

Current Biology

Morphologically Specialized Termite Castes and Advanced Sociality in the Early Cretaceous

Highlights

- Until now, the oldest worker and soldier termites were 17 million years old
- Workers of five termite species are reported in 100-million-year-old amber from Myanmar
- One new species, *Krishnatermes yoddha*, has winged, worker, and soldier castes
- Another new species has one of the largest soldiers ever, *Gigantotermes rex*

Authors

Michael S. Engel, Phillip Barden,
Mark L. Riccio, David A. Grimaldi

Correspondence

msengel@ku.edu (M.S.E.),
grimaldi@amnh.org (D.A.G.)

In Brief

Highly social animals with castes have recruitment with efficient foraging and defense, making these species competitively superior. Engel et al. report the first soldiers and definitive worker termites from the Cretaceous, which have adaptations very similar to modern species, indicating that termites probably had the original societies.



Morphologically Specialized Termite Castes and Advanced Sociality in the Early Cretaceous

Michael S. Engel,^{1,2,3,*} Phillip Barden,^{3,4} Mark L. Riccio,⁵ and David A. Grimaldi^{3,*}

¹Department of Ecology & Evolutionary Biology, University of Kansas, Lawrence, KS 66045-4415, USA

²Division of Entomology, Natural History Museum, University of Kansas, Lawrence, KS 66045, USA

³Division of Invertebrate Zoology, American Museum of Natural History, New York, NY 10024-5192, USA

⁴Department of Biological Sciences, Rutgers University, Newark, NJ 07102, USA

⁵Institute of Biotechnology, Cornell University, Ithaca, NY 14853, USA

*Correspondence: msengel@ku.edu (M.S.E.), grimaldi@amnh.org (D.A.G.)

<http://dx.doi.org/10.1016/j.cub.2015.12.061>

SUMMARY

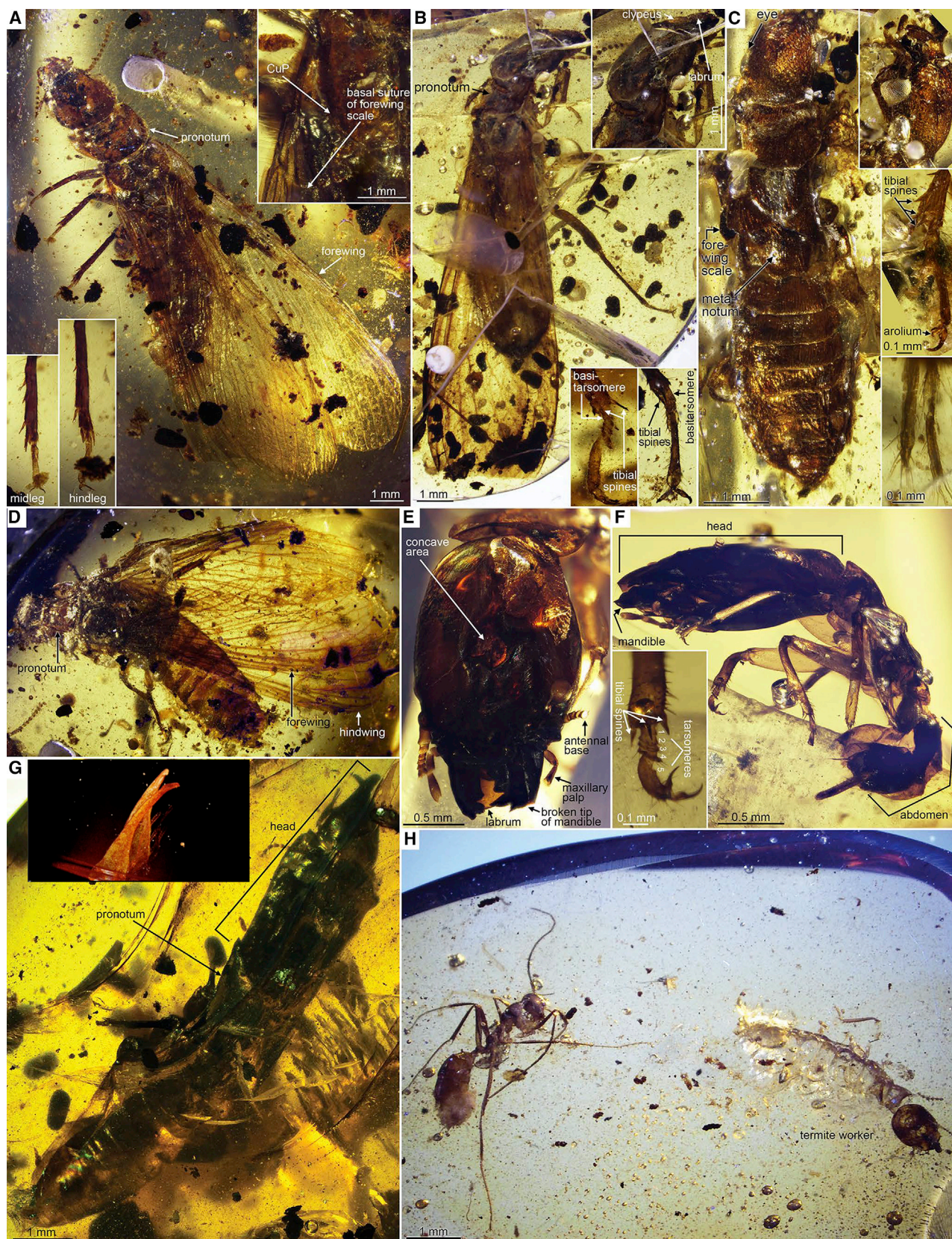
A hallmark of animals that are eusocial, or those with advanced sociality, is reproductive specialization into worker and queen castes [1–3]. In the most derived societies, these divisions are essentially fixed and in some arthropods, include further specialization—a tripartite system with a soldier caste that defends the colony [1]. Eusociality has originated numerous times among insects but is believed to have appeared first in the termites (Isoptera), in the Early Cretaceous [4]. However, all termites known from the Cretaceous have, until now, only been winged reproductives (alates and dealates); the earliest soldiers and definitive workers were known from just the Miocene (ca. 17–20 million years ago [mya]) [4]. Here, we report six termite species preserved in Early Cretaceous (ca. 100 mya) amber from Myanmar, one described as *Krishna-termes yoddha* gen. et sp. nov., comprising the worker/pseudergate, winged reproductive, and soldier, and a second species, *Gigantotermes rex* gen. et sp. nov., based on one of the largest soldier termites yet known. Phylogenetic analysis indicates that *Krishna-termes* are in the basal “*Meiatermes-grade*” of Cretaceous termites. Workers/pseudergates of another four species are briefly described, but not named. One of these workers/pseudergates reveals that ants—the most serious enemies of modern termites—lived in close proximity to termites in the Burmese paleofauna. These discoveries demonstrate the Mesozoic antiquity of specialized termite caste systems and corroborate that among all social species, termites probably had the original societies.

RESULTS AND DISCUSSION

Advanced sociality, or eusociality, in which a colony of parents with several cohorts of their offspring are specialized into castes behaviorally and sometimes morphologically [1–5], is essentially an arthropod phenomenon. The only vertebrate exceptions to

this are two species of African mole rats; otherwise, eusociality occurs in such myriad arthropods as a genus of snapping shrimp, a genus each of gall-forming aphids and thrips, a species of bark beetle, seven lineages of stinging (aculeate) wasps (including all ants, four groups of bees, one crabronid wasp, and most Vespidae), as well as in all 3,100 species of termites [4]. All of these taxa inhabit durable nests that are provisioned for feeding offspring and defended. In the earliest stages of eusociality, siblings and offspring remain in the nest and take on the behavioral role of workers, while retaining some reproductive capacity. In subsequent evolutionary stages this system was modified by the appearance of morphologically specialized workers who lost their fertility, further augmented by a third and even more specialized caste, the soldier, which exists solely for colony defense and in some cases is even unable to feed itself [1]. Eusociality evolved most often in aculeate wasps apparently because the hymenopteran sex-determining mechanism of haplodiploidy substantially increases the inclusive fitness of siblings [6, 7], although this has been disputed [8, 9]. Indeed, close genetic relatedness among nestmates, via inbreeding or some form of parthenogenesis, is the rule in eusocial arthropods [4], the major exception being termites.

The origin and maintenance of eusociality in termites is generally attributed to their feeding habits. Except for the recently evolved Macrotermitinae, colonies of which cultivate a symbiotic fungus on which they feed [10], all other termites depend on a diverse flora of symbiotic intestinal protists or bacteria that metabolize cellulose and exist exclusively in termites. Every non-macrotermitine termite must obtain its gut microbiota via anal trophallaxis from nestmates. The Isoptera is the only major group of arthropods in which all species have a morphologically distinctive worker and/or pseudergate caste; in basal ants (e.g., poneromorphs) and eusocial bees (basal corbiculates and some halictines), the morphological differentiation between workers and reproductives is slight, and soldiers do not exist [5, 11, 12]. Pseudergates can regress late in nymphal development into worker-like individuals; the development of true workers is established early and irreversibly, including atrophy of the gonads [13]. The distinction is an important one, but, for simplicity, our use of “worker” here refers to “worker and/or pseudergate” unless specified. For termites, in contrast to ants, the soldier caste is nearly ubiquitous, lost only in several recently evolved genera [14]. Isopterans have an arsenal of soldier defenses: greatly enlarged heads, many with mandibles that are either



(legend on next page)

elongate and heavily toothed or scissor-like and twisted (which interlock and snap), or in many Nasutitermitinae, the mandibles are vestigial and the nozzle-shaped heads spray gluey secretions on the enemy. Nasute soldiers with tiny mandibles, in fact, cannot feed themselves and depend upon nestmate workers.

The fossil record of termites has been essentially one of only alates, the winged, reproductive individuals. The earliest definitive fossilized workers and soldiers have been, until now, those of six species in the Mastotermitidae, Rhinotermitidae, and Termitidae preserved in Miocene amber (ca. 17–20 million years ago [mya]) from the Dominican Republic [4, 15, 16]. Dominican amber termites are remarkably diverse and the species extremely similar to modern ones. Oddly, worker and soldier termites have not been found even in Eocene Baltic amber, which is the most productive amber deposit and probably the most diverse fossil insect assemblage [4, 17, 18]. The report of a worker specimen with possible affinities to the Cretaceous genus *Meiatermes* (otherwise known from alates and isolated wings) is based on a wingless specimen in limestone from the Early Cretaceous of Spain [19]. If this is a worker, its preservation does not exhibit detail that can exclude it being an imago with shed wings or simply a nymph. It was identified as a worker since eyes were not visible (their absence is not definitive), and mandibular dentition is not fully preserved. Also, the head is rectangular, not rounded as occurs in all known termite workers. Although there are various Paleogene fossil termite nests and several definitive ones from the Late Cretaceous [14, 20], family attributions of the latter in particular are uncertain and so have not refined our understanding of the earliest origins of termite social behavior.

Phylogenetic evidence predicts that termites extend into the Late Jurassic [21], possibly into the mid-Jurassic or even Late Triassic, 180–226 mya [22]. These studies were based on the morphology of fossil and exemplar Recent termites [21], as well as total-evidence (morphology + molecular data) analyses [22], and consistently indicate that Cretaceous alate termites form an extensive basal grade in the isopteran tree. Only one Cretaceous fossil termite is more basal than the most primitive living species, *Mastotermites darwiniensis* from northern Australia, so sociality in Cretaceous termites has been inferred from the fact that *M. darwiniensis* is eusocial. Definitive, direct evidence for specialized termite castes or eusociality in the Cretaceous has been lacking until now.

The termites reported here were recovered from mid-Cretaceous amber of northern Myanmar (earliest Cenomanian, ca. 100 mya), famous for its diversity of arthropod and even vertebrate inclusions [23]. Termites in these deposits, like all Cretaceous outcrops, are uncommon and represent less than 1%

of all inclusions [21]. A prior study reported five genera and six species of Burmese amber termites, all based on alates [24]. Our present material comprises four large reproductives (Figures 1A–1D), three complete with wings, the fourth of which had removed its wings (a dealate: Figure 1C); nine workers (in six amber pieces) (Figure 2); and the soldiers of two distinctively different species (Figures 1E–1G). The soldier specimens have some unique traits but otherwise possess the complete suite of specializations found in modern termite soldiers and are utterly unlike any major workers of extant eusocial groups [14]; their mandibular dentition, in fact, is nearly identical to soldiers of the living relict family Archotermopsidae [14, 25]. The fossil workers are clearly separable into five species, one of which is associated with an alate and the small soldier. This species, *Krishnatermes yoddha*, n. gen. et n. sp., is the first Cretaceous termite known from all three castes. The four other species known only from workers are not formally described (Supplemental Information). Details of the imago wings aided phylogenetic placement of *K. yoddha* among living and extinct families and genera of Isoptera [14, 21] (Figure 4). Complete descriptive details and discussion of affinities of the taxa are provided in the Supplemental Information.

Systematic Paleontology

Infraorder Isoptera Brullé, 1832.

Parvorder Euisoptera Engel, Grimaldi, et Krishna, 2009 [21].

“*Meiatermes* Grade” (sensu Engel et al., 2007 [17]).

***Krishnatermes yoddha* Engel, Barden, et Grimaldi, gen. et sp. nov.**

ZooBank LSID (generic name) urn:lsid:zoobank.org:act:FE022235-B2F0-42D8-A3E8-529F4D23B0CC.

ZooBank LSID (species name): urn:lsid:zoobank.org:act:ODA40661-D141-40BA-A3A4-B8A55F85E4C8.

Etymology. The generic name is a combination of a prefix honoring the late Kumar Krishna (1928–2014), world authority on termites, and the suffix *termes*, Greek for “termite.” The gender of the name is masculine. The specific epithet is from the Hindi Yōd’dhā, meaning “warrior,” in reference to the earliest termite soldier (it is unknown whether the name of the fictional Jedi Master from Star Wars, Yoda, was adapted from this Hindi word).

Referred Material. Holotype imago (Figures 1, 2, 3, S1, and S2), JZC-Bu1839a; paratype alate (Bu1839b), same piece as holotype; paratype soldier, JZC-Bu183; paratype workers, AND Bu942a, b. All are preserved in amber from the Albian-Cenomanian boundary (ca. 100 mya) [26], Kachin Province, northern Myanmar.

Figure 1. Alate and Soldier Termites in 100-Million-Year-Old Burmese Amber

Alate (A–D) and soldier (E–G) termites in 100-million-year old Burmese amber (at different magnifications).

(A) Holotype alate of *Krishnatermes yoddha* gen. et sp. nov., JZC Bu1839a. Insets: base of left forewing; mesothoracic and metathoracic tibiae and tarsi.

(B) Paratype of *K. yoddha*, JZC Bu155. Insets: head, ventrolateral view; right protarsus (to left, mesal view), left protarsus (lateral view).

(C) Dealate of *Krishnatermes* sp., JZC Bu156.

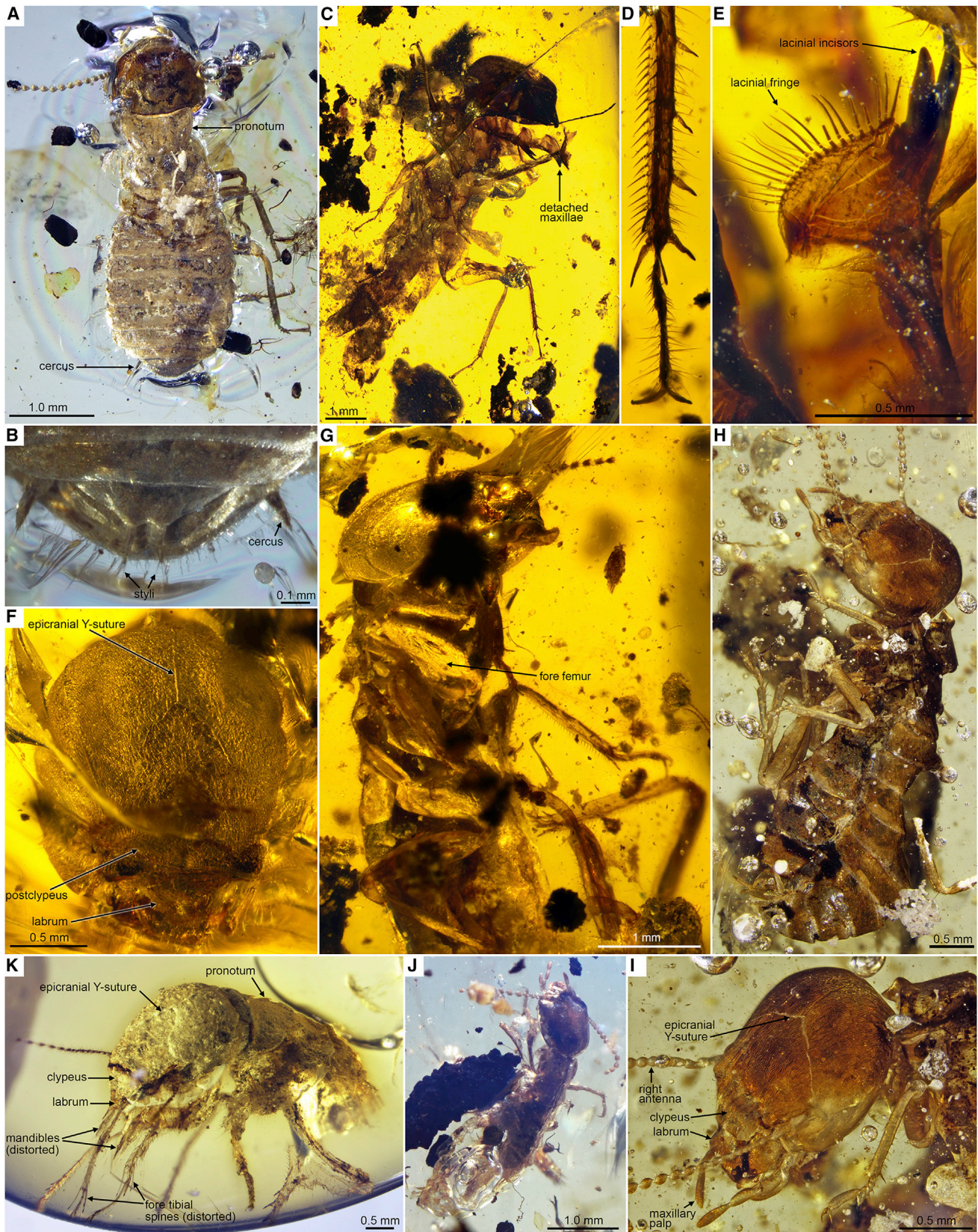
(D) Alate, *Krishnatermes yoddha*, JZC Bu-1839b.

(E and F) Soldier, paratype of *K. yoddha*, JZC Bu183. Head, frontal view (E). Habitus, lateral view (F). Inset: right protarsus (mesal view).

(G) Holotype soldier of *Gigantotermes rex* gen. et sp. nov., AMNH Bu-TJ001. Inset: CT scan movie of frontal view of head, showing mandibles and other mouthparts. See also Document S2 for the online version of Figure 1 containing a video.

(H) Unique Cretaceous co-occurrence of a worker ant, *Gerontoformica gracilis*, and a termite worker (morphospecies 3), AMNH TJ Bu-002.

See also Figures S1–S3.



(legend on next page)

Diagnosis, All Castes. Right mandible with at least two marginal teeth, each tooth about as long as apical tooth, subsidiary tooth present; antenna moniliform, with 14–18 articles; compound eyes (when present) circular, without emargination, well separated from posterior border of head; ocelli absent; fontanelle absent; ventral cervical sclerite absent; procoxa with shallow ventral keel; femora not carinate or keeled ventrally; all tarsi wholly pentamerous; tibial spur formula 3-4-4, spurs serrated, asymmetrical; 2-3 short cercomeres.

Diagnosis, Imago. Mandible completely covered by labrum; pronotum large, flat, broader than head, with prominent apico-lateral angles; tibia with outer spines along length; pretarsal arolium present but very small; wing membrane hyaline, reticulate; forewing scale large, greatly overlapping hind wing base, humeral margin convex, basal suture convex, all veins originating within scale, with faint reticulation in scale posterior to M and CuA; vein Sc long; multiple, elongate R veins; R₁ simple, terminating in apical fifth of wing; R₂ bifurcating near wing margin, terminating just anterior to Rs termination; Rs long, terminating just anterior to wing apex; radial field not expanding apically, relatively uniform across length; M branching near wing mid-length, encompassing apical third of posterior wing margin, anterior branch terminating just posterior to wing apex; hind wing without defined scale, lacking basal suture (wings chewed off at jagged margin in dealate), without anal lobe.

Diagnosis, Worker/Pseudergate. Mandible completely covered by labrum; eye present, ca. 0.10 mm diameter, without facets, slightly separated from antennal socket; pronotum with anterior margin thickened, slightly upturned and concave, apico-lateral angles acute but rounded; pretarsal arolium minute or absent.

Diagnosis, Soldier. Head dorsoventrally compressed, darkly sclerotized, long relative to body length; mandibles extending beyond labral apex; compound eye reduced (no facets); pronotal angles slightly more acute; arolium absent or highly reduced.

***Gigantotermes rex* Engel, Barden, et Grimaldi, gen. et sp. nov.**

ZooBank LSID (generic name): urn:lsid:zoobank.org:act:052379CA-5B56-4038-BA07-08C6196C432D.

ZooBank LSID (specific epithet): urn:lsid:zoobank.org:act:7518E6CC-3FBE-4F0D-9E53-5F4915992348.

Etymology. The generic name is a combination of a prefix in reference to the large size of the soldier and the typical Greek suffix for termites, *termes*. Gender of the name is masculine. The specific epithet, *rex*, is from the Latin, meaning “king” or “ruler” (also in reference to the size of the soldier).

Referred Material. Holotype soldier (Figures 1G and 3), AMNH Bu-TJ001; in Early Cretaceous amber from northern Myanmar [26].

Diagnosis, Soldier. Unique among all known soldier termites, very large, ca. 2 cm in body length; head large, ca. 0.4× total length of body, lateral margins parallel. Mandibles large, with two inner marginal teeth (similar in many details to the soldier mandibles of *Archotermopsis wroughtoni*); apical tooth long, pointed, curved. Portion of gena below antennal insertion pointed and projecting; compound eyes vestigial, epicranial Y-shaped ecdysial cleavage scar present. Pronotum distinct, massive (slightly wider than head, greatest length approximately half that of head); anterior margin with deep concavity, producing distinctive anterolateral points. Tibiae with spines having serrated edges; metafemur very large, swollen; tarsi wholly pentamerous; hind pretarsal claws enlarged, arolium absent or highly reduced.

The *Meiatermes*-grade of genera, to which *Krishnatermes* belongs, lies between the basal-most termites (*Garmitermes*, *Cratomastotermes*, and *Mastotermitidae*) and the remainder of the Isoptera. *Mastotermitidae* was global during the Cretaceous and much of the Cenozoic [14, 27] but contains now just the relict species *M. darwiniensis*. Like mastotermitids, *K. yoddha* primitively retains fully pentamerous tarsi, well-developed and serrated tibial spines, a 3-4-4 tibial spur formula, a large forewing scale in which all of the primary veins originate and that bears distinct reticulations, multiple R veins, and a very large imago pronotum that is slightly produced apicolaterally. Interestingly, the dealate specimen JZC Bu156 (Figure 1C), which is an undescribed species of *Krishnatermes*, has a hind wing scale that lacks a basal suture. In those mastotermitids where the hind wing scale can be carefully observed, the basal suture is also absent. In all living termites except *M. darwiniensis*, both pairs of wings are shed along the basal suture; in *M. darwiniensis*, the hind wings are chewed off at the base, producing a distinctive ragged edge in dealates similar to that observed in *Garmitermes succineus* in Baltic amber [17] and the dealate female studied

Figure 2. Worker Termites in Burmese Amber, at Various Magnifications

(A and B) *Krishnatermes yoddha*, paratype AND Bu-942b.

(A) Habitus, ventral view.

(B) Apex of abdomen, ventral view.

(C–E) Morphospecies 2, AMNH SD. Bu-001.

(C) Ventrolateral habitus.

(D) Left mesothoracic tibia and tarsus, dorsal view.

(E) Left maxilla.

(F and G) Morphospecies 4, AND Bu935a.

(F) Head, frontal view.

(G) Habitus, anterior end, lateral view.

(H and I) Morphospecies 1, AMNH Bu235.

(H) Habitus, lateral view.

(I) Head, dorsolateral view.

(J) *Krishnatermes yoddha*, paratype AND Bu-942a, habitus.

(K) *Meiatermes*-grade worker termite, AND Bu-886. The mouthparts and forelegs are distended as an artifact of preservation.

See also Figure S3.

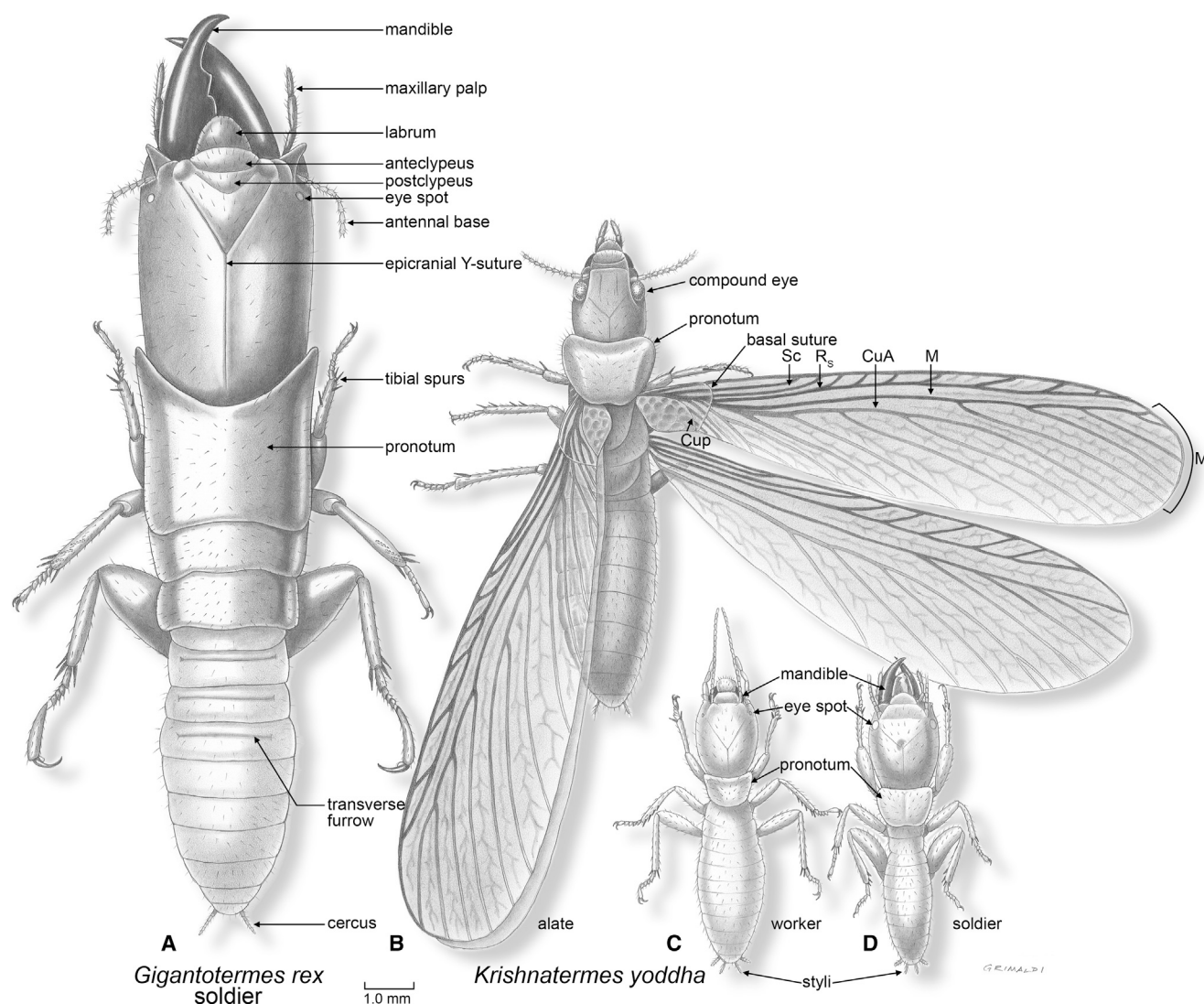


Figure 3. Tripartite Eusocial Castes in the Early Cretaceous

(A–D) Reconstructions, to scale, of the soldier of *Gigantotermes rex* gen. et sp. nov. and all three castes of *Krishnatermes yoddha* gen. et sp. nov. See also Figures S1–S3.

herein. Derived features shared between *K. yoddha* and the Euisoptera [21] are loss of the hind wing anal lobe and the occipital suture (which distinctively traverses the length of the gena in *M. darwiniensis* and other primitive termites).

Placement of *Gigantotermes* and the other species of Burmese amber workers is imprecise in lieu of alates and the other castes. In *Gigantotermes*, the pronotum is relatively larger (at least twice the size) than in any living species of termite soldier; the head is most similar in overall shape to that of the genus *Stolotermes* (Stolotermitidae: Neogene to Recent), differences being that the latter has smaller mandibles, a pronotum about half the size, and four (instead of five) tarsomeres. The mandibular dentition of *Gigantotermes* is generally similar to that of *Archotermopsis* and to a lesser degree *Hodotermopsis* [25] of the primitive family Archotermopsidae [21], and all have soldier mandibles that project well in front of the head. However, these similarities in dentition are apparently plesiomorphic, and it is un-

likely that *Gigantotermes* is an early archotermopsid since it lacks the broadened and dorsoventrally compressed head capsule bearing well-developed temples [25]. Based on the plesiomorphic conditions of pentamerous tarsi, a Y-shaped epicranial scar, mandibular structure and dentition, and at least three serrated, asymmetrical tibial spines on each leg, *Gigantotermes* probably also lies within the basal *Meiatermes*-grade of Cretaceous termites. The four unnamed species of workers (Figures 2 and S3) have the same conditions of the tarsi, leg spines, mandibles, and Y-shaped ecdysial scar and are probably all within this basal grade.

The body size of termite soldiers varies widely, but, with the exception of modern *Archotermopsis* and *Porotermes adamsoni*, soldiers are on average 0.80× the length of alates (refer to Supplemental Information). Given the proportions of the soldier of *Gigantotermes rex*, it should correspond to an as-of-yet unknown alate termite from the Cretaceous with a body

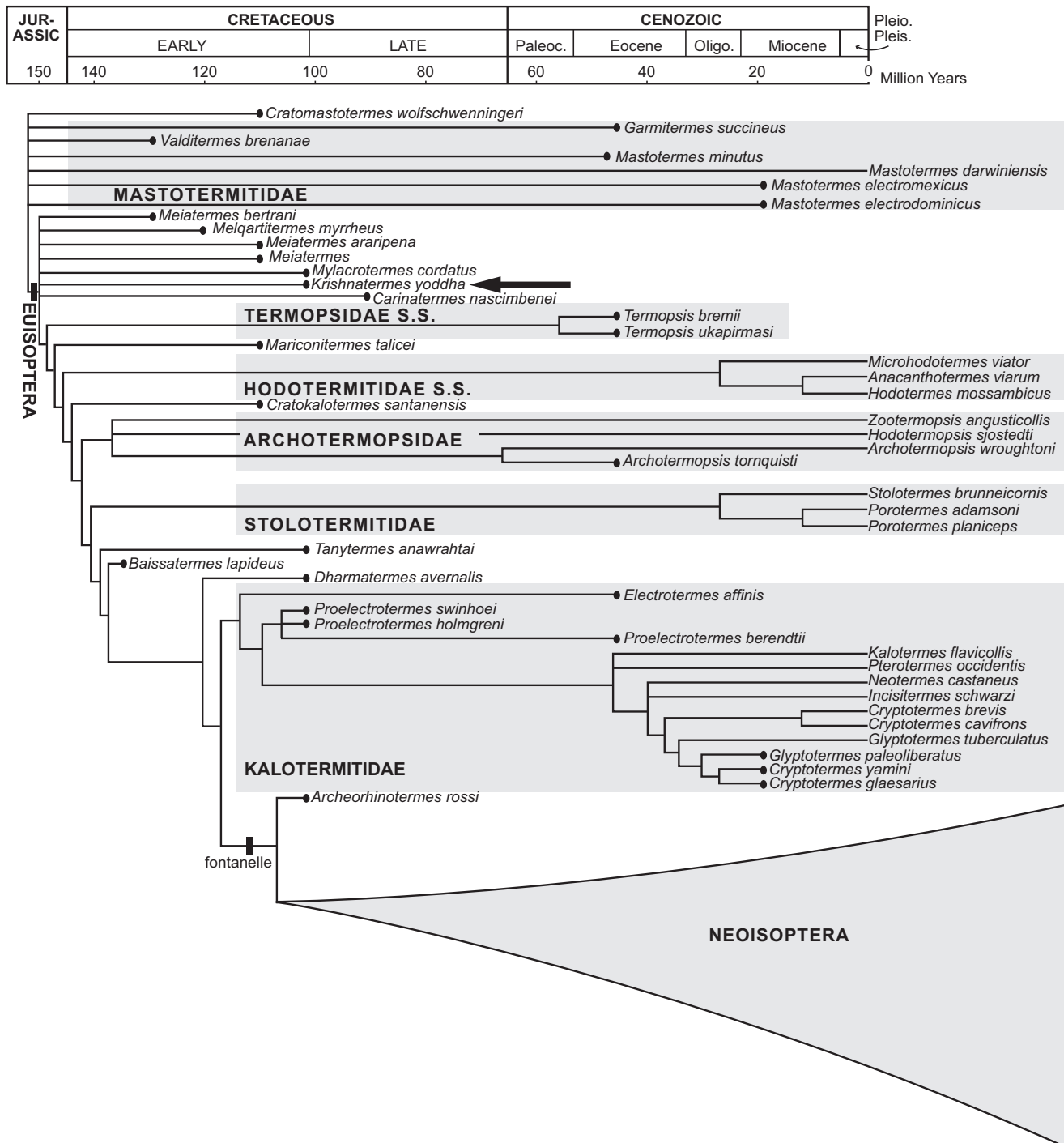


Figure 4. Phylogeny of Basal Living and Fossil Taxa of the Termites—Isoptera

Cladogram based on unweighted tree using 111 characters (mostly morphological) [21] (see Supplemental Information; matrix at <http://purl.org/phylo/treebase/phyloids/study/TB2:S18665>). Relationships within speciose living families (i.e., Neoisoptera: Rhinotermitidae, Termitidae) are not depicted; the position of *Krishnatermes yoddha* gen. et sp. nov. is shown with a bold arrow. *Gigantotermes* gen. nov. and the unnamed species of Burmese amber workers probably lie within the *Meiatermes*-grade of Cretaceous genera. Ages of nodes do not necessarily reflect divergence times. See also Figure S4, which gives full topologies and support values.

length of approximately 2.4 cm and a wing span of approximately 7 cm. The largest known termites are in the South American genus *Syntermes* (Termitidae: Syntermitinae), which have a

forewing length of up to 3.5 cm; the other largest living termites are Termopsidae and *Mastotermes*, which have forewing lengths up to 2.6 cm. (most other living termites are significantly smaller).

A very large primitive termite (*Gyatermes styriensis*) is known as an isolated forewing from the Upper Miocene (ca. 11.3 megannum [Ma]) of Austria, which has a length of 3.35 cm [28]. The soldiers of the largest species of *Syntermes* are slightly larger than *Gigantotermes* (e.g., *Syntermes aculeosus*, *S. spinosus* 2.05–2.15 cm body length; [Supplemental Information](#)). Thus, the extraordinary size of *Gigantotermes* is comparable to that of two unrelated genera that have the largest known body sizes. Body size of workers is always smaller than that of alates (on average 0.73×); the worker of *K. yoddha* is small (0.41×) relative to the alate, the soldier slightly larger (0.51×).

A unique piece of amber (AMNH TJ Bu-002) was discovered containing a worker ant of *Gerontoformica gracilis* and a worker termite (not of *K. yoddha*) ([Figure 1H](#) and [Supplemental Information](#)). The termite is partially decayed but preserves diagnostic characters of the mandibles, head capsule, pronotum, and tarsal structure. The ant is better preserved, with all appendages articulated and a long sting protruding; both specimens lie on the same flow surface. The ant faces the termite, its head approximately 5.5 mm away from the posterior end of the termite abdomen, less than either body length. Burmese amber preserves a diverse array of ants [12, 29–32] and alate termites [24, 33], but this is the closest co-occurrence of the two groups from the Cretaceous. Modern ants are notorious enemies of termites [34]: “The two groups have undoubtedly been locked in struggle for the greater part of the 100 million years of their coexistence, with ants acting as the active aggressors for the most part and termites as the prey and resisters” [4]. Many ants are opportunistic predators of termites, but some are specialized, obligate termitivores, particularly among the poneromorphs [35] (e.g., some species of *Leptogenys*, *Megaponera*, *Paliothyreus*, and *Pachycondyla*), but even including some small Myrmecinae such as *Tetramorium*, *Eurhopalothrix*, and *Proatta*. Today, ants have effects on termites at the scale of biological communities [36–39].

The scarcity of ants and termites in the Cretaceous makes it unlikely that the former was a major selective force on termites at this time, especially since the earliest termites preceded the earliest ants by at least 30 million years based on direct fossil evidence. Whether the earliest termites had soldier castes is unknown. Phylogenetic estimates of ant age are based on morphology and fossils [40] and molecular models [41–43] and range from 116 mya to 168 mya. Since the earliest definitive fossils of aculeate wasps (a group to which ants belong) are from the Early Cretaceous ca. 130 mya [4], the younger estimates of ant age (116–125 mya) are realistic. The phylogenetic position of the oldest fossil termite *Baissatermes lapideus*, a lithified alate from the Early Cretaceous of Siberia (ca. 130 million years old), is immediately basal to the Kalotermitidae and Neoisoptera ([Figures 4 and S4](#)) [21], suggesting that it was eusocial. This, plus the discovery that a *Meiatermes*-grade genus in the Cretaceous, *Krishnatermes*, possessed all three fully developed castes, indicates that termite eusociality extended into the Late Jurassic. As such, and if eusociality indeed imparts such adaptive superiority, why did it take about 50 million years for termites to become ecologically dominant [21]? Also, if ants today impose major selection pressures for the maintenance and diversity of termite soldiers, it remains to be explained what apparently caused soldier termites to appear tens of millions of years prior to ants.

EXPERIMENTAL PROCEDURES

The new taxonomic names are registered in ZooBank urn:lsid:zoobank.org:pub:D2412BFB-2B1C-4D62-9CB0-6F0D338868A0. Type specimens are deposited in the American Museum of Natural History, New York (AMNH), some on indefinite loan. Inclusions were prepared by trimming, grinding, and embedding in EpoTek 301-T synthetic resin for optimal observation and imaging using stereomicroscopy (Nikon SMZ1500 with NIS Elements software) and compound microscopy (Nikon Eclipse with Nikon D3 DSLR camera and HeliconFocus software). Scans were performed at Cornell University with a Zeiss VERSA XRM-520 nano-CT scanner utilizing various specimen-dependent voltages, currents, and exposure settings. Image stacks were rendered and analyzed in OsiriX (64 bit v.5.5) and Avizo 8.0 (VSG). Specimens of the three castes of *Krishnatermes yoddha* were morphologically coded using the earlier data matrix of living and fossil termites [21], supplemented with three additional characters (refer to [Supplemental Information](#)), for 111 characters in total. Only 14 characters were unobservable for *K. yoddha*, so 87% of the characters could be coded for this fossil species. The morphological matrix (which can be found in the TreeBASE data repository at <http://purl.org/phylo/treebase/phylo/study/TB2:S18665>) was run using the parsimony-based program TNT v.1.1 [44], using both weighted and unweighted parameters (unweighted tree summarized in [Figure 4](#); weighted and unweighted trees with support values given in [Figure S4](#)).

ACCESSION NUMBERS

The accession number for the morphological data reported in this paper is TreeBase: TB2:S18665.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, four figures, and three tables and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2015.12.061>.

AUTHOR CONTRIBUTIONS

D.A.G. and M.S.E. designed the research. D.A.G. and M.S.E. performed morphological and comparative studies. P.B. performed phylogenetic analyses. M.L.R. performed nano-CT scanning. D.A.G. produced the raw images and illustrations. D.A.G. and M.S.E. drafted the manuscript, to which P.B. and M.L.R. contributed.

ACKNOWLEDGMENTS

We are grateful to James S. Zigras, Scott Anderson, Tyler Janovitz, and Scott Davies for providing specimens for study and for deposition of types in the American Museum of Natural History; to the late Kumar Krishna for early discussions on the character combinations embodied by *Krishnatermes*; to Steve Thurston (AMNH) for compiling the plates and producing the diagrams; and to Valerie Krishna for a careful reading of the text. This work was partly supported by U.S. National Science Foundation grants DEB-0542909 and DEB-1144162 (to M.S.E.) and DDIG-1313547 (to D.A.G. and P.B.), an NSF Predoctoral Fellowship (to P.B.), and a 2014 College of Liberal Arts & Sciences (University of Kansas) Travel Award (to M.S.E.).

Received: November 5, 2015

Revised: December 27, 2015

Accepted: December 31, 2015

Published: February 11, 2016

REFERENCES

1. Wilson, E.O. (1971). *The Insect Societies* (Cambridge: Harvard University Press).
2. Lin, N., and Michener, C.D. (1972). Evolution of sociality in insects. *Q. Rev. Biol.* 47, 131–159.

3. Wilson, E.O. (1975). *Sociobiology: The New Synthesis* (Cambridge: Harvard University Press).
4. Grimaldi, D., and Engel, M.S. (2005). *Evolution of the Insects* (Cambridge: Cambridge University Press).
5. Hölldobler, B., and Wilson, E.O. (1990). *The Ants* (Cambridge: Harvard University Press).
6. Hamilton, W.D. (1964). The genetical evolution of social behaviour. I. *J. Theor. Biol.* 7, 1–16.
7. Hamilton, W.D. (1964). The genetical evolution of social behaviour. II. *J. Theor. Biol.* 7, 17–52.
8. Nowak, M.A., Tarnita, C.E., and Wilson, E.O. (2010). The evolution of eusociality. *Nature* 466, 1057–1062.
9. Wilson, E.O., and Nowak, M.A. (2014). Natural selection drives the evolution of ant life cycles. *Proc. Natl. Acad. Sci. USA* 111, 12585–12590.
10. Rouland-Lefèvre, C., and Bignell, D.E. (2002). Cultivation of symbiotic fungi by termites of the subfamily Macrotermitinae. In *Symbiosis: Mechanisms and Model Systems*, J. Seckbach, ed. (Berlin: Springer), pp. 731–756.
11. Michener, C.D. (1974). *The Social Behavior of the Bees: A Comparative Study* (Cambridge: Harvard University Press).
12. Barden, P., and Grimaldi, D. (2016). Adaptive radiation in socially advanced stem-group ants from the Cretaceous. *Curr. Biol.* Published online February 11, 2016. <http://dx.doi.org/10.1016/j.cub.2015.12.060>.
13. Noiro, C., and Pasteels, J.M. (1987). Ontogenetic development and evolution of the worker caste in termites. *Experientia* 43, 851–860.
14. Krishna, K., Grimaldi, D.A., Krishna, V., and Engel, M.S. (2013). Treatise on the Isoptera of the world. *Bull. Am. Mus. Nat. Hist.* 377, 1–2704.
15. Krishna, K. (1996). New fossil species of termites of the subfamily Nasutitermitinae from Dominican and Mexican amber (Isoptera, Termitidae). *Am. Mus. Novit.* 3176, 1–13.
16. Krishna, K., and Grimaldi, D. (2009). Diverse Rhinotermitidae and Termitidae (Isoptera) in Dominican amber. *Am. Mus. Novit.* 3640, 1–48.
17. Engel, M.S., Grimaldi, D.A., and Krishna, K. (2007). A synopsis of Baltic amber termites (Isoptera). *Stuttgarter Beitr. Naturk. Ser. B* 372, 1–20.
18. Engel, M.S. (2008). Two new termites in Baltic amber (Isoptera). *J. Kans. Entomol. Soc.* 81, 194–203.
19. Martínez-Delclòs, X., and Martinell, J. (1995). The oldest known record of social insects. *J. Paleontol.* 69, 594–599.
20. Genise, J.F., Bellosi, E.S., Melchor, R.N., and Cosarinsky, M.I. (2005). Comment—Advanced early Jurassic termite (Insecta: Isoptera) nests: evidence from the Clarens Formation in the Tuli Basin, southern Africa (Bordy et al., 2004). *Palaos* 20, 303–308.
21. Engel, M.S., Grimaldi, D.A., and Krishna, K. (2009). Termites (Isoptera): their phylogeny, classification, and rise to ecological dominance. *Am. Mus. Novit.* 3650, 1–27.
22. Ware, J.L., Grimaldi, D.A., and Engel, M.S. (2010). The effects of fossil placement and calibration on divergence times and rates: an example from the termites (Insecta: Isoptera). *Arthropod Struct. Dev.* 39, 204–219.
23. Grimaldi, D., Engel, M.S., and Nascimbene, P.C. (2002). Fossiliferous Cretaceous amber from Myanmar (Burma): Its rediscovery, biotic diversity, and paleontological significance. *Am. Mus. Novit.* 3361, 1–72.
24. Engel, M.S., Grimaldi, D.A., and Krishna, K. (2007). Primitive termites from the Early Cretaceous of Asia (Isoptera). *Stuttgarter Beitr. Naturk. Ser. B* 371, 1–32.
25. Emerson, A.E. (1933). A revision of the genera of fossil and Recent Termopsidae (Isoptera). *Univ. Calif. Publ. Entomol.* 6, 163–195.
26. Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q., and Li, X. (2012). Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretac. Res.* 37, 155–163.
27. Wappler, T., and Engel, M.S. (2006). A new record of *Mastotermes* from the Eocene of Germany (Isoptera: Mastotermitidae). *J. Paleontol.* 80, 380–385.
28. Engel, M.S., and Gross, M. (2009). A giant termite from the late Miocene of Styria, Austria (Isoptera). *Naturwissenschaften* 96, 289–295.
29. Engel, M.S., and Grimaldi, D.A. (2005). Primitive new ants in Cretaceous amber from Myanmar, New Jersey, and Canada (Hymenoptera: Formicidae). *Am. Mus. Novit.* 3485, 1–23.
30. Barden, P., and Grimaldi, D. (2012). Rediscovery of the bizarre Cretaceous ant *Haidomyrmex* Dlussky (Hymenoptera: Formicidae), with two new species. *Am. Mus. Novit.* 3755, 1–16.
31. Barden, P., and Grimaldi, D. (2013). A new genus of highly specialized ants in Cretaceous Burmese amber (Hymenoptera: Formicidae). *Zootaxa* 3681, 405–412.
32. Barden, P., and Grimaldi, D. (2014). A diverse ant fauna from the mid-Cretaceous of Myanmar (Hymenoptera: Formicidae). *PLoS ONE* 9, e93627.
33. Krishna, K., and Grimaldi, D. (2003). The first Cretaceous Rhinotermitidae (Isoptera): a new species, genus, and subfamily in Burmese amber. *Am. Mus. Novit.* 3390, 1–10.
34. Bugnion, E. (1922). La guerre des fourmis et des termites, la genèse des instincts expliquée par cette guerre. In *Le Monde Social des Fourmis, Volume III*, A. Forel, ed. (Geneva: Kundig), pp. 173–225.
35. Wheeler, W.M. (1936). Ecological interactions of Ponerinae and other ants to termites. *Proc. Am. Acad. Arts Sci.* 71, 159–243.
36. Mill, A.E. (1982). Faunal studies on termites (Isoptera) and observations on their ant predators (Hymenoptera: Formicidae) in the Amazon Basin. *Rev. Bras. Entomol.* 26, 253–260.
37. Gonçalves, T.T., Reis, R., Jr., DeSouza, O., and Ribeiro, S.P. (2005). Predation and interference competition between ants (Hymenoptera: Formicidae) and arboreal termites (Isoptera: Termitidae). *Sociobiology* 46, 409–419.
38. Lepage, M., Roisin, Y., and Pasteels, J.M. (1999). Community interactions between ants and arboreal-nest termites in New Guinea coconut plantations. *Insectes Soc.* 46, 126–130.
39. Pequeno, P.A.C., and Pantoja, P.O. (2012). Negative effects of *Azteca* ants on the distribution of the termite *Neocapritermes braziliensis* in Central Amazonia. *Sociobiology* 59, 1–10.
40. Grimaldi, D., and Agosti, D. (2000). A formicine in New Jersey Cretaceous amber (Hymenoptera: formicidae) and early evolution of the ants. *Proc. Natl. Acad. Sci. USA* 97, 13678–13683.
41. Brady, S.G., Schultz, T.R., Fisher, B.L., and Ward, P.S. (2006). Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proc. Natl. Acad. Sci. USA* 103, 18172–18177.
42. Moreau, C.S., Bell, C.D., Vila, R., Archibald, S.B., and Pierce, N.E. (2006). Phylogeny of the ants: diversification in the age of angiosperms. *Science* 312, 101–104.
43. Moreau, C.S., and Bell, C.D. (2013). Testing the museum versus cradle tropical biological diversity hypothesis: phylogeny, diversification, and ancestral biogeographic range evolution of the ants. *Evolution* 67, 2240–2257.
44. Goloboff, P.A., Farris, J.S., and Nixon, K.C. (2008). TNT, a free program for phylogenetic analysis. *Cladistics* 24, 774–786.

Current Biology, Volume 26

Supplemental Information

**Morphologically Specialized Termite Castes
and Advanced Sociality in the Early Cretaceous**

Michael S. Engel, Phillip Barden, Mark L. Riccio, and David A. Grimaldi

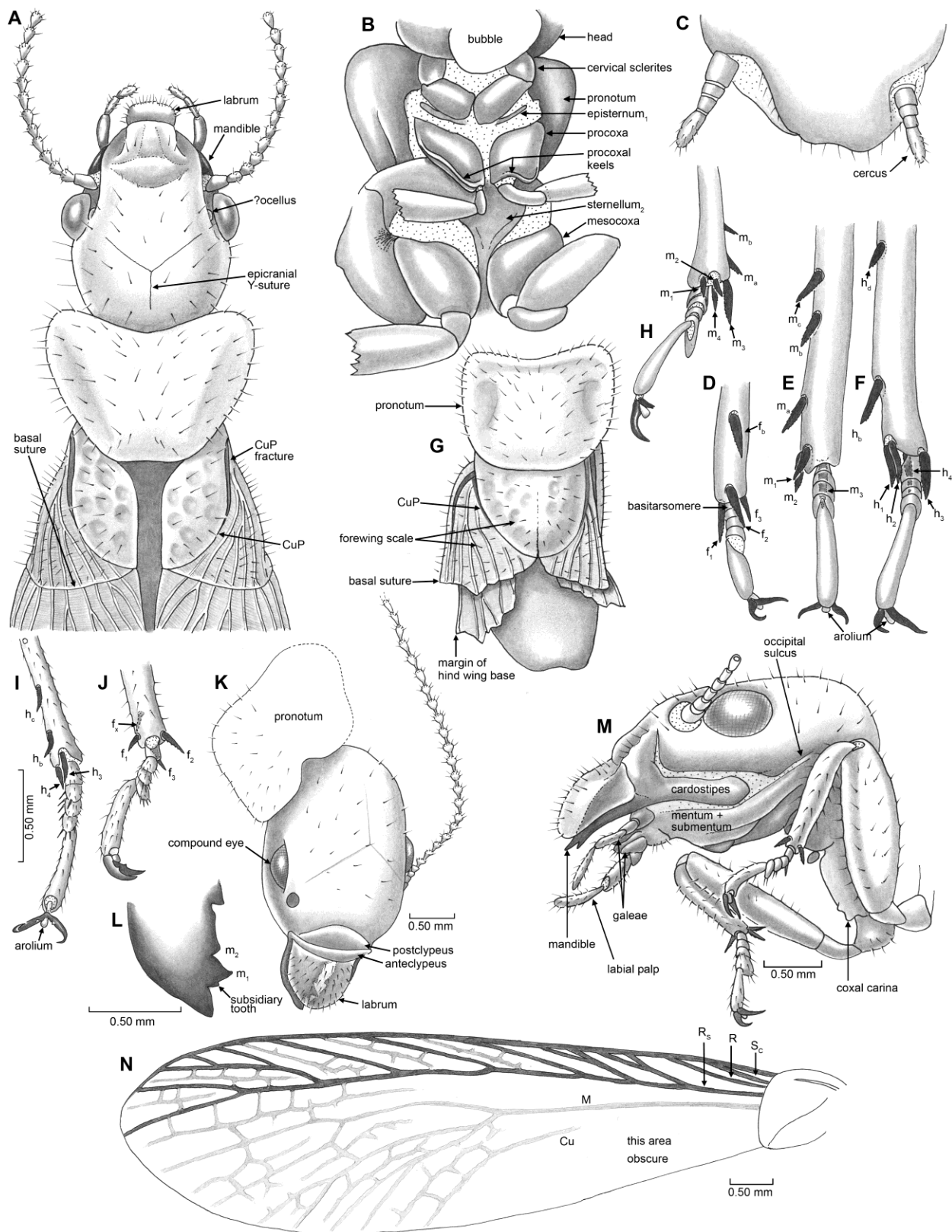


Figure S1. Alate holotype of *Krishnatermes yoddha* gen. et sp. nov., JZC Bu1839a (A–F); dealate of *Krishnatermes* sp. JZC Bu156 (G–H); alate paratypes of *Krishnatermes yoddha*, JZC Bu1839b. Related to Figs. 1, 3. (A) Dorsal view of anterior portion of body. (B) Ventral view of thorax. (C) Apex of abdomen, dorsal view. (D) Protibial apex, protarsus, and propretarsus, lateral view (as preserved). Nomenclature of spination follows that established elsewhere[14]. (E) Mesotibia, mesotarsus, and mesopretarsus, dorsal view (as preserved). (F) Metatibia, metatarsus, and metapretarsus, dorsal view (as preserved). (G) Dorsal view of thorax, showing bases of fore and hind wings (wing scales). (H) Midleg, showing spination. (I) Metatibia, metatarsus, and metapretarsus, ventral view. (J) Protibial apex, protarsus, and propretarsus, lateral view. (K) Oblique dorsal view of head and pronotum. The labrum is transparent, allowing observation of the mandibles. (L) Right mandible. (M) Head and forelegs, oblique ventrolateral view. (N) Forewing.

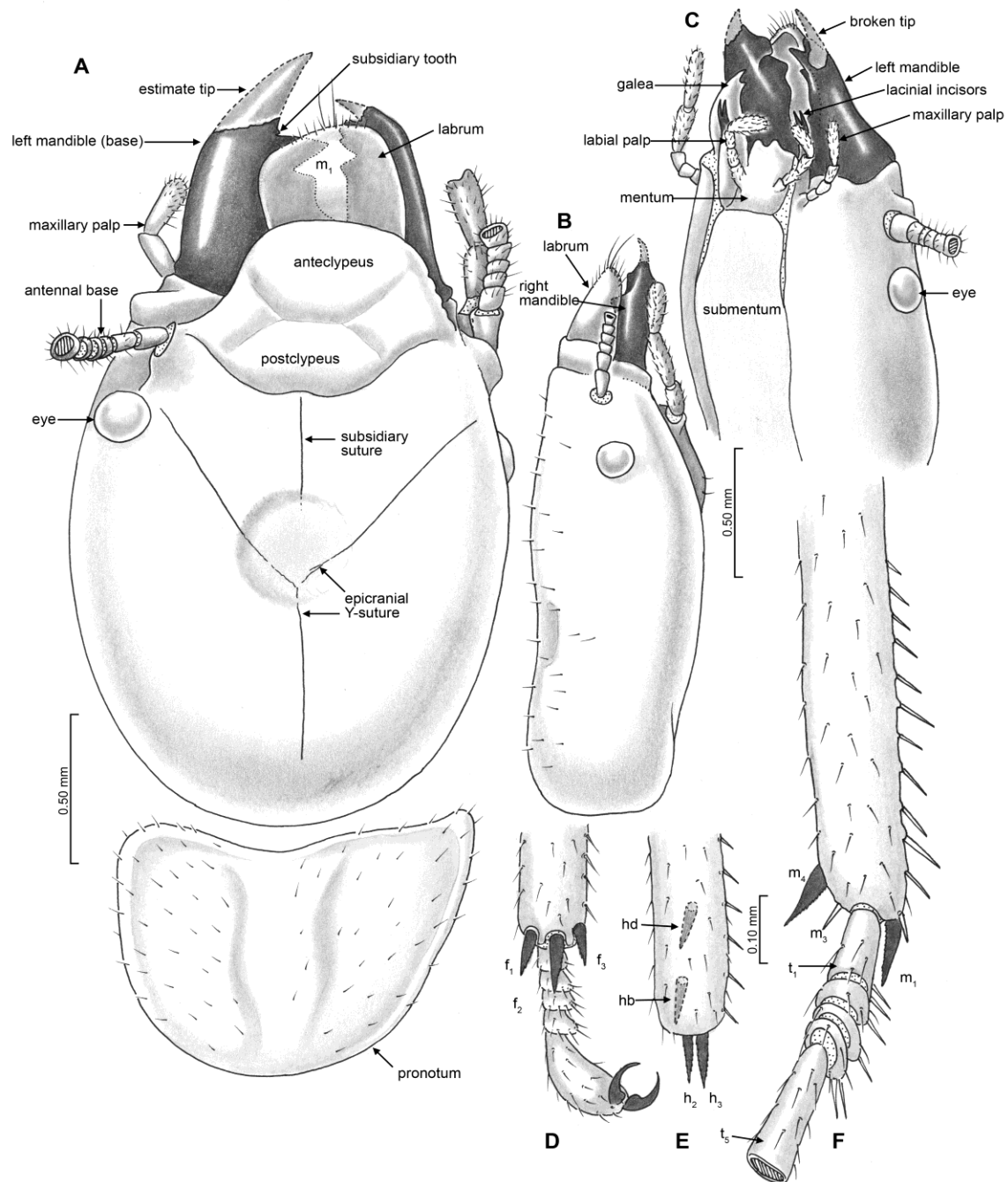


Figure S2. Paratype soldier of *Krishnatermes yoddha* gen. et sp. nov. (JZC Bu183). Related to Figures 1, 3. (A) Head and thorax in dorsal view. Tips of mandibles were broken off, with reconstructed tips shown here. (B) Head in full lateral view, showing its flatness. (C) Head, oblique ventral view of anterior portion. (D) Protibial apex, protarsus, and propretarsus (as preserved), ventral view. (E) Metatibial apex (as preserved). (F) Mesotibia and mesotarsus (as preserved).

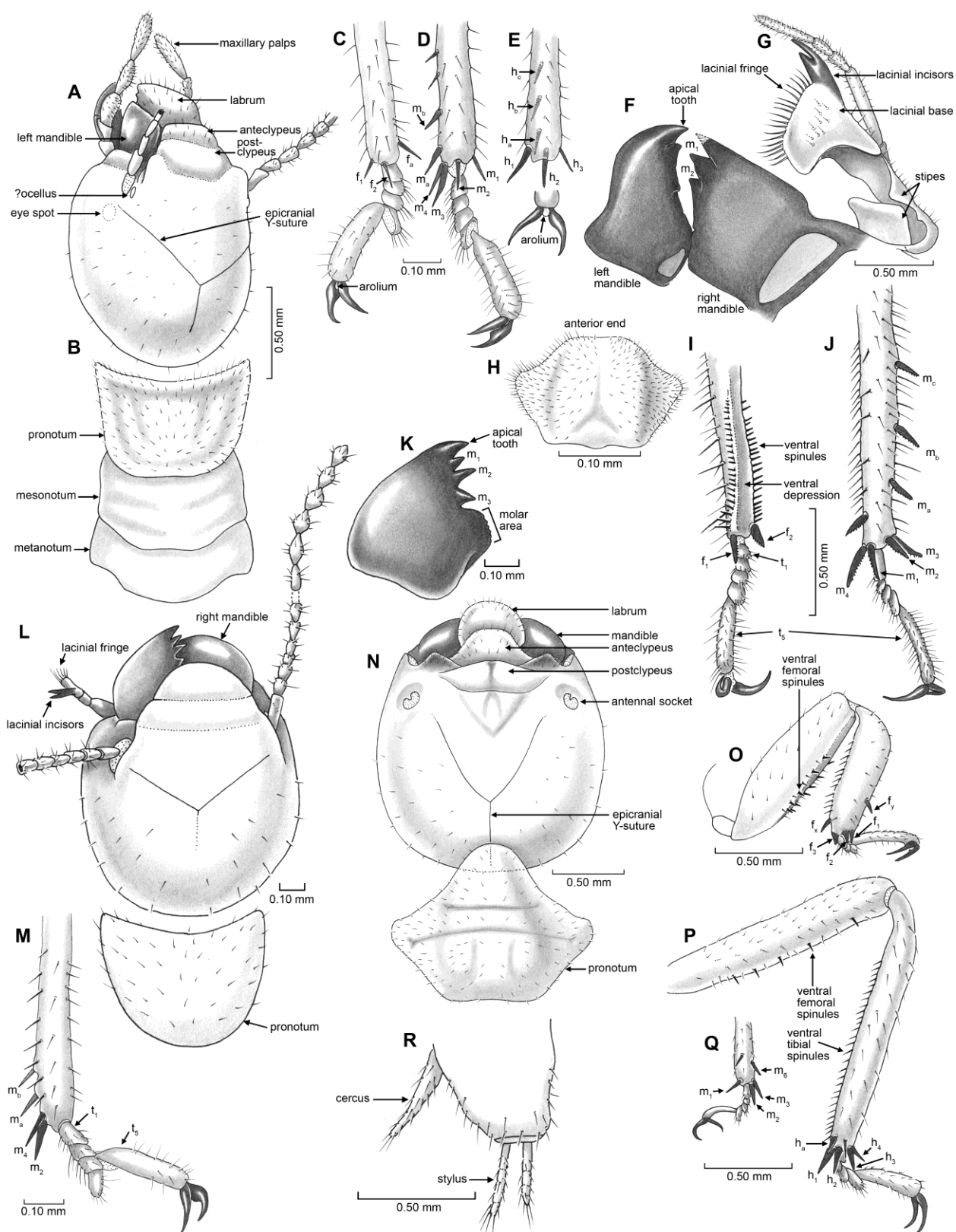


Figure S3. Workers/pseudergates of *Meiatermes*-grade termites. Related to Figures 2, 3. A-E: Morphospecies 1 (JZC Bu235). (A) Head, dorsal view. (B) Thoracic nota, dorsal view. (C) Protibia, protarsus, and propretarsus, lateral view. (D) Mesotibia, mesotarsus, and mesopretarsus, lateral view. (E) Metatibial apex and metapretarsus, dorsal view. **F- J Morphospecies 2 (AMNH Bu-SD001).** (F) Mandibles. (G) Left maxilla. (H) Pronotum. (I) Protibia, protarsus, and propretarsus, ventrolateral view. (J) Mesotibia, mesotarsus, and mesopretarsus, dorsal view. **K-M: Morphospecies 3 (TJ Bu002).** (K) Detail of left mandible, showing dentition. The base of the mandible is visible through the translucent labrum. (L) Dorsal views of head and pronotum. (M) Detail of midleg, showing spination of tibia and segmentation of tarsus. **N-R: Morphospecies 4 (AND Bu935a).** (N) Dorsal view of head and pronotum. (O) Entire foreleg, mesal view, showing stout profemur and protibia, spination, and tarsal segmentation. (P) Entire hind leg, mesal view, showing metafemur and metatibia, spination, and tarsal segmentation. (Q) Apex of mesotibia and all tarsomeres of midleg. (R) Apex of abdomen showing both styli and one of the cerci.

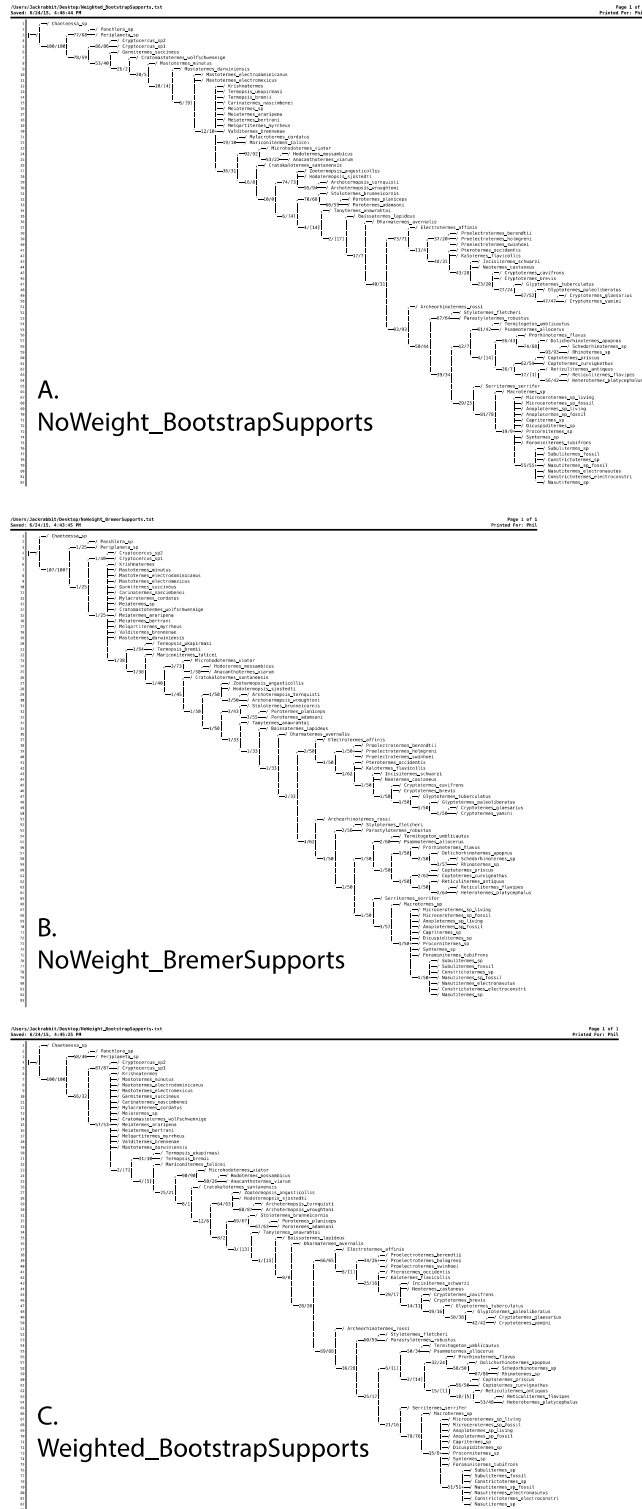


Figure S4. Strict consensus cladograms of fossil and living basal Isoptera. Related to Figure 4. Details of characters and analysis provided in Supplemental Information. (A) Unweighted, showing bootstrap support values. (B) Unweighted, showing Bremer Support values. (C) Weighted, with bootstrap values.

Table S1. Linear measurements (mm) and meristic values of Burmese amber termite castes. Related to Figures 1-4. *Designations:* L = Length; W = Width; PN = Pronotum; FW = Forewing; No. Ant. = Number of antennomeres (>X indicates apical antennomeres are missing; =X indicates all antennomeres are intact; ≥X indicates equivocal).

Specimen No.-caste	Body L	Head L/W	PN L/W	FW L	No. Ant.	Species
JZC Bu1839a-alate	10.04	2.24/2.05	1.58/2.00	11.39	>16	<i>yoddha</i>
JZC Bu1839b-alate	—	—/—	—/—	—	=18	<i>yoddha</i>
AND Bu942a-worker	4.09	1.23/1.10	0.50/0.86	—	=14	<i>yoddha</i>
AND Bu942b-worker	3.51	1.06/0.84	0.44/0.59	—	=15	<i>yoddha</i>
JZC Bu183-soldier	5.20	2.38/1.35	0.80/1.02	—	>6	<i>yoddha</i>
JZC Bu155-alate	10.07	2.65/—	1.25/1.52	9.93	=24	sp.
JZC Bu156-dealate	8.70	2.19/1.37	1.06/1.29	—**	=21	sp.
JZC Bu235-worker*	4.70	1.68/—	0.64/0.87	—	≥20	1
AMNH Bu-SD001-worker	>9.00	1.54/—	1.54/—	—	>21	2
AMNH Bu-TJ002-worker	<5.51	1.29/1.00	0.54/0.72	—	>13	3
AND Bu935a-worker	~7.15	1.93/1.80	1.04/1.30	—	=17	4
AND Bu935b-worker	—	—/—	—/—	—	=18	4
AND Bu886-worker	—**	2.61/—	—/2.07	—	>16	?
AMNH BuTJ001-soldier	19.00	7.60/3.40	3.70/3.60	—	>10	<i>rex</i>

* “Worker” designation also applies to any possible pseudergates.

** These measurements missing because either inapplicable (e.g., wings) or preservation does not allow measurement.

Table S2. Linear measurements (mm) of each caste of representative species of living and fossil termites. Related to Figures 1-4, main text.

	Body length	Wing length	Head length	Head width	Pronotal width
<i>Mastotermes darwiniensis</i> (Recent, Australia)					
alate	14.01	24.25	2.33	2.94	3.47
soldier	12.29	n.a.	2.84	3.23	3.43
worker	11.40	n.a.	2.07	2.71	2.73
<i>Mastotermes electrodanicus</i> (Miocene, Dominican Republic)					
alate	14.75	20.70	2.75	—	2.80
soldier	10.63	n.a.	3.52	—	2.12
worker	8.41	n.a.	2.71	—	1.94
<i>Krishnatermes yoddha</i> (mid-Cretaceous, Burma)					
alate	10.04	11.39	2.24	—	2.00
soldier	5.20	n.a.	2.38	1.35	1.02
worker	4.15	n.a.	0.95	1.16	0.75
<i>Microhodotermes viator</i> (Recent, Africa)					
alate	14.01	24.75	2.29	2.41	2.11
soldier	8.36	n.a.	2.61	2.25	1.68
worker	8.77	n.a.	2.30	2.18	1.53
<i>Hodotermes mossambicus</i> (Recent, Africa)					
alate	15.17	21.0	2.25	2.70	2.56
soldier	12.94	n.a.	3.68	3.81	2.31
worker	8.74	n.a.	2.0	2.0	1.62
<i>Archotermopsis wroughtoni</i> (Recent, Himalayan)					
alate	12.50	—	2.17	2.42	2.21
soldier	16.25	n.a.	4.80	4.40	3.22
worker	11.65	n.a.	2.16	2.38	1.88
<i>Zootermopsis angusticollis</i> (Recent, western North America)					
alate	13.04	18.75	2.41	2.53	2.13
soldier	13.50	n.a.	4.40	3.98	2.70
worker	12.53	n.a.	2.24	2.60	2.22
<i>Stolotermes victoriensis</i> (Recent, Australia)					
alate	5.83	8.20	1.27	0.92	0.77
soldier	5.45	n.a.	1.80	1.17	0.61
worker	4.76	n.a.	0.78	0.93	0.64
<i>Porotermes adamsoni</i> (Recent, Australia)					
alate	9.32	13.40	1.63	1.60	1.54
soldier	11.81	n.a.	4.00	3.13	2.26
worker	9.01	n.a.	1.98	2.05	1.62
<i>Kalotermes flavicollis</i> (Recent, Palearctic)					
alate	7.54	—	1.06	1.08	1.41
soldier	6.97	n.a.	1.99	1.29	1.47
worker	6.55	n.a.	1.26	1.08	1.37
<i>Stylotermes fletcheri</i> (Recent, India)					
alate	7.19	—	1.37	1.19	1.06
soldier	6.71	n.a.	2.53	1.56	1.38
worker	4.39	n.a.	1.07	1.00	0.82
<i>Reticulitermes flavipes</i> (Recent, Nearctic)					
alate	6.02	7.30	1.28	1.11	0.94
soldier	5.39	n.a.	2.06	1.24	0.94
worker	4.93	n.a.	1.08	0.97	0.67
<i>Coptotermes priscus</i> (Miocene, Dominican Republic)					
alate	7.50	7.75	1.30	—	1.02
soldier	3.53	n.a.	1.21	—	0.46

worker	3.26	n.a.	0.82	—	0.42
--------	------	------	------	---	------

Table S3. Proportions of total body length of worker and soldier castes relative to that of alates. Related to Figure 3, main text.

Species	Worker	Soldier
† <i>Krishnatermes yoddha</i>	0.41	0.51
Mastotermitidae		
<i>Mastotermes darwiniensis</i>	0.81	0.87
† <i>Mastotermes electrodominicus</i>	0.56	0.71
Hodotermitidae		
<i>Microhodotermes viator</i>	0.77	0.73
<i>Hodotermes mossambicus</i>	0.57	0.85
Archotermopsidae		
<i>Archotermopsis wroughtoni</i>	0.93	1.30
<i>Zootermopsis angusticollis</i>	0.96	1.03
Stolotermitidae		
<i>Stolotermes victoriensis</i>	0.81	0.93
<i>Porotermes adamsoni</i>	0.96	1.26
Kalotermitidae		
<i>Kalotermes flavicollis</i>	0.87	0.92
Stylotermitidae		
<i>Stylotermes fletcheri</i>	0.61	0.93
Rhinotermitidae		
<i>Reticulitermes flavipes</i>	0.81	0.89
† <i>Coptotermes priscus</i>	0.43	0.47

Supplemental Experimental Procedures

All of the termite specimens were assembled by screening thousands of pieces of Burmese amber containing inclusions. After trimming and polishing of the amber pieces, diagnostic details of the head (including mandibular dentition), prothorax, and legs were observed, measured and photographed. Morphological terminology and format used in the descriptions follows that employed elsewhere for basal termite lineages[S1-S3]. The higher classification adopted here is that supported by recent comprehensive phylogenetic analyses of living and fossil termites[S6, S7], and presented in the revised classification of the *Treatise on the Isoptera of the World*[S8].

Infraorder Isoptera Brullé, 1832

‘*Meiatermes* Grade’ (*sensu* Engel et al., 2007)

Krishnatermes Engel, Barden, et Grimaldi, gen. nov.

ZooBank LSID urn:lsid:zoobank.org:act:FE022235-B2F0-42D8-A3E8-529F4D23B0CC

Type species

Krishnatermes yoddha Engel, Barden, et Grimaldi, sp. nov.

Diagnosis

As for the species, by monotypy.

Comments

As noted in the main text, the group occupies an intermediate phylogenetic position between the more basal Mastotermitidae and the clade Euisoptera as defined in prior cladistic studies. Primitive features shared symplesiomorphically with Mastotermitidae include the presence of well-developed, serrated, asymmetrical tibial spines (also shared with roaches); a 3-4-4 tibial spur formula, fully pentamerous tarsi (i.e., with five full tarsomeres); a large pronotum that is apicolaterally produced; a large forewing scale, with all primary veins originating within the scale, and with distinct reticulated network developed between the primary veins within the scale; the forewing with multiple, elongate R veins, encompassed within a uniformly wide radial field; and the absence of the hind wing scale (in the dealate specimen JZC Bu156, diagnosed below as a species separate from the type species, *K. yoddha*), the hind wings showing a jagged edge resulting from chewing with the mandibles to remove them, in contrast to the smoothly cleaved edge of the forewing scale in which wings are shed along a suture or line of dehiscence — in the alates the developed forewing scale suture can be observed clearly. An anal lobe is absent, but the venation is plesiomorphically similar to Masotermitidae, with branching of Rs noticeably less developed than in mastotermitids; in this regard venation is more similar to primitive euisopteran families such as Archotermopsidae and Hodotermitidae (*Krishnatermes* has fewer Rs branches than these latter lineages). Derived features demonstrating the closer relationship between *Krishnatermes* and Euisoptera include a small procoxal keel; loss of the hind wing anal lobe; and absence of the occipital sulcus. The presence of a subsidiary tooth is similar to the primitive euisopteran family Archotermopsidae, a group today relict in western North America and isolated pockets in far eastern Palearctic Asia and northern localities in the Oriental Region[S8]. The presence of this subsidiary tooth is likely primitive in these two clades, as are their pentamerous tarsi and full forewing venation. Archotermopsidae have a derived form of soldier in which the head has become greatly enlarged, broadened, and somewhat dorsoventrally compressed, often with well-developed temples and posterior angles, and the mandibles are greatly developed and elongate, projecting well forward in front of the head, while the soldier of *Krishnatermes* has a more typical form of head capsule. The soldier of *Krishnatermes* has mandibles more prominent than those of their corresponding worker or reproductive castes, but they do not approximate anything analogous to the condition observed in archotermopsids. It is difficult to detect in the available specimens, but there appears to be no ventral cervical sclerites, which would be in accordance with the phylogenetic placement of the group near Euisoptera, although the genus routinely is nested among the basal *Meiatermes*-grade of Cretaceous genera.

Krishnatermes yoddha Engel, Barden, et Grimaldi, sp. nov.

(Figs. 1A, B, D-F; 2A, J; S3-5)

ZooBank LSID urn:lsid:zoobank.org:act:0DA40661-D141-40BA-A3A4-B8A55F85E4C8

Type series

Holotype imago, JZC-Bu1839a; paratype alate (Bu1839b), same piece as holotype; paratype soldier, JZC-Bu183; paratype workers, AND-Bu942a, b. All in Early Cretaceous amber from Kachin Province, northern Myanmar.

Description

Integument dark brown throughout; sparsely pubescent. *Imago*. Head robust, longer than wide, posterior border broadly and gently rounded, lateral borders parallel-sided; right mandible (as seen through cleared postclypeus and labrum) with at least two marginal teeth, each tooth about as long as apical tooth, subsidiary tooth present, mandibles not projecting beyond apex of labrum; labrum subquadrate; postclypeus transverse, much wider than long, relatively flat; antenna moniliform, with 18 articles; compound eyes without anterior emargination, circular, separated from lower margin of head by slightly less than eye diameter, separated from posterior border of head by about eye diameter; ocelli ('ocelloids') absent; fontanelle absent; Y-shaped ecdysial cleavage scar present; ventral cervical sclerite absent. Pronotum large, flat, and broad, broader than head; anterior border concave, with rounded apicolateral angles produced; lateral borders slightly convergent posteriorly, weakly convex, with posterior corners gently rounded inward; posterior border relatively straight; forming a moderately trapezoidal shape. Procoxa with small ventral keel; femora apparently not carinate or keeled ventrally; all tarsi completely pentamerous; tibiae with three outer spines along length, tibial spur formula 3-4-4, spurs of all legs serrated and asymmetrical; arolium present but small, pretarsal ungues (claws) simple. Wings largely hyaline, membrane reticulate, not pimplate or nodulate. Forewing (veins best seen in specimens JZC Bu1839) veins Sc, R, and Rs more strongly pigmented than remainder of veins; forewing scale large, well overlapping hind wing base, scale longer than medial length of pronotum, humeral margin convex, basal suture convex; all major longitudinal veins originating inside wing scale, with faint reticulations posterior to M and CuA within scale; Sc long, simple, terminating along anterior wing margin at about one-third wing length; R₁ and R₂ elongate, R₁ simple over length, terminating in apical fifth of wing length, R₂ branching dichotomously apically and terminating just anterior to Rs tip near wing apex; radial field not greatly expanded apically, comparatively uniform in width across wing length; Rs long, simple over most of length, branching near wing apex, terminating just anterior to wing apex; wing apex encompassed by narrow space between Rs and anterior-most branch of M; M long, branching at about wing midlength, anterior-most branch terminating immediately posterior to wing apex, medial field broad, encompassing apical third of posterior wing margin; CuA branching within forewing scale, posterior-most branches simple, remaining branches with significant subsidiary branching, CuA field encompassing most of posterior wing margin. Hind wing without basal suture, wings torn rather than shed (evidenced in dealate where forewings are shed at smooth suture line and hind wings are jaggedly torn, a condition found today only within *Mastotermes*); without anal lobe. Abdomen relatively narrow, cylindrical, sides generally parallel; cerci well developed, three-segmented.

Integument brown, with generally sparsely scattered, fine, erect to suberect setae; head and pronotum with scattered, erect, simple setae, those on lateral margins of pronotum slightly longer and more prominent; setae of remainder of thorax and abdomen sparse, erect, and fine, those of abdomen somewhat longer than those of thorax; legs with similarly fine, sparse, erect, long setae; forewing scales almost devoid of setae, where present setae short, fine (not bristly), suberect; cerci with several, short, simple, apically-directed setae.

Relatively large termites; total body length ca. 10.04 mm; head longer than wide, length of head to apex of labrum 2.24 mm, width across compound eyes 2.05, width posterior to compound eyes 1.8 mm; postclypeus median length 0.23 mm; labrum slightly wider than long, length 0.39 mm, width 0.43 mm; compound eye diameter 0.55 mm; median length of pronotum 1.58 mm; maximum width of pronotum (across apicolateral angles) 2.00 mm, depth of anterior concavity 0.23 mm; length of metatibia 1.8 mm; length of forewing scale 1.5 mm; forewing length (including scale) ca. 11.39 mm, maximum width 3.5 mm.

Worker. As described for the imago except in typical caste differences and as follows: compound eyes present but small (diameter approximately equal to that of antennal socket), without facets; Y-shaped ecdysial cleavage scar present; mandibles with dentition as in imago, mandibles not extending beyond labral apex (fortunately, labral integument is cleared through preservation permitting a clear view of the dentition); postclypeus wider than long, but not as dramatically as in imago, surface slightly convex; integument light brown, almost yellowish ventrally and on legs, pronotum smaller than in imago but still broader than head and with most of surface flattened, with anterior border upturned and thickened, apicolateral corners less strongly produced, apicolateral angles more acutely rounded, lateral borders more straight and weakly convergent posteriorly; tibial spurs 3-4-4, without most spines present in imago except three spines on inner surface of mesotibia; tarsi pentamerous; 3 cercomeres present.

Total body length ca. 3.80 mm; head longer than wide, length of head to apex of labrum 1.8 mm, maximum width 0.97 mm; postclypeus median length 0.25 mm; labrum length 0.39 mm; median length of pronotum 0.47 mm; maximum width of pronotum (across apicolateral angles) 0.72 mm; length of metatibia 1.3 mm.

Soldier. As described for the imago except in typical caste differences and as follows: head very darkly sclerotized, much more so than in worker or imago, integument throughout relatively smooth to faintly imbricate, with very sparsely scattered, fine, short, erect to suberect setae, except head with virtually no setae; head more developed than in worker or imago (typical for this caste) relative to pronotum, slightly wider than pronotum, head

more dorsoventrally compressed than in worker or imago; postclypeus flat (as in imago); compound eye reduced, diameter 0.19 mm, circular, separated from lower border of head by slightly more than twice eye diameter, separated from posterior border of head by more than six times eye diameter, eye lacking facets; mandibles elongate, extending when complete well beyond apex of labrum (mandibles are cleaved broadly and shortly beyond labral apex, indicating that a significant portion is missing, but no additional marginal teeth would have been present between apical tooth and first preserved marginal tooth as evidenced by presence of subsidiary tooth, which is present only along first marginal tooth in some basal termite lineages[S8]); subsidiary tooth present, two marginal teeth present, first apparently longer than second. Pronotum similar to that of worker, i.e., anteriorly rimmed, with apicolateral lobes more acute than in imago or worker, but smaller than in imago. Legs as in worker (*vide supra*).

Soldier partially preserved, with abdomen largely crumpled and apparently small; head longer than wide, length of head to apex of labrum 2.3 mm, maximum width 1.4 mm; labrum length 0.39 mm; median length of pronotum 0.70 mm; maximum width of pronotum (across apicolateral angles) 1.1 mm; length of metatibia 1.1 mm.

***Krishnatermes* sp.**

(Figs. 1C; S1G)

Material

Dealate, JZC Bu156, in mid-Cretaceous amber from Myanmar.

Description

A species distinguished from *K. yoddha* by the smaller body size (8.70 mm, vs. 10.04–10.07 mm); antenna with 21 articles (vs. 18); pronotum almost square (vs. trapezoidal); mesotibia with four (vs. three) apical spurs, two (m_a , m_b) (vs. three: m_a , m_b , m_c) mid-lateral spurs; forewing scale with costal fracture well developed (vs. not).

Comments

This species is not being named in lieu of its wings, wing structure providing many diagnostic characters in fossil termites (particularly for the many lithified taxa). Other than the diagnostic differences between this dealate and *K. yoddha*, listed above, this specimen is very similar and is therefore placed in *Krishnatermes* pending discovery of specimens with wings.

***Gigantotermes rex* Engel, Barden, et Grimaldi, gen. et sp. nov.**

(Figs. 1G [including movie of CT scan], Fig. 2)

ZooBank LSID (generic name): urn:lsid:zoobank.org:act:052379CA-5B56-4038-BA07-08C6196C432D

ZooBank LSID (specific epithet): urn:lsid:zoobank.org:act:7518E6CC-3FBE-4F0D-9E53-5F4915992348

Type species

Gigantotermes rex Engel, Barden, et Grimaldi, sp. nov.

Holotype

Soldier, AMNH Bu-TJ001, in mid-Cretaceous amber from Myanmar.

Description

Soldier. Among the largest known soldier termites, body length 19.0 mm from tip of mandible to apex of abdomen, but tip of abdomen is slightly decayed so total length slightly greater (otherwise, specimen is virtually complete; specimen in a dark piece of lens-shaped Burmese amber 25 mm dia. x 9 mm thick, somewhat occluded with fine particles and bubbles, fractures, flow lines and about 20 frass pellets; no other arthropod inclusions are visible).

Head massive, width 3.4 mm, length 5.65 mm from anterior margin of labrum to posterior margin of head, 7.60 mm total (including mandibles); head capsule virtually rectangular, much longer than wide; lateral margins virtually parallel; posterior border inserted deep into concavity of anterior margin of pronotum. Mandibles very heavily sclerotized, completely prognathous, dentate. Left mandible overlapping right one; both approximately equal in size and length. Dentition visible on left mandible only; apex of left mandible slender, very pointed and hooked, with triangular median tooth and shallow, cutting basal tooth near margin of labrum (compare with *A. wroughtoni*[S9]). Left mandible length 2.90 mm, greatest exposed width 1.05 mm. Labrum small, rounded lobe 1.15 mm W x 0.60 mm L. Anteclypeus shallow, lenticular, 1.20 mm W, 0.50 mm L; postclypeus somewhat triangular, 1.2 mm W, 0.4 mm L. Clypeus flanked by pair of small, shallow lobes, lateral to each a ledge-like lobe overhanging insertion of antenna. Anterior to antennal insertion a projecting, triangular, pointed lobe 0.5 mm L. Both antennae missing apical flagellomeres; antenna with >10 antennomeres. Compound eye reduced to small, pale, facet-less, pale spot posterior and slightly lateral to antennal insertion. Head capsule with a faint Y-shaped epicranial ecdysial cleavage scar. Maxillary palps with 4 palpomeres, basal palpomere shortest, penultimate one longest; labial palps with 3 palpomeres, basal palpomere shortest, apical one longest. Galea, cardo, stipes and other mouthparts not visible under light microscopy. Cervical sclerites very large, robust, 2-segmented (an inner cervical sclerite and lateral cervical sclerite on each side), V-shaped.

Pronotum massive, with deeply concave anterior margin producing long anterolateral points; lateral margins nearly parallel (very slightly concave), posterior margin concave. Pronotal dimensions: median length 2.3 mm; greatest length 3.7 mm (laterally, including anterolateral projections); greatest width 3.6 mm (across anterior portion). Median portion of pronotum raised longitudinally, depressed lateral to this. Mesonotum and metanotum largely transverse, median lengths 0.95 and 1.10 mm, respectively; greatest widths 3.15 and 2.95 mm respectively. Meso- and metanotum each with small posterolateral lobe. Legs with tarsi wholly pentamerous (i.e., no cryptic tarsomere as in some Archotermopsidae), tibiae spinose, tibial spines slightly asymmetrical, with finely serrate margin; arolium absent between pretarsal claws. Foreleg smallest, procoxa small (no evidence of keel), protibia slender, ca. 1.2 mm L, protarsus 1.0 mm, pretarsal claws 0.20 mm; profemur thick, stout. Mesocoxa and mesofemur not visible; mesotibia fairly stout, 1.9 mm L, mesotarsus 0.95 mm L, pretarsal claws small. Hind leg largest of legs, metafemur extremely stout, ≥ 1.2 mm thick; metatibia 1.8 mm L, with 3 spines, metatarsus long, 2.0 mm L, metapretarsal claw very large (0.55 mm L). Tibial spines (terminology as employed elsewhere[S8]): protibia with f_1 , f_3 , plus more proximal one (x) and mid-dorsal one (y); mesotibia with 6 spines m_1 , m_2 , m_3 , plus row of 3 ventral spines (m_a , m_b , m_c); metatibia with 3 spines h_1 , h_2 , h_4 .

Ten abdominal terga visible dorsally, lengths along midline, from TI–TX (in mm): 0.40, 0.70, 0.70, 0.75, 0.70, 0.70, 0.70, 0.50, 0.30, 0.20. Terga II, III, and IV with shallow, incompletely transverse sulcus on anterior half. Total length of abdomen 5.6 mm. Styli not observed, but cerci slender, short (0.55 mm), and with 8 cercomeres, basal two cercomeres longest. Sterna well developed.

Worker morphospecies 1

(Figs. 2; S3)

Referred Material

Worker, JZC Bu235, in mid-Cretaceous amber from Myanmar.

Distinguishing Features

Small bodied worker, body length 4.70 mm. Head with epicranial Y-shaped scar, sparse pilosity, head length 1.68 mm; anteclypeus and postclypeus well defined, labrum slightly pilose; mandibles (e.g., dentition) not observable; compound eye highly vestigial (present only as a light spot; no lens-like structure). Pronotum with fine, sparse pilosity; anterior margin slightly concave, with moderate anterolateral angles, lateral margins virtually parallel; pronotal length/width 0.64/0.87 mm. Antenna with ≥ 20 articles. Tibial spines at best with very fine, very sparse serrations, barely discernable at 150X; arolium present but small; pretarsal claws without subapical tooth. Protibia with three apical spines (f_1 , f_2 , f_a), mesotibia with 4 apical and 2 subapical spines (m_1 , m_2 , m_3 , m_4 , m_a , m_b), metatibia with 3 apical and 3 subapical (h_1 , h_2 , h_3 , h_a , h_b , h_c). Tibiae without ventrolateral longitudinal rows of spinules. Tarsi fully pentamerous, basitarsomere short.

Worker morphospecies 2

(Figs. 2; S3)

Referred Material

Worker, AMNH Bu-SD001, in mid-Cretaceous amber from Myanmar.

Distinguishing Features

Large bodied worker, body length >9.00 mm. Head with epicranial Y-shaped scar, sparse pilosity, head length 1.54 mm; anteclypeus and postclypeus well defined, labrum slightly pilose. Mandibles and maxilla very exposed, all details observable: right mandible with 3 triangular teeth (1 apical [tip broken], 2 marginal), left mandible with apical tooth slightly hooked, M1 and M2 separated by very fine notch, incisor-like; no subsidiary tooth. Maxilla with 4 palpomeres; lacinia with two sclerotized incisors, one of them subapical (not both apical); lacinia lobe-like with fringe of setae on distal margin, sparse setae on outer surface. Compound eye entirely absent. Antenna with >21 articles. Pronotum roughly hexagonal in shape, with short anterior and posterior margins, lateral margins produced into a middle point/lobe; central portion of pronotum raised; pronotum with short pilosity, denser laterally; pronotal length 1.54 mm. Tibiae with stout, coarsely serrated spines; protibia with two apical spines (f_1 , f_2), mesotibia with four apical spines (m_1 , m_2 , m_3 , m_4) and four longitudinal/preapical spines (m_a , m_b , m_c , plus subsidiary dorsolateral spine). Tibiae with two ventrolateral, parallel rows of stout, short spinule-like setae. Tarsi fully pentamerous, basitarsomere short; pretarsal claws well developed, without preapical tooth; arolium either highly reduced or absent.

Worker morphospecies 3

(Figs. 2; S3)

Referred Material

Worker, TJ Bu002, in mid-Cretaceous amber from Myanmar.

Distinguishing Features

Moderate sized worker, body length <5.51 mm. Head oval in dorsal view, head length/width 1.29/1.00 mm; head dorsally with epicranial Y-shaped scar (arms best developed, median scar barely developed). Compound eye completely absent. Anteclypeus and postclypeus barely differentiated, if at all; labrum small, almost hemispherical in shape. Left maxilla exposed, showing fringe of setae on distal margin; pair of sclerotized lacinial incisors (appear to both be apical; in not one is only slightly subapical). Left mandible with dentition fully visible: teeth narrow, pointed, apical tooth slightly curved, M1 is smallest tooth, M2 longest marginal tooth (slender), M3 pointed slightly basad; molar area well developed. Antenna with >13 articles. Pronotum slightly U-shaped, with anterior margin concave and posterior margin convex; with very sparse pilosity; frontolateral margins slightly pointed; pronotal length/width 0.54/0.72 mm. Tibial spurs slender, if serrations present they are very fine and sparse; if asymmetrical, then barely so. Mesotibia with two apical (m_2 , m_4) and two subapical (m_a , m_b) spines. Tarsi fully pentamerous, with tarsomere four projecting beneath distitarsomere; arolium either very small or absent; pretarsal claw without preapical tooth.

Comments

This is an oval, flattened piece of clear yellow amber 24 mm length x 15 mm width x 2.5 mm thick, which also contains a worker of the ant *Gerontoformica gracilis*. The piece has two fine layers in it, each with fine bubbles; the ant and termite lie on one layer. There are no other arthropod inclusions in the piece besides the ant and termite. The termite is 6.5 mm in length, but the ventral portion of the body is largely decayed away and the abdominal tergites are very separated, indicating that the abdomen is unnaturally distended. The head capsule is largely preserved; a portion of the right antenna is disarticulated and distant from the intact basal segments. The right fore legs and a very small portion of the left one are partially preserved; a portion of the right mid leg is preserved (distal half of femur, all of tibiae and tarsi), and only small fragments of the hind leg. The end of the termite lies 5.5 mm away from the head of the ant, which is facing toward the termite. The ant is better preserved than the termite, with all appendages complete and articulated; the distal portion of the ant's metasoma is decayed, with a long sting protruding through some frothy material. A pair of apical lacinial incisors (vs. one tooth being preapical) is a feature of Hodotermitidae s.str., though the leg and mandible structure indicate otherwise. The formula and structure of the tibial spines indicate that this species is more derived than the other four species for which workers are known.

Worker morphospecies 4

(Figs. 2; S3)

Referred Material

Worker, AND Bu935a, b, c, in mid-Cretaceous amber from Myanmar.

Distinguishing Features

Worker of average size, body length 7.15 mm (based on Bu935a). Head broadly oval dorsally, almost circular; head length/width 1.93/1.80 mm. Head with well-developed epicranial scar; dorsum with very sparse pilosity. Compound eye completely absent. Postclypeus and anteclypeus entirely differentiated; postclypeus shallow, with slight median trough, devoid of setae; anteclypeus produced into a median lobe, finely pilose. Between and lateral to the ante- and postclypeus a pair of short, slightly pointed, sclerotized lobes. Labrum almost circular in shape, with fine pilosity near margin. Mandibles (e.g., dentition), maxilla not exposed or visible. Antenna with 17–18 articles. Pronotum with distinctive pentagonal shape, posterior margin straight, lateral and frontal margins each distended into projecting lobe. Pronotum with very fine pilosity; pronotal length/width 1.04/1.30 mm. Legs distinctive: profemur and protibia very stout, femur with two ventral rows of 5–6 fine spinules; profemur with ventral row of >10 stiff, stout setae; metafemur and metatibia long, slender, femur with ventral row of 6 thin spinules, tibia with ca. 35 spinules. Tibial spine formula 3-3-4; protibia with three apical (f_1 , f_2 , f_3) spines, two subapical ones (f_x , f_y ; see Fig.S3); mesotibia with three apical (m_1 , m_2 , m_3) spines and two subapical spines (m_b , m_x); metatibia with four apical (h_1 , h_2 , h_3 , h_4) and one thick subapical (h_a). Tarsi fully pentamerous; basitarsomere small, tarsomere four produced ventral to distitarsomere; pretarsal claws long, slender, without preapical tooth; arolium either very small or absent. Styli present; slender, digitate, segmentation obscure; cercus slightly thicker, segmentation obscure.

Comments

The piece contains three workers (one, 935c is very fragmentary); their distinctive morphology indicates these are clearly conspecific.

Measurements and Proportions of Specimens and Castes

In an effort to estimate the size of the alate of *Gigantotermes rex*, five measurements were made of representative specimens of all three castes of ten Recent species of termites and three extinct species (*K. yoddha* [herein],

Mastotermes electrodanicus, and *Coptotermes priscus*, the latter two in Miocene Dominican amber) (Tables S2 and S3). Fossils and exemplar specimens of living species were measured using a Nikon SMZ1500 stereoscope with NIS Elements© software. For fossils, the amber was trimmed and polished to maximize a dorsal and lateral view of the body, and a frontal view of the head. Amber specimens were positioned by gently pressing the amber piece into a piece of dental wax affixed to a glass microscope slide. Amber specimens were assigned a unique catalogue number. Linear measurements were made for fossil and living species of the body length (from anterior margin of clypeus to tip of abdomen), forewing length, head length, (greatest) head width, and (greatest) pronotal width. Specimens of living species came from the AMNH termite collection, belonging to the following collection series:

Mastotermitidae: *Mastotermes darwiniensis* (Australia: Koolpinyah, New South Wales; Darwin, Northern Territory).

Hodotermitidae: *Microhodotermes viator* (Ras Raman area, Israel); *Hodotermes mossambicus* (USA: Olivewood, California [introduced]; Republic of South Africa: Cape Province).

Archotermopsidae: *Archotermopsis wroughtoni* (India: Badyar, Jharja); *Zootermopsis angusticollis* (Canada: Garrow Bay, British Columbia; USA: Olympia, Washington).

Stolotermitidae: *Stolotermes victoriensis* (Australia: Belgrave, Victoria); *Porotermes adamsoni* (Australia: Nundle, New South Wales; Monbulk, Victoria; Lees Spring, FCT).

Kalotermitidae: *Kalotermes flavicollis* (Megiddo, Jaffa Israel).

Stylotermitidae: *Stylotermes fletcheri* (India: Coimbatore).

Rhinotermitidae: *Reticulitermes flavipes* (USA: Niles, Michigan).

Measurements of individuals in early Miocene Dominican amber were made of the following specimens:

†*Mastotermes electrodanicus*: AMNH DR14-595 (soldier), AMNH DR8-41 (soldier), AMNH DR14-238 (soldier), AMNH DR16-1529 (worker), AMNH DR14-237 (worker), AMNH DR99-139 (worker), AMNH DR-PB270 (alate), AMNH DR-V2 (alate), AMNH DR12-14 (alate), AMNH DR99-129 (alate).

†*Coptotermes priscus*: AMNH DR14-1179A, AMNH DR14-1179B (soldiers), AMNH DR10-1248 (worker), AMNH DR PB277 (alates).

Body size of soldiers (measured as total body length) varies widely, from 0.47x the size of the alate in the Miocene species *C. priscus*, to 1.30x the alate in *A. wroughtoni*. With the exception of *Archotermopsis* and *Porotermes adamsoni* (the latter 1.26x the alate size), soldier termites are on average 0.80x the length of alates.

Phylogenetics

To assess relationships among extant and fossil termites, 111 morphological characters were scored across a total of 82 taxa. The matrix is essentially the one used in an earlier study of living and fossil Isoptera[S6], but with three additional characters and one additional taxon (*Krishnatermes yoddha*, described herein). The additional characters are:

109. Soldier head anterior to vertex: not dorsoventrally flattened [state 0]; flattened [state 1]. State 1 applies to *Archotermopsis*, *Hodotermopsis*, and *Zootermopsis* (Archotermopsidae), which differs from the flattened head observed in *Psammotermes*, &c. (Rhinotermitidae: Psammotermitinae).

110. Soldier head with lateral striations: absent [state 0]; present [state 1]. State 1 applies to the two species of *Archotermopsis* in the matrix.

111. Soldier head capsule with posterolateral temples: tapered or rounded [state 0]; greatly produced and lobed [state 1]. State 1 applies uniquely to the two species of *Archotermopsis* in the matrix.

The complete, revised matrix is available at <http://purl.org/phylo/treebase/phyloids/study/TB2:S18665>.

This revised matrix was analyzed in TNT v.1.1[S10] under equal- and implied-weighting, to explore the impact of reduced homoplasy on overall tree topology[S11]. Implied-weighting requires an *a priori* assignment for a constant of concavity (K-value) that determines how strongly homoplastic characters are downweighted. Therefore, a script titled “setk,” developed by Salvador Arias, was implemented to identify an appropriate K value given this particular dataset through the formula suggested elsewhere[S10]. The script returned a K-value of 12.15 that was utilized in implied-weighting searches. Regardless of weighting regime, all heuristic searches were performed using the *xmult* command in TNT with sectorial searches, drifting, fusing, and ratchet functions until the best score was located 100 times. Nodes were evaluated with Bremer supports and bootstrap resampling (1000 pseudoreplicates). The unweighted search produced 370 most parsimonious trees with 315 steps (CI=0.39, RI=0.82); the weighted search recovered 168 trees of optimal length (score 10.74; CI=0.41, RI=0.83). Both analyses produced nearly

identical results with respect to overall polarity and major relationships (Fig. S4). As expected, implied weighted analyses were more resolved across the paraphyletic assemblage of basal termites but the nodes are poorly supported and some nodes may be spurious. The irresolution of relationships within this grade appears to be a stable result, reflective probably of an early radiation of termites.

Supplemental References

- S1. Engel, M.S., Grimaldi, D.A., and Krishna, K. (2007). A synopsis of Baltic amber termites (Isoptera). *Stuttgarter Beitr. Naturk. Ser. B* 372, 1–20.
- S2. Engel, M.S., Grimaldi, D.A., and Krishna, K. (2007). Primitive termites from the Early Cretaceous of Asia (Isoptera). *Stuttgarter Beitr. Naturk. Ser. B* 371, 1–32.
- S3. Engel, M.S., and Gross, M. (2009). A giant termite from the late Miocene of Styria, Austria (Isoptera). *Naturwissen.* 96, 289–295.
- S4. Grimaldi, D.A., Engel, M.S., and Krishna, K. (2008). The species of Isoptera (Insecta) from the Early Cretaceous Crato Formation (Isoptera): A revision. *Am. Mus. Novit.* 3626, 1–30.
- S5. Engel, M.S., Nel, A., Azar, D., Soriano, C., Tafforeau, P., Néraudeau, Colin, J.-P., and Perrichot, V. (2011). New, primitive termites (Isoptera) from Early Cretaceous ambers of France and Lebanon. *Palaeodiversity* 4, 39–49.
- S6. Engel, M.S., Grimaldi, D.A., and Krishna, K. (2009). Termites (Isoptera): their phylogeny, classification, and rise to ecological dominance. *Am. Mus. Novit.* 3650, 1–27.
- S7. Ware, J.L., Grimaldi, D.A., and Engel, M.S. (2010). The effects of fossil placement and calibration on divergence times and rates: an example from the termites (Insecta: Isoptera). *Arthropod Structure and Development* 39, 204–219.
- S8. Krishna, K., Grimaldi, D.A., Krishna, V., and Engel, M.S. (2013). Treatise on the Isoptera of the world. *Bull. Am. Mus. Nat. Hist.* 377, 1–2704.
- S9. Emerson, A.E. (1933). A revision of the genera of fossil and Recent Termopsidae (Isoptera). *Univ. Calif. Publ. Entomol.* 6, 163–195.
- S10. Goloboff, P.A., Farris, J.S., and Nixon, K.C. (2008). TNT, a free program for phylogenetic analysis. *Cladistics* 24, 774–786.
- S11. Goloboff, P.A. (1993). Estimating character weights during tree search. *Cladistics* 9, 83–91.