



Phylogeny, classification, and species-level taxonomy of ants (Hymenoptera: Formicidae)*

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*In: Zhang, Z.-Q. & Shear, W.A. (Eds) (2007) Linnaeus Tercentenary: Progress in Invertebrate Taxonomy. *Zootaxa*, 1668, 1–766.

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Abstract

The current state of ant systematics is reviewed. In recent years substantial progress has been made in identifying the major clades of ants and the relationships among them. Earlier inferences about ant phylogeny based on morphology have been refined and modified as a result of a recent influx of molecular (DNA sequence) data and new fossil discoveries. It is now apparent that much of the biological and taxonomic diversity of ants is contained within the “formicoid clade” which comprises 14 of the 20 extant subfamilies and about 90% of all species. Whether the remaining groups of extant ants (Leptanillinae and the poneroid subfamilies) represent a clade or a grade at the base of the ant tree remains unresolved. The fossil record for crown group ants extends back to 90–100 mya. Stem ants (sphecomyrmines, armaniines) were also present during this period. Molecular divergence date estimates that take into account the fossil record of both ants and other Hymenoptera suggest that crown group ants arose ~115–135 mya. Most of the extant ant subfamilies and genera are well defined morphologically and likely monophyletic, but there are some notable exceptions including the subfamily Cerapachyinae and several large and ambiguously delimited genera such as *Pachycondyla*. Several tribes in the large subfamilies Formicinae and Myrmicinae also represent artificial assemblages. Finally, while the species-level taxonomy of some ant genera is in a satisfactory state, taxonomic anarchy reigns in others, with numerous ill-defined species and many names of uncertain applicability. Progress in this area of ant systematics will require sustained individual efforts, expansion of job opportunities, enlistment of new technologies, and a deeper understanding of the nature of ant species and the differences between them.

Key words: ant systematics, molecular phylogenetics, alpha-taxonomy, fossils, formicoid clade

Introduction

Ants are a conspicuous component of terrestrial biodiversity. With more than 12,000 described species (Bolton *et al.* 2006) and many others awaiting description, ants are the most species-rich of all social insects. They have come to occupy virtually all major terrestrial habitats, with the exception of tundra and cold ever-wet forests. They display a remarkable range of social behaviors, foraging habits and associations with other organisms (Hölldobler & Wilson 1990), which has generated intense scientific and public interest.

Ant systematics has a long history, summarized in Brown (1955) and Bolton (2003), yet our understanding of the species-level diversity and phylogeny of these organisms is far from complete. Perhaps this is not surprising in view of the large number of species involved, the rarity of many of these, and the predominant focus in ant systematics on the non-reproductive, or worker, caste. For most species of ants workers are the most readily available form, but the differences among workers of closely related species can be quite subtle, and are often obscured by substantial intraspecific variation and worker caste polymorphism.

Until recently worker morphology has also been the foundation for the higher classification of ants. It is becoming increasingly apparent, however, that some aspects of worker morphology show a strong tendency towards convergence, making it challenging to infer phylogenetic relationships from morphological characters alone. The incorporation of additional sources of evidence, especially DNA sequences, has revealed a clearer picture of the evolutionary history of these remarkable social insects.

Ant phylogeny

Although impressionistic tree-like diagrams can be found in earlier literature (e.g., Wheeler 1920, Emery 1920, Morley 1938), a useful starting point for discussing modern work on ant phylogeny is Brown's (1954) paper on the internal phylogeny and subfamily classification of ants, appearing in the inaugural issue of *Insectes Sociaux*. Brown recognized nine subfamilies, divided into two major lineages: the "myrmecoid complex", comprising the subfamilies Myrmeciinae, Pseudomyrmecinae, Dolichoderinae and Formicinae, and the "poneroid complex", containing Cerapachyinae, Ponerinae, Myrmicinae, Dorylinae and Leptanillinae. He presented a "tentative phylogenetic tree" of the ants, which reflected the systematic philosophy prevailing at the time in that several subfamilies are depicted as paraphyletic. Thus, Pseudomyrmecinae are shown arising within Myrmeciinae and Myrmicinae emerge from within Ponerinae. Brown's (1954) paper, based on an intuitive integration of a large body of morphological evidence, had a strong influence on later work.

Subsequent discoveries, especially the finding of the Cretaceous fossil *Sphecomyrma freyi* (Wilson *et al.* 1967) and the rediscovery of the so-called "living-fossil" ant *Nothomyrmecia macrops* (Taylor 1978), led to further modification of Brown's (1954) scheme. On the basis of differences in abdominal structure Taylor (1978) transferred Myrmeciinae and Pseudomyrmecinae to the poneroid complex, and placed the remaining ants in a "formicoid complex", comprising Formicinae, Dolichoderinae, Aneuretinae and Nothomyrmeciinae, the latter reflecting removal of *Nothomyrmecia* from Myrmeciinae. The first explicitly quantitative cladistic analyses of ant subfamily relationships (Baroni Urbani *et al.* 1992, Grimaldi *et al.* 1997) yielded results further at variance with earlier work. For example, they suggested that Pseudomyrmecinae is sister to Myrmeciinae, contradicting Brown's (1954) tree, and they found *Nothomyrmecia* to be closely related to Myrmeciinae, in disagreement with Taylor (1978). These newer results from cladistic analyses of morphology began to acquire canonical status (e.g., Grimaldi & Agosti 2000b, Wilson & Hölldobler 2005) even though the support for most groups—as measured by bootstrap values or decay indices—was very weak. One group that was consistently recovered, however, was the doryline section, the army ants and their relatives, which had been carefully scrutinized and delimited in an exemplary morphological study by Bolton (1990a, 1990c).

Another key contribution by Bolton was his landmark reclassification of ants (Bolton 2003). Although it did not contain an explicit phylogenetic analysis, this study represented an important advance in ant systematics because it recognized the artificiality of certain higher taxa, especially the subfamily Ponerinae (*sensu lato*), and divided them into smaller, morphologically coherent units, diagnosed (as far as possible) by autapomorphies. Bolton's (2003) monograph provides a very useful framework for testing and refining phylogenetic hypotheses, and for designing appropriate taxon sampling schemes in molecular studies.

Beginning about a decade ago but with much greater prominence in the last five years, molecular (DNA sequence) data have come to play a crucial role in attempts to reconstruct the ant "tree of life". Molecular phylogenetic analyses based on multiple nuclear genes have yielded robust results that reinforce some preexisting views but overturn others—and suggest that there has been considerable morphological convergence among some ant lineages (Ward & Brady 2003, Saux *et al.*, 2004, Ward & Downie 2005, Brady *et al.* 2006, Moreau *et al.* 2006, Ouellette *et al.* 2006). Molecular data provide very strong support for a novel group, the "formicoid clade", not revealed by previous morphological work. This clade comprises 14 of the 20 extant ant subfamilies and about 90% of all described ant species. Formicoids include such widespread and species-rich subfamilies as Myrmicinae, Formicinae and Dolichoderinae, as well as the army ants (Ecitoninae, Aenictinae, Dorylinae, Aenictogitoninae) (Figure 1). Non-formicoids comprise five "poneroid" subfamilies (Agroecomyrmecinae, Amblyoponinae, Paraponerinae, Ponerinae, and Proceratiinae) and the enigmatic Leptanillinae. Relationships among these remaining six subfamilies are less well resolved. In Bayesian analyses of multi-gene data sets Leptanillinae is sister to all other ants, while the poneroids form a clade that is sister to the formicoids, but this result appears to be confounded by data artifacts including long-branch attraction (Bergsten 2005) between Leptanillinae and other aculeate outgroups. It does not have statistically stronger support than alternatives in which the ant root lies within the poneroids or on the bipartition separating formicoids from other ants (Brady *et al.* 2006).

Within the formicoids, there are several well-supported supra-subfamilial clades: (1) dorylomorphs (army ants and relatives, including the paraphyletic Cerapachyinae); (2) myrmeciomorphs (Myrmeciinae and Pseudomyrmecinae); (3) dolichoderomorphs (Aneuretinae and Dolichoderinae); and (4) ectaheteromorphs (Ectatomminae and Heteroponerinae) (Figure 1). These groups are less unexpected—they had been proposed at one time or another on the basis of various lines of morphological evidence (Bolton 2003). The question of the position of Pseudomyrmecinae is now resolved in favor of Brown's (1954) original proposition, except that subfamily Myrmeciinae is sister to, rather than progenitor of, the pseudomyrmecines. The monophyly of the Myrmeciinae, including *Nothomyrmecia*, is strongly upheld. Bolton's (2003) splitting of the old Ponerinae into multiple subfamilies has been fully vindicated. In fact, two of the new subfamilies, Ectatomminae and Heteroponerinae, have no close relationship with the other ex-ponerines. Rather, they are formicoids, nested well up in the tree as part of a clade that includes Myrmicinae and Formicinae (Brady *et al.* 2006, Moreau *et al.* 2006).

Nearly all of the 21 subfamilies that Bolton (2003) recognized appear to be monophyletic, with the notable exception of the Cerapachyinae. Cerapachyines are essentially the paraphyletic core of the dorylomorphs (the erstwhile "doryline section"), out of which the more specialized army ants and leptanilloidines evolved. In addition, the monotypic subfamily Apomyrminae is now known to be nested within the subfamily Amblyoponinae (Saux *et al.* 2004). Despite the inclusion of *Apomyrma* in Amblyoponinae, there is still a possibility that the subfamily is paraphyletic. There are some suggestive similarities in morphology and behavior between Leptanillinae and Amblyoponinae (Brown *et al.* 1971, Bolton 1990b, Masuko 1990, Ward 1994), which indicate that leptanillines might be highly modified amblyoponines. The molecular data cannot decisively reject the hypothesis of a close relationship between the two groups (Brady *et al.* 2006).

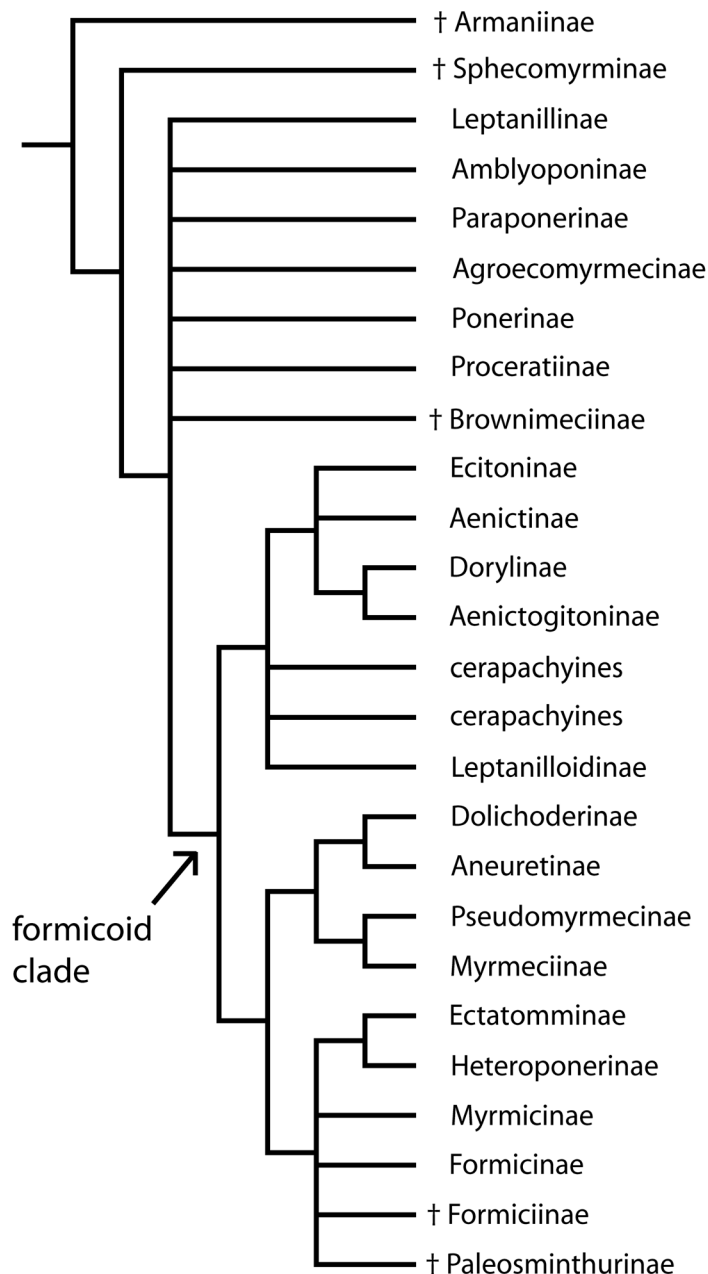


FIGURE 1. Current understanding of relationships among the ant subfamilies as inferred from molecular phylogenetic studies (Ward & Brady 2003, Saux *et al.* 2004, Brady *et al.* 2006, Moreau *et al.* 2006, Ouellette *et al.* 2006). Placement of extinct taxa is based on Grimaldi *et al.* (1997), Dlussky (1999), Ward & Brady (2003) and Bolton (2003).

The fossil record and the origin of ants

There is an extensive fossil record of ants and ant-like wasps, dating back to the middle of the Cretaceous (Carpenter 1992, Bolton 2003, Grimaldi & Engel 2005, Perrichot *et al.* 2007). Ant fossils are scarce in the Cretaceous, typically comprising 1% or less of all insect specimens, but they become increasingly common in Tertiary deposits (Grimaldi & Agosti 2000b). They account for about 5% of all insects in Baltic amber (Eocene), 20% of insects in Florissant shales (early Oligocene) and 36% of insect specimens in Dominican amber (Miocene) (Carpenter 1930, Dlussky & Rasnitsyn 2003). The fossil record provides an incomplete but tantalizing picture of changing ant diversity and taxonomic composition at selected periods in the past. To the

extent that fossils can be placed in extant higher taxa, they are also very useful in providing multiple calibration points for estimating divergence times in molecular phylogenies.

Debate about the occurrence of the first “true ant” in the fossil record (Poinar *et al.* 1999, 2000, Grimaldi & Agosti 2000a) can be clarified by first distinguishing between crown group and stem group taxa (Magallón 2004). Crown group ants are the clade encompassing the most recent common ancestor of living ants and their descendants. The stem group is defined more inclusively: all taxa more closely related to ants than to any other extant organisms. Extinct lineages which lie outside the crown group, but which are considered more closely related to ants than to any other living aculeate wasps, are members of this more inclusive stem group. They are here termed “stem ants”. Thus, phylogenetic analyses place the fossil *Sphecomyrma* as sister to the living ants (Grimaldi *et al.* 1997, Ward & Brady 2003), so it is clearly a stem ant—a member of the stem group but not the crown group. The extinct Armaniinae (treated as family Armaniidae by some workers) are more distantly related but arguably the next closest known relatives to extant ants after the Sphecomyrminae (Dlussky 1999). Hence they can also be considered stem ants. Of course, if the fossil record were sufficiently detailed we would eventually encounter stem ants with little resemblance to their modern counterparts because they lack most of the synapomorphies that we associate with ants. This is a dilemma that we do not currently face, but it has affected arguments about the origin of other fossil-rich groups such as mammals and flowering plants (de Queiroz & Gauthier 1990, Doyle & Donoghue 1993). An alternative would be to adopt an *apomorphy-based* definition of the Formicidae: all organisms that possess a metapleural gland, for example. This would place the origin of ants somewhere on the branch below the crown group. Sphecomyrminae have this gland (Grimaldi *et al.* 1997), whereas it cannot be discerned in Armaniinae, although this could be a function of poorer preservation in these impression fossils.

When do we see the first appearance of crown group ants in the fossil record? The answer to this question depends on the confidence we have in assigning fossils to pre-defined clades within the crown group. Most of the Tertiary ants can be easily placed to subfamily—many are assignable without controversy to extant genera (Dlussky & Rasnitsyn 2003). But the same cannot be said for Cretaceous ant fossils. None of these appears to belong to living genera or tribes, and for most of them even subfamily assignment is uncertain.

Kyromyrma neffi from New Jersey amber (Turonian, 90 mya) is an exception: it clearly has an acidopore (Grimaldi & Agosti 2000b), a distinctive derived feature found only in the Formicinae, making *Kyromyrma* more closely related to this clade than to any other extant subfamily, and therefore an undoubted crown group ant. Using relaxed clock divergence dating Brady *et al.* (2006) obtained an estimated age for crown group Formicinae of ~80 my, consistent with the interpretation that *Kyromyrma* is a stem Formicinae. Another ant from New Jersey amber, *Brownimecia clavata*, was placed initially in Ponerinae (Grimaldi *et al.* 1997) and later in its own subfamily within the “poneromorphs” (Bolton 2003), a group roughly equivalent to the present day “poneroids” plus the ectaheteromorphs. It seems probable that *Brownimecia* is also a crown group ant, but uncertainty about relationships among the poneroids (see above) leaves open some room for doubt.

Competing candidates for the title of oldest crown group ant include two fossils from Burmese amber of Albian age (100 mya): *Burmomyrma rossi*, a possible aneuretine (Dlussky 1996) and *Myanmyrma gracilis*, a possible myrmeciine (Engel & Grimaldi 2005; but see Archibald *et al.* 2006); and *Gerontoformica cretacica* (Nel *et al.* 2004) from French amber of similar age. Nel *et al.* (2004) treated *Gerontoformica* as *incertae sedis* within Formicidae, but noted possible affinities to Formicinae or Dolichoderinae. It seems likely that *Burmomyrma* and *Gerontoformica* are either crown group ants or very close to that clade. They have a habitus suggestive of modern ants including, in the case of *Gerontoformica*, an elongate scape, which is characteristic of crown group ants and absent from *Sphecomyrma* and armaniines. The *Burmomyrma* fossil is headless but other features of its morphology, and the fact that another putative aneuretine is reported from Canadian amber (Campanian, 80 mya) (Engel & Grimaldi 2005), speak in favor of treating it as a crown group formicid. *Myanmyrma* is more puzzling—despite the specialized abdominal morphology (presence of petiole and post-petiole) it has a very short scape, like other stem ants.

Probable crown group ants also occur in younger (Turonian, 90 mya) compression fossils from Botswana: *Afropone* and *Afromyrma* were placed in Ponerinae and Myrmicinae, respectively (Dlussky *et al.* 2004), although their assignment to these specific subfamilies has been questioned (Wilson & Hölldobler 2005, Archibald *et al.* 2006).

In summary, on the basis of the fossil record it is highly probable that crown group ants had originated by the late Albian (~100 mya) and they were certainly present before the Turonian (90 mya). There is considerable diversity of body form among putative crown group ants from this period. Stem ants (sphecomyrmines, armaniines) are known from contemporaneous deposits. The earliest records of both groups are from the northern hemisphere (France, Myanmar), with the later appearances in eastern North America and southern Africa. This suggests that ants originated and diversified in Laurasia, before dispersing to other regions (Perrichot *et al.* 2007).

It is worth belaboring the crown group/stem group distinction not only because it affects our thinking about ant origins (and has been overlooked in previous discussions on this topic), but also because it becomes important when incorporating fossil data into molecular divergence date estimates. When using a fossil to constrain the minimum age of a node on a molecular tree the constraint applies to the *stem group* of the least inclusive clade to which the fossil belongs (Magallón 2004). *Kyromyrma*, for example, cannot be placed in any subclade of Formicinae, so it supplies a minimum age estimate of 90 my for stem group Formicinae, i.e., for the node that represents the most recent common ancestor of this clade and its nearest extant relative. On the other hand, the age estimates that are generated by divergence dating methods are typically reported as *crown group* ages. Thus, an estimate for the age of crown group ants of, say, 115 my would not be contradicted by the finding of stem ants (sphecomyrmines or armaniines) in older deposits.

Using a large molecular data set consisting of seven nuclear genes from 162 taxa, Brady *et al.* (2006) estimated divergence dates for the major clades of ants by employing the penalized likelihood approach implemented in the program r8s (Sanderson 2003). Fossils were used to constrain the minimum ages of 41 nodes within the tree, and the root node—located deep within the aculeate wasp outgroups—was fixed with two different ages (one high, one low) reflecting a range of values consistent with the fossil record of Hymenoptera as a whole. This yielded age estimates for crown group ants in the range of ~115 to 135 million years, in agreement with conjecture in the paleontological literature (Grimaldi & Engel 2005), but contradicting previous molecular studies that inferred a Jurassic origin of ants (Crozier *et al.* 1997, Moreau *et al.* 2006).

Divergence date estimates for clades within the Formicidae indicate that most ant subfamilies originated (at the crown group level) in the late Cretaceous, followed by extensive within-subfamily diversification in the Paleogene (Brady *et al.* 2006). It has been hypothesized that the ants diversified in concert with the angiosperms and that their evolutionary success is linked to inhabitation of the complex leaf litter layer of angiosperm-dominated forests and the tending of plant-feeding hemipteran insects (Wilson & Hölldobler 2005, Moreau *et al.* 2006). The fossil record and divergence date estimates are not inconsistent with this hypothesis, but additional work on this problem is called for.

Higher classification

In volume 1 of *Systema Naturae* Linnaeus (1758) described seventeen species of ants. All were placed in the single genus *Formica*, although within a few decades additional genera had been recognized, and this trend continued in the ensuing years, together with the development of a more complex hierarchical classification in which genera were apportioned among subfamilies and tribes. The ant species described by Linnaeus (1758) are now dispersed in eleven different genera, belonging to four subfamilies.

A comprehensive account of the history of changes in the higher classification of ants is given in Bolton (2003). For much of the twentieth century the number of recognized ant subfamilies varied from seven to ten,

with the Aneuretinae, Cerapachyinae, Leptanillinae, Myrmeciinae and Pseudomyrmecinae being variously treated as separate subfamilies or (at different times) subsumed within Dolichoderinae, Ponerinae, Dorylinae, Ponerinae, and Myrmicinae, respectively. The last three decades have seen a proliferation of subfamily names, as a result of three factors: (1) the realization that some subfamilies were assemblages of unrelated taxa; (2) abandonment of paraphyletic taxa, and (3) the discovery of novel fossil taxa. Twenty extant subfamilies of ants are currently recognized, along with five extinct subfamilies (Table 1). One of the fossil taxa, Armaniinae, is often given family rank within the superfamily Formicoidea (Engel & Grimaldi 2005).

TABLE 1. List of valid subfamily and tribe names in Formicidae (from Engel & Grimaldi 2005 and Bolton *et al.* 2006). Subfamilies are arranged in putative clades (Ward & Brady 2003, Brady *et al.* 2006), but the placement of Leptanillinae, poneroids, and some fossils is uncertain. † = extinct taxon.

stem ants

- †Armaniinae Dlussky (1983)
- †Sphecomyrminae Wilson & Brown (1967)
 - †Haidomyrmecini Bolton (2003)
 - †Sphecomyrmini Wilson & Brown (1967)

incertae sedis

- Leptanillinae Emery (1910)
 - Anomalomyrmini Taylor (1990)
 - Leptanillini Emery (1910)

poneroids

- Agroecomyrmecinae Carpenter (1930)
- Amblyoponinae Forel (1893)
- †Brownimeciinae Bolton (2003)
- Paraponerinae Emery (1901)
- Ponerinae Lepeletier de Saint Fargeau (1835)
 - Platythyreini Emery (1901)
 - Ponerini Lepeletier de Saint Fargeau (1835)
 - Thaumatomyrmecini Emery (1901)
- Proceratiinae Emery (1895)
 - Probolomyrmecini Perrault (2000)
 - Proceratiini Emery (1895)

formicoids: dorylomorphs

- Aenictinae Emery (1901)
 - Aenictogitoninae Ashmead (1905)
 - Cerapachyinae Forel (1893)
 - Acanthostichini Emery (1901)
 - Cerapachyini Forel (1893)
 - Cylindromyrmecini Emery (1901)
 - Dorylinae Leach (1815)
 - Ecitoninae Forel (1893)
 - Cheliomyrmecini Wheeler, W. M. (1921)
 - Ecitonini Forel (1893)
 - Leptanilloidinae Bolton (1992)
-

.....continued

TABLE 1 (continued).

formicoids: myrmeciomorphs

- Myrmeciinae Emery (1877)
 - Myrmeciini Emery (1877)
 - Prionomyrmecini Wheeler, W. M. (1915)
- Pseudomyrmecinae Smith, M. R. (1952)

formicoids: dolichoderomorphs

- Aneuretinae Emery (1913)
- Dolichoderinae Forel (1878)
 - Dolichoderini Forel (1878)
 - Iridomyrmecini Dubovikoff (2005)

formicoids: ectaheteromorphs

- Ectatomminae Emery (1895)
 - Ectatommini Emery (1895)
 - Typhlomyrmecini Emery (1911)
- Heteroponerinae Bolton (2003)

formicoids: Formicinae

- Formicinae Latreille (1809)
 - Camponotini Forel (1878)
 - Dimorphomyrmecini Emery (1895)
 - Formicini Latreille (1809)
 - Gigantiopini Ashmead (1905)
 - Lasiini Ashmead (1905)
 - Melophorini Forel (1912)
 - Myrmecorhynchini Wheeler, W. M. (1917)
 - Myrmoteratini Emery (1895)
 - Notostigmatini Bolton (2003)
 - Oecophyllini Emery (1895)
 - Plagiolepidini Forel (1886)

formicoids: Myrmicinae

- Myrmicinae Lepeletier de Saint Fargeau (1835)
 - Adelomyrmecini Fernández (2004)
 - Ankylomyrmini Bolton (2003)
 - Attini Smith, F. (1858)
 - Basicerotini Brown (1949)
 - Blepharidattini Wheeler & Wheeler (1991)
 - Cataulacini Emery (1895)
 - Cephalotini Smith, M. R. (1949)
 - Crematogastrini Forel (1893)
 - Dacetini Forel (1892)
 - Formicoxenini Forel (1893)
 - Lenomyrmecini Bolton (2003)
 - Liomyrmecini Bolton (2003)
 - Melissotarsini Emery (1901)
 - Meranoplinae Emery (1914)
 - Metaponini Forel (1911)
 - Myrmecini Ashmead (1905)
 - Myrmecini Lepeletier de Saint Fargeau (1835)

.....continued

TABLE 1 (continued).

Myrmicini Lepeletier de Saint Fargeau (1835)
Paratopulini Bolton (2003)
Phalacromyrmecini Dlussky & Fedoseva (1988)
Pheidolini Emery (1877)
Solenopsidini Forel (1893)
Stegomyrmecini Wheeler, W. M. (1922)
Stenammini Ashmead (1905)
Tetramoriini Emery (1895)

formicoids: others

†Formiciinae Lutz (1986)

†Paleosminthurinae Pierce & Gibrion (1962)

The acceptance of the principle that the supraspecific taxa recognized in a classification should be monophyletic has come slowly to ant systematics. This is largely because there has been persistent sentiment in favor of the notion that the primary criterion for recognition of higher taxa is that they should be “sufficiently distinct” from one another. Application of this “degree of difference” rule can lead to the creation (or the persistence from past classifications) of paraphyletic taxa. This is the situation with the subfamily Cerapachyinae, which essentially represents the more generalized members of the dorylomorph clade. As a result of molecular phylogenetic studies the non-monophyly of Cerapachyinae, already suggested from morphological considerations (Brady & Ward 2005), has become readily apparent (Brady 2003, Brady *et al.* 2006, Moreau *et al.* 2006). Yet, there is no simple solution to this problem because the precise details of cerapachyine paraphyly remain unclear. There is insufficient resolution at the base of the dorylomorph tree to realign subfamily boundaries, short of treating the entire clade as one subfamily (Dorylinae).

Recent molecular analyses indicate that several tribes within the Formicinae (Lasiini, Plagiolepidini) and Myrmicinae (Dacetini, Pheidolini, Solenopsidini, Stenammini) are also non-monophyletic (Brady *et al.* 2006). Again, the non-monophyly manifests itself in bushy parts of the tree, where some relationships are ambiguous. Establishing a phylogenetic classification of Formicinae and Myrmicinae that is underpinned by well resolved and well supported trees will require much more extensive sampling of taxa and genes.

The genus-level classification of ants is more stable, with about 288 extant ant genera currently recognized (Bolton *et al.* 2006). Most of these are reasonably well demarcated and readily identified (e.g., Bolton 1994). But there are more than a dozen ant genera which are either weakly or very broadly defined, and which appear to be non-monophyletic by virtue of their exclusion of derivative (satellite) genera.

One of the most egregious cases involves *Pachycondyla*, a genus of Ponerinae, which is almost synonymous with the entire tribe Ponerini except that, under the current definition of *Pachycondyla*, a number of morphologically specialized clades (genera) are removed from it. Comprehensive molecular studies by Chris Schmidt (pers. comm.) have confirmed what was long suspected: *Pachycondyla* species are scattered all over the Ponerini phylogeny, interspersed among ~20 other genera. Clearly a major overhaul of the classification of the entire tribe is needed. Placement of all species into one genus coincident with Ponerini itself would create a highly variable genus with more than 1000 species—not a desirable solution. If we are to retain a Linnaean (i.e., ranked) phylogenetic classification system for ants, with named taxa that are recognizable with reasonable facility, then what is required here—and in other taxa where comparable problems arise—is a robust molecular phylogeny and identification of a set of mutually exclusive clades that are relatively easily distinguished morphologically. This is a challenging task, and given considerable heterogeneity in rates of morphological evolution it remains unclear if this goal can always be achieved.

Other ant genera known or strongly suspected to be non-monophyletic include *Amblyopone*, *Cerapachys*, *Tetraponera*, *Camponotus*, *Trachymyrmex*, *Leptothorax*, *Nesomyrmex*, *Temnothorax*, *Aphaenogaster*, *Messor*, *Monomorium*, and *Tetramorium*. Resolving these into mutually exclusive monophyletic groups that can be diagnosed with obvious phenotypic features will require comprehensive sampling of the relevant species, selection of genes of appropriate variability, and careful scrutiny of morphological variation.

The placement of fossil taxa within the higher classification of ants also poses challenges. It becomes increasingly difficult to do this for older material and for specimens preserved as impression fossils rather than in fossilized resins. Fossils are vitally important for enhancing our understanding of ant evolution. They reveal unexpected character combinations, geographical distributions, and instances of past co-occurrence with other organisms. Fossils also provide the best source of independent evidence on clade ages, and permit us to obtain estimates (however approximate) of the absolute timeline of ant history. Despite this, considerable subjectivity and uncertainty accompanies attempts to place fossils on a phylogeny. This is reflected in the substantial number of fossil ants with *incertae sedis* status (Bolton 2003, Bolton *et al.* 2006), and by the use of naming conventions (collective taxa, form-taxa) that signify fossils of uncertain affinity (Dlussky & Rasnitsyn 2003).

Species-level taxonomy

Recent progress in ant phylogenetics has not been accompanied by a comparable improvement in the species-level taxonomy (alpha-taxonomy) of these organisms. This is unfortunate because for hyperdiverse taxa such as ants there is a great deal of unfinished taxonomic work. The enterprise of discovering, describing and distinguishing species can be rewarding and stimulating. Species delimitation is (or should be) closely linked to population and evolutionary biology. It is, after all, concerned with identifying the very place in the tree of life where within-population processes give way to between-population divergence and speciation. But the pedestrian aspects of alpha-taxonomy (specimen examination and description, preparation of illustrations, scrutiny of types, search for reliable diagnostic features) can be quite tedious and time-consuming—and are made more difficult in ant taxonomy by reliance on the worker caste in which morphology is often reduced relative to that of reproductives. A further disincentive is the great scarcity of jobs for those engaged primarily in descriptive taxonomy. Museum and university positions in systematics that would have been filled by such individuals fifty years ago are increasingly going to those whose primary focus is molecular phylogenetics. This trend is easy to understand, but the imbalance needs to be redressed if we wish to have the capability of using morphology to confidently identify terminal taxa on the tree of life.

Figure 2 depicts the historical pattern of ant species descriptions. The rate of description of new ant species and subspecies remained quite low for almost a century after Linnaeus (1758), with scattered contributions by Fabricius, Latreille, Nylander, Westwood and other workers. There was a notable increase from about 1850 onwards, starting with a series of papers by ant specialists such as F. Smith, Roger, and Mayr, and reaching a peak in the early twentieth century during a flurry of taxonomic activity by Emery, Forel, Santschi and W. M. Wheeler. There was a marked decline in the number of species described annually from about 1930 to 1960, and a modest increase since then. The decline should not necessarily be interpreted as a lack of activity. The naming of ants in the late nineteenth and early twentieth centuries resulted in many weakly defined species and infraspecific forms. With the advent of the “new systematics” in the 1940’s and 1950’s, ant taxonomists such as Creighton, Brown and Wilson began taking a more nuanced view of species, accepting more intraspecific variation and abandoning the use of subspecies (Buhs 2000, Ward 2007). Under this non-typological view of species it became apparent that there were considerable numbers of synonyms among the names that had accumulated in the literature—notwithstanding the continued occurrence of undescribed species in nature.

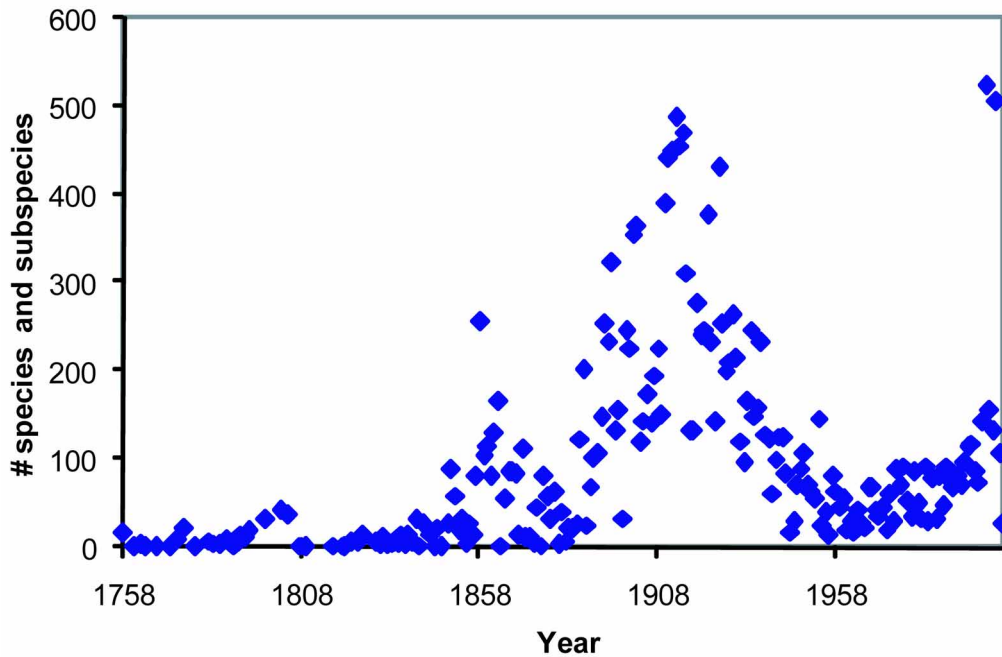


FIGURE 2. Numbers of species and subspecies of ants described each year from 1758 to 2005. Modified from Bolton *et al.* (2006).

The older literature in ant taxonomy is replete with isolated descriptions of species, subspecies and “varieties”, in which the new taxa are not integrated into a more comprehensive taxonomy of the genus to which they are assigned. These names have accumulated in a piece-meal fashion and remain a substantial taxonomic burden in those ant genera that have not been monographed within the last fifty years. This situation is particularly acute in large and diverse genera such as *Crematogaster*, *Pheidole*, *Hypoponera*, *Paratrechina*, *Solenopsis*, and *Camponotus*. Some of these have been revised regionally (e.g., Trager 1984, Eguchi 2001, Longino 2003, Wilson 2003) and these contributions represent valuable building blocks, but global treatments remain elusive. For any one of these hyperdiverse genera a useful first step would be the identification of mutually exclusive clades (species groups or subgenera) that are applicable globally.

On the other hand, thanks to the energetic efforts of a few individuals, several species-rich and widely distributed ant genera have been revised at a worldwide level, including *Neivamyrmex* (Borgmeier 1955, Watkins 1976), *Cataulacus* (Bolton 1974a, 1982), *Tetramorium* (Bolton 1976, 1977, 1979, 1980), *Rogeria* (Kugler 1994), *Gnamptogenys* (Lattke 1995, 2004, Lattke *et al.* 2007), *Cephalotes* (de Andrade & Baroni Urbani 1999), *Strumigenys* (Bolton 2000), *Pyramica* (Bolton 2000), *Proceratium* (Baroni Urbani & de Andrade 2003) and *Acropyga* (LaPolla 2004). Of course, no taxonomic revision should be considered final and these genera will continue to be affected by new discoveries and interpretations, but their species-level taxonomy is in a much better state than that of most other large ant genera.

For smaller (more species-poor) genera of ants and for geographically restricted regions the situation is much better, especially in Europe (e.g., Seifert 2007) and Japan (Imai *et al.* 2003). The literature on ant taxonomy is highly dispersed, however, and sometimes difficult to locate. Bolton’s (2003) monograph on ant classification provides an excellent entrée into this literature, including identification guides and keys. Ant identification resources are becoming increasingly available online, through sites such as AntWeb (www.antweb.org), Antbase (www.antbase.org), Australian Ants Online (www.ento.csiro.au/science/ants), Ants of Costa Rica (<http://academic.evergreen.edu/projects/ants/AntsofCostaRica.html>) and Japanese Ant Image Database (<http://ant.edb.miyakyo-u.ac.jp/E>).

Several technological developments hold the promise of facilitating ant species-level taxonomy. These include improvements in imaging (e.g., Automontage system), specimen measurement, distribution mapping,

and electronic organization of data. DNA bar-coding has the potential to provide valuable information about species boundaries in ants (Smith *et al.* 2005), and to assist in the targeting of additional population samples in poorly resolved complexes. The use of multiple independent genes is likely to improve this procedure. Interactive keys such as Lucid (www.lucidcentral.org) offer increased flexibility for species identification and more efficient handling and sharing of character state information.

While these new tools will undoubtedly assist in the task of delimiting species and inferring relationships among them, it is worth remembering that the process of population differentiation and speciation is a complex one—perhaps especially so in ants—and we must expect there to be some evolutionarily intermediate situations that will frustrate the pigeon-holing aspirations of a taxonomist. Advances in technology will not simplify nature, nor obviate the need for comprehensive sampling of populations. Recent documentation of transpecific social polymorphisms (Krieger & Ross 2002), cryptic species (Schlick-Steiner *et al.* 2006), interdependent hybrid lineages (Helms Cahan *et al.* 2002, Helms Cahan & Vinson 2003, Andersen *et al.* 2006), and clonal reproduction (Pearcy *et al.* 2004, Fournier *et al.* 2005) hint at the possible complications that await the student of ant taxonomy, and highlight the need for a population perspective when tackling taxonomic challenges.

Conclusions

Ant systematics is at an exciting crossroads, where new lines of evidence and methods of inquiry promise much improved understanding of the species-level diversity and phylogeny of these organisms. The broad outline of the evolutionary history of ants is becoming increasingly well defined, thanks in large measure to the use of DNA sequence data, but many of the details of that history remain to be clarified. Outstanding challenges include resolving the branching sequence among “poneroids” at the base of the ant tree, and refining our understanding of the timing and sequence of events leading to the modern ants. The current higher classification of ants is broadly phylogenetic, but there are some troublesome non-monophyletic genera and tribes (and one subfamily) whose parsing into clades will test our ability to retain a ranked classification system in which all higher taxa are morphologically diagnosable. Few would argue that all nodes in a tree should be named, but with the advent of more detailed phylogenies one can expect an increased need for interpolation of names between subfamilies, tribes and genera. At the species-level there is much room for improvement in ant taxonomy, and concerted—indeed heroic—efforts will be needed to create “species pages” for all of the world’s ants.

Acknowledgements

My research on ant systematics has been supported by the University of California (Davis) and the US National Science Foundation. Many of the molecular phylogenetic findings summarized here have emerged from the Ant AToL (Assembling the Tree of Life) Project, supported by NSF grant EF-0431330, and carried out in collaboration with colleagues Brian Fisher (California Academy of Sciences) and Seán Brady and Ted Schultz (Smithsonian Institution). I am grateful to Seán Brady, Michael Branstetter, Eli Sarnat, and two anonymous reviewers for helpful comments on the manuscript.

References

- Anderson, K.E., Gadau, J., Mott, B.M., Johnson, R.A., Altamirano, A., Strehl, C. & Fewell, J.H. (2006) Distribution and evolution of genetic caste determination in *Pogonomyrmex* seed-harvester ants. *Ecology*, 87, 2171–2184.

- Archibald, S.B., Cover, S.P. & Moreau, C.S. (2006) Bulldog ants of the Eocene Okanagan Highlands and history of the subfamily (Hymenoptera: Formicidae: Myrmeciinae). *Annals of the Entomological Society of America*, 99, 487–523.
- Baroni Urbani, C. & de Andrade, M.L. (2003) The ant genus *Proceratium* in the extant and fossil record (Hymenoptera: Formicidae). *Museo Regionale di Scienze Naturali Monografie (Turin)*, 36, 1–492.
- Baroni Urbani, C., Bolton, B. & Ward, P.S. (1992) The internal phylogeny of ants (Hymenoptera: Formicidae). *Systematic Entomology*, 17, 301–329.
- Bergsten J. (2005) A review of long-branch attraction. *Cladistics*, 21, 163–193.
- Bolton, B. (1974) A revision of the Palaeotropical arboreal ant genus *Cataulacus* F. Smith (Hymenoptera: Formicidae). *Bulletin of the British Museum (Natural History). Entomology*, 30, 1–105.
- Bolton, B. (1976) The ant tribe Tetramoriini (Hymenoptera: Formicidae). Constituent genera, review of smaller genera and revision of *Triglyphothrix* Forel. *Bulletin of the British Museum (Natural History). Entomology*, 34, 281–379.
- Bolton, B. (1977) The ant tribe Tetramoriini (Hymenoptera: Formicidae). The genus *Tetramorium* Mayr in the Oriental and Indo-Australian regions, and in Australia. *Bulletin of the British Museum (Natural History). Entomology*, 36, 67–151.
- Bolton, B. (1979) The ant tribe Tetramoriini (Hymenoptera: Formicidae). The genus *Tetramorium* Mayr in the Malagasy region and in the New World. *Bulletin of the British Museum (Natural History). Entomology*, 38, 129–181.
- Bolton, B. (1980) The ant tribe Tetramoriini (Hymenoptera: Formicidae). The genus *Tetramorium* Mayr in the Ethiopian zoogeographical region. *Bulletin of the British Museum (Natural History). Entomology*, 40, 193–384.
- Bolton, B. (1982) Afrotropical species of the myrmicine ant genera *Cardiocondyla*, *Leptothorax*, *Melissotarsus*, *Messor* and *Cataulacus* (Formicidae). *Bulletin of the British Museum (Natural History). Entomology*, 45, 307–370.
- Bolton, B. (1990a) Abdominal characters and status of the cerapachyine ants (Hymenoptera, Formicidae). *Journal of Natural History*, 24, 53–68.
- Bolton, B. (1990b) The higher classification of the ant subfamily Leptanillinae (Hymenoptera: Formicidae). *Systematic Entomology*, 15, 267–282.
- Bolton, B. (1990c) Army ants reassessed: the phylogeny and classification of the doryline section (Hymenoptera, Formicidae). *Journal of Natural History*, 24, 1339–1364.
- Bolton, B. (1994) *Identification guide to the ant genera of the world*. Harvard University Press, Cambridge, Massachusetts, 222 pp.
- Bolton, B. (2000) The ant tribe Dacetini. *Memoirs of the American Entomological Institute*, 65, 1–1028.
- Bolton, B. (2003) Synopsis and classification of Formicidae. *Memoirs of the American Entomological Institute*, 71, 1–370.
- Bolton, B., Alpert, G., Ward, P.S. & Nasrecki, P. (2006) *Bolton's Catalogue of ants of the world*. Harvard University Press, Cambridge, Massachusetts, CD-ROM.
- Borgmeier, T. (1955) Die Wanderameisen der neotropischen Region. *Studia Entomologica*, 3, 1–720.
- Brady, S.G. (2003) Evolution of the army ant syndrome: the origin and long-term evolutionary stasis of a complex of behavioral and reproductive adaptations. *Proceedings of the National Academy of Sciences U. S. A.*, 100, 6575–6579.
- Brady, S.G., Fisher, B.L., Schultz, T.R. & Ward, P.S. (2006) Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proceedings of the National Academy of Sciences U. S. A.*, 103, 18172–18177.
- Brady, S.G. & Ward, P.S. (2005) Morphological phylogeny of army ants and other dorylomorphs (Hymenoptera: Formicidae). *Systematic Entomology*, 30, 593–618.
- Brown, W.L., Jr. (1954) Remarks on the internal phylogeny and subfamily classification of the family Formicidae. *Insectes Sociaux*, 1, 21–31.
- Brown, W.L., Jr. (1955) Ant taxonomy. In: Kessel, E.W. (Ed.) *A century of progress in the natural sciences, 1853–1953*. California Academy of Sciences, San Francisco, pp. 569–572.
- Brown, W.L., Jr., Gotwald, W.H., Jr. & Léveux, J. (1971) A new genus of ponerine ants from West Africa (Hymenoptera: Formicidae) with ecological notes. *Psyche (Cambridge)*, 77, 259–275.
- Buhs, J.B. (2000) Building on bedrock: William Steel Creighton and the reformation of ant systematics, 1925–1970. *Journal of the History of Biology*, 33, 27–70.
- Carpenter, F.M. (1930) The fossil ants of North America. *Bulletin of the Museum of Comparative Zoology*, 70, 1–66.
- Carpenter, F.M. (1992) *Treatise on invertebrate paleontology. Part R. Arthropoda 4. Volume 4. Superclass Hexapoda*. Geological Society of America, Boulder, pp. i–ii, 279–655.
- Crozier, R.H., Jermini, L.S. & Chiotis, M. (1997) Molecular evidence for a Jurassic origin of ants. *Naturwissenschaften*, 84, 22–23.
- de Andrade, M.L. & Baroni Urbani, C. (1999) Diversity and adaptation in the ant genus *Cephalotes*, past and present. *Stuttgarter Beiträge zur Naturkunde. Serie B (Geologie und Paläontologie)*, 271, 1–889.
- de Queiroz, K. & Gauthier, J. (1990) Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. *Systematic Zoology*, 39, 307–322.

- Dlussky, G.M. (1999) The first find of the Formicoidea (Hymenoptera) in the lower Cretaceous of the northern hemisphere. [In Russian.] *Paleontologicheskii Zhurnal*, 1999(3), 62–66.
- Dlussky, G.M., Brothers, D.J. & Rasnitsyn, A.P. (2004) The first Late Cretaceous ants (Hymenoptera: Formicidae) from southern Africa, with comments on the origin of the Myrmicinae. *Insect Systematics and Evolution*, 35, 1–13.
- Dlussky, G.M. & Rasnitsyn, A.P. (2003) Ants (Hymenoptera: Formicidae) of Formation Green River and some other Middle Eocene deposits of North America. *Russian Entomological Journal*, 11, 411–436.
- Doyle, J.A. & Donoghue, M.J. (1993) Phylogenies and angiosperm diversification. *Paleobiology*, 19, 141–167.
- Eguchi, K. (2001) A revision of the Bornean species of the ant genus *Pheidole* (Insecta: Hymenoptera: Formicidae: Myrmicinae). *Tropics Monograph Series*, 2, 1–154.
- Emery, C. (1920) La distribuzione geografica attuale delle formiche. Tentativo di spiegarne la genesi col soccorso di ipotesi filogenetiche e paleogeografiche. *Atti della Reale Accademia dei Lincei. Memorie. Classe di Scienze Fisiche, Matematiche e Naturali*, (5)13, 357–450.
- Engel, M.S. & Grimaldi, D.A. (2005) Primitive new ants in Cretaceous amber from Myanmar, New Jersey, and Canada (Hymenoptera: Formicidae). *American Museum Novitates*, 3485, 1–23.
- Fournier, D., Estoup, A., Orivel, J., Foucaud, J., Jourdan, H., Le Breton, J. & Keller, L. (2005) Clonal reproduction by males and females in the little fire ant. *Nature* (London), 435, 1230–1234.
- Grimaldi, D. & Agosti, D. (2000a) The oldest ants are Cretaceous, not Eocene: comment. *Canadian Entomologist*, 132, 691–693.
- Grimaldi, D. & Agosti, D. (2000b) A formicine in New Jersey Cretaceous amber (Hymenoptera: Formicidae) and early evolution of the ants. *Proceedings of the National Academy of Sciences U. S. A.*, 97, 13678–13683.
- Grimaldi, D., Agosti, D. & Carpenter, J.M. (1997) New and rediscovered primitive ants (Hymenoptera: Formicidae) in Cretaceous amber from New Jersey, and their phylogenetic relationships. *American Museum Novitates*, 3208, 1–43.
- Grimaldi, D. & Engel, M.S. (2005) *Evolution of the insects*. Cambridge University Press, Cambridge, xv + 755 pp.
- Helms Cahan, S., Parker, J.D., Rissing, S.W., Johnson, R.A., Polony, T.S., Weiser, M.D. & Smith, D.R. (2002) Extreme genetic differences between queens and workers in hybridizing *Pogonomyrmex* harvester ants. *Proceedings of the Royal Entomological Society of London. Series B*, 269, 1871–1877.
- Helms Cahan S. & Vinson S.B. (2003) Reproductive division of labor between hybrid and non hybrid offspring in a fire ant hybrid zone. *Evolution*, 57, 1562–1570.
- Hölldobler, B. & Wilson, E.O. (1990) *The ants*. Harvard University Press, Cambridge, Massachusetts, xii + 732 pp.
- Imai, H. T., Kihara, A., Kondoh, M., Kubota, M., Kuribayashi, S., Ogata, K., Onoyama, K., Taylor, R. W., Terayama, M., Tsukii, Y., Yoshimura, M. & Ugawa, Y. (2003) *Ants of Japan*. Gakken, Tokyo, 224 pp.
- Krieger, M.J. & Ross, K.G. (2002). Identification of a major gene regulating complex social behavior. *Science* (Washington, D.C.), 295, 328–332.
- Kugler, C. (1994) A revision of the ant genus *Rogeria* with description of the sting apparatus (Hymenoptera: Formicidae). *Journal of Hymenoptera Research*, 3, 17–89.
- LaPolla, J.S. (2004) *Acropyga* (Hymenoptera: Formicidae) of the world. *Contributions of the American Entomological Institute*, 33(3), 1–130.
- Lattke, J.E. (1995) Revision of the ant genus *Gnamptogenys* in the New World (Hymenoptera: Formicidae). *Journal of Hymenoptera Research*, 4, 137–193.
- Lattke, J.E. (2004) A taxonomic revision and phylogenetic analysis of the ant genus *Gnamptogenys* Roger in Southeast Asia and Australasia (Hymenoptera: Formicidae: Ponerinae). *University of California Publications in Entomology*, 122, 1–266.
- Lattke, J.E., Fernández, F. & Palacio, E.E. (2007). Identification of the species of *Gnamptogenys* Roger in the Americas. *Memoirs of the American Entomological Institute*, 80, 254–270.
- Linnaeus, C. (1758) *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata*. L. Salvii, Holmiae [= Stockholm], 824 pp.
- Longino, J.T. (2003) The *Crematogaster* (Hymenoptera, Formicidae, Myrmicinae) of Costa Rica. *Zootaxa*, 151, 1–150.
- Magallón, S. (2004) Dating lineages: molecular and paleontological approaches to the temporal framework of clades. *International Journal of Plant Science*, 165(4 Suppl.), S7–S21.
- Masuko, K. (1990) Behavior and ecology of the enigmatic ant *Leptanilla japonica* Baroni Urbani (Hymenoptera: Formicidae: Leptanillinae). *Insectes Sociaux*, 37, 31–57.
- Moreau, C.S., Bell, C.D., Vila, R., Archibald, S.B. & Pierce, N.E. (2006) Phylogeny of the ants: diversification in the age of angiosperms. *Science* (Washington D. C.), 312, 101–104.
- Morley, B.D.W. (1938) An outline of the phylogeny of the Formicidae. *Bulletin de la Société Entomologique de France*, 43, 190–194.
- Ouellette, G.D., Fisher, B.L. & Girman, D.J. (2006) Molecular systematics of basal subfamilies of ants using 28S rRNA (Hymenoptera: Formicidae). *Molecular Phylogenetics and Evolution*, 40, 359–369.
- Pearcy, M., Aron, S., Doums, C. & Keller, L. (2004) Conditional use of sex and parthenogenesis for worker and queen production in ants. *Science* (Washington D. C.), 306, 1780–1783.

- Perrichot, V., Lacau, S., Néraudeau, D. & Nel, A. (2007) Fossil evidence for the early ant evolution. *Naturwissenschaften*, doi: 10.1007/s00114-007-0301-8.
- Poinar, G., Jr., Archibald, B. & Brown, A. (1999) New amber deposit provides evidence of early Paleogene extinctions, paleoclimates, and past distributions. *Canadian Entomologist*, 131, 171–177.
- Poinar, G., Baroni Urbani, C. & Brown, A. (2000) The oldest ants are Cretaceous, not Eocene: reply. *Canadian Entomologist*, 132, 695–696.
- Sanderson M.J. (2003) r8s: inferring absolute rates of molecular evolution and divergence times in the absence of a molecular clock. *Bioinformatics*, 19, 301–302.
- Saux, C., Fisher, B.L. & Spicer, G.S. (2004) Dracula ant phylogeny as inferred by nuclear 28S rDNA sequences and implications for ant systematics (Hymenoptera: Formicidae: Amblyoponinae). *Molecular Phylogenetics and Evolution*, 33, 457–468.
- Seifert, B. (2007) *Die Ameisen Mittel- und Nordeuropas*. Iutra Verlags- und Vertriebsgesellschaft, Tauer, 368 pp.
- Schlick-Steiner, B.C., Steiner, F.M., Moder, K., Seifert, B., Sanetra, M., Dyreson, E., Stauffer, C. & Christian, E. (2006) A multidisciplinary approach reveals cryptic diversity in western Palearctic *Tetramorium* ants (Hymenoptera: Formicidae). *Molecular Phylogenetics and Evolution*, 40, 259–273.
- Smith, M.A., Fisher, B.L. & Hebert, P.D.N. (2005) DNA barcoding for effective biodiversity assessment of a hyperdiverse arthropod group: the ants of Madagascar. *Philosophical Transactions of the Royal Society of London. B. Biological Sciences*, 360, 1825–1834.
- Taylor, R.W. (1978) *Nothomyrmecia macrops*: a living-fossil ant rediscovered. *Science* (Washington D. C.), 201, 979–985.
- Trager, J.C. (1984) A revision of the genus *Paratrechina* (Hymenoptera: Formicidae) of the continental United States. *Sociobiology*, 9, 49–162.
- Ward, P.S. (1994) *Adetomyrma*, an enigmatic new ant genus from Madagascar (Hymenoptera: Formicidae), and its implications for ant phylogeny. *Systematic Entomology*, 19, 159–175.
- Ward, P.S. (2007) Edward O. Wilson and his contributions to ant systematics. *Memoirs of the American Entomological Institute*, 80, 3–7.
- Ward, P.S. & Brady, S.G. (2003) Phylogeny and biogeography of the ant subfamily Myrmeciinae (Hymenoptera: Formicidae). *Invertebrate Systematics*, 17, 361–386.
- Ward, P.S. & Downie, D.A. (2005) The ant subfamily Pseudomyrmecinae (Hymenoptera: Formicidae): phylogeny and evolution of big-eyed arboreal ants. *Systematic Entomology*, 30, 310–335.
- Watkins, J.F., II. (1976) *The identification and distribution of New World army ants (Dorylinae: Formicidae)*. Baylor University Press, Waco, Texas, 102 pp.
- Wheeler, W.M. (1920) The subfamilies of Formicidae, and other taxonomic notes. *Psyche* (Cambridge), 27, 46–55.
- Wilson, E.O. (2003) *Pheidole in the New World. A dominant, hyperdiverse ant genus*. Harvard University Press, Cambridge, Massachusetts, [ix] + 794 pp.
- Wilson, E.O., Carpenter, F.M. & Brown, W.L., Jr. (1967) The first Mesozoic ants, with the description of a new subfamily. *Psyche* (Cambridge), 74, 1–19.
- Wilson, E.O. & Hölldobler, B. (2005) The rise of the ants: a phylogenetic and ecological explanation. *Proceedings of the National Academy of Sciences U. S. A.*, 102, 7411–7414.

