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

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

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Running Header: New Miocene drywood termite

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Introduction

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

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

The kalotermitids have a rather extensive fossil record, with 74 registered occurrences ranging from the Cretaceous to Quaternary periods (http://fossilworks.org/). The oldest representative of the family was described from the Brazilian Crato Formation, as *Cratokalotermes santanensis* Bechly, 2007, and the family seems to have diversified during the mid-Cretaceous, with various species reported from Cenomanian Burmese amber (Cockerell, 1916, 1917; Engel et al., 2007; Poinar, 2009; Zhao et al., 2021).

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

Material and methods

The studied specimen is preserved in a piece of amber originating from a deposit located in the North Shewa Zone of Ethiopia. The exact locality is unknown but is undoubtedly among the four localities reported by Bouju et al. (2021, fig. 2), as the material was accessed through an amber trader from Addis Ababa who obtains amber exclusively from those four localities. Apparently, the amber is dug from the same geological layer in the four deposits. The amber bed corresponds to a siltstone situated within a series of Pre-Oligocene to Miocene basalts and ignimbrite (Coulié et al., 2003; Kieffer et al., 2004; Belay et al., 2009) that are exposed down the gorges of the Jema and Wenchit Rivers or their tributaries (Bouju and Perrichot, 2020). Unfortunately, no radiometric age could be obtained from the adjacent basaltic rocks sampled by two of us in 2019 from the locality of Woll (see Bouju et al., 2021: fig. 2). However, the geological data, combined with studies of the amber chemistry, organismic inclusions, and palynomorphs of the amber-bearing sediment, support an early Miocene age for the amber (Bouju and Perrichot, 2020; Bouju et al., 2021).

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

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

Systematic paleontology

Order Blattodea Brunner von Wattenwyl, 1882

Infraorder Isoptera Brullé, 1832

Family Kalotermitidae Froggatt, 1897

Genus *Glyptotermes* Froggatt, 1897

Type species.—*Glyptotermes tuberculatus* Froggatt, 1897 by subsequent designation in Snyder, 1949: 45.

Glyptotermes abyssinicus new species

Figures 1–3

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

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

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

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

Wings (Fig. 3.1–3.5) 4.75 mm long (measured from suture to apex), membrane reticulate; fore wing scale 0.75 mm long, not covering hind wing scale, with humeral margin nearly straight, claval suture (CuP) straight, slightly curved distally, basal suture straight; fore wing with M and CuA veins arising independently from inside the wing scale; Sc short and simple; RA and RP fused basally, RA short, RP long with 2 anterior branches or fusion point with C; M sclerotized, running to wing apex, close and parallel to RP, with at least 1 anterior, short branch located near wing apex, and maybe two unsclerotized anterior branches located respectively in basal and apical wing third; CuA unsclerotized, with 8–9 posterior branches and maybe two unsclerotized anterior branches; hind wing not describable; anal lobe absent on both wings.

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

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

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

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

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

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

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

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

Discussion

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

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

Conclusion

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

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Figure captions

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.

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 = 25 µm (**4**), or 100 µm (**6–8**), or 125 µm (**1–3, 5**).

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**) line drawing of right wing scales in dorsal view; (**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 µm (**1–3**), or 750 µm (**4, 5**).

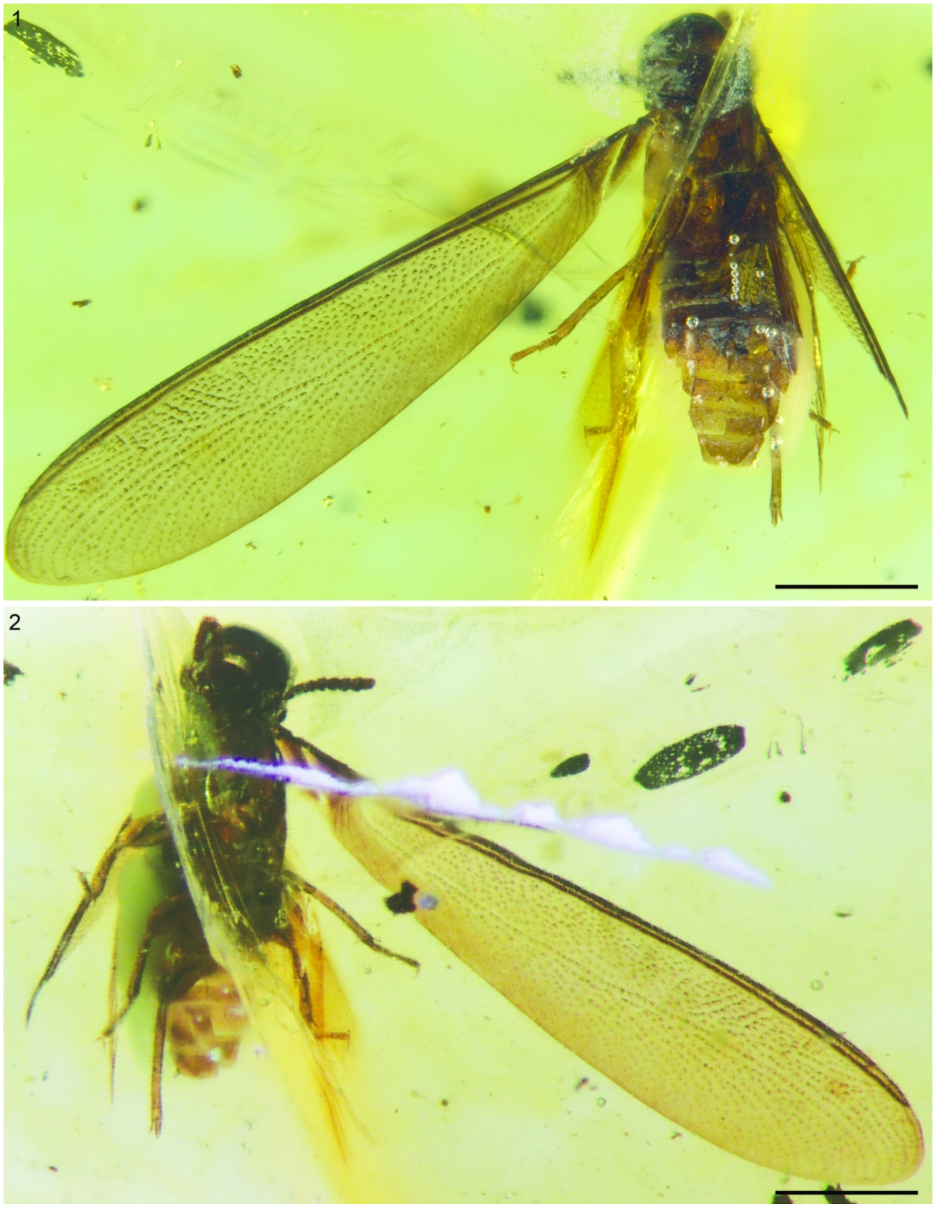

Figure 1. *Glyptotermes abyssinicus* n. sp., holotype IGR.ET2020/017, from early Miocene Ethiopian amber. (1) Habitus in dorsal view; (2) habitus in ventral view. Scale bars = 1 mm.

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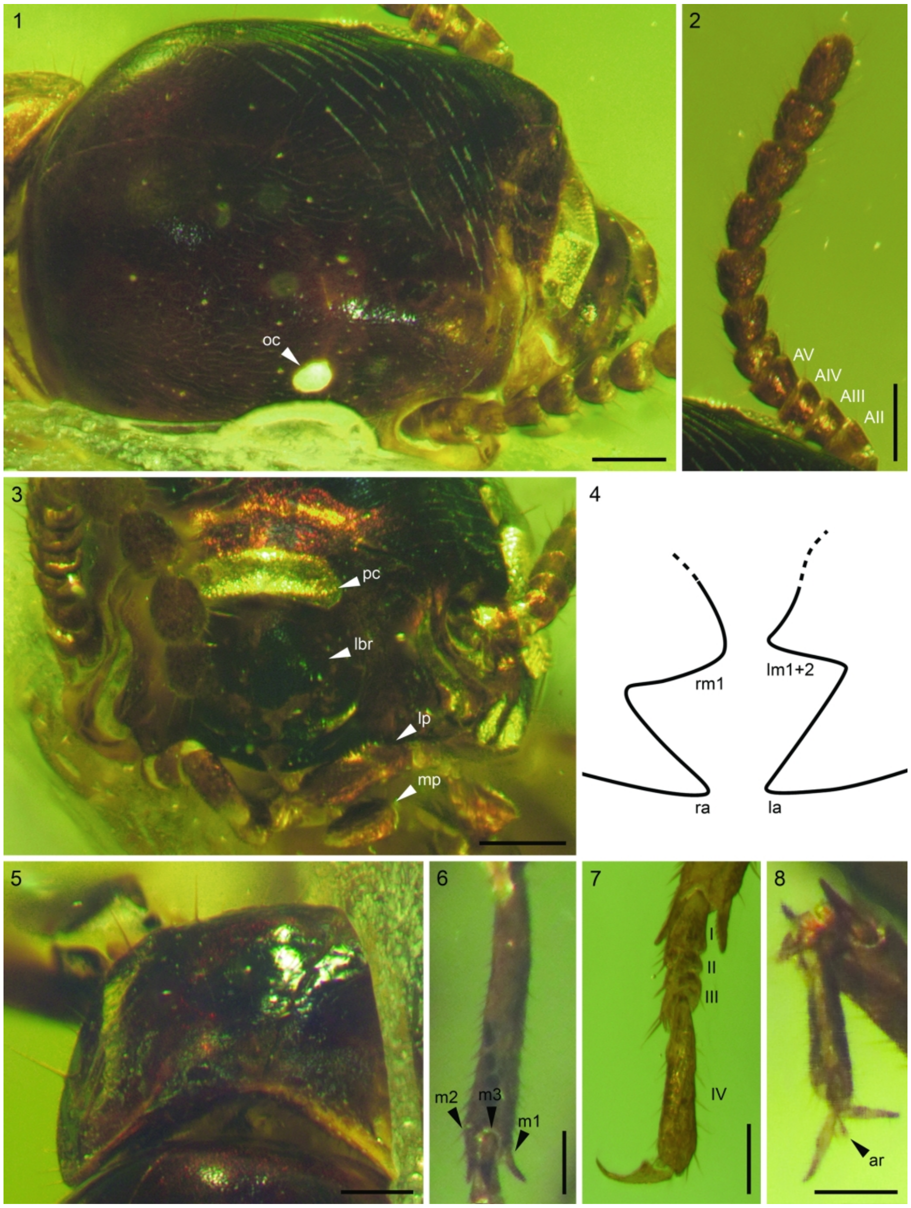

Figure 2. *Glyptotermes abyssinicus* n. sp., holotype IGR.ET2020/017, from early Miocene Ethiopian amber. (1) Head in dorsal view; (2) left antenna in dorsal view; (3) mouthparts in frontal view; (4) line drawing of mandibles in frontal view; (5) pronotum in anterodorsal view; (6) right mesotibia in 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 µm (1–3, 5), or 100 µm (6–8).

170x225mm (300 x 300 DPI)

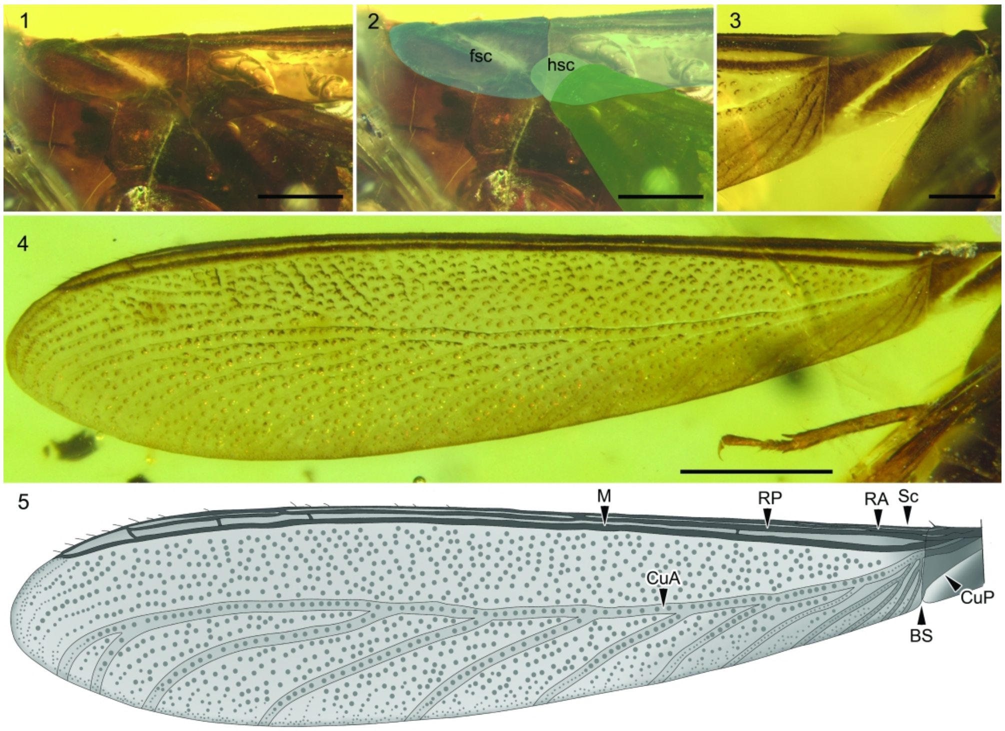

Figure 3. *Glyptotermes abyssinicus* n. sp., holotype IGR.ET2020/017, from early Miocene Ethiopian amber. (1) Right hind and fore wing bases in dorsal view; (2) same as 1, but colour-marked to highlight the wing scales; (3) left fore wing scale in dorsal view; (4) left fore wing in dorsal view; (5) explanatory 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 μm (1–3), or 750 μm (4).

179x133mm (600 x 600 DPI)