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Ants: Phylogeny and Classification



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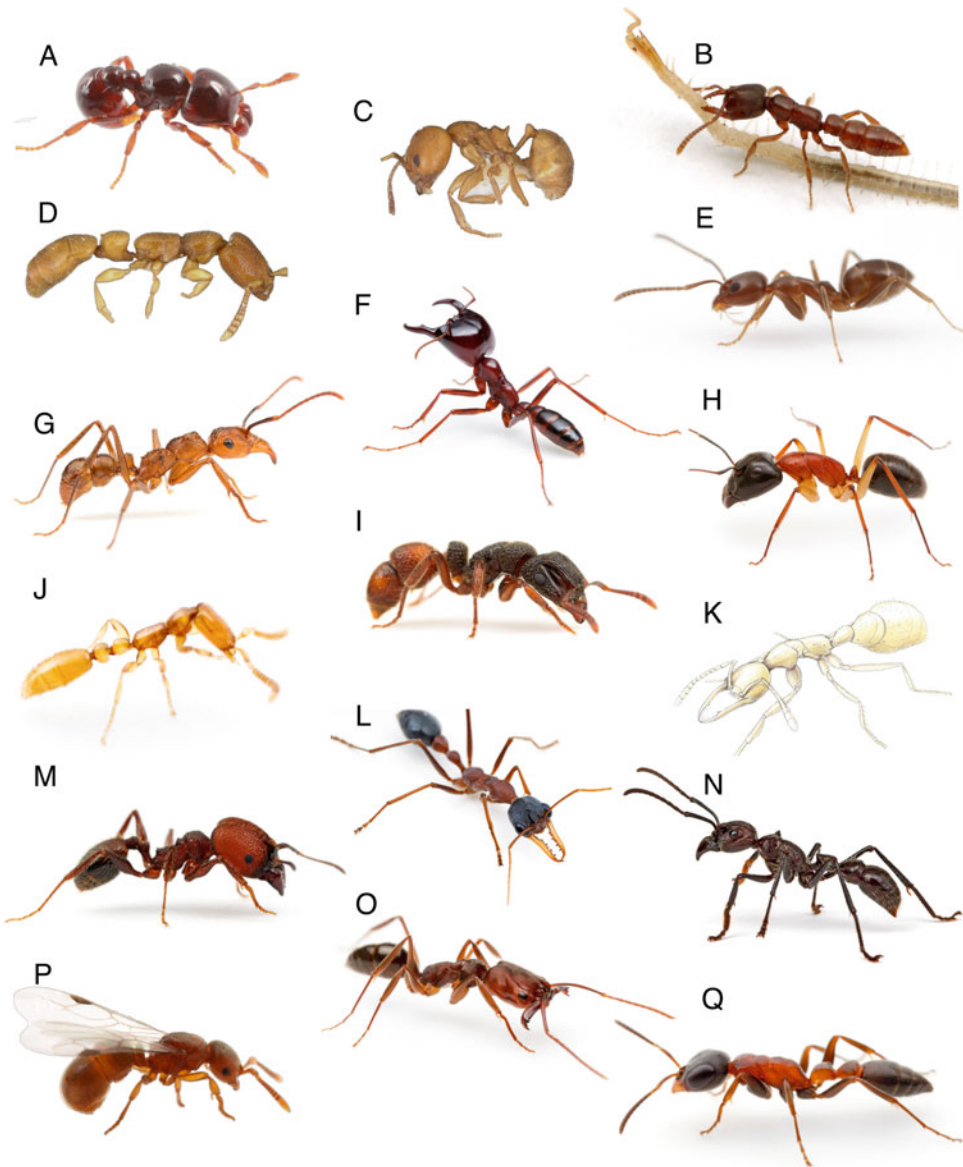
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Ants are the most ubiquitous and ecologically dominant insects on the face of our Earth. This is believed to be due in large part to the cooperation allowed by their sociality. At the time of writing, about 13,500 ant species are described and named, classified into 334 genera that make up 17 subfamilies (Fig. 1). This diversity makes the ants the world's by far the most speciose group of eusocial insects, but ants are not only diverse in terms of numbers of species. They exhibit an amazing diversity of form and function exemplified by a number of charismatic taxonomic or functional groups known as ► [army ants](#), ► [trap-jaw ants](#), ► [turtle ants](#), ► [fungus-growing ants](#), exploding ants, and ► [socially parasitic ants](#), to only name a few. Taxonomic and phylogenetic research helps to discover, describe, and organize the diversity of organisms, as well as to reveal their evolutionary histories. The timeline of modern zoological nomenclature officially begins in

1758 when the Swedish botanist Carl von Linné published the tenth edition of his catalog of all plant and animal species known at the time. Among the approximately 4,200 animals that he included were 17 species of ants. The succeeding two and a half centuries have seen tremendous progress in the theory and practice of biological classification. Here we provide a summary of the current state of phylogenetic and systematic research on the ants.

Ants Within the Hymenoptera Tree of Life

Ants belong to the order Hymenoptera, which also includes wasps and bees. ► [Eusociality](#), or true sociality, evolved multiple times within the order, with ants as by far the most widespread, abundant, and species-rich lineage of eusocial animals. Within the Hymenoptera, ants are part of the ► [Aculeata](#), the clade in which the ovipositor has been modified into a ► [venom-injecting organ](#), or stinger, and where all known instances of hymenopteran eusociality are concentrated. Although the ants' status as aculeates has been long known, their affinities within the group have been the subject of different proposals. Application of genome-scale data to phylogenetics in the last 5 years reveals that ants are most closely related to the Apoidea, the lineage that includes bees and sphecoid wasps [14, 21].



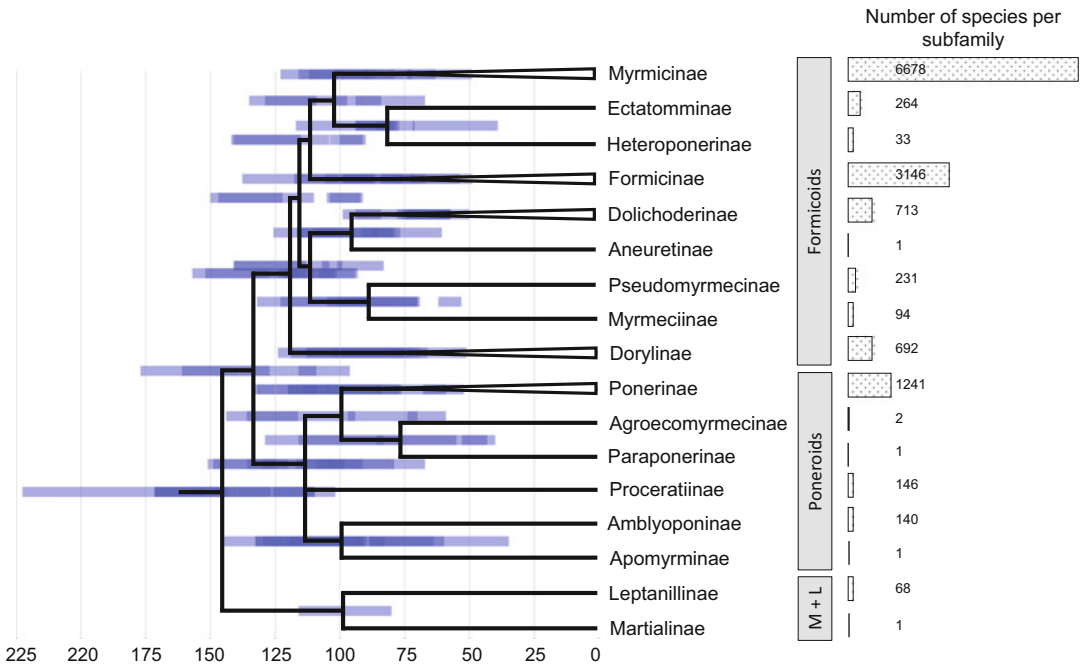
Ants: Phylogeny and Classification, Fig. 1 Diversity of extant ant subfamilies. (a) Agroecomyrmecinae (b) Amblyoponinae (c) Aneuretinae (d) Apomyrminae (e) Dolichoderinae (f) Dorylinae (g) Ectatomminae (h) Formicinae (i) Heteroponerinae (j) Leptanillinae (k) Martialinae (l) Myrmeciinae (m) Myrmicinae (n)

Paraponerinae (o) Ponerinae (p) Proceratiinae (q) Pseudomyrmecinae. All photos by Alex Wild (<http://www.alexanderwild.com>), except (a) by Micheal Branstetter, (c & d) from Antweb.org (<http://www.antweb.org>), and drawing of (k) by Barrett Klein

Phylogeny of the Extant Ants

The great diversity of extant ant species is distributed among 17 subfamilies grouped into 3 major clades, the leptanilloid, poneroid, and formicoid

clades (Fig. 2). The leptanilloid clade comprises a single Neotropical species from the subfamily Martialinae, *Martialis heureka*, and about 70 described species of the subfamily Leptanillinae, which are confined to the Old World. There is



Ants: Phylogeny and Classification, Fig. 2 Relationships among extant ant subfamilies and their species counts. Blue bars show ranges of age estimates for crucial

nodes from studies listed in Table 1. Estimates from each study are superimposed so that darker colors indicate more overlap. Age scale in millions of years

some uncertainty as to whether leptanilloids are indeed a natural, monophyletic group, as *Martialis* was earlier inferred to be the sister lineage to all other ants and its position has been sensitive to the way phylogenetic analysis is carried out. Recent studies, however, support a sister-group relationship between *Martialis* and the Leptanillinae, placing the leptanilloids as sister to all remaining ants [11].

The poneroids include more than 1,500 valid described species and are distributed across 6 subfamilies: Agroecomyrmecinae, Apomyrminae, Amblyoponinae, Paraponerinae, Ponerinae, and Proceratiinae. The Ponerinae harbor more than 80% of the poneroid diversity with roughly 1,250 extant species. Poneroid ants are mostly confined to the tropics, with only isolated species in several genera extending into the north temperate regions. While it is almost universally agreed that poneroids are a clade, phylogenetic relationships among poneroid subfamilies are less well resolved. Apomyrminae and Amblyoponinae are sister groups, but relative placements of other

subfamilies remain uncertain, even following application of genome-scale phylogenetic data. The observed phylogenetic uncertainty probably reflects rapid initial diversification of poneroid lineages during the late Cretaceous.

The formicoid clade encompasses the vast majority of all ant species (~12,000) and contains all remaining ant subfamilies: Aneuretinae, Dolichoderinae, Dorylinae, Ectatomminae, Formicinae, Heteroponerinae, Myrmeciinae, Myrmicinae, and Pseudomyrmecinae. Although as a rule these ants are more diverse in (or even confined to) the tropics at the subfamily level, two formicoid subfamilies, the Formicinae and Myrmicinae, have been particularly successful in temperate zones. The majority of ant species found in the Nearctic and Palearctic regions belong to these two subfamilies. In contrast to the poneroids, there exists broad consensus regarding the phylogenetic relationships of subfamilies in the formicoid clade.

As can be seen in Fig. 2, species diversity of extant ants is unequally distributed across the

phylogeny. Martialinae plus Leptanillinae contain only 1% of species diversity, while poneroids and formicoids account for the remaining 11% and 88%, respectively.

Overview of Ant Subfamilies

For ease of reference, the following summary of the 17 extant and 3 known extinct subfamilies is presented in alphabetic order, rather than grouping them by major clades.

Agroecomyrmecinae

A poneroid subfamily consisting of only two living species, *Tatuidris tatusia* (Fig. 1a) and *Ankylomyrma coronacantha*. Both are rarely encountered. *Tatuidris*, found in Central and South America, is thought to be a specialized predator, foraging for yet undetermined prey in the leaf litter of mid-elevation rainforests. Workers of *Ankylomyrma* have been collected a handful of times in West Africa. It is an arboreal species, but nothing else is known of its natural history. Agroecomyrmecinae was presumably more diverse in the past, as three fossil species have been described from Eocene Baltic and Rovno ambers of Europe, whose exact dating is controversial, and from ca. 34 million years old North American Florissant shale.

Amblyoponinae

A poneroid subfamily of about 140 currently described extant species distributed among 9 genera. Recent phylogenetic work shows two major clades, one comprising the genera *Amblyopone*, *Onychomyrmex*, and *Prionopelta*, and the other the remaining six genera [30]. With more than 50 species, *Stigmatomma* (Fig. 1b) is the largest genus. Species belonging to this small subfamily are known as *Dracula ants*, because adults bite their own larvae and consume their hemolymph, a behavior also observed in Leptanillinae and Proceratiinae. This mode of feeding is thought to be an adaptation to unstable food supplies affecting specialized predators that are unable to regurgitate and share food within the colony. As such, it can be seen as an alternative to ► [trophallaxis](#). Crown-

group Amblyoponinae likely started to diversify in the mid-Cretaceous, and, despite low species diversity, the subfamily is distributed worldwide and exhibits a variety of morphologies and life histories. Many species are small in body and colony sizes and are cryptic dwellers of the soil, leaf litter, or rotting wood. Some are specialized predators of geophilomorph centipedes, while the large species *Myopopone castanea* is known to prey on wood-boring cerambycid beetle larvae. *Onychomyrmex* species have an army-ant-like life history and wingless queens. Certain *Mystrium* species possess queens that are smaller than and of conspicuously different color than the workers. Several Eocene impression fossils of the extinct genus *Casaleia* from the ~47 million years old Messel formation have been assigned to Amblyoponinae, and two Baltic amber species of *Stigmatomma* have been described.

Aneuretinae

This formicoid subfamily is currently represented by a single extant species, ► [Aneuretus simoni](#), which is confined to isolated sites in Sri Lanka. The Aneuretinae are the sister group to the Dolichoderinae. *Aneuretus simoni* (Fig. 1c) is a rarely found species nesting predominantly in rotten wood, with polygynous and ► [polydomous colonies](#) generally containing fewer than 100 workers. The worker caste is polymorphic, and the species exhibits generalized predatory and scavenging habits. Aneuretine ants were much more widespread and speciose in the past. Nine extinct genera and 12 species have been described from Cretaceous and Eocene amber as well as from impression fossils from Europe, Asia, and North America. The Cretaceous fossils include the genera *Burmomyrma* and *Cananeuretus*, whose assignment to Aneuretinae is uncertain. *Napakimyрма paskapooensis* is the oldest undisputed aneuretine and the only confirmed ant fossil known from the Paleocene. This impression fossil is known from the 56–60 million-year-old Paskapoo Formation in Canada.

Apomyrminae

Apomyrminae is a monotypic poneroid subfamily, represented by *Apomyrma stygia* (Fig. 1d).

Apomyrminae are sister to Amblyoponinae. *Apomyrma stygia* is known from sub-Saharan Africa, and very little is known of its habits, except for subterranean nesting and indirect evidence of predation on geophilomorph centipedes. Fossils remain unknown from the Apomyrminae.

†Brownimeciinae

This extinct monotypic subfamily is known from Cretaceous New Jersey amber dated to approximately 92 million years ago. The sole species, *Brownimecia clavata*, is similar to sphecomyrmines but distinguished by a long antennal scape, which is thought to be a derived feature. *Brownimecia* has been inferred to be the sister lineage to all crown-group ants.

Dolichoderinae

The Dolichoderinae are a highly diverse formicoid subfamily of more than 700 extant species. The classification and phylogeny of this group have been studied extensively, and at present the extant taxa are organized into 4 tribes and 28 genera [25, 28]. One of the tribes, Leptomyrmecini, contains a clade that encompasses a massive Australian radiation that began some 25 million years ago, making Australia the center of dolichoderine diversity.

As a large subfamily, the dolichoderines show a variety of morphologies and life histories and therefore defy easy synopsis. Characteristic morphological traits include a nonfunctional stinger and thin cuticle devoid (with the exception of the genus *Dolichoderus*) of much of the sculpture or armament that is typical for most other ants. Colonies range from monogynous and containing a few hundred workers to highly populous polygynous colonies inhabiting polydomous nests. As one example, nests of the Australian *Iridomyrmex purpureus* can house upwards of 300,000 workers. One of the world's most significant invasive ants, the ► [argentine ant](#) *Linepithema humile* (Fig. 1e), is also a member of the Dolichoderinae. The argentine ant and the noninvasive North American odorous house ant *Tapinoma sessile* form ► [supercolonies](#) with no apparent upper size limit. Instead of defending themselves by stinging, dolichoderines are armed with an

impressive battery of chemical defenses and are known for their advanced chemical communication systems. The Neotropical genus ► [Azteca](#) is known for its diverse ecological ► [interactions with plants](#) and ► [scale insects](#) and has been the focus of many studies on coevolution and adaptation. The subfamily also has an impressive fossil record comprising 135 fossil species in 20 genera. New and currently undescribed species from ca. 72 million-year-old Myanmar amber and *Chronomyrmex medicinehatensis* from 78–79 million-year-old Cretaceous amber of Canada are the oldest known dolichoderines. It appears likely that dolichoderines were more diverse in the past and that later arrivals on the ant evolutionary stage, such as the Myrmicinae and rapidly diversifying lineages within the Formicinae, displaced the Dolichoderine on continents other than Australia.

Dorylinae

This diverse formicoid subfamily contains almost 700 described extant species distributed among 27 genera, including the charismatic true army ants [9]. The dorylines have a worldwide distribution, but the vast majority of species occurs in the tropics. The phylogeny of this group has been difficult to infer with certainty, likely because dorylines experienced an ancient rapid radiation [10, 13]. Due to a lack of characteristic morphological traits that would allow for grouping multiple genera and uncertainty in phylogenetic placement of several other genera, no tribal classification is currently in use.

The army ants, the most conspicuous and best-known members of the Dorylinae, are characterized by a suite of behavioral and morphological characteristics dubbed “the army ant syndrome.” This includes collective foraging, frequent colony relocation, and highly derived queen and male morphologies. The true army ants are among the most bizarre and impressive social insects. They forage in coordinated swarms that have no scouts or leaders; colonies move nesting sites periodically; and young queens ► [found new colonies](#) by budding. Army ant colonies are among the largest insect societies. An estimate of 22 million workers has been made for a single colony of the

African army ant *Dorylus wilverthi*. Young *Dorylus* queens mate with as many as 20 different males and are capable of storing more than 800 million spermatozoa used to lay an estimated 250 million eggs during their lifetimes.

New World army ant colonies undergo cycles of alternating phases of foraging and reproduction, during which the queen is either physogastric and producing eggs and the colony is not changing nesting sites (the so-called stately phase) or the queen ceases egg production, workers forage intensively, and the colony moves between nesting places each day (nomadic phase). In many species the workers and even queens are completely blind, and males have conspicuously robust, large bodies. In spite of the high level of morphological and behavioral specialization, molecular phylogenetic studies indicate that New World army ants (genera *Cheliomyrmex*, *Eciton*, *Labidus*, *Neivamyrmex*, and *Nomamyrmex*) and Old World army ants *Aenictus* and *Dorylus* (Fig. 1f) evolved convergently in South America and Africa, respectively. In addition to the true army ants, the Dorylinae contains a number of lineages whose biology, taxonomy, and phylogeny are poorly known. It is uncertain whether any species in these non-army ant lineages acquired all components of the army ant syndrome, but each individual trait described above has been reported for some species. There is one extinct genus, *Procerapachys*, known from Eocene Baltic and Bitterfeld ambers. Extant doryline genera are also known from Baltic, Dominican, and Chiapas amber deposits.

Ectatomminae

The Ectatomminae are a medium-sized formicoid subfamily with over 250 described species classified in 4 genera: ► *Ectatomma* (Fig. 1g; 15 extant species), *Gnamptogenys* (138 species), ► *Rhytidoponera* (104 species), and *Typhlomyrmex* (7 species). The Ectatomminae are the sister group to the Heteroponerinae, and together they form a clade sister to the Myrmicinae (Fig. 2). *Ectatomma* and *Typhlomyrmex* are confined to the New World, *Rhytidoponera* occurs in Southeast Asia and Australasia, and *Gnamptogenys* is found both in the

New World as well as in Southeast Asia and Australia. Despite the relatively low species diversity, ectatommines are common and conspicuous elements of tropical New World and Australian ant faunas. The subfamily is absent from Africa and from most parts of the northern temperate regions.

Most ectatommines appear to be generalized predators and scavengers although specialized predators of fungus-growing ants and millipedes have been reported in the genus *Gnamptogenys*. One species of *Ectatomma* was described as obligate ► [social parasite](#). Ectatommines often nest in rotting wood or in the soil. Both ground foraging and arboreal foraging species are known. *Typhlomyrmex* species are generally cryptic and live and forage underground. Colony sizes are relatively small, rarely exceeding several hundred workers. Both monogynous and polygynous colonies have been recorded. Many ectatommines, especially in the genus *Rhytidoponera*, have lost the true queen caste and reproduce through mated workers (► [gamergates](#)). Certain species of *Ectatomma* are considered pest control agents for crops in the Neotropics. The subfamily has a rather extensive fossil record, and some 14 species in several genera are known from the Miocene Dominican and Eocene amber of Europe, as well as Eocene impression fossils. The affinity of the 78–79 million-year-old Cretaceous Canadian amber fossil *Canapone dentata* is uncertain, but it has been suggested to represent an early ectatommine. *Pseudectatomma* impression fossils from ~47 million-year-old European Messel Formation and *Electroponera dubia* from Eocene Baltic amber are the oldest undisputed ectatommine fossils.

†Formiciinae

The Formiciinae – note the close similarity in name to the next subfamily – are an extinct subfamily of giant ants currently containing six species in two genera: *Titanomyrma* and *Formicium*. These are impression fossils known from four localities in North America and Europe, all dated to the Eocene when the two continents were connected by land bridges in the north Atlantic [1]. Only alates (*Titanomyrma*) and wing

impressions (*Formicium*) have been collected. *Titanomyrma* species are both the largest ants and Hymenoptera known, with queens reaching a body length of 6 cm. The oldest Formiciinae fossils are 49–54 million years old from the North American Green River formation. The exact phylogenetic placement of the Formiciinae is uncertain, but they are currently placed within the formicoid clade.

Formicinae

The Formicinae are the second-largest subfamily of ants with 51 extant genera and more than 3,000 described and many known but undescribed species. Two genera in one massive radiation, the ► **carpenter ants** (*Camponotus*) and their close relatives the ► **spiny ants** (*Polyrhachis*), account for more than 1,700 species. The formicines have a global distribution and are important components of both tropical and temperate faunas. In north temperate regions, at around 45°N, the Formicinae become the most species-rich subfamily. The phylogeny and higher classification of the subfamily have recently been revised, dividing the subfamily into 11 monophyletic tribes [3]. Workers can be diagnosed by the acidopore, a circular opening formed by a fold of the last abdominal sternite, which is surrounded by a fringe of setae. The Formicinae lack a stinger and use this opening to spray formic acid, a venom unique to the subfamily.

The tribe Camponotini contains *Camponotus* (Fig. 1h) and *Polyrhachis*, as well as several lesser known ant genera, such as the large-eyed Australasian strobe ants *Opisthopsis*, the spectacularly iridescent *Calomyrmex*, the often intricately sculptured *Echinopla*, and one of the world's largest ants, the Southeast Asian *Dinomyrmex gigas*. All Camponotini have a bacterial symbiont, *Blochmannia*, found in cells lining the midgut and in the ovaries. *Blochmannia* is vertically transmitted from generation to generation and provides essential nutrients to the ants.

Formicines have successfully radiated into the world's arid zones, with three unrelated genera occupying this niche in different parts of the world: the species-rich genus *Melophorus* in Australia, ► **Cataglyphis** in North Africa and Asia,

and *Myrmecocystus* in North America. *Myrmecocystus* is a prime example of the *honeypot ants*, which can store liquid food in highly expandable abdomens, thus forming living pantries. The food storage behavior of the honeypot ants evolved independently in desert ants from several genera, all of the subfamily Formicinae.

Formicine ants also engage in obligate symbioses with mealybugs (genus *Acropyga*) and ant plants (*Cladomyrma*, *Myrmelachista*). The jumping ant *Gigantiops destructor* is common throughout the Amazon basin, where its very large eyes and unusual, highly visually oriented behavior make it conspicuous. Southeast Asian *Myrmoteras* are an example of trap-jaw ants, or ants in which spring-loaded mandible action generates extremely fast-snapping movement. There is also a high number of socially parasitic species in the Formicinae, especially temporary parasites and ► **dulotic** species in the genera *Formica*, *Polyergus*, and *Rossumyrmex*. The fossil record of Formicinae is impressive, with 31 extinct genera and 197 fossil species. The Cretaceous New Jersey amber fossil *Kyromyrmex neffi* was dated at approximately 92 million years, exhibits a well-developed acidopore, and is the oldest undisputed formicine ant.

Heteroponerinae

The Heteroponerinae are a small formicoid subfamily of 3 genera and 33 species. Heteroponerines have a remarkably disjunct biogeographic distribution: 28 species of *Heteroponera* (Fig. 1i) are found in Australia, New Zealand, and in the Neotropics. Four species of *Acanthoponera* are Neotropical, and the single species of *Aulacopone* is known from only two queens collected in Azerbaijan. Heteroponerinae are sister to Ectatomminae (Fig. 2), and the two subfamilies can be difficult to separate based on morphological characters. The Heteroponerinae can be recognized by a longitudinal carina running down the top of the head. Little is known of this group's biology. Some heteroponerines nest in or under rotting wood, in the soil, and under stones. Some species were observed to feign death when disturbed. Colonies are small and monogynous, and both winged and ► **ergatoid queens** are

known. There are no heteroponerine fossils known at the time of writing.

Leptanillinae

This small leptanilloid subfamily of rarely encountered subterranean ants currently comprises about 70 described Old World species, although the group's cryptic habits make it likely that many more species await discovery. Leptanillines are currently classified in eight genera. There are three major lineages within the subfamily: the sister lineage to all other leptanillines, represented by the single species *Opamyrra hungvuong*, species with somewhat larger workers that are currently classified in the genera *Anomalomyrra* and *Protanilla*, and species with miniscule workers in the genus *Leptanilla*. The genera *Noonilla*, *Phaulomyrra*, *Scyphodon*, and *Yavnella* are known only from males.

Little is known about the biology of leptanillines, and only a couple of species have been studied in the laboratory. Colonies are probably small (not more than several hundred workers) in most species and either monogynous (*Leptanilla*; Fig. 1j) or polygynous with ergatoid queens (*Protanilla*). Like the amblyoponine Dracula ants that feed on their own larvae, leptanilline queens and workers engage in larval hemolymph feeding. Unlike the amblyoponines, however, they do not puncture the larval cuticle. Instead, they feed through a pair of specialized duct organs located on the larval abdomen. *Leptanilla* also appear to be specialized predators of soil centipedes and have been shown to produce brood in reproductive bouts similar to those observed in the true army ants. Fossil leptanillines are not known.

Martialinae

The Martialinae are a monotypic subfamily known from only few specimens collected in the Brazilian Amazon [22]. The phylogenetic position of *Martialis heureka* (Fig. 1k) was initially inferred as the sister lineage to all extant ants. However, recent phylogenetic studies suggest a sister group relationship between the New World Martialinae and the Old World Leptanillinae. The

difficulties associated with establishing the phylogenetic position of *Martialis* are related to compositional heterogeneity of molecular sequence data and the old age of this lineage [11]. Nothing is known about the biology of *Martialis*, although the complete lack of eyes and the pale-yellow cuticle strongly suggest a subterranean life. Elongate, forceps-like mandibles suggest specialized predatory habits. Fossils are unknown from the Martialinae.

Myrmeciinae

This is a formicoid subfamily presently confined to Australia and New Caledonia. Two extant genera comprise this group: *Myrmecia* (Fig. 1l), also known as bull ants or bulldog ants, and *Nothomyrmecia*, the dawn ants. There are about 100 described species of *Myrmecia*, whereas *Nothomyrmecia* is represented by the single extant species *Nothomyrmecia macrops* [26]. The Myrmeciinae are the closest relatives of the big-eyed arboreal ants Pseudomyrmecinae (Fig. 2). Due to their diurnal habits, large body sizes, and pugnacity, bulldog ants are the most characteristic element of the Australian myrmecofauna. *Myrmecia* exhibits a variety of reproductive strategies. Young queens either establish new colonies independently or via pleometrosis (dependent colony foundation). Colonies can be monogynous or polygynous, and queens can be singly or multiply mated. Queens of some species are winged, while others are ergatoid, and in a few species the queen caste has been replaced by gamergates (reproductive workers). Colony sizes range from a few dozen to a couple of thousand workers. Nests are typically built in the soil but occasionally also in rotting logs, and one species, *M. mjobergi*, nests arboreally. The workers are effective solitary foragers with large eyes and correspondingly good vision. *Myrmecia* deliver exceptionally painful stings. They are also known for rapid karyotype evolution and the high variability in chromosome numbers among species. *M. croslandi* is the only ant species known to have only a single pair of chromosomes, a remarkable condition known only in one other metazoan, a nematode.

In contrast to many bulldog ants, the dawn ant *Nothomyrmecia macrops* is extremely rare and

known from only a few localities in South Australia. *Nothomyrmecia* are nocturnal and exhibit traits that were historically associated with ancestral ant societies, including small colony size, solitary foraging, lack of division of labor, and queens foraging while raising the first brood. The Myrmeciinae are represented by a diverse fossil record revealing an almost global distribution during the Eocene. Six extinct genera represented by 16 species are known from Eocene and Oligocene impression fossils and ambers of Europe, Asia, North America, and South America.

Myrmicinae

With more than 6,500 described species, the Myrmicinae are by far the largest ant subfamily. According to recent taxonomic rearrangements based on molecular phylogenetic results, this formicoid subfamily is currently classified into 6 monophyletic tribes and 143 extant genera [29]. Their biogeographic distribution is global, and myrmicines are present in every habitat where ants are found. Because of their great species diversity, the myrmicines exhibit biological and morphological variation that spans most of the range observed in the family as a whole. Specialized functional groups found in the myrmicines include ► **fungus-growing ants**, arboreal ► **turtle ants**, ► **seed-harvesting ants**, ► **social parasites**, and numerous lineages of independently evolved ► **trap-jaw ants**. Myrmicines gave rise to several spectacular adaptive radiations. Only 5 of the 143 genera, ► *Pheidole* (Fig. 1m), *Strumigenys*, ► *Crematogaster*, *Tetramorium*, and ► *Temnothorax*, contain more than half of the subfamily's species. The six myrmicine tribes are well supported by molecular data but poorly defined by morphological characters. Myrmicini is the only myrmicine tribe that is endemic to north temperate regions. The two constituent genera, *Myrmica* and *Manica*, are relatively unspecialized scavengers, common in boreal and subboreal habitats. The tribe Pogonomyrmecini contains three genera that are restricted to the New World. *Patagonomyrmex* and *Pogonomyrmex* are granivores, while *Hylomyrma* is a likely omnivorous scavenger. The Stenamini are another moderately-sized tribe with several

seed-harvesting lineages comprising mostly the north temperate genera *Aphaenogaster*, *Messor*, *Stenamma*, *Veromessor*, and others.

The Solenopsidini are a tribe with global distribution and two highly speciose genera: ► *Monomorium* and ► *Solenopsis*. Some of the world's most notorious invasive ants are the fire ants *Solenopsis invicta* and *S. geminata*. Other *Solenopsis* species, known as thief ants, often nest close to larger ants from which they steal resources and even consume brood. *Monomorium* includes several seed-harvesting species and the common greenhouse and house pest *M. pharaonis*. *Monomorium* is a large genus that was recently recognized as polyphyletic and is currently undergoing a taxonomic reevaluation.

The Attini are the tribe that originated and diversified largely in the New World, with three large radiations of some of the world's most remarkable ants: the genera *Pheidole*, *Strumigenys*, and fungus-growing ants in the *Atta* genus group. At just over 1,000 described and many unnamed species, *Pheidole* competes with the formicine genus *Camponotus* for the title of the most speciose ant genus. *Pheidole* species are dimorphic or trimorphic with a well-developed major worker caste. *Pheidole* reached their exceptional species richness within the last 40 million years and colonized all continents except Antarctica. With more than 800 described cryptic, leaf-litter dwelling species, *Strumigenys* is not far behind. *Strumigenys* is a genus in which a spring-loaded (trap-jaw) mandible-closing mechanism evolved independently several times, each time *Strumigenys* colonized a new major geographic region. The *Atta* genus group is endemic to the New World and comprises the only ants that cultivate fungus for food. Leaf-cutting ants in the genera *Acromyrmex* and *Atta* are among the most characteristic Neotropical ants, often seen harvesting great amount of vegetation that serves as substrate for their fungus gardens. Other members of the tribe include the Neotropical *Cephalotes* turtle ants and the invasive little fire ant *Wasmannia auropunctata*. The Attini and its core genera originated and diversified mainly in the Neotropics but subsequently spread across the world.

All other myrmicines are classified in the tribe Crematogastrini [4]. This clade contains 64 genera and approximately 40% of the myrmicine species. The Crematogastrini originated and diversified mostly in the Paleotropics, especially in the Indomalayan region. A few crematogastrine lineages are also present in the New World, including by far the largest northern temperate genus, the acorn ants *Temnothorax*, and the mostly tropical *Carebara*, *Crematogaster*, and *Nesomyrmex*, among others. *Tetramorium* is another hyperdiverse ant genus that belongs to this tribe and is mostly confined to the Old World except for several desert-adapted native North American species and two recent introductions. Certain species of *Carebara* ants exhibit extreme worker-queen or worker polymorphism. In the case of Southeast Asian *Carebara diversa* and related species, known as ► [marauder ants](#), the largest workers can weigh 500 times as much as their smallest sisters. Marauder ants forage in self-organized groups, as do true army ants, and their colonies attain sizes of hundreds of thousands of workers. The Myrmicinae have an extensive fossil record with 37 described extinct genera and 170 fossil species. The 89–94 million-year-old Cretaceous impression fossil *Afromyrma petrosa* is the earliest putative myrmicine, although its affinities are uncertain. The oldest undisputed myrmicines are known from 52 million-year-old Chinese Fushun amber.

Paraponerinae

Paraponera clavata (Fig. 1n), the infamous ► [bullet ant](#) of the Neotropics, is the sole species in this formicoid subfamily. This species has a remarkably broad distribution, occurring from Honduras in Central America to Paraguay and Rio Grande do Sul state in Southern Brazil, and it is common throughout most of its range. *Paraponera clavata* is famous for its extremely painful sting. Its Tupí-Guaraní name, *tuca-ndy*, means “the one wounding deeply.” The nests of *P. clavata* are built at the base of trees or arboreally, and colonies can reach a couple of thousand workers. Queens forage while raising the first brood, and workers forage individually. Their diet consists of invertebrate prey and scavenged

arthropods as well as nectar. Although *Paraponera* does not now occur in the Caribbean, a single fossil species, *P. dieteri*, is known from 15–26 million-year-old Miocene Dominican amber.

Ponerinae

The Ponerinae are the third largest subfamily of ants with 47 genera and more than 1,200 species [23, 24]. Because of their diversity, ponerines are difficult to characterize, although many species are large and possess thick cuticle. The subfamily is mostly tropical, with few lineages extending into the temperate regions. Ponerines are currently divided into two tribes, the Platythyreini and the Ponerini. The Platythyreini contain a single genus with some 40 species, forming the sister group to all other ponerines. ► [Platythyrea punctata](#) is found in Central America and the Caribbean. It shows a remarkable diversity of reproductive strategies, where regular queens, intercastes, and mated workers can reproduce either sexually or via thelytokous ► [parthenogenesis](#). All other genera are classified within the tribe Ponerini. The colonies of ponerines are generally small compared to many other ants, and no species is considered an invasive pest. The reproductive biology of many ponerines is remarkable, because many species have lost the queen caste in favor of gamergates. The presence of gamergates is also known from other subfamilies, although it is most widespread in ponerines.

The Ponerinae are another subfamily in which ► [trap-jaw mechanisms](#) evolved convergently. The sister genera *Anochetus* and *Odontomachus* (Fig. 1o) evolved powerful snapping mandibles used for prey capture. Interestingly, the trap-jaw mandibles can also be employed to propel individual ants into the air, a behavior that in some species may represent active predator avoidance. The South American ► [Dinoponera](#) ants have arguably the largest workers of any living ants, and they rely exclusively on gamergates for reproduction. *Dinoponera* have, with maximally 60 pairs, the highest number of chromosomes reported in any Hymenopteran. Although primarily scavengers of dead invertebrates, *Dinoponera*

have been observed to prey on small vertebrates such as frogs.

Southeast Asian *Harpegnathos* are unusual in that jumping is their main mode of locomotion, otherwise known in certain species of *Odontomachus* and Australian *Myrmecia* ants and the Neotropical formicine *Gigantiops*. Spectacular morphological adaptations to specialized prey can be seen in Neotropical *Thaumatomyrmex* ants, which use their highly modified mandibles to prey on very setose polyxenid millipedes, and some *Centromyrmex* species are extremely robust, presumably as an adaptation to hunting termites. Ponerines also have an extensive fossil record with 12 extinct genera and 86 species. Undescribed species reported from ca. 72 million-year-old Burmese amber are the oldest undisputed ponerine fossils.

Proceratiinae

The Proceratiinae are a poneroid subfamily of some 145 extant species currently classified into three genera: *Discothyrea*, *Probolomyrmex*, and *Proceratium* (Fig. 1p). Many species likely remain to be described, as these are cryptic ants that dwell in the leaf litter and soil. Proceratiines belong to the poneroid clade, but their exact phylogenetic placement remains elusive. Currently they are inferred as the sister group to a monophyletic clade consisting of Amblyoponinae and Apomyrminae (Fig. 2). The three proceratiine genera are distributed throughout various habitats of the tropics and warm temperate regions of the world. Colony sizes are small, often fewer than 100 workers. Nests are built deep in the soil and in rotting wood, and occasionally they nest arboreally. Very few direct observations of Proceratiinae biology have been made, but the few species studied appear to be predators of arthropod eggs. The queens of the African *Discothyrea oculata* start colonies in spider egg sacs where they find shelter and abundant food for their first brood. *Proceratium* and *Discothyrea* are known from Dominican and Chiapas ambers, and the single extinct genus, *Bradoponera*, consists of four species which are known from the Eocene Baltic, Bitterfeld, and Rovno ambers of Europe.

Pseudomyrmecinae

This is a medium-sized formicoid subfamily of big-eyed arboreal ants comprising 230 described extant species that are classified into three genera. *Pseudomyrmex* (Fig. 1q) and the monotypic genus *Myrcidris* are endemic to tropical and warm temperate regions of the New World, while *Tetraponera* occurs in the Old World tropics [27]. This subfamily's closest relatives are the Myrmeciinae (Fig. 2). Pseudomyrmecines are known for their mutualistic relationships with plants, which evolved at least a dozen times in the subfamily. Perhaps the best-known example is the obligate mutualism between members of the Central American *Pseudomyrmex ferrugineus* group and swollen-thorn *Vachellia* acacias. In this system, the acacias provide nesting space in swollen thorns and food in the form of extrafloral nectaries and nutritious structures produced at the tips of leaves called food bodies or Beltian bodies. In exchange the ants aggressively protect acacias from herbivores. Although the vast majority of pseudomyrmecines are arboreal, a few species nest in the soil. Colonies are of small to moderate size of several hundred workers, except for the ant-plant mutualists, whose colonies can exceed 10,000 workers. Temporary social parasitism and workerless social parasitism have been reported from the subfamily. A total of 20 fossil species are known from Eocene Baltic, Bitterfeld, and Rovno ambers of Europe (*Tetraponera*) and 15–26 million-year-old Miocene Dominican amber (*Pseudomyrmex*).

†Sphecomyrminae

The Sphecomyrminae are considered stem-group fossils of the family Formicidae. Recently the taxonomic scope of Sphecomyrminae was broadened by inclusion of taxa that had previously been placed in the subfamily Armaniinae, although this taxonomic change could soon be reversed. The classification of the Armaniinae has been in flux and some authors considered this subfamily a stem-group representative of the Formicidae, whereas others regarded the Armaniinae as a family outside of the Formicidae. Armaniinae are Cretaceous impression fossils known exclusively from alates. There are 33 currently recognized

species of Sphecomyrminae classified in 14 genera. The oldest known sphecomyrmines are *Baikuris*, *Gerontoformica*, and *Haidomyrmodes* from ~100 million-year-old French Charentese amber.

Fossil Record and Timeline of Early Ant Evolution

Snapshots of the ants' evolutionary history are seen in an impressive fossil record. Over 750 fossil ant species have been described, more than the currently known number of dinosaur species [2]. The timeline of ant evolution begins with an early Hymenopteran fossil showing affinities to the lineage containing both ants and Apoidea. One of these early fossils is *Cariridris bipetiolata*, a 112–122 million-year-old impression fossil from Brazil. It was once postulated to be the earliest known ant but more likely represents a relative of the sphecooid family Ampulicidae.

Cretaceous amber deposits from 100–125 million years ago contain insect fossils but no known ant inclusions. Ants appear in the fossil record around 100 million years ago, and they are at first very uncommon, representing less than 2% of all Cretaceous insect inclusions from then onwards. Despite their low abundance, these early ants already exhibited a variety of distinct morphologies. The extinct subfamily Sphecomyrminae is the most diverse, with genera such as *Gerontoformica* and *Sphecomyrma*, which have generalized wasp-like mandibles, as well as a number of forms with spectacular mandibular and head morphologies not seen in modern ants. Ants in the genera *Haidomyrmex*, *Haidomyrmodes*, and *Haidoterminus* possess remarkable L-shaped or scythe-like mandibles. The tips of these mandibles point toward the frons and likely functioned as trap-jaw mechanics. *Ceratomyrmex* and *Linguamyrmex* are even more extreme, sporting a massive clypeal horn with an apical lobe, apparent trigger hairs, and extremely long mandibles that point toward the lobe. No such structures are known in extant ants.

Sphecomyrmines are most often considered a stem lineage of all extant ants, which means that

all representatives are extinct and members of the Sphecomyrminae are not more closely related to any particular extant lineage but instead more closely related to other extinct lineages. In parallel to some stem-group ants, however, some Cretaceous fossils certainly belong to crown-group ants, that is, they can be placed inside the clade formed by currently living ant lineages. The most spectacular example is the ca. 92 million-year-old amber fossil *Kyromyrma neffi*, which can unmistakably be recognized as a formicine ant due to its well-developed and plainly visible acidopore.

No definitive fossil ants were known from the period 55–78 million years ago until very recently when the aneuretine impression fossil *Napakimyrmex paskapooensis* was described from the Canadian Paleocene Paskapoo Formation, which is 56–60 million years old.

By the time Eocene amber deposits formed in Europe, most contemporary subfamilies are known to have been present. Exceptions are the subterranean subfamilies Apomyrminae, Leptanillinae, and Martialinae, as well as the monotypic Paraponerinae and species-poor Heteroponerinae. Unfortunately, confident dating of the Eocene European amber deposits (Baltic, Bitterfeld, and Rovno ambers) has been notoriously difficult, and various authors have proposed either Lutetian (41–48 million years old) or Priabonian (34–38 million years) ages for Baltic and Rovno ambers, and an even wider range of estimates for Bitterfeld amber, suggested to be as young as Upper Oligocene (23–28 million years ago). Regardless of the exact age of the deposits, ants evidently became more abundant in terrestrial ecosystems and account for 10% or more of the insect inclusions in Eocene ambers. Although fossil Eocene ant faunas of Europe and North America contain extant genera, their taxonomic composition differs from today's faunas from the same regions. Not only are many lineages currently confined to the tropics, but frequently a mixture of tropical and temperate genera is found. This pattern has been observed for other faunas and floras of the Eocene, including fossil termites, dragonflies, and floras from Yellowstone National Park, USA. Several explanations have been proposed to explain this pattern, including

transport and mixing of fossils from places with different paleoclimates, time averaging of deposits that were actually laid down over periods of millions of years, and Eocene climates with reduced seasonality and no modern equivalents.

The study of fossils is crucial for our understanding of ant evolution. It provides a window into past morphologies, behaviors, and faunas. It is also necessary for modern phylogenetic inference that has been focused on molecular data and sophisticated statistical analysis. Molecular phylogenies require fossils in order to accurately calibrate nodes on the phylogenetic tree and obtain divergence dates in absolute time. Without a solid understanding of the phylogenetic position of fossils, which can only be obtained through morphological investigations, confident dating of events in ant evolution is impossible, regardless of theoretical advances in computer modeling. The same logic extends to biogeographic inference, where past species ranges and dispersal events are reconstructed from patterns of modern distributions and phylogeny. Because the fossil record reveals that distributions of modern taxa have changed over time, often dramatically, such inferences are incomplete or biased without consideration of fossils. Ant systematists are becoming increasingly aware of these limitations, fossils are being discovered or reevaluated, and ways in which modeling of the evolutionary past is done are being often revised. These factors lead to constant refinement of our understanding of the timeline of ant evolution.

With the above caveats in mind, it is no surprise that estimates of the age of crown-group ants and major ant clades have varied among studies (Fig. 2, Table 1). Most phylogenetic work places the most recent common ancestor of modern ants in the Early Cretaceous period, between 145 and 110 million years ago. This is before the time when first Cretaceous amber ant fossils become available and suggests that the presumed stem-group sphecomyrmines remained dominant in terrestrial habitats for some time after crown-group ants first appeared on the scene. This timeline also shows that modern ants rose to prominence alongside angiosperms and that bursts of ant diversification occurred throughout their evolutionary

past. Examples of rapid radiations include early diversification of the poneromorph clade, the dorylines, tribe Crematogastrini, and several of the hyperdiverse genera. These patterns are further discussed below.

Diversification of Modern Ants: Geography, Innovation, Dispersal, and Coevolution

The majority of ant species live in the tropics: Costa Rica is home to about the same number (~900) of ant species as Canada and the USA combined despite occupying a land area almost 400 times smaller. Approximately 79% of ant species and subspecies have ranges that are at least in part within tropical latitudes (23.5° north and south), despite the fact that the tropics account for only 36% of the Earth's dry land surface. This pattern of species richness is reflected in higher phylogenetic diversity in the tropics and the fact that most ant genera and subfamilies are either restricted to the tropics or present in the tropics as well as temperate regions.

Several hypotheses have been put forward to explain high tropical diversity, exemplified by ants and many other animal and plant taxa. Comparative phylogenetic research suggests that tropical ant lineages are much older than temperate lineages and that tropical and temperate lineages give rise to new species at similar rates. Accordingly, most familiar north temperate ant genera, such as *Formica*, *Lasius*, or *Temnothorax*, must be regarded as evolutionary newcomers. This suggests that there are fewer ants in colder regions because these faunas are relatively young [16].

Recent molecular phylogenetic studies revealed other large-scale geographic patterns in ant evolution. Many old clades show affinity to major biogeographic regions, suggesting that diversification often remains confined to a particular region over long periods. For example, the myrmicine tribe Attini of 45 genera and more than 2,500 species originated in the New World approximately 65 million years ago. Its diversification proceeded mainly in the Neotropics until a few lineages, most notably the hyperdiverse

Ants: Phylogeny and Classification, Table 1 Age range estimates for select major ant clades and five largest subfamilies from major phylogenetic studies. Numbers in square brackets next to references correspond to reference number. Age ranges are reported in millions of years before present

Clade/reference	Brady et al. 2006 [12]	Moreau et al. 2006 [19]	Ward et al. 2010 [28]	Schmidt 2013 [23]	Moreau and Bell 2013 [18]	Brady et al. 2014 [13]	Ward et al. 2015 [29]	Blaimer et al. 2015 [3]	Ward and Fisher 2016 [30]	Blanchard and Moreau 2017 [5]	Economato et al. 2018 [16]	Borowiec 2019 [10]	Borowiec et al. 2019 [11]
Formicidae	111–137	141–169		111–152	128–169					145–220	154–169		103–123
Leptamillioidea													82–114
Poneroids	100–115	122–134		93–128	69–107					105–147	127–149		81–102
Formicoids	103–120	118–131		95–122	104–118					115–155	129–150		96–106
Amblyoponinae	92–118	113–143		66–114	37–87				93–128	85–131	93–131		62–87
+Apomyrminae													
Dolichoderinae	87–106	103–113	81–114	62–97	80–85					98–108	100–123		78–89
+Aneuretinae													
Heteroponerinae	81–92				80–84					79–92	73–115		41–70
+Ectatomminae													
Pseudomyrmecinae	91–103			72–99	55–60					72–121	95–130		71–92
+Myrmecinae													
Dolichoderinae	71–76	86–97	59–74		59–72					60–73	62–92		52–62
Dorylinae	71–94	99–117			68–93	74–101				77–111	95–122	53–101	
Formicinae	77–83	92–104		56–82	69–90			88–136		89–97	73–116		51–71
Myrmicinae	81–89	100–114		65–88	74–90		88–110			91–100	94–121		51–72
Ponerinae	79–103	111–132		78–112	54–66					86–118	106–130		61–84

genera *Pheidole* and *Strumigenys*, started dispersing out of this realm within the last 30 million years. A parallel Old World example is another myrmicine tribe, the tribe Crematogastrini, with 64 extant genera and more than 2,600 species. In this case most of the diversification occurred within the Indomalayan and Afrotropical regions, with few lineages eventually dispersing into the north temperate zone and Neotropics. Other examples of old species-rich clades mostly confined to a single biogeographic region include the largely Afrotropical formicine tribes Plagiolepidini, the north temperate Formicini, and the Australian Melophorini, as well as the large clade comprising almost all of New World doryline species and the ponerine *Odontomachus* genus group, the latter distributed mainly in the Paleotropics. Similar patterns of long-term geographic affinity of clades can also be seen in less speciose groups, such as the Amblyoponinae, and the exclusively Old World subfamily Leptanillinae.

In addition to radiations spanning large biogeographic regions, molecular phylogenies combined with extensive faunal surveys provide a clearer picture of island ant faunas and have uncovered numerous examples of island radiations. The Malagasy ant fauna has been the focus of intensive surveys in the last 25 years. Approximately 96% of its 745 species are endemic to the island, and the fauna includes several lineages that represent recent dispersals of species-rich genera such as *Crematogaster* and *Pheidole*, arriving on the island approximately 25 and ten million years ago, respectively. In contrast, the clade of Malagasy-endemic genera *Eutetramorium*, *Malagidris*, *Royidris*, and *Vitsika* colonized Madagascar approximately 50 million years ago, but these endemic genera are currently species poor, perhaps representing a remnant of the original ant radiation now curbed by competition from more recent arrivals. Islands are also home to phylogenetically isolated, relict species, such as *Aneuretus simoni* of Sri Lanka or *Pilotrochus besmerus* of Madagascar.

Diversification rates across the tree of life are highly uneven, and the ants are no exception. As already discussed, this pattern is obvious at the

subfamily level (Fig. 2), but it is also present within subfamilies. Although currently 334 extant ant genera are recognized, eight of the most speciose taxa, *Camponotus*, *Crematogaster*, *Monomorium*, *Pheidole*, *Polyrhachis*, *Strumigenys*, *Temnothorax*, and *Tetramorium* together account for over 5,400 species, or about 40% of all described ant species. Moreover, these lineages are often sister groups to much less speciose clades and are relatively young, their crown groups having originated throughout the last 40 million years or later.

Much attention has been paid to the causes of this uneven proliferation of species in ants and other taxa. This research is carried out in the context of understanding that relative rates of both speciation and extinction contribute to overall diversification of a lineage. Common factors that promote diversification include colonization of a new region, where competition is reduced, or a key innovation, a trait that promotes diversification or reduces extinction, perhaps by allowing expansion into new niches. Identification of any trait as directly responsible for increased diversification, however, is difficult. In ants, candidates for key innovations include, but are not limited to, the *Blochmannia* symbiosis of the Camponotini, the dimorphic worker caste of *Pheidole*, the convergently evolved trap-jaw mandibles in distantly related myrmicine, formicine, and ponerine lineages, as well as the fungus-growing behavior in the *Atta* genus group and the specialized hunting behavior in the army ants. The factors responsible for the ecological success of most species-rich ant groups, however, are difficult to know with certainty.

A contrasting pattern is found in lineages that are remarkably species poor but have persisted through long periods of geologic time without significant diversification [20]. The many examples of such lineages among ants include monotypic genera such as *Aneuretus*, *Martialis*, *Opamyrra*, *Paraponera*, *Phalacromyrmex*, and *Tatuidris*. Many of these are cryptobiotic, and it may be that these lineages experience both low extinction and low speciation rates as a result of adaptations to their ecologically stable subterranean environments. This does not explain,

however, cases of *Aneuretus* or *Paraponera*, which forage above ground. In the case of *Aneuretus*, at least, it appears that it represents the last living lineage of a once more diverse group now in decline.

Present State of Ant Systematics

The publication of the landmark monographs *Identification Guide to the Ant Genera of the World* and *A New General Catalogue of the Ants of the World* marked a turning point in ant systematics [6, 7], not long after the comprehensive monograph *The Ants* [17]. These resources created a major upsurge in myrmecology, as the resulting synergy promoted it as a prominent field of entomological inquiry and accelerated the pace of taxonomic research. The average number of new ant taxa described each year more than doubled between the two decades prior to 1995 and the two decades since, with more than 200 new ant taxa described annually in recent years. This trend shows no sign of abating, so that the formal description of new taxa, both extant and fossil species, is predicted to continue for the foreseeable future.

Since the publication of these landmark books in the 1990s, there has been an effort to move the taxonomic catalog and literature online and to foster a more community-driven cataloging effort. Web portals such as antbase.org and, more recently, AntCat.org are providing easy access to taxonomic literature and information. Web portals such as AntWeb.org and AntWiki.org link these resources to specimen-based distribution data and images, including many type specimens from natural history collections around the world, contributing to further democratization of taxonomic information.

In addition to the recent improvements in access to taxonomic information and the increased pace of description of new taxa, advances in DNA sequencing technologies and phylogenetic methodology have sparked a revolution in our understanding of evolutionary relationships among ants. The molecular phylogenetic studies produced in the last

15 years or so provide a picture of ant relationships and evolution that often differ from the scenarios drawn from morphology-based phylogenies, especially at the subfamily and tribe level. It highlights the frequency of morphological convergence in ant evolution and allows reexamination of ant morphology in the light of independent tests of evolutionary relationships provided by molecular data. Myrmecologists are also increasingly taking advantage of micro-computed tomography, which reveals unprecedented detail of skeleto-musculature in even the smallest animals, living or fossil, and allows rendering of three-dimensional models of external and internal structure. The field of ant systematics is thus ripe for a revival of morphological research.

The molecular revolution has provided us with a relatively stable and complete picture of phylogenetic relationships of ants at the subfamily and even genus level [12, 15, 19]. An ongoing effort of the Global Ant Genome Alliance is seeking to understand ant diversity from a new perspective, and providing a genome-based phylogeny for all ant genera is likely to further solidify this framework [8]. However, much phylogenetic work remains to be done in species-level phylogeny. Most ant genera currently lack a comprehensive phylogenetic tree, although much progress has been made in elucidating relationships within hyperdiverse lineages such as *Crematogaster*, *Pheidole*, or *Polyrhachis*. Efforts targeting other massive genera such as *Camponotus*, *Strumigenys*, and *Tetramorium* are ongoing.

The future of ant systematics will likely continue to abound in discoveries of new ant species, to see a fuller integration and accessibility of taxonomic literature, cataloging efforts, and specimen data, as well as bringing exciting new insights into the morphology of living and extinct ants. New molecular techniques and theoretical advances will continue to build on this foundation to achieve higher phylogenetic resolution toward the tips of the ant tree of life, enhance stability in ant taxonomy and classification, and decipher ant evolution in a comprehensive framework

integrating genetic, morphological, behavioral, ecological, and evolutionary information.

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