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4 The Ants

On several counts ants can be regarded as the premier social insects. They are the most widely distributed of the major eusocial groups, ranging from the arctic tree line south to Tierra del Fuego, to the tip of South Africa, and to Tasmania, and occurring on virtually every oceanic island between Iceland and the Aleutians in the north and Tristan da Cunha and Campbell in the south. They are numerically the most abundant of social insects. At any given moment there are at least 10^{15} living ants on the earth assuming that C. B. Williams (1964) is correct in estimating a total of 10^{18} individual insects—and taking 0.1 percent as a conservative estimate of the proportion made up of ants. The ants contain a greater number of known genera and species than all other eusocial groups combined. The diversity of their ecological and social adaptations is truly remarkable. Food specialization is extreme, exemplified by the species of the ponerine genus *Leptogenys* that prey only on isopods; by species of the ponerine genera *Discothyrea* and *Proceratium* that feed only on arthropod eggs (Brown, 1957); by certain members of the myrmicine tribe Dacetini that prey only on entomobryomorph and symphypleonan collembolans (Brown and Wilson, 1959a); and by members of the subfamily Cerapachyinae, all of which, so far as we know, prey exclusively on other ants (Wilson, 1958a; Gotwald and Brown, 1966). The majority of ant groups exhibit a highly variable degree in prey choice, while a few have come to subsist primarily on seeds. Still others rely entirely on the "honeydew" secretions of homopterous insects reared in their nests or on special mutualistic fungi cultured on insect dung or vegetation (Way, 1963; Weber, 1966).

Social parasitism attains its most advanced development in these insects. A finely graded series of stages in the

evolution of the phenomenon is displayed by various species up to and including degenerate forms of slavery in which the slave-maker workers are capable only of conducting raids and are totally dependent for minute-to-minute care on their slave workers. Other evolutionary lines lead to totalinquilism, in which the worker caste is lost; in one remarkable species (*Teleutomyrmex schneideri*) the parasite queens have turned into ectoparasites, their bodies having become modified for riding on the backs of the host queens (Chapter 19).

Nesting habits are no less diverse. A few ant species, such as the fungus growers of the genus *Atta* and the extreme desert dwellers *Monomorium salomonis* and *Myrmecocystus melliger*, excavate deep galleries and shafts down into the soil, sometimes to depths of six meters or more (Bernard, 1951; Jacoby, 1952; Creighton and Crandall, 1954). In contrast, there are the arboreal species, some of which are limited to cavities of one or a very few species of plants. A few of the host plants in turn are highly specialized to house and nourish ant colonies and are unable to survive without these insect guests (Janzen, 1967). The tiny myrmicine *Cardiocondyla wroughtoni* sometimes nests in cavities left in dead leaves by leaf-mining caterpillars, while a few formicine species—*Oecophylla longinoda* and *O. smaragdina*, *Camponotus senex*, and certain species of *Polyrhachis*—have evolved the habit of using silk drawn from their own larvae to construct tent-like arboreal nests (Forel, 1896).

The reason for the numerical preeminence of ants is a matter for conjecture. Surely it has something to do with the innovation, achieved as far back as the mid-Cretaceous period, of a wingless worker caste able to forage deeply into soil and plant crevices. It must also stem partly

from the fact that primitive ants began as predators on other arthropods and were not bound, as were the termites, to a cellulose diet and to the restricted nesting sites that place colonies within range of adequate quantities of cellulose. Finally, the success of ants might be explained in part by the ability of all the primitive species and most of their descendants to nest in the soil and leaf mold, a location that gave them an initial advantage in the exploitation of these most energy-rich terrestrial microhabitats. And perhaps this behavioral adaptation was made possible in turn by the origin of the metapleural gland, the acid secretion of which inhibits growth of microorganisms in the nest chambers (Maschwitz *et al.*, 1970).

In 1968, according to Francis Bernard, 7600 living species of ants had been described from the entire world. W. L. Brown (personal communication) believes that the true number, including those remaining to be described, probably falls between 12,000 and 14,000. These comprise about 250 unequivocal genera. There is more variety of species in the tropics, and this diversity declines sharply with increasing latitude (Kusnezov, 1957a; Wilson, 1968a). The fauna of North America north of Mexico, for example, one of the best studied taxonomically, was known to contain only 455 species in 1950 (Creighton). Only 3 of the more widespread of these species make it to the tree line of the American arctic, and they are very rare or absent on the tundra beyond (Weber, 1950; W. Briggs, personal communication).

The ants constitute all of the single superfamily Formicoidea and, within that, the single family Formicidae. Brown (1954) divided the Formicidae into two major branches, the myrmecioid and poneroid "complexes" of subfamilies. The names of the complexes were derived from the most primitive subfamilies known to belong to them at that time, namely the Myrmeciinae and Ponerinae. This taxonomic decision has since come to be supported by a growing amount of solid evidence, and it has some potentially profound evolutionary implications to be discussed later in this chapter. Within the two complexes can be recognized the eleven subfamilies listed in Table 4-1. Some authorities place the Aneuretinae as a tribe within the Dolichoderinae and the Cerapachyinae as a tribe within the Ponerinae; both are clearly no more than borderline candidates for subfamilial rank. Representatives of some of the most diverse ant genera are illustrated in Figures 4-1 to 4-6.

TABLE 4-1. Subfamilies of ants (family Formicidae), together with the principal tribes and genera and their world distribution. (Some authors place the Aneuretinae within the Dolichoderinae and the Cerapachyinae within the Ponerinae.)

Division	Distribution
THE MYRMECIOID COMPLEX	
Subfamily Sphecomyrminae <i>Sphecomyrma</i>	Fossil only; Cretaceous of New Jersey
Subfamily Myrmeciinae <i>Nothomyrmecia</i> <i>Myrmecia</i> <i>Prionomyrmex</i> <i>Ameghinoia</i>	Australia Australia, New Caledonia Fossil only; Oligocene of Europe Fossil only; early Tertiary of South America
Subfamily Aneuretinae <i>Aneuretus</i> <i>Mianeuretus</i> , <i>Paraneuretus</i> , <i>Protaneuretus</i>	Ceylon Fossil only; Oligocene of United States and Europe
Subfamily Pseudomyrmecinae <i>Pseudomyrmex</i> <i>Tetraponera</i> <i>Pachysima</i> , <i>Viticicola</i>	New World tropics Africa, Asia, Australia Africa
Subfamily Dolichoderinae Tribe Dolichoderini <i>Dolichoderus</i> , <i>Monacis</i> * <i>Hypoclinea</i> <i>Acanthoclinea</i> , <i>Diceratoclinea</i> Tribe Leptomyrmecini * <i>Leptomyrmex</i> Tribe Tapinomini <i>Tapinoma</i> * <i>Iridomyrmex</i> * <i>Technomyrmex</i> <i>Liometopum</i> <i>Bothriomyrmex</i> <i>Conomyrma</i> , <i>Dorymyrmex</i> , <i>Ecilius</i>	New World tropics World-wide Australia Australia World-wide New World, Asia, Australia Asia, Australia Eurasia, North America Widespread in Old World New World
Subfamily Formicinae Tribe Myrmecorhynchini <i>Myrmecorhynchus</i> Tribe Dimorphomyrmecini <i>Dimorphomyrmex</i> * <i>Gesomyrmex</i> Tribe Myrmoteratini <i>Myrmoteras</i> Tribe Melophorini <i>Notoncus</i> , <i>Prolasius</i> , <i>Melophorus</i>	 Australia Asia Asia Asia Australia

Division	Distribution
Subfamily Formicinae (<i>continued</i>)	
Tribe Plagiolepidini <i>Acantholepis</i> , <i>Anoplolepis</i> , <i>Plagiolepis</i> <i>Acropyga</i>	Widespread in Old World Asia, Australia, New World tropics
Tribe Oecophyllini * <i>Oecophylla</i>	Australia, Asia, Africa
Tribe Formicini * <i>Formica</i> , * <i>Lasius</i> , <i>Polyergus</i> <i>Acanthomyops</i> <i>Brachymyrmex</i> * <i>Prenolepis</i> <i>Euprenolepis</i> , <i>Pseudolasius</i> <i>Paratrechina</i>	Eurasia, North America North America North America Eurasia, North America Asia, Australia World-wide
Tribe Camponotini * <i>Camponotus</i> <i>Calomyrmex</i> , <i>Opisthopsis</i> <i>Polyrhachis</i>	World-wide Australia Asia, Africa, Australia
THE PONEROID COMPLEX	
Subfamily Ponerinae	
Tribe Amblyoponini <i>Amblyopone</i> <i>Prionopelta</i> <i>Myopopone</i> <i>Mystrum</i> <i>Onychomyrmex</i>	World-wide Asia, Australia, New World tropics Asia, New Guinea Asia, Africa, Australia Australia
Tribe Ectatommini <i>Ectatomma</i> <i>Heteroponera</i> <i>Rhytidoponera</i> <i>Discothyrea</i> , <i>Proceratium</i> <i>Gnamptogenys</i>	New World tropics Pantropical Asia, Australia World-wide New World, Asia, Melanesia
Tribe Platythyreini <i>Platythyrea</i>	Pantropical
Tribe Ponerini <i>Hypoponera</i> , * <i>Ponera</i> <i>Diacamma</i> , <i>Myopias</i> , <i>Ectomomyrmex</i> <i>Bothroponera</i> , <i>Brachyponera</i> , <i>Cryptopone</i> <i>Leptogenys</i> , <i>Trachymesopus</i>	World-wide Asia, Australia Old World tropics Pantropical
Tribe Odontomachini <i>Anochetus</i> , <i>Clontomachus</i>	Pantropical
Subfamily Cerapachyinae	
Tribe Sphinctomyrmecini <i>Sphinctomyrmex</i>	Asia, Australia, New World tropics
Tribe Cerapachyini <i>Cerapachys</i> <i>Lioponera</i> , <i>Phyracaces</i> , <i>Syscia</i> <i>Acanthostichus</i>	Pantropical Old World tropics New World tropics
Subfamily Leptanillinae <i>Leptanilla</i>	Pantropical

Division	Distribution
Subfamily Dorylinae	
Tribe Dorylini <i>Aenictus</i> <i>Dorylus</i> <i>Anomma</i>	Old World tropics Asia, Africa Africa
Tribe Cheliomyrmecini <i>Cheliomyrmex</i>	New World tropics
Tribe Ecitonini <i>Eciton</i> , <i>Labidus</i> <i>Neivamyrmex</i>	New World tropics New World
Subfamily Myrmicinae	
Tribe Myrmicini (broad sense) <i>Manica</i> , * <i>Myrmica</i> , <i>Stenamma</i> <i>Aphaenogaster</i> , <i>Leptothorax</i> , <i>Monomorium</i> , <i>Myrmecina</i> , <i>Pheidole</i> , <i>Solenopsis</i> <i>Cardiocondyla</i> , <i>Oligomyrmex</i> , <i>Pheidologeton</i> , <i>Pristomyrmex</i> , <i>Rhoptromyrmex</i> , <i>Triglyphothrix</i> <i>Lordomyrma</i> , <i>Podomyrma</i> , <i>Vollenhovia</i> <i>Chelaner</i> , <i>Machomyrma</i> <i>Xiphomyrmex</i>	Eurasia, North America World-wide Old World tropics Asia, Australia Australia Asia, Australia, New World tropics Melanesia, New World tropics Old World New World
Tribe Ochetomyrmecini <i>Rlepharidatta</i> , <i>Ochetomyrmex</i> , <i>Wasmannia</i>	New World tropics
Tribe Attini <i>Acromyrmex</i> , <i>Apterostigma</i> , <i>Atta</i> , <i>Cyphomyrmex</i> , <i>Trachymyrmex</i>	New World, mostly tropical
Tribe Meranoplini <i>Calyptomyrmex</i> , <i>Meranoplus</i> <i>Mayriella</i>	Old World tropics Australia
Tribe Crematogastrini <i>Crematogaster</i>	World-wide
Tribe Metaponini <i>Metapone</i>	Pantropical
Tribe Dacetini <i>Acanthognathus</i> , <i>Daceton</i> <i>Strumigenys</i> <i>Smithis</i> , <i>uma</i> <i>Colobostruma</i> , <i>Epopostruma</i> , <i>Mesostruma</i> , <i>Orectognathus</i>	New World tropics World-wide Asia, Australia, New World tropics Australia
Tribe Basicerotini <i>Basiceros</i> <i>Eurhopalothrix</i> , <i>Rhopalothrix</i>	New World tropics Pantropical

* Genus also known from early Tertiary fossils.

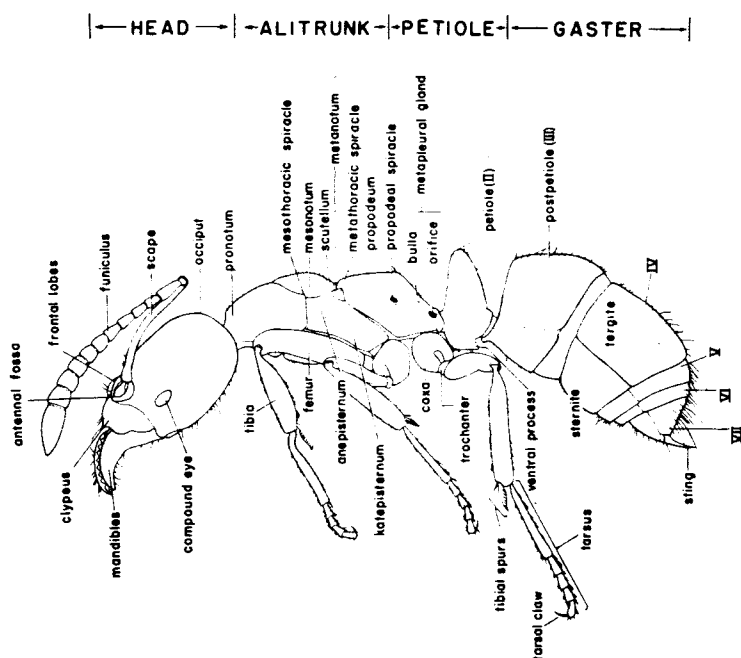


FIGURE 4-1. Worker of the New Zealand ponerine ant *Mesoponera castanea* showing some of the principal morphological features used in taxonomy (from Brown, 1958).

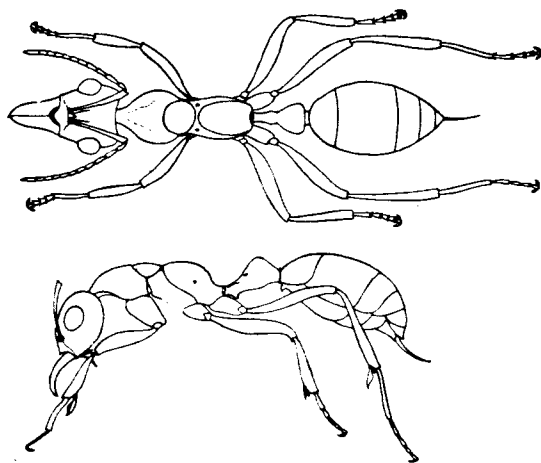


FIGURE 4-2. The worker caste of *Nothomyrmecia macrops*, considered to be the most primitive living member of the Australian subfamily Myrmeciinae and hence of the entire myrmecoid complex (modified from Clark, 1934).

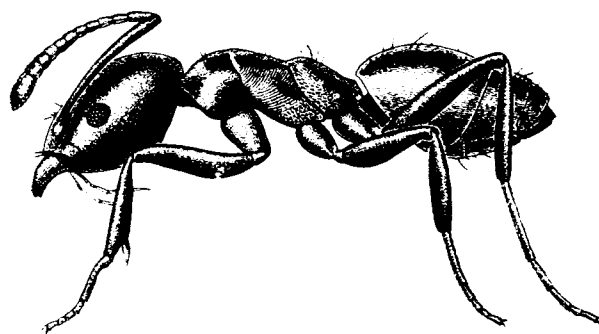


FIGURE 4-3. The worker of *Technomyrmex albipes*, a member of the Dolichoderinae (from Wilson and Taylor, 1967).



FIGURE 4-4. The worker of *Paratrechina longicornis*, a member of the Formicinae (from M. R. Smith, 1947).



FIGURE 4-5. The worker of *Trachymesopus stigmus*, a member of the Ponerinae (from Wilson and Taylor, 1967).

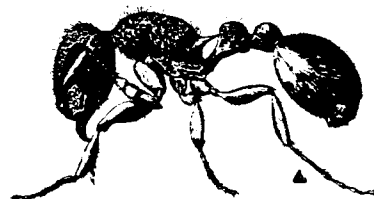


FIGURE 4-6. The worker of *Triglyphothrix striatidens*, a member of the Myrmicinae (from M. R. Smith, 1947).

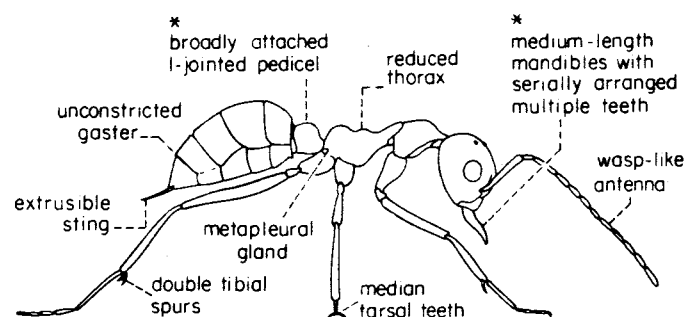
The Origin of the Ants

Until very recently the search for the ancestry of ants has resulted in frustration. To be sure, a vast number of fossils were available for study. In examining 9,527 Baltic amber specimens, of Oligocene age, Wheeler (1914) recognized no less than 92 species belonging to 43 genera. Comparably rich Oligocene deposits were described from rock fossils in North America (Carpenter, 1930), and additional finds were made in Miocene amber from Sicily (Emery, 1891), Miocene rocks from East Africa (Wilson and Taylor, 1964), early Tertiary rocks from South America (Viana and Haedo Rossi, 1957), and amber of middle to late Tertiary age from the Dominican Republic and Chiapas, Mexico (Brown and Wilson, unpublished). These Tertiary faunas are for the most part modern in aspect. In the Oligocene deposits, for example, the most abundant genera are *Iridomyrmex* and *Lasius*, in that order. *Iridomyrmex* is still a prominent element of the tropical and warm temperate faunas of the New World and both numerically dominant and species-rich in Australia and New Guinea. *Lasius* remains one of the several most abundant and species-rich genera in the cooler portions of Europe, Asia, and North America. The Oligocene species of *Lasius* fit well within the range of variation exhibited by the living species but are morphologically as distinct from them as the living species are from each other (Wilson, 1955a). This is also true for the other ant genera that have persisted since Oligocene times, including *Camponotus*, *Formica*, *Iridomyrmex*, *Myrmica*, *Oecophylla*, *Ponera*, and *Technomyrmex*. There are also quite a few extinct genera and even some primitive forms among the Tertiary fossils. But the most primitive of all of these, *Prionomyrmex longiceps* of the Baltic amber, is a member of the Myrmeciinae, a group still represented by two living genera and many species in Australia and New Caledonia. Furthermore, the most generalized known member of the Myrmeciinae is a living Australian species—*Nothomyrmecia macrops* (see Figure 4-2). This remarkable ant was described by John Clark in 1934 on the basis of two workers collected somewhere within a 10,000-square-mile area of dry, uninhabited heath and eucalyptus forest between Esperance and Balladonia, in southwestern Australia. Several expeditions, including one by C. P. Haskins and the present author, have attempted to recover additional, living specimens, but they have not been successful. The story of the discovery and subsequent

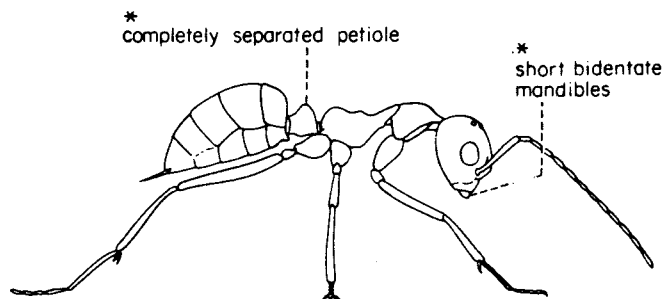
unrewarded search for *Nothomyrmecia*, together with a more detailed description of the type specimens, is given by Brown and Wilson (1959b).

In sum, the known Tertiary faunas are essentially modern in character, and they offer no strong clues to the origin of the ants. In order to find fossils that link the primitive ants to the nonsocial wasps, myrmecologists were forced to look to the Mesozoic era. Their hopes were slow in being realized, because insect fossils from Mesozoic times are scarce, and this is particularly true for the Cretaceous period, the most recent and promising section of the Mesozoic era. In 1967 Wilson, Carpenter, and Brown (1967a,b) were fortunate enough to acquire the first ant remains of Cretaceous age. The species, *Sphecomyrma freyi*, and the new subfamily founded on it (Sphecomyrminae), were described from two well-preserved workers in New Jersey (United States) amber dating to the lowermost portion of the upper half of the Cretaceous age (see frontispiece). The age of the specimens was estimated to be about 100 million years, or nearly twice that of the Baltic amber ants. *Sphecomyrma* displays most of the characteristics earlier projected for the hypothetical ancestor of the ant from morphological studies of the rest of the Formicidae, as illustrated in Figure 4-7. It departs in only one important regard: its petiole is ant-like, while its mandibles are wasp-like—that is, very short and bearing only two teeth. We had expected just the reverse. We had guessed that the mandibles, which are the principal working tools of the worker ant and which vary to an extreme degree within the living Formicidae in ways correlated with food habits, would have been altered from the primitive wasp condition early in the evolution of the group. Also, there is a tribe of living ponerine ants, the Amblyoponini, in which the mandibles are modified but the petiole is not (see Figure 4-8).

This second piece of contrary evidence created a seemingly insoluble problem in the reconstruction of early ant phylogeny. The problem can be most clearly phrased in terms of the following abstract question. How is it possible for an ancestral form, in our case the proformicid wasp, to possess two primitive character states *a* and *b*, then to give rise to an annectant form (*Sphecomyrma*) with one derived state *a'*, and one original state *b*, finally for the annectant form to give rise to a more advanced group (the Amblyoponini) with the *reversed* set of character states, *a* and *b'*? The only way out seems to be to assume that the Amblyoponini, which are the most primitive known



PREVIOUSLY HYPOTHESIZED ANCESTOR



SPHECOMYRMA

FIGURE 4-7. Comparison of the worker of *Sphecomyrma freyi*, the first ant of Mesozoic age discovered, with the hypothetical ancestor projected from earlier morphological studies. The principal character states are indicated, and the trivial details in the hypothetical ancestor, which could not be guessed in advance, are made the same as in *Sphecomyrma* solely for convenience (from Wilson, Carpenter, and Brown, 1967a).

members of the poneroid complex, and *Sphecomyrma*, which is the probable antecedent of the myrmecoid complex, represent independent derivations from the protoformicid Tiphidae. In other words, the ants may have originated twice in evolution. The possibilities are indicated in Figure 4-9. Of course, we are in no position to know about the degree of sociality of *Sphecomyrma*, so that the moment of origin of eusociality in the Mesozoic era and the number of times it originated independently remain matters for conjecture.

Whatever the source of the Amblyoponini as opposed to the remainder of the poneroid complex, *Sphecomyrma freyi* forms an excellent connecting step between the

Myrmeciinae and the nonsocial wasps of the family Tiphidae. The similarities between *Sphecomyrma* and the tiphid genus *Methocha* (Figure 4-10) are particularly close. The conditions under which eusociality might have arisen in the early ants will be discussed at greater length later in this chapter.

The Taxonomy of Ants

The taxonomy of the world ant fauna is still relatively inadequate. There are, to begin with, few useful regional monographs. Creighton's (1950) review of the ants of North America north of Mexico is one of the best, and it has the added distinction of being the first major work to dispense with the clumsy and meaningless polynomials that plagued ant taxonomy for a hundred years. Creighton substituted a much simpler and more efficient system of binomials and trinomials based on modern population concepts (for example, "*Camponotus herculeanus pennsylvanicus* var. *whymperi*" was placed as a synonym under *Camponotus herculeanus*). Bernard (1968) has made a similar valuable revision of the ants of Europe. Other useful regional works include compendiums by Gallardo (1916-1932) and Arnold (1915-1926) on the ants of Argentina and South Africa, respectively; the pioneering but fragmentary work by Wheeler (1922) on the fauna of Africa south of the Sahara and the Malagasy Region*; the old but still useful review of the ants of India by Bingham (1903); and monographs on the ants of Puerto Rico by M. R. Smith (1936a), of New Zealand by Brown (1958), and of Polynesia as a whole by Wilson and Taylor (1967). The fauna of New Guinea and surrounding islands has been reviewed in part by Wilson (1959a and included references). Individual taxa revised in recent years include the primitive Australian genus *Myrmecia* (Clark, 1951; Brown, 1953a); the ponerine tribes Amblyoponini, Platythyreini, Ectatommini, and Typhlomyrmecini (Brown, 1960a, 1965, and included references); the genus *Ponera* (Taylor, 1967); the New World doryline army ants (Borgmeier, 1955); the doryline army ants of Asia and Australia (Wilson, 1964); the myrmicine harvesting ants of the genus *Pogonomyrmex* in North America (Cole,

*The massive work in which Wheeler's articles appear (*Bull. Amer. Mus. Nat. Hist.*, 45: 1-1139; 1922), along with contributions on the biology of African ants by I. W. Bailey, J. C. Bequaert, W. M. Mann, and F. Santschi, is lightly referred to by ant taxonomists as the Congo Bible.

1968); most sections of the large myrmicine tribe Dacetini (Brown, 1948, 1952, 1953c,d, 1959, 1964a, and contained references); the myrmicine tribes Solenopsidini (Ettershank, 1966) and Basicerotini (Brown and Kempf, 1960); the fungus-growing myrmicine genera *Atta* (Borgmeier, 1959), *Mycocepurus* (Kempf, 1963), and *Cyphomyrmex* (Kempf, 1965); the myrmicine tribe Cephalotini (Kempf, 1951, 1958); the Aneuretinae (Wilson *et al.*, 1956); the myrmicine genus *Crematogaster* of North America (Buren,

1958, 1968b); the dolichoderine genus *Monacis* (Kempf, 1959); and the formicine genera *Notoncus* (Brown, 1955a), *Lasius* (Wilson, 1955a), and *Acanthomyops* (Wing, 1968). Ant larvae have been systematically described by G. C. and Jeanette Wheeler (1951–1965 and included references). The generic characteristics of male ants in the North American fauna have been treated by M. R. Smith (1943). These studies, along with other, smaller revisions too numerous to list here, cover only a small part of the



FIGURE 4-8. A worker of the primitive ant *Amblyopone australis* stands over a pupa (enclosed in its cocoon) and an assortment of eggs and larvae. The broad posterior attachment of the petiole (a primitive trait) and heavy, elongate mandibles (an advanced trait) can be seen clearly in this individual. In the upper left and lower right corners of the photograph, larvae feed by thrusting their mandibles directly into the bodies of the insect prey (photograph courtesy of R. W. Taylor).

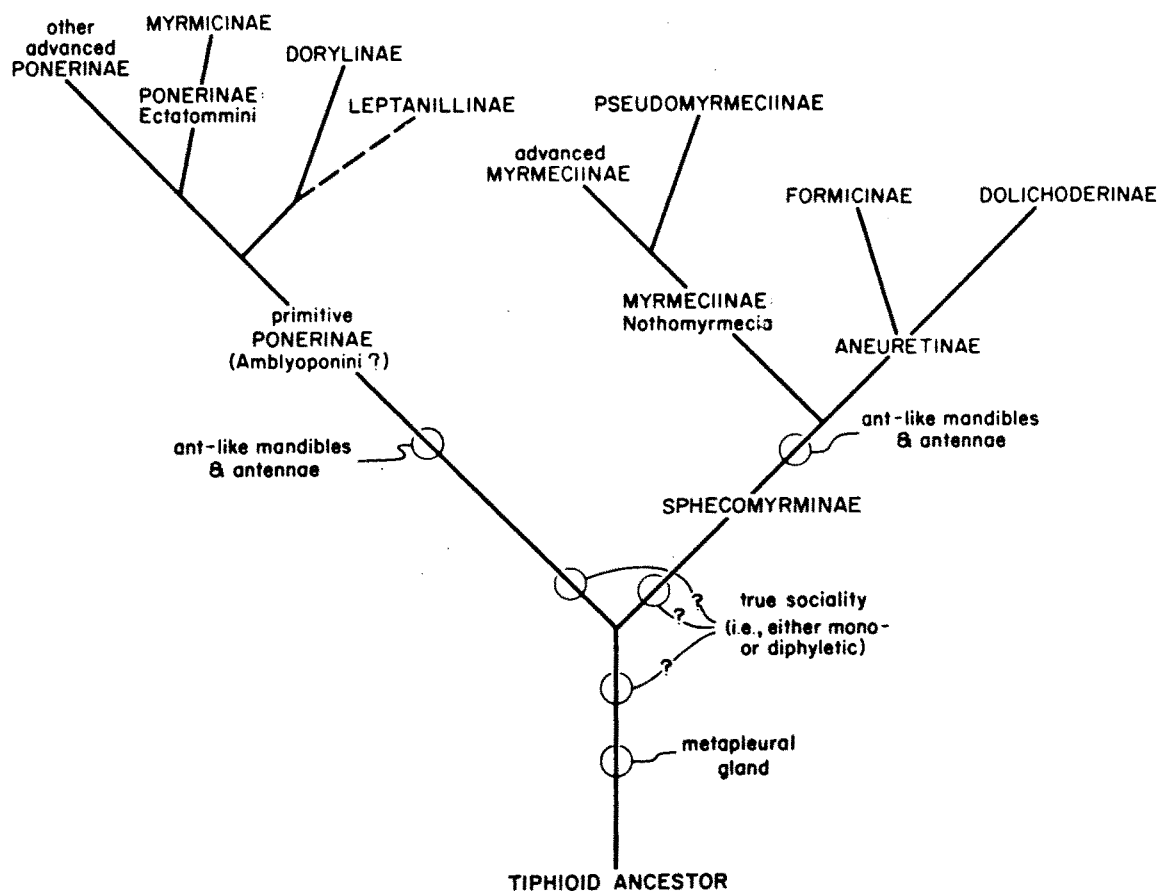


FIGURE 4-9. Phylogenetic diagram of the simple branching form, showing the inferred relationships of the subfamilies of ants. The possible dual origin of eusociality during the early evolution of the ants is indicated (from Wilson, Carpenter, and Brown, 1967a).

world fauna. The tropical groups are especially poorly known. A key to the genera of the world has been presented by Wheeler (1922), who based it in large part on Carlo Emery's earlier key (1902) and genus-level review in the *Genera Insectorum* (1910–1925), but it is cumbersome in use and has grown increasingly out of date. The cytotaxonomy of ants, which is a young but potentially very important subject, has been reviewed by Elisabeth Hauschteck (1963) and Crozier (1968). A perceptive and entertaining history of ant taxonomy has been written by Brown (1955b).

Culturing and Observational Techniques

The culture and study of ants in the laboratory is a simple operation. Colonies of many species can be main-

tained in nothing more than a bottle containing the natural nesting material (for example, soil or decaying wood) or even a thick pad of moist paper or cotton. Ants are generally very adaptable and will conduct most of their normal activities under conditions more favorable to the observer than to them. Ideally, however, the artificial nest should be constructed so that the dimensions and microclimate of the nest chambers closely simulate those in the wild, the brood chambers should be kept dark or in red light, and the colonies should have a constant food source in a foraging arena apart from the nest. Some species require special food. Many dacetine species, for example, accept only collembolans, while fungus-growing ants need to be provided with substratum suitable for culturing their special kinds of fungi. A variety of culturing methods adaptable to most kinds of ants are described in the

popular books by Wheeler (1910) and Skaife (1961). Freeland (1958) invented an excellent vertical observation nest for *Myrmecia* and other very large ants. Wilson (1962a) designed a plastic nest which serves for the simultaneous observation of large colonies inside and outside the nest during foraging activity. A completely defined synthetic diet for ants has been invented by Ettershank (1967), while diets and several mass culturing techniques for various ant species have been reviewed by Carney (1970).

The Natural History of the Primitive Ants of the Genus *Myrmecia*

The "bull-dog ants" of the genus *Myrmecia* have proven to be exceptionally rewarding subjects for the study of social biology in several respects. They are among the largest ants, workers ranging in various species from 10 to 36 mm in length, and yet are easy to culture in the laboratory. They are also, next to *Nothomyrmecia* and

perhaps *Amblyopone*, the most primitive of the living ants. The first encounter with foraging *Myrmecia* workers in the field in Australia is always a memorable experience for an entomologist. One gains the strange impression of a wingless wasp just on its way to becoming an ant: "In their incessant restless activity, in their extreme agility and rapidity of motion, in their keen vision and predominant dependence on that sense, in their aggressiveness and proneness to use the powerful sting upon slight provocation, the workers of many species of *Myrmecia* and *Promyrmecia* show more striking superficial resemblances to certain of the Myrmecidae or Mutillidae than they do to higher ants" (Haskins and Haskins, 1950a). According to Brown (1953a), *Myrmecia* and *Promyrmecia* should be joined on morphological grounds into a single genus. Thus enlarged, *Myrmecia* contains approximately 120 species, all of which are limited to Australia except for a single representative on the island of New Caledonia (*M. apicalis*).

Through the efforts of Wheeler (1933a), Clark (1934 and

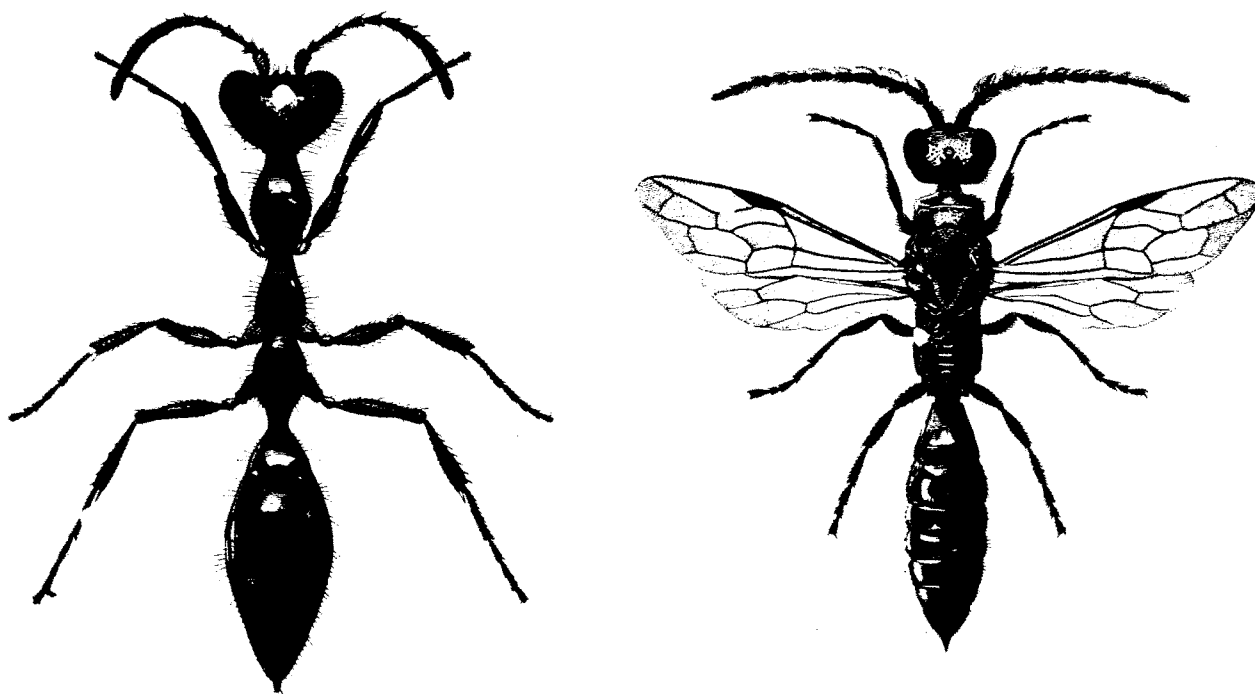


FIGURE 4-10. Adults of the tiphid wasp *Methocha fimbriicornis* (left, female; right, male), a representative of the living genus of nonsocial wasps that bear the closest resemblance to *Sphecomyrma freyi* and through it to the more advanced ants of the myrmecioid complex. This species occurs in the Philippine Islands (from F. X. Williams, 1919).