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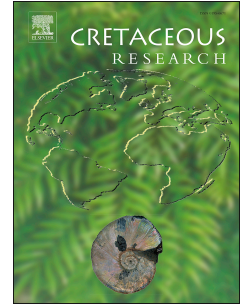
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Potential new evidences of bee fly parasitoidism on ground-dwelling insects in 'mid'-Cretaceous Burmese amber (Diptera: Bombyliidae)

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2 **Potential new evidences of bee fly parasitoidism on ground-dwelling insects in ‘mid’–**  
3 **Cretaceous Burmese amber (Diptera: Bombyliidae)**

4  
5 Running head

6 ‘mid’–Cretaceous bee fly parasitoidism

7  
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9  
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18  
19 **ABSTRACT**

20 Two new ‘Tomophthalmae’ bee flies *Paleocytherea pouilloni* gen. et sp. nov., and *Nidergasia*  
21 *neraudeaui* gen. et sp. nov. are described from the ‘mid’–Cretaceous Burmese amber. They  
22 are provisionally not attributed to a precise subfamily. The female of *Paleocytherea pouilloni*  
23 has terminalia modified into a very wide chamber with acanthophorite spines on tergites 9+10  
24 and a row of ventral setae evocating a specialized hair brush. These structures allowed  
25 digging into sand to lay eggs, and possibly would characterize a sand chamber similar to those

26 of several extant Bombyliidae that use it to coat eggs with sand and attack ground-dwelling  
27 insects. Eggs are wrapped with sand, avoiding desiccation and/or direct competition with  
28 more efficient parasitoids, including wasps. This discovery suggests a potential great antiquity  
29 for this behavior (*e.g.*, potential competitors like angarosphecids wasps are recorded in  
30 Burmese amber). Potential bee fly hosts were antlions, pygmy mole crickets, and the earliest  
31 bees, also known in the Burmese amber.

32

33 *Keywords:* Insecta; Diptera; female sand chamber; Cenomanian; gen. et sp. nov.;  
34 paleodiversity.

35

### 36 **1. Introduction**

37 Bombyliidae, also known as bee flies, are renowned to be important pollinator taxa that  
38 commonly inhabit in arid and semi-desert regions, feeding on nectar and pollen (Hull, 1973;  
39 Armstrong, 1979). Bombyliidae also have the particularity of possessing parasitoid larvae.  
40 This is a diversified family among Diptera (Brachycera) which displays a range of size from  
41 minute (Mythicomyiinae) to large species (Anthracinae) with beautiful color patterns. Since  
42 the first monography of the family proposed by Hull (1973) and the recent catalog of the  
43 family by Evenhuis & Greathead (2015) more than 4780 extant species have been described.  
44 The Bombyliidae family is at the ‘base’ of the Asiloidea and Empidoidea (Wiegmann *et al.*  
45 2003; Shin *et al.* 2018), as either sister group to all other asiloids (Woodley, 1989; Yeates,  
46 2002; Wiegmann *et al.*, 2011; Shin *et al.*, 2018), or as sister group to all other heterodactylan  
47 flies (Trautwein *et al.*, 2010; Shin *et al.*, 2018). The Cenozoic bombyliid fossil record is,  
48 compared to the Cretaceous record, well known with 35 genera and nearly 55 species  
49 described from fossil compressions and amber inclusions (Evenhuis, 1994; Hennig, 1966;  
50 Evenhuis, 2002; Nel & De Ploëg, 2004; Nel, 2006, 2008; Wedmann & Yeates, 2008;

51 Evenhuis, 2013; Greenwalt *et al.*, 2015). However, the oldest records of this family are from  
52 the Burmese amber with only seven described species of bee flies (Grimaldi, 2016; Zhang &  
53 Wang, 2016; Ye *et al.*, 2019), all characterized by a short proboscis, brush-shaped flagellum,  
54 a relatively ‘plesiomorphic’ venation, and variable female terminalia. These oldest bee flies  
55 belong to the crown group Bombyliidae, suggesting that this family has greater antiquity,  
56 which is also supported by the presence of a Mythicomyiidae in the middle Jurassic of the  
57 Russian Federation (Kovalev, 1985). Recently, Ye *et al.* (2019) described three females of  
58 ‘mid’-Cretaceous Burmese amber bombyliid flies with possible sand chambers, a specialized  
59 structure present in some extant bombyliid subfamilies. It is used to coat eggs in sand before  
60 deposition while hovering. Herein, we described two new genera and species of bee flies from  
61 the same Burmese amber, with well-preserved bodies and novel wing venation highlighting  
62 the evolution of Cretaceous Bombyliidae and their underestimated diversity. Both are  
63 attributed to the ‘Tomophthalmae’ group, otherwise known from the Paleocene of France, the  
64 Middle Eocene Baltic amber, and the Oligocene of France. These fossils are potentially of  
65 great interest in dating the antiquity of bee fly parasitoidism behavior on ground-dwelling  
66 hosts.

67

## 68 **2. Material and method**

69 The type specimens of *Paleocytherea pouilloni* gen. et sp. nov. and *Nidergasia neraudeaui*  
70 gen. et sp. nov. are embedded in two small clear pieces of amber. They have been prepared  
71 using a diamond disk or polished with a grinder polisher (Buehler EcoMet 30) by using a very  
72 thin silicon carbide sanding paper (grit size = 7000). Specimens were examined using a Nikon  
73 binocular microscope SMZ 1500 or a Leica MZ APO stereomicroscope. Photographs have  
74 been taken with a Nikon camera D800 and a Canon 5D Mark II camera, and are digitally  
75 stacked photomicrographic composites of several individual focal planes, which were

76 obtained using HeliconFocus. The figures were composed with Adobe Illustrator and  
77 Photoshop software.

78 The pieces of Burmese amber derive from the deposits of Noije Bum in the Hukawng  
79 Valley (26° 29' N, 96° 35' E), Kachin State, northern Myanmar (See detailed map in Grimaldi  
80 & Ross, 2017: fig. 2). Radiometric data established an early Cenomanian age (98.79 ±0.62  
81 Ma) for Kachin amber, based on zircons from volcanic clasts found within the amber-bearing  
82 sediments (Shi *et al.*, 2012). Some ammonites found in the amber-bearing bed and within  
83 amber corroborates a late Albian–early Cenomanian age (Cruickshank & Ko, 2003; Yu *et al.*,  
84 2019). The classification follows Yeates (1994) and the morphological nomenclature follows  
85 Cumming & Wood (2017).

86  
87 Institutional abbreviations

88 IGR: Geological Department and Museum of the University of Rennes, France.

89  
90 Anatomical abbreviations

91 C costal vein; h crossvein between C and Sc; sc-r crossvein between Sc and R; Sc subcostal  
92 vein; R radial vein, R1, R2, R3, R4, R5 branches of R; M median vein, M1, M2 branches of  
93 M; dm cell between M and Cu; CuA vein cubitus anterior; br and bm basal cells of wing; A  
94 anal vein.

### 96 **3. Systematic palaeontology**

97 Class Insecta Linnaeus, 1758

98 Order Diptera Linnaeus, 1758

99 Family Bombyliidae Latreille, 1802

100 Genus *Paleocytherea* Ngô-Muller & Nel, gen. nov.

101 urn:lsid:zoobank.org:act:54D9555D-7274-4BEB-981C-7F89B0CE3ED6

102 Type species: *Paleocytherea pouilloni* Ngô-Muller & Nel sp. nov.

103 *Diagnosis.* Postcranium with deep concavity surrounding occipital foramen; scape and  
104 pedicel short, without any dorsal spine; antennal sockets widely separated; antennal flagellum  
105 with very long and flat first segment and two short apical articles plus a style; clypeus not  
106 reaching base of antennae; ocellar tubercle on vertex; posterior eye margin simple; head wider  
107 than high in anterior view; gena bare; no notopleural setae, laterotergite/ anatergite bare; tibial  
108 spur formula 1,2,0; apex of R2+3 straight; cell br longer than bm; cell cua closed; R4 weakly  
109 less sigmoidal; no interradiial crossvein; a widely opened chamber at apex of abdomen with an  
110 internal row of acanthophorite spines and a row of setae ventrally inside sternite VII, these  
111 possibly corresponding to an hair brush.

112 *Etymology.* Named after ‘paleo’ in reference to its antiquity, and the extant genus *Cytherea*.

113 Gender feminine.

114

115 ***Paleocytherea pouilloni*** Ngô-Muller & Nel, sp. nov.

116 Figures 1–4

117 urn:lsid:zoobank.org:act:44C382A0-804F-4BC1-B697-BF7AB8485976

118 *Etymology.* Named after Jean-Marc Pouillon, who allowed us to study the type specimen. The  
119 species epithet is to be treated as a noun in the genitive case.

120 *Holotype.* MHNE.2020.3.1 (Po16, nearly complete female, with apices of mid and hind tarsi  
121 missing), collection Jean-Marc Pouillon, deposited in the Musée d’Histoire Naturelle of  
122 Colmar.

123 *Horizon and locality.* Noije Bum Hill, Hukawng Valley, Kachin State, Myanmar; lower  
124 Cenomanian, Upper Cretaceous.

125 *Diagnosis.* As for the genus; wing hyaline with a darkened stigma.

126 *Description.* Head 0.5 mm long, 1.1 mm wide; wider than high in anterior view, roughly  
127 hemispherical in shape; anterior half convex; eye large, bare, no differentiation of facets; eye  
128 occupying all of lateral, much of dorsal and ventral surfaces of head; posterior edge of eye not  
129 emarginate; eye without fine transverse line through middle; no emargination near antennal  
130 base; ocelli present, but small; ocellar triangle on vertex, small, barely raised above surface of  
131 vertex; frons well developed, 0.26 mm wide, width  $0.23 \times$  that of head, lateral margins  
132 diverging slightly anteriorly; clypeus not reaching base of antennae; postgena deeply sunken,  
133 forming deep concavity into which neck inserts, with a weak and sparse pilosity; gena nearly  
134 bare; occiput flat posterior to frons and to eyes; postcranium with deep concavity surrounding  
135 occipital foramen; antennal sockets widely separated, *ca.* four times the diameter of an  
136 antennal socket; antenna apically tapered; scape cylindrical,  $1.5 \times$  length of pedicel; pedicel  
137 cylindrical, very slightly wider at apex, with apical ring of fine setae; flagellum flat with three  
138 definite articles, basal article very long,  $11 \times$  length of distal articles combined, these with  
139 faint appearance of vestigial segments; 3rd flagellar article half the size of 2nd; minute stylus  
140 present, apical; proboscis short, projecting forward, prelabellar portion recessed into oral  
141 cavity; labellum exposed, slightly projecting beyond frontal surface of eyes. Labium short,  
142 broad, length and height both twice its width, with short fine pilosity; lacinia long, laterally  
143 flanking labium; tip blunt, reaching to middle of labellum; labellar lobes rounded and fleshy.  
144 Thorax *ca.* 2.0 mm long, 1.5 mm high, rather long and narrow in dorsal view, narrower than  
145 head; neck long, dorsally with few long, fine, stiff setae, hardly visible; most of scutum and  
146 pleura covered with fine pilosity; notopleural area without macrosetae (bristles), one  
147 macroseta on supraalar area; laterotergite/ anatergite bare; transverse suture short, entirely  
148 vertical on lateral surface of scutum; scutum pinched in near middle at transverse suture.  
149 Wing slender, 3.3 mm long, 1.2 mm wide, W/L 2.75; basicosta light, well developed; C  
150 circumambient, black proximally, greatly thinned posterior to R4 apex; crossvein H faint;



151 small, faint crossvein sc-r present; Sc complete, sclerotized, apex ending slightly distal to  
152 midwing length; R-R1 thickest, most heavily sclerotized vein, length  $0.6 \times$  that of wing;  
153 darkened pterostigmatic area between apical third of R1 and C; R2+3 arising at an acute angle  
154 and in rather distal position, straight, and not upturned at apex; fork of R4+5 asymmetrical,  
155 branch of R4 longer and slightly sinuous, apices encompassing wing tip; M1 and M2 slightly  
156 sinuous, short, attached to apex of cell dm; Y-juncture of M1-M2 not weakened; CuA1  
157 attached near base of cell dm; cell br much longer than bm; apices of CuA2 and A1 meeting  
158 at wing margin (cell cup close); vein A2 present, but nebulous; anal lobe well-developed;  
159 alula rather broad; upper calypter well-developed.

160 Legs: bases of all coxae closely situated, coxae suspended beneath thorax (not projecting  
161 forward or laterally); all coxae with brush of fine, long, golden setae, on anterior surface of  
162 procoxa, lateral surfaces of meso- and metacoxae; femora with fine, decumbent setae; length  
163 metafemur  $>$  meso  $>$  profemur; mesotibia with dorso-longitudinal row of six black short,  
164 spinelike setae, none visible ventrally; tibial spurs 1-2-2; basitarsomeres as long as distal  
165 tarsomeres combined; pretarsal structures small; pulvilli small; empodium setiform.

166 Abdomen 2.0 mm long, 0.7 mm wide, slender, no wider than thorax in dorsal view, with  
167 dense vestiture of fine, decumbent setae; mediotergite covered in long setulae; lateral margins  
168 of tergites and sternites meeting; tergite 1 with long pubescence; sternites well-developed; a  
169 rather large chamber with an internal row of acanthophorite spines (Fig. 3B arrow Spb)  
170 (Spatelborsten sensu Mühlenberg 1971); also a row of setae ventrally inside sternite 7 (Fig.  
171 3B arrow Hpi?) possibly corresponding to an hair brush (Haarpinsel sensu Mühlenberg 1971).

172

173 Genus *Nidergasia* Jouault & Nel, gen. nov.

174 urn:lsid:zoobank.org:act:7ACB688A-425F-47C1-BCF8-9D980D29E786

175 *Type species: Nidergasia neraudeaui* Jouault & Nel sp. nov.

176 *Diagnosis.* Eyes holoptic; proboscis short; scape elongated, about twice as long as pedicel;  
177 pedicel short and trapezoidal-shaped, without any dorsal spine; antennal sockets widely  
178 separated; antennal flagellum with very long, slightly curved first segment tapered apically  
179 and two short apical articles plus a style; face absent; ocellar tubercle on vertex; posterior eye  
180 margin simple; head wider than high in anterior view; gena bare; scutum arched, with three  
181 notopleural macrosetae; tibial spur formula 0-2-0; wings with R2 and R3 separated; R3 not  
182 reaching wing margin; with apex of R2 straight; vein m-m strongly zigzag; vein R4 reduced,  
183 arched and not reaching wing margin; cell br longer than bm; cell cua open; no interradiial  
184 crossvein.

185 *Etymology.* Named after Valentin Nidergas, passionate student in dipterology. Gender  
186 feminine.

187

188 *Nidergasia neraudeaui* Jouault & Nel, sp. nov.

189 Figures 5–7

190 urn:lsid:zoobank.org:act:D8D4EF7C-F760-4B18-80A0-F407C59C9669

191 *Etymology.* Named after our friend and colleague Pr. Didier Néraudeau, renowned  
192 paleontologist. The species epithet is to be treated as a noun in the genitive case.

193 *Holotype.* Male number IGR.BU-008 (nearly complete, with left wing partially polished).

194 *Diagnosis.* As for the genus.

195 *Horizon and locality.* Noiye Bum Hill, Hukawng Valley, Kachin State, Myanmar; lower  
196 Cenomanian, Upper Cretaceous.

197 *Description.* Head 0.5 mm long, 0.8 mm wide (measured in dorsal view) (Figs. 5–6); wider  
198 than high in anterior view, hemispherical in lateral view; anterior half convex; eyes large,  
199 bare, no differentiation of facets; eyes occupying all of lateral, much of dorsal and ventral  
200 surfaces of head; posterior edge of eyes not emarginate; eye without fine transverse line

201 through middle; no emargination near antennal base; ocelli present, but small; ocellar triangle  
202 on vertex, small, barely raised above surface of vertex; frons well developed, 0.34 mm wide,  
203 width  $0.23 \times$  that of head, lateral margins diverging slightly anteriorly; face absent; postgena  
204 slightly sunken, forming small concavity into which neck inserts; gena nearly bare; occiput  
205 slightly convex posterior to frons and to eyes; postcranium with deep concavity surrounding  
206 occipital foramen; antennal sockets widely separated, *ca.* four times diameter of antennal  
207 socket; antenna apically tapered; scape cylindrical, about 0.1 mm long; pedicel trapezoidal  
208 shaped, slightly tapering at apex, without apical ring of fine setae, about 0.06 mm long;  
209 three definite flagellomeres, basal flagellomere very long, about 0.3 mm long, slightly curved  
210 and tapered apically; two remaining flagellomeres with faint appearance of vestigial  
211 segments; 3rd flagellomere subequal to 2nd; minute apical stylus present; proboscis short,  
212 projecting antero-ventrally (Figs. 5, 6, 7).

213 *Thorax* (Fig. 5) *ca.* 1 mm long, 1.12 mm high, rather stout and large in dorsal view, larger  
214 than head; conspicuously convex; neck short, dorsally covered with few long, fine, stiff setae;  
215 most of scutum and pleura covered with fine pilosity; notopleural area with three macrosetae  
216 (bristles); prealar bristle present; laterotergite/ anatergite with sparse setae; scutum convex  
217 covered with sparse appressed setae.

218 *Wing* slender, at least 2.3 mm long, at least 0.8 mm wide (Figs. 7, A–B); basicosta as same  
219 color as body; C probably circumambient, black proximally, thinned posteriorly to R2+3  
220 apex; crossvein h conspicuous; crossvein sc-r not visible; Sc complete, sclerotized, apex  
221 ending slightly distal to midwing length; R-R1 thickest, most heavily sclerotized vein;  
222 darkened pterostigmatic area between apical third of R1 and C; R2 nearly straight, forked  
223 apically into R2 and R3; R2 slightly curved; R3 partial; fork of R4+5 asymmetrical, R4 very  
224 short and curved; M1 and M2 curved to straight, short, attached to apex of cell dm; Y-  
225 juncture of M1-M2 not weakened; CuA1 attached near base of cell dm; cell br much longer

226 than bm and thin; apices of CuA2 and A1 not meeting at wing margin (cell cua close) (Fig.  
227 7B); anal lobe well-developed; alula rather broad; upper calypter well-developed (Fig. 7A).  
228 *Legs* (Fig. 5) coxa separated by a long a triangular shaped pleural projection; bases of all  
229 coxae closely situated (with midcoxa equidistant from pro- and meta-coxa), coxae suspended  
230 beneath thorax (not projecting forward or laterally); all coxae with brush of fine, long, golden  
231 setae, on anterior surface of procoxa, lateral surfaces of meso- and metacoxae; femora with  
232 fine, decumbent setae; length of metafemur (about 0.45 mm) > mesofemur (about 0.71 mm) >  
233 profemur (about 0.63 mm); metatibia with dorso-longitudinal row of black spinelike setae;  
234 tibial spurs formula 0-2-0; basitarsomeres longer than other tarsomeres and as long as  
235 combined lengths of distal tarsomeres; pretarsal structures small; pulvilli small (not exceeding  
236 tarsal claws); empodium setiform; tarsal claws simple.  
237 *Abdomen* (Fig. 5) 0.9 mm long, 0.56 mm high, slender, no wider than thorax in dorsal view,  
238 with dense vestiture of fine, decumbent setae; tergite with posterior margin covered in long  
239 setulae; lateral margins of tergites and sternites meeting; all tergites short and curved  
240 backward pubescence; sternites well-developed; genitalia hardly visible.

241

#### 242 **4. Discussion**

243 Following the key to fly families of Marshall *et al.* (2017), *Paleocytherea* gen. nov. and  
244 *Nidergasia* gen. nov. key out as Bombyliidae because of the following characters: wing fully  
245 developed; body not strikingly modified; wing membrane without a pattern of folds between  
246 veins; cell cua very long; vein R4+5 forked; empodium bristle-like; no spurious vein; veins  
247 not conspicuously curved anteriorly before wing apex; basal median cell with veins arising  
248 from three corners; and arculus present.

249 Grimaldi (2016) described a series of Bombyliidae from Burmese amber. *Pioneeria*  
250 *bombylia* Grimaldi, 2016 is the most similar to *Paleocytherea* gen. nov. In particular, they

251 share the most remarkable characters of *Pioneeria*, after Grimaldi (2016: 67), viz., antennal  
252 flagellum with two short apical articles; and two mesotibial spurs. Actually, two short apical  
253 flagellomeres (plus a style) are also present in some extant *Bombyliidae*, e.g., *Cacoplox* Hull,  
254 1970, *Sericusia* Edwards, 1936, *Crocidium* Loew, 1860 (Hull 1973). Two mesotibial spurs  
255 are also present in several extant bombyliid groups, e.g., some Bombyliinae and the  
256 Lordotinae (Li & Yeates, 2019). These characters are thus not sufficient to consider that  
257 *Paleocytherea* gen. nov. is closely related to *Pioneeria*. Furthermore, there are some  
258 significant differences between the two taxa, viz. the first flagellomere of *Paleocytherea* gen.  
259 nov. is flat and much longer than the subcylindrical one of *Pioneeria*; the gena is bare in  
260 *Paleocytherea* gen. nov., instead of being setose in *Pioneeria*; *Paleocytherea* gen. nov.  
261 displays no notopleural setae, instead of four in *Pioneeria*; the laterotergite/ anatergite of  
262 *Paleocytherea* gen. nov. are bare, instead of being setose in *Pioneeria*; tibial spur formula 1-  
263 2-2 instead of 0-2-?; apex of R2+3 is straight in *Paleocytherea* gen. nov., while it is curved in  
264 *Pioneeria*; cell br is longer than bm in *Paleocytherea* gen. nov., instead of being of equal  
265 length in *Pioneeria*. These characters justify a new genus and species. Grimaldi (2016)  
266 noticed that the genus and species *Pseudorhagio zhangi* Zhang *et al.*, 2016 from Burmese  
267 amber, originally placed in Tabanomorpha family *incertae sedis*, could belong to the  
268 Bombyliidae, and also resembles *Pioneeria bombylia*. *Pseudorhagio* has a very long first  
269 flagellomere, as in *Paleocytherea* gen. nov. Unfortunately, Zhang *et al.* (2016) did not  
270 indicate whether this flagellomere is cylindrical or flat. *Paleocytherea* gen. nov. differs from  
271 *Pseudorhagio* in the following points: cell cup closed at the wing margin instead of being  
272 clearly open in *Pseudorhagio*; tibial spur formula 1-2-2 instead of 0-2-0; R4 much less  
273 sigmoidal than in *Pseudorhagio*; R2+3 straight at apex instead of being strongly curved in  
274 *Pseudorhagio*. Unfortunately, Zhang *et al.* (2016) did not indicate whether *Pseudorhagio* had  
275 antennal flagellum with two short apical articles, or notopleural setae.

276 After the key to the extant bombyliid subfamilies of Yeates (1994), *Paleocytherea*  
277 gen. nov. and *Nidergasia* gen. nov. would fall near the Cythereinae because of the following  
278 characters: postcranium with deep concavity surrounding occipital foramen; scape and pedicel  
279 without any dorsal spine; ocellar tubercle found on vertex; posterior eye margin simple; head  
280 wider than it is high in anterior view; two mesotibial spurs (in *Amictus* Wiedemann, 1817).  
281 *Paleocytherea* gen. nov. also shares an elongate first palpomere with Cythereinae, but its cell  
282 cua is closed, unlike in the Cythereinae; also it has no interrarial crossvein, which is a  
283 putative synapomorphy of this subfamily, 'present in most' of the extant representatives  
284 (Yeates, 1994: 154) and in *Nidergasia* gen. nov. This last taxon has also a rudimentary  
285 interrarial crossvein, a putative synapomorphy of this subfamily.

286 The deep concavity of postcranium of *Paleocytherea* gen. nov. and *Nidergasia* gen.  
287 nov. supports their attribution to the Tomophthalmae (clade '57' of Yeates 1994: fig. 7), viz.,  
288 (Sericosoma + (Mariobezziinae + (Oniromyiinae + (Cythereinae + (Lomatiinae +  
289 (Anthracinae + (Tomomyzinae + Antoniinae)))))). The 'antennal sockets widely separated' is  
290 also a character of *Cytherea* Fabricius, 1794, *Sericosoma* Macquart, 1849, and *Pantarbes*  
291 Osten Sacken, 1877, which are three genera of the Tomophthalmae, after Yeates (1994). After  
292 the molecular phylogenetic analysis of Trautwein *et al.* (2011), this group of subfamilies is  
293 paraphyletic. This molecular phylogeny is quite different from the morphological phylogeny  
294 of Yeates concerning the placements of the subfamilies. Thus the exact phylogenetic position  
295 of *Paleocytherea* gen. nov. and *Nidergasia* gen. nov. remain uncertain, although they are  
296 certainly nested in the bombyliid crown group with one of the Tomophthalmae subfamilies,  
297 but their affinities with a precise subfamily remain uncertain.

298 According to Ye *et al.* (2019), *Paleocytherea* gen. nov. would fall near the Burmese  
299 amber *Cretabomylia* Ye *et al.*, 2019, but it differs from the latter in having the third

300 flagellomere clearly longer than the second flagellomere, crossvein m-m with apical part  
301 nearly straight, and lacking notopleural macrosetae and acanthophorite spines.

302 *Nidergasia* gen. nov. differs from all the extant and fossil Cythereinae in the wing  
303 venation and antennae. *Nidergasia* gen. nov. strongly differs from all the other Burmese  
304 amber Bombyliidae in the presence of the distal separation of R2 and R3 and the rudimentary  
305 R4. However, following Ye *et al.* (2019) *Nidergasia* gen. nov. keys out near the Burmese  
306 amber *Cretabombylia* Ye *et al.*, 2019, but it differs in having three notopleural macrosetae,  
307 the presence of the distal separation of R2 and R3, and the presence of a rudimentary R4.

308

## 309 5. Conclusion

310 *Paleocytherea pouilloni* has a broad posterior opening of its abdomen with a dorsal row of  
311 acanthophorite spines and a ventral row of setae that could correspond to a hair brush. Very  
312 similar structures are also present in *Similipioneeria mirantenna* Ye *et al.*, 2019 and  
313 *Cretabombylia spinifera* Ye *et al.*, 2019 and (Ye *et al.*, 2019: Figs. 2, 4). Of course it is not  
314 possible to see inside these chambers, but these ventral setae are in the same position as in the  
315 extant Bombyliidae that have a sand chamber. At least these bee flies were able to dig into  
316 sand to lay their eggs because of the presence of acanthophorites spines. An abdominal sand  
317 chamber with a row of specialized setae is a character present in Bombyliinae, Crocidiinae,  
318 Mariobezziinae, Oniromyiinae, Cythereinae, Lomatiinae, Tomomyzinae, and Anthracinae  
319 (Yeates, 1994: 163). Trautwein *et al.* (2011) confirmed the hypothesis of Yeates (1994) about  
320 parallel evolution of sand chambers in Bombyliidae. The known larvae of the extant bee flies  
321 are parasitoids on Arachnida, Orthoptera, Blattodea, Diptera, Lepidoptera, Hymenoptera,  
322 Coleoptera, and Neuroptera larvae or pupae (Yeates & Greathead, 1997; El-Hawagry & Al  
323 Dhafer, 2019). Many bee fly species parasitize wasps or solitary bees that dig holes and lay  
324 eggs in the sand, in which the fly goes and deposits its eggs. Yeates (1994: 163) indicated that

325 bee flies with a sand chamber 'have a complex mode of oviposition in which they first alight  
326 and charge the sand chamber with small particles of substrate, using vigorous movements of  
327 tergites 8, 9, and 10. The particles are used to protectively coat their eggs with sand while  
328 they are discharged from the common oviduct into the sand chamber. Females search for a  
329 suitable oviposition site and oviposit by flicking coated eggs with vigorous motions of the  
330 abdomen while hovering'. This sand chamber allows bee flies to protect eggs from  
331 desiccation, and/or to 'ensures a specialization to ground-dwelling hosts .... to avoid direct  
332 competition with more efficient parasitoids, including wasps and tachinid flies', after  
333 Trautwein *et al.* (2011: 5). Cerretti *et al.* (2017: 12) estimated the age for Tachinidae at 33.7  
334 Ma. at the earliest. However the extinct family Angarosphecidae (Apoidea of the 'sphecoid  
335 group') of sand wasps are recorded from Burmese amber (Melo & Rosa, 2018). In addition, a  
336 larva of a rhopalosomatid wasp parasitising a cricket was found in this amber (Lohrmann &  
337 Engel, 2017). Competitions of this kind may thus have already occurred in Burmese amber  
338 paleobiota. It is not possible to precisely determine which type of insect was parasitized by  
339 *Paleocytherea* gen. nov. However all the orders for potential hosts listed above are recorded  
340 in Burmese amber, including the oldest known 'true' solitary bee (Poinar & Danforth, 2006;  
341 Poinar, 2009). Antlions (Neuroptera: Myrmeleontoidea), which lay their eggs in sand, and  
342 pygmy mole crickets (Orthoptera: Tridactylidae), which burrow, live in tunnel and brood in  
343 sand, were also found in this amber (Heads, 2009; Hu *et al.*, 2018), and were thus potential  
344 hosts for ancient bee flies. The discovery of *Paleocytherea* gen. nov. would suggest the great  
345 antiquity of parasitoidism behavior on ground-dwelling hosts for Bombyliidae. The presence  
346 in the 'mid'-Cretaceous Burmese amber of no less than nine genera also shows that the  
347 Bombyliidae were not only present during that period, but already highly diverse.  
348 Nevertheless, if the Mythicomyiidae are known in the late Jurassic and early Cretaceous, only  
349 a poorly preserved and undescribed 'Bombyliidae gen. sp.' is recorded from the Aptian of



350 Mongolia (Tatarinov *et al.*, 1986: fig. 121a). Early Cretaceous Bombyliidae remain to be  
351 discovered.

352

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360

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490

491 **FIG. 1.** *Paleocytherea pouilloni* Ngô-Muller & Nel, gen. et sp. nov., holotype  
492 MHNE.2020.3.1. A, habitus, left side. B, wing. Scale bars represent 1 mm.

493 **FIG. 2.** *Paleocytherea pouilloni* Ngô-Muller & Nel, gen. et sp. nov., holotype  
494 MHNE.2020.3.1. A, mouthparts. B, legs, left: fore tarsus, center: mid tibia, right: hind tibia,  
495 arrows: spurs. Scale bars represent 0.5 mm (A); 0.2 mm (B).

496 **FIG. 3.** *Paleocytherea pouilloni* Ngô-Muller & Nel, gen. et sp. nov., holotype  
497 MHNE.2020.3.1. A, head above, arrows: second and third flagellomeres. B, apex of

498 abdomen, arrows Spb Spatelborsten, row of ventral inner setae (Hpi?). Scale bars represent  
499 0.5 mm.

500 **FIG. 4.** *Paleocytherea pouilloni* Ngô-Muller & Nel, gen. et sp. nov., holotype  
501 MHNE.2020.3.1. A, habitus right side. B, head from above and thorax, arrow: macroseta on  
502 supraalar area. Scale bars represent 1.0 mm.

503 **FIG. 5.** *Nidergasia neraudeaui* Jouault & Nel, gen. et sp. nov., holotype number IGR.BU-  
504 008. A, habitus, left lateral view. B, habitus, right lateral view. Scale bars represent 1 mm.

505 **FIG. 6.** *Nidergasia neraudeaui* Jouault & Nel, gen. et sp. nov., holotype number IGR.BU-  
506 008. A, Head in dorsal view. B, Line drawing of antennae. C, Head in ventrolateral view.  
507 Scale bars represent 0.5 mm (A,C); 0.12 mm (B).

508 **FIG. 7.** *Nidergasia neraudeaui* Jouault & Nel, gen. et sp. nov., holotype number IGR.BU-  
509 008. A, wing in dorsal view. B, line drawing of wing. Scale bars represent 0.5 mm.

All authors equally contributed to the paper

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