



**Mastigocoleidae fam. nov., a New Mesozoic Beetle Family  
and the Early Evolution of Dryopoidea (Coleoptera)**

Journal:	<i>Insect Systematics and Diversity</i>
Manuscript ID	ISD-2021-0061.R1
Manuscript Type:	Research
Date Submitted by the Author:	n/a
Complete List of Authors:	Tihelka, Erik; University of Bristol, School of Earth Sciences Jäch, Manfred ; Naturhistorisches Museum Wien, Entomology Kundrata, Robin; Palacký University, Department of Zoology, Faculty of Science Li, Yan-Da; Nanjing Institute of Geology and Palaeontology Chinese Academy of Sciences, State Key Laboratory of Palaeobiology and Stratigraphy Engel, Michael; University of Kansas Department of Ecology and Evolutionary Biology, Department of Ecology and Evolutionary Biology Lozano-Fernandez, Jesus; University of Barcelona, Department of Genetics, Microbiology and Statistics Huang, Di-Ying; Nanjing Institute of Geology and Palaeontology Chinese Academy of Sciences, State Key Laboratory of Palaeobiology and Stratigraphy Cai, Chenyang; Nanjing Institute of Geology and Palaeontology Chinese Academy of Sciences, State Key Laboratory of Palaeobiology and Stratigraphy
<b>Please choose a section from the list</b>:	Evolution
Organism Keywords:	Coleoptera
Field Keywords:	Evolution, Paleontology, Phylogeny

SCHOLARONE™  
Manuscripts

1 **Mastigocoleidae fam. nov., a New Mesozoic Beetle Family and the Early Evolution of**  
2 **Dryopoidea (Coleoptera)**

3  
4 Erik Tihelka<sup>1</sup>, Manfred Jäch<sup>2</sup>, Robin Kundrata<sup>3</sup>, Yan-Da Li<sup>4</sup>, Michael S. Engel<sup>5,6</sup>, Jesus Lozano-  
5 Fernandez<sup>7,8</sup>, Diying Huang<sup>4</sup> and Chenyang Cai<sup>1,4,10</sup>

6 <sup>1</sup>School of Earth Sciences, University of Bristol, Life Sciences Building, Tyndall Avenue, Bristol, BS8, United  
7 Kingdom, <sup>2</sup>Naturhistorisches Museum Wien, Burgring 7, A-1010 Wien, Austria, <sup>3</sup>Department of Zoology, Faculty of  
8 Science, Palacký University, 77900 Olomouc, Czech Republic, <sup>4</sup>State Key Laboratory of Palaeobiology and  
9 Stratigraphy, Nanjing Institute of Geology and Palaeontology, and Center for Excellence in Life and  
10 Paleoenvironment, Chinese Academy of Sciences, Nanjing 210008, China, <sup>5</sup>Division of Entomology, Natural  
11 History Museum, University of Kansas, Lawrence, KS 66045, U.S.A., <sup>6</sup>Department of Ecology & Evolutionary  
12 Biology, University of Kansas, Lawrence, KS 66045-4415, U.S.A., <sup>7</sup>Department of Genetics, Microbiology and  
13 Statistics, University of Barcelona, Barcelona, Spain, <sup>8</sup>School of Biological Sciences, University of Bristol, Life  
14 Sciences Building, Tyndall Avenue, Bristol BS8 1TQ, United Kingdom, and <sup>10</sup>Corresponding author, e-mail:  
15 cycai@nigpas.ac.cn

16  
17 **Abstract**

18 With some 3,700 described species, Dryopoidea are a moderately diverse superfamily of beetles whose  
19 position within basal Polyphaga has been historically difficult to elucidate. Members of most extant  
20 dryopoid families are set apart from the majority of other polyphagans by their association with aquatic  
21 habitats, but little is known about the origin of these derived life habits and the phylogeny of the  
22 superfamily. Here we describe Mastigocoleidae Tihelka & Cai **fam. nov.**, a new family of Mesozoic  
23 dryopoids represented by fossils from the Cretaceous Yixian Formation in northeastern China  
24 (undescribed species; ~125 Ma), Crato Formation in northeastern Brazil (*Mastigocoleus rhinoceros*  
25 Tihelka & Cai **gen. et sp. nov.**; ~113 Ma), and amber from northern Myanmar (*Mastigocoleus resinicola*  
26 Tihelka & Cai **gen. et sp. nov.** and *Cretaceocoleus saetosus* Tihelka, Kundrata & Cai **gen. et sp. nov.**;  
27 ~99 Ma). Integrating the findings of recent molecular and morphological phylogenetic analyses, we  
28 recover Mastigocoleidae as an early diverging dryopoid clade sister to the families Lutrochidae and  
29 Dryopidae, or less likely as a group of putative stem dryopoids. Mastigocoleidae are most distinctly  
30 separated from all other dryopoid families by their whip-like antennae, with 11 antennomeres, reaching to  
31 the pronotal base, and with the scape broadest and longest, a short pedicel, and antennomeres II–XI more  
32 or less distinctively gradually tapering towards the apex. Mastigocoleidae indicate that the last common  
33 ancestor of Dryopoidea was likely terrestrial in the adult stage, and document character acquisitions  
34 associated with a specialization for aquatic life.

35

36 **Key words:** Dryopoidea, Byrrhoidea, phylogeny, new family, aquatic adaptations, sexual dimorphism,  
37 fossil record

## 38 **Introduction**

39 As one of the basalmost lineages of the megadiverse beetle suborder Polyphaga, the superfamily  
40 Dryopoidea occupies an important position for understanding the early evolution of coleopteran  
41 biodiversity. Dryopoidea, as defined by Cai et al. (2021), contain 12 families with over 3,700 described  
42 species (Ślipiński et al. 2011). Aside from their species richness, dryopoid beetles exhibit an extraordinary  
43 morphological diversity. Some, such as Eulichadidae, have relatively large and colourful adults with  
44 ornamental elytra living on vegetation, while others, such as the aquatic Dryopidae, are usually small,  
45 unicoloured, with strongly reduced antennae and dense hydrofuge pubescence, at least on the ventral side  
46 of the body. Such morphological modifications are correlated with aquatic lifestyles. While some larvae  
47 and adults are truly aquatic, often remaining submerged for prolonged periods of time, others occur on  
48 plant debris accumulated along water courses, on river banks, vegetation near riparian habitats, and some  
49 are completely terrestrial (Emden 1942, Brown 1987, Costa et al. 1996, Jäch 1998).

50 On the whole, members of Dryopoidea are morphologically variable, such that finding larval and  
51 adult characters supporting the monophyly of the group has been difficult. Dryopoidea were defined by  
52 Crowson (1955, 1960, 1973, 1978, 1982) and Kasap & Crowson (1975), as including the families  
53 Chelonariidae, Dryopidae, Elmidae, Eulichadidae, Heteroceridae, Limnichidae, Lutrochidae, Psephenidae,  
54 and Ptilodactylidae. Lawrence and Newton (1982) transferred Callirhipidae to Dryopoidea, which were  
55 previously considered as part of Armatopodea or Rhipicerodea, and Lawrence (1988) further  
56 transferred the family Cneoglossidae from Cantharoidea and placed dryopoid beetles in a redefined  
57 broader concept of Byrrhoidea, which was adopted by subsequent authors (Lawrence and Newton 1995,  
58 Beutel 2016). The monophyly of the expanded Byrrhoidea proved difficult to verify with adult, larval, and  
59 combined morphological datasets (Beutel 1995, Lawrence et al. 1995, 2011, Costa et al. 1999). Early  
60 molecular studies based on a handful of genes have likewise yielded mixed results (Hunt et al. 2007,  
61 Bocak et al. 2014, McKenna et al. 2015, Kunderata et al. 2017). New phylogenomic studies have supported  
62 Byrrhidae as sister to Buprestidae (McKenna et al. 2019, Cai et al. 2021), thus rendering the old  
63 Byrrhoidea polyphyletic. Hence, in the updated classification of Coleoptera incorporating recent  
64 phylogenomic findings, Cai et al. (2021) re-established Dryopoidea to include the 12 dryopoid families  
65 without Byrrhidae, along with Protelmidae which were raised to family rank by Jäch *et al.* (2016).  
66 Podabrocephalidae, originally treated as a separate family (Pic 1930, Lawrence et al. 1999) and included  
67 in Byrrhoidea by Bouchard et al. (2011), was shown to be a lineage of Ptilodactylidae (Kunderata et al.  
68 2019). The adult and larval morphological characters defining the superfamily were discussed by Cai *et al.*  
69 (2021); on the molecular level the monophyly of Dryopoidea is supported by a unique rearrangement of  
70 tRNA gene order (Timmermans and Vogler 2012). However, the internal relationships among all the  
71 constituent dryopoid families have not yet been addressed with genome-scale datasets and await

72 resolution. In particular, the relationships of Eulichadidae and Callirhipidae remain to be resolved, as well  
73 as the position of Cneoglossidae, Protelmidae, and the apparent paraphyly of Ptilodactylidae and  
74 Limnichidae (McKenna et al. 2015, 2019, Kundrata et al. 2017, 2019, Cai et al. 2021). The family  
75 Protelmidae, while not included in a molecular phylogeny to date, appears to be closely related with  
76 Dryopidae and Lutrochidae, based on morphological characters.

77 The convoluted taxonomic history of Dryopoidea and uncertain phylogenetic relationships among  
78 its families are exacerbated by the sparsity of the group's fossil record. Molecular clock studies suggest a  
79 Triassic to Jurassic origin of crown Dryopoidea (McKenna et al. 2015, Toussaint et al. 2017, Zhang et al.  
80 2018, Cai et al. 2021). The enigmatic Jurassic and Cretaceous genera *Mesodascilla* Martynov, 1926 and  
81 *Mesaphus* Hong, 1983 have been tentatively affiliated with Eulichadidae (Kirejtshuk and Azar 2013),  
82 although relationships with Dascillidae and the extinct families Lasiosynidae and Triaplidae have been  
83 proposed as well (Martynov 1926, Crowson 1971, Hong 1983, Kirejtshuk et al. 2010). The earliest  
84 reliable dryopoid fossil is the chelonariid *Eochelonarium belle* Kirejtshuk, 2013 from Cretaceous  
85 Lebanese amber collected at the Kfar Selouane outcrop in central Lebanon (Kirejtshuk and Azar 2013),  
86 which has been conservatively dated to the Early Barremian (Maksoud et al. 2017, Maksoud and Azar  
87 2020). Other early fossil dryopoids include the only slightly younger heterocerid *Heterocerites magnus*  
88 Prokin & Ren, 2011 from the Barremian–Aptian Yixian Formation in China (Prokin and Ren 2011, Li et  
89 al. 2020), indicating that the superfamily had already diversified by the Early Cretaceous.

90 Studies of the fossil record of beetles can contribute important information about the timing of  
91 origin and extinction of lineages, tracing eco-morphological changes throughout the course of coleopteran  
92 evolution, and understanding changes in beetle diversity through geological time. Here we describe a new  
93 family of dryopoid beetles based on specimens from three exceptional Cretaceous fossil deposits: the  
94 Barremian–Aptian Cretaceous Yixian Formation in eastern China, the Aptian–Albian Crato Formation in  
95 northeastern Brazil, and Albian–Cenomanian amber from northern Myanmar. This diverse set of fossils in  
96 various modes of preservation enable us to formally address the placement of the new family in a total-  
97 evidence phylogenetic context. The new family shares most characters with the basal dryopoid families  
98 Lutrochidae and Dryopidae. This discovery adds to our knowledge of the early diversity of dryopoids and  
99 the evolution of aquatic habits in Dryopoidea.

100

## 101 **Methods**

### 102 ***Geological background***

103 The fossil material studied herein originates from three Cretaceous deposits with exceptional preservation  
104 (Konservat-Lagerstätten).

105 The Jehol Biota, preserved in the lacustrine sediments of the Yixian Formation at Huangbanjigou,  
106 Beipiao City, Liaoning Province and Liutiaogou, Ningcheng County, Inner Mongolia in China, is most  
107 famous for its exquisitely preserved feathered dinosaurs and Cretaceous mammals but also hundreds of  
108 well-preserved insects, including numerous beetles (Huang et al. 2012, Pan et al. 2013, Cai et al. 2014).  
109 The Yixian Formation is Early Cretaceous in age.  $^{40}\text{Ar}/^{39}\text{Ar}$  dating produced a mean age of  $124.6 \pm 0.1$  Ma  
110 for sanidine from tuff interbedded in the fossiliferous horizons of the lower Yixian Formation near  
111 Jianshangou village, and  $^{40}\text{Ar}/^{39}\text{Ar}$  single-grain total fusion analyses provided an age of  $124.6 \pm 0.25$  Ma  
112 for the same tuff from Sihetun village (Swisher et al. 1999), an age consistent with the fossil fauna (Zhou  
113 and Wang 2017). The single specimen from the Yixian Formation studied by us (QZYX0013) is deposited  
114 in the private collection of Mr. Zhe Qu, Harbin, China.

115 The Crato Formation, sometimes referred to as the Crato Member of the Santana Formation, is a  
116 limestone deposit outcropping near Nova Olinda in the Ceará Province in northeastern Brazil (Martill et  
117 al. 2007). The location and local geology of the deposit have been discussed by Barling *et al.* (2015),  
118 among others. The fossil-bearing unit has been dated to the Late Aptian or perhaps Early Albian on the  
119 basis of palynological evidence ( $\sim 112.6$  Ma; Pons *et al.*, 1990). The Crato palaeoenvironment has been  
120 reconstructed as a sheltered lake system (Heimhofer et al. 2010, Warren et al. 2016), and arthropods  
121 associated with lacustrine habitats are not uncommon in the deposit (e.g. Nel & Pella, 2020; Nel &  
122 Pouillon, 2020). The fossils are partly compressed, three dimensional mineralized replicas preserved in  
123 yellowish limestone. The original cuticle has been replaced by dark brown iron oxide, while internally  
124 bodies are composed largely of calcite and apatite (Dias and Carvalho 2020, Jouault et al. 2020). Two  
125 specimens from Crato were studied: AMNH SA43296, which was provided with a label stating, “?  
126 Dryopoidea”, by Roy. A. Crowson and subsequently illustrated in Grimaldi & Engel (2005, Fig. 10.35);  
127 and SMNS 66552, figured in Martill *et al.* (2007) and labelled as, “Archostemata, probably Cupedidae”.

128 Amber mines in the Hukawng Valley, Kachin State in northern Myanmar preserves one of the most  
129 diverse Cretaceous insect faunas in terms of its sheer abundance and diversity of preserved inclusions (Cai  
130 et al. 2019, Ross 2019, 2020). Radiometric dating of the amber-bearing horizon suggested  $\sim 99$  Ma as the  
131 minimum age of the deposit (Shi et al. 2012, Mao et al. 2018). Palaeontological evidence indicates that the  
132 amber is no older than the latest Albian (Yu et al. 2019). It is presumed that the fossilised resin was  
133 produced by dawn redwood trees of the genus *Metasequoia* standing near the sea (Smith and Ross 2016,  
134 Grimaldi and Ross 2017, Mao et al. 2018). At the time of secretion, the West Burma Block was an  
135 isolated tropical island in the Tethys Ocean (Westerweel et al. 2019). The West Burma Block is  
136 considered to have drifted from Australia between the late Triassic and Cretaceous, since a high share of  
137 the taxa preserved in amber from northern Myanmar biota is today endemic to Australasia and Southeast  
138 Asia (Gimmel et al. 2019, Poinar 2019, Liu et al. 2020). Myanmar amber inclusions examined by us

139 include specimens NIGP174708, NIGP174709, NM-T3501, and BUR0006. The amber pieces were  
140 purchased in late 2016 from a Myanmar amber dealer whose family has been working in the amber  
141 business for many years. The material was mined prior to the start of the armed conflict in the Hukawng  
142 Valley, and thus the material is open to legitimate study, with respect to the laws of Myanmar and China  
143 (Engel 2020). Myanmar amber inclusions examined by us include specimens NIGP174708, NIGP174709,  
144 NM-T3501, and BUR0006. Based on their field numbers, the specimens deposited in the NIGP were  
145 acquired in late 2016 from a local Myanmar amber dealer. The remaining specimens were purchased by a  
146 well-established amber collector in Myitkyina before 2016. As the material was mined prior to the start of  
147 the armed conflict in the Hukawng Valley, it is open to legitimate study (Engel 2020)..

148

### 149 ***Specimen preparation, photography and measurements***

150 The amber fossils were prepared by polishing with sandpaper and diatomite powder. Fossils were  
151 photographed using a Canon EOS 5D Mark III digital camera, equipped with a Canon MP-E 65 mm  
152 macro lens (F2.8, 1–5X), and with an attached Canon MT-24EX twin flash or a Canon EOS 7D camera  
153 with a MP-E 65 mm macro lens (F2.8, 1–5X) and a Canon MT-26EX-RT flash mounted on a WeMacro  
154 Auto-Rail. Fine morphological details were captured using an Axio Imager 2 microscope. To increase the  
155 depth of field, images taken at different distances from the specimen were stacked in Helicon Focus. The  
156 Yixian Formation specimen (QZYX0013) was wetted with ethanol to improve contrast and enable easier  
157 observation. Body length herein refers to the distance from clypeus to abdominal apex, while body width  
158 was measured at the broadest point across the elytra.

159 This published work has been registered in ZooBank (www.zoobank.org):

160 [http://zoobank.org/urn:lsid:zoobank.org:pub:\[to be added upon acceptance\]](http://zoobank.org/urn:lsid:zoobank.org:pub:[to be added upon acceptance])

161

### 162 ***Phylogenetic analyses***

163 To elucidate the systematic position of the new beetle family in a formal phylogenetic context, the type  
164 species, *Mastigocoleus resinicola* gen. et sp. nov., was scored for 41 out of the 112 available characters  
165 for all dryopoid families compiled by Lawrence (1988), of which 87 pertain to adult morphology and 25  
166 to larvae. When multiple possible character states were listed as available in the original matrix, we opted  
167 to use plesiomorphic states as defined by Lawrence (1988). The following two new character states were  
168 added to Lawrence's (1988) matrix: 7:3 (antennal sensory modification beginning on antennomere II);  
169 14:3 (apical maxillary palpomere cylindrical and diagonally truncate at apex). Taxon sampling was  
170 restricted to the 11 sampled dryopoid families *sensu* Cai *et al.* (2021). The family Byrrhidae was used as  
171 the outgroup, following the results of recent phylogenomic studies that indicate a sister relationship  
172 between Byrrhidae (sole member of Byrrhoidea) and Dryopoidea (McKenna *et al.* 2019, Cai *et al.* 2021).

173 The resultant character matrix in .tnt format is available in the Supplementary Information. Parsimony  
174 analyses were conducted in TNT v. 1.5 (Goloboff and Catalano 2016) using implied weights. The  
175 recommended concavity value ( $K$ ) of 12 was used, which has been shown to yield better topologies  
176 against homoplastic characters (Goloboff et al. 2018). Collapsing rules were set to ‘none’ and the analysis  
177 was run using default settings with the ‘New Technology Search’ algorithm. To assess tree support, a  
178 nonparametric bootstrap analysis was run with 1,000 replicates. Character states were mapped using  
179 ASADO v. 1.61 (Nixon 2004).

180 Recent molecular studies focused on Dryopoidea have provided new insights into the deep  
181 phylogeny of the superfamily, suggesting that morphological analyses may have been confounded by  
182 convergent evolution of adaptations for aquatic life and are not alone sufficient for resolving the early  
183 divergences (Kundrata et al. 2017, McKenna et al. 2019, Cai et al. 2021). To complement the results of  
184 our morphological analysis and to provide a robust resolution of intrafamilial relationships within  
185 Dryopoidea, we re-visited the four-gene dataset of Kundrata *et al.* (2017) sampling 10 out of the 12  
186 recognised families (i.e., without Cneoglossidae and Protelmidae). Since recent phylogenomic studies  
187 have redefined the limits of Dryopoidea and clarified its sister relationships, the decisive dataset of  
188 Kundrata *et al.* (2017) was re-analysed to reflect these findings. The taxon sampling was restricted to the  
189 10 ingroup dryopoid families, represented by 108 taxa, and seven representatives of Byrrhidae were used  
190 as outgroups. Topologies were reconstructed using the Bayesian site-heterogeneous infinite mixture model  
191 CAT-GTR+G4, which has been shown to suppress artefacts such as long-branch attraction (Lartillot et al.  
192 2007), implemented in PhyloBayes MPI 1.7 (Lartillot et al. 2013). Two independent Markov chain Monte  
193 Carlo (MCMC) chains were run until convergence ( $\text{maxdiff} < 0.3$ ).

194 To reconstruct the deep nodes among Dryopoidea we also considered the results of the recent  
195 phylogenomic studies of Zhang *et al.* (2018), McKenna *et al.* (2019), and Cai *et al.* (2021), which sampled  
196 nine dryopoid families represented by 68 single-copy nuclear protein coding genes (Cai *et al.* 2021) and  
197 89 genes (McKenna et al. 2019), respectively.

198

### 199 ***Collection abbreviations***

200 AMNH – American Museum of Natural History, New York, NY, USA

201 NIGP – Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, Jiangsu  
202 Province, China

203 NMPC, National Museum, Prague, Czechia

204 PCRK – private collection of Robin Kundrata, Olomouc, Czechia

205 SMNS – State Museum of Natural History Stuttgart, Stuttgart, Baden-Württemberg, Germany

206 QZYYX – private collection of Ze Qu, Harbin, Heilongjiang Province, China



207  
208 **Systematic Entomology**  
209 Order Coleoptera Linnaeus, 1758  
210 Superfamily Dryopoidea Billberg, 1820  
211 Family †Mastigocoleidae Tihelka & Cai **fam. nov.**  
212  
213 <http://zoobank.org/urn:lsid:zoobank.org:act:> [to be added after acceptance]  
214  
215 *Type genus. Mastigocoleus* Tihelka & Cai **gen. nov.**  
216  
217 *Diagnosis.* Apical maxillary palpomere not expanded apically and distinctly truncate. Compound eyes  
218 with interfacetal setae. Head not grooved beneath compound eyes for reception of antennae. Maxillary  
219 palpomere IV wide and diagonally truncate apically. Antenna with 11 articles, filiform, not pectinate or  
220 clubbed, with basal antennomere distinctively broadest of all articles, antennomere II shortest, attached  
221 subapically to preceding antennomere, antennomeres II–XI more or less distinctively gradually tapering  
222 apically. Hypomeron without posterior depression or grooves for reception of leg podites. Anterior edge  
223 of prosternum forming a chin-piece. Procoxae separated by more than 0.4× their width. Prosternal process  
224 less high apically and curving dorsally. Mesocoxae longitudinally oriented, separated by less than their  
225 width. Mesoventrite short, with median groove (as in Lutrochidae); mesoventrite-metaventrite suture  
226 distinct. Metacoxa subtriangularly transverse, sulcate posteriorly for reception of metafemur. Ventrites not  
227 connate; apical margins arcuate, sometimes weakly so.  
  
228 *Systematic placement.* The new family can be assigned to Dryopoidea by the possession of the following  
229 combination of characters: procoxae transverse; head with distinct labrum; antennae filiform; tarsomere V  
230 elongate, approximately as long as preceding four tarsomeres in metatarsi (Crowson 1955, Cai et al.  
231 2021).  
  
232 *Description.* Body elongate oval, moderately convex. Body length 4.59–9.77 mm, body width 2.65–3.77  
233 mm. Specimens not preserving their original colour, in various hues of dark brown to grey. Body surfaces  
234 finely punctate, with short moderately dense erect setae most prominent on frontal region, antennal base,  
235 legs, pronotum, and elytra, but more or less covering entire body.  
236       Head hypognathous, approximately subpentagonal in dorsal view, broadest at compound eyes,  
237 deeply retracted into prothorax. Labrum transverse, apical margin straight, lacking apical setal brush.  
238 Frontoclypeal sulcus absent. Frontoclypeal margin almost straight, representing less than eighth of head  
239 width across eyes, with a minute incision medially. Frontal region with or without a raised medial ridge.

240 Epicranium without prominent Y-shaped carina or ecdysial scar. Mandible robust, short and wide, apex  
241 with at least two teeth. Maxillary palpus tetramerous; palpomere II equally wide throughout, cylindrical;  
242 palpomere III subtriangular, expanding apically, about half as long as preceding palpomere; apical  
243 palpomere equally wide throughout, diagonally truncate at apex (Fig. 2C: mp4). Labial palpus trimerous,  
244 shorter than maxillary palpus; apical palpomere fusiform, subequal in length to palpomere II. Mentum flat,  
245 wide, possessing a medial pit, with anterior margin arcuate, lacking apical setae. Submentum short,  
246 transverse, with a medial incision in anterior margin. Compound eyes large and protuberant or small and  
247 slightly protuberant, subcircular to ellipsoidal in dorsal and lateral views, erect interfacetal setae present,  
248 distributed across eye. Ocelli absent. Antennal insertion exposed from above, narrowly separated by  
249 scarcely more than maximum width of basal antennomere. Subantennal grooves absent. Antenna with 11  
250 antennomeres, filiform, not pectinate or clubbed, reaching beyond elytral humeri (not reaching posterior of  
251 head in Lutrochidae), with short erect setae longest and densest at antennal base, scape without abundant  
252 elongate setae (such setae present in Lutrochidae). Basal antennomere (scape) distinctly broadest,  
253 expanding apically. Antennomere II (pedicel) shortest, attached subapically to scape. Antennomere III  
254 only slightly longer than preceding antennomere. Antennomeres II–XI more or less distinctly gradually  
255 tapering towards apex (more pronounced in *Mastigocoleus*, less so in *Cretaceocoleus*), giving antenna a  
256 whip-like shape. Temples absent. Vertex of head finely punctate, lacking long setae.

257 Pronotum broader than long, distinctly broader than head at eyes, as wide as elytral humeri  
258 posteriorly. Anterior margin of pronotum distinctly bisinuate, such that pronotum longest medially.  
259 Anterior angles strongly angulate, nearly orthogonal (*Cretaceocoleus*) to more acute (*Mastigocoleus*,  
260 undescribed Yixian specimen), distinctly produced anteriorly. Disc lacking a longitudinal medial line,  
261 slightly convex (*Mastigocoleus resinicola* and *Cretaceocoleus saetosus*), medially depressed (*M.*  
262 *rhinoceros*), or with a raised medial ridge (undescribed specimen from Yixian Formation). Lateral  
263 pronotal carinae complete. Posterior angles of pronotum indistinctly (*Mastigocoleus*) to strongly produced  
264 and angulate (*Cretaceocoleus*), orthogonal (*Mastigocoleus*) to acute (*Cretaceocoleus*). Posterior edge of  
265 pronotum distinctly bisinuate in dorsal view, more pronouncedly than anterior margin. Hypomeron  
266 without grooves for reception of femur. Scutellum broader than wide, widest medially, with anterior  
267 margin straight and posterior margin approximately semi-circular to slightly pointed apically.

268 Anterior edge of prosternum forming a broadly rounded and strongly projecting chin-piece.  
269 Prosternum in front of procoxae over 5× as long as procoxal length. Procoxae oval, slightly transverse,  
270 open posteriorly, separated by approximately distance equivalent to their width. Prosternal process of  
271 variable width, with lateral carinae or not, equally wide throughout, abruptly narrowing distally,  
272 lanceolate, with apex slightly curving towards thorax. Mesoventerite short, with a medial groove for  
273 reception of prosternal process. Mesocoxae suboval, longitudinal, subcontiguous to moderately separated.

274 Meso- and metaventral processes acute, not touching. Mesoventrite-metaventricle suture distinct.  
275 Metaventricle short, not much longer than maximum width of metacoxae. Metaventricle longer than  
276 mesoventrite, slightly shorter than prothorax. Metathoracic discrimen distinct, almost complete.  
277 Metakatepisternal suture well developed. Metepisternum relatively short and broad. Intercoxal process of  
278 ventrite I well developed, reaching to anterior third of coxae, pointed apically. Metacoxal cavities large,  
279 transverse, subcontiguous, partly separated by anterior ventral projection.

280       Legs long, metathoracic legs longer than elytra. Trochantins exposed. Metacoxa transverse,  
281 posteriorly sulcate for reception of metafemur. Trochanters large, femoral attachment oblique. Femora  
282 stout, excavate for reception of tibiae. Tibiae stout, tibial spurs straight. Tarsal formula 5-5-5, tarsi  
283 elongate or stout, with ventral rami on mesotarsus present or absent. Pretarsal claws well developed,  
284 simple; empodium apparently with two long setae.

285       Elytra elongate, completely covering abdomen, parallel-sided from posthumeral region to apical  
286 third. Anterior margin slightly crenulate. Lateral margin slightly explanate, densely setose. Elytral disc  
287 with nine striae, either punctate (*Cretaceocoleus*) or formed by shallowly impressed furrows  
288 (*Mastigocoleus*). Elytral apices acute, meeting at suture (but see note, below). Epipleura widest basally,  
289 abruptly narrowed in metaventral region, almost complete or nearly so.

290       Abdomen sparsely pubescent, with five ventrites; ventrites not connate. Acute anterior process of  
291 ventrite I reaching to apical third of mesocoxae. Margins of ventrites strongly (*Cretaceocoleus*) to weakly  
292 (*Mastigocoleus*) arcuate. Basal ventrite longest, ventrites II–IV generally shortening apically, ventrite V  
293 longer. Apical ventrite broadly rounded. Morphology of genitalia unknown.

294  
295 *Note.* The elytral suture appears to be deflected in the compression fossils from the Yixian and Crato  
296 Formations, while this is not the case for *M. resinicola* preserved in amber. This taphonomic artefact  
297 occurs frequently in compression fossils, where the apices of the elytra were pushed apart from each other  
298 during fossilisation. We thus regard it as taxonomically uninformative.

299

300

301 *Mastigocoleus* Tihelka & Cai **gen. nov.**

302 [http://zoobank.org/urn:lsid:zoobank.org:act: \[to be added after acceptance\]](http://zoobank.org/urn:lsid:zoobank.org:act:[to be added after acceptance])

303 Figs 1–4

304

305 *Type species.* *Mastigocoleus resinicola* Tihelka & Cai sp. nov.

306

307 *Included species.* *Mastigocoleus resinicola* and *M. rhinoceros*.

308

309 *Occurrence.* Aptian–Albian Crato Formation in Brazil (*M. rhinoceros*, represented by two specimens);  
310 and Albian–Cenomanian amber from northern Myanmar (*M. resinicola*, represented by two specimens).

311

312 *Diagnosis.* Antennomeres II–XI pronouncedly tapering apically. Mesotarsi without ventral rami. Anterior  
313 pronotal angles acute. Posterior angles of pronotum indistinctly produced and orthogonal. Procoxae  
314 separated by less than their width. Prosternal process thinner, not bordered laterally. Mesocoxae almost  
315 contiguous. Metatibia not distinctly expanded at apex. Tibial spurs elongate and stout, longer than  
316 metatarsomere I. Elytra with nine longitudinal striae. Margins of ventrites weakly arcuate.

317

318 *Etymology.* The name is a combination of the Ancient Greek nouns ‘*mástigos*’ (μάστιγος, feminine  
319 genitive singular of μάστιξ / mástix), meaning, ‘whip’, and ‘*koleós*’ (κολεός), meaning, ‘scabbard’ and  
320 from which the ordinal name Coleoptera is derived. Gender: masculine.

321

322

323 *Mastigocoleus resinicola* Tihelka & Cai **sp. nov.**

324 <http://zoobank.org/urn:lsid:zoobank.org:act:> [to be added after acceptance]

325 Figs 1–2

326

327 *Material.* Holotype, NIGP174708, sex unknown, a single well-preserved amber inclusion (NIGP).

328

329 *Type locality and horizon.* Amber mine in the Hukawng Valley, Myitkyina District, Kachin State,  
330 Myanmar; latest Albian to Albian/Cenomanian boundary (Lower–Upper Cretaceous boundary).

331

332 *Diagnosis.* As for genus together with: clypeus lacking a horn (although this may be a sexually dimorphic  
333 character); pronotal disc slightly convex; pronotum broadest medially.

334

335 *Description.* Body length 6.53 mm, body width 2.24 mm. Head 1.25 mm long, 1.4 × wider than long.  
336 Antennomere I broadening apically, 1.8 × wider than following antennomere; antennomere II attached  
337 subapically to antennomere I; antennomere III longer than preceding antennomere, 1.1 × longer;  
338 antennomeres V–XI gradually thinning and lengthening apically; antennomere XI pointed apically, 1.1 ×  
339 longer than preceding antennomere, maximum width at base representing less than 0.1 × maximum width  
340 of antennomere I. Ratio of antennomere lengths (in mm): 0.49 : 0.20 : 0.22 : 0.32 : 0.38 : 0.35 : 0.41 : 0.36  
341 : 0.38 : 0.31 : 0.41. Pronotum 1.38 mm long, 1.4 × wider than long, broadest medially. Anterior pronotal

342 angles acute. Pronotal disc slightly convex. Posterior angles of pronotum indistinctly produced,  
343 orthogonal, rounded apically. Procoxae separated by less than their width. Prosternal process thinner, not  
344 bordered laterally. Apex of prosternal process lanceolate, with apex thinner and slightly curving towards  
345 thorax. Medial mesoventral cavity deeply impressed, broadest in basal third, narrowing apically (Fig. 2F:  
346 mca). Mesocoxae almost contiguous. Elytra 3.90 mm long, 1.7× longer than their combined width. Elytrae  
347 with nine faint, complete striae. Hind wings present, apex of folded wings visible under elytra (Fig. 1A).  
348 Protibia slightly longer than profemur, mesotibia as long as mesofemur, metatibia slightly longer than  
349 metafemur. Metatibia not abruptly expanded at apex, with a wide groove (Fig. 2G: tb2). Metatibial spur  
350 reaching to middle of metatarsomere IV. Tarsomeres I–III short, wider than long; tarsomere IV slightly  
351 longer, longer than wide; tarsomere V as long as combined lengths of preceding tarsomeres. Pretarsal  
352 claws more or less straight; mesopretarsal claws as long as two thirds of mesotarsomere V, metapretarsal  
353 claws as long as combined lengths of metatarsomeres IV and V. Margins of ventrites weakly arcuate.  
354 Ratios of ventrite lengths: 0.71 : 0.59 : 0.41 : 0.40 : 0.56.

355  
356 *Etymology.* The specific epithet refers to the preservation of the species in fossil resin, combining the  
357 Latin noun *rēsīna*, meaning, ‘resin’, with the masculine suffix *-cola*, which denotes an ‘inhabitor’.

358  
359  
360 *Mastigocoleus rhinoceros* Tihelka & Cai **sp. nov.**

361 [http://zoobank.org/urn:lsid:zoobank.org:act: \[to be added after acceptance\]](http://zoobank.org/urn:lsid:zoobank.org:act:[to be added after acceptance])

362 Figs 3–4

363  
364 *Material.* Holotype, SMNS 66552, sex unknown, a single compression fossil preserving antennae and legs  
365 exposed in dorsal aspect (SMNS). Paratype, AMNH SA43296, sex unknown, a single compression fossil  
366 preserving body and basal two antennomeres (AMNH).

367  
368 *Type locality and horizon.* Chapada do Araripe, northeastern Brazil, Nova Olinda Member of the Crato  
369 Formation; Aptian–Albian (Lower Cretaceous) Crato Formation in Brazil.

370  
371 *Diagnosis.* As for genus together with: frontoclypeus with a medial horn-like process (although this may  
372 be a sexually dimorphic character); pronotal disc with a medial depression; pronotum broadest in posterior  
373 half.

374

375 *Description.* Body length 7.84–8.16 mm, body width 3.42–3.77 mm. Head 0.87–1.06 mm long, 1.8–2.1×  
376 wider than long, with uniform fine punctation. Frontoclypeus with a medial horn-like process.  
377 Antennomere I broadening apically, 1.7× wider than following antennomere; antennomere II attached  
378 subapically to antennomere I; antennomere III longer than preceding antennomere; antennomeres V–XI  
379 gradually thinning and lengthening apically, except slightly shorter antennomeres V and VIII;  
380 antennomere XI pointed apically, 1.3× longer than preceding antennomere, maximum width at base  
381 representing less than 0.1× maximum width of antennomere I. Ratio of antennomere lengths: 1.25 : 0.40:  
382 0.59 : 0.95 : 0.78 : 1.00 : 1.01 : 0.96 : 0.98 : 0.99 : 1.18. Pronotum 1.56–1.58 mm long, 1.8–2.0× wider  
383 than long, broadest in posterior half. Anterior pronotal angles acute. Posterior angles of pronotum  
384 indistinctly produced, orthogonal, rounded apically. Pronotal disc depressed medially. Posterior angles of  
385 pronotum indistinctly produced, orthogonal, rounded apically. Elytra 5.39–5.71 mm, 1.5–1.7× longer than  
386 their combined width. Mesotibia shorter than mesofemur. Ventral characters not visible, legs poorly  
387 preserved.

388  
389 *Etymology.* The specific epithet is taken from the Ancient Greek *rhīnókerōs* (ῥῖνόκερωϝ: itself a  
390 combination of *rhīs* (ῥῖϝ), meaning, „nose“, and *kéras* (κέραϝ), meaning, „horn“, and refers to the horn-  
391 like process on the frontoclypeus.

392

393

394 *Cretaceocoleus* Tihelka & Cai **gen. nov.**

395 [http://zoobank.org/urn:lsid:zoobank.org:act: \[to be added after acceptance\]](http://zoobank.org/urn:lsid:zoobank.org:act:[to be added after acceptance])

396 Figs 5–7

397

398 *Type and only included species.* *Cretaceocoleus saetosus* Tihelka, Kundrata & Cai sp. nov.

399

400 *Occurrence.* Albian–Cenomanian amber from northern Myanmar (*Cretaceocoleus saetosus* represented  
401 by three known specimens).

402

403 *Diagnosis.* Antennomeres II–XI less pronouncedly tapering towards apex. Mesotarsus with or without  
404 ventral rami (Fig. 5E: vr, Fig. 7C). Anterior pronotal angles approximately orthogonal. Posterior angles of  
405 pronotum strongly produced and acute. Procoxae separated by approximately their width. Prosternal  
406 process wider, bordered laterally. Mesocoxae separated by close to half their width. Metatibia distinctly  
407 expanded apically. Tibial spurs short and thin, no longer than tarsomere I (Fig. 5F: ts). Elytra with nine  
408 punctate striae. Margins of ventrites strongly arcuate.

409

410 *Etymology.* Combination of “Cretaceous” and ‘*koleós*’ (κολεός), after Coleoptera. Gender: masculine.

411

412 *Cretaceocoleus saetosus* Tihelka, Kundrata & Cai **sp. nov.**

413 <http://zoobank.org/urn:lsid:zoobank.org:act:> [to be added after acceptance]

414 Figs 5–7

415

416 *Material.* Holotype, NIGP174709, sex unknown, a single well-preserved amber inclusion (NIGP).

417 Paratype, NM-T3501 (ex PCRK, BUR0027), sex unknown, a single well-preserved amber inclusion

418 (NMPC); Paratype, BUR0006, sex unknown, a single well-preserved amber inclusion (PCRK).

419

420 *Note.* The three studied specimens are similar in terms of their overall morphology and size. However,  
421 both paratypes differ in lacking distinct attachment modifications on the mesotarsi. Instead of establishing  
422 a separate taxon, we conservatively interpret these differences as possible sexual dimorphism.

423

424 *Type locality and horizon.* Amber mine in the Hukawng Valley, Myitkyina District, Kachin State,

425 Myanmar; latest Albian to Albian/Cenomanian boundary (Lower–Upper Cretaceous boundary).

426

427 *Diagnosis.* As for the genus (*vide supra*).

428

429 *Description.* Body length 4.43–4.59 mm, body width 1.58–2.65 mm. Head 0.55–0.56 mm long, 1.6×  
430 wider than long. Apical maxillary palpomere distinctly truncate (Fig. 7A: mp). Antennomere I slightly

431 broadening apically, 1.4× wider than following antennomere; antennomere II attached subapically to

432 antennomere I; antennomere III longer than preceding antennomere; antennomeres V–XI gradually

433 thinning and lengthening apically, except slightly shorter antennomeres VII and IX; antennomere XI

434 pointed apically, 1.5× longer than preceding antennomere, maximum width at base representing

435 approximately 0.3× maximum width of antennomere I. Ratio of antennomere lengths: 0.38 : 0.10 : 0.16:

436 0.18 : 0.18 : 0.20 : 0.18 : 0.21 : 0.17 : 0.17 : 0.24. Pronotum 0.96–1.08 mm long, 1.4× wider than long,

437 broadest medially. Anterior pronotal angles strongly angulate, approximately orthogonal. Pronotal disc

438 slightly convex. Posterior angles of pronotum indistinctly strongly produced posteriorly, acutely pointed

439 apically. Procoxae separated by approximately their width. Prosternal process wider, bordered laterally,

440 apex not clearly visible. Medial mesoventral groove faintly impressed, subtriangular, broadest anteriorly.

441 Mesocoxae more widely separated than in *Mastigocoleus*, by close to half their width. Protibia

442 approximately 0.5 × as length of profemur, mesotibia as long as mesofemur, metatibia distinctly longer

443 than metafemur. Metatibia abruptly expanded apically. Tibial spurs short, thin, no longer than tarsomere I  
444 (Fig. 5F: ts). Protarsomeres I–IV densely setose, propretarsal claws sickle-shaped, representing two thirds  
445 of protarsomere V length. Mesotarsus with ventral rami in holotype (Fig. 5E: vr), absent in paratype (Fig.  
446 7C), mesotarsomere V longer than combined lengths of preceding tarsomeres, mesopretarsal claws sickle-  
447 shaped, representing approximately half of tarsomere V length. Metatarsus distinctly thinner than  
448 metatibia, metatarsomere V as long as combined lengths of preceding metatarsomeres, metapretarsal  
449 claws sickle-shaped representing approximately half of metatarsomere V length. Elytra 2.91–2.96 mm  
450 long, 1.8× longer than their combined width. Elytra with nine punctate striae. Margins of ventrites  
451 strongly arcuate. Ratio of ventrite lengths: 0.44–0.48 : 0.27–0.31 : 0.20–0.21 : 0.28–0.29 : 0.45–0.94.

452  
453 *Etymology.* The specific epithet is taken from the Latin adjective *saetōsus*, meaning, “bristly”, in reference  
454 to the distinctly setose body.

455

#### 456 **Undescribed specimen**

457 Fig. 8

458

459 *Material.* QZYX0013, part and counterpart.

460

461 *Occurrence.* Huangbanjigou, Beipiao, Liaoning, northeastern China; Barremian–Aptian (Lower  
462 Cretaceous) Yixian Formation.

463

464 *Note.* The oldest member of Mastigocoleidae is represented by a single compression fossil from the  
465 Yixian Formation, (QZYX0013). Since the specimen is not deposited in a public institutional collection  
466 and in accordance with the recommendations of the ICZN, we refrain from formally describing it. The  
467 specimen nonetheless seems to represent a new species close to *Mastigocoleus* as indicated by the shape  
468 of its antennae, similar body size (9.77 mm), and striate elytra. It differs from *Mastigocoleus* most  
469 distinctly by its distinct medial groove on the pronotum. The seemingly projecting horn-like anterior  
470 pronotal angles may represent a genuine morphological character or alternatively a taphonomic artefact  
471 resulting from compression.

472

#### 473 **Results and Discussion**

##### 474 *Early evolution of Dryopoidea and the position of Mastigocoleidae*

475 Early morphological studies divided dryopoids into two major clades, one including families that  
476 commonly co-occur in riparian habitats (e.g., Heteroceridae, Limnichidae, Dryopidae, Lutrochidae) and



477 another partly terrestrial clade (Eulichadidae and Callirhipidae, sometimes grouping with other families)  
478 (Crowson 1960, 1978, Lawrence 1988, Costa et al. 1999, Lawrence et al. 2011). A similar view of  
479 dryopoid relationships emerged from our re-analysis of Lawrence's (1988) matrix including  
480 Mastigocoleidae. A single most parsimonious tree of 192 steps (Fig. 9B; consistency index: 0.542,  
481 retention index: 0.553) was recovered under parsimony that divided the superfamily into two clades: a  
482 well-supported (bootstrap value = 91) clade of Heteroceridae, Limnichidae, Dryopidae, and Lutrochidae  
483 on one hand, and a moderately supported (bootstrap value = 67) clade comprising Elmidae, Psephenidae,  
484 Cneoglossidae, Ptilodactylidae, Chelonariidae, Callirhipidae, and Eulichadidae, on the other.

485 Molecular studies conducted over the past decade have substantially altered our understanding of  
486 dryopoid evolution. The Dryopoidea of Crowson (1955, 1960) and Cai et al. (2021) was supported as  
487 monophyletic in the 89-gene phylogeny of McKenna *et al.* (2019), the 95-gene phylogeny of Zhang *et al.*  
488 (2018), the 68-gene phylogeny of Cai *et al.* (2021), the eight-gene phylogeny of McKenna *et al.* (2015),  
489 and in our reanalysed four-gene phylogeny of Kundrata *et al.* (2017). In agreement with the morphological  
490 analysis, Dryopidae + Lutrochidae form a well-supported clade (Bayesian Posterior Probability [BPP] =  
491 100), equivalent to the 'dryopid clade' of Kundrata *et al.* (2017). The close relationship between  
492 Dryopidae and Lutrochidae has been noted for as long as the two families have been recognised.  
493 *Lutrochus* Erichson, 1847 was originally described in Dryopidae and was only placed into a separate  
494 family later by Crowson (1978). Lutrochids and dryopids are the only members of the superfamily  
495 Dryopoidea possessing interfacetal setae (Lawrence et al. 1999). Furthermore, they share elongate, curved,  
496 and cylindrical male genitalia (Maier 2016); functional ventral longitudinal muscles in sternite IV  
497 (Crowson 1978); and some dryopids also share a free abdominal sternite V with Lutrochidae (Lawrence  
498 and Newton 1982). Both families share the absence of ommatidia without expanded corneal lenses, while  
499 exocone lenses are present throughout most Elateriformia (Lawrence et al. 2011). Preliminary molecular  
500 analyses based on three genes and focused on Lutrochidae even indicate that a merger of the two families  
501 may be substantiated, provided that novel morphological evidence and datasets with more extensive gene  
502 sampling may support such integration (Maier 2016).

503 In molecular analyses, the dryopid clade is recovered as the earliest-diverging lineage of  
504 Dryopoidea, sister to the remaining families (Fig. 9A,C,D; Kundrata *et al.*, 2017; Zhang *et al.*, 2018;  
505 McKenna *et al.*, 2019; Cai *et al.*, 2020). The early-diverging position of Dryopidae and Lutrochidae  
506 within Dryopoidea is supported by several characters shared symplesiomorphically with Buprestidae,  
507 specifically the morphology of the testes, ventral nerve cord, transverse sulcus of the metasternum, along  
508 with several larval features cited by Kasap & Crowson (1975). Some systematists (e.g., Jan Obenberger  
509 and later in life Roy A. Crowson) were even inclined to consider their 'Buprestoidea' as likely nested

510 within Dryopoidea, pointing out similarities shared with Lutrochidae, among other families (Crowson  
511 1982).

512 Outside of the dryopid clade, the family Eulichadidae (or Eulichadidae + Callirhipidae) forms the  
513 sister group to the remaining families in the analyses of McKenna *et al.* (2019) and Cai *et al.* (2021),  
514 while deep relationships were poorly resolved in our four-gene analyses. Incongruities regarding the  
515 paraphyly of Limmichidae with respect to Heteroceridae were only recovered in datasets with broad gene  
516 sampling but not in the smaller four-gene dataset. Regardless of these inconsistencies, these topologies  
517 imply that that aquatic habits present in Dryopidae and Lutrochidae were lost in the short-lived adults of  
518 the early-diverging family Eulichadidae (although the immatures are principally aquatic), as well as in all  
519 life stages of Callirhipidae, only to be subsequently regained in most derived dryopids. Such convergent  
520 evolution towards an aquatic or semiaquatic lifestyle, at least in some life stages, may explain why many  
521 of the aquatic dryopoid families often group together in morphological analyses.

522 The extinct family Mastigocoleidae shares important characters with the early-diverging families  
523 Lutrochidae and Dryopidae: compound eyes with interfacetal setae, anterior edge of the prosternum  
524 forming a chin-piece, procoxae separated by more than  $0.4\times$  their width, and elytral epipleura abruptly  
525 narrowed next to the junction of the thorax and abdomen. These characters are absent or occur only rarely  
526 and sporadically in other members of Dryopoidea (Lawrence 1988, Lawrence *et al.* 2011). It is difficult to  
527 determine if Mastigocoleidae are more closely related to Dryopidae or Lutrochidae. In common with  
528 Dryopidae, Mastigocoleidae possess nine elytral striae (although some dryopids have less), while elytral  
529 striae are entirely absent in Lutrochidae. Whip-antennate beetles also share with some dryopids their  
530 narrowly separated mesocoxae (Kodada *et al.* 2016). On the other hand, the truncate apical maxillary  
531 palpomere and the straight apical margin of the frontoclypeus are more reminiscent of Lutrochidae (Ide *et al.*  
532 2016, Maier 2016). However, unlike both Dryopidae and Lutrochidae, species of Mastigocoleidae have  
533 an occipital area shorter than the compound eye diameter, or at most equally long (possibly in  
534 *Cretaceocoleus* but difficult to judge given that the head is deeply inserted into the prothorax). The  
535 morphology of the antennae, the absence of antennal grooves, and shapes of the head and the prosternal  
536 process also separate mastigocoleids from either family (Lawrence *et al.* 1999, 2011, Ide *et al.* 2016,  
537 Maier 2016). Affinity with the Lutrochidae + Dryopidae clade is further supported by the analysis of  
538 morphological characters based on the matrix of Lawrence (1987), where whip-antennate beetles were  
539 sister to Lutrochidae, next to Dryopidae (Fig. 9B). We note that the results of our morphological  
540 phylogenetic analysis must be interpreted with caution, since most deep relationships within this tree are  
541 incongruent with recent phylogenomic data, as discussed above. This likely reflects prevalent homoplasy  
542 in the morphological dataset, which has been recognised as a considerable problem in elateriform  
543 morphological phylogenies (Kundrata *et al.* 2014, Li *et al.* 2021). Because the fossils possess a

544 combination of characters from both families, we regard Mastigocoleidae as closely allied with these two,  
545 either as sister to the clade Lutrochidae + Dryopidae or as a stem group to Dryopoidea. This is supported  
546 by molecular studies (Fig. 9A, CD), which imply that key characters of the family such as dilated basal  
547 antennomeres, presence of interfacetal setae, prosternum forming a chin-piece, and elytral epipleura  
548 abruptly narrowed next to the junction of the thorax and abdomen are plesiomorphic within Dryopoidea,  
549 while specializations for life in aquatic habitats evolved later in the ancestor of crown Lutrochidae +  
550 Dryopidae (Fig. 10). Mastigocoleidae are less likely to represent stem-Dryopoidea, although characters  
551 such as similarities of its antennae with those of Chelonariidae should be given consideration in future  
552 studies.

553

### 554 ***Morphological comparison with other lineages of Dryopoidea***

555 The monophyly of Mastigocoleidae is supported by the following conspicuous characters: (1) antennae  
556 with 11 antennomeres, not pectinate or clubbed, with basal antennomere distinctly broadest, antennomere  
557 II shortest, and antennomeres II–XI more or less distinctly gradually, but noticeably, tapering towards the  
558 apex (more distinct in *Mastigocoleus*, less so in *Cretaceocoleus*); (2) apical maxillary palpomere not  
559 expanded apically and distinctly diagonally truncate; (3) compound eyes with interfacetal setae; (4) head  
560 without subantennal grooves; (5) anterior edge of prosternum forming a chin-piece; (6) prosternal process  
561 curved and tapering apically, longer than the precoxal prosternal distance; (7) mesocoxae longitudinally  
562 oriented, separated by less than their width. These characters are further elaborated on below.

563 (1) The shape of antennae seen in Mastigocoleidae, with antennomere I widest and longest, and the  
564 remaining antennomeres not modified and gradually tapering apically, is unique within  
565 Dryopoidea and likely within the whole of Coleoptera. Accordingly, it represents the most  
566 distinctive putative apomorphy of the group. The most similar antennal morphology to the one  
567 observed in Mastigocoleidae is present in some members of the small dryopoid family  
568 Chelonariidae. However, the chelonariid genera *Chelonarium* Fabricius, 1801 and  
569 *Pseudochelonarium* Pic, 1916 have their basal antennomeres dilated and the remainder of the  
570 antennomeres of subequal width, which differs from Mastigocoleidae where antennomeres taper  
571 towards the apex gradually. The new fossil family also differs from Chelonariidae in not having  
572 enlarged antennomeres III and IV that fit into a cavity of the mesoventrite. However, the  
573 enlargement of the basal antennomeres is notably present in Dryopidae and Lutrochidae.  
574 Antennomere I or antennomeres I and II are enlarged in Dryopidae, while in Lutrochidae both  
575 antennomeres I and II are always enlarged. However, both Dryopidae and Lutrochidae have the  
576 remaining antennomeres forming a serrate club, which is certainly not the case in  
577 Mastigocoleidae. Unlike Dryopidae and Lutrochidae, Mastigocoleidae have antennomere II

- 578           shortest of all antennomeres and the antenna are long, extending well beyond the posterior  
579           pronotal margin.
- 580       (2) Another notable diagnostic character of the family is the shape of the fourth maxillary palpomere.  
581           While it is cylindrical, subulate, or slightly expanded and truncate apically in most species of  
582           Dryopoidea (Lawrence 1982), mastigocoleids have the apical palpomere roughly subcylindrical  
583           but diagonally truncate apically. Within Dryopoidea, this condition is most similar to that in  
584           Lutrochidae, where palpomere IV is slightly expanded and truncate to subtriangular apically. In  
585           Dryopidae the terminal palpomere is always cylindrical to fusiform.
- 586       (3) Within Dryopoidea, the presence of interfacetal setae is restricted to Dryopidae, Lutrochidae, and  
587           Mastigocoleidae. All other dryopoid families lack setose compound eyes, at least in their  
588           groundplan.
- 589       (4) The head in mastigocoleids is deeply inserted into the prothorax. It lacks grooves under the  
590           compound eyes for the reception of the antennae, contrary to what can be observed in Lutrochidae  
591           and Dryopidae, where such grooves are at least faintly present. The presence of antennal grooves  
592           may be associated with the shortening of antennae observed in aquatic dryopoids, which is not the  
593           case in Mastigocoleidae.
- 594       (5) All three families share a distinctly produced anterior edge of the prosternum forming a chin-  
595           piece, which is otherwise rare in Dryopoidea and occurs only in some Psephenidae (some  
596           Eubriinae), Elmidae, Limnichidae, and Heteroceridae (Lawrence et al. 1999).
- 597       (6) The prosternal process of mastigocoleids is elongate, extending well beyond the procoxae and  
598           fitting into a mesoventral cavity. The prosternal process is equally wide throughout but becomes  
599           less ventrally protruding towards the apex and curves dorsad. This condition is distinct from  
600           Lutrochidae where the prosternal process is about as wide as long and with bead laterally. The  
601           nature of the prosternal process is more variable in Dryopidae, but the process is always shorter  
602           than the precoxal prosternal distance. In Mastigocoleidae, the prosternal process is slightly longer  
603           than the prosternum in front of the procoxae.
- 604       (7) Mesocoxae are always transverse in Dryopidae, they are circular to slightly transverse in  
605           Lutrochidae. The mesocoxae of *Mastigocoleus* and *Cretaceocoleus* are longest longitudinally.  
606           Although the degree of mesocoxal separation differs in the two mastigocoleids genera, it never  
607           exceeds more than two thirds of the mesocoxal width. Mesocoxae are always widely separated in  
608           Lutrochidae, while in Dryopidae they are narrowly to moderately separated.

609

### 610 ***The Mesozoic history of Dryopoidea***

611 The discovery of a diverse set of fossils belonging to the stem-dryopid clade from three fossil deposits  
612 (Fig. 12) and spanning roughly ~23 Ma from Early to Late Cretaceous (Fig. 11) enables us to place the  
613 origin and early evolution of Dryopoidea into a wider palaeobiological context. Cretaceous whip-  
614 antennate beetles suggest that the last common ancestor of Dryopidae was terrestrial, at least during the  
615 adult stage. The general body shape is not boat-like, suggesting that adult beetles probably did not occupy  
616 fast-flowing water. The moderately dense hair-like erect setae and the complete absence of dense  
617 recumbent hair-like setae variously flattened or forming scales resembles terrestrial dryopoids (Kodada et  
618 al. 2016). While aquatic dryopoids typically possess shortened antennae, correlated with the presence of  
619 antennal grooves, the antennae of mastigocoleids are long and stout. The terrestrial ancestry of dryopoids  
620 is further supported by the fact that most larval Dryopidae are terrestrial (although the larvae of aquatic  
621 genera live close to water and are referred to as “paraquatic”), while the larvae of Lutrochidae occupy  
622 submerged wood (Ide et al. 2016, Kodada et al. 2016).

623 Extant members of the family Chelonariidae, the group with antennae most similar to  
624 mastigocoleids, are possibly phytophagous, although some species appear to be associated with ants and  
625 termites (Spangler 1980). It is possible that whip-antennate beetles shared some attributes with  
626 chelonariids, but it must be noted that the latter represent a rather derived family in Dryopoidea.

627 Mastigocoleidae possessed morphological characters possibly related to sexual selection. The  
628 most conspicuous of these are the pronotal horns in the Yixian Formation specimen and clypeal horns in  
629 *M. rhinoceros* (Fig. 4A, B: ch). Similarity with the head and pronotal modifications seen in extant horned  
630 beetles suggest that they may have been used as weapons in male-to-male combat (Emlen 2000), implying  
631 that heightened sexual selection and competition for females was present in stem-dryopoids. Assuming  
632 that the angulate pronotal processes performed an adaptive function, another possibility is that they simply  
633 offered protection from predators; testing this hypothesis is contingent upon discovering unequivocally  
634 female specimens of *M. rhinoceros*. The frontoclypeal mesial horn present in *M. rhinoceros* is a structure  
635 unparalleled in basal dryopoids except of the flightless terrestrial dryopid *Geoparnus rhinoceros* Kodada,  
636 Jäch, Čiampor & Čiamporová-Zaťovičová, 2007. Little is known about the biology of this species aside  
637 the fact that it occurs in decaying plant material in the lowland forests of Borneo (Kodada et al. 2007),  
638 however since the clypeal modifications only occur in males, it is likely that they are the product of sexual  
639 selection. The mesotarsal rami (Fig. 5E: vr, Fig. 7C) present in the holotype of *C. saetosus* but absent in  
640 the paratype may represent sexually dimorphic characters associated with attachment to the partner during  
641 mating.

642 The unnamed whip-antennate beetle fossil from the Yixian Formation in China is the earliest  
643 representative of the family Mastigocoleidae. While the earliest reliable dryopoid fossil, the chelonariid  
644 *Eochelonarium belle*, is Early Barremian (Kirejtshuk and Azar 2013), molecular clock studies suggest a

645 Late Triassic to Early Cretaceous origin of Dryopoidea (Hunt et al. 2007, McKenna et al. 2015, Toussaint  
646 et al. 2017, Zhang et al. 2018), with most studies employing the greatest number of calibrations  
647 converging on a Late Triassic to Early Jurassic date (Toussaint et al. 2017, Cai et al. 2021). Considering  
648 that mastigocoleids are likely younger than stem-dryopoids, then taking the Triassic origin of Dryopoidea  
649 estimated by molecular clock studies as given and considering the earliest Cenomanian age of amber from  
650 northern Myanmar, the lineage would have persisted at most for ~100–130 Ma. When Mastigocoleidae  
651 went extinct is open to speculation. If Mastigocoleidae were phytophagous occupants of Mesozoic near-  
652 limnic habitats, it is possible that the replacement of gymnosperms by angiosperms by the Late Cretaceous  
653 removed the habitats or food sources for the beetles (Barba-Montoya et al. 2018, Condamine et al. 2020).  
654 Another biotic crisis that may have severely impacted mastigocoleids was the end-Cretaceous (K-Pg)  
655 mass extinction event. However, the K-Pg crisis seems to not have been instrumental in shaping the  
656 modern diversity of Coleoptera, at least at the family level, since almost all beetle families known from  
657 the Cretaceous have persisted until the present (Labandeira and Sepkoski 1993, Cai et al. 2021, but see  
658 Peris et al. 2020). It is therefore equally possible that mastigocoleids crossed the K-Pg boundary and  
659 persisted into the Cenozoic, although this scenario is again purely speculative and depends on further  
660 exploration of younger insect-bearing fossil deposits.

661

## 662 **Conclusions**

663 We describe a new family of dryopoid beetles, Mastigocoleidae, based on exceptionally well-preserved  
664 compression fossils and amber inclusions from three Early to Late Cretaceous deposits. The beetles are  
665 most readily distinguished from other members of the superfamily by the apical maxillary palpomere not  
666 expanded apically and distinctly truncate, compound eyes with interfacetal setae, head without antennal  
667 grooves, and the characteristic shape of the whip-like antennae. Compound eyes with interfacetal setae, a  
668 prosternum forming a chin-piece anteriorly, procoxae separated by more than 0.4× their width, and the  
669 abrupt narrowing of the elytral epipleura at the junction of the thorax and abdomen suggest an affinity  
670 with the earliest-diverging dryopoid families Lutrochidae and Dryopidae, corroborated by a formal  
671 phylogenetic analysis. Our phylogenetic analyses highlight a growing consensus in dryopoid relationships,  
672 with the dryopid clade (Lutrochidae + Dryopidae) supported as sister to the rest of the superfamily. The  
673 discovery of early-diverging dryopoids sheds light on the ancestral character states of Dryopoidea and its  
674 early evolution. The fossils reveal that stem-dryopoids were likely terrestrial as adults, and so associations  
675 with riparian and littoral habitats evolved later independently in several dryopoid clades. Specialization  
676 for aquatic lifestyles in Dryopoidea resulted in a progressive modification of the antennae (from  
677 ancestrally elongate antennae to short and compact forms), the associated development of antennal  
678 grooves, and hydrofuge pubescence.

679

**680 Supplementary Data**

681 Supplementary data are available at *Insect Systematics and Diversity* online.

682

**683 Author Contributions**

684 C.C. and E.T. conceived the study, C.C. and E.T. prepared and photographed the fossils, E.T. ran the  
685 phylogenetic analyses, E.T. drafted the manuscript with input from all authors. All authors contributed to  
686 morphological studies and descriptions of specimens.

687

**688 Acknowledgements**

689 We thank two anonymous reviewers for their valuable comments. E.T. is grateful to Günter Schweigert  
690 (Staatliches Museum für Naturkunde, Stuttgart) for loan of Crato material from the SMNS, and Martin  
691 Fikáček (National Sun Yat-sen University, Kaohsiung & National Museum, Prague) for loan of extant  
692 dryopoids for comparison. This study was supported by the Strategic Priority Research Program of the  
693 Chinese Academy of Sciences (grant nos. XDB26000000 and XDB18000000), the National Natural  
694 Science Foundation of China (grant no. 42072022), and the Second Tibetan Plateau Scientific Expedition  
695 and Research project (grant no. 2019QZKK0706).

696

**697 Data Availability**

698 Analysis files are available for download from Mendeley Data, doi: 10.17632/x8cmpmsfyg.1.

699

700 **References Cited**

- 701 **Barba-Montoya, J., M. dos Reis, H. Schneider, P. C. J. Donoghue, and Z. Yang. 2018.** Constraining  
702 uncertainty in the timescale of angiosperm evolution and the veracity of a Cretaceous Terrestrial  
703 Revolution. *New Phytologist*. 218: 819–834.
- 704 **Barling, N., D. M. Martill, S. W. Heads, and F. Gallien. 2015.** High fidelity preservation of fossil insects  
705 from the Crato Formation (Lower Cretaceous) of Brazil. *Cretac. Res.* 52: 605–622.
- 706 **Beutel, R. G. 1995.** Phylogenetic analysis of Elateriformia (Coleoptera: Polyphaga) based on larval  
707 characters. *J. Zool. Syst. Evol. Res.* 33: 145–171.
- 708 **Bocak, L., C. Barton, A. Crampton-Platt, D. Chesters, D. Ahrens, and A. P. Vogler. 2014.** Building the  
709 Coleoptera tree-of-life for >8000 species: composition of public DNA data and fit with Linnaean  
710 classification. *Syst. Entomol.* 39: 97–110.
- 711 **Bouchard, P., Y. Bousquet, A. E. Davies, M. A. Alonso-Zarazaga, J. F. Lawrence, C. H. C. Lyal, A. F.  
712 Newton, C. A. M. Reid, M. Schmitt, S. A. Ślipiński, and A. B. T. Smith. 2011.** Family-group names  
713 in Coleoptera (Insecta). *Zookeys*. 1–972.
- 714 **Brown, H. P. 1987.** Biology of riffle beetles. *Annu. Rev. Entomol.* 32: 253–273.
- 715 **Cai, C., J. F. Lawrence, S. Yamamoto, R. A. B. Leschen, A. F. Newton, A. Ślipiński, Z. Yin, D. Huang, and  
716 M. S. Engel. 2019.** Basal polyphagan beetles in mid-Cretaceous amber from Myanmar:  
717 biogeographic implications and long-term morphological stasis. *Proc. Roy. Soc. B.* 286: 20182175.
- 718 **Cai, C., M. K. Thayer, M. S. Engel, A. F. Newton, J. Ortega-Blanco, B. Wang, X.-D. Wang, and D.-Y.  
719 Huang. 2014.** Early origin of parental care in Mesozoic carrion beetles. *Proc. Natl. Acad. Sci.* 111:  
720 14170–14174.
- 721 **Cai, C., E. Tihelka, M. Giacomelli, J. F. Lawrence, A. Ślipiński, R. Kundrata, S. Yamamoto, M. K. Thayer,  
722 A. F. Newton, R. A. B. Leschen, M. L. Gimmel, L. Lü, M. S. Engel, D. Huang, D. Pisani, and P. C. J.  
723 Donoghue. 2021.** Integrated phylogenomics and fossil data illuminate the evolution of beetles.  
724 *bioRxiv*. 2021.09.22.461358.
- 725 **Condamine, F. L., D. Silvestro, E. B. Koppelhus, and A. Antonelli. 2020.** The rise of angiosperms pushed  
726 conifers to decline during global cooling. *Proc. Natl. Acad. Sci.* 117: 28867–28875.
- 727 **Costa, C., S. Ide, S. A. Vanin, and E. P. Teixeira. 1996.** Larvae of Neotropical Coleoptera XXIII: *Lutrochus*  
728 *germari* Grouvelle, descriptions of immatures, redescription of adults and bionomics  
729 (Dryopoidea, Lutrochidae). *Rev. Bras. Entomol.* 40: 47–56.
- 730 **Costa, C., S. A. Vanin, and S. Ide. 1999.** Systematics and bionomics of Cneoglossidae with a cladistic  
731 analysis of Byrrhoidea *sensu* Lawrence & Newton (1995) (Coleoptera, Elateriformia). *Arq. Zool.*  
732 35: 231–300.
- 733 **Crowson, R. A. 1955.** *The Natural Classification of the Families of Coleoptera*, 1st ed. Nathaniel Lloyd &  
734 Co., Ltd., London.
- 735 **Crowson, R. A. 1960.** The phylogeny of Coleoptera. *Annu. Rev. Entomol.* 5: 111–134.
- 736 **Crowson, R. A. 1971.** Observations on the superfamily Dascilloidea (Coleoptera: Polyphaga), with the  
737 inclusion of Karumiidae and Rhipiceridae. *Zool. J. Linn. Soc.* 50: 11–19.
- 738 **Crowson, R. A. 1973.** On a new superfamily Armatopoidea of polyphagan beetles, with the definition  
739 of two new fossil genera from the Baltic Amber. *J. Nat. Hist.* 7: 225–238.
- 740 **Crowson, R. A. 1978.** Problems of phylogenetic relationships in Dryopoidea (Coleoptera). *Entomol.*  
741 *Germ.* 4: 250–257.
- 742 **Crowson, R. A. 1982.** On the dryopoid affinities of Buprestidae. *Coleopt. Bull.* 36: 22–25.
- 743 **Dias, J. J., and I. de S. Carvalho. 2020.** Remarkable fossil crickets preservation from Crato Formation  
744 (Aptian, Araripe Basin), a Lagerstätten from Brazil. *J. S. Am. Earth Sci.* 98: 102443.
- 745 **Emden, F. I. van. 1942.** Die larven der Callirhipini, eine mutmassliche *Cerophytum*-Larve und Familien-  
746 Bestimmungstabelle der Larven der Malacodermata-Sternoxia-Reihe (Coleoptera). *Bull. Ann. Soc.*  
747 *Entomol. Belg.* 72: 199–259.



- 748 **Emlen, D. J. 2000.** Integrating development with evolution: a case study with beetle horns: results from  
749 studies of the mechanisms of horn development shed new light on our understanding of beetle  
750 horn evolution. *BioScience*. 50: 403–418.
- 751 **Engel, M. S. 2020.** Myanmar: palaeontologists must stop buying conflict amber. *Nature*. 584: 525–525.
- 752 **Gimmel, M. L., K. Szawaryn, C. Cai, and R. A. B. Leschen. 2019.** Mesozoic sooty mould beetles as living  
753 relicts in New Zealand. *Proc. Roy. Soc. B*. 286: 20192176.
- 754 **Goloboff, P. A., and S. A. Catalano. 2016.** TNT version 1.5, including a full implementation of  
755 phylogenetic morphometrics. *Cladistics*. 32: 221–238.
- 756 **Goloboff, P. A., A. Torres, and J. S. Arias. 2018.** Weighted parsimony outperforms other methods of  
757 phylogenetic inference under models appropriate for morphology. *Cladistics*. 34: 407–437.
- 758 **Grimaldi, D., and M. S. Engel. 2005.** *Evolution of the Insects*, 1st ed. Cambridge University Press,  
759 Cambridge.
- 760 **Grimaldi, D., and A. J. Ross. 2017.** Extraordinary Lagerstätten in amber, with particular reference to the  
761 Cretaceous of Burma, pp. 287–342. *In* Fraser, N.C., Sues, H.-D. (eds.), *Terrestrial Conservation*  
762 *Lagerstätten: Windows into the Evolution of Life on Land*. Dunedin Academic Press, Edinburgh.
- 763 **Heimhofer, U., D. Ariztegui, M. Lenniger, S. P. Hesselbo, D. M. Martill, and A. M. Rios-Netto. 2010.**  
764 Deciphering the depositional environment of the laminated Crato fossil beds (Early Cretaceous,  
765 Araripe Basin, North-eastern Brazil). *Sedimentology*. 57: 677–694.
- 766 **Hong, Y. 1983.** *Middle Jurassic Fossil Insects in North China*, 1st ed. Geological Publishing House, Beijing.
- 767 **Huang, D., M. S. Engel, C. Cai, H. Wu, and A. Nel. 2012.** Diverse transitional giant fleas from the  
768 Mesozoic era of China. *Nature*. 483: 201–204.
- 769 **Hunt, T., J. Bergsten, Z. Levkanicova, A. Papadopoulou, O. S. John, R. Wild, P. M. Hammond, D. Ahrens,  
770 M. Balke, M. S. Caterino, J. Gómez-Zurita, I. Ribera, T. G. Barraclough, M. Bocakova, L. Bocak,  
771 and A. P. Vogler. 2007.** A comprehensive phylogeny of beetles reveals the evolutionary origins of  
772 a superradiation. *Science*. 318: 1913–1916.
- 773 **Ide, S., C. Costa, and S. A. Vanin. 2016.** Lutrochidae Kasap & Crowson, 1975, pp. 602–605. *In* Beutel,  
774 R.G., Leschen, R.A.B. (eds.), *Handbook of Zoology. Arthropoda: Insecta. Coleoptera, Beetles. Vol.*  
775 *1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga Partim)*. De  
776 Gruyter, Berlin, Boston.
- 777 **Jäch, M. A. 1998.** Annotated check list of aquatic and riparian/littoral beetle families of the world  
778 (Coleoptera), pp. 25–42. *In* Jäch, M.A., Ji, L. (eds.), *Water Beetles of China. Vol. II. Zoologisch-*  
779 *Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein*, Vienna.
- 780 **Jäch, M., J. Kodada, M. Brojer, W. D. Shepard, and F. Čiampor. 2016.** Coleoptera: Elmidae and  
781 Protelmidae. *World Catalogue of Insects, Volume 14, Coleoptera: Elmidae and Protelmidae*. Brill,  
782 Leiden.
- 783 **Jouault, C., J.-M. Pouillon, and A. Nel. 2020.** The first fossil horntail wasp (Hymenoptera: Siricidae) from  
784 Lower Cretaceous Crato Formation in Brazil. *Palaeoentomol.* 3: 382–389.
- 785 **Kasap, H., and R. A. Crowson. 1975.** A comparative anatomical study of Elateriformia and Dascilloidea  
786 (Coleoptera). *Trans. Roy. Entomol. Soc. Lond.* 126: 441–495.
- 787 **Kirejtshuk, A. G., and D. Azar. 2013.** Current knowledge of Coleoptera (Insecta) from the Lower  
788 Cretaceous Lebanese amber and taxonomical notes for some Mesozoic groups. *Terrestrial*  
789 *Arthropod Rev.* 6: 103–134.
- 790 **Kirejtshuk, A. G., H. Chang, D. Ren, and S. C. Kun. 2010.** Family Lasiosynidae n. fam., new palaeoendemic  
791 Mesozoic family from the infraorder Elateriformia (Coleoptera: Polyphaga). *Ann. Soc. Entomol.*  
792 *Fr.* 46: 67–87.
- 793 **Kodada, J., M. A. Jäch, and F. Čiampor. 2016.** Dryopidae Bilberg, 1820 (1817), pp. 590–600. *In* Beutel,  
794 R.G., Leschen, R.A.B. (eds.), *Handbook of Zoology. Arthropoda: Insecta. Coleoptera, Beetles. Vol.*

- 795 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga Partim). De  
796 Gruyter, Berlin, Boston.
- 797 **Kodada, J., M. A. Jäch, F. Čiampor, and Z. Čiamporová-Zaťovičová. 2007.** *Geoparnus rhinoceros* sp. nov.,  
798 a new edaphic dryopid with unusual sexual dimorphism (Coleoptera: Dryopidae). *Zootaxa*. 1481:  
799 59–68.
- 800 **Kundrata, R., M. Bocakova, and L. Bocak. 2014.** The comprehensive phylogeny of the superfamily  
801 Elateroidea (Coleoptera: Elateriformia). *Mol. Phylogenet. Evol.* 76: 162–171.
- 802 **Kundrata, R., M. A. Ivie, and L. Bocak. 2019.** *Podabrocephalus* Pic is the morphologically modified  
803 lineage of Ptilodactylinae (Coleoptera: Elateriformia: Ptilodactylidae). *Insect Syst. Evol.* 50: 147–  
804 161.
- 805 **Kundrata, R., M. A. Jäch, and L. Bocak. 2017.** Molecular phylogeny of the Byrrhoidea–Buprestoidea  
806 complex (Coleoptera, Elateriformia). *Zool. Scr.* 46: 150–164.
- 807 **Labandeira, C. C., and J. J. Sepkoski. 1993.** Insect diversity in the fossil record. *Science*. 261: 310–315.
- 808 **Lartillot, N., H. Brinkmann, and H. Philippe. 2007.** Suppression of long-branch attraction artefacts in the  
809 animal phylogeny using a site-heterogeneous model. *BMC Evol. Biol.* 7: S4.
- 810 **Lartillot, N., N. Rodrigue, D. Stubbs, and J. Richer. 2013.** PhyloBayes MPI: Phylogenetic reconstruction  
811 with infinite mixtures of profiles in a parallel environment. *Syst. Biol.* 62: 611–615.
- 812 **Lawrence, J. F. 1988.** Rhinorhipidae, a new beetle family from Australia, with comments on the  
813 phylogeny of the Elateriformia. *Invert. Taxonom.* 2: 1–53.
- 814 **Lawrence, J. F., A. M. Hastings, M. J. Dallwitz, T. A. Paine, and E. J. Zurcher. 1999.** Beetles of the World:  
815 A Key and Information System for Families and Subfamilies. CD-ROM. Version 1.0 for MS-  
816 Windows. CSIRO Publishing, Melbourne.
- 817 **Lawrence, J. F., and A. F. Newton. 1982.** Evolution and classification of beetles. *Annu. Rev. Ecol. Syst.* 13:  
818 261–290.
- 819 **Lawrence, J. F., N. B. Nikitsky, and A. G. Kirejtshuk. 1995.** Phylogenetic position of Decliniidae  
820 (Coleoptera: Scirtoidea) and comments on the classification of Elateriformia (sensu lato), pp.  
821 375–410. *In* Pakaluk, J., Ślipiński, A.S. (eds.), *Biology, Phylogeny, and Classification of Coleoptera:*  
822 *Papers Celebrating the 80th Birthday of Roy A. Crowson.* Muzeum i Instytut Zoologii PAN,  
823 Warsaw.
- 824 **Lawrence, J. F., A. Ślipiński, A. E. Seago, M. K. Thayer, A. F. Newton, and A. E. Marvaldi. 2011.**  
825 Phylogeny of the Coleoptera based on morphological characters of adults and larvae. *Ann. Zool.*  
826 61: 1–217.
- 827 **Li, Y., E. Tihelka, D. Huang, and C. Cai. 2020.** Specialized variegated mud-loving beetles from mid-  
828 Cretaceous Burmese amber (Coleoptera: Heteroceridae). *Palaeontol.* 3: 059–067.
- 829 **Li, Y.-D., R. Kundrata, E. Tihelka, Z. Liu, D. Huang, and C. Cai. 2021.** Cretophengodidae, a new  
830 Cretaceous beetle family, sheds light on the evolution of bioluminescence. *Proc. Roy. Soc. B.* 288:  
831 20202730.
- 832 **Liu, Z., E. Tihelka, T. C. McElrath, S. Yamamoto, A. Ślipiński, B. Wang, D. Ren, and H. Pang. 2020.** New  
833 minute clubbed beetles (Coleoptera, Monotomidae, Lenacini) from mid-Cretaceous amber of  
834 Northern Myanmar. *Cretaceous Research.* 107: 104255.
- 835 **Maier, C. 2016.** Phylogeny, Ecology, and Taxonomic Revision of the Travertine Beetles (Coleoptera:  
836 Lutrochidae) (PhD thesis).
- 837 **Maksoud, S., and D. Azar. 2020.** Lebanese amber: latest updates. *Palaeontol.* 3: 125–155.
- 838 **Maksoud, S., D. Azar, B. Granier, and R. Gèze. 2017.** New data on the age of the Lower Cretaceous  
839 amber outcrops of Lebanon. *Palaeoworld.* 26: 331–338.
- 840 **Mao, Y. Y., K. Liang, Y. Su, J. G. Li, X. Rao, H. Zhang, F. Xia, Y. Fu, C. Cai, and D. Huang. 2018.** Various  
841 amberground marine animals on Burmese amber with discussions on its age. *Palaeontol.* 1:  
842 91–103.

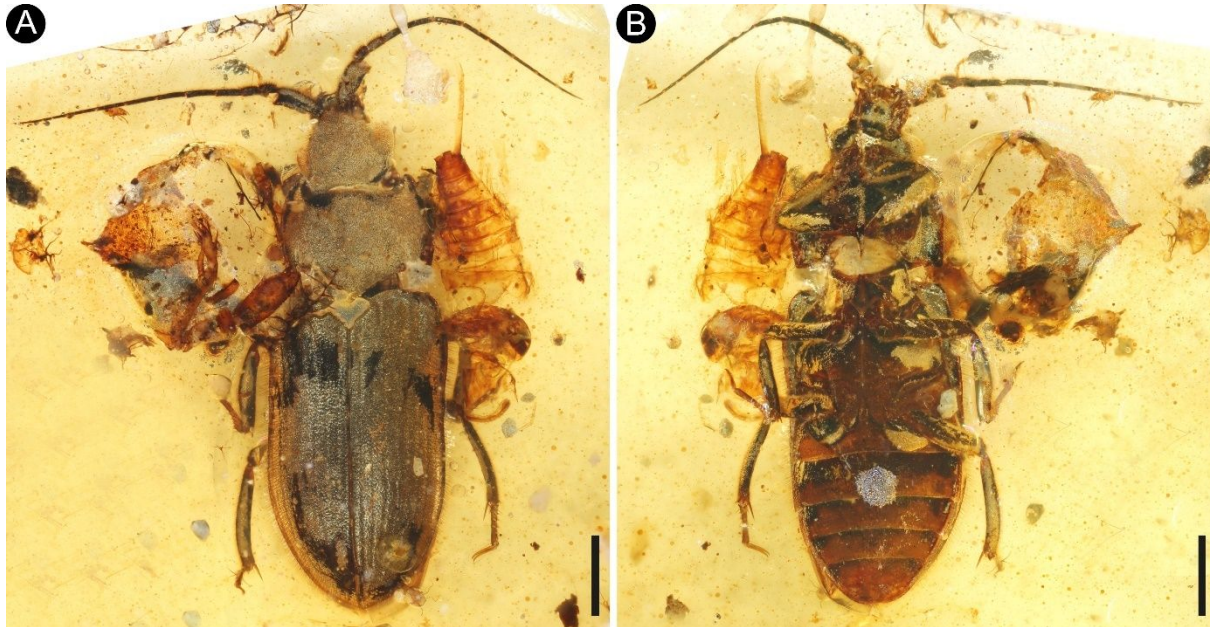
- 843 **Martill, D. M., G. Bechly, and R. F. Loveridge. 2007.** The Crato Fossil Beds of Brazil: Window into an  
844 Ancient World. Cambridge University Press.
- 845 **Martynov, A. V. 1926.** K poznaniyu iskopaemykh nasekomykh yurskikh slantsev turkeстана. 5. O  
846 nekotorykh formakh zhukov (Coleoptera). *Ezh. Rus. Paleontol. Obsh.* 5: 1–39.
- 847 **McKenna, D. D., S. Shin, D. Ahrens, M. Balke, C. Beza-Beza, D. J. Clarke, A. Donath, H. E. Escalona, F.**  
848 **Friedrich, H. Letsch, S. Liu, D. Maddison, C. Mayer, B. Misof, P. J. Murin, O. Niehuis, R. S.**  
849 **Peters, L. Podsiadlowski, H. Pohl, E. D. Scully, E. V. Yan, X. Zhou, A. Ślipiński, and R. G. Beutel.**  
850 **2019.** The evolution and genomic basis of beetle diversity. *Proc. Natl. Acad. Sci.* 116: 24729–  
851 24737.
- 852 **McKenna, D. D., A. L. Wild, K. Kanda, C. L. Bellamy, R. G. Beutel, M. S. Caterino, C. W. Farnum, D. C.**  
853 **Hawks, M. A. Ivie, M. L. Jameson, R. a. B. Leschen, A. E. Marvaldi, J. V. Mchugh, A. F. Newton, J.**  
854 **A. Robertson, M. K. Thayer, M. F. Whiting, J. F. Lawrence, A. Ślipiński, D. R. Maddison, and B.**  
855 **D. Farrell. 2015.** The beetle tree of life reveals that Coleoptera survived end-Permian mass  
856 extinction to diversify during the Cretaceous terrestrial revolution. *Syst. Entomol.* 40: 835–880.
- 857 **Nel, A., and C. Pella. 2020.** The oldest water scorpion discovered in the Early Cretaceous Crato  
858 Formation (Hemiptera: Nepidae). *Palaeontomol.* 3: 301–308.
- 859 **Nel, A., and J.-M. Pouillon. 2020.** The second genus of the ‘libelluloid’ family Araripephlebiidae  
860 (Odonata, Clavilabiata). *Palaeontomol.* 3: 240–244.
- 861 **Nixon, K. C. 2004.** ASADO version 1.5 Beta. Program and Documentation Distributed by the Author. Self-  
862 published, Ithaca.
- 863 **Pan, Y., J. Sha, Z. Zhou, and F. T. Fürsich. 2013.** The Jehol Biota: definition and distribution of  
864 exceptionally preserved relicts of a continental Early Cretaceous ecosystem. *Cretaceous Res.* 44:  
865 30–38.
- 866 **Peris, D., R. Kundrata, X. Delclòs, B. Mähler, M. A. Ivie, J. Rust, and C. C. Labandeira. 2020.** Unlocking  
867 the mystery of the mid-Cretaceous Mysteriomorphidae (Coleoptera: Elateroidea) and modalities  
868 in transiting from gymnosperms to angiosperms. *Sci. Rep.* 10: 16854.
- 869 **Pic, M. 1930.** Contribution a l’étude de Coléoptères malacodermes (2e article). II. - Quelques données  
870 générales sur la systématique et cas particuliers. *Ann. Soc. Entomol. Fr.* 99: 311–314.
- 871 **Poinar, G. 2019.** Burmese amber: evidence of Gondwanan origin and Cretaceous dispersion. *Hist. Biol.*  
872 31: 1304–1309.
- 873 **Pons, D., P.-Y. Berthou, and D. A. Campos. 1990.** Quelques observations sur la palynologie de l’Aptien  
874 sup’erieur et de l’Albien du Bassin d’Araripe. in Atas do I Simposio sobre a Bacia do Araripe e  
875 bacias interiores do nordeste, Crato, 14 a 16 de junho de 1990 (eds. Campos, D. de A., Viana, M.  
876 S. S., Brito, P. M. & Beurlen, G.) 241–252 (Crato, 1990)., pp. 241–252. *In* Campos, D.A., Viana,  
877 M.S.S., Brito, P.M., Beurlen, G. (eds.), Atas Do Simposio Sobre a Bacia Do Araripe e Bacias  
878 Interiores Do Nordeste, Crato, 14–16 de Junho de 1990. Crato.
- 879 **Prokin, A. A., and D. Ren. 2011.** New species of variegated mud-loving beetles (Coleoptera:  
880 Heteroceridae) from mesozoic deposits of China. *Paleontol. J.* 45: 284–286.
- 881 **Ross, A. J. 2019.** Burmese (Myanmar) amber checklist and bibliography 2018. *Palaeontomology.* 2: 22–  
882 84.
- 883 **Ross, A. J. 2020.** Supplement to the Burmese (Myanmar) amber checklist and bibliography, 2019.  
884 *Palaeontomol.* 3: 103–118.
- 885 **Shi, G., D. A. Grimaldi, G. E. Harlow, J. Wang, J. Wang, M. Yang, W. Lei, Q. Li, and X. Li. 2012.** Age  
886 constraint on Burmese amber based on U–Pb dating of zircons. *Cretaceous Res.* 37: 155–163.
- 887 **Ślipiński, A., R. A. B. Leschen, and J. F. Lawrence. 2011.** Order Coleoptera Linnaeus, 1758. in Zhang, Z.  
888 (ed.) *Animal biodiversity: an outline of higher-level classification and survey of taxonomic*  
889 *richness.* *Zootaxa.* 3148: 203–208.

- 890 **Smith, R. D. A., and A. J. Ross. 2016.** Amberground pholadid bivalve borings and inclusions in Burmese  
891 amber: implications for proximity of resin-producing forests to brackish waters, and the age of  
892 the amber. *Earth Environ. Sci. Trans. Roy. Soc. Edinb.* 107: 239–247.
- 893 **Spangler, P. J. 1980.** Chelonariid larvae, aquatic or not? (Coleoptera: Chelonariidae). *Coleopt. Bull.* 34:  
894 105–114.
- 895 **Swisher, C. C., Y. Wang, X. Wang, X. Xu, and Y. Wang. 1999.** Cretaceous age for the feathered dinosaurs  
896 of Liaoning, China. *Nature.* 400: 58–61.
- 897 **Timmermans, M. J. T. N., and A. P. Vogler. 2012.** Phylogenetically informative rearrangements in  
898 mitochondrial genomes of Coleoptera, and monophyly of aquatic elateriform beetles  
899 (Dryopoidea). *Mol. Phylogenet. Evol.* 63: 299–304.
- 900 **Toussaint, E. F. A., M. Seidel, E. Arriaga-Varela, J. Hájek, D. Král, L. Sekerka, A. E. Z. Short, and M.  
901 Fikáček. 2017.** The peril of dating beetles. *Syst. Entomol.* 42: 1–10.
- 902 **Warren, L. V., F. G. Varejão, F. Quaglio, M. G. Simões, F. T. Fürsich, D. G. Poiré, B. Catto, and M. L.  
903 Assine. 2016.** Stromatolites from the Aptian Crato Formation, a hypersaline lake system in the  
904 Araripe Basin, northeastern Brazil. *Facies.* 63: 3.
- 905 **Westerweel, J., P. Roperch, A. Licht, G. Dupont-Nivet, Z. Win, F. Poblete, G. Ruffet, H. H. Swe, M. K. Thi,  
906 and D. W. Aung. 2019.** Burma Terrane part of the Trans-Tethyan arc during collision with India  
907 according to palaeomagnetic data. *Nat. Geosci.* 12: 863–868.
- 908 **Yu, T., R. Kelly, L. Mu, A. Ross, J. Kennedy, P. Broly, F. Xia, H. Zhang, B. Wang, and D. Dilcher. 2019.** An  
909 ammonite trapped in Burmese amber. *Proc. Natl. Acad. Sci.* 116: 11345–11350.
- 910 **Zhang, S.-Q., L.-H. Che, Y. Li, D. Liang, H. Pang, A. Ślipiński, and P. Zhang. 2018.** Evolutionary history of  
911 Coleoptera revealed by extensive sampling of genes and species. *Nat. Commun.* 9: 205.
- 912 **Zhou, Z.-H., and Y. Wang. 2017.** Vertebrate assemblages of the Jurassic Yanliao Biota and the Early  
913 Cretaceous Jehol Biota: Comparisons and implications. *Palaeoworld, Geologic and biotic events  
914 on the continent during the Jurassic/Cretaceous transition.* 26: 241–252.  
915  
916  
917

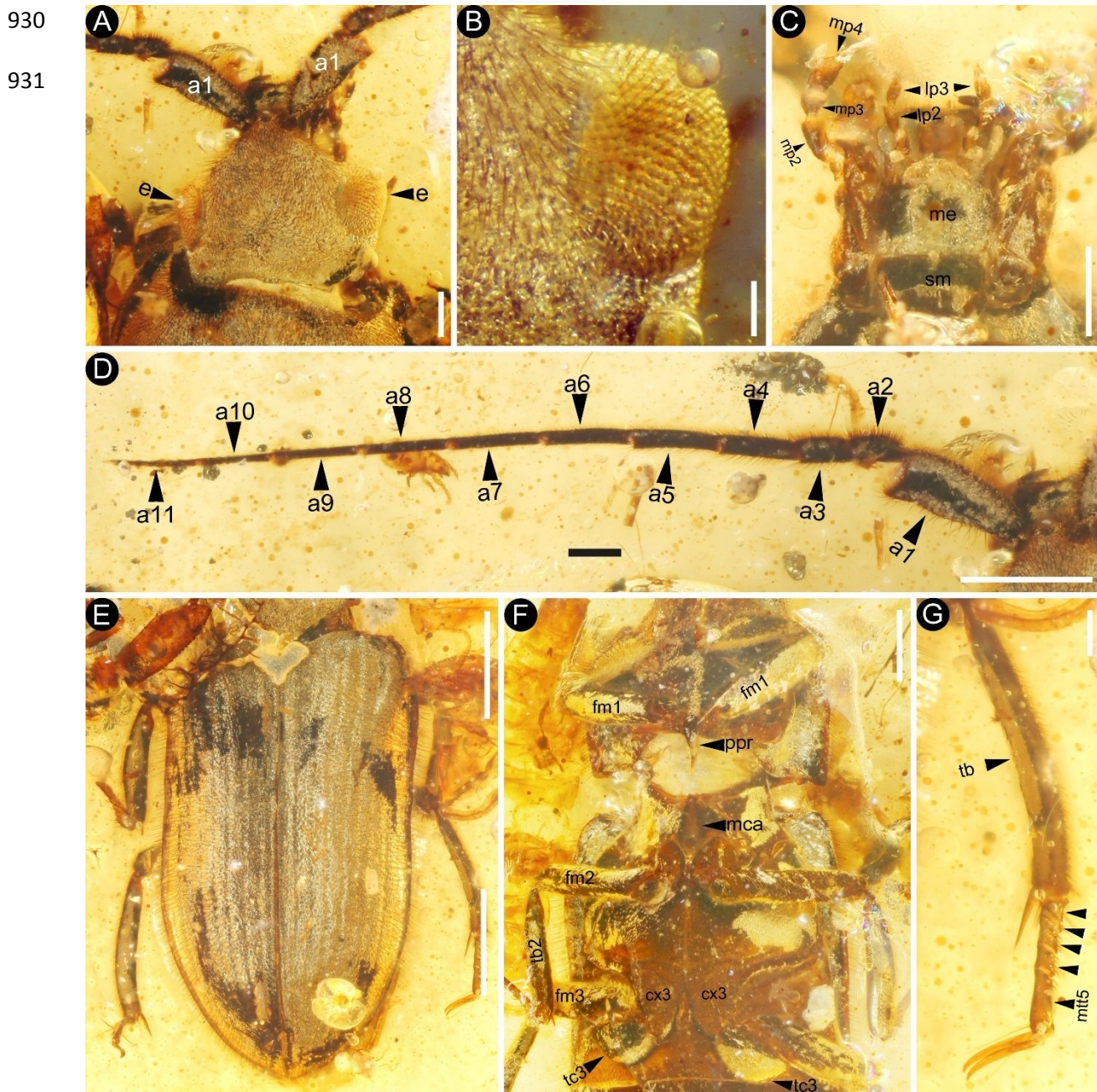
918 **Fig. 1.** Habitus of *Mastigocoleus resinicola* Tihelka & Cai gen. et sp. nov. (NIGP174708) from the mid-  
919 Cretaceous amber from northern Myanmar in (A) dorsal; and (B) ventral views. Scale bars = 1 mm.

920

921



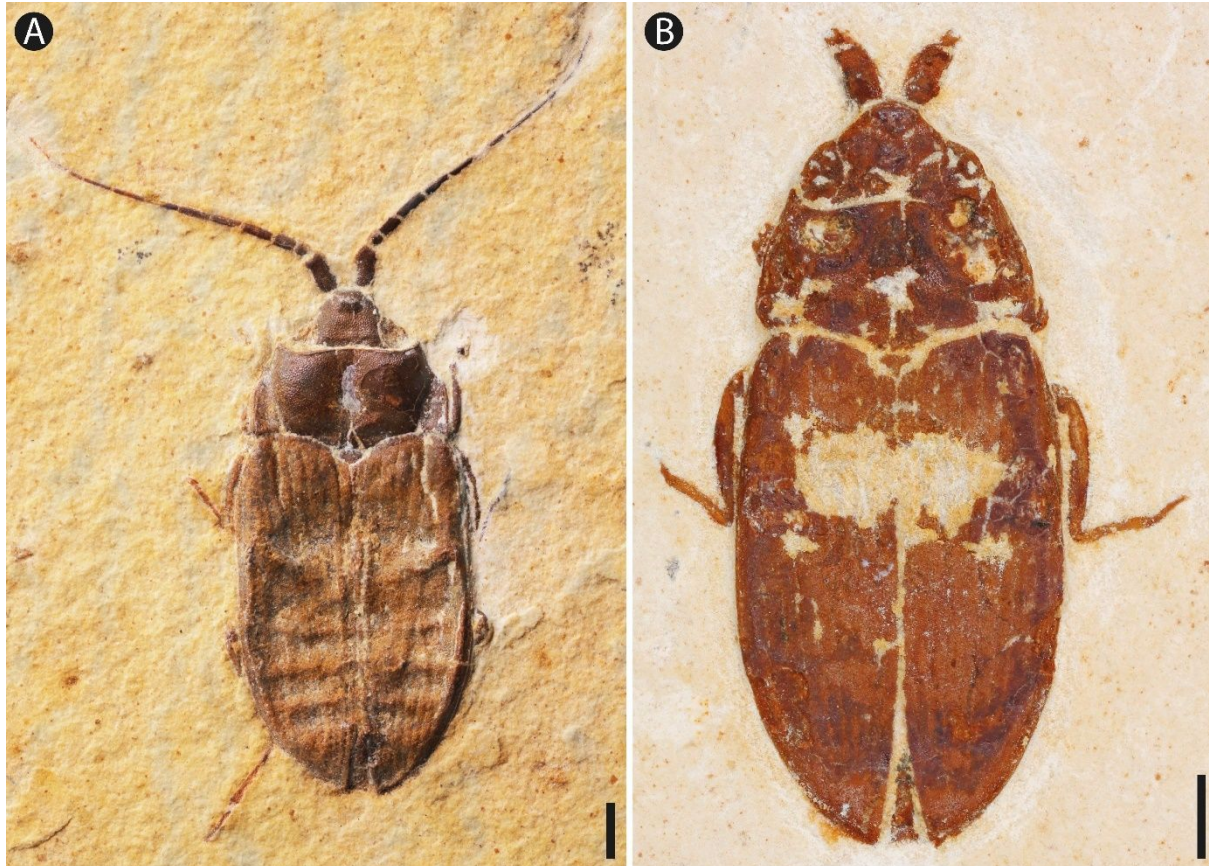
922 **Fig. 2.** Morphological details of *Mastigocoleus resinicola* Tihelka & Cai gen. et sp. nov. (NIGP174708)  
 923 from the mid-Cretaceous amber from northern Myanmar. (A) head in dorsal view; (B) Compound eye in  
 924 dorsal view; (C) Mouthparts in ventral view; (D) Antenna; (E) Elytra; (F) Thorax in ventral view; (G)  
 925 Metathoracic leg. Abbreviations: a1–11, antennomeres 1–11; cx3, metacoxa; e, compound eye; fm1,  
 926 profemur; fm2, mesofemur; fm3, metafemur; lb2–3, labial palpomeres 2–3; mca, mesoventral cavity; me,  
 927 mentum; mp2–4, maxillary palpomeres 2–4; mtt5, metatarsus 5; ppr, prosternal process; sm, submentum;  
 928 tb, metatibia; tb2, mesotibia; tc3, trochanter of metathoracic leg. Scale bars = 100  $\mu$ m (B, G); 250  $\mu$ m (A,  
 929 C); 500  $\mu$ m (D, F), 1 mm (E).



932 **Fig. 3.** Habitus of *Mastigocoleus rhinoceros* Tihelka & Cai gen. et sp. nov. from the Early Crato  
933 Formation in northeastern Brazil. (A) holotype (SMNS 66552); (B) paratype (AMNH SA43296). Scale  
934 bars = 1 mm.

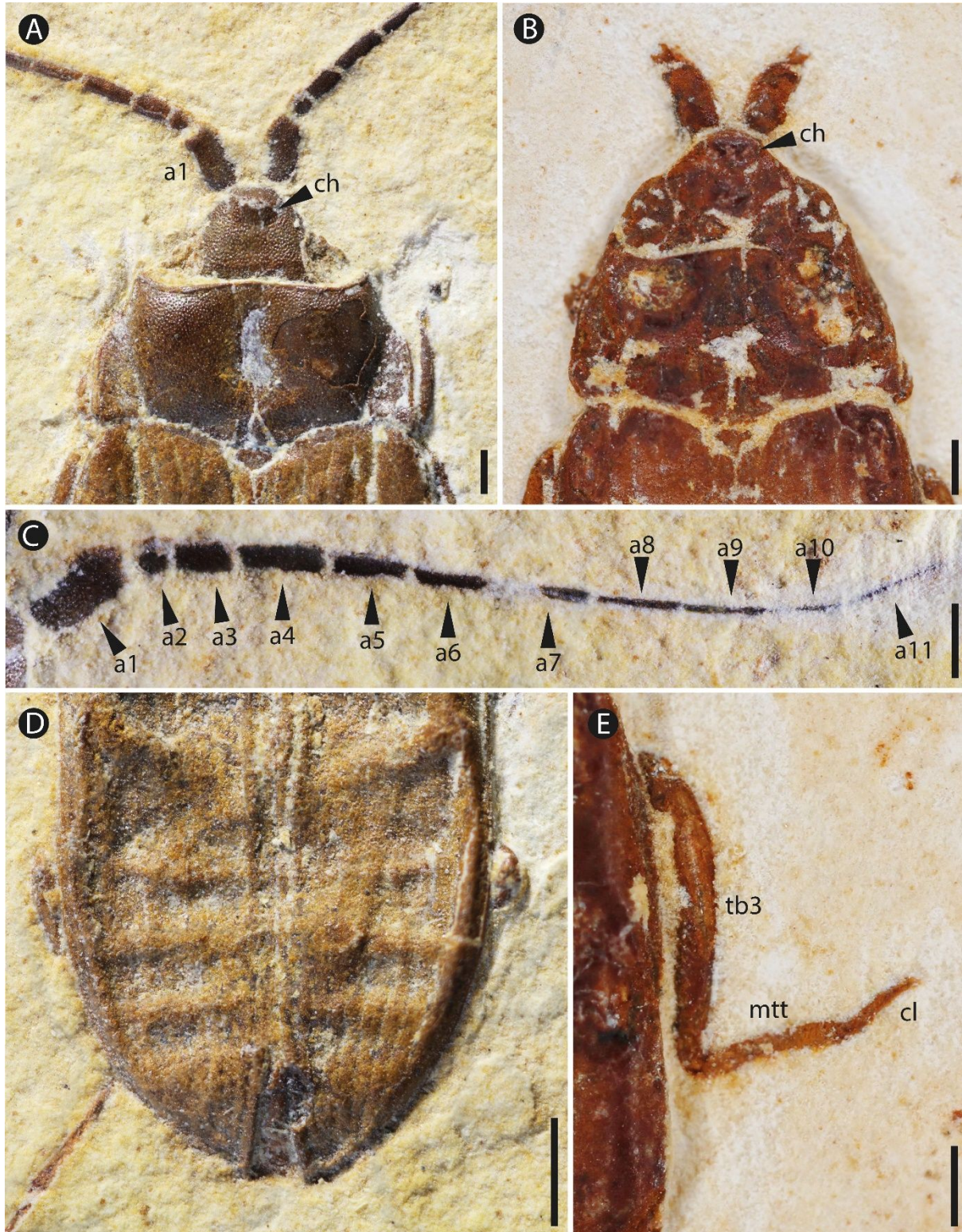
935

936



937 **Fig. 4.** Morphological details of *Mastigocoleus rhinoceros* Tihelka & Cai gen. et sp. nov. holotype (A, C,  
 938 D) and paratype (B, E) from the Early Crato Formation in northeastern Brazil. (A, B) head and pronotum  
 939 in dorsal view; (C) Antenna; (D) Elytral apex; (E) Metathoracic leg; (E) Elytra. Abbreviations: a1–11,  
 940 antennomeres 1–11; ch, clypeal horn; cl, claw; mtt, metatarsus; tb3, metatibia. Scale bars = 500  $\mu$ m (A–C,  
 941 E), 1 mm (D).

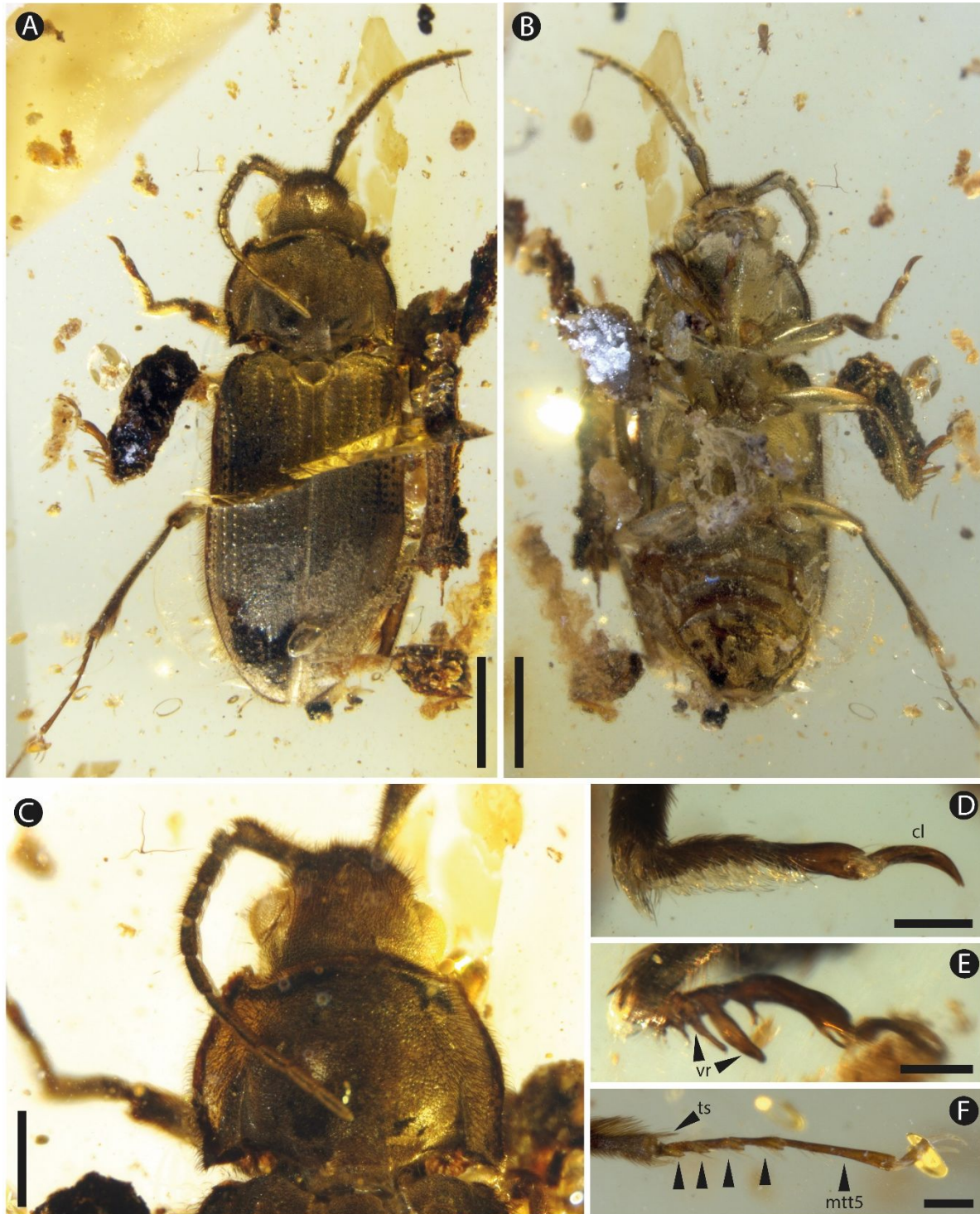
942



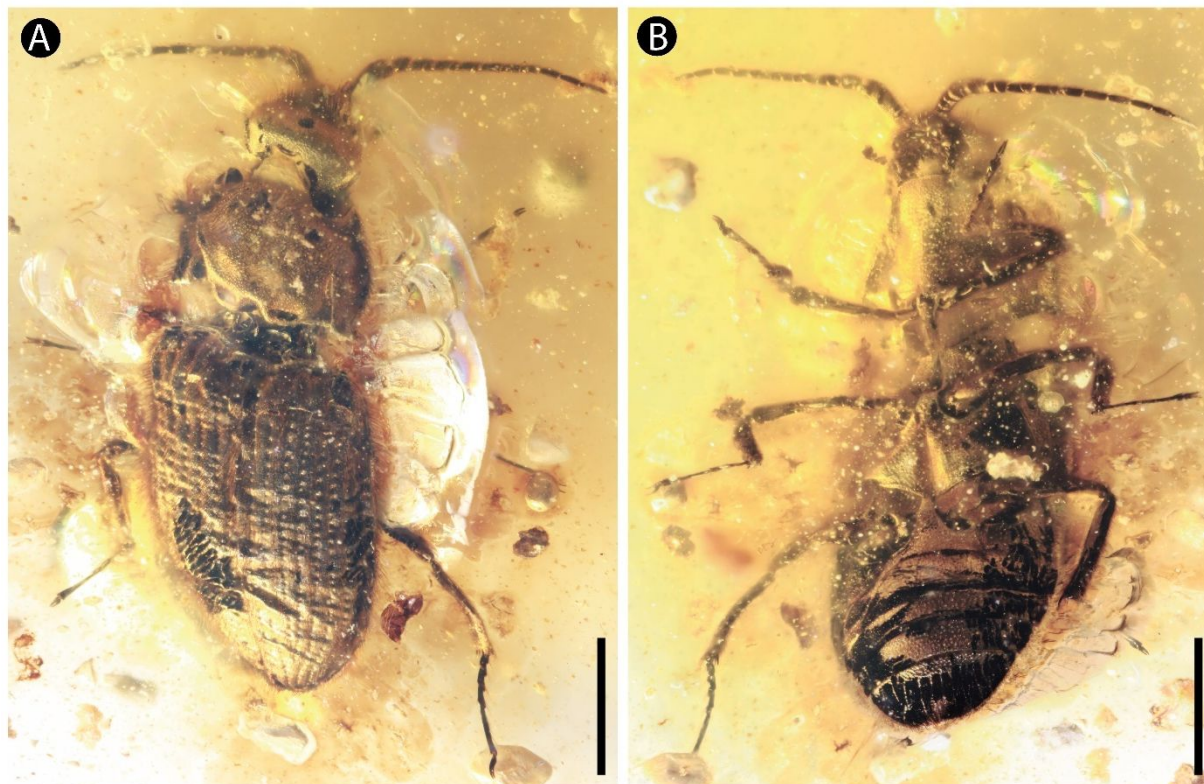


943 **Fig. 5.** *Cretaceocoleus saetosus* Tihelka, Kundrata & Cai gen. et sp. nov. (holotype, NIGP174709) from  
 944 the mid-Cretaceous amber from northern Myanmar. (A) Habitus in dorsal view; (B) Habitus in ventral  
 945 view; (C) Head and pronotum in dorsal view; (D) Protarsus; (E) Mesotarsus; (F) Metatarsus.  
 946 Abbreviations: c, claws; mtt5, metatarsus 5; ts, tibial spur; vr, mesotarsal ventral rami. Scale bars = 500  
 947  $\mu\text{m}$  (D–F), 500  $\mu\text{m}$  (C), 1 mm (A, B).

948  
 949



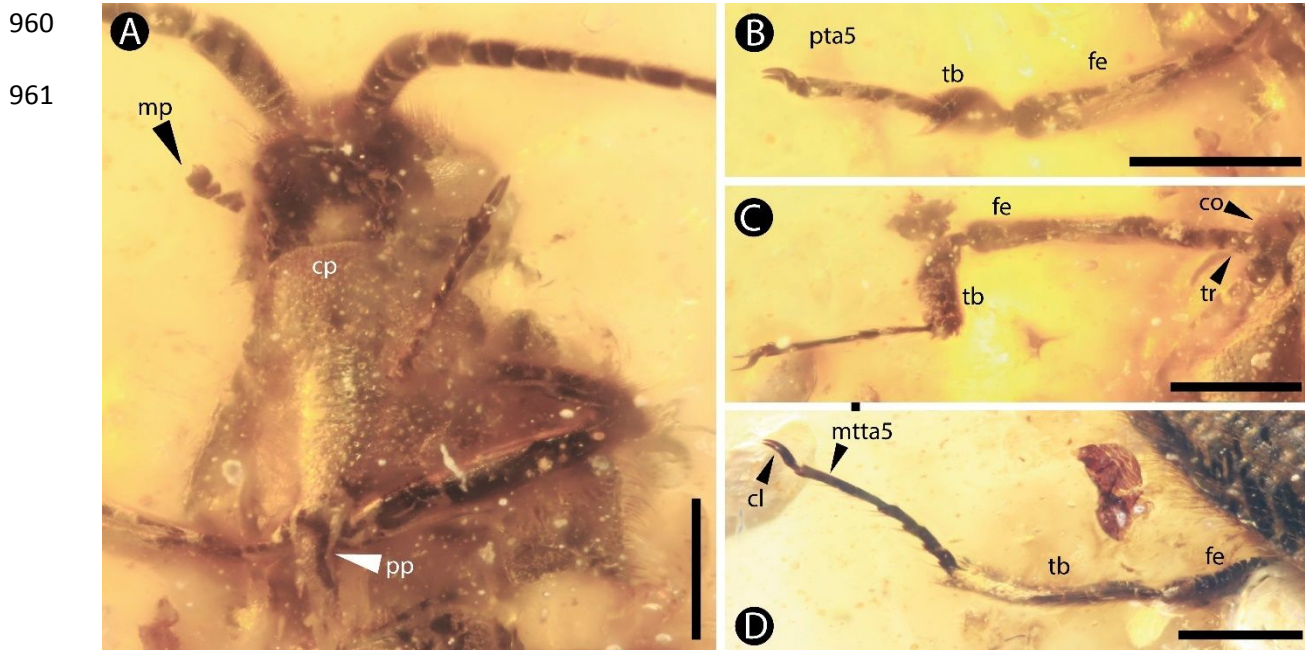
950 **Fig. 6.** *Cretaceocoleus saetosus* Tihelka, Kundrata & Cai gen. et sp. nov. (paratype, NM-T3501) from the  
951 mid-Cretaceous amber from northern Myanmar. Habitus in dorsal (A) and ventral (B) views. Scale bars =  
952 1 mm.



953

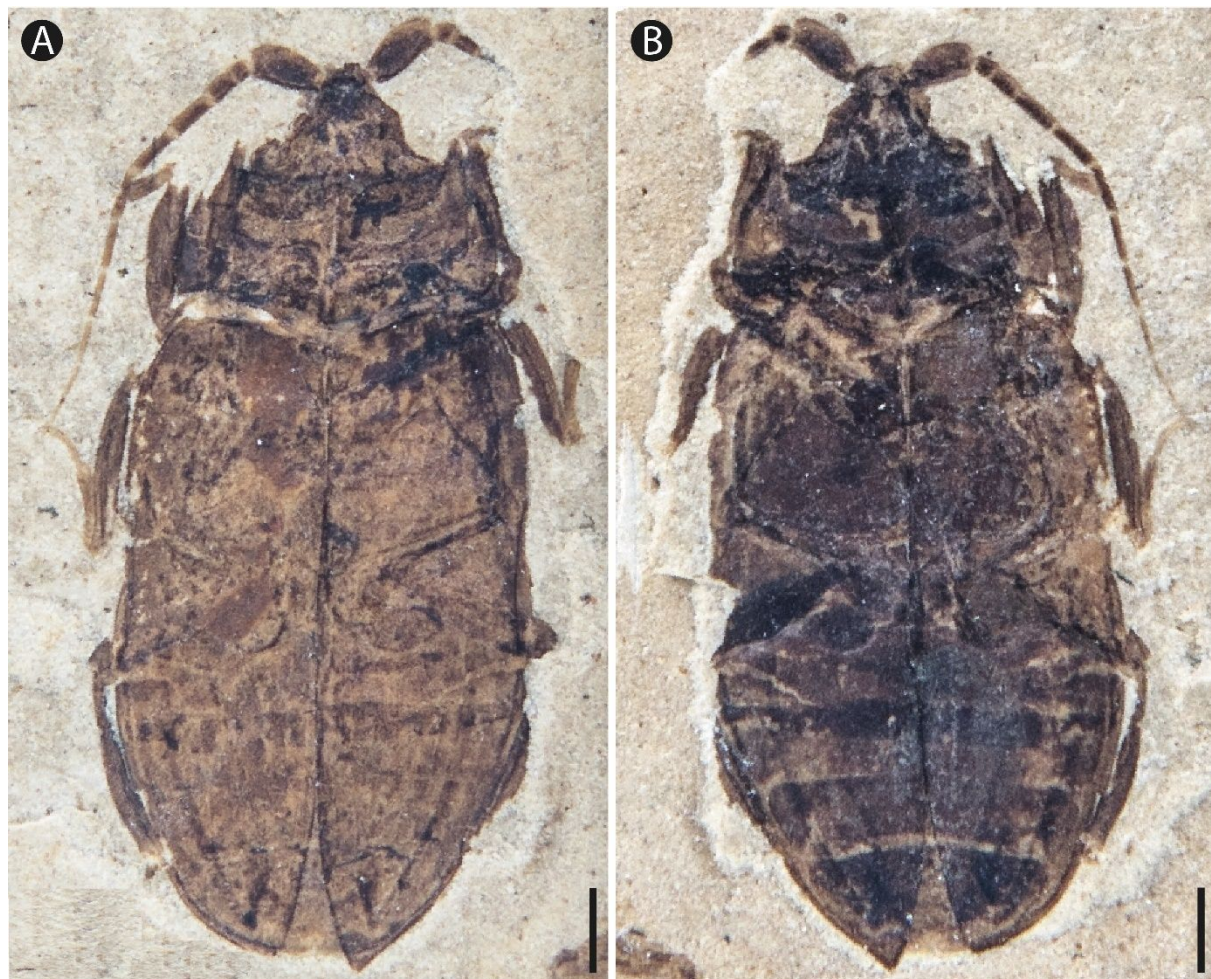
954

955 **Fig. 7.** Morphological details of *Cretaceocoleus saetosus* Tihelka, Kundrata & Cai gen. et sp. nov.  
956 (paratype, NM-T3501) from the mid-Cretaceous amber from northern Myanmar. (A) Head and prothorax  
957 in ventral view. (B) Prothoracic leg. (C) Mesothoracic leg. (D) Metathoracic leg. Abbreviations: cl,  
958 co, coxa; cp, prosternal chin-piece; fe, femur; mp, maxillary palp; mta, metatarsomere 5; pp, prosternal  
959 process; pta5, protarsomere 5; tb, tibia; tr, trochanter. Scale bars = 500  $\mu\text{m}$  (A), 250  $\mu\text{m}$  (B–D).



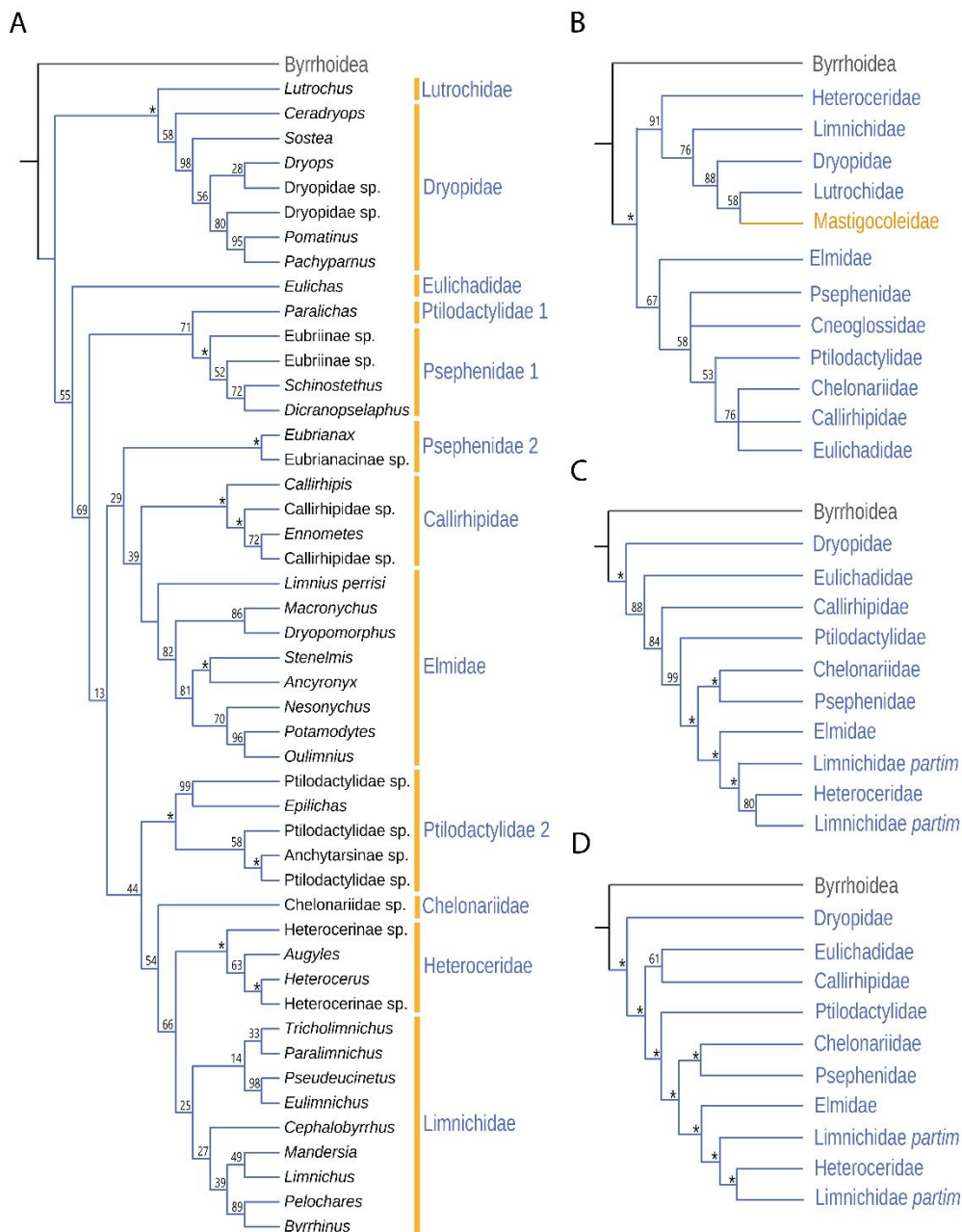
962 **Fig. 8.** Undescribed mastigocoleid (QZYX0013) from the Lower Cretaceous Yixian Formation in  
963 northeastern China in (A) dorsal; and (B) ventral views. Scale bars = 1 mm.

964  
965

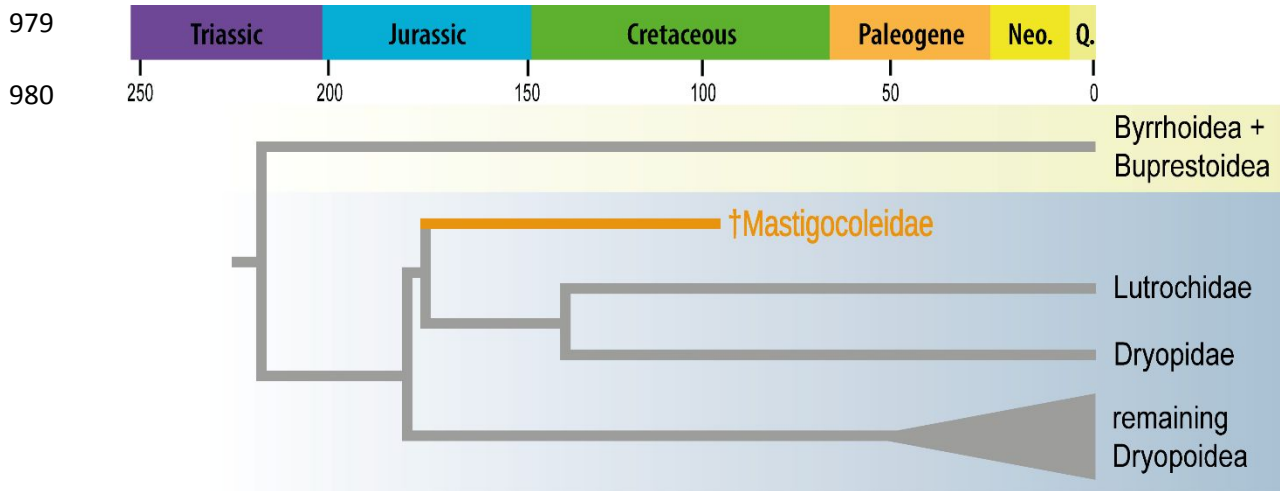


966 **Fig. 9.** Recent phylogenetic hypotheses of Dryopoidea. (A) A four-gene dataset from Kundrata *et al.*  
 967 (2017) sampling only members of Dryopoidea as ingroups and Byrrhidae as outgroup, re-analysed using  
 968 the Bayesian site-heterogeneous CAT-GTR+G model. Branch lengths omitted and nodes for major genera  
 969 collapsed for clarity. For full tree see Fig. S1. (B) Morphological phylogenetic analysis using a matrix  
 970 adapted from Lawrence (1988), sampling 112 adult and larval characters with *Mastigocoleus resinicola*  
 971 scored for 41 characters (tree length: 192 steps; consistency index: 0.542; retention index: 0.553). For  
 972 mapped character states see Fig. S2. (C) Phylogeny of Dryopoidea recovered by Cai *et al.* (2021),  
 973 sampling 68 genes analysed under a Bayesian site-heterogeneous framework. (D) Phylogeny of  
 974 Dryopoidea recovered by McKenna *et al.* (2019), sampling 89 genes analysed under a maximum  
 975 likelihood site-homogeneous framework.

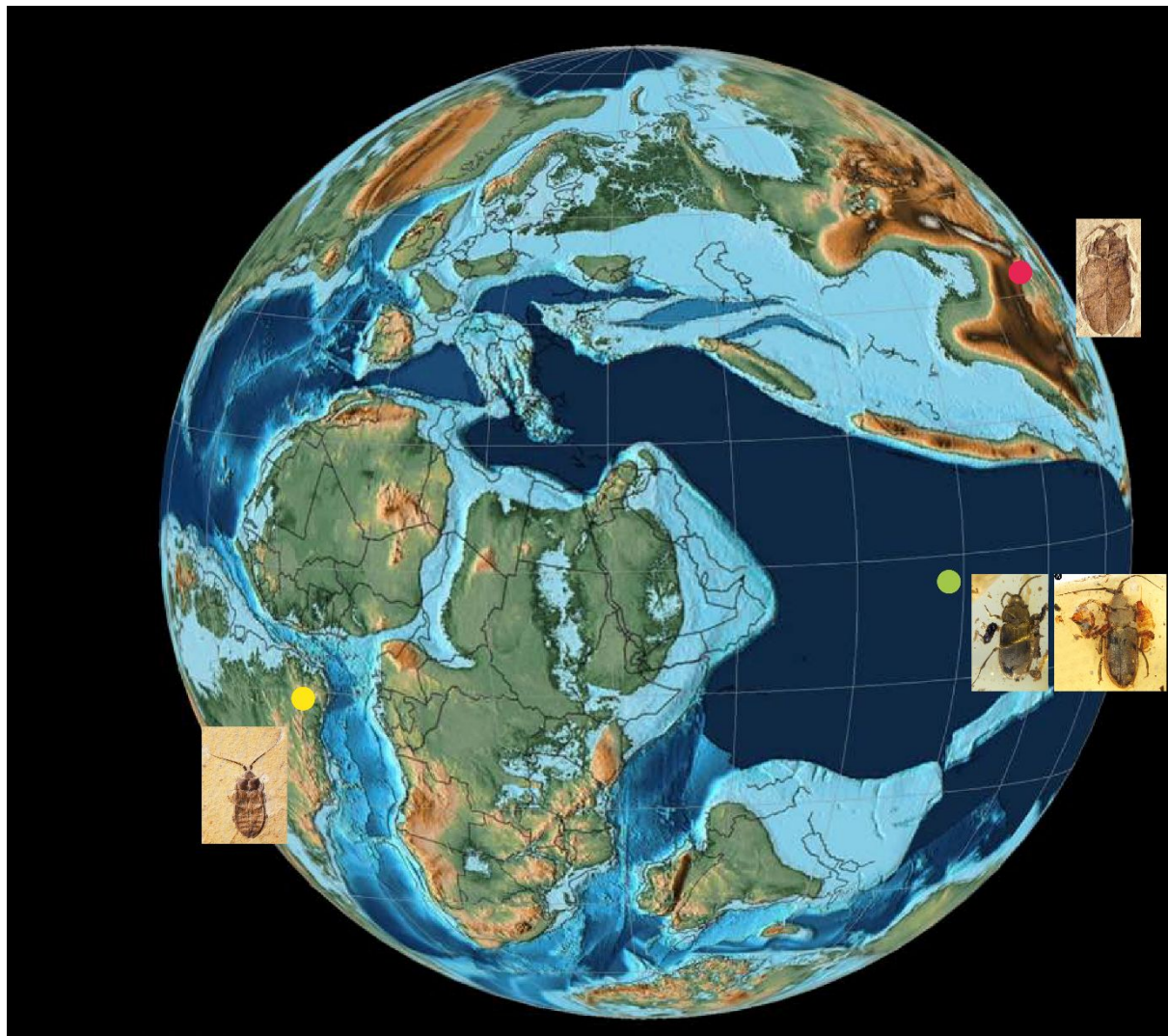
976



977 **Fig. 10.** A simplified consensus phylogenetic tree of Dryopoidea, highlighting the probable position of  
978 Mastigocoleidae. Timescale after Cai *et al.* (2021). Abbreviations: Neogene; Q., Quaternary.



981 **Fig. 11.** Geographical distribution of Mastigocoleidae during the Cretaceous (late Albian, 101 Ma),  
982 marking the locations of the fossil deposits preserving whip-antennate beetles.



983 ● Yixian Formation      ● Crato Formation      ● Burmese amber

984

985 **Graphical abstract**



†*Mastigocoleus resinicolus*



†*Mastigocoleus rhinoceros*



986



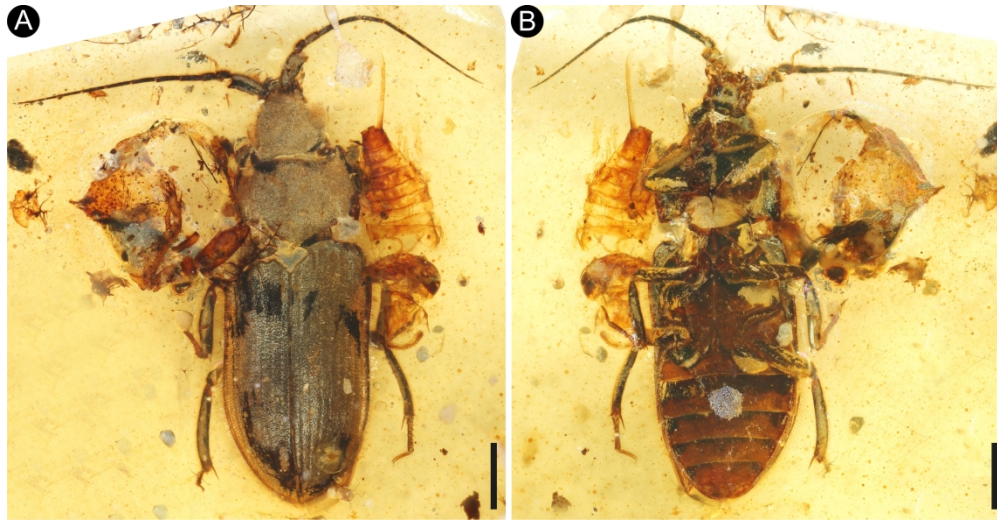


Fig. 1. Habitus of *Mastigocoleus resinicola* Tihelka & Cai gen. et sp. nov. (NIGP174708) from the mid-Cretaceous amber from northern Myanmar in (A) dorsal; and (B) ventral views. Scale bars = 1 mm.

180x92mm (600 x 600 DPI)

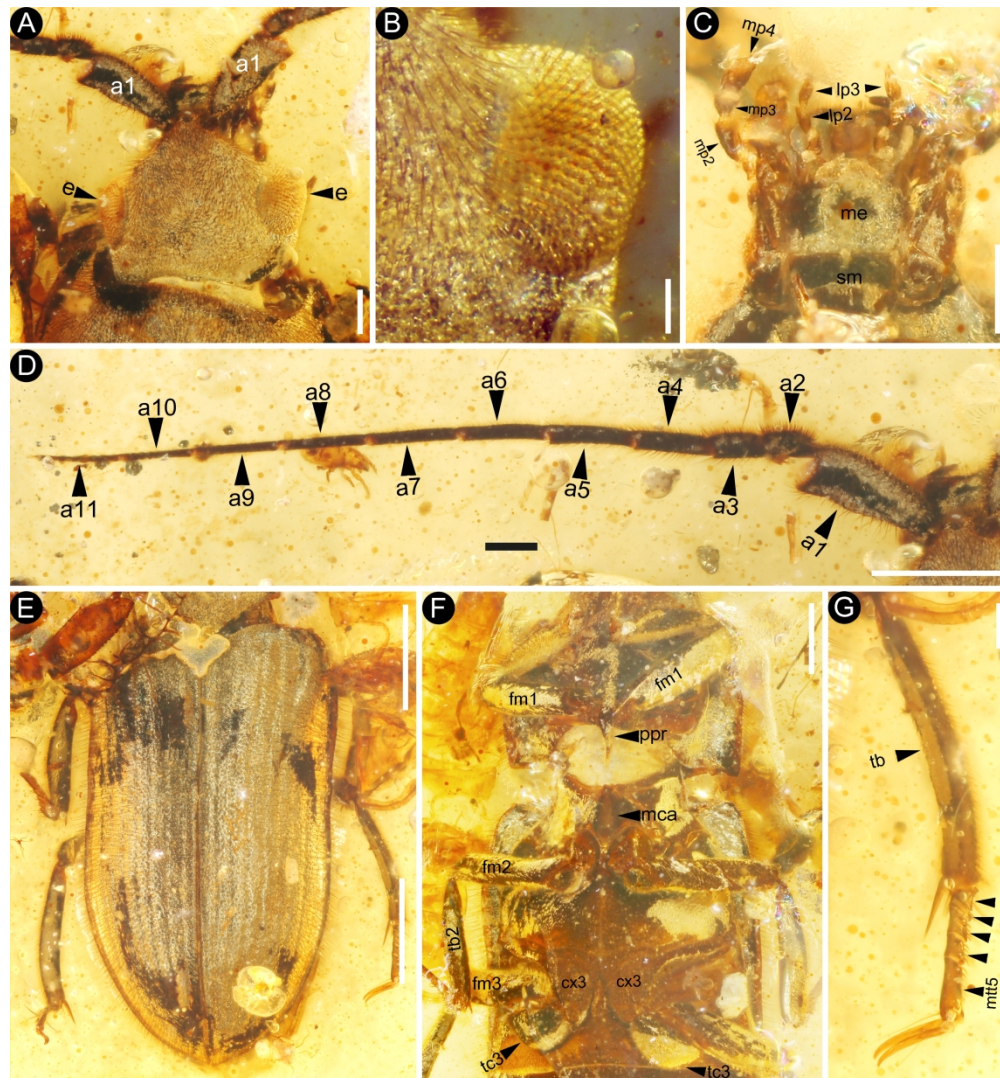


Fig. 2. Morphological details of *Mastigocoleus resinicola* Tihelka & Cai gen. et sp. nov. (NIGP174708) from the mid-Cretaceous amber from northern Myanmar. (A) head in dorsal view; (B) Compound eye in dorsal view; (C) Mouthparts in ventral view; (D) Antenna; (E) Elytra; (F) Thorax in ventral view; (G) Metathoracic leg. Abbreviations: a1–11, antennomeres 1–11; cx3, metacoxa; e, compound eye; fm1, profemur; fm2, mesofemur; fm3, metafemur; lb2–3, labial palpomeres 2–3; mca, mesoventral cavity; me, mentum; mp2–4, maxillary palpomeres 2–4; mtt5, metatarsus 5; ppr, prosternal process; sm, submentum; tb, metatibia; tb2, mesotibia; tc3, trochanter of metathoracic leg. Scale bars = 100  $\mu$ m (B, G); 250  $\mu$ m (A, C); 500  $\mu$ m (D, F), 1 mm (E).

180x193mm (600 x 600 DPI)

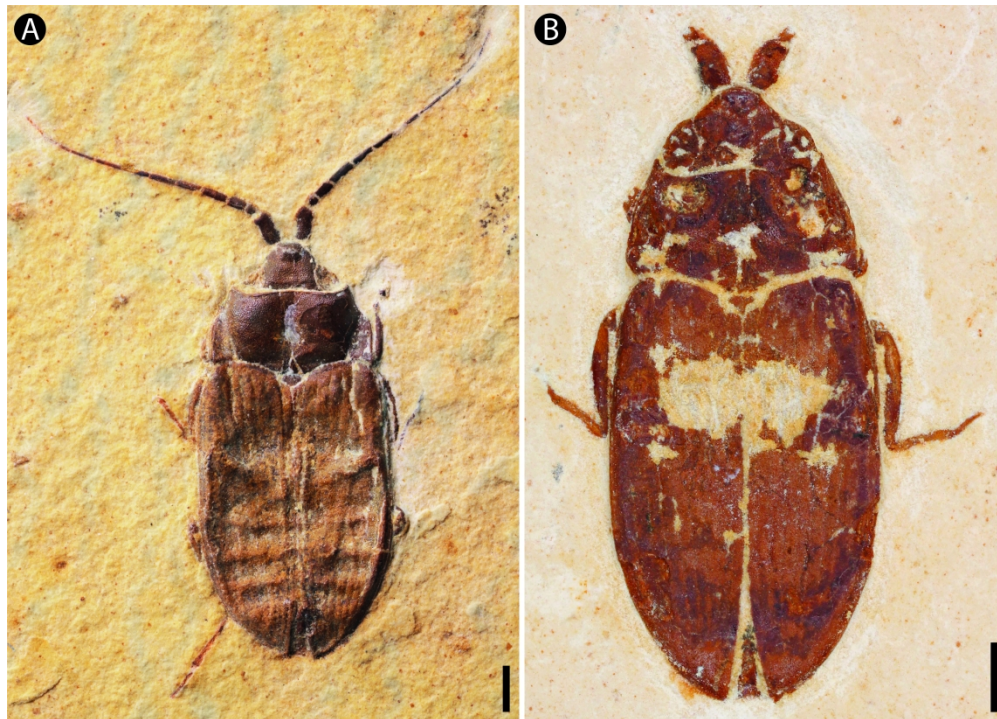


Fig. 3. Habitus of *Mastigocoleus rhinoceros* Tihelka & Cai gen. et sp. nov. from the Early Crato Formation in northeastern Brazil. (A) holotype (SMNS 66552); (B) paratype (AMNH SA43296). Scale bars = 1 mm.

204x146mm (600 x 600 DPI)

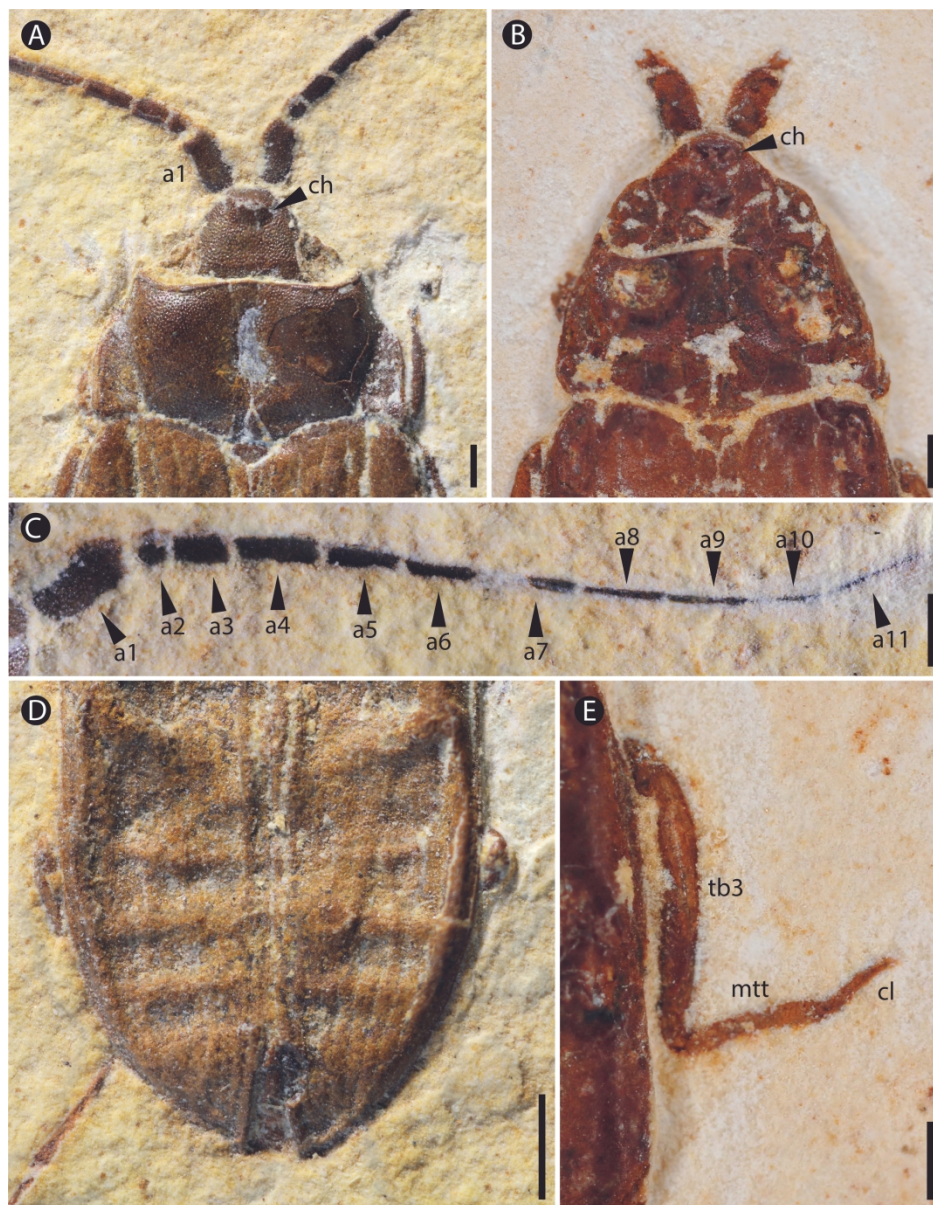


Fig. 4. Morphological details of *Mastigocoleus rhinoceros* Tihelka & Cai gen. et sp. nov. holotype (A, C, D) and paratype (B, E) from the Early Crato Formation in northeastern Brazil. (A, B) head and pronotum in dorsal view; (C) Antenna; (D) Elytral apex; (E) Metathoracic leg; (E) Elytra. Abbreviations: a1–11, antennomeres 1–11; ch, clypeal horn; cl, claw; mtt, metatarsus; tb3, metatibia. Scale bars = 500  $\mu$ m (A–C, E), 1 mm (D).

205x262mm (300 x 300 DPI)

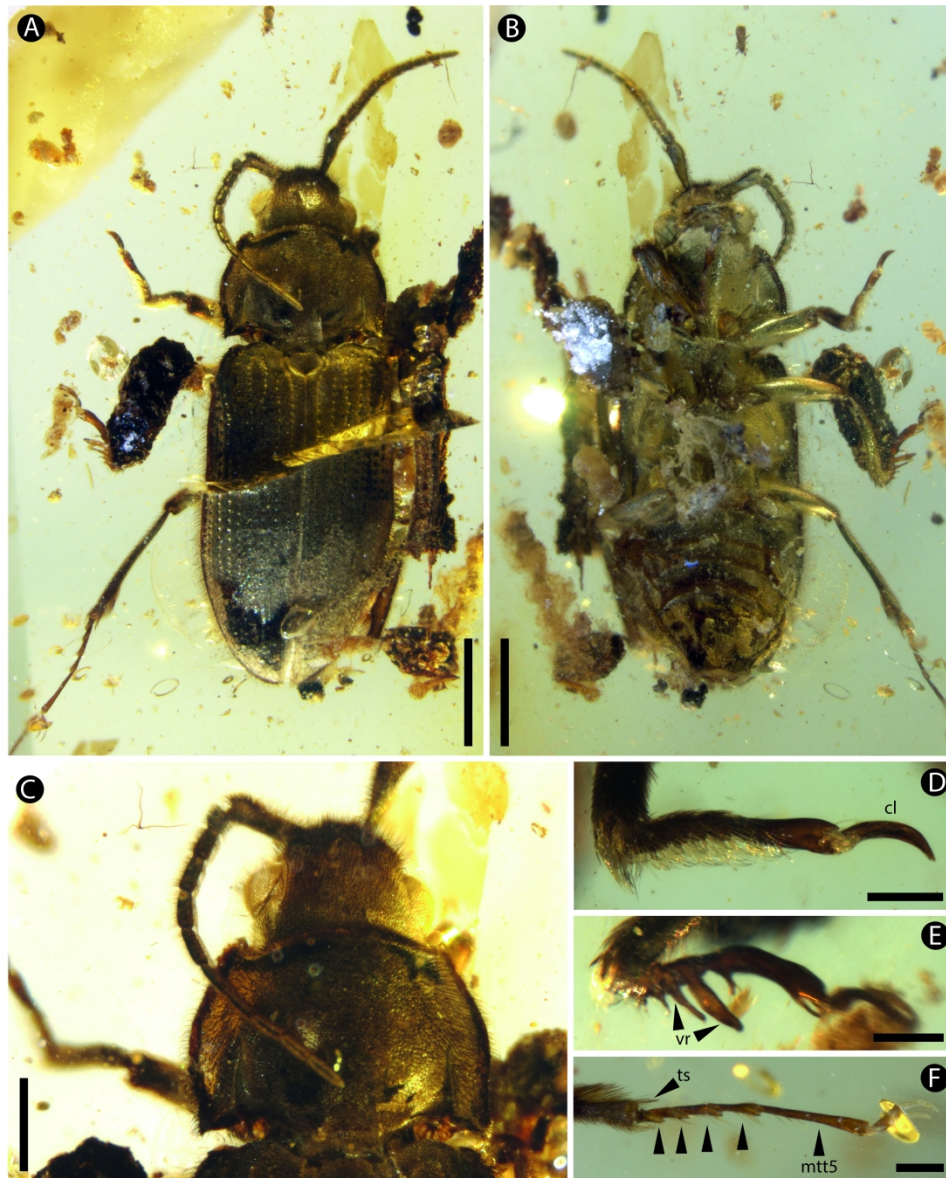


Fig. 5. *Cretaceocoleus saetosus* Tihelka, Kundrata & Cai gen. et sp. nov. (holotype, NIGP174709) from the mid-Cretaceous amber from northern Myanmar. (A) Habitus in dorsal view; (B) Habitus in ventral view; (C) Head and pronotum in dorsal view; (D) Protarsus; (E) Mesotarsus; (F) Metatarsus. Abbreviations: c, claws; mtt5, metatarsus 5; ts, tibial spur; vr, mesotarsal ventral rami. Scale bars = 500  $\mu$ m (D–F), 500  $\mu$ m (C), 1 mm (A, B).

165x204mm (600 x 600 DPI)

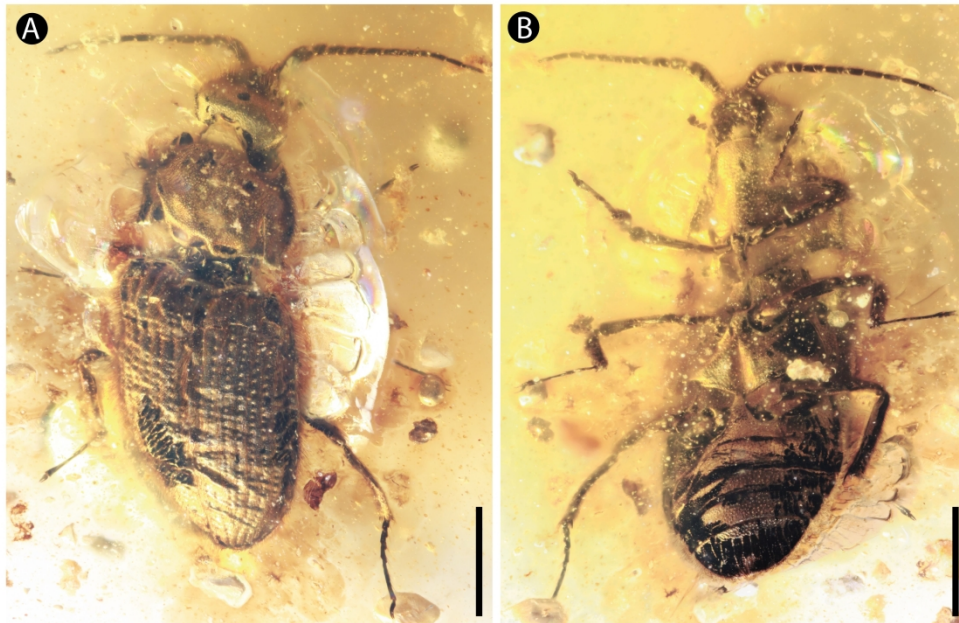


Fig. 6. *Cretaceocoleus saetosus* Tihelka & Cai gen. et sp. nov. (paratype, NM...) from the mid-Cretaceous amber from northern Myanmar. Habitus in dorsal (A) and ventral (B) views. Scale bars = 1 mm.

206x167mm (600 x 600 DPI)

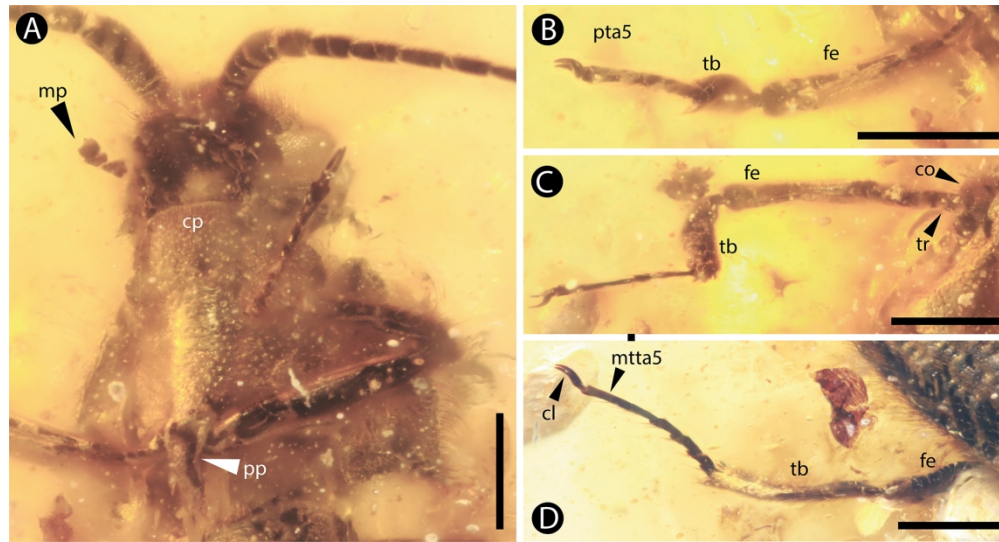


Fig. 7. Morphological details of *Cretaceocoleus saetosus* Tihelka, Kundrata & Cai gen. et sp. nov. (paratype, NM-T3501) from the mid-Cretaceous amber from northern Myanmar. (A) Head and prothorax in ventral view. (B) Prothoracic leg. (C) Mesothoracic leg. (D) Metathoracic leg. Abbreviations: cl, claw; co, coxa; cp, prosternal chin-piece; fe, femur; mp, maxillary palp; mtt5, metatarsomere 5; pp, prosternal process; pta5, protarsomere 5; tb, tibia; tr, trochanter. Scale bars = 500  $\mu$ m (A), 250  $\mu$ m (B–D).

714x384mm (72 x 72 DPI)



Fig. 8. Undescrbed mastigocoleid (QZYX0013) from the Lower Cretaceous Yixian Formation in northeastern China in (A) dorsal; and (B) ventral views. Scale bars = 1 mm.

160x129mm (220 x 220 DPI)



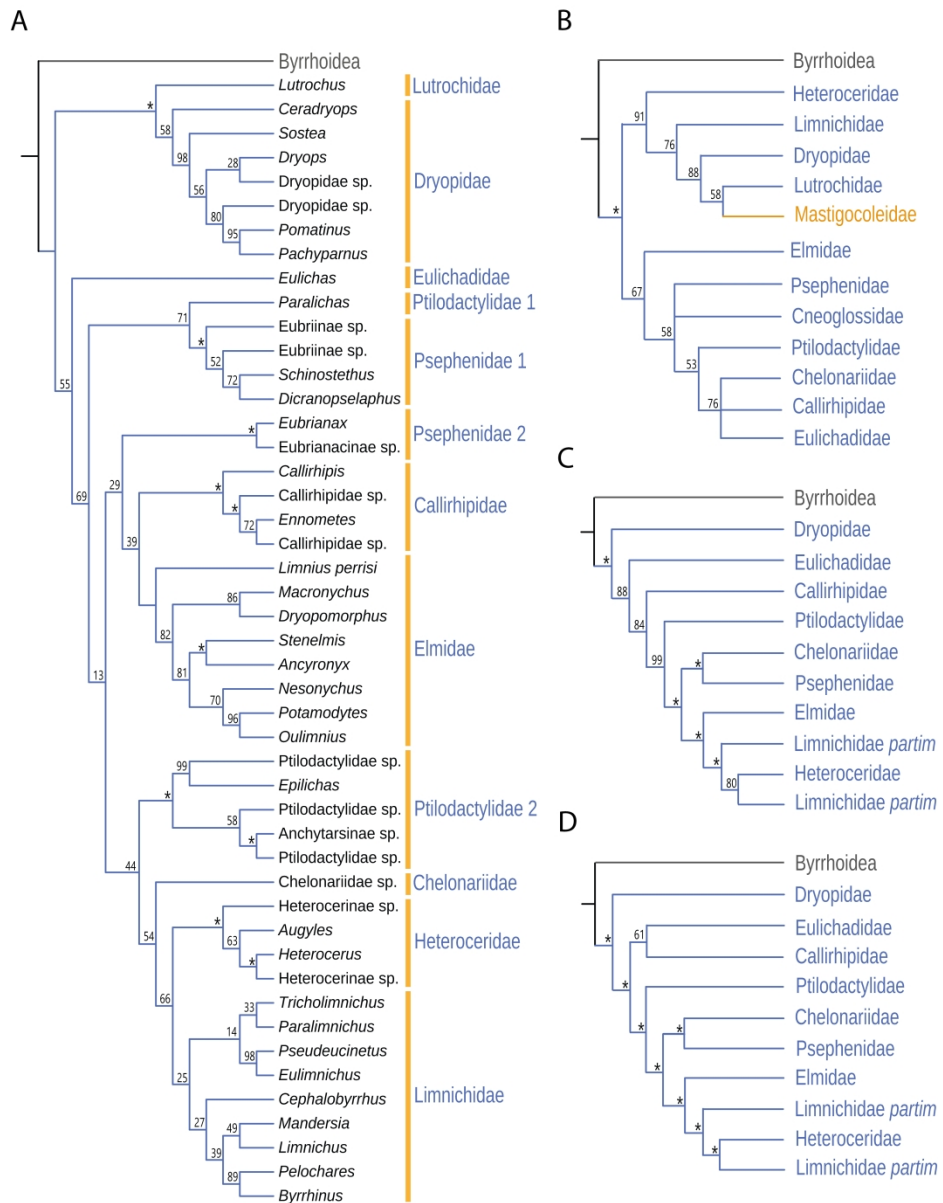


Fig. 9. Recent phylogenetic hypotheses of Dryopoidea. (A) A four-gene dataset from Kundrata et al. (2017) sampling only members of Dryopoidea as ingroups and Byrrhidae as outgroup, re-analysed using the Bayesian site-heterogeneous CAT-GTR+G model. Branch lengths omitted and nodes for major genera collapsed for clarity. For full tree see Fig. S1. (B) Morphological phylogenetic analysis using a matrix adapted from Lawrence (1988), sampling 112 adult and larval characters with *Mastigocoleus resinicola* scored for 41 characters (tree length: 192 steps; consistency index: 0.542; retention index: 0.553). For mapped character states see Fig. S2. (C) Phylogeny of Dryopoidea recovered by Cai et al. (2021), sampling 68 genes analysed under a Bayesian site-heterogeneous framework. (D) Phylogeny of Dryopoidea recovered by McKenna et al. (2019), sampling 89 genes analysed under a maximum likelihood site-homogeneous framework.

202x261mm (600 x 600 DPI)

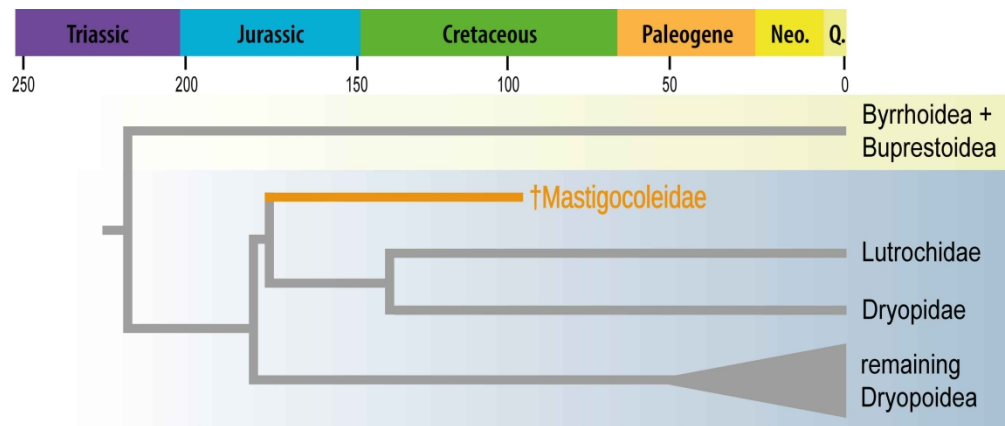


Fig. 10. A simplified consensus phylogenetic tree of Dryopoidea, highlighting the probable position of Mastigocoleidae. Timescale after Cai et al. (2021). Abbreviations: Neogene; Q., Quaternary.

153x64mm (600 x 600 DPI)

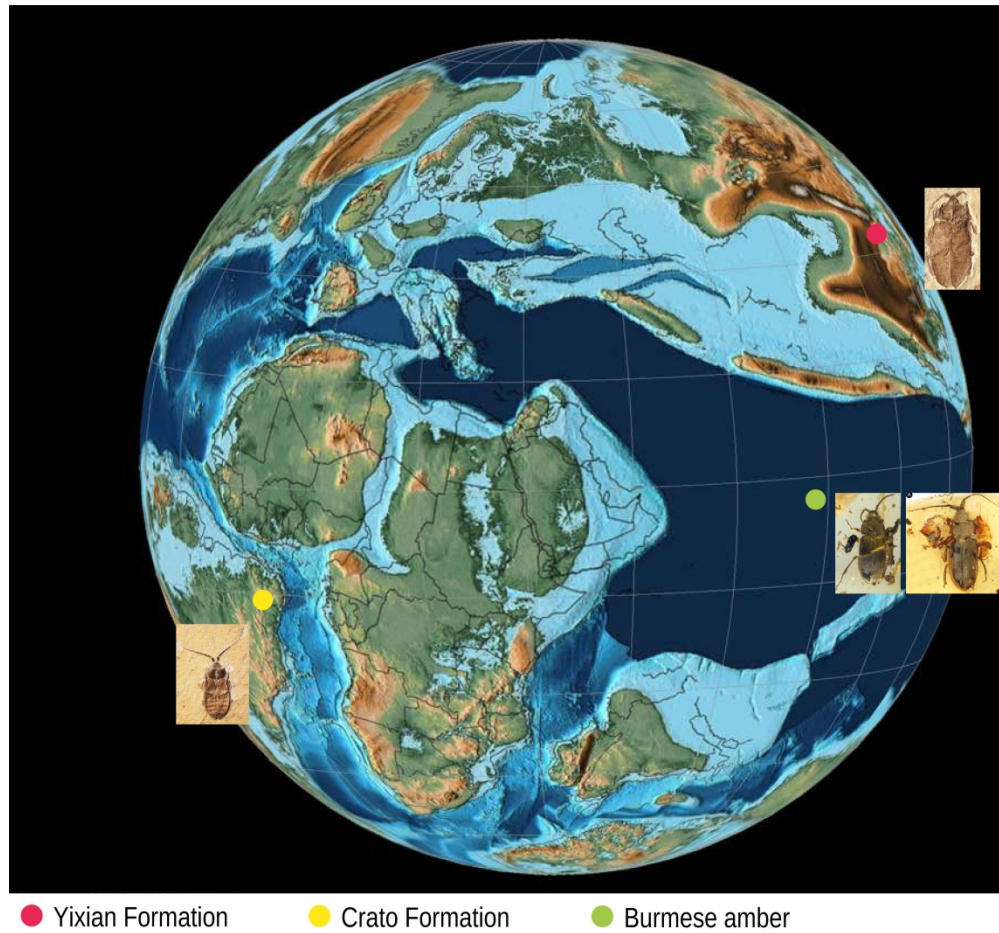


Fig. 11. Geographical distribution of Mastigocoleidae during the Cretaceous (late Albian, 101 Ma), marking the locations of the fossil deposits preserving whip-antennate beetles.

209x194mm (600 x 600 DPI)

## Supporting Information for

### **Mastigocoleidae fam. nov., a new Mesozoic family of whip-antennate beetles and the early evolution of Dryopoidea (Coleoptera)**

Erik Tihelka, Manfred Jäch, Robin Kundrata, Yan-Da Li, Michael S. Engel, Jesus Lozano-Fernandez, Diying Huang and Chenyang Cai

Journal: *Insect Systematics and Diversity*

#### **Supplemental Figures**

**Figure S1** Phylogeny of Dryopoidea based on a four-gene alignment from Kundrata et al. (2017) with restricted taxon sampling analysed with the CAT-GTR+G4 model in PhyloBayes.

**Figure S2** Most parsimonious tree of Dryopoidea obtained in tnt v. 1.5 with 'New Technology Search' under implied weighting showing the position of *Mastigocoleus resinicola*, with mapped character states.

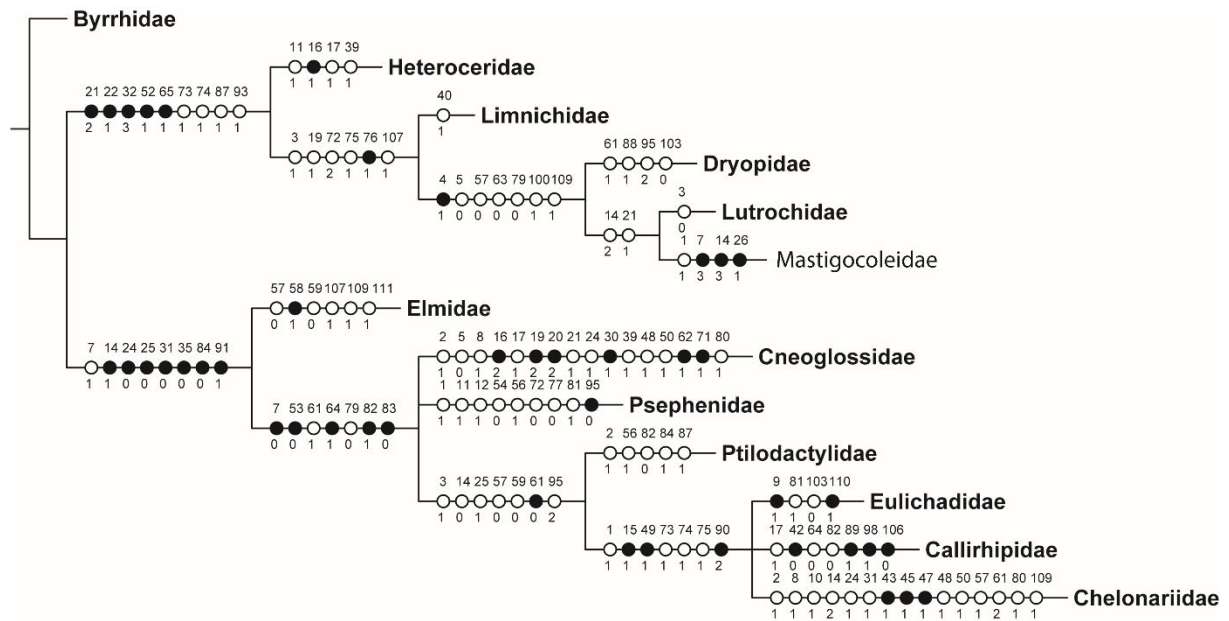
#### **Supplemental Tables**

**Table S1** GenBank accessions for the selected taxa from Kundrata et al. (2017) re-analysed with the CAT-GTR+G4 model.

**Table S2** Morphological matrix for Dryopoidea, modified from Lawrence (1988), including *Mastigocoleus resinicola*, in .tnt format.



**Figure S2.** Most parsimonious tree of Dryopoidea obtained in tnt v. 1.5 with ‘New Technology Search’ under implied weighting showing the position of *Mastigocoleus resinicola*, with mapped character states. Character matrix adapted from Lawrence (1988).



**Table S1.** GenBank accessions for the selected taxa from Kundrata et al. (2017) re-analysed with the CAT-GTR+G4 model.

Superfamily/family	Taxon	18S	28S	<i>rrnL</i>	<i>coxI</i>
<b>BYRRHOIDEA</b>					
Byrrhidae	<i>Byrrhus pilula</i>	AF427604	DQ198705	DQ198625	DQ198548
Byrrhidae	<i>Byrrhus</i> sp.	KX092934	KX093068	N	KX092799
Byrrhidae	<i>Curimus erichsoni</i>	KX092935	KX093069	KX092676	KX092800
Byrrhidae	<i>Simplocaria</i> sp.	–	KM364160	KM364303	N
Byrrhidae	<i>Chalcosphaerium</i> sp.	–	EF214158	N	EF214030
Byrrhidae	<i>Chaetophora spinosa</i>	AF451929	DQ198706	N	N
Byrrhidae	<i>Curimopsis setigera</i>	AF451930	DQ198707	N	N
<b>DRYOPOIDEA</b>					
Callirhipidae	Callirhipidae sp1	DQ100490	DQ198726	DQ198637	DQ198560
Callirhipidae	Callirhipidae sp2	KF625511	KF626112	KF625818	KF625211
Callirhipidae	<i>Callirhipis dissimilis</i>	KX092944	KX093078	KX092685	KX092809
Callirhipidae	<i>Callirhipis suturalis</i>	KX092942	KX093076	KX092683	KX092807
Callirhipidae	<i>Callirhipis</i> sp.	KX092943	KX093077	KX092684	KX092808
Callirhipidae	<i>Ennometes cf. testaceicornis</i>	KX092946	KX093080	KX092686	KX092810
Chelonariidae	Chelonariidae sp1	KX092998	KX093126	KX092733	KX092859
Chelonariidae	Chelonariidae sp2	DQ100488	DQ198724	DQ198635	DQ198558
Chelonariidae	Chelonariidae sp3	KX092997	KX093125	KX092732	KX092858
Chelonariidae	Chelonariidae sp4	KF625509	KF626110	KF625817	KF625210
Dryopidae	Dryopidae sp1	KX092972	KX093102	KX092710	KX092836
Dryopidae	Dryopidae sp2	KX092995	KX093123	KX092730	KX092856
Dryopidae	Dryopidae sp3	KX092974	KX093104	KX092712	KX092838
Dryopidae	<i>Ceradryops matei</i>	–	EF209494	N	EF209434
Dryopidae	<i>Dryops lutulentus</i>	KX092976	KX093106	KX092714	KX092840
Dryopidae	<i>Dryops</i> sp.	KX092971	KX093101	KX092709	KX092835
Dryopidae	<i>Pachyarnus</i> sp1	KX092973	KX093103	KX092711	KX092837
Dryopidae	<i>Pachyarnus</i> sp2	KX092975	KX093105	KX092713	KX092839
Dryopidae	<i>Pomatinus substriatus</i>	AF451924	DQ198708	DQ198626	DQ198549
Dryopidae	<i>Sostea</i> sp1	KX092989	KX093118	KX092725	KX092851
Dryopidae	<i>Sostea</i> sp2	KX092982	KX093111	KX092720	KX092845
Dryopidae	<i>Sostea</i> sp3	KX092992	KX093120	KX092728	KX092854
Dryopidae	<i>Sostea</i> sp4	KX092987	KX093116	KX092724	KX092849
Dryopidae	<i>Sostea</i> sp5	KX092977	KX093107	KX092715	KX092841
Dryopidae	<i>Sostea</i> sp6	KX092983	KX093112	KX092721	KX092846
Dryopidae	<i>Sostea</i> sp7	KX092985	KX093114	KX092723	KX092847
Dryopidae	<i>Sostea</i> sp.8	KX092990	KX093119	KX092726	KX092852

Dryopidae	<i>Sostea</i> sp9	KX092979	KX093109	KX092717	KX092842
Dryopidae	<i>Sostea</i> sp10	KX092980	KX093110	KX092718	KX092843
Elmidae	<i>Ancyronyx raffaelacatharina</i>	KX093016	KX093141	KX092744	KX092877
Elmidae	<i>Dryopomorphus</i> sp	KX093000	KX093128	KX092734	KX092861
Elmidae	<i>Limnius perrisi</i>	AF451915	AJ862767	AJ862736	AJ862800
Elmidae	<i>Macronychus quadrituberculatus</i>	AF451920	DQ198713	EF209458	EF209578
Elmidae	<i>Oulimnius rivularis</i>	AF451913	DQ198714	DQ198628	DQ198551
Elmidae	<i>Potamodytes</i> sp1	KX093001	KX093129	KX092735	KX092862
Elmidae	<i>Potamodytes</i> sp2	AF451912	DQ198715	DQ198629	DQ198552
Elmidae	<i>Potamodytes</i> sp3	KX093014	KX093140	KX092742	KX092875
Elmidae	<i>Stenelmis</i> sp1	KX093003	KX093131	N	KX092864
Elmidae	<i>Stenelmis</i> sp2	KX093018	KX093143	KX092745	KX092879
Elmidae	<i>Stenelmis</i> sp3	KX093004	KX093132	KX092737	KX092865
Elmidae	<i>Stenelmis</i> sp4	KX093017	KX093142	N	KX092878
Elmidae	<i>Stenelmis</i> sp5	KX093013	KX093139	N	KX092874
Elmidae	<i>Stenelmis</i> sp6	KX093019	KX093144	N	KX092880
Elmidae	<i>Stenelmis</i> sp7	KX093005	KX093133	N	KX092866
Elmidae	<i>Stenelmis</i> sp8	KX093006	KX093134	N	KX092867
Elmidae	<i>Stenelmis</i> sp9	KX093008	KX093135	EF209466	KX092869
Elmidae	<i>Nesonychus</i> sp.	KX093012	KX093138	KX092741	KX092873
Eulichadidae	<i>Eulichas baeri</i>	KX092940	KX093074	KX092681	KX092805
Eulichadidae	<i>Eulichas dudgeoni</i>	KX092936	KX093070	KX092677	KX092801
Eulichadidae	<i>Eulichas</i> cf. <i>fasciolata</i>	KX092937	KX093071	KX092678	KX092802
Eulichadidae	<i>Eulichas funebris</i> 1	KX092938	KX093072	KX092679	KX092803
Eulichadidae	<i>Eulichas funebris</i> 2	KX092939	KX093073	KX092680	KX092804
Eulichadidae	<i>Eulichas</i> sp.1	KX092941	KX093075	KX092682	KX092806
Eulichadidae	<i>Eulichas</i> sp.2	DQ100489	DQ198725	DQ198636	DQ198559
Heteroceridae	<i>Augyles maritimus</i>	AF451927	DQ198717	N	N
Heteroceridae	<i>Heterocerus</i> sp1	AF451928	DQ198718	DQ198630	DQ198553
Heteroceridae	Heterocerinae sp1	KX093032	KX093157	KX092757	KX092893
Heteroceridae	Heterocerinae sp2	KX093031	KX093156	KX092756	KX092892
Limnichidae	<i>Byrrhinus</i> sp1	KX093028	KX093153	KX092753	KX092889
Limnichidae	<i>Byrrhinus</i> sp2	KX093027	KX093152	KX092752	KX092888
Limnichidae	<i>Byrrhinus</i> sp3	EF209533	N	EF209473	EF209593
Limnichidae	<i>Cephalobyrrhus</i> sp.	EF209534	N	EF209474	EF209594
Limnichidae	<i>Eulimnichus</i> sp.	AF451922	HQ634240	N	N
Limnichidae	<i>Limnichus pygmaeus</i>	AF451923	DQ198719	DQ198631	DQ198554
Limnichidae	<i>Limnichus</i> sp1	KX093025	KX093150	KX092751	KX092886
Limnichidae	<i>Limnichus</i> sp2	KX093022	KX093147	KX092748	KX092883
Limnichidae	<i>Mandersia</i> sp1	KX093029	KX093154	KX092754	KX092890
Limnichidae	<i>Mandersia</i> sp2	KX093030	KX093155	KX092755	KX092891



Limnichidae	<i>Pelochares</i> sp1	KX093023	KX093148	KX092749	KX092884
Limnichidae	<i>Pelochares</i> sp2	KX093024	KX093149	KX092750	KX092885
Limnichidae	<i>Paralimnichus</i> sp.	KX093020	KX093145	KX092746	KX092881
Limnichidae	<i>Tricholimnichus</i> sp.	KX093026	KX093151	N	KX092887
Lutrochidae	<i>Lutrochus</i> sp.	EF209539	HQ634239	EF209479	EF209599
Psephenidae	<i>Eubrianax</i> sp.	DQ100485	DQ198721	DQ198632	DQ198555
Psephenidae	Eubrianacinae sp1	KF625503	KF626103	KF625811	KF625204
Psephenidae	Eubriinae sp1	KX092947	N	KX092687	KX092813
Psephenidae	Eubriinae sp2	KX092948	N	KX092688	KX092815
Psephenidae	<i>Dicranopselaphus</i> sp1	KX092949	N	KX092689	KX092812
Psephenidae	<i>Dicranopselaphus</i> sp2	KF625514	KF626115	KF625820	KF625214
Psephenidae	<i>Dicranopselaphus</i> sp3	KF625515	KF626116	KF625821	KF625215
Psephenidae	<i>Dicranopselaphus</i> sp4	KX092951	KX093082	KX092691	KX092811
Psephenidae	<i>Schinostethus brevis</i>	KX092950	KX093081	KX092690	KX092814
Ptilodactylidae	Anchytarsinae sp1	KX092963	KX093094	KX092702	KX092827
Ptilodactylidae	<i>Epilichas</i> sp1	KX092968	KX093099	KX092706	KX092832
Ptilodactylidae	<i>Paralichas pectinatus</i>	DQ100486	DQ198722	DQ198633	DQ198556
Ptilodactylidae	<i>Ptilodactyla serricornis</i>	AF451931	DQ198723	DQ198634	DQ198557
Ptilodactylidae	<i>Ptilodactyla</i> sp1	KX092956	KX093087	KX092696	KX092820
Ptilodactylidae	<i>Ptilodactyla</i> sp2	KX092954	KX093085	KX092694	KX092818
Ptilodactylidae	<i>Ptilodactyla</i> sp3	KX092969	KX093100	KX092707	KX092833
Ptilodactylidae	Ptilodactylinae sp1	KX092952	KX093083	KX092692	KX092816
Ptilodactylidae	Ptilodactylinae sp2	KX092958	KX093089	KX092698	KX092822
Ptilodactylidae	Ptilodactylinae sp3	KX092959	KX093090	KX092699	KX092823
Ptilodactylidae	Ptilodactylinae sp4	KF625520	KF626121	KF625825	KF625219
Ptilodactylidae	Ptilodactylinae sp5	KF625522	KF626123	KF625827	KF625221
Ptilodactylidae	Ptilodactylinae sp6	KX092955	KX093086	KX092695	KX092819
Ptilodactylidae	Ptilodactylinae sp7	KX092957	KX093088	KX092697	KX092821
Ptilodactylidae	Ptilodactylinae sp8	KF625518	KF626119	KF625824	KF625217
Ptilodactylidae	Ptilodactylinae sp9	KX092953	KX093084	KX092693	KX092817
Ptilodactylidae	Ptilodactylidae sp1	KF625521	KF626122	KF625826	KF625220
Ptilodactylidae	Ptilodactylidae sp2	KX092964	KX093095	KX092703	KX092828
Ptilodactylidae	Ptilodactylidae sp3	KX092965	KX093096	KX092704	KX092829
Ptilodactylidae	Ptilodactylidae sp4	KX092961	KX093092	KX092700	KX092825
Ptilodactylidae	Ptilodactylidae sp5	KF625517	KF626118	KF625823	KF625222
Ptilodactylidae	Ptilodactylidae sp6	KX092962	KX093093	KX092701	KX092826

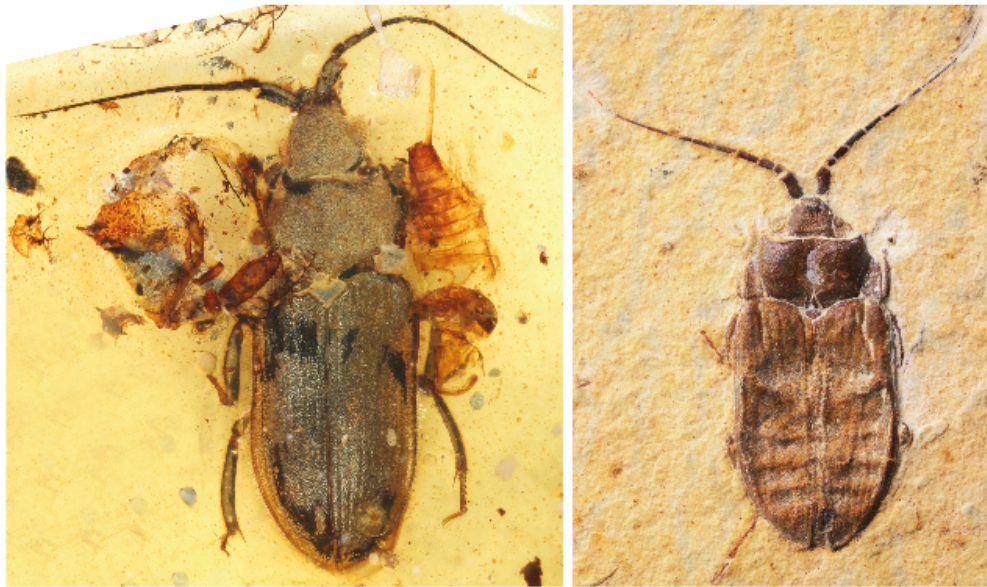
**Table S2.** Morphological matrix for Dryopoidea, modified from Lawrence (1988), including *Mastigocoleus resinicola*, in .tnt format.

```

xread
112 13
Byrrhidae
    010010200000000000000001110000011001101010100000000011021-
1220000000000000000001000110001000000110000010111010000
Dryopidae 001100100000000000102111100000130010010001000000001--
0200121000100100021111100000110011000010210011010111101000
Lutrochidae    0001001000000200001011111000001-
00100100010000000000100100122000100100021111100000110010000000010011
111111101010
Mastigocoleus
1011?03000??03??00101111110??0130010010??00000??00??????????00?????
????????????????????????????????????????????????????????
Eulichadidae    1010100010000010001100001000000-
00010100110000001000000200010011011001021110110011?00?002-
100210000010111000100
Callirhipidae
    101010000011101010100000100000010001010000000000100000020001001
00000010211101100000000011--01021011111-110000000
Ptilodactylidae 0110100000000000001000001000000-
00010100010000000000010100020011000000020000110000010010001000210000
011111000000
Cneoglossidae    01000001-10001021-221001000001010001011001000001-
10001021-221111000000120000110101????????????????????????????
Chelonariidae    1110100101111210001100011000001-0001010011101011-
10001021-022011011000021110110101?????102-11021001111111001000
Psephenidae
    10001000011101000000000000000002000001000100000000000011-
22101100000000000000011000000001000010000001111000000
Elmidae
    000011100000010000000000000000020000010001000000000011020102201
0000100010000101000100000001000110010001111101010
Limnichidae    00101120000000000001021111000001-
00100101010000000001--021-
22201010010002111110100011001000001011001011111100000
Heteroceridae
    0000112000100001100021011000001300100110010000000001--021-
222010100100001100001000110010000010110010011111000000
;

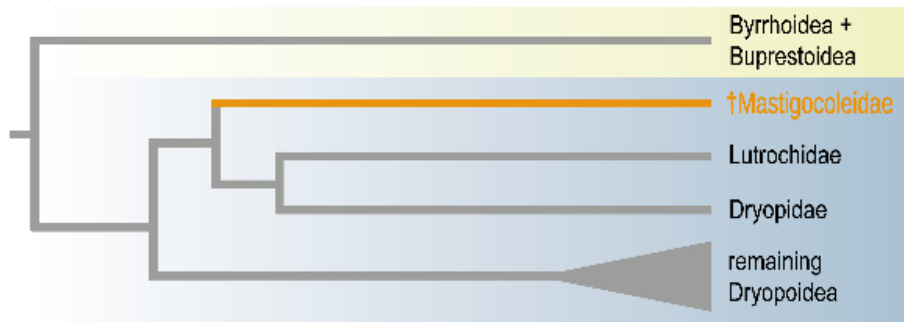
proc /;
comments 0
;

```



†*Mastigocoleus resinicola*

†*Mastigocoleus rhinoceros*



108286

169x162mm (96 x 96 DPI)

10<sup>th</sup> February 2022  
Bristol, UK

**Response to reviewer comments: ISD-2021-0061**

Dear Dr. Bond,

Thank you for your consideration of our manuscript entitled “ **Mastigocoleidae fam. nov., a New Mesozoic Beetle Family and the Early Evolution of Dryopoidea (Coleoptera)**”. We thank the reviewers for the time and attention they have dedicated to providing insightful feedback on the manuscript. We have reviewed the comments and revised the manuscript accordingly, please find our responses detailed point-by-point below. Changes to the text have been marked in the ‘track changes mode’ in the annotated file. A ‘clean’ version of the manuscript without annotations is attached as well.

Among the main changes, we now uploaded the data to the Mendeley online repository. The accession numbers for molecular data are provided in the Supplementary Information.

We hope that the revised version addresses all the reviewer’s comments and look forward to hearing from you soon.

Kind regards,

*Erik Tihelka*      *Chenyang Cai*

Erik Tihelka

Chenyang Cai

**REVIEWER #1**

This manuscript is an excellent contribution that describes new fossil taxa that reflect on the evolution of the Superfamily Dryopoidea. The information it provides and the authors' analysis is new and they help to unravel the development of the "dryopoid" life style. I recommend that it is accepted "As Is" and I look forward to seeing it in print.

Thank you very much for your comments. We made a few minor editing changes to the manuscript and activated the data repository on Mendeley Data, so our data are freely available to the entomological community.

**REVIEWER #2**

Dear Authors,

I have really appreciated the work done and the great effort put in presenting the new beetle family and in its contextualization within the Dryopoidea clade.

I generally agree with all comments, results and notes provided; there are only a few minor issues I would like being addressed before the final acceptance (check the revised draft).

I remain available for further help or an open confrontation if needed.

Sincerely

Thank you very much for your comments. We made all the changes indicated in the review file. Many thanks for spotting mistakes that we overlooked.

As suggested in the annotated PDF file, we double-checked if *M. resinicola* is the correct form of the name. Although counterintuitive, in Latin '-cola' is the masculine form of this suffix. This represents an exception to the rule of thumb that -us is masculine in Latin, and -a or -ae are feminine, which does not apply universally. We confirm that the masculine form of the name is "*resinicola*".