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2 **Ontogenetic modifications produce similar phenotypes in distantly related click beetles**
3 **(Coleoptera: Elateridae)**

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12
13 **Abstract**

14 The study analyzes the relationships of click beetles (Elateridae) *Paulusiella* Löbl, 2007, and
15 *Analestesa* Leach, 1824 (= *Cebriognathus* Chobaut, 1899), both incapable of jumping, with soft-
16 bodied habitus, and unknown females. Due to divergent morphology, their positions have been an
17 uncertain issue. We use mitochondrial genomes to test their current placement in Cebriionini
18 (=Cebriognathini) and Elaterinae *incertae sedis*, respectively. We recover *Paulusiella* as a sister to
19 *Hemiops* Laporte, 1838 (Hemiopinae) and *Analestesa* as one of the serially splitting branches in
20 Cardiophorinae, both with robust support. Paulusiellinae **subfam. nov.** is proposed for *Paulusiella*.
21 *Analestesa* is transferred to Cardiophorinae, and Cebriognathini Paulus, 1981, an earlier synonym of
22 Elaterinae: Cebriionini, is a synonym of Cardiophorinae Candèze, 1859. The click beetles affected by
23 ontogenetic modifications converge to similar forms lacking derived states. As a result, their
24 phylogenetic position cannot be reliably inferred by morphological analyses and needs to be validated
25 by molecular data. Paulusiellinae and *Analestesa* represent two additional cases of the shift to
26 incomplete sclerotization in elaterids raising the total number to six. The present transfers of extant
27 taxa between subfamilies call for a cautious interpretation of morphology in other soft-bodied groups,
28 including the taxa described from amber deposits.

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30 Key words: classification, molecular phylogeny, morphology, evolution, ontogeny.
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33 **Introduction**

34 Click beetles (Elateroidea: Elateridae) are well known for their jumping adults (Ribak &
35 Weihs 2011). Still, some click beetles lost their thoracic click mechanism and differ from their
36 relatives in general appearance. Omalids, drilids (false firefly beetles), and plastocerids were
37 separate families considered the relatives of fireflies, soldier- and net-winged beetles (Crowson 1972,
38 Branham & Wenzel 2003, Lawrence et al. 2011). Only recently, they were included in Elateridae
39 (Bocak et al. 2018, Kusy et al. 2019). Cebriionids (Elaterinae) traditionally contained other non-
40 clicking, soft-bodied elaterids. Although cebriionids were earlier treated as a family (Crowson 1955),
41 they are so slightly modified (Arnett 1949, Rattu 2016) that they were included in Elateridae since
42 applying Hennig's phylogenetic systematics (Crowson 1981, Bouchard et al. 2011). Later, they were
43 downranked to the tribe Cebriionini in Elaterinae (Kundrata et al. 2014). Still, their classification has
44 never benefited from a molecular study, and the relationships of constituent genera have been poorly
45 corroborated. Concerning the known effect of modified metamorphosis on the phenotype of elateroids
46 (Kusy et al. 2019, 2021), reexamining the phylogenetic position of non-clicking elaterids is needed
47 not only to update the classification but also to understand the evolution of ontogenetic modifications.

48 Metamorphosis is a crucial innovation that is supposedly connected with the enormous
49 diversity of insects (Nicholson et al. 2014). The transition between larva, pupa and adult is a complex,
50 fine-tuned cascade of steps (Jindra et al. 2015, Jindra 2019) that can be prematurely terminated. Then,
51 some larval and pupal characteristics can persist in adults (Gould 1977, Bocak & Brlik 2008,
52 McMahon & Hayward 2016, Bocek et al. 2019). In the most severely affected elateroids, the imaginal
53 characters are not expressed, and larva-like females are sexually mature (Cicero 2008, Wong 1996,
54 Masek et al. 2014, 2015, Makarov & Kazantsev 2022). The ontogenetic modifications are usually
55 similar within a single group. Still, different levels are known in various lineages (Crowson 1972,
56 McMahon & Hayward 2016).

57 The phenotypically divergent adults are weakly sclerotized, and never use the clicking
58 mechanism known in their relatives (e.g., drilids, omalisids, cebrionids, etc.). Further, we can
59 encounter shortened or vestigial elytra, sometimes connected with a loss of wings. The abdomen can
60 be larviform (drilids), or at least the ventrites are loose (e.g., Dendrometrinae: Plastocerini; Kusy et al.
61 2018). The incomplete metamorphosis results in the loss of phylogenetically younger traits in
62 agreement with Baer's recapitulation law (Løvtrup 1978). The modified soft-bodied forms have been
63 confusing to systematists till an independent source of phylogenetic information became available
64 with the sequencing of DNA. Due to absent apomorphic traits, some affected lineages have been
65 assigned inappropriate high ranks. Alternatively, the unrelated groups were merged into a single taxon
66 (Lawrence et al. 2011, Kazantsev 2013). In such a way, the morphologists defined the earlier
67 superfamily Cantharoidea, and the cantharoid clade in Elateroidea (Crowson 1972, Lawrence 1988,
68 Lawrence et al. 2011).

69 There are several obstacles that have delayed the studies on modified elaterids. Most neotenic
70 groups are rare compared to their close relatives, and obtaining individuals properly fixed for
71 molecular analyses has not been easy. Additionally, some females often remain unknown. We only
72 estimate that the females are affected by the paedomorphic syndrome from the morphology of males,
73 the relationships, and the absence of females in contrast with numerous males deposited in
74 collections. Wingless females remain in the soil, and some only expose the abdomen during the
75 copulation (observed in *Cebrio*, [https://www.youtube.com/watch?v=MIEz6jHCgLo&ab_](https://www.youtube.com/watch?v=MIEz6jHCgLo&ab_channel=RobertoLascaro)
76 [channel=RobertoLascaro](https://www.youtube.com/watch?v=MIEz6jHCgLo&ab_channel=RobertoLascaro) accessed on Nov. 3, 2022); Bocak et al. 2013, Bocek et al. 2018).

77 Our study reinvestigates the relationships of the soft-bodied forms placed in the tribe
78 Cebrionini (Elaterinae). We revisit morphological evidence for the earlier proposed concept of
79 cebrionids and look for the morphological traits that could potentially support the molecular
80 relationships. We intend to show that morphologically divergent lineages may converge to similar
81 phenotypes even if they are distantly related. The results affect the Linnean classification of
82 investigated taxa. We believe that revising the traditional placement of extant soft-bodied elaterids
83 might contribute to a better understanding of morphological evolution. We expect, analogically to
84 click beetle phylogeny, further changes in the placement of other strongly modified groups. The
85 difficulties with classifying extant soft-bodied forms should also be considered in works on fossils for
86 which only morphological and often incomplete data are available.

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88 **Methods**

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90 The compilation of the dataset

91 The mitogenomic dataset was assembled from newly sequenced mitogenomes of *Cebrio* sp.,
92 *Cebriorhipis* sp., *Analestesa arabica* (Paulus, 1981), *Paulusiella serraticornis* (Paulus, 1972),
93 *Quasimus* sp., and *Hemiops* sp. The voucher numbers and complete locality data are reported in Tab.
94 1. Further mitogenomic data were taken from the dataset published by Kusy et al. (2021).

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96 Table 1. The list of newly sequenced samples. For the list of publicly available samples, see Supp.
97 Tab. S1.

Taxon	Voucher	Geographic origin
<i>Paulusiella serraticornis</i>	G21004	Iran, Kerman prov., Gebal Barez mts., 1345 m, 26 km N of Jiroft, wadi, 28°54'14"N 57°40'32"E, 27. May 2018, Vit Kuban leg., coll. V. Kuban.
<i>Analestesa arabica</i>	G21003	Kingdom of Saudi Arabia, Hieth, 2. May 1975, 40 km S of Riyadh, 24°18'9", 46°42'27", W. Büttiker leg., coll. L. Bocak.
<i>Cebrio</i> sp.	G19010	Italy, Sardinia, 2 km W of Irgutosu, 62 m, 39°31'31"N, 8°28'20"E, D. Ahrens & S. Fabrizzi leg., coll. L. Bocak.
<i>Cebriorhipis</i> sp.	G22001	Indonesia, Bali, Tamblingan Lake, 1000–1300 m, 8°15'33"S, 115°6'14"E. 2.–17. Feb 2004, S. Jakl leg., coll. D. Kusy.
<i>Quasimus</i> sp.	R19010	Japan, Kunimidake, 35°27'3 "N, 136°21'37"E, 14. May 2015, T. Sota leg., coll. L. Bocak.
<i>Hemiops</i> sp.	G19002	Malaysia, Perak, km 24 Rd Tapah-Ringlet, 230 m, 4°18'39"N, 101°19'52"E, 19. Apr. 2013, L. Dembicky leg., coll. L. Dembicky.

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99 Laboratory procedures, data handling, and morphological investigation

100 The total DNA was isolated from alcohol-preserved or dry-mounted samples. The vouchers were used
101 for morphological investigation. They were dissected after short relaxation in 50% ethanol. The
102 structures were treated in hot 10% KOH for a short time. The photographs were taken by a Canon M6
103 Mark II camera attached to an Olympus SZX16 binocular microscope. Stacks were assembled using
104 Helicon Focus software and processed in Photoshop 6.0. Vouchers are deposited in the collections of
105 the collectors and of Biodiversity & Molecular Evolution at CATRIN, Olomouc.

106 DNA was extracted using Qiagen MagAttract HMW DNA extraction kit, and eluted in AE
107 buffer. Short insert size library constructions (~320 bp) and subsequent paired-end (2 × 150 bp)
108 sequencing of the samples were done by Novogene, Inc., Beijing, using Illumina NovaSeq 6000. Raw
109 Illumina reads were quality checked with FastQC and filtered with fastp 0.21.0 (Chen et al. 2018)
110 using -q 28 -u 50 -n 15 -l 50 settings. Filtered reads were used for final mitogenome assemblies. The
111 mitogenomes were built de novo using the NOVOPlasty v.2.7.2 pipeline (Dierckxsens et al. 2017).
112 NOVOPlasty was run with the default settings except the kmer value when we used a multi-kmer
113 strategy with the following kmer sizes of 25, 39, 45, and 51. We used as seed the single fragment of
114 *Oxyntopus* sp. cox1 gene available in GenBank (HQ333982). In the case of *Quasimus* sp., the
115 mitochondrial fragments were mined from unpublished transcriptomic data that were mapped on the
116 mitochondrial genome of *Cardiophorus signatus*, and manually curated in Geneious v.7.1.9. The
117 newly assembled mitochondrial genomes were annotated using the MITOS2 webserver (Bernt et al.
118 2013) with the invertebrate genetic code and RefSeq 63 metazoa reference. The annotation,
119 circularization, and start + stop codons corrections of protein-coding genes (PCSGs) were performed
120 manually in Geneious v.7.1.9. The sequences of newly produced mitochondrial genomes were
121 deposited into the Mendeley database DOI:10.17632/73dmw4czm3.1.

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123 Phylogenetic analyses

124 The six mitochondrial genomes of click beetles were merged for the purpose of phylogenetic analyses
125 with thirty earlier published mitochondrial genomes (36 ingroup taxa and 1 outgroup, Kusy et al.
126 2021). The dataset contained terminals belonging to ten subfamilies of Elateridae. The nucleotide
127 sequences of protein-coding genes (PCG) were aligned using TransAlign (Bininda-Emonds 2005). In
128 addition, nucleotide sequences of rRNA genes and translated amino acid sequences of PCGs were
129 aligned with Mafft v.7.407 using the L-INS-i algorithm (Katoh & Standley, 2013). The aligned data
130 were concatenated with FASconCAT-G v.1.04 (Kück & Longo 2014). We compiled the following
131 datasets: (A) 13 PCG mtDNA and 2 rRNA mtDNA genes partitioned by gene or unpartitioned; (B) 13
132 mitochondrial PCGs and by gene or unpartitioned; (C) 13 mitochondrial PCGs masked by degen

133 software (Steenwyk et al. 2020) partitioned by a gene or unpartitioned; (D) amino acid level analysis
134 of 13 mitochondrial PCGs. The degree of missing data and overall pairwise completeness scores
135 across all datasets was inspected using AliStat v.1.7. (Thomas et al. 2020) (Supp. Fig. S1).

136 Phylogenetic inferences were performed under maximum likelihood (ML) optimization using
137 IQ-Tree2.1.2 (Minh et al. 2020), and Bayesian inference (BI) using PhyloBayes MPI v.1.8 (Lartillot
138 et al. 2013). Before ML tree searches, best-fitting model selection for each partition was performed
139 with ModelFinder (Chernomor et al. 2016, Kalyaanamoorthy et al. 2017) using the -MFP. All datasets
140 were tested against a complete list of models. We used the edge-linked partitioned model for tree
141 reconstructions (-spp option) allowing each partition to have its own rate.

142 Ultrafast bootstrap values (Hoang et al. 2018) were calculated for each tree using -bb 5000
143 option. In the PhyloBayes analysis, unpartitioned datasets A, and D were analyzed under the site-
144 heterogeneous mixture CAT + GTR + Γ 4 model for all searches. Two independent Markov chain
145 Monte Carlo (MCMC) were run for each dataset. We checked for the convergence in the tree space
146 with bpcomp program and generated output of the largest (maxdiff) and mean (meandiff) discrepancy
147 observed across all bipartitions and generated a majority-rule consensus tree using a burn-in of 30%
148 and sub-sampling every 10th tree. Additionally, we used the program tracecomp to check for
149 convergence of the continuous parameters of the model.

150 We employed several tests to investigate alternative phylogenetic relationships, including the
151 approximately unbiased AU-test (Shimodaira 2002), the p-SH (p-value of the Shimodaira-Hasegawa
152 test) (Shimodaira & Hasegawa 1999), the KH-test (one-sided Kishino-Hasegawa test) (Kishino &
153 Hasegawa 1989), the p-WKH (p-value of weighted KH test), the p-WSH (p-value of weighted SH
154 test), c-ELW (Expected Likelihood Weight) (Strimmer & Rambaut 2002), and bp-RELL (bootstrap
155 proportion using RELL method) (Kishino et al. 1990). To evaluate the hypothesized placement of
156 focal taxa (*Analestesa arabica*, *Cebriorhipis* sp., and *Paulusiella serraticornis*) within Elaterinae, we
157 tested the maximum likelihood (ML) tree topology against three alternative topologies suggested by
158 earlier classifications: (A) *Analestesa arabica* as sister to *Cebrio* and *Cebriorhipis*, (B) *Paulusiella*
159 *serraticornis* as sister to *Cebrio* and *Cebriorhipis*, and (C) the clade containing all focal taxa. IQ-
160 TREE2 (Minh et al. 2020) was used to perform all tests, with per-site log-likelihoods calculated using
161 the --test-weight --test-au --sitelh parameters and 10,000 replications

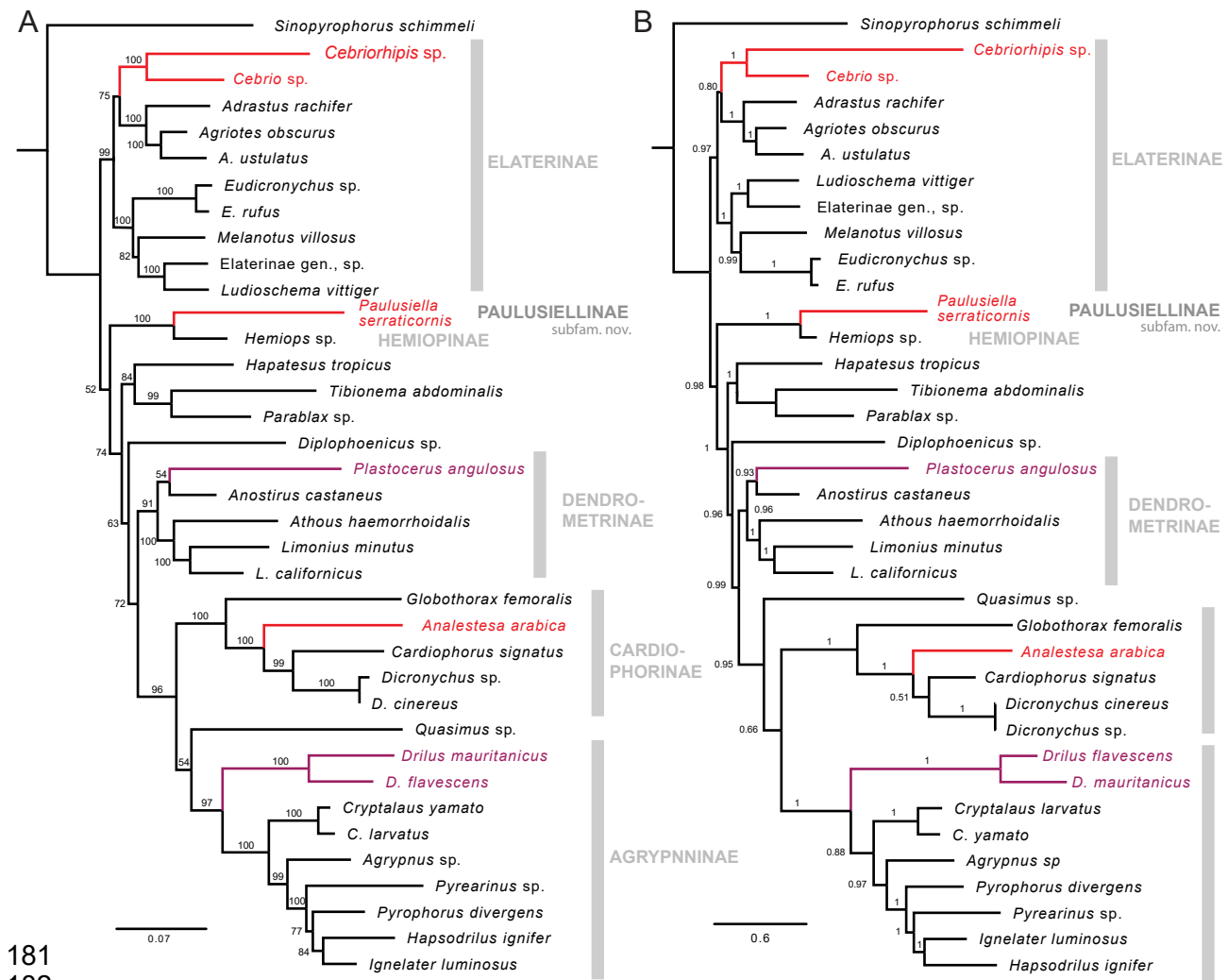
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163 Results

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165 Molecular phylogeny

166 The Bayesian and maximum likelihood mitogenomic analyses indicate high support for the polyphyly
167 of Cebriionini in the traditional sense (Figs. 1A, B; Supp. Figs. S2-S11). Only *Cebrio* sp. and
168 *Cebriorhipis* sp. are members of Elaterinae (BS 99%, PP 0.97). *Paulusiella serraticornis* was
169 regularly a sister to *Hemiops* sp. (BS 100%, PP 1.00). Still, the clade was variably a sister to the
170 remaining elaterid subfamilies or a sister to the non-Elaterinae subfamilies (Fig. 1A, B, Supp. Figs.
171 S2-S11). *Analestesa arabica* was firmly placed within Cardiophorinae (BS 100%, PP 1.00) as the
172 second split following *Globothorax femoralis*. The position of Negastrinae as a putative sister of
173 Cardiophorinae was recovered only by some analyses (Supp. Figs. S5, S6, S8). Alternatively, the
174 genus was found as a sister to the Agrypninae (Fig. 1A), or the Cardiophorinae + Agrypninae clade
175 (Fig. 1B). No analysis suggested alternative positions for the focal taxa. The tests rejected the
176 relationships of *Paulusiella* and *Analestesa* with Cebriionini (*Cebriorhipis* and *Cebrio*; Elaterinae;
177 Tab. 2). We separately considered both genera in Cebriionini, and alternatively, either of them as a
178 sister to *Cebrio* and *Cebriorhipis* (Tab. 2). We did not test the relationships between subfamilies and
179 the monophyly of Elateridae as the dataset does not provide enough support for the deepest
180 relationships.



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184 **Figure 1.** The mitogenomic relationships of soft-bodied and/or non-clicking genera *Paulusiella*,
 185 *Cebrio*, *Scaptolenus*, *Analestesa*, *Plastocerus*, *Drilus*, and their clicking relatives. The numbers at
 186 branches designate bootstrap values and posterior probabilities. A – the maximum likelihood analysis
 187 of thirteen protein-coding mitochondrial genes at the nucleotide level with coding masked by the
 188 degen software and partitioned by genes. B – The Bayesian analysis using PhyloBayes at the
 189 nucleotide level. The trees with full-length branches and the results of additional analyses are shown
 190 in Supp. Figs. S2–S11. Red – the taxa earlier placed in Cebriorhini; magenta – non-clicking elaterids
 191 earlier placed in families Drilidae and Plastoceridae.

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195 Morphology

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197 *Paulusiella serraticornis* (Paulus, 1972)

198 *Escalerina serraticornis* Paulus, 1972: 38 (in Karumiidae; now Dascillidae: Karumiinae).

199 (Figs. 2A–P)

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201 Redescription

202 Male. Body 5–7 mm long, slender, slightly flattened, light brown colored, vestiture of upper surfaces
 203 with erect, long bristles (Figs. 2A–C).

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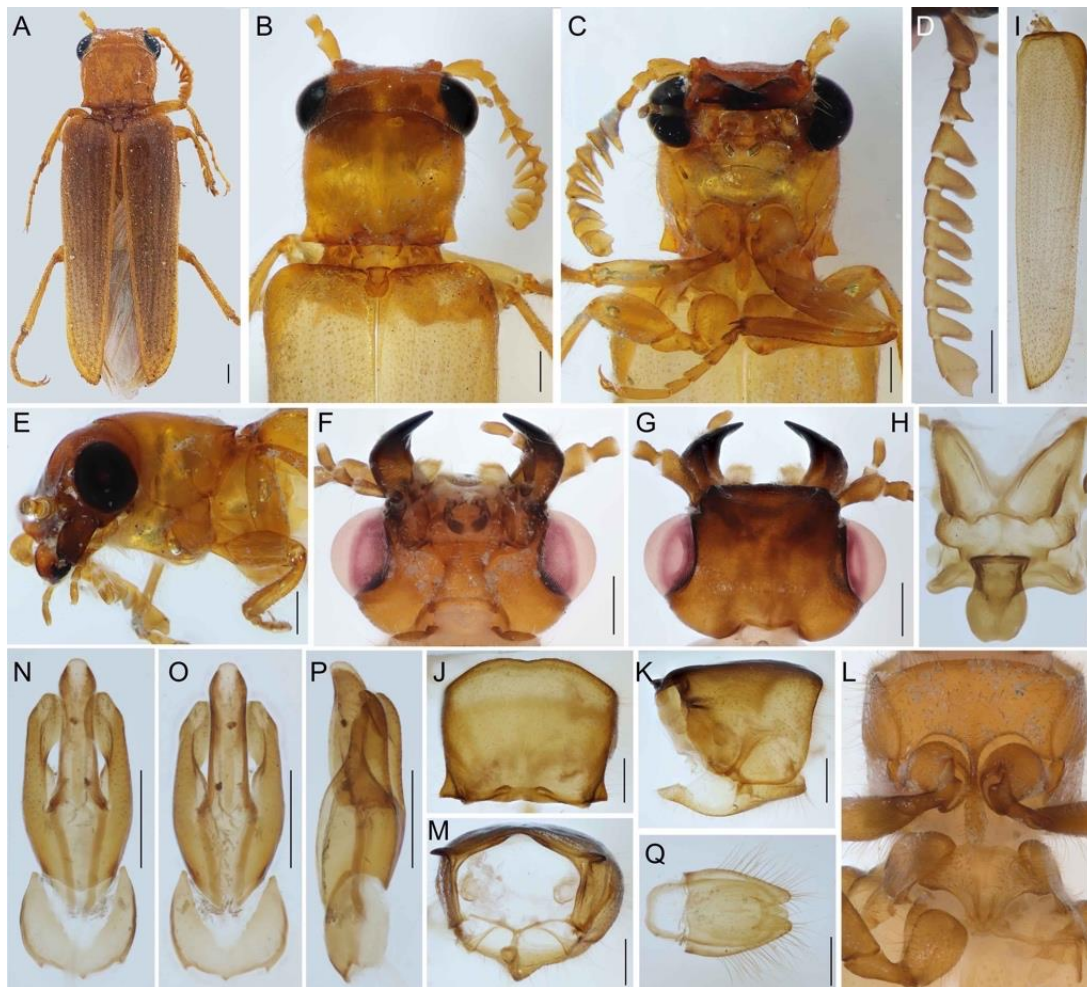
Table 2. Results of the alternative tree topologies likelihood testing. Aa: *Analestesa arabica*; Ce: *Cebrio* sp.; Cr: *Cebriorhipis* sp.; Ps: *Paulusiella serraticornis*; deltaL: logL difference from the maximal logL in the set; bp-RELL: bootstrap proportion using REll method; p-KH: p-value of one-sided Kishino–Hasegawa); p-SH: p-value of Shimodaira–Hasegawa test; p-WKH: p-value of weighted KH test; p-WSH: p-value of weighted SH test; c-ELW: Expected Likelihood Weight; p-AU: p-value of approximately unbiased (AU) test. Bold text represents the accepted test.

Topology	logL	deltaL	bp-RELL	p-KH	p-SH	p-WKH	p-WSH	c-ELW	p-AU
ML	-79060.25	0.00	0.823	0.826	1.000	0.826	0.994	0.819	0.820
PB	-79069.89	9.64	0.177	0.174	0.570	0.174	0.370	0.181	0.181
(Aa(Ce,Cr))	-79486.96	426.70	0.000	0.000	0.000	0.000	0.000	0.000	0.000
(Ps(Ce,Cr))	-79109.91	49.66	0.000	0.000	0.098	0.000	0.000	0.000	0.000
(Ps(Aa(Ce,Cr)))	-79532.71	472.46	0.000	0.000	0.000	0.000	0.000	0.000	0.000

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Head slightly declined, transverse, with small antennal sockets, including eyes greater than prothoracic width, gradually narrowed posteriorly. Frons and vertex flat, with lateral carinae behind antennal pits, without ocelli (Figs. 2F, G). Eyes protuberant, rounded, finely faceted. Antennal insertions widely separated, covered by protuberant edge from above (Fig. 2B). Anterior edge of clypeus straight (Fig. 2C), gular sutures narrowly separated, and cervical sclerites well-sclerotized (Fig. 2F). Antennae reaching elytral humeri, antennomere 1 robust, long, antennomere 2 small, but longer than width, antennomeres 4-10 flabellate, terminal antennomere flat (Fig. 2D). Labrum concealed beneath clypeus; mandibles robust, curved, with dorso- and ventrolateral edges (Fig. 2E). Mandibular apex unidentate, incisor edge simple, without mola (Figs. 2F, G), maxilla with setose mala; maxillary palpi slender, 4-segmented, apical palpomere cylindrical; labium tiny, labial palpi 3-segmented, cylindrical (Fig. 2F).

Prothorax transverse (Fig. 2B), pronotum without carinae, maximum width 1.23 times length, widest in anterior third, only slightly narrower at base, sides sinuate (Figs. 2B, J). Prothorax basally narrower than elytral bases; lateral pronotal carina visible posteriorly. Posterior angles of pronotum strongly acute (Fig. 2K). Posterior edge of pronotum sinuate. Prosternum about as long as prosternal process, process long slender, edge curved in lateral view (Figs. 2C, K); apex of prosternal process does not reach mesosternal pit (Fig. 2L); promesothoracic clicking mechanism non-functional; procoxal cavities open, narrowly separated (Fig. 2C). Elytra cover whole abdomen, tapering to apex, widest at humeri, without apparent costae or rows of punctures (Fig. 2I). Elytra free apically (Fig. 2A), Elytral pleuron very short. Scutellum well developed; abruptly elevated; anteriorly straight, posteriorly broadly rounded and surpassing elytral surface, anterior edge of mesoventrite rounded (Fig. 2H), meso- and meta coxal cavities narrowly separated. Metasternum long, discrimen complete, posterior transverse suture apparent, posterior margin deeply emarginate between coxae. Hind wing present.



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243 **Fig. 2.** *Paulusiella serraticornis* from Iran. A – general appearance, dorsal view; B, C – frontal part
244 of the body, dorsally and ventrally; D – antenna; E – head and pronotum in lateral view; F, G – head,
245 ventral and dorsal view; H – mesonotum; I – elytron; J–L –pronotum, dorsally, laterally, posterior
246 view, M prosternal process, and mesosternal pit; N–P male genitalia, ventrally, dorsally, laterally;
247 Q – terminal abdominal segments. Scales 0.5 mm.

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249 Legs slightly compressed, with long, gradually widened trochanters, femoral attachments
250 oblique; femora twice wider than tibiae (Fig. 2C), tibiae with simple outer edge and two long apical
251 spines; tarsomeres slender, five segmented, without ventral pads, claws paired, long, slender, and
252 simple.

253 Abdomen with six visible abdominal ventrites, ventrite 1 divided by metacoxae, ventrite 2
254 without process; penultimate tergite deeply emarginate, ultimate tergite very small, narrow (Fig. 2Q).
255 Male genitalia trilobate; symmetrical. Phallus stout, short, basally merged with parameres (Figs. 2N–
256 P).

257 Females of all species unknown.

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259 Biology, distribution and species diversity

260 All species have been reported from semidesert ecosystems of southwestern Asia, and the highest
261 diversity is known from Iran. Males are commonly collected at the light. The biology is unknown, and
262 the larvae and females are presumably endogenous. The mite species *Trochometridium kermanicum*
263 Mortazavi & Hajiqanbar, 2011 was found on *Paulusiella* sp. in Iran (Mortazavi et al. 2011).

264 The genus contains six species: *P. serraticornis* (Paulus, 1972) (Iran); *P. richteri* (Mandl,
265 1974) (Iran); *P. fossulatipennis* (Mandl, 1974) (Pakistan); *P. pallida* (Mandl, 1974) (Iran); *P.*
266 *holzschuhi* (Mandl, 1979) (Iran); *P. sweihana* (Geisthardt, 2009) (United Arab Emirates).

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268 ***Analestesa arabica* (Paulus, 1981)**

269 *Cebriognathus arabicus* Paulus, 1981: 261.

270 (Figs. 3A–P)

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272 Redescription

273 Male. Body 6 mm long, slender, slightly flattened, light brown colored, vestiture dense and short (Fig.
274 3A).

275 Head prognathous, slightly transverse, including eyes equals prothoracic width. gradually
276 narrowed posteriorly; dorsally flat, without ocelli (Figs. 3B–D). Eyes slightly protuberant, rounded,
277 finely faceted. Antennal insertions widely separated, covered by protuberant edge from above (Figs.
278 3B, C, E); clypeus concave (Fig. 3C), gular sutures narrowly separated, and cervical sclerites
279 sclerotized (Fig. 3D). Antennae reaching mid of elytra, antennomere 1 robust, long, antennomere 2
280 small, antennomeres 4–11 filiform, terminal antennomere shorter than preceding one (Fig. 3I).

281 Labrum concealed beneath clypeus; mandibles robust, abruptly curved (Fig. 3E). Mandibular apex
282 and incisor edge simple, maxilla with setose mala; maxillary palpi slender, 4-segmented, apical
283 palpomere parallel-sided; labium tiny, labial palpi 3-segmented (Fig. 3D).

284 Prothorax transverse, pronotum without carinae, maximum width 1.18 times length, widest in
285 middle, sides convex (Fig. 3B). Prothorax basally narrower than elytral bases; lateral pronotal edge
286 absent (Figs. 3F–H). Posterior angles of pronotum short, acute. Posterior edge of pronotum sinuate.
287 Prosternum slightly longer than prosternal process, process slender, edge curved in lateral view (Figs.
288 3F, G); procoxal cavities open, narrowly separated (Fig. 3D); promesothoracic clicking mechanism
289 non-functional. Elytra cover abdomen, tapering to apex, widest at humeri, with inconspicuous costae
290 (Fig. 3A). Elytra free apically, independently rounded. Scutellum well developed; widest anteriorly
291 (Fig. 3A) Hind wing well developed.

292 Legs slightly compressed, with long trochanters (Fig. 3D), tibiae with simple outer edge,
293 bearing setae, and two apical, long spines; tarsomeres slender, five segmented, without ventral pads,
294 claws paired, long, slender, and simple.

295 Abdomen with six free abdominal sternites, ventrite 1 entire, with inter-coxal process;
296 penultimate tergite simple, ultimate tergite large (Fig. 3P). Male genitalia trilobate; symmetrical.
297 Phallus slender, short (Figs. 3K, M).

298 Females of all species unknown, putatively incapable of flight.

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300 ***Cebrio igelmimen* Rattu et François, 2021**

301 (Fig. 4A)

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303 Remark

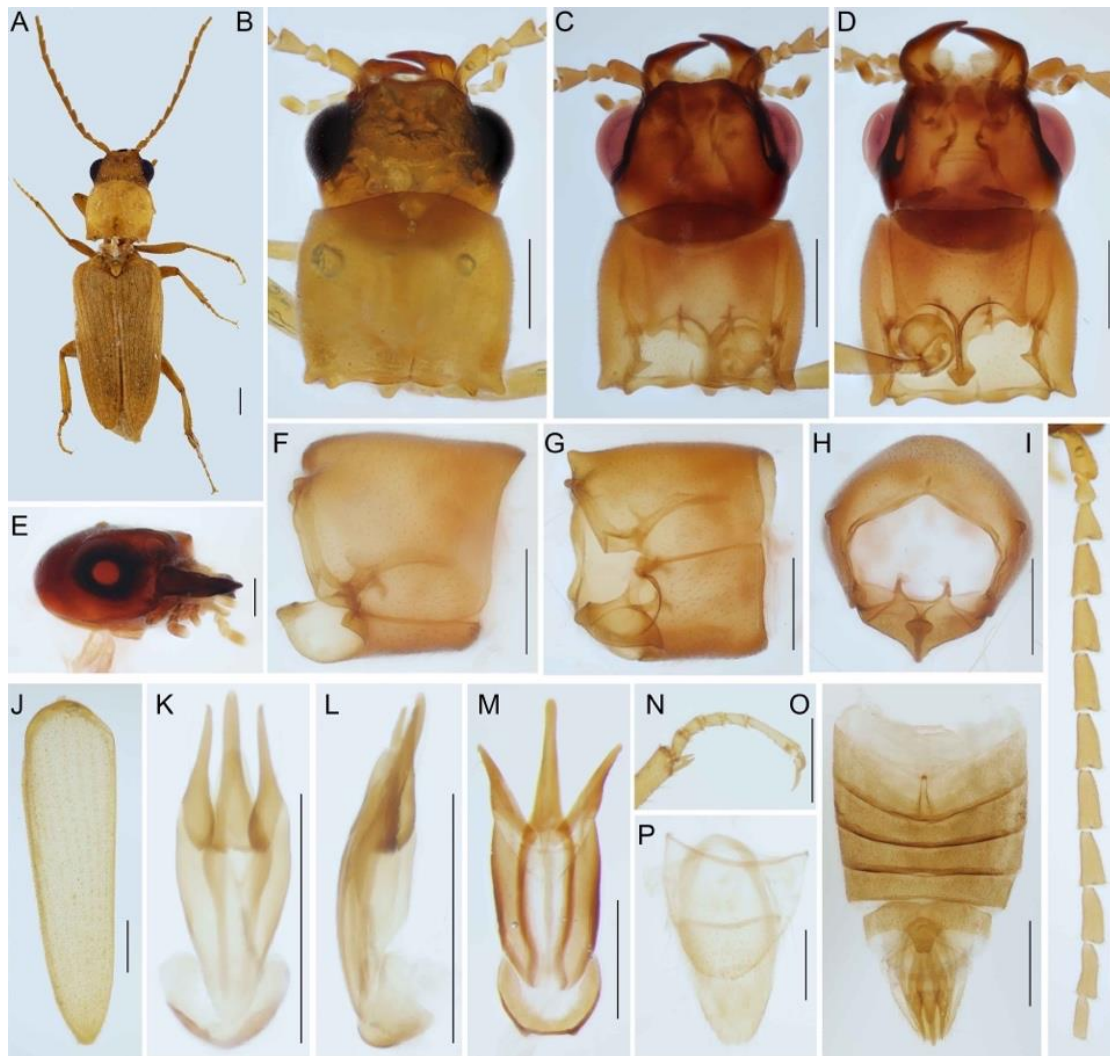
304 The *Cebrio* females are rare in collections. Recently, two females were described in detail by Rattu
305 (2016) and Rattu & François (2021). Fig. 4A shows the female *Cebrio igelmimen* (photo provided by
306 R. Rattu).

307 The *Cebrio* females differ from conspecific males in several traits: substantially larger body,
308 small eyes, short antennae, and legs, especially tarsi are substantially shorter than in

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314 **Fig. 3.** *Analestesa arabica* (Paulus, 1981) from Saudi Arabia (except for Fig. 3I). A – general
315 appearance, dorsal view; B–D – frontal part of the body, dorsally (B, C) and ventrally); E – head in
316 lateral view; F–H – pronotum, lateral, dorsolateral, and posterior view; I – antenna; J – elytron; K, M
317 – male genitalia, ventrally, dorsally, laterally; l – Male genitalia of *Dicronychus cinereus* (Herbst,
318 1784); N – hind tarsus and apical part of tibia; O – abdomen, ventral view; P – terminal abdominal
319 segments. Scales 0.5 mm.

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322 males (compare Figs. 4A and 4L), often shortened elytra, physogastrous abdomen, weak
323 sclerotization of the cuticle.

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325

326 *Cebriorhipis* sp.

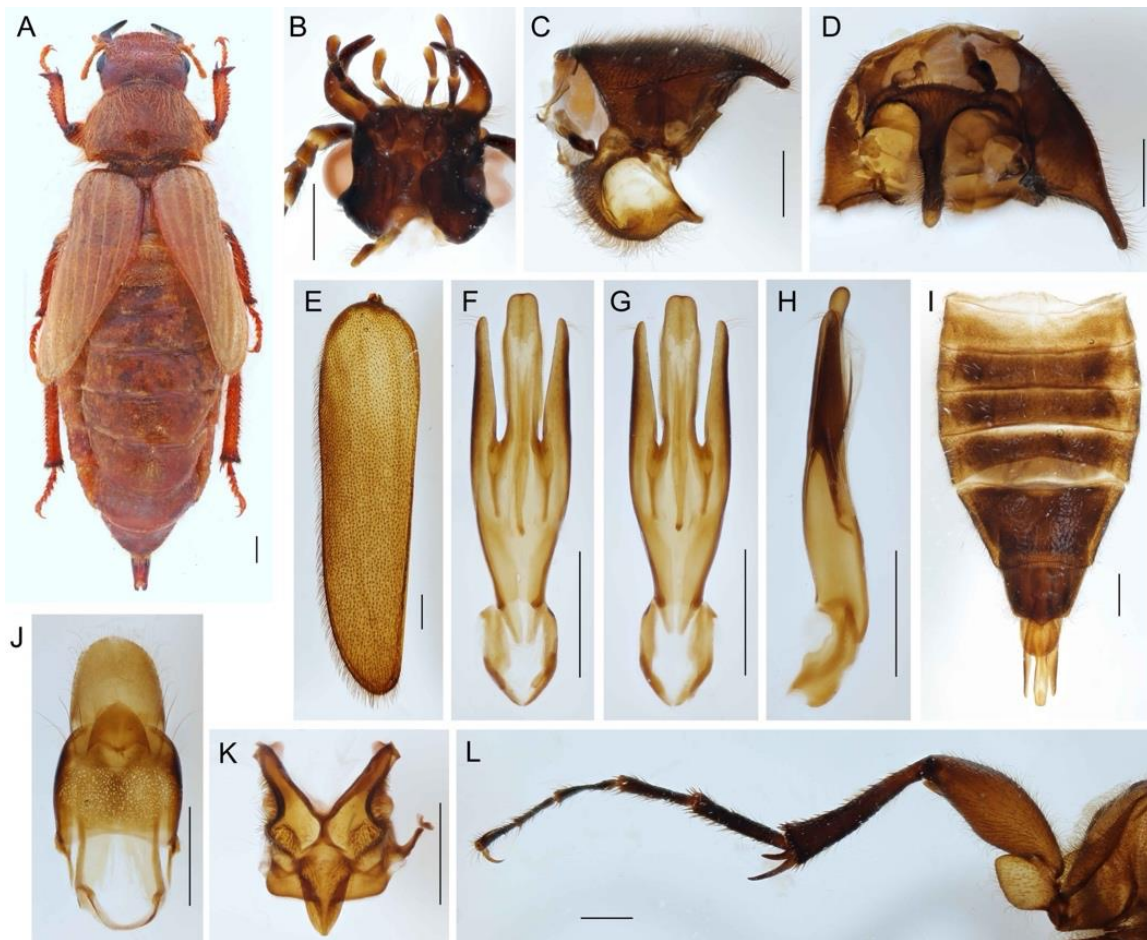
327 (Fig. 4B–M)

328

329 Description

330 Male. Body 12–14 mm long, robust, slightly flattened, brown colored, vestiture dense, long short
331 (Figs. 4B–E).

332



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334

335 **Fig. 4.** A – *Cebrio (Tibesia) igelmimen* Rattu et François, 2021 from Morocco, female, general
336 appearance. *Cebriorhipis* sp. from Bali. B – head, ventral view; C, D – pronotum, lateral and
337 ventral view; E – elytron; F–I male genitalia, ventral, dorsal and lateral view; J – abdomen, ventral view; K –
338 terminal abdominal segments; L – mesoscutellum; M – metathoracic leg. Scales 1.0 mm. Fig. 4A was
339 published by Rattu & François (2021) and is here reprinted with permission of the authors who retain
340 the copyright of this photo.

341

342 Head prognathous to slightly declined, transverse, including eyes narrower than prothoracic
343 width, gradually narrowed posteriorly (Fig. 4B). Eyes slightly protuberant, rounded, ocelli absent.
344 Antennal insertions widely separated, gular sutures narrowly separated, and cervical sclerites
345 sclerotized (Fig. 4B). Antennae slender, shortly flabellate, reaching almost mid of elytra, antennomere
346 1 robust, long, antennomeres 2 and 3 short, antennomeres 4–11 with short lamella, terminal
347 antennomere similar length as preceding one. Mandibles robust, abruptly curved (Fig. 4E).
348 Mandibular apex and incisor edge simple, maxilla with short setose mala; maxillary palpi slender, 4-
349 segmented, apical palpomere parallel-sided; labium tiny, labial palpi 3-segmented (Fig. 4B).

350 Prothorax transverse, pronotum without carinae, maximum width 1.5 times length, widest at
351 posterior angles, sides convex (Figs. 4C, D). Prothorax basally narrower than elytral bases; lateral
352 pronotal edge conspicuous in whole length (Fig. 4C). Posterior angles of pronotum ling, acute.
353 Prosternal process four times longer than prosternum (Fig. 5D); procoxal cavities open, narrowly
354 separated; promesothoracic clicking mechanism non-functional (Fig. 4D). Elytra cover abdomen,
355 tapering to apex, widest at humeri, with inconspicuous costae (Fig. 4E). Elytral suture almost
356 complete. Scutellum well developed; pointed posteriorly (Fig. 4K) Hind wings well developed.

357 Legs slightly compressed, with tarsi longer than femora and tibiae; slender pro- and
358 mesotrochanters and widened metathoracic trochanters (Fig. 4L), tibiae with simple outer edge
359 bearing setae, and two apical, long spines; tarsomeres slender, five segmented, without ventral pads,
360 claws paired, long, slender, and simple (Fig. 4L).

361 Abdomen with seven free abdominal sternites, ventrite 1 entire, without inter-coxal process;
362 penultimate tergite simple (Fig. 4J). Male genitalia trilobate; symmetrical. Phallus robust, basally
363 fused with parameres (Figs. 4F–H). Females of *Cebriorhipis* unknown.

364

365

366 **Taxonomy**

367 **Paulusiellinae Kusy, Motyka & Bocak, new subfamily**

368

369 Type genus

370 *Paulusiella* Löbl, 2007 (monotypic).

371 =*Paulusiella* Mandl, 1974 (invalid name).

372

373 Diagnosis

374 The erection of the new subfamily is based on molecular relationships that recovered *Paulusiella* as a
375 sister to *Hemiops* Laporte, 1838 (Elateridae: Hemiopinae; Fig. 1). The subfamily is monogeneric, and
376 the description of *Paulusiella serraticornis* is given above. The morphology is illustrated in Fig. 2 and
377 summarized in Tab. 3.

378

379 Justification of the erection of the subfamily Paulusiellinae

380 The morphology does not provide sufficient guidance for the placement of the genus in a natural
381 classification. The absence of apparent diagnostic characters is documented by the initial invalid
382 description of *Paulusiella* in Dascilloidea (Mandl 1974, 1979), the inclusion of an originally karumid
383 species in the genus (*Escalerina serraticornis* Paulus, 1972; Dascilloidea: Dascillidae), and the recent
384 description of a *Paulusiella* species in *Selasia* (*Selasia sweithana* Geisthardt, 2009; Elateridae:
385 Agrypninae: Drilini; Geisthardt 2009; Ivie & Branham 2011). The type-genus *Paulusiella* was validly
386 erected in Cebriioninae (now Elaterinae: Cebriionini) by Löbl (2007) and later transferred to Elateridae
387 *incertae sedis* (Ivie & Barclay 2011).

388 Here, *Paulusiella* was recovered with robust support as a sister to *Hemiops* Laporte, 1838 by
389 all analyses (Fig. 1A, B, 5A–P, Supp. Figs. S2–S11). Hemiopinae is a small elaterid subfamily with
390 only four genera – *Hemiops* Laporte, 1838 (Figs. 5A–P; East and Southeast Asia), *Legna* Walker,
391 1858 (Sri Lanka), *Parhemiops* Candèze, 1878 (Nepal) and morphologically somewhat distant
392 *Exoeolus* Broun, 1893 (New Zealand) (Douglas 2011). Comparing *Paulusiella* and *Hemiops*, we can
393 see similar abruptly elevated scutellum that is anteriorly straight in *Paulusiella* but bilobate in
394 *Hemiops* (Figs. 2H, 5M) and similar morphology of trochanters (Figs. 2D, 5B, K; Paulus 1972, Fig.
395 3). In both taxa, the scutellum posteriorly surpasses the elytral surface, but projected posterior part of
396 the scutellum is commonly encountered in elateroids. The antennae are different, but the relative
397 length of the three basal antennomeres is similar (Figs. 2D, 5D). There are several structures that are
398 present in *Hemiops* and absent in *Paulusiella*: the sharp lateral prothoracic edge (Figs. 2K, 5F),
399 apparent elytral longitudinal costae (Figs. 2I, 5A), the complex posterior shape of the prothorax (Figs.
400 2J, M, 5N, O). The taxa also differ in the relative length of the prosternal process, prosternum, shape
401 of elytra, abdominal terminal segments, and the shape of phallus (Figs. 2A–Q; 5A–P).

402 We prefer to assign the subfamily rank to the *Paulusiella*-based taxon as we cannot propose
403 any reliable diagnostic character that would morphologically define the clade of all hemiopine genera
404 and *Paulusiella*.

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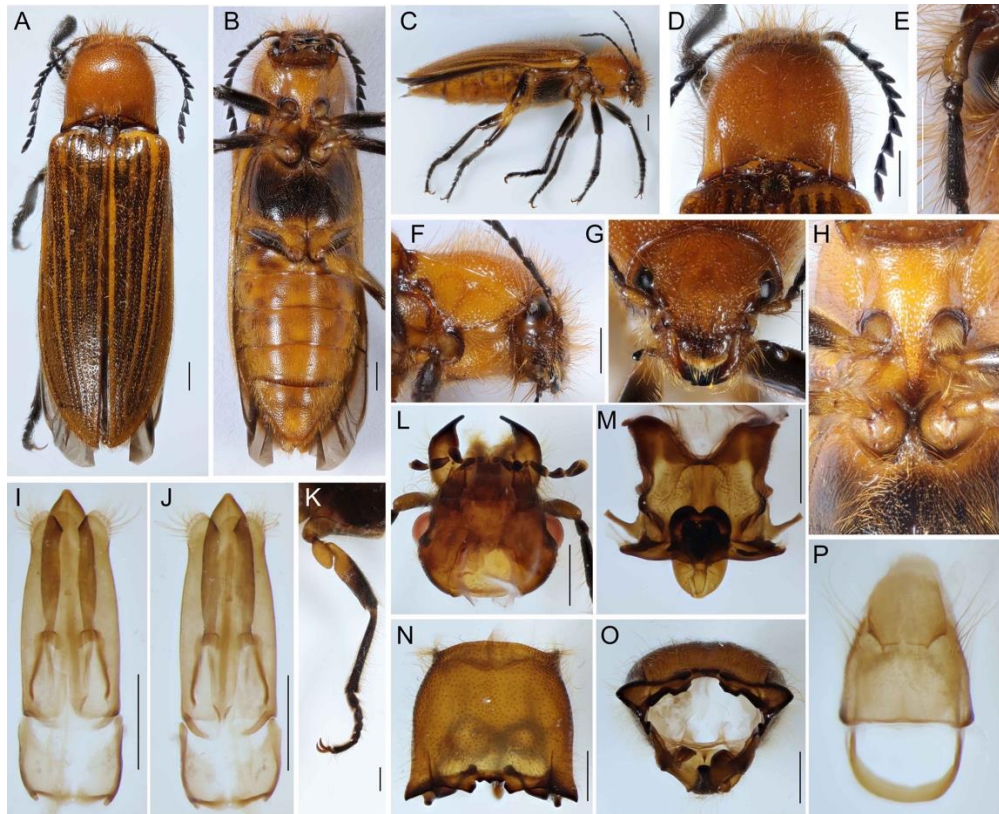
Tab. 3. The overview of elaterid morphological characters in the lineages with modified or unknown females and clicking *Hemiopus* sp.

Character Taxon	Male							Female
	anten- nae	apical antenna- meres	prosternum/ prosternal process	lateral pronotal edge	elytral rows or costae / suture; shape	abdominal segments	mesocox. process (ventr. 1)	Differences when compared with conspecific male
<i>Hemiopus</i> (Hemiopinae)	short	10<11	long / long, clicking	present	present / full; widest in middle	connate	present	fully sclerotized, flying, similar male
<i>Cebrio</i> (Elaterinae)	short	10<11	short / long, non-clicking	present	absent / divergent, widest basally	free	absent	some females with short elytra and wingless; physogastric abdomen, short antennae, and legs (Fig. 4A).
<i>Paulusiella</i> (Paulusiellinae)	short	10<11	short / short, non-clicking	vestige posteriorly	absent / divergent, widest basally	free	absent	unknown
<i>Analestesa</i> (Cardiophorinae)	long	10>11	long / short, non-clicking	absent	absent / absent; widest basally	free	present	unknown
<i>Plastocerus</i> (Dendrometrinae)	long	10<11	long / short, non-clicking	present	present / full; parallel-sided	free	short	obtuse posterior pronotal angles, shorter antennae than male
<i>Drilus</i> (Agrypninae)	short	10<11	short / short, non-clicking	present	absent / full suture; widest posteriorly	free	absent	head and appendages adult-like, rest of body larviform
<i>Omalisus</i> (Omalisinae)	long	10<11	short / short, non-clicking	present	present; full suture, parallel-sided	free	absent	pupa-like: short legs and antennae, vestigial elytra, similar length of meso- and metathorax

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433 **Fig. 5.** *Hemiopus* sp. from Laos. A–C general appearance, dorsal, ventral, and lateral aspects; D –
434 pronotum; E – basal antennomeres; F – pronotum and head, ventrolateral view; G – head, dorsally; H
435 – prosternal process and mesosternal pit; I, J – male genitalia; K – metathoracic leg; L – head
436 ventrally; M – mesonotum; N, O ° pronotum, dorsal, and posterior view; P – terminal abdominal
437 segments. Scales 1.0 mm.

438

439 **Subfamily Cardiophorinae Candèze, 1859**

440 *Cardiophorites* Candèze, 1859: 4.

441 *Cardiophori*: LeConte 1861: 166.

442 *Cardiophorinae*: Burakowski et al. 1985: 227.

443

444 Type genus

445 *Cardiophorus* Eschscholtz, 1829.

446

447 =*Aphrici* LeConte, 1861: 173.

448 Type genus: *Aphricus* LeConte, 1853.

449 =*Aptopina* Jakobson, 1913: 760.

450 Type genus: *Aptopus* Eschscholtz, 1829.

451 =*Esthesopinae* Fleutiaux, 1919: 76.

452 Type genus: *Esthesopus* Eschscholtz, 1829.

453 =*Nyctorini* Semenov-Tian-Shanskij et Pjatakova, 1936: 102.

454 Type genus: *Nyctor* Semenov-Tian-Shanskij et Pjatakova, 1936 [= *Cardiophorus* Eschscholtz,
455 1829 *sensu* Cate (2007) but not Douglas (2017)].

456 =*Cebriognathinae* Paulus, 1981: 264 (recently *Elaterinae*: *Cebrionini* or as a synonym of

457 *Cebrioninae*), **a new synonym of Cardiophorinae.**

458 Type genus: *Cebriognathus* Chobaut, 1899 (= *Analestesa* Leach, 1824).

459

460 Remark

461 The molecular analysis robustly recovered *Analestesa arabica* in close relationships with *Globothorax*
462 Fleutiaux, 1891 (= *Teslasena* Fleutiaux, 1892), *Cardiophorus* Eschscholtz, 1829, and *Dicronychus*
463 Brullé, 1832 (Figs. 1A, B, Supp. Figs. S2–S11). The position is also supported by the structure of
464 male genitalia (Figs. 3K–M). Although Paulus (1981) erected Cebriognathinae within that time
465 accepted Cebriionidae, he mentioned the here confirmed similarity of the male genitalia of
466 *Cebriognathus* and Cardiophorinae and discussed the possibility that *Cebriognathus* is a modified
467 click beetle. Bouchard et al. (2011) listed Cebriognathinae as a synonym of Cebriioninae, and the
468 GBIF database (<https://www.gbif.org/species/4428817> accessed on Nov. 7, 2022) lists *Analestesa* as a
469 junior synonym of *Cebrio*. Still, *Analestesa* is a valid name and must be considered one of the
470 Cardiophorinae genera.

471 *Analestesa* is much less sclerotized than most cardiophorine click beetles and has no clicking
472 mechanism (Figs. 3A, D). It differs from most Cardiophorinae in a quadrate mesoscutellar shield and
473 the small and short prosternal process that does not reach the mesothoracic pit. The only
474 cardiophorine species with weakly sclerotized cuticle has been *Nyctor expallidus* Semenov-Tian-
475 Shanskij et Pjatakova, 1936 (= *Cardiophorus expallidus*, *sensu* Cate 2007). The males have possibly
476 slender antennae, and the females shortened, robust antennae. Although Douglas (2017) described
477 both illustrated specimens as males, the intraspecific variability in the morphology of antennae is
478 improbable (Douglas 2017; Figs. 60, 61).

479 There are several characters defining Cardiophorinae + Negastrinae and the monophyly of
480 Cardiophorinae (Douglas 2017) that could be sought in *Analestesa*: the shape of the parameres (Figs.
481 3K–M) and the straight lateral edge of the prosternum. Another diagnostic character was defined in
482 female genitalia, but females are unknown for *Analestesa*. The modified external morphology does
483 not provide evidence for the placement of *Analestesa* in Cardiophorinae, and only the similar male
484 genitalia support the recovered DNA-based topology. The recovered relationships
485 (*Globothorax*(*Analestesa*(*Cardiophorus*, *Dicronychus*)) suggest that the earlier proposed morphology-
486 based topology (*Dicronychus*(*Cardiophorus*, *Globothorax*)) might need further investigation (Douglas
487 2017).

488

489

490 **Subfamily Elaterinae Leach, 1815**

491 Elaterides Leach, 1815: 85.

492 Type genus: *Elater* Linnaeus, 1758.

493 **Cebriionini Latreille, 1802**

494 Cebriionates Latreille, 1802: 97.

495 Type genus: *Cebrio* Olivier, 1790.

496

497 Remark

498 Females of *Cebrio* have variably developed elytra and large bodies. The known females are flightless
499 (Fig. 5A; Rattu 2016, Rattu & François, 2021, Martinez-Luque et al. 2022). The females differ from
500 conspecific males in smaller eyes and a different shape of the cranium, shorter appendages: very short
501 antennae, with low differentiation between the antennomeres, short legs, with longer femora and
502 tibiae than tarsi, shortened elytra, and vestigial wings. *Cebrio gigas* (F., 1787) has a physogastric
503 female but the elytra that form complete elytral suture, although they do not completely cover the
504 abdomen
505 (https://inpn.mnhn.fr/espece/cd_nom/240515 – accessed on 3 Nov 2022).

506

507 Revised composition of Cebrionini

508 Cebrionina Latreille, 1802: *Cebrion* Olivier, 1790; *Cebriorhipis* Chevrolat, 1875, *Musopsis* Chevrolat,

509 1875, *Scaptolenus* LeConte, 1853; *Selonodon* Latreille, 1834; *Stenocebrion* Solervicens, 1988.

510 Aplastina Stibick, 1979: *Aplastus* LeConte, 1859; *Euthysanius* LeConte, 1853; *Octinodes* Candèze,

511 1863 (= *Plastocerus* LeConte, 1853); *Cylindroderus* Latreille, 1834 (= *Cylindroderoides* Schwarz,

512 1907); *Dodecacius* Schwarz, 1902 (Arnett 1949, Johnson 2002, Sánchez-Ruiz & Löbl 2007, Johnson

513 & Chaboo 2015).

514 Stibick (1979) listed Pleonomini Semenov et Pjatakova, 1936 as a coordinate taxon of

515 Aplastini in Aplastinae. The group was listed as Pleonominae by Cate (2007) and as the tribe

516 Pleonomini in Dendrometrinae by Bouchard et al. (2011). *Pleonomus* Ménétrés, 1849 has both sexes

517 with fully developed elytra but apparent sexual dimorphism (Reitter 1900) resembling the

518 modifications observed in other soft-bodied elaterids.

519

520

521 Discussion

522

523 Origins of soft-bodied forms

524 Some fifteen years ago, the Elateridae was a morphologically homogenous beetle family with few

525 slightly modified, weakly sclerotized taxa concentrated in Cebrionini (Elaterinae; Sánchez-Ruiz &

526 Löbl 2007, Lawrence et al. 2011, Bouchard et al. 2011). Until now, cebrionids have served as a

527 collective taxon for at least partly soft-bodied, non-clicking elaterids with flightless or unknown

528 females (Arnett 1949, Johnson 2002, Rattu 2016, Rattu & François 2021, etc.). Since 2007, several

529 DNA-based studies have targeted soft-bodied elateroids. They have advocated that Drilidae,

530 Omalidae, and Plastoceridae (Cantharoidea are modified click beetles (Bocakova et al. 2007,

531 Kundrata & Bocak 2011, Bocak et al. 2018, Kusy et al. 2018). Additionally, the relationships between

532 widely defined Elateridae and lampyroid families were suggested by Kusy et al. (2021). Other studies

533 recovered a similar clade but rejected the monophyly of Elateridae (Zhang et al. 2018, McKenna et al.

534 2019, Douglas et al. 2021).

535 The earlier phylogenetic hypotheses had a clear evolutionary connotation: the shift leading to

536 flightless, soft-bodiedness, the retention of some larva- or pupa-like characters in adults, and even

537 larviform females of some taxa, was understood as a rare phenomenon. Therefore, almost all elateroid

538 lineages with weak sclerotization, including some taxa with neotenic females, shared a hypothesized

539 common ancestor (the Cantharoidea and cantharoid clade concepts; Crowson 1955, 1972, Branham &

540 Wenzel 2003, Lawrence et al. 2011). The rejection of the cantharoid clade (Bocakova et al. 2007,

541 Sagegami-Oba et al. 2007) and the robust placement of some ‘cantharoid’ groups in Elateridae (Kusy

542 et al. 2019) suggested a different view: the process of metamorphosis is less stable than previously

543 thought, and numerous elaterid groups independently lost the clicking mechanism, are soft-bodied

544 (i.e., cantharoid-like), their known females are physogastric, have short appendages, and short,

545 vestigial or absent elytra (Fig. 4A, Tab. 3).

546 Here, we studied the position of two taxa, *Paulusiella* and *Analestesa* (= *Cebriognathus* or

547 *Cebrion*), earlier placed in Elateridae *incertae sedis* or Elaterinae: Cebrionini (Sánchez-Ruiz & Löbl

548 2007, Ivie & Barclay 2011). Both genera are known only in males, and their females are putatively

549 flightless. These are small-bodied, non-clicking, weakly sclerotized beetles, with shortened and

550 posteriorly slender elytra, without a full-length elytral suture and coadaptation between the lateral

551 elytral margins of the abdomen (Figs. 2, 3). Due to these traits, they are superficially similar to some

552 Cebrionini, but the DNA analysis placed them in very distant positions (Figs. 1A, B, Supp. Figs. S2–

553 S11). *Paulusiella serraticornis* was recovered as a sister to Hemipopinae and *Analestesa arabica* as

554 one of the serial splits in Cardiophorinae. These positions are robustly supported by molecular data
555 (Tab. 2). Conversely, their relationships are hardly supported by morphology (see Results). Still, the
556 comparative morphology neither clearly supports their relationships to *Cebrio* (Figs. 2–4). Cebriionini,
557 i.e., *Cebrio*, *Cebriorhipis*, and *Scaptolenus*, contain medium-sized beetles with a characteristically
558 robust body, short prosternum, fully developed sharp lateral pronotal margin, and seven segments of
559 the abdomen (Fig. 5; Tab. 3). Small-bodied and weakly sclerotized Aplastini, i.e., *Aplastus*,
560 *Euthysanius*, and *Octinodes*, are more similar due to small and slender body. Still, all have elaterid-
561 like pronotum with acutely projected posterior angles. *Selonodon* is an elaterid-like cebriionid (Galley
562 1999), and *Stenocebrio* is similar in general appearance to *Paulusiella* or *Analestesa* (Solervicens
563 1988), but the genus was unavailable for the study.

564 Although the divergent morphology is sometimes referred to only as flightlessness and soft-
565 bodiedness, the morphological modifications affect almost all body parts, and similar modifications
566 are known in unrelated lineages (e.g., Paulus 1972, Johnston & Gimmel 2020, Tab. 3). Besides
567 shortened to vestigial elytra and wings, we often notice the shortened antennae and legs; the loss or
568 substantial simplification of complex structures, e.g., the pronotum (keels, lateral edge, shortened
569 prosternum, shortened prosternal process, the loss of acutely projected posterior angles, unfunctional
570 click mechanism), a lower ratio between the length of meta and mesothorax (the female of *Omalisus*;
571 Bocak & Brlik 2008), free abdominal segments, the loss of inter-coxal keel in visible abdominal
572 segment 1, loss of costae of rows of punctures in elytra (Figs. 2, 3, 4; Tab. 3).

573 The fully sclerotized elaterids have thick-walled thoracic segments, strong muscles, a
574 mesosternal pit, long prosternum, and the elytra are held closed by the mesoscutellar catch.
575 Additionally, the prothorax and mesothorax are coadapted, and pivots and flanges enable precisely
576 defined click action (Ewans 1972). This complex mechanism is lost in all soft-bodied groups. The
577 affected groups do not necessarily have all traits modified (e.g., compare the antennal length of
578 *Analestesa* and *Paulusiella*; Figs. 2D, 3I), but the presence of these characters is often recorded in the
579 males of elateroid taxa for which we have proved or hypothesized the modified, flightless females
580 (Crowson 1972, Cicero 1988, Bocakova et al. 2007, Bocek et al. 2018, Kundrata & Bocak 2019, Kusy
581 et al. 2019, Rosa et al. 2020).

582 The phylogenetic distribution of non-flying and soft-bodied groups is biased to Elateroidea or
583 Elateriformia, respectively (Gould 1977, McMahon & Hayward 2016). Within click beetles, modified
584 forms are known in Elaterinae: Cebriionini, Omalisinae, Dendrometrinae: Plastocerini, and
585 Agrypninae: Drilini (Bocakova et al. 2007, Kundrata & Bocak 2011, Bocak et al. 2018, Bocek et al.
586 2018, Kusy et al. 2019). The relationships of *Analestesa* and *Paulusiella* are hypothesized as further
587 two independent origins of these modifications: Paulusiellinae is a sister to Hemioptinae, and
588 *Analestesa* is one of the numerous genera of Cardiophorinae (Figs. 1A, B, Supp. Figs. S2–S11).
589 Similar phenotypes are known in the lampyroid families. Telegeusinae (Omethidae), which are
590 closely related to Armatopodidae, and Jurasaidae, related to Eucnemidae and Cerophytidae, are
591 further examples of the independent origin of soft-bodied forms (Bocakova et al. 2007, Bocak et al.
592 2014, Zhang et al. 2018, McKenna et al. 2019, Rosa et al. 2020). An additional case of lost
593 sclerotization was hypothesized in Ptilodactylidae, which now contains one morphologically modified
594 species, earlier the type of Podabrocephalidae (Kundrata et al. 2019). Analogical modifications were
595 also reported in one species of *Anorus* (Dascillidae; Johnston & Gimmel 2020) and other dascillids
596 (Karumiinae; Paulus 1972). We suppose, in agreement with earlier studies, that the morphological
597 modifications result from earlier termination of metamorphosis that strongly affects females but also
598 has some effect on males (Gould 1977, Bocak et al. 2008, McMahon & Hayward 2016, etc.).

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602 Modified morphology and systematics

603 The modification caused by incomplete metamorphosis (i.e., the retention of some larval
604 characters and the loss of some derived traits) leads to two kinds of taxonomic misplacements. These
605 beetles are often merged into a single clade as the modifications have a similar effect on unrelated
606 lineages. Then, the morphological analyses using the parsimony criterion prefer these shared
607 characters before fewer, if any, contradicting characters shared with close, yet unmodified, relatives.
608 In such a way, earlier authors defined taxa as Cantharoidea and the cantharoid clade (Crowson 1972,
609 Lawrence et al. 2011), the subfamily Cebrioninae or the tribe Cebrionini (Arnett 1949, Bouchard et al.
610 2011), the clade of neotenic lineages in net-winged beetles (Kazantsev, 2013), or suggested
611 *Podabrocephalus* Pic, 1913 (Byrrhoidea) as a sister of the cantharoid clade (Lawrence et al. 2011).
612 Additionally, some taxa were initially placed in distantly related but similarly modified groups. For
613 example, Paulus (1972) described *Paulusiella serraticornis* as *Escalerina serraticornis* in Dascillidae,
614 and Geisthardt (2009) described *P. sweihana* in *Selasia* (Agrypninae: Drilini; Ivie & Barclay 2011).

615 The unrealistically deep rooting of modified forms is a second kind of misplacement. The loss
616 of derived character states leads to the inference of a deeper position of incompletely metamorphosed
617 groups than those of their fully sclerotized relatives. Consequently, the inappropriately high rank is
618 given to modified lineages. This effect led to the earlier discussion on the ancient origin of neotenic
619 (Crowson 1972, Kazantsev 2005), the proposed sister-relationships of *Selonodon* Latreille
620 (Cebrionini) and other elaterids (Lawrence et al. 2011) or descriptions of elaterid subfamilies
621 Pleonominae (=Pleonomini, Dendrometrinae) and Nyctorini (=Cardiophorinae). The absence of
622 female characters in the analyzed matrices (unknown or sometimes completely larviform females)
623 lowers the number of informative characters coded for neotenic taxa. Then, missing data negatively
624 affect the stability of phylogenies.

625 The above-described pitfalls cannot be solved by any methodological modification of the
626 morphology-based phylogenetic analyses. The earlier analyses handled many taxa and characters and
627 were correctly conducted by experienced comparative morphologists (Branham & Wenzel 2003,
628 Lawrence et al. 2011). In these groups, we urgently need information unaffected by pedogenetic
629 syndrome. Now, we can access information-rich genetic data and reinvestigate the traditionally
630 accepted relationships. The growing evidence suggests common shifts from the clicking, well-
631 sclerotized elaterids to weakly sclerotized forms with highly modified females (Figs. 1A, B, Supp.
632 Figs. Figs. S2–S11). We can look for similar evolutionary pathways in other groups and test the new
633 hypotheses with even more extensive data in the future. The striking conflict between morphology-
634 and DNA-based relationships of extant lineages also calls for cautious analyses of soft-bodied forms
635 preserved in amber deposits, as their relationships cannot be validated with molecular data.

636

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641 photograph of a *Cebrio* female (Fig. 5A).

642

643 Authors' contribution and funding

644 Conceptualization, L.B., D.K., M.M.; molecular analyses, M.M., D.K.; writing, original draft
645 preparation, D.K. M.M., L.B.; comparative morphology, L.B.; reviewing and editing, all co-authors;
646 visualization, L.B., M.M.; funding acquisition, L.B., M.M., D.K. All authors have read and agreed to
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649

650 **Conflict of interest**

651 None declared.

652

653 **Data availability statement**

654 The analyzed sequences are available in the Mendeley depository. Kusy, Dominik; Motyka, Michal;
655 Bocak, Ladislav (2023), "Data for „Ontogenetic modifications produce similar phenotypes in distantly
656 related click beetles (Coleoptera: Elateridae),” DOI:10.17632/73dmw4czm3.1.

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