

A giant termite from the Late Miocene of Styria, Austria (Isoptera)

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Received: 9 September 2008 / Revised: 11 November 2008 / Accepted: 13 November 2008
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Abstract A giant termite is described and figured from the Late Miocene of the Styrian Basin in southeastern Austria. *Gyatermes styriensis* gen. n. et sp. n. is represented by a relatively complete forewing, with basal scale. The fossil approximates in size the largest of all termites today and is the largest fossil termite on record. The presence of this species in the Late Miocene fauna of Europe indicates that climatic conditions were appropriate for the persistence of species and colonies requiring relatively stable, warm conditions. The genus is primitive in overall features but shares some similarity with the dampwood termites.

Keywords Insecta · Isoptera · Termites · Miocene · Tertiary · Austria

Introduction

Termites belong to a triumvirate of social insects which dramatically shape terrestrial ecosystems throughout the world. Although they have modest species numbers, comprising 2,958 living species (compared to the bees

and ants with 19,254 and 12,463 species, respectively: numbers valid as of 7 November 2008), without the vital role of termites, entire ecosystems would crash (Grimaldi and Engel 2005). Like honeybees, ants, some wasps, and a few other organisms, all termites are advanced eusocial, with individuals behaviorally and anatomically specialized for specific tasks within the colony. This organization accounts for the efficiency with which termites process the most abundant terrestrial biomolecule, lignocellulose, and for the billions of dollars of damage colonies impose on human architectural structures. For good or bad, the termites are a dominant force in the world, impacting both natural and human-created ecosystems. Yet, the history that shaped this force has historically been obscured or ignored (Grimaldi and Engel 2005).

Extensive study of the Cenozoic record has revealed to date little insight into the diversity of higher termites, although the order appears to not have become as ecologically ubiquitous as it is today until sometime during the latter half of this period (Thorne et al. 2000; Grimaldi and Engel 2005; Engel et al. 2009). Tertiary faunas preserved in amber have documented relatively modern faunas (e.g., Engel 2008; Engel and Krishna 2007a, b; Engel et al. 2007a), although those in the Baltic region during the middle Eocene (45 million years ago) were principally composed of primitive families, and species were of moderate abundance (Nel and Bourguet 2006; Engel et al. 2007a; Engel 2008). Nonetheless, all hitherto documented Tertiary species were of proportions similar to their modern counterparts and, although some could be relatively large as species of the order are concerned, none were of gargantuan size despite the existence of climatic conditions more suitable to larger insects and their associated colonies. Recently, however, a giant termite, representing an undescribed genus and species similar in

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some respects to the primitive genus *Termopsis* Heer (1849) (also from the Tertiary of Europe, with wings ranging from 12 to 26 mm), was recovered from Late Miocene sediments of the Styrian Basin in Austria. Herein, we document this giant primitive termite, with its wing length of 33.5 mm (and possible wing span of nearly 76 mm when thoracic width is also considered), demonstrating that the paleoclimate was such to support species of far greater than average proportions and that such primitive species persisted in Europe well into the Neogene.

The format and morphological terminology for the descriptions follow that of Engel et al. (2007a, b). Photomicrographs were prepared using a Nikon D1x digital camera attached to an Infinity® K-2 long-distance microscopic lens. Metrics were made using an ocular micrometer on an Olympus SZX12 stereomicroscope.

Geological setting and paleoecology

The prodigious species discussed herein was discovered in Upper Miocene (Lower Pannonian [Lower Tortonian, equivalent global stage]) fluviolacustrine deposits from Paldau in the eastern Styrian Basin at the western margin of the Pannonian Basin System (Ebner and Sachsenhofer 1991; Gross et al. 2007; Fig. 1). Paleogeographically, the Styrian Basin belongs to the area of the Central Paratethys, which became restricted to the Pannonian Basin during the onset of the Late Miocene. A vast, long-lived, successively freshening lake evolved, the so-called Lake Pannon (Magyar et al. 1999; Piller et al. 2007).

Lake level fluctuations triggered by geotectonics and climate caused short-term trans- and regressions and thus repeated interchanges between lacustrine Lake Pannon and its adjacent terrestrial environments. Supported by lithostratigraphy, paleomagnetical investigations, and biostratigraphy with well-known endemic mollusc lineages and mammals, these oscillations enabled also the introduction of high-resolution sequence stratigraphical schemes for intra- and extrabasinal correlations (Kosi et al. 2003; Harzhauser et al. 2004; Schreilechner and Sachsenhofer 2007).

At the gravel-pit of Paldau, a complete fluvial fining-upward cycle of a gravel-bed to gravel-sand meandering river (sensu Miall 1996) is exposed and intensively studied in respect to its various subfacies units and vegetational habitats (Gross 1998; Krenn 1998; Gross et al. 2000; Fig. 2). Stratigraphical correlations argue for an age of ca. 11.3 Ma (Gross 2003, 2004).

The termite wing was found close to the top of the outcrop in a plant-rich, pelitic layer together with some other insect remains (e.g., beetle elytra and fly and ant wings). Sedimentological analyses and paleobotanic contents refer to a deposition in a eutrophic floodplain pond with free-floating water plants bordered by a dense reed zone and a backswamp forest. Based on the nearest living relative approach applied to the fossil leaf-flora, Krenn (1998) suggested a warm temperate climate with mean annual temperatures (MAT) of about 10–16°C, 18–22°C for the mean warmest month temperature, and mean values above 0°C for the coldest month (CMT). Inference about mean annual precipitation (MAP) was obscured due to the azonal character of the vegetation but was suggested to vary

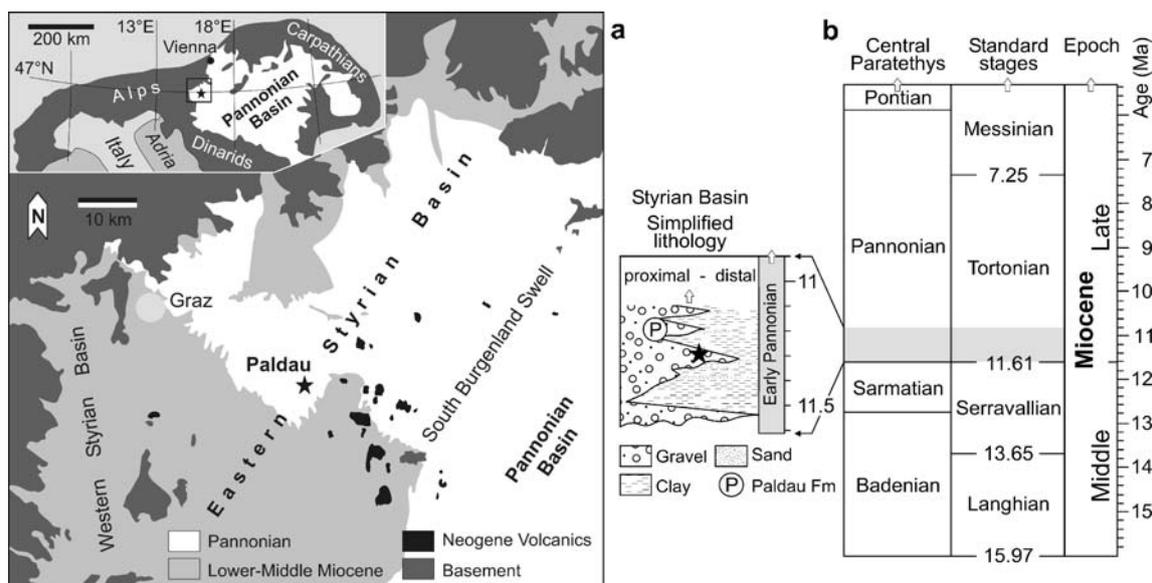


Fig. 1 Geological (a) and stratigraphical (b) position of the Paldau locality, Styrian Basin (15°48'38" E/46°56'17" N). Locality indicated by star

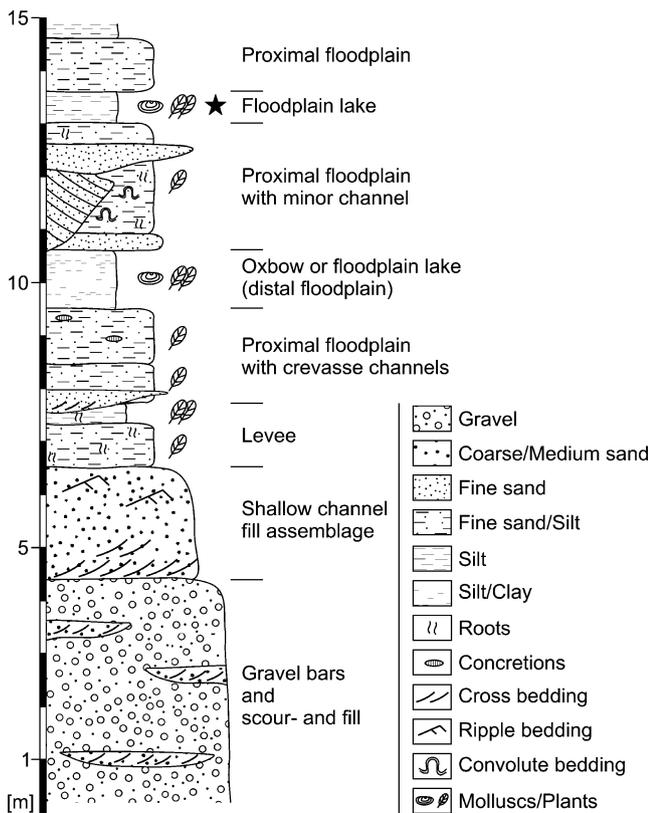


Fig. 2 Lithological profile and facies interpretation of the gravel pit Paldau (=type section of the Paldau Formation). Layer with termite fossil indicated by *star*

between 1,000 and 2,000 mm. Paldau occurred at the end of a relatively dry period (c. 13.2–11.5 Ma) and just prior to the start of a “washhouse” climatic period (Böhme et al. 2008). Perhaps rough modern environmental analogs to that of Paldau would be floodplains or back swamp forests of southern Florida.

These estimations are in agreement with evaluations from geo- and stratigraphically close sites, for which the following climate data are proposed: MAT 15–19°C, CMT >0°, MAP 1,280–1,950 mm (Kovar-Eder and Hably 2006). Recent reviews and quantifications for the climate in Central Europe during the Late Miocene yielded similar results (Bruch et al. 2006, 2007; Erdei et al. 2007).

Systematic paleontology

Genus *Gyatermes* gen. n.

Type species Gyatermes styriensis sp. n.

Diagnosis Imago. Large termites (forewing length, with suture ca. 33.5 mm), with densely reticulate archedictyon

on wing membranes; forewing scale with basal cleavage suture convex, CuP (claval fissure) terminating into suture just prior to posterior wing margin, with reticulations present between CuA and CuP, and posterior to CuP, humeral margin apparently straight; Sc and R elongate; R with at least four branches; Rs with superior and two inferior branches, encompassing wing apex; M extensively developed, encompassing most of posterior wing margin; CuA forming pectinate series of branches in proximal quarter of wing.

Etymology The new genus-group name is a combination of the Latin terms *Gyas* (name for a mythical giant) and *termes* (meaning, “termite”) and is a reference to the large size of the animal. The name is masculine.

Gyatermes styriensis sp. n. (Fig. 3)

Holotype Imago forewing; LMJ 204.148, Late Miocene (Early Pannonian, ca. 11.3 Ma), Paldau, Paldau Formation, Styrian Basin, Austria; deposited in the Landesmuseum Joanneum (LMJ), Graz, Austria.

Diagnosis As for the genus (*vide supra*).

Description Imago forewing. Length including scale (as preserved) 33.50 mm; length of forewing scale (as preserved) 2.34 mm; length of forewing to basal cleavage suture 31.16 mm; forewing maximum width 8.1 mm. Coloration of wings not preserved, membrane densely reticulate with well-developed archedictyon (Fig. 3), membrane between apparently lacking other sculpturing (e.g., no nodulations). Forewing scale with all veins originating within scale (Fig. 3); humeral margin straight (note, however, that preservation along leading edge is less than ideal, and sometimes a convex border can be slightly bent ventrally, e.g., holotype of *Termopsis ukapirmasi* Engel et al. 2007a, giving the appearance of a relatively straight border); forewing basal cleavage suture complete across entire wing (not evanescent posteriorly as in some primitive termites), suture convex; scale surface relatively tegminous, with faint reticulations present between CuA and CuP, and in claval area (area posterior to CuP) (Fig. 3); CuP present as a well-defined vein (sometimes present in other species as weakened line or claval fissure), simple, terminating into basal cleavage suture just prior to posterior wing margin. Veins Sc, R, and Rs (except for a single inferior branch of Rs) more heavily pigmented than other veins; Sc apparently long (only partially preserved), extending at least to one third wing length; R long, extensively developed apically, extending nearly to wing apex, with four anterior branches, R₁ originating in basal third of wing and apparently simple,

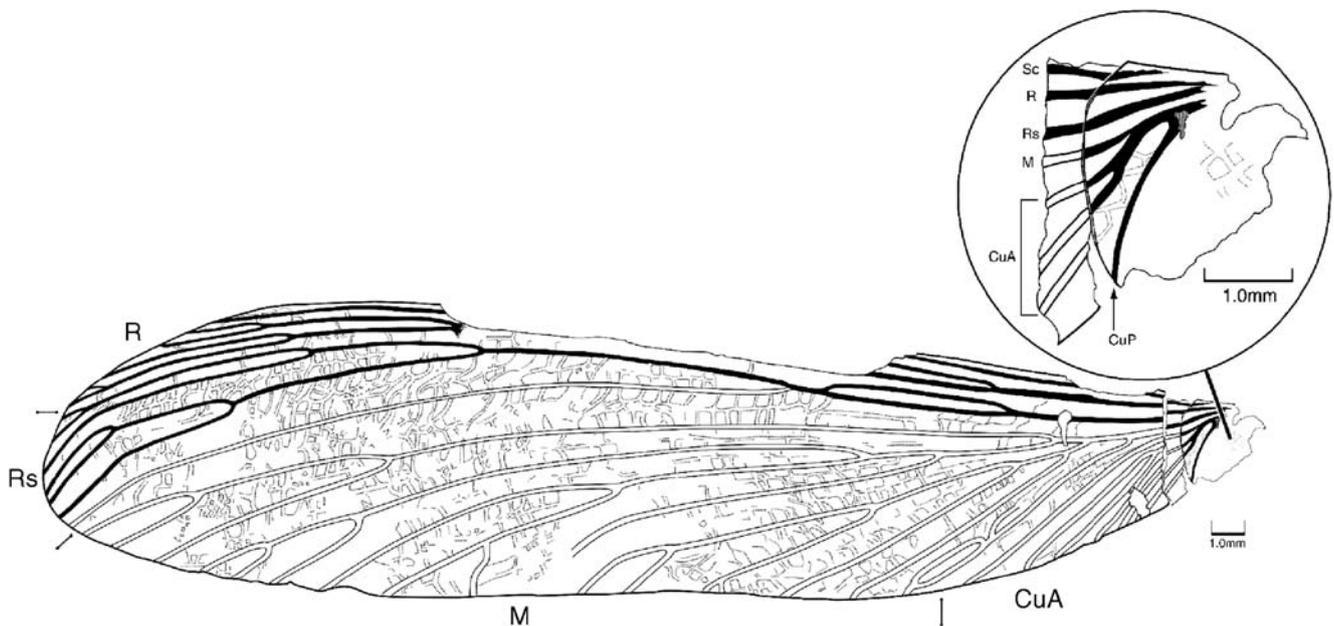


Fig. 3 Photomicrograph (*above*) and line drawing (*below*, as preserved and with details of forewing scale and basal fractured portion of wing enlarged) of holotype of *G. styriensis* gen. et sp. n. (LMJ 204.148), length of wing (including scale) from base to apex

33.5 mm. Note that the wing is fractured near its base slightly distal of the basal cleavage suture, with the scale and the basalmost section of the wing slightly offset (shifted slightly posterior) from the remainder of the wing

terminating on anterior wing margin in apical sixth of wing, remaining branches originating in basal third of wing and terminating on anterior wing margin in apical sixth of wing and before rounded wing apex, R_2 forking before terminating on anterior margin, R_3 simple, R_4 forking right at wing margin; R_s encompassing rounded wing margin, with three

primary branches, Rs_1 branching shortly before its mid-length, anteriormost branch forking at wing margin, posterior branch of Rs_1 simple and terminating at wing apex, R_s with two inferior branches terminating immediately behind wing apex, first inferior branch (Rs_2) forking just beyond its midlength, anteriormost branch forking again

along its midlength, posteriormost branch simple, second inferior branch originating just past basal third of wing length and less sclerotized than remainder of Rs system, simple for its entire length; M extensively developed (Fig. 3), first branch terminating on posterior wing margin just posterior to wing apex, posteriormost branch terminating on posterior wing margin in basal quarter of wing length, with at least 12 main branches and five of those forking near posterior wing margin; CuA very short (as in *T. ukapirmasi* and *Zootermopsis*, albeit more developed in the latter insect), forming series of pectinate branches in basal quarter of wing.

Etymology The specific epithet is based on that province of Austria from which the fossil originates.

Conclusions

Giant insects typically conjure up images of modern tropical beetles, moths, katydids, walking-sticks, or the Paleozoic monsters such as griffenflies, some with over 71-cm wingspans (Grimaldi and Engel 2005). The majority of today's insect diversity, as well as those since the close of the Paleozoic, are of more trifling proportions and certainly those with more robust body sizes are confined to typically warmer and often more humid climates, owing to their physiological requirements. Typically, termites are included among those legions of insect species with more diminutive body sizes, although their numbers and level of organization permit them to wield an ecological impact far greater than their sizes might imply.

Certainly, the cold temperate environs of modern Europe have proved unsuitable for a diversity of termite lineages and have been definitely unable to sustain populations of large termite species such as those seen in the tropics. Nonetheless, such larger species are actually few in number even in the tropics, the largest winged reproductives being those of the genus *Syntermes* (Termitidae: Syntermitinae) from the New World tropics, with individual wings up to 35 mm in length (Emerson 1945; Constantino 1995). Among more primitive termite families, several species of the family Termopsidae *sensu lato* and the sole survivor of the Mastotermitidae, *Mastotermes darwiniensis*, are all robust and can have wing lengths up to 26 mm (e.g., Emerson 1933, 1965) but live in warmer tropical or arid environments. The new discovery, with its wing length of 33.5 mm, was certainly a giant among living and fossil termites and rivals those alates of *Syntermes* from South America. By comparison, most other species of termites, living or extinct, were relative dwarves, with the previously largest termites from the Tertiary of Europe being several

Eocene or Oligocene Mastotermitidae at about 20–27 mm in length (e.g., Krishna and Grimaldi 1991; Wappler and Engel 2006). It is largely speculative what the total body length of *Gyatermes styriensis* imagoes may have been. However, given that total body length in many modern species of “giant” termites tends to be 70–80% of the forewing length, a gross approximation of total body length for *G. styriensis* would be a little over 25 mm. Primitive termites with large body sizes generally have small colony sizes (e.g., 100–1,000 individuals), although those of *M. darwiniensis* are massive, with individuals numbering into the millions. Although *M. darwiniensis* is anomalous among living primitive termites, colony size is not inhibited by body size given that colonies of *Syntermes* typically number more than 30,000 individuals (e.g., Mill 1984). Nonetheless, given that *Gyatermes* is not related to *Mastotermes* and does not belong among the higher termites (see below), colony sizes were likely modest, perhaps more analogous to modern-day colonies of *Zootermopsis* or *Archotermopsis*.

Despite its similar proportions, *Gyatermes* is clearly not related to the giants of the Syntermitinae, which belong to the derived family Termitidae (Engel and Krishna 2004) and all of which have characteristically simplified wing venation. Similarly, the genus can be excluded from the Mastotermitidae by the straight humeral margin, the reduced cubital field and extensively developed medial field, and the presence of a single radial vein, although this vein is branched along its length. Instead, *Gyatermes* exhibits a suite of features primitive among termites and indicative of a basal, paraphyletic grade of groups comprising the Mastotermitidae, Termopsidae *sensu lato*, Hodotermitidae, and numerous living and extinct genera related to them. Primitive termites among this unnatural assemblage typically exhibit the primitive wing features of a densely reticulate archediacyon present between the main longitudinal veins, a relatively tegminous basal scale, reticulations present on the scale between veins CuA and CuP and posterior to CuP, some development of inferior branches present on vein Rs, a multiple-branched radial vein, and often a long subcosta and radius, among other plesiomorphic traits. Much of the termites exhibiting these features were present during the Cretaceous, with a relatively few surviving by the Late Tertiary and even fewer today (e.g., living members of the families Mastotermitidae, Hodotermitidae, and Termopsidae *sensu lato*). All of these wing features are present in *Gyatermes*, indicating that, in its day, it was a surviving relic of this primitive grade of termites.

Among all of these lineages, *Gyatermes* appears to have most affinity with the Termopsidae, as it has historically been defined (Emerson 1933; Engel and Krishna 2004), although this family is demonstrably paraphyletic (or even

polyphyletic) and its composition is undergoing revision (Engel et al. 2009). In many primitive features, the wings of *Gyatermes* resemble those of the Tertiary genus *Termopsis*. Both genera have extensively developed Rs veins that encompass the wing apex, extensively developed medial systems, and a relatively reduced CuA that forms a series of pectinate veins near the wing base. In addition, both genera show some degree of vein reticulation and fusion. For example, in *T. ukapirmasi*, the branches of CuA rejoin at some points or heavily sclerotized portions of the arch-dictyon merged with the veins, creating cells in the wing (Fig. 3). A similar condition is seen in the basalmost branches of M and basally in Rs in *Gyatermes*. Indeed, in primitive termites, the venation is more variable and such fusions of veins are relatively commonly encountered (e.g., Weidner 1967; Engel et al. 2007b), and such vein fusions have sometimes misled authors to erect higher categories in order to accommodate them, failing to recognize that they are merely teratologies or variations (e.g., Schlüter 1989). While the presence of a cell basally in Rs and a cell apically in the basalmost branch of M would appear to be features of *Gyatermes*, given how labile such features are in primitive termites (e.g., Emerson 1933, 1968; Weidner 1967; Coaton 1949, 1958; Roonwal and Bose 1988), these are considered not to be diagnostic traits for the genus or species.

Gyatermes can be readily distinguished from *Termopsis* by its much more abbreviated CuA and correspondingly more developed medial field, by the elongate Sc and R (apomorphically shortened in *Termopsis*), multibranching R (simple in *T. ukapirmasi*, somewhat branched in *T. breinii*), the smaller number of superior branches to Rs, and straight humeral margin to the forewing scale (primitively arched in *Termopsis*), in addition to its much larger size. In some features, *Gyatermes* appears more primitive than *Termopsis*—namely, the elongate Sc and R and the more extensively developed R. In contrast, the putatively straight humeral margin to the forewing scale is a derived feature reminiscent of the primitive living genera *Archotermopsis*, *Hodotermopsis*, and *Zootermopsis*, a group historically classified with *Termopsis* but actually not closely related (Engel et al. 2009). These three genera (a.k.a. the dampwood termites) comprise approximately 11 modern species that generally live in damp, rotting wood (hence their name) and in warm temperate to arid climates. *Archotermopsis*, with two species living in Southeast Asia and the Himalayan region (Afghanistan, Pakistan, northern India), is a distinctly monophyletic group supported by the presence of large lenticular compound eyes in imagoes and the large quadrate heads of soldiers with lateral striations. There is a single species of *Archotermopsis* in Baltic amber (Engel et al. 2007a). The genus apparently most closely related to *Archotermopsis* appears to be *Hodotermopsis*, with a single variable species occurring throughout Asia, owing to the

deep incision between the left apical tooth and the first marginal tooth in the soldier mandible. The last genus, *Zootermopsis*, has three species living in western North America (western USA into southwestern Canada and northern Mexico). Despite having a flat humeral margin as in these other genera, *Gyatermes* has an elongate Sc and R, both of which are more reduced in the aforementioned taxa. Moreover, the cubital field is more developed in all except *Zootermopsis*, which, although reduced in comparison to *Archotermopsis*, is nonetheless more developed than that seen in *Gyatermes*. Lastly, these genera lack the reticulations of the forewing scale primitively seen between CuA and CuP and posterior to CuP in *Gyatermes*.

For now, we have not formally placed *Gyatermes* with any particular lineage of primitive termites. The classification and relationships of the termite families and subfamilies are presently under revision based on a cladistic analysis of living and fossil material (Engel et al. 2009). Moreover, many features of the body, particularly of the pronotum, legs (number of spurs, number and arrangement of tarsal articles), and head, may significantly revise our understanding of *Gyatermes*'s relationship to other primitive termite genera. Accordingly, we await the future discovery of additional, more complete material so that we can obtain a thorough understanding of Europe's lost giant termites.

Acknowledgements It is our pleasure to dedicate this contribution to K. Krishna of the American Museum of Natural History (New York). Dr. Krishna is the reigning authority on the systematics of living and fossil termites and has laid the modern foundation upon which evolutionary work on the order is built. Financial support for this work was provided by National Science Foundation (USA) grant DEB-0542909 (to MSE). The illustration of the wing venation was executed by S. Taliaferro, made possible by the University of Kansas Engel Illustration Fund. We are also grateful to three anonymous reviewers for comments on an earlier version of the manuscript. This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

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