Commentary

In search of ant ancestors

Ted R. Schultz*

Department of Entomology, MRC 188, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560-0188

Ants are arguably the greatest success story in the history of terrestrial metazoa. On average, ants monopolize 15–20% of the terrestrial animal biomass, and in tropical regions where ants are especially abundant, they monopolize 25% or more. But ants did not always run the world. They do not appear in the fossil record until the mid-Cretaceous, and for more than the first half of their history—a period spanning 60 to 80 million years—ants occupied a relatively modest position in the terrestrial biosphere. To understand the factors, both ecological and historical, that contributed to the rise of the ants, we require a clearer picture of the stepwise evolution of the major ant lineages. Now, Grimaldi and Agosti (1) report in a recent issue of PNAS the remarkable discovery of a worker ant, preserved in amber for over 90 million years, that is clearly assignable to a modern ant subfamily that contains many familiar extant species, including carpenter ants. Combined with other paleontological and phylogenetic information, this unexpected fossil strongly indicates that the diversification of many ant subfamilies occurred earlier and more rapidly than previously suspected.

Ants represent the family Formicidae in the insect order Hymenoptera and, like the yellow jackets, hornets, and paper wasps to which they are closely related, ants are stinging wasps. All ants are eusocial, that is, they live in colonies in which a wingless neuter daughter caste cooperates to raise subsequent generations of their mother queen's offspring. Like all of its descendants, the ancestral ant was almost certainly eusocial, with colonies made up of small bands of hunter–gatherers living in simple temporary nests in the soil. From this modest beginning arose the current diversity of the family Formicidae, numbering over 9,500 described species and an estimated 3,000 to 9,000 additional species as yet unknown to science. Today ants occupy keystone positions in most terrestrial environments, serving as major conduits of energy and organic material. They are, for example, important turners of the soil, matching or exceeding the activity of earthworms in this role. They are among the leading predators of invertebrates in most ecosystems, and in the Neotropics they are the leading herbivores as well, with leaf-cutter ants taking more than 15% of the fresh vegetation (feeding it

to a symbiotic fungus, which they in turn eat). Interactions with ants have shaped the evolution of diverse organisms to an astonishing degree. Ants participate in symbioses—some facultative, some obligate—with over 465 plant species in over 52 families (2), with thousands of arthropod species (3, 4), and with as-yet-unknown numbers of fungi and microorganisms (5, 6). Clearly, the study of most ecosystems must include the study of the resident ant species. Because of their complex colony-level behaviors, ants serve as model organisms for the highly visible disciplines of behavioral ecology and sociobiology, particularly in studies focused on the dynamics of kin selection, within-colony conflicts of interest, caste differentiation, and division of labor.

Given the strong interest in ants from a range of biological disciplines, it is especially important that we understand the unique evolutionary history of this group. Fortunately, during the last decade, a solid foundation has been established for ant systematics and, indeed, for ant biology in general by Hölldobler and Wilson (4) (exhaustive biological overview), Bolton (7, 8) (taxonomic catalog and genus-level keys), Ward *et al.* (9) (exhaustive bibliographic database), and Agosti *et al.* (10) (manual for using ants as bioindicators). During this same time period, partial progress toward reconstructing the subfamily-level phylogeny of ants has been achieved in studies using extant species (11–13), but these studies have been impeded by the lack of critically informative paleontological data.

Ant paleontology has evolved as a subdiscipline of ant systematics ever since the latter's origins in the mid-19th century. Among the first ant fossils to receive serious attention were those found in Baltic amber (14, 15), which we now know originated in the early Oligocene [≈30 million years ago (mya)]. Except for indicating that ant distributions have changed dramatically, the Baltic amber ant fossils are strikingly modern—so much so, in fact, that at least one author was inspired to suggest that they might be fakes (16). Most other significant sources of Tertiary ants reveal a similarly modern ant fauna, including the North American Florrisant (Colorado) and Green River (Wyoming) shales (Oligocene, ≈30 mya) (17), the Dominican amber (Miocene, ≈20 mya) (e.g., ref. 18), and others listed by

Grimaldi and Agosti (ref. 1, table 1). In the Eocene as in the present, ants comprise a significant proportion of the insect biota, and ant species are easily assigned to extant subfamilies and, in most cases, to extant genera as well. Whatever the story of the ants' rise to dominance, it obviously unfolded before the deposition of these Tertiary fossil remains.

In the absence of Cretaceous ant fossils, the quest for ant origins relied until recently on comparative studies of the morphology, behavior, and ecology of the likeliest "most primitive" extant species. Between 1951 and 1977, this quest drew a series of myrmecologists to Western Australia's outback in search of the ant-origin "holy grail," the species *Nothomyrmecia macrops*. Known from two imperfectly labeled worker specimens collected by members of a frontier excursion in 1931, *N. macrops* was subsequently declared the world's most primitive ant (19, 20). After years of failed efforts, living colonies were finally located in 1977 (21), and *N. macrops* quickly became one of the most studied ants on the planet.

Comparisons of *Nothomyrmecia* with plesiomorphic ("primitive") members of other ant lineages provided important hypotheses about the morphology of the earliest ants and, in 1966, ant systematists were able to test those hypotheses directly. In that year, two rock hounds, Mr. and Mrs. Edmund Frey, collected a relatively large piece of amber from a clay embankment in Cliffwood Beach, New Jersey. Although originating from a site that is, in modern times, less exotic than that of Dominican or even Baltic amber, the New Jersey amber is far older, most likely originating in the mid-Cretaceous Turonian stage (90–94 mya). Peering backward in time through a window polished in the Frey's amber nugget, Wilson *et al.* (22, 23) became the first myrmecologists to examine an ant from the Cretaceous, nearly three times as old as any previously known ant fossil. Subsequently named *Sphe-*

comyrma freyi and representing a new subfamily, the Sphecomyrminae, the New Jersey specimen was found to possess many (but not all) of the characters that had been predicted for a truly primeval ant. Unfortunately, some doubt remained about whether *S. freyi* was a true ant because of uncertainty about the presence of the antibiotic-producing metapleural gland, a defining feature of ants.

Despite this discovery, the New Jersey amber remained understudied for nearly 20 years until in 1986 D. Grimaldi took up the task, aided by a number of fossil collectors and American Museum of Natural History volunteers. As a result, Grimaldi *et al.* (13) described additional specimens of *Sphecomyrma,* including a winged male, and banished lingering doubts about the formicid affiliations of *S. freyi* by confirming the presence of a metapleural gland. Four genera and eight species of the Sphecomyrminae are now known from New Jersey, Siberian, and Canadian Cretaceous ambers, including *Cretomyrma* (two species), *Dlusskyidris* (one species), *Baikuris* (three species based on males), and *Sphecomyrma* (two species). From this fossil record, we may conclude that "the most primitive known group of ants, the Sphecomyrminae, lived over much of the Northern hemisphere during middle and late Cretaceous times" (24). A possibly earlier ant, *Cariridris,* tentatively assigned to the subfamily Myrmeciinae (represented today by the Australian bulldog ants and *Nothomyrmecia*), has been described from the Brazilian Aptian (110 mya) (13, 25). Earlier fossils in the family Armaniidae may or may not be ants (13, 26, 27); they are treated as a linking form between ants and other stinging wasps by Grimaldi and Agosti (ref. 1, figure 2).

After the discovery of *Sphecomyrma*, it was generally believed that the major lineages of ants (i.e., the subfamilies) must have arisen gradually during the interval between 90 and 50 mya, i.e., during the time frame bounded by the *Sphecomyrma* fossils on the one hand and by the Eocene ant fossils on the other. By demonstrating that the subfamily Formicinae was contemporaneous with the Sphecomyrminae, however, Grimaldi and Agosti (1) render this view untenable. In fact, because of Grimaldi *et al.* (13), we know that the extant subfamily Ponerinae was also contemporaneous; more doubtfully, the Dolichoderinae (28) and the Myrmeciinae (25) may have been present. This unexpected information allows the assignment of minimum dates to several of the most basal nodes of the cladogram for the family Formicidae (ref. 1, figure 2) and thus provides a calibrated standard for future ant systematic research. Combined with additional fossil data and phylogenetic information for the Hymenoptera, this information also permits the plausible dating of the origin of ants. Grimaldi and Agosti (1), Agosti *et al.* (29), and Grimaldi *et al.* (13) argue convincingly that the ancestral ant diverged from aculeate wasp during the Cretaceous, no earlier than 140 mya, and more likely between 110 and 130 mya, for the following reasons: (*i*) Ant-like fossils (including the Armaniidae) originating before 115 mya are entirely unknown; (*ii*) the oldest known hymenopteran fossils date from the Triassic and are represented solely by the most plesiomorphic hymenopteran family, the Xyelidae; (*iii*) the earliest aculeate fossils, representing the most primitive stinging wasps, appear in the late Jurassic; and (*iv*) there is strong fossil evidence for a Cretaceous origin for the Vespidae, which, together with the Scoliidae and the Bethylidae, is the most likely sister group to the ants. The only dissenting opinion, that of Crozier *et al.* (30) for a Jurassic ant origin based on a molecular clock, has been questioned by Grimaldi *et al.* (13) and Rust and Andersen (31).

As pointed out earlier, Grimaldi and Agosti's (1) conclusion that at least some ant subfamilies diverged before 90 mya suggests a diversification of major ant body plans during the first 30 million years of ant evolution; the rarity of ant fossils of this age relative to those of other insects implies, however, that this diversification of form was not accompanied by an increase in ecological dominance (ref. 1, table 1). In contrast, by the mid-Eocene (roughly 50 mya), ants had achieved their current levels of abundance, with nearly all extant subfamilies and many extant genera in place. This increase in abundance suggests an explosive radiation of ants during the second third of their history.

What ecological and historical factors account for these two broad phases of ant diversification, the first resulting in the principal morphological differences between major lineages, and the second resulting in ecological dominance? This question will be answered only when reliable paleoecological data are combined with a well-supported phylogeny. Ideally, this phylogeny must incorporate character data from a variety of sources, including DNA sequences of extant ant species and morphological characters of both extant and fossil forms. Only fossil information, however, permits the assignment of minimum dates to the internal nodes of the phylogeny—even molecular dating techniques must be calibrated by paleontological data. Indeed, since the discovery of *S. freyi,* fossils have played an increasingly influential role in ant phylogenetics. In the last 6 years, the standard-reference cladogram proposed in 1994 by Baroni Urbani *et al.* (11) has been revised twice because of new fossil data (1, 13) and once because of the discovery of an enigmatic extant species (12). We can only hope that this cycle of discovery and revision will continue or even accelerate, so that our current clouded picture of ant phylogeny will come increasingly into focus—in much the same way, perhaps, that the initially vague but evocative form of a Cretaceous ant becomes progressively clearer when a nugget of amber is painstakingly prepared and polished by D. Grimaldi and colleagues.

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