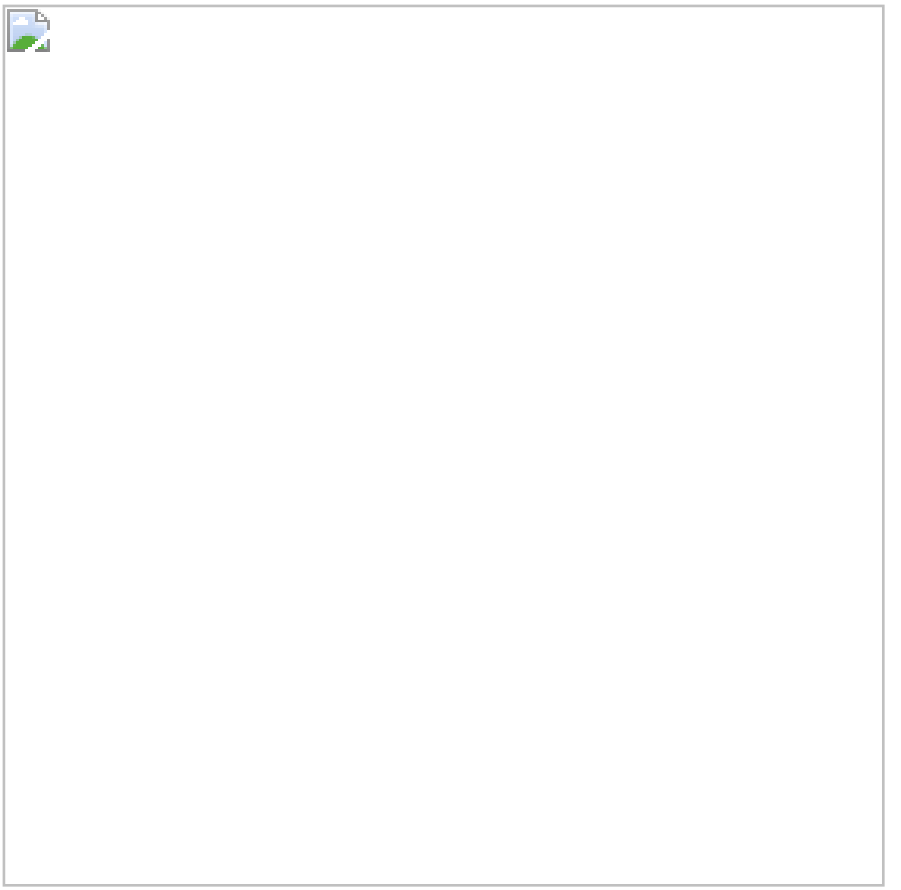

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Primitive New Ants in Cretaceous Amber from Myanmar, New Jersey, and Canada (Hymenoptera: Formicidae)

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CONTENTS

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ABSTRACT

New information is provided on the oldest fossil ants (Formicidae), including the description of a new species of †*Sphecomyrma* (†Sphecomyrminae), a new genus of sphecomyrmines, a new genus of apparent myrmeciines, and a new genus of apparent aneuretines. New material from New Jersey amber (Turonian) includes workers of †*Sphecomyrma freyi* Wilson and Brown preserved together in the same piece of amber, a worker of an unidentifiable †*Sphecomyrma* species, and a worker of †*Brownimecia clavata* Grimaldi, Agosti, and Carpenter (†Brownimeciinae). A new species of †*Sphecomyrma* in New Jersey amber is described and figured from a worker as †*S.* ***mesaki,*** new species. Two worker specimens in Campanian amber from Canada are described, one of which is described as †***Cananeuretus occidentalis,*** new genus and species, and is tentatively placed in Aneuretinae. From Burmese amber (Albian-Cenomanian) are the oldest, definitive ants, along with ones in amber from Charente-Maritime of France (approximately contemporaneous in age). A new genus and species, allied to †*Sphecomyrma*, is described from these deposits as †***Sphecomyrmodes orientalis,*** along with a remarkable new ''poneroid'', †***Myanmyrma gracilis,*** new genus and species (Myrmeciinae?). A key to the species of †*Sphecomyrma* is provided, the classification of ants summarized, and the Cretaceous records of Formicidae briefly outlined.

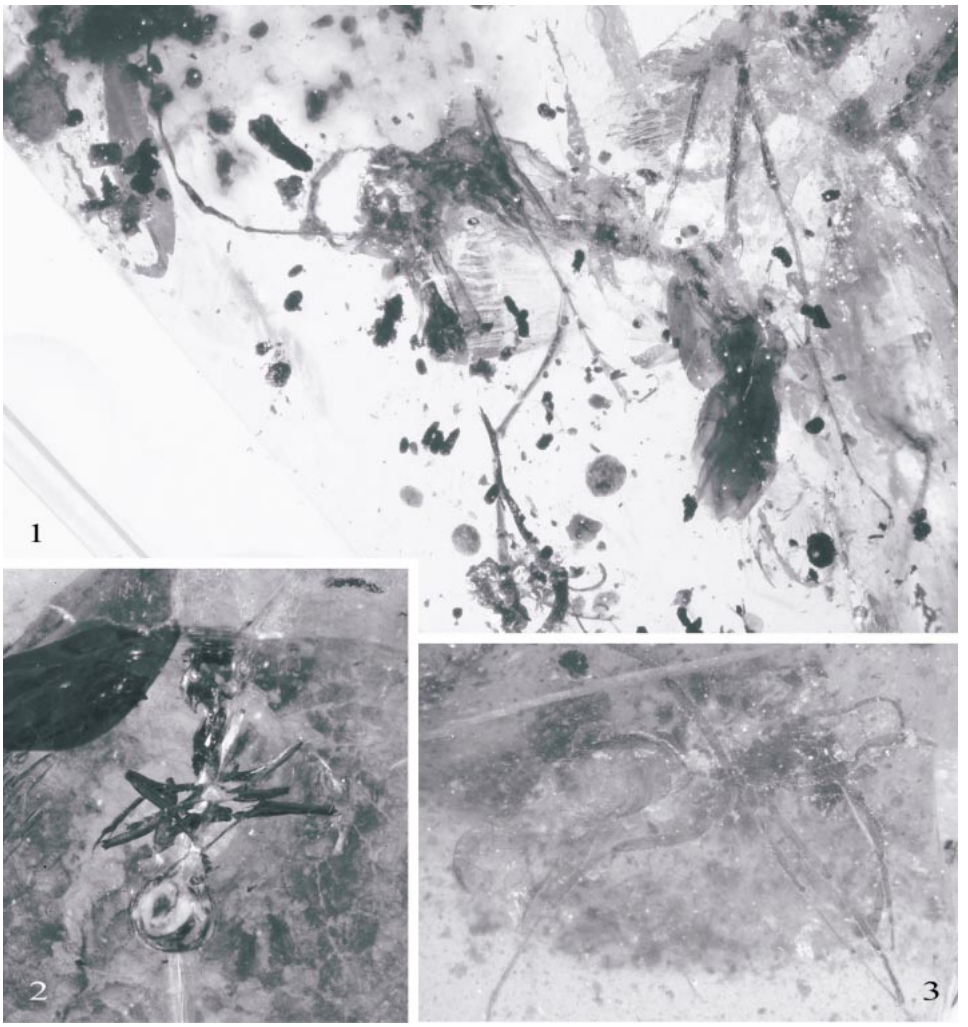
INTRODUCTION

Ants can truly be said to shape the terrestrial world. Of the 11,833 species of Formicidae[3], many have a profound impact on natural and manmade ecosystems, which is made possible by their eusociality, frequently large colony sizes, and abundance. There is scarcely a place outside of the polar regions where one cannot find these insects or their effects. Ants are among the most common and diverse kind of insect in various Cenozoic deposits, and are particularly well known in the fossilized faunas of Dominican, Sicilian, and Baltic ambers (Rasnitsyn and Kulicka, 1990; Skalski and Veggiani, 1990; Wilson, 1985a), as are the less spectacularly preserved compressions from Lagerstätte such as Florissant (Carpenter, 1930), Green River (Dlussky and Rasnitsyn, 2003), and other Tertiary localities throughout the world. Although Formicidae came into their own during the Cenozoic, in the Mesozoic and Early Tertiary (Paleocene) formicids were rare, and their earliest evolution has been gradually unveiled with each new fossil discovery (e.g., Wilson et al., 1967; Wilson, 1985b; Grimaldi et al., 1997; Grimaldi and Agosti, 2000a; Dlussky and Rasnitsyn, 2003; Dlussky et al., 2004; Nel et al., 2004).

Until 1985, the only true formicid known from the Cretaceous Period was †*Sphecomyrma freyi* Wilson and Brown, in New Jersey amber. Since 1985, ants have been reported in Cretaceous amber from Siberia, France, Canada, Burma, and additional new specimens and taxa in New Jersey amber (reviewed in Grimaldi et al., 1997, with additions by Dlussky, 1999; Grimaldi and Agosti, 2000a; Grimaldi et al., 2002; Nel et al., 2004: *vide* appendix 1). Here we report important new specimens of described ant taxa recently discovered in New Jersey amber, new species of †sphecomyrmines in both New Jersey and Burmese amber, as well as three new genera in Burmese and Canadian ambers (e.g., figs. 1–3). While it is well established that New Jersey amber is of Turonian age (Grimaldi et al., 2000) and that Canadian amber is Campanian (Borkent, 1995), the dating of Burmese amber has been contentious. Formerly believed to be of Tertiary age, recent work has demonstrated that the Burmese deposit dates from the mid-Cretaceous (e.g., Zherikhin and Ross, 2000; Grimaldi et al., 2002; Cruickshank and Ko, 2003). Thus, those taxa in Burmese amber (Albian-Cenomanian) are among the current oldest records of ants along with ants in amber of approximately contemporaneous age from Charente-Maritime, France (Nel et al., 2004), being at least 8–10 million years older than previous records of the family.

In keeping with myrmecological tradition and literature, we generally use terminology for morphological structures (e.g., antennal

[3] Species total accurate as of 17 June 2005 (*vide* www.antbase.org).



Figs. 1–3. Three Cretaceous amber ants. 1. †***Myanmyrma gracilis,*** new genus and species (AMNH Bu-014) in Burmese amber. 2. †***Cananeuretus occidentalis,*** new genus and species (TMP 8.89.7) in Canadian amber. 3. †***Sphecomyrmodes orientalis,*** new genus and species (AMNH Bu-351) in Burmese amber.

parts) as outlined by Hölldobler and Wilson (1990) and Bolton (1994); however, for body regions we have used head, mesosoma (= alitrunk), and metasoma (= petiole + gaster), as is standard in apocritan Hymenoptera. Throughout, ''head length'' is measured from the apex of the vertex to the anterior border of the clypeus. The higher classification of the ants has recently undergone a major rearrangement owing to the work of Bolton (2003) (summarized with minor modifications in table 1). We have employed that classification, herein, noting in various places where we believe it might eventually be modified. Material considered herein is deposited in the Amber Collection, Division of Invertebrate Zoology, American Museum of Natural History, New York (AMNH); the Department of Palaeontology of the Natural History Museum, London (NHML); and Royal Tyrell Museum of Palaeontology, Drumheller, Canada (TMP). Specimens in the AMNH collection were embedded in epoxy for preparation and study, using the pro-

TABLE 1

Hierarchical Suprageneric Classification of the Ants (Formicidae) and Antlike Wasps (Armaniidae) (modified from Bolton, 2003)[a]

Family †ARMANIIDAE Dlussky
Family FORMICIDAE Latreille

- Subfamily †Sphecomyrminae Wilson & Brown
  - Tribe †Sphecomyrmini Wilson & Brown
  - Tribe †Haidomyrmecini Bolton
- "poneromorph" group [*paraphyletic*]
  - Subfamily †Brownimeciinae Bolton
  - Subfamily Amblyoponinae Forel[b]
  - Subfamily Paraponerinae Emery
  - Subfamily Heteroponerinae Bolton
  - Subfamily Ponerinae Lepeletier de Saint Fargeau
    - Tribe Ponerini Lepeletier de Saint Fargeau
    - Tribe Thaumatomyrmecini Emery
    - Tribe Platythyreini Emery
  - Subfamily Proceratiinae Emery
    - Tribe Proceratiini Emery
    - Tribe Probolomyrmecini Perrault
  - Subfamily Ectatomminae Emery
    - Tribe Ectatommini Emery
    - Tribe Typhlomyrmecini Emery
- leptanillomorph group[b]
  - Subfamily Leptanillinae Emery
    - Tribe Anomalomyrmini Taylor
    - Tribe Leptanillini Emery
- dorylomorph group
  - Subfamily Cerapachyinae Forel
    - Tribe Acanthostichini Emery
    - Tribe Cylindromyrmecini Emery
    - Tribe Cerapachyini Forel
  - Subfamily Leptanilloidinae Bolton
  - Subfamily Aenictinae Emery
  - Subfamily Aenictogitoninae Ashmead
  - Subfamily Ecitoninae Forel
    - Tribe Cheliomyrmecini Wheeler
    - Tribe Ecitonini Forel
  - Subfamily Dorylinae Leach
- myrmeciomorph group
  - Subfamily Myrmeciinae Emery
    - Tribe Myrmeciini Emery
    - Tribe Prionomyrmecini Wheeler
  - Subfamily Pseudomyrmecinae Smith
- myrmicomorph group
  - Subfamily Agroecomyrmecinae Carpenter
  - Subfamily Myrmicinae Lepeletier de Saint Fargeau
    - Tribe Stegomyrmecini Wheeler
    - Tribe Myrmecinini Ashmead
    - Tribe Metaponini Forel
    - Tribe Melissotarsini Emery
- myrmicomorph group, Subfamily Myrmicinae (*continued*)
  - dacetite tribal group
    - Tribe Basicerotini Brown
    - Tribe Dacetini Forel[c]
    - Tribe Phalacromyrmecini Dlussky & Fedoseeva
  - cataulacite tribal group
    - Tribe Cataulacini Emery
    - Tribe Cephalotini Smith
  - attite tribal group
    - Tribe Blepharidattini Wheeler & Wheeler
    - Tribe Attini Smith
  - solenopsidite tribal group
    - Tribe Stenammini Ashmead
    - Tribe Solenopsidini Forel
  - myrmicite tribal group
    - Tribe Myrmicini Lepeletier de Saint Fargeau
    - Tribe Tetramoriini Emery
    - Tribe Pheidolini Emery
    - Tribe Lenomyrmecini Bolton
    - Tribe Paratopulini Wheeler
  - formicoxenite tribal group
    - Tribe Crematogastrini Forel
    - Tribe Ankylomyrmini Bolton
    - Tribe Liomyrmecini Mayr
    - Tribe Meranoplini Emery
    - Tribe Myrmicariini Forel
    - Tribe Formicoxenini Forel
- formicomorph group
  - Subfamily †Formiciinae Lutz
  - Subfamily Formicinae Latreille
    - Tribe Dimorphomyrmecini Emery[d]
    - Tribe Myrmecorhynchini Wheeler
  - plagiolepidite tribal group
    - Tribe Lasiini Ashmead
    - Tribe Plagiolepidini Forel
    - Tribe Myrmoteratini Emery
  - formicite tribal group
    - Tribe Oecophyllini Emery
    - Tribe Gigantiopini Ashmead
    - Tribe Camponotini Forel[e]
    - Tribe Notostigmatini Bolton
    - Tribe Formicini Latreille
    - Tribe Melophorini Forel
  - Subfamily Aneuretinae Emery
  - Subfamily Dolichoderinae Forel

[a]Bolton's (2003) informal groups of subfamilies as well as informal tribal groups are employed herein. As continued phylogenetic work refines the higher classification of the Myrmicinae and Formicinae, these tribal groups may warrant formalization as supertribes. If so, then we recommend that the suffix -iti be employed for the supertribal rank as has been done for other aculeate lineages (e.g., Engel, 2005). In advance of this, we have used informal names for these tribal groups based on this suffix as to avoid confusion when referring informally to a particular tribe (i.e., to avoid confusion caused by, for example, using "attine" for members of the attine tribal group [which might also include *Blepharidatta*] or for actual members of the Attini).

[b]The subfamily Apomyrminae Dlussky and Fedoseeva (formerly in the leptanillomorph group, sensu Bolton, 2003) is herein considered a synonym of Amblyoponinae as proposed by Saux et al. (2004).

[c] In Grimaldi and Engel (2005) this name appeared as "Dacetonini" based on a misinterpretation of the Greek root on the part of MSE. The name is taken from the Greek word *daketon*, meaning "biting animal". MSE erroneously believed the word to terminate in Greek as δακετων which would result in an augmented stem and require the retention of the terminal "-on" in the family-group name (apparently Forel, 1892, himself, believed this as well since he originally proposed the name as "Dacetonini", and innumerable myrmecologists also used this form, alongside the form "Dacetini", until recently). However, the original Greek terminates with omicron (rather than omega), i.e., δακετον, which necessitates the dropping of the "-on" and leaving the combining stem as "dacet-". Hence the family-group name is correctly spelled as Dacetini (in this case with the tribal suffix). The name appears here in its correct form and will so in future editions of Grimaldi and Engel (2005)

[d]Bolton (2003) used the junior name Gesomyrmecini since the type genus of Dimorphomyrmecini (i.e., *Dimorphomyrmex*) is a synonym of *Gesomyrmex*. However, ICZN (1999: Art. 40.1) states that a family-group name cannot be rejected even if its type genus is considered a junior synonym of another genus. Since Dimorphomyrmecini dates from Emery (1895: as Dimorphomyrmii) and Gesomyrmecini from Ashmead (1905: as Gesomyrmicinae), the former name should be employed for the tribe.

[e]The subfamily †Palaeosminthurinae has recently been synonymized with Camponotini (Snelling, in press).

cedure outlined by Nascimbene and Silverstein (2000).

SYSTEMATIC PALEONTOLOGY

Family Formicidae Latreille

DIAGNOSIS: Head prognathous; dorsal rim of torulus often tuberculate or concealed under vertical lamella of frons; antenna geniculate. Primitively with anterior margin of clypeus spiculate (apomorphically lost in many modern lineages: *vide infra*). Infrabuccal sac present between labium and hypopharynx. Pronotum with posterodorsal margin weakly concave; posterolateral apex truncate anterior to tegula. Metapleural gland present in females, opening above metacoxa (rarely absent); meso- and metacoxae contiguous; inner metatibial spur modified as calcar. Hind wing typically without jugal lobe (presence of the lobe is plesiomorphic within the family and likely part of the familial ground plan). Metasoma petiolate; first metasomal segment forming true node (strongly constricted anteriorly and posteriorly); first metasomal sternum separated from second metasomal sternum by deep constriction. Morphologically distinct, sterile worker caste typically present[4] (i.e., advanced eusocial); reproductives typically macropterous, workers apterous. Workers with pronotum fused to mesothorax (a freely articulating pronotum, present in some species, is plesiomorphic and undoubtedly part of the formicid ground plan), remaining segments typically fused. Species advanced eusocial.

COMMENTS: The ants, currently including 11,833 species (Bolton, 1995; www.antbase.org) have a cosmopolitan distribution and are among the most recognizable of all insects. Numerous species exist in Cenozoic deposits around the world and are relatively commonly encountered. Species of Cretaceous formicids, which are very rare, are briefly outlined in appendix 1.

Bolton (2003) considered the antlike wasps of the Cretaceous family Armaniidae to represent the basalmost subfamily of the ants. We have, however, retained armaniids at the family rank and as the sister group (perhaps paraphyletic?) to Formicidae (*vide* table 1 and appendix 1).

It is interesting to note that many primitive ants have clypeal spicules with rounded apices (e.g., †*Sphecomyrmodes*, †*Myanmyrma*; Amblyoponinae). Apomyrma has similar spicules, but these are located on the labrum rather than along the anterior clypeal margin. The significance of this trait is as of yet unclear (e.g., a ground-plan feature with numerous, apomorphic losses; or functional convergence).

Subfamily †Sphecomyrminae Wilson and Brown

†***Sphecomyrmodes,*** new genus

TYPE SPECIES: †*Sphecomyrmodes orientalis*, new species.

DIAGNOSIS: Distinguished from all other species of the tribe Sphecomyrmini by the minute, peglike denticles running along the entirety of the anterior margin of the clypeus and from †*Sphecomyrma* by the absence of a medial extension or process on the clypeal margin.

ETYMOLOGY: The new genus-group name is a combination of †*Sphecomyrma*, type genus of the subfamily, and the suffix–*odes*, meaning ''with the form of''. The name is masculine.

†*Sphecomyrmodes* ***orientalis,*** new species
Figures 3–4

DIAGNOSIS: As for the genus (*vide supra*).

DESCRIPTION: **Head.** Relatively large, height of head slightly less than length of alitrunk. Length of head 1.23 mm (with mandibles closed). No apparent microsculpture on cuticle of head. Clypeus setose; setae of moderate length and widely separated. Mandible simple, with only two teeth; outer surface with numerous, widely scattered, fine setae. Antenna of moderate length, with scape short, funicular article I (pedicel) shortest antennal article, funicular article II the longest article of funiculus. Lengths of antennal articles (in mm): scape 0.23, pedicel (funicular article [fa] I) 0.13, faII 0.32, faIII 0.15, faIV 0.15, faV 0.15, faVI 0.15, faVII 0.17, faVIII 0.17, faIX 0.17, faX 0.17, faXI 0.27. **Mesosoma.** Mesosomal length 1.33

[4] Some inquilines have apomorphically lost the worker caste.

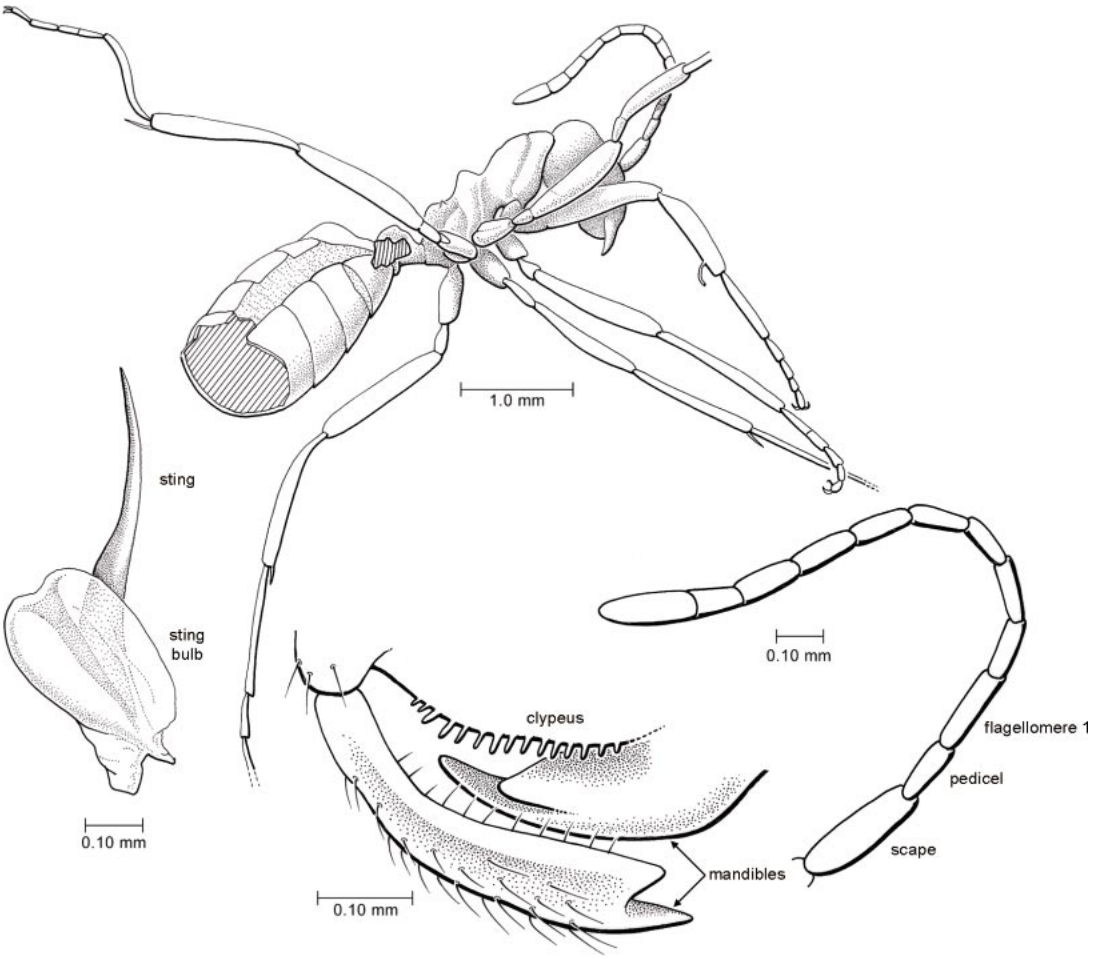


Fig. 4. Holotype worker of †***Sphecomyrmodes orientalis,*** new genus and species (AMNH Bu-351); general habitus, sting, clypeal margin and mandibles, and antenna.

mm; without apparent microsculpturing, with scattered fine, short setae on all visible surfaces, those on propodeum about twice as long as other setae. Coxae large, slightly inflated, ventrally setose, setae numerous and fine. Legs moderate length. Foreleg with tarsomere I distinctly longer than combined lengths of more distal tarsomeres; tarsomere I with ''antennal cleaner'' (strigil) a velvety notch on ventral margin of proximal end; calcar present, length slightly longer than greatest width of profemur, ventral margin with row of fine teeth and (apically) setae. Patch of dense, elongate setae opposite strigil on profemur; inner posterior surface of protibial apex with three stout, spinelike setae minutely curved inward at their extreme apices (visible on left foreleg). Pairs of stiff setae on ventral surface of protarsomeres: tarsomeres I-III with three pairs, IV with two small pairs. Pretarsal claw with minute subapical tooth. **Metasoma.** Attachment of petiole to propodeum not particularly thick; thickness (measured in lateral view) of anterior end of petiolar peduncle 0.3× greatest depth of propodeum. Petiole length 0.38 mm, height 0.37 mm. Preserved portion of gaster 1.73 mm in length. Integument without apparent microsculpturing, with scattered, fine setae. Distalmost metasomal segments torn apart, although sting bulb and sting well preserved beneath metasoma (fig. 4).

TYPE MATERIAL: **Holotype.** AMNH Bu-351, an incompletely preserved worker in a piece of reddish-orange amber, from Myanmar. Collected in Kachin state, Tanai village, on Ledo Road, 105 km NW Myitkyna, via Leeward Capital Corp., 1999.

ETYMOLOGY: The specific epithet is the Latin word *orientalis*, meaning ''of the east'' and is a reference to this being the first species of the tribe †Sphecomyrmini (sensu Bolton, 2003) recorded from Myanmar.

Genus †*Sphecomyrma* Wilson and Brown

†*Sphecomyrma* Wilson and Brown, *In* Wilson et al., 1967: 8. Type species: †*Sphecomyrma freyi* Wilson and Brown, 1967, monobasic and original designation.

DIAGNOSIS: Scape short; funiculus long and filiform, about four times length of scape; promesothoracic suture complete and well developed; trochantellus absent; petiole with distinct, domed node widely separated from propodeum and remainder of metasoma by deep constrictions; cuticle without sculpturing, superficial microscopic relief, with scattered and sparse setae.

COMMENTS: The genus, which is defined largely by plesiomorphies, is doubtfully monophyletic. It contains three species: †*Sphecomyrma canadensis* Wilson in Canadian amber, and †*S. freyi* Wilson and Brown and a new species in New Jersey amber (*vide infra*). In addition, we provide information from newly identified material of †*S. freyi*.

Key to Species of †*Sphecomyrma* (based on the worker caste)

1. Anterior margin of clypeus with short, broad extension, surface with two, long setae at most; compound eye round 2
— Anterior margin of clypeus with long, medial lobe (fig. 5), surface with numerous, long setae; compound eye oval [New Jersey amber] . . . . . †*S. mesaki* Engel and Grimaldi, n.sp.
2. Third antennal article slightly more than twice as long as second article [New Jersey amber] . . . . . †*S. freyi* Wilson and Brown
— Third antennal article about as long as second article [Canadian amber] . . . . . †*S. canadensis* Wilson

†*Sphecomyrma **mesaki,*** new species
Figure 5

DIAGNOSIS: Distinguished from all other species of the genus by the median portion of the clypeus having a long ventral lobe, length of the clypeus through the lobe is 0.46× the greatest width of clypeus; clypeus setose; and scape very short (1.2× the length of longest funicular article). The species can be further distinguished from †*S. freyi* (the other species of the genus in New Jersey amber) by broad, shallow scrobes at base of antennae; an eye that is approximately 1/3 larger and oval (vs. almost perfectly round in †*S. freyi*); and a large head (length of head/length of mesosoma = 0.83, vs. 0.65 in †*S. freyi*).

DESCRIPTION: Petiole and gaster not preserved, so only head, mesosoma, and legs preserved. **Head.** Large, length of head slightly less than length of alitrunk. Length of head 2.20 mm (with mandibles closed); width of head 1.95 mm; length of eye 0.66 mm. No microsculpture on cuticle of head. Vertex with fine, sparse pilosity, setae ca. 0.2 mm long. Ocelli present, median ocellus situated just above dorsal tangent of compound eyes. Face bare. Bases of antennae situated in shallow, broad scrobes; length of scrobe about equal to length of scape and articulating base. Eyes well developed, bare, situated well above bases of antennae; gena deep. Lateral portions of clypeus quadrate; median portion distended into long ventral lobe that extends to ventral margin of closed right mandible. Clypeus setose, except on middle part. Mandibles simple, with only two teeth. Antennae of moderate length, with scape short, funicular article I (pedicel) shortest antennal article, funicular article II the longest article of funiculus. Lengths of antennal articles (in mm): scape 0.53, pedicel (funicular article [fa] I) 0.20, faII 0.43, faIII 0.35, faIV 0.30, faV 0.23, faVI 0.23, faVII 0.30, faVIII 0.22, faIX 0.26, faX 0.30, faXI 0.33. **Mesosoma.** Mesosomal length 2.66 mm; without microsculpturing, except at posterolateral margin of promesonotal suture, where eight fine grooves occur. Dome of promesonotum setose; several fine setae on dorsal surface of metanotum and propodeum. Coxae large, inflated, ventrally setose. Attachment of petiole

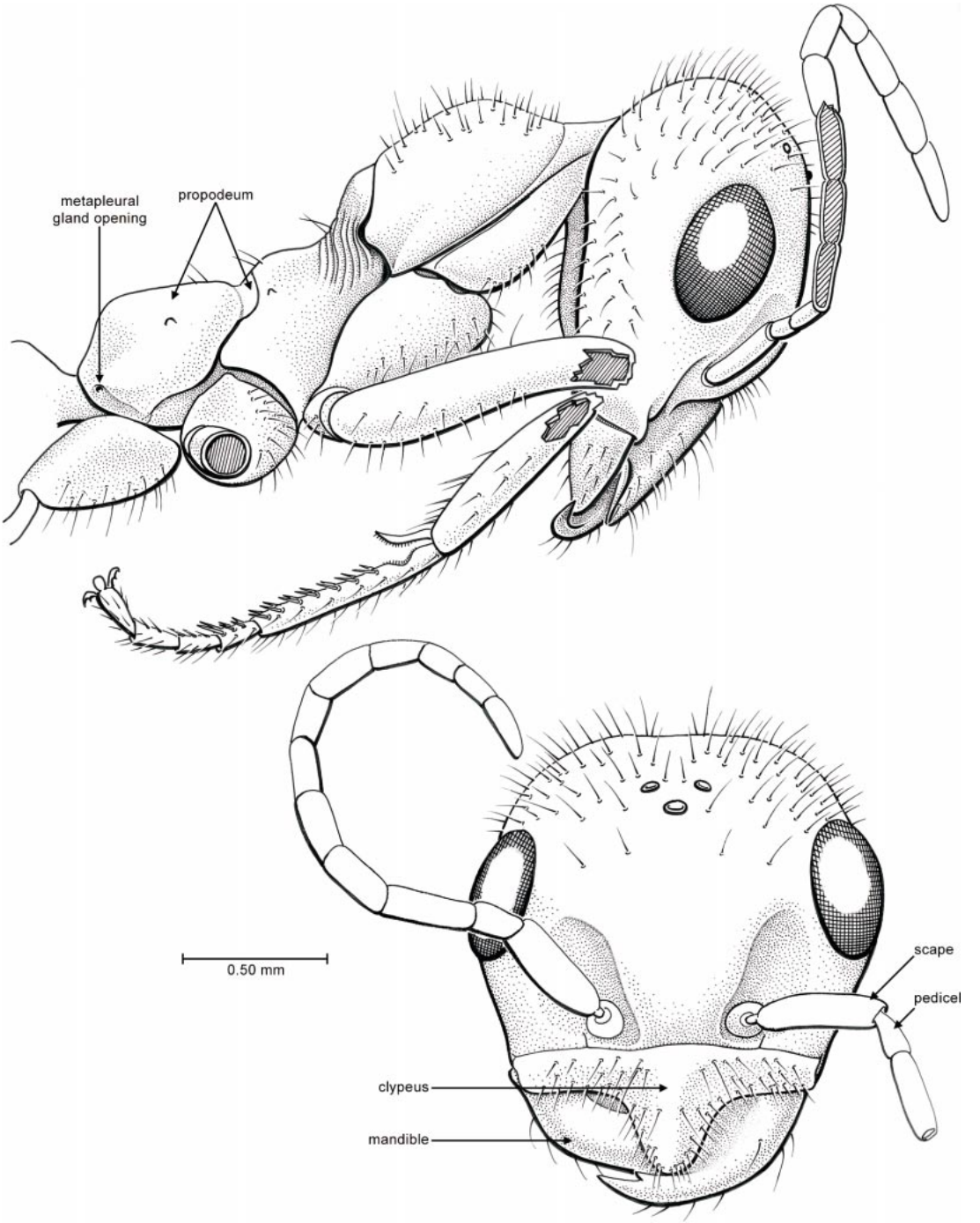


Fig. 5. Holotype worker of †*Sphecomyrma* ***mesaki,*** new species (AMNH NJ-1023); lateral habitus and facial view.

to propodeum not particularly thick; thickness (measured in lateral view) of anterior end of petiolar peduncle 0.3x greatest depth of propodeum. Metapleural gland opening (MGO) and MG bulla obvious, situated on posterolateral part of propodeum just above metacoxa. MGO small, with groove running between it and extended almost to vental margin of propodeum. Legs moderate length. Foreleg with tarsomere I slightly longer than combined length of more distal tarsomeres; tarsomere I with ''antennal cleaner'' (strigil) a velvety notch on ventral margin of proximal end; calcar present, length slightly longer than greatest width of femur, ventral margin with row of fine teeth and (apically) hairs. Stiff setae on ventral surface of protarsomeres: tarsomere I with 7 pairs, II with 3 pairs, III with 3 small pairs, IV with 2 small pairs. Pretarsal claw with subapical tooth. Metasoma not preserved.

TYPE MATERIAL: **Holotype.** AMNH NJ-1023, an incompletely preserved worker in a piece of amber barely larger than the ant, from Sayreville, New Jersey (Middlesex Co.), White Oaks outcrop, coll. Bob Mesak (fig. 5). The amber is an irregularly shaped drop, 7 × 5 × 4 mm, made of clear yellow amber. Portions of some appendages are breached at the surface, and the petiole and gaster were similarly lost at the surface. Since very little amber exists between the ant and surface of the amber piece, no trimming or polishing was possible. Still, details through the rough surface are highly visible by immersing the piece in glycerine.

ETYMOLOGY: The specific epithet is a patronymic for Bob Mesak, who collected and donated this valuable specimen to the AMNH.

†*Sphecomyrma freyi* Wilson and Brown
Figure 6

†*Sphecomyrma freyi* Wilson and Brown, *In* Wilson et al., 1967: 8. Grimaldi et al., 1997: 12 (redescription of some features, new specimens, neotype).

MATERIAL: AMNH NJ-943, in amber from New Jersey: Middlesex Co., Sayreville, White Oaks outcrop, collected by Keith Luzzi (fig. 6). The piece is transparent yellow, originally much larger than now; was embedded and trimmed to 14 × 15 × 4 mm. The piece contains two workers of †*S. freyi*.

DESCRIPTIVE NOTES: Both workers are largely but not completely preserved. Specimen A has the frontal half of the head missing; most of the antenna is present except for bases of the scapes; the entirety of the remainder of the body is preserved and the sting appears largely or fully extruded. Specimen B has the dorsal and apical part of the gaster missing, as well as portions of the right hind leg; the anterior third of the head is obscured by Schimmel and a bubble.

Measurements of body: Width of head (specimen B), 1.03 mm; length of head (B, approximate), 1.20 mm; length of mesosoma 1.39 mm (B), 1. 40 mm (A); length of petiole 0.29 mm (B), 0.33 mm (A); length of gaster (A) 1.72 mm; length of extruded portion of sting (A), 0.33 mm. Measurements of antennal articles (as measured for right antenna in A, left antenna in B) presented in table 2. Measurements of leg segmentation (as measured on specimen A) presented in table 3.

COMMENTS: The discovery of this piece of amber is highly significant and addresses questions of the social behavior of primitive ants like †*Sphecomyrma*. As reviewed in Grimaldi et al. (1997), Dlussky (1987, 1988), and Poinar et al. (1999) questioned whether †*Sphecomyrma* was a true ant since it had such a short scape [but see response to Poinar et al. (1999) by Grimaldi and Agosti (2000b)]. With such a short scape, Dlussky argued that it would be impossible for †*Sphecomyrma* to antennate, and therefore it was considered highly unlikely for †*Sphecomyrma* to have been social. Among the approximately 1700 fossiliferous pieces of New Jersey amber in the AMNH collection thus far, four pieces contain worker or male sphecomyrmine ants. These ants are (and probably originally were) exceedingly rare, and the probability that two workers would be preserved in one piece *by chance alone* is extremely remote. It is most parsimonious to explain the occurrence of two workers in the same piece as a result of social behavior.

†*Sphecomyrma* sp.

MATERIAL: AMNH NJ-942, a male in amber from New Jersey: Middlesex Co., Say-

Fig. 6. Two workers of †*Sphecomyrma freyi* Wilson and Brown preserved in a single piece of New Jersey amber (AMNH NJ-943).

reville, White Oaks outcrop. Collected by the late Steve Swolensky. Specimen is in a clear yellow piece of amber 5 × 7 mm, embedded in epoxy and trimmed to 1.5 mm thickness for a full lateral view of the ant.

COMMENTS: Venation and other details of this specimen are indistinguishable from AMNH NJ-242, described and figured by Grimaldi et al. (1997) as †*Sphecomyrma*? sp. Measurements: Length of hind wing (forewing

TABLE 2
Measurements of Antennal Articles for †*Sphecomyrma freyi* (AMNH NJ-943)

	Specimen	
Antennal article	A[a]	B[b]
Scape	—	0.33 mm
fa1 (pedicel)	0.16 mm	0.12 mm
fa2	0.28 mm	0.24 mm
fa3	0.16 mm	0.16 mm
fa4	0.16 mm	0.16 mm
fa5	0.16 mm	0.16 mm
fa6	0.16 mm	0.17 mm
fa7	0.16 mm	0.18 mm
fa8	0.16 mm	0.17 mm
fa9	0.17 mm	0.17 mm
fa10	0.16 mm	0.17 mm
fa11	0.23 mm	0.26 mm

[a]Measurements taken from right antenna.
[b]Measurements taken from left antenna.
fa = funicular article.

apices are lost), 1.97 mm; length of mesosoma 1.29 mm; length of petiole 0.36 mm; length of gaster 1.05 mm; length of antenna 2.40 mm.

Genus †*Haidomyrmex* Dlussky

†*Haidomyrmex* Dlussky, 1996: 84. Type species: †*Haidomyrmex cerberus* Dlussky, 1996, monobasic and original designation.

DIAGNOSIS: Clypeus a small, hemispheric lobe lying just below antennal bases, possessing brush of ca. 60 fine, stiff, whitish setae; setae are evenly arranged, those on ventral margin thickened at base but taper to a fine point apically. Compound eyes small, length ca. 0.2× length of head capsule; ocelli absent. Mandibles elongate, scimitar-shaped, without serrations or teeth. Propodeum rounded in profile. Petiole one-segmented, nodiform, with distinct constriction at articulation with remainder of metasoma. Known from the worker caste only.

COMMENTS: The head of †*Haidomyrmex* is enigmatic (fig. 7) and much of the detail is obscured below the clypeus and where the mandibles articulate. Indeed, it is likely that there has been significant distortion at the manibular bases resulting in the rather ''deep'' appearance they have relative to the clypeus.

The peculiar clypeal setae may have served a sensory function, perhaps as trigger hairs for the large mandibles, much the way gaff-shaped mandibles of various myrmecines and ''poneroids'' function. In those living ants long, fine, stiff trigger setae lie on the inside surface of the mandibles and on the oral margin. †*Haidomyrmex* has no such setae, so perhaps the clypeal brush functioned analogously. How †*Haidomyrmex* might have fed itself is an enigma. It is possible that this worker is similar to the major workers of *Eciton*, which cannot feed themselves.

†*Haidomyrmex cerberus* Dlussky
Figures 7–8

†*Haidomyrmex cerberus* Dlussky, 1996: 85.

HOLOTYPE: NHML In.20182, partial worker specimen in amber from Myanmar.

COMMENTS: We have tentatively followed past authors in placing †*Haidomyrmex* within †Sphecomyrminae (e.g., Bolton, 2003). However, it is important to note the significant similarities between this genus and †*Brownimecia* in New Jersey amber (*vide infra*). Both genera have large, dome-shaped heads, with relatively small compound eyes, lack ocelli, have large mandibles devoid of serrations or dentition, and an elongate anterior extension, or collar, of the pronotum.

TABLE 3
Leg Measurements (in mm) for †*Sphecomyrma freyi* (AMNH NJ-943)

			Tarsomeres				
	Femur	Tibia	1	2	3	4	5
Fore	0.82	0.73	0.49	0.13	0.12	0.08	0.13
Mid	0.97	0.83	0.58	0.20	0.17	0.13	0.19
Hind	1.20	1.10	0.74	0.29	0.19	0.14	0.20

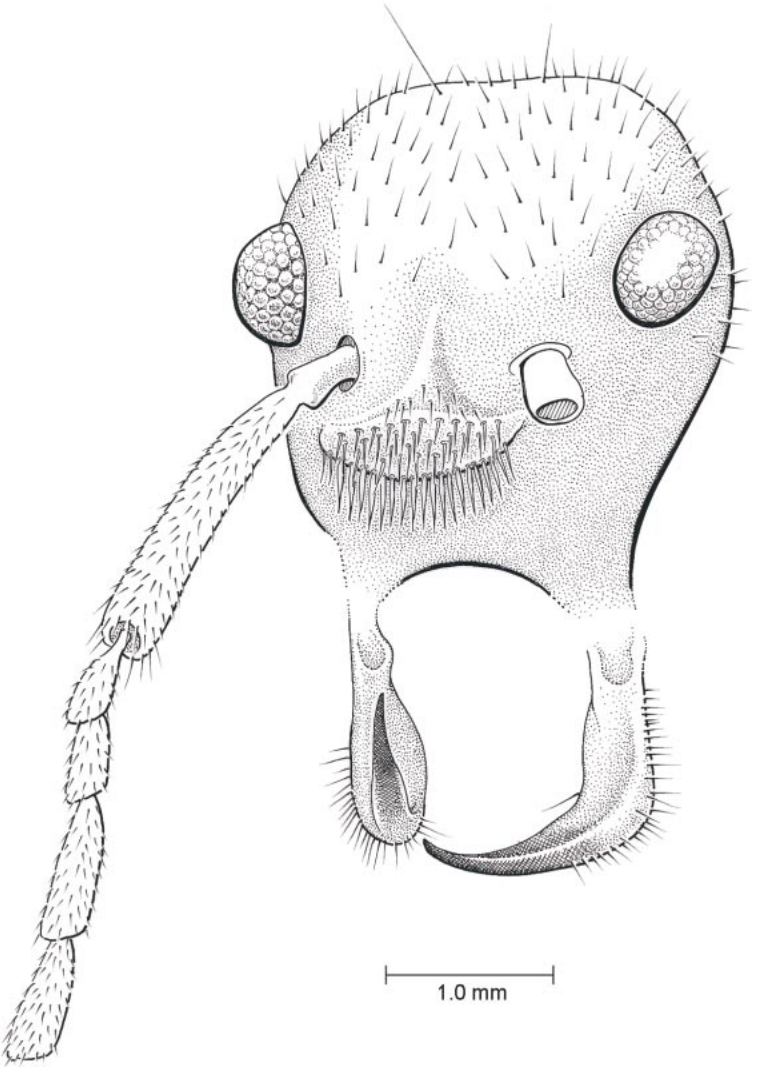


Fig. 7. Facial view of holotype worker of †*Haidomyrmex cerberus* Dlussky (NHML In.20182).

SUBFAMILY †BROWNIMECIINAE BOLTON

Genus †*Brownimecia* Grimaldi, Agosti, and Carpenter

†*Brownimecia* Grimaldi, Agosti, and Carpenter, 1997: 20. Type species: †*Brownimecia clavata*. Grimaldi, Agosti, and Carpenter, 1997, monobasic and original designation.

DIAGNOSIS: Antenna distinctly clubbed, apical funicular article twice the width of basal ones and pedicel. Ocelli absent. Mandibles long, thin, scimitar-shaped, strongly cruciate, without teeth or crenulations, but with oral surface bearing about 30 short, spiculelike setae. Metasoma with slight but definite constriction between second and third segment (also known as abdominal segments III and IV; gastral segments 1 and 2). Known from the worker caste only.

†*Brownimecia clavata* Grimaldi, Agosti, and Carpenter

†*Brownimecia clavata* Grimaldi, Agosti, and Carpenter, 1997: 20.

MATERIAL: AMNH NJ-941, in amber from

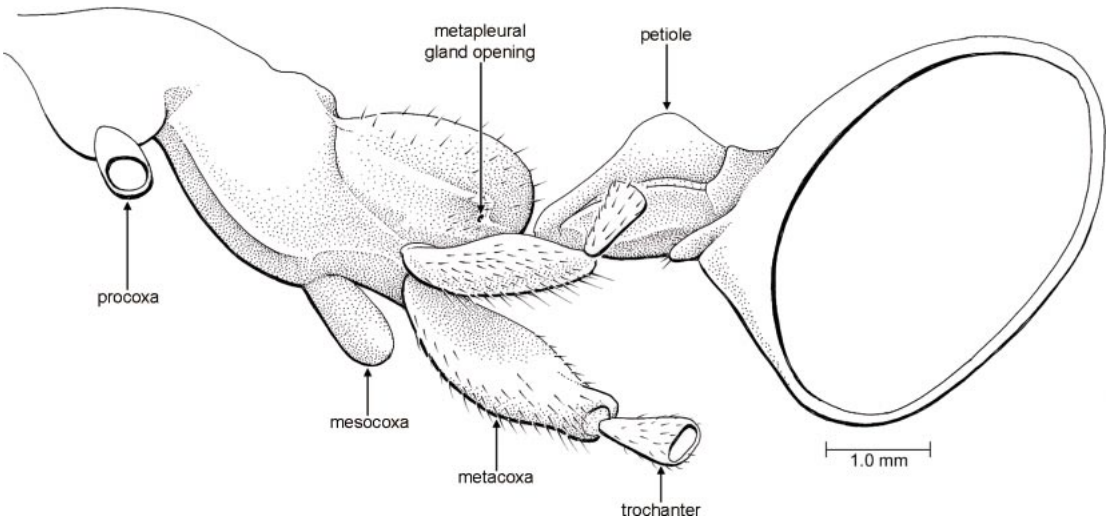


Fig. 8. Lateral view of mesosoma and petiole, as preserved, of holotype worker of †*Haidomyrmex cerberus* Dlussky (NHML In.20182).

New Jersey: Middlesex Co., Sayreville, White Oaks outcrop, collected by Steve Swolensky.

COMMENTS: A beautifully preserved specimen in clear yellow amber, 5 × 8 mm, which was embedded in epoxy and trimmed to 2 mm thickness. Like the holotype which was described in 1997, it is curled up and the sting is extruded. The piece also contains some wood fragments and a frass pellet. The length of head (including closed mandibles) 0.88 mm, greatest width of head 0.74 (between outer margins of eyes), length of eye 0.24 mm, length of trunk 0.94 mm, length of petiole 0.32 mm. The mandibles are tightly closed, so details are less visible than in the holotype. The front portion of the head, however, and especially the clypeus, are more visible. The clypeus has fine, parallel crenulations along and perpendicular to the dorsal margin of the clypeus. Most significantly, ocelli are definitively absent (rather than vestigial or minute). Three large ocelli are rare in ants, with scattered occurrence (e.g., Cerapachyinae [*Cylindromyrmex*, *Simopone*], Formicinae [*Aphophomyrmex*, *Notostigma*, *Alloformica*, *Cataglyphis*], Myrmeciinae [*Myrmecia*]), otherwise the ocelli are repeatedly lost, reduced, or modified secondarily (as is true for †*Brownimecia*). The large, well-developed ocelli of †*Sphecomyrma* are clearly a plesiomorphic feature and part of the formicid ground plan.

SUBFAMILY INCERTAE SEDIS

†***Myanmyrma,*** new genus

TYPE SPECIES: †*Myanmyrma gracilis*, new species.

DIAGNOSIS: Gracile ''poneroid'' ant with extremely long legs; mandibles nearly equal to length of head, sickle-shaped, with a long, apical sharp tooth and blunt subapical one; clypeal margin bilobate, denticulate; long, spatulate genal process; antennal sockets inclined, antennal funiculus very long, second article longest; articles slightly shorter apically; integument of head spinose; clypeus deeply incised along anterior margin and with distinct peglike setae; eyes and ocelli not apparent (but may be present); pretarsal claws with minute tooth; petiole with distinct nodus; gastral constriction distinct; sting well developed. Easily distinguished from †*Haidomyrmex*, another highly modified ant in Burmese amber, by the mandibular and clypeal structure, head microsculpturing, metasomal constriction, long genal processes, and very long legs.

ETYMOLOGY: Taken directly from Myanmar, the country of the amber's origin; and–

myrma, a common suffix for ant genera. The name is feminine.

†*Myanmyrma* ***gracilis,*** new species
Figures 1, 9

DIAGNOSIS: As for the genus (*vide supra*).

DESCRIPTION: Specimen has been compressed, but body form was clearly extremely gracile, with very long legs. **Head.** Proportions difficult to determine due to compression; length ca. 1.76 mm. Front of head with pair of carinae diverging dorsally; blunt spines on ridges of carinae and on frons; spines absent below ventral limit of carinae, with irregular cuticular foveae on clypeus. Ventral margin of clypeus with deep median emargination; clypeus with two lobes, margin of two lobes with row of ca. 14 minute denticles on each lobe, labrum similarly bilobed and denticulate. Lateral portion of clypeus lobed, without denticles. Gena with spatulate process, exact length difficult to discern, but ca. 0.3× length of mandible. Mandibles long, 1.61 mm. (right one), nearly equal to length of head, sickle-shaped; apical tooth long, sharp; blunt subapical tooth, no other teeth. No fine setae apparent. Apex of right mandible longer than left, especially apical tooth. Eyes well developed (difficult to observe since they are sunken in a cavity), length ca. 0.25× length of head. Antenna very long (7.2 mm); scape fairly short, with wide base; funicular article (fa) 1 shortest, fa2 longest; lengths of antennal articles (in mm): scape 0.63, funicular article (fa) [pedicel] I 0.44, faII 1.05, faIII 0.62, faIV 0.53, faV 0.61–faVI 0.45, faVII 0.40, faVIII 0.41, faIX 0.48, faX 0.48, faXI 0.65. **Mesosoma.** Elongate, not deep, length ca. 3.52 mm; small opening to metapleural gland (MPG) apparent just above hind coxa. Legs extremely long (*vide* measurements in table 4); trochantellus apparently absent. Protibia with dorsal, preapical brush of fine setae; one large, two finer apical spurs; ventral surface of probasitarsus with fine pilosity, six pairs of stiff setae; all tarsomeres with four apical spines; each pretarsal claw with median tooth. Mesotibia with pair of ventroapical spurs; ventral surface of mesobasitarsus with three rows of 10 stiff setae each; metatibia with pair of apical spurs, one larger and pectinate; ventral surface of metabasitarsus with fine pilosity, 10 pairs of setae. **Metasoma.** Petiole attachment to second metasomal segment narrow; petiole with high, narrow node; length of petiole 1.26 mm; posterior portion of petiole narrow, tubular; deep constriction between second and third metasomal segments. Metasoma overall quite small, ca. 0.3x length of body (excluding antennae). Terga and sterna telescoped in specimen, as shown in figure 9; gaster (i.e., metasoma excluding petiole) approximately 2.95 mm long. Sting well developed, only partly extruded but internally visible; pygidium with long fine setae.

HOLOTYPE: AMNH Bu-014, a worker, in amber from northern Myanmar (Burma) (figs. 1, 9). Collected in Kachin state, Tanai village, on Ledo Road, 105 km NW Myitkyna, via Leeward Capital Corp., 1999. The ant is in a transparent yellow piece of amber, which was originally more than 20 mm in diameter and 30 mm in length. The piece was occluded with fractures and debris, so it required epoxy embedding and then trimming to better observe the ant. The piece is now rhomboid-shaped, 17 × 22 × 4 mm, the broad surfaces being parallel to the lateral surface of the ant. A flat edge also permits a frontal view of the head. Other inclusions in the piece are numerous frass pellets and wood fragments, further suggestive (besides body form) of arboreal/wood nesting habits of the ant. The ant specimen shows a great deal of distortion due to compression. The cuticle is transparent, facilitating observation of some internal structures (such as unextruded portions of the sting), but some compressed surfaces could easily be mistaken for flanges and other structures.

ADDITIONAL MATERIAL: Two additional, fragmentary specimens are perhaps representative of †*M. gracilis*; however, because of their poor preservation, we hesitate to designate them as paratypes. Both are preserved in amber from northern Myanmar and with the same collection data as the holotype. AMNH Bu-225, a poorly preserved worker but very similar to holotype in observable traits. AMNH Bu-1509, a badly compressed worker preserved in yellow amber; head mostly crushed and difficult to discern, metasoma similarly compressed; somewhat

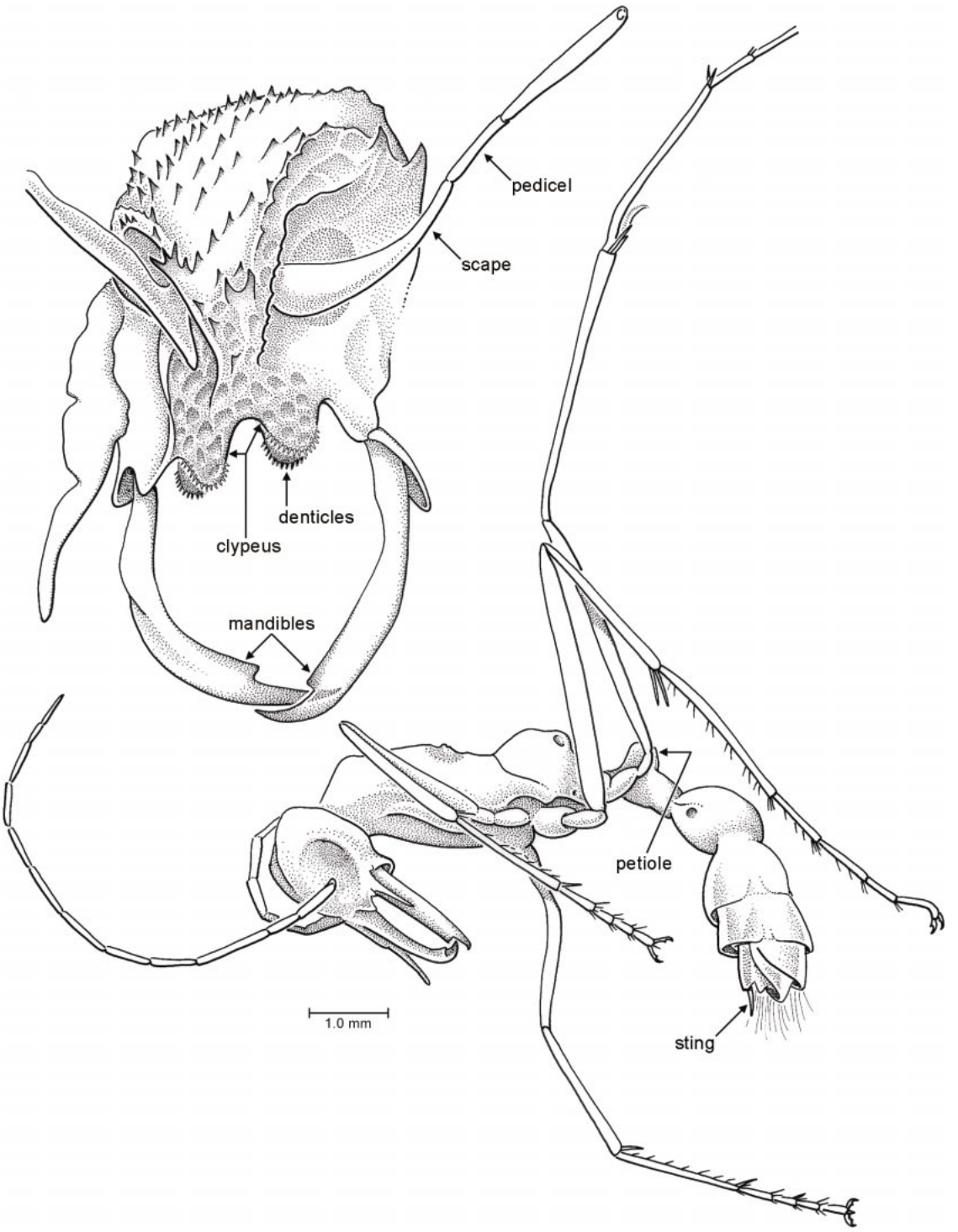


Fig. 9. Holotype worker of †***Myanmyrma gracilis,*** new genus and species (AMNH Bu-014); facial view and general habitus.

TABLE 4
Leg Measurements[a] of Holotype Worker of †*Myanmyrma gracilis* (in mm)

			Tarsomeres					
	Femur	Tibia	1	2	3	4	5	Claw
Fore	2.33	1.50	1.47	0.52	0.42	0.31	0.38	0.28
Mid	3.10	2.22	2.16	0.82	0.72	0.47	0.55	0.22
Hind	3.67	3.23	2.49	—	—	—	—	—

[a]As measured on the left legs.

smaller than holotype and Bu-225 but still exhibiting the same elongate, slender legs, constriction in first gastral segments, etc., this individual may represent a minor worker.

ETYMOLOGY: The specific epithet is the Latin word *gracilis*, meaning ''slender'', as a reference to elongate legs and structure of this ant.

COMMENTS: Constriction of the metasoma indicates the specimen is a ''poneroid'', which is the third and oldest Cretaceous record of this paraphyletic grade of primitive ants (the poneroid grade includes the poneromorph and myrmeciomorph subfamilies of Bolton, 2003). The other Cretaceous ''poneroids'' are †*Brownimecia clavata* (in New Jersey amber: Turonian), and †*Canapone dentata* Dlussky (in Canadian amber: Campanian). It is interesting that †*Myanmyrma* is only the fourth record of ants in Burmese amber, but two of these records are for highly modified species. †*Burmomyrma rossi* Dlussky is based on a single, alate, incomplete specimen, with head and portion of the alitrunk missing. The most distinctive feature of †*Burmomyrma* is the wing with highly reduced venation; thus, the taxonomic concept of this genus is not entirely comparable with that of the other two Burmese amber genera. †*Burmomyrma*, as discussed again later (*vide infra*), has been tentatively placed in the Aneuretinae (Dlussky, 1996; Bolton, 2003). Both †*Haidomyrmex* and †*Myanmyrma* are extremely gracile and relatively large ants, with large, highly modified mouthparts and genae. The extremely long legs and slender body are analogous to *Leptomyrmex* (Dolichoderinae) and *Oecophylla* (Formicinae), the latter of which is entirely arboreal. †*Haidomyrmex* and †*Myanmyrma* presumably had similar habits. †*Haidomyrmex* and †*Myanmyrma* are clearly not closely related, the former placed in the †Sphecomyrminae by Dlussky. The type and only specimen of †*Haidomyrmex*, however, has only the second metasomal (i.e., first gastral) segment preserved, so the lack of a constriction posterior to this segment is suggested, not definitive (*vide supra*).

The lengths of basal articles of the antenna of †*Myanmyrma* are highly significant. Funicular article 2 is the longest article in the funiculus, as is the case for most †Sphecomyrminae (except †*S. canadensis* Wilson). This condition does not exist in the other Cretaceous ''poneroids'', †*Brownimecia* and †*Canapone*. A long funicular article 2 was proposed by Grimaldi et al. (1997: 8) as one of only two or three possible synapomorphies for the †Sphecomyrminae. If truly apomorphic, the long funicular article 2 would have been independently derived in †*Myanmyrma*. If a long funicular article 2 was plesiomorphic, the monophyly of the †Sphecomyrminae would be seriously doubtful. Outgroup evidence from closely related aculeate families suggests that, indeed, this feature is symplesiomorphic for basal ants, including †*Myanmyrma*.

Placement of †*Myanmyrma* in a subfamily is challenging. As noted, the metasomal constriction implies placement among the poneroid grade where it best approximates species of the Ponerinae (poneromorph) or the Myrmeciinae (myrmeciomorph). Neither placement is entirely satisfactory, but we believe inclusion in the latter subfamily is more likely (although we tentatively retain the genus as subfamily incertae sedis). Like myrmeciines, †*Myanmyrma* has a metasomal

constriction, the antennal sockets inclined to nearly a vertical position, 12-segmented antennae, pectinate inner metatibial spur, and elongate mandibles. Unlike typical myrmeciines, however, the the new genus has mandibles that are sickle-shaped, with dentition only at the apices; has a deeply incised clypeal margin, with distinct spicules on the lobes; has a spinose integument on the head; has gracile legs; and elongate genal processes. These traits are, however, autapomorphic and do not preclude placement in Myrmeciinae. Within Myrmeciinae, †*Myanmyrma* would appear to be closest to the tribe Myrmeciini (sensu Bolton, 2003; Ward and Brady, 2003) as evidenced by the elongate second funicular segment and distinctly two-segmented waist. The latter trait is likely plesiomorphic as it occurs in *Myrmecia* and weakly so in †*Prionomyrmex*, perhaps being apomorphically lost in *Nothomyrmecia*. The presence of spicules along the clypeal margin in †*Myanmyrma* is an interesting and enigmatic feature that should be further explored for its systematic implications.

This is the species that is referred to by Grimaldi and Engel (2005) as ''undescribed Myrmeciinae?''

Subfamily Aneuretinae? Emery

†***Cananeuretus,*** new genus

Type Species: †*Cananeuretus occidentalis*, new species.

Diagnosis: Compound eyes present, small; ocelli absent. Antennal sockets slightly inclined; scape elongate. Mandible of primitive construction, with four distinct teeth (fig. 10), basalmost tooth largest. Preoccipital carina absent; ocelli absent. Alitrunk elongate, slender; pronotal neck elongate. Meso- and metatibia with a single spur; pretarsal claws simple. Propodeal lobes, denticles, and spines absent; petiole one-segmented, anterior peduncle elongate, with distinct tubular, postnodal section (more elongate than in *Aneuretus*) articulating high on anterior surface of second metasomal segment, petiolar tergum and sternum fused; nodus not very high. Metasoma excluding petiole short and globular; without U-shaped emargination on anterior margin of second metasomal segment; sting present and well developed. Known from the worker caste only.

Etymology: The new genus-group name is a combination of Canada, the country from which this amber originates, and *Aneuretus*, type genus of the Aneuretinae. The name is masculine.

Comments: †*Cananeuretus* might at first be confused for †*Eotapinoma*, a dolichoderine described from Canadian amber (Dlussky, 1999). †*Cananeuretus* differs notably from †*Eotapinoma* in the presence of a well-developed sting (apparently vestigial in †*Eotapinoma*, like all dolichoderines), the more elongate petiole with a distinct nodus (shorter petiole, which does not have an elongate peduncle and without developed nodus in †*Eotapinoma*), and the reduced compound eyes (large in †*Eotapinoma*).

This new genus is tentatively placed in Aneuretinae, although the group shows mostly what are presumed plesiomorphies for the subfamily. The presence of a strong, well-developed sting and absence of an acidopore excludes placement in Dolichoderinae or Formicinae. However, the genus is best placed among the formicomorph subfamilies (sensu Bolton, 2003) where it most closely approximates the Aneuretinae. As more material is recovered of these ants and a cladistic framework for fossil aneuretines achieved, it is possible that †*Cananeuretus* and others may prove to be stem-group Aneuretinae or even represent stem groups to Aneuretinae + Dolichoderinae.

Today the subfamily Aneuretinae consists of a single species occurring in Sri Lanka. During the Tertiary aneuretines were distributed widely in the Northern Hemisphere as evidenced by their occurrence in Baltic amber (Wheeler, 1914) and Florissant, Colorado (Carpenter, 1930). The mid-Cretaceous genus †*Burmomyrma*, in amber from Myanmar, has been tentatively placed in the Aneuretinae (Dlussky, 1996; Bolton, 2003) and, until now, represented the sole Mesozoic record for the subfamily. It is increasingly apparent that aneuretines were widely distributed during the Mesozoic and early Tertiary, and that *Aneuretus* is a notable relict in Sri Lanka today. The significant extinction of northern aneuretines was perhaps a result of the infamous Eocene-Oligocene

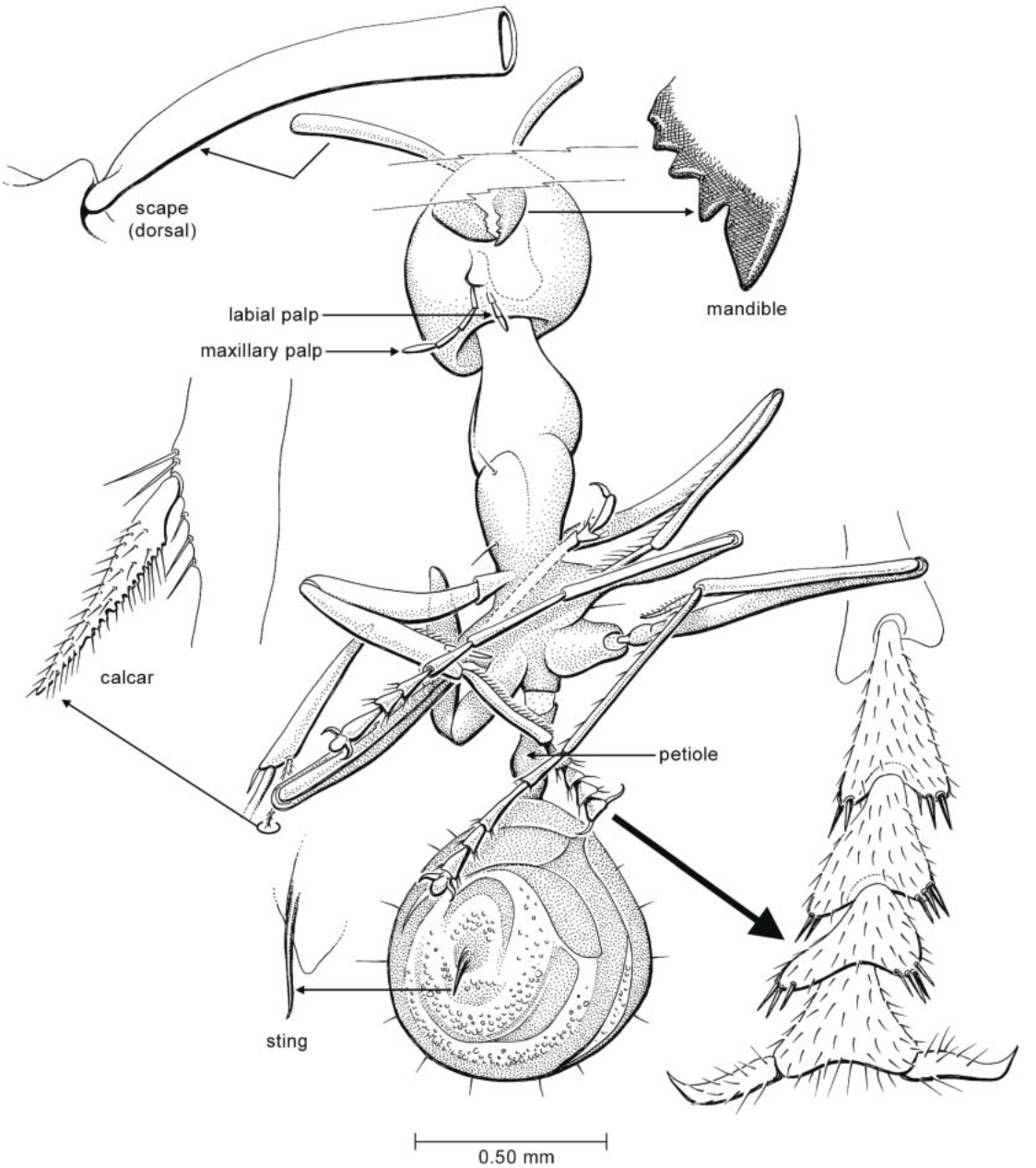


Fig. 10. Holotype worker of †***Cananeuretus occidentalis,*** new genus and species (TMP 8.89.7).

climatic shift, a cooling event that dramatically altered the evolutionary history and biogeography of numerous insect lineages that are today austral relicts (Grimaldi and Engel, 2005).

†*Cananeuretus* ***occidentalis,*** new species
Figures 2, 10–11

DIAGNOSIS: As for the genus (*vide supra*).
DESCRIPTION: Body with sparsely scattered,

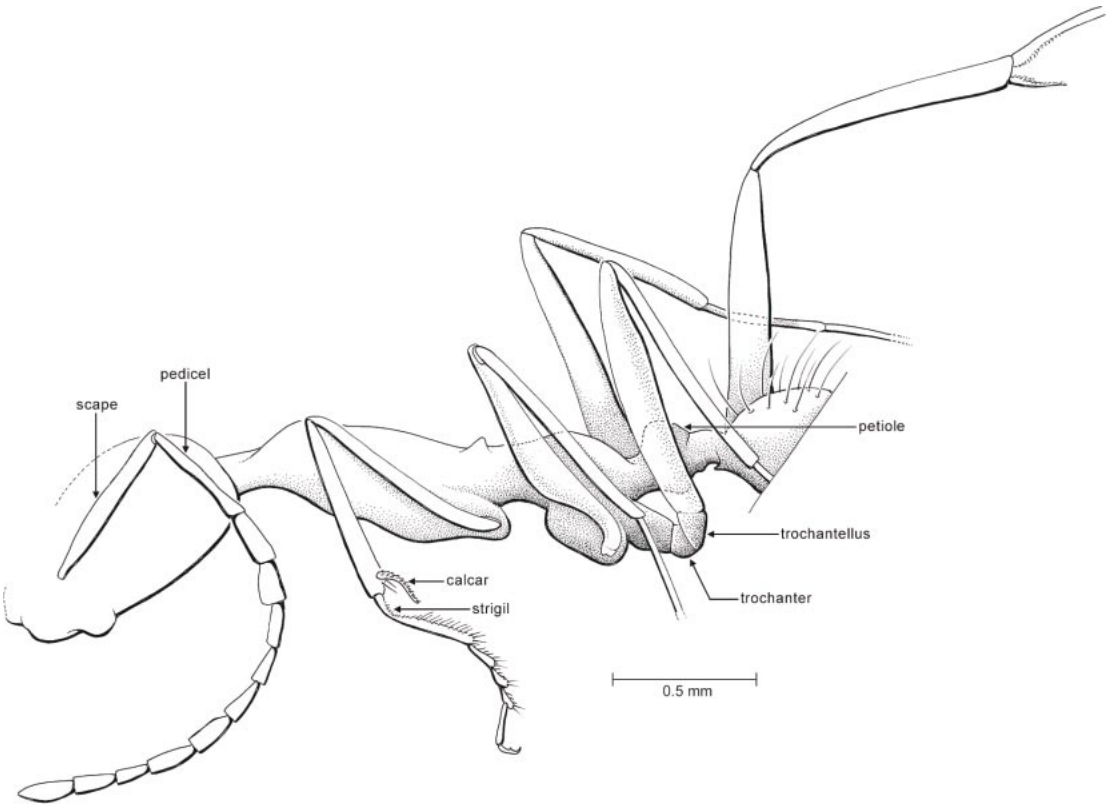


Fig. 11. Partial worker of †*Cananeuretus occidentalis*? (TMP 91.149.3).

fine setae; integument finely imbricate. **Head.** Length ca. 0.52 mm; narrowed slightly toward apex; vertex gently rounded. Mandibles with short, pointed teeth, basalmost apical tooth largest. Eyes present, relatively small and low on head (difficult to observe). Scape fairly long (0.46 mm), narrowed slightly at base for articulation with bulb (fig. 10); pedicel 0.65× length of scape. **Mesosoma.** Elongate, not deep, length ca. 3.10 mm; pronotum forming a distinct neck anteriorly. Legs slender and long; trochantellus present (fig. 11). Inner surfaces of protibia and probasitarsus with row of short, fine setae forming weakly defined brushes (fig. 10); tarsomeres beyond basitarsus triangular, laterally with short, distinct, stiff setae; pretarsal claws simple. Mesotibia and metatibia with a single spur; metatibial spur distinctly and minutely setose (fig. 10). Propodeum without lobes or spines, broadly rounded and gently sloping to articulation with petiole. **Metasoma.** Petiole with elongate peduncle, distinct nodus, and relatively long posterior, tubular section, articulating high on second metasomal segment; petiolar tergum and sternum fused; metasoma without constriction between second and third segments (i.e., gastral segments 1 and 2); metasoma overall quite globular. Sting well developed, extruded.

HOLOTYPE: TMP 8.89.7, labeled, ''Grassy Lake, Alberta, Campanian, Foremost Formation, Formicidae'' (figs. 2, 10). Worker in amber that is embedded in a thin block of epoxy and slide mounted.

ADDITIONAL MATERIAL: TMP 91.149.3, labeled, ''Hymenoptera, Grassy Lake, Alberta, Campanian, Foremost Formation, Formicidae'' (fig. 11). Worker in amber that is embedded in a thin block of epoxy and slide mounted. The specimen is partial and owing to some minor differences in the shape of the petiole, we have considered it best to only tentatively assign it to this species.

ETYMOLOGY: The specific epithet is the

term *occidentalis*, meaning ''of the west'', and is a reference to this being the first aneuretine or aneuretine-like ant from the Mesozoic of the Western Hemisphere.

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REFERENCES

Ashmead, W.H. 1905. A skeleton of a new arrangement of the families, subfamilies, tribes and genera of the ants, or the superfamily Formicoidea. Canadian Entomologist 37: 381–384.

Bolton, B. 1994. Identification guide to the ant genera of the world. Cambridge: Harvard University Press, 222 pp.

Bolton, B. 1995. A new general catalogue of the ants of the world. Cambridge: Harvard University Press, 504 pp.

Bolton, B. 2003. Synopsis and classification of Formicidae. Memoirs of the American Entomological Institute 71: 1–370.

Borkent, A. 1995. Biting midges in the Cretaceous amber of North America (Diptera: Ceratopogonidae). Leiden: Backhuys Publishers, 237 pp.

Carpenter, F.M. 1930. The fossil ants of North America. Bulletin of the Museum of Comparative Zoology 70: 1–66.

Cruickshank, R.D., and K. Ko. 2003. Geology of an amber locality in the Hukawng Valley, northern Myanmar. Journal of Asian Earth Sciences 21: 441–455.

Dlussky, G.M. 1987. New Formicoidea (Hymenoptera) from Late Cretaceous. Paleontologicheskiy Zhurnal 1987: 131–135. [In Russian]

Dlussky, G.M. 1988. Ants from the amber of Sakhalin (Paleocene?). Paleontologicheskiy Zhurnal 1988: 50–61. [In Russian]

Dlussky, G.M. 1996. Ants (Hymenoptera, Formicidae) of Burmese amber. Paleontologicheskiy Zhurnal 3: 83–89. [In Russian]

Dlussky, G.M. 1999. New ant taxa (Hymenoptera, Formicidae) from Canadian amber. Paleontologicheskiy Zhurnal 4: 73–76. [In Russian]

Dlussky, G.M., D.J. Brothers, and A.P. Rasnitsyn. 2004. The first Late Cretaceous ants (Hymenoptera: Formicidae) from southern Africa, with comments on the origin of the Myrmicinae. Insect Systematics and Evolution 35: 1–13.

Dlussky, G.M., and A.P. Rasnitsyn. 2003. Ants (Hymenoptera: Formicidae) of Formation Green River and some other middle Eocene deposits of North America. Russian Entomological Journal 11: 411–436.

Emery, C. 1895. Die Gattung *Dorylus* Fab. und die systematische Eintheilung der Formiciden. Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere 8: 685–778.

Engel, M.S. 2005. Family-group names for bees (Hymenoptera: Apoidea). American Museum Novitates 3476: 1–33.

Forel, A. 1892. Attini und Cryptocerini. Zwei neue *Apterostigma*-Arten. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 8: 344–349.

Grimaldi, D., and D. Agosti. 2000a. A formicine in New Jersey Cretaceous amber (Hymenoptera: Formicidae) and early evolution of the ants. Proceedings of the National Academy of Sciences of the United States of America. 97: 13678–13683.

Grimaldi, D., and D. Agosti. 2000b. The oldest ants are Cretaceous, not Eocene: Comment. Canadian Entomologist 132: 691–693.

Grimaldi, D., D. Agosti, and J.M. Carpenter. 1997. New and rediscovered primitive ants (Hymenoptera: Formicidae) in Cretaceous amber from New Jersey, and their phylogenetic relationships. American Museum Novitates 3208: 1–43.

Grimaldi, D., and M.S. Engel. 2005. Evolution of the insects. Cambridge: Cambridge University Press, xv+755 pp.

Grimaldi, D., A. Shedrinsky, and T. Wampler. 2000. A remarkable deposit of fossiliferous amber from the Upper Cretaceous (Turonian) of New Jersey. *In* D. Grimaldi (editor), Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey: 1–76. Leiden: Backhuys Publishers, viii + 498 pp.

Grimaldi, D.A., M.S. Engel, and P.C. Nascimbene. 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. American Museum Novitates 3361: 1–72.

Hölldobler, B., and E.O. Wilson. 1990. The ants. Cambridge: Harvard University Press, xii+ [1]+732 pp.

International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature [4th ed.]. London: International Trust for Zoological Nomenclature, xxix+ [1]+306 pp.

Jell, P.A. 2004. The fossil insects of Australia. Memoirs of the Queensland Museum 50(1): 1–124.

Jell, P.A., and P.M. Duncan. 1986. Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra fossil bed (Korumberra Group), South Gippsland, Victoria. Memoir of the Association of Australasian Paleontologists 3: 111–205.

Nascimbene, P., and H. Silverstein. 2000. The preparation of fragile Cretaceous ambers for conservation and study of organismal inclusions. *In* D. Grimaldi (editor), Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey: 93–102. Leiden: Backhuys Publishers, viii + 498 pp.

Naumann, I.D. 1993. The supposed Cretaceous ant *Cretacoformica explicata* Jell and Duncan (Hymenoptera). Journal of the Australian Entomological Society 32: 355–356.

Nel, A., G. Perrault, V. Perrichot, and D. Néraudeau. 2004. The oldest ant in the lower Cretaceous amber of Charente-Maritime (SW France) (Insecta: Hymenoptera: Formicidae). Geologica Acta 2(1): 23–29.

Poinar, G., Jr., B. Archibald, and A. Brown. 1999. New amber deposit provides evidence of Early Paleogene extinctions, paleoclimates, and past distributions. Canadian Entomologist 131: 171–177.

Rasnitsyn, A.P., and R. Kulicka. 1990. Hymenopteran insects in Baltic amber with respect to the overall history of the order. Prace Muzeum Ziemi 41: 53–64.

Rasnitsyn, A.P., and D.L.J. Quicke. 2002. History of insects. Dordecht: Kluwer, xii + 517 pp.

Saux, C., B.L. Fisher, and G.S. Spicer. 2004. Dracula ant phylogeny as inferred by nuclear 28S rDNA sequences and implications for ant systematics (Hymenoptera: Formicidae: Amblyoponinae). Molecular Phylogenetics and Evolution 33: 457–468.

Skalski, A.W., and A. Veggiani. 1990. Fossil resin in Sicily and the northern Apennines: geology and organic content. Prace Muzeum Ziemi 41: 37–49.

Snelling, R.R. In press. The identity of the fossil ant, ''*Palaeosminthurus juliae*'' Pierce and Gibron (Hymenoptera: Formicidae). Journal of the Kansas Entomological Society.

Verhaagh, M. 1996. Warum die älteste bekannte Ameise keine ist. Beiträge der Hymenopterologen-Tagung in Stuttgart 1996: 11.

Ward, P.S., and S.G. Brady. 2003. Phylogeny and biogeography of the ant subfamily Myrmecinae (Hymenoptera: Formicidae). Invertebrate Systematics 17: 361–386.

Wheeler, W.M. 1914 [1915]. The ants of the Baltic amber. Schriften der Physikalisch-ökonomischen Gesellschaft zu Königsberg 55: 1–142.

Wilson, E.O. 1985a. Invasion and extinction in the West Indian ant fauna: evidence from the Dominican amber. Science 229: 265–267.

Wilson, E.O. 1985b. Ants from the Cretaceous and Eocene amber of North America. Psyche 92: 205–216.

Wilson, E.O., F.M. Carpenter, and W.L. Brown, Jr. 1967. The first Mesozoic ants, with the description of a new subfamily. Psyche 74: 1–19.

Zherikhin, V.V., and A.J. Ross. 2000. A review of the history, geology and age of Burmese amber (Burmite). Bulletin of the Natural History Museum London (Geology) 56: 3–10.

APPENDIX

Cretaceous Ants (Formicidae) and Related Taxa

The following table summarizes the described species of ants and antlike wasps (i.e., Armaniidae) from the Cretaceous. The classificatory structure generally follows that of Bolton (2003). The fossil *Cretacoformica explicata* Jell and Duncan (1986) from the Lower Cretaceous (Aptian) Koonwara beds of Australia is excluded since it is not only not a formicid, but not even an aculeate (Naumann, 1993; Grimaldi et al., 1997: *vide etiam* Jell, 2004).

Taxon	Deposit	Age
Family FORMICIDAE Latreille		
Poneromorph Group		
Subfamily †Sphecomyrminae Wilson and Brown		
Genus †*Sphecomyrmodes* Engel and Grimaldi, n.gen.		
†*S. orientalis* Engel and Grimaldi, n.sp.	Burmese (A)	Alb
Genus †*Sphecomyrma* Wilson and Brown		
†*S. canadensis* Wilson	Canadian (A)	Cam
†*S. freyi* Wilson and Brown	New Jersey (A)	Tur
†*S. mesaki* Engel and Grimaldi, n.sp.	New Jersey (A)	Tur
Genus †*Baikuris* Dlussky		
†*B. casei* Grimaldi, Agosti, and Carpenter	New Jersey (A)	Tur
†*B. mandibularis* Dlussky	Taymyr (A)	San
†*B. mirabilis* Dlussky	Taymyr (A)	San
Genus †*Cretomyrma* Dlussky		
†*C. arnoldii* Dlussky	Taymyr (A)	San
†*C. unicornis* Dlussky	Taymyr (A)	San
Genus †*Dlusskyidris* Bolton		
†*D. zherichini* (Dlussky)	Taymyr (A)	San
Genus †*Haidomyrmex* Dlussky	Burmese (A)	Alb
†*H. cerberus* Dlussky	Burmese (A)	Alb
Subfamily Ponerinae? Lepeletier de Saint Fargeau		
Genus †*Afropone* Dlussky, Brothers, and Rasnitsyn		
†*A. oculata* Dlussky, Brothers, and Rasnitsyn	Botswana (C)	Tur
†*A. orapa* Dlussky, Brothers, and Rasnitsyn	Botswana (C)	Tur
Genus †*Canapone* Dlussky		
†*C. dentata* Dlussky	Canadian (A)	Cam
Subfamily †Brownimeciinae Bolton		
Genus †*Brownimecia* Grimaldi, Agosti, and Carpenter		
†*B. clavata* Grimaldi, Agosti, and Carpenter	New Jersey (A)	Tur
Myrmeciomorph Group?		
Subfamily Incertae Sedis (perhaps Myrmeciinae Emery)		
Genus †*Myanmyrma* Engel and Grimaldi, n.gen.		
†*M. gracilis* Engel and Grimaldi, n.sp.	Burmese (A)	Alb
Myrmicomorph Group		
Subfamily Myrmicinae Lepeletier de Saint Fargeau		
Genus †*Afromyrma* Dlussky, Brothers, and Rasnitsyn		
†*A. petrosa* Dlussky, Brothers, and Rasnitsyn	Botswana (C)	Tur
Formicomorph Group		
Subfamily Incertae Sedis		
Genus †*Gerontoformica* Nel and Perrault		
†*G. cretacica* Nel and Perrault	France (A)	Alb
Subfamily Formicinae Latreille		
Genus †*Kyromyrma* Grimaldi and Agosti		
†*K. neffi* Grimaldi and Agosti	New Jersey (A)	Tur
Subfamily Dolichoderinae Forel		
Genus †*Eotapinoma* Dlussky		
†*E. macalpini* Dlussky	Canadian (A)	Cam

APPENDIX
(Continued)

Taxon	Deposit	Age
Formicomorph Group (continued)		
Subfamily Aneuretinae? Emery		
Genus †*Burmomyrma* Dlussky		
†*B. rossi* Dlussky	Burmese (A)	Alb
Genus †*Cananeuretus* Engel and Grimaldi, n.gen.		
†*C. occidentalis* Engel and Grimaldi, n.sp.	Canadian (A)	Cam
Family †ARMANIIDAE Dlussky		
Subfamily †Armaniinae Dlussky		
Genus †*Archaeopone* Dlussky		
†*A. kyzlzharica* Dlussky	Kazakhstan (C)	Alb
†*A. taylori* Dlussky	Magadan (C)	Cen
Genus †*Armania* Dlussky (= †*Armaniella* Dlussky)		
†*A. robusta* Dlussky	Magadan (C)	Cen
†*A. capitata* Dlussky	Ulya (C)	Alb
†*A. pristina* Dlussky	Ulya (C)	Alb
†*A. curiosa* (Dlussky)	Magadan (C)	Cen
Genus †*Dolichomyrma* Dlussky		
†*D. longiceps* Dlussky	Kazakhstan (C)	Alb
Genus †*Khetania* Dlussky		
†*K. mandibulata* Dlussky	Ulya (C)	Alb
Genus †*Orapia* Dlussky, Brothers, and Rasnitsyn		
†*O. minor* Dlussky, Brothers, and Rasnitsyn	Botswana (C)	Tur
†*O. rayneri* Dlussky, Brothers, and Rasnitsyn	Botswana (C)	Tur
Genus †*Poneropterus* Dlussky		
†*P. sphecoides* Dlussky	Magadan (C)	Cen
Genus †*Pseudarmania* Dlussky		
†*P. rasnitsyni* Dlussky	Magadan (C)	Cen
†*P. aberrans* Dlussky	Magadan (C)	Cen
ACULEATA Family Incertae Sedis (*nec* Formicidae)		
Genus †*Cariridris* Brandão and Martins-Neto[a]		
†*C. bipetiolata* Brandão and Martins-Neto	Santana (C)	Apt
Genus †*Cretopone* Dlussky[b]		
†*C. magna* Dlussky	Kazakhstan (C)	Alb
Genus †*Petropone* Dlussky[b]		
†*P. petiolata* Dlussky	Kazakhstan (C)	Alb

[a]Verhaagh (1996) indicated a placement in Sphecidae (Apoidea) for †*Cariridis*, while Rasnitsyn (*in* Rasnitsyn and Quicke, 2002) suggested Ampulicidae (Apoidea).

[b]Grimaldi et al. (1997) indicated †*Cretopone* and †*Petropone* to be best considered as Aculeata incertae sedis. More recently Bolton (2003) has suggested that they may be genera of poneromorph ants but not assignable as to subfamily.

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