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### Primitive termites from the Early Cretaceous of Asia (Isoptera)

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#### Abstract

New fossil termites (Isoptera) are described and figured from four Early Cretaceous deposits across Asia, including some of the oldest records for the order. In total seven new genera and six new species are established from these sites. A single, alate specimen is documented from the Zaza Formation (Berriasian) of Baissa, Transbaikalia (Siberia, Russia) and is described as *Baissatermes lapideus* n. gen. n. sp. *Baissatermes lapideus* n. gen. n. sp. is the oldest fossil termite presently known and the oldest known example of a social organism. *Valditermes acutipennis* PONOMARENKO, from the Aptian of Mongolia, is transferred to a new genus, *Khanitermes* n. gen. (resulting in the new combination, *Khanitermes acutipennis* n. comb.). *Melqartitermes myrrheus* n. gen. n. sp. is described in Neocomian amber from Lebanon. The latest Albian Burmese amber (Myanmar) harbors the greatest diversity of termites hitherto discovered from any Cretaceous amber locality. In total six species are documented in Burmese amber, including the following new taxa and combinations: *Mylacrotermes cordatus* n. gen. n. sp., *Dharmatermes avernalis* n. gen. n. sp., *Proelectrotermes swinhoi* (COCKERELL) n. comb., *P. holmgreni* n. sp., *Kachinitermes* n. gen., *Kachinitermes tristis* (COCKERELL) n. comb., *Tanytermes anawrahtai* n. gen. n. sp. The significance of these new taxa for understanding early termite evolution and basal relationships within Isoptera is discussed. A checklist of Cretaceous termites is provided.

Key words: Asia, Isoptera, Mesozoic, paleontology, phylogeny, taxonomy.

#### Zusammenfassung

Es werden neue fossile Termiten (Isoptera) aus Ablagerungen der frühen Kreide von Asien beschrieben und abgebildet, darunter einige der ältesten Nachweise der Ordnung. Insgesamt werden sieben neue Gattungen und sechs neue Arten eingeführt. Aus der Zaza Formation (Berriasium) von Baissa, Transbaikalien (Sibirien, Russland) wird ein einzelnes, beflügeltes Exemplar als *Baissatermes lapideus* n. gen. n. sp. beschrieben. Es ist die älteste gegenwärtig bekannte fossile Termitenart und das älteste Beispiel für einen sozialen Organismus. *Valditermes acutipennis* PONOMARENKO aus dem Aptium der Mongolei wird einer neuen Gattung, *Khanitermes* n. gen., zugeordnet (das ergibt die neue Kombination *Khanitermes acutipennis* n. comb.). Aus dem Bernstein des Libanon (Neokom) wird *Melqartitermes myrrheus* n. gen. n. sp. beschrieben. Der Burmesische Bernstein (Oberstes Albium; Myanmar) beherbergt die größte Vielfalt an Termiten, die bisher aus einem kreidezeitlichen Bernstein bekannt ist. Insgesamt sind sechs Arten belegt, die die folgenden neuen Taxa und Kombinationen umfassen: *Mylacrotermes cordatus* n. gen. n. sp., *Dharmatermes avernalis* n. gen. n. sp., *Proelectrotermes swinhoi* (COCKERELL) n. comb., *P. holmgreni* n. sp., *Kachinitermes* n. gen., *Kachinitermes tri-*

*stis* (COCKERELL) n. comb., *Tanytermes anawrahtai* n. gen. n. sp. Die Bedeutung dieser neuen Taxa für das Verständnis der frühen Evolution der Termiten sowie deren basaler Verwandtschaftsverhältnisse werden diskutiert. Eine Checkliste kreidezeitlicher Termiten wird erstellt.

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## 1. Introduction

Among the 30 living orders of insects traditionally recognized, termites have singular biological significance. They are the only group of eusocial insects without haplodiploid sex determination, and the only significant group among all insects to feed on wood and other forms of cellulose and lignocellulose. Their diet, in conjunction with advanced sociality, makes termites of pivotal ecological importance. For example, termites process prodigious amounts of wood, grass, humus, dung, and mycelia in the tropical and subtropical regions of the world, and thus have profound effects on the carbon cycling and soils of these regions (reviewed in GRIMALDI & ENGEL 2005). The question of how these insects became so significant is thus not a trivial one.

One approach to addressing the success of termites is historical, specifically based on fossils and phylogenetics. The closest living relative of termites is the relict genus of wood roaches, *Cryptocercus* (e. g., LO et al. 2000; GRANDCOLAS & D'HAESE 2001; KLASS & MEIER 2006), which is traditionally placed in its own family (e. g., MCKITTRICK 1964) but more recently put in the apparently paraphyletic roach family Polyphagidae (GRANDCOLAS 1996). Though no Jurassic termite has yet been found, Isoptera putatively diverged from a xylophagous “polyphagid” ancestor – one line leading to *Cryptocercus*, the other to termites – in the Late Jurassic, ca. 150–160 mya.

The Mesozoic record of termites (Table 1) was unveiled with the first Cretaceous termite, *Cretatermes*, described 40 years ago (EMERSON 1967) from the Late Cretaceous of Labrador. It was not until 14 years later that the second Cretaceous species was reported (JARZEMBOWSKI 1981), and by the mid and late 1980's an additional four species became known, three from Europe and one from central Asia (LACASARUIZ & MARTÍNEZ-DELCLÓS 1986; PONOMARENKO 1988; SCHLÜTER 1989). An ad-

ditional ten species were described in the 1990's, seven of them from the Early Cretaceous of China (REN 1995). The only other North American Cretaceous termite, *Carinatermes*, was described in 2000 from the Late Cretaceous amber of New Jersey (KRISHNA & GRIMALDI 2000). The only Cretaceous Rhinotermitidae, *Archeorhinotermes*, was described soon thereafter in Burmese amber (KRISHNA & GRIMALDI 2003). To the three species from the Early Cretaceous Crato (Santana) Formation of Brazil (KRISHNA 1990; FONTES & VULCANO 1998) have recently been added reports of a putative six additional species (MARTINS-NETO et al. 2006; BECHLY in press), though the species concepts of the MARTINS-NETO taxa are vague and it is likely some, if not all, will be synonyms.

Herein we describe six new species (some 19% of the known Cretaceous fauna), including the first one in Early Cretaceous Lebanese amber, as well as four additional species from Burmese amber and the oldest known termite fossil (from the Berriasian of Baissa, Transbaikalia, Russia). We also propose three new combinations. As of now Asia (including Central Asia and Asia Minor) has the greatest diversity, with 17 species; in addition, there are nine South American species (all Crato Formation, but which need re-study), four European, and two North American, for a total of 32 species (including the three records of BECHLY (in press)) – a far cry from 40 years ago.

The main purpose of this paper is descriptive, to delineate and figure the new species in detail for a companion study on the phylogeny of living and extinct basal termites (GRIMALDI, ENGEL & KRISHNA in prep.).

#### Acknowledgements

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## 2. Materials and methods

### 2.1. Material and specimen preparation

All of the specimens considered herein are from the Early Cretaceous of Asia, ranging from the westernmost edges of the continent (in Lebanon), to the Far East in Russia (Siberia) and Mongolia, and to the southern tropics (in northern Myanmar). Compression fossils were studied dry and, at times, with polarized light. Amber pieces were embedded in epoxy following the methods and procedures of NASCIMBENE & SILVERSTEIN (2000) and then trimmed and polished to afford the maximal view of specimen features. Inclusions were then studied using compound and stereomicroscopy. Photomicrographs were prepared using a MicroOptics ML-1000 digital imaging system. Measurements were made for observable features and, therefore, are not entirely consistent across the taxa considered (e. g., the metatibial length was not measurable in all specimens). Type material is located in the following institutions:

AMNH American Museum of Natural History, New York  
 NHML Natural History Museum, London  
 PIN Paleontological Institute, Russian Academy of Sciences, Moscow  
 SEMC University of Kansas Natural History Museum, Lawrence

## 2.2. Terminology and descriptions

Morphological terminology in the descriptions is generally that employed widely in isopteran systematics except as noted here. Typically termed “humeral suture”, we employ the name “basal cleavage suture” or “basal suture” for the distinctive suture demarcating the apex of the wing scale, where the wings are shed. “Humeral suture” is a misnomer as “humeral” refers to the anterior, i. e., costal, margin of the extreme wing base where there is often in insects a small sclerite called the humeral plate. This anterior basal section of the costal margin, inside the wing scale, is accordingly termed the “humeral margin” herein. The vein CuP is a short, typically arched vein that runs entirely within the wing scale, terminating at, or just before, the posterior edge of the basal suture. This vein is sometimes termed the “claval suture”, a misnomer since there is no break made along this vein and while certainly deeply incised it is more appropriately termed the “claval fissure” but is herein referred to strictly as CuP, and as demarcating the anterior and apical margin of the claval area. Lastly, the issue of tarsal reduction is a prominent one in Isoptera. In the basalmost termites the tarsus is pentamerous (i. e., with five articles) but gradually becomes reduced to a tetramerous condition (i. e., with four articles). This reduction results from the gradual minimization of the second tarsal article as is evidenced by the slight reduction of the second article in *Termopsis* relative to the completely pentamerous condition seen in *Mastotermes*. The reduction becomes even more advanced in genera such as *Archotermopsis* in which the metatarsus becomes cryptically pentamerous. In this latter condition the second tarsal article is further reduced such that in dorsal aspect the tarsus appears tetramerous, but the second article is fully visible ventrally demonstrating that it is in fact pentamerous. In its ultimate state, the second tarsal article is lost entirely giving a truly tetramerous tarsus (an even more derived condition seen only in a few Tertiary or modern genera such as *Stylotermes* or *Parastylotermes*, is a trimerous tarsus). However, in order to denote the correct serial homology for this process of reduction we number tarsal articles based on their homologues rather than their physical position in relation to each other. Thus, in tetramerous tarsi the tarsal articles present are the first, third, fourth, and fifth, as accordingly numbered as such (e. g., Figs. 10c–e, 12b).

Nearly all of the genera considered herein are monotypic and we have, therefore, constructed detailed generic descriptions, highlighting characters that are most significant for comparison with modern and other fossil termite genera as presently defined. Specific descriptions are, accordingly, abbreviated and may need to incorporate features presently considered “generic” should additional species be discovered that can be readily included with slight modification of the generic diagnosis. Taxa are purposefully not assigned to higher categories (i. e., families) pending an on-going phylogenetic study of basal living and fossil termites designed to redefine the families and subfamilies of Isoptera (GRIMALDI, ENGEL & KRISHNA in prep.). Recent assertions to place termites as a single family within Blattaria (INWARD et al. 2007)

are without merit and do nothing to provide nomenclatural stability. The placement of termites among roaches has been known for nearly a century and they had even been considered a suborder of Dictyoptera at times in the past (e.g., MCKITTRICK 1964). The Isoptera could be easily once again considered a suborder or infraorder within Blattaria without altering the internal classification of termites and immediately eliminating the paraphyly of Blattaria (LO et al. 2007), or the latter could be segregated into multiple orders. The application of the ordinal rank is merely semantic and serves only to indicate relative degrees of inclusiveness of a particular taxon in relation to other taxa. Regardless, the Isoptera are herein rightfully retained as a distinct, multi-familial lineage of the Dictyoptera.

### 3. Systematic Paleontology

#### 3.1. Zaza Formation, Russia

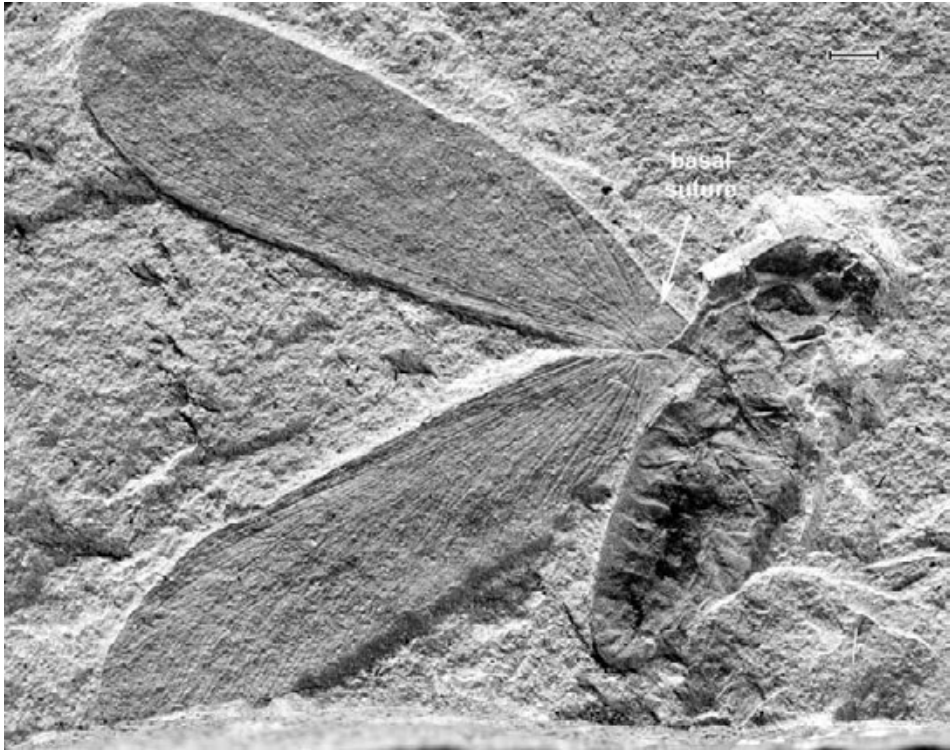
Baissa is widely considered one of, if not the, most important Early Cretaceous localities for compression fossils of insects. The fidelity of preservation is relatively high and the fauna is remarkably diverse, with many species being outright abundant. To date, more than 10,000 fossil insects have been recovered by the scientists of the Paleontological Institute's Arthropoda Laboratory (RASNITSYN & QUICKE 2002). The locality is composed of marls and limestones in the Zaza Formation (RASNITSYN & QUICKE 2002) of approximately Berriasian age (RASNITSYN et al. 1998). Baissa is located along the Vitim River in Central Siberia (western Transbaikalia).

#### Genus *Baissatermes* n. gen.

Type species: *Baissatermes lapideus* n. gen. n. sp.

Etymology: The new genus-group name is a combination of the locality Baissa (from which the fossil originates) and *Termes*, the oldest generic name in Isoptera. The name is masculine.

Diagnosis. – Imago. Head robust; Y-shaped coronal ecdysial cleavage line faintly visible; right mandibular apex evident, with two, pointed marginal teeth, first marginal tooth about as long as apical tooth; subsidiary tooth absent. Pronotum large, anterior margin apparently slightly emarginate, lateral border straight, parallel with longitudinal axis of body. Wings with well-defined basal suture (Figs. 1, 2b, c); forewing narrow, with rounded apex; forewing scale with basal suture weakly convex, with veins apparently originating inside scale; Sc short, terminating on anterior wing margin shortly after basal suture; R simple and short, terminating at basal third of wing length; Rs extending to wing apex and gradually broadening radial field toward apex such that Rs branches encompass anterior wing apex, with about seven main branches evident, some apically with minute, secondary branches along anterior wing margin; M running about equidistant from Rs and CuA, branches of M not well preserved, with at least some evidence of dichotomous branching in distal half of wing length, apparently terminating just posterior of wing apex and with posteriormost branch terminating on posterior wing margin at point one-third of wing



**Fig. 1.** Photomicrograph of holotype imago of *Baissatermes lapideus* n. gen. n. sp. (PIN 3064/8583); Zaza Formation, Berriasian; Baissa, Russia. – Scale bar = 1 mm.

length from apex; CuA pectinately branched, terminating on posterior wing margin at about two-thirds wing length.

Comments. – Although preserved such that relatively few characters can be gleaned from the single specimen, the significance of *Baissatermes lapideus* n. gen. n. sp. is its age. The Baissa locality dates from the Berriasian (vide supra), making this the oldest record of a termite yet documented and the oldest evidence of a eusocial organism. Previously *Meiatermes bertrani* LACASA-RUIZ & MARTÍNEZ-DELCLÒS (1986), from the important Montsec locality in Spain, was believed to be the oldest termite and social insect (MARTÍNEZ-DELCLÒS & MARTINELL 1995), but these deposits are of Early Barremian age (ANSORGE 1993; MARTÍN-CLOSAS & LÓPEZ-MORÓN 1995), not Berriasian-Valanginian.

*Baissatermes lapideus* n. gen. n. sp.

Figs. 1, 2b, c

2002 Hodotermitid sp. – RASNITSYN & QUICKE, p. 272, fig. 380.

Holotype: Imago, PIN 3064/8583 (Fig. 1).

Stratum typicum: Zaza Formation, Berriasian.

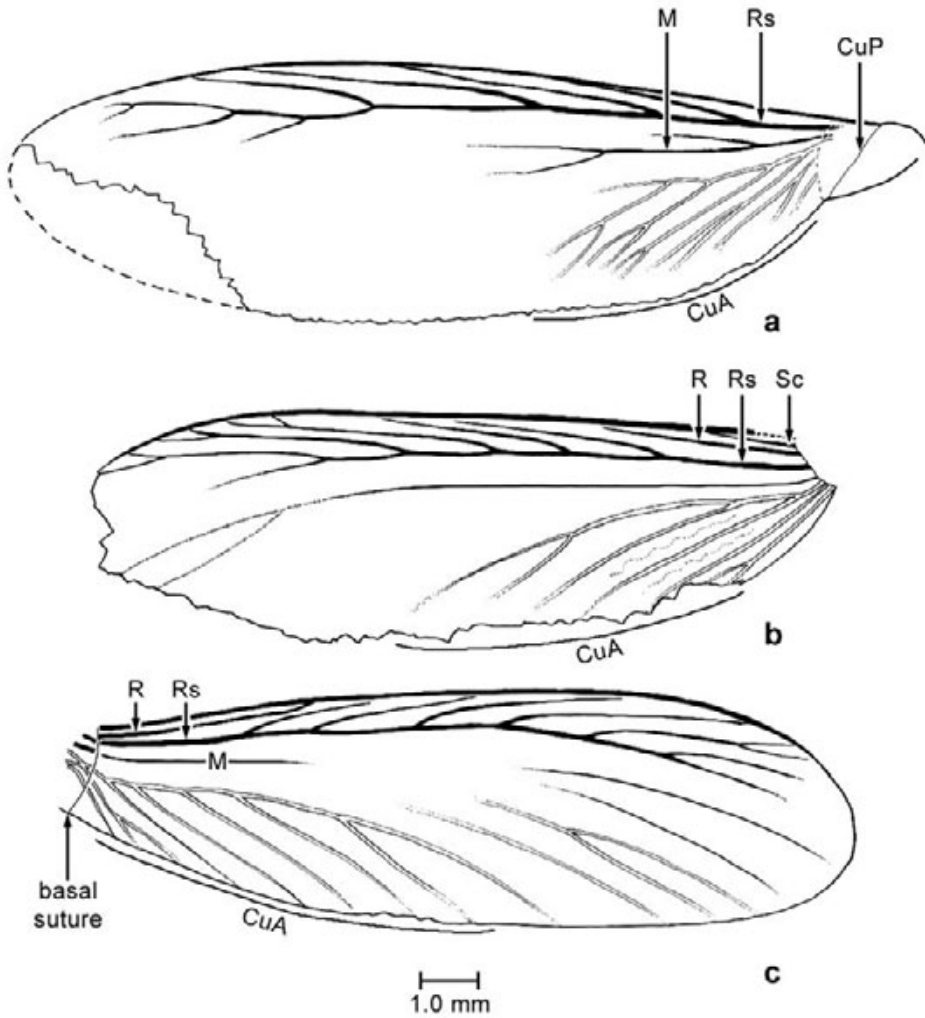


Fig. 2. Wing venation of compression fossil termites from the Early Cretaceous of Mongolia and Siberia. a: Forewing venation of holotype of *Khanitermes acutipennis* (PONOMARENKO) n. comb. (PIN 4271/1); Shar-Tologoy Formation, Early Cretaceous; Shar-Tologoy, Mongolia. b–c: Holotype of *Baissatermes lapideus* n. gen. n. sp. (PIN 3064/8583); Zaza Formation, Berriasian; Baissa, Transbaikalia, Russia. b: Discernible left forewing venation. c: Discernible details of right forewing venation.

Locus typicus: Baissa, Transbaikalia.

Etymology: The specific epithet is the Latin word *lapideus*, meaning “of stone”.

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

Description. – Imago. Head length 2.2 mm, width 2.1 mm; median pronotum length 1.0 mm. Length of forewing from basal suture to apex 12.7 mm; forewing width 4.0 mm; length of hind wing from basal suture 13.1 mm; hind wing width 3.7 mm; forewing with Sc, R, and Rs more distinctly sclerotized than M and CuA; Sc

relatively short, terminating on anterior wing margin in basal quarter of wing not far from basal suture; R simple and short, terminating on anterior wing margin in basal third of wing just beyond termination of Sc; Rs running relatively parallel to anterior wing margin until about wing midlength, then gently curving posteriorly toward wing apex, with six branches, more apical branches with short, secondary branches along wing margin; M relatively simple, apparently branching beyond wing midlength, curving slightly toward posterior wing margin, total number of branches indeterminate, medial field just posterior of wing apex and ending in apical third of wing; CuA pectinately branched, branches simple except one basal branch with short secondary fork, cubital field encompassing nearly basal two-thirds of posterior wing margin.

### 3.2. Shar-Tologoy Formation, Mongolia

The Mesozoic deposits of Mongolia have proven to be a great source of Early Cretaceous insects (reviewed in RASNITSYN & QUICKE 2002). The Shar-Tologoy Formation, in particular, has yielded a wealth of species in diverse orders such as Ephemeroptera (e.g., the giant mayfly *Ephemeropsis melanurus* COCKERELL), Odonata, Orthoptera, Hemiptera, Neuroptera, Coleoptera, Diptera (e.g., *Prospeolepta brevicubita* BLAGODEROV), and Trichoptera. A single termite has also been described from the Aptian-aged Shar-Tologoy locality (PONOMARENKO 1988), and we herewith take the opportunity to provide new information on this species.

#### Genus *Khanitermes* n. gen.

Type species: *Valditermes acutipennis* PONOMARENKO, 1988.

Etymology: The new genus-group name is a combination of Khan, the title of political and military leaders in the ancient Mongol Empire, and *Termes* (meaning, “termite”), the first generic name of the Isoptera. The generic name is a reference to the most famous Khan of ancient Mongolia, GENGHIS KHAN (c. 1162–18 August 1227, born BORJIGIN TEMÜJIN, the former being his surname, was bestowed with the title Khan and became GENGHIS KHAN in 1206). He united the Mongol Tribes into the Mongol Empire in 1206. The name is masculine.

Diagnosis. – Imago. Forewing narrow, with rounded apex (not acutely pointed as indicated by the original description and the specific epithet); forewing scale with basal suture gently convex, with veins apparently originating inside of forewing scale; CuP relatively straight, not forming a distinct, convex arch (Fig. 2a); R not evident as basal anterior margin of wing apparently folded; Rs with pectinate branches extending anteriorly, those branches in apical third of wing with some secondary branches, first branch originating in basal quarter of forewing not far beyond basal suture, Rs relatively straight along its course (not curved posteriorly), although not parallel with costal margin of wing and ultimately terminating at wing apex in more posterior position (thus radial field widens toward wing apex) (Fig. 2a); M running about equidistant from Rs and Cu; M dichotomously branching, with apparent total of four branches, although small stub of possible fifth, basal, anteriorly-directed branch apparently present (this branch appears in basal quarter of forewing and not far beyond basal suture), first distinct branching of M at basal third of forewing

length, next branching apparently near forewing midlength; Cu apparently terminating just beyond forewing midlength, with various branches and some secondary branches; CuP straight, demarcating an apically-pointed claval area (Fig. 2a).

Comments. – PONOMARENKO (1988) placed his Early Aptian fossil in the genus *Valditermes*, a group previously known only from a single Hauterivian species from England (JARZEMBOWSKI 1981). Two of us (M. S. E. and D. A. G.) were afforded the opportunity to study PONOMARENKO's holotype in Moscow in late July 2002 and the new figure of the wing venation is based upon observations and notes taken at that time (Fig. 2a). While the wing is relatively narrow, the apex is not as truly pointed as indicated by PONOMARENKO's (1988) original reconstruction. Instead, the more posterior portions of the forewing apex are simply not preserved, giving those surviving components a rather apically acute appearance.

Notable differences between the Mongolian (Shar-Tologoy) species (*Khanitermes* n. gen.) and the British (Lower Weald Clay) species (*Valditermes*) include: Rs extending to wing apex and slightly toward posterior but overall relatively straight along its course and not distinctly curved posteriorly (Rs distinctly, albeit gently, curving posteriorly in apical third of wing in *Valditermes*); and M with dichotomous branching, apparently with maximally four branches (M pectinate in *Valditermes*).

*Khanitermes acutipennis* (PONOMARENKO) n. comb.

Fig. 2a

- 1988 *Valditermes acutipennis* PONOMARENKO, sp. nov. – PONOMARENKO, p. 71, table 13, fig. 1.  
 1991 *Valditermes acutipennis* PONOMARENKO. – JARZEMBOWSKI, p. 93.  
 1993 *Valditermes acutipennis* PONOMARENKO, 1988. – NEL & PAICHELER, p. 136.  
 1995 *Valditermes acutipennis*. – MARTÍNEZ-DELCLÒS & MARTINELL, p. 595.  
 2000 *Valditermes acutipennis*. – KRISHNA & GRIMALDI, p. 133.  
 2000 *Valditermes acutipennis* PONOMARENKO. – THORNE et al., p. 81, 85, fig. 2.  
 2005 *Valditermes acutipennis*. – GRIMALDI & ENGEL, p. 250.  
 2006 *Valditermes acutipennis* PONOMARENKO. – MARTINS-NETO et al., p. 125.

Holotype: Imago, PIN 4271/1.

Stratum typicum: Bon-Tsagan Group, Shar-Tologoy Formation, Early Cretaceous, Aptian.

Locus typicus: Mongolia, Bayan Khongor District, Gobi Altai, 33 km North Bayan-Leg area, Shar-Tologoy.

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

### 3.3. Amber from Lebanon

The Neocomian amber from various localities in Lebanon represents the oldest amber with macroscopic biological inclusions. The diversity of taxa preserved in Lebanese amber is remarkable, with thousands of inclusions representing 13 insect orders (not including the order Isoptera, newly reported herein), as well as various arachnids, feathers, and even a lizard. Here we describe the first termite from Lebanese amber (Fig. 3), although the precise outcrop in Lebanon from which this specimen originated is unknown.



**Fig. 3.** Photomicrograph of holotype imago of *Melqartitermes myrrheus* n. gen. n. sp. (AMNH L-Iso1); Lebanese amber; Neocomian. – Scale bar = 1 mm.

### Genus *Melqartitermes* n. gen.

Type species: *Melqartitermes myrrheus* n. gen. n. sp.

**Etymology:** The new genus group name is a combination of the Phoenician name MELQART and *Termes* (meaning, “termite”), the first generic name of the Isoptera. MELQART (also known as MELKURT), son of BAAL, was the Phoenician god of the underworld and patron of ancient Tyre, the city famously besieged and conquered by ALEXANDER THE GREAT in 332 B.C. when his request to make sacrifice to MELQART was denied by the Tyrians. The name is masculine.

**Diagnosis.** – Imago. Head robust (Fig. 3, 4a), posterior border faintly curved, lateral borders parallel-sided; right mandible (as seen ventrally) with at least two marginal teeth (Fig. 4a), each tooth about as long as apical tooth, subsidiary tooth not present; antenna moniliform, with at least 13 articles (total article number unknown), flagellar articles progressively larger from base to preserved apex; compound eyes without anterior emargination, apparently circular, separated from lower margin of head by less than eye diameter, separated from posterior border of head by about eye diameter or slightly less; ocelli absent; fontanelle apparently absent; ventral cervical sclerite present (Fig. 4a), sclerite transverse, narrowly rectangular, with faint medial depression and scattered minute setae. Pronotum large, flat, and broad, slightly broader than head; anterior border weakly concave; lateral borders apparently parallel-sided, with posterior corners gently rounded inward; posterior border straight, thus pronotum with a largely quadrate shape. Procoxa apparently without ventral keel or carina; femora apparently not carinate or keeled ventrally; all

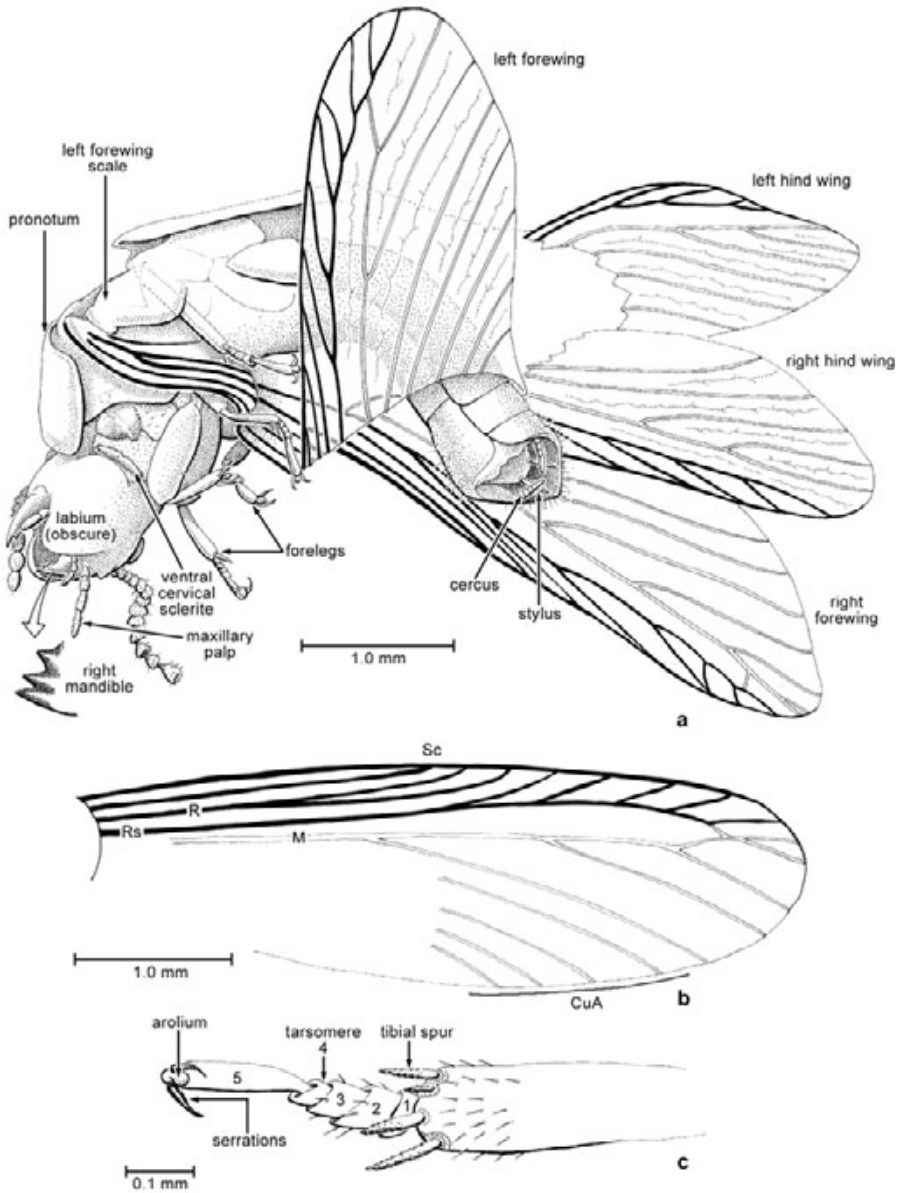


Fig. 4. Holotype imago of *Melqartitermes myrrheus* n. gen. n. sp. (AMNH L-Iso1); Lebanese amber; Neocomian. a: Lateral habitus. b: Reconstruction of visible portions of forewing venation. c: Metatarsus, metapretarsus, and apex of metatibia.

tarsi completely pentamerous (Fig. 4c); tibial spur formula 3-4-4, spurs of all legs serrated; large arolium present on all legs (Fig. 4c), pretarsal ungues with minute, apical serrations along inner margin. Wings largely hyaline, slightly infuscate on membrane; membrane not reticulate, although with some more faintly infuscate lines apically between longitudinal veins. Forewing veins Sc, R, and Rs heavily pigmented,

remainder lightly pigmented (Fig. 4b); forewing scale large, overlapping hind wing base, humeral margin weakly convex, basal suture convex; all veins originating inside wing scale; Sc and R elongate, Sc terminating on costal margin just prior to wing midlength, R forking in basal third of wing, with branches terminating at wing midlength and slightly beyond wing midlength, respectively; Rs with 5–6 anterior branches, first branch arising beyond wing midlength; Rs running generally parallel to costal wing margin for entire length, near wing apex connecting to anteriormost branch of M; radial field relatively narrow for entire length of wing; visible portion of M with five long, pectinate branches gently curved toward posterior margin, apicalmost branch connected to apicalmost branch of Rs and terminating at wing apex, first branch of M apparently arising at forewing midlength; hind wing without anal lobe. Abdomen relatively narrow, cylindrical (Fig. 4a), sides generally parallel; cerci well developed (Fig. 4a), apparently six-segmented; styli present (Fig. 4a), length slightly more than one-half length of cercus.

Comments. – *Melqartitermes* n. gen. has many notable plesiomorphic features including the presence of the ventral cervical sclerite (absent in all Isoptera except *Mylacrotermes* n. gen., vide infra); fully pentamerous tarsi in which the second tarsomere is neither reduced nor partially obscured when viewed from above (in genera such as *Archotermopsis*, *Hodotermopsis*, and *Zootermopsis* the tarsus is cryptically pentamerous, appearing tetramerous when viewed from above); the presence of a large arolium; the serrated edges to the spurs; the large forewing scale; the large and relatively flat pronotum (i. e., not bowed transversely and saddle-shaped in profile); the long, multi-segmented cerci, and the presence of styli. Definitive assignment of this fossil to family and/or subfamily awaits the completion of presently ongoing phylogenetic studies combining neontological and paleontological material. However, comments can be made on some features of *Melqartitermes* n. gen. and their distribution among the higher lineages of basal Isoptera as they are presently defined.

The presence of the ventral cervical sclerite, fully pentamerous tarsi, multi-segmented cerci, serrated spurs, and a large arolium attest to the primitive nature of this fossil. Nonetheless, the absence of an anal lobe in the hind wing is a peculiar apomorphy of *Melqartitermes* n. gen. In the current system of the Isoptera (e. g., as outlined by ENGEL & KRISHNA 2004), this genus might most closely approximate *Stolotermes* and *Porotermes* or *Hodotermes* and *Anacanthotermes*, particularly the former two owing to the narrow radial field, with Rs generally parallel to the costal margin. However, *Melqartitermes* n. gen. differs from all of these in its large pronotum with a straight anterior border and the presence of the ventral cervical sclerite, and from the latter two in the completely pentamerous tarsi and narrow radial field. The genus *Archotermopsis* has an apical mandibular structure and venation that perhaps most resembles those of *Melqartitermes* n. gen., although significant differences remain between these genera.

As noted, *Melqartitermes* n. gen. has a narrow radial field along the entire anterior margin of the forewing, with Rs not branching extensively near the wing apex but instead simply joining the anteriormost branch of M near the wing apex. This differs notably from other primitive Cretaceous fossils such as *Carinatermes* and *Meiatermes*, as well as the Tertiary fossil genus *Ulmeriella*, all of which have fully pentamerous tarsi. In addition, *Melqartitermes* n. gen. differs from *Carinatermes* in the presence of arolia (absent in *Carinatermes*), a pronotum with a straight anterior mar-

gin (deeply concave in *Carinatermes*), and the humeral border of its forewing scale weakly convex (straight in *Carinatermes*). From *Meiatermes* the new genus further differs by the longer Sc and R, with Sc extending to about the forewing midlength (both terminating before the forewing midlength in *Meiatermes*), and the more extensively branched M.

The absence of the fontanelle and the procoxal keel is somewhat uncertain as both of these surfaces are exceedingly difficult to see owing to the nature of preservation of the holotype of the type species.

*Melqartitermes myrrheus* n. gen. n. sp.

Figs. 3, 4

Holotype: Imago (Fig. 3), AMNH L-Iso1.

Age: Early Cretaceous, Neocomian.

Locus typicus: Lebanon.

Etymology: The specific epithet is a reference to myrrh, an aromatic gum-resin exuded by *Commiphora abyssinica* (O. BERG.) ENGL. (Burseraceae) and related species, and used in trade by the ancient people of the Mediterranean.

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

Description. – As described for the genus with the following additions: Imago. Width of head 0.82 mm; compound eye diameter 0.29 mm; lateral length of pronotum 0.82 mm; length of forewing from basal suture to apex 4.6 mm; width of forewing 1.38 mm; length of forewing scale 0.74 mm; width of hind wing 1.38 mm. Integument dark brown and (where evident) faintly imbricate; setation not evident except on ventral cervical sclerite and pleura, setae short, simple, and anteriorly- or laterally-directed. Forewing with R branched near its midlength; Rs terminating just slightly before wing apex, with five branches, apically joined to M by rs-m just before midlength of apicalmost branch; M terminating at wing apex, with at least five main branches evident, all branches simple, basalmost branch terminating at apical fifth of wing along posterior wing margin; only four apical branches of CuA visible, all apparently simple, cubital field apparently occupying about three-quarters of posterior wing margin.

### 3.4. Amber from Myanmar

While long believed to be of Tertiary age, amber from northeastern Burma was recently and correctly revealed to be Early Cretaceous in age, dating from the latest Albian (GRIMALDI et al. 2002; CRUICKSHANK & KO 2003). The fauna is remarkably diverse, perhaps more so than any other Cretaceous amber assemblage. Concomitantly, the termite fauna of Burmese amber is similarly important, representing the most diverse Cretaceous amber assemblage of Isoptera. Two species have been documented (COCKERELL 1916, 1917; WILLIAMS 1968), to which we here add a further four (Figs. 5–12).

Genus *Mylacrotermes* n. gen.

Type species: *Mylacrotermes cordatus* n. gen. n. sp.

Ety mology: The new genus-group name is a combination of *Mylacris* (meaning, “roach”) and *Termes* (meaning, “termite”). The name is masculine.

Diagnosis. – Imago. Head rounded, lateral and posterior margins gently rounded; antenna filiform basally with articles becoming more moniliform apically, with 14 articles; compound eyes circular, relatively small (Fig. 5a), separated from lower margin of head by apparently less than diameter, separated from posterior border of head by about 2.75 times diameter; ocelli absent; fontanelle absent; occipital carina present (Fig. 5b); single, well-sclerotized, ventral cervical sclerite present (Fig. 5b), sclerite large and roughly U-shaped; lateral cervical sclerites elongate, apparently without longitudinal groove. Pronotum large, slightly wider than head (Figs. 5a, b), cordate (Fig. 5a) (i. e., anterior margin deeply concave, lateral borders converging posteriorly, posterior margin rounded). Tibial spur formula 2-2-3 (two spurs on midleg, with a closely approximated subapical spine that appears as a third spur), with a single subapical spine on inner surface of meso- and metatibia (Figs. 5d, e), spurs minutely serrated; tarsi completely pentamerous (Figs. 5d, e); arolium absent. Wings not preserved except for bases; forewing scale very large, apparently without defined basal suture or well-defined scales (i. e., wings roughly torn when shed), all veins originating in wing scale; venation at wing base distinctly corrugated (Fig. 5a); humeral margin broadly arched and costal area broad (Fig. 5a); membrane of scale relatively well-sclerotized (i. e., tegminous), with distinct reticulations posterior to CuA (Fig. 5a); termination of CuP (claval fissure) on posterior wing margin distinctly basal to and separated from apical margin of wing scale; hind wing without defined basal suture, margin roughly torn (as in modern *Mastotermes darwiniensis* FROGGATT). Cerci long (Fig. 5c), surpassing apex of abdomen; segmentation not visible.

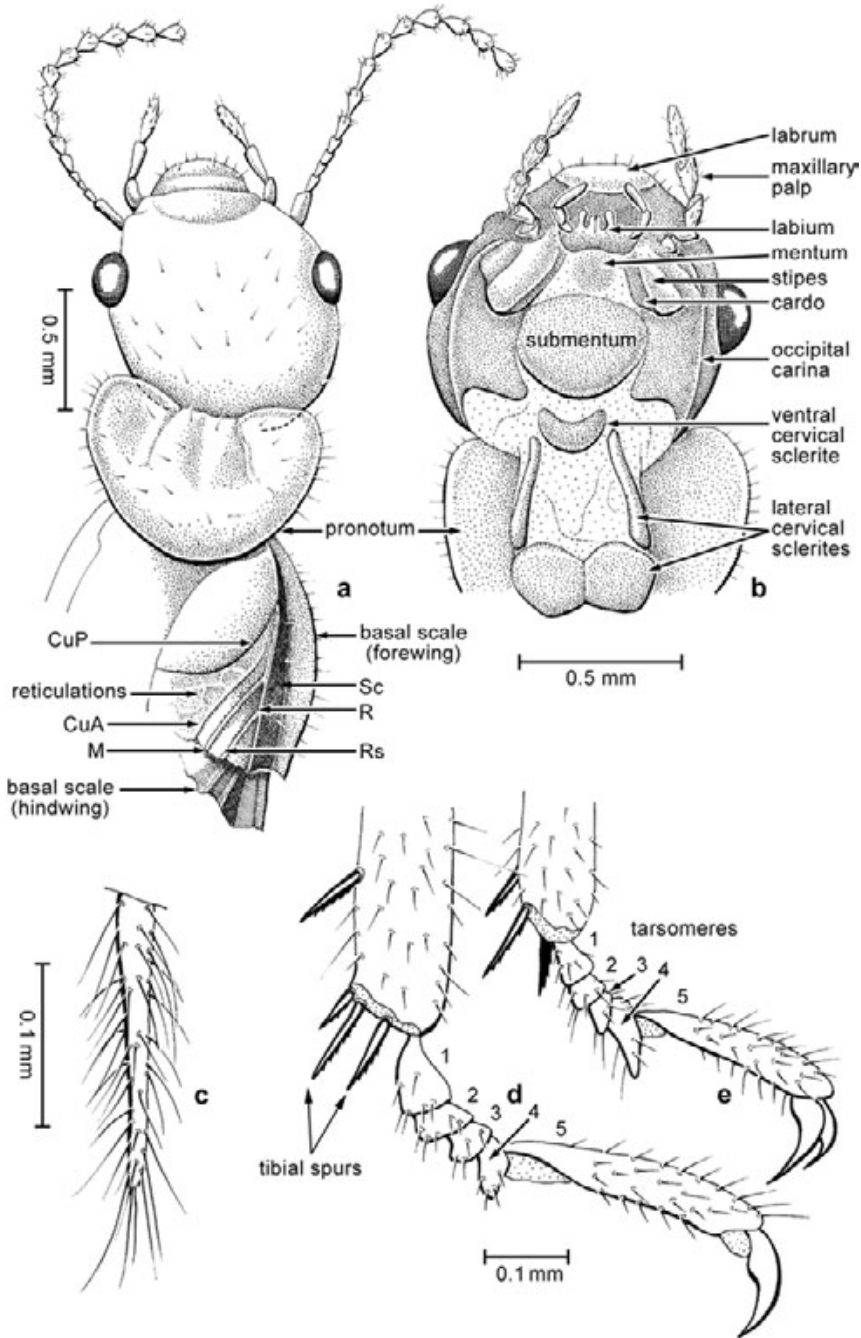
Comments. – *Mylacrotermes* n. gen. is, along with *Melqartitermes* n. gen. (vide supra), one of the most primitive known termites, exhibiting some clearly roach-like features such as the presence of ventral cervical sclerites as well as notable pleiomorphies for the Isoptera. Like *Mastotermes* the new genus has completely pentamerous tarsi on all legs, a well-defined occipital carina, a strong procoxal carina (i. e., “keeled procoxae”), a relatively well-sclerotized wing base with reticulations present posterior to CuA, a relatively broad costal area in the wing base, a broadly arched humeral margin to the wing base, a broad pronotum, and long cerci. Unlike *Mastotermes*, however, *Mylacrotermes* n. gen. lacks an arolium, lacks a basal cleavage suture in the forewing, and primitively retains a ventral cervical sclerite and corrugated wing veins. We can only presume that *Mylacrotermes* n. gen. would also have primitively retained a large anal lobe or fan in the hind wing owing to its presumed position as basal relative to *Mastotermes*.

*Mylacrotermes cordatus* n. gen. n. sp.

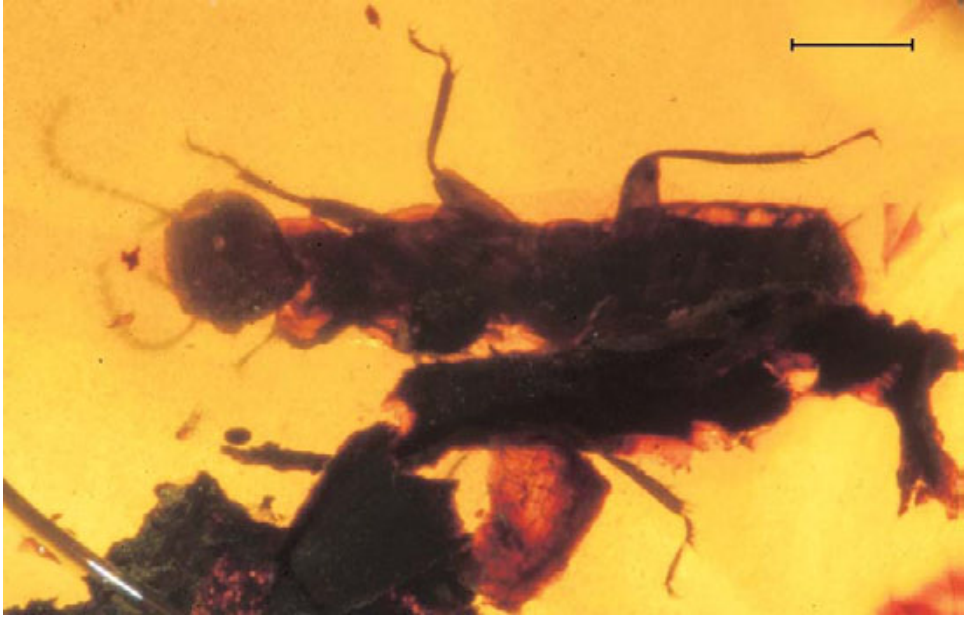
Figs. 5–6

Holotype: Imago (dealate) (Fig. 6), SEMC KU-Bu-045.

Age: Early Cretaceous, latest Albian.



**Fig. 5.** Holotype imago of *Mylacrotermes cordatus* n. gen. n. sp. (SEMC KU Bu-045); Burmese amber, latest Albian; Tanai Village, Myanmar. **a:** Detail of head (dorsal aspect), prothorax, and wing bases. **b:** Detail of head and anterior prothorax (ventral aspect). **c:** Cercus. **d:** Metatarsus, metapretarsus, and apex of metatibia. **e:** Mesotarsus, mesopretarsus, and apex of mesotibia.



**Fig. 6.** Photomicrograph of holotype imago of *Mylacrotermes cordatus* n. gen. n. sp. (KU Bu-045); Burmese amber, latest Albian; Tanai Village, Myanmar. – Scale bar = 1 mm.

Locus typicus: Myanmar (Burma), Kachin, Tanai Village (on Ledo Road 105 km NW Myitkyna).

Etymology: The specific epithet is the Latin term *cordatus* (meaning “heart-shaped”) and refers to the heart-shaped pronotum, characteristic of the species.

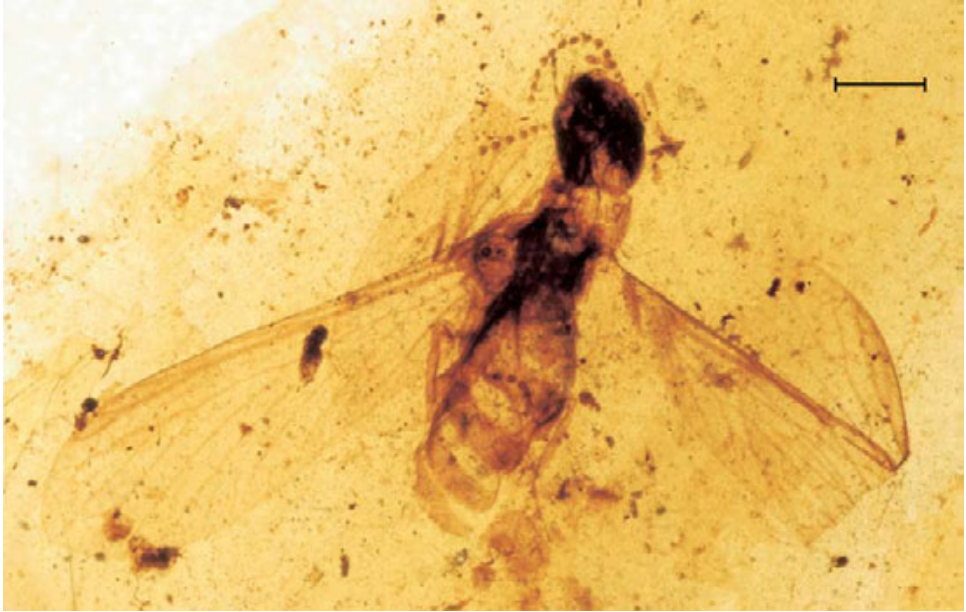
Diagnosis. – As for the genus (vide supra).

Description. – Imago (dealate). Length of head to apex of labrum 1.28 mm; approximate width of head 1.02 mm; compound eye diameter 0.33 mm; maximum length of pronotum 0.74 mm; length of pronotum along midline 0.62 mm; length of metatibia 1.07 mm; length of forewing scale 0.97 mm. Integument dark brown except ventrally on legs, cervix, and thorax brown, apparently faintly imbricate. Head and pronotum with scattered, erect, simple setae, those on lateral margins of pronotum slightly longer and more prominent; setae of remainder of thorax and abdomen slightly shorter and more sparse except at apex of abdomen setae slightly longer than those of pronotum and more dense than elsewhere on body; short, erect, simple setae along humeral margin of wing scale but not evident on surface of scale; cerci with numerous, elongate, simple, apically-directed, suberect setae.

#### Genus *Dharmatermes* n. gen.

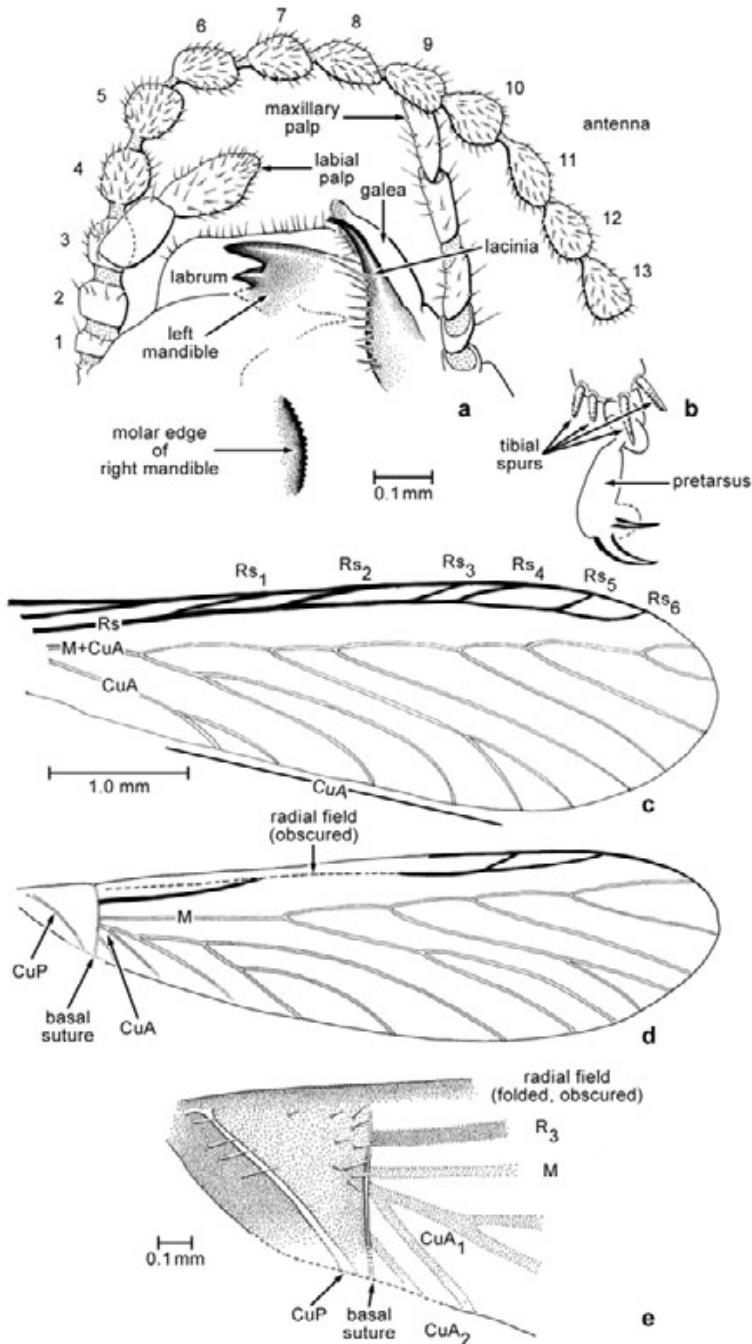
Type species: *Dharmatermes avernalis* n. gen. n. sp.

Etymology: The new genus-group name is a reference to the Dharmic faiths (the principal Dharmic faiths being Hinduism, Buddhism, Jainism, and Sikhism) predominant in Myanmar and surrounding countries. The name is, accordingly, a combination of Dharma and *Termes*, the oldest generic name in Isoptera. The name is masculine.



**Fig. 7.** Photomicrograph of holotype imago of *Dharmatermes avernalis* n. gen. n. sp. (AMNH Bu-313); Burmese amber, latest Albian; Tanai Village, Myanmar. – Scale bar = 1 mm.

**Diagnosis.** – Imago. Head broader than long, roughly rectangular, lateral borders parallel, posterior border gently rounded (Fig. 7); left mandible (as seen ventrally) with at least two, sharply-pointed marginal teeth (Fig. 8a), each tooth shorter than apical tooth, subsidiary tooth not present; lacinia with inner margin fringed with setae (Fig. 8a), possibly with two teeth (a smaller, subapical one) but this is obscure; molar edge of right mandible serrate (Fig. 8a) (as seen in shadowed profile; serrations likely corresponding to transverse ridges running across molar surface); antenna moniliform, with at least 14 articles (total article number unknown), basal articles smaller and ring-like; compound eyes circular, apparently separated from lower margin of head by less than one-half compound eye diameter, separated from posterior border of head by about 2.25 times compound eye diameter; ocelli absent; fontanelle absent. Pronotum large, flat, and broad, slightly broader than head; anterior border almost straight to weakly convex; lateral borders apparently parallel-sided, with posterior corners gently rounded inward; posterior border straight, thus pronotum with a largely quadrate shape. Metatibia with four spurs, spurs minutely serrated, metatibia without subpical spines; tarsi apparently pentamerous; pretarsus with arolium apparently present (Fig. 8b). Wings hyaline, membrane not reticulate; basal suture very weakly curved, nearly straight; CuP (claval fissure) similarly nearly straight, terminating slightly basad posterior point of termination of basal suture; diagnosis of venation based on right forewing (Fig. 8d) (vide Comments, infra); veins Sc, R, and Rs heavily pigmented, remainder lightly pigmented; forewing scale large, overlapping hind wing base, humeral margin almost straight (Fig. 8e), basal suture nearly straight (Fig. 8e); all veins originating inside wing scale (Fig. 8e); Sc short, terminating on costal margin in basal fifth of wing; R simple and short, terminating in



**Fig. 8.** Holotype imago of *Dharmatermes avernalis* n. gen. n. sp. (AMNH Bu-313); Burmese amber, latest Albian; Tanai Village, Myanmar. a: Anteriormost portion of head (ventral aspect). b: Metatarsus, metapretarsus, and extreme apex of metatibia (as preserved). c: Left forewing venation (teratological: vide text). d: Right forewing venation. e: Right forewing base.

basal quarter of wing; Rs with six anterior branches, first branch arising at basal third of wing; Rs running parallel to costal wing margin for entire length; radial field relatively narrow for entire length of wing (as in Termopsidae); M with long, pectinate branches, branches relatively straight and angled toward posterior margin except basalmost branches slightly and gently curved, first branch of M arising before forewing midlength, medial field encompassing wing apex; apicalmost branch of CuA terminating on posterior wing margin just before apical third of forewing length; hind wing without anal lobe; hind wing broader than forewing (likely teratological: vide Comments, infra). Apical segments of abdomen damaged.

Comments. – The venations of the two forewings in the holotype of *Dharmatermes avernalis* n. gen. n. sp. exhibit striking differences (cf. Figs. 8c, d), clearly resulting from a teratology in the formation of the left forewing (Fig. 8c). The right forewing depicts a more typical venation (Fig. 8d), with the stems of M and CuA separate at the basal suture. In the left forewing, however, M and CuA are partially fused, resulting in a composite venation whereby the more apical branches of CuA appear as a basal, forked branch of M. A nearly identical form of teratological fusion of M and CuA is seen in modern termites. For example, individuals of the kalotermitid *Neotermes fletcheri* HOLMGREN & HOLMGREN are known to sometimes have M and CuA partially fused, giving rise to the same condition in which the basal, forked branch or branches of “M” are actually the more apical branches of CuA (e. g., ROONWAL & SEN-SARMA 1960). Interestingly, in the formation of this teratology the hind wing is correspondingly broadened such that the wings are no longer homonomous, similar to the condition seen in the holotype of *D. avernalis* n. gen. n. sp.

The right forewing venation of *Dharmatermes* n. gen. (Fig. 8d) is not without similarity to that of *Stolotermes* and *Porotermes* (vide etiam *Tanytermes* n. gen., infra). All three genera have a narrow radial field running parallel to the anterior wing margin.

The tarsi are apparently pentamerous and the pretarsi apparently bear an arolium but these are difficult to discern owing to incomplete preservation of the holotype and these features should be considered tentative. In addition, it was not possible to determine the spur number of the pro- and mesotibia as these legs are damaged in the holotype.

*Dharmatermes avernalis* n. gen. n. sp.

Figs. 7–8

2002 *Kalotermes ?swinhoei*. – GRIMALDI et al., p. 33, 35, fig. 22f.

Holotype: Imago (Fig. 7), AMNH Bu-313.

Age: Early Cretaceous, latest Albian.

Locus typicus: Myanmar, Kachin, Tanai Village (on Ledo road, 105 km NW Myitkyna).

Etymology: The specific epithet is the Latin term *avernalis* and means “of Avernus” (Avernus was the term for the nether world and the name, therefore, means “of the nether world”).

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

Description. – Imago. Length of head to labral apex 1.30 mm; length of head to

mandibular base 0.94 mm; head width 0.89 mm; compound eye diameter 0.20 mm; pronotal length 0.66 mm; pronotal width 0.92 mm; metatibial length 0.89 mm; length of forewing from basal suture to apex 5.0 mm; length of forewing scale 0.89 mm; forewing width 1.58 mm. Integument of head dark brown, remainder brown; microsculpturing not evident. Setae of head and pronotum not evident; wing scale with a few, erect, apically-directed setae basal to claval suture (CuP), additional, shorter, erect to suberect setae beyond claval suture and closer to basal suture (Fig. 8e). Forewing (based on right forewing venation: Fig. 8d) with Rs terminating before wing apex; M terminating at wing apex, with five main branches, first and second with secondary branches, basalmost branch terminating at apical quarter of wing along posterior wing margin; CuA with four main branches, all originating outside wing scale, third with secondary branches shortly after origin, cubital field occupying about two-thirds posterior wing margin. Abdomen incomplete.

### Genus *Tanytermes* n. gen.

Type species: *Tanytermes anawrahtai* n. gen. n. sp.

Etymology: The new genus-group name is a combination of the Greek prefix *tany* (meaning, "long") and *Termes*, the oldest generic name in Isoptera. The name is a reference to the elongate shape, particularly of the head, in this fossil. The name is masculine.

Diagnosis. – Imago. Head elongate (Figs. 9, 10a), posteriormost section tapering slightly to form "neck-like" attachment to prothorax, lateral borders roughly parallel-sided; right mandible (as seen through cleared labrum) with at least two, sharply-pointed marginal teeth, subsidiary tooth not present, apical tooth elongate (Fig. 10a); antenna with 14 articles, flagellar articles progressively larger from base to about midpoint and then approximately equal in length and width until apicalmost article which is slightly more elongate and narrow; compound eyes without anterior emargination, circular, relatively small (Fig. 10a), posteriad of antennal articulation by distance slightly less than compound eye length, separated from lower margin of head by less than eye diameter, separated from posterior border of head by many times eye diameter; ocelli absent; fontanelle absent. Pronotum elongate, longer than wide (Fig. 10a), maximal width slightly less than width of head, relatively flat; anterior border straight; lateral borders slightly convergent anteriorly; posterior border straight. All tarsi tetramerous (Figs. 10c–e); tibial spur formula 2-3-2 (Figs. 10c–e), spurs of all legs minutely serrated; pretarsus with ungues simple, with large arolium present on all legs (Figs. 10c–e). Wing membranes hyaline and not reticulate; veins Sc, R, and Rs heavily pigmented, remainder lightly pigmented; forewing scale large, overlapping hind wing scale, humeral margin almost straight, basal suture convex (Fig. 10a); all veins originating inside wing scale, termination of CuP (claval fissure) on posterior margin well prior to basal cleavage suture (Fig. 10a); Sc terminating on costal margin in basal quarter of wing length, at distance from basal suture slightly less than forewing scale length (Fig. 10b); R simple, terminating at about one-third wing length; Rs first branching in basal third of wing, no inferior branches present, with eight superior branches, the first minutely branched right along anterior wing margin; Rs running generally parallel to costal wing margin for entire length, thereby forming narrow radial field, Rs separate from M along its entire length; M relatively simple, running about half way between Rs and CuA, first branching in apical



**Fig. 9.** Photomicrograph of holotype in *Tanytermes anawrahtai* n. gen. n. sp. (AMNH Bu-1608); Burmese amber, latest Albian; Tanai Village, Myanmar. – Scale bar = 1 mm.

third of wing, with first branch terminating at wing apex, forming relatively narrow medial field encompassing wing apex; CuA highly pectinate along its entire length (Fig. 10b), some branches with shorter, apical branches as well, CuA-field encompassing nearly entire posterior margin of forewing. Abdomen relatively narrow, cylindrical; tenth tergum with deep medioapical division (Fig. 10f); cerci not preserved.

**Comments.** – While the venation of *Tanytermes* n. gen. is generally termopsine-like, other aspects of its morphology are quite autapomorphic. In particular, the elongate, snakefly-like shape of the head, with the exophthalmic compound eyes positioned far anterior on the head is dramatically distinctive and differs from all other Cretaceous Isoptera. In addition, the pronotum is elongate, although still narrower than the head capsule. The venation of *Tanytermes* n. gen. is reminiscent of *Stolotermes* and particularly *Porotermes* owing to the relatively narrow radial field that does not widen near the wing apex, the lack of a connection between Rs and M, with a more simplistic M extending to the wing apex. However, *Tanytermes* n. gen. lacks a subsidiary tooth on the right mandible, has a peculiarly elongate apical tooth, has an elongate pronotum and head capsule, wing membrane that is not reticulate (reticulate in *Porotermes*), a long and extensively branched CuA (much shorter in *Stolotermes* and *Porotermes*, with a corresponding expansion in the branching of M), and it possesses a distinct arolium.

It is worth noting that the “snakefly-like” head and labral shape of *Tanytermes* n. gen. (Figs. 9, 10) is remarkably similar to the overall head structure of soldiers in *Stolotermes* and *Porotermes*, although in both of these the compound eyes are dra-

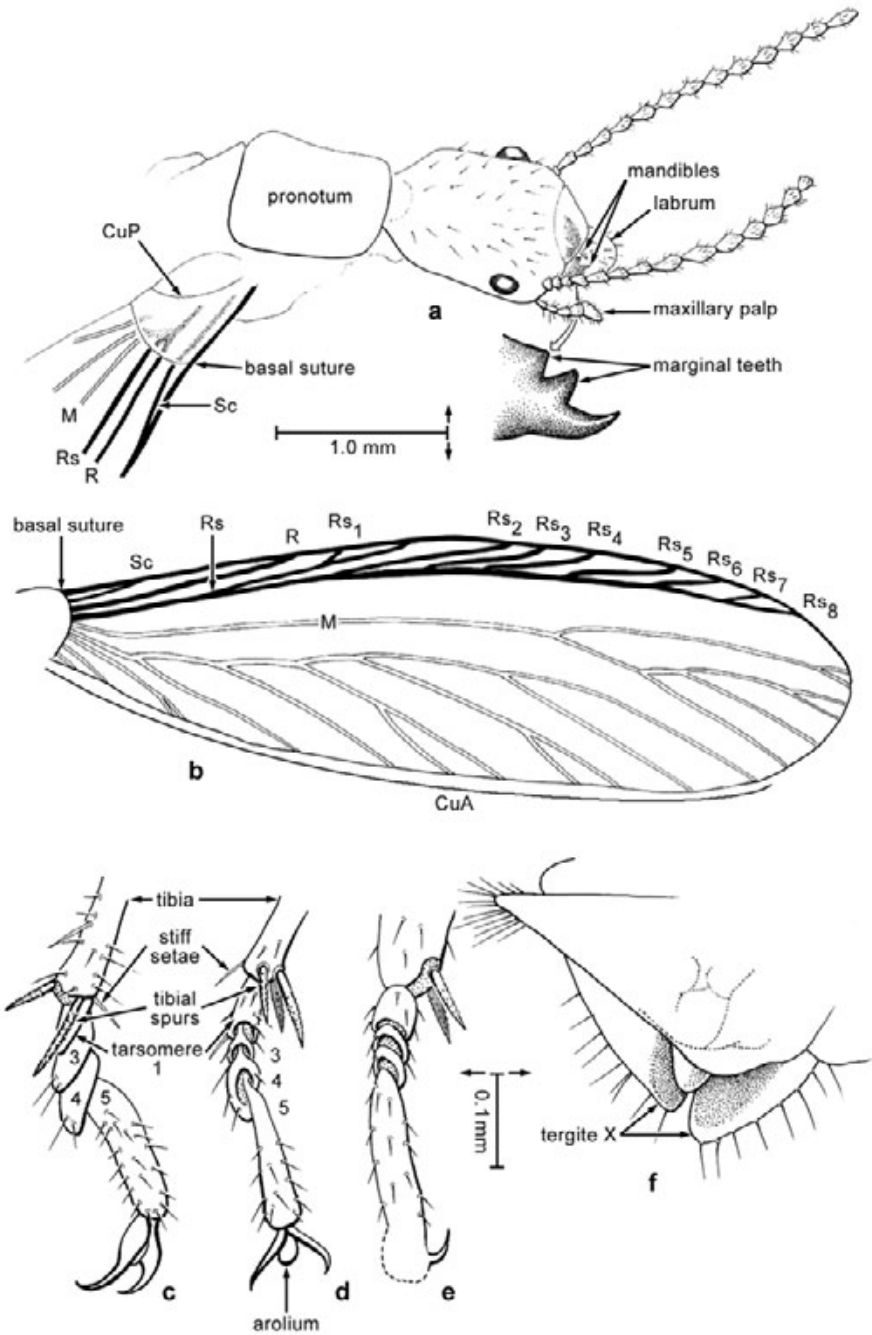


Fig. 10. Holotype imago of *Tanytermes anawrahtai* n. gen. n. sp. (AMNH Bu-1608); Burmese amber, latest Albian; Tanai Village, Myanmar. a: Detail of head, prothorax, and forewing base. b: Forewing venation. c: Protarsus, propretarsus, and apex of protibia (tarsal articles are numbered based on their homologies with other Isoptera whereby the second tarsal article is reduced and eventually lost, thus leaving only four total articles, but those being present are the first, third, fourth, and fifth, as accordingly numbered in the figure). d: Mesotarsus, mesopretarsus, and apex of mesotibia. e: Metatarsus, metapretarsus, and apex of metatibia. f: Abdominal apex as preserved.

matically reduced and the mandibles are much more elongate and pronounced. Nonetheless, if the head were found in isolation one might suspect it was closer to that of a soldier, than to an imago.

*Tanytermes anawrahtai* n. gen. n. sp.

Figs. 9–10

Holotype: Imago (Fig. 9), AMNH Bu-1608.

Age: Early Cretaceous, latest Albian.

Locus typicus: Myanmar, Kachin, Tanai Village (on Ledo road, 105 km NW Myitkyna).

Etymology: The specific epithet is a patronymic honoring King ANAWRAHTA who reigned from 1044 A.D. until his death in 1077, and the first ruler of a unified Burmese Empire who also converted the country to Theravada Buddhism.

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

Description. – Imago. Length of head to apex of labrum 1.02 mm; length of head to mandibular base 0.77 mm; head width 0.66 mm; compound eye diameter 0.10 mm; distance from compound eye to lower head margin 0.05 mm; pronotal length 0.66 mm; pronotal width 0.46 mm; metatibial length 0.74 mm; length of forewing with scale 4.95 mm; length of forewing scale 0.51 mm; forewing width 1.53 mm. Integument dark brown except legs brown, microsculpturing of head apparently imbricate, microsculpturing on remainder of body not evident. Head with scattered, short, simple, suberect, anteriorly-directed setae, similar setae on labrum; setae not evident on pronotum. Rs with eight branches, first with short secondary branches at wing margin, Rs terminating just before wing apex; M with four main branches, first and second with short secondary branches at wing margin, M terminating at wing apex, basalmost branch terminating just before wing apex along posterior wing margin; CuA pectinately branched, with nine branches, three originating in wing scale, third, sixth, and seventh branches with short secondary branches, cubital field occupying nearly entire posterior wing margin.

Genus *Proelectrotermes* ROSEN

1913 *Calotermes* (*Proelectrotermes*). – ROSEN, p. 331. Type species: *Termes* (*Kalotermes*) *berendtii* PICTET-BARABAN in: PICTET-BARABAN & HAGEN, 1856, by monotypy.

1941 *Calotermes* (*Neotermes*). – ARMBRUSTER, p. 18. Type species: *Calotermes* (*Neotermes*) *roseni* ARMBRUSTER, 1941, by original designation.

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 *Neotermes* 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. Herein we expand the genus to include two other amber fossil species, and extend its range back an additional 50 Ma. KRISHNA (1961) and EMERSON (1969) have provided the most recent, detailed diagnoses for *Proelec-*

*trotermes*, recognizing the genus as primitive kalotermitids with at least three tibial spurs, with two outer spines and a single inner spine (all seen in the new fossil species described herein). In the forewing of *Proelectrotermes* the radial vein is simple and elongate, extending near to the wing's midlength (or even slightly beyond, as in *P. berendtii*). The kalotermitid fossils considered herein exhibit these same attributes and in the absence of any other distinguishing traits are, accordingly, considered as members of this lineage.

*Proelectrotermes swinhoei* (COCKERELL) n. comb.

- 1916 *Termopsis swinhoei* n. sp. – COCKERELL, p. 138, fig. 4.  
 1920 *Termopsis swinhoei* COCKERELL. – FLETCHER, p. 988, pl. 166, fig. 23.  
 1925 *Termopsis? Swinhoei*. – SNYDER, p. 157, chart 1.  
 1933 *Termopsis swinhoei* COCKERELL. – EMERSON, p. 190.  
 1941 *Miotermes? swinhoei* COCKERELL. – ARMBRUSTER, p. 41.  
 1949 *Termopsis? swinhoei* COCKERELL, 1916. – SNYDER, p. 370.  
 1953 *Termopsis swinhoei* COCKERELL. – LAL & MENON, p. 7.  
 1968 *Kalotermes swinhoei* (COCKERELL). – WILLIAMS, p. 547, figs. 1–3.  
 1969 *Kalotermes swinhoei* (COCKERELL). – EMERSON, p. 34.  
 1978 *Kalotermes swinhoei* (COCKERELL). – BURNHAM, p. 89.  
 1978 *Kalotermes swinhoei* (COCKERELL, 1916). – SCHLÜTER, p. 55.  
 1978 *Kalotermes swinhoei* COCK. – ZHERIKHIN, p. 114.  
 1982 *Kalotermes swinhoe* [sic] (COCKERELL, 1916). – KEILBACH, p. 214.  
 1992 *Kalotermes swinhoei* (COCKERELL, 1916). – SPAHR, p. 30, 79.  
 1992 *Kalotermes swinhoei* (COCKERELL). – POINAR, p. 104.  
 1993 *Kalotermes swinhœi* (COCKERELL, 1916). – NEL & PAICHELER, p. 120.  
 2000 *Kalotermes swinhoei* (COCKERELL, 1916). – ROSS & YORK, p. 11, 17, fig. 3.  
 2002 *Kalotermes swinhoei* (COCKERELL). – GRIMALDI et al., p. 35.  
 2005 “*Kalotermes*” *swinhoei*. – GRIMALDI & ENGEL, p. 247.

Holotype: Imago, NHML In. 19096.

Age: Early Cretaceous, latest Albian.

Locus typicus: Northern Myanmar.

Diagnosis. – This species was rather extensively described by WILLIAMS (1968) and we have not repeated that material here. Instead we provide only the most salient features for distinguishing the species from other *Proelectrotermes* and for documenting its place in the genus. The venation of this species is very similar to that of *P. holmgreni* n. sp. described below except that M branches apical to the final primary branching of CuA, while in *P. holmgreni* n. sp. the situation is reversed with M first forking well prior to the terminal branching of CuA. The species is also slightly smaller with a forewing length from the basal cleavage suture of 4.81 mm, and forewing width of 1.49 mm (nearly a third of the size of *P. berendtii* in Baltic amber!). Like the Tertiary species of *Proelectrotermes* the metabasitarsus is not distinctly elongate as is the case in *P. holmgreni* n. sp. The legs are unfortunately not sufficiently preserved to determine with accuracy the condition of the tibial spination.

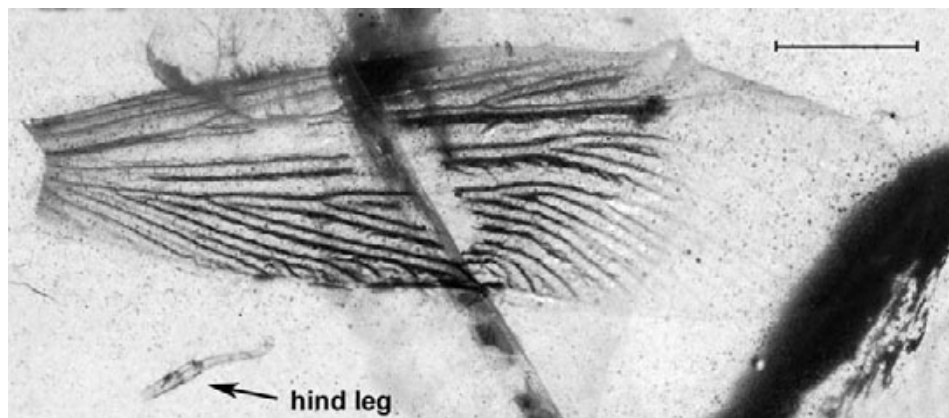


Fig. 11. Photomicrograph of holotype forewing and hind leg fragment (to the lower left of the forewing) of *Proelectrotermes holmgreni* n. gen. n. sp. (AMNH Bu-043); Burmese amber, latest Albian; Tanai Village, Myanmar. – Scale bar = 1 mm.

*Proelectrotermes holmgreni* n. sp.

Figs. 11–12

Holotype: Fragmentary imago (forewing and hind leg fragment: Fig. 11), AMNH Bu-043.

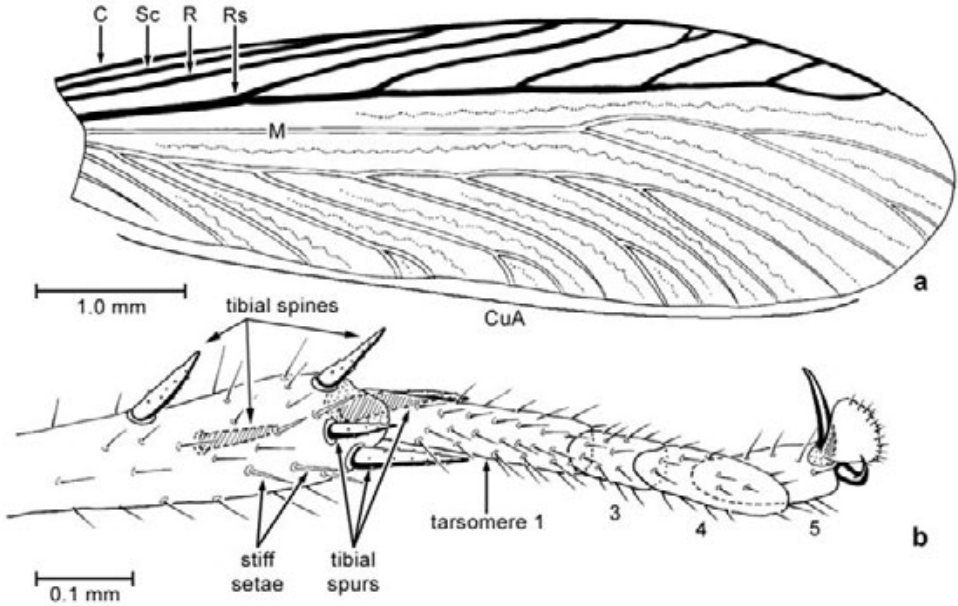
Age: Early Cretaceous, latest Albian.

Locus typicus: Myanmar, Kachin, Tanai Village (on Ledo road, 105 km NW Myitkyna).

Etyymology: The specific epithet is a patronymic honoring of NILS FRITHIOF HOLMGREN (1877–1954), the foremost isopterist of his era and perhaps the greatest comparative anatomist of the Isoptera ever. HOLMGREN developed the first phylogenetic hypotheses for the various groups of termites, recognizing most of the lineages as we understand them today, and laid a sturdy foundation for the subsequent evolutionary studies of KEMNER, EMERSON, HARE, KRISHNA, and many others.

Diagnosis. – The new species can be distinguished from all other congeners by the more elongate first tarsomere (apparently of the hind leg) which is slightly longer than the immediately following two tarsal articles (Fig. 12b). In addition, *P. holmgreni* n. sp. is slightly larger than *P. swinhoei* with a forewing length (as measured from the basal cleavage suture) of 6.0 mm and a width of 1.8 mm (refer also to the diagnosis for *P. swinhoei*, vide supra), but about one-half the size of the Baltic amber species, *P. berendtii* (refer to measurements of that species provided by EMERSON 1969). In addition, the radial field is slightly broader than in the Tertiary species.

Description. – Imago. Fragmentary specimen represented solely by shed forewing and fragment of hind leg (all other features of the species are unknown). Length of forewing from basal cleavage suture to apex 6.0 mm; width of forewing 1.8 mm; basal suture broadly curved; Sc, R, and Rs more heavily pigmented than M and CuA; Sc and R simple and elongate, Sc terminating on anterior wing margin in basal third of wing (Fig. 12a), R terminating near wing midlength; Rs running parallel to anterior wing margin, with six branches, third branch with minute secondary branches at wing margin, radial field relatively broad, Rs terminating before wing apex; M running at midpoint between Rs and CuA, not branching until apical third



**Fig. 12.** Holotype of *Proelectrotermes holmgreni* n. sp. (AMNH Bu-043); Burmese amber, latest Albian; Tanai Village, Myanmar. **a:** Forewing venation. **b:** Incomplete hind-leg; metatarsus, metapretarsus, and apex of metatibia (tarsal articles are numbered based on their homologies with other Isoptera whereby the second tarsal article is reduced and eventually lost, thus leaving only four total articles, but those being present are the first, third, fourth, and fifth, as accordingly numbered in the figure).

of wing, with three branches, second branch with minute secondary branches at wing margin, terminal branch of M reaching wing apex, basalmost branch terminating just before wing apex along posterior wing margin; CuA pectinately branched, with ten branches, two originating in wing scale, fourth, fifth, and seventh branches with short secondary branches, cubital field occupying nearly entire posterior wing margin. Three metatibial spurs minutely and sparsely serrate (pimplate); three metatibial spines (one close to arthrodial membrane bearing spurs) (Fig. 12b); metabasitarsus elongate (Fig. 12b), length about equal to combined length of succeeding tarsomeres; arolium present, large; pretarsal ungues simple, not serrate.

Genus *Kachinitermes* n. gen.

Type species: *Hodotermes tristis* COCKERELL, 1917.  
 Etymology: The new genus-group name is a combination of Kachin, the northeastern state of Myanmar from which the amber originates, and *Termes*, the oldest generic name in Isoptera. The name is masculine.

Diagnosis. – Imago. Small, kalotermitid-like species (hind wing length 3.95 mm, as preserved, maximal width 1.17 mm). Wing membrane hyaline, without pigment-

ed nodules; hind wing R terminating on anterior wing margin in basal quarter of wing, shortly beyond basal cleavage suture; Rs with apparently six, simple branches, M basally branching from radial stem in basal quarter of wing, simple along its entire length, running about midway between Rs and CuA; CuA occupying entire posterior margin of wing, with nine main branches, first originating inside wing scale, third, fourth, and fifth branches with secondary branches.

Comments. – The placement of type species has been controversial and, sadly, some of this ambiguity remains. Only a hind wing is preserved, with the extreme apex missing. COCKERELL (1917) originally placed his fossil in *Hodotermes*, without justification, while WILLIAMS (1968) transferred the species to Kalotermitidae and to the genus *Kalotermes* in particular. While it does seem as though attribution to Kalotermitidae is likely accurate, the species does not really appear to have true affinity to *Kalotermes*. Despite the fragmentary nature of the holotype and the degree of deterioration, there is no evidence that the wing membrane ever possessed pigmented nodules as is present in modern *Kalotermes*. Moreover, the hind wing R is much shorter than in modern *Kalotermes*, the vein scarcely extending to one-quarter of the wing length before terminating on the costal margin. The affinity of this new genus among kalotermitids is entirely unknown and we must await the discovery of new, more completely preserved material to elaborate further on its identity with any accuracy.

*Kachinitermes tristis* (COCKERELL) n. comb.

- 1917 *Hodotermes tristis* sp. n. – COCKERELL, p. 329, fig. 10.  
 1920 *Hodotermes tristis* COCKERELL. – FLETCHER, p. 988, pl. 166, fig. 24.  
 1933 *Hodotermes tristis* COCKERELL. – EMERSON, p. 190.  
 1941 *Hodotermes tristis* COCKERELL. – ARMBRUSTER, p. 40.  
 1941 *Rhinotermes? tristis* COCKERELL. – ARMBRUSTER, p. 41.  
 1949 *Hodotermes tristis* COCKERELL, 1917. – SNYDER, p. 370.  
 1953 *Hodotermes tristis* COCKERELL. – LAL & MENON, p. 4.  
 1968 *Kalotermes tristis* (COCKERELL). – WILLIAMS, p. 549, fig. 4.  
 1969 *Kalotermes tristis* (COCKERELL). – EMERSON, p. 35.  
 1978 *Kalotermes tristis* (COCKERELL). – BURNHAM, p. 89.  
 1978 *Kalotermes tristis* (COCKERELL, 1916 [sic]). – SCHLÜTER, p. 55.  
 1978 *Kalotermes tristis* COCK. – ZHERIKHIN, p. 114.  
 1982 *Kalotermes tristis* (COCKERELL, 1917). – KEILBACH, p. 214.  
 1992 *Kalotermes tristis* (COCKERELL, 1917). – SPHAR, p. 30, 79.  
 1992 *Kalotermes tristis* (COCKERELL). – POINAR, p. 104.  
 1993 *Kalotermes tristis* (COCKERELL, 1917). – NEL & PAICHELER, p. 120.  
 2000 *Kalotermes tristis* (COCKERELL, 1917). – ROSS & YORK, p. 11.  
 2002 *Kalotermes tristis* (COCKERELL). – GRIMALDI et al., p. 35.

Holotype: Imago, NHML In. 19103.

Age: Early Cretaceous, latest Albian.

Locus typicus: Northern Myanmar.

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

Tab. 1. Described Mesozoic Isoptera<sup>1</sup> (presented in order by age, from oldest to most recent). Three additional taxa, not listed or considered further herein since formal descriptions have yet to be published, are reported by BECHLY (in press).

Taxon	Locality	Type <sup>2</sup>	Age
<i>Baissatermes lapideus</i> n. gen. n. sp.	Baissa, Transbaikalia, Russia	C	Cretaceous (Berriasian)
<i>Valditermes brenanae</i> JARZEMBOWSKI, 1981	Wealden, England	C	Cretaceous (Hauterivian)
<i>Melqitermes myrribeus</i> n. gen. n. sp.	Lebanese amber	A	Cretaceous (Neocomian)
<i>Melqitermes bertrami</i> LACASA-RUIZ & MARTÍNEZ-DELCLÓS, 1986	Montsec, Spain	C	Cretaceous (Barremian)
<i>Jitermes tsaii</i> REN, 1995	Lushangfen, Beijing, China	C	Cretaceous (Barremian)
<i>Huaxitermes huangt</i> REN, 1995	Lushangfen, Beijing, China	C	Cretaceous (Barremian)
<i>Yanjiangtermes giganteus</i> REN, 1995	Lushangfen, Beijing, China	C	Cretaceous (Barremian)
<i>Yongdingia optipara</i> REN, 1995	Lushangfen, Beijing, China	C	Cretaceous (Barremian)
<i>Asiatermes reticulatus</i> REN, 1995	Lushangfen, Beijing, China	C	Cretaceous (Barremian)
<i>Mesotermopsis incompleta</i> (REN, 1995)	Lushangfen, Beijing, China	C	Cretaceous (Barremian)
<i>Mesotermopsis lata</i> (REN, 1995)	Lushangfen, Beijing, China	C	Cretaceous (Barremian)
<i>Melqitermes araripena</i> KRISHNA, 1990	Santana, Brazil	C	Cretaceous (Aptian)
<i>Cretatermes peireirai</i> FONTES & VULCANO, 1998	Santana, Brazil	C	Cretaceous (Aptian)
<i>Martconitermes talicei</i> FONTES & VULCANO, 1998	Santana, Brazil	C	Cretaceous (Aptian)
<i>Caatingatermes megacephalus</i> MARTINS-NETO et al., 2006 <sup>3</sup>	Santana, Brazil	C	Cretaceous (Aptian)
<i>Araripetermes nativa</i> MARTINS-NETO et al., 2006 <sup>3</sup>	Santana, Brazil	C	Cretaceous (Aptian)
<i>Nordestinatermes obesa</i> MARTINS-NETO et al., 2006 <sup>3</sup>	Santana, Brazil	C	Cretaceous (Aptian)
<i>Khanitermes acutipennis</i> (PONOMARENKO, 1988), n. comb.	Shar-Tologoy, Mongolia	C	Cretaceous (Aptian)
<i>Kachinitermes tristis</i> (COCKERELL, 1917), n. comb.	Burmese amber	A	Cretaceous (Albian)
<i>Proelectrotermes swimhoeti</i> (COCKERELL, 1916), n. comb.	Burmese amber	A	Cretaceous (Albian)
<i>Proelectrotermes holmgreni</i> n. sp.	Burmese amber	A	Cretaceous (Albian)
<i>Archeorhinotermes rossi</i> KRISHNA & GRIMALDI, 2003	Burmese amber	A	Cretaceous (Albian)
<i>Mylacrotermes cordatus</i> n. gen. n. sp.	Burmese amber	A	Cretaceous (Albian)
<i>Dharmatermes avernalis</i> n. gen. n. sp.	Burmese amber	A	Cretaceous (Albian)
<i>Tanytermes anawrahtai</i> n. gen. n. sp.	Burmese amber	A	Cretaceous (Albian)
<i>Mastotermes sarthibensis</i> SCHLÜTER, 1989	French amber	A	Cretaceous (Albian)
<i>Luettitermes priscus</i> SCHLÜTER, 1989, nom. emend.	French amber	A	Cretaceous (Cenomanian)
<i>Cretatermes carpenteri</i> EMERSON, 1967	Labrador, Canada	C	Cretaceous (Cenomanian)
<i>Carinatermes nascimbenei</i> KRISHNA & GRIMALDI, 2000	New Jersey amber, USA	A	Cretaceous (Turonian)

<sup>1</sup> Although described as a termite, *Hebeitermes weichangensis* HONG (1982) from Jiuquan, Gansu, China (Cretaceous: Barremian) is actually a roach wing.

<sup>2</sup> Type of preservation indicated as amber inclusion (A) or compression fossil (C).

<sup>3</sup> The validity of these taxa is of serious debate and the poor descriptions and figures suggest these may prove to be synonyms, a thorough revision of Cretaceous Isoptera from Brazil is needed from actual isopterists.

#### 4. Discussion

It is interesting to note that the history of Cretaceous termite research, outlined in the introduction, has mimicked that of the discovery and study of Cretaceous ants, another ecologically-ubiquitous and abundant social insect lineage today. As for the termites, the first Cretaceous ant was discovered and described in the late 1960's (WILSON et al. 1967) (note that at the time EMERSON (1967) described the "first" Cretaceous termite COCKERELL's species were mistakenly believed to be of Miocene age), with a few more trickling in during the 1980's (e. g., WILSON 1985; DLUSSKY 1987), but with the real explosion in their study and the full force of their implications not come to fruition until the late 1990's and earliest years of the current century (e. g., DLUSSKY 1996, 1999; GRIMALDI et al. 1997; GRIMALDI & AGOSTI 2000; ENGEL & GRIMALDI 2005). In this way, the studies of these two dominant social animals have mirrored each other. Interestingly, the total number of Cretaceous ants, including the armaniids, is 36 species (again close to the current total for termites) and there too the greatest diversity is from Asiatic deposits (21 species, or an overwhelming 58%, admittedly this may be slightly biased owing to looser species concepts for some of the Asiatic taxa but the fauna remains diverse nonetheless) (ENGEL & GRIMALDI 2005).

The taxa discussed herein demonstrate the great utility Cretaceous fossils will ultimately have in resolving basal relationships within Isoptera. Species such as *Melgartitermes myrrheus* n. gen. n. sp. and *Mylacrotermes cordatus* n. gen. n. sp. exhibit attributes more primitive than any modern termites, particularly in the presence of ventral cervical sclerites and it must be wondered whether some Early Cretaceous species described as compressions may have also exhibited such a trait but is unobservable owing to fidelity of preservation. More importantly, various Cretaceous species have character combinations that will provide unique insights into the resolution of relationships among basal lineages (GRIMALDI, ENGEL & KRISHNA in prep.).

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