

# The Phylogeny and Evolution of Ants

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## Keywords

Formicidae, fossil record, long-branch attraction, process heterogeneity, convergence, divergence

## Abstract

Originating most likely in the early Cretaceous, ants have diversified to become the world's most successful eusocial insects, occupying most terrestrial ecosystems and acquiring a global ecological footprint. Recent advances in our understanding of ant evolutionary history have been propelled by the use of molecular phylogenetic methods, in conjunction with a rich (and still growing) fossil record. Most extant ants belong to the formicoid clade, which contains ~90% of described species and has produced the most socially advanced and dominant forms. The remaining ants are old lineages of predominantly cryptobiotic species whose relationships to one another and to the formicoids remain unclear. Rooting the ant tree is challenging because of (*a*) a long branch separating ants from their nearest outgroup, and (*b*) heterogeneity in evolutionary rates and base composition among ant lineages. These factors will need to be given careful consideration in future phylogenomic studies of ants.

## INTRODUCTION

Eusociality, a state of cooperation involving overlapping generations, collective care of the young, and reproductive division of labor, has evolved in relatively few animal groups, most notably in the Hymenoptera (ants, bees, and wasps) and the Blattodea (cockroaches) (Wilson 1971, Inward et al. 2007). By most measures the ants (Hymenoptera: Formicidae) represent the most successful of all such experiments in eusocial life. They have diversified into tens of thousands of species, colonized most of the world's terrestrial ecosystems, and acquired multifarious ecological roles. Ants have a significant impact on populations of other organisms through their varied activities as scavengers, predators, seed harvesters, honeydew feeders, herbivores, and ecosystem engineers (Hölldobler & Wilson 1990, Folgarait 1998, Lach et al. 2009). In some tropical forests the biomass of ants exceeds that of terrestrial vertebrates severalfold (Fittkau & Klinge 1973), and ants are the dominant consumers of plant resources in the canopy of lowland rainforests (Davidson et al. 2003). Many ant species have developed symbiotic relationships with other life-forms, participating in a complex web of interactions with microbes, fungi, plants, and other animals (Hölldobler & Wilson 1990, Davidson & McKey 1993, Mueller et al. 2001, Russell et al. 2009).

There are approximately 13,000 described species of ants (AntCat 2014), but the actual number of extant species may well be two or three times this. We are far from having a complete inventory at the species level: Numerous ant species remain undiscovered and/or undescribed, especially from tropical regions, and many of the larger ant genera are in a state of taxonomic disarray (Ward 2007). This review focuses on the major lineages of ants and summarizes our current understanding of their evolutionary history. In contrast to species-level taxonomy, progress on the higher-level phylogeny of ants has been rapid in recent years, although there are still some thorny issues remaining to be resolved. This is a fast-moving field, and with the increasing use of genomic data in phylogeny estimation (Lemmon & Lemmon 2013) we can expect to see further advances in our knowledge in the near future.

## HISTORICAL CONTEXT: ANTS AS MODIFIED WASPS

### Hymenopteran Heritage

Ants are members of the order Hymenoptera, a large and successful group of haplodiploid insects, comprising wasps and their derivative cousins, the ants and bees. The oldest lineages of Hymenoptera are a series of broad-waisted wasps, the “Symphyta,” that are predominantly phytophagous and relatively species-poor (Huber 2009). Most hymenopteran diversity resides in a large clade known as the Apocrita, which arose within a subgroup of symphytans, probably in the Triassic or early Jurassic (Rasnitsyn 1975, Ronquist et al. 2012). Characterized by the fusion of the first abdominal segment to the thorax and the presence of a strong constriction between the first and second abdominal segments, the Apocrita include an enormous variety of parasitoid and predatory wasps, as well as some plant-feeding taxa (Gauld & Bolton 1988).

The reconfiguration of body segments in this group is associated with considerable dexterity of abdominal movement. This may have been of particular importance in one subclade of Apocrita, the Aculeata, in which the ovipositor was modified into a stinging device used to inject paralyzing venom into hosts or prey and to defend against enemies. The aculeate Hymenoptera include various parasitoids and cleptoparasites (such as cuckoo wasps, bethylids, tiphiids, scoliids, and mutillids), and several groups of predatory wasps (such as vespids, spider wasps, and spheciform wasps) that show variable nesting and social behavior (Gauld & Bolton 1988). It is within the aculeate Hymenoptera that ants and bees evolved.

## The Closest Relatives of Ants

There is compelling morphological and molecular evidence for the monophyly of ants (Brothers 1975, Bolton 2003, Brady et al. 2006, Moreau & Bell 2013), but until recently their relationship to other groups of aculeate Hymenoptera was unclear. The conventional view was that ants evolved from a nonsocial parasitoid wasp (Wheeler 1928, Wilson 1971, Dlussky 1983), perhaps similar in biology to the extant tiphoid wasp *Methoca*, which parasitizes tiger beetle larvae (Wilson et al. 1967). Morphological cladistic studies of the Aculeata by Brothers (1975, 1999) suggested that ants are sister to a clade comprised of two groups with contrasting biology: (a) scoliid wasps, which are ectoparasitoids on subterranean beetle larvae, and (b) vespids, which are mostly predatory nest-building wasps (such as potter wasps and yellow jackets), and include both solitary and eusocial species (Gauld & Bolton 1988). In some of the analyses by Brothers the ants were recovered as sister to the family Bradynobaenidae, a rather obscure group of wingless female wasps, whose biology is almost unknown but which are presumed to be parasitoids of other arthropods.

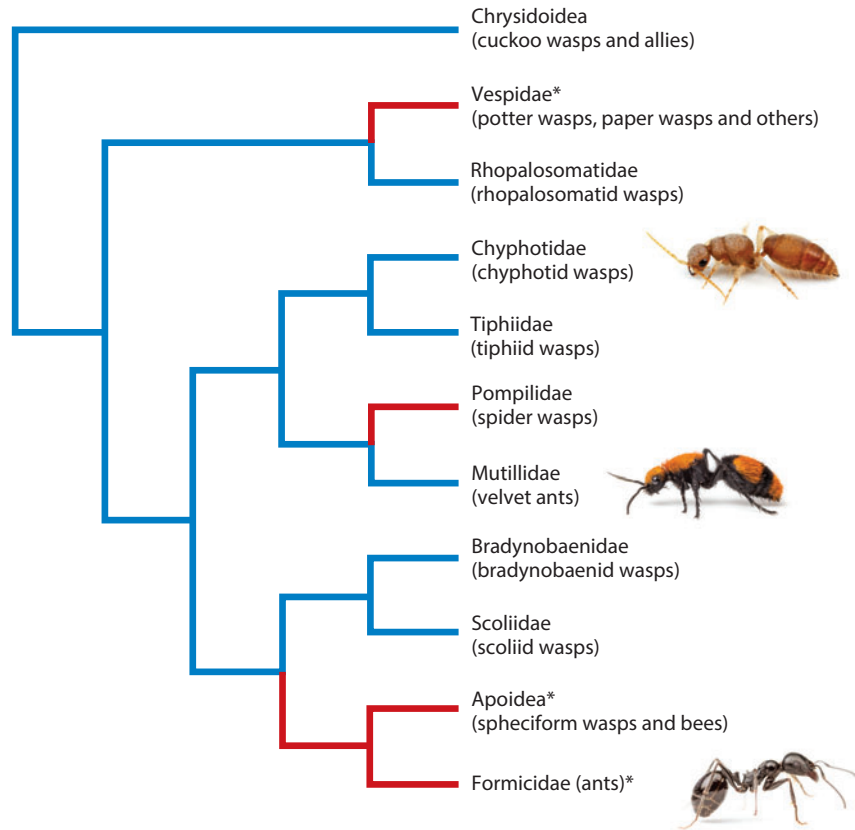
Molecular phylogenetic analyses have produced contradictory conclusions about aculeate relationships, with ants being positioned as sister to apoidea and scolioid wasps (Scoliidae and Bradynobaenidae) (Pilgrim et al. 2008, Debevec et al. 2012), sister to scolioid wasps only (Wilson et al. 2013), sister to a diverse group of mostly ectoparasitoid wasps in the tiphoid-pompiloid complex (Heraty et al. 2011), or sister to the small ectoparasitoid family Rhopalosomatidae (Klopfstein et al. 2013). These investigations have been based on a relatively small number (3–7) of gene fragments, with apparently limited power to recover some relationships within the Aculeata.

A recent phylogenomic study (Johnson et al. 2013) based on several hundred genes generated a well-resolved and strongly supported phylogeny of the major lineages of Aculeata (**Figure 1**). Among the primary conclusions are that vespid wasps are not closely related to ants or scoliids; bradynobaenids are nonmonophyletic, with true bradynobaenids being sister to scoliids and other bradynobaenid-like taxa being members of the tiphoid complex; and the closest relatives of ants are the spheciform wasps and bees, known collectively as the Apoidea (Johnson et al. 2013). If these results hold up under more extensive taxon sampling (Danforth 2013), then they suggest that the early branching lineages of Apoidea, represented by solitary wasps such as mud daubers (Sphecidae) and cockroach wasps (Ampulicidae), might provide greater insight into the origin of ants than the ectoparasitoid wasps, such as scoliids, bradynobaenids, and tiphoids, to which ants were thought to be more closely related (Wilson 1971, Dlussky 1983, Brothers 1999).

## Comparisons with Apoidea

Spheciform wasps capture and paralyze arthropod prey and transport the food items to a nest or cavity. Some species of the sphecid genus *Chorion* have parasitoid-like habits, abandoning the host after paralysis without placing it in a nest (Bohart & Menke 1976). This is presumably a secondary condition, but it does emphasize that there is a rather fluid boundary between parasitoid behavior and predation. Nest construction and food provisioning have long been considered important prerequisites for the evolution of eusociality, which is restricted within the Hymenoptera to three lineages possessing these characteristics: vespid wasps, ants, and Apoidea (Wilson 1971, Gauld & Bolton 1988). All ants are eusocial, but this is true of only some members of the vespid and apoid clades. The finding that ants and Apoidea are each other's closest relatives suggests that the nesting and food collection habits favorable to eusociality arose only once in their common ancestor, rather than separately in ectoparasitoid predecessors (Johnson et al. 2013).

Ants possess several traits that are not characteristic of Apoidea, including an apterous worker caste, the shedding of wings by colony-founding queens and subsequent feeding of larvae on the products of flight muscle histolysis, the rearing of young in communal brood chambers, and



**Figure 1**

A phylogeny of the aculeate Hymenoptera, derived from analysis of a 308-gene data matrix (Johnson et al. 2013). In this study all nodes had strong support, with Bayesian posterior probabilities of 1.00 and maximum likelihood bootstrap percentages of 100. Placement of Rhopalosomatidae is based on studies by Pilgrim et al. (2008) and Debevec et al. (2012). Blue branches indicate parasitoidism, the ancestral condition for Aculeata; red branches indicate nest construction and prey transport. Clades containing eusocial species are marked with an asterisk. Chyphotid wasps (formerly in Bradynobaenidae) and velvet ants are superficially similar to ants but not closely related. Images copyright of Alex Wild, used with permission.

progressive provisioning of food items to the larvae (Wilson 1971). Spheciform wasps and bees, both solitary and eusocial, retain wings as adults, usually rear young in separate cells, and often mass provision (Matthews 1991). These contrasts need to be considered in any attempt to infer the sequence of events involved in the transition to eusociality in ants.

Independent colony foundation by single queens is prevalent in ants and evidently represents the ancestral condition (Cronin et al. 2013, Keller et al. 2014). Together with the observation that all ant larvae are progressively provisioned, these natural history features support the hypothesis that ants achieved eusociality via the “subsocial route” (Wilson 1971), in which a nesting female engaged in extended parental care to the point where there was overlap between mother and adult offspring—with the latter then having an opportunity to forego reproduction and assist their mother in further offspring production. Under this scenario reproductive altruism in ants evolved among female siblings of high relatedness, probably offspring of a monandrous female (Hughes et al. 2008), consistent with a strong role for kin selection (Bourke 2011). A comparable situation

probably applies to most eusocial lineages of Apoidea. Ant eusociality has its own peculiarities, however, which undoubtedly influenced the direction of ant evolution. Wing shedding by queens and the deployment of an apterous worker caste, for example, would have given the first ants access to a range of cryptic nest sites and hidden food items not available to their winged wasp relatives, perhaps leading to a stronger propensity to nest and forage in the soil (Lucky et al. 2013). Another unique feature of ants, the metapleural gland, produces secretions with antibacterial activity. This is thought to have facilitated nesting in moist, pathogen-rich environments (Wilson 1987), although other functions of the gland cannot be ruled out (Yek & Mueller 2011). Ants further diverged from their wasp ancestors with the acquisition of serially dentate mandibles and geniculate (elbowed) antennae, which, it has been argued, aided in nest building and manipulation of small objects (food particles and brood) in the communal nest chamber (Dlussky 1983).

## INFERRING THE ANT TREE OF LIFE

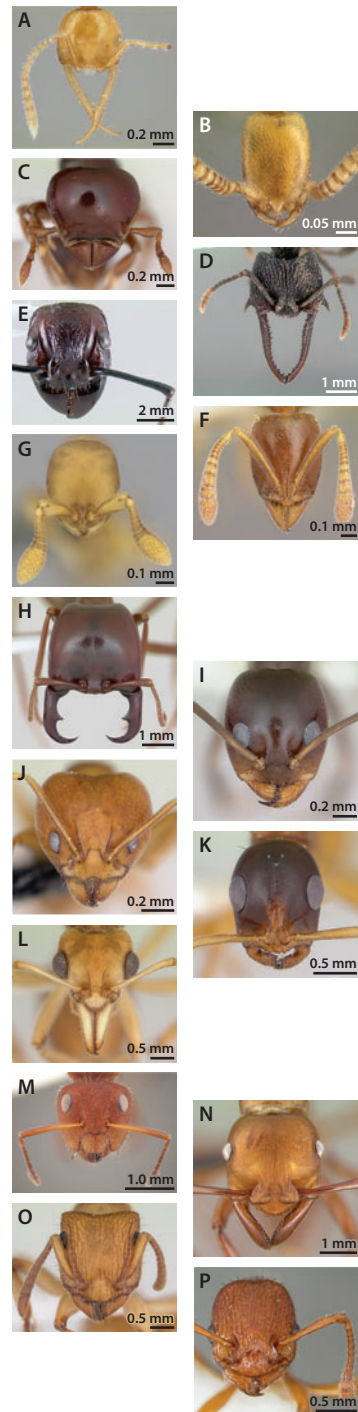
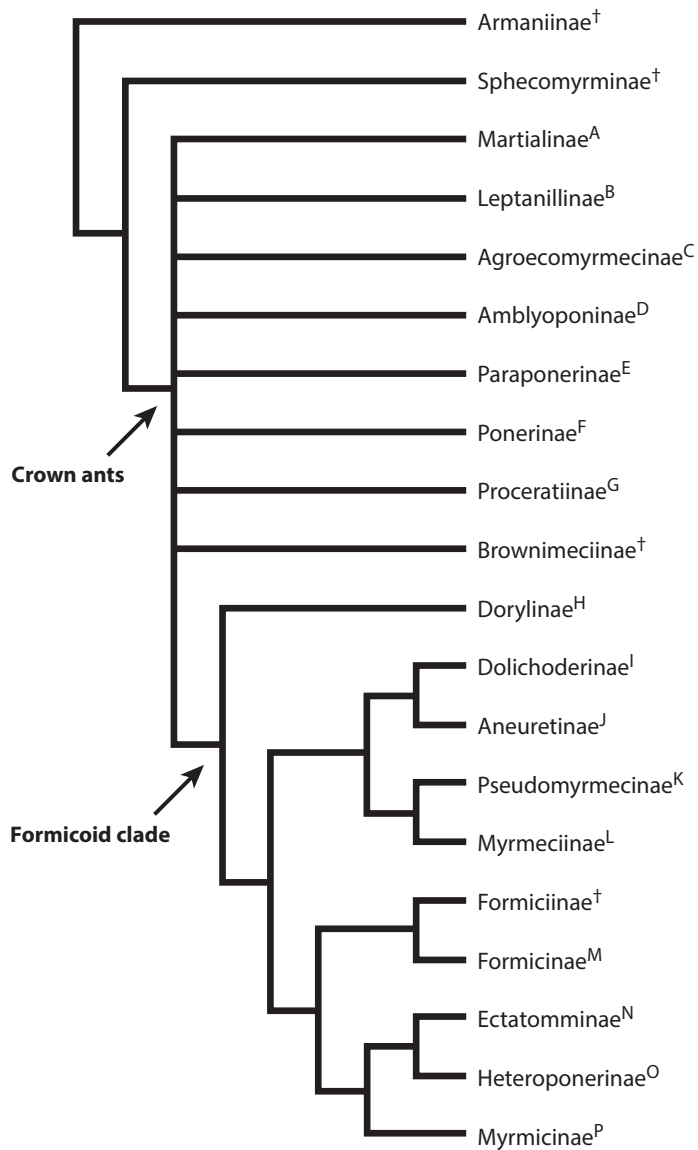
### Phylogenetic Relationships Among the Major Ant Lineages

The internal phylogeny of ants has been a matter of debate for many decades. Until about ten years ago the arguments were primarily based on evidence derived from external morphology (e.g., Brown 1954, Wilson et al. 1967, Taylor 1978, Baroni Urbani et al. 1992, Ward 1994, Grimaldi et al. 1997). Such studies helped to delimit major lineages of ants, i.e., subfamilies and tribes, but they did not produce a consensus on the relationships among those lineages (Ward 2007). Different approaches and character systems yielded contradictory results, and the higher classification of ants varied accordingly. Even the few studies based on quantitative cladistic analysis of large morphological data sets generated trees in which most nodes, except those subtending well-defined subfamilies, had weak support.

Just before ant molecular phylogenetics began to gather momentum, Bolton (2003) published a landmark reclassification of ants. Solely based on morphology and lacking an explicit phylogenetic analysis, this study nevertheless synthesized a large body of information on morphological variation in ants, recognized the artificiality of certain higher taxa, especially the subfamily Ponerinae as then circumscribed, and proposed a series of smaller, better defined subfamilies. This monograph came at an opportune time, providing a framework for taxon sampling and hypothesis testing in subsequent studies.

The past decade has seen substantial progress in illuminating the broad outlines of ant evolutionary history, largely due to the use of molecular phylogenetic approaches (Moreau 2009, Ward 2011), but also aided by Bolton's (2003) synthesis and by new fossil discoveries (LaPolla et al. 2013). From molecular studies there has emerged unanimous support for a large group of ants known as the formicoid clade (Saux et al. 2004, Ward & Downie 2005, Brady et al. 2006, Moreau et al. 2006, Moreau & Bell 2013), containing about 90% of all known ant species and 9 of the 16 extant subfamilies (AntCat 2014, Brady et al. 2014) (**Figure 2**). This clade includes three exceptionally species-rich subfamilies, Dolichoderinae, Formicinae, and Myrmicinae, as well as the army ants and their relatives (Dorylinae, formerly the dorylomorph clade), bulldog ants (Myrmecinae), big-eyed arboreal ants (Pseudomyrmecinae), and three smaller groups. Accompanying this taxonomic variety is also a great diversity in nesting, feeding, and social behavior (Ward 2009) (**Table 1**). Most of the “movers and shakers” in the ant world belong to the formicoid clade. It has produced the most socially advanced species and those that tend to dominate—numerically and behaviorally—in ant communities.

All of the formicoid subfamilies, originally delimited on the basis of morphology alone (Bolton 2003), are strongly supported as monophyletic by the molecular data, a pleasing concordance



between two disparate lines of evidence. Morphology could not fully clarify relationships among the subfamilies, but that knowledge gap has been filled by analysis of DNA sequence data (**Figure 2**). Some of these findings, such as the Pseudomyrmecinae/Myrmeciinae and Dolichoderinae/Aneuretinae clades and a close relationship of Myrmicinae to Ectatomminae, had been proposed in a seminal paper by the renowned ant taxonomist William L. Brown, Jr. (1954). Brown's ruminations were intuitive and nonquantitative—and even somewhat ambiguous because of his acceptance of paraphyletic groups (Keller 2011)—yet in some respects they turned out to be more accurate than later quantitative cladistic analyses based on large morphological data sets (Ward 1990, Baroni Urbani et al. 1992, Grimaldi et al. 1997, Keller 2011).

Despite overwhelming molecular support for the formicoid clade there is no known morphological synapomorphy of the group, and the clade was never recovered in any of the phylogenetic analyses based on morphology. Recently it has been proposed that a duplication in the Vitellogenin (Vg) gene, and associated caste- and behavior-specific expression of the paralogs, is a synapomorphy of the formicoids (Corona et al. 2013, Oxley et al. 2014). This duplication has been detected in several formicoids (from four subfamilies) whose genomes have been sequenced and is absent in the one nonformicoid ant that has been examined. This is an exciting finding, and if additional sampling confirms absence of the duplication in nonformicoids, then it suggests a possible link between gene duplication and the evolutionary success of the formicoid clade.

What of the remaining 10% of ant diversity? This is comprised of several groups whose relationships to one another and to the formicoids are somewhat uncertain (Ward 2009) (**Figure 2**). The bulk of this diversity is contained within a group of five subfamilies known collectively as the poneroids: Agroecomyrmecinae, Amblyoponinae, Paraponerinae, Ponerinae, and Proceratiinae. Many of these are biologically cryptic species, living in soil or leaf litter, with relatively simple social organization (Wilson & Hölldobler 2005) (**Table 1**). The members of the subfamily Ponerinae have amassed considerable diversity, however, and some species are conspicuous and aggressive predators (Schmidt & Shattuck 2014). In molecular studies the poneroids appear as either a clade, sister to the formicoids, or a paraphyletic group within which the formicoids arise (Brady et al. 2006, Moreau et al. 2006, Rabeling et al. 2008, Kück et al. 2011, Moreau & Bell 2013).

There are two other groups of nonformicoid ants: the Leptanillinae are a small clade of pale, blind subterranean ants (Bolton 1990); and the subfamily Martialinae is represented by a single recently discovered species, *Martialis heureka*, also with blind workers and presumed to be subterranean, and known from only two collections from Manaus, Brazil (Rabeling et al. 2008). These two lineages have vied for the position of sister group to all other ants. Different analyses of the same molecular data set have come to opposite conclusions (Rabeling et al. 2008, Kück et al. 2011), and analysis of a larger data set yielded an ambiguous outcome (Moreau & Bell 2013).

## Rooting the Ant Tree

We are faced, then, with continuing uncertainty about the relationships among early branching lineages of ants, including the placement of the root. In the first comprehensive molecular

### Figure 2

The ant tree of life: a summary of well-supported relationships among the ant subfamilies, based on molecular phylogenetic analyses by Brady et al. (2006, 2014), Moreau et al. (2006), Rabeling et al. (2008), Kück et al. (2011), Moreau & Bell (2013), and Ward et al. (2014). Relationships among extant taxa are supported by Bayesian posterior probabilities in the range of 0.91–1.00 (mostly 1.00). Fossil taxa (†) are placed provisionally, based on Lutz (1986), Grimaldi et al. (1997), Dlussky (1999), Ward & Brady (2003) and Bolton (2003). The head of a worker ant is depicted for each extant subfamily. Images reprinted from AntWeb ([www.antweb.org](http://www.antweb.org)) with permission.



**Table 1 Diversity, distribution, and biology of extant ant subfamilies**

Taxon	# spp.	Known distribution	Biology
<b>Martialine clade</b>			
Martialinae	1	Brazilian Amazon	Unknown; assumed to be hypogeic and specialist predator (Rabeling et al. 2008)
<b>Leptanilline clade</b>			
Leptanillinae	59	Paleotropical	Hypogeic; specialist predators; some have army ant–like behavior
<b>Poneroids</b>			
Agroecomyrmecinae	2	Neotropical, Afrotropical	Hypogeic and epigeic; feeding habits unknown, likely specialist predators
Amblyoponinae	125	Widespread	Hypogeic; specialist predators
Paraponerinae	1	Neotropical	Epigeic; generalist predator and scavenger
Ponerinae	1155	Widespread, mostly tropical	Hypogeic and epigeic; mostly predators, both generalist and specialist
Proceratiinae	135	Widespread, mostly tropical	Hypogeic; specialist predators
<b>Formicoid clade</b>			
Aneuretinae	1	Sri Lanka	Epigeic; generalist predator and scavenger
Dolichoderinae	706	Widespread	Mostly epigeic; generalist predators and scavengers
Dorylinae	677	Widespread, mostly tropical	Hypogeic and epigeic; predators, especially of other ants; includes army ants
Ectatomminae	267	Neotropical, Australian	Epigeic; mostly generalist predators and scavengers
Formicinae	3007	Widespread	Mostly epigeic; generalist predators and scavengers, some granivores
Heteroponerinae	24	Neotropical, Australian	Epigeic; generalist predators and scavengers
Myrmeciinae	92	Australian	Epigeic; generalist predators and scavengers
Myrmicinae	6440	Widespread	Mostly epigeic; generalist and specialist predators, scavengers, granivores, herbivores
Pseudomyrmecinae	229	Widespread, mostly tropical	Epigeic; generalist predators and scavengers

“# spp.” refers to number of described extant species, taken from AntCat (2014). Hypogeic species are those that forage underground; epigeic species forage aboveground, on the soil surface and/or vegetation. Information on biology is from various sources, summarized by Hölldobler & Wilson (1990) and Brown (2000).

phylogenetic studies of ants (Brady et al. 2006, Moreau et al. 2006) the Leptanillinae emerged as “basal,” that is, sister to all other ants, with strong support under both maximum likelihood and Bayesian inference (this was before the discovery of *Martialis*). The poneroids were also a strongly supported clade, sister to the formicoids. Brady et al. (2006) argued, however, that the placement of Leptanillinae at the base of the ant tree could be an artifact of long-branch attraction (LBA) (Holland et al. 2003, Bergsten 2005), with the leptanilline clade being attracted to the long branch separating ants from their distant outgroups (Lartillot et al. 2007). When Brady et al. (2006) performed an analysis of the same data set with outgroups removed, the resulting unrooted tree differed in topology such that the leptanillines were clustered within the poneroids, as part of a bipartition separating poneroids and formicoids. Adding outgroups and rooting this tree in such a way as to make Leptanillinae sister to all other ants yielded a tree that could not be distinguished statistically, using the Shimodaira-Hasegawa (S-H) test (Shimodaira & Hasegawa 1999), from those in which the root was placed elsewhere within the poneroid cluster or on the branch separating poneroids and formicoids (Brady et al. 2006) (**Figure 2**). A more recent analysis, using



the S-H test on a data set with more taxa, but fewer genes, did detect significant support for a basal position of Leptanillinae and *Martialis* (Moreau & Bell 2013). In addition, Lucky et al. (2013) applied a likelihood mapping test with quartet puzzling (Strimmler & von Haeseler 1997) to the Brady et al. (2006) data set and also found strong support for a basal position of Leptanillinae. Thus the weight of evidence would seem to favor the hypothesis that Leptanillinae and *Martialis* are the earliest branching lineages of extant ants.

However, these statistical tests cannot overcome misleading signal due to phylogenetic artifacts. If there is heterogeneity of the substitution process (across sites or lineages) and if the employed models do not adequately capture this process heterogeneity, this can cause robust, statistically significant support for the wrong tree (Jeffroy et al. 2006, Lartillot et al. 2007). LBA has been implicated, for example, in the incorrect placement of nematodes at the base of the Bilateria (Philippe et al. 2005) and of monocots as sister to all other angiosperms (Stefanovic et al. 2004). In addition, data sets of limited size may yield spurious trees. One of the first empirical uses of the quartet puzzling likelihood mapping test gave strong support to a (Chelicerata + Myriapoda) clade within the Arthropoda (Strimmler & von Haeseler 1997), a hypothesis now disfavored in light of more extensive data (Rota-Stabelli et al. 2011).

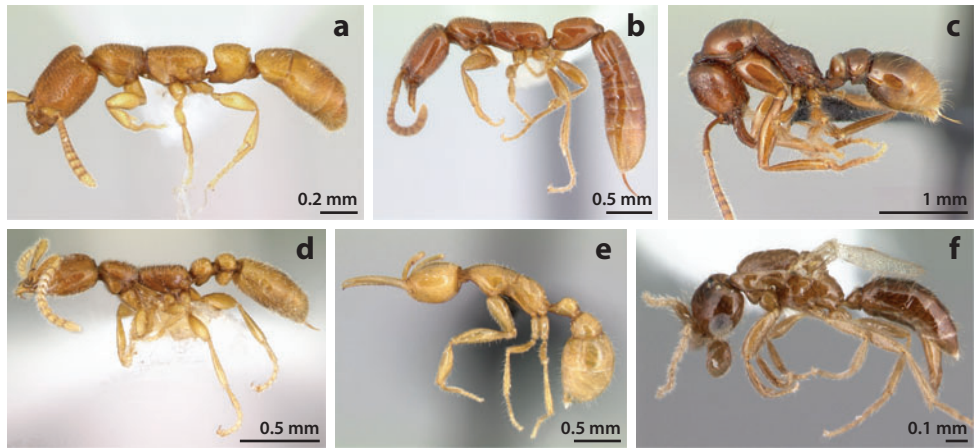
Another complicating factor is base frequency heterogeneity among lineages, which is prevalent in ants (Ward et al. 2010, Brady et al. 2014) and is known to mislead phylogenetic inference (Jeffroy et al. 2006, Rota-Stabelli et al. 2013). Compared with other aculeate Hymenoptera most ants tend to be GC (guanine-cytosine)-biased at third codon positions, whereas Leptanillinae are relatively AT (adenine-thymine)-rich (P.S. Ward, unpublished.). If the AT bias of leptanillines is a derived trait—possibly as a result of reduced selection for thermostability in their cool subterranean habitats—this could bias results in favor of a basal position for the group.

There are interesting parallels with attempts to root the tree of placental mammals. As with the ants there is compression of early branching events (in the Cretaceous), and the in-group is separated by a relatively long branch from the closest extant relatives. Rooting of the mammalian tree has been shown to be sensitive to taxon and gene sampling, choice of substitution model (Morgan et al. 2013), and base frequency heterogeneity (Romiguier et al. 2013). A consensus on the placement of the root has not been achieved (Teeling & Hedges 2013), despite the application of extensive genomic data to this question. Now consider the ants: The amount of molecular data applied to the problem has been much smaller (3–7 genes, as opposed to thousands of genes), taxon sampling has been much less complete, and there has not been a concerted effort to deal with process heterogeneity. This is all the more reason, therefore, to remain cautious in our conclusions.

To summarize, there are two major issues to be resolved about basal relationships in ants:

1. Are Leptanillinae and *Martialis*, either sequentially or together, (a) sister to all other ants or (b) highly derived poneroids?
2. Are the poneroids (a) a monophyletic group or (b) a paraphyletic group within which formicoids evolved?

Although most studies support 1(a) and 2(a), the suspicion that LBA or other artifacts are biasing these results is based on the simple observation that removal of outgroups alters the in-group-only (unrooted) tree, precluding monophyly of the poneroids unless they are redefined to include Leptanillinae and *Martialis* (Brady et al. 2006; P.S. Ward, unpublished data). Resolution of these questions will clearly be aided by the use of more extensive (i.e., phylogenomic) data, but this alone may not be sufficient (Philippe et al. 2011). It will also be important to (a) filter the sequence data to reduce the likelihood of phylogenetic artifacts (Lemmon & Lemmon 2013), (b) employ models that better capture process heterogeneity (Lartillot et al. 2007, Ronquist &



**Figure 3**

Enigmatic subterranean ants of uncertain placement in the ant tree. (a) *Apomyrma stygia*, worker; (b) *Opamyрма bungvuong*, worker; (c) *Anomalomyrma boltoni*, worker; (d) *Leptanilla* sp., worker; (e) *Martialis beureka*, worker; (f) *Scyphodon anomalum*, male. Current subfamily assignments are (a,b) Amblyoponinae, (c,d) Leptanillinae, (e) Martialinae, and (f) unplaced. Images reprinted from AntWeb ([www.antweb.org](http://www.antweb.org)) with permission; photographers Michael Branstetter (e), April Nobile (a, b, d, f), and Erin Prado (c).

Deans 2010), and (c) sample a sufficiently representative diversity of taxa, both within ants and among aculeate outgroups.

### Exploring Ant Diversity and Expanding Taxon Representation

The world of ant diversity has not been exhaustively explored, and there is still the potential to discover new species that improve our inferences about relationships among the major ant lineages. The discovery of *Martialis*, a key taxon in our attempts to unravel the earliest branching events in ant phylogeny, was recent and serendipitous (Rabeling et al. 2008). The rare Sri Lankan ant species, *Aneuretus simoni*, the sole surviving member of its subfamily, contributes importantly to accurate reconstruction of relationships in its species-rich sister group, the Dolichoderinae (Ward et al. 2010). Among other relictual taxa, the ant *Opamyрма bungvuong*, described recently from two pale, blind workers found in Vietnam, manifests a peculiar mixture of leptanilline-like and poneroid-like features (Yamane et al. 2008) (**Figure 3**). It is similar to the Afrotropical genus *Apomyrma* and has been placed, along with that genus, in the subfamily Amblyoponinae, but in preliminary molecular phylogenetic analyses it is a short-branched sister to Leptanillinae (P.S. Ward, unpublished).

*Apomyrma* itself is a paradoxical ant. Known from one described and several undescribed species, all from the Afrotropical region, this rare subterranean ant has been variously placed in the Amblyoponinae (Brown et al. 1971), in the Leptanillinae (Bolton 1990), and in its own subfamily Apomyrminae (Baroni Urbani et al. 1992). The first studies to include a valid *Apomyrma* sequence (Brady et al. 2006, Moreau et al. 2006) situated this taxon near the base of the subfamily Amblyoponinae, but without strong support for any particular position. The morphological similarities between *Apomyrma* and *Opamyрма* are intriguing (**Figure 3**), but because of instability in their placement in molecular trees it is uncertain whether these are shared derived features, shared ancestral similarities, or convergent traits associated with underground living.

Even more mysterious is the taxon *Scyphodon anomalum*, known only from a few males collected in Sumatra and Kalimantan, Indonesia (**Figure 3**). This species was originally described as a wasp,

of uncertain affinity, possibly in the Braconidae, Proctotrupidae, or Bethyridae (Brues 1925). It was subsequently treated as an ant in the subfamily Leptanillinae (Petersen 1968), but some authors have argued it should be considered *incertae sedis* (of uncertain placement) in the Aculeata (Ogata et al. 1995). *Noonilla copiosa* is another enigmatic Asian species, known only from males and placed in Leptanillinae (Petersen 1968) or as *incertae sedis* in Formicidae (Ogata et al. 1995). Sequence data are not yet available for these taxa, but they and other as-yet-undiscovered species could prove to be useful additions to the ant tree, shortening the branch leading to Leptanillinae or perhaps even reducing the long branch separating ants from their nearest outgroup.

## THE CHRONOLOGY OF ANT DIVERSIFICATION

### The Fossil Record

There is an extensive fossil record of ants and other aculeate Hymenoptera (Grimaldi & Engel 2005), which provides critical information about their evolutionary history. Some of these fossils are impressions in sedimentary deposits, but many are inclusions in fossil resin (amber), often with strikingly well-preserved features (LaPolla et al. 2013). Ant-like fossils first appear about 100 Mya, but they are scarce in Cretaceous deposits, typically comprising 1% or less of all insect specimens. Ants become increasingly common in the Tertiary, accounting for 20–30% of all insects in some Oligocene and Miocene deposits (LaPolla et al. 2013). Thus there is a clear signature in the fossil record of the increasing prominence of ants in the last 50–60 million years.

In the following discussion “crown group ants” refers to the clade comprising the most recent common ancestor of living ants and their descendants, whereas the “stem group” includes all taxa more closely related to ants than to any other extant organisms (Magallón 2004). Members of the stem group that lie outside the crown group are here termed stem ants. Fossils that appear to represent stem ants occur in deposits over a 26-Myr period from the middle Albian (~105 Mya) to the middle Campanian (~79 Mya) (LaPolla et al. 2013). Placed in the subfamilies Armaniinae and Sphecomyrminae, these fossils exhibit some but not all the features associated with modern ants. Sphecomyrminae, for example, possess an ant-like petiole (a constricted second abdominal segment) and a metapleural gland, but lack the elongate first antennal segment (scape) seen in crown group ants (Bolton 2003). Armaniinae have an ant-like petiole, but the presence of a metapleural gland has not been confirmed in this group (LaPolla et al. 2013). Armaniinae are the first to appear (and disappear) in the fossil record, and they are likely sister to all other known ants (Bolton 2003, Ward 2007). The Sphecomyrminae encompass considerable morphological diversity (Perrichot 2014), including species with bizarrely modified mandibles (Barden & Grimaldi 2012), but neither they nor the Armaniinae apparently survived the K/Pg (Cretaceous–Paleogene) extinction event.

Several putative crown group ants have been recorded from the Cretaceous (LaPolla et al. 2013). None can be placed in living genera, and even assignment to a subfamily is often problematic. The oldest definitive crown group ants are (a) a member of the subfamily Dolichoderinae in Ethiopian amber (Late Cenomanian, 95 Mya) (Schmidt et al. 2010, LaPolla et al. 2013), and (b) a representative of the subfamily Formicinae in New Jersey amber (Turonian, 90 Mya) (Grimaldi & Agosti 2000). Other ant fossils, placed provisionally in or near extant subfamilies, have been recorded from French Charentese amber (100 Mya), Burmese amber (99 Mya), and Botswanan Orapa mudstone (91 Mya) (summarized by LaPolla et al. 2013). In younger Canadian amber (78 Mya) there is a greater diversity; putative members of the extant subfamilies Aneuretinae, Dolichoderinae, and Ectatomminae coexist with the now extinct Sphecomyrminae (McKellar et al. 2013).

In contrast to their muted appearance in the Cretaceous, crown group ants become increasingly abundant and diverse in the Paleogene. By the late Eocene (40 Mya) 12 of 16 extant subfamilies are represented in the fossil record, and prominent contemporary genera, such as *Camponotus*, *Dolichoderus*, *Formica*, *Lasius*, *Myrmica*, *Oecophylla*, and *Tetraponera*, are recognizable (Bolton 2003, Dlussky & Rasnitsyn 2009, LaPolla et al. 2013). Recent discoveries of substantial ant diversity in early Eocene amber deposits (Rust et al. 2010, Aria et al. 2011) suggest that this shift to a “modern” ant fauna took place around the time of the Paleocene-Eocene thermal maximum (McInerney & Wing 2011), although the paucity of ant fossils in the Paleocene reduces confidence in the timing of this event. Another peculiarity of the Eocene ant fauna is giant winged ants of the extinct subfamily Formiciinae, some as large as small hummingbirds (Archibald et al. 2011). The worker caste of Formiciinae has not been discovered, and the winged forms appear in the fossil record for only a short time period in the early and middle Eocene.

Among Neogene deposits, the ants in Dominican amber (early Miocene, 15–20 Mya) have been particularly well studied (Wilson 1985, Arillo & Ortuño 2005), revealing a rich Neotropical fauna, composed almost entirely of representatives of extant genera. Some of these taxa, such as *Neivamyrmex* army ants, the giant poneroid *Paraponera*, and dolichoderine ants of the genera *Azteca* and *Dolichoderus*, are now extinct in the Greater Antilles but survive in mainland Central and South America, attesting to less favorable environmental conditions on Hispaniola since the Miocene.

## Divergence Dating

The foregoing discussion touches upon some of the highlights of the ant fossil record (for a more detailed review see LaPolla et al. 2013). The diversity of ants in these deposits, along with a respectable fossil record for other Hymenoptera (Rasnitsyn & Kulicka 1990, Grimaldi & Engel 2005), affords great opportunity for fossil-calibrated divergence dating of ants, in conjunction with molecular phylogenies. The estimates of clade ages resulting from such studies have been somewhat variable, however, even when based on similar data sets and modes of analysis (Brady et al. 2006, Moreau et al. 2006), indicating sensitivity to methods of calibration and the range of fossil taxa considered (Brady 2011, LaPolla et al. 2013). Moreau et al. (2006), for example, inferred that crown ants originated 140–168 Mya, whereas Brady et al. (2006) obtained estimates of 115–135 Mya using similar data and methods.

The most recent evaluation, employing Bayesian dating inference, yielded age estimates for crown ants of 139–158 Mya (Moreau & Bell 2013). As with many molecular studies this is somewhat at variance with the fossil record and implies a 50-Myr gap between the time that crown ants arose and their first appearance in the fossil record (95 Mya). The absence of even stem ants from any formations older than 105 Mya, including a geographically diverse selection of insect-rich early Cretaceous deposits (Perrichot et al. 2008, LaPolla et al. 2013), would seem to argue against such an early origin of crown ants. Nevertheless, it is increasingly recognized that, for all but the most complete series, fossils do not provide direct estimates of clade ages, owing to the vagaries of fossil preservation and discovery (Wilkinson et al. 2011). Significant fossil ant discoveries continue to be made and timelines are being expanded—only twenty-five years ago, for example, the oldest definitive crown ants were from Paleocene deposits (~60 Mya) (Dlussky 1988). From this perspective an early Cretaceous (i.e., Neocomian) origin of stem ants is not unreasonable, especially because the fossil record of Apoidea, the likely sister group of ants, extends back to this time period (Brady et al. 2009).

Topological uncertainty, particularly that associated with rooting of the ant tree (see above), must introduce some uncertainty to node dating. This includes the phylogeny of the outgroup taxa

because they also supply crucial fossil calibration points. The Moreau & Bell (2013) chronogram places ants as sister to all other Aculeata including Chrysidoidea, an arrangement that is not consistent with any previous hypothesis of aculeate Hymenoptera relationships (Debevec et al. 2012, Johnson et al. 2013) and one that tends to overestimate the age of ants because the crown group is situated abnormally deep in the tree relative to other aculeates. Correcting for this misalignment of the tree might bring the crown age estimates more in line with other studies that suggest an origin of ants about 125 Mya (Brady et al. 2006, LaPolla et al. 2013, Schmidt 2013).

Crown age estimates of the major lineages (subfamilies) of formicoid ants show greater agreement among multiple studies and methods of analysis and less conflict with fossil evidence (LaPolla et al. 2013). The formicoid clade itself has a consistently estimated age of about 110 Mya; Dorylinae appear to have arisen about 85 Mya; and the three large subfamilies Dolichoderinae, Formicinae, and Myrmicinae have estimated crown ages of 60–70 Mya, 70–80 Mya, and 80–100 Mya, respectively (Brady et al. 2006, 2014; Ward et al. 2010, 2014; Moreau & Bell 2013; Schmidt 2013). Thus there is an emerging consensus that the major groups of formicoid ants all arose in the late Cretaceous rather than the early Paleogene. Ancestral range reconstruction across an ant-wide phylogeny placed the origin of most of these lineages in the Neotropics (Moreau & Bell 2013), suggesting that this region was an important setting for early ant evolution, although one of the larger subfamilies, Dolichoderinae, appears to have had a Paleotropical origin (Ward et al. 2010).

## Diversification Rate Shifts

There have been several attempts to estimate changes in ant diversification rates, motivated in part by the hypothesis that ants codiversified with angiosperms, as a result of the increased habitat complexity of soil and ground litter in angiosperm-dominated forests (Wilson & Hölldobler 2005, Moreau et al. 2006). Using a lineage-through-time (LTT) plot derived from a molecular phylogeny, Moreau et al. (2006) found evidence for an increase in the diversification rate of ants about 100 Mya, corresponding to the rise of angiosperm dominance. Pie & Tschá (2009) argued on the basis of simulation studies that the apparent shift was an artifact of incomplete taxon sampling. Using an expanded data set, Moreau & Bell (2013) contended that there was indeed a late Cretaceous increase in diversification rate on the basis of an LTT plot that departed from null expectations. It remains unclear how much these results are biased by other factors such as among-lineage rate variation, inclusion/exclusion of outgroups, and phylogenetic uncertainty in the deeper parts of the ant tree. Estimation of diversification rate shifts is a challenging problem in general (Stadler 2011), and this will be a fruitful area of further investigation.

Pie & Tschá (2009) and Moreau & Bell (2013) both found significant changes in diversification rates among ant lineages, although the assignment of shifts to particular nodes was method sensitive (Pie & Tschá 2009). The detection of lineage-specific shifts in diversification rates is hardly surprising in view of the large discrepancies in species richness among some sister pairs of ant taxa. The subfamily Dolichoderinae, for example, has 706 described species (AntCat 2014) and many others as yet undescribed, compared with its sister group, the subfamily Aneuretinae, with one extant species; the tribe Camponotini contains 1,840 described species, against its putative sister group, *Myrmoterus*, with 39 species. Such examples abound and although it is often possible to identify potential causes, such as enhanced chemical defenses in Dolichoderinae (Blum & Hermann 1978) and obligate intracellular symbionts in Camponotini (Wernegreen et al. 2009), these ad hoc explanations are difficult to test if the putative cause is evolutionarily unique (Nunn 2011). The success of ants as a whole is often attributed to the development in many ant taxa of close associations with trophobionts: plant-feeding, honeydew-producing insects, primarily Hemiptera (Delabie 2001, Wilson & Hölldobler 2005). This is an appealing idea, especially considering the



importance of carbohydrate-rich resources in contemporary ant communities (Davidson et al. 2003, Kay et al. 2014), but a rigorous phylogenetic test of this hypothesis has not been conducted.

## EVOLUTIONARY TRENDS: CONVERGENCE, DIVERGENCE, AND STASIS

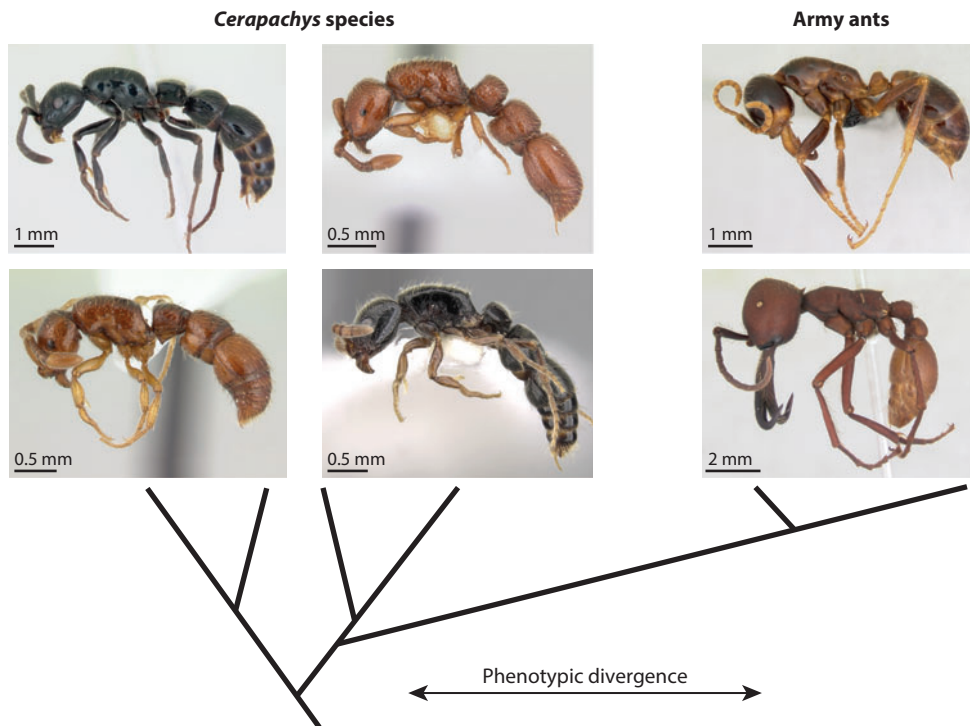
It has long been evident that certain morphological features of ants have evolved repeatedly in different lineages—examples include the formation of a second node-like structure (postpetiole) on the abdomen, loss of the sting, fusion of body sclerites, reduction of antennal segments, evolution of specialized mandibles, and the development of phragmotic (plug-shaped) heads (Hölldobler & Wilson 1990, Bolton 2003). Loss of stinging ability has occurred independently in several formicoid lineages and has been accompanied by (a) deployment of alternate modes of defense, such as modified biting mandibles or chemical repellents, and (b) a reduced dependency upon capture of live arthropod prey (Kugler 1979). Convergent evolution has also occurred in many social traits such as polygyny, polyandry, and worker caste polymorphism (Hölldobler & Wilson 1977, Oster & Wilson 1978, Hughes et al. 2008).

One of the findings to emerge from new molecular phylogenies is that convergence is even more widespread than previously appreciated. For example, the ant genera *Ankylomyrma* and *Tatuidris*, placed in the Myrmicinae on the basis of morphological characteristics shared with members of that subfamily, are now known to be poneroid ants, far removed phylogenetically from Myrmicinae (Brady et al. 2006, Moreau et al. 2006, Ward et al. 2104). It is now apparent that several well-known ant genera, including *Camponotus* and *Messor*, are nonmonophyletic because convergently similar species have been placed erroneously in the same genus (**Table 2**). More often, however, nonmonophyletic ant taxa can be traced to a different cause: marked heterogeneity in evolutionary rates, with highly divergent taxa found to be nested within others that show much greater stasis (**Table 2**). This is well illustrated by the iconic army ants, segregated in their own genera while more conservative members of the doryline clade in which they arose have been lumped together mistakenly in a single genus *Cerapachys* (**Figure 4**).

**Table 2** Examples of ant genera whose nonmonophyly has been revealed by molecular phylogenetic studies

Subfamily	Genus	Cause	Comments
Dorylinae	<i>Sphinctomyrmex</i>	Convergence	Independent evolution in Neotropics and Paleotropics
Formicinae	<i>Camponotus</i>	Convergence	Subgenus <i>Colobopsis</i> is an independent lineage
Myrmicinae	<i>Messor</i>	Convergence	Independent evolution of granivores in Nearctic region and Old World
Myrmicinae	<i>Monomorium</i>	Convergence	Species in the <i>destructor</i> - and <i>scabriceps</i> -groups form an independent lineage
Amblyoponinae	<i>Stigmatomma</i>	Divergence	Divergent in-groups ( <i>Adetomyrma</i> , <i>Myopopone</i> , <i>Mystrium</i> etc.) are excluded
Dorylinae	<i>Cerapachys</i>	Divergence	Generalized dorylines within which army ants and others evolved
Myrmicinae	<i>Aphaenogaster</i>	Divergence	Generalized predators and scavengers, within which specialized clades evolved
Myrmicinae	<i>Cyphomyrmex</i>	Divergence	Paraphyletic with respect to fungus-growing ants with “higher” agriculture
Myrmicinae	<i>Trachymyrmex</i>	Divergence	Leaf-cutter ants ( <i>Atta</i> and <i>Acromyrmex</i> ) evolved within the group
Ponerinae	<i>Pachycondyla</i>	Divergence	Recently reconfigured to restore monophyly (see Schmidt & Shattuck 2014)
Pseudomyrmecinae	<i>Tetraponera</i>	Divergence	Paraphyletic with respect to <i>Myrcidris</i> and <i>Pseudomyrmex</i>

Sources: Brady et al. (2006, 2014), Schultz & Brady (2008), Schmidt & Shattuck (2014), Ward (2011), and Ward et al. (2014).



**Figure 4**

Heterogeneity in rates of morphological and social evolution as exemplified by doryline ants. Many of the more generalized members of the doryline clade have been assigned to the catch-all genus *Cerapachys*. The highly derivative army ants are placed in their own genera. Based on Brady et al. (2014). Images reprinted from AntWeb ([www.antweb.org](http://www.antweb.org)) with permission. Photographers: (first row, left to right) April Nobile; (second row, left to right) Erin Prado, Shannon Hartman, April Nobile.

More generally, across the entire sweep of ant diversity, variation in rates of morphological and social evolution has produced a striking comingling of “primitive” and highly derived species. Attention is often focused on the more conspicuous and socially advanced ants, those with large colony sizes, dense foraging trails, specialized worker subcastes, and well-organized systems of communication and defense. These species justly excite our imagination and motivate the view of ant colonies as superorganisms (Hölldobler & Wilson 1990). Yet it is worth remembering that in many of the same communities there are ant species living in small colonies, with much more limited division of labor and less expansive capabilities of foraging, communication, and defense. How is it that since their divergence from a common ancestor in the Cretaceous different ant lineages have reached such different levels of social and anatomical complexity? What factors have propelled some groups to diverge extensively while others have retained many ancestral characteristics? Investigation of these questions will require detailed scrutiny of ecological, historical, and phylogenetic influences.

## CONCLUDING REMARKS

As this brief survey demonstrates, many aspects of ant evolutionary history have been clarified in recent years, especially concerning the phylogeny of the formicoid clade. Although not a focus of this review, there has also been substantial progress toward elucidating phylogenetic relationships



within some ant subfamilies (Schultz & Brady 2008; Ward et al. 2010, 2014; Schmidt 2013; Brady et al. 2014) and larger genera (Moreau 2008, Jansen et al. 2010, Blaimer 2012, Branstetter 2012, Price et al. 2014). These studies at shallower taxonomic levels have employed more extensive taxon sampling, which has enhanced inferences about diversification, biogeographic history, and trait evolution. At deeper levels in the ant phylogeny there remains the challenging problem of identifying the root of the tree, made difficult because of a long branch separating ants from the nearest outgroup, and further complicated by heterogeneity of the evolutionary process within ants. Phylogenomic approaches offer the prospect of resolving these basal relationships if sufficient attention is paid to data filtering, model selection, and taxon sampling. As phylogenetic uncertainty is reduced, this will in turn allow more precise testing of hypotheses about the tempo and mode of evolution in ants.

Future work on ant phylogeny would benefit from greater integration of paleontological and molecular data (Barden & Grimaldi 2012, LaPolla et al. 2013), ideally through analyses of data matrices that combine character information from both fossils and extant taxa (Ronquist et al. 2012). This will require a renewed emphasis on morphology-based ant taxonomy, an activity that has been eclipsed by the success of molecular phylogenetics. Detailed knowledge of morphology is essential not only for understanding the relationship of fossils to extant taxa, and employing them more effectively in divergence dating, but also to provide a pragmatic framework for identification of living species. The taxonomy of many ant genera and tribes is in a chaotic state, with unknown numbers of undescribed species and a woeful lack of clarity about the species limits of named forms. It will be difficult to achieve complete taxon sampling in phylogenetic analyses of these groups—or even obtain reliable estimates of species richness for subsampled clades—without greater investment in taxonomy and better morphological characterization of species and higher taxa.

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