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New and Rediscovered Primitive Ants (Hymenoptera: Formicidae) in Cretaceous Amber from New Jersey, and Their Phylogenetic Relationships*

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ABSTRACT

All Cretaceous records of ants are reviewed, and evidence originally given for their placement is evaluated. Cretaceous Formicoidea preserved in rocks lack preservation of critical ant synapomorphies like the metapleural gland, which are preserved in specimens in amber. For this reason, the Armaniidae Dlussky, from the Cretaceous of Russia, are placed here as Formicoidea incertae sedis, not in the Formicidae proper. The oldest amber with ants is from New Jersey.

Seven complete and partial specimens of Formicidae, recently discovered in Turonian (92 Ma) amber from central New Jersey, are described and discussed. The specimens consist of four males and three workers. One complete and well-preserved worker is *Sphecomyrma freyi* Wilson and Brown 1967, known previously from two workers in a piece of Turonian amber from Cliffwood Beach, New Jersey. Well preserved in the new worker are external and even some internal features of the metapleural gland—a definitive formicid synapomorphy—which are described in detail for the first time. This specimen is designated as a neotype to replace the disintegrated holotype of this species. One complete male specimen is tentatively assigned to *Sphecomyrma*, which would be the first known male of the genus. One complete and one partial male, both from the same piece of amber, are a new, plesiomorphic species of *Baikuris* Dlussky (*Baikuris casei*, n. sp.), the genus previously known only from upper Cretaceous (Santonian) amber of Taymyr, northern Siberia. Two workers represent a new genus and species of Cretaceous Formicidae, ***Brownimecia clavata*** n. gen., n. sp., based on distinctively clubbed antennae, proportions of the antennal articles, and thin mandibles that lack teeth and extensively cross, and a ponerine-like constriction

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between abdominal segments III and IV (gaster segments I and II). *Brownimecia* is more closely related to extant Formicidae than are Sphecomyrminae, the genus being the earliest known member of the extant subfamily Ponerinae. The fourth male belongs to a third genus, undescribed. These are the oldest definitive ants.

Composition, monophyly, and systematic position of the subfamily Sphecomyrminae are discussed. Modifications were made to the data of Baroni Urbani et al. (1992) and reanalyses were made of the basal relationships of the Formicidae including *Sphecomyrma* and *Brownimecia*. Discrepencies with the cladograms of Baroni Urbani et al. (1992) are discussed. Including the fossil taxon Formiciinae Lutz (compressed remains from the Eocene of Germany) in the cladistic analysis, as done by Baroni Urbani et al., imparts too many missing values for meaningful analysis. *Sphecomyrma*, not discussed by Baroni Urbani et al., retains its basal position in the Formicidae in the present analysis. Discovery of new and exclusively primitive ants in upper Cretaceous ambers indicates an origin of the ants probably in the lowermost Cretaceous, but no older, contrary to a recent molecular hypothesis.

INTRODUCTION

The ants can arguably be said to be the ecologically and numerically dominant family of insects—perhaps of all organisms—on earth. As Hölldobler and Wilson (1990) discussed, ants are so abundant that approximately 3 million exist in a hectare of Amazonian forest soil, and they represent some 10–15% of the entire animal biomass in terrestrial ecosystems. On this basis alone, the origins of the ants would be important for understanding the evolution of modern terrestrial biological communities.

The outstanding hallmark of the ants is that all species are eusocial, which is what probably caused their tremendous success. The wingless workers can easily penetrate minute niches. Their array of glands and secretions enables sophisticated chemical communication, such that they can rapidly recruit workers for sequestering food; defend the colony, especially with soldiers and stinging workers; and even subdue large prey. Eusociality has actually evolved 12 times in the Hymenoptera: once in the ants, and all other times in the Vespoidea (social/paper wasps) and the Apoidea s.s. (bees). It was the ants that became predominant, though, because they are thought to have been the earliest, perhaps the first, eusocial insect predators on the ground (Hölldobler and Wilson, 1990). Clearly, knowing the earliest history of the ants can allow much better understanding of the unparalleled success of this remarkable group. It is a history that began in the late Mesozoic.

SPHECOMYRMA AND NEW JERSEY AMBER

The first Mesozoic ant to be discovered and described was *Sphecomyrma freyi* Wilson and Brown, in Cretaceous amber from New Jersey. The piece of amber that contained two workers was discovered in 1966 by an amateur collector, Edmund Frey, who found it in strata of the Raritan-Magothy Formations exposed in bluffs at Cliffwood Beach, New Jersey. It was studied and reported by Wilson et al. (1967a, 1967b). Despite such a sensational find, little attention was paid to New Jersey amber other than by another fossil collector, Gerard R. Case. Case collected Cretaceous amber from at least a dozen localities between 1962 and 1986, all of it found in rather trace quantities on the surface of lignitic exposures. Many of his samples were given to Princeton University (Dept. of Geology) where they were examined for inclusions. (The other samples were given to the AMNH [American Museum of Natural History] in 1992.) The only piece with inclusions was found in 1966—the same year as the *Sphecomyrma* discovery—in the Such Clay Pits in Parlin, New Jersey. It contained a ceratopogonid and two chironomid midges. Case's collections revealed that amber in New Jersey was actually widespread in appropriate Cretaceous exposures, and that other insects existed in the amber besides *Sphecomyrma*. These collections remained largely unnoticed for more than 20 years, and even the ceratopogonid wasn't described until 1986, as *Culicoides casei*.

In 1976 Gerard Case brought Robert Langenheim (University of Illinois, Champagne-Urbana) to several of the amber localities in Sayreville and adjacent towns in New Jersey, where they collected samples. Langenheim had worked on the stratigraphy of late Oligocene amber from Mexico and Cretaceous amber from Alaska. No results were reported from those samples from New Jersey. From 1986–1989 the senior author resumed the collection of amber from various Cretaceous exposures in New Jersey, some of them visited 20 years earlier by Case. The samples collected by Grimaldi were used in a stratigraphic and chemical study of the amber (Grimaldi et al., 1989), and only one piece was found to contain an insect inclusion (a partial midge). By 1986, some sites had been developed and were no longer accessible. The bluffs at Cliffwood Beach—type locality for *Sphecomyrma freyi*—for example, were covered in 1974–75 with boulders and a skin of cyclone steel fencing onto which concrete was poured. All collecting done in New Jersey up until 1989 uncovered small amounts of amber, and the likelihood of discovering pieces with insects seemed so remote that prospecting was then abandoned.

In 1992 Gerard Case brought to Grimaldi's attention two remarkable new deposits from central New Jersey rich in fossiliferous Cretaceous amber. They lay between some of the sites prospected earlier that were only a few miles apart. Exact locations and maps are available through the senior author, but they correspond most closely to site number five on the map in Grimald et al. (1989), approximately 7 km NW of Cliffwood Beach. Since November 1992, excavations by dedicated AMNH volunteers (see below) have amassed several hundred pounds of amber and hundreds of inclusions. Among these inclusions were the additional specimens treated here. The new material allows us to more carefully consider the phylogenetic position of the sphecomyrmines. Although amber has been known from New Jersey and other places in the Atlantic Coastal Plain for at least 150 years (reviewed in Grimaldi et al., 1989), it was the 1966 discovery of *Sphecomyrma* that brought serious attention to the substance.

MATERIALS AND METHODS

Specimens were excavated with hundreds of other inclusions in approximately 80 kg of raw amber. The amber occurred in veins of compacted, lignitic peat, just above the very deep deposits of the South Amboy Fire Clay (Turonian). The peats are the stranded remains of deltaic deposits, probably formed by coastal cedar swamps. Inclusions of leafy shoots and fibrous bark indicate that the botanical origin of the amber is not Araucariaceae, as originally proposed based on chemistry (Langenheim, 1969; Grimaldi et al., 1989), but in the Cupressaceae. A detailed account of the stratigraphy, taphonomy, and paleoecology of the amber sites is provided elsewhere (Grimaldi, 1997).

Approximately 70% of the amber is virtually opaque, due to a thick suspension of particulate debris and bubbles. The transparent pieces are mostly very brittle and fracture easily. To trim and polish a window in this amber with an orientation crucial for observation, a technique of vacuum-embedding needed to be developed. The technique is described in more detail elsewhere (Silverstein and Nascimbene, 1997), but involves embedding the amber in a synthetic casting resin of low viscosity and refractive index (see also appendix). While the resin is still fluid, the preparation is subjected to a reduced pressure of approximately 4 psi in a bell jar attached to a vacuum pump. This removes air from the fine cracks and allows resin to seep in. Filling cracks not only cements the fragile piece, but allows one to see through cracks where the air would otherwise cause a crack to be like a small mirror.

Work on the manuscript was as follows: Grimaldi did the final trims and polishing of specimens for observation, did sketches and final drawings, photographs, and wrote the manuscript, including descriptions. Agosti also examined morphology, checked the sketches and descriptions, and worked with Carpenter on the cladistics.

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THE SPHECOMYRMINAE AND MESOZOIC "FORMICOIDEA"

A synopsis of all taxa described as ants and close relatives from the Mesozoic, in the order in which they were reported, is given below. Dlussky (1975, 1983, 1987) described 16 species and 11 genera from the Cretaceous of Russia and Kazakhstan, based on 30 compression fossils and inclusions in amber. The family Armaniidae was described for several new "formicoid" forms: *Archaeopone, Armania, Armaniella, Poneropterus*, and *Pseudarmania*. Dlussky (1975) originally kept the Sphecomyrminae as a subfamily of the Formicidae, but later (Dlussky, 1983) elevated Sphecomyrminae to family, maintaining that the primitive condition of two teeth on the mandible and an antenna with a short scape and long, flexible funiculus excluded them from the Formicidae. Wilson (1987), using a morphometric analysis, showed that Dlussky's genera are possibly allometric variations of the gynes and workers for only two taxa. He placed Dlussky's genera into two genera: *Sphecomyrma* and *Cretomyrma*. In lieu of reexamining original material, as E. O. Wilson did for some taxa, we will not address the identity of Armaniidae here, but our results do bear on the identities and relationships of the genera that Dlussky placed in the Sphecomyrminae/-idae: *Baikuris, Cretomyrma, Paleomyrmex* (later renamed *Dlusskyidris*), and *Sphecomyrma*. Bolton (1994) placed the Armaniidae as a subfamily of the Formicidae (along with the Sphecomyrminae), which was a classification adopted yet again by Dlussky (1996). As we discuss below, until more completely preserved material becomes available, it is most prudent to regard the Armaniidae as Formicoidea incertae sedis.

THE MESOZOIC FORMICOIDS

Sphecomyrma freyi Wilson and Brown, 1967. Described on the basis of two well-preserved workers in a piece of amber from Cliffwood Beach, New Jersey. It was originally thought (Wilson et al., 1967a, 1967b) that this amber was Cenomanian (ca. 100 Ma), then late Santonian, ca. 80 Ma (Wilson, 1985; Hölldobler and Wilson, 1990) (this was a date quoted by Dlussky, 1975). Dlussky (1983: p. 63 of Paleontol. J. translation) later mentioned that "in the past few years they [the New Jersey amber deposits] have been redated as Santonian or even early Campanian," which is erroneous. Like the material we are reporting, the type material of *S. freyi* is probably Turonian (90–94 Ma). In the original paper describing the species (Wilson et al., 1967b), they mentioned the piece of amber as being in the private collection of Edmund Frey, of Mountainside, New Jersey. It was donated to the Museum of Comparative Zoology, Harvard, soon after publication of the paper, residing in the fossil insect collection. The specimen disintegrated during the vacuum-embedding process, for which a neotype is designated, below.

Cretomyrma arnoldii Dlussky, 1975: 116. Known from a partial worker in a piece of amber from Yantardakh, Taymyr Peninsula, northern Siberia (Paleontological Institute Nauka [PIN] number 3130/113). It is largely headless (only imprints of some mouthparts and the second segment of the antenna remain), but details of petiole, gaster, and legs are well described. This deposit is dated as Santonian. *Cretomyrma* was placed by Dlussky (1975; 1987) in the Sphecomyrminae/-idae.

Cretomyrma unicornis Dlussky, 1975: 116. A worker specimen even more partial than *C. arnoldii*, with just a portion of the propodeum, petiole, gaster, and the entire left middle leg preserved. From the same deposit as *C. arnoldii*, PIN 3311/363.

Dlusskyidris zherichini (Dlussky), 1975: 118. *Dlusskyidris* Bolton, 1994, is a replacement name for *Paleomyrmex* Dlussky (preoccupied by *Paleomyrmex* Heer, 1865). Known from a virtually complete male (holotype, PIN 3311/364) and two incomplete males (PIN 3311/365 and 3311/366) in Siberian amber. Placed by Dlussky (1975; 1987) in the Sphecomyrminae/-idae.

Petropone petiolata Dlussky, 1975: 119. Compression fossil of an apparent wingless specimen, possibly a worker, from the Cretaceous (Turonian) of southern Kazakhastan [PIN 2783/158]. Dlussky actually placed this (and two other genera, immediately below) in the Ponerinae, but later (Dlussky, 1983: p. 64 Paleontol. J. translation) mentioned that the "systematic position of these genera [*Petropone* and *Cretopone*] must be changed .... [but] remains unclear, because their impressions are incompletely preserved." Carpenter (1992) mentioned this taxon to be only doubtfully assigned to the Formicidae.

Cretopone magna Dlussky, 1975: 119. Compression of a partial and badly distorted insect from the same deposit as *Petropone*. Dlussky (1983) removed it, and *Petropone*, from the Ponerinae to a genus incertae sedis in the Formicoidea. In our view, based on Dlussky's (1975) illustration, it is impossible to assign the specimen to any aculeate family.

Archaeopone kzylzharica Dlussky, 1975: 121. Based on a single, incomplete compression fossil from the Cretaceous of Kazakhastan (same deposit as previous two taxa) (PIN 2383/263). Originally placed in the Ponerinae (Dlussky, 1975), it was later placed in the Armaniidae (Dlussky, 1983). Carpenter (1992) gave this taxon a doubtful assignment to the Formicidae, with which we must concur. As illustrated (Dlussky, 1975, p. 120, fig. 132), the specimen is headless and virtually legless. The alitrunk and gaster are preserved; a petiole also shows but without an obvious node.

Dolichomyrma longiceps Dlussky, 1975: 121. Cretaceous of Kazakhastan (same deposit as previous taxa). Like *Archaeopone*, Dlussky originally placed this unique specimen (PIN 2383/145) and a similar one (described as *Dolichomyrma*? *latipes* Dlussky, 1975 [PIN 2383/144]) in the Ponerinae, then in the Armaniidae. Carpenter (1992) mentioned this taxon also to be of doubtful assignment as a formicid. The type and only known specimen of *D. longiceps* has proportions of the head, alitrunk, and gaster similar to that of a worker ant, and a possible petiole is rendered in his figure of it, but no other "diagnostic" features are obvious.

Armania robusta Dlussky, 1983. Based on a large, winged female compressed in rocks from the Al'skaya Formation (Cenomanian) of Ten'ki District, Magadan region, Russia. Holotype (PIN 3901/155) is in lateral view showing a distinct, large petiole; paratype (PIN 3901/160), also winged, is preserved dorsally with a petiole barely preserved.

Pseudarmania rasnitsyni Dlussky, 1983. Known only from a single winged, well-preserved female from the same deposit as *Armania* (PIN 3901/156). Head, alitrunk, and gaster, some legs, are well preserved, and only basal portions of the wings.

Pseudarmania aberrans Dlussky, 1983: as for *P. rasnitsyni*, except that the unique specimen (PIN 3901/152) is missing the head and anterior portion of the alitrunk.

Armaniella curiosa Dlussky, 1983. Described on basis of a single, incomplete female (PIN 3901/158) from the Al'skaya Formation of Ten'ki, Magadan. Portions of the head, antenna, wing, legs, gaster, and the petiole are preserved.

Archaeopone taylori Dlussky, 1983. Based on two specimens from the Al'skaya Formation of Magadan. The holotype (PIN 3901/154) is an apparent male with the head, antenna, alitrunk, anterior half of gaster, and portions of wing preserved.

Poneropterus sphecoides Dlussky, 1983. Complete apparent male specimen (PIN 3901/157) from the Al'skaya Formation of Magadan. Virtually entire body preserved, in dorsal aspect.

Sphecomyrma canadensis Wilson, 1985. Known from a well-preserved worker (holotype) and poorly preserved one in amber from near Medicine Hat, Alberta, Canada, numbers 330 (holotype) and 205 (paratype) in Biosystematics Research Institute, Agriculture Canada, Ottawa. These specimens were from collections made by McAlpine and Martin (1966), who also collected Cretaceous amber from Cedar Lake, Manitoba. It is generally believed that the amber from Medicine Hat and the redeposited amber from Cedar Lake is the same age as amber from Grassy Lake, Alberta, dated in situ (according to Pike, 1995) as from the upper part of the Judith River Group of the Foremost Formation, ca. 78–79 Ma.

Pike (1995) reported three additional ants, identified as "*Sphecomyrma* sp.," in the amber from Grassy Lake. These are in the Royal Tyrrell Museum, Drumheller, Alberta. The specimens were examined by E. O. Wilson, two of them being *Sphecomyrma* [*canadensis*?], the other being a poorly preserved worker with mandibles and antenna more highly derived than in *Sphecomyrma* (Pike, personal commun. to DG, Jan. 1997).

Cretacoformica explicata Jell and Duncan, 1986. Based on (an) alate specimen(s) from the Lower Cretaceous of Koonwarra, Victoria, Australia, in the Aptian (ca. 115 Ma) Koonwarra Fossil Bed Formation. The specimen is not well preserved. For example, the petiole, if present, is obscured. Naumann (1993) reexamined the unique specimen (no. NMVP 102501A,B in Museum of Victoria, Melbourne), and presented a detailed, corrected description. He could not place it to a family of Apocrita, but discussed features that were both consistent and inconsistent with the Diapriidae, as proposed by Darling and Sharkey (1990). The genus was cited as *Cretaceoformica* [sic] in Poinar (1992).

Baikuris mandibularis Dlussky, 1987. Known from three males in a piece of amber from Lake Taymyr, Baykura-Neru Bay, Taymyr Peninsula of Siberia, Russia (amber piece is PIN 3730/5 in the Paleontological Institute, Moscow). This amber is dated as Santonian.

Baikuris mirabilis Dlussky, 1987. Known from an incomplete male in a piece of amber from the same locality as *B. mandibularis* (PIN 3730/8).

Cariridris bipetiolata Brandão and Martins-Neto, 1989: Based on an apterous specimen in Lower Cretaceous (Santana Formation, Aptian, ca. 110 Ma) limestone from Ceará, Brazil, and interpreted as a worker. This specimen has a definite, narrow and elongate petiole, and a scape that appears slightly longer than in *Sphecomyrma* or *Cretomyrma* workers; but the bases of the antennae, on the other hand, are obscured. Examination by DG of an excellent color slide of the specimen indicates that the proposed existence of a postpetiole in the specimen (a constriction just anterior to true abdominal segment IV) may be a preservational artifact. Prior and continuing studies of Santana Formation insects (e.g., Grimaldi, 1990) document excellent and detailed preservation of external cuticles, the study of which requires proper physical cleaning and removal of matrix with acetic acid digestion. There are substantial areas of the specimen still uncleaned, with limestone matrix still covering the pronotum, bases of the legs, all of the mid left leg, and margins of the alitrunk and petiole. What is interpreted as petiole and gastric constriction could be an appearance due to the overburden of matrix in these areas. As we discuss later, placement of *Cariridris* as possibly in the Myrmiciinae (Brandão et al., 1990) is consistent with the basal phylogenetic position of this subfamily. However, since mandibular dentition, calcars, and presence of a metapleural gland cannot be observed, placement of *Cariridris* in the family Formicidae cannot be confirmed with present material.

Lastly, Poinar (1992: 203) published an unclear photograph of an aculeate in Lebanese amber (Neocomian) from the Acra Collection, as "The earliest known ant?" That specimen is preserved very well and was examined in 1990 by the senior author. Although an aculeate, it is definitely not Formicoidea.

Using a criterion of just the presence of a petiole—a feature easily fossilized even as a compression—there is certainty in the identity of the following genera being formicoids: *Armania, Amaniella, Archaeopone taylori, Cariridris, Dolichomyrma, Poneropterus*, and *Pseudarmania.* Wilson (1987) reexamined Dlussky's holotypes of *Armania robusta* and *Pseudarmania rasnitsyni*, and found that a trochantellus was actually absent, as is the case in all living Formicidae. Dlussky used its apparent primitive presence to exclude the Armaniidae from the formicids. It is an intriguing character, since it occurs as a ground plan of the Vespidae, the sister group (with Scoliidae) to the Formicidae (Brothers, 1975; Brothers and Carpenter, 1993; Rasnitsyn, 1988). The character, however, seems as if it would be exceedingly difficult to resolve in a compression fossil, since it is a segment largely fused to the base of the femur, demarcated merely by a fine suture. A trochantellus definitely occurs in at least the New Jersey amber specimens, making it plausible that the Armaniidae also possessed it. In Dlussky's diagnosis of the Armaniidae he mentioned the broad attachment of the petiole to the gaster (a plesiomorphic feature), which Wilson also critiqued. If the large gasters of the winged females described by Dlussky indicate that they are indeed queens, as argued by Wilson, the most parsimonious argument is that the broadly attached petiole is a sexually dimorphic feature, as in living Formicidae. Lack of preserved details like dentition of the mandible and presence of a metapleural gland precludes a more detailed placement of these taxa, at least with the present material.

Incomplete and/or poor preservation of *Archaeopone kzylzharica, Cretacoformica, Cretopone*, and *Petropone* (as described by Dlussky) makes their identities even as formicoids questionable in our view. This leaves the four genera described in Cretaceous amber from Siberia, Canada, and New Jersey: *Sphecomyrma, Cretomyrma, Baikuris*, and *Dlusskyidris.* The latter two genera are known only from males, and metapleural glands cannot be observed. The first two genera are known from workers where the metapleural gland can be observed, making these the oldest true ants, family Formicidae (see below, for discussion of taxonomy). The oldest definitive Formicidae is still *Sphecomyrma*, along with the new taxa in New Jersey amber described below. We mostly agree with the classification of Wilson (1987), in that Sphecomyrminae are the most primitive and oldest known subfamily of the Formicidae (see cladistic results, below). However, we are unprepared for the formal synonymies of Dlussky's genera made by Wilson, without the basis of definitive synapomorphies.

The following is a proposed summary classification of Cretaceous aculeate fossils that have been described as convincing ants or close ant relatives:

APOCRITA, incertae sedis
        Cretacoformica
ACULEATA, incertae sedis
        Cretopone
        Petropone
    Superfamily FORMICOIDEA
        Family ARMANIIDAE (monophyly uncertain)
            Armania
            Armaniella
            Archaeopone
            Dolichomyrma
            Poneropterus
            Pseudarmania
        Family uncertain
            Cariridris
        Family FORMICIDAE (true ants)
            Subfamily Sphecomyrminae
            ?*Baikuris* (♂♂ only)
            Cretomyrma
            Dlusskyidris
            Sphecomyrma
            ?*Haidomyrmex* (Burmese amber: Tertiary?)
            Subfamily Ponerinae
            Brownimecia

FAMILY FORMICIDAE

SUBFAMILY SPHECOMYRMINAE

INCLUDED GENERA: *Baikuris, Cretomyrma, Dlusskyidris*, and *Sphecomyrma.*

All features diagnostic for the subfamily as given by Wilson et al. (1967b) and Dlussky (1975, 1983, 1987) are symplesiomorphic at the level of the family: worker with short mandibles with only two teeth; antennae with short scape and long, flexible funiculus; low, rounded petiole; presence of metapleural gland; an unconstricted gaster;

extrusible sting; mid and hind tibiae with double spurs.

The only synapomorphies we could find for the group are: presence of a short pedicel, which has a length slightly longer than its width; a second funicular segment (first flagellar segment) twice or more the length of other segments (an exception would be *Sphecomyrma canadensis*, see below); and males without a distal, evanescent segment of wing vein CuA (CuA^1). All three features are unique within the Formicidae. However, the short pedicel also appears in some Vespidae, so it is possibly plesiomorphic.

Dlussky removed sphecomyrmines from the Formicidae, as mentioned above, based on the structure of the antenna and the mandibles. Specifically, the antenna has a first segment too short for the antenna to be sufficiently elbowed—a condition necessary, Dlussky maintained, for eusociality, since it allows brood and food manipulation. If not social, Dlussky concluded, then *Sphecomyrma* and relatives cannot be ants. Although he did not cite studies that address how ants manipulate objects with their antennae, Dlussky presumably meant that the apices of the antennae must not be too distant from the mandibles, for optimal manipulation of food and tactile communication (“antennation”). Indeed, antennation is a behavior commonly used for such social activities as trophallaxis, although (as Wilson [1987] pointed out), trophallaxis may not occur among workers of many primitive ants such as *Nothomyrmecia*, Amblyoponini, Apomyrminae and even some advanced species like *Pogonomyrmex badius* (reviewed in Hölldobler and Wilson, 1990). Workers of some ants merely transport larvae to cached prey and do not engage in trophallaxis.

Evidence in favor of Dlussky's argument, however, is the fact that the proportions of the scape and funiculus appear to be grossly maintained throughout the ants. For example, there is a convergent development in ants with extremely long, gaff-shaped mandibles and a corresponding lengthening of the scape (e.g., *Acanthognathus, Harpegnathos, Myrmecia*, and *Myrmomoteras*). This suggests a functional constraint in proportions of the antennae and mandibles. Dlussky attempted to quantify the relationship between antennal proportions and social existence in aculeates. Using 37 genera in various families, he devised several indices of the antennae, which for purposes here are best represented by his IK1 index (length of scape/total length of antenna). This index and the other two were divided into three categories: one represented by the parasitoid aculeates (IK1 = 10–25%), the second by the solitary provisioning wasps and bees (IK1 = 17–35%), and the third by the social bees, ants, and a few solitary bees (IK1 = 30–40%). In lieu of seeing the complete data, it is reasonable to assume these are arbitrary groupings. Statistics on ANOVA or confidence limits were not given, and the great overlap in the ranges would suggest that the groupings are not significant.

We do not want to belabor the antennal index argument, because the manipulation of the antennae in any sphecomyrmine will never be observed, only inferred. For Dlussky (1983) to claim that “[sphecomyrmines] could not have transported their brood or entered into trophallaxis with their larvae,” is thus speculation at this point. As Wilson (1987) pointed out, the eusocial wasps have antennal proportions similar to those of the sphecomyrmines, and this obviously hasn't prevented them from feeding their larvae. In fact, an extremely short antennal scape is present in various leptanilloidine ants, which are eusocial like other ants. Morphology of sphecomyrmines is not at all inconsistent with a social existence, but perhaps the only way to confirm sociality would be the discovery of part of a fossilized colony. Portions of fossilized colonies occur, rarely, in younger, Tertiary ambers, such as with some dolichoderines like *Azteca*, and another (undescribed) genus in Miocene amber from the Dominican Republic (Waggensberg et al., 1996). Wilson's (1987) morphometric evidence on the relative size of the gaster is strongly supportive of castes in the Cretaceous formicoids.

Dlussky probably underestimated the significance of the metapleural gland, a feature agreed even by Dlussky to be in sphecomyrmines. The metapleural gland, which produces large quantities of microcidal and fungistatic phenylacetic acid, is unique to ants. It presumably acts as a disinfectant, and allows nesting in soil/leaf litter without infection of the brood and colony (Hölldobler and Wilson, 1990), which explains its loss in tree-nesting genera (*Oecophylla, Polyrachis, Dendromyrmex*, and most *Camponotus*) and some socially parasitic ants. Despite claims by Dlussky (1987) that sphecomyrmines were solitary or semicommunal, the metapleural gland is almost certainly evidence of a social existence.

Brandão et al. (1990) stated that the position of sphecomyrmines as ancestral/primitive to all Formicidae " . . . was challenged by Dlussky [sic] 1987, with whom we concur." They then concluded that *Cariridris* is the oldest formicid on the basis of its differentiated scape and the presence of a petiole. Baroni-Urbani (1988) (and as cited in Poinar, 1992) also offered a conclusion similar to that of Dlussky, that *Sphecomyrma* could not be an ant because of the short basal antennal article, and "the apparent absence of a metapleural gland." This is one reason why Baroni-Urbani et al. (1992) did not include *Sphecomyrma* in their phylogenetic analysis of ant tribes (personal commun. CBU to DG and DA). Our new material definitively proves the existence of the gland. Also, Baroni Urbani and de Andrade (1994: p48) commented that "only one probably true ant is known from the lower Cretaceous [*Cariridris*] . . . other presumed Cretaceous Formicidae are currently regarded as non-formicid Aculeates." As discussed above, crude preservation of *Cariridris* in limestone prevents observation of critical details.

The other reason given by Baroni Urbani et al. (1992) for not including sphecomyrmines in their ant cladogram was that "many of the characters . . . cannot be assessed . . . " Oddly, they included the Formiciinae, an extinct subfamily described from compressed remains in Eocene oil shales of Messel, Germany (Lutz, 1988), the preservation of which is hardly as fine as that in amber. Indeed, only 20% of the characters in their matrix can be scored for the Formiciinae, but slightly over 40% can be scored for *Sphecomyrma* workers (67% if characters of the apparent male are included, but which were unavailable to Baroni Urbani et al. [1992]). This probably explains why the Formiciinae was the basalmost lineage in their analysis, which we discuss in the cladistic section of this paper.

Genus *Cretomyrma* Dlussky

DIAGNOSIS (extracted and translated from Dlussky, 1975, 1983): Known only from workers. Propodeum: low; with single, toothlike process; spiracles circular; differs from *Sphecomyrma* on the basis of a petiole that is lower and rounder, with anterior and posterior connections that are less constricted. Legs elongate, with calcars on mid and hind tibiae. Mandibles with "additional tooth on top."

One character mentioned by Dlussky, the size of the sting, is questionable, since the extent that it is extruded will affect estimates of its size.

TYPE SPECIES: *C. arnoldii* Dlussky.

Genus *Dlusskyidris* Bolton

Paleomyrmex Dlussky, 1975: 118 (preoccupied by *Paleomyrmex* Heer, 1865: 91).

Dlusskyidris Bolton, 1994: 187 (replacement name).

DIAGNOSIS (extracted and translated from Dlussky, 1975): Known only on basis of male. Mid and hind tibia with calcars. Wing venation complete and primitive, with closed cells 1r + 2r, 3r, 2rm and 1mcu [Dlussky's terminology]. Subgenital plate triangular, reaching valvulae. Last tergite of abdomen triangular, with well-developed cerci. Parameres narrow, pointed, and slightly curved medially.

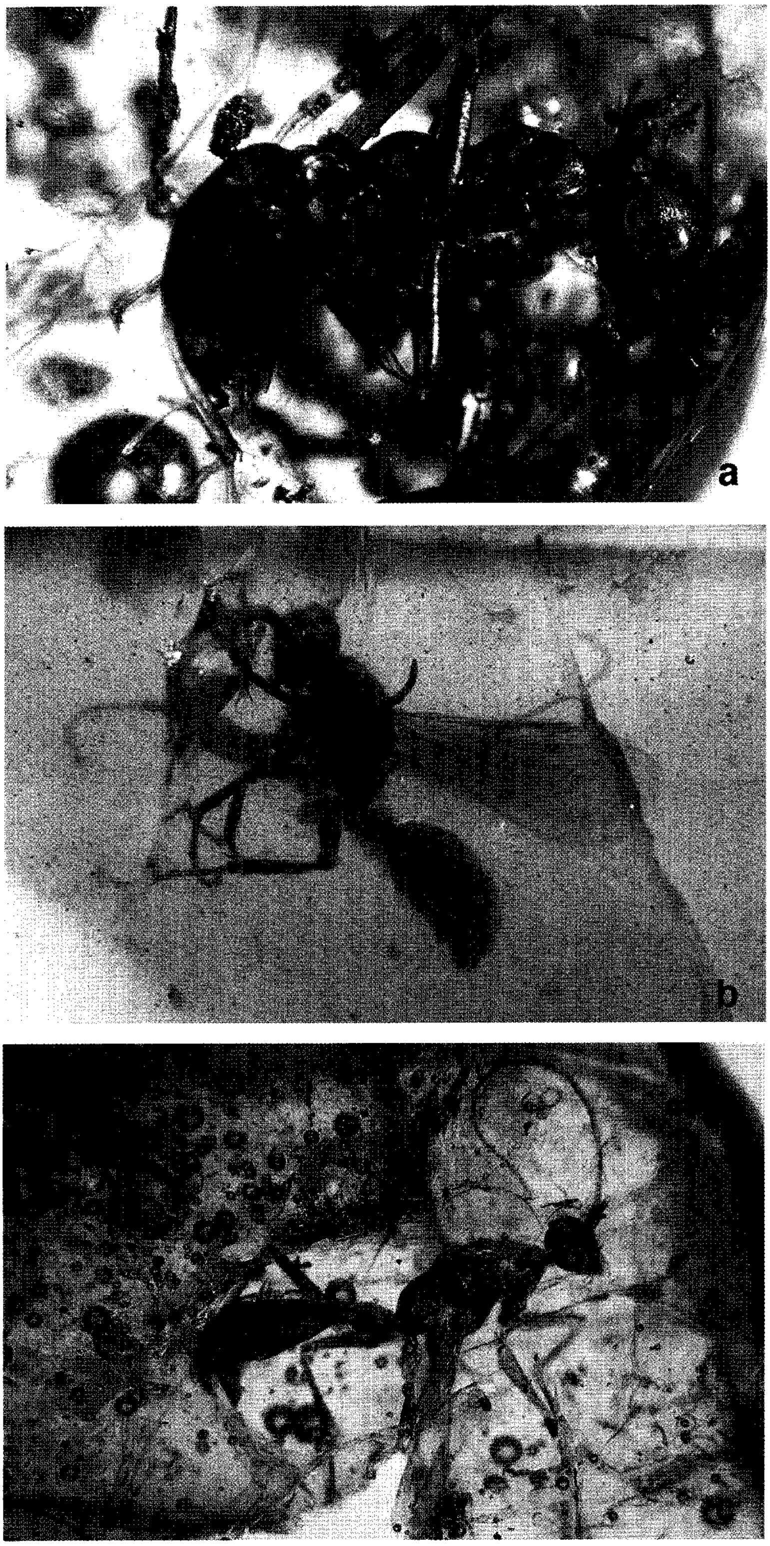
Dlussky mentioned that, on the basis of hardly being able to associate males and workers in ants, it is "quite possible that *Paleomyrmex* are males of *Sphecomyrma* or *Cretomyrma*."

TYPE SPECIES: *D. zherikhini* (Dlussky)

Genus *Sphecomyrma* Wilson and Brown

DIAGNOSIS: Scape short, 0.57–0.68 mm; funiculus long and filiform, approximately four times the length of scape; pro/mesothoracic suture complete and well formed; petiole with distinct, domed node widely separated from propodeum and gaster by deep constrictions; cuticle without sculpturing, just superficially microscopic relief, with scattered and sparse setae.

Significant features not mentioned in the original reports (Wilson et al., 1967a,b),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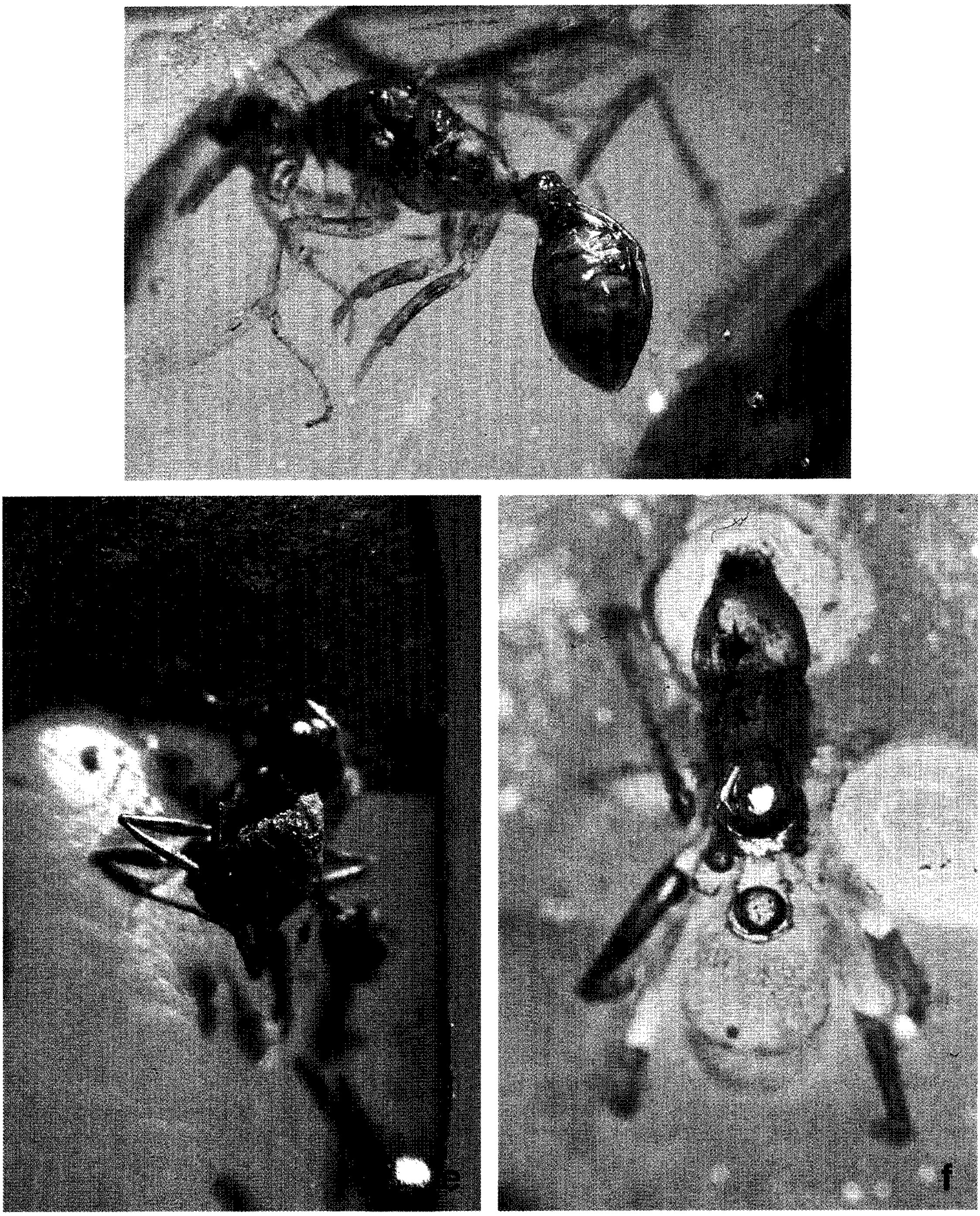


Fig. 1. Photomicrographs of Formicidae in Turonian amber from New Jersey. [Left page] **a.** *Sphecomyrma freyi*, AMNH NJ-112. **b.** Male, *Sphecomyrma*? AMNH NJ-242. **c.** Male, *Baikurus casei* (holotype), AMNH NJ-90bb. [Above] **d.** Male, undetermined genus, AMNH NJ-107. **e–f:** *Brownimecia clavata*. **e.** Holotype. **f.** Paratype, AMNH NJ-231.

which we report here based on AMNH NJ-112, are: helcium apparently lacking; trochantellus lacking; and a pair of long, extremely fine setae present in the middle of the clypeus.

Type Species: *S. freyi* Wilson and Brown.

Sphecomyrma freyi Wilson and Brown

Figures 1a, 2, 3

Specimen (Neotype): AMNH NJ-112, from the "Sunrise Landing" site, East Brunswick, New Jersey. Collected by Gerard Case, James Leggett, and Paul Borodin, 1994. The ant is a complete and beautifully preserved wingless female in a transparent, deep amber-colored piece that originally was half filled with debris. After embedding, the debris half was sliced off; now the piece is 18 × 14 × 5 mm, and contains some debris, bubbles, as well as one mite, six podurid Collembola, stellate trichomes, and portion of a spider. A piece of debris is lying in front of the head, obscuring a portion of the face. Deposited in the Museum of Comparative Zoology, Harvard University, in replacement for the original type specimen (see appendix).

Description: Measurements of AMNH NJ-112: total length 4.1 mm; head width 1.08; eye depth 0.28; scape length 0.57; funiculus length 2.02; alitrunk length 1.48; gaster length 1.51. These measurements and other features agree in virtually all respects with the detailed descriptions and illustrations in Wilson et al. (1967a,b), to which we can add some observations on the metapleural gland (MG). The MG was distinctly observed under 60–100× magnifications, although better results were obtained using a Leitz stereoscope at 144× and different angles of fiber optic illumination. Best results were obtained by examining the propodeum at 160× and 400× using a Zeiss compound microscope and *reflected* fiber optic illumination. This method of examination absolutely requires a flat amber surface parallel to and very close to the surface of the structure, as in the preparation of AMNH NJ-112. In the original report by Wilson et al. (1967b: p. 11), there was some equivocation as to the presence of the gland, which perhaps explained why it was not described in any detail: "... if we are mistaken about the presence of the metapleural gland, it would be possible to consider *Sphecomyrma* as a wasp rather than an ant."

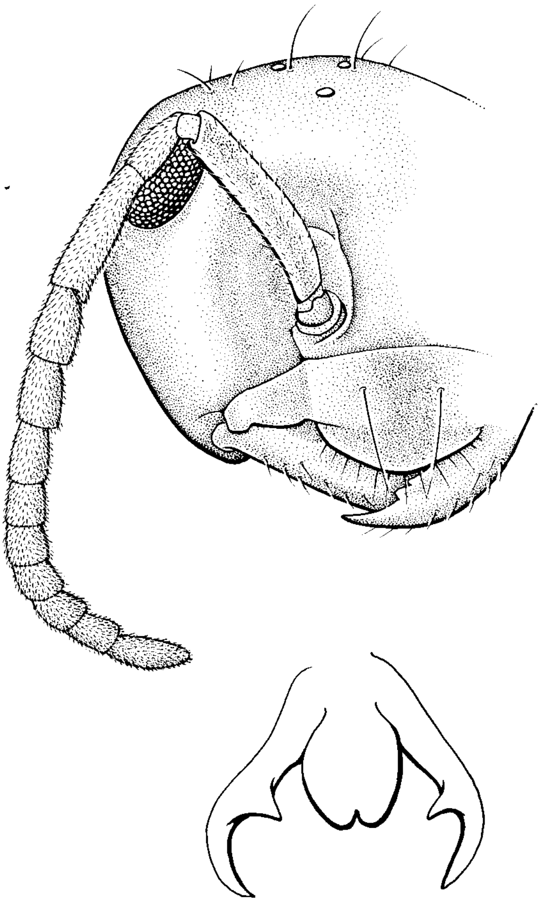


Fig. 2. Newly discovered worker and neotype of *Sphecomyrma freyi* (AMNH NJ-112, now in the MCZ). **Above.** Detail of head, frontal view (at a slight ventrolateral angle). Total length of funiculus and relative size of flagellomeres are distorted, since the antenna is curled back and somewhat underneath the head. The left side of the head is obscured by a large piece of debris. Note that short space between scape and pedicel is a membranous area, not an antennomere. **Below.** Detail of pretarsal claws.

The metapleural gland in AMNH NJ-112 distinctly shows a wide oval orifice, virtually round, with a shallow lip extended anteroventrad to it for a length of approximately 6 to 7 diameters of the orifice. Distance of the orifice from the posterior margin of the pro-

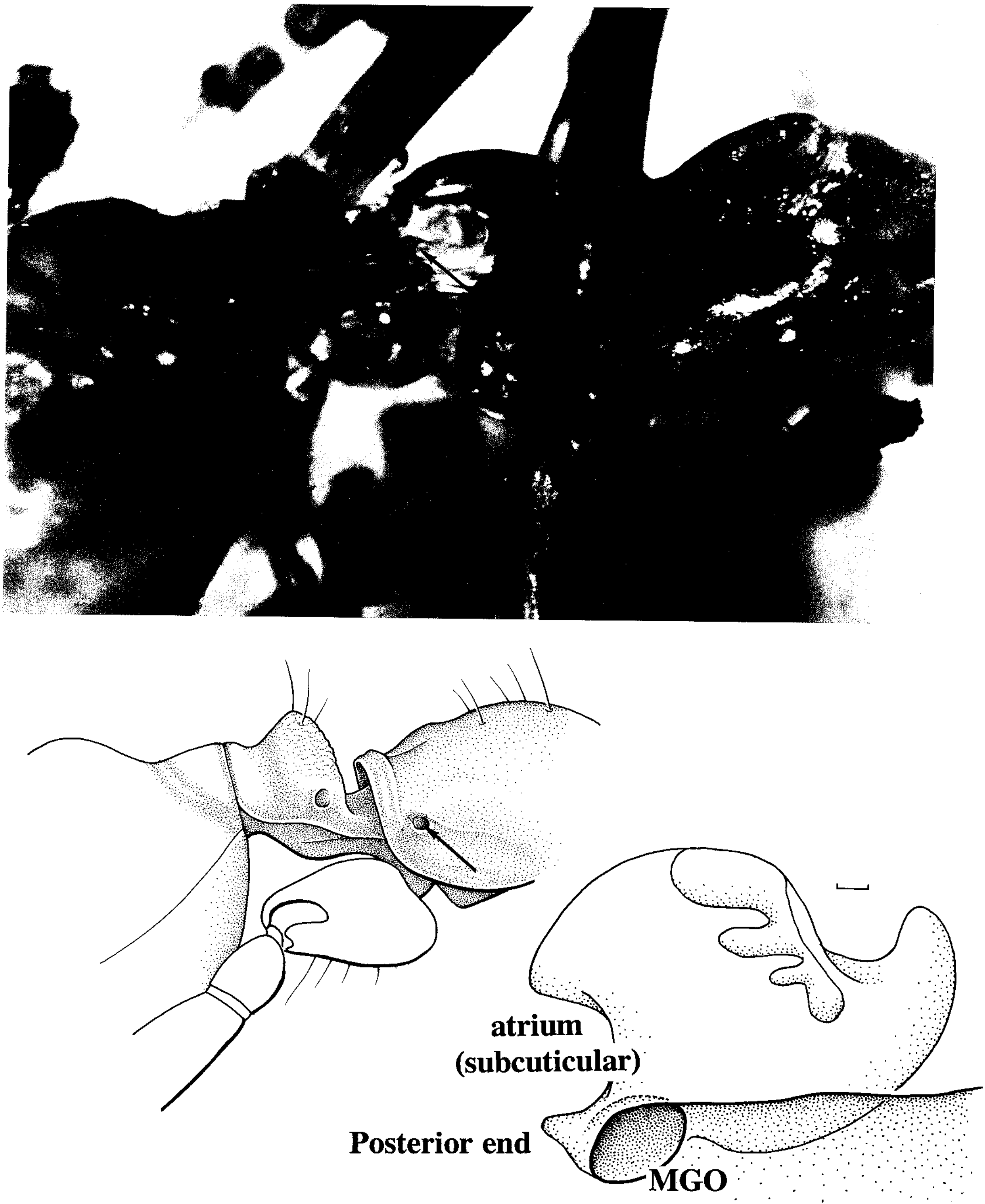


Fig. 3. *Sphecomyrma freyi* worker, AMNH NJ-112. Photomicrograph and illustrated rendering (to the same scale) of the alitrunk and anterior portion of the gaster, showing details of the metapleural gland opening [MGO] (arrows) and petiole. The cuticle of the bulla appears thinner than surrounding cuticle and, as shown in the photo, this area is actually collapsed into a slight depression. The bulla was rendered in the drawing as it might have appeared: slightly bulging.

Subcuticular detail beneath the MGO is also shown, which is probably the atrium of the gland, with remnants of the glandular tissue to one corner. Scale = 0.1 mm.

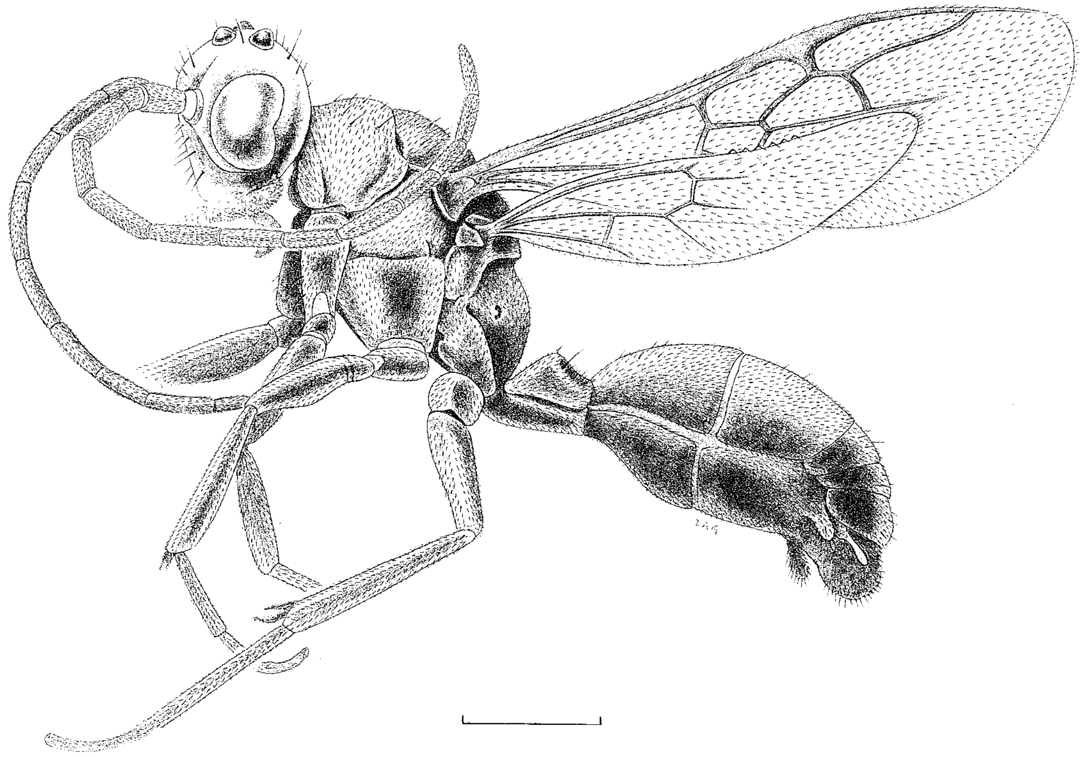


Fig. 4. Male, AMNH NJ-242, probably *Sphecomyrma*. Scale = 0.5 mm.

podeum is approximately twice the diameter of the orifice. The cuticle of the area anterior to the orifice is quite transparent and shows little sclerotization, suggesting it to be considerably thinner than surrounding cuticle of the alitrunk. What was probably a slightly raised area (the bulla) is now a shallow concavity, perhaps compressed because of the thinner cuticle in this area. Consequently, an irregularly shaped chamber is visible beneath the cuticle, probably the atrium for the secretions of the metapleural gland. In the anterodorsal corner of the lightly sclerotized subcuticular chamber is a whitish mass with four small lobes: perhaps the gland itself, shrunken from its normal size.

Sphecomyrma canadensis Wilson

The only other sphecomyrmine known from North America can be distinguished from *S. freyi* (according to Wilson [1985]) based on the workers with a more robust trunk and a shorter third antennal segment (which is about as long as the second antennal segment; in *freyi* the third segment is slightly more than twice the length of segment two).

Sphecomyrma? sp.
Figures 1b, 4, 12a

Specimen: Male, AMNH NJ-242, from White Oaks site, Sayreville, New Jersey, collected by Keith Luzzi, 1995. A superbly preserved, complete, and well-displayed specimen in a piece of amber that was originally cylindrical and 5 mm diameter, 10 mm long, with the ant occupying almost the entire diameter. The amber is slightly turbid with minute particles and bubbles, and contains a few fine cracks. The piece was vacuum-embedded and sliced lengthwise to remove the debris-filled half and improve visibility of the wings and venation.

Description: Total length 3.13 mm. HEAD: With three large ocelli on vertex, but not on tubercle(s); pair of fine, stiff hairs on frons, vertex, and postocciput, with finer hairs interspersed. Face with two pairs of longer, fine setae and several smaller ones. Eye reniform, with middle of hind margin emarginate, indented to a depth of about 4 facets. Eye large, its depth 0.6× depth of head; width of eye 0.72× depth of eye. Supra-antennal suture present, extended to level of anterior ocellus. No microtrichia on head. Antennal proportions: scape short, approximately same length as flagellomere I (funicular segment II); pedicel very short, ca. 0.3× length of flagellomere I. Flagellomere I 1.1–1.2× length of longest distal funicular segments. Antenna with 11 flagellomeres, densely covered with fine microtrichia, total length of antenna 2.6 mm. Mouthparts largely covered with bubbles, with two palpal segments protruding.

ALITRUNK: 1.25 mm long, length of petiole 0.35 mm. Petiole covered with microtrichia, having pair of longer setae on apex of nodus, and shorter setae posteriad. Depth of petiole under node 1.5× depth of where it is attached to trunk or gaster. Trunk largely covered with fine microtrichia, nota with scattered, larger setae. Legs distal to and including femora with microtrichia in even, longitudinal rows. Mid and hind tibia each with a pair of setose, apical spurs; one on the hind tibia is pectinate. Propodeal spiracle slitlike, with small lobe covering part of orifice. WINGS: Forewing length 2.25 mm. Hindwing 0.7× length of forewing, shapes typically formicid, with hindwing having more acute apex and angulate posteroapical margin. Distinctive features of forewing are: costal vein thickened beyond pterostigma, tapering to nearly wing apex; vein R + Sc with small spur just before it meets with pterostigma; discoidal cell narrow, with distinctive veins connecting it with R + Sc and M + CuA. Hindwing with 7 fine, long distal hamuli, no anterior hamuli; basal part of vein M straight, distal spur virtually lost; vein Cu fairly long, nearly reaching wing margin.

GASTER: Length 1.22 mm; segments 1 and 2 equal in length, comprising approximately ⅔ of gaster. Terminalia largely obscured by layer of froth, with two pairs of setose lobes protruding (cerci?). Anterior pair (parameres) twice as broad as posterior ones.

DISCUSSION: Genera of ants are not routinely surveyed for males, the systematics of which is based mostly on workers. Without males taken directly from a colony, assignment of them to a particular species or even genus is rarely done. Nonetheless, some features allow us to tentatively associate this male with *Sphecomyrma* workers: similar size; similarity in structure of the petiole, which has a pair of fine, long setae on the apex of the node (albeit widespread in many ants); lack of a trochantellus; and the proportions of the basal segments of the antenna. This male is certainly not *Baikurus* or the same genus as AMNH NJ-231.

GENUS *Baikuris* Dlussky

DIAGNOSIS: According to Dlussky (1987): Only males known, having eyes kidney-shaped; mandibles narrow, margins virtually parallel and without teeth; base of outer surface with oval area and ridge (opening of mandibular gland?); "lower jaw" palps long, 6-segmented; labral palps evidently 3-segmented; scutum with deep parapsidal grooves; forewing with cell 1r + 2r (Dlussky terminology) partly divided by rudimentary crossvein; mid and hind legs with small trochantellus; tibial spurs 2, 2, 2; claws with preapical tooth; petiole distinct, with small node; indistinct constriction between first and second segment of abdomen [sic?][gaster]; genitalia small, retracted into abdominal segments; cerci well developed.

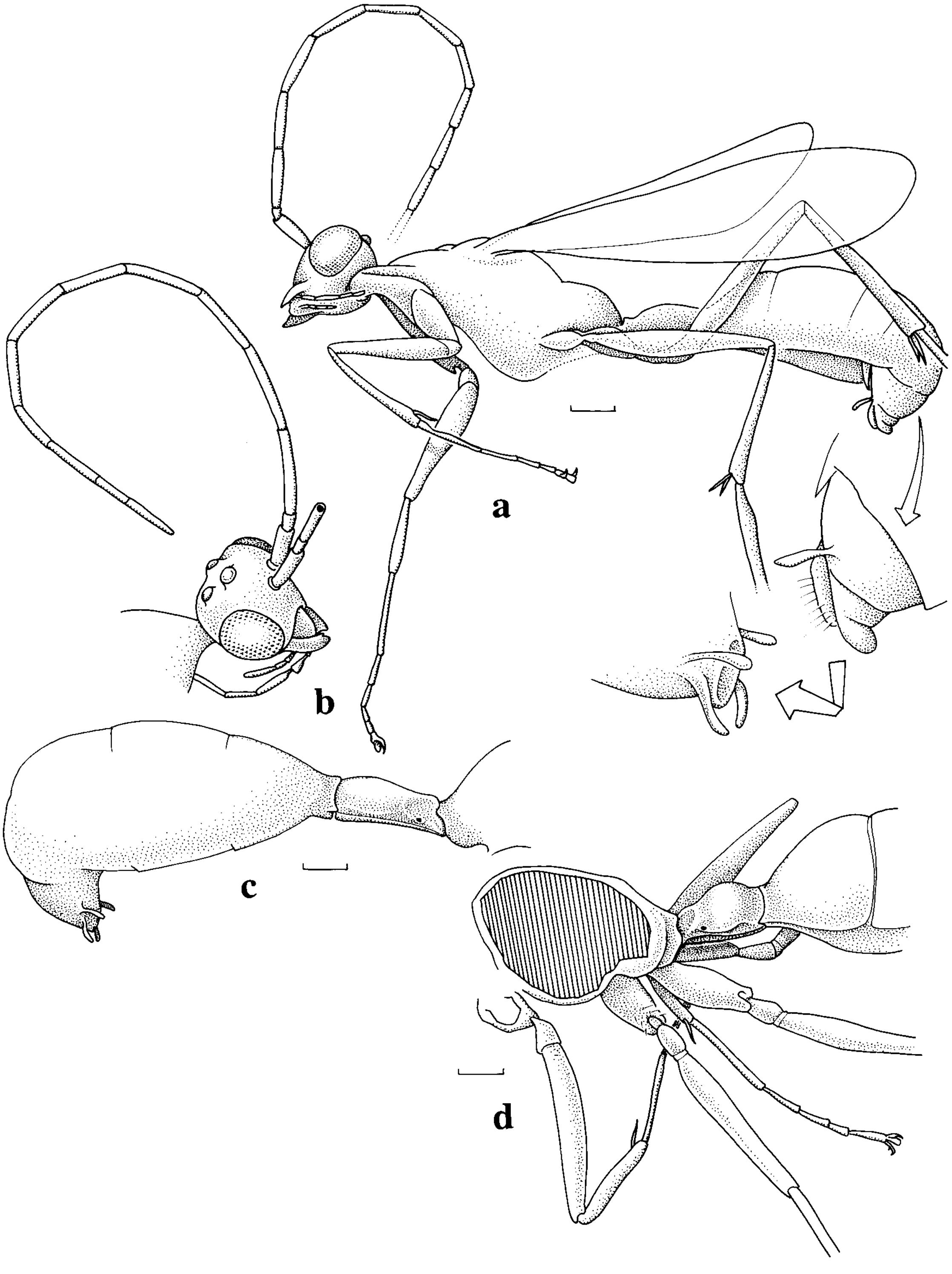
Baikurus casei, new species

Figures 1c, 5a–d, 12b

DIAGNOSIS: Known only from male specimens, and distinguished from other males of genus on basis of eyes not being reniform and there being no complete or partial crossvein between cell 1r + 2r. Otherwise, similarities with *Baikurus* are striking: mandibles have no or virtually no teeth; labial palps are long, 6 segmented; alitrunk with deep parapsidal grooves; small trochantellus present on mid and hind legs; petiole elongate, as in *Baikurus mirabilis*; and genitalia very similar.

DESCRIPTION: Males large, 7.5 mm body length, forewing length 5.0 mm.

HEAD: With three large ocelli, hind pair on low tubercles; head bare of setae. Eyes


a
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d

large, oval (not reniform or emarginate), depth ca. 0.6× depth of head. No supra-antennal suture seen. Antennal proportions: scape short, 0.5× length of flagellomere 1 (antennal segment 3); pedicel very small, 0.45× length of scape; antennal segment 3 slightly longer than immediately distal one, segments increasingly shorter distad, narrowly tapered at apex. Antenna with 11 flagellomeres. Labial palps long, 5 segments visible; maxillary palps shorter, 4 segments visible. Mandibles barely toothed; clypeus well developed.

ALITRUNK: Pleura somewhat obscured; legs long and slender, forelegs with one apical tibial spur; mid and hind tibia with two apical tibial spurs; mid and hind coxa (best seen in NJ-90aa) with slight suture at proximal end of femur (the trochantellus). Petiole long and slender: in NJ-90bb length is 2.3× the width, in NJ-90aa length is only 1.7× width, difference possibly due to angles of observation. WINGS: Forewing with vein C not reaching pterostigma, vein R tapering out midway between pterostigma and apex of Rs. Vein M + 1m-cu with slight bend in middle, but no extra crossvein intersecting submarginal cell-1. Discal cell and subdiscal cell-1 trapezoidal. Hindwing with apical half of posterior margin acute and very straight; 10 minute apical hamuli, no proximal hamuli.

GASTER: First segment 1.2–1.3× length of petiole, with slight constriction between gaster segments 1 and 2. Genitalia best seen in ventral view of NJ-90bb, with two pairs of lobes apparent: anterior pair slightly clavate, posterior pair with apices tapered.

HOLOTYPE: AMNH NJ-90bb, a large, completely preserved male in a large, extensively fractured, clear yellow piece of amber. Piece AMNH NJ-90 is one of the most remarkable pieces of New Jersey amber discovered thus far, containing 40 whole organism inclusions, including the oldest fossil mushrooms (Hibbett et al., 1996) (details of the piece are presented elsewhere [Grimaldi, 1997]). A large sliver from the entire piece, measuring 30 × 30 × 8 mm, was vacuum-embedded, and the portion with the ant isolated by cutting out a pielike slice. One surface of the slice with the ant is irregular and coarsely ground, requiring glycerine with a glass coverslip on top for viewing the inclusion. Observing the wing venation requires viewing from both sides.

ETYMOLOGY: Patronym in recognition of the collecting efforts of Gerard R. Case.

OTHER SPECIMENS: NJ-90aa. A very partial male in a thin, chipped, clear yellow piece 10 × 6 × 2 mm, which also contains the remains of a very large insect unidentifiable to order. The dorsal portion of the ant's alitrunk is lost at the surface of the amber, the head is completely gone, and only one-third of the wing is preserved. However, the entire fore and mid legs are well preserved and the hind legs up to the femur. The petiole and base of the gaster are well preserved, and have proportions very similar to that of specimen NJ-90bb. That, plus the fact that both specimens came from the same large piece, makes it almost certain they are the same species, perhaps even males from a swarm.

DISCUSSION: Wilson et al. (1967b) discussed the similarities between *Sphecomyrma* and amblyoponines, the latter being the most primitive or among the most primitive "poneroids," by virtue of the petiole being broadly attached to the gaster (much more so than in *Sphecomyrma* or *Cretomyrma*). Interestingly, they mentioned that "one character that has never received any particular attention is the form of the amblyoponine male mandibles . . . " which are "narrow . . . sometimes bidentate, and sometimes tapering to a single acute point . . . [and] close tightly against the . . . clypeal margin." This is the situation in *Baik-*

←

Fig. 5. *Baikurus casei*, n. sp. **a–c**. Holotype (AMNH NJ-90bb). **a.** Left habitus, with a slightly ventral view, also showing details of genitalia. **b.** Oblique dorsal view of head. **c.** Oblique dorsal view of gaster and petiole. **d.** Incomplete specimen (AMNH NJ-90aa), showing petiole, legs, and portions of alitrunk and gaster. Scales = 0.5 mm.

uris, which also has a slight constriction between gaster segments 1 and 2.

GENUS?

Figures 1d, 6, 13c

DESCRIPTION: Male, AMNH NJ-107: A virtually complete specimen in a small, clear yellow chip of amber, 7 × 9 × 3 mm, missing distal portions of forelegs, antennae distal to first two segments.

HEAD: Eyes large, oval, posterior margin not emarginate. Position of specimen in the amber prevents measurements on proportions of the eye and head. Mouthparts largely obscured by forthy coating, although two pairs palps protrude, each with four visible segments. Only three basal segments of right antenna remain, the pedicel being very short (ca. 0.3× length of scape). If portion of the right antenna distal to pedicel is a complete first flagellomere, it is relatively short (ca. 2.2× length of pedicel).

ALITRUNK: Mesonotum with spare, short, erect hairs, cuticle otherwise devoid of microtrichia. Scutellum with shallow transverse trough on anterior margin, containing row of 5 pits; pair of widely separated, fine setae on dorsal surface. Mesothoracic spiracle recessed in deep, large pit. Propodeum large; spiracle centrally placed and aperture not slitlike (no flap covers the aperture), with pair of fine setae dorsally. Posterior face of propodeum with very lightly rugose oval area, bordered by 8 erect fine setae. Petiole relatively short; conically shaped; narrow and articulating with propodeum, with a central ring of 8 fine setae. Where gaster articulates with petiole, short collar is formed on anterior margin of first gaster segment. LEGS: Foreleg with apical tibial spur and proximal tarsal segment with basal "kink" and comb of 8–10 fine setae that oppose spur (antennal cleaner). Mid and hind tibia each with pair of apical spurs, one spur half the length of other. Mid and hind femora with short trochantellus at proximal end, faintly sutured from femur. Tarsal claws with small preapical tooth.

WINGS: Shape of submarginal cell most like that of *Baikurus casei*, with slight bend in vein M + 1m-cu. Easily distinguished from *B. casei* and other Cretaceous ant wings by the open discal cell-1 (lacking the apical cross vein) and subdiscal cell-1 not being trapezoidal but with the anterior vein curved down toward posterior vein.

DISCUSSION: Although this male is distinct from the *Baikuris* and probably *Sphecomyrma* males also in the deposit, we prefer not to formally name it. Ant taxonomy presently relies on diagnoses using worker characters, which is a criterion that should apply to extinct taxa until modern taxa are better surveyed for males. Genera named for isolated males and workers are very likely to lead to a confusing taxonomy. We describe a new species of *Baikuris* above, based on males, because this genus is presently diagnosed only by males.

Unfortunately, critical features of the antenna are lost that would confirm this ant as a sphecomyrmine, which appears very likely. It primitively possesses the trochantellus (*Sphecomyrma* lacks a trochantellus), and wing venation—although with a few deviant features—is very similar to that of other male sphecomyrmines. The apparent absence of a distal spur on vein CuA would also place this ant in the Sphecomyrminae.

WING VENATION: Perhaps not surprisingly, there is little comparative work on the wing venation in the living Formicidae. Ant systematists have concentrated their collecting, and thus the systematic characters, on the apterous workers. One of the few studies on comparative wing venation was done by Brown and Nutting (1949); on which many of our comments on Cretaceous taxa are based.

In general, the venation of aculeates is rather conservative, particularly so in the Formicidae. The discal/discoidal cell of the forewing, for example is virtually constant, very rarely lost in ants. The second submarginal cell ("discal cell 2") is apomorphically absent in some ants; the cell is present in many primitive ants and in the Cretaceous taxa. But, valuable insight in sphecomyrmine monophyly, for example, was provided by wing venation: loss of the evanescent distal section of vein Cu-A (also termed Cu-A1). Conversely, wing venation reinforces the primitive nature of sphecomyrmines. The presence of vein 1r,

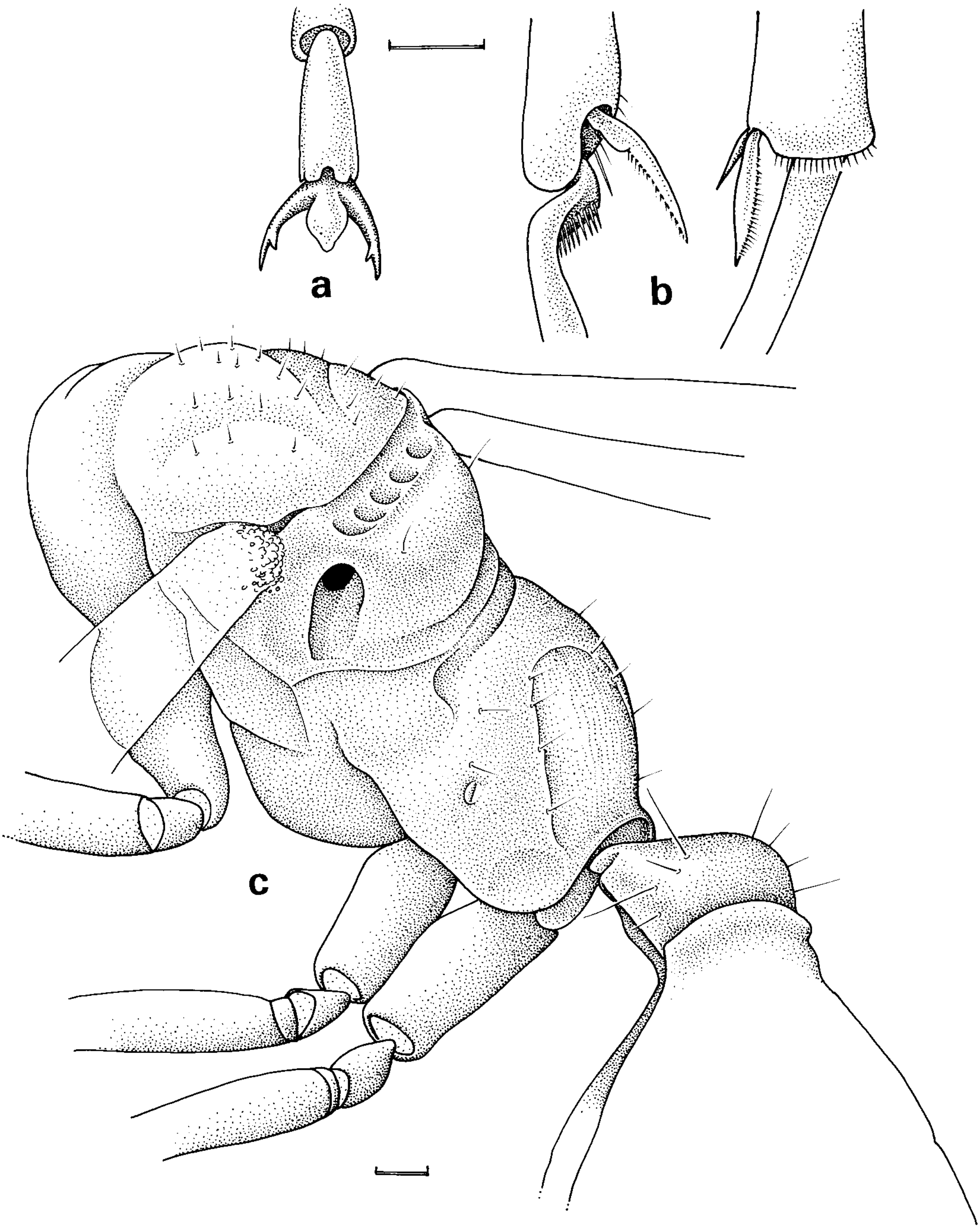


Fig. 6. Male, AMNH NJ-107: genus unknown. **a.** Detail of pretarsal claw. **b.** Detail of spurs/calcar at apex of tibia on fore and hind legs. **c.** Alitrunk, petiole, and anterior portion of gaster, dorsolateral view. Scale = 0.1 mm.

for example, which bisects the submarginal cell, is seen in primitive, extant Myrmeciinae and some Ponerinae, as well as in the Cretaceous *Baikuris mandibularis*. Loss of this vein occurs early in ant cladogenesis. Likewise, the absence of vein Mf2 (the distal wall of the second submarginal cell) is apomorphic, but the vein is present in *Baikuris, Dlusskyidris,* and the apparent male *Sphecomyrma* reported here.

Brownimecia, new genus

DIAGNOSIS: Distinguished from other Cretaceous worker ants by antenna (seen in both specimens) and the mandibles (seen in AMNH NJ-667). Antenna distinctly clubbed, apical flagellomere twice the width of basal ones and pedicel. Mandibles long, thin, scimitar-shaped, strongly cruciate, without teeth or crenulations, but with oral surface bearing ca. 30 short, spiculelike setae. Gaster with slight but definite constriction between first and second segment (abdominal segments III and IV).

ETYMOLOGY: For the renowned systematist on ants, the late William L. Brown, Jr., whom the senior author had the pleasure of knowing while a graduate student at Cornell University. Bill died suddenly on March 31, 1997, several days after reviewing this manuscript. We are grateful he was able to learn of the discoveries and see the patronym in his honor.

TYPE SPECIES: *B. clavata,* new species.

Brownimecia clavata, new species

Figures le, f; 7–11

DESCRIPTION: Body largely covered with microtrichia, sparsest on notum, absent on propodeum.

HEAD: Large, width (excluding eyes) 1.6× greatest width of notum. Eye relatively small, length 0.3× length of head, virtually round, with about 100 ommatidia. Ocelli not observed. Postocciput with recessed, trapezoidal area bearing no microtrichia. Antenna distinctively clubbed, with apical segment 2.0× width of basal flagellar segments plus pedicel. Relative lengths of funicular segments: for AMNH NJ-231: pedicel 2.1 : flagellomere-I 1.6: 1.0 : 1.1. : 1.3 : 1.3 : 1.1 : 1.3 : 1.3 : 1.6 :apical flagellomere 2.3. For AMNH NJ-667: pedicel 1.4 : 1.8 : 1.2 : 1 : 1 : 1 : 1: 1.2 : 1.2 : 1.7 : apical flagellomere 3.2. Shortest funicular segments are the third through sixth; second funicular segment slightly swollen in middle. Scape lost in AMNH NJ-231; in AMNH NJ-667 scape is 0.4× length of funiculus, 1.7× height of eye. Mouthparts intact only in NJ-667. Clypeus shallow and very broad, nearly width of head. Mandibles distinctive: apical half of left mandible protruding beyond clypeus (but best seen in lateral view of specimen), right mandible adpressed against anterior margin of clypeus, but oral surface visible in anterodorsal view: mandibles are narrow, toothless, scimitarshaped, crossing approximately at midlength, oral surface with about 30 short and spiculelike setae. Basal portion of gena with a lateral tooth. Palps long and thin: labial palp with 4 segments (basal one minute), maxillary palp with 2 visible segments (probably more present). Fimbricate glossa present (observable only in lateral view).

ALITRUNK: Dorsally constricted at level of middle of mesonotum; pronotum and mesonotum with sparse microtrichia, mesonotum with flat, oval-shaped dorsal surface. Metathoracic spiracle raised on small cone-shaped protuberance. Articulation between propodeum and mesonotum largely fused (suture barely visible). Propodeum with dome smooth and hairless, in lateral view helmet-shaped. Propodeal spiracle situated in middle. Metapleural gland orifice obscured by froth of fine bubbles, but transverse ridge to MGO is visible (this is also seen in a scanning electron micrograph of the cavity of AMNH NJ-231, see below). Area surrounding the MGO not conspicuously raised into a bulla. Legs densely covered with microtrichia, except coxae. Calcars on mid and hind tibiae. Pretarsal claw with preapical tooth. Petiole with dome of node not hemispherical but slightly pointed, microtrichose, with pair of fine setae near summit. Petiolar spiracle at basal third of petiole. Petiole narrowly attached to propodeum, broadly attached to gaster.

GASTER: Helcium well developed, with slight crenulations on gastral edge (best seen in SEMs). Abdominal segment 3 (gaster segment 1) microsetose, 1.5× length of petiole, with slight constriction between abdominal segments 3 and 4. Abdomen lost at surface of amber in AMNH NJ-231. In AMNH NJ-667, tip of abdomen is obscured by a coating of froth, through which a sting is discernible.

	Measurements (in mm)	
	holotype	paratype
Body length	3.43	—
Head width	—	0.79
Scape length	0.52	—
Funiculus length	1.02	—
Alitrunk length	1.32	1.20
Gaster length	1.29	—

TYPES: Holotype, AMNH NJ-667, a superbly preserved, complete specimen in a clear yellow piece of amber. It was vacuum embedded for better observation of certain details. Collected by Yale Goldman at White Oaks site.

Paratype, partial remains of a worker, AMNH NJ-231 in a tiny, oval, clear yellow piece, only 2 × 3 × 6 mm. We are grateful to Alan Graffam of Geological Enterprises (Ardmore, OK), who sent it to us, having obtained it from a private collector whose identity was not disclosed. Almost undoubtedly this piece was collected at the White Oaks site, since this is where virtually all New Jersey amber collectors obtained their material. Someone had obviously tumbled the piece since the surface is rather polished, and the ant is merely an exposed and clean cast on the flat surface of the piece. The front legs are virtually all gone, the mid and hind legs lost distally from the middle of the tibiae. A cast of the dorsal part of the head remains (including the ommatidia), but the ventral half of the head is lost. Funiculus of left antenna is intact, but scape is largely lost (the right antenna is entirely lost). The entire alitrunk is largely intact *within* the amber. Exposure of the specimen is fortuitous, since it exposed casts of some critical areas and details, particularly the petiole, which allowed viewing with an SEM. The specimen was first gold coated for SEM and examined at low voltage (5 kV) using a Zeiss DSM-1 scanning EM. Details of the exposed cuticle were observable, the most significant being the propodeum, petiole, and helcium. The specimen was then vacuum embedded, trimmed close and parallel to the lateral and dorsal surfaces of the body, which exposed windows into the gold-coated amber. Surprisingly, translucency of the coated surface was retained.

ETYMOLOGY: In reference to the distinctively clubbed antennae.

DISCUSSION: *Brownimecia* is not referable to the Sphecomyrminae, by virtue of its more derived proportions of antennal segments, the pedicel being relatively longer and the first flagellomere relatively shorter than in all the other sphecomyrmine workers in Canadian, Siberian, and New Jersey ambers. The scape is much longer in proportion to the funiculus (1:2) than in the worker sphecomyrmines (e.g., 1:4 in *Sphecomyrma freyi*). The mandibles are distinctively autapomorphic, and the clavate funiculus is found in most living ants, probably a groundplan feature of the living ants. The slight gastric constriction indicates *Brownimecia* to be a primitive ponerine.

Ward (1994) discussed many characters of primitive ponerines, and amblyoponines in particular, which are useful in assessing the phylogenetic position of *Brownimecia*. One feature that he did not mention, however, was genal spurs, which occur in some amblyoponines like *Amblyopone* and *Mystrium*. Other features that *Brownimecia* shares with certain amblyoponines are: mandibles narrow, long, articulation points very widely separated, and mandibles extensively crossing (again, much like *Amblyopone* and *Mystrium*); eyes small; and the mesonotum short and flattened. In virtually all other respects, though, *Brownimecia* is extremely primitive compared to extant Amblyoponini or Ponerinae: the genus lacks tergosternal fusion of abdominal segments III and IV, anterior margin of the clypeus is simple (without peglike setae), and the eyes are situated near the middle of the sides of the head (not slightly posterior to the middle). Unfortunately, some characters discussed by Ward (1994) could not be observed in either specimen of *Brownimecia*: metacoxal cavities, metapleural gland orifice, abdominal sternum and tergum II, stridulatory file on abdominal termite IV, and details of the sting.

Very recently, Dlussky (1996) described a bizarre ant in the Sphecomyrminae. His report is of exceptional interest because of the

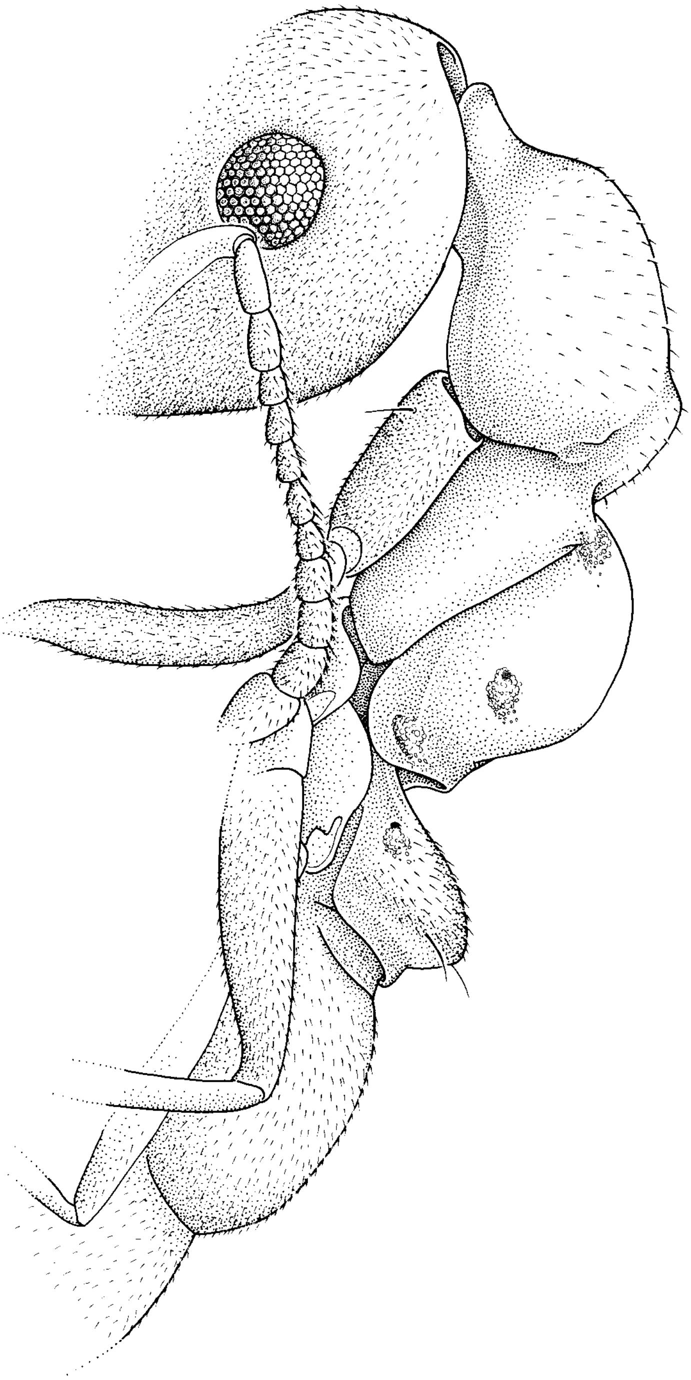


Fig. 7. *Brownimecia clavata*, n. gen., n. sp., paratype (AMNH NJ-231). **Above,** left lateral view. **Right,** dorsal view. Bubbles are emanating from spiracles and the metapleural gland orifice, obscuring the shapes of the apertures. Scale = 0.5 mm.

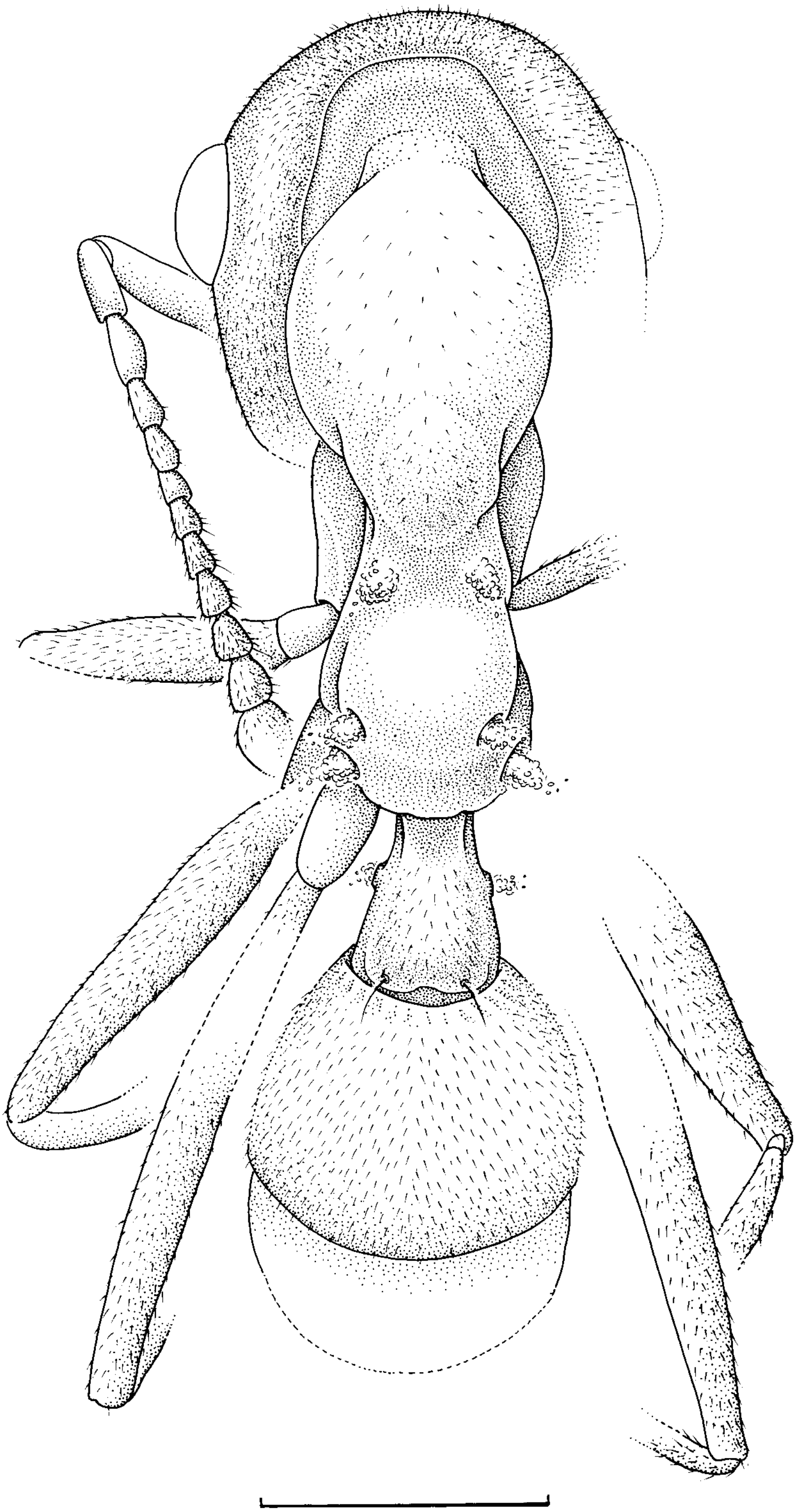
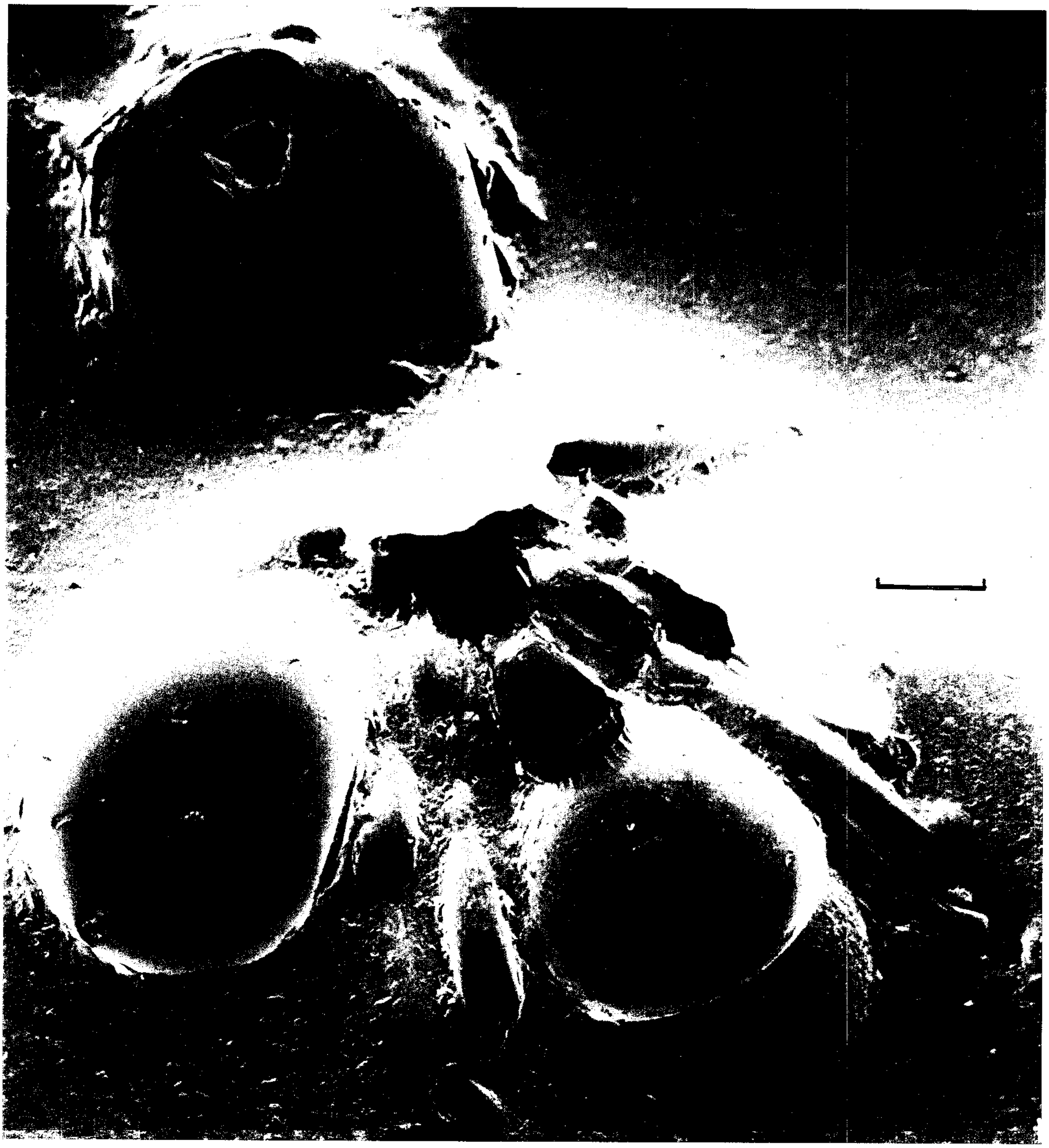


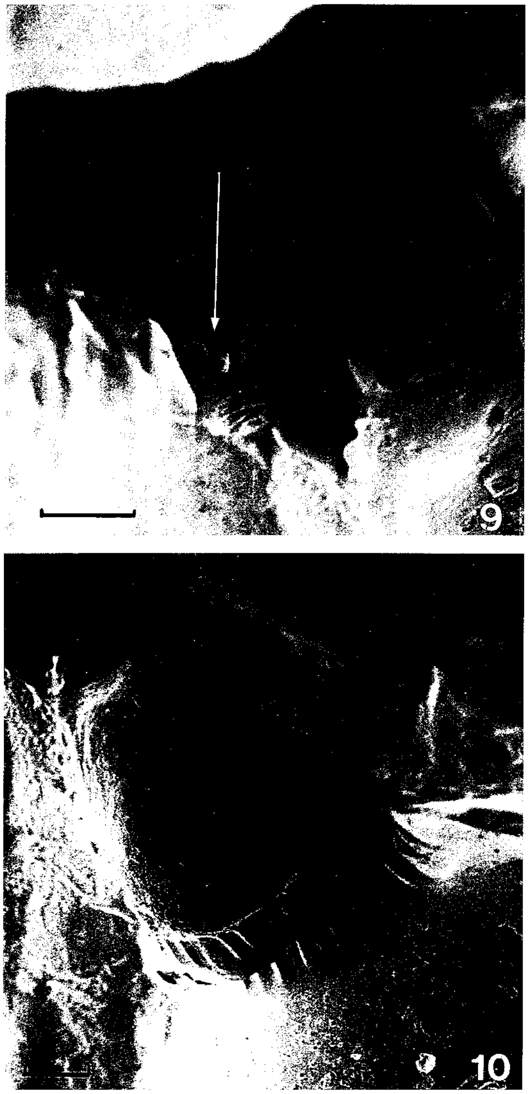
Fig. 7. (*Continued*)



Figs. 8–10. Scanning electron micrographs of *Brownimecia clavata*, paratype AMNH NJ-231. **8:** (above) Entire specimen, as exposed on surface of amber (compare fig. 7). Scale = 200 μm.

structure of the ant, and its preservation in Burmese amber. Moreover, it had been suggested to us that perhaps *Haidomyrmex* Dlussky and *Brownimecia* were closely related, on the basis of the bizarre, sickle-shaped, toothless mandibles (they also both possess a narrow, elongate pronotal "neck," and small eyes).

First, a great deal of mystique has surrounded amber from northern Burma, which was mined for at least a millennium until the early quarter of the 20th century (Grimaldi, 1996). The only museum with a significant collection of the material having inclusions is the Natural History Museum, London. Cockerell (1922), who originally studied the NHM material, stated that the material was no younger than mid-Eocene, but, unfortu-



Figs. 9, 10. **9:** Detail of propodeum, showing channels leading to the metapleural gland opening. **10:** Petiole, showing crenulate helcium. Scales = 50 μm.

nately, the stratigraphy of Burmese amber has never been reliably determined. Recently, Rasnitsyn (1996) surveyed 1200 arthropod inclusions in the NHM Burmese amber collection, and concluded, at least on the basis of the Hymenoptera (including the ants described by Dlussky), that the amber was most likely upper Cretaceous in origin. A sphecomyrmine in Burmese amber would suggest a Cretaceous age of this amber, providing the ant is accurately placed (see below). Composition of the Burmese amber, based on visual inspection by D. Grimaldi and pyrolysis gas chromatography by Alexander Shedrinsky (unpubl.), suggests it to be Tertiary. Granted, there are no means presently known that perfectly correlate amber's color, hardness, brittleness, or any other physical and chemical features of "maturation," with age. Nonetheless, all Cretaceous ambers are brittle and often highly fractured; Burmese amber is soft enough that it had been used for carvings, as early as 1000 A.D. and before Baltic amber became so available (Grimaldi, 1996). The general features of Burmese amber *suggest* a Paleocene or early Eocene age.

Secondly, the ant itself, *Haidomyrmex*, is startling: it possesses small eyes, huge genae, and huge, L-shaped mandibles. Depth and width of the mandible are approximately equal to those of the ant's cranium; the outer margin of the mandible has a squared angle, the inner margin being curved and toothless. These mandibles may have functioned in a manner analogous to that of other, living ants with "trap jaws," where long, fine hairs trigger the mandibles to suddenly snap closed. *Haidomyrmex* has a pair of such hairs on the margin of the clypeus.

We doubt that this new genus is in the Sphecomyrminae, for the lack of ocelli and structure of the head, and a scape that is distinctly shorter than any definitive, Cretaceous sphecomyrmine. Its lack of a trochantellus (cited by Dlussky) does not differ from the situation in *Sphecomyrma* (reported here in the new worker of *S. freyi*). Clearly, *Haidomyrmex* and *Brownimecia* are unrelated, based at the very least on proportions of the antennae, apparent lack of a gastral constriction in *Haidomyrmex*, position of spiracles, and pilosity of the alitrunk. *Haidomyrmex* may be a sphecomyrmine, but until more definitive worker synapomorphies are discovered for the subfamily, its exact position will remain obscure.

PHYLOGENETICS

It is virtually self-evident that the fullest systematic value of fossils can be revealed by an understanding of phylogenetic posi-

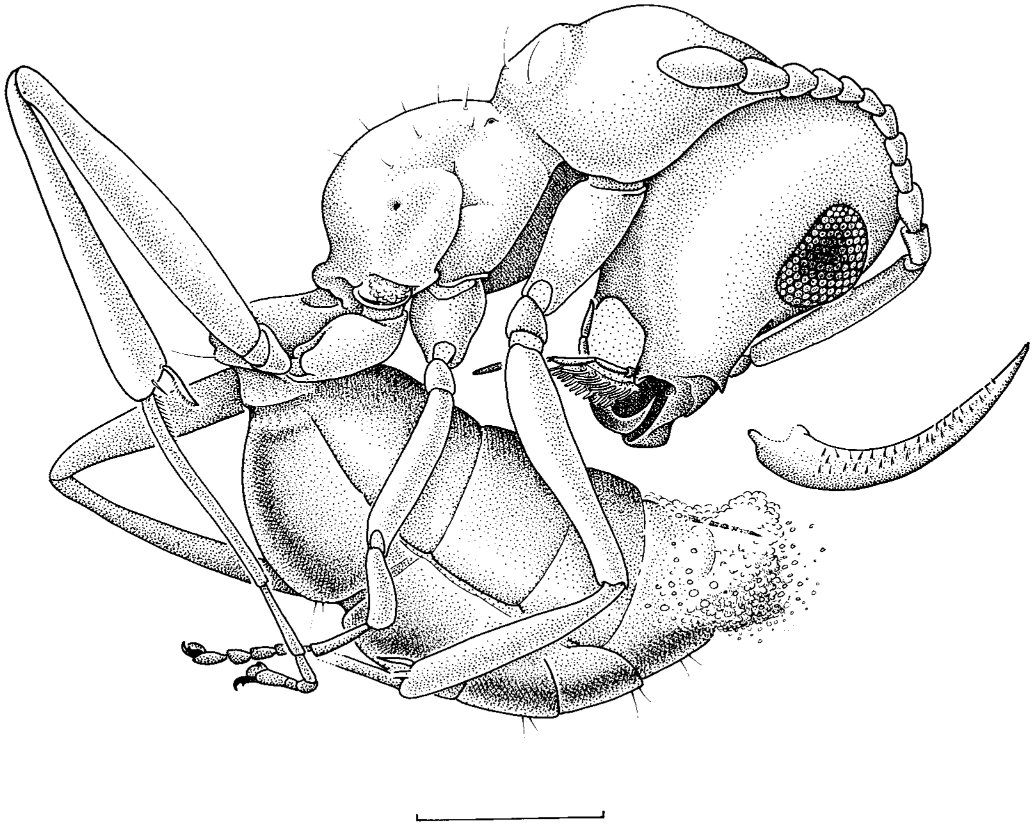


Fig. 11. *Brownimecia clavata*, holotype: lateral habitus. Scale line: 0.5 mm (for habitus). Detail of left mandible (slightly more magnified) from anterodorsal view, showing spiculate oral surface.

tion. Species diversity and rich morphology of modern forms have dictated the bases for insect phylogenies, including the Hymenoptera. Indeed, the lack of many characters in fossil forms compromises the resolution of phylogenetic hypotheses (Wheeler, 1992), and the placement of fossils accordingly depends on preserved characters whose phylogenetic values are known.

The most comprehensive and widely cited study on ant phylogeny is by Baroni Urbani et al. (1992), which provides a cladistic framework for our discussion of the positions of *Sphecomyrma* and *Brownimecia,* the oldest definitive worker ants. First, we discuss some character recoding for the matrix of Baroni Urbani et al. (1992), reanalyze the slightly revised data, then discuss implications of the revised (albeit, still unstable) cladograms for placing the two Cretaceous genera.

METHODS: Cladistic analysis (Hennig, 1966) was implemented using the programs Hennig86 (Farris, 1988), Nona (Goloboff, 1996a), Phast (Goloboff, 1996b), Dada (Nixon, 1995a) and Clados (Nixon, 1995b). Dada was used for data matrix editing, and as a shell for submission of character matrices to Hennig86, Nona, and Clados. Hennig86 was used for cladogram construction, and successive weighting with the rescaled consistency index (Farris, 1989). Typically, the multiple tree search command was applied with branch swapping (mhennig*), followed by branch breaking (bb*). This procedure was supplemented by use of the "autospin" feature of Dada, which randomly shuffles order of taxa in the matrix and resubmits the matrix to Hennig86. Autospin was run 100 times with mhennig* to try to find separate stands of multiple equally parsimonious trees, with the results all subjected to bb*.

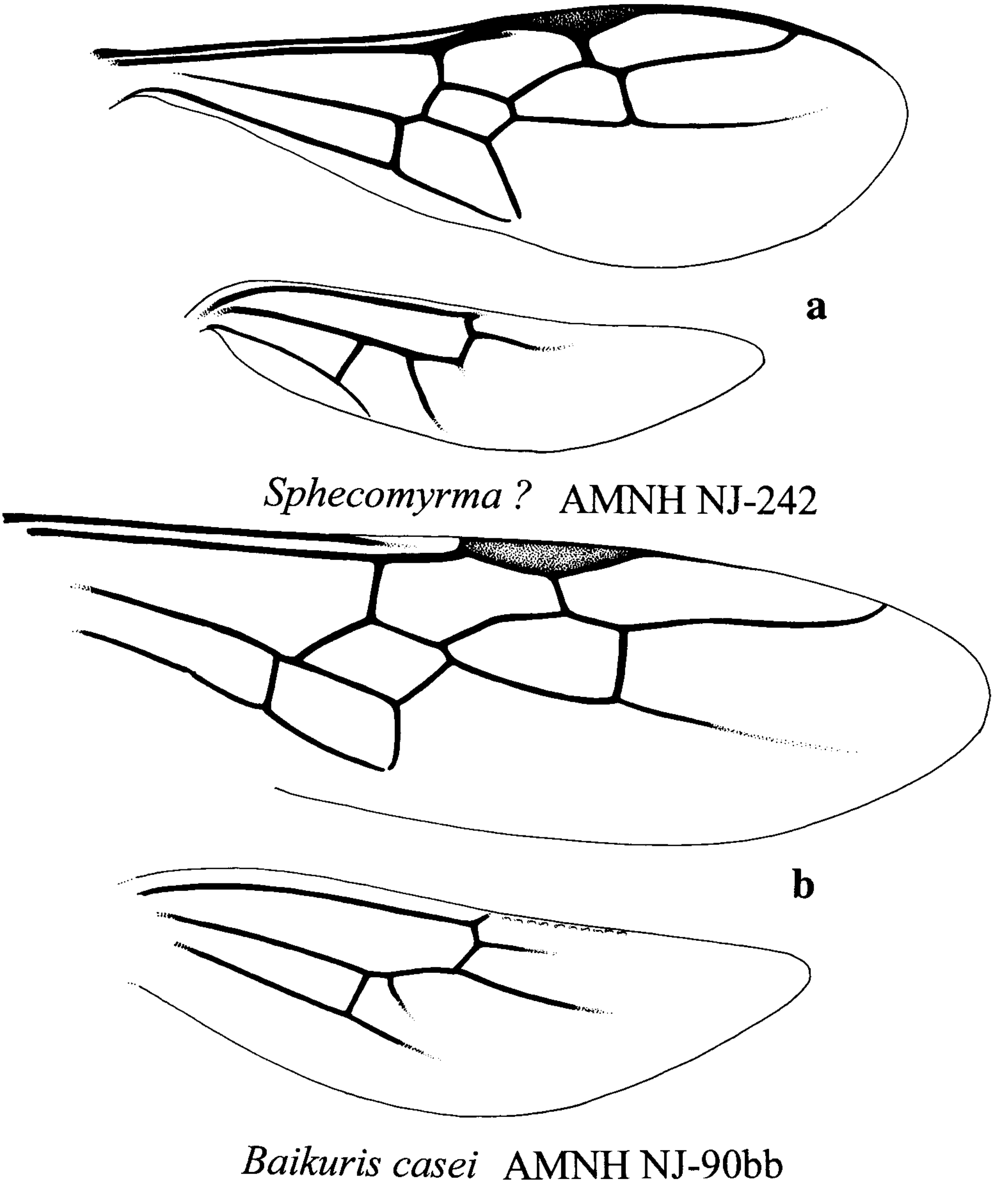


Fig. 12. Fore and hind wing venation of male sphecomyrmines. **a.** AMNH NJ-242 (*Sphecomyrma*?). **b.** *Baikurus casei*, holotype, AMNH NJ-90bb.

Because Hennig86 does not support analysis of polymorphic data, such characters are recoded as missing by Dada before submission to Hennig86. Results of Hennig86 analyses were checked with Nona, which does support polymorphisms. Because Hennig86 also outputs semistrictly supported trees (with resolutions supported by just one among the possible optimizations; see Nixon and Carpenter, 1996), Nona was used as a filter for strictly supported trees, as described by Carpenter (1996), using the "unique" command after reading in Hennig86 trees. Nona was also used for cladogram construction, by applying the multiple tree search command via random addition sequence, with tree-bisection-reconnection branch swapping (mult* with 20–50 random additions), followed by ad-

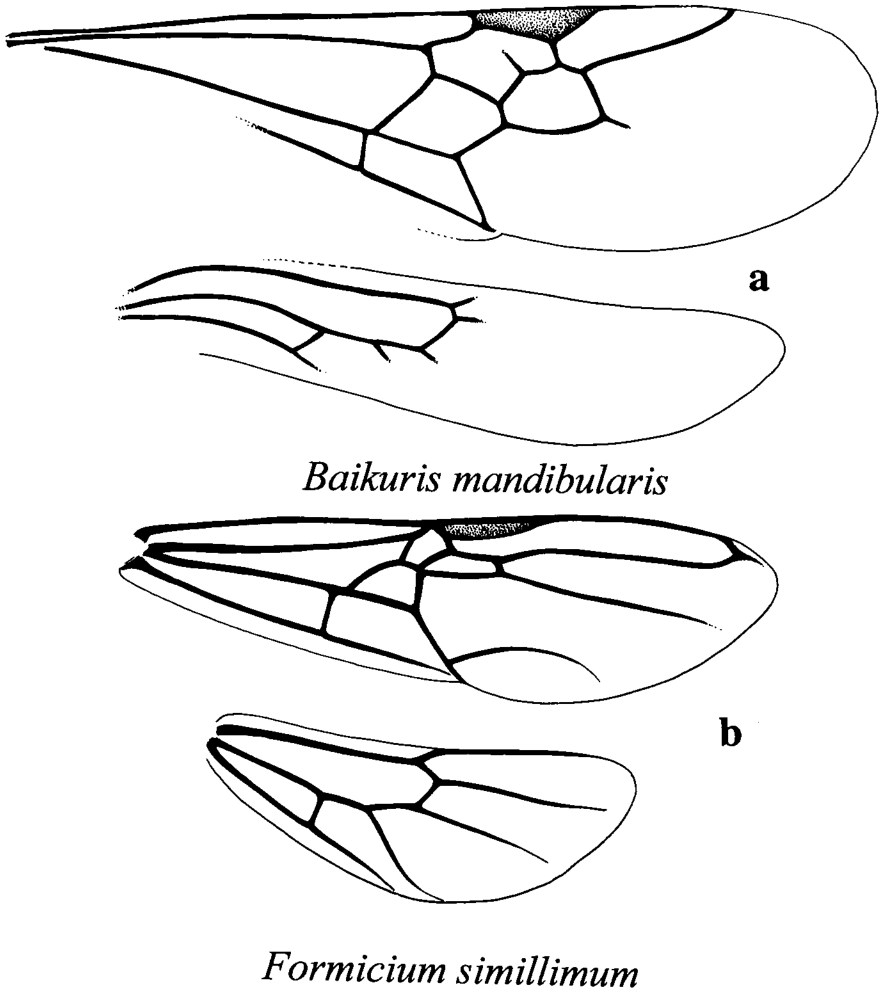


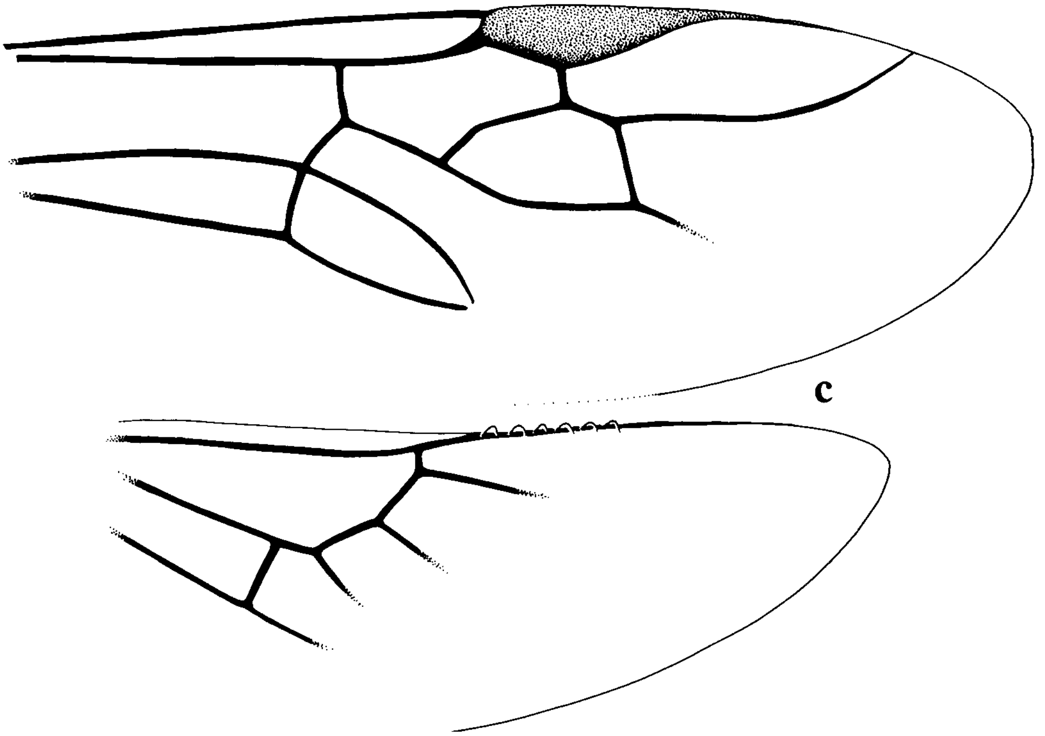
Fig. 13. Wing venation of male sphecomymines in upper Cretaceous amber from Taymyr, Siberia (a,d), New Jersey (c), and the Eocene Formiciinae (Messel, Germany; redrawn from Lutz, 1988). **a.** *Baikuris mandibularis* Dlussky (redrawn from Dlussky, 1987 [fig. 2]). **b.** *Formicium simillimum*. **c.** AMNH NJ-107, genus unknown. **d.** *Dlusskyidris zherichini* (Dlussky) (redrawn from Dlussky, 1975 [fig. 130]).

ditional branch swapping (command max*). Results were filtered for collapsibility as described by Nixon and Carpenter (1996), using the "ksv" and "best" commands on tree files. Clados was used for tree visualization and manipulation, checking for strict support, calculation of consensus trees, and printing. Bremer support values (Bremer, 1988) were calculated using Phast, by invoking the "bsupport" command and searching on suboptimal trees up to six steps longer.

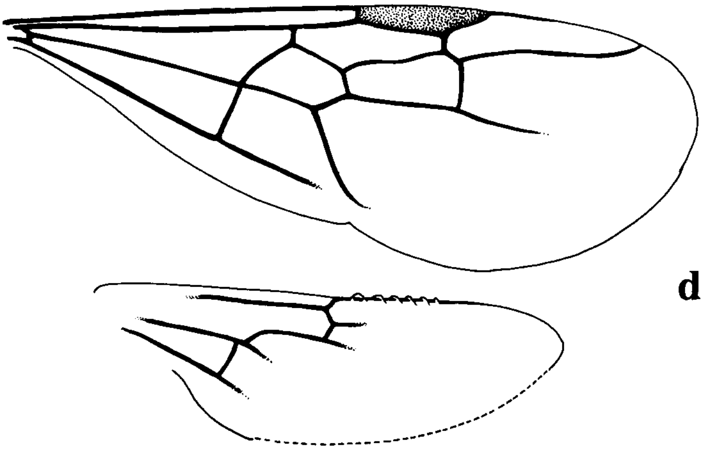
The following analyses were based on modifications to the original data matrix by Baroni Urbani et al. (1992) (see appendix, table 1).

1. Character **30** of the matrix was recoded for Leptanilloidinae (1 instead of 0), a correction suggested by Phil Ward (personal commun.). The results from analysis of the corrected matrix are shown, which are essentially the same as those reported by Baroni Urbani et al. (1992).

2. The corrected data matrix was expand-



AMNH NJ-107



Dlusskyidris zherikhini

Fig. 13. (*Continued*)

ed by the addition of *Adetomyrma*, a genus that complicates the proposed phylogeny of Baroni Urbani et al, as this new genus does not fall within their interpretation of the Ponerinae (Ward, 1994).

3. The following characters used in the matrix of Baroni Urbani et al (1992) were recoded, due to unnecessary splitting of multistate characters: **11** and **12** (new character **9**): metapleural gland absent (0), present

TABLE 1

Characters 1–62

Multistate characters are treated as nonadditive, as noted. A question mark denotes an unknown state, while a dash denotes an inapplicable trait. An asterisk denotes a polymorphism showing all applicable states; a dollar sign denotes a subset polymorphism.

	5 10 15 20 25 30 35 40 45 50 55 60
Vespidae	00000000000000000000000--00000000000000000000000000000000000-0
Bradynobaenidae	0000000$00000101000000$--000000000???0000000000000*0000000??-?
Aenictinae	10010100121100100011001000100100010100110001010101011010000010
Aenictogiton	???????0??1?????????????????????????????0??111011100101000????
Aneuretinae	10000001010001010000000--0000000011010100000000110000100100000
Anomalomyrmini	10-0110002100111011100200000000000000010010???????????????????
Apomyrmini	11010100011000110101000--000000000000010000000????????????0000
Cerapachyinae	100*0000*21*001000*100$100101000010000*0000*010111100010000000
Dolichoderinae	10000*01011001*10000000--0000000011010*000000*01100001*0100010
Dorylinae	10010100121100100001001000110000010100110011010101001010000010
Ecitoninae	10010*001211001000*10010001001000100001100000101001000110000*0
Formicinae	10-00001*11001110000000--0000001111000100000010110000**01000*0
Leptanillini	1011010002100111011100200000000000000011001*011111?00010111011
Leptanilloides	10-1010002100?100011?01000100110000000*???????????????????????
Myrmeciini	10000011020010010010002100000000000001000100000000100100100000
Myrmicinae	10100*0$111001*11*10*0$0100000000*0000*001000*0110100**0*00010
Nothomyrmeciinae	10-0000102001001000001--000000000000100000000000000?110100000
Ponerinae	10-*0**$*1*0**1100*1**210100*0000*0000*00*0*0*0*11100**0*000*0
Pseudomyrmecinae	100000010210*00100101010100000000000000001000001101001001001 10
Formiciinae	???????????????????????????????000?????010?000??0???????00????
Prionomyrmecini	10?00001??????????1????????????00???????0??00000??????????????
Adetomyrma	10010101010001110000000??010000000???0????????????????????????
Sphecomyrma	10?0000102?00??1?0000?0???0000000??????????0000?1?00010000????
Platythyrea	10000001010001100001002001000000000???1000?00000111100000 0????
Paraponera	100000010100011100000121000000000000???1000?00000001100000 0????
Amblyopone	10000001011000110000002001000000000 0??1000?00001100100000 0????
Brownimecia	10?0000?11??0????0010?100?00?000?0????????????????????????????

CHARACTER LIST

1. Head: hypognathous (0); prognathous (1).
2. Labrum: without rows of peglike teeth (0); with 2 rows of peglike teeth (1).
3. Labium: with pair of cylindrical pegs (0); without (1).
4. Clypeus: normally developed (0); extremely reduced (1).
5. Clypeus: rounded (0); with flat medial surface (10.
6. Worker eyes: present (0); absent (1).
7. Malar area in dorsal view: visible (0); reduced (1).
8. Antennal socket: exposed (0); not covered (1); covered by torulus (2) [nonadditive].
9. Worker promesonotal suture: mobile (0); fused (1).
10. Metapleural gland: absent (0); not covered (1); covered by cuticular flange (2) [nonadditive].
11. Metacoxal cavities: open or sutured (0); closed (1).
12. Metatibial gland: absent (0); present (1).
13. Basitarsal sulcus on metatarsi: absent (0); present (1).
14. Petiole: without tergosternal fusion (0); with (1).
15. Worker helcium: unfused (0); fused (1).
16. Helcium sternite: protruding ventrally (0); not (1).
17. Helcium sternite: overlapped laterally by pretergite (0); not (1).
18. Worker spiracle of III: situated posteriorly (0); situated close to anterior face of tergite (1).
19. Worker diameter of segment III: subequal to segment IV (0); smaller (1).
20. Worker segment III: tergum and sternum not fused (0); with complete fusion (10).
21. Worker dorsal stridulatory organ: absent (0); present between segments III & IV (1).
22. Worker ventral stridulatory organ: absent (0); present between segments III & IV (1).
23. Segment IV: without presclerites (0); with presternite & pretergite, unfused (1); fused (2) [nonadditive].
24. Segment IV presclerite length: <.5 IV (0); >.5 IV (1).

without a dorsally covering flange (1), covered with a flange (2); **25** and **26** (new character **22**): abdominal segment IV without presclerites (0), with presclerites and pretergites unfused (1), with presclerites and pretergites fused (2). Baroni Urbani et al. (1992) scored only binary variables in their data matrix, but in doing so, they potentially lost information (Pogue and Mickevich, 1990). Multistate characters are readily analyzed as additive, if states are in a morphocline or similarity is nested, or as nonadditive. The two new variables were treated as nonadditive.

The following characters were deleted: **9**, the "short scape" is difficult to define, and furthermore present in Leptanilloidinae. Dlussky (1983) and Baroni Urbani (1989) introduced this character essentially as a surrogate for social behavior (also see our previous discussion, p. 8). **51**, basal hamuli have not been seen in *Amblyopone* spp. and in *Nothomyrmecia*. **67** and **68**, we consider the empirical basis too meager to include these two behavioral characters in the analyses.

Polymorphic characters were resolved for the ponerines by splitting the ponerines into monomorphic subtaxa (admittedly, still a slim

←

25. Presternite of IV: subequal to pretergite (0); shorter (1).
26. Segment IV tergum & sternum: not fused (0); completely fused (1).
27. Spiracles of V–VII: not visible (0); visible (1).
28. Pygidium: not bidentate (0); bidentate (1).
29. Pygidial spines: absent (0); present (1).
30. Pygidial reduction: absent (0); narrow U-shaped sclerite (1).
31. Worker pygidium: not covered by tergum VI (0); covered (10.
32. Acidopore: absent (0); present (1).
33. Sting and lancets: articulated (0); disarticulated (1).
34. Furcula: well developed (0); reduced to absent (1).
35. Proventriculus: flaccid (0); sclerotized (1).
36. Dufour gland epithelium: not crenellate (0); crenellate (1).
37. Pavan's gland: absent (0); present (1).
38. Sting bulb gland: absent (0); present (1).
39. Worker-gyne dimorphism: limited to wings & alar sclerites (0); pronounced (1).
40. Gyne: not dichthadiiform (0); dichthadiiform (1).
41. Wing venation: not crowded (0); crowded (1).
42. Gyne segment III: poorly differentiated (0); forming postpetiole (1).
43. Bursa copulatrix: not exposed (0); exposed (1).
44. Male antennal sockets: clypeus visible (0); at anterior margin of head (1).
45. Male head incision: absent (0); present posteriorly (1).
46. Male antennal scape: shorter than next 2 articles (0); longer (1).
47. Male forewing pterostigma: present (0); absent (1).
48. Male hindwing jugal lobe: present (0); absent (1).
49. Male propodeal spiracle: slit-shaped (0); round to elliptical (1).
50. Male segment III: no tergosternal fusion (0); present (1).
51. Male segment IV: without presclerites (0); with differentiated presclerites (1).
52. Male tergite VII: sclerotized (0); desclerotized (1).
53. Male sternite VIII: without anterior apodemes (0); with long anterior apodemes (1).
54. Male cerci: present (0); absent (1).
55. Male subgenital plate: not biaculeate (0); biaculeate (1).
56. Lamina annularis: thin (0); enlarged (1).
57. Male genitalia: retractile (0); not retractile (1).
58. Male genitalia size: normal (0); larger than rest of gaster (1).
59. Larval hemolymph feeding organ: absent (0); present on abdominal segment III (1).
60. Larval mandibles: inner masticatory margin (0); outer (1).
61. Trophothylax: absent (0); present (1).
62. Pupa: with cocoon (0); naked (1).

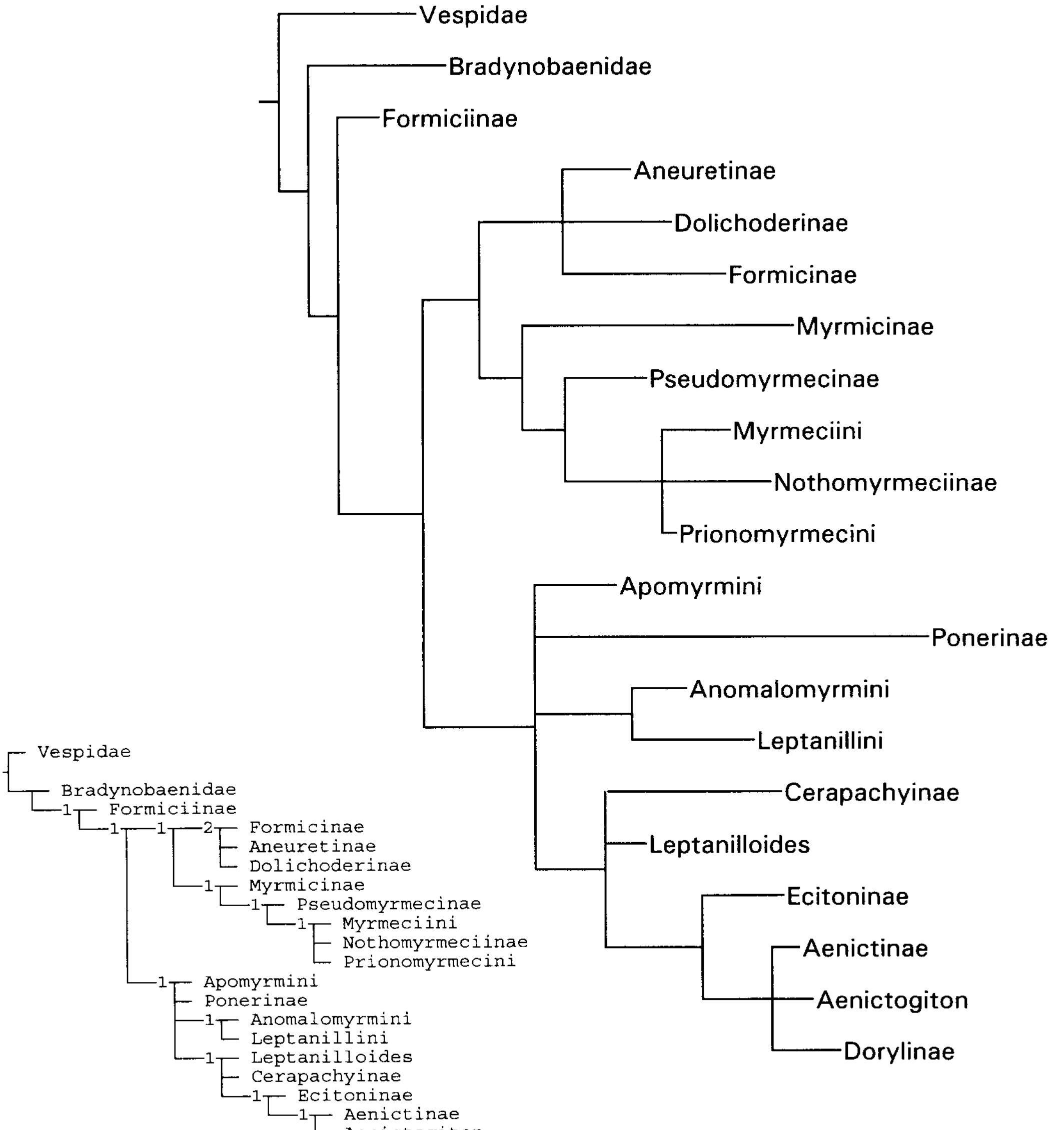


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Fig. 14. Consensus cladogram based on successive weighting of 54 trees with length of 537, using data revised from Baroni Urbani et al. (1992).

Fig. 15. Bremer support values for cladogram in fig. 14.

sampling), which is preferable to the ambiguity introduced by polymorphic scorings (Nixon and Davis, 1991; Nixon, 1996). For that reason, *Paraponera, Platythyrea,* and *Amblyopone* were scored and included. For the outgroups, Vespidae and Bradynobaenidae, some polymorphism was resolved by extrapolation, based on the groundplans established by Brothers and Carpenter (1993).

4. The New Jersey amber fossils *Sphecomyrma* and *Brownimecia* were added to the

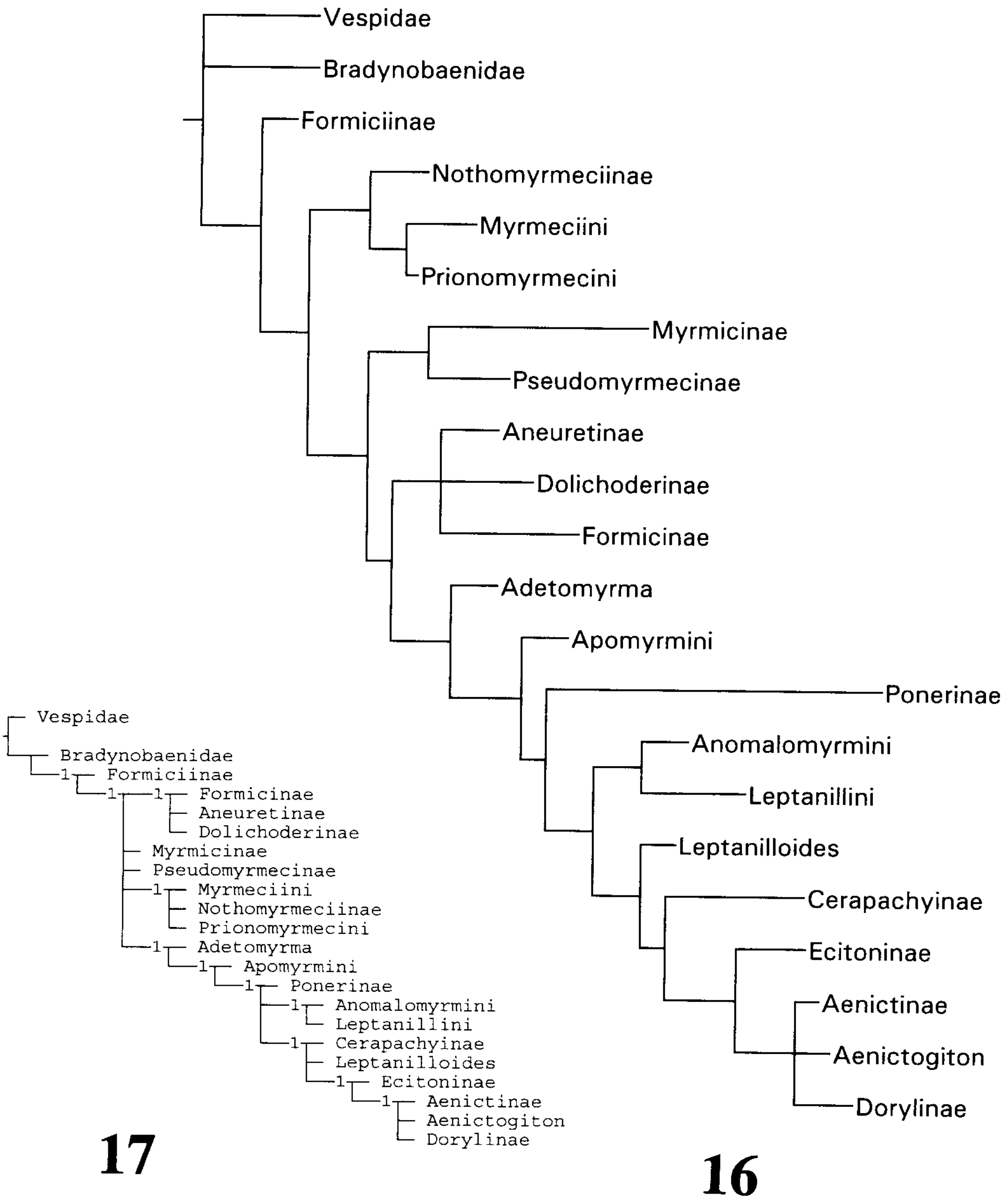
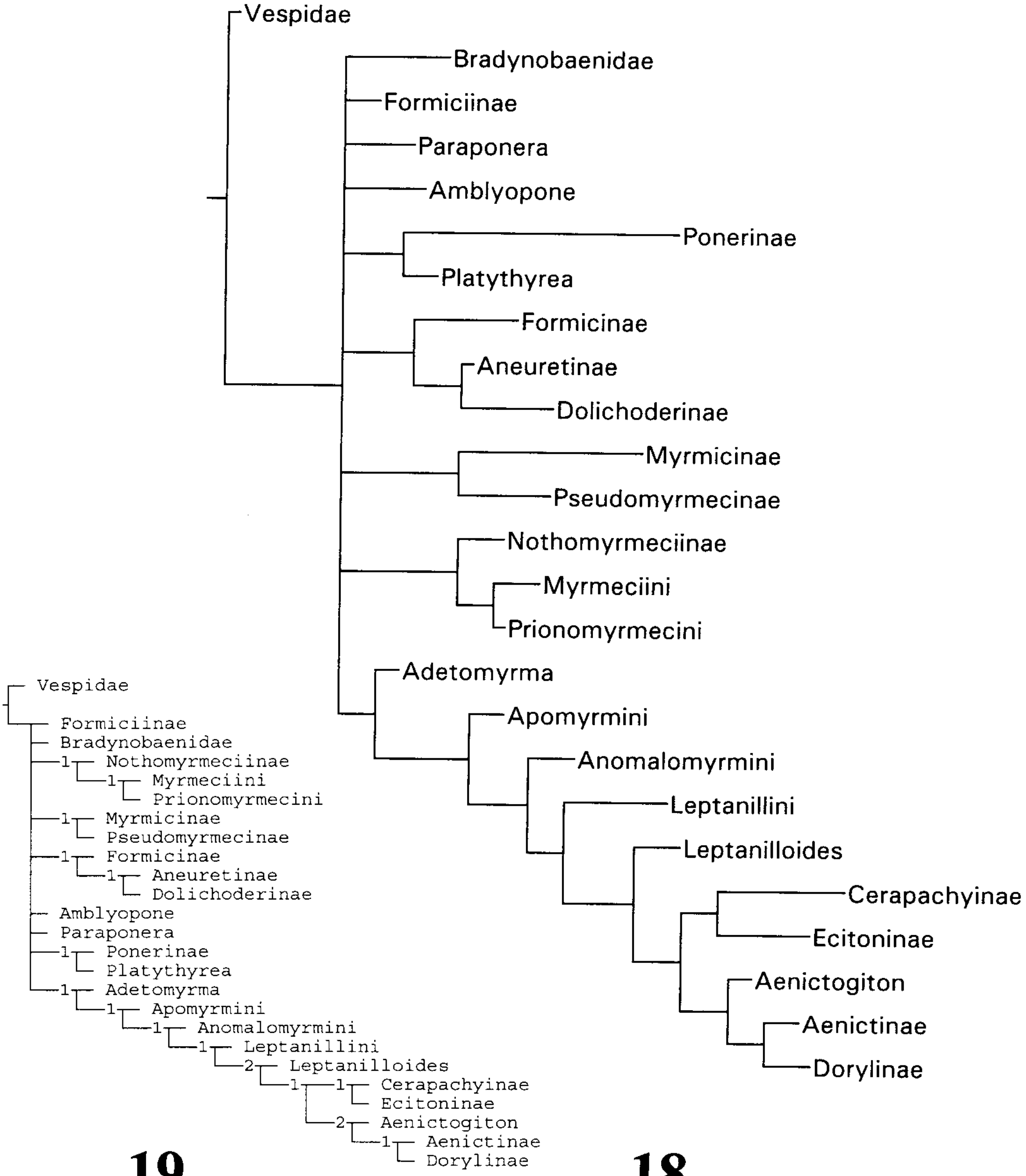


Fig. 16. Consensus cladogram with the Malagasy genus *Adetomyrma* added.
Fig. 17. Bremer support values for cladogram in fig. 16.

matrix, scoring characters for the worker of *Sphecomyrma* and the apparent male.

5. Finally, all taxa with more than 70% missing values were excluded, i.e., Formiciinae (81%), Prionomyrmecinae (75%), and Aenictogitoninae (71%). The overall effect of high levels of missing data is to weaken the application of the parsimony criterion (Nixon, 1996), and this is seen in the present study, where the taxon Formiciinae (an Eocene compression fossil) in particular introduces instability into the results, with no discernible benefit.



19 **18**

Fig. 18. Cladogram using revised characters and the ponerines divided into three smaller taxa. Strict consensus of successively weighted trees.

Fig. 19. Bremer support values for cladogram in fig. 18.

CLADISTIC RESULTS

1. The reanalysis of Baroni Urbani et al.'s revised data resulted in 144 cladograms of length 110; the original result was 72 cladograms of that length. However, of these 144 cladograms, only eight are strictly supported when filtered by Nona (four for the original, uncorrected matrix). Successive weighting results in 54 cladograms of weighted length 537; their consensus tree (fig. 14) is slightly less resolved than the consensus presented by

Baroni Urbani et al. (1992: fig. 4), with *Leptanilloides* and Cerapachyinae now part of a trifurcation.

Baroni Urbani et al. (1992) reported various statistical tests of "structure" in their matrix. They cited the PTP test (Faith and Cranston, 1991) as indicating "significant" phylogenetic structure in the data, but the problems and validity of that test have been presented (Källersjö et al., 1992; Carpenter, 1997). Baroni Urbani et al. also reported results of bootstrapping (Felsenstein, 1985), another technique that has been critiqued (Carpenter, 1992); but, criticism aside, the bootstrapping result (Baroni Urbani et al., 1992: fig. 7) was notable for showing no "significant" nodes. Indeed, their bootstrapped tree, a fully resolved majority-rule consensus, contained a great majority of nodes with replicate frequencies of less than 50%! Although commonly presented, this is certainly a misapplication: groups with frequencies less than 50% may be contradicted more often than they appear (see examples in Farris et al., 1996). The Bremer support was calculated for the data matrix, and the results (fig. 15) confirm low support for all groupings—only one clade has a Bremer support of as much as two steps, all other nodes being supported by one step, or with no support (unresolved in that figure).

2. The addition of the data for the living Malagasy genus *Adetomyra* produced a rather different tree (fig. 16). Hennig86 reported 264 cladograms of length 114, consistency index 0.59, and retention index of 0.71. Only 40 of these trees are strictly supported, and successive weighting resulted in six cladograms of weighted length 532. The consensus of these six cladograms (fig. 16) shows major rearrangements of basal nodes, and that the enigmatic, apparent ponerine genus *Adetomyra* is not the sister group of the Ponerinae, as already indicated by Ward (1994). Bremer supports (fig. 17) remain low.

3. Recoding of the abovementioned characters, and the addition of three more ponerine taxa produced yet another topology (fig. 18). Hennig86 reports four cladograms (with autospin) of length 121, consistency index 0.52, and retention index 0.69. Only two of these are strictly supported, and the results are stable to successive weighting (weighted length 468). The consensus tree of the two strictly supported trees is poorly resolved basally, but examination of the underlying trees shows that this is caused by alternative placements of one taxon: Formiciinae is either the sister group of Bradynobaenidae, or of *Paraponera*! Clearly, that taxon is contributing little useful information. Aside from that (artifactual) instability, a notable difference is the grouping within the army ant clade sensu Bolton (cf. the position of Cerapachyinae). Bremer supports remain low, although now two clades have supports of two steps (fig. 19).

4. The addition of the two fossil taxa, *Brownimecia* and *Sphecomyrma*, leads to a report of 120 cladograms by Hennig86, with length of 124, consistency index of 0.51, and retention index 0.68. Just 16 of these are strictly supported, and successive weighting results in 12 cladograms (weighting length 470). The consensus of these 12 cladograms (fig. 20) is again poorly resolved basally, but again that results primarily from instability brought about by inclusion of the Formiciinae. The position of the sphecomyrmines is thus ambiguous, but *Brownimecia* turns out to be part of a distant ponerine clade. The Bremer supports did not change overall (fig. 21).

5. The deletion of taxa with more than 70% missing values caused significant changes in topology, as predicted in simulations by Wheeler (1992). Hennig86 reports 356 cladograms of length 122, consistency index 0.50, and retention index 0.67. Just 82 of these cladograms are strictly supported, and successive weighting results in 36 cladograms (weighted length 449). The consensus of these 36 cladograms (fig. 22) is much better resolved. The basal formicid node is a quadritomy with *Sphecomyrma,* Myrmeciini + Nothomyrmeciinae, Myrmicinae + Pseudomyrmecinae, and the remaining taxa. *Brownimecia* is part of a larger ponerine clade, apparently a very basal member (not reflected in the cladistic analysis); and, there are two changes in the army ant clade (Apomyrmini to Dorylinae). The Bremer supports (fig. 23) are low.

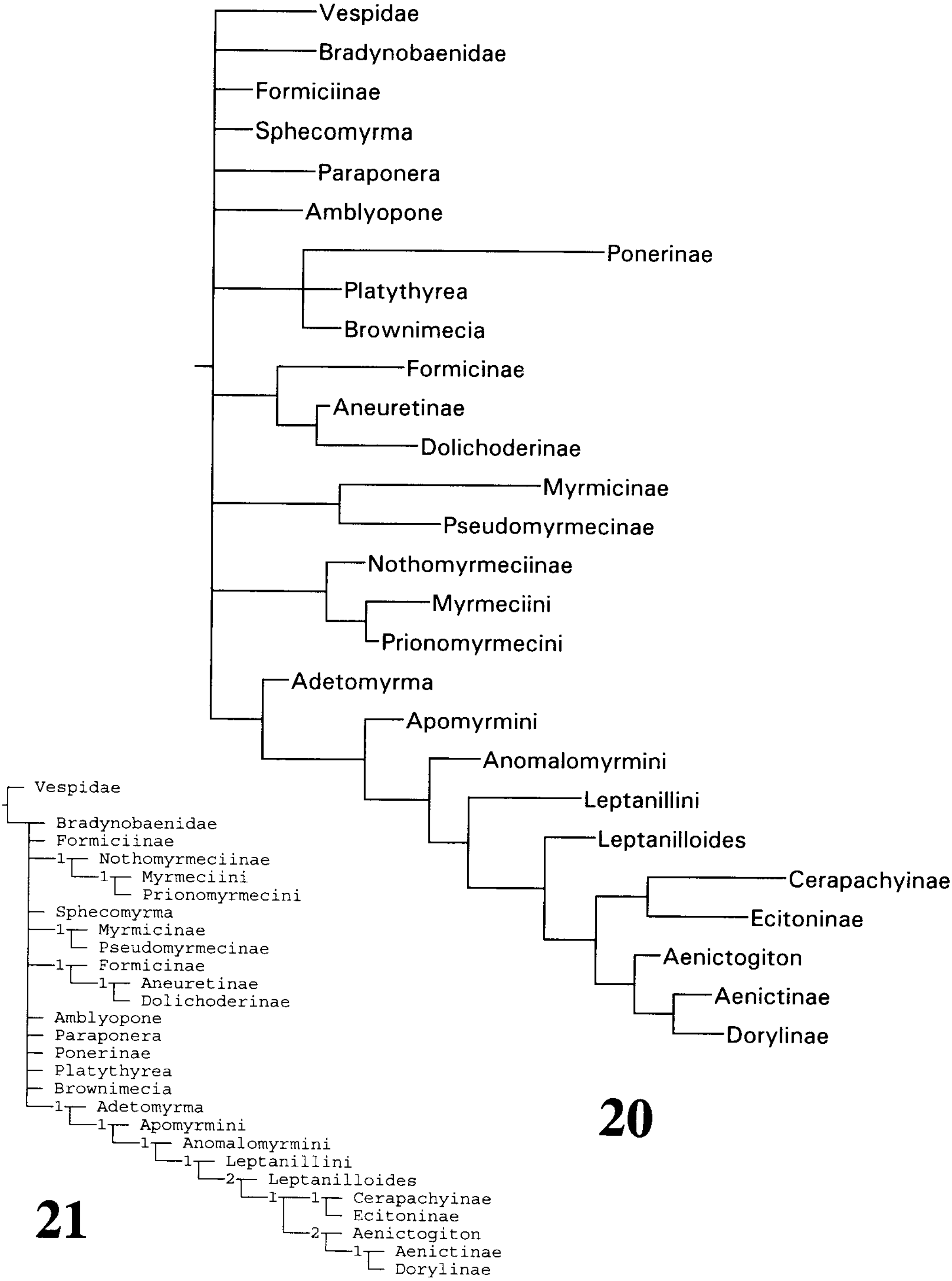
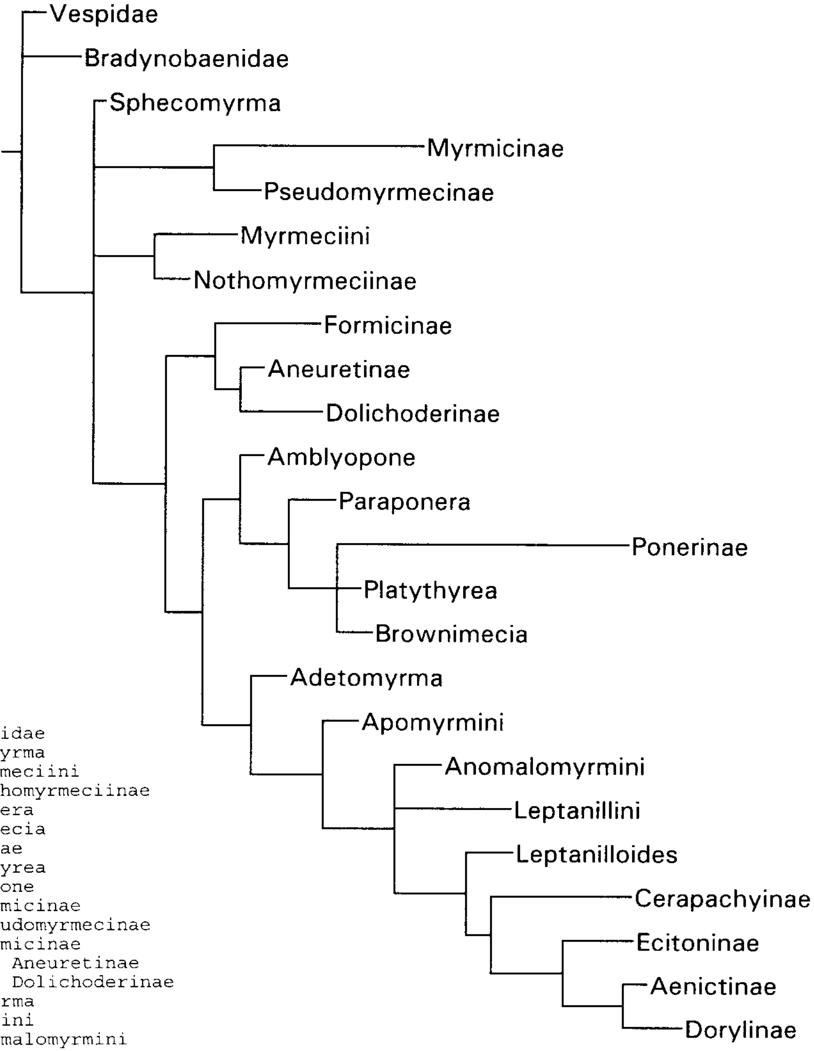


Fig. 20. Consensus of 12 successively weighted cladograms, with the New Jersey amber Cretaceous fossils *Sphecomyrma* and *Brownimecia* incorporated.

Fig. 21. Bremer support values for cladogram in fig. 20.



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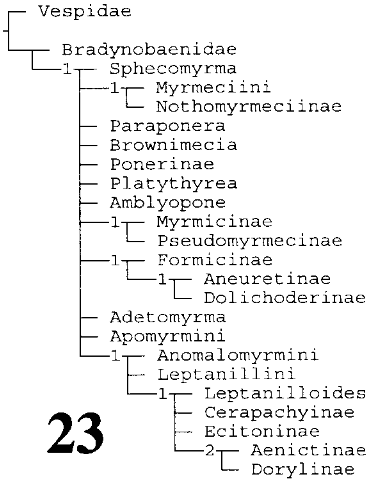

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Fig. 22. Preferred cladogram: consensus of 36 successively weighted cladograms, deleting three taxa with >70% missing values (Formiciinae [Eocene compression fossil], and the living subfamilies Prionomyrmecinae and Aenictogitoninae).

Fig. 23. Bremer support values for cladogram in fig. 22.

DISCUSSION: CLADISTICS

Our preferred result (fig. 22) differs in some fundamental ways from that of Baroni Urbani et al. (their figs. 9–15). The grouping of army ants is stable through both analyses, reflecting the numerous synapomorphies revealed in the studies by Bolton (1994). *Adetomyrma*, however, replaces the Ponerinae as their sister group in figure 22, confirming Ward's (1994) comment that *Adetomyra*, if considered a ponerine, would render the subfamily polyphyletic. Even more fundamental is the finding that the clade ((Aneuretinae +

Dolichoderinae) + Formicinae) is now the sister group to the Ponerinae s.l. + (*Adetomyrma* + army ants), and not to (Myrmeciinae, Nothomyrmeciinae, Pseudomyrmecinae, Myrmicinae). Also, the basal node of Formicidae is now unresolved, whereas it was resolved in Baroni Urbani et al.'s (1992) trees. In the hand-derived cladogram by Ward (1994), the most significant difference is the switch of the Myrmicinae from being one of the most basal clades, to perhaps being allied with a portion of the Ponerinae.

The analyses presented here raise caution concerning the robustness of the proposed phylogeny of the ants, caused by the addition and deletion of taxa as well as the reinterpretation of some of the character states, which have great effects on the topology of the trees. First, many missing values, especially in three taxa (*Aenictogiton*, *Prionomyrmex,* and the fossil *Formicium*) create a highly ambiguous matrix—with 16% of the cells missing. Second, many taxa have a high degree of polymorphism (6% of cells). These two factors result in an ambiguous matrix (more than 22% of the cells), which is accordingly problematic (Nixon, 1996). The addition or deletion of taxa always resulted in different topologies, in our view another clear sign of insufficient data.

As important as phylogenetic analyses of Formicidae are for evolutionary studies, the understanding of ant phylogeny still requires serious attention. The fine preservation of fossils in amber allows retention of many more characters than in compression fossils, which is made abundantly clear in how much less ambiguous is the placement of the New Jersey amber ants as compared to the Eocene compression fossil taxon. Placement of even the finest fossils, though, depends on a stable phylogeny, itself subject to the discovery of fossils with unpredicted combinations of characters. Ultimately, all robust phylogenies depend on the discovery of new characters and close scrutiny of the homologies of known characters.

CONCLUSION: THE AGE OF ANTS

The discovery of further sphecomyrmine ants in amber and the detailed structure of their metapleural gland clearly show that sphecomyrmines are ants. The reanalyses of earlier published data and the inclusion of fossil data (indeed, data on fossilized inclusions!), for which more than 35% of the characters could be coded, confirm the basal position of the sphecomyrmines. The discovery in particular of *Brownimecia*, a new and primitive Cretaceous ponerine, and the presence of four taxa from the same deposit, indicate that the radiation of ants 90–94 Ma was more developed than previously believed. Stratigraphic distribution of fossil Formicoidea is thus: the oldest known forms are from ca. 110 Ma, and the oldest definitive Formicidae are known from approximately 20 Ma later; only primitive taxa occur throughout the first 50 Ma—or pre-Tertiary—history of fossil ants.

A reasonable estimation would place the origin of the ants in the lowermost Cretaceous, but almost certainly no earlier. This conclusion is also consistent with the close relationship of the Formicidae to the Vespidae + Scoliidae (Brothers and Carpenter, 1993), and the phylogenetic position of Cretaceous Vespidae (Carpenter and Rasnitsyn, 1990). Vespid fossils belonging only to the two basalmost clades of the family occur in sediments from the Barremian (ca. 118 Ma) to Turonian of Russia. Vespids may extend to the earliest Cretaceous. Recently, Crozier et al. (1997) estimated a controversial age of the Formicidae as being in the lower Jurassic. This hypothesis was based on estimated divergence times of mitochondrial cytochrome b sequences compared among extant species of *Myrmecia*, calibrating nucleotide substitution rates using *Cariridris*, and an assumption of clocklike rates. Previously we discussed the ambiguous nature of *Cariridris*, but Crozier et al. regard it as an "undoubted ant" and a myrmeciine in particular. Our reanalyses have confirmed a basal phylogenetic position of the myrmeciines, making the existence of a lower Cretaceous one like *Cariridris* plausible. While *Cariridris*, like other insects from the Crato Member of the Santana Formation, is assignable to the Aptian (Maisey, 1990), an absolute age of 124.5 Ma (cited by Crozier et al., 1997) is too old: 110 Ma is the recognized age. Use of an ambiguous fossil to calibrate nucleotide change among *extant species* of *Myrmecia* no doubt has led to an estimate of ant origins that is contrary to the whole fossil record of the Hymenoptera. Despite the vicissitudes of insect fossilization, given the consistent preservation of Symphyta and basal Apocrita in the Jurassic, and the appearance of most living and extinct families of Aculeata in the lower to mid-Cretaceous (Rasnitsyn, 1988), a lower Jurassic origin of the ants is highly improbable. The earliest Hymenoptera, in fact, are xyelid sawflies from the Triassic, and the earliest aculeates are the extinct family Bethylonymidae from the upper Jurassic of Russia.

With little doubt, ant origins do not predate 140 Ma, or the earliest Cretaceous. Latest Cretaceous and earliest Tertiary records of ants are paultry to nonexistent, but all evidence thus far indicates that by the early Tertiary there is consistent preservation of living subfamilies and even some extant genera (Dlussky, 1988, 1996; W. M. Wheeler, 1915; Wilson, 1985). The radiations that spawned approximately 11,000 living species of ants occurred only 40–50 million years ago, or one-third to one-half the approximate duration of ants. Why the ants did not become abundant, diverse, and dominant until the Tertiary is a matter for future consideration.

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APPENDIX

Vacuum Embedding and Disintegration of the Type of *Sphecomyrma freyi*

The holotype of Sphecomyrma freyi occurred in a deep red piece of amber collected in 1966 from Cliffwood Beach, New Jersey. The piece originally contained two workers, but it cracked, separating the two workers (Wilson et al., 1967a,b). The piece containing the holotype (photograph in Hölldobler and Wilson, 1990) was roughly cubical, approximately 22 × 18 × 17 mm, very brittle, with some fine, superficial cracks; larger cracks permeated deeply into the piece. It was stored in a wooden cabinet in an uncovered drawer of the fossil insect collection in the Museum of Comparative Zoology for 30 years, padded with cotton in a small plastic box with a snap clasp. Over the years there had been deterioration of the piece; it become darker and more fractured, which is typical of even softer, less brittle amber like Baltic material (Grimaldi, 1993). Cretaceous material is even more susceptible to oxidative damage. To slow or prevent further deterioration, Canada Balsam had been applied to one or more faces of the piece (F. M. Carpenter, personal commun. to DG, 1988), although when and how often is unknown.

The ant itself was very close (ca. 0.3 mm) to a flat, prepared surface. This surface had numerous, fine, parallel scratches, the result of grinding/polishing by Carpenter or others. On top of this surface was a layer of clear, hardened material with a slightly irregular surface, 0.1–0.2 mm thick, that prevented detailed observation of the holotype. A cotton swab moistened with 70% ethanol gently rubbed on the surface resulted in no visible effect.

Balsam would become tacky under such treatment. The coating(s) applied just over the ant no doubt were made to reduce surface distortions for photography and close examinations. It later became apparent that this material was almost certainly dried mineral oil, or perhaps a synthetic slide mounting medium like Euparol (or both), based on the manner in which this substance behaved during curing in a synthetic embedding resin, and some other observations.

Mineral oil has traditionally been used for extremely clear observation of inclusions in amber (e.g., Grimaldi, 1993). F. M. Carpenter used mineral oil, in fact, to store some pieces of Baltic and Canadian amber in the MCZ, as a method to prevent oxidative decomposition, but he also embedded some pieces in Canada Balsam (Grimaldi, 1993; also see comments below). Lastly, the cotton stored in the box with the type specimen was stained yellowish, similar to mineral oil residues on cotton from specimens in the AMNH collection. If the layer was even partially dried mineral oil, numerous coatings must have been applied over the years, perhaps by various investigators inspecting the specimen.

To prevent further deterioration of the MCZ specimen, a process of vacuum embedding in a synthetic resin was used, refined from that of Schlee and Dietrich (1970), who developed it for preserving and studying very brittle Lebanese amber. The technique not only seals the piece from atmospheric oxygen, it is an excellent physical protection from accidental shattering, and is the only reliable way to trim into a piece of cracked amber for accurate views of inclusions without further fracturing or splitting the piece. The technique has been used successfully and consistently on over 800 pieces of New Jersey and Lebanese amber at the AMNH. A detailed, illustrated description will be presented elsewhere (Silverstein, and Nascimbene, 1997), but with basic techniques mentioned here.

The embedding medium is an epoxide (Buehler, Inc.) that is hardened using a polymerization/catalyzing agent. Heat is generated during the polymerization; the larger the volume of medium, the hotter the reaction. Epoxide and catalyzing agent are mixed in a separate container, then poured into shallow cylindrical rubber molds (Buehler, Inc). The amber piece is then gently slipped beneath the surface of the liquid epoxy, bubbles removed from the epoxide, and the preparation placed under a bell jar that is sealed and brought to approximately 4 psi of pressure (atmospheric pressure at sea level being 14 psi). The reduced pressure removes air from fine cracks in the amber, allowing epoxide to seep into the cracks and bind fractures together (it also improves visibility, by eliminating mirrorlike fractures filled with air). After 10 minutes under vacuum, the rubber cups are removed and the specimen is allowed to hardened at room temperature and pressure, generally taking several hours. The hardened block can then be trimmed with a water-fed diamond saw and ground with water-fed emory wheels of 320 and 600 grits.

Shortly after the MCZ piece was removed from the vacuum, a foam of bubbles suddenly appeared on the coated surface over the ant, signaling a reaction within the epoxide no doubt initiated by the heat of polymerization. Within several minutes the epoxide had become thickened enough to prevent removing the amber without damage. Numerous previous embeddings done in this manner, using pieces of New Jersey amber and epoxide volume several times this size, never yielded visible effects to the amber, let alone a froth of bubbles. The heat alone from the polymerization reaction would not cause such an effect on the amber (amber, in fact, requires temperatures in excess of 350°F for any softening to occur). The coating over the ant had caused the intense bubbling, since uncoated surfaces were largely unaffected. To our deep disappointment, we found that the coating had penetrated several millimeters *into* the amber.

After the epoxy was completely hardened, it was trimmed and polished. No view of the ant could be found, the surface where it now was being opaque with a suspension of yellowish bubbles. The block was cut through the middle of the amber piece, distant from the ant, in an attempt to view the ant from the other, interior side. (In cutting through the center, other, minute insects may have been obliterated, which we considered worth sacrificing for the sake of the ant. One unusual psychodid midge deep in the piece, though, was revealed this way and remains very well preserved and displayed, a silent and enduring witness). Cutting through the interior of the amber exposed highly fractured and brittle amber too deep for the epoxide to have permeated, even under vacuum. Both halves were vacuum embedded again, with perfect results (the coated surface of the amber was already sealed). Since the exposed inner surface of the amber was cemented by the second embedding, grinding of the interior surface toward the outer surface with the ant could now be done safely. Reaching 2 mm within the presumed surface of the ant revealed no specimen. It was only after a cross section was ground away from one edge that it became apparent that the bubbling involved the 1–2 mm of surface amber containing the ant. During the bubbling of the coating + amber mixture, the ant had become dis-

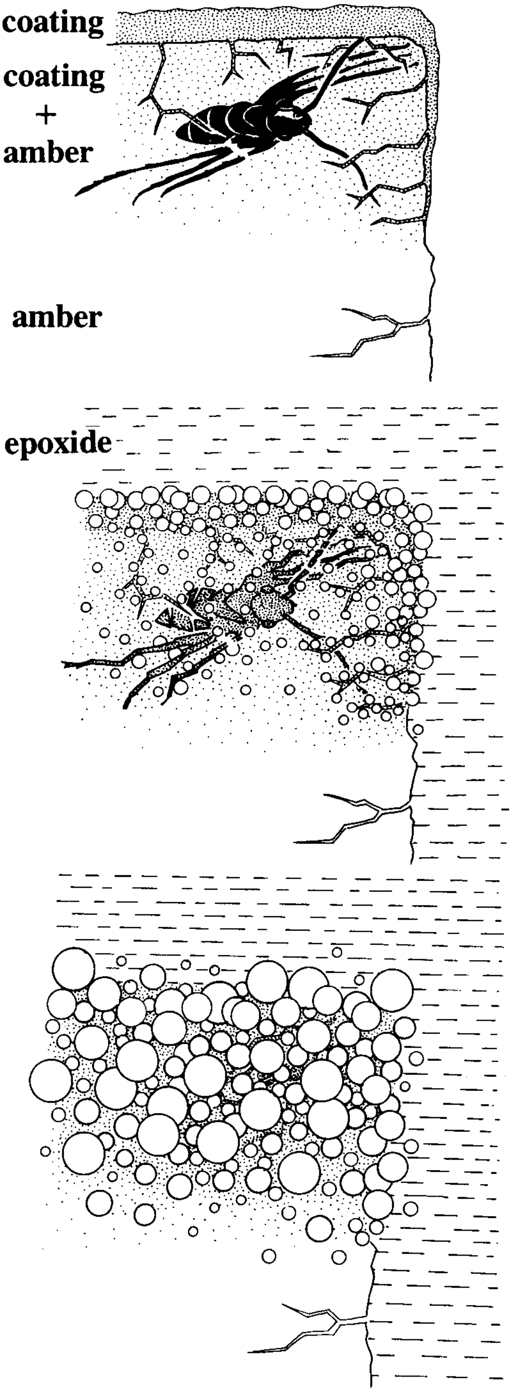

Fig. 24. Schematic interpretation in cross section of damaged incurred to the amber piece containing the type of *Sphecomyrma freyi* during embedding process. **Top,** prior to embedding. **Middle,** formation of reaction bubbles. **Bottom,** end result. Uncoated surfaces were largely unaffected.

articulated and the parts entirely obscured, with the specimen effectively disintegrated.

What was so stunning was the dramatic and destructive effect of the coating on the amber itself, a substance popularly considered inert. The effect must have been greatly enhanced by oil that penetrated numerous fine fractures in the piece, and by presumably 30 years of contact with and replenishment of oil. If any of these microscopic and oil-laden fractures extended to the ant, its body cavity would probably have contained the coating too. Oddly, Baltic amber stored for decades in vials of mineral oil at the MCZ showed little surface degradation (D. Grimaldi, personal obs., 1995). A small collection of Arkansas amber, however, given to the AMNH and stored for 20 years in mineral oil at the Univ. Illinois by Ellis MacLeod, was soft and malleable even to the core of pieces 20 mm thick, and totally degraded. Mineral oil obviously has dramatically different effects on different ambers. Even though Baltic and Arkansas ambers are similar in age, they have completely different botanical origin and chemistry, which must account for the different reactivity. New Jersey amber is no different. The fact that this amber visibly reacts with organic solvents like acetone, whereas most other ambers (including Cretaceous amber from Lebanon and Canada) do not, indicates a particularly fragile and reactive composition.

This preparation is a tragic lesson in the study and stewardship of valuable amber fossils. First, the use of mineral oil—almost certainly the coating that caused the disintegration—must be stringently avoided. Despite advocacy of the use of mineral oil for viewing inclusions (e.g., Grimaldi, 1993; Poinar, 1992), this oil clearly chemically reacts with some ambers much more than others. Sugar syrup or glycerine, or other water-based substance, should be used. Hopefully it is not too late for some specimens. Many pieces of amber in the Acra collection of Lebanese amber, and even some of the New Jersey amber ants reported in this study, had been coated with mineral oil at various times for better viewing of inclusions. Thin films of the oil must still reside on the surface and in the fine cracks.

Secondly, failures like this must temper future curatorial decisions. Given a particularly valuable amber fossil that will gradually disintegrate with age, but which has been treated in unknown ways, keen insight must be excercised as to the appropriate method of conservation.

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