



# Taxonomy, Phylogenetics, and Evolution

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## 1.1 Introduction

Since their origin about 120 million years ago (Mya), ants have evolved to become the most species-rich and ecologically diverse group of social insects (Grimaldi and Engel 2005; Hölldobler and Wilson 1990). Currently there are about 12,500 described species of extant ants (Bolton *et al.* 2006), but this statistic is undermined by several sources of uncertainty. On the one hand, as taxonomic knowledge improves, some of these species names will prove to be redundant (synonyms of older names). On the other hand, it is also evident that there are many ant species remaining to be discovered and/or formally described. In recent taxonomic monographs the number of new synonyms is typically less than the number of new species, sometimes by a wide margin (e.g. Bolton 2000, 2007, Wilson 2003), suggesting that the total diversity of ants could well exceed 25,000 species.

Ant systematics is concerned with delimiting species and understanding the phylogenetic relationships among them. Demarcation of ant species typically entails detailed morphological scrutiny of the worker caste – supplemented by examination of queens and males, if available – with the aim of discovering phenotypic gaps that indicate the existence of distinct evolutionary lineages (Ward 2001). Phylogenetics involves application of various methods of inference in an attempt to estimate the historical relationships among taxa. In recent years there has been a surge of interest in ant phylogeny, with DNA sequences supplanting morphology as the principal source of evidence. Such molecular

studies promise to provide robust phylogenies that will be of great benefit to ant ecologists and behaviourists. This phylogenetic knowledge is also leading to an improved higher classification of ants, one that reflects the main features of evolutionary history. Species-level taxonomy has advanced more fitfully than ant phylogenetics, however, and a great deal remains to be accomplished before most ant species are well characterized (Ward 2007c).

This chapter summarizes recent progress in ant phylogeny and provides an outline of the higher classification of ants that is consistent with this new knowledge. The major lineages of ants are identified and features of their biology are discussed. The state of species-level taxonomy is evaluated, and resources that are available to ecologists for the identification of ant species and genera are documented. The emphasis is on extant taxa, with occasional reference to the fossil record where relevant to the discussion. Ant biogeography is considered in Chapter 2 of this volume by Fisher.

## 1.2 Phylogeny: inferring the evolutionary history of ants

Our knowledge of ant phylogeny has improved remarkably over the last decade. Several factors have contributed to this: a new comprehensive classification of ants based on reevaluation of the morphological evidence (Bolton 2003), a series of molecular phylogenetic studies employing multiple nuclear genes (Brady 2003; Brady *et al.* 2006; Moreau *et al.* 2006; Rabeling *et al.* 2008; Schultz and

Brady 2008a; Ward and Downie 2005), and new fossil discoveries (Dlussky *et al.* 2004; Engel and Grimaldi 2005; Grimaldi and Agosti 2000; Nel *et al.* 2004; Perrichot *et al.* 2008a; Perrichot *et al.* 2008b). As a result we are now at a stage where the broad outlines of ant evolutionary history are becoming apparent. This situation was preceded by an earlier period of uncertainty and disagreement over the relationships among the main lineages of ants, and a lack of consensus on the delimitation of these lineages (Baroni Urbani *et al.* 1992; Brown 1954; Grimaldi *et al.* 1997; Taylor 1978; Wilson *et al.* 1967). In retrospect it seems that these difficul-

ties arose because of insufficient appreciation of the potential for extensive morphological convergence, especially in the worker caste, from which most evidence about ant phylogeny had been taken.

Twenty-one extant subfamilies of ants are currently recognized, and for most of these there is compelling evidence of monophyly (Rabeling *et al.* 2008; Ward 2007c). From molecular phylogenetic studies it is now evident that most of these subfamilies belong to a well-supported group, known as the formicoid clade (Figure 1.1). This includes three large ant subfamilies, Dolichoderinae, Formicinae, and Myrmicinae, as well as army ants and relatives

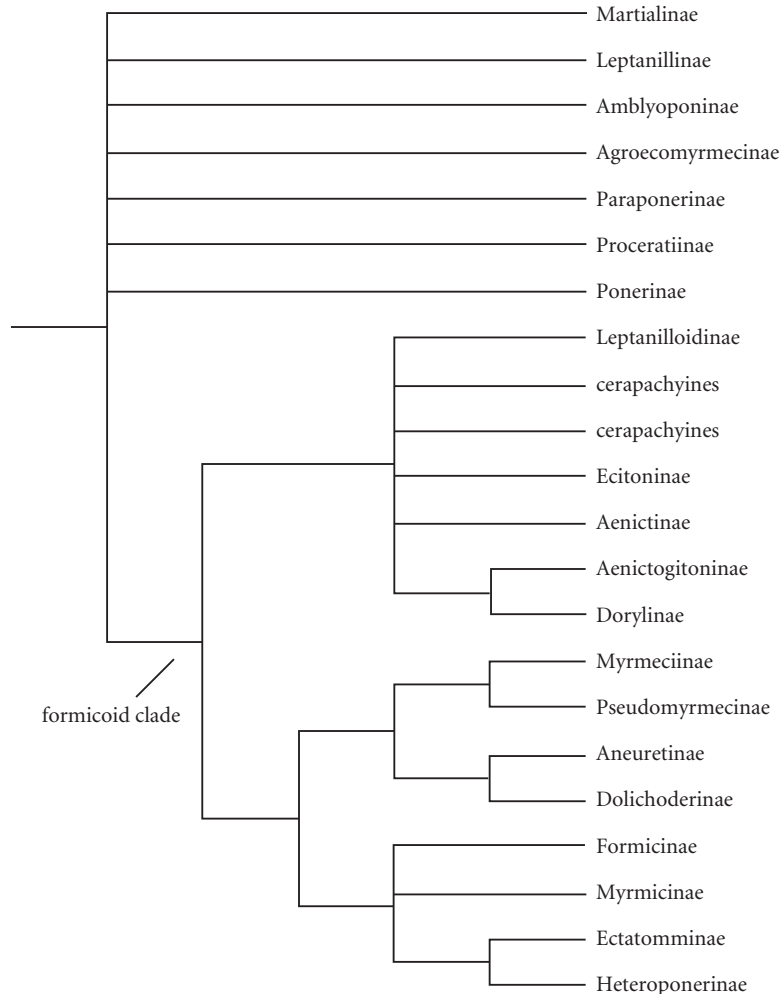


Figure 1.1 Summary of well supported relationships among the extant ant subfamilies. Modified from Ward (2007c).

(dorylomorphs), bulldog ants (Myrmecinae), big-eyed arboreal ants (Pseudomyrmecinae), and a scattering of other smaller groups. No single morphological feature has been discovered that distinguishes formicoids from other ants but they emerge as a solid group in all molecular phylogenetic analyses (Brady *et al.* 2006; Moreau *et al.* 2006; Ohnishi *et al.* 2004; Ouellette *et al.* 2006; Saux *et al.* 2004; Ward and Brady 2003; Ward and Downie 2005).

The evolutionary history of formicoid ants is becoming increasingly well known. At the base of the formicoid tree, as sister to the others, is the well-supported dorylomorph clade, comprising army ants, cerapachyines, and leptanilloidines. Within this group, the subfamily Cerapachyinae is not monophyletic, however, and the question of army ant monophyly remains an open one (cf. Brady 2003), although the enigmatic subfamily Aenictogitoninae, known until recently only from isolated males, is now clearly shown to be sister to army ants in the genus *Dorylus* (Brady *et al.* 2006). Additional research is needed to resolve relationships among the cerapachyine lineages and to clarify the history of army ant evolution within the dorylomorph clade.

Among the remaining formicoids there is strong support for five major clades: (a) myrmeciomorphs, consisting of Myrmecinae and Pseudomyrmecinae; (b) dolichoderomorphs (Dolichoderinae and Aneuretinae); (c) ectaheteromorphs (Ectatomminae and Heteroponerinae); (d) Myrmicinae; and (e) Formicinae. Inferred relationships among these groups are shown in Figure 1.1. The last three clades are treated as a trichotomy because current molecular data cannot clearly resolve relationships among them.

Outside the formicoids we can recognize two major groups of ants: (a) highly modified subterranean species belonging to the subfamily Leptanillinae, and (b) five 'poneroid' subfamilies (Agroecomyrmecinae, Amblyoponinae, Paraponerinae, Ponerinae, and Proceratiinae). The relationship of poneroids and leptanillines to one another and to the formicoids remains uncertain. In some molecular phylogenetic analyses, Leptanillinae is recovered as sister to all other ants, with poneroids forming a clade that is sister to the formicoids (Brady *et al.* 2006; Moreau *et al.* 2006; Saux *et al.*

2004), but this result may be an artefact of long-branch attraction (Bergsten 2005; Holland *et al.* 2003) between leptanillines and aculeate wasp out-groups. When Brady *et al.* (2006) performed an unrooted analysis on a seven-gene data set, excluding aculeate wasp out-groups but including representatives of all ant subfamilies, they obtained a strongly supported bipartition between formicoids and all other ants. However, the poneroids could not be made monophyletic under any possible rooting of this tree, because Leptanillinae was nested *within* the poneroids close to Agroecomyrmecinae and Amblyoponinae. The root of the ant tree could still be on the leptanilline branch, but this would imply that poneroids are paraphyletic. Under the likelihood-based Shimodaira–Hasegawa test, Brady *et al.* (2006) could not reject alternate placements of the root within poneroids or on the bipartition separating poneroids plus leptanillines from formicoids.

The recent discovery of a bizarre new ant species from the Amazon rainforest has generated further insight and intrigue into questions of early ant evolution (Rabeling *et al.* 2008). Given the name *Martialis heureka*, this species has a pale, blind worker caste, and a suite of unusual morphological features (Figure 1.2). Based on Bayesian analyses of three nuclear genes (18S rDNA, 28S rDNA, and elongation factor 1- $\alpha$  F2), *Martialis* appears to be sister to all other extant ants, with Leptanillinae as sister to the remaining ants (Rabeling *et al.* 2008). It remains to be seen whether the inclusion of additional genes will strengthen support for this result. In any event, the prevalence of hypogaic habits in *Martialis*, Leptanillinae, and poneroids suggests that either the ancestral ant was subterranean and cryptic (contrary to the impression given by early ant fossils – discussed later) or that the surviving members of these old lineages have retreated to subterranean habitats, and convergently lost sight and pigment.

It is now clear that some features of worker ant morphology have indeed undergone greater convergence than previously realized. For example, the subfamily Agroecomyrmecinae, represented by the extant genus *Tatuidris*, had been placed in or near the Myrmicinae (Bolton 2003), on the basis of their common possession of



**Figure 1.2** The recent discovery of *Martialis heureka* in the Amazon rainforest near Manaus, Brazil, has shed light on the general pattern of ant evolution and radiation. The species is in a monotypic genus representing a new subfamily (Martialinae) that appears to be a sister lineage to all other living ants. (Photo: Rabeling *et al.* 2008)

certain features of abdominal morphology, including the presence of a postpetiole and tergosternal fusion of the petiole sclerites. Yet we now know that these two groups are only distantly related, with the Agroecomyrmecinae falling outside the formicoid clade. Within the formicoids there is an intermingling of taxa with both highly derived social behaviour and morphology as well as those with more generalized (ancestral) habits and appearance, suggesting that the characteristics associated with the derived taxa (such as trophallaxis, complex chemical communication, marked worker–queen differentiation, and worker caste polymorphism) arose independently multiple times.

The fossil record provides an additional source of information about the evolutionary history of ants, particularly concerning their first appearance and the timeline of their diversification. When considering the contribution of fossils, it is useful to make a distinction between crown group and stem group taxa (Magallón 2004). Crown group ants are

the clade composed of the most recent common ancestor of all extant ants and their descendants. Stem group ants are more inclusive, containing all organisms more closely related to ants than to any other extant taxa. We can employ the term ‘stem ants’ to refer to extinct taxa that are outside the crown group but that are inferred to be more closely related to ants than to any other living aculeate wasps. Comparable stem and crown group distinctions can be made at any level in the taxonomic hierarchy.

By this criterion the ant-like Cretaceous fossils assigned to the subfamilies Sphecomyrminae and Armaniinae (the latter is sometimes treated as its own family, Armaniidae) can be regarded as stem ants (Ward 2007c). They have been recorded from Cretaceous deposits ranging in age from about 80 to 100 Mya, mostly from the northern hemisphere (Perrichot *et al.* 2008a). Interestingly, a few putative crown group ants are known from the same time period, but assignment of most of these to extant subfamilies is problematic. An exception is the remarkable fossil *Kyromyрма neffi* from New Jersey amber (Turonian, 90 Mya). This taxon belongs to the Formicinae (Grimaldi and Agosti 2000) and establishes a minimum age of 90 million years for stem group formicines. Earlier in the Cretaceous there are fossil aculeate wasps, going as far back as 140 Mya (Grimaldi and Engel 2005), but no ants (Perrichot *et al.* 2008a).

Divergence date estimates based on molecular data that incorporate the full range of information from the hymenopteran fossil record suggest that crown group ants arose about 115–135 Mya (Brady *et al.* 2006). This is consistent with the fossil record (Grimaldi and Engel 2005) but contradicts other molecular studies that inferred a Jurassic origin for ants (Crozier *et al.* 1997; Moreau *et al.* 2006).

Ants are scarce as Cretaceous fossils and increase markedly in abundance in Tertiary deposits (Grimaldi and Agosti 2000), making up 5% of all insects in Baltic amber (Eocene), 20% in Florissant shales (early Oligocene), and 36% in Dominican amber (Dlussky and Rasnitsyn 2003). The increasing ascendance of ants in the Paleogene has been attributed to codiversification with angiosperms (Moreau *et al.* 2006; Wilson and Hölldobler 2005), with the success of ants being linked to the

development of angiosperm forests with a complex leaf litter layer, and to the tending of honeydew-producing hemipterans. This is an intriguing idea, but a rigorous test remains elusive.

### 1.3 Higher classification: a survey of the major lineages

Table 1.1 provides an outline of the higher classification of ants that is consistent with the new findings about phylogeny. In this Section I briefly review the biology and distribution of these groups at the subfamily level. Brown (2000) produced a useful compendium of similar information, arranged by genus.

#### 1.3.1 Martialinae

This new subfamily was erected for a remarkable ant species discovered recently in lowland Amazon rainforest near Manaus, Brazil (Rabeling *et al.* 2008). *Martialis heureka* is known from a single stray worker collected on the rainforest floor at dusk. Judging from its pale cuticle, absence of eyes, and small size (~2.5 mm in length) *Martialis* is likely to be a hypogaecic species, foraging in concealed locations. The enlarged fore legs, bulbous head, and elongate, slender mandibles suggest specialized predatory habits. Great interest awaits the discovery of additional specimens of *Martialis* and the elucidation of its biology.

#### 1.3.2 Leptanillinae

Leptanillines are small to minute, pale, blind ants, known only from tropical and warm temperate regions of the Old World. Colonies of these ants are apparently restricted to subterranean habitats, and the most frequent indication of their presence is the occurrence of males in light traps and pan traps (Robertson 2000). Little is known about the biology of most leptanillines, but Masuko (1990) documented nomadic, army ant-like behaviour in *Leptanilla japonica*, whose workers prey on geophilomorph centipedes. He also discovered that the adult ants feed on larval haemolymph from a special gland located on the fourth abdominal segment (Masuko 1989). Queens of Leptanillini are wingless and

dichthadiiform, while those of Anomalomyrmini are deciduously winged (Baroni Urbani and de Andrade 2006; Bolton 2003).

#### 1.3.3 Poneroids

Poneroids are a heterogeneous assemblage of ants that represents either a grade or a clade at the base of the ant tree (discussed earlier). One of the more unusual groups in this assemblage is the subfamily Agroecomyrmecinae, consisting of an extant genus of Neotropical ants (*Tatuidris*), whose small cryptic workers are associated with rainforest leaf litter, and two fossil genera, described from Colorado Florissant shales and Baltic amber, respectively (Bolton 2003; Brown and Kempf 1968). Nothing is known about the biology of these ants. Based on the specialized mandibles and well-developed sting, Brown and Kempf (1968) speculated that the ants attack ‘some active or slippery live arthropod prey in the soil or soil cover’. The unique species *Paraponera clavata*, the sole living representative of the subfamily Paraponerinae (Bolton 2003), emerges in some molecular analyses as sister to *Tatuidris*. *P. clavata* is a large aggressive ant that inhabits Neotropical rainforests. Workers are generalist predators and scavengers, and also collect substantial quantities of extrafloral nectar (Young and Hermann 1980).

The Amblyoponinae (~100 described species) comprise several genera of ants with distinctive morphology and specialized predatory behaviour (Brown 1960). The workers are small-eyed and generally cryptic in their foraging habits. Recorded prey items include geophilomorph centipedes, beetle larvae, and diplurans. Workers have been shown to consume larval haemolymph by puncturing the integument at specific locations (Masuko 1986; Wild 2005). Members of the genus *Onychomyrmex* exhibit nomadic behaviour and synchronized brood cycles in the manner of army ants (Miyata *et al.* 2003). Amblyoponines are found in all biogeographic regions, but they are most common in forested habitats. They are often treated as exemplars of ‘primitive’ ant behaviour (Thorne and Traniello 2003), although some of their traits are highly derived.

The subfamily Proceratiinae (~120 species) is another group of specialized predators with hypogaecic nesting and foraging habits. The eyes of the

**Table 1.1.** A higher classification of extant ants (Hymenoptera: Formicidae) consistent with recent molecular phylogenetic findings. The table lists currently valid names of subfamilies (-inae) and tribes (-ini). Extinct taxa are excluded. Groups that are known or suspected to be non-monophyletic—as they are currently defined—are marked with an asterisk. A few of these taxa can be readily transformed into monophyletic groups (e.g., Ponerini becomes a clade when Thaumatomyrmecini is subsumed within it) but others represent more problematic situations. Based on Engel and Grimaldi (2005), Bolton *et al.* (2006), Brady *et al.* (2006), Ward (2007b), Rabeling *et al.* (2008) and Ward *et al.* (2009).

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<b>Martialine clade</b>	*Ectatommini
Martialinae	Typhlomyrmecini
<b>Leptanilline clade</b>	Heteroponerinae
Leptanillinae	<b>Formicoid clade: Formicinae</b>
Anomalomyrmini	Formicinae
Leptanillini	Camponotini
<b>*Poneroids</b>	Dimorphomyrmecini
Agroecomyrmecinae	Formicini
*Amblyoponinae	Gigantiopini
Paraponerinae	*Lasini
Ponerinae	Melophorini
Platythyreini	Myrmecorhynchini
*Ponerini	Myrmoteratini
Thaumatomyrmecini	Notostigmatini
Proceratiinae	Oecophyllini
Probolomyrmecini	*Plagiolepidini
Proceratiini	<b>Formicoid clade: Myrmicinae</b>
<b>Formicoid clade: dorylomorphs</b>	Myrmicinae
Aenictinae	Adelomyrmecini
Aenictogitoninae	Ankylomyrmini
*Cerapachyinae	Attini
Acanthostichini	Basicerotini
*Cerapachyini	Blepharidattini
Cylindromyrmecini	Cataulacini
Dorylinae	Cephalotini
Ecitoninae	Crematogastrini
Cheliomyrmecini	*Dacetini
*Ecitonini	*Formicoxenini
Leptanilloidinae	Lenomyrmecini
<b>Formicoid clade: myrmeciomorphs</b>	Liomyrmecini
Myrmeciinae	Melissotarsini
Myrmeciini	Meranoplini
Prionomyrmecini	Metaponini
Pseudomyrmecinae	Myrmecinini
<b>Formicoid clade: dolichoderomorphs</b>	*Myrmicini
Aneuretinae	Paratopulini
Dolichoderinae	Phalacromyrmecini
Bothriomyrmecini	*Pheidolini
Dolichoderini	*Solenopsidini
Leptomymecini	Stegomyrmecini
Tapinomini	*Stenammini
<b>Formicoid clade: ectaheteromorphs</b>	Tetramoriini
Ectatomminae	

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workers are reduced or absent. These ants are widespread but infrequently encountered in tropical and warm temperate regions, nesting in the ground or in rotten wood. Species of *Proceratium* and *Discothyrea* have been recorded preying on eggs of spiders and other arthropods (Brown 1980).

The largest and most diverse of the poneroid subfamilies is the Ponerinae, with more than 1,100 described species (Bolton *et al.* 2006). These are predacious ants, and include both large-eyed epigaeic (above-ground foraging) species as well as small-eyed hypogaeic taxa. Ponerines are widespread in warm temperate and tropical habitats, becoming especially abundant in the wet tropics. While most species appear to be rather generalized in their choice of prey, some have become specialized hunters of particular kinds of arthropods such as termites, millipedes, and isopods (Hölldobler and Wilson 1990). A few ponerine species have acquired group-raiding and nomadic behaviour (Maschwitz *et al.* 1989).

### 1.3.4 Dorylomorphs

This is a very distinctive clade of mostly tropical ants, that includes not only army ants (Aenictinae, Aenictogitoninae, Dorylinae, and Ecitoninae) but also the core group (cerapachyines) from which they evidently evolved. The army ants possess a unique suite of characteristics: mass foraging, nomadism, and highly modified (dichthadiiform) queens (Brady 2003). The more common species have been the subject of extensive scientific study (summary in Gotwald 1995). Much less attention has been focused on the biology of cerapachyine ants. Most *Cerapachys* species appear to be brood predators of other ants, while species of *Acanthostichus* and *Cylindromyrmex* are reported to prey on termites (Brown 1975). Also included in the dorylomorph clade is the subfamily Leptanilloidinae, a small group of blind, subterranean ants confined to the New World tropics (Brandão *et al.* 1999; Ward 2007b).

### 1.3.5 Myrmeciomorphs

The myrmeciomorphs comprise two groups of active, large-eyed stinging ants: the Myrmeciinae

(~100 species) and the Pseudomyrmecinae (~300 species). There are two extant genera of myrmeciines, *Myrmecia* and *Nothomyrmecia*, both confined to the Australian region. The fossil record reveals that myrmeciines were formerly present in South America and the northern hemisphere (Archibald *et al.* 2006; Ward and Brady 2003). The living species of Myrmeciinae are generalist predators and scavengers and they nest mostly in the ground. In contrast, ants in the subfamily Pseudomyrmecinae are almost exclusively arboreal, nesting in dead twigs and, in a minority of cases, in live plant domatia (Ward 1991). Pseudomyrmecines are widespread in tropical Africa and Australasia, but reach their highest diversity in the New World tropics (Ward and Downie 2005).

### 1.3.6 Dolichoderomorphs

The subfamily Dolichoderinae is one of the 'big three' among the formicoids, with about 880 described species and a worldwide distribution. These ants are generalist scavengers and predators, and avid consumers of hemipteran honeydew. In many ant communities – but especially in Australia – they are among the most numerically and behaviourally dominant ants (Andersen 1995). Dolichoderines have produced several prominent invasive species, most notably the Argentine ant (*Linepithema humile*) which has severely disrupted native ant communities in most places where it has been introduced (Holway *et al.* 2002a; see also Part IV). The sister taxon to Dolichoderinae is the Aneuretinae, represented by a single living species confined to the wet forests of Sri Lanka (Wilson *et al.* 1956). Aneuretines were more widespread and diverse in the past, being known from Paleogene fossils in Europe, Asia, and North America (Dlussky and Rasnitsyn 2003).

### 1.3.7 Ectaheteromorphs

The two subfamilies, Ectatomminae (~260 species) and Heteroponerinae (22 species), that make up this group were previously placed in the Ponerinae (*sensu lato*). Most ectaheteromorphs appear to be generalist predators and scavengers but some

species in the genus *Gnamptogenys* have become specialized predators on millipedes, beetles, and other ants (Lattke 1995). Ectatomminae and Heteroponerinae are widespread and mostly tropical or subtropical in distribution but they are absent from the Afrotropical region.

### 1.3.8 Myrmicinae

This is the largest of all ant subfamilies, with more than 6,700 described species and many others awaiting description. Myrmicines encompass an extraordinary range of foraging behaviours, nesting habits, and colony structure. They include omnivores, generalized predators and scavengers, specialist predators, seed harvesters, primitive fungus-growers, and leaf-cutting ants (Hölldobler and Wilson 1990). They are found on all major land masses and in essentially all habitats occupied by ants. Myrmicines well known to the public include fire ants (*Solenopsis* spp.), leaf-cutting ants (*Atta*, *Acromyrmex*), and seed harvesters (*Pogonomyrmex*, *Messor*).

### 1.3.9 Formicinae

The subfamily Formicinae is another cosmopolitan group, with about 3,600 described species. Formicines are very diverse in nesting and feeding habits, although in comparison to myrmicines they show less of a tendency towards reduction in size and occupation of concealed microhabitats. Most species appear to be generalist predators and scavengers; specialized predation is rare (Hölldobler and Wilson 1990). A few formicine lineages are predominantly hypogaecic and have developed trophobiotic relationships with subterranean root-feeding hemipterans. Familiar formicines include carpenter and sugar ants (*Camponotus*), wood ants and congeners (*Formica*), honeypot ants (*Myrmecocystus*), and weaver ants (*Oecophylla*).

## 1.4 Species-level taxonomy and identification

For most ant ecologists the aspect of ant systematics of greatest practical importance is the availability of tools for species identification. This in turn depends on the quality of species-level taxonomic research

that has been carried out. Progress in ant species delimitation has been mixed, however, and overshadowed in recent years by advances in ant phylogeny. We are a long way from having the ability to recognize most species of ants, especially in the species-rich tropics. This inability to employ species names of universal applicability (Box 1.1) results in a continuing impediment to studies of ant biology.

The rate of description of new ant species was quite modest until the middle of the nineteenth century (Ward 2007c). Then the pace picked up as ant specialists appeared on the scene, and descriptive activity reached a peak in the early twentieth century when myrmecologists such as Emery, Forel, Santschi, and Wheeler engaged in prolific naming of numerous ant species, subspecies, and 'varieties'. Unfortunately many of these named taxa were poorly characterized, described in isolation from related species, and not incorporated into a more comprehensive taxonomic framework. In the last 60 years infraspecific taxa have been abandoned in ant taxonomy, and a 'population perspective' of species-level variation has been gradually adopted. But the earlier legacy of uncertain and dubious names is still with us and retards progress, especially in large widespread genera such as *Pheidole*, *Camponotus*, and *Crematogaster*.

There are also features intrinsic to ants that make species delimitation challenging (see Box 1.2). The worker caste is the most readily available form and the one on which most ant taxonomy is based. Yet workers often exhibit less pronounced differences among species than the sexual queens and males. Interspecific differences can also be obscured by worker caste polymorphism within species. Recent reports of cryptic species of ants (Pusch *et al.* 2006; Schlick-Steiner *et al.* 2006b), clonal reproduction (Foucaud *et al.* 2007; Kobayashi *et al.* 2008; Pearcy *et al.* 2004), and hybridization (Feldhaar *et al.* 2008; Helms-Cahan *et al.* 2002; Schwander *et al.* 2007) add further complications to the task of inferring species boundaries in ants.

Despite this, the situation for identification of ant species continues to improve. The generic classification of ants is relatively stable, and keys for identification of ant genera are widely available. Bolton's guide (1994) to ant genera of the world is the gold standard. There are also up to date

**Box 1.1 Applications of taxonomy: why should we name ants?****Philip S. Ward**

Scientific names are labels applied to taxa to aid in communication. Under the conventions of the current (fourth) edition of the *International Code of Zoological Nomenclature* (ICZN) (International Commission on Zoological Nomenclature 1999), animal species have compound names, comprising the genus name (first letter capitalized) and the species name (all lower case), with the name of the author, the person who described the species, as an optional third component. The year of publication of the original species description may also be inserted after the author's name. If the author's name is placed in parentheses, this signifies that he or she originally described the species in a genus different from the one in which it is currently placed. For example, *Lasius flavus* (Linnaeus, 1758) was originally described by Linnaeus in the genus *Formica*, and later transferred to *Lasius*.

Such generic transfers occur because taxonomists refine their concepts of the limits of a given genus or other higher taxon (tribe, subfamily, etc.). For example, the 17 species of ants described by Linnaeus (1758) were all placed in the genus *Formica*, but they are now allocated to 11 different genera in four subfamilies (Ward 2007c). The higher-level classification of ants has gradually stabilized, however, to the point where about 290 extant genera are currently recognized (Bolton *et al.* 2006), and this number is not likely to change radically.

The ICZN specifies rules for determining whether a scientific name is available (properly published) and valid (considered the correct name for a taxon). If two or more different names have been proposed for what is considered to be the same species then, in general, the oldest available name becomes the valid name, while the younger name is relegated to the status of junior synonym (an invalid name). Junior synonyms are common in ant taxonomy,

largely due to a spate of species descriptions that occurred in the late nineteenth and early twentieth centuries, often unaccompanied by clear diagnostic features. At that time, names were also commonly applied to intraspecific forms (subspecies, varieties), a practice now largely abandoned in ant taxonomy.

An ant species by any other name would smell as sweet (or foul), but sharing information about the species is greatly facilitated by having a universal label. The scientific name of a species provides a link to information about phylogenetic relationships, distribution, ecology, behaviour, and other aspects of the species' biology. When non-systematists study ants there is sometimes a tendency – encouraged by situations where taxonomic knowledge is incomplete or inaccessible – to identify specimens to genus only and then assign morphospecies tags (*Pheidole* sp. A., *Pheidole* sp. B., etc.). This precludes linkage to other studies of the same species identified with different monikers, and as a result the development of global knowledge about the species is inhibited. In some instances there may be no other option, but it is then especially important to deposit voucher specimens in a public institution so that species identities can be checked by future investigators. This is true even for specimens identified to species – the identifications might be in error, or concepts of species limits might change in the future.

At a more applied level, having a unique and universal label for each ant species enhances our ability to use these organisms in biodiversity assessment and conservation planning. In particular, if we wish to evaluate not just local richness (alpha-diversity) but also species turnover (beta-diversity), or if we seek to understand the phylogenetic heritage of ant communities, then accurate identification of species assumes critical importance.

## Box 1.2 How to identify ants

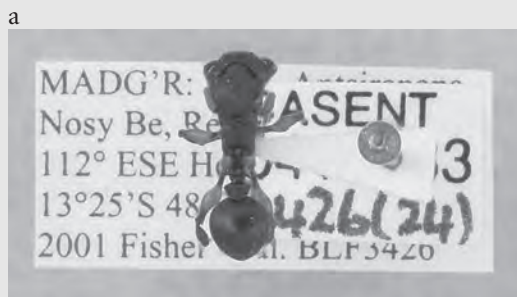
Brian L. Fisher

There is a great satisfaction and reward in establishing the identity of an ant, especially if it is one you encountered in the field. After spending days or weeks collecting and preparing a series of specimens, there is nothing like that first look under the scope. What do these ants have to tell us about their species, their environment, and their place on the planet?

To answer these questions, you must first identify the genus and species of the ant. In theory, identification should be a straightforward process of comparing characteristics in published keys. In practice, however, the technical background required and the paucity of taxonomic references represent considerable challenges. Ants may be among the most dominant and important groups of terrestrial organisms, but we have a long way to go before taxonomic knowledge and identification tools for this group matches those of birds and butterflies.

lection data, including locality name, latitude and longitude (using the decimal degrees format to an accuracy of five decimal places), elevation, date, habitat, method, and collector.

Learn to be skilled at point-mounting (Fig. 1.2.1), and practise it regularly. Properly label specimens, and always deposit voucher specimens at a museum of your choice. Learn ant morphology (Fig. 1.2.2). The glossary in Bolton (1994) provides a solid foundation in morphological terminology for ants, and Richards (1977) provides the same for the broader Hymenoptera. With this background and preparation, both online and printed resources (e.g. Bolton 1994; Bolton 2003; www.AntWeb.org) can help to distinguish the worker castes of the more than 280 described ant genera. With experience, identification to a genus is possible in the field using a 20x hand lens.

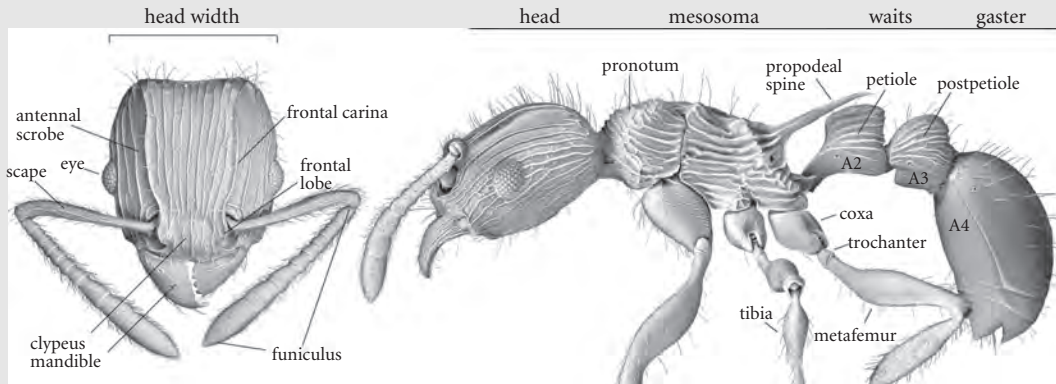


**Figure 1.2.1** Views from above and side of a point-mounted ant specimen showing position of ant on point and labels on pin. The specimen here is *Terataner alluaudi* from Madagascar. (Photos: www.AntWeb.org and Erin Prado)

Like any task worth doing, ant identification demands some preparation. First, collect the specimens into 95% EtOH. Because of intra-specific variation, be sure to obtain an adequate series of workers and soldier castes and, if present, queens and males. For each collection, record at least minimal locality and col-

continues

## Box 1.2 continued



**Figure 1.2.2** Common morphological features used to identify ant genera and species. Measurements are often necessary to distinguish similar species. Abdominal segments A2-A4 are indicated. Shown here is a worker of *Tetramorium* from Madagascar.

Not all genera, however, are well defined or identified, even based on the worker caste (Brady *et al.* 2006; Ward 2007c), and keys to genera based on males are lacking for most regions (Yoshimura and Fisher 2007).

Molecular analyses and faunal inventories will allow a more comprehensive diagnosis of clades (i.e. genera) based on characters from workers, queens, and males, and will remain an active and productive area of research over the next decade.

The next step in the enterprise, species-level identification, is often fraught with frustration and failure. The odds are stacked against you, since as many as half of all ant species have yet to be described. Furthermore, keys for many groups are non-existent, and published species descriptions are not much help since many species were described in isolation without comparisons to similar taxa (Ward 2007c). Meanwhile, differences among polymorphic worker and soldier castes within a species may obscure the subtle differences that exist between species. Many characters are used to identify ants at the species level, including hairs (location, number, length, shape, direction), scape (shape, length), mandible (shape, length, dentition), sculpturing, spines (location,

length), head (width, length), and eye (location, size). Complicating the process further is the fact that population differentiation and speciation are ongoing, meaning that intermediates and hybrids are to be expected occasionally. The bottom line is that species-level taxonomy in ants is difficult.

The good news is that several changes underway are facilitating the practice of good taxonomy and the publication of user friendly keys: (a) Taxonomic resources are increasingly available in digital format. (b) Large-scale inventories are capturing specimens across their entire range of variation. (c) DNA techniques are facilitating the linkage of sexes and castes, highlighting taxa requiring further study (Fisher and Smith 2008). (d) The identification of monophyletic species groups, especially in hyperdiverse genera such as *Pheidole*, *Monomorium*, *Solenopsis*, *Crematogaster*, and *Camponotus*, provide smaller taxonomic units for taxonomic study (divide and conquer). (e) The use of matrix-based online interactive keys such as Lucidcentral.org provide flexibility in character selection during identification and are updatable as new species are discovered.

**Box 1.2 continued**

For many of us, the delimitation of higher ant taxa and species cannot happen fast enough. In the meantime, a taxonomist's best options are to consult the literature (Bolton 2003, and see Table 1.2) and scan the Web for regional keys and images. In

many cases an expert may be needed to confirm your identifications. Your chances of having an expert look at your material increases if you first mount, label, and sort specimens to morphospecies, labelling them with your tentative identifications.

regional keys to ant genera of Central Europe (Seifert 2007), Japan (Imai *et al.* 2003), Taiwan (Lin and Wu 2003), Borneo (Hashimoto 2003), North America (Fisher and Cover 2007), the Neotropics (Palacio and Fernández 2003), and Australia (Shattuck 1999). Within the last three decades, several large ant genera and numerous smaller ones have received the benefit of global species-level revisions or comprehensive treatment over large geographic regions. For some countries in Europe and Asia, there are well illustrated identification guides for all ant species (e.g. Imai *et al.* 2003; Seifert 2007). Identification resources and high-quality images of ants are becoming increasingly available on the internet, through such sources as AntWeb ([www.AntWeb.org](http://www.AntWeb.org)), Antbase ([www.antbase.org](http://www.antbase.org)), Australian

Ants Online (<http://anic.ento.csiro.au/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>).

The literature concerned with species identification of ants is quite scattered, but Brown (2000) and Bolton (2003) provide helpful documentation. For identification of ants from specific regions or countries, researchers are advised to first consult the list in Bolton (2003: 78–9). Under the treatment of individual subfamilies and genera Bolton (2003) also indicates what species keys, if any, are available. More recent publications that are not cited in Bolton (2003) are listed in Table 1.2.

**Table 1.2** Recently published ant species identification keys not cited in Bolton (2003).

Taxon	Region/Country	Reference(s)
Formicidae	Central Europe	Seifert (2007)
Formicidae	Serbia and Montenegro	Petrov (2006)
Formicidae	North Korea	Radchenko (2005a)
Formicidae	Micronesia	Clouse (2007)
Formicidae	Socotra Archipelago	Collingwood <i>et al.</i> (2004)
Poneroids, ectaheteromorphs	Colombia	Jiménez <i>et al.</i> (2008)
<i>Acropyga</i>	Worldwide	LaPolla (2004); LaPolla and Fisher (2005)
<i>Adelomyrmex</i>	Worldwide	Fernández (2003)
<i>Aenictus</i>	Australia	Shattuck (2008b)
<i>Allomerus</i>	Neotropical	Fernández (2007a)
<i>Anochetus</i>	Malagasy	Fisher and Smith (2008)
<i>Aphaenogaster</i>	Australia	Shattuck (2008a)
<i>Axinidris</i>	Afrotropical	Snelling (2007)
<i>Azteca</i>	Costa Rica	Longino (2007)
<i>Basiceros</i>	Neotropical	Feitosa <i>et al.</i> (2007)
<i>Camponotus</i>	Australia	McArthur (2007)
<i>Camponotus</i>	Poland	Suchocka <i>et al.</i> (2008)
<i>Camponotus</i> ( <i>Karavaievia</i> )	Southeast Asia	Dumpert <i>et al.</i> (2006)

<i>Camponotus (festinatus group)</i>	United States	Snelling (2006)
<i>Carebara</i>	New World	Fernández (2004, 2006)
<i>Carebara</i>	China	Xu (2003)
<i>Centromyrmex</i>	Afrotropical	Bolton and Fisher (2008a)
<i>Crematogaster</i>	Morocco	Cagniant (2005)
<i>Crematogaster (Physocrema)</i>	Indochinese Peninsula	Hosoishi and Ogata (2008)
<i>Diacamma</i>	Australia	Shattuck and Barnett (2006)
<i>Eurhopalothrix</i>	Neotropical	Ketterl <i>et al.</i> (2004)
<i>Forelius (part)</i>	New World	Guerrero and Fernández (2008)
<i>Formica (pallidefulva group)</i>	Nearctic	Trager <i>et al.</i> (2007)
<i>Gnamptogenys</i>	Oriental and Australian	Lattke (2004)
<i>Gnamptogenys</i>	New World	Lattke <i>et al.</i> (2007)
<i>Lachnomyrmex</i>	Neotropical	Feitosa and Brandão (2008)
<i>Lasius (Dendrolasius)</i>	East Palearctic	Radchenko (2005b)
<i>Leptothorax</i>	East Palearctic	Radchenko (2004)
<i>Linepithema</i>	New World	Wild (2007b)
<i>Lordomyrma</i>	Fiji	Sarnat (2006)
<i>Mayriella</i>	Oriental and Australian	Shattuck (2007); Shattuck and Barnett (2007)
<i>Meranoplus (part)</i>	Australia	Andersen (2006)
<i>Meranoplus (diversus group)</i>	Australia	Schödl (2007)
<i>Metapone</i>	Madagascar	Alpert (2007)
<i>Monomorium</i>	Madagascar	Heterick (2006)
<i>Monomorium</i>	Neotropical	Fernández (2007b)
<i>Mycetarotes</i>	Neotropical	Mayhé-Nunes and Brandão (2006)
<i>Mycocepurus</i>	North and Central America	Mackay <i>et al.</i> (2004)
<i>Myrmelachista</i>	Costa Rica	Longino (2006)
<i>Myrmica (social parasites)</i>	Palaearctic	Radchenko and Elmes (2003)
<i>Myrmica</i>	Korea	Lyu (2006)
<i>Mystrium</i>	Indo-Australian	Bihn and Verhaagh (2007)
<i>Neivamyrmex</i>	United States	Snelling and Snelling (2007)
<i>Nesomyrmex</i>	Southern Africa	Mbanyana and Robertson (2008)
<i>Odontomachus</i>	Malagasy	Fisher and Smith (2008)
<i>Oxyepoecus (vezenyii group)</i>	Neotropical	Albuquerque and Brandão (2004)
<i>Perissomyrmex</i>	Worldwide	Zhou and Huang (2006)
<i>Perissomyrmex</i>	Worldwide	Ogata and Okido (2007)
<i>Peronomyrmex</i>	Australia	Shattuck (2006)
<i>Pheidologeton</i>	China	Zhou <i>et al.</i> (2006)
<i>Pheidole</i>	Northern Vietnam	Eguchi (2008)
<i>Pheidole (roosevelti group)</i>	Fiji	Sarnat (2008)
<i>Phrynonoponera</i>	Afrotropical	Bolton and Fisher (2008b)
<i>Polyrhachis</i>	India	Karmaly (2004)
<i>Polyrhachis</i>	Sulawesi	Kohout (2008b)
<i>Polyrhachis (Aulacomyrma)</i>	Melanesia	Kohout (2007b)
<i>Polyrhachis (Campomyrma)</i>	Borneo	Kohout (2007a)
<i>Polyrhachis (Cyrtomyrma)</i>	Borneo, Melanesia, Australia	Kohout (2006)
<i>Polyrhachis (flavoflagellata-grp)</i>	Southeast Asia	Kohout (2008a)
<i>Prionopelta</i>	Indo-Pacific	Shattuck (2008c)
<i>Pristomyrmex</i>	Philippines	Zettel (2006)
<i>Probolomyrmex</i>	Oriental	Eguchi <i>et al.</i> (2006)
<i>Proceratium</i>	Worldwide	Baroni Urbani and de Andrade (2003)

(Continued)

Table 1.2 Continued

Taxon	Region/Country	Reference(s)
<i>Pyramica</i>	China	Xu and Zhou (2004)
<i>Rogeria</i>	Guyana	Lapolla and Sosa-Calvo (2006)
<i>Solenopsis</i>	Galápagos Islands	Pacheco <i>et al.</i> (2007)
<i>Stegomyrmex</i>	Neotropical	Feitosa <i>et al.</i> (2008)
<i>Strumigenys</i>	China	Zhou and Xu (2003)
<i>Technomyrmex</i>	Worldwide	Bolton (2007)
<i>Technomyrmex</i>	New World	Fernández and Guerrero (2008)
<i>Temnothorax</i>	southeast United States	Deyrup and Cover (2004)
<i>Temnothorax</i>	East Palearctic	Radchenko (2004)
<i>Tetramorium (chefkети complex)</i>	Palearctic	Csoz <i>et al.</i> (2007)
<i>Tetramorium (tortuosum group)</i>	México	Vásquez-Bolaños (2007)
<i>Tetraopenera</i>	China	Xu and Chai (2004)
<i>Tetraopenera (ambigua group)</i>	Afrotropical	Ward (2006)
<i>Trachymyrmex (part)</i>	New World	Mayhé-Nunes and Brandão (2005, 2007)
<i>Trachymyrmex</i>	Nearctic	Rabeling <i>et al.</i> (2007)
<i>Wasmannia</i>	New World	Longino and Fernández (2007)

### 1.5 Future directions in species delimitation

Effective species-level taxonomy requires the accumulation and comparison of large population samples and an intelligent consideration of the factors generating intra- and interspecific variation. By its very nature this work is laborious, and requires sustained dedication of time and energy. New developments in technology can be employed to facilitate many aspects of the process, however. Improvements in imaging (e.g. the Automontage system) allow colour illustrations of unprecedented quality to become a standard feature in taxonomic revisions. We can envisage a time in the near future when colour images of most of the world's described ants, including type specimens, will be available online, along with the relevant taxonomic literature. For working taxonomists this will largely obviate the need for expensive museum visits to Europe, where many of the type specimens of the numerous poorly characterized ant taxa have been deposited. Electronic capture of specimen data and measurements will continue to facilitate the analysis and dissemination of this information. Interactive keys such as Lucid ([www.lucidcentral.org](http://www.lucidcentral.org)) offer increased flexibility for species identification

and more efficient handling and sharing of character state information. For ant ecologists seeking more user-friendly identification tools such interactive keys present an attractive alternative to conventional dichotomous keys.

Nevertheless in some taxonomically challenging situations it may be difficult to clearly demarcate ant species on the basis of morphology alone. If we consider ant species to be evolutionarily independent lineages that are reproductively isolated from one another, then genetic data should be informative about species boundaries. DNA barcoding, using a 658 bp fragment of the mitochondrial gene cytochrome c oxidase I (COI), has been touted as an effective tool both for species identification (Hebert *et al.* 2003) and for species discovery and delimitation (Smith *et al.* 2006). This gene – alone or in combination with COII – has proven to be informative about species boundaries in *Cardiocondyla* (Heinze *et al.* 2005), *Tetramorium* (Schlick-Steiner *et al.* 2006b), and in various groups of Malagasy ants (Smith *et al.* 2005). There are other instances in which COI has performed less effectively in the discrimination of ant species, for example in the genera *Anochetus* (Fisher and Smith 2008), *Solenopsis* (Ross and Shoemaker 2005), *Cataglyphis* (Knaden *et al.* 2005), and *Linepithema* (Wild 2009). In the last three cases nuclear gene markers showed

greater species fidelity than mitochondrial DNA (mtDNA), a result that could be attributed to the greater tendency of organelle DNA to leak cross species boundaries (Hudson and Coyne 2002). This argues, of course, for the use of multiple lines of evidence when evaluating species limits. Under the most favourable conditions one can anticipate a process of reciprocal illumination, where inferences from morphology guide initial taxon sampling and then subsequent results from DNA sequencing lead to reevaluation of morphological differences, which in turn generates further exploration of genetic and phenotypic variation.

Another potential complication with the use of mtDNA markers is posed by nuclear pseudogenes of mitochondrial origin, or numts (Bensasson *et al.* 2001), which compete with the targeted mitochondrial gene(s) during amplification. Recently numts have been documented in *Atta cephalotes*, in which they were found in all 67 individual ants examined (Martins *et al.* 2007) and they are known or suspected to occur in a variety of other ant taxa (Kronauer *et al.* 2007b; Ward unpubl. data). Numts are abundant in the genome of the honeybee, *Apis mellifera* (Pamilo *et al.* 2007). Thus, when sequencing mitochondrial genes in ants care is needed to ensure that the protocols for extraction and amplification yield the targeted mtDNA genes rather than pseudogenes.

Although inferences about species boundaries are strengthened by the use of multiple independent markers, we are hampered by a dearth of nuclear genes with appropriate levels of variability for evaluating relationships among closely related populations and species of ants. Other methods for capturing genetic differences among populations, such as the use of amplified fragment length polymorphisms (AFLPs) (Vos *et al.* 1995) or microsatellites (e.g. Goodisman and Hahn 2005) may have greater utility. Genomic approaches to species delimitation (Shaffer and Thomson 2007) also show

promise. In applying new molecular techniques to species-level taxonomy it is important to avoid falling into the trap of typological thinking – if there is an overarching lesson to be learned from evolutionary biology it is that species are usually variable entities, and that speciation is a gradual and complicated process.

## 1.6 Summary

As the most species-rich and biologically eclectic of all social insects, ants present considerable challenges to the process of cataloguing and understanding their remarkable diversity. Substantial progress has been made in recent years, however, in identifying the major clades of ants and clarifying their evolutionary history. We now have a higher classification of ants in which most of the subfamilies and tribes appear to be monophyletic and well diagnosed, with a few notable exceptions. Uncertainty persists regarding the phylogenetic relationships among old lineages at the base of the ant tree and concerning the time frame of ant evolution. The species-level taxonomy of ants has advanced more fitfully, and ant ecologists have an extensive but far-from-complete set of resources for identifying ant species. Ongoing and sustained effort is needed in the area of species discovery and delimitation, and in the delivery of this information to potential users.

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