

Current Biology

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

Highlights

- 99 million-year-old amber from Myanmar preserves adaptively diverse early ants
- Fossils preserve distinct castes, worker aggregations, and interspecific conflict
- These early ants are basal lineages distinct from modern ants
- Despite sociality and diversity, stem-group ants did not persist into the Cenozoic

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In Brief

Barden and Grimaldi detail the early history of ants through descriptions and analyses of ants in Burmese amber, preserved with life-like fidelity. Most Cretaceous species belong to stem-group basal lineages and were morphologically diverse. In addition, amber preserves multiple lines of evidence suggestive of sociality.

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 *Gerontofornica* 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., Chrysoidea, 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 *Gerontofornica*, 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

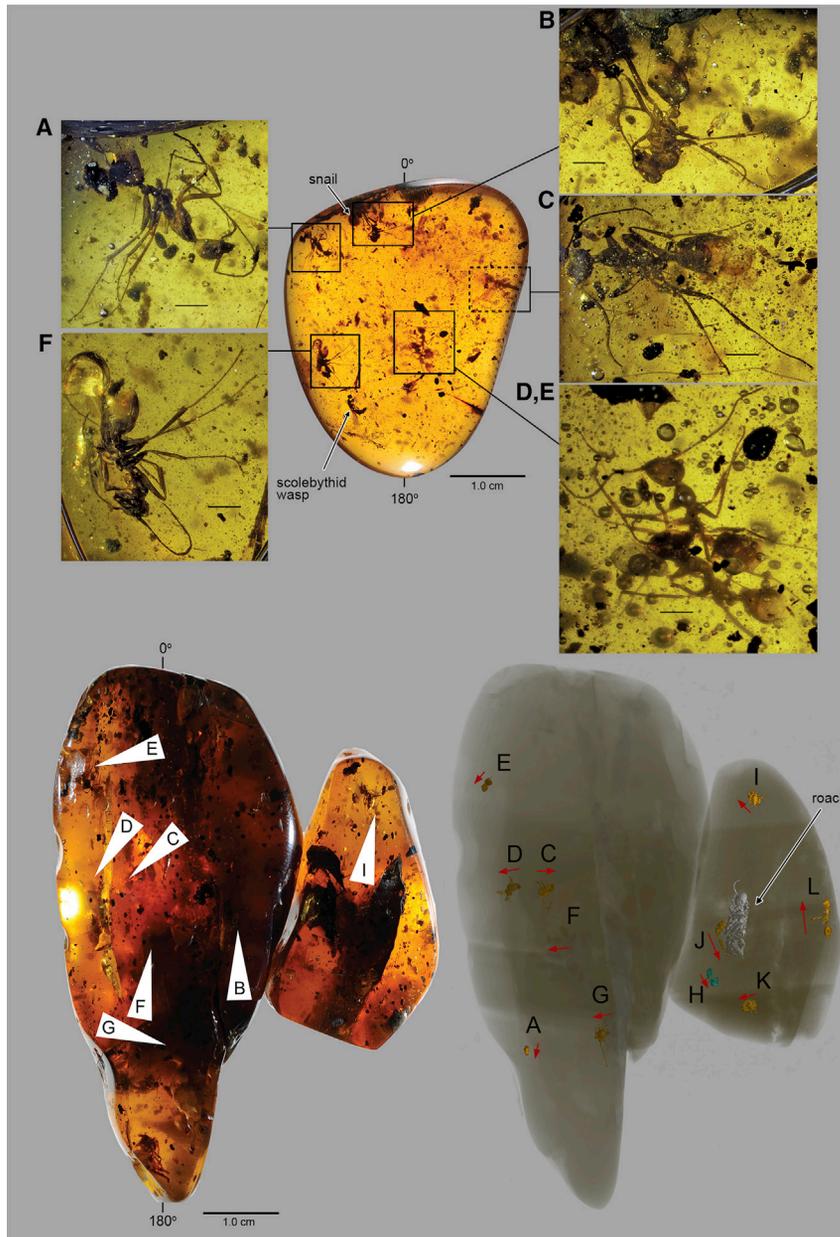


Figure 1. Social Assemblages of Cretaceous Worker Ants

(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 Bu166 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 Bu166 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.

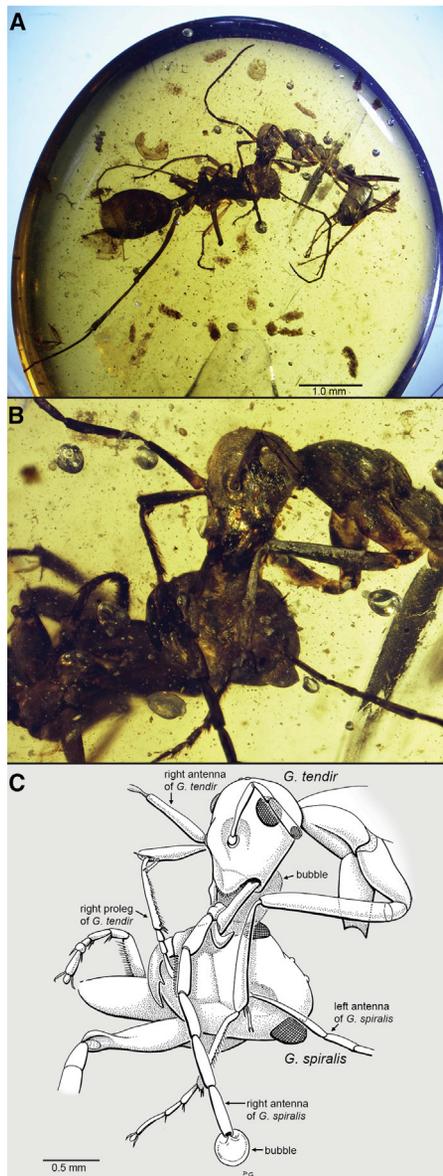


Figure 2. Workers of Two Species of *Gerontoformica* in Burmese Amber, *G. tendir* and *G. spiralis*, Captured while Fighting
Specimen JZC Bu1646.

(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

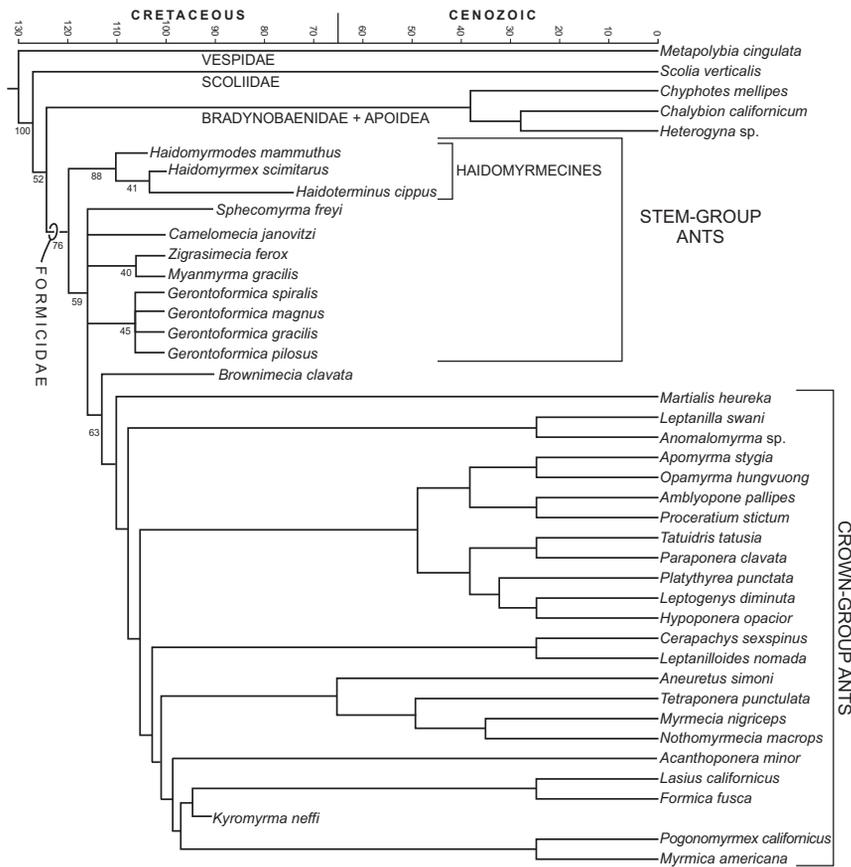


Figure 3. Preferred Timescaled Consensus Cladogram of Cretaceous and Exemlar Extant Ants

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 (Bethylnomyidae) 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.

Gerontofornica Nel and Perrault

Gerontofornica Nel and Perrault, 2004: pg. 24. Type species: *G. cretacea* 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 *Gerontofornica*.

Gerontofornica maraudera Barden and Grimaldi, New Species, Figure S2

Diagnosis (Brief). Distinguishable from other *Gerontofornica* 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. janovitzii*, 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

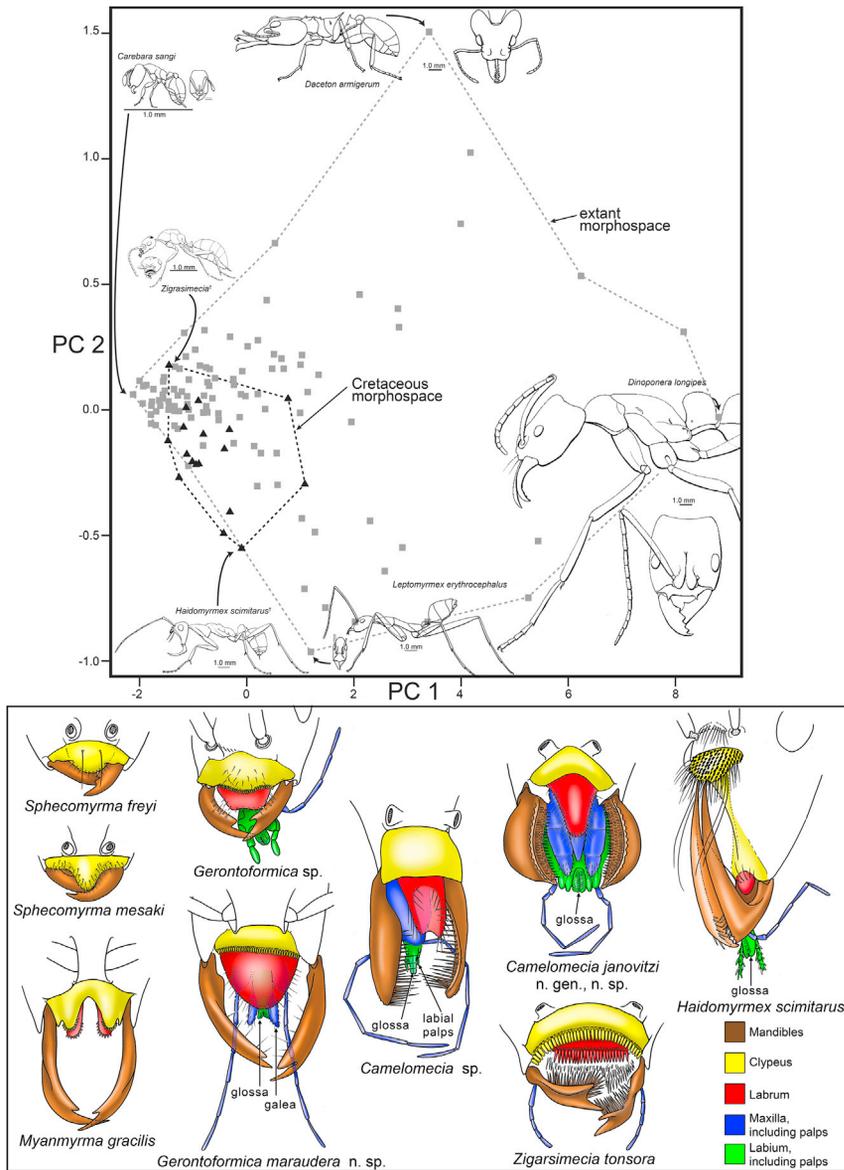


Figure 4. PCA Plot of Exempler Living and Cretaceous Ant Workers and Assemblage of Mouthpart Diversity in Cretaceous Stem-Group Ants

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 magna* (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 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

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

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*, *Zigrasimecia*). 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

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