



HAL
open science

Ants (Hymenoptera: Formicidae) from Miocene Ethiopian amber: filling gaps in the geological record of African terrestrial biota

Vincent Perrichot, Brendon Boudinot, Michael Engel, Chunpeng Xu, Blażej Bojarski, Jacek Szwedo

► To cite this version:

Vincent Perrichot, Brendon Boudinot, Michael Engel, Chunpeng Xu, Blażej Bojarski, et al.. Ants (Hymenoptera: Formicidae) from Miocene Ethiopian amber: filling gaps in the geological record of African terrestrial biota. *Zoological Journal of the Linnean Society*, 2022, pp.zlac053. 10.1093/zoolinnean/zlac053 . insu-03734903

HAL Id: insu-03734903

<https://insu.hal.science/insu-03734903v1>

Submitted on 21 Jul 2022

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

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



**Ants (Hymenoptera: Formicidae) from Miocene Ethiopian
amber: filling gaps in the geological record of African
terrestrial biota**

Journal:	<i>Zoological Journal of the Linnean Society</i>
Manuscript ID	ZOJ-01-2022-4863.R1
Manuscript Type:	Original Article
Keywords:	Africa < Geography, biogeography < Geography, morphological systematics < Taxonomy, Miocene < Palaeontology, computed tomography < Anatomy, Insecta < Taxa
Abstract:	<p>The early Miocene (16–23 Mya) amber of Ethiopia constitutes a new source of fossil ants for Africa, where they are otherwise very poorly documented. Here we report a diversified assemblage of six subfamilies and at least 19 genera that are still predominantly alive in the Afrotropics today. In this first account, a particular reference is made to the subfamily Dolichoderinae, with the description of two new species: <i>Technomyrmex svojtakai</i> Perrichot & Engel sp. nov. and <i>Ravavy goldmani</i> Boudinot & Perrichot sp. nov. The former species is illustrated and described based on synchrotron-radiation micro-computed tomography, while the latter represents the first fossil record for the tribe Bothriomyrmecini and <i>Ravavy</i> Fisher, 2009, a Malagasy and Afrotropical genus that was hitherto monotypic. The ant composition in Ethiopian amber is congruent with the global pattern emerging across ants and showing a Neogene diversification almost exclusively within extant genera.</p>

1
2
3
4
5
6
7
8
9
10 1 **Ants (Hymenoptera: Formicidae) from Miocene Ethiopian amber:**
11
12 2 **filling gaps in the geological record of African terrestrial biota**
13
14
15 3

16
17 4 Running title: Ants from Miocene Ethiopian amber
18

19 5
20 6 VINCENT PERRICHOT^{1,*}, BRENDON E. BOUDINOT^{2,3}, MICHAEL S. ENGEL^{4,5},
21
22 7 CHUNPENG XU⁶, BŁAŻEJ BOJARSKI⁷ and JACEK SZWEDO⁷
23
24 8

25
26 9 ¹*Univ Rennes, CNRS, Géosciences Rennes - UMR 6118, 35000 Rennes, France*

27 10 ²*Friedrich-Schiller-Universität Jena, Institut für Zoologie und Evolutionsforschung, Erberstraße 1,*
28
29 11 *07743 Jena, Germany*

30 12 ³*University of California, Davis, One Shields Ave, Davis, California 95616, USA*

31
32 13 ⁴*Division of Entomology, Natural History Museum, and Department of Ecology & Evolutionary*
33
34 14 *Biology, University of Kansas, Lawrence, Kansas 66045, USA*

35 15 ⁵*Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th*
36
37 16 *Street, New York, New York 10024, USA*

38 17 ⁶*State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and*
39
40 18 *Palaeontology, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China*

41
42 19 ⁷*Laboratory of Evolutionary Entomology and Museum of Amber Inclusions, Department of*
43
44 20 *Invertebrate Zoology and Parasitology, Faculty of Biology, University of Gdansk, 59 Wita Stwosza*
45 21 *St., 80-309 Gdansk, Poland*

46 22 *Corresponding author. E-mail: vincent.perrichot@univ-rennes1.fr
47
48 23

49
50 24 [Version of record, published online XX XXXX XXXX; <http://zoobank.org/>

51 25 [urn:lsid:zoobank.org:pub:35706103-4302-459E-A72F-769063E2DB21](http://zoobank.org/pub:35706103-4302-459E-A72F-769063E2DB21)]
52
53
54
55
56
57
58
59
60

1
2
3
4
5
6
7
8
9
10 26 **Abstract**

11
12 27 The early Miocene (16–23 Mya) amber of Ethiopia constitutes a new source of fossil ants for
13
14 28 Africa, where they are otherwise poorly documented. Here we report a diversified assemblage
15
16 29 of six subfamilies and at least 19 genera that are still predominantly alive in the Afrotropics
17
18 30 today. In this first account, a particular reference is made to the subfamily Dolichoderinae,
19
20 31 with the description of two new species: *Technomyrmex svojtkai* Perrichot & Engel, sp.
21
22 32 **nov.** and *Ravavy goldmani* Boudinot & Perrichot, sp. nov. The first is illustrated and
23
24 33 described based on synchrotron-radiation microcomputed tomography, and the second
25
26 34 represents the first fossil record for the tribe Bothriomyrmecini and *Ravavy*, a Malagasy and
27
28 35 Afrotropical genus that was hitherto monotypic. The ant composition in Ethiopian amber is
29
30 36 congruent with the global pattern emerging across ants and showing a Neogene diversification
31
32 37 almost exclusively within extant genera.

33 39 **Additional keywords:**

Commented [MC1]: AUTHOR: please provide up to 10 keywords that are not mentioned in the title, thanks.

34 40
35 41
36 42 **INTRODUCTION**

37 43 The fossil record of ants (Hymenoptera: Formicidae), although generally extensive, is
38 44 exceedingly scarce in Africa. To date, only four deposits from the continent have been
39 45 reported to yield ants, primarily as compression fossils of incomplete preservation: 10 alate
40 46 specimens representing four species in three genera of uncertain affinity were described from
41 47 the Late Cretaceous of Botswana (Turonian, ca. 91 Mya; Dlussky *et al.*, 2004; see also
42 48 Archibald *et al.*, 2006; LaPolla *et al.*, 2013); a petrified colony of *Oecophylla* Smith, 1860
43 49 (Formicinae) was described from the early Miocene of Kenya (16–23 Mya; Wilson & Taylor,
44 50 1964); and a single, undetermined individual was mentioned but not figured from the Middle
45 51
46 52
47 53
48 54
49 55
50 56
51 57
52 58
53 59
54 60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

51 Eocene of Tanzania (Lutetian, 45 Mya; Harrison *et al.*, 2001: 62; Schlüter, 2018). Based on a
52 photograph of this specimen kindly provided by Terry Harrison, this latter specimen is
53 assignable to the subfamily Ponerinae (pers. obs., 2014).

54 Recently, the likelihood for obtaining more substantial material has increased with the
55 discovery of the first African fossiliferous amber in Ethiopia, from which two ants have been
56 reported so far. Ethiopian amber was initially assigned a Cretaceous age (Schmidt *et al.*,
57 2010), but this notion was soon challenged by the examination of further material (Perrichot
58 *et al.*, 2016, 2018) and the first description of species belonging to extant or derived, post-
59 Cretaceous genera, such as the ant genus *Melissotarsus* Emery, 1877 and the salticid spider
60 †*Gorgopsina* Petrunkevitch, 1955 (Coty *et al.*, 2016; Wunderlich, 2017). Since then, further
61 geological and palynological studies have enabled a revised dating of Ethiopian amber to the
62 early Miocene (16–23 Mya; see Bouju & Perrichot, 2020; Bouju, 2021), and taxonomic
63 studies of additional arthropod inclusions have invariably revealed extant genera (Ulitzka,
64 2020, Bouju *et al.*, 2021, 2022b; Szadziewski *et al.*, 2021; Solórzano-Kraemer *et al.*, 2022).

65 Apart from the myrmicine *Melissotarsus ethiopiensis* Coty, Lebon & Nel, 2016, thus far
66 only one other ant individual of uncertain subfamilial attribution was reported and figured
67 from Ethiopian amber (Schmidt *et al.*, 2010: fig. 3A). This ant fossil was later identified as a
68 member of Dolichoderinae (LaPolla *et al.*, 2013: suppl. fig. 5). Here we formally describe this
69 fossil and further subsequently discovered dolichoderines from Ethiopian amber, comprising
70 one new species each in the extant genera *Technomyrmex* Mayr, 1872 and *Ravavy* Fisher,
71 2009. We also provide an overview of the ant diversity in Ethiopian amber, including an
72 inventory of other subfamilies and genera identified from four institutional collections, of
73 which a detailed taxonomic treatment will be proposed in future studies.

74 75 MATERIAL AND METHODS

1
2
3
4
5
6
7
8
9
10 7611
12 77 AMBER SPECIMENS

13 78 The studied specimens are contained in four amber pieces housed in the following public
14 79 repositories: Nanjing Institute of Geology and Palaeontology (NIGPAS, China), the
15 80 University of Rennes (IGR, France), the Museum of Amber Inclusions of the University of
16 81 Gdansk (MAIG, Poland) and the Natural History Museum of Vienna (NHMW, Austria). The
17 82 fossils originated from various deposits of the North Shewa and South Wollo Zones of the
18 83 Amhara region (refer to Bouju *et al.*, 2021, 2022a, for details on the localities). Ethiopian
19 84 amber is generally collected from siltstone exposed in gorges of rivers incising the north-
20 85 western Ethiopian Plateau. Analyses of the palynomorphs from the amber-bearing siltstone
21 86 indicate an early Miocene age for all these deposits.

22 87 Specimen NHMW-N6976 was part of the sample surveyed by Schmidt *et al.* (2010) and
23 88 originates from a deposit near Alem Ketema, in the North Shewa Zone. While the ant is
24 89 preserved in a piece of translucent amber, its detailed examination was made particularly
25 90 difficult owing to its position of preservation, *i.e.*, with legs and antennae retracted along the
26 91 curled body so that the face, mesosoma, petiole and apex of the gaster are rendered mostly
27 92 invisible (Fig. 1A). Therefore, the specimen was imaged using X-ray synchrotron
28 93 microtomography and the different structures visualized after a virtual dissection (see below
29 94 for details on the imaging technique).

30 95 Specimen MAIG 6020 comes from a deposit near the town of Weldiya in the south-east
31 96 of the South Wollo Zone (see details about this deposit in Bouju *et al.*, 2021). The amber
32 97 piece contains diverse remains of cryptogams and insects, including four dolichoderine ant
33 98 workers missing various body parts such as the head, gaster or legs.

34 99 Specimens NIGP180512 and IGR.ET2015/001a were purchased from a gem trader in
35 100 Addis Ababa and come from one of the four deposits of the North Shewa Zone mentioned by

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Bouju *et al.* (2022a: fig. 2), although the exact locality is unknown. Both amber pieces originally contained one male dolichoderine together with various myrmicine ants and other arthropod or plant inclusions. These pieces were cut into six and two fragments, respectively, and each fragment was ground and polished from all sides in order to enhance the visibility of inclusions and facilitate their study and photography. All amber pieces were legally purchased from a licensed gemstone trader in Addis Ababa, and export permits obtained from the Ethiopian Ministry of Mines and Petroleum.

EXAMINATION AND IMAGING

The specimens were examined, measured and photographed using various optical stereomicroscopes equipped with a digital camera. For best photographic results, a drop of water was applied to the amber surface above the region of interest and covered with a glass coverslip (see Sadowski *et al.*, 2021, for recommendations on the preparation and imaging of amber inclusions). All images are digitally stacked composites of multiple focal planes, and most were obtained using Helicon Focus software, with the exception of the two specimens of *Ravavy*. The latter were imaged with a Canon EOS 7D equipped with a Canon MP-E 65 mm macro lens, with the camera attached to a StackShot rail (Cognisys Inc.); lighting was provided by a pair of synchronized YN560 Speedlite (Yongnuo Photographic Equipment Co.) flashes; stacks were then exported as tiffs using Adobe Lightroom and montaged using Zerene Stacker (Zerene Systems LLC). All figures were composed with Adobe Photoshop.

The specimen NHMW-N6976 was imaged at the European Synchrotron Radiation Facility (ESRF, Grenoble) using a propagation phase-contrast X-ray microtomography protocol described in detail by Lak *et al.* (2008). The amber piece was scanned using a monochromatic beam with an acceleration voltage of 17 keV, an isotropic voxel size of 0.678 μm , and a propagation distance of 145 mm between the sample and the detector. The

1
2
3
4
5
6
7
8
9
10 126 tomography consisted of 1500 projections acquired through a 180° rotation and 0.5 seconds
11 127 of exposure time. After the acquisition, the volume was reconstructed using filtered back-
12 128 projection algorithms adapted for local tomography applications (PyHST, ESRF), and later
13 129 segmented using a manual region growing protocol in VGStudioMax 3.0 software (Volume
14 130 Graphics, Germany). Virtual dissections were made using the same software.
15
16
17
18
19

20 132 MORPHOLOGICAL TERMINOLOGY

21 133 Terminology for the head follows Richter *et al.* (2020); the head is described as if it were
22 134 prognathous for both the worker and male. Mesosomal terms for the worker follow Bolton
23 135 (1994, 2007) and Keller (2011), while alate-specific terms including wing venation follow
24 136 Boudinot (2015). Genitalic terminology follows Boudinot (2013, 2018); the following terms
25 137 are favoured from the latter work: gonopods (= “parameres”), gonocoxite (= “basimere”),
26 138 gonostylus (= “telomere”) and penite (= penisvalva). “Imbricate” is used in the sense of
27 139 Harris (1979) for sculpture, *i.e.*, with an even pattern of polygonal scutes which demarcate the
28 140 underlying epithelial cell margins (Mikó *et al.*, 2013).
29
30
31
32
33
34
35

36 141 MEASUREMENTS AND INDICES

37 142 Measurements (all in mm) and indices follow Bolton’s (2007) revision of *Technomyrmex*.
38 143 Specimens were measured from photographs in Adobe Illustrator, or from 3D reconstruction
39 144 in VGStudioMax; measurement files and values for males of *Ravavy* species are provided in
40 145 Appendix S1. Except male-specific variables indicated by an asterisk (*), the main metrics
41 146 can be visualized on Figure 2:
42
43
44
45
46
47

48 148 BL Body length: the total body length from the anterior margin of the head excluding
49 149 mandibles to the apex of the abdomen, measured in dorsal view.
50
51
52
53
54

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

- 150 HL Head length: the length of the head capsule excluding the mandibles; measured in
151 full-face view in a straight line from a line that spans the anteriormost points of the
152 clypeal lobes to the level of a line that spans the posterior corners of the head
153 capsule.
- 154 HW Head width: the maximum width of the head immediately behind the eyes, measured
155 in full-face view.
- 156 HWE* Head width, eyes: the maximum width of the head, including the compound eyes.
- 157 SL Scape length: the maximum straight-line length of the scape, excluding the basal
158 constriction or neck that occurs just distal of the condylar bulb.
- 159 FcW Frontal carinae width: the distance across the separation of the frontal carinae at
160 medium level of toruli, measured in full-face view.
- 161 EL Eye length: in profile, the maximum measurable length of the compound eye.
- 162 OLL* Ocellus length, lateral: the maximum length of the lateral ocellus, measured in full-
163 face view.
- 164 OIL* Inter-ocellus length: the minimum distance between the lateral ocelli, measured in
165 full-face view.
- 166 WL Weber's length: the diagonal length of the mesosoma in profile, from the angle at
167 which the pronotum meets the cervix to the posterior basal angle of the metapleuron.
- 168 ML* Mesoscutum length: the maximum length of the mesoscutum, measured in dorsal
169 view.
- 170 MW* Mesoscutum width: the maximum width of the mesoscutum, measured in dorsal
171 view.
- 172 FWL* Forewing length: the maximum length of the forewing from the apices of the axillary
173 sclerites to the wing apex.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

- 174 PH Petiole height: the maximum height of petiole (abdominal segment 2), measured in
profile view.
- 175
- 176 PL Petiole length: the maximum length of petiole (abdominal segment 2), measured in
dorsal view.
- 177
- 178 PW Petiole width: the maximum width of petiole (abdominal segment 2), measured in
dorsal view.
- 179
- 180 GL Gaster length: the maximum length of gaster (abdominal tergites 3 to 7), measured in
dorsal view.
- 181
- 182 GW Gaster width: the maximum width of gaster, measured in dorsal view.
- 183 CI Cephalic index: $HW/HL \times 100$.
- 184 HWI* Head width index: $HW/HWE \times 100$.
- 185 SI Scape index: $SL/HW \times 100$.
- 186 OI Ocular index: $EL/HL \times 100$.
- 187 OCI* Ocellar index: $OLL/OIL \times 100$.
- 188 EPI Eye Position Index: in full-face view, the distance from a horizontal line that spans
the anterior clypeal margin to one that spans the anterior margins of the eyes, divided
by the distance from a horizontal line that spans the posterior margins of the eyes to
one that spans the posterior corners of the head, $\times 100$.
- 189
- 190
- 191
- 192 MI* Mesoscutum index: $MW/ML \times 100$.
- 193 PI* Petiolar index: $PL/PH \times 100$.
- 194

SYSTEMATIC PALAEOLOGY

FAMILY FORMICIDAE LATREILLE, 1809

SUBFAMILY DOLICHODERINAE FOREL, 1878

TRIBE TAPINOMINI EMERY, 1913

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

199 GENUS *TECHNOMYRMEX* MAYR, 1872

200 *Type species. Technomyrmex strenuus* Mayr, 1872: 147.

201

202 ***TECHNOMYRMEX SVOJTKAI* PERRICHOT & ENGEL SP. NOV.**

203 (FIGS 1–3, S1, S2)

204 *Zoobank registration.* urn:lsid:zoobank.org:act:565B4980-A80E-450B-A09B-603264A91F50

205 *Type material.* Holotype NHMW-N6976, a complete worker; in early Miocene (16–23 Mya)

206 amber from the North Shewa Zone, Amhara region, Ethiopia; housed in the Department of

207 Mineralogy and Petrography, Naturhistorisches Museum Wien (NHMW, Austria). Paratypes

208 MAIG 6020, two workers missing portions of legs; in early Miocene (16–23 Mya) amber

209 from the South Wollo Zone, Amhara region, Ethiopia; housed in the Museum of Amber

210 Inclusions of the University of Gdansk (MAIG, Poland).

211 *Other material.* MAIG 6020, one worker missing the head, portions of legs and gaster, but

212 similar to the associated paratypes in its size and preserved structures, particularly the

213 subcylindrical petiole, the shape and position of metathoracic and propodeal spiracles, thus

214 considered here as conspecific; housed in the Museum of Amber Inclusions of the University

215 of Gdansk (MAIG, Poland).

216 *Etymology.* The specific epithet honours Mr. Matthias Svojtka (University of Vienna) who

217 discovered the fossil representing the holotype and generously made it available for study.

218 *Diagnosis.* The species is uniquely identified within *Technomyrmex* by the following

219 combination of worker characters: (1) anterior clypeal margin with a deep V-shaped median

220 incision; (2) inner margins of incision continuously arched, with no marked angle with

221 broadly semicircular anterolateral clypeal margins; (3) dorsum of head with a single pair of

222 stiff setae situated above posterior level of eyes; (4) compound eyes situated around

223 midlength of head (EPI 59), with about 40 ommatidia; (5) palp formula 6,4; (6) mandible with

1
2
3
4
5
6
7
8
9
10 224 six conspicuous teeth apically on masticatory margin; (7) counting from the apex, first tooth
11
12 225 longest, third and fifth teeth subequal in length, smaller than second and fourth, third to sixth
13
14 226 teeth each separated by one denticle, sixth tooth followed by a continuous series of smaller
15
16 227 teeth gradually decreasing in size along masticatory margin and basal angle, becoming
17
18 228 denticles along entire basal margin; (8) the basal angle indistinct, continuously arched
19
20 229 between margins; (9) mesosoma devoid of erect setae; (10) propodeal dorsum as long as
21
22 230 declivitous face, their junction broadly rounded.
23
24 231 *Description.* Holotype. Body integument minutely asperous, mostly glabrous except sparse
25
26 232 stiff setae on anterior head margin and gaster. Head only slightly longer than wide.
27
28 233 Compound eye oval, moderately large and feebly convex, its outer margin barely surpassing
29
30 234 the outline of sides in full-face view, with 38–40 ommatidia. Ocelli absent. Frontal carinae
31
32 235 well distant, closer to inner margin of eyes than to each other, not surpassing posterior margin
33
34 236 of eyes, and without frontal lobe such that antennal sockets entirely exposed although laterad.
35
36 237 Antenna 12-merous, scape surpassing vertexal margin by more than one third its length; first
37
38 238 and terminal funicular antennomeres subequal in length, nearly twice as long as broad; all
39
40 239 other antennomeres cylindrical, only slightly longer than broad. Vertex with an erect seta
41
42 240 (likely paired, but upper left side of head altered) longitudinally aligned with frontal carina, in
43
44 241 profile situated at midlength between posterior margins of eye and head. Anterior clypeal
45
46 242 margin bordered by seven stiff, short setae inclined ventrally; posterior clypeal margin
47
48 243 semicircular, even with posterior level of toruli. Mesosoma: in profile, mesonotal dorsal
49
50 244 outline feebly convex in its anterior third, flat and sloped in its posterior two thirds.
51
52 245 Mesonotum and propodeum forming a distinct angle at metanotal groove. Metathoracic
53
54 246 spiracles raised into distinct tubercles, conspicuously breaking outline of mesosoma in
55
56 247 lateral view, distinctly anterior to metanotal groove. Dorsal surface of propodeum flat,
57
58 248 declivitous surface convex. In profile, propodeal spiracle at junction of lateral and declivitous

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

249 surfaces, slightly above midheight of sclerite. Dorsal surface of mesosoma apparently without
250 erect setae. Legs: mesotibia and metatibia each with one spur, that of metatibia pectinate.

251 Metasoma: petiole more than twice as long as wide, nearly as wide as high, broadest around
252 its midlength; ventral and dorsal surfaces feebly convex; ventral surface without lobe, with
253 two anterior longitudinal rows of three short setae. Gaster: abdominal tergite III largest,
254 ventral surface of its anterior projection with a groove that accommodates entire petiole.
255 Tergites III–VI with posterior margin bordered by a row of short appressed setae barely
256 surpassing margin. Tergite VII in dorsal view small, trapezoidal.

257 *Paratypes and other specimens.* As the holotype, although incomplete or partially invisible by
258 preservation, but with posterior margin of head intact, not emarginate (MAIG 6020
259 paratypes); palpomeres clearly exposed (MAIG 6020 paratype 1), revealing a palp formula
260 6,4, with maxillary palp relatively long, exceeding hypostomal margin but not reaching
261 occiput, and labial palp short, about one third length of maxillary palp; mesonotum
262 constricted and elongate (MAIG 6020 additional worker).

263 *Measurements and indices.* Abbreviations are explained in material & methods. Holotype: BL
264 ~ 2.00, HL 0.50, HW 0.49, EL 0.15, FcW 0.18, SL 0.59, WL 0.77, PL 0.30, PW 0.13, PH
265 0.12, GL 0.80, GW 0.55, CI 98, OI 30, EPI 59, SI 129. Paratypes and additional worker: HL
266 0.52–0.54, HW 0.46, EL 0.11–0.15, SL 0.52, WL 0.77, PL 0.25–0.35, PW 0.20, SI 110.

267 *Note.* Amber piece MAIG 6020 also contains a fourth, partially preserved worker, which
268 displays a similar petiole and can probably be attributed to *Technomyrmex*. However, only the
269 mesosoma and petiole are preserved, and it differs by a larger size (WL ~ 2.40 vs. 0.77; PL
270 0.77 vs. 0.25–0.35) and the presence of a dense, short pubescence covering all sclerites; it
271 probably belongs to another species.

272 Among the dolichoderines, the petiole reduced to a low segment without a node or scale
273 and overhung by the first gastral segment which is anteriorly grooved is shared by

1
2
3
4
5
6
7
8
9
10 274 *Technomyrmex* and *Tapinoma* Förster, 1850. The pygidium exposed in dorsal view, thus with
11
12 275 five gastral tergites visible, as is seen on the new fossil, warrants placement in *Technomyrmex*
13
14 276 (whereas the pygidium is reflexed ventrally, exposing only four gastral tergites in dorsal view
15
16 277 in *Tapinoma*; see, e.g., Bolton, 2007; Fisher & Bolton, 2016).

17 278 The new species is readily recognizable by its anterior clypeal margin with a deep V-
18
19 279 shaped incision and broadly rounded lateral margins, the almost complete lack of erect setae
20
21 280 on the dorsum of head, mesosoma and first gastral tergite (with the exception of a single pair
22
23 281 of setae posterior to the frontal carinae), and the propodeal dorsum that is as long as or even
24
25 282 slightly longer than the declivitous surface. In all other species of *Technomyrmex* with a
26
27 283 deeply incised clypeal margin, the median notch is either U-shaped or semicircular, but never
28
29 284 V-shaped. These and other features such as the elongate mesosoma and metathoracic spiracles
30
31 285 raised on tubercles, suggest that *T. svojtakai* may belong to the *bicolor* group of species as
32
33 286 defined by Bolton (2007).

34 288 TRIBE BOTHRIOMYRMECINI DUBOVIKOFF, 2005

35
36 289 GENUS *RAVAVY* FISHER, 2009

37
38 290
39
40 291 *Type species. Ravavy miafina* Fisher, 2009: 47, figs 6, 7b.

41 292
42
43 293 ***RAVAVY GOLDMANI* BOUDINOT & PERRICHOT SP. NOV.**

44
45 294 (FIGS 4–5)

46
47 295
48 296 *Zoobank registration.* urn:lsid:zoobank.org:act:693FB2F0-817E-4BD6-B2E4-

49
50 297 5585AFC99EA2

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

298 *Type material.* Holotype NIGP180512, male, housed in the Nanjing Institute of Geology and
299 Palaeontology (NIGPAS, China); paratype IGR.ET2015/001a, male, housed in the Geological
300 Museum of the University of Rennes (IGR, France). In early Miocene (16–23 Mya) amber
301 from the North Shewa Zone, Amhara region, Ethiopia.

302 *Etymology.* The specific epithet honours Mr Yale Goldman (Bloomfield, Connecticut) who
303 kindly facilitated access to the type specimens of the new species.

304 *Diagnosis.* Because of the limited knowledge of male ants at the global scale, this diagnosis is
305 broken into four parts in order to establish the identity of the treated specimens: identification
306 at the subfamilial, tribal, generic and species levels. **(I)** Identifiable as Dolichoderinae by the
307 following combination: (1) clypeal condyle large, rhomboidal [*note 1*]; (2) forewing crossvein
308 cu-a prefurcal, *i.e.*, joining M+Cu proximad branching point of M and Cu; (3) helcium
309 infraaxial; (4) abdominal segment III unpetiolated, *i.e.*, not reduced in size relative to segment
310 IV; (5) prora absent; (6) abdominal segment IV without cinctus; (7) gonostylus dorsoventrally
311 short relative to gonocoxite, proximally constricted and not extending proximad gonocoxite
312 [*note 2*]; (8) basivolsellar process present [*note 3*]. **(II)** Identifiable as Bothriomyrmecini by
313 the following combination [*note 4*]: (9) clypeus not extending posteriorly between toruli; (10)
314 medial hypostomal lamina absent; and (11) forewing cross-vein 2rs-m absent. **(III)**
315 Identifiable as *Ravavy* by the following features, all of which are unique within
316 Bothriomyrmecini [*note 5*]: (12) mandible unidentate, spatulate with an apical spiniform tooth
317 (*vs.* mandible multidentate, strap-shaped to spiniform) [*note 6*]; (13) palp formula 6,3 (*vs.* 6,4
318 or $\leq 4,3$) [*note 7*]; (14) pterostigma situated immediately proximad forewing midlength (*vs.*
319 situated distad); (15) marginal cell extremely long, somewhat more than twice the length of
320 submarginal cell 1; (16) Rf appendix, *i.e.*, distalmost free abscissa of R, long, somewhat
321 shorter than pterostigma; (17) discal cell subrectangular, longer proximodistally than wide
322 anteroposteriorly and size small; (18) petiolar node broadly convex in profile view (*vs.*

1
2
3
4
5
6
7
8
9
10 323 anteroposteriorly narrow and squamiform); (19) penite apices not downcurved, but being
11 324 produced distally as long, linear processes. **(IV)** Distinguished from *Ravavy miafina* by the
12 325 following [note 8]: (20) smaller, BL ~ 2.57–2.34, WL ~ 0.43–0.46, FWL ~ 2.17–2.52 (vs.
13 326 larger, BL ~ 3.33–4.46, WL ~ 1.30–1.67, FWL ~ 3.85–3.99); (21) head somewhat broader, CI
14 327 ~ 122 (vs. narrower, CI ~ 112–114 although 122 in one specimen); (22) malar space relatively
15 328 long, MSI ~ 6 and space distinctly longer than proximal width of mandible in lateral view (vs.
16 329 relatively short, MSI ~ 28–32 and distinctly shorter than proximal mandibular width); (23)
17 330 eye relatively long, OI ~ 40–39 (vs. eye relatively short, OI ~ 14–18); (24) ocelli relatively
18 331 small, OCI ~ 38 (vs. 44–62); (25) antennomere III but not IV slightly kinked (vs. both
19 332 antennomeres kinked); (26) mesoscutum relatively long, MI ~ 80 (vs. short, MI ~ 104–131);
20 333 (27) scutoscutellar sulcus distinctly broad (vs. short, almost line-like); (28) petiole relatively
21 334 long, PI ~ 80 (vs. short, PI ~ 51–67); (29) bristle-like setae apparently not developed on
22 335 gastral sternites (vs. such setae present on all gastral sternites except the first); (30) abdominal
23 336 sternum IX posterior margin broadly convex (vs. broadly emarginate); (31) gonostyli
24 337 relatively long, length ~ 2–3 × height (vs. short, length ~ 1 × height); (32) gonostylar apices
25 338 narrowly pointed (vs. broadly rounded); (33) ventral margin of penite more-or-less linear
26 339 from base to apex (vs. base produced ventrally as a dorsoventrally long, anteroposteriorly
27 340 narrow, serrate lobe); (34) apicoventral penite processes short, length from proximodorsal
28 341 inflection point ~ 1 × height (vs. long, length ~ 4 × height).

29 342 *Notes on diagnosis.*

- 30 343 1. A large, rhomboidal clypeal condyle is an apparent synapomorphy of the
31 344 Dolichoderomorpha, *i.e.*, Dolichoderinae + Aneuretinae. The clypeal condyle of
32 345 Formicinae and other subfamilies is variable in shape, often anteroposteriorly narrow.
33 346 2. The form of the gonopod is an apparent synapomorphy of Dolichoderinae as it is not
34 347 shared with Aneuretinae.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

- 348 3. Most dolichoderines have a posteroventral (ventroapical) basivolsellar process, which
349 may be short and triangular to elongate and digitate. The process is absent in *Azteca*
350 Forel, 1878 and *Gracilidris* Wild & Cuzzo, 2006 (sister taxa), *Ochetellus* Shattuck,
351 1992 and some *Dolichoderus* Lund, 1831. Formicines do not have a basivolsellar
352 process; such a process is present convergently in the Amblyoponinae, which is a
353 synapomorphy for that subfamily (Yoshimura & Fisher, 2012; Boudinot, 2015).
- 354 4. In their recent phylogenetic revision of the Dolichoderinae, Ward *et al.* (2010)
355 provided reduction or loss of the medial hypostomal lamina as a synapomorphy of the
356 Bothriomyrmecini that occurs in both sexes. Subsequently, Boudinot *et al.* (2016)
357 recognized loss of forewing cross-vein 2rs-m as another diagnostic condition. Here,
358 we propose the “short” condition of the clypeus as an additional synapomorphy of the
359 tribe. The clypeus in both males and females extends posteriorly between the antennal
360 toruli in the majority of dolichoderine genera with only a few exceptions (Shattuck,
361 1992; Boudinot, 2015), such as the *neotropicus* and *macro* clades of *Leptomyrmex*
362 Mayr, 1862 (Lucky & Ward, 2010; Boudinot *et al.*, 2016; Barden *et al.*, 2017).
- 363 5. Males and queens of the Bornean genus *Loweriella* Shattuck, 1992 are unknown in
364 contrast to the other three bothriomyrmecine genera (*Bothriomyrmex* Emery, 1869a,
365 *Chronoxenus* Santschi, 1919, *Ravavy*). Because *Loweriella* is the sister group of
366 *Ravavy* (Ward *et al.*, 2010), a number of the diagnostic traits of the latter genus
367 adduced here may be synapomorphies of the two genera.
- 368 6. Yoshimura & Fisher (2011) tentatively remarked that additional, vestigial denticles
369 may be present in *R. mifina* and label a possible denticle on a dissected mandible
370 imaged with a compound microscope. Because this apparent denticle is on the lateral
371 mandibular margin and as the apical tooth is a consistent feature of even “edentate”

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

372 mandibles (Boudinot *et al.*, 2021), we interpret the mandible of *R. miafina* as strictly
373 unidentate.

374 7. The 6,3 palpomere count is an apparent synapomorphy of *Ravavy* within the
375 Bothriomyrmecini. *Loweriella* has a plesiomorphic 6,4 count, while *Bothriomyrmex*
376 and *Chronoxenus* share a derived, reduced count which is $\leq 4,3$ (Bolton, 2003; Fisher,
377 2009; Yoshimura & Fisher, 2011).

378 8. The fine anatomy and morphology of *R. miafina* is illustrated in Fisher (2009) and
379 especially Yoshimura & Fisher (2011). The latter work provided a revised diagnosis
380 of this species plus a comparative analysis of genitalic form. Comparisons were made
381 to the images in the literature, on AntWeb (2022), and to specimens examined at the
382 California Academy of Sciences.

383 *Description.* Integument uniformly imbricate, apparently with a more-or-less even vestiture of
384 extremely short and appressed pubescence; bristle-like setae not visible on body with
385 exception of tarsi, gastral tergites and gonostyli, those of gastral tergites sparse. Head roughly
386 rectangular, narrow anterad eyes and broader posteriorly; malar space relatively broad, being
387 longer than proximal width of mandible in lateral view; posterior head margin emarginate.
388 Compound eye bulging, length slightly less than half head length, subreniform with subtle
389 emargination occurring on along ventral eye margin and with > 175 ommatidia but probably
390 not more than 200 (complete count not possible). Ocelli small; lateral ocelli relatively
391 wideset, separated from one another by somewhat more than three lateral ocellar lengths.
392 Frontal carinae poorly developed. Antenna 13-merous, scape about as long as compound eye
393 and about 3 × as long as pedicel; pedicel about twice as long as wide and slightly more than
394 half the length of antennomere III; antennomere III slightly kinked at about midlength;
395 antennomeres III–XIII subequal in length and about 4 × as long as wide. Ocellar sensilla
396 (setae) not visible. Anterior clypeal margin more-or-less linear; clypeal setation not

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

397 observable; posterior clypeal margin convex, portion of epistomal sulcus anterad and between
398 toruli linear, weakly concave. Mandibles spiniform, tapering to their unidentate apices, thus
399 appearing wedge-shaped in dorsal view. Labrum deeply notched apically, sides distinctly
400 narrowing apicomediad. Palp formula 6,3; maxillary palp relatively long, exceeding
401 hypostomal margin but not occiput; labial palp short, about one fourth length of maxillary
402 palp. Prementum elongate diamond shaped. Stipes without transverse carina. Medial
403 hypostomal lamina absent. Pronotum short, strap-like. Mesoscutum relatively long, with
404 maximum length greater than maximum width; notauli absent; parapsides diverging
405 anteriorly; scutoscutellar sulcus distinctly broad; lateral mesopectal sulcus sinuate. Upper
406 metapleural region distinct, about 4 × as long as broad; lower metapleural region indistinct.
407 Propodeum without distinct dorsal and posterior surfaces; propodeal spiracle small, circular,
408 set slightly below metaphragmal pit. Femora puny, thin; metafemur and metatibia slightly
409 sinuate. Tibial spur formula 1,1. Arolia small, barely visible. Petiole elliptical in lateral view,
410 with broadly convex tergum and sternum; node not squamiform. Abdominal tergum III with
411 broad but shallow concavity anteriorly above helcium. Abdominal segments III–VII similar in
412 size, unmodified. Abdominal sterna VII–VIII broadly emarginate posteriorly. Abdominal
413 sternum IX posterior margin convex, simple. Cerci not visible. Cupula not visible.
414 Gonocoxite length uncertain; gonocoxital apex distinctly offset from gonostylar base.
415 Gonostylus elongate, triangular; length about 2–3 × width; apex narrowly pointed. Volsellae
416 incompletely visible; basivolsellar process present, acute; cuspis absent; lateropenite (= *digitus*)
417 apex directed ventrad at nearly right angle relative to body of volsella; dorsal margin
418 of *digitus* almost lobate; digital apices narrowing, almost rod-like and curved laterad. Ventral
419 margins of penites more-or-less linear from base to apex; dorsal margins broadly convex in
420 lateral view; apical processes directed posterad and relatively short, length from

1
2
3
4
5
6
7
8
9
10 421 proximodorsal inflection point $\sim 1 \times$ height. Fore- and hindwing venation virtually identical to

11
12 422 *R. miafina*. Jugal lobe absent.

13
14 423 *Measurements and indices*. Dashes indicate metric could not be taken or calculated. Holotype:

15 424 BL ~ 2.34 , HL 0.54, HW 0.41, HWE 0.50, EL 0.21, MSL 0.09, FcW –, SL –, OLL –, OIL –,

16
17 425 WL 0.91, ML 0.43, MW –, FWL 2.17, PL –, PW 0.09, PH 0.12, GL 0.86, GW 0.43, CI 92,

18
19 426 HWI 122, MSI 6, SI –, OI 39, EPI –, OCI –, MI –, PI –. Paratype: BL ~ 2.57 , HL 0.54, HW

20
21 427 0.41, HWE 0.48, MSL 0.09, EL 0.22, FcW 0.12, SL 0.22, OLL 0.04, OIL 0.011, WL 0.98,

22
23 428 ML 0.46, MW 0.37, FWL 2.52, PL 0.12, PW –, PH 0.15, GL 0.93, GW 0.54, CI 90, HWI –,

24 429 MSI 6, SI –, OI 40, EPI –, OCI 38, MI 80, PI 80.

25
26 430 *Note*. For comparison, see the metrics for *R. miafina* provided below.

27 431

28
29 432 *RAVAVY MIAFINA* FISHER, 2009

30 433

31
32
33 434 *Measurements and indices*. (N = 4, taken from CASENT0078664, CASENT0080308,

34 435 CASENT0115570, CASENT0474633.) BL ca. 3.33–4.46, HL 2.37–2.45, HW 1.84–1.91,

35 436 HWE 2.13–2.25, EL 0.34–0.43, MSL 0.08–0.09, FcW 0.49–0.55, SL 0.074–0.98, OLL 0.24–

36 437 0.28, OIL 0.44–0.56, WL 1.30–1.67, ML 0.68–0.78, MW 0.81–0.92, FWL 3.85–4.24, PL

37
38 438 0.15–0.19, PW –, PH 0.28–0.31, GL 1.64–2.29, GW 0.58–0.70, CI 88–92, HWI 112–114

39
40 439 (122), MSI 28–32, SI 39–53, OI 14–18, EPI –, OCI 44–62, MI 104–129, PI 51–67.

41 440

42
43
44 441 DISCUSSION

45 442

46
47
48 443 The fossil record of Dolichoderinae spans the Cenozoic to the Late Cretaceous, with $\sim 16\%$ of

49 444 the total species-level diversity of the subfamily represented by extinct taxa (Bolton, 2022).

50
51 445 Of the 137 valid extinct dolichoderine species, 48 are attributed to 20 extinct genera and the

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

446 remainder are distributed among extant genera of the Dolichoderini (*Dolichoderus* †50 spp.),
447 Leptomyrmecini (*Gracilidris* †1 sp., *Iridomyrmex* Mayr, 1862 †5 spp., *Leptomyrmex* †1 sp.),
448 and Tapinomini (*Liometopum* Mayr, 1861 †20 spp., *Tapinoma* Förster, 1850 †6 spp.,
449 *Technomyrmex* †4 spp.). *Ravavy goldmani* is only the second described species of the genus
450 and also constitutes the first fossil member of Bothriomyrmecini. Based on the enhanced
451 application of SR- μ -CT (Figs 1–2), *Technomyrmex svojtikai* expands the knowledge of this
452 genus.

453 The genus *Ravavy* was recently established to accommodate a series of males collected
454 in Madagascar, all attributed to a single species, *R. miafina* (Fisher, 2009; Yoshimura &
455 Fisher, 2011). Although they remain undescribed, workers were associated with the male by
456 the Ant Tree of Life research group. Based on this association, it has been found by the
457 myrmecological community that *Ravavy* likely comprises multiple species and is distributed
458 throughout the Afrotropics, including the Democratic Republic of Congo, Ghana,
459 Mozambique, South Africa, Tanzania and Zambia (see data on AntWeb, 2022). As the new
460 records are based almost entirely on workers, plus a dealate queen, the documentation of
461 morphological diversity for male *Ravavy* remains limited to specimens identified as *R.*
462 *miafina*. The diversity of Malagasy *Ravavy* is certainly underappreciated as well, as a second
463 morphospecies is also known. In any case, the new species described above, *R. goldmani*,
464 represents the first male of the genus recorded from Africa, and it shares a suite of derived
465 traits with *R. miafina*, in addition to displaying the diagnostic features of Dolichoderinae and
466 Bothriomyrmecini. Although these species are superficially similar, detailed examination
467 revealed 15 discretized trait differences between the two, as listed in part IV of the diagnosis,
468 thus indicating some degree of phylogenetic distance. The lack of identified male
469 *Loweriella*—the sistergroup of *Ravavy* (Ward *et al.*, 2010)—unfortunately complicates the
470 interpretation of generic boundaries. Because *Ravavy* males of other extant morphospecies

1
2
3
4
5
6
7
8
9
10 471 have yet to be recorded, we cannot provide further discussion on the specific relationship of
11
12 472 the fossil to modern lineages.

13
14 473 *Technomyrmex* comprises 94 living species primarily distributed in the Afrotropical,
15
16 474 Indomalayan and Australian bioregions (Bolton, 2022). Two species, *T. fulvus* (Wheeler,
17
18 475 1934) and *T. gorgona* Fernández & Guerrero, 2008, are endemic to the Neotropics (Fernández
19
20 476 & Guerrero, 2008). Besides an unsubstantiated report of *Technomyrmex* from Canadian Hat
21
22 477 Creek amber (Poinar *et al.*, 1999; see Ward *et al.*, 2010; Archibald *et al.*, 2018), four extinct
23
24 478 species have hitherto been attributed to the genus: *T. hispaniolae* Wilson, 1985 and *T.*
25
26 479 *caritatis* Brandão *et al.*, 1999 from Miocene Dominican amber; *T. septentrionalis* Zhang,
27
28 480 1989 from Miocene imprints of Shanwang, China; and *T. deletus* Emery, 1891 from Sicilian
29
30 481 amber. While the generic identities of the first three species have been questioned (Bolton,
31
32 482 2007; Fernández & Guerrero, 2008), the placement of *T. deletus* is considered more certain
33
34 483 due to preservation and exposure of its proventriculus (Bolton, 2007). The Sicilian and
35
36 484 Ethiopian amber species are thus the only definite fossil species of *Technomyrmex*, with *T.*
37
38 485 *deletus* previously hypothesized to have affinity with the *T. albipes* group (Bolton, 2007) and
39
40 486 *T. sjojtakai* here assumed to be related to the *T. bicolor* group. It is worth noting that the age of
41
42 487 Sicilian amber is controversial, being from late Eocene, Oligocene or middle Miocene (14–34
43
44 488 Mya; Ragazzi & Roghi, 2014).

41 489 The overall morphological similarity of *T. sjojtakai* and *R. goldmani* to extant species
42
43 490 provides further information about the timing and pattern of ant diversification. The ages of
44
45 491 these fossils are congruent with the divergence dating estimates of Ward *et al.* (2010) for the
46
47 492 *Ravavy* + *Loweriella* and *Technomyrmex* crown clades, with suggested age ranges of ~17–42
48
49 493 Mya and ~18–33 Mya, respectively. The Miocene species described here are readily
50
51 494 attributable to *Technomyrmex* and *Ravavy* based on a suite of synapomorphies. Indeed, it is
52
53 495 possible that *T. sjojtakai* and *R. goldmani* are members of the crown clades of their respective
54

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

496 genera given that *Technomyrmex* was represented by three terminals in Ward *et al.* (2010) and
497 the undescribed Afrotropical morphospecies of *Ravavy* were not sampled in that study.
498 Whereas Eocene to Oligocene amber deposits include a mixture of extant and extinct genera
499 plus stemgroup species (*e.g.*, Barden, 2017; Boudinot *et al.*, 2022), Miocene deposits are
500 dominated by modern genera and crown-group species (*e.g.*, Barden, 2017; Barden *et al.*,
501 2017; Prebus, 2017). With the direct fossil record and divergence time estimates (for
502 summary of the latter, see Borowiec *et al.*, 2021), the larger pattern emerging across ants is
503 the diversification of clades attributable to extant subfamilies during the Late Cretaceous, to
504 extant genera in the Palaeogene and to modern species since the Miocene.

505 Finally, we provide further corroborating evidence for a Miocene age of Ethiopian
506 amber (Bouju & Perrichot, 2020; Bouju, 2021) via the high abundance and species
507 composition of ants among the total arthropod inclusions. We have examined 84 fossiliferous
508 amber pieces from four collections housed in the NIGPAS, IGR, MAIG and NHMW
509 collections. This material yielded 192 ant individuals (104 males, 85 workers and 3 alate
510 females), representing six subfamilies and at least 19 genera, as summarized in Table 1.
511 Importantly, the examined material comprised two unbiased samples of 17 and 43
512 fossiliferous pieces ('IGR' and 'MAIG' samples, respectively) obtained directly from the
513 market at Addis Ababa and purchased without pre-selection for particular insect or plant taxa.
514 The ant prevalence reaches 48% of total insects in the IGR sample and 52% in the MAIG
515 sample; these values are congruent only with Neogene fossil insect deposits such as the
516 Miocene Dominican or Mexican amber (LaPolla *et al.*, 2013; Barden, 2017). Further, within
517 the ants, the prevalence of Myrmicinae (75% of all ants in the IGR sample, 54% in the MAIG
518 sample) also supports a Miocene age (Barden, 2017). In contrast, the subfamily
519 Dolichoderinae studied herein is infrequent, accounting for less than 4% of the total ant

1
2
3
4
5
6
7
8
9
10 520 assemblage examined. We will report on the species identities and morphological diversity of
11
12 521 further Ethiopian amber ants in future taxonomic treatments.

13 522
14
15 523 ACKNOWLEDGEMENTS
16

17 524
18
19 525 We warmly thank Matthias Svojtka (University of Vienna), Yale Goldman (Bloomfield,
20 526 Connecticut) and Marcin Buzalski (Gdansk) for facilitating access to various specimens
21
22 527 described or reported here. We are grateful to Amde Zewdalem (Jacksonville, Florida) and
23
24 528 Binyam Teferi (Addis Ababa) for information and access to the amber deposits of the North
25
26 529 Shewa Zone, Ethiopia; the Ethiopian Ministry of Mines and Petroleum for delivering the
27
28 530 export permits; Valentine Bouju and Cédric Chény (Univ. Rennes) for contributing data and
29
30 531 preparation of ants from Ethiopian amber; Alexander Schmidt (University of Göttingen) for
31
32 532 invaluable discussions, advices and contribution regarding the study of Ethiopian amber; Paul
33
34 533 Tafforeau and Carmen Soriano (ESRF) for the exquisite synchrotron imaging of specimen
35
36 534 NHMW-N6976; and Bo Wang (NIGPAS) for acquisition and provision of the male
37
38 535 specimens described here. We thank Hans Pohl (Friedrich Schiller University Jena) for
39
40 536 allowing use of his imaging station. Finally, we thank the editor and anonymous reviewers for
41
42 537 their comments. This research was supported by the Alexander von Humboldt Foundation via
43
44 538 Research Fellowships to V.P. (2006–2008) and B.E.B. (2020–2022), Harvard Ernst Mayr
45
46 539 travel grants (B.E.B.), the Tellus-INTERRVIE program CNRS INSU (project
47
48 540 AMBRAFRICA to V.P.), the Strategic Priority Research Program of the Chinese Academy of
49
50 541 Sciences (XDB26000000), the National Natural Science Foundation of China (42125201,
51
52 542 41688103) and the ESRF through attribution of inhouse beamtime on the beamline ID19.

53
54
55 543
56
57 544 REFERENCES
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

- 545
546 **AntWeb. 2022.** *AntWeb Version 8.68.7*. Berkeley: California Academy of Sciences.
547 Available at: <https://www.antweb.org> (accessed 7 January 2022).
- 548 **Archibald SB, Cover SP, Moreau CS. 2006.** Bulldog ants of the Eocene Okanagan
549 Highlands and history of the subfamily (Hymenoptera: Formicidae: Myrmeciinae). *Annals*
550 *of the Entomological Society of America* **99**: 487–523.
- 551 **Archibald SB, Rasnitsyn AP, Brothers DJ, Mathewes RW. 2018.** Modernisation of the
552 Hymenoptera: ants, bees, wasps, and sawflies of the early Eocene Okanagan Highlands of
553 western North America. *The Canadian Entomologist* **150**: 205–257.
- 554 **Barden P. 2017.** Fossil ants (Hymenoptera: Formicidae): ancient diversity and the rise of
555 modern lineages. *Myrmecological News* **24**: 1–30.
- 556 **Barden P, Boudinot BE, Lucky A. 2017.** Where fossils dare and males matter: combined
557 morphological and molecular analysis untangles the evolutionary history of the spider ant
558 genus *Leptomymex* Mayr (Hymenoptera: Dolichoderinae). *Invertebrate Systematics* **31**:
559 765–780.
- 560 **Bolton B. 1994.** *Identification guide to the ant genera of the World*. Cambridge: Harvard
561 University Press.
- 562 **Bolton B. 2003.** Synopsis and classification of Formicidae. *Memoirs of the American*
563 *Entomological Institute* **71**: 1–370.
- 564 **Bolton B. 2007.** Taxonomy of the dolichoderine ant genus *Technomyrmex* Mayr
565 (Hymenoptera: Formicidae) based on the worker cast. *Contributions of the American*
566 *Entomological Institute* **35**: 1–150.
- 567 **Bolton B. 2022.** *An online catalogue of the ants of the world*. Available at:
568 <http://www.antcat.org> (accessed 7 January 2022]

- 1
2
3
4
5
6
7
8
9
10 569 **Borowiec ML, Moreau CS, Rabeling C. 2021.** Ants: phylogeny and classification. In: Starr
11 C, ed. *Encyclopedia of social insects*. Cham: Springer International Publishing, 52–69.
12 570
13 **Boudinot BE. 2013.** The male genitalia of ants: musculature, homology, and functional
14 571
15 572 morphology (Hymenoptera, Aculeata, Formicidae). *Journal of Hymenoptera Research* **30**:
16 573 29–49.
17 574
18 **Boudinot BE. 2015.** Contributions to the knowledge of Formicidae (Hymenoptera, Aculeata):
19 575 A new diagnosis of the family, the first global male-based key to subfamilies, and a
20 576 treatment of early branching lineages. *European Journal of Taxonomy* **120**: 1–62.
21 577
22 **Boudinot BE, Probst RS, Brandão CRF, Feitosa RM, Ward PS. 2016.** Out of the
23 578 Neotropics: newly discovered relictual species sheds light on the biogeographical history
24 579 of spider ants (*Leptomyrmex*, Dolichoderinae, Formicidae). *Systematic Entomology* **41**:
25 580 658–671.
26 581
27 **Boudinot BE. 2018.** A general theory of genital homologies for the Hexapoda (Pancrustacea)
28 582 derived from skeletomuscular correspondences, with emphasis on the Endopterygota.
29 583 *Arthropod Structure & Development* **47**: 563–613.
30 584
31 **Boudinot BE, Moosdorf OTD, Beutel RG, Richter A. 2021.** Anatomy and evolution of the
32 585 head of *Dorylus helvolus* (Formicidae: Dorylinae): patterns of sex- and caste-limited traits
33 586 in the sausagefly and the driver ant. *Journal of Morphology* **282**: 1616–1658.
34 587
35 **Boudinot BE, Borowiec ML, Prebus MM. 2022.** Phylogeny, evolution, and classification of
36 588 the ant genus *Lasius*, the tribe Lasiini, and the subfamily Formicinae (Hymenoptera:
37 589 Formicinae). *Systematic Entomology* **47**: 113–151.
38 590
39 **Bouju V. 2021.** *Paléobiodiversité et paléoenvironnements des gisements à ambre du Crétacé*
40 591 *et du Miocène d’Afrique*. Unpublished Ph.D. Thesis, Université de Rennes 1.
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

- 592 **Bouju V, Feldberg K, Kaasalainen U, Schäfer-Verwimp A, Hedenäs L, Buck WR, Wang**
593 **B, Perrichot V, Schmidt AR. 2022a.** Miocene Ethiopian amber: a new source of fossil
594 cryptogams. *Journal of Systematics and Evolution*. <https://doi.org/10.1111/jse.12796>
- 595 **Bouju V, Jouault C, Perrichot V. 2022b.** The termite genus *Glyptotermes* (Isoptera:
596 Kalotermitidae) in Miocene amber from Ethiopia. *Journal of Paleontology* **96**: 387–393.
- 597 **Bouju V, Perrichot V. 2020.** A review of amber and copal occurrences in Africa and their
598 paleontological significance. *BSGF-Earth Sciences Bulletin* **191**: 17.
- 599 **Bouju V, Rosse-Guillevic S, Griffon M, Bojarski B, Szwedó J, Perrichot V. 2021.** The
600 genus *Allodia* (Diptera: Mycetophilidae) in Miocene Ethiopian amber. *Fossil Record* **24**:
601 339–346.
- 602 **Brandão CRF, Baroni Urbani C, Wagensberg J, Yamamoto C. 1999 ('1998').** New
603 *Tecnomyrme* in Dominican amber (Hymenoptera: Formicidae), with a reappraisal of
604 Dolichoderinae phylogeny. *Entomologica Scandinavica* **29**: 411–428.
- 605 **Coty D, Lebon M, Nel A. 2016.** When phylogeny meets geology and chemistry: doubts on
606 the dating of Ethiopian amber. *Annales de la Société Entomologique de France* **52**: 161–
607 166.
- 608 **Dlussky GM, Brothers DJ, Rasnitsyn AP. 2004.** The first Late Cretaceous ants
609 (Hymenoptera: Formicidae) from southern Africa, with comments on the origin of the
610 Myrmicinae. *Insect Systematics and Evolution* **35**: 1–13.
- 611 **Dubovikoff DA. 2005.** The system of taxon *Bothriomyrmex* Emery, 1869 *sensu*
612 *lato* (Hymenoptera: Formicidae) and relatives genera. *Caucasian Entomological Bulletin*
613 **1**: 89–94. [In Russian].
- 614 **Emery C. 1869a.** Descrizione di una nuova formica italiana. *Annuario del Museo Zoologico*
615 *della Reale Università de Napoli* **5**: 117–118.

- 1
2
3
4
5
6
7
8
9
10 616 **Emery C. 1869b.** Enumerazione dei formicidi che rinvenngonsi nei contorni di Napoli con
11
12 617 descrizioni di specie nuove o meno conosciute. *Annali dell'Accademia degli Aspiranti*
13
14 618 *Naturalisti. Secunda Era* **2**: 1–26.
- 15 619 **Emery C. 1877.** Catalogo delle formiche esistenti nelle collezioni del Museo Civico di
16
17 620 Genova. Parte prima. Formiche provenienti dal Viaggio dei signori Antinori, Beccari e
18
19 621 Issel nel Mar Rosso e nel paese dei Bogos. [concl.]. *Annali del Museo Civico di Storia*
20
21 622 *Naturale* **9**: 369–381.
- 22 623 **Emery C. 1891.** Le formiche dell' ambra Siciliana nel Museo Mineralogico dell'Universita di
23
24 624 Bologna. *Memorie della Reale Accademia delle Scienze dell'Istituto di Bologna* **5**: 141–
25
26 625 165 [pagination of separate 568–591], pl. 1–3.
- 27 626 **Emery C. 1893 ('1892')**. [Untitled. Introduced by: "M. C. Emery, de Bologne, envoie les
28
29 627 diagnoses de cinq nouveaux genres de Formicides"]. *Bulletin Bimensuel de la Société*
30
31 628 *Entomologique de France* **1892**: 275–277.
- 32
33 629 **Emery C. 1913 ('1912')**. Hymenoptera. Fam. Formicidae. Subfam. Dolichoderinae. *Genera*
34
35 630 *Insectorum* **137**: 1–50.
- 36 631 **Fernández F, Guerrero RJ. 2008.** *Technomyrmex* (Formicidae: Dolichoderinae) in the New
37
38 632 World: synopsis and description of a new species. *Revista Colombiana de Entomología*
39
40 633 **34**: 110–115.
- 41 634 **Fisher BL. 2009.** Two new dolichoderine ant genera from Madagascar: *Aptinoma* gen. n. and
42
43 635 *Ravavy* gen. n. (Hymenoptera: Formicidae). *Zootaxa* **2118**: 37–52.
- 44
45 636 **Fisher BL, Bolton B. 2016.** *Ants of Africa and Madagascar: a guide to the genera*. Berkeley:
46
47 637 University of California Press.
- 48 638 **Forel A. 1878.** Études myrmécologiques en 1878 (première partie) avec l'anatomie du gésier
49
50 639 des fourmis. *Bulletin de la Société Vaudoise des Sciences Naturelles* **15**: 337–392.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

- 640 **Forel A. 1891.** Les Formicides. [part]. In: Grandidier A, ed. *Histoire physique, naturelle, et*
641 *politique de Madagascar. Volume XX. Histoire naturelle des Hyménoptères. Deuxième*
642 *partie (28e fascicule)*. Paris: Hachette et Cie, v + 237 pp.
- 643 **Forel A. 1900.** Un nouveau genre et une nouvelle espèce de Myrmicide. *Annales de la*
644 *Société Entomologique de Belgique* **44**: 24–26.
- 645 **Förster A. 1850.** *Hymenopterologische Studien. 1. Formicariae*. Aachen: Ernst Ter Meer.
- 646 **Harris RA. 1979.** A glossary of surface sculpturing. *Occasional Papers in Entomology, State*
647 *of California Department of Food and Agriculture* **28**: 1–31.
- 648 **Harrison T, Msuya CP, Murray AM, Jacobs BF, Báez AM, Mundil R, Ludwig KR.**
649 **2001.** Paleontological investigations at the Eocene locality of Mahenge in North-Central
650 Tanzania, East Africa. In: Gunnell GF, ed. *Eocene biodiversity: unusual occurrences and*
651 *rarely sampled habitats*. Boston: Springer, Topics in Geobiology, vol. **18**: 39–74.
- 652 **Keller RA. 2011.** A phylogenetic analysis of ant morphology (Hymenoptera: Formicidae)
653 with special reference to the poneromorph subfamilies. *Bulletin of the American Museum*
654 *of Natural History* **355**: 1–90.
- 655 **Lak M, Néraudeau D, Nel A, Cloetens P, Perrichot V, Tafforeau P. 2008.** Phase contrast
656 X-ray synchrotron imaging: opening access to fossil inclusions in opaque amber.
657 *Microscopy and Microanalysis* **14**: 251–259.
- 658 **LaPolla JS, Dlussky GM, Perrichot V. 2013.** Ants and the fossil record. *Annual Reviews of*
659 *Entomology* **58**: 609–630.
- 660 **Latreille PA. 1809.** *Genera crustaceorum et Insectorum secundem ordinem naturalem in*
661 *familias disposita, iconibus exemplisque plurimis explicata*. Tomus 4. Paris and
662 Strasbourg: A. Koenig, 399 pp.
- 663 **Lucky A, Ward PS. 2010.** Taxonomic revision of the ant genus *Leptomyrme* Mayr
664 (Hymenoptera: Formicidae). *Zootaxa* **2688**: 1–67.

- 1
2
3
4
5
6
7
8
9
10 665 **Lund PW. 1831.** Lettre sur les habitudes de quelques fourmis du Brésil, adressée à M.
11
12 666 Audouin. *Annales des Sciences Naturelles* **23**: 113–138.
- 13 667 **Mayr G. 1855.** Formicina austriaca. Beschreibung der bisher im österreichischen Kaiserstaate
14
15 668 aufgefundenen Ameisen, nebst Hinzufügung jener in Deutschland, in der Schweiz und in
16
17 669 Italien vorkommenden Arten. *Verhandlungen der Zoologisch-Botanischen Vereins in*
18
19 670 *Wien* **5**: 273–478.
- 20 671 **Mayr G. 1861.** *Die europäischen Formiciden. Nach der analytischen Methode bearbeitet.*
21
22 672 Wien: C. Gerolds Sohn.
- 23 673 **Mayr G. 1862.** Myrmecologische Studien. *Verhandlungen der Kaiserlich-Königlichen*
24
25 674 *Zoologisch-Botanischen Gesellschaft in Wien* **12**: 649–776.
- 26 675 **Mayr G. 1865.** Formicidae. In: Novara Expedition 1865. *Reise der Österreichischen Fregatte*
27
28 676 *"Novara" um die Erde in den Jahren 1857, 1858, 1859. Zoologischer Theil. Bd. II. Abt. 1.*
29
30 677 Wien: K. Gerold's Sohn.
- 31 678 **Mayr G. 1872.** Formicidae Borneensis collectae a J. Doria et O. Beccari in territorio Sarawak
32
33 679 annis 1865–1867. *Annali del Museo Civico di Storia Naturale* **2**: 133–155.
- 34 680 **Mikó I, Trietsch C, Sandall EL, Yoder MJ, Hines H, Deans AR. 2016.** Malagasy
35
36 681 *Conostigmus* (Hymenoptera: Ceraphronoidea) and the secret of scutes. *PeerJ* **4**: e2682.
- 37 682 **Perrichot V, Boudinot BE, Cole J, Delhaye-Prat V, Esnault J, Goldman Y, Nohra YA,**
38
39 683 **Schmidt AR. 2016.** African fossiliferous amber: a review. In: Penney D, Ross AJ, eds.
40
41 684 *Abstracts of the 7th international conference on fossil insects, arthropods, and amber, held*
42
43 685 *in Edinburgh, Scotland, in April–May 2016.* Manchester: Siri Scientific Press, 41.
- 44 686 **Perrichot V, Boudinot BE, Chény C, Cole J, Jeanneau L, Schmidt A, Szewdo J, Wang B.**
45
46 687 **2018.** The age and paleobiota of Ethiopian amber revisited. *5th International*
47
48 688 *Palaeontological Congress, held in Paris, France, in July 2018.* Abstract book, 23.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

- 689 **Petrunkevitch AI. 1955.** Arachnida. In: Moore RC, ed. *Treatise on invertebrate*
690 *palaeontology, part P. Arthropoda 2.* Lawrence: Geological Society of America &
691 University of Kansas Press, 42–162.
- 692 **Poinar G Jr, Archibald B, Brown A. 1999.** New amber deposit provides evidence of early
693 Paleogene extinctions, paleoclimates, and past distributions. *The Canadian Entomologist*
694 **131:** 171–177.
- 695 **Prebus MM. 2017.** Insights into the evolution, biogeography and natural history of the acorn
696 ants, genus *Temnothorax* Mayr (Hymenoptera: Formicidae). *BMC Evolutionary Biology*
697 **17:** 250.
- 698 **Ragazzi E, Roghi G. 2014.** Simetite, the Sicilian amber. In: Kustatscher E, Roghi G, Bertini
699 A, Miola A, eds. Palaeobotany of Italy. *Publication of the Museum of Nature South Tyrol*
700 **9:** 232–237.
- 701 **Richter A, Hita Garcia F, Keller RA, Billen J, Economo EP, Beutel, RG. 2020.**
702 Comparative analysis of worker head anatomy of *Formica* and *Brachyponera*
703 (Hymenoptera: Formicidae). *Arthropod Systematics & Phylogeny* **78:** 122–170.
- 704 **Sadowski EM, Schmidt AR, Seyfullah LJ, Solórzano-Kraemer MM, Neumann C,**
705 **Perrichot V, Hamann C, Milke R, Nascimbene PC. 2021.** Conservation, preparation
706 and imaging of diverse ambers and their inclusions. *Earth-Science Reviews* **220:** 103653.
- 707 **Santschi F. 1914.** *Voyage de Ch. Alluaud et R. Jeannel en Afrique Orientale, 1911–1912.*
708 *Résultats scientifiques. Insectes Hyménoptères. II. Formicidae.* Paris: Libr. A. Schulz.
- 709 **Santschi F. 1919.** Fourmis du genre *Bothriomyrmex* Emery (Système et mœurs). *Revue*
710 *Zoologique Africaine* **7:** 201–224.
- 711 **Santschi F. 1938.** Notes sur quelques *Ponera* Latr. *Bulletin de la Société Entomologique de*
712 *France* **43:** 78–80.

- 1
2
3
4
5
6
7
8
9
10 713 **Schlüter T. 2018.** Eocene insects from a Maar Lagerstätte at Mahenge, northern Tanzania.
11
12 714 *Entomologia Generalis* **37**: 375–392.
- 13 715 **Schmidt AR, Perrichot V, Svojtka M, Anderson KB, Belet KH, Bussert R, Dörfelt H,**
14
15 716 **Jancke S, Mohr B, Mohrmann E, Nascimbene PC, Nel A, Nel P, Ragazzi E, Roghi,**
16
17 717 **G., Saupe EE, Schmidt K, Schneider H, Selden PA, Vávra N. 2010.** Cretaceous
18
19 718 African life captured in amber. *Proceedings of the National Academy of Sciences of the*
20
21 719 *USA* **107**: 7329–7334.
- 22 720 **Shattuck SO. 1992.** Generic revision of the ant subfamily Dolichoderinae (Hymenoptera:
23
24 721 Formicidae). *Sociobiology* **21**: 1–181.
- 25 722 **Smith F. 1852.** Descriptions of some hymenopterous insects captured in India, with notes on
26
27 723 their economy, by Ezra T. Downes, Esq., who presented them to the Honourable the East
28
29 724 India Company. *Annals and Magazine of Natural History* **(2)9**: 44–50.
- 30 725 **Smith F. 1853 ('1854').** Monograph of the genus *Cryptocerus*, belonging to the group
31
32 726 Cryptoceridae – family Myrmicidae – division Hymenoptera Heterogyna. *Transactions of*
33
34 727 *the Entomological Society of London* **(2)2**: 213–228.
- 35 728 **Smith F. 1860.** Catalogue of hymenopterous insects collected by Mr. A. R. Wallace in the
36
37 729 islands of Bachian, Kaisaa, Amboyna, Gilolo, and at Dory in New Guinea. *Journal and*
38
39 730 *Proceedings of the Linnean Society of London. Zoology* **5(17b)(suppl. to vol. 4)**: 93–143.
- 40 731 **Solórzano-Kraemer MM, Hammel JU, Kunz R, Xu C, Cognato AI. 2022.** Miocene
41
42 732 pinhole borer ambrosia beetles: new species of *Diapus* (Coleoptera: Curculionidae:
43
44 733 Platypodinae). *Palaeoworld* **31**. Available from:
45
46 734 <https://doi.org/10.1016/j.palwor.2021.10.001>
- 47 735 **Szadziewski R, Sontag E, Pankowski MV. 2021.** A new biting midge of the genus
48
49 736 *Forcipomyia* Meigen, 1818 from Miocene Ethiopian amber (Diptera: Ceratopogonidae).
50
51 737 *Palaeoentomology* **4**: 441–444.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

- 738 **Ulitzka MR. 2020.** Two fossil thrips from Ethiopian amber (Thysanoptera) with description
739 of *Merothrips aithiopicus* sp. n. (Thysanoptera: Merothripidae). *Zootaxa* **4786**: 283–288.
- 740 **Ward PS, Brady SG, Fisher BL, Schultz TR. 2010.** Phylogeny and biogeography of
741 dolichoderine ants: effects of data partitioning and relict taxa on historical inference.
742 *Systematic Biology* **59**: 342–362.
- 743 **Westwood JO. 1839.** *An introduction to the modern classification of insects; founded on the*
744 *natural habits and corresponding organisation of the different families. Volume 2. Part*
745 *XI.* London: Longman, Orme, Brown, Green and Longmans.
- 746 **Westwood JO. 1840.** Observations on the genus *Typhlopone*, with descriptions of several
747 exotic species of ants. *Annals and Magazine of Natural History* **6**: 81–89.
- 748 **Wheeler WM. 1934.** Neotropical ants collected by Dr. Elisabeth Skwarra and others. *Bulletin*
749 *of the Museum of Comparative Zoology at Harvard College* **77**: 160–240.
- 750 **Wild AL, Cuzzo F. 2006.** Rediscovery of a fossil dolichoderine ant lineage (Hymenoptera:
751 Formicidae: Dolichoderinae) and a description of a new genus from South America.
752 *Zootaxa* **1142**: 57–68.
- 753 **Wilson EO. 1985.** Ants of the Dominican amber (Hymenoptera: Formicidae). 3. The
754 subfamily Dolichoderinae. *Psyche* **92**: 17–37.
- 755 **Wilson EO, Taylor RW. 1964.** A fossil ant colony: new evidence of social antiquity. *Psyche*
756 **71**: 93–103.
- 757 **Wunderlich J. 2017.** Description of a derived spider taxon in Ethiopian amber (Araneae:
758 Salticidae). *Beiträge zur Araneologie* **10**: 280–284.
- 759 **Yoshimura M, Fisher BL. 2011.** A revision of male ants of the Malagasy region
760 (Hymenoptera: Formicidae): key to genera of the subfamily Dolichoderinae. *Zootaxa*
761 **2794**: 1–34.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

762 **Zhang J. 1989.** *Fossil insects from Shanwang, Shandong, China*. Jinan, China: Shandong
763 Science and Technology Publishing House. [in Chinese, with English summary].

764

For Review Only

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60**Figure captions**

Figure 1. *Technomyrmex svojtkai* holotype worker NHMW-N6976. A, photomicrograph in right lateral view, with tip of gaster curled toward the mouthparts. B, 3D model in nearly the same position, imaged by synchrotron microtomography. C–E, 3D model of body with antennae and legs virtually removed. C, frontal view. D, left lateral view. E, posterior (dorsal) view. Scale bar: 0.5 mm. Animated versions of this are available in Supporting Information online (Figs S1, S2).

Figure 2. *Technomyrmex svojtkai*. Phase contrast X-ray synchrotron microtomography of holotype worker NHMW-N6976, with indication of measurements as reported in Material and methods. A, lateral view of body with legs and antennae virtually removed, and with petiole and gaster virtually uncurled to approximate the life position. The left lateral side of the head and mesosoma being crushed, the figure shows them from the horizontally flipped right side in standard left profile view. B, reconstruction in dorsal view, without legs and antennae, and with gaster largely concealing the petiole as in approximate life position. C, head in full-face view. D, head without antennae in full-face view. E, mandibles in dorsal view. F, petiole in dorsal view, with articulation with gaster as preserved. G, gaster in ventral view, with articulation with petiole as preserved, showing the first gastral tergite concavity for accommodation of petiole. Abbreviations: AIII–AVII, abdominal segments III to VII. Scale bars: 0.5 mm, except 0.2 mm for E.

Figure 3. *Technomyrmex svojtkai* photomicrographs of paratype workers and additional, partial worker, specimen MAIG 6020. A, paratype 1, ventral view. B, paratype 2, dorsal

1
2
3
4
5
6
7
8
9
10 789 view. C, paratype 2, left lateral view, anterior-oblique orientation. D, non-type, partially
11 preserved worker, right lateral view. Scale bars: 0.25 mm.

12 790
13 791
14
15 792 **Figure 4.** *Ravavy goldmani* holotype male NIGP180512, photomicrographs. A, left lateral
16 view, slightly anterior-oblique orientation. B, ventral view, slightly left-lateral-oblique
17 793 orientation. Scale bars: 0.5 mm.
18 794

19 795
20
21 796 **Figure 5.** *Ravavy goldmani* photomicrographs. A–B, holotype male NIGP180512, C–F,
22 paratype male IGR.ET2015/001a. A, right lateral view, slightly posterodorsal-oblique
23 orientation. B, oral view, slightly right-lateral-oblique orientation. C, dorsal view,
24 797 slightly right lateral, anterior oblique orientation. D, ventral view, slightly right-lateral,
25 798 posterior oblique orientation. E, right lateral, slightly ventral, anterior oblique view. F,
26 799 caudal view of genitalia, slightly right lateral oblique. Scale bars: 0.5 mm for A, B, F;
27 800 1.0 mm for C–E.
28 801
29 802
30 803

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

804 **Table 1.** Diversity and specimen count of ants known from Ethiopian amber (acronyms of
805 collections are explained in material and methods).

Taxa	Number of specimens and castes in each collection			
	IGR	MAIG	NIGPAS	NHMW
Dolichoderinae				
Bothriomyrmecini				
<i>Ravavy</i> Fisher, 2009	1m		1m	
Tapinomini				
<i>Technomyrmex</i> Mayr, 1872		4w		1w
Dorylinae				
gen. indet.		1w		
Formicinae				
Plagiolepidini				
<i>Anoplolepis</i> Santshi, 1914	1w			
Myrmicinae				
Attini				
<i>Pheidole</i> Westwood, 1839	1w			
Crematogastrini				
<i>Cardiocondyla</i> Emery, 1869b		1w		
<i>Carebara</i> Westwood, 1840	5m	2m, 1w	5m	
<i>Cataulacus</i> Smith, 1853		1w		
<i>Melissotarsus</i> Emery, 1877	3w	4w	1m, 1w	
<i>Rhopalomastix</i> Forel, 1900			1aq, 1w	
<i>Trichomyrmex</i> Mayr, 1865	3m, 37w		1m, 2w	
gen. indet.			1m	
Solenopsidini				
<i>Monomorium</i> Mayr, 1855	11w	1m, 1w	1m	
Tribe incertae sedis				
gen. indet.	3m, 1w	2aq, 32m, 5w	1w	
Ponerinae				
Ponerini				
<i>Cryptopone</i> Emery, 1893		6m	1m	
<i>Hypoponera</i> Santshi, 1938		1m	1m	
<i>Euponera</i> ? Forel, 1891	2m			
gen. indet.	3m	12m, 1w	2m	
Pseudomyrmecinae				
<i>Tetraoponera</i> Smith, 1852			1w	
Subfamily incertae sedis				
gen. indet.	2m, 3w	17m, 2w		
	TOTAL, ants: 192			

806

807

1
2
3
4
5
6
7
8
9
10 808 SUPPORTING INFORMATION

11
12 809
13
14 810 Additional Supporting Information may be found in the online version of this article at the
15 811 publisher's website:

16
17 812
18
19 813 **Figure S1.** Animated 3D volume rendering of *Technomyrmex svojtakai*, holotype worker
20 814 NHMW-N6976.

21
22 815
23
24 816 **Figure S2.** Animated 3D volume rendering of *Technomyrmex svojtakai*, holotype worker
25 817 NHMW-N6976. Body view with legs removed.

26
27 818
28
29 819 **Appendix S1.** Measurement file and values for males of *Ravavy* species.
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54

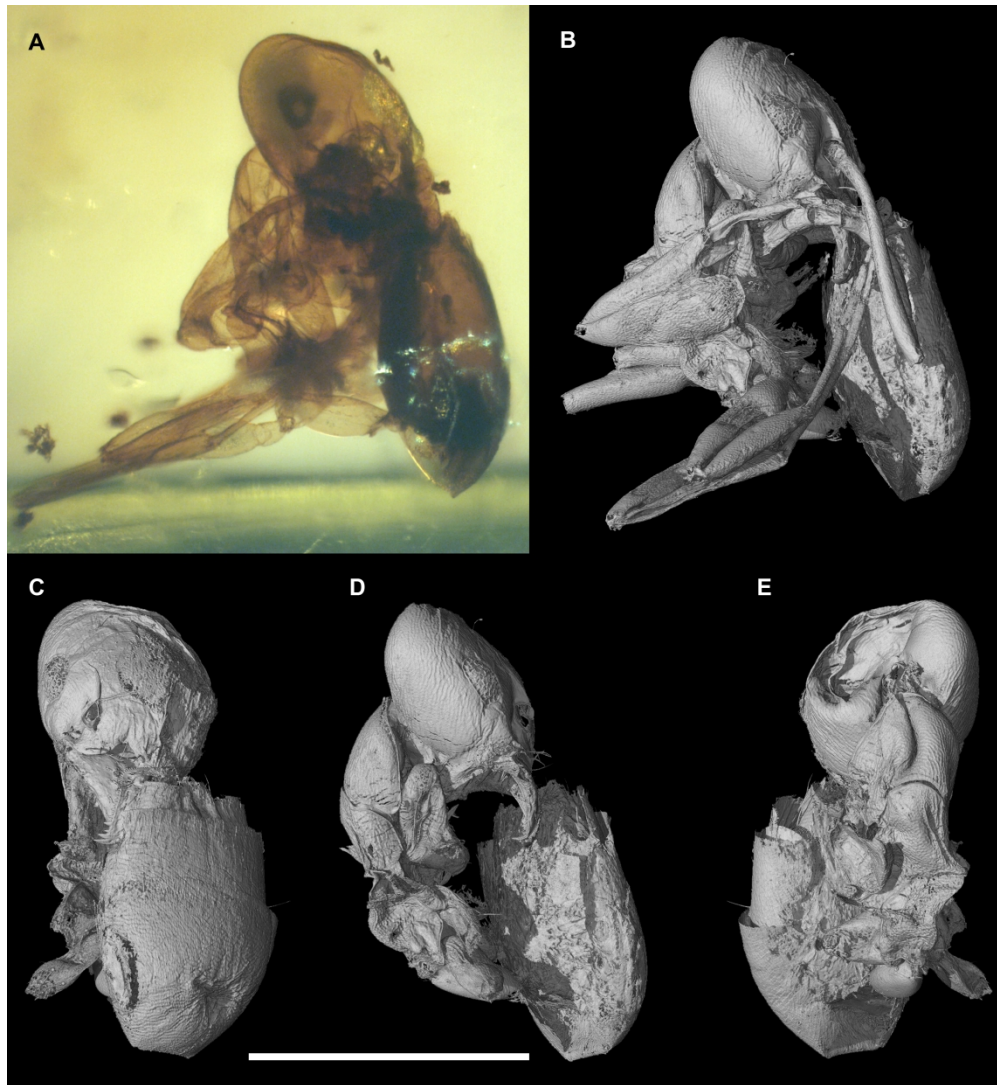


Figure 1. *Technomyrmex svojtkai* sp. nov., holotype worker NHMW-N6976. A, photomicrograph in right lateral view, with tip of gaster curled toward the mouthparts. B, 3D model in nearly the same position, imaged by synchrotron microtomography. C–E, 3D model of body with antennae and legs virtually removed. C, frontal view. D, left lateral view. E, posterior (dorsal) view. Scale bar: 0.5 mm. Animated versions of this are available in Supporting Information online (Figs. S1, S2).

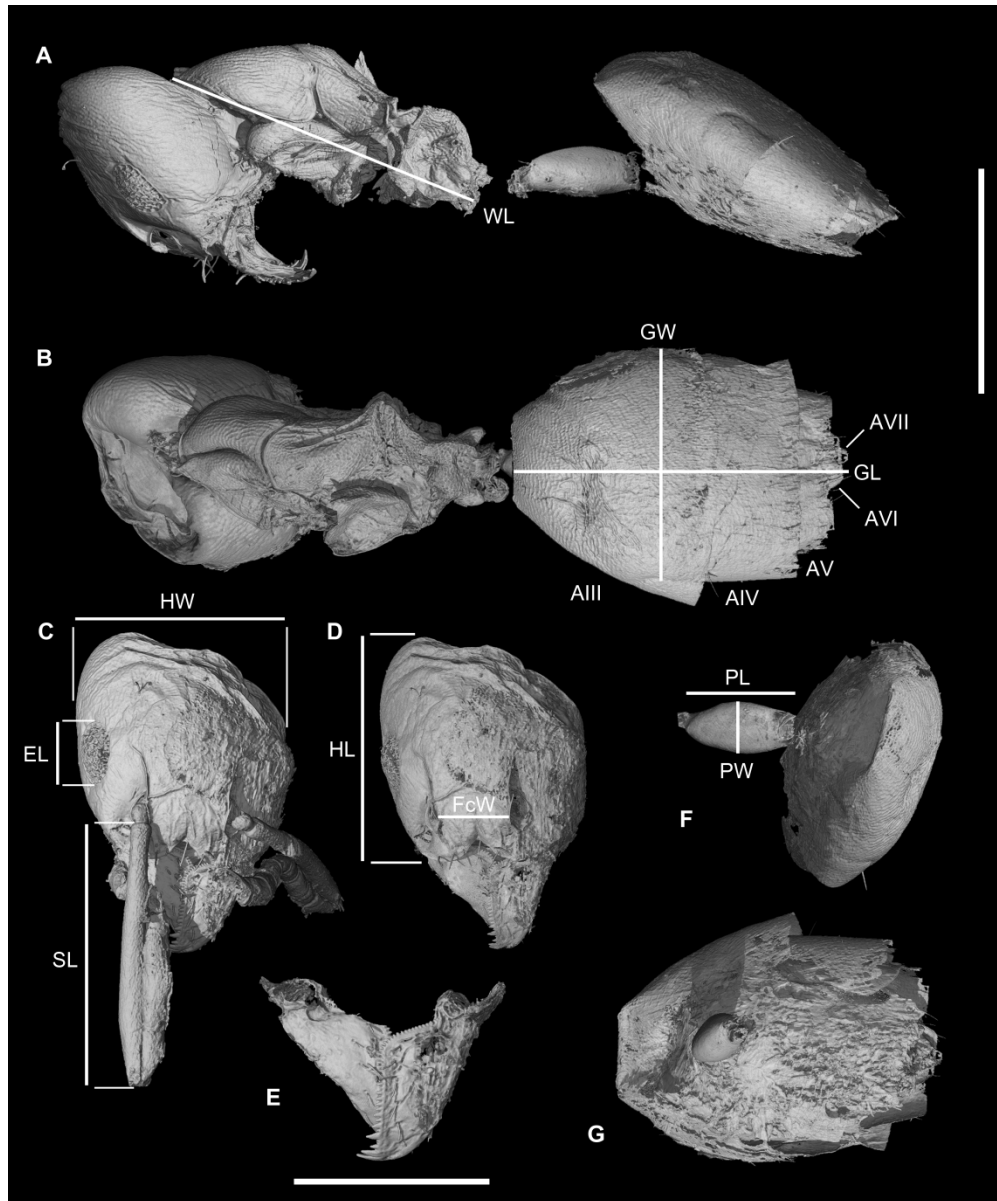


Figure 2. *Technomyrmex svojtkai* sp. nov. Phase contrast X-ray synchrotron microtomography of holotype worker NHMW-N6976, with indication of measurements as reported in Material and methods. A, lateral view of body with legs and antennae virtually removed, and with petiole and gaster virtually uncurled to approximate the life position. The left lateral side of the head and mesosoma being crushed, the figure shows them from the horizontally flipped right side in standard left profile view. B, reconstruction in dorsal view, without legs and antennae, and with gaster largely concealing the petiole as in approximate life position. C, head in full-face view. D, head without antennae in full-face view. E, mandibles in dorsal view. F, petiole in dorsal view, with articulation with gaster as preserved. G, gaster in dorsal view, with articulation with petiole as preserved, showing the first gastral tergite concavity for accommodation of petiole. Abbreviations: AIII–AVII, abdominal segments III to VII. Scale bars: 0.5 mm, except 0.2 mm for E.

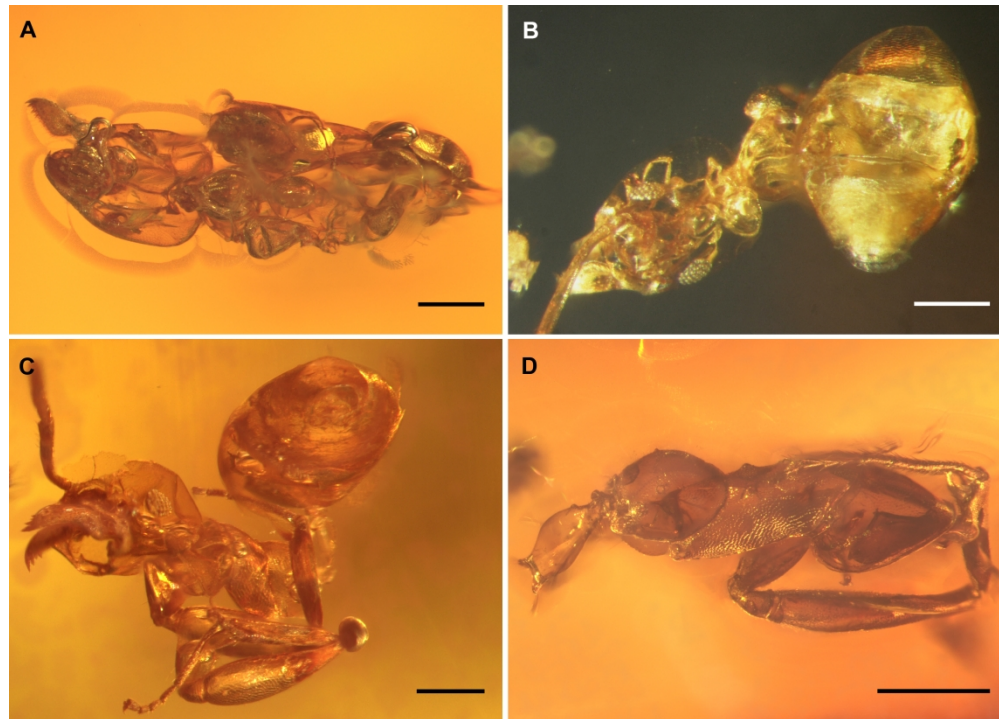


Figure 3. *Technomyrmex svojtkai* sp. nov., photomicrographs of paratype workers and additional, partial worker, specimen MAIG 6020. A, paratype 1, ventral view. B, paratype 2, dorsal view. C, paratype 2, left lateral view, anterior-oblique orientation. D, non-type, partially preserved worker, right lateral view. Scale bars: 0.25 mm.



Figure 4. *Ravavy goldmani* sp. nov., holotype male NIGP180512, photomicrographs. A, left lateral view, slightly anterior-oblique orientation. B, ventral view, slightly left-lateral-oblique orientation. Scale bars: 0.5 mm.

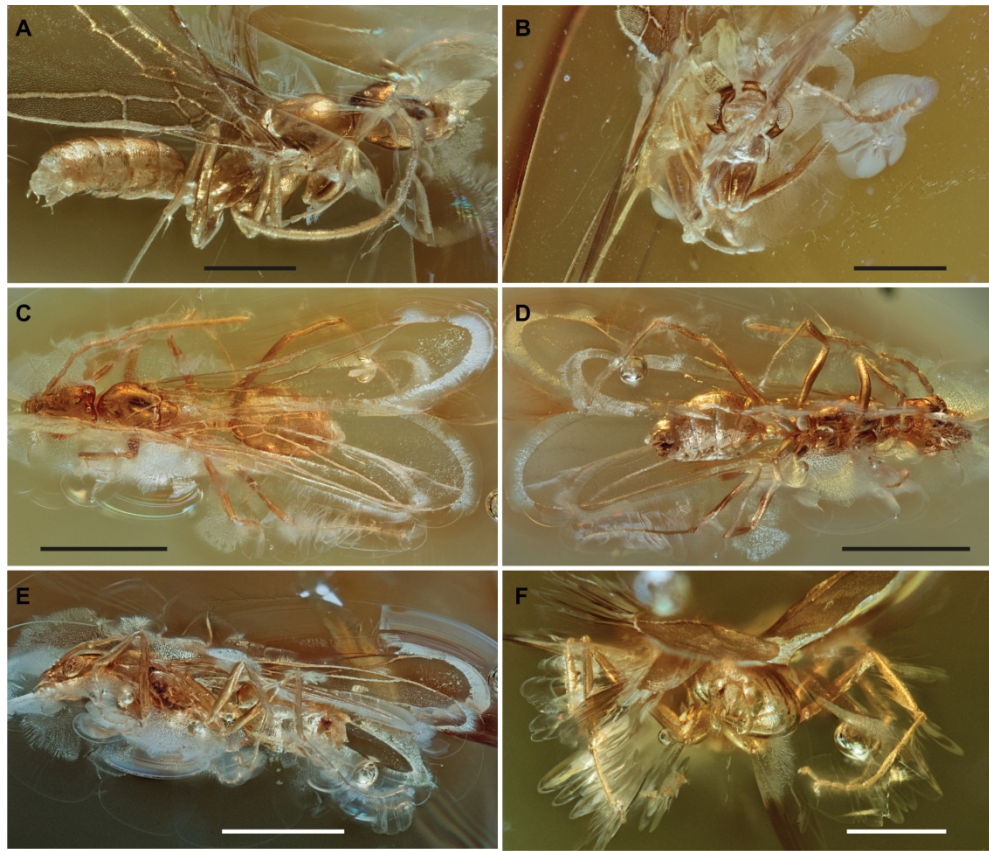


Figure 5. *Ravavy goldmani* sp. nov., photomicrographs. A–B, holotype male NIGP180512, C–F, paratype male IGR.ET2015/001a. A, right lateral view, slightly posterodorsal-oblique orientation. B, oral view, slightly right-lateral-oblique orientation. C, dorsal view, slightly right lateral, anterior oblique orientation. D, ventral view, slightly right-lateral, posterior oblique orientation. E, right lateral, slightly ventral, anterior oblique view. F, caudal view of genitalia, slightly right lateral oblique. Scale bars: 0.5 mm for A, B, F; 1.0 mm for C–E.