

Adaptive Radiation in Socially Advanced Stem-Group Ants from the Cretaceous

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<http://dx.doi.org/10.1016/j.cub.2015.12.060>

SUMMARY

Across terrestrial ecosystems, modern ants are ubiquitous. As many as 94 out of every 100 individual arthropods in rainforests are ants [1], and they constitute up to 15% of animal biomass in the Amazon [2, 3]. Moreover, ants are pervasive agents of natural selection as over 10,000 arthropod species are specialized inquilines or myrmecomorphs living among ants or defending themselves through mimicry [4, 5]. Such impact is traditionally explained by sociality: ants are the first major group of ground-dwelling predatory insects to become eusocial [3], increasing efficiency of tasks and establishing competitive superiority over solitary species [6, 7]. A wealth of specimens from rich deposits of 99 million-year-old Burmese amber resolves ambiguity regarding sociality and diversity in the earliest ants. The stem-group genus *Gerontoformica* maintained distinct reproductive castes including morphotypes unknown in solitary aculeate (stinging) wasps, providing insight into early behavior. We present rare aggregations of workers, indicating group recruitment as well as an instance of interspecific combat; such aggression is a social feature of modern ants. Two species and an unusual new genus are described, further expanding the remarkable diversity of early ants. Stem-group ants are recovered as a paraphyletic assemblage at the base of modern lineages varying greatly in size, form, and mouthpart structure, interpreted here as an adaptive radiation. Though Cretaceous stem-group ants were eusocial and adaptively diverse, we hypothesize that their extinction resulted from the rise of competitively superior crown-group taxa that today form massive colonies, consistent with Wilson and Hölldobler's concept of "dynastic succession."

RESULTS

Molecular-based estimates suggest that ants diverged from their nearest relatives sometime between the Late Jurassic and Early

Cretaceous [8–10]; however, the earliest known fossil ants are considerably younger—perhaps due to preservation biases. Ants occur in five major amber deposits during the Cretaceous Period from approximately 100 to 78 million years ago and have attracted substantial study. Initial discoveries were made in amber from New Jersey, USA (ca. 92 mega-annum [Ma]) [11–13], western Canada (ca. 78 Ma) [14–17], and northern Siberia (ca. 85 Ma) [18]. The oldest ants are from the latest Albian of France, ca. 100 Ma [19, 20], but the deposit that has attracted the most attention is from northern Myanmar, dated radiometrically at 99 Ma [21] near the boundary between the Early and Late Cretaceous. With 19 described species, this is the largest and biotically most diverse of all Cretaceous amber deposits, comprising over 50% of Cretaceous ant species [16, 22–26].

Ants are rare in the Cretaceous, constituting less than 1% of all individual insects from various deposits [13, 27]. By the Early to mid-Eocene, 52–42 Ma, they rise in abundance from between 5% and 12% [28–30], coinciding with the proliferation of major modern ant subfamilies. In Miocene Dominican amber (ca. 20 Ma), all ants belong to modern subfamilies and comprise 20% of all insect inclusions [13].

While all modern ants are social, the 13,000 described species vary greatly in behavior and morphology, ranging from groups of less than a hundred solitary hunters in conflict for reproductive rights to colonies of millions exhibiting morphologically specialized and rigid division of labor [3]. The first described Cretaceous ants were similar to modern solitary aculeate wasps in which the female is wingless and the male winged (e.g., Chrysidoidea, Brachynobaenidae, methochine Tiphiidae, all Mutillidae, rhopalosomatids and pompilids). In addition, most Cretaceous ants lack distinctive elbowed antennae exhibited by modern ants, which, it was proposed, could have prevented social activities such as brood care [31]. These solitary affinities were disputed based on the antennal structure of eusocial bees and vespids, as well as morphological similarities between the four Cretaceous species known at the time and modern, social ants [32].

Here, we present further morphological evidence for reproductive caste differentiation in two genera of Cretaceous ants and very rare preserved instances of social behavior in the extinct genus *Gerontoformica*, known from the Cretaceous of France and Myanmar.

Evidence for Sociality

There is compelling morphological evidence for sociality in Cretaceous ants. Ants uniquely possess a specialized, complex

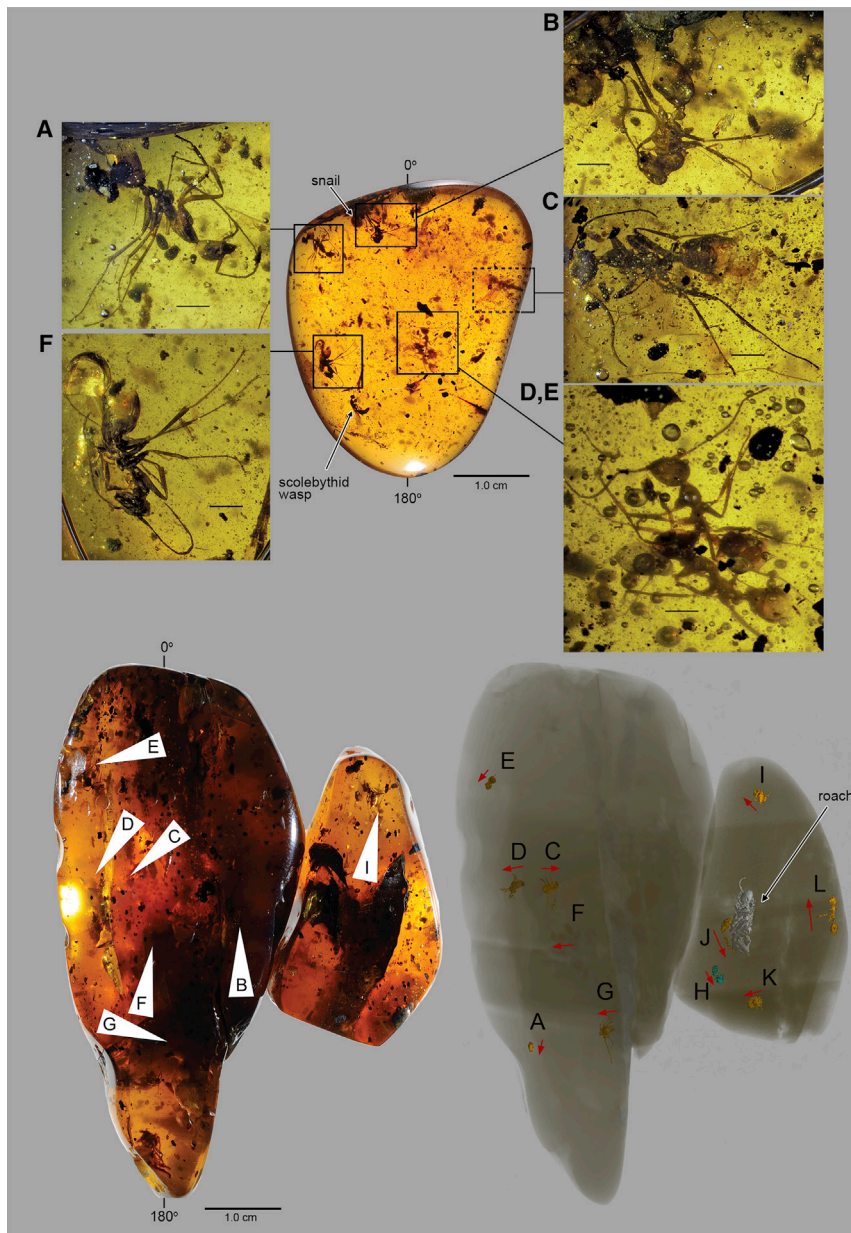


Figure 1. Social Assemblages of Cretaceous Worker Ants

(A–F) Top: photomicrograph of entire piece of JZC Bu1814, with detailed views of its six workers of *Gerontoformica spiralis*. The 0° to 180° axis was used to measure orientations of the ants. Bottom: JZC Bu116 sections A and B, containing 12 worker ants (labeled A–L). Bottom left: photomicrographs of entire piece with two sections fitting together as in the original resin flow. Bottom right: CT scans, with 10 of the 11 *Gerontoformica spiralis* workers in orange and one *Haidomyrmex zigrasi* Barden and Grimaldi in blue (one *G. spiralis* worker, labeled B, was not recovered by X-ray imaging); red arrows indicate orientation of body axis. The large insect is a roach. See also Figure S1.

ants and another eusocial group of insects, termites (Isoptera) [35]. Also, many modern ants exhibit claustral founding, in which a queen sequesters herself in a cavity and raises an initial generation of workers rather than foraging herself, sustained by metabolizing her highly developed flight muscles [36]. In *Gerontoformica*, *Haidomyrmex*, *Haidomyrmodes*, and *Zigrasimecia* (Cretaceous genera where queens are known), such metabolic stores appear absent as there is very little size dimorphism between queens and workers ([20, 23, 24, 26]; Figure S3). This also provides a possible explanation for why three dealate females (founding queens) in three of the four genera were captured in Burmese amber ([23, 24]; Figure S3): these queens were initially foraging while founding their colony; they were not cloistered. Dealate queens are rare relative to alate queens in Cenozoic amber, with three times more winged females than dealate females recorded in a monograph of over 9,000 Baltic amber specimens [37], contrasted with an equal number of both

metapleural gland, visible as an external opening on the posterior region of the mesosoma. The gland function is not certain, but its secretions have been hypothesized to aid in defense, social interactions, and colony hygiene [33]. All Cretaceous ants have a gaping, fully exposed metapleural gland opening [12, 23–25]. Most importantly, four morphs are known in Burmese and French amber ant genera (Table S1; [12, 16, 20, 23–26]), including conspecific worker and queen morphotypes suggestive of social behavior [34]: (1) entirely wingless females (workers); (2) females that are fully winged (alates); (3) individuals that have lost the wings but retain small wing stubs (dealates) (both alates and dealates are queens); and (4) fully winged males.

The presence of dealate females from the Cretaceous is highly significant. In modern ants, newly mated queens remove their own wings shortly after the nuptial flight, a behavior unique to

forms known in stem-group taxa. Foraging by founding queens was probably typical of early ants.

While there are reports of worker syninclusions from the Cretaceous ranging from two to five individuals [13, 20, 26] consistent with sociality, these specimens have not been thoroughly analyzed, and the largest aggregations have been lost due to preparation. Here, very rare examples preserve behavioral evidence for sociality in four species of *Gerontoformica* in Burmese amber. Three samples of amber contain the largest assemblages of worker ants known from the Cretaceous, imaged for the first time.

Specimen JZC Bu1814 contains six workers of *Gerontoformica spiralis* (Figure 1). Specimen JZC Bu116 contains 11 *Gerontoformica spiralis* workers and one worker of *Haidomyrmex zigrasi*. The piece is broken into two contiguous sections, portions of which are lost, so this assemblage may have been larger.

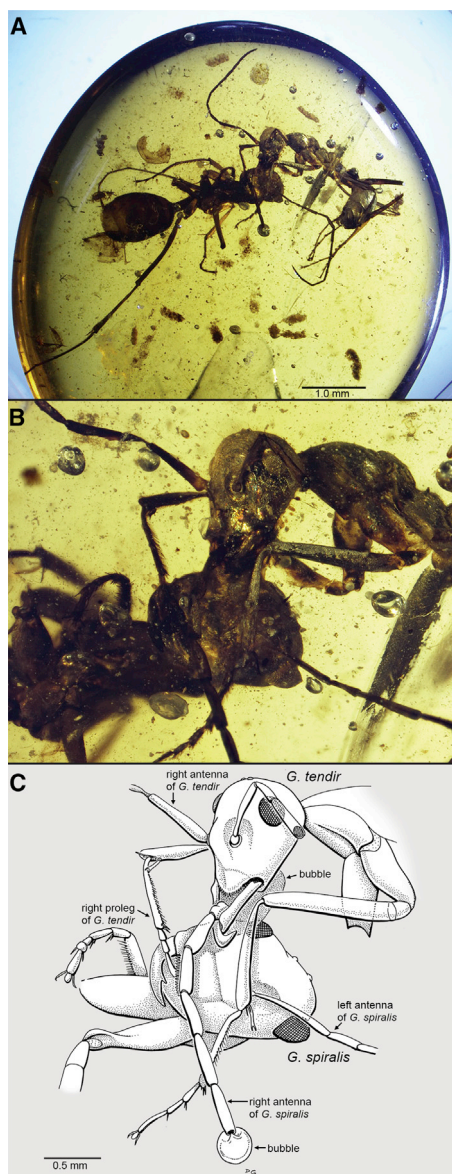


Figure 2. Workers of Two Species of *Gerontoformica* in Burmese Amber, *G. tendir* and *G. spiralis*, Captured while Fighting
Specimen JZC Bu1646.

(A) Photomicrograph of entire specimens.

(B) Photomicrographic detail of interaction.

(C) Illustration of anterior portion of specimens, clarifying positions of appendages.

Both sections were CT scanned for three-dimensional rendering of the ants, as well as a large roach (Figures 1 and S1). Specimen JZC Bu1645 is a broad piece of amber containing 21 ants constituting three species of *Gerontoformica* (*G. orientalis*, *G. contegus*, *G. robustus*). Although there are three distinct groupings of workers, the groupings do not appear to be species specific, nor are there signs of aggression in this assemblage (Figure S1).

Based on raw samples, ants are very rare in Cretaceous amber [13, 27, 38, 39], so the probability of finding an assemblage of

conspecific worker ants in Burmese amber based on chance alone is highly remote; in the case of amber piece JZC Bu116, we calculated it as approximately 3.1×10^{-16} . Clearly there is a biological explanation for these assemblages, for which there are three possibilities: (1) the ants are solitary and aggregating at a common food source. The presence of two ant species in Bu116, together with a large roach, suggests that attraction to a prey item may have had some effect; however, this remains inconclusive. This explanation may pertain as well to piece JZC Bu1646, although it contains no large, potential prey. However, there are 19 named species of ants in Burmese amber, so the probability is even more remote that many individuals in two of these pieces, and all individuals in piece JZC Bu1814, are conspecific, unless sociality is involved. (2) The ants were social, and the resin captured them near a nesting site. There is no evidence for this, although rare specimens of Dominican and Baltic amber exhibit workers with or even carrying their brood. (3) The ants were social and engaging in recruitment foraging. There is some evidence for this interpretation in piece Bu116, since it contains a large roach (12.5 mm body length) with nine ants close by (within four ant-body lengths), as well as the remains of a large spirobolidan millipede. Piece 1814 has no obvious prey item, though commercial processing of the amber may have obliterated any traces of one.

It is commonly thought that the early branching lineages of extant ants exhibit solitary hunting; however, some species utilize group recruitment in attacking and retrieving large prey (e.g., *Stigmatomma* [40]), as well as in prey searches (e.g., *Leptogenys* [41]). Hunting recruits in these species usually form a procession, but in the amber fossils analyzed there appears to be no regular orientation of the individual ants. This situation is inconclusive as the lack of an orientation pattern could be due either to the possibility that *Gerontoformica* did not form hunting processions (e.g., they did not use trail pheromones) or that the flowing resin mixed the original arrangement of workers.

A remarkable piece of Burmese amber (JZC Bu1646) contains two worker ants, *Gerontoformica tendir* (specimen A) and *Gerontoformica spiralis* (specimen B) (Figure 2), captured while fighting, with mandibles of each clasped around an appendage of its opponent. Interspecific aggression is unknown among females of solitary aculeates; however, ants are notorious for warfare, typically fighting by grasping the antennae and legs of opponents. There is a spectrum of intraspecific and interspecific aggression of ants, ranging from protection of the nest (in virtually all species), to protection of the nest and food supply, to aggressive exclusion of any invaders within the foraging territory [3]. Mortal combat by ant workers is common, possibly because the deaths of sterile individuals represent “only an energy and labor deficit” [3], resulting in a slight or negligible diminishment of reproductive capacity [42, 43].

Diverse Cretaceous Stem-Group Ant Lineages

While some Cretaceous ants are attributable to modern groups [13], the vast majority are distinct from living taxa. Initial Cretaceous discoveries fit predictions of what a transitional stem-group ant might look like: morphologically plesiomorphic and generalized with affinities to both modern ants and wasps [11]. Subsequently uncovered taxa have significantly altered this view with the discovery of highly unusual and

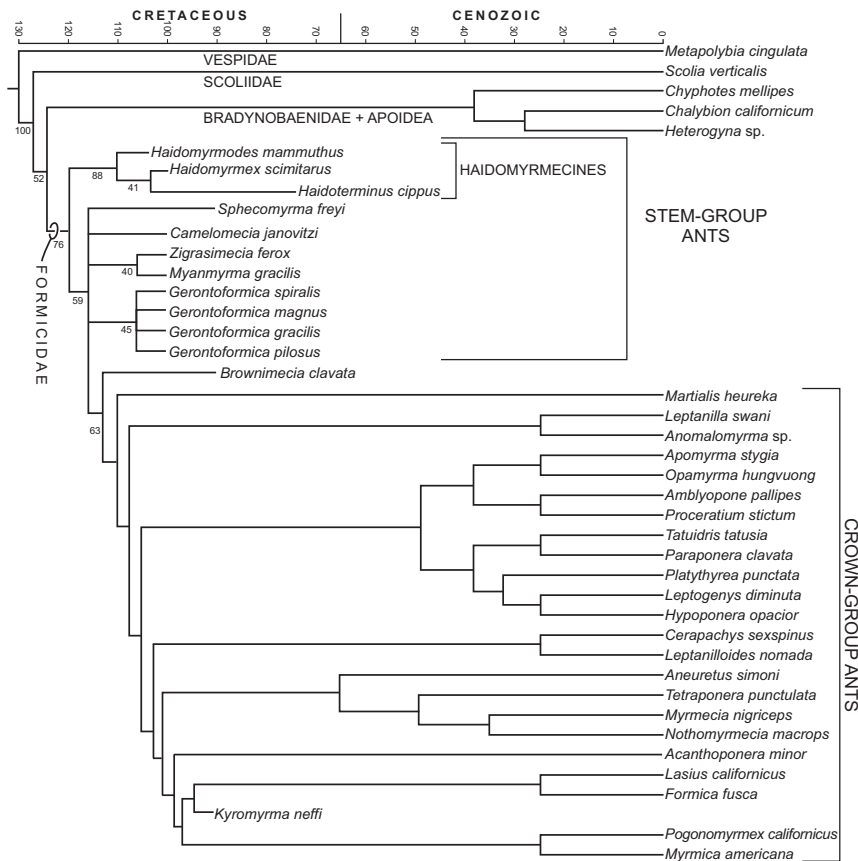


Figure 3. Preferred Timescaled Consensus Cladogram of Cretaceous and Exemplar Extant Ants

Based on a parsimony-based analysis of 42 morphological characters using implied weighting ($K = 6.875$) and a crown-group topology constrained by previous molecular hypotheses [9]. Timescale included to demonstrate range of Cretaceous fauna: nodes and branch lengths do not correspond to actual diversification times or morphological change, although the earliest divergences are constrained not to exceed the age of the earliest aculeates (Bethyloymidae) in the very Late Jurassic [42]. Node values represent bootstrap support measures. See [Supplemental Information](#) for details of analytical procedures.

Etymology. As in English “marauder,” in reference to the fierce appearance and dramatic mandibles.

Camelomecia Barden and Grimaldi, New Genus, Figures S2–S4

Diagnosis (Brief). Head and mandibular structure unique. Gena with V-shaped incision accommodating lateral articulation of mandible. Mandibles broad, cup-like (mesally concave), with anterior margin of inner surface with rows of dense, scale-like setae. Anterior margin of pronotum uniquely with collar of

enigmatic adaptations [17, 22, 24, 26]. The species and morphotypes reported here, from mid-Cretaceous amber of northern Myanmar, further expand this early diversity; additionally, several Cretaceous taxa are phylogenetically treated for the first time.

Systematics

See [Supplemental Information](#) for complete descriptions.

Gerontoformica Nel and Perrault

Gerontoformica Nel and Perrault, 2004: pg. 24. Type species: *G. cretatica* Nel and Perrault, by original designation. In Albian-aged amber from France.

Sphecomyrmodes Grimaldi and Engel, 2005: pg. 5. Type species: *Sphecomyrmodes orientalis*, by original designation. In Burmese amber. New synonymy.

Diagnosis (Emended). Distinguished from other Cretaceous genera by an uninterrupted row of peg-like denticles on the anterior margin of the clypeus; mandibles falcate, with one large apical tooth and one preapical tooth. The revised diagnosis and new generic synonymy is based on re-examination by one author (P.B.) of the type specimen, officially housed at the National Museum of Natural History, Paris. Species formerly placed in *Sphecomyrmodes* [16, 20, 25] are now placed in *Gerontoformica*.

Gerontoformica maraudera Barden and Grimaldi, New Species, Figure S2

Diagnosis (Brief). Distinguishable from other *Gerontoformica* species by elongate gaff-like mandibles; frontal lobe with pointed and projected anterolateral margin.

dense, fine pilosity. Petiole pedunculate, broadly attached to gaster.

Species. *C. janovitzi*, new Species. See [Supplemental Information](#) for description.

Etymology. Derived directly from English “camel,” referring to the head in profile, and *-mecia*, a common suffix in ant generic names derived from Greek.

DISCUSSION

All phylogenetic analyses recover Cretaceous lineages outside of crown-group ants, while *Brownimecia* (from the Late Cretaceous of New Jersey) was recovered either among a polytomy of living subfamilies or as the sister to all modern ants. Weighted analyses yield a paraphyletic grade of Cretaceous taxa at the base of the Formicidae, a finding consistent with a stem-group relationship (Figure 3). The placement of haidomyrmecines—the bizarre, tusk-jawed “hell ants”—as sister to all remaining ants is novel and largely based on mesosoma structure as well as head orientation and attachment. Monophyly of the three genera and five described species of haidomyrmecines is indisputable, based on their unique mandible and head morphology. Sphecomyrminae was formerly defined by the short antennal scape [44, 45], but this is a plesiomorphic character widespread in aculeate wasps and lost in the haidomyrmecine *Haidotermis cippus*. While the metanotum is obvious as a well-developed dorsal sclerite in most aculeates and in stem-group ants, its great reduction to a narrow groove, or its entire loss, is a striking

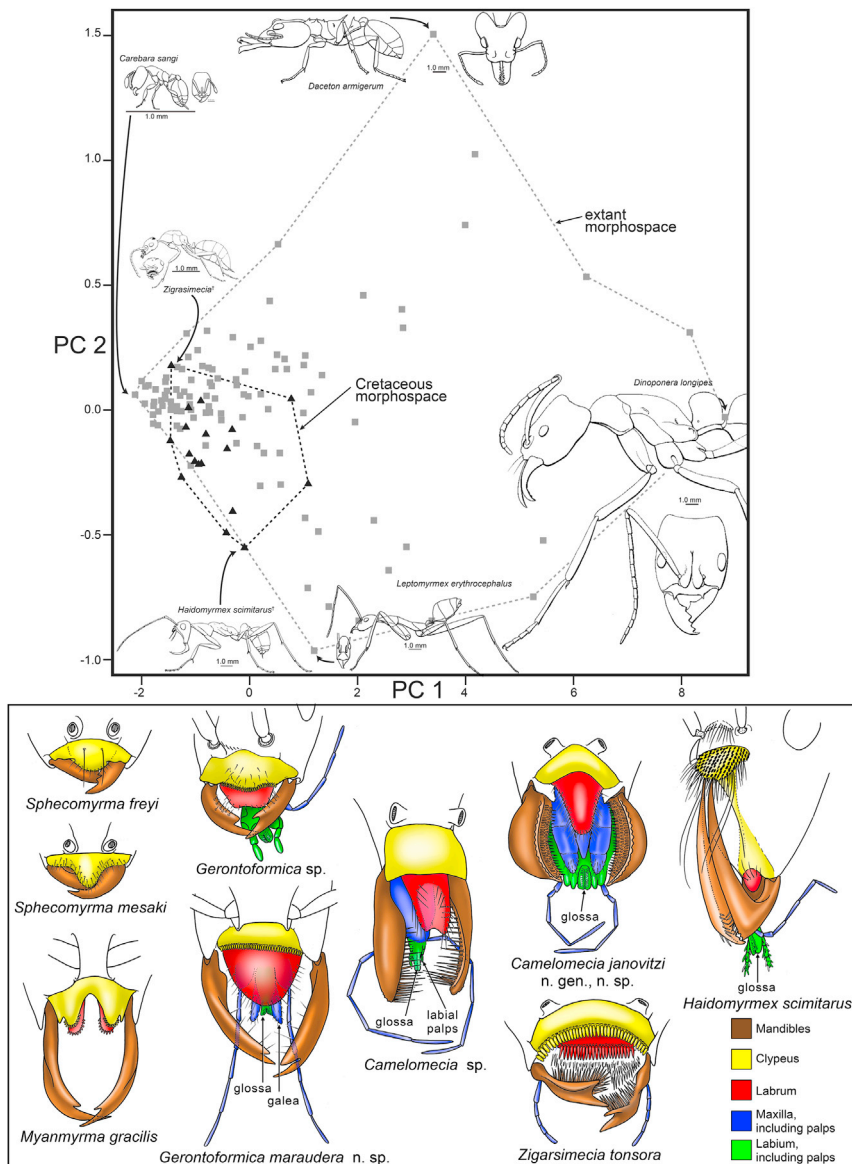


Figure 4. PCA Plot of Exemplar Living and Cretaceous Ant Workers and Assemblage of Mouthpart Diversity in Cretaceous Stem-Group Ants

Top: generated by PCA analysis (PC1 96% and PC2 3% of variance) of four body proportions of 107 living species in 96 genera and 19 Cretaceous species in five genera. For data and analyses see [Supplemental Information](#). Gray and black lines circumscribe living and Cretaceous morphospace, respectively. Body shapes and sizes of six living and extinct exemplar species are presented to same scale, with the exception of the minute ants *Carebara* and *Zigrasimecia* (which are greatly enlarged). Bottom: a summary of diversity and homology among Cretaceous stem-group ant mouthparts. Note that not all structures are preserved in known specimens of *Sphecomyrma freyi*, *S. mesaki*, and *Myanmyrma gracilis*, and, therefore, some components are missing. See also [Figures S2 and S3](#).

structure. Stem-group ants represent an extinct adaptive radiation, ranging from tiny, stout *Zigrasimecia* (2 mm body length) with short, setose mandibles; to the bulky *Gerontoformica magnus* (8.5 mm), built like some modern poneroids; to the slender, long-legged *Gerontoformica gracilis* and *Myanmyrma gracilis*, resembling modern spider ants (*Leptomymex*) and weaver ants (*Oecophylla*). Perhaps the most striking aspect of stem-group ants, and yet difficult to quantify, is the assortment of mandibular structures ([Figures 4 and S2–S4](#)). In the case of haidomyrmecine species, there are no analogs among modern insect taxa, and the feeding modes of *Zigrasimecia* and *Camelomecia* defy explanation.

Queen ants in Burmese and French amber were largely undifferentiated from workers beyond the development of

but overlooked synapomorphy of crown-group ants (some formicine and pseudomyrmecine workers possess this feature, presumably secondarily regained).

Morphometric analysis of Cretaceous ant workers indicates that stem-group ants were diverse and morphologically similar to modern ant workers ([Figure 4](#)). The morphospace of Cretaceous ants lies almost entirely within that of the modern species. Remarkably, even though species diversity of modern ants is nearly three orders of magnitude greater than that of the known Cretaceous ants, size and elongational morphospace of stem-group taxa occupies 10% that of living lineages (23% of the size diversity and 29% of the degree of elongation). This is a substantial underestimate for three reasons. (1) Ants in Cretaceous amber are known from five Laurasian localities only. (2) Preservation in amber biases against capture of larger specimens. (3) Our principal-component analysis (PCA) does not measure various other adaptive features, such as discrete traits and mouthpart

wings and flight-associated sclerites; in addition, dealate foundresses appear to have foraged—both of these primitive social features. Early ants probably formed small colonies of several dozen uniform individuals and were flexible in reproductive capacity among female nest mates, similar to basal living ants such as poneroids [46–48]. Social hierarchy is plastic in some ants with small colonies (generally <100 individuals), such as *Harpegnathos*, where workers retain the ability to reproduce and are morphologically very similar to founding queens [49]. This state contrasts with highly social taxa living in huge colonies (>100,000 individuals), such as *Atta* leaf-cutter ants and *Eciton* army ants, in which the dimorphism between reproductives and workers is profound. Still, these Cretaceous colonies were well developed enough to form aggregations, apparently coordinate in foraging, as well as aggressively engage other ants. One lineage, the haidomyrmecines, ranged from what is now western France to southeast Asia and western Canada and were clearly a

Cretaceous counterpart of modern trap-jawed ants. *Gerontofornica* extended throughout Laurasia, from present-day France to Myanmar. Other stem-group lineages were apparently more geographically restricted but strikingly diverse.

Although there is a 15–20 million year gap surrounding the K-Pg (Cretaceous–Paleogene) boundary for ants, we surmise that the lack of stem-group ants in the Cenozoic represents definitive absence after this boundary. Given the great competitive advantage of sociality, why did these diverse, social lineages become extinct? The bulk of ant biomass today is dominated by groups like dolichoderines, dorylines, formicines, and myrmicines [50], many of which form large to massive colonies with extreme caste specialization. The radiation of modern ants in the latest Cretaceous and early Paleogene probably ecologically overwhelmed Cretaceous stem groups, consistent with Wilson and Hölldobler's [51] concept of “dynastic succession.” Several stem-group ant lineages possessed uniquely specialized mouthparts—perhaps their reliance on particular food sources made them especially susceptible to extinction. Exploration for insect fossils around the critical 15–20 million year gap straddling the K-Pg boundary will no doubt further clarify patterns of ant extinction and modern radiation, enriching the increasingly complex history of one of nature's greatest success stories.

EXPERIMENTAL PROCEDURES

Described taxa are registered in ZooBank under LSIDs urn:lsid:zoobank.org:pub:7F08DE99-7838-40CB-BD40-8123E8C5AC94; full systematic descriptions are available in [Supplemental Information](#). Orientations of individual ants were measured to test for positional patterns within each piece ([Figure 1](#); [Figure S1](#); [Supplemental Information](#)). Type specimens are deposited in the American Museum of Natural History, New York (AMNH). Phylogenetic relationships of nine Cretaceous genera were estimated using exemplars from 12 well-preserved species, plus exemplars of 24 living species in most major living subfamilies, employing weighted and unweighted parsimony-based analyses of 42 morphological characters. For morphometric analyses, 107 species were sampled across 96 genera and all 16 extant subfamilies, measuring head and post-cephalic proportions. Our sampling deliberately included extant extremes, such as the largest (*Dinoponera*: ~3 cm total length) to smallest (*Carebara*: ~1.3 mm) living ants. Cretaceous ants are represented by 19 species in five genera (*Haidomyrmex*, *Haidomyrmodes*, *Gerontofornica*, *Sphecomyrma*, *Zigrasimexia*). A PCA identified two factors explaining nearly all variance: overall size (PC1) and degree of head and body elongation (PC2).

ACCESSION NUMBERS

The accession number for the morphological data reported in this paper is TreeBase: TB2:S18555.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, four figures, and one table and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2015.12.060>.

AUTHOR CONTRIBUTIONS

P.B. and D.A.G. designed the research. P.B. conducted morphological and phylogenetic analyses. P.B. and D.A.G. drafted the manuscript.

ACKNOWLEDGMENTS

We thank Tyler Janovitz, James Zigras, and Scott Anderson for providing specimens; Stefan Cover, Gavin Broad, and Vincent Perrichot for advice, host-

ing visits, and providing access to specimens in the Museum of Comparative Zoology, Natural History Museum in London, and University of Rennes, respectively; Morgan Hill and Henry Towbin at the AMNH Microscopy and Imaging Facility and Mark Riccio at the Cornell Biotechnology Resource Center Imaging Facility for assistance with CT imaging; Paul Nascimbene (AMNH) for amber preparation of delicate and important specimens; and Steve Thurston for figure preparation. Valerie Krishna, Phil Ward, and two anonymous reviewers provided careful comments that improved this manuscript. Funding was provided by the Richard Gilder Graduate School (AMNH) and the National Science Foundation (Graduate Research Fellowship to P.B. and Doctoral Dissertation Improvement Grant #1313547 to D.A.G. and P.B.).

Received: November 5, 2015

Revised: December 16, 2015

Accepted: December 17, 2015

Published: February 11, 2016

REFERENCES

- Davidson, D.W., Cook, S.C., Snelling, R.R., and Chua, T.H. (2003). Explaining the abundance of ants in lowland tropical rainforest canopies. *Science* 300, 969–972.
- Fittkau, E.J., and Klinge, H. (1973). On biomass and trophic structure of the central Amazonian rain forest ecosystem. *Biotropica* 5, 2–14.
- Hölldobler, B., and Wilson, E.O. (1990). *The Ants* (Cambridge: Harvard University Press).
- McIver, J.D., and Stonedahl, G. (1993). Myrmecomorphy: morphological and behavioral mimicry of ants. *Annu. Rev. Entomol.* 38, 351–377.
- Parker, J., and Grimaldi, D.A. (2014). Specialized myrmecophily at the ecological dawn of modern ants. *Curr. Biol.* 24, 2428–2434.
- Oster, G.F., and Wilson, E.O. (1978). *Caste and Ecology in the Social Insects* (Princeton: Princeton University Press).
- Beshers, S.N., and Fewell, J.H. (2001). Models of division of labor in social insects. *Annu. Rev. Entomol.* 46, 413–440.
- 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.
- 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.
- 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.
- Wilson, E.O., Carpenter, F.M., and Brown, W.L., Jr. (1967). The first Mesozoic ants with the description of a new subfamily. *Psyche* (Camb Mass) 74, 1–19.
- Grimaldi, D.A., Agosti, D., and Carpenter, J.M. (1997). New and rediscovered primitive ants (Hymenoptera: Formicidae) in Cretaceous amber from New Jersey and their phylogenetic relationships. *Am. Mus. Novit.* 3208, 1–43.
- 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.
- Wilson, E.O. (1985). Ants from the Cretaceous and Eocene amber of North America. *Psyche* (Camb Mass) 92, 205–216.
- Blusky, G.M. (1999). New ant taxa (Hymenoptera Formicidae) from Canadian amber. *Палеонтол. ж.* 4, 73–76.
- 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.
- McKellar, R.C., Glasier, J., and Engel, M.S. (2013). A new trap-jawed ant (Hymenoptera: Formicidae: Haidomyrmecini) from Canadian Late Cretaceous amber. *Can. Entomol.* 145, 454–465.

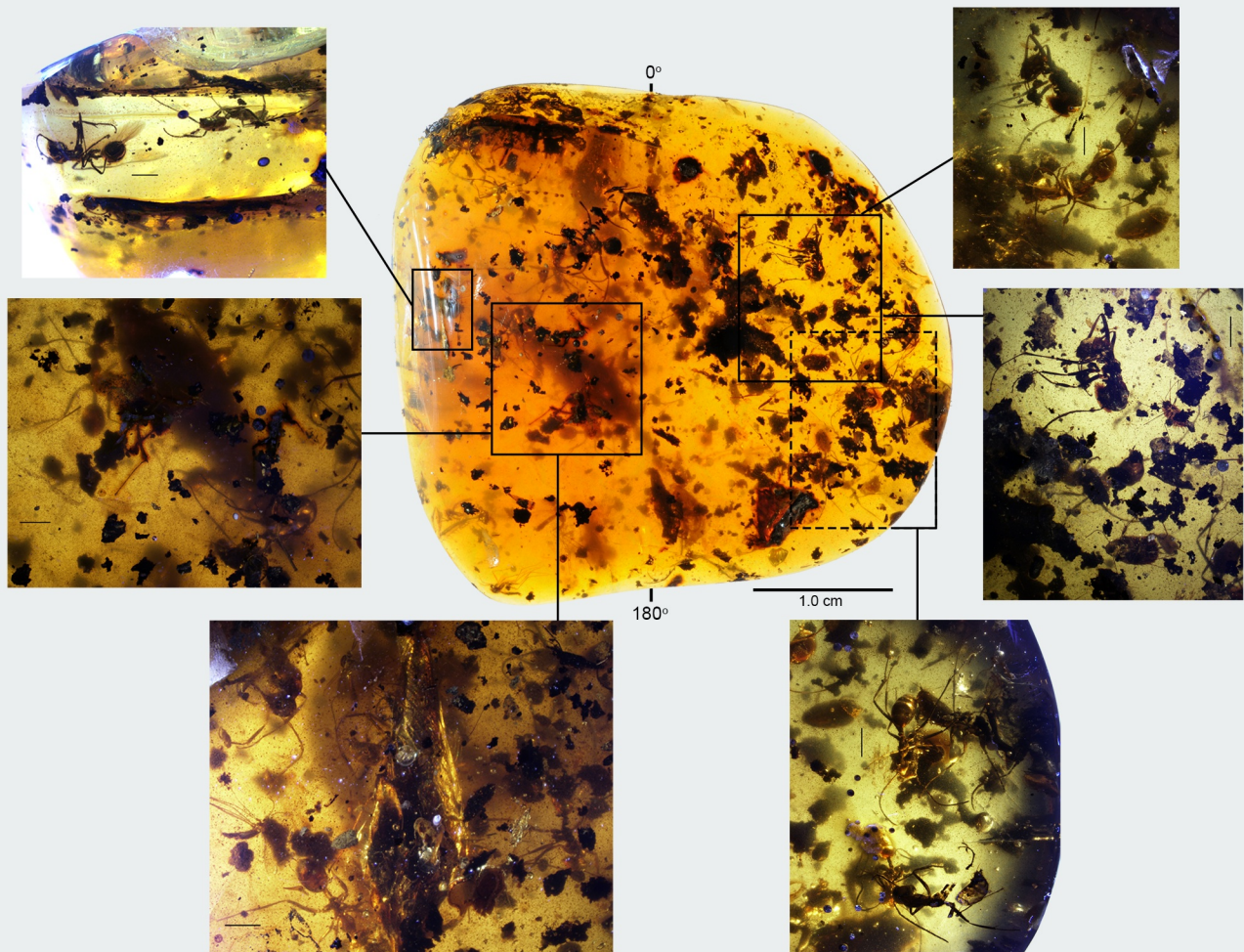
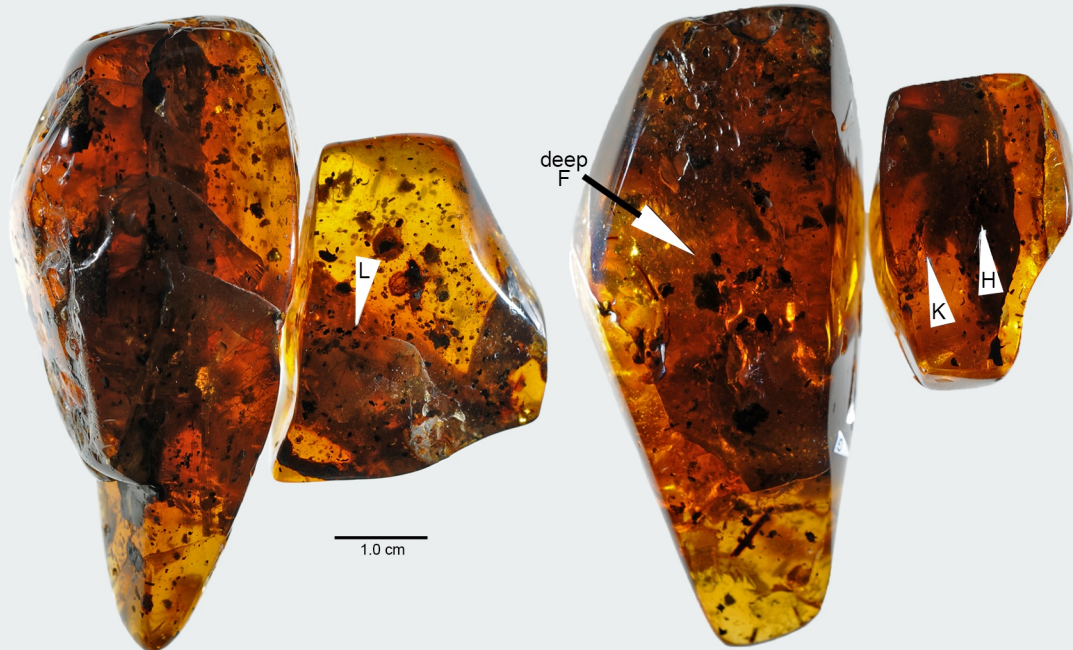
18. Dlussky, G.M. (1987). New Formicoidea (Hymenoptera) of the Upper Cretaceous. *Палеонтол. ж.* 20, 131–135.
19. Nel, A., Perrault, G., Perrichot, V., and Néraudeau, D. (2004). The oldest ant in the lower cretaceous amber of Charente-maritime (SW France) (Insecta: Hymenoptera: Formicidae). *Geol. Acta.* 2, 23–29.
20. Perrichot, V., Nel, A., Néraudeau, D., Lacau, S., and Guyot, T. (2008). New fossil ants in French Cretaceous amber (Hymenoptera: Formicidae). *Naturwissenschaften* 95, 91–97.
21. 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.
22. Dlussky, G.M. (1996). Ants (Hymenoptera Formicidae) of Burmese amber. *Палеонтол. ж.* 30, 449–454.
23. 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.
24. Barden, P., and Grimaldi, D. (2013). A new genus of highly specialized ants in Cretaceous Burmese amber (Hymenoptera: Formicidae). *Zootaxa* 3681, 405–412.
25. Barden, P., and Grimaldi, D. (2014). A diverse ant fauna from the mid-cretaceous of Myanmar (Hymenoptera: Formicidae). *PLoS ONE* 9, e93627.
26. Perrichot, V. (2014). A new species of the Cretaceous ant *Zigrasimecia* based on the worker caste reveals placement of the genus in the Sphecomyrminae (Hymenoptera: Formicidae). *Myrmecol. News* 19, 165–169.
27. LaPolla, J.S., Dlussky, G.M., and Perrichot, V. (2013). Ants and the fossil record. *Annu. Rev. Entomol.* 58, 609–630.
28. Dlussky, G.M., and Rasnitsyn, A.P. (2007). Paleontological record and stages of ant evolution. *Usp. Sovrem. Biol.* 127, 118–134.
29. Rust, J., Singh, H., Rana, R.S., McCann, T., Singh, L., Anderson, K., Sarkar, N., Nascimbene, P.C., Stebner, F., Thomas, J.C., et al. (2010). Biogeographic and evolutionary implications of a diverse paleobiota in amber from the early Eocene of India. *Proc. Natl. Acad. Sci. USA* 107, 18360–18365.
30. Wang, B., Rust, J., Engel, M.S., Szewdo, J., Dutta, S., Nel, A., Fan, Y., Meng, F., Shi, G., Jarzembowski, E.A., et al. (2014). A diverse paleobiota in early eocene Fushun amber from China. *Curr. Biol.* 24, 1606–1610.
31. Dlussky, G.M. (1983). New subfamily of Late Cretaceous Hymenoptera: “missed link” between ants and Scoliidae. *J. Paleontol.* 17, 65–78.
32. Wilson, E.O. (1987). The earliest known ants: an analysis of the Cretaceous species and an inference concerning their social organization. *Paleobiology* 13, 44–53.
33. Yek, S.H., and Mueller, U.G. (2011). The metapleural gland of ants. *Biol. Rev. Camb. Philos. Soc.* 86, 774–791.
34. Perrichot, V., Lacau, S., Néraudeau, D., and Nel, A. (2008). Fossil evidence for the early ant evolution. *Naturwissenschaften* 95, 85–90.
35. Engel, M.S., Barden, P., Riccio, M.L., and Grimaldi, D.A. (2016). Morphologically Specialized Termite Castes and Advanced Sociality in the Early Cretaceous. *Curr. Biol.* Published online on February 11, 2016. <http://dx.doi.org/10.1016/j.cub.2015.12.061>.
36. Keller, R.A., Peeters, C., and Beldade, P. (2014). Evolution of thorax architecture in ant castes highlights trade-off between flight and ground behaviors. *eLife* 3, e01539.
37. Wheeler, W.M. (1915). The ants of the Baltic amber. *Schrift. Phys. Ökonom. Ges. Königsberg* 55, 56–59.
38. Grimaldi, D.A., and Nascimbene, P.C. (2010). Raritan (New Jersey) amber. In *Biodiversity of Fossils in Amber from the Major World Deposits*, D. Penney, ed. (Manchester: Siri Scientific Press), pp. 167–191.
39. Perrichot, V., Néraudeau, D., Tafforeau, P., and Penney, D. (2010). Charentese amber. In *Biodiversity of Fossils in Amber from the Major World Deposits*, D. Penney, ed. (Manchester: Siri Scientific Press), pp. 192–207.
40. Ito, F. (1993). Observation of group recruitment to prey in a primitive ponerine ant *Amblyopone* sp. (*reclinata* group) (Hymenoptera: Formicidae). *Insectes Soc.* 40, 163–167.
41. Duncan, F.D., and Crewe, R.M. (1994). Group hunting in a ponerine ant *Leptogenys nitida* Smith. *Oecologia* 97, 118–123.
42. Porter, S.D., and Jorgensen, C.D. (1981). Foragers of the harvester ant *Pogonomyrmex owyheei*: a disposable caste? *Behav. Ecol. Sociobiol.* 9, 247–256.
43. Schmid-Hempel, P., and Schmid-Hempel, R. (1984). Life duration and turnover of foragers in the ant *Cataglyphis bicolor* (Hymenoptera Formicidae). *Insectes Soc.* 31, 345–360.
44. Grimaldi, D., and Engel, M.S. (2005). *Evolution of the Insects* (Cambridge: Cambridge University Press).
45. Bolton, B. (2003). Synopsis and Classification of Formicidae. *Mem. Am. Entomol. Inst.* 71, 1–370.
46. Ito, F. (1993). Social organization in a primitive ponerine ant: queenless reproduction dominance hierarchy and functional polygyny in *Amblyopone* sp. (*reclinata* group) (Hymenoptera: Formicidae: Ponerinae). *J. Nat. Hist.* 27, 1315–1324.
47. Peeters, C. (1993). Monogyny and polygyny in Ponerine ants with or without queens. In *Queen Number and Sociality in Insects*, L. Keller, ed. (Oxford: Oxford University Press), pp. 234–261.
48. Peeters, C. (1997). Morphologically “primitive” ants: comparative review of social characters and the importance of queen-worker dimorphism. In *The Evolution of Social Behavior in Insects and Arachnids*, J.C. Choe, and B.J. Crespi, eds. (Cambridge: Cambridge University Press), pp. 372–391.
49. Peeters, C., Liebig, J., and Hölldobler, B. (2000). Sexual reproduction by both queens and workers in the ponerine ant *Harpegnathos saltator*. *Insectes Soc.* 47, 325–332.
50. Ward, P.S. (2014). The phylogeny and evolution of ants. *Annu. Rev. Ecol. Evol. Syst.* 45, 23–43.
51. Wilson, E.O., and Hölldobler, B. (2005). The rise of the ants: a phylogenetic and ecological explanation. *Proc. Natl. Acad. Sci. USA* 102, 7411–7414.

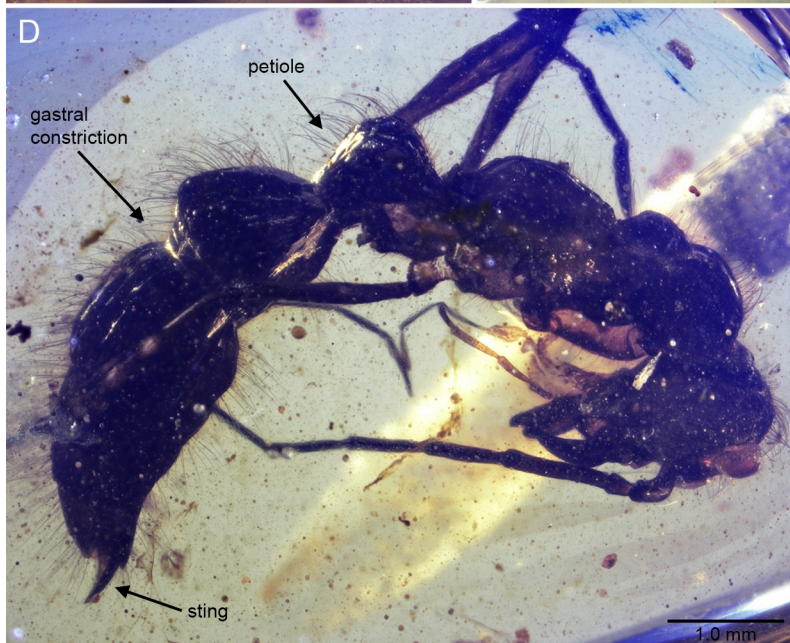
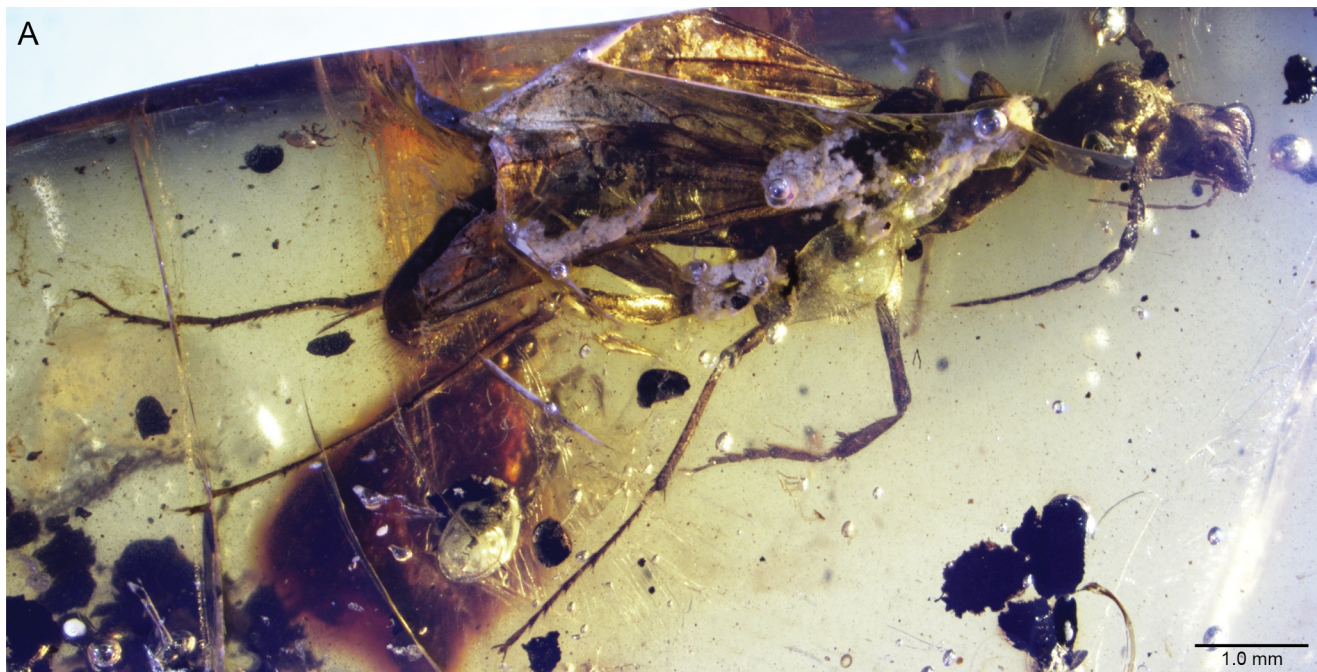
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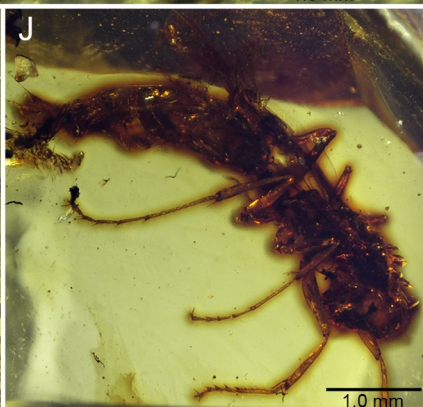
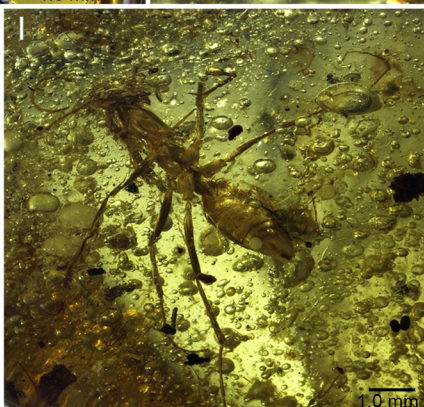
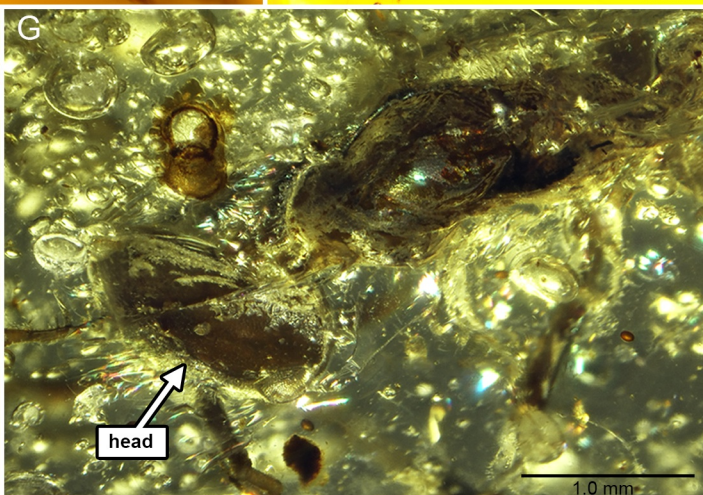
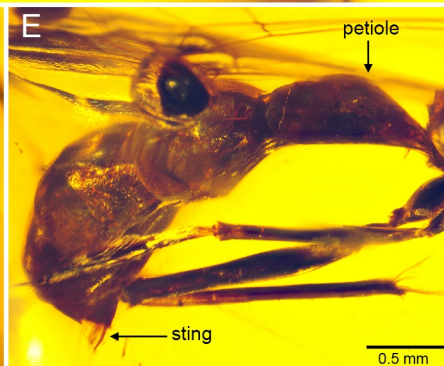
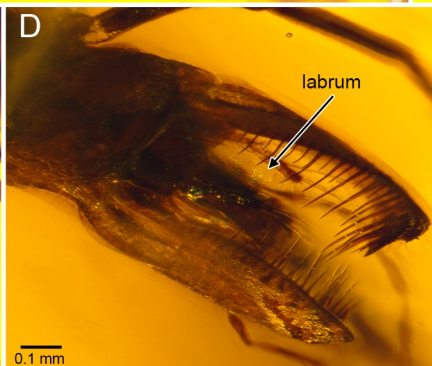
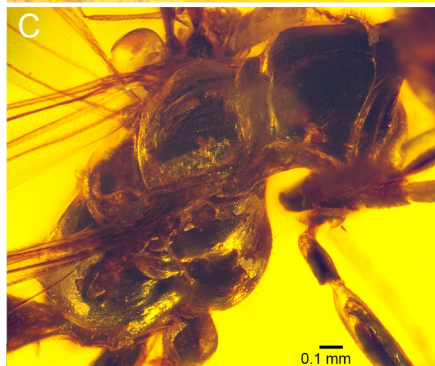
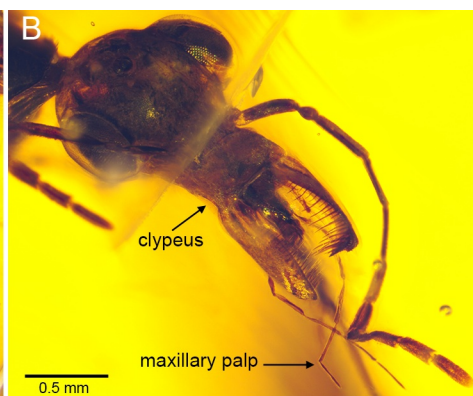
Supplemental Information

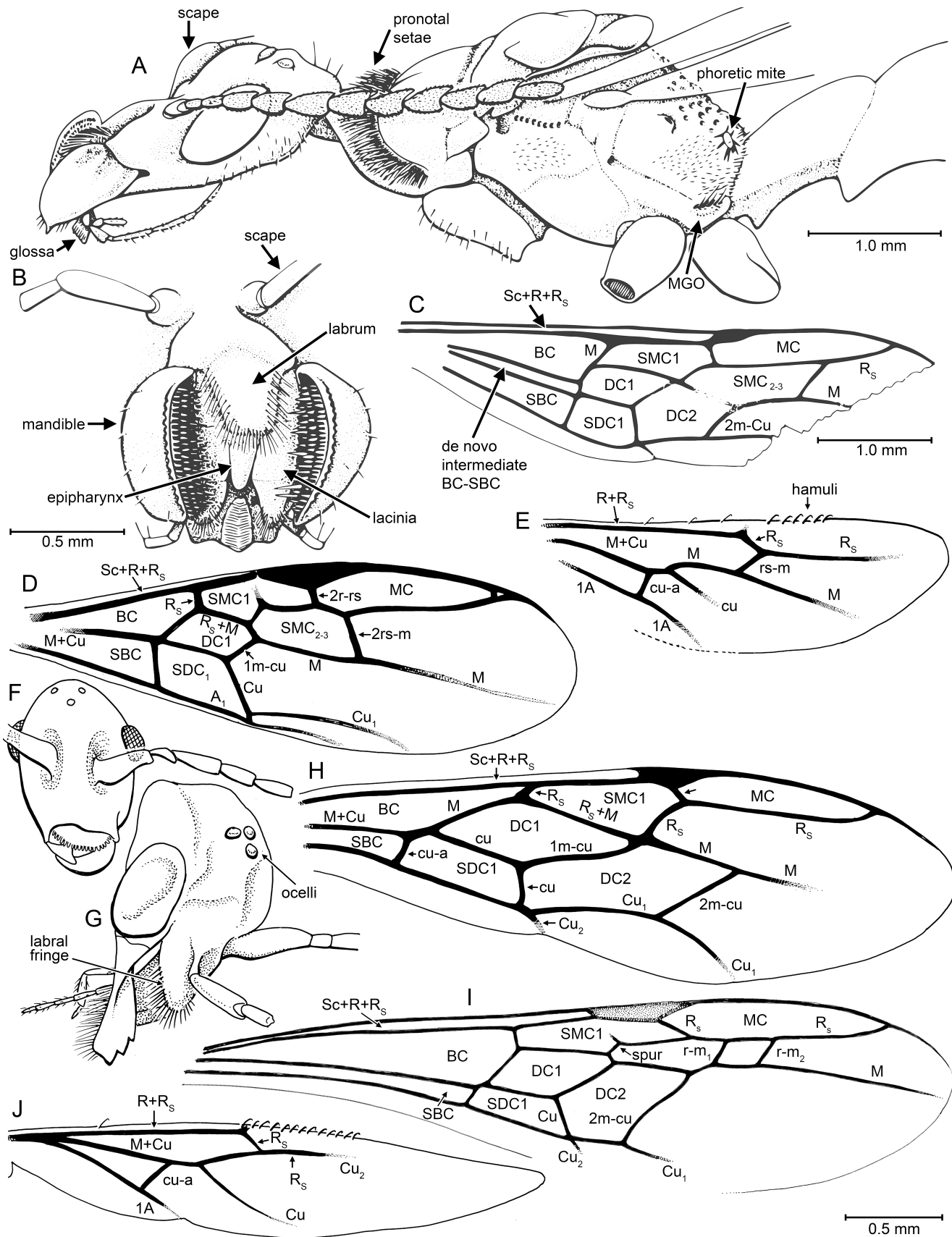
**Adaptive Radiation in Socially Advanced
Stem-Group Ants from the Cretaceous**

Phillip Barden and David A. Grimaldi









Supplemental Figure Legends

Figure S1. Photographs of Cretaceous worker ant assemblage specimens. **Top.** Complimentary views of JZC Bu16 shown in Figure 1, bottom left. **Bottom.** Large assemblage of Cretaceous worker ants comprising three species. Photomicrograph of entire piece of JZC Bu1645, containing 21 worker ants of *Gerontoformica orientalis* (Engel and Grimaldi), *G. contegus* (Barden and Grimaldi), and *G. robustus* (Barden and Grimaldi), with detailed views of worker aggregations. Scale bars in detailed views equal to 1.0 mm. Also related to Figure 1.

Figure S2. Photomicrographs of *Camelomecia janovitzi* and *Gerontoformica maraudera* holotypes. **A.** Lateral view of entire *Camelomecia janovitzi* holotype, AMNH Bu-TJ003. **B.** Frontal view of head featuring setose mouthparts AMNH Bu-TJ003. **C.** Alternate lateral view AMNH Bu-TJ003. **D.** Lateral view of entire *Gerontoformica maraudera* holotype, JZC Bu1846. **E.** Head from frontal view featuring long, gaff-like mandibles JZC Bu1846. See also Figure 4.

Figure S3. Photomicrographs of ant reproductives in Burmese amber. **A.** Dorsolateral view of entire *Camelomecia* sp specimen Tong-112. **B.** Dorsolateral view of head, specimen Tong-112. **C.** Dorsolateral view of mesosoma, specimen Tong-112. **D.** Enlarged dorsolateral view of mouthparts, highlighting sharp, teeth-like setae, specimen Tong-112. **E.** Dorsolateral view of metasoma, beginning at abdominal segment II (petiole) on the right, specimen Tong-112. **F.** Dorsolateral view of winged queen *Gerontoformica* sp., specimen JZC Bu313. **G.** Head and mesosoma of JZC Bu1821. **H.** Lateral view of male ?*Camelomecia* sp., specimen JZC Bu1818. **I.** Ventral view of dealate queen *Gerontoformica* sp., specimen JZC Bu1821. **J.** Dorsolateral view of winged queen *Gerontoformica* sp., specimen JZC Bu318. See also Table S1.

Figure S4. Reconstruction of *Camelomecia janovitzi* and diagnostic positions of ant reproductives in Burmese amber. **A.** Entire visible lateral view of *C. janovitzi*. **B.** Frontal view of *C. janovitzi* mouthparts as preserved. **C.** Forewing of *C. janovitzi* as preserved. **D.** Forewing of *Gerontoformica* sp., queen JZC Bu313. **E.** Hindwing of JZC Bu313. **F.** Head of JZC Bu313. **G.** Head of ?*Camelomecia* sp., male JZC Bu1818. **H.** Forewing of JZC Bu1818. **I.** Forewing of *Camelomecia* sp., queen Tong-112. **J.** Hindwing of JZC Bu1818. Reconstructions D-J Correspond to scale bar at bottom right. See also Figure 4.

Table S1 | Summary of multiple castes known among Cretaceous stem-group amber ants.

Group	Worker		Queens		Male	References
	♀	♀	Alate	Dealate	♂	
			♀			
<i>Haidomyrmex</i>	x			x		[S18]
<i>Haidomyrmodes</i>	x		x			[S17]
<i>Gerontoformica</i>	x		x	x		[S12]; Herein
<i>Zigrasimecia</i>	x			x		[S19,S20]
<i>Camelomecia</i>			x		x	Herein
<i>Sphecomyrma</i>	x				x	[S1]

Supplemental Experimental Procedures

Phylogenetic analysis

While some Cretaceous ants are attributable to modern groups, the vast majority are distinct from living taxa. To explore the position of Cretaceous ants not attributable to modern subfamilies, a morphological matrix was assembled with special consideration to avoid including characters known to be homoplastic within crown-group ants; some characters were redrafted from Grimaldi et al.[S1] and Keller[S2]. A total of forty-one taxa were represented by forty-two morphological characters scored from traditional light microscopy, descriptions, and high-resolution CT-scan reconstructions. Numerous sister groups have been proposed for ants. To accommodate this ambiguity, included in the taxonomic sampling were five outgroup representatives from vespoidea relatives. These comprise members of the families Scoliidae, Heterogynaidae, and Sphecidae. The latter two groups reflect the recent hypothesis that Apoidea is sister to Formicidae[S3]. Seven putative stem-group Cretaceous species and genera were included in order to explore their position relative to modern ant groups. Excluded from the analysis were very poorly preserved specimens as well as additional species of genera already represented and known to vary with features that are highly homoplastic within crown group ants (i.e. pilosity, sculpturing, head and body shape). Twenty-four crown-group ant species were included to represent all major modern subfamilies, with a slight overrepresentation toward basal lineages. Included in the crown-group sampling to evaluate fossil reliability was a single undisputed crown-group fossil from the Cretaceous, *Kyromyrmex neffi* (Late Cretaceous of New Jersey). This fossil possesses a complex derived feature known as an acidopore, a synapomorphy of the subfamily Formicinae. In all unconstrained analyses *Kyromyrmex* was recovered within Formicinae.

Because worker ants are most often recovered in amber, and modern taxonomy is based largely on workers, we chose to focus the character matrix on the morphology of wingless female ants. The comparison of apterous worker castes and winged females of non-social outgroups may appear problematic. However, some fossil taxa are known from reproductive and worker castes, and in the cases of *Haidomyrmex*, *Haidomyrmodes*, and *Zigrasimecia* where queen and worker castes are known, there appears to be little morphological differentiation—beyond flight-associated thoracic sclerites—between workers and reproductives even at the generic level. This is also the case in a single, putative *Gerontoformica* alate presented herein. It must be noted that Wilson[S4] proposed that lithified Cretaceous fossils of winged aculeates, described by Dlussky[S5] as a formicid family, the Armaniidae, are the queens of *Sphecomyrmex* and *Cretomyrmex* ants, genera which are known as wingless females in Canadian, New Jersey, and Siberian amber, an inference based on gaster proportions. Although not discussed by Wilson, the wing venation of Armaniidae is very similar to that of male *Sphecomyrmex*[S1]. However, armaniids are quite large and have a distinctly thicker petiole. Our results presented here based on finely preserved, uncompressed specimens in amber support much less dimorphism between queen and worker ants from the Cretaceous. Therefore, Armaniidae appear to be a lineage distinct from true Formicidae. Thus, in the absence of wing venation characters, the comparisons made here are valid.

The dataset was analyzed under parsimony with TNT v. 1.1[S6] under a variety of conditions to explore the sensitivity of novel hypotheses to search parameters. Searches were performed under both equal- and implied-weighting as in Goloboff[S7]. It has been shown that weighting against homoplastic characters can lead to more stable topologies and improved resampling support[S8]. Implied-weighting procedures involve assigning an *a priori* constant of concavity (K value); therefore the TNT setk script, developed by Salvador Arias, was utilized to identify the most appropriate K value through the formula suggested by Goloboff et al.[S8]. A value of 6.875 was returned and subsequently implemented in implied weighting runs. To incorporate hypotheses generated from molecular phylogenetics, the topology of crown-group ants was constrained in some searches to reflect the subfamilial relationships presented in Brady et al [S9]. In these instances, well-supported relationships among living subfamilies were enforced, rendering a static, monophyletic crown-group. This constraint was enforced only after weighted and unweighted unconstrained analyses found that Cretaceous ants were not recovered inside the clade of crown-group Formicidae. A total of four search protocols were implemented comprising constrained and unconstrained analyses for both weighting regimes (unweighted; K=6.875). Regardless of weight or constraints, 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 20 times. Nodes were evaluated with Bremer supports and bootstrap resampling (1000 pseudoreplicates).

In no unconstrained analyses were sphecomyrmine ants placed among crown-group lineages. Both unweighted analyses found sphecomyrmine terminals recovered as a polytomy along with the branch leading to modern ants. *Brownimecia* was recovered as sister to all modern, crown-group ants in all weighted, unconstrained analyses; however it occurs among a basal polytomy of modern subfamilies in the unweighted, unconstrained analysis. *Brownimecia clavata* possesses a long scape, as well as a metanotal groove, which are features of modern ants and likely contribute to this position. Weighted search protocols yielded a grade of stem-group Cretaceous genera at the

base of the ant tree, regardless of topology constraint. Weighting protocols also recovered Haidomyrmecini as sister to all other ants. The positions of *Gerontoformica*, *Sphecomyrma*, and *Zigrasimecia* were somewhat variable, although the placements of the Haidomyrmecini and *Brownimecia* were fairly constant. A preferred weighted ($K=6.875$) and constrained tree was selected based on a low homoplasy index and congruence with molecular hypotheses. Unconstrained topologies resulted in incongruence with previous molecular results, particularly with regard to the polarity of the tree. Bootstrap values were low for many stem-group clades, likely a reflection of few defining synapomorphies among a suite of convergent morphologies. Morphological matrix and all generated trees can be found in the TreeBASE data repository at <http://purl.org/phylo/treebase/phyloids/study/TB2:S18555>.

Morphometrics

To create temporal comparisons of morphospace, a morphometric dataset was generated of extant and stem-group worker ants comprising approximately 1400 individual measurements. Four measurements of each specimen were taken utilizing museum specimens, descriptions, and Antweb.org: Head Length (HL) measured medially in frontal view; Head Width (HW) measured at its greatest in frontal view (excluding outer margins of eyes); Mesosoma Length (MsL) also known as Weber's length, taken in lateral view from the anterodorsal-most point of the pronotum (excluding any collar) to the posteroventral-most point of the propodeum; Mesosoma Height (MsH) taken in lateral view from the ventral-most point of the propleuron to the dorsal-most margin of the pronotum. These measurements, while certainly excluding some morphological diversity, were selected to best allow for direct comparison of basic body shape between fossil and extant taxa. This procedure is particularly important in fossil specimens with limited viewing angles or distortion. All sixteen subfamilies and 96 extant genera were sampled totaling 107 crown-ant morphotypes. Included were three instances of multiple castes within the same species and eight instances of multiple species within a genus. Taxonomic sampling of extant morphospace is not exhaustive, but rather is largely meant to capture the extremes and boundaries in morphospace. Five Cretaceous genera were included totaling 18 morphotypes (equal to species). Some taxa were not included due to degradation or visual impediments preventing reliable measurement. In all possible cases, three specimens were measured for each morphotype and a mean was generated for each. Means were then concatenated and transformed utilizing a principal components analysis implemented in R (v. 3.1.1, R Core Team, 2014). Principal component 1 (general body size) and principal component 2 (degree of body/head elongation) explain 96% and 3% of the variance, respectively.

Imaging Protocols

CT scanning took place at the American Museum of Natural History and the Cornell University Biotechnology Resource Center Imaging Facility, Ithaca, New York.

American Museum of Natural History

Specimens were scanned utilizing a General Electric Phoenix vtomex s, which has both 180 and 240kV x-ray tubes. Tube voltage and current were set according to each individual specimen to maximize refraction between amber matrix and insect inclusions. Amber fossils were mounted atop a custom chuck allowing for a precise center of rotation. Subsequent 2-dimensional x-ray images were then transformed into projected Z-stacks utilizing the program phoenix datos|x reconstruction v2.2.1 RTM. Z-stacks were imported into VGStudio Max (64-bit v2.2.2.62189) for rendering and analysis. In some cases, multiple scans were taken of single specimens and stitched together using ImageJ v1.48 (Rasband 1997-2014).

Cornell Biotechnology Resource Center Imaging Facility

Scans were performed with a Zeiss VERSA XRM-520 utilizing a variety of specimen dependent voltage, current, and exposure settings. Resulting TIFF stacks were then rendered and analyzed in OsiriX (64 bit v5.5) and Avizo 8.0 (VSG).

Morphological Characters

1. **Orientation of head:** 0) hypognathous 1) prognathous.
 - a. Axial position of head. Hypognathous with the head vertical and ventrally positioned mouthparts; prognathous with the head horizontal and anteriorly facing mouthparts.
2. **Mandibular orientation:** 0) parallel to axial plane of head 1) perpendicular to axial plane of head.
 - a. In which plane the mandibles primarily maneuver. While all known modern ants possess mandibles that maneuver in a horizontal plane, there is evidence that ants within the tribe Haidomyrmecini articulated their mandibles vertically.
3. **Anterior margin of clypeus with row of peg-like denticles:** 0) absent 1) present.
 - a. Short, peg-like setae present along the anterior margin of the clypeus. There is considerable variation in the structure of these setae among extant amblyponine species, particularly with

regard to their apices (flattened, sheer angled face, sharp). There is no apparent variation among Cretaceous species that possess this feature.

4. **Labral pegs:** 0) absent 1) present.
 - a. Stout setae exhibited along the exposed anterior labral surface. Such setae are present in some extant amblyoponine species, as well as the Cretaceous genus *Zigrasimecia*.
5. **Clypeus development:** 0) highly reduced 1) a clearly visible sclerite 2) extending to vertex of head.
 - a. The size and degree of clypeal development. Highly reduced, indicating the clypeus does not appear visible in frontal view, often in cases where the antennal sockets are abutting the anterior margin of the head. This is the case in some extant taxa including *Martialis* and Proceratiinae.
6. **Clypeal suture syndrome:** 0) clypeal sulci absent 1) highly reduced 2) developed.
 - a. In reference to sulci, the overall development of the posterior and lateral clypeal margins. Absent refers to completely obliterated or smooth margins; reduced refers to faint outlines, developed as clear depressed demarcations but without a distinct sulcus.
7. **Position of antennal sockets:** 0) posterior to clypeus 1) anterior.
 - a. Position of antennal sockets with reference to median portion of posterior clypeal margin.
8. **Clypeal process:** 0 absent 1) present.
 - a. A distinct protrusion not associated with the antenna as in the case of a frontal lobe. Often setose and with a sheer anterior face. A defining character of the Haidomyrmecini.
9. **Torulus syndrome:** 0) torular sclerite not visibly raised 1) developed as shield covering antennal base 2) developed and fused with frontal lobe.
 - a. The development of the torulli. The fusion of the torulus and frontal lobe is considered to be a synapomorphy of ponerine ants[S2].
10. **Frontal lobe:** 0) absent 1) single lobe not derived from frontal carina 2) present and bilobed 3) originating as broad and bifurcating.
 - a. A medial lobe present between the antennal sockets. The state “broad form” refers to a raised medial process between antennal sockets, apparently resulting from dorsal expansion of the head capsule, not associated with development of the frontal carina, although the frontal carina may abut this feature. States two and three correspond with the dorsolateral expansion of the frontal carina[S2].
State three with frontal lobe splitting into two distinct ridges surrounding clypeus as in *Camelomecia*.
11. **Frontal lobe syndrome:** 0) bulbous 1) pinched-in posteriorly
 - a. Overall shape of the frontal lobe. While most frontal lobes are anteriorly situated, a posteriorly narrowed state is thought to be a synapomorphy of Ponerinae + Paraponerinae + Amblyoponinae (the relationship among these three subfamilies still not clear).
12. **Scape length:** 0) equal to all other flagellomeres individually 1) larger than any other antennal segments but less than 0.25x antenna length 2) greater than 0.25x total antenna length.
 - a. The proportion of the scape relative to total antenna length.
13. **Antennal segments:** Continuous character.
 - a. The total number of antennal segments comprising the antenna. A continuous character state ranging from 7 to 13 for included taxa.
14. **Ocelli:** 0) absent 1) present.
 - a. The presence of simple eye structures on the head vertex. These can be quite variable in size.
15. **Compound eye:** 0) absent 1) present as single ommatidium 2) present as compound facets.
 - a. Laterally positioned visual organ. Apparently single ommatidium condition is the result of secondary fusion of ommatidia, although the structure acts like a single lens or ocellus.
16. **Development of posterior portion of pronotum:** 0) narrow strip 1) developed.
 - a. The degree of pronotal development in the posterior axis. State zero indicates the mesonotum comprises most of the anterior thoracic region, state one reflects a pronotum that extends posteriad. Outgroup taxa possess a highly developed mesonotal sclerite, presumably associated with flight.
17. **Pronotal lobe:** 0) absent 1) present.
 - a. Pronotum with or without a rounded lobe visible in lateral view along posterior margin. This lobe jutting into the mesopleuron—a key feature of Apoidea. (To improve and test out-group relationships).
18. **Propleuron:** 0) reduced, not visible in lateral view 1) developed, visible in lateral view.

- a. Development of propleuron, reflected in visibility from lateral view.
- 19. **Pro-mesonotal suture:** 0) absent 1) present and flexible (articulating) 2) present and rigid (not articulating).
 - a. The state of the promesonotal suture, best viewed in lateral view.
- 20. **Metanotum:** 0) Distinct sclerite 1) reduced to a groove 2) obliterated.
 - a. The development of the metanotum, visible in lateral or from dorsal view. Nearly all described Cretaceous and out-group taxa possess a distinct metanotal sclerite, which is not the case in modern ants. In nearly all extant species, the metanotum may be a vestigial narrow groove (called the metanotal groove) or obliterated entirely. Some derived crown-group ants within Formicinae and Pseudomyrmecinae possess this feature.
- 21. **Propodeal suture:** 0) absent 1) present.
 - a. The presence of an anterior propodeal suture in lateral view.
- 22. **Mesopleural sutures:** 0) absent/obliterated 1) anterior suture present only 2) posterior suture present only 3) both sutures present.
 - a. Degree to which the mesopleuron is guarded both anteriorly and posteriorly by distinct sutures.
- 23. **Metapleural gland:** 0) absent 1) present.
 - a. Presence of a distinct gland, with an opening on the posterior portion of the mesopleuron.
- 24. **Trochantellus:** 0) absent 1) present.
 - a. A “sub-segment” with a faint sulcus between the trochanter and the femur, which is actually part of the femur.
- 25. **Pretarsal claw:** 0) simple 1) with subapical tooth 2) pectinate 3) with basal tooth
 - a. Pretarsal claw state (latter two states from Keller[S2]).
- 26. **Petiole:** 0) absent 1) present.
 - a. The second abdominal segment modified as a node-like waist segment.
- 27. **Petiole peduncle:** 0) absent 1) present.
 - a. Peduncle defined as an anteriorly narrowed region of the petiole.
- 28. **Petiole development:** 0) no dorsal expansion, cylindric 1) gradually sloped, rounded dorsally, dome-shaped 2) anteroposteriorly flattened, tall and broad 3) narrowed anteroposteriad into a scale-like structure.
 - a. Overall shape of the petiole node as it expands in height.
- 29. **Posterior face of petiole:** 0) narrowed 1) broadly attached to gaster.
 - a. Posterior margin of petiole. State zero indicates a narrowing before its connection to the gaster; state one reflects a broad attachment at the greatest petiole height.
- 30. **Petiole fusion:** 0) fused tergosternally 1) no fusion, suture visible.
 - a. Presence of a suture along medial axis of petiole when viewed laterally.
- 31. **Helcium:** 0) concealed 1) exposed, extends to reach petiole.
 - a. The presclerite of abdominal segment two (either as postpetiole or gaster segment one).
- 32. **Third abdominal segment:** 0) first gastral segment 1) postpetiole present.
 - a. Condition of the third abdominal segment. In ants the “gaster” begins at the third proper abdominal segment; however, in some groups such as myrmecines, the third segment is developed into a second petiolar node.
- 33. **Sternal projection on abdominal segment 3:** 0) absent 1) present.
 - a. A ventral projection found just below the attachment point of the petiole to abdominal segment 3 (either as postpetiole or gaster segment one)
- 34. **Constriction between abdominal segments 3 and 4 (not postpetiole):** 0) absent 1) present dorsally 2) present ventrally 3) present dorsally and ventrally.
 - a. A brief, narrowed region between the third and fourth abdominal segments.
- 35. **Abdominal segments 3 and 4:** 0) tergosternally fused 1) no such fusion 2) 2+3 fused 3) Only 3 fused.
 - a. The presence of a suture between the gastral tergites and sternites. State two specific to *Anomalomyrma*. State three specific to *Apomyrma*.
- 36. **Sting:** 0) absent 1) present.
- 37. **Acidopore:** 0) absent 1) present.
- 38. **Clypeal denticle structure:** 0) largely subcuticular 1) extending well outside of cuticle with tapered apex 2) extending well outside of cuticle with flattened apex.
 - a. In some amblyoponine ants, the clypeal setae are largely subcuticular, with only their very apex impacting the surface of the cuticle: giving the appearance of a clypeus made dentiform by

cuticular sculpturing. In most extant and all Cretaceous species, clypeal setae are well developed and are entirely external.

- 39. Metapleural gland opening:** 0) gaping 1) opening a narrow slit.
a. Variation in the overall size and shape of the metapleural gland opening. Coded as a gap in the event the metapleural gland is not present altogether.
- 40. Frontal carina:** 0) absent 1) longitudinal sculpturing leading from the clypeus posteriad 2) circular sculpturing leading around antennal base.
b. A pair of ridges found between the antennae.
- 41. Pygidial teeth:** 0) absent 1) present
a. Pygidium armed with teeth-like setae posteriorly.
- 42. Mandibular shape:** 0) scythe-like with single apical tooth 1) simple with bidentate apex 2) scythe-like with multiple teeth 3) broad, flattened apex 4) broad and triangular throughout 5) flattened basally with dramatically rounded and pointed apical tooth 6) cup-like with setose inner margin.
a. Overall shape of mandibles. State 0 without subapical teeth. State 1 may possess teeth subapical teeth such as in *Opamyrra*. States 3 and 4 with no regard to teeth present on or near apex. State 4 broad throughout inner margin as in *Aneuretus*. State 5 as in Haidomyrmecini. State 6 as in *Camelomecia*.

Expanded Descriptions of Multiple-Ant Pieces

All specimens housed at the American Museum of Natural History and dated to the Albian-Cenomanian boundary (ca. 99 Ma) [S10] from Kachin Province, northern Myanmar.

JZC Bu1814 (Fig. 1): This piece is a flattened, 40 L x 31 mm W x 8 mm thick, roughly triangular, transparent piece of amber, which contains six *Gerontoformica spiralis* worker ants (specimens A to F), none of them dealates. The piece also contains a thin suspension of particulate organic debris and organismal inclusions. Among the inclusions are minute fragments of wood, disarticulated bits of arthropods, a minute snail with conical whorls and fine striae (located between ants A and B); a scolebythid wasp, wings of two specimens of the scorpionfly *Parapolycentropus* (Mecoptera: Pseudopolycentropodidae), an unidentified larva, a small fragment of (scaled) reptile skin, one minute beetle (Scydmaenidae), and frass pellets. Interestingly, the apex of the metasoma on all ant specimens is decayed away and separated from the rest of the metasoma; in three of the specimens the detached apex is lying behind or near the ant; in the other three this portion is completely lost (indicating some significant post-mortem flow). Two of the workers, D and E, lie adjacent to each other. In a tangent lying between the middle of the broad end (0°) and the opposite, narrower end (180°), the head-to-gaster positions of the ants are as follows: (A) 152°, (B) 187°, (C) 85°, (D) 335°, (E) 335°, (F) 172°. Four of the six specimens are directed toward the center of the amber piece, and two of these ants are adjacent. There are no obvious flow lines or layers separating specimens, so they all appear to have been trapped on the same surface.

JZC Bu116 (Fig. 1, bottom; S1, top): This is a large piece of dark, occluded amber with 12 worker ants (none are dealates), 11 *Gerontoformica spiralis* (specimens A-J, L) and one *Haidomyrmex zigrasi* (specimen K). The piece occurs in two sections: Section A (roughly drop-shaped) is 66 mm L x 31 mm W (a surface with 6 ants) x 30 mm thick (with one ant, specimen F); Section B is roughly trapezoidal with proportions 30 mm W (a flat end that had been trimmed and polished) x 32 mm L x 34 mm along the longest side. The two sections belong to what was obviously an even larger piece, as there are sections that would fit along the sides of A and B. Thus, the 12 ants in this piece are a minimal number; more may have been preserved in the lost sections. The pieces are shown where the slightly irregular surface of each fits together; this fit is also indicated by the position of a calcite seam that continues from one piece into the other. Light photomicrography shows the natural colors and surfaces of the amber (Fig. 1, bottom left; S1, top); CT scans (Fig. 1, bottom right) were used to map the positions and orientations of the ants and several large arthropods that were potential prey. The piece is highly occluded with a suspension of organic particles, debris, and various arthropods.

Section A: The core of Section A has a thick, calcite-filled fracture and bark pieces running longitudinal to the piece, ending near a fracture that forms a shallow, external shelf. It contains 7 ants (specimens A-G). Besides soil particles, frass pellets, plant fragments and assorted fragments of bark, the other organismal inclusions are the following: 2 Arachnida (1 mite [Acari], 1 ground spider [8 mm body length]); 1 Myriapoda (Spirobolida); 1 Hymenoptera (family indet.); 7 Diptera: 1 Cecidomyiidae, 2 Empididae, 3 Sciaroidea, 1 Scatopsidae; 1 Archaeognatha (bristletail), 1 early instar roach (Blattaria), 1 early instar earwig (Dermaptera), 1 mite (Acari), 1 Coleoptera (Curculionoidea?), 1 Collembola (Sminthuridae), and 1 Orthoptera (Tridactylidae). With the narrow end

of section A as 0° and the middle of the opposite, broader end as 180°, the head-mesosomal orientations with respect to this axis as measured in a 2-d projection of the piece are the following: (A) 76°, (B) 185°, (C) 305°, (D) 76°, (E) 76°, (F) 255°, (G) 110°.

Section B: Contains 5 ants, including a specimen of *Haidomyrmex* (specimens H-L); other arthropod inclusions are 3 mites (Acari: Oribatida), 2 partial Archaeognatha, 5 Coleoptera (3 Ptiliidae, 1 Cucujoidea, 1 partial), 1 Heteroptera (Dipsocoromorpha), 1 nymphal plant hopper (Auchenorrhyncha), 1 bark louse (Psocoptera), as well as a large, adult roach (12.5 mm body L) that may have been a prey item. There are also several large fragments of bark, ca. 6-7 mm L. Head-to-mesosoma orientations of the ants were done on two projections of Section B: one a view of the broadest face, and another of the end (Fig. S1, top). Orientations of the ants from 0° are the following: for the broad face: (H) 61°, (I) 180°, (J) 240°, (K) 265°, (L) 315°. For the end-projection: (H) 0°, (I) 238°, (J) 185°, (K) 161°, (L) 185°. Four specimens (I, J, K, and L) are clustered near the roach (2.66, 6.63, 3.97, 8.99 mm respectively), 3 of which are in the same orientation (specimens I, J, and K [*Haidomyrmex*]). Proximity and orientations indicate that the roach may be a potential or actual prey item. Obvious directionality would confirm recruitment hunting in the ants, but a lack of directionality is equivocal and inconclusive (due possibly to non-behavioral reasons, e.g., effects of resin flows).

JZC Bu1645 (Fig. S1, bottom): This is a flattened piece of dark amber, 37 mm greatest width x 40 mm greatest length x 15 mm greatest thickness, filled with over 40 arthropods and a suspension of fine to coarse debris. It includes an assemblage of 21 worker ants.

Scattered densely throughout the piece are many small to large dark, irregular masses, within which are sand grains and plant fragments. The irregular masses are probably soil and/or humus particles. Some stellate plant trichomes and disarticulated bits of arthropod appendages are sparsely scattered throughout. Besides the ants there are at least 20 other arthropods: 9 "fungus gnats" in 3 families (Diptera: Sciarioidea); 1 small, early instar nymph of earwig (Dermaptera); 2 roaches (Blattodea), including one entire nymph and the legs of a larger specimen; one spiny, early instar nymph of a true bug (Heteroptera); 1 mite (Acari); 1 early instar snakefly (Raphidioptera) larva; two spring tails (Collembola); one early instar nymph of cricket (Grylloidea); one early instar Polyxonida millipede; and a portion of what appears to be a scorpion tail (three segments). There is also a bud-like structure, 4 x 13 mm, which appears to be the rolled-up wing of an adult roach (Blattodea). The presence of the dermapteran nymph, roaches, collembolans, millipede, and humus/soil masses indicate that the resin was formed or deposited on or near the ground.

The piece has three layers, each layer comprised of approximately 5 mm of clear dark amber, with two thin boundary layers between them. Most of the humus particles lie on the boundary layers. Layer three is the smallest in area, lying as a small mound on layer two; layer one comprises the broadest surface of the piece. Ants are embedded within all three layers, although there are groups of ants that correspond to different layers. It is difficult to know if the time between layers (resin flows) is on the scale of hours or days.

There are 21 worker ants (labelled A through U), all but four of which are completely preserved or nearly so. Depth of amber, position of the ant, and partial preservation obscures detailed observation of many ants, but otherwise all of them appear to be workers; none appear to be dealates. Based on visible body size and proportions, they belong to at least three species of the genus *Gerontoformica* (*G. orientalis* [Engel and Grimaldi], *G. contegus* [Barden and Grimaldi], *G. robustus* [Barden and Grimaldi]). It is not possible to confidently identify all inclusions to species, however; it appears that most are *G. orientalis*. There are three groups of ants, separated by layers and distance: Group 1 is comprised of 7 ants (specimens A to G), all lying near one edge of layer one; Group 2 is comprised of just three ants, lying in layer two, near a distant edge; and Group 3 is comprised of 11 ants (ants H, L through U), all embedded within layer three. Moreover, specimens in Group 1 are aggregated into an area ca. 23 x 11 mm, separated by about 11 mm from Groups 2+3 (ants of which are aggregated into an area ca. 27 x 20 mm). There appears to be no directionality among the ants in Groups 1 or 2; in Group 3 six of the 11 ants are pointing "north" or near-north (0°), though the others show little such orientation.

Directions of the head-gaster body orientation of all ants are the following: ant A 130°; B 215°; C 50°; D 90°; E 325°; F 180°; G 70°; H 210°; I 20°; J 20°; K 155°; L 170°; M 5°; N 355°; O 85°; P 305°; Q 255°; R 50°; S 90°; T 0°; U 0°.

Expanded Descriptions of Multi-Ant Assemblages

The only unbiased record of ant abundance in Burmese amber is from a large, 75 kg supply of rough, unpolished and unscreened Burmese amber[S11], which generated 3100 inclusions of terrestrial arthropods. Among these were two ants, each of a different species. The probability of finding an ant in Burmese amber, based on this sample, is approximately 3×10^{-3} . Pieces JZC Bu116 and JZC Bu1814, however, contain 12 and 6 ants, respectively

(11 of the 12 in Bul16 are conspecifics). Therefore, the probability of finding an assemblage of conspecific worker ants *based on chance alone* is astronomically remote; in the case of amber piece JZC Bul16 approximately 3.1×10^{16} .

Expanded Description of Fighting Ants

Piece JZC Bul1646 is an oval cabochon-shaped piece 13 mm W x 16 mm L x 6 mm thick composed of deep, transparent yellow amber, completely enclosing a conspecific pair of *Gerontoformica* ants (Fig. 2). The ants have stings but no wing stubs, and so are clearly workers. The mandibles of each ant are closed around an appendage of the other. Also in the piece is an oribatid mite and small, unidentified blobs of organic material. Ant A (*Gerontoformica tendir*) is smaller than Ant B (*Gerontoformica spiralis*) by ca. 84%, based on head length/mesosomal lengths, and has its mandibles closed around the base of B's right antenna. In ant A the left antenna is missing antennomeres three and ones distal to this; the right antenna is fully intact (12 antennomeres); its right protarsus appears to be trapped between the left mandible and clypeal comb of ant B. In ant B the left antenna is intact (also having 12 antennomeres); the right antenna is grasped by ant A at its base (apparently the scape); six basal segments of the antenna are preserved, the six distal ones lost. The broken apex of the grasped, right antenna of ant B is exuding an air bubble, indicating that the ant was living while mired in the soft resin. Ant B is also missing the postfemoral portion of the left proleg. Ant A is preserved in its entirety; in B the apical segments of the metasoma are detached from the rest of the body. In neither specimen is the metasoma curled under the body, as if stinging its opponent. The two ants, however, were clearly fighting, based on the loss of some distal antennomeres, and the mandibles of each ant grasping an appendage of its opponent. Ants typically fight by grasping antennae and legs of opponents.

Species identification was based primarily on the presence of a distinct apomorphy, and secondarily on the proportion of the head capsule. Ant A possesses a medial projection of the anterior clypeal margin, a feature known only in *G. tendir*, while Ant B possesses a broadly rounded clypeal margin seen in other *Gerontoformica* species. To assess proportional and size differences between both workers, we measured only head and mesosomal length, as ant B is missing components of the abdomen. The head of Ant A measures 1.07mm at its greatest length, with a maximum width of 0.72mm (~14% smaller, but approximately equal to proportions of the *G. tendir* holotype); ant B head length is 1.03mm with a width of 1.04mm (~10% larger, but equal in proportionality to the *G. spiralis* holotype, among others). The approximately equal head length and width exhibited by ant B is present in four *Gerontoformica* species: *G. gracilis*, *G. robustus*, *G. spiralis*, and *G. subcuspsis*. It is possible to exclude *G. gracilis*, *G. robustus*, and *G. subcuspsis* based on the lack of an elongated mesosoma (~7x longer than height between fore and mid-coxae), robust mesosoma combined with sessile petiole, or subpetiole projection, respectively. The mesosoma of ant A (putatively *G. tendir*) is 1.99mm while ant B (putatively *G. spiralis*) is 2.34mm in length. This is of note as the size range for the *G. spiralis* type material is between 4.22mm and 5.11mm while the *G. tendir* holotype is 6.93mm in length [S12]. Regarding this size disparity: the gaster and petiole of the *G. tendir* type specimen (there is also a single paratype that is highly partial and desiccated) are extremely elongate – likely due to preservational distortion – and together account for ~48% of the total length. Overall, the mesosomal length of the *G. tendir* holotype (2.35mm) is approximately 18% larger than that of ant A, within the intraspecific variance known for the genus so far (in the case of *G. robustus*, the largest workers appear to be as much as 40% larger than the smallest individuals). With respect to ant A, the mesosoma length is approximately 15% larger than that of the largest well-preserved paratype (~2.05mm).

This rare preserved instance of interspecific aggression between two *Gerontoformica* workers is best explained in the context of sociality. Intraspecific male-male competition (combat or ritualized fighting) is common in solitary species of insects controlling access to females, but interspecific aggression is rare, and unknown in wingless female aculeates, except ants (all living species of which are social). Although ants are infamous for their warfare, there is actually a continuum in intra- and interspecific aggression, ranging from protection of the nest (in virtually all species), to protection of the nest and food supply, to protection of these plus the foraging area (i.e., territoriality) [S13]. Territoriality can be conditional (e.g., dependent on the invading species) or absolute. For example, some species of *Formica* that form large colonies can force the extirpation of other local ant species (e.g., *F. polycetena*[S14], *F. yessensis*[S15]); *Oecophylla* weaver ants are very aggressive in defending the trees in which their colonies reside[S13]. Aggressive territoriality is also why some exotic, invasive species like *Solenopsis invicta* and *Iridomyrmex humilis* severely impact native species.

Expanded Systematic Paleontology

Family Formicidae Latreille 1809

Camelomecia Barden and Grimaldi, **New Genus**, Figs. S2A-C; S3A-E,H; S4G,I

Diagnosis (gyne): Based on alate specimens. A unique morphotype with unusual head and mandibular structure. Head broad posteriorly, narrowed sharply at anterior margin of eyes and antennal sockets. Antenna with 12 segments, scape short; flagellomeres narrow at base, most broadened apically with inner pointed lobe. Gena with V-shaped incision accommodating lateral articulation of mandible. Mandibles broad, cup-like (mesally concave), with anterior margin of inner surface with rows of dense, scale-like setae. Labrum a tongue-like sclerite between mandibles, its margin rimmed with fine setae. Eyes and ocelli well developed. Anterior margin of pronotum with unique collar of long, dense, fine pilosity. Petiole pedunculate, broadly attached to gaster.

Type Species: *C. janovitzi*, new species.

Etymology: Derived directly from camel, referring to the head in profile; and *-mecia*, a common suffix in ant generic names derived from Greek.

Camelomecia janovitzi, Barden and Grimaldi, **New Species**, Figs. S2A-C; S4A-C

Diagnosis: As for genus.

ZooBank LSID. urn:lsid:zoobank.org:act:5040EF0A-7286-4644-947E-EED4CF79E063

Description (gyne): all measurements in millimeters (mm).

Head: Elongate, broad posteriorly, narrowed anteriorly; head depth (length) (including clypeus) 2.26; width 1.03 at greatest (excluding eyes), 0.71 at narrowed apex. Prognathous, postgena with ventral declivity around cervical connection. Vertex of head rounded broadly. Eyes large and ellipsoid; 0.93 length, 0.41 width. Ocelli 0.10 in diameter, atop slightly raised cuticular ridge. Antenna with 12-segments: scape 0.37 in length; pedicel 0.16, flagellomeres I-X: 0.46, 0.36, 0.36, 0.33, 0.30, 0.30, 0.31, 0.29, 0.24, 0.31. Total antenna length 3.79. Antennomeres 4-11 with narrow base, apex broadened and asymmetrical, inner portion of apex extended and pointed, giving flagellum a slightly serrate appearance. Head capsule narrowed approximately 30% near anterior margin of eye and antennal socket. Frontal lobe originating medially near antennal sockets, bifurcating into two distinct ridges leading to anterior margin of head, flanking the clypeus base. Labrum 0.53 in length, 0.34 at greatest width near posterior margin, medially depressed, surface glabrous; extending 0.31 anteriorly between mandibles with narrowing lateral margins meeting 0.20 wide anterior margin at ~90° angle. Lateral edges of labrum possessing array of long, tapered setae directed anteriorly; anterior edge of labrum with more fine setae, ~5x shorter in length. Sharp, concave incision visible in lateral view separating gena into two separate pointed dorsal and ventral processes, accommodating lateral articulation of mandible. Mandible cup-like (inner surface strongly concave), length approximately 0.76, height 0.47 at greatest; developed primarily dorsoventrally, with some lateral bowing resulting in a bulging external surface; ventral edge largely flattened with single apical tooth, dorsal edge broadly rounded, external margin without setae or fine sculpturing, anterior portion of internal margin with many thick, pointed and scale-like setae ranging 0.07 to 0.21 in length; dorsoventral edge with fine serrate denticles. Basal-most region of mandible largely obscured by gena, appearing slightly rugose and narrowed. Maxillary palp with 5 segments, palpomere I-X length: 0.10, 0.11, 0.36, 0.36, 0.33, 0.36; Labial palp with 3 segments, last two segments 0.20 and 0.16 in length.

Mesosoma: Depth (maximum dorsoventral height) 2.03 from mesopleuron to mesonotum, Weber's length 3.59. Length of individual dorsal sclerites: pronotum 0.46; mesoscutum 0.53; mesoscutellum 0.29; scutellum 0.86; metanotum distorted; propodeum 0.89. Pronotum and propleuron separated by deep sulci, both sclerites extending beneath occipital suture; propleuron ventrally expanded near head capsule and visible in lateral view; pronotum dorsally reduced near head, sharply expanding into broad collar posteriorly, coated in long and flattened setae originating near posterior margin and extending to anterior-most edge of collar. Mesoscutum largely glabrous, with long anteriorly-projecting setae near anterior margin. Tegula broadly rounded. Scutellum with slightly elevated medial ridge. Wings damaged, partially obscured, though most of forewing venation visible. Mesopleuron and propodeum highly developed, together comprising ~70% of mesosoma in lateral view. Metapleuron narrow with distinct sulci, highly pilose, notably more so than mesopleuron or propodeum. Metapleural gland opening visible as narrow slit, having 3-4 fine upright setulae on ventral margin. Propodeum with steep anterior face, spiracle atop slight cuticular elevation. Procoxa broad, 0.97 long; protrochanter 0.40; profemur 1.56; protibia 1.23, sparsely setose; protibial spur well developed, laterally accompanied by four stiff setae in linear arrangement. Mesocoxa

broad, 0.57 long; mesotrochanter 0.29; mesofemur 1.39, sparsely setose near apex; mesotibia 1.51 with occasional sharp setae; two mesotibial spurs, the larger approximately 1.3x in length. Metacoxa 1.11 long; metatrochanter 0.31; metafemur 2.03; metatibia 2.24; two metatibial spurs present, the larger approximately 1.3x longer with distinct brush. Trochantellus present; pretarsal claw with subapical tooth.

Metasoma: Largely obscured, total length approximately 4.57 including petiole. Petiole broad and pedunculate, 1.64 in length; attaches anteriorly at an approximate height of 0.40, sharply rising to an overall height of 1.16; gradually rounded dorsally; longitudinal sulcus highly developed; small sub-petiolar process present near anterior margin; posterior attachment broad 0.71 in height with longitudinal sulcus aligned with sulcus present on gastral segment I. Gastral segment I (abdominal segment III) with thick, dark sulcus, gradually pointed ventral projection present anteriorly. Gastral segment II obscured, apparently comprising majority of gaster length. Terminal regions of telescoped gastral segments III, IV, and V visible, each highly setose. Sting present.

Type: Holotype, AMNH Bu-TJ003, alate female. Myanmar: Kachin State dated to the Albian-Cenomanian boundary (ca. 99 Ma) [S10]. Housed at the American Museum of Natural History.

Etymology: Patronym in honor of Tyler Janovitz and his generosity with the type specimen.

Description (gyne) *Camelomecia* sp.: Tong-112: fully winged (Figs. S3A-E; S4I) Specimen preserved within large (2.5 x 2.8 x 1.1cm) piece of light yellow amber.

Description: Total length of ant approximately 6.3; some desiccation apparent in mouthparts, petiole, and gaster. Head shape very similar to *C. janovitzi*, 1.38 in length; eyes elongate, 0.58 long; ocelli large, bulging. Mandibles more elongate than *C. janovitzi* specimen, with overall cup-like shape with internal margin of sharp setae. Labrum partially cleared with few setae near posterior margin; lateral margins darkened, possessing sparse setae. Clypeus distinct from *C. janovitzi*, dorsally flattened with distinct posterior margin spanning width of head. Antennal segments flattened and distorted, preventing reliable measurement; scape approximately 0.75x length of flagellomere I. Pronotum with faint row of short setae along anterior margin, anteriorly pronotum narrowing greatly into neck before meeting head; promesonotal suture highly visible, appearing flexible, mesosoma constricted ventrally at this suture; scutellum bulbous, developed dorsally; propodeum with sheer posterior face, broadly rounded at posterodorsal margin, possessing stout spines; metapleural gland opening present, gaping. Propleuron reduced; mesopleuron developed, rounded laterally. Mid- and hind-legs with visible trochantellus; pretarsal claw with subapical tooth; tibial spurs as in *C. janovitzi*. Petiole pedunculae and elongate, gradually expanded to meet abdominal segment III, with single ventral spicule near anterior margin. Gaster elongate, distinct constriction between III and IV abdominal segments; third valvulae and sting visible.

Description (male) ?*Camelomecia* sp.: JZC Bu1818 (Figs. S3H; S4G,H,J) A rather large, gracile ant preserved in a large piece of transparent yellow amber 45 x 22 x 20 mm (untrimmed); the piece also containing two beetle larvae (one minute, early instar; the other larger and distinctive, resembling Brachypsectridae), plus 21 oblong frass pellets that are fairly uniform in size. Body length of the ant approximately 8.5; mesosoma distorted as preserved. Pronotum extended into long, slender neck; propodeum long, gradually sloping; petiole not well preserved, but apparently long, slender, not well developed; gaster relatively short. Head: Eye large, oval; ocelli present, large, barely separated (by distances less than their diameter); antenna with 11 antennomeres (9 flagellomeres). Lengths: scape 0.27; pedicel 0.58, flagellomere I 0.57, II 0.55, III 0.46, IV + V unclear, VI 0.32, VII 0.27, VIII 0.25, IX 0.35. Clypeus apparently without pegs but with fringe of stiff, fine setae. Mandibles distinctive, very similar to those of alate *Camelomecia*: short, scoop-shaped, with two short, subapical teeth; fringe of stiff, spicule-like setae on ventral margin and mesal surface. Legs relatively short compared to body length. Protibia with pectinate calcar, calcar notched in middle of the surface facing tibia. Mesotibia with one large ventroapical spur; metatibia with pair of ventroapical spurs, approximately equal in length. Pretarsal claws with small, subapical tooth, arolium well developed. Male genitalia slender, conical, parameres adjoining.

Wing and Venation: Relatively short and slender, forewing length 4.96, width 1.56; hind wing length 3.96, width 0.77. Hind wing with row of 13 thicker hamuli distal to Rs, one fine hamulus anterior to midline of R + Rs. Wing venation distinct, divergent from *Sphecomyrma* and *Gerontoformica*: Forewing with SMC1 complete, undivided; cell DC very large, forming parallelogram (vs. pentagonal); large DC2 cell present (i.e. vein 2m-cu present) (vs. absent); cell SMC2-3 absent (vs. present). Hind wing with long row of hamuli posterior to Rs (vs. shorter, ≤ 6); venation reduced: vein M absent (vs. present, apically evanescent). Venation very similar to that of alate female (AMNH Bu-TJ003) This specimen is placed in *Camelomecia* on the basis of the distinctive mandibles, oral setae, and similar wing venation.

***Gerontoformica* Nel & Perrault**

Gerontoformica Nel & Perrault, 2004: pg. 24. Type species: *G. cretatica* Nel & Perrault, by original designation. In Late Albian-aged amber from Charente-Maritime, France.

Sphecomyrmodes Grimaldi & Engel, 2005: pg. 5. Type species *Sphecomyrmodes orientalis*, by original designation. In Burmese amber dated to the Albian-Cenomanian boundary (ca. 99 Ma). **NEW SYNONYMY.**

Diagnosis (emended): Distinguished from other Cretaceous genera by the presence of an uninterrupted row of peg-like denticles on the anterior margin of the clypeus; mandibles falcate, with one large apical tooth and one preapical tooth; labrum without denticles.

The revised diagnosis and new generic synonymy are based on re-examination by one author (P.B.) of the type specimen, housed at the National Museum of Natural History, Paris. The original description of *G. cretatica* reports peg-like teeth on the labrum, which actually occur on the clypeus [S20]. Also, the antenna is distorted, giving the false appearance of an elongate scape. Finally, the apparent lack of a sting in the type specimen can be attributed to preservation, as other major features (dorsal mesosomal sclerites) are missing. Species formerly placed in *Sphecomyrmodes* [S12,S16,S17] are now placed in *Gerontoformica*, as follows:

New Combinations:

Gerontoformica occidentalis (Perrichot, Nel, Néraudeau, Lacau and Guyot) 2008: 95. **New Combination.**

Gerontoformica orientalis (Engel and Grimaldi) 2005: 5. **New Combination.**

Gerontoformica contegus (Barden and Grimaldi) 2014: 2. **New Combination.**

Gerontoformica gracilis (Barden and Grimaldi) 2014: 4. **New Combination.**

Gerontoformica magnus (Barden and Grimaldi) 2014: 7. **New Combination.**

Gerontoformica pilosus (Barden and Grimaldi) 2014: 10. **New Combination.**

Gerontoformica robustus (Barden and Grimaldi) 2014: 12. **New Combination.**

Gerontoformica rugosus (Barden and Grimaldi) 2014: 15. **New Combination.**

Gerontoformica spiralis (Barden and Grimaldi) 2014: 16. **New Combination.**

Gerontoformica subcuspsis (Barden and Grimaldi) 2014: 17. **New Combination.**

Gerontoformica tendir (Barden and Grimaldi) 2014: 17. **New Combination.**

Gerontoformica maraudera, Barden and Grimaldi, **New Species**, Fig. S2D,E

Diagnosis (worker): Readily distinguishable from other *Gerontoformica* species by elongate mandibles incapable of full adduction against clypeus; frontal lobe with pointed and projected anterolateral margin; sparse, thick setae coating head and body; five maxillary palpomeres; reduced metanotum; distinct band-like constriction between first and second gaster segments. Total length 8.67.

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Description (worker): all measurements in millimeters (mm).

Head: Sparsely setose, setae up to 0.36 length; head 1.21 length from posterior margin of head to anterior margin of clypeus in frontal view; 1.06 wide excluding eyes. Ocelli present. Occipital foramen broadly rounded. Vertex of head flattened, its posterolateral margins broadly rounded. Eyes situated high on head, 65% the distance above anterior margin of clypeus to posterior margin of head. Eyes bulging, 0.43 long, 0.24 deep. Cuticle between antennae raised into frontal lobe, frontal carina originate at inner margin of eye, diagonally leading to anterior margin of frontal lobe, terminating as a slight pointed expansion. Antenna total length 6.07: scape 0.66, pedicel 0.19, funicular segment I 0.89, II 0.63, III 0.63, IV 0.60, V 0.61, VI 0.54, VII 0.56, VIII 0.54, IX 0.51, X 0.56. Clypeus appearing reduced, anterior and lateral margins obscured by desiccation; anterolateral margin with small pointed projection; anterior margin with characteristic stout, setae-like denticles (0.03 long), difficult to enumerate, >15. Mandibles elongate, 1.00 long, exceeding width of clypeus preventing flush retraction as in other *Gerontoformica*; apex with two denticles, apical tooth slightly larger; external margins slightly setose. Labium broad, possessing at least six interwoven rows of small, pointed denticles; anterior margin with fine, tapered setae. Labial palps with two palpomeres (damaged and not possible to measure accurately); maxillary palp with five palpomeres: I 0.13, II 0.23, III 0.33, IV 0.44, V unclear.

Mesosoma: Weber's length 2.90. Dorsal lengths: Pronotum 1.07, mesonotum 0.70, propodeum 1.44. Dorsal sclerites with sparse setae throughout. Pronotum broadly rounded with high collar; depression situated just anterior to collar. Propleuron reduced, slightly visible in lateral view. Mesonotum expanded dorsally; thoracic gemmae appear to be present. Metanotum apparently lost or highly reduced. Pronotum elongate, gradually rounded;

metapleural gland opening gaping, facing posteriorly. Forelegs lost beyond the forecoxae; one midleg preserved; hind legs lost beyond femur. Procoxa with tapered setae along anterior edge, 0.69 long. Mesocoxa 0.53 long; mesotrochanter 0.36 long; mesofemur 1.69 long, trochantellus present; mesotibia highly setose, measurement obscured by fracturing and distortion, mesotibial spur not visible; tarsal segments highly setose, pretarsal claw with subapical tooth. Metacoxae 0.74 long; metatrochanter 0.37 long; metafemur 2.46 long.

Metasoma: Petiole not tergosternally fused, with broad anterior face, nodiform; approximately 1.06 total length. Node broadly rounded with setae along dorsal face; maximum height 0.67, decreasing to 0.57 at gaster attachment (sternal projection comprising 50% of this height). Underside of petiole and sternite of gaster segment I (abdominal segment III) possessing narrow projection that appears to be attached to both sclerites, projection with perpendicular anterior and ventral margins, anteroventral margin with sharp hook. Helcium distinct, rugose segment expanding to reach petiole. Gaster rugose throughout, with sparse elongate setae. Distinct band-like constriction between gaster segments I and II. Sting exuded slightly.

Type: Holotype JCZ Bu1846. Wingless female (presumed worker). Preserved in a 11 x 7 x 5 mm piece of transparent yellow amber previously shaped into bead. Myanmar: Kachin State dated to the Albian-Cenomanian boundary (ca. 99 Ma) [S10]. Housed at the American Museum of Natural History.

Etymology: As in “marauder,” in reference to the fierce appearance and dramatic mandibles.

Description (gyne) *Gerontoformica* sp.: JZC Bu313 (Figs. S3F; S4D-F) This is a virtually complete specimen in a piece that was originally bead-shaped, with a hole bored through it. It was trimmed flat on two faces, one face providing a full frontal view of the head; size is now 8 x 5 x 4 mm. The ant is missing its apical antennomeres (just the four basal ones remain), and the apex of the metasoma (e.g., sting), which were obliterated at the surface of the bead. The piece also contains a Collembola, a small Hemiptera (Dipsocoromorpha), and a tiny empidoid fly (the first two of these suggests capture near or on the surface of the ground). Other than loss of some small portions the ant is quite well preserved, with little preservational distortion and the cuticle cleared in most regions (thus facilitating observation of fine details). The wings are particularly well preserved.

Head length 0.81; head width 0.62; eye length 0.20; mesosomal length 1.89 (likely distorted by dessication); petiole length 0.54; gaster length (preserved portion) 1.73; forewing length 4.25, width 1.34; hindwing length 2.83, width 1.06. Head: oral margin broad, with comb of ca. 18 clypeal pegs; mandible structure typical of *Gerontoformica*: broad, with single preapical tooth (plus apical one). Ocelli present, small; head with numerous fine, erect setae; bases of antennae surrounded by large, round, shallowly concave area. Pronotum projected into long, narrowed neck; metapleural gland opening large, facing posteriad (mesosoma strongly compressed laterally). Mesoscutellum and postnotum well developed; propodeum shallow, sloping; petiole distorted, not fully discernable. Protibia with long, slender, bare (non-pectinate) calcar having bifid apex, smaller spur mesally (0.5x the length). Mesotibia with slender ventroapical spur; metatibia with pair of ventroapical spurs (approximately equal in size).

Wing and Venation: Hind wing with row of six thicker hamuli distal to Rs; 3 finer, widely spaced ones distal to this. Venation very similar to that of male *Sphecomyrma* sp. in Turonian-aged New Jersey amber (AMNH NJ-242) [S1]. Main forewing differences are that *Gerontoformica* sp. (Bu313) has a partial division of cell SMC1, as in *Baikurus mandibularis* Dlussky (vs. undivided); basal cells BC and SBC are shorter; vein Cu1 is present, though weaker than the other veins (vs. absent); vein M gradually fades apicad but nearly complete (vs. evanescent well before the wing margin). Main hind wing differences are Rs and M evanescent apically (vs. barely developed in *Sphecomyrma*).

Description (gyne) *Gerontoformica* sp.: JZC Bu318 (Fig. S3J) A complete specimen enclosed within a 9 x 5 x 4 mm piece of clear yellow amber; the entire cuticle covered with a reddish layer, indicating oxidation and/or initial pyritization of the specimen (the red layer obscures many structures). Wings are folded over each other, the distal halves of each being crumpled; the venation is nearly impossible to reconstruct. Ocelli present, small; face long, details of clypeal comb and mandibular dentition not visible. Antenna with 12 antennomeres (10 flagellomeres). Protibia with calcar bare (not pectinate), having bifid apex. Claws with small preapical tooth, arolium large and well developed. Structure of mesosoma obscured by some distortion. Mesotibia with two ventro-apical spurs (1 small, 1 longer posterior one); metatibia with two ventroapical spurs, both approximately the same length. Sting long, well-developed. Petiole broadly rounded dorsally, dome-like; sternite I with obvious ventral projection; gaster slender (some internal contents preserved, visible through cuticle). Head length 1.02; head width 0.62; eye depth 0.19; mesosomal length 1.48; petiole length 0.48; gaster length 1.96; forewing and hind wing length obscured due to degradation. Lengths of antennomeres: scape 0.37; pedicel 0.18; flagellomere I 0.32; 0.21; 0.19; 0.17; 0.17; 0.20; 0.15; 0.17; 0.14; 0.17; 0.15; 0.27.

Venation: Not visible.

Description (gyne) *Gerontoformica* sp.: JZC Bu1821 (Fig S3G,I) A well-preserved but partially obscured specimen. The dealate ant is suspended in a resin flow among hundreds of bubbles, preventing some lateral views. The piece is 2.5 x 1.4 x 0.9 cm, trimmed flat on one surface to provide a clear ventral view of the head and body. Head length 1.43; head width 1.38; eye length 0.50; mesosomal length 2.37; petiole length 0.60; gaster length 2.61; antenna: scape 0.57; pedicel 0.31, flagellomere I+II+III +IV obscured, V 0.32, VI 0.31, VII 0.25, VIII 0.23, IX 0.28, X 0.43. Head broadly rounded square, slightly narrowing anteriorly. Mandibles bidentate, anterior margin of clypeus with peg-like denticles, difficult to enumerate (>12), characteristic of other *Gerontoformica* taxa. Antennal sockets posterior to clypeal margin, surrounded by slightly depressed area relative to medially elevated cuticle between antennae. Frontal carina spiraling out from just lateral to inner margin of antennal socket to anterior margin of eye, as in *G. orientalis* and *G. spiralis*. Ocelli present. Pronotum with anteriorly expanded neck: propleuron visible in lateral view. Mesoscutum highly developed, flattened dorsally; transscutal fissure very faint; scutellum raised dorsally; wing stubs clearly visible. Metapleural gland opening gaping, projecting posteriorly. Propodeum reduced, sloping dramatically. Protibial spur bifurcating near apex, pectinate between these two apices; mesotibia and metatibia each with two approximately equal length spurs, one pectinate; trochantellus present, pretarsal claw with subapical tooth. Petiole pedunculate, apparently attached somewhat broadly although attachment point mostly obscured by a fissure. Gaster segment I with slight ventral projection; gastral segments not terg-sternally fused, largely obscured. Sting present.

Supplemental References

- [S1]. Grimaldi, D.A., Agosti, D., and Carpenter, J.M. (1997). New and rediscovered primitive ants (Hymenoptera: Formicidae) in Cretaceous amber from New Jersey and their phylogenetic relationships. *Am. Mus. Novit.* 3208, 1-43.
- [S2]. Keller, R.A. (2011). A phylogenetic analysis of ant morphology (Hymenoptera: Formicidae) with special reference to the poneromorph subfamilies. *Bull. Am. Mus. Nat. Hist.* 355, 1-90.
- [S3]. Johnson, B.R., et al. (2013). Phylogenomics resolves evolutionary relationships among ants bees and wasps. *Curr. Biol.* 23(20), 2058-2062.
- [S4]. Wilson, E.O. (1987). The earliest known ants: an analysis of the Cretaceous species and an inference concerning their social organization. *Paleobiology* 13(1), 44-53.
- [S5]. Dlussky, G.M. (1983). New subfamily of Late Cretaceous Hymenoptera: "missed link" between ants and Scolioidea. *J. Paleontol.* 17, 65-78.
- [S6]. Goloboff, P.A., Farris, J.S.M., and Nixon, K.C. (2008) TNT a free program for phylogenetic analysis. *Cladistics* 24(5), 774-786.
- [S7]. Goloboff, P.A. (1993). Estimating character weights during tree search. *Cladistics* 9(1), 83-91.
- [S8]. Goloboff, P.A., Carpenter, J.M., Arias, J.S., and Esquivel, D.R.M. (2008). Weighting against homoplasy improves phylogenetic analysis of morphological data sets. *Cladistics* 24(5), 758-773.
- [S9]. 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(48), 18172-18177.
- [S10]. Shi, G., et al. (2012). Age constraint on Burmese amber based on U–Pb dating of zircons. *Cretaceous Res.* 37, 155-163.
- [S11]. Grimaldi, D.A., 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, 1-71.
- [S12]. Barden, P., and Grimaldi, D. (2014). A Diverse Ant Fauna from the Mid-Cretaceous of Myanmar (Hymenoptera: Formicidae). *PLoS One* 9(4), e93627.
- [S13]. Hölldobler, B., and Wilson, E.O. (1990). *The Ants* (Cambridge: Harvard University Press).
- [S14]. Savolainen, R., and Vepsäläinen, K. (1988). A competition hierarchy among boreal ants: impact on resource partitioning and community structure. *Oikos* 151(2), 135-155.
- [S15]. Higashi, S., and Yamauchi, K. (1979). Influence of a supercolonial ant *Formica (Formica) yessensis* Forel on the distribution of other ants in Ishikari Coast [Japan]. *Jpn. J. Ecol.* 29, 257-264.
- [S16]. 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.
- [S17]. Perrichot, V., Nel, A., Néraudeau, D., Lacau, S., and Guyot, T. (2008). New fossil ants in French Cretaceous amber (Hymenoptera: Formicidae). *Naturwissenschaften* 95(2), 91-97.
- [S18]. 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.
- [S19]. Barden, P., and Grimaldi, D. (2013). A new genus of highly specialized ants in Cretaceous Burmese amber (Hymenoptera: Formicidae). *Zootaxa* 3681(4), 405-412.
- [S20]. Perrichot, V. (2014). A new species of the Cretaceous ant *Zigrasimecia* based on the worker caste reveals placement of the genus in the Sphecomyrminae (Hymenoptera: Formicidae). *Myrmecol. News* 19, 165-169.