

The oldest known mastotermitids (Blattodea: Termitoidea) and phylogeny of basal termites

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Abstract. Five finely preserved termites from the mid-Cretaceous (Cenomanian) amber of Myanmar provide new information allowing a reanalysis of the phylogeny of basal termites. The Mastotermitidae family is recovered as monophyletic, and a redefined Hodotermitidae *sensu lato* is also monophyletic to include Archotermopsidae, Hodotermitidae and Stolotermitidae. Such a phylogenetic relationship agrees with the results from previous molecular phylogeny. Alongside these findings, there are many taxa that can only be shown to be termites with no other phylogenetically informative data. These form a comb of ‘grade groups’ emerging in the Late Jurassic. The new amber specimens are described as two new species. *Anisotermes xiai* **gen. et sp.n.** is described from multiple castes and has symplesiomorphic characteristics: large body size, a broad pronotum, well-developed reticulated veins, and a large anal lobe of the hindwings. It shares wing features with the other new species, *Mastotermes monostichus* **sp.n.** Both new taxa are assigned to the Mastotermitidae, as they are shown to have synapomorphies that unite the family.

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Introduction

Termites are widespread insects that are of considerable economic and ecological importance, mostly inhabiting the tropics and subtropics (Jones & Eggleton, 2011). There are approximately 3000 described termite species (Krishna *et al.*, 2013). Their ecological dominance is attributed to their eusociality (Engel *et al.*, 2009), similar to ants, eusocial vespid wasps and eusocial bees. However, termite castes are diploid, whereas eusocial Hymenoptera have haploid males and diploid females. In addition, termites and eusocial Hymenoptera are not closely related (Grimaldi & Engel, 2005; Engel *et al.*, 2009) and their similar extended phenotype (e.g. overlapping generations and sterile helper castes) is a living example of evolutionary convergence. Termites and the subsocial wood-feeding cockroach,

Cryptocercus, are believed to have a common ancestor (Inward *et al.*, 2007; Misof *et al.*, 2014) and termites are now classified as Termitoidea, an epifamily of Blattodea (Eggleton *et al.*, 2007; Xiao *et al.*, 2012; Beccaloni & Eggleton, 2013).

Among the Termitoidea, *Mastotermes* Froggatt, 1896 is acknowledged to be the most basal living genus, using both morphology and molecules (Engel *et al.*, 2009; Bourguignon *et al.*, 2015; Engel *et al.*, 2016a). However, there have been no synapomorphies available to define Mastotermitidae precisely, as more and more primitive termites are found. If Mastotermitidae is a monophyly, it is also poorly known. The identification characters are all plesiomorphies (Krishna *et al.*, 2013). This uncertainty is not helped by the description of only one extant species of Mastotermitidae, *Mastotermes darwiniensis* Froggatt, 1897, found naturally only in Northern Australia. Other records are wholly based on fossils, which do not give full morphological information. Extant mastotermitids have hindwings with large anal lobes, strongly reticulated wing venation, and eggs in two rows with a covering similar to a cockroach ootheca;

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these are all symplesiomorphies with other cockroaches, which tell us nothing about their phylogenetic position within the termites.

Fossil termites

The fossil record and phylogenetic reconstructions suggest that the earliest termites were from the Jurassic (Grimaldi & Engel, 2005; Bourguignon *et al.*, 2015). The oldest definitively identified fossil termite is an imago (winged adult) named *Baissatermes lapideus* Engel, Grimaldi and Krishna, 2007 from the Cretaceous Zaza Formation, Berriasian (140 Ma; Engel *et al.*, 2007a). However, other castes of this species are not known, so we cannot assume that *Baissatermes lapideus* was necessarily eusocial.

A checklist for the described mastotermitids through geological time was given by Wappler & Engel (2006). Subsequently, another mastotermitid, *Mastotermes aethiopicus* Engel *et al.*, 2015, was described from Africa (Engel *et al.*, 2015). There are now five genera in Mastotermitidae; among them, *Mastotermes* is the largest genus, but they are mostly described from fragmentary specimens, and so are hard to characterize fully. The taxonomic status of reported 'mastotermitids' in the Cretaceous – *Khanitermes acutipennis* Ponomarenko, 1988, *Mastotermes sarthensis* Schlüter, 1989, and *Valditermes brentanae* Jarzembowski, 1981 – has been controversial because several of them have only incomplete wings, with few phylogenetically useful characters preserved. Here, we undertake a new phylogenetic analysis of basal termites, augmented with new amber mastotermitids, showing that their fossil records do indeed stretch back to the Cretaceous.

Materials and methods

Taxon sampling and character choice

The discovery of new basal-termite fossils provided incentive for our reanalysis of the phylogeny of the basal termites, especially Mastotermitidae. Previous phylogenetic analyses used morphological characters from both fossil and extant termites (Engel *et al.*, 2009, 2016a). In this study, we reanalysed the data from those papers with additional taxa and new characters (File S1). We only examined basal termites (non-Neoisoptera), based on our collections, and we concentrated on the early evolution of termites. We used specimens with the body preserved (specimens with only wings preserved were excluded), which left us with 55 species of basal termites, including 33 fossil species, to be reanalysed. Seven fossil species (Table 1) have been described since 2007 (Engel, 2008; Poinar Jr, 2009; Engel & Delclòs, 2010; Engel *et al.*, 2011) and are included in an analysis for the first time. All the species used can be found in the phylogenetic tree (Fig. 1A) or in a NEXUS file (File S2). Seventy-four characters were extracted from the previous analyses (Engel *et al.*, 2009, 2016a) and nine new characters were added for this analysis. Several previously miscoded states,

Table 1. New fossil termite species added for this phylogenetic analysis.

Species	Materials	Age
<i>Anisotermes xiai</i> gen. et sp.n.	Burmese amber	Albian–Cenomanian
<i>Idanotermes desioculus</i> Engel, 2008	Baltic amber	Lutetian
<i>Kachinitermopsis burmensis</i> Poinar, 2009	Burmese amber	Albian–Cenomanian
<i>Morazatermes krishnai</i> Engel & Delclòs, 2010	Spain amber	Aptian
<i>Santonitermes chloaeae</i> Engel, Nel & Perrichot, 2011	French amber	Albian–Cenomanian
<i>Syagriotermes salomeae</i> Engel, Nel & Perrichot, 2011	French amber	Albian–Cenomanian
<i>Lebanotermes veltzae</i> Engel, Azar & Nel, 2011	Lebanese amber	Lower Aptian

even though innocuous, were corrected (Table 2). In Engel *et al.* (2009, 2016a), the characters 51 and 52 for dehiscent winged *Periplaneta* should have a value of 0, but they were given null values. For the character 88, only *Psamnotermes allocerus* and *Termitogeton umblicautus* were coded with state 1 (soldier head flattened), but the heads of stotermitids are general obviously flattened (an adaptation for their shuttling through the tunnels in the wood; see Fig. 2).

Phylogenetic analysis

Phylogenetic analysis was conducted using maximum parsimony (MP) in TNT v1.5 (Goloboff & Catalano, 2016) and WINCLADA v1.00.08, with the NONA script (Goloboff, 1997; Nixon, 2002). The analysis in TNT used 'New Technology Search' with Sectorial search, Ratchet, Drift and Tree fusing analyses. The minimum length was set to be found 100 times. Consensus trees were calculated through the strict method and Bremer support was calculated through the script 'bremer.run' of the program. A repeated analysis was run in WINCLADA using NONA and set to keep 10 000 maximum trees, 1000 replications and 100 starting trees per replication. The consensus trees were calculated through the strict, Nelsen and majority-rule methods. The final phylogenetic tree (Fig. 1A) is based on the strict consensus from WINCLADA with synapomorphies and plesiomorphies on the nodes.

Materials

The five new amber specimens were collected from a mine on the Noije Bum hill, about 20 km away from Tanai, Hukawng Valley, in Kachin State, northern Myanmar. They are from the mid-Cretaceous (Grimaldi *et al.*, 2002; Cruickshank &

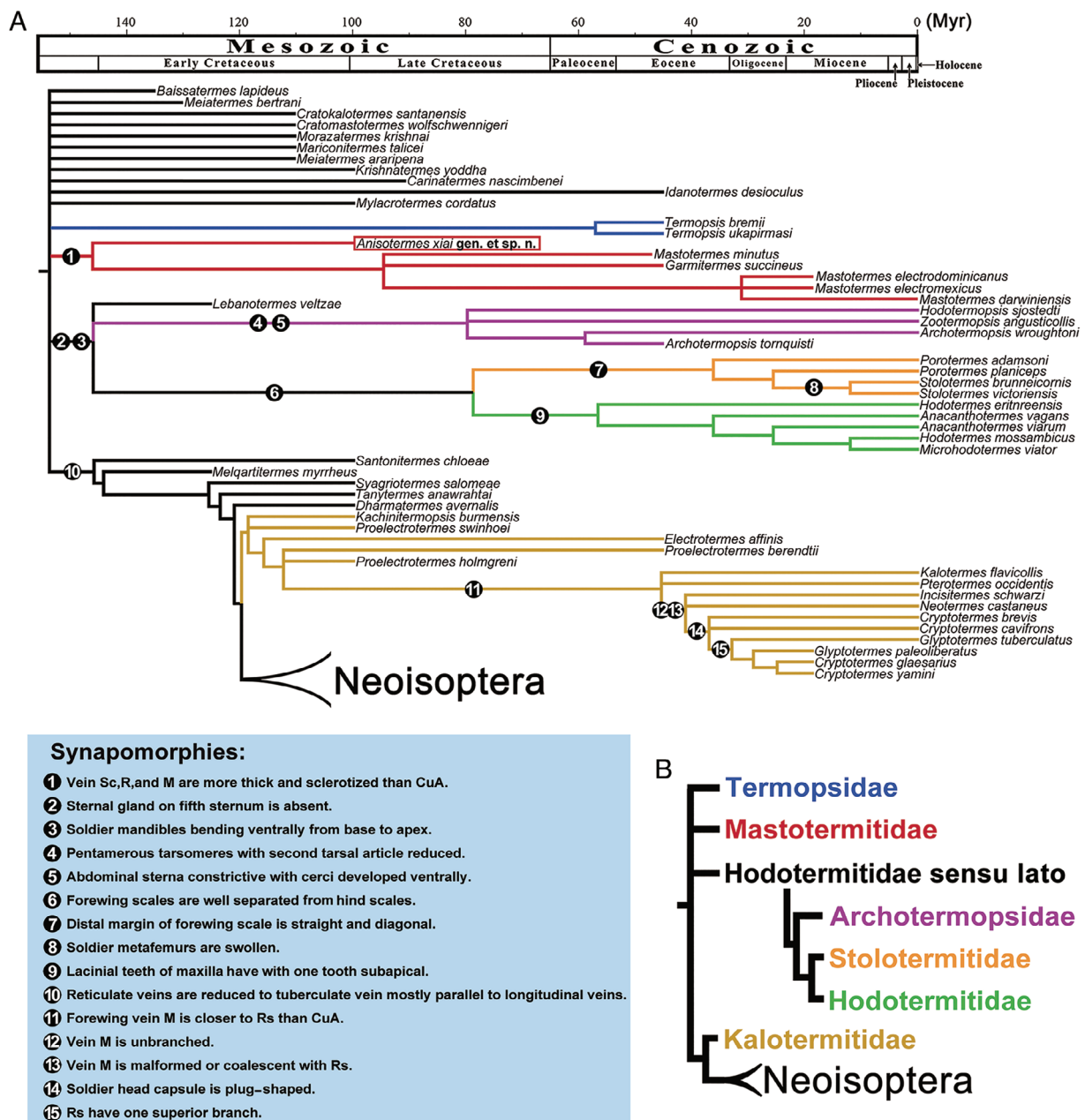


Fig. 1. Phylogeny of Termitoidae based on 55 species and 74 characters (analysed with TNT v1.5 and WINCLADA with NONA script). ‘Neoisoptera’ are added manually, and the divergence time are estimated for clarity. (A) Strict consensus tree; numbers on nodes show the synapomorphies. (B) Diagram of the family relationships of basal termites, with colours corresponding to clades in (A). [Colour figure can be viewed at wileyonlinelibrary.com].

Table 2. Correction of character states from previous matrices in Engel *et al.* (2009, 2016a).

Character in Engel <i>et al.</i> (2009)	Species	Original state	Corrected state
51. Fore- and hindwings, not dehiscent = 0, dehiscent = 1	<i>Periplaneta</i> sp.	–	0
52. Forewing basal cleavage suture, absent = 0, present = 1	<i>Periplaneta</i> sp.	–	0
88. Soldier heads, normal = 0, flattened = 1	<i>Poroterme adamsoni</i>	0	1
	<i>Poroterme planiceps</i>	0	1
	<i>Stoloterme brunneicornis</i>	0	1

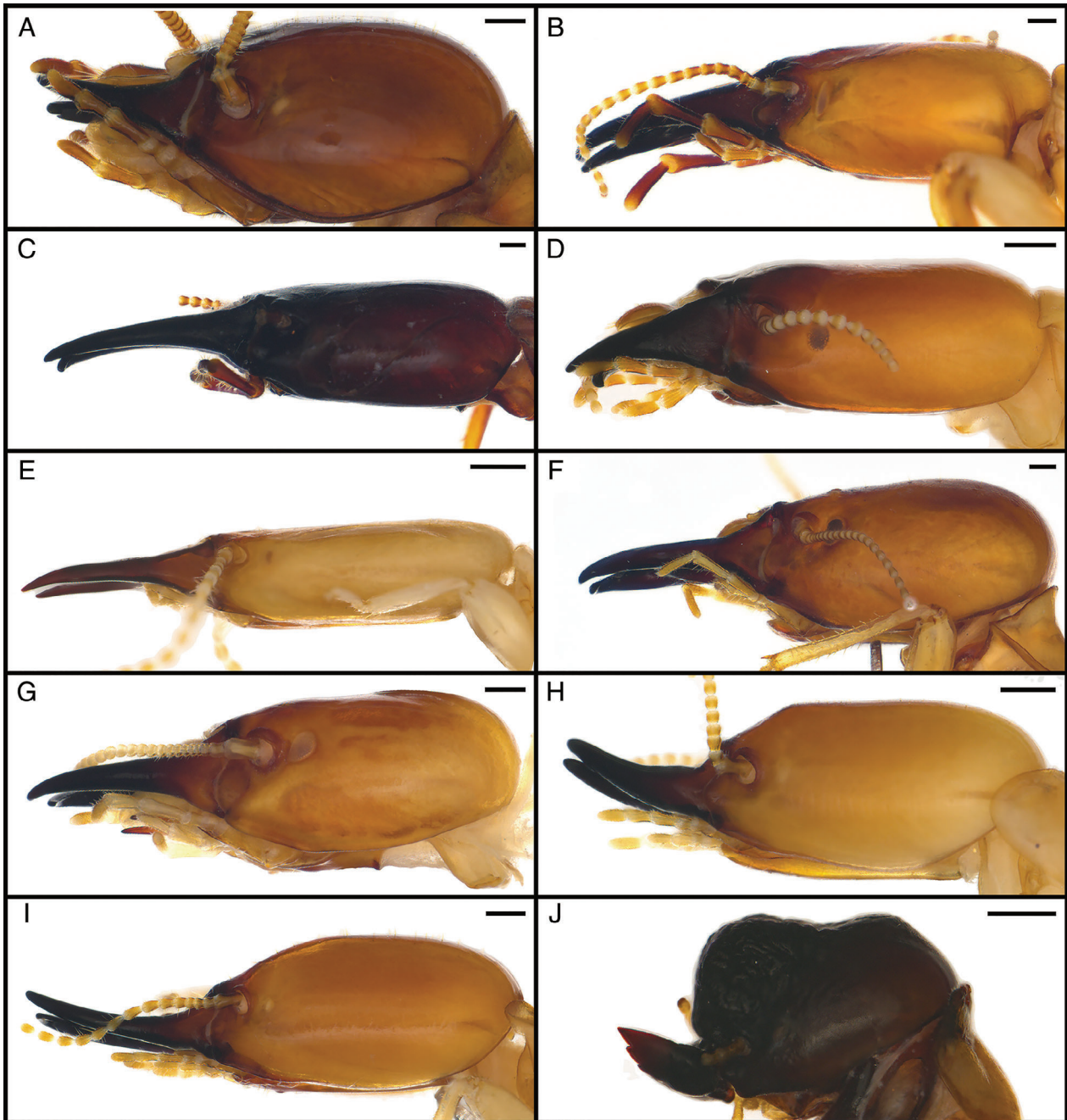


Fig. 2. Soldier heads of basal termites. Mastotermitidae and Kalotermitidae show upswept mandibles, whereas Archotermopsidae, Stolotermitidae and Hodotermitidae show deflexed mandibles. (A) *Mastotermes darwiniensis* Froggatt; (B) *Archotermopsis wroughtoni* Desneux; (C) *Zootermopsis angusticollis* Hagen; (D) *Porotermes planiceps* Sjostedt; (E) *Stolotermes victoriensis* Hill; (F) *Anacanthotermes viarum* König; (G) *Microhodotermes viator* Latrielle; (H) *Kalotermes flavicollis* Fabricius; (I) *Neotermes castaneus* Burmeister; (J) *Cryptotermes brevis* Walker. Scale bars: 0.4 mm. [Colour figure can be viewed at wileyonlinelibrary.com].

Ko, 2003; Ross, 2015). Many stem-group insects have been found in this locality with evolutionary significance (Engel *et al.*, 2016a; Chen *et al.*, 2018a,b). Imago specimens were observed and photographed with a Nikon SMZ25 (CNU). Worker/pseudergate and soldier specimens were photographed with a Zeiss AXIO Zoom V16 (Natural History Museum,

London). The specimens were submerged in water to reduce refraction, which gives rise to image distortion (refractive index: amber, *c.* 1.54; water, 1.33; air, 1). Simplified drawings were prepared using Adobe ILLUSTRATOR CC and further modified through Adobe PHOTOSHOP CC; the final drawings were adjusted for distorted preservation recovery.

Results

Systematic palaeontology

Order Blattodea, Brunner von Wattenwyl, 1882

Epifamily Termitoidae, Latreille, 1802

Family Mastotermitidae Desneux, 1904

Genus *Anisotermes* Zhao, Eggleton & Ren gen.n.

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Type species. Anisotermes xiai sp.n.

Etymology. The generic name is a combination of the Greek prefix 'Aniso-', which reflects the fact that the venations of wings of the specimen are asymmetric, and 'termes', which is the usual suffix for the generic name in Termitoidae. Gender masculine.

Diagnosis. Imago: Head approximately rounded; ocelli absent; fontanelle absent; Y-suture absent; mandible not exceeding labrum; antenna moniliform with about 25 articles, terminal 8 articles tapered; compound eyes hemispheric, lying on the middle position of the head; pronotum definitely saddle shape, slightly wider than head in dorsal view; lateral margin weakly turnup; procoxal carina present; tibial spines of all legs present; tibial spur formula 3–4–4; tarsi pentamerous; arolium absent; wings membranous, heavily reticulated; forewing scale large, overlapping hindwing base, basal suture convex, veins Sc, R, Rs and M more heavily pigmented than CuA. Forewing: all major veins origin in scale; Sc simple; Rs with five to six main branches, terminating on costal margin anterior to wing apex; radial field with moderate width, parallel to costal margin; M running about the midway between Rs and CuA, terminating on posterior margin; medial field relatively narrow; CuA branched, terminating about the same distance with Rs to wing apex; CuP (claval suture) arched, meeting with basal suture on posterior margin. Hindwing: without basal suture, large anal lobe present; M first inferior branch fading away, terminating in the centre of hindwings; cerci short, trimerous or tetramerous; abdominal styli absent in female but present in male.

Worker/pseudergate. Whole body pilous; head plumply rounded in dorsal view; clypeus relatively flat; Y-suture present but not strong; antenna moniliform, not tapered along length, with about 24 articles; pronotum slightly saddle-shaped, anterior margin convex but dorsally elevated for head movements, anterolateral corners, lateral margin evenly converging posteriorly; mesonotum lateral margin converging anteriorly; procoxal carina present; meso- and metatibia with extra spines on the inner side; tibial spur formula 3–4–4; tarsi pentamerous; meso- and metatibia with a row of macrosetae.

Soldier. Whole body pilous with setae slightly longer than worker/pseudergate; head capsule extended, plumply elliptical; antenna moniliform, with about 22 articles; compound eyes absent; ocelli absent; Y-suture absent; mandibles stout

but short, left mandible with two margin teeth, right mandible with one margin tooth; pronotum remarkable, roundly rhombic, slightly saddle shape; procoxal carina present; tibial spur formula 3–4–4; tarsi pentamerous; meso- and metatibia with extra spines and rows of macrosetae; Abdomen plump; styli slender.

Comments. *Anisotermes* gen.n. is morphologically assigned to Mastotermitidae on account of the distinct feature that M vein in the imago wing is sclerotized as well as Sc, R and Rs, but stronger than CuA. Compared with the described mastotermitids, *Anisotermes* shares most characters with *Mastotermes*, especially the relic species *Mastotermes darwiniensis*, which is the best reference point as it has fully accessible characters. The pronotum of *Anisotermes* imagoes have a similar shape to that of *Garmitermes* (Engel *et al.*, 2007b) except that *Anisotermes* has a weakly turned up lateral margin. However, *Anisotermes* imagoes do not have ocelli, and the first inferior vein of hindwing M fading away along length is intrinsically conserved which are never found in other mastotermitids. The pronotal shape of *Anisotermes* worker/pseudergate is similar within *Mastotermes*, whereas the pronotum length of *Anisotermes* soldier is greater than that of the soldiers in *Mastotermes*. Besides, the single marginal tooth near the base of right mandible in the *Anisotermes* soldier is unique, different from other known mastotermitid soldiers.

Anisotermes xiai Zhao, Eggleton & Ren gen. et sp.n.

[http://zoobank.org/urn:lsid:zoobank.org:act:C8A7A4DB-](http://zoobank.org/urn:lsid:zoobank.org:act:C8A7A4DB-AB12-4CBA-BACE-55EC732FB35C)
AB12-4CBA-BACE-55EC732FB35C.

Etymology. The specific name 'xiai' is in honour of Mr Fangyuan Xia, Director of Lingpoge Amber Museum, recognising his contribution to this study of termites in Burmese amber.

Diagnosis. As for the genus.

Holotype. Female imago: BA32001 (Figs 3–5) is temporarily housed at the Capital Normal University and will eventually be deposited in the Lingpoge Amber Museum in Shanghai (specimens are available for study by contacting DR or FX). It is a well-preserved termite imago (alate), with an almost complete body except that the majority of the antennae is missing; all wings are preserved.

Paratypes. Male imago: CNU-TER-BU-2017001 (Fig. 6), deposited in CNU, a well-preserved termite imago (dealate), with a fraction of forewing and hindwing preserved discretely. Worker/pseudergate: CNU-TER-BU-2017002 (Fig. 7A, B). Soldier: CNU-TER-BU-2017003 (Fig. 7C–E). Measurements of paratypes are shown in Table 3.

Type locality. Hukawng Village, Kachin State, northern Myanmar.

Stratigraphic horizon. Mid-Cretaceous (Cenomanian).

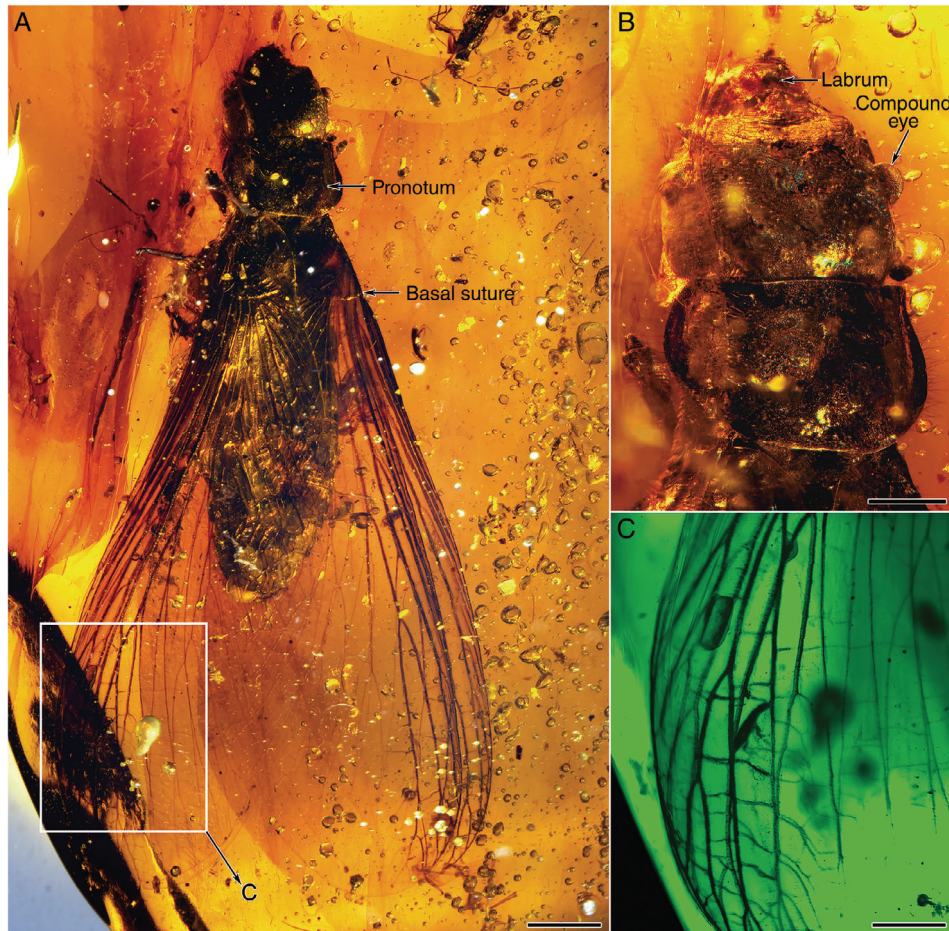


Fig. 3. Photographs of *Anisotermes xiai* gen. et sp.n., holotype specimen BA32001 (female imago). (A) Habitus (dorsal view); (B) head and pronotum; (C) 'cross-veins' shown on left wings. Scale bars: 2 mm (A); 1 mm (B, C). [Colour figure can be viewed at wileyonlinelibrary.com].

Description. Imago: body 15.5 mm long, well sclerotized, entirely dark brown; head length 3.2 mm, width 2.6 mm, with sparse setae; sclerotized labrum breaking away from anteclypeus, width approximate with approximately equal to length, anterior margin with short setae; apical tooth of mandibles not reaching the apex of labrum, margin teeth not visible; anteclypeus and postclypeus corrugated, much wider than long; antennae gracile, left antenna with 11 articles preserved, right antenna lost; compound eye small but plump, hemispheric, diameter 0.6 mm, lying on the middle position of the head, ommatidia diameter *c.* 25 μ m; pronotum pilous, width 3.3 mm, centronal length 1.9 mm in dorsal view, slightly covering head; tibial spurs and spines not serrated; Wings long and broad, length 19.0 mm, apex rounded; reticulated veins obviously pigmented among radial field and medial field; venation varying intraindividually. Forewing: humeral margin convex, with weakly arched lobe present, basal suture curved; left forewing vein Sc simple, terminating on basal quarter of wing length; R with a branch in scale, terminating along anterior wing margin in half wing length; Radial field occupying about 1/8 wing area, occupying about 1/8 left forewing with five branches, right

forewing with six branches, first branching in basal 1/5 of wing length; M first branching in basal third of wing length, left M with five main branches, right M varying with five branches in total; CuA first branching in scales, with high density near wing scales. Hindwings: without basal suture; large anal lobe present; left Rs with six branches, right Rs with three branches; CuP separating CuA from anal veins; A₁ not evident; A₂, A₃ invisible; abdomen broad and short; cerci trimerous or tetramerous, segmentation not obvious; abdominal styli absent.

Order Blattodea, Brunner von Wattenwyl, 1882

Epifamily Termitoidae, Latreille, 1802

Family Mastotermitidae, Desneux, 1904

Genus *Mastotermes* Froggatt, 1896

Mastotermes monostichus Zhao, Eggleton & Ren sp.n.

<http://zoobank.org/urn:lsid:zoobank.org:act:EE8BFB1B-7682-4C56-A305-E7CE86CE1F0E>.

Etymology. The specific name '*monostichus*' means 'monostichous' and is derived from the fact that the specimen has a forewing and a hindwing on one side.

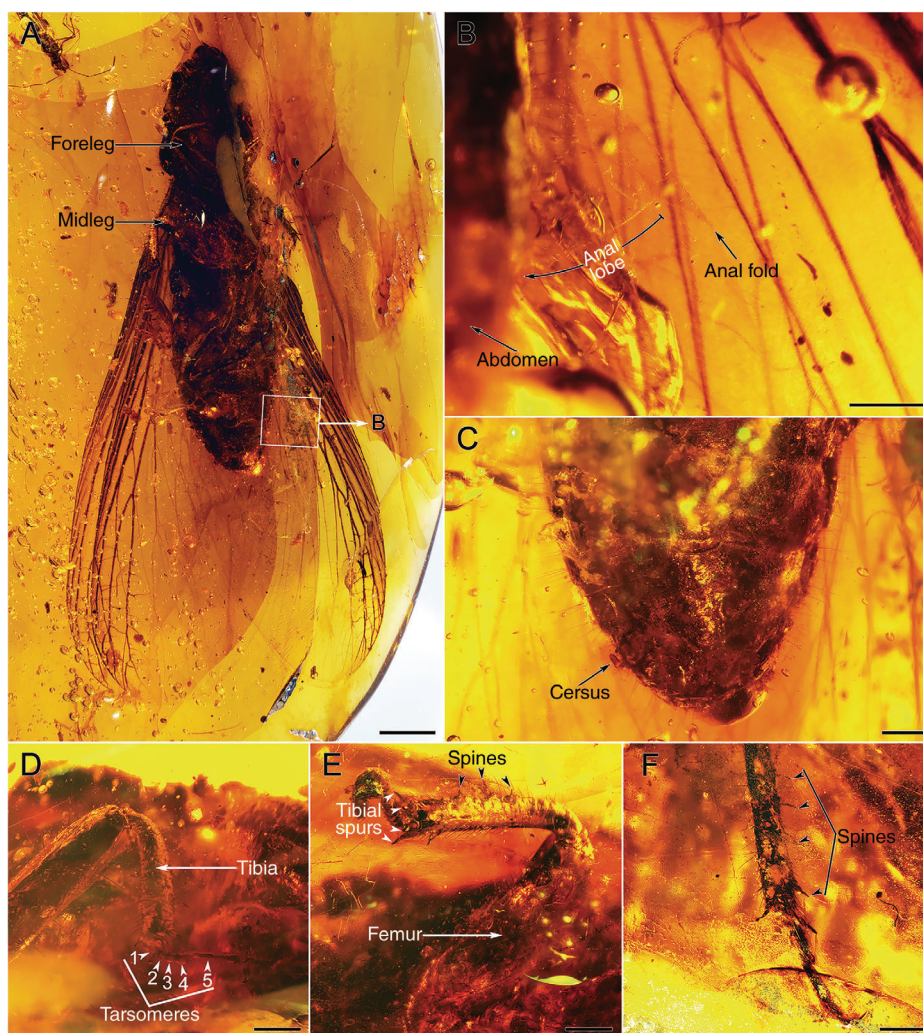


Fig. 4. Photographs of *Anisotermes xiai* gen. et sp.n., holotype specimen BA32001 (female imago). (A) Habitus (ventral view); (B) anal lobe of right hindwing; (C) genitalia in ventral view; (D–F) tibia, tarsi, and claw of right foreleg, mid-leg and hind leg. Scale bars: 2 mm (A); 0.5 mm (B–F). [Colour figure can be viewed at wileyonlinelibrary.com].

Diagnosis. *Imago*: wings membranous, long and broad, heavily reticulated with ‘cross-veins’ present; veins Sc, R, Rs and M more heavily pigmented than CuA, reticulated veins obviously pigmented among radial field and medial field; forewing Sc with a faint branch; R with two branches; radial field width moderate, Rs with five main branches; medial field encompassing wing apex, M main vein closely parallel to Rs main vein, with five main branches, first branch of M arising just before forewing mid-length, M terminating on costal margin anterior to wing apex; CuA with modest branches, apicalmost branch of CuA terminating on posterior margin about apical third of forewing length. Hindwing with large anal lobe; Sc simple, terminating on costal margin at about basal third of hindwing length; R long, terminating on costal margin before apical third of hindwing length; Rs with two branches; medial field encompassing wing apex, weakly narrower than forewing; M main vein separating with Rs near the wing base, relatively close parallel to Rs, with

two main branches, secondary branches present; CuA branching uniformly, terminating posterior to wing apex.

Comments. Compared with the known mastotermitids, *M. monostichus* sp.n. shows slightly simpler venation, intervals between longitudinal veins are wider. Besides, Sc + R + Rs extremely wide near basal suture. Hindwing A_1 without branches different from the multi-branch of A_1 in *Mastotermes darwiniensis*, and $A_2 + A_3$ have only one extra branch out of scale.

Holotype. CNU-TER-BU-2017004 (Fig. 8), deposited in CNU, only a pair of left forewings and left hindwings preserved.

Type locality. Hukawng Village, Kachin State, northern Myanmar.

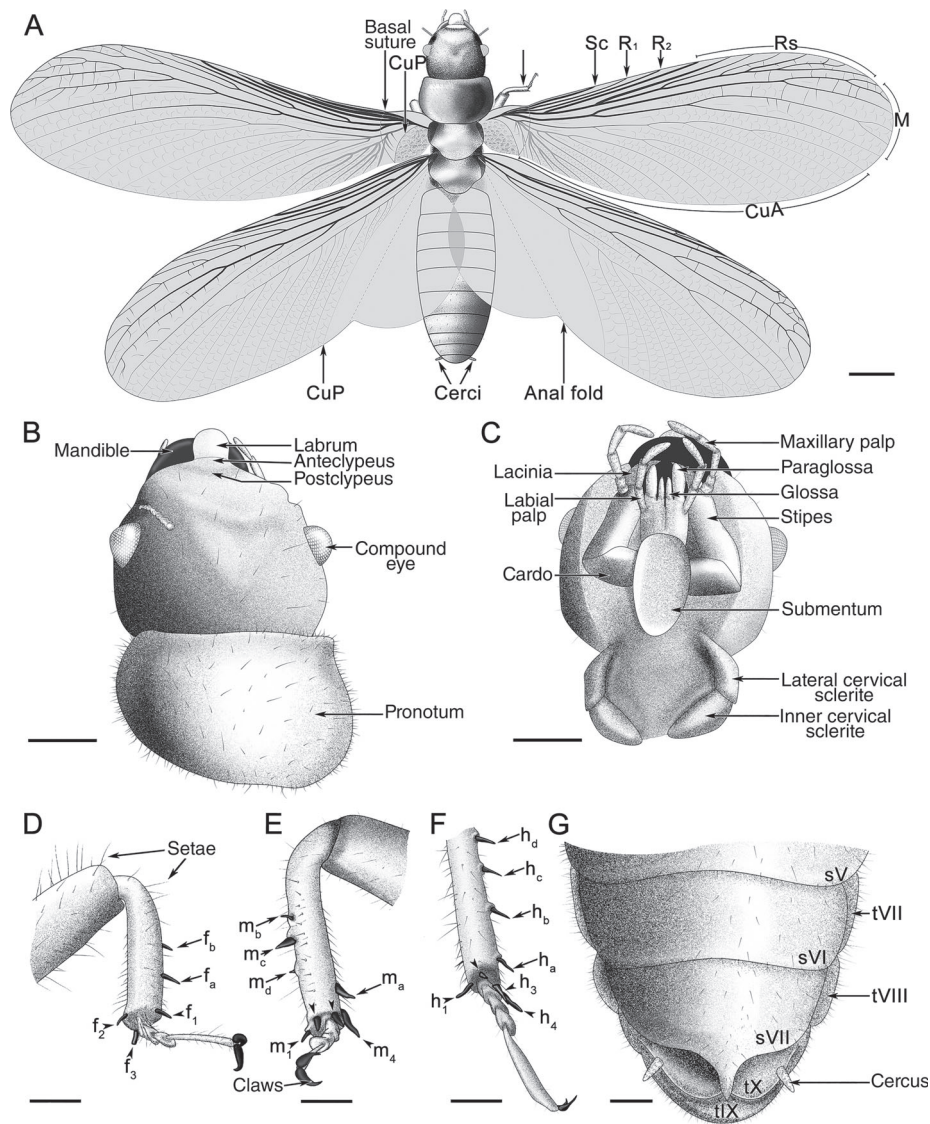


Fig. 5. Drawings of *Anisotermes xiai* gen. et sp.n., holotype specimen BA32001 (female imago). (A) Reconstruction with wings unfolded, part of the regular reticulated wings is speculative; (B) head and pronotum in dorsal view; (C) head and ‘cervix’ in dorsal view; (D–F) tibial spurs (labelled with numbers) and spines (labelled with letters) of the foreleg (f), mid-leg (m) and hind leg (h); (G) genitalia (ventral view). S, sternum; t, tergum. Scale bars: 2 mm (A); 1 mm (B, C); 0.5 mm (D–G).

Stratigraphic horizon. Mid-Cretaceous (Cenomanian).

Description. Imago: wings membranous, reticulated veins present; forewing basal part missing, preserved part length 12.1 mm, width 4.2 mm, apex rounded, middle section of posterior margin flat; veins Sc, R, Rs and M more heavily pigmented than CuA and A; forewing Sc short, with a faint branch; R with two branches, terminating on costal margin at about basal third of forewing length; radial field width moderate, occupying about one-fifth area on average; Rs with five main branches; medial field encompassing wing apex, M main vein closely parallel to Rs main vein, with five main branches, first branch of M arising just before forewing mid-length, fourth branch has a

secondary branch terminating on wing apex, M finally terminating on costal margin anterior to wing apex; CuA with modest branches, apicalmost branch of CuA terminating on posterior margin about apical third of forewing length. Hindwing with large anal lobe, preserved part with length of 12.9 mm, width 4.4 mm; Sc longer than that of forewing, terminating on costal margin at about basal third of hindwing length; R long, terminating on costal margin before apical third of hindwing length; Rs with two simple branches, first branch just before Sc terminates; medial field encompassing wing apex, weakly narrower than forewing; M main vein separating from Rs away from wing base, then closely parallel to Rs main vein, second branch of M having a secondary branch and a tertiary branch, terminating on

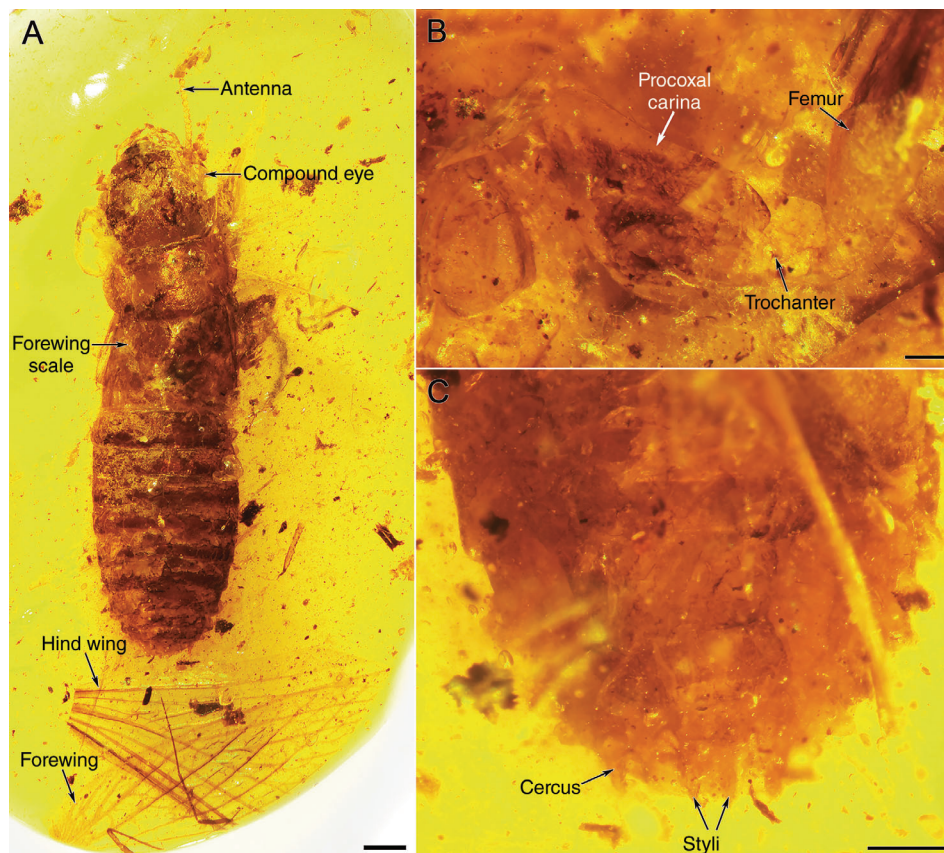


Fig. 6. Photographs of *Anisotermes xiai* gen. et sp.n., paratype specimen CNU-TER-2017001 (male imago). (A) Habitus, part of wings is isolated. (B) Procoxal carina on right fore-coxa. (C) Genitalia (ventral view). Scale bars: 1 mm in (A); 0.2 mm in (B); 0.5 mm in (C). [Colour figure can be viewed at wileyonlinelibrary.com].

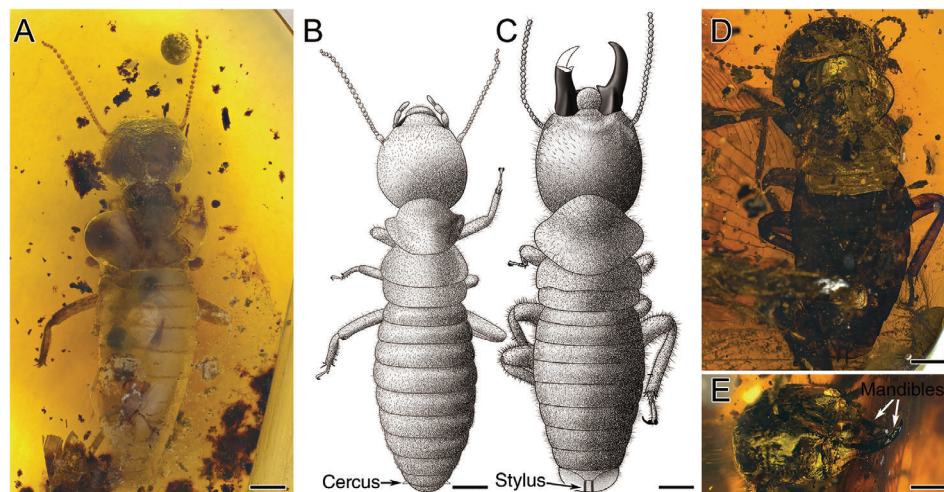


Fig. 7. Photographs and drawings of worker/pseudergate and soldier of *Anisotermes xiai* gen. et sp.n. (A, B) Worker/pseudergate habitus (dorsal view): paratype specimen CNU-TER-2017002; (C, D) soldier habitus (dorsal view): paratype specimen CNU-TER-2017003; (E) head of soldier, with left mandible broken. Scale bars: 1 mm. [Colour figure can be viewed at wileyonlinelibrary.com].

Table 3. Measurements of paratypes of *Anisotermes xiai* gen. et sp.n.: male (CNU-TER-BU-2017001), worker/pseudergate (CNU-TER-BU-2017002), soldier (CNU-TER-BU-2017003).

Measurement (mm)	Male	Worker/pseudergate	Soldier
Body length	12.6	11.0	12.9
Head capsule width	2.7	2.6	3.0
Head capsule length	2.9	3.1	3.8
Pronotum width	3.2	2.3	3.1
Pronotum length	1.8	1.6	2.3

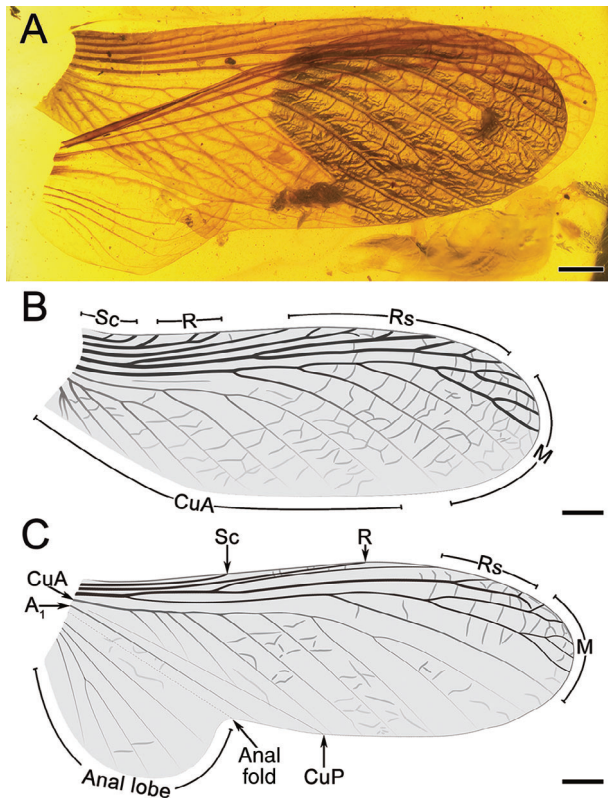


Fig. 8. Photograph and drawings of *Mastotermes monostichus* sp.n., holotype specimen CNU-TER-2017004 (isolated left wings). (A) Photograph of overlapped left wings; (B) drawing of the venation of left forewing; (C) drawing of the venation of left hindwing. Scale bars: 1 mm. [Colour figure can be viewed at wileyonlinelibrary.com].

wing apex; CuA branching uniformly, terminating posterior to wing apex.

Phylogenetic analysis of basal termites

WINCLADA (with the NONA program) found 12 most parsimonious trees with a best score of 265 (consistency index = 37, retention index = 74). We show the strict consensus tree in simplified form with only synapomorphies marked (Fig. 1A). Figure 1B is a diagram showing the relationship among the

families of basal termites. Original strict consensus can be found in Figure S1. Majority method consensus and Nelsen consensus are also shown in the Figures S2 and S3. TNT calculated the same results within WINCLADA and Bremer supports were calculated to show supports for nodes in the trees (Figure S4); all branches with synapomorphies receive scores ≥ 1 .

In this morphological phylogenetics analysis using the MP method, mainly based on fossil termites, the relationship between genera within families is generally the same as that in previous studies (Engel *et al.*, 2009, 2016a). Where the tree does differ from earlier studies is in the relationship between the families. Our trees show Mastotermitidae as monophyletic with *Anisotermes xiai* gen. et sp.n. at the base of that clade. Mastotermitids have a synapomorphy in that the M vein is thick and sclerotized, like Sc, R and Rs, and much stronger than CuA, whereas nonmastotermitid termites have narrow M veins as weak as CuA and cockroach main wing veins are all uniformly sclerotized. A clade includes Archotermopsidae, Stolotermitidae and Hodotermitidae, and *Lebanotermes* is recovered to be monophyletic, sharing the following synapomorphies: the sternal gland is absent on the fifth sternum and the soldier mandibles are bent ventrally from base to apex, whereas Mastotermitidae and Kalotermitidae have mandibles bent dorsally (Fig. 2). In this clade, Archotermopsidae is the sister group of two families, based on the reduced second tarsal articles and abdominal sterna constriction, with cerci developed ventrally. Stolotermitidae and Hodotermitidae are a sister group, sharing a synapomorphy of the separated fore- and hindwing bases, which distinguishes them from other basal termites. In addition, the straight and diagonal basal sutures of forewings define Stolotermitidae, and lacinial teeth with one tooth subapical define Hodotermitidae.

Discussion

Due to the low number of described Mastotermitidae species, the topology of this family was shaky with low support under phylogenetic analyses. Mastotermitids were clustered into a branch but without synapomorphies (Engel *et al.*, 2009) or shown as a pectinate paraphyly (Engel *et al.*, 2016a) located at the base of Termitoidae. In this study, with the new species involved and the support of synapomorphies, the monophyletic Mastotermitidae and its definition become clearer. The synapomorphies provide evidence to confirm the phylogenetic location of suspected 'Mastotermitids'. *Mastotermes monostichus* sp.n. and *Mastotermes aethiopicus* have their M vein more strongly sclerotized and more heavily pigmented than CuA. However, *Valditermes brenanae*, *Khanitermes acutipennis* and *Idanotermes desioculus*, which were placed into Mastotermitidae, do not show a strongly sclerotized M vein, and thus they cannot be classified as mastotermitids by this definition. Factors such as body size, habitat and behaviour influence the preservation of insects in amber (Weitschat & Wichard, 2002). Mastotermitids are rarely found in the Cretaceous and are particularly rare in amber. More resin flow was required for larger insects to be embedded and they were so strong that

they often escaped from the resin flow (Labandeira, 2014). Mastotermitids have a general body size > 10 mm, imagoes have strong sclerotized wings, and they can fly a long way (but directionlessly) (Weesner, 1965). Therefore, it is likely that few mastotermitids were trapped and the diversity of Mastotermitidae in the Cretaceous is probably underestimated. Besides, the caste differentiation and the presence of true worker is a synapomorphy of termites (Figure S1) and *Mastotermes* has true workers in comparison with known pseudergates generally appearing in Archotermopsidae, Stolotermitidae, Kalotermitidae and a few Rhinotermitidae. Therefore, we speculate that *Anisotermes* **gen.n.** might have had true workers, as did *Mastotermes* did, but only based on parsimony.

Archotermopsidae, Stolotermitidae and Hodotermitidae were thought to be in a single family: the same was thought to be true for Hodotermitidae in the early years (Ahmad, 1950). However, owing to their different biology, and as a result of morphological phylogenetics, each of them was assigned as a single family (Engel, 2011; Krishna *et al.*, 2013). In this study, the monophyly of a clade that includes all three families is recovered on account of new characters added. Interestingly, this clade agrees with the recent studies of mitochondrial genome phylogenetics and hybrid molecular phylogenetics (Legendre *et al.*, 2008; Cameron *et al.*, 2012; Bourguignon *et al.*, 2015). Therefore, we propose the clade Hodotermitidae *sensu lato* (Archotermopsidae + Stolotermitidae + Hodotermitidae), representing the monophyly, to help us better understand the relationships among the three families in relation to basal termites. The phylogenetic relationships among these families are different from previous studies (Legendre *et al.*, 2008; Cameron *et al.*, 2012; Bourguignon *et al.*, 2015). What is consistent is that Hodotermitidae is the most derived family of the Hodotermitidae *sensu lato*. Whether Archotermopsidae or Stolotermitidae is more basal is debatable. To better test the phylogeny of Hodotermitidae *sensu lato* with higher resolution, additional fossil specimens and molecular data are required. Engel *et al.* (2016a,b) described *Ginormotermes rex*, based solely on a giant termite soldier preserved in Burmese amber. The specimen shows similar morphological characteristics to *Archotermopsis*, *Hodotermopsis* and *Stolotermes*, such as the mandibles bending ventrally from the base to the apex, pale compound eyes and the swollen hind femora, whereas *G. rex* was thought to lie in the *Meiatermes*-grade. Our new synapomorphies support monophyletic Hodotermitidae *sensu lato* (and its contained families), and we believe *Ginormotermes* is a stem group of Hodotermitidae *sensu lato*, although the presumably large alates which might help to test this are unlikely to be preserved in amber.

Meiatermes-grade was defined as a paraphyletic grade group, which includes many fossil termites located between Mastotermitidae and the more apical families (Engel *et al.*, 2016a). ‘Loss of the anal lobe of the hindwing’ is a potential synapomorphy for non-Mastotermitidae termites but was not found to be a synapomorphy in our phylogenetic trees. In this study, an indeterminate grade group includes species of *Meiatermes*-grade and other Family incertae sedis fossil species and has a position that is similarly unresolved, as for the Mastotermitidae and Hodotermitidae. This probably represents an early evolutionary radiation

of basal termites in the Late Jurassic. In addition, more recently discovered fossil termites (*Morazatermes krishnai*, *Idanotermes desioculus*) are assigned to this grade. A branch including *Cratokalotermes santanensis*, *Idanotermes desioculus*, *Morazatermes krishnai* and *Mylacrotermes cordatus* is only shown in the majority consensus and the Nelsen consensus (Figures S2 and S3) but is not found in the strict consensus tree in our phylogenetic analysis. As no synapomorphies unambiguously support the branch, we conservatively treat it as unresolved above the Termitoidea level.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Original strict consensus calculated using WINCLADA (NONA).

Figure S2. Majority-rule consensus calculated using WINCLADA (NONA).

Figure S3. Nelsen consensus calculated using WINCLADA (NONA).

Figure S4. Bremer support for the branches of strict consensus in TNT.

File S1. Excel file (.xls).

File S2. Nexus file (.nex).

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