



HAL
open science

The first flat wasps (Hymenoptera: Bethylidae) from Miocene Mexican amber

Manuel Brazidec, Vincent Perrichot

► To cite this version:

Manuel Brazidec, Vincent Perrichot. The first flat wasps (Hymenoptera: Bethylidae) from Miocene Mexican amber. *Journal of South American Earth Sciences*, 2022, 116, pp.103838. 10.1016/j.jsames.2022.103838 . insu-03664482

HAL Id: insu-03664482

<https://insu.hal.science/insu-03664482>

Submitted on 11 May 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.

Journal Pre-proof

The first flat wasps (Hymenoptera: Bethyloidea) from Miocene Mexican amber

Manuel Brazidec, Vincent Perrichot



PII: S0895-9811(22)00128-6

DOI: <https://doi.org/10.1016/j.jsames.2022.103838>

Reference: SAMES 103838

To appear in: *Journal of South American Earth Sciences*

Received Date: 4 April 2022

Revised Date: 3 May 2022

Accepted Date: 3 May 2022

Please cite this article as: Brazidec, M., Perrichot, V., The first flat wasps (Hymenoptera: Bethyloidea) from Miocene Mexican amber, *Journal of South American Earth Sciences* (2022), doi: <https://doi.org/10.1016/j.jsames.2022.103838>.

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

© 2022 Published by Elsevier Ltd.

1 **The first flat wasps (Hymenoptera: Bethylinae) from Miocene Mexican amber**

2 MANUEL BRAZIDEC^{1,2*}, VINCENT PERRICHOT¹

3 ¹Univ Rennes, CNRS, Géosciences Rennes, UMR 6118, 35000 Rennes, France.

4 manuel.brazidec@gmail.com / <https://orcid.org/0000-0002-0860-8972>;

5 vincent.perrichot@univ-rennes1.fr / <https://orcid.org/0000-0002-7973-0430>

6 ²State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and
7 Palaeontology and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of
8 Sciences, 39 East Beijing Road, Nanjing 210008, China.

9 *corresponding author

10 **Abstract**

11 Despite a fairly good number of Miocene insect-bearing deposits available worldwide, the
12 bethylinid wasps from this period are yet very poorly known. Here, we describe and figure three
13 new species in three subfamilies, from the early to middle Miocene of Totolapa (Mexico):
14 *Goniozus cotyi* sp. nov. (Bethylinae), *Bakeriella nanyhela* sp. nov. (Epyrinae), and *Solepyris*
15 *electromexicanus* sp. nov. (Scleroderminae). The cosmopolitan *Goniozus* Förster, 1856 was
16 already known from the Miocene of Dominican Republic, whereas the Pan-American
17 *Bakeriella* Kieffer, 1910 and the South-American *Solepyris* Azevedo, 2006 are recorded for
18 the first time as fossil. Our finding expands the geographical distribution of the latter genus
19 much northward in the New World.

20 **Keywords:** Insecta; Chrysidoidea; Bethylinae; Epyrinae; Scleroderminae; Chiapas amber;

21 **1. Introduction**

22 Wasps of the family Bethyridae (Chrysidoidea) are cosmopolitan, although more diverse
23 in tropical regions. Today the family comprises more than 2900 extant species that are mainly
24 parasitoids of lepidopteran and coleopteran larvae (Azevedo et al., 2018; Evans, 1964). The
25 diversity of bethylid wasps is also witnessed through geological times, with about 100 fossil
26 species described, principally from the long-surveyed Baltic Eocene amber. But whereas it is
27 often repeated that Cretaceous bethylids are poorly documented, Miocene representatives did
28 not receive much attention either. This is particularly surprising when considering that highly
29 fossiliferous deposits such as Dominican and Mexican amber have been studied for more than
30 six decades (e.g., Sanderson and Farr, 1960; Snyder, 1960). In fact, only five species are
31 known from the Miocene, all but one from the New World: *Goniozus respectus* Sorg, 1988
32 (Bethylinae), *Anisepyrus gradatus* Sorg, 1988 (Epyrinae), *Apenesia miki* (Terayama, 2004)
33 (Pristocerinae), and *Alongatepyrus pedrocai* Colombo and Azevedo (in Colombo et al., 2022a)
34 (Scleroderminae), from Dominican amber; *Parascleroderma palaeosinica* Brazidec and
35 Perrichot, 2022 (Pristocerinae) from Chinese amber of Zhangpu; and *Epyrus deletus* Brues,
36 1910 (Epyrinae) from rock-imprints of Florissant, USA. However, it is worth mentioning that
37 the latter specimen was attributed to *Epyrus* s.l., since many diagnostic features cannot be
38 observed on the compression fossil (Brues, 1910: fig. 1). Another bethylid from Florissant
39 was briefly characterized but not named (Brues, 1906), and an unnamed species of *Goniozus*
40 Förster, 1856 was also figured from compression fossils of Rubielos de Mora, in Spain
41 (Peñalver-Mollá, 1998). In general, however, bethylids are poorly preserved and even rarely
42 observed in sedimentary rocks, maybe due to the small size and fossorial habits of these
43 wasps. As small insects frequently moving on bark, these are more prone to fossilization in
44 tree resin (Solórzano Kraemer et al., 2018). The scant Miocene record of Bethyridae may
45 therefore be particularly enriched by screening amber, notably that of poorly investigated
46 deposits such as Totolapa (Mexico), or recently discovered deposits from New Zealand,

47 Ethiopia, and China (Solórzano Kraemer et al., 2015; Schmidt et al., 2018; Bouju and
48 Perrichot, 2020; Wang et al., 2021).

49 Here, we propose three new species of Bethyridae from the Totolapa deposit, one of the
50 earliest-known amber sites from Chiapas, Mexico (Bryant, 1983). This is the first report of the
51 family from this site, the biota of which being still largely unknown (Solórzano Kraemer,
52 2010; Coty and Nel, 2013; Durán-Ruiz et al., 2013; Ross et al., 2016).

53

54 **2. Material and methods**

55 The studied specimens are contained in three amber pieces originating from the Totolapa
56 deposit, State of Chiapas, southwestern Mexico, more specifically from a mine owned by the
57 Ramirez family along the Río Salado (see map in Durán-Ruiz et al., 2013: fig. 1). Ambers
58 from Totolapa and Simojovel are chemically identical and have been assigned their own
59 variety, the Simojovelite (Lambert et al., 1989; Riquelme et al., 2014). Furthermore, the
60 amber-bearing strata in Totolapa have been correlated with the Mazantic shale and Balumtum
61 sandstone from the Simojovel deposits, and are thus similarly dated as early-middle Miocene
62 (Perrilliat et al., 2010; Durán-Ruiz et al., 2013; Riquelme and Menéndez-Acuña, 2017; Hegna
63 et al., 2020 and references therein). The pieces studied herein have been collected and bought
64 to the mine owners in 2007 by M. David Coty (France) who recently offered them to one of
65 us (M.B.) for study. We subsequently donated the specimens for permanent repository in the
66 paleontological collection of the Museo de Paleontología de la Facultad de Ciencias (FCMP),
67 Universidad Nacional Autónoma de México.

68 The amber pieces have been polished to facilitate the observation of the specimen, using
69 thin silicon carbide sanding papers on a grinder polisher (Buehler EcoMet 30). The

70 examination and photographs were conducted with a Leica DMC4500 camera attached to a
71 Leica M205C stereomicroscope. All images are digitally stacked photomicrographic
72 composite of several focal planes, which were obtained using Helicon Focus 6.7. Adobe
73 Illustrator CC2019 and Photoshop CC2019 software were used to compose the figures and
74 ImageJ 1.53 for measurements (Schneider et al., 2012). Details of the body have been
75 redrawn digitally from sketch drawings made with a camera lucida attached to the
76 stereomicroscope. The morphological nomenclature follows Lanes et al. (2020), except Harris
77 (1979) for the surface sculpturing. Main measurements and indices used are as follows: length
78 of forewing (LFW); length of head, measured from top of vertex to apex of clypeus (LH);
79 width of head above eyes (WH); width of frons (WF); height/width of eye (HE); ocello-ocular
80 line (OOL); width of ocellar triangle (WOT); diameter of anterior ocellus (DAO); vertex-
81 ocular line (VOL).

82 This published work and its new nomenclatural acts are registered in ZooBank with the
83 following LSID (reference): urn:lsid:zoobank.org:pub:E1861647-9624-4AC1-9201-
84 B362CDFEC545

85

86 **3. Systematic palaeontology**

87 **Superfamily** Chrysidoidea Latreille, 1802

88 **Family** Bethylidae Haliday, 1839

89 **Subfamily** Bethylinae Haliday, 1839

90 **Genus** *Goniozus* Förster, 1856

91 *Goniozus cotyi* sp. nov.

92 Fig. 1

93 LSID (species): urn:lsid:zoobank.org:act:37E8ABCD-D609-45BE-9389-EB5D77F07BAB

94 Material. Holotype number FCMP-1464, a complete male, with some features hidden by air
95 bubbles.

96 Etymology. This species honours David Coty, for his generous donation of the specimen and
97 in this way contributing to the knowledge of the Totolapa amber. The specific epithet is to be
98 treated as a noun in a genitive case.

99 Diagnosis. (Male) Body stout; head wider than high (Fig. 1A); mandible thick, with four short
100 teeth (Fig. 1C); flagellomeres slightly longer than wide; flagellomere 1 thinner than following
101 ones; parapsidal signum deeply impressed (Fig. 1C); [1M] cell closed; prestigma triangular;
102 pterostigma large, rounded; 2r-rs&Rs contiguous, only slightly arched toward anterior wing
103 margin (Fig. 1D); femora enlarged; profemur largest, laterally flattened (Fig. 1B).

104 Type locality. Río Salado Mine, Totolapa, State of Chiapas, southwestern Mexico.

105 Age. Early to middle Miocene, ca. 23–15 Ma

106 Description. Body rather flattened, stout (length 3.70 mm). Head prognathous, ovoid, longer
107 than wide; LH: 0.71 mm, WH: 0.58 mm; WF: 0.41 mm, HE: 0.25 mm; frons flat, punctuate,
108 sparsely pubescent; compound eyes elliptical, longer than high; clypeus with median lobe
109 acutely angular, clypeal carina outcurved in profile, extending on frons; mandibles widely
110 opened, thick, with four small teeth apically; antennae short, with 11 flagellomeres;
111 flagellomeres slightly longer than wide (length ca. 0.06 mm); flagellomere 1 thinner than
112 following one(s); flagellomeres 2–5 stout; flagellomeres 6–11 thin; flagellomere 11 tapering
113 at apex.

114 Mesosoma with dorsum smooth (length 1.16 mm); propleuron not visible dorsally; dorsal
115 pronotal area with lateral margin straight; anteromesoscutum as long as pronotum, parapsidal
116 signum well impressed, notauli absent; scuto-scutellar suture without sulcus; mesopleuron not
117 prominent. Fore wing macropterous, hyaline (LFW: 2.07 mm); C, Sc+R, M+Cu, A tubular;
118 Rs&M curved; Rs+M tubular; [1M] cell (areolet) closed; prestigma triangular; pterostigma
119 large, rounded; 2r-rs&Rs contiguous, slightly arched toward wing margin, distal segment
120 absent. Legs pubescent; profemur largest, slightly flattened; meso and metafemora enlarged;
121 tarsal claws curved.

122 Metasoma about as long as head + mesosoma combined, not distinctly pubescent (length 1.83
123 mm); petiole inconspicuous; segments subequal in length.

124 Systematic remarks. The specimen possesses numerous features reminiscent of the
125 Bethylinae, such as the thick mandibles with four teeth, the clypeal carina extending on the
126 frons and outcurved as seen in profile, the tarsal claws strongly angled, the fore wing with
127 Rs+M tubular and Rs&M widely angled, allowing attribution to this subfamily. Following the
128 key of the bethyline genera of Azevedo et al. (2018), it keys in *Goniozus* for the following
129 characters: antenna with 11 flagellomeres, dorsal pronotal area regularly long, fore wing with
130 less than five closed cells, mesopleuron not prominent and fore wing with [2R1] cell opened.
131 It differs from *Goniozus respectus*, known from the more or less contemporary Dominican
132 amber in having the 2r-rs&Rs vein shorter, not conspicuously angled apically, the cu-a vein
133 arched (vs. straight) and the pterostigma more rounded (Sorg, 1988: fig. 22). It also differs
134 from the unnamed *Goniozus* from compressions of Rubielos de Mora, Spain, in having the
135 [1M] cell closed (but this might be due to the coarser preservation of rock-imprints), the
136 pterostigma more rounded and the 2r-rs&Rs vein not angled apically (Peñalver-Mollá, 1998:
137 fig. 36).

138

139 **Subfamily** Epyrinae Kieffer, 1914

140 **Genus** *Bakeriella* Kieffer, 1910

141 *Bakeriella nanyhela* sp. nov.

142 Fig. 2

143 LSID (species): urn:lsid:zoobank.org:act:urn:lsid:zoobank.org:act:F310FE17-B8F7-4648-

144 9C86-A49B9A10109C

145 Material. Holotype number FCMP-1465, a complete female.

146 Etymology. Nanyhela is the female divinity of fertility and harvests in the Chiapanec

147 mythology. The specific epithet is to be treated as a noun in a genitive case.

148 Diagnosis. Body punctate, with metallic reflections; head ovoid (Figs. 2.A, B); median

149 clypeal lobe wide, obtuse triangle-shaped; mandibles thick, with three stout teeth;

150 flagellomere 1 shortest, shorter than pedicel (Fig. 2.F); propleuron visible dorsally; notauli

151 sinuous, convergent posteriorly; mesoscuto-mesoscutellar pits large, bean-shaped, separated

152 by thin septum (Fig. 2.B); metapectal-propodeal complex carinate, median carina complete;

153 [2R1] cell narrow (Fig. 2.A); meso- and metafemora more enlarged than profemur and

154 flattened; mesotibia shorter than mesofemur, with row of spines distally along outer margin

155 (Fig. 2.E); metasoma slightly longer than mesosoma, with sparse but long pubescence on

156 posterior segments (Fig. 2.D).

157 Type locality. Río Salado Mine, Totolapa, State of Chiapas, southwestern Mexico.

158 Age. Early to middle Miocene, ca. 23–15 Ma

159 Description. Body stout, uniformly punctate, blackish, with metallic reflections (length 6.70
160 mm). Head prognathous, ovoid, longer than wide; LH: 1.28 mm, WH: ca. 0.82 mm; WF: 0.55
161 mm, HE: 0.32 mm; OOL: 0.26 mm; WOT: 0.10 mm; DAO: 0.07 mm; VOL: 0.24 mm; frons
162 slightly convex, bearing very short pubescence; compound eyes elliptical, longer than high,
163 glabrous, closer to mandibles insertion than to occipital carina; clypeus with wide obtuse
164 triangle median lobe, clypeal carina short, not extending on frons, lateral lobes poorly
165 developed; mandibles thick, slightly overlapping, with three stout teeth, ventralmost tooth
166 longest; scape punctate, 2.6 times longer than pedicel; pedicel longer than wide; 11
167 flagellomeres, barely longer than wide; flagellomere 1 shortest (0.07 mm vs. 0.08–0.11 mm),
168 shorter than pedicel; flagellomere 11 tapering at apex; ocellar triangle posteriad on head;
169 occipital carina complete.

170 Mesosoma sparsely pubescent (length 2.51 mm); propleuron visible in dorsal view; dorsal
171 pronotal area ecarinate, long, without anterior depression or elevation, without pronounced
172 corners; anteromesoscutum with parapsidal signum impressed posteriorly, with notauli
173 complete, convergent posteriorly and sinuous; mesoscuto-mesoscutellar pits large, bean-
174 shaped, separated by thin septum; mesoscutellum diamond-shaped with blunted apex nearly
175 in contact with metapectal-propodeal complex; mesopleuron not prominent, with
176 transepisternal line; metapectal-propodeal complex carinate, metapostnotal median carina
177 complete, metapostnotal-propodeal carina not curved, no posterior spines or projections. Fore
178 wing hyaline and micropubescent (LFW: 3.82 mm); C, Sc+R, M+Cu, A, Rs&M and cu-a
179 tubular; pterostigma short, not rounded; 2r-rs&Rs contiguous, long and poorly arched toward
180 wing margin; [2R1] cell narrow, opened apically. Legs swollen; meso- and metafemora more

181 enlarged than profemur, flattened; mesotibia shorter than mesofemur (0.59 mm vs. 0.64 mm),
182 with 8–10 spines along outer margin; tibial spurs configuration 1-2-2.

183 Metasoma slightly longer than mesosoma, fusiform (length 2.91 mm); petiole inconspicuous;
184 metasomal segments decreasing in length posteriorly; pubescence absent on anterior
185 segments, long pubescence sparse but present on posterior segments; sting exerted, long
186 (length 0.66 mm).

187 Systematic remarks. Following the key to the subfamilies of Bethylidae of Azevedo et al.
188 (2018), this specimen keys in the Epyrinae for the fully-developed wings, without Rs+M, the
189 metanotum short, the metapectal-propodeal complex without posterior spines, the metasomal
190 segment 2 regularly long, the mesopleuron with transepisternal line, the fore wing with
191 anterior margin straight and C present. Following the key to the genera of Epyrinae of
192 Colombo et al. (2022b), it keys between *Epyris* Kieffer, 1914 and *Bakeriella* Kieffer, 1910 for
193 the mesoscuto-mesoscutellar foveae not connected by sulcus, the posterior ocelli broadly
194 separated, the dorsal pronotal area without elevation anteriorly and the anterior margin not
195 incurved, the anterior area of sternite 2 without flap and the antennae not pectinate, the
196 mesoscuto-mesoscutellar foveae separated by less than half their own length, the metapectal-
197 propodeal disc with distinct metapostnotal-propodeal carina. However, some features merely
198 indicate *Bakeriella* for the present fossil: the body with metallic reflections, as is visible in
199 some *Bakeriella* but not in *Epyris* (Azevedo et al., 2018); the mesoscuto-mesoscutellar foveae
200 subelliptical rather than rectangular, a pattern of *Bakeriella* (e.g., Azevedo, 2014: figs. 1, 6,
201 9); the mesoscutellum not contacting the metapectal-propodeal complex, a diagnostic
202 character of *Bakeriella* (Azevedo, 2014); and the strong metapostnotal-propodeal carina also
203 merely indicates *Bakeriella* (Azevedo, 2014; Azevedo et al., 2018). Following the key to the
204 species of *Bakeriella* of Azevedo (2014), the specimen keys between *Bakeriella*

205 *quinquepartita* (Kieffer, 1910) and *Bakeriella lindigi* (Kieffer, 1910) for the dorsal pronotal
206 area without carina, the mesoscuto-mesoscutellar foveae not connected, the median clypeal
207 lobe angulate and the mesoscuto-mesoscutellar foveae wider than long. It differs from both
208 species in having the notauli complete and the mandibles with three teeth. Therefore, we
209 propose the new species *Bakeriella nanyhelae* sp. nov. for this specimen.

210 **Subfamily** Scleroderminae Kieffer, 1914

211 **Genus** *Solepyris* Azevedo, 2006

212 *Solepyris electromexicanus* sp. nov.

213 Fig. 3

214 LSID (species): urn:lsid:zoobank.org:act:urn:lsid:zoobank.org:act:130FED75-1BCA-48CB-
215 83FA-00F0D5F6C829

216 Material. Holotype number FCMP-1466, a complete female but accidentally damaged during
217 preparation (head separated from body).

218 Etymology. Combination of *electro-*, from the Greek *electron* meaning amber, and -
219 *mexicanus*, for the geographical origin.

220 Diagnosis. (Female) Body much flattened (Figs. 3A, C); mandibles with three teeth,
221 ventralmost two teeth longest (Figs. 3.D, G); occipital carina present; dorsal pronotal area
222 1.53 times longer than anteromesoscutum; mesoscuto-mesoscutellar grooves elongate,
223 separate by thin septum (Fig. 3.B); fore wing with only Sc+R, Rs&M and A tubular; Sc+R
224 thickened distally (Fig. 3.F); femora enlarged (Fig. 3.C).; metasoma smooth, with last tergites
225 more pubescent

- 226 Type locality. Río Salado Mine, Totolapa, State of Chiapas, southwestern Mexico.
- 227 Age. Early to middle Miocene, ca. 23–15 Ma
- 228 Description. Body much depressed, elongate and poorly pubescent (length 5.05 mm). Head
229 prognathous, ovoid, longer than wide; LH: 0.89 mm, WH: 0.76 mm; WF: 0.48 mm, HE: ca.
230 0.19 mm; OOL: 0.43 mm; WOT: 0.08 mm; DAO: ca. 0.05 mm; VOL: 0.24 mm; frons flat;
231 compound eyes elliptical, longer than high, as high as head laterally, glabrous, located
232 anteriorly on head; clypeus with median lobe poorly projecting forward; mandibles rather
233 long, with three teeth, ventralmost two teeth longest; antennae filiform; scape 2.3 times longer
234 than pedicel; 11 flagellomeres slightly longer than wide (length ca. 0.09 mm); flagellomere 11
235 longest; vertex convex with corner rounded; ocellar triangle compact, anterior ocellus
236 posterior to supra ocular line; occipital carina present.
- 237 Mesosoma with dorsum coriaceous (length 1.68 mm: height 0.44 mm); propleuron visible
238 dorsally, anterior corner rather angulate; prosternum large, larger than procoxa, triangular
239 with anterior margin outcurved; dorsal pronotal area elongate, depressed anteriorly, lateral
240 margin strongly incurved, posterior margin slightly incurved with corners overlapped by
241 anteromesoscutum; anteromesoscutum with parapsidal signum, without notauli; mesoscuto-
242 mesoscutellar grooves elongate, separate by thin septum; mesoscutellum trapezoidal with
243 blunt corners, large; metanotum barely visible; metapectal-propodeal complex smooth,
244 without posterior spines; propodeal declivity short. Fore wing macropterous, hyaline (LFW:
245 2.32 mm); venation reduced to Sc+R, Rs&M and A; Sc+R thickened distally, reaching
246 anterior margin in basal half of wing. Hind wing without venation. Legs slightly pubescent;
247 protochanter originating from apex of procoxa; all femora swollen.

248 Metasoma longer than mesosoma, fusiform, with denser pubescence on last segments (length
249 2.48 mm; height 0.32 mm); petiole inconspicuous; six tergites visible, subequal in length; no
250 modifications of tergites; short sting visible.

251 Systematic remarks. Considering the general habitus and the large prosternum, our specimen
252 could easily be mistaken for a Scolebythidae. But the reduced fore wing venation, the
253 protochanter inserted on apex of coxa instead of laterally, and the prosternum triangular
254 rather than diamond-shaped, rather suggest that it belongs to the Scleroderminae. Following
255 the keys to the Scleroderminae, our specimen keys in *Solepyris* Azevedo, 2006 for the
256 antennae with 11 flagellomeres, the body much depressed with the eye as high as head
257 laterally, the fore wing macropterous, the prosternum large, triangular and the vein A and
258 Rs&M complete. The large prosternum is much uncommon within the Bethylidae and our
259 specimen additionally shares numerous characters with *Solepyris*: the head wider than
260 mesosoma, the clypeus short, the number of mandibular teeth, the notauli absent, the dorsal
261 pronotal area depressed anteriorly with lateral margins incurved, the anteromesoscutum
262 slightly overlapping posterolateral corners of pronotum, the Sc+R vein dilated distally, and
263 the stigma absent. It differs from the two known species of the genus, *S. unicus* Azevedo,
264 2006 and *S. montuosus* Azevedo, 2009, by the body more depressed, the femora more
265 enlarged, and a different shape of the mandibles, with the dorsalmost tooth more basad
266 (Azevedo, 2009).

267

268 **4. Discussion**

269 Of the three species studied here, two belong to genera with a wide distribution:
270 *Gonozius*, which is cosmopolitan, and *Bakeriella*, a Pan-American genus. Approximately

271 thirty living species of *Goniozus* were recognized by Evans (1978) in Mexico. Judging by the
272 presence of *G. respectus* in the more or less contemporary deposit of Dominican amber, its
273 diversity was probably already settled by this epoch. This is supported by its presence in the
274 fossil record since the Upper Eocene (Ramos et al., 2014). It is therefore not surprising to
275 record it in the Chiapas amber and demonstrates that *Goniozus* is well distributed around the
276 globe since the Miocene at least. Similarly, Azevedo (2014) records six extant species of
277 *Bakeriella* in Mexico but *Bakeriella nanyhelae* sp. nov. is the first fossil of the genus. Given
278 that Bethyridae from Mexican and Dominican ambers have been poorly investigated and that
279 *Bakeriella* is almost restricted to the Neotropics, with a few species in Northern Mexico and
280 the United States, this is not surprising. However, it denotes a long occurrence of both genera
281 in the Neotropical region.

282 *Solepyris* is much more uncommon nowadays. The genus and type species *S. unicus*
283 were erected by Azevedo (2006) based on three females with a scolebythid-like habitus from
284 Ecuador (Rio Palengue) and Brazil (Belo Horizonte). Later, Azevedo (2009) found another
285 species from Brazil (Espírito Santo) and investigated several sclerodermine collections but
286 failed to find additional specimens. The few specimens collected showed that *Solepyris* might
287 have a broad distribution throughout South America but our finding geographically expands it
288 about 2,500 km northward in the Neotropics. However, the type specimens of *S. unicus* are
289 distant of more than 4,000 km. Recently, Colombo et al. (2022a) proposed a hypothesis for
290 the exclusive presence of strongly flattened sclerodermine wasps in tropical regions. They
291 based it on the observation that Coleoptera larvae living in cryptic habitats, their hosts, occur
292 widely in these regions. Unfortunately, nothing is known about the biology of *Solepyris* and
293 none of the sclerodermine genera with such particular morphology listed in Colombo et al.
294 (2022a) occur as north in Central America as *Solepyris electromexicanus* sp. nov. According
295 to Azevedo (2009), *Solepyris* might be closely related to *Megaprosternum* Azevedo, 2006,

296 which has been reported to parasitise *Cleonaria bicolor* Thomson, 1864 (Coleoptera:
297 Cerambycidae; see Gupta et al., 2017). It would have been possible for *Solepyris*
298 *electromexicanus* sp. nov. to have a similar feeding habit since some Cerambycidae have been
299 recorded emerging from *Hymenaea* tree (Tavakilian et al., 1997). The *Hymenaea* genus is
300 considered to be the producer of Chiapas amber (Poinar and Brown, 2002; Solórzano
301 Kraemer, 2010) and Cerambycidae are known from this deposit, but are yet undescribed
302 (Ross et al., 2016: fig. 15). Further living observations and collection of additional specimens
303 might help to better understand both the biology and biogeography of *Solepyris*.

304 The age of Totolapa amber has been widely debated since its discovery, because its
305 geological settings could not have been studied precisely *in situ*. It was first thought to be
306 Eocene, based on the geological map of the central depression region of Chiapas (INEGI,
307 1985), which would largely predate the other amber deposits of Mexico, dated late Oligocene-
308 middle Miocene. Lambert et al. (1989) contradicted this hypothesis by showing that ambers
309 from Simojovel and Totolapa are chemically similar and hence likely from a same
310 paleobotanical source. Further taxonomic studies of included arthropods (e.g Barrios-Izás and
311 Coty, 2016; Coty et al., 2014; Durán-Ruiz et al., 2013; Riquelme et al. 2014) revealed a
312 paleofauna widely composed of extant genera of tropical to temperate affinities, which better
313 correspond to a Miocene dating rather than Eocene. Our discovery of three modern genera of
314 Bethylidae, of cosmopolitan or neotropical distribution, strengthens the proposal of a Miocene
315 age for Totolapa amber.

316

317 **Acknowledgments**

318 We are in debt to David Coty for the generous donation of the material, discussion on
319 the mining and geology of the deposit, and valuable comments on our work. We sincerely
320 thank Manuel and Heriberto Ramirez, owners and miners of the Río Salado Mine, and their
321 whole family for allowing David Coty's collecting on their property. We also thank Dr.
322 Francisco Sour Tovar (Universidad Nacional Autónoma de México) and Dr. Mónica M.
323 Solorzano-Kraemer (Senckenberg Research Institute, Germany), for advice and help with the
324 final repository of the studied material. We finally express our gratitude to two anonymous
325 reviewers for their comments on the first version of the manuscript. This work is part of
326 Manuel Brazidec Ph.D. project on "The role of greenhouses on the diversification and
327 evolution of chrysidoid wasps".

328

329 **References**

- 330 Azevedo, C.O., 2006. Two new genera of Sclerodermini (Hymenoptera: Bethylidae;
331 Epyrinae) with large, scolebythid-like prosternums. *Zootaxa* 1191, 35–47.
- 332 Azevedo, C.O., 2009. A new species of *Solepyris* Azevedo (Hymenoptera, Bethylidae) from
333 Brazil, with amended diagnosis of the genus. *Revista Brasileira de Entomologia* 53: 327–
334 330.
- 335 Azevedo, C.O., 2014. Synopsis of *Bakeriella* Kieffer, 1910 (Hymenoptera, Bethylidae).
336 *Zootaxa* 3878, 501–535. <http://dx.doi.org/10.11646/zootaxa.3878.6.1>
- 337 Azevedo, C.O., Alencar, I.D.C.C, Ramos, M.S., Barbosa, D.N., Colombo, W.D., Vargas,
338 J.M., Lim, J., 2018. Global guide of the flat wasps (Hymenoptera, Bethylidae). *Zootaxa*
339 4489, 1–294. <https://doi.org/10.11646/zootaxa.4489.1.1>

- 340 Barrios-Izás, M., Coty, D., 2016. A new fossil species of *Caulophilus* Wollaston, 1854
341 (Coleoptera: Curculionidae: Cossoninae) from Mexican amber. *The Coleopterists Bulletin*
342 70, 177–179. <https://doi.org/10.1649/072.070.0126>
- 343 Bouju, V., Perrichot, V., 2020. A review of amber and copal occurrences in Africa and their
344 paleontological significance. *BSGF-Earth Sciences Bulletin* 191(17), 11 pp.
345 <https://doi.org/10.1051/bsgf/2020018>
- 346 Brues, C.T., 1906. Fossil parasitic and phytophagous Hymenoptera from, Colorado. *Bulletin*
347 *of the American Museum of Natural History* 22, 481–498.
- 348 Brues, C.T., 1910. The parasitic Hymenoptera of the Tertiary of Florissant, Colorado. *Bulletin*
349 *of the Museum of Comparative Zoology* 44, 3–125.
- 350 Bryant D.D., 1983. A recently discovered amber source near Totolapa, Chiapas, Mexico.
351 *American Antiquity* 48, 354–357.
- 352 Colombo, W.D., Perkovsky, E.E., Azevedo, C.O., 2022a. Synopsis of the rare genus
353 *Alongatepyris* (Hymenoptera, Bethylidae), with description of the first extinct species from
354 Dominican amber. *Palaeoentomology* 5, 57–65.
355 <https://doi.org/10.11646/palaeoentomology.5.1.6>
- 356 Colombo, W.D., Tribull, C.M., Waichert, C., Azevedo, C.O., 2022b. Integrative taxonomy
357 solves taxonomic impasses: a case study from Epyrinae (Hymenoptera, Bethylidae).
358 *Systematic Entomology*. <https://doi.org/10.1111/syen.12544>
- 359 Coty, D., Aria, C., Garrouste, R., Wils, P., Legendre, F., Nel, A., 2014. The first ant-termite
360 syninclusion in amber with CT-scan analysis of taphonomy. *PLoS ONE* 9, e104410.
361 <https://doi.org/10.1371/journal.pone.0104410>

- 362 Coty, D., Nel, A., 2013. New fossil Pachygastrinae from Mexican amber (Diptera:
363 Stratiomyidae). *Annales de la Société Entomologique de France* 49, 267–272.
364 <https://doi.org/10.1080/00379271.2013.845473>
- 365 Durán-Ruiz, C., Riquelme, F., Coutiño-José, M., Carbot-Chanona, G., Castaño-Meneses,
366 Ramos-Arias, M., 2013. Ants from the Miocene Totolapa amber (Chiapas, Mexico), with
367 the first record of the genus *Forelius* (Hymenoptera, Formicidae). *Canadian Journal of*
368 *Earth Sciences* 50, 495–502. <https://doi.org/10.1139/cjes-2012-0166>
- 369 Evans, H.E., 1964. A synopsis of the American Bethylidae (Hymenoptera, Aculeata). *Bulletin*
370 *of the Museum of Comparative Zoology* 132, 1–222.
- 371 Evans, H.E., 1978. The Bethylidae of America North of Mexico. *Memoirs of the American*
372 *Entomological Institute* 27, 1–332.
- 373 Gupta, A., Rajeshwari, S.K., Azevedo, C.O., 2017. Biology and description of
374 *Megaprosternum cleonarovororum* sp. nov. (Hymenoptera: Bethylidae) a gregarious larval
375 ectoparasitoid of *Cleonaria bicolor* Thomson (Coleoptera: Cerambycidae) from India.
376 *Zootaxa* 4237, 78–90. <https://doi.org/10.11646/zootaxa.4237.1.4>
- 377 Harris, R.A., 1979. A glossary of surface sculpturing. *Occasional Papers in Entomology, State*
378 *of California Department of Food and Agriculture* 28, 1–31.
- 379 Hegna, T.A., Lazo-Wasem, E.A., Serrano-Sánchez, M.d.L., Barragán, R., Vega, F.J., 2020. A
380 new fossil talitrig amphipod from the lower early Miocene Chiapas amber documented
381 with microCT scanning. *Journal of South American Earth Sciences* 98, 102462.
382 <https://doi.org/10.1016/j.jsames.2019.102462>
- 383 INEGI, 1985. Carta geológica, E15-11 (Tuxtla Gutiérrez), escala 1:250,000. Mexico City,
384 Mexico: SPP/INEGI, Instituto Nacional de Estadística, Geografía y informática.

- 385 Lambert, J.B., Frye, J.S., Lee Jr., T.A., Welch, C.J., Poinar Jr., G.O., 1989. Analysis of
386 Mexican amber by Carbon-13 NMR Spectroscopy. *Archeological Chemistry* 4, 381–388.
387 <https://doi.org/10.1021/ba-1988-0220.ch021>
- 388 Lanes, G.O., Kawada, R., Azevedo, C.O., Brothers, D.J., 2020. Revisited morphology applied
389 for Systematics of flat wasps (Hymenoptera, Bethylidae). *Zootaxa* 4752, 1–127.
390 <https://doi.org/10.11646/zootaxa.4752.1.1>.
- 391 Peñalver-Mollá, E., 1998. *Estudio tafonómico y paleoecológico de los insectos del Mioceno*
392 *de Rubielos de Mora (Teruel)*. Instituto de estudios Turolenses, Teruel, 179 pp.
- 393 Perrilliat, M.C., Vega, F.J., Coutiño, M.A., 2010. Miocene mollusks from the Simojovel area
394 in Chiapas, southwestern Mexico. *Journal of South American Earth Sciences* 30, 111–119.
395 <https://doi.org/10.1016/j.jsames.2010.04.005>
- 396 Poinar Jr., G., Brown, A.E., 2002. *Hymenaea mexicana* sp. nov. (Leguminosae:
397 Caesalpinioidea) from Mexican amber indicates Old World connections. *Botanical Journal*
398 *of the Linnean Society* 139, 125–132. <https://doi.org/10.1046/j.1095-8339.2002.00053.x>
- 399 Ramos, M.S., Perkovsky, E.E., Rasnitsyn, A.P., Azevedo, C.O., 2014. Revision of Bethylinae
400 fossils (Hymenoptera: Bethylidae) from Baltic, Rovno and Oise amber, with comments on
401 the Tertiary fauna of the subfamily. *Neues Jahrbuch für Geologie und Paläontologie* 271,
402 203–228. <https://doi.org/10.1127/0077-7749/2014/0385>
- 403 Riquelme, F., Menéndez-Acuña, M., 2017. Miocene spider *Maevia eureka* nov. sp. (Araneae:
404 Salticidae). *PeerJ* 5, e3614. <https://doi.org/10.7717/peerj.3614>
- 405 Riquelme, F., Ruvalcaba-Sil, J.L., Alvarado-Ortega, J., Estrada-Ruiz, E., Galicia-Chávez,
406 Porras-Múzquiz, H., Stojanoff, V., Siddons, D.P., Miller, L., 2014. Amber from México:
407 Coahuilite, Simojovelite and Bacalite. *MRS Proceeding* 1618, 169–180.
408 <https://doi.org/10.1557/opl.2014.466>

- 409 Ross, A.J., Mellish, C.J.T., Crighton, B., York, P.V., 2016. A catalogue of the collections of
410 Mexican amber at the Natural History Museum, London and National Museums Scotland,
411 Edinburgh, UK. *Boletín de la Sociedad Geológica Mexicana* 68, 45–55.
- 412 Sanderson, M.W., Farr, T.H., 1960. Amber with insect and plant inclusions from the
413 Dominican Republic. *Science* 131, 1313–1314.
- 414 Schmidt, A.R., Kaulfuss, U., Bannister, J.M., Baranov, V., Beimforde, C., Bleile, N., Borkent,
415 A., Busch, A., Conran, J.G., Engel, M.S., Harvey, M., Kennedy, E.M., Kerr, P.H.,
416 Kettunen, E., Kiecksee, A.P., Lengeling, F., Lindqvist, J.K., Maraun, M., Mildenhall, D.
417 C., Perrichot, V., Rikkinen, J., Sadowski, E.M., Seyfullah, L.J., Stebner, F., Szwed, J.,
418 Ulbrich, P., Lee, D.E., 2018. Amber inclusions from New Zealand. *Gondwana Research*
419 56, 135–146. <https://doi.org/10.1016/j.gr.2017.12.003>
- 420 Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of
421 image analysis. *Nature Methods* 9, 671–675. <https://doi.org/10.1038/nmeth.2089>
- 422 Solórzano Kraemer, M.M., 2010. Mexican amber. In: Penney D. (Ed.), *Biodiversity of fossils*
423 *in amber from the major world deposits*. Siri Scientific Press, 42–56.
- 424 Solórzano Kraemer, M.M., Delclòs, X., Slapham, M., Arillo, A., Peris, D., Jäger, P., Stebner,
425 F., Peñalver, E., 2018. Arthropods in modern resin reveal if amber accurately recorded
426 forest arthropod communities. *Proceedings of the National Academy of Sciences of the*
427 *USA* 115, 6739–6744. <https://doi.org/10.1073/pnas.1802138115>
- 428 Solórzano Kraemer, M.M., Kraemer, A.S., Stebner, F., Bickel, D.J., Rust, J., 2015.
429 Entrapment bias of arthropods in Miocene amber revealed by trapping experiments in a
430 tropical forest in Chiapas, Mexico. *PLoS ONE* 10, e0118820.
431 <https://doi.org/journal.pone.0118820>

- 432 Sorg, M., 1988. Zur Phylogenie und Systematik der Bethyridae (Insecta, Hymenoptera,
433 Chrysoidea). Sonderveröffentlichungen des Geologischen Instituts der Universität zu
434 Köln 63, 1–146.
- 435 Snyder, T.E., 1960. Fossil termites from Tertiary amber of Chiapas, Mexico (Isoptera).
436 Journal of Paleontology 34, 493–494.
- 437 Tavakilian, G., Berkov, A., Meurer-Grimes, B., Mori, S., 1997. Neotropical tree species and
438 their faunas of xylophagous longicorns (Coleoptera: Cerambycidae) in French Guiana. The
439 Botanical Review 63, 303-355.
- 440 Wang, B., Shi, G., Xu, C., Spicer, R.A., Perrichot, V., Schmidt, A.R., Feldberg, K., Heinrichs,
441 J., Chény, C., Pang, H., Liu, X., Gao, T., Wang, Z., Ślipiński, A., Solórzano Kraemer,
442 M.M., Heads, S.W., Thomas, M.J., Sadowski, E.-M., Szwed, J., Azar, D., Nel, A., Liu,
443 Y., Chen, J., Zhang, Qi, Zhang, Q., Luo, C., Yu, T., Zheng, D., Zhang, H., Engel, M.S.,
444 2021. The mid-Miocene Zhangpu biota reveals an outstandingly rich rainforest biome in
445 East Asia. Science Advances 7(18), eabg0625. <https://doi.org/10.1126/sciadv.abg0625>

446

447

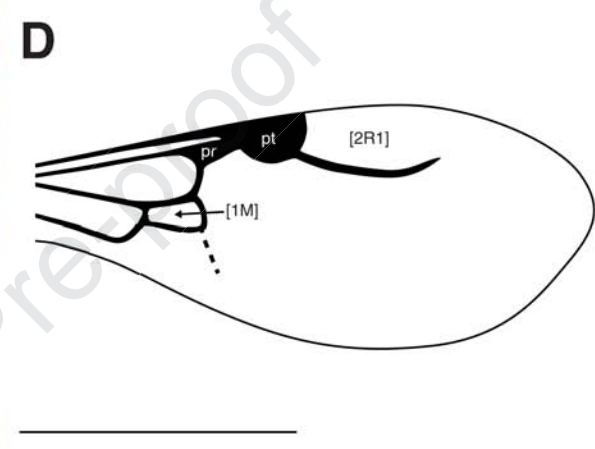
448 **Figure captions:**

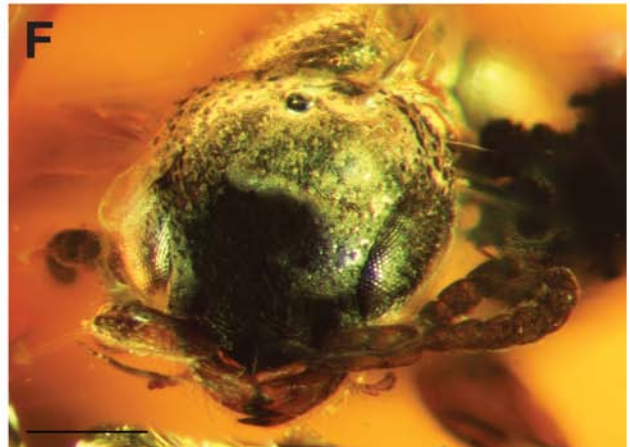
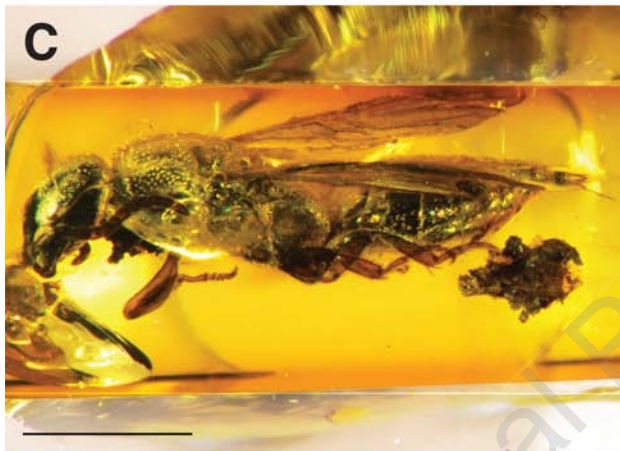
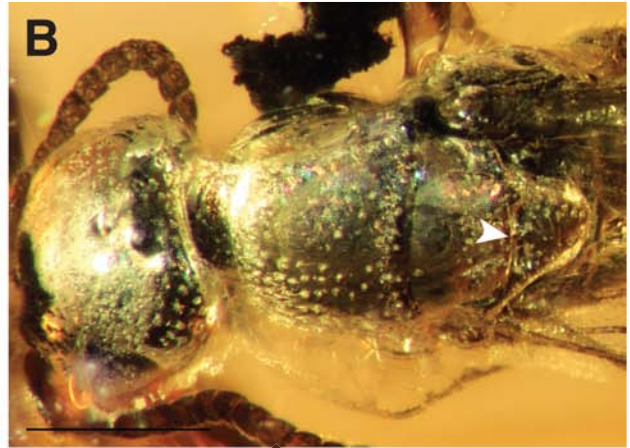
449 **Figure 1.** *Goniozus cotyi* sp. nov., holotype male FCMP-1464; A. habitus in dorsal view; B.
450 habitus in lateral view; C. head and anterior mesosoma in lateral view (white arrow:
451 parapsidal signum); D. line drawing of fore wing (abbreviations: pr = prestigma; pt =
452 pterostigma). Scale bars: A, B, D = 1 mm; C = 0.5 mm. (2-column fitting image)

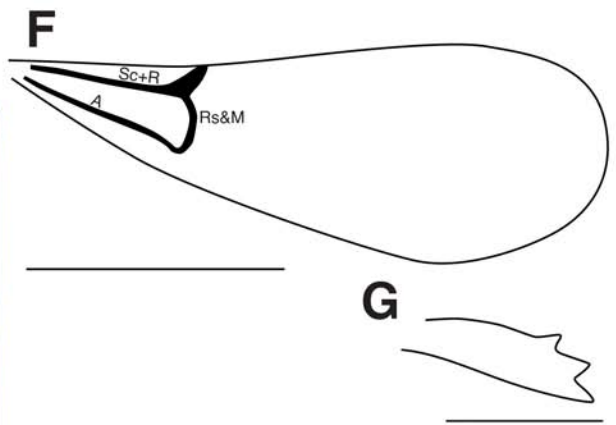
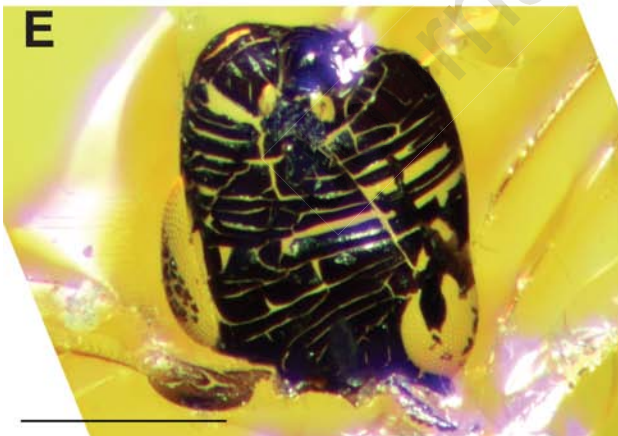
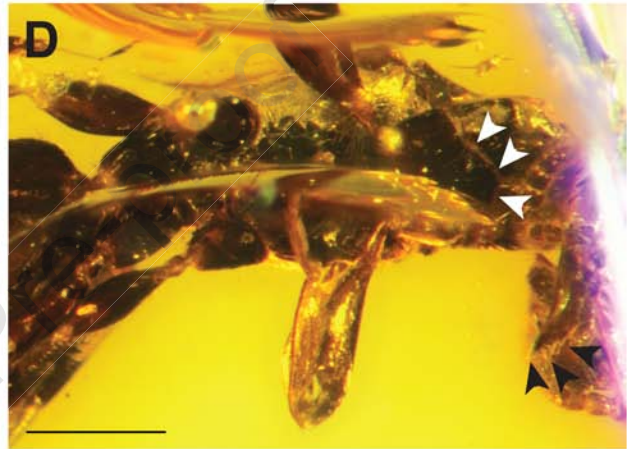
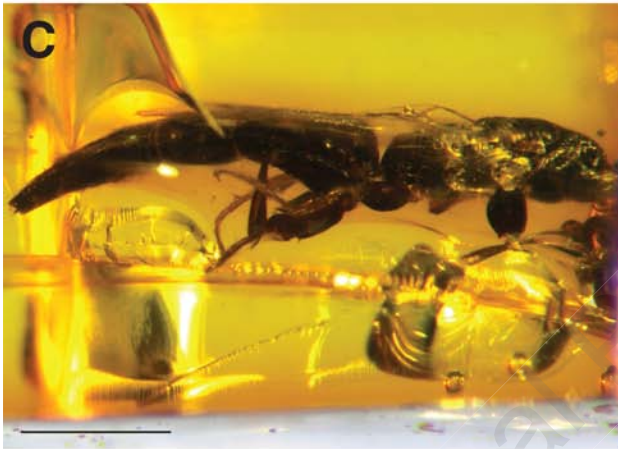
453 **Figure 2.** *Bakeriella nanyhela* sp. nov., holotype female FCMP-1465; A. habitus in dorsal
454 view; B. head and anterior mesosoma in dorsal view (arrow: septum separating scuto-

455 scutellar pits); C. habitus in lateral view; D. metasoma in lateral view; E. meso and
456 metalegs in lateral view; F. head in frontal view. Scale bars: A, C = 2 mm; B, D, E = 1
457 mm; F = 0.5 mm. (2-column fitting image)

458 **Figure 3.** *Solepyris electromexicanus* sp. nov., holotype female FCMP-1466; A. habitus in
459 dorsal view; B. mesosoma in dorsal view; C. mesosoma and metasoma in lateral view; D.
460 mesosoma in ventral view (white arrows: anterior margin of prosternum; black arrows:
461 mandibular teeth); E. dorsal surface of head in internal view; F. line drawing of fore wing;
462 G. line drawing of right mandible in frontal view. Scale bars: A, C, F = 1 mm; B, D, E =
463 0.5 mm; G = 0.25 mm. (2-column fitting image)







Highlights

- Description of the three first species of Bethylidae in Miocene Mexican amber
- Diverse *Goniozus* and *Bakeriella* found to have a long occurrence in Neotropics
- New *Solepyris* helps discuss its particular disjunct biogeographical pattern
- Modern genera provide additional support for a Miocene age of Totolapa amber

Journal Pre-proof

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.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Journal Pre-proof