



The first mastotermitid termite from Africa (Isoptera: Mastotermitidae): a new species of *Mastotermes* from the early Miocene of Ethiopia

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Abstract.—The first mastotermitid termite from Africa is described and figured from wing fragments recovered from the early Miocene (22–21 Ma) deposits of the Mush Valley, Amhara Region, central Ethiopia. *Mastotermes aethiopicus* new species is the second fossil termite recorded from Africa and expands the known paleo-distribution of the genus from tropical North America and Europe into northeastern Africa during the Miocene. *Mastotermes aethiopicus* is distinguished from the living *M. darwiniensis* Froggatt and other Neogene species of the genus, and comments are provided regarding the occurrence of this genus in the tropical fauna of Miocene Ethiopia.

Introduction

Among the termites (Isoptera), one of the more interesting and spectacular of large taxa is *Mastotermes darwiniensis* Froggatt, 1897, a relict species living today in northern Australia and comprising the sole extant member of its family, Mastotermitidae (Grimaldi and Engel, 2005). *Mastotermes darwiniensis* has drawn the attention of termite workers for generations owing to its basal position among the clade of living Isoptera and the large number of plesiomorphic traits relative to roaches that it retains (Engel et al., 2009; Ware, Grimaldi, and Engel, 2010; Krishna et al., 2013). Notably primitive features include the large body size (alates ca. 18 mm in length, excluding wings, and with a forewing length ca. 27 mm); ocelli; keeled procoxae; wholly pentamerous tarsi; numerous branched Rs, M, and Cu veins; lack of a developed hind wing basal suture (the hind wings are typically chewed off); well-developed anojugal lobe in the hind wing; multisegmented cerci; ovipositor with valvulae; laying of eggs in an ootheca-like pod; and mycetocytes that house *Blattabacterium* Hollande and Favre, 1931 (Flavobacteriales: Blattabacteriaceae), a symbiont also found in roaches (Emerson, 1965; Krishna et al., 2013). Among this litany of traits, the well-developed anojugal lobe and egg pods are unique among living termites. Colonies are found in tropical, non-forested areas living in the stumps of trees, felled logs, or underground, and if conditions are right, may have a worker force that numbers over a million individuals. Where it occurs, the species can be a damaging pest, with a very

broad diet (Hill, 1921, 1942; Calaby and Gay, 1959; Gay and Calaby, 1970; Krishna et al., 2013). Colonies were accidentally introduced into southern New Guinea during the Second World War and have become established (Barrett, 1965; Gay, 1967; Gray, 1968; Miller, 1986; Watson, Miller, and Abbey, 1998); otherwise, the distribution of the species appears to be limited only by climate and historical factors (Hill, 1942; Emerson, 1965; Krishna et al., 2013). As noted above, the genus is relict and fossil mastotermitids are known from Cretaceous and Cenozoic deposits throughout the world (Emerson, 1965; Wappler and Engel, 2006; Engel, Grimaldi, and Krishna, 2007a; Engel, 2008), and most of these fossil species are assigned to the genus *Mastotermes* Froggatt, 1897 (Wappler and Engel, 2006; Krishna et al., 2013). Indeed, 13 fossil species of *Mastotermes* have been documented, whereas there are presently only 12 other fossil mastotermitids (Krishna et al., 2013). Four species of *Mastotermes* are known from amber inclusions ranging from the early Miocene of Mexico and the Dominican Republic (Krishna and Emerson, 1983; Krishna and Grimaldi, 1991), to the Eocene and late Cenomanian of France (Schlüter, 1989; Nel and Bourguet, 2006), while the remainder are represented by a variety of compressions from the Eocene through Miocene of Europe, and all are far afield from the modern occurrence of *M. darwiniensis*. Quite interestingly, virtually all of these fossil occurrences are in moist tropical (e.g., Dominican amber) or subtropical environments (e.g., Eckfeld Maar) (Wappler and Engel, 2006), which stand in contrast to the ecological tolerances of *M. darwiniensis*.

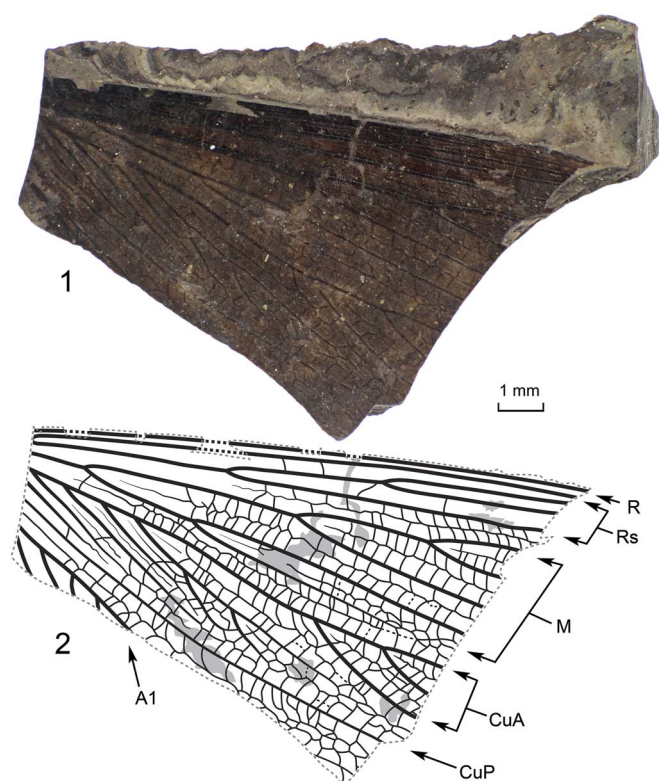


Figure 1. Photograph and illustration of holotype hind wing fragment (MU34-12) of *Mastotermes aethiopicus* n. sp. (1) Photograph of specimen as preserved, (2) illustration of discernible venational details.

Herein we present the description of a new species of *Mastotermes* (Fig. 1) recovered from the early Miocene shales of the Mush deposits in central Ethiopia. This represents the first record of the Mastotermitidae in Africa and only the second fossil termite species for the continent (Engel et al., 2013). Prior to this, fossil termites have been well documented from all other regions except Antarctica (Krishna et al., 2013). The species discussed herein is also the first insect reported from the Mush deposits, the other Ethiopian fossil termite having originated from the late Oligocene Chilga deposits.

Material and methods

Three fragments of hind wings were recovered from the Mush Valley localities of northern Ethiopia. Two fragments preserve only portions of the anterior veins (Fig. 2), whereas the third (Fig. 1.1), and most complete, encompasses a very well-preserved section through the basal portion of a hind wing and including important characters indicative of *Mastotermes*. Venational and other terminology follows that of Engel et al. (2007b, 2009, 2011a), whereas the format for the description is augmented from that of Engel et al. (2007a, 2011b), Engel and Gross (2009), and Engel and Delclòs (2010). The classification adopted herein is that of Engel et al. (2009) and Krishna et al. (2013). Photography for Figure 1.1 was done with a Canon EOS 7D attached to an Infinity K-2 long-distance microscope lens; photographs for Figure 2 were taken with a Canon EOS 7D using a MP-E 65mm f/2.8 1×–5× Macro lens on a tripod with remote shooting. Measurements were prepared using an

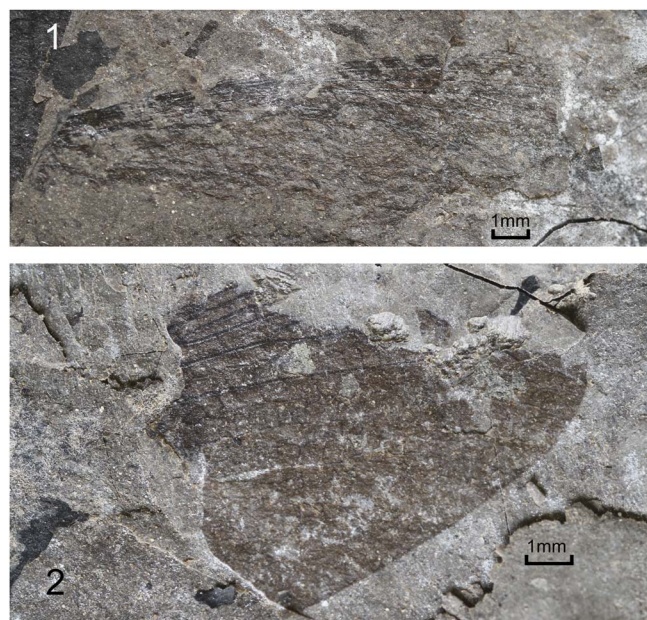


Figure 2. Photographs of additional, poorly preserved wing fragments referred to *Mastotermes aethiopicus* n. sp. (1) Specimen MU13-32(2), (2) specimen MU30-2A.

ocular micrometer. This paper is registered under ZooBank LSID urn:lsid:zoobank.org:pub:9134EA7B-5816-4970-AD00-B2E5506C48EE.

Geological setting

The Mush Valley fossil site is located approximately 160 km northeast of Addis Ababa, Ethiopia, approaching the western shoulder of the Main Ethiopian Rift and at a present-day elevation of about 2500 m. The modern small spring-fed Mush River exposes fossiliferous early Miocene sediments and volcanoclastic deposits on its way, ultimately, to the Blue Nile River. Fossils are found in lacustrine, carbonaceous shales deposited in what appears to have been a volcanic crater lake, as hypothesized on the basis of stratigraphic and geographic relationships among ignimbrites, ashes, and the fossiliferous sediments themselves. The volcanics, which exhibit abundant postdepositional faults, represent one part of Miocene volcanism on a regional scale on the Ethiopian Plateau (Kieffer et al., 2004). Evidence for lacustrine deposition includes the presence of fine sedimentary laminations, fossil frogs, fish, and aquatic plants, and apparent anoxic conditions at the time of burial. Terrestrial input of organic matter includes remarkably well-preserved leaves, fruits, seeds, and less commonly, the bones of large mammals, crocodiles, and at least one rodent tooth. Exquisitely preserved frog fossils also occur in some horizons (Clemens et al., unpublished data). Ignimbrites and ashes occur stratigraphically immediately below and above the fossiliferous carbonaceous shales. The age of the fossils is well-constrained by ^{238}U - ^{206}Pb dates of 21.736 ± 0.054 Ma and 21.73 ± 0.01 Ma on ashes below and above the shales, respectively (Mark Schmitz, personal communication). Thus, the Mush Valley site is the earliest Neogene macrofossil site in East Africa.

Systematic paleontology

Family Mastotermitidae Desneux, 1904

Genus *Mastotermes* Froggatt, 1897

Mastotermes aethiopicus new species

Figures 1.1, 2.1, 2.2

Diagnosis.—The new species may be distinguished by the following combination of traits: hind wing R long; Rs forking before fork in M, not pectinately branched; M rather extensively branching, with initial branching shifted proximad; posterior branch of M forking, disappearing into reticulations, not extending to wing margin as a well-defined longitudinal vein.

Description.—Imago (hind wing). Total length of preserved fragment along anterior (leading) edge 14 mm (estimated total length in life, ca. 30–35 mm), total length of posterior edge of fragment 11 mm, maximum width of preserved fragment 8.5 mm, basal width of preserved fragment 3.5 mm. Membrane without reticulations between R and Rs, and only a few faint reticulations between branches of Rs, remainder of membrane with strongly developed reticulations (Fig. 1), membrane not nodulose or wrinkled. Anterior veins R, Rs, and M more heavily sclerotized than remaining veins, membranes between these veins more darkly pigmented than elsewhere (Fig. 1.1); radial vein simple as preserved, running along anterior of fragment for full length (Fig. 1.2); Rs branching at extreme base of fragment and before branching in any other preserved longitudinal veins (Fig. 1.2), anteriormost branch running close to and parallel with R, simple across entire preserved length, posteriormost branch forking twice along preserved length, first fork at point slightly beyond tangent of first fork in posterior branch of M, second fork at point near tangent with midpoint between first and second forks in anterior branch of M, no secondary branching in Rs veins (Fig. 1.2); radial sector field only broadening slightly toward apex of fragment; M branching relatively basally, first branching slightly beyond first fork of Rs, posteriormost branch forking at point slightly before tangent with first fork in posterior branch of Rs, posterior branch from this fork disappearing into reticulations at point near apicalmost preserved fork in CuA, anterior branch from this fork simple, extending to apex of fragment; anteriormost branch of M forking at point near tangent of midpoint between first and second fork in posteriormost branch of Rs and then again apical to apicalmost preserved fork in Rs, all branches of anteriormost section of M simple; CuA well developed, branching dichotomously (Fig. 1.2), at least second branches preserved, all except apicalmost three disappearing into reticulations (as preserved, Fig. 1.2), the final course of the apical three branches cannot be ascertained), CuP well developed and sclerotized, extending across entire field of preserved fragment (Fig. 1.2); A1 evident near base of fragment, branching dichotomously, with at least four branches preserved (apicalmost inferior branch very minute at edge of fragment) (Fig. 1.2).

Holotype.—Alate hind wing fragment (Fig. 1.1); MU34-12; Mush collections, National Museum of Ethiopia, Addis Ababa, Ethiopia. The specimen is a trapezoidal fragment of a hind wing

near base but not encompassing the basalmost edge and extending for perhaps what might have been one quarter or slightly more of wing length; anteriorly, fragment preserves the posteriormost R, which must have been long and posteriorly the basal section of A1 (attesting to presence of an anal lobe) and a long section of CuP.

Additional material.—Two additional wing fragments [MU13-32(2) and MU30-2A] of *Mastotermes* were also identified and are likely of the same species. Given that they preserve far fewer traits they are not included in the type series. Both are preserved in the Mush collections, National Museum of Ethiopia, Addis Ababa, Ethiopia.

MU13-32(2) (Fig. 2.1) (imago hind wing fragment, only leading edge clear, length of preserved portion 15.5 mm, maximum width of fragment 5 mm) is a relatively long fragment, incomplete at base and apically, only anterior veins clearly discernible; wing appears crumpled upon itself with posterior margin crumpled toward anterior margin resulting in jumbling of veins; only those longitudinal veins along anterior section discernible and apparently not tied up in crumpled remigium. Apparently short Sc terminating into costal margin; R1 and R2 evident, R1 short and terminating into costal margin, R2 long and apparently terminating into costal margin; preserved portions of R apparently without branches, although if some short anterior branches were present then they might not be discernible given the state of preservation; RS forming a broad field apically with at least three main branches, the first two apparently fused basally and diverging in basal third of preserved wing fragment, both apparently simple although if faint anterior branches were present they might not be discernible as preserved; posteriormost branch of Rs more extensively branching and forming bulk of preserved radial field at least four branches in apical portion of preserved fragment, anterior branch simple, posterior branching twice, first branch with dichotomous branch apical in fragment, second simple within preserved fragment; M simple basally, branching in basal third of preserved fragment, anterior branch simple, posterior branch with at least one inferior branch shortly after separation of M1 and M2; CuA only discernible in basal portion of fragment.

MU30-2A (Fig. 2.2) (imago hind wing fragment, total maximum preserved length 10 mm, maximum length of portion with anterior veins 5 mm, maximum width of fragment 7 mm) is a very tiny fragment through a wing and appears to be from near the wing apex; only anterior five veins preserved, two branching apically, darkened area appears to represent portions of remigial membrane but no veins or reticulations are discernible over lightly browned area relative to surrounding gray matrix. Generally resembles the above fragments in preservation of anterior veins.

Etymology.—The specific epithet refers to the origin of the fossil from Africa and Ethiopia in particular (Aethiopia being a classical Greek name for parts of Africa then known to Europeans), and that this is the sole species of Mastotermitidae from the African continent. The specific name is registered under ZooBank LSID urn:lsid:zoobank.org:act:57C79903-F132-4501-B036-C91B94B71AC9.

Comments.—The presence of a distinct hind wing anojugal lobe (MU34-12) as evidenced by the distinctive arrangement of a

straight CuP (claval fold) posterior to the basal branches of CuA and then the basal part of A1 with its characteristic pectinate branches, are indicative of the Mastotermitidae (Krishna et al., 2013), while the arrangement of the anterior veins is indicative of *Mastotermes* (e.g., compare against *Blattotermes* Riek, 1952, *Spargotermes* Emerson, 1965, *Valditermes* Jarzembowski, 1981, *Khanitermes* Engel et al., 2007b: vide Emerson, 1965; Jarzembowski, 1981; Engel et al., 2007b). *Miotermes* Rosen, 1913, albeit a very ill-defined group of taxa, have a more reduced medial and cubital field (Emerson, 1965), not suggested by the position, orientation, and direction of these veins in the holotype. As discussed above, Mastotermitidae are the only extant termites, as well as the sole family from the Cenozoic, that primitively retain the anojugal lobe. Naturally, it would be ideal to have more of the wing and information from the body (e.g., tarsal segmentation, head structure, pronotal shape), but the available fragments preserve important characters permitting confident identification. The hind wing fragments available preserve multiple radial veins (R1 and R2), another distinctive feature of mastotermitids (other termites have branching within a single radial stem).

Given the generally global Paleogene-Neogene distribution of mastotermitids, relative to their modern restriction to northern Australia, it is perhaps little surprise that one should be found in the Miocene of eastern Africa. Virtually all of the localities from which mastotermitids have been recovered are distinctively tropical or subtropical, and this certainly meshes nicely with the paleoenvironmental reconstruction of the Mush locality (Pan et al., 2012; Pan et al., 2014).

Discussion

Although fragmentary, the preserved venational details of *M. aethiopicus* are diagnostic and permit meaningful comparison with other fossil and living species. From *M. darwiniensis* the new species differs by M with its initial branching nearer to the wing base (in *M. darwiniensis* M does not branch until midwing), and with the posterior branch forking shortly thereafter and disappearing into reticulations slightly before the tangent of the second fork in the anterior branch (in *M. darwiniensis* the posterior branch is simple). The early branching of M is similar to *M. electrodanicus* Krishna and Grimaldi, 1991 from the Dominican Republic, but in that species the first fork in Rs is beyond the fork of M, while in *M. aethiopicus* the fork is before that of M. The new species is most dissimilar to *M. electromexicus* Krishna and Emerson, 1983 in early Miocene amber from southern Mexico (Krishna and Emerson, 1983), particularly in the sequence of basal branching which differs greatly from that of *M. aethiopicus* (cf. Krishna and Emerson, 1983: fig. 2, with our Fig. 1.2). Among other Neogene species of *Mastotermes* the new species can be distinguished by: Rs is pectinately branched in *M. croaticus* Rosen, 1913 (not pectinately branched in *M. aethiopicus*), M bifurcates and then its branches bifurcate apically in *M. croaticus* (M is more extensively branched in *M. aethiopicus*), R1 is very short in *M. croaticus* (R is long in *M. aethiopicus*), the medial system is simplified in *M. minor* Pongrácz, 1928 (extensively branched in *M. aethiopicus*), and the posterior branch of M is simple and reaches the wing margin in *M. haidingeri*

(Heer, 1849) (posterior branch of M is clearly branched and partially disappears into the wing reticulations in *M. aethiopicus*) (Rosen, 1913; Pongrácz, 1928). *Mastotermes aethiopicus* shares with the Oligocene *M. gallica* Nel, 1986 and *M. picardi* Nel and Paicheler, 1993 the early branching of M, although in the former M is less developed than in the other two species. The African species can be distinguished from *M. gallica* by the more extensively developed Rs, while from *M. picardi* it differs in the more simplified medial system and the elongate R (the medial field is broad and composed of numerous branches and R is exceptionally short, terminating shortly after the first fork in Rs, in the latter species) (Nel and Paicheler, 1993).

Mastotermes was clearly once quite global in its distribution, with species extending from the Miocene of Mesoamerica and the Caribbean to the once subtropical forests of Europe. With the gradual loss of suitable habitats across much of this area, it is understandable that many mastotermitids contracted in their range and became extinct. *Mastotermes* was at least still widely distributed by the middle Miocene, and it is at this time unclear what were the precise factors resulting in the loss of diversity and restriction of the genus to non-forested regions in northern Australia. Introductions and persistence of living *M. darwiniensis* in New Guinea (Evans et al., 2013), with significantly higher annual rainfalls than their native occurrences in Australia, suggest that although more humid tropical climates are not ideal, colonies of *Mastotermes* remain capable of surviving, albeit not thriving, in such habitats. Since the various fossil species form an effective grade with respect to *M. darwiniensis*, it is unclear to what extent the ecology of the latter may be applicable to the former, although given that close relatives often share ecological niches, it seems safe to assume some degree of broad overlap (e.g., Peterson et al., 1999). Indeed, if extinct species of *Mastotermes* were more broadly suited to humid environments, the preference of extant *M. darwiniensis* for drier habitats may be a specialization that came about during Miocene-Pliocene drying, and its ability to persist when introduced into humid areas represents nothing more than phylogenetic inertia of past ecological tolerances within the genus. The more dramatic drying events of the Miocene-Pliocene may have had an impact on populations of *Mastotermes*, while other groups of termites such as hodo-termitids and macrotermitines were poised to take advantage of the growing tropical savannas.

The Mush locality likely represents a secondary tropical moist forest (Pan et al., 2012, 2014), which would be in general accordance with an environment suitable for the occurrence of *Mastotermes* based on *M. darwiniensis* and the extinct species from Mexican and Dominican ambers (Krishna and Emerson, 1983; Krishna and Grimaldi, 1991), and suggests that the general restriction of the genus to drier environments had not yet occurred by this time. Given that modern *M. darwiniensis* may have colonies numbering up to a million individuals and be quite damaging, it is likely that *M. aethiopicus* played a significant role in the broader ecology of the Mush forest, contributing to the breakdown of lignocellulose accumulating from the turnover of falling trees. Naturally, the small number of and fragmentary nature of the available specimens hampers any broader ecological or phylogenetic interpretation. Nonetheless, these tantalizing glimpses into the insect fauna of the early

Miocene of the Horn of Africa should encourage future workers to hunt more enthusiastically for hexapods, particularly given the heavy ecological weight wielded by most insects, particularly termites.

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