Current Biology

Early Evolution of Specialized Termitophily in Cretaceous Rove Beetles

Highlights

- Until now, the oldest unequivocal termitophiles were 19 million years old

- The earliest termitophile is reported in 99-million-year-old amber from Myanmar

- *Cretotrichopsenius* represents the oldest record for the tribe Trichopseniini

- It shows that ancient termite societies were relatively quickly invaded by beetles

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In Brief

Understanding the early evolution of inquilines and parasites of insect societies is challenging. Cai et al. report the first unequivocal termitophile from mid-Cretaceous Burmese amber, with a protective limuloid body similar to modern species, indicating that ancient termite societies were invaded by beetles at least 99 million years ago.

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Early Evolution of Specialized Termitophily in Cretaceous Rove Beetles

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SUMMARY

Termitophiles, symbionts that live in termite nests, include a wide range of morphologically and behaviorally specialized organisms. Complex adaptive mechanisms permit these animals to integrate into societies and to exploit their controlled physical conditions and plentiful resources, as well as to garner protection inside termite nests. An understanding of the early evolution of termitophily is challenging owing to a scarcity of fossil termitophiles, with all known reliable records occurring from the Miocene (approximately 19 million years ago [mya]) [1–6], and an equivocal termitophile belonging to the largely free-living Mesoporini from the mid-Cretaceous [7]. Here we report the oldest, morphologically specialized, and obligate termitophiles from mid-Cretaceous Burmese amber (99 mya). *Cretotrichopsenius burmiticus* gen. et sp. nov. belongs to Trichopseniini, a group of distinctive termitophilous aleocharine rove beetles, all of which possess specialized swollen or horseshoe-crab-shaped body plans. *Cretotrichopsenius* display the protective horseshoe-crab-shaped body form typical of many modern termitophiles, with concealed head and antennae and strong posteriorly directed abdominal setae. *Cretotrichopsenius* represent the earliest definitive termitophiles, shedding light on host associations in the early evolution of termite societies. The fossil reveals that ancient termite societies were quickly invaded by beetles and by multiple independent lineages of social parasites over the subsequent eons.

RESULTS AND DISCUSSION

Eusocial insects include some of the most ecologically ubiquitous of terrestrial animals and are dominated by ants, social wasps and bees, and termites [8, 9]. The nests within which these societies operate are well protected and provide for a safe, communal space for the storing of resources and production of brood [8]. Given this, it is little wonder that the nests of eusocial insects are often cohabited by a diversity of highly specialized symbionts that take advantage of the abundant resources and protection inside the nests [8, 10]. The successful invasion of eusocial societies entails a plethora of frequently elaborate morphologies, behaviors, and chemical cues. Termitophiles are morphologically specialized organisms that live in termite nests during at least one complete stage of their life cycle [11]. A wide variety of arthropods have been found as termitophiles, and termitophilous species have evolved independently many times in groups as diverse as pill bugs (Crustacea), millipedes (Diplopoda), mites (Arachnida), and insects. Among insects, one of the most remarkable radiations of termitophiles involves lineages in the beetle family Staphylinidae (rove beetles), and particularly within the subfamily Aleocharinae [12].

Understanding the early evolution of specialized termitophily has been severely hindered by a scarcity of definitive fossil termitophiles, especially those from the Mesozoic. Fossils of highly modified inquilines are extremely rare owing to their peculiar biology, which frequently involves species spending the vast majority of their life cycle within the hosts' nests. To date, definitive fossil termitophiles, all of early Miocene age (approximately 19 mya), are known among termite bugs (Hemiptera: Termitaphididae) [1–4] and trichopseniine rove beetles (Coleoptera: Staphylinidae) [5, 6]. In addition, presumably termitophilous beaded lacewing larvae (Neuroptera: Berothidae) are recorded from mid-Eocene Baltic amber (approximately 45 mya) [13]. Recently, Yamamoto et al. [7] reported a probable termitophile from mid-Cretaceous Burmese amber, but the lifestyle of *Mesosymbion* is problematic (see below). The evolution of termitophily in trichopseniine beetles has been tentatively studied based on modern representatives [6, 14], but the suggested hypotheses contradict each other, and there has been no direct evidence of inquilines early in their history. Thus, the origin and subsequent evolution of termitophily in Trichopseniini remains elusive. Our discovery of significantly ancient termitophiles from the mid-Cretaceous provides a unique window for understanding when a group of specialized beetles became integrated into termite nests and reveals that the appearance of elaborate, fully specialized termitophiles took place about 99 million years ago.
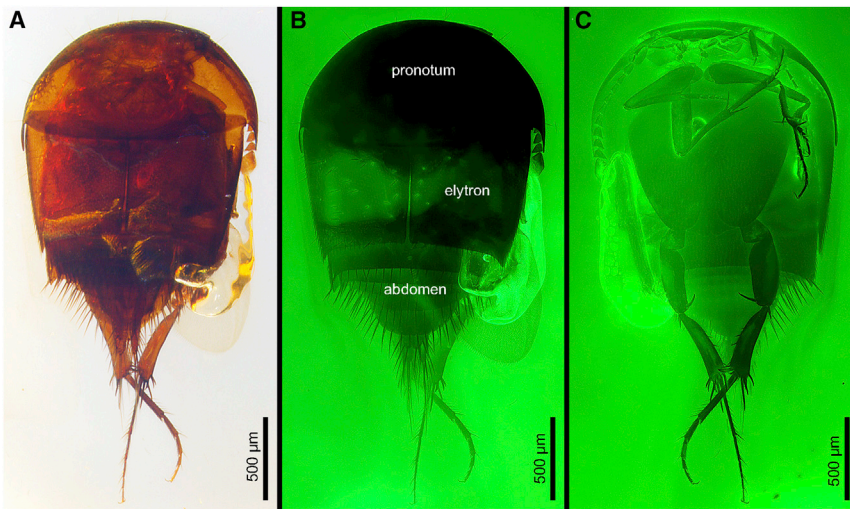
Figure 1. Termitophilous Trichopseniine, *Cretotrichopsenius burmiticus* gen. et sp. nov., in Mid-Cretaceous Amber from Myanmar, Holotype NIGP164518

(A) General habitus, dorsal view, under normal light.

(B) General habitus, dorsal view, under epifluorescence.

(C) General habitus, ventral view, under epifluorescence.

See also Figures S1 and S3.

Systematic Paleontology

Order Coleoptera Linnaeus, 1758

Family Staphylinidae Latreille, 1802

Subfamily Aleocharinae Fleming, 1821

Tribe Trichopseniini LeConte and Horn, 1883

Cretotrichopsenius burmiticus gen. et sp. nov.

ZooBank LSID (generic name): urn:lsid:zoobank.org:act:C4E629CA-79A0-403D-B2A7-C7CE647A8712

ZooBank LSID (species name): urn:lsid:zoobank.org:act:D636DD94-F69E-4C62-BA6E-D8B6A2CF227D

Material

Holotype, NIGP164518 (Figures 1, 2, and S1A–S1C); paratype, NIGP164519 (Figures S1D–S1F); both housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Etymology

The generic name *Cretotrichopsenius* is derived partly from the Cretaceous, in reference of the age of the fossils, and the genus *Trichopsenius*. The specific name *burmiticus* refers to the occurrence of the fossil in amber known as Burmite.

Locality and Age

The specimens are derived from an amber mine located near Noije Bum, Tanaing, Kachin, Myanmar. The U-Pb dating of zircons from the volcanoclastic matrix yielded an age of 98.79 ± 0.62 million years [15].

Diagnosis

Cretotrichopsenius is distinguished from all other Trichopseniini by the following combination of characters: body limuloid (horse-shoe-crab-shaped) and large (~0.7 mm in pronotal length); antenna elongate, laterally flattened with exposed pedicel, slightly clavate; elytron densely setose; metafemur with a large and stout spine at inner-apical margin; outer margin of metatibia without spines; apical margins of abdominal segments with dense, strong, posteriorly directed setae.

Description

Refer to online Supplemental Information for a complete description.

Aleocharinae are widespread and taxonomically the largest rove beetle subfamily, comprising over 16,500 described spe-

cies and approximately 1,300 genera grouped in 63 tribes. Among this diversity there are approximately 740 species (204 genera in 22 tribes) that are associated with termites, of which 12 tribes consist exclusively of termitophilous species [16]. Aleocharinae represent one of the most distinctive and arguably the most successful radiations of termitophiles [11]. To integrate into the hosts' societies, termitophilous aleocharines have repeatedly and independently evolved physogastry (i.e., swollen, largely membranous abdomens) and limuloid body shapes, representing the two principal ecomorphs of these beetles [10, 11]. Both morphological adaptations have arisen convergently many times in beetles (Coleoptera) as well as in flies (Diptera) [11]. Physogastry, the inflation of the abdomen and sometimes the thorax, is likely for a mutual exchange of exudates between termitophiles and their hosts [11], and in some cases is hypothesized to have a mimetic function [17, 18]. Physogastric species are generally well integrated into the termite society, actively interacting with their hosts and notable for their slow movements. Limuloid species, exhibiting extremely compact appendages and cavities to receive structures more vulnerable to host aggression, are specialized for defense, an adaptation commonly found in myrmecophiles and termitophiles [17]. Unlike physogastric taxa, limuloid species are faster moving and usually do not actively interact with their hosts, preferring instead to effectively go about unnoticed within the society.

Cretotrichopsenius exhibits the characteristic features of the modern aleocharine tribe Trichopseniini, including the peculiar articulation of the hind leg whereby the coxae are fully fused and incorporated into the metaventrite [14, 19], the presence of a large lamella fused to the metaventrite, and the absence of abdominal paratergites and pentamerous tarsi [20]. *Cretotrichopsenius* has a typical limuloid shape (Figure 1 and Figures S1A–S1F), although other trichopseniines vary in overall shape, including taxa that are more elongate (Figure S3C) and distinctly physogastric (Figure S3B) [14, 19]. Their teardrop-shaped body plan is hypothesized to serve a protective function [17] and is commonly found in diverse myrmecophilous beetles [21]. In particular, similar body shapes occur in many extant termitophilous trichopseniines (Figure S3A) and in other termitophilous tribes such as Termitodiscini (e.g., *Termitodiscus*) and Termitohospitini (e.g., *Termitohospes*). The head capsule is broadly oval, completely covered and dorsally protected by the pronotum (Figures 2A, 2B, and S2A), and not visible in dorsal view. The elongate and slender antennae with nine flagellomeres
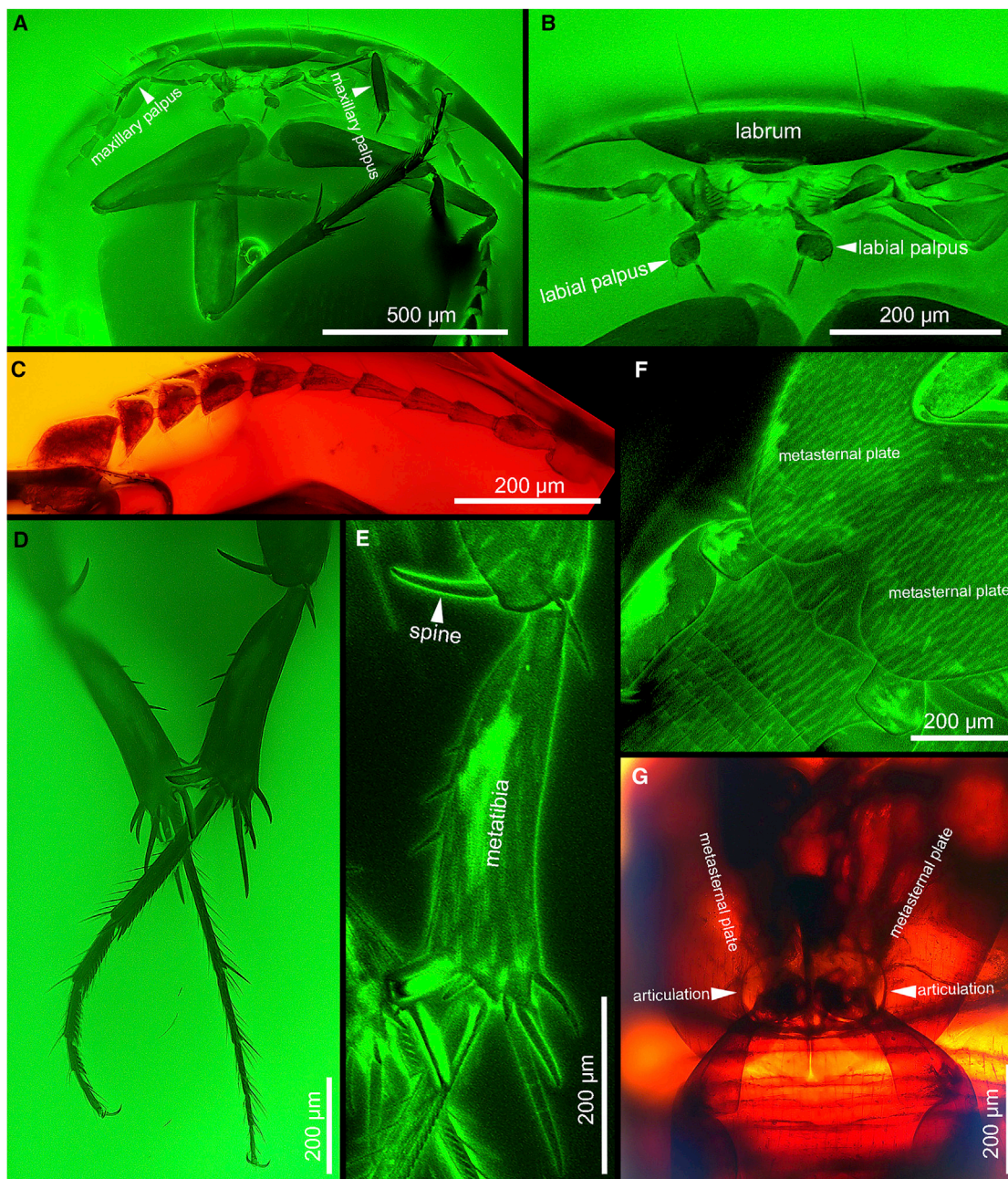
Figure 2. Details of *Cretotrichopsenius burmiticus* gen. et sp. nov., Holotype; Photomicrographs in Green under Epifluorescence and Confocal Laser Scanning Microscopy, and Photomicrographs in Red under Transmitted Light
(A) Ventral view of head and prothorax.
(B) Enlargement of (A), showing mouth parts.
(C) Right antenna.
(D) Hind legs.
(E) Enlargement of metatibia and metafemoral apex, with metafemoral spine indicated.
(F) Metasternal plates and basal parts of hind legs.
(G) Same as (F), showing the characteristic articulation.
See also Figure S2.

(Figure 2C), possibly representing a plesiomorphic form because this resembles the antenna of free-living out-group Aleocharinae (Figure 3), are quite distinctive among all limuloid trichopse-

niines, since modern Trichopseniini have antennae that are usually short and compact, as in *Congopsenius*, *Seeversia*, *Prorhinopsenius*, *Schedolimulus*, and *Papuapsenius* [14, 19].
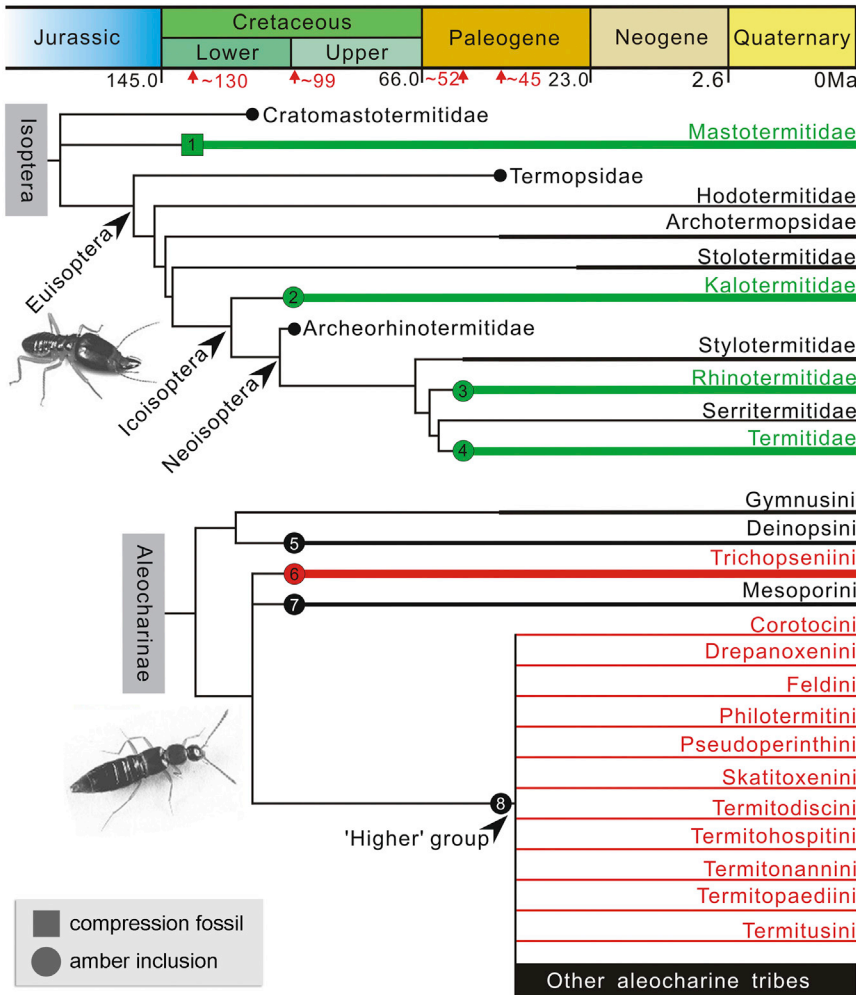
Figure 3. Evolutionary History of Termites and Aleocharinae, with Emphasis on All Obligately Termitophilous Tribes

Phylogeny of termites is modified from Krishna et al. [28], and phylogeny of Aleocharinae is based on Ashe [30]. Green lines refer to hosts of termitophiles; red lines refer to obligate termitophiles; thick black lines indicate fossil ranges for termite lineages not presently known as associates of Trichopseniini. (1) Earliest Mastotermitidae from Early Cretaceous Wealden clay of England. (2) Earliest Kalotermitidae from mid-Cretaceous Burmese amber (approximately 99 mya). (3) Earliest Rhinotermitidae from early Eocene Indian amber (approximately 52–55 mya). (4) Earliest Termitidae from early Eocene Indian amber. (5–7) Earliest Deinopsini, Mesoporini, and Trichopseniini from Burmese amber. (8) Earliest "higher" group aleocharines from Baltic amber (approximately 45 mya).
See also Figure S4 and Tables S1–S3.

By contrast, the physogastric trichopseniines, such as *Mastopsenius*, *Rhinotermopsenius*, and *Termitona* (Figure S3B), appear to have elongate and completely exposed antennae, implying a different mechanism of integration into the termite colony from those of limuloid termitophiles. Like the head, the antennae of *Cretotrichopsenius* were concealed completely under the explanate pronotum, representing another protective modification. The pronotum of *Cretotrichopsenius* is semicircular, broad, and greatly explanate, with a bisinuate posterior margin and posterolateral angles, serving a protective function for the elytra (forewings). The elytra are short and truncate, with pronounced posterolateral angles and dense, irregularly arranged microsetae and several long macrosetae. The abdomen strongly tapers toward its apex, with the apex of each abdominal tergite and sternite (segments III–VIII) and lateral tergal sclerite IX armed with dense, strong, and posteriorly directed setae (Figure S2B), which might protect the beetle from being disturbed by its hosts. The legs (Figure 2D) are relatively long, similar to those of *Prorhinopsenius*, *Trichopsenius*, and *Termitopsenius*, when compared to other genera with short and compact legs, such as *Schedolimulus* and *Seeversia*.

The most impressive leg morphology is the modification of the hind legs. The hind legs appear to be articulated directly to the metaventrite by the trochanter (Figure 2G), representing the most characteristic trait of Trichopseniini and demonstrating its definitive inclusion within this clade. The metafemur (Figure 2E and Figure S2C) is robust, with a large and strong spine at the inner-apical margin, a structure also developed in some extant limuloid trichopseniines, including *Congopsenius*, *Schedolimulus*, and *Termitopsenius*. The exact function of the metafemoral spine remains elusive. The metatibia (Figure 2E and Figure S2C), armed with three long spurs and about seven shorter strong spines at the apex, is likely used for kicking the ground as the beetles scuttle around. The basal four metatarsomeres have a row of dense comb-like spines (Figure 2D and Figures S1H and S2D), which may at least serve to support and protect the tarsus. Another remarkable feature of *Cretotrichopsenius* is the transformation of the coxa into a "metasternal plate" (Figures 2F and 2G), under which the hind leg can be retracted. The plate is well developed in almost all trichopseniines, except in some physogastric forms such as *Schizelythron* [14]. The innovation of the metasternal plate and modifications of the hind leg, together with the limuloid body shape, might have enabled early trichopseniine beetles to integrate into termite societies. Behavioral observations of modern trichopseniines demonstrate that some species are capable of leaping for surprisingly long distances, considering their very small body size [19]. *Cretotrichopsenius*, with robust femora, strong spines on the tibiae and tarsi, and metasternal plates, likely had a similar leaping behavior, especially because similar modifications of the hind legs are also known in other jumping beetles, such as Eucinetidae and thaumastodine Limnichidae [22]. Although it is difficult to regard the peculiar articulation of the hind leg as an adaptation for escape, it might have played an important role in the early evolution of Trichopseniini [19]. Given the above, along with its placement

within a tribe of obligate termite inquilines, it is highly likely that *Cretotrichopsenius* was termitophilous, particularly owing to the protective limuloid body shape and many other specialized adaptive modifications.

Recent species of Trichopseniini are usually associated with derived neoisopteran termites of Rhinotermitidae [6, 12, 14, 19] (Table S1), and less frequently with Termitidae [19]. Interestingly, some trichopseniines are known to live within nests of the basal-most termites (Mastotermitidae) [6] and drywood termites (Kalotermitidae) [23]. It is exceptionally remarkable that extant species of *Prorhinopsenius* are associated with three host families, including Mastotermitidae, Kalotermitidae, and Rhinotermitidae (Table S2). Multiple hypotheses have been proposed for elucidating the origin and early associations between the termitophilous Trichopseniini and their termite hosts [6, 14, 17], but they contradict each other, and the challenge is to distinguish among the alternative hypotheses in the absence of a comprehensive phylogeny for Trichopseniini and, more importantly, the hitherto dearth of Mesozoic fossils.

Phylogenetic studies based on fossil and recent termites predict that termites originated in the Late Jurassic [24, 25]. The oldest fossil termite is from the Early Cretaceous of Siberia (approximately 135 mya [9]), and its phylogenetic position is among a morphological grade of early termites paraphyletic to Icoisoptera (Kalotermitidae + Neoisoptera), indicating that it was already eusocial [24]. This fact, along with the recent discovery that a more basal group had fully developed—tripartite castes during mid-Cretaceous—demonstrates that termite eusociality had arisen by the latest Jurassic [25]. Termites in Burmese amber (nine genera and ten species) are represented by several species of the "*Meiatermes*-grade," a distinctive paraphyletic assemblage of basal genera between Mastotermitidae and all other termites [24, 25], as well as four species of Kalotermitidae [25, 26] (Table S3). Considering that the societies of Burmese termites were already well developed, it is fascinating to find that trichopseniines had similarly already become highly specialized for living within those settings, as evidenced by *C. burmiticus*. The limuloid *C. burmiticus* possessed innovations demonstrating one of the two principal ecomorphs associated with termitophile-termite integration [11]. Although some extant trichopseniines can biosynthesize the same cuticular hydrocarbons as those of their host termites, so as to integrate into the colony [27], it is impossible to verify whether such a chemical system was already present in *Cretotrichopsenius*. *Cretotrichopsenius* clearly displays a body shape similar to the putatively primitive genus *Prorhinopsenius*, and as supported by analyses of the external and internal morphology of extant Trichopseniini [19]. Given that *Prorhinopsenius* are termitophiles of termites spanning the full phylogenetic spread of Isoptera (Figure 3 and Table S2), it is possible that *Cretotrichopsenius* either had a similar host breadth or could have occurred with any termites of the *Meiatermes*-grade, the early kalotermitids, or even the earliest Neoisoptera. Burmese amber harbors the earliest fossil evidence of Neoisoptera (Archaeorhinotermitidae) [25, 28], and these, too, might have served as possible hosts for *Cretotrichopsenius*. Host specificity is rather low in extant trichopseniines, and as such it is certainly likely that *Cretotrichopsenius* may have been associated with the variety of groups known from Burmese amber [25, 26]. Regardless, *C. burmiticus* demonstrates

that trichopseniines had not only originated before the mid-Cretaceous but had also become remarkably specialized as elusive termitophiles by this time, relatively early in the evolution of neoisopteran termites, suggesting a long co-association of the beetles with their hosts [6].

Aleocharinae are a hyper-diverse group of Staphylinidae, but their fossil record is sparse. Burmese amber has revealed the earliest known Mesozoic aleocharine, and it belonged to the basal tribes Deinopsini [29] and Mesoporini [7]. Deinopsini, along with Gymnusini, are sister to Mesoporini + Trichopseniini (another putatively basal group), and then to the remaining majority of Aleocharinae ("higher" aleocharines), as supported by available phylogenetic analyses [7, 30] (Figure 3). Yamamoto et al. [7] reported the first Mesozoic Mesoporini, *Mesosymbion compactus*, from Burmese amber, and *M. compactus* was suspected as a probable termitophile. In addition, another two new fossils belonging to Mesoporini, closely related to Trichopseniini, are known from Burmese amber (Figure S4). Mesoporini, with 16 extant species (in nine genera) and four extinct species (in four genera), are a small lineage occurring in all zoogeographical regions. Six mesoporine species in five genera have been collected with associated termites, including *Anacyptus goeldii* [31], *A. testaceus* [12], *Callopsenius clavicornis* [12], *Dictyon termitophilum* [32], *Kistnerium japonicum* [33], and *Mesoporus rufoflavus* [34]. However, two of these species, *A. testaceus* and *M. rufoclavus*, have also been collected under bark or in leaf litter and appear to not be obligate termitophiles [20]. The remaining ten modern species, in five genera (*Ampheida*, *Dictyon*, *Mimodictyon*, *Paraconosoma*, and *Paradictyon*), are generally found under bark and in rotting wood or leaf litter, with no known association with termites [35–37]. Mesoporini thus appear to be associated with decaying trees, but with only a few species associated with termites that nest in such trees. More importantly, those Mesoporini are entirely associated with Neoisoptera, such as Rhinotermitidae (*Coptotermes*, *Heterotermes*, and *Reticulitermes*) and Termitidae (*Diversitermes*) [12, 31–33], suggesting that the termite association in Mesoporini originated much later, not earlier than early Eocene. Phylogenetic analyses by Yamamoto et al. [7] suggest that the Cretaceous *Mesosymbion* is a sister group to the New Zealand-endemic *Paraconosoma*, a small group with both species occuring only in forest leaf litter, rotting nikau palm leaf bases on the ground [37]. Therefore, *Mesosymbion* with a protective "limuloid" body plan and clubbed antennae are not necessarily termitophilous. Other lineages of termitophilous Aleocharinae are found among the "higher" aleocharines, such as Corotocini, Termitodiscini, Termitohospitini, Termitonannini, Termitopaediini, and Termitusini, and they are usually associated with derived Rhinotermitidae or Termitidae [12] (Figure 3), crown groups of which are not known until the earliest Eocene [38]. It would therefore appear that the mid-Cretaceous *Cretotrichopsenius* were among the first obligate termitophiles, taking advantage of the secluded and controlled environment and accessing numerous resources within early termite nests (Figure 4).

The discovery of a definite trichopseniine from the Mesozoic represents the earliest unequivocal termitophile and pushes back the age of these obligate termite associates by 80 million years. *Cretotrichopsenius burmiticus* indicates that trichopseniines successfully invaded and became specialized for living

Figure 4. Ecological Reconstruction of the Mid-Cretaceous Termitophilous Trichopseniine, *Cretotrichopsenius burmiticus* gen. et sp. nov.

within ancient termite societies and were present early in the evolution of both termites and aleocharine beetles. The fossil reveals a richer ecology within early insect societies during the Cretaceous and a lengthy period of co-evolution between termites, the first of all social insects, and their numerous arthropod associates.

EXPERIMENTAL PROCEDURES

The new taxonomic names are registered in ZooBank urn:lsid:zoobank.org:pub:6290B579-F8DA-4FFB-8FD7-6FE9F8E131C0. The amber was polished with sand paper of gradually finer grit sizes, and lastly with diatomite mud. Observations and photographs were taken using a Zeiss Discovery V20 stereo microscope and a Zeiss Axio Imager 2 light microscope with a digital camera attached. Photomicrographs with green background were taken using fluorescence as light source attached to a Zeiss Axio Imager 2 light microscope (Figures 1B, 1C, 2A, 2B, and 2D and Figures S1C–S1E, S4A–S4D, S4F, and S4G) and a confocal laser scanning microscopy Zeiss LSM 710 with 10× objectives using a laser at 488 nm (Figures 2E, 2F, and S2). Focus stacking software (Helicon Focus 3.10) was used to increase depth of field.

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.2017.03.009.

AUTHOR CONTRIBUTIONS

C.C. designed the research. C.C. drafted the manuscript, to which M.S.E., A.F.N., and K.T.E. contributed. D.H., M.S.E., and A.F.N. participated in morphological studies.

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