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A synopsis of Baltic amber termites (Isoptera)

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Abstract

A brief overview and dichotomous key is provided for those termites (Isoptera) occurring in middle Eocene (Lutetian) Baltic amber. Ten species in seven genera are presently documented from Baltic amber, these being as follows: *Garmitermes succineus* n. gen. n. sp., *Termopsis bremii* (Heer), *T. ukapirmasi* n. sp., *Archotermopsis tornquisti* Rosen, *Proelectrotermes berendtii* (Pictet-Baraban), *Electrotermes affinis* (Hagen), *E. girardi* (Giebel), *Reticulitermes antiquus* (Germar), *R. minimus* Snyder, and *Parastylotermes robustus* (Rosen). *Garmitermes succineus* n. gen. n. sp. is the first *Mastotermes*-like termite discovered in Baltic amber. *Hemerobites* Germar, a senior synonym of *Reticulitermes* Holmgren, is designated as a nomen oblitum under the ICZN rules. *Maresa* Giebel, another senior synonym of *Reticulitermes*, is tentatively suppressed pending a petition to the ICZN to preserve the latter name.
Keywords: Amber, distribution, Isoptera, paleontology, taxonomy, termite, Tertiary, Eocene.

Zusammenfassung

Es wird ein kurzer Überblick über die Termiten (Isoptera) aus dem Mitteleozän des Baltischen Bernsteins gegeben sowie ein dichotomer Bestimmungsschlüssel für diese Arten erstellt. Die folgenden sieben Gattungen mit zehn Arten sind gegenwärtig aus dem Baltischen Bernstein dokumentiert: *Garmitermes succineus* n. gen. n. sp., *Termopsis bremii* (Heer), *T. ukapirmasi* n. sp., *Archotermopsis tornquisti* Rosen, *Proelectrotermes berendtii* (Pictet-Baraban), *Electrotermes affinis* (Hagen), *E. girardi* (Giebel), *Reticulitermes antiquus* (Germar), *R. minimus* Snyder und *Parastylotermes robustus* (Rosen). *Garmitermes succineus* n. gen. n. sp. ist die erste *Mastotermes*-ähnliche Termite, die im Baltischen Bernstein entdeckt worden ist. *Hemerobites* Germar, ein älteres Synonym von *Reticulitermes* Holmgren, wird entsprechend den Regeln der ICZN als nomen oblitum eingestuft. *Maresa* Giebel, ein weiteres älteres Synonym von *Reticulitermes*, wird vorläufig unterdrückt, bis über den Antrag an die ICZN, den letzteren Namen beizubehalten, entschieden ist.

Contents

1. Introduction

Baltic amber has an ancient allure. PLINY the Elder (GAIUS PLINIUS SECUNDUS, 23–79 A. D.) recorded that during the reign of NERO CLAUDIUS CAESAR AUGUSTUS GERMANICUS (37–68 A. D., reigned 54–68 A. D., last of the Julio-Claudian Dynasty) the value of an amber object exceeded that of a healthy, male slave, so great was the emperor's passion for the prized commodity. At the same time, many gazed with awe at the insects elegantly preserved therein and even the great Roman poet MARCUS VALERIUS MARTIALIS (c. 40–c. 103 A. D.) composed epigrams immortalizing the insects he observed in succinite. The same intrigue with Baltic amber inclusions continues today, although with a more refined view that they represent species from the long extinct tropical forests of the Eocene epoch. The Eocene was the last global "hot house" climate, and Europe was covered by seasonal paratropical forests, with the southern portions of the continent composed of archipelagos in a warm, relatively shallow sea. It was during this Early Paleogene episode (i. e., Paleocene-Eocene) when termites (order Isoptera) appear to have risen to dominance (GRIMALDI & ENGEL 2005). The Tertiary termite fauna is, therefore, of considerable significance for understanding the formation of modern termite diversity.

Herein we provide a brief overview of the Baltic amber termite fauna. Most species have received relatively recent and thorough treatments by other authors and so we provide only a brief review of those genera occurring in Baltic amber and provide descriptions for two new species (one in a new genus). The rhinotermitids have been thoroughly described by EMERSON (1971), the kalotermitids by KRISHNA (1961) and EMERSON (1969), and the termopsines by EMERSON (1933). In addition, WEIDNER (1955) provided a brief account of each species known to him and these were subsequently catalogued by KEILBACH (1982) and SPAHR (1992).

The age and origin of Baltic amber has been discussed by various authors, most recently by ENGEL (2001), WEITSCHAT & WICHARD (2002), and GRIMALDI & ENGEL (2005). The types of the new species are deposited in the Amber Fossil Collection, Division of Invertebrate Zoology, American Museum of Natural History, New York (AMNH).

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2. Systematic paleontology

2.1. Key to termites in Baltic amber

The following key is based solely on imagoes, the only caste hitherto known from Baltic amber.

1 Metatarsus pentamerous, either completely or cryptically (i. e., with second tarsomere not evident in dorsal aspect, but visible in lateral or ventral aspect) **2**
– Metatarsus tetramerous or trimerous **5**
2 Ocelli absent; pronotum narrower than head; costal area of forewing scale relatively narrow; cleavage suture of forewing weakly arched; hind wings with defined cleavage suture **3**
– Ocelli present; pronotum much broader than head, saddle-shaped; costal area of forewing scale large; cleavage suture of forewing strongly arched; hind wings without cleavage suture, torn when shed . . . . . ***Garmitermes succineus*** n. gen. n. sp.
3 Compound eye circular, not enlarged, anterior border not concave or emarginate; metatarsus completely pentamerous; antenna with 22–24 articles **4**
– Compound eye large, anterior border distinctly concave; metatarsus cryptically pentamerous (i. e., with second tarsal article visible ventrally but hidden dorsally); antenna with 18–19 articles . . . . . ***Archotermopsis tornquisti*** Rosen
4 Length of forewing from basal cleavage suture ca. 14.8–16.2 mm; forewing basal suture complete, clearly meeting posterior margin; stems of Rs and M joined for short distance in forewing scale . . . . . ***Termopsis bremii*** (Heer)
– Length of forewing from basal cleavage suture ca. 12 mm; forewing basal suture evanescent in posterior third; stems of Rs and M separate in forewing scale . . . . . ***Termopsis ukapirmasi*** n. sp.
5 Fontanelle absent; tarsi tetramerous; wing membrane wrinkled or with weak reticulations between some of the longitudinal veins **6**
– Fontanelle present; tarsi trimerous or tetramerous; wing membrane densely reticulate between veins (Fig. 10b) **8**
6 Mesotibia with two outer spines, inner spine absent; R terminating on anterior wing margin in basal third of forewing; CuP (claval fissure) terminating on posterior margin prior to basal suture; 15–18 antennal articles **7**
– Mesotibia with two outer spines and one inner spine; R terminating on anterior wing margin near forewing midpoint; CuP (claval fissure) terminating at posterior edge of basal suture; 19–20 antennal articles . . . . . ***Proelectrotermes berendtii*** (Pictet-Baraban)
7 Forewing length with scale 8.84–8.94 mm . . . . . ***Electrotermes affinis*** (Hagen)
– Forewing length with scale 6 mm . . . . . ***Electrotermes girardi*** (Giebel)
8 Setae of head and pronotum sparse and short (setae distinctly shorter than length of scape); pronotum slightly narrower than head; tarsi tetramerous **9**
– Setae of head and pronotum more numerous and long, particularly on the latter (setae as long as or longer than scape); pronotum distinctly narrower than head; tarsi trimerous . . . . . ***Parastylotermes robustus*** (Rosen)
9 Body size moderate, length of forewing from suture 6.5–8.8 mm; antenna with 17–20 articles; ocellus separated from compound eye by slightly less than ocellar width; anterior border of pronotum with slight medial indentation . . . . . ***Reticulitermes antiquus*** (Germar)
– Body size minute, length of forewing from suture 3.94 mm; antenna with 13–14 articles; ocellus separated from compound eye by ocellar width; anterior border of pronotum straight . . . . . ***Reticulitermes minimus*** Snyder

2.2. Baltic amber genera and new species

The following account provides brief comments on those termite genera occurring in Baltic amber. In addition, we include the description of the two new species (one in a new genus) and discuss the status of the previously proposed taxa. Family-group names follow those of Engel & Krishna (2004a, 2004b, 2007).

Family Mastotermitidae DESNEUX, 1904a

Genus *Garmitermes* n. gen.

Type species: *Garmitermes succineus* n. sp.

Etymology: The new genus-group name is a combination of the names GARM, from Norse mythology, and *Termes*, meaning termite and the type genus of Isoptera. GARM was the CERBERUS of Norse mythology, and was a giant, ferocious dog living in the cave Gnipahellir and guarding Helheim, land of the dead (ruled by HEL, goddess of the underworld). The name is masculine.

Diagnosis. – Head robust and approximately circular, lateral borders parallel-sided (Figs. 1–2a), distinctly opisthognathous; Y-shaped coronal (epicranial) ecdysial cleavage line very faint (Fig. 2a); compound eyes large, circular; ocelli present, large, adjoining compound eyes (Fig. 2a); fontanelle absent; antenna moniliform, with 26 articles, distinctly tapered for apical 7–8 articles; occipital carina present (Fig. 3). Lateral cervical sclerites enlarged (Fig. 3). Pronotum very large, saddle-shaped (covering most of prothoracic pleura) (Figs. 1–2a), anterior margin weakly concave, lateral margins gently converging posteriorly, medio-posterior margin almost straight. Metascutellum broad, plate-like, slightly projecting posteriorly over abdominal base. Procoxae with distinct ventral carina (i. e., "procoxae keeled"); tibial spur formula 3-5-4, spurs stout, asymmetrical, each with ventral concavity, minutely serrate (Fig. 2b, c); protibia without subapical spines; mesotibia with two outer spines; metatibia with a single, subapical spine; all tarsi completely pentamerous, with distinct plantular pads (Fig. 2b, c), with papillae, present on apico-ventral surfaces of basal four tarsal articles; pretarsal ungues simple, arolium either greatly vestigial or absent (a small stub can be seen between the ungues that is either the apex of the unguitractor or perhaps a highly reduced arolium). Forewing scale large, almost entirely covering hind wing base (Figs. 1–2a), heavily sclerotized and pigmented (nearly tegminous), apical margin broadly convex, humeral margin broadly convex, intersects CuP, with broad costal area (as in *Mastotermes*); fine fracture between R and M (as in *Mastotermes*) (Fig. 2a); claval area with scattered, faint dimples (rudimentary archedictyon); CuP (claval fissure) broadly arched, terminating at posterior edge of basal suture; venation of scale distinctly corrugated, pattern of venation as in *Mastotermes*, with all veins originating in scale, single stems of Sc and R, Rs pectinately branching in scale (two branches within scale), M+CuA stem giving rise to M and CuA, the latter forming two branches in scale; distinct reticulations present between CuA and CuP (claval fissure). Hind wing without basal suture, margin roughly torn. Sternites narrow, apical sternite with posterior margin cleft along medial line of sternite (cleft extends approximately one-third sternal length); two slightly protruding lobes at apex of sternite (perhaps membranous) (Fig. 3a); cerci extending beyond abdominal apex, segmentation not discernible (perhaps with at least four articles but this is entirely uncertain and total number of articles, if any, is not ascertainable as the cerci are largely obscured), densely covered with stout, apically-directed setae (styli are also likely present but obscured).

Comments. – *Garmitermes* is the first mastotermitid-like fossil discovered in Baltic amber. Like *Mastotermes*, *Garmitermes* has a large pronotum that is broader than the head, ocelli, has a large forewing scale that almost completely overlaps the hind wing base, the hind wings torn rather than shed along a basal suture, a radial fracture, the tarsi of all legs completely pentamerous, and a primitive 3-5-4 tibial

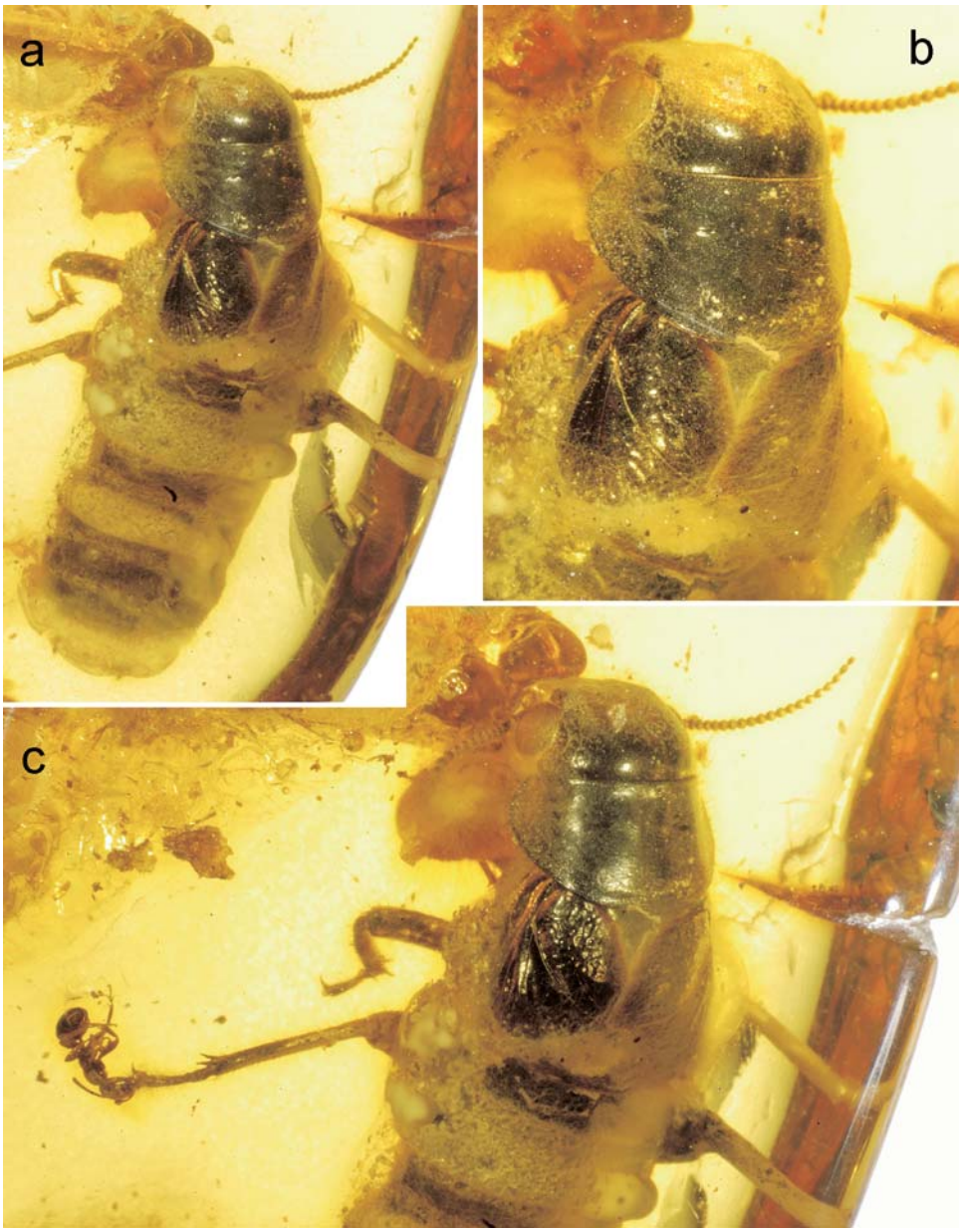

Fig. 1. Dealate imago of *Garmitermes succineus* n. gen. n. sp., holotype (AMNH B-JH-118). **a**: Dorsal aspect. **b**: Detail of head, pronotum, and forewing scales. **c**: Anterior half of specimen showing extended hind leg with worker of *Liometopum oligocenicum* WHEELER grasping tarsus. The pronotum serves as the best scale for all images, the median length being 2.20 mm.

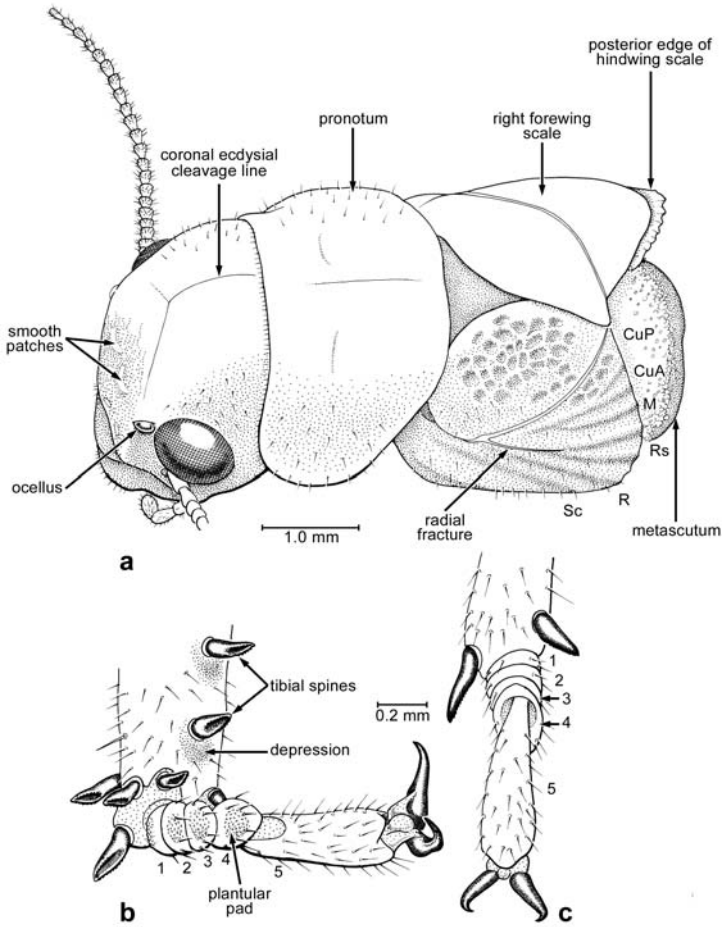

Fig. 2. *Garmitermes succineus* n. gen. n. sp., holotype (AMNH B-JH-118). **a**: Oblique dorsal view of head and thorax. **b**: Detail of mid leg showing mesotarsus and mesotibial apex as preserved; view of mesotibia is slightly distal looking proximad, view of mesotarsus is ventral. **c**: Detail of foreleg showing protarsus and protibial apex in dorsal view.

spur formula. In contrast to *Mastotermes*, the head is opisthognathous, the lateral cervical sclerites are distinctly larger, the pronotum extremely bowed and wrapped laterally, the metascutellum is greatly enlarged, the mesosternum is well-developed (Fig. 3b), the arolium of the new genus is either greatly vestigial or absent, the tarsal plantular pads are present on the ventro-apical surfaces of the basal four tarsal articles, the number of antennal articles is reduced (26 in *Garmitermes* versus 29–32 in *Mastotermes*) and the apical articles are tapered. We have retained *Garmitermes* in the Mastotermitidae pending the results of an on-going phylogenetic analysis of basal living and fossil termites (GRIMALDI, ENGEL & KRISHNA in prep.).

Mastotermes is well documented in the Tertiary faunas of Europe, including the roughly contemporaneous fauna of Eckfeld Maar in Germany (WAPPLER & ENGEL 2006). Accordingly, it had been considered somewhat enigmatic that mastotermitids were unknown from the Baltic amber fauna. Indeed, NEL & BOURGET (2006), not-

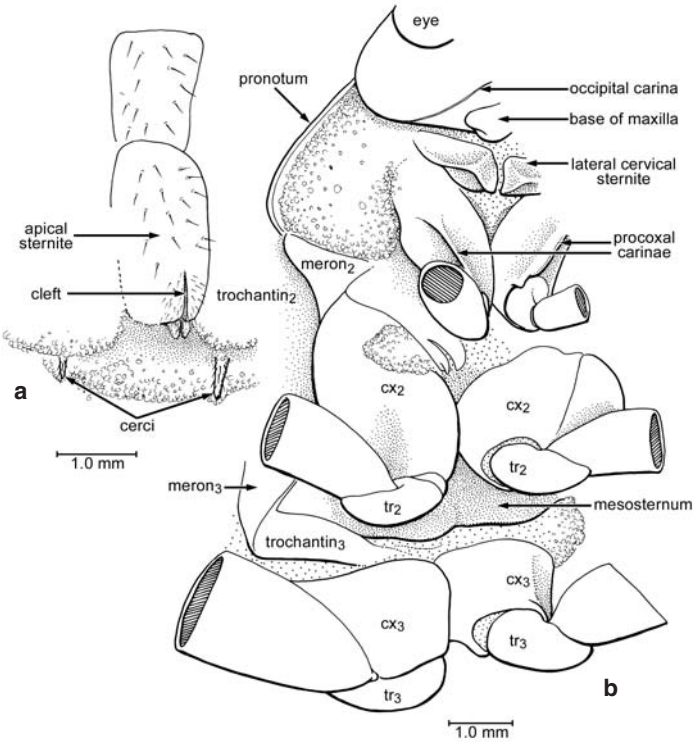

Fig. 3. Ventral structures of *Garmitermes succineus* n. gen. n. sp., holotype (AMNH B-JH-118). **a**: apex of abdomen, showing those structures obscured by froth and bubbles, depicted are the apical two sternites and apices of cerci. **b**: ventral view of thorax and extreme posterior of head.

ing this conspicuous absence, suggested that mastotermitids are preserved only in ambers of angiosperm origin and that the chemical composition of the coniferous resin comprising Baltic amber had a "repulsive action" on such termites. The discovery of the mastotermitid *G. succineus* n. gen. n. sp. in Baltic amber now nicely eliminates that absence and clearly the chemical composition of succinite has not served as an effective repellent.

Garmitermes succineus n. gen. n. sp.

Figs. 1–3

Holotype: Imago (Fig. 1); AMNH B-JH-118; middle Eocene (Lutetian), "Blaue Erde" deposit, Baltic amber.

Etymology: The specific epithet is the Latin term succineus, meaning "amber".

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

Description. – Imago. Length of head to mandibular base 2.70 mm; head width 2.50 mm; compound eye diameter 1.07 mm; distance between compound eye and lower head margin 0.26 mm; ocellar length 0.30 mm; maximum length of pronotum

2.50 mm; median length of pronotum 2.20 mm; width of pronotum 3.80 mm; metatibial length 3.06 mm; length of forewing scale 2.86 mm. Integument faintly imbricate, apparently dark brown on head, pronotum, and wing scales; antennae light brown; legs brown; abdomen (where evident through Schimmel) apparently brown. Head and pronotum with exceedingly sparse pilosity, mostly confined to margins, setae short (length of setae shorter than ocellar length); forewing scale with scattered, erect, short setae, mostly in anterior half.

Comments. – Interestingly, the holotype is preserved with a small worker ant, apparently of *Liometopum oligocenicum* WHEELER (Hymenoptera: Formicidae: Dolichoderinae), biting its apicalmost metatarsomere (Fig. 1c); evidence that the bitter feud between termites and ants has lasted far longer than the battles between the tribes and nations of men.

Family Termopsidae HOLMGREN, 1911

Genus *Termopsis* HEER, 1849

1849 *Termes (Termopsis).* – HEER, p. 23. Type species: *Termes bremii* HEER, 1849, by subsequent designation of ICZN (2005).
1913 *Xestotermopsis.* – ROSEN, p. 329. Type species: *Termes bremii* HEER, 1849, by original designation.

Comments. – The genus *Termopsis* was originally established as a subgenus of *Termes* (at that time encompassing all known termites) but was quickly elevated to generic rank as LINNAEUS's genus was subdivided. Four species are presently classified in *Termopsis*, although only one of these, namely the type species *T. bremii*, is found in Baltic amber. The other three species are known only as later Tertiary compressions: *T. gracilipennis* THÉOBALD from the Oligocene of France, *T. mallaszi* PONGRÁCZ and *T. transsylvanica* PONGRÁCZ from the Miocene of Hungary. Among termopsine termites, *Termopsis* can be immediately recognized by the compound eyes circular, not prominent or large (Figs. 5a, 7a); the absence of ocelli; the pronotum slightly narrower than head, with its lateral borders about parallel to weakly convergent posteriorly; the completely pentamerous tarsi (but see *T. ukapirmasi*, infra), with all five articles visible in dorsal as well as ventral aspect; the absence of the arolium (but see *T. ukapirmasi*, infra); the forewing basal suture only slightly curved (nearly straight); and the long cerci, extending beyond the apex of the abdomen but not elongate as in *Archotermopsis* and with 5–6 articles. Herein we describe a second, much smaller, species of *Termopsis*.

Termopsis ukapirmasi n. sp.

Figs. 4, 5–6

Holotype: Imago (Fig. 4); AMNH B-JH-Iso4; middle Eocene (Lutetian), "Blaue Erde" deposit, Baltic amber.

Paratype: Imago; AMNH B-JH-Iso2; middle Eocene (Lutetian), "Blaue Erde" deposit, Baltic amber.

Etymology: The specific epithet is taken from ancient Prussian mythology and is the name, UKAPIRMAS, of the god who created the world.

Fig. 4. Imago of *Termopsis ukapirmasi* n. sp., holotype (AMNH B-JH-Iso4). – Scale bar = 1 mm.

Diagnosis. – The new species can be readily distinguished from the only other *Termopsis* in Baltic amber, *T. bremii* (Fig. 7), by the smaller body size, the form and venation of the wing scale, and the posteriorly evanescent basal suture and claval fissure (CuP) (vide etiam Key, supra). In overall size the new species approximates *Archotermopsis tornquisti* from which it can be distinguished by the smaller and circular compound eye, the 23 antennal articles, and the pentamerous tarsi, among other characters distinguishing these two genera.

Description. – Imago. Total length with wings 16.2 mm; body length 10.5 mm; length of head to mandibular base 1.80 mm; head width 2.10 mm; compound eye diameter 0.59 mm; distance between compound eye and lower head margin 0.23 mm; maximum length of pronotum 1.07 mm; width of pronotum 1.99 mm; metatibial length 2.65 mm; forewing length to basal suture 12.0 mm; forewing width 4.1 mm; length of forewing scale 1.33 mm. Integument, where evident, faintly imbricate. Head rounded and dark brown; compound eyes not large, circular, not prominent (Fig. 5a); separated from posterior border of head by nearly twice their diameter; antenna with 23 articles, brown; head with exceedingly sparse, short, erect to suberect setae. Pronotum brown, slightly narrower than head, anterior margin faintly concave, lateral borders weakly converging posteriorly, posterior border almost straight; setae exceedingly short, suberect, and sparse, mostly on lateral borders. Legs brown; tibial spur formula 3-4-3 (Fig. 5c, d); protibia with three apical spurs, without spines; mesotibia with four apical spurs, with one subapical spine; metatibia with three apical spurs, with one subapical spine; arolium present. Forewing scale with all veins originating inside scale; humeral margin with weakly arched lobe present, otherwise relatively straight (Fig. 5a: depicted as preserved with the lobe partially folded ventral to the plane of the wing); forewing basal suture evanescent in posterior third; CuP (claval fissure) evanescent near posterior wing margin, relative-

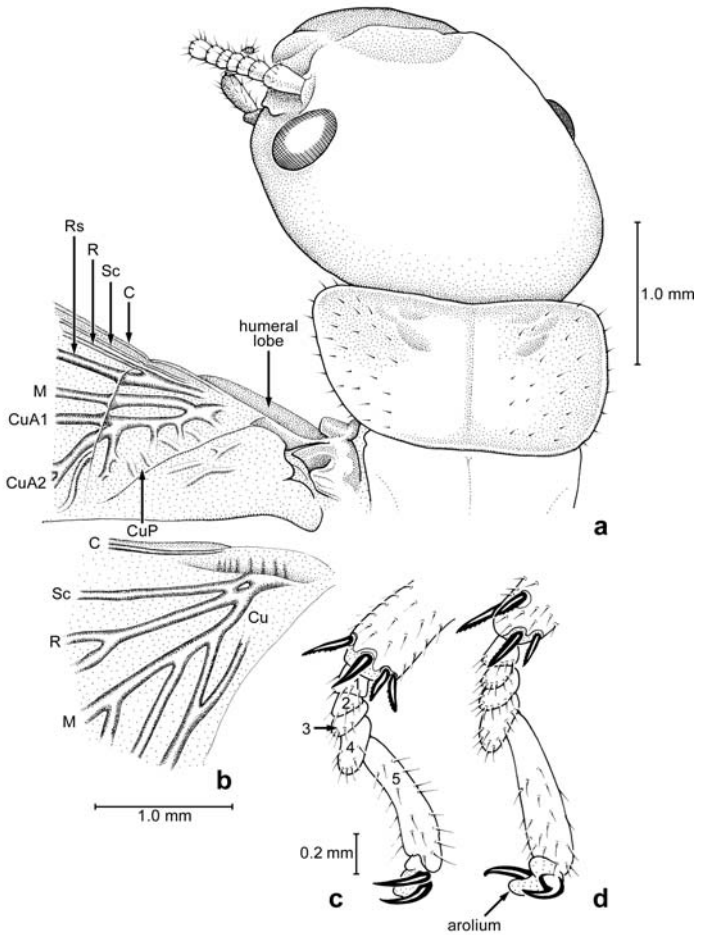

Fig. 5. *Termopsis ukapirmasi* n. sp., holotype (AMNH B-JH-Iso4). **a**: Head, thorax, and base of left forewing. **b**: Base of left hind wing. **c**: Left mesotarsus and mesotibial apex, mesal view. **d**: Right metatarsus and metatibial apex, ventro-mesal view.

ly straight (Fig. 5a); some faint reticulation present between CuA and CuP (claval fissure) and in claval area; veins Sc, R, and Rs (except inferior branches and apicalmost stub) more heavily pigmented than other veins (Fig. 6); Sc short, terminating on anterior wing margin shortly beyond basal suture; R simple and short, terminating on anterior wing margin in basal quarter of wing; radial field gradually widening toward and encompassing wing apex; Rs with six superior branches and three inferior branches, branches without secondary branches, last (apicalmost) four branches not sclerotized; M running closer to CuA than to Rs, attached to CuA in basal third of wing; CuA pectinately branched, with at least seven principal branches; well developed archedictyon (reticulations between main branches) present (Fig. 6); wing hyaline except scale brown, stems of veins M and CuA near basal suture brown (Sc, R, and Rs are uniformly brown as noted), and radial field slightly fuscous; wing membrane wrinkled between veins and archedictyon. Abdomen brown, where evident.

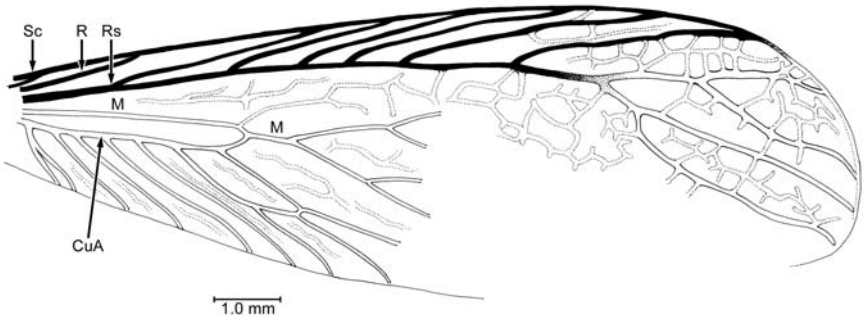

Fig. 6. Forewing of *Termopsis ukapirmasi* n. sp., holotype (AMNH B-JH-Iso4), omitting basal scale.

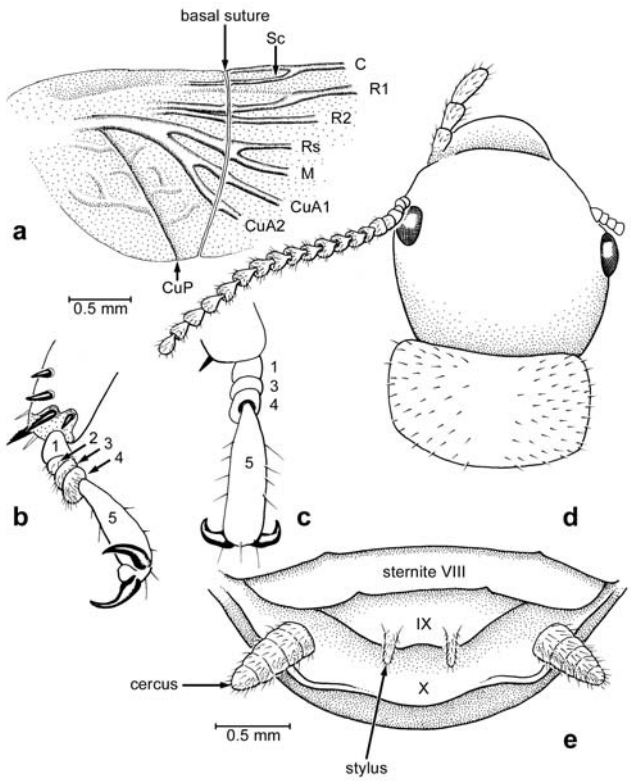

Fig. 7. *Termopsis bremii* (Heer) (AMNH C88891). **a**: Base of forewing. **b**: Left metatarsus and metatibial apex, oblique ventral view. **c**: Left metatarsus and metatibial apex, dorsal view. **d**: Dorsal view of head and pronotum. **e**: Ventral view of apex of abdomen.

Genus *Archotermopsis* Desneux, 1904

1904b *Termopsis (Archotermopsis).* – Desneux, p. 13. Type species: *Termopsis (Archotermopsis) wroughteni* Desneux, 1904b, by monotypy.

Material examined: We have not had the opportunity to personally examine *A. tornquisti*.

Comments. – *Archotermopsis* is a primitive genus of termopsine termites known from two modern species, one living in the Himalayan Region of India and Pakistan as well as northeastern Afghanistan, the other in Vietnam. In addition, there is a single fossil species in Baltic amber, *A. tornquisti* (ROSEN 1913). This distribution, with living species in Asia and extinct taxa in the Paleocene-Eocene of Europe, is a relatively commonly observed biogeographic pattern. The genus can be recognized in the imago caste by the cryptically pentamerous metatarsus; the large compound eyes, with their conspicuously concave anterior margin (near the antennal articulation); antennae with 18–19 articles (23–27 articles in living species); the narrow pronotum, with its lateral borders distinctly converging posteriorly, and with the anterior and posterior borders emarginate; the tibial spur formula of 4-3-2 or 4-4-2 (based on living species); the tibiae of all legs with additional spines (varying from 1–6 in living species); the presence of the arolium; the straight and rather weak basal suture; and the elongate cerci (greatly surpassing the abdominal apex) with 6–8 long articles.

Family Kalotermitidae FROGGATT, 1897

Genus *Proelectrotermes* ROSEN, 1913

1913 *Calotermes (Proelectrotermes).* – ROSEN, p. 331. Type species: *Termes (Kalotermes) berendtii* PICTET-BARABAN in PICTET-BARABAN & HAGEN, 1856, by monotypy.
1941 *Calotermes (Neotermites).* – ARMBRUSTER, p. 18. Type species: *Calotermes (Neotermites) roseni* ARMBRUSTER, 1941, by original designation.

Material examined: One of us (K. K.) has examined a specimen of *P. berendtii* in the collection of the Chicago Natural History Museum and designated it as the neotype (KRISHNA 1961).

Comments. – The genus *Proelectrotermes* was originally established by ROSEN (1913) as an extinct subgenus of *Kalotermes*, at that time encompassing all kalotermitids. The group was later elevated to generic rank by EMERSON (1942) and combined with *Neotermites* by EMERSON (1971). Since that time the genus has been employed for the middle Eocene, Baltic amber species *P. berendtii* as well as two Tertiary compressions, *P. fodinae* (SCUDDER) from the Eocene-Oligocene boundary of Florissant, Colorado and *P. roseni* (ARMBRUSTER) from the Miocene Randeck Maar near Stuttgart, Germany, and, most recently, two species in mid-Cretaceous amber from Myanmar (ENGEL et al. 2007). KRISHNA (1961) and EMERSON (1969) have provided the most recent, detailed diagnoses for *Proelectrotermes*, recognizing the genus as encompassing primitive kalotermitids with at least three tibial spurs, with two outer spines and a single inner, subapical spine on the mesotibia. In addition, the radial field of *Proelectrotermes* is relatively broad in comparison to other kalotermitids and the radial vein is simple and elongate, extending near to the wing's midlength.

Genus *Electrotermes* ROSEN, 1913

1913 *Calotermes (Electrotermes).* – ROSEN, p. 331. Type species: *Termes affinis* HAGEN in PICTET-BARABAN & HAGEN, 1856, by original designation.

Material examined: Two imagoes; AMNH B-E-2; AMNH B-E-5 (Fig. 8); middle Eocene (Lutetian), "Blaue Erde" deposit, Baltic amber.

Comments. – Like *Proelectrotermes*, the genus *Electrotermes* was originally established as a subgenus in *Kalotermes* before being elevated to generic rank by EMERSON (1942). The genus is similar to *Proelectrotermes* except that the radial field is slightly narrower, the number of antennal articles is 14–18 (versus 19–20 in *Proelectrotermes*), the claval fissure (CuP) terminates prior to the basal suture (terminating at the posterior edge of the basal suture in *Proelectrotermes*), and the inner, subapical spine of the mesotibia is absent (only the two outer mesotibial spines are present).

Three species have generally been recognized in *Electrotermes* – two in Baltic amber, *E. affinis* (HAGEN) (Fig. 8) and *E. girardi* (GIEBEL), and one in contemporaneous Parisian amber, *E. flecki* NEL & BOURGUET. The two taxa in Baltic amber differ solely in forewing length with the scale (6 mm in *E. girardi* versus 8.84–8.94 mm in *E. affinis*). HAGEN (1858) considered *E. girardi* a synonym of *E. affinis*, and various authors have considered the validity of the former as suspicious (e. g., EMERSON 1969). Like EMERSON (1969) we have tentatively retained *E. girardi* as a valid species and hopefully continued exploration of Baltic amber inclusions will bring further material to light.

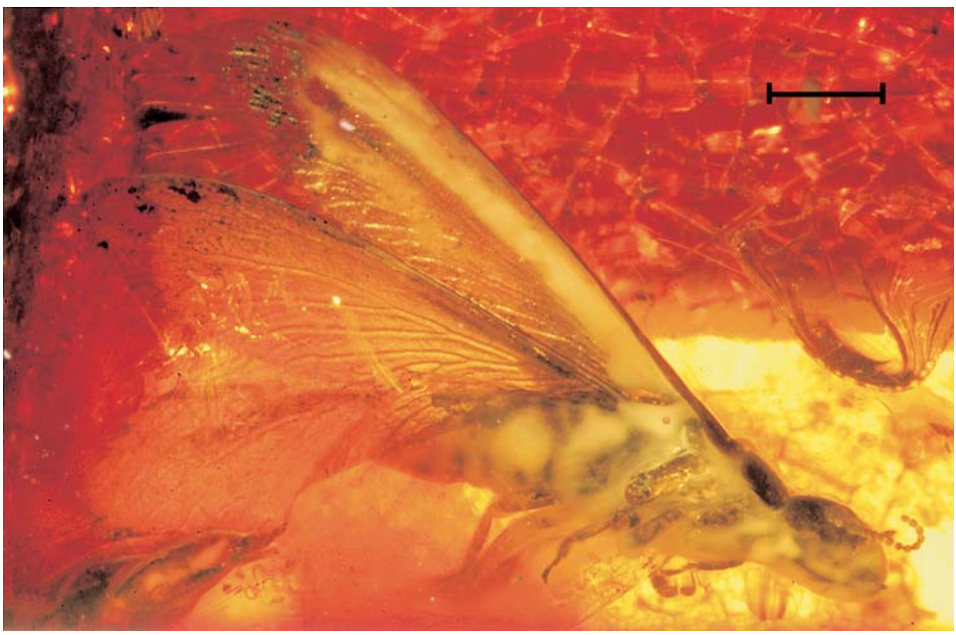

Fig. 8. Imago of *E. affinis* (specimen originally from the collection of KURT VON ROSEN, donated by ROSEN to ALFRED E. EMERSON in 1927) (AMNH B-E-5). – Scale bar = 1 mm.

Family Rhinotermitidae Froggatt, 1897
Genus *Reticulitermes* Holmgren, 1913

1813 *Hemerobites.* – Germar, p. 16. Type species: *Hemerobites antiquus* Germar, 1813, by monotypy. Nomen oblitum (vide Comments, infra).
1856 *Maresa.* – Giebel, p. 298. Type species: *Maresa plebeja* Giebel, 1856, by monotypy. Nomen rejiciendum (vide Comments, infra).
1913 *Leucotermes (Reticulitermes).* – Holmgren, p. 60. Type species: *Termes flavipes* Kollar, 1837, by original designation. Nomen protectum.
1977 *Reticulitermes (Frontotermes).* – Tsai et al., p. 465. Type species: *Reticulitermes chinensis* Snyder, 1923, by original designation.
1977 *Reticulitermes (Planifrontotermes).* – Tsai et al., p. 465. Type species: *Termes speratus* Kolbe, 1885, by original designation.
1983 *Tsaitermes.* – Li & Ping, p. 239. Type species: *Reticulitermes (Planifrontotermes) yingdeensis* Tsai & Li in Tsai et al., 1977, by original designation.

Material examined: Eight imagoes of *R. antiquus*; AMNH B-JWJ-359 (specimen figured in Janzen 2002: fig. 155); AMNH B-E-3; AMNH B-E-4; AMNH B-E-6 (Fig. 9a); AMNH C88891-B; AMNH B-JH-Iso1 (Fig. 9b); AMNH B-JH-Iso3; AMNH B-JH-Iso5; middle Eocene (Lutetian), "Blaue Erde" deposit, Baltic amber.

Comments. – The genus *Reticulitermes* is today widespread with 143 modern species. Various fossil species have been described, mostly as compressions, with two species documented in Baltic amber – *Reticulitermes antiquus* (Germar) and *R. minimus* Snyder, both redescribed in detail by Emerson (1971). *Reticulitermes antiquus* is the most common termite in Baltic amber (Fig. 9) and *R. minimus* is the smallest known termite (Snyder 1928). *R. antiquus* can be distinguished most readily from *R. minimus* by its larger body size (length of forewing from basal suture 6.5–8.8 mm in *R. antiquus* versus 3.94 mm in *R. minimus*) and more numerous antennal articles (17–20 in *R. antiquus* versus 13–14 in *R. minimus*), among other characters (vide etiam Key, supra).

The genus-group name *Hemerobites* has priority over *Reticulitermes* (vide supra) but this name has not been used as valid after 1899 and literally hundreds of articles by dozens of authorities have employed the name *Reticulitermes* for these ubiquitous and economically important termites that are significant pests throughout the world. In accordance with ICZN (1999) Art. 23.9.1 we hereby consider *Hemerobites* as a nomen oblitum and *Reticulitermes* as a nomen protectum, automatically suppressing the former for purposes of priority whenever these two genera are considered synonyms (vide etiam Engel & Krishna in press).

The genus-group name *Maresa* similarly has priority over *Reticulitermes* (vide supra) and has been used only a couple of times as a valid taxon. Unfortunately, the last usage of the name was by Handlirsch (1907), thereby rendering ICZN (1999) Art. 23.9.1 unusable for the conservation of *Reticulitermes*. We have, therefore, prepared a petition to suppress *Maresa* as a nomen rejiciendum for the purposes of priority (Engel & Krishna in press). In accordance with the ICZN (1999) current usage (i. e., with *Reticulitermes* as the valid generic name) must be maintained until a decision has been rendered by the Commission.

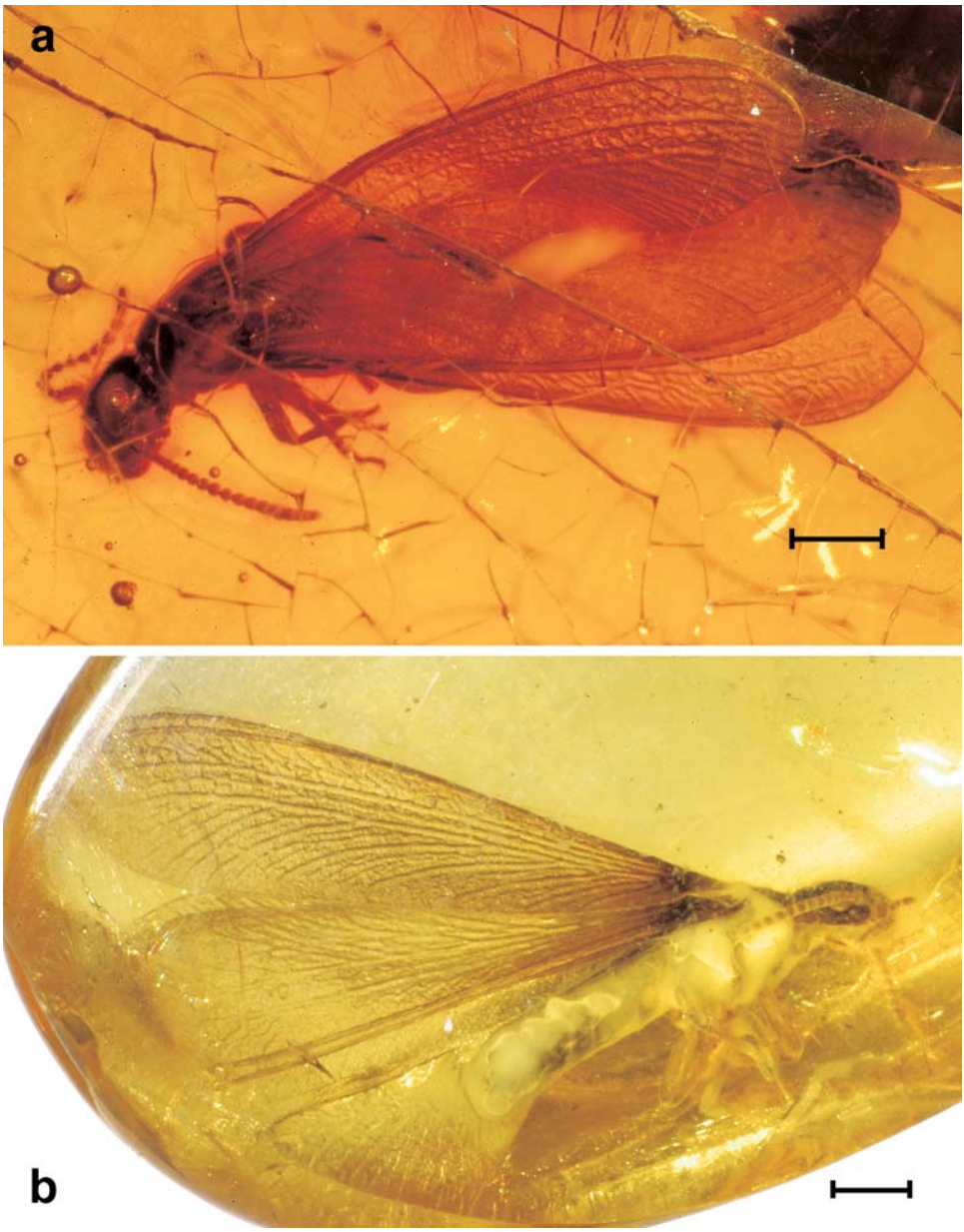

Fig. 9. Imagoes of *Reticulitermes antiquus* (GERMAR). **a**: Specimen originally from the collection of KURT VON ROSEN (donated by ROSEN to ALFRED E. EMERSON in 1927) (AMNH B-E-6). **b**: More recently excavated and identified specimen (AMNH B-JH-Iso1). – Scale bars = 1 mm.

Genus *Parastylotermes* SNYDER & EMERSON, 1949

1949 *Parastylotermes.* – SNYDER & EMERSON in SNYDER, p. 378. Type species: *Stylotermes washingtonensis* SNYDER, 1931, by original designation.

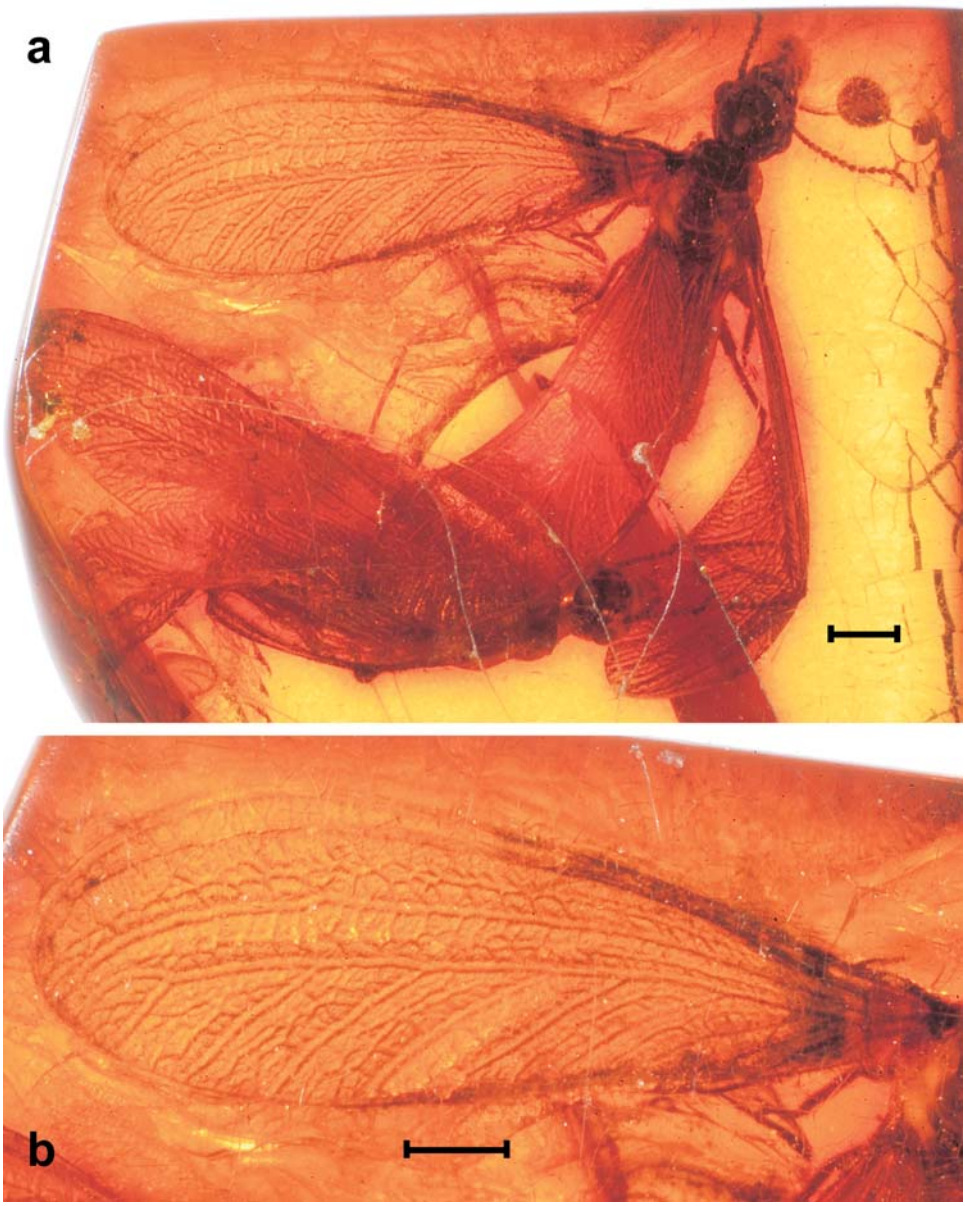

Fig. 10. Imagoes of *Parastylotermes robustus* (ROSEN). **a**: Photomicrograph of lectotype and paralectotype imagoes (syntype specimens originally from the collection of KURT VON ROSEN, donated by ROSEN to ALFRED E. EMERSON in 1927) (AMNH B-E-7), uppermost specimen with wings spread is the lectotype selected by EMERSON (1971). **b**: Forewing detail of lectotype. – Scale bars = 1 mm.

Material examined: Lectotype and paralectotype imagoes of *P. robustus* (Fig. 10); AMNH B-E-7; middle Eocene (Lutetian), "Blaue Erde" deposit, Baltic amber; lectotype and paralectotype designated by EMERSON (1971).

Comments. – *Parastylotermes* was established for a Miocene species from the Latah Formation (State of Washington, USA) and for a single Baltic amber species previously placed in *Reticulitermes* (SNYDER 1949). Two additional species from the Miocene of California were subsequently added by SNYDER (1955) and PIERCE (1958). The species from the Neogene of western North America are all known as compressions, with *Parastylotermes robustus* (ROSEN) the sole amber representative of the genus (Fig. 10). It is unclear whether or not the Baltic amber species is truly congeneric with the North American taxa. The differences between the subfamilies Heterotermitinae and Stylotermitinae, and between *Stylotermes* and *Parastylotermes*, are subtle and largely quantitative. As such, the Paleogene *P. robustus* might rightfully belong in a genus distinct from the younger North American fossils. Unfortunately, the compressions do not afford fine enough detail to permit such discernment and *P. robustus* is most prudently retained in *Parastylotermes* despite the temporal separation and apparently peculiar disjunct distribution of the included species. *Parastylotermes* can be distinguished from the other rhinotermitids in Baltic amber by the more numerous and long setae of the head and pronotum (the individual setae are as long as or longer than the scape) and the pronotum distinctly narrower than the head.

3. Discussion

It is interesting to note that the Baltic amber termite fauna consists almost exclusively of primitive isopterans. *Garmitermes*, *Termopsis*, *Archotermopsis*, *Electrotermes*, and *Proelectrotermes* are all representative of primitive lineages. Only *Reticulitermes* and *Parastylotermes* are representative of the "higher" termites and therein only of the Rhinotermitidae. The today ubiquitous Termitidae are unknown from the Baltic amber fauna. Certainly termitids must have been present as evidenced by the occurrence of their sister group, the Rhinotermitidae. However, the family was apparently not even remotely as abundant as they are today and were, perhaps, represented during the latest Cretaceous and Early Tertiary merely by stem-groups, unassignable to modern subfamilies.

The distribution of the various taxa represented in Baltic amber is also most interesting. Many genera are wholly extinct (e. g., *Garmitermes*, *Termopsis*, *Electrotermes*, *Proelectrotermes*, and *Parastylotermes*) but have affinities to lineages today not occurring in Europe. *Garmitermes* is allied to the genus *Mastotermes*, a lineage that today consists of a single species restricted to Australia, but whose distribution included at least North America and Europe during the Tertiary and latest Cretaceous. *Termopsis* appears to have been entirely restricted to Europe, with species surviving through to the Miocene before eventually becoming extinct. The kalotermitid genera *Electrotermes* and *Proelectrotermes* are apparently related to a clade principally comprising Oriental genera, but also, in a more derived position of that same lineage, some widespread taxa also encompassing the African and Neotropical regions. Interestingly, while *Electrotermes* is confined to the Tertiary of Europe, *Proelectrotermes* encompasses two fossil species from the mid-Cretaceous of Myanmar in addition to a compression fossil species from the Miocene of Europe, the latter representing the last occurrence of the genus. A single species from the Eocene-Oligocene boundary of North America has also been included in *Proelectrotermes* but this

species is represented solely by a fragmentary compression and its placement within *Proelectrotermes* may be erroneous. Similarly, *Parastylotermes* has been considered to encompass a Baltic amber species as well as two Miocene species from western North America. The North American compressions, however, are difficult to assign as the subtle characters of the Stylotermitinae are challenging to observe with great detail in minute compressions and this enigmatic, northern disjunct distribution may be an artifact (vide supra).

The remaining two genera, *Reticulitermes* and *Archotermopsis*, are both found in the modern fauna. *Reticulitermes*, the infamous subterranean termites so destructive to human habitation, is a remarkably diverse Holarctic genus. Relationships among the 143 currently recognized species, however, are unclear and it is unknown whether the species occurring in Baltic amber are allied to species today living in Asia or elsewhere. *Archotermopsis*, on the other hand, today consists of two species living in Asia, one in the Himalayan Region and the other in Vietnam. Such a connection between the Eocene fauna of Europe and modern taxa in Asia is a common biogeographic pattern seen for Baltic amber fossils (e. g., ANDER 1942; LARSSON 1978; ENGEL 2001).

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