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

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

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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: <b><i>Technomyrmex svojtakai</i></b> Perrichot &amp; Engel <b>sp. nov.</b> and <b><i>Ravavy goldmani</i></b> Boudinot &amp; Perrichot <b>sp. nov.</b> 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>

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12 2 **filling gaps in the geological record of African terrestrial biota**  
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17 4 Running title: Ants from Miocene Ethiopian amber  
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51 25 [urn:lsid:zoobank.org:pub:35706103-4302-459E-A72F-769063E2DB21](http://zoobank.org/pub:35706103-4302-459E-A72F-769063E2DB21)]  
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## Abstract

The early Miocene (16–23 Mya) amber of Ethiopia constitutes a new source of fossil ants for Africa, where they are otherwise 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: *Technomyrmex svojtkai* Perrichot & Engel, sp. nov. and *Ravavy goldmani* Boudinot & Perrichot, sp. nov. The first is illustrated and described based on synchrotron-radiation microcomputed tomography, and the second represents the first fossil record for the tribe Bothriomyrmecini and *Ravavy*, 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.

Additional keywords:

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

## INTRODUCTION

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

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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

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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

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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  $\mu\text{m}$ , and a propagation distance of 145 mm between the sample and the detector. The

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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.  
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#### 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).  
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#### 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:  
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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.  
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- 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.

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- 174 PH Petiole height: the maximum height of petiole (abdominal segment 2), measured in  
profile view.
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- 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,  $\times 100$ .
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- 192 MI\* Mesoscutum index:  $MW/ML \times 100$ .
- 193 PI\* Petiolar index:  $PL/PH \times 100$ .
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## SYSTEMATIC PALAEOLOGY

FAMILY FORMICIDAE LATREILLE, 1809

SUBFAMILY DOLICHODERINAE FOREL, 1878

TRIBE TAPINOMINI EMERY, 1913

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199 GENUS *TECHNOMYRMEX* MAYR, 1872

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

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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

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10 224 six conspicuous teeth apically on masticatory margin; (7) counting from the apex, first tooth  
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12 225 longest, third and fifth teeth subequal in length, smaller than second and fourth, third to sixth  
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14 226 teeth each separated by one denticle, sixth tooth followed by a continuous series of smaller  
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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  
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32 235 well distant, closer to inner margin of eyes than to each other, not surpassing posterior margin  
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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  
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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  
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54 246 spiracles raised into distinct tubercles, conspicuously breaking outline of mesosoma in  
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56 247 lateral view, distinctly anterior to metanotal groove. Dorsal surface of propodeum flat,  
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58 248 declivitous surface convex. In profile, propodeal spiracle at junction of lateral and declivitous

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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

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10 274 *Technomyrmex* and *Tapinoma* Förster, 1850. The pygidium exposed in dorsal view, thus with  
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12 275 five gastral tergites visible, as is seen on the new fossil, warrants placement in *Technomyrmex*  
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14 276 (whereas the pygidium is reflexed ventrally, exposing only four gastral tergites in dorsal view  
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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-  
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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  
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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  
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33 286 defined by Bolton (2007).

34 288 TRIBE BOTHRIOMYRMECINI DUBOVIKOFF, 2005

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36 289 GENUS *RAVAVY* FISHER, 2009

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

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43 293 ***RAVAVY GOLDMANI* BOUDINOT & PERRICHOT SP. NOV.**

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45 294 (FIGS 4–5)

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

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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.*

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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.

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- 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”

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

7. The 6,3 palpomere count is an apparent synapomorphy of *Ravavy* within the Bothriomyrmecini. *Loweriella* has a plesiomorphic 6,4 count, while *Bothriomyrmex* and *Chronoxenus* share a derived, reduced count which is  $\leq 4,3$  (Bolton, 2003; Fisher, 2009; Yoshimura & Fisher, 2011).
8. The fine anatomy and morphology of *R. miafina* is illustrated in Fisher (2009) and especially Yoshimura & Fisher (2011). The latter work provided a revised diagnosis of this species plus a comparative analysis of genitalic form. Comparisons were made to the images in the literature, on AntWeb (2022), and to specimens examined at the California Academy of Sciences.

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

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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

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10 421 proximodorsal inflection point  $\sim 1 \times$  height. Fore- and hindwing venation virtually identical to

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

12 423 *Measurements and indices*. Dashes indicate metric could not be taken or calculated. Holotype:

13 424 BL  $\sim 2.34$ , HL 0.54, HW 0.41, HWE 0.50, EL 0.21, MSL 0.09, FcW –, SL –, OLL –, OIL –,

14 425 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,

15 426 HWI 122, MSI 6, SI –, OI 39, EPI –, OCI –, MI –, PI –. Paratype: BL  $\sim 2.57$ , HL 0.54, HW

16 427 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,

17 428 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 –,

18 429 MSI 6, SI –, OI 40, EPI –, OCI 38, MI 80, PI 80.

19 430 *Note*. For comparison, see the metrics for *R. miafina* provided below.

20 431

21 432 *RAVAVY MIAFINA* FISHER, 2009

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23 434 *Measurements and indices*. (N = 4, taken from CASENT0078664, CASENT0080308,

24 435 CASENT0115570, CASENT0474633.) BL ca. 3.33–4.46, HL 2.37–2.45, HW 1.84–1.91,

25 436 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–

26 437 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

27 438 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

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

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#### 441 DISCUSSION

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

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

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

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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- $\mu$ -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

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10 471 have yet to be recorded, we cannot provide further discussion on the specific relationship of  
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12 472 the fossil to modern lineages.

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

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

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10 520 assemblage examined. We will report on the species identities and morphological diversity of  
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12 521 further Ethiopian amber ants in future taxonomic treatments.

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765 **Figure captions**

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

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

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

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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.

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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.  
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22 796 **Figure 5.** *Ravavy goldmani* photomicrographs. A–B, holotype male NIGP180512, C–F,  
23 paratype male IGR.ET2015/001a. A, right lateral view, slightly posterodorsal-oblique  
24 797 orientation. B, oral view, slightly right-lateral-oblique orientation. C, dorsal view,  
25 798 slightly right lateral, anterior oblique orientation. D, ventral view, slightly right-lateral,  
26 799 posterior oblique orientation. E, right lateral, slightly ventral, anterior oblique view. F,  
27 800 caudal view of genitalia, slightly right lateral oblique. Scale bars: 0.5 mm for A, B, F;  
28 801 1.0 mm for C–E.  
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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
<b>Dolichoderinae</b>				
Bothriomyrmecini				
<i>Ravavy</i> Fisher, 2009	1m		1m	
Tapinomini				
<i>Technomyrmex</i> Mayr, 1872		4w		1w
<b>Dorylinae</b>				
gen. indet.		1w		
<b>Formicinae</b>				
Plagiolepidini				
<i>Anoplolepis</i> Santshi, 1914	1w			
<b>Myrmicinae</b>				
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	
<b>Ponerinae</b>				
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	
<b>Pseudomyrmecinae</b>				
<i>Tetraoponera</i> Smith, 1852			1w	
<b>Subfamily incertae sedis</b>				
gen. indet.	2m, 3w	17m, 2w		
	TOTAL, ants: 192			

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10 808 SUPPORTING INFORMATION

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

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

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

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27 818  
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29 819 **Appendix S1.** Measurement file and values for males of *Ravavy* species.  
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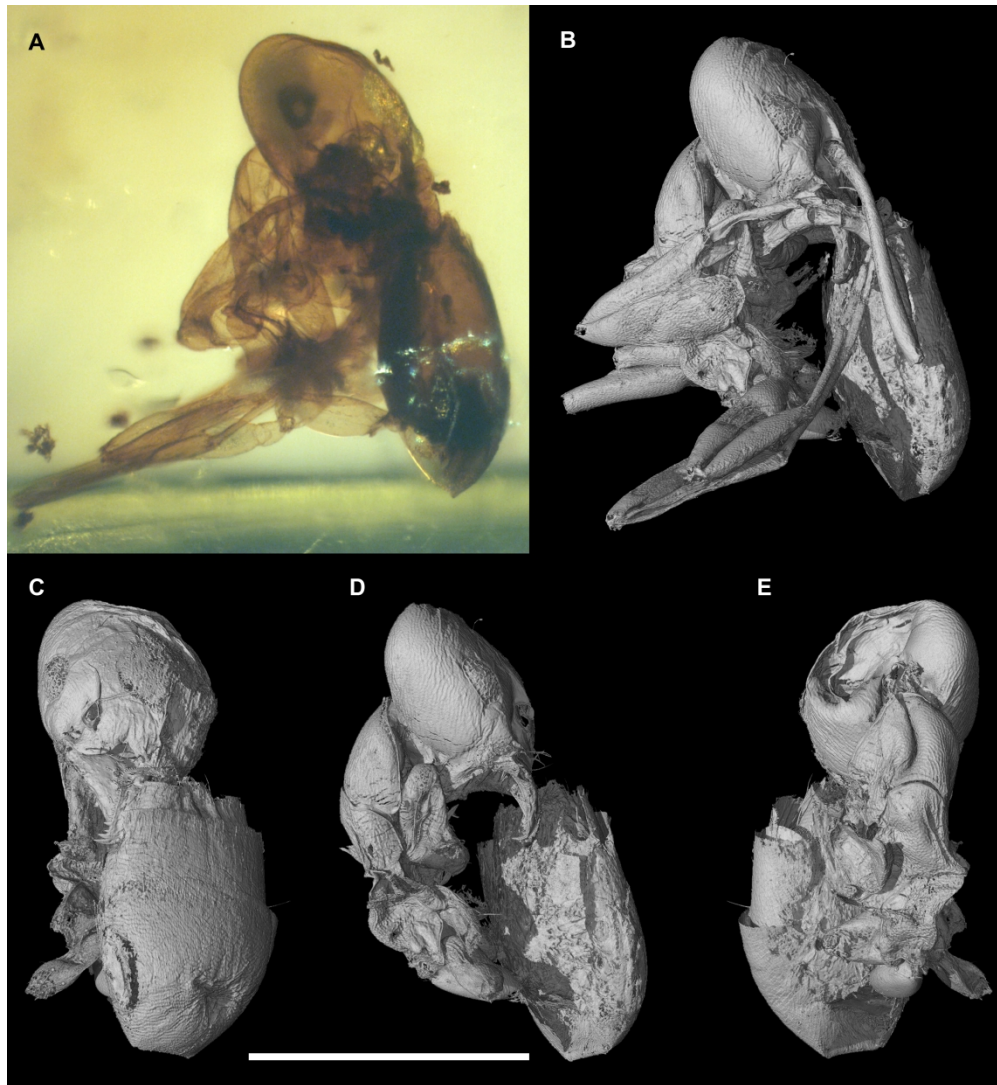


Figure 1. *Technomyrmex svojtkai* sp. nov., holotype worker NHMW-N6976. A, photomicrograph in right lateral view, with tip of gaster curled toward the mouthparts. B, 3D model in nearly the same position, imaged by synchrotron microtomography. C–E, 3D model of body with antennae and legs virtually removed. 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).

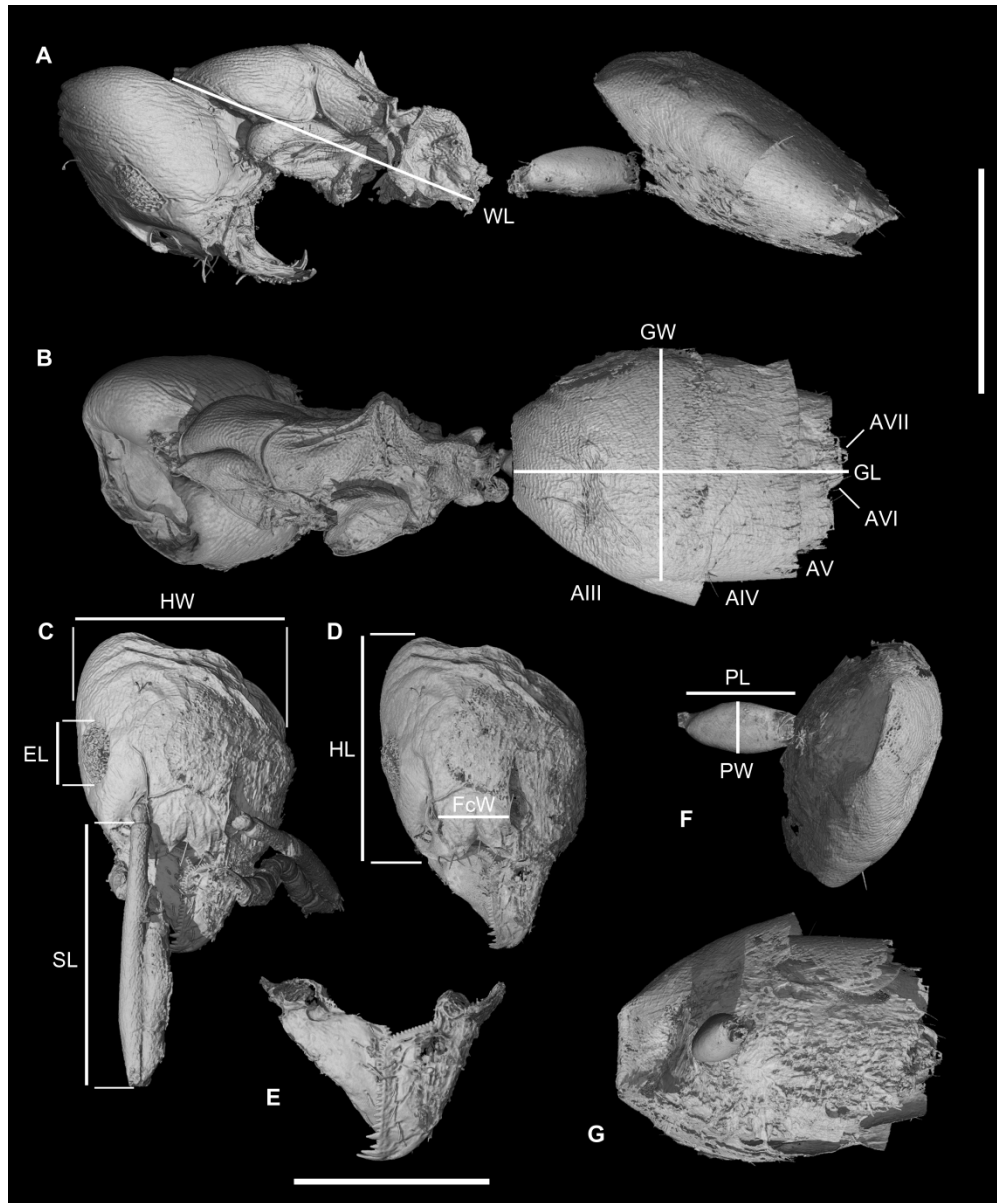


Figure 2. *Technomyrmex svojtkai* sp. nov. Phase contrast X-ray synchrotron microtomography of holotype worker NHMW-N6976, with indication of measurements as reported in Material and methods. A, lateral view of body with legs and antennae virtually removed, and with petiole and gaster virtually uncurled 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 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.

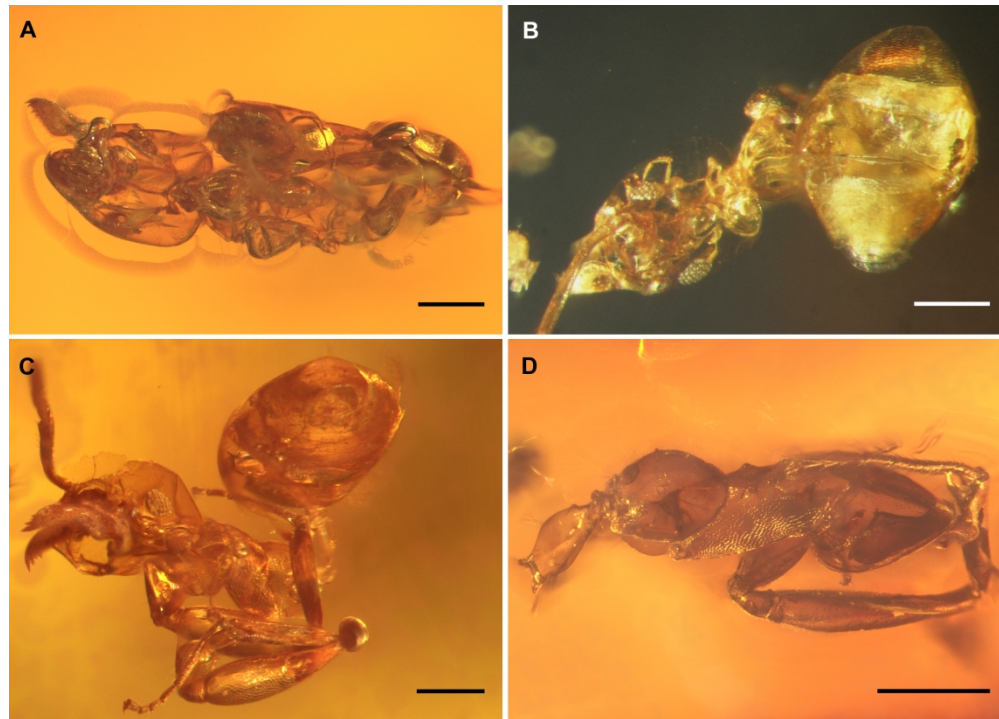


Figure 3. *Technomyrmex svojtkai* sp. nov., photomicrographs of paratype workers and additional, partial worker, specimen MAIG 6020. A, paratype 1, ventral view. B, paratype 2, dorsal view. C, paratype 2, left lateral view, anterior-oblique orientation. D, non-type, partially preserved worker, right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

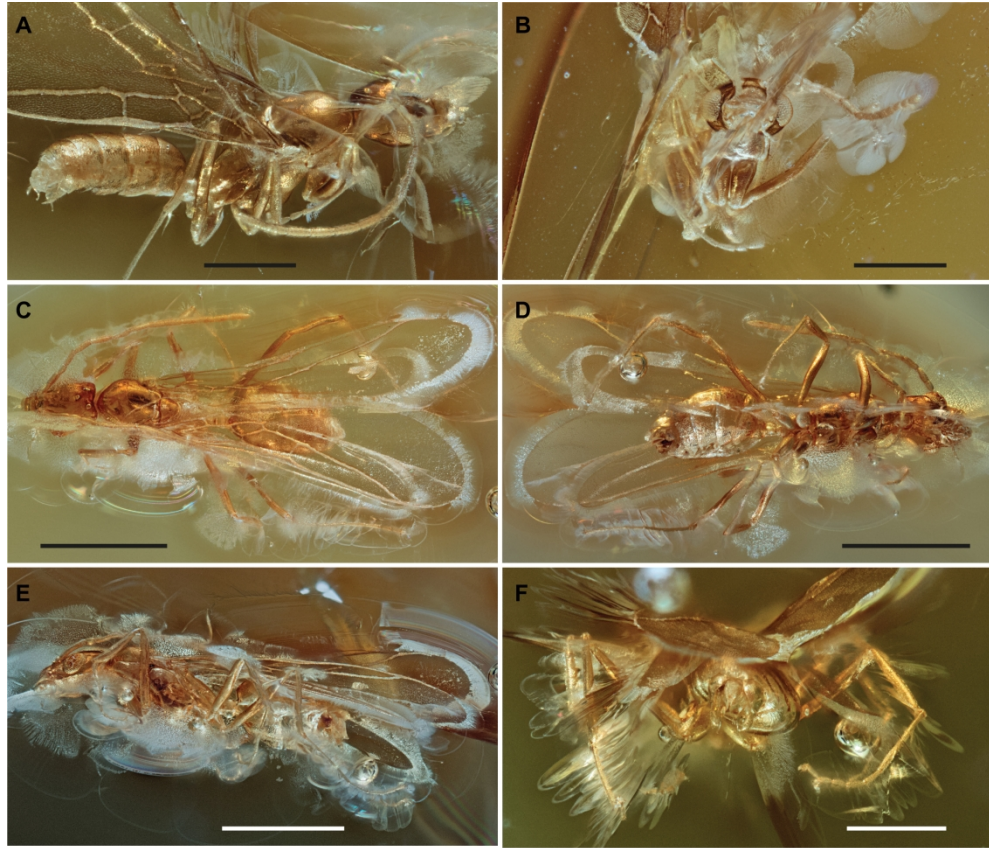


Figure 5. *Ravavy goldmani* sp. nov., photomicrographs. A–B, holotype male NIGP180512, C–F, paratype male IGR.ET2015/001a. A, right lateral view, slightly posterodorsal-oblique orientation. B, oral view, slightly right-lateral-oblique orientation. C, dorsal view, slightly right lateral, anterior oblique 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.