Ant, paleontology of

The most important single fossil-ant find yet reported is the recent discovery of *Sphecomyrma freyi*. *Sphecomyrma* is the type genus of the new subfamily Sphecomyrminae. Not only is it by far the geologically oldest known ant fossil, but also it is the earliest certainly assignable member of the upper, or aculeate, suborder of the order Hymenoptera. The aculeate Hymenoptera, which in present times include the bees and the true wasps as well as the ants, can now for the first time be traced with certainty to the early Upper Cretaceous, some 100,000,000 years ago.

Cretavus. Previously discovered ant and other aculeate fossils had all been found in Cenozoic formations, with the single exception of the Siberian Upper Cretaceous fossil named *Cretavus sibiricus* by A. G. Sharov in 1957. Since this specimen consists of a single forewing with venation something like that of the living aculeate wasp family Plumariidae, a little-known group confined to southern South America and South Africa, *Cretavus* has been called an aculeate. Without some knowledge of the rest of the body, however, the subordinal placement of *Cretavus* must remain in doubt.

Sphecomyrma. This "wasp-ant" is known from two worker specimens found in 1966 in a lump of amber in the Magothy formation exposure on the beach bluffs at Cliffwood, in Raritan Bay, N.J. Edmund Frey and his wife, discoverers of the fossils, found a single large lump of crumbly amber in a layer of clay. This lump subsequently fell apart into smaller pieces, two of which contained each a single ant, as well as some small dipterous flies. The amber fragments were ground, polished, and photographed by F. Carpenter; they were well preserved, considering age and state of matrix.

Morphology. The appearance of the ants is shown in Figs. 1 and 2. The general habitus is antlike, but closer examination shows that certain characters of the ancestral solitary wasps have been retained: The mandibles are narrow, short, and curved and are bidentate at the apex; the antennae are long and filiform, with the scape (basal segment) not very markedly elongate; the mesonotum (middle segment of thorax) is complex, and two of its plates (the scutum and the scutellum) are still distinct and are separated by an intervening axillary surface.

The two worker specimens conform remarkably well to the archetypal ant as projected by myrmecologists previous to this discovery. The chief departures from the expected archetypal characters concern the form of the mandibles and petiole,

Fig. 1. Photograph of holotype worker of *Sphecomyrma freyi* fossilized in amber. (*E. O. Wilson, F. M. Carpenter, and W. L. Brown, Jr., The first Mesozoic ants, with the description of a new subfamily, Psyche, 74:1–19, 1967*)

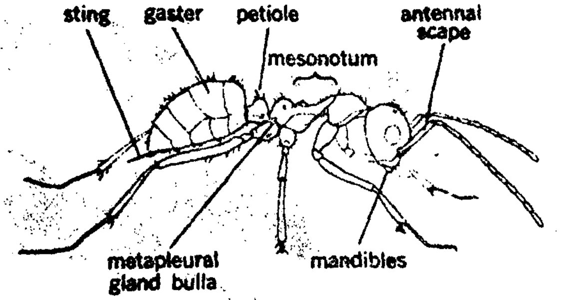

Fig. 2. Drawing of holotype worker of *Sphecomyrma freyi*, corrected from original. (*E. O. Wilson, F. M. Carpenter, and W. L. Brown, Jr., The first Mesozoic ants, with the description of a new subfamily, Psyche, 74:1–19, 1967*)

or waist segment. It was previously thought that in ant evolution the mandibles became antlike (that is, lost their wasplike form) before the petiole was constricted behind to a single-segmented node quite separate from the trunk (thorax) in front and the gaster (abdomen) in the rear. In *Sphecomyrma* the mandibles are more like those of a tiphiid solitary wasp (for example, *Methocha*) than they are like those of any ant worker, yet the petiolar node is clearly and rather deeply pinched off behind in the manner of many higher ants, particularly in the subfamily Formicinae.

In fact, in overall impression of form *Sphecomyrma* is startlingly like a formicine ant, such as *Prenolepis*, and it is only on closer examination that primitive characteristics not possessed by the Formicinae are noticed. These details are the wasplike mandibles, well-developed exsertile sting, toothed tarsal claws, short antennal scapes, and two tibial spurs on middle and hindlegs. (The smaller of two spurs shown on each of the fore tibiae in the drawn figures of the original published descriptions of *S. freyi* are in error, for they do not exist in the type specimens; these spurs have been deleted from the reproduction of the original figure printed here as Fig. 2.)

Relationships to Amblyoponini. The Formicidae include a relict, living tribe of predatory ants, the Amblyoponini, which is not known from fossils but which certainly carries some very primitive characters. The amblyoponine male has mandibles like those of *Sphecomyrma*—slender, short, and curved, with a bidentate or simple apex, and capable of closing up tightly under the free clypeal margin. The worker-queen mandibles of Amblyoponini, although usually more elaborate than those of tiphiid wasps, can be derived from the tiphiid pattern without much strain. However, it is the form of the petiole that most clearly links the Amblyoponini to the ant-ancestral Tiphiidae. Not only is the amblyoponine petiole usually broadly joined to the gaster behind, but it is in most cases very like those of various tiphiid wasps in its general plan and is presumably derived earlier than the stock with a postconstricted petiole that gave rise to *Sphecomyrma*. This means that the ants must have split into at least two (and probably more) major stocks during the Cretaceous.

Phylogeny. The stock including *Sphecomyrma* may have led to the subfamily Formicinae, if the habitus resemblances mean anything. The ecological specialty of the Formicinae, insofar as the subfamily can be said to have one, is the exploitation of the sugary excreta of homopteran plant lice as a major source of food. Of course, other subfamilies in the Formicidae have similar feeding habits, and the subfamily Dolichoderinae in particular appears to be at least as completely committed to this ecological niche as are the Formicinae.

The similarity in external appearance between the subfamilies Formicinae and Dolichoderinae has in the past usually led to conclusions that these stocks are phyletically closely related. It now seems more realistic to consider them as convergent; the proventriculus, the damming valve of the crop, or "social stomach," has evolved in very different ways in the two subfamilies, and the radical evolution of the sting apparatus and its venom glands has taken a very different direction (and apparently at a very different rate) in dolichoderines as compared to formicines. Thus, internally they are as different as ants are known to be. It may well be that the Dolichoderinae arose from a stock represented by the living (Australian) and Oligocene (Baltic amber) subfamily Myrmeciinae, or perhaps from another lineage of which a surviving trace, living or fossil, does not exist. (A large, winged ant fossil, possibly a myrmeciine, was found in mid-Tertiary beds in Argentina and described by M. J. Viana and J. A. Haedo Rossi; no Myrmeciinae are known to survive in the New World.) If *Sphecomyrma* (subfamily Sphecomyrminae) is considered to be the ancestral line of the Formicinae and if early poneroid (predaceous) and myrmecioid (predaceous and nectar-feeding) lines are postulated, it seems likely that the adaptive radiation of the Formicidae was well launched by the end of the Cretaceous.

Tertiary ants. By Oligocene (Baltic amber) times, as is well known, this radiation had produced many modern genera, some even identical with modern forms at the species-group level. It should be borne in mind, however, that dominant currently world-wide genera containing hundreds of species (such as *Pheidole* and *Crematogaster*) are completely absent in the mid-Tertiary formations. (The old report of *Pheidole* from the Miocene Florissant Shales in Colorado is nullified by recent taxonomic changes.) Surely representatives of these huge genera, which contain many living tree-foraging and even tree-dwelling species, would have turned up in amber or as winged forms in the lacustrine deposits had they been present in these areas in mid-Tertiary times. Perhaps their radiation, if not their origins, occurred at a post-Miocene date. If so, the speciation and distribution of these genera have taken place at a remarkably rapid rate, but at a rate that is tending to be more accepted as normal as evidence from animals and plants accumulates.

Ant origin. On the early end of the scale, the origin of the ants (and the aculeate Hymenoptera) may now be dated as probably mid-Cretaceous. Certainly, as has long been maintained, the evolution of the aculeates was tied in with the radiation of the flowering plants (angiosperms), which started early in the Cretaceous. The insectiferous amber deposits of the Canadian Cretaceous contain a fair representation of Hymenoptera, as well as many other insects, but so far no aculeates have been found in this formation. From this fact alone, it is probably justifiable to consider the Canadian amber as being earlier than the Magothy formation.

Magothy amber. The Magothy, known for over 100 years, lies atop the Raritan formation, at the very bottom of the Upper Cretaceous. The Magothy outcrops at many sites on the east coast from Maryland to Nantucket, and amber has been found widely over this range. The amber is associated directly with lignites and leaf and twig impressions derived from *Sequoia* trees or a closely related genus. It seems clear that these were the source of the resin that became the amber. Although many pieces of Magothy amber have been found and undoubtedly exist in private and public collections, no insect inclusions had been reported up to the time of the Freys' find. The Magothy and Raritan formations are now the focus of great interest, mainly because of the demonstrated possibility that important amber insect fossils can be found there.

For background information *see* ANT; HYMENOPTERA in the McGraw-Hill Encyclopedia of Science and Technology. [WILLIAM L. BROWN, JR.]

Bibliography: M. J. Viana and J. A. Haedo Rossi, *Ameghiniana*, 1:108–113, 1957; E. O. Wilson, F. M. Carpenter, and W. L. Brown, Jr., *Psyche*, 74:1–19, 1967; *Science*, Sept. 1, 1967.