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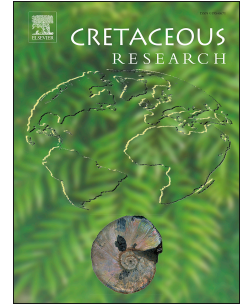


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1 A new mid-Cretaceous fossil genus of stonefly (Plecoptera: Perlidae) from the Bur-
2 mese amber

3

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15

16 ABSTRACT

17 A new genus and species of stonefly is described and figured from the mid-Cretaceous Burmese
18 amber as †*Burmaperla pouilloni* Jouault & Nel gen. et sp. nov. The placement of this new genus
19 and species within the Perlidae is corroborated by an in-depth comparison of apomorphies. This
20 new species differs from all other Acroneuriinae from the mid-Cretaceous Burmese amber biota,
21 *inter alia*, owing to its wing venation with ScP reaching RA beyond ra-rp, RP with three branches,
22 MP partially fused with the upper branch of CuA, CuA with four branches, its hammer nearly circu-
23 lar and its genitalia with paraprocts weakly sclerotized, abruptly upcurved, thinning towards the
24 apex and symmetrical. This new species increases the diversity of Acroneuriinae stoneflies in the
25 Burmese amber biota, and combined with the geological history of the Burmese terrane is used to
26 discuss the putative presence of Antarctoperlaria in mid-Cretaceous Burmese amber.

27

28 *Keywords:*

29 Fossil record, gen. et sp. nov., Insecta, paleobiogeography, taxonomy

30

31 **1. Introduction**

32 The order Plecoptera, also called stoneflies because the adults are often found on rocks near streams
33 or ponds, is the sister group of a clade that would comprise all the other polyneopteran orders ex-
34 cept the more inclusive clade Zoraptera + Dermaptera (Wipfler et al., 2019: fig. 1). The current di-
35 versity of Plecoptera is greater than 3497 species (Fochetti and de Figueroa 2007). The number of
36 families of Plecoptera varies according to the authors but greatly benefits from the advances related
37 to the study of molecular data (South et al., 2021) despite this the position of some taxa remains
38 doubtful (e.g. *Megaleuctra*). The fossil record of Plecoptera represents ca. 300 species distributed in
39 ca. 25 families (sensu <http://fossilworks.org/>, last accessed September 29, 2021). Based on the fossil
40 record, the oldest described stem-groups Plecoptera date back to the Moscovian (ca. 314.6–311.45
41 Ma) from the Yanghugou Formation of China (Béthoux et al., 2011), and from France (ca. 308–306
42 Ma; Schubnel et al., 2019). Using molecular data, Letsch et al. (2021) inferred one of the most
43 comprehensive time-calibrated trees for extant Plecoptera, which filled an important gap on the di-
44 vergence time estimates of all the main clades of extant stoneflies. Relying on seven fossil calibra-
45 tions, this dated tree suggests that the crown-Plecoptera arose during the Guadalupian, ca. 265 Ma
46 (294.2 – 235.5 Ma, 95% HPD) (Letsch et al., 2021: fig. 2).

47 Among the Plecoptera, the family Perlidae has its crown-group estimated in the Jurassic, ca.
48 165 Ma, and is recovered as sister to the clade (Chloroperlidae + Perlodidae) (Letsch et al., 2021:
49 fig. 2). Their oldest representatives are known from the mid-Cretaceous Burmese amber (ca. 98 Ma)
50 and some are confidently placed in the subfamily Acroneuriinae (e.g., Chen, 2018, 2019a,b). The
51 other subfamily, the Perlinae, has its oldest representatives known from Baltic amber (37.2–33.9 Ma)
52 (Pictet and Hagen, 1856).

53 In this study, we describe a new genus and species of Perlidae based on a well-preserved
54 male specimen from the mid-Cretaceous Burmese amber. This discovery increases the diversity of
55 stoneflies documented from the Burmese amber biota.

56

57 **2. Material and methods**

58 The amber piece containing the specimen comes from the deposits of Noije Bum in the Hukawng
59 Valley (26° 29' N, 96° 35' E), Kachin State, Northern Myanmar (see detailed map in Grimaldi and
60 Ross, 2017: fig. 2). This amber deposit was located on the West Burma block (WBB) a terrane that
61 migrated from the south-east of Gondwana, across the Tethys Ocean during the Jurassic and Creta-
62 ceous and then collided with Asia (e.g. Seton et al., 2012). Radiometric data established an early
63 Cenomanian age (98.79 ± 0.62 Ma) for Kachin amber, based on zircons from volcanic clastes found
64 within the amber-bearing sediments (Shi et al., 2012). Some ammonites found in the amber-bearing
65 bed and within amber corroborate a late Albian–early Cenomanian age (Cruickshank and Ko, 2003;
66 Yu et al., 2019).

67 The holotype of †*Burmaperla pouilloni* gen. et sp. nov. (Figs. 1-3) is from the collection of
68 one of us (JMP), and is complete and well preserved. The amber piece was polished to facilitate the
69 observation of the specimen using a grinder polisher (Buehler EcoMet 30), and a thin silicon car-
70 bide sanding paper (grit size = 7000). The specimen was examined and photographed with a Leica
71 MZ APO with an attached Canon EOS 5D Mark II camera. All images are digitally stacked photo-
72 micrographic composites of several individual focal planes, which were obtained using Helicon Fo-
73 cus 6.7. The figures were composed with Adobe Illustrator CC2019 and Photoshop CC2019 soft-
74 ware. Wing venation nomenclature follows Béthoux (2005). The amber piece is housed in the
75 Musée d'Histoire Naturelle et d'Ethnographie (Colmar, France) under the collection number
76 MHNE.2021.11.1.

77 Published work and nomenclatural acts are registered in ZooBank (<http://zoobank.org/>, last
78 access: 19 12 2021), with the following LSID (reference): urn:lsid:zoobank.org:pub:D6201846-
79 BF5F-46CB-A893-4F2DD7BAC430.

80

81 **3. Systematic Paleontology**

82 Order Plecoptera Burmeister, 1839

83 Suborder Arctoperlaria Zwick, 1973

84 Infra-order Systellognatha Enderlein, 1909

85 Superfamily Perloidea Latreille, 1802

86 Family Perlidae Latreille, 1802

87 Subfamily Acroneuriinae Klapálek, 1914

88

89 Genus *Burmaperla* Jouault & Nel gen. nov.

90 urn:lsid:zoobank.org:act:A8E2792B-682B-474B-9FDC-B69ACB8FD4F0

91

92 Etymology. The genus name is a combination of the prefix ‘burma’ referring to the originating
93 country of the amber piece (Myanmar) and *Perla*, type genus of the family Perlidae. Gender femi-
94 nine.

95 Type species. *Burmaperla pouilloni* sp. nov. Jouault & Nel (only species included).

96 Diagnosis. Triocellate; pronotum slightly trapezoidal with broadly curved anterior and posterior
97 corners, sutures distinct; first two tarsomeres shortest with euplantulae; forewing with ScP reaching
98 RA beyond ra-rp; two extra crossvein beyond ScP and RA fusion point; at least eight crossveins
99 between ScP and anterior margin; ScP+RA terminating well before wing apex; RP originating in
100 basal third of forewing and with three branches; MP partially fused with upper branch of CuA; CuA
101 with four branches; AA2 with three branches; abdomen near half of body length; with all segments
102 not extended; abdominal terga unmodified; posterior margin of sternum 9 rounded; hammer distinct,

103 nearly circular, length $1.14 \times$ longer than wide; paraproct weakly sclerotized, abruptly upcurved,
104 thinning towards apex and symmetrical; cercomeres with long bristles.

105 Remark: A detailed discussion for the placement and comparison with other Acroneuriinae genera
106 is available in the discussion part.

107

108 *Burmaperla pouilloni* Jouault & Nel sp. nov.

109 (Figs. 1-3)

110 urn:lsid:zoobank.org:act:D9546CAA-D08F-49BC-97B0-7FA8411B12A9

111 Etymology. Named after Jean-Marc Pouillon, who donated the holotype. The species epithet is to
112 be treated as a noun in the genitive case.

113 Material. Holotype MHNE.2021.11.1 (a complete specimen preserved in an ovoid piece of amber
114 measuring $15 \times 19 \times 4$ mm), deposited at the Musée d'Histoire Naturelle et d'Ethnographie (Colmar,
115 France).

116 Locality and horizon: Noiye Bum Hill, Hukawng Valley, Kachin State, Myanmar; upper Albian to
117 lower Cenomanian, mid-Cretaceous.

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

119 Description. Macropterous; body length (excluding antennae and cerci) ca. 8.0 mm, stout, generally
120 brown. Wings folded and overlapped on body so only forewings are visible. Dorsal aspect of termi-
121 nalia covered by wings but visible under microscope.

122 Head trapezoidal, ca. 1.05 mm long and 1.75 mm wide (eyes include) not overlapped by an-
123 terior part of pronotum, with an elliptical spot covering three ocelli and anterior half of head; two
124 posterior ocelli larger than anterior one; compound eyes rounded. Antenna brown and filiform, with
125 at least 45 antennomeres (hardly discernible basally since covered with bubbles), $0.81 \times$ as long as
126 body, each antennomere thinning towards apex. Maxillary palps long, with five visible palpomeres,
127 lengths from basal to apical ones (in mm): at least 0.07; 0.23; 0.43; 0.34; 0.20. Labial palps with
128 three(?) palpomeres, length from basal to apical ones (in mm): > 0.26 ; 0.40; 0.32.

129 Pronotum narrower than head, ca. 0.90 mm long and ca. 1.33 mm wide, slightly trapezoidal
130 with broadly curved corners, mostly brown except for a wide, pale median band. Dorsal part of
131 mesothorax and metathorax, similarly colored as pronotum, sclerotized except for median area,
132 nearly as wide as pronotum. Gill remnant maybe present, hidden inside bubbles. Furcal pit,
133 mesosternal Y-arm present; mesosternal Y-stem apparently present (not fully visible). Legs brown;
134 two tibia spurs present; fore femur ca. 0.42 mm wide and ca. 1.12 mm long, tibia ca. 0.17 mm wide
135 and ca. 1.5 mm long, tarsus ca. 0.52 mm long; mid femur ca. 0.42 mm wide and ca. 1.45 mm long,
136 tibia ca. 0.25 mm wide and ca. 1.67 mm long, tarsus ca. 0.62 mm long; hind femur ca. 0.45 mm
137 wide and ca. 1.87 mm long, tibia ca. 0.29 mm wide and ca. 2.25 mm long, tarsus ca. 0.63 mm long;
138 first two tarsal segments shortest with conspicuous euplantulae; arolium broad and setose; tarsal
139 claws simple.

140 Wings hyaline, veins brown. Forewing length ca. 7.80 mm; M forked at wing midlength; six
141 crossveins present between M and CuA; CuA forked basal to fork of M, with four branches; CuP
142 and AA1 simple; AA2 with three branches; area between CuA and CuP with five crossveins. Hind
143 wings hidden under forewings.

144 Abdomen length about half-length of body, with dark lateral surfaces and pale ventral sur-
145 face; posterolateral margins of each segment slightly extended. Lengths of sternites, in ventral view
146 from base to apex (in mm): 0.3; 0.35; 0.35; 0.37; 0.42; 0.40; 0.42; 0.9; 0.01. Posterior margin of
147 sternum 9 rounded, posteromedially with an oval hammer. Paraproct weakly sclerotized, abruptly
148 upcurved, thinning towards apex and symmetrical. Cerci hairy and curved, with at least 10 cerco-
149 meres, basal cercomere much longer than other segments.

150

151 **4. Discussion**

152 This specimen displays several characters allowing a confident placement within the Perlidae and
153 Acroneuriinae. More precisely, a hammer on sternite 9 is an apomorphy of the Arctoperlaria (Zwick,
154 2000). The short first tarsomere, setose arolium, and small and weak mandibles are apomorphic

155 characters supporting the subclade Systellognatha (Sroka et al., 2018; Zwick, 2000). The current
156 classification of Plecoptera supports the superfamilies Perloidea and Pteronarcyioidea within the
157 Systellognatha. Although Zwick (2000) proposed a series of apomorphic characters to define these
158 two clades, they are all based either on the internal morphology or on nymph morphology and are
159 therefore not visible on our specimen.

160 We do not place our specimen within the families included in the superfamily Pteronarcyoi-
161 dea because it lacks laterally expanded arolium (Zwick, 2000), has a more reduced forewing vena-
162 tion (Béthoux, 2005), and a hammer/ventral vesicle that is not reduced. Additionally, wing venation
163 character have been proposed to distinguish the Pteronarcyidae (Cui et al., 2016): numerous
164 crossveins between M and CuA in distal half of wing, a character not recorded on this specimen.
165 Similarly, we cannot place this specimen within the Styloperlidae since it lacks a dense setal brush
166 on male sternite nine (replacing the vesicle or hammer) and lacks a X-shaped sclerotization normal-
167 ly recorded on the sternite 10 of male styloperlids (Zwick, 2000). The last pteronarcyoid family, the
168 Peltoperlidae, is distinguishable from the other Plecoptera by a short head strongly inserted into the
169 angulate prothorax (Chen and Xu, 2020), and by labial palps not visible in dorsal view (Fenoglio et
170 al., 2021). These characters are not recorded on our specimen preventing its placement within the
171 Peltoperlidae.

172 The particular configuration of the tarsus, with a short basal tarsomere, has been considered
173 differently according to the authors. This character is a synapomorphy of the Perloidea for Zwick
174 (1973), a synapomorphy of Perloidea with (Peltoperlidae + Styloperlidae) for Zwick (1980), and
175 independently derived in these lineages for Zwick (2000) and Nelson (2009). Therefore, there is no
176 doubt that this specimen belongs to the Perloidea (the other families being previously excluded).
177 Among the Perloidea (Perlodidae + Perlidae + Chloroperlidae), we can exclude affinities of our
178 specimen with the Chloroperlidae because it does not possess a slender body or an oval pronotum
179 (Zwick, 2000). Similarly, it cannot be placed within the Perlodidae because it does not possess
180 submental gills or lateral stylets of male epiproct, apomorphic characters of the Perlodinae (Zwick,

181 2000). It differs from the Isoperlinae and Perlodinae in having a more developed wing venation
182 (e.g., RP with three branches). Based on the original diagnosis of the family (Klapálek, 1909), our
183 specimen differs from perlodid stoneflies in having a pronotum whose sides are not parallel, a char-
184 acter state found in numerous extant species (Huo and Du, 2021).

185 Therefore we place it within the family Perlidae, already well documented in Burmese am-
186 ber. We exclude affinities with the Perlinae because the specimen does not possess hemitergites 10
187 modified into anteriorly curved hooks; also the hammer is fully visible, while no hairbrush on mesal
188 areas of abdominal sternites is visible (Zwick, 2000). Additionally, our specimen shows the
189 apomorphic character of the Acroneuriinae, viz. the paraprocts transformed into anteriorly up-
190 curved hooks (Zwick, 2000).

191 This specimen does not correspond to the putative imago of †*Electroneuria ronwoodi* Sroka
192 et al., 2018 (known by a nymph), since it has short cerci while †*Electroneuria ronwoodi* has long
193 ones. Zwick (1980) noticed a correlation between the length of cerci in nymphs and adults in the
194 Systellognatha.

195 We cannot place the specimen in the genus †*Cretacroneuria* Chen, 2020 since it has a dif-
196 ferent wing venation and genitalia configuration (Chen, 2020). Our specimen has a RP with three
197 branches (vs. four in †*Cretacroneuria*), its MP is fused with CuA for a short distance (vs. complete-
198 ly separated) and it has more m-cua crossveins. Additionally, the pronotum is less trapezoidal and
199 the anterior corners are not angulate. The paraproct are not directed laterally but upcurved and
200 hook-shaped (vs. digitiform in †*Cretacroneuria*).

201 We do not assign the studied fossil to the genus †*Burmesoperla* Chen, 2019 since it has a
202 circular hammer (vs. C-shaped) and a forewing with MP and CuA partially fused (vs. completely
203 separated) (Chen, 2019b).

204 Finally, Chen (2018) proposed a fossil tribe †Largusoperlini to accommodate the particular
205 genus †*Largusoperla* Chen, Wang & Du, 2018. He used the following characters to distinguish it
206 from the other Acroneuriinae: ‘triocellate; male hammer transverse, elevated, usually elliptical in

207 shape; male paraprocts distinctly enlarged, asymmetrical; cercus with approximately 10 segments;
208 male tergum 9 with patches of long hairs; cleft of male tergum 10 at least in posterior half; male
209 epiproct sclerite present' (Chen, 2018: 297). The proposed list of characters prevents us from plac-
210 ing the new fossil within the †Largusoperlini based on, at least, the hammer shape that is circular to
211 slightly ovoid but not transverse, and the paraproct shape that is neither distinctly enlarged nor
212 asymmetrical in the new fossil (Chen, 2018). Therefore, we proposed a new genus to accommodate
213 this new specimen.

214 The description of *Burmaperla pouilloni* gen. et sp. nov. complements the relatively well-
215 diversified plecopteran fauna of the West Burma block (WBB). The current stonefly diversity on
216 the West Burma block is however restricted to the sub-order Arctoperlaria, which is quite surprising
217 considering the distribution of the extant representatives of the sub-order. In fact, the majority of
218 Arctoperlaria are today found in the northern hemisphere, except the Notonemouridae, and are con-
219 sidered to be of Holarctic origin (Letsch et al., 2021: fig. 3). As a result, the colonization of West
220 Burma block by the Arctoperlaria may have been late, when the WWB came closer to Laurasia dur-
221 ing the Late Cretaceous (e.g. Westerweel et al., 2019), the alternative being that the Arctoperlaria
222 were more widely distributed before the Cretaceous (Cui et al., 2018).

223 The path of the West Burma block through the Meso-Tethys Ocean—the West Burma block
224 was originally located near the Australian block in east Gondwana during the Early Jurassic (e.g.
225 Seton et al., 2012)—is used as an argument to strengthen the assumption that West Burma block
226 was isolated (an island) during its migration and that fauna transfers have taken place only before its
227 separation or lately when it approached Laurasia. Therefore, early faunal inputs are supposed to
228 have Gondwana origins (e.g. Poinar, 2018) and later inputs to be of Laurasia origins (e.g. Jouault,
229 2021). Consequently, some representatives of the Antarctoperlaria inhabiting the Gondwana may
230 have colonized the WBB prior to its separation from Gondwana. This assumption would be corrob-
231 orated by the presence of several Antarctoperlaria (e.g. *Gondwanoperlidium*: Pinto and Purper,
232 1978; Riek, 1956; or *Euxenoperla* Riek, 1976a,b) in South America, Africa, and Australia. There-

233 fore, it seems possible that an antarctoperlarian fauna was trapped in Burmese amber but not yet
234 described.

235

236 **5. Conclusion**

237 Amber from northern Myanmar provides a unique glimpse to the paleodiversity of stoneflies during
238 the Cretaceous and particularly during the migration of the West Burma block (from South Gond-
239 wana to Asia during the Cretaceous). The current distribution of Plecoptera, their fossil record, and
240 the particular geological history of West Burma block suggest that the Antarctoperlaria may have
241 been present on WBB during the Cretaceous and trapped in amber but not yet described. The de-
242 scription of *Burmaperla pouilloni* gen. et sp. nov. also increases the diversity of Acroneuriinae
243 stoneflies and suggests that the subfamily was more diversified than previously thought. If the fossil
244 record of the order continues to grow, an analysis of the fossil record to decipher the evolutionary
245 dynamics of stoneflies over geological time will be needed to clarify the evolutionary history of the
246 order and better understand their diversification.

247

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254

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361 **Figure captions**

362 **Fig. 1.** *Burmaperla pouilloni* Jouault & Nel gen. et sp. nov., holotype MHNE.2021.11.1. Habitus. A,
363 dorsal view. B, ventral view. Scale bars = 1 mm.

364 **Fig. 2.** *Burmaperla pouilloni* Jouault & Nel gen. et sp. nov., holotype MHNE.2021.11.1. A, detailed
365 view of anterior part of body in dorsal view. B, detailed view of head in ventral view. Scale bars
366 = 0.5 mm.

367 **Fig. 3.** *Burmaperla pouilloni* Jouault & Nel gen. et sp. nov., holotype MHNE.2021.11.1. A, detailed
368 view of tarsus with euplantulae. B, detailed view of posterior part of body in ventral view. C, de-
369 tailed view of genitalia in postero-ventral view. D, line drawing of forewing venation with veins
370 labelled. Scale bars = 0.5 mm (A, B, C); 1 mm (D).

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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