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A termite from the Late Oligocene of northern Ethiopia

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Termites of the family Stolotermitidae are a relict lineage of primitive Isoptera. The fossil record of Stolotermitidae is exceptionally poor, with only two Miocene (Neogene) species documented to date. Herein, a new genus and species of Paleogene termites is described and figured from the Late Oligocene (28–27 Ma, Early Chattian) of northwestern Ethiopia (Amhara Region, Chilga Woreda). *Chilgatermes diamatensis* gen. et sp. nov., is most similar to genera of the Stolotermitidae, Archotermopsidae, and Termopsidae but can be distinguished on the basis of forewing venational details. The genus is tentatively placed in the Stolotermitidae: Porotermitinae. *Chilgatermes diamatensis* is the first fossil termite from Ethiopia and, indeed, the first from the entire African continent.

Introduction

The family Stolotermitidae comprise ten living species in Australia, sub-Saharan Africa, and the Neotropics (Emerson 1942; Krishna et al. 2013). The family has historically been included in the Termopsidae s.l., a heterogeneous lineage of primitive Isoptera widely known as the "dampwood termites". Recently, Termopsidae has been recognized as paraphyletic and its constituents segregated into three separate families—Termopsidae for the fossil genus *Termopsis* Heer, 1849, Stolotermitidae for the former subfamilies Porotermitinae (*Porotermes* Hagen, 1858, three extant species) and Stolotermitinae (*Stolotermes* Hagen, 1858, seven extant species), and Archotermopsidae for the genera *Archotermopsis* Desneux, 1904, *Zootermopsis* Emerson, 1933, *Hodotermopsis* Holmgren, 1911, *Parotermes* Scudder, 1883, and likely also *Gyatermes* Engel and Gross, 2009 (Engel et al. 2009). This arrangement has garnered support from morphological, paleontological, behavioral, biochemical, and DNA sequence data sources (Engel et al. 2009; Ware et al. 2010; Lacey et al. 2011).

Only two fossil species were documented to date, both of *Stolotermes* and both from the Miocene (Neogene). The first species attributed to the genus was *Stolotermes amanoi* Fujiyama, 1983, described from a shed wing recovered from the Late Miocene Anadozawa Formation of Japan (Fujiyama 1983). The most recent record came from a similarly shed forewing described as *Stolotermes kupe* Kaulfuss, Harris, and Lee, 2010 from the Early Miocene (Otaian Stage) of New Zealand (Kaulfuss et al. 2010). Aside from these two specimens, no other records for the family have been documented. *Tanytermes* Engel, Grimaldi, and Krishna, 2007 and *Dharmatermes* Engel, Grimaldi, and Krishna, 2007 from the mid-Cretaceous of Myanmar have wing venations superficially similar to Stolotermitidae and were compared with *Stolotermes* and *Porotermes* when first discovered (Engel et al. 2007b). However, in all cladistic treatments *Tanytermes* and *Dharmatermes* group elsewhere, albeit often near Stolotermitidae—e.g., related to the Kalotermitidae + Neoisoptera clade (= Icoisoptera) (Engel et al. 2009) or as progressive sisters to Neoisoptera (Ware et al. 2010) or Kalotermitidae alone (Lo and Eggleton 2010).

Herein is described an enigmatic fossil species, again based on a pair of shed wings, from the Late Oligocene (Paleogene) of northeastern Africa. The new fossil is loosely attributable to the Stolotermitidae although it is plesiomorphic in many details to the two subfamilies, Stolotermitinae and Porotermitinae, and may represent a stem-group to Stolotermitidae or Porotermitinae (less likely). While wings alone often do not provide a sufficiently rich source of character data for definitive placement of a particular fossil, this species is noteworthy as it is the first fossil record of a termite, of any age, from Africa thereby representing a significant new record for the paleontology of Isoptera.

Institutional abbreviations.—CH, Chilga collections, National Museum of Ethiopia, Addis Ababa, Ethiopia.

Geological setting

Fossiliferous sediments are located on the Ethiopian Plateau, approximately 60 km west of Gondar. The regional geology consists of massive (approximately 2000 m thick) Oligocene trap basalts with interspersed tuffs, lignites, and fluvial volcaniclastic and clastic sediments exposed along streams and gully cuts (Hoffmann et al. 1997; Kappelman et al. 2003; Jacobs et al. 2005). The study site is located in a nearly 100 m thick sedimentary section of strata that overlies a 32.4 ± 1.6 Ma whole rock K/Ar dated basalt next to the Guang River (Kappelman et al. 2003). Compression fossils, including the specimen discussed herein, were excavated from a 22 to 36 cm thick, greenish-gray to yellow-green massive mudstone layer within the section. The layer represents an overbank (or pond) deposit derived from a weathered ash (Pan 2007). The fossil termite was found with a relatively diverse autochthonous or parautochthonous tropical moist forest paleoflora, the Guang River flora, composed of compressions of leaves and reproductive structures, logs, in situ stumps, and pollen (Jacobs et al. 2005; Pan 2007, 2010; Pan and Jacobs 2009; Pan et al. 2010). All of these fossils are dated to 27.23 ± 0.1 Ma by a ^{206}Pb/^{238}U analysis of zircon crystals extracted from an ash layer stratigraphically correlated with the mudstone (Pan 2010).

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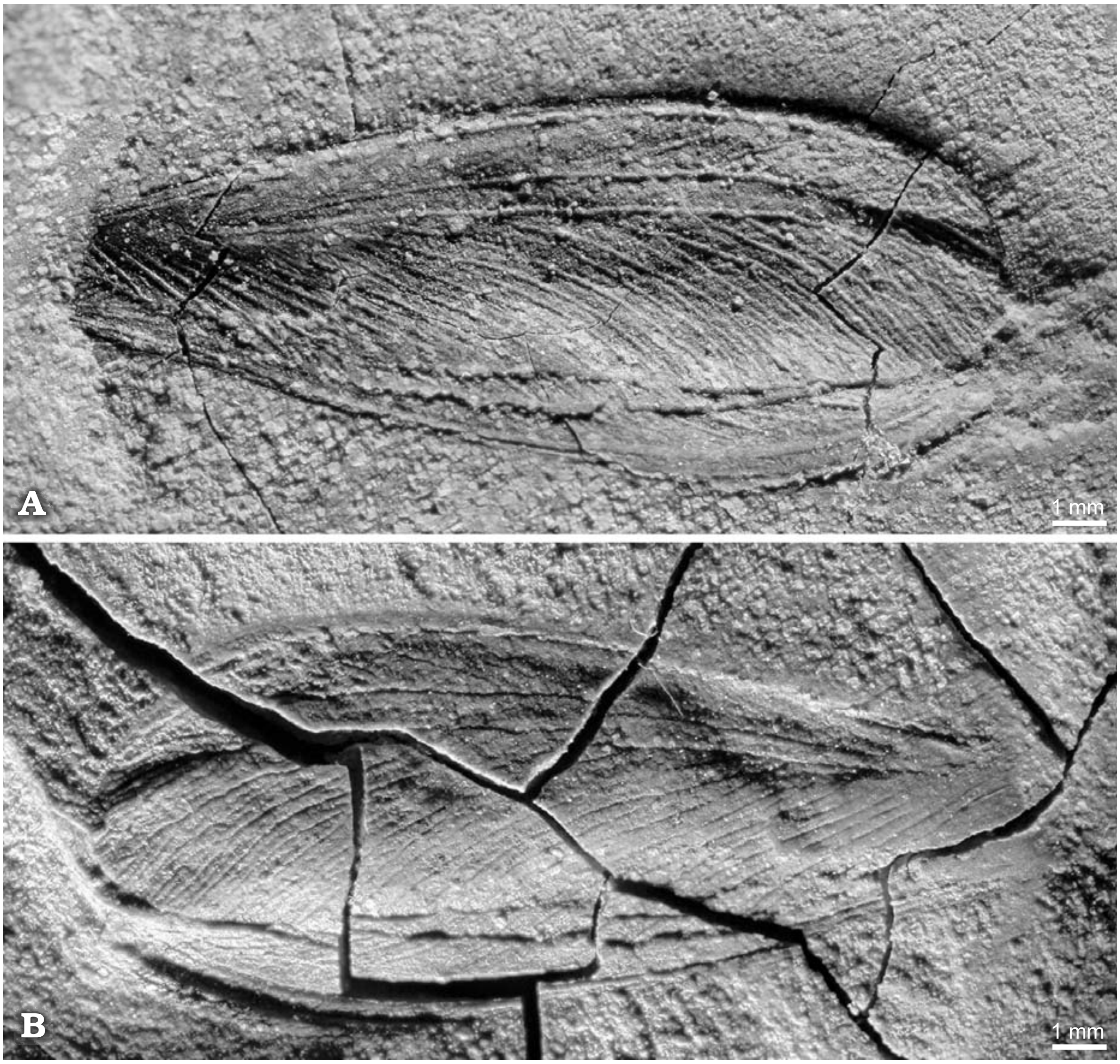

Fig. 1. Termite *Chilgatermes diamatensis* gen. et sp. nov. (CH 52-70), Chilga Woreda, Ethiopia, Early Chattian (Oligocene). Photomicrographs of part (**A**) and counterpart (**B**).Photomicrographs by MSE.

Systematic paleontology

Morphological terminology follows that of Engel et al. (2007a, b, 2011a), and Grimaldi et al. (2008), while the format for the description is that of Engel et al. (2007b), Engel and Gross (2009), and Engel et al. (2011b). The classification adopted herein is that of Engel et al. (2009).

Family Stolotermitidae Holmgren, 1910

Subfamily Porotermitinae? Emerson, 1942

Genus *Chilgatermes* nov.

Type species: *Chilgatermes diamatensis* gen. et sp. nov.; see below.

Etymology: A combination of Chilga, from the name of the geographic region, and *termes*, "wood-borer", common stem for isopteran genera (gender masculine).

Diagnosis.—As for the type species; see below.

Chilgatermes diamatensis sp. nov.

Figs. 1–2.

Etymology: The specific epithet is taken from the ancient kingdom of D'mt (a.k.a. Diamat), which ruled portions of modern Eritrea and northern Ethiopia from ca. 700–400 BCE, and which encompassed in its southernmost regions the Chilga deposits.

Holotype: Alate wings, overlapping with only forewing venation discernible; CH 52-70 (a and b), part and counterpart; deposited in the Chilga collections, National Museum of Ethiopia, Addis Ababa, Ethiopia.

Type locality: Sublocality 2 (CH 52) of Guang River flora, northwestern Ethiopia (Amhara Region, Chilga Woreda, approximately 60 km west of Gondar (Jacobs et al. 2005).

Type horizon: Late Oligocene (Early Chattian, 28–27 Ma).

Diagnosis.—Alate forewing: Membrane reticulate; all veins originating inside scale; basal suture gently convex, not straight or oblique (straight and oblique in modern Stolotermitidae); radial field relatively wide, not as narrow as in extant Stolotermitidae, of approximately same width for most of wing length, widening to encompass wing apex in ex-

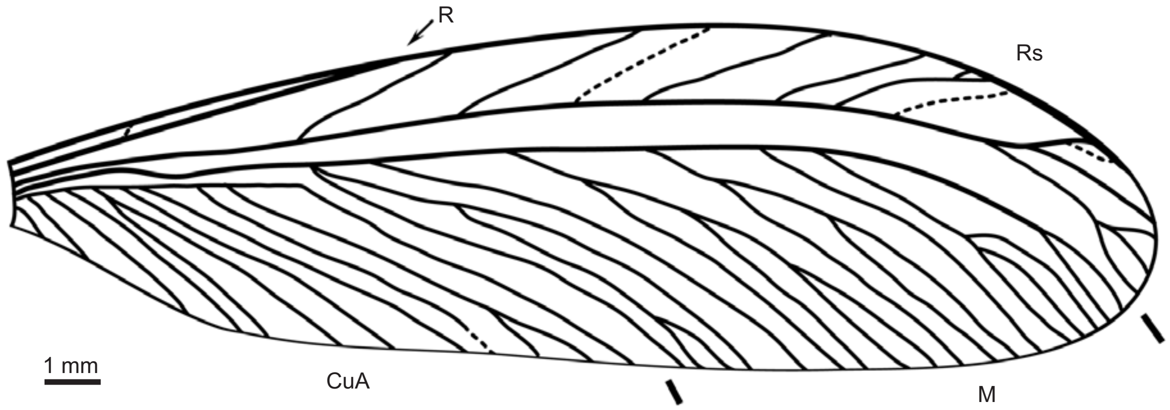

Fig. 2. Reconstruction of forewing venation of termite *Chilgatermes diamatensis* gen. et sp. nov. (CH 52-70) from Chilga Woreda, Ethiopia, Early Chattian (Oligocene), membrane reticulations omitted. Drawing by Ismael A. Hinojosa-Díaz. Abbreviations: CuA, anterior cubital vein; M, medial vein; R, radial vein; Rs, radial sector vein.

treme apical portion of wing; R (radial vein) simple, extending to about one-third wing length, apparently with a single, short veinlet extending to costal margin in basal third; Rs (radial sector vein) strong, with several (8), largely-simple branches extending to costal margin; M (medial vein) strong, running closer to CuA (anterior cubital vein) than to Rs in proximal third of wing, extensively developed, with numerous (7), mostly dichotomously-branching primary branches extending to posterior wing margin, apicalmost branch terminating just posterior to wing apex, basalmost branch terminating on posterior margin near wing midlength; CuA extensively developed in proximal half of wing, with numerous (at least 10), largely-simple branches.

Description.—As in the diagnosis, with the following minor additions: Total length (as preserved) from basal suture to apex 17.4 mm; maximum width 5.9 mm. Sc (subcostal vein) not evident; apex of Rs stem branching dichotomously just posterior to wing apex, apicalmost superior branch forking near its base, posteriormost fork terminating at wing apex; penultimate branch of CuA forking near posterior wing margin.

Stratigraphic and geographic range.—Type locality only.

Discussion and conclusions

Chilgatermes differs from extant Stolotermitidae, including *Porotermes*, in the broader radial field; the much more extensively-developed medial vein, with more than seven primary branches; the gently convex basal suture; and the more densely-branched CuA. In the absence of the wing scale and structures of the body it is impossible to give a more precise phylogenetic association of the fossil. However, it is likely that its biology was similar to other stolotermitids, living in somewhat temperate regions and nesting in dead wood, often stumps and root systems but logs (i.e., not standing erect and with roots still embedded in the soil) are also prone. Nests are built entirely within the timber, with colonies established by reproductives entering gaps or cracks on surfaces exposed above the soil level. However, nests are extended downward by the workers, typically into the root systems, thereby developing a connection with the soil, necessary for the maintenance of sufficient moisture levels within the colony. The nests themselves consist of irregular, flattened chambers which either border one another directly or are connected by narrow tunnels. Given the abundance of plant material from Chilga it is entirely possible that entire nests may be recovered from the deposits.

Hopefully continued exploration in Chilga will reveal not only more complete material of *C. diamatensis* but additional termite and other insect species. The Cenozoic record of insects in Africa is confined to a small handful of localities, with about 120 specimens recorded from the most "prolific" of these (e.g., Schlüter 2003). Given the diversity of insects today and in the past (Grimaldi and Engel 2005), this is a paltry record for such an ecologically significant and diversity dominant lineage of terrestrial animals. By the Cenozoic insects had already been around for at least 345 million years, diversified into all of their major lineages, and nearly all of these had been dominant in their respective ecosystems for eons (Grimaldi and Engel 2005). By the time of the Late Oligocene the termites had diversified and arisen in abundance, becoming one of the most significant recyclers of carbon (Engel et al. 2009), with diverse faunas documented in the preceding and following epochs of Chilga (e.g., Engel et al. 2007a, 2009, 2011a; Wappler and Engel 2006; Engel and Gross 2009; Krishna and Grimaldi 2009). The ecosystem of Chilga in the Late Oligocene was certainly ideal habitat for termites of several families. Given the usual development of large numbers of workers and soldiers, particularly in the Rhinotermitidae and Termitidae, as well as swarms of reproductives at certain times of the year, the potential for isopteran material is considerable and wings and other termite fragments should be sought actively in the region.

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