elateridae, Trixagidae et Melasidae. Voyage de Ch. Alluaud et R. Jeannel en Afrique Orientale (1911 – 1912) résultats scientifiques. Coleoptera. Vol. XIII. – L’homme, Paris. 119 pp.

Fleutiaux E. 1947. Révision des Élatérides (Coléoptères) de l’Indo-Chine Française. – Notes d’Entomologie Chinoise **11**: 233 – 420.

Froggatt W.W. 1917. Entomological notes. A remarkable click beetle (*Tetralobius fortnumi* Hope). – The Agricultural Gazette of New South Wales **28**: 894 – 895.

Girard C. 1971. Les Coléoptères Elateridae de Lamto (Côte d’Ivoire). – Bulletin de l’Institut Fondamental d’Afrique Noire **33**: 549 – 650.

Girard C. 1979. Contribution a l’étude des *Tetralobus* de l’Éthiopie (Coleoptera Elateridae Tetralobinae). – Revue Française d’Entomologie (N.S.) **1**: 174 – 178.

Girard C. 1987. Un Tetralobinae afrotropical nouveau: *Neotetralobus africanus* nov. gen., n. sp. (Coleoptera, Elateridae). – Annales de la Société Entomologique de France (N.S.) **23**: 49 – 52.

Girard C. 2003. Étude des peuplements d’Elateridae (Coleoptera) de la région du mont Nimba et descriptions de taxons nouveaux. In: Lamotte M., Roy R. (eds), Le peuplement animal du mont Nimba (Guinée, Côte d’Ivoire, Liberia). – Mémoires du Muséum National d’Histoire Naturelle **190**: 393 – 549.

Girard C. 2016. Six Elateridae nouveaux de l’Afrique intertropicale (Coleoptera). – Bulletin de la Société Entomologique de France **121**: 225 – 232.

Girard C., Costa C., Rosa S.P. 2007. Présence insolite de larves et de nymphes de *Tetralobus* (Coleoptera: Elateridae), dans des termitières mortes de *Macrotermes* (Isoptera): données sur la morphologie et la bionomie de larves et de nymphes de trois espèces. – Annales de la Sociéte Entomologique de France (N.S.) **43**: 49 – 56.

Gunter N.L., Leavengood J.M., Bartlett J.S., Chapman E.G., Cameron S.L. 2013. A molecular phylogeny of the checkered beetles and a description of Epiclininae a new subfamily (Coleoptera: Cleroidea: Cleridae). – Systematic Entomology **38**: 626 – 636.

Gunter N.L., Weir T.A., Ślipiński S.A., Bocak L., Cameron S.L. 2016. If dung beetles (Scarabaeidae: Scarabaeinae) arose in association with dinosaurs, did they also suffer a mass co-extinction at the K-Pg boundary? – PLoS ONE **11**: e0153570.

Gur’yeva Y.L. 1974. Thoracic structure of click beetles (Coleoptera, Elateridae) and the significance of the structural characters for the system of the family. – Entomologicheskoe Obozrenie **53**: 96 – 113.

Han T., Lee W., Lee S., Park I.G., Park H. 2016. Reassessment of species diversity of the subfamily Denticollinae (Coleoptera: Elateridae) through DNA Barcoding. – PLoS ONE **11**: e0148602.

Hayek C.M.F. 1974. On some Coleoptera Elateridae from East Africa. – Monitore Zoologico Italiano, Supplemento **5**: 91 – 99.

Hope F.W. 1842. A monograph on the coleopterous family Phyllophoridae. – Proceedings of the Zoological Society of London **10**: 73 – 79.

Huelsenbeck J.P., Ronquist F. 2001. MRBAYES: Bayesian inference of phylogenetic trees. – Bioinformatics **17**: 754 – 755.

Hyslop J.A. 1917. The phylogeny of the Elateridae based on larval characters. – Annals of the Entomological Society of America **10**: 241 – 263.

Jamal A. 1994. Major insect pests of gum arabic trees *Acacia senegal* Willd. and *Acacia seyal* L. in Western Sudan. – Journal of Applied Entomology **117**: 10 – 20.

Johnson P.J. 2002. Elateridae Leach 1815. Pp. 160 – 173 in: Arnett R.H., Thomas M.C., Skelley P.E., Frank J.H. (eds), American Beetles, Vol. 2. – Boca Raton, FL, CRC.

Katoh K., Misawa K., Kuma K., Miyata T. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. – Nucleic Acids Research **30**: 3059 – 3066.

Katoh K., Standley D.M. 2013. MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability. – Molecular Biology and Evolution **30**: 772 – 780.

Kearse M., Moir R., Wilson A., Stones-Havas S., Cheung M., Sturrock S., Buxton S., Cooper A., Markowitz S., Duran C., Thierer T., Ashton B., Mentjies P., Drummond A. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. – Bioinformatics **28**: 1647 – 1649.

Kubaczkova M., Kundrata R. 2017. Annotated catalogue of the click-beetle subfamily Tetralobinae (Coleoptera: Elateridae). – Zootaxa **4323**: 151 – 184.

Kundrata R., Bocak L. 2011. The phylogeny and limits of Elateridae (Insecta, Coleoptera): is there a common tendency of click beetles to soft-bodiedness and neoteny? – Zoologica Scripta **40**: 364 – 378.

Kundrata R., Bocakova M., Bocak L. 2014. The comprehensive phylogeny of the superfamily Elateroidea (Coleoptera: Elateriformia). – Molecular Phylogenetics and Evolution **76**: 162 – 171.

Kundrata R., Gunter N.L., Douglas H., Bocak L. 2016. Next step toward a molecular phylogeny of click-beetles (Coleoptera: Elateridae): redefinition of Pityobiinae, with a description of a new subfamily, Parablacinae, from the Australasian Region. – Austral Entomology **55**: 291 – 302.

Lacordaire J.T. 1857. Histoire naturelle des Insectes. Genera des Coléoptères ou exposé méthodique et critique de tous les genres proposés jusqu’ici dans cet ordre d’insectes. Tome quatrième contenant les familles des Buprestides, Throscides, Eucnémides, Élatérides, Cébrionides, Cérophytides, Rhipicérides, Dascyllides, Malacodermes, Clérides, Lyméxylones, Cupésides, Ptinio res, Bostrichides et Cissides. – Librairie Encyclopédique de Roret, Paris. 579 pp.

Lanfear R., Calcott B., Ho S.Y.W., Guindon S. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. – Molecular Biology and Evolution **29**: 1695 – 1701.

Laporte F.L.N.C. 1840. Histoire naturelle des insectes Coléoptères. Avec une introduction renfermant l’anatomie et la physiologie des animaux articulés, par M. Brullé. Tome premier. Histoire naturelle des animaux articulés, annelides, crustacés, arachnides, myriapodes et insectes. – P. Duménil, Paris. 324 pp.

Laurent L. 1964a. Tetralobinae de la région Aethiopienne (Coleoptera Elateridae). – Bulletin de la Société Royale des Sciences de Liège **33**: 214 – 238.

Laurent L. 1964b. Tetralobinae de la région Aethiopienne (Coleoptera Elateridae). – Bulletin de la Société Royale des Sciences de Liège **33**: 354 – 372.

Laurent L. 1964c. Tetralobinae de la région Aethiopienne (Coleoptera Elateridae). – Bulletin de la Société Royale des Sciences de Liège **33**: 495 – 506.

Laurent L. 1964d. Tetralobinae de la région Aethiopienne (Coleoptera Elateridae). – Bulletin de la Société Royale des Sciences de Liège **33**: 857 – 877.

Laurent L. 1965a. Tetralobinae de la région Aethiopienne (Coleoptera Elateridae). – Bulletin de la Société Royale des Sciences de Liège **34**: 669 – 685.

Laurent L. 1965b. Oxynopterinae et Tetralobinae de l’Angola (Coleoptera, Elateridae). – Museu do Dundo, subsídios para o estudo da biologia na Lunda **28**: 35 – 40.

Laurent L. 1967. La sous-famille Tetralobinae (Coleoptera, Elateridae). – Bulletin & Annales de la Société Royale d’Entomologie de Belgique **103**: 83 – 109.

Laurent L. 1968. Un nouveau sous-genre de *Tetralobus* (Coleoptera Elateridae). – Bulletin des Recherches Agronomiques de Gembloux **3**: 328 – 330.

Lawrence J.F., Newton A.F. 1995. Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). Pp. 779 – 1083 in: Pakaluk J., Ślipiński A. (eds), Biology, Phylogeny, and Classification of Coleoptera. Papers Celebrating the 80th Birthday of Roy A. Crowson. Volumes 1 – 2. – Muzeum i Instytut Zoologii PAN, Warszawa.

Miller M.A., Pfeiffer W., Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. – Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010. New Orleans, LA.

Muona J. 1995. The phylogeny of Elateroidea (Coleoptera), or which tree is the best today? – Cladistics **11**: 317 – 341.

Neboiss A. 1956. A check list of Australian Elateridae (Coleoptera). – Memoirs of the National Museum of Victoria **22**: 1 – 75.

Neboiss A. 1961. Additions and corrections to the check list of Australian Elateridae (Coleoptera). – Memoirs of the National Museum of Victoria **22**: 1 – 29.

Quedenfeldt G. 1886. Verzeichniss der von Herrn Major a. D. von Mechow in Angola und am Quango-Strom 1878 – 1881 gesammelten Buprestiden und Elateriden. – Berliner Entomologische Zeitschrift **30**: 1 – 38.

Rambaut A. 2009. FigTree 1.3.1. – Available at http://tree.bio.ed.ac.uk/software/figtree/.

Rambaut A., Drummond A.J. 2007. Tracer 1.5. – Institute of Evolutionary Biology University of Edinburgh, Edinburgh. – Available at http://beast.bio.ed.ac.uk/Tracer.

Rosa S.P., Albertoni F.F., Bená D.C. 2015. Description of the immature stages of *Platycrepidius dewynteri* Chassain (Coleoptera, Elateridae, Agrypninae, Platycrepidiini) from Brazil with a synopsis of the larval characters of Agrypninae tribes. – Zootaxa **3914**: 318 – 330.

Sagegami-Oba R., Oba Y., Ôhira H. 2007. Phylogenetic relationships of click beetles (Coleoptera: Elateridae) inferred from 28S ribosomal DNA: Insights into the evolution of bioluminescence in Elateridae. – Molecular Phylogenetics and Evolution **42**: 410 – 421.

Schenkling S. 1925. Elateridae I. Pp. 1 – 263 in: Schenkling S. (ed.), Coleopterorum Catalogus. Pars 80. – W. Junk, Berlin.

Schwarz O. 1906. Coleoptera. Fam. Elateridae. Pp. 1 – 370 in: Wytsman P. (ed.), Genera Insectorum. Fascicule 46. – P. Wytsman, Bruxelles.

Stamatakis A. 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. – Bioinformatics **22**: 2688 – 2690.

Stamatakis A., Hoover P., Rougemont J. 2008. A rapid bootstrap algorithm for the RAxML web servers. – Systematic Biology **57**: 758 – 771.

Stibick J.N.L. 1979. Classification of the Elateridae (Coleoptera). Relationships and classification of the subfamilies and tribes. – Pacific Insects **20**: 145 – 186.

Suzuki W. 2002. Notes on two elaterid beetles of the genus *Pseudotetralobus* (Coleoptera, Elateridae) from New Guinea and Halmahera Islands. – Elytra **30**: 183 – 188.

Van Zwaluwenburg R.H. 1959. Some type designations, with notes on Pacific Elateridae (Coleoptera). – Pacific Insects **1**: 347 – 414.

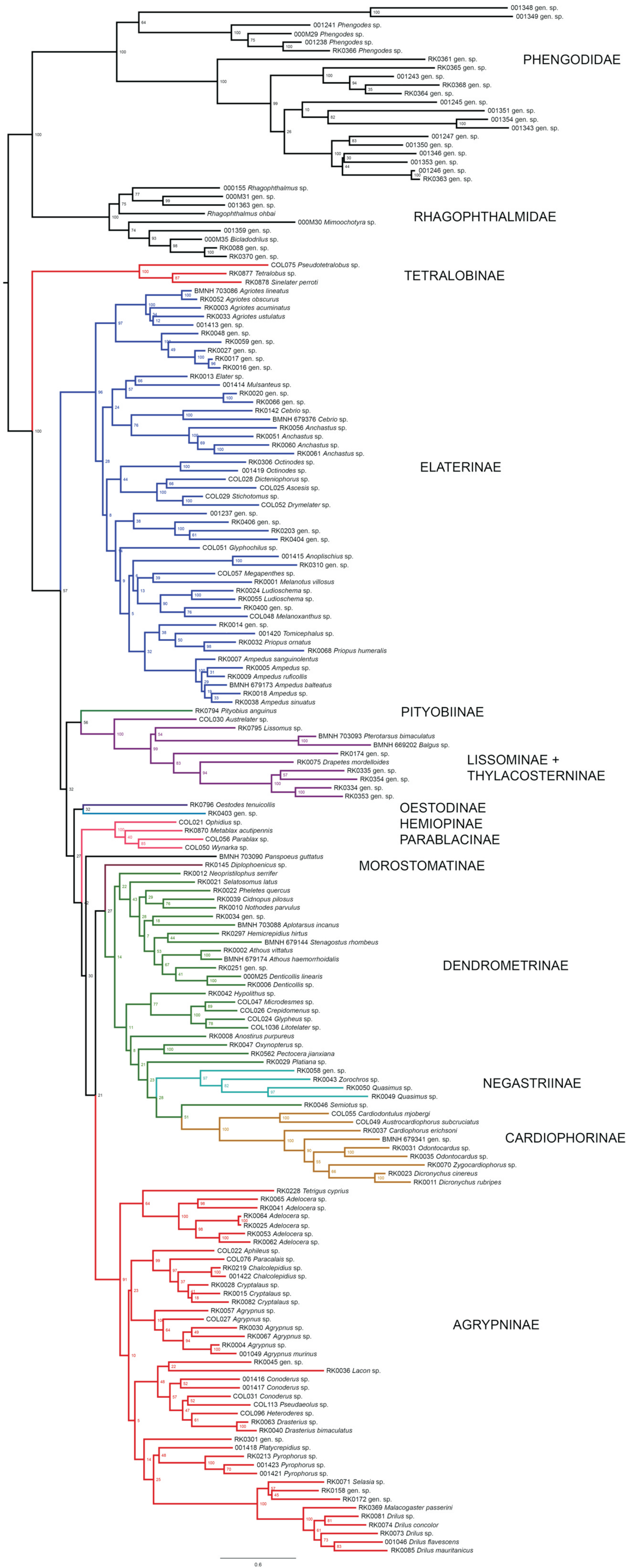
Electronic Supplement Files

at http://www.senckenberg.de/arthropod-systematics

File 1: kundrata&al-tetralobinae-asp2018-electronicsupplement-1.pdf — **Fig. S1**. Phylogenetic hypothesis for Elateridae, resulting from the ML analysis of concatenated Mafft alignment of four molecular markers (18S rRNA, 28S rRNA, *rrnL* mtDNA and *cox1* mtDNA) for 181 terminals. Values at branches indicate ML bootstrap support.

File 2: kundrata&al-tetralobinae-asp2018-electronicsupplement-2.pdf — **Fig. S2**. Phylogenetic hypothesis for Elateroidea, resulting from the ML analysis of concatenated Mafft alignment of four molecular markers (18S rRNA, 28S rRNA, *rrnL* mtDNA and *cox1* mtDNA) for 451 terminals. Values at branches indicate ML bootstrap support.

File 3: kundrata&al-tetralobinae-asp2018-electronicsupplement-3.doc — **Table S1.** List of Tetralobinae species examined in this study.


001348 gen. sp.
001349 gen. sp.
001241 *Phengodes* sp.
000M29 *Phengodes* sp.
001238 *Phengodes* sp.
RK0366 *Phengodes* sp.
RK0361 gen. sp.
RK0365 gen. sp.
001243 gen. sp.
RK0368 gen. sp.
RK0364 gen. sp.
001245 gen. sp.
001351 gen. sp.
001354 gen. sp.
001343 gen. sp.
001247 gen. sp.
001350 gen. sp.
001346 gen. sp.
001353 gen. sp.
001246 gen. sp.
RK0363 gen. sp.
PHENGODIDAE
000155 *Rhagophthalmus* sp.
000M31 gen. sp.
001363 gen. sp.
Rhagophthalmus ohbai
000M30 *Mimoochotyra* sp.
001359 gen. sp.
000M35 *Bicladodrilus* sp.
RK0088 gen. sp.
RK0370 gen. sp.
RHAGOPHTHALMIDAE
COL075 *Pseudotetralobus* sp.
RK0877 *Tetralobus* sp.
RK0878 *Sinelater perroti*
TETRALOBINAE
BMNH 703086 *Agriotes lineatus*
RK0052 *Agriotes obscurus*
RK0003 *Agriotes acuminatus*
RK0033 *Agriotes ustulatus*
001413 gen. sp.
RK0048 gen. sp.
RK0059 gen. sp.
RK0027 gen. sp.
RK0017 gen. sp.
RK0016 gen. sp.
RK0013 *Elater* sp.
001414 *Mulsanteus* sp.
RK0020 gen. sp.
RK0066 gen. sp.
RK0142 *Cebrio* sp.
BMNH 679376 *Cebrio* sp.
RK0056 *Anchastus* sp.
RK0051 *Anchastus* sp.
RK0060 *Anchastus* sp.
RK0061 *Anchastus* sp.
RK0306 *Octinodes* sp.
001419 *Octinodes* sp.
COL028 *Dicteniophorus* sp.
COL025 *Ascesis* sp.
COL029 *Stichotomus* sp.
COL052 *Drymelater* sp.
001237 gen. sp.
RK0406 gen. sp.
RK0203 gen. sp.
RK0404 gen. sp.
COL051 *Glyphochilus* sp.
001415 *Anoplischius* sp.
RK0310 gen. sp.
COL057 *Megapenthes* sp.
RK0001 *Melanotus villosus*
RK0024 *Ludioschema* sp.
RK0055 *Ludioschema* sp.
RK0400 gen. sp.
COL048 *Melanoxanthus* sp.
RK0014 gen. sp.
001420 *Tomicephalus* sp.
RK0032 *Priopus ornatus*
RK0068 *Priopus humeralis*
RK0007 *Ampedus sanguinolentus*
RK0005 *Ampedus* sp.
RK0009 *Ampedus ruficollis*
BMNH 679173 *Ampedus balteatus*
RK0018 *Ampedus* sp.
RK0038 *Ampedus sinuatus*
ELATERINAE
RK0794 *Pityobius anguinus*
PITYOBIINAE
COL030 *Austrelater* sp.
RK0795 *Lissomus* sp.
BMNH 703093 *Pterotarsus bimaculatus*
BMNH 669202 *Balgus* sp.
RK0174 gen. sp.
RK0075 *Drapetes mordelloides*
RK0335 gen. sp.
RK0354 gen. sp.
RK0334 gen. sp.
RK0353 gen. sp.
LISSOMINAE +
THYLACOSTERNINAE
RK0796 *Oestodes tenuicollis*
RK0403 gen. sp.
COL021 *Ophidius* sp.
RK0870 *Metablax acutipennis*
COL056 *Parablax* sp.
COL050 *Wynarka* sp.
OESTODINAE
HEMIOPINAE
PARABLACINAE
BMNH 703090 *Panspoeus guttatus*
RK0145 *Diplophoenicus* sp.
MOROSTOMATINAE
RK0012 *Neopristilophus serrifer*
RK0021 *Selatosomus latus*
RK0022 *Pheletes quercus*
RK0039 *Cidnopus pilosus*
RK0010 *Nothodes parvulus*
RK0034 gen. sp.
BMNH 703088 *Aplotarsus incanus*
RK0297 *Hemicrepidius hirtus*
BMNH 679144 *Stenagostus rhombeus*
RK0002 *Athous vittatus*
BMNH 679174 *Athous haemorrhoidalis*
RK0251 gen. sp.
000M25 *Denticollis linearis*
RK0006 *Denticollis* sp.
RK0042 *Hypolithus* sp.
COL047 *Microdesmes* sp.
COL026 *Crepidomenus* sp.
COL024 *Glypheus* sp.
COL1036 *Litotelater* sp.
RK0008 *Anostirus purpureus*
RK0047 *Oxynopterus* sp.
RK0562 *Pectocera jianxiana*
RK0029 *Platiana* sp.
DENDROMETRINAE
RK0058 gen. sp.
RK0043 *Zorochros* sp.
RK0050 *Quasimus* sp.
RK0049 *Quasimus* sp.
NEGASTRIINAE
RK0046 *Semiotus* sp.
COL055 *Cardiodontulus mjobergi*
COL049 *Austrocardiophorus subcruciatus*
RK0037 *Cardiophorus erichsoni*
BMNH 679341 gen. sp.
RK0031 *Odontocardus* sp.
RK0035 *Odontocardus* sp.
RK0070 *Zygocardiophorus* sp.
RK0023 *Dicronychus cinereus*
RK0011 *Dicronychus rubripes*
CARDIOPHORINAE
RK0228 *Tetrigus cyprius*
RK0065 *Adelocera* sp.
RK0041 *Adelocera* sp.
RK0064 *Adelocera* sp.
RK0025 *Adelocera* sp.
RK0053 *Adelocera* sp.
RK0062 *Adelocera* sp.
COL022 *Aphileus* sp.
COL076 *Paracalais* sp.
RK0219 *Chalcolepidius* sp.
001422 *Chalcolepidius* sp.
RK0028 *Cryptalaus* sp.
RK0015 *Cryptalaus* sp.
RK0082 *Cryptalaus* sp.
RK0057 *Agrypnus* sp.
COL027 *Agrypnus* sp.
RK0030 *Agrypnus* sp.
RK0067 *Agrypnus* sp.
RK0004 *Agrypnus* sp.
001049 *Agrypnus murinus*
AGRYPNINAE
RK0045 gen. sp.
RK0036 *Lacon* sp.
001416 *Conoderus* sp.
001417 *Conoderus* sp.
COL031 *Conoderus* sp.
COL113 *Pseudaeolus* sp.
COL096 *Heteroderes* sp.
RK0063 *Drasterius* sp.
RK0040 *Drasterius bimaculatus*
RK0301 gen. sp.
001418 *Platycrepidius* sp.
RK0213 *Pyrophorus* sp.
001423 *Pyrophorus* sp.
001421 *Pyrophorus* sp.
RK0071 *Selasia* sp.
RK0158 gen. sp.
RK0172 gen. sp.
RK0369 *Malacogaster passerini*
RK0081 *Drilus* sp.
RK0074 *Drilus concolor*
RK0073 *Drilus* sp.
001046 *Drilus flavescens*
RK0085 *Drilus mauritanicus*
0.6


OUTGROUP
BUPRESTOIDEA
BYRRHOIDEA
ARTEMATOPODIDAE
OMETHIDAE
EUCNEMIDAE
THROSCIDAE
CEROPHYTIDAE
LYCIDAE
LAMPYRIDAE
CANTHARIDAE
OMALISIDAE
RHAGOPHTHALMIDAE
PHENGODIDAE
Negastriinae
Lissominae
Tetralobinae
Cardiophorinae
Morostomatinae
ELATERIDAE
Elaterinae
Dendrometrinae
Agrypninae

Table S1. A list of Tetralobinae species examined in this study.
ANIC - Australian National Insect Collection, CSIRO, Canberra, Australia; HNHM - Hungarian Natural History Museum, Budapest, Hungary; MNHN - Museum National d'Histoire Naturelle, Paris, France; NHMW - Naturhistorisches Museum, Vienna, Austria; RMCA - Royal Museum for Central Africa, Tervuren, Belgium; SDEI - Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany.

Subfamily Tetralobinae Candèze, 1857

Tribe Tetralobini Candèze, 1857

Genus *Neotetralobus* Girard, 1987

Neotetralobus africanus Girard, 1987
Holotype + 2 paratypes (MNHN)

Genus *Paratetralobus* Laurent, 1964a

Paratetralobus hemirhipoides (Fleutiaux, 1919)
Holotype + 8 paratypes (MNHN), determined material (HNHM, MNHN, RMCA)

Genus *Pseudalaus* Laurent, 1967

Pseudalaus dohrni (Candèze, 1881)
Determined material (MNHN, RMCA, SDEI)

Genus *Pseudotetralobus* Schwarz, 1902

Pseudotetralobus australasiae (Gory, 1836)
Determined material (ANIC, MNHN, SDEI)

Pseudotetralobus capucinus (Candèze, 1881)
Paralectotype (MNHN)

Pseudotetralobus corrosus (Candèze, 1878b)
Determined material (HNHM, MNHN, SDEI)

Pseudotetralobus fortnumi (Hope, 1842)
Determined material (MNHN, SDEI)

Pseudotetralobus murrayi (Candèze, 1857)
Determined material (MNHN, SDEI)

Pseudotetralobus pumilus (Candèze, 1893)
Determined material (MNHN)

Pseudotetralobus quadrifoveatus (Macleay, 1888)
Lectotype + paralectotype (ANIC), determined material (ANIC, HNHM, SDEI)

Pseudotetralobus thoracius (Blackburn, 1890)
Determined material (MNHN)

Genus *Sinelater* Laurent, 1967

Sinelater perroti (Fleutiaux, 1940)
Holotype + paratype (MNHN), determined material (MNHN, NHMW)

Genus *Tetralobus* Lepeletier & Audinet-Serville, 1828

Tetralobus arbonnieri Girard, 2003
Holotype (MNHN), determined material (MNHN, RMCA)

Tetralobus auratilis Schwarz, 1903
Lectotype + 2 paralectotypes (SDEI), determined material (MNHN, RMCA)

Tetralobus auricomus Hope, 1842
Determined material (MNHN, RMCA, SDEI)

Tetralobus auripilis Laurent, 1964a
Determined material (MNHN, RMCA)

Tetralobus bifoveolatus Boheman, 1851
Determined material (MNHN, RMCA)

Tetralobus candezei Fleutiaux, 1919
2 syntypes (MNHN), determined material (RMCA, SDEI)

Tetralobus cavifrons Fairmaire, 1887
Determined material (HNHM, MNHN, NHMW, RMCA, SDEI)

Tetralobus chassaini Girard, 1979
Holotype + paratype (MNHN), paratype (RMCA)

Tetralobus chevrolati Candèze, 1857
Determined material (NHMW, SDEI)

Tetralobus crassicollis Laurent, 1964a
Determined material (HNHM, MNHN, RMCA)

Tetralobus curticollis Candèze, 1893
Determined material (HNHM, MNHN, RMCA)

Tetralobus dabbenei Candèze, 1893
Determined material (HNHM, MNHN, RMCA)

Tetralobus flabellicornis (Linnaeus, 1767)
Determined material (HNHM, MNHN, NHMW, RMCA, SDEI)

Tetralobus gabunensis Schwarz, 1903
Lectotype (SDEI), determined material (HNHM, MNHN, RMCA)

Tetralobus gigas (Fabricius, 1801)
Determined material (HNHM, MNHN, RMCA, SDEI)

Tetralobus grandidieri Candèze, 1889
Holotype (MNHN), determined material (MNHN, RMCA)

Tetralobus hiekei Laurent, 1967
Determined material (MNHN, RMCA)

Tetralobus hopei Guérin-Méneville, 1847
Determined material (HNHM, NHMW, RMCA, SDEI)

Tetralobus hunti Laurent, 1964b
Determined material (HNHM, MNHN, RMCA, SDEI)

Tetralobus insularis Candèze, 1889
Lectotype (MNHN), determined material (MNHN)

Tetralobus kivuensis Laurent, 1964d
Holotype (RMCA)

Tetralobus latus Laurent, 1964b
Determined material (RMCA)

Tetralobus macari Candèze, 1889
Determined material (HNHM, MNHN, RMCA)

Tetralobus macer Laurent, 1964d
Holotype + paratype (RMCA), determined material (RMCA)

Tetralobus mechowi (Quedenfeldt, 1886)
Determined material (MNHN, RMCA, SDEI)

Tetralobus mirei Girard, 2016
Holotype + 5 paratypes (MNHN), 3 paratypes (RMCA

Tetralobus mystacinus Candèze, 1857
Determined material (HNHM, MNHN, RMCA, SDEI)

Tetralobus natalensis Candèze, 1857
Determined material (HNHM, RMCA, SDEI)

Tetralobus parallelus Schwarz, 1901
Syntype (SDEI)

Tetralobus polyphemus Boheman, 1851
Determined material (MNHN, RMCA)

Tetralobus punctatus Candèze, 1857
Determined material (MNHN, RMCA)

Tetralobus raffrayi Candèze, 1881
Determined material (HNHM, MNHN, RMCA)

Tetralobus recticollis Schwarz, 1903
Lectotype + paralectotype (SDEI), determined material (MNHN)

Tetralobus rotundifrons Guérin-Méneville, 1847
Determined material (HNHM, RMCA, SDEI)

Tetralobus rougeoti Girard, 1979
Holotype (MNHN), determined material (HNHM)

Tetralobus savagei Hope, 1842
Determined material (HNHM, MNHN, RMCA, SDEI)

Tetralobus scutellaris Schwarz, 1902
Lectotype (SDEI), determined material (MNHN, RMCA. SDEI)

Tetralobus sennaariensis Candèze, 1857
Determined material (HNHM, MNHN, SDEI)

Tetralobus shuckhardi (Hope, 1842)
Determined material (HNHM, MNHN, RMCA, SDEI)

Tetralobus sobrinus Candèze, 1889
Determined material (HNHM, MNHN, RMCA)

Tetralobus subsulcatus Guérin-Méneville, 1847
Determined material (HNHM, MNHN, RMCA, SDEI)

Tetralobus tuberculatus Laurent, 1964a
Holotype (RMCA), determined material (MNHN)

Tetralobus villosus Fleutiaux, 1918
Holotype (MNHN), determined material (HNHM, MNHN, RMCA, SDEI)

Tribe Piezophyllini Laurent, 1967

Genus *Piezophyllus* Hope, 1842

Piezophyllus benitensis Fleutiaux, 1902
Type (MNHN), determined material (MNHN, RMCA)

Piezophyllus borneensis Fleutiaux, 1902
Type (MNHN)

Piezophyllus lavaudeni Fleutiaux, 1932
2 syntypes (MNHN), determined material (MNHN, SDEI)

Piezophyllus macrocerus (Laporte, 1838)
Determined material (MNHN)

Piezophyllus spencei Hope, 1842
Determined material (MNHN, RMCA)

Příloha 7

Douglas, H., **Kundrata, R.**, Janošíková, D. & Bocák, L. (2018) Molecular and morphological evidence for new genera in the click-beetle subfamily Cardiophorinae (Coleoptera: Elateridae). *Entomological Science*, 21: 292–305.
[IF 1,069; 2 citace na WoS]
[korespondující autor; autorský podíl: 35 %]

Entomological Science (2018) **21**, 292–305 doi: 10.1111/ens.12306

ORIGINAL ARTICLE

Molecular and morphological evidence for new genera in the click-beetle subfamily Cardiophorinae (Coleoptera: Elateridae)

Hume B. DOUGLAS[1], Robin KUNDRATA[2], Dominika JANOSIKOVA[2] and Ladislav BOCAK[2]

[1]*Canadian National Collection of Insects, Arachnids and Nematodes, Agriculture and Agri-Food Canada, Ottawa, Canada and* [2]*Department of Zoology, Faculty of Science, Palacky University, Olomouc, Czech Republic*

Abstract

The Cardiophorinae is consistently at the subfamily rank in recent classifications. Conversely, generic limits and relationships remain unstable. Here, we use two nuclear (18S and 28S) and three mitochondrial (*rrnL*, *cox1–3′* and *cox1–5′*) markers to test phylogenetic hypotheses for the Cardiophorinae. We investigate the positions of *Paracardiophorus buettikeri* Chassain from the Arabian Peninsula and a simple-clawed Argentinian *Horistonotus* Candèze species, neither of which matches the diagnoses of their assigned genera. Additionally, we test the monophyly of the widely defined *Cardiophorus* Eschscholtz by including representatives of *Cardiophorus* (*Cardiophorus*), *Cardiophorus* (*Coptostethus* Wollaston) and the former subgenus *Zygocardiophorus* Iablokoff-Khnzorian and Mardjanian. Molecular analyses recover three clades, which are also supported by morphological traits. Using inferred relationships we propose three new genera: *Arandelater* Douglas and Kundrata gen. nov., *Chassainphorus* Douglas and Kundrata gen. nov., and *Huarpelater* Douglas and Kundrata gen. nov. for *Horistonotus canescens* Steinheil, *P. buettikeri* and an undescribed species perhaps historically mistaken for *H. canescens*. *Horistonotus tumidicollis* Schwarz is synonymized under *H. canescens*. *Coptostethus* is raised from a subgenus of *Cardiophorus* to the genus level with revision of its definition. Eighteen *Cardiophorus* (*Cardiophorus*) and *Dicronychus* Brullé species are newly assigned to *Coptostethus*. All species currently included in *Coptostethus* are listed. All *Coptostethus* species from South Africa are transferred to *Cardiophorus* (*Cardiophorus*). *Huarpelater cordobae* Douglas and Kundrata sp. nov. is described, and *Horistonotus quillu* Aranda is transferred to *Huarpelater* gen. nov. The replacement name *Coptostethus cobosi* nom. nov. and comb. nov. is proposed for *Cardiophorus inflatus* Cobos. We provide diagnoses and illustrated descriptions for the new genera and their types.

Key words: *Cardiophorus*, *Coptostethus*, *Dicronychus*, flightlessness, *Horistonotus*, *Paracardiophorus*, taxonomy.

INTRODUCTION

The Cardiophorinae is an ecologically diverse subfamily of predatory, herbivorous, and pollinator Elateridae inhabiting most terrestrial biomes. It contains more than 1,200 species classified into 34 extant genera distributed in all major zoogeographic regions (Douglas 2017). Although it is among the most stable elaterid subfamilies (Hyslop 1917; Fleutiaux 1947; Dolin 1975; Stibick 1979; Johnson 2002; Costa *et al*. 2010), limits of cardiophorine genera and their relationships remain unstable (Gur'yeva 1974; Douglas 2011, 2017). Most phylogenetic analyses including Cardiophorinae were DNA-based, focused on subfamily-level relationships, and included few representatives (six spp., Sagegami-Oba *et al*. 2007; seven spp., Kundrata & Bocak 2011; nine spp., Kundrata *et al*. 2016). Douglas (2011) was the first to test the phylogenetic position and monophyly of Cardiophorinae using adult morphology.

Correspondence: Robin Kundrata, Department of Zoology, Faculty of Science, Palacky University, 17. Listopadu 50, 771 46 Olomouc, Czech Republic.
Email: robin.kundrata@upol.cz
http://zoobank.org/References/8FC58FDE-95F5-4E73-BB4D-E1636734A0A4
Reproduced with the permission of the Minister of Agriculture and Agri-Food.

Received 21 September 2017; accepted 24 January 2018; first published 23 March 2018.

Douglas (2017) revised the genus level classification, providing diagnoses and a key to genera. While Douglas' morphological analysis of adult Cardiophorinae indicated that many genera were non-monophyletic, the resulting trees did not allow establishment of monophyletic genera for many species. Because DNA-based phylogenetic analyses have brought taxonomic resolution to some Elateridae (e.g. Kundrata *et al.* 2016), molecular markers were expected to improve resolution of the Cardiophorinae.

Recently, we have identified several taxa that do not fit diagnoses of the existing genera. Chassain (1979) suggested that *Paracardiophorus buettikeri* Chassain, 1979 did not belong to *Paracardiophorus* Schwarz. Some South American *Horistonotus* including *H. canescens* Steinheil, 1874 have simple tarsal claws, a character state contradicting the diagnosis of the genus *Horistonotus* Candèze (Douglas 2017). To test their positions within the Cardiophorinae, we sequenced DNA of two nuclear (18S and 28S) and three mitochondrial (*rrnL*, *cox1–3′* and *cox1–5′*) markers for representatives of *Horistonotus* and *Paracardiophorus*. We also sequenced and examined representatives of the nominate subgenus of *Cardiophorus* Eschscholtz, the subgenus *Coptostethus* Wollaston, and *Zygocardiophorus* Iablokoff-Khnzorian and Mardjanian (a former subgenus of *Cardiophorus*) to test the monophyly of the broadly defined genus *Cardiophorus*. The results of these analyses are applied to the classification of Cardiophorinae.

MATERIALS AND METHODS

Taxon sampling and laboratory methods

We report here 12 newly sequenced representatives of Cardiophorinae from the Nearctic, Neotropical, and western Palaearctic regions. In our study, we included representative specimens of the type species for *Cardiophorus*, *Paracardiophorus*, and *Zygocardiophorus*. For *Horistonotus* and *Coptostethus*, we sequenced specimens morphologically similar to their respective type species. The voucher specimens are deposited in the collection of R. Kundrata, Palacky University (Olomouc, Czech Republic) (Table 1). Specimens were fixed in 96% alcohol and stored at –20°C. Whole genomic DNA was extracted using Wizard SV96 Purification System kit (Promega, Madison, WI, USA) following standard protocols. Extraction yield was measured using a NanoDrop-1000 Spectrophotometer (Thermo Fisher Scientific, Wilmington, DE, USA). The polymerase chain reaction (PCR) and cycle sequencing conditions followed Bocakova *et al.* (2007) and Kundrata and Bocak (2011); primers used are listed in Table S1. Two nuclear markers, a fragment of 18S rRNA (~1,000 bp) and the D2 loop of 28S rRNA (~640 bp), and three fragments of the mitochondrial genome, *rrnL* (~520 bp) and two non-overlapping portions of *cox1*, *cox1–3′* (723 bp) and *cox1–5′* mtDNA (658 bp), were sequenced. Sequences of the *cox1–5′* fragment were additionally generated for the already sequenced taxa to complement the matrix (Table 1). Polymerase chain reaction products were purified using PCRμ96 plates (Millipore, Bedford, MA, USA) and sequenced with the ABI 3130 Genetic Analyzer using Big Dye Terminator 1.1 Cycle Sequencing kit (Applied Biosystems, Waltham, MA, USA). GenBank accession numbers of new sequences are in Table 1.

Dataset assembling and phylogenetic analyses

Sequences were edited using Geneious 7.1.7 (Biomatters; www.geneious.com). We merged newly produced sequences with data extracted from GenBank (Table 1; Bocakova *et al.* 2007; Kundrata & Bocak 2011; Kundrata *et al.* 2014, 2016; Hendrich *et al.* 2015). We used representatives of Dendrometrinae *sensu lato* and Negastriinae as outgroups, and trees were rooted with *Diplophoenicus* Candèze (Morostomatinae) (Kundrata *et al.* 2016). Our dataset contained 41 terminal taxa for which at least four markers were available (Morostomatinae 1 sp., Dendrometrinae 15 spp., Negastriinae 4 spp. and Cardiophorinae 21 spp.; Table 1). To test the relationships of *Chassainphorus* gen. nov. with the morphologically similar genera *Ryukyucardiophorus* Ôhira and *Allocardiophorus* Ôhira, we additionally supplemented our dataset with the *cox1–5′* sequences from GenBank for the latter two (Table 1; Oba *et al.* 2015). These complete datasets are referred to as FL41 and FL43, respectively.

Sequences were aligned using Mafft 7.157 at default parameters (Katoh *et al.* 2002; Katoh & Standley 2013). Alignments of the length-invariable protein-coding *cox1* sequences were checked by amino acid translation. To evaluate the occurrence of substitution saturation in our data, we estimated the Iss statistic using an entropy-based Xia's nucleotide substitution saturation test (Xia *et al.* 2003) implemented in DAMBE 5.6.14 (Xia & Lemey 2009; Xia 2013) for each non-coding gene and each position of the protein-coding *cox1* fragments. We estimated the empirical proportion of invariant sites from the data and used 10,000 replicates on the fully resolved sites to perform the analyses. Because the 3rd codon positions in the *cox1* fragments showed substitution saturation (Table S2), we discarded these from the dataset, preparing reduced datasets RED41 and RED43. The best-fit partitioning schemes and partition-specific substitution models were tested using a greedy algorithm in

Table 1 Sequences used in this study, with GenBank and voucher numbers

		Marker					
Subfamily/genus/species	Geographic origin	18S	28S	*rrnL*	*cox1–3′*	*cox1–5′*	Specimen voucher
Morostomatinae							
Diplophoenicus sp.	Madagascar	KF625753	KF626335	KF626050	KF625454	N	UPOL RK0145
Dendrometrinae							
Anostirus purpureus	Slovakia	HQ333761	HQ333856	HQ333679	HQ333945	MG230726	UPOL RK0008
Athous vittatus	Czech Republic	HQ333755	HQ333850	HQ333674	HQ333939	MG230722	UPOL RK0002
Cidnopus pilosus	Slovakia	HQ333792	HQ333887	HQ333703	HQ333974	MG230724	UPOL RK0039
Crepidomenus sp.	Australia	KT460137	KT460151	KT460112	KT460169	N	COL026
Denticollis sp.	Japan	HQ333759	HQ333854	KF626041	HQ333943	MG230721	UPOL RK0006
Hemicrepidius hirtus	Bulgaria	KF625754	KF626340	KF626054	KF625448	N	UPOL RK0297
Hypolithus sp.	Japan	HQ333795	HQ333890	HQ333705	HQ333977	N	UPOL RK0042
Neopristilophus serrifer	Japan	HQ333765	HQ333860	HQ333682	HQ333948	N	UPOL RK0012
Nothodes parvulus	Slovakia	HQ333763	HQ333858	HQ333681	KF625443	MG230723	UPOL RK0010
Oxynopterus sp.	Philippines	HQ333800	HQ333895	HQ333710	HQ333982	MG230719	UPOL RK0047
Pectocera jianxiana	China	KT447368	KT447374	KT447365	KT447379	N	UPOL RK0562
Pheletes quercus	Czech Republic	HQ333775	HQ333870	HQ333692	HQ333958	MG230725	UPOL RK0022
Platiana sp.	Indonesia	HQ333782	HQ333877	HQ333696	HQ333964	N	UPOL RK0029
Selatosomus latus	Czech Republic	HQ333774	HQ333869	HQ333691	HQ333957	MG230720	UPOL RK0021
Semiotus sp.	Chile	HQ333799	HQ333894	HQ333709	HQ333981	N	UPOL RK0046
Negastriinae							
Hypdonus cf. *fasciatus*	Malaysia	HQ333796	HQ333891	HQ333706	HQ333978	N	UPOL RK0043
Quasimus sp.	Malaysia	HQ333802	HQ333897	HQ333712	HQ333984	MG230718	UPOL RK0049
Quasimus sp.	Malaysia	HQ333803	HQ333898	HQ333713	HQ333985	MG230716	UPOL RK0050
Zorochros sp.	Malaysia	HQ333811	HQ333906	N	HQ333992	MG230717	UPOL RK0058
Cardiophorinae							
Austrocardiophorus subcruciatus	Australia	KT460140	KT460148	KT460116	KT460177	N	COL049
Cardiodontulus mjobergi	Australia	KT460139	KT460149	KT460117	KT460181	N	COL055
Cardiophorus erichsoni	Slovakia	HQ333790	HQ333885	HQ333701	HQ333972	MG230733	UPOL RK0037
Cardiophorus gramineus	Hungary	MG230682	MG230694	MG230671	MG230706	KM452020[a]	UPOL RK0621
Cardiophorus ruficollis	Czech Republic	MG230691	MG230703	MG230679	MG230715	MG230736	UPOL RK0912
Cardiophorus ulcerosus	Italy (Sardinia)	MG230680	MG230692	MG230669	MG230704	MG230739	UPOL RK0294
Chassainphorus buettikeri	Oman	MG230689	MG230701	N	MG230713	MG230728	UPOL RK0906
Coptostethus skulei	Oman	MG230685	MG230697	MG230674	MG230709	MG230730	UPOL RK0853
Coptostethus sp.	Spain (Canary Isl.)	MG230686	MG230698	MG230675	MG230710	MG230731	UPOL RK0862
Coptostethus sp.	Spain (Canary Isl.)	MG230687	MG230699	MG230676	MG230711	MG230732	UPOL RK0863
Craspedostethus dilutus	Oman	MG230690	MG230702	MG230678	MG230714	N	UPOL RK0907
Dicronychus cinereus	Czech Republic	HQ333776	HQ333871	KF626024	HQ333959	MG230735	UPOL RK0023
Dicronychus rubripes	Slovakia	HQ333764	HQ333859	KF626023	HQ333947	MG230734	UPOL RK0011
Horistonotus cf. *simplex*	USA	MG230683	MG230695	MG230672	MG230707	MG230727	UPOL RK0834
Huarpelater cordobae	Argentina	MG230684	MG230696	MG230673	MG230708	MG230729	UPOL RK0846
Odontocardus sp.	Indonesia	HQ333784	HQ333879	KF626025	HQ333966	N	UPOL RK0031
Odontocardus sp.	Indonesia	HQ333788	HQ333883	KF626026	HQ333970	MG230737	UPOL RK0035
Paracardiophorus musculus	Hungary	MG230688	MG230700	MG230677	MG230712	MG230738	UPOL RK0889
Zygocardiophorus nigratissimus	Turkey	MG230681	MG230693	MG230670	MG230705	N	UPOL RK0512
Zygocardiophorus sp.	Morocco	HQ333823	HQ333918	HQ333730	HQ334003	N	UPOL RK0070
gen. sp.	Namibia	AF451942	DQ198739	DQ198649	DQ198571	N	BMNH 679341
Allocardiophorus nigroapicalis	Japan	N	N	N	N	KM612432[b]	Anign1

(*Continues*)

Table 1 Continued

Subfamily/genus/species	Geographic origin	Marker 18S	 28S	 *rrnL*	 *cox1–3′*	 *cox1–5′*	Specimen voucher
Ryukyucardiophorus loochooensis	Japan	N	N	N	N	KM613003[b]	RI001

[a]Chimera; the *cox1–5′* sequence for *C. gramineus* was taken from Hendrich *et al.* (2015), sample voucher GBOL_Col_FK_5380.
[b]Sequences taken from Oba *et al.* (2015).
The sequences with MG accession numbers were produced in the current study. Previously sequenced material was reported by Bocakova *et al.* (2007), Kundrata and Bocak (2011) and Kundrata *et al.* (2014, 2016). N, not available.

PartitionFinder 1.1.1 (Lanfear *et al.* 2012) under the corrected Akaike information criteria.

Maximum likelihood (ML) analyses were carried out using RAxML 8.1.24 (Stamatakis 2006) by the CIPRES web server (www.phylo.org; Miller *et al.* 2010). We applied the GTR+I+G model and the partitioning scheme as defined by PartitionFinder. Branch support was calculated using the Rapid Bootstrap algorithm (Stamatakis *et al.* 2008) with 1,000 bootstrap replicates. Bootstrap values ≥90% were considered strong nodal support. Datasets were further analyzed under Bayesian inference (BI) using MrBayes 3.2.6 (Huelsenbeck & Ronquist 2001) on the CIPRES portal (Miller *et al.* 2010), with partitioning schemes and nucleotide substitution models identified in PartitionFinder. Four chains were run for 4×10^7 generations using the Markov chain Monte Carlo method. Stationary phase and convergence were detected in Tracer 1.5 (Rambaut & Drummond 2007) and the first 20% of generations were discarded as burn-in. A 50% majority-rule consensus tree was constructed to determine the posterior probabilities from the remaining trees. Posterior probabilities ≥95% indicate strong statistical support (Felsenstein 2004). The resulting trees were visualized and edited in FigTree 1.3.1 (Rambaut 2009).

Morphology

Adult specimens from the following collections were used for a detailed morphological examination: Canadian National Collection of Insects, Arachnids, and Nematodes, Agriculture and Agri-Food Canada, Ottawa, Canada (CNCI), Muséum national d'Histoire naturelle, Paris, France (MNHN), Naturhistorisches Museum Basel, Switzerland (NHMB), collection of Robin Kundrata, Olomouc, Czech Republic (PCRK), Royal Belgian Institute of Natural Sciences (RBINS) and Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany (SDEI). Genitalia were dissected after a short treatment in 85% lactic acid. Diagnostic characters were photographed using a digital camera attached to a stereoscopic microscope. The following measurements of the type specimens were taken with an ocular micrometer on a microscope: BL, body length, measured from the anterior edge of head capsule to the apex of elytra; BW, body width, measured at the widest part of the body; EL, elytral length; WHe, width of head including eyes; WHum, width at humeri; PL, pronotal length at midline; PW, pronotal width at the widest part; Edist, minimum interocular distance at the frontal part of cranium; Ediam, maximum eye diameter in the lateral view. Specimen label data are cited verbatim. Lectotypes were designated for *Horistonotus canescens* Steinheil, 1874 and *H. tumidicollis* Schwarz, 1906 to fix species concepts. Morphological terminology follows Douglas (2017).

RESULTS

Dataset/alignment parameters

Both 41-taxa and 43-taxa aligned datasets included 3,646 homologous positions (1,003, 713, 549, 723 and 658 positions for 18S, 28S, *rrnL*, *cox1–3′* and *cox1–5′*, respectively). Datasets without 3rd codon positions of the *cox1–3′* and *cox1–5′* had 3,186 homologous positions. The full-length 41-taxa matrix contained 2,557 conserved, 1,028 variable and 882 parsimony informative characters. The reduced dataset contained 2,341 conserved, 784 variable, and 649 parsimony informative characters. For nuclear genes, nucleotide percentage composition was nearly unbiased (18S: A = 25.7, C = 23.4, T = 23.5, G = 27.3; 28S: A = 25.5, C = 23.3, T = 20.4, G = 30.9). The mitochondrial genes showed a higher AT content (*rrnL*: A = 32.0, C = 10.0, T = 40.0, G = 18.0; *cox1–3′*: A = 32.1, C = 19.0, T = 34.0, G = 14.9; *cox1–5′*: A = 28.9, C = 21.9, T = 32.8, G = 16.4). PartitionFinder identified eight partitions for the full-length datasets (18S, 28S, *rrnL* and the codon positions of *cox1* fragments as follows: 1st *cox1–3′*, 2nd *cox1–3′*, 3rd *cox1–3′* + 1st *cox1–5′*, 2nd *cox1–5′*, 3rd *cox1–5′*) as the optimal scheme, and seven partitions for the reduced datasets (each gene and codon position). The nucleotide substitution model GTR+I+G was selected for most partitions, SYM+I+G for 18S rRNA and the 1st codon position of *cox1–3′*, and SYM+G and GTR+I for the 2nd and 3rd positions of *cox1–5′*, respectively (Table S3).

Phylogenetic analyses

Full-length and reduced datasets of 41 and 43 taxa analyzed by ML and BI methods yielded very similar tree topologies and support values. In order to summarize results and congruence among analyses, we mapped support values on phylogenetic trees inferred from BI analyses of FL41 and FL43 datasets (Figs 1 and S1, respectively). We identified Negastriinae as sister to Cardiophorinae in most analyses with variable support. Cardiophorinae was always monophyletic, mostly with maximal statistical support. Analyses of the 41-taxa datasets (Fig. 1) identified three strongly supported major clades within Cardiophorinae. The first clade included simple-clawed *Horistonotus* species from Argentina (i.e. *Huarpelater* gen. nov.), true *Horistonotus*, *Paracardiophorus buettikeri* (i.e. *Chassainphorus* gen. nov.), *Austrocardiophorus* Douglas, and *Cardiodontulus* Van Zwaluwenburg. Neither *Horistonotus* nor *Paracardiophorus* was recovered as monophyletic. *Huarpelater* gen. nov. was sister to the rest of the clade, and *Chassainphorus* gen. nov. was sister to *Horistonotus*. Interrelationships within this clade were robustly supported. The second clade was formed by *Craspedostethus* Schwarz and the remaining cardiophorine lineages (third clade). The genus *Cardiophorus* was always recovered as polyphyletic, with most *Cardiophorus* sensu stricto species sister to *Odontocardus* Fleutiaux. *Cardiophorus skulei* Platia & Schimmel, 1997 formed a strongly supported clade with *Coptostethus*, and *Zygocardiophorus* was sister to the type species of *Paracardiophorus*. Analyses of the 43-taxa datasets, containing *cox1–5′* sequences of *Allocardiophorus* and *Ryukyucardiophorus*, recovered the same topology; however, with generally lower support values. Neither *Allocardiophorus* nor *Ryukyucardiophorus* formed a clade with *Chassainphorus* gen. nov. (Fig. S1).

TAXONOMY

Below we provide a shortened version of the taxonomic information for genera *Huarpelater* Douglas and Kundrata gen. nov., *Arandelater* Douglas and Kundrata gen. nov., *Chassainphorus* Douglas and Kundrata gen. nov., and *Coptostethus* Wollaston, 1854 stat. rev. The full descriptions and redescriptions of the here examined genera and species are provided in Appendix S1. Likewise, more details regarding the distribution and other relevant notes for the studied taxa are in the Appendix S1. The updated list of cardiophorine genera, with numbers of species included, is given in Table 2.

Huarpelater Douglas and Kundrata gen. nov.

(Figs 2–4)

Type species

Huarpelater cordobae Douglas and Kundrata sp. nov.

Diagnosis

Male. Antennae with sensory elements beginning on antennomere III; mandible apices bidentate. Pronotum with lateral carinae (not distinguishable from hind-angle carinae) restricted to posterior 1/4 (Fig. 3); anterior prosternal lobe not short, covering labium. Scutellar shield with anterior edge emarginate (Fig. 2), anterolateral edges straight or concave posterior to anterolateral corners. Tarsi without apically extending lobes or pads; tarsal claws each with 1 apex per side. Aedeagus with paramere apices flattened. The detailed description of this genus is given in Appendix S1.

Etymology

Named for the Huarpe people, indigenous to the Mendoza region of Argentina. Gender: masculine.

Huarpelater cordobae Douglas and Kundrata sp. nov.

(Figs 2–4)

Type material

Holotype, ♂, "ARGT. [ARGENTINA], San-Luis, Dept. Belgraus, Buan Putor, II.72, Bolle"; and with the authors' red label: "Holotype *Huarpelater cordobae* Douglas and Kundrata 2017" (CNCI). Paratype, ♂, "Argentina central [ARGENTINA, Catamarca Province], –28.21729, –65.885181, 19.12.13, leg. Aleš Buček lgt., RK0846"; and with the authors' yellow label: "Paratype *Huarpelater cordobae* Douglas and Kundrata 2017" (PCRK).

Diagnosis

Male. Antennae long, reaching to midlength of body; frons with supra-antennal carina little elevated above labrum. Pronotum slightly wider than long. Elytra with edges micro-serrate. Aedeagus with basal struts length 1.0 times median lobe length; parameres with apices flattened without apicolateral expansions (Fig. 4). Males of this species differ from those of *Huarpelater quillu* (Aranda, 2009) comb. nov. in having antennae

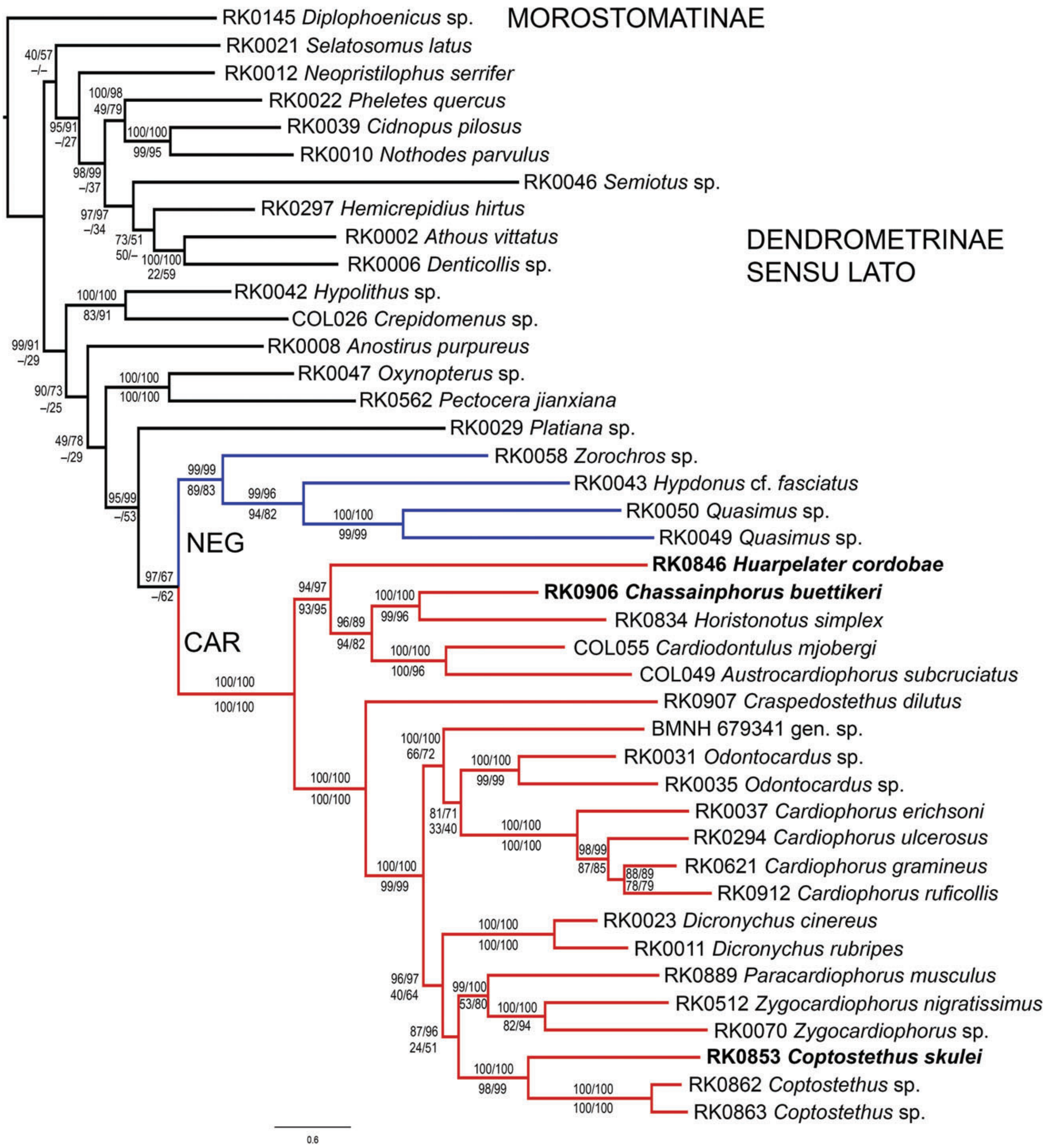


Figure 1 Phylogenetic hypothesis for Cardiophorinae based on the Bayesian inference performed on the 41-taxa dataset aligned by Mafft. Numbers at the branches indicate Bayesian posterior probabilities for the full-length dataset (upper left) and the dataset with 3rd codon positions discarded (upper right), and maximum likelihood bootstrap values for the full-length dataset (lower left) and the dataset with 3rd codon positions discarded (lower right). For taxa in bold we propose new taxonomic acts. –, Clade not recovered. CAR, Cardiophorinae; NEG, Negastriinae.

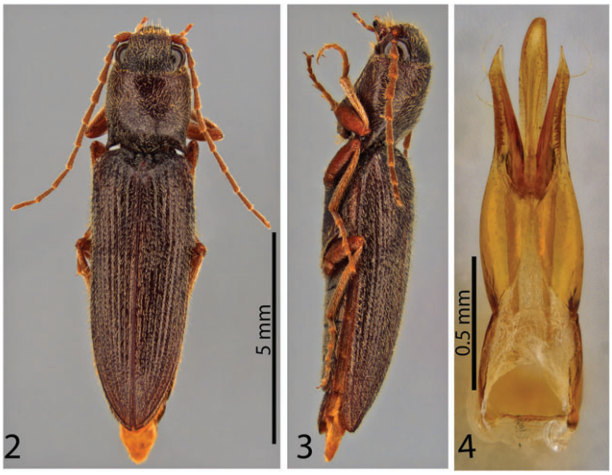
exceeding pronotal hind angles by the length of the four apical antennomeres (three in *H. quillu*) and elytral intervals costate (rounded in *H. quillu*). The detailed description of *H. cordobae* is given in Appendix S1.

Etymology

Named for Silvia Córdoba (Fundación Miguel Lillo, Tucumán, Argentina) in honor of her contributions to knowledge of Elateridae.

Table 2 List of genera and subgenera classified in Cardiophorinae, with the numbers of described species. Modified from Douglas (2017)

Extant genera	
Allocardiophorus Ôhira, 1989	2 spp.
Aphricus LeConte, 1853	8 spp.
=*Patricia* Van Zwaluwenburg, 1947	
=*Patriciella* Van Zwaluwenburg, 1953	
Aptopus Eschscholtz, 1829	35 spp.
=*Eniconyx* Horn, 1884	
Arandelater Douglas and Kundrata **gen. nov.**	1 sp.
Austrocardiophorus Douglas, 2017	59 spp.
Blaiseus Fleutiaux, 1931	10 spp.
Buckelater Costa, 1973	1 sp.
Cardiodontulus Van Zwaluwenburg, 1963	2 spp.
Cardiophorellus Cobos, 1970	
Subgenus *Cardiophorellus* Cobos, 1970	1 sp.
Subgenus *Parapleonomus* Cobos, 1970	1 sp.
Cardiophorus Eschscholtz, 1829	
=*Caloderus* Stephens, 1830	
=*Paradicronychus* Dolin and Gurjeva, 1975	
Subgenus *Cardiophorus* Eschscholtz, 1829	548 spp.
Subgenus *Lasiocerus* Buysson, 1912	2 spp.
Subgenus *Perrinellus* Buysson, 1899	12 spp.
Cardiotarsus Eschscholtz, 1836	51 spp.
Chassainphorus Douglas and Kundrata **gen. nov.**	1 sp.
Chileaphricus Douglas, 2017	1 sp.
Coptostethus Wollaston, 1854 **stat. rev.**	67 spp.
Craspedostethus Schwarz, 1898	19 spp.
=*Craspedonotus* Schwarz, 1898	
Dicronychus Brullé, 1832	114 spp.
=*Gauroderus* Thomson, 1859	
=*Paramecus* Dillwyn, 1829	
Diocarphus Fleutiaux, 1947	1 sp.
Displatynychus Ôhira, 1987	2 spp.
Esthesopus Eschscholtz, 1829	50 spp.
Floridelater Douglas, 2017	1 sp.
Globothorax Fleutiaux, 1891	3 spp.
=*Teslasena* Fleutiaux, 1892	
Horistonotus Candèze, 1860	103 spp.
Huarpelater Douglas and Kundrata **gen. nov.**	2 spp.
Margogastrius Schwarz, 1903	1 sp.
=*Gastrimargus* Schwarz, 1902	
Metacardiophorus Gurjeva, 1966	3 spp.
Neocardiophorus Gurjeva, 1966	2 spp.
Nyctor Semenov-Tian-Shanskij and Pjatakova, 1936	2 spp.
Odontocardus Fleutiaux, 1931	6 spp.
Pachyelater Lesne, 1897b	6 spp.
=*Lesnelater* Fleutiaux, 1935	
=*Parelater* Lesne, 1897	
Paracardiophorus Schwarz, 1895	54 spp.
Paraplatynychus Fleutiaux, 1931	4 spp.
Phorocardius Fleutiaux, 1931	15 spp.
Platynychus Motschulsky, 1858	18 spp.
Ryukyucardiophorus Ôhira, 1973	5 spp.
Triplonychoidus Schwarz, 1906	2 spp.
Triplonychus Candèze, 1860	17 spp.
Tropidiplus Fleutiaux, 1903	4 spp.
Zygocardiophorus Iablokoff-Khnzorian and Mardjanian, 1981	1 sp.
Extinct genus	
Mionelater Becker, 1963	1 sp.



Figures 2–4 *Huarpelater cordobae* Douglas and Kundrata sp. nov., holotype. **2** Dorsal habitus. **3** Lateral habitus. **4** Aedeagus.

Huarpelater quillu (Aranda, 2009) comb. nov.

Horistonotus quillu Aranda, 2009: 39.

Remark

This species is transferred to *Huarpelater* gen. nov. because the original description and illustrations match the diagnostic characters of this genus.

Arandelater Douglas and Kundrata gen. nov.

(Figs 5–14)

Type species

Horistonotus canescens Steinheil, 1874.

Diagnosis

Frons with supra-antennal carina forked near juncture with compound eye. Pronotum with carina along lateral edge visible in dorsal view, not reaching anterior edge. Scutellar shield with anterior edge narrowly emarginate. Tarsi non-lobed and tarsal claws with 1 apex per side. Bursa copulatrix with paired proximal (largest) sclerites elongate-ovoid with largest spines along mesal edge (Fig. 9). The detailed description of this genus is given in Appendix S1.

Etymology

Named for Dr. Susana G. Aranda (Fundación Miguel Lillo, Tucumán, Argentina) in honor of her contributions to knowledge of Elateridae. Gender: masculine.

Arandelater canescens (Steinheil, 1874) comb. nov.

Horistonotus canescens Steinheil, 1874: 568.
Horistonotus tumidicollis Schwarz, 1906: 145. Syn. nov.

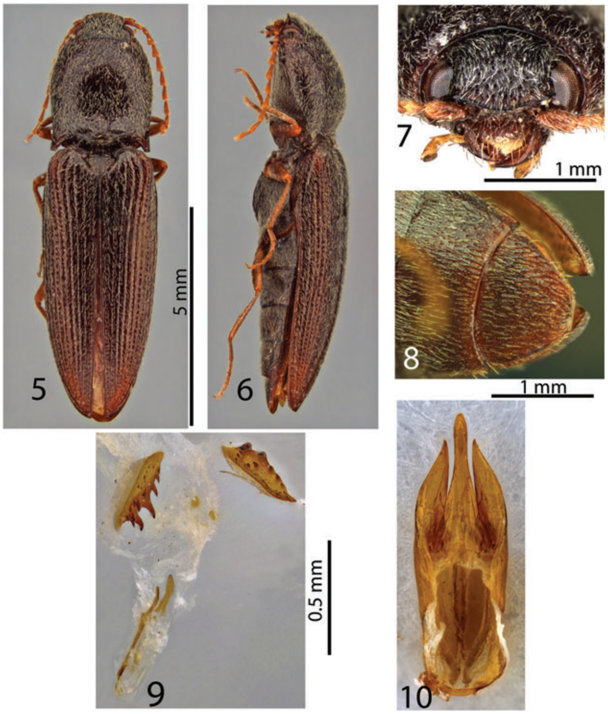
Type material

Type material of *H. canescens* (Figs 11–14). Lectotype, ♂, here designated: "[ARGENTINA] Mendoza; *Horistonotus canescens* Strobel Steinh; Ex Museo E. Steinheil; Museum Paris, 1952, coll. R. Oberthur; Syntype; Syntype *Horistonotus canescens* Steinheil; MNHN EC7462"; and with the authors' red label: "Lectotype *Horistonotus canescens* Steinheil Douglas and Kundrata 2017" (MNHN).

Type material of *H. tumidicollis* (Figs 5–10). Lectotype, ♂, here designated: "[ARGENTINA] Mendoza, Coll. Schwarz, Syntypus, DEI Müncheberg, Col-07603"; and with the authors' red label: "Lectotype *Horistonotus tumidicollis* Schwarz Douglas and Kundrata 2017" (SDEI). Paralectotype, ♀: "[ARGENTINA] Mendoza, Coll. Schwarz, Syntypus [handwritten], *tumidicollis* Schw., DEI Müncheberg, Col-07601"; and with the authors' orange label: "Paralectotype *Horistonotus tumidicollis* Schwarz Douglas and Kundrata 2017" (SDEI). Paralectotype, ♂: Labels same as for female, with number "Col-07602″ (SDEI).

Diagnosis

Male. Antennae not reaching beyond pronotal hind-angles (Figs 5,6); frons with supra-antennal carina elevated above labrum (Fig. 7), nasale concave in lateral profile (Fig. 6); aedeagus (Fig. 10) with basal struts length 0.8 times median lobe length; parameres broad basally, tapered evenly to pointed apex, without apicolateral or apicomedial expansions; median lobe slightly pedunculate, simple. The detailed redescription of *A. canescens* is given in Appendix S1.



Figures 5–10 *Arandelater canescens* (Steinheil, 1874), types of *Horistonotus tumidicollis* Schwarz, 1906. **5** Dorsal habitus. **6** Lateral habitus. **7** Frons. **8** Abdominal ventrite (V). **9** Ovipositor and sclerites of the bursa copulatrix. **10** Aedeagus.

Remark

Schwarz (1906) did not mention the very similar *H. canescens* in his description of *H. tumidicollis*. So, it seems likely that Schwarz was not aware of the similarity between *H. tumidicollis* and *H. canescens*. We propose to consider *H. tumidicollis* a junior synonym of *H. canescens* because of their seemingly identical morphology, and because *H. tumidicollis* was apparently described in error.

Chassainphorus **Douglas and Kundrata gen. nov.**

(Figs 15–17)

Type species

Paracardiophorus buettikeri Chassain, 1979.

Diagnosis

Male. Mandibles with apices bidentate. Pronotum with lateral carinae (not distinguishable from hind-angle carinae), single carina at side of pronotum reaching only to anterior half (Fig. 16), separate dorsal carina of each hind angle absent. Prosternum with anterior prosternal lobe long covering labium. Scutellar shield with anterior edge straight (Fig. 15) to narrowly emarginate. Tarsi simple; tarsal claws with 1 apex per side. Abdominal ventrites micro-serrate laterally. The detailed description of this genus is given in Appendix S1.

Etymology

The genus name combines the words "Chassain" (in honour of Jacques Chassain (Thomary, France), author of the type species for this genus) and "*Cardiophorus*" Eschscholtz (the type genus of Cardiophorinae). Gender: masculine.

Chassainphorus buettikeri **(Chassain, 1979) comb. nov.**

(Figs 15–17)

Paracardiophorus buettikeri Chassain, 1979: 210.

Type material

Holotype, ♂, "[SAUDI ARABIA] Wadi Mizbil, 13. IV.1977, W. Büttiker leg." (NHMB).

Other material studied

♂, "OMAN, Dhofar prov., Wadi Mughsayl, 120 m, 16°52′N 53°43′E, 2–3 Oct 2013, J. Halada and P. Kučera lgt., RK0906" (PCRK).

Diagnosis

Male. Supra-antennal carinae raised above frons in posterodorsal view, frons with supra-orbital grooves weak or absent. Scutellar shield with anterior edge straight to narrowly emarginate (Fig. 15). Tarsal claws simple, but swollen at base. Aedeagus narrow; parameres (Fig. 17) without apicolateral or apicomedial expansions; basal struts approximately 0.8 times median lobe length, median lobe slightly pedunculate, tapered apically. The redescription of *Ch. buettikeri* is given in Appendix S1.

Coptostethus **Wollaston, 1854 stat. rev.**

(Figs 18–24)

Coptostethus Wollaston, 1854: 238.

Type species

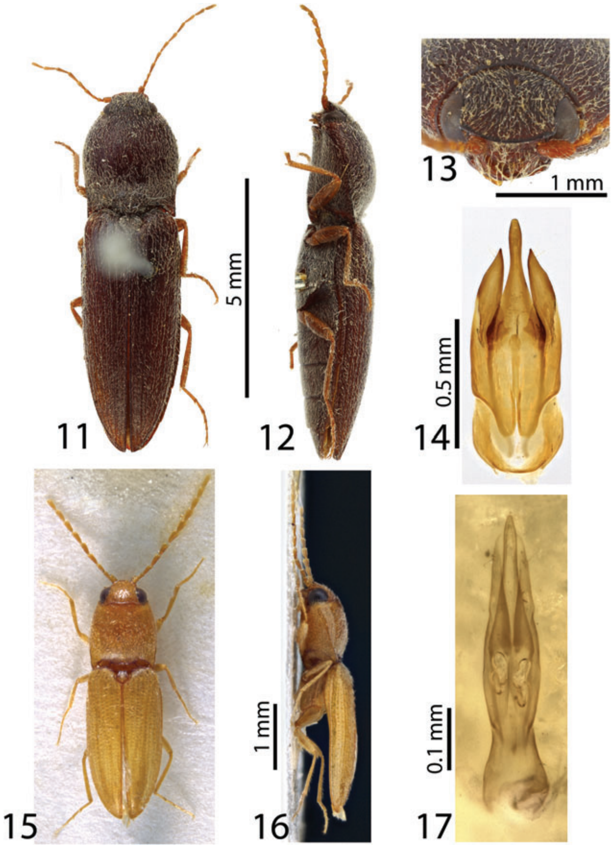
Coptostethus femoratus Wollaston, 1854: 240, by monotypy.

Diagnosis

Mandibles with apices bidentate. Pronotum with carina along lateral edge absent or hidden by edge of pronotum in dorsal view, reaching less than halfway to anterior edge. Prosternum with anterior edge not short, produced as lobe, concealing labium when head not extended. Scutellar shield with middle of anterior edge abruptly emarginate, and posterior apex pointed. No tarsomeres lobed or lamellate; tarsal claws with 1 or 2 apices per side. Urosternites III–VII with or without serrations along sides. Bursa copulatrix with proximal sclerites ovoid, each nearly bilaterally symmetrical with longest spines near midline and a median groove along midline to constricted base; spermathecal gland duct with weakly sclerotized ring-like sclerotization surrounding base. A detailed redescription of *Coptostethus* is given in Appendix S1.

Remarks

The included *Coptostethus* species are phylogenetically distant from *Cardiophorus gramineus* (Scopoli, 1763), the type species of *Cardiophorus*, and therefore *Coptostethus* should be elevated to the genus rank. Using Douglas' (2017) key, *Coptostethus femoratus* (the type species for the genus) would be keyed to *Coptostethus*, but other species to *Cardiophorus* Eschscholtz or *Dicronychus* Brullé. However, *Coptostethus* females have proximal sclerites of the bursa copulatrix with a narrow, straight-sided base and the largest spines near the midline of the sclerite. Proximal sclerites of *Cardiophorus* and *Dicronychus* are ovoid with the largest spines along one edge. *Coptostethus* females also have a ring-like sclerotization around the base of the spermathecal gland duct, which is absent from most or all *Cardiophorus* and *Dicronychus*. Dissection of females of other *Cardiophorus* and *Dicronychus* species from North Africa, West Asia and perhaps elsewhere could show that other members of these genera also belong to *Coptostethus*.



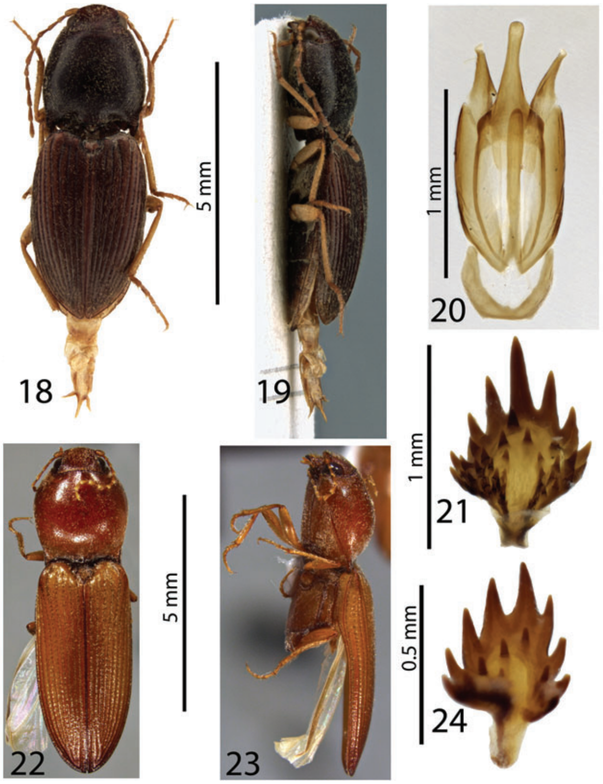
Figures 11–17 *Arandelater canescens* (Steinheil, 1874), male lectotype of *Horistonotus canescens* (**11–14**) and *Chassainphorus beuttikeri* (Chassain, 1979), male lectotype (**15–17**). **11,15** Dorsal habitus. **12,16** Lateral habitus. **13** Frons. **14,17** Aedeagus.

All available illustrations of *Coptostethus* species were examined (Cobos 1970, 1978, 1983; Németh & Platia 2014; Platia 2015a, 2015b; Platia & Kakiopoulos 2015) to identify variability in diagnostic characters in the bursa copulatrix sclerites. The following species had proximal sclerites moderate to broad (Figs 21,24), nearly symmetrical with a median groove and narrow (petiolate) base; distal sclerites fused and weakly sclerotized, and base of spermathecal gland duct surrounded by sclerotized ring: *Coptostethus buci* Németh & Platia, 2014; *C. salvatoi*

Platia in Platia & Kakiopoulos, 2015; *C. oromii* (Cobos, 1978); *C. machadoi* (Cobos, 1983); *C. vittatus* (Lindberg, 1953); *C. crassiusculus* Wollaston, 1864; *C. vestitus* Lindberg, 1953; *C. minutus* Lindberg, 1953; *C. canariensis* Wollaston, 1858; *C. hayeki* (Cobos, 1970); *C. obtusus* Wollaston, 1864: 213; *C. palmensis* (Cobos, 1970); *C. mateui* (Cobos, 1970); *C. obscurus* Wollaston, 1864. The following species differed in that the distal sclerites did not have a petiole-like base: *C. globulicollis* Wollaston, 1862; *C. brunneipennis* Wollaston, 1863; *C. mendizabili* (Cobos, 1970); *C. arozarenai* (Cobos, 1970), distal sclerites absent; *C. fernandezi* (Cobos, 1970); *C. gomerensis* (Cobos, 1970).

Species currently recognized as *Coptostethus* Wollaston, 1854

The morphological evidence (as well as the source of evidence) for transfer of species marked with "*" is given in Appendix S1. These are species not described in *Coptostethus* or *Cardiophorus* (*Coptostethus*). Species listed as "comb. nov." without an asterisk were described in *Cardiophorus* (*Coptostethus*).



Figures 18–24 *Coptostethus* sp. from Canary Islands (**18–21**) and *C. skulei* (Platia & Schimmel, 1997) comb. nov. (**22–24**). **18,22** Dorsal habitus. **19,23** Lateral habitus. **20** Aedeagus. **21,24** Proximal sclerite of bursa copulatrix.

Coptostethus abora (Wurst and Cate, 1994) **comb. nov.**; *Coptostethus aegyptiacus* (Platia in Platia & Kakiopoulos, 2015) **comb. nov.*** (from *Dicronychus aegyptiacus* Platia in Platia & Kakiopoulos, 2015: 47); *Coptostethus alepensis* (Pic, 1914) **comb. nov.*** (from *Cardiophorus alepensis* Pic, 1914: 10); *Coptostethus arozarenai* (Cobos, 1969) **comb. nov.**; *C. attilai* Németh & Platia, 2014; *Coptostethus auarita* (Liberto and Wurst, 1999) **comb. nov.**; *C. bonitaensis* Platia, 2015; *Coptostethus brancuccii* (Platia & Schimmel, 1997) **comb. nov.*** (from *Dicronychus brancuccii* Platia & Schimmel, 1997: 309); *C. brunneipennis* Wollaston, 1863; *Coptostethus buettikeri* (Platia & Schimmel, 1997) **comb. nov.*** (from *Dicronychus buettikeri* Platia & Schimmel, 1997: 310); *C. buci* Németh & Platia, 2014; *Coptostethus cabrerai* (Cobos, 1970) **comb. nov.**; *C. canariensis* Wollaston, 1858; *Coptostethus cobosi* Douglas and Kundrata, 2018 **nom. nov.** (and **comb. nov.***) (replacement name for *Cardiophorus* (*Coptostethus*) *inflatus* Cobos, 1970: 94, which is preoccupied by *Cardiophorus inflatus* Candèze, 1882: 78); *Coptostethus cobossanchezi* (Díaz de Castro and Sánchez-Ruiz, 2002) **comb. nov.**; *C. crassiusculus* Wollaston, 1864; *Coptostethus divergens* (Cobos, 1983) **comb. nov.**; *C. eggeri* Platia, 2015; *C. femoratus* Wollaston, 1854; *Coptostethus fernandezi* (Cobos, 1970) **comb. nov.**; *Coptostethus ferruginosus* (Platia & Schimmel, 1997) **comb. nov.*** (from *Dicronychus ferruginosus* Platia & Schimmel, 1997: 311); *C. globulicollis* Wollaston, 1862; *Coptostethus gomerensis* (Cobos, 1970) **comb. nov.**; *C. gracilis* Wollaston, 1864; *Coptostethus guanche* (Cobos, 1970) **comb. nov.**; *Coptostethus guayote* (Wurst and Cate, 1994) **comb. nov.**; *Coptostethus hameti* (Platia, 2015) **comb. nov.*** (from *Cardiophorus hameti* Platia, 2015a: 18); *Coptostethus hayeki* (Cobos, 1970) **comb. nov.**; *Coptostethus hierrensis* (Franz, 1980) **comb. nov.**; *Coptostethus ilniczkyi* (Németh & Platia, 2014) **comb. nov.*** (from *Dicronychus ilniczkyi* Németh & Platia, 2014: 475); *Coptostethus inflatus* (Cobos, 1970) **comb. nov.**; *Coptostethus kandaharensis* (Németh & Platia, 2014) **comb. nov.*** (from *Dicronychus kandaharensis* Németh & Platia, 2014: 477); *Coptostethus karolyvigi* (Németh & Platia, 2014) **comb. nov.*** (from *Dicronychus karolyvigi* Németh & Platia, 2014: 478); *C. kundratai* Németh & Platia, 2014; *Coptostethus larseni* (Platia & Schimmel, 1997) **comb. nov.*** (from *Dicronychus larseni* Platia & Schimmel, 1997: 312); *Coptostethus latescapulatus* (Buysson, 1906) **comb. nov.*** (from *Cardiophorus latescapulatus* Buysson, 1906: 19); *Coptostethus lindbergi* (Cobos, 1970) **comb. nov.**; *C. longicornis* Lindberg, 1953; *Coptostethus machadoi* (Cobos, 1983) **comb.**

nov.; *C. mantici* Platia, 2016; *Coptostethus mateui* (Cobos, 1970) **comb. nov.**; *Coptostethus mendizabali* (Cobos, 1970) **comb. nov.**; *C. minutus* Lindberg, 1951; *C. nemethi* Platia, 2015; *C. obscurus* Wollaston, 1864; *C. obtusus* Wollaston, 1864; *C. opaculus* Platia, 2015; *Coptostethus oromii* (Cobos, 1978) **comb. nov.**; *Coptostethus palmensis* (Cobos, 1970) **comb. nov.**; *Coptostethus paternus* (Candèze, 1889) **comb. nov.*** (from *Cardiophorus paternus* Candèze, 1889: 109); *C. petterssoni* Platia, 2015; *Coptostethus platai* (Cobos, 1979) **comb. nov.**; *Coptostethus povolnyi* (Németh & Platia, 2014) **comb. nov.*** (from *Dicronychus povolnyi* Németh & Platia, 2014: 480); *C. putzeri* Schimmel, 2008; *C. salvatoi* Platia in Platia & Kakiopoulos, 2015; *Coptostethus scapulatus* (Candèze, 1878) **comb. nov.*** (from *Cardiophorus scapulatus* Candèze, 1878: clxi); *C. selvagensis* Schimmel, 2008; *C. skoupyi* Platia, 2015; *Coptostethus skulei* (Platia & Schimmel, 1997) **comb. nov.*** (from *Cardiophorus skulei* Platia & Schimmel, 1997: 307); *Coptostethus stolatus* (Erichson, 1840) **comb. nov.*** (from *Dicronychus stolatus* Erichson, 1840: 315); *Coptostethus talhouki* (Platia & Schimmel, 1997) **comb. nov.*** (from *Dicronychus talhouki* Platia & Schimmel, 1997: 314); *Coptostethus taylori* (Cobos, 1970) **comb. nov.**; *C. vestitus* Lindberg, 1951; *C. vilaflorensis* Platia, 2015; *C. vittatus* Lindberg, 1953; *Coptostethus wittmeri* (Platia & Schimmel, 1997) **comb. nov.*** (from *Dicronychus wittmeri* Platia & Schimmel, 1997: 315); *Coptostethus wollastoni* (Cobos, 1970) **comb. nov.**

Species previously assigned to *Cardiophorus* (*Coptostethus*) and newly assigned to *Cardiophorus* (*Cardiophorus*)

Species listed as "comb. nov." were described in the genus *Coptostethus*.

Cardiophorus basilaris Candèze, 1865 [South Africa]; *Cardiophorus capensis* Laurent, 1974 [South Africa]; *Cardiophorus guttatus* (Candèze, 1865) **comb. nov.** [South Africa]; *Cardiophorus majusculus* (Candèze, 1889) **comb. nov.** [South Africa]; *Cardiophorus sexpunctatus* (Candèze, 1878) **comb. nov.** [South Africa]; *Cardiophorus tenuipes* (Candèze, 1889) **comb. nov.** [South Africa]. This includes all former *Coptostethus* species not from the islands of the eastern Atlantic Ocean west of Morocco. These species, described as *Coptostethus* because of their short wings, do not match the revised *Coptostethus*. These species are reassigned to the nominate subgenus *Cardiophorus* (*Cardiophorus*).

DISCUSSION

Here we used for the first time DNA sequences to infer the relationships within the Cardiophorinae. Our results revealed three major lineages within Cardiophorinae, all robustly supported statistically (Figs 1,S1) and morphologically diagnosable. The first lineage includes three of the five genera subjected to this analysis, that is, *Horistonotus*, *Cardiodontulus*, *Austrocardiophorus* (but not *Craspedostethus* and *Odontocardus*) that were a part of Douglas' (2017) "Southern Clade", and newly described *Chassainphorus* gen. nov. and *Huarpelater* gen. nov. The position of *Allocardiophorus* and *Ryukyucardiophorus* within this clade, despite using only a single gene fragment, is also strongly supported (Fig. S1). Representatives of this clade share bilobed or multilobed proximal sclerites (partially membranous in many, but single-lobed in *Horistonotus*) and lack distal sclerites of the bursa copulatrix. Most species have closed procoxal cavities, lack separate pronotal hind-angle carinae and lateral carinae, and lack lateral expansions of the parameres. The second lineage contains *Craspedostethus*, which has separate pronotal lateral and hind angles carinae, uniquely slipper-like flexible bursal sclerites, and a coil-like spermatheca. The third clade contains species (including the type species of *Cardiophorus*) with fully sclerotized, single-lobed proximal bursal sclerites and a pair of distal sclerites (separate or fused). Most of these also have separate pronotal hind-angle carinae and lateral carinae, and many have parameres with pre-apical lateral expansions.

The molecular phylogeny suggests that none of the former *Horistonotus*, *Paracardiophorus* or *Cardiophorus* is monophyletic, which is consistent with the morphology-based analysis of Douglas (2017). We report here two new genera based on species previously assigned to *Horistonotus*, which differ in having simple tarsal claws from other *Horistonotus* species. The type species of *Huarpelater* gen. nov. was probably misidentified as *Horistonotus canescens* by Golbach (1979) and Córdoba and Aranda (2013), while true *Horistonotus canescens* is here transferred to *Arandelater* gen. nov. Although we have no DNA sequences for *Arandelater* gen. nov., the morphology of the bursal sclerites has no affinity to *Horistonotus* or *Huarpelater* gen. nov. Additionally, we find *Paracardiophorus buettikeri* not closely related to the type species of *Paracardiophorus* (Figs 1,S1). This was already suggested by several authors based on morphology (Chassain 1979; Platia & Schimmel 1997; Platia 2007). Because *Paracardiophorus buettikeri* is similar in several morphological aspects to the East Asian genera *Allocardiophorus* and *Ryukyucardiophorus* (see Taxonomy section for more detail), before deciding its placement we included published DNA sequences (Oba *et al.* 2015) of these East Asian genera into our dataset. Our molecular phylogenetic results support the placement of *P. buettikeri* in a newly established genus, *Chassainphorus* gen. nov. Furthermore, we tested the monophyly of the broadly defined *Cardiophorus* by including the representatives of *Cardiophorus*, *Zygocardiophorus* and *Coptostethus* into the analyses. The remaining two *Cardiophorus* subgenera, *Lasiocerus* Buysson and *Perrinellus* Buysson, were not available for molecular analysis, and should be sequenced when possible. The former subgenus *Zygocardiophorus* was already elevated to the generic rank by Douglas (2017), and this status is confirmed here by molecular data. Additionally, we find *Coptostethus*, until now a subgenus of *Cardiophorus*, as phylogenetically distinct from *Cardiophorus* (Figs 1,S1). Some authors already treated *Coptostethus* as a separate genus, but without analysis or other evidence (Dajoz 1963; Németh & Platia 2014; Platia & Kakiopoulos 2015; Platia 2016). *Coptostethus* was originally defined by the short wings of its species (Wollaston 1854), with most representatives known from the Canary Islands (Cobos 1970, 1978, 1983). This led to placement of dissimilar short-winged Cardiophorinae from other world regions in *Coptostethus* (Douglas 2017). However, the present analyses suggest that the long-winged *Cardiophorus skulei* is the closest relative of the *Coptostethus* species studied here. Furthermore, all known *Coptostethus* species and *Cardiophorus skulei* share distinctive sclerites of the bursa copulatrix (Figs 21,24), which are not observed in other monophyletic genera of Cardiophorinae (Douglas 2017). We propose to redefine *Coptostethus* to include the long-winged species with similar bursal sclerites, which have been classified in the non-monophyletic genera *Cardiophorus* and *Dicronychus*. The presence of species with fully developed or reduced wings within a single genus is also known for some other Elateridae, for example, *Selatosomus* Stephens or several Dimini (Dolin 1975; Schimmel 1996).

Here we have shown that integrative taxonomy using both molecular markers and morphology is highly effective for Cardiophorinae. Our major cardiophorine clades mostly agree with topologies of morphological analyses by Douglas (2017), but with more resolution and support. Further taxa, especially from the speciose and morphologically diverse genera, should be included in the future molecular analyses and morphologically re-examined in order to establish a stable phylogenetic classification for Cardiophorinae.

ACKNOWLEDGMENTS

We are very obliged to colleagues and institutions for providing us with the material studied herein, namely M. Borer (NHMB, Switzerland), S. Blank (SDEI, Germany), J. Constant (RBINS), J. Halada, P. Kučera and A. Buček (Czech Republic). Antoine Mantilleri (Paris, France) helped us with locating the type of *P. buettikeri*. Karine Savard prepared specimen images and plates. We thank G. Platia for literature and comments on the morphology of *Ch. buettikeri*. We thank S. Cordoba for comments on Cardiophorinae of Argentina. Most species transfers were possible thanks to past efforts of Christine von Hayek to dissect types of Cardiophorinae, and female genitalic illustrations published by G. Platia, and A. Cobos. We thank P. Bouchard (CNCI, Canada) for his comments on applications of the ICZN Code. This study was supported by the internal grant of the Faculty of Science UP (IGA_PrF_2017_023; RK, DJ) and the Synthesys grant FR-TAF 6701 (RK).

REFERENCES

Aranda SG (2009) Dos nuevas especies de *Horistonotus* Candèze 1860 (Coleoptera: Elateridae) y redescripción de *Horistonotus farinosus* Candèze 1891. *Acta Zoológica Lilloana* **53**, 29–48.

Bocakova M, Bocak L, Hunt T, Teraväinen M, Vogler AP (2007) Molecular phylogenetics of Elateriformia (Coleoptera): Evolution of bioluminescence and neoteny. *Cladistics* **23**, 477–496.

Buysson H (1906) Note sur les élatérides récoltés en Perse par M. J. de Morgan en 1894. *Bulletin du Muséum d'Histoire Naturelle* **12**, 17–21.

Candèze ECA (1878) Élatérides nouveaux. *Annales de la Société Entomologique de Belgique* **21**, li–lxi, lxxv–lxxxv, cxxxv–cxliii, clxi–clxxii, clxxxix–cxcix.

Candèze ECA (1882) Élatérides nouveaux (troisième fascicule). *Mémoires de la Société Royale des Sciences de Liège (2e Série)* **9**, 1–117.

Candèze ECA (1889) Élatérides nouveaux. *Vol. IV. Annales de la Société Entomologique de Belgique* **33**, 67–123.

Chassain J (1979) Insects of Saudi Arabia. Coleoptera: Fam. Elateridae. *Fauna of Saudi Arabia* **1**, 193–211.

Cobos A (1970) Ensayo monographico sobre los *Cardiophorus* Esch., 1829 de Canarias. *Instituto Espanol de Entomologia* **126**, 1–68.

Cobos A (1978) *Sobre Cardiophorus atlanticos extracanarios del subgenero Coptostethus (Coleoptera, Elateridae). Museo de Ciencias Naturales del Cabildo Insular de Santa Cruz de Tenerife. Contribucion al estudio de la Historia Natural de las Islas Salvajes. Resultados de la expedicion cientifica 'Agamenon 76' (23 de febrero–3 de Marzo de 1976)*. Aula de Cultura de Tenerife, Canary Islands.

Cobos A (1983) Tres nuevas especies de *Cardiophorus* eschs (Col. Elateridae) de Canarias. *Boletín de la Asociación española de Entomología* **6**, 237–243.

Córdoba SP, Aranda SG (2013) Descripción de una nueva especie del género *Horistonotus* (Coleoptera: Elateridae) y clave ilustrada para la determinación de especies presentes en la Argentina. *Acta Zoológica Lilloana* **57**, 3–13.

Costa C, Lawrence JF, Rosa SP (2010) Elateridae Leach, 1815. In: Leschen RAB, Beutel RG, Lawrence JF (eds) *Coleoptera, Beetles. Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)*, Vol. **2**, pp 75–103. In: Kristensen NP, Beutel RG (eds) *Handbook of Zoology, Arthropoda: Insecta.* Walter de Gruyter, Berlin/New York.

Dajoz R (1963) Note preliminaire sur la classification des Cardiophorinae d'Europe et de la région Mediterranéene. *Revue Francaise d'Entomologie* **30**, 164–173.

Dolin VG (1975) Wing venation in click beetles and its significance for the taxonomy of the family. *Zoologicheskii Zhurnal* **54**, 1618–1633.

Douglas H (2011) Phylogenetic relationships of Elateridae inferred from adult morphology, with special reference to the position of Cardiophorinae. *Zootaxa* **2900**, 1–45.

Douglas H (2017) World reclassification of the Cardiophorinae (Coleoptera, Elateridae), based on phylogenetic analyses of morphological characters. *ZooKeys* **655**, 1–130.

Erichson WF (1840) Ueber Elateriden ohne Bruststachel (Cardiophorus). *Zeitschrift für die Entomologie* **2**, 279–341.

Felsenstein J (2004) *Inferring Phylogenies.* Sinauer Associates, Sunderland.

Fleutiaux E (1947) Révision des Élatérides (Coléoptères) de l'Indo-Chine Française. *Notes d'Entomologie Chinoise* **11**, 233–420.

Golbach R (1979) *Horistonotus latus* nueva especie (Col. Elateridae). *Acta Zoológica Lilloana* **35**, 411–415.

Gur'yeva YL (1974) Thoracic structure of click beetles (Coleoptera, Elateridae) and the significance of the structural characters for the system of the family. *Entomologicheskoye Obozreniye* **53**, 96–113.

Hendrich L, Morinière J, Haszprunar G *et al.* (2015) A comprehensive DNA barcode database for central European beetles with a focus on Germany: Adding more than 3500 identified species to BOLD. *Molecular Ecology Resources* **15**, 795–818.

Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**, 754–755.

Hyslop JA (1917) The phylogeny of the Elateridae based on larval characters. *Annals of the Entomological Society of America* **10**, 241–263.

Johnson PJ (2002) Elateridae Leach 1815. In: Arnett RH, Thomas MC, Skelley PE, Frank JH (eds) *American Beetles*, Vol. **2**, pp 160–173. CRC, Boca Raton, FL.

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution* **30**, 772–780.

Katoh K, Misawa K, Kuma K, Miyata T (2002) MAFFT: A novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* **30**, 3059–3066.

Kundrata R, Bocak L (2011) The phylogeny and limits of Elateridae (Insecta, Coleoptera): Is there a common tendency of click beetles to soft-bodiedness and neoteny? *Zoologica Scripta* **40**, 364–378.

Kundrata R, Bocakova M, Bocak L (2014) The comprehensive phylogeny of the superfamily Elateroidea (Coleoptera: Elateriformia). *Molecular Phylogenetics and Evolution* **76**, 162–171.

Kundrata R, Gunter NL, Douglas H, Bocak L (2016) Next step toward a molecular phylogeny of click-beetles (Coleoptera: Elateridae): Redefinition of Pityobiinae, with a description of a new subfamily, Parablacinae, from the Australasian region. *Austral Entomology* **55**, 291–302.

Lanfear R, Calcott B, Ho SYW, Guindon S (2012) PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* **29**, 1695–1701.

Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*; 14 Nov 2010, New Orleans, LA, USA, pp 1–8.

Németh T, Platia G (2014) On some Palaearctic click beetles deposited in the Hungarian Natural History Museum, 2 (Coleoptera: Elateridae). *Zootaxa* **3841**, 451–490.

Oba Y, Ôhira H, Murase Y, Moriyama A, Kumazawa Y (2015) DNA barcoding of Japanese click beetles (Coleoptera, Elateridae). *PLoS ONE* **10**, Artical ID e0116612. https://doi.org/10.1371/journal.pone.0116612

Pic M (1914) Notes diverses, descriptions et diagnoses. *L'Échange. Revue Linnéenne* **30**, 10–13.

Platia G (2007) Order Coleoptera, family Elateridae. *Arthropod Fauna of the UAE* **1**, 194–210.

Platia G (2015a) Description of new species of click beetles from the Palearctic region with interesting new records (Coleoptera, Elateridae). *Boletín de la Sociedad Entomológica Aragonesa* **56**, 13–25.

Platia G (2015b) Contribution to the knowledge of the click beetles of the Maldives (Coleoptera: Elateridae). *Boletín de la Sociedad Entomológica Aragonesa* **57**, 182–184.

Platia G (2016) New species and new records of click beetles from the Palearctic Region (Coleoptera, Elateridae). *Boletín de la Sociedad Entomológica Aragonesa* **59**, 23–28.

Platia G, Kakiopoulos G (2015) Eleven new click beetles and records from the Canary Islands, Greece, Egypt, Turkey and Iran (Coleoptera, Elateridae). *Boletín de la Sociedad Entomológica Aragonesa* **57**, 45–52.

Platia G, Schimmel R (1997) Click-beetles (Coleoptera: Elateridae) from the Sultanate of Oman with additional new species and records from neighbouring regions. *Fauna of Saudi Arabia* **16**, 291–318.

Rambaut A (2009) *FigTree, Version 1.3.1*. Available from URL: http://tree.bio.ed.ac.uk/software/figtree/

Rambaut A, Drummond AJ (2007) *Tracer, Version 1.5*. Institute of Evolutionary Biology University of Edinburgh, Edinburgh. Available from URL: http://beast.bio.ed.ac.uk/Tracer

Sagegami-Oba R, Oba Y, Ôhira H (2007) Phylogenetic relationships of click beetles (Coleoptera: Elateridae) inferred from 28S ribosomal DNA: Insights into the evolution of bioluminescence in Elateridae. *Molecular Phylogenetics and Evolution* **42**, 410–421.

Schimmel R (1996) *Das Monophylum Diminae Candèze, 1863 (Insecta: Coleoptera: Elateridae)*, Vol. **33**. Pollichia, Bad Dürkheim.

Schwarz O (1906) Neue Elateriden aus Amerika. *Deutsche Entomologische Zeitschrift* **1906**, 97–158.

Stamatakis A (2006) RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22**, 2688–2690.

Stamatakis A, Hoover P, Rougemont J (2008) A rapid bootstrap algorithm for the RAxML web servers. *Systematic Biology* **57**, 758–771.

Steinheil E (1874) Symbolae ad historian Coleopterorum Argentiniae Meridionales, ossia enumerazione dei coleotteri raccolti dal Prof. Strobel nell' Argentinia Meridionale e descrizione delle specie nuove. *Atti della Società Italiana di Scienze Naturali* **15**, 554–578.

Stibick JNL (1979) Classification of the Elateridae (Coleoptera). Relationships and classification of the subfamilies and tribes. *Pacific Insects* **20**, 145–186.

Wollaston TV (1854) *Insecta Maderensia: Being an Account of the Insects of the Islands of the Madeiran Group*. John van Voorst, London.

Xia X (2013) DAMBE 5: A comprehensive software package for data analysis in molecular biology and evolution. *Molecular Biology and Evolution* **30**, 1720–1728.

Xia X, Lemey P (2009) Assessing substitution saturation with DAMBE. In: Lemey P, Salemi M, Vandamme A-M (eds) *The Phylogenetic Handbook: A Practical Approach to DNA and Protein Phylogeny*, 2nd edn, pp 615–630. Cambridge University Press, Cambridge.

Xia X, Xie Z, Salemi M, Chen L, Wang Y (2003) An index of substitution saturation and its application. *Molecular Phylogenetics and Evolution* **26**, 1–7.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Appendix S1 Detailed taxonomic information for genera *Huarpelater* Douglas and Kundrata gen. nov., *Arandelater* Douglas and Kundrata gen. nov., *Chassainphorus* Douglas and Kundrata gen. nov., and *Coptostethus* Wollaston stat. rev.

Figure S1 Phylogenetic hypothesis on Cardiophorinae based on the Bayesian inference performed on the 43-taxa dataset aligned by Mafft. Numbers at the branches indicate Bayesian posterior probabilities for the full-length dataset (upper left) and the dataset with 3rd codon positions discarded (upper right), and maximum likelihood bootstrap values for the full-length dataset (lower left) and the dataset with 3rd codon positions discarded (lower right). CAR - Cardiophorinae; NEG - Negastriinae. For taxa marked with asterisk only the *cox1–3'* mtDNA sequences are available. For taxa in bold we propose new taxonomic acts.

Table S1 Primers used for the polymerase chain reaction amplifications of the studied markers.

Table S2 Results of the Xia's nucleotide substitution saturation test in DAMBE, based on simulations with 32 operational taxonomic units (10,000 replicates).

Table S3 Summary of the PartitionFinder results.

Appendix S1. Detailed taxonomic information for genera *Huarpelater* Douglas and Kundrata gen. nov., *Arandelater* Douglas and Kundrata gen. nov., *Chassainphorus* Douglas and Kundrata gen. nov., and *Coptostethus* Wollaston, 1854 stat. rev.

Generic descriptions follow Douglas' (2017, p. 40) template for description of new genera of Cardiophorinae.

Huarpelater Douglas and Kundrata gen. nov.

(Figs 2–4)

Type species. *Huarpelater cordobae* Douglas and Kundrata sp. nov.

Diagnosis. Male. Antennae with sensory elements beginning on antennomere III; mandible apices bidentate. Pronotum with lateral carinae (not distinguishable from hind-angle carinae) restricted to posterior 1/4 (Fig. 3); anterior prosternal lobe not short, covering labium. Scutellar shield with anterior edge emarginate (Fig. 2), anterolateral edges straight or concave posterior to anterolateral corners. Tarsi without apically extending lobes or pads; tarsal claws each with 1 apex per side. Aedeagus with paramere apices flattened.

Description. Male. Head. Antennae with sensory elements beginning on antennomere 3; mandible apices bidentate. Labrum short and convex; area between each antennal fossa and adjacent compound eye unsculptured. Frons with supra-antennal carina not forked near junctures with compound eyes, with supra-orbital grooves present. *Prothorax*. Pronotum with sublateral incisions present and carinae absent; posterior edge of pronotum with 3 apices mesally; lateral carinae (not distinguishable from hind-angle carinae) restricted to posterior 1/4 (Fig. 3); hind angles not truncate dorsally; separate dorsal carina of each hind angle absent; rectangularly emarginate immediately meso-ventrad of hind angles; procoxal cavities narrowly open. Prosternum with sides concave ventral view; anterior prosternal lobe not short, covering labium; prosternal process curved dorsad, ventral surface not carinate. *Pterothorax*. Scutellar shield with anterior edge emarginate (Fig. 2), anterolateral edges straight or concave posterior to anterolateral corners, posterior apex pointed. Mesoventral cavity with lateral edges sinuate anterad of mesocoxae. Mesanepisternum and mesepimeron not reaching mesocoxal cavity; mesotrochantin not exposed. Hind wings not notched in anal area. *Legs*. Tarsi without apically extending lobes or pads; tarsal claws each with 1 apex per side; metacoxal plate covers 1/3 of metatrochanter with legs withdrawn. *Abdomen*. Ventrites not micro-serrate laterally. *Male terminalia*. Abdominal segment IX with tergite and sternites articulated at sides; aedeagus with 2 setae at paramere apices (Fig. 4). *Female*. Unknown.

Etymology. Named for the Huarpe people, indigenous to the Mendoza region of Argentina. Gender: masculine.

Distribution. Argentina.

Remarks.

Huarpelater gen. nov. keys in Douglas (2017) to *Cardiophorus* (*Perinellus*) *argentatus* Abeille de Perrin, 1894, from Israel. However, paramere apices of *Huarpelater* are flat (cylindrical in *Perinellus*). Within South America, *Huarpelater* gen. nov. differs from *Chileaphricus* Douglas in sensory elements beginning on antennomere III (antennomere IV in *Chileaphricus*), supra-antennal carina not forked (forked in *Chileaphricus*), prosternal anterior lobe not short, directed ventrad (short in *Chileaphricus*), mesotrochantin not exposed (exposed in type species *Chileaphricus*), elytral intervals 2–8 costate apically (intervals 4–6 costate apically in *Chileaphricus*), and parameres each with 2 setae (4 setae in *Chileaphricus*). We expect the undescribed female to also match the above diagnosis based on patterns of sexual dimorphism and observed in other genera (Douglas 2017).

Huarpelater cordobae **Douglas and Kundrata sp. nov.**

(Figs 2–4)

Type material. Holotype, ♂, "ARGT. [ARGENTINA], San-Luis, Dept. Belgraus, Buan Putor, II.72, Bolle"; and with the authors' red label: "Holotype *Huarpelater cordobae* Douglas and Kundrata 2017" (CNCI). Paratype, ♂, "Argentina central [ARGENTINA, Catamarca Province], -28.21729, -65.885181, 19.12.13, leg. Aleš Buček lgt., RK0846"; and with the authors' yellow label: "Paratype *Huarpelater cordobae* Douglas and Kundrata 2017" (PCRK).

Type locality. Argentina: San Luis Province, Belgrano Department.

Diagnosis. Male. Antennae long, reaching to midlength of body. Parameres with apices flattened without apicolateral expansions (Fig. 4). Males of this species differs from those of

Huarpelater quillu (Aranda, 2009) comb. nov. in having antennae exceeding pronotal hind angles by the length of the four apical antennomeres (three in *A. quillu*) and elytral intervals costate (rounded in *A. quillu*).

Description. Male. Length 7–10 mm. Integument brown; dorsal surface double-punctured with punctures and setae of two discrete size-classes, pale setae partially hiding integument. Antennae long, reaching to midlength of body; frons with supra-antennal carina little elevated above labrum. Pronotum slightly wider than long. Elytra with edges micro-serrate; intervals costate in apical third. Aedeagus with basal struts length 1.0 times median lobe length; median lobe straight basally, tapered at apex; parameres without apicolateral expansions (Fig. 4). *Female.* Unknown.

Measurements. BL 9.1 mm, EL 6.3 mm, WHe 1.6 mm, WHum 2.4 mm, PL 2.1 mm, PW 2.2 mm, Edist 1.2 mm, Ediam 0.6 mm.

Distribution. Argentina: Catamarca; Mendoza; San Luis; and perhaps nearby provinces.

Etymology. Named for Silvia Córdoba (Fundación Miguel Lillo, Tucumán, Argentina) in honour of her contributions to knowledge of Elateridae.

Remarks. This or a similar species was apparently already studied by Golbach (1979) and Córdoba and Aranda (2013), but misidentified as *Horistonotus canescens* Steinheil, 1874 (redescribed below). In both publications *H. canescens* is the only Argentinian species with simple tarsal claws, costate elytral intervals, and male antennae reaching beyond the midlength of the body. *H. canescens* sensu Córdoba and Aranda (2013) also matches all other characters of *H. cordobae* sp. nov. including the simple supra-antennal carina, elongate pronotum, and costate elytral interstriae. Species concepts of Golbach (1979) and Córdoba and Aranda (2013) do not match the type specimen of *H. canescens* (Figs 5–14) in that *H. canescens* has antennae not reaching pronotal hind angles, and the pronotum has a carina at the sides extending from the hind angle to the anterior ¼.

Huarpelater quillu (Aranda, 2009) comb. nov.

Horistonotus quillu Aranda, 2009: 39.

Remark. This species is transferred to *Huarpelater* gen. nov. because the original description and illustrations match the diagnostic characters of this genus.

***Arandelater* Douglas and Kundrata gen. nov.**

(Figs 5–14)

Type species. *Horistonotus canescens* Steinheil, 1874.

Diagnosis. Frons with supra-antennal carina forked near juncture with compound eye. Pronotum with carina along lateral edge visible in dorsal view, not reaching anterior edge. Scutellar shield with anterior edge narrowly emarginate. Tarsi non-lobed and tarsal claws with one apex per side. Bursa copulatrix with paired proximal (largest) sclerites elongate-ovoid with largest spines along mesal edge (Fig. 9).

Description. Length 7–11 mm. Integument brown to black. *Head.* Antennae weakly serrate; antennal sensory elements beginning on antennomere IV; mandibles with apices bidentate. Labrum convex; area between each antennal fossa and adjacent compound eye unsculptured, with low carina joining fossa and eye, with pit on either side of carina. Frons with supra-antennal carina forked near juncture with compound eye (Fig. 7); frons with supra-orbital grooves present (Fig. 7). *Prothorax*. Pronotum with punctures oval; sublateral incisions present; posterior edge of pronotum with 2 apices mesally (adjacent to scutellar shield); lateral carinae (not distinguishable from hind-angle carinae) not reaching beyond pronotal midlength if present (Fig. 6), not situated ventrad of lateral edge of pronotum; hind angles complete dorsally (Fig. 6); dorsal carina of each hind angle single, not visible as separate from pronotal lateral carina; hypomeral hind edges rectangularly emarginate (Fig. 6) immediately meso-ventrad of hind angles; procoxal cavities narrowly open or closed. Prosternum with sides weakly concave in ventral view; anterior prosternal lobe long, covering labium; prosternal process curved dorsad somewhat, ventral surface not carinate laterally. *Pterothorax*. Scutellar shield with anterior edge emarginate (Fig. 5), posterior apex pointed. *Legs*. Tarsi simple; tarsal claws with 1 apex per side; metacoxal plate covers 1/2 of metatrochanter with legs withdrawn. *Abdomen*. Abdominal ventrite 5 with punctures arranged into irregular longitudinal grooves, apex flattened (Fig. 8). *Male terminalia*. Abdominal segment IX with tergite and sternites articulated at sides; parameres with apices not forked

(Fig. 10), sides with 2 setae; aedeagus with basal struts approximately 0.8 times median lobe length; median lobe weakly pedunculate. *Female genitalia.* Ovipositor with baculae present; coxites flexible. Bursa copulatrix without sclerotized spermathecae; paired spine-bearing sclerites present (Fig. 9), proximal simple-elongate with longest spines along mesal edge, distal sclerites present as weakly sclerotized discs; spermathecal gland duct with base not sclerotized; anterior end of bursa with 1 pedunculate sac.

Etymology. Named for Dr. Susana G. Aranda (Fundación Miguel Lillo, Tucumán, Argentina) in honour of her contributions to knowledge of Elateridae. Gender: masculine.

Distribution. Argentina.

Remarks. DNA for this species was unavailable for analysis, but morphology sets this species clearly outside the concept of any other genus. The simple claws and simple elongate bursal sclerites both exclude it from *Horistonotus* (Douglas 2017), and most other South American genera (*Aptopus* Eschscholtz, *Buckelater* Costa, *Esthesopus* Eschscholtz, *Globothorax* Fleutiaux, *Triplonychoidus* Schwarz, *Triplonychus* Candèze). *Austrocardiophorus* (present in Chile) shares simple tarsal claws with this species, but differs in having the scutellar shield uniformly concave ateriorly, and the sclerites of the bursa copulatrix bilobed (Douglas 2017). *Arandelater* gen. nov. differs from the also simple-clawed *Huarpelater* gen. nov. (*Huarpelater* gen. nov. characters in in parentheses) in having the supra-antennal carina divided at the intersection (undivided) with the compound eye; antennal sensory elements beginning on the fourth antennomere (third). The bursa copulatrix of this species matches the clade containing *Cardiophorus* (Fig. 1; BMNH 679341 through *Coptostethus*), although the pronotal lateral carina is not distinguishable from the hind angle carina. In Douglas' (2017) key to genera this genus would lead users to *Cardiophorus* (*Coptostethus*) Wollaston (part) at couplet 42. However, this genus can be distinguished from *Coptostethus* by the elongate asymmetrical posterior sclerites of the bursa copulatrix. In *Arandelater* gen. nov., the sclerites have most spines along the mesal edge, where in *Coptostethus* they are evenly distributed along both edges.

Arandelater canescens **(Steinheil, 1874) comb. nov.**

(Figs 5–14)

Horistonotus canescens Steinheil, 1874: 568; Schwarz, 1906b: 179 (misspelled as *castanescens*); Schenkling, 1925: 258; Blackwelder, 1944: 302; Golbach, 1979: 412; Golbach, 1994: 32; Córdoba & Aranda, 2013: 10.

Horistonotus tumidicollis Schwarz, 1906a **syn.n.**; Schwarz, 1906a: 145; Schwarz, 1906b: 178; Schenkling, 1925: 259; Blackwelder, 1944: 303; Golbach, 1979: 411; Golbach, 1994: 32; Córdoba & Aranda, 2013: 10.

Type material of *H. canescens* (Figs 11–14). Lectotype, ♂, here designated: "[ARGENTINA] Mendoza; *Horistonotus canescens* Strobel Steinh; Ex Museo E. Steinheil; Museum Paris, 1952, coll. R. Oberthur; Syntype; Syntype *Horistonotus canescens* Steinheil; MNHN EC7462; and with the authors' red label: "Lectotype *Horistonotus canescens* Steinheil Douglas and Kundrata 2017" (MNHN).
Type material of *H. tumidicollis* (Figs 5–10). Lectotype, ♂, here designated: "[ARGENTINA] Mendoza, Coll. Schwarz, Syntypus, DEI Müncheberg, Col-07603"; and with the authors' red label: "Lectotype *Horistonotus tumidicollis* Schwarz Douglas and Kundrata 2017" (SDEI). Paralectotype, ♀: "[ARGENTINA] Mendoza, Coll. Schwarz, Syntypus [handwritten], *tumidicollis* Schw., DEI Müncheberg, Col-07601"; and with the authors' orange label: "Paralectotype *Horistonotus tumidicollis* Schwarz Douglas and Kundrata 2017" (SDEI). Paralectotype, ♂: Labels same as for female, with number "Col-07602" (SDEI).

Type locality. Argentina: Mendoza and San Luis Provinces.

Diagnosis. Male. Antennae not reaching beyond pronotal hind-angles (Figs 5–6); aedeagus (Fig. 10) with basal struts length 0.8 times median lobe length; parameres broad basally, tapered evenly to pointed apex, without apicolateral or apicomedial expansions; median lobe slightly pedunculate, simple.

Redescription. *Male.* Length 7–11 mm. Integument brown-black; dorsal surface double-punctured with punctures and setae of two discrete size-classes, pale setae partially hiding integument. Antennae not reaching beyond pronotal hind-angles (Figs 5–6); frons with supra-antennal carina elevated above labrum (Fig. 7), nasale concave in lateral profile (Fig. 6). Elytra with edges micro-serrate; intervals costate in apical third. Abdominal ventrites with edges not microserrate. Aedeagus (Fig. 10) with basal struts length 0.8 times median lobe length; parameres broad basally, tapered evenly to pointed apex, without apicolateral or apicomedial expansions; median lobe slightly pedunculate, simple. *Female.* Like male except antennae shorter. Genitalia: as described for the genus.

Measurements (lectotype of *H. canescens*). BL 7.8 mm, EL 5.3 mm, WHe 1.1 mm, WHum 2.0 mm, PL 2.1 mm, PW 2.1 mm, Edist 0.8 mm, Ediam 0.3 mm.

Distribution. Argentina (Mendoza).

Remarks. Schwarz (1906a) did not mention the very similar *H. canescens* in his description of *H. tumidicollis*. So, it seems likely that Schwarz was not aware of similarity between *H. tumidicollis* and *H. canescens*. We propose to consider *H. tumidicollis* a junior synonym of *H. canescens* because of their seemingly identical morphology, and because *H. tumidicollis* was apparently described in error.
Córdoba and Aranda (2013) reported two more simple-clawed species of *Horistonotus* from Argentina: *H. farinosus* Candèze, 1891 and *H. humeralis* Candèze, 1860. However, their morphologies do not match *Huarpelater* or *Arandelater*. Generic placement and confirmation of their occurence in Argentina requires further research.

***Chassainphorus* Douglas and Kundrata gen. nov.**
(Figs 15–17)

Type species. *Paracardiophorus buettikeri* Chassain, 1979: 210.

Diagnosis. Male. Mandibles with apices bidentate. Pronotum with lateral carinae (not distinguishable from hind-angle carinae), single carina at side of pronotum reaching only to anterior half (Fig. 16), separate dorsal carina of each hind angle absent. Prosternum with anterior prosternal lobe long covering labium. Scutellar shield with anterior edge straight (Fig. 15) to narrowly emarginate. Tarsi simple; tarsal claws with 1 apex per side. Abdominal ventrites micro-serrate laterally.

Description. Male. Head. Antennae with antennal sensory elements beginning on antennomere III; mandibles with apices bidentate. Labrum convex; area between antennal fossa and compound eye with carina connecting fossa and eye. Frons with supra-antennal carinae forked near junctures with compound eyes. *Prothorax*. Pronotum with sublateral incisions present and carinae absent; posterior edge of pronotum with 3 apices mesally (adjacent to scutellar shield, Fig. 17); lateral carinae (not distinguishable from hind-angle carinae), single carina at side of pronotum reaching only to anterior half (Fig. 16); hind angles not truncate dorsally; separate dorsal carina of each hind angle absent; rectangularly emarginate immediately meso-ventrad of hind angles; procoxal cavities closed. Prosternum with sides straight at midlength in ventral view; anterior prosternal lobe long, covering labium; prosternal process curved dorsad only near apex, ventral surface not carinate laterally. *Pterothorax*. Scutellar shield with anterior edge straight (Fig. 15) to narrowly emarginate, posterior apex pointed. Hind wings notched in anal area. *Legs*. Tarsi simple; tarsal claws with 1 apex per side. *Abdomen*. Ventrites micro-serrate laterally. *Male terminalia*. Abdominal segment IX with tergite and sternites articulated at sides; aedeagus with parameres with 2 setae each (Fig. 17). *Female*. Unknown.

Distribution. Oman, Saudi Arabia, United Arab Emirates, Yemen.

Etymology. The genus name combines the words "Chassain" (in honour of Jacques Chassain (Thomary, France), author of the type species for this genus) and "*Cardiophorus*" Eschscholtz (the type genus of Cardiophorinae). Gender: masculine.

Remarks. This genus shares similar pronotal morphology with *Ryukyucardiophorus* Ôhira from Japan and Taiwan but it differs from the latter in having tarsal claws with a single point (although the base of each claw is expanded by about 2x). Another similar genus, *Allocardiophorus* Ôhira (from Japan), shares the pronotal morphology and simple claws and tarsi with *Chassainphorus* gen. nov., but lacks microserrate abdominal edges. We expect the undescribed female to also match the above diagnosis based on patterns of sexual dimorphism and observed in other genera (Douglas 2017). Discovery of members of *Chassainophorus* gen. nov. with external morphology like that of *Cardiophorus* and *Dicronychus* means that assignment of species to genera will require dissection of female genitalia.

Chassainphorus buettikeri **(Chassain, 1979) comb. nov.**

(Figs 15–17)

Paracardiophorus buettikeri Chassain, 1979: 210; Platia & Schimmel, 1997: 316; Cate, 2007: 206; Platia, 2007: 209; Löbl & Smetana, 2008: 24.

Type material. Holotype, ♂, "[SAUDI ARABIA] Wadi Mizbil, 13.IV.1977, W. Büttiker leg." (NHMB).

Other material studied. ♂, "OMAN, Dhofar prov., Wadi Mughsayl, 120 m, 16°52'N 53°43'E, 2.–3.Oct.2013, J. Halada and P. Kučera lgt., RK0906" (PCRK).

Type locality. Saudi Arabia: "Wadi Mizbil".

Diagnosis. Male. Aedeagus narrow; parameres (Fig. 17) without apicolateral or apicomedial expansions; basal struts approximately 0.8 times median lobe length, median lobe slightly pedunculate, tapered apically.

Redescription. Male. Body 3.0 times longer than wide. Integument red-brown with elytra yellow-brown; double-punctured with punctures and setae of two discrete size-classes; vestiture pale and not obscuring integument (Fig. 15). Supra-antennal carinae raised above frons in posterodorsal view, frons with supra-orbital grooves weak or absent. Scutellar shield with anterior edge straight to narrowly emarginate (Fig. 15). Elytra with intervals flattened; lateral carina microserrate. Tarsal claws simple, but swollen at base. Aedeagus narrow; parameres (Fig. 17) without apicolateral or apicomedial expansions; basal struts approximately 0.8 times median lobe length, median lobe slightly pedunculate, tapered apically. *Female*. Unknown.

Measurements. BL 3.7 mm, EL 2.5 mm, WHe 0.8 mm, WHum 1.1 mm, PL 0.9 mm, PW 1.1 mm, Edist 0.4 mm, Ediam 0.4 mm.

Distribution. Oman, Saudi Arabia, Yemen, United Arab Emirates.

Remarks. Chassain (1979) suggested in his original description that this species perhaps does not belong in genus *Paracardiophorus*. Evidence for the establishment of a new genus to accommodate this species is mainly from the DNA-based phylogeny (Fig. 1), and morphology also does not indicate placement of this within any described genera in

Cardiophorinae. Further morphological evidence could come from eventual discovery of females of this species.

Coptostethus **Wollaston, 1854 stat. rev.**

(Figs 18–24)

Coptostethus Wollaston, 1854: 238.

Type species. *Coptostethus femoratus* Wollaston, 1854: 240, by monotypy.

Diagnosis. Mandibles with apices bidentate. Pronotum with carina along lateral edge absent or hidden by edge of pronotum in dorsal view, reaching less than halfway to anterior edge. Prosternum with anterior edge not short, produced as lobe, concealing labium when head not extended. Scutellar shield with middle of anterior edge abruptly emarginate, and posterior apex pointed. No tarsomeres lobed or lamellate; tarsal claws with one or two apices per side. Urosternites III–VII with or without serrations along sides. Bursa copulatrix with proximal sclerites ovoid, each nearly bilaterally symmetrical with longest spines near midline and a median groove along midline to constricted base; spermathecal gland duct with weakly sclerotized ring-like sclerotization surrounding base.

Redescription. Length 3.5–9.0 mm. Integument yellow-brown to black, some with longitudinal stripes on elytra. *Head.* Antennal sensory elements beginning on antennomere III or IV; mandibles with apices bidentate. Labrum evenly convex or with transverse ridge; area between antennal fossa and compound eye unsculptured. Frons convex; with nasale concave between supra-antennal carinae and labral base concave in side view or not, supra-antennal carina forked near juncture with compound eye; frons with supra-orbital grooves present. *Prothorax.* Pronotum with sublateral incisions present; posterior edge of pronotum with 3 apices mesally (adjacent to scutellar shield); lateral carinae not reaching anterior edge or absent (Fig. 19), situated ventrad of lateral edge of pronotum where present; hind angles complete dorsally (Fig. 19); dorsal carina of hind angle single; hypomeral hind rectangularly emarginate immediately meso-ventrad of hind angles; procoxal cavities narrowly open. Prosternum with sides concave to straight in ventral view; anterior prosternal lobe long, covering labium; prosternal process with ventral surface carinate laterally in most or all. *Pterothorax.* Scutellar shield with anterior edge emarginate (Fig. 18), anterolateral edges straight or evenly rounded, posterior apex pointed. Mesoventral cavity with lateral edges sinuate anterad of mesocoxae in ventral view. Elytra with intervals weakly convex; sides serrate or not. Hind wings short or capable of flight, notched in anal area. *Legs.* Tibiae with spine-like setae dorsally or antero-dorsally; tarsi simple; tarsal claws each with 1–2 apices per side; metacoxal plate covers 1/8–2/3 of metatrochanter with legs withdrawn. *Abdomen.* Sides of ventrites 1–5 micro-serrate or not. *Male terminalia.* Abdominal segment IX with tergite and sternites articulated at sides; parameres with (Fig. 20) or without apicolateral expansions, each with 2 setae; aedeagus with basal struts as long as median lobe; median lobe evenly tapered to weakly pedunculate. *Female genitalia.* Ovipositor with baculae present; coxites flexible. Bursa copulatrix without sclerotized spermathecae; spine-bearing sclerites present; proximal sclerites ovoid, each nearly bilaterally symmetrical with longest spines near midline (Figs 21, 24) and a median groove along midline to constricted base; paired distal sclerites absent to sclerotized and fused as “U” shape; spermathecal gland duct with weakly sclerotized ring-like sclerotization surrounding base, several short diverticulae along duct; anterior end of bursa with 1 pedunculate sac.

Distribution. Portugal: Madeira, Savage Islands; Spain: Canary Islands; Morocco; Tunisia; Eritrea; Yemen; Oman; Saudi Arabia; Qatar; United Arab Emirates; Kuwait; Syria; Iran; Afghanistan; Maldives; Burma.

Remarks. The included *Coptostethus* species are phylogenetically distant from *Cardiophorus gramineus* (Scopoli, 1763), the type species of *Cardiophorus*, and therefore *Coptostethus* should be elevated to the genus rank. Using Douglas’ (2017) key, *Coptostethus femoratus* (the type species for the genus) would be keyed to *Coptostethus*, but other species to *Cardiophorus* Eschscholtz or *Dicronychus* Brullé. However, *Coptostethus* females have proximal sclerites of the bursa copulatrix with a narrow, straight sided base and the largest spines near the midline of the sclerite. Proximal sclerites of *Cardiophorus* and *Dicronychus* are ovoid with the largest spines along one edge. *Coptostethus* females also have a ring-like sclerotization around the base of the spermathecal gland duct, which is absent from most or all *Cardiophorus* and *Dicronychus*. Dissection of females of other *Cardiophorus* and *Dicronychus* species from North Africa, West Asia, and perhaps elsewhere could show that other members of these genera also belong to *Coptostethus*.

All available illustrations of *Coptostethus* species were examined (Cobos 1970, 1978, 1983; Németh & Platia 2014; Platia 2015a, b; Platia & Kakiopoulos 2015) to identify variability in diagnostic characters in the bursa copulatrix sclerites. The following species had proximal sclerites moderate to broad (Figs 21, 24), nearly symmetrical with a median groove and narrow (petiolate) base; distal sclerites fused and weakly sclerotized, and base of spermathecal gland duct surrounded by sclerotized ring: *Coptostethus buci* Németh and Platia, 2014; *C. salvatoi* Platia in Platia and Kakiopoulos, 2015; *C. oromii* (Cobos, 1978); *C. machadoi* (Cobos, 1983); *C. vittatus* (Lindberg, 1953); *C. crassiusculus* Wollaston, 1864; *C. vestitus* Lindberg, 1953; *C. minutus* Lindberg, 1953; *C. canariensis* Wollaston, 1858; *C. hayeki* (Cobos, 1970); *C. obtusus* Wollaston, 1864: 213; *C. palmensis* (Cobos, 1970); *C. mateui* (Cobos, 1970); *C. obscurus* Wollaston, 1864. The following species differed in that the distal sclerites did not have a petiole-like base: *C. globulicollis* Wollaston, 1862; *C. brunneipennis* Wollaston, 1863; *C. mendizabili* (Cobos, 1970); *C. arozarenai* (Cobos, 1970), distal sclerites absent; *C. fernandezi* (Cobos, 1970); *C. gomerensis* (Cobos, 1970).

Species currently recognized as *Coptostethus* Wollaston, 1854.

Supporting evidence is provided below for species marked with "*". These are species not described in *Coptostethus* or *Cardiophorus* (*Coptostethus*). Species listed as "comb. nov." without an asterisk were described in *Cardiophorus* (*Coptostethus*).

Coptostethus abora (Wurst and Cate, 1994) **comb. nov.**
Coptostethus aegyptiacus (Platia in Platia and Kakiopoulos, 2015) **comb. nov.***
Coptostethus alepensis (Pic, 1914) **comb. nov.***
Coptostethus arozarenai (Cobos, 1969) **comb. nov.**
Coptostethus attilai Németh and Platia, 2014
Coptostethus auarita (Liberto and Wurst, 1999) **comb. nov.**
Coptostethus bonitaensis Platia, 2015a
Coptostethus brancuccii (Platia and Schimmel, 1997) **comb. nov.***
Coptostethus brunneipennis Wollaston, 1863
Coptostethus buettikeri (Platia and Schimmel, 1997) **comb. nov.***
Coptostethus buci Németh and Platia, 2014
Coptostethus cabrerai (Cobos, 1970) **comb. nov.**
Coptostethus canariensis Wollaston, 1858
Coptostethus cobosi Douglas and Kundrata, 2018 **nom. nov.** (and **comb. nov.***) Replacement name for *Cardiophorus* (*Coptostethus*) *inflatus* Cobos, 1970: 94, which is preoccupied by *Cardiophorus inflatus* Candèze, 1882: 78.

Coptostethus cobossanchezi (Díaz de Castro and Sánchez-Ruiz, 2002) **comb. nov.**

Coptostethus crassiusculus Wollaston, 1864

Coptostethus divergens (Cobos, 1983) **comb. nov.**

Coptostethus eggeri Platia, 2015a

Coptostethus femoratus Wollaston, 1854

Coptostethus fernandezi (Cobos, 1970) **comb. nov.**

Coptostethus ferruginosus (Platia and Schimmel, 1997) **comb. nov.***

Coptostethus globulicollis Wollaston, 1862

Coptostethus gomerensis (Cobos, 1970) **comb. nov.**

Coptostethus gracilis Wollaston, 1864

Coptostethus guanche (Cobos, 1970) **comb. nov.**

Coptostethus guayote (Wurst and Cate, 1994) **comb. nov.**

Coptostethus hameti (Platia, 2015a) **comb. nov.***

Coptostethus hayeki (Cobos, 1970) **comb. nov.**

Coptostethus hierrensis (Franz, 1980) **comb. nov.**

Coptostethus ilniczkyi (Németh and Platia, 2014) **comb. nov.***

Coptostethus inflatus (Cobos, 1970) **comb. nov.**

Coptostethus kandaharensis (Németh and Platia, 2014) **comb. nov.***

Coptostethus karolyvigi (Németh and Platia, 2014) **comb. nov.***

Coptostethus kundratai Németh and Platia, 2014

Coptostethus larseni (Platia and Schimmel, 1997) **comb. nov.***

Coptostethus latescapulatus (Buysson, 1906) **comb. nov.***

Coptostethus lindbergi (Cobos, 1970) **comb. nov.**

Coptostethus longicornis Lindberg, 1953

Coptostethus machadoi (Cobos, 1983) **comb. nov.**

Coptostethus mantici Platia, 2016

Coptostethus mateui (Cobos, 1970) **comb. nov.**

Coptostethus mendizabali (Cobos, 1970) **comb. nov.**

Coptostethus minutus Lindberg, 1951

Coptostethus nemethi Platia, 2015a

Coptostethus obscurus Wollaston, 1864

Coptostethus obtusus Wollaston, 1864

Coptostethus opaculus Platia, 2015a

Coptostethus oromii (Cobos, 1978) **comb. nov.**

Coptostethus palmensis (Cobos, 1970) **comb. nov.**

Coptostethus paternus (Candèze, 1889) **comb. nov.***

Coptostethus petterssoni Platia, 2015a

Coptostethus platai (Cobos, 1979) **comb. nov.**

Coptostethus povolnyi (Németh and Platia, 2014) **comb. nov.***

Coptostethus putzeri Schimmel, 2008

Coptostethus salvatoi Platia in Platia and Kakiopoulos, 2015

Coptostethus scapulatus (Candèze, 1878) **comb. nov.***

Coptostethus selvagensis Schimmel, 2008

Coptostethus skoupyi Platia, 2015a

Coptostethus skulei (Platia and Schimmel, 1997) **comb. nov.***

Coptostethus stolatus (Erichson, 1840) **comb. nov.***

Coptostethus talhouki (Platia and Schimmel, 1997) **comb. nov.***

Coptostethus taylori (Cobos, 1970) **comb. nov.**

Coptostethus vestitus Lindberg, 1951

Coptostethus vilaflorensis Platia, 2015a

Coptostethus vittatus Lindberg, 1953

Coptostethus wittmeri (Platia and Schimmel, 1997) **comb. nov.***

Coptostethus wollastoni (Cobos, 1970) **comb. nov.**

Supporting evidence for transfers of other *Cardiophorus* and *Dicronychus* species to *Coptostethus*.

Supporting evidence for taxonomic changes to species above marked with “*”. All are species transferred to *Coptostethus* based on characters of the bursa copulatrix. Most or all are fully-winged species. Unless noted otherwise, the following morphological evidence for transfer to *Coptostethus* was observed: posterior sclerites nearly symmetrical, with median groove and narrow parallel-sided base; spermathecal gland duct with sclerotized ring surrounding base.

***Coptostethus aegyptiacus* (Platia in Platia and Kakiopoulos, 2015) comb. nov.**, from *Dicronychus aegyptiacus* Platia in Platia and Kakiopoulos, 2015: 47. Source of evidence for transfer: illustration in original description (Platia and Kakiopoulos, 2015). Evidence for transfer: as above.

***Coptostethus alepensis* (Pic, 1914) comb. nov.**, from *Cardiophorus alepensis* Pic, 1914: 10. Source of evidence for transfer: microscope slide of genitalia labelled: "*Cardiophorus* *alepensis* Pic, ♀ genitalia of TYPE, palmate sp., C. M. F. von Hayek det.1962" (MNHN). Evidence for transfer: as above.

***Coptostethus brancuccii* (Platia and Schimmel, 1997) comb. nov.**, from *Dicronychus brancuccii* Platia and Schimmel, 1997: 309. Source of evidence for transfer: illustration in original description. Evidence for transfer: as above, except unknown whether base of spermathecal gland duct is sclerotized.

***Coptostethus buettikeri* (Platia and Schimmel, 1997) comb. nov.**, from *Dicronychus buettikeri* Platia and Schimmel, 1997: 310. Source of evidence for transfer: illustration in original description. Evidence for transfer: as above, except unknown whether base of spermathecal gland duct is sclerotized.

***Coptostethus ferruginosus* (Platia and Schimmel, 1997) comb. nov.**, from *Dicronychus ferruginosus* Platia and Schimmel, 1997: 311. Source of evidence for transfer: illustration in original description. Evidence for transfer: as above, except unknown whether base of spermathecal gland duct is sclerotized.

***Coptostethus hameti* (Platia, 2015a) comb. nov.**, from *Cardiophorus hameti* Platia, 2015a: 18. Source of evidence for transfer: illustration in original description (Platia, 2015a). Evidence for transfer: as above.

***Coptostethus ilniczkyi* (Németh and Platia, 2014) comb. nov.**, from *Dicronychus ilniczkyi* Németh and Platia, 2014: 475. Source of evidence for transfer: illustration in original description. Evidence for transfer: as above, except proximal sclerite only somewhat symmetrical.

***Coptostethus kandaharensis* (Németh and Platia, 2014) comb. nov.**, from *Dicronychus kandaharensis* Németh and Platia, 2014: 477. Source of evidence for transfer: illustration in original description. Evidence for transfer: as above.

***Coptostethus karolyvigi* (Németh and Platia, 2014) comb. nov.**, from *Dicronychus karolyvigi* Németh and Platia, 2014: 478. Source of evidence for transfer: illustration in original description original description. Evidence for transfer: as above.

***Coptostethus larseni* (Platia and Schimmel, 1997) comb. nov.**, from *Dicronychus larseni* Platia and Schimmel, 1997: 312. Source of evidence for transfer: illustration in original description. Evidence for transfer: as above, except unknown whether base of spermathecal gland duct is sclerotized.

***Coptostethus latescapulatus* (Buysson, 1906) comb. nov.**, from *Cardiophorus latescapulatus* Buysson, 1906: 19. Source of evidence for transfer: microscope slide of genitalia labelled: "*Cardiophorus latescapulatus* Buyss. sp. nov., Type, Museum Paris, Poucht é Kouh

Galougah, Alt. 750 m, D. du Morgan, 1904, TYPE, ♀ genitalia; Palmate" (MNHN). Evidence for transfer: as above.

***Coptostethus paternus* (Candèze, 1889) comb. nov.**, from *Cardiophorus paternus* Candèze, 1889: 109. Source of evidence for transfer: pinned specimens and slide of genitalia labelled: "Coll. R.I.Sc.N.B, ETHIOPIE, Bogos 1871, Keren Maz. Antinoni, Collection E. Candèze, n. sp?, Paternus cd., dét. E. Candèze, TYPE" (RBINS). Evidence for transfer: as above.

***Coptostethus povolnyi* (Németh and Platia, 2014) comb. nov.**, from *Dicronychus povolnyi* Németh and Platia, 2014: 480. Source of evidence for transfer: illustration in original description. Evidence for transfer: as above.

***Coptostethus scapulatus* (Candèze, 1878) comb. nov.**, from *Cardiophorus scapulatus* Candèze, 1878: clxi. Source of evidence for transfer: illustration in Dajoz (1963). Evidence for transfer: as above, except unknown whether base of spermathecal gland duct is sclerotized.

***Coptostethus skulei* (Platia and Schimmel, 1997) comb. nov.**, (Figs 22–24), from *Cardiophorus skulei* Platia and Schimmel, 1997: 307. Source of evidence for transfer: illustration in original description. Evidence for transfer: Original description, phylogenetic analysis in present paper (Fig. 1), dissection of a specimen used for a phylogenetic analysis.

***Coptostethus stolatus* (Erichson, 1840) comb. nov.**, from *Dicronychus stolatus* (Erichson, 1840: 315). Source of evidence for transfer: illustration in Platia (2015b). Evidence for transfer: as above.

***Coptostethus talhouki* (Platia and Schimmel, 1997) comb. nov.**, from *Dicronychus talhouki* Platia and Schimmel, 1997: 314. Source of evidence for transfer: illustration in original description. Evidence for transfer: as above, except unknown whether base of spermathecal gland duct is sclerotized.

***Coptostethus wittmeri* (Platia and Schimmel, 1997) comb. nov.**, from *Dicronychus wittmeri* Platia and Schimmel, 1997: 315. Source of evidence for transfer: illustration in original description. Evidence for transfer: as above, except unknown whether base of spermathecal gland duct is sclerotized.

Species previously assigned to *Cardiophorus* (*Coptostethus*) and newly assigned to *Cardiophorus* (*Cardiophorus*).

Species listed as “comb. nov.” were described in genus *Coptostethus*.

Cardiophorus basilaris Candèze, 1865 [South Africa]; *Cardiophorus capensis* Laurent, 1974 [South Africa]; *Cardiophorus guttatus* (Candèze, 1865) **comb. nov.** [South Africa]; *Cardiophorus majusculus* (Candèze, 1889) **comb. nov.** [South Africa]; *Cardiophorus sexpunctatus* (Candèze, 1878) **comb. nov.** [South Africa]; *Cardiophorus tenuipes* (Candèze, 1889) **comb. nov.** [South Africa]. This includes all former *Coptostethus* species not from the islands of the eastern Atlantic Ocean west of Morocco. These species, described as *Coptostethus* because of their short wings, do not match the revised *Coptostethus*. These species are reassigned to the nominate subgenus *Cardiophorus* (*Cardiophorus*).

References to Appendix S1

Aranda SG (2009) Dos nuevas especies de *Horistonotus* Candèze 1860 (Coleoptera: Elateridae) y redescripción de *Horistonotus farinosus* Candèze 1891. *Acta Zoológica Lilloana* **53**, 29–48.

Blackwelder RE (1944) Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America. Part 2. *Bulletin of the United States National Museum* **185**, 189–341.

Buysson H (1906) Note sur les élatérides récoltés en Perse par M. J. de Morgan en 1894. *Bulletin du Muséum d'Histoire Naturelle* **12**, 17-21.

Candèze ECA (1878) Élatérides nouveaux. *Annales de la Société Entomologique de Belgique* **21**, li–lxi, lxxv–lxxxv, cxxxv–cxliii, clxi–clxxii, clxxxix–cxcix.

Candèze ECA (1882) Élatérides nouveaux (troisième fascicule). *Mémoires de la Société Royale des Sciences de Liège (2e Série)* **9**, 1–117.

Candèze ECA (1889) Élatérides nouveaux. Vol. IV. *Annales de la Société Entomologique de Belgique* **33**, 67–123.

Cate PG (2007) Family Elateridae. In: Löbl I, Smetana A (eds) *Catalogue of Palaearctic Coleoptera, Vol. 4. Elateroidea - Derodontoidea - Bostrichoidea - Lymexyloidea - Cleroidea - Cucujoidea*, pp. 89–209. Apollo Books, Stenstrup.

Chassain J (1979) Insects of Saudi Arabia. Coleoptera: Fam. Elateridae. *Fauna of Saudi Arabia* **1**, 193–211.

Cobos A (1970) Ensayo monographico sobre los *Cardiophorus* Esch., 1829 de Canarias. *Instituto Espanol de Entomologia* **126**, 1–68.

Cobos A (1978) *Sobre Cardiophorus atlanticos extracanarios del subgenero Coptostethus (Coleoptera, Elateridae). Museo de Ciencias Naturales del Cabildo Insular de Santa Cruz* *de Tenerife. Contribucion al estudio de la Historia Natural de las Islas Salvajes. Resultados de la expedicion cientifica 'Agamenon 76' (23 de febrero–3 de Marzo de 1976).* Aula de Cultura de Tenerife, Canary Islands.

Cobos A (1983) Tres nuevas especies de *Cardiophorus* eschs (Col. Elateridae) de Canarias *Boletín de la Asociación española de Entomología* **6**, 237–243.

Córdoba SP, Aranda SG (2013) Descripción de una nueva especie del género *Horistonotus* (Coleoptera: Elateridae) y clave ilustrada para la determinación de especies presentes en la Argentina. *Acta Zoológica Lilloana* **57**, 3–13.

Douglas H (2017) World reclassification of the Cardiophorinae (Coleoptera, Elateridae), based on phylogenetic analyses of morphological characters. *ZooKeys* **655**, 1–130.

Erichson WF (1840) Ueber Elateriden ohne Bruststachel (Cardiophorus). *Zeitschrift für die Entomologie* **2**, 279–341.

Golbach R (1979) *Horistonotus latus* nueva especie (Col. Elateridae). *Acta Zoológica Lilloana* **35**, 411–415.

Golbach R (1994) Elateridae (Col.) de la Argentina. Historia, Catálogo actualizado hasta 1991 inclusive y Clave de subfamilias y de géneros de Centro y Sudamérica. *Opera Lilloana* **41**, 1–48.

Löbl I, Smetana A (2008) Errata for Volume 4. In: Löbl I, Smetana A (eds) *Catalogue of Palaearctic Coleoptera, Vol. 5. Tenebrionoidea*, pp. 22–27. Apollo Books, Stenstrup.

Németh T, Platia G (2014) On some Palaearctic click beetles deposited in the Hungarian Natural History Museum, 2 (Coleoptera: Elateridae). *Zootaxa* **3841**, 451–490.

Pic M (1914) Notes diverses, descriptions et diagnoses. *L`Échange, Revue Linnéenne* **30**, 10–13.

Platia G (2007) Order Coleoptera, family Elateridae. *Arthropod fauna of the UAE* **1**, 194–210.

Platia G (2015a) Description of new species of click beetles from the Palearctic region with interesting new records (Coleoptera, Elateridae). *Boletín de la Sociedad Entomológica Aragonesa* **56**, 13–25.

Platia G (2015b) Contribution to the knowledge of the click beetles of the Maldives (Coleoptera: Elateridae). *Boletín de la Sociedad Entomológica Aragonesa* **57**, 182–184.

Platia G, Kakiopoulos G (2015) Eleven new click beetles and records from the Canary Islands, Greece, Egypt, Turkey and Iran (Coleoptera, Elateridae). *Boletín de la Sociedad Entomológica Aragonesa* **57**, 45–52.

Platia G, Schimmel R (1997) Click-beetles (Coleoptera: Elateridae) from the Sultanate of Oman with additional new species and records from neighbouring regions. *Fauna of Saudi Arabia* **16**, 291–318.

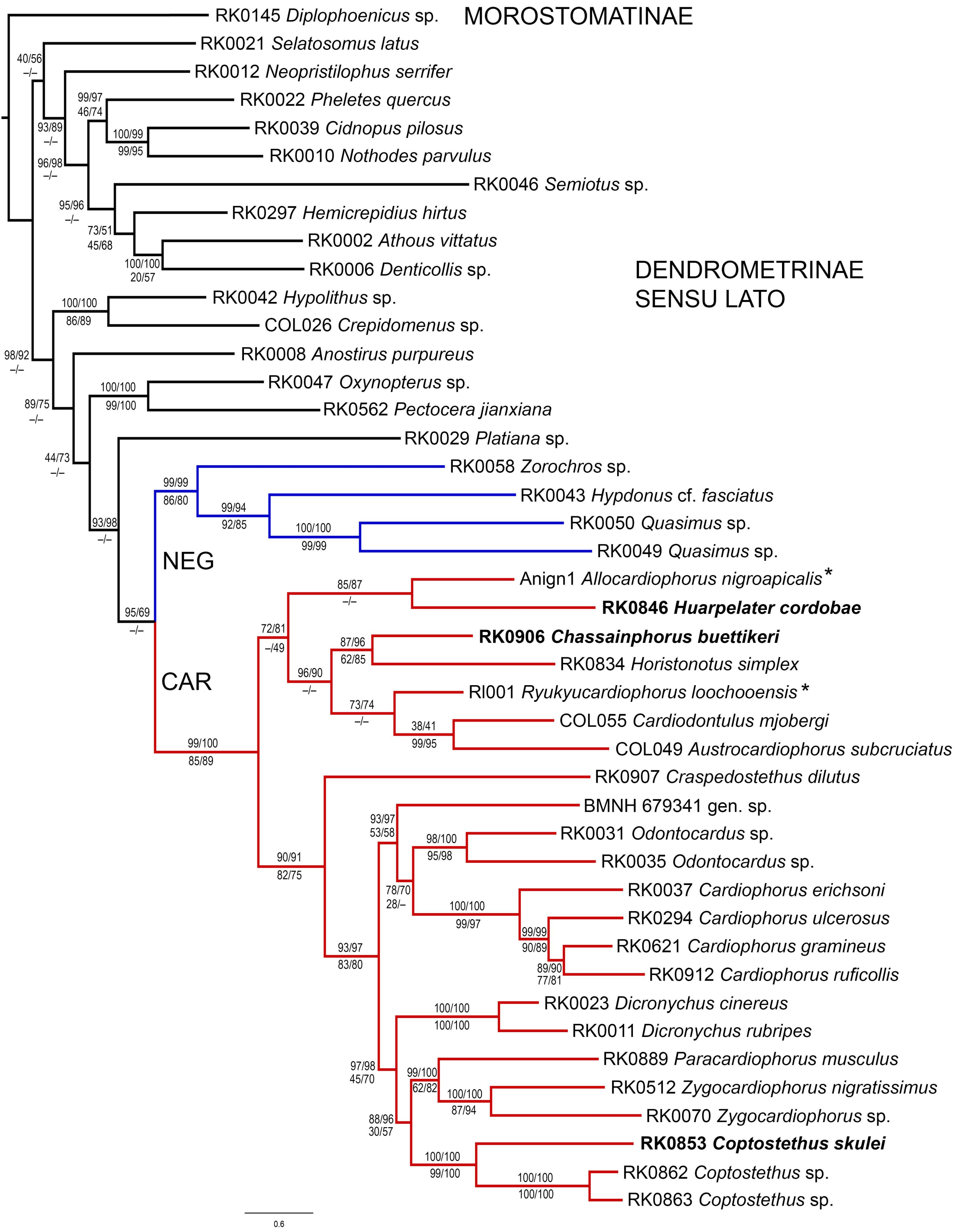
Schenkling S (1925) Elateridae I. *Coleopterorum Catalogus, auspiciis et auxilio W. Junk*, Pars 80. W. Junk, Berlin, Germany.

Schwarz O (1906a) Neue Elateriden aus Amerika. *Deutsche Entomologische Zeitschrift* **1906**, 97–158.

Schwarz O (1906b) *Coleoptera. Fam. Elateridae. Genera Insectorum de P. Wytsman, Fasc. 46*. P. Wytsman, Brussels.

Steinheil E (1874) Symbolae ad historian Coleopterorum Argentiniae Meridionales, ossia enumerazione dei coleotteri raccolti dal Prof. Strobel nell' Argentinia Meridionale e descrizione delle specie nuove. *Atti della Società Italiana di Scienze Naturali* **15**, 554–578.

Wollaston TV (1854) *Insecta Maderensia: being an account of the insects of the islands of the Madeiran Group*. John van Voorst, London, UK.


MOROSTOMATINAE
RK0145 Diplophoenicus sp.
40/56
–/–
RK0021 Selatosomus latus
RK0012 Neopristilophus serrifer
99/97
46/74
RK0022 Pheletes quercus
93/89
–/–
100/99
99/95
RK0039 Cidnopus pilosus
RK0010 Nothodes parvulus
96/98
–/–
95/96
–/–
RK0046 Semiotus sp.
RK0297 Hemicrepidius hirtus
73/51
45/68
RK0002 Athous vittatus
100/100
20/57
RK0006 Denticollis sp.
DENDROMETRINAE
SENSU LATO
100/100
86/89
RK0042 Hypolithus sp.
COL026 Crepidomenus sp.
98/92
–/–
RK0008 Anostirus purpureus
100/100
99/100
RK0047 Oxynopterus sp.
89/75
–/–
RK0562 Pectocera jianxiana
RK0029 Platiana sp.
44/73
–/–
99/99
86/80
RK0058 Zorochros sp.
RK0043 Hypdonus cf. fasciatus
99/94
92/85
93/98
–/–
100/100
99/99
RK0050 Quasimus sp.
RK0049 Quasimus sp.
NEG
85/87
–/–
Anign1 Allocardiophorus nigroapicalis*
95/69
–/–
RK0846 Huarpelater cordobae
72/81
–/49
87/96
62/85
RK0906 Chassainphorus buettikeri
RK0834 Horistonotus simplex
CAR
96/90
–/–
RI001 Ryukyucardiophorus loochooensis*
73/74
–/–
38/41
99/95
COL055 Cardiodontulus mjobergi
99/100
85/89
COL049 Austrocardiophorus subcruciatus
RK0907 Craspedostethus dilutus
93/97
53/58
BMNH 679341 gen. sp.
98/100
95/98
RK0031 Odontocardus sp.
90/91
82/75
RK0035 Odontocardus sp.
78/70
28/–
RK0037 Cardiophorus erichsoni
100/100
99/97
99/99
90/89
RK0294 Cardiophorus ulcerosus
93/97
83/80
RK0621 Cardiophorus gramineus
89/90
77/81
RK0912 Cardiophorus ruficollis
100/100
100/100
RK0023 Dicronychus cinereus
RK0011 Dicronychus rubripes
97/98
45/70
99/100
62/82
RK0889 Paracardiophorus musculus
100/100
87/94
RK0512 Zygocardiophorus nigratissimus
88/96
30/57
RK0070 Zygocardiophorus sp.
RK0853 Coptostethus skulei
100/100
99/100
100/100
100/100
RK0862 Coptostethus sp.
RK0863 Coptostethus sp.
0.6

Příloha 8

Baalbergen, E., Helwerda, R., Schelfhorst, R., Castillo Cajas, R.F., van Moorsel, C.H.M., **Kundrata, R.**, Welter-Schultes, F.W., Giokas, S. & Schilthuizen, M. (2014) Predator-prey interactions between shell-boring beetle larvae and rock-dwelling land snails. *PLoS ONE*, 9: e100366.
[IF 3,234; 14 citací na WoS; celkem 7 citací bez autorových autocitací]
[autorský podíl: 12 %]

Predator-Prey Interactions between Shell-Boring Beetle Larvae and Rock-Dwelling Land Snails

Els Baalbergen[1]☯, Renate Helwerda[1]☯, Rense Schelfhorst[1]☯, Ruth F. Castillo Cajas[2,3], Coline H. M. van Moorsel[4,5], Robin Kundrata[6], Francisco W. Welter-Schultes[7], Sinos Giokas[8], Menno Schilthuizen[1,2,5]*

1 Focus Group Character Evolution, Naturalis Biodiversity Center, Leiden, The Netherlands, **2** Centre for Ecological and Evolutionary Studies, Rijksuniversiteit Groningen, Groningen, The Netherlands, **3** Department of Animal Ecology and Tropical Biology, University of Würzburg, Würzburg, Germany, **4** St Antonius Hospital, Nieuwegein, The Netherlands, **5** Institute Biology Leiden, Leiden University, Leiden, The Netherlands, **6** Department of Zoology, Palacky University, Olomouc, Czech Republic, **7** Zoologisches Institut der Universität, University of Göttingen, Göttingen, Germany, **8** Department of Biology, University of Patras, Rio (Patras), Greece

Abstract

Drilus beetle larvae (Coleoptera: Elateridae) are specialized predators of land snails. Here, we describe various aspects of the predator-prey interactions between multiple *Drilus* species attacking multiple *Albinaria* (Gastropoda: Clausiliidae) species in Greece. We observe that *Drilus* species may be facultative or obligate *Albinaria*-specialists. We map geographically varying predation rates in Crete, where on average 24% of empty shells carry fatal *Drilus* bore holes. We also provide first-hand observations and video-footage of prey entry and exit strategies of the *Drilus* larvae, and evaluate the potential mutual evolutionary impacts. We find limited evidence for an effect of shell features and snail behavioral traits on inter- and intra-specifically differing predation rates. We also find that *Drilus* predators adjust their predation behavior based on specific shell traits of the prey. In conclusion, we suggest that, with these baseline data, this interesting predator-prey system will be available for further, detailed more evolutionary ecology studies.

Citation: Baalbergen E, Helwerda R, Schelfhorst R, Castillo Cajas RF, van Moorsel CHM, et al. (2014) Predator-Prey Interactions between Shell-Boring Beetle Larvae and Rock-Dwelling Land Snails. PLoS ONE 9(6): e100366. doi:10.1371/journal.pone.0100366

Editor: Fabio S. Nascimento, Universidade de São Paulo, Faculdade de Filosofia Ciências e Letras de Ribeirão Preto, Brazil

Received December 10, 2013; **Accepted** May 26, 2014; **Published** June 25, 2014

Funding: Funding for this study came from NWO-ALW (grant 819.01.012, awarded to M.S.), the Jan-Joost ter Pelkwijkfonds (awarded to E.B, R.S., and R.H.), the Uyttenboogaart-Eliasen Fonds (awarded to M.S.), the Kees Bakker award (awarded to R.H.), and a doctoral fellowship to F.W.-S. from the Evangelisches Studienwerk. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

* Email: menno.schilthuizen@naturalis.nl

☯ These authors contributed equally to this work.

Introduction

Gastropods are among the most diverse groups of animals, and the most readily observable aspect of this diversity is in their shell form and ornamentation. Gastropod shell shape is generally considered to evolve under a strong direct influence of biotic and abiotic agents, and, at least in marine gastropods, predator-prey interactions are paramount among these [1–2]. On land, however, the influence of predators on snail shell evolution is less clear [3].

One particularly diverse group of land snails is the clausiliid genus *Albinaria*, of which the >100 species occur abundantly on limestone rocks throughout Greece and surrounding regions (fig. 1A) [4], with most species occupying small, usually non-overlapping ranges [5–7]. The animals actively forage on micro-flora on the rocks during the wet months (roughly October to April), but estivate, usually with their apertures firmly sealed to the rock, and often in dense clusters, during the dry part of the year. Species differentiation is most apparent in various shell traits, such as radial ribbing, apertural folds and lamellae, and the structure of the clausilium (a door-like aperture closing apparatus and a Clausiliidae synapomorphy; figs. 1B, C).

Although *Albinaria* snails are preyed upon by a wide range of predators, including rodents, molluscivorous snails, and carabid beetles [8], their chief enemies appear to be larvae of the elaterid beetle genus *Drilus* (fig. 1D–F). These enter *Albinaria* snails by boring a hole through the shell wall (fig. 1G), killing and eating the snail's soft body, and, after molting or pupating, leaving via a second bore-hole (fig. 1H) [9–10]; but see below. Often, the entry and exit holes can be distinguished by their shape [8]. In many locations, more than 50% of the empty shells carry such *Drilus* bore-holes [11].

Given their intimate relationship with *Albinaria* and their shells, we expect that *Drilus* might be an important selective agent in *Albinaria* shell evolution. Indications of non-random predation by *Drilus* already exist, since Mesher and Welter-Schultes [11] found that on the island of Día (off Crete), *Drilus* attack was high in the three native *Albinaria* species, but low in a fourth, possibly introduced, species. To assess such possibilities further, we have investigated in more detail the interaction between *Albinaria* and *Drilus* in various regions in Greece.

Biogeography and Diversity of *Drilus* Predators

We first investigated the geographic variation in predation rate, by mapping the proportions, relative to the total number of empty shells, of shells with *Drilus* bore-holes, which have a characteristic size and shape, and are easily distinguished from other types of shell damage—see fig. S1 and [8]—throughout Crete. We did this by measuring the proportion of shells with *Drilus* holes in each of 1,160 museum samples. (With "sample" we mean a number of

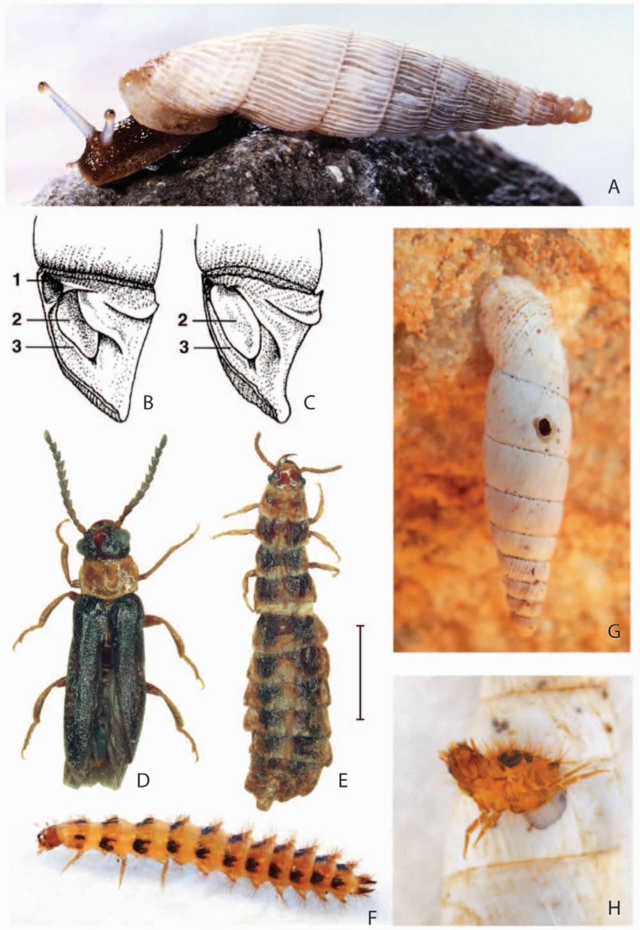


Figure 1. Greek *Albinaria* snails and their *Drilus* predators. A, *Albinaria hippolyti* from Crete (photo: V. Wiese). B and C, the clausilium, shown in the shell aperture after removal of the left lateral shell wall (B shows a less-obstructing, N-type clausilium, C shows a more obstructing, G-type clausilium). D and E, a male and a female, respectively, of a yet undescribed *Drilus* species from Crete (scale: 2 mm). F, a full-grown larva of *Drilus* "L" from the Peloponnese (same scale as D and E). G, an estivating *A. discolor* from the Peloponnese, with a *Drilus* exit bore hole. H, a *Drilus* "L" exiting from its prey, an *A. menelaus* from the Peloponnese.
doi:10.1371/journal.pone.0100366.g001

empty shells from a single location, usually taken in a 50×50 m area; see Data files S1 and S3.) These show a pattern of high, but regionally varying predation rates, with an average of 0.239±0.168 (fig. 2). In the Peloponnese and Kephalonia, where our geographic coverage was much less complete, we found predation rates that appeared lower than in Crete, but still substantial: average = 0.082±0.079 (n = 18 samples, 7,450 shells in total; in view of the mixed character of the samples, we refrained from testing for significance in the Crete vs. Peloponnese+Kephallonia difference). *Drilus* predation therefore accounts for a large proportion of total adult mortality [12].

We then used a combination of larval and adult characters, and mtDNA sequencing, to determine the number of *Drilus* species in the region, as well as their prey specificity (see Data file S2). We found that at least nine species can be distinguished (for the taxonomic and phylogenetic details we refer to Ref. [13], and Kundrata et al. unpublished manuscript; we provide a preliminary map of the species' distributions in fig. S2). For the four species that occur in Crete, we did not assess prey specificity, but for the remaining five, occurring in the Peloponnese, Zakynthos, and Kephalonia, we were able to do this by investigating bore holes and exuviae in shells of the entire snail fauna in 39 locations. The results (Fig. 3A) show that *Drilus* includes obligate *Albinaria*-specialists (e.g., *Drilus* "L") as well as generalists that only rarely attack *Albinaria* (e.g., *Drilus* "E"). Although these results may be somewhat confounded by differences in the snail species abundance distributions, the data from two locations, Paralíon Ástros and Koutróufa, where two *Drilus* species (*D.* "D" and *D.* "E") occur syntopically, confirm the differences in prey specificity between these two species (Fig. 3B). As in other members of the genus, our *Drilus* species tend to have small geographic ranges (e.g., *Drilus* "D," "L," and "M" may have range lengths of 50 km or less), which may be explained by the fact that *Drilus* females are wingless (fig. 1E) [14].

Behavior of *Drilus* preying on *Albinaria*

Unexpectedly, we found that *Drilus* may successfully attack *Albinaria* without leaving any bore-holes in the shell. We opened 645 dead *Albinaria* shells from the Peloponnese, and out of 169 shells that had been preyed by *Drilus* (judged by the presence of exuviae or a live larva), 60 contained exuviae but showed no trace of a bore-hole. This means not only that predation rates calculated from bore-hole frequencies are underestimates, but also that *Drilus* employs more than one attack strategy.

To understand better the predatory behavior of *Drilus*, we obtained three live pseudopupae (an immobile resting stage) from field-collected *Albinaria* shells, as well as live *Albinaria*, and used these for observations in the laboratory. Of these three, one remained in pseudopupal state. The other two (both *Drilus* "L") molted into active larvae. One (obtained from an *A. edmundi*) entered an *Albinaria edmundi* via the aperture and killed it. It remained inside for 28 days, bored a hole in the shell wall to exit, but then died while emerging. However, the third one (obtained from an *A. discolor*) stayed alive and active for almost two years, and during that time consumed eight adult prey individuals. In all eight predation events (which took place under dark conditions in a box with several loose *Albinaria* individuals, i.e., not adhering to any substrate), the larva entered the snail via the aperture (after having inspected several potential prey), never boring a hole in the shell wall nor into the clausilium (Video S2). After entering a snail, it apparently attacked and ate (part of) the snail immediately, because it moved fragments of dried, undigested snail tissue outside of the aperture within three days. In total, it would remain in a shell for 22–32 days, except for one very lengthy stay inside a prey shell that lasted from September 19th until May 1st, and possibly indicated hibernation. Each time the larva exited from an empty prey shell, it left behind an exuvia, meaning that the number of larval stages may be much larger than the three to four that had been suspected previously [15–16]. In all cases except one, the larva did bore a hole from within the prey shell to exit. Boring was done with the jaws and a copious amount of (possibly acidic) saliva and, based on the one occasion when it was observed from start to finish (Video S1; fig. 4) took seven hours.

These observations confirm that a *Drilus* may enter an *Albinaria* prey either by apertural-entry or by shell-boring (see also Video S2 for these behaviors in Cretan species). Similarly, it may also exit the (empty) prey shell either via the aperture or via a new bore-hole. As in other snail-predator interactions [16–18], each of these entry and exit strategies have their advantages and disadvantages. For example, apertural entry as well as exit may be hindered by the clausilium and/or by apertural folds that project into the lumen of the whorl. On the other hand, it may be less costly than

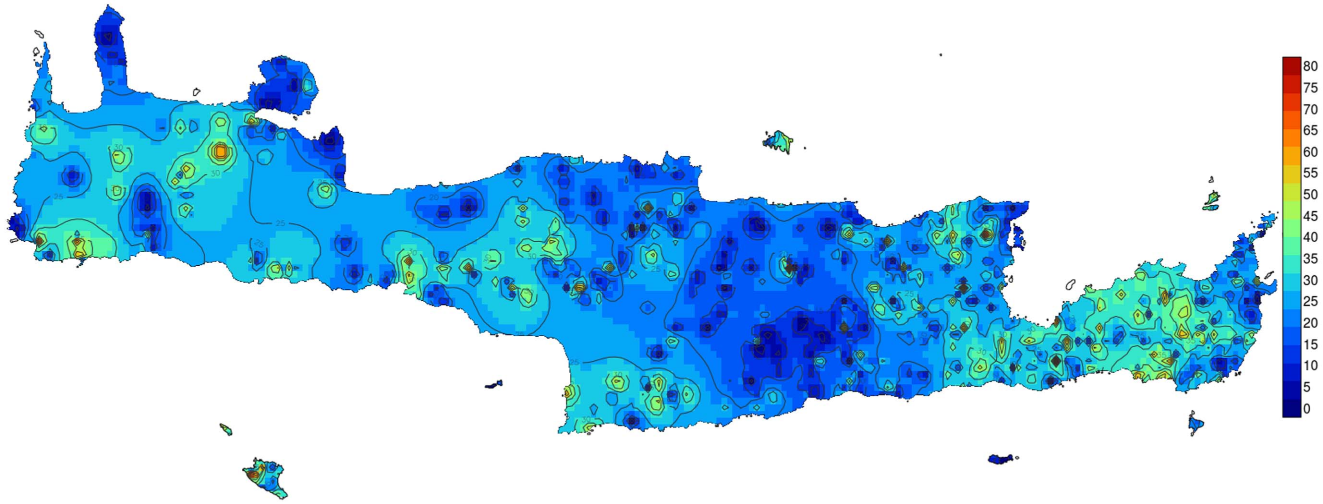


Figure 2. Map of Crete and surrounding islands, showing contours of regionally varying *Drilus* predation rates (given as percentages attacked shells per sample) in *Albinaria*, derived from bore-hole frequencies in 1,160 museum samples from Naturalis Biodiversity Center, Leiden, The Netherlands, Haus der Natur, Cismar, Germany, and Natural History Museum, Budapest, Hungary. Maps were drawn using inverse kriging distance calculation in R v.2.15.2 [23], with packages gstat [24], maptools (R v.0.8-27), rgdal (R v.0.8-12) and rgeos (R v.0.3-2).
doi:10.1371/journal.pone.0100366.g002

boring in terms of time, energy, and saliva (if the saliva indeed helps dissolve the shell). Entering and perhaps also exiting the shell by boring may be hindered by the presence of dense and/or tall radial ribs on the shell surface, but is more costly. Finally, it should be noted that shell features that impede predator entry will primarily impose a selection pressure on the prey (by ensuring its survival), whereas those that impede predator exit will primarily select for predator traits (by causing the predator to die within the prey shell).

Potential Evolutionary Impact of Predator-Prey Interaction on the Prey

We may predict that more heavily-ribbed *Albinaria* species [19] are better protected against boring (and therefore show a lower proportion of bored shells and/or more bore-hole failures) and that *Albinaria* species with a more completely obstructed aperture [20] are better protected against apertural-entry (and therefore show more bored shells). As a preliminary test of these predictions, we scored numbers of bored and intact shells in pairs of syntopic *Albinaria* species, exposed to the same *Drilus* species, but differing in either radial rib height or apertural obstructions. Our results (Table S1) do not provide consistent support for the predictions. At Argínia, the strongly ribbed *A. adrianae* has, as predicted, a lower proportion of bored shells than the smooth *A. contaminata*, but at Póros, no difference was found. Bore-hole failures do not differ among the four populations. At one of the three sites where a species with a partly-obstructed aperture (an N-type clausilium) co-occurs with a species with a completely obstructed (G-type) aperture, the latter has fewer bored shells, while at the other two locations, no difference was found. Obviously, these results are inconclusive since they are based on small numbers of populations and should be repeated with a larger-scale study, including more species and more locations.

We also obtained some data that suggest that predation by *Drilus* may be non-random within a single *Albinaria* population and hence may cause natural selection on variable traits. In a population of *A. krueperi*, preyed upon by *Drilus* "G", we found that predation (derived from exuviae in the shells) was predominantly towards the smaller individuals; however, such a response was not found in a population of *A. adriani*, preyed upon by *Drilus* "D" and "E" (Table S2). In addition, in a population of *A. caerulea* from the Cyclades, we found that predation risk (derived from bore-hole data) was greater in snails estivating in isolation than in snails estivating in clusters (fig. 3C), which may be one way in which such clustered estivation (a conspicuous behavioral pattern in most *Albinaria* species) evolved.

Potential Evolutionary Impact of Predator-Prey Interaction on the Predator

In contrast to the evolutionary impact that the predator may have on the prey, the reverse may also be the case. *Albinaria* snails are, at least during the dry months of the year, often firmly sealed against the substrate, whereas most of the other species that we recorded as *Drilus* prey tend to estivate in the soil. We may therefore expect that *Drilus* species that are more specialized in feeding on *Albinaria*, have a greater tendency to bore holes for entering, and, probably more importantly, for exiting the shell (an inability to do the latter would mean death for the *Drilus* larva). Indeed, we find a positive correlation between *Albinaria*-specificity and hole-boring tendency among the five *Drilus* species from the Peloponnese and Kephalonia (fig. 3A).

Finally, another indication that the prey shell morphology affects the predator was obtained when we compared the positions of entrance holes in shells of species with an N-type clausilium (*A. argynnis*, *A. discolor*, and *A. solicola*; all from the Eastern Peloponnese) with those in shells of species with a G-type clausilium (*A. adriani*, *A. edmundi*, and *A. campylauchen*, all roughly sympatric with the previous three). We found that in the N-type group, more shells had a bore-hole in the outer shell wall between the aperture and the clausilium than in the G-type group (fig. 3D). Since the N-type species have a clausilium that does not completely close off the aperture, whereas the G-type clausilium does, these data may indicate that predator populations faced with G-type prey have evolved a shell entry strategy by which the hole is bored at a

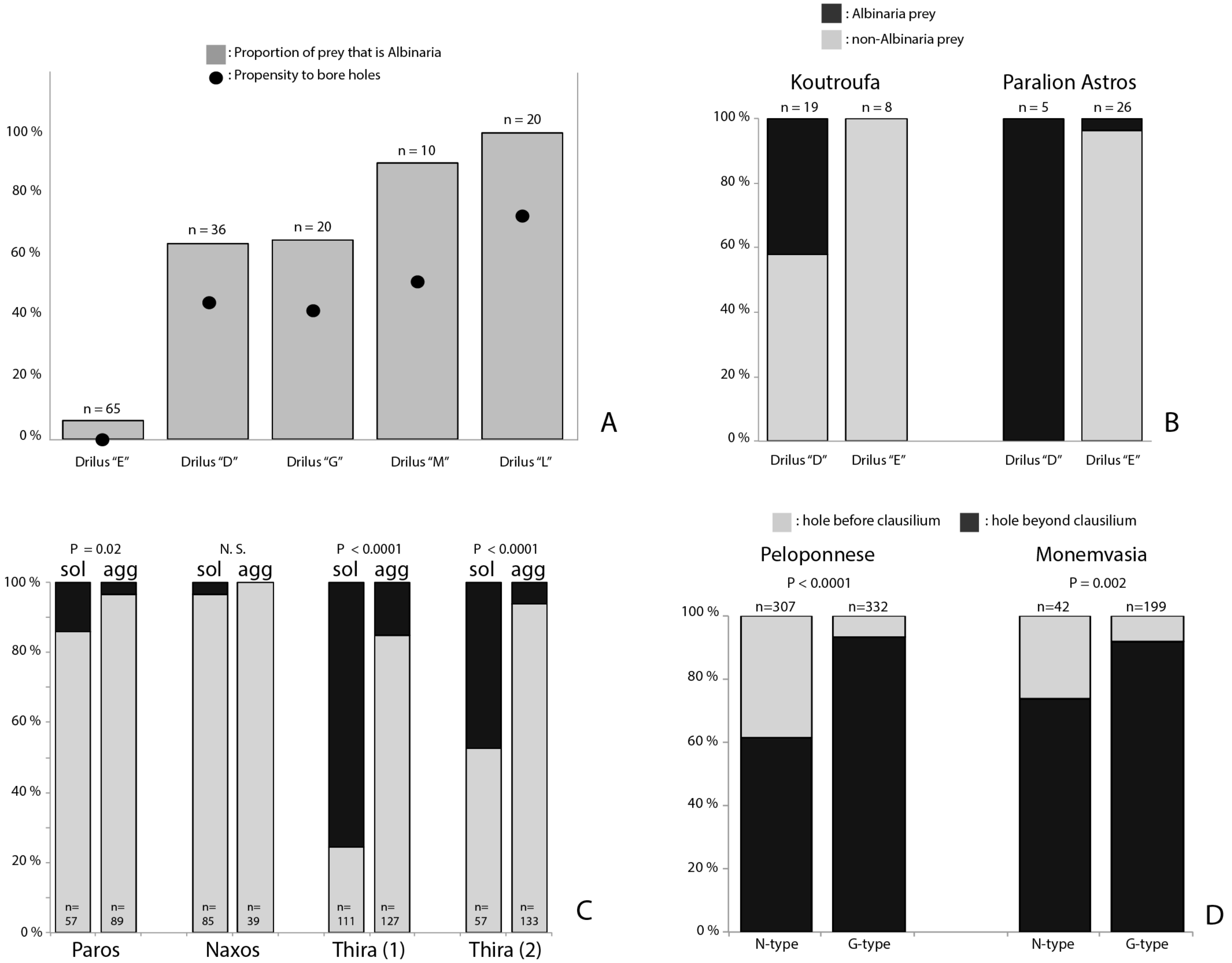


Figure 3. A, five *Drilus* species from the Peloponnese have different specificities for *Albinaria* as prey, and concomitant propensities to bore holes in the shell (calculated as the number of bore holes divided by the total number of prey). B, difference ($P<0.05$, Fisher's exact test) in prey specificity between *Drilus* "D" (more *Albinaria*-specific) and "E" (less *Albinaria* specific) in two localities where both species occur syntopically (these data are not included in fig. 3A). C, differences in *Drilus* predation rate (dark portion of the bar) between solitarily ("sol") and group-wise ("agg") estivating snails of *A. caerulea* in four 5 m^2 plots in the islands of Paros, Naxos, and Thira (voucher numbers RMNH.MOL.84354-84363, RMNH.MOL.85192, and RMNH.MOL.85193). An aggregate was defined as a cluster of >20 snails, with distances of <2 cm separating them. A snail was considered solitary if it was >20 cm distance from a conspecific (significance tested with Chi-square test). D, positions of entrance holes in shells of species with an N-type clausilium compared with those in shells of species with a G-type clausilium, shown for the entire eastern Peloponnese as well as for the site Monemvasia, where both clausilium types occur microsympatrically. (*P*-values are derived from Fisher's exact test.)
doi:10.1371/journal.pone.0100366.g003

position beyond the obstruction. However, the same difference is seen in Monemvasia, where the N-type *A. discolor* lives syntopically with the G-type *A. campylauchen*. This suggests that, rather than an evolved behavioral difference between predator populations, the predator may also be able to detect the clausilium type before boring a hole and that the difference in strategy is due to a behavioral response, rather than an evolved, fixed behavior (fig. 3D).

Conclusion

Given the complexity of this predator-prey system, with multiple predator species, multiple prey species, varying prey specificity, and complex small-scale biogeographic patterns, we will not hazard a conclusion on the impact of these interactions on shell evolution in *Albinaria*. However, we think we have shown that detailed study of the natural history of these ecological interactions reveal a potential for such evolutionary responses. Elements from our study may provide starting points for further work, specifically targeted at understanding the possible predator-prey arms races or patterns of escalation in this system, an approach that has proved successful in a similar terrestrial system consisting of tropical micro-snails and shell-boring slugs [21–22].

Additional Methods Details

Sampling of live specimens was done at the locations with the following coordinates: 37°09.694′ N, 22°48.745′ E and 37°20.132′ N, 22°45.769′ E. No specific permissions were required for the accomplished field sampling activities by the University of Patras. The field studies were conducted exclusively in public and not protected land areas. The field studies did not involve any endangered or protected species. Sampling was

Figure 4. Still from Video S1, showing a *Drilus* "L" larva (in the lab) creating an exit bore-hole from within a prey *Albinaria meleaus*, followed by the lengthy procedure by which the larva emerges from the shell.
doi:10.1371/journal.pone.0100366.g004

conducted according to the main legal texts in the field of biodiversity (UN Convention on Biodiversity), which became part of the Greek legislation in 1994 (law 2204), and the EU Directive 2004/35 regulating environmental liability. Animal capturing, handling and killing was designed to avoid distress and unnecessary suffering to the animals as laid down in the Council Directive 86/609/EEC, art. 7.4 and the Council of Europe (CoE) European Convention for the protection of vertebrate animals used for experimental and other scientific purposes (1986, ETS 123). All relevant information was also given to the Bioethics Committee of the University of Patras".

Supporting Information

Figure S1 Fig. S1. *Drilus* bore hole proportions (both entry and exit holes), based on measurements taken from shells of *A. discolor* and *A. adriani* from Agios Andreas and in *A. discolor, A. campylauchen* and *A. discolor x A. campylauchen* hybrids from Monemvasia.
(PDF)

Figure S2 Distribution map for *Drilus* morphospecies in the Peloponnese and surrounding area. In addition to morphospecies "D," "E," "G," "L," and "M," mentioned in the text, a location for a sixth species, "U," is also shown. Each dot represents one or more specimens. Bicolor dots indicate syntopic occurrence of multiple species. Scale bar = 100 km.
(PDF)

Data File S1 Data Collection Codes: This file contains detailed data on the snail samples, containing *Drilus* larvae, adults, or exuviae, collected in Greece for this study, as well as on the field localities. Data available from the Dryad Digital Repository:.
(XLSX)

Data File S2 Data Voucher Numbers: This file contains detailed information on all *Drilus* specimens used for this study. Data available from the Dryad Digital Repository:.
(XLSX)

Data File S3 Data Predation Crete: This file contains data used to assess geographic distribution of *Drilus* predation rates in *Albinaria* prey across Crete. Material derived from Naturalis Biodiversity Center, Leiden, and Haus der Natur, Cismar. Data available from the Dryad Digital Repository:.
(XLS)

Table S1 *Drilus* predation in co-occurring prey species pairs differing in shell traits. Significance was tested with Fisher's exact test.
(DOCX)

Table S2 Five shell traits in *Albinaria krueperi* and *A. adriani* populations, with indications for selection by *Drilus* predation. Shell height and width were measured with hand-held calipers, the other traits with a graded ocular. *Drilus* attack was ascertained by the presence of a bore hole and/or an exuvia in the shell. Significance was tested with 2-sample t-test in R.
(DOCX)

Video S1 A *Drilus* "L" larva (in the lab) creating an exit bore-hole from within a prey *Albinaria meleaus*, followed by stills from the lengthy procedure by which the larva emerges from the shell.
(WMV)

Video S2 Series of three clips (footage sped up 64x), taken in the lab: First, *Drilus longulus* larva entering an *Albinaria* (*cretensis* complex) shell via an entry bore-hole, followed by footage in which entry is made by a *Drilus* sp. via the aperture of an *Albinaria* (*cretensis* complex) snail. Finally, a *Drilus* "L" larva selecting and entering an *A. menelaus* snail via the aperture.
(WMV)

Acknowledgments

We thank Edmund Gittenberger and Robert Cameron for help with the identification of certain species of Greek snails, and Bertie-Joan van Heuven and Marcel Eurlings for lab assistance. Paulien de Jong, Heike Kappes, Theo Kemperman, Thor-Seng Liew, Aydin Örstan, Ton de Winter, and Nikita van Zeijl served as valuable discussion partners during various parts of the study. Material from the Natural History Museum, Budapest, was kindly provided by P. Subai and L. Pintér, from Naturalis Biodiversity Center by Jeroen Goud and Bram van der Bijl, and from the Haus der Natur by Vollrath Wiese, who also supplied the photo of *Albinaria hippolyti*. In Patras, Evi Thanou provided logistical support.

Author Contributions

Conceived and designed the experiments: EB RH RS RC CvM RK MS SG FWS. Performed the experiments: EB RH RS RC CvM RK MS SG FWS. Analyzed the data: EB RH RS RC CvM RK MS SG FWS. Contributed reagents/materials/analysis tools: MS SG FWS. Wrote the paper: MS.

References

1. Vermeij GJ (1987) Evolution and Escalation: An Ecological History of Life. Princeton: Princeton University Press. 544 p.
2. Vermeij GJ (2011) The energetics of modernization: the last one hundred million years of biotic evolution. Palaeontol Res 15: 54–61.
3. Goodfriend GA (1986) Variation in land-snail shell form and size and its causes: a review. Syst Zool 35: 204–223.
4. Nordsieck H (1999) Annotated check-list of the species of the *Albinaria-Isabellaria* group (Gastropoda: Stylommatophora: Clausiliidae). Mitt Dt Malakozool Ges 62/63: 1–21.
5. Gittenberger E (1991) What about nonadaptive radiation? Biol J Linn Soc 43: 263–272.
6. Welter-Schultes FW (2010) Revision of the genus *Albinaria* in Crete (Greece): presence of geographically variable monotypic and polytypic species. Archiv Molluskenk 139: 143–245.

7. Welter-Schultes FW (2012) European non-marine molluscs, a guide for species identification. Göttingen: Planet Poster Editions. 760 p.
8. Schilthuizen M, Kemperman TCM, Gittenberger E (1994) Parasites and predators in *Albinaria* (Gastropoda Pulmonata: Clausiliidae). Bios (Macedonia, Greece) 2: 177–186.
9. Roth JR (1855) Spicilegium molluscorum orientalium annis 1852 et 1853 collectorum. Malakozool Bl 2: 17–58.
10. Örstan A (1999) Drill holes in land snail shells from Western Turkey. Schr Malakozool 13: 31–36.
11. Mesher CS, Welter-Schultes FW (2008) Studies on range expansion, predation pressure, and insolation in *Albinaria* on the island of Dia (Greece), focused on a recently introduced species (Gastropoda: Clausiliidae). Species Phyl Evol 1: 129–140.
12. Giokas S, Mylonas M (2002) Spatial distribution, density and life-history in four *Albinaria* species (Gastropoda, Pulmonata, Clausiliidae). Malacologia 44: 33–46.
13. Baalbergen E (2013) Larvae of Drilini (Coleoptera: Elateridae) beetles preying on snails. M.Sc. thesis, Leiden University. 65 p.
14. Kundrata R, Bocak L (2011) The phylogeny and limits of Elateridae (Insecta, Coleoptera): is there a common tendency of click beetles to soft-bodiedness and neoteny? Zool Scr 40: 364–378.
15. Schilthuizen M (1994) Differentiation and Hybridisation in a Polytypic Snail. Ph. D. thesis, Leiden University. 178 p.
16. Vermeij GJ (1979) Shell architecture and causes of death of Micronesian reef snails. Evolution 33: 686–696.
17. DeWitt TJ, Robinson BW, Wilson DS (2000) Functional diversity among predators of a freshwater snail imposes an adaptive trade-off for shell morphology. Evol Ecol Res 2: 129–148.
18. Konuma J, Chiba S (2007) Trade-offs between force and fit: Extreme morphologies associated with feeding behavior in carabid beetles. Am Nat 170: 90–100.
19. Kemperman TCM, Gittenberger E (1988) On morphology, function and taxonomic importance of the shell ribs in Clausiliidae (Mollusca: Gastropoda Pulmonata) with special reference to those in *Albinaria*. Basteria 52: 77–100.
20. Van Moorsel CHM, Dijkstra EGM, Gittenberger E (2000) Molecular evidence for repetitive parallel evolution of shell structure in Clausiliidae. Mol Phyl Evol 17: 200–208.
21. Schilthuizen M, van Til A, Salverda M, Liew TS, James SS, et al. (2006) Microgeographic evolution of snail shell shape and predator behavior. Evolution 60: 1851–1858.
22. Liew TS, Schilthuizen M (2014) Association between shell morphology of micro-land snails (genus *Plectostoma*) and their predator's predatory behaviour. PeerJ 2: e329 Available: https://peerj.com/articles/329/. Accessed 1 June 2014.
23. R Core Team (2012) R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.
24. Pebesma EJ (2004) Multivariable geostatistics in S: the gstat package. Computers Geosci 30: 683–691.

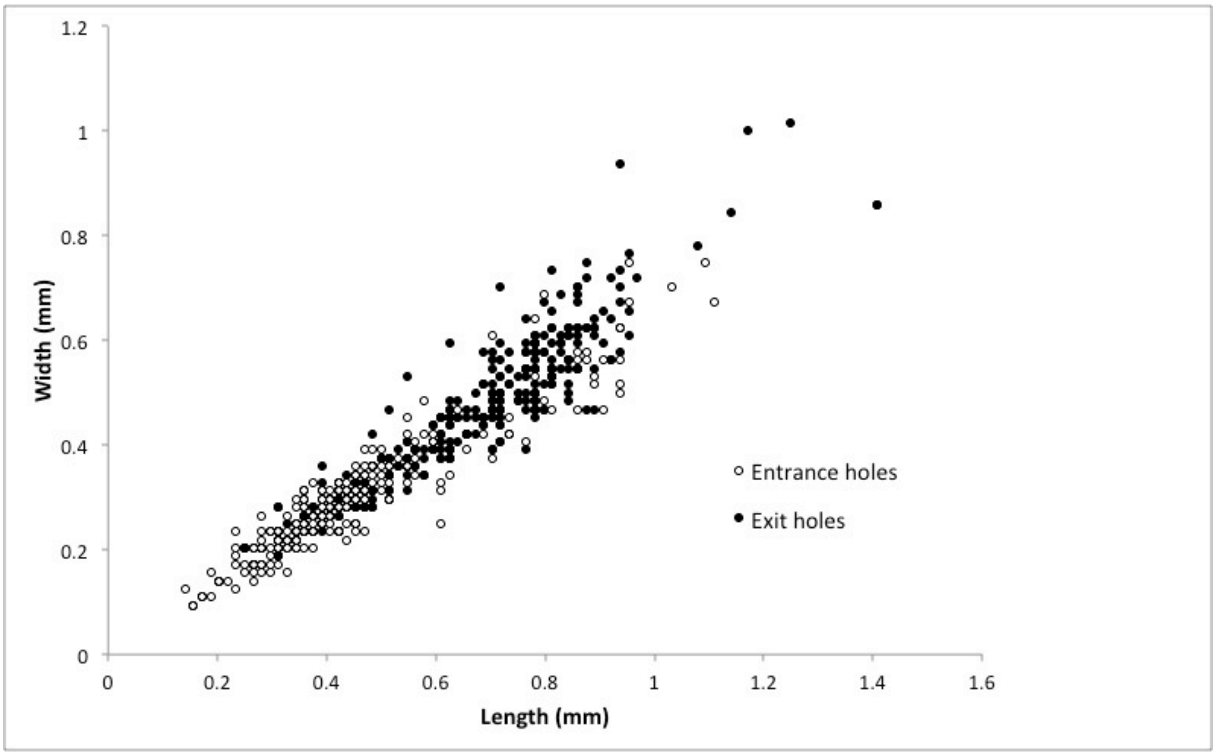


Fig. S1. *Drilus* bore hole proportions (both entry and exit holes), based on measurements taken from shells of *A. discolor* and *A. adriani* from Agios Andreas and in *A. discolor, A. campylauchen* and *A. discolor x A. campylauchen* hybrids from Monemvasia.

Distribution of morphospecies in the Peloponnese and Ionian Islands

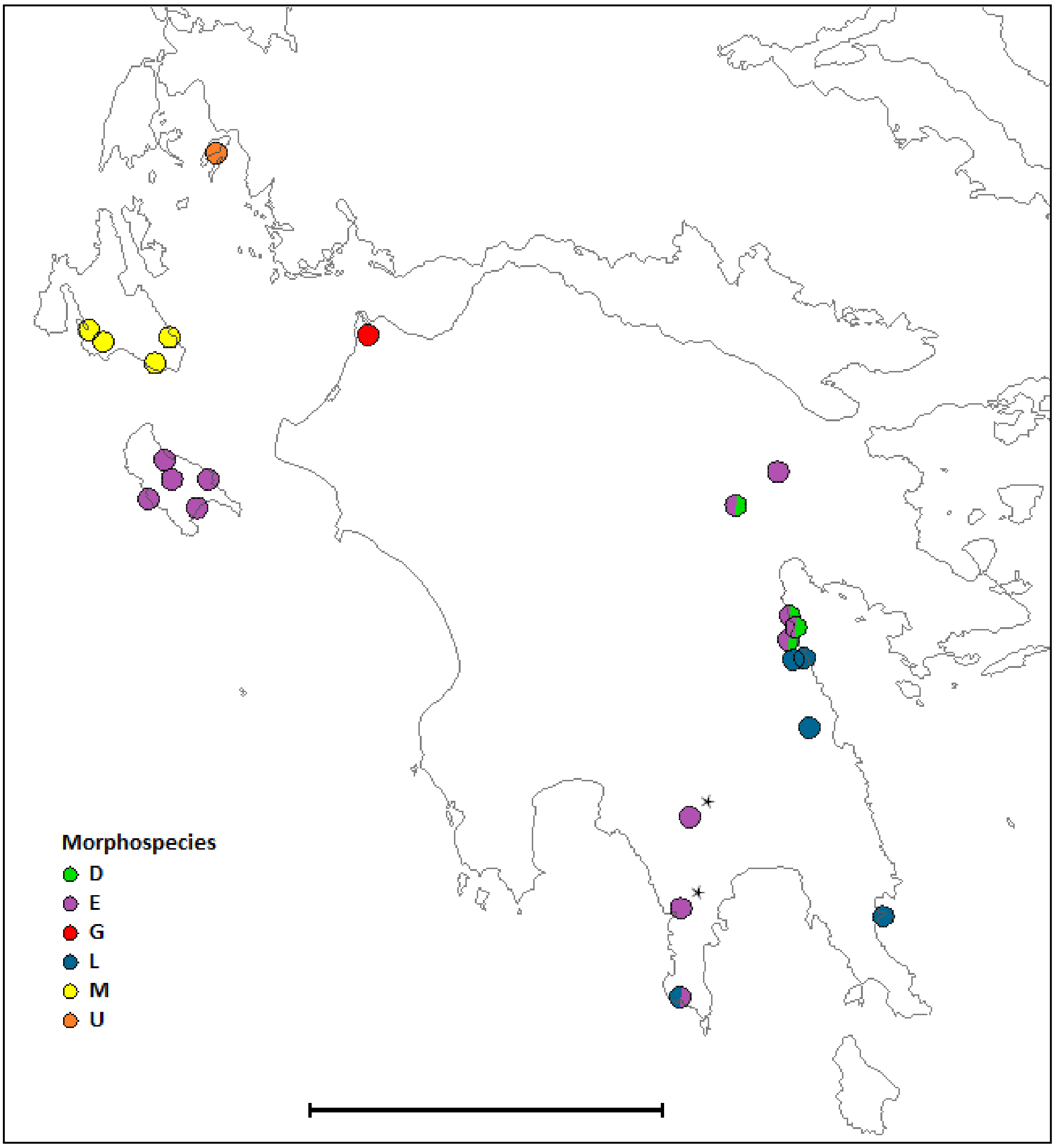


Figure S2. Distribution map for *Drilus* morphospecies in the Peloponnese and surrounding area. In addition to morphospecies “D,” “E,” “G,” “L,” and “M,” mentioned in the text, a location for a sixth species, “U,” is also shown. Each dot represents one or more specimens. Bicolor dots indicate syntopic occurrence of multiple species. Scale bar = 100 km.

Příloha 9

Kundrata, R., Baena, M. & Bocák, L. (2015) Classification of Omalisidae based on molecular data and morphology, with description of Paradrilinae subfam. nov. (Coleoptera: Elateroidea). *Zootaxa*, 3915: 413–422.
[IF 0,994; 7 citací na WoS; celkem 4 citace bez autorových autocitací]
[autorský podíl: 40 %]

Zootaxa 3915 (3): 413–422
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3915.3.6
http://zoobank.org/urn:lsid:zoobank.org:pub:248111C9-0C68-4F1C-A9B0-B5F1E0DAB54B

Classification of Omalisidae based on molecular data and morphology, with description of Paradrilinae subfam. nov. (Coleoptera: Elateroidea)

ROBIN KUNDRATA[1], MANUEL BAENA[2] & LADISLAV BOCAK[1,3]

[1]*Department of Zoology, Faculty of Science, Palacky University, 17. listopadu 50, 771 46, Olomouc, Czech Republic.*
E-mails: robin.kundrata@upol.cz, ladislav.bocak@upol.cz
[2]*Departamento de Biología y Geología, I.E.S. Trassierra, c/Avenida Arroyo del Moro, s/n, 14011 Córdoba, Spain.*
E-mail: tiarodes@gmail.com
[3]*Corresponding author*

Abstract

Omalisidae, a species-poor family of elateroid beetles, are distributed mostly in the Mediterranean region. The morphology of females is modified due to neotenic development and the males share some traits with other neotenic lineages in Elateroidea, namely Drilini (Elateridae: Agrypninae) and Lyropaeinae (Lycidae). A molecular phylogeny was inferred from six omalisid species representing four genera and the previously published dataset of Elateroidea. The DNA based phylogeny suggests that small-bodied males, reduced pronotal carinae and missing elytral costae evolved independently in multiple elateroid lineages. The limits of Omalisidae are redefined and seven genera, *i.e.*, *Omalisus* Geoffroy, 1762, *Phaeopterus* Costa, 1857, *Thilmanus* Gemminger, 1869, *Euanoma* Reitter, 1889, *Pseudeuanoma* Pic, 1901, *Paradrilus* Kiesenwetter, 1865 and *Cimbrion* Kazantsev, 2010, are currently placed in the family. Thilmaninae Kazantsev, 2005 and *Paradrilus* Kiesenwetter, 1865 are transferred from Drilini (Elateridae: Agrypninae) to Omalisidae and the Paradrilinae subfam. nov. is proposed. *Paradrilus* differs from other Omalisidae in prolonged cranium, wide robust prosternum with two apical processes and absent sharp edge of the pronotum. The morphology of *Paradrilus* is described in detail, illustrated and all taxa currently classified in Omalisidae are listed.

Key words: Drilini, Elateroidea, molecular phylogeny, morphology, new subfamily, *Paradrilus*, *Phaeopterus*, taxonomy

Introduction

The Elateroidea represent a morphologically diverse lineage of both well sclerotized and soft-bodied beetles (Lawrence 1988, Bocakova *et al.* 2007). Major families, such as click beetles (Elateridae), fireflies (Lampyridae), soldier beetles (Cantharidae), and net-winged beetles (Lycidae), each with thousands of extant species, are well defined by morphological synapomorphies (Crowson 1972, Leschen *et al.* 2010). On the other hand, relationships, limits and status of Omalisidae have been subject of contradictory views (Crowson 1972, Kazantsev 2010, Kundrata & Bocak 2011a). Omalisidae kept either family rank or were included as a subfamily in Lycidae (*e.g.*, Bourgeois 1882, Kleine 1933, Crowson 1972). Altogether seven genera have been placed in Omalisidae since the family was erected, but only a type genus *Omalisus* Geoffroy, *Phaeopterus* Costa and *Cimbrion* Kazantsev have always been classified within the family (Tab. 1). *Thilmanus* Gemminger was placed in Lycidae or Drilidae and *Euanoma* Reitter, *Pseudeuanoma* Pic and *Paradrilus* Kiesenwetter in Drilidae (Tab. 1). These genera share similar weakly sclerotized, usually small-bodied males and incompletely metamorphosed females (*e.g.*, Crowson 1972, Kundrata & Bocak 2007, 2011a).

The molecular data suggested phylogenetic hypotheses in conflict with previous views: (1) refuted relationships of Omalisidae + Lycidae, (2) proposed the Phengodidae + Rhagophthalmidae + Omalisidae + Elateridae clade, and (3) recovered drilids as a terminal clade within Elateridae: Agrypninae. However, in the past molecular analyses, the number of included omalisid genera was limited to *Omalisus* and later *Pseudeuanoma* due to the rareness of these beetles (Bocakova *et al.* 2007, Kundrata & Bocak 2011a, Bocak *et al*. 2014, Kundrata *et al.* 2014).

Accepted by P. Johnson: 13 Jan. 2015; published: 4 Feb. 2015

TABLE 1. An overview of the classification of Omalisidae.

Genus	Bourgeois (1882)	Kleine (1933)	Crowson (1972)	Bocak & Brlik (2008)
Omalisus Geoffroy, 1762	present	present	present	present
Phaeopterus Costa, 1857	present	present	present	present
Euanoma Reitter, 1889	-	present	no (omitted)	no
Pseudeuanoma Pic, 1901	-	present	no (Drilidae)	no
Thilmanus Gemminger, 1869	present	present	no (Lycidae)	present
Paradrilus Kiesenwetter, 1865	present	no (Drilidae)	no	no
Cimbrion Kazantsev, 2010	-	-	-	-

continued.

Genus	Kazantsev (2010)	Kundrata &Bocak (2011)	This study
Omalisus Geoffroy, 1762	present	present	present
Phaeopterus Costa, 1857	present	present	present
Euanoma Reitter, 1889	no	present	present
Pseudeuanoma Pic, 1901	no	present	present
Thilmanus Gemminger, 1869	no (Drilidae)	present	present
Paradrilus Kiesenwetter, 1865	no	no	present
Cimbrion Kazantsev, 2010	present	-	present

Omalisidae are distributed in the western Palearctic region. *Omalisus fontisbellaquaei* Geoffroy, 1785 is the only common and widely distributed species. Other species are typically known from several specimens from a few localities in the Mediterranean region. The species level taxonomy of *Omalisus*, *Phaeopterus* and *Thilmanus* was revised by Bocak & Brlik (2008), and the genera *Euanoma* and *Pseudeuanoma* by Kundrata & Bocak (2007). These studies refrained from discussion on higher classification as the first DNA analyses have already shown a possibility that the neotenic modifications might result in simplifications of multiple complex morphological structures (*e.g*., simplified wing venation, modified thoracic morphology, vestigial mouthparts, and reduced elytral costae).

Recent field research yielded specimens of *Paradrilus* and *Phaeopterus* for DNA isolation. With the current dataset of four genera of Omalisidae and almost complete representation of other elateroid families (Bocakova *et al*. 2007, Kundrata *et al.* 2014), we are able to investigate internal relationships among omalisid genera. Additionally, a secondary aim of the current study is to provide morphological redescription of *Paradrilus* and to modify the classification of Omalisidae.

Material and methods

Laboratory procedures and concatenation of the dataset. The dataset of 557 terminals, most of them previously reported by Bocakova *et al.* (2007) and Kundrata *et al.* (2014), was expanded by the newly produced sequences of *Paradrilus opacus* and *Phaeopterus unicolor*. The voucher specimens are deposited in the authors' voucher collection. The sequences were deposited in GenBank with accession numbers KJ909284–KJ909287. The extensive dataset of Elateroidea was used to confirm the position of Omalisidae. Laboratory procedures and primers were reported by Bocakova *et al.* (2007) and Kundrata *et al.* (2014).

Sequence handling, alignment and phylogenetic analyses. Sequences were edited using Sequencher 4.9 (Gene Codes Corp., Ann Arbor, MI, USA). The length invariable *cox1* sequences were aligned by Mafft 7.149 (Katoh *et al.* 2002). The rRNA fragments were aligned using Mafft and BlastAlign 2.1, the later algorithm omits length variable parts when reliable alignment cannot be inferred (Belshaw & Katzourakis 2005). The concatenated datasets were partitioned by genes and codon positions and analyzed under the maximum likelihood criterion using

RAxML 7.3.1 (Stamatakis 2006) via the CIPRES web server (www.phylo.org; Miller *et al.* 2010). Bootstrap values (BS) were calculated using the rapid bootstrap algorithm (Stamatakis *et al.* 2008) with 1,000 bootstrap iterations under the GTRCAT model. The phylogenetic trees were visualized and edited in FigTree 1.3.1 (Rambaut 2009).

Morphology. Morphological examinations are based on adult males. DNA grade specimens of *Paradrilus opacus* and *Phaeopterus unicolor* were collected in Spain, Córdoba, Santa María de Trassierra, Arroyo del Molino by M. Baena (Fig. 19) and in Italy, Elba, Monte Perone by M. Geiser, respectively. Body parts were disarticulated after treatment in hot 10% aqueous solution of potassium hydroxide. The line drawings were derived from the photographs taken by camera mounted on a stereoscopic microscope. The measures were taken using ocular grid in a stereomicroscope.

Results

Three gene fragments, 18S rRNA (~1850 bp), 28S rRNA (~650 bp), and *cox1* mtDNA (723 bp) were produced for *Paradrilus opacus* and only the *cox1* mtDNA fragment for *Phaeopterus unicolor*. The 557-taxa 4-gene concatenated dataset aligned by BlastAlign and Mafft contained 5,339 and 5,434 positions, respectively. The aligned 18S represented 2,454 and 2,729 positions, 28S 1,255 and 1,310, and *rrnL* 907 and 672 positions. The *cox1* mtDNA fragment was aligned along protein coding codons (723 positions). The individual markers provided 34.6% (18S), 20.5% (28S), 20.1% (*rrnL*) and 24.9% (*cox1*) of the total number of parsimony informative positions in the Blast alignment.

The Omalisidae were recovered as a sister to Phengodidae + Rhagophthalmidae in the clade ((Omalisidae (Phengodidae, Rhagophthalmidae)) Elateridae) although with low bootstrap support (Fig. 1). No alternative placement of Omalisidae was recovered under described settings of analyses. The internal tree topology of Omalisidae was similar in both analyses: *Pseudeuanoma* was recovered a sister to other omalisids and *Paradrilus* a sister to the *Omalisus* + *Phaeopterus* clade (Fig. 2). However, also these internal branches obtained low support.

Discussion

Knowledge on Omalisidae had been limited to original generic and specific descriptions until recently as most species are rare and occur in very limited ranges (Kundrata & Bocak 2007, Bocak & Brlik 2008). Due to the very low number of extant taxa in Drilidae and Omalisidae and unclear relationships, family-group taxa had not been proposed by previous students and only recently, Kazantsev (2005, 2010) described Thilmaninae Kazantsev, 2005 and Euanomini Kazantsev, 2010 for *Thilmanus* and *Euanoma* + *Pseudeuanoma*, respectively. Thilmaninae were described in Lycidae and later transferred to Drilidae (Kazantsev 2005, 2010), Euanomini in Drilidae (Kazantsev 2010) and transferred to Omalisidae (Kundrata & Bocak 2011a). Kazantsev (2010) proposed close relationships of *Thilmanus* and *Euanoma* + *Pseudeuanoma* and merged Euanomini and Thilmanini in Thilmaninae (in Drilidae).

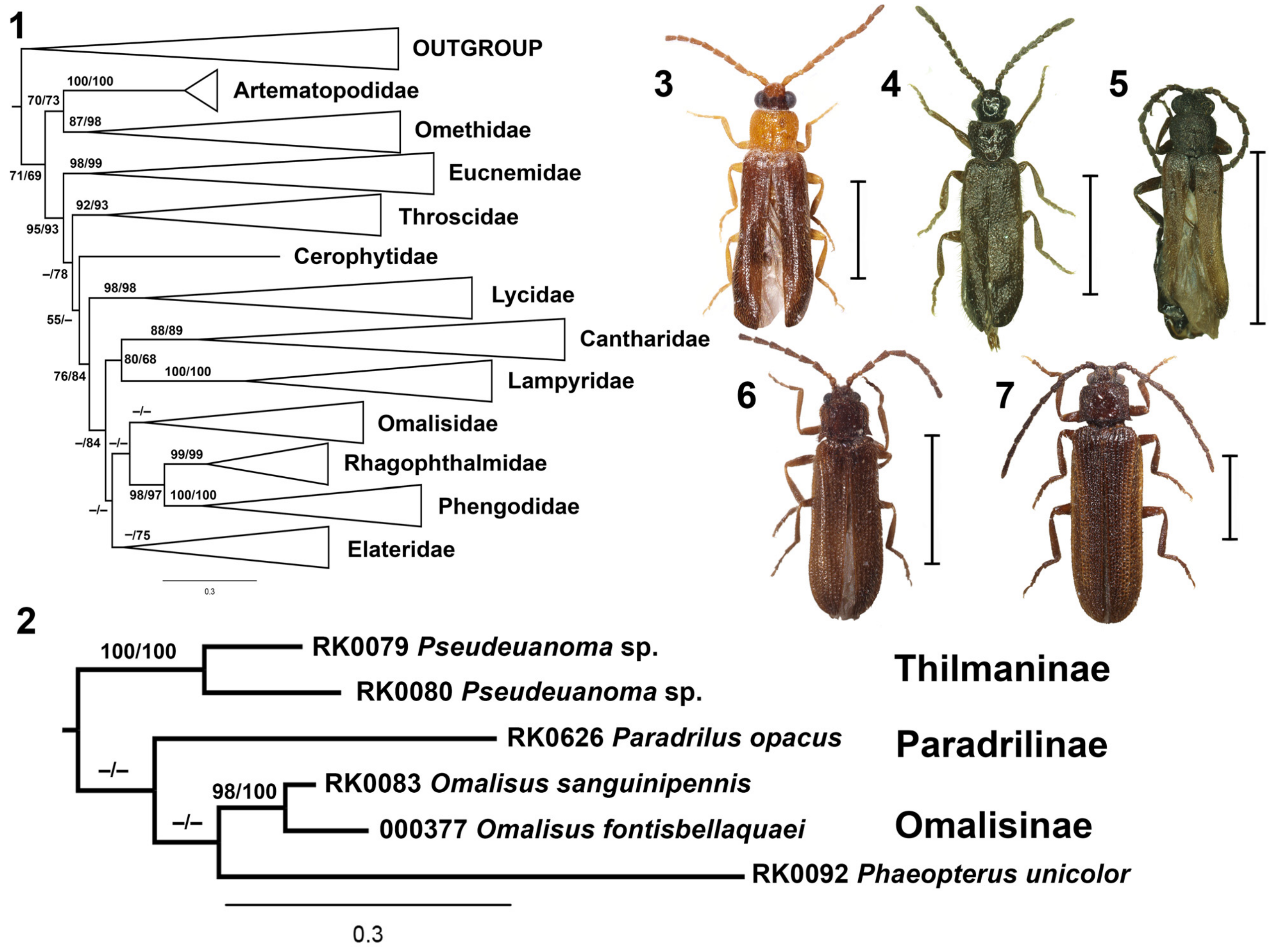
The current molecular analyses suggest the relationships of *Paradrilus* and *Omalisus* + *Phaeopterus*, confirm placement of *Pseudeuanoma* (Thilmaninae: Euanomini) in Omalisidae (Figs 1–2), and position of Omalisidae in the Rhagophthalmidae + Phengodidae + Elateridae clade in a distant relationships to Lycidae.

We assembled DNA data representing all omalisid family-group taxa except Thilmanini (a monogeneric tribe). Relationships of *Thilmanus* and various elateroid taxa were inferred from morphology and its position was hypothesized in Lycidae (Crowson 1972, Kazantsev 2005), Drilidae (Medvedev & Kazantsev 1992, Kazantsev 2010) or Omalisidae (Kleine 1933, Bocak & Bocakova 1990, Bocak & Brlik 2008). All molecular analyses place Euanomini, represented by two species of *Pseudeuanoma*, as a sister to the remaining omalisids (the present analysis—Fig. 2; Kundrata & Bocak 2011a, Bocak *et al.* 2014, Kundrata *et al.* 2014) and with respect to relationships ((*Euanoma*, *Pseudeuanoma*) *Thilmanus*)) defended by Kazantsev (2010), we re-transfer *Thilmanus* and Thilmaninae to Omalisidae.

Paradrilus has been another elateroid genus with unclear relationships. Kiesenwetter (1865, 1866) described *Paradrilus* in Drilidae, Bourgeois (1882) placed it in Omalisidae and Olivier (1910) re-transferred it to Drilidae, where it remained until now (Wittmer 1944, Bocak 2007). The widely delimited Drilidae (*sensu* Wittmer 1944) contained numerous genera currently placed in various elateroid families (Crowson 1972; Kundrata & Bocak

2011a, b; Jeng 2012; Janisova & Bocakova 2013), but *Paradrilus* remained in Drilini, as no DNA data were available (Bocak 2007). Currently, *Paradrilus* is recovered as a sister to the *Phaeopterus* + *Omalisus* clade. Morphologically, *Paradrilus* represents a distinct lineage and its relationships to the *Phaeopterus* + *Omalisus* clade has never been suggested. *Paradrilus* differs from other omalisids in the prolonged cranium, absence of pronotal carinae and sharp pronotal margins (Fig. 13; both carinae and sharp margin well developed in *Omalisus* and *Phaeopterus*), absence of elytral costae (Fig. 5; costae present in *Phaeopterus* and *Omalisus*), two-segmented labial palpi (unique character state in Omalisidae, Fig. 11), and the shape of prosternum (Fig. 14). The male genitalia of *Paradrilus* and *Phaeopterus* are similar (Fig. 18). The absence of pronotal carinae and elytral costae, reduction of mouthparts, hypognathous head, and tiny body are commonly encountered in males of neotenic lineages. We often observe strong sexual dimorphism in body size of neotenic beetles and K- and r-strategies were hypothesized for respective sexes (Bocak *et al*. 2008).

We recovered an independent position of *Paradrilus* in molecular phylogeny (Fig. 2) and found very distant morphology of *Paradrilus* when the genus is compared with Thilmaninae: Euanomini and Omalisinae. The definitions of subfamilies in Omalisidae (Kazantsev 2005, 2010) force us to erect a subfamily Paradrilinae subfam. nov. for *Paradrilus*, despite the fact that utility of these subfamilies is questioned by the number of genera included in each of them. The diagnosis, description and comparison of morphology are provided in the taxonomy section.



FIGURES 1–7. 1—The maximum likelihood (ML) Elateroidea phylogenetic tree of 557 taxa aligned by BlastAlign and inferred from RAxML; 2—Omalisidae phylogeny inferred from RAxML. The values at branches represent bootstrap values inferred from ML analyses of datasets aligned by BlastAlign and Mafft, respectively. 3—*Euanoma marketae* Kundrata & Bocak, 2007 (holotype); 4—*Pseudeuanoma* sp.; 5—*Paradrilus opacus* Kiesenwetter, 1865 (lectotype); 6—*Phaeopterus unicolor* Costa, 1857 (holotype); 7—*Omalisus fontisbellaquaei* Geoffroy, 1762. Scale 2 mm (Figs 3–7).

Taxonomy

Paradrilinae subfam. nov.

Type genus. *Paradrilus* Kiesenwetter, 1865.

Diagnosis. *Paradrilus* is similar in the small, very slender and black-colored body to *Thilmanus* (body lengths: *Paradrilus* 2.2–2.7 mm, *Thilmanus* 1.9–3.1 mm). Other Omalisidae have a stouter body: *Phaeopterus* 3.1–3.8 mm, *Pseudeuanoma* 3.2–4.9 mm, *Euanoma* 4.3–6.8 mm, *Cimbrion* 5.3–7.9 mm and *Omalisus* 5.0–8.5 mm (Kundrata & Bocak 2007, Bocak & Brlik 2008). *Paradrilus* shares with other Omalisidae the strengthened lateral margins of the phallobase (Fig. 18), and with *Thilmanus* and *Phaeopterus* the membranous apexes of parameres (the parameres of *Omalisus* have the sclerotized processes; Bocak & Brlik 2008). A number of traits is unique for *Paradrilus*: the two-segmented labial palpi, wide, t-shaped hypopharynx, parallel-sided, wide prosternum, absent sharp lateral edges in pronotum, prolonged frontal part of the cranium with laterally inserted antennae, and absent elytral costae (the trait shared with *Pseudeuanoma* and *Thilmanus*).

Description of the subfamily. The same as for *Paradrilus opacus* below.

Genera classified in Paradrilinae. *Paradrilus* only, the monogeneric subfamily.

Paradrilus opacus Kiesenwetter, 1865

(Figs 5, 8–18)

Paradrilus opacus Kiesenwetter, 1865: 369.

Type material. Lectotype [here designated], male, "Andalusia, Kiesenwetter, 326. 33." [invalidly designated as a paratype by a local curator]; Paralectotype [here designated], male, the same data as lectotype (Hungarian Natural History Museum, Budapest).

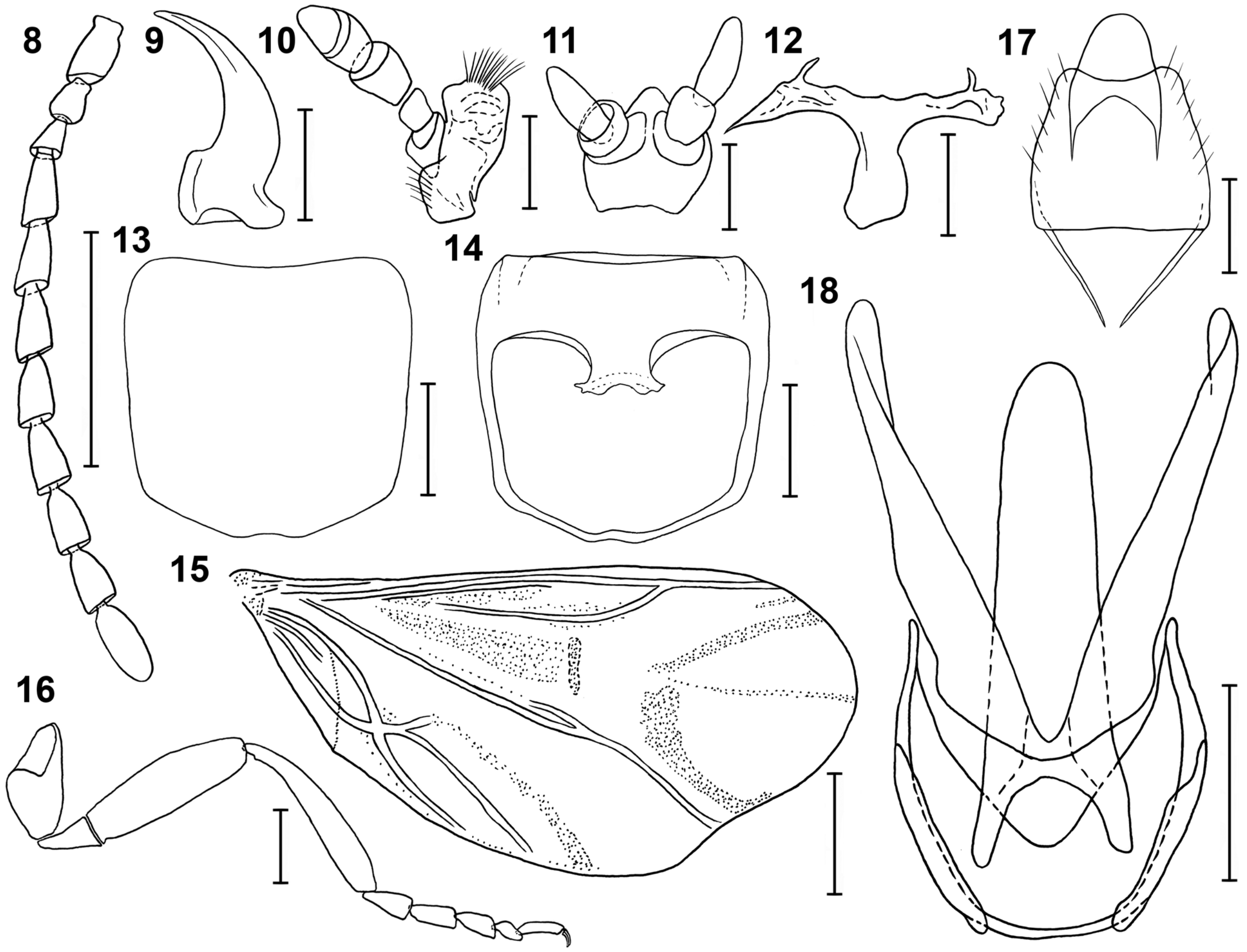
Other material examined. 2 males, "Andalusien" (Naturhistorisches Museum, Basel), 2 males, "Andalus., Kratz, 64." (Muséum national d'Histoire naturelle, Paris), 1 male, "Spain, Córdoba, Santa María de Trassierra, Arroyo del Molino, 20.–25. v. 2012, M. Baena leg." (DNA voucher specimen RK0626; Laboratory of Molecular Systematics, UP, Olomouc).

Redescription. Adult, male. Body slender, 2.2–2.7 mm long, 3.7 times longer than width at humeri, weakly dorso-ventrally flattened, parallel-sided (Fig. 5); moderately sclerotized, cuticle of elytra and abdomen soft, flexible; dark brown to black colored, surface mat, finely punctured, with dense, short vestiture.

Head small, hypognathous, slightly narrower than prothorax, exposed from prothorax, with fully developed mouthparts; cranium prolonged anteriorly, with inconspicuous antennal sockets, antennal insertions fronto-lateral, separated by narrow bridge, about 0.6 times width of maximum diameter of antennal cavity. Eyes small, moderately prominent, eye diameter 1.4 times their frontal distance. Antennae filiform, 11-segmented, antennomeres round in cross section (Fig. 8); scape robust, parallel-sided, constricted at base, apex asymmetrical; pedicel slightly triangular, robust, constricted at base, widely rounded apically; antennomere 3 shortest, triangular; antennomere 4 much longer; following antennomeres gradually shortened except terminal one. All antennomeres with moderately dense, erect pubescence. Fronto-clypeal suture absent; anterior edge of clypeus concave; labrum membranous, hypopharynx T-shaped, sclerotized, lateral processes long, suboesophaginal ring absent (Fig. 12). Mandibles slender apically, robust at base, slightly curved; incisor without teeth (Fig. 9). Maxilla with small cardo, stipes well developed, plate-shaped; galea and lacinia fused in setose, mala basally sclerotized; palpifer triangular, robust; maxillary palpi four-segmented, palpomere 1 small, transverse, palpomeres 2 and 3 robust, about as long as wide, apical palpomere twice longer than width at base, slender apically, apex widely rounded (Fig. 10). Labium small, praementum short, wide, reduced to convex plate with extensive palpal cavities, projected and pointed apically, without ligula or apical setae; postmentum fused with gula, sclerotized, plate-like, about as long as width; labial palpi tiny, two-segmented, basal palpomere wide, transverse, apical palpomere slender, almost parallel-sided, weakly pointed at apex (Fig. 11).

Prothorax about as long as width (pronotum length/width ratio=0.9), anterior edge straight, frontal angles obtuse, anterior foramen widely rounded; posterior angles obtuse, posterior margin weakly emarginate in middle;

lateral edges widely convex, widest in frontal fourth, straight posteriorly, pronotum narrower basally than elytral humeri, disc convex, lateral margins bent downwards, with inconspicuous pleura anteriorly, disc without any carinae or keel, mat, finely structured, with punctures at frontal and posterior corners (Fig. 13). Prosternum moderately long, with wide parallel-sided prosternal process bearing divergent short and robust branches at apex (Fig. 14). Scutellum bilobate. Mesoventrite wide, coxae in extensive cavities laterally. Metasternum long, pleural part connected to metasternum with membrane, epimeron and episternum slender. Elytra very slender, tapering to apex, with humeral edge and pleura present in basal third, posterior half of elytra flat, elytra without longitudinal costae, surface with fine papillae bearing apical setae; elytral apexes separately rounded (Fig. 5). Wing as in Fig. 15. Legs slender, compressed (Fig. 16); coxae separated, elongate; trochanters slender, moderately long, transversally cut at apex; femora moderately robust; tibiae slender, with pair of small spurs apically; tarsi with five slender tarsomeres, tarsomeres 1–3 subequal, tarsomere 4 short, tarsomere 5 slender, long; pulvilli absent; claws simple (Fig. 16).



FIGURES 8–18. *Paradrilus opacus* Kiesenwetter, 1865; 8—antenna; 9—mandible; 10—maxilla; 11—labium; 12—hypopharynx; 13—pronotum; 14—prosternum; 15—wing; 16—leg; 17—last abdominal segments; 18—aedeagus. Scale 0.05 mm (Fig. 11), 0.1 mm (Figs 9–10, 12, 17–18), 0.2 mm (Figs 13–14, 16), 0.5 mm (Figs 8, 15).

Abdomen with eight visible ventrites, basal ventrite membranous in middle part, terminal male segments as in Fig. 17. Aedeagus of trilobate type, with long parameres; apices of parameres simple, partly membranous; internal sac inconspicuous, membranous; phallobase plate-like, v-shaped, with strengthened lateral margins and postero-lateral processes (Fig. 18).

Measurements (lectotype). Body length 2.70 mm, width at humeri 0.73 mm, pronotum length 0.50 mm; pronotum width 0.57 mm, minimum frontal distance between eyes 0.30 mm, maximum eye diameter in lateral view 0.21 mm.

Distribution. Southern Spain (Andalusia: Córdoba, Huelva, Jaén, and Sevilla provinces; Kiesenwetter 1866, Bahillo de la Puebla & López Colón 2005).

Biology and ecology. The specimens were collected by sweeping of the herbal stratum in a forested place near Santa María de Trassierra, Córdoba, Spain (Fig. 19).

Remarks. The female and larva are unknown. As only males are present in all examined collections, we suppose that the females of *Paradrilus* do not complete metamorphosis similarly to other Omalisidae (Kiesenwetter 1866, Bocak & Brlik 2008).

The type material is not present in the Kiesenwetter collection in Zoologische Staatssammlung München, Germany (K. Neven, personal communication) and might be distributed in several museums. We were able to locate types only in the Budapest museum and several conspecific individuals elsewhere. The specimens in the Budapest collection were designated by a curator as paratypes, but there is no indication in the original description that holotype and paratypes were designated and all types must be considered as syntypes (ICZN 1999). We prefer to designate lectotype as the beetles with limited dispersal propensity tend to produce separate, evolutionary isolated populations in a limited geographical space (Malohlava & Bocak 2010) and the original series can include several species. The here fixed morphological concept of *Paradrilus* follows that represented by identified specimens in several European collections.

FIGURE 19. Habitat of *Paradrilus opacus* Kiesenwetter, 1865—Arroyo del Molino, Santa María de Trassierra, Córdoba, Spain.

A taxonomic checklist of the family Omalisidae.

Family Omalisidae Lacordaire, 1857

Subfamily Omalisinae Lacordaire, 1857
Genus *Omalisus* Geoffroy, 1762
    Type species: *Omalisus fontisbellaquaei* Geoffroy, 1785
    O. fontisbellaquaei Geoffroy, 1785 (Europe; see Bocak 2007)
    O. nicaeensis Lesne, 1921 (France)
    O. sanguinipennis Laporte, 1840 (Croatia, Italy, Montenegro)
    O. taurinensis Baudi di Selve, 1872 (Italy)
    O. victoris Mulsant, 1852 (France)
Genus *Phaeopterus* Costa, 1857
    Type species: *Phaeopterus unicolor* Costa, 1857
    P. unicolor Costa, 1857 (Italy, Corsica)
Genus *Cimbrion* Kazantsev, 2010
    Type species: *Cimbrion nigricorne* (Reitter, 1881)
    C. nigricorne (Reitter, 1881) (Bosnia and Herzegovina, Croatia)
Subfamily Thilmaninae Kazantsev, 2005
Tribe Thilmanini Kazantsev, 2005
Genus *Thilmanus* Gemminger, 1869
    Type species: *Thilmanus obscurus* Baudi di Selve, 1872
    Thilmanus laticeps Pic, 1913 (France)
    Thilmanus obscurus Baudi di Selve, 1872 (Sardinia, Corsica)
Tribe Euanomini Kazantsev, 2010
Genus *Euanoma* Reitter, 1889
    Type species: *Euanoma starcki* Reitter, 1889
    E. argonauta Kazantsev, 2010 (Georgia)
    E. curvata Kundrata & Bocak, 2007 (Turkey)
    E. elongata Pic, 1932 (Ossetia)
    E. graeca (Pic, 1901) (Greece)
    E. kolchica Kazantsev, 2010 (Georgia)
    E. marketae Kundrata & Bocak, 2007 (Turkey)
    E. semitestacea Pic, 1907 (Turkey)
    E. starcki Reitter, 1889 (Russia, Georgia)
    E. svihlai Kundrata & Bocak, 2007 (Turkey)
Genus *Pseudeuanoma* Pic, 1901
    Type species: *Pseudeuanoma obscura* Pic, 1901
    P. caligo Kazantsev, 2010 (Turkey)
    P. ionica Pic, 1901 (Greece)
    P. obscura Pic, 1901 (Turkey)
    P. reitteri Pic, 1901 (Greece)
Subfamily Paradrilinae Kundrata, Baena & Bocak, subfam. nov.
Genus *Paradrilus* Kiesenwetter, 1865
    Type species: *Paradrilus opacus* Kiesenwetter, 1865
    P. opacus Kiesenwetter, 1865 (Spain)

A key to the genera of Omalisidae.

1. Pronotum with rounded, obtuse lateral margins . . . . *Paradrilus*
\- Pronotum with sharp edge forming lateral margins 2
2. Elytra with rows of regular rounded punctures, which form nine longitudinal costae in elytra, pronotum with keel attached to posterior margin and parallel with lateral margin of pronotum 3
\- Elytra with inconspicuous obtuse shallow punctures or irregularly sculptured, pronotum without any lateral keels or vestiges of keels present at base of pronotum, not reaching further than one quarter of pronotum length. 4
3. Parameres with externally curved apices, body size 5.0–8.5 mm, pronotal keels inconspicuous anteriorly, well developed in basal half, elytral costa 6 strongly elevated, antennomere 4 about 1.3 times longer than combined length of antennomeres 2 and

3 . . . . *Omalisus*

\- Parameres with simple apices, membranous apically, body length 3.1–3.8 mm, lateral pronotal keels very sharp in whole length, reaching frontal margin of pronotum, costa 6 prominent in humeral half, antennomere 4 about as long as combined length of antennomeres 2 and 3. *Phaeopterus*

4\. Prosternum with long slender process as in *Omalisus* . . . . *Cimbrion*

\- Prosternum without slender median process. 5

5\. Body slender, elytra about 6 times longer than width at humeri, dark brown to black colored, legs and antennae uniformly dark colored, small bodied, 1.9–4.9 mm long. 6

\- Body robust, about 5 times longer than width at humeri, elytra variably colored, with light humeri, brown or testaceous; when elytra and pronotum dark colored at least some antennomeres and legs light brown to testaceous, body medium-sized, 4.3–6.8 mm long. *Euanoma*

6\. Apical part of parameres slender, sometimes pointed . . . . *Thilmanus*

\- Apical part of parameres robust, widely rounded. *Pseudeuanoma*

Acknowledgements

We would like to thank M. Geiser (London) for providing the *Phaeopterus* sample and to the curators and institutions that provided us with the material in their care. This study was supported by GAČR P506/11/1757 (LB) and the internal grant of Faculty of Science, UP Olomouc (RK). We are obliged to N. Gunter for comments on the manuscript and proof reading.

References

Bahillo de la Puebla, P. & López Colón, J.I. (2005) Los Drilidae Lacordaire, 1857 de la Península Ibérica e Islas Baleares (Coleoptera). *Boletín Sociedad Entomológica Aragonesa*, 37, 119–128.

Belshaw, R. & Katzourakis, A. (2005) BlastAlign: a program that uses blast to align problematic nucleotide sequences. *Bioinformatics*, 21, 122–123.
http://dx.doi.org/10.1093/bioinformatics/bth459

Bocak, L. (2007) Drilidae. *In*: Löbl, I. & Smetana, A. (Eds.), *The Palaearctic Catalogue of Coleoptera. Vol. 4*. Apollo Books, Stenstrup, pp. 209–210. [Denmark]

Bocak, L., Barton, C., Crampton-Platt, A., Chesters, D., Ahrens, D. & Vogler, A.P. (2014) Building the Coleoptera tree-of-life for >8000 species: composition of public DNA data and fit with Linnaean classification. *Systematic Entomology*, 39, 97–110.
http://dx.doi.org/10.1111/syen.12037

Bocak, L. & Bocakova, M. (1990) Revision of the supergeneric classification of the family Lycidae (Coleoptera). *Polskie Pismo Entomologiczne*, 59, 623–676.

Bocak, L., Bocakova, M., Hunt, T. & Vogler, A.P. (2008) Multiple ancient origins of neoteny in Lycidae (Coleoptera): consequences for ecology and macroevolution. *Proceedings of the Royal Society B*, 275, 2015–2023.
http://dx.doi.org/10.1098/rspb.2008.0476

Bocak, L. & Brlik, M. (2008) Revision of the family Omalisidae (Coleoptera, Elateroidea). *Insect Systematics & Evolution*, 39, 189–212.
http://dx.doi.org/10.1163/187631208788784101

Bocakova, M., Bocak, L., Hunt, T., Teravainen, M. & Vogler, A.P. (2007) Molecular phylogenetics of Elateriformia (Coleoptera): evolution of bioluminescence and neoteny. *Cladistics*, 23, 477–496.
http://dx.doi.org/10.1111/j.1096-0031.2007.00164.x

Bourgeois, J. (1882) Lycidae de l'ancient monde. *L'Abeille*, 20, 1–92.

Crowson, R.A. (1972) A review of the classification of Cantharoidea (Coleoptera), with the definition of two new families: Cneoglossidae and Omethidae. *Revista de la Universidad de Madrid*, 21, 35–71.

ICZN (1999) *International Code of Zoological Nomenclature. 4th Edition*. The International Trust for Zoological Nomenclature, London, 305 pp.

Janisova, K. & Bocakova, M. (2013) Revision of the subfamily Ototretinae (Coleoptera: Lampyridae). *Zoologischer Anzeiger*, 252, 1–19.
http://dx.doi.org/10.1016/j.jcz.2012.01.001

Jeng, M.L. (2012) Re-classification of *Rhipidiomorphus malaccanus* Pic, a long-neglected genus and species of Psephenoidinae (Coleoptera: Psephenidae). *Zootaxa*, 3180, 66–68.

Katoh, K., Misawa, K., Kuma, K. & Miyata, T. (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research*, 30, 3059–3066.
http://dx.doi.org/10.1093/nar/gkf436

Kazantsev, S.V. (2005) Morphology of Lycidae with some considerations on evolution of the Coleoptera. *Elytron*, 17/18, 49–226. [(2003–2004) et *Coleopterological Monographs*, 3, 73–248]

Kazantsev, S.V. (2007) Comparative morphology of the genus *Euanoma* Reitter, 1889 (Coleoptera: Drilidae). *Russian Entomological Journal*, 16, 439–449.

Kazantsev, S.V. (2010) New taxa of Omalisidae, Drilidae and Omethidae, with a note on systematic position of Thilmaninae (Coleoptera). *Russian Entomological Journal*, 19, 51–60.

Kiesenwetter, E.A.H. (1865) Eine entomologische Excursion nach Spanien in Sommer 1865. *Berliner Entomologische Zeitschrift*, 9, 369–375.
http://dx.doi.org/10.1002/mmnd.18650090316

Kiesenwetter, E.A.H. (1866) Beiträge zur Käferfauna Spaniens. Erstes Stück. Malacodermata, Melyridae. *Berliner Entomologische Zeitschrift*, 10, 241–274.
http://dx.doi.org/10.1002/mmnd.18660100117

Kleine, R. (1933) *Coleopterorum Catalogus auspiciis et auxilio W. Junk editus S. Schenkling. Pars 128: Lycidae*. W. Junk, Berlin, 145 pp.

Kundrata, R. & Bocak, L. (2007) A revision of *Euanoma* and *Pseudeuanoma* (Coleoptera: Drilidae). *Annales Zoologici*, 57, 427–441.

Kundrata, R. & Bocak, L. (2011a) The phylogeny and limits of Elateridae (Insecta, Coleoptera): is there a common tendency of click beetles to soft-bodiedness and neoteny? *Zoologica Scripta*, 40, 364–378.
http://dx.doi.org/10.1111/j.1463-6409.2011.00476.x

Kundrata, R. & Bocak, L. (2011b) Redescription and relationships of *Pseudothilmanus* Pic (Coleoptera: Rhagophthalmidae) – a long-term neglected glow-worm beetle genus from the Himalayas. *Zootaxa*, 2794, 57–62.

Kundrata, R., Bocakova, M. & Bocak, L. (2014) The comprehensive phylogeny of the superfamily Elateroidea (Coleoptera: Elateriformia). *Molecular Phylogenetics and Evolution*, 76, 162–171.
http://dx.doi.org/10.1016/j.ympev.2014.03.012

Leschen, R.A.B., Beutel, R.G. & Lawrence, J.F. (Eds.) (2011) *Coleoptera, Beetles. Vol. 2. Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). In:* Kristensen, N.P. & Beutel, R.G. (Eds.), *Handbook of Zoology, Arthropoda: Insecta*. Walter de Gruyter GmbH & Co. KG, Berlin/New York, xiii + 786 pp.

Medvedev, L.N. & Kazantsev, S.V. (1992) A new subfamily and a new genus of lycid beetles from Southeast Asia. *In*: Medvedev, L.N. (Ed.), *Systematics and ecology of insects of Vietnam*. Nauka Publishers, Moscow, pp. 55–60.

Malohlava, V. & Bocak, L. (2010) Evidence of extreme habitat stability in a Southeast Asian biodiversity hotspot based on the evolutionary analysis of neotenic net-winged beetles. *Molecular Ecology*, 19, 4800–4811.
http://dx.doi.org/10.1111/j.1365-294X.2010.04850.x

Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *In*: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 November 2010, pp. 1–8. [New Orleans, LA]

Olivier, E. (1910) Rhagophthalmidae, Drilidae. *In*: Schenkling, S. (Ed.), *Coleopterorum Catalogus*. *Pars 10*. W. Junk, Berlin, pp. 1–10.

Rambaut, A. (2009) FigTree 1.3.1. Available from: http://tree.bio.ed.ac.uk/software/figtree/ (accessed 20 January 2015)

Stamatakis, A. (2006) RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690.
http://dx.doi.org/10.1093/bioinformatics/btl446

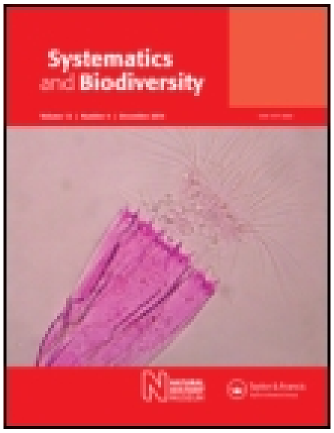
Stamatakis, A., Hoover, P. & Rougemont, J. (2008) A Rapid Bootstrap Algorithm for the RAxML Web Servers. *Systematic Biology*, 57, 758–771.
http://dx.doi.org/10.1080/10635150802429642

Wittmer, W. (1944) Catalogue des Drilidae E. Oliv. (Coleoptera - Malacodermata). *Revista de la Sociedad Entomológica Argentina*, 12, 203–221.

Příloha 10

Kundrata, R., Baalbergen, E., Bocák, L. & Schilthuizen, M. (2015) The origin and diversity of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) in Crete based on mitochondrial phylogeny. *Systematics and Biodiversity*, 13: 52–75.
[IF 1,985; 10 citací na WoS; celkem 6 citací bez autorových autocitací]
[korespondující autor; autorský podíl: 30 %]

This article was downloaded by: [Knihovna Univerzity Palackeho], [Robin Kundrata]
On: 29 December 2014, At: 01:12
Publisher: Taylor & Francis
Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Click for updates

Systematics and Biodiversity
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tsab20

The origin and diversity of Drilus Olivier, 1790 (Elateridae: Agrypninae: Drilini) in Crete based on mitochondrial phylogeny

Robin Kundrata[a], Els Baalbergen[b], Ladislav Bocak[a] & Menno Schilthuizen[bcd]

[a] Department of Zoology, Faculty of Science, Palacky University, 17 listopadu 50, 771 46, Olomouc, Czech Republic

[b] Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, the Netherlands

[c] Rijksuniversiteit Groningen, Centre for Ecological and Evolutionary Studies, Nijenborgh 7, 9747AG Groningen, the Netherlands

[d] Leiden University, Institute Biology Leiden, P.O. Box 9516, 2300 RA Leiden, the Netherlands

Published online: 17 Nov 2014.

To cite this article: Robin Kundrata, Els Baalbergen, Ladislav Bocak & Menno Schilthuizen (2015) The origin and diversity of Drilus Olivier, 1790 (Elateridae: Agrypninae: Drilini) in Crete based on mitochondrial phylogeny, Systematics and Biodiversity, 13:1, 52-75, DOI: 10.1080/14772000.2014.968236

To link to this article: http://dx.doi.org/10.1080/14772000.2014.968236

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the “Content”) contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at http://www.tandfonline.com/page/terms-and-conditions

Systematics and Biodiversity (2015), **13(1)**: 52−75

Research Article

The origin and diversity of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) in Crete based on mitochondrial phylogeny

ROBIN KUNDRATA[1]*, ELS BAALBERGEN[2], LADISLAV BOCAK[1] & MENNO SCHILTHUIZEN[2,3,4]

[1]Department of Zoology, Faculty of Science, Palacky University, 17 listopadu 50, 771 46, Olomouc, Czech Republic
[2]Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, the Netherlands
[3]Rijksuniversiteit Groningen, Centre for Ecological and Evolutionary Studies, Nijenborgh 7, 9747AG Groningen, the Netherlands
[4]Leiden University, Institute Biology Leiden, P.O. Box 9516, 2300 RA Leiden, the Netherlands

(Received 20 June 2014; accepted 11 September 2014)

We investigated the phylogeography and speciation of *Drilus* in the Mediterranean, with focus on the Aegean and especially Crete. Altogether 12 species were sequenced for two fragments of the cytochrome c oxidase subunit I gene (*cox1−3′* and *cox1−5′* mtDNA) and provided 1381 nucleotides. Both fragments were analysed under the maximum likelihood criterion and Bayesian inference separately and concatenated as a single dataset. The *Drilus* species from the Peloponnese, the Ionian islands and Crete did not form a monophylum. *Drilus* sp. E from the Peloponnese and Zakynthos was sister to *D. mauritanicus* Lucas from Spain in most cases. The remaining Greek *Drilus* species formed a robustly supported clade in all analyses; however, the species from Crete do not seem to be monophyletic. Estimating species divergences using BEAST, we found out that the key dates in the west Aegean *Drilus* phylogeography appeared to be the Tortonian Crete−Peloponnese separation (12−9 Mya), the desiccation of the Mediterranean basin during the Messinian Salinity Crisis (5.96−5.33 Mya), and the repeated fragmentation of Crete during the Pliocene and Pleistocene. Within the *Drilus* lineages, we obtained a substitution rate estimate of 2.75% divergence per million years, which is in excellent agreement with previous studies. A Generalized Mixed Yule Coalescent (GMYC) analysis suggested the presence of six *Drilus* species in Crete (seven species in total, since the DNA sequences were not available for *D. creticus* Pic); however, we formally identified and (re)described only four which can be morphologically defined: *D. creticus*, *D. longulus* Kiesenwetter, *D. horasfakionus* sp. nov. and *D. baenai* sp. nov. These species are endemic to Crete and surrounding islets. Their diagnostic characters are illustrated and an identification key to males of these species is provided. The intraspecific variability, distribution and ecology of all species are discussed and suggestions for further research are given.

http://zoobank.org/urn:lsid:zoobank.org:pub:F8DDBCC1-C2D1-48F7-BE99-55D9ED4C2234

Key words: Coleoptera, *cox1* mtDNA, DNA barcoding, Elateroidea, Greece, Messinian Salinity Crisis, neoteny, new species, phylogeny, taxonomy

Introduction

The former beetle family Drilidae, recently transferred as the tribe Drilini to Elateridae (Kundrata & Bocak, 2011), represents a lineage with morphology and ecology strongly affected by the neotenic development of females, which remain wingless and larviform (Kundrata & Bocak, 2007; Figs 35−37). The larvae and females of Drilini prey on snails (Baalbergen et al., 2014; Schilthuizen, Kemperman, & Gittenberger, 1994; Williams, 1951). Drilini are represented in the Mediterranean Region by *Malacogaster* Bassi (all 11 species) and *Drilus* Olivier (most of 30 species; Bocak, 2007; Wittmer, 1944). Almost half of the Mediterranean *Drilus* species are endemic to various Mediterranean islands (Bocak, 2007). Despite their occurrence in Europe, most species are only known from the original 19th century descriptions and since then have only been mentioned in catalogues (Bocak, 2007; Wittmer, 1944). Therefore, the diversity, species-limits, data on the immature stages and females and relationships among *Drilus* species are poorly known and the lack of proper descriptions, diagnoses and identification keys precludes further progress in *Drilus* research. This is also the situation for the *Drilus* of the island of Crete. Only *Drilus longulus* Kiesenwetter, 1859 and *D. creticus* Pic, 1905

---

*Correspondence to: Robin Kundrata. Email: robin.kundrata@upol.cz

ISSN 1477-2000 print / 1478-0933 online

http://dx.doi.org/10.1080/14772000.2014.968236

have been described from Crete and no other taxonomic work dealing with Cretan *Drilus* species has been carried out. Bocak (2007) and Wittmer (1944) also mentioned *Drilus funebris* Reitter in Brenske & Reitter, 1884 from the Greek mainland as a Cretan species. The *Drilus* fauna of the island of Crete had not been the focus of systematic, biogeographic and ecological studies until Schilthuizen et al. (1994) briefly described the morphology of two species and discussed their predation on *Albinaria* snails (see also Welter-Schultes, 2000). Due to the chaotic taxonomic situation in Drilini, these species have not been formally described.

Recently, several studies have made use of molecular data for a variety of animal taxa in order to elucidate their biogeographic affinities in the Aegean region including Crete. These studies tried to examine how the key geological events such as the formation of the Mid-Aegean trench (MAT), the separation of Crete from the Peloponnese and the central Aegean islands during the Tortonian (∼12−9 million years ago (Mya); Creutzburg, 1963), the Messinian Salinity Crisis (MSC; 5.9−5.33 Mya; Krijgsman, Hilgen, Raffi, Sierro, & Wilson, 1999), and climatic oscillations during the Pleistocene (Lymberakis & Poulakakis, 2010) influenced the phylogeography and speciation processes in Mediterranean vertebrates and invertebrates (e.g. Akın et al., 2010; Kyriazi et al., 2013; Parmakelis et al., 2005; Poulakakis, Lymberakis, Valakos, Zouros, & Mylonas, 2005). Herein, we study *Drilus* as a lineage with limited dispersal propensity (1) to taxonomically review this genus in Crete, redescribe species already known and describe ones new to science, provide diagnoses and an identification key, (2) to determine how many *Drilus* species occur in the Ionian islands (incl. Zakynthos, Kefalonia and Kalamos), Peloponnese and Crete, (3) use mtDNA data to investigate the phylogeographic pattern of *Drilus* species in the Aegean region, and (4) to suggest further research on *Drilus* in the Mediterranean.

Materials and methods

Taxon sampling, laboratory procedures and dataset assembling

The majority of *Drilus* specimens used in this phylogenetic study were obtained from the molluscan collection of the Naturalis Biodiversity Center, Leiden, the Netherlands. After collection of molluscan hosts, drilines crawled out of their prey shells. All preserved museum specimens were collected between 1986 and 2003. Additional material was collected during fieldwork in 2011−2013.

To investigate the phylogenetic position of Cretan *Drilus* species, we sequenced two fragments of the mitochondrial cytochrome c oxidase subunit I gene for 40 and 24 specimens, respectively (*cox1−3′* mtDNA, 723 bp; *cox1−5′* mtDNA, 645 bp; Table 1). Total DNA was extracted using the DNeasy® Blood & Tissue kit or Wizard SV96 Purification System (Promega Corp., Madison, WI, USA). The *cox1−3′* mtDNA was amplified either as a single fragment (Simon et al., 1994) or two fragments (Ribera et al., 2010) and *cox1−5′* mtDNA was amplified as a single fragment (Folmer, Black, Hoeh, Lutz, & Vrijenhoek, 1994). Primer pairs are listed in Table S1 (see online supplemental material, which is available from the article's Taylor & Francis Online page at http://dx.doi.org/10.1080/14772000.2014.968236). The fragments were amplified using 1U Taq polymerase (BioTaq DNA Polymerase, Bioline), 2−4 mM $MgCl_2$, 50 μM dNTP, 0.5 mM each primer and 1−5 μL template DNA in 25 μL reaction volume. Cycle conditions were 3 min at 94 °C; 15 s at 94 °C, 30 s at 50 °C, 40 s at 72 °C (repeated for 40 cycles) and 5 min at 72 °C. The amplification products were purified and sequenced by Macrogen (Macrogen Europe Inc., Amsterdam, the Netherlands).

The newly obtained data were merged with previously published *cox1−3′* mtDNA sequences deposited in GenBank (Table 1; Bocakova, Bocak, Hunt, Teraväinen, & Vogler, 2007; Hunt et al., 2007; Kundrata & Bocak, 2011). A *Selasia* sp. (Agrypninae: Drilini) was used for rooting the trees (Kundrata & Bocak, 2011). We analysed both fragments separately (*cox1−3′*, 49 taxa; *cox1−5′*, 24 taxa), but also the concatenated dataset containing all available Drilini taxa (49 taxa), and the reduced dataset containing taxa with both fragments present (24 taxa). Voucher and GenBank accession numbers are listed in Table 1. The classification used herein follows that of Kundrata and Bocak (2011).

Sequence handling, alignment and phylogenetic analyses

Sequences were edited using Sequencher 4.9 (Gene Codes Corp., Ann Arbor, MI, USA) and aligned by ClustalW 1.83 (Thompson, Higgins, & Gibson, 1994). The resulting alignment contained no indels. The fragments were analysed separately with partitions defined by codon positions. The concatenated datasets (49 and 24 taxa) were partitioned by fragment and codon positions, yielding a total of six partitions. The partial and concatenated datasets were analysed under the maximum likelihood criterion using RAxML 7.3.1 (Stamatakis, 2006) via the CIPRES web server (www.phylo.org; Miller, Pfeiffer, & Schwartz, 2010). Bootstrap values (BS) were calculated using the rapid bootstrap algorithm (Stamatakis, Hoover, & Rougemont, 2008) with 1000 bootstrap iterations under the GTRCAT model. Further, all datasets were analysed under Bayesian inference using MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2001). Four chains were run for 40×10^6 generations using the Markov chain Monte Carlo

Table 1. The list of material used in this study, with GenBank accession and voucher numbers. * Sequences downloaded from GenBank; ** pseudopupa (an immobile resting larval stage).

Genus/Species	Sex/Stage	Geographic origin	*cox1-3′*	*cox1-5′*	Specimen voucher	Source
Selasia sp.	Male	South Africa	HQ334004*	KJ572952	UPOL RK0071	Kundrata & Bocak 2011
Selasia sp.	Male	South Africa	HQ334005*	KJ572953	UPOL RK0072	Kundrata & Bocak 2011
Drilus flavescens	Male	Malta	DQ198579*	N	UPOL 001046	Bocakova et al. 2007
Drilus flavescens	Male	Malta	KJ572890	KJ572942	UPOL RK0446	
Drilus flavescens	Male	Great Britain	DQ222003*	N	BMNH 679287	Hunt et al. 2007
Drilus flavescens	Larva	The Netherlands	KJ572927	KJ572943	EB2013-265	
Drilus mauritanicus	Male	Spain	HQ334015*	KJ572948	UPOL RK0084	Kundrata & Bocak 2011
Drilus mauritanicus	Male	Spain	HQ334016*	KJ572949	UPOL RK0085	Kundrata & Bocak 2011
Drilus concolor	Male	Hungary	HQ334007*	KJ572946	UPOL RK0074	Kundrata & Bocak 2011
Drilus concolor	Larva	The Netherlands	KJ572892	N	RMNH.INS.871829	
Drilus concolor	Female	The Netherlands	KJ572893	KJ572945	RMNH.INS.559215	
Drilus concolor	Larva**	The Netherlands	KJ572894	KJ572944	RMNH.INS.559216	
Drilus sp. A	Male	Turkey	HQ334013*	KJ572947	UPOL RK0081	Kundrata & Bocak 2011
Drilus sp. E	Male	Greece, Peloponnese	HQ334006*	KJ572950	UPOL RK0073	Kundrata & Bocak 2011
Drilus sp. E	Larva**	Greece, Zakynthos	KJ572891	KJ572951	RMNH.INS.559217	
Drilus sp. L	Larva**	Greece, Peloponnese	KJ572919	N	RMNH.INS.559209	
Drilus sp. L	Larva	Greece, Peloponnese	KJ572920	N	RMNH.INS.559210	
Drilus sp. L	Larva	Greece, Peloponnese	KJ572917	KJ572938	RMNH.INS.559211	
Drilus sp. L	Larva	Greece, Peloponnese	KJ572918	KJ572937	RMNH.INS.871796	
Drilus sp. L	Larva	Greece, Peloponnese	KJ572915	KJ572939	UPOL RK0539	
Drilus sp. L	Larva**	Greece, Peloponnese	KJ572916	N	UPOL RK0540	
Drilus sp. D	Male	Greece, Kalamos	KJ572912	KJ572932	RMNH.INS.559213	
Drilus sp. D	Male	Greece, Peloponnese	KJ572911	N	RMNH.INS.559219	
Drilus sp. M	Larva	Greece, Kefalonia	KJ572913	KJ572933	RMNH.INS.871808	
Drilus sp. G	Larva	Greece, Peloponnese	KJ572914	KJ572934	RMNH.INS.559218	
Drilus baenai sp. nov.	Female	Greece, Crete	KJ572909	KJ572935	RMNH.INS.871921	
Drilus baenai sp. nov.	Larva	Greece, Crete	KJ572910	N	EB2013-304	
Drilus baenai sp. nov.	Female	Greece, Crete	KJ572907	KJ572936	EB2013-307	
Drilus baenai sp. nov.	Male	Greece, Crete	KJ572908	N	RMNH.INS.559175	
Drilus longulus	Female	Greece, Crete	KJ572922	KJ572930	RMNH.INS.559192	
Drilus longulus	Larva	Greece, Crete	KJ572926	N	RMNH.INS.559191	
Drilus longulus	Larva	Greece, Crete	KJ572925	N	RMNH.INS.559205	
Drilus longulus	Larva	Greece, Crete	KJ572921	N	RMNH.INS.559206	
Drilus longulus	Larva	Greece, Crete	KJ572923	N	RMNH.INS.559207	
Drilus longulus	Male	Greece, Crete	KJ572924	KJ572931	UPOL RK0638	
Drilus horasfakionus sp. nov.	Female	Greece, Crete	KJ572897	N	RMNH.INS.871814	
Drilus horasfakionus sp. nov.	Larva**	Greece, Crete	KJ572895	N	RMNH.INS.871818	
Drilus horasfakionus sp. nov.	Larva**	Greece, Crete	KJ572896	N	RMNH.INS.871820	
Drilus horasfakionus sp. nov.	Male	Greece, Crete	KJ572899	N	RMNH.INS.559153	
Drilus horasfakionus sp. nov.	Male	Greece, Crete	KJ572898	N	RMNH.INS.559154	
Drilus horasfakionus sp. nov.	Male	Greece, Crete	KJ572902	N	RMNH.INS.559155	
Drilus horasfakionus sp. nov.	Female	Greece, Crete	KJ572905	N	EB2013-299	
Drilus horasfakionus sp. nov.	Larva	Greece, Crete	KJ572906	N	EB2013-300	
Drilus horasfakionus sp. nov.	Female	Greece, Crete	KJ572900	KJ572941	RMNH.INS.559163	
Drilus horasfakionus sp. nov.	Male	Greece, Crete	KJ572901	KJ572940	RMNH.INS.559169	
Drilus horasfakionus sp. nov.	Male	Greece, Crete	KJ572903	N	EB2013-320	
Drilus horasfakionus sp. nov.	Female	Greece, Crete	KJ572904	N	RMNH.INS.559204	
Drilus horasfakionus sp. nov.	Female	Greece, Crete	KJ572928	N	EB2013-456	
Drilus horasfakionus sp. nov.	Female	Greece, Crete	KJ572929	N	EB2013-457	

(MCMC) method, with trees sampled every 1000 generations. The stationarity was detected in Tracer 1.5 (Rambaut & Drummond, 2007). For each analysis, the initial 10% of the trees were discarded as burn-in and the posterior probabilities (PP) were determined from the remaining trees.

Estimation of divergence times, substitution rates and species delimitation

To estimate the divergence times and substitution rates, we used a Bayesian approach as implemented in BEAST 1.7.5 (Drummond & Rambaut, 2007; Suchard & Rambaut, 2009) on the CIPRES web server (www.phylo.org; Miller et al., 2010). The 44-taxa *cox1−3'* mtDNA dataset containing only sequences in a full length was run partitioned by codon positions (1+2, 3). We used a GTR+I+G model with a relaxed molecular clock and an uncorrelated lognormal model of rate variation among branches (Drummond, Ho, Phillips, & Rambaut, 2006). As the tree prior we used a random starting tree and a Yule model. There are no known fossils of the soft-bodied Drilini, which makes any calibration difficult. Therefore, we used one of the most suitable geotectonic events of the Aegean region – the separation of Crete from the Peloponnese during the formation of the Mid-Aegean trench (Tortonian; 12−9 Mya) – as a calibration point (CP). This event has had a great impact on biodiversity in the area (Akın et al., 2010; Lymberakis & Poulakakis, 2010) and has been used and verified in many biogeographic studies (e.g. Parmakelis et al., 2005; Solà, Sluys, Gritzalis, & Riutort, 2013). Crete was probably at least in some degree reconnected to the mainland during the Messinian Salinity Crisis (5.96−5.33 Mya; Krijgsman et al., 1999) and became permanently isolated again after the end of the MSC (Bache et al., 2012). Therefore, we used the end of the MSC as the alternative hypothesis for the calibration point. Two hundred million generations of the MCMC were run, sampling trees every 1000 generations. The results were visualized using Tracer 1.5 (Rambaut & Drummond, 2007) to check that parameter values were fluctuating at stable levels. We obtained the effective sample sizes of more than 200 samples for all parameters. The first 10% of the trees were discarded as burn-in. The remaining trees were summarized in TreeAnnotator 1.6.2. (Drummond & Rambaut, 2007) and the maximum credibility tree was visualized and edited in FigTree 1.3.1 (Rambaut, 2009). We compared the two alternative calibration scenarios using Bayes factors (implemented in Tracer 1.5; Rambaut & Drummond, 2007) and Kass & Raftery's (1995) approach.

For species delimitation, we employed the Generalized Mixed Yule Coalescent method (GMYC; Fontaneto et al., 2007; Pons et al., 2006) implemented in R (http://www.r-project.org/) using the splits package (Ezard, Fujisawa, & Barraclough, 2009) on a rooted normalized tree of 44 *cox1−3′* Drilini sequences. The single threshold model (Fujisawa & Barraclough, 2013; Pons et al., 2006) was performed on the dataset. We applied the DNA barcoding strategy for the association of different semaphoronts (Bergsten et al., 2012; Hebert, Cywinska, Ball, & deWaard, 2003). The intraspecific genetic distances were computed using PAUP* 4.03b10 (Swofford, 2002).

Morphological taxonomy

We examined the morphology of both adult sexes and immature stages. The material was either stored dried in capsules (larvae, females, some males) or pinned (most males). Genitalia were dissected after treatment in hot 10% aqueous solution of potassium hydroxide and photographed using a digital camera mounted on a stereoscopic microscope. The membranous parts of female genitalia were dyed with chlorazol black. The SEM photographs were made with a JSM 5300 Scanning Electron Microscope. The line drawings were derived from the photographs, and scanned and edited using Adobe Photoshop CS6.

The following measurements were taken with an ocular scale bar on a binocular microscope: BL, body length, measured from the fore margin of head to the apex of the elytra (in males) or apex of the body (females, larvae); BW, body width, measured at the widest part of the body; EL, elytral length; WHe, width of head including eyes; WHum, elytral width at humeri; PL, pronotal length at midline; PWA, pronotal width between anterior angles; PWP, pronotal width between posterior angles; Edist, minimum interocular distance in the frontal part of the head; Ediam, maximum eye diameter in lateral view. Only maximum values for body length and width in larvae were recorded.

The material included in this study is deposited in the following collections: Hungarian Natural History Museum, Budapest, Hungary (HNHM; curator: O. Merkl), Lund Museum of Zoology, Lund University, Sweden (MZLU; R. Danielsson), Naturhistorisches Museum, Vienna, Austria (NHMW; H. Schillhammer, M. Jäch), Naturhistorisches Museum Basel, Switzerland (NHMB; E. Sprecher), Naturalis Biodiversity Center, Leiden, the Netherlands (RMNH; H. Huijbregts; including Zoological Museum, Amsterdam; ZMAN; B. Brugge), private collections of A. Teunissen, Eindhoven, the Netherlands (ATPC), F. Houška, České Budějovice, Czech Republic (FHPC), R. Schuh, Wiener Neustadt, Austria (RSPC), L. Bocak, Olomouc, Czech Republic (LBPC), and R. Kundrata, Olomouc, Czech Republic (RKPC). The sequenced specimens from RMNH and HNHM were labelled by voucher numbers RMNH.INS. and six digits or EB2013- and three digits. The *Drilus* specimens from Crete were compared with their congeners from other Mediterranean regions deposited in aforementioned museums, Natural History Museum, London, UK (BMNH; M. Barclay) and Národní muzeum, Prague, Czech Republic (NMPC; J. Hájek). The morphological terminology used herein follows that of Bocak, Branham, and Kundrata (2010).

Results

Molecular phylogeny

The 49-taxa concatenated dataset contained 1381 homologous positions with 38.5% parsimony-informative characters. The numbers of homologous positions and constant, variable parsimony-informative and parsimony-uninformative characters for total matrix and individual markers are listed in Table S2 (see supplemental material online).

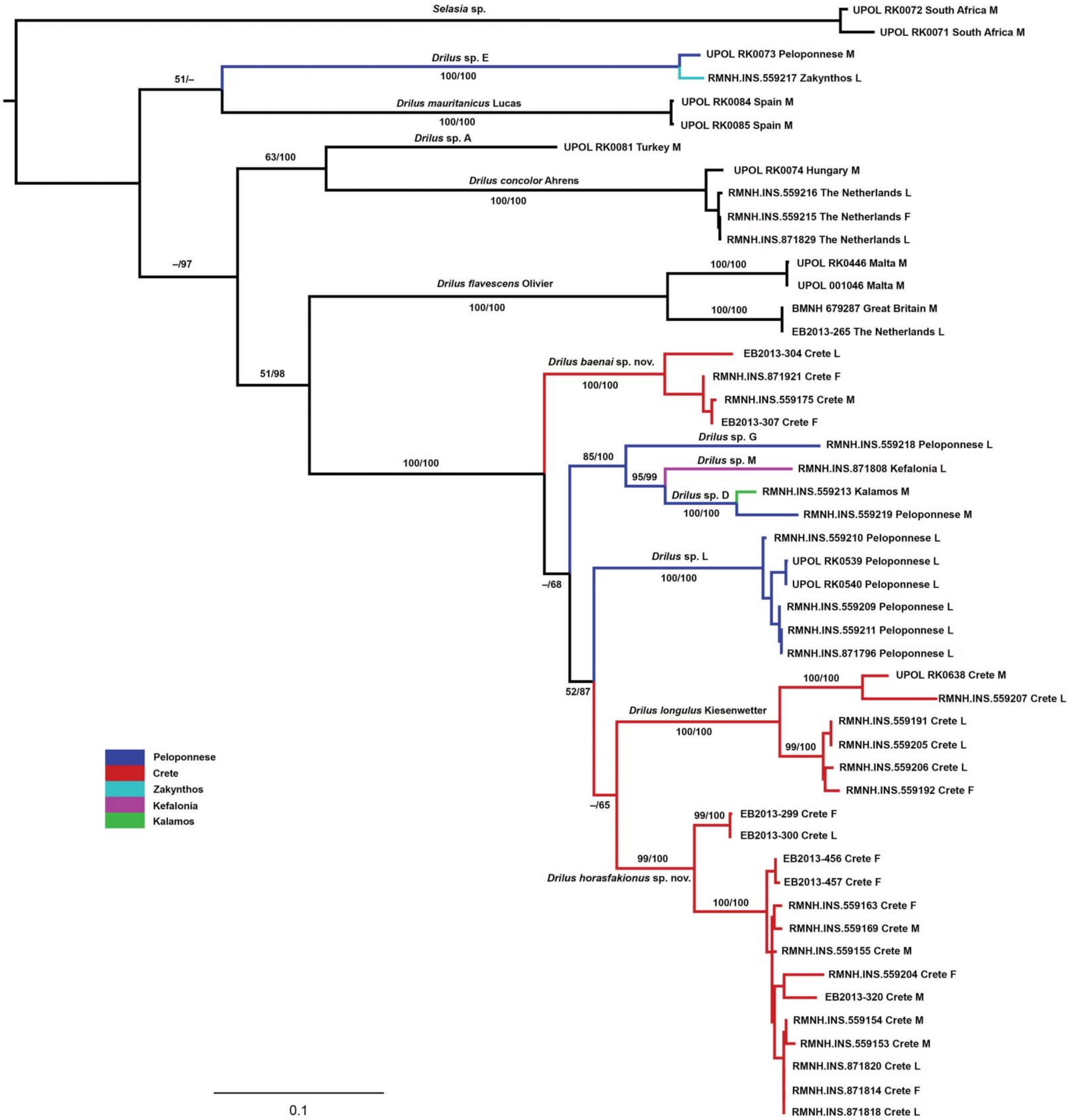


Fig. 1. Maximum likelihood (ML) phylogenetic tree of the 49-taxa concatenated dataset. Numbers at branches represent ML bootstrap values and Bayesian posterior probabilities, respectively. The voucher numbers are followed by the geographic origin and the semaphoront. M, male; F, female; L, larva.

The maximum uncorrected pairwise distances among *Drilus* species varied between 21.3% for *cox1−5′* mtDNA and 21.9% for *cox1−3′* mtDNA (Table S2, see supplemental material online).

The phylogenetic analyses of available Drilini *cox-1* sequences revealed that *Drilus* species from the Peloponnese, Ionian islands and Crete do not form a monophylum (Fig. 1, Table 2). Species E from the Peloponnese and Zakynthos was not included in the Greek *Drilus* clade in all analyses and in most cases formed a weakly supported clade with *D. mauritanicus* Lucas, 1842, i.e. both Cretan and the Peloponnese + Ionian islands *Drilus* species were always paraphyletic. *Drilus* species from the Ionian islands, the Peloponnese and Crete except sp. E formed a robustly supported clade in all analyses (further referred to as the 'Greek clade'; ML analysis BS 93−100%, Bayesian PP 100%). All species of the Greek clade obtained robust support (Fig. 1, Table 2). Within the Greek clade, five subclades with low support are included. These subclades are (1) *D. baenai* sp. nov. from Crete, (2) a subclade including *Drilus* sp. D, M and G from the Peloponnese and Ionian islands, (3) *Drilus* sp. L from the Peloponnese, (4) *D. longulus* from Crete, and (5) *D. horasfakionus* sp. nov. from Crete (Fig. 1, Table 2). In most cases, *D. longulus* and *D. horasfakionus* sp. nov. formed a clade, which was with low but consistent support sister to *Drilus* sp. L (Fig. 1, Table 2). The *Drilus flavescens* Olivier, 1790 was sister to the Greek clade in all but one analyses (Table 2).

In the chronogram obtained using the 10.5 ± 1.5 Mya calibration point (Fig. 2), *Drilus baenai* sp. nov. diverged from the other Greek clade species 11.8 Mya and *Drilus* species D, G and M 10.9 Mya. *Drilus longulus* and *D. horasfakionus* sp. nov. were separated 8.6 Mya. Within the Cretan species, lineages started to diverge 4.5 Mya (*D. horasfakionus* sp. nov.), 4.3 Mya (*D. longulus*) and 3.4 Mya (*D. baenai* sp. nov.; Fig. 2). Using the 5.3 ± 0.3 Mya CP, the separations of *D. baenai* sp. nov. and the *Drilus* spp. D, G and M clade date back to 5.8 Mya and 5.2 Mya, respectively. *Drilus longulus* and *D. horasfakionus* sp. nov. diverged 4.6 Mya. The divergence within the Cretan species started 2.3 Mya (*D. horasfakionus* sp. nov.), 2.4 Mya (*D. longulus*) and 1.8 Mya (*D. baenai* sp. nov.; Table S3, see supplemental material online).

The scenario with 5.3 ± 0.3 Mya CP obtained slightly higher marginal log-likelihood (−5279.809 ± 0.069), but the 10.5 ± 1.5 Mya CP scenario achieved a very similar value (−5280.135 ± 0.066) and therefore, using Kass and Raftery's (1995) guidelines, no alternative is significantly better. However, the comparison between the dated phylogeny of the 'Greek clade' and the geological history of the Aegean region (e.g. Creutzburg, 1963; Lymberakis & Poulakakis, 2010; Meulenkamp, 1985) suggests that using the 5.3 ± 0.3 Mya CP produces some discrepancies (e.g. no *Drilus* lineages present in Crete after the Tortonian

Table 2. Recovery of selected clades with bootstrap support in maximum likelihood (ML) and posterior probabilities in Bayesian (BI) analyses from ClustalW alignment of partial (49 and 24 taxa), concatenated all-taxa (49 taxa) and pruned (24 taxa) datasets. Only values above 50% are shown. M, monophylum; P, paraphylum; A, E, L, D, M, G, species identified in the main text (see also Table 1); CR/PE$^+$, clade of *Drilus* spp. from Crete, Peloponnese and Ionian islands; CR/PE$^-$, CR/PE$^+$ minus *Drilus* sp. E; Crete, *Drilus* spp. from Crete; Pelop., *Drilus* spp. from Peloponnese and Ionian islands; flav, *Drilus flavescens* Olivier, 1790; mauri, *Drilus mauritanicus* Lucas, 1842; hora, *Drilus horasfakionus* sp. nov.; long, *Drilus longulus* Kiesenwetter, 1859; baenai, *Drilus baenai* sp. nov.

Type of dataset	Number of taxa	Type of analysis	mauri + sp. E	flav+					hora +long	hora+ long+ L	hora+long +L+DMG	D+M+G	D+M	baenai	long	hora	sp. L	sp. D
				CR/PE$^+$	CR/PE$^-$	CR/PE$^-$	Crete	Pelop.										
cox1-3′ mtDNA	49	BI	M(98)	P	M(100)	M	P	P	M(70)	M	P	M(100)	M(98)	M(100)	M(100)	M(98)	M(100)	M(100)
cox1-3′ mtDNA	49	ML	M(57)	P	M(96)	P	P	P	M(55)	P	P	M(76)	M(94)	M(99)	M(99)	M(85)	M(100)	M(99)
cox1-5′ mtDNA	24	BI	P	P	M(100)	P	P	P	M	M	M	M(85)	P	M(100)	M(100)	–	M(100)	–
cox1-5′ mtDNA	24	ML	P	P	M(93)	M(55)	P	P	P	M	M	M(62)	P	M(100)	M(100)	–	M(98)	–
concatenated	24	BI	M	P	M(100)	M(95)	P	P	M	M(84)	M(72)	M(100)	M(99)	M(100)	M(100)	–	M(100)	–
concatenated	24	ML	M	P	M(100)	M(60)	P	P	M	M	M	M(75)	M(96)	M(100)	M(100)	–	M(100)	–
concatenated	49	BI	M	P	M(100)	M(98)	P	P	M(65)	M(87)	M(68)	M(100)	M(99)	M(100)	M(100)	M(100)	M(100)	M(100)
concatenated	49	ML	M(51)	P	M(100)	M(51)	P	P	M	M(52)	M	M(85)	M(95)	M(100)	M(100)	M(99)	M(100)	M(100)

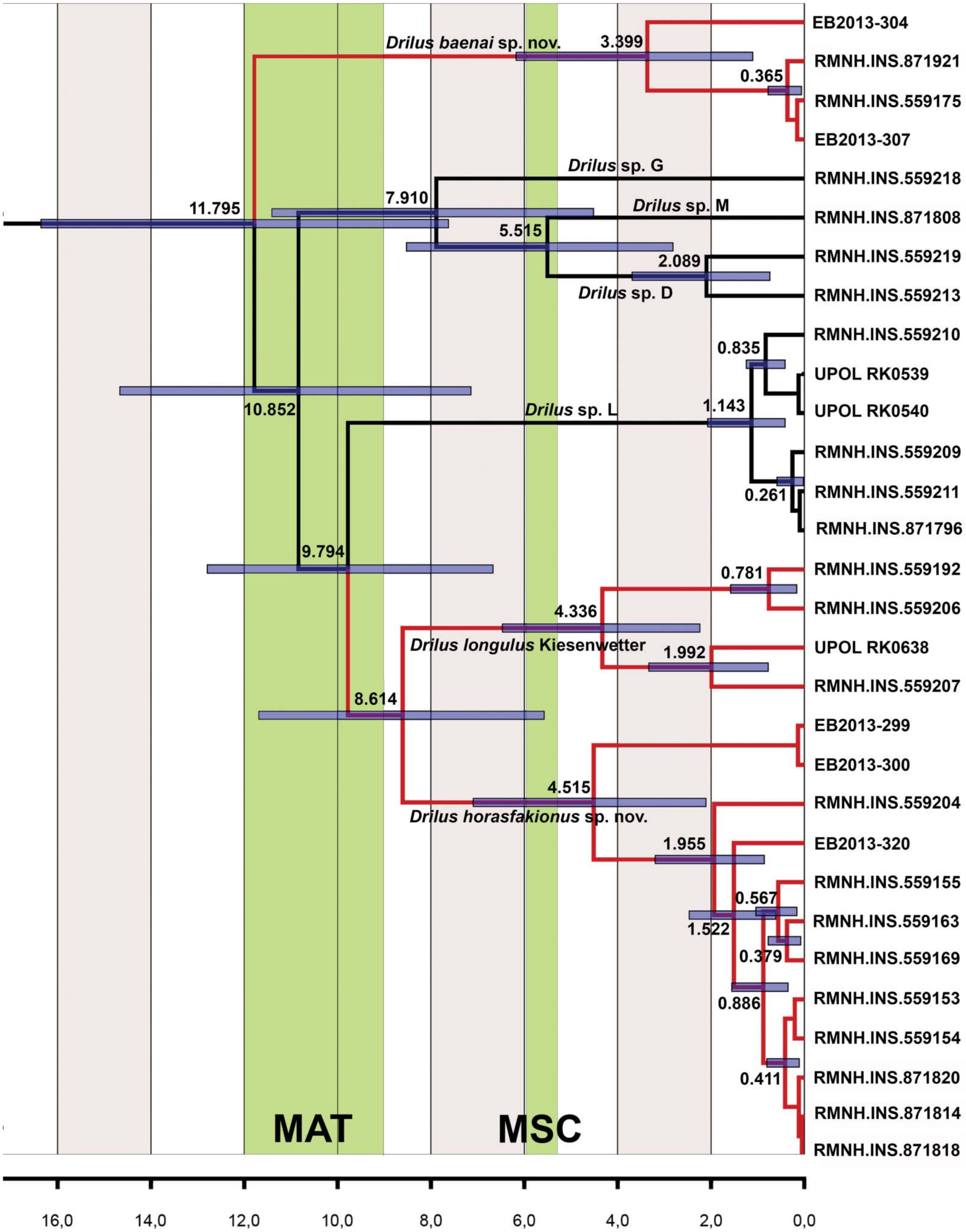


Fig. 2. Time-calibrated maximum clade credibility tree of the 44-taxa *cox1–3′* mtDNA dataset obtained under a relaxed molecular clock and an uncorrelated lognormal model as implemented in BEAST. Mean node ages are indicated at each node. The blue bars represent the 95% highest posterior density distributions for the estimated divergence time of each node. MAT, the formation of the Mid-Aegean trench; MSC, the Messinian Salinity Crisis.

isolation of Crete, the separation of *D. baenai* sp. nov. predates the MSC). Therefore, we will not discuss this CP scenario further. Molecular substitution rate estimates for both scenarios are reported in Table S3 (see supplemental material online).

The GMYC model for species delimitation identified 17 (confidence interval 10−22) independent entities including singletons and 12 (9−12) clusters, i.e. entities with more than one individual. The likelihood values of the null and the GMYC models were 21.04159 and 28.67791, respectively. The GMYC model had a significantly better fit to the data than the null model ($P < 0.001$). The Maltese and NW European populations of *Drilus flavescens* were inferred as two independent species. Similarly, broadly defined *D. baenai* sp. nov., *D. horasfakionus* sp. nov. and *D. longulus* were divided each into two entities (Table S4, see supplemental material online). The intraspecific genetic distances are listed in Table S5 (see supplemental material online).

Taxonomy

Drilus Olivier, 1790

Drilus Olivier, 1790: 1.

Type species. *Drilus flavescens* Olivier, 1790: 1.
= *Cochleoctonus* Mielzinsky, 1824: 74.

Type species. *Cochleoctonus vorax* Mielzinsky, 1824: 74.

Diagnosis. *Drilus* differs from *Selasia* Laporte by the deeply emarginate frontal margin of mesoventrite (slightly concave in *Selasia*) and from *Malacogaster* by convex lateral margins of pronotum (subparallel-sided in *Malacogaster*) and almost complete sharp edges at lateral prothoracic margins (short in *Malacogaster*; Kundrata & Bocak, 2007; Kundrata, Kobieluszova, & Bocak, 2014). The detailed morphology of *Drilus* adults and larva was described by Bocak et al. (2010).

Drilus baenai sp. nov.

(Figs 6, 10, 14, 18, 22, 26, 30, 34, 37, 40, 43, 46, 51)

Type locality. Greece, Crete, Palon Horion.

Holotype. Male, ‘Kreta, Palon Horion, Palm, 18.5’ (MZLU). **Paratypes.** 2 males, ‘Kreta, Palon Horion, 19/5 75’ (MZLU), 1 male, ‘Kreta, 17.5.70, U. Pfizer, // D. longulus Kies., det. W. Wittmer, NMB, coll. Wittmer’ (NHMB), 1 male (RMNH.INS.559173), ‘GREECE, Crete, Iraklion, Asfendilis Mt., UTM: LU3773, 2-10-1991, Leg. M. Schilthuizen’ (RMNH), 1 male (RMNH.INS.559175), ‘Greece, Crete, 2 km W of Kalí Liménes, UTM KU9766, 26.7.1995, G. Lindner leg.’ (RMNH), 1 male (RMNH.INS.559181), ‘Greece, Central Crete, 1 km SW of Avdoú, UTM LU5698, 7.8.1994, F. Welter-Schultes leg.’ (RMNH), 1 male (RMNH.INS.559184), ‘Greece, E Crete, 0.4 km E of Anatolí, UTM LU7778, 13.5.1990, Holger Fischer leg.’ (RMNH), 1 female (EB2013−307), ‘Greece, Central Crete, 3.5 km S of Apesokári, UTM LU1372, 6.7.1993, Pintér and Varga leg.’ (HNHM), 1 female (RMNH.INS.871921), ‘Greece, Crete, prov. Iraklion 2 km (4.8 km measured along road) S of Rotas[s]I (= 2.2 km SE of Pirgos) 580 m alt., UTM LU3373, 2.10.1991, E. Gittenberger leg.’ (RMNH).

Other material examined. 2 males (RMNH.INS.559170, RMNH.INS.559171), ‘Greece, Crete, prov. Lasithi, NW point of Lasitiou-plain 0.6 km N of Kato Methohi (= 4.8 km S of Avdhou) alt. 790 E-NE exposed, UTM LU5795, 25.5.1992, E. & E. J. Gittenberger & M. Lombaerts leg.’ (RMNH), 1 male (RMNH.INS.559174), ‘Greece, Central Crete, Limín Chersonísou, UTM LV5309, 16.1.1987, F. Welter-Schultes leg.’ (RMNH), 1 male (RMNH.INS.559176), ‘Greece, Central Crete, 2 km NE of Kastéli, UTM LU4798, 4.8.1994, F. Welter-Schultes leg.’ (RMNH), 1 male (RMNH.INS.559177), ‘Greece, Central Crete, 2 km NE of Péfkos, UTM LU6380, 7.12.1990, F. Welter-Schultes leg.’ (RMNH), 1 male (RMNH.INS.559178), ‘Greece, Central Crete, Moní Agarathou near Sambás, UTM LU4099, 7.5.1990, Holger Fischer leg.’ (RMNH), 1 male (RMNH.INS.559179), ‘Greece, Central Crete, Iráklio, UTM LV3112, 15.1.1987, F. Welter-Schultes leg.’ (RMNH), 1 male (EB2013−390), ‘Greece, E Crete, Vai near Palékastro, UTM MV3201, 14.7.1994, Drimmer, Pintér and Varga leg.’ (HNHM), 1 male (RMNH.INS.559180), ‘Greece, Central Crete, 2 km E of Laráni, UTM LU2686, 4.12.1990, F. Welter-Schultes leg.’ (RMNH), 1 male (RMNH.INS.903266), ‘Greece, Central Crete, 1 km NW of Panórama, UTM LU3490, 15.12.1990, F. Welter-Schultes leg.’ (RMNH), 1 male (EB2013−313), ‘Greece, E Crete, 1 km SE of Sitía, UTM MU2095, 9.7.1993, Pintér and Varga leg.’ (HNHM), 1 male (RMNH.INS.559182), ‘Greece, E Crete, gorge 2 km W of Kavoúsi, UTM LU9487, 14.7.1990, F. Welter-Schultes and J. Fischer leg.’ (RMNH), 1 male (RMNH.INS.559183), ‘Greece, E Crete, 5 km W Lástros, UTM LU9990, 3.1.1986, F. Welter-Schultes leg.’ (RMNH), 1 male (RMNH.INS.559185), ‘Greece, E Crete, 0.5 km E of Máles, UTM LU7282, 17.1.1987, F. Welter-Schultes leg.’ (RMNH), 1 male (RMNH.INS.559186), ‘Greece, Central Crete, Chárakas, UTM LU2974, 28.12.1990, F. Welter-Schultes leg.’ (RMNH), 1 male (RMNH.INS.559187), ‘Greece, Central Crete, 1 km E of Keratókambos, UTM LU5376, 12.12.1990, F. Welter-Schultes leg.’ (RMNH), 1 male (RMNH.INS.559188), ‘Greece, E Crete, 2 km NE of Chandrás, UTM MU2084, 27.4.1996, F. Welter-Schultes leg.’ (RMNH), 1 male (RMNH.INS.559189), ‘Greece, E Crete, 1 km E Azokéramos, UTM MU3388, 26.4.1996, F.

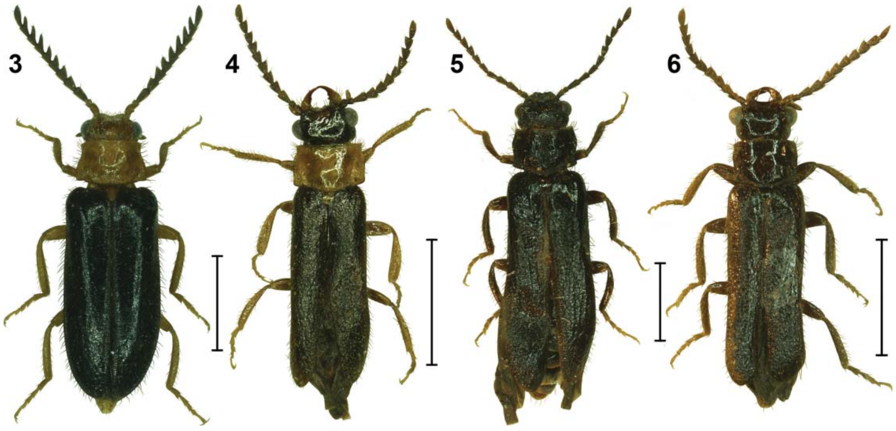
Welter-Schultes leg.' (RMNH), 1 male (RMNH. INS.559190), 'Greece, Island of Día, N of central Crete, UTM LV3924, 25.6.1990, F. Welter-Schultes & J. Fischer leg.' (RMNH), 1 male (EB2013–407), 'Greece, Greece: E Crete, 2 km E of Sitía, UTM MU2195, 9.7.1993, Pintér and Varga leg.' (HNHM), 1 larva (EB2013–309), 'Greece, Gávdos island S of Crete, 3.1992, F. Welter-Schultes' (HNHM), 1 male (EB2013–363), 1 larva (EB2013–304), 'Greece, E Crete, Moní Faneroménis, 3 m W of Sitía, UTM MU1597, 13.7.1994, Drimmer, Pintér and Varga leg.' (HNHM), 1 larva (EB2013–310), 'Greece, Central Crete, 2.5 km W of Sambás, UTM LU4097, 30.7.1992, Pintér and Varga leg.' (HNHM), 3 larvae (RMNH.INS.903261, RMNH.INS.903273, RMNH.INS.903281), 'Greece, E Crete, Yuktas, mountain south of Iraklion, 450 m alt., 35.238588′N 25.151182′E, 5–2013, M. Schilthuizen leg.' (RMNH), 1 larva (RMNH. INS.871924), 'Crete, Asterousia range (south coast, Iraklion prov.) 4.7 km from Miamou along the road in northerly direction, 410 m alt., M. Schilthuizen leg.' (RMNH).

Diagnosis. Males. *Drilus baenai* sp. nov. differs from similarly coloured *D. longulus* by larger eyes (Figs 9–10, 13–14), short clypeus with shallowly emarginate anterior margin (Figs 13–14), head rather smooth, with fine, sparse punctures, more robust antennae (Figs 21–22), and sharply V-shaped mesoventrite with short deep median depression (Figs 25–26).

Females. *Drilus baenai* sp. nov. is the only known Cretan *Drilus* species with valviferes and coxites fully separated (Fig. 51).

Larvae. *Drilus baenai* sp. nov. is distinguishable from its Cretan congeners by cerci with a thick short hair in middle part of outer margin (missing in *D. horasfakionus*, slenderer in *D. longulus*; Figs 44–46).

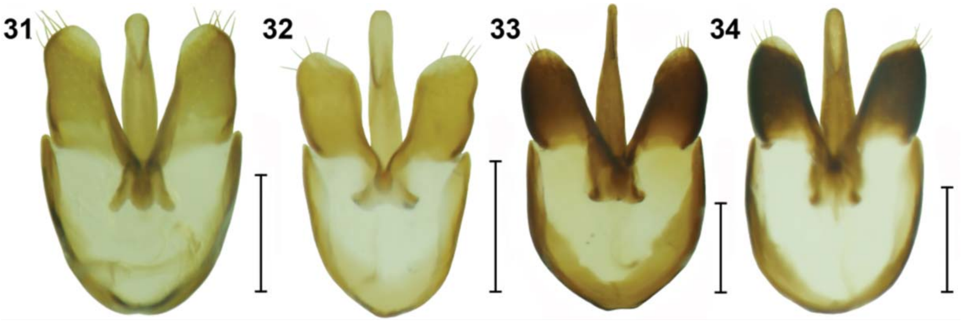
Description. Male. Body medium-sized, elongate, almost parallel-sided, 3.8 times as long as wide at humeri, moderately convex dorsally (Fig. 6). All body parts dark brown to black, legs and antennae brown, antennomeres 1–2 and tarsi lighter. Entire body covered by golden pubescence. Head including eyes 1.1–1.2 times wider than anterior margin of pronotum, smooth, very sparsely and finely punctured, with shallow and wide frontal depression; clypeus short, anterior clypeal edge smooth, widely concave between antennal sockets; cranium dorsally with sparse, semi-erect pubescence (Figs 10, 14). Eyes medium-sized, their frontal distance 1.8 times eye diameter. Mandibles robust, sharp, shiny, considerably curved, basally covered with long setae, with basal part broader, incisor margin with conspicuous tooth in middle part (Fig. 18). Antennae robust, serrate, reaching one third of elytral length, scapus robust, pear-shaped, pedicel short, minute, antennomere 3 only slightly serrate, antennomeres 4–10 moderately serrate, subequal in length; apical antennomere longest, simple (Fig. 22). Pronotum slightly convex, widest in one third, in posterior angles 1.2 times wider than length at midline. Anterior margin almost straight; lateral margins convex, widened in one third; posterior margin about as wide as anterior margin, convex, slightly sinuate in middle part. Anterior angles obtuse, posterior angles almost rectangular, rounded, slightly turned upward (Fig. 10); surface of disc punctured, with sparse, semi-erect, long setae. Prosternum transverse, with frontal margin almost straight, prosternal process short, elevated in middle part (Fig. 30). Scutellum flat, U-shaped, almost as long as wide. Mesoventrite narrow, sharply V-shaped, with deep, narrow median depression in frontal margin (Fig. 26). Metaventrite with wide depression in middle part, with fine, sparse punctures and semi-erect pubescence. Elytral outer margins almost parallel-sided, inner margins dehiscent in apical third; elytra 1.3 times wider than posterior margin of pronotum,



Figs. 3–6. General appearance of the Cretan *Drilus* spp. (males): (3) *Drilus creticus*, (4) *D. horasfakionus* sp. nov., (5) *D. longulus*, (6) *D. baenai* sp. nov. Scale bars: 2 mm.

2.6 times longer than width at humeri, irregularly wrinkled, covered by sparse pubescence; each elytron rounded independently, tapered apically (Fig. 6). Abdomen short, slender; with long pubescence sparse in middle part, denser around margins. Legs moderately long, slender, slightly compressed, with sparse, long, erected setae, coxae long, robust, trochanters slender, obliquely attached to femora, tarsomeres 1–3 gradually shortened; tarsomere 4 minute, shortest; apical tarsomere long, narrow, slightly longer than tarsomeres 3 and 4 together, claws simple, slender, slightly curved. Phallus strong, longer than parameres, considerably curved, almost parallel-sided, parameres apically with sparse setae, phallobase robust, longer than parameres (Fig. 34).

Figs. 7–30. Head and pronotum, dorsal view (males): (7) *Drilus creticus*, (8) *D. horasfakionus* sp. nov., (9) *D. longulus*, (10) *D. baenai* sp. nov.; head, dorsofrontal view: (11) *D. creticus*, (12) *D. horasfakionus* sp. nov., (13) *D. longulus*, (14) *D. baenai* sp. nov.; right mandible: (15) *D. creticus*, (16) *D. horasfakionus* sp. nov., (17) *D. longulus*, (18) *D. baenai* sp. nov.; antenna: (19) *D. creticus*, (20) *D. horasfakionus* sp. nov., (21) *D. longulus*, (22) *D. baenai* sp. nov.; mesoventrite: (23) *D. creticus*, (24) *D. horasfakionus* sp. nov., (25) *D. longulus*, (26) *D. baenai* sp. nov.; prosternum: (27) *D. creticus*, (28) *D. horasfakionus* sp. nov., (29) *D. longulus*, (30) *D. baenai* sp. nov. Scale bars: 1 mm (7–10, 19–22), 0.5 mm (11–14), 0.25 mm (15–18, 23–30).



Figs. 31−34. Male genitalia: (31) *Drilus creticus*, (32) *D. horasfakionus* sp. nov., (33) *D. longulus*, (34) *D. baenai* sp. nov. Scale bars: 0.25 mm.

Female. Larviform, body elongate**.** All body parts yellowish to light brown, only dorsal surface of thoracic and abdominal segments laterally dark brown (Fig. 37). Head prognathous, well sclerotized, small, narrower than pronotal anterior margin, with shallow depression between antennal sockets; clypeus short, widely concave anteriorly. Eyes small, their frontal distance 3.7−4.0 times eye diameter. Antennae not present in examined material. Mandibles robust, shiny, considerably curved, incisor margin with small tooth in middle part (Fig. 43). Pronotum widest posteriorly; thoracic and abdominal tergites wrinkled, with longitudinal narrow depression. Legs short, robust. Abdomen widest in posterior third, apical segment much narrower and smaller. Ovipositor with tiny valviferes, separated from robust coxites. Styli small, connected to coxites by extensive membrane. Vagina simple, slender, sac-like, with unpaired glands (Fig. 51).

Larva. Body elongate, slightly widened towards apex. All body parts dark yellow to light brown, markings on the dorsal surface of thoracic and abdominal segments dark brown, head with large dark band around stemmata, expanding towards the rear (Fig. 40). Head prognathous, well sclerotized, small, narrower than frontal pronotal margin. Antennae three-segmented. Mandibles well developed, sclerotized, narrow and falcate. Legs five-segmented, short, robust. Abdomen with sclerotized and pigmented tergites, with long setae, especially dorsally (Fig. 40). Lateral pleural processes well developed, lateral tergal processes slightly developed; both more developed towards the apex, but less developed on penultimate and ultimate segments. Last segment small, slender. Cerci bent upward and slightly inward, covered with thin long pubescence, with a thick short hair in middle part of outer margins (usually two times thicker than width of thin hairs), cerci apically cuspidate; apex short (Fig. 46).

Variability. Males. Antennae light brown to brown, antennomeres 1−2 mostly lighter than rest of antennae; legs either concolor brown or tarsi lighter. Anterior angles obtuse or almost rectangular, posterior angles slightly to distinctly turned upward. Metaventrite with depression variable in shape and size.

Measurements. Holotype: BL 6.8 mm, EL 4.7 mm, WHe 1.4 mm, WHum 1.8 mm, PL 1.1 mm, PWA 1.4 mm, PWP 1.4 mm, Edist 0.8 mm, Ediam 0.5 mm. Variability in males: BL 3.5−6.8 mm, EL 3.0−4.7 mm, WHe 1.0−1.4 mm, WHum 1.0−1.8 mm, PL 0.7−1.1 mm, PWA 0.8−1.4 mm, PWP 0.9−1.4 mm, Edist 0.5−0.8 mm, Ediam 0.3−0.5 mm. Females: BL 10.5−16.8 mm, BW 2.3−3.7 mm, WHe 0.8−1.0 mm, PL 0.9−1.1 mm, PWA 1.0−1.4 mm, PWP 1.2−2.0 mm, Edist 0.80 mm, Ediam 0.20 mm. Larvae: BL 13.3 mm, BW 3.0 mm.

Distribution. *Drilus baenai* sp. nov. occurs in central and eastern Crete (Heraklion and Lasithi regional units including the Dia islet) and in Gavdos islet (Chania regional unit; Fig. 52).

Biology and ecology. *Drilus baenai* sp. nov. was found in shells of Albinaria corrugata corrugata, *A. inflata draparnaldi, A. rebeli, A. retusa, A. terebra* and *A. teres.*

Etymology. The species name ‘*baenai*’ is a patronym in honour of Manuel Baena (Córdoba, Spain).

Remarks. Schilthuizen et al. (1994) returned the types of *D. creticus* and *D. longulus* to the MNHN in the mid-1990s but these specimens have been apparently misplaced in the collection. Until now, *Drilus longulus* was the only uniformly dark-coloured species in Crete. We found two dark-coloured *Drilus* species: the first one has elongated clypeus forming narrowed nasal part, and the second one has short clypeus with frontal margin widely concave (Figs 13−14). *Drilus longulus* is morphologically similar to *D. funebris* from the Greek mainland (Brenske & Reitter, 1884). Because *D. funebris* has an elongated clypeal part, we consider the specimens with long nasal part to be *D. longulus* and specimens with short, widely emarginated clypeus *D. baenai* sp. nov. Schilthuizen et al. (1994) briefly described the black coloured *Drilus* form I stating: 'The frontal edge of the clypeus, between the antennal bases, is concave' (p. 183). From that description it is clear that the *Drilus* form I is conspecific with *D. baenai* sp. nov.

Drilus creticus Pic, 1905
(Figs 3, 7, 11, 15, 19, 23, 27, 31)

Drilus creticus Pic, 1905: 170.

Type locality. 'Crête: Assistaes' (Pic, 1905)

Material examined. 1 male, 'CRETE, Rethymno pref., Mariou, 30. v. 2010, Lgt. F. Houška' (FHPC); 1 male, 'Kreta, Kritsa, 17.5.75' (MZLU), 1 male, 'Kreta, Palon Horion, Palm' (MZLU), 1 male, 'GREECE, Crete, Milatos, 29-IV-1988, K.W.R. Zwart' (RMNH), 1 male, 'Graecia, Kreta, Mirsini, 18.6.1998, ex. coll. Keukelaar, *Drilus creticus* Pic, A. Teunissen det.' (ATPC), 1 male, 'GREECE: E-Crete (10), rd. to Lasithi Plateau, 5 km SSW Malia, 0.5 km N Gonies, 300 m, 4.6.2010, leg. Schuh' (RSPC).

Diagnosis. Males. *Drilus creticus* Pic, 1905 differs clearly from *D. longulus* Kiesenwetter, 1859 and *D. baenai* sp. nov. by shorter, more robust habitus (Figs 3, 5–6) and golden brown pronotum (Figs 7, 9–10). *Drilus creticus* is easily distinguishable from similarly coloured *D. horasfakionus* sp. nov. by the following combination of characters: more robust general appearance (Figs 3–4), lighter head colouration (Figs 7–8), mandibular incisor margin with conspicuous tooth closer to apical part (Figs 15–16), more serrate antennae (Figs 19–20), pronotum with more prominent, acute posterior angles (Figs 7–8), prosternum less transverse (Figs 27–28), mesoventrite distinctly wider and more transversal (Figs 23–24), and longer parameres (Figs 31–32).

Redescription. Male. Body medium-sized, elongate, almost parallel-sided, 3.1–3.2 times as long as wide at humeri, moderately convex dorsally (Fig. 3). Antennomeres 1–2, prothorax, scutellum, mesoventrite, legs and last visible ventrite golden to golden brown, head golden brown to brown, antennomeres 3–11 and metaventrite dark brown, elytra and abdomen black. Entire body covered by golden pubescence. Head including eyes 1.1–1.2 times wider than anterior margin of pronotum, sparsely punctured, with shallow and wide frontal depression, anterior clypeal edge moderately concave, dorsally with sparse, semi-erect pubescence (Figs 7, 11). Eyes medium-sized, their frontal distance 1.7–1.9 times eye diameter. Mandibles robust, shiny, considerably curved, basally covered with long setae, incisor margin with robust tooth near apical part (Fig. 15). Antennae strongly serrate, reaching one third of elytral length, scapus robust, pear-shaped, pedicel short, minute, antennomere 3 long, simple, slightly widened apically; antennomeres 4–10 serrate, subequal in length, apical antennomere longest, simple (Fig. 19). Pronotum slightly convex, widest in posterior angles, 1.5–1.6 times wider than length at midline. Anterior margin slightly emarginate in middle; lateral margins convex, gradually widened posteriorly; posterior margin 1.2–1.3 times wider than anterior margin, slightly sinuate in middle part. Anterior angles almost rectangular, posterior angles prominent, acute, slightly turned upward (Fig. 7); surface of disc finely punctured, with sparse, erected, long setae. Prosternum transverse, with frontal margin almost straight, prosternal process short, elevated in middle part (Fig. 27). Scutellum flat, subtriangular, posteriorly narrowly rounded. Mesoventrite transverse, widely V-shaped, frontal margin shallowly emarginate, with short median depression (Fig. 23). Elytra subparallel-sided, widest at humeri, 1.2–1.3 times wider than posterior margin of pronotum, 2.2–2.3 times longer than width at humeri, irregularly wrinkled, covered by sparse pubescence, with slight longitudinal keel running from humeri to interior margin of elytral apex, inconspicuous in apical third of elytra; basal part of elytra grooved (Fig. 3). Abdomen slender; with long pubescence sparse in middle part and very dense around margins; penultimate ventrite with smooth, shallow emargination in posterior margin. Aedeagus with strong phallus; phallus slightly longer than parameres, considerably curved, almost parallel-sided; parameres long, apically with sparse setae; phallobase robust, wide, only slightly longer than parameres (Fig. 31). Female. Unknown. Larva. Unknown.

Measurements. Males: BL 5.7–6.1 mm, EL 4.2–4.5 mm, WHe 1.3–1.5, WHum 1.8–2.0 mm, PL 0.9–1.0 mm, PWA 1.2–1.3 mm, PWP 1.5–1.6 mm, Edist 0.8 mm, Ediam 0.4–0.5 mm.

Distribution. *Drilus creticus* is known from central and eastern Crete (Rethymno, Heraklion and Lasithi regional units). The type locality 'Assistaes' might be the misspelling of Asites; = Kato Asites; *c.* 25 km SW of Heraklion city. The place 'Palon Horion' written on the label in one of the MZLU paratypes might be the misspelling of Kalo Horio, a village near Kritsa in eastern Crete.

Biology and ecology. Unknown.

Remarks. Type specimen should be deposited in the Pic collection in Muséum national d'histoire naturelle, Paris, France (Pic, 1905). However, the type is probably lost (see the remarks under the *D. baenai* sp. nov. section). According to the original description (Pic, 1905), this species should be 12 mm long. However, no male specimen of any Cretan species known by the authors reaches this length (Schilthuizen et al., 1994; this study).

Drilus horasfakionus sp. nov.
(Figs 4, 8, 12, 16, 20, 24, 28; 32; 35, 38, 41, 44, 47−49)

Type locality. Greece, Crete, Imbros.

Holotype. Male, 'Greece, Creta, Imbros, 27. VII. 1992, leg. L. Pintér & A. Varga' (HNHM). **Paratypes.** 3 males, 1 female, the same data as holotype, 1 male, 'Greece, Creta, Hora Sfakion, 27. VII. 1992, leg. L. Pintér & A. Varga' (HNHM), 2 males, 2 females (EB2013−456, EB2013−457), 'Greece, Creta, Aradena, 27. VII. 1992, leg. L. Pintér & A. Varga' (HNHM), 1 male, 'Greece, Creta, Koundoura, 26. VII. 1992, leg. L. Pintér & A. Varga' (HNHM), 1 male (RMNH.INS.559153), 'Greece, Crete, Khanion, Imbros gorge, 4 km NE of Khora Sfakion, UTM: KV418021, 470 m alt., From shells of *Albinaria* spp., 31-7-1996, Leg. E. Gittenberger' (RMNH), 1 female (RMNH.INS.559204), 'Greece, Crete, Gorge north of Spili, 380 m alt., 24.5714'N, 35.2573′N 24.5714′E, M. Schilthuizen leg.' (RMNH), 1 female (RMNH.INS.559163), 'Greece, Gávdos island, S of Crete, UTM, 3.1992, F. Welter-Schultes leg.' (RMNH).

Other material examined. 1 male (RMNH.INS.559154), 2 females (RMNH.INS.871813, RMNH.INS.871814), 3 larvae (RMNH.INS.871820, RMNH.INS.871815, RMNH.INS.871818), 'Greece, Crete, Khanion, Imbros gorge, 4 km NE of Khora Sfakion, 470 m alt., UTM KV418021, 31.7.1996, E. Gittenberger leg.' (RMNH), 1 male (RMNH.INS.559155), 'Greece, Crete, prov. Khanion (= Khania, = Hania, = Chania) Imbros gorge, 4 km NE of Khora Sfakion, 455 m alt., UTM KV4101, 5.5.1998, E. Gittenberger leg.' (RMNH), 1 male (RMNH.INS.559157), 1 larva (RMNH.INS.871812), 'Greece, Crete, prov. Khanion (= Khania, = Hania, = Chania) NE-side of Khora Sfakion, left side gorge, 85 m alt., UTM KU383996, 6.5.1998, E. Gittenberger leg.' (RMNH), 1 male (EB2013−357), 2 females (EB2013−354, EB2013−355), 1 larva (EB2013−356), 'Greece, W Crete, Arádena gorge W of Anópoli, UTM KV3201, 27.7.1992, Pintér and Varga leg.' (HNHM), 2 males (EB2013−303, EB2013−359), 2 females (EB2013−358, EB2013−301), 2 larvae (EB2013−353, EB2013−302), 'Greece, W Crete, Agios Ioánis W of Anópoli, UTM KV2802, 27.7.1992, Pintér and Varga leg.' (HNHM), 2 males (RMNH.INS.559159, RMNH.INS.559160), 1 female (RMNH.INS.559158), 'Greece, W Crete, 1.5 km ENE of Anidri near Paleochóra, UTM GE4804, 5.1.1987, F. Welter-Schultes leg.' (RMNH), 1 male (EB2013−371), 3 females (EB2013−368, EB2013−369, EB2013−370), 'Greece, W Crete, Farági Kourtaliótiko N of Asómatos, UTM KU6897, 21.7.1986, K. Sin leg.' (HNHM), 1 male (RMNH.INS.559162), 1 male (EB2013−375), 2 females (EB2013−374, EB2013−306), 'Greece, W Crete, Imbros gorge, southern entry, UTM KV4200, 18.7.1994, Drimmer, Pintér and Varga leg.' (HNHM), 1 male (EB2013−379), 1 female (EB2013−378), 'Greece, W Crete, Samaria gorge, uppermost 2 km, UTM GE6710, 17.7.1986, K. Sin leg.' (HNHM), 1 male (EB2013−385), 'Greece, W Crete, Moní Chrisoskalítisas, UTM GE3010, 17.7.1993, Pintér and Varga leg.' (HNHM), 1 male (RMNH.INS.559165), 'Greece, Gavdopoúla island, S of Crete, UTM, 7.3.1992, F. Welter-Schultes leg.' (RMNH), 1 male (RMNH.INS.559166), 'Greece, Gavdopoúla island, S of Crete, UTM, 7.3.1992, F. Welter-Schultes leg.' (RMNH), 1 male (EB2013−396), 'Greece, W Crete, Paralía Korakás near Rodákino, UTM KU5596, 18.7.1994, Drimmer, Pintér and Varga leg.' (HNHM), 1 male (EB2013−397), 'Greece, W Crete, Soúgia, UTM GE5503, 19.7.1993, Pintér and Varga leg.' (HNHM), 1 male (RMNH.INS.559167), 'Greece, W Crete, 6.3 km E of Paleochóra, UTM GE5003, 8.1.1987, F. Welter-Schultes leg.' (RMNH), 1 male (RMNH.INS.559168), 'Greece, West Crete, UTM GE2809, 1.1987, F. Welter-Schultes leg.' (RMNH), 1 male (RMNH.INS.559169), 'Greece, W Crete, 6 km W of Paleochóra, UTM GE3703, 24.10.2003, H. Turni leg.' (RMNH), 1 male (EB2013−319), 'Greece, Central Crete, Knosós, UTM LV3307, 12.7.1994, Drimmer, Pintér and Varga leg.' (HNHM), 1 male (EB2013−320), 'Greece, W Crete, Moní Préveli, UTM KU6893, 20.7.1994, Drimmer, Pintér and Varga leg.' (HNHM), 1 male (RMNH.INS.559161), 1 female (RMNH.INS.559161), 'Greece, W Crete, Farági Kourtaliótiko N of Asómatos, UTM KU6897, 21.7.1986, K. Sin leg.' (RMNH), 1 female (EB2013−299), 1 larva (EB2013−300), 'Greece, W Crete, 2 km N of Rodopós, UTM GE4940, 16.7.1993, Pintér and Varga leg.' (HNHM), 1 larva (RMNH.INS.559164), 'Greece, W Crete, 8 km N of Kalivianí, UTM GE3539, 16.7.1993, Pintér and Varga leg.' (RMNH), 2 larvae (RMNH.INS.903262, RMNH.INS.903275), 'Greece, W Crete, Theriso, gorge south of Chania, 580 m alt., 35.4175'N 23.9867'E, 5−2013, M. Schilthuizen leg.' (RMNH), 1 larva (EB2013−345), 'Greece, W Crete, Farági Kotsífou 2 km NE of Selia, UTM KV6200, 23.7.1994, Drimmer, Pintér and Varga leg.' (HNHM), 1 larva (EB2013−398), 'Greece, W Crete, between Paleochóra and Koundoúra, UTM GE4102, 26.7.1992, Pintér and Varga leg.' (HNHM).

Diagnosis. Males. *Drilus horasfakionus* sp. nov. can be easily distinguished from *D. longulus* and *D. baenai* sp. nov. by the golden brown pronotum (Figs 4−6, 8−10) and from similarly coloured *D. creticus* by the following combination of characters: slender habitus (Figs 3−4), dark head (Figs 7−8, 11−12), mandibular incisor margin with small tooth in middle part (Figs 15−16), less strongly serrate antennae (Figs 19−20), pronotum with less prominent posterior angles (Figs 7–8), prosternum more transverse (Figs 27–28), mesoventrite distinctly narrower and less transverse (Figs 23–24), and shorter parameres (Figs 31–32).

Females. *Drilus horasfakionus* sp. nov. shares fused valvifer and coxites with *D. longulus* (Figs 49–50). These species can be distinguished by the following characters: *D. horasfakionus* sp. nov. has a paler pronotum than other thoracic and abdominal tergites (uniformly coloured in *D. longulus*; Figs 35–36), mandibular incisor margin with short tooth in middle part (robust, closer to apical part in *D. longulus*; Figs 41–42), and long slender vagina (short, wide in *D. longulus*; Figs 49–50).

Larvae. *Drilus horasfakionus* sp. nov. is the only Cretan *Drilus* species without a thick short hair in the middle part of outer margins of cerci (Fig. 44).

Description. Male. Body medium-sized, slender, elongate, almost parallel-sided, 3.8 times as long as wide at humeri, moderately convex dorsally (Fig. 4). Head, elytra and abdomen dark brown to black, frontoclypeal depression brown, antennae and metaventrite brown to dark brown; mouthparts, gula, prothorax, scutellum, legs, last visible ventrite golden brown, mesoventrite and mesepisternum darker. Entire body covered by golden pubescence. Head including eyes as wide as anterior margin of pronotum, sparsely punctured, with wide and shallow frontal depression; anterior clypeal edge concave, dorsally with sparse, semi-erect pubescence (Figs 8, 12). Eyes with their frontal distance 1.8 times eye diameter. Mandibles robust, incisor margin with small tooth in middle part (Fig. 16). Antennae serrate, reaching one third of elytral length, scapus robust, pear-shaped, pedicel shorter, minute, antennomere 3 long, widened apically, antennomeres 4–10 serrate, subequal in length, apical antennomere longest, simple, slightly rounded apically (Fig. 20). Pronotum slightly convex, widest in one third, in posterior angles 1.6 times wider than length at midline. Anterior margin almost straight; lateral margins convex, widened in one third, posterior margin 1.1 times wider than anterior margin, widely and smoothly sinuate in middle part. Anterior angles almost rectangular, posterior angles obtuse, rounded (Fig. 8), lateral margins and posterior angles distinctly turned upward, surface of disc punctured, with sparse, erected, long setae. Prosternum transverse, with frontal margin slightly concave, prosternal process short, widely rounded (Fig. 28). Scutellum flat, subtriangular, widely rounded posteriorly. Mesoventrite narrow, sharply V-shaped, with short median depression in frontal margin (Fig. 24). Elytral outer margins almost parallel-sided, inner margins distinctly dehiscent in apical third; elytra as wide as posterior margin of pronotum, 2.8 times longer than width at humeri, irregularly wrinkled, covered by sparse pubescence, with very slight longitudinal keel running from humeri to interior margin of elytral apex, inconspicuous in apical third of elytra, each elytron rounded independently, tapered apically (Fig. 4). Abdomen covered with long pubescence, sparse in middle part, denser around margins; penultimate ventrite with smooth, shallow emargination in posterior margin. Phallus strong, distinctly longer than parameres, considerably curved, almost parallel-sided, parameres short, robust, apically with sparse setae, phallobase robust, longer than parameres (Fig. 32).

Female. Larviform, body elongate. All body parts yellowish to brown, thoracic and abdominal tergites laterally dark brown (in specimen from Gavdos almost whole surface of tergites dark brown, Fig. 35), pronotum paler. Head small, including eyes slightly narrower than pronotal anterior margin, with shallow depression between antennal sockets; clypeus short, widely concave anteriorly. Eyes small, their frontal distance 2.4–3.1 times eye diameter. Antennae short, with 10–11 antennomeres, ultimate antennomere either well developed or probably fused with the penultimate one, bearing small conical appendage (see the remarks below; Figs 47–48). Mandibles robust, shiny, considerably curved, incisor margin with small tooth in middle part (Fig. 41). Legs short, robust. Abdomen widest in posterior third, apical segment much narrower and smaller. Ovipositor with fused valvifers and coxites; vagina long, slender (Fig. 49).

Larva. Body elongate, slightly widened towards apex. All body parts yellow to orange brown, markings on the dorsal surface of abdominal segments brown, on thoracic segments usually lighter (Fig. 38). Head with dark band around stemmata, expanding towards the rear (Fig. 38). Cerci slightly bent upward and inward, apically cuspidate, covered with thin long pubescence, apex short (Fig. 44).

Variability. Males. Antennae mostly brown to dark brown, but one of the paratypes has scapuses lighter and the other paratype has the first antennomere uniformly brown and the second one gradually lighter towards apex. Femora mostly golden brown, sometimes darker. Entire penultimate abdominal ventrite mostly dark brown, only in some cases its apical part ventrite golden to golden brown. Frontal depression of head variable in size and depth; posterior angles slightly to distinctly turned upward.

Remarks. The females of the *Drilus* species have 10 or 11 antennomeres (Bocak et al., 2010; Faucheux & Agnas, 2011). We were not able to study the antennal morphology among the Cretan species since antennae have been missing in most of the studied specimens including all females of *D. baenai* sp. nov. and *D. longulus*. In *D.*

horasfakionus sp. nov. females, only four individuals have well-preserved antennae. The three females bear antennae with 11 fully developed antennomeres (Fig. 48). These females have a small conical appendage located in the last antennomere (Figs 47–48). One female has only 10 visible antennomeres, however the last one is apparently prolonged and it may actually consist of fused 10th and 11th antennomeres (with the small conical appendage also present; Fig. 47). Faucheux and Agnas (2011) observed the similar antennal morphology for the *D. mauritanicus* female. The non-uniform peculiar morphology of the female antennae may be affected by the neotenic development connected with the persistence of the larval characters in Drilini (Cros, 1930). More detailed study is needed for better understanding of the morphology and possible functions of the apical parts of ultimate antennomeres and small conical appendages (Faucheux & Agnas, 2011).

Measurements. Holotype: BL 4.5 mm, EL 3.3 mm, WHe 1.1 mm, WHum 1.2 mm, PL 0.7 mm, PWA 1.1 mm, PWP 1.2 mm, Edist 0.6 mm, Ediam 0.4 mm. Variability in males: BL 3.4–5.8 mm, EL 2.5–4.2 mm, WHe 0.9–1.3 mm, WHum 1.0–1.4 mm, PL 0.6–0.9 mm, PWA 0.8–1.1 mm, PWP 1.0–1.3 mm, Edist 0.5–0.8 mm, Ediam 0.3–0.4 mm. Females: BL 5.5–10.5 mm, BW 1.2–2.2 mm, WHe 0.6–1.0 mm, PL 0.6–0.9 mm, PWA 0.7–1.1 mm, PWP 0.9–1.5 mm, Edist 0.5–0.7 mm, Ediam 0.2–0.3 mm. Larvae: BL 9.1 mm, BW 2.6 mm.

Distribution. *Drilus horasfakionus* sp. nov. is distributed mainly in the western and central parts of Crete (Chania and Rethymno regional units) including the Gavdos and Gavdopoula islets, but one specimen was found also near Heraklion (Fig. 52).

Biology and ecology. *Drilus horasfakionus* sp. nov. was found in shells of *Albinaria sublamellosa, A. sphakiota sphakiota* and *Albinaria tenuicostata*.

Etymology. This species is named after Hora Sfakion, where part of the type series was collected.

Drilus longulus Kiesenwetter, 1859
(Figs 5, 9, 13, 17, 21, 25, 29, 33, 36, 39, 42, 45, 50)

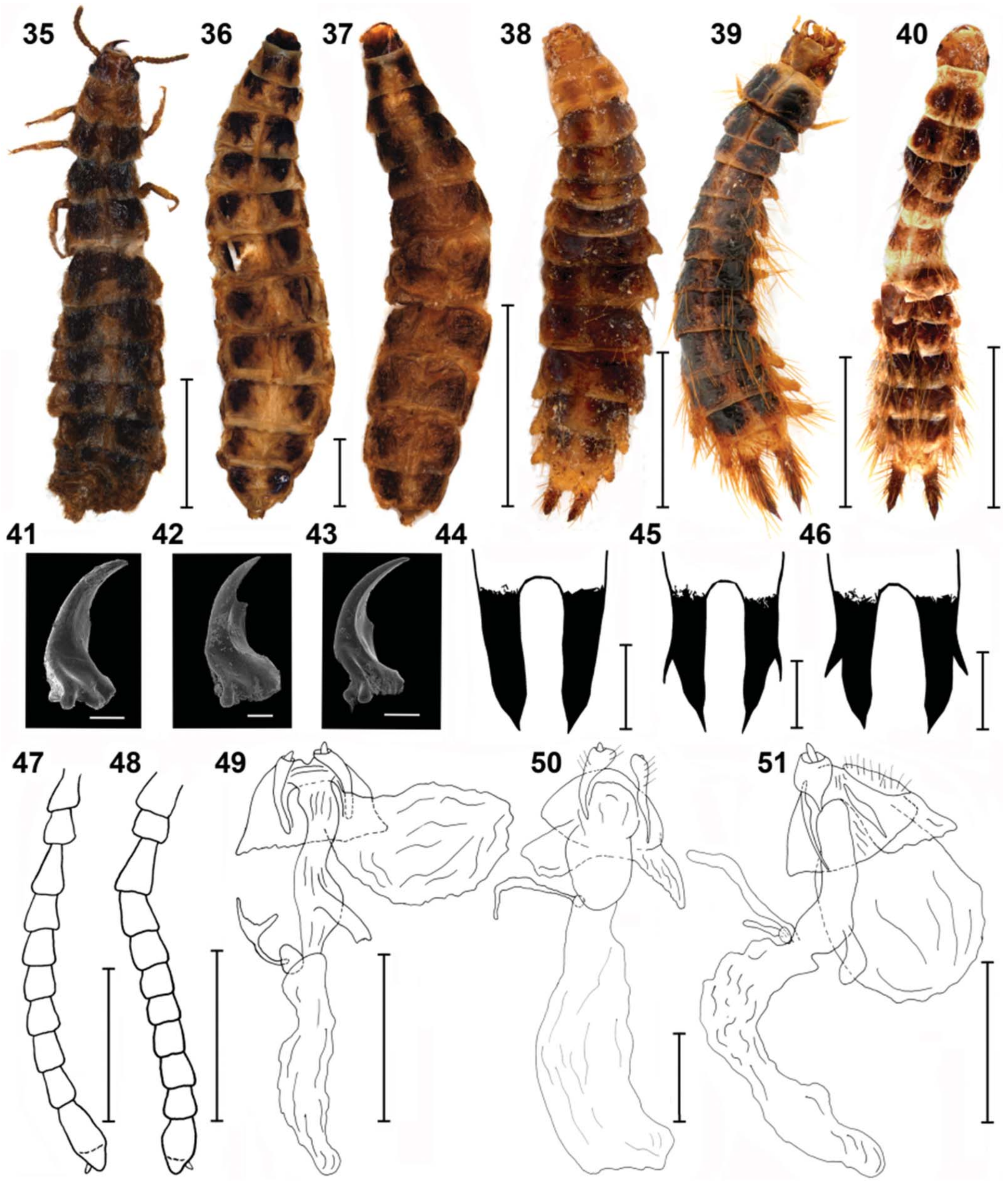
Drilus longulus Kiesenwetter, 1859: 159.

Type locality. Crete (Kiesenwetter, 1859).

Material examined. 1 male, 'Kreta mer., Matala, 28.-30.3.1980, Vl. Lapáček lgt.' (LBPC), 1 male, 'Creta, Biró, Herakleion, 1906. IV.' (HNHM), 1 male, 'Assitaes, Creta or., Holtz, 5.03, *Drilus funebris* var Reitt.' (NHMW), 1 male, 'Candia, Mitte Mai, Kreta, Rebel' (NHMW), 1 male, ' Hellas, Kriti, Chania, Epanochori, 17. V. 2013, Vitali & Trandafir' (RKPC), 1 male, 'Grekl., Kreta, Malia 1 km, S om. I fruktodling, loc. 3, 10.V.1979, leg. R. Danielsson, NMB, coll. Wittmer' (NHMB), 1 male, 'Kreta, 7.4.71, Iraklion, leg. Wewalka, NMB, coll. Wittmer' (NHMB), 1 male, 'Chania, 21.4.71, Kreta 1971, W. Wittmer, NMB, coll. Wittmer' (NHMB), 1 male, 'Rethimnon, 17.4., Kreta 1971, W. Wittmer, NMB, coll. Wittmer' (NHMB), 1 male, 'Ierapetra, Kreta 1971, W. Wittmer, 10.4., NMB, coll. Wittmer' (NHMB), 1 male, 'Cerigotto, Collectie C. & O. Vogt, Acq. 1960' (ZMAN), 1 female (RMNH.INS.559192), 'Greece, Crete, prov. Iraklion, SE-side of Pirgos rocky site, 300 m alt., UTM LU3175, 2.10.1991, E. Gittenberger leg.' (RMNH), 1 larva (RMNH.INS.559191), 'Greece, Central Crete, 35°13.736′N 24°56.367′E, 2011, M. Schilthuizen and Y. Lammers leg.' (RMNH), 1 larva (RMNH.INS.559205), 'Greece, Crete, Mountains west of Kroussonas, 1160 m alt., 35.235731′N 24.951646′E, 5–2013, M. Schilthuizen leg.' (RMNH), 1 larva (RMNH.INS.559206), 'Greece, Crete, Mountains west of Kroussonas, 1029 m alt., 35.238054′N 24.942653′E, 5–2013, M. Schilthuizen leg.' (RMNH), 1 larva (RMNH.INS.559207), 'Greece, Crete, Gorge north of Spili, 380 m alt., 35.2573′N 24.5714′E, 5–2013, M. Schilthuizen leg.' (RMNH), 1 larva (RMNH. INS.903260), 'Greece, Crete, Mountains west of Kroussonas, 1196 m alt., 35.234863′N 24.951100′E, 5–2013, M. Schilthuizen leg.' (RMNH), 1 larva (RMNH. INS.871922), 'Crete; north slopes of Psilorithis plateau 1.1 km from Drosia along the road in the direction of Rethimnon, 350 m alt., M. Schilthuizen leg.' (RMNH), 1 larva (RMNH.INS.871923), 'Crete; north slopes of Psilorithis plateau: 10.4 km from Arkhadi Monastery along the road in the direction of Mt. Psilorithis, 860 m alt., M. Schilthuizen leg.' (RMNH).

Diagnosis. Males. *Drilus longulus* shares with *D. funebris* from Attika (mainland Greece) the prolonged clypeus but can be easily recognized by darker body colouration, longer antennae and shape of male genitalia (Fig. 33). *Drilus longulus* is very similar in colouration to *D. baenai* sp. nov. (Figs 5–6). However, *D. longulus* has a distinctly prolonged clypeus, anteriorly notched with sharp median emargination in middle part (Figs 9, 13), head wrinkled, with larger and denser punctures, smaller eyes (Figs 9, 13), thin antennae (Fig. 21), and mesoventrite not so sharply V-shaped, without deep median depression (Fig. 25).

Females. *Drilus longulus* differs from *D. baenai* sp. nov. by fused valvifers and coxites (Figs 50–51) and from *D. horasfakionus* sp. nov. by robust tooth in mandibular incisor margin (Figs 41–42) and much shorter and wider vagina (Figs 49–50).



Figs. 35–51. General appearance of the Cretan *Drilus* spp. (females): (35) *D. horasfakionus* sp. nov., (36) *D. longulus*, (37) *D. baenai* sp. nov.; larvae: (38) *D. horasfakionus* sp. nov., (39) *D. longulus*, (40) *D. baenai* sp. nov.; female mandibles: (41) *D. horasfakionus* sp. nov., (42) *D. longulus*, (43) *D. baenai* sp. nov.; larval cerci: (44) *D. horasfakionus* sp. nov., (45) *D. longulus*, (46) *D. baenai* sp. nov.; antennae of different *D. horasfakionus* sp. nov. female specimens (47–48); female genitalia: (49) *D. horasfakionus* sp. nov., (50) *D. longulus*, (51) *D. baenai* sp. nov. Scale bars: 2 mm (35–40), 1 mm (49–51), 0.5 mm (44–48), 0.1 mm (41–43).

Larvae. *Drilus longulus* is distinguishable from its Cretan congeners by cerci with one moderately thick short hair in middle part of outer margin (no in *D. horasfakionus*, much thicker in *D. baenai* sp. nov.) and with long acuminate apex (short in other species; Figs 44–46).

Redescription. Male. Body medium-sized, elongate, almost parallel-sided, 3.5–3.8 times as long as wide at humeri, moderately convex dorsally (Fig. 5). All body parts dark brown to black, legs and antennomeres 1–2 (in some cases only tarsi and whole antennae) slightly lighter. Entire body covered by golden pubescence. Head including eyes 1.0–1.1 times wider than anterior margin of pronotum, irregularly wrinkled, coarsely, moderately deeply punctured, with very shallow and wide frontal depression, clypeus prolonged, forming nasal part; anterior clypeal edge almost straight to slightly concave, notched, with sharp emargination in the middle part (Figs 9, 13). Cranium covered dorsally by sparse, semi-erect pubescence; antennal sockets conspicuous, partly covered by lateral margins of cranial nasal part (Fig. 13). Eyes with their frontal distance 2.4–2.6 times eye diameter. Mandibles robust, shiny, considerably curved, incisor margin with conspicuous tooth in middle part, apex slightly rounded (Fig. 17). Antennae serrate, scapus robust, pear-shaped, pedicel shorter, minute, antennomere 3 only slightly serrate, antennomeres 4–10 moderately serrate, subequal in length; apical antennomere longest, simple (Fig. 21). Pronotum slightly convex, widest in one third, in posterior angles 1.2–1.4 times wider than length at midline. Anterior margin almost straight; lateral margins convex, slightly turned upward, widened in one third; posterior margin 1.0–1.1 times wider than anterior margin, moderately convex, slightly sinuate in middle part. Anterior angles almost rectangular, posterior angles obtuse, rounded (Fig. 9); posterior angles slightly turned upward; surface of disc wrinkled, moderately punctured, with sparse, semi-erect, long setae. Prosternum transverse, with frontal margin straight, prosternal process short, widely rounded (Fig. 29). Scutellum flat, U-shaped, almost as long as wide. Mesoventrite narrow, V-shaped, with short, broad median depression in frontal margin (Fig. 25). Elytral outer margins almost parallel-sided, inner margins dehiscent in apical third; elytra 1.2–1.4 times wider than posterior margin of pronotum, 2.5–2.8 times longer than width at humeri, irregularly wrinkled, covered by sparse pubescence, with very slight longitudinal keel running from humeri to interior margin of elytral apex, inconspicuous in apical third of elytra; each elytron rounded independently, tapered apically (Fig. 5). Abdomen with long pubescence sparse in middle part, denser around margins. Phallus longer than parameres, considerably curved, almost parallel-sided; parameres apically with sparse setae; phallobase robust, longer than parameres (Fig. 33).

Female. Larviform, body elongate, All body parts yellowish to brown, thoracic and abdominal tergites laterally dark brown (Fig. 36). Head small, slightly narrower than pronotal anterior margin, with shallow depression between antennal sockets; clypeus slightly prolonged; eyes small, their frontal distance 2.8 times eye diameter. Antennae missing in studied material. Mandibles robust, shiny, considerably curved, incisor margin with conspicuous tooth in middle part (Fig. 42). Legs short, robust. Abdomen widest in posterior third, apical segment much narrower and smaller. Ovipositor with fused valvifers and coxites; vagina sac-like, short, wide (Fig. 50).

Larva. Body elongate, slightly widened towards apex. All body parts dark yellow to orange brown, markings on the dorsal surface of thoracic and abdominal segments dark brown (Fig. 39). Head with large dark band around stemmata, expanding towards the rear. Cerci bent slightly upward and more inward, covered with thin long pubescence, with a moderately thick short hair in middle part of outer margins (usually less than two times thicker than width of thin hairs), cerci apically cuspidate to acuminate; apex long (Fig. 45).

Variability. Males. There are only slight differences in the coloration (see the description above), shape of lateral pronotal margins, clypeal margin, and the density of punctures on head and pronotum among the specimens from different collecting sites.

Measurements. Males: BL 5.8–7.7 mm, EL 4.4–5.7 mm, WHe 1.2–1.6 mm, WHum 1.6–2.1 mm, PL 1.0–1.2 mm, PWA 1.1–1.6 mm, PWP 1.2–1.7 mm, Edist 0.9–1.1 mm, Ediam 0.4 mm. Female: BL 15.0 mm, BW 3.6 mm, WHe 1.1 mm, PL 1.2, PWA 1.3 mm, PWP 1.7 mm, Edist 0.8 mm, Ediam 0.3 mm. Larvae: BL 11.0 mm, BW 3.0 mm.

Distribution. *Drilus longulus* is distributed throughout Crete and in the island of Antikythera (Fig. 52).

Biology and ecology. *Drilus longulus* was found in shells of *Albinaria corrugata corrugata, A. hippolyti aphrodite*, *A. h. holtzi, A. idaea* and *A. spratti*.

Identification key for the males of the Cretan *Drilus* species.

1. Prothorax golden to golden brown, much paler than elytra **2**

- Prothorax and elytra concolor dark brown to black **3**

2. Body robust, head pale (Figs 3, 7, 11); antennae strongly serrate (Fig. 19), mandibular incisor margin with conspicuous tooth close to apical part (Fig. 15), pronotal hind angles prominent, acute (Fig. 7), scutellum posteriorly narrowly rounded (Fig. 3), mesoventrite wide, widely V-shaped (Fig. 23); parameres long (Fig. 31)..............***Drilus creticus*** Pic

- Body slender, elongate, head dark (Figs 4, 8, 12); antennae moderately serrate (Fig. 20), mandibular incisor margin with small tooth in middle part (Fig. 16), pronotal hind angles almost rectangular (Fig. 4B), scutellum posteriorly widely rounded (Fig. 4), mesoventrite narrow, sharply V-shaped (Fig. 24); parameres short (Fig. 32)..................***Drilus horasfakionus*** sp. nov.

3. Head wrinkled, with large, dense punctures; clypeus elongated; clypeal frontal margin either straight or slightly concave, notched, sharply emarginated in middle part (Fig. 13); Edist/Ediam ratio 2.4−2.6 (Figs 9, 13).................***Drilus longulus*** Kiesenwetter

- Head rather smooth, with fine, sparse punctures; clypeus short; clypeal frontal margin smooth, widely emarginated (Fig. 14); Edist/Ediam ratio 1.6−1.8 (Figs 10, 14) . . . . ***Drilus baenai*** sp. nov.

Discussion

The morphological diversity of *Drilus* species in Crete

In this study, we examined the *Drilus* species diversity in the island of Crete. Although only two species, *D. longulus* and *D. creticus*, were described from the island, some authors mentioned that *D. funebris* also occurred in Crete (Bocak, 2007; Wittmer, 1944). However, we could not confirm the occurrence of this species in Crete despite studying the Mediterranean *Drilus* diversity in major European museums. The type locality of *D. funebris* is Attica in central Greece and this species differs from *D. longulus* by the coloration, shape of antennae, pronotum and male genitalia (Brenske & Reitter, 1884; R. Kundrata, pers obs). However, these species share the apparently prolonged clypeal part of the head and this character may have led some entomologists to confuse both species.

Because of the general lack of information on larval stages and females, previous species descriptions of *D. longulus* and *D. creticus* were exclusively based on adult males (Kiesenwetter, 1859; Pic, 1905). During our studies on Cretan *Drilus*, we found material belonging to four morphologically clearly recognizable species in major European collections (Fig. 3). These species are endemic to Crete and surrounding islets (see Taxonomy part for the species distribution information), which is in concordance with a high degree of Cretan endemism in many flightless animal taxa (e.g. Giokas & Sfenthourakis, 2008; Legakis & Kypriotakis, 1994; Sfenthourakis & Legakis,

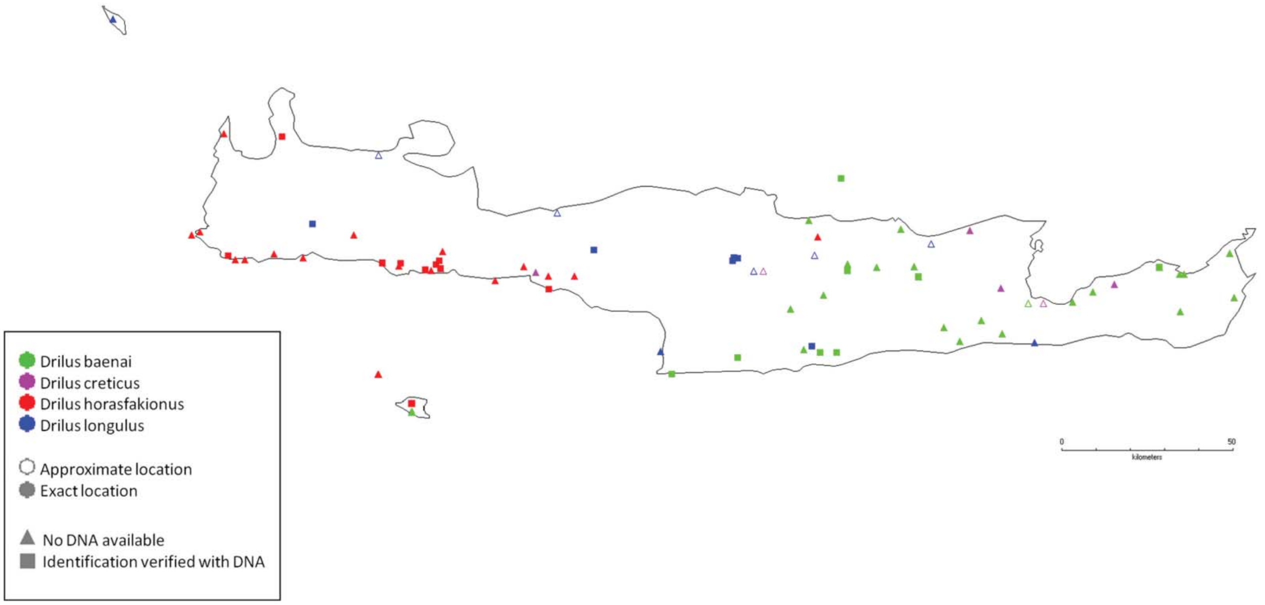


Fig. 52. The distribution of *Drilus* spp. in Crete and adjacent islets.

2001). Neither of the Cretan species was represented in the museums by more than a few specimens and only the recent effort of malacologists yielded larger series of these beetles (Baalbergen et al. 2014; Schilthuizen et al., 1994; this study). *Drilus creticus* is the most distinct species with its robust body, strongly serrate antennae and parameres almost as long as the phallus (Figs 3, 19, 31). *Drilus longulus* is the only Cretan *Drilus* species with a prolonged clypeus (Figs 9, 13).

For sequencing purposes, we mostly had at our disposal the material collected by malacologists as a by-product of snail shell collecting. We failed to find males corresponding to *D. creticus* among our material, although we cannot exclude the possibility that some subclades of *D. baenai* sp. nov. (EB2013–304), *D. horasfakionus* sp. nov. (EB2013–299, EB2013–300) or *D. longulus* (RMNH. INS.599192, RMNH.INS.599206), which contain only larvae and/or females, might be in fact *D. creticus*. However, taking into consideration the male morphology of *D. creticus*, which is distinct from other Cretan species, we consider it improbable. One of the possible explanations why *D. creticus* was not present in our material is that the malacologists who collected *Drilus* beetles focused on *Albinaria* snails, and *D. baenai* sp. nov., *D. horasfakionus* sp. nov. and *D. longulus* are important predators of these snails, whereas *D. creticus* might feed on other snail taxa, like *Drilus* sp. E from the Peloponnese, which feeds on *Rumina* and other large-bodied snails (Baalbergen, 2013; Baalbergen et al., 2014).

The genetic diversity of *Drilus* species in Crete

We used the *cox1* mtDNA fragments, widely used in DNA-based taxonomy, for matching the larvae, neotenic females and males (e.g. Ahrens, Monaghan, & Vogler, 2007; Levkanicova & Bocak, 2009; Sipek & Ahrens, 2011). The GMYC analysis identified six species in Crete (i.e. seven species in total, since the DNA sequences were not available for *D. creticus*; Table S4, see supplemental material online). Unfortunately, males were available only for three of them; the remaining terminals represent only larvae or larvae and females (Fig. 1). The males of the three species were identified as *D. baenai* sp. nov., *D. horasfakionus* sp. nov. and *D. longulus*. The GMYC analysis and intraspecific genetic distances suggested that there are at least two independent lineages within each of the above-mentioned taxa (Fig. 1; Tables S4 and S5, see supplementary material online). However, for several reasons we have decided not to consider these lineages as separate species. We have only a single larva as a subclade of *D. baenai* sp. nov. In the *D. longulus* clade, there are two branches – the first containing male and larva, and the second containing female and larvae. As the larval morphology is quite conservative and not always reliable for species identification, we are unable to separate particular entities morphologically. In *D. horasfakionus* sp. nov., females are present in both subclades. However, the female external morphology is strongly affected by neoteny (Bocak et al., 2010) and is similar in all known Cretan species (Figs 35–37). The female genitalia in Agrypninae mainly bear supraspecific characteristics (e.g. Prosvirov & Savitsky, 2011) and although there are some differences in female genitalia among the studied Cretan species, we did not find any well-defined characters for the separation of the females from two *D. horasfakionus* sp. nov. subclades. Moreover, we only have a very limited number of specimens for the detailed study of the morphological variability of the genitalia. Therefore, we treat the respective subclades within each species (i.e. *D. baenai* sp. nov., *D. horasfakionus* sp. nov. and *D. longulus*) as conspecific despite their genetic distances and long time of separation (Figs 1–2; Tables S3 and S5, see supplementary material online). This decision is further supported by the realization that it would be inappropriate to establish new taxa based only on larvae and/or females as these would be vaguely defined and impossible to identify by morphological characters.

Similar to previous studies (e.g. Fujisawa & Barraclough, 2013), we assume that the GMYC model overestimates the number of species entities in these slowly dispersing *Drilus* and that the subclades of the three species are only genetically differentiated geographic populations. Indeed, all branches follow a strict geographic pattern and specimens from the individual subclades were collected at distant sites; the lack of sequences from the intervening populations may heavily affect the GMYC outcome (Hamilton, Hendrixson, Brewer, & Bond, 2014). Ikeda, Nishikawa, and Sota (2012) showed that flightless beetle species have, as expected, a greater degree of geographic subdivision and deeper genetic branching in comparison to species where all or at least some populations are able to fly (for review, see Vogler & Timmermans, 2012). This might be the case for the neotenic *Drilus* species with limited vagility due to the flightless larviform females. Therefore, we should treat the results of the GMYC model carefully, and take into account not only the genetic distance but also the morphology, biology and ecology of the investigated taxa as well as their phylogeographic history (see e.g. Brower, 2006; Fujisawa & Barraclough, 2013). On the other hand, the great genetic distances between the British/Dutch and Maltese lineages of *D. flavescens* or between the *D. longulus* subclades may indicate the presence of yet undescribed species. Malohlava and Bocak (2010) studied the diversity of other neotenic elateroids (Lycidae, genus *Scarelus*) and showed great genetic differentiation of neotenics within relatively small areas in South-East Asia.

The phylogeny of the Mediterranean *Drilus* species

In this paper, we use mtDNA data to investigate the phylogeny of *Drilus* species in the Mediterranean. Our analyses reveal a non-monophyletic origin of *Drilus* species from the Ionian islands, the Peloponnese and Crete. *Drilus* sp. E from the Peloponnese and Zakynthos was found as a sister species to *Drilus mauritanicus* from Spain in very distant relationship to the clade formed by the remaining Greek species (Fig. 1, Table 2). The position of *Drilus* sp. E close to *D. mauritanicus* is also supported by their biology as both these species mainly prey on *Rumina* spp. (Baalbergen 2013; Cros, 1926). The species of the Greek clade, on the other hand, mainly or exclusively prey on *Albinaria* snails (see the Taxonomy section). *Drilus flavescens* was found sister to the Greek clade in most analyses, although with poor support in some occassions. However, our dataset does not cover the whole diversity of the Mediterranean *Drilus* and it is possible that addition of further species would affect the *Drilus* tree topology.

Our dataset confirmed that neither the species from the Peloponnese + Ionian islands nor from Crete are of monophyletic origin (Fig. 1, Table 2). We did not study in detail the morphology of *Drilus* species from the Peloponnese and Ionian islands and therefore the species from those regions are here designated as tentative, using a single-letter code (see Baalbergen, 2013 for more information). However, these species form two lineages within the Greek clade – the first consists of species from the Peloponnese and Ionian islands and the second is species L from the eastern Peloponnese. The latter was consistently found (although with low support) as sister taxon to the *D. longulus* + *D. horasfakionus* clade from Crete. The relationship between *D. longulus* and *D. horasfakionus* from Crete is supported by the morphology of female genitalia as both species share fused valvifers and coxites (Figs 49–50). On the other hand, the evolution of male morphological characters is more complicated. The males of *D. longulus* share the prolonged clypeus with some of the Peloponnese *Drilus* species. According to the here presented molecular phylogeny, this character must have originated several times independently in the *Drilus* evolution (Fig. 1). Furthermore, *D. longulus* has been until now confused with another black Cretan species, *D. baenai* sp. nov. These species, however, do not seem to be closely related (Fig. 1) and also greatly differ in some morphological aspects (see Taxonomy part for more details).

Phylogeography, estimation of divergence times, and substitution rates in the Greek *Drilus* clade

The Aegean region was part of a united landmass during the Upper and Middle Miocene (23–12 million years ago). At the end of the Middle Miocene (Serravallian/Tortonian; 12 Mya), the formation of the Mid-Aegean trench (east of Crete and west of Kasos-Karpathos islands) began and was fully completed *c.* 9 Mya (Creutzburg, 1963). During the same period (Tortonian), the submergence of Crete started slowly from east to west and the land connection to the central Aegean island-landmass and the Peloponnese began to lower (Meulenkamp, 1985). The separation of the eastern Cretan *Drilus baenai* sp. nov. in the initial period of isolation is therefore in agreement with the geological events in the area (Fig. 2). Some 9 Mya, Crete was fully isolated from the Peloponnese and partly submerged. Several palaeo-islands were present, which correspond roughly with the highest Cretan mountains (e.g. Meulenkamp, 1985; Schilthuizen et al., 2004; Welter-Schultes & Williams, 1999), and eastern Crete was probably well separated from the western and central parts (e.g. Fig. 2 in Lymberakis & Poulakakis, 2010). The location of the palaeo-islands corresponds with distributions of many Cretan taxa (e.g. Legakis & Kypriotakis, 1994; Parmakelis et al., 2005; Schilthuizen et al., 2004; Velonà, Ghesini, Luchetti, Marini, & Mantovani, 2010). The central-western Cretan *Drilus* species separated from their Peloponnese congeners (the calibration point used herein) approximately 9 Mya and *D. longulus* and *D. horasfakionus* sp. nov. were isolated from each other soon after that (Fig. 2, Table S3, see supplemental material online). According to the known distributional data, these species occur sympatrically in western Crete (Fig. 52).

The palaeo-islands of Crete probably maintained stable habitats for *Drilus* species during a number of palaeogeographic events (Parmakelis et al., 2005; Welter-Schultes & Williams, 1999). During the Messinian Salinity Crisis (5.96–5.33 Mya), the closing of the Strait of Gibraltar resulted in the drying out of the entire Mediterranean basin (Krijgsman et al., 1999). The islands became mountains in the dry steppe so that the migration between islands and mainland was possible for some animal taxa as documented by e.g. Akın et al. (2010), Lymberakis and Poulakakis (2010), and Poulakakis et al. (2005). However, Crete was isolated from the surrounding areas by deep canyons (Schüle, 1993) and therefore, migration in the dried basin with unfavourable climatic conditions was difficult or impossible for some taxonomic groups (e.g. Solà et al., 2013). Schilthuizen et al. (2004) suggested that the saline conditions may have prevented dispersal of land snails between the palaeo-islands. Those conditions probably also affected *Drilus* as the major land snail predator in Crete (Schilthuizen et al., 1994, 2004; Welter-Schultes, 2000) so that the previously isolated species remained in their original distributional areas. In addition, the Messinian Salinity Crisis probably influenced the *Drilus* speciation in the Peloponnese/Ionian islands area (Fig. 2). The island of Crete became permanently isolated again after the re-flooding of the Mediterranean basin at the end of the MSC (Bache et al., 2012). Crete was partially submerged and subdivided into smaller islands (e.g. Meulenkamp, 1985). The repeated fragmentation of Crete caused by sea level changes and climatic fluctuations during the Pleistocene together with the low vagility of *Drilus* as well as land snails probably provide the reason for the subsequent branching events within the Cretan *Drilus* species (Fig. 2). This is in agreement with many recent studies which show a Pliocene/Pleistocene species radiation in the Aegean region (e.g. Jesse, Grudinski, Klaus, Streit, & Pfenninger, 2011; Schilthuizen et al., 2004; Simaiakis, Dimopoulou, Mitrakos, Mylonas, & Parmakelis, 2012; Solà et al., 2013; Velonà et al., 2010). To sum up, we suggest that the key events in the west Aegean *Drilus* phylogeography are the Tortonian Crete-Peloponnese separation (12−9 Mya), the desiccation of the Mediterranean basin during the MSC (5.96−5.33 Mya), and the climatic oscillations during the Plio-Pleistocene.

Recently, several studies investigated the molecular substitution rates within insect lineages including Coleoptera (e.g. Allegrucci, Trucchi, & Sbordoni, 2011; Papadopoulou, Anastasiou, & Vogler, 2010; Pons, Ribera, Bertranpetit, & Balke, 2010; Pons & Vogler, 2005). Using 10.5 ± 1.5 Mya as a calibration point, we obtained a mean rate of 0.014 nucleotide substitutions per site per million years per lineage (= 2.75% of pairwise sequence divergence). The rate estimates for *cox1* obtained in the present paper are in excellent agreement with previous studies (2.3−4.0%; Brower, 1994; Papadopoulou et al., 2010 and the references therein). Therefore, we consider that the 10.5 ± 1.5 Mya calibration point scenario and our subsequent biogeographic conclusions are quite plausible.

Prospects for further research on Drilini in the Aegean region, including Crete

We are aware of the fact that our study has limited data and is of a preliminary character. Although this is the most robust phylogenetic hypothesis of the genus *Drilus* so far, we have mtDNA sequences available for only a limited number of species, and we also lack denser sampling at the intraspecific level. Furthermore, incomplete data are available for immature stages and females for the vast majority of Mediterranean species. We need to find the complete series of semaphoronts of different species to examine their morphological diversity. The lack of information on *Drilus* taxonomy, biology and ecology precludes evolutionarily oriented studies. More detailed data on the predator−prey relationship between *Drilus* and the land snails are also needed (e.g. prey specificity, attack strategies and their successfulness; see Baalbergen et al., 2014). Although this study doubled the number of described species from Crete and provides us with a comprehensive overview of the *Drilus* problematics in the Aegean region, there are still some questions to be solved (e.g. the position of *Drilus creticus*). The much finer sampling and using the additional markers are crucial for the elucidation of the Aegean *Drilus* phylogeny, the detailed biogeographic structure of the populations, and the internal relationships of the individual *Drilus* lineages. Such results with the known palaeogeographic history of Crete may help to reveal in detail the influence of the palaeoislands and climatic oscillations on the distributional patterns of *Drilus* in Crete.

Acknowledgements

We would like to thank E. Gittenberger, E. J. Van Nieukerken, F. Welter-Schultes, F. Vitali (Luxembourg) and F. Fanti (Italy) for the material used for the DNA extraction. We are very obliged to the curators, institutions and colleagues who provided us with the material in their care.

Funding

This study was supported by grants from the Uyttenboogaart-Eliasen Foundation and the Jan Joost ter Pelkwijk Fund (EB, MS), the Naturalis Focus Group Character Evolution (RK, MS), GAČR P506/11/1757 (LB), the internal grant of Faculty of Science, UP Olomouc (LB, RK) and the EU-Synthesys BE-TAF-2193 and AT-TAF-3921 projects (RK). This support is gratefully acknowledged.

Supplemental data

Supplemental data for this article can be accessed here.

References

Ahrens, D., Monaghan, M. T., & Vogler, A. P. (2007). DNA-based taxonomy for associating adults and larvae in multi-species assemblages of chafers (Coleoptera: Scarabaeidae). *Molecular Phylogenetics and Evolution, 44*, 436−449. doi:10.1016/j.ympev.2007.02.024

Akın, Ç., Bilgin, C. C., Beerli, P., Westaway, R., Ohst, T., Litvinchuk, S. N., . . . Plötner, J. (2010). Phylogeographic patterns of genetic diversity in eastern Mediterranean water frogs were determined by geological processes and climate change in the Late Cenozoic. *Journal of Biogeography, 37*, 2111−2124. doi: 10.1111/j.1365−2699.2010.02368.x

Allegrucci, G., Trucchi, E., & Sbordoni, V. (2011). Tempo and mode of species diversification in *Dolichopoda* cave crickets (Orthoptera, Rhaphidophoridae). *Molecular Phylogenetics and Evolution, 60*, 108−121. doi: 10.1016/j.ympev.2011.04.002

Baalbergen, E. (2013). *Larvae of Drilini (Coleoptera: Elateridae) beetles preying on snails* (Unpublished master's thesis). Leiden: Leiden University.

Baalbergen, E., Helwerda, R., Schelfhorst, R., Castillo Cajas, R. F., van Moorsel, C. H. M., Kundrata, R., . . . Schilthuizen, M. (2014). Predator-prey interactions between shell-boring beetle larvae and rock-dwelling land snails. *Public Library of Science, 9*, e100366. doi:10.1371/journal.pone.0100366

Bache, F., Popescu, S.-M., Rabineau, M., Gorini, C., Suc, J.-P., Clauzon, G., . . . Çakır, Z. (2012). A two-step process for the reflooding of the Mediterranean after the Messinian Salinity Crisis. *Basin Research, 24*, 125−153. doi:10.1111/j.1365−2117.2011.00521.x

Bergsten, J., Bilton, D. T., Fujisawa, T., Elliott, M., Monaghan, M. T., Balke, M., . . . Vogler, A. P. (2012). The effect of geographical scale of sampling on DNA barcoding. *Systematic Biology, 61*, 851−869. doi:10.1093/sysbio/sys037

Bocak, L. (2007). Drilidae. In I. Löbl & A. Smetana (Eds.), *The Palaearctic catalogue of Coleoptera,* (pp. 209−210). Volume 4. Stenstrup: Apollo Books.

Bocak, L., Branham, M. A., & Kundrata, R. (2010). Family Drilidae Blanchard, 1845. In R. A. B. Leschen, R. G. Beutel, & J. F. Lawrence (Vol. Eds.), *Coleoptera, Beetles; Volume 2: morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim),* (pp. 104−110). In N. P. Kristensen & R. G. Beutel (Eds.), *Handbook of zoology, Arthropoda: Insecta,*. Berlin: Walter de Gruyter GmbH & Co. KG.

Bocakova, M., Bocak, L., Hunt, T., Teraväinen, M., & Vogler, A. P. (2007). Molecular phylogenetics of Elateriformia (Coleoptera): evolution of bioluminescence and neoteny. *Cladistics, 23*, 477−496. doi: 10.1111/j.1096-0031.2007.00164.x

Brenske, E., & Reitter, E. (1884). Neuer Beitrag zur Käferfauna Griechenlands. *Deutsche Entomologische Zeitschrift, 28*, 17−100.

Brower, A. V. Z. (1994). Rapid morphological radiation and convergence among races of the butterfly *Heliconius erato* inferred from patterns of mitochondrial DNA evolution. *Proceedings of the National Academy of Sciences USA, 91*, 6491−6495. doi: 10.1073/pnas.91.14.6491

Brower, A. V. Z. (2006). Problems with DNA barcodes for species delimitation: ‘ten species’ of *Astraptes fulgerator* reassessed (Lepidoptera: Hesperiidae). *Systematics and Biodiversity, 4*, 127−132. doi: 10.1017/S147720000500191X

Creutzburg, N. (1963). Paleogeographic evolution of Crete from Miocene till our days. *Cretan Annals, 15/16*, 336−342.

Cros, A. (1926). Moeurs et évolution du *Drilus mauritanicus* Lucas. *Bulletin Société d'Histoire Naturelle de l'Afrique du Nord, 17*, 181−206.

Cros, A. (1930). *Malacogaster passerini* Bassi: Moeurs, évolution. *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord,* 21, 133−160.

Drummond, A. J., Ho, S. Y. W., Phillips, M. J., & Rambaut, A. (2006). Relaxed phylogenetics and dating with confidence. *Public Library of Science Biology, 4*, e88. doi:10.1371/journal.pbio.0040088

Drummond, A. J., & Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by sampling trees. *BioMed Central Evolutionary Biology, 7*, 214. doi:10.1186/1471-2148-7-214

Ezard, T., Fujisawa, T., & Barraclough, T. (2009). splits: SPecies' LImits by Threshold Statistics. R package version 1.0−11/r29. Retrieved from http://R-Forge.R-project.org/projects/splits/, accessed 13 October 2014.

Faucheux, M. J., & Agnas, M. (2011). *Drilus mauritanicus* Lucas, 1849 et *Malacogaster passerinii* Bassi, 1883 présents dans le meme biotope á Oualida (Maroc atlantique), (Coleoptera: Elateroidea: Drilidae). *Bulletin de la Société des sciences naturelles de l'Ouest de la France, 32*, 79−90.

Folmer, O., Black, M., Hoeh, W., Lutz, R., & Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology, 3*, 294−299.

Fontaneto, D., Herniou, E. A., Boschetti, C., Caprioli, M., Melone, G., Ricci, C., & Barraclough, T. G. (2007). Evidence for independently evolving species in bdelloid rotifers. *PloS Biology, 5*, 914−921. doi:10.1371/journal.pbio.0050087

Fujisawa, T., & Barraclough, T. G. (2013). Delimiting species using single-locus data and the Generalized Mixed Yule Coalescent (GMYC) Approach: a revised method and evaluation on simulated datasets. *Systematic Biology, 62*, 707−724. doi: 10.1093/sysbio/syt033

Giokas, S., & Sfenthourakis, S. (2008). An improved method for the identification of areas of endemism using species co-occurrences. *Journal of Biogeography, 35*, 893−902. doi:10.1111/j.1365−2699.2007.01840.x

Hamilton, C. A., Hendrixson, B. E., Brewer, M. S., & Bond, J. E. (2014). An evaluation of sampling effects on multiple DNA barcoding methods leads to an integrative approach for delimiting species: a case study of the North American tarantula genus *Aphonopelma* (Araneae, Mygalomorphae, Theraphosidae). *Molecular Phylogenetics and Evolution, 71*, 79−93. doi: 10.1016/j.ympev.2013.11.007

Hebert, P. D. N., Cywinska, A., Ball, S. L., & deWaard, J. R. (2003). Biological identifications through DNA barcodes. *Proceedings of the Royal Society B−Biological Sciences, 270*, 313−321. doi:10.1098/rspb.2002.2218

Huelsenbeck, J. P., & Ronquist, F. (2001). MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics, 17*, 754−755. doi: 10.1093/bioinformatics/17.8.754

Hunt, T., Bergsten, J., Levkanicova, Z., Papadopoulou, A., St-John, O., Wild, R., . . . Vogler, A. P. (2007). A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. *Science, 318*, 1913−1916. doi: 10.1126/science.1146954

Ikeda, H., Nishikawa, M., & Sota, T. (2012). Loss of flight promotes beetle diversification. *Nature Communications, 3*, 648. doi: 10.1038/ncomms1659

Jesse, R., Grudinski, M., Klaus, S., Streit, B., & Pfenninger, M. (2011). Evolution of freshwater crab diversity in the Aegean region (Crustacea: Brachyura: Potamidae). *Molecular Phylogenetics and Evolution, 59*, 23−33. doi: 10.1016/j.ympev.2010.12.011

Kass, R. E., & Raftery, A. E. (1995). Bayes factors. *Journal of the American Statistical Association, 90*, 773−795. doi: 10.1080/01621459.1995.10476572

Kiesenwetter, E. A. H. (1859). Beitrag zur Käferfauna Griechenlands. Sechstes Stück: Malacodermata, Cleridae, Ptinidae, Anobiidae. *Berliner Entomologische Zeitschrift, 3*, 158−192.

Krijgsman, W., Hilgen, F. J., Raffi, I., Sierro, F. J., & Wilson, D. S. (1999). Chronology, causes and progression of the Messinian salinity crisis. *Nature, 400*, 652−655. doi: 10.1038/23231

Kundrata, R., & Bocak, L. (2007). A revision of *Euanoma* and *Pseudeuanoma* (Coleoptera: Drilidae). *Annales Zoologici, 57*, 427−441.

Kundrata, R., & Bocak, L. (2011). The phylogeny and limits of Elateridae (Insecta, Coleoptera): is there a common tendency of click beetles to soft-bodiedness and neoteny? *Zoologica Scripta, 40*, 364−378. doi: 10.1111/j.1463−6409.2011.00476.x

Kundrata, R., Kobieluszova, L., & Bocak, L. (2014). A review of Drilini (Coleoptera: Elateridae: Agrypninae) of the Northern Levant, with description of a new species from Syria and a key to Levantine species. *Zootaxa, 3755*, 457−469. doi:10.11646/zootaxa.3755.5.5

Kyriazi, P., Kornilios, P., Nagy, Z. T., Poulakakis, N., Kumlutaş, Y., Ilgaz, Ç., . . . Lymberakis, P. (2013). Comparative phylogeography reveals distinct colonization patterns of Cretan snakes. *Journal of Biogeography, 40*, 1143−1155. doi:10.1111/jbi.12057

Legakis, A., & Kypriotakis, Z. (1994). A biogeographical analysis of the Island of Crete, Greece. *Journal of Biogeography, 21*, 441−445. doi: 10.2307/2845761

Levkanicova, Z., & Bocak, L. (2009). Identification of net-winged beetle larvae (Coleoptera: Lycidae) using three mtDNA fragments: a comparison of their utility. *Systematic Entomology, 34*, 210−221. doi: 10.1111/j.1365−3113.2008.00457.x

Lymberakis, P., & Poulakakis, N. (2010). Three continents claiming an archipelago: The evolution of Aegean's herpetofaunal diversity. *Diversity, 2*, 233−255. doi: 10.3390/d2020233

Malohlava, V., & Bocak, L. (2010). Evidence of extreme habitat stability in a Southeast Asian biodiversity hotspot based on the evolutionary analysis of neotenic net-winged beetles. *Molecular Ecology, 19*, 4800−4811. doi: 10.1111/j.1365-294X.2010.04850.x

Meulenkamp, J. E. (1985). Aspects of the Late Cenozoic evolution of the Aegean region. In D. J. Stanley, & F. C. Wezel (Eds.), *Geological evolution of the Mediterranean Basin,* (pp. 307−321). New York: Springer.

Miller, M. A., Pfeiffer, W., & Schwartz, T. (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In *Proceedings of the Gateway Computing Environments Workshop (GCE),* (pp. 1−8). 14 November 2010, New Orleans.

Papadopoulou, A., Anastasiou, I., & Vogler, A. P. (2010). Revisiting the insect mitochondrial molecular clock: the Mid-Aegean Trench Calibration. *Molecular Biology and Evolution, 27*, 1659−1672. doi: 10.1093/molbev/msq051

Parmakelis, A., Pfenninger, M., Spanos, L., Papagiannakis, G., Louis, C., & Mylonas, M. (2005). Inference of a radiation in *Mastus* (Gastropoda, Pulmonata, Enidae) on the Island of Crete. *Evolution, 59*, 991−1005. doi: 10.1554/04−489

Pic, M. (1905). Capture diverses, noms nouveaux et diagnoses (Colóptères). *L`Échange, Revue Linnéenne, 21*, 169−171.

Pons, J., Barraclough, T. G., Gomez-Zurita, J., Cardoso, A., Duran, D. P., Hazell, S., . . . Vogler, A. P. (2006). Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Systematic Biology, 55*, 595−609. doi: 10.1080/10635150600852011

Pons, J., Ribera, I., Bertranpetit, J., & Balke, M. (2010). Nucleotide substitution rates for the full set of mitochondrial protein-coding genes in Coleoptera. *Molecular Phylogenetics and Evolution, 56*, 796−807. doi: 10.1016/j.ympev.2010.02.007

Pons, J., & Vogler, A. P. (2005). Complex pattern of coalescence and fast evolution of a mitochondrial rRNA pseudogene in a recent radiation of tiger beetles. *Molecular Biology and Evolution, 22*, 991−1000. doi: 10.1093/molbev/msi085

Poulakakis, N., Lymberakis, P., Valakos, E., Zouros, E., & Mylonas, M. (2005). Phylogenetic relationships and biogeography of *Podarcis* species from the Balkan Peninsula, by Bayesian and maximum likelihood analyses of mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution, 37*, 845−857. doi:10.1016/j.ympev.2005.06.005

Prosvirov, A. S., & Savitsky, V. Y. (2011). On the significance of genital characters in supraspecific systematics of the elaterid subfamily Agrypninae (Coleoptera, Elateridae). *Entomological Review, 91*, 755−772. doi: 10.1134/S0013873811060091

Rambaut, A. (2009). FigTree 1.3.1. Retrieved from http://tree.bio.ed.ac.uk/software/figtree/, accessed 13 October 2014.

Rambaut, A., & Drummond, A. J. (2007). *Tracer 1.5*. Edinburgh: Institute of Evolutionary Biology, University of Edinburgh. Retrieved from http://beast.bio.ed.ac.uk/Tracer, accessed 13 October 2014.

Ribera, I., Fresneda, J., Bucur, R., Izquierdo, A., Vogler, A. P., Salgado, J. M., & Cieslak, A. (2010). Ancient origin of a Western Mediterranean radiation of subterranean beetles. *BioMed Central Evolutionary Biology, 10*, 29. doi: 10.1186/147121481029

Schilthuizen, M., Gutteling, E., van Moorsel, C. H. M., Welter-Schultes, F. W., Haase, M., & Gittenberger, E. (2004). Phylogeography of the land snail *Albinaria hippolyti* (Pulmonata: Clausiliidae) from Crete, inferred from ITS-1 sequences. *Biological Journal of the Linnean Society, 83*, 317−326. doi: 10.1111/j.1095−8312.2004.00391.x

Schilthuizen, M., Kemperman, T. C. M., & Gittenberger, E. (1994). Parasites and predators in *Albinaria* (Gastropoda Pulmonata: Clausiliidae). *Bios, 2*, 177−186.

Schüle, W. (1993). Mammals, vegetation and the initial human settlement of the Mediterranean islands: a palaeoecological approach. *Journal of Biogeography, 20*, 399−411. doi: 10.2307/2845588

Sfenthourakis, S., & Legakis, A. (2001). Hotspots of endemic terrestrial invertebrates in southern Greece. *Biodiversity and Conservation, 10*, 1387−1417. doi: 10.1023/A:1016672415953

Simaiakis, S. M., Dimopoulou, A., Mitrakos, A., Mylonas, M., & Parmakelis, A. (2012). The evolutionary history of the Mediterranean centipede *Scolopendra cingulata* (Latreille, 1829) (Chilopoda: Scolopendridae) across the Aegean archipelago. *Biological Journal of the Linnean Society, 105*, 507−521. doi: 10.1111/j.1095−8312.2011.01813.x

Simon, C., Frati, F., Beckenbach, A., Crespi, B., Liu, H., & Flook, P. (1994). Evolution, weighting and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America, 87*, 651−701.

Sipek, P., & Ahrens, D. (2011). Inferring larval taxonomy and morphology in *Maladera* species (Coleoptera: Scarabaeidae: Sericini) using DNA taxonomy tools. *Systematic Entomology, 36*, 628−643. doi: 10.1111/j.1365−3113.2011.00582.x

Solà, E., Sluys, R., Gritzalis, K., & Riutort, M. (2013). Fluvial basin history in the northeastern Mediterranean region underlies dispersal and speciation patterns in the genus *Dugesia* (Platyhelminthes, Tricladida, Dugesiidae). *Molecular Phylogenetics and Evolution, 66*, 877−888. doi: 10.1016/j.ympev.2012.11.010

Stamatakis, A. (2006). RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics, 22*, 2688−2690. doi: 10.1093/bioinformatics/btl446

Stamatakis, A., Hoover, P., & Rougemont, J. (2008). A rapid bootstrap algorithm for the RAxML Web Servers. *Systematic Biology, 57*, 758−771. doi: 10.1080/10635150802429642

Suchard, M. A., & Rambaut, A. (2009). Many-core algorithms for statistical phylogenetics. *Bioinformatics, 25*, 1370−1376. doi: 10.1093/bioinformatics/btp244

Swofford, D. L. (2002). *PAUP*: Phylogenetic analysis using parsimony (*and other methods)*, v.4.0b10. Sunderland, MA: Sinauer Associates.

Thompson, J. D., Higgins, D. G., & Gibson, T. J. (1994). CLUSTAL W: improving the sensitivity of progressive multiple sequence alignments through sequence weighting, position specific gap penalties and weight matrix choice. *Nucleic Acids Research, 22*, 4673−4680. doi: 10.1093/nar/22.22.4673

Vogler, A. P., & Timmermans, M. J. T. N. (2012). Speciation: don’t fly and diversify? *Current Biology, 22*, R284−R286. doi: 10.1016/j.cub.2012.03.015

Velonà, A., Ghesini, S., Luchetti, A., Marini, M., & Mantovani, B. (2010). Starting from Crete, a phylogenetic re-analysis of the genus *Reticulitermes* in the Mediterranean area. *Molecular Phylogenetics and Evolution, 56*, 1051−1058. doi: 10.1016/j.ympev.2010.04.037

Williams, F. X. (1951). Life history studies of East African *Achatina* snails. *Bulletin of the Museum of Comparative Zoology, 105*, 295−317.

Welter-Schultes, F. W., & Williams, M. R. (1999). History, island area and habitat availability determine land snail species richness of Aegean islands. *Journal of Biogeography, 26*, 239−249. doi: 10.1046/j.1365−2699.1999.00276.x

Welter-Schultes, F. W. (2000). The pattern of geographical and altitudinal variation in the land snail *Albinaria idaea* from Crete (Gastropoda: Clausiliidae). *Biological Journal of the Linnean Society, 71*, 237−250. doi: 10.1111/j.1095−8312.2000.tb01256.x

Wittmer, W. (1944). Catalogue des Drilidae E. Oliv. (Coleoptera − Malacodermata). *Revista de la Sociedad Entomológica Argentina, 12*, 203−221.

Associate Editor: Eirik Rindal

Table S1. The list of primers used in this study.

Fragment	Code	-mer	Sequence (5’ >> 3’)	Reference
cox1-3′	Pat	25	TCCAATGCACTAATCTGCCATATTA	Simon *et al.*, 1994
cox1-3′	SPat	21	GCACTAWTCTGCCATATTAGA	Simon *et al.*, 1994 (modified)
cox1-3′	Jerry	23	CAACATTTATTTTGATTTTTTGG	Simon *et al.*, 1994
cox1-3′	SJerry	23	CAACATYTATTYTGATTYTTTGG	Simon *et al.*, 1994 (modified)
cox1-3′	Tom	22	ACRTAATGAAARTGGGCTACWA	Ribera *et al.*, 2010
cox1-3′	Chy	22	TWGTAGCCCAYTTTCATTAYGT	Ribera *et al.*, 2010
cox1-5′	LCO1490K	26	TCAACWAAYCATAAAGACATTGGAAC	Folmer *et al.*, 1994 (modified)
cox1-5′	HCO2198K	26	TAAACTTCTGGGTGWCCAAARAATCA	Folmer *et al.*, 1994 (modified)

References for Table S1.

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294-299.

Ribera I, Fresneda J, Bucur R, Izquierdo A, Vogler AP, Salgado JM, Cieslak A. 2010. Ancient origin of a Western Mediterranean radiation of subterranean beetles. *BMC Evolutionary Biology* 10: 29.

Simon C, Frati F, Beckenbach A, Crespi B, Liu H, Flook P. 1994. Evolution, weighting and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America* 87: 651-701.

Table S2. Numbers of characters, base frequencies and maximum uncorrected pairwise distances.* – only *Drilus* sequences included

Dataset/ Nr. of taxa	Number of characters	Constant characters	Parsimony uninformative	Parsimony informative	Base frequencies (%)				Max. uncorrec. pairw. dist. (%)
					A	C	G	T	
cox1-3′ mtDNA	723	418	17	288	32.38	18.81	16.75	32.07	21.87*
cox1-5′ mtDNA	658	403	11	244	28.05	21.98	18.52	31.46	21.27*
Total dataset	1381	821	28	532	30.97	19.83	17.35	31.85	21.90*

Table S3. Estimated ages of selected nodes inferred from the Beast analyses. * the node used for calibration; long[1] = including all *D. longulus* sequences; long[2] = *D. longulus* including only UPOL RK0638 and RMNH.INS.559207; hora[1] = including all *D. horasfakionus* sp. nov. sequences; hora[2] = *D. horasfakionus* sp. nov. excluding EB2013-299 and EB2013-300. S. E. = standard error

	calibration point 10.5±1.5 mya		calibration point 5.3±0.3 mya	
selected node	mean (my)	95% HPD	mean (my)	95% HPD
CRETE/PELOP	11.795	7.510–16.208	6.320	5.055–7.793
hora+long+DGML	10.852	7.131–14.677	5.816	4.828–6.944
hora+long+L*	9.794	6.720–12.833	5.249	4.664–5.844
hora+long	8.614	5.551–11.660	4.620	3.671–5.512
DGM	7.910	4.453–11.465	4.243	2.797–5.643
DM	5.515	2.748–8.485	2.957	1.696–4.270
hora[1]	4.515	2.183–7.162	2.429	1.377–3.660
long[1]	4.336	2.251–6.546	2.332	1.409–3.303
baenai	3.399	1.153–6.276	1.810	0.696–3.213

D	2.089	0.736–3.712	1.124	0.427–1.897
long^2	1.992	0.765–3.351	1.071	0.465–1.722
hora^2	1.955	0.853–3.280	1.045	0.522–1.661
L	1.143	0.400–2.105	0.606	0.240–1.062
mean rate (subs/s/my/l)	0.014	0.008–0.020	0.023	0.016–0.030
	(2.75%)		(4.54%)	
ln P (model/data)	-5280.135 (S.E. +/-0.066)		-5279.809 (S.E. +/-0.069)	

Table S4. Species entities delimitation using the GMYC approach. M=male, F=female, L=larva, P=pseudopupa (an immobile resting larval stage).

GMYC entities	Morphological species, geographical origin, semaphoront	Voucher numbers
1	*Selasia* sp. Africa M	UPOL RK0071
	Selasia sp. Africa M	UPOL RK0072
2	*Drilus* sp. E Zakynthos P	RMNH.INS.559217
	Drilus sp. E Greece M	UPOL RK0073
3	*Drilus mauritanicus* Spain M	UPOL RK0084
	Drilus mauritanicus Spain M	UPOL RK0085
4	*Drilus concolor* Hungary M	UPOL RK0074
	Drilus concolor The Netherlands P	RMNH.INS.559216
	Drilus concolor The Netherlands L	RMNH.INS.871829
	Drilus concolor The Netherlands F	RMNH.INS.559215
5	*Drilus flavescens* Malta M	UPOL 001046
	Drilus flavescens Malta M	UPOL RK0446
6	*Drilus baenai* Crete F	RMNH.INS.871921
	Drilus baenai Crete M	RMNH.INS.559175
	Drilus baenai Crete F	EB2013-307
7	*Drilus* sp. D Greece M	RMNH.INS.559219
	Drilus sp. D Kalamos M	RMNH.INS.559213
8	*Drilus* sp. L Greece L	RMNH.INS.559210
	Drilus sp. L Greece L	UPOL RK0539

	Drilus sp. L Greece P	UPOL RK0540
	Drilus sp. L Greece P	RMNH.INS.559209
	Drilus sp. L Greece L	RMNH.INS.871796
	Drilus sp. L Greece L	RMNH.INS.559211
9	*Drilus longulus* Crete L	RMNH.INS.559207
	Drilus longulus Crete M	UPOL RK0638
10	*Drilus longulus* Crete F	RMNH.INS.559192
	Drilus longulus Crete L	RMNH.INS.559206
11	*Drilus horasfakionus* Crete F	EB2013-299
	Drilus horasfakionus Crete L	EB2013-300
12	*Drilus horasfakionus* Crete F	RMNH.INS.559204
	Drilus horasfakionus Crete M	EB2013-320
	Drilus horasfakionus Crete M	RMNH.INS.559155
	Drilus horasfakionus Crete M	RMNH.INS.559169
	Drilus horasfakionus Crete F	RMNH.INS.559163
	Drilus horasfakionus Crete M	RMNH.INS.559153
	Drilus horasfakionus Crete M	RMNH.INS.559154
	Drilus horasfakionus Crete F	RMNH.INS.871814
	Drilus horasfakionus Crete P	RMNH.INS.871820
	Drilus horasfakionus Crete L	RMNH.INS.871818
13	*Drilus* sp. A Turkey M	UPOL RK0081
14	*Drilus flavescens* Great Britain M	BMNH 679287
15	*Drilus baenai* Crete L	EB2013-304
16	*Drilus* sp. G Greece L	RMNH.INS.559218
17	*Drilus* sp. M Kefalonia L	RMNH.INS.871808

Table S5. The maximum uncorrected pairwise distances in *Drilus* lineages (%). *D. baenai* a = *D. baenai minus* EB2013-304; *D. longulus* a = UPOL RK0638 and RMNH.INS.559207; *D. longulus* b = *D. longulus* Kiesenwetter *minus D. longulus* a; *D. horasfakionus* b = *D. horasfakionus* sp. nov. *minus* EB2013-299 and EB2013-300.

Taxon	*cox1-3′* mtDNA	*cox1-5′* mtDNA	Total dataset
D. sp. E	2.21	2.89	2.53
D. concolor Ahrens	1.94	1.67	1.74
D. flavescens Olivier	12.45	8.51	12.50
D. baenai sp. nov.	5.39	0.77	5.55
D. baenai a	0.55	–	0.55
D. sp. D	3.87	–	3.93
D. sp. L	1.94	1.06	1.79
D. longulus Kiesenwetter	9.14	7.14	9.34
D. longulus a	4.70	–	4.71
D. longulus b	1.44	–	1.50
D. horasfakionus sp. nov.	6.50	–	6.50
D. horasfakionus b	3.73	1.22	3.73

Příloha 11

Kundrata, R. & Bocák, L. (2017) Taxonomic review of Drilini (Elateridae: Agrypninae) in Cameroon reveals high morphological diversity, including the discovery of five new genera. *Insect Systematics & Evolution*, 48: 441–492.
[IF 0,763; 8 citací na WoS; celkem 2 citace bez autorových autocitací]
[korespondující autor; autorský podíl: 50 %]

BRILL

Insect Systematics & Evolution 48 (2017) 441–492

brill.com/ise

Taxonomic review of Drilini (Elateridae: Agrypninae) in Cameroon reveals high morphological diversity, including the discovery of five new genera

Robin Kundrata* and Ladislav Bocak

Department of Zoology, Faculty of Science, Palacky University, 17. listopadu 50, 771 46,
Olomouc, Czech Republic
*Corresponding author, e-mail: robin.kundrata@upol.cz

Version of Record, published online 7 April 2017; published in print 1 November 2017

Abstract

The first comprehensive survey of the Cameroonian Drilini fauna is presented. High diversity was identified in the zone of tropical rain forest and five genera are proposed: *Flabelloselasia* gen. n., *Kupeselasia* gen. n., *Lolosia* gen. n., *Microselasia* gen. n., and *Wittmerselasia* gen. n. with the subgenus *Latoselasia* subgen. n. The following species are described: *Flabelloselasia oculata* sp. n., *Kupeselasia minuta* sp. n., *Lolosia transversalis* sp. n., *Microselasia barombi* sp. n., *M. elongata* sp. n., *M. gracilis* sp. n., *M. grandis* sp. n., *M. kupensis* sp. n., *M. lolodorfensis* sp. n., *M. macrocephala* sp. n., *M. obscura* sp. n., *M. pseudograndis* sp. n., *Wittmerselasia camerooniana* sp. n., *W. davidsoni* sp. n., *W. geiseri* sp. n., *W. variabilis* sp. n., and *W.* (*Latoselasia*) *similis* sp. n. *Selasia maculata* Wittmer, 1989 is redescribed and transferred to *Wittmerselasia* gen. n. as *W. maculata* (Wittmer, 1989), comb. n. Taxonomically important characters are illustrated for all genera and species and an identification key for Drilini from Cameroon is provided.

Keywords
Elateroidea; *Selasia*; Africa; diversity hot-spot; distribution

Introduction

Drilini is a small morphologically distinct beetle lineage with the soft-bodied, fully winged males and larviform apterous females (Crowson 1972; Bocak et al. 2010). Due to their "cantharoid" appearance they had been long classified in their own family Drilidae (Lawrence et al. 2011). In contrast with morphology-based phylogenies, numerous molecular studies on Elateroidea confirmed their relationships within the click-beetle subfamily Agrypninae (Kundrata & Bocak 2011a; Kundrata et al. 2016; Timmermans et al. 2016) or with other elaterids (McKenna et al. 2015). Historically, Drilini contained many only superficially similar elateroid genera from different regions of the world (e.g., Wittmer 1944; Kundrata & Bocak 2011a,b; Janisova &

DOI 10.1163/1876312X-48022161

Bocakova 2013). Crowson (1972) substantially reduced the concept of the lineage and after further studies only six genera remained in Drilini (Bocak et al. 2010), three of them later being transferred to Omalisidae based on the DNA analyses (Kundrata & Bocak 2011a; Kundrata et al. 2015b). The current concept of Drilini is limited to genera *Drilus* Olivier (45 spp.), *Malacogaster* Bassi (11 spp.) and *Selasia* Laporte (65 spp.), which are distributed in the Afrotropical, Palaearctic and Oriental Regions (e.g., Bocak 2007; Bocak et al. 2010). Recently, several taxonomic studies on Palaearctic Drilini were published (e.g., Kundrata et al. 2014, 2015a; Petrzelkova & Kundrata 2015; Trllova & Kundrata 2015), but the African lineages have remained underinvestigated. Most species from the tropical Africa were briefly and insufficiently described by Maurice Pic (e.g., Pic 1914, 1918, 1931, 1946). Recently, only Wittmer (1989) and Geisthardt (2007a,b) studied the African fauna and described a number of new species mainly from the southern Africa. The diversity and classification of the Drilini from rain forests in the Gulf of Guinea has not yet been studied, primarily because of the unavailability of samples from this region. The recent expedition to Cameroon specifically targeted the neotenic lineages in Cameroon and yielded a quite high number of previously unknown Drilini and these are used for a taxonomic study here. We describe new genus- and species-group taxa of Drilini from Cameroon which represents one of the World biodiversity hotspots (Stuart & Adams 1990; Myers 2000). Hitherto, only *Selasia maculata* Wittmer, 1989 has been reported from Cameroon, but new samples from several localities revealed much higher diversity. Using morphology, five new genera are delimited, and 17 new species are described.

Material and methods

We studied the morphology of adult males; the females and larvae of the examined species are unavailable. The genitalia were dissected after treatment in hot 10% KOH. Diagnostic characters were photographed using a digital camera attached to a stereoscopic microscope. The following measurements were taken with a scale bar in an eyepiece: BL–body length, measured from the fore margin of head to the apex of elytra; WHe–head width including eyes; EL, elytral length; WHum, width at humeri; PL, pronotal length at midline; PW, pronotal width at widest part; Edist, minimum interocular distance in the frontal part of cranium; Ediam, maximum eye diameter in the lateral view. The locality labels are cited verbatim. Morphological terminology follows Bocak et al. (2010) and Kundrata et al. (2014, 2015a). The types are deposited in the Natural History Museum, London, United Kingdom (BMNH), Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA (CMNH), Muséum national d'Histoire naturelle, Paris, France (MHNP), and the voucher collection of the Department of Zoology, Palacky University, Olomouc, Czech Republic (UPOL).

Systematics

Order Coleoptera Linnaeus, 1758
Suborder Polyphaga Emery, 1886

Superfamily Elateroidea Leach, 1815
Family Elateridae Leach, 1815
Subfamily Agrypninae Candèze, 1857
Tribe Drilini Blanchard, 1845

All Drilini representatives from Cameroon known to the authors are herein accommodated to the newly established genera. The genus *Selasia*, which is the most speciose Drilini lineage in Africa, differs from *Flabelloselasia* gen. n., *Kupeselasia* gen. n., *Microselasia* gen. n., and *Wittmerselasia* gen. n. in having much shorter and wider fronto-clypeal region between antennal insertions, gradually declined to the base of labrum, and from *Lolosia* gen. n. in having strongly serrate to flabellate antennae, ultimate maxillary and labial palpomeres never subacute apically, and U-shaped phallobase. The occurrence of *Selasia* in Cameroon is highly probable as 14 species of this genus are known from the surrounding regions (Nigeria, Republic of the Congo, Democratic Republic of the Congo; Wittmer 1944, Pic 1946, Barker 1969). We have studied all described species whose types are deposited in major European museums. None of them is conspecific with the here presented species from Cameroon.

Genus *Flabelloselasia* gen. n.

Type species

Flabelloselasia oculata sp. n.

Diagnosis

Flabelloselasia gen. n. is recognizable by the flabellate antennae with the branches about 20 times longer than the stems of the corresponding antennomeres VI–X (Fig. 28), the rather narrow, high fronto-clypeal region (Fig. 19), large, prominent eyes (Figs 19, 25), maxillary and labial palpi elongate, apically slightly widened and obliquely cut (Fig. 27), pronotum with the sublateral carinae almost reaching frontal margin (Fig. 25), sternite IV deeply notched basally (Fig. 33), phallobase V-shaped, and the parameres short, almost rectangular (Fig. 107).

Description

Male. Body 2.80 times longer than width at humeri; reddish brown to brown, mesoventrite, coxae and apical abdominal segments lighter, legs and mouthparts yellowish; body surface covered with yellow pubescence (Fig. 1).

Head including eyes 0.90 times as wide as pronotum; surface smooth, with wide, shallow median depression, sparsely punctured, covered with sparse, long, semi-erect pubescence; frons slightly convex, narrowed apically; antennal sockets narrowly separated, supra-antennal carinae indistinct; fronto-clypeal region narrow, high, with two weakly developed, divergent, smooth carinae; its surface sparsely punctate, basally covered with sparse, long, erect pubescence (Fig. 19). Eyes large, prominent, their frontal distance 1.00–1.05 times eye diameter (Fig. 25). Labrum transverse, sclerotized, with frontal margin widely concave, sparsely punctate. Mandibles robust, moderately long, sickle-shaped, with apical oblique tooth and another tooth located in middle part of incisor; base of mandible with long setae, apical part bare, shiny (Fig. 26). Maxillary palpi tetramerous, slender, palpomere I short, wide, palpomere II less than twice longer than wide, palpomere III short, about as long as wide, ultimate palpomere elongate, more than 3 times as long as palpomere III, apically slightly widened, flattened, obliquely cut (Fig. 27). Labium short, wide; labial palpi trimerous, tiny, apical palpomere pointed apically. Antennae 11-segmeneted, flabellate, scapus robust, widened apically, pedicel short, small, antennomere III long, more than 3 times longer than pedicel, with robust branch, which is longer than body of antennomere III but less than half as long as branch of antennomere IV, antennomeres IV–X minute, short, subequal in length, basally with very long, flattened lamellae of about the same lengths, apical antennomere simple, longest, about as long as lamella of penultimate antennomere; all antennomeres covered with moderately dense pubescence (Fig. 28).

Pronotum slightly convex, transverse, widest at posterior angles, 1.75 times wider than length at midline. Anterior margin almost straight, slightly emarginate medially, lateral margins diverging posteriorly, posterior margin simple, widely convex. Anterior angles inconspicuous; posterior angles obtuse. Disc with narrow, transverse carina near anterior margin, and with distinct sublateral carinae almost reaching anterior margin (Fig. 25). Lateral carina separating pronotum from hypomeron distinct, incomplete anteriorly. Surface of disc sparsely shallowly punctured, with sparse semi-erect pubescence. Hypomeron carinate sublaterally, moderately densely punctate; prosternal suture very short. Prosternum transverse, prosternal lobe short, with frontal margin widely convex, with long semi-erect setae; prosternal process short, sledner, gradually narrowed toward apex, constricted subapically, rounded apically. Scutellum flat, triangular, long, about 1.4 times as long as wide, with anterior margin gradually declivitous (Fig. 29). Mesoventrite widely V-shaped, with frontal margin widely concave; mesoventral cavity shallow, with poorly defined walls. Mesocoxal cavity open to both mesepimeron and mesepisternum. Metaventrite large, subtrapezoidal, sparsely covered with shallow punctures. Elytra subparallel-sided, 0.75 times as long as body; basally wrinkled, indistinctly striate, with longitudinal, weakly developed stria running from humeri towards apex, remaining striae indistinct, more developed basally (Fig. 1). Each elytron with apices separately rounded, very sparsely punctate, covered with long, semi-erect pubescence, sparser basally, denser laterally and apically; elytral suture distinct, wide, depressed. Hind wing venation as in Fig. 31. Legs slender, slightly compressed, with sparse, long, semi-erect setae, coxae robust, trochanters slender, elongate, widened apically, obliquely attached to femora; tarsomeres I–II subequal in length, tarsomere III slightly shorter than preceding ones, about 1.5 times longer than tarsomere IV; tarsomere IV shortest, minute, extended ventrally, apical tarsomere slender, long, about 2.5 times longer than tarsomere IV (Fig. 30); claws simple, slender, slightly curved, each with long seta basally.

Abdomen soft, slender, ventrites with very sparse, shallow punctures, sparsely covered with semi-erect pubescence; penultimate ventrite slightly emarginate medially. Tergites IX and X weakly connected by membrane; tergite IX basally with two sublateral processes (Fig. 32). Sternite IX 1.6 times as long as wide, deeply notched basally, rounded apically, with apex finely punctate and sparsely setose (Fig. 33); sternite X small, wider than long, partly membranous, with basal margin emarginate, apically rounded, connected by membrane to sternite IX.

Male genitalia trilobate, 1.6 times as long as wide; median lobe robust, longer than parameres, slightly longer than phallobase, moderately curved in lateral view, basally with two short, divergent struts, dorsally with robust, long, subapical hook; parameres short, subrectangular, about as long as wide, setose apically; phallobase robust, slightly wider than long, basally narrowed, V-shaped (Fig. 107).

Females and immature stages unknown.

Distribution

This genus is known from the Southwest Region in Cameroon (Fig. 125).

Etymology

The name is derived from the long antennal branches and the general similarity of this genus to *Selasia* Laporte, 1836. Gender: feminine.

Flabelloselasia oculata **sp. n.**

(Figs 1, 19, 25–33, 107)

Type material

Holotype, male, "Cameroon, SW Prov., Nyassoso, Mt. Kupé, 900 m, 4°49.59' N 9°40.54' E, 9.–11. Mar 2008, Bolm lgt." (UPOL); paratype, male, "Cameroon: SW Prov., Fako dist., Bakingili, 25 km W Limbe, VII. 11.–20.1984, coll. R. Davidson" (CMNH).

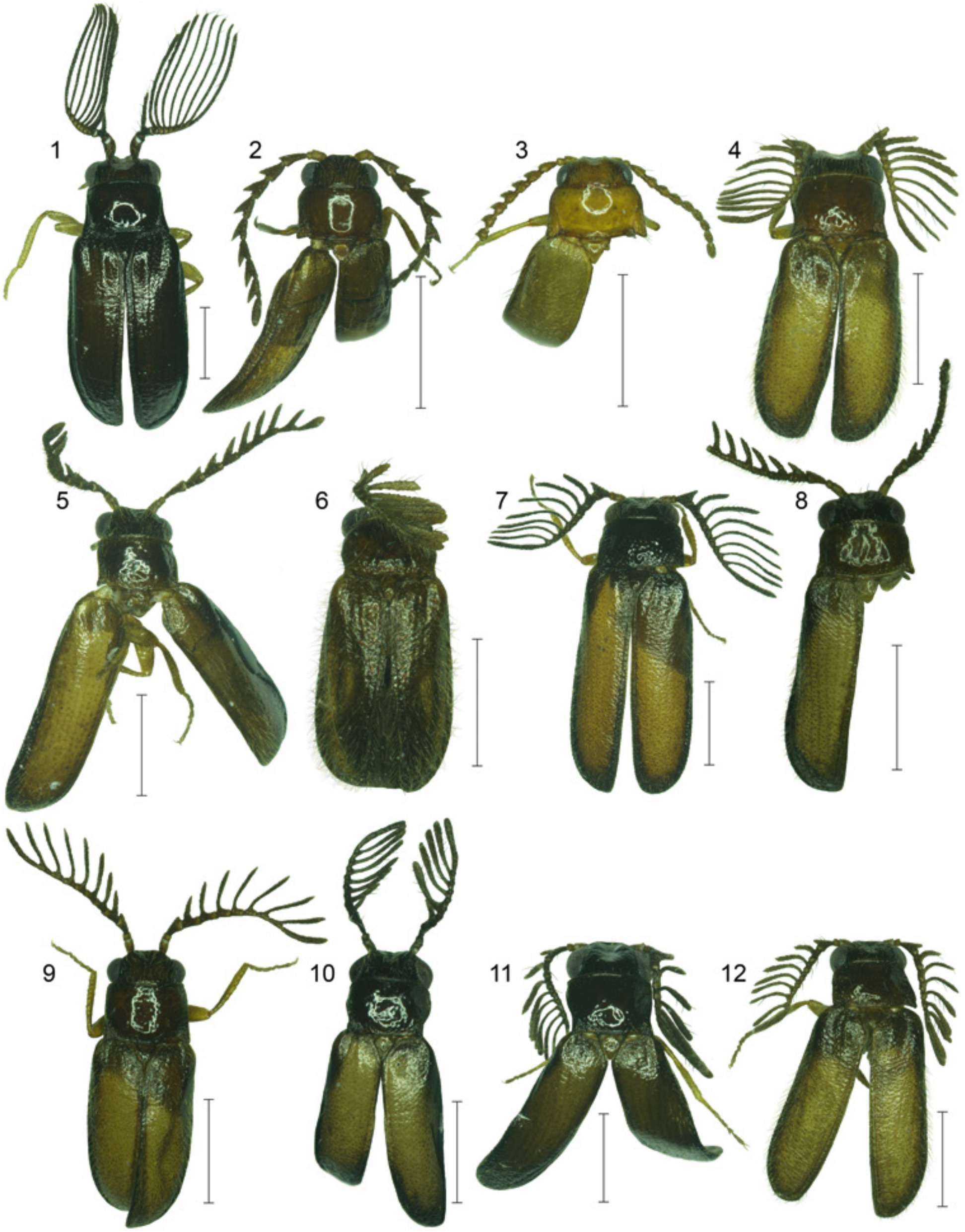
Diagnosis

Flabelloselasia oculata sp. n. is easily recognizable by the strongly flabellate antennae with the branches about 20 times longer than their respective stems in antennomeres VI–X (Fig. 28) and the male genitalia with V-shaped phallobase and short, subrectangular parameres (Fig. 107). Other Drilini in the region have antennal branches maximally 12 times longer than their stems, their male genitalia mostly have U-shaped phallobases (except for *Lolosia* gen. n.), and their parameres are never subrectangular.

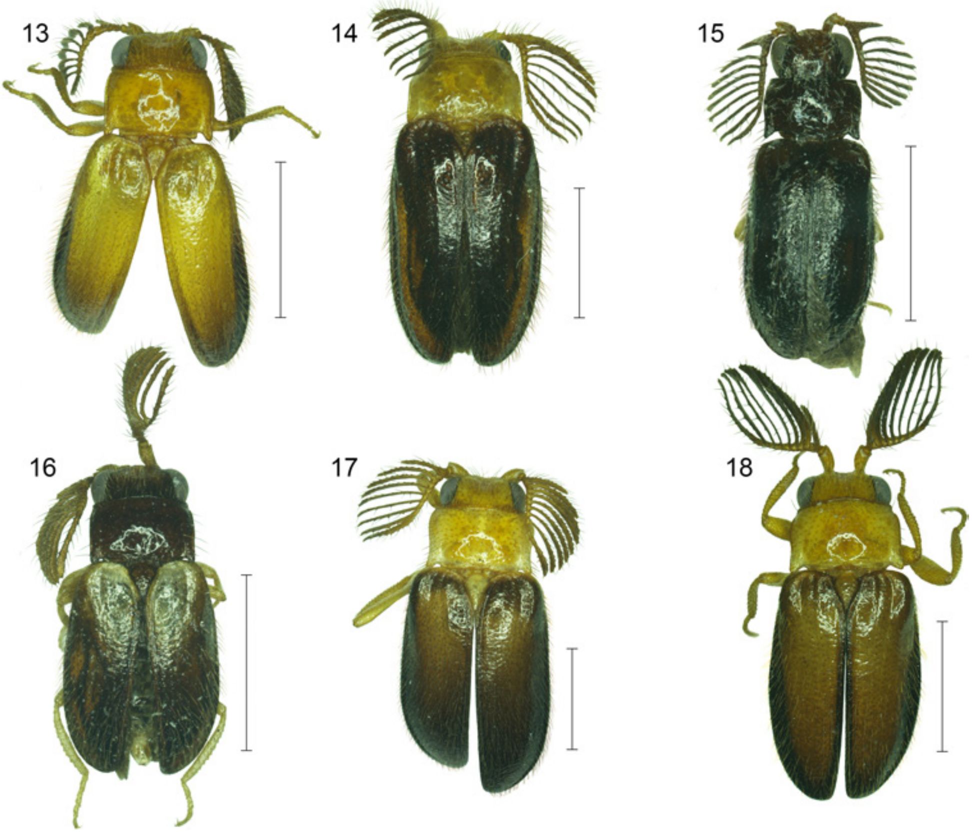
Description

Body mostly brown, only pronotum lighter in a single paratype, mesoventrite; coxae and abdominal apical segments lighter, legs and mouthparts yellowish; body surface covered with yellow pubescence (Fig. 1).

Head slightly narrower than pronotum. Eyes large, their frontal distance same as eye diameter (Fig. 25). Antennae flabellate, pedicel short, antennomere III long, with



Figs 1–12. Habitus images of Drilini from Cameroon. (1) *Flabelloselasia oculata* sp. n.; (2) *Kupeselasia minuta* sp. n.; (3) *Lolosia transversalis* sp. n.; (4) *Microselasia barombi* sp. n.; (5) *M. elongata* sp. n.; (6) *M. gracilis* sp. n.; (7) *M. grandis* sp. n.; (8) *M. kupensis* sp. n.; (9) *M. lolodorfensis* sp. n.; (10) *M. macrocephala* sp. n.; (11) *M. obscura* sp. n.; (12) *M. pseudograndis* sp. n. Scale bars = 1.0 mm.



Figs 13–18. Habitus images of *Wittmerselasia* gen. n. (13) *W. camerooniana* sp. n.; (14) *W. davidsoni* sp. n.; (15) *W. geiseri* sp. n.; (16) *W. maculata* (Wittmer 1989); (17) *W. variabilis* sp. n.; (18) *W.* (*Latoselasia*) *similis* sp. n. Scale bars = 2.0 mm.

robust branch, antennomeres IV–X short, with long, flattened branches, apical antennomere simple, about as long as lamella of preceding antennomere (Fig. 28).

Pronotum widest at posterior angles, 1.7 times wider than length at midline, with transverse carina near anterior margin, and with distinct sublateral carinae almost reaching anterior margin (Fig. 25). Elytra 0.75 times as long as body, 2.05 times as long as wide at humeri (Fig. 1).

Abdominal terminal segments as in Figs 32–33. Male genitalia with median lobe longer than parameres; parameres short, subrectangular, about as long as wide; phallobase slightly wider than long, V-shaped (Fig. 107).

Measurements

Holotype. BL 3.90 mm, WHum 1.40 mm, EL 2.85 mm, WHe 1.00 mm, PL 0.65 mm, PW 1.15 mm, Edist 0.45 mm, Ediam 0.45 mm. Paratype. BL 4.10 mm, EL 3.00

Figs 19–24. Frontoclypeal regions of Drilini from Cameroon. (19) *Flabelloselasia oculata* sp. n.; (20) *Kupeselasia minuta* sp. n.; (21) *Lolosia transversalis* sp. n.; (22) *Microselasia obscura* sp. n.; (23) *Wittmerselasia variabilis* sp. n.; (24) *Wittmerselasia* (*Latoselasia*) *similis* sp. n. Scale bars = 0.5 mm.

mm, WHe 1.10 mm, WHum 1.45 mm, PL 0.70 mm, PW 1.25 mm, Edist 0.45 mm, Ediam 0.45 mm.

Distribution

Cameroon: Southwest Region (Fig. 125).

Etymology

The specific name refers to the large eyes.

Genus *Kupeselasia* gen. n.

Type species

Kupeselasia minuta sp. n.

Diagnosis

This genus is superficially similar to *Microselasia* gen. n. in the body coloration, general appearance, complete frontal carina, subacute apices of palpi, the shape of the frontoclypeal region and the U-shaped phallobase, which is as long as or longer than wide (Figs 2, 4–12, 20, 22, 36, 54, 108, 110–118). However, *Kupeselasia* gen. n. has acutely serrate antennae unlike the flabellate antennae of *Microselasia* gen. n.; Figs 37, 71–79), slender mandibles (Figs 35, 53), sternite IX not emarginate basally (more or less emarginate in *Microselasia* gen. n.; Figs 42, 60–61), and parameres characteristically slender and elongate (Fig. 108).

Description

Male. Body 3.05 times longer than width at humeri; brown, head, pronotum, antennomeres III–XI, and ventral parts darker; body surface covered with yellow pubescence (Fig. 2).

Head including eyes 0.9 times as wide as pronotum; surface smooth, with shallow median depression, sparsely punctured, covered with sparse, semi-erect pubescence; frons slightly produced and narrowed apically, slightly surpassing fronto-clypeal region; antennal sockets rather narrowly separated, supra-antennal carinae form distinct, sinuate frontal carina; fronto-clypeal region high, narrow, abruptly declined between antennal insertions, sloping to base of labrum, sparsely punctate, basally covered with sparse, semi-erect setae (Fig. 20). Eyes moderately large, prominent, their frontal distance 1.45 times eye diameter (Fig. 34). Labrum sclerotized, transverse, short, with frontal margin widely concave. Mandibles rather long, sickle-shaped, bidentate, with long apical oblique tooth and another tooth located in middle part of incisor; mandibles basally setose, apically bare, shiny (Fig. 35). Maxillary palpi tetramerous, slender, palpomere I short, wide, palpomere II less than twice longer than wide, about 1.5 longer than palpomere III, palpomere III short, about as long as wide, palpomere IV elongate, about 3 times as long as palpomere III, apically slightly constricted, pointed (Fig. 36). Labium short, wide; labial palpi trimerous, tiny, palpomeres I–II short, apical palpomere elongate, wide basally, apically narrowed, pointed. Antennae 11-segmeneted, strongly serrate, scapus robust, widened apically, pedicel short, small, antennomere III long, weakly serrate, more than 3 times longer than antennomere II, antennomeres IV–X strongly serrate, slightly shorter than antennomere III, subequal in length, apical antennomere simple, elongate, slightly longer than penultimate antennomere (Fig. 37); all antennomeres covered with moderately dense pubescence.

Pronotum slightly convex, transverse, widest at posterior angles, 1.55 times wider than length at midline. Anterior margin almost straight, lateral margins sinuate, diverging posteriorly, posterior margin simple, widely convex. Anterior angles inconspicuous; posterior angles obtuse, slightly produced postero-laterally, with wrinkled surface. Disc with transverse carina near anterior margin, distinct sinuate sublateral carinae almost reaching anterior margin, and transverse carina near posterior margin (Fig. 34); its surface smooth, very sparsely covered with shallow punctures, denser at lateral margins, with sparse semi-erect pubescence, denser at lateral margins and posterior angles. Lateral carina separating pronotum from hypomeron distinct, almost reaching pronotal frontal margin. Hypomeron smooth, with indistinct, short sublateral carina near prosternal suture, sparsely punctate, with short semi-erect setae near lateral carina; prosternal suture very short. Prosternum transverse, prosternal lobe short, with frontal margin widely convex, with long semi-erect setae; prosternal process short, narrowly rounded apically. Scutellum flat, triangular, smooth, about as long as wide, narrowly rounded posteriorly (Fig. 40). Mesoventrite widely V-shaped, with frontal margin widely concave; mesoventral cavity shallow, with poorly defined walls. Mesocoxal cavity open to both mesepimeron and mesepisternum. Metaventrite large, subtrapezoidal, smooth, very sparsely covered with shallow punctures. Elytra subparallel-sided, 0.70 times as long as body, with narrow epipleura; basally wrinkled, with traces of indistinct striae in humeral part (Fig. 2). Each elytron with apices separately rounded, very sparsely punctate, covered with moderately long, semi-erect pubescence, sparser basally, denser laterally and apically; elytral suture distinct, wide, depressed. Hind wing venation as in Fig. 38. Legs slender, slightly compressed, with sparse, long, semi-erect setae, coxae robust, trochanters slender, elongate, widened apically, obliquely attached to femora; tarsomeres I–III subequal in length, about twice longer than tarsomere IV; tarsomere IV shortest, minute, extended ventrally, apical tarsomere slender, long, about 3 times longer than tarsomere IV (Fig. 39); claws simple, slender, slightly curved, setose basally.

Abdomen soft, slender, ventrites with very sparse, shallow punctures, sparsely covered with semi-erect pubescence, denser laterally; tergite and sternite I reduced, sternite II formed only by two separate sclerites; tergites IX and X weakly connected by membrane; tergite IX basally with two sublateral processes; tergite X partly membranous apically (Fig. 41). Sternite IX elongate, 1.9 times as long as wide, apex rounded, punctate, with sparse short setae; sternite X almost rounded, partly membranous, connected by membrane to sternite IX (Fig. 42).

Male genitalia trilobate, 1.9 times as long as wide; median lobe robust, more than twice longer than parameres, slightly longer than phallobase, moderately curved in lateral view, basally with two long struts, dorsally with short subapical hook; parameres slender, elongate, about twice as long as wide, truncate apically; phallobase robust, U-shaped, longer than wide (Fig. 108).

Females and immature stages unknown.

Distribution

This genus is known only from the Southwest Region in Cameroon (Fig. 125).

Etymology

The generic name combines "Kupé", the name of the type locality, and "*Selasia*" Laporte, 1836, a genus in Drilini. Gender: feminine.

Kupeselasia minuta **sp. n.**

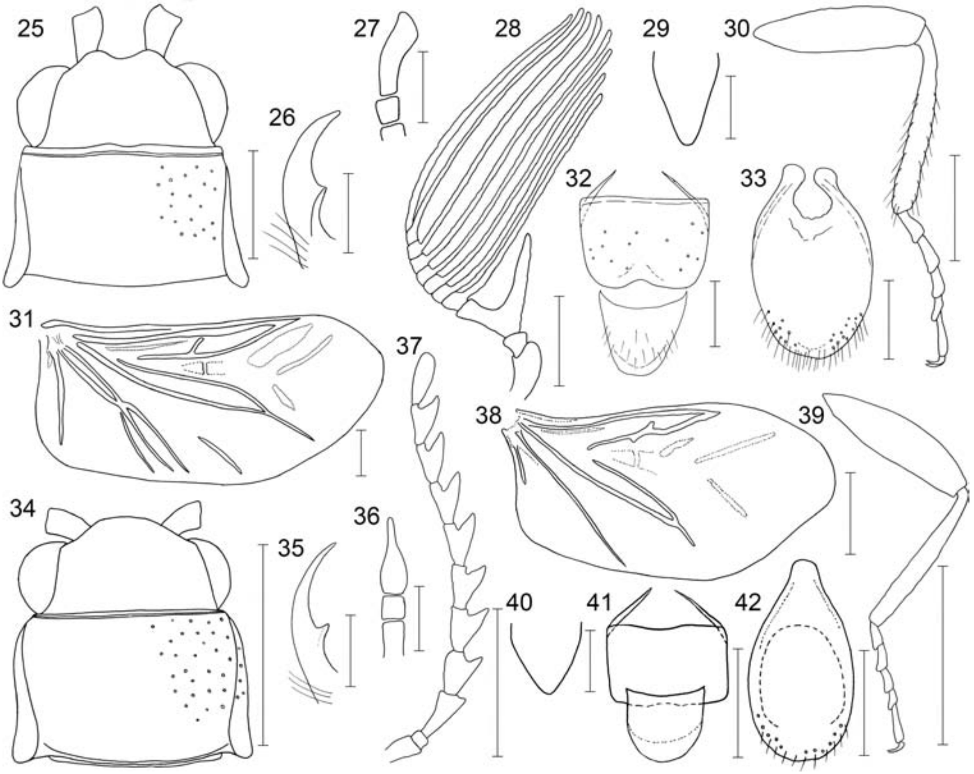
(Figs 2, 20, 34–42, 108)

Type material

Holotype, male, "Cameroon, SW Prov., Nyassoso, Mt. Kupé, 900 m, 4°49.59' N 9°40.54' E, 9.–11. Mar 2008, Bolm lgt." (UPOL).

Diagnosis

Kupeselasia minuta sp. n. can be easily recognized due to its complete frontal carina, narrow and high fronto-clypeal region (Fig. 20), strongly serrate antennae (Fig. 37),



Figs 25–42. Body parts of *Flabelloselasia* gen. n. and *Kupeselasia* gen. n. *Flabelloselasia oculata* sp. n. (25) head and pronotum; (26) mandible; (27) last maxillary palpomeres; (28) antenna; (29) scutellum; (30) leg; (31) hind wing; (32) abdominal tergites IX–X; (33) abdominal sternite IX. *Kupeselasia minuta* sp. n. (34) head and pronotum; (35) mandible; (36) last maxillary palpomeres; (37) antenna; (38) hind wing; (39) leg; (40) scutellum; (41) abdominal tergites IX–X; (42) abdominal sternite IX. Scale bars = 0.1 mm (Figs 35–36, 40), 0.2 mm (Figs 26–27, 29, 32–33, 41–42), 0.5 mm (Figs 25, 28, 30–31, 34, 37–39).

distinct sublateral pronotal carinae almost reaching frontal margin (Fig. 34), U-shaped, elongate phallobase, and the distinctly narrowed and elongate parameres (Fig. 108).

Description

Body brown, head, pronotum, antennomeres III–XI, and ventral parts darker; body surface covered with yellow pubescence (Fig. 2).

Head including eyes slightly narrower than pronotum. Eyes moderately large, their frontal distance 1.45 times eye diameter (Fig. 34). Antennae serrate, antennomere III weakly serrate, more than 3 times longer than antennomere II, antennomeres IV–X serrate, shorter, subequal in length, apical antennomere simple, slightly longer than penultimate antennomere (Fig. 37).

Pronotum widest at posterior angles, 1.55 times wider than length at midline, with transverse carina near anterior margin, distinct sinuate sublateral carinae almost reaching anterior margin, and transverse carina near posterior margin (Fig. 34). Elytra 0.70 times as long as body, 2.15 times as long as wide at humeri (Fig. 2).

Abdominal terminal segments as in Figs 41–42. Male genitalia with median lobe more than twice longer than parameres; parameres slender, elongate, about twice as long as wide; phallobase longer than wide, U-shaped (Fig. 108).

Measurements

BL 2.10 mm, WHum 0.70 mm, EL 1.50 mm, WHe 0.55 mm, PL 0.40 mm, PW 0.60 mm, Edist 0.30 mm, Ediam 0.21 mm.

Distribution

Cameroon: Southwest Region (Fig. 125).

Etymology

The specific epithet refers to the small body of this species.

Genus *Lolosia* gen. n.

Type species

Lolosia transversalis sp. n.

Diagnosis

Lolosia gen. n. can be recognized by using the following combination of characters: the incomplete frontal carina, wide fronto-clypeal region (Fig. 21), ultimate maxillary and labial palpomeres narrowed, subacute apically (Fig. 46), serrate antennae (Fig. 43), pronotum 1.85 times wider than long, with distinct, sinuate sublateral carinae (Fig. 44), scutellum about as long as wide (Fig. 48), sternite IX elongate, 2.1 times longer than wide (Fig. 50), V-shaped phallobase, and relatively long, apically rounded parameres (Fig. 109).

Description

Male. Body 2.25 times longer than width at humeri. Body yellowish to light brown, pronotum, antennomeres I–II and legs lighter, abdomen darker; body surface covered with yellow pubescence (Fig. 3).

Head including eyes 0.75 times as wide as pronotum; surface smooth, very shallowly depressed medially, sparsely punctured, covered with sparse, long semi-erect pubescence; antennal sockets moderately widely separated, supra-antennal carinae distinct, short, not meeting medially; fronto-clypeal region slightly wider than long, convex; its surface rough, sparsely punctate, basally covered with sparse, semi-erect setae (Fig. 21). Eyes large, prominent, their frontal distance 1.20 times eye diameter (Fig. 44). Labrum sclerotized, transverse, short, produced forwards, with frontal margin slightly concave.

Mandibles robust, moderately long, sickle-shaped, bidentate, with long apical oblique tooth and another, robust tooth located in middle part of incisor; mandibles basally setose, apical part bare, shiny (Fig. 45). Maxillary palpi tetramerous, slender, palpomere I short, wide, palpomere II more than 1.5 times longer than wide, slightly more than 1.5 longer than palpomere III, palpomere III short, slightly wider than long, palpomere IV elongate, apically slightly constricted, pointed, about 3.5 times as long as palpomere III (Fig. 46). Labium short, wide; labial palpi trimerous, tiny, palpomeres I–II short, apical palpomere elongate, pointed apically. Antennae 11-segmeneted, serrate, scapus robust, widened apically, pedicel short, small, antennomeres III–X serrate, rugose, antennomere III long, more than twice longer than antennomere II, antennomeres IV–X slightly shorter than antennomere III, subequal in length, apical antennomere simple, longest, about 1.5 times as long as penultimate antennomere (Fig. 43); all antennomeres covered with moderately dense pubescence.

Pronotum slightly convex, transverse, widest at posterior angles, 1.85 times wider than length at midline. Anterior margin almost straight, lateral margins diverging posteriorly, posterior margin widely convex, slightly bent upwards, slightly emarginate medially. Anterior angles inconspicuous; posterior angles obtuse, with wrinkled surface. Disc smooth, with indistinct transverse carina near anterior margin, distinct sinuate sublateral carinae almost reaching anterior margin, and transverse carina near posterior margin (Fig. 44). Lateral carina separating pronotum from hypomeron distinct, incomplete anteriorly. Surface of disc very sparsely covered with shallow punctures, with sparse semi-erect pubescence, denser at posterior angles. Hypomeron with sublateral carina near prosternal suture, moderately densely punctate; prosternal suture very short. Prosternum transverse, prosternal lobe short, with frontal margin widely convex, with long semi-erect setae; prosternal process short, slender, subparallel-sided, pointed apically. Scutellum flat, triangular, smooth, about as long as wide, narrowly rounded posteriorly (Fig. 48). Mesoventrite V-shaped, with frontal margin widely concave; mesoventral cavity shallow, with poorly defined walls. Metaventrite large, subtrapezoidal, smooth, very sparsely covered with shallow punctures. Elytra subparallel-sided, 0.75 times as long as body, with narrow epipleura; basally wrinkled, with longitudinal, weakly developed stria running from humeri towards apex, but inconspicous at apical half (Fig. 3). Each elytron with apices separately rounded, very sparsely punctate, covered with moderately long, semi-erect pubescence, sparser basally, denser laterally and apically; elytral suture distinct, wide, depressed. Hind wing venation as in Fig. 47. Legs slender, slightly compressed, with sparse, long, semi-erect setae, coxae robust, trochanters slender, elongate, widened apically, obliquely attached to femora; tarsomeres I–II subequal in length, tarsomere III slightly shorter, about 1.5 times longer than tarsomere IV; tarsomere IV shortest, minute, extended ventrally, apical tarsomere slender, long, about 3 times longer than tarsomere IV (Fig. 49); claws simple, slender, slightly curved, each with long seta basally.

Abdomen soft, slender, ventrites with very sparse, shallow punctures, sparsely covered with semi-erect pubescence, denser laterally. Tergites IX and X weakly connected by membrane; tergite IX basally with two sublateral processes (Fig. 51). Sternite IX elongate, 2.1 times as long as wide, notched basally, apex rounded, with sparse short setae (Fig. 50); sternite X almost rounded, partly membranous, connected by membrane to sternite IX.

Male genitalia trilobate, 1.9 times as long as wide; median lobe robust, longer than parameres, about as long as phallobase, moderately curved in lateral view, basally with two short struts, dorsally with robust subapical hook; parameres elongate, rounded apically, apex sparsely setose; phallobase robust, slightly wider than long, basally narrowed, V-shaped (Fig. 109).

Females and immature stages unknown.

Distribution

This genus is known only from the South Region in Cameroon (Fig. 125).

Etymology

The name *Lolosia* gen. n. is a combination of words Lolodorf (type locality) and *Selasia* Laporte, 1836 (genus in Elateridae: Drilini). Gender: feminine.

Lolosia transversalis **sp. n.**

(Figs 3, 21, 43–51, 109)

Type material

Holotype, male, “Cameroon, South Prov., Lolodorf, 550 m, 3°14.06' N 10°43.52', 31 E. Mar 2008, Bolm lgt.” (UPOL).

Diagnosis

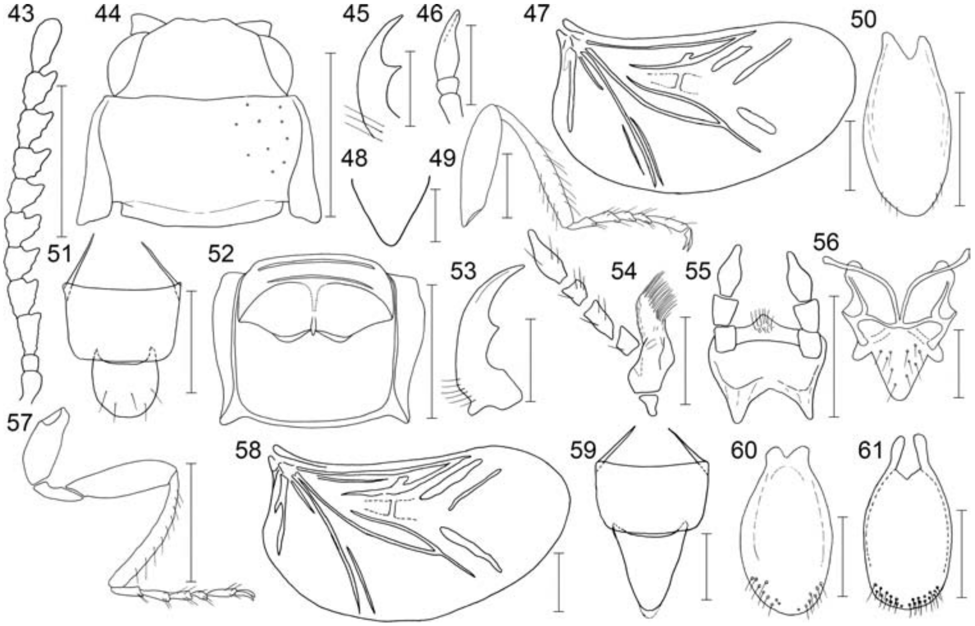
Lolosia transversalis sp. n. is characteristic by the incomplete frontal carina (Fig. 21), maxillary and labial palpi with ultimate palpomeres subacute apically (Fig. 46), serrate antennae (Fig. 43), and male genitalia with V-shaped phallobase (Fig. 109).

Description

Body yellowish to light brown, pronotum, antennomeres I–II and legs lighter, abdomen darker; body surface covered with yellow pubescence (Fig. 3).

Head including eyes slightly narrower than pronotum. Eyes large, their frontal distance 1.20 times eye diameter (Fig. 44). Antennae serrate, pedicel short, antennomere III more than twice longer than antennomere II, antennomeres IV–X shorter, subequal in length, apical antennomere simple, about 1.5 times as long as penultimate antennomere (Fig. 43).

Pronotum widest at posterior angles, 1.85 times wider than length at midline, with indistinct transverse carina near anterior margin, distinct sinuate sublateral carinae almost reaching anterior margin, and transverse carina near posterior margin (Fig. 44). Elytra 0.75 times as long as body, 1.60 times as long as wide at humeri (Fig. 3).



Figs 43–61. Body parts of *Lolosia* gen. n. and *Microselasia* gen. n. *Lolosia transversalis* sp. n.: (43) antenna; (44) head and pronotum; (45) mandible; (46) last maxillary palpomeres; (47) hind wing; (48) scutellum; (49) leg; (50) abdominal sternite IX; (51) abdominal tergites IX–X. *Microselasia obscura* sp. n.: (52) prosternum; (53) mandible; (54) maxilla; (55) labium; (56) scutellum; (57) leg; (58) hind wing; (59) abdominal tergites IX–X; (60) abdominal sternite IX. *Microselasia barombi* sp. n.: (61) abdominal sternite IX. Scale bars = 0.1 mm (Figs 45–46, 48), 0.2 mm (Figs 49–51, 53–56, 59–61), 0.5 mm (Figs 43–44, 47, 52, 57–58).

Abdominal terminal segments as in Figs 50–51. Male genitalia with median lobe longer than parameres, parameres elongate, rounded apically; phallobase slightly wider than long, V-shaped (Fig. 109).

Measurements

BL 2.10 mm, WHum 0.95 mm, EL 1.50 mm, WHe 0.55 mm, PL 0.40 mm, PW 0.70 mm, Edist 0.30 mm, Ediam 0.25 mm.

Distribution

Cameroon: South Region (Fig. 125).

Etymology

The name “transversalis” refers to the transverse pronotum of this species.

Genus *Microselasia* gen. n.

Type species

Microselasia obscura sp. n.

Diagnosis

Microselasia gen. n. shares the minute body and apically narrowed, subacute ultimate maxillary and labial palpomeres with *Lolosia* gen. n. and *Kupeselasia* gen. n. *Lolosia* gen. n. differs from *Microselasia* gen. n. in having an incomplete frontal carina, wide fronto-clypeal region (Figs 21–22), more transverse pronotum (1.85 times wider than long in *Lolosia* gen. n.; 1.40–1.75 in *Microselasia* gen. n.; Figs 44, 62–70), and the V-shaped phallobase (Figs 109–118). *Kupeselasia*, which is superficially similar to *Microselasia* gen. n., differs in the strongly serrate antennae (flabellate in *Microselasia* gen. n.; Figs 37, 71–79), more slender mandibles (Figs 35, 53), sternite IX not emarginate basally (more or less emarginate in *Microselasia* gen. n.; Figs 42, 60–61), and distinctly elongate parameres (Fig. 108).

Description

Male. Body slender, 2.35–3.60 mm long, 2.65–3.15 times longer than width at humeri, dorsally weakly convex; moderately sclerotized, with cuticle of elytra and abdomen soft. Body light brown to dark brown, legs and mouthparts usually lighter; surface covered with yellow to light brown pubescence (Figs 4–12).

Head including eyes slightly narrower than width of pronotum in most species, only in *M. macrocephala* sp. n. and *M. obscura* sp. n. slightly wider, and in *M. gracilis* sp. n. of about the same width (Figs 62–70); surface smooth, shallowly depressed medially, very sparsely punctate, covered with sparse, long, semi-erect pubescence; frons slightly produced and narrowed apically, slightly surpassing fronto-clypeal region; antennal sockets rather narrowly separated, supra-antennal carinae meet medially, forming distinct, sinuate frontal carina (less distinct in *M. grandis* sp. n. and *M. pseudograndis* sp. n.); fronto-clypeal region high, narrow, abruptly declined between antennal insertions, sloping to base of labrum, with more or less sharply defined longitudinal carina running from frontal carina, divergent anteriorly; its surface sparsely punctate, basally covered with sparse, semi-erect setae (Fig. 22). Eyes medium-sized to large, hemispherically prominent, their frontal distance 1.10–1.60 times eye diameter (Figs 62–70). Labrum sclerotized, transverse, sparsely punctate, with frontal margin more or less widely concave. Mandibles relatively long, falcate, bidentate, with apical oblique tooth and another tooth located in middle part of incisor; mandibles basally more robust, with long setae, apical part slender, bare, shiny (Fig. 53). Maxilla with small cardo, stipes plate-like, galea and lacinia fused, setose, partly membranous, maxillary palpi tetramerous, slender, palpomeres I short, wide, obliquely cut apically, palpomere II about two times as long as wide, obliquely cut basally, palpomere III short, slightly longer than wide, ultimate palpomere elongate, about 3 times as long as wide, fusiform, subacute apically (Fig. 54). Labium small, wide, plate-like, moderately well-sclerotized, medio-anteriorly slightly produced, subacute, basally deeply emarginate; labial palpi trimerous, tiny, palpomeres I–II short, about as long as wide, apical palpomere longer than wide, fusiform, subacute apically (Fig. 55). Antennae 11-segmeneted, flabellate; scapus robust, slightly widened apically, pedicel short, small; antennomere III serrate, long, more than 2.5 times longer than pedicel, either subequal in legth with antennomeres IV–X (in species with weakly flabellate antennomeres IV–X, i.e., *M. elongata* sp. n. and *M. kupensis* sp. n.) or 1.1–1.7 times longer than antennomere IV; antennomere IV 1.1–1.5 times longer than antennomere V, antennomere V 1.2–1.6 times longer than antennomere VI, antennomeres VI–X short, subequal in legth (in species with strongly flabellate antennomeres IV–X); branches of antennomeres IV–X either about 1.5–2.0 times longer than stems of respective antennomeres (in species with weakly flabellate antennae) or about 3–9 times longer than stems of respective antennomeres (in species with strongly flabellate antennae); antennomere XI simple, longest, about same length as branch of penultimate antennomere, about 1.5 times longer than stem of penultimate antennomere in *M. elongata* sp. n., about 3–7 times longer than penultimate antennomere in remaining species; all antennomeres covered with moderately dense pubescence (Figs 71–79).

Pronotum slightly convex, more or less transverse, widest at posterior angles in most species (at anterior two fifths in *M. gracilis* sp. n., *M. macrocephala* sp. n. and *M. obscura* sp. n.), 1.40–1.75 times wider than length at midline. Anterior margin almost straight, lateral margins from concave to convex, diverging posteriorly, posterior margin simple, widely convex. Anterior angles inconspicuous; posterior angles variable, from acute, produced postero-laterally to obtuse, rectangular, and rounded. Disc with narrow, transverse carina near anterior margin, and with or without distinct sublateral carinae; if present, sublateral carinae short, often inconspicuous, only in *M. pseudograndis* sp. n. almost reaching anterior margin (Figs 62–70). Lateral carina separating pronotum from hypomeron distinct, incomplete anteriorly; hypomeron smooth; prosternal suture very short. Surface of disc sparsely covered with shallow punctures, with sparse semi-erect pubescence. Prosternum transverse, produced forward, surpassing pronotum at lateral view, with two transverse carinae medially; prosternal lobe very short, with frontal margin almost straight, with row of long semi-erect setae; posterior margin produced medially to form narrow ridge, apically with short, sharply defined, subparallel-sided, subacute prosternal process (Fig. 52).

Scutellum flat, triangular, about as long as wide, posteriorly widely rounded (Fig. 56). Mesoventrite widely V-shaped, with frontal margin widely concave; mesoventral cavity shallow, with poorly defined walls. Mesocoxal cavity open to both mesepimeron and mesepisternum. Metaventrite large, subtrapezoidal, sparsely covered with shallow punctures. Elytra subparallel-sided, 0.65–0.75 times as long as body, 1.90–2.30 times as long as wide, with narrow, closed epipleura (Figs 4–12). Each elytron more or less basally wrinkled, with apices separately rounded, sparsely covered with shallow punctures, arranged irregularly in indistinct rows; covered with long, semi-erect pubescence, sparser basally, denser laterally and apically; elytral suture distinct, wide, depressed. Hind wing venation reduced, as in Fig. 58. Legs slender, slightly compressed, with sparse, long, semi-erect setae, coxae robust, trochanters slender, elongate, widened apically, obliquely attached to femora; tibia and tarsi relatively long; tarsi almost as long as tibia, tarsomeres I–II subequal in length, tarsomere III slightly shorter, tarsomere IV shortest, minute, extended ventrally, apical tarsomere long, slender (Fig. 57); claws simple, slender, slightly curved, each with long seta basally.

Abdomen soft, slender, ventrites with very sparse, shallow punctures, sparsely covered with semi-erect pubescence; tergite and sternite I reduced, sternite II formed only by two separate sclerites; penultimate ventrite slightly emarginate medially. Tergites IX and X weakly connected by membrane; tergite IX basally with two sublateral processes (Fig. 59). Sternite IX 1.7–2.0 times as long as wide, more or less deeply notched basally, rounded apically, with apex finely punctate and sparsely setose, especially at lateral portions (Figs 60–61); sternite X partly membranous, connected by membrane to sternite IX.

Male genitalia trilobate, 1.5–1.9 times as long as wide, with median lobe slender to stout, shorter to longer than phallobase, longer than parameres, moderately curved in lateral view, basally with two short to relatively long struts, dorsally with more or less robust, short or long subapical hook; parameres minute, short, variously shaped, more or less setose apically; phallobase robust, U-shaped, about as long as wide to 1.3 times longer than wide (Figs 110–118).

Females and immature stages unknown.

Distribution

All known species of *Microselasia* gen. n. are distributed in the Southwest and South Regions in Cameroon (Fig. 125).

Etymology

The generic name refers to the small size of the included species and their similarity to genus *Selasia* Laporte, 1836. Gender: feminine.

***Microselasia barombi* sp. n.**

(Figs 4, 61–62, 71, 110)

Type material

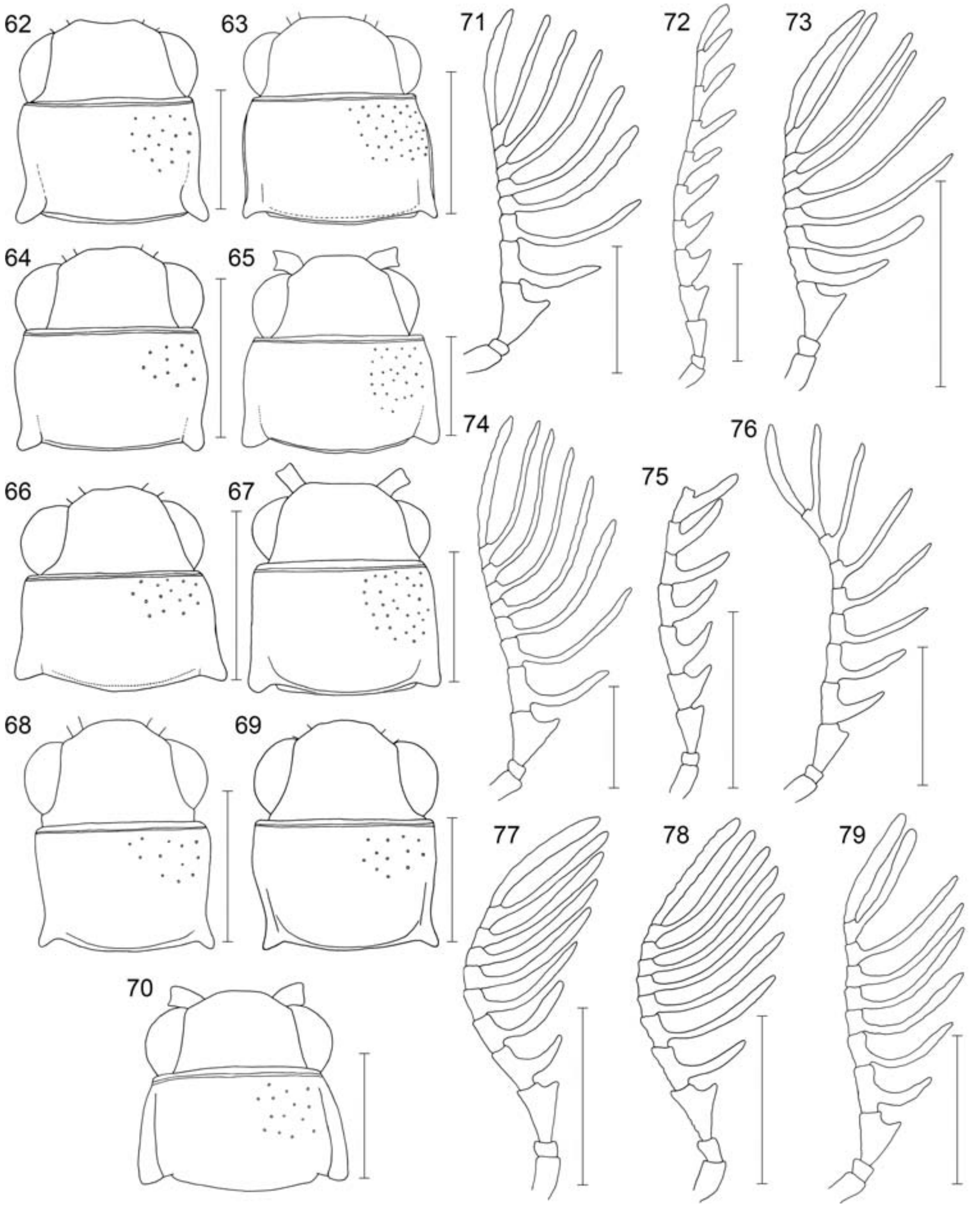
Holotype, male, "Cameroon, SW Prov., Kumba env., Barombi Mbo, 4°38.53' N 9°24.51' E, 280 m, 8. Mar 2008, Bolm lgt." (UPOL); paratypes, 2 males, "Cameroon, SW Prov., Nyassoso, Mt. Kupé, 900 m, N4°49.59' E9°40.54', 9.–11. Mar 2008, Bolm lgt." (UPOL).

Diagnosis

Microselasia barombi sp. n. is superficially similar to *M. gracilis* sp. n., *M. macrocephala* sp. n. and *M. obscura* sp. n. These species share strongly flabellate antennae (Figs 71, 73, 77–78) and the pronotum with distinctly sinuate lateral margins and posterior angles postero-laterally projected (Figs 62, 64, 68–69). It differs from all above mentioned species in the relatively smaller eyes (Edist/Ediam = 1.30–1.35), the head including eyes slightly narrower than pronotum, and the pronotum widest at posterior angles (Fig. 62).

Description

Body 2.65–2.80 times longer than width at humeri. Body light brown to brown (one paratype generally darker), head darker, mouthparts and legs yellowish to light brown; body covered with yellow pubescence (Fig. 4).



Figs 62–79. Body parts of *Microselasia* gen. n. Head and pronotum. (62) *M. barombi* sp. n.; (63) *M. elongata* sp. n.; (64) *M. gracilis* sp. n.; (65) *M. grandis* sp. n.; (66) *M. kupensis* sp. n.; (67) *M. lolodorfensis* sp. n.; (68) *M. macrocephala* sp. n.; (69) *M. obscura* sp. n.; (70) *M. pseudograndis* sp. n. Antenna. (71) *M. barombi* sp. n.; (72) *M. elongata* sp. n.; (73) *M. gracilis* sp. n.; (74) *M. grandis* sp. n.; (75) *M. kupensis* sp. n.; (76) *M. lolodorfensis* sp. n.; (77) *M. macrocephala* sp. n.; (78) *M. obscura* sp. n.; (79) *M. pseudograndis* sp. n. Scale bars = 0.5 mm.

Head including eyes 0.95 times as wide as pronotum. Eyes medium-sized, their frontal distance 1.30–1.35 times eye diameter (Fig. 62). Antennae flabellate; antennomere III strongly serrate, long, about 1.4 times longer than antennomere IV; antennomere IV 1.5 times longer than antennomere V, antennomere V 1.5 times longer than antennomere VI, antennomeres VI–X short, subequal in legth, branches of antennomeres VI–X about 8 times longer than stems of respective antennomeres; antennomere XI simple, longest, about same length as branch of penultimate antennomere, about 7 times longer than penultimate antennomere (Fig. 71).

Pronotum transverse, widest at posterior angles, 1.50–1.55 times wider than length at midline, with lateral margins sinuate, posterior angles slightly rounded, produced postero-laterally; disc with short sublateral carinae near posterior angles (Fig. 62). Elytra moderately long, 0.70 times as long as body, 1.90–2.00 times longer than wide.

Abdominal sternite IX 1.9 times as long as wide, moderately deeply notched basally (Fig. 61). Male genitalia 1.7 times as long as wide, with median lobe stout, shorter than phallobase, curved in lateral view, basally with two moderately long struts, dorsally with moderately long, robust subapical hook; parameres minute, short, almost rounded apically; phallobase robust, relatively long, 1.2 times longer than wide (Fig. 110).

Measurements

Holotype. BL 2.65 mm, WHum 1.00 mm, EL 1.90 mm, WHe 0.80 mm, PL 0.50 mm, PW 0.80 mm, Edist 0.45 mm, Ediam 0.35 mm. Paratypes. BL 3.30 mm, WHum 1.15 mm, EL 2.30 mm, WHe 0.80–0.90 mm, PL 0.60 mm, PW 0.90 mm, Edist 0.47–0.50 mm, Ediam 0.36 mm.

Distribution

Cameroon: Southwest Region. Two localities from where the species has been recorded are only about 35 km far from each other (Fig. 125).

Etymology

The specific epithet refers to Barombi Mbo where the holotype was collected.

***Microselasia elongata* sp. n.**

(Figs 5, 63, 72, 111)

Type material

Holotype, male, "Cameroon, SW Prov., Nyassoso, Mt. Kupé, 900 m, 4°49.59' N 9°40.54' E, 9.–11. Mar 2008, Bolm lgt." (UPOL).

Diagnosis

This species shares the weakly flabellate antennae with *M. kupensis* sp. n. (Figs 72, 75), but differs in the relatively smaller eyes (Edist/Ediam 1.40; in *M. kupensis* sp. n. 1.10), less transverse pronotum (1.45 times wider than long; in *M. kupensis* sp. n. 1.75 times wider than long; Figs 63, 66), relatively longer male genitalia including phallobase, and more slender median lobe (Figs 111, 114).

Description

Body 2.95 times longer than width at humeri. Body brown to dark brown, mouthparts, antennomeres I–II and legs lighter; body covered with yellow pubescence (Fig. 5).

Head including eyes 0.95 times as wide as pronotum. Eyes medium-sized, their frontal distance 1.40 times eye diameter (Fig. 63). Antennae flabellate, antennomere III long, slightly serrate, subequal in length with antennomeres IV–X, antennomeres IV–X shortly flabellate, with branches as long as or slightly longer than respective stems, antennomere XI simple, longest, about 1.5 times longer than penultimate antennomere (Fig. 72).

Pronotum transverse, widest at posterior angles, 1.45 times wider than length at midline, with lateral margins slightly sinuate, posterior angles acute; disc with short, inconspicuous sublateral carinae near posterior angles (Fig. 63). Elytra moderately long, 0.65 times as long as body, 1.95 times longer than wide.

Abdominal sternite IX 1.8 times as long as wide, moderately deeply notched basally. Male genitalia 1.8 times as long as wide, with median lobe slender, shorter than phallobase, curved in lateral view, basally with two short struts, dorsally with short subapical hook; parameres short, subacute apically; phallobase robust, relatively long, 1.3 times longer than wide (Fig. 111).

Measurements

BL 3.10 mm, WHum 1.05 mm, EL 2.05 mm, WHe 0.65 mm, PL 0.45 mm, PW 0.70 mm, Edist 0.39 mm, Ediam 0.28 mm.

Distribution

Cameroon: Southwest Region (Fig. 125).

Etymology

The species name “elongata” is derived from the Latin word “elongatus” and refers to its long phallobase (Fig. 111).

***Microselasia gracilis* sp. n.**

(Figs 6, 64, 73, 112)

Type material

Holotype, male, “Cameroon, Southwest Prov., 2 km N Bakingili, 200 m, 28.–30. July 1984, J. Rawlins, J. DiGiulio, Holotypus [red printed label], *Selasia gracilis* Wittm. [handwritten], det. W. Wittmer” (CMNH).

Diagnosis

Microselasia gracilis sp. n. shares relatively large eyes, strongly flabellate antennae and pronotum widest at anterior half with *M. macrocephala* sp. n. and *M. obscura* sp. n. (Figs 64, 68–69, 73, 77–78). *Microselasia gracilis* sp. n. differs from the above mentioned species in having more transverse pronotum (1.65 times wider than long; versus 1.40–1.45; Figs 64, 68–69), antennomere III about 1.7 times longer than antennomere IV (versus 1.2–1.3), and phallobase about as long as wide (versus longer than wide; Figs 112, 116–117).

Description

Body 2.95 times longer than width at humeri. Body brown, palpi and legs yellowish to light brown; body covered with yellow pubescence (Fig. 6).

Head including eyes as wide as pronotum. Eyes large, their frontal distance 1.10 times eye diameter (Fig. 64). Antennae flabellate; antennomere III strongly serrate, long, about 1.7 times longer than antennomere IV; antennomere IV 1.5 times longer than antennomere V, antennomere V 1.2 times longer than antennomere VI, antennomeres VI–X short, subequal in legth, branches of antennomeres VI–X about 9 times longer than stems of respective antennomeres; antennomere XI simple, longest, about 7 times longer than penultimate antennomere (Fig. 73).

Pronotum transverse, widest at anterior two fifths, 1.65 times wider than length at midline, with lateral margins convex, posterior angles short, produced postero-laterally; disc without distinct sublateral carinae (Fig. 64). Elytra moderately long, 0.70 times as long as body, 2.05 times longer than wide.

Abdominal sternite IX 1.8 times as long as wide, moderately deeply notched basally. Male genitalia 1.6 times as long as wide, with median lobe short, stout, slightly shorter than phallobase, curved in lateral view, basally with two short struts, dorsally with short subapical hook; parameres short, subacute apically; phallobase robust, about as long as wide (Fig. 112).

Measurements

BL 2.30 mm, WHum 0.80 mm, EL 1.60 mm, WHe 0.65 mm, PL 0.40 mm, PW 0.65 mm, Edist 0.30 mm, Ediam 0.28 mm.

Distribution

Cameroon: Southwest Region (Fig. 125).

Etymology

There is a label "*Selasia gracilis* Wittm., det. W. Wittmer" pinned under the beetle, and because this name have not been formally published by W. Wittmer, we decided to use a species name *gracilis* for this species, following the Wittmer's label. The name "gracilis" is a Latin adjective meaning slender or gracile.

Microselasia grandis sp. n.

(Figs 7, 65, 74, 113)

Type material

Holotype, male, "Cameroon, SW Prov., Nyassoso, Mt. Kupé, 900 m, 4°49.59' N 9°40.54' E, 9.–11. Mar 2008, Bolm lgt." (UPOL).

Diagnosis

This species shares the strongly flabellate antennae, rather transverse pronotum (1.62–1.64 times wider than long), and the shape of male genitalia with *M. pseudograndis* sp. n. (Figs 65, 70, 74, 79, 113, 118). However, *M. grandis* sp. n. has larger body (3.60 mm; 2.95 mm in *M. pseudograndis* sp. n.), relatively smaller eyes, missing long sublateral carina on pronotum (Figs 65, 70), and the relatively longer phallobase and shorter median lobe (Figs 113, 118).

Description

Body 3.15 times longer than width at humeri. Body dark brown, mouthparts, antennomeres I–II and legs light brown; body covered with light brown pubescence (Fig. 7).

Head including eyes 0.85 times as wide as pronotum, with moderately sharply defined frontal carina. Eyes medium-sized, their frontal distance 1.30 times eye diameter (Fig. 65). Antennae flabellate; antennomere III strongly serrate, long, about 1.2 times longer than antennomere IV; antennomere IV 1.5 times longer than antennomere V, antennomere V 1.3 times longer than antennomere VI, antennomeres VI–X short, subequal in legth, branches of antennomeres VI–X about 8 times longer than stems of respective antennomeres; antennomere XI simple, longest, about 7 times longer than penultimate antennomere (Fig. 74).

Pronotum transverse, widest at posterior angles, 1.60 times wider than length at midline, with lateral margins slightly sinuate, posterior angles subrectangular, rounded; disc with indistinct, short sublateral carinae (Fig. 65). Elytra relatively long, 0.75 times as long as body, 2.30 times longer than wide.

Abdominal sternite IX 1.9 times as long as wide, moderately deeply notched basally. Male genitalia 1.7 times as long as wide, with median lobe elongate, about as long as phallobase, slightly constricted subapically, curved in lateral view, basally with two short struts, dorsally with short subapical hook; parameres short, subacute apically; phallobase robust, relatively long, 1.2 times longer than wide (Fig. 113).

Measurements

BL 3.60 mm, WHum 1.15 mm, EL 2.65 mm, WHe 0.80 mm, PL 0.60 mm, PW 0.95 mm, Edist 0.45 mm, Ediam 0.34 mm.

Distribution

Cameroon: Southwest Region (Fig. 125).

Etymology

The specific epithet refers to the relatively large body of this species.

***Microselasia kupensis* sp. n.**

(Figs 8, 66, 75, 114)

Type material

Holotype, male, "Cameroon, SW Prov., Nyassoso, Mt. Kupé, 900 m, 4°49.59' N 9°40.54' E, 9.–11. Mar 2008, Bolm lgt." (UPOL).

Diagnosis

Microselasia kupensis sp. n. and *M. elongata* sp. n. are the only two known species of *Microselasia* gen. n. which have the weakly flabellate antennae with branches less than twice as long as their stems (Figs 72, 75). They differ in the relative eye size (Edist/Ediam 1.10 in *M. kupensis* sp. n., 1.40 in *M. elongata* sp. n.), the shape of pronotum (1.75 times wider than long in *M. kupensis* sp. n., 1.45 in *M. elongata* sp. n.; Figs 63, 66), and male genitalia (1.5 times longer than wide, phallobase about as long as wide, and median lobe robust in *M. kupensis* sp. n.; 1.8 times longer than wide, phallobase 1.3 times longer than wide, and median lobe slender in *M. elongata* sp. n.; Figs 111, 114).

Description

Body 3.00 times longer than width at humeri. Body brown to dark brown, mouthparts, antennomeres I–II, scutellum and legs lighter; body covered with yellow pubescence (Fig. 8).

Head including eyes 0.85 times as wide as pronotum. Eyes large, their frontal distance 1.09 times eye diameter (Fig. 66). Antennae flabellate, antennomere III long, slightly serrate, subequal in length with antennomeres IV–IX; antennomeres IV–IX shortly flabellate, with branches from about as long as to 1.5 times longer than respective stems (antennomeres X–XI missing; Fig. 75).

Pronotum transverse, widest at posterior angles, 1.75 times wider than length at midline, with lateral margins slightly sinuate, diverged posteriorly, posterior angles subacute, rounded, slightly produced postero-laterally; disc without distinct sublateral carinae (Fig. 66). Elytra relatively long, 0.75 times as long as body 2.30 times longer than wide.

Abdominal sternite IX 1.9 times as long as wide, moderately deeply notched basally. Male genitalia 1.5 times as long as wide, with median lobe stout, slightly shorter than phallobase, curved in lateral view, basally with two moderately long struts, dorsally with short robust subapical hook; parameres short, subacute apically; phallobase robust, about as long as wide (Fig. 114).

Measurements

BL 2.45 mm, WHum 0.80 mm, EL 1.85 mm, WHe 0.55 mm, PL 0.35 mm, PW 0.65 mm, Edist 0.27 mm, Ediam 0.25 mm.

Distribution

Cameroon: Southwest Region (Fig. 125).

Etymology

The specific epithet refers to the type locality of this species, i.e., Mt. Kupé.

***Microselasia lolodorfensis* sp. n.**

(Figs 9, 67, 76, 115)

Type material

Holotype, male, "Cameroon, South Prov., Lolodorf, 550 m, 3°14.06' N 10°43.52', 31 E. Mar 2008, Bolm lgt." (UPOL); paratype, male, the same data as for the holotype; paratype, male, "Cameroon, South Prov., Lolodorf, 550 m, N3°14.06' E10°43.52', 1.–5. Mar 2008, Bolm lgt." (UPOL).

Diagnosis

Microselasia lolodorfensis sp. n. is characteristic by the relatively small eyes (Edist/Ediam 1.50–1.60), all antennomeres with branches less than 4 times as long as their respective stems, antennomere XI more than 3 times longer than penultimate antennomere (Fig. 76), male genitalia elongate, 1.8 times longer than wide, and median lobe with very long subapical hook (Fig. 115).

Description

Body 2.85–3.00 times longer than width at humeri. Body brown to dark brown, elytra, and antennomeres I–II lighter, mouthparts and legs yellowish to light brown; body covered with yellow pubescence (Fig. 9).

Head including eyes 0.90–0.95 times as wide as pronotum. Eyes medium-sized, their frontal distance 1.50–1.60 times eye diameter (Fig. 67). Antennae flabellate; antennomere III serrate, only slightly longer than antennomere IV; antennomere IV almost as long as antennomere V, antennomere V 1.3 times longer than antennomere VI, antennomeres VI–X short, subequal in legth, branches of antennomeres VI–X 3–4 times longer than stems of respective antennomeres; antennomere XI simple, longest, more than 3 times longer than penultimate antennomere (Fig. 76).

Pronotum transverse, widest at posterior angles, 1.40–1.45 times wider than length at midline, with lateral margins almost straight, slightly diverged posteriorly, posterior angles rounded; disc without sublateral carinae (Fig. 67). Elytra moderately long, 0.70–0.75 times as long as body, 2.00–2.15 times longer than wide.

Abdominal sternite IX 2.0 times as long as wide, moderately deeply notched basally. Male genitalia 1.8 times as long as wide, with median lobe elongate, slender, longer than phallobase, curved in lateral view, basally with two moderately long struts, dorsally with long, distinct subapical hook; parameres short, subacute apically; phallobase robust, slightly longer than wide (Fig. 115).

Measurements

Holotype. BL 2.75 mm, WHum 0.95 mm, EL 2.05 mm, WHe 0.70 mm, PL 0.55 mm, PW 0.80 mm, Edist 0.44 mm, Ediam 0.28 mm. Paratypes. BL 2.60–2.75 mm, WHum 0.85–0.95 mm, EL 1.80–1.90 mm, WHe 0.65–0.70 mm, PL 0.45–0.50 mm, PW 0.65–0.75 mm, Edist 0.39 mm, Ediam 0.25 mm.

Distribution

Cameroon: South Region (Fig. 125).

Etymology

The specific epithet refers to the type locality of this species, i.e., Lolodorf.

***Microselasia macrocephala* sp. n.**

(Figs 10, 68, 77, 116)

Type material

Holotype, male, "Cameroon, SW Prov., Nyassoso, Mt. Kupé, 900 m, 4°49.59' N 9°40.54' E, 9.–11. Mar 2008, Bolm lgt." (UPOL); paratype, male, the same data as for the holotype (UPOL).

Diagnosis

Microselasia macrocephala sp. n. is superficially similar to *M. gracilis* sp. n. and *M. obscura* sp. n. due to the large eyes, strongly flabellate antennae, and the pronotum widest at anterior half (Figs 64, 68–69, 73, 77–78). *Microselasia gracilis* sp. n. has more transverse pronotum (1.65 times wider than long; 1.40–1.45 in *M. macrocephala* sp. n.; Figs 64, 68), antennomere III about 1.7 times longer than antennomere IV (1.2 in *M. macrocephala* sp. n.; Figs 73, 77), and phallobase about as long as wide (1.3 times longer than wide in *M. macrocephala* sp. n.; Figs 112, 116). *Microselasia obscura* sp. n. is larger (3.10–3.50 mm long; 2.35–2.75 mm in *M. macrocephala* sp. n.), has branches of antennomeres VI–X about 8 times longer than their respective stems (6 times in *M. macrocephala* sp. n.; Figs 77–78), smaller, apically almost rounded parameres (larger, subacute apically in *M. macrocephala* sp. n.), and subapical hook on median lobe robust, widened (slender, short hook in *M. macrocephala* sp. n.; Figs 116–117).

Description

Body 2.75 times longer than width at humeri. Body brown to dark brown, antennomeres I–II slightly lighter, legs yellowish to light brown; body covered with yellow pubescence (Fig. 10).

Head including eyes as wide as pronotum. Eyes large, their frontal distance 1.15 times eye diameter (Fig. 68). Antennae flabellate; antennomere III strongly serrate, long, about 1.2 times longer than antennomere IV; antennomere IV 1.3 times longer than antennomere V, antennomere V 1.3 times longer than antennomere VI, antennomere VI 1.3 times longer than antennomere VII, antennomeres VII–X short, subequal in legth, branches of antennomeres VI–X about 6 times longer than stems of respective antennomeres; antennomere XI simple, longest, about 6 times longer than penultimate antennomere (Fig. 77).

Pronotum transverse, widest just behind anterior margin, 1.40–1.45 times wider than length at midline, with lateral margins sinuate, posterior angles slightly rounded, produced postero-laterally; disc without sublateral carinae (Fig. 68). Elytra moderately long, 0.70 times as long as body, 1.90 times longer than wide.

Abdominal sternite IX 1.9 times as long as wide, moderately deeply notched basally. Male genitalia 1.8 times as long as wide, with median lobe robust, slightly shorter than phallobase, curved in lateral view, basally with two long struts, dorsally with short subapical hook; parameres short, subacute apically; phallobase robust, relatively long, 1.3 times longer than wide (Fig. 116).

Measurements

Holotype. BL 2.75 mm, WHum 1.00 mm, EL 1.90 mm, WHe 0.70 mm, PL 0.50 mm, PW 0.70 mm, Edist 0.34 mm, Ediam 0.30 mm. Paratype. BL 2.35 mm, WHum 0.85 mm, EL 1.60 mm, WHe 0.65 mm, PL 0.45 mm, PW 0.65 mm, Edist 0.32 mm, Ediam 0.28 mm.

Distribution

Cameroon: Southwest Region (Fig. 125).

Etymology

The name "macrocephala" comes from the Latin expression for the "large head".

***Microselasia obscura* sp. n.**

(Figs 11, 22, 52–60, 69, 78, 117)

Type material

Holotype, male, "Cameroon, SW Prov., Nyassoso, Mt. Kupé, 900 m, 4°49.59' N 9°40.54' E, 9.–11. Mar 2008, Bolm lgt." (UPOL); 3 paratypes, males, same data as for the holotype (UPOL).

Diagnosis

Microselasia obscura sp. n. is very similar to *M. macrocephala* sp. n. Both species share large head and eyes, strongly flabellate antennae and the shape of pronotum (Figs 68–69, 77–78), but they differ in the body length (3.10–3.50 mm for *M. obscura* sp. n.; 2.34–2.74 mm for *M. macrocephala* sp. n.), relative length of antennal branches (longer in *M. obscura* sp. n.; Figs 77–78), and the shape of male genitalia (parameres smaller, apically almost rounded, median lobe more robust, widened apically, with subapical hook robust in *M. obscura* sp. n.; parameres larger, subacute apically, median lobe more slender, with subapical hook short in *M. macrocephala* sp. n.; Figs 116–117).

Description

Body 2.90–2.95 times longer than width at humeri. Body dark brown, head darker, antennomeres I–II and scutellum light brown, mouthparts and legs yellowish to light brown; body covered with yellow pubescence (Fig. 11).

Head including eyes as wide as pronotum. Eyes large, their frontal distance 1.15 times eye diameter (Figs 22, 69). Antennae flabellate; antennomere III strongly serrate, long, 1.2–1.4 times longer than antennomere IV; antennomere IV 1.4 times longer than antennomere V, antennomere V 1.7 times longer than antennomere VI, antennomeres VI–X short, subequal in legth, branches of antennomeres VI–X about 8 times longer than stems of respective antennomeres; antennomere XI simple, longest, about 7 times longer than penultimate antennomere (Fig. 78).

Pronotum transverse, widest at anterior two fifths, 1.40 times wider than length at midline, with lateral margins sinuate, posterior angles slightly rounded, produced postero-laterally; disc without sublateral carinae (Fig. 69). Elytra moderately long, 0.65–0.70 times as long as body, 1.95–2.00 times longer than wide.

Abdominal sternite IX 1.9 times as long as wide, very slightly notched basally. Male genitalia 1.9 times as long as wide, with median lobe robust, about as long as phallobase, widened apically, curved in lateral view, basally with two moderately long struts, dorsally with distinct, robust subapical hook; parameres minute, short, apically almost rounded; phallobase robust, relatively long, 1.2 longer than wide (Fig. 117).

Intraspecific variability

One paratype has lighter disc of pronotum and dark brown to black elytra. There are slight differences in the lengths of branch of antennomere III among the studied specimens.

Measurements

Holotype. BL 3.10 mm, WHum 1.05 mm, EL 2.10 mm, WHe 0.75 mm, PL 0.55 mm, PW 0.75 mm, Edist 0.39 mm, Ediam 0.33 mm. Paratypes. BL 3.10–3.50 mm, WHum 1.05–1.20 mm, EL 2.10–2.35 mm, WHe 0.75–0.95 mm, PL 0.55–0.65 mm, PW 0.75–0.95 mm, Edist 0.38–0.47 mm, Ediam 0.33–0.41 mm.

Distribution

Cameroon: Southwest Region (Fig. 125).

Etymology

The specific epithet means “dark” in Latin and refers to the body coloration of this species.

Microselasia pseudograndis **sp. n.**

(Figs 12, 70, 79, 118)

Type material

Holotype, male, “Cameroon, South Prov., Lolodorf, 550 m, N3°14.06' E10°43.52', 31. Mar 2008, Bolm lgt.” (UPOL).

Diagnosis

Microselasia pseudograndis sp. n. is similar to *M. grandis* sp. n. in having the strongly flabellate antennae, pronotum 1.60–1.65 times wider than long, and the median lobe of male genitalia slightly constricted subapically, with typically very short subapical hook (Figs 65, 70, 74, 79, 113, 118). These species differ in the body size (body 2.95 mm long in *M. pseudograndis* sp. n.; 3.60 mm in *M. grandis* sp. n.), relative size of eyes (Edist/Ediam 1.20 in *M. pseudograndis* sp. n.; 1.30 in *M. grandis* sp. n.), sublateral carina on pronotum (distinct, almost reaching anterior margin in *M. pseudograndis* sp. n.; short, indistinct in *M. grandis* sp. n.; Figs 65, 70), and the shape of male genitalia (phallobase relatively shorter and median lobe longer in *M. pseudograndis* sp. n.; Figs 113, 118).

Description

Body 2.95 times longer than width at humeri. Body brown, mouthparts, antennomeres I–II and legs lighter; body covered with yellowish pubescence (Fig. 12).

Head including eyes 0.90 times as wide as pronotum; frontal carina moderately sharply defined. Eyes relatively large, their frontal distance 1.20 times eye diameter (Fig. 70). Antennae flabellate; antennomere III strongly serrate, long, about 1.1 times longer than antennomere IV; antennomere IV 1.4 times longer than antennomere V, antennomere V 1.4 times longer than antennomere VI, antennomeres VI–X short, subequal in legth, branches of antennomeres VI–X about 5 times longer than stems of respective antennomeres; antennomere XI simple, longest, about 5 times longer than penultimate antennomere (Fig. 79).

Pronotum transverse, widest at posterior angles, 1.65 times wider than length at midline, with lateral margins convex, posterior angles subrectangular, widely rounded; disc with distinct sublateral carinae almost reaching anterior margin (Fig. 70). Elytra relatively long, 0.75 times as long as body, 2.25 times longer than wide.

Abdominal sternite IX 1.7 times as long as wide, moderately deeply notched basally. Male genitalia 1.7 times as long as wide, with median lobe elongate, longer than phallobase, slightly constricted subapically, curved in lateral view, basally with two short struts, dorsally with short subapical hook; parameres short, subacute apically; phallobase robust, slightly longer than wide (Fig. 118).

Measurements

BL 2.95 mm, WHum 0.95 mm, EL 2.15 mm, WHe 0.75 mm, PL 0.50 mm, PW 0.80 mm, Edist 0.41 mm, Ediam 0.34 mm.

Distribution

Cameroon: South Region (Fig. 125).

Etymology

The specific epithet refers to the morphological similarity of this species to *M. grandis* sp. n.

Genus *Wittmerselasia* gen. n.

Type species

Wittmerselasia camerooniana sp. n.

Diagnosis

This genus can be recognized by using the following combination of characters: body moderately large, 3.15–6.60 mm long, fronto-clypeal region high, narrow, abruptly declined between antennal insertions, with characteristic two rows of long setae laterally (Figs 23–24), terminal maxillary palpomere hatchet-like (Figs 82, 90), eyes large, their frontal distance 1.00–1.15 times eye diameter, antennae strongly flabellate (Figs 101–106), pronotum subrectangular, very sparsely punctured, its posterior margin with a distinct angular emargination (Figs 95–100), prosternal process long, slender (Fig. 80), scutellum triangular, slightly longer than wide (Fig. 85), abdominal sternite IX about 1.4–1.7 times as long as wide, rounded apically (Fig. 88), and male genitalia robust, with basal struts of median lobe relatively short, and parameres distinctly setose (Figs 119–124).

The genus *Selasia* differs from *Wittmerselasia* gen. n. in having much wider fronto-clypeal region, gradually declined to the base of labrum, and male genitalia with differently shaped parameres and longer basal struts of median lobe, *Flabelloselasia* gen. n. in much longer antennal branches (Fig. 28), pronotum with distinct sublateral carinae almost reaching frontal margin (never reaching first half of pronotum in *Wittmerselasia* gen. n.; Figs 25, 95–100), and male genitalia with V-shaped phallobase and subrectangular parameres (Fig. 107), and *Lolosia* gen. n., *Kupeselasia* gen. n. and *Microselasia* gen. n. in having apically narrowed and subacute ultimate maxillary and labial palpomeres (Figs 36, 46, 54).

Distribution

All known species of this genus occur in the Southwest, Centre and South Regions in Cameroon (Fig. 125).

Etymology

The generic name is dedicated to late W. Wittmer (Basel, Switzerland) and refers to the similarity of this genus to *Selasia* Laporte, 1836. Gender: feminine.

Subgenus *Wittmerselasia* subgen. n.

Type species

Wittmerselasia camerooniana sp. n.

Diagnosis

The genus *Wittmerselasia* gen. n. contains two subgenera, the nominotypical *Wittmerselasia* subgen. n. and *Latoselasia* subgen. n. (Figs 13–18). They differ in the shape of labrum (larger and only partly sclerotized in *Wittmerselasia* subgen. n.; sclerotized, subpentagonal, widely rounded apically in *Latoselasia* subgen. n.; Figs 23–24), the length and shape of apical maxillary palpomere (longer, constricted subapically in *Wittmerselasia* subgen. n.; shorter and wider in *Latoselasia* subgen. n.; Figs 82, 90), and the shape of male genitalia (phallobase never longer than wide, median lobe longer than phallobase, parameres larger, more pointed apically in *Wittmerselasia* subgen. n.; phallobase slightly longer than wide, median lobe shorter than phallobase, parameres smaller, rounded apically in *Latoselasia* subgen. n.; Figs 119–124).

Description

Male. Body 3.15–6.60 mm long, 2.50–2.80 times longer than width at humeri. Body yellowish to dark brown, antennal branches often darker, elytra either uniformly colored or with basal parts lighter or with apical and partly lateral portions darker, dark brown to black, legs lighter, body surface covered with yellowish to light brown pubescence (Figs 13–17).

Head including eyes 0.75–0.95 times as wide as pronotum; surface smooth, very shallowly depressed medially, sparsely punctate, covered with sparse, long, semi-erect pubescence; antennal sockets moderately widely separated, frons narrowed apically, slightly surpassing fronto-clypeal region; fronto-clypeal region high, narrow, partly membranous, abruptly declined between antennal insertions, sloping toward base of labrum; its surface smooth medially, rough laterally, basally with two lateral rows of punctures with long erected setae (Fig. 23). Eyes large, prominent, their frontal distance 1.05–1.15 times eye diameter (Figs 95–100). Labrum transverse, basally sclerotized, with transverse row of long setae, apically partly membranous. Mandibles robust, moderately long, falcate, bidentate, with long apical oblique tooth and another, robust tooth located in middle part of incisor; mandibles basally setose, apical part bare, shiny (Fig. 81). Maxillary palpi tetramerous, slender, palpomere I short, palpomere II elogate, about twice longer than wide, slightly more than twice longer than palpomere III, palpomere III short, about as long as wide, palpomere IV more than 3 times longer than palpomere III, about 2.5 times as long as wide, hatchet-like, slightly constricted subapically, flattened, widened and slightly rounded apically (Fig. 82). Labium short, wide, partly membranous; labial palpi trimerous, tiny, palpomeres I–II short, wide, apical palpomere elongate, fusiform, subacute apically (Fig. 83). Antennae 11-segmeneted, flabellate; scapus robust, slightly widened apically, pedicel short, small; antennomere III long, 2.5–3.3 times longer than following antennomeres, its branch from about the same legth as stem to more than twice longer than stem; antennomeres IV–X short, subequal in length, with branches distinctly flattened, branch of antennomere IV slightly shorter than branches of antennomeres V–X, which are about 8–12 times longer than their stems; antennomere XI simple, longest, of about same length as branches of preceding antennomeres; all antennomeres with surface uneven, rough, sparsely covered with long setae, arising from the edges of branches (Figs 101–106).

Pronotum slightly convex, transverse, widest at half or posterior angles, 1.60–1.80 times wider than length at midline. Anterior margin more or less straight; lateral margins almost straight to convex (slightly converged posteriorly in *W. variabilis* sp. n.), bent upwards; posterior margin with wide angular emargination medially. Anterior angles inconspicuous; posterior angles short, widely rounded. Disc smooth, without or with short sublateral carinae near posterior angles, never reaching first half of pronotum (Figs 95–100). Lateral carina separating pronotum from hypomeron distinct, almost reaching pronotal frontal margin. Surface of disc very sparsely covered with shallow punctures, with sparse semi-erect, long pubescence, both punctures and setae equally distributed. Hypomeron smooth, with indistinct sublateral carina, slightly wrinkled near edges; prosternal suture very short. Prosternum transverse, prosternal lobe short, with frontal margin widely rounded, with long semi-erect setae; prosternal process moderately long, slender, subparallel-sided, subacute apically (Fig. 80). Scutellum flat, triangular, slightly longer than wide, subacute apically, sparsely covered with shallow punctures and semi-erect setae (Fig. 85). Mesoventrite widely V-shaped, with frontal margin widely emarginate, posterior margin produced medially to form narrow, shallow mesoventral cavity. Mesocoxal cavity open to both mesepimeron and mesepisternum. Metaventrite large, subtrapezoidal, smooth, very sparsely covered with shallow punctures. Elytra subparallel-sided to ovoid, combined 0.65–0.70 times as long as body; basally wrinkled (Figs 13–17). Each elytron with apex separately rounded, sparsely punctate, covered with long, semi-erect pubescence; elytral suture distinct, wide, depressed. Hind wing venation as in Fig. 86. Legs slightly compressed, with surface rough, covered with sparse, long, semi-erect pubescence; coxae robust, trochanters slender, elongate, widened apically, obliquely attached to femora; tarsomeres I–II subequal in length, tarsomere III slightly shorter, tarsomere IV shortest, minute, extended ventrally, apical tarsomere elongate, slender, about 3 times longer than tarsomere IV (Fig. 84); claws simple, slender, slightly curved; each claw basally with long seta.

Abdomen soft, slender, ventrites with very sparse, shallow punctures, sparsely covered with semi-erect pubescence, denser laterally. Tergites I–II reduced; tergites IX and

X connected by membrane; tergite IX more than 0.5 times as long as wide, basally with two sublateral processes; tergite X longer than wide, rounded apically (Fig. 87). Sternite IX 1.4–1.7 times as long as wide, deeply emarginate basally, apex rounded, punctate, with sparse short setae (Fig. 88); sternite X connected by membrane to sternite IX, partly membranous.

Male genitalia trilobate, 1.7–1.8 times as long as wide; median lobe strong, slightly longer than phallobase, moderately curved in lateral view, basally with two short, robust struts, dorsally with short to long subapical hook; parameres robust, subacute or slightly rounded apically, covered with moderately long setae, mainly on inner margin and apical portion; phallobase robust, about as wide as long or slightly wider than long, U-shaped (Figs 119–123).

Females and immature stages unknown.

***Wittmerselasia camerooniana* sp. n.**

(Figs 13, 80–88, 95, 101, 119)

Type material

Holotype, male, "Cameroon, South Prov., Lolodorf, 550 m, 3°14.06' N 10°43.52' E, 31. Mar 2008, Bolm lgt." (UPOL); 2 paratypes, males, "Cameroon, South Prov., Lolodorf, 550 m, 3°14.06' N 10°43.52' E, 1.–5. Mar 2008, Bolm lgt." (UPOL); paratype, male, "Cameroun, Batanga, Museum Paris, Collection Léon Fairmaire, 1906" (MHNP).

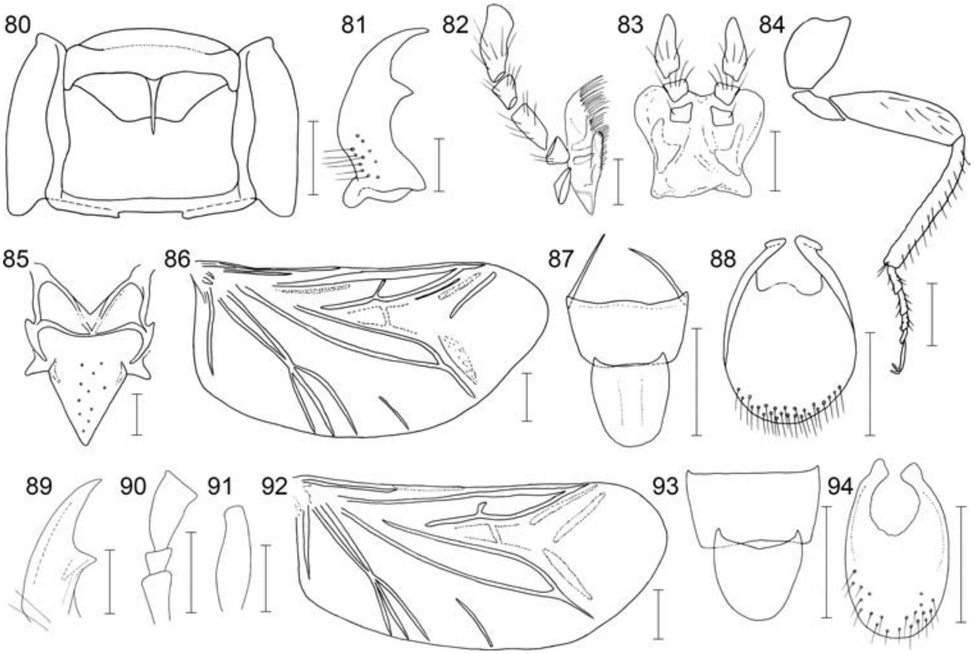
Diagnosis

Wittmerselasia camerooniana sp. n. is similar by the body size and light body coloration with yellowish to light brown pronotum to *W. davidsoni* sp. n. and *W. variabilis* sp. n., but it can be recognized by the relatively shorter branch of antennomere III, which is about as long as stem (almost or more than twice longer than respective stems in two other species; Figs 101–102, 105). Additionally, *Wittmerselasia variabilis* sp. n. differs in the more transverse pronotum with more distinctly produced posterior angles (Figs 95–96, 99), and in the shorter hook of median lobe (Figs 119–120, 123).

Description

Body 2.55–2.65 times longer than width at humeri. Body yellowish to light brown, antennal branches darker, apex and lateral portions of elytra dark brown to black; body covered with yellow pubescence (Fig. 13).

Head including eyes 0.75–0.85 times as wide as pronotum. Eyes large, their frontal distance 1.10 times eye diameter (Fig. 95). Antennae flabellate, with antennomere III about 2.5 times longer than following antennomeres, its branch about the same length as stem; antennomeres V–X with branches about 9 times longer than their stems (Fig. 101).



Figs 80–94. Body parts of *Wittmerselasia* gen. n. *Wittmerselasia camerooniana* sp. n. (80) prosternum; (81) mandible; (82) maxilla; (83) labium; (84) leg; (85) scutellum; (86) hind wing; (87) abdominal tergites IX–X; (88) abdominal sternite IX. *Wittmerselasia* (*Latoselasia*) *similis* sp. n.: (89) mandible; (90) last maxillary palpomeres; (91) terminal labial palpomere; (92) hind wing; (93) abdominal tergites IX–X; (94) abdominal sternite IX. Scale bars = 0.1 mm (Fig. 91), 0.2 mm (Figs 81–83, 85, 89–90), 0.5 mm (Figs 80, 84, 86–88, 92–94).

Pronotum transverse, widest at half, 1.65–1.75 times wider than length at midline, with lateral margins slightly convex, bent upwards; posterior margin with wide angular emargination medially; posterior angles short, widely rounded, produced backward; disc with short sublateral carinae near posterior angles (Fig. 95). Elytra 0.70 times as long as body, 1.70–1.85 times as long as wide at humeri.

Abdominal sternite IX 1.4 times as long as wide. Male genitalia with median lobe dorsally with robust, long subapical hook, parameres robust, subacute apically; phallobase about as wide as long (Fig. 119).

Measurements

Holotype. BL 4.40 mm, WHum 1.70 mm, EL 3.00 mm, WHe 1.15 mm, PL 0.80 mm, PW 1.35 mm, Edist 0.52 mm, Ediam 0.47 mm. Paratypes. BL 4.35–5.60 mm, WHum 1.70–2.20 mm, EL 3.10–3.80 mm, WHe 1.20–1.40 mm, PL 0.85–1.05 mm, PW 1.45–1.85 mm, Edist 0.53–0.72 mm, Ediam 0.48–0.66 mm.

Distribution

Cameroon: South Region (Fig. 125).

Etymology

The specific epithet refers to the geographic origin of this species.

***Wittmerselasia davidsoni* sp. n.**

(Figs 14, 96, 102, 120)

Type material

Holotype, male, "Cameroon: Southwest Prov., 25 km W Limbe, Bakingili, 1–10 July 1984, 10 m, J. Rawlins, R. Davidson" (CMNH); paratype, male, "Cameroon: Southwest Prov., 25 km W Limbe, Bakingili, intercept trap, 4 August 1984, James A. DiGiulio" (CMNH).

Diagnosis

This species shares the similar body size and lightly colored body with yellowish to light brown pronotum with *W. camerooniana* sp. n. and *W. variabilis* sp. n. (Figs 13–14, 17). *Wittmerselasia davidsoni* sp. n. differs from *W. camerooniana* sp. n. in the darker elytra (Figs 13–14) and relatively longer branch of antennomere III (Figs 101–102), and from *W. variabilis* sp. n. in the relatively less transverse pronotum with shorter and less produced posterior angles (Figs 96, 99), relatively shorter branch of antennomere III (Figs 102, 105), and the longer hook of median lobe (Figs 120, 123).

Description

Body 2.60–2.70 times longer than width at humeri. Body yellowish to light brown, antennal branches darker, elytra dark brown; body covered with yellowish to light brown pubescence (Fig. 14).

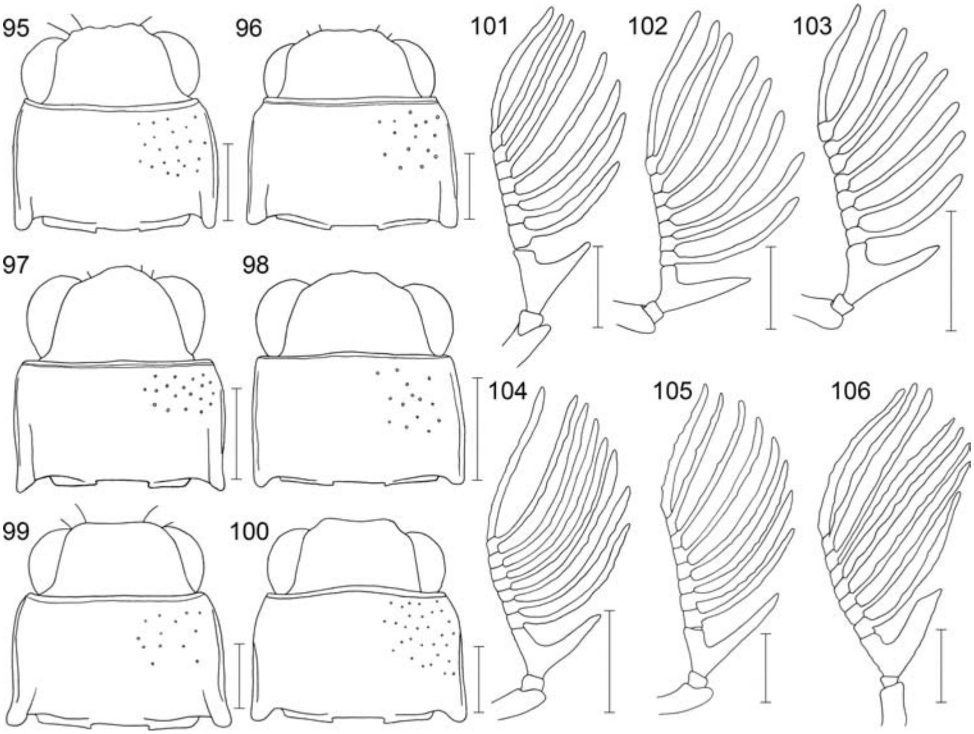
Head including eyes 0.80–0.85 times as wide as pronotum. Eyes large, their frontal distance 1.10–1.15 times eye diameter (Fig. 96). Antennae flabellate, with antennomere III about 3 times longer than following antennomeres, its branch about twice longer than stem; antennomeres V–X with branches about 9 times longer than their stems (Fig. 102).

Pronotum transverse, widest at half, 1.60–1.65 times wider than length at midline, with lateral margins almost straight, bent upwards; posterior margin with wide angular emargination medially; posterior angles short, widely rounded; disc with short sublateral carinae near posterior angles (Fig. 96). Elytra 0.70 times as long as body, 1.80–1.85 times longer than width at humeri.

Abdominal sternite IX 1.5 times as long as wide. Male genitalia with median lobe dorsally with robust, long subapical hook, parameres robust, subacute apically; phallobase slightly wider than long (Fig. 120).

Measurements

Holotype. BL 5.10 mm, WHum 2.00 mm, EL 3.55 mm, WHe 1.30 mm, PL 1.00 mm, PW 1.60 mm, Edist 0.64 mm, Ediam 0.56 mm. Paratype. BL 6.20 mm, WHum



Figs 95–106. Body parts of *Wittmerselasia* gen. n. Head and pronotum. (95) *W. camerooniana* sp. n.; (96) *W. davidsoni* sp. n.; (97) *W. geiseri* sp. n.; (98) *W. maculata* (Wittmer, 1989); (99) *W. variabilis* sp. n.; (100) *W.* (*Latoselasia*) *similis* sp. n. Antenna. (101) *W. camerooniana* sp. n.; (102) *W. davidsoni* sp. n.; (103) *W. geiseri* sp. n.; (104) *W. maculata* (Wittmer, 1989); (105) *W. variabilis* sp. n.; (106) *W.* (*Latoselasia*) *similis* sp. n. Scale bars = 0.5 mm.

2.30 mm, EL 4.30 mm, WHe 1.50 mm, PL 1.10 mm, PW 1.80 mm, Edist 0.66 mm, Ediam 0.61 mm.

Distribution

Cameroon: Southwest Region (Fig. 125).

Etymology

The specific epithet is a patronym in honor of R. Davidson (CMNH).

***Wittmerselasia geiseri* sp. n.**

(Figs 15, 97, 103, 121)

Type material

Holotype, male, "Cameroon: Mbalmayo F. Res., TIGER Survey, BM 1994–148, Ebogo, (?).vii.1993, FITrap 1, 722 [white/yellow], n. genus, det. M. A. Ivie, 2010"

(BMNH); 2 paratypes, males, with the same data as for the holotype (BMNH); paratype, male, “Cameroon: Mbalmayo F. Res., TIGER Survey, BM 1994–148, Eboufek, 28.vii.1993, FITrap 1, 721 [white/green]”, 351 [yellow]” (BMNH); paratype, male, “Cameroon, SW Prov., Fako Dist., Bakingili, 25 km W Limbe, VII. 21.–31. 1984, Coll. R. Davidson, *Selasia* spec., longer series needed [handwritten]” (CMNH).

Diagnosis

Wittmerselasia geiseri sp. n. shares the body size and dark body coloration with *W. maculata* (Wittmer, 1989) (Figs 15–16). They differ in the sublateral carina on the pronotum (distinct, reaching almost half of pronotum in *W. geiseri* sp. nov; absent in *W. maculata*; Figs 97–98), the relative lengths of branches of antennomeres IV–X (Figs 103–104), and in the shape of male genitalia (median lobe with short hook, parameres slightly rounded apically in *W. geiseri* sp. n.; median lobe with long hook, parameres subacute apically in *W. maculata*; Figs 121–122).

Description

Body 2.50–2.80 times longer than width at humeri. Body dark brown, in some cases elytra basally slightly lighter, antennomeres I–II lighter, mouthparts and legs yellowish to light brown; body covered with yellowish to light brown pubescence (Fig. 15).

Head including eyes 0.80–0. 90 times as wide as pronotum. Eyes large, their frontal distance 1.05–1.10 times eye diameter (Fig. 97). Antennae flabellate, with antennomere III more than 3 times longer than following antennomeres, its branch about twice longer than stem; antennomeres V–X with branches about 8 times longer than their stems (Fig. 103).

Pronotum transverse, widest at half, 1.65–1.70 times wider than length at midline, with lateral margins almost straight, bent upwards; posterior margin with wide angular emargination medially; posterior angles short, widely rounded, produced backward; disc with sublateral carinae near posterior angles, reaching about half of pronotum (Fig. 97). Elytra 0.65–0.70 times as long as body, 1.70–1.95 times as long as wide at humeri.

Abdominal sternite IX 1.7 times as long as wide. Male genitalia with median lobe dorsally with short subapical hook, parameres robust, slightly rounded apically; phallobase slightly wider than long (Fig. 121).

Measurements

Holotype. BL 3.80 mm, WHum 1.35 mm, EL 2.45 mm, WHe 0.95 mm, PL 0.65 mm, PW 1.10 mm, Edist 0.40 mm, Ediam 0.38 mm. Paratypes. BL 3.95–4.80 mm, WHum 1.45–1.95 mm, EL 2.75–3.35 mm, WHe 1.05–1.30 mm, PL 0.70–0.90 mm, PW 1.20–1.60 mm, Edist 0.46–0.55 mm, Ediam 0.44–0.51 mm.

Intraspecific variability

The specimen from Eboufek has slightly less transverse pronotum (PW/PL = 1.65) than remaining specimens of *W. geiseri* sp. n. (PW/PL = 1.70). The specimen from

Bakingili is larger and relatively shorter (BL 4.80 mm, BL/Whum 2.50) than specimens from the Centre Region (BL 3.80–4.65 mm, BL/Whum 2.70–2.80).

Distribution

Cameroon: Centre Region, Southwest Region (Fig. 125).

Etymology

The name of this species is a patronym in honor of M. Geiser (BMNH).

***Wittmerselasia maculata* (Wittmer, 1989) comb. n.**

(Figs 16, 98, 104, 122)

Selasia maculata Wittmer, 1989: 202.

Type material

Holotype, male, "Cameroon: Southwest Prov., 25 km W Limbe, Bakingili, Malaise Trap, 12 July 1984, James DiGiulio" (CMNH); 2 paratypes, males, "Cameroon: Southwest Prov., 25 km W Limbe, Bakingili, Malaise Trap, 16 July 1984, James DiGiulio" (CMNH); 2 paratypes, males, "Cameroon: Southwest Prov., 25 km W Limbe, Bakingili, Malaise Trap, 23 July 1984, James DiGiulio" (CMNH); 2 paratypes, males, "Cameroon: Southwest Prov., 25 km W Limbe, Bakingili, 10 m, Malaise Trap, July 13, 1984, J. DiGiulio" (CMNH); 2 paratypes, males, "Cameroon: Southwest Prov., 25 km W Limbe, Bakingili, 16 July 1984, J. DiGiulio" (CMNH).

Other material examined

Male, "Cameroon: Southwest Province, Bakingili, 10 m, 11.–12. Jun 1984, James A. DiGiulio" (erroneously designated as paratype) (CMNH); male, "Cameroon: Southwest Province, Bakingili, 10 m, 21 July 1984, John E. Rawlins" [erroneously designated as paratype] (CMNH); male, "Cameroon: Southwest Prov., 25 km W Limbe, Bakingili, Malaise Trap, 30 June 1984, James A. DiGiulio" (CMNH); male, "Cameroon: Southwest Prov., 25 km W Limbe, Bakingili, intercept trap, 14 July 1984, James A. DiGiulio" (CMNH); male, "Cameroon: Southwest Prov., 25 km W Limbe, Bakingili, intercept trap, 29 July 1984, James A. DiGiulio" (CMNH); male, "Cameroon, SW Prov., Fako Dist., Bakingili, 25 km W Limbe, VII. 1.–10. 1984, Coll. R. Davidson" (CMNH); male, "Cameroon, SW Prov., Fako Dist., Bakingili, 25 km W Limbe, VII. 11.–20. 1984, Coll. R. Davidson" (CMNH).

Diagnosis

This species is superficially similar to *W. geiseri* sp. n. by the small body size and dark coloration (Figs 15–16), but it differs from the latter in absence of sublateral pronotal carina (Figs 97–98), relatively longer branches of antennomeres IV–X (Figs 103–104), longer hook of median lobe, and parameres subacute apically (Figs 121–122).

Redescription

Body 2.50–2.65 times longer than width at humeri. Body brown to dark brown, head and pronotum reddish dark brown (in some cases edges of pronotum and head lighter), basal portion of elytra lighter, legs yellowish to light brown; body covered with yellowish to light brown pubescence (Fig. 16).

Head including eyes 0.85–0.95 times as wide as pronotum. Eyes large, their frontal distance 1.05–1.10 times eye diameter (Fig. 98). Antennae flabellate, with antennomere III more than 3 times longer than following antennomeres, its branch about 1.5 times as long as stem; antennomeres V–X with branches about 12 times longer than their stems (Fig. 104).

Pronotum widest at half, 1.65–1.70 times wider than length at midline, with lateral margins slightly convex, bent upwards; posterior margin with wide angular emargination medially; posterior angles short, widely rounded; disc without distinct sublateral carinae near posterior angles (Fig. 98). Elytra 0.65–0.70 times as long as body, 1.70–1.85 times as long as wide at humeri.

Abdominal sternite IX 1.5 times as long as wide. Male genitalia with median lobe dorsally with robust, long subapical hook, parameres robust, subacute apically; phallobase slightly wider than long (Fig. 122).

Measurements

Holotype. BL 3.60 mm, WHum 1.40 mm, EL 2.40 mm, WHe 1.00 mm, PL 0.65 mm, PW 1.10 mm, Edist 0.45 mm, Ediam 0.41 mm. Paratypes and non-type material. BL 3.15–4.65 mm, WHum 1.25–1.80 mm, EL 2.20–3.20 mm, WHe 0.95–1.25 mm, PL 0.60–0.90 mm, PW 1.05–1.50 mm, Edist 0.42–0.56 mm, Ediam 0.39–0.53 mm.

Distribution

Cameroon: Southwest Region (Fig. 125).

Remark

Wittmer (1989) designated the holotype and eight paratypes in the original description. He stated, that the holotype and four paratypes should be deposited in the CMNH and the remaining four paratypes in the Naturhistorisches Museum in Basel, Switzerland. However, there are no specimens of *W. maculata* deposited in Basel (M. Geiser, E. Sprecher, pers. commun.) and there are 10 specimens labelled as “paratypus” in the CMNH. Based on the original description, the type series should include specimens with the following data: “Cameroon: Southwest Prov., 25 km W Limbe Bakingili, 12.–23.VII.1984, Malaise trap, James DiGiulio”. Therefore, two other specimens designated as paratypes, but with different data, are herein removed from the type series.

***Wittmerselasia variabilis* sp. n.**

(Figs 17, 23, 99, 105, 123)

Type material

Holotype, male, "Cameroon, South Prov., Lolodorf, 550 m, 3°14.06' N 10°43.52' E, 31. Mar 2008, Bolm lgt." (UPOL); paratype, male, "Cameroon, SW Prov., Nyassoso, Mt. Kupé, 900 m, 4°49.59' N 9°40.54' E, 9.–11. Mar 2008, Bolm lgt." (UPOL).

Diagnosis

Wittmerselasia variabilis sp. n. is the only species within the subgenus *Wittmerselasia* subgen. n. with the branch of antennomere III more than twice longer than its stem (Fig. 105) and the pronotum widest at posterior angles, with posterior angles distinctly produced postero-laterally (Fig. 99).

Description

Body 2.50–2.65 times longer than width at humeri. Body yellowish to light brown, antennal branches darker, elytra either completely dark brown (holotype) or only apical portion dark brown to black; body covered with yellowish to light brown pubescence (Fig. 17).

Head including eyes 0.80–0.85 times as wide as pronotum. Eyes large, their frontal distance 1.05 times eye diameter (Fig. 99). Antennae flabellate, with antennomere III about 2.5 times longer than following antennomeres, its branch slightly more than twice longer than stem; antennomeres V–X with branches about 9 times longer than their stems (Fig. 105).

Pronotum widest at posterior angles, 1.75–1.80 times wider than length at midline, with lateral margins slightly sinuate, bent upwards, diverged posteriorly; posterior margin with wide angular emargination medially; posterior angles widely rounded, produced postero-laterally; disc with short sublateral carinae near posterior angles (Fig. 99). Elytra 0.70 times as long as body, 1.80–1.90 times as long as wide at humeri.

Abdominal sternite IX 1.6 times as long as wide. Male genitalia with median lobe dorsally with robust, short subapical hook, parameres robust, subacute apically; phallobase about as long as wide (Fig. 123).

Intraspecific variability

The holotype has antennal branches brown and elytra completely dark brown, whereas the paratype has antennal branches dark brown to black and elytra yellowish-brown with apical portion dark brown to black.

Measurements

Holotype. BL 6.60 mm, WHum 2.50 mm, EL 4.70 mm, WHe 1.65 mm, PL 1.15 mm, PW 2.00 mm, Edist 0.72 mm, Ediam 0.68 mm. Paratype. BL 6.00 mm, WHum 2.40 mm, EL 4.25 mm, WHe 1.45 mm, PL 1.00 mm, PW 1.85 mm, Edist 0.67 mm, Ediam 0.63 mm.

Distribution

Cameroon: South Region, Southwest Region (Fig. 125).

Etymology

The specific epithet refers to the variable coloration of elytra in this species.

Subgenus *Latoselasia* subgen. n.

Type species

Latoselasia similis sp. n.

Diagnosis

Latoselasia subgen. n. differs from the nominotypical *Wittmerselasia* subgen. n. in the sclerotized, subpentagonal, apically widely rounded labrum (larger and only partly sclerotized in *Wittmerselasia* subgen. n.; Figs 23–24), shorter and wider apical maxillary palpomere (longer, constricted subapically in *Wittmerselasia* subgen. n.; Figs 82, 90), phallobase slightly longer than wide, median lobe shorter than phallobase, and parameres smaller, rounded apically (phallobase never longer than wide, median lobe longer than phallobase, and parameres larger, more pointed apically in *Wittmerselasia* subgen. nov; Figs 119–124).

Description

Male. Body 4.80–5.30 mm long, 2.60–2.80 times longer than width at humeri. Body yellowish, yellowish-brown or brown, elytra either uniformly brown or yellowish to brown with lateral and apical parts dark brown, antennomeres III–XI brown to dark brown, branches darker; body surface covered with yellowish to light brown pubescence (Fig. 18).

Head including eyes 0.80–0.85 times as wide as pronotum; surface smooth, very shallowly depressed medially, sparsely punctate, covered with sparse, long, semi-erect pubescence; antennal sockets moderately widely separated, frons narrowed apically, slightly surpassing fronto-clypeal region; fronto-clypeal region high, narrow, partly membranous, abruptly declined between antennal insertions, sloping toward base of labrum; its surface smooth medially, rough laterally, basally with two lateral rows of punctures with long erected setae (Fig. 24). Eyes large, prominent, their frontal distance 1.00–1.05 times eye diameter. Labrum sclerotized, subpentagonal, short, produced forwards, with frontal margin widely rounded. Mandibles robust, moderately long, falcate, bidentate, with long apical oblique tooth and another, robust tooth located in middle part of incisor; mandibles basally setose, apical part bare, shiny (Fig. 89). Maxillary palpi tetramerous, slender, palpomere I short, palpomere II elogate, about twice longer than wide, more than twice longer than palpomere III, palpomere III short, about as long as wide, palpomere IV more than 3 times longer than palpomere III, less than twice as long as wide, hatchet-like, apically distinctly flattened and widened (Fig. 90). Labium short, wide; labial palpi trimerous, tiny, palpomeres I–II short, wide, apical palpomere elongate, fusiform (Fig. 91). Antennae 11-segmeneted, flabellate, scapus robust, widened apically, pedicel short, small, antennomere III long, more than 2.5 times longer than antennomeres IV–X, with robust, wide branch, longer than stem; antennomeres IV–X short, subequal in length, strongly flabellate, with branches distinctly flattened, about 12 times longer than respective stems, apical antennomere simple, elongate, about as long as branch of penultimate antennomere (Fig. 106); all antennomeres with surface uneven, sparsely covered with long setae, arising from the edges of branches.

Pronotum slightly convex, transverse, widest at posterior angles, 1.55–1.70 times wider than length at midline. Anterior margin slightly convex, slightly bent upwards, lateral margins almost straight, bent upwards, posterior margin with wide angular emargination medially. Anterior angles inconspicuous; posterior angles short, widely rounded. Disc smooth, without or with slightly developed short sublateral carinae (Fig. 100). Lateral carina separating pronotum from hypomeron distinct, almost reaching pronotal frontal margin. Surface of disc very sparsely covered with shallow punctures, with sparse semi-erect, long pubescence, both punctures and setae equally distributed. Hypomeron almost smooth; prosternal suture very short. Prosternum transverse, prosternal lobe short, with frontal margin almost straight, with long semi-erect setae; prosternal process moderately long, slender, subparallel-sided, subacute apically. Scutellum flat, triangular, slightly longer than wide, subacute apically, sparsely covered with shallow punctures and semi-erect setae. Mesoventrite widely V-shaped, with frontal margin widely emarginate, posterior margin produced medially to form narrow mesoventral cavity. Mesocoxal cavity open to both mesepimeron and mesepisternum. Metaventrite large, subtrapezoidal, smooth, very sparsely covered with shallow punctures. Elytra subparallel-sided, 0.70 times as long as body; basally wrinkled (Fig. 18). Each elytron with apices separately rounded, sparsely punctate, covered with long, semi-erect pubescence; elytral suture distinct, wide, depressed. Hind wing venation as in Fig. 92. Legs slender, slightly compressed, with sparse, long, semi-erect setae, coxae robust, trochanters slender, elongate, widened apically, obliquely attached to femora; tarsomeres I–III subequal in length, tarsomere 4 shortest, minute, extended ventrally, apical tarsomere long, slender; claws simple, slender, slightly curved, each basally with long seta.

Abdomen soft, slender, ventrites with very sparse, shallow punctures, sparsely covered with semi-erect pubescence, denser laterally. Tergites IX and X connected by membrane; tergite IX about 0.5 times as long as wide; tergite X rounded apically (Fig. 93). Sternite IX elongate, 1.8 times as long as wide, deeply emarginate basally, apex rounded, punctate, with sparse short setae; sternite X connected by membrane to sternite IX, transverse, partly membranous (Fig. 94).

Male genitalia trilobate, 1.6 times as long as wide; median lobe robust, short, less than twice longer than parameres, shorter than phallobase, moderately curved in lateral view, basally with two short, robust struts, dorsally with rather short subapical hook; parameres small, elongate, more or less rounded apically, inner margin and apex covered with moderately long setae; phallobase robust, slightly longer than wide, U-shaped (Fig. 124).

Females and immature stages unknown.

Etymology

The generic name is a combination of words “latus” (Latin), which means wide and refers to the typically widened apex of the apical maxillary palpomere, and *Selasia* Laporte, 1836. Gender: feminine.

***Latoselasia similis* sp. n.**

(Figs 18, 24, 89–94, 100, 106, 124)

Type material

Holotype, male: “Cameroon, SW Prov., Kumba env., Barombi Mbo, 4°38.53' N 9°24.51' E, 280 m, 8. Mar 2008, Bolm lgt.” (UPOL); paratype, male, same data as for the holotype (UPOL); paratype, male, “Cameroon, Lolodorf, A. I. Good, Acc. 7789, June 1925” (CMNH); paratype, male, “Cameroon, SW Prov., Fako Dist., Bakingili 25 km W Limbe, VI. 11.–20. 1984, Coll. R. Davidson” (CMNH).

Diagnosis

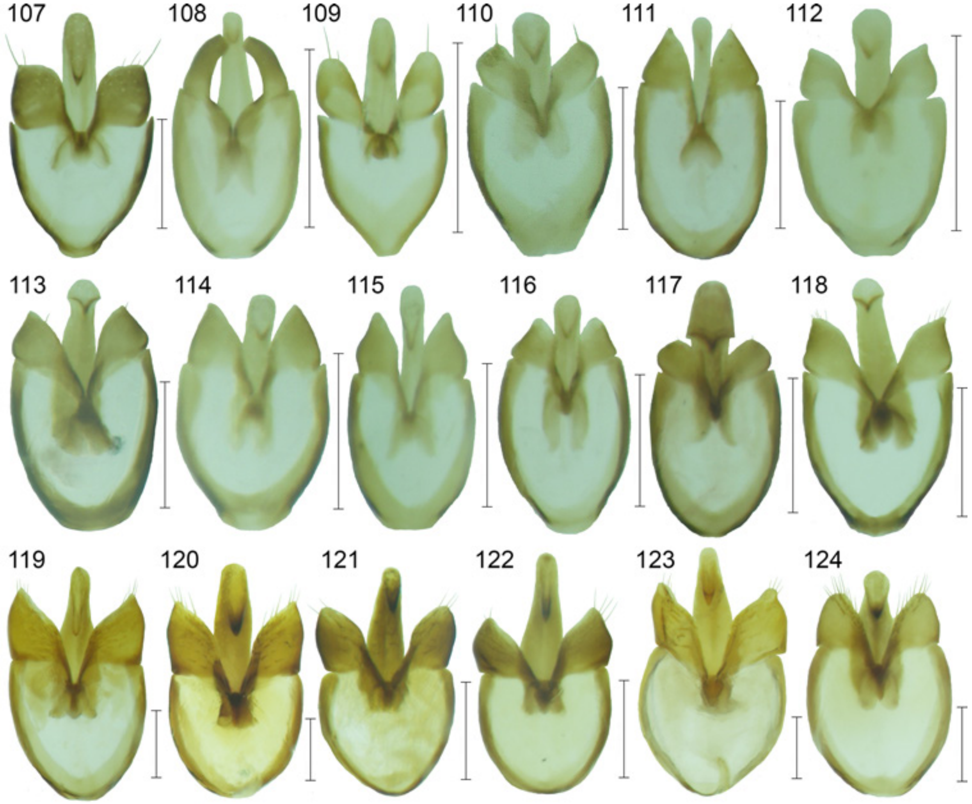
Latoselasia similis sp. n. is by general appearance and the light body coloration with yellowish to light brown pronotum similar to *Wittmerselasia camerooniana* sp. n., *W. davidsoni* sp. n. and *W. variabilis* sp. n. (Figs 13–14, 17–18). These species differ from *L. similis* sp. n. in the subgeneric characters (i.e., shape of labrum, maxillary palpi and genitalia; Figs 23–24, 82, 91, 119–124; see the subgeneric diagnoses above), and additionally, *W. camerooniana* sp. n. and *W. davidsoni* sp. n. have all antennal branches relatively shorter (Figs 101–102), and *W. variabilis* sp. n. has pronotum more transverse, with more distinctly produced posterior angles (Fig. 99), relatively longer branch of antennomere III, and all subsequent branches shorter (Fig. 105).

Description

Body 2.60 times longer than width at humeri. Body yellowish to brown, antennal branches dark brown, elytra either uniformly brown or yellowish to brown with lateral and apical parts dark brown (incl. holotype); body surface covered with yellowish pubescence (Fig. 18).

Head including eyes 0.80 times as wide as pronotum. Eyes large, their frontal distance 1.00 times eye diameter (Fig. 100). Antennae flabellate, with antennomere III more than 2.5 times longer than following antennomeres, its branch less than twice longer than stem; antennomeres V–X with branches about 12 times longer than their stems (Fig. 106).

Pronotum widest at posterior angles, 1.70 times wider than length at midline, with anterior and lateral margins slightly bent upwards, without sublateral carinae, with transverse carina near posterior margin (Fig. 100). Lateral carina separating pronotum



Figs 107–124. Male genitalia of Drilini in Cameroon. (107) *Flabelloselasia oculata* sp. n.; (108) *Kupeselasia minuta* sp. n.; (109) *Lolosia transversalis* sp. n.; (110) *Microselasia barombi* sp. n.; (111) *M. elongata* sp. n.; (112) *M. gracilis* sp. n.; (113) *M. grandis* sp. n.; (114) *M. kupensis* sp. n.; (115) *M. lolodorfensis* sp. n.; (116) *M. macrocephala* sp. n.; (117) *M. obscura* sp. n.; (118) *M. pseudograndis* sp. n.; (119) *Wittmerselasia camerooniana* sp. n.; (120) *W. davidsoni* sp. n.; (121) *W. geiseri* sp. n.; (122) *W. maculata* (Wittmer, 1989); (123) *W. variabilis* sp. n.; (124) *W.* (*Latoselasia*) *similis* sp. n. Scale bars = 0.2 mm.

from hypomeron distinct, almost reaching pronotal frontal margin. Elytra subparallel-sided, 0.70 times as long as body, 1.80–1.85 times as long as wide at humeri.

Abdominal terminal segments as in Figs 93–94. Male genitalia with median lobe shorter than phallobase; parameres elongate, setose, more or less rounded apically; phallobase slightly longer than wide, U-shaped (Fig. 124).

Intraspecific variability

The specimens from Kumba, which include the holotype, have relatively wider pronota than those from Limbe and Lolodorf (1.65–1.70 versus 1.55–1.60, respectively). Even within a single population we identified some variability in coloration when a specimen from Kumba has yellowish base and the middle part of elytra and the other specimens are completely brown. The paratype from Lolodorf (South Region)

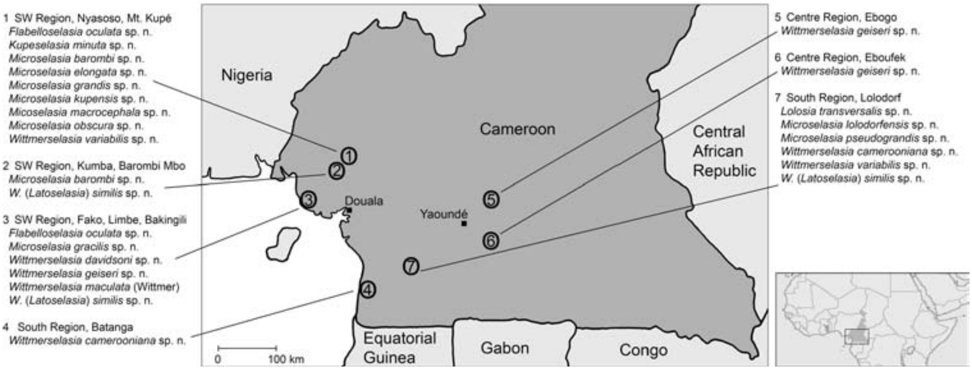


Fig. 125. The distribution of Drilini in Cameroon.

has uniformly brown elytra and scutellum, and distinct pronotal sublateral carinae on pronotum. The paratype from Limbe has slightly smaller eyes (Edist/Ediam ratio 1.05; 1.00 for the typical representatives). These subtle differences cannot be used for reliable definition of formal taxa and we prefer to merge all populations in a single species concept. Molecular data can potentially show the deeper divergence that morphology indicates as has been shown in other neotenic lineages of elateroid beetles (e.g., Bray & Bocak 2016).

Measurements

Holotype. BL 5.20 mm, WHum 2.00 mm, EL 3.60 mm, WHe 1.40 mm, PL 1.00 mm, PW 1.70 mm, Edist 0.55 mm, Ediam 0.55 mm. Paratypes. BL 4.80–5.30 mm, WHum 1.75–2.00 mm, EL 3.25–3.65 mm, WHe 1.20–1.30 mm, PL 0.85–1.00 mm, PW 1.45–1.55 mm, Edist 0.50–0.55 mm, Ediam 0.50–0.51 mm.

Distribution

Cameroon: Southwest Region, South Region (Fig. 125).

Etymology

The specific epithet refers to the external morphological similarity of this species to the representatives of the subgenus *Wittmerselasia* subgen. n. (Latin; similis = similar, resembling).

An identification key for the genera and species of Drilini in Cameroon (based on adult males)

1. Antennae strongly flabellate, antennomere III 2.5–3.5 times longer than antennomere IV, antennomeres IV–X subequal in length, not longer than wide (without branches); ultimate maxillary palpomere apically widened, never subacute or pointed.. 2

–. Antennae serrate, weakly or strongly flabellate, antennomere III 1.0–1.7 times as long as antennomere IV; antennomeres IV–X subequal in length or gradually shortened, longer than wide (without branches); ultimate maxillary palpomere apically subacute or pointed 8

2. Branches of antennomeres VI–X about 20 times longer than their stems (Fig. 28); pronotum with sublateral carina almost reaching anterior margin (Fig. 25); mandibles long, slender (Fig. 26); male genitalia with V-shaped phallobase and subrectangular parameres (Fig. 107) .... (*Flabelloselasia* gen. n.) *F. oculata* sp. n.

–. Branches of antennomeres VI–X about 8–12 times longer than their stems (Figs 101–106); pronotum either without sublateral carina or with carina short, never reaching anterior half of pronotum (Figs 95–100); mandibles wider, robust (Figs 81, 89); male genitalia with U-shaped phallobase and parameres longer than wide (Figs 119–124).. (*Wittmerselasia* gen. n.) 3

3. Apical maxillary palpomere less than twice as long as wide, apically cut, straight (Fig. 90); labrum sclerotized, subpentagonal, apically widely rounded; phallobase slightly longer than wide, median lobe shorter than phallobase, and parameres smaller, rounded apically (Fig. 124)............(*Latoselasia* subgen. n.) *L. similis* sp. n.

–. Apical maxillary palpomere about 2.5 times as long as wide, slightly constricted subapically, apically slightly rounded (Fig. 82); labrum transverse, large, only partly sclerotized; phallobase never longer than wide, median lobe longer than phallobase, and parameres larger, more or less pointed apically (Figs 119–123) .... (*Wittmerselasia* subgen. n.) 4

4. Body including pronotum yellowish to light brown; mostly larger specimens (4.35–6.60 mm long).. 5

–. Body brown to dark brown, pronotum reddish dark brown to dark brown; mostly smaller specimens (3.15–4.80 mm long) 7

5. Antennomere III with branch of about the same length as stem (Fig. 101).......... .... *W. camerooniana* sp. n.

–. Antennomere III with branch distinctly longer than stem 6

6. Pronotum less transverse (1.60–1.65 times as wide as long), lateral margins almost straight, posterior angles short (Fig. 96); phallobase slightly wider than long; median lobe of male genitalia with robust long hook (Fig. 120)............ *W. davidsoni* sp. n.

–. Pronotum more transverse (1.75–1.80 times as wide as long), lateral margins sinuate, posterior angles prominent, produced postero-laterally (Fig. 99); phallobase about as long as wide; median lobe of male genitalia with short hook (Fig. 123).. .... *W. variabilis* sp. n.

7. Pronotum with distinct sublateral carina (Fig. 97); branches of antennomeres V–X about 8 times longer than their stems (Fig. 103); median lobe of male genitalia with short hook; parameres slightly rounded apically (Fig. 121)............ *W. geiseri* sp. n.

–. Pronotum without sublateral carina (Fig. 98); branches of antennomeres V–X about 12 times longer than their stems (Fig. 104); median lobe of male genitalia with robust long hook; parameres subacute apically (Fig. 122)...................... .... *W. maculata* (Wittmer, 1989)

8. Frontal carina incomplete; fronto-clypeal region wide (Fig. 21); pronotum 1.85 times wider than long (Fig. 44); phallobase V-shaped (Fig. 109).. (*Lolosia* gen. n.) *L. transversalis* sp. n.
–. Frontal carina complete; fronto-clypeal region narrow (Figs 20, 22); pronotum 1.40–1.75 times wider than long (Figs 34, 62–70); phallobase U-shaped (Figs 108, 110–118).. 9
9. Body 2.10 mm long; antennae strongly serrate (Fig. 37); mandibles more slender (Fig. 35); sternite IX not emarginate basally (Fig. 42); parameres distinctly elongate, slender (Fig. 108)................................ (*Kupeselasia* gen. n.) *K. minuta* sp. n.
–. Body 2.30–3.60 mm long; antennae flabellate (Figs 71–79); mandibles more robust (Fig. 53); sternite IX emarginate basally (Figs 60–61); parameres not distinctly elongate (Figs 110–118)..(*Microselasia* gen. n.) 10
10. Head including eyes about same as or wider than maximal pronotal width; pronotum widest at anterior half.. 11
–. Head including eyes narrower than maximal pronotal width; pronotum widest at posterior angles.. 13
11. Pronotum more transverse, 1.65 times wider than long (Fig. 64); antennomere III about 1.7 times longer than antennomere IV (Fig. 73); phallobase about as long as wide (Fig. 112) .... *M. gracilis* sp. n.
–. Pronotum less transverse, 1.40–1.45 times wider than long (Figs 68–69); antennomere III about 1.2–1.3 times longer than antennomere IV (Figs 77–78); phallobase 1.2–1.3 times longer than wide (Figs 116–117) 12
12. Body length 2.35–2.75 mm; branches of antennomeres VI–X about 6 times longer than their respective stems (Fig. 77); parameres subacute apically; subapical hook on median lobe slender, short (Fig. 116)..................*M. macrocephala* sp. n.
–. Body length 3.10–3.50 mm; branches of antennomeres VI–X about 8 times longer than their respective stems (Fig. 78); parameres minute, almost rounded apically; subapical hook on median lobe robust, widened (Fig. 117).. *M. obscura* sp. n.
13. Eyes relatively larger (Edist/Ediam 1.10–1.20); pronotum more transverse, 1.65–1.75 times wider than long.. 14
–. Eyes medium-sized (Edist/Ediam 1.30–1.60); pronotum less transverse, 1.40–1.60 times wider than long.. 15
14. Body length 2.45 mm; antennae weakly flabellate (Fig. 75); pronotum 1.75 times wider than long, without distinct sublateral carina (Fig. 66); eyes relatively larger (Edist/Ediam 1.10); male genitalia 1.5 times as long as wide, median lobe slightly shorter than phallobase, with relatively longer subapical hook (Fig. 114).. *M. kupensis* sp. n.
–. Body length 2.95 mm; antennae strongly flabellate (Fig. 79); pronotum 1.65 times wider than long, with distinct sublateral carina almost reaching anterior margin (Fig. 70); eyes relatively smaller (Edist/Ediam 1.20); male genitalia 1.7 times as long as wide, median lobe longer than phallobase, with relatively shorter subapical hook (Fig. 118) .... *M. pseudograndis* sp. n.

15. Antennae weakly flabellate, antennomere III slightly serrate, 1.0–1.1 times as long as antennomere IV, branches of antennomeres IV–X less than 4 times longer than stems of respective antennomeres, antennomere XI less than 4 times longer than penultimate antennomere; minimal frontal distance between eyes 1.40–1.60 times eye diameter; male genitalia relatively longer, 1.8 times longer than wide 16
–. Antennae strongly flabellate, antennomere III strongly serrate, 1.2–1.4 times as long as antennomere IV, branches of antennomeres IV–X about 8 times longer than stems of respective antennomeres, antennomere XI about 7 times longer than penultimate antennomere; minimal frontal distance between eyes 1.30–1.35 times eye diameter; male genitalia relatively shorter, 1.7 times longer than wide 17
16. Body length 3.10 mm; antennae only weakly flabellate, antennomeres III–VII subequal in length, branches of antennomeres IV–X less than 1.5 times longer than stems of respective antennomeres, antennomere XI less than twice longer than penultimate antennomere (Fig. 72); minimal frontal distance between eyes 1.40 times eye diameter; phallobase elongate, 1.3 times longer than wide, median lobe slightly shorter than phallobase, with subapical hook short (Fig. 111) .... *M. elongata* sp. n.
–. Body length 2.60–2.75 mm; antennae more strongly flabellate, antennomeres III–VII gradually shortened, branches of antennomeres IV–X about 3–4 times longer than stems of respective antennomeres, antennomere XI more than 3 times longer than penultimate antennomere (Fig. 76); minimal frontal distance between eyes 1.50–1.60 times eye diameter; phallobase only slightly longer than wide, median lobe longer than phallobase, with subapical hook robust, long (Fig. 115) .... *M. lolodorfensis* sp. n.
17. Head including eyes only slightly narrower than pronotum (Whe/PW 0.95); pronotum 1.50–1.55 times wider than long, with lateral sides distinctly sinuate, with posterior angles produced postero-laterally (Fig. 62); median lobe robust, short, shorter than phallobase, with apical hook robust, relatively longer (Fig. 110) .... *M. barombi* sp. n.
–. Head including eyes distinctly narrower than pronotum (Whe/PW 0.85); pronotum 1.60 times wider than long, with lateral sides almost straight, with posterior angles only slightly produced posteriorly (Fig. 65); median lobe elongate, slender, about as long as phallobase, with apical hook short (Fig. 113).... .... *M. grandis* sp. n.

Discussion

The tropical rain forests in the Gulf of Guinea are one of the biodiversity hotspots and host many endemic animal species (e.g., Stuart et al. 1990; Oates et al. 2004), including the neotenic elateroid beetles which are well known for their low dispersal propensity and the occurrence limited to the stable habitats, e.g., the Cameroonian endemics in the net-winged beetles *Dexoris* Waterhouse and *Lolodorfus* Bocakova (Bocak & Bocakova 1990; Bocak et al. 2008, 2013; Bocakova 2014). The forest zone is limited to a few dozens of kilometres along the coast and is strongly affected by climatic fluctuation resulting in fragmentation during dry and cold periods, but even in the driest periods the refugia were available for animals with very low dispersal propensity like neotenic beetles. Two major Afrotropical forest ecoregions are represented in Cameroon. The western part of the country belongs to the coastal Lower Guinean forests and has been identified as the West African Forests biodiversity hotspot, while the region south of the Sanaga River belongs to the Congolian forests (Fjeldså & Lovett 1997; Myers 2000; Oates et al. 2004). The general stability of this area supports a high diversity of neotenic beetles which have very limited ranges and usually define regions with extreme phylogenetic diversity (Bocak et al. 2008).

The diversity of Drilini in the western and central Africa has never been systematically studied. Hitherto, only a few species have been reported from this area, from which only *Wittmerselasia maculata* was described from the Lower Guinean forests (Wittmer 1989). Our study is the first review of the Drilini fauna in Cameroonian rain forest zone which was possible when new highly diverse material from this region become available. We report 18 species from the whole region, eleven of them being endemic to the Southwest and four to the South Region. Only three species are known from large ranges. *Wittmerselasia variabilis* sp. n. and *W.* (*Latoselasia*) *similis* sp. n. are distributed across Southwest and South Regions, i.e., more than 200 km far from each other, and *W. geiseri* sp. n. occurs in localities in the Southwest and Central Regions, more than 300 km far from each other. Although Sanaga River serves as the natural barrier for many animal species (i.e., Mitchell et al. 2015), it seems that at least some Drilini species are distributed on both its banks. The geographic structure of populations and possibly the presence of partly isolated populations is suggested by a relatively high intraspecific morphological variability in *Wittmerselasia geiseri* sp. n. and *W.* (*Latoselasia*) *similis* sp. n. The limited ranges and a morphological divergence of populations and closely related species have been reported in other neotenic elateroid lineages such as Omalisidae (Bocak & Brlik 2008), Iberobaeniidae (Bocak et al. 2016), and Lycidae (Bray & Bocak 2016). The molecular data will be needed for validation of morphology-based delimitation of species, and we preferred the wider species concepts when morphology of geographically distant population is similar as in the cases of *Wittmerselasia geiseri* sp. n. and *W.* (*Latoselasia*) *similis* sp. n.

Besides high diversity in the whole area, we also found a high number of Drilini occurring sympatrically in a single locality. Nine species in four genera were recorded from Mt. Kupé, six species in three genera in the vicinity of Lolodorf and six species in three genera near Bakingili (Fig. 125). Similar high local diversity was reported for some Palaearctic Drilini and it was attributed to the prey specificity (Faucheux & Agnas 2011; Baalbergen et al. 2014, 2016; Kundrata et al. 2015a). Neither immature stages nor presumably larviform females of the Cameroonian Drilini were observed and we can only suppose the same biology and ecology as in other Drilini which are all predators of land snails (e.g., Barker 1969; Baalbergen et al. 2014; Kobieluszova & Kundrata 2015). De Winter & Gittenberger (1998) studied the diversity of the land snails of a square kilometer plot in southern Cameroonian rainforest and identified 97 species, which has been the world's highest sympatric land snail diversity reported to date. Taking into consideration the enormous diversity of the prey in a single locality, the presence of several Drilini species in the same area is in agreement with previous observations. A plenitude of food, the presence of the long-term stable habitats (Fjeldså & Lovett 1997; Bocak et al. 2008) and the fact, that all 18 known Cameroonian species were collected only in a few localities, suggest probably the much higher real diversity of Drilini in this region than until now expected.

Acknowledgements

We are very obliged to R. Davidson (CMNH, Pittsburgh, PA, USA), M. Geiser (BMNH, London, UK) and A. Mantilleri (MHNP) for the loan of material in their care. This study was supported by the Czech Science Foundation (P506/11/1757, LB). The short-term stays of RK in the Koninklijk Museum voor Midden-Afrika, Tervuren, Belgium (BE-TAF 6078) and the Muséum national d'Histoire naturelle, Paris, France (FR-TAF 6701) were funded by the EU-SYNTHESYS grants.

References

Baalbergen, E., Helwerda, R., Schelfhorst, R., Castillo Cajas, R.F., van Moorsel, C.H.M., Kundrata, R., Welter-Schultes, F.W., Giokas, S. & Schilthuizen, M. (2014) Predator–prey interactions between shell-boring beetle larvae and rock-dwelling land snails. *PLoS One* **9**: e100366.

Baalbergen, E., Schelfhorst, R. & Schilthuizen, M. (2016) *Drilus* larvae in the Netherlands (Coleoptera: Elateridae: Drilini). *Entomologische Berichten* **76**: 165–173.

Barker, J.F. (1969) Notes on the life cycle and behaviour of the drilid beetle *Selasia unicolor* (Guérin). *Proceedings of the Royal Entomological Society of London (Series A)* **44**: 169–172.

Bocak, L. (2007) Drilidae. In: Löbl, I. & Smetana, A. (Eds) Catalogue of Palaearctic Coleoptera, Volume **4**, Apollo Books, Stenstrup, Denmark: pp. 209–210.

Bocak, L. & Brlik, M. (2008) Revision of the family Omalisidae (Coleoptera, Elateroidea). *Insect Systematics and Evolution* **39**: 189–212.

Bocak, L., Bocakova, M., Hunt, T. & Vogler, A.P. (2008) Multiple ancient origins of neoteny in Lycidae (Coleoptera): consequences for ecology and macroevolution. *Proceedings of the Royal Society London Series B: Biological Sciences* **275**: 2015–2023.

Bocak, L., Branham, M.A. & Kundrata, R. (2010) Family Drilidae Blanchard, 1845. In: Leschen, R.A.B., Beutel, R.G. & Lawrence, J.F. (volume Eds) Coleoptera, Beetles, Volume 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). In: Kristensen, N.P. & Beutel, R.G. (Eds) *Handbook of Zoology, Arthropoda: Insecta*. de Gruyter, Berlin, pp. 104–110.

Bocak, L., Grebennikov, V.V. & Masek, M. (2013) A new species of *Dexoris* (Coleoptera: Lycidae) and parallel evolution of brachyptery in the soft-bodied elateroid beetles. *Zootaxa* **3721**: 495–500.

Bocak, L., Kundrata, R., Andújar Fernández, C. & Vogler, A.P. (2016) The discovery of Iberobaeniidae (Coleoptera: Elateroidea), a new family of beetles from Spain, with immatures detected by environmental DNA sequencing. *Proceedings of the Royal Society B-Biological Sciences* **283**: 20152350.

Bocakova, M. (2014) *Lolodorfus*, a new genus of net-winged beetles (Coleoptera: Lycidae: Dexorinae) from Cameroon. *Zootaxa* **3811**: 374–380.

Bray, T. & Bocak, L. (2016) Slowly dispersing neotenic beetles can speciate on a penny coin and generate space-limited diversity in the tropical mountains. *Scientific Reports* **6**: 33579.

Crowson, R.A. (1972) A review of the classification of Cantharoidea (Coleoptera), with definition of two new families, Cneoglossidae and Omethidae. *Revista de la Universidad de Madrid* **21**: 35–77.

de Winter, A.J. & Gittenberger, E. (1998) The land snail fauna of a square kilometer patch of rainforest in southwestern Cameroon: high species richness, low abundance and seasonal fluctuations. *Malacologia* **40**: 231–250.

Faucheux, M.J. & Agnas, M. (2011) *Drilus mauritanicus* Lucas, 1849 et *Malacogaster passerinii* Bassi, 1883 présents dans le même biotope à Oualidia (Maroc atlantique) (Coleoptera: Elateroidea: Drilidae). *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France (nouvelle série)* **33**: 79–90.

Fjeldså, J. & Lovett, J.C. (1997) Geographical patterns of old and young species in African forest biota: the significance of specific montane areas as evolutionary centres. *Biodiversity and Conservation* **6**: 325–346.

Geisthardt, M. (2007a) Remarks on some African *Selasia*-species and description of new species (Coleoptera: Drilidae). *Mitteilungen des Internationalen Entomologischen Vereins* **32**: 27–43.

Geisthardt, M. (2007b) Neue und bekannte *Selasia* Laporte, 1836 Arten aus dem südliche Afrika (Coleoptera, Drilidae). *Entomologica Basiliensia et Collectionis Frey* **29**: 31–40.

Janisova, K. & Bocakova, M. (2013) Revision of the subfamily Ototretinae (Coleoptera: Lampyridae). *Zoologischer Anzeiger* **252**: 1–19.

Kobieluszova, L. & Kundrata, R. (2015) Taxonomic review of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) from Asia Minor, with descriptions of seven new species and comments on the female antennal morphology in Drilini. *Zootaxa* **4012**: 78–96.

Kundrata, R. & Bocak, L. (2007) A revision of *Euanoma* and *Pseudeuanoma* (Coleoptera: Drilidae). *Annales Zoologici* **57**: 427–441.

Kundrata, R. & Bocak, L. (2011a) The phylogeny and limits of Elateridae (Insecta, Coleoptera): is there a common tendency of click beetles to soft-bodiedness and neoteny? *Zoologica Scripta* **40**: 364–378.

Kundrata, R. & Bocak, L. (2011b) Redescription and relationships of *Pseudothilmanus* Pic (Coleoptera: Rhagophthalmidae) – a long-term neglected glow-worm beetle genus from the Himalayas. *Zootaxa* **2794**: 57–62.

Kundrata, R., Kobieluszova, L. & Bocak, L. (2014) A review of Drilini (Coleoptera: Elateridae: Agrypninae) of the Northern Levant, with description of a new species from Syria and a key to Levantine species. *Zootaxa* **3755**: 457–469.

Kundrata, R., Baalbergen, E., Bocak, L. & Schilthuizen, M. (2015a) The origin and diversity of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) in Crete based on mitochondrial phylogeny. *Systematics and Biodiversity* **13**: 52–75.

Kundrata, R., Baena, M. & Bocak, L. (2015b) Classification of Omalisidae based on molecular data and morphology, with description of Paradrilinae subfam. nov. (Coleoptera: Elateroidea). *Zootaxa* **3915**: 413–422.

Kundrata, R., Gunter, N.L., Douglas, H. & Bocak, L. (2016) Next step toward a molecular phylogeny of click-beetles (Coleoptera: Elateridae): redefinition of Pityobiinae, with a description of a new subfamily, Parablacinae, from the Australasian Region. *Austral Entomology* **55**: 291–302.

Laporte, F.L. (1836) Études entomologiques, ou descriptions d'insectes nouveaux, et observations sur la synonymie. *Revue Entomologique* **4**: 5–60.

Lawrence, J.F., Ślipiński, A., Seago, A.E., Thayer, M.K., Newton, A.F. & Marvaldi, A.E. (2011) Phylogeny of the Coleoptera based on morphological characters of adults and larvae. *Annales Zoologici* **61**: 1–217.

McKenna, D.D., Wild, A.L., Kanda, K., Bellamy, C.L., Beutel, R.G., Caterino, M.S., Farnum, C.W., Hawks, D.C., Ivie, M.A., Jameson, M.L., Leschen, R.A.B., Marvaldi, A.E., McHugh, J.V., Newton, A.F., Robertson, J.A., Thayer, M.K., Whiting, M.F., Lawrence, J.F., Ślipiński, A., Maddison, D.R. & Farrell, B.D. (2015). The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Systematic Entomology* **40**: 835–880.

Mitchell, M.W., Locatelli, S., Sesink Clee, P.R., Thomassen, H.A. & Gonder, M.K. (2015) Environmental variation and rivers govern the structure of chimpanzee genetic diversity in a biodiversity hotspot. *BMC Evolutinary Biology* **15**: 1.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858.

Oates, J.F., Bergl, R.A. & Linder, J.M. (2004) Africa's Gulf of Guinea forests: Biodiversity patterns and conservation priorities. *Advances in Applied Biodiversity Science* **6**: 1–90.

Petrzelkova, I. & Kundrata, R. (2015) The genus *Drilus* (Elateridae: Agrypninae) from the Levant: a new species, new records and updated key to the males. *Annales Zoologici* **65**: 483–490.

Pic, M. (1914) Nouveaux Coléoptères de diverses familles. *Mélanges Exotico-Entomologiques* **10**: 7–20.

Pic, M. (1918) Courtes descriptions diverses. *Mélanges Exotico-Entomologiques* **28**: 1–24.

Pic, M. (1931) Coléoptères Malacodermes Hétéromères nouveaux. *Revue de Zoologie et de Botanique Africaines* **21**: 37–50.

Pic, M. (1946) Coléoptères du globe (suite). *L'Échange, Revue Linnéenne* **62**: 1–4.

Stuart, S.N., Adams, R.J. & Jenkins, M.D. (1990) Biodiversity in sub-saharan Africa and its islands. Conservation, management and sustainable use. A contribution to the Biodiversity Conservation Strategy Programme. Occasional Papers of the IUCN Species Survival Commission, No. 6. IUCN, Gland.

Timmermans, M.J.T.N., Barton, C., Haran, J., Ahrens, D., Culverwell, C.L., Ollikainen, A., Dodsworth, S., Foster, P.G., Bocak, L. & Vogler, A.P. (2016). Family-level sampling of mitochondrial genomes in Coleoptera: compositional heterogeneity and phylogenetics. *Genome Biology and Evolution* **8**: 161–175.

Trllova, S. & Kundrata, R. (2015) A review of the genus *Selasia* (Elateridae: Agrypninae: Drilini) in the Palaearctic Region. *Zootaxa* **3920**: 563–571.

Wittmer, W. (1944) Catalogue des Drilidae E. Oliv. (Coleoptera - Malacodermata). *Revista de la Sociedad Entomológica Argentina* **12**: 203–221.

Wittmer, W. (1989) Die Familie Drilidae (Coleoptera) in Südafrika, sowie Beschreibung von neuen Arten aus dem südlichen Afrika (30. Beitrag zur Kenntnis der Fauna Afrikas). *Entomologica Basiliensia* **13**: 187–205.

Příloha 12

Šormová, E., Kramp, K. & **Kundrata, R.** (2018) Diversity and phylogenetic relationships of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) in Cyprus. *Zoologischer Anzeiger*, 275: 1–12.

[IF 1,345; 2 citace na WoS; celkem 1 citace bez autorových autocitací]

[korespondující autor; autorský podíl: 45 %]

Zoologischer Anzeiger 275 (2018) 1–12

Contents lists available at ScienceDirect

Zoologischer Anzeiger

journal homepage: www.elsevier.com/locate/jcz

Zoologischer Anzeiger

Diversity and phylogenetic relationships of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) in Cyprus

Eliska Sormova[a], Katja Kramp[b], Robin Kundrata[a,*]

[a] *Department of Zoology, Faculty of Science, Palacky University, 17. listopadu 50, 771 46, Olomouc, Czech Republic*
[b] *Senckenberg Deutsches Entomologisches Institut, Eberswalder Str. 90, 15374 Müncheberg, Germany*

ARTICLE INFO

Article history:
Received 14 September 2017
Received in revised form 3 April 2018
Accepted 3 April 2018
Available online 11 April 2018
Corresponding Editor: Sven Bradler

Keywords:
DNA barcoding
Distribution
Elateroidea
The Mediterranean
Morphology
Neoteny
Variability

ABSTRACT

The neotenic elaterid genus *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) contains more than 40 species distributed primarily in the Mediterranean region. The precise number of species remains ambiguous due to the insufficient taxonomic investigation in several areas. Herein, we study *Drilus* diversity in Cyprus and we recognize the following species: *D. humeralis* Pic, 1931, *D. rectus* Schaufuss, 1867, and *D. rufipes* (Baudi di Selve, 1871). *Drilus testaceipes* Pic, 1933 syn. nov. is synonymized under *D. rectus*, and *D. truquii* (Baudi di Selve, 1871) syn. nov. is synonymized under *D. rufipes*. As consequence of these taxonomic changes, *Drilus humeralis* remains the only species endemic to Cyprus. Females of *D. rectus* and *D. rufipes* are described and figured for the first time, as well as the larvae of *D. rufipes*. A key to the males of *Drilus* species in Cyprus is given. *Drilus rectus* is recorded in Syria for the first time and *D. rufipes* is recorded in Rhodes. To examine the phylogenetic relationships of *Drilus* in Cyprus, we produced the *cox1*-3′, *cox1*-5′ and *rrnL* mtDNA sequences for available specimens of *D. rectus* and *D. rufipes* and merged them with data from GenBank. Results of the maximum likelihood analysis and Bayesian inference suggest a close relationship between *D. rectus* and *Drilus* cf. *mertliki* from Turkey, and a sister position of *D. rufipes* to a clade formed by the species from the Ionian Islands, Peloponnese, and Crete. Using the multigene barcoding approach including the above mentioned mitochondrial markers and the nuclear arginine kinase, we have been able to associate the different larval stages from Cyprus with the adult males of *D. rufipes*, and confirm the intraspecific variability in male body size and antennal coloration. Moreover, the low genetic difference in the *cox1*-3′ fragments indicates the close relationship between *D. rectus* populations from Cyprus and southern Turkey.

1. Introduction

The representatives of click-beetle tribe Drilini are characterized by the weakly sclerotized body and the strong sexual dimorphism having males fully winged and capable of flight, and neotenic females larviform and wingless (Crowson, 1972; Kundrata et al., 2015a). After several taxonomic changes in the past years Drilini currently contains about 130 species classified in eight genera of which only *Drilus* Olivier, 1790 and *Malacogaster* Bassi, 1834 occur in the Mediterranean region (Kundrata et al., 2015b; Kundrata and Bocak, 2011a,b, 2017; Trllova and Kundrata, 2015). Drilini fauna was studied for the Iberian Peninsula and Balearic Islands, Crete, Asia Minor and the Levantine mainland (Bahillo De La Puebla and López Colón et al., 2005; Kobieluszova and Kundrata, 2015; Kundrata et al., 2014b, 2015a; Petrzelkova and Kundrata, 2015). These contributions increased the number of known Drilini species in the Mediterranean up to more than 50 and helped us to improve the knowledge on their morphological variability, biology and ecology. However some areas in the region, as for example Cyprus, still remain underinvestigated.

Cyprus is a part of the Mediterranean Basin biodiversity hotspot (Myers et al., 2000) and represents a relatively isolated island with a high degree of endemism. New beetle species are being discovered regularly in Cyprus (Assmann et al., 2015; Háva, 2014; Makranczy, 2014; Petrzelkova et al., 2017) but still, no recent taxonomic studies or at least identification keys have been available for many lineages including Drilini. The first contribution to the Drilini of Cyprus was published by Baudi di Selve (1871) who described two species of *Malacogaster* and reported two species of *Drilus*. Later, Zurcher (1911) transferred both *Malacogaster* to *Drilus*, and Pic (1931, 1933) described two additional *Drilus* species from Cyprus. Since then, all

---

[*] Corresponding author.
E-mail addresses: kkramp@senckenberg.de (K. Kramp), robin.kundrata@upol.cz (R. Kundrata).

https://doi.org/10.1016/j.jcz.2018.04.001
0044-5231/

above mentioned species were only listed in catalogues by Wittmer (1944) and Bocak (2007); not a single comprehensive study of the Cypriot Drilini have ever been made. In this study, we used the collection material as well as the molecular data to investigate the intraspecific variability, phylogeny and distribution of *Drilus* species in Cyprus.

2. Material and methods

2.1. Morphology

We studied primarily adult male and female morphology of *Drilus* from Cyprus but we also examined diagnostic characters for available larval stages of *D. rufipes* (Baudi di Selve, 1871). The material cited in this paper was borrowed from the following institutional and personal collections: Natural History Museum, London, United Kingdom (BMNH), Muséum national d'Histoire naturelle, Paris, France (MNHN), Naturkundemuseum Erfurt, Germany (NKME), Naturhistorisches Museum Basel, Switzerland (NMBS), Národní muzeum, Prague, Czech Republic (NMPC), Hungarian Natural History Museum, Budapest, Hungary (HNHM), collection of Andreas Link, Haid/Ansfelden, Austria (PCAL), collection of George Kakiopoulos, Athens, Greece (PCGK), collection of Jan Batelka, Prague, Czech Republic (PCJB), collection of R. Kundrata, Olomouc, Czech Republic (PCRK), collection of R. Schuh, Wiener Neustadt, Austria (PCRS), and National Collection of Insects, The Steinhardt Museum of Natural History and Israel National Center for Biodiversity Studies, Department of Zoology, Tel Aviv University, Tel Aviv, Israel (SMNH-TAU). Genitalia were dissected after a short treatment in hot 10% aqueous solution of potassium hydroxide. The membranous parts of the female genitalia were dyed with chlorazol black. Habitus and important diagnostic characters were photographed using a digital camera attached to a stereoscopic microscope. Images were stacked using Helicon Focus 6 software (Helicon Soft Ltd.). The line illustrations of the female genitalia were derived from the photographs. The following measurements were taken with an ocular micrometer on a microscope: BL–body length, measured from the fore margin of head to the apex of elytra (in males) or body (females, larvae); BW–body width, measured at the widest part of the body; EL–elytral length; WHe–width of head including eyes; WHum–width at humeri; PL–pronotal length at midline; PW–pronotal width at the widest part; Edist–minimum interocular distance at the frontal part of cranium; Ediam–maximum eye diameter in the lateral view. If not stated otherwise, the width was measured at the widest part of the structure. Exact label data are cited for the examined material, with additional information placed within square brackets. Since *Drilus rectus* Schaufuss, 1867 and *D. rufipes* were recently treated by Kundrata et al. (2014b) we do not repeat the full descriptions here; instead we provide diagnoses and observations about the variability for these species. The morphological terminology follows (Kundrata et al. (2014b, 2015a) and Kundrata and Bocak (2017).

2.2. Taxon sampling and laboratory procedures

In the molecular dataset, we included 13 specimens (nine adults and four larvae) of *D. rufipes* from five different sites in Cyprus and two specimens of *D. rectus* from Cyprus and Turkey (Table 1). The voucher specimens are deposited in the collection of R. Kundrata, UP Olomouc (PCRK). Whole genomic DNA was extracted using the E.Z.N.A Tissue Kit (Omega Bio-tek Inc. Norcross, USA) according to the manufacturer protocol for tissue DNA. Elution was

Table 1

The list of material used in this study, with GenBank accession and voucher numbers. The codes starting with MF50 indicate sequences newly produced in this study.

Genus/Species	Geographical origin	*cox1-3'*	*cox1-5'*	*rrnL*	argK	Specimen voucher
Malacogaster passerinii	Italy, Sardinia	KF625432	MF507028	KF626029	N	UPOL RK0369
Drilus flavescens	Malta	KJ572890	KJ572942	MF506988	N	UPOL RK0446
Drilus flavescens	The Netherlands	KJ572927	KJ572943	N	N	EB2013-265
Drilus mauritanicus	Spain	HQ334016	KJ572949	HQ333743	N	UPOL RK0085
Drilus concolor	Hungary	HQ334007	KJ572946	HQ333734	N	UPOL RK0074
Drilus concolor	The Netherlands	KJ572893	KJ572945	N	N	RMNH.INS.559215
Drilus cf. *mertliki*	Turkey	HQ334013	KJ572947	HQ333739	N	UPOL RK0082
Drilus sp. E	Greece, Peloponnese	HQ334006	KJ572950	HQ333733	N	UPOL RK0073
Drilus sp. E	Greece, Zakynthos	KJ572891	KJ572951	N	N	RMNH.INS.559217
Drilus sp. L	Greece, Peloponnese	KJ572917	KJ572938	N	N	RMNH.INS.559211
Drilus sp. L	Greece, Peloponnese	KJ572918	KJ572937	N	N	RMNH.INS.871796
Drilus sp. L	Greece, Peloponnese	KJ572915	KJ572939	MF506990	N	UPOL RK0539
Drilus sp. D	Greece, Kalamos	KJ572912	KJ572932	N	N	RMNH.INS.559213
Drilus sp. M	Greece, Kefalonia	KJ572913	KJ572933	N	N	RMNH.INS.871808
Drilus sp. G	Greece, Peloponnese	KJ572914	KJ572934	N	N	RMNH.INS.559218
Drilus baenai	Greece, Crete	KJ572909	KJ572935	N	N	RMNH.INS.871921
Drilus baenai	Greece, Crete	KJ572907	KJ572936	N	N	EB2013-307
Drilus longulus	Greece, Crete	KJ572922	KJ572930	N	N	RMNH.INS.559192
Drilus longulus	Greece, Crete	KJ572924	KJ572931	N	N	UPOL RK0638
Drilus horasfakionus	Greece, Crete	KJ572900	KJ572941	N	N	RMNH.INS.559163
Drilus horasfakionus	Greece, Crete	KJ572901	KJ572940	N	N	RMNH.INS.559169
Drilus rectus	Turkey, Hatay Province	MF507014	N	MF506989	N	UPOL RK0205
Drilus rectus	Cyprus, Larnaka	MF507015	N	N	N	UPOL RK0916
Drilus rufipes	Cyprus, Limassol, Akrotiri	MF507018	MF507031	MF506994	N	UPOL RK1003
Drilus rufipes	Cyprus, Paphos, Amargeti	MF507020	N	MF506991	N	UPOL RK0788
Drilus rufipes	Cyprus, Paphos, Amargeti	MF507017	MF507030	MF506993	N	UPOL RK1002
Drilus rufipes	Cyprus, Paphos, Tsada	MF507016	MF507029	MF506992	N	UPOL RK1001
Drilus rufipes	Cyprus, Paphos, Tsada	MF507021	MF507033	MF506995	MF507006	UPOL RK1005
Drilus rufipes	Cyprus, Paphos, Tsada	MF507022	MF507034	MF506996	MF507007	UPOL RK1006
Drilus rufipes	Cyprus, Limassol, Zakaki	MF507019	MF507032	N	MF507005	UPOL RK1004
Drilus rufipes	Cyprus, Limassol, Zakaki	MF507023	MF507035	N	N	UPOL RK1007
Drilus rufipes	Cyprus, Limassol, Zakaki	MF507024	MF507036	N	MF507008	UPOL RK1008
Drilus rufipes	Cyprus, Paphos, Vretsia	MF507025	MF507037	MF506997	MF507009	UPOL RK1032
Drilus rufipes	Cyprus, Paphos, Vretsia	MF507026	MF507038	MF506998	MF507010	UPOL RK1033
Drilus rufipes	Cyprus, Paphos, Vretsia	N	MF507039	MF506999	MF507011	UPOL RK1034
Drilus rufipes	Cyprus, Paphos, Vretsia	MF507027	MF507040	N	N	UPOL RK1035

Table 2
List of primers used for PCR amplifications.

Fragment	Code	F/R	Sequence (5′ » 3′)	Reference
cox1-3'	SAR-L	F	CGCCTGTTTATCAAAAACAT	Palumbi et al. (1991)
	SBRH	R	CCGGTCTGAACTCAGATCACGT	
cox1-5'	LCO1490	F	GGTCAACAAATCATAAAGATATTGG	Folmer et al. (1994)
	HCO2198	R	TAAACTTCAGGGTGACCAAAAAATCA	
rrnL	C1-J-2183 (Jerry)	F	CAACAYTTATTTTGATTYTTTGG	Simon et al. (1994)
	TL2-N-3014 (Pat)	R	ATCCATTACATATAATCTGCCATA	
ArgK	AK168F	F	CAGGTTTGGARAAYCACGAYTCYGG	Wild and Maddison (2008)
	AK939R	R	GCCNCCYTCRGCYTCRGTGTGYTC	

performed twice with 100 µl Elution buffer each. A fragment of the nuclear gene arginine kinase (argK; 718 bp) and three fragments of the mitochondrial genome, i.e. *rrnL* (~510 bp) and two non-overlapping portions of cytochrome oxidase subunit I, *cox1*-3′ (723 bp) and *cox1*-5′ (658 bp), were sequenced. Amplifications were performed in 15 µl reactions containing 7.5 µl 2 × Qiagen Multiplex PCR Plus Master Mix (Qiagen, Hilden, Germany), 0.3 µM of each primer, RNase-free water and 0.5 µl template DNA. Amplification conditions were as follows: initial PCR activation step at 95 °C 5 min, 38 (40 for argK) cycles of 30 s denaturing at 95 °C, 90 s annealing (45 °C for *rrnL*, 47 °C for *cox1*, 57 °C for argK), 90 s extension at 72 °C, followed by a final extension of 30 min at 68 °C. Primers used for *cox1*-3′ (Simon et al., 1994), *cox1*-5′ (Folmer et al., 1994), *rrnL* (Palumbi et al., 1991) and argK (Wild and Maddison, 2008) are listed in Table 2. The PCR products were visualized on a 1.4% agarose gel stained with Gel Red (0.1, Biotium, Hayward, USA), purified with Exonuclease I and FastAP Thermosensitive Alkaline Phosphatase (Life Technologies, Darmstadt, Germany), and sequenced on an ABI3730XL sequencer using Big Dye v. 3.1 Terminator Kit (Thermo Fisher Scientific, Darmstadt, Germany) by Macrogen, Netherlands. GenBank accession numbers of new sequences are in Table 1.

2.3. Dataset assembling, alignment and phylogenetic analyses

Sequences were assembled and manually checked using Geneious 9.1.8 (Kearse et al., 2012). To investigate the phylogenetic position of Cypriot *Drilus* species, we merged the new sequences with the already exisiting data (Kundrata and Bocak 2011a; Kundrata et al., 2014a, 2015a). *Malacogaster passerinii* Bassi, 1834 was used to root the phylogenetic trees (Faucheux and Kundrata, 2017). Final dataset contained 35 terminals for which at least two markers out of three (*cox1*-3′, *cox1*-5′, *rrnL*) were available, with an exception of *D. rectus* from Cyprus, Larnaka (RK0788) for which only *cox1*-3′ was successfully amplified (Table 1). *Drilus* spp. D, E, G, L, M were designated as such following Kundrata et al. (2015a).

Sequences were aligned using the Mafft plugin for Geneious (default parameters; Katoh et al., 2002). Alignments of the length invariable protein-coding sequences were checked by amino acid translation. To assess the influence of noise due to saturation of the third codon positions, we used the index of substitution saturation (Iss) described by Xia et al. (2003) as implemented in DAMBE 5.6.14 (Xia, 2013) for all markers. Basic sequence statistics were calculated using MEGA 6.06 (Tamura et al., 2013). The best-fit partitioning schemes and partition-specific substitution models were tested using a greedy algorithm in PartitionFinder 1.1.1 (Lanfear et al., 2012) under the corrected Akaike information criterion (AICc). Maximum likelihood (ML) analysis was performed in RAxML 8.2.10 (Stamatakis, 2006) using the CIPRES web portal (Miller et al., 2010). We applied the GTR + I + G model and the partitioning scheme as defined by PartitionFinder. Bootstrap analysis was performed using the rapid bootstrapping option with 1000 iterations (Stamatakis et al., 2008). Bayesian inference (BI) was conducted in MrBayes 3.2.6 (Huelsenbeck and Ronquist, 2001) running on the CIPRES Science Gateway (Miller et al., 2010), with partitions and nucleotide substitution models as identified in PartitionFinder. Four chains were run for 40 million generations using the Markov chain Monte Carlo method. Results were checked in Tracer 1.5 (Rambaut and Drummond, 2007); the first 20% of trees were discarded as burn-in, and the posterior probabilities (PP) were determined from remaining trees.

3. Results

3.1. Taxonomy

3.1.1. Drilus species in Cyprus

Drilus humeralis Pic, 1931 (Fig. 1E,F,J)

Drilus humeralis Pic, 1931: 9.

Material examined. Holotype. Male, “CHYPRE [Cyprus], Mv. armenien [handwritten], type [handwritten], Type [red printed label], *humeralis* n. sp., *D. humeralis*” (MNHN).

Type locality. Northern Cyprus, Magaravank (= Sourp Magar), Armenian monastery located in the Kyrenia Mountains.

Diagnosis. *Drilus humeralis* is a distinctive species, easily recognizable from its congeners by the following combination of characters: head reddish brown; head including eyes distinctly wider than anterior pronotal margin; antennae serrate; pronotum subquadrate, 1.2 times as wide as long; median lobe only slightly surpassing parameres apically (Fig. 1E,F, J).

Redescription. Male. Size: Body 6.9 mm long, 3.5 times longer than width at humeri. Coloration: reddish brown to dark brown, with head, antennomeres I–II, pro- and mesothorax, and legs lighter; body covered with yellowish pubescence (Fig. 1A).

Head: including eyes slightly wider than anterior margin of pronotum (Fig. 1F), sparsely shallowly punctured; frontoclypeal part with wide shallow central depression, lateral margins above antennal sockets elevated, covered with sparse semierect pubescence; clypeal margin widely concave. Eyes medium-sized, their frontal distance 2.1 times eye diameter. Mandibles long, curved, basally covered with long erected setae; incisor margin with tooth medially. Labrum sclerotized, transverse, with smooth surface, sparsely covered with semi-erect setae; maxillary palpi 4-segmented, slender, basal palpomere short, palpomere II longest, about 1.5 times longer than palpomere III, palpomere III short, apical palpomere fusiform, apically flattened, obliquely cut; labial palpi 3-segmented, tiny, apical palpomere fusiform, pointed. Antennae 11-segmented, serrate, reaching one third of elytral length, scape robust, pear-shaped, pedicel short, minute, attached subapically to scape, antennomere III elongate, widened apically, antennomeres 4–10 serrate, slightly shorter than antennomere III, subequal in length, apical antennomere simple, longest (Fig. 1E).

Thorax: pronotum slightly convex, subquadrate, widest at middle, 1.2 times wider than length at midline; anterior margin slightly sinuous; lateral margins convex, slightly elevated, mainly posteriorly; posterior margin bisinuate, produced posteromedially; anterior angles inconspicuous, posterior angles obtuse (Fig. 1F);

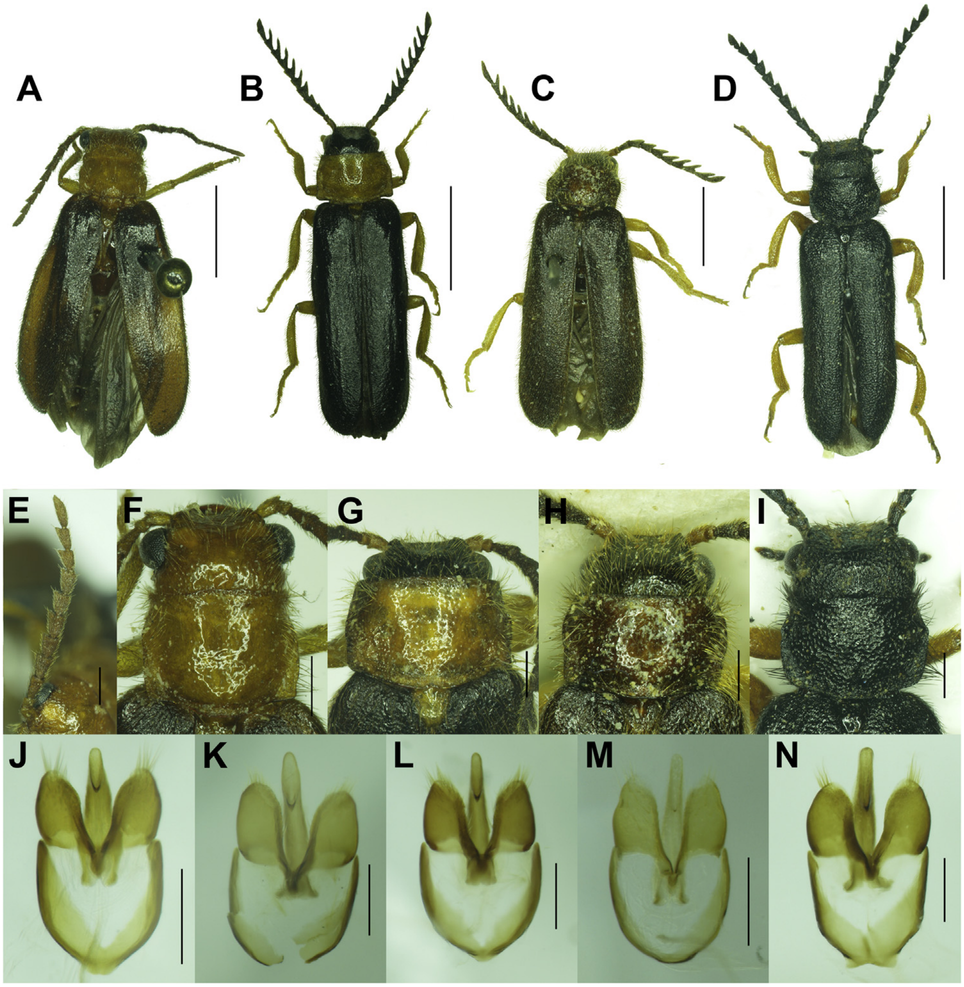


Fig. 1. *Drilus* spp. from Cyprus, males. Habitus. (A) *D. humeralis* Pic, 1931, holotype. (B) *D. rectus* Schaufuss, 1867. (C) *D. rectus* Schaufuss, 1867 (syntype of *D. testaceipes* Pic, 1933). (D) *D. rufipes* (Baudi di Selve, 1867). Antenna. (E) *D. humeralis* Pic, 1931. Pronotum. (F) *D. humeralis* Pic, 1931. (G) *D. rectus* Schaufuss, 1867. (H) *D. rectus* Schaufuss, 1867 (syntype of *D. testaceipes* Pic, 1933). (I) *D. rufipes* (Baudi di Selve, 1867). Aedeagus. (J) *D. humeralis* Pic, 1931. (K) *D. rectus* Schaufuss, 1867. (L) *D. rectus* Schaufuss, 1867 (syntype of *D. testaceipes* Pic, 1933). (M) *D. rufipes* (Baudi di Selve, 1867), a specimen from Livadia, Larnaca (3.8 mm). (N) *D. rufipes* (Baudi di Selve, 1867), a specimen from Alassa, Limassol (7.9 mm). Scale bars – 2.0 mm (A–D), 0.5 mm (E–I), 0.3 mm (J–N).

surface of disc almost smooth, covered sparsely with shallow punctures, with sparse semierect pubescence, denser at angles and lateral margins. Scutellum linguiform, slightly longer than wide, sparsely punctate, covered with semi-erect setae; apically rounded. Prosternum transverse, its surface uneven, with anterior margin almost straight, posterior margin medially elevated and produced, forming minute ridge-like prosternal process. Mesoventrite v-shaped, with shallow furrow medially. Elytra relatively long, about 0.7 times as long as body, combined about 2.5 times as long as wide, subparallel-sided, wrinled (mainly basally), covered with short semierect pubescence. Legs slender, slightly compressed, with sparse, long, semierect setae, tarsomeres 1–4 gradually shortened, tarsomere 4 shortest, with lobe ventrally, apical tarsomere longest, slender, slightly longer than combined lengths of tarsomeres 3 and 4; claws simple, slender, basally with long setae. Male genitalia: phallus robust, considerably curved (in lateral view), slightly longer than phallobase, with short subapical hook; parameres shorter than phallus, rounded at apex, with long setae apically; phallobase robust, about as long as wide (Fig. 1J).

Female and immature stages unknown.

Measurements. BL 6.9 mm, EL 5.0 mm, WHe 1.4 mm, WHum 2.0 mm, PL 1.2 mm, PW 1.4 mm, Edist 0.90 mm, Ediam 0.45 mm.

Distribution. Northern Cyprus (Fig. 3).

Drilus rectus Schaufuss, 1867 (Figs. 1B,C,G,H,L,M; 2 A, C, E)

Drilus rectus Schaufuss, 1867: 84.

Drilus *testaceipes* Pic, 1933: 9, **syn. nov.**

Material examined. CYPRUS. Syntype of *D. testaceipes*. Male, "Cyprus, Nicosia, 30.iv.32, H. M. Morris, Pres. by Imp. Inst. Ent. Brit. Mus. 1933-295, 701, Type [white round label with red margin; printed], gardé 1 ex, sans antennes, *Drilus testaceipes* n. sp." (BMNH). Syntype of *D. testaceipes*. Male, "Cyprus, Nicosia, 30.iv.32, H. M. Morris, 701, *Drilus testaceipes* n. sp." (MNHN). – Male, "Cyprus, Nicosia, 30.iv.32, H. M. Morris, 701, Pres by Imp. Inst. Ent. Brit. Mus. 1933-47, *Drilus rectus* Schauf, det. W. Wittmer, *Drilus rectus* Schf., G. E. Bryant det." (BMNH); male, "Cyprus, Skarinou, 29.–31.v.1933, leg. Krajcik, coll. general National Museum Prague, Czech Republic" (NMPC); male, "Cyprus, Kyrenia, Karavas, 469, Dr. Pfeffer lgt., ex coll. Pfeffer, Nat. Mus. Prague, *rectus*" (NMPC); male, "Cyprus, Distr. Lemesos, Lemesos E, 06.–13.iv.2012, 34°42′20″N 33°06′11″E, 0–40 m NN, leg. A. Kopetz, #01" (NKME); male (in vial with 96% alcohol), "Cyprus, Larnaka distr., 2.2 km W Pano Lefkara, 625 m, 12.iv.2013, Z. Lucbauer leg., RK0916" (PCRK); female, "Cyprus, Nicosia, 30. IV. 32, H. M. Morris, *Drilus rectus* ♀ Sch., 701, Pres. by Imp. Inst. Ent. Brit. Mus. 1933-47" (BMNH); SYRIA. Male, "Syria, Qardaha, Latakia env., 2.v.1982, A. Olexa, J. Batelka, Praha, Purchase 2005, coll. Aldo Olexa" (PCJB).

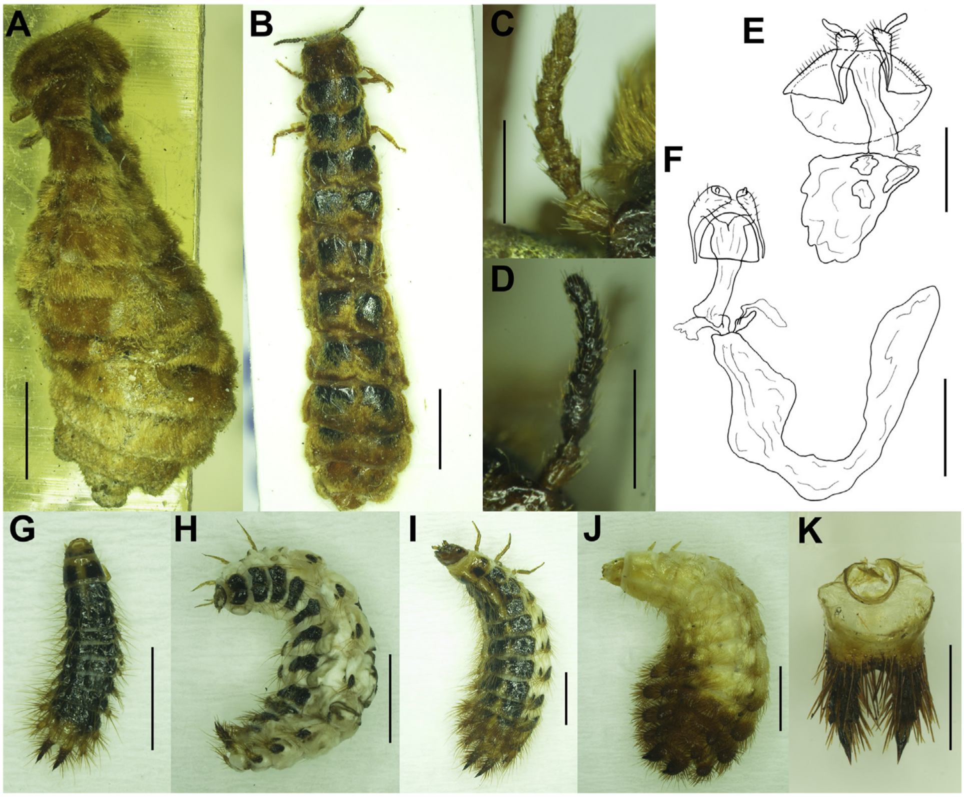


Fig. 2. *Drilus* spp. from Cyprus, females and larvae. Females. Habitus. (A) *D. rectus* Schaufuss, 1867. (B) *D. rufipes* (Baudi di Selve, 1871). Antenna. (C) *D. rectus* Schaufuss, 1867. (D) *D. rufipes* (Baudi di Selve, 1871). Female genitalia. (E) *D. rectus* Schaufuss, 1867. (F) *D. rufipes* (Baudi di Selve, 1871). Larvae of *D. rufipes* (Baudi di Selve, 1871). (G) early instar of active larva. (H–I) late instars of active larva. (J) pseudopupa. (K) larval cerci. Scale bars – 2.0 mm (A–B, G–J), 1.0 mm (E–F, K), 0.5 mm (C–D).

Type locality. *Drilus rectus*: Lebanon: Beirut; southern Turkey: Antiochia. *Drilus testaceipes*: Cyprus: Nicosia.

Diagnosis. Male. *Drilus rectus* differs from *D. rufipes* in having paler pronotum (black in *D. rufipes*; Fig. 1G–I), pectinate antennae (serrate in *D. rufipes*; Fig. 1B–D), and body surface not rugose, sparsely punctate (rugose, wrinkled, with contiguous large punctures in *D. rufipes*; Fig. 1G–I). *Drilus humeralis* has reddish head and antennae, serrate antennae, subquadrate pronotum, and relatively shorter and more robust median lobe of aedeagus (Fig. 1E,F,J). Female. *Drilus rectus* is characteristic by its robust body, thorax and abdomen covered completely with very dense setae, conspicuously elongate styli, and short robust bursa copulatrix (Fig. 2A,E).

Description of female. Larviform, body elongate. Size: BL 10 mm, BW 4 mm. Coloration: light brown to brown, head darker, medially reddish brown, dorsal surface of thoracic and abdominal segments with slightly darker sublateral markings, less apparent in last segments; body (especially thorax and abdomen) covered with very dense yellowish pubescence (Fig. 2A). Head: prognathous, well sclerotized, small, narrower than pronotal anterior margin. Eyes small, located laterally. Antennae 11-segmented, 0.8 times as long as head width, filiform, sparsely covered with long semierect setae; apical antennomere minute, narrow, with small conical appendage attached apically (Fig. 2C). Mandibles robust, shiny, considerably curved, incisor margin medially with small tooth (only part of right mandible present). Labrum well sclerotized, transverse. Thorax: pronotum widest at posterior two thirds; surface of thoracic and abdominal tergites uneven. Abdomen: with nine visible segments, apical segment much narrower and smaller. Genitalia: ovipositor with fused valviferes and coxites; styli elongate, about 3.5 times as long as wide, about 1.3 times as long as coxite width, less than 3 times shorter that fused valvifer and coxite. Vagina simple, slender, elongate, sac-like; bursa copulatrix short, robust, sac-like (Fig. 2E).

Measurements of *D. testaceipes* syntypes. BL 7.1–8.4 mm, EL 5.4–6.1 mm, Whum 2.1–2.5 mm, Whe 1.4–1.6 mm, PL 1.0–1.2 mm, PW 1.7–2.0 mm, Edist 0.90–1.10 mm, Ediam 0.45–0.50 mm.

Variability. Males. This species exhibits the intraspecific variability in the coloration (body paler or darker brown, thorax and abdomen yellowish brown to chestnut brown), body size (BL 5.1–10.4 mm; specimens from Cyprus: 6.0–9.0 mm), shape of pronotum (PW/PL 1.3–1.6, including the specimens from Cyprus), and parameres (more or less elongate and rounded apically). A specimen from Limassol (NKME) has pronotum with reduced posterior angles and male genitalia with a relatively slightly longer phallus but until more material is available, we keep this specimen under *D. rectus*.

Distribution. Cyprus (Fig. 3), Israel, Lebanon, Syria, Turkey. **First record for Syria.**

Remarks. We found three adult males collected by H. M. Morris in 1932 in Nicosia; two of them are labelled as *D. testaceipes* syntypes and one as *D. rectus*. The specimens of *D. testaceipes* have slightly darker pronota (Fig. 1H) but there is a gradation in coloration of pronotum within all *D. rectus*/*testaceipes* specimens and similar variable coloration was reported for *D. rectus* from the mainland Levant (Petrzelkova and Kundrata, 2015). Furthermore, both external morphology and male genitalia of all examined representatives of *D. testaceipes* and *D. rectus* suggest that they represent a single species (Fig. 1B,C,G,H,K,L) so we herein synonymize *Drilus testaceipes* Pic, 1933 with *Drilus rectus* Schaufuss, 1867. For more information on the populations of *D. rectus* in Lebanon, Turkey and Israel see Kundrata et al. (2014b), Kobieluszova and Kundrata (2015), and Petrzelkova and Kundrata (2015).

Drilus rufipes (Baudi di Selve, 1871) (Figs. 1D,I, M,N; 2B,D,F–K)
Malacogaster rufipes Baudi di Selve, 1871: 62.

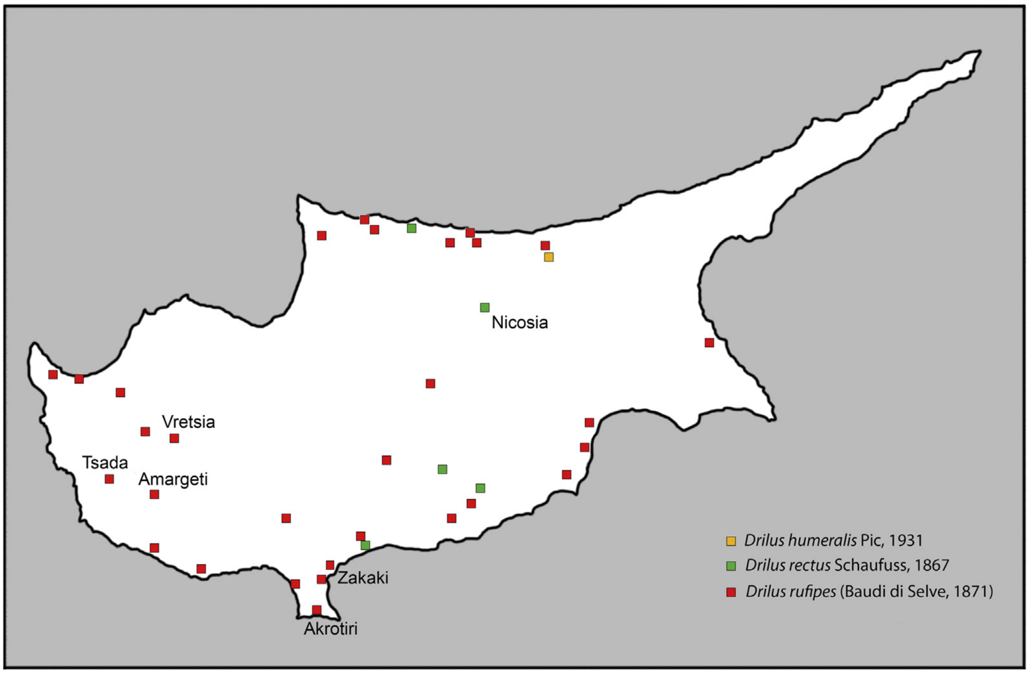


Fig. 3. The distribution of *Drilus* species in Cyprus.

Drilus rufipes: Zurcher (1911): 243

Drilus reitteri Bourgeois, 1908: 241; synonymized by Zurcher (1911: 243).

Malacogaster truquii Baudi di Selve, 1871: 61, **syn. nov.**

Drilus truquii: Zurcher (1911): 243.

Material examined. CYPRUS. Male, "Cyprus, Pentalia, 21 km NE Pafos, 34°50.4′N 32°36.2′E, 555 m, 9.iv.2008, L. Friedman" (SMNH-TAU); male, "Cyprus, Akrotiri Bay, 26.iii.1947, G. A. Mavromoustakis, B. M. 1947-397, Akrotiri Bay, 26.iii.47" (BMNH); male, "Livadia, Cyprus, ex Orig. Samlg., J. Breit Wien, *Malacogaster rufipes* Bdi."(NMBS); male, "Cyprus, Akrotiri Forest, 18.iv.1937, G. A. Mavromoustakis, B. M. 1937-808" (BMNH); male, "Cyprus, Famagusta, 13.iii.1932, E. E. Green, B. M. 1932-503, *Malacogaster rufipes* Bdi, det. W. Wittmer désire" (BMNH); 2 males, "Cyprus, Akrotiri Bay, 26.iii.1947, G. A. Mavromoustakis, B. M. 1947-397" (BMNH); male, "Cyprus, Larnaka, Glaszner, *Malacogaster rufipes* Bdi, det. W. Wittmer" (HNHM); male, "Cyprus, Akrofiri Forest, 18.iv.1937, G. A. Mavromoustakis, B. M. 1937-808" (BMNH); male, Livadia, Cyprus, ex Orig. Samlg, J. Breit Wien" (NMBS); 4 males, "Cyprus env., Larnaca, Kiti, III. 2006, leg. W. Hansely, coll. R. Schuh (Austria)" (PCRK, PCRS); male, "Kiti - Zypern, 2008, leg. W. Hansely" (PCRS); 2 males, "Cyprus, Paphos, Amargeti, 21.iv.2012, Ch. Makris lgt., RK0788, RK1002" (PCRK); male, "Panagia, April 2007, Ch. Makris lgt." (PCRK); male, "CY-Pafos, Panagia, 800 m, 9-4-2010, On a white wall, Leg. Ch. Makris" (PCRK); male, "Cyprus, Distr. Lemesos, Lemesos, 16 km NW Alassa, W 34°46′19″N 32°54′38″E, 08.iv.2012, 250 mNN, leg. A. Kopetz #07" (NKME); male, "Cyprus, Distr. Lemesos, Lemesos, 15 km NW Alassa, NW 34°46′02″N 32°54′25″E, 250 m NN, 10.iv.2012, leg. A. Kopetz #16" (NKME); male, "CY, Prov. Lefkosia 82, Politiko 1 km S, Macchia, 400 m, Fritzlar leg., 21.iii.2012" (NKME); male, "CY, Prov. Lemesos 73, Pissouri S, beweidetes, Plateau, 200 m, Fritzlar leg., 15.iii.2012" (NKME); male, "Cyprus, Distr. Lemesos, Lemesos, 16 km NW, Alassa, W, 250 mNN, 34°46′19″N 32°54′38″E, 08.iv.12, leg. D. Frenzel #07" (NKME); 2 males, "CY, Prov. Larnaka 74, Kalavasos 2 km N, Flusstal, 100 m, Fritzlar leg., 16.iii.2012" (NKME); male, "CY, Prov. Larnaka 76, Choirokoitia 2 km NW, Loulas Farm, 10 m, Fritzlar leg., 17.iii.2012" (NKME); male, "Cyprus, N, Lapta, 5 km SW, stony meadow with bushes, 560 m NN, 35°19′36″N, 33°07′20″E, 31.II.15, leg. D. Frenzel #31" (NKME); male, "Cyprus, Polis, SE, Lysos, N, dry slope, peach trees, bushes, 35°00′11″N, 32°30′26″E, 430 m NN, 31.III.2016, leg. D. + M. Frenzel #65" (NKME); 2 males, "N-Cyprus, Girne, 5 km SW, Saint Hilarion Castle, 31.III.2015 35°18′37″N, 33°16′53″E–35°18′45″N, 33°16′23″E, 475 m – 575m NN leg. A. Kopetz #28" (NKME); male, "N-Cyprus, Girne, 22 km E, Karaağaç, S, olive grove, sheep-run, 350 m NN, 35°18′41″N, 33°33′25″E, 29.III.2015, leg. A. Kopetz #24" (NKME); male, "N-Cyprus, Girne, 19 km W, Karsiyaca, scrubby slope, 90 m NN, 35°20′53″N, 33°06′46″E, 03.IV.2015, leg. A. Kopetz #40" (NKME); male, "N-Cyprus, Çamlibel, 6 km SW,Tepebasi, W, pine forest, macchia, 180 m NN, 35°18′10″N, 33°00′11″E, 30.III.2015, leg. A. Kopetz #25" (NKME); 3 males, "N-Cyprus, Girne SE, urban area, 50 m NN, 35°19′41″N, 33°20′18″E, 28.III.–06.IV.2015, leg. D. Frenzel #23" (NKME); male, "Cyprus m., 26.iii.2004, Akrotiri env., 16 km S of Lemesos, S. Kadlec lgt., ex coll. S. Kadlec, National Museum Prague, Czech Republic" (NMPC); 2 males, "Cyprus, 1.iv.2000, Germasogeia env. (NE of Limassol), St. Kadlec lgt., ex coll. S. Kadlec, National Museum Prague, Czech Republic" (NMPC); male, "Cyprus centr., Trodos mts., Odou env., 27.iii., 1.iv.2004, leg. P. Kabátek, coll. general National Museum Prague, Czech Republic" (NMPC); 3 males, "Cyprus, Kouklia (n. Pafos), 2.iv.2000, S. Kadlec leg." (NMPC); 3 males, "Cyprus, Germasogeina [= Germasogeia] env. (NE of Limassol), 1.iv.2000, S. Kadlec leg." (NMPC); 4 males, "Cyprus, 5 km W of Latsi (Akamas Peninsula), 1.–10.iv.2000, S. Kadlec leg." (NMPC); male, "CYP, Fyti, 34°55′40″N 32°33′09″E, 25.iii.2014 (11,180), leg. Andreas Link" (PCAL); male, "Cyprus, Limassol, Akrotiri, 25.ii.2012, Ch. Makris lgt., RK1003" (PCRK); 3 males, "Cyprus, Limassol, Zakaki, 23.iii.2012, Ch. Makris lgt., RK1004, RK1007–1008" (PCRK); 3 males, "Cyprus, Paphos, Tsada, 3.iv.2012, Ch. Makris lgt., RK1001, RK1005–1006" (PCRK); male, "Bellapais nr. Kyrenia, Cyprus, 13. iv. 1974, BMNH {E} 1998-129. W R B Hynd" (BMNH); female, "Cyprus, April 2005, Ch. Makris lgt." (PCRK); 17 larvae (6 active larvae, 13 pseudopupae; in vials with 96% alcohol), "Cyprus, Pafos, Vretsia, 03–05.vii.2015, in shell of *Monacha syriaca*, Kundrata & Petrželková leg., RK1032–RK1035" (RKPC). GREECE. Male, "Dodecannesus, Rhodes island, inside Lindos town, on white wall of a house, 31.iii. 2009, Kakiopoulos lgt.:" (PCGK).

Type locality. Both *D. rufipes* and *D. truquii*: Cyprus (with no additional data).

Diagnosis. Male. *Drilus rufipes* is easily recognizable by its dark brown to black body with yellowish femora, tibiae, basal 2–3 tarsomeres and apical two abdominal ventrites, and body surface coarsely wrinkled, rugose, with large contiguous punctures, which is a unique character among *Drilus* species (Fig. 1D,I). Female. *Drilus rufipes* differs from *D. rectus* in having relatively slenderer and more elongate body, darker dorsal sublateral markings, sparser body vestiture, conspicuously shorter styli, and much more elongate bursa copulatrix (Fig. 2A,B,E,F).

Description of female. Larviform, body elongate. Size: BL 12 mm, BW 2.8 mm. Coloration: light brown to reddish brown, head darker, reddish brown, antennomeres III–XI dark brown, dorsal surface of meso- and metathoracic and abdominal segments with large dark brown markings; body covered with dense yellowish pubescence, pubescence sparse or absent on dorsal markings (Fig. 2B). Head: prognathous, well sclerotized, small, narrower than pronotal anterior margin. Eyes small, located laterally. Antennae with 10 or 11 antennomeres [unfortunately, the only available specimen has antennae with different numbers of antennomeres, i.e. left with 10, right with 11], 0.8 times as long as head width, filiform, sparsely covered with long semierect setae; apical antennomere with small conical appendage attached apically (Fig. 2D). Mandibles shiny, considerably curved, incisor margin medially with small tooth. Labrum well sclerotized, transverse. Thorax: pronotum subparallel-sided; surface of thoracic and abdominal tergites uneven. Abdomen: with nine visible segments, apical segment much narrower and smaller. Genitalia: ovipositor with fused valviferes and coxites; styli short, minute, slightly longer than wide, about 0.3 times as long as coxite width, more than 10 times shorter than fused valvifer and coxite. Vagina simple, slender, relatively long, sac-like; bursa copulatrix elongate, sac-like (Fig. 2F).

Description of larva. Active larva. Body elongate, slightly widened towards apex, often twisted to C-shape. Size: BL up to 9 mm, BW up to 3 mm. Coloration: yellowish to light brown, head orange to reddish brown, dorsally with black markings (larger in early instars, smaller in later instars), with black spots laterally near eyes, dorsal surface of thoracic and abdominal segments either black with only pro- and mesonotum light brown medially (early instars) or black with all segments light brown medially (later instars), ventral surface of abdominal segments 1–7 either black (early instars) or with two pairs of black spots on each side, sublateral one small, one near middle large (later instars); lateral pleural and tergal processes black, with apices brown, cerci dark brown to black; body covered with long yellowish to light brown pubescence, denser and longer on abdomen (Fig. 2G–I). Head: prognathous, well sclerotized, small, narrower than frontal pronotal margin. Mandibles sclerotized, narrow and falcate. Thorax and abdomen: with heavily sclerotized and pigmented tergites, with long setae, especially dorsally. Lateral pleural and tergal processes well developed, lateral ones larger than tergal ones. Last segment small, slender. Cerci slightly bent upward, densely covered with long pubescence, cerci apically acuminate; with long apical part (Fig. 2K).

Pseudopupa. Body twisted to C-shape, robust, widened apically, less sclerotized than previous instars. Size: BL up to 9 mm, BW up to 4 mm. Coloration: pale yellowish, with last abdominal tergites brown, covered with long semi-erct setae, denser dorsally and apically (Fig. 2J). Head: mouthparts reduced, mandibles shorter than in previous instars. Thorax and abdomen: lateral pleural and tergal processes well developed, lateral ones considerably larger than tergal ones. Legs reduced, shorter than in previous instars. Cerci thickened, apically acuminate, covered densely with long setae (Fig. 2J).

Table 3
The list of adult male specimens of *Drilus rufipes* (Baudi di Selve, 1871) from Cyprus sequenced in this study, with information on the variability in their body size and antennal coloration. L - body length (mm), Wh - width at humeri (mm), A - antennomere.

Voucher	District, locality	L	Wh	L/Wh	coloration of antennae
RK1003	Limassol, Akrotiri	3.8	1.2	3.2	entire antennae black
RK1004	Limassol, Zakaki	5.0	1.6	3.1	entire antennae black
RK1007	Limassol, Zakaki	4.6	1.4	3.3	entire antennae black
RK1008	Limassol, Zakaki	4.3	1.3	3.3	A1 reddish black, A2–A11 black
RK0788	Paphos, Amargeti	7.5	2.4	3.1	A1 dark red, A2–A11 black
RK1002	Paphos, Amargeti	6.8	2.3	3.0	A1 reddish black, A2–A11 black
RK1001	Paphos, Tsada	7.6	2.6	2.9	A1 pale red, A2–A11 black
RK1005	Paphos, Tsada	4.9	1.5	3.3	A1 reddish black, A2–A11 black
RK1006	Paphos, Tsada	5.7	2.0	2.9	A1 reddish black, A2–A11 black

Variability. Males. There is an intraspecific variability in the coloration of antennae in *D. rufipes*. Typical specimens have antennae black with only the scape reddish to reddish black, however some specimens have both scape and pedicel reddish to reddish black, several specimens (mainly those collected in the first half of 20th century) have entire antennae reddish brown, and several specimens have entire antennae black (Tables 3, S1). Additionally, this species shows variability in the body size (3.0–8.7 mm), the relative body width (BL/Whum 2.9–3.5), the relative width of pronotum (PW/PL 1.3–1.6), and the relative eye size (Edist/Ediam 2.3–3.0).

Distribution. Cyprus (Fig. 3), Greece (Rhodes), Israel. **First record for Greece**.

Remarks. Baudi di Selve (1871) described *D. rufipes* and *D. truquii* from Cyprus (both under the genus *Malacogaster*) and differentiated them mainly by the size (*D. rufipes* smaller, *D. truquii* larger) and the coloration of the antennae (scape and pedicel more or less black in *D. rufipes*, scape reddish in *D. truquii*). We failed to find the type material of these species in the main European collections but we consider the identity of these species to be firmly established and confirmed based on the original descriptions and by the study of the small specimens from the historical collections identified as *D. rufipes*. Zurcher (1911) reported the variability in pronotum punctation and coloration of antennae for *D. rufipes*, however, he kept both species as valid. Here, we examined in detail a large series of *D. rufipes* and we observed a gradation in both body size (from smaller and relatively narrower specimens to larger and relatively wider specimens) and antennae coloration (from entirely reddish brown antennae through dark brown to black antennae with only scape or scape and pedicel reddish to entirely black antennae) (Tables 3, S1). Therefore, we herein synonymize *Drilus truquii* (Baudi di Selve, 1871) under *Drilus rufipes* (Baudi di Selve, 1871). For more information on the populations from the mainland Levant see Kundrata et al. (2014b) and Petrzelkova and Kundrata (2015).

The examined larvae were collected in the shells of *Monacha syriaca* (Ehrenberg, 1831) (Gastropoda: Hygromiidae) in the leaf litter under the oak in Vretsia, Paphos (locality figured in Petrzelkova et al., 2017). The different larval stages of *Drilus* were described in detail by Baalbergen et al. (2014, 2016). We identified several instars of active larvae and the pseudopupae among the collected material (Fig. 2G–J), and additionally, we detected a large number of larval exuviae in the snail shells. This is the first report of *Drilus* larvae from Cyprus.

3.1.2. Drilus *species not confirmed in Cyprus*

***Drilus adustus*(Chevrolat, 1854)**

Malacogaster adustus Chevrolat, 1854: 433.

Drilus adustus (Chevrolat, 1854): Kundrata et al. (2014b): 458.

Drilus posticus Schaufuss, 1867: 82; synonymized by Kundrata et al. (2014b: 458).

Remark. This species was originally described from Lebanon (Chevrolat, 1854) and later reported (as *D. posticus*) from Cyprus by Baudi di Selve (1871). Subsequent authors, however, reported this species only from the mainland Levant (Olivier, 1910; Wittmer, 1944; Bocak, 2007; Kundrata et al., 2014b). We have not found any specimen of *D. adustus* from Cyprus despite the intensive search in most European collections.

3.1.3. An identification key to males of Drilus *species in Cyprus*

1. Pronotum black; tarsi bicolor (basally yellowish, apically dark brown); antennae slightly serrate; body surface distinctly coarsely wrinkled . . . . *D. rufipes* (Baudi di Selve, 1871)

– Pronotum yellowish to reddish brown; tarsi unicolor, pale; antennae serrate to pectinate; body surface not coarsely wrinkled. 2

2. Head of the same color as pronotum; antennae pale brown, serrate; pronotum subquadrate, 1.2 times as wide as long . . . . *D. humeralis* Pic, 1931

– Head darker than pronotum; antennae dark brown, serrate to pectinate; pronotum transverse, 1.3–1.6 times as wide as long . . . . *D. rectus* Schaufuss, 1867

3.2. Alignment parameters, substitution saturation and PartitionFinder results

The aligned concatenated dataset of 35 terminals included 1906 homologous positions (723, 658 and 525 positions for *cox1*-3′, *cox1*-5′ and *rrnL*, respectively), with 1229 conserved, 675 variable, and 566 parsimony informative characters. The nucleotide composition for individual markers was as follows: *rrnL*: A = 29.2, C = 10.8, T = 41.8, G = 18.2; *cox1*-3′: A = 33.1, C = 18.6, T = 32.1, G = 16.2; *cox1*-5′: A = 28.1, C = 22.3, T = 31.4, G = 18.2). The substitution saturation index (Iss) values for *rrnL* and all codon positions in both *cox1* fragments were significantly lower than the critical values for the symmetrical tree topology. The significantly higher Iss values were present only for the 3rd codon positions in *cox1*-5′ for the extremely asymmetrical (and probably not realistic) tree topology. The detailed results of the saturation tests are provided in Table S2. These results indicate that there is little substitution saturation in our sequence data. PartitionFinder identified the following five partitions for the given dataset as the optimal scheme: *cox1*-3′ position 1 + *cox1*-5′ position 2, *cox1*-3′ position 2 + *cox1*-5′ position 3, *cox1*-3′ position 3, *cox1*-5′ position 1, and *rrnL*. The GTR + I + G, HKY + I, HKY + G, GTR + I + G, and GTR + I + G nucleotide substitution models were selected for the above mentioned partitions, respectively.

3.3. Phylogenetic analyses

The ML and BI analyses produced almost identical tree topologies with roughly similar statistical support for major clades (Fig. 4). *Drilus rectus* was recovered as a sister to *Drilus* cf. *mertliki* from Turkey, and both were in a clade with *D. concolor*. The *cox1*-3′ mtDNA sequences differ in 1.4% bases between *D. rectus* specimens from Turkey (Hatay province) and Cyprus. *Drilus rufipes* was sister to a clade of *Drilus* species from the Ionian Islands, Peloponnese and Crete with the maximal statistical support in both analyses (Fig. 4). *Drilus* larvae from Cyprus were recovered within the *D. rufipes* clade. There was no clear geographic structure within *D. rectus* populations, only the specimens from Limassol: Zakaki and Paphos: Vretsia formed a robustly supported subclade. The maxi-

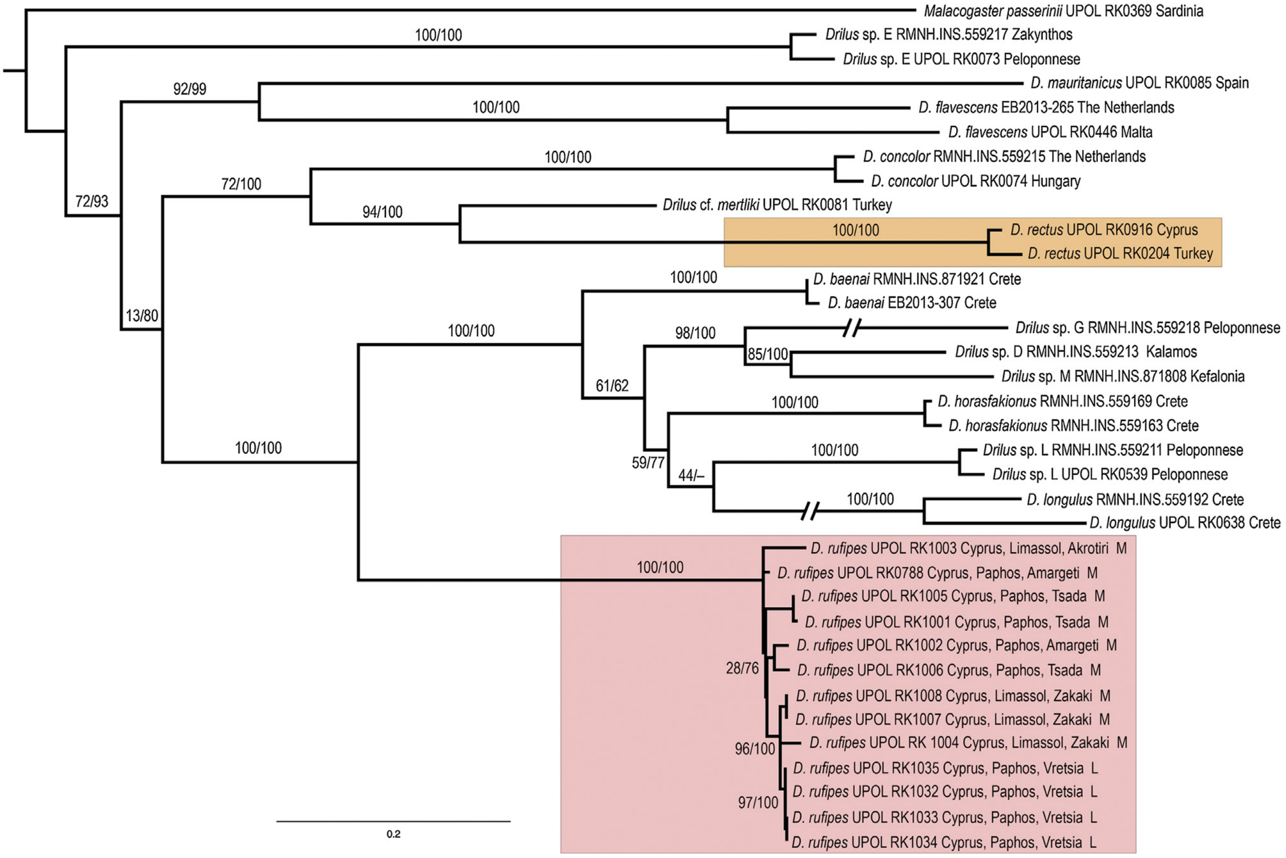


Fig. 4. The phylogenetic hypothesis for *Drilus* Olivier, 1790 based on the ML analysis of the concatenated dataset (*cox1*-3′, *cox1*-5′, *rrnL*) for 35 terminals aligned by Mafft. Numbers at the branches indicate ML bootstrap values and Bayesian posterior probabilities, respectively. "–" refers to clades contradicted by the analyses. "M" and "L" in *D. rufipes* individuals refer to male and larva, respectively.

Table 4
The maximum uncorrected pairwise genetic distances (p-distances) among populations of *Drilus rufipes* (Baudi di Selve, 1871) from Cyprus. Numbers in parentheses represent numbers of individuals included.

District, locality		p-distances (%)			
	Voucher numbers	*cox1-3’*	*cox1-5’*	*rrnL*	argK
Limassol, Zakaki	RK1004, 1007–08	1.0 (3)	0.9 (3)	–	0.1 (2)
Paphos, Amargeti	RK0788, 1002	1.4 (2)	–	0.0 (2)	–
Paphos, Tsada	RK1001, 1005–06	2.2 (3)	2.1 (3)	0.8 (3)	0.0 (2)
Paphos, Vretsia	RK1032–1035	0.1 (3)	0.2 (4)	0.0 (3)	0.4 (3)
all	RK0788, 1001–08, 1032–35	3.0 (12)	3.6 (12)	1.0 (9)	0.4 (7)

mum uncorrected pairwise distances among *D. rufipes* individuals were 3.0% for *cox1*-3′, 3.6% for *cox1*-5′, 1.0% for *rrnL*, and 0.4% for argK (Tables 4, S3–S6).

4. Discussion

4.1. Diversity and distribution of Drilus species in Cyprus

Studies on *Drilus* are complicated by the lack of data on their inter- and intraspecific variability, ecology and species distributions. Here, we carried out the first comprehensive study on *Drilus* diversity in Cyprus since Baudi di Selve (1871). Previous studied reported six species from this island, three of them endemic (Baudi di Selve, 1871; Pic, 1931, 1933; Zurcher 1911). We confirm the presence of *D. humeralis*, *D. rectus*, *D. rufipes*, *D. testaceipes*, and *D. truquii*, but we have not been able to locate any specimen of *D. posticus* (synonymized with *D. adustus* by Kundrata et al., 2014b) which is known from Lebanon and was reported from Cyprus only by Baudi di Selve (1871). Based on the original descriptions, *D. testaceipes* differs from *D. rectus* only in the darker pronotum, and *D. truquii* from *D. rufipes* in the body size and coloration of antennae (Baudi di Selve, 1871; Pic, 1933; Schaufuss, 1867). However, intraspecific variability in body size and coloration is commonly encountered in Drilini (Kundrata, 2012; Kundrata and Bocak, 2017). Indeed, we found the pronotal color gradation from pale reddish to reddish brown in *D. rectus* (Fig. 1G,H) and the gradation in body size and antennae coloration in *D. rufipes* (Tables 3, S1) so we synonymize *D. testaceipes* with *D. rectus* and *D. truquii* with *D. rufipes*. Both here synonymized species were known only from Cyprus, and after our taxonomic investigation the only remaining Cypriot endemic is *D. humeralis* known from a single specimen collected in the Kyrenia Mountains in the northern part of the island (Fig. 3). Remaining two species, i.e. *D. rectus* and *D. rufipes*, seem to be quite widespread compared to most *Drilus* species in the Mediterranean. *Drilus rectus* is known from several localities in Cyprus (Fig. 3) and also from the region ranging from the southern Turkey to Israel. *Drilus rufipes* was originally described from Cyprus, where it is known mainly from the southern part of the island (Fig. 3). Later, this species was synonymized with *D. reitteri* Bourgeois, 1908 from Israel (Zurcher, 1911). Here, we report a specimen of *D. rufipes* collected in Rhodes, the largest of the Dodecanese islands near the Anatolian coast of Turkey. It is obvious from the current distributional map of *Drilus* species in Cyprus that the collecting effort is biased towards the southern regions of the island as only a few specimens have been reported from the northern part (Fig. 3).

4.2. Phylogenetic relationships and species limits in Drilus from Cyprus based on molecular data

The phylogenetic relationships among *Drilus* species were first examined by Kundrata et al. (2015a) using two non-overlapping fragments of the cytochrome oxidase subunit I but no representative from Cyprus was included in the analyses. Here, we produced new sequences for *D. rufipes* from Cyprus and *D. rectus* from Cyprus and Turkey, and merged them with the already published data to construct the *Drilus* phylogeny based on the fragment of *rrnL* and two fragments of *cox1* (Table 1). *Drilus rectus* is closely related to *Drilus* cf. *mertliki* from Turkey (Fig. 4). Their relationship is supported also by morphology; both species share similar habitus, pectinate antennae, shape of pronotum, and male genitalia (Fig. 1B,G,H,K,L; Kobieluszova and Kundrata 2015). On the other hand, *D. rufipes* is a sister to the clade of species from the Peloponnese, Ionian islands, and Crete (Fig. 4). These lineages share relatively narrow body shape in both males and females, and the shape of pronotum in males (Figs. 1D,I; 2B; Kundrata et al. 2015a). The phylogenetic position of the third Cypriot species, *D. humeralis*, could not be tested as no additional material has been found after the holotype. Its remarkable morphology, especially the large head and subquadrate pronotum (Fig. 1F), suggests this species is most probably distant from both *D. rectus* and *D. rufipes*.

Further, we tested if the adult males matching the descriptions of *D. rufipes* and *D. truquii* form monophyletic groups in the phylogenetic tree. According to the original descriptions by Baudi di Selve (1871), *D. rufipes* is a small species with black antennae (antennomeres I–II more or less black), and *D. truquii* is a larger species with the scape reddish and remaining antennomeres black. We found a gradation in body size and coloration of antennae among the examined specimens, and the DNA-based analysis confirms that neither small specimens with entirely black antennae nor larger specimens with reddish scape form monophyletic lineages (Fig. 4, Table 3). This is an additional evidence for the synonymization of both species. Another challenge we faced was identifying the immature stages of *Drilus* collected for the first time in Cyprus. However, an identification of insect larvae to a species level based on morphology is often difficult or impossible due to the scarce knowledge on the immature stages. Such is the case of the Mediterranean *Drilus*; larvae were described only for a few species (e.g. Kobieluszova and Kundrata, 2015; Kundrata et al., 2015a) and until this study, no *Drilus* larvae from Cyprus were known. Recently, the identification of insect larvae through DNA barcodes becomes popular and this method has been successful for various taxonomic groups (e.g. Ahrens et al., 2007; Bocak et al., 2016; Gattolliat and Monaghan, 2010; Levkanicova and Bocak, 2009; Vivero et al., 2017). Using molecular data we have been able to associate the different larval stages including several active instars and a resting stage (pseudopupa) with the adult males of *D. rufipes* (Fig. 4).

The DNA barcodes are nowadays widely used also for the species delimitations (e.g. Hausmann et al., 2016; Hebert et al., 2003; Monaghan et al., 2005; Schmidt et al., 2017). In this study, we assessed the genetic distances within *D. rectus* and *D. rufipes* clades. *Drilus rectus* is a relatively widespread species described originally from the southern Turkey and Lebanon (Schaufuss, 1867). Since this species exhibits a great intraspecific variability in the coloration and several morphological features including the cuticular structure of head, shape of pronotal hind angles and parameral apices, Kundrata et al. (2014b) and Petrzelkova and Kundrata (2015) called for the DNA-based investigation of the Cypriot and mainland populations. Here, we sequenced two representatives from Cyprus and southern Turkey (Hatay province) but only a single fragment of *cox1* was available for both specimens. They differ in 1.4% bases which indicates a low genetic divergence and a close relationship between the island and mainland populations. Therefore, although only a limited number of populations was available for the molecular study, our results indicate that *D. rectus* is a species with high intraspecific variability rather than a complex of cryptic species. For *D. rufipes*, we assessed the genetic distances using using the multigene barcoding approach, including the widely used mitochondrial *rrnl* and *cox1* (two non-overlapping portions) and for the first time in *Drilus*, the nuclear protein-coding arginine kinase. Maximum intraspecific distances were low for the *rrnL* and arginine kinase, whereas in *cox1*-3′ and *cox1*-5′ (the standard barcode region) they reached 3.0% and 3.6%, respectively (Tables 4, S3–S6). Such divergence slightly surpasses the widely accepted 3% threshold indicating separate species in many insect groups (Hebert et al., 2003) but even higher intraspecific genetic distances were reported for some *Drilus* species from Crete (Kundrata et al., 2015a), the slowly dispersing net-winged beetles (Li et al., 2015), and other beetle lineages (e.g. Hendrich et al., 2015; Pentinsaari et al., 2014). This is not surprising because species with limited dispersal propensity retain higher genetic differentiation among populations than good dispersers (Ikeda et al., 2012). *Drilus* species have restricted vagility due to the presence of neotenic wingless females. Therefore, we should also include further lines of evidence such as e.g. morphology when evaluating the species limits using molecular markers (i.e. integrative taxonomy; Will et al., 2005). *Drilus rufipes* is easily recognizable on the base of the external morphology (e.g. in habitus, bicolor tarsi, typical structure of body surface, shape of pronotum) and although there is a relatively higher genetic variability as well as a gradual variability in body size and antennal coloration among its representatives, we consider the different populations as a single species.

4.3. Morphology and ecology of Drilus females and larvae in Cyprus

Females of *Drilus* are morphologically modified due to the incomplete metamorphosis; they retain a larvae-like morphology throughout their lives (Crowson, 1972; Cicero, 1988). Therefore, they bear a lower number of taxonomically important characters than their male counterparts (Kundrata et al., 2015a) and it is mostly unreliable to associate the conspecific males and females without using DNA or collecting them in copula. In this study, we examined two females belonging to two different *Drilus* species (Fig. 2A,B). The first female bears a determination label that states it is *D. rectus*. This specimen was collected by H. M. Morris on the same locality and date as three male specimens of *D. rectus* so we can assume that this female really belongs to *D. rectus*. The second female specimen was collected by Ch. Makris (as a larva) on the locality where he found also males of *D. rufipes*. What more, the narrow body and dark antennae of the female corresponds with the body shape and antennal coloration of adult males, and the body coloration including the black dorsal markings corresponds with the coloration of larvae of *D. rufipes* (Fig. 2B,D,G–I). Further DNA analysis involving males and females of both species should be carried out to confirm our conclusions.

There are only a few *Drilus* species for which the females are known, and these differ mainly in the body coloration and the morphology of antennae and genitalia (Kobieluszova and Kundrata, 2015; Kundrata et al., 2015a). The body coloration, although often variable within the adult males of a single species, can be used for the differentiation of females including those from Cyprus (Baalbergen et al., 2016; Kundrata et al., 2015a). The use of antennae as an important diagnostic character in *Drilus* females is hindered by the common misinterpretation of their morphology (for a review, see Kobieluszova and Kundrata, 2015). Unlike males, which have serrate to pectinate antennae with 11 antennomeres, females bear filiform antennae which consist in natural conditions of 10–12 antennomeres including the very small apical one. However, in artificial or laboratory conditions they have often peculiar number of antennomeres as well as other malformations (loss of antennomeres, two antennomeres united into one, etc.). Therefore, it is not surprising that the female of *D. rufipes* which was reared at home by Ch. Makris (personal communication) has different number of antennomeres on each antenna. Further study involving more female specimens of *Drilus* species from Cyprus is crucial for understanding the importance of antennae in the species determination. Regarding the female genitalia, *D. rufipes* shares short styli and elongate bursa copulatrix with most of the known females, and it closely resembles *D. horasfakionus* Kundrata et al., 2015a, from Crete (Kundrata et al., 2015a). On the other hand, the female of *D. rectus* exhibits a unique morphology of genitalia among the described *Drilus* species; it has elongate styli which are longer than the coxite width (shorter in all other *Drilus* spp.) and about 1/3 of length of the fused valvifer and coxite (1/8 or less in other species).

The *Drilus* larvae are predators of terrestrial snails and the Mediterranean species prey on Helicidae (*Eobania* Hesse, 1913, *Theba* Risso, 1826), Clausiliidae (*Albinaria* Vest, 1867, *Bulgarica* Boettger, 1877) and Subulinidae (*Rumina* Risso, 1826) (e.g. Baalbergen et al., 2014; Faucheux and Agnas, 2011; Gittenberger, 1994; Kobieluszova and Kundrata, 2015; Örstan, 1999; Schilthuizen et al., 1994). Members of the above-mentioned families occur also in Cyprus (Gittenberger, 2016). However, larvae of *D. rufipes* from Cyprus were collected from shells of the hygromiid snail *Monacha syriaca*. Until now, only *D. flavescens* (Geoffroy, 1785) and *D. concolor* from the mainland Europe were identified as predators of *Monacha* spp. (Baalbergen et al., 2016; Drees, 2014; Kundrata, unpublished information). Baalbergen et al. (2014) confirmed the differences in prey specifity among the Aegean *Drilus* species. There are about 100 described species of terrestrial snails in Cyprus, and about one quarter of them are endemics (Gittenberger, 2016). Unfortunately, we have almost no information on the predator-prey relationships between *Drilus* and snails in Cyprus. Further investigation of both taxa is crucial for understanding the prey specifity in the Cypriot *Drilus* spp. Particularly interesting would be to find out if *D. rectus* and *D. rufipes* populations from outside Cyprus prey on the same snail taxa as populations in Cyprus or alternatively, if the prey varies between these populations.

5. Conclusions

The Mediterranean region is one of the World's biodiversity hotspots (Myers et al., 2000) and hosts a vast majority of *Drilus* species (Kobieluszova and Kundrata, 2015, Kundrata et al., 2014b, 2015a; Wittmer 1944). Integrative taxonomic studies including molecular, morphological and ecological data should be employed to more thoroughly examine the *Drilus* diversity as this group of beetles is interesting from the evolutionary (neotenic development of females) as well as the ecological (beetle-snail predator-prey system) point of view (Baalbergen et al., 2014). This is the first comprehensive study on *Drilus* diversity of Cyprus and we provide the first phylogenetic hypothesis for the Cypriot *Drilus*, taxonomic review including information on the intraspecific variability and species distributions, and descriptions of females and immature stages. However, many questions still remain to be answered. Much more samples are available from the southern part of the island and therefore, more effort should be put to the entomological investigation of the northern Cyprus. For example, furhter data are required about *D. humeralis*, species known on the base of a single specimen collected in the Kyrenia Mountains (Fig. 3). In order to specify the positions of Cypriot *Drilus* in detail, further comparative material from the surrounding areas should be added into the phylogenetic analysis; the identity of females studied here should be confirmed using DNA analysis, and special emphasis should be placed on the investigation of the immature stages and their prey. This study serves as a solid systematic base for future evolutionary and ecological research on *Drilus* in the Mediterranean region.

Acknowledgements

We are grateful to M. Barclay, M. Geiser (BMNH), A. L. L. Friedman, O. Rittner (SMNH-TAU), J. Hájek (NMPC), M. Hartmann (NKME), T. Deuve, O. Montreuil (MNHN), E. Sprecher (NMBS), J. Batelka (Czech Republic), G. Kakiopoulos (Greece), A. Link (Austria), and R. Schuh (Austria) for loan of material in their care. We thank Ch. Makris (Cyprus) for the continuous support on Drilus research in Cyprus, Z. Lucbauer (United Kingdom) and P. Hajdaj (Czech Republic) for donation of material used for the DNA extraction, E. Baalbergen (Netherlands) for the comments on larvae of D. rufipes, M. Geiser (BMNH) for the comments on material deposited in the BMNH, R. Poggi (Italy) and M. Appelhans (Germany) for help with literature, and J. Kundratova (Czech Republic) for the technical assistance. The short-term stays of RK in the Naturhistorisches Museum Wien, Austria (AT-TAF 6821; M. Jäch, I. Plonski), the Museum National d'Histoire Naturelle, Paris, France (FR-TAF 6701; O. Montreuil, A. Mantilleri), and the Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany (DE-TAF 7085; S. Blank, T. Schmitt) were funded by the EU-SYNTHESYS grants. This study was supported by the internal grant of the Faculty of Science UP Olomouc (IGA_PrF_2018_026).

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.jcz.2018.04.001.

References

Ahrens, D., Monaghan, M.T., Vogler, A.P., 2007. DNA-based taxonomy for associating adults and larvae in multi-species assemblages of chafers (Coleoptera: Scarabaeidae). Mol. Phylogenet. Evol. 44, 436–439.

Assmann, T., Austin, K., Boutaud, E., Buse, J., Chikatunov, V., Drees, C., Felix, R.F.F.L., Friedman, A.L.L., Khoury, F., Marcus, T., Renan, I., Schmidt, C., Wrase, D.W., 2015. The ground beetle supertribe Zuphiitae in the southern Levant (Coleoptera, Carabidae). Spixiana 38, 237–262.

Baalbergen, E., Helwerda, R., Schelfhorst, R., Castillo Cajas, R.F., van Moorsel, C.H.M., Kundrata, R., Welter-Schultes, F.W., Giokas, S., Schilthuizen, M., 2014. Predator-prey interactions between shell-boring beetle larvae and rock-dwelling land snails. PLoS One 9, e100366, http://dx.doi.org/10.1371/journal.pone.0100366.

Baalbergen, E., Schelfhorst, R., Schilthuizen, M., 2016. *Drilus* larvae in the Netherlands (Coleoptera: Elateridae: Drilini). Entomol. Berichten 76, 165–173.

Bahillo De La Puebla, P., López Colón, J.I., 2005. Los Drilidae Lacordaire, 1857 de la Península Ibérica e Islas Baleares (Coleoptera). Boletín de la S.E.A. 37, 119–128.

Baudi Di Selve, F., 1871. Coleopterorum messis in insula Cypro et Asia minore ab Eugenio Truqui congregatae recensitio: de Europaeis notis quibusdam additis. Pars quarta. Berliner Ent. Zeit. 15, 49–71.

Bocak, L., 2007. Drilidae. In: Löbl, I., Smetana, A. (Eds.), Catalogue of Palaearctic Coleoptera 4: Apollo Books. Stenstrup, Denmark, pp. 209–210.

Bocak, L., Kundrata, R., Andújar Fernández, C., Vogler, A.P., 2016. The discovery of Iberobaeniidae (Coleoptera: Elateroidea), a new family of beetles from Spain, with immatures detected by environmental DNA sequencing. Proc. R. Soc. Lond. B Biol. Sci. 283, 20152350, doi: 10.1098/rspb.2015.2350.

Cicero, J.M., 1988. Ontophylogenetics of cantharoid larviforms (Coleoptera: Cantharoidea). Coleopt. Bull. 42, 105–151.

Crowson, R.A., 1972. A review of the classification of Cantharoidea (Coleoptera), with definition of two new families, Cneoglossidae and Omethidae. Rev. Univ. Madrid 21, 35–77.

Drees, M., 2014. Leuchtkäfer und Verwandte aus dem Raum Hagen (Coleoptera: Lycidae, Lampyridae et Drilidae). Nat. Heim. 74, 13–20.

Faucheux, M.J., Agnas, M., 2011. *Drilus mauritanicus* Lucas, 1849 et Malacogaster passerinii Bassi, 1883 présents dans le meme biotope á Oualida (Maroc atlantique), (Coleoptera: Elateroidea: Drilidae). Bull. Soc. Sci. Nat. Ouest Fr. 33, 79–90.

Faucheux, M.J., Kundrata, R., 2017. Comparative antennal morphology of male Drilini with special reference to the sensilla (Coleoptera: Elateridae: Agrypninae). Zool. Anz. 266, 105–119, http://dx.doi.org/10.1016/j.jcz.2016.11.002.

Folmer, O., Black, M.B., Hoeh, W.R., Lutz, R.A., Vrijenhoek, R.C., 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Mol. Mar. Biol. Biotechnol. 3, 294–299.

Gattolliat, J.-L., Monaghan, M.T., 2010. DNA-based association of adults and larvae in Baetidae (Ephemeroptera) with the description of a new genus *Adnoptilum* in Madagascar. J. North Am. Benthol. Soc. 29, 1042–1057, http://dx.doi.org/10.1899/09-119.1.

Gittenberger, E., 2016. Chapter 22: Mollusca (Gastropoda). Non-marine snails and slugs. In: Sparrow, D.J., John, E. (Eds.), An Introduction to the Wildlife of Cyprus. Terra Cypria, Limassol, pp. 569–585.

Hausmann, A., Miller, S.E., Holloway, J.D., deWaard, J.R., Pollock, D., Prosser, S.W.J., Hebert, P.D.N., 2016. Calibrating the taxonomy of a megadiverse insect family: 3000 DNA barcodes from geometrid type specimens (Lepidoptera, Geometridae). Genome 59, 671–684, http://dx.doi.org/10.1139/gen-2015-0197.

Háva, J., 2014. Thorictus procerus John, 1962. New myrmecophilous species for Cyprus (Coleoptera: Dermestidae: Thorictinae). Arq. Entomol. 12, 79.

Hebert, P.D.N., Cywinska, A., Ball, S.L., Dewaard, J.R., 2003. Biological identifications through DNA barcodes. Proc. R. Soc. Lond. B Biol. Sci. 270, 313–321, http://dx.doi.org/10.1098/rspb.2002.2218.

Hendrich, L., Morinière, J., Haszprunar, G., Hebert, P.D.N., Hausmann, A., Köhler, F., Balke, M., 2015. A comprehensive DNA barcode database for Central European beetles with a focus on Germany: adding more than 3500 identified species to BOLD. Mol. Ecol. Res. 15, 795–818, http://dx.doi.org/10.1111/1755-0998.12354.

Huelsenbeck, J.P., Ronquist, F., 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17, 754–755, http://dx.doi.org/10.1093/bioinformatics/17.8.754.

Ikeda, H., Nishikawa, M., Sota, T., 2012. Loss of flight promotes beetle diversification. Nat. Commun. 3, 648, http://dx.doi.org/10.1038/ncomms1659.

Katoh, K., Misawa, K., Kuma, K., Miyata, T., 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Res. 30, 3059–3066, http://dx.doi.org/10.1093/nar/gkf436.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P., Drummond, A.J., 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28, 1647–1649, http://dx.doi.org/10.1093/bioinformatics/bts199.

Kobieluszova, L., Kundrata, R., 2015. Taxonomic review of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) from Asia Minor, with descriptions of seven new species and comments on the female antennal morphology in Drilini. Zootaxa 4012, 78–96, http://dx.doi.org/10.11646/zootaxa.4012.1.4.

Kundrata, R., 2012. Taxonomic review of the Himalayan species of *Selasia* Laporte, 1836 (Coleoptera: Elateridae: Agrypninae: Drilini). Ann. Zool. 62, 261–266, http://dx.doi.org/10.3161/000345412X652783.

Kundrata, R., Baalbergen, E., Bocak, L., Schilthuizen, M., 2015a. The origin and diversity of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) in Crete based on mitochondrial phylogeny. Syst. Biodivers. 13, 52–75, http://dx.doi.org/10.1080/14772000.2014.968236.

Kundrata, R., Baena, M., Bocak, L., 2015b. Classification of Omalisidae based on molecular data and morphology, with description of Paradrilinae subfam. nov. (Coleoptera: Elateroidea). Zootaxa 3915, 413–422, http://dx.doi.org/10.11646/zootaxa.3915.3.6.

Kundrata, R., Bocak, L., 2011a. The phylogeny and limits of Elateridae (Insecta, Coleoptera): is there a common tendency of click beetles to soft-bodiedness and neoteny? Zool. Scr. 40, 364–378, http://dx.doi.org/10.1111/j.1463-6409.2011.00476.x.

Kundrata, R., Bocak, L., 2011b. Redescription and relationships of *Pseudothilmanus* Pic (Coleoptera: Rhagophthalmidae) a long-term neglected glow-worm beetle genus from the Himalayas. Zootaxa 2794, 57–62, http://dx.doi.org/10.5281/zenodo.207021.

Kundrata, R., Bocak, L., 2017. Taxonomic review of Drilini (Elateridae: Agrypninae) in Cameroon reveals high morphological diversity, including the discovery of five new genera. Insect Syst. Evol. 48, 441–492, http://dx.doi.org/10.1163/1876312X-48022161.

Kundrata, R., Bocakova, M., Bocak, L., 2014a. The comprehensive phylogeny of the superfamily Elateroidea (Coleoptera: Elateriformia). Mol. Phylogenet. Evol. 76, 162–171, http://dx.doi.org/10.1016/j.ympev.2014.03.012.

Kundrata, R., Kobieluszova, L., Bocak, L., 2014b. A review of Drilini (Coleoptera: Elateridae: Agrypninae) of the Northern Levant, with description of a new species from Syria and a key to Levantine species. Zootaxa 3755, 457–469, http://dx.doi.org/10.11646/zootaxa.3755.5.5.

Lanfear, R., Calcott, B., Ho, S.Y.W., Guindon, S., 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Mol. Biol. Evol. 29, 1695–1701, http://dx.doi.org/10.1093/molbev/mss020.

Levkanicova, Z., Bocak, L., 2009. Identification of net-winged beetle larvae (Coleoptera: Lycidae) using three mtDNA fragments: a comparison of their utility. Syst. Entomol. 34, 210–221, http://dx.doi.org/10.1111/j.1365-3113.2008.00457.x.

Li, Y., Gunter, N., Pang, H., Bocak, L., 2015. DNA-based species delimitation separates highly divergent populations within morphologically coherent clades of poorly dispersing beetles. Zool. J. Linn. Soc. 175, 59–72, http://dx.doi.org/10.1111/zoj.12262.

Makranczy, G., 2014. Revision of the genus *Ochthephilus* Mulsant & Rey, 1856 (Coleoptera: Staphylinidae, Oxytelinae). Rev. Suisse Zool. 121, 457–694.

Miller, M.A., Pfeiffer, W., Schwartz, T., 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), 14 November, New Orleans, pp. 1–8.

Monaghan, M.T., Balke, M., Gregory, T.R., Vogler, A.P., 2005. DNA-based species delineation in tropical beetles using mitochondrial and nuclear markers. Philos. Trans. R. Soc. Lond. B Biol. Sci. 360, 1925–1933, http://dx.doi.org/10.1098/rstb.2005.1724.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858, http://dx.doi.org/10.1038/35002501.

Örstan, A., 1999. Drill holes in land snail shells from western Turkey. Schr. Malakozool. Haus Nat. Cismar. 13, 31–36.

Palumbi, S.R., Martin, A., Romano, S., Mc-Millan, W.O., Stice, L., Grabawski, G., compiled by S. Palumbi 1991. The Simple Fool's Guide to PCR, Version 2.0. (Privately Published). University of Hawaii, Honolulu.

Pentinsaari, M., Hebert, P.D.N., Mutanen, M., 2014. Barcoding beetles: a regional survey of 1872 species reveals high identification success and unusually deep interspecific divergences. PLoS One 9, e108651, http://dx.doi.org/10.1371/journal.pone.0108651.

Petrzelkova, I., Kundrata, R., 2015. The genus *Drilus* (Elateridae: Agrypninae) from the Levant: a new species, new records and updated key to the males. Ann. Zool. 65, 483–490, http://dx.doi.org/10.3161/00034541ANZ2015.65.3.005.

Petrzelkova, I., Makris, C., Kundrata, R., 2017. The genus *Brachypsectra* LeConte, 1874 (Coleoptera: Brachypsectridae) in the Palaearctic Region. Eur. J. Taxon. 276, 1–14, http://dx.doi.org/10.5852/ejt.2017.276.

Pic, M., 1931. Notes diverses, nouveautes. L‘Échange, Rev. Linn. 47, 9–10.

Pic, M1933. Notes diverses, nouveautes. L‘Échange, Rev. Linn. 49, 9–11.

Rambaut, A., Drummond, A.J., Available at 2007. Tracer 1.5. Edinburgh, Institute of Evolutionary Biology University of Edinburgh http://beast.bio.ed.ac.uk/Tracer.

Schaufuss, L.W., 1867. Beitrag zur Gruppe der Malacodermata. Entomol. Zeit. 28, 81–86.

Schilthuizen, M., Kemperman, T.C.M., Gittenberger, E., 1994. Parasites and predators in *Albinaria* (Gastropoda Pulmonata: Clausiliidae). BIOS 2, 177–186.

Schmidt, S., Taeger, A., Morinière, J., Liston, A., Blank, S.M., Kramp, K., Kraus, M., Schmidt, O., Heibo, E., Prous, M., Nyman, T., Malm, T., Stahlhut, J., 2017. Identification of sawflies and horntails (Hymenoptera, 'Symphyta') through DNA barcodes: successes and caveats. Mol. Ecol. Resour. 17, 670–685, http://dx.doi.org/10.1111/1755-0998.12614.

Simon, C., Frati, F., Beckenbach, A.T., Crespi, B., Liu, H., Flook, P., 1994. Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. Ann. Entomol. Soc. Am. 87, 651–701, http://dx.doi.org/10.1093/aesa/87.6.651.

Stamatakis, A., 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22, 2688–2690, http://dx.doi.org/10.1093/bioinformatics/btl446.

Stamatakis, A., Hoover, P., Rougemont, J., 2008. A Rapid bootstrap algorithm for the RAxML web servers. Syst. Biol. 57, 758–771, http://dx.doi.org/10.1080/10635150802429642.

Tamura, K., Stecher, G., Peterson, D., Filipski, A., Kumar, S., 2013. MEGA6: molecular evolutionary genetics analysis version 6.0. Mol. Biol. Evol. 30, 2725–2729, http://dx.doi.org/10.1093/molbev/mst197.

Trllova, S., Kundrata, R., 2015. A review of the genus *Selasia* (Elateridae: Agrypninae: Drilini) in the Palaearctic Region. Zootaxa 3920, 563–571, http://dx.doi.org/10.11646/zootaxa.3920.4.5.

Vivero, R.J., Bejarano, E.E., Estrada, L.G., Florez, F., Ortega-Gomez, E., Aparicio, Y., Torres-Gutierrez, C., Uribe-Soto, S., Muskus-Lopez, C., 2017. DNA barcode for identification of immature stages of sand flies (Diptera: Psychodidae) collected from natural breeding sites. Zootaxa 4277, 228–236, http://dx.doi.org/10.11646/zootaxa.4277.2.3.

Wild, A.L., Maddison, D.R., 2008. Evaluating nuclear protein-coding genes for phylogenetic utility in beetles. Mol. Phylogenet. Evol. 48, 877–891, http://dx.doi.org/10.1016/j.ympev.2008.05.023.

Will, K.W., Mishler, B.D., Wheeler, Q.D., 2005. The perils of DNA barcoding and the need for integrative taxonomy. Syst. Biol. 54, 844–851.

Wittmer, W., 1944. Catalogue des Drilidae E. Oliv. (Coleoptera - Malacodermata). Rev. Soc. Entomol. Arg. 12, 203–221.

Xia, X., 2013. DAMBE 5: a comprehensive software package for data analysis in molecular biology and evolution. Mol. Biol. Evol. 30, 1720–1728, http://dx.doi.org/10.1093/molbev/mst064.

Xia, X., Xie, Z., Salemi, M., Chen, L., Wang, Y., 2003. An index of substitution saturation and its application. Mol. Phylogenet. Evol. 26, 1–7, http://dx.doi.org/10.1016/S1055-7903(02)00326-3.

Zurcher, C., 1911. Note sur deux *Drilus* de l'île de Chypre (Col. Drilini). Bull. Soc. Entomol. Fr., 243–244.

Table S1. List of the non-sequenced adult male specimens of *Drilus rufipes* (Baudi di Selve, 1871) from Cyprus, with information on the variability in their body size and antennal coloration. L - body length (mm), Wh - width at humeri (mm), A - antennomere.

Nr.	District, locality	L	Wh	L/Wh	coloration of antennae
01	Limassol, Akrotiri	3.2	1.1	2.9	A1–A2 reddish, A3–A11 reddish brown
03	Limassol, Akrotiri	4.0	1.2	3.3	A1–A2 reddish, A3–A11 reddish brown
05	Limassol, Akrotiri	3.5	1.2	2.9	A1–A2 reddish brown, A3–A11 missing
06	Limassol, Akrotiri	3.2	1.0	3.2	A1 reddish, A2–A11 dark reddish brown
08	Limassol, Akrotiri	3.8	1.2	3.2	entire antennae reddish brown
22	Limassol, Akrotiri	8.7	2.9	3.0	A1 reddish, A2–A11 black
14	Limassol, Alassa	6.3	1.8	3.4	A1 reddish black, A2–A11 black
15	Limassol, Alassa	5.8	1.7	3.4	A1 reddish, A2–A11 black
18	Limassol, Alassa	7.9	2.5	3.1	A1 reddish, A2–A11 black
17	Limassol, Pissouri	4.5	1.3	3.5	A1 reddish black, A2–A11 black
23	Lim., Germasogeia	6.7	2.2	3.0	A1–A2 reddish black, A3–A11 black
24	Lim., Germasogeia	6.2	1.9	3.4	A1–A2 reddish black, A3–A11 black
29	Lim., Germasogeia	6.4	2.1	3.0	A1–A2 reddish black, A3–A11 black
30	Lim., Germasogeia	5.0	1.6	3.1	A1–A2 dark reddish brown, A3–A11 reddish black
31	Lim., Germasogeia	6.8	2.1	3.2	A1–A2 reddish black, A3–A11 black
12	Paphos, Panagia	7.6	2.5	3.0	A1 reddish, A2–A11 black
13	Paphos, Panagia	6.6	2.0	3.3	A1 reddish, A2–A11 black
26	Paphos, Kouklia	8.2	2.7	3.0	A1–A2 reddish black, A3–A11 black
27	Paphos, Kouklia	6.0	1.8	3.4	A1 reddish black, A2–A11 black
28	Paphos, Kouklia	5.0	1.5	3.3	A1–A2 reddish brown, A3–A11 black
32	Paphos, Latsi	6.5	2.0	3.3	A1 reddish black, A2–A11 black
33	Paphos, Latsi	5.8	1.8	3.2	A1 reddish, A2–A11 black
34	Paphos, Latsi	6.6	2.1	3.1	A1 reddish, A2–A11 black
35	Paphos, Latsi	6.6	2.1	3.1	A1 reddish, A2–A11 black
36	Paphos, Fyti	6.8	2.1	3.2	A1 reddish, A2–A11 black
16	Nicosia, Politiko	6.0	1.8	3.4	entire antennae black
07	Larnaca	3.5	1.2	2.9	entire antennae reddish brown
02	Larnaca, Livadia	3.8	1.2	3.2	entire antennae reddish brown
09	Larnaca, Livadia	3.8	1.2	3.1	A1–A2 reddish, A3–A11 dark reddish brown
10	Larnaca, Larnaca	4.9	1.4	3.5	A1 reddish, A2–A11 reddish black
19	Larnaca, Kalavasos	5.4	1.6	3.5	A1 reddish, A2–A11 black
20	Larnaca, Kalavasos	5.3	1.6	3.4	A1–A2 reddish brown, A3–A11 reddish black
21	Larnaca, Choirokoitia	5.8	1.7	3.5	A1 reddish black, A2–A11 black
25	Larnaca, Odou	8.3	2.5	3.3	A1 reddish, A2–A11 black
04	Famagusta	4.0	1.3	3.1	A1 reddish, A2–A11 reddish brown

Table S2. Results of the Xia's nucleotide substitution saturation test in DAMBE. Analyses were performed on fully resolved sites only. Iss - index of substitution saturation; Iss.c^S - critical value for symmetrical tree topology; Iss.c^A - critical value for extremely assymetrical tree topology; T - T value; DF - degrees of freedom; P^S, P^A - probability that Iss is significantly different from the critical value (Iss.c^S or Iss.c^A, respectively); Pinv - proportion of invariable sites; pos. - codon position.

Marker /pos.	Iss	Iss.c^S	T	DF	P^S	Iss.c^A	T	DF	P^A	Pinv
rrnL	0.134	0.721	28.710	340	0.000	0.543	19.996	340	0.000	0.343
cox1-3′/1st	0.169	0.489	6.619	85	0.000	0.356	3.868	85	0.000	0.250
cox1-3′/2nd	0.171	0.548	5.064	22	0.000	0.417	3.315	22	0.003	0.801
cox1-3′/3rd	0.481	0.693	5.513	113	0.000	0.469	0.310	113	0.757	0.015
cox1-5′/1st	0.121	0.610	16.101	148	0.000	0.372	8.275	148	0.000	0.315
cox1-5′/2nd	0.013	0.758	93.362	215	0.000	0.721	88.646	215	0.000	0.004
cox1-5′/3rd	0.485	0.638	5.332	209	0.000	0.360	4.333	209	0.000	0.034

Table S3. The maximum uncorrected pairwise genetic distances (p-distances) for the *cox1-3'* sequences of *Drilus rufipes* (Baudi di Selve, 1871) from Cyprus. [1] RK1001 Paphos, Tsada, [2] RK1002 Paphos, Amargeti, [3] RK1003 Limassol, Akrotiri, [4] RK1004 Limassol, Zakaki, [5] RK0788 Paphos, Amargeti, [6] RK1005 Paphos, Tsada, [7] RK1006 Paphos, Tsada, [8] RK1007 Limassol, Zakaki, [9] RK1008 Limassol, Zakaki, [10] RK1032 Paphos, Vretsia, [11] RK1033 Paphos, Vretsia, [12] RK1035 Paphos, Vretsia.

	[1]	[2]	[3]	[4]	[5]	[6]	[7]	[8]	[9]	[10]	[11]	[12]
[1]												
[2]	0.026											
[3]	0.029	0.025										
[4]	0.030	0.026	0.024									
[5]	0.024	0.014	0.019	0.018								
[6]	0.001	0.028	0.030	0.029	0.022							
[7]	0.021	0.014	0.019	0.018	0.011	0.022						
[8]	0.024	0.017	0.019	0.010	0.011	0.022	0.008					
[9]	0.024	0.017	0.019	0.010	0.011	0.022	0.008	0.000				
[10]	0.028	0.021	0.024	0.014	0.015	0.026	0.012	0.004	0.004			
[11]	0.026	0.019	0.022	0.012	0.014	0.025	0.011	0.003	0.003	0.001		
[12]	0.026	0.019	0.022	0.012	0.014	0.025	0.011	0.003	0.003	0.001	0.000	

Table S4. The maximum uncorrected pairwise genetic distances (p-distances) for the *cox1-5'* sequences of *Drilus rufipes* (Baudi di Selve, 1871) from Cyprus. [1] RK1001 Paphos, Tsada, [2] RK1002 Paphos, Amargeti, [3] RK1003 Limassol, Akrotiri, [4] RK1004 Limassol, Zakaki, [5] RK1005 Paphos, Tsada, [6] RK1006 Paphos, Tsada, [7] RK1007 Limassol, Zakaki, [8] RK1008 Limassol, Zakaki, [9] RK1032 Paphos, Vretsia, [10] RK1033 Paphos, Vretsia, [11] RK1034 Paphos, Vretsia, [12] RK1035 Paphos, Vretsia.

	[1]	[2]	[3]	[4]	[5]	[6]	[7]	[8]	[9]	[10]	[11]	[12]
[1]												
[2]	0.014											
[3]	0.026	0.030										
[4]	0.018	0.020	0.032									
[5]	0.005	0.015	0.024	0.017								
[6]	0.020	0.012	0.036	0.020	0.021							
[7]	0.018	0.017	0.029	0.009	0.017	0.017						
[8]	0.018	0.017	0.029	0.009	0.017	0.017	0.000					
[9]	0.015	0.017	0.027	0.006	0.014	0.017	0.006	0.006				
[10]	0.017	0.018	0.029	0.008	0.015	0.018	0.008	0.008	0.002			
[11]	0.017	0.018	0.029	0.008	0.015	0.018	0.008	0.008	0.002	0.000		
[12]	0.015	0.017	0.027	0.006	0.014	0.017	0.006	0.006	0.000	0.002	0.002	

Table S5. The maximum uncorrected pairwise genetic distances (p-distances) for the *rrnL* sequences of *Drilus rufipes* (Baudi di Selve, 1871) from Cyprus. [1] RK0788 Paphos, Amargeti, [2] RK1001 Paphos, Tsada, [3] RK1002 Paphos, Amargeti, [4] RK1003 Limassol, Akrotiri, [5] RK1005 Paphos, Tsada, [6] RK1006 Paphos, Tsada, [7] RK1032 Paphos, Vretsia, [8] RK1033 Paphos, Vretsia, [9] RK1034 Paphos, Vretsia.

	[1]	[2]	[3]	[4]	[5]	[6]	[7]	[8]	[9]
[1]									
[2]	0.006								
[3]	0.000	0.006							
[4]	0.004	0.010	0.004						
[5]	0.006	0.000	0.006	0.010					
[6]	0.002	0.008	0.002	0.006	0.008				
[7]	0.002	0.008	0.002	0.006	0.008	0.004			
[8]	0.002	0.008	0.002	0.006	0.008	0.004	0.000		
[9]	0.002	0.008	0.002	0.006	0.008	0.004	0.000	0.000	

Table S6. The maximum uncorrected pairwise genetic distances (p-distances) for the arginie kinase sequences of *Drilus rufipes* (Baudi di Selve, 1871) from Cyprus. [1] RK1004 Limassol, Zakaki, [2] RK1005 Paphos, Tsada, [3] RK1006 Paphos, Tsada, [4] RK1008 Limassol, Zakaki, [5] RK1032 Paphos, Vretsia, [6] RK1033 Paphos, Vretsia, [7] RK1034 Paphos, Vretsia.

	[1]	[2]	[3]	[4]	[5]	[6]	[7]
[1]							
[2]	0.001						
[3]	0.001	0.000					
[4]	0.001	0.000	0.000				
[5]	0.001	0.000	0.000	0.000			
[6]	0.003	0.004	0.004	0.004	0.004		
[7]	0.001	0.000	0.000	0.000	0.000	0.004	

Příloha 13

Kundrata, R. & Bocák, L. (v tisku) Molecular phylogeny reveals the gradual evolutionary transition to soft-bodiedness in click-beetles and identifies Sub-Saharan Africa as a cradle of diversity for Drilini (Coleoptera: Elateridae). *Zoological Journal of the Linnean Society*.
[IF 2,685]
[korespondující autor; autorský podíl: 50 %]

The LINNEAN SOCIETY of London
ZOOLOGICAL Journal of the Linnean Society

Molecular phylogeny reveals the gradual evolutionary transition to soft-bodiedness in click-beetles and identifies Sub-Saharan Africa as a cradle of diversity for Drilini (Coleoptera: Elateridae)

Journal:	*Zoological Journal of the Linnean Society*
Manuscript ID	Draft
Manuscript Type:	Original Article
Keywords:	Evolution, molecular systematics < Genetics, Africa < Geography, Phylogenetics, maximum likelihood < Phylogenetics, Bayesian inference < Phylogenetics, phylogenetic systematics < Phylogenetics, entomology < Taxa, Taxonomy, new genera < Taxonomy

Abstract:

Drilini are soft-bodied predatory click-beetles (Elateridae: Agrypninae) with incompletely metamorphosed females. Due to divergent morphology, their classification has been contentious. We present the first densely sampled molecular phylogeny of Drilini based on nuclear and mitochondrial markers. Altogether 44 species, representing all genera, were analysed using maximum likelihood and Bayesian approach. Molecular analyses recovered five major clades well-supported by morphology. Afrotropical lineages mark deep splits; most Palearctic species belong to a terminal clade, and a few species of the predominantly Afrotropical *Selasia* are distributed from Arabia up to the Himalayas and Thailand. The origin of Drilini is dated to the late Eocene (~35.5 Mya) and rapid radiation is identified from the Eocene/Oligocene to the mid-Miocene. We describe the gradual transformation of male morphological traits, e.g., the level of sclerotization, structure of mouthparts, loss of the thoracic interlocking mechanism, shortened elytra, and expanded larviform abdomen. *Austroselasia* gen. nov., *Habeshselasia* gen. nov., *Illubaboria* gen. nov., *Malacodrilus* gen. nov., and *Mashaselasia* gen. nov. are proposed as new. *Latoselasia* stat. rev., earlier the subgenus of *Wittmerselasia*, is elevated to the genus rank. *Habeshselasia bicolor* sp. nov., *H. illubaborensis* sp. nov., *Illubaboria bicolor* sp. nov., *Malacodrilus hajeki* sp. nov., and *Mashaselasia aethiopica* sp. nov. are described.

Abstract

Drilini are soft-bodied predatory click-beetles (Elateridae: Agrypninae) with incompletely metamorphosed females. Due to divergent morphology, their classification has been contentious. We present the first densely sampled molecular phylogeny of Drilini based on nuclear and mitochondrial markers. Altogether 44 species, representing all genera, were analysed using maximum likelihood and Bayesian approach. Molecular analyses recovered five major clades well-supported by morphology. Afrotropical lineages mark deep splits; most Palearctic species belong to a terminal clade, and a few species of the predominantly Afrotropical *Selasia* are distributed from Arabia up to the Himalayas and Thailand. The origin of Drilini is dated to the late Eocene (~35.5 Mya) and rapid radiation is identified from the Eocene/Oligocene to the mid-Miocene. We describe the gradual transformation of male morphological traits, e.g., the level of sclerotization, structure of mouthparts, loss of the thoracic interlocking mechanism, shortened elytra, and expanded larviform abdomen. *Austroselasia* gen. nov., *Habeshselasia* gen. nov., *Illubaboria* gen. nov., *Malacodrilus* gen. nov., and *Mashaselasia* gen. nov. are proposed as new. *Latoselasia* stat. rev., earlier the subgenus of *Wittmerselasia*, is elevated to the genus rank. *Habeshselasia bicolor* sp. nov., *H. illubaborensis* sp. nov., *Illubaboria bicolor* sp. nov., *Malacodrilus hajeki* sp. nov., and *Mashaselasia aethiopica* sp. nov. are described.

Keywords: Agrypninae - biogeography - dating - morphology - neoteny - Paleogene - systematics - taxonomy - transformation

Introduction

The extraordinary species richness of beetles (Ślipiński *et al.*, 2011) is the result of their long evolution and ecological plasticity (Hunt *et al.*, 2007). The transformation of morphological traits is an important part of the diversification process and understanding underlying processes is important in evolutionary and taxonomic research (e.g., Short & Fikáček, 2013; Karolyi *et al.*, 2016; Toussaint *et al.*, 2016; Stanger-Hall *et al.*, 2018). The presence of sclerotized elytra connected by interlocking devices with pterothorax and abdomen is a key innovation that has facilitated the successful radiation of beetles (Lawrence & Britton, 1991; i.e., exoskeletalization of Tomoyasu *et al.*, 2009). A well-sclerotized compact body is characteristic for most beetles, but some lineages are soft-bodied and have lost interlocking devices, e.g., Micromalthidae, Lymexyloidea, Dascillidae: Karumiinae, multiple lineages of Elateroidea and Cleroidea, and some Tenebrionoidea. It is not surprising that body form had long been used for building a beetle classification. However, some taxa defined by a weakly sclerotized cuticle were polyphyletic. For example, the historical Malacodermata consisted mainly of families now classified in the Elateroidea and Cleroidea (Lawrence *et al.*, 1995). Similarly, Cantharoidea contained various elateriform lineages including the byrrhoid Cneoglossidae and dascilloid Karumiinae (Crowson, 1955, 1972). Later, Cantharoidea were included in the widely delimited Elateroidea (Lawrence, 1988). Using morphological analyses, the soft-bodied lineages were regularly recovered as a clade (e.g., Lawrence *et al.*, 2011), but molecular phylogenetic studies showed multiple origins of soft-bodiedness in Elateroidea (Bocakova *et al.*, 2007; Kundrata & Bocak, 2011) and Cleroidea (Bocakova *et al.*, 2015).

The transitions from a completely to poorly sclerotized body form include changes in external morphology: e.g., the loss of interlocking devices, reduction of the prosternum, including the prosternal process, the presence of freely movable, transverse procoxae with exposed trochantins, reduction or loss of the intercoxal process of the first abdominal ventrite, and presence of free abdominal ventrites (Crowson, 1972; Lawrence, 1988; Bocak *et al.*, 2018). Additionally, due to the loss of well-sclerotized cuticle and interlocking mechanisms protecting them from predators, soft-bodied beetles commonly evolved different anti-predator strategies such as unpalatability associated with aposematic coloration or bioluminescence (Bocakova *et al.*, 2007, 2012, 2015). An interesting phenomenon often connected with incomplete sclerotization is neoteny, i.e., the presence of larval features in sexually mature adults. Females are regularly affected and their morphology spans from forms with only a larviform abdomen, modified pterothorax, brachyptery or winglessness, to completely larviform females (e.g., Bocak *et al.*, 2008, 2018; Bocek *et al.*, 2018). The modifications represent a continuum from soft-bodiedness to strongly neotenic females (Bocak *et al.*, 2008, 2018; Jeng, 2008). The gradual nature of the incomplete sclerotization is clearly documented in Cleroidea, where there is a continuum in degree of sclerotization from hard-bodied groups such as majority of Trogossitidae through intermediately sclerotized Cleridae to the highly soft-bodied representatives of the melyrid lineages (Bocakova *et al.*, 2012, 2015). The evolution of neoteny in Elateroidea has a similar character (Bocak *et al.*, 2008; Bocak & Brlik, 2008; Masek *et al.*, 2015; Kundrata *et al.*, 2015a).

Multiple origins of soft-bodied forms was reported in click-beetles (Elateridae; Kundrata & Bocak, 2011; Bocak *et al.*, 2018). The vast majority of Elateridae are well sclerotized beetles with a unique promesothoracic clicking mechanism. Three morphologically disparate lineages, earlier given family rank (Plastoceridae, Cebrionidae, and Drilidae), were recovered in disparate terminal positions in DNA-based analyses, and were downgraded to the subfamily or tribal level: Plastocerinae, Elaterinae: Cebrionini, and Agrypninae: Drilini, respectively (Kundrata & Bocak, 2011; Kundrata *et al.*, 2014; Bocak *et* *al.*, 2018). They show different levels of morphological modifications in both sexes due to incomplete metamorphosis, with *Plastocerus* Schaum as the least modified and Drilini on the opposite end of the spectrum.

Currently, the Drilini comprise ~120 species in eight genera, all from the Old World (Bocak *et al.*, 2010; Kundrata & Bocak, 2017). Adults are sexually dimorphic. The soft-bodied males are capable of flight and resemble other soft-bodied elateroids, and grub-like wingless females have only the head and legs completely metamorphosed and the rest of the body remains larviform (Bocak *et al.*, 2010). The soft-bodied, almost eruciform driline larvae differ from elaterid wireworms and they feed on land snails (e.g., Kundrata *et al.*, 2015a; Faucheux & Agnas, 2016). Drilini were placed in relationships with other soft-bodied elateroid lineages such as Lampyridae, Cantharidae, and Phengodidae, based mainly on their superficial morphological similarity (e.g., Crowson, 1972; Lawrence, 1988; Branham & Wenzel, 2003; Lawrence *et al.* 2011). Conversely, Bocakova *et al.* (2007) and Hunt *et al.* (2007) suggested the close relationships of Drilidae and Elateridae, and Kundrata & Bocak (2011) investigated the position of drilids, recovered them nested within Agrypninae in Elateridae, and lowered their status to a tribe. Since then, molecular-based studies recovered Drilini as a sister to some elaterid genera or embedded within Agrypninae (Bocak *et al.*, 2014, 2016; Kundrata *et al.*, 2014, 2016, 2018; McKenna *et al.*, 2015; Amaral *et al.*, 2016; Timmermans *et al.*, 2016; Martin *et al.*, 2017; Kusy *et al.*, 2018). The limits of Drilini have recently substantially changed. Olivier's (1910) and Wittmer's (1944) classifications listed up to 35 genera from various zoogeographical regions but Crowson (1972) transferred most of them to other elateriform families. Bocak (2007) listed six genera and Kundrata & Bocak (2011) and Kundrata *et al.* (2015b) transferred three of them to Omalisidae. Currently, Drilini contains *Drilus* Olivier and *Malacogaster* Bassi from the West Palearctic Region, *Selasia* Laporte from Africa, Arabian Peninsula, Himalayas, India, Sri Lanka and Thailand, and five species-poor genera from Sub-Saharan Africa (Kundrata & Bocak, 2017). Drilini genera have been mostly identified based on the shape of antennae (e.g., all taxa with flabellate antennae were placed in *Selasia*) in contrast with the plasticity of this character in some elateroids (e.g., Bocek & Bocak, 2017; Kundrata & Bocak, 2017). Recent taxonomic studies focused mainly on the Mediterranean (e.g., Kundrata *et al.*, 2015a), and the tropical fauna remains under-investigated. Wittmer (1989) and Geisthardt (2007a, b) described several species of *Selasia*. Kundrata & Bocak (2017) identified highly morphologically disparate drilines in Cameroon. Some Drilini DNA sequences have been reported in the phylogenetic studies of Elateridae or Elateroidea (Kundrata & Bocak, 2011; Kundrata *et al.*, 2014), and in the phylogenies dealing with the Mediterranean fauna (Kundrata *et al.*, 2015a; Sormova *et al.*, 2018). Driline relationships need to be rigorously tested and the Afrotropical forms are critical for understanding the evolution of Drilini (Kundrata & Bocak, 2017).

The main aims of this study are a) to propose a phylogenetic hypothesis for Drilini and estimate divergence times for the major splits, b) to assess diversity, distribution, and morphology of major lineages, c) to examine in detail the morphological transformation from fully sclerotized and clicking elaterids to soft-bodied Drilini, and d) to modify the classification of Drilini according to these results.

Material and Methods

This dataset represents 66 sampled specimens belonging to 44 species and all 14 known Drilini genera including those described here (Table S1). The sampling covers the entire geographic range of Drilini and represents about a third of the described species-level diversity. Seven genera are represented by at least two species; all other genera except *Lolosia* Kundrata & Bocak, 2017 are presently monotypic. The position of genera previously tentatively placed into Drilini, i.e., *Euanoma* Reitter, *Pseudeuanoma* Pic and *Paradrilus* Kiesenwetter, has been resolved and they are not included in the current analysis (Kundrata & Bocak, 2011; Kundrata *et al.*, 2015b). The Agrypninae were used as outgroups (6 tribes, 17 genera, 33 species) (Table S2; Kundrata & Bocak, 2011; Kundrata *et al.*, 2014) and *Denticollis* sp. (Elateridae: Dendrometrinae), as a non-agrypnine click-beetle, was used for rooting (Table S1; Kundrata & Bocak, 2011; Kundrata *et al.*, 2014).

Specimens were fixed in 96% ethanol and stored at -20ºC. Total genomic DNA was extracted using DNeasy Blood & Tissue kit (Qiagen, Hilden, Germany) according to the manufacturer protocol. The PCR amplification and sequencing were carried out as described in Bocakova *et al.* (2007) and Kundrata & Bocak (2011); the primers are listed in Table S3. Six markers were sequenced: 18S rRNA (~1850 bp), the D2 loop of 28S rRNA (~635 bp), and the fragments of *rrnL* (~530 bp), *cox1-3'* (723 bp), *cox1-3'* (658 bp), and *nad5* + tRNAs (~1200 bp) mtDNA (Tables S1, S2). GenBank accession numbers are listed in Tables S1–S2. Voucher specimens are deposited at the Laboratory of Molecular Systematics, Palacky University, Olomouc (UPOL).

Sequence handling, datasets and alignment methods

Sequence chromatograms were edited using Sequencher 4.9 (Gene Codes Corp., Ann Arbor, MI, USA). Assembled contigs were queried against the online NCBI Nucleotide BLAST database to identify possible contaminants. Newly produced sequences were merged with publicly available data (Tables S1, S2). The dataset contained 100 terminals (34 outgroups, 66 Drilini, further referred to as "full dataset"). Due to missing markers for some individuals, we additionally analyzed a 68-taxa dataset (further referred as "reduced dataset") with at most one marker missing, except for a representative of *Malacodrilus* gen. nov. (Tab. S1).

Single-fragment alignments were performed in Geneious 7.1.7 (Biomatters Inc., Newark, NJ, USA) using the Mafft 7.017 plug-in (default parameters; Katoh & Standley, 2013). Protein-coding *cox1-3′*, *cox1-5′*, and *nad5* markers were unambiguously aligned due to length conservation and subsequently checked by amino acid reading frames to identify paralogs. The length variability in the non-coding gene sequences was low in the ingroup, therefore a single alignment was produced and no potentially ambiguously aligned regions were identified. To test the effect of outgroups with length-variable regions, we further aligned and analyzed the dataset of only 66 ingroup taxa (further referred to as "ingroup-only dataset"). Individual gene alignments were concatenated in Geneious, and sequence statistics were calculated using MEGA 6.06 (Tamura *et al.*, 2013).

Substitution saturation test and model selection

To test the effect of substitution saturation in the phylogenetic inferences, we conducted an entropy-based Xia's nucleotide substitution saturation test (Xia *et al.*, 2003) implemented in DAMBE 6.4.107 (Xia & Lemey, 2009; Xia, 2017) for each non-coding gene and each position of the protein-coding markers (Table S4). This test is based on the index of substitution saturation statistic (Iss) compared to the critical substitution saturation index, assuming either a symmetrical or extremely asymmetrical tree topology ($\mathrm{Iss.c}^{S}$ or $\mathrm{Iss.c}^{A}$, respectively). The P values were obtained to assess if Iss is significantly different from the critical value. An Iss significantly lower than Iss.c means that the sequences have experienced little substitution saturation, and Iss higher than Iss.c means that the sequences have experienced high level of saturation and are of a limited use in the phylogenetic reconstruction (Xia & Lemey, 2009). We estimated the empirical proportion of invariant sites from the data and used 10 000 replicates on the fully resolved sites to perform the analyses.

We detected no saturation in the non-coding genes and the first two codon positions of the protein-coding genes (Iss < Iss.c). The third codon positions of *cox1-3′* were not saturated when assuming a symmetrical tree topology (Iss < Iss.c^S; P = 0) and experienced some level of saturation when assuming an extreme asymmetrical tree (Iss > Iss.c^A; P = 0.113). For the third codon positions of *cox1-5′* and *nad5*, substantial (Iss < Iss.c^A; P = 0.465) to full substitution saturation (Iss > Iss.c^A; P = 0.309) was detected for the symmetric tree topology, respectively. Additionally, Iss values were significantly higher than Iss.c^A for asymmetric tree topologies in both *cox1-5′* and *nad5* (P=0; Table S4). Since the extreme asymmetrical trees are generally very unlikely, we followed the recommendations by Xia & Lemey (2009) and kept the third codon positions of *cox1-3′* but discarded the third codon positions of *cox1-5′* and *nad5*.

The best-fit partitioning schemes and appropriate substitution models for each gene and codon positions of the protein-coding markers were determined in PartitionFinder 2.1.1 (Lanfear *et al.*, 2016) using the linked branch lengths, the greedy heuristic algorithm, and the corrected Akaike information criterion as recommended in the manual. We identified 11 partitions (18S, 28S, *rrnL*, tRNAs, the first and second codon positions for the protein-coding *cox1-5′* and *nad5*, and all codon positions for *cox1-3′*) as the optimal scheme, with nucleotide substitution model GTR+I+G for most partitions, SYM+I+G for the first codon positions of *cox1-5′* and HKY+I+G for tRNAs in the 100- and 68-taxa datasets, and K80+I+G for 28S in the 100-taxa dataset (Table S5).

Phylogenetic analyses

Phylogenetic inferences were conducted using maximum likelihood (ML) and Bayesian inference (BI). ML analyses were conducted using RAxML 8.1.24 (Stamatakis, 2006) via the

CIPRES web server (Miller *et al.*, 2010). We applied the GTR+I+G model and the partitioning scheme by genes and codons as defined by PartitionFinder (Table S5). Branch support was calculated using the Rapid Bootstrap algorithm (Stamatakis *et al.*, 2008) with 1,000 bootstrap replicates. The GTRCAT model was used during the rapid bootstrapping and GTRGAMMA for optimal topology search. Bootstrap values (BS) ≥ 70% were considered as moderate support whereas BS ≥ 90% indicated strong support for a node. Bayesian inference was carried out using MrBayes 3.2.6 (Huelsenbeck & Ronquist, 2001) on the CIPRES portal (Miller *et al.*, 2010), with partitioning schemes and nucleotide substitution models identified in PartitionFinder (Table S5). Four chains were run for 4×10^7 generations using the Markov chain Monte Carlo method. Adequate sampling, mixing and convergence to the stationary distribution (i.e., the effective sample size values higher than 200 for all parameters) were checked using Tracer 1.6 (Rambaut *et al.*, 2014) and the first 20% of generations were discarded as burn-in. A 50% majority-rule consensus tree was constructed to determine the posterior probabilities (PP) from the remaining trees. Posterior probabilities ≥ 95% indicate strong statistical support (Felsenstein, 2004). The resulting trees were visualized and edited in FigTree 1.3.1 (Rambaut, 2009).

Divergence time estimation

For the estimation of divergence times we used a mtDNA dataset of 67 terminals representing all Drilini and *Adelocera* sp. RK0065. Taxa with missing data were kept in analyses as these have a minimal impact on the accuracy of divergence dating (Zheng & Wiens, 2015). Trees were dated using a Bayesian approach implemented in BEAST 1.8.2 (Drummond *et al.*, 2012) on the CIPRES web server. jModelTest 2.1.6 (Darriba *et al.*, 2012) proposed GTR+I+G as the best model using the both versions of Akaike information criterion (AIC, AICc), and HKY + I + G using the Bayesian information criterion and Decision Theory method. The analyses using GTR+I+G model did not reach the stationary phase. Therefore, we used the less complex model HKY + I + G. The genes and codon positions were partitioned and each partition was provided with its own parameters. The analyses were performed using a relaxed molecular clock and an uncorrelated lognormal model of rate variation among branches (Drummond *et al.*, 2006). A Yule model or Birth-Death process tree priors were tested in separate analyses and compared using the Bayes factor scores calculated in Tracer 1.6. The criterion 2 ln Bayes factor > 10 (Kass & Raftery, 1995) was used to decide if a given model was superior (Table S8). Because no fossil record is available for dating the divergence times in Drilini, we calibrated topology using the mtDNA rate estimates for beetles from the literature. We used a mean rate of 0.0115 substitutions per site per million years per lineage (subs/s/my/l) for *cox1* (Brower, 1994), 0.0054 subs/s/my/l for *rrnL* (Papadopoulou *et al.*, 2010), and 0.0167 subs/s/my/l for *nad5* (Pons *et al.*, 2010). These rates have been satisfactorily applied in in previous studies (e.g., Malohlava & Bocak, 2010; Motyka *et al.*, 2017, 2018). The statistically improper priors, such as intervals extending to infinity, were converted to proper priors with a large, finite upper bound. Analyses were set to 50 million generations with sampling every 2,500 generations with the first 10% of trees discarded as burn-in. Stationary phase and adequate sample sizes were confirmed using Tracer 1.6. For each tested prior and for each parameter, effective sample size (ESS) values were always above 500, and usually much higher. The resulting trees were summarized in TreeAnnotator 1.8.2 and the maximum credibility tree was visualized and edited in FigTree 1.3.1. Divisions of geological time and their boundaries follow the ICS International Chronostratigraphic Chart v. 2018/07 (Cohen, 2013; updated).

Morphology

The Drilini specimens used for the morphological part of the study are deposited in the following collections: The Natural History Museum, London (BMNH), Koninklijk Museum voor Midden-Afrika, Tervuren (RMCA), Museum National d'Histoire Naturelle, Paris (MNHN), Natural History Museum, Budapest (HNHM), Naturkundemuseum Erfurt (NKME), Naturhistorisches Museum, Vienna (NHMW), National Museum, Prague (NMPC), Naturalis Biodiversity Center, Leiden (RMNH), Naturhistorisches Museum, Basel (NHMB), Museo Civico di Storia Naturale, Genova (MSNG), Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin (MFNB), Senckenberg Deutsches Entomologisches Institut, Müncheberg (SDEI), and the collection of Department of Zoology, Palacky University, Olomouc (UPOL). The morphological terminology follows Kundrata & Bocak (2017). Genitalia were dissected after a short treatment in 10% KOH. Diagnostic characters were photographed using a digital camera attached to a stereoscopic microscope. The following measurements were taken with an ocular micrometer on a microscope: BL, body length, measured from the anterior edge of head capsule to the apex of elytra; WHum, width at humeri; EL, elytral length; WHe, width of head including eyes; PL, pronotal length at midline; PW, pronotal width at the widest part; Edist, minimum interocular distance at the frontal part of cranium; Ediam, maximum eye diameter in the lateral view. Specimen label data are cited verbatim.

Results

DNA data and alignments

The six-gene full and reduced datasets aligned by the Mafft algorithm comprised 5154 and 5151 homologous positions, respectively. Dataset containing only the ingroup included 5093 homologous positions. Numbers of conserved, variable and parsimony informative characters in various datasets are summarized in Table S6. Nucleotide composition of markers is given in Table S7. The full dataset consisted of 100 specimens and comprised 78 18S sequences, 77 28S sequences, 79 *rrnL* sequences, 95 *cox1-3′* sequences, 72 *cox1-5′* sequences, and 61 *nad5*+tRNAs sequences (Tables S1, S2).

Molecular phylogenetic analyses

The detailed topology of Drilini was investigated using the 100 and 68-taxa datasets including outgroups (rooted with the non-agrypnine *Denticollis* sp.), and the 66-taxa dataset including only the ingroup (unrooted). The ML phylogenetic hypothesis for the 100-taxa dataset and the BI phylogenetic hypothesis for the 68-taxa dataset are shown in Figs 1 and S1. An overview of the recovered clades with the bootstrap values for ML analyses and posterior probabilities for BI analyses is given in Table 1. All analyses recovered a monophyletic Drilini (BS and PP 100%) split into five moderately to strongly supported clades: clade A (*Austroselasia* gen. nov., 4 spp.), clade W (*Habeshselasia* gen. nov., 2 spp.; *Mashaselasia* gen. nov., 1 sp.; *Latoselasia* Kundrata & Bocak, 1 sp.; *Wittmerselasia* Kundrata & Bocak, 4 spp.), clade S (*Illubaboria* gen. nov., 1sp.; *Selasia*, 3 spp.), clade M (*Flabelloselasia* Kundrata & Bocak, 1 sp.; *Lolosia* Kundrata & Bocak, 1 sp.; *Kupeselasia* Kundrata & Bocak, 1 sp.; *Microselasia* Kundrata & Bocak, 8 spp.), and clade D (*Malacogaster*, 2 spp.; *Malacodrilus* gen. nov., 1 sp.; *Drilus*, 14 spp.) (Fig. 1, Table 1). Almost no statistical support was recovered for backbone splits and so the relationships among the five major clades remained ambiguous. The bootstrap support remained low (Fig. S1, Table 1) in analyses without outgroups (66-taxa dataset) or taxa with missing fragments (68-taxa reduced dataset). Despite the lack of statistical support, the reconstructed topologies regardless of the filtering of data and presence of outgroups were congruent, except for a few nodes. The clade A (i.e., *Austroselasia* gen. nov.) was sister to all remaining Drilini in most analyses, and the following topology was inferred: clade A (clade W (clade S (clade M + clade D))) (Figs 1 and S1). Only the 68-taxa ML analysis inferred clades A + W sister to all remaining Drilini. All genera were recovered monophyletic and usually moderately to strongly supported; only *Drilus* was rendered paraphyletic to the inclusion of clade *Malacogaster* + *Malacodrilus* gen. nov. in the analyses of the reduced dataset (Fig. S1).

Within clade W, there was a strong support for the subclade *Mashaselasia* gen. nov. + *Latoselasia* + *Wittmerselasia* (BS 97–100%, PP 100%) which was sister to *Habeshselasia* gen. nov. (Figs 1 and S1). The former *Wittmerselasia* sensu lato (i.e., *Wittmerselasia* + *Latoselasia*) was monophyletic in all analyses but usually with low support. Within the M clade, *Flabelloselasia* was usually sister to *Lolosia* + (*Kupeselasia* + *Microselasia*); only in two BI analyses *Flabelloselasia* formed a clade with *Lolosia*. *Kupeselasia* was sister to *Microselasia* always with the maximal support. Within clade D, *Drilus* was usually sister to the well-supported clade of *Malacogaster* and *Malacodrilus* gen. nov. The latter subclade was recovered embedded within *Drilus* in the analyses of the reduced dataset although without support (Figs 1 and S1).

Divergence dating

The chronograms obtained using the different tree priors achieved very similar values of the marginal log-likelihood (-47658.848±0.468 for the Birth-Death process, -47659.477±0.382 for the Yule model; Table S8) and therefore, using Kass & Raftery's (1995) guidelines, no alternative is significantly better. Since both trees yielded almost the same divergence time estimates for the recovered nodes, we further discuss only the results from the analysis with the Birth-Death process which obtained slightly higher marginal log-likelihood (Table S8). The time of origin of Drilini is estimated at 35.5 Mya in the late Eocene, with a 95% HPD of 39.6–31.7 Mya. The origins of major Drilini clades date back to the Eocene/Oligocene boundary and Oligocene (Fig. 2, Table S8), and most divergence events at the genus level within these clades occurred since Oligocene until the mid-Miocene. The diversification within Greek *Drilus* was estimated in late Miocene and Pliocene (Fig. 2). The complete results are given in Table S8.

Systematics: Updated generic classification of Drilini

Order Coleoptera Linnaeus, 1758

Suborder Polyphaga Emery, 1886

Superfamily Elateroidea Leach, 1815

Family Elateridae Leach, 1815

Subfamily Agrypninae Candèze, 1857

Tribe Drilini Blanchard, 1845

Drilites Blanchard, 1845: 53.

Type genus. *Drilus* Olivier, 1790.

Diagnosis. The Drilini as currently defined share the following combination of characters in males: body soft, only weakly sclerotized; mandible bidentate; antenna with 11 antennomeres; antennomere II minute, always distinctly shorter than antennomere III; tarsomere IV shortest, ventrally with membranous lobe; pretarsal claw with basal setae; abdomen with seven or eight visible sternites; phallus considerably curved laterally, dorsally with subapical hook; and phallobase without any posterolateral processes. Known females are larviform, grub-like, and wingless, with body elongate, head small, prognathous, eyes relatively small, mandible bidentate, antenna consisting of 8–12 antennomeres, terminal antennomere minute, ovipositor with subapically attached short styli, and bursa copulatrix without any sclerites or spines. Larvae share the following characteristics: elongate body, slightly widened towards apex, hairy, especially dorsally, pubescence denser towards apex; prognathous, well sclerotized head with relatively small eyes; antenna with three antennomeres; mandible simple, narrow and falcate; abdomen with sclerotized and pigmented tergites, with long setae; lateral pleural and tergal processes usually well developed; last abdominal segment small, slender; cerci elongate, apically cuspidate or acuminate, densely covered with long pubescence.

Remark. The following generic diagnoses are based only on the male morphology since immature stages and females are known only for the Mediterranean *Drilus* and *Malacogaster*. Some larvae and females earlier reported for the Afrotropical *Selasia* might in fact belong to another genus and need to be re-examined in future.

Clade A (*Austroselasia* gen. nov.)

Relationships. The internal relationships within this clade have not been fully resolved using the available data. *Austroselasia pulchra* from South Africa was sister to the remaining species from Zambia and Kenya in the analyses of full and ingroup-only datasets (Fig. 1) but it was recovered as a terminal lineage in the analyses of the reduced dataset (Fig. S1). The *Austroselasia* sp. B from Zambia and sp. C from Kenya form a monophylum supported by both DNA and morphology; they share a similarly shaped pronotum and short, stout male genitalia.

Genus *Austroselasia* gen. nov.

(Figs 3A, 4A–N, 9O)

Type species. *Selasia pulchra* Pascoe, 1887; here designated.

Species included. Two species formerly described in *Selasia*, i.e., *Austroselasia pulchra* (Pascoe, 1887) comb.n. and *Austroselasia jaegeri* (Geisthardt, 2007) comb.n., and several undescribed species.

Diagnosis. *Austroselasia* can be recognized by the following combination of characters: fronto-clypeal region short and wide, gradually declined towards base of labrum to almost vertical (Fig. 4A); eyes large, their frontal separation 1.05–1.25 times eye diameter; antenna flabellate (Fig. 4E); pronotum transverse, 1.55–1.80 times as wide as long, with posterior margin rectangularly emarginate (Fig. 4F–G), lateral carina almost complete, sublateral carina usually forming more or less distinct ridge of various lengths; prosternum transverse, with prosternal process forming a narrow plate (Fig. 4G); scutellar shield longer than wide (Fig. 4H); abdominal ventrites I–IV connate (Fig. 9O); sternite IX basally emarginate (Fig. 4M); paramere apically obliquely cut (Fig. 4N).

Description. Male. Body 4.0–12.0 mm long, 2.40–2.70 times longer than width at humeri; yellowish brown to brown, sometimes with elytra blackish from humeri obliquely to apex; body surface covered with yellow pubescence (Fig. 3A).

Head (Fig. 4A) including eyes 0.80–0.90 times as wide as pronotum; surface smooth, covered with sparse, shallow punctures and sparse, long, semi-erect pubescence; antennal insertions widely separated, region between antennal insertions longitudinally depressed; fronto-clypeal region short and wide, gradually declined towards base of labrum to almost vertical. Eyes (Fig. 4A, F) large, prominent, their frontal separation 1.05–1.25 times eye diameter. Labrum transverse, sclerotized, with frontal margin widely concave, sparsely punctate. Mandible (Fig. 4B) robust, moderately long, sickle-shaped, with apical oblique tooth and another distinct tooth located in middle part of incisor; base of mandible with long setae, apical part bare, shiny. Maxilla (Fig. 4C) with small cardo, stipes plate-like, partly membranous, galea and lacinia partly membranous, setose; maxillary palpus tetramerous, palpomere I short, palpomere II longer than palpomeres I and III, terminal palpomere longer or about as long as palpomere II, apically usually widened, flattened, obliquely cut. Labium (Fig. 4D) short, partly membranous; labial palpus trimerous, tiny; terminal palpomere longest, fusiform, apically flattened, obliquely cut. Antenna (Fig. 4E) with 11 antennomeres, flabellate, scapus robust, widened apically, pedicel short, small, antennomere III long, about twice as long as wide (without branch), with robust branch, which is longer than body of antennomere III, antennomeres IV–X minute, short, subequal in length, with long, flattened lamellae of about the same lengths (only branch of antennomere IV shorter), apical antennomere simple, longest, about as long as lamella of penultimate antennomere; all antennomeres covered with moderately dense pubescence.

Pronotum (Fig. 4F) slightly convex, transverse, widest at posterior angles, 1.55–1.80 times as wide as long. Anterior margin almost straight to slightly rounded, lateral margins slightly sinuate to almost straight, posterior margin rectangularly emarginate, emargination shallow, about as wide as scutellar shield. Anterior angles inconspicuous; posterior angles obtuse, usually not prominent. Disc usually with sublateral carina forming more or less distinct ridge of various lengths. Lateral carina distinct, almost complete. Surface of disc almost smooth, somewhat shiny, sparsely shallowly punctate, with sparse semi-erect pubescence. Hypomeron almost smooth, with distinct longitudinal carina; prosternal suture very short. Prosternum (Fig. 4G) transverse, sparsely punctate, covered with long semi-erect setae; prosternal lobe very short, with frontal margin rounded; prosternal process slender, forming a narrow plate. Scutellar shield (Fig. 4H) flat, triangular, longer than wide, with anterior margin gradually declivitous, apex narrowly rounded to subacute. Mesoventrite (Fig. 4I) transverse, with frontal margin widely concave; mesoventral process elongate, narrow; mesoventral cavity shallow, narrowed posteriorly, with indistinctly defined walls. Mesocoxal cavity open to both mesepimeron and mesanepisternum. Metaventrite large, subtrapezoidal, sparsely covered with shallow punctures. Elytra (Fig. 3A) subparallel-sided, basally wrinkled, then almost smooth, with indistinct lines of punctures, moderately sparsely covered with long, semi-erect pubescence, lateral margins, apex and suture distinctly swollen, somewhat depressed, apex rounded. Hind wing venation as in Fig. 4J. Leg (Fig. 4K) moderately long, slightly compressed, with sparse, long, semi-erect setae; coxa robust; trochanter small but robust, obliquely attached to femur; tarsomeres I–II subequal in length, tarsomere III shorter than tarsomeres I and II, ventrally with minute membranous lobe; tarsomere IV shortest, minute, ventrally with membranous lobe, apical tarsomere slender, long; claws simple, slender, slightly curved, each with long seta basally.

Abdomen (Fig. 9O) soft, with seven ventrites (sternites III–IX), the first four of which are connate; all ventrites with sparse, shallow punctures, sparsely covered with semi-erect pubescence; penultimate ventrite slightly emarginate medially. Tergites IX and X (Fig. 4L) connected by membrane; tergite IX basally with two sublateral processes. Sternite IX (Fig. 4M) about 1.7 times as long as wide, deeply notched basally, rounded apically, with apex finely punctate and sparsely covered with setae; sternite X about 0.5 times as long as sternite IX, partly membranous, connected by membrane to sternite IX.

Male genitalia (Fig. 4N) trilobate, longer than wide, about 0.75 times as long as sternite IX; median lobe of variable length, robust, moderately curved in lateral view, basally with two short struts, dorsally with stout subapical hook; paramere of various lengths (usually short as in the type species), apically obliquely cut, partly membranous, with sparse setae; phallobase v-shaped or u-shaped, of various lengths.

Females and immature stages unknown.

Distribution. Southern and eastern Africa (Botswana, Kenya, Malawi, Mozambique, South Africa, Swaziland, Tanzania, Zambia, Zimbabwe) (Fig. 1).

Clade W (*Habeshselasia* gen. nov., *Mashaselasia* gen. nov., *Latoselasia*, *Wittmerselasia*)

Relationships. Our molecular phylogeny recovers *Habeshselasia* gen. nov. sister to the subclade formed by *Mashaselasia* gen. nov., *Latoselasia*, and *Wittmerselasia* (Figs 1 and S1). Both subclades are clearly distinguishable by morphological characters. *Habeshselasia* gen. nov. has the fronto-clypeal region short and relatively wide, sloping backwards to base of labrum, and smaller eyes, with their frontal separation 1.55–1.65 times eye diameter (Fig. 5A–B). The three remaining genera typically have a narrow and high fronto-clypeal region, which is abruptly declined between the antennal insertions and frontally excavated, partly membranous; the eyes large, with their frontal separation up to 1.15 times eye diameter; and the pronotal disc with the lateral margins turned upwards (Kundrata & Bocak, 2017).

Genus *Habeshselasia* gen. nov.

(Figs 3B–C, 5A–U, 9P)

Type species. *Habeshselasia bicolor* sp. nov.; here designated.

Species included. *Habeshselasia bicolor* sp. nov. and *H. illubaborensis* sp. nov.

Diagnosis. *Habeshselasia* gen. nov. can be recognized by the following combination of characters: dorsal body surface smooth, glabrous (Fig. 3B–C); fronto-clypeal region short and relatively wide, sloping backwards to base of labrum (Fig. 5A–B); eyes medium-sized, their frontal separation 1.55–1.65 times eye diameter; antenna weakly flabellate, with antennomeres IV–X elongate, with branches longer than their respective stems (Fig. 5F–G); posterior margin of pronotum rectangularly emarginate (Fig. 5H–J); abdominal ventrites I–IV connate (Fig. 9P).

Description. Male. Body 3.10–5.30 mm long, 2.80–2.90 times longer than width at humeri; dark brown to black with elytra yellowish (*H. bicolor* sp. nov.), or yellowish to light reddish brown with antennomeres III–XI and most of abdomen dark brown (*H. illubaborensis* sp. nov.) (Fig. 3B–C).

Head (Fig. 5A–B, H) including eyes 0.80–0.90 times as wide as pronotum; surface smooth, glabrous, dorsally with shallow median depression, very sparsely punctate, covered with sparse, long, semi-erect pubescence; antennal insertions moderately widely separated; frons apically rounded in lateral view; fronto-clypeal region short and relatively wide, sloping backwards to base of labrum. Eyes medium-sized, prominent, their frontal separation 1.55–1.65 times eye diameter. Labrum relatively small, transverse, sparsely punctate and covered with semi-erect setae, apically partly membranous, with frontal margin concave. Mandible (Fig. 5C) robust, moderately long, sickle-shaped, with apical oblique tooth and another distinct tooth located between middle part of incisor and apex; base of mandible with uneven surface and long setae, apical part bare, shiny. Maxilla (Fig. 5D) with small cardo, stipes plate-like, partly membranous, galea and lacinia partly membranous, setose; maxillary palpus tetramerous, palpomere I short, transverse, palpomere II longer than palpomeres I and II, palpomere III short, about as long as wide, terminal palpomere elongate, fusiform, apically flattened, obliquely widely rounded. Labium (Fig. 5E) short, partly membranous; labial palpus trimerous, tiny, palpomeres I and II short, wide; apical palpomere long, fusiform, distinctly narrowed toward apex, apically obliquely cut. Antenna (Fig. 5F–G) with 11 antennomeres, flabellate; scapus robust, elongate, pedicel short, small, antennomere III long, more than twice as long as wide (without branch), with robust short branch, antennomeres IV–X elongate, about 2.5–3.0 times as long as wide, gradually shortened toward apex, with long lamellae arising from base, lamellae about 1.1–3.0 times as long as their respective stems, relatively slightly shorter in antennomeres IV–V; apical antennomere simple, longest, about as long as lamella of penultimate antennomere; all antennomeres covered with moderately dense pubescence.

Pronotum (Fig. 5H–I) slightly convex, transverse, widest at posterior angles, 1.60–1.65 times wider than length at midline. Anterior margin almost straight or slightly emarginate medially, lateral sides weakly sinuate, posterior margin shallowly, rectangularly emarginate, emargination about as wide as scutellar shield. Anterior angles inconspicuous; posterior angles either prominent and slightly diverging or short, obtuse, oriented posteriorly. Disc with narrow, transverse carina near anterior margin, and with distinct sublateral carinae almost reaching anterior margin. Lateral carina distinct, almost reaching anterior margin of pronotum. Surface of disc smooth, glabrous, very sparsely and shallowly punctate, with only several semi-erect setae near and at margins. Hypomeron smooth, with oblique longitudinal carina; prosternal suture very short. Prosternum (Fig. 5J) transverse, sparsely punctate, prosternal lobe short, excavated and oriented ventrally, with frontal margin rounded, with long semi-erect setae; prosternal process sledner, relatively short, forming narrow plate. Scutellar shield (Fig. 5K) flat, triangular, slightly longer than wide, with anterior margin gradually declivitous, apex narrowly rounded. Mesoventrite (Fig. 5L) transverse, with frontal margin almost straight to widely concave; anterior part separated from rest by transverse sinuate carina, slightly depressed; mesoventral process elongate, narrow; mesoventral cavity shallow, with poorly defined walls. Mesocoxal cavity open to both mesepimeron and mesanepisternum. Metaventrite large, subtrapezoidal, sparsely covered with shallow punctures. Elytra (Fig. 3B–C) subparallel-sided, 0.75 times as long as body; basally slightly wrinkled, smooth, glabrous, indistinctly shallowly punctate, sparsely covered with moderately long semi-erect setae; elytral suture distinct, depressed, apex rounded. Hind wing venation as in Fig. 5M. Leg (Fig. 5N) moderately long, slightly compressed, with sparse, long, semi-erect setae; coxa robust; trochanter elongate, obliquely attached to femur; tarsomeres I–II subequal in length, tarsomere III slightly shorter than tarsomeres I and II, ventrally with minute membranous expansion, tarsomere IV shortest, minute, ventrally with small membranous lobe, apical tarsomere slender, long; all tarsomeres widened apically; claws simple, slender, slightly curved, each with long seta basally.

Abdomen (Fig. 9P) soft, with seven ventrites (sternites III–IX), the first four of which are connate; all ventrites with sparse, fine punctures, sparsely covered with semi-erect pubescence; penultimate ventrite slightly emarginate medially. Sternite IX (Fig. 5O, S) 1.8 times as long as wide, deeply notched basally, rounded apically, with apex finely punctate and sparsely covered with setae; sternite X small, partly membranous, apically rounded, connected by membrane to sternite IX. Tergites IX and X (Fig. 5P, T) connected by membrane; tergite IX basally with two sublateral processes.

Male genitalia (Fig. 5R, U) trilobate, 1.6–1.7 times as long as wide, about 0.75 times as long as sternite IX; median lobe robust, longer than phallobase, moderately curved in lateral view, basally with two minute struts, dorsally with short or long subapical hook; paramere elongate, with setae apically; phallobase robust, wider than long, u-shaped.

Females and immature stages unknown.

Distribution. Ethiopia.

Etymology. The name is a combination of the words Habesha, referring to the people of Ethiopia, and *Selasia* Laporte, 1838 (a genus in Drilini). Gender: feminine.

Habeshselasia bicolor **sp. nov.**

(Figs 3B; 5A, C–F, H, K–R; 9P)

Type material. Holotype, ♂, "ETHIOPIA, Welega Prov., 6 km W Nekemte, 2300 m, 9°06'07" N, 36°37'43" E, 5.–6. June 2009, Bolm lgt." (UPOL); paratypes, 8 ♂♂, same data as for the holotype (UPOL).

Diagnosis. *Habeshselasia bicolor* sp. nov. differs from *H. illubaborensis* sp. nov. in having body black with elytra yellowish (yellowish to reddish brown with only antennomeres III–XI and abdomen dark brown in *H. illubaborensis* sp. nov.; Fig. 3B–C), antennomeres III–X with shorter branches (e.g., branches of antennomeres IV–V only slightly longer than their respective stems in *H. bicolor* sp. nov., and about 1.2 and 1.7 times as long as their respective stems in *H. illubaborensis* sp. nov.; Fig. 5F–G), pronotum widest posteriorly, with posterior angles diverging (widest at anterior third, with hind angles oriented posteriorly in *H. illubaborensis* sp. nov.; Fig. 5H–I), and the relatively longer subapical hook on median lobe, shorter phallobase, and longer paramere with narrowly rounded apex (Fig. 5R, U).

Description. Holotype, male. Body 5.30 mm long, 1.80 mm wide at humeri. Body (Fig. 3B) dark brown to black, labrum and mandibles lighter, elytra yellowish; body surface covered with yellow pubescence, antennae with brown pubescence.

Head (Fig. 5A) 0.80 times as wide as pronotum. Eyes medium-sized, their frontal separation 1.55 times eye diameter. Antenna (Fig. 5F) flabellate, antennomere III long, with short, robust, triangular branch, antennomeres IV–X elongate, with elongate narrow branches, antennomeres IV–V with branches slightly longer than their respective stems, antennomeres VI–X with branches about 1.5–2.7 times as long as their respective stems; apical antennomere simple, about as long as lamella of preceding antennomere.

Pronotum (Fig. 5H) widest at posterior angles, 1.65 times as wide as long at midline, anterior margin almost straight, lateral sides weakly sinuate, posterior angles prominent, slightly diverging; disc with indistinct transverse carina near anterior margin, and with distinct sublateral carinae almost reaching anterior margin. Elytra (Fig. 3B) 0.75 times as long as body, together 2.15 times as long as wide at humeri.

Abdominal terminal segments as in Fig. 5O–P. Male genitalia (Fig. 5R) with median lobe longer than paramere, subapical hook relatively long; paramere long, narrowly rounded apically, with setae at apical half; phallobase slightly wider than long, u-shaped, slightly shorter than paramere.

Variability. Body length: 3.75–5.30 mm; interocular distance 1.55–1.60 times eye diameter; pronotum 1.60–1.65 times as wide as long. Mouthparts are lighter in some paratypes.

Distribution. Western Ethiopia.

Etymology. The specific epithet refers to the body coloration of this species.

Habeshselasia illubaborensis **sp. nov.**

(Figs 3C; 5B, G, I–J, S–U)

Type material. Holotype, ♂, "ETHIOPIA, Illubabor Pr., 12 km N Masha, 1770 m, 7°51'07" N, 35°27'16" E, 12. June 2009, Bolm lgt." (UPOL); paratypes, 3 ♂♂, the same data as for the holotype (UPOL).

Diagnosis. *Habeshselasia illubaborensis* sp. nov. can be recognized by the following combination of characters: body yellowish to reddish light brown, with only antennomeres III–XI and abdomen dark brown (Fig. 3C), antennomeres IV–V with branches about 1.2–1.7 times as long as their respective stems (Fig. 5G), pronotum widest at anterior third, with hind angles short, oriented posteriorly (Fig. 5I), median lobe with short subapical hook, and paramere shorter than phallobase, with well rounded apex (Fig. 5U).

Description. Holotype, male. Body 3.10 mm long, 1.10 mm wide at humeri. Body (Fig. 3C) yellowish to reddish light brown, antennomeres III–XI and abdomen (except last ventrite) dark brown; body surface covered with yellow pubescence.

Head (Fig. 5B) 0.90 times as wide as pronotum. Eyes medium-sized, their frontal separation 1.65 times eye diameter. Antenna (Fig. 5G) flabellate, antennomere III long, with very short, robust, triangular branch, antennomeres IV–X elongate, with elongate narrow branches, antennomeres IV–V with branches about 1.2–1.7 times as long as their respective stems, antennomeres VI–X with branches about 2.3–3.2 times as long as their respective stems; apical antennomere simple, about as long as lamella of preceding antennomere.

Pronotum (Fig. 5I) widest at anterior third, 1.65 times as wide as long at midline, anterior margin slightly emarginate medially, lateral sides weakly sinuate, posterior angles short, obtuse, oriented posteriorly; disc with transverse carina near anterior margin, and with distinct sublateral carinae almost reaching anterior margin. Elytra (Fig. 3C) 0.75 times as long as body, together 2.10 times as long as wide at humeri.

Abdominal terminal segments as in Fig. 5S–T. Male genitalia (Fig. 5U) with median lobe longer than paramere, subapical hook very short; paramere long, well rounded apically, with setae at apical half; phallobase only slightly wider than long, u-shaped, slightly longer than paramere.

Variability. Body length: 3.10–4.10 mm; interocular distance 1.60–1.65 times eye diameter; pronotum 1.60–1.65 times as wide as long.

Distribution. Southwestern Ethiopia.

Etymology. The specific name refers to Illubabor, which is the name for a former province in Ethiopia.

Genus *Mashaselasia* gen. nov.

(Figs 3D; 6A–I)

Type species. *Mashaselasia aethiopica* sp. nov.; here designated.

Species included. Type species only.

Diagnosis. *Mashaselasia* can be recognized by the following combination of characters: body surface smooth, glabrous (Fig. 6B); fronto-clypeal region (Fig. 6B) rather narrow, high, abruptly declined between antennal insertions, frontally excavated, partly membranous; eyes (Fig. 6A–B) large, their frontal separation equals eye diameter; labrum transverse, apically membranous; terminal maxillary palpomere (Fig. 6C) more than twice as long as wide, hatchet-like, slightly constricted subapically, widened and slightly rounded apically; antenna

(Fig. 6D) flabellate, with antennomeres IV–X elongate, with narrow branches; pronotum transverse, subrectangular, 1.60 times as wide as long, very sparsely punctate, its posterior margin with a shallow angulate emargination; scutellar shield (Fig. 6E) triangular, longer than wide; abdominal ventrites I–IV connate; abdominal sternite IX (Fig. 6G) twice as long as wide; median lobe (Fig. 6I) slightly longer than phallobase, paramere longer than wide, narrowly rounded apically, distinctly setose; phallobase slightly wider than long.

Description. Male. Body 4.65 mm long, 3.00 times longer than width at humeri. Body (Fig. 3D) yellowish to light brown, head slightly darker, antennomeres III–XI and abdomen dark brown, body surface covered with yellowish pubescence.

Head (Fig. 6A–B) including eyes about as wide as pronotum; surface smooth, very shallowly depressed medially, sparsely punctate, covered with sparse, long, semi-erect pubescence; antennal insertions moderately widely separated, frons narrowed apically, slightly surpassing fronto-clypeal region; fronto-clypeal region high, narrow, partly membranous, abruptly declined between antennal insertions, frontally excavated; its surface smooth medially, uneven laterally. Eyes (Fig. 6A–B) large, prominent, their frontal separation equals eye diameter. Labrum (Fig. 6B) transverse, basally sclerotized, with transverse row of long setae, apically partly membranous. Mandible (Fig. 6B) robust, moderately long, falcate, bidentate, with long apical oblique tooth and another, robust tooth located in middle part of incisor; mandibles basally covered with long setae, apical part bare, shiny. Maxilla with small cardo, stipes plate-like, partly membranous, galea and lacinia partly membranous, setose; maxillary palpus tetramerous, slender, palpomere I short, palpomere II elogate, about twice as long as wide, palpomere III short, slightly longer than wide, palpomere IV more than 3 times longer than palpomere III, about 2.3 times as long as wide, hatchet-like, slightly constricted subapically, flattened, widened and slightly rounded apically (Fig. 6C). Labium short, partly membranous; labial palpus trimerous, tiny, apical palpomere elongate, fusiform, subacute apically. Antenna (Fig. 6D) with 11 antennomeres, flabellate; scapus robust, slightly widened apically, pedicel short, small; antennomere III long, about 1.5 times as long as antennomere IV, with short, triangular branch, stems of antennomeres IV–X about 2.5 times as long as wide, subequal in length, with branches arising from base (except antennomere X where it arises from apex), gradually slightly longer from towards apical antennomere, from two to four times as long as their respective stems; apical antennomere simple, longest, slightly longer than lamella of penultimate antennomere; all antennomeres covered with moderately dense pubescence.

Pronotum (Fig. 6A) slightly convex, transverse, widest at posterior angles, 1.60 times as wide as long. Anterior margin more or less straight; lateral margins very slightly sinuate, bent upwards; posterior margin medially with wide shallow rectangular emargination. Anterior angles inconspicuous; posterior angles short, rounded, slightly diverfing. Disc smooth, with sublateral carinae almost reaching anterior margin of pronotum. Lateral carina distinct, almost reaching pronotal frontal margin. Surface of disc very sparsely covered with shallow punctures, with sparse semi-erect, long pubescence, both punctures and setae equally distributed. Hypomeron with smooth surface, with indistinct medial depression, slightly uneven near edges; prosternal suture very short. Prosternum transverse, slightly uneven, prosternal lobe short, with frontal margin almost straight, with long semi-erect setae; prosternal process forming slender narrow plate. Scutellar shield (Fig. 6A) flat, triangular, about 1.4 as long as wide, subacute apically, surface almost smooth, spasely covered with shallow punctures and semi-erect setae. Mesoventrite (Fig. 6E) with frontal slighttly concave; mesoventral process elongate, narrow; mesoventral cavity shallow, with poorly defined walls. Mesocoxal cavity open to both mesepimeron and mesanepisternum. Metaventrite large, subtrapezoidal, almost smooth, very sparsely covered with shallow punctures. Elytra (Fig.

3D) subparallel-sided, 0.75 times as long as body; basally slightly wrinkled, with slightly uneven, almost smotth surface. Each elytron with apex separately rounded, sparsely punctate and covered with long, semi-erect pubescence; elytral suture distinct, depressed. Hind wing venation as in Fig. 6F. Leg slightly compressed, with surface rough, covered with sparse, long, semi-erect pubescence, thicker on tibia; coxae robust, trochanters slender, elongate, widened apically, obliquely attached to femora; tarsomeres I–II subequal in length, tarsomere III slightly shorter, tarsomere IV shortest, minute, ventrally lobate, apical tarsomere elongate, slender; claw simple, slender, slightly curved, basally with long seta.

Abdomen soft, with seven ventrites (sternites III–IX), the first four of which are connate; all ventrites with sparse, fine punctures, sparsely covered with long semi-erect pubescence; penultimate ventrite emarginate medially. Sternite IX (Fig. 6G) elongate, twice as long as wide, emarginate basally, apex rounded, punctate, with sparse short setae; sternite X connected by membrane to sternite IX, partly membranous. Tergites IX and X (Fig. 6H) connected by membrane; tergite IX transverse, basally with two sublateral processes; tergite X longer than wide, widely rounded apically, apex partly membranous.

Male (Fig. 6I) genitalia trilobate, 1.6 times as long as wide, 0.65 times as long as sternite IX; median lobe stout, longer than parameres, slightly longer than phallobase, moderately curved in lateral view, dorsally with robust, moderately long subapical hook; paramere moderately long, longer than wide, apically narrowly rounded, covered with sparse setae; phallobase robust, slightly wider than long, u-shaped.

Females and immature stages unknown.

Distribution. Ethiopia.

Etymology. The name is a combination of Masha (the city in the southwestern Ethiopia) and *Selasia* Laporte, 1838, a genus in Elateridae: Drilini. Gender: feminine.

Mashaselasia aethiopica **sp. nov.**

(Figs 3D; 6A–I)

Type material. Holotype, ♂, "ETHIOPIA, Illubabor Pr., 12 km N Masha, 1770 m, 7°51'07" N, 35°27'16" E, 12. June 2009, Bolm lgt." (UPOL).

Diagnosis. This species differs from the remaining Drilini by the combination of the smooth and glabrous body surface (Fig. 3D), narrow, frontally excavated fronto-clypeal region (Fig. 6B), large eyes (Fig. 6A–B), elongate terminal maxillary palpomere, constricted subapically and widened apically (Fig. 6C), elongate antennomeres IV–X (Fig. 6D), and connate abdominal ventrites I–IV.

Description. Body 4.65 mm long, 1.55 mm wide at humeri. Body (Fig. 3D) yellowish brown, head, pedicel, scutellar shield, middle and hind femora darker; antennomeres III–XI, meso- and metathorax, and abdomen brown to dark brown; body surface covered with yellow pubescence.

Head about as wide as pronotum (Fig. 6A). Eyes (Fig. 6A–B) large, their frontal separation equals eye diameter. Antenna (Fig. 6D) flabellate, antennomere III about 1.5 times as long as antennomere IV, with short branch, stems of antennomeres IV–X about 2.5 times as long as wide, with branches about 2–4 times as long as their respective stems; apical antennomere simple, slightly longer than lamella of penultimate antennomere.

Pronotum (Fig. 6A) widest at posterior angles, 1.60 times as wide as long, with distinct sublateral carinae almost reaching anterior margin. Elytra (Fig. 3D) 0.75 times as long as body, together 2.20 times as long as wide at humeri.

Abdominal terminal segments as in Fig. 6G–H. Male genitalia (Fig. 6I) with median lobe longer than parameres; paramere longer than wide; phallobase u-shaped.

Distribution. Southwestern Ethiopia.

Etymology. The specific name refers to the type locality.

Genus *Latoselasia* Kundrata & Bocak, 2017 stat. rev.

Latoselasia Kundrata & Bocak, 2017: 481 [as a subgenus of *Wittmerselasia*].

Type species. *Latoselasia similis* Kundrata & Bocak, 2017; by original designation.

Species included. Type species only.

Diagnosis. *Wittmerselasia* can be recognized by the following combination of characters: body surface smooth, usually glabrous; fronto-clypeal region narrow, high, abruptly declined between antennal insertions, frontally excavated, partly membranous, with two rows of long setae laterally; eyes large, their frontal separation 1.00–1.05 times eye diameter; labrum sclerotized, subpentagonal, short, produced forward; terminal maxillary palpomere less than twice as long as wide, hatchet-like, distinctly widened apically; antenna strongly flabellate; pronotum transverse, subrectangular, 1.55–1.70 times as wide as long, very sparsely punctate, its posterior margin with a distinct angulate emargination; prosternal process forming a narrow plate; scutellar shield triangular, only slightly longer than wide; abdominal ventrites I–

IV connate; abdominal sternite IX basally deeply emarginate; median lobe shorter than phallobase, with short basal struts; paramere relatively narrow, small, covered with setae mainly subapically and at apex; phallobase longer than wide. See Kundrata & Bocak (2017) for more details.

Distribution. Cameroon.

Remark. *Latoselasia* Kundrata & Bocak, 2017 is given here the full genus status based on the both DNA analysis and morphology (Figs 1 and S1; Kundrata & Bocak, 2017).

Genus *Wittmerselasia* Kundrata & Bocak, 2017

Wittmerselasia Kundrata & Bocak, 2017: 470.

(Fig. 9B, H)

Type species. *Wittmerselasia camerooniana* Kundrata & Bocak, 2017; by original designation.

Species included. Five described and several undescribed species are known. *Wittmerselasia camerooniana* Kundrata & Bocak, 2017, *W. davidsoni* Kundrata & Bocak, 2017, *W. geiseri* Kundrata & Bocak, 2017, *W. maculata* (Wittmer, 1989), *W. variabilis* Kundrata & Bocak, 2017.

Diagnosis. *Wittmerselasia* can be recognized by the following combination of characters: body surface usually smooth, glabrous; fronto-clypeal region narrow, high, abruptly declined between antennal insertions, frontally excavated, partly membranous, with two rows of long setae laterally; eyes large, their frontal separation 1.00–1.15 times eye diameter; labrum large, apically membranous; terminal maxillary palpomere about 2.5 times as long as wide, hatchet-like, slightly constricted subapically, widened and slightly rounded apically; antenna strongly flabellate; pronotum transverse, subrectangular, 1.60–1.80 times as wide as long, very sparsely punctate, its posterior margin with a distinct angulate emargination; prosternal process (Fig. 9B) forming a narrow plate; scutellar shield triangular, only slightly longer than wide; mesoventral process (Fig. 9H) elongate, narrowed towards apex; abdominal ventrites I–IV connate; abdominal sternite IX basally deeply emarginate; median lobe usually longer than phallobase, with short basal struts, paramere relatively wide, somewhat obliquely subacute apically, distinctly covered with setae; phallobase never longer than wide. See Kundrata & Bocak (2017) for more details.

Relationships. *Wittmerselasia* sp. A from Ghana, if present, was sister to the remaining congeners, and *W. camerooniana* from Cameroon formed a clade with *Wittmerselasia* sp. B from Ghana (Figs 1 and S1).

Distribution. All described species are known from Cameroon. Several undescribed species occur in western and central Africa.

Clade S (*Illubaboria* gen. nov., *Selasia*)

Relationships. *Illubaboria* gen. nov. differs from *Selasia* in the shape of the labrum (Fig. 7A; about 2.5 times wider than long; in *Selasia* more than four times wider than long, and often reduced), shape of the antenna (Fig. 7F; stems of antennomeres V–X considerably longer than wide; in *Selasia* as long as wide or only slightly longer than wide), thickness of the outer margin of elytra (simply edged; in *Selasia* swollen), and the shape of sternite IX (Fig. 7L; basally truncate; in *Selasia* emarginate). Another morphological character which might be considered as supporting this clade is the presence of latero-apical prostrusions on the paramere apex in *Illubaboria* gen. nov. and some *Selasia* (e.g., *S. arabica*) (Fig. 7N).

Further detailed investigations in the *Selasia* lineage are necessary because all three species included in our analysis differ in the morphology of mouthparts (mainly labrum) and male genitalia. We refrain from making any taxonomic changes in this group based on the limited number of specimens analyzed here, and tentatively keep most species previously classified in *Selasia* in this genus.

Genus *Illubaboria* gen. nov.

(Figs 3E; 7A–O; 9R)

Type species. *Illubaboria bicolor* sp. nov.; here designated.

Species included. Type species only.

Diagnosis. *Illubaboria* gen. nov. can be recognized by the following combination of characters: fronto-clypeal region (Fig. 7A) short, sloping backwards to base of labrum; eyes (Fig. 7A–B) medium-sized, their frontal 1.55–1.70 times eye diameter; antenna (Fig. 7F) weakly flabellate; pronotum (Fig. 7B) transverse, smooth, glabrous, without distinct sublateral carinae, with posterior margin simple, with only shallow arcuate emargination; mesoventrite (Fig. 7I) medio-laterally with short transverse carinae; abdominal ventrites (Fig. 9R) free; median lobe (Fig. 7N–O) long compared to paramere, with very long subapical hook.

Description. Male. Body (Fig. 3E) 2.80–6.60 mm long, 2.90–3.10 times longer than width at humeri; dark brown, head and antennae black, prothorax, most of mouthparts and first pair of legs yellowish to light brown; body surface covered with yellowish to light brown pubescence.

Head (Fig. 7A–B) including eyes 0.95–1.00 times as wide as pronotum; surface smooth, glabrous, dorsally with shallow median depression, very sparsely punctate, covered with sparse, long, semi-erect pubescence; antennal insertions relatively narrowly separated; frons apically rounded in lateral view; fronto-clypeal region short, sloping backwards to base of labrum. Eyes (Fig. 7A–B) medium-sized, their frontal 1.55–1.70 times eye diameter. Labrum (Fig. 7A) transverse, sclerotized, sides narrowed towards apex, with frontal margin widely concave, sparsely punctate. Mandible (Fig. 7C) robust, elongate, sickle-shaped, with apical oblique tooth and another tooth located in middle part of incisor; base of mandible with long setae, apical part bare, shiny. Maxilla (Fig. 7D) with small cardo, stipes plate-like, partly membranous, galea and lacinia partly membranous, setose; maxillary palpus tetramerous, palpomere I short, transverse, palpomere II elongate, about twice as long as wide, palpomere III short, slightly longer than wide, terminal palpomere longest, fusiform, apex narrowed, flattened, widely obliquely rounded. Labium (Fig. 7E) short, partly membranous; labial palpus trimerous, tiny, palpomeres I and II short, apical palpomere elongate, narrowed towards apex. Antenna (Fig. 7F) with 11 antennomeres, weakly flabellate, scapus robust, elongate, pedicel short, small, antennomere III long, triangular, about as twice as long as wide, stems of antennomeres IV–X about 2.5 times as long as wide, subequal in length, with branches arising from base, triangular and short in basal antennomeres and toward apex gradually more elongate, about 1.75 times as long as their respective stems; apical antennomere simple, longest, slightly longer than lamella of penultimate antennomere; all antennomeres covered with moderately dense pubescence.

Pronotum (Fig. 7B) slightly convex, transverse, widest at anterior third, 1.40–1.50 times as wide as long. Anterior margin almost straight, lateral margins sinuate, distinctly constricted before posterior angles, posterior margin simple, with shallow arcuate emargination. Anterior angles inconspicuous; posterior angles short and narrow, slightly diverging. Disc with narrow, transverse carina near anterior margin, without sublateral carinae, but surface near lateral sides wrinkled. Lateral carina distinct, almost complete. Surface of disc smooth, glabrous, sparsely shallowly punctate, with sparse semi-erect pubescence. Hypomeron smooth, with oblique longitudinal carina; prosternal suture very short. Prosternum (Fig. 7G) transverse, prosternal lobe very short, with frontal margin almost straight, with long semi-erect setae; prosternal process short, narrow, plate-like. Scutellar shield (Fig. 7H) flat, triangular, slightly longer than wide, with anterior margin gradually declivitous, apex narrowly rounded. Mesoventrite (Fig. 7I) with frontal margin almost straight, medio-laterally with short transverse carinae; mesoventral process elongate, narrowed towards apex; mesoventral cavity shallow, with poorly defined walls. Mesocoxal cavity open to both mesepimeron and mesanepisternum. Metaventrite large, subtrapezoidal, sparsely covered with shallow punctures. Elytra (Fig. 3E) subparallel-sided, 0.75 times as long as body; basally wrinkled, indistinctly striate, surface slightly uneven, glabrous, covered with long, semi-erect pubescence; elytral suture distinct, depressed; apices separately rounded. Hind wing venation as in Fig. 7J. Leg (Fig. 7K) moderately long, slightly compressed, with sparse, long, semi-erect setae; coxa robust; trochanter elongate, widened apically, obliquely attached to femur; tarsomeres I–II elongate, subequal in length, tarsomere III shorter than tarsomeres I and II; tarsomere IV shortest, minute, apical tarsomere slender, elongate; claws simple, slender, slightly curved, each with long seta basally.

Abdomen (Fig. 9R) soft, with seven free ventrites (sternites III–IX); all ventrites with sparse, fine punctures, sparsely covered with semi-erect pubescence, mainly at margins; penultimate ventrite very slightly emarginate medially. Sternite IX (Fig. 7L) about 1.6 times as long as wide, basally truncate, almost straight, apically widely rounded, with apex finely punctate and sparsely covered with long setae; sternite X small, longer than wide, partly membranous, connected by membrane to sternite IX. Tergites IX and X (Fig. 7M) weakly connected by membrane; tergite IX basally with two sublateral processes.

Male genitalia (Fig. 7N–O) trilobate, elongate, about 2.4 times as long as wide, about as long as sternite IX; median lobe robust, elongate, less than twice as long as paramere, longer than phallobase, moderately curved in lateral view, basally with two very short, divergent struts, dorsally with robust, long, subapical hook, reaching almost half of median lobe; paramere longer than wide, inner margin almost straight, outer margin slightly rounded, apically truncate, with long setae, with latero-apical projection on inner side; phallobase robust, longer than wide, basally truncate, u-shaped.

Females and immature stages unknown.

Distribution. Ethiopia.

Etymology. The name is derived from Illubabor, the former province of Ethiopia. Gender: feminine.

***Illubaboria bicolor* sp. nov.**

(Figs 3E; 7A–O; 9R)

Type material. Holotype, ♂, "ETHIOPIA, Illubabor Pr., 4 km W Tora, 1950 m, 8°20'45" N, 36°05'23" E, 9. June 2009, Bolm lgt." (UPOL); 8 paratypes: 7 ♂♂, same data as for the holotype (UPOL), 1 ♂, "ETHIOPIA, Illubabor Pr., 2 km N Bedele, 2000 m, 8°27'22" N, 36°21'09" E, 8. June 2009, Bolm lgt." (UPOL).

Diagnosis. *Illubaboria bicolor* sp. nov. is similar in its body size, moderately-sized eyes and weakly flabellate antennae to the species of *Habeshselasia* gen. nov. but it differs e.g., in having pronotal hind margin arcuately emarginate (rectangularly emarginate in *Habeshselasia* spp.; Figs 5H–I, 7B), all abdominal ventrites free (first four connate in *Habeshselasia* spp.), and differently shaped male genitalia (Figs 5R, U; 7N–O). This species resembles *Selasia pulchella* Gestro (also from Ethiopia) by the pale pronotum and dark antennae and elytra but *I. bicolor* sp. nov. has the head and the first two antennomeres dark brown (yellowish in *S. pulchella*), antennal branches shorter, and the apex of the terminal maxillary palpomere narrowed (widely truncate in *S. pulchella*).

Description. Holotype, male. Body 6.60 mm long, 2.20 mm wide at humeri. Body (Fig. 3E) dark brown, head and antennae black, prothorax, labrum, maxilla except palpomeres II–IV, labium except apical palpomeres, procoxae, protrochanters, and most of profemora yellowish to light brown; body surface covered with yellowish to light brown pubescence.

Head (Fig. 7A–B) 0.95 times as wide as pronotum. Eyes medium-sized, their frontal separation 1.60 times eye diameter. Antenna (Fig. 7F) weakly flabellate, pedicel short, antennomere III long, triangular, about as twice as long as wide, antennomeres IV–X (without branches) about 2.5 times as long as wide; branches triangular in basal antennomeres and toward apex gradually more elongate, about 1.75 times as long as their respective stems; apical antennomere simple, longest, slightly longer than lamella of penultimate antennomere.

Pronotum (Fig. 7B) widest at posterior angles, 1.45 times as wide as long at midline, lateral sides sinuate before posterior angles; posterior angles short, slightly diverging; disc with transverse carina near anterior margin, and with indistinct wrinkles sublaterally near posterior angles. Elytra (Fig. 3E) 0.75 times as long as body, together 2.20 times as long as wide at humeri.

Abdominal terminal segments as in Fig. 7L–M. Male genitalia (Fig. 7N–O) with median lobe elongate, about 1.75 times as long as paramere, with short basal struts, subapical hook very long; paramere slightly longer than half of median lobe, elongate, laterally rounded, apically truncate, with latero-apical projection on inner side, apex with setae; phallobase about 1.1 times as long as wide, u-shaped.

Variability. Body length: 2.80–6.60 mm; head 0.95–1.00 times as wide as pronotum; interocular distance 1.55–1.70 times eye diameter; pronotum 1.40–1.50 times as wide as long. The paratype from Bedele has slightly less sinuate sides of pronotum, with posterior angles more divergent, and more distinct sublateral wrinkles on pronotal disc.

Distribution. Central Ethiopia.

Etymology. The specific epithet refers to the body coloration of this species.

Genus *Selasia* Laporte, 1838

Selasia Laporte, 1838: 19.

(Fig. 9C, I, S)

Type species. *Selasia rhipiceroides* Laporte, 1838; by monotypy.

Diagnosis. *Selasia* as defined here can be recognized by the following combination of characters: frontoclypeal region short and wide; labrum transverse, more than four times wider than long, sometimes membranous; antenna flabellate; pronotum transverse, 1.60–1.90 times as wide as long (about 1.35 times in *S. socotrana*), with posterior margin shallowly and widely arcuately emarginate (Fig. 9C), lateral carina almost complete, sublateral carina usually missing; prosternum (Fig. 9C) transverse, with prosternal process reduced or short and narrow; scutellar shield longer than wide; mesoventrite (Fig. 9I) with anterior margin slightly concave, without distinct margin; seven free abdominal ventrites (Fig. 9S); and sternite IX basally emarginate.

Species included. 64 species. *Selasia apicalis* Pic, 1914, *S. arabica* Geisthardt, 2003, *S. atriventris* Pic, 1914, *S. auberti* Pic, 1921, *S. basalis* Gorham, 1895, *S. boruckae* Kundrata, 2012, *S. decipiens* Guérin-Méneville, 1829, *S. dembickyi* Kundrata & Sormova, 2018, *S. erlangeri* Geisthardt, 2007, *S. etoshaensis* Wittmer, 1989, *S. fulva* Gorham, 1883, *S. grandis* Pic, 1914, *S. incognita* Geisthardt, 2007, *S. jenisi* Kundrata & Sormova, 2018, *S. kilimana* Kolbe, 1897, *S. lata* Pic, 1954, *S. laticeps* Pascoë, 1887, *S. merkli* Kundrata, 2012, *S. minuta* Kolbe, 1897, *S. nigrobrunnea* Kundrata, 2017, *S. oberprieleri* Wittmer, 1989, *S. obscura* Wittmer, 1962, *S. pectoralis* Pic, 1946, *S. pulchella* Gestro, 1878, *S. raffrayi* Pic, 1921, *S. rhipiceroides* Laporte, 1836, *S. robecchii* Gestro, 1892, *S. sabatinellii* Kundrata, 2017, *S. socotrana* Kundrata, 2012, *S. striata* (Pic, 1929), *S. variabilis* Wittmer, 1989, *S. venusta* Olivier, 1914, *S. widenmanni* Kolbe, 1897. The type material of *S. asperulipennis* Fairmaire, 1893 and *S. isabellae* Bourgeois, 1909 is most probably lost and their identity cannot be confirmed from the brief original descriptions. The following species currently placed in this genus differ morphologically from the here defined *Selasia* but are not yet placed elsewhere: *Selasia angustior* Pic, 1954, *S. atricornis* Pic, 1946, *S. basipennis* Pic, 1913, *S. bicolor* Wittmer, 1953, *S. castanea* Wittmer, 1989, *S. chaboti* Pic, 1921, *S. curtipennis* Pic, 1918, *S. diversicornis* Pic, 1929, *S. dumosa* Geisthardt, 2007, *S. endroedyi* Wittmer, 1989, *S. fuscula* (Boheman, 1851), *S. homhilia* Geisthardt, 2003, *S. incostata* Wittmer, 1989, *S. intermedia* Wittmer, 1997, *S. maynei* Pic, 1931, *S. murtulai* Pic, 1930, *S. nigricollis* Wittmer, 1989, *S. nigripennis* Pic, 1925, *S. pectinata* Wittmer, 1989, *S. posticalis* Pic, 1931, *S. pseudopectinata*

Geisthardt, 2007, *S. ruficolor* Pic, 1946, *S. sibutensis* Pic, 1914, *S. testaceicolor* Pic, 1914, *S. transkeiensis* Wittmer, 1989, *S. transvaalensis* Wittmer, 1989; *S. unicolor* Guérin-Méneville, 1829, *S. wittmeri* Geisthardt, 2007, *S. zernyi* Hicker, 1944. The systematic placement of these species will be examined in detail in future studies.

Relationships. *Selasia arabica* from Yemen and *Selasia* sp. from Nigeria formed an unsupported clade sister to *S. erlangeri* from Kenya in all but one analysis (Figs 1 and S1).

Distribution. Afrotropical Region, southern part of the Arabian Peninsula, Socotra, Pakistan, Nepal, India, Sri Lanka, Thailand.

Clade M (*Flabelloselasia*, *Lolosia*, *Kupeselasia*, *Microselasia*)

Relationships. The molecular phylogeny suggests *Flabelloselasia* is sister to the remaining genera in the clade, and this is also supported by morphology. *Flabelloselasia* has the apical maxillary palpomeres apically cut, the scutellar shield distinctly longer than wide, and the wing venation more developed. Conversely, the subclade formed by *Lolosia*, *Kupeselasia* and *Microselasia* contains very tiny species (usually about 3 mm) with the apical maxillary and labial palpomeres subacute or almost pointed, the scutellar shield about as long as wide, and highly reduced wing venation (Kundrata & Bocak, 2017). Both DNA and morphology suggest a close relationship between *Kupeselasia* and *Microselasia* (Figs 1 and S1, Table S1). These genera are superficially similar to each other and share the body coloration, general appearance, complete frontal carina, shape of the frontoclypeal region, and the U-shaped phallobase (Kundrata & Bocak, 2017). The internal relationships within *Microselasia* have not been fully resolved using our dataset; however, we consistently recovered two monophyletic groups with the morphological support. The first group consists of *M. kupensis*

Kundrata & Bocak, *M. grandis* Kundrata & Bocak, and *M. pseudograndis* Kundrata & Bocak, which all have a transverse pronotum which is 1.60–1.75 times as wide as long. The second group includes the species which share the pronotum with distinctly sinuate lateral sides and the posterior angles projected postero-laterally, and male genitalia with a short robust median lobe and small parameres (Kundrata & Bocak, 2017). *Microselasia barombi* Kundrata & Bocak and *M. macrocephala* Kundrata & Bocak were always included in that subclade, whilst *M. obscura* was part of it only in the ML analyses (Figs 1 and S1, Table x1). This is most probably casused by the incomplete fragment representation as only the *cox1-3′* fragment was available for this species (Table S1). *Microselasia gracilis* Kundrata & Bocak, which is morphologically similar to the species of this group, should also belong here but we had no DNA-grade material of this species.

Genus *Flabelloselasia* Kundrata & Bocak, 2017

Flabelloselasia Kundrata & Bocak, 2017: 443.

Type species. *Flabelloselasia oculata* Kundrata & Bocak, 2017; by original designation.

Species included. Type species only.

Diagnosis. *Flabelloselasia* can be recognizable among other genera of Drilini by the following combination of characters: dorsal body surface smooth, glabrous; fronto-clypeal region rather narrow, high, with two longitudinal divergent carinae; eyes large, their frontal separation 1.00–1.05 times eye diameter; terminal maxillary and labial palpomere elongate, apically slightly widened and obliquely cut; antenna flabellate, with branches of the antennomeres VI–X about 20 times longer than the respective stems; pronotum transverse, 1.75 times as wide as long, lateral carina almost complete, sublateral carinae distinct, almost reaching frontal margin of pronotum; scutellar shield about 1.40 times as long as wide; abdominal ventrites free; phallobase v-shaped; paramere short, almost rectangular (see Kundrata & Bocak 2017 for more details).

Distribution. Cameroon.

Genus *Lolosia* Kundrata & Bocak, 2017

Lolosia Kundrata & Bocak, 2017: 452.

Type species. *Lolosia transversalis* Kundrata & Bocak, 2017; by original designation.

Species included. Three described species. *Lolosia gajduskovae* Kundrata, 2018, *L. smetkovae* Kundrata, 2018, *L. transversalis*.

Diagnosis. *Lolosia* can be recognized by the following combination of characters: body minute, with smooth, glabrous surface; frontal carina incomplete; fronto-clypeal region wide; eyes large, their frontal separation 1.20 times eye diameter; terminal maxillary and labial palpomere narrowed, subacute apically; antenna serrate; pronotum transverse, 1.85 times wider than long, lateral carina almost complete, sublateral carinae distinct, sinuate, almost reaching anterior margin; scutellar shield about as long as wide; abdominal ventrites free; sternite IX elongate, 2.1 times longer than wide; phallobase v-shaped; paramere relatively long, apically rounded (see Kundrata & Bocak, 2017 for more details).

Distribution. Cameroon, Central African Republic, Democratic Republic of the Congo.

Genus *Kupeselasia* Kundrata & Bocak, 2017

Kupeselasia Kundrata & Bocak, 2017: 448.

Type species. *Kupeselasia minuta* Kundrata & Bocak, 2017; by original designation.

Species included. Type species only.

Diagnosis. *Kupeselasia* can be recognized by the following combination of characters: body minute, 2.10 mm long; frontoclypeal region narrow, high, with frontal carina complete; eyes medium-sized, their frontal separation 1.45 times eyes diameter; antenna serrate; terminal maxillary and labial palpomere apically narrowed, subacute; pronotum 1.55 times as wide as long, with posterior margin simple, lateral carina almost complete, sublateral carinae distinct, sinuate, almost reaching anterior margin; scutellar shield about as long as wide; abdominal ventrites free; sternite IX basally not emarginate; paramere typically slender and elongate. See Kundrata & Bocak (2017) for more details.

Distribution. Cameroon.

Genus *Microselasia* Kundrata & Bocak, 2017

Microselasia Kundrata & Bocak, 2017: 455.

(Fig. 9D, J, T)

Type species. *Microselasia obscura* Kundrata & Bocak, 2017; by original designation.

Species included. 11 described and several undescribed species. *Microselasia barombi* Kundrata & Bocak, 2017, *M. burgeoni* (Pic, 1930), *M. elongata* Kundrata & Bocak, 2017, *M. gracilis* Kundrata & Bocak, 2017, *M. grandis* Kundrata & Bocak, 2017, *M. kupensis* Kundrata & Bocak, 2017, *M. lolodorfensis* Kundrata & Bocak, 2017, *M. macrocephala*

Kundrata & Bocak, 2017, *M. obscura* Kundrata & Bocak, 2017, *M. pseudograndis* Kundrata & Bocak, 2017, *M. sormovae* Kundrata, 2018.

Diagnosis. *Microselasia* can be recognized by the following combination of characters: body minute, 2.35–3.60 mm long; frontoclypeal region narrow, high, with frontal carina complete; eyes medium-sized to large, their frontal separation 1.10–1.60 times eyes diameter; antenna weakly to strongly flabellate; terminal maxillary and labial palpomere apically narrowed, subacute; pronotum more or less transverse, 1.40–1.75 times as wide as long, with posterior margin simple, lateral carina almost complete; scutellar shield about as long as wide; abdominal ventrites free (Fig. 9T); sternite IX notched basally, with lateral sides more or less rounded; paramere minute, short. See Kundrata & Bocak (2017) for more details.

Relationships. We recovered two maximally supported subclades within *Microselasia*; the first consisted of *M. kupensis* + (*M. grandis* + *M. pseudograndis*), and the second of *M. macrocephala* + *M. barombi*. *Microselasia obscura* was sister either to the first subclade (BI analyses) or to the second clade (ML analyses) (Figs 1 and S1).

Distribution. Cameroon, Democratic Republic of the Congo. Undescribed species are known from the surrounding areas in western and central Africa.

Clade D (*Malacogaster*, *Malacodrilus* gen. nov., *Drilus*)

Relationships. All three genera included in this clade are easily recognizable based on their morphology. The subclade formed by *Malacodrilus* gen. nov. and *Malacogaster* obtained robust statistical support (Figs 1 and S1). The adult males of the latter two genera share the typically distinctly widened frontal part of head (not widened in *Drilus*), serrate antennae (serrate or weakly pectinate in *Drilus*), subquadrate or subtrapezoidal pronotum (never transverse as in vast majority of *Drilus* spp.), and the first abdominal ventrite complete (reduced to two lateral sclerites in *Drilus*) (Figs 8A–B, F–G; 9E–F, U–W). Females and larvae of *Drilus* and *Malacogaster* also differ in external morphology (for more details, see Kobieluszova & Kundrata, 2015 and Faucheux & Agnas, 2016, respectively) but unfortunately, no females and immature stages are known for *Malacodrilus* gen. nov.

Malacogaster differs from *Malacodrilus* gen nov. in having the lateral pronotal carina short, extending usually no more than half of pronotal length (amost complete in *Malacodrilus* gen. nov.; Fig. 8H), mandible with only a small tooth medially at incisor (distinct tooth in *Malacodrilus* gen. nov.; Fig. 8C), sternite IX and tergite X distinctly elongate, about or more than twice as long as wide (not elongate, less than twice as long as wide in *Malacodrilus* gen. nov.), and the parameres with latero-apical projection (without projections in *Malacodrilus* gen. nov.; Fig. 8P).

Genus *Drilus* Olivier, 1790

Drilus Olivier, 1790: 3.

(Fig. 9E, K, U)

Type species. *Drilus flavescens* (Geoffroy, 1785); by monotypy.

Species included. 45 described and several undescribed species. *Drilus adustus* Chevrolat, 1854, *D. akbesianus* (Fairmaire, 1895), *D. amabilis* Schaufuss, 1867, *D. attenuatus* Pic, 1914, *D. badius* Kobieluszova & Kundrata 2015, *D. baenai* Kundrata *et al.* 2015, *D. bleusei* (Olivier, 1913), *D. bicolor* Schaufuss, 1867, *D. concolor* Ahrens, 1812, *D. creticus* Pic, 1905, *D. distincticollis* Pic, 1907, *D. flavescens* (Geoffroy, 1785), *D. frontalis* Schaufuss, 1867, *D. fulvicollis* Audouin, 1824, *D. fulvicornis* Kiesenwetter, 1859, *D. fulvitarsis* Baudi di Selve, 1872, *D. funebris* Reitter, 1884, *D. horasfakionus* Kundrata *et al.* 2015, *D. huijbregtsi* Kobieluszova & Kundrata 2015, *D. humeralis* Pic, 1931, *D. iljini* Barovskij 1922, *D. iranicus* Wittmer, 1967, *D. latithorax* Pic, 1902, *D. longulus* Kiesenwetter, 1859, *D. mauritanicus* Lucas, 1842, *D. mertliki* Kobieluszova & Kundrata 2015, *D. nemethi* Kundrata *et al.* 2014, *D. novoathonius* Sumakow, 1903, *D. obscuricornis* Pic, 1899, *D. posticus* Schaufuss, 1867, *D. rectus* Schaufuss, 1867, *D. rittneri* Petrzelkova & Kundrata 2015, *D. robustus* Kobieluszova & Kundrata 2015, *D. rufipes* (Baudi di Selve, 1872), *D. sanliurfensis* Kobieluszova & Kundrata 2015, *D. schwarzi* Reitter, 1891, *D. subparallelus* Pic, 1934, *D. testaceipes* Pic, 1933, *D. teunisseni* Kobieluszova & Kundrata 2015, *D. turcicus* Kobieluszova & Kundrata 2015. The following five species described from the Afrotropical Region have morphology different from the here defined *Drilus* and will be revised in near future: *D. atripennis* Pic, 1934, *D. basilewskyi* Wittmer, 1962, *D. impressiceps* Pic, 1913, *D. ramosus* Fairmaire, 1883, *D. testaceipennis* Pic, 1918.

Diagnosis. *Drilus* can be recognized by the following combination of characters: dorsal body surface uneven, usually matt; eyes relatively small to medium-sized, their frontal separation 1.60–3.00 times eye diameter; antenna slightly serrate to weakly flabellate; pronotum transverse, 1.20–1.70 times as wide as long, with lateral sides sinuate or rounded, lateral carina almost complete, and posterior margin usually only shallowly arcuately emarginate; prosternum (Fig. 9E) with reduced prosternal process; mesoventrite (Fig. 9K) v-shaped, with only indistinctly defined or shallow mesoventral cavity; surface of elytra usually without distinct striae or lines of punctures; abdominal ventrites free (Fig. 9U), sternite IX and tergite X not apparently elongate, with more or less rounded sides, usually not more than 1.80 times as long as wide; paramere without latero-apical projection.

Relationships. The phylogenetic relationships among the *Drilus* lineages are only partly resolved based on the six-marker phylogeny (Figs 1 and S1). The presence of the monophyletic group informally known as the "Greek clade", which is formed by the elongate, usually tiny species with the serrate antennae which are specialized predators of the *Albinaria* snails and are distributed in the Peloponnese, the Ionian islands and Crete, is consistent with the results of the *cox1* analysis by Kundrata *et al.* (2015a), and its statistically strongly supported sister group relationship with *D. rufipes* (Baudi di Selve) from Cyprus is in agreement with the results of the three-marker analysis by Sormova *et al.* (2018). The remaining species, which include usually more robust and hairy representatives with weakly flabellate antennae and a strongly transverse pronotum, formed a gradual branching in previous studies (Kundrata *et al.*, 2015a; Sormova *et al.*, 2018) but they were found to be monophyletic in this study, although with low support (Figs 1 and S1). This clade included two branches, i.e., *D. fulvicornis* + (*D. flavescens* + *D. mauritanicus*), and *D. concolor* + (*D. rectus* + *D.* cf. *mertliki*). More species in the analysis in combination with a detailed morphological investigation of this genus are needed for a better understanding of *Drilus* phylogenetic interrelationships.

Distribution. Northern Africa (Algeria, Morocco), Europe, Asia Minor, Levant, Caucasus, Iran. Species from the tropical Africa do not belong to the genus (see comment above).

Genus *Malacodrilus* gen. nov.

(Figs 3F; 8A–P; 9V)

Type species. *Malacodrilus hajeki* sp. nov.; here designated.

Diagnosis. *Malacodrilus* can be recognized by the following combination of characters: body relatively short, robust (Fig. 3F), fronto-clypeal region (Fig. 8A–B) slightly produced forwards, short, wide, widely depressed; eyes (Fig. 8A–B) small, their frontal separation 2.00–2.30 times eye diameter; antenna (Fig. 8F) robust, serrate; pronotum (Fig. 8G) subquadrate, 1.25–1.40 times as wide as long, lateral carina almost complete; prosternum (Fig. 8H) with reduced prosternal process; scutellar shield (Fig. 8I) apically subtruncate; mesoventrite (Fig. 8J) v-shaped, with anterior margin emarginate; elytra (Fig. 3F) relatively short, dehiscent; abdominal ventrites free (Fig. 9V); sternite IX and tergite X (Fig. 8N–O) not apparently elongate, about 1.5 times as long as wide; paramere (Fig. 8P) without latero-apical projection.

Description. Male. Body (Fig. 3F) 4.30–6.20 mm long, slightly convex dorsally, 2.60 times longer than width at humeri; yellowish brown to brown, most of elytra and whole metaventrite black; body surface covered with yellow pubescence.

Head (Fig. 8A–B) including eyes 0.90–1.10 times as wide as pronotum; surface irregularly wrinkled and punctate; frons wide, with large, more or less deep medial depression, lateral margins elevated above antennal insertions; anterior edge distinct but not carinate, slightly produced forwards. Eyes (Fig. 8A–B) relatively small, prominent, their frontal separation 2.00–2.30 times eye diameter. Labrum sclerotized, transverse, subtrapezoidal, with frontal margin slightly concave; sparsely punctate, covered with semi-erect setae. Mandible (Fig. 8C) bidentate, robust, pigmented, sickle-shaped, with apical oblique tooth, incisor margin medially with moderately long second tooth; base with long setae, apical part bare, shiny. Maxilla (Fig. 8D) with small cardo, stipes small, plate-like, partly membranous; galea and lacinia apparently fused, reduced, setose; maxillary palpus tetramerous, robust, about as long as mandible, palpomere I short, wider than long, palpomere

II robust, about 1.4 times as long as wide, palpomere III only slightly longer than wide, terminal palpomere longest, fusiform, apically narrowed, with apex obliquely cut. Labium (Fig. 8E) short, partly membranous; labial palpus trimerous, tiny, about half length of maxillary palpus, palpomere I short, transverse, terminal palpomere about 2.5 times as long as wide, fusiform, apically gradually narrowed, obliquely cut. Antenna (Fig. 8F) with 11 antennomeres, serrate, robust, reaching humeri; scapus elongate, about 1.75 times as long as wide, pedicel minute, about as long as wide, antennomere III simple, elongate, more than 1.5 times as long as wide, widened apically, antennomeres IV–X serrate, slightly longer than wide, terminal antennomere simple, elongate, more than 2.5 times as long as wide, apically slightly narrowed, obliquely cut; all antennomeres covered with moderately dense, semi-erect pubescence.

Pronotum (Fig. 8G) moderately convex, subquadrate, widest at about anterior two fifths or at posterior angles, 1.25–1.40 times as wide as long. Anterior margin slightly rounded, usually slightly emarginate medially, sides slightly widened at anterior two fifths, posterior margin simple, bisinuate, arcuately, moderately deeply emarginate medially. Anterior angles inconspicuous; posterior angles obtuse, almost rectangular or slightly divergent. Lateral carina incomplete anteriorly. Surface of disc sparsely, moderately deeply punctate, with sparse semi-erect pubescence, mainly at sides and angles. Hypomeron almost smooth, sparsely covered with semi-erect setae; prosternal suture very short. Prosternum (Fig. 8H) transverse, its surface uneven, sparsely punctate and covered with semi-erect setae, mainly at frontal margin; prosternal lobe inconspicuous, frontal margin widely concave; prosternal process reduced. Scutellar shield (Fig. 8I) flat, tongue-like, elongate, more than 1.3 times as long as wide, with anterior margin gradually declivitous, apex subtruncate. Mesoventrite (Fig. 8J) widely v-shaped, with frontal margin emarginate, posterior margin rounded; mesoventral cavity in form of large shallow median depression, with poorly defined walls. Mesocoxal cavity open to both mesepimeron and mesanepisternum. Metaventrite large, subtrapezoidal, covered with fine punctures and semi-erect pubescence. Elytra (Fig. 3F) subparallel-sided, relatively short, 0.70 times as long as body; with uneven, rough surface, basally wrinkled, without any striae or distinct lines of punctures, covered with long, semi-erect pubescence, with apices dehiscent, separately rounded. Hind wing venation as in Fig. 8K. Leg (Fig. 8L) moderately long, slightly compressed, with sparse, long, semi-erect setae; coxa robust; trochanter elongate, slightly widened apically, attached obliquely to femur; tarsomeres I–III elongate, widened apically, gradually decreasing in length, tarsomere IV short, ventrally with short membranous lobe, terminal tarsomere long, slender; claws simple, slender, slightly curved, each with seta basally.

Abdomen (Fig. 9V) soft, with seven free ventrites (sternites III–IX); all ventrites with sparse, shallow punctures, sparsely covered with semi-erect pubescence, mainly at margins; penultimate ventrite very slightly emarginate medially. Sternite IX (Fig. 8N) about 1.5 times as long as wide, narrowed basally, widely rounded apically, finely punctate and sparsely covered with setae; sternite X small, about 0.5 times as long as sternite IX, longer than wide, partly membranous, with basal margin almost straight, apically rounded, connected by membrane to sternite IX. Tergites IX and X (Fig. 8O) weakly connected by membrane; tergite IX basally with two sublateral processes.

Male genitalia (Fig. 8P) trilobate, about 2.1 times as long as wide, about 0.85 times as long as sternite IX; median lobe robust, slightly longer than paramere, moderately curved in lateral view, basally with two very short, divergent struts, dorsally with robust subapical hook; paramere elongate, slightly longer than phallobase, apically rounded, with long setae; phallobase robust, about as long as wide, u-shaped.

Females and immature stages unknown.

Distribution. Pakistan.

Etymology. The genus name is a combination of the two generic names in Drilini, i.e., *Malacogaster* Bassi, 1834 and *Drilus* Olivier, 1790. Gender: masculine.

Malacodrilus hajeki **sp. nov.**

(Figs 3F; 8A–P; 9V)

Type material. Holotype, ♂, "PAKISTAN, NWFP, Khyber agency, Up. stream Kabul river, 30.8.–7.9. 2004, 700 m, leg. V. Gurko" (NMPC); 24 paratypes, males, same data as for the holotype (NMPC, UPOL).

Diagnosis. *Malacodrilus hajeki* sp. nov. is similar in habitus to some species of *Drilus* but it can be recognized by the following combination of characters: the short compact body (Fig. 3F), typically wide, depressed fronto-clypeal region (Fig. 8A–B), robust serrate antennae (Fig. 8F), subquadrate pronotum (Fig. 8G), and relatively short, diverging elytra (Fig. 3F).

Description. Holotype, male. Body 5.50 mm long, 2.10 mm wide at humeri. Body (Fig. 3F) yellowish brown to brown, elytra (except basalmost portions and basal part of suture) and metaventrite black; body surface covered with yellow pubescence.

Head (Fig. 8A–B) 0.95 times as wide as pronotum. Eyes small, their frontal separation 2.00 times eye diameter. Antenna (Fig. 8F) serrate, antennomere III simple, elongate, more than 1.5 times as long as wide, widened apically, antennomeres IV–X serrate, about 1.2–1.4 times as long as wide, terminal antennomere simple, elongate, more than 2.5 times as long as wide, apically slightly narrowed, obliquely cut.

Pronotum (Fig. 8G) widest at posterior angles, 1.30 times as wide as long at midline, sides sinuate, posterior margin simple, slightly emarginate medially; posterior angles obtuse, slightly divergent; surface of disc sparsely punctate, with sparse semi-erect pubescence. Elytra (Fig. 3F) 0.70 times as long as body, together 1.80 times as long as wide at humeri.

Abdominal terminal segments as in Fig. 8N–O. Male genitalia (Fig. 8P) with median lobe longer than paramere, subapical hook moderately long; paramere elongate, rounded apically, with setae at apex; phallobase about as wide as long, u-shaped.

Variability. Body length: 4.30–6.20 mm; interocular distance 2.00–2.30 times eye diameter; pronotum 1.25–1.40 times as wide as long. The soft, weakly sclerotized abdomen of this species is highly flexible. Therefore, known specimens show a great variation in the relative length of abdomen within a single population, from specimens with abdomen short, fully covered by elytra to specimens with the abdomen considerably elongated, surpassing the elytral apices by several segments.

Distribution. This species is known only from the type locality in Khyber Agency, Pakistan.

Etymology. The specific epithet is a patronym in honor of Jiří Hájek (National Museum Prague, Czech Republic).

Genus *Malacogaster* Bassi, 1834

Malacogaster Bassi, 1834: pl. 99.

(Fig. 9F, L, W)

Type species. *Malacogaster passerinii* Bassi, 1834; by monotypy.

Species included. 11 species. *Malacogaster bassii* Lucas, 1870, *M. holomelas* Peyerimhoff, 1949, *M. maculiventris* Reitter, 1894, *M. nigripes* Schaufuss, 1867, *M. olcesei* Pic, 1951, *M. parallelocollis* Reitter, 1894, *M. passerinii* Bassi, 1833, *M. rubripes* Peyerimhoff, 1949, *M. rutllanti* Alcaide, 1946, *M. theryi* Pic, 1951, *M. tilloides* Wollaston, 1864.

Diagnosis. *Malacogaster* can be recognized by the combination of the following characters: fronto-clypeal region short and wide; eyes small, their frontal separation 2.20–2.65 times eye diameter; labrum large, subtrapezoidal; mandible with only small tooth medially at incisor; terminal maxillary and labial palpomeres short, gradually narrowed toward apex, apically obliquely truncate; antenna serrate; pronotum subquadrate to subtrapezoidal, about 1.10–1.40 times as wide as long, with lateral sides almost straight, usually gradually widened towards posterior margin, posterior margin with small arcuate median emargination; lateral carina short, reaching usually no more than half of pronotal length; prosternum (Fig. 9F) with reduced prosternal process; mesoventrite (Fig. 9L) v-shaped, with only indistinctly defined or shallow mesoventral cavity; elytra usually relatively short, dehiscent, with abdomen surpassing the tip of elytra; surface of elytra uneven, without striae or lines of punctures; abdominal ventrites free (Fig. 9W); sternite IX and tergite X typically elongate, about or more than twice as long as wide; paramere with latero-apical projection on inner side.

Distribution. Spain (Canary Islands, Iberian Peninsula, Balearic Islands), Italy (Sardinia, Sicily, Italian Peninsula), northern Africa (Morocco, Algeria, Tunisia, Libya).

An identification key for the genera of Drilini based on adult males

1. Posterior margin of pronotum rectangularly emarginate, emargination about as wide as scutellar shield (Fig. 5H); abdominal ventrites I–IV connate; antenna flabellate ....
2

–. Posterior margin of pronotum simple, without emargination or shallowly, arcuately emarginate (Fig. 7B); abdominal ventrites I–IV never connate; antenna serrate to flabellate 6

2. Eyes large, their frontal separation 1.00–1.25 times eye diameter; scutellar shield apically subacute 3

–. Eyes medium-sized, their frontal separation 1.55–1.65 times eye diameter (Fig. 5A–B, H); scutellar shield apically rounded (Fig. 5K) .... *Habeshselasia* gen. nov.

3. Fronto-clypeal region narrow, high, abruptly declined between antennal insertions, frontally excavated 4

–. Fronto-clypeal region short and wide, gradually declined to base of labrum to almost vertical (Fig. 4A) .... *Austroselasia* gen. nov.

4. Antennomere III 2.5–3.3 times as long as antennomere IV, with its branch about as long as or longer than stem; antennomeres IV–X short, about as long as wide or slightly longer than wide; branches of antennomeres V–X about 8–12 times as long as their respective stems; sublateral pronotal carina missing or short, never reaching anterior half of pronotum 5

–. Antennomere III only about 1.5 times as long as antennomere IV, with its branch distinctly shorter than stem; antennomeres IV–X distinctly longer than wide; branches of antennomeres V–X about 2–4 times as long as their respective stems (Fig. 6D); sublateral pronotal carina almost reaching anterior margin of pronotum (Fig. 6A) .... *Mashaselasia* gen. nov.

5. Apical maxillary palpomere less than twice as long as wide, apically cut, straight; labrum sclerotized, subpentagonal, apically widely rounded; phallobase slightly longer than wide,

median lobe shorter than phallobase; paramere smaller, apically rounded .... *Latoselasia* Kundrata & Bocak, 2017

–. Apical maxillary palpomere about 2.5 times as long as wide, slightly constricted subapically, apically slightly rounded; labrum transverse, large, only partly sclerotized; phallobase never longer than wide, median lobe longer than phallobase; paramere larger, apically subacute .... *Wittmerselasia* Kundrata & Bocak, 2017

6. Fronto-clypeal region narrow, high, with a more or less developed vertical median carina or two lateral carinae 7

–. Fronto-clypeal region wide, never carinate (Fig. 8A) 9

7. Antenna strongly flabellate, branches of antennomeres VI–X about 20 times longer than their stems; frontal carina incomplete; antennomere III more than 3 times as long as antennomere IV; terminal maxillary palpomere apically widely truncate; phallobase v-shaped; paramere subrectangular .... *Flabelloselasia* Kundrata & Bocak, 2017

–. Antenna serrate to flabellate, branches of antennomeres VI–X not more than 10 times longer than their stems; frontal carina complete; antennomere III 1.0–1.7 times as long as antennomere IV; terminal maxillary palpomere apically narrowed, subacute; phallobase u-shaped; paramere variously shaped but never subrectangular 8

8. Body 2.10 mm long; antenna strongly serrate; mandible slender; sternite IX not emarginate basally; paramere distinctly elongate, slender .... *Kupeselasia* Kundrata & Bocak, 2017

–. Body 2.30–3.60 mm long; antenna flabellate; mandibles robust; sternite IX emarginate basally; paramere not distinctly elongate .... *Microselasia* Kundrata & Bocak, 2017

9. Pronotum transverse, with distinct sinuate sublateral carinae almost reaching anterior margin of pronotum; terminal maxillary palpomere apically narrowed, subacute; antenna serrate, with uneven surface; scutellar shield as long as wide .... *Lolosia* Kundrata & Bocak, 2017

–. Pronotum subquadrate to transverse, without distinct sublateral carinae; terminal maxillary palpomere variously shaped; antenna serrate to flabellate, with more or less even surface; scutellar shield longer than wide 10

10. Fronto-clypeal region almost vertical or steeply declivous to base of labrum (Fig. 7A); antenna weakly to strongly flabellate; scutellar shield apically narrowly rounded to subacute; mesoventrite posteriorly narrowly produced (Fig. 9I); elytral surface usually almost smooth; seven abdominal ventrites; sternite IX basally truncate or emarginate 11

–. Fronto-clypeal region more or less produced forwards between antennae (Fig. 8A); antenna serrate to weakly flabellate; scutellar shield apically widely rounded to subtruncate; mesoventrite v-shaped, posteriorly simply rounded (Figs 8J, 9K–L); elytral surface uneven, often wrinkled; eight abdominal ventrites; sternite IX basally narrowed, usually rounded 12

11. Labrum more or less sclerotized, more than four times wider than long, sometimes reduced and almost completely membranous; stems of antennomeres V–X as long as wide or only slightly longer than wide; outer margin of elytra apically swollen; sternite IX basally emarginate .... *Selasia* Laporte, 1838

–. Labrum sclerotized, about 2.5 times wider than long (Fig. 7A); stems of antennomeres V–X considerably longer than wide (Fig. 7F); outer margin of elytra apically simple; sternite IX basally truncate (Fig. 7L) .... *Illubaboria* gen. nov.

12. Lateral pronotal carina short, reaching usually no more than half of pronotal length; mandible with only small tooth medially at incisor; sternite IX and tergite X distinctly elongate, about or more than twice as long as wide; paramere with latero-apical projection .... *Malacogaster* Bassi, 1838

–. Lateral pronotal carina almost complete; mandible with distinct tooth medially at incisor (Fig. 8C); sternite IX and tergite X not elongate, always less than twice as long as wide (Fig. 8N–O); paramere without latero-apical projection (Fig. 8P) 13

13. Frons not distinctly widened; antenna serrate or weakly flabellate; pronotum usually transverse (exceptionally subquadrate); anterior margin of prosternum rounded or straight (Fig. 9E); first abdominal ventrite formed by two lateral sclerites (Fig. 9U) .... *Drilus* Olivier, 1790

–. Frons distinctly widened (Fig. 8A–B); antenna serrate (Fig. 8F); pronotum subquadrate (Fig. 8G); anterior margin of prosternum concave (Fig. 8H); first abdominal ventrite complete (Fig. 9V) .... *Malacodrilus* gen. nov.

Discussion

Relationships and monophyly of Drilini

All molecular analyses have suggested a phylogenetic position of Drilini that is in conflict with morphology-based classifications (Crowson, 1972; Lawrence *et al.*, 2011). Drilini have never been placed with the the so-called 'cantharoid' families and have always been recovered closely related to the click beetles or specifically Agrypninae (e.g., Kundrata & Bocak, 2011; Bocak *et al.*, 2014, 2016; Kundrata *et al.*, 2014, 2016, 2018; McKenna *et al.*, 2015; Amaral *et al.*, 2016; Timmermans *et al.*, 2016**)**. Due to their strongly modified morphology compared to their inferred closest relatives, limited morphological support is available for the DNA-based placement. Notable exceptions include the presence of basal setae on pretarsal claws and the absence of the wedge cell in hind wing venation which are shared with Agrypninae. However, these characters evolved multiple times within Elateridae, therefore they must be treated with caution (Kundrata *et al.*, 2018). Current results indicate close relationships of Drilini with *Ludioctenus* Fairmaire, *Lacon* Laporte and *Adelocera* Latreille in agreement with previous analyses (Kundrata *et al.*, 2014, 2016; Figs 1 and S1). Here, we recovered the monophyly of Drilini as currently defined with robust support, i.e., *Drilus*, *Malacogaster* and *Selasia*, plus newly identified lineages (Kundrata *et al.*, 2014; Kundrata & Bocak, 2017; Figs 1 and S1).

Major clades of Drilini

The phylogenetic analyses identify five main clades which are present across all recovered DNA-based topologies and they are supported by morphology of adult males (see below). Their interrelationships are sensitive to applied algorithms, but all analyses show deep splits among four Afrotropical clades and a single terminal clade consisting of Palearctic species (Figs 1 and S1).

Clade A (*Austroselasia* gen. nov.)

Clade A contains species with a short and wide fronto-clypeal region, which is gradually declined towards base of labrum or almost vertical (Fig. 4A), flabellate antennae (Fig. 4E), the pronotum with posterior margin rectangularly emarginate, sublateral carina usually forming a distinct ridge (Fig. 4F), the transverse prosternum with prosternal process forming a narrow plate (Fig. 4G), seven abdominal ventrites with the first four connate (Fig. 9O), and the parameres apically obliquely cut (Fig. 4N). All species in this clade are superficially similar to *Selasia* (Fig. 1; Wittmer, 1989; Geisthardt, 2007a, b), which however differs by the almost imperceptibly and arcuately emarginate pronotal margin, the sublateral carina on pronotal disc indistinct or missing, all ventrites free (Fig. 9S), and the apical portions of parameres usually rounded.

Clade W (*Habeshselasia* gen. nov., *Mashaselasia* gen. nov., *Latoselasia*, *Wittmerselasia*)

Clade W is characterized by the glabrous body surface (Fig. 3B–D), the rectangularly emarginate posterior pronotal margin (Figs 5H–I, 6A), the transverse prosternum with a prosternal process forming a narrow plate (Figs 5J, 9B), seven abdominal ventrites with the first four connate (Fig. 9P), and conspicuously hairy parameres (Figs 5U, 6I; Kundrata & Bocak, 2017). Molecular phylogeny recovered *Habeshselasia* gen. nov. as sister to the other three genera (Figs 1 and S1), and both subclades are strongly supported by morphological characters (see below).

Clade S (*Illubaboria* gen. nov., *Selasia*)

Clade S is characterized by the pronotum with a simple posterior margin which has the median part only shallowly arcuately emarginate, the pronotal disc without distinct sublateral carinae (Fig. 7B), and the abdomen with seven free ventrites (Fig. 9R–S). Most species share the transverse prosternum with prosternal process forming a narrow plate (Fig. 7G); however, the prosternal process is highly reduced in some *Selasia*. Until recently, *Selasia* was used as a 'waste-basket genus' for Afrotropical Drilini with flabellate antennae (e.g., Wittmer, 1989; Geisthardt, 2007a, b). The current analysis shows that the Afrotropical fauna of Drilini is not represented by a single clade, but consists of several lineages representing an early radiation. The type species of *Selasia* (*S. rhipiceroides* Laporte from Senegal) was unavailable but we included in the analysis an undescribed species from Nigeria (RK0566; Table S1) which is morphologically close to the type species. We limit *Selasia* to the species with short antennomeres V–X, slightly arcuately emarginate posterior margin of pronotum, swollen outer margin of elytral apex, and seven free ventrites.

Clade M (*Flabelloselasia*, *Lolosia*, *Kupeselasia*, *Microselasia*)

Clade M contains species with a dark coloured, slender, minute body (2.10–4.10 mm), a high fronto-clypeal region (widened and shortened in *Lolosia*), a smooth glabrous pronotal disc usually with distinct sublateral carinae (commonly reduced or missing in *Microselasia*), the transverse prosternum with a prosternal process forming a narrow plate (Fig. 9D), and the abdomen with two additional lateral sclerites supposedly derived from the fragmented sternite II (shared with *Drilus*, but not with *Malacogaster* and *Malacodrilus* gen. nov.; Fig. 9T–W; Kundrata & Bocak, 2017). It must be noted, however, that no synapomorphy was identified except a minute body. *Flabelloselasia* is morphologically somewhat different from the remaining genera and its distinctiveness is confirmed by the molecular phylogeny (Fig. 1). The subclade formed by *Lolosia*, *Kupeselasia* and *Microselasia* is characterized by the very tiny body (usually about 3 mm), apical maxillary and labial palpomeres subacute or almost pointed, the scutellar shield about as long as wide, and highly reduced wing venation (Kundrata & Bocak, 2017).

Microselasia is variable in the shape of antennae, from weakly flabellate with elongate antennomere stems to strongly flabellate antennae with short antennomere stems (Kundrata & Bocak, 2017). The molecular phylogeny reveals that the form of the antennae is not a phylogenetically informative character. Closely related species have different antennae, and two species with weakly flabellate antennomeres (*M. kupensis* and *M. elongata* Kundrata & Bocak) were never inferred as sister taxa (Fig. 1). These results indicate rapid evolution of some traits due to their supposed role in inter-sexual communication (e.g. Bocek & Bocak, 2017; Stanger-Hall *et al.*, 2018).

Clade D (*Malacogaster*, *Malacodrilus* gen. nov., *Drilus*)

This clade contains species with serrate to pectinate antennae, a flattened head with the frontal region often produced forwards (Fig. 8A–B), relatively small eyes, with their frontal separation 1.60–3.00 times eye diameter, usually less transverse pronotum without sublateral carinae (Fig. 8G), less transverse prosternum with a reduced prosternal process (Figs 8H, 9E–F), v-shaped mesoventrite with a reduced mesoventral process (Figs 8J, 9K–L), elytra often divergent or reduced, with a rough surface (Fig. 3F), and the abdomen with eight free ventrites (although the first ventrite is often formed by two separate sclerites; Fig. 9U–W). Our molecular phylogenies are ambiguous regarding the monophyly of *Drilus* with respect to the *Malacogaster* + *Malacodrilus* gen. nov. clade (Figs 1 and S1, Table S1). When all taxa, i.e. also those with some markers missing, are included, *Drilus* is monophyletic and a sister to *Malacogaster* + *Malacodrilus* gen. nov. (compare Fig. 1 and S1). Both conflicting topologies obtained low statistical support. We prefer the results of the analyses of the larger dataset with the higher proportion of missing data, because adding taxa even with extensive missing data can be beneficial and improve phylogenetic accuracy especially in cases where analyses are misled by limited taxon sampling (e.g., Wiens & Morrill, 2011; Wiens & Tiu, 2012; Jiang *et al.*, 2014), and because *Drilus*, *Malacodrilus* gen. nov. and *Malacogaster* differ in their morphology (see the Systematics section below).

Both molecular phylogeny and morphology suggest a basal position for the clades A and W, whose males have the prosternal process present, well-developed mesoventral process, the connate basal abdominal ventrites, and the intercoxal process present on the first ventrite (Figs 4G, I; 5J, L; 6E; 9B, H, O–P). More terminal lineages have the pronotum with slightly arcuately emarginate posterior margin and all abdominal ventrites free. Members of clade S still have an apparent prosternal process (with exception of some *Selasia* species), well developed mesoventral process, seven abdominal ventrites, and at least a slightly developed intercoxal process on the first ventrite (Figs 7G, I; 9C, I, R–S). Clades M and D have partly reduced maxillae (Fig. 8D), a highly reduced mesoventral process (Figs 8J, 9J–L), softer elytra with uneven surface, eight abdominal ventrites, and the intercoxal process on the first ventrite highly reduced or absent (Fig. 9T–W). Members of clade M have still an apparent prosternal process, and the first ventrite is divided into two lateral sclerites (Fig. 9D, T). The representatives of clade D do not have a prosternal process, and the first ventrite is formed by two lateral sclerites in *Drilus*, but it is more or less complete in *Malacodrilus* gen. nov. and *Malacogaster* (Figs 8H, 9E–F, U–W), with the latter often having shortened and divergent elytra.

Origin, diversity, distribution, and divergence time estimates of Drilini

Until recently, genera in Drilini have been poorly characterized and their limits have been based on general appearance and coloration. Earlier authors placed all species with relatively long antennal branches into *Selasia*, species with a reddish pronotum and dark elytra and with several abdominal ventrites surpassing the tip of elytra to *Malacogaster*, and other forms to *Drilus* (e.g., Baudi di Selve, 1871; Olivier, 1913; Wittmer, 1962; Kundrata & Bocak, 2007). The Afrotropical Drilini have been collectively treated as *Selasia* as their morphology and diversity has not been properly studied. Only recently, Kundrata & Bocak (2017) described several genera from Cameroon and questioned the earlier concepts.

Here, based on the DNA phylogeny and morphological evidence, we confirm that the Afrotropical Drilini form multiple genetically and morphologically distinct lineages. Our results indicate that Subsaharan Africa is an area where all deeply rooted clades occur and this region is most probably the center of early divergence for Drilini followed by at least two colonization events to the Palearctic region (*Selasia* and the clade D) and at least one reaching the Oriental region (Fig. 1). The low dispersal capacity of Drilini similar to other groups with incompletely metamorphosed females (Masek *et al.*, 2015) and the relatively recent origin of Drilini (Fig. 2) make an alternative hypothesis of secondary dispersal to the Afrotropical region improbable. The origin of Drilini was dated to the late Eocene (ca. 35.5 Mya), when the relative position of landmasses was already similar to the present state (Scotese 2014). The five main clades originated shortly after the rise of the group; most early splits occurred between the Eocene/Oligocene boundary and the mid-Miocene when the global climate was undergoing drastic fluctuations (Fig. 2; Zachos *et al.*, 2001; Feakins & deMenocal, 2010). This scenario is in agreement with other studies focused on different organisms (e.g., Aduse-Poku *et al.*, 2009; Klak *et al.*, 2017). Further, our study is one of the numerous recent "out-of-Africa" examples for various insect taxa (e.g., Eberle *et al.*, 2017; Ye *et al.*, 2017; Sahoo *et al.*, 2018).

The splits among deep Afrotropical branches are supported also by morphology if we suppose the gradual progressive shift to incomplete metamorphosis (Bocak *et al.*, 2008, 2018; Jeng, 2008). The presence of four connate ventrites, similar to the morphology of a typical click-beetle abdomen, is present in the Afrotropical clades A and W. The representatives of clade A (i.e., *Austroselasia* gen. nov.) occur in southern and eastern Africa, while those of clade W are distributed in western, central, and northeastern Africa. Combined, these clades contain about 30 species including some undescribed forms. According to our results, clade S with the highest diversity in tropical Africa branched off next (Fig. 2). *Selasia arabica* Geisthardt from the Arabian Peninsula forms a terminal lineage in this clade, and based on their morphology, the species from the Himalayas, India, Sri Lanka, and Indochina should also belong to this clade. These relationships together with the divergence time estimates indicate that *Selasia* dispersed from eastern Africa to the Indian subcontinent probably through the Arabian Peninsula in the early Miocene, in agreement with some other animals (e.g., Kodandaramaiah & Wahlberg, 2007; Aduse-Poku *et al.*, 2009). Further data is needed for the robust support of this hypothesis as the sampling from the Himalayas and Oriental region is poor. More material can also help us to understand the limits and diversity of the genus *Selasia*, which is, with about 60 species, still the most species-rich genus in Drilini. The lineages of clade M, which includes about 25 rainforest species from western and central Africa, gradually diversified through the Oligocene soon after their separation from clade D, which includes about 60 species distributed in the Palearctic region. The Palearctic clade diversified mainly during the early and middle Miocene, and the Greek *Drilus* diversification was probably influenced by the formation of the Mid-Aegean Trench in the Tortonian (ca. 12–9 Mya), as was already documented by Kundrata *et al.* (2015a) (Fig. 2).

The Mediterranean houses a single lineage, but is an apparent diversification hot-spot with about 50 species of *Drilus* and *Malacogaster*. Similarly, further incompletely metamorphosed elateroids are known from this regios: almost 200 species of Cebrionini (*Cebrio* Olivier, *Analestesa* Leach), and *Plastocerus* (Plastocerinae; Cate, 2007; Bocak *et al.*, 2018). Additionally, most species of another neotenic soft-bodied elateroid family, Omalisidae, and all representatives of Iberobaeniidae are endemic to the Mediterranean area (Bocak & Brlik, 2008; Bocak *et al.*, 2016; Bocek *et al.*, 2018). Myers *et al.* (2000) identified high ancient diversity in the Mediterranean and these poorly dispersing beetle lineages support the uniqueness of the Mediterranean fauna.

Sclerotization and interlocking devices in Elateridae and Drilini

Incomplete metamorphosis and hence an incomplete body sclerotization can be observed in three independent clades within Elateridae (Bocak *et al.*, 2018; Kundrata *et al.*, 2018). The affected lineages show different levels of morphological modifications in both sexes, but this can be best documented in the females. The female of *Plastocerus* (Plastocerinae) resembles typical Elateridae, but it is slightly less sclerotized, lacks the functional clicking mechanism, and has free abdominal ventrites (Bocak *et al.*, 2018). Cebrionini females are more modified; they are brachypterous, with most of the abdomen exposed. Known females of Drilini are wingless and almost completely larviform, with only head partly adult-like (Crowson, 1972; Kundrata *et al.*, 2015a). Although we cannot identify a sister group of Drilini using the available data, we can see that other Agrypninae, including putative sister clades, contain only fully sclerotized lineages with a functional clicking mechanism. The soft-bodied Drilini are a terminal lineage and accordingly, for the purpose of the study of evolution of soft-bodiedness, it does not matter which particular group of Agrypninae is in fact the sister group of Drilini.

The complex of morphological traits shared by neotenic lineages include a weakly sclerotized, flexible cuticle and various changes, often reductions, in the structure of the mouthparts, thorax, and abdomen (Crowson, 1972; Lawrence, 1988; Bocak & Bocakova, 2008; Bocak *et al.*, 2018). The molecular phylogeny indicates a gradual transition from the slightly affected lineages to the severely affected groups (Figs 1 and 9). All Drilini have only a lightly sclerotized body, and the most loosely articulated and also the least sclerotized body can be found in the terminal clade D. Elateroid beetles affected by incomplete metamorphosis often have a tendency towards reduction of the male body size (e.g., Bocak & Brlik, 2008; Kundrata *et al.*, 2015b; Bocak *et al.*, 2016). This phenomenon is observed in some males of Drilini. Taxa recovered in deeply rooted branches are mostly medium-sized to large-bodied while clade M contains only small-bodied species, and many species in clade D also have a reduced body size (Kundrata *et al.*, 2015a; Kundrata & Bocak, 2017). The most important and often gradual changes in morphology due to the neotenic development include modifications of mouthparts, ventral part of thorax, and abdomen.

Mouthparts

Modified elateroids have often reduced maxillae and labium, and sometimes also a smaller number of palpomeres (Bocak & Bocakova, 2008; Kundrata *et al.*, 2015b; Bocak *et al.*, 2016). Plastocerinae and Cebrionini have well-developed mouthparts (Bocak *et al.*, 2018; personal observation), but the head and mouthparts of Drilini are modified. *Mashaselasia* gen. nov., *Latoselasia*, and *Wittmerselasia* (all members of the clade W) have a unique partly membranous fronto-clypeal region. Several *Selasia* have a partly or almost completely membranous labrum. All Drilini have a reduced and partly membranous labium, with only two small sclerotized plates near the palpi. The membranous apical portion of the labium is distinct and bilobate in clades A, W and S (Figs 4D, 5E, 7E); however, it is highly reduced in the terminal clades M and D (Fig. 8E). The galea and lacinia are highly reduced in clades M and especially D, which has the cardines much smaller than the palpi (Fig. 8D).

Thorax

The clicking elateroids have an elongate prosternum, promesothoracic interlocking mechanism, mesoventrite with distinct mesoventral process, globular procoxae, and highly reduced and concealed protrochantins. Unlike them, soft-bodied elateroids have short and transverse prosternum with the prosternal process variably reduced, promesothoracic clicking mechanism absent, mesoventrite usually without a distinct mesoventral process and mesoventral cavity, transversely elongate procoxae, and exposed and freely movable protrochantins (Crowson, 1955; Lawrence & Newton, 1982; Lawrence, 1988; Bocak & Bocakova, 2008; Lawrence *et al.*, 2011; Bocak *et al.*, 2018).

Within Elateridae, some cebrionines have a loosely organized and weakly sclerotized body, but they retain thoracic structures characteristic for the well-sclerotized groups (Lawrence, 1988). *Plastocerus* displays intermediate conditions in the thoracic morphology: it has a relatively well-sclerotized body and a typical elaterid-like mesoventrite, but its promesothoracic interlocking mechanism is only weakly developed and non-functional; a relatively wide prosternum with a somewhat reduced prosternal process; thecoxae are transverse, and exposed protrochantins are rigid (Lawrence & Newton, 1982; Bocak *et al.*, 2018).

In Drilini, the deeply rooted clades A, W and S share the short and wide prosternum with a prosternal process reduced to a narrow laterally flattened plate-like structure, the mesoventrite has a narrow elongate mesoventral process, and the mesoventral cavity is reduced anteriorly and moderately deep to shallow posteriorly (Figs 4G, I; 5J, L; 6E; 7G, I; 9B–C, H–I). In clade M, the prosternum is wide and has a narrow prosternal process (Fig. 9D), but the mesoventrite is reduced to a v-shaped sclerite without a distinct mesoventral process, and with a reduced and usually very shallow mesoventral cavity (Fig. 9J). In clade D, prosternum is usually less transverse than in the previous clades, and the prosternal process is absent (Figs 8H; 9E–F). The mesoventrite in the representatives of clade D is similarly reduced as in clade M, and often with a membranous and not clearly defined anterior margin (Figs 8J; 9K–L).

Adult male elytra and hind wings are commonly reduced in elateroids, mostly in groups with incompletely metamorphosed females, e.g., Cantharidae: Chauliognathinae: Ichthyurini, Omethidae: Telegeusinae, Lycidae: *Alyculus* Kazantsev, *Dexoris* Waterhouse or Lampyridae: *Phosphaenus* Laporte (Branham & Wenzel, 2003; Bocak *et al.*, 2013; Takahashi *et al.*, 2016). In Drilini, females are wingless but all known males possess both elytra and hind wings. However, we can identify certain differences in their sclerotization and structure. Some deeply rooted clades have the elytra relatively well-sclerotized, usually covering all but the terminal abdominal segment, and their inner margins are subparallel for most of their length. In contrast with these, the taxa belonging to the terminal clade D have the least sclerotized and often shortened elytra (mainly in *Malacogaster*) and their inner margins are distinctly divergent (Fig. 3F). Analogous differences can be found in their cuticle structure. The representatives of clades A, W and S and *Flabelloselasia* from the clade M usually have a relatively smooth elytral surface with apparent elytral striae and interstriae or at least their remnants. Unlike them, most members of clade M and all members of clade D have the elytral surface rough, wrinkled, with striae inconspicuous, and often present only at humeri.

Additionally, although all Drilini have somewhat reduced wing venation compared to most clicking Elateridae, we can observe a tendency to an even more radical reduction of a wing venation within clades M and D. *Lolosia*, *Kupeselasia* and *Microselasia* (clade M) are characterized by a reduction of veins in both apical and medial regions. *Flabelloselasia*, which is sister to these genera, has substantially less reduced wing venation (Kundrata & Bocak, 2017). *Drilus*, *Malacodrilus* gen. nov. and *Malacogaster* (i.e., clade D) have mainly the median region reduced (Fig. 8K). The reduction of wing venation is regularly triggered by body miniaturization and we must consider such a possibility. However, there are some drilines which have a small body, but only weakly reduced wing venation (e.g., some *Selasia*, *Flabelloselasia*), and conversely, some *Drilus* or *Malacogaster* are relatively large-bodied, but they have apparently simplified wing venation. These examples indicate that the reduction of the wing venation in Drilini correlates more with phylogeny than with body size.

Abdomen

The number of ventrites and if and how many of them are connate have long been used as important characters (Lawrence *et al.*, 2011). The well-sclerotized elateroids have usually five ventrites (i.e., sternites III–VII exposed) and all five (Artematopodidae, Throscidae, most Eucnemidae), the basal four (Cerophytidae, most Elateridae, Eucnemidae: *Phyllocerus* Lepeletier & Serville) or three (Eucnemidae: Anischiinae) are connate. In contrast, the soft-bodied elateroids have usually seven or eight ventrites (i.e. sternites II–VIII or IX), all are free and often connected by extensive membranes (Lawrence, 1988; Lawrence *et al.*, 2007; Bocak & Bocakova, 2008; Bocak *et al.*, 2018). The degree of connation and number of exposed sternites varies considerably and there is a continuum ranging from five connate to nine free ventrites.

The five well-sclerotized ventrites and the connation of the first four (Fig. 9N) have been used as a diagnostic character for the Elateridae, mostly in combination with other features such as the clicking mechanism (Calder, 1996). However, some Elateridae, e.g., *Denticollis* Piller & Mitterpacher and *Pleonomus* Ménétriés, have six ventrites, of which the first four are connate. This unusual number of sternites led earlier authors to merge those genera into a single group (Schwarz, 1906). Additionally, Cebrionini usually have seven ventrites, and males have the first four connate (Fig. 9M) whereas females have all ventrites free. In *Plastocerus*, the female has six free ventrites and the male seven ventrites, of which the first three are connate. However, although *Plastocerus* has free ventrites, these are clearly well-sclerotized compared with the soft-bodied elateroids (Bocak *et al.*, 2018). These cases represent a continuum between the fully-sclerotized and soft-bodied Elateridae.

The distribution of these character states is analogous in Drilini. Considering the recovered relationships, although weakly statistically supported, we can see the gradual transition from partly-sclerotized to soft-bodied forms. The males in the clades A and W have seven ventrites, with the first four connate (Fig. 9O–P). Their abdomen is quite well-sclerotized and less flexible than in other Drilini, and it is usually fully covered by elytra or with only the apical segment surpassing the elytral apices. Conversely, members of the clades S, M and D have the abdomen with all ventrites freely movable, usually with extensive membranous connections between abdominal segments. Their abdomen is soft and highly flexible, capable of wagging and stretching, and thus exhibits a great variation in its length relative to the elytra. Not surprisingly, a graded series of morphological modifications can be identified: seven ventrites are found in clade S (Fig. 9R–S), eight ventrites and the first ventrite consisting of two lateral sclerites in clade M and *Drilus* from clade D (Fig. 9T–U), eight more or less complete ventrites in *Malacogaster* and *Malacodrilus* gen. nov. from the clade D (Fig. 9V–W). Unfortunately, we have only very scarce information on females as the only reliably identified females belong to *Drilus* and *Malacogaster*, both from clade D. Females from the African clades A, W and M remain unknown, and those earlier reported as belonging to *Selasia* (Barker, 1969) need re-examination as there is no certainty if they are really members of that genus. Therefore, we are unable to assess if all Drilini females are modified to the same extent. The known females have a larviform abdomen with nine visible sternites, and previous studies confirmed that these incompletely metamorphosed females bear a lower number of taxonomically important characters than males in agreement with the delayed evolution of distinguishing traits in ontogeny (e.g., Gould, 1977; Kundrata *et al.*, 2015a; Masek *et al.*, 2015).

Another abdominal modification possibly connected with incomplete metamorphosis is the presence and shape of the intercoxal process on the first abdominal ventrite (Crowson, 1972; Lawrence, 1988; Bocak *et al.*, 2018). While this process is usually well developed and distinct in the clicking elateroids, it is reduced or missing in soft-bodied lineages. The intercoxal process is well developed in most elaterid taxa (Fig. 9N), but weakly developed in Cebrionini and *Plastocerus*. In Drilini, it is either considerably reduced in length (e.g., in *Illubaboria* gen. nov.; Fig. 9R), forming only an indistinct tubercle, or absent in *Drilus* and *Malacogaster* (Fig. 9U, W).

Conclusions

Drilini were commonly perceived as a Palearctic lineage due to their diversity in the Mediterranean. Most studies focused on *Drilus* and *Malacogaster* from Europe and northern Africa, and knowledge on the tropical *Selasia* has remained limited to primary descriptions and brief distributional records. Here, we demonstrate that the Afrotropical fauna contains morphologically and genetically disparate taxa with a long evolutionary history, and Mediterranean *Drilus*, *Malacogaster* and *Malacodrilus* gen. nov. form a terminal clade (Figs 1–2, S1). Four of five major lineages diversified in the Afrotropical region. Palearctic species belong to two clades: most are included in the clade D, and a few of them (roughly 20% of diversity in clade S) are distributed along the southern coast of Asia up to northern Thailand.

The molecular phylogeny of Drilini and morphological characters suggest a gradual transition from lineages weakly affected by incomplete metamorphosis to highly modified soft-bodied groups. The gradual series of morphological changes in males includes a transition from a well-sclerotized to a soft body, reduction of mouthparts, shortened prosternum with reduced prosternal process, reduction of the mesoventral cavity and mesoventral process, relative shortening of the elytra and roughening of the elytral surface, reduction of the hind wing venation, a higher number of ventrites, and a loss of connation of abdominal ventrites and the intercoxal process on the first ventrite.

The gradual character of morphological modifications connected with the incomplete metamorphosis as well as the homoplastic character of these changes have been known for different taxa within Elateriformia. The multiple origins of neoteny and soft-bodied "cantharoid" lineages within the superfamily Elateroidea were repeatedly documented (Bocakova *et al.*, 2007; Kundrata & Bocak, 2011; Kundrata *et al.*, 2014; Bocak *et al.*, 2008). At the family level, different modifications were reported for Eucnemidae (various degrees of abdominal ventrite connation in certain groups; Lawrence *et al.*, 2007), Lampyridae (differences in numbers of ventrites among various groups; Branham, 2010), Lycidae (origins of larviform females; Bocak *et al.*, 2008), and Elateridae (incompletely sclerotized lineages; Kundrata & Bocak, 2011; Bocak *et al.*, 2018). Outside Elateroidea, analogous modifications are known also in Dermestidae, where most lineages have five ventrites and the intercoxal process on the first ventrite but *Thylodrias* Motschulsky with the neotenic female has eight ventrites and lack the intercoxal process on the first ventrite (Lawrence & Ślipiński, 2010).

Various and mostly phylogenetically conservative morphological modifications have been documented in many lineages (e.g., Bocakova *et al.*, 2007; Bocak *et al.*, 2008, 2016, 2018). The linked progressive loss of sclerotization and adult traits in both sexes of *Omalisus* Geoffroy and *Thilmanus* Gemminger were described in Omalisidae (Bocek *et al.*, 2018). Our study is the first one describing in detail the gradual morphological modifications from more sclerotized to soft-bodied males within a single diversified lineage. Both molecular and morphological evidence suggest the basal position of the clades A and W, whose males have at least a short plate-like prosternal process, a well-developed mesoventral process, connate basal abdominal ventrites, and the intercoxal process on the first ventrite present (Figs 4G, I; 5J, L; 6E; 9B, H, O–P). More modified terminal lineages usually have reduced prosternal, mesoventral and intercoxal abdominal processes, and have all abdominal ventrites free (Figs 8H, J; 9E–F, J–L, R–W). The females are known only for a fraction of species and only from the clades with more modified male morphology, therefore further research is needed to link the modifications in various semaphoronts. Additionally, a detailed morphological study and molecular phylogeny may reveal similar gradual modifications in another click-beetle group, Cebrionini.

References

Aduse-Poku K, Vingerhoedt E, Wahlberg N. 2009. Out-of-Africa again: A phylogenetic hypothesis of the genus *Charaxes* (Lepidoptera: Nymphalidae) based on five gene regions. *Molecular Phylogenetics and Evolution* **53**: 463–478.

Amaral DT, Mitani Y, Ohmiya Y, Viviani VR. 2016. Organization and comparative analysis of the mitochondrial genomes of bioluminescent Elateroidea (Coleoptera: Polyphaga). *Gene* **586**: 254–262.

Barker JF. 1969. Notes on the life cycle and behaviour of the drilid beetle *Selasia unicolor* (Guérin). *Proceedings of the Royal Entomological Society of London (Series A)* **44**: 169–172.

Baudi di Selve F. 1871. Coleopterorum messis in insula Cypro et Asia minore ab Eugenio Truqui congregatae recensitio: de Europaeis notis quibusdam additis. Pars quarta. *Berliner Entomologische Zeitschrift* **15**: 49–71.

Bocak L. 2007. Drilidae. In: Löbl I, Smetana A, eds. *Catalogue of Palearctic Coleoptera, Volume 4*. Stenstrup: Apollo Books, 209–210.

Bocak L, Barton C, Crampton-Platt A, Chesters D, Ahrens D, Vogler AP. 2014. Building the Coleoptera tree-of-life for >8000 species: composition of public DNA data and fit with Linnaean classification. *Systematic Entomology* **39**: 97–110.

Bocak L, Bocakova M. 2008. Phylogeny and classification of the family Lycidae (Insecta: Coleoptera). *Annales Zoologici* **58**: 695–720.

Bocak L, Brlik M. 2008. Revision of the family Omalisidae (Coleoptera, Elateroidea). *Insect Systematics & Evolution* **39**: 189–212.

Bocak L, Grebennikov VV, Masek M. 2013. A new species of *Dexoris* (Coleoptera: Lycidae) and parallel evolution of brachyptery in the soft-bodied elateroid beetles. *Zootaxa* **3721**: 495–500.

Bocak L, Bocakova M, Hunt T, Vogler AP. 2008. Multiple ancient origins of neoteny in Lycidae (Coleoptera): consequences for ecology and macroevolution. *Proceedings of the Royal Society London Series B: Biological Sciences* **275**: 2015–2023.

Bocak L, Kundrata R, Andújar Fernández C, Vogler AP. 2016. The discovery of Iberobaeniidae (Coleoptera: Elateroidea), a new family of beetles from Spain, with immatures detected by environmental DNA sequencing. *Proceedings of the Royal Society B: Biological Sciences* **283**: 20152350.

Bocak L, Branham MA, Kundrata R. 2010. Family Drilidae Blanchard, 1845. In: Leschen RAB, Beutel RG, Lawrence JF, eds. *Handbook of Zoology, Arthropoda: Insecta; Coleoptera, Beetles, Volume 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim*. Berlin: Walter de Gruyter, 104–110.

Bocak L, Motyka M, Bocek M, Bocakova M. 2018. Incomplete sclerotization and phylogeny: The phylogenetic classification of *Plastocerus* (Coleoptera: Elateroidea). *PLoS ONE* **13**: e0194026.

Bocakova M, Bocak L, Hunt T, Teraväinen M, Vogler AP. 2007. Molecular phylogenetics of Elateriformia (Coleoptera): evolution of bioluminescence and neoteny. *Cladistics* **23**: 477–496.

Bocakova M, Constantin R, Bocak L. 2012. Molecular phylogenetics of the melyrid lineage (Coleoptera: Cleroidea). *Cladistics* **28**: 117–129.

Bocakova M, Bocak L, Gimmel ML, Motyka M, Vogler AP. 2015. Aposematism and mimicry in soft-bodied beetles of the superfamily Cleroidea (Insecta). *Zoologica Scripta* **45**: 9–21.

Bocek M, Bocak L. 2017. The comparison of molecular and morphology-based phylogenies of trichaline net-winged beetles (Coleoptera: Lycidae: Metriorrhynchini) with description of a new subgenus. *PeerJ* **5**: e3963.

Bocek M, Fancello L, Motyka M, Bocakova M, Bocak L. 2018. The molecular phylogeny of Omalisidae (Coleoptera) defines the family limits and demonstrates low dispersal propensity and ancient vicariance patterns. *Systematic Entomology* **43**: 250–261.

Branham MA. 2010. Lampyridae Latreille, 1817. In: Leschen RAB, Beutel RG, Lawrence JF, eds. *Handbook of Zoology, Arthropoda: Insecta; Coleoptera, Beetles, Volume 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim*. Berlin: Walter de Gruyter, 141–149.

Branham MA, Wenzel JW. 2003. The evolution of photic behavior and the evolution of sexual communication in fireflies (Coleoptera: Lampyridae). *Cladistics* **19**: 1–22.

Brower AVZ. 1994. Rapid morphological radiation and convergence among races of the butterfly *Heliconius erato* inferred from patterns of mitochondrial-DNA evolution. *Proceedings of the National Academy of Sciences of the United States of America* **91**: 6491–6495.

Calder AA. 1996. *Click Beetles: Genera of the Australian Elateridae (Coleoptera). Monographs on invertebrate taxonomy, Vol. 2.* Victoria: CSIRO Publishing.

Cate P. 2007. Elateridae. In: Löbl I, Smetana A, eds. *Catalogue of Palearctic Coleoptera, Volume 4*. Stenstrup: Apollo Books, 89–209.

Cohen KM, Finney SC, Gibbard PL, Fan JX. 2013. The ICS International Chronostratigraphic Chart. *Episodes* **36**: 199–204. [updated]

Crowson RA. 1955. *The natural classification of the families of Coleoptera*. London: Nathaniel Lloyd & Co., Ltd.

Crowson RA. 1972. A review of the classification of Cantharoidea (Coleoptera), with definition of two new families, Cneoglossidae and Omethidae. *Revista de la Universidad de Madrid* **21**: 35–77.

Darriba D, Taboada GL, Doallo R, Posada D. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* **9**: 772.

Drummond AJ, Ho SYW, Phillips MJ, Rambaut A. 2006. Relaxed phylogenetics and dating with confidence. *PLoS Biology* **4**: e88.

Drummond AJ, Suchard MA, Xie D, Rambaut A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* **29**: 1969–1973.

Eberle J, Fabrizi S, Lago P, Ahrens D. 2017. A historical biogeography of megadiverse Sericini—another story "out of Africa"? *Cladistics* **33**: 183–197.

Faucheux MJ, Agnas M. 2016. Les hypermétamorphoses de deux Drilini (Coleoptera: Elateridae), *Drilus mauritanicus* Lucas 1849 et *Malacogaster passerinii* Bassi 1833. Notion de larves primaire, secondaire et tertiaire. *Bulletin de la Société des sciences naturelles de l'Ouest de la France* **38**: 59–99.

Feakins SJ, deMenocal PB. 2010. Global and African regional climate during the Cenozoic. In: Werdelin F, Sanders EJ, eds. *Cenozoic Mammals of Africa*. Berkeley: University of California Press, 45–55.

Felsenstein J. 2004. *Inferring Phylogenies*. Sunderland: Sinauer Associates, Inc.

Geisthardt M. 2007a. Remarks on some African *Selasia*-species and description of new species (Coleoptera: Drilidae). *Mitteilungen des Internationalen Entomologischen Vereins* **32**: 27–43.

Geisthardt M. 2007b. Neue und bekannte *Selasia* Laporte, 1836 Arten aus dem südliche Afrika (Coleoptera, Drilidae). *Entomologica Basiliensia et Collectionis Frey* **29**: 31–40.

Gould SJ. 1977. *Ontogeny and phylogeny*. Cambridge: Harvard University Press.

Huelsenbeck JP, Ronquist F. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**: 754–755.

Hunt T, Bergsten J, Levkanicova Z, Papadopoulou A, St. John O, Wild R, Hammond PM, Ahrens D, Balke M, Caterino MS, Gómez-Zurita J, Ribera I, Barraclough TG, Bocakova M, Bocak L, Vogler AP. 2007. A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. *Science* **318**: 1913–1916.

Jeng ML. 2008. Comprehensive phylogenetics, systematics, and evolution of neoteny of Lampyridae (Insecta: Coleoptera). Unpublished D. Phil. Thesis, University of Kansas.

Jiang W, Chen SY, Wang H, Li DZ, Wiens JJ. 2014. Should genes with missing data be excluded from phylogenetic analyses? *Molecular Phylogenetics and Evolution* **80**: 308–318.

Karolyi F, Hansal T, Krenn HW, Colville JF. 2016. Comparative morphology of the mouthparts of the megadiverse South African monkey beetles (Scarabaeidae: Hopliini): feeding adaptations and guild structure. *PeerJ* **4**: e1597.

Kass RE, Raftery AE. 1995. Bayes factors. *Journal of the American Statistical Association* **90**: 773–795.

Katoh K, Standley DM. 2013. MAFFT Multiple sequence alignment sftware version 7: Improvements in performance and usability. *Molecular Biology and Evolution* **30**: 772–780.

Klak C, Hanáček P, Bruyns PV. 2017. Out of southern Africa: Origin, biogeography and age of the Aizooideae (Aizoaceae). *Molecular Phylogenetics and Evolution* **109**: 203–216.

Kobieluszova L, Kundrata R. 2015. Taxonomic review of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) from Asia Minor, with descriptions of seven new species and comments on the female antennal morphology in Drilini. *Zootaxa* **4012**: 78–96.

Kodandaramaiah U, Wahlberg N. 2007. Out-of-Africa origin and dispersal-mediated diversification of the butterfly genus *Junonia* (Nymphalidae: Nymphalinae). *Journal of Evolutionary Biology* **20**: 2181–2191.

Kundrata R, Bocak L. 2007. A revision of *Euanoma* and *Pseudeuanoma* (Coleoptera: Drilidae). *Annales Zoologici* **57**: 427–441.

Kundrata R, Bocak L. 2011. The phylogeny and limits of Elateridae (Insecta, Coleoptera): is there a common tendency of click beetles to soft-bodiedness and neoteny? *Zoologica Scripta* **40**: 364–378.

Kundrata R, Bocak L. 2017. Taxonomic review of Drilini (Elateridae: Agrypninae) in Cameroon reveals high morphological diversity, including the discovery of five new genera. *Insect Systematics & Evolution* **48**: 441–492.

Kundrata R, Bocakova M, Bocak L. 2014. The comprehensive phylogeny of the superfamily Elateroidea (Coleoptera: Elateriformia). *Molecular Phylogenetics and Evolution* **76**: 162–171.

Kundrata R, Baalbergen E, Bocak L, Schilthuizen M. 2015a. The origin and diversity of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) in Crete based on mitochondrial phylogeny. *Systematics and Biodiversity* **13**: 52–75.

Kundrata R, Baena M, Bocak L. 2015b. Classification of Omalisidae based on molecular data and morphology, with description of Paradrilinae subfam. nov. (Coleoptera: Elateroidea). *Zootaxa* **3915**: 413–422.

Kundrata R, Gunter NL, Douglas H, Bocak L. 2016. Next step toward a molecular phylogeny of click-beetles (Coleoptera: Elateridae): redefinition of Pityobiinae, with a description of a new subfamily, Parablacinae, from the Australasian Region. *Austral Entomology* **55**: 291–302.

Kundrata R, Gunter NL, Janosikova D, Bocak L. 2018. Molecular evidence for the subfamilial status of Tetralobinae (Coleoptera: Elateridae), with comments on parallel evolution of some phenotypic characters. *Arthropod Systematics & Phylogeny* 76: 137–145.

Kusy D, Motyka M, Andujar C, Bocek M, Masek M, Sklenarova K, Kokas F, Bocakova M, Vogler AP, Bocak L. 2018. Genome sequencing of *Rhinorhipus* Lawrence exposes an early branch of the Coleoptera. *Frontiers in Zoology* **15**: 21.

Lanfear R, Frandsen PB, Wright AM, Senfeld T, Calcott B. 2016. PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution* **34**: 772–773.

Lawrence JF. 1988. Rhinorhipidae, a new beetle family from Australia, with comments on the phylogeny of the Elateriformia. *Invertebrate Taxonomy* **2**: 1–53.

Lawrence JF, Britton EB. 1991. Coleoptera (beetles). CSIRO Division of Entomology, ed. *The Insects of Australia: A Textbook for Students and Research Workers, Second Edition, Volume 2*. Carlton: Melbourne University Press, 543–564.

Lawrence JF, Newton AF. 1982. Evolution and classification of beetles. *Annual Review of Ecology and Systematics* **13**: 261–290.

Lawrence JF, Ślipiński SA. 2010. Dermestidae Latreille, 1804. In: Leschen RAB, Beutel RG, Lawrence JF, eds. *Handbook of Zoology, Arthropoda: Insecta; Coleoptera, Beetles, Volume 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim*. Berlin: Walter de Gruyter, 198–206.

Lawrence JF, Ślipiński SA, Pakaluk J. 1995. From Latreille to Crowson: a history of the higher-level classification of beetles. Pakaluk J., Ślipiński SA, eds. *Biology, Phylogeny, and Classification of Coleoptera. Papers Celebrating the 80th Birthday of Roy A. Crowson. Volumes 1–2*. Warszawa: Muzeum i Instytut Zoologii PAN, 87–154.

Lawrence JF, Muona J, Teräväinen M, Ståhls G, Vahtera V. 2007. *Anischia*, *Perothops* and the phylogeny of Elateroidea (Coleoptera: Elateriformia). *Insect Systematics & Evolution* **38**: 205–239.

Lawrence JF, Ślipiński SA, Seago AE, Thayer MK, Newton AF, Marvaldi AE. 2011. Phylogeny of the Coleoptera based on morphological characters of adults and larvae. *Annales Zoologici* **61**: 1–217.

Malohlava V, Bocak L. 2010. Evidence of extreme habitat stability in a Southeast Asian biodiversity hotspot based on the evolutionary analysis of neotenic net-winged beetles. *Molecular Ecology* **19**: 4800–4811.

Martin GJ, Branham MA, Whiting MF, Bybee SM. 2017. Total evidence phylogeny and the evolution of adult bioluminescence in fireflies (Coleoptera: Lampyridae). *Molecular Phylogenetics and Evolution* **107**: 564–575.

Masek M, Palata V, Bray TC, Bocak L. 2015. Molecular phylogeny reveals high diversity and geographic structure in Asian neotenic net-winged beetles *Platerodrilus* (Coleoptera: Lycidae). *PLoS ONE* **10**: e0123855.

McKenna DD, Wild AL, Kanda K, Bellamy CL, Beutel RG, Caterino MS, Farnum CW, Hawks DC, Ivie MA, Jameson ML, Leschen RAB, Marvaldi AE, McHugh JV, Newton AF, Robertson JA, Thayer MK, Whiting MF, Lawrence JF, Ślipiński SA, Maddison DR, Farrell BD. 2015. The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Systematic Entomology* **40**: 835–880.

Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 Nov. 2010, New Orleans, Louisiana, 1–8.

Motyka M, Masek M, Bocak L. 2017. Congruence between morphology and molecular phylogeny: the reclassification of Calochromini (Coleoptera: Lycidae) and their dispersal history. *Zoological Journal of the Linnean Society* **180**: 47–65.

Motyka M, Kampova L, Bocak L. 2018. Phylogeny and evolution of Müllerian mimicry in aposematic *Dilophotes*: evidence for advergence and size-constraints in evolution of mimetic sexual dimorphism. *Scientific Reports* **8**: 3744.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858.

Olivier E. 1910 Rhagophthalmidae, Drilidae. Schenkling S, ed., *Coleopterorum Catalogus, Pars 10*. Berlin: W. Junk, 1–10.

Olivier E. 1913. Description d'une nouvelle espèce de Drilidae [Col.]. *Bulletin de la Société Entomologique de France* **1913**: 92–93.

Papadopoulou A, Anastasiou I, Vogler AP. 2010. Revisiting the insect mitochondrial molecular clock: The mid-Aegean trench calibration. *Molecular Biology and Evolution* **27**: 1659–1672.

Pons J, Ribera I, Bertranpetit J, Balke M. 2010. Nucleotide substitution rates for the full set of mitochondrial protein-coding genes in Coleoptera. *Molecular Phylogenetics and Evolution* **56**: 796–807.

Rambaut A. 2009. FigTree 1.3.1. Available at http://tree.bio.ed.ac.uk/software/figtree/.

Rambaut A, Suchard MA, Xie D, Drummond AJ. 2014. Tracer 1.6. Available from http://beast.bio.ed.ac.uk/Tracer.

Sahoo RK, Lohman DJ, Wahlberg N, Müller CJ, Brattström O, Collins SC, Peggie D, Aduse-Poku K, Kodandaramaiah U. 2018. Evolution of *Hypolimnas* butterflies (Nymphalidae): Out of-Africa origin and *Wolbachia*-mediated introgression. *Molecular Phylogenetics and Evolution* **123**: 50–58.

Schwarz O. 1906. Coleoptera. Fam. Elateridae. In: Wytsman P., ed. *Genera Insectorum, Fascicule 46*. Bruxelles: P. Wytsman, 1–370.

Scotese CR. 2014. Atlas of Paleogene Paleogeographic Maps (Mollweide Projection), Maps 8–15, Volume 1, The Cenozoic. *PALEOMAP Atlas for ArcGIS*. PALEOMAP Project, Evanston, Illinois.

Short AEZ, Fikáček M. 2013. Molecular phylogeny, evolution and classification of the Hydrophilidae (Coleoptera). *Systematic Entomology* **38**: 723–752.

Ślipiński SA, Leschen RAB, Lawrence JF. 2011. Order Coleoptera Linnaeus, 1758. In: Zhang ZQ, ed. *Animal Biodiversity: An Outline of Higher-Level Classification and Survey of Taxonomic Richness*. *Zootaxa* **3148**: 203–208.

Sormova E, Kramp K, Kundrata R. 2018. Diversity and phylogenetic relationships of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) in Cyprus. *Zoologischer Anzeiger* **275**: 1–12.

Stamatakis A. 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22**: 2688–2690.

Stamatakis A, Hoover P, Rougemont J. 2008. A Rapid Bootstrap Algorithm for the RAxML Web Servers. *Systematic Biology* **57**: 758–771.

Stanger-Hall KF, Sander Lower SE, Lindberg L, Hopkins A, Pallansch J, Hall DW. 2018. The evolution of sexual signal modes and associated sensor morphology in fireflies (Lampyridae, Coleoptera). *Proceedings of the Royal Society B: Biological Sciences* **285**: 20172384.

Takahashi N, Bocak L, Abd Ghani I. 2016. Discovery of a new species of the brachyelytrous net-winged beetle genus *Alyculus* (Coleoptera: Lycidae) from Peninsular Malaysia. *Zootaxa* **4144**: 145–150.

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S. 2013. MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution* **30**: 2725–2729.

Timmermans MJTN, Barton C, Haran J, Ahrens D, Culverwell CL, Ollikainen A, Dodsworth S, Foster PG, Bocak L, Vogler AP. 2016. Family-level sampling of mitochondrial genomes in Coleoptera: compositional heterogeneity and phylogenetics. *Genome Biology and Evolution* **8**: 161–175.

Tomoyasu Y, Arakane Y, Kramer KJ, Denell RE. 2009. Repeated co-options of exoskeleton formation during wing-to-elytron evolution in beetles. *Current Biology* **19**: 2057–2065.

Toussaint EFA, Hendrich L, Escalona HE, Porch N, Balke M. 2016. Evolutionary history of a secondary terrestrial Australian diving beetle (Coleoptera, Dytiscidae) reveals a lineage of high morphological and ecological plasticity. *Systematic Entomology* **41**: 650–657.

Wiens JJ, Morrill MC. 2011. Missing data in phylogenetic analysis: Reconciling results from simulations and empirical data. *Systematic Biology* **60**: 719–731.

Wiens JJ, Tiu J. 2012. Highly incomplete taxa can rescue phylogenetic analyses from the negative impacts of limited taxon sampling. *PLoS ONE* **7**: e42925.

Wittmer W. 1944. Catalogue des Drilidae E. Oliv. (Coleoptera - Malacodermata). *Revista de la Sociedad Entomológica Argentina* **12**: 203–221.

Wittmer W. 1962. LXXVII - Coleoptera Drilidae, Cantharidae, Malachiidae, Dasytidae et Prionoceridae. Mission zoologique de l'I.R.S.A.C. en Afrique orientale. (P. Basilewsky et N. Leleup, 1957). *Annales du Musée Royal de l'Afrique Centrale* **110**: 259–270.

Wittmer W. 1989. Die Familie Drilidae (Coleoptera) in Südafrika, sowie Beschreibung von neuen Arten aus dem südlichen Afrika (30. Beitrag zur Kenntnis der Fauna Afrikas). *Entomologica Basiliensia* **13**: 187–205.

Xia X. 2017. DAMBE6: New tools for microbial genomics, phylogenetics and molecular evolution. *Journal of Heredity* **108**: 431–437.

Xia X, Lemey P. 2009. Assessing substitution saturation with DAMBE. In: Lemey P, Salemi M, Vandamme AM, eds. *The Phylogenetic Handbook: A Practical Approach to DNA and Protein Phylogeny, 2nd edition*. Cambridge University Press, 615–630.

Xia X, Xie Z, Salemi M, Chen L, Wang Y. 2003. An index of substitution saturation and its application. *Molecular Phylogenetics and Evolution* **26**: 1–7.

Ye Z, Zhen YH, Zhou YY, Bu WJ. 2017. Out of Africa: Biogeography and diversification of the pantropical pond skater genus *Limnogonus* Stål, 1868 (Hemiptera: Gerridae). *Ecology and Evolution* **7**: 793–802.

Zachos J, Pagani M, Sloan L, Thomas E, Billups K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* **292**: 686–693.

Zheng Y, Wiens JJ. 2015. Do missing data influence the accuracy of divergence-time estimation with BEAST? *Molecular Phylogenetics and Evolution* **85**: 41–49.

Table 1. Recovery of selected clades with bootstrap support in the maximum likelihood (ML) analyses and posterior probabilities in the Bayesian analyses (BI) from the concatenated Mafft alignments of full (100 terminals), reduced (68 terminals), and ingroup-only (66 terminals) datasets.

Number of terminals	100		68		66	
Clade/ Method of analysis	ML	BI	ML	BI	ML	BI
clade A (*Austroselasia*)	88	100	89	100	97	100
clade W (*Habesh-+Masha-+Lato-+Wittmerselasia*)	78	100	90	100	73	100
clade S (*Illubaboria+Selasia*)	77	100	77	99	85	100
clade M (*Flabello-+Lolosia+Kupe-+Microselasia*)	88	100	82	100	96	100
clade D (*Drilus+Malacogaster+Malacodrilus*)	100	100	100	100	100	100
Selasia	69	100	n.a.	n.a.	78	100
Habeshselasia	92	100	100	100	95	100
Mashaselasia+Latoselasia+Wittmerselasia	97	100	100	100	98	100
Latoselasia+Wittmerselasia	75	95	47	46	68	64
Wittmerselasia (*sensu stricto*)	80	85	98	100	93	100
Lolosia+Kupeselasia+Microselasia	40	–	50	95	62	–
Kupeselasia+Microselasia	100	100	100	100	100	100
Microselasia	63	80	69	100	89	100
Malacogaster+Malacodrilus	100	100	100	100	99	100
Malacogaster	100	100	100	100	100	100
Drilus	68	56	–	–	87	79

Figure captions

Figure 1. A) A phylogenetic hypothesis for Drilini based on the maximum likelihood (ML) analysis of the 100-taxa concatenated Mafft alignment. Numbers at branches represent ML bootstrap values and Bayesian posterior probabilities, respectively. The representatives of Elateridae: Agrypninae from upper left to lower right are as follows: *Agrypnus murinus* (Linnaeus, 1758); *Cryptalaus* sp.; *Lacon querceus* (Herbst, 1748); *Austroselasia pulchra* (Pascoe, 1887) gen. et comb. nov.; *Selasia arabica* Geisthardt, 2003; *Drilus concolor* Ahrens, 1812. Not to scale. Credit for the first and third photographs: Udo Schmidt. B) Distribution of the clades A and W; C) Distribution of the clade S; D) Distribution of the clades M and D.

Figure 2. Chronogram for Drilini from the BEAST analysis. The node bars depict the confidence interval of node ages (95% node height HD).

Figure 3. Habitus images of the newly described Drilini. A) *Austroselasia pulchra* (Pascoe, 1887) gen. et comb. nov., male; B) *Habeshselasia bicolor* gen. et sp. nov., male; C) *H. illubaborensis* gen. et sp. nov., male; D) *Mashaselasia aethiopica* gen. et sp. nov., male; E) *Illubaboria bicolor* gen. et sp. nov., male; F) *Malacodrilus hajeki* gen. et sp. nov., male. Scale bars = 1.0 mm.

Figure 4. Body parts of *Austroselasia pulchra* (Pascoe, 1887) gen. et comb. nov., male. A) head, frontal view; B) mandible; C) maxilla; D) labium; E) antenna; F) pronotum; G) prosternum; H) scutellum; I) mesoventrite; J) hind wing; K) midleg; L) abdominal tergite X; M) abdominal sternite IX; N) aedeagus, dorsal view. Scale bars = 0.2 mm (Figs B–D, I, L–N), 0.5 mm (Figs A, E–H), 1.0 mm (Fig. K), 2.0 mm (Fig. J).

Figure 5. Body parts of *Habeshselasia* gen. nov., male. A) head of *H. bicolor* sp. nov., frontal view; B) head of *H. illubaborensis* sp. nov., frontal view; *H. bicolor* sp. nov.: C) mandible; D) maxilla; E) labium; F) antenna; G) antenna of *H. illubaborensis* sp. nov.; H) pronotum of *H. bicolor* sp. nov.; I) pronotum of *H. illubaborensis* sp. nov.; J) prosternum of *H. illubaborensis* sp. nov.; *H. bicolor* sp. nov.: K) scutellum; L) mesoventrite; M) hind wing; N) midleg; O) abdominal sternite IX; P) abdominal tergites IX–X; R) aedeagus; *H. illubaborensis* sp. nov.: S) abdominal sternite IX; T) abdominal tergites IX–X; U) aedeagus, dorsal view. Scale bars = 0.2 mm (Figs B–E, K–L, O–U), 0.5 mm (Figs A, F–J, M–N).

Figure 6. Body parts of *Mashaselasia aethiopica* gen. et sp. nov., male. A) anterior part of the holotype showing head, pronotum and scutellar shield; B) head, frontal view; C) apical maxillary palpomeres; D) antenna; E) mesoventrite; F) hind wing; G) abdominal sternite IX; H) abdominal tergites IX–X; I) aedeagus, dorsal view. Scale bars = 0.1 mm (Fig. C), 0.2 mm (Figs B, D–E, G–I), 0.5 mm (Figs A, F).

Figure 7. Body parts of *Illubaboria bicolor* gen. et sp. nov., male. A) head, frontal view; B) head and pronotum, dorsal view; C) mandible; D) maxilla; E) labium; F) antenna; G) prosternum; H) scutellum; I) mesoventrite; J) hind wing; K) midleg; L) abdominal sternite IX; M) abdominal tergite X; N) aedeagus, dorsal view; O) aedeagus, lateral view. Scale bars = 0.1 mm (Figs H–I), 0.2 mm (Figs A–E, G, L–O), 0.5 mm (Figs F, J–K).

Figure 8. Body parts of *Malacodrilus hajeki* gen. et sp. nov., male. A) head, fronto-dorsal view; B) head, frontal view; C) mandible; D) maxilla; E) labium; F) antenna; G) pronotum; H) prosternum; I) scutellum; J) mesoventrite; K) hind wing; L) midleg; M) metacoxae; N)

abdominal sternite IX; O) abdominal tergites IX–X; P) aedeagus, dorsal view. Scale bars = 0.1 mm (Figs D–E, J), 0.2 mm (Figs C, G–I, N–P), 0.5 mm (Figs A–B, F, K–M).

Figure 9. Body parts of the Drilini representatives (all males). Prosternum. A) *Agrypnus murinus* (Linnaeus, 1758); B) *Wittmerselasia camerooniana* Kundrata & Bocak, 2017; C) *Selasia erlangeri* Geisthardt, 2007; D) *Microselasia obscura* Kundrata & Bocak, 2017; E) *Drilus rectus* Schaufuss, 1867; F) *Malacogaster passerinii* Bassi, 1834. Mesoventrite. G) *Agrypnus murinus* (Linnaeus, 1758); H) *Wittmerselasia camerooniana* Kundrata & Bocak, 2017; I) *Selasia erlangeri* Geisthardt, 2007; J) *Microselasia obscura* Kundrata & Bocak, 2017; K) *Drilus rectus* Schaufuss, 1867; L) *Malacogaster passerinii* Bassi, 1834. Abdomen. M) *Cebrio* sp. (Elaterinae: Cebrionini); N) *Agrypnus murinus* (Linnaeus, 1758); O) *Austroselasia pulchra* (Pascoe, 1887) gen. et comb. nov.; P) *Habeshselasia bicolor* gen. et sp. nov.; R) *Illubaboria bicolor* gen. et sp. nov.; S) *Selasia* sp.; T) *Microselasia barombi* Kundrata & Bocak, 2017; U) *Drilus rectus* Schaufuss, 1867; V) *Malacodrilus hajeki* gen. et sp. nov.; W) *Malacogaster passerinii* Bassi, 1834. Scale bars = 0.2 mm (Figs G–L), 0.5 mm (Figs A–F), 1.0 mm (Figs M–W).

Supporting Information

Figure S1. The Bayesian phylogenetic hypothesis for Drilini inferred from the 68-taxa concatenated Mafft alignment. Numbers at branches represent ML bootstrap values and Bayesian posterior probabilities, respectively.

Table S1. The list of ingroup terminals used in this study, with GenBank accession and voucher numbers.

Table S2. The list of outgroup terminals used in this study, with GenBank accession and voucher numbers.

Table S3. Primers used for the PCR amplifications of the studied genes.

Table S4. Results of the Xia's nucleotide substitution saturation test in DAMBE, based on simulations with 32 operational taxonomic units (10 000 replicates).

Table S5. Summary of the PartitionFinder results.

Table S6. Numbers and types of characters in the analyzed datasets.

Table S7. Nucleotide composition of markers used in this study (in %).

Table S8. Estimated dates (in mya) of the main nodes in Drilini inferred from the BEAST analysis of the concatenated mtDNA fragments using various tree priors and previously published mutation rates (nucleotide substitutions/site/mya/lineage) for mtDNA markers. A, W, S, M and D designate the Drilini clades as defined in the main text. The numbers in parentheses designate 95% probability intervals.

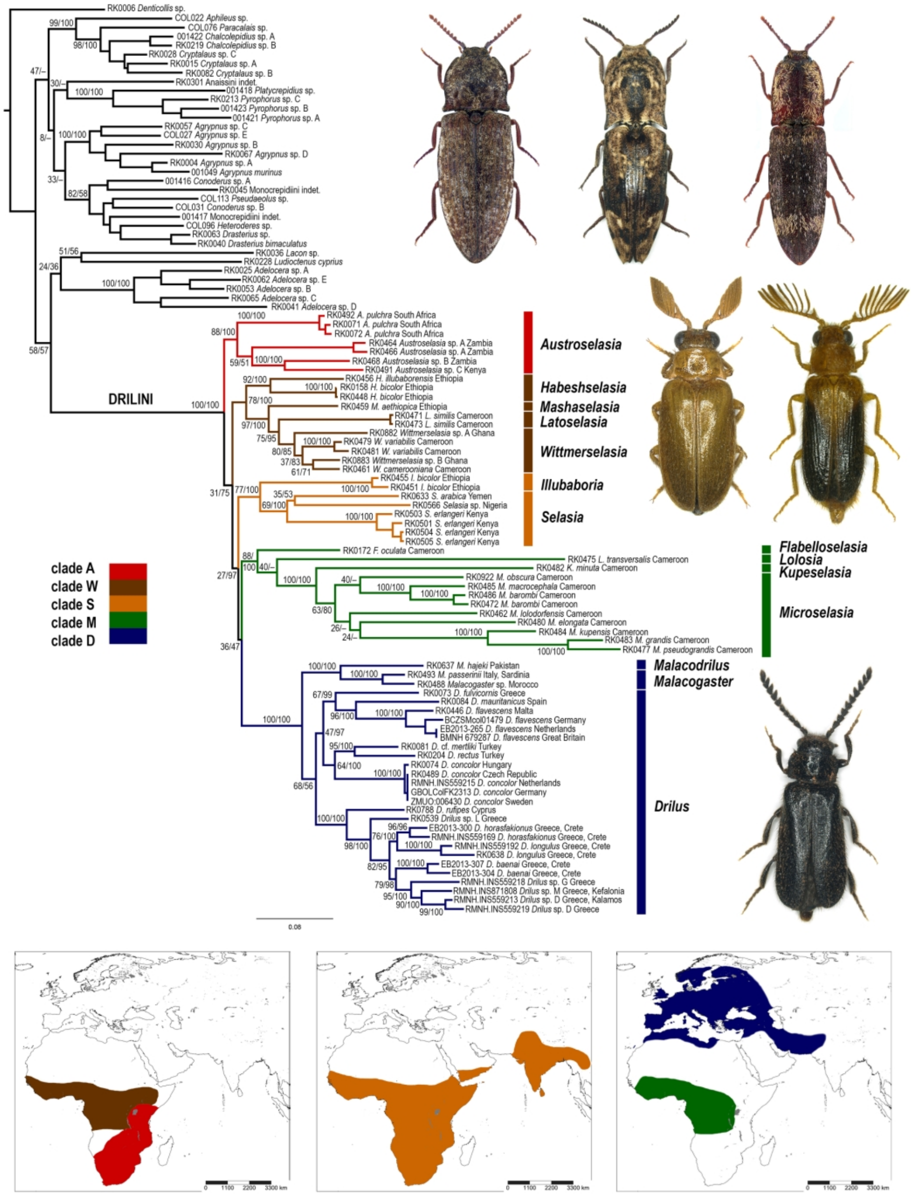


Figure 1. A) A phylogenetic hypothesis for Drilini based on the maximum likelihood (ML) analysis of the 100-taxa concatenated Mafft alignment. Numbers at branches represent ML bootstrap values and Bayesian posterior probabilities, respectively. The representatives of Elateridae: Agrypninae from upper left to lower right are as follows: Agrypnus murinus (Linnaeus, 1758); Cryptalaus sp.; Lacon querceus (Herbst, 1748); Austroselasia pulchra (Pascoe, 1887) gen. et comb. nov.; Selasia arabica Geisthardt, 2003; Drilus concolor Ahrens, 1812. Not to scale. Credit for the first and third photographs: Udo Schmidt. B) Distribution of the clades A and W; C) Distribution of the clade S; D) Distribution of the clades M and D.

170x223mm (300 x 300 DPI)

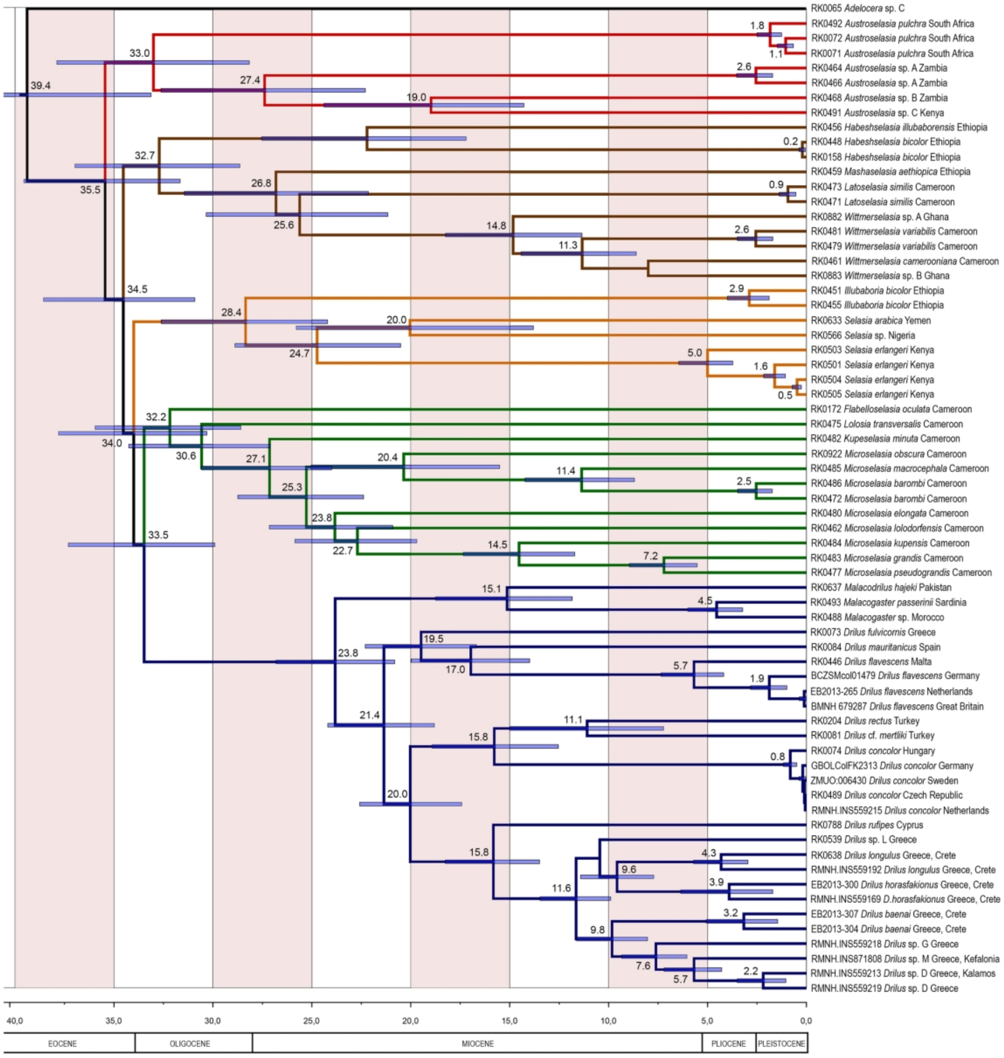


Figure 2. Chronogram for Drilini from the BEAST analysis. The node bars depict the confidence interval of node ages (95% node height HD).

170x182mm (300 x 300 DPI)

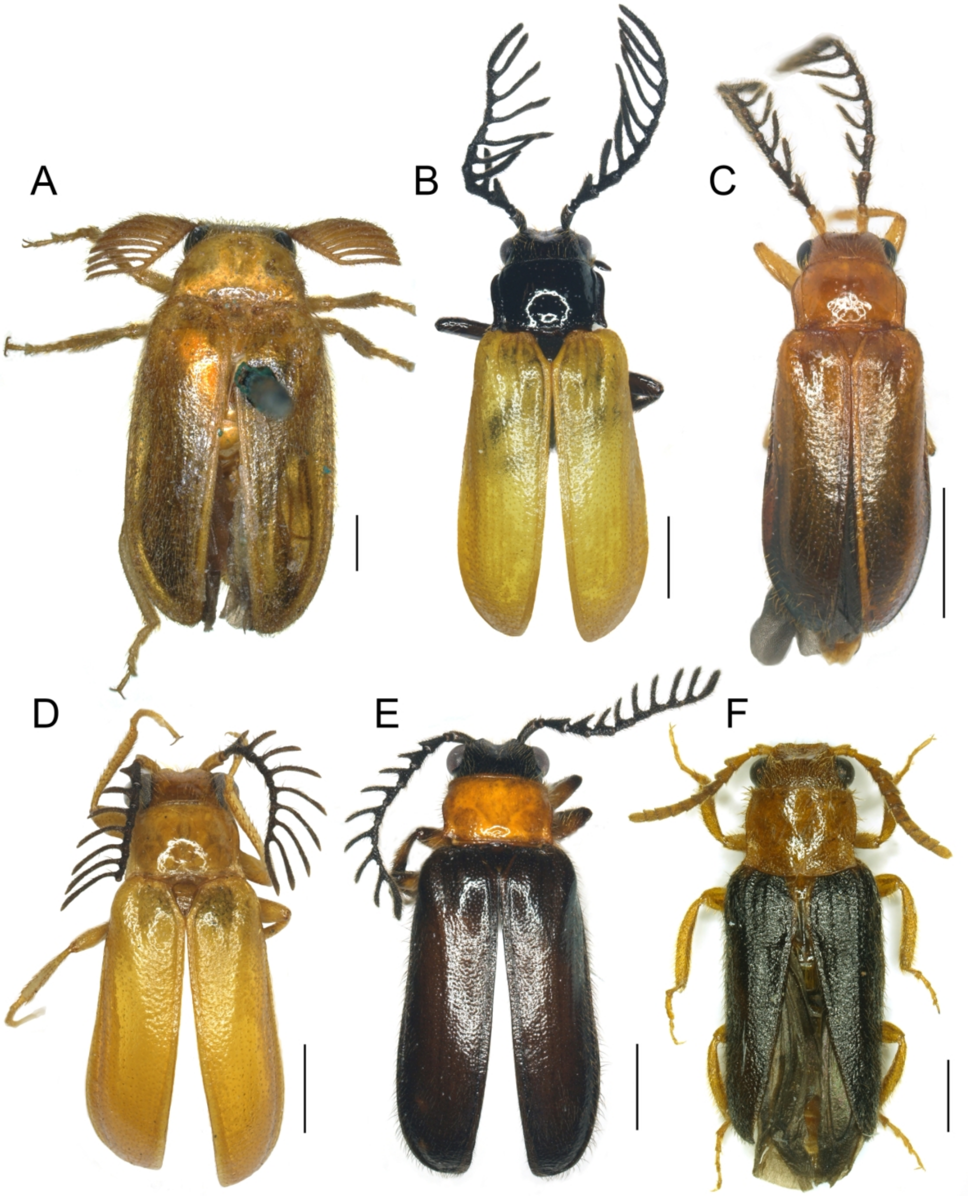


Figure 3. Habitus images of the newly described Drilini. A) Austroselasia pulchra (Pascoe, 1887) gen. et comb. nov., male; B) Habeshselasia bicolor gen. et sp. nov., male; C) H. illubaborensis gen. et sp. nov., male; D) Mashaselasia aethiopica gen. et sp. nov., male; E) Illubaboria bicolor gen. et sp. nov., male; F) Malacodrilus hajeki gen. et sp. nov., male. Scale bars = 1.0 mm.

170x209mm (300 x 300 DPI)

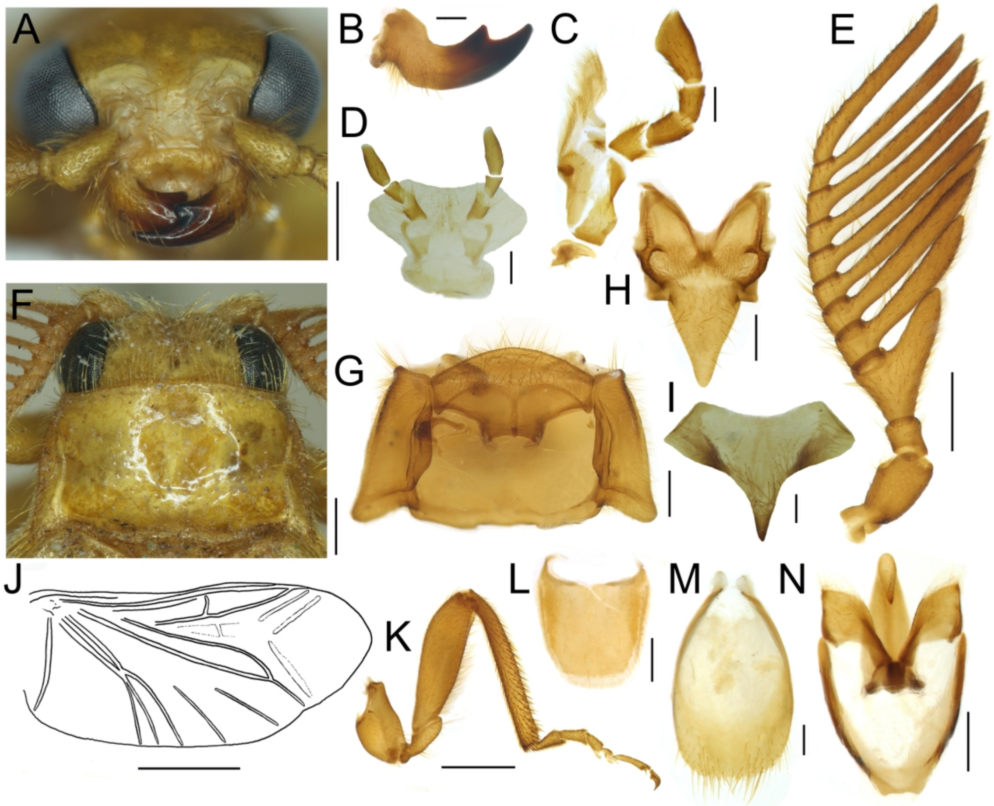


Figure 4. Body parts of Austroselasia pulchra (Pascoe, 1887) gen. et comb. nov., male. A) head, frontal view; B) mandible; C) maxilla; D) labium; E) antenna; F) pronotum; G) prosternum; H) scutellum; I) mesoventrite; J) hind wing; K) midleg; L) abdominal tergite X; M) abdominal sternite IX; N) aedeagus, dorsal view. Scale bars = 0.2 mm (Figs B–D, I, L–N), 0.5 mm (Figs A, E–H), 1.0 mm (Fig. K), 2.0 mm (Fig. J).

169x138mm (300 x 300 DPI)

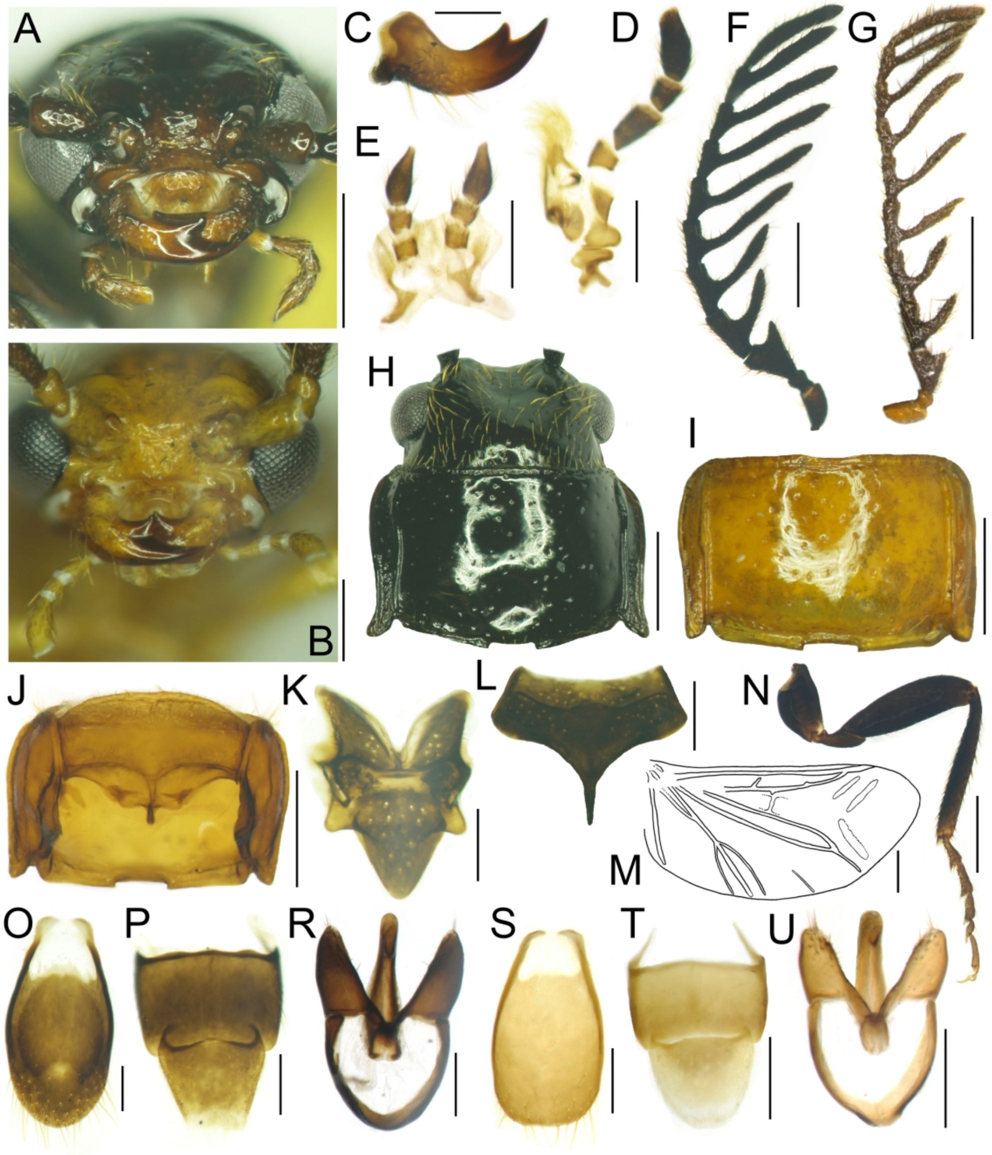


Figure 5. Body parts of Habeshselasia gen. nov., male. A) head of H. bicolor sp. nov., frontal view; B) head of H. illubaborensis sp. nov., frontal view; H. bicolor sp. nov.: C) mandible; D) maxilla; E) labium; F) antenna; G) antenna of H. illubaborensis sp. nov.; H) pronotum of H. bicolor sp. nov.; I) pronotum of H. illubaborensis sp. nov.; J) prosternum of H. illubaborensis sp. nov.; H. bicolor sp. nov.: K) scutellum; L) mesoventrite; M) hind wing; N) midleg; O) abdominal sternite IX; P) abdominal tergites IX–X; R) aedeagus; H. illubaborensis sp. nov.: S) abdominal sternite IX; T) abdominal tergites IX–X; U) aedeagus, dorsal view. Scale bars = 0.2 mm (Figs B–E, K–L, O–U), 0.5 mm (Figs A, F–J, M–N).

170x197mm (300 x 300 DPI)

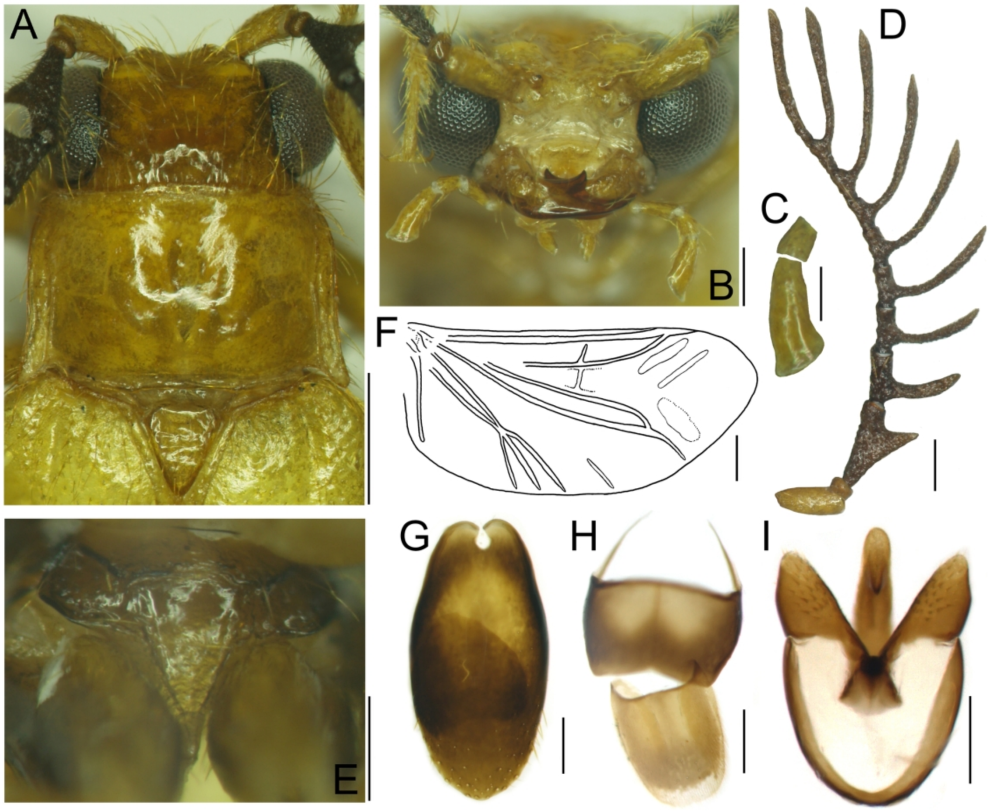


Figure 6. Body parts of Mashaselasia aethiopica gen. et sp. nov., male. A) anterior part of the holotype showing head, pronotum and scutellar shield; B) head, frontal view; C) apical maxillary palpomeres; D) antenna; E) mesoventrite; F) hind wing; G) abdominal sternite IX; H) abdominal tergites IX–X; I) aedeagus, dorsal view. Scale bars = 0.1 mm (Fig. C), 0.2 mm (Figs B, D–E, G–I), 0.5 mm (Figs A, F).

170x138mm (300 x 300 DPI)

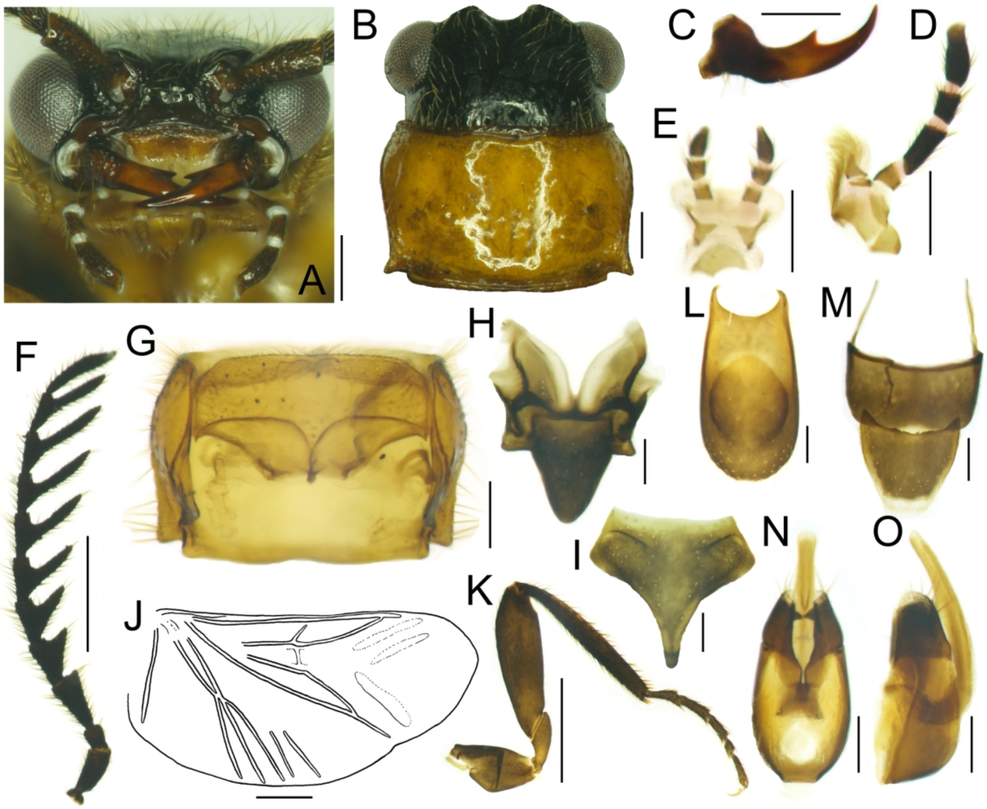


Figure 7. Body parts of Illubaboria bicolor gen. et sp. nov., male. A) head, frontal view; B) head and pronotum, dorsal view; C) mandible; D) maxilla; E) labium; F) antenna; G) prosternum; H) scutellum; I) mesoventrite; J) hind wing; K) midleg; L) abdominal sternite IX; M) abdominal tergite X; N) aedeagus, dorsal view; O) aedeagus, lateral view. Scale bars = 0.1 mm (Figs H–I), 0.2 mm (Figs A–E, G, L–O), 0.5 mm (Figs F, J–K).

170x138mm (300 x 300 DPI)

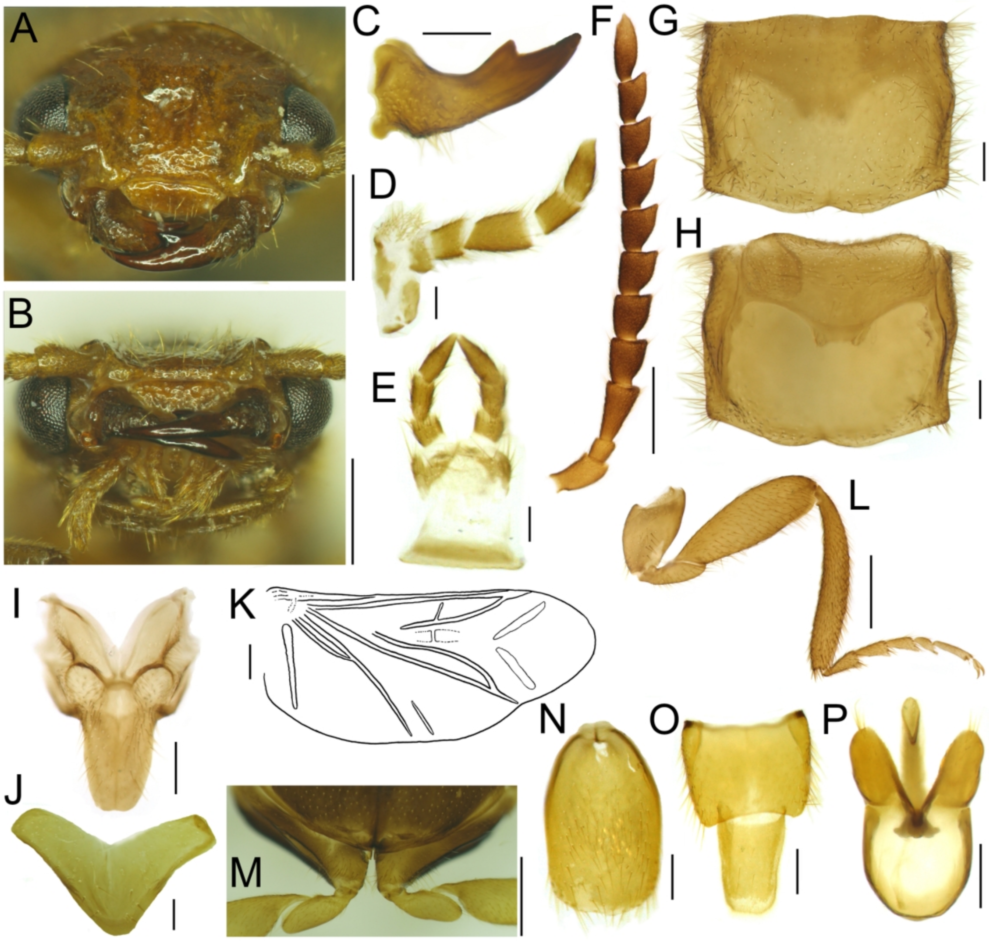


Figure 8. Body parts of Malacodrilus hajeki gen. et sp. nov., male. A) head, fronto-dorsal view; B) head, frontal view; C) mandible; D) maxilla; E) labium; F) antenna; G) pronotum; H) prosternum; I) scutellum; J) mesoventrite; K) hind wing; L) midleg; M) metacoxae; N) abdominal sternite IX; O) abdominal tergites IX–X; P) aedeagus, dorsal view. Scale bars = 0.1 mm (Figs D–E, J), 0.2 mm (Figs C, G–I, N–P), 0.5 mm (Figs A–B, F, K–M).

170x160mm (300 x 300 DPI)

Figure 9. Body parts of the Drilini representatives (all males). Prosternum. A) Agrypnus murinus (Linnaeus, 1758); B) Wittmerselasia camerooniana Kundrata & Bocak, 2017; C) Selasia erlangeri Geisthardt, 2007; D) Microselasia obscura Kundrata & Bocak, 2017; E) Drilus rectus Schaufuss, 1867; F) Malacogaster passerinii Bassi, 1834. Mesoventrite. G) Agrypnus murinus (Linnaeus, 1758); H) Wittmerselasia camerooniana Kundrata & Bocak, 2017; I) Selasia erlangeri Geisthardt, 2007; J) Microselasia obscura Kundrata & Bocak, 2017; K) Drilus rectus Schaufuss, 1867; L) Malacogaster passerinii Bassi, 1834. Abdomen. M) Cebrio sp. (Elaterinae: Cebrionini); N) Agrypnus murinus (Linnaeus, 1758); O) Austroselasia pulchra (Pascoe, 1887) gen. et comb. nov.; P) Habeshselasia bicolor gen. et sp. nov.; R) Illubaboria bicolor gen. et sp. nov.; S) Selasia sp.; T) Microselasia barombi Kundrata & Bocak, 2017; U) Drilus rectus Schaufuss, 1867; V) Malacodrilus hajeki gen. et sp. nov.; W) Malacogaster passerinii Bassi, 1834. Scale bars = 0.2 mm (Figs G–L), 0.5 mm (Figs A–F), 1.0 mm (Figs M–W).

170x250mm (300 x 300 DPI)

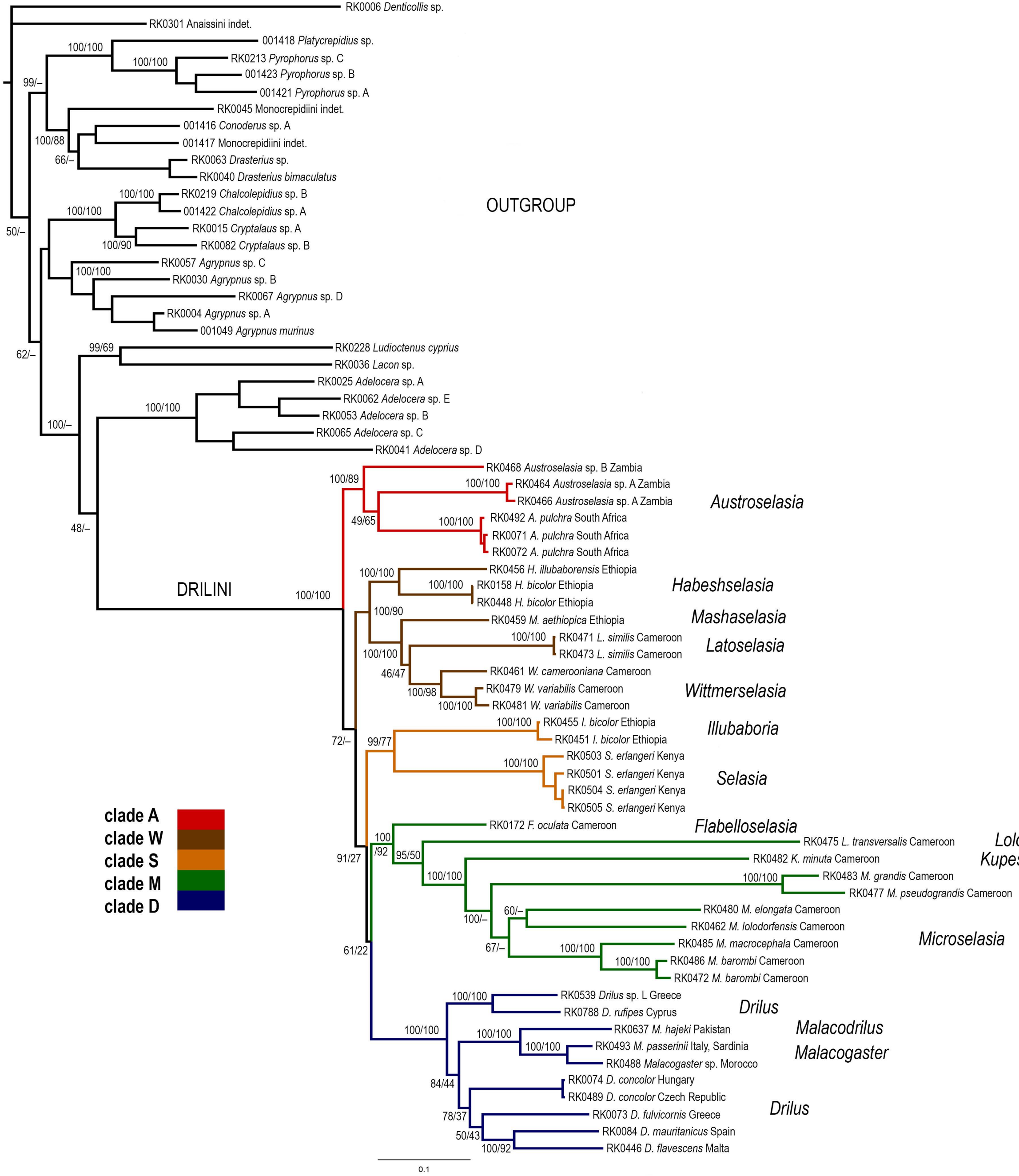

RK0006 Denticollis sp.
RK0301 Anaissini indet.
100/100
001418 Platycrepidius sp.
100/100
RK0213 Pyrophorus sp. C
001423 Pyrophorus sp. B
001421 Pyrophorus sp. A
99/–
RK0045 Monocrepidiini indet.
001416 Conoderus sp. A
100/88
001417 Monocrepidiini indet.
66/–
RK0063 Drasterius sp.
RK0040 Drasterius bimaculatus
100/100
RK0219 Chalcolepidius sp. B
100/100
001422 Chalcolepidius sp. A
OUTGROUP
RK0015 Cryptalaus sp. A
50/–
100/90
RK0082 Cryptalaus sp. B
RK0057 Agrypnus sp. C
100/100
RK0030 Agrypnus sp. B
RK0067 Agrypnus sp. D
RK0004 Agrypnus sp. A
001049 Agrypnus murinus
99/69
RK0228 Ludioctenus cyprius
62/–
RK0036 Lacon sp.
RK0025 Adelocera sp. A
100/100
RK0062 Adelocera sp. E
RK0053 Adelocera sp. B
100/–
RK0065 Adelocera sp. C
RK0041 Adelocera sp. D
RK0468 Austroselasia sp. B Zambia
100/89
100/100
RK0464 Austroselasia sp. A Zambia
RK0466 Austroselasia sp. A Zambia
Austroselasia
49/65
100/100
RK0492 A. pulchra South Africa
48/–
RK0071 A. pulchra South Africa
RK0072 A. pulchra South Africa
100/100
RK0456 H. illubaborensis Ethiopia
100/100
RK0158 H. bicolor Ethiopia
Habeshselasia
DRILINI
100/100
RK0448 H. bicolor Ethiopia
100/90
RK0459 M. aethiopica Ethiopia
Mashaselasia
100/100
RK0471 L. similis Cameroon
Latoselasia
100/100
RK0473 L. similis Cameroon
46/47
RK0461 W. camerooniana Cameroon
100/98
RK0479 W. variabilis Cameroon
Wittmerselasia
100/100
RK0481 W. variabilis Cameroon
100/100
RK0455 I. bicolor Ethiopia
Illubaboria
72/–
99/77
RK0451 I. bicolor Ethiopia
RK0503 S. erlangeri Kenya
100/100
RK0501 S. erlangeri Kenya
Selasia
RK0504 S. erlangeri Kenya
RK0505 S. erlangeri Kenya
clade A 🟥
RK0172 F. oculata Cameroon
Flabelloselasia
clade W
100
RK0475 L. transversalis Cameroon
Lolosia
clade S
91/27
/92
95/50
RK0482 K. minuta Cameroon
Kupeselasia
clade M 🟩
100/100
100/100
RK0483 M. grandis Cameroon
RK0477 M. pseudograndis Cameroon
clade D
60/–
RK0480 M. elongata Cameroon
100/–
RK0462 M. lolodorfensis Cameroon
Microselasia
67/–
100/100
RK0485 M. macrocephala Cameroon
61/22
100/100
RK0486 M. barombi Cameroon
RK0472 M. barombi Cameroon
100/100
RK0539 Drilus sp. L Greece
RK0788 D. rufipes Cyprus
Drilus
100/100
100/100
RK0637 M. hajeki Pakistan
Malacodrilus
100/100
RK0493 M. passerinii Italy, Sardinia
RK0488 Malacogaster sp. Morocco
Malacogaster
84/44
RK0074 D. concolor Hungary
RK0489 D. concolor Czech Republic
Drilus
78/37
RK0073 D. fulvicornis Greece
50/43
RK0084 D. mauritanicus Spain
100/92
RK0446 D. flavescens Malta
0.1

Table S1. The list of ingroup taxa used in this study, with GenBank accession and voucher numbers. 1 – Caterino *et al*. (2005); 2 – Bocakova *et al*. (2007); 3 – Hunt *et al*. (2007); 4 – Hendrich *et al*. (2015); 5 – Kundrata & Bocak (2011); 6 – Kundrata *et al*. (2014); 7 – Kundrata *et al*. (2015); 8 – Pentinsaari *et al*. (2014); 9 - Sormova *et al*. (2018); * - *cox1-5'* taken from the conspecific specimen RK1003.
[Note: xxxxxxxx will be replaced by the GenBank accession numbers if/when the manuscript is accepted for publication]

Genus/Species	Geographical origin	18S rRNA	28S rRNA	*rrnL*	*cox1-3'*	*cox1-5'*	*nad5*	Specimen voucher
Austroselasia pulchra	South Africa, Limpopo	HQ333824[5]	HQ333319[5]	HQ333731[5]	HQ334004[5]	xxxxxxxx	xxxxxxxx	UPOL RK0071
Austroselasia pulchra	South Africa, Limpopo	HQ333825[5]	HQ333320[5]	HQ333732[5]	HQ334005[5]	xxxxxxxx	xxxxxxxx	UPOL RK0072
Austroselasia pulchra	South Africa, KwaZulu-Natal	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	N	UPOL RK0492
Austroselasia sp. A	Zambia, Northern Prov.	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	N	UPOL RK0464
Austroselasia sp. A	Zambia, NW Province	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0466
Austroselasia sp. B	Zambia, Northern Prov.	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0468
Austroselasia sp. C	Kenya, Coast Province	N	N	N	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0491
Illubaboria bicolor	Ethiopia, Illubabor Prov.	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	N	UPOL RK0451
Illubaboria bicolor	Ethiopia, Illubabor Prov.	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0455
Habeshselasia bicolor	Ethiopia, Welega Prov.	KF625739[6]	KF626323[6]	KF626027[6]	KF625433[6]	N	xxxxxxxx	UPOL RK0158
Habeshselasia bicolor	Ethiopia, Welega Prov.	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0448
Habeshselasia illubaborensis	Ethiopia, Illubabor Prov.	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0456
Wittmerselasia camerooniana	Cameroon, South Region	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0461
Wittmerselasia variabilis	Cameroon, South Region	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0479
Wittmerselasia variabilis	Cameroon, SW Region	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0481
Wittmerselasia sp. A	Ghana, Eastern Region	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	N	UPOL RK0882
Wittmerselasia sp. B	Ghana, Eastern Region	N	N	xxxxxxxx	N	N	N	UPOL RK0883
Latoselasia similis	Cameroon, SW Region	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0471
Latoselasia similis	Cameroon, SW Region	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0473
Mashaselasia aethiopica	Ethiopia, Illubabor Prov.	xxxxxxxx	xxxxxxxx	N	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0459
Selasia arabica	Yemen, Al Hudaydah	xxxxxxxx	N	N	xxxxxxxx	xxxxxxxx	N	UPOL RK0633
Selasia erlangeri	Kenya, Eastern Province	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0501
Selasia erlangeri	Kenya, NE Province	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0504
Selasia erlangeri	Kenya, Coast Province	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0505
Selasia erlangeri	Kenya, Eastern Province	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0503
Selasia sp.	Nigeria, Abuja State	N	N	xxxxxxxx	xxxxxxxx	N	xxxxxxxx	UPOL RK0566
Flabelloselasia oculata	Cameroon, SW Region	KF625740[6]	KF626324[6]	KF626028[6]	KF625434[6]	N	xxxxxxxx	UPOL RK0172
Lolosia transversalis	Cameroon, South Region	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0475
Kupeselasia minuta	Cameroon, SW Region	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0482
Microselasia barombi	Cameroon, SW Region	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0472
Microselasia barombi	Cameroon, SW Region	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0486
Microselasia elongata	Cameroon, SW Region	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	N	UPOL RK0480
Microselasia grandis	Cameroon, SW Region	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0483
Microselasia kupensis	Cameroon, SW Region	xxxxxxxx	xxxxxxxx	N	xxxxxxxx	xxxxxxxx	N	UPOL RK0484
Microselasia lolodorfensis	Cameroon, South Region	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0462
Microselasia macrocephala	Cameroon, SW Region	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0485
Microselasia obscura	Cameroon, SW Region	N	N	N	xxxxxxxx	N	N	UPOL RK0922
Microselasia pseudograndis	Cameroon, South Region	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0477
Malacodrilus hajeki	Pakistan, Khyber Agency	N	N	xxxxxxxx	xxxxxxxx	xxxxxxxx	N	UPOL RK0637
Malacogaster passerinii	Italy, Sardinia	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0493
Malacogaster sp.	Morocco, Casablanca-Settat	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0488
Drilus baenai	Greece, Crete	N	N	N	KJ572910[7]	N	N	EB2013-304
Drilus baenai	Greece, Crete	N	N	N	KJ572907[7]	KJ572936[7]	N	EB2013-307
Drilus concolor	Hungary	HQ333827[5]	KF626322[6]	HQ333734[5]	HQ334007[5]	KJ572946[7]	xxxxxxxx	UPOL RK0074
Drilus concolor	Czech Republic	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	xxxxxxxx	UPOL RK0489

Drilus concolor	Sweden	N	N	N	N	KJ962998[8]	N	ZMUO:006430
Drilus concolor	The Netherlands	N	N	N	KJ572893[7]	KJ572945[7]	N	RMNH.INS559215
Drilus concolor	Germany	N	N	N	N	KM450682[4]	N	GBOLColFK2313
Drilus flavescens	United Kingdom	AY745559[1]	DQ202663[3]	DQ202597[3]	DQ222003[3]	N	N	BMNH 679287
Drilus flavescens	The Netherlands	N	N	N	KJ572927[7]	KJ572943[7]	N	EB2013-265
Drilus flavescens	Germany	N	N	N	N	KM450710[4]	N	BCZSMcol01479
Drilus cf. *flavescens*	Malta	xxxxxxxx	xxxxxxxx	MF506988[9]	KJ572890[7]	KJ572942[7]	xxxxxxxx	UPOL RK0446
Drilus fulvicornis	Greece, Peloponnese	HQ333826[5]	HQ333921[5]	HQ333733[5]	HQ334006[5]	KJ572950[7]	xxxxxxxx	UPOL RK0073
Drilus horasfakionus	Greece, Crete	N	N	N	KJ572901[7]	KJ572940[7]	N	RMNH.INS559169
Drilus horasfakionus	Greece, Crete	N	N	N	KJ572906[7]	N	N	EB2013-300
Drilus longulus	Greece, Crete	N	N	N	KJ572922[7]	KJ572930[7]	N	RMNH.INS559192
Drilus longulus	Greece, Crete	N	N	N	KJ572924[7]	KJ572931[7]	N	UPOL RK0638
Drilus cf. *mertliki*	Turkey, Artvin Province	N	N	HQ333739	HQ334013	KJ572947[7]	N	UPOL RK0081
Drilus mauritanicus	Spain, Córdoba	HQ333836[5]	HQ333927[5]	HQ333742[5]	HQ334015[5]	KJ572948[7]	N	UPOL RK0084
Drilus rectus	Turkey, Hatay Province	N	N	MF506989[9]	MF507014[9]	N	xxxxxxxx	UPOL RK0204
Drilus rufipes	Cyprus	xxxxxxxx	xxxxxxxx	MF506991[9]	MF507020[9]	MF507031[9]	N	UPOL RK0788*
Drilus sp. D	Greece, Kalamos	N	N	N	KJ572912[7]	KJ572932[7]	N	RMNH.INS559213
Drilus sp. D	Greece, Peloponnese	N	N	N	KJ572911[7]	N	N	RMNH.INS559219
Drilus sp. G	Greece, Peloponnese	N	N	N	KJ572914[7]	KJ572934[7]	N	RMNH.INS559218
Drilus sp. L	Greece, Peloponnese	xxxxxxxx	xxxxxxxx	MF506990[9]	KJ572915[7]	KJ572939[7]	xxxxxxxx	UPOL RK0539
Drilus sp. M	Greece, Kefalonia	N	N	N	KJ572913[7]	KJ572933[7]	N	RMNH.INS871808

References for Table S1.

Bocakova, M., Bocak, L., Hunt, T., Teraväinen, M. & Vogler, A.P. (2007) Molecular phylogenetics of Elateriformia (Coleoptera): evolution of bioluminescence and neoteny. Cladistics, 23, 477–496.

Caterino, M. S., Hunt, T. & Vogler, A. P. (2005) On the constitution and phylogeny of Staphyliniformia (Insecta: Coleoptera). Molecular Phylogenetics and Evolution, 34, 655–672.

Hendrich, L., Morinière, J., Haszprunar, G., Hebert, P.D.N., Hausmann, A., Köhler, F.,Balke, M. (2015) A comprehensive DNA barcode database for Central Europeanbeetles with a focus on Germany: adding more than 3500 identified species toBOLD. Molecular Ecology Resources, 15, 795–818.

Hunt, T., Bergsten, J., Levkanicova, Z., Papadopoulou, A., St. John, O., Wild, R., Hammond, P. M., Ahrens, D., Balke, M., Caterino, M. S., Gómez-Zurita, J., Ribera, I., Barraclough, T. G., Bocakova, M., Bocak, L. & Vogler, A. P. (2007) A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. Science, 318, 1913–1916.

Kundrata, R., Baalbergen, E., Bocak, L. & Schilthuizen, M. (2015a) The origin and diversity of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) in Crete based on mitochondrial phylogeny. Systematics and Biodiversity, 13, 52–75.

Kundrata, R. & Bocak, L. (2011) The phylogeny and limits of Elateridae (Insecta, Coleoptera): is there a common tendency of click beetles to soft-bodiedness and neoteny? Zoologica Scripta, 40, 364–378.

Kundrata, R., Bocakova, M. & Bocak, L. (2014) The comprehensive phylogeny of the superfamily Elateroidea (Coleoptera: Elateriformia). Molecular Phylogenetics and Evolution, 76, 162–171.

Pentinsaari, M., Hebert, P.D.N., Mutanen, M. (2014) Barcoding beetles: a regionalsurvey of 1872 species reveals high identification success and unusually deepinterspecific divergences. PLoS One, 9, e108651.

Sormova, E., Kramp, K. & Kundrata, R. (2018) Diversity and phylogenetic relationships of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) in Cyprus. Zoologischer Anzeiger, 275, 1–12.

Table S2. Outgroup taxa used in the analyses. Sequences taken from Kundrata & Bocak (2011) and Kundrata et al. (2014, 2016); only the KM sequence taken from Hendrich et al. (2015), and the XX sequences newly generated in this study. * - sequence taken from the conspecific specimen (RK0064); ** - tRNA missing.

[Note: xxxxxxxx will be replaced by the GenBank accession numbers if/when the manuscript is accepted for publication]

Subfamily/Tribe	Genus/Species	Geographical origin	18S rRNA	28S rRNA	*rrnL* mtDNA	*cox1-3′* mtDNA	*cox1-5′* mtDNA	*nad5* mtDNA	Specimen voucher
Dendrometrinae									
Denticollini	*Denticollis* sp.	Japan	HQ333759	HQ333854	KF626041	HQ333943	xxxxxxxx	xxxxxxxx	UPOL RK0006
Agrypninae									
Agrypnini	*Agrypnus murinus*	Slovakia	AF451943	DQ198735	DQ198645	DQ198567	KM451787	N	UPOL 001049
Agrypnini	*Agrypnus* sp. A	Japan	HQ333757	HQ333852	HQ333676	HQ333941	N	xxxxxxxx	UPOL RK0004
Agrypnini	*Agrypnus* sp. B	Indonesia	HQ333783	HQ333878	HQ333697	HQ333965	N	xxxxxxxx	UPOL RK0030
Agrypnini	*Agrypnus* sp. C	Japan	HQ333810	HQ333905	HQ333719	HQ333991	N	xxxxxxxx	UPOL RK0057
Agrypnini	*Agrypnus* sp. D	Indonesia	HQ333820	HQ333915	HQ333727	HQ334000	xxxxxxxx	xxxxxxxx	UPOL RK0067
Agrypnini	*Agrypnus* sp. E	Australia	KT460125	KT460144	KT460118	KT460170	N	N	COL027
Agrypnini	*Adelocera* sp. A	Japan	HQ333778	HQ333873	HQ333694	HQ333961	xxxxxxxx*	xxxxxxxx	UPOL RK0025
Agrypnini	*Adelocera* sp. B	Indonesia	HQ333806	HQ333901	HQ333715	HQ333987	xxxxxxxx	xxxxxxxx**	UPOL RK0053
Agrypnini	*Adelocera* sp. C	Malaysia	HQ333818	HQ333913	HQ333725	HQ333998	xxxxxxxx	xxxxxxxx	UPOL RK0065
Agrypnini	*Adelocera* sp. D	Indonesia	HQ333794	HQ333889	KF626035	HQ333976	N	xxxxxxxx	UPOL RK0041
Agrypnini	*Adelocera* sp. E	Indonesia	HQ333815	HQ333910	KF626033	KF625439	xxxxxxxx	N	UPOL RK0062
Agrypnini	*Lacon* sp.	Indonesia	HQ333789	HQ333884	KF626036	HQ333971	xxxxxxxx	N	UPOL RK0036
Anaissini	indet.	Panama	KF625761	KF626341	KF626055	KF625452	N	xxxxxxxx	UPOL RK0301
Hemirhipini	*Aphileus* sp.	Australia	KT460123	KT460142	KT460122	KT460166	N	N	COL022
Hemirhipini	*Chalcolepidius* sp. A	Panama	HQ333752	HQ333847	HQ333671	HQ333937	xxxxxxxx	xxxxxxxx	UPOL 001422
Hemirhipini	*Chalcolepidius* sp. B	French Guyana	KF625743	KF626326	KF626031	KF625437	N	xxxxxxxx**	UPOL RK0219
Hemirhipini	*Cryptalaus* sp. A	Japan	HQ333768	HQ333863	HQ333685	HQ333951	N	xxxxxxxx	UPOL RK0015
Hemirhipini	*Cryptalaus* sp. B	Malaysia	HQ333834	HQ333926	HQ333740	HQ334014	xxxxxxxx	N	UPOL RK0082
Hemirhipini	*Cryptalaus* sp. C	Indonesia	HQ333781	HQ333876	KF626034	N	N	xxxxxxxx**	UPOL RK0028
Hemirhipini	*Ludioctenus cyprius*	Greece	KF625744	KF626327	KF626032	KF625438	N	xxxxxxxx**	UPOL RK0228
Hemirhipini	*Paracalais* sp.	Australia	KT460124	KT460143	KT460121	KT460184	N	N	COL076
Monocrepidiini	*Conoderus* sp. A	Panama	HQ333746	HQ333841	HQ333665	HQ333931	xxxxxxxx	xxxxxxxx	UPOL 001416
Monocrepidiini	*Drasterius* sp.	Morocco	HQ333816	HQ333911	HQ333723	HQ333996	xxxxxxxx	xxxxxxxx	UPOL RK0063
Monocrepidiini	*Drast. bimaculatus*	Slovakia	HQ333793	HQ333888	HQ333704	HQ333975	N	xxxxxxxx	UPOL RK0040
Monocrepidiini	indet.	Panama	HQ333747	HQ333842	HQ333666	HQ333932	xxxxxxxx	xxxxxxxx	UPOL 001417
Monocrepidiini	indet.	Malaysia	HQ333798	HQ333893	HQ333708	HQ333980	N	xxxxxxxx	UPOL RK0045
Monocrepidiini	*Conoderus* sp. B	Australia	KT460126	KT460147	KT460119	KT460174	N	N	COL031
Monocrepidiini	*Heteroderes* sp.	Australia	KT460127	KT460145	KT460120	KT460185	N	N	COL096
Monocrepidiini	*Pseudaeolus* sp.	Australia	KT460128	KT460146	N	KT460186	N	N	COL113
Platycrepidiini	*Platycrepidius* sp.	Panama	HQ333748	HQ333843	HQ333667	HQ333933	xxxxxxxx	xxxxxxxx	UPOL 001418
Pyrophorini	*Pyrophorus* sp. A	Panama	HQ333751	HQ333846	HQ333670	HQ333936	xxxxxxxx	xxxxxxxx	UPOL 001421
Pyrophorini	*Pyrophorus* sp. B	Panama	HQ333753	HQ333848	HQ333672	KF625435	xxxxxxxx	xxxxxxxx	UPOL 001423
Pyrophorini	*Pyrophorus* sp. C	French Guyana	KF625742	KF626325	KF626030	KF625436	N	xxxxxxxx	UPOL RK0213

Table S3. Primers used for the PCR amplifications* of the studied genes.

Gene	Code	-mer	Sequence (5’ >> 3’)
rRNA			
18S	fragment A		
	18S 5'	24	GACAACCTGGTTGATCCTGCCAGT
	18S b5.0	19	TAACCGCAACAACTTTAAT
	fragment B		
	18S ai	22	CCTGAGAAACGGCTACCACATC
	18S b2.5.1	22	CGTTTTTGGCAAATGCTTTCGC
	fragment C		
	18S a1.0.1	20	GGTGAAATTCTTGGATCGTC
	18S bi	20	GAGTCTCGTTCGTTATCGGA
	fragment D		
	18S a2.0	19	ATGGTTGCAAAGCTGAAAC
	18S 3'Irk1	20	TACGACTTTTACTTCCTCTA
28S	28S ff	20	TTACACACTCCTTAGCGGAT
	28S dd	19	GGGACCCGTCTTGAAACAC
mtDNA			
rrnL	16a	20	CGCCTGTTTAACAAAAACAT
	16bb	22	CCGGTTTAAACTCAGATCATGT
	ND1-A	27	GGTCCCTTACGAATTTGAATATATCCT
cox1-3'	S-Pat	21	GCACTAWTCTGCCATATTAGA
	S-Jerry	23	CAACATYTATTYTGATTYTTTGG
cox1-5'	LCO1490K	26	TCAACWAAYCATAAAGACATTGGAAC
	HCO2198K	26	TAAACTTCTGGGTGWCCAAARAATCA
nad5	OF1DRI**	29	CCTACCCCCGTTTCATCTCTAGTTCATTC
	OF1PYR**	29	CCTACACCTGTTTCTTCCTTGGTTCACTC
	R6ELA**	29	GAAACAAAWATTTGTAATTAGTTTCGACCT

* PCR conditions included an initial denaturation step of 1–2 min at 94–96°C, followed by 40 cycles as follows: 30–60 sec at 94°C, 30–60 sec at 41–50°C (depending on the melting temperatures of primer pairs used), 1–2 min at 72°C, and a final step of 10 min at 72°C. ABI technology was used for the DNA sequencing.

** Primers newly designed in this study.

Table S4. Results of the Xia's nucleotide substitution saturation test in DAMBE, based on simulations with 32 operational taxonomic units (10 000 replicates). Analysis performed on fully resolved sites only. Iss - index of substitution saturation; Iss.c^{S} - critical value for symmetrical tree topology; Iss.c^{A} - critical value for extremely asymmetrical tree topology; T - T value; DF - degrees of freedom; P^{S}, P^{A} - probability that Iss is significantly different from the critical value (Iss.c^{S} or Iss.c^{A}, respectively); Pinv - proportion of invariable sites.

Marker/codon pos.	Iss	Iss.c^{S}	T	DF	P^{S}	Iss.c^{A}	T	DF	P^{A}	Pinv
18S rRNA	0.016	0.742	142.82	520	0.000	0.431	81.673	520	0.000	0.431
28S rRNA	0.049	0.704	44.835	336	0.000	0.378	22.508	336	0.000	0.346
rrnL mtDNA	0.233	0.701	19.281	427	0.000	0.375	5.866	427	0.000	0.120
cox1-3' mtDNA/1st	0.195	0.796	10.995	92	0.000	0.571	6.877	92	0.000	0.096
cox1-3' mtDNA /2nd	0.087	0.793	20.902	78	0.000	0.566	14.187	78	0.000	0.244
cox1-3' mtDNA /3rd	0.636	0.796	3.973	102	0.000	0.571	1.600	102	0.113	0.002
cox1-5' mtDNA/1st	0.150	0.687	16.770	183	0.000	0.368	6.802	183	0.000	0.150
cox1-5' mtDNA /2nd	0.038	0.687	39.788	137	0.000	0.368	20.214	137	0.000	0.363
cox1-5' mtDNA /3rd	0.665	0.687	0.732	216	0.465	0.368	10.234	216	0.000	0.000
nad5 mtDNA/1st	0.373	0.690	7.650	186	0.000	0.375	0.056	186	0.955	0.076
nad5 mtDNA /2nd	0.232	0.690	11.978	177	0.000	0.375	3.740	177	0.000	0.118
nad5 mtDNA /3rd	0.723	0.691	1.020	199	0.309	0.376	10.931	199	0.000	0.003
tRNA	0.208	0.973	16.518	60	0.000	0.880	14.513	60	0.000	0.086

Table S5. Summary of the PartitionFinder results. Settings: branchlengths = linked, models of evolution = mrbayes/raxml, search algorithm = greedy. #par. - number of parameters; #sub. - number of subsets. Partition scheme with 11 subsets = (18S) (28S) (*rrnL*) (*cox1-3'*_pos1) (*cox1-3'*_pos2) (*cox1-3'*_pos3) (*cox1-5'*_pos1) (*cox1-5'*_pos2) (*nad5*_pos1) (*nad5*_pos2) (tRNAs).

Dataset (taxa/aln)	AICc	lnL	#par.	#sub.	Best Model
Bayesian inference (mrbayes)					
100/Mafft	112389.40	-55872.71	303	11	GTR+I+G, K80+I+G (28S), SYM+I+G (*cox1-5'*_pos1), HKY+I+G (tRNA)
68/Mafft	94067.15	-46777.39	244	11	GTR+I+G, SYM+I+G (*cox1-5'*_pos1), HKY+I+G (tRNA)
66/Mafft (ingroup)	71391.20	-35433.75	249	11	GTR+I+G
Maximum likelihood (raxml)					
100/Mafft	112403.93	-55864.12	317	11	GTR+I+G
68/Mafft	94079.81	-46775.99	251	11	GTR+I+G
66/Mafft (ingroup)	71391.20	-35433.75	249	11	GTR+I+G

Table S6. Numbers and types of characters in the analyzed datasets.

Number of taxa/	Characters	rRNA		mtDNA							parsimony
Alignment type	total	18S	28S	*rrnL*	*cox1-3'*	*cox1-5'*	*nad5*	*tRNA*	conserved	variable	informative
100/Mafft	5154	1880	686	535	723	438	681	211	3550	1546	1274
68/Mafft	5151	1880	682	536	723	438	681	211	3588	1503	1259
66/Mafft (ingroup)	5093	1847	671	531	723	438	681	202	3732	1332	1089

Table S7. Nucleotide composition of markers used in this study (in %).

Base	18S	28S	*rrnL*	*cox1-3'*	*cox1-5'*	*nad5*	tRNAs
A	24.0	24.9	29.2	32.9	29.6	23.7	37.5
T	23.4	19.8	41.5	33.0	31.7	49.8	40.5
C	24.5	24.0	10.6	18.5	21.2	9.9	8.9
G	28.1	31.3	18.6	15.6	17.5	16.6	13.1

Table S8. Estimated dates (in mya) of the main nodes in Drilini inferred from the BEAST analysis of the concatenated mtDNA fragments using the Yule Process and Birth-Death tree priors and previously published mutation rates for mtDNA markers. A, W, S, M and D designate the Drilini clades as defined in the main text. The numbers in parentheses designate 95% probability intervals.

Tree prior	Yule Process	Birth-Death
lnP (model/data)	-47659.477	-47658.848
Drilini	35.4 (31.4–39.6)	35.5 (31.7–39.6)
Clade W+S+M+D	34.5 (30.7–38.5)	34.5 (30.9–38.6)
Clade S+M+D	34.0 (30.1–37.8)	34.0 (30.3–37.8)
Clade M+D	33.4 (29.7–37.3)	33.5 (29.9–37.3)
Clade A (*Austroselasia*)	32.9 (28.1–38.1)	33.0 (28.2–37.9)
Clade W	32.7 (28.5–37.0)	32.7 (28.6–37.0)
Habeshselasia	22.2 (17.1–27.8)	22.2 (17.2–27.5)
Masha+Lato+Wittmerselasia	26.8 (22.4–31.7)	26.8 (22.1–31.4)
Lato+Wittmerselasia	25.6 (21.0–30.2)	25.6 (21.2–30.3)
Latoselasia	00.9 (00.5–01.3)	00.9 (00.5–01.4)
Wittmerselasia	14.9 (11.4–18.4)	14.8 (11.3–18.3)
Clade S	28.2 (24.1–32.6)	28.3 (24.2–32.6)
Illubaboria	02.9 (01.9–04.0)	02.9 (01.9–04.0)
Selasia	24.6 (20.3–28.9)	24.7 (20.5–28.9)
Clade M	32.1 (28.4–35.9)	32.2 (28.6–36.0)
Lolosia+Kupe+Microselasia	30.6 (27.0–34.3)	30.6 (27.1–34.3)
Kupeselasia+Microselasia	27.2 (23.8–30.6)	27.1 (24.0–30.6)
Microselasia	25.3 (22.1–28.6)	25.3 (22.4–28.7)
Clade D	23.9 (20.9–26.9)	23.8 (20.8–26.8)
Malacogaster+Malacodrilus	15.2 (11.6–18.6)	15.1 (11.8–18.8)
Malacogaster	04.5 (03.1–06.0)	04.5 (03.2–06.0)
Drilus	21.4 (18.9–24.1)	21.4 (18.8–24.2)

Potvrzení autorského podílu na publikacích zařazených v habilitační práci, u nichž uchazeč není korespondujícím autorem

Potvrzení autorského podílu Robina Kundraty

Tímto potvrzuji, že jsem korespondujícím autorem následujících publikací a současně potvrzuji autorský podíl R. Kundraty v daném rozsahu:

Bocak, L., Kundrata, R., Andújar Fernández, C. & Vogler, A. P. (2016) The discovery of Iberobaeniidae (Coleoptera: Elateroidea), a new family of beetles from Spain, with immatures detected by environmental DNA sequencing. *Proceedings of the Royal Society B: Biological Sciences*, 283: 20152350.

Podíl R. Kundraty na publikaci: 35 %

Kundrata, R., Baena, M. & Bocak, L. (2015) Classification of Omalisidae based on molecular data and morphology, with description of Paradrilinae subfam. nov. (Coleoptera: Elateroidea). *Zootaxa*, 3915: 413–422.

Podíl R. Kundraty na publikaci: 40 %

V Olomouci, 27. 2. 2019,

Prof. Ing. Ladislav Bocák, Ph.D.
Katedra zoologie PřF UP v Olomouci
17. listopadu 50, 779 00 Olomouc
tel.: +420585634906
e-mail: ladislav.bocak@upol.cz

To Whom It May Concern

datum
February 11th, 2019

betreft

Dear Sir, Madam,

I hereby confirm that I am the corresponding author of the following paper:

Baalbergen, E., Helwerda, R., Schelfhorst, R., Castillo Cajas, R. F., van Moorsel, C. H. M., Kundrata, R., Welter-Schultes, F. W., Giokas, S. & Schilthuizen, M. (2014) Predator-prey interactions between shell-boring beetle larvae and rock-dwelling land snails. *PLoS ONE*, 9: e100366.

I also confirm that the overall contribution of Dr. Robin Kundrata to the paper amounts to 12%.

Yours sincerely,

Prof. Dr. Menno Schilthuizen

Senior researcher (Naturalis Biodiversity Center)
Professor of Character Evolution and Biodiversity (Leiden University)

Naturalis
Biodiversity
Center

Darwinweg 2
Postbus 9517
2300 RA Leiden

T 071 751 91 91
po@naturalis.nl
www.naturalis.nl

KvK 411 695 15
BTW NL 803595943 B01
IBAN NL34RABO0114477000