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.
Published online at www.senckenberg.de/arthropod-systematics on 30.iv.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).

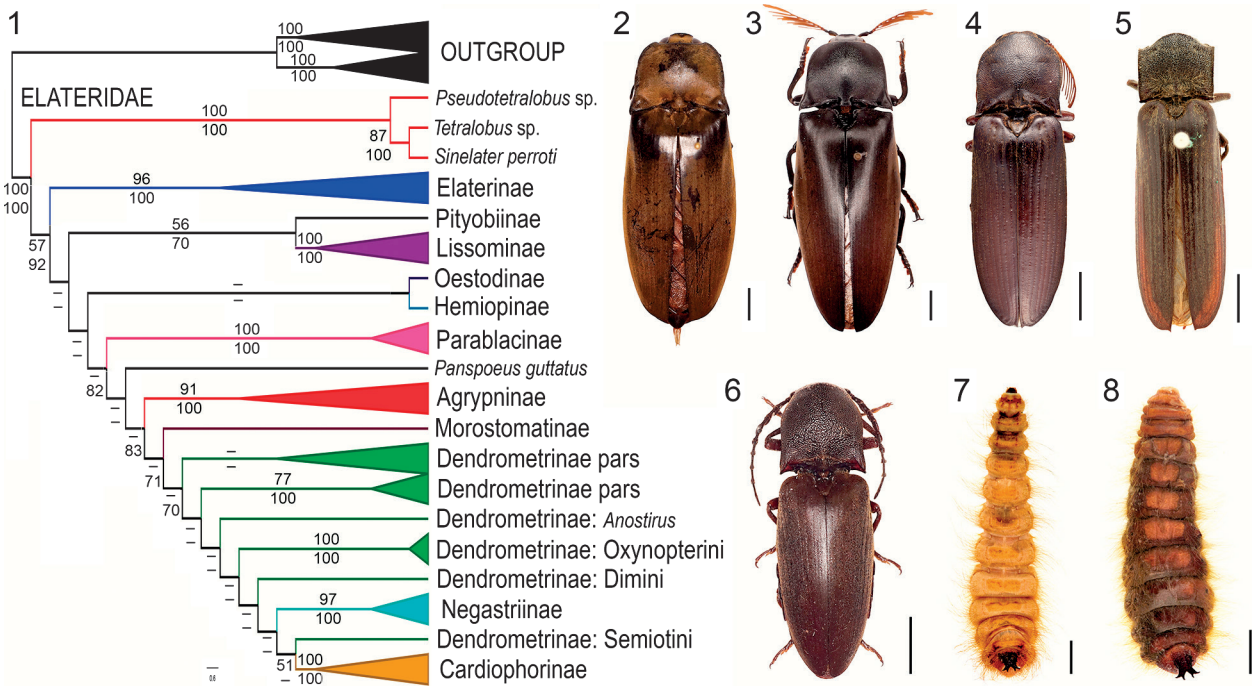
3. Results

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., Teravāinen 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 Société 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. Partition Finder: 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., Benà 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.