A new arceotermitid species from mid-Cretaceous Kachin amber (Isoptera: Teletisoptera)

Corentin Jouault[1,*], Ru Smith[2] & Michael S. Engel[3]

[1]*Oxford University Museum of Natural History, University of Oxford, Parks Road, Oxford OX1 3PW, UK.*

[2]*Jabatan Geologi, Universiti Malaya, 50603 Kuala Lumpur, Wilayah Persekutuan Kuala Lumpur, Malaysia*

[3]*Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY, 10024, USA*

jouaultc0@gmail.com; https://orcid.org/0000-0002-3680-5172

ru.d.a.smith@gmail.com; XXX

mengel@amnh.org; https://orcid.org/0000-0003-3067-077X

**Corresponding author*

Abstract

The mid-Cretaceous termite genus *Arceotermes* Engel & Jiang (Arceotermitidae) has hitherto been known from a single species in Kachin amber (Myanmar). Here we report a second species, which is described and figured as *Arceotermes bellator* **sp. nov.**, permitting an emendation of the generic diagnosis. The new species is distinguished from the type species by mandibular dentition and number of antennomeres. We discuss its systematic placement in detail, and propose of brief summary of the defensive strategy used by termite soldiers during the mid-Cretaceous.

Keywords: Termites, soldiers, diversity, taxonomy, mandibles

Introduction

Colony defense is one of the main factors that has contributed to the evolutionary success of termites (Wilson, 1971). Defense is achieved through both passive — such as cryptic way of life or nest fortifications— and active mechanisms (Deligne *et al.*, 1981; Prestwich, 1984; Noirot & Darlington, 2000; Šobotník *et al.*, 2010a,b, 2012). Active defense is mainly accompished by a defense-dedicated caste, the soldiers. This caste is found in most termite species and has also evolved in several other eusocial lineages, showing a critical importance in the evolution of sociality (Crespi, 1992; Duffy, 1996; Tian & Zhou, 2014).

As early as the mid-Cretaceous, Isoptera employed a specialized soldier caste for defense against opponents or predators (*e.g.*, Engel *et al.*, 2016; Jouault *et al.*, 2021). It is hypothesized that the environmental changes during the Angiosperm Terrestrial Revolution (ATR) (Benton *et al.*, 2022) exerted considerable pressure on termites, leading to the development of a distinct caste exclusively dedicated to colony defense (Engel *et al.*, 2016; Jouault *et al.*, 2022a, 2024). Additionally, the first records of termite soldiers coincide with the rise of ants, long-term enemies of termites (Barden, 2017). Consequently, it is assumed that the ATR and the concurrent rise of ants played a collaborative role in promoting the development of a defensive caste in Isoptera (Jouault *et al.*, 2022a).

During the Cretaceous, termite soldiers exhibited two types of mandible shapes: biters and reapers (Deligne, 1971). These mandibular variations not only suggest that termites employed diverse defensive strategies against predators but also indicate that earlier defense mechanisms likely relied primarily on brute force rather than kinetic energy associated with the rapid and powerful opening and closing of mandibles (*i.e.*, soldiers with slashing mandibles). Despite this diversity, our understanding of the morphological variations in termite

soldiers from the Cretaceous is limited, with only six documented species, all originating from Kachin amber (Engel *et al.*, 2016; Zhao *et al.*, 2019, 2020; Jiang *et al.*, 2021; Jouault *et al.*, 2021).

The most recently described soldier is a specimen of *Arceotermes hospitis* Engel & Jiang, 2021. This genus was established based on a specimen from mid-Cretaceous Kachin amber, and placed in its own family, Arceotermitidae (Jiang *et al.*, 2021). The family Arceotermitidae includes two subfamilies: Arceotermitinae (*Arceotermes*) and Cosmotermitinae (*Cosmotermes* Zhao, Yin, Shih & Ren, 2020). The latter was reclassified from Stolotermitidae to Arceotermitidae (Zhao *et al.*, 2020; Jiang *et al.*, 2021). The mandible shape, tarsomere number, and morphology of *Arceotermes* and *Cosmotermes*, and by extension of the Arceotermitidae, strongly support their placement within Teletisoptera (for a detailed discussion see Jiang *et al.*, 2021: 380-382). Members of this family share similarities with the Stolotermitidae but can be distinguished by several key features: their head is not dorsoventrally compressed (*vs.* strongly dorsoventrally compressed in Stolotermitidae), their pronotum is approximately equal in width to the head (*vs*. narrower), and their mandibles have deeply incised teeth. However, like many extinct termite lineages, the diversity of Arceotermitidae remains poorly understood due to limited fossil evidence. This highlights the need for further studies on Cretaceous termite soldiers to better understand the defensive strategies of Isoptera during this period and to more thoroughly document the early diversity of termite species.

Embracing this view, we describe a new arceotermitid soldier from mid-Cretaceous Kachin amber of Myanmar. The specimen, representing a new species, is well-preserved, facilitating clear observation of both mandibles and body. This discovery enables us to refine the diagnosis of the genus *Arceotermes*.

Material and methods

Origin of amber piece

The piece of amber containing *Arceotermes bellator* sp. nov. originated from the deposits of Noije Bum in the Hukawng Valley (26°29′N, 96°35′E), Kachin State, northern Myanmar (*vide* Grimaldi & Ross, 2017: fig. 2). Radiometric data established an early Cenomanian age (98.79 ± 0.62 Mya) for Kachin amber, based on zircons from volcanic clasts found within the amber-bearing sediments (Shi *et al.*, 2012). Some ammonites found in the amber-bearing bed and within amber corroborated a late Albian/early Cenomanian age (Cruickshank & Ko, 2003; Yu *et al.*, 2019). The specimen was photographed with an UltraMacro/WeMacro auto-rail with an attached Sony A7R IV camera. All images are digitally stacked photomicrographic composites of several individual focal planes, which were obtained using Helicon Focus 6.7. The figures were composed with Adobe Illustrator CC2019 and Photoshop CC2019 software. The piece of amber is housed in the collection of Ru Smith with accession number RS.P1596 and is accessible upon reasonable request.

Terminology and measurements

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), 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)]. The following abbreviations are used for mandibular dentition: LAt, RAt for left and right apical teeth; LMt_n, RMt_n for left and right marginal teeth numbered from apical to proximal.

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Systematic paleontology

Infraorder Isoptera Brullé, 1832

Parvorder Euisoptera Engel *et al.*, 2009

Minorder Teletisoptera Barden & Engel, 2021

Family Arceotermitidae Engel, 2021 (in Jiang *et al.*, 2021)

Remarks. The soldiers of this family can be distinguished from those of Mastotermitidae and Archotermopsidae by their tetramerous tarsi, smaller number of antennomeres (less than 20 articles). Unlike the dorsoventrally compressed heads of Stolotermitidae soldiers, their heads are not compressed in this manner. The pronotum is about as wide as the head capsule, while in Archotermopsidae, Hodotermitidae, and Stolotermitidae the pronotum is narrower. Key mandibular features further separate this group from Stolotermitidae. The right marginal teeth are broad, with the second marginal tooth possessing a distinct gnathal edge. The right apical tooth has a distinct constriction at its base. Additionally, there is no subsidiary tooth, and the mandibular teeth are deeply incised, unlike the shallow incisions seen in Stolotermitidae. As in Archotermopsidae and Stolotermitidae, the pronotum is flat, contrasting with the weakly saddle-shaped pronotum typical of Hodotermitidae. Finally, the tibiae lack the prominent lateral spines characteristic of Archotermopsidae.

Genus *Arceotermes* Engel & Jiang, 2021 (in Jiang *et al.*, 2021: 381)

Included species. *Arceotermes hospitis* Engel & Jiang, 2021 (type species; in Jiang *et al.*, 2021), and *Arceotermes bellator* **sp. nov.**

Emended diagnosis. Head large, longer than broad, posterior temples not tumid, head not dorsoventrally compressed. Lateral surface of head without striations, lateral margins largely parallel. Dorsal head surface without clearly visible Y-shaped ecdysial cleavage scar (it is difficult, though, to determine whether it is absent or merely exceedingly faint), fontanelle absent. Compound eyes absent, ocelli absent, antennae composed of 15–17, largely moniliform articles. Mandibles large, elongate, and gently bent ventrad toward their apices, with prominent apical and marginal teeth. Soldier mandibles with two right marginal teeth and three left marginal teeth (in addition to the apical tooth), right marginal teeth broad, and simple (sometimes with two points). Apical teeth long, pointed, and curved. Postmentum greatly broadened anteriorly, with concave lateral margins tapering posteriorly. Pronotum broad, and about as wide as head, with anterior margin broadly concave and lateral margins faintly convex, roughly parallel, and broadly rounded posteriorly to a broadly and weakly convex posterior margin. Surface of pronotum flat. Tibial-spur formula: 3-3-3, tarsi tetramerous, without arolium. Cerci with at least four cercomeres.

***Arceotermes bellator* sp. nov.**

(Figures 1–3)

urn:lsid:zoobank.org:act:06C37E90-2D4C-498A-A049-6874A0AA065E

Material. Holotype RS.P1596, soldier, preserved in a rectangular piece of amber, measuring 11 × 10 × 6 mm, housed in the amber collection of Ru Smith, York, England.

Etymology. The specific epithet is the Latin noun *bellātor*, meaning, "warrior".

Locality and horizon. Noije Bum Hill, Hukawng Valley, Kachin State, Myanmar; uppermost Albian to lowermost Cenomanian, mid-Cretaceous.

Diagnosis. Antennae with 15 antennomeres (*vs*. 17 in *A. hospitis*). Left mandible with LMt_1 nearly as wide as LMt_2, leaf-shaped (*vs*. much narrower than LMt_2 and elongate in *A. hospitis*); LMt_2 pointed apically, leaf-shaped (*vs*. not so pointed apically, blunt in *A. hospitis*). Right mandible with constriction at RAt base faint (*vs*. well impressed); RAt thin and much longer than RMt_1 (*vs*. stout and short in *A. hospitis*).

Description. Soldier. Total body length (as preserved) about 6.2 mm (mandibles included); head enlarged, nearly squared, slightly longer than wide, head length (excluding mandibles) 1.82 mm, maximum width 1.44 mm, chestnut brown, with virtually no setae, remainder of body with sparsely scattered, fine, suberect setae; head not compressed dorsoventrally, slightly wider than pronotum, lateral sides roughly parallel, posterolateral angles not tumid, lateral surface without stridulatory file, posterior border gently and broadly convex; fontanelle absent; labrum longer than wide, projecting over about 0.75× mandibular length, labrum length 0.6 mm, width 0.55 mm; anteclypeus pale, flat, transverse, subequal in length to postclypeus; postclypeus transverse; clypeus flanked by small, shallow lobes lateral to each lobe overhanding antennal insertion; mandibles heavily sclerotized, approximately equal in size and length, left mandible length about 1 mm, slightly overlapping apically, elongate, extending well beyond apex of labrum, gently bent ventrad apically; dentition prominent, with two right marginal teeth and three left marginal teeth; right marginal teeth broad, apical teeth long,

pointed, curved; subsidiary tooth lacking; compound eyes absent; maxillary palpus long, overpassing mandibles, with five palpomeres, first two palpomeres short, third widest, fifth apically rounded, slightly thinner than fourth; antenna with 15 moniliform articles, 1.8 mm long; weak occipital carina present anteriorly, disappearing by tangent with widest point of postmentum.

Pronotum broad, about as wide as head (1.3 mm in dorsal view), anterior margin broadly and gently concave, lateral margins faintly convex, roughly parallel, broadly rounded posterolaterally, posterior border weakly convex, surface flat.

Legs. Procoxa without carina, profemur 0.90 mm, protibia length 0.75 mm, protarsus length 0.30 mm. Mesofemur 0.85 mm, mesotibia length 0.73 mm, mesotarsus length 0.35 mm. Metafemur 1.05 mm, metatibia length 0.85 mm; metatarsus length ca. 0.45 mm. Tibial-spur formula 3-3-3; tarsi tetramerous; pretarsal claws simple; arolium absent.

Abdomen 2.3 mm long, 1.3 mm wide; cercus with at least four cercomeres (perhaps more), combined length 0.25 mm.

Remarks. The mandibular dentition is a robust character suite for discriminating species within most extant genera of Isoptera (*e.g.*, Scheffrahn, 2022; Schiff *et al.*, 2023). Here, we record important differences between the mandibles of the new species and those of *A. hospitis*.

Discussion

Systematic placement

The systematic placement of Cretaceous termites can be mired in difficulty and controversy, especially for those known largely from wing venation with few or no characters from the body and especially when lacking critical information from the mandibular dentition and tarsal structure. Fortunately, the current specimen is easily attributed to a specific family owing to its excellent preservation (Fig. 1). The absence of a fontanelle immediately allows for the exclusion of the families of Neoisoptera (Krishna *et al.*, 2013). Similarly, the comparatively longer cerci composed of four cercomeres precludes affinity with the Kalotermitidae or Tanytermitidae (Jiang *et al.*, 2021). In addition, the new specimen further differs from Kalotermitidae in the absence of a clear Y-shaped ecdysial cleavage scar (*vs*. always present in Kalotermitidae and most of the time strongly impressed) (Krishna, 1961; Krishna *et al.*, 2013). Note that the transparency of the head may be misleading when interpreting this structure on fossil specimens because the shape of the basal part of the submentum may look a bit triangular and be seen through the head capsule (Fig. 2). In addition, the gently downcurved soldier mandibles is not present in Icoisoptera (Figs. 2-3).

The remaining possibilities for an assignment of the fossil are to be sought among the Teletisoptera, Mastotermitidae, and several extinct families and unplaced genera of Cretaceous termites (Jouault *et al.*, 2022b). Some groups can be rather quickly dismissed such as the extinct Melqartitermitidae and Mylacrotermitidae as both of these have ventral cervical sclerites and wholly pentamerous tarsi, the former character otherwise absent in other Isoptera (where known) and certainly lacking in the current fossil, and the tarsi are tetramerous in the specimen reported here (Engel et al. 2007). Krishnatermitidae also have pentamerous tarsi (Engel *et al.*, 2016). Similarly, Mastotermitidae have wholly pentamerous tarsi,

more than 20 antennomeres, and a slightly saddle-shaped pronotum, while the fossil has tetramerous tarsi, fewer than 20 antennomeres, and a flat pronotum (Krishna *et al.*, 2013).

Naturally, there remain several Cretaceous groups for which it is not possible to make a meaningful comparison as they are known only from alates or even isolated wings. Cratomastotermitidae are known only from alates but once again the pentamerous tarsi help to exclude them as a possibility (Bechly, 2007). This is also the case for Termopsidae, an extinct family that has consistently grouped apart from Archotermopsidae and even other Teletisoptera (*e.g.*, Engel *et al.*, 2009, 2016; Jouault *et al.*, 2021).

Archotermopsidae and Hodotermopsidae (*sensu* Wang *et al.*, 2022) are excluded owing to the possession of pentamerous tarsi, albeit cryptically pentamerous. In addition, the current fossil further differs from the soldiers of Archotermopsidae by the comparatively short and apically strongly arched mandibles (vs. linear and not strongly arched in Archotermopsidae) (Krishna *et al.*, 2013: figs. 31–32).

Among the remaining groups, the Hodotermitidae, Arceotermitidae, and Stolotermitidae all have tetramerous tarsi, like the fossil described herein. The 15 antennomeres preclude affinities with Hodotermitidae, which have 22–33 antennomeres (Krishna *et al.*, 2013), and the tongue-shape of the mandibular teeth and the flat pronotum further differ from the pointed teeth of extant hodotermitid mandibles and their weakly saddle-shaped pronotum (Krishna *et al.*, 2013: figs. 33–35). Affinities with the Stolotermitidae are excluded because the right marginal teeth are elongate and comparatively thinner, with the second marginal tooth possessing a distinct gnathal edge (Fig. 3); the right apical tooth has a distinct constriction at its base; a subsidiary tooth is absent; and all mandibular teeth are deeply incised (Jiang *et al.*, 2021). Through elimination, the sole clade remaining is that of Arceotermitidae and, indeed,

the new soldier can be readily attributed to this family as it possesses the whole suite of character states used to circumscribe arceotermitids from other Teletisoptera, and more precisely to diagnose the genus *Arceotermes* (Jiang *et al.*, 2021).

Termite early defensive specializations in soldiers

Extant termite soldiers have an arsenal of defenses ranging from greatly enlarged and phragmotic heads (plug defense) to various mandible-shapes: elongated, heavily toothed, scissor-like or twisted mandibles. Termites soldiers have, therefore, been originally classed into four main categories based on the way they use their mandibles: biters, reapers, symmetrical snappers, and asymmetrical snappers (Deligne, 1971). Some recently diverged taxa, in the Neoisoptera, also possess nozzle-shaped heads spraying gluey secretions on the enemy, with the earliest fossil possessing such character being recorded from the mid-Cretaceous (Krishna & Grimaldi, 2003; Krishna *et al.*, 2013; Hellemans *et al.*, 2024).

Cretaceous termite soldiers already possessed diversified mandible shapes while there is to date no record of the soldiers with fontanelles from this period: *Milesitermes engeli* Jouault & Nel, 2021 had hooked mandibles with one small median tooth (although the mandibles are likely incomplete; Fig. 4A); *Anisotermes xiai* Zhao, Eggleton & Ren, 2019 had massive and moderately elongated mandibles with one pre-apical tooth (Fig. 4B); *Ginormotermes rex* Engel, Barden & Grimaldi, 2016 had massive and moderately elongated mandibles with pre-apical teeth (Fig. 4C); *Krishnatermes yoddha* Engel, Barden & Grimaldi, 2016 had scissor-like, elongated but apparently feebly toothed mandibles (Fig. 4D); *Cosmotermes multus* Zhao, Yin, Shih & Ren, 2020 had massive and heavily toothed mandibles (Fig. 4E); and *Arceotermes hospitis* Engel & Jiang, 2021 had massive and heavily toothed man-

dibles (Figs. 3B-4F) (Engel *et al.*, 2016; Zhao *et al.*, 2019, 2020; Jouault *et al*., 2021). Following the classification detailed previously (Deligne, 1971), only two soldier types are recorded during the Cretaceous period, namely biters in Mastotermitidae (*i.e.*, *Milestermes*, *Anisotermes*, and *Ginormotermes*) and Arceotermitidae (*i.e.*, *Cosmotermes*, and *Arceotermes*), and reapers in Mastotermitidae (*i.e.*, *Krishnatermes*). These different shapes of mandibles not only suggest that termites had various defense strategies during the mid-Cretaceous but also point out that earlier defense strategies relied mainly on the use of brute force and not on kinetic energy (linked to the wide opening and slamming of the mandibles). Rather unsurprisingly, the size of the soldiers from this period is relatively large (*e.g.*, *Ginormotermes*) since mandible power is directly linked to the size and mass of the adductor muscles (themselves conditioned by the size of the cephalic capsule and the size of the soldier).

Future research is expected to shed light on whether soldiers with fontanelles existed during this period and to document the early diversity of Neoisoptera more comprehensively. Currently, our understanding of their evolution's initial stages remains limited and requires further investigation. Similarly, an increasing number of termite soldier specimens is anticipated, from Kachin amber, to enhance our understanding of the defensive strategies employed by Cretaceous termites and may offer valuable insights into the evolutionary success of certain lineages.

Conclusion

The scarce diversity of Mesozoic Isoptera limits our understanding of the onset of their evolutionary history. To increase their fossil record, a new species from the Cretaceous period, identified as a member of the extinct Arceotermitidae family, is described from Kachin am-

ber. The description of *Arceotermes bellator* **sp. nov.** highlights the underestimated diversity of Isoptera in Cretaceous deposits. Finally, this new taxon allows for examining previously invisible features, enabling a revision of the generic diagnosis.

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References

Barden, P. (2017) Fossil ants (Hymenoptera: Formicidae): ancient diversity and the rise of modern lineages. *Myrmecological News*, 14, 1–30.

Bechly, G. (2007) Isoptera: termites. *In*: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds), *The Crato Fossil Beds of Brazil: Window into an Ancient World.* Cambridge University Press, Cambridge, pp. 249–262.

Benton, M.J., Wilf, P. & Sauquet, H. (2022) The Angiosperm Terrestrial Revolution and the origins of modern biodiversity. *New Phytologist*, 233, 2017–2035. https://doi.org/10.1111/nph.17822

Crespi, B.J. (1992) Eusociality in Australian gall thrips. *Nature*, 359, 724–726. https://doi.org/10.1038/359724a0

Cruickshank, R.D. & Ko, K. (2003) Geology of an amber locality in the Hukawng Valley, northern Myanmar. *Journal of Asian Earth Sciences*, 21, 441–455. https://doi.org/10.1016/S1367-9120(02)00044-5

Deligne, J. (1971) Mécanique du comportement de combat chez les soldats de termites (Insecta: Isoptera). *Forma et Functio*, 4, 176–187.

Deligne, J., Quennedey, A. & Blum, M.S. (1981) The enemies and defense mechanisms of termites. *Social Insects*, 2, 1–76. https://doi.org/10.1016/B978-0-12-342202-6.50008-3

Duffy, J.E. (1996) Eusociality in a coral-reef shrimp. *Nature*, 381, 512–514. https://doi.org/10.1038/381512a0

Engel, M.S., Grimaldi, D.A. & Krishna, K. (2007) Primitive termites from the Early Cretaceous of Asia (Isoptera). *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie)*, 371, 1–32.

Engel, M.S., Grimaldi, D.A. & Krishna, K. (2009) Termites (Isoptera): their phylogeny, classification, and rise to ecological dominance. *American Museum Novitates*, 3650: , 1–27. https://doi.org/10.1206/651.1

Engel, M.S., Barden, P., Riccio, M.L. & Grimaldi, D.A. (2016) Morphologically specialized termite castes and advanced sociality in the Early Cretaceous. *Current Biology*, 26, 522–530. https://doi.org/10.1016/j.cub.2015.12.0614

Grimaldi, D.A. & Ross, A. (2017) Extraordinary Lagerstätten in amber, with particular reference to the Cretaceous of Burma. *In*: Fraser, N.C., Sues, H.-D. (Eds), *Terrestrial*

conservation Lagerstätten: windows into the evolution of life on land. Dunedin Academic Press, Edinburgh, pp. 287–342.

Hellemans, S., Rocha, M.M., Wang, M., Aanen, D.K., Bagnères, A.-G., Buček, A., Carrijo, T.F., Chouvenc, T., Cuezzo, C., Constantini, J.P., Constantino, R., Dedeine, F., Deligne, J., Eggleton, P., Evans, T.A., Josens, G., Hanus, R., Harrison, M., Harry, M., Jouault, C., Kalleshwaraswamy, C.M., Kaymak, E., Korb, J., Lee, C.-Y., Legendre, F., Li, H.-F., Lo, N., Lu, T., Matsuura, K., Maekawa, K., McMahon, D., Mizumoto, N., Oliveira, D.E., Poulsen, M., Romero Arias, J., Sillam-Dussès, D., Su, N.-Y., Tokuda, G., Vargo, E., Ware, J.L., Šobotník, J., Scheffrahn, R.H., Cancello, E., Roisin, Y., Engel, M.S. & Bourguignon, T. (2024) Genomic data bring a new dawn to the classification of extant termites. *Nature Communications*, 15, 6724. https://doi.org/10.1038/s41467-024-51028-y

Jiang, R.-X., Zhang, H.-R., Eldredge, K.T., Song, X.-B., Li, Y.-Y., Tihelka, E., Huang, D.-Y., Wang, S., Engel, M.S. & Cai, C.-Y. (2021) Further evidence of Cretaceous termitophily: description of new termite hosts of the trichopseniine *Cretotrichopsenius* (Coleoptera: Staphylinidae), with emendations to the classification of lower termites (Isoptera). *Palaeoentomology*, 4, 374–389. https://doi.org/10.11646/palaeoentomology.4.4.13

Jouault, C., Condamine, F.L., Legendre, F. & Perrichot, V. (2024) The Angiosperm Terrestrial Revolution buffered ants against extinction. *Proceedings of the National Academy of Sciences of the USA*, 121, e2317795121. https://doi.org/10.1073/pnas.2317795121

Jouault, C., Legendre, F., Grandcolas, P., Nel, A. (2021) Revising dating estimates and the antiquity of eusociality in termites using the fossilized birth-death process. *Systematic Entomology*, 46, 592–610. https://doi.org/10.1111/syen.12477

Jouault, C., Engel, M.S., Legendre, F., Huang, D.-Y., Grandcolas, P. & Nel, A. (2022b) Incrementing and clarifying the diversity and early evolution of termites (Blattodea: Isoptera). *Zoological Journal of the Linnean Society*, 196, 608–629. https://doi.org/10.1093/zoolinnean/zlac064

Jouault, C., Engel, M.S., Huang, D., Berger, J., Grandcolas, P., Perkovsky, E.E., Legendre, F. & Nel, A. (2022a) Termite Valkyries: soldier-like alate termites From the Cretaceous and task specialization in the early evolution of Isoptera. *Frontiers in Ecology and Evolution*, 10, 737367. https://doi.org/10.3389/fevo.2022.737367

Krishna, K.A. (1961) Generic revision and phylogenetic study of the family Kalotermitidae. *Bulletin of the American Museum of Natural History*, 122, 303–408.

Krishna, K. & Grimaldi, D.A. (2003) The first Cretaceous Rhinotermitidae (Isoptera): a new species, genus, and subfamily in Burmese amber. *American Museum Novitates*, 3390, 1–10. https://doi.org/10.1206/0003-0082(2003)390%3C0001:TFCRIA%3E2.0.CO;2

Krishna, K.A., Grimaldi, D.A., Krishna, V. & Engel, M.S. (2013) Treatise on the Isoptera of the world. *Bulletin of the American Museum of Natural History*, 377, 1–2704. https://doi.org/10.1206/377.1

Lo, N., Engel, M.S., Cameron, S., Nalepa, C.A., Tokuda, G., Grimaldi, D.A., Kitade, O., Krishna, K., Klass, K.-D., Maekawa, K., Miura, T. & Thompson, G.J. (2007) Save Isop-

tera: a comment on Inward *et al*. *Biology Letters*, 3, 562–563. https://doi.org/10.1098/rsbl.2007.0264

Noirot, C. & Darlington, J.P.E.C. (2000) Termite nests: architecture, regulation and defence. *In*: Abe, T., Bignell, D.E. & Higashi, M. (Eds). *Termites: evolution, sociality, symbioses, ecology.* Springer publishing pp. 121–139.

Prestwich, G.D. (1984) Defense mechanisms of termites. *Annual Review of Entomology*, 29, 201–232. https://doi.org/10.1146/annurev.en.29.010184.001221

Scheffrahn, R.H. (2022) *Amitermes californicus* Banks, 1920 (Isoptera, Termitidae, Termitinae) resurrected after ninety years of synonymy and *A. floridensis* Scheffrahn, 1989 synonymized into *A. wheeleri* (Desneux, 1906). *Zootaxa*, 5128, 581–588. https://doi.org/10.11646/zootaxa.5128.4.7

Schiff, N.M., Myles, T.G., Pham, T.H., Lancaster, A., Scheffler, B., Hanner, R. & deWard, J. (2023) A new species of *Parrhinotermes* (Isoptera: Rhinotermitidae: Rhinotermitinae) from Vietnam. *Transactions of the American Entomological Society*, 149, 299–313. https://doi.org/10.3157/061.149.0302

Shi, G.-H., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M.-C., Lei, W.-Y., Li, Q.-L. & Li, X.-H. (2012) Age constraint on Burmese amber based on U–Pb dating of zircons. *Cretaceous Research*, 37, 155–163. https://doi.org/10.1016/j.cretres.2012.03.014

Šobotník, J., Bourguignon, T., Hanus, R., Weyda, F. & Roisin, Y. (2010a) Structure and function of defensive glands in soldiers of *Glossotermes oculatus* (Isoptera: Serritermiti-

dae). *Biological Journal of the Linnean Society*, 99, 839–848. https://doi.org/10.1111/j.1095-8312.2010.01392.x

Šobotník, J., Jirošová, A. & Hanus, R. (2010b) Chemical warfare in termites. *Journal of Insect Physiology*, 56, 1012–1021. https://doi.org/10.1016/j.jinsphys.2010.02.012

Šobotník, J., Bourguignon, T., Hanus, R., Demianová, Z., Pytelková, J., Mareš, M., Foltynová, P., Preisler, J., Cvačka, J., Krasulová, J. & Roisin, Y. (2012) Explosive backpacks in old termite workers. *Science*, 337, 436. https://doi.org/10.1126/science.1219129

Tian, L. & Zhou, X. (2014) The soldiers in societies: defense, regulation, and evolution. *International Journal of Biological Sciences*, 10, 296–308. https://doi.org/10.7150/ijbs.6847

Wang, M.-L., Hellemans, S., Šobotník, J., Arora, J., Buček, A., Sillam-Dussès, D., Clitheroe, C., Lu, T., Lo, N., Engel, M.S., Roisin, Y., Evans, T.A. & Bourguignon, T. (2022) Phylogeny, biogeography, and classification of Teletisoptera (Blattaria: Isoptera). *Systematic Entomology*, 47, 581–590. https://doi.org/10.1111/syen.12548

Wilson, E.O. (1971) The Insect societies. Harvard University Press, Cambridge, pp. 562.

Yu, T.-T., Thomson, U., Mu, L., Ross, A., Kennedy, J., Broly, P., Xia, F.-Y., Zhang, H.-C., Wang, B. & Dilcher, D. (2019) An ammonite trapped in Burmese amber. *Proceedings of the National Academy of Sciences of the USA*, 116, 11345–11350. https://doi.org/10.1073/pnas.1821292116

Zhao, Z., Eggleton, P., Yin, X., Goa, T., Shih, C. & Ren, D. (2019) The oldest known mastotermitids (Blattodea: Termitoidae) and phylogeny of basal termites. *Systematic Entomology*, 44, 612–623. https://doi.org/10.1111/syen.12344

Zhao, Z., Yin, X., Shih, C., Gao, T. & Ren, D. (2020) Termite colonies from mid-Cretaceous Myanmar demonstrate their early eusocial lifestyle in damp wood. *National Science Review*, 7, 381–390. https://doi.org/10.1093/nsr/nwz141

Figure captions:

Figure 1. *Arceotermes bellator* **sp. nov. A**, Habitus, ventral view. **B**, Habitus, dorsal view. Scale bar: 1 mm.

Figure 2: *Arceotermes bellator* **sp. nov. A**, Detailed dorsal view of the head. **B**, Head in dorsal view. **C**, Detailed view of pro- and mesotibial apices with spurs indicated by black arrows. **D**, Detailed view of right midleg with spurs indicated by black arrows. **E**, Detailed view of left hindleg with spurs indicated by black arrows and metatarsomeres by white arrows. Scale bars: 1 mm (A, B, C, E), 0.5 mm (D).

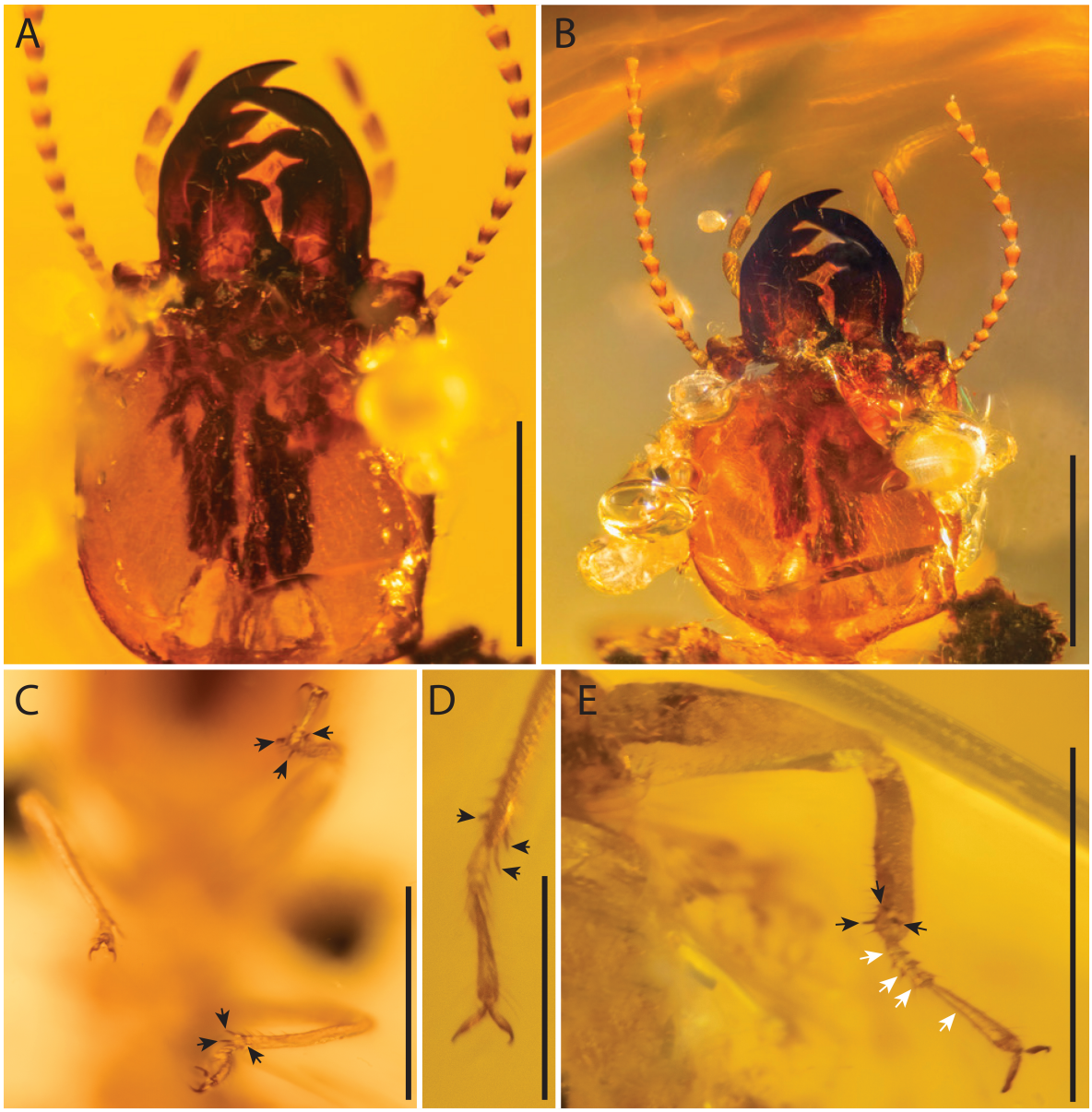

Figure 3. Comparison of mandibular dentition of species of *Arceotermes* Engel & Jiang, with dentary names labelled. **A**, *Arceotermes bellator* **sp. nov. B**, *Arceotermes hospitis* Engel & Jiang (from Jiang et al., 2021). Scale bar: 1 mm.

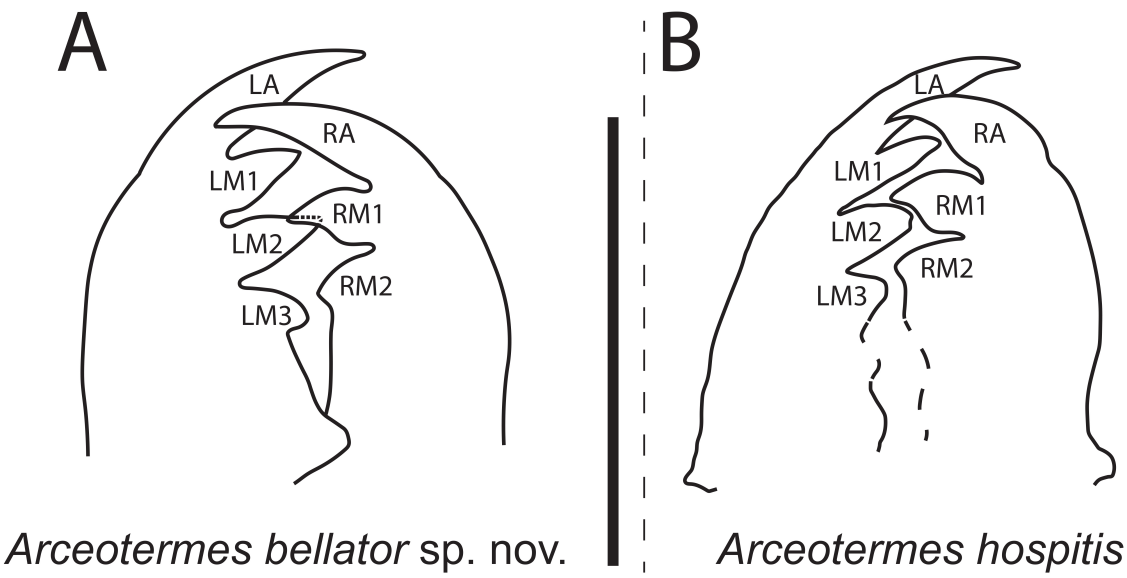

Figure 4. ‘mid’-Cretaceous termite soldiers. A, *Milestermes engeli* Jouault & Nel 2021. B, *Anisotermes xiai* Zhao *et al.* 2019. C, *Ginormotermes rex* Engel *et al.* 2016. D, *Krishnatermes yoddha* Engel *et al.* 2016. E, *Cosmotermes multus* Zhao *et al.* 2020. F, *Arceotermes hospitis* Engel & Jiang, 2021 (head modified from Engel *et al.* 2016; Zhao *et al.* 2019, 2020; Jiang *et al.*, 2021; Jouault *et al.* 2021).