




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

Valentine Bouju,<sup>1</sup>  Corentin Jouault,<sup>1,2</sup>  and Vincent Perrichot<sup>1\*</sup> 

<sup>1</sup>Université de Rennes, CNRS, Géosciences Rennes, UMR 6118, 35000, Rennes, France <[valentine.bouju@univ-rennes1.fr](mailto:valentine.bouju@univ-rennes1.fr)>  
<[vincent.perrichot@univ-rennes1.fr](mailto:vincent.perrichot@univ-rennes1.fr)>

<sup>2</sup>Muséum National d'Histoire Naturelle, Institut de Systématique, Evolution, Biodiversité (ISYEB), CNRS, Sorbonne Université, EPHE, Université des Antilles, CP50, 57 Rue Cuvier, 75005 Paris, France <[jouaultc0@gmail.com](mailto:jouaultc0@gmail.com)>

**Abstract.**—A new species of drywood termite (Isoptera: Kalotermitidae) is described from a nearly complete alate specimen preserved in early Miocene Ethiopian amber. *Glyptotermes abyssinicus* new species is distinguished by its U-shaped head with 12-segmented antennae, the ocelli separated from the eye margin, the right mandible with an obtuse angle between the apical and first marginal teeth, the left mandible with an obtuse angle between the apical and first + second marginal teeth, and the wing venation. This is the first termite reported from Ethiopian amber, and the fourth Miocene species of the extant genus *Glyptotermes* Froggatt, 1897, 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, *G. abyssinicus* n. sp. constitutes an interesting new record for the biogeographical history of the kalotermitid lineage.

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

## 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). Although some discrepancies were 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 rise of the kalotermitids (Bourguignon et al., 2015; Bucek et al., 2019; Jouault et al., 2021).

Comprehension of the Kalotermitidae has 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 (Behrensmeyer and Turner, 2013). 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 because 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 true fossil record of the genus, and one of the very few fossil kalotermitids, from Africa.

## Materials 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), because the material was accessed through an amber trader from Addis Ababa who obtains amber exclusively from those four localities.

\*Corresponding author.

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 Jamma 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 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, Huntsman Advanced Materials, Basel, Switzerland) following the method of 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 (Helicon Soft, Kharkiv, Ukraine). Illustrations were made using Adobe Illustrator and Photoshop CC 2019 software. We follow the morphological terminology and classification of termites as presented by Krishna et al. (2013), except for the wing venation that follows Schubnel et al. (2019).

Abbreviations used in the text: AI–AV = antennomeres 1–5; C = costal vein; CuA = anterior cubitus; CuP = claval suture (posterior cubitus); f1–f3 = protibial spurs 1–3; h1–h3 = metatibial spurs 1–3; M = medial vein; m1–m3 = mesotibial spurs 1–3; RA = anterior radius; RP = posterior radius; Sc = subcostal vein.

*Repository and institutional abbreviation.*—The type specimen examined in this study is deposited in the amber collection of the Geological Department and Museum of the Université de Rennes (IGR), France, under 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 (Snyder, 1949, p. 45).

*Glyptotermes abyssinicus* new species  
 Figures 1–3

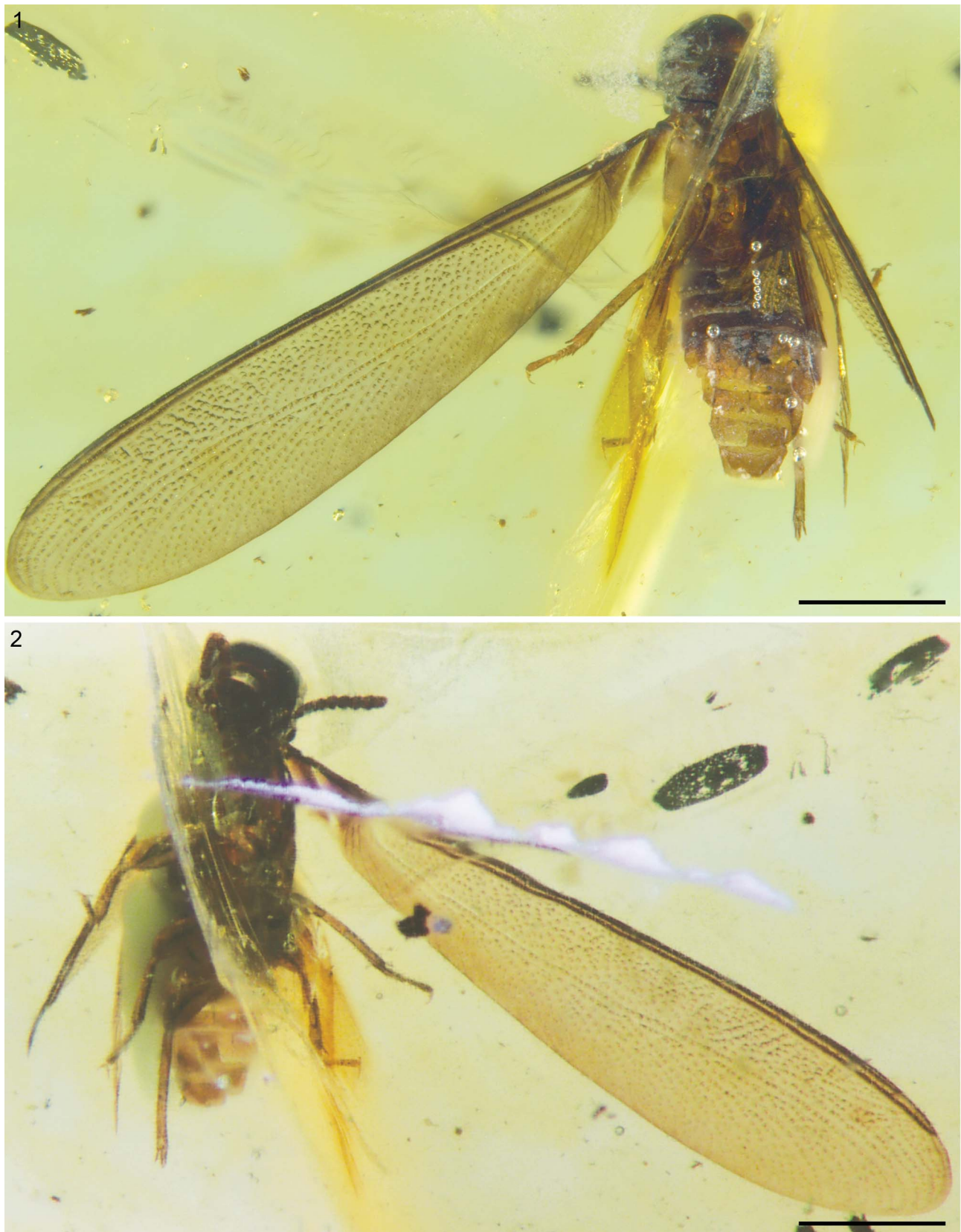
*Holotype.*—One alate specimen, IGR.ET2020/017, in amber from the lower Miocene (16–23 Myr) of the North Shewa Zone, Amhara and Oromia regions, Northwestern Plateau of Ethiopia.

*Diagnosis.*—Head U-shaped in posterodorsal view; eyes small, subcircular 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; forewing scale not fully overlapping hind wing scale; forewing 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 eight or nine 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 subcircular, slightly wider than long, ~0.25 mm wide, protruding from head, separated from posterior head margin by more than its length; ocelli white, ovoid (~0.06 mm long and 0.05 mm wide), located above eye midlength, 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 three segments (Fig. 2.3); labrum ~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 (~0.24 mm wide and 0.06 mm long).

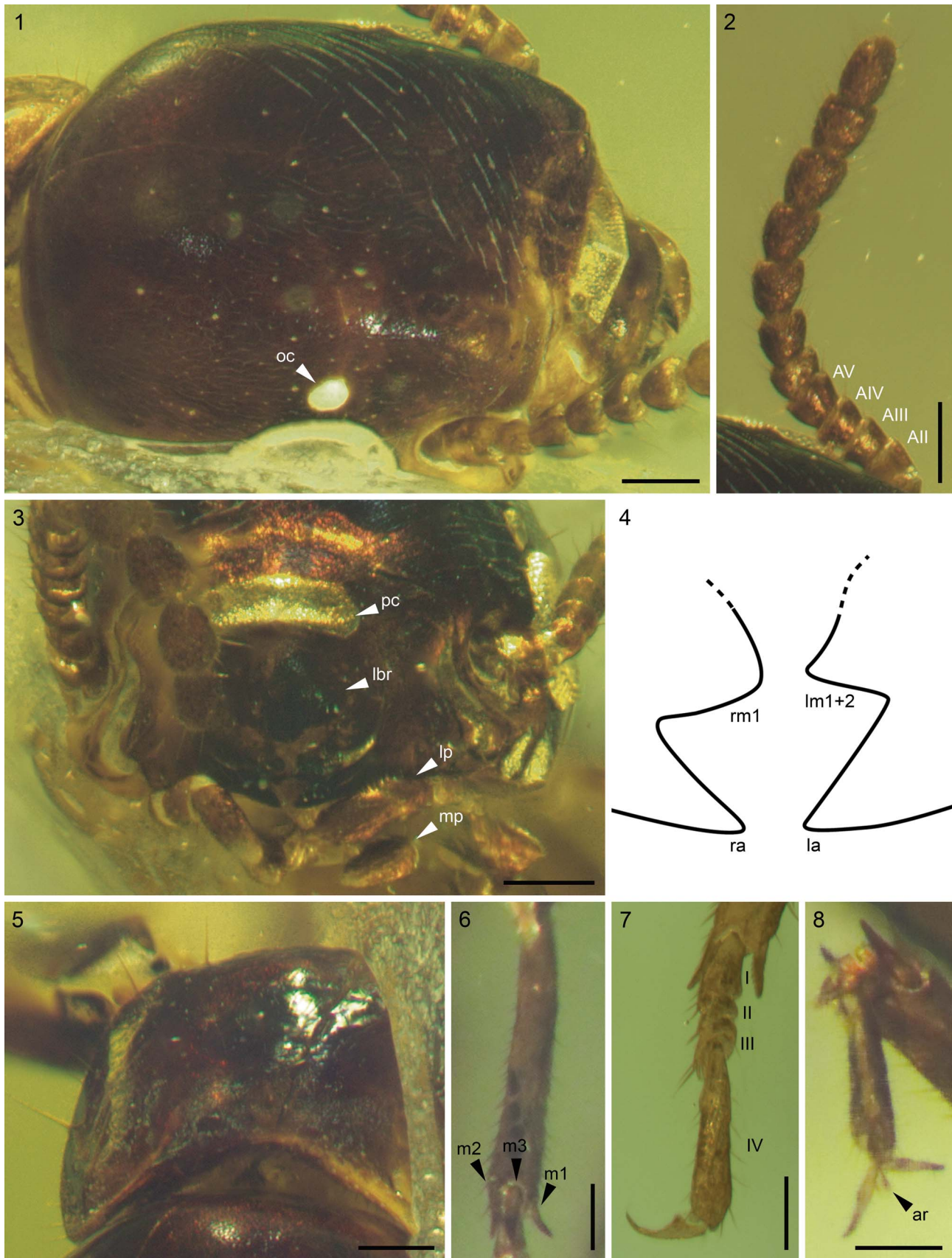
Pronotum (Fig. 2.5) flat to slightly arched in lateral view; anterior margin slightly concave; sides rounded, slightly narrower than head. Legs slender; profemur ~0.5 mm long, protibia ~0.4 mm long, protarsus at least 0.2 mm long; protibia with three spurs (f1, f2, f3); mesofemur ~0.5 mm long; mesotibia ~0.5 mm long; mesotarsus at least 0.4 mm long; mesotibia with three spurs (m1, m2, m3; Fig. 2.6); metafemur ~0.5 mm long; metatibia ~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; forewing scale 0.75 mm long, not overlapping hind wing scale, with humeral margin nearly straight, CuP straight, slightly curved distally, with straight basal suture; forewing with M and CuA veins arising independently from inside the wing scale; Sc short, simple; RA and RP fused basally; RA short; RP long with two anterior branches or fusion point with C; M sclerotized, running to wing apex, close and parallel to RP, with at least one anterior, short branch located near wing apex, and maybe two unsclerotized anterior

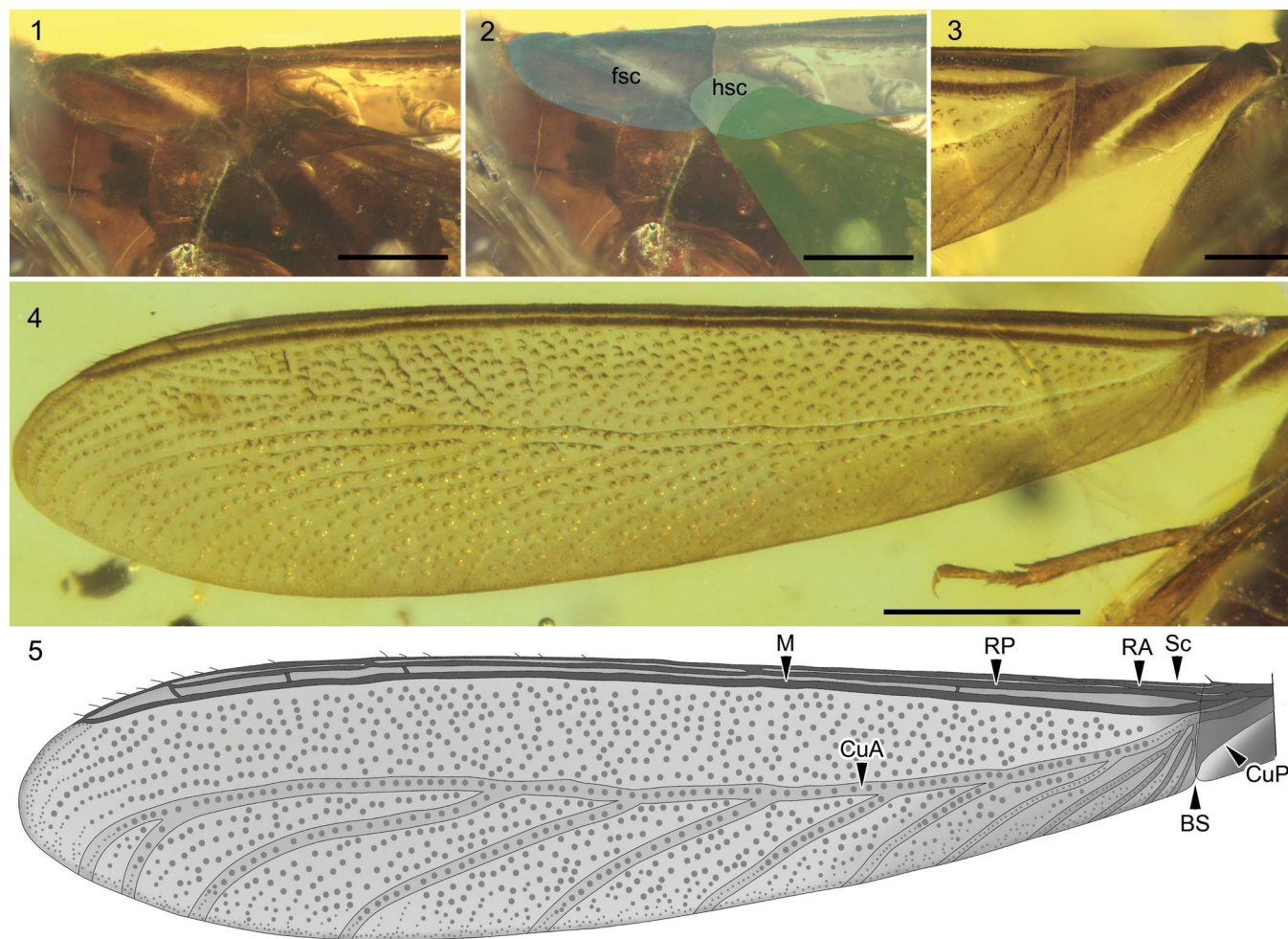


**Figure 1.** *Glyptotermes abyssinicus* n. sp., holotype IGR.ET2020/017, from early Miocene Ethiopian amber: (1) habitus in dorsal view; (2) habitus in ventral view. Scale bars = 1 mm.





**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) diagrammatic 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 first + second marginal tooth; lp = labial palp; m1–m3 = mesotibial spurs 1–3; mp = maxillary palp; oc = ocellus; pc = postclypeus; ra = right mandible apical tooth; rm1 = right mandible first marginal tooth. Scale bars = 125  $\mu$ m (1–3, 5), 100  $\mu$ m (6–8).



**Figure 3.** *Glyptotermes abyssinicus* n. sp., holotype IGR.ET2020/017, from early Miocene Ethiopian amber: (1) right hind- and forewing bases in dorsal view; (2) overlay of right wing scales in (1); (3) left forewing scale in dorsal view; (4) left forewing in dorsal view; (5) explanatory drawing of (4). BS = basal suture; CuA = anterior cubitus; CuP = claval suture (posterior cubitus); fsc = forewing scale; hsc = hind wing scale; M = medial vein; RA = anterior radius; RP = posterior radius; Sc = subcostal vein. Scale bars = 750  $\mu$ m (4, 5), 250  $\mu$ m (1–3).

branches located respectively in basal and apical wing third; CuA unsclerotized, with eight or nine posterior branches and maybe two unsclerotized anterior branches; hind wing not describable; anal lobe absent on both wings.

Abdomen not fully preserved,  $\sim$ 1.4 mm long, with at least six or seven observable segments (Fig. 1.1); abdominal segments apparently widest at midlength. Cerci and styli not visible.

**Etymology.**—The specific epithet refers to the Abyssinian origin of the amber piece, and is to be treated as an adjective.

**Remarks.**—The new fossil does not fit in the early diverged termite families, including the extinct Cratomastotermitidae and Termopsidae, because it combines the following series of derived characters: reduced wing venation (versus more complete, RP with at least several branches, and no costalization of veins in early diverged families), four-segmented tarsi (versus five-segmented, plesiomorphic character), a reduced tibial spur formula 3-3-3 (versus enriched with additional spurs along tibiae), and the head wider than the pronotum (versus smaller than the 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: hind wing without anal lobe, tarsi four-segmented, antenna 12-segmented, fontanelle absent, forewing 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 (versus 13 or 14 in *Calcaritermes*, 17 or 18 in *Proneotermes*). Additionally, it differs from *Proneotermes* but concords with *Glyptotermes* by the small eye diameter (0.25 mm versus 0.39–0.43 mm in *Proneotermes*) and the forewing with M as heavily sclerotized as the radial sector, running very close and parallel to the radial sector to reach the apex of the wing, with



faint branches between M and radial sector, and radial sector very close to the costal vein.

*Glyptotermes abyssinicus* n. sp. can be distinguished from the extant Neotropical and African *Glyptotermes* spp. 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, and the African *G. sinomalatus* Krishna and Emerson, 1962, by a U-shaped head (versus circular or semicircular in the other species). It differs from other species by the 12-segmented antennae—versus 11-segmented in *G. marlatti* (Snyder, 1926) and *G. planus* (Snyder, 1925), or > 12-segmented in *G. amplus* Scheffrahn et al., 2001, *G. kawandae* Wilkinson, 1954, or *G. longiusculus* Krishna and Emerson, 1962.

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

Finally, *Glyptotermes abyssinicus* n. sp. differs from the fossil species *G. grimaldii* and *G. paleoliberatus* by a smooth head capsule (versus granulate) and the ocelli separated from the eye margin (versus touching). The old description of *G. pusillus* from East African copal challenges its comparison with the other *Glyptotermes* spp. However, it is clear that our specimen does not belong to *G. pusillus* owing to the differential of temporal range (Pleistocene versus 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 of 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 might 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 for 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* spp., however, are very tolerant to environmental conditions and

can live in swamp forests or mangroves (Johnson et al., 1980; Tho, 1992). According to Scheffrahn (2021, p. 24), 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, because 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 the amber (Bouju and Perrichot, 2020; Bouju et al., 2021).

## Conclusions

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, morphology-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, Pan, and Jacobs, 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.

## Acknowledgments

We are grateful to Y. Goldman (Bloomfield, Connecticut) who provided the Ethiopian amber piece studied here. We thank A. Zewdalem (Jacksonville, Florida) and B. Teferi (Addis Ababa, Ethiopia) for information and access to the amber deposits of the North Shewa Zone, Ethiopia; and the reviewers and editor for their helpful comments. Partial support for this work was provided by the Tellus-INTERRVIE program of CNRS INSU (project AMBRAFRICA to V. Perrichot, 2019), enabling fieldwork in Ethiopia for V. Bouju and V. Perrichot.

## References

- Bechly, G., 2007, Isoptera: Termites, in Martill, D.M., Bechly, G., and Loveridge, R.F., eds., *The Crato Fossil Beds of Brazil: Window into an Ancient World*: Cambridge, UK, Cambridge University Press, p. 249–262.
- Behrensmeier, A. K., and Turner, A., 2013, Taxonomic occurrences of Kalotermitidae recorded in the Paleobiology Database: Fossilworks, <http://fossilworks.org> (accessed 27 September 2021).
- Belay, T., Tesfay, I., Ayalew, A., Yohannes, G., Zewdie, T., Bekele, H., Tadesse, M., Demisse, T., and Alemu, T., 2009, Geology of the Were-Ilu Area: Geological Survey of Ethiopia Memoir no. 25, 56 pp. 27 September 2021
- Bouju, V., and Perrichot, V., 2020, A review of amber and copal occurrences in Africa and their paleontological significance: BSGF—Earth Sciences Bulletin, v. 191, p. 17, <http://doi.org/10.1051/bsgf/2020018>.
- Bouju, V., Feldberg, K., Kaasalainen, U., Schaefer-Verwimp, A., Hedenäs, L., Buck, W.R., Wang, B., Perrichot, V., and Schmidt, A.R., 2021, Miocene Ethiopian amber: A new source of fossil cryptogams: Journal of Systematics and Evolution, <https://doi.org/10.1111/jse.12796>.
- Bourguignon, T., Lo, N., Cameron, S.L., Šobotník, J., Hayashi, Y., Shigenobu, S., Watanabe, D., Roisin, Y., Miura, T., and Evans, T.A., 2015, The evolutionary

- history of termites as inferred from 66 mitochondrial genomes: *Molecular Biology and Evolution*, v. 32, p. 406–421, <https://doi.org/10.1093/molbev/msu308>.
- Brullé, G.A., 1832, *Insectes: Expédition scientifique de Morée, Section des Sciences Physiques, Tome 3, Partie 1, Zoologie, Sect. 2, Des Animaux Articulés*: Paris, F.G. Levrault, p. 1–29 + 64–395.
- Brunner von Wattenwyl, K., 1882, *Prodromus der Europäischen Orthopteren*: Leipzig, Germany, W. Engelmann, 466 p.
- Bucek, A., Sobotník, J., He, S., Shi, M., McMahon, D.P., Holmes, E.C., Roisin, Y., Lo, N., and Bourguignon, T., 2019, Evolution of termite symbiosis informed by transcriptome-based phylogenies: *Current Biology*, v. 29, p. 3728–3734, <https://doi.org/10.1016/j.cub.2019.08.076>.
- Cockerell, T.D.A., 1916, *Insects in Burmese amber*: *American Journal of Science*, ser. 4, v. 42, p. 135–138.
- Cockerell, T.D.A., 1917, *Insects in Burmese amber*: *Annals of the Entomological Society of America*, v. 10, p. 323–329.
- Coulié, E., Quidelleur, X., Gillot, P.-Y., Courtillot, V., Lefèvre, J.-C., and Chiesa, S., 2003, Comparative K-Ar and Ar/Ar dating of Ethiopian and Yemenite Oligocene volcanism: Implications for timing and duration of the Ethiopian traps: *Earth and Planetary Science Letters*, v. 206, p. 477–492, [https://doi.org/10.1016/S0012-821X\(02\)01089-0](https://doi.org/10.1016/S0012-821X(02)01089-0).
- Cowie, R.H., Wood, T.G., Barnett, E.A., Sands, W.A., and Black, H.J.J., 1990, A checklist of the termites of Ethiopia with a review of their biology, distribution and pest status: *African Journal of Ecology*, v. 28, p. 21–33.
- Debelo, D.G., and Degaga, E.G., 2014, Termite species composition in the central rift valley of Ethiopia: *Agriculture and Biology Journal of North America*, v. 5, no. 3, p. 123–134.
- Emerson, A.E., 1969, A revision of the Tertiary fossil species of the Kalotermitidae (Isoptera): *American Museum Novitates*, v. 2359, p. 1–57.
- Engel, M.S., and Kaulfuss, U., 2017, Diverse, primitive termites (Isoptera: Kalotermitidae, incertae sedis) from the early Miocene of New Zealand: *Austral Entomology*, v. 56, p. 94–103, <https://doi.org/10.1111/aen.12216>.
- Engel, M.S., and Krishna, K., 2007, Drywood termites in Dominican amber (Isoptera: Kalotermitidae): *Beiträge zur Entomologie*, v. 57, p. 263–275, <https://doi.org/10.21248/contr.entomol.57.2.263-275>.
- Engel, M.S., Grimaldi, D.A., and Krishna, K., 2007, Primitive termites from the Early Cretaceous of Asia (Isoptera): *Stuttgarter Beiträge zur Naturkunde B*, v. 371, p. 1–32.
- Engel, M.S., Grimaldi, D.A., and Krishna, K., 2009, Termites (Isoptera): Their phylogeny, classification, and rise to ecological dominance: *American Museum Novitates*, v. 3650, p. 1–27, <https://doi.org/10.1206/651.1>.
- Engel, M., Pan, A.D., and Jacobs, B.F., 2013, A termite from the late Oligocene of northern Ethiopia: *Acta Palaeontologica Polonica*, v. 58, p. 331–334, <https://doi.org/10.4202/app.2011.0198>.
- Froggatt, W.W., 1897, *Australian Termitidae, Part 2: Proceedings of the Linnean Society of New South Wales*, v. 21, p. 510–552.
- Heer, O., 1849, *Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien, Zweiter Teil: Heuschrecken, Florfliegen, Aderflügler, Schmetterlinge und Fliegen*. Leipzig, Germany, W. Engelmann, iv + 264 p.
- Holmgren, N., 1911, *Termitenstudien, 2, Systematik der Termiten, Die Familien Mastotermitidae, Protermitidae und Mesotermitidae*: *Kungliga Svenska Vetenskaps-Akademiens Handlingar*, v. 46, no. 6, p. 1–86, 6 pls.
- Johnson, R.A., Lamb, R.W., Sands, W.A., Shittu, M.O., Williams, R.M.C., and Wood, T.G., 1980, A checklist of Nigerian termites (Isoptera) with brief notes on their biology and distribution: *Nigerian Field*, v. 45, p. 50–64.
- Jouault, C., Legendre, F., Grandcolas, P., and Nel, A., 2021, Revising dating estimates and the antiquity of eusociality in termites using the fossilized birth-death process: *Systematic Entomology*, v. 46, p. 592–610, <https://doi.org/10.1111/syen.12477>.
- Kieffer, B., Arndt, N., Lapiere, H., Bastien, F., Bosch, D., Pecher, A., Yirgu, G., Ayalew, D., Weis, D., Jerram, D.A., Keller, F., and Meugnot, C., 2004, Flood and shield basalts from Ethiopia: Magmas from the African superswell: *Journal of Petrology*, v. 45, p. 793–834, <https://doi.org/10.1093/petrology/egg112>.
- Krishna, K., 1961, A generic revision and phylogenetic study of the family Kalotermitidae (Isoptera): *Bulletin of the American Museum of Natural History*, v. 122, p. 303–408.
- Krishna, K., and Emerson, A.E., 1962, New species of the genus *Glyptotermes* Froggatt from the Papuan, Oriental, Ethiopian, and Neotropical regions (Isoptera, Kalotermitidae): *American Museum Novitates*, v. 2089, p. 1–65.
- Krishna, K., Grimaldi, D.A., Krishna, V., and Engel, M.S., 2013, Treatise on the Isoptera of the world: *Bulletin of the American Museum of Natural History*, v. 377, p. 1–2704, <https://doi.org/10.1206/377.1>.
- Legendre, F., Nel, A., Svenson, G.J., Robillard, T., Pellens, R., and Grandcolas, P., 2015, Phylogeny of Dictyoptera: Dating the origin of cockroaches, praying mantises and termites with molecular data and controlled fossil evidence: *PLoS ONE*, v. 10, p. e0130127, <https://doi.org/10.1371/journal.pone.0130127>.
- Nel, A., and Paicheler, J.C., 1993, Les Isoptera fossiles: Etat actuel des connaissances, implications paléocologiques et paléoclimatologiques (Insecta, Dictyoptera): *Cahiers de Paléontologie, CNRS Éditions, Paris*, p. 101–179.
- Poinar, G., Jr., 2009, Description of an Early Cretaceous termite (Isoptera: Kalotermitidae) and its associated intestinal protozoa, with comments on their co-evolution: *Parasites & Vectors*, v. 2, no. 1, p. 12, <https://doi.org/10.1186/1756-3305-2-12>.
- Sadowski, E.M., Schmidt, A.R., Seyfullah, L.J., Solórzano-Kraemer, M.M., Neumann, C., Perrichot, V., Hamann, C., Milke, R., and Nascimbene, P.C., 2021, Conservation, preparation and imaging of diverse ambers and their inclusions: *Earth-Science Reviews*, v. 220, p. 103653, <https://doi.org/10.1016/j.earscirev.2021.103653>.
- Scheffrahn, R.H., 2021, The termite genus *Glyptotermes* (Isoptera: Kalotermitidae) from Paraguay: *ZooKeys*, v. 1059, p. 23–33, <https://doi.org/10.3897/zookeys.1059.70500>.
- Scheffrahn, R.H., Su, N.Y., and Křeček, J., 2001, *Glyptotermes amplus*, a new dampwood termite (Isoptera: Kalotermitidae) from St. Lucia: *Florida Entomologist*, v. 84, p. 426–430.
- Schubnel, T., Desutter-Grandcolas, L., Legendre, F., Prokop, J., Mazurier, A., Garrouste, R., Grandcolas, P., and Nel, A., 2019, To be or not to be: Post-cubital vein in insects revealed by microtomography: *Systematic Entomology*, v. 45, p. 327–336, <https://doi.org/10.1111/syen.12399>.
- Snyder, T.E., 1925, New American termites, including a new subgenus: *Journal of the Washington Academy of Sciences*, v. 15, p. 152–162.
- Snyder, T.E., 1926, New termites from Guatemala, Costa Rica, and Colombia: *Journal of the Washington Academy of Sciences*, v. 16, p. 18–28.
- Snyder, T.E., 1949, *Catalogue of termites (Isoptera) of the world: Smithsonian Miscellaneous Collections*, v. 112, p. 1–490.
- Tho, Y.P., 1992, *Termites of Peninsular Malaysia*: Kuala Lumpur, Malaysia, Forest Research Institute Malaysia (Malayan Forest Records, v. 36), 224 p.
- Wilkinson, W., 1954, Three new species of Kalotermitidae (Isoptera) from East Africa: *Proceedings of the Royal Entomological Society of London, ser. B, Taxonomy*, v. 23, p. 75–82.
- Wilkinson, W., 1959, Four new species of Kalotermitidae from East Africa (Isoptera): *Proceedings of the Royal Entomological Society of London, ser. B, Taxonomy*, v. 28, p. 61–72.
- Yashiro, T., Takematsu, Y., Ogawa, N., and Matsuura, K., 2019, Taxonomic assessment of the termite genus *Neotermes* (Isoptera: Kalotermitidae) in the Ryukyu-Taiwan Island arc, with description of a new species: *Zootaxa*, v. 4604, p. 549–561, <https://doi.org/10.11646/zootaxa.4604.3.10>.
- Zhang, J.F., 1989, [Fossil Insects from Shanwang, Shandong, China]: Jinan, Shandong Science and Technology Publishing House, 459 p. (in Chinese, with English summary)
- Zhang, J.F., Sun, B., and Zhang, X., 1994, [Miocene Insects and Spiders from Shanwang, Shandong]: Beijing, Science Press, 298 p. (in Chinese, with English summary)
- Zhao, Z., Eggleton, P., Yin, X., Gao, T., Shih, C., and Ren, D., 2019, The oldest known mastotermitids (Blattodea: Termitoidea) and phylogeny of basal termites: *Systematic Entomology*, v. 44, p. 612–623, <https://doi.org/10.1111/syen.12344>.
- Zhao, Z., Shih, C., Gao, T., and Ren, D., 2021, Termite communities and their early evolution and ecology trapped in Cretaceous amber: *Cretaceous Research*, v. 117, p. 104612, <https://doi.org/10.1016/j.cretres.2020.104612>.

Accepted: 17 October 2021