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**The first predatory dance fly of the subfamily
Ocydromiinae with specialized, raptorial legs in
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Hybotidae)**

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1 **The first predatory dance fly of the subfamily Ocydromiinae with specialized, raptorial**
2 **legs in mid-Cretaceous amber from Myanmar (Diptera: Hybotidae)**

3

4 Running head

5 mid-Cretaceous hunter dance fly

6

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22

23 **ABSTRACT**

24 The first ocydromiine hybotid fly is described and illustrated from a remarkable male preserved
25 in mid-Cretaceous amber from northern Myanmar. *Pouillonhybos venator*, gen. et sp. nov., is

26 distinguished from other members of the subfamily Ocydromiinae as well as other lineages of
27 living and fossil Hybotidae. The holotype of *P. venator* exhibits spectacular specializations of
28 the mid and hind legs, modifications likely linked to the grasping of prey either during capture
29 and/or while feeding. The species reported here is the earliest evidence of significant leg
30 modifications in Hybotidae indicating an early appearance of such specializations in the
31 family's history.

32

33

34 *Keywords:* Brachycera; Cenomanian; Empidoidea; predatory dance flies; taxonomy

35

36 **1. Introduction**

37 The family Hybotidae largely includes predaceous flies that typically frequent on fallen logs or
38 semi-aquatic vegetation in forested environments. Although generally predators, a few are
39 known to feed on pollen. Where known for the predatory taxa, many species capture preys
40 while in flight although tachydromiines more readily subdue their prey on plant surfaces
41 (Chvála, 1983). During feeding, hybotids grasp the prey item with their hind legs while
42 manipulating their food and stabilizing themselves with their fore and midlegs (Wilder, 1974).
43 Accordingly, various modifications of the hind legs have arisen among Hybotidae which appear
44 to be associated with capturing and holding their prey, the most elaborate of which belong to
45 groups believed to take their victims while in flight. The fossil record of the family is scanty,
46 with comparatively few records (Evenhuis, 1994). Hybotid flies are quite rare in the Mesozoic,
47 with only the Early Cretaceous genus *Pseudoacarterus* Waters, 1989, the mid-Cretaceous
48 *Electrocyrtoma* Cockerell, 1917, and the Late Cretaceous *Archiplatypus* Kovalev, 1974. Herein
49 we report from the mid-Cretaceous Burmese amber a remarkable new hybotid fly of the
50 subfamily Ocydromiinae with highly specialized male hind legs, implying that the evolution of

51 such features appeared early in the family's history. We provide a description of this new taxon
52 and comparisons with the diversity of modern and other extinct genera.

53

54 **2. Material and methods**

55 The specimen comes from the earliest Cenomanian amber (98.79 ± 0.62 Ma, based on U-Pb
56 zircon dating of the volcanoclastic matrix; Shi et al., 2012); location map of amber-bearing
57 locality in Yin et al. (2018: fig. 1A). It is preserved in a piece of clear, yellow amber. The amber
58 piece was cut, shaped, and polished using a diamond disk under water and diatomite, and was
59 then mounted between two coverslips with sugar medium dissolved at saturation in water,
60 before being examined and photographed. The inclusion was examined and measured under
61 incident light with an Olympus SZX9 and Leitz Wetzlar binocular microscopes. The holotype
62 is deposited in the amber collection of the Musée d'Histoire Naturelle et d'Ethnographie de
63 Colmar (MHNEC), France under collection number MHNE.2020.7.1. We follow the
64 terminology of Cumming & Wood (2009) and the empidoid classification of Sinclair &
65 Cumming (2006).

66

67 **3. Systematic palaeontology**

68 Order Diptera Linnaeus, 1758

69 Superfamily Empidoidea Latreille, 1809

70 Family Hybotidae Meigen, 1820

71 Subfamily Ocydromiinae Schiner, 1862

72 Genus *Pouillonhybos* Ngô-Muller, Engel & Nel, gen. nov.

73 urn:lsid:zoobank.org:act:39BCAEAE-6677-496A-A30B-1B9691ADA0FD

74 Type species: *Pouillonhybos venator* Ngô-Muller, Engel & Nel, sp. nov.

75 *Diagnosis.* Proboscis short, oriented ventrally. Antenna with stylus elongate, arista-like, longer
76 than postpedicel. Protibial gland present. Mesofemur crassate, with four stout, elongate, ventral
77 setae; mesotibia elongate, basally slightly geniculate, with two outer rows of short, oblique
78 setae and a single, elongate, apical spur. Hind legs greatly modified; metacoxa with one
79 elongate seta; metafemur with pronounced inner curvature, with two stout, thickened, elongate
80 subapical spines and a series of stout, elongate setae ventrally as well as a row of shorter, curved
81 prolateral (ectal) setae; metatibia strongly arched with a prominent, thick, subapical, hook-like
82 lobe, and a row of long inner setae, and an apical spur; metabasitarsus broadened, with an ectal
83 row of curved setae and an ental row of long, rather straight setae. Wings well developed, much
84 longer than abdomen; pterostigma lacking; C terminating at wing apex, on M₁; stem of Rs short;
85 R₂₊₃ comparatively straight; R₄₊₅ and M₁ roughly parallel; *dm* present, elongate; m-m arched,
86 with faint nebulous trace of M₂, trace disappearing after length about 0.5× m-m length; two
87 veins emitted from *dm* reaching wing margin (M₁ and M₄); *cua* present, elongate, about as long
88 as *bm*, with apex oblique, with outer angle obtuse, without spur vein; vein dm-m strongly
89 oblique; CuA not broadly arching apically to CuA+CuP; CuP and CuA+CuP faint, not reaching
90 wing margin; anal lobe narrow; alula absent. Epandrium with pair of articulated surstyli
91 apically.

92 *Etymology.* The new generic name is a combination of the surname Pouillon, honoring Jean-
93 Marc Pouillon, who donated the type specimen, and *Hybos* Meigen, the type genus of the
94 family. The gender of the name is masculine.

95

96 ***Pouillonhybos venator*** Ngô-Muller, Engel & Nel, sp. nov.

97 Figs 1–3

98 urn:lsid:zoobank.org:act:AB82FF4F-897E-4784-ADCC-5F3D8D025C1C

99 *Etymology.* The specific epithet is taken from the Latin word '*venator*', meaning, 'hunter',
100 referring to the specialized metatibiae of this species.

101 *Material.* Holotype MHNE.2020.7.1 (a complete specimen in amber, coll. Jean-Marc Pouillon);
102 Musée d'Histoire Naturelle et d'Ethnographie de Colmar, France.

103 *Horizon and locality.* Noiye Bum Hill, Hukawng Valley, Kachin State, Myanmar; lower
104 Cenomanian, mid-Cretaceous.

105 *Diagnosis.* As for genus; only one included species.

106 *Description.* Male, body 2.03 mm long (Fig. 1); head 0.22 mm long, 0.30 mm wide; compound
107 eyes apparently setose, with few visible very short setae, large, meeting at one point above (a
108 gas bubble occludes views of the upper part of the head); ptilinal fissure absent; occiput and
109 frons bare; apex of antenna with lengthened, arista-like stylus (Fig. 3A), possibly dimerous as
110 a very short structure is present between it and postpedicel, apical on postpedicel; postpedicel
111 pear-shaped, 0.06 mm long, quite shorter than stylus (0.66 mm long) and shorter than pedicel;
112 pedicel with an apical crown of strong setae, longer than scape; proboscis short, oriented
113 ventrad.

114 Thorax 0.64 mm long, 0.45 mm wide, with bare laterotergite; two elongate setae on scutellum
115 and three near base of wing.

116 Wing hyaline (Fig. 1B), longer than abdomen, apex rounded, 2.22 mm long, 0.45 mm wide,
117 covered with microtrichia, without darkened pterostigma; Sc ending on C, 1.08 mm from wing
118 base; C extending to wing apex, terminating at apex of M1; Rs originating well distad level of
119 humeral vein (h), 0.39 mm from it; branches of Rs not strongly thickened and crowded
120 anterobasally; R2+3 elongate and straight, 0.08 mm long; R4+5 unbranched, 1.29 mm long,
121 nearly straight and parallel to M1; cell *dm* present, 0.69 mm long, 0.13 mm wide, with three
122 veins distally emerging from it: M1 (0.6 mm long), M2 (present as an exceedingly faint
123 nebulous vein disappearing well before wing margin, distinctly shorter than m-m crossvein),

124 and M4 (0.19 mm long); CuA forming a distinct angle with basal part of CuP; cell *cua* scarcely
125 shorter than cell *bm* (*bm-cm* and CuA nearly confluent), with outer angle obtuse; CuA+CuP
126 vein not reaching wing margin; narrow anal lobe, 0.13 mm wide; lunule absent; a series of long
127 setae on anal margin; haltere elongate, 0.41 mm long, 0.08 mm wide.

128 Legs (Figs 2, 3A). Pretarsal claws simple, empodia setiform; protibial gland present; profemur
129 0.29 mm long, 0.06 mm wide, curved, with a series of at least five long setae along inner
130 surface; protibia 0.29 mm long, 0.04 mm wide, with three rows of stout setae, one apical spur;
131 probasitarsus elongate, 0.18 mm long, with two series of long setae; protarsomere II 0.11 mm
132 long; protarsomere III 0.08 mm long; protarsomere IV 0.04 mm long; protarsomere V 0.06 mm
133 long; mesofemur crassate, approximately 0.42 mm long, 0.06 mm wide, with four stout,
134 thickened, erect, spine-like setae on ventral surface; mesotibia 0.53 mm long, 0.04 mm wide,
135 basally geniculate, with two series of rather short, oblique setae, a single elongate apical spur;
136 mesotarsus ca. 0.53 mm long; metacoxa with a single, elongate, posteroventral seta, 0.29 mm
137 long; metafemur 0.76 mm long, 0.09 mm wide, with a pronounced inner curvature and two
138 stout, thickened, enlarged, subapical spurs (0.16 mm long) and a series of long, stout, erect,
139 spine-like setae along ventral surface, a series of shorter, finer, curved, oblique setae along
140 dorsal surface (Fig. 2); metatibia basally geniculate, strongly curved, with a subapical hook-
141 like lobe (0.1 mm long), apex of lobe narrowly rounded, a row of long, oblique setae on inner
142 surface, a single, short, basally thickened apical spur, outer surface with a row of erect to
143 semierect, short, fine setae; metabasitarsus greatly broadened and somewhat trapezoidal as
144 lateral margins slightly converge apically, 0.09 mm long, 0.04 mm wide, outer edge with a row
145 of short, strongly curved setae, inner edge with a row of longer, obliquely erect, largely straight
146 setae; metarsomere II elongate, 0.16 mm long, 0.01 mm wide, with two rows of fine, long setae;
147 metatarsomere III 0.09 mm long, 0.01 mm wide, metatarsomere IV 0.08 mm long, 0.008 mm
148 wide, metatarsomere V 0.08 mm long, 0.008 mm wide.

149 Abdomen elongate (Fig. 2), rather narrow, 1.0 mm long, 0.24 mm wide, with a single, elongate
150 spine-like seta laterally on segments II–V; male terminalia asymmetrical and rotated 90° (Fig.
151 3B); cercus thin with a small inner extension; hypoproct small near cercal base; phallus large,
152 as long as and broader than cerci; epandrium greatly enlarged, spoon-shaped, apparently with
153 an apical pair of articulated surstyli.

154 Female unknown.

155

156 **4. Discussion**

157 *Pouillonhybos* gen. nov. can be placed within the Empidoidea owing to the following
158 characters: ptilinal fissure and lunule absent; empodia setiform; pedicel shorter than flagellum;
159 flagellum with three flagellomeres; cell *cua* small; stylus elongate and thin; wing apex rounded;
160 branches of R not strongly thickened and crowded anterobasally; C extending to wing apex;
161 CuA+CuP not reaching wing margin. Using those traits outlined by recent authors (*e.g.*,
162 Steyskal & Knutson, 1981; Sinclair & Cumming, 2006, 2017), the new fossil genus falls among
163 the Hybotidae based on the following characters: apex of antenna with lengthened, bristle-like
164 stylus (stylus also not setulose); thorax with bare laterotergite; protibial gland present; C ending
165 at wing apex, instead of circumambient (but some empidids also have a costa terminating at the
166 wing apex); Rs originating well distal to level of humeral vein (h); R4+5 unbranched; CuA
167 forming a distinct angle with basal part of CuP. It should be noted that some Empididae have a
168 wing venation quite similar to that of *Pouillonhybos* (*viz.* *Macrostomus* Wiedemann, 1817),
169 especially in the narrow anal lobe and shape of cell *cua*, and even in the C terminating on M1.
170 Such empidids, however, differ from *Pouillonhybos* in the setulose scape (not so in the fossil),
171 shape of the more elongate flagellum, and, in the case of *Macrostomus*, lacking a defined stylus
172 (Smith, 1961: fig. 3; Rafael & Cumming, 2004: figs 1, 3).

173 Wahlberg & Johanson (2018) presented a molecular phylogenetic analysis of the
174 Empidoidea, in which Hybotidae are subdivided into six subfamilies: Bicellariinae Sinclair &
175 Cumming, 2006; Ocydromiinae Schiner, 1862; Oedaleinae Chvála, 1983; Hybotinae Meigen,
176 1820; Tachydromiinae Meigen, 1822; and Trichininae Chvála, 1983. Most recently, Sinclair
177 (2019) added the subfamily Stuckenbergomyiinae Sinclair, 2019. Affinities between the new
178 fossil and Trichininae (*Trichinomyia* Tuomikoski, 1959 and *Trichina* Meigen, 1830) are
179 excluded because of the absence of an alula, the narrow anal lobe, the absence of a pterostigma,
180 and the elongate stylus (Tuomikoski, 1959). The Tachydromiinae are excluded because M₂ is
181 present, albeit only as a short, faintly nebulous vein, cell *dm* present, and cell *cua* elongate
182 (Sinclair & Cumming, 2006, 2017). Similarly, the subfamily Bicellariinae (*Bicellaria*
183 Macquart, 1823) can be discounted owing to the narrow anal area and presence of cell *dm* (Kato,
184 1971). The Oedaleinae have a branched M₁₊₂ and an anterad projecting proboscis, quite unlike
185 *Pouillonhybos*, and the Stuckenbergomyiinae differ from the new fossil genus in the truncate
186 cell *cua*, shortened stylus, and three veins emitted from cell *dm*.

187 Affinities with the Hybotinae would also be excluded because of the presence of M₂ in
188 *Pouillonhybos*, but as it is rudimentary in the present fossil we prefer to compare the new genus
189 to extant and fossil hybotine genera. The short proboscis of *Pouillonhybos* excludes affinities
190 with *Syneches* Walker, 1852 (incl. *Parahybos* Kertész, 1899, *Harpamerus* Bigot, 1859, and
191 *Epiceia* Walker, 1860), *Hybos* Meigen, 1803, *Smithybos* Ale-Rocha, 2000, *Syndyas* Loew,
192 1857, and *Lactistomyia* Melander, 1902. In the genera *Afrohybos* Smith, 1967, *Cerathybos*
193 Bezzi, 1909, *Euhybus* Coquillett, 1895, and *Neohybos* Ale-Rocha & Carvalho, 2003 cell *cua*
194 extends far distal to cell *bm* (Melander, 1902; Smith, 1967; Ale-Rocha, 2000, 2002, 2008; Ale-
195 Rocha & Carvalho, 2003; Grootaert & Yang, 2009; Sinclair, 1996, 2011; Liu et al., 2012, 2014),
196 quite unlike *Pouillonhybos* in which these cells are about subequal in length, with *cua* only
197 scarcely shorter than *bm*. *Acarterus* Loew, 1858, *Lamachella* Melander, 1928, and the

198 Cretaceous genus *Pseudoacarterus* Waters, 1989 have cell *cua* apically convex (*i.e.*, CuA is
199 convexly arched), while in the new genus CuA is straight and oblique (Waters, 1989; Sinclair,
200 1996). Additionally, in *Lamachella* *cua* is distinctly shorter than *bm*, a pterostigma is usually
201 present, m-cu is more elongate and not in near alignment with CuA, and R₂₊₃ is sinuate, unlike
202 *Pouillonhybos* (Smith, 1969: figs 137-138; Sinclair & Cumming, 2017). *Chillcottomyia*
203 Saigusa, 1986, *Stenoproctus* Loew, 1858, and the Miocene genus *Syneproctus* Solórzano-
204 Kraemer et al., 2020 have cell *cua* quite shorter than *bm*, and with apex convex, nearly
205 perpendicular to the two veins CuA and CuP, unlike *Pouillonhybos* (Smith, 1969: figs 127-128,
206 130; Yang & Grootaert, 2004; Solórzano-Kraemer et al., 2020).

207 The fossil shares many traits with the subfamily Ocydromiinae, in which cell *cua* is
208 shorter than or about as long as cell *bm*, with its outer angle obtuse; the postpedicel shorter than
209 the arista-like stylus; a cell *dm* present; and the proboscis oriented ventrad, all as in
210 *Pouillonhybos* (Sinclair & Cumming, 2000, 2006; Wahlberg & Johanson, 2018). In addition,
211 ocydromiines also have an epandrium with an apical pair of articulated surstyli, another trait
212 apparently present in *Pouillonhybos*, pointing to a placement within the subfamily for this new
213 Cretaceous genus.

214 Within this subfamily, *Leptopezella* Sinclair & Cumming, 2007 has no discal cell, a
215 pterostigma, cell *cua* clearly shorter than *bm*, and no metatibial extension, and is therefore quite
216 different from *Pouillonhybos* (Sinclair & Cumming, 2007). *Abocciputa* Plant, 1989 and
217 *Chvalaea* Papp & Földvári, 2001 differ from *Pouillonhybos* in that cell *cua* is significantly
218 shorter than cell *bm*, there is no trace of M₂, and R₄₊₅ is not parallel to M₁ (Plant, 1989; Papp
219 & Földvári, 2002; Shamshev et al., 2017), and the genera *Austropeza* Plant, 1989,
220 *Pseudoscelolabes* Collin, 1933, and *Leptodromiella* Tuomikoski, 1936 also have cell *bm* much
221 longer than cell *cua* (Tuomikoski, 1936; Collin, 1926, 1928, 1933; Chvála, 1983; Plant, 1989).
222 *Oropezella* also has a rather long cell *dm* and quite short veins emerging from it, unlike

223 *Pouillonhybos* (Chvála, 1983; Ale Rocha, 2007). In the genus *Stylocydromia* Saigusa, 1986
224 there is a long cell *dm*, while the base of Rs is much closer to h than to r-m, unlike the condition
225 in *Pouillonhybos* (Saigusa, 1986). The genus *Leptopeza* Macquart, 1827 has a rudimentary M₁
226 and cell *bm* much longer than cell *cua* (Chvála, 1983), while in *Ocydromia* Meigen, 1820, the
227 stylus is supra-apical rather than apical in *Pouillonhybos*, and moreover cell *bm* is much longer
228 than cell *cua* and there is no trace of a third vein emerging from *dm* (Chvála, 1983).
229 *Apterodromia* Oldroyd, 1949 shares with *Pouillonhybos* a cell *cua* nearly as long as *bm*, but it
230 has an anal area much more reduced than *Pouillonhybos* and a well-defined M₂ (Sinclair &
231 Cumming, 2000). *Neotrichina* Sinclair & Cumming, 2000 has the stylus scarcely as long as the
232 postpedicel, three veins emitted from *dm* that reach the wing margin, cell *cua* much shorter than
233 *bm*, an anal vein almost complete to the wing margin, CuA closing *cua* almost straight, all quite
234 distinct from the character states present in *Pouillonhybos*; also some species of *Neotrichina*
235 have the metatibia dilated apically but without a lateral expansion, and therefore unlike that in
236 *Pouillonhybos* (Collin, 1933; Sinclair & Cumming, 2000). *Hoplopeza* Bezzi, 1909 and
237 *Scelolabes* Philippi, 1865 can be excluded from having any affinity with the new fossil genus
238 because they have Rs short, arising near the apex of cell *bm*, and cell *cua* much shorter than *bm*
239 (Collin, 1933; Rafael, 1995; Sinclair & Cumming, 2000). Lastly, *Leptodromia* Sinclair &
240 Cumming, 2000 has cell *cua* two-thirds length of cell *bm* and a short M₁ that does not reach the
241 wing margin (Bezzi, 1904; Sinclair & Cumming, 2000).

242 Among known extinct genera, the Eocene Baltic amber genus *Palaeoleptopeza*
243 Meunier, 1908, was considered as near to “*Leptopeza* but with spinose hind femora” by
244 Melander (1928: 371), and differs from *Pouillonhybos* in that the postpedicel is as long as the
245 stylus, R₂₊₃ is distinctly arcuate, and M₂ is more clearly defined as a fuscous nebulous trace
246 (Meunier, 1908: pl. 7, fig. 15, pl. 8, fig. 4). *Ecommocydromia difficilis* Schlüter, 1978 is the
247 unique Cretaceous taxon currently attributed to the Ocydromiinae; it is based on an incomplete

248 specimen in amber with numerous characters of wing venation missing (in particular, the
249 relative positions of r-m, base of Rs, and h are unknown), rendering it impossible to determine
250 if this assignment is valid or whether it might belong to the Dolichopodidae. It has three long
251 veins emerging from an elongate cell *dm*, which is quite unlike any other Ocydromiinae. The
252 cells *bm* and *cua* are not preserved, and we believe that attribution to Ocydromiinae is difficult
253 to justify (Schlüter, 1978: figs 86-89). *Ecommocydromia difficilis* is perhaps best considered as
254 incertae sedis until more completely preserved specimens are recovered. The Eocene Baltic
255 amber genus *Meghyperella* Meunier, 1908 was considered by Melander (1928: 370) as
256 “apparently related to *Leptopeza*” (Ocydromiinae), and possibly a “predecessor of
257 *Stenoproctus*” (Hybotinae). It differs from *Pouillonhybos* in the exceptionally short stylus
258 (Meunier, 1908), and needs to be revised. Evenhuis (1994) listed it among the fossil
259 ‘Empididae’. Note that the alleged Oligocene hybotine genus *Eternia* Martins-Neto et al., 1992
260 is based on a poorly preserved fossil, but it preserves *cua* as long as *bm* with an obtuse outer
261 angle, suggesting it belongs to the Ocydromiinae (Martins-Neto et al., 1992). Lastly, the
262 putative Oligocene hybotine genus *Tremembella* Martins-Neto et al., 1992 is based on an
263 exceptionally poorly preserved specimen and until more complete material is discovered it
264 remains impossible to compare with the other genera.

265 The only other Hybotidae from Burmese amber is *Electrocyrtoma burmanica* Cockerell,
266 1917, a genus that differs from *Pouillonhybos* in the absence of cell *dm*, a much broader cell
267 *bm*, and a cell *cua* much shorter than *bm* (Cockerell, 1917: fig. 5). Melander (1928: 368)
268 indicated that *Electrocyrtoma* resembled *Bicellaria*, while Grimaldi & Cumming (1999: 51)
269 considered it as belonging to Tachydromiinae.

270

271 **5. Conclusions**

272 *Pouillonhybos* is the first ocydromiine from Burmese amber and probably the only definitive
273 representative of this subfamily from the Cretaceous. Modern Ocydromiinae are predators
274 (Chvála, 1976), and like other hybotids often hold their prey with the hind legs while feeding.
275 However, no living ocydromiines have a massive prominence on the metatibia like the one
276 present in *Pouillonhybos*. This structure, together with the stout setae and spines on the
277 metafemur, erect and spine-like setae on ventral surface of mesofemur, and setae on the other
278 femora and tibiae, coxae, and abdomen, strongly suggest that *Pouillonhybos* was a predator
279 who, like surviving relatives, captured and hold prey with its hind legs. The hybotine genera
280 *Hybos*, *Syndyas*, and *Syneches* have raptorial hind legs (Grootaert, 1996), with strong spines on
281 the metafemur but no prominent extension on the metatibia. Some species of *Lactistomyia* also
282 have raptorial hind legs with a metatibial lateral extension, albeit situated in a distinctly more
283 proximal position than that of *Pouillonhybos* (Ale-Rocha, 2008). *Afrohybos* has also a highly
284 modified hind leg with a ventral extension of the metafemur and strong spines on the metatibia
285 (Smith, 1969: fig. 96), while the hybotine genus *Syneproctus* has a metatibia with an apical
286 extension most analogous to that of the fossil, but quite a bit smaller than that of *Pouillonhybos*.

287 Many Hybotidae and Dolichopodidae have raptorial fore and/or mid legs with greatly
288 modified femora and/or tibiae, and some dolichopodids have a strong spine on an apical
289 extension of the meso- and/or metatibia and/or structures on the metabasitarsus, resembling the
290 metatibial extension of *Pouillonhybos* and *Syneproctus* (Bickel, 1985: figs 7-8; Zhu et al., 2005;
291 Runyon, 2008; Grichanov & Brooks, 2017). It is clear that not only various leg modifications
292 have evolved convergently among empidoid lineages for subduing and handling prey, but such
293 traits also appeared in the early phases of their diversification as evidence by their presence in
294 at least one Cretaceous ocydromiine. The special shape of the legs of *Pouillonhybos* suggests
295 that it was catching its preys during flight, as for the extant Ocydromiinae (Daugeron, 1997).

296 Many Empidoidea are well-known for their complex mating behavior, with gifts to the
297 female and semaphore behaviors. Nevertheless, after Downes (1969: 290), both sexes of ‘the
298 extant Hybotinae and some Ocydromiinae’ ‘capture prey and the feeding habits have no
299 relationship to the flight in the mating swarm’. Even if the extant Ocydromiinae are making
300 swarms without mating (Daugeron, 1997), in absence of information on the morphology of the
301 female of *Pouillonhybos*, it is not possible to infer hypotheses about the mating behavior in this
302 ancient Hybotidae.

303

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307

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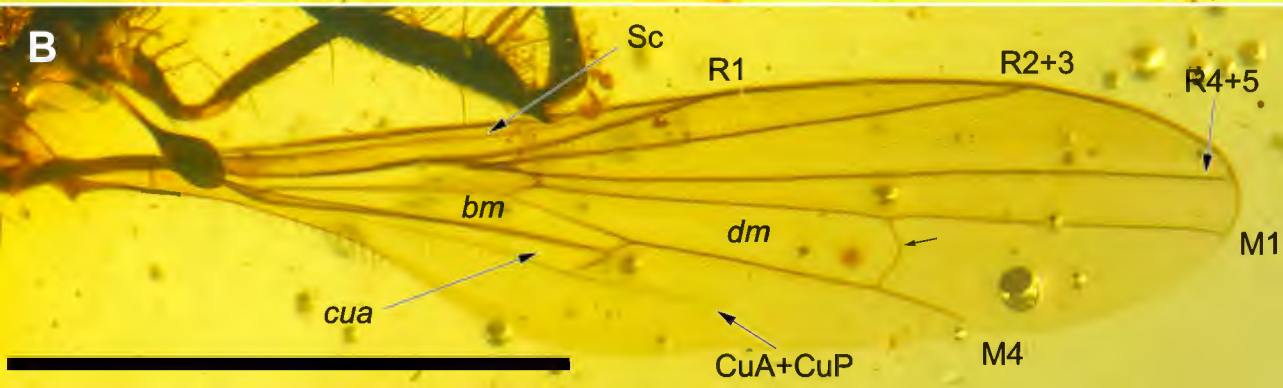
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505 **FIG. 1.** *Pouillonhybos venator* Ngô-Muller, Engel, & Nel, gen. et sp. nov., holotype
506 MHNE.2020.7.1. A, habitus, ventral view. B, wing, arrow base of vein M2. Scale bars = 1 mm.

507 **FIG. 2.** *Pouillonhybos venator* Ngô-Muller, Engel, & Nel, gen. et sp. nov., holotype
508 MHNE.2020.7.1. Hind leg, c.s. coxal seta, bt. basitarsus, f. femur, t. tibia, s. spur. Scale bar =
509 1 mm.

510 **FIG. 3.** *Pouillonhybos venator* Ngô-Muller, Engel, & Nel, gen. et sp. nov., holotype
511 MHNE.2020.7.1. A, head, above. B, male terminalia, lateral view; ce cercus, ep epandrium, ph
512 phallus. Scale bar = 0.5 mm (A), 0.1 mm (B).

513

A**B**



f.

f.

s.

C.S.

t.

s.

bt.



