



## **Incrementing and clarifying the diversity and early evolution of termites (Blattodea: Isoptera)**

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## Abstract

The past diversity of Isoptera is relatively poorly documented. Many early diverging families are only represented today by relicts of their Mesozoic and Cenozoic richness. Therefore, the onset of their evolutionary history and the transitions between families or even between subsocial and eusocial ways of life remain difficult to decipher and require additional fossil occurrences. Here, we report the oldest worker/pseudergate trapped in amber and a new Mastotermitidae, both from Hkamti amber. We document a diverse assemblage of species representing early diverging families from the ‘mid’-Cretaceous of Kachin, including two new genera and four new species in as many different genera: *Anisotermes bourguignoni* sp. nov., *Longitermes pulcher* gen. et sp. nov., *Magnifitermes krishnai* gen. et sp. nov., and *Mastotermes myanmarensis* sp. nov. These descriptions provide significant morphological evidence to discuss the placement of the genus *Anisotermes*, confidently place the new genera, and confirm the monophyly of Mastotermitidae. The diversity of Cretaceous isopterans, in light of the biology of their extant representatives, is used to discuss paleoecological implications and highlights the radiation of early diverged Isoptera in the complex Cretaceous ecosystem. The validity of the species *Meiatermes cretacicus* is discussed.

ADDITIONAL KEYWORDS: Eusociality – Insecta – New taxa – Paleodiversity, Paleoecosystems – Systematic positions

## INTRODUCTION

With as many extinct as extant families, the isopteran non-termitid lineages—which are now clearly less speciose than termitids—have a rich diversity in the Mesozoic. Fossils of these lineages have much to tell us about the early stages of termite evolution, which would remain highly partial and speculative if those fossils were ignored (Barden and Engel, 2020; Chouvenc et al., 2021). A typical example is the relict *Mastotermes darwiniensis* Froggatt. As a unique extant representative of Mastotermitidae, the first-diverging lineage of extant termites, *M. darwiniensis* is found only in Australia while the family was much more widespread in the past (Krishna et al., 2013). Ruling on a biogeographic scenario while considering only the relict distribution of *M. darwiniensis* would be nonsensical (Grandcolas et al., 2014). Similarly, deciphering the early stages of social or morphological evolution in termites requires a strong knowledge and a clear taxonomy of their Mesozoic fossils.

Seven out of the eight extinct families of termites are known from Cretaceous deposits. Known from the Eocene, the Termopsidae Holmgren, 1911 was described a long time ago, but the seven others were defined much more recently (Archeorhinotermitidae Krishna and Grimaldi, 2003; Cratomastotermitidae Engel et al., 2009; Melqartitermitidae, Mylacrotermitidae, Krishnatermitidae, Arceotermitidae, and Tanytermitidae, all described by Engel in Jiang et al. 2021). In the meantime, fossil descriptions have accumulated (e.g., Martínez-Delclòs and Martinell, 1995; Nel and Bourguet, 2006; Engel et al., 2007a,b, 2016; Zhao et al., 2019, 2020; Bezerra et al., 2020; Jouault et al., 2021a), but difficulties remain to unambiguously disentangle plesiomorphic from apomorphic character states, mostly because of incomplete specimens in the fossil record. This has resulted in ill-defined taxa, as exemplified by the ‘*Meiatermes*-grade’ that mainly includes fragmentary or poorly preserved fossils, from which key characters and apomorphies cannot be observed. Their familial attributions cannot be determined. The ‘*Meiatermes*-grade’ is thus a heterogeneous set of taxa. This grade illustrates, however, the remarkable diversity of termites during the Cretaceous and the need to clarify their taxonomy to gain access to the early stages of termite evolution.

Embracing this vision recently led authors to formally describe several new extinct families of termites from the ‘*Meiatermes*-grade’ (Jiang et al. 2021) and to elevate the Hodotermopsidae (*Hodotermopsis*) to family rank (clarifying the former paraphyly of Archotermopsidae; Wang et al., 2022). In the same spirit, we describe herein four new species—and two new genera—from Cretaceous deposits (ca. 110-98 Ma). We take advantage of those descriptions to help refine the taxonomic outline of a few extinct taxa and clarify what can be learned from these fossils in regard to termite evolution. More specifically, *Magnifitermes krishnai* gen. et sp. nov., *Anisotermes bourguignoni* sp. nov., and *Mastotermes myanmarensis* sp. nov. add to our knowledge of mastotermitid diversity (and its subfamilies: Mastotermitinae and Idanotermitinae), the earliest-diverging family with an extant (and relict) representative. *Longitermes pulcher* gen. et sp. nov. is the oldest putative representative of the Hodotermopsidae (sensu Wang et al., 2022) and fills a gap of ca. 80 Ma, which is critical for any study relying on calibrated dating. Specimens of *Meiatermes* previously described or illustrated specimens of the ‘*Meiatermes*-grade’ are used to suggest how to move away from heterogeneous assemblages like the ‘*Meiatermes*-grade’, while continuing to document termite diversity in the deep past, a pivotal period of termite evolution. Finally, a worker or pseudergate trapped in the latest Albian Hkamti amber, and likely belonging to the family Mastotermitidae, provides the earliest direct evidence of a termite worker caste found in amber.

## **MATERIAL AND METHODS**

### **BURMESE AMBER**

The amber pieces containing the specimens come from two Myanmar deposits, viz. Noiye Bum and Hkamti sites. Noiye Bum is in the Hukawng Valley (26°29' N, 96°35' E), Kachin State, northern Myanmar (see detailed map in Grimaldi and Ross, 2017: fig. 2). The Hkamti site is about 80 km southwest of the Angbamo site (see detailed map in Xing and Qiu, 2020: fig 1). The amber from Myanmar was produced on a paleo-island isolated from the mainland (Laurasia and Gondwana) for

at least 10 Ma (Jouault et al., 2021b), and located in the midsection of the paleo-Tethys (Seton et al., 2012).

The amber piece containing the specimen of *Mastotermes myanmarensis* and the worker/pseudergate comes from the deposits of Hkamti site, Hkamti District, Sagaing Region, Myanmar. Zircon U-Pb analyses established an early Albian age ( $109.7 \pm 0.4$  Ma) for Hkamti amber, based on zircon analyses of clastic sediments at the surface (Xing and Qiu, 2020).

The amber pieces containing the other specimens studied herein come from the deposits of Noiye Bum in the Hukawng Valley ( $26^{\circ} 29' \text{ N}$ ,  $96^{\circ} 35' \text{ E}$ ), Kachin State, northern Myanmar (see detailed map in Grimaldi and Ross, 2017: fig. 2). Taphonomic analyses of pholadids and radiometric data, based on zircons from volcanic clasts found within the amber-bearing sediments, established an early Cenomanian age ( $98.7 \pm 0.62$  Ma) for Kachin amber (Shi et al., 2012; Smith & Ross, 2017). Some ammonites found in the amber-bearing bed and within amber corroborate a late Albian / early Cenomanian age (Cruickshank and Ko, 2003; Yu et al., 2019).

## AMBER PREPARATION, EXAMINATION, AND SPECIMEN PHOTOGRAPHS

The amber pieces were prepared using a diamond disk and polished with a polisher (Buehler EcoMet 30) by using a thin silicon carbide sanding paper (grit size = 7000). The specimens are housed in the amber collection of the Geological Department and Museum (IGR) of the University of Rennes, France or in the collection of the Nanjing Institute of Geology and Palaeontology Chinese Academy of Sciences (NIGPAS). The specimens were examined using a Leica MZ APO stereomicroscope, a Nikon SMZ25 stereomicroscope or a Zeiss V20 stereomicroscope. Photographs have been taken with a Canon 5D Mark II or a Nikon D800 cameras, and are digitally stacked photomicrographic composites of several individual focal planes, which were obtained using HeliconFocus 6.7. The figures were composed with Adobe Illustrator CC2019 and Photoshop CC2019 software. We follow the morphological terminology and the classification of termites as presented in Krishna et al. (2013), with recent additions of Jiang et al. (2021) and Wang et al.

(2022), except for modifications to wing venation terms adapted from Schubnel et al. (2019), and we retain the name Isoptera (Lo et al., 2007), although as subordinate to Blattodea (as advocated by Lo et al., 2007; and Krishna et al., 2013).

This published work and its included nomenclatural acts are registered in ZooBank (<http://www.zoobank.org/>, last access: XX XX 2021), with the following LSID (reference):

## C-T SCAN RECONSTRUCTION

To observe important morphological characters on the head of *Anisotermes bourguignoni*, we used high-resolution X-ray microtomography (Zeiss Xradia 520 versa) at the micro-CT laboratory of NIGP. Based on the comparatively large size of the fossil specimen, a CCD-based 4× objective was used, providing isotropic voxel sizes of 3.9677 μm with the help of geometric magnification. During the scan, the acceleration voltage for the X-ray source was 50 kV, and a thin filter (LE2) was used to avoid beam-hardening artifacts. To improve signal-to-noise ratio, 2801 projections over 360° were collected, and the exposure time for each projection was 1s. The tomographic data were analyzed using Drishti (version v2.6.4) software.

## ABBREVIATIONS

Body abbreviations are as follows: gl, glossa; la, left apical tooth; lb, labrum; lc, lacinia; lci, lacinial incisor; LM<sub>1</sub>-LM<sub>3</sub>, left marginal teeth (number corresponding); Lp, Labial palp; mb, mandibles; Mp, maxillary palp; mt, mentum; pc, postclypeus; pgl, paraglossa; ra, right apical tooth; RM<sub>1</sub>-RM<sub>2</sub>, right marginal teeth (number corresponding); sm, submentum; st, stipe; ttp, tentorial pit. Wing venation abbreviations are as follows: A1, first anal vein; CuA, anterior cubitus; MA, media; PCu, postcubitus; RA, anterior radius; RP, posterior radius; Sc, subcosta.

## SYSTEMATIC PALAEOLOGY

ORDER BLATTODEA BRUNNER VON WATTENWYL, 1882

INFRAORDER ISOPTERA BRULLÉ, 1832

FAMILY HODOTERMOPSIDAE ENGEL in Jiang et al. (2021)

GENUS ***LONGITERMES*** Jouault, Engel, Legendre, & Nel, **GEN. NOV.**

<http://zoobank.org/urn:lsid:XXXXX>

*Type species: Longitermes pulcher* Jouault, Engel, Legendre, & Nel, sp. nov.

*Etymology:* The generic name is a combination of the Latin *longus*, meaning “long” which refers to the elongate head of the new species, and *Termes* commonly used to designate Isoptera. Gender masculine.

*Diagnosis:* Imago. Head elongate, with anterior corners rounded orthogonal and posterior corners broadly rounded; occiput and frons convex; epicranial ecdysial line visible; ocelli absent; postclypeus trapezoidal; anteclypeus small; left mandible apical tooth elongate, sharp, three marginal teeth, LM<sub>1</sub>-LM<sub>2</sub> interdental space small, v-shaped, LM<sub>1</sub> small, LM<sub>2</sub> elongate, forming broad cutting edge, LM<sub>2</sub>-LM<sub>3</sub> separated by a notch, LM<sub>3</sub> bent toward base of mandible; right mandible with long, sharp apical tooth, and at least one marginal tooth of similar shape and length; pronotum slightly wider than head, anterior margin concave, posterior margin broadly convex with a median concavity, sides broadly convex; tarsi pentamerous (fourth tarsomere cryptic); tibial spur formula 3-4-2; all tibiae with strong setae but no additional spines; arolium present; forewing with scale large, with humeral margin nearly straight, claval suture straight (PCu), basal suture faintly arched; Sc, RA, RP heavily sclerotized; R branched within scale; RP nearly encompassing wing apex, with main branch bending to wing apex, with five secondary branches; M and CuA weaker than other surrounding veins; CuA with three branches in scales; anal veins absent; hind wing with delineated scale.

***LONGITERMES PULCHER*** Jouault, Engel, Legendre, & Nel, **SP. NOV.**

Figs. 1–2

<http://zoobank.org/urn:lsid:XXXXX>

*Material:* Holotype, IGR.BU-052, preserved in an ovoid piece of amber measuring  $18 \times 12 \times 2$  mm, housed in the amber collection of the Geological Department and Museum (IGR), Rennes, France.

*Locality and horizon:* Noiye Bum Hill, Hukawng Valley, Kachin State, Myanmar; upper Albian to lower Cenomanian, ‘mid’-Cretaceous.

*Etymology:* The specific epithet is from the Latin adjective *pulcher*, meaning “beautiful”.

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

*Description:* Imago specimen, body ca. 7.34 mm long (as preserved and measured from tip of labrum to abdominal apex). Head elongate, ca. 1.44 mm long (measured from posterior margin to tip of labrum) and ca. 0.82 mm wide excluding compound eyes (measured beyond eyes), trapezoidal in dorsal view, prognathous, sides slightly convex, postclypeus ca. 0.11 mm long, anteclypeus ca. 0.11 mm long, labrum lobe-shape, sides nearly parallel, slightly narrower basally, apical margin nearly straight, with few setae; mandibles triangular shaped, ca. 0.20 mm high, covered by labrum; left mandible apical tooth elongate, sharp; three marginal teeth, LM<sub>1</sub> small, LM<sub>1</sub>-LM<sub>2</sub> interdental space small, v-shaped, LM<sub>2</sub> elongate, forming broad cutting edge, LM<sub>2</sub>-LM<sub>3</sub> separated by a notch, LM<sub>3</sub> bend toward base of mandible (general aspect similar to left imago mandible of *Hodotermopsis*); right mandible with long, sharp apical tooth, and at least one marginal tooth of similar shape and length; buccal pieces: glossa with two visible segments, paraglossa with three segments, length from base to apex (in mm) 0.05, 0.06, 0.1; lacinial incisor with two teeth; five maxillary palpomeres visible, length from base to apex (in mm): 0.06, 0.05, 0.08, 0.09, 0.12; three labial palpomeres present, total length as preserved ca. 0.21 mm; compound eyes, ca. 0.37 mm long, ovoid, situated laterally near head mid-length, and separated from posterior head margin by more than their length; ocelli absent; fontanelle absent; antennae moniliform with 14 antennomeres. Pronotum ca. 0.54 mm long and ca. 1.0 mm wide, nearly flat with anterior margin concave, anterior corners arched, sides broadly convex and posterior margin convex with a medial indentation, posterior corners broadly arched.



Legs robust; profemur medially swollen, *ca.* 0.63 mm long, protibia *ca.* 0.37 mm long, protarsus *ca.* 0.22 mm long; protibia with three spurs f1, f2, f3; mesofemur medially swollen *ca.* 0.63 mm long, mesotibia *ca.* 0.42 mm long, mesotarsus *ca.* 0.22 mm long; mesotibia with four observable spurs m1, m2, m3, m4; metafemur *ca.* 0.51 mm long, metatibia *ca.* 0.52 mm long, with two observable spurs h1, h2, mesotarsus *ca.* 0.25 mm long; all tarsi pentamerous, with arolium. Forewing scale *ca.* 0.80 mm long, and 0.54 mm wide (measured distally), RP with additional tertiary branches joining costal margin; median (M) weak, closer to cubitus (Cu) than to radial sector (RP), with five branches terminating at lower margin; CuA with six primary and secondary branches extending to lower margin; anal vein absent. Hind wing (folded or damage): humeral suture weak, barely visible; wing venation apparently similar to forewing except anal vein present.

Abdomen at least 4.0 mm long (damaged during the fossilization process) with at least 10 observable segments; abdominal segments apparently slightly wider near mid-length. Cerci multi-merous *ca.* 0.16 mm long, five(?) cercomeres (sometimes fused so not clearly countable).

Color. Not preserved.

*Remarks:* *Longitermes pulcher* is unique among Cretaceous termites, with an unprecedented combination of diagnostic characters making it close to the family Archotermopsidae, as treated in Jiang et al. (2021), i.e., encompassing *Hodotermopsis*, *Archotermopsis*, and *Zootermopsis*. Here we follow the new system of Wang et al. (2022: tabl. 1), which recently resolved paraphyly of Archotermopsidae by elevating the Hodotermopsinae to family rank. In fact, *L. pulcher* shares with the Archotermopsidae and Hodotermopsidae the lack of a fontanelle; a Y-shaped ecdysial line present; large compound eyes; ocelli absent; pronotum faintly arched, slightly wider than head; left mandible with an apical tooth and three marginal teeth. Legs: five tarsomeres (some cryptic); tibial spur formula 3-4-2; arolium present. Cerci with five(?) cercomeres. Forewing: costal margin flat to faintly arched; humeral suture well defined, almost straight; Sc, RA, RP sclerotized, RP with the main branch bending to apex of wing, 5–6 secondary branches and additional tertiary branches joining costal margin; M weak, with secondary branches terminating at lower margin; Cu with

primary and secondary branches extending to lower margin; anal vein absent. The wing venation with the radial field encompassing most of the wing apex and the shape of the left mandibular teeth, nearly similar to that of *Hodotermopsis*, strengthen the taxonomic placement. However, the phylogenetic position of the new genus is hard to ascertain and it may be a stem representative of the Hodotermopsidae or of the Archotermopsidae (sensu Wang et al., 2022). Since the new specimen differs from the genera *Archotermopsis* and *Zootermopsis* (Archotermopsidae sensu Wang et al., 2022), at least based on its mandibular shape with LM<sub>2</sub> elongate and forming a broad cutting edge (vs. sharp and not forming a cutting edge in the aforementioned genera) (Krishna et al., 2013), and resembles more the genus *Hodotermopsis* in its wing venation and mandibular configuration, we presume that *Longitermes* is likely a stem-Hodotermopsidae (sensu Wang et al., 2022). *Hodotermopsis* differs from the new specimen in possessing small eyes while they are large in *Longitermes*, but also in having numerous antennomeres (at least 23) while the new specimen only possesses 14 (the antenna might not be complete but the number of antennomeres seems to be lower than in *Hodotermopsis*) (Krishna et al., 2013). Recently, several families were erected based on Cretaceous specimens from Kachin amber (e.g., Melqartitermitidae, Mylacrotermitidae) but our specimen cannot be placed in any of them (Jiang et al., 2021). Its broad radial field precludes affinities with the Melqartitermitidae and the presence of a well-defined forewing basal suture demarcating the scale precludes affinities with the Mylacrotermitidae (Jiang et al., 2021). Similarly, the new specimen differs from representatives of the family Krishnatermitidae, at least, because of its forewing with PCu straight (vs. arched in *Krishnatermes*), RP encompassing the wing apex (variable in *Krishnatermes*), and its hind wing with a defined scale (vs. absent in *Krishnatermes*). However, the habitus of *Longitermes* and *Krishnatermes* are at first sight quite similar, which, if not symplesiomorphic, may indicate a proximity between the two genera and a hypothetical proximity of *Krishnatermes* with the Teletisoptera.

#### FAMILY MASTOTERMITIDAE DESNEUX, 1904

SUBFAMILY IDANOTERMITINAE ENGEL in Jiang et al. (2021)

GENUS *ANISOTERMES* Zhao, Eggleton, & Ren, 2019

Included species; *Anisotermes xiai* Zhao, Eggleton, & Ren 2019 (type species) and *A. bourguignoni* Jouault, Engel, Huang, & Nel, sp. nov.

*Emended diagnosis*: Head approximately rounded; ocelli absent; fontanelle absent; Y-shaped ecdysial line absent; mandible not exceeding labrum, with la and ra conspicuously longer than LM<sub>1</sub> and RM<sub>1</sub>; antenna moniliform, with about 25 antennomeres, terminal eight antennomeres tapered; compound eyes hemispheric, lying at head mid-length; pronotum definitely saddle-shaped, slightly wider than head in dorsal view; lateral margin weakly upcurved; procoxal carina present; additional tibial spines present on all legs; tibial spur formula 3-4-4; tarsi wholly pentamerous; arolium variable (absent in *A. xiai* but present in *A. bourguignoni*); wings membranous, densely reticulate; forewing scale large, overlapping hind wing base, basal suture convex, veins Sc, RA, RP, and M more heavily pigmented than CuA. Forewing: all major veins originate within scale; Sc simple or double; RP with five to six main branches, terminating on costal margin anterior to wing apex; radial field of moderate width, parallel to costal margin; M running about midway between RP and CuA, terminating on posterior margin; medial field relatively narrow; CuA branched, terminating about same distance with Rs to wing apex; PCu (claval suture) arched, meeting basal suture on posterior margin. Hind wing without basal suture, large anal lobe present; M first inferior branch fading away, terminating in center of hind wing; cerci short, trimerous or tetramerous (with additional indented rings); abdominal styli absent in female but present in male.

***ANISOTERMES BOURGUIGNONI*** Jouault, Engel, Huang, & Nel, **SP. NOV.**

Figs 3–5

ZooBank LSID (species name): urn:lsid:zoobank.org:act: XXX

*Holotype*: Specimen identifier NIGP177751 (a complete dealate specimen preserved in a rounded amber piece), housed in the collection of the Nanjing Institute of Geology and Palaeontology Chinese Academy of Sciences (NIGPAS), Nanjing, China.

*Etymology*: The specific epithet honors Dr. Thomas Bourguignon for his work on termite evolution; and is to be treated as a noun in the genitive case.

*Locality and age*: Noiye Bum Hill, Hukawng Valley, Kachin State, Myanmar; late Albian to early Cenomanian, 'mid'-Cretaceous.

*Diagnosis*: Imago. Head rounded, with anterior corners slightly orthogonal and posterior corners rounded; left mandible with  $la$  longer than  $LM_1$ , both sharp; right mandible with an apical and two marginal teeth,  $ra$  shorter than  $RM_1$ ,  $RM_1$  and  $RM_2$  separated by a sharp angle; occiput and frons convex; postclypeus trapezoidal; anteclypeus small; ocelli absent; pronotum massive, trapezoidal, wider than head, anterior margin concave surrounding head, posterior margin broadly convex, with dorsal surface flatly arched in profile, sides convex; tarsi pentamerous; tibial spur formula 3-4-4; protibia with two additional spine ( $fa$ ,  $fb$ ); mesotibia with six additional spines ( $ma$ - $mf$ ); metatibia with at least three additional spines ( $ha$ - $hc$ ); arolium present; forewing with scale large, with humeral margin well-defined and slightly arched, claval suture strongly curved ( $PCu$ ), basal suture convex;  $Sc$ ,  $RA$ ,  $RP$  and  $CuA$  heavily sclerotized;  $Sc$  branched within scale and going outside of scale;  $R$  branched within scale;  $M$  weaker than other surrounding veins;  $CuA$  with three branches in scales;  $PCu$  strongly curved; anal veins not discernable within scale.

*Description*: Imago, body ca. 10 mm long (from tip of labrum to abdomen apex). Head robust, ca. 2.20 mm long (measured from under the pronotum to the tip of the labrum) and ca. 1.93 mm wide excluding compound eyes, square-shaped in dorsal view, hypognathous, sides slightly convex, anterolateral corner slightly orthogonal, postero-lateral corners rounded, Y-shaped ecdysial scar absent; tentorial pit visible ( $ttp$ ); postclypeus ( $pc$ ) 0.32 mm long, trapezoidal; labrum ca. 0.50 mm long, lobe-shape, narrower basally; mandibles massive, triangular shaped, at least 0.53 mm high; buccal pieces with glossa ( $gl$ ), paraglossa ( $gl$ ), stipe ( $st$ ), mentum ( $mt$ ), submentum ( $sm$ ) visible but

not clearly describable; five maxillary palpomeres, combined length as preserved ca. 1.2 mm; four(?) labial palpomeres present, with three discernible palpomeres, combined length ca. 0.75 mm; compound eyes, ca. 0.45 mm long, circular, situated laterally near head mid-length, and separated from posterior head margin by more than their length; fontanelle not visible and probably absent; antenna moniliform with at least 22 antennomeres. Pronotum ca. 1.60 mm long and ca. 2.73 mm wide, overlapping head dorsally, sides slightly upturned.

Legs robust; procoxa ca. 1.38 mm long, profemur ca. 1.51 mm long, protibia ca. 1.41 mm long, protarsus at least 0.76 mm long; protibia with three spurs f1, f2, f3, and additional spines; mesocoxa ca. 1.13 mm long, mesofemur medially swollen ca. 1.57 mm long, mesotibia ca. 1.72 mm long, mesotarsus ca. 0.64 mm long; mesotibia with four observable spurs m1, m2, m3, m4, and additional spines; metacoxa at least 1.10 mm long, metafemur at least 2.24 mm long, metatibia at least 1.50 mm long, with three observable spurs h1, h2, h3, h4, and additional spines; all spurs flattened with serration; all tarsi pentamorous; pretarsal arolium present. Forewing scale ca. 2.36 mm long, and 1.41 mm wide (measured distally), sclerotized, especially in anal area, with sparse setation. Hind wing scale not visible but proximal part of hind wing clearly cut beyond basal suture.

Abdomen at least 6.0 mm long with at least 11 observable segments; abdominal segments widest at mid-length. Cerci multi-merous ca. 0.52 mm long, 5–7 cercomeres (sometimes fused so not clearly countable).

*Color:* Not preserved.

*Remarks:* *Anisotermes bourguignoni* differs from most other Cretaceous ‘lower’ Isoptera in having a plesiomorphic character in scale configuration (e.g., fine reticulation between veins in the scale), tarsi pentamorous (plesiomorphic character), a tibial spur formula of 3-4-4, and an overall massive trapezoidal-shaped pronotum. The wholly pentamorous tarsi and enriched tibial spur formula tend to imply an early diverged position within Isoptera, among groups like Mastotermitidae, Archotermopsidae, Hodotermitidae, and their various extinct relatives. Additionally, its general habitus, and particularly its large pronotum, suggests that *A. bourguignoni* is related to the

Mastotermitidae, or to taxa belonging to the ‘*Meiatermes*’-grade. Interestingly, the hind wings of *A. bourguignoni* were cut slightly distal from the hind wing basal scale suture, while in the forewing the cut follows the basal suture. The hind wing basal scale suture was probably not fragile enough to break alone after the mating swarm, as it normally happens in a majority of extant termites. This suggests that the suture of the hind wing is rudimentary (symplesiomorphy) as in *Mastotermes darwiniensis* Froggatt (Tillyard, 1931), and that the new specimen could be related to the Mastotermitidae. Another character suggesting placement of *Anisotermes* within Mastotermitidae is the mandibular shape. In fact, *Anisotermes* and *Mastotermes* exhibit a similar configuration of teeth on both mandibles, and length variations ( $RM_1$  conspicuously longer than  $ra$  vs. equal in length) are usually indicative of different genera from the same family. Additionally, this placement is strengthened by the diagnostic characters of the new species: ocelli absent, procoxal carina present, arolium present, and the aforementioned scale characters. The absence of ocelli indicates affinities with the Idanotermitinae, but the new fossil differs from the genus *Idanotermes* Engel, 2008 in at least its different tibial spur formula (i.e., 3-4-4 vs. 3-4-3). The genus *Anisotermes* is here tentatively considered as a member of the Idanotermitinae (Jiang et al., 2021: 379); we confirm this placement mainly based on the presence of the anal lobe (characteristics of the Mastotermitidae within the Isoptera) and based on the absence of ocelli. The new species differs from *A. xiai* by, *inter alia*, the presence of the pretarsal arolium and more additional spines along the tibiae.

#### SUBFAMILY MASTOTERMITINAE DESNEUX, 1904

#### GENUS **MAGNIFITERMES** Jouault, Engel, & Nel, **GEN. NOV.**

<http://zoobank.org/urn:lsid:XXXXX>

*Etymology*: The generic name is a combination of the Latin adjective *magnificus*, meaning “magnificent” and the noun *termes*, meaning, “termite”, and commonly used as the root for most genera of Isoptera. Gender masculine.

*Type species*: *Magnifitermes krishnai* Jouault, Engel, & Nel, sp. nov.

*Diagnosis:* Imago. Head massive, square-shaped, dorsally flattened, with posterior corners broadly rounded; epicranial scar present; ocelli present, located just above compound eyes (not separated from eyes by a space greater than their length); postclypeus trapezoidal and flat; anteclypeus anteriorly convex; left mandible with an apical and two distinct marginal teeth, LM<sub>1</sub>-LM<sub>2</sub> interdental space broad, v-shaped, posterior margin of LM<sub>1</sub> slightly longer than anterior margin LM<sub>2</sub>; pronotum massive, trapezoidal, wider than head, anterior margin concave surrounding head, posterior margin broadly convex, with dorsal surface flatly arched in profile, sides convex; tarsi pentamerous, with fifth tarsomere extremely elongate; tibial spur formula 3-4-4; protibia with two additional spines (fa, fb); mesotibia with four(?) additional spines (ma, mb, mc, md); metatibia with at least three additional spines (ha, hb, hc); pretarsal arolium present; forewing scale quite large, overlapping hind wing scale, claval suture (PCu) broadly arched, basal suture broadly arched; Sc, RA, RP, M heavily sclerotized; Sc with two main branches; R branched within scale; RP running parallel to costal margin, with at least five branches joining costal margin; M slightly closer to RP than to CuA, with at least four secondary branches radiating to apical margin; CuA less sclerotized, with several branches joining lower margin. Hind wing: scale (basal) suture absent; anal lobe (an-jugal) developed (folded).

***MAGNIFITERMES KRISHNAI*** Jouault, Engel, & Nel, **SP. NOV.**

Figs. 6–7

<http://zoobank.org/urn:lsid:XXX>

*Holotype:* Specimen identifier IGR.BU-053 (a complete alate specimen preserved in a drop-shaped amber piece measuring 18 × 29 × 5 mm), housed in the amber collection of the Geological Department and Museum (IGR), Rennes, France.

*Etymology:* The specific epithet honors the late Dr. Kumar Krishna (1928–2014), eminent termitologist and beloved friend and collaborator of MSE. Dr. Krishna's work also inspired CJ to study fossil termites. He is sorely missed. The name is treated as a noun in the genitive case.

*Locality and age:* Noiye Bum Hill, Hukawng Valley, Kachin State, Myanmar; upper Albian to lower Cenomanian, 'mid'-Cretaceous.

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

*Description:* Imago, body ca. 13.5 mm long (as preserved and measured from tip of labrum to abdomen apex). Head massive, ca. 2.87 mm long (measured from posterior margin to tip of labrum) and about 1.5 mm wide excluding compound eyes (measured beyond eyes), slightly trapezoidal, prognathous, sides convex, postclypeus and anteclypeus combined length ca. 0.32 mm long, labrum lobe-shape, sides nearly parallel, slightly narrower basally, apical margin nearly straight, with few setae; mandibles triangular shaped, ca. 0.46 mm high, covered by labrum; left mandible apical tooth sharp, two marginal teeth, LM<sub>1</sub>-LM<sub>2</sub> interdental space broad, v-shaped, LM<sub>2</sub> elongate; right mandible not visible; glossa (gl) and paraglossa (gl), lacinial incisor with at least one long tooth; five maxillary palpomeres visible, combined length ca. 0.9 mm; three labial palpomeres present, at least 0.60 mm long; compound eyes, ca. 0.52 mm long, circular, situated laterally near head mid-length, and separated from posterior head margin by more than their length; ocelli present; fontanelle absent; antennae moniliform with 28(?) antennomeres. Pronotum massive, ca. 1.58 mm long, trapezoidal, wider than head, anterior margin concave surrounding head, posterior margin broadly convex, with dorsal surface flatly arched in profile, sides convex.

Legs slender; profemur, ca. 1.37 mm long, protibia ca. 0.90 mm long, protarsus ca. 0.54 mm long; protibia with three spurs f1, f2, f3, *plus* additional spines (see Diagnosis, *supra*); mesotibia ca. 1.31 mm long, mesotarsus ca. 0.57 mm long; mesotibia with four observable spurs m1, m2, m3, m4, additional spines (see Diagnosis, *supra*); metatibia ca. 1.87 mm long, with four observable spurs h1, h2, h3, h4, *plus* additional spines (see Diagnosis, *supra*), mesotarsus ca. 0.75 mm long; all spurs flattened with serration; all tarsi pentamerous; pretarsal arolium present. Forewing scale at least 1.50 mm long. Hind wing hidden under forewing.



Abdomen at least 6.46 mm long (damaged during fossilization), with at least nine observable segments; abdominal segments apparently slightly wider near mid-length. Cerci with five cercomeres, stylus preserved but covered by a white coat.

Color: Not preserved.

*Remarks:* *Magnifitermes krishnai* differs from most other Cretaceous Isoptera in combining a series of plesiomorphic characters in the wings (e.g., fine reticulation between veins in the scale, anal lobe present), tarsi wholly pentamerous (plesiomorphic character), a tibial spur formula of 3-4-4, and an overall massive trapezoidal-shaped pronotum. The wholly pentamerous tarsi and enriched tibial spur formula suggest an early diverging position among Isoptera, among groups like Mastotermitidae, Archotermopsidae, Hodotermitidae, Hodotermopsidae, and their various extinct relatives. Additionally, its general habitus and particularly its large pronotum and anal lobe suggest that *M. krishnai* is related to the Mastotermitidae. Recently, the Mastotermitidae were split into two distinct subfamilies Mastotermitinae and Idanotermitinae (Jiang et al., 2021). The Idanotermitinae are mainly characterized by the absence of ocelli on the head of imagoes. Due to the presence of ocelli, the new fossil is placed in the subfamily Mastotermitinae. It differs from the other Mastotermitinae, in particular *Mastotermes*, by a distinct Y-shaped ecdysial scar. Potential paraphyly of Mastotermitinae relative to Idanotermitinae is in need of clarification.

GENUS *MASTOTERMES* FROGGATT, 1897

***MASTOTERMES MYANMARENSIS* Jouault, SP. NOV.**

Figs. 9–10

<http://zoobank.org/urn:lsid:XXX>

*Material:* Holotype, IGR.BU-054, preserved in an elongate, pale, and ovoid piece of amber measuring 50 × 20 × 9 mm, housed in the amber collection of the Geological Department and Museum (IGR), Rennes, France.

*Locality and horizon:* Hkamti site, Hkamti District, Sagaing Region, Myanmar; early Albian (ca. 110 Ma), Early Cretaceous.

*Etymology:* The specific epithet refers to country of origin of the amber piece, Myanmar, combining the country name with the Latin toponymic adjectival suffix *-ēnsis*, meaning, “from”.

*Diagnosis:* Imago: wings membranous, long and broad, densely reticulate, with ‘cross-veins’ present; veins Sc, RA, RP, and M more heavily sclerotized than CuA, reticulate veins obviously pigmented among radial and medial fields; forewing Sc with two main branches; R with two branches; width of radial field moderate, RA simple, RP with five main branches; medial field encompassing wing apex, M main vein closely parallel to RP main vein, with three main branches, first branch of M arising near apical third of wing; CuA with five main branches, apical-most branch of CuA terminating into posterior margin and in apical third of forewing length. Hind wing with large anal lobe; costal space wide; Sc simple, terminating on costal margin at basal third of hind wing length; RA long, simple and terminating on costal margin before apical third of hind wing length; RP with two main branches; medial field encompassing wing apex; M separating from RP near wing base, relatively closely parallel to RP, with three main branches, secondary branches present; CuA uniformly branching, terminating just posterior to wing apex.

*Description:* Imago: wings membranous, reticulate veins present; forewing scale part missing, forewing preserved part at least 10.70 mm long and 4.62 mm wide, apex rounded, middle section of posterior slightly convex basally then convex; veins Sc, RA, RP, and M more heavily sclerotized than CuA and A; forewing Sc short, bifurcate at suture, posterior branch with a faint subbranch at margin; RA with one branch; radial field width moderate, occupying about one-sixth area on average; RP with five branches, proximal branch fading apically before anterior wing margin; M closely parallel to RP, with three main branches; CuA with numerous posterior branches, apicalmost branch of CuA terminating on posterior margin well proximal to apex, more proximal branches loosely pectinate, apical-most of these branches terminating on margin near wing mid-length.

Hind wing with large anal lobe, scale not preserved, 14.10 mm long and 6.0 mm wide with anal lobe and 5.16 mm wide without anal lobe; Sc longer than that of forewing; RA long, simple and terminating on costal margin before apical third of hind wing length; RP with three branches, first branch originating just before point of contact between Sc and wing margin; M with four branches, separating from RP away from wing base, then closely parallel to RP, apical branch of M with a secondary branch; CuA with numerous posterior branches, some dichotomous, terminating posterior to wing apex.

Color: Not preserved.

*Remarks:* Compared with the known ‘mid’-Cretaceous fossil and the extant mastotermitids, *M. myanmarensis* stands out in having broadly rounded wings, wider intervals between the longitudinal veins (shared with *M. monostichus* Zhao, Eggleton, & Ren, 2019), and a broad space above Sc on the hind wing. Additionally, the space occupied by Sc+RA+RP is extremely wide near the basal suture. *Mastotermes myanmarensis* has a hind wing with vein A1 without branches while the extant *M. darwiniensis* has a vein A1 with numerous posterior branches (similar to *M. monostichus*), and the anal veins in the anal lobe are all simple (vs. with some dichotomies in *M. darwiniensis* and *M. monostichus*). *Mastotermes myanmarensis* can be differentiated from *M. monostichus* by the forewing with RA simple, M with only a reduced number of branches and the first dichotomy far from the wing base, CuA with more dichotomous branches; hind wing with a broad space above Sc, and the anal field with more branches. *Mastotermes myanmarensis* also differs from the extant *M. darwiniensis* by its temporal range (‘mid’-Cretaceous vs. extant).

FAMILY INCERTAE SEDIS

GENUS ET SPECIES INDETERMINATE 1

Figs. 11–12

*Material examined:* Specimen identifier IGR.BU-055, housed in the amber collection of the Geological Department and Museum (IGR), Rennes, France.

*Localities and ages:* Noiye Bum Hill, Hukawng Valley, Kachin State, Myanmar; upper Albian to lower Cenomanian, ‘mid’-Cretaceous.

*Remarks:* This species is likely one of those unrelated genera falling into the ‘*Meiatermes* grade’ (sensu Engel et al., 2007), which cannot be assigned to any currently circumscribed families but that can be excluded from the Neoisoptera.

## GENUS ET SPECIES INDETERMINATE 2

Fig. 13

*Material examined:* Specimen identifier IGR.BU-056, housed in the amber collection of the Geological Department and Museum (IGR), Rennes, France.

*Locality and horizon:* Hkamti site, Hkamti District, Sagaing Region, Myanmar; early Albian (ca. 110 Ma), Early Cretaceous.

*Remarks.* This specimen possesses moniliform antennae, a relatively broad pronotum, numerous tibial spurs, pentamerous tarsi and it lacks a fontanelle (apomorphy of the Neoisoptera). This combination of characters is typical of the early diverged termites (Krishna et al., 2013). However, we can neither observe the mandible configuration nor the configuration of the clypeal area, precluding a confident placement in a given family. On the other hand, the absence of wing and of defensive specializations (e.g., elongate mandibles or phragmotic head) indicates that this specimen is likely a worker or a pseudergate. Because the developmental pathways of Cretaceous termites are unknown, it is impossible to attribute this specimen to a worker (with bifurcated pathways) or pseudergate ‘caste’ (with linear pathways).

## DISCUSSION

## CLARIFYING THE TAXONOMY OF THE EARLIEST-DIVERGING LINEAGES AMONG TERMITES: LIMITS OF CRATOMASTOTERMITIDAE AND OF THE *MEIATERMES*-GRADE

Several authors (Engel et al., 2009: 9; Krishna et al., 2013) have placed *Cratomastotermes* from the Early Cretaceous in the family Cratomastotermitidae, and not within Mastotermitidae. The diagnosis is based on putative plesiomorphies or characters of unknown polarity, none of which argues against its validity, but emphasizes the need for further study. For example, the arched humeral margin of the forewing scale is also present in Mastotermitidae and Mylacrotermitidae, and this form is presumed to be ancestral for Isoptera, although this remains to be conclusively tested. Similarly, the large rectangular pronotum is a character putatively inherited from a dictyopteran ancestor of Isoptera. More definitively, pentamerous tarsi are shared between several families (e.g., Mastotermitidae, Archotermopsidae *sensu* Jiang et al., 2021), and are not only recovered as a plesiomorphy for Isoptera but for even higher clades of insects. The lack of ocelli is known in the mastotermitid subfamily Idanotermitinae (Jiang et al., 2022) and elsewhere in other isopteran lineages, although it is unknown whether or not this is a shared loss in the case of Idanotermitinae and *Cratomastotermes*. The most distinctive character is ‘the primitive retention of distinct cross veins, archedictyon between veins’, but an archedictyon is also present in recent *Mastotermes*, but absent in other fossil mastotermitids, meaning that the distribution of this feature is difficult to discern. Moreover, the actual definition of the ‘archedictyon’ is confused, and this patterning of crossveins or veinlike features between the longitudinal sectors in various insect lineages may not be homologous at all. Certainly the combination of features in *Cratomastotermes* is differentially diagnostic, but whether it is distinct from other clades of early diverging Isoptera is unclear. In a recent phylogenetic analysis, the family was found nested within the Mastotermitidae (Jouault et al., 2021: fig. 5). Accordingly, we prefer not to give this group familial rank basal to Mastotermitidae, while noting that the reliance of the recent analysis on the fossilized birth-death (FBD) model can be problematic in the placement of fossil taxa and some estimations, particularly as not all fossils are appropriate for the FBD process (e.g., Luo et al., 2020, 2022).

The ‘*Meiatermes*-grade’ encompasses fragmentary or poorly preserved fossils, in which key characters and apomorphies cannot be observed, and is an informal means of referring to those taxa excluded from Icoisoptera but otherwise as “Family Incertae sedis” (i.e., unassignable to family but definitively excludable from higher isopteran clades). Therefore, this grade serves as a ‘taxonomic bin’ including fossils that simply cannot be assigned with confidence to any of the early diverging termite families, living or fossil. Nor can these be definitively determined as stem groups to any one or subset of these groups. The major problem is the impossibility to observe complete wing venation (Fig. 11), while the antennae (moniliform) (Fig. 12A), tibial spurs (when fully preserved; Figs. 12B, C), wholly pentamerous tarsi (when fully preserved; Fig. 12C), forewing scale (Fig. 12D), and pronotum (Fig. 11), all suggest a proximity among early diverging families. All these symplesiomorphies challenge confident placements in any of the non-Icoisoptera families, and lack sufficient details as to allow more precision. This problem particularly applies to fossil termites preserved as compressions. While preservation in amber is often of excellent quality—the observation of morphological characters typically limited only by bubbles, fractures, or other inclusions—preservation in rock is usually of lower quality and specimens may be damaged when extracted from the matrix or prepared (Grimaldi et al. 2008). The placements of fossil compressions are, therefore, mainly based on the wings, often better preserved than the remainder of the body, although some body parts other than the wings are also preserved in some exceptional formations, allowing further studies (Grimaldi et al. 2008). Nonetheless, the typical absence of so many key characters often excludes a more refined clarification of phylogenetic affinities.

Recently a new species of *Meiatermes*, namely *M. cretacicus*, was described from the Crato Formation based on partial specimens—illustrating our previous statements concerning the rare preservation of legs and tarsi—and the use of wing veins as the sole support to establish a separate species (Bezerra et al., 2021). *Meiatermes cretacicus* is doubtful and, worse, might contribute to the chaos in the taxonomy of the earliest-diverging lineages, specifically those that are so important to any understanding of early termite evolution. In fact, the authors proposed the following diagnosis

to distinguish the species from the other *Meiatermes* spp. (Bezerra et al. 2021: 3): 'Small body-size termite. Head rounded, lateral borders slightly rounded, and Y-shaped line present' [in their discussion they indicated that the body size of *M. cretacicus* is smaller than that of *M. araripena* whereas the size ca. 7.0 mm fits with the body size variation of *M. araripena* and *M. hariolus* (Grimaldi et al., 2008: tab. 1)]; 'Pronotum slightly broader than head, anterior border concave, lateral borders broadly rounded, and posterior border slightly straight' [a similar configuration is recorded in other *Meiatermes* (e.g. *M. araripena*)]. The challenge is that the diagnosis as presented does not present a unique combination of traits that differentially exclude other congeners. More importantly, the specimens figured in Bezerra et al. (2021) are in ventral views. In fact, hind wings pass under the abdomen and thorax, and the cubito-anal fields and wing bases are not visible. Therefore, the putative absence of concavity on the posterior margin of the pronotum is not visible and over-interpreted. Moreover, when the specimens are preserved dorso-ventrally, the veins are 'printed' on the body, which is not the case here. 'Forewing veins Sc, R, Rs, and M more heavily pigmented than CuA. Rs extensively branched and encompassing majority of the posterior wing margin. M branching near wing mid-length with only two branches. CuA well-developed, with modest posterior branches terminating on inner margin of the wing' [these wing venation characters are not sufficient to distinguish the new species from other *Meiatermes* spp.; see variation in wing venation in Grimaldi et al., 2008: fig. 10)]. 'Cerci short and three-segmented' [also the case in *M. araripena* (Grimaldi et al., 2008: fig. 3)]. Therefore, based on the proposed diagnosis, the specimens used to describe *M. cretacicus* undoubtedly belong to the genus *Meiatermes* but not necessarily to a distinct species. The only character that would justify a separate species, but not used in the diagnosis of *M. cretacicus*, is the anterior branch of M located in the lower half of the wing and directed towards the anterior margin (Bezerra et al., 2021; figs 2–5). This character is currently only documented from *M. cretacicus*. Because the variability of wing venation in other Crato *Meiatermes* is relatively well documented (see numerous wing drawings of other *Meiatermes*

in Grimaldi et al., 2008: fig. 3), we have retained the validity of *M. cretacicus* and wait for new specimens to decide whether or not the species should be synonymized.

## FOSSIL CALIBRATIONS, RADIATION, AND GHOST LINEAGES

Currently, two hypotheses can be proposed to explain the diversification of Isoptera in the onset of their evolutionary history. They rely on different dating for the origin of termites and are based on two different approaches: molecular data on extant taxa (e.g., Legendre et al., 2015; Bucek et al., 2019) and morphological data on extant and fossil taxa (Jouault et al., 2021). Under the first hypothesis, termites are assumed to have arisen ca. 150 Ma ago during the latest Jurassic (e.g., Legendre et al., 2015; Bucek et al., 2019), suggesting, when combined with the fossil record, a relatively rapid radiation of Isoptera at the beginning of their evolutionary history, because they are already quite diverse during the Early Cretaceous. This hypothesis is in agreement with the direct fossil evidence (i.e., the termite fossils) but in disagreement with the existence of putative Triassic or Early and Late Jurassic nests, and controversially assigned to termites (Hasiotis and Dubiel, 1995; Bordy et al., 2004, 2009, 2010; Genise et al., 2005; Genise, 2016; Smith et al., 2020), although attribution to Isoptera has been vigorously refuted (e.g., Genise et al., 2005). These nests, if they were truly from termites, would suggest an older origin of termites and their presence may actually be counter-indicative of a rapid radiation. A Triassic age for Isoptera would also imply that termites diverged from among roachoids (with complete ovipositors) and reduced their ovipositor independent from that of other crown-group Blattodea, even implying Isoptera would be outside of Blattodea s.str. altogether. Such an assertion is not supported by any phylogenetic estimate and is refuted by virtually all morphological, molecular, developmental, and paleontological evidence. Instead, Isoptera are repeatedly placed in crown-Blattodea and as a clade near Cryptocercidae.

Another argument in favor of the rapid diversification of termites is the simultaneous presence of several representatives of stem groups of different families (e.g., *Longitermes*) that diverged precociously in termite evolution. Under the second hypothesis, termites are assumed to



have arisen during the Triassic or earliest Jurassic, at latest, with a steadier evolution, but beginning coincident with roachoids. This second hypothesis is further challenged by the lack of termite fossils in all early or middle Jurassic fossil deposits. The Cretaceous corresponds, in all analyses (e.g., Legendre et al., 2015; Bucek et al., 2019; Jouault et al., 2021), with the initial diversification of crown-Isoptera or with the diversification of crown-groups of extant families, thereby making this a critical period for study and from which to seek further termite fossils, particularly any from the early stages, like those from Lebanese amber, Crato, and other Early Cretaceous deposits.

Ghost lineages have always challenged the understanding of organismal diversification. They emphasize how much the fossil record and phylogenetic dating estimates might diverge (Ronquist et al., 2016). They directly result from fossilization biases and organismal biology. Ghost lineages also participate in the misinterpretation of radiations, migrations, and life habits of fossil taxa. Naturally, ghost lineages can also be deceiving as they do not necessarily represent the entire line of a given crown group, but instead an undefined period of stem groups followed by the crown group appearing at least by the time of its first fossil occurrence. Thus, a ghost lineage does not indicate that a given crown group extends that far back into the fossil record, but instead indicates that at minimum the stem group likely extends back to that point of common ancestry, with the crown groups appearing anywhere along that line. Ghost lineages are especially numerous in the insect fossil record (Nel et al., 2018). In termites, ghost lineages are reduced since this clade is (maybe) less prone to fossilization biases than many other insect groups thanks to their swarming behavior that potentially leads to the entombment of multiple specimens in the same deposit (e.g., *Meiatermes araripena*: Grimaldi et al., 2008). Nevertheless, four major ghost lineages are notable among termites, viz. in Archotermopsidae, Hodotermitidae, Hodotermopsidae, and Termopsidae.

The family Archotermopsidae (sensu Jiang et al., 2021) encompasses the genera *Archotermopsis* Desneux 1904, *Gyatermes* Engel and Gross 2009, *Hodotermopsis*, *Parotermes* Scudder 1883, and *Zootermopsis* Emerson 1933. However, its internal composition has been modified to resolve paraphyly with Hodotermitidae (Wang et al., 2022), by elevating the

Hodotermopsinae and the Archotermopsinae (subfamilies of Archotermopsidae in Jiang et al., 2021) to familial rank: Hodotermopsidae (*Hodotermopsis*) and Archotermopsidae (*Archotermopsis*, *Zootermopsis*) (Wang et al., 2022). Archotermopsidae sensu Wang et al. (2022) is assumed to have its crown-group diversifying after the early Eocene, and its ghost lineage (including its stem groups) diverging during the Early Cretaceous (e.g., Bucek et al., 2019; Jouault et al., 2021; Wang et al., 2022). Hodotermopsidae sensu Wang et al. (2022) is assumed to have its crown-group diversifying after the Miocene, but also seems to have at least its stem group diverging during the Early Cretaceous (e.g., Bucek et al., 2019; Jouault et al., 2021; Wang et al., 2022). Therefore, there is a huge gap in the fossil record between crown-Hodotermopsidae and their estimated divergence from the common ancestor with Archotermopsidae, resulting in a ghost lineage of ca. 80 Ma. The description of *Longitermes* seems to partially fill this gap and suggests that Hodotermopsidae may be older than previously estimated by molecular analyses. *Longitermes* can be used conservatively as a new calibration point for stem-Hodotermopsidae. Similarly, Archotermopsidae sensu Wang et al. (2022) do not have any stem-representatives from the Cretaceous period, suggesting that future works should focus on documenting any potential stem group.

## CONCLUSION

The diversity of Mesozoic Isoptera, which have much to tell us about the early steps of termite evolution, is increased with the descriptions of four new species and two new genera from the Cretaceous of Myanmar. Those new taxa provide noteworthy evidence to discuss the validity of some other taxa (e.g., *Meiatermes* and Cratomastotermitidae) but also highlight the underestimated diversity of termites in Cretaceous deposits. The description of a new stem representative of the extant family Hodotermopsidae helps to fill a major ghost lineage in termite evolutionary history and sheds light on the early evolutionary dynamics of termites. Finally, the discovery of the oldest worker/pseudergate trapped in Hkamti amber (Fig. 13) underlines that task division was already established in the Burmese amber biota since the Aptian.

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Figure caption:

**Figure 1:** *Longitermes pulcher* gen. et sp. nov., holotype IGR.BU-052. Photograph of habitus.

Scale bar: 1 mm.

**Figure 2:** *Longitermes pulcher* gen. et sp. nov., holotype IGR.BU-052. Detailed photographs. A:

Head; B: Mandibles; C: Apical part of left foreleg; D: Mesotibia; E: Metatibia; F: Metatibia; G:

Forewing. Scale bars: 0.5 mm (A, B, C, D, G); 0.25 mm (E, F).

**Figure 3:** *Anisotermes bourguignoni* sp. nov., holotype NIGP177751. Photographs of habitus. A:

Dorsal view; B: Ventral view. Scale bars: 1 mm.

**Figure 4:** *Anisotermes bourguignoni* sp. nov., holotype NIGP177751. Detailed photographs. A:

Head and pronoun in dorsal view; B: Head in ventral view; C: High-resolution X-ray

microtomography reconstruction of head in ventral view; D: High-resolution X-ray

microtomography reconstruction of head in anterolateral view; E: Line drawing of mandibles; F:

Line drawing of *Mastotermes darwinensis* mandibles. Scale bars 0.5 mm (A, C, D); 1 mm (B).

**Figure 5:** *Anisotermes bourguignoni* sp. nov., holotype NIGP177751. Detailed photographs. A:

Protarus; B: Mesotarsus; D: Apex of metatibia; E: Line drawing of scale venation with names of

veins labelled; E: Scale; F: Cerci in ventral view with arrows pointing cercomeres; G: Cerci in

dorsal view; H: Interpretative drawing of protibia; I: Interpretative drawing of mesotibiae; J:

Interpretative drawing of metatibiae. Scale bars: 0.2 mm (A, F, G); 0.5 mm (B, C, D, E, G, H, I, J).

**Figure 6:** *Magnifitermes krishnai* gen. et sp. nov., holotype IGR.BU-053. Photograph of habitus.

Scale bar: 2 mm.

**Figure 7:** *Magnifitermes krishnai* gen. et sp. nov., holotype IGR.BU-053. Detailed photographs.

A: Head and pronotum; B: Antenna; C: Fore leg; D: Mid leg; E: Hind leg. Scale bar: 1 mm (A, B,

C, D); 0.5 mm (E).

**Figure 8:** *Magnifitermes krishnai* gen. et sp. nov., holotype IGR.BU-053. A: Detailed photograph

of mandibles; B: Line drawing of forewing venation. Scale bar: 0.5 mm (A); 2 mm (B).



**Figure 9:** *Mastotermes myanmarensis* sp. nov., holotype IGR.BU-054. A: Forewing. B: Hind wing. Scale bars: 2 mm.

**Figure 10:** *Mastotermes myanmarensis* sp. nov., holotype IGR.BU-054. Line drawings with veins labelled (crossveins omitted); A: Forewing. B: Hind wing. Scale bars: 2 mm.

**Figure 11:** Specimen IGR.BU-055 belonging to the ‘*Meiatermes*-grade’. Photograph of habitus. Scale bar: 20 mm.

**Figure 12:** Specimen IGR.BU-055 belonging to the ‘*Meiatermes*-grade’. Detailed photographs. A: Left antenna; B: Right protibia (arrow indicating tibial spurs); C: Right mesotibia (arrow indicating tarsomeres); D: Forewing scale. Scale bars: 1 mm.

**Figure 13:** Worker or pseudergate IGR.BU-056, from Hkamti amber. A: Habitus in left view; B: Habitus in right view; C: Details of tibia (with arrow indicating tarsomeres). Scale bars: 0.5 mm.