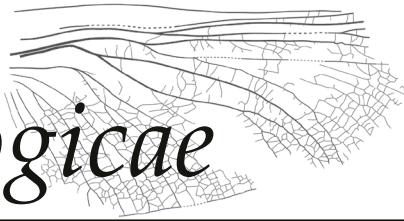


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A giant termite of the genus *Gyatermes* from the Late Miocene of Nagano Prefecture, Japan (Isoptera)

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Abstract. A new species of the termite genus *Gyatermes* Engel & Gross (Archotermopsidae) is described and figured from a beautifully preserved forewing in late Neogene sediments of Nagano Prefecture, central Japan. The approximately 27-mm long forewing of *Gyatermes naganoensis* Engel & Tanaka, new species, is preserved in Late Miocene (late Messinian) mudstone of the Ogawa Formation (*ca.* 6 Ma), and is distinguished from its slightly older and larger congener *G. styriensis* Engel & Gross, from the early Tortonian of Styria, Austria. Comments are provided regarding the paleoclimatic implications of a giant termite in the Miocene fauna of Nagano.

INTRODUCTION

The approximately 3110 species of living termites (Dictyoptera: Isoptera) are among the most influential of insect lineages, their highly organized eusocial colonies wielding considerable ecological dominance in almost every environment in which they are known to occur. These often maligned insects reshape landscapes, break-down large volumes of lignocellulose, augment atmospheric gases, and, among a comparatively small subset of species, have the power to ravage human habitations and agricultural ecosystems (Grimaldi & Engel, 2005). Termites have been about since at least the earliest Cretaceous and likely the latter part of the Jurassic (Grimaldi & Engel, 2005; Engel *et al.*, 2009; Ware *et al.*, 2010; Krishna *et al.*, 2013), although the group did

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not radiate considerably in number of species and abundance until later in the Paleogene (Engel *et al.*, 2009). There is today a rather robust fossil record for Isoptera, with a diversity of phylogenetically primitive lineages spanning the Cretaceous and Cenozoic (Engel *et al.*, 2009). While many of these are preserved with considerable fidelity and have illuminated much of the early history of the termites (Engel *et al.*, 2009), there remain just as many that are challenging to interpret, regardless of whether preserved in amber or as compressions/impressions, given that they are known only from wings shed by dispersing alates or are exceedingly fragmentary (*e.g.*, Pongrácz, 1928; Emerson, 1965, 1967; Weidner, 1967; Weidner & Riou, 1986; Nel & Paicheler, 1993; Prokop & Nel, 1999; Engel & Delclòs, 2010; Engel *et al.*, 2011a; Engel, 2014). Despite the challenges of ascertaining the phylogenetic relationships of such taxa, they do aid faunal reconstructions as well as give insights into the diversity (and disparity) of termites living within a given geological formation and region. Not surprisingly, the largest number of fossil termite species and available specimens come from Cenozoic, largely Neogene, sediments, with particularly well studied faunas being those in amber from the early Eocene of India (Engel *et al.*, 2011b), the Middle Eocene of Europe (Rosen, 1913; Weidner, 1955; Engel *et al.*, 2007a; Engel, 2008), the Early Miocene of Chiapas (Snyder, 1960; Krishna & Emerson, 1983; Emerson, 1969, 1971; Krishna, 1996; Engel & Krishna, 2007a, 2007b), and the Early Miocene of the Dominican Republic (Krishna & Grimaldi, 2009), the latter of which is the most diverse fossil termite fauna known at this time.

While fossil insects are well known and studied from across the islands of Japan, termites are relatively rarely encountered. Prior records of fossil termites from Japan have largely originated from Late Miocene deposits in the Tohoku and Chugoku Regions (Prefectures of Akita, Iwate, Miyagi, Tottori, and Yamagata) (Fujiyama, 1983; Yamana & Maruo, 1992; Hayashi & Nagasawa, 2000), or the Early Pliocene of central Japan (Koshimizu, 1982). Fujiyama (1983) recorded five Late Miocene termite species, almost all of which represented primitive isopteran families (*i.e.*, all families basal to the clade Icoisoptera and consisting of the families Mastotermitidae, Termopsidae, Hodotermitidae, Archotermopsidae, and Stolotermitidae: Engel *et al.*, 2009, 2013; Krishna *et al.*, 2013), and included two species of the extinct genus *Ulmeriella* Meunier (possibly Archotermopsidae but its actual phylogenetic position remains controversial), a species of *Hodotermopsis* Holmgren (Archotermopsidae), and a species of *Stolotermes* Hagen (Stolotermitidae). The fifth species was putatively of the neoisopteran family Rhinotermitidae, but was not assignable beyond familial attribution (Fujiyama, 1983). Interestingly, among primitive termite families the modern Japanese fauna includes only a single species, *Hodotermopsis sjostedti* Holmgren (Krishna *et al.*, 2013). Hayashi & Nagasawa (2000) recorded further material considered near to the *Hodotermopsis* originally documented by Fujiyama (1983). Koshimizu's (1982) material was attributed to 'Hodotermitidae', and Yamana & Maruo (1992) listed two specimens of 'Mastotermitidae' and 'Hodotermitidae', but all of these require confirmation and future study. No other species of fossil Isoptera have been hitherto added to the paleofaunas of Japan.

Here we provide the description of a new giant termite (Figs. 1–2) from the Neogene sediments of Nagano Prefecture, Japan. The specimen was discovered among plant material preserved in tuffaceous mudstone and recorded by Koike & Tanaka (2015) as "Termopsidae gen. et sp. indet.", representing the first record of a termite from the Miocene of central Japan. Further study of the details of the venation of the present specimen reveals that it is representative of a new species in the archotermopsid genus *Gyatermes* Engel & Gross, known previously from the Late Miocene of



Figures 1–2. Photographs of holotype (CHAF-20038) of *Gyatermes naganoensis*, new species, from the Miocene of central Japan. 1. Entire slab containing the termite and plant debris. 2. Detail of wing.

the Styrian Basin in Austria (Engel & Gross, 2009). This is the first Asiatic record of *Gyatermes* and, together with the aforementioned *H. sjostedti* and the Miocene *H. iwantensis* Fujiyama, are the only archotermopsids from the islands of Japan (Krishna *et al.*, 2013). The enigmatic genus *Ulmeriella* Meunier is likely also an archotermopsid and perhaps near *Archotermopsis* Desneux as both have a uniquely apomorphic lenticular compound eye (Weidner, 1955; Emerson, 1968; Engel *et al.*, 2007a; Engel, pers. obs.), and there are two putative species of the genus in the Miocene of Japan – *Ulmeriella uemurai* Fujiyama and *U. shizukuishiensis* Fujiyama (Fujiyama, 1983). However, *Ulmeriella* are poorly defined and various forms ascribed to the genus may belong to different, potentially unrelated groups, including those species described from Japan (Engel, pers. obs.). Reflection on the botheration posed by *Ulmeriella* is beyond the scope of the present contribution but remains a pernicious puzzle in the systematics of Cenozoic Isoptera.



Figure 3. Photograph of the cliff face at Mt. Chausuyama from which the holotype (CHAF-20038) of *Gyatermes naganoensis*, new species, was recovered (photograph by T. Tanaka).

MATERIAL AND METHODS

The wing was recovered along with numerous botanicals (Fig. 1) from the Mt. Chausuyama locality of Nagano, central Japan, and is deposited in the Shinshushinmachi Fossil Museum. The specimen originated in the Ronji Mudstone Member of the Ogawa Formation at Mt. Chausuyama, Nagano City. The south side of Mt. Chausuyama is a cliff formed by repeated landslides (Fig. 3). The lower part of the cliff exposes the Susobana Tuff Member with the Ronji Mudstone Member conformably deposited above it (Fig. 4). The wing was found in the tuffaceous mudstone situated on a bed of lignite within the cliff face (Fig. 4). Also within the same tuffaceous mudstones were recovered several specimens of *Taxodium dubium* (Sternberg) Heer (Cupressaceae) and species of *Alnus* Mill. (Betulaceae). Over 60 species of plants have been reported from the stratum, collectively referred to as the Mt. Chausuyama Fossil Plant Flora (Ohta, 1950; Tomizawa, 1962). Species of the mussel genera *Cristaria* Schumacher and *Anodonta* Lamarck (both Unionoida: Unionidae) and clams of the genus *Corbicula* Megerle von Mühlfeld (Veneroida: Corbiculidae), all of which inhabit fresh or brackish waters, were found in the silt bed just beneath the lignite layer (Fig. 4). It is believed that the stratum was deposited in a river delta and marsh environment. The wing is remarkably complete and only portions of the base and apex are damaged, and with a small bit of the basal leading edge covered by overlying matrix (Fig. 2). The fine details of the membrane surface are preserved, and the high fidelity of the fossil lends hope to the discovery of further insects and their possible implica-

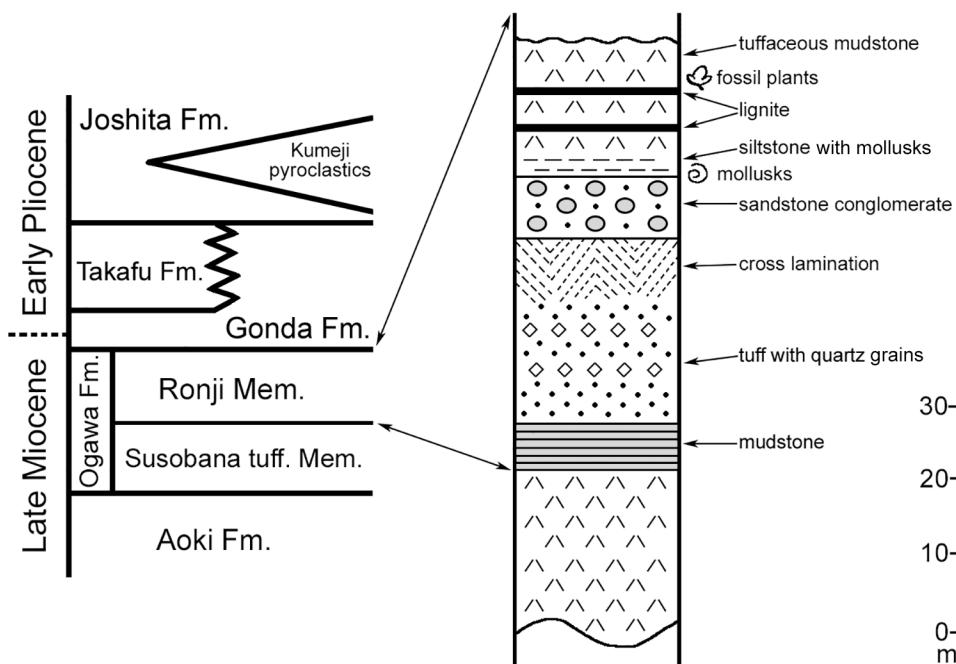


Figure 4. Generalized stratigraphic section (at left) from Shinshushinmachi near Mt. Chausuyama and columnar section of the cliff at Mt. Chausuyayama (at right) (redrawn and modified from Handa, 2014, and Tomizawa, 1962). ‘Fm.’ denotes formation, ‘Mem.’ denotes member.

tions for the fauna. Unfortunately, the stratum at Chausuyama is not laminated and when broken, cleaves into irregular blocks, thereby making it difficult to find such fossils. This is in stark contrast to the Early Pliocene laminites at the nearby Mt. Kabutoiwa where 116 insects from 10 orders and 28 families have been recovered, including some termites (Koshimizu, 1982, 1984).

Although descriptive work or science within the comparative method is mistakenly considered not synthetic or of limited value, it is in reality one of the more fundamental and critical of efforts and is the basis from which broader patterns and explanations are extrapolated (Grimaldi & Engel, 2007), and the below descriptive account is provided in that context. For the systematic descriptions and consideration we follow the forewing terminology of Engel *et al.* (2007b, 2009), Grimaldi *et al.* (2008), and Krishna *et al.* (2013), and the format employed elsewhere for primitive fossil termite species (*e.g.*, Wappler & Engel, 2006; Engel & Gross, 2009; Engel *et al.*, 2013, *in press*). We have followed the classification of Krishna *et al.* (2013), and retained use of the name Isoptera as advocated by Lo *et al.* (2007) and others (*e.g.*, Engel & Krishna, 2004; Engel *et al.*, 2009; Engel, 2011). Photography was done using an Olympus Stylus TG-2 ‘Tough’ digital camera, with images arranged in Adobe Photoshop®.

SYSTEMATIC PALEONTOLOGY

Infraorder Isoptera Brullé
Parvorder Euisoptera Engel *et al.*
Family Archotermopsidae Engel *et al.*

Genus *Gyatermes* Engel & Gross

Gyatermes Engel & Gross, 2009: 291. Type species: *Gyatermes styriensis* Engel & Gross, 2009, by original designation.

DIAGNOSIS (after Engel & Gross, 2009): **Imago.** Large termites (forewing length, including wing scale *ca.* 26.5–33.5 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 (known only for *Gyatermes styriensis* Engel & Gross), with reticulations present between CuA and CuP, and posterior to CuP (known only for *G. styriensis*), humeral margin apparently straight; Sc and R elongate; R branched, with up to four branches; Rs with superior and at least some 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.

INCLUDED SPECIES: *Gyatermes styriensis* from the Late Miocene of Styria, Austria (Engel & Gross, 2009), and the new species *G. naganoensis* from the Late Miocene of Nagano Prefecture, Japan.

Gyatermes naganoensis Engel & Tanaka, new species

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(Figs. 1–2)

Termopsidae gen. et sp. indet.: Koike & Tanaka, 2015: 2 (figs. 2–4).

DIAGNOSIS: New species differs from its congener, *G. styriensis*, in its slightly smaller size (length from base to apex 26.5 mm in *G. naganoensis* versus 33.5 mm in *G. styriensis*), pectinately-branched R2 (R2 more dichotomously branched in *G. styriensis*), less-developed Rs with only two distinct branches apically and numerous incomplete inferior branches (Rs with several complete superior and inferior branches in *G. styriensis*), termination of Rs just posterior to wing apex (Rs encompassing larger field in *G. styriensis*), and initial branching of M within scale (M does not branch until outside of scale in *G. styriensis*).

DESCRIPTION: **Imago forewing.** Length including scale (as preserved) 26.5 mm; forewing maximum width (as preserved) 7.0 mm. Coloration of wing not preserved, membrane densely reticulate with well-developed archedictyon, membrane lacking nodulation or other texturing. Wing scale with all veins originating within scale (basal cleavage suture faint, discernible anteriorly as preserved), M and CuA with their initial forks inside of scale; scale surface not clearly preserved; veins Sc, R, and Rs apparently stronger than other veins; Sc long (partially preserved), extending to between one-third and one-half wing length; R long (partially preserved), forking into R1 and R2 inside of scale, R1 apparently simple (the leading edge is not fully exposed and we cannot exclude the possibility of short anterior branches on R1), R1 apparently terminating on anterior wing margin just beyond wing midlength, R2 branching in apical two-thirds of wing length, with at least 5 anterior branches, each branch simple and arising in pectinate arrangement, posterior-apicalmost branch of R2 apparently terminating just anterior wing apex; Rs apparently encompassing wing apex, with several incomplete posterior branches that merge into archedictyon, forking more distinctly in apical fifth of wing length, posteriormost branch apparently terminating

just posterior to wing apex; M extensively developed, anteriormost branch apparently terminating on posterior wing margin just posterior to wing apex, posteriormost branch terminating on posterior wing margin at basal quarter of wing length, with at least 13 main branches, several with subsidiary branches and forking near wing margin, although most in basal half of wing length simple; CuA short (similar to that of *G. styriensis*, *Zootermopsis* Emerson, and *Termopsis ukapirmasi* Engel *et al.*), forming series of pectinate branches in basal quarter of wing length, all branches terminating along posterior wing margin.

HOLOTYPE: Imago forewing; CHAF-20038, Late Miocene (late Messinian, *ca.* 6 Ma), Ronji Member, Ogawa Formation, Mt. Chausuyama, Shinonoi, Nagano City, Nagano Prefecture, Chūbu Region, Honshu, Japan, collector Shigeru Karasawa; deposited in the Shinshushimachi Fossil Museum, Nagano, Japan.

ETYMOLOGY: The specific epithet is based on Nagano Prefecture, from which the specimen originates.

DISCUSSION

It is remarkable that a giant termite referable to *Gyatermes* might be recovered from Late Miocene deposits of central Japan, and at considerable distance from the Styrian Basin where *G. styriensis* was discovered. During the Miocene and Early Pliocene Honshu was already separated from mainland Asia, and as would be expected, the climate was generally warmer than at present. The flora of the deposits is indicative of a mixed temperate and moist environment, with many deciduous plants of both warm and some cool temperate clades, as well as some subtropical elements, such as *Glyptostrobus* Endlicher (Tomizawa, 1962). The preceding Tortonian was characterized by generally warm temperate, fully humid, and hot summer conditions across Japan (Tang *et al.*, 2011), and this would have persisted to some degree through to the Early Pliocene (Zanclean), when seemingly permanent 'El Niño' effects were still present (Wara *et al.*, 2005). The presence of a large-bodied termite such as *G. naganoensis* in the fauna around Nagano is certainly consistent with a warmer, more humid climate. It is not surprising that with the much later close of the Pliocene and the dramatic shift into the colder global environment of the Pleistocene (Filippelli & Flores, 2009), species such as *G. naganoensis* would have been unable to survive, although it is at present unknown to what degree such large-bodied, primitive dampwood termites would have extended beyond the Messinian. Unfortunately, aside from its occurrence in the Late Miocene, there is little more than we can infer from or deduce about *G. naganoensis* given the currently available information. It will be critical to continue exploration of these deposits for more completely preserved material, and perhaps even evidence of their feeding or nest-building behaviors. It is possible that the biology of *Gyatermes* was much like modern genera such as *Zootermopsis* or *Archotermopsis*, suggesting a possible preference for nesting in moist, rotting wood, and which would accord with a near coastal, forested, riverine environment such as appears to be the case in Late Miocene Nagano. Given the possible environmental conditions that were present, it is likely there was a more developed isopteran fauna, particularly for mastotermitid, stolotermitid, and other archotermopsid species, all of whom exhibit relict modern distributions (Krishna *et al.*, 2013). The presence of Late Miocene species of the same genus in central Europe and central Japan indicates that the genus was either widespread across Eurasia during the Neogene, or was disjunct and perhaps already relict by the closing stages of the epoch. Extensive paleoentomological exploration is

needed across the Neogene in order to expand and refine our understanding of termite evolution during the period as at present the vast majority of fossils come from a surprisingly restricted number of deposits (summarized in Krishna *et al.*, 2013), impeding for the moment broader generalizations of isopteran historical biogeography.

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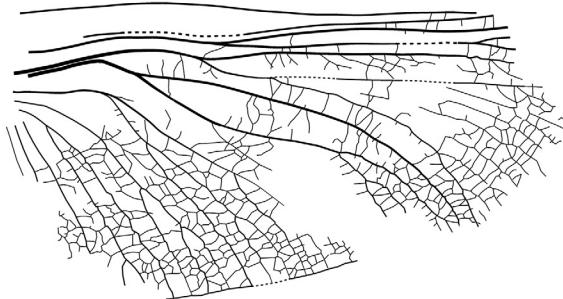
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Pharciphyzelus lacefieldi Beckemeyer & Engel, 2011

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Occasional Contributions to Paleoentomology

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