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► **To cite this version:**

Valentine Bouju, Corentin Jouault, Vincent Perrichot. The termite genus *Glyptotermes* (Isoptera: Kalotermitidae) in Miocene amber from Ethiopia. *Journal of Paleontology*, 2022, 96 (2), pp.387-393. 10.1017/jpa.2021.106 . insu-03435971

HAL Id: insu-03435971

<https://insu.hal.science/insu-03435971v1>

Submitted on 19 Nov 2021

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Journal of Paleontology



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UNIVERSITY PRESS**

**The termite genus *Glyptotermes* (Isoptera: Kalotermitidae)
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Journal:	<i>Journal of Paleontology</i>
Manuscript ID	JPA-RA-2021-0060.R2
Manuscript Type:	Regular Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Bouju, Valentine; Université de Rennes 1, Géosciences Jouault, Corentin; Université de Rennes 1, Géosciences; Muséum National d'Histoire Naturelle, Institut de Systématique, Evolution, Biodiversité (ISYEB) Perrichot, Vincent; Université de Rennes 1, Géosciences
Taxonomy:	Insecta, Blattodea < Insecta, Isoptera
Broad Geologic Time:	Neogene < Cenozoic
Detailed Geologic Time:	Miocene < Neogene
Subject area Geographic Location:	Africa, Ethiopia
Abstract:	A new species of drywood termite (Isoptera: Kalotermitidae) is described from a nearly complete alate specimen preserved in early Miocene Ethiopian amber. <i>Glyptotermes abyssinicus</i> n. sp., is distinguished by its U-shaped head with 12-segmented antennae, the ocelli separated from eye margin, the right mandible with obtuse angle between apical and first marginal teeth, the left mandible with obtuse angle between apical and first + second marginal teeth, and its wing venation. This is the first termite reported from Ethiopian amber, and the fourth Miocene species of the extant genus <i>Glyptotermes</i> , together with species previously described from diatomites of China and amber from the Dominican

	Republic. As the oldest report of the genus known from Africa, <i>G. abyssinicus</i> n. sp. constitutes an interesting new record for the biogeographical history of the kalotermitid lineage.

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1 **The termite genus *Glyptotermes* (Isoptera: Kalotermitidae) in Miocene**
2 **amber from Ethiopia**

3
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12
13 **Running Header:** New Miocene drywood termite

14
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17 is distinguished by its U-shaped head with 12-segmented antennae, the ocelli separated from eye
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24

25 UUID: <http://zoobank.org/7670b045-fb31-4809-8116-4d14c4dd275b>

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27

28 **Introduction**

29

30 The Kalotermitidae, also named drywood termites for their high tolerance to dry conditions, is a
31 monophyletic family consistently retrieved as sister to the Neoisoptera in recent molecular and
32 morphological phylogenetic analyses (Engel et al., 2009; Bourguignon et al., 2015; Legendre et al.,
33 2015; Bucek et al., 2019; Zhao et al., 2019; Jouault et al., 2021). While some discrepancies are
34 observed regarding the divergence time estimates of several isopteran constitutive families, depending
35 on the method or dataset used, molecular- and morphology-based analyses agree for an Early
36 Cretaceous appearance of the kalotermitids (Bourguignon et al., 2015; Bucek et al., 2019; Jouault et al.,
37 2021).

38 The comprehension of the Kalotermitidae have greatly benefited from the outstanding work of
39 Kumar Krishna who proposed the first phylogenetic hypothesis and described tens of new species and
40 genera, e.g., *Bifiditermes* Krishna, 1961, *Incisitermes* Krishna, 1961, *Postelectrotermes* Krishna, 1961,
41 and the fossil species *Incisitermes peritus* Engel and Krishna, 2007, or *Cryptotermes glaesarius* Engel
42 and Krishna, 2007.

43 The kalotermitids have a rather extensive fossil record, with 74 registered occurrences ranging
44 from the Cretaceous to Quaternary periods (<http://fossilworks.org/>). The oldest representative of the
45 family was described from the Brazilian Crato Formation, as *Cratokalotermes santanensis* Bechly,
46 2007, and the family seems to have diversified during the mid-Cretaceous, with various species

47 reported from Cenomanian Burmese amber (Cockerell, 1916, 1917; Engel et al., 2007; Poinar, 2009;
48 Zhao et al., 2021).

49 *Glyptotermes* Froggatt, 1897 is a cosmopolitan genus principally represented in tropical
50 environments and is the most speciose of kalotermitid genera, with at least 128 living species (Krishna
51 et al., 2013; Scheffrahn, 2021). *Glyptotermes* is commonly found infesting sound or rotting dry wood,
52 as well as wood scars in live trees (Scheffrahn et al., 2001; Engel and Krishna, 2007). Like all
53 kalotermitids, *Glyptotermes* reproductives are likely to be trapped in resin during their swarming flight
54 since they commonly land on tree trunks and rarely reach the ground, and in fact the genus is recorded
55 by the numerous wings and winged specimens mentioned from many deposits worldwide (Cowie et al.,
56 1990; Nel and Paicheler, 1993; Engel and Krishna, 2007; Krishna et al., 2013; Engel and Kaulfuss,
57 2017). As for many extant genera, the fossil record of *Glyptotermes* remains relatively scarce, with
58 only four species described: *G. grimaldii* Engel and Krishna, 2007, and *G. paleoliberatus* Engel and
59 Krishna, 2007, from early Miocene Dominican amber; *G. shandongianus* (Zhang, 1989), from Miocene
60 diatomitic deposits of Shanwang, China (Zhang, 1989; Zhang et al., 1994); and *G. pusillus* (Heer,
61 1849), from Pleistocene or younger East African copal (Heer, 1849; Snyder, 1949; Krishna et al.,
62 2013). The new specimen described herein represents the first fossil record of the genus, and one of the
63 very few fossil kalotermitids, from Africa.

64

65 **Material and methods**

66

67 The studied specimen is preserved in a piece of amber originating from a deposit located in the North
68 Shewa Zone of Ethiopia. The exact locality is unknown but is undoubtedly among the four localities
69 reported by Bouju et al. (2021, fig. 2), as the material was accessed through an amber trader from
70 Addis Ababa who obtains amber exclusively from those four localities. Apparently, the amber is dug

71 from the same geological layer in the four deposits. The amber bed corresponds to a siltstone situated
72 within a series of Pre-Oligocene to Miocene basalts and ignimbrite (Coulié et al., 2003; Kieffer et al.,
73 2004; Belay et al., 2009) that are exposed down the gorges of the Jema and Wenchit Rivers or their
74 tributaries (Bouju and Perrichot, 2020). Unfortunately, no radiometric age could be obtained from the
75 adjacent basaltic rocks sampled by two of us in 2019 from the locality of Woll (see Bouju et al., 2021:
76 fig. 2). However, the geological data, combined with studies of the amber chemistry, organismic
77 inclusions, and palynomorphs of the amber-bearing sediment, support an early Miocene age for the
78 amber (Bouju and Perrichot, 2020; Bouju et al., 2021).

79 The specimen was found preserved in syninclusion with a tiny chalcid wasp (Pteromalidae?) in
80 a piece of greenish amber. The raw amber piece was ground and polished using thin silicon carbide
81 papers for an optimal observation of the insect specimens in frontal, dorsal, and ventral views. The
82 amber piece was ultimately embedded in a block of epoxy resin (Araldite 2020) following the method
83 in Sadowski et al. (2021, fig. 8) for consolidation and long-term conservation. Photographs and
84 examination of the specimen were made using a Leica M205 C stereomicroscope equipped with a
85 Leica DMC4500 digital camera. The series of photographs taken at multiple focal planes were stacked
86 using Helicon Focus 6.7 software. Illustrations were made using Adobe Illustrator and Photoshop CC
87 2019 softwares. We follow the morphological terminology and classification of termites as presented in
88 Krishna et al. (2013), except for the wing venation that follows Schubnel et al. (2019).

89

90 *Repository and institutional abbreviations.*—The type specimen examined in this study is deposited in
91 the amber collection of the Geological Department and Museum of the University of Rennes (IGR),
92 France, under the registration number IGR.ET2020/017.

93

94 **Systematic paleontology**

95 Order Blattodea Brunner von Wattenwyl, 1882

96 Infraorder Isoptera Brullé, 1832

97 Family Kalotermitidae Froggatt, 1897

98 Genus *Glyptotermes* Froggatt, 1897

99
100 *Type species.*—*Glyptotermes tuberculatus* Froggatt, 1897 by subsequent designation in Snyder, 1949:

101 45.

102
103 *Glyptotermes abyssinicus* new species

104 Figures 1–3

105

106 *Holotype.*—One alate specimen, IGR.ET2020/017, in amber from the lower Miocene (16–23 Ma) of
107 the North Shewa Zone, Amhara and Oromia regions, Northwestern Plateau of Ethiopia.

108

109 *Diagnosis.*—Head U-shaped in posterodorsal view; eyes small, sub-circular and feebly protruding from
110 head laterally; ocelli distinctly separated from eye margin, longest obliquely; antenna 12-segmented,
111 AII longer than AIII, AIII subequal to slightly shorter than AIV; left mandible with apical tooth stout,
112 angle between apical and first + second marginal teeth right to nearly obtuse; right mandible with long,
113 stout apical tooth, angle between apical and first marginal teeth obtuse; fore wing scale not fully
114 overlapping hind wing scale; fore wing with Sc and RA short, RP long with two anterior branches, M
115 sclerotized, running very close to and parallel to RP to reach wing apex, with faint cross-veins between
116 M and radial sector, CuA with at least 8–9 posterior branches.

117

118 *Description*.—Body 3.8 mm long (from tip of labrum to abdomen apex), 7.0 mm with wings (Fig. 1).
119 Head (Fig. 2.1, 2.2) prognathous, 1.1 mm long and 0.65 mm wide excluding compound eyes, with
120 straight sides, anterolateral corners slightly angulate, posterolateral corners rounded; compound eye
121 sub-circular, slightly wider than long, ca. 0.25 mm wide, protruding from head, separated from
122 posterior head margin by more than its length; ocelli white, ovoid (about 0.06 mm long and 0.05 mm
123 wide), located above eye mid-length, very close to but not touching eye margin; fontanelle absent;
124 antenna (Fig. 2.2) moniliform, with 12 antennomeres, AII longer than AIII, AIII subequal to slightly
125 shorter than AIV, AIV shorter than AV, following antennomeres progressively increasing in length
126 toward apex; left mandible with slightly obtuse to nearly right angle between apical and first + second
127 marginal teeth, third marginal tooth hidden; right mandible with obtuse angle between apical and first
128 marginal teeth; maxillary palps hidden by labial palps in frontal view; labial palps with 3 segments
129 (Fig. 2.3); labrum about 0.18 mm long and 0.24 mm wide, posterior margin convex, anterior margin
130 straight or nearly so; postclypeus slightly raised medially (Fig. 2.1, 2.3), rectangular and conspicuously
131 wider than long (about 0.24 mm wide and 0.06 mm long).

132 Pronotum (Fig. 2.5) flat to slightly arched in lateral view, anterior margin slightly concave,
133 sides rounded, slightly narrower than head. Legs slender; profemur *ca.* 0.5 mm long, protibia *ca.* 0.4
134 mm long, protarsus at least 0.2 mm long; protibia with three spurs f1, f2, f3; mesofemur *ca.* 0.5 mm
135 long, mesotibia *ca.* 0.5 mm long, mesotarsus at least 0.4 mm long; mesotibia with three spurs m1, m2,
136 m3 (Fig. 2.6); metafemur *ca.* 0.5 mm long, metatibia *ca.* 0.8 mm long, metatarsus at least 0.4 mm long;
137 metatibia with three spurs h1, h2, h3; no additional spine on meso- and metatibiae; tarsi tetramerous,
138 with apical tarsomere as long as or slightly longer than combined length of preceding ones (Fig. 2.7);
139 arolium present (Fig. 2.8).

140 Wings (Fig. 3.1–3.5) 4.75 mm long (measured from suture to apex), membrane reticulate; fore
141 wing scale 0.75 mm long, not covering hind wing scale, with humeral margin nearly straight, claval
142 suture (CuP) straight, slightly curved distally, basal suture straight; fore wing with M and CuA veins

143 arising independently from inside the wing scale; Sc short and simple; RA and RP fused basally, RA
144 short, RP long with 2 anterior branches or fusion point with C; M sclerotized, running to wing apex,
145 close and parallel to RP, with at least 1 anterior, short branch located near wing apex, and maybe two
146 unsclerotized anterior branches located respectively in basal and apical wing third; CuA unsclerotized,
147 with 8–9 posterior branches and maybe two unsclerotized anterior branches; hind wing not describable;
148 anal lobe absent on both wings.

149 Abdomen not fully preserved, ca. 1.4 mm long, with at least 6 to 7 observable segments (Fig.
150 1.1); abdominal segments apparently widest at mid-length. Cerci and styli not visible.

151 *Etymology*.—The specific epithet *abyssinicus* refers to the Abyssinian origin of the amber piece.

152

153 *Remarks*.—The new fossil does not fit in the early diverged termite families, including the extinct
154 Cratomastotermitidae and Termopsidae, since it combines the following series of derived characters: a
155 reduced wing venation (vs. more complete, RP with at least several branches and no costalisation of
156 veins in early diverged families), 4-segmented tarsi (vs. 5-segmented, plesiomorphic character), a
157 reduced tibial spur formula 3-3-3 (vs. enriched with additional spurs along tibiae), and a head wider
158 than pronotum (vs. smaller than pronotum). Compared to most of the other families, the fossil lacks a
159 fontanelle (apomorphic character of the Neoisoptera; Krishna et al. 2013). Following the key to the
160 families based on imago characters by Krishna et al. (2013, p. 69), the new fossil keys out in the
161 Kalotermitidae for its hind wing without anal lobe, tarsi 4-segmented, antenna 12-segmented,
162 fontanelle absent, fore wing scale not overlapping hind wing scale, ocelli present, and pronotum flat.
163 Using the key to the kalotermitid genera of Krishna et al. (2013: p. 75–76), the new fossil species keys
164 out either in *Glyptotermes*, *Calcaritermes* Snyder, 1925, or *Proneotermes* Holmgren, 1911, depending
165 on character states detailed in the sixth and thirteenth couplets but invisible on the fossil, i.e., the left
166 mandibular portion posterior to the first + second marginal tooth. However, the specimen differs from
167 *Calcaritermes* and *Proneotermes* by the 12 antennomeres (vs. 13–14 in *Calcaritermes*, 17–18 in

168 *Proneotermes*). Additionally, it differs from *Proneotermes* but concords with *Glyptotermes* by the
169 small eye diameter (0.25 mm vs. 0.39–0.43 mm in *Proneotermes*) and the fore wing with M as heavily
170 sclerotized as the radial sector, running very close to and parallel to the radial sector to reach apex of
171 wing, with faint branches between M and radial sector, and radial sector very close to costal vein.

172 *Glyptotermes abyssinicus* n. sp. can be distinguished from the extant Neotropical and African
173 *Glyptotermes* species, by the combination of characters stated in the diagnosis. More precisely, *G.*
174 *abyssinicus* n. sp. differs from *G. adamsoni* Krishna and Emerson, 1962, *G. sicki* Krishna and Emerson,
175 1962, or the African *G. sinomalatus* Krishna and Emerson, 1962, by a U-shaped head (vs. circular or
176 semi-circular in the other species). It differs from other species by the 12-segmented antennae (vs. 11-
177 segmented in *G. marlatti* (Snyder, 1926) and *G. planus* (Snyder, 1925); more than 12-segmented in *G.*
178 *amplus* Scheffrahn et al., 2001, *G. kawandae* Wilkinson, 1954, or *G. longisculus* Krishna and
179 Emerson, 1962.

180 *Glyptotermes abyssinicus* n. sp. can also be distinguished from other species by the antennae
181 with AII longer than AIII (vs. AII shorter than AIII in *G. asperatus* (Snyder, 1926), *G. ignotus*
182 Wilkinson, 1959, or *G. tuberifer* Krishna and Emerson, 1962; by measurements such as the body, head
183 and wing length (*G. rotundifrons* Krishna and Emerson, 1962 and *G. suturis* (Snyder, 1925) are larger
184 species with wider head and pronotum, and longer fore wings; *G. contracticornis* (Snyder, 1925) and
185 *G. longipennis* Krishna and Emerson, 1962 are about twice as large as *G. abyssinicus* n. sp.); by the
186 ocelli separated from the eye margin (vs. ocelli touching eye margin in *G. jurioni* Krishna and
187 Emerson, 1962, *G. parki* Krishna and Emerson, 1962, *G. parvoculatus* Krishna and Emerson, 1962 or
188 *G. truncatus* Krishna and Emerson, 1962.

189 Finally, *Glyptotermes abyssinicus* n. sp. differs from the fossil species *G. grimaldii* Engel and
190 Krishna, 2007 and *G. paleoliberatus* Engel and Krishna, 2007 by a smooth head capsule (vs. granulose)
191 and the ocelli separated from the eye margin (vs. touching). The old description of *G. pusillus* (Heer,
192 1849), from East African copal, challenges its comparison with the other *Glyptotermes* species.

193 However, it is clear that our specimen does not belong to *G. pusillus* owing to the differential of
194 temporal range (Pleistocene vs. Early Miocene).

195 **Discussion**

196

197 The genus *Glyptotermes* has a worldwide distribution with a higher diversity in tropical areas
198 (Scheffrahn et al., 2001; Krishna et al., 2013; Debelo and Degaga, 2014; Yashiro et al., 2019;
199 Scheffrahn, 2021). Our current knowledge on the *Glyptotermes* fossil record, and its correlation with
200 the distribution of the extant representatives of the genus, seems to indicate that *Glyptotermes* was also
201 widely distributed in the tropical region during the Miocene period and may have experimented
202 successive dispersal events during older geological periods (Krishna and Emerson, 1962; Emerson,
203 1969; Nel and Paicheler, 1993; Engel and Krishna, 2007).

204 The kalotermitids are generally of particular importance in extant and past ecosystems due to
205 their biology. In fact, they are the only termites that do not need to construct their nest in contact with
206 soil (a direct adaptation from their high tolerance to dryness). The kalotermitids can live exclusively
207 within the wood and participate in its active degradation by consuming the trunk in which they
208 construct their nest. Extant *Glyptotermes* species, however, are very tolerant to environmental
209 conditions and can live in swamp forests or mangroves (Johnson et al., 1980; Tho, 1992). And
210 according to Scheffrahn (2021), extant, Neotropical '*Glyptotermes* species have a rather high wood
211 moisture requirement and, therefore, are not found in arid parts of the Neotropics'. The same was likely
212 true for the Miocene species newly described here, as this accords with indications of a generally
213 humid, tropical, forest environment with freshwater suggested by the palynomorphs associated with
214 Ethiopian amber as well as by other organismal inclusions in amber (Bouju and Perrichot, 2020; Bouju
215 et al., 2021).

216

217 **Conclusion**

218

219 Although Isoptera are relatively well known from the fossil record, numerous fossil species have been
220 described based on compression or imprint fossils of isolated wings, challenging placements and
221 questioning some systematic attributions (Krishna et al., 2013). The present description of a nearly
222 complete, three-dimensional, *Glyptotermes* specimen provides elements for more comprehensive,
223 morphological-based phylogenetic studies. Additionally, *Glyptotermes abyssinicus* n. sp. can be
224 considered as the oldest and first « true » *Glyptotermes* fossil from Africa. This discovery confirms the
225 presence of the genus since the Miocene period and will allow further inference on the biogeographical
226 history of the genus. The genus *Chilgatermes* Engel et al., 2013 (Stolotermitidae), described from an
227 Oligocene imprint fossil, was hitherto the only fossil termite known from Ethiopia. Therefore, the
228 description of *Glyptotermes abyssinicus* n. sp. extends our knowledge of the Isoptera fossil diversity in
229 Ethiopia.

230

231 **Acknowledgments**

232 We are grateful to Yale Goldman, Bloomfield, Connecticut, who provided the Ethiopian amber piece
233 studied here. We thank Amde Zewdalem, Jacksonville, Florida, and Benyam Teferi, Addis Ababa,
234 Ethiopia, for information and access to the amber deposits of the North Shewa Zone, Ethiopia; and the
235 reviewers and editor for their helpful comments. Partial support for this work was provided by the
236 Tellus-INTERRVIE programme of CNRS INSU (project AMBRAFRICA to V. Perrichot, 2019),
237 enabling field work in Ethiopia for V. Bouju and V. Perrichot.

238

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356 **Figure captions**

357

358 **Figure 1.** *Glyptotermes abyssinicus* n. sp., holotype IGR.ET2020/017, from early Miocene Ethiopian
359 amber. (1) Habitus in dorsal view; (2) habitus in ventral view. Scale bars = 1 mm.

360

361 **Figure 2.** *Glyptotermes abyssinicus* n. sp., holotype IGR.ET2020/017, from early Miocene Ethiopian
362 amber. (1) Head in dorsal view; (2) left antenna in dorsal view; (3) mouthparts in frontal view; (4)
363 line drawing of mandibles in frontal view; (5) pronotum in anterodorsal view; (6) right mesotibia in
364 ventral view; (7) left mesotarsus in ventral view; (8) right protarsus in ventral view. I–IV =
365 tarsomeres 1–4; AII–AV = antennomeres 2–5; ar = arolium; la = left mandible apical tooth; lbr =
366 labrum; lm1+2 = left mandible 1st + 2nd marginal tooth; lp = labial palp; m1, m2, m3 = mesotibial
367 spurs 1–3; mp = maxillary palp; oc = ocellus; pc = postclypeus; ra = right mandible apical tooth;
368 rm1 = right mandible 1st marginal tooth. Scale bars = 25 μm (4), or 100 μm (6–8), or 125 μm (1–3,
369 5).

370

371 **Figure 3.** *Glyptotermes abyssinicus* n. sp., holotype IGR.ET2020/017, from early Miocene Ethiopian
372 amber. (1) Right hind and fore wing bases in dorsal view; (2) line drawing of right wing scales in
373 dorsal view; (3) left fore wing scale in dorsal view; (4) left fore wing in dorsal view; (5) explanatory
374 drawing of fore wing venation. BS = basal suture; CuA = anterior cubital vein; CuP = claval suture;
375 fsc = fore wing scale; hsc = hind wing scale; M = medial vein; RA = anterior radial vein; RP =
376 posterior radial vein; Sc = subcostal vein. Scale bars = 250 μm (1–3), or 750 μm (4, 5).

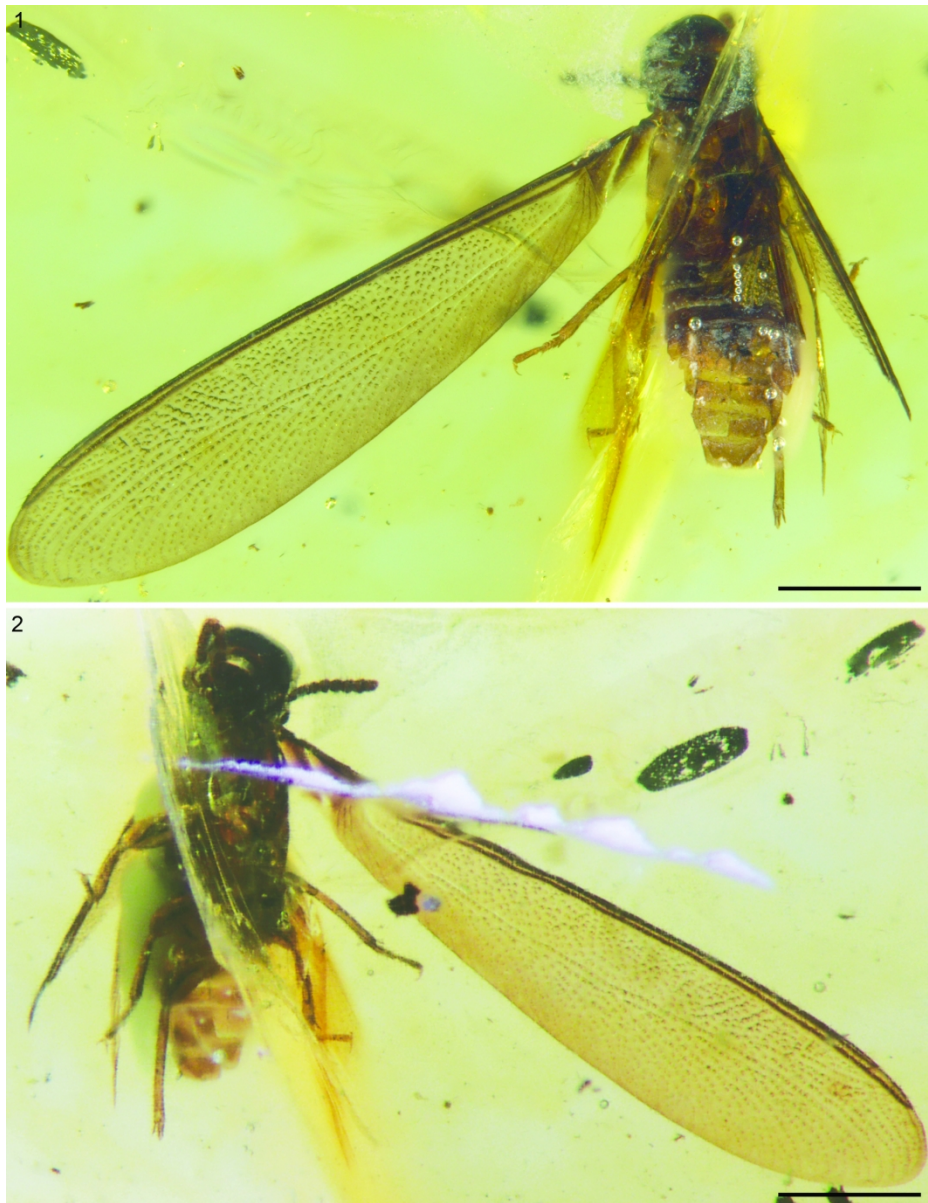


Figure 1. *Glyptotermes abyssinicus* n. sp., holotype IGR.ET2020/017, from early Miocene Ethiopian amber. (1) Habitus in dorsal view; (2) habitus in ventral view. Scale bars = 1 mm.

170x218mm (300 x 300 DPI)

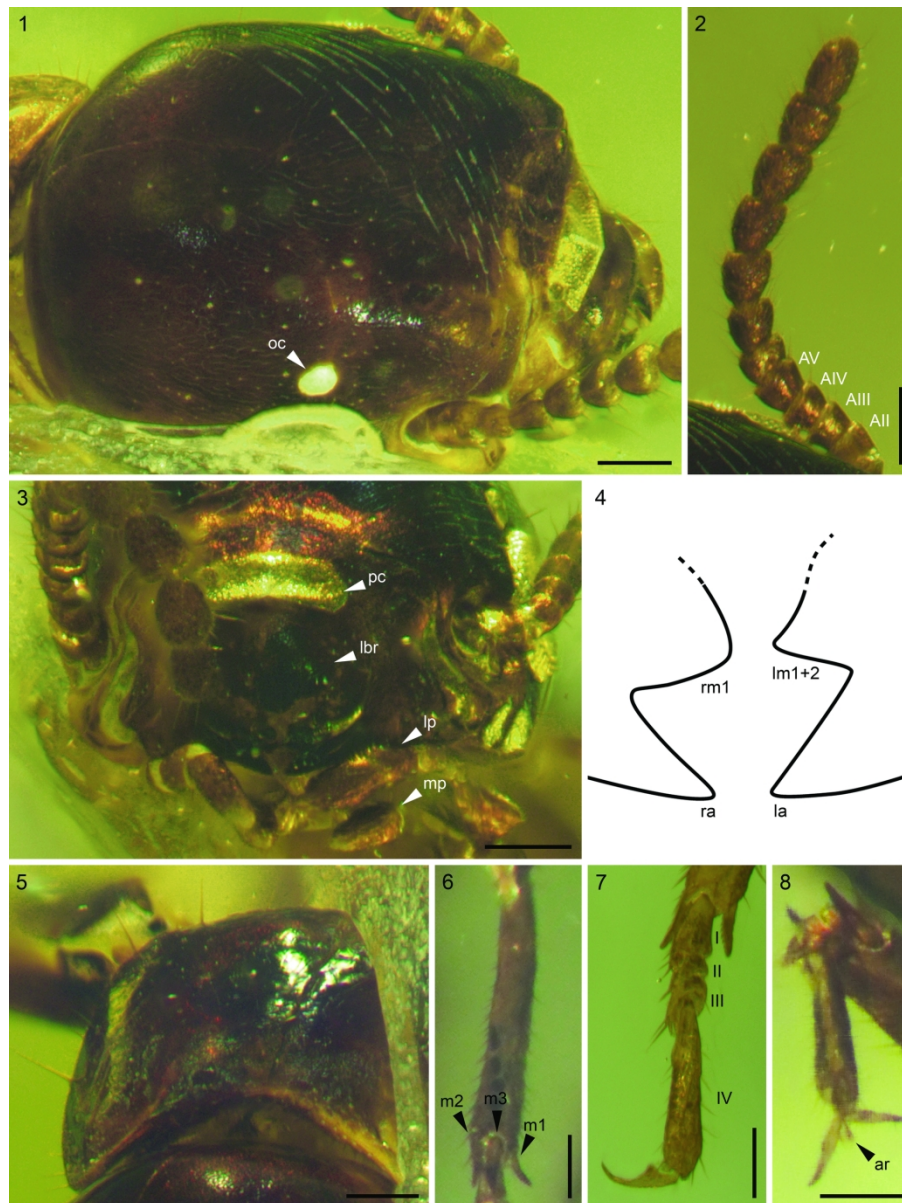


Figure 2. *Glyptotermes abyssinicus* n. sp., holotype IGR.ET2020/017, from early Miocene Ethiopian amber. (1) Head in dorsal view; (2) left antenna in dorsal view; (3) mouthparts in frontal view; (4) line drawing of mandibles in frontal view; (5) pronotum in anterodorsal view; (6) right mesotibia in ventral view; (7) left mesotarsus in ventral view; (8) right protarsus in ventral view. I–IV = tarsomeres 1–4; AII–AV = antennomeres 2–5; ar = arolium; la = left mandible apical tooth; lbr = labrum; lm1+2 = left mandible 1st + 2nd marginal tooth; lp = labial palp; m1, m2, m3 = mesotibial spurs 1–3; mp = maxillary palp; oc = ocellus; pc = postclypeus; ra = right mandible apical tooth; rm1 = right mandible 1st marginal tooth. Scale bars = 125 μ m (1–3, 5), or 100 μ m (6–8).

170x225mm (300 x 300 DPI)

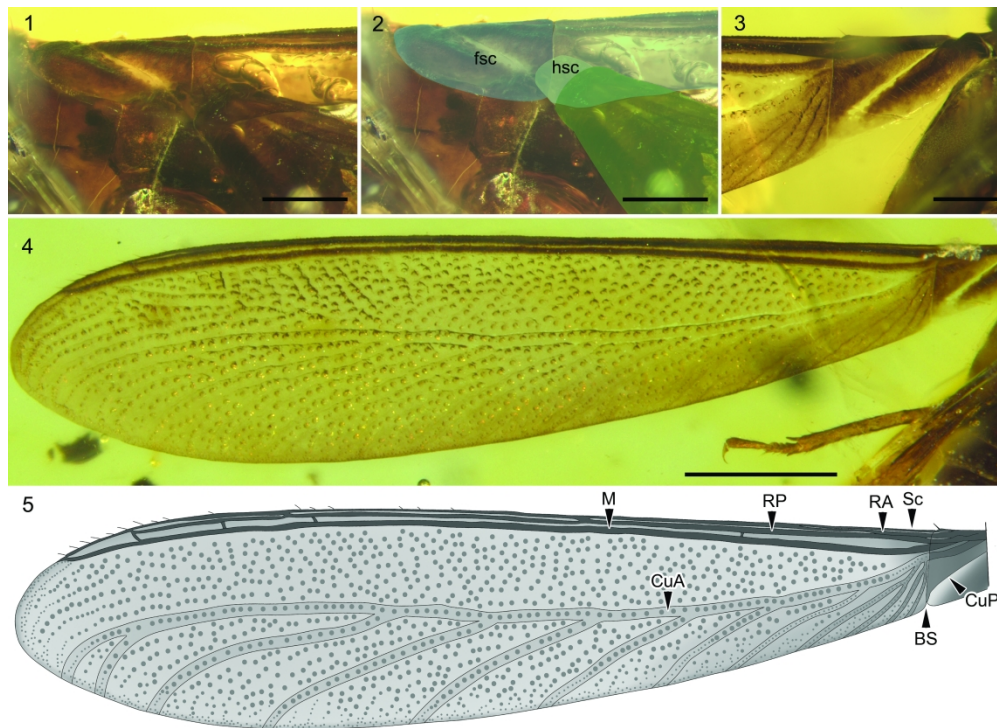


Figure 3. *Glyptotermes abyssinicus* n. sp., holotype IGR.ET2020/017, from early Miocene Ethiopian amber. (1) Right hind and fore wing bases in dorsal view; (2) same as 1, but colour-marked to highlight the wing scales; (3) left fore wing scale in dorsal view; (4) left fore wing in dorsal view; (5) explanatory drawing of fore wing venation. BS = basal suture; CuA = anterior cubital vein; CuP = claval suture; fsc = fore wing scale; hsc = hind wing scale; M = medial vein; RA = anterior radial vein; RP = posterior radial vein; Sc = subcostal vein. Scale bars = 250 μ m (1–3), or 750 μ m (4).

179x133mm (600 x 600 DPI)