not apply to the adult sex ratio when it comes to lifetime offspring production. For example, if the sex ratio at maturation is 1:1 then at ,maturity males and females have the same expected mean number of offspring, even if the sexes differ in adult mortality rates so that the adult sex ratio becomes very biased. The reason why the adult sex ratio predicts the breeding system in shorebirds might simply be because it is correlated with the sex ratio at maturation. Also, if the sexes differ in their mortality rates while caring for young (i.e., a different cost of reproduction), then the sex that has a lower cost of reproduction can afford to invest more in care because it is cheaper. All else being equal, however, a sex difference in mortality means that the adult sex ratio will be biased towards the sex with the lower cost of reproduction.

Where can I find out more?

Fairbairn, D.J. (2013). Odd Couples: Extraordinary Differences between the Sexes in the Animal Kingdom (Princeton: Princeton University Press).

Fritzsche, K., Booksmythe, I., and Arnqvist, G. (2016). Sex ratio bias leads to the evolution of sex role reversal in honey locust beetles. Curr. Biol. *26*, 2522–2526.

Hamilton, W.D. (1967). Extraordinary sex ratios. Science *156*, 477–488.

Jennions, M.D., and Fromhage, L. (2017). Not all sex ratios are equal: the Fisher condition, parental care and sexual selection. Phil. Trans. R. Soc. B (in press).

Kahn, A.T., Jennions, M.D., and Kokko, H. (2015). Sex allocation, juvenile mortality and the costs imposed by offspring on parents and siblings. J. Evol. Biol. *28*, 428–437.

Liker, A., Freckleton, R.P., and Szekely, T. (2013). The evolution of sex roles in birds is related to adult sex ratio. Nat. Comm. *4*, 1587.

McNamara, J. M., Székely, T., Webb, J.N., and Houston, A.I. (2000). A dynamic game-theoretic model of parental care. J. Theor. Biol. *205*, 605–623.

Queller, D.C. (1997). Why do females care more than males? Proc. R. Soc. B *264*, 1555–1557.

Schacht, R., Rauch, K.L., and Borgerhoff Mulder, M. (2014). Too many men: the violence problem? Trends Ecol. Evol. *29*, 214–222.

Székely, T., Weissing, F. J., and Komdeur, J. (2014). Adult sex ratio variation: implications for breeding system evolution. J. Evol. Biol. *27*, 1500–1512.

West, S.A. (2009). Sex Allocation (Princeton: Princeton University Press).

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Evidence from amber for the origins of termitophily

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Fossil morphology is often used to infer the ecology of extinct species. In a recent report in *Current Biology*, Cai and colleagues [1] described an extinct rove beetle, *Cretotrichopsenius burmiticus*, from two specimens in mid-Cretaceous Burmese amber (~99 million years old). Based on morphology and the taxonomic group to which the specimens belong, the authors proposed that *Cretotrichopsenius* was a termitophile — a socially parasitic symbiont of termite colonies. Moreover, the new taxon was claimed to represent the oldest “unequivocal” termitophile so far discovered, pushing back the known evolutionary history of termitophily by ~80 million years, close to the origin of termite eusociality. *Cretotrichopsenius* is certainly an important discovery for understanding the evolutionary steps leading to this type of social insect symbiosis. However, we issue a caveat here concerning the authors’ assertion that *Cretotrichopsenius* was truly termitophilous. Additionally, we question the authors’ representation of a previously published, likely-termitophilous rove beetle in Burmese amber [2].

Cretotrichopsenius belongs to the staphylinid subfamily Aleocharinae, a speciose group with numerous termitophilous lineages [3]. The morphology of *Cretotrichopsenius* indicates membership of the tribe Trichopseniini. This tribe, together with its putative sister tribe Mesoporini [4], contains many termitophiles: all species of Trichopseniini are termitophilous, whereas multiple species of Mesoporini have independently evolved termitophily (the remainder of Mesoporini are presumed to be free-living) [2]. That the Trichopseniini–Mesoporini clade is an early-diverging branch of the aleocharine phylogeny [4] made it likely, *a priori*, that extinct members of these tribes could have been evolutionarily ancient termitophiles. Importantly, beetles in both tribes have a limuloid (horseshoe crab-like) body shape, with a hood-like thorax that protects the head. Such limuloid anatomy is seen in a diversity of social parasite groups in Aleocharinae, attesting to its functional utility for survival inside ant and termite nests [3].

Cai and colleagues’ assertion that *Cretotrichopsenius* was definitively termitophilous rests on its systematic placement in Trichopseniini and limuloid body shape [1]. However, in the case of the Trichopseniini–Mesoporini clade, limuloid morphology, though adaptive for termitophily, may not be *per se* an adaptation for this way of life. Rather, the defensive limuloid body shape likely arose in a free-living common ancestor of the two tribes [2,4,5]. This body plan is seen in all trichopseniine and mesoporine species (including free-living taxa), and is present to varying degrees in members of the earlier-diverging, entirely free-living aleocharine tribes Gymnusini and Deinopsini, as well as in members of predominantly free-living subfamilies closely related to Aleocharinae, the Tachyporinae, Habrocerinae and Trichophyinae. In other words, the limuloid shape arose prior to the convergent evolution of termitophily in multiple lineages of Mesoporini and in crown-group Trichopseniini (Figure 1A). Consequently, free-living, stem-group trichopseniines with limuloid anatomy once existed. For this reason, the authors’ assertion that *Cretotrichopsenius* represents an “unequivocal” termitophile based on its limuloid body shape and membership of Trichopseniini is questionable. Critically, the authors failed to conduct a phylogenetic analysis to evaluate the placement of *Cretotrichopsenius*, so a position outside of termitophilous crown-group Trichopseniini remains possible (Figure 1A). Indeed, the authors note that unlike extant limuloid trichopseniines, which have short, compact antennae, *Cretotrichopsenius* has long, thin antennae with exposed pedicels, resembling those of free-living out-group Aleocharinae [1]. Moreover, based on the data in the paper, it is unclear if *Cretotrichopsenius* possesses any overt anatomical adaptations for termitophily: the additional characters

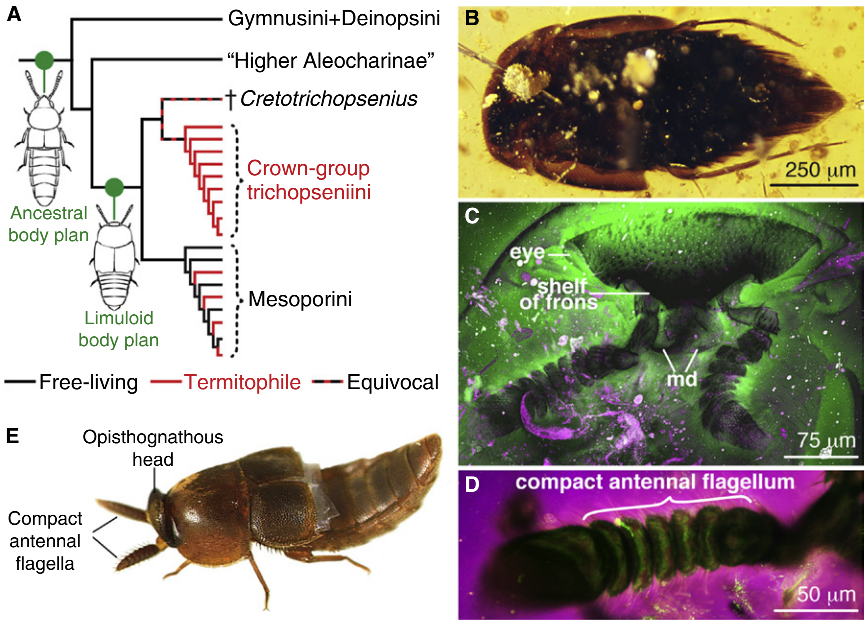

Figure 1. Early evolution of termitophily in aleocharine rove beetles.
(A) Possible interpretation of the biology and phylogenetic position of *Cretotrichopsenius* based on evidence presented by Cai *et al.* [1]. Phylogeny of basal aleocharine relationships (topology from [2,4]) reveals that evolution of the limuloid body plan occurred along the branch leading to Trichopseniini and Mesoporini, prior to the evolution of termitophily in both tribes (red branches), and possibly even earlier, with the common ancestor of Aleocharinae potentially having "quasi-limuloid" shape with moderately expanded prothorax partially covering the head. A position for *Cretotrichopsenius* as a limuloid free-living stem-group of wholly termitophilous crown-group Trichopseniini is possible, based on data presented in [1]. The numbers of lineages in Trichopseniini and Mesoporini do not represent actual diversity, but convey that all crown-group trichopseniines are termitophiles, whereas termitophily has evolved convergently in Mesoporini. (B–D) *Mesosymbion compactus* (Mesoporini) from Burmese amber (images from [2]). (B) Dorsal habitus (light microscopy) showing limuloid shape. (C) Ventral view (confocal microscopy) revealing defensively modified opisthognathous head, with short, robust antennae inserted under shelf-like edges of frons; md: mandibles. (D) Sagittal confocal section through right antenna shows segments of the flagellum compacted into each other which conceals the interconnecting pedicels, a hallmark of social parasites. (E) The extant termitophile *Athexenia* (Aleocharinae: Termitodiscini) exhibits defensive morphology that is convergent with *Mesosymbion*: a limuloid body shape, with an opisthognathous head and compact antennal flagella. (Photo: Steven Marshall.)

discussed as playing defensive roles against termites (e.g., structures of the hind legs, presence of metasternal plates) are features diagnostic of the tribe Trichopseniini without demonstrated roles in termitophily. Such traits are putatively plesiomorphic in the tribe — whether they evolved before or after termitophily is unknown; so, they too were potentially present in free-living, stem-trichopseniines.

We agree with Zyła *et al*. [6] that despite the recent explosion of work on Cretaceous staphylinids, rigorous phylogenetic placement of new taxa has been carried out in only a minority of studies. Yet, such analysis becomes essential if the goal is to infer accurate patterns of character evolution, distinguish adaptation from preadaptation, or ascribe a likely palaeoecology to a fossil taxon. Based on the evidence presented by Cai *et al.* [1], one cannot conclude that *Cretotrichopsenius* was definitively a termitophile; the taxon can be justifiably interpreted as a stem-group trichopseniine that evolved prior to termitophily in the crown-group.

This absence of demonstrated symbiotic specializations in *Cretotrichopsenius* contrasts with another extinct aleocharine in Burmese amber, described earlier and phylogenetically placed in Mesoporini [2]. *Mesosymbion compactus* is limuloid (Figure 1B) but additionally bears anatomical hallmarks of social parasites that are evolutionarily derived — that is, features appearing to be adaptations for social parasitism that were not merely inherited from free-living trichopseniine–mesoporine common ancestors (nor features plesiomorphic within Mesoporini). These are: a backward-pointing (opsithognathous) head with mandibles directed posteriorly (Figure 1C); antennae inserted under protective shelf-like margins of the frons, so their attachment points on the head are unexposed (Figure 1C); defensively-modified robust, compact antennae that are short, thick and composed of transverse, telescoping segments which are compacted together, concealing the weak, interconnecting pedicels (Figure 1D). As discussed before [2], these three adaptations, when co-occurring with the limuloid body shape, define a socially parasitic ecomorph that has evolved convergently in rove beetles, including some limuloid Trichopseniini and a variety of other termitophilous lineages of Aleocharinae. The genus *Athexenia* (Figure 1E) exemplifies a taxon with this convergent morphology among extant termitophilous aleocharines. Regardless of *Mesosymbion*'s tribal taxonomic affinity, its suite of characters alone argues for its symbiotic ecology, and such a hypothesis is only bolstered by *Mesosymbion*'s membership of Mesoporini, a tribe with a repetitive tendency toward evolving termitophily.

Nevertheless, Cai *et al.* [1] consider *Mesosymbion* an "equivocal" termitophile because: some termitophilous mesoporines appear less tightly associated with hosts than do trichopseniines do; some mesoporines are free-living; mesoporines are associated with Neoisoptera, a termite group known only from the Cenozoic, implying that termitophilous relationships in general in Mesoporini must have evolved post-Cretaceous. However, none of these arguments weaken the case for *Mesosymbion* being a termitophile; like many aleocharine groups that have taken up with social insects, the strengths of symbiotic associations simply vary between mesoporine species, from free-living to obligately termitophilous. Similarly, host associations can be evolutionarily dynamic, and liable to change across aleocharine clades composed wholly or predominantly of symbiotic species (see for example the varied ant and termite hosts of Lomechusini [7]). Indeed, like termitophilous mesoporines, thirteen of fifteen extant trichopseniine genera are also associated with Neoisoptera (and in the two remaining trichopseniine genera associated with termite families with likely Cretaceous or earlier origins, one species has also switched to Neoisoptera, further emphasizing the prevailing lack of host fixity over time). Finally, Cai *et al.* [1] misrepresent *Mesosymbion* as merely “limuloid with clubbed antennae”, without acknowledging its suite of adaptations that betray a probable symbiotic ecology (note that *Mesosymbion*’s specialized antennal form differs to the simple “clubbed” antennae of non-symbiont aleocharines, as Cai *et al.* imply [1]). *Mesosymbion* and *Cretotrichopsenius* provide insights into a biologically fascinating group of beetles in the mid-Cretaceous. We hope that this correspondence clarifies interpretations of their possible palaeoecologies.

REFERENCES

1. Cai C., Huang, D., Newton, A.F., Eldredge, K.T., and Engel, M.S. (2017). Early evolution of specialized termitophily in Cretaceous rove beetles. Curr. Biol. *27*, 1229–1235.
2. Yamamoto, S., Maruyama, M., and Parker, J. (2016). Evidence for social parasitism of early insect societies by Cretaceous rove beetles. Nat. Commun. *7*, 13658.
3. Parker, J. (2016). Myrmecophily in beetles (Coleoptera): evolutionary patterns and biological mechanisms. Myrmecol. News *22*, 65–108.
4. Ashe, J.S. (2005). Phylogeny of the tachyporine group subfamilies and ‘basal’lineages of the Aleocharinae (Coleoptera: Staphylinidae) based on larval and adult characteristics. Syst. Entomol. *30*, 3–37.
5. Pasteels, J.M., and Kistner, D.H. (1971). Revision of the termitophilous subfamily Trichopseniinae (Coleoptera: Staphylinidae). II. The remainder of the genera with a representational study of the gland systems and a discussion of their relationships. Misc. Publ. Entomol. Soc. Am. *7*, 351–399.
6. Żyła, D., Yamamoto, S., Wolf-Schwenninger, K., and Solodovnikov, A. (2017). Cretaceous origin of the unique prey-capture apparatus in mega-diverse genus: stem lineage of Steninae rove beetles discovered in Burmese amber. Sci Rep, *7*, 45904.
7. Hlaváč, P., Newton, A.F., and Maruyama, M. (2011). World catalogue of the species of the tribe Lomechusini (Staphylinidae: Aleocharinae). Zootaxa *3075*, 1–151.

[1]The Kyushu University Museum, Hakozaki 6-10-1, Higashi-ku, Fukuoka 812-8581, Japan. [2]Department of Genetics and Development, Columbia University, 701 West 168th Street, New York, NY 10032, USA. [3]Division of Invertebrate Zoology, American Museum of Natural History, New York, NY 10024, USA. [4]Co-first author.
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Response to “Evidence from amber for the origins of termitophily”

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In a recent *Current Biology* paper [1], we reported the oldest, morphologically specialized, and obligate termitophiles, *Cretotrichopsenius burmiticus* (Figure 1, left), from mid-Cretaceous Burmese amber, about 99 million years old. *Cretotrichopsenius*, belonging to the obligately termitophilous rove beetle tribe Trichopseniini, display the protective horseshoe-crab-shaped body typical of many extant termitophiles. However, the termitophilous lifestyle of *Cretotrichopsenius* is being questioned by Yamamoto *et al*. [2] based on their representation of the termitophile-related features and premature and presumptive phylogenetic placement of *Cretotrichopsenius* within Trichopseniini. We stand by our interpretation that *Cretotrichopsenius* are obligate termitophiles, and *Mesosymbion* [3], a member of the largely free-living Mesoporini, are not necessarily termitophilous.

Our argument that *Cretotrichopsenius* was termitophilous is based on its systematic placement in Trichopseniini and is also “owing to the protective limuloid body shape and many other specialized adaptive modifications” [1]. Yamamoto *et al*. [2] represented our evidence as “its systematic placement in Trichopseniini and limuloid body shape”. However, “many other specialized adaptive modifications” of *Cretotrichopsenius* obviously indicate an obligate, symbiotic association with early social insects, such as the explanate pronotum covering the head and antennae, abdomen armed with strong posteriorly-directed setae, robust jumping hind legs, strong apical metatibial spurs and spines, tarsomeres with a row of comb-like spines and inner-apical margin of metafemur with a strong spine, traits congruent with other termitophiles. Yamamoto *et al*. [2] pointed out that “the authors failed to conduct a phylogenetic analysis to evaluate the placement of *Cretotrichopsenius*, so a position outside of termitophilous crown-group Trichopseniini remains a possibility”. However, the absense of a cladistic analysis *per se* does not fail to support the placement of a certain taxon, and the attribution of our species is supported (regardless how analyzed) by specific morphological characters. In *Cretotrichopsenius*, the elongate antennae are probably plesiomorphic within the limuloid group of genera [1], but antennal length varies among species: the termitophilous *Prorhinopsenius* usually have clubbed and compact antennae (Figure 1, middle), whereas one of the Miocene species, *Prorhinopsenius mexicanus*, bears elongate antennae [4], similar to those of *Cretotrichopsenius*. Additionally, *Cretotrichopsenius* display many highly derived features, including a setose abdomen, comb-like spines on the tarsi, and metafemoral apex with a strong spine. Moreover, there is evidence that the limuloid body shape is a derived bodyplan within the Trichopseniini, since *Trichopsenius* (Figure 1, right) and *Xenistusa* with an elongate body and exposed, elongate antennae together may represent a basal clade of this tribe [4]. As such, *Cretotrichopsenius* is demonstrably not a sister group to all extant taxa, contradicting Yamamoto and colleagues’ [2] unfounded assumption that *Cretotrichopsenius* were a free-living, stem-group of the exclusively termitophilous crown-group Trichopseniini.

A rigorous phylogenetic analysis of extant and extinct taxa is important for understanding evolutionary history. However, there is a trend that many analyses are based on the integration of fossil taxa into an established character matrix with a limited and untargeted sampling of the studied groups. In Yamamoto *et al*. [3], the character matrix and studied taxa are derived from Ashe [5], an analysis which was aimed at understanding the phylogeny of the tachyporine group subfamilies and the ‘basal’ lineages of Aleocharinae (*i.e.*, those tribes lacking a tergal gland). The Mesoporini in Ashe [5] and subsequently in Yamamoto *et al*. [3] are represented by only