



HAL
open science

Sexual conflict during Mesozoic: The first Cretaceous damselfly in Burmese amber (Hemiptera: Heteroptera: Nabidae)

Romain Garrouste, Thomas Schubnel, Diying Huang, Dany Azar, Chenyang Cai, André Nel

► To cite this version:

Romain Garrouste, Thomas Schubnel, Diying Huang, Dany Azar, Chenyang Cai, et al.. Sexual conflict during Mesozoic: The first Cretaceous damselfly in Burmese amber (Hemiptera: Heteroptera: Nabidae). *Cretaceous Research*, 2020, 108, pp.104344 -. 10.1016/j.cretres.2019.104344 . hal-03488649

HAL Id: hal-03488649

<https://hal.science/hal-03488649v1>

Submitted on 21 Jul 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

1 Sexual conflict during Mesozoic: the first Cretaceous damsel bug in Burmese amber
2 (Hemiptera: Heteroptera: Nabidae)

3

4 Romain Garrouste^a, Thomas Schubnel^a, Diying Huang^{b*}, Dany Azar^{b,c}, Chenyang Cai^b, André
5 Nel^{a,*}

6

7 ^a *Institut de Systématique, Évolution, Biodiversité, ISYEB - UMR 7205 – CNRS, MNHN, UPMC,*
8 *EPHE, Muséum national d'Histoire naturelle, Sorbonne Universités, 57 rue Cuvier, CP 50,*
9 *Entomologie F-75005, Paris, France (garroust@mnhn.fr, thomas.schubnel@wanadoo.fr,*
10 *anel@mnhn.fr)*

11 ^b *State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and*
12 *Palaeontology, Chinese Academy of Sciences, Nanjing 210008, People's Republic of China*
13 *(dyhuang@nigpas.ac.cn, cycai@nigpas.ac.cn)*

14 ^c *Lebanese University, Faculty of Sciences II, Department of Biology, Fanar Matn P.O. Box*
15 *26110217, Lebanon (danyazar@ul.edu.lb)*

16

17 * Corresponding author

18

19 ABSTRACT

20 The oldest Nabidae, *Cretanazgul camillei* gen. et sp. nov., is described from the mid Cretaceous
21 Burmese amber and attributed to the extant subfamily Prostemmatinae. This new record is in
22 accordance with the emergence of the Nabidae between 150 and 130 Ma. This new fossil should
23 help to precise future dating of this family. As the amber area of Myanmar was probably an
24 island of the Thetys Ocean during the mid-Cretaceous, originating from the Gondwana, it is
25 possible that the Nabidae have a Gondwanian origin. *Cretanazgul* possibly practiced traumatic

26 insemination as all extant Prostemmatinae, but it was not possible to find the male internal
27 organ linked to this behavior in this fossil despite 3D reconstruction with CT-scan data and
28 fluorescence imaging.

29

30 *Keywords:*

31 Insecta

32 Heteroptera

33 Nabidae

34 Prostemmatinae

35 Traumatic insemination

36

37 **1. Introduction**

38 The Nabidae (sensu Schuh and Štys, 1991) is a relatively small family of cimicomorphan bugs,
39 with 31 genera and 386 modern species (after Coscarón et al., 2015). It is currently divided into
40 Nabinae and Prostemmatinae (Li et al., 2012a). All the extant Prostemmatinae are involved in
41 traumatic insemination via several ways, including perforation of the female abdomen
42 teguments by a sharp acus in apical position of the intromittent organ. Traumatic insemination
43 is a bizarre form of mating practiced by some insects in which males use hypodermic genitalia
44 to penetrate female's body wall during copulation, frequently bypassing the genital tract and
45 ejaculating in the hemocoel (Tatarnic et al., 2014). There are very few data on the fossil Nabidae
46 sensu stricto. After a biogeographical inference, Asquith and Lattin (1990) proposed a Late
47 Cretaceous age for the genus *Nabacula* Kirby, 1837 (Nabinae). Kerzhner (1981) cited
48 *Metatropiphorus succini* (Jordan, 1952) from the Eocene Baltic amber in the subfamily Nabinae
49 (Jordan, 1952). *Nabis gracillimus* (Heer, 1865) (Late Miocene, Germany), *Nabis lividus* (Heer,
50 1853) (Early Miocene, Croatia), and *Nabis vagabundus* (Heer, 1853) (Early Miocene, Croatia)

51 are based on compression fossils that have never been revised (Heer, 1853, 1865). Kerzhner
52 (1981) considered these fossils as probably dubious, and added that only ‘*Nabis lucidus* Germar
53 and Berendt, 1856’ (Eocene Baltic amber) could belong to the Prostematinae (see also
54 Péricart, 1987). This fossil taxon has never been revised. Lastly *Nabis strausi* Jordan, 1969 was
55 described from the Pliocene of Germany on the basis of an apparently poorly preserved
56 compression fossil (Jordan, 1969). *Karanabis kiritshenkoi* Becker-Migdisova, 2008 (Late
57 Jurassic of Kazakhstan) resembles Nabinae but Popov and Bechly (2007) put it in the
58 Mesoveliidae and Damgaard (2008) considered it as a Gerromorpha. The Early Cretaceous
59 genera *Izinabis* Shcherbakov, 2008, *Juracipeda* Shcherbakov, 2008, *Saldonabis* Shcherbakov,
60 2008, *Vetanthocoris* Yao, Cai et Ren, 2006, *Collivetanthocoris* Yao, Cai et Ren, 2006,
61 *Byssoidecerus* Yao, Cai et Ren, 2006, and *Mecopodus* Yao, Cai et Ren, 2006 are Velocipedidae
62 after Shcherbakov (2008) who considered this group as a subfamily of the Nabidae (but see
63 Yao et al., 2006; Hou et al., 2012). In summary, the oldest relatively ‘accurate’ Nabidae sensu
64 stricto are Middle Eocene. Nevertheless, Jung and Lee (2012) considered that ‘the split of
65 Nabidae and Lasiochilidae most probably occurred in the Jurassic’, after a molecular
66 phylogenetic analysis of the Cimicoidea, using the Eocene *Metatropiphorus succini* as
67 calibrating point. Here we describe the first Mesozoic representative of this family from the
68 mid Cretaceous Burmese amber.

69 Like many Cimicomorpha, most of the recent Nabidae (especially all Prostematinae) are
70 involved in processes of sexual conflict through several traumatic insemination modes
71 (Tatarnic, 2014). We have performed a CT-Scan of this bug inclusion to check the preservation
72 and to have access to the morphology and fine anatomy of its genitalia.

73

74 **2. Material and methods**

75 The amber piece was polished before being examined and photographed. The fossil was
76 examined and measured using an incident light stereomicroscope (Nikon SMZ 1500 and SMZ
77 25). Photographs were taken using a Zeiss Discovery V20 microscope system. Optical
78 instruments were equipped by camera lucida and digital cameras. The raw digital images were
79 processed with focus stacking software, and figure plates prepared with Adobe Photoshop™.
80 Fluorescence Imaging have been realized on Zeiss V16 AxioZoom in MNHN Microcopy
81 Platform. Microtomography CT-scan was done on a GE Sensing & Inspection Technologies
82 Phoenix X|ray v|tome|x 240 L with the following parameters: voxel size: 0.0019 mm; 2200
83 projections; exposure time: 2.000 s with two images per projection; voltage: 50 kV; current:
84 200 μA. Scan was performed without filter.

85 Fossil-bearing Burmite amber has mostly been collected from the Hukawng Valley in northern
86 Myanmar (formerly known as Burma) (Dong et al., 2015). For an overview of the amber deposit
87 and its geological setting see Zherikhin & Ross (2000), Cruickshank & Ko (2003) and Ross et
88 al. (2010), and for the list of described fossils see Ross (2019). Radiometric U–Pb zircon dating
89 (Shi et al., 2012) recently constrained this amber to a minimum age of 98.79 ± 0.62 Ma, which
90 is equivalent to the mid-Cretaceous (earliest Cenomanian). The original habitat of the amber
91 forest is still controversial, in fact it has originally been assumed to be a ‘tropical’ araucarian
92 forest (Grimaldi et al., 2002; Poinar et al., 2007), possibly with Dipterocarpaceae as another
93 source for the fossil resin. However, the first detailed report on the macromolecular nature and
94 palaeobotanical affinity of Burmite amber (Dutta et al., 2011), based on gas chromatography -
95 mass spectrometry, rejected Araucariaceae and Dipterocarpaceae in favour of Pinaceae as
96 Burmite amber tree.

97 We follow the subfamily classification of Schuh and Štys (1991), based on a
98 morphological cladistics analysis, in defining the Nabidae as including only the Nabinae and
99 Prostemmatinae, and considering the Medocostidae Štys, 1967 and Velocipedidae Bergroth,

100 1891 as separate families, contra Péricart (1987), Shcherbakov (2008) or Novoselsky et al.
101 (2014) who considered these two groups as nabid subfamilies. Tian et al. (2008) supported well-
102 separated positions for the Nabidae and the Velocipedidae in a molecular phylogenetic analysis
103 that did not include the Medocostidae.

104

105 **3. Systematic paleontology**

106 Order: Hemiptera Linnaeus, 1758

107 Suborder: Heteroptera Latreille, 1810

108 Family: Nabidae Costa, 1853

109 Subfamily: Prostemmatinae Reuter, 1890

110 Genus: *Cretanazgul* gen. nov.

111 Type species: *Cretanazgul camillei* sp. nov.

112 urn:lsid:zoobankxxxx

113 *Diagnosis.* This genus can be separated from the other Prostemmatinae with the following
114 characters: pronotum not clearly divided into an anterior and a posterior part; scutellum with
115 two pairs of long trichobothria located on its lateral margins; costal fracture rudimentary;
116 forefemur without a distinct angle, and only small spines on the inner side; no clear row of setae
117 on hind tibia corresponding to stiff setae associated to Ekblom's organ.

118 *Etymology.* Named after the Cretaceous and the Nazgul, evil hunter characters in the book 'The
119 Lord of the Rings' by British writer J. R. R. Tolkien, like extant Prostemmatidae, mainly active
120 hunter of heteropteran. Gender masculine.

121

122 *Cretanazgul camillei* sp. nov.

123 **Figs. 1–3**

124 **Material.** Holotype NIGP 164903 (male), deposited at Nanjing Institute of Geology and
125 Paleontology, P.R. China.

126 *Etymology.* Named after Camille Garrouste, daughter of the first author RG.

127 *Type locality and stratum.* Tanai Village, Hukawng Valley, Kachin State, northern Myanmar.
128 Burmite amber, mid-Cretaceous (earliest Cenomanian), ca. 99 Ma (Shi et al., 2012).

129

130 **Description**

131 Body 2.6 mm long; head 0.22 mm long, 0.6 mm wide; mandibular plates not enlarged; labium
132 short and stout, four-segmented, and inserted anteriorly on head, reaching base of head; head
133 not neck-like behind eyes; two high tubercles aligned with bases of antennae; two ocelli placed
134 posteriorly to eyes; a pair of long trichobothria near eyes; antennal prepedicellite present;
135 antennae with four long segments plus one extra at base of antennal segment II, antennal
136 segment I 0.1 mm long, II 0.4 mm long, III 0.3 mm long, IV 0.26 mm long; thorax 0.96 mm
137 wide; pronotum 0.4 mm long, 0.8 mm wide, not clearly divided into an anterior and a posterior
138 part, a pair of long trichobothria in anterior part and another in posterior part, plus a row of
139 short curved setae along lateral margins; pronotal collar weakly indicated; no prosternal sulcus;
140 scutellum 0.67 mm long, 0.8 mm wide, with two pairs of long trichobothria located on its lateral
141 margins; tegmen 2.2 mm long, 0.6 mm wide, embolium distinct; costal fracture short and
142 rudimentary; clavus not widened posteriorly; membrane 1.1 mm long, with a stub on a vein
143 diverging from corium-membrane boundary and three cells with emanating veins; ‘fossettes
144 parastigmatiques’ only present on abdominal segment 3; abdominal spiracles 2-8 not visible on
145 laterosternites; ventral laterotergites not visible and fused with abdominal sternum; male
146 abdominal segment 8 reduced and for the most part telescoped within segment 7; male
147 parameres well visible, and very acute, blade shape slightly twisted; fore femur greatly
148 broadened, without a distinct angle, 0.6 mm long, 0.22 mm wide; two longitudinal rows of

149 small spines on inner side of forefemur; foretibia widened from base to apex, 0.6 mm long, with
150 a large apico-ventral fossula spongiosa clothed with modified microtrichia; hind femur 0.66
151 mm long, 0.16 mm wide, hind tibia 0.87 mm long, no clear row of setae on hind tibia
152 corresponding to stiff setae associated to Ekblom's organ, which is not visible, if present.

153

154 **4. Discussion**

155 After Schuh and Štys (1991), *Cretanazgul* gen. nov. falls in the Nabidae (= Nabinae +
156 Prostemmatinae) because of the following apomorphies: prepedicellite present; labium inserted
157 anteriorly on head; ventral laterotergites not visible and fused with abdominal sternum; fossula
158 spongiosa well-developed apico-ventrally on foretibiae, clothed with modified microtrichia;
159 membrane with a stub on a vein diverging from corium-membrane boundary; costal fracture
160 reduced; male abdominal segment 8 reduced and for the most part telescoped within segment
161 7; 'fossettes parastigmatiques' present.

162 *Cretanazgul* gen. nov. differs from the Velocipedidae in its weak costal fracture; antenna
163 **with five apparent segments**; and foretibia with a fossula spongiosa (Van Doesburg, 2004). It
164 differs from the Medocostidae in its antenna **with five apparent segments**; fossula spongiosa
165 present; and scutellum with trichobotria (Štys, 1967; Schuh and Slater, 1995).

166 Also, after the key to the cimicomorphan families of Schuh and Slater (1995),
167 *Cretanazgul* gen. nov. can be attributed to the Prostemmatinae for the following characters:
168 mandibular plates not enlarged; labium short and stout, four-segmented, and inserted anteriorly
169 on head; fossula spongiosa present in protibial; no prosternal sulcus; head not neck-like behind
170 eyes; antenna with five apparent segments; membrane with a stub; antennal prepedicellite
171 present; membrane with three cells with emanating veins; two pairs of trichobothria located on
172 lateral margins of scutellum.

173 Brailovsky (2018) listed the following characters for the Prostematinae: body oblong
174 and stout; antennae with four segments plus a supplementary one, rostrum moderately stout,
175 collar narrow or absent, scutellum with 1-7 pairs of conspicuous trichobothria along the lateral
176 margins, hemelytra with the embolium distinct and clavus not or only scarcely widened
177 posteriorly, fore femora strongly incrassate, provided with a tooth or angula process on the
178 ventral surface, and tibiae with a fossa spongiosa at the apex. All these characters are present
179 in *Cretanazgul* gen. nov.

180 Other characters of this subfamily, present in *Cretanazgul* gen. nov., are: profemur
181 greatly broadened; protibia widened from base to apex; pronotal collar weakly indicated;
182 ‘fossettes parastigmatiques’ only present on abdominal segment 3; costal fracture rudimentary;
183 abdominal spiracles 2-8 not visible on laterosternites; antennae four segmented plus one extra
184 at the base of antennal segment II (Carayon, 1948, 1950; Péricart, 1987; Kerzhner, 2007;
185 Cornelis and Coscaron, 2013).

186 Nevertheless, *Cretanazgul* gen. nov. has only small teeth on forefemur as in some recent
187 taxa (e.g. *Pagasa* Stål 1862) (Kerzhner, 2007). Also it has no clear row of setae on the hind
188 tibia that would correspond to the stiff setae associated to the Ekblom’s organ normally present
189 in these bugs (Schuh and Slater, 1995). These character states are probably plesiomorphic.

190 The Prostematinae comprise the following modern genera: *Alloeorhynchus* Fieber,
191 1860, *Pagasa*, *Prostemma* Laporte, 1832 (Prostematini), *Phorticus* Stål, 1860, and
192 *Rhamphocoris* Kirkaldy, 1901 (Phorticini). In the genera *Rhamphocoris*, *Alloeorhynchus*,
193 *Pagasa*, and *Phorticus*, the pronotum is clearly divided into an anterior and a posterior part,
194 unlike in *Cretanazgul* gen. nov. (Harris, 1936; Carayon, 1970; Blinn, 1995; Cassis, 2016;
195 Brailovsky and Barrera, 2017). Furthermore *Phorticus* has the supplementary antennal segment
196 obsolete or absent, unlike in *Cretanazgul* gen. nov. (Harris, 1928; Brailovsky, 2018). In
197 *Prostemma*, the pronotum is sometime weakly divided, especially in macropterous forms, as in

198 our fossil (Péricart, 1987). *Cretanazgul* gen. nov. differs from *Prostemma* in the forefemur
199 without a distinct angle (Péricart, 1987: fig. 16a). Thus we can attribute it to a new extinct
200 genus.

201

202 **5. Conclusion**

203

204 Extant Nabidae are predaceous, mainly on small insects. The strong and short mouthparts of
205 *Cretanazgul camillei* gen. et sp. nov. support the inference of similar feeding habits for this
206 Cretaceous taxon. After the phylogenetic analysis of Li et al. (2012b), the Cimicomorpha would
207 originate in the Late Triassic, and the Nabidae could be dated between 150 and 130 Ma. Our
208 discovery is congruent with these hypotheses. It should help to precise future dating of these
209 clades. As the amber area of Myanmar was probably an island of the Thetys Ocean during the
210 mid-Cretaceous (Metcalf, 2011; Zahirovic et al., 2014; Rasnitsyn and Öhm-Kühnle, 2018),
211 originating from the Gondwana, it is possible that the Nabidae have a Gondwanian origin.

212 The assignment of *Cretanazgul camillei* gen. et sp. nov. to the Prostemmatinae could
213 direct us to the fact that this Cretaceous insect could have practiced this mode of reproduction
214 also well-represented in the extant representatives of many cimicomorphan lineages. But it was
215 not possible to have information on internal structures with intromittant organ characteristic of
216 the Prostemmatinae and involved in traumatic insemination (Carayon, 1977), even under X-ray
217 imaging, due to the poor preservation of the inner structures. The traumatic insemination could
218 also involve acute parameres, but we cannot accurately infer sexual behavior of this type for
219 *Cretanazgul* gen. nov.

220

221 **Acknowledgements**

222 We sincerely thank two anonymous referees for their useful remarks on the first version of the
223 paper. This work was supported by the Strategic Priority Research Program of the Chinese
224 Academy of Sciences (XDB18030501), the National Natural Science Foundation of China
225 (41672011), and the French CNRS and MNHN. Authors thanks Miguel Garcia-Sanz for CT-
226 Scan Tomography on AST-RX MNHN platform (OMSI), and Marc Geze for Fluorescence
227 Microscopy Imaging (PM/MNHN)

228

229 **References**

230 Asquith, A., Lattin, J.D., 1990. *Nabicula (Limnonabis) propinqua* (Reuter) (Heteroptera:
231 Nabidae): dimorphism, phylogenetic relationships and biogeography. Tijdschrift voor
232 Entomologie 133, 3–16.

233 Blinn, R.L., 1995. *Phorticus collaris* Stål: a nabid new to Eastern North America (Heteroptera:
234 Nabidae). Journal of the New York Entomological Society 103, 216–218.

235 Brailovsky, H., 2018. A review of the subfamily Prostemmatinae from Honduras (Hemiptera:
236 Heteroptera: Nabidae), with the description of a new species, new records, and a key.
237 Proceedings of the Entomological Society of Washington 120, 1–8.

238 Brailovsky, H., Barrera, E., 2017. A review of the Mexican species of *Alloeorhynchus* Fieber
239 (Hemiptera: Heteroptera: Nabidae: Prostemmatinae) with description of six new species, new
240 distributional records, and key to the species. Zootaxa 4338, 305–318.

241 Carayon, J., 1948. Les organes parastigmatiques des Hémiptères Nabidae. Comptes-Rendus de
242 l'Académie des Sciences de Paris 227, 864–866.

243 Carayon, J., 1950. Les fossettes tégumentaires abdominales des Nabidés (Hemiptera
244 Heteroptera). Proceedings of the 8th International Congress of Entomology, Stockholm, 207–
245 213.

246 Carayon, J., 1970. Etude des *Alloeorhynchus* d'Afrique Centrale avec quelques remarques sur
247 la classification des Nabidae (Hemiptera). Annales de la Société Entomologique de France
248 (N.S.) 6, 899–931.

249 Carayon, J., 1977. Insémination extra-génitale traumatique. In: Grassé, P.P. (ed.). Traité de
250 Zoologie 7, 351–390.

251 Cassis, G., 2016. Four new species, first Australian records and review of the phorticine genus
252 *Rhamphocoris*, and key to genera and review of Australian Nabidae (Hemiptera: Heteroptera:
253 Nabidae). Entomologica Americana 122, 169–198.

254 Cornelis, M., del Carmen Coscarón, M., 2013. The Nabidae (Insecta, Hemiptera, Heteroptera)
255 of Argentina. ZooKeys 333, 1–30.

256 Coscarón, S., Braman, S.K., Cornelis, M., 2015. Chapter 11: damsel bugs (Nabidae). pp. 287-
257 305. In: Panizzi, A.R., Grazia, J. (eds). True bugs (Heteroptera) of the Neotropics. Entomology
258 in Focus 2, i–xxii + 1–901.

259 Cruickshank, R.D., Ko, K., 2003. Geology of an amber locality in the Hukaung Valley, northern
260 Myanmar. Journal of Asian Earth Sciences 21, 441–455.

261 Damgaard, J., 2008. Evolution of the semi-aquatic bugs (Hemiptera: Heteroptera:
262 Gerromorpha) with a re-interpretation of the fossil record. Acta Entomologica Musei Nationalis
263 Pragmae 48, 251–268.

264 Dong, F., Shih, C.-K., Ren, D., 2015. A new genus of Tanyderidae (Insecta: Diptera) from
265 Myanmar amber, Upper Cretaceous. Cretaceous Research 54, 260–265.

266 Dutta, S., Mallick, M., Kumar, K., Mann, U., Greenwood, P.F., 2011. Terpenoid composition
267 and botanical affinity of Cretaceous resins from India and Myanmar. International Journal of
268 Coal Geology 85, 49–55.

269 Grimaldi, D., Engel, M.S., Nascimbene, P., 2002. Fossiliferous Cretaceous amber from
270 Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American*
271 *Museum Novitates* 3361, 1–72.

272 Harris, H.M., 1928. A monographic study of the hemipteran family Nabidae as it occurs in
273 North America. *Entomologica Americana* 9, 1–90.

274 Harris, H.M., 1936. Notes on the species of *Psilistus* Stal (Hemiptera, Nabidae). *Proceedings*
275 *of the Royal Entomological Society of London (B)* 6, 191–196.

276 Heer, O., 1853. Die Insektenfauna der Tertiärgebilde von Ceningen und von Radoboj in
277 Croatien. 3 Abtheilung: Rhynchoten. Leipzig. In: Englemann, W. (ed.). *Neue Denkschriften*
278 *Allgemeinen Schweizerische Gesellschaft für die Gesammten Naturwissenschaften* 13, 1–138.

279 Heer, O., 1865. *Die Urwelt der Schweiz*. Schultheß, F. Verlag (publ.), Zürich, i–xxix + 1–628.

280 Hou, W.-J., Yao, Y.-Z., Zhang, W.-T., Ren, D., 2012. The earliest fossil flower bugs
281 (Heteroptera: Cimicomorpha: Cimicoidea: Vetanthocoridae) from the Middle Jurassic of Inner
282 Mongolia, China. *European Journal of Entomology* 109, 281–288.

283 Jordan, K.H.C., 1952. *Nabis succini* n. sp., eine Nabide aus den Bernstein Ostpreussens
284 (Hemiptera, Heteroptera). *Beiträge für Entomologie* 2, 455–457.

285 Jordan, K.H.C., 1969. Eine neue terrestrische Wanze aus dem Pliozän von Willershausen.
286 *Berichte der Naturhistorischen Gesellschaft zu Hannover* 113, 107–108.

287 Jung, S., Lee, S., 2012. Correlated evolution and Bayesian divergence time estimates of the
288 Cimicoidea (Heteroptera: Cimicomorpha) reveal the evolutionary history. *Systematic*
289 *Entomology* 37, 22–31.

290 Kerzhner, I.M., 1981. *Faunas SSSR. Nasekomye Khabotnye*. 13. Vyp. 2 Poluzhestkokrylye
291 *semeyetva Nabidae*. Leningrad, 326 pp. (record of fossil taxa: 74–76.)

292 Kerzhner, I.M., 2007. Nabidae of the West Indies (Heteroptera). *Zoosystematica Rossica* 16,
293 225–234.

294 Li, H., Liu, H.-y., Song, F., Shi, A.-m., Zhou, X.-g., and Cai, W.-z., 2012a. Comparative
295 mitogenomic analysis of damsel bugs representing three tribes in the family Nabidae (Insecta:
296 Hemiptera). PLoS One 7 (9) (e45925), 1–9.

297 Li, M., Tian, Y., Zhao, Y., Bu, W.-j., 2012b. Higher level phylogeny and the first divergence
298 time estimation of Heteroptera (Insecta: Hemiptera) based on multiple genes. PLoS One 7 (2)
299 (e32152), 1–17.

300 Metcalfe, I., 2011. Palaeozoic–Mesozoic history of SE Asia. In: Hall, R., Cottam, M.A.,
301 Wilson, M.E.J. (eds.), The SE Asian gateway: history and tectonics of the Australia-Asia
302 collision. Geological Society of London, Special Publications 355, 7–35.

303 Novoselsky, T., Freidberg, A., Dorchin, N., Meltzer, N., Kerzhner, I., 2014. The Nabidae
304 (Hemiptera: Heteroptera) of Israel and the Sinai Peninsula. Zootaxa 3827, 471–492.

305 Péricart, J., 1987. Hémiptères Nabidae d'Europe occidentale et du Maghreb. Faune de France
306 71, 1–185.

307 Poinar, G.O., Jr., Lambert, J.B., Wu, Y., 2007. Araucarian source of fossiliferous Burmese
308 amber: spectroscopic and anatomical evidence. Journal of the Botanical Research Institute of
309 Texas 1, 449–455.

310 Popov, Yu.A., Bechly, G., 2007. Heteroptera: bugs. pp. 317-328. In: Martill, D., Bechly, G.,
311 Loveridge, R. (eds). The Crato fossil beds of Brazil: Window into an ancient world. Cambridge
312 University Press, Cambridge, 624 pp.

313 Rasnitsyn, A.P., Öhm-Kühnle, C., 2018. Three new female *Aptenoperissus* from mid-
314 Cretaceous Burmese amber (Hymenoptera, Stephanoidea, Aptenoperissidae): unexpected
315 diversity of paradoxical wasps suggests insular features of source biome. Cretaceous Research
316 91, 168–175.

317 Ross, A.J., 2019. Burmese (Myanmar) amber checklist and bibliography 2018.
318 Palaeoentomology 2, 22–84.

319 Ross, A., Mellish, C., York, P., Crighton, B., 2010. Burmese amber. In: Penney, D. (ed.),
320 Biodiversity of fossils in amber from the major world deposits. Siri Scientific Press,
321 Manchester, 208–235.

322 Schuh, R.T., Slater, J.A., 1995. True bugs of the World (Hemiptera: Heteroptera). Classification
323 and natural history. Comstock Publishing Associates, Cornell University Press, Ithaca and
324 London, i–xii + 1–336.

325 Schuh, R.T., Štys, P. 1991. Phylogenetic analysis of cimicomorphan family relationships
326 (Heteroptera). Journal of New York Entomological Society 99, 298–350.

327 Shcherbakov, D.E., 2008. Mesozoic Velocipedinae (Nabidae s.l.) and Ceresopseidae
328 (Reduvidioidea), with notes on the phylogeny of Cimicomorpha (Heteroptera). Russian
329 Entomological Journal 16, 401–414.

330 Shi, G.-H., Grimaldi, D.A., Harlow, G.E., Wang, J., Yang, M.-C., Lei, W.-Y., Li, Q., Li, X.-H.,
331 2012. Age constraints on Burmese amber based on U-Pb dating of zircons. Cretaceous Research
332 37, 155–163.

333 Štys, P., 1967. Medocostidae - a new family of cimicomorphan Heteroptera based on a new
334 genus and two new species from tropical Africa. 1. Descriptive part. Acta Entomologica
335 Bohemoslovaca 64, 439–465.

336 Tatarnic, N.J., Cassis, G., Siva-Jothy, M.T., 2014. Traumatic insemination in terrestrial
337 arthropods. Annual Review of Entomology 59, 245–261.

338 Tian, Y., Zhu, W., Li, M., Xie, Q., Bu, W., 2008. Influence of data conflict and molecular
339 phylogeny of major clades in cimicomorphan true bugs (Insecta: Hemiptera: Heteroptera).
340 Molecular Phylogenetics and Evolution 47, 581–597.

341 Van Doesburg, P.H.Jr., 2004. A taxonomic revision of the family Velocipedidae Bergroth, 1891
342 (Insecta: Heteroptera). Zoologische Verhandelingen 347, 1–110.

343 Yao, Y.-z., Cai, W.-z., Ren, D., 2006. Fossil flower bugs (Heteroptera: Cimicomorpha:
344 Cimicoidea) from the Late Jurassic of Northeast China, including a new family,
345 Vetanthocoridae. Zootaxa 1360, 1–40.

346 Zahirovic, S., Seton, M., Müller, R.D., 2014. The Cretaceous and Cenozoic tectonic evolution
347 of Southeast Asia. Solid Earth 5, 227–273.

348 Zherikhin, V.V., Ross, A.J., 2000. A review of the history, geology and age of Burmese amber
349 (Burmite). Bulletin of the Natural History Museum, Geological Series 56, 3–10.

350

351 **Fig. 1.** *Cretanazgul camillei* gen. et sp. nov., holotype NIGP 164903,. A, habitus dorsal; B,
352 habitus lateral; C, tegmen. Scale bars = 1 mm.

353 **Fig. 2.** *Cretanazgul camillei* gen. et sp. nov., holotype NIGP 164903. A, fore femur; B, fore
354 tibia; C, head dorsal; D, hind leg. Scale bars = 0.2 mm (A, B, C), 0.5 mm (D).

355 **Fig. 3.** *Cretanazgul camillei* gen. et sp. nov., holotype NIGP 164903. Male parameres (arrows).
356 A, right; B, left. Scale bars = 0.1 mm.







