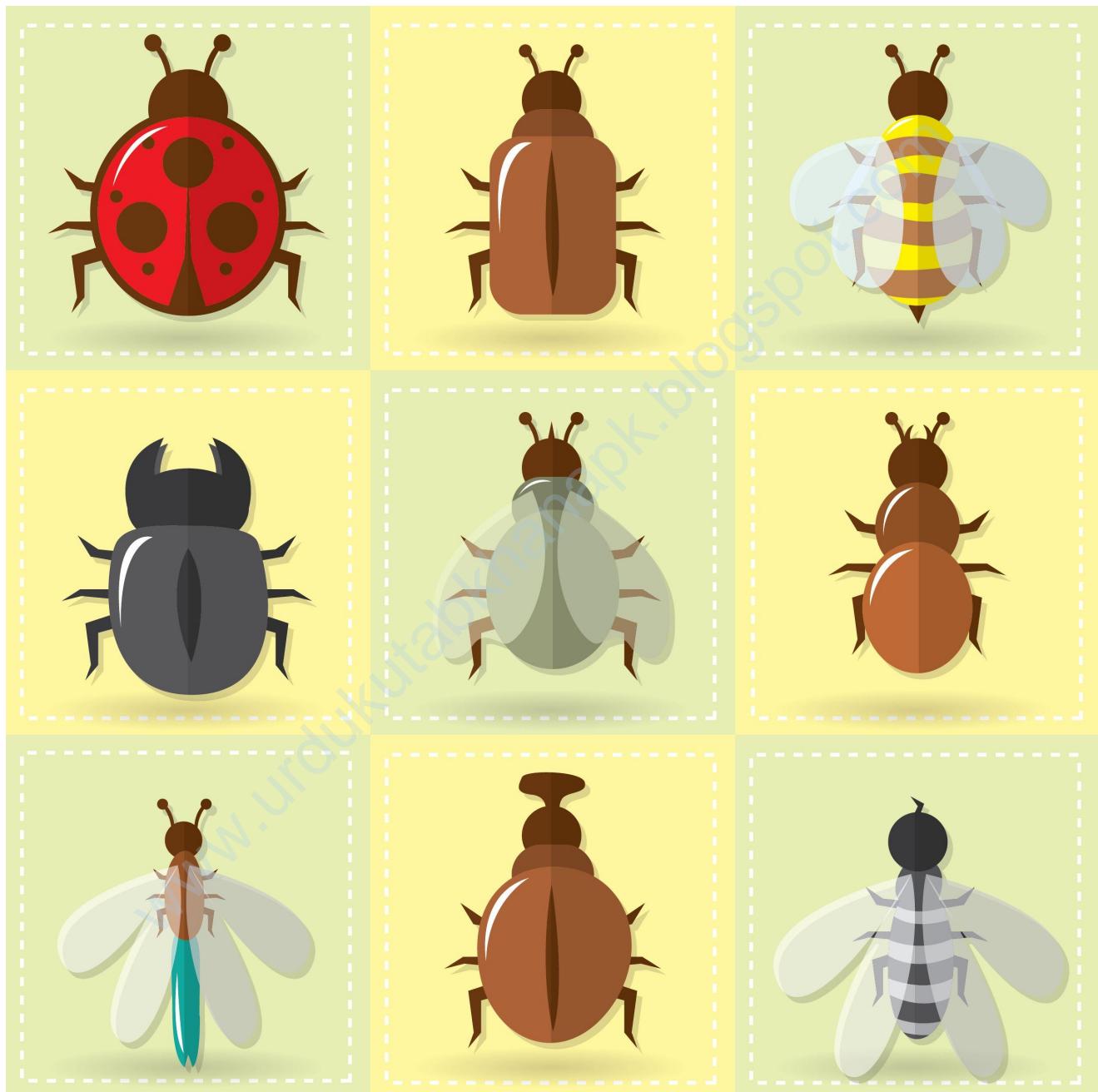


# Ants



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# Main article

## Ant

Ants Temporal range: 100–0Ma	
Albian – Recent	
	
Army ants forming a bridge	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Suborder:	Apocrita
Superfamily:	Vespoidea
Family:	<b>Formicidae</b> Latreille, 1809
Subfamilies	
<ul style="list-style-type: none"><li>• Aenictogitoninae</li><li>• Agroecomyrmecinae</li><li>• Amblyoponinae (incl. "Apomyrminae")</li><li>• Aneuretinae</li><li>• Cerapachyinae</li><li>• Dolichoderinae</li><li>• Ecitoninae (incl. "Dorylinae" and "Aenictinae")</li><li>• Ectatomminae</li></ul>	

- Formiciinae
- Formicinae
- Heteroponerinae
- Leptanillinae
- Leptanilloidinae
- Martialinae
- Myrmeciinae (incl. "Nothomyrmecinae")
- Myrmicinae
- Paraponerinae
- Ponerinae
- Proceratiinae
- Pseudomyrmecinae
- †Sphecomyrminae

**Ants** are social insects of the family **Formicidae** /fɔr'mɪsidi:/ and, along with the related wasps and bees, belong to the order Hymenoptera. Ants evolved from wasp-like ancestors in the mid-Cretaceous period between 110 and 130 million years ago and diversified after the rise of flowering plants. More than 12,500 out of an estimated total of 22,000 species have been classified.<sup>[1][2]</sup> They are easily identified by their elbowed antennae and a distinctive node-like structure that forms a slender waist.

Ants form colonies that range in size from a few dozen predatory individuals living in small natural cavities to highly organised colonies that may occupy large territories and consist of millions of individuals. Larger colonies consist mostly of sterile wingless females forming castes of "workers", "soldiers", or other specialised groups. Nearly all ant colonies also have some fertile males called "drones" and one or more fertile females called "queens". The colonies sometimes are described as superorganisms because the ants appear to operate as a unified entity, collectively working together to support the colony.<sup>[3]</sup>

Ants have colonised almost every landmass on Earth. The only places lacking indigenous ants are Antarctica and a few remote or inhospitable islands. Ants thrive in most ecosystems and may form 15–25% of the terrestrial animal biomass.<sup>[1]</sup> Their success in so many environments has been attributed to their social organisation and their ability to modify habitats, tap resources, and defend themselves. Their long co-evolution with other species has led to mimetic, commensal, parasitic, and mutualistic relationships.<sup>[4]</sup>

Ant societies have division of labour, communication between individuals, and an ability to solve complex problems.<sup>[1]</sup> These parallels with human societies have long been an inspiration and subject of study. Many human cultures make use of ants in cuisine, medication, and rituals. Some species are valued in their role as biological pest control agents.<sup>[5]</sup> Their ability to exploit resources may bring ants into conflict with humans, however, as they can damage crops and invade buildings. Some species, such as the red imported fire ant, are regarded as invasive species, establishing themselves in areas where they have been introduced accidentally.<sup>[1]</sup>

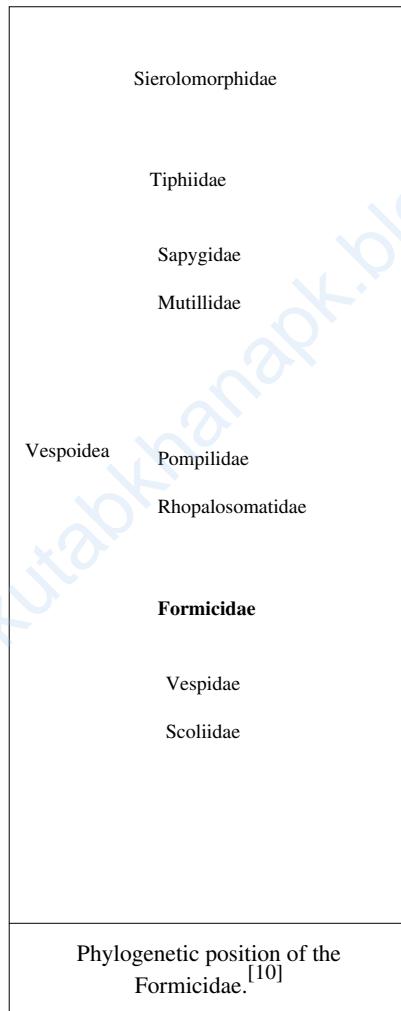
## Etymology

The word *ant* is derived from *ante* of Middle English which is derived from *aemette* of Old English and is related to the Old High German *āmeiza*, hence the modern German *Ameise*. All of these words come from West Germanic \**amaitjo*, and the original meaning of the word was "the biter" (from Proto-Germanic \**ai-*, "off, away" + \**mait-*"cut").<sup>[6][7]</sup> The family name *Formicidae* is derived from the Latin *formīca* ("ant")<sup>[8]</sup> from which the words in other Romance languages such as the Portuguese *formiga*, Italian *formica*, Spanish *hormiga*, Romanian *furnică* and French *fourmi* are derived. It has been hypothesized that a Proto-Indo-European word \**morwi-* was used, cf. Sanskrit *vamrah*, Latin *formīca*, Greek μύρμηξ *mýrmēx*, Old Church Slavonic *mrviji*, Old Irish *moirb*, Old Norse *maurr*.<sup>[9]</sup>

## Taxonomy and evolution



Ants fossilised in Baltic amber.



The family Formicidae belongs to the order Hymenoptera, which also includes sawflies, bees, and wasps. Ants evolved from a lineage within the vespid wasps. In 1966, E. O. Wilson and his colleagues identified the fossil remains of an ant (*Sphecomyrma*) that lived in the Cretaceous period. The specimen, trapped in amber dating back to around 92 million years ago, has features of both ants and wasps.<sup>[11]</sup> *Sphecomyrma* possibly was a ground forager, while *Haidomyrmex* and *Haidomyrmodes*, related genera in subfamily Sphecomyrminae are reconstructed as active arboreal predators.<sup>[1]</sup> After the rise of flowering plants about 100 million years ago they diversified and assumed ecological dominance around 60 million years ago.<sup>[1][12][13]</sup> Some groups such as the Leptanillinae and Martialinae

are suggested to have diversified from early primitive ants which were likely to have been predators underneath the surface of the soil.<sup>[10]</sup>

During the Cretaceous period, a few species of primitive ants ranged widely on the Laurasian super-continent (the northern hemisphere). They were scarce in comparison to the populations of other insects, representing only approximately 1% of the entire insect population. Ants became dominant after adaptive radiation at the beginning of the Paleogene period. By the Oligocene and Miocene ants had come to represent 20–40% of all insects found in major fossil deposits. Of the species that lived in the Eocene epoch, approximately one in ten genera survive to the present. Genera surviving today comprise 56% of the genera in Baltic amber fossils (early Oligocene), and 92% of the genera in Dominican amber fossils (apparently early Miocene).<sup>[11][14]</sup>

Termites, although sometimes called *white ants*, are not ants. They belong to the order Isoptera. Termites are more closely related to cockroaches and mantids. Termites are eusocial, but differ greatly in the genetics of reproduction. That their social structure is similar to that of ants, is attributed to convergent evolution.<sup>[15]</sup> Velvet ants look like large ants, but are wingless female wasps.<sup>[16][17]</sup>

## Distribution and diversity

Region	Number of species <sup>[18]</sup>
Neotropics	2162
Nearctic	580
Europe	180
Africa	2500
Asia	2080
Melanesia	275
Australia	985
Polynesia	42

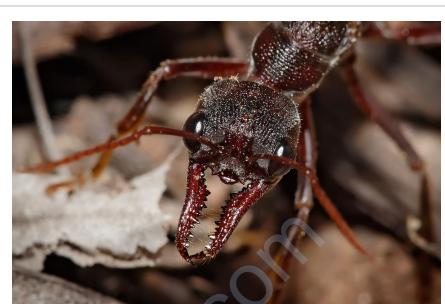
Ants are found on all continents except Antarctica, and only a few large islands such as Greenland, Iceland, parts of Polynesia and the Hawaiian Islands lack native ant species.<sup>[19][20]</sup> Ants occupy a wide range of ecological niches, and are able to exploit a wide range of food resources either as direct or indirect herbivores, predators, and scavengers. Most species are omnivorous generalists, but a few are specialist feeders. Their ecological dominance may be measured by their biomass and estimates in different environments suggest that they contribute 15–20% (on average and nearly 25% in the tropics) of the total terrestrial animal biomass, which exceeds that of the vertebrates.<sup>[1]</sup>

Ants range in size from 0.75 to 52 millimetres (0.030–2.0 in),<sup>[21]</sup> the largest species being the fossil *Titanomyrmex giganteum*, the queen of which was 6 centimetres (2.4 in) long with a wingspan of 15 centimetres (5.9 in).<sup>[1]</sup> Ants vary in colour; most ants are red or black, but a few species are green and some tropical species have a metallic lustre. More than 12,000 species are currently known (with upper estimates of the potential existence of about 22,000) (see the article List of ant genera), with the greatest diversity in the tropics. Taxonomic studies continue to resolve the classification and systematics of ants. Online databases of ant species, including AntBase and the Hymenoptera Name Server, help to keep track of the known and newly described species.<sup>[22]</sup> The relative ease with which ants may be sampled and studied in ecosystems has made them useful as indicator species in biodiversity studies.<sup>[23][24]</sup>

## Morphology

Ants are distinct in their morphology from other insects in having elbowed antennae, metapleural glands, and a strong constriction of their second abdominal segment into a node-like petiole. The head, mesosoma, and metasoma are the three distinct body segments. The petiole forms a narrow waist between their mesosoma (thorax plus the first abdominal segment, which is fused to it) and gaster (abdomen less the abdominal segments in the petiole). The petiole may be formed by one or two nodes (the second alone, or the second and third abdominal segments).<sup>[25]</sup>

Like other insects, ants have an exoskeleton, an external covering that provides a protective casing around the body and a point of attachment for muscles, in contrast to the internal skeletons of humans and other vertebrates. Insects do not have lungs; oxygen and other gases such as carbon dioxide pass through their exoskeleton via tiny valves called spiracles. Insects also lack closed blood vessels; instead, they have a long, thin, perforated tube along the top of the body (called the "dorsal aorta") that functions like a heart, and pumps haemolymph toward the head, thus driving the circulation of the internal fluids. The nervous system consists of a ventral nerve cord that runs the length of the body, with several ganglia and branches along the way reaching into the extremities of the appendages.<sup>[26]</sup>



Bull ant showing the powerful mandibles and the relatively large compound eyes that provide excellent vision

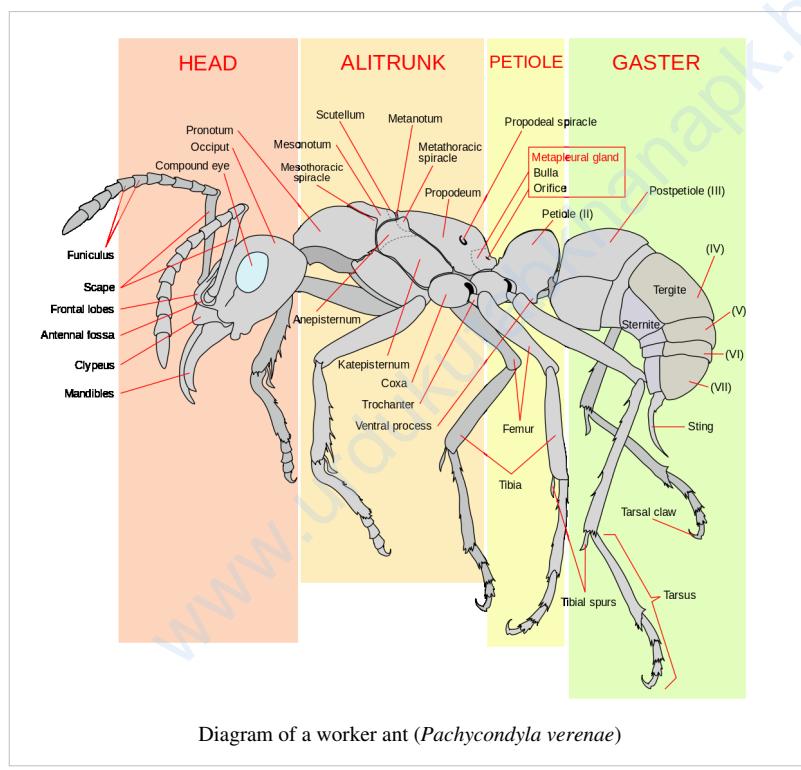


Diagram of a worker ant (*Pachycondyla verenae*)

<sup>[28]</sup> away.

### Head

An ant's head contains many sensory organs. Like most insects, ants have compound eyes made from numerous tiny lenses attached together. Ant eyes are good for acute movement detection, but do not offer a high resolution image. They also have three small ocelli (simple eyes) on the top of the head that detect light levels and polarization.<sup>[27]</sup> Compared to vertebrates, most ants have poor-to-mediocre eyesight and a few subterranean species are completely blind. Some ants such as Australia's bulldog ant, however, have excellent vision and are capable of discriminating the distance and size of objects moving nearly a metre

Two antennae ("feelers") are attached to the head; these organs detect chemicals, air currents, and vibrations; they also are used to transmit and receive signals through touch. The head has two strong jaws, the mandibles, used to carry food, manipulate objects, construct nests, and for defence.<sup>[26]</sup> In some species a small pocket (infrabuccal chamber) inside the mouth stores food, so it may be passed to other ants or their larvae.<sup>[29]</sup>

## Legs

All six legs are attached to the mesosoma ("thorax"). A hooked claw at the end of each leg helps ants to climb and to hang onto surfaces.

## Wings

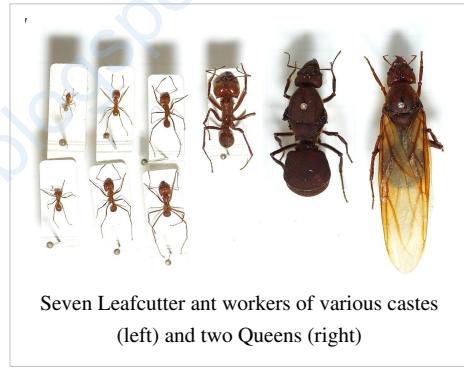
Most queens and the small number of drones in a colony (the male ants), have wings; queens shed the wings after the nuptial flight, leaving visible stubs, a distinguishing feature of queens. Wingless queens (ergatoids) and males occur in a few species, however.<sup>[26]</sup>

## Metasoma

The metasoma (the "abdomen") of the ant houses important internal organs, including those of the reproductive, respiratory (tracheae), and excretory systems. Workers of many species have their egg-laying structures modified into stings that are used for subduing prey and defending their nests.<sup>[26]</sup>

## Polymorphism

In the colonies of a few ant species, there are physical castes—workers in distinct size-classes, called minor, median, and major workers. Often the larger ants have disproportionately larger heads, and correspondingly stronger mandibles. Such individuals sometimes are called "soldier" ants because their stronger mandibles make them more effective in fighting, although they still are workers and their "duties" typically do not vary greatly from the minor or median workers. In a few species the median workers are absent, creating a sharp divide between the minors and majors.<sup>[30]</sup> Weaver ants, for example, have a distinct bimodal size distribution.<sup>[31][32]</sup> Some other species show continuous variation in the size of workers. The smallest and largest workers in *Pheidologeton diversus* show nearly a 500-fold difference in their dry-weights.<sup>[33]</sup> Workers cannot mate; however, because of the haplodiploid sex-determination system in ants, workers of a number of species can lay unfertilised eggs that become fully fertile, haploid males. The role of workers may change with their age and in some species, such as honeypot ants, young workers are fed until their gasters are distended, and act as living food storage vessels. These food storage workers are called *repletes*.<sup>[34]</sup> This polymorphism in morphology and behaviour of workers initially was thought to be determined by environmental factors such as nutrition and hormones that led to different developmental paths; however, genetic differences between worker castes have been noted in *Acromyrmex* sp.<sup>[35]</sup> These polymorphisms are caused by relatively small genetic changes; differences in a single gene of *Solenopsis invicta* can decide whether the colony will have single or multiple queens.<sup>[36]</sup> The Australian jack jumper ant (*Myrmecia pilosula*) has only a single pair of chromosomes (with the males having just one chromosome as they are haploid), the lowest number known for any animal, making it an interesting subject for studies in the genetics and developmental biology of social insects.<sup>[37][38]</sup>



Seven Leafcutter ant workers of various castes (left) and two Queens (right)

## Development and reproduction

The life of an ant starts from an egg. If the egg is fertilised, the progeny will be female (diploid); if not, it will be male (haploid). Ants develop by complete metamorphosis with the larva stages passing through a pupal stage before emerging as an adult. The larva is largely immobile and is fed and cared for by workers.

Food is given to the larvae by trophallaxis, a process in which an ant regurgitates liquid food held in its crop. This is also how adults share food, stored in the "social stomach". Larvae may also be provided with solid food such as trophic eggs, pieces of prey, and seeds brought back by foraging workers and the larvae may even be transported directly to captured prey in some species. Wikipedia:Please clarify



Ants eating food particle

The larvae grow through a series of moults and enter the pupal stage. The pupa has the appendages free and not fused to the body as in a butterfly pupa.<sup>[39]</sup> The differentiation into queens and workers (which are both female), and different castes of workers (when they exist), is influenced in some species by the nutrition the larvae obtain. Genetic influences and the control of gene expression by the developmental environment are complex and the determination of caste continues to be a subject of research.<sup>[40]</sup> Larvae and pupae need to be kept at fairly constant temperatures to ensure proper development, and so often, are moved around among the various brood chambers within the colony.<sup>[41]</sup>

A new worker spends the first few days of its adult life caring for the queen and young. She then graduates to digging and other nest work, and later to defending the nest and foraging. These changes are sometimes fairly sudden, and define what are called temporal castes. An explanation for the sequence is suggested by the high casualties involved in foraging, making it an acceptable risk only for ants who are older and are likely to die soon of natural causes.<sup>[42][43]</sup>



Fertilised meat-eater ant queen beginning to dig a new colony

Most ant species have a system in which only the queen and breeding females have the ability to mate. Contrary to popular belief, some ant nests have multiple queens while others may exist without queens. Workers with the ability to reproduce are called "gamergates" and colonies that lack queens are then called gamergate colonies; colonies with queens are said to be queen-right.<sup>[44]</sup> The winged male ants, called drones, emerge from pupae along with the breeding females (although some species, such as army ants, have wingless queens), and do nothing in life except eat and mate.

Most ants are univoltine, producing a new generation each year.<sup>[1]</sup>

During the species-specific breeding period, new reproductives, females and winged males leave the colony in what is called a nuptial flight. Typically, the males take flight before the females. Males then use visual cues to find a common mating ground, for example, a landmark such as a pine tree to which other males in the area converge. Males secrete a mating pheromone that females follow. Females of some species mate with just one male, but in some others they may mate with as many as ten or more different males.<sup>[4]</sup>

Mated females then seek a suitable place to begin a colony. There, they break off their wings and begin to lay and care for eggs. The females store the sperm they obtain during their nuptial flight to selectively fertilise future eggs. The first workers to hatch are weak and smaller than later workers, but they begin to serve the colony immediately. They enlarge the nest, forage for food, and care for the other eggs. This is how new colonies start in most ant species. Species that have multiple queens may have a queen leaving the nest along with some workers to found a colony at a new site,<sup>[45]</sup> a process akin to swarming in honeybees.

A wide range of reproductive strategies have been noted in ant species. Females of many species are known to be capable of reproducing asexually through thelytokous parthenogenesis<sup>[46]</sup> and one species, *Mycocepurus smithii*, is known to be all-female.<sup>[47]</sup>

Ant colonies can be long-lived. The queens can live for up to 30 years, and workers live from 1 to 3 years. Males, however, are more transitory, being quite short-lived and surviving for only a few weeks.<sup>[48]</sup> Ant queens are estimated to live 100 times longer than solitary insects of a similar size.<sup>[1]</sup>

Ants are active all year long in the tropics, but, in cooler regions, they survive the winter in a state of dormancy or inactivity. The forms of inactivity are varied and some temperate species have larvae going into the inactive state, (diapause), while in others, the adults alone pass the winter in a state of reduced activity.<sup>[49]</sup>



Ants mating

## Behaviour and ecology

### Communication

Ants communicate with each other using pheromones, sounds, and touch.<sup>[50]</sup> The use of pheromones as chemical signals is more developed in ants than in other hymenopteran groups. Like other insects, ants perceive smells with their long, thin, and mobile antennae. The paired antennae provide information about the direction and intensity of scents. Since most ants live on the ground, they use the soil surface to leave pheromone trails that may be followed by other ants. In species that forage in groups, a forager that finds food marks a trail on the way back to the colony; this trail is followed by other ants, these ants then reinforce the trail when they head back with food to the colony. When the food source is exhausted, no new trails are marked by returning ants and the scent slowly dissipates. This behaviour helps ants deal with changes in their environment. For instance, when an established path to a food source is blocked by an obstacle, the foragers leave the path to explore new routes. If an ant is successful, it leaves a new trail marking the shortest route on its return. Successful trails are followed by more ants, reinforcing better routes and gradually identifying the best path.<sup>[51]</sup>



An ant trail

Ants use pheromones for more than just making trails. A crushed ant emits an alarm pheromone that sends nearby ants into an attack frenzy and attracts more ants from farther away. Several ant species even use "propaganda pheromones" to confuse enemy ants and make them fight among themselves.<sup>[52]</sup> Pheromones are produced by a wide range of structures including Dufour's glands, poison glands and glands on the hindgut, pygidium, rectum, sternum, and hind tibia.<sup>[1]</sup> Pheromones also are exchanged, mixed with food, and passed by trophallaxis, transferring information within the colony.<sup>[53]</sup> This allows other ants to



A *Plectroctena* sp. attacks another of its kind to protect its territory

detect what task group (*e.g.*, foraging or nest maintenance) to which other colony members belong.<sup>[54]</sup> In ant species with queen castes, when the dominant queen stops producing a specific pheromone, workers begin to raise new queens in the colony.<sup>[55]</sup>

Some ants produce sounds by stridulation, using the gaster segments and their mandibles. Sounds may be used to communicate with colony members or with other species.<sup>[56][57]</sup>

## Defence

*See also Insect defences*

Ants attack and defend themselves by biting and, in many species, by stinging, often injecting or spraying chemicals such as formic acid. Bullet ants (*Paraponera*), located in Central and South America, are considered to have the most painful sting of any insect, although it is usually not fatal to humans. This sting is given the highest rating on the Schmidt Sting Pain Index.

The sting of Jack jumper ants can be fatal,<sup>[58]</sup> and an antivenom has been developed for it.<sup>[59]</sup>

Fire ants, *Solenopsis* spp., are unique in having a poison sac containing piperidine alkaloids.<sup>[60]</sup> Their stings are painful and can be dangerous to hypersensitive people.<sup>[61]</sup>



A weaver ant in fighting position, mandibles wide open

Trap-jaw ants of the genus *Odontomachus* are equipped with mandibles called trap-jaws, which snap shut faster than any other predatory appendages within the animal kingdom.<sup>[1]</sup> One study of *Odontomachus bauri* recorded peak speeds of between 126 and 230 km/h (78 – 143 mph), with the jaws closing within 130 microseconds on average. The ants were also observed to use their jaws as a catapult to eject intruders or fling themselves backward to escape a threat.<sup>[1]</sup> Before striking, the ant opens its mandibles extremely widely and locks them in this position by an internal mechanism. Energy is stored in a thick band of muscle and explosively released

when triggered by the stimulation of sensory organs resembling hairs on the inside of the mandibles. The mandibles also permit slow and fine movements for other tasks. Trap-jaws also are seen in the following genera: *Anochetus*, *Orectognathus*, and *Strumigenys*,<sup>[1]</sup> plus some members of the Dacetini tribe,<sup>[62]</sup> which are viewed as examples of convergent evolution.

A Malaysian species of ant in the *Camponotus cylindricus* group has enlarged mandibular glands that extend into their gaster. When disturbed, workers rupture the membrane of the gaster, causing a burst of secretions containing acetophenones and other chemicals that immobilise small insect attackers. The worker subsequently dies.<sup>[63]</sup>

Suicidal defences by workers are also noted in a Brazilian ant, *Forelius pusillus*, where a small group of ants leaves the security of the nest after sealing the entrance from the outside each evening.<sup>[64]</sup>

In addition to defence against predators, ants need to protect their colonies from pathogens. Some worker ants maintain the hygiene of the colony and their activities include undertaking or *necrophagy*, the disposal of dead nest-mates.<sup>[65]</sup> Oleic acid has been identified as the compound released from dead ants that triggers necrophobic behaviour in *Atta mexicana*<sup>[66]</sup> while workers of *Linepithema humile* react to the absence of characteristic chemicals (dolichodial and iridomyrmecin) present on the cuticle of their living nestmates to trigger similar behavior.<sup>[67]</sup>



Ant mound holes prevent water from entering the nest during rain

Nests may be protected from physical threats such as flooding and overheating by elaborate nest architecture.<sup>[68][69]</sup> Workers of *Cataulacus muticus*, an arboreal species that lives in plant hollows, respond to flooding by drinking water inside the nest, and excreting it outside.<sup>[70]</sup> *Camponotus anderseni*, which nests in the cavities of wood in mangrove habitats, deals with submergence under water by switching to anaerobic respiration.<sup>[71]</sup>

## Learning

Many animals can learn behaviours by imitation, but ants may be the only group apart from mammals where interactive teaching has been observed. A knowledgeable forager of *Temnothorax albipennis* will lead a naive nest-mate to newly discovered food by the process of tandem running. The follower obtains knowledge through its leading tutor. The leader is acutely sensitive to the progress of the follower and slows down when the follower lags and speeds up when the follower gets too close.<sup>[72]</sup>

Controlled experiments with colonies of *Cerapachys biroi* suggest that an individual may choose nest roles based on her previous experience. An entire generation of identical workers was divided into two groups whose outcome in food foraging was controlled. One group was continually rewarded with prey, while it was made certain that the other failed. As a result, members of the successful group intensified their foraging attempts while the unsuccessful group ventured out fewer and fewer times. A month later, the successful foragers continued in their role while the others had moved to specialise in brood care.<sup>[73]</sup>

## Nest construction

Complex nests are built by many ant species, but other species are nomadic and do not build permanent structures. Ants may form subterranean nests or build them on trees. These nests may be found in the ground, under stones or logs, inside logs, hollow stems, or even acorns. The materials used for construction include soil and plant matter,<sup>[45]</sup> and ants carefully select their nest sites; *Temnothorax albipennis* will avoid sites with dead ants, as these may indicate the presence of pests or disease. They are quick to abandon established nests at the first sign of threats.<sup>[74]</sup>



Leaf nest of weaver ants, Pamalican, Philippines

The army ants of South America and the driver ants of Africa do not build permanent nests, but instead, alternate between nomadism and stages where the workers form a temporary nest (bivouac) from their own bodies, by holding each other together.<sup>[75]</sup>

Weaver ant (*Oecophylla* spp.) workers build nests in trees by attaching leaves together, first pulling them together with bridges of workers and then inducing their larvae to produce silk as they are moved along the leaf edges. Similar forms of nest construction are seen in some species of *Polyrhachis*.<sup>[76]</sup>

Some ant species build nests in and on buildings. Interior spaces in walls, windows, and even electric appliances such as clocks, lamps, and radios in the interior of buildings may be used as sites for nests.

## Cultivation of food



*Myrmecocystus*, honeypot ants, store food to prevent colony famine

Most ants are generalist predators, scavengers, and indirect herbivores,<sup>[1]</sup> but a few have evolved specialised ways of obtaining nutrition. Leafcutter ants (*Atta* and *Acromyrmex*) feed exclusively on a fungus that grows only within their colonies. They continually collect leaves which are taken to the colony, cut into tiny pieces and placed in fungal gardens. Workers specialise in related tasks according to their sizes. The largest ants cut stalks, smaller workers chew the leaves and the smallest tend the fungus. Leafcutter ants are sensitive enough to recognise the reaction of the fungus to different plant material, apparently detecting chemical signals from the fungus. If a particular type of leaf is found to be toxic to the fungus, the colony will no longer collect it. The ants feed on structures produced by the fungi called *gongylidia*. Symbiotic bacteria on the exterior surface of the ants produce antibiotics that kill bacteria introduced into the nest that may harm the fungi.<sup>[77]</sup>

## Navigation

Foraging ants travel distances of up to 200 metres (700 ft) from their nest<sup>[1]</sup> and scent trails allow them to find their way back even in the dark. In hot and arid regions, day-foraging ants face death by desiccation, so the ability to find the shortest route back to the nest reduces that risk. Diurnal desert ants of the genus *Cataglyphis* such as the Sahara desert ant navigate by keeping track of direction as well as distance travelled. Distances travelled are measured using an internal pedometer that keeps count of the steps taken<sup>[78]</sup> and also by evaluating the movement of objects in their visual field (optical flow).<sup>[79]</sup> Directions are measured using the position of the sun.<sup>[80]</sup> They integrate this information to find the shortest route back to their nest.<sup>[81]</sup> Like all ants, they can also make use of visual landmarks when available<sup>[82]</sup> as well as olfactory and tactile cues to navigate.<sup>[83][84]</sup> Some species of ant are able to use the Earth's magnetic field for navigation.<sup>[85]</sup> The compound eyes of ants have specialised cells that detect polarised light from the Sun, which is used to determine direction.<sup>[86][87]</sup> These polarization detectors are sensitive in the ultraviolet region of the light spectrum.<sup>[88]</sup> In some army ant species, a group of foragers who become separated from the main column sometimes may turn back on themselves and form a circular ant mill. The workers may then run around continuously until they die of exhaustion.<sup>[89]</sup> Such wheels have been observed in other ant species, notably when a group has fallen into or been overcome with water, whereby the group rotates in a partially submerged circle on the surface of the water. The behavior could allow survival of a brief flooding.

## Locomotion

The female worker ants do not have wings and reproductive females lose their wings after their mating flights in order to begin their colonies. Therefore, unlike their wasp ancestors, most ants travel by walking. Some species are capable of leaping. For example, Jerdon's jumping ant (*Harpegnathos saltator*) is able to jump by synchronising the action of its mid and hind pairs of legs.<sup>[90]</sup> There are several species of gliding ant including *Cephalotes atratus*; this may be a common trait among most arboreal ants. Ants with this ability are able to control the direction of their descent while falling.<sup>[91]</sup>

Other species of ants can form chains to bridge gaps over water, underground, or through spaces in vegetation. Some species also form floating rafts that help them survive floods. These rafts may also have a role in allowing ants to colonise islands.<sup>[92]</sup> *Polyrhachis sokolova*, a species of ant found in Australian mangrove swamps, can swim and live in underwater nests. Since they lack gills, they go to trapped pockets of air in the submerged nests to breathe.<sup>[93]</sup>

## Cooperation and competition

Not all ants have the same kind of societies. The Australian bulldog ants are among the biggest and most basal of ants. Like virtually all ants, they are eusocial, but their social behaviour is poorly developed compared to other species. Each individual hunts alone, using her large eyes instead of chemical senses to find prey.<sup>[1]</sup>

Some species (such as *Tetramorium caespitum*) attack and take over neighbouring ant colonies. Others are less expansionist, but just as aggressive; they invade colonies to steal eggs or larvae, which they either eat or raise as workers or slaves. Extreme specialists among these slave-raiding ants, such as the Amazon ants, are incapable of feeding themselves and need captured workers to survive.<sup>[94]</sup> Captured workers of the enslaved species *Temnothorax* have evolved a counter strategy, destroying just the female pupae of the slave-making *Protomognathus americanus*, but sparing the males (who don't take part in slave-raiding as adults).<sup>[95]</sup>



Meat-eater ants feeding on a cicada, social ants cooperate and collectively gather food



A worker *Harpegnathos saltator* (a jumping ant) engaged in battle with a rival colony's queen

Ants identify kin and nestmates through their scent, which comes from hydrocarbon-laced secretions that coat their exoskeletons. If an ant is separated from its original colony, it will eventually lose the colony scent. Any ant that enters a colony without a matching scent will be attacked.<sup>[96]</sup> Also, the reason why two separate colonies of ants will attack each other even if they are of the same species is because the genes responsible for pheromone production are different between them. The argentine ant, however, does not have this characteristic, due to lack of genetic diversity, and has become a global pest because of it.

Parasitic ant species enter the colonies of host ants and establish themselves as social parasites; species such as *Strumigenys xenos* are entirely parasitic and do not have workers, but instead, rely on the food gathered by their *Strumigenys perplexa* hosts.<sup>[97][98]</sup> This form of parasitism is seen across many ant genera, but the parasitic ant is usually a species that is closely related to its host. A variety of methods are employed to enter the nest of the host ant. A parasitic queen may enter the host nest before the first brood has hatched, establishing herself prior to development of a colony scent. Other species use pheromones to confuse the host ants or to trick them into carrying the parasitic queen into the nest. Some simply fight their way into the nest.<sup>[99]</sup>

A conflict between the sexes of a species is seen in some species of ants with these reproductives apparently competing to produce offspring that are as closely related to them as possible. The most extreme form involves the production of clonal offspring. An extreme of sexual conflict is seen in *Wasmannia auropunctata*, where the queens produce diploid daughters by thelytokous parthenogenesis and males produce clones by a process whereby a diploid egg loses its maternal contribution to produce haploid males who are clones of the father.<sup>[100]</sup>

## Relationships with other organisms

Ants form symbiotic associations with a range of species, including other ant species, other insects, plants, and fungi. They also are preyed on by many animals and even certain fungi. Some arthropod species spend part of their lives within ant nests, either preying on ants, their larvae, and eggs, consuming the food stores of the ants, or avoiding predators. These inquilines may bear a close resemblance to ants. The nature of this ant mimicry (myrmecomorphy) varies, with some cases involving Batesian mimicry, where the mimic reduces the risk of predation. Others show Wasmannian mimicry, a form of mimicry seen only in inquilines.<sup>[101][102]</sup>

Aphids and other hemipteran insects secrete a sweet liquid called honeydew, when they feed on plant sap. The sugars in honeydew are a high-energy food source, which many ant species collect.<sup>[103]</sup> In some cases, the aphids secrete the honeydew in response to ants tapping them with their antennae. The ants in turn keep predators away from the aphids and will move them from one feeding location to another. When migrating to a new area, many colonies will take the aphids with them, to ensure a continued supply of honeydew. Ants also tend mealybugs to harvest their honeydew. Mealybugs may become a serious pest of pineapples if ants are present to protect mealybugs from their natural enemies.<sup>[104]</sup>

Myrmecophilous (ant-loving) caterpillars of the butterfly family Lycaenidae (e.g., blues, coppers, or hairstreaks) are herded by the ants, led to feeding areas in the daytime, and brought inside the ants' nest at night. The caterpillars have a gland which secretes honeydew when the ants massage them. Some caterpillars produce vibrations and sounds that are perceived by the ants.<sup>[105]</sup> Other caterpillars have evolved from ant-loving to ant-eating: these myrmecophagous caterpillars secrete a pheromone that makes the ants act as if the caterpillar is one of their own larvae. The caterpillar is then taken into the ant nest where it feeds on the ant larvae.<sup>[106]</sup>

Fungus-growing ants that make up the tribe Attini, including leafcutter ants, cultivate certain species of fungus in the *Leucoagaricus* or *Leucocoprinus* genera of the Agaricaceae family. In this ant-fungus mutualism, both species depend on each other for survival. The ant *Allomerus decemarticulatus* has evolved a three-way association with the host plant, *Hirtella physophora* (Chrysobalanaceae), and a sticky fungus which is used to trap their insect prey.<sup>[107]</sup>



The spider *Myrmarachne plataleoides* (female shown) mimics weaver ants to avoid predators.



An ant transporting an aphid



Ants may obtain nectar from flowers such as the dandelion but are only rarely known to pollinate flowers.

Lemon ants make devil's gardens by killing surrounding plants with their stings and leaving a pure patch of lemon ant trees, (*Duroia hirsuta*). This modification of the forest provides the ants with more nesting sites inside the stems of the *Duroia* trees.<sup>[108]</sup> Although some ants obtain nectar from flowers, pollination by ants is somewhat rare.<sup>[109]</sup> Some plants have special nectar exuding structures, extrafloral nectaries that provide food for ants, which in turn protect the plant from more damaging herbivorous insects.<sup>[110]</sup> Species such as the bullhorn acacia (*Acacia cornigera*) in Central America have hollow thorns that house colonies of stinging ants (*Pseudomyrmex ferruginea*) who defend the tree against insects, browsing mammals, and epiphytic vines. Isotopic labelling studies suggest that plants also obtain nitrogen

from the ants.<sup>[111]</sup> In return, the ants obtain food from protein- and lipid-rich Beltian bodies. Another example of this type of ectosymbiosis comes from the *Macaranga* tree, which has stems adapted to house colonies of *Crematogaster* ants.

Many tropical tree species have seeds that are dispersed by ants.<sup>[112]</sup> Seed dispersal by ants or myrmecochory is widespread and new estimates suggest that nearly 9% of all plant species may have such ant associations.<sup>[113][114]</sup> Some plants in fire-prone grassland systems are particularly dependent on ants for their survival and dispersal as the seeds are transported to safety below the ground. Many ant-dispersed seeds have special external structures, elaiosomes, that are sought after by ants as food.<sup>[115]</sup>

A convergence, possibly a form of mimicry, is seen in the eggs of stick insects. They have an edible elaiosome-like structure and are taken into the ant nest where the young hatch.<sup>[116]</sup>

Most ants are predatory and some prey on and obtain food from other social insects including other ants. Some species specialise in preying on termites (*Megaponera* and *Termitopone*) while a few Cerapachyinae prey on other ants.<sup>[1]</sup> Some termites, including *Nasutitermes corniger*, form associations with certain ant species to keep away predatory ant species.<sup>[117]</sup> The tropical wasp *Mischocyttarus drewseni* coats the pedicel of its nest with an ant-repellant chemical.<sup>[118]</sup> It is suggested that many tropical wasps may build their nests in trees and cover them to protect themselves from ants. Stingless bees (*Trigona* and *Melipona*) use chemical defences against ants.<sup>[1]</sup>

Flies in the Old World genus *Bengalia* (Calliphoridae) prey on ants and are kleptoparasites, snatching prey or brood from the mandibles of adult ants.<sup>[1]</sup> Wingless and legless females of the Malaysian phorid fly (*Vestigipoda myrmolarvoidea*) live in the nests of ants of the genus *Aenictus* and are cared for by the ants.<sup>[1]</sup>

Fungi in the genera *Cordyceps* and *Ophiocordyceps* infect ants. Ants react to their infection by climbing up plants and sinking their mandibles into plant tissue. The fungus kills the ants, grows on their remains, and produces a fruiting body. It appears that the fungus alters the behaviour of the ant to help disperse its spores<sup>[119]</sup> in a microhabitat that best suits the fungus.<sup>[120]</sup> Strepsipteran parasites also manipulate their ant host to climb grass stems, to help the parasite find mates.<sup>[121]</sup>

A nematode (*Myrmeconema neotropicum*) that infects canopy ants (*Cephalotes atratus*) causes the black-coloured gasters of workers to turn red. The parasite also alters the behaviour of the ant, causing them to carry their gasters high. The conspicuous red gasters are mistaken by birds for ripe fruits such as *Heronima alchorneoides* and eaten. The droppings of the bird are collected by other ants and fed to their young, leading to further spread of the nematode.<sup>[122]</sup>

South American poison dart frogs in the genus *Dendrobates* feed mainly on ants, and the toxins in their skin may come from the ants.<sup>[123]</sup>

Army ants forage in a wide roving column, attacking any animals in that path that are unable to escape. In Central and South America, *Eciton burchellii* is the swarming ant most commonly attended by "ant-following" birds such as antbirds and woodcreepers.<sup>[1][124]</sup> This behaviour was once considered mutualistic, but later studies found the birds to be parasitic. Although direct kleptoparasitism (birds stealing food from the ants' grasp) is rare, the birds eat many prey insects that the ants would otherwise eat and thus decrease their foraging success.<sup>[125]</sup> Birds indulge in a peculiar behaviour called anting that, as yet, is not fully understood. Here birds rest on ant nests, or pick and drop ants onto their wings and feathers; this may be a means to remove ectoparasites from the birds.

Anteaters, aardvarks, pangolins, echidnas, and numbats have special adaptations for living on a diet of ants. These adaptations include long, sticky tongues to capture ants and strong claws to break into ant nests. Brown bears (*Ursus arctos*) have been found to feed on ants. About 12%, 16%, and 4% of their faecal volume in spring, summer, and autumn, respectively, is composed of ants.<sup>[126]</sup>



Spiders sometimes feed on ants.

## Relationship with humans

Ants perform many ecological roles that are beneficial to humans, including the suppression of pest populations and aeration of the soil. The use of weaver ants in citrus cultivation in southern China is considered one of the oldest known applications of biological control.<sup>[5]</sup> On the other hand, ants may become nuisances when they invade buildings, or cause economic losses.

In some parts of the world (mainly Africa and South America), large ants, especially army ants, are used as surgical sutures. The wound is pressed together and ants are applied along it. The ant seizes the edges of the wound in its mandibles and locks in place. The body is then cut off and the head and mandibles remain in place to close the wound.<sup>[127][128][129]</sup>

Some ants of the family Ponerinae have toxic venom and are of medical importance. The species include *Paraponera clavata* (*Tocandira*) and *Dinoponera* spp. (false *Tocandiras*) of South America<sup>[130]</sup> and the *Myrmecia* ants of Australia.<sup>[131]</sup>

In South Africa, ants are used to help harvest rooibos (*Aspalathus linearis*), which are small seeds used to make a herbal tea. The plant disperses its seeds widely, making manual collection difficult. Black ants collect and store these and other seeds in their nest, where humans can gather them *en masse*. Up to half a pound (200 g) of seeds may be collected from one ant-heap.<sup>[132][133]</sup>

Although most ants survive attempts by humans to eradicate them, a few are highly endangered. Mainly, these are island species that have evolved specialized traits. They include the critically endangered Sri Lankan relict ant (*Aneuretus simoni*) and *Adetomyrma venatrix* of Madagascar.<sup>[134]</sup>

It has been estimated by E.O. Wilson that the total number of individual ants alive in the world at any one time is between one and ten quadrillion (short scale) (i.e. between  $10^{15}$  and  $10^{16}$ ). According to this estimate, the total biomass of all the ants in the world is approximately equal to the total biomass of the entire human race.<sup>[135]</sup>



Weaver ants are used as a biological control for citrus cultivation in southern China

## As food



Ants and their larvae are eaten in different parts of the world. The eggs of two species of ants are used in Mexican *escamoles*. They are considered a form of insect caviar and can sell for as much as USD 40 per pound (USD 90/kg) because they are seasonal and hard to find. In the Colombian department of Santander, *hormigas culonas* (roughly interpreted as "large-bottomed ants") *Atta laevigata* are toasted alive and eaten.<sup>[136]</sup>



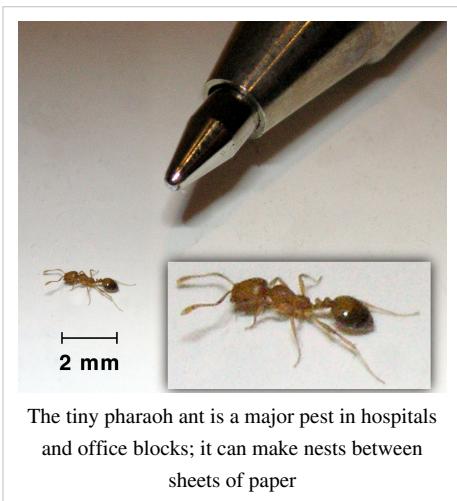
In areas of India, and throughout Burma and Thailand, a paste of the green weaver ant (*Oecophylla smaragdina*) is served as a condiment with curry.<sup>[137]</sup> Weaver ant eggs and larvae, as well as the ants, may be used in a Thai salad, *yam* (Thai: ยำ), in a dish called *yam khai mot daeng* (Thai: ยำไข่มดแดง) or red ant egg salad, a dish that comes from the Issan or north-eastern region of Thailand. Saville-Kent, in the *Naturalist in Australia* wrote "Beauty, in the case of the green ant, is more than skin-deep. Their attractive, almost sweetmeat-like translucency possibly invited the first essays at their consumption by the human species". Mashed up in water, after the manner of lemon squash, "these ants form a pleasant acid drink which is held in high favor by the natives of North Queensland, and is even appreciated by many European palates".<sup>[1]</sup>

In his *First Summer in the Sierra*, John Muir notes that the Digger Indians of California ate the tickly, acid gasters of the large jet-black carpenter ants. The Mexican Indians eat the replete workers, or living honey-pots, of the honey ant (*Myrmecocystus*).<sup>[1]</sup>

## As pests

Some ant species are considered pests,<sup>[1]</sup> and because of the adaptive nature of ant colonies, eliminating the entire colony is nearly impossible. Therefore pest management is a matter of controlling local populations, instead of eliminating an entire colony, and most attempts at control are temporary solutions.

Ants classified as pests include the pavement ant, yellow crazy ant, sugar ants, the Pharaoh ant, carpenter ants, Argentine ant, odorous house ants, red imported fire ant, and European fire ant. Populations are controlled using insecticide baits, either in granule or liquid formulations. Bait is gathered by the ants as food and brought back to the nest where the poison is inadvertently spread to other colony members through trophallaxis. Boric acid and borax are often used as insecticides that are relatively safe for humans. Bait may be broadcast over a large area to control species such as the red fire ants that occupy large areas. Nests of red fire ants may be destroyed by following the ant trails back to the nest and then pouring boiling water into the nest to kill the queen. This works in approximately 60% of the mounds and requires about 14 litres (3 imp gal; 4 US gal) per mound.<sup>[138]</sup>

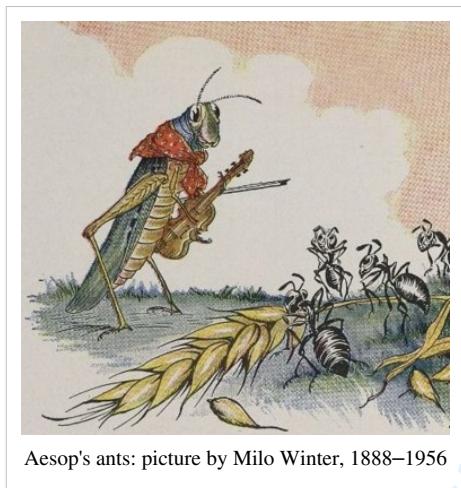


## In science and technology

Observed by humans since the dawn of history, the behavior of ants has been documented and the subject of early writings and fables passed from one century to another. Those using scientific methods, myrmecologists, study ants in the laboratory and in their natural conditions. Their complex and variable social structures have made ants ideal model organisms. Ultraviolet vision was first discovered in ants by Sir John Lubbock in 1881.<sup>[139]</sup> Studies on ants have tested hypotheses in ecology and sociobiology, and have been particularly important in examining the predictions of theories of kin selection and evolutionarily stable strategies.<sup>[140]</sup> Ant colonies may be studied by rearing or temporarily maintaining them in *formicaria*, specially constructed glass framed enclosures.<sup>[141]</sup> Individuals may be tracked for study by marking them with dots of colours.<sup>[141]</sup>

The successful techniques used by ant colonies have been studied in computer science and robotics to produce distributed and fault-tolerant systems for solving problems, for example Ant colony optimization and Ant robotics. This area of biomimetics has led to studies of ant locomotion, search engines that make use of "foraging trails", fault-tolerant storage, and networking algorithms.<sup>[142]</sup>

## In culture



Aesop's ants: picture by Milo Winter, 1888–1956

Anthropomorphised ants have often been used in fables and children's stories to represent industriousness and cooperative effort. They also are mentioned in religious texts.<sup>[142][143]</sup> In the Book of Proverbs in the Bible, ants are held up as a good example for humans for their hard work and cooperation. Aesop did the same in his fable The Ant and the Grasshopper. In the Quran, Sulayman (Arabic: سليمان) is said to have heard and understood an ant warning other ants to return home to avoid being accidentally crushed by Sulayman and his marching army.<sup>[Quran 27:18 [144]]</sup><sup>[145]</sup> In parts of Africa, ants are considered to be the messengers of the deities. Some Native American mythology, such as the Hopi mythology, considers ants as the very first animals. Ant bites are often said to have curative properties. The sting of some species of *Pseudomyrmex* is claimed to give fever relief.<sup>[146]</sup> Ant bites are used in

the initiation ceremonies of some Amazon Indian cultures as a test of endurance.<sup>[147][148]</sup>

Ant society has always fascinated humans and has been written about both humorously and seriously. Mark Twain wrote about ants in his 1880 book *A Tramp Abroad*.<sup>[149]</sup> Some modern authors have used the example of the ants to comment on the relationship between society and the individual. Examples are Robert Frost in his poem "Departmental" and T. H. White in his fantasy novel *The Once and Future King*. The plot in French entomologist and writer Bernard Werber's *Les Fourmis* science-fiction trilogy is divided between the worlds of ants and humans; ants and their behaviour is described using contemporary scientific knowledge. H.G. Wells wrote about intelligent ants destroying human settlements in Brazil and threatening human civilization in his 1905 science-fiction short story, *The Empire of the Ants*. In more recent times, animated cartoons and 3-D animated movies featuring ants have been produced including *Antz*, *A Bug's Life*, *The Ant Bully*, *The Ant and the Aardvark*, and *Atom Ant*. Renowned myrmecologist E. O. Wilson wrote a short story, "Trailhead" in 2010 for *The New Yorker* magazine, which describes the life and death of an ant-queen and the rise and fall of her colony, from an ants' point of view.<sup>[150]</sup>

From the late 1950s through the late 1970s, ant farms were popular educational children's toys in the United States. Later versions use transparent gel instead of soil, allowing greater visibility.<sup>[150]</sup> In the early 1990s, the video game SimAnt, which simulated an ant colony, won the 1992 Codie award for "Best Simulation Program".<sup>[151]</sup>

Ants also are quite popular inspiration for many science-fiction insectoids, such as the Formics of *Ender's Game*, the Bugs of *Starship Troopers*, the giant ants in the films *Them!* and *Empire of the Ants*, Marvel Comics' super hero

Ant-Man, and ants mutated into super-intelligence in *Phase IV*. In strategy games, ant-based species often benefit from increased production rates due to their single-minded focus, such as the Klackons in the *Master of Orion* series of games or the ChCht in *Deadlock II*. These characters are often credited with a hive mind, a common misconception about ant colonies.<sup>[152]</sup>

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- [5] Hölldobler & Wilson (1990), pp. 619–629
- [14] Hölldobler & Wilson (1990), pp. 23–24
- [18] Hölldobler & Wilson (1990), p. 4
- [21] Hölldobler & Wilson (1990), p. 589
- [25] Borror, Triplehorn & Delong (1989), p. 737
- [26] Borror, Triplehorn & Delong (1989), pp. 24–71
- [41] Hölldobler & Wilson (1990), pp. 351, 372
- [45] Hölldobler & Wilson (1990), pp. 143–179
- [55] Hölldobler & Wilson (1990), p. 354
- [75] Hölldobler & Wilson (1990), p. 573
- [95] See also New Scientist, April 9, 2009
- [99] Hölldobler & Wilson (1990), pp. 436—448
- [144] <http://www.usc.edu/org/cmje/religious-texts/quran/verses/027-qmt.php#027.018>

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## Further reading

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## External links

- Antweb from The California Academy of Sciences (<http://www.antweb.org/>)
- AntBase – a taxonomic database with literature sources (<http://antbase.org/>)
- Ant Genera of the World – distribution maps ([http://www.antmacroecology.org/ant\\_genera/index.html](http://www.antmacroecology.org/ant_genera/index.html))
- The super-nettles. A dermatologist's guide to ants-in-the-plants (<http://www.botanical-dermatology-database.info/BotDermReviews/Myrmecophytes.html>)
- Australian Ants, A CSIRO guide to their identification and distribution (<http://anic.ento.csiro.au/ants/index.aspx>)

# Behaviour and ecology

## Ant colony

An **ant colony** is the basic family unit around which ants organize their lifecycle. Ant colonies are eusocial, and are very much like those found in other social Hymenoptera, though the various groups of these developed sociality independently through convergent evolution. The typical colony consists of one or more egg-laying queens, a large number of sterile females ("workers") and, seasonally, a large number of winged sexual males and females. Periodically, swarms of the winged sexuals (known as alates) depart the nest in great nuptial flights. The males die shortly thereafter, along with most of the females. A small percentage of the females survive to initiate new nests.<sup>[1]</sup>

## Supercolonies

Until 2000, the largest known ant supercolony was on the Ishikari coast of Hokkaidō, Japan. The colony was estimated to contain 306 million worker ants and one million queen ants living in 45,000 nests interconnected by underground passages over an area of 2.7 km<sup>2</sup> (670 acres).<sup>[2]</sup> In 2000, an enormous supercolony of Argentine ants was found in Southern Europe (report published in 2002). Of 33 ant populations nested along the 6,004-kilometre (3,731 mi) stretch along the Mediterranean and Atlantic coasts in Southern Europe, 30 belonged to one supercolony with estimated millions of nests and billions of workers, interspersed with three populations of another supercolony.<sup>[3]</sup> The researchers claim that this case of unicoloniality cannot be explained by loss of their genetic diversity due to the genetic bottleneck of the imported ants. In 2009, it was demonstrated that the largest Japanese, Californian and European Argentine ant supercolonies were in fact part of a single global "megacolony".<sup>[4]</sup>

Another supercolony, measuring approximately 100 km (62 mi) wide, was found beneath Melbourne, Australia in 2004.<sup>[5]</sup>

## Organizational Terminology

The following terminology is commonly used among myrmecologists to describe the behaviours demonstrated by ants when founding and organizing colonies:<sup>[1]:page 209</sup>

### Monogyny

An ant colony established under a single, egg-laying, queen.



A plaster cast of an ant nest.



Ant hill and ant tracks, Oxley Wild Rivers National Park, New South Wales

**Polygyny**

An ant colony established under multiple, egg-laying, queens.

**Oligogyny**

A polygynous colony where the multiple, egg-laying, queens remain far apart from one another in the nest.

**Haplometrosis**

The founding of a colony by a single queen.

**Pleometrosis**

The founding of a colony by multiple queens.

**Monodomy**

An ant colony established in a single nest site.

**Polydomy**

An ant colony occupying multiple nest sites.



Entrance to a Harvester Ant nest (Pune, Maharashtra, India)

## **Ant-hills**

An *ant-hill*, in its simplest form, is a pile of earth, sand, pine needles, or clay or a composite of these and other materials that build up at the entrances of the subterranean dwellings of ant colonies as they are excavated. A colony is built and maintained by legions of worker ants, who carry tiny bits of dirt and pebbles in their mandibles and deposit them near the exit of the colony. They normally deposit the dirt or vegetation at the top of the hill to prevent it from sliding back into the colony, but in some species they actively sculpt the materials into specific shapes, and may create nest chambers within the mound.

In some areas of the world including English-speaking countries of Africa, in common speech the term *ant-hill* (also written as "anthill") refers to a termite mound. Note that termites are not ants.

Giant ant hills like the one on the right found in Zambia are often used to make clay bricks as the clay in the anthills is above the surface which saves time digging large holes in the ground to get to it. They are built by termites which are photosensitive so it is safe to dig into their hills without them attacking anyone.



A clay ant hill

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  - [3] Tatiana Giraud, Jes S. Pedersen, and Laurent Kelle. *Evolution of supercolonies: The Argentine ants of southern Europe* (<http://www.ncbi.nlm.nih.gov/articlerender.fcgi?artid=122904>). The National Academy of Sciences, 2002.
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  - [5] **Super ant colony hits Australia** (<http://news.bbc.co.uk/1/hi/sci/tech/3561352.stm>). BBC News, 2004.

## External links

- AntBlog, UK based ant website (<http://www.antblog.co.uk>)
  - Journal of Insect Science: The nest architecture of the Florida harvester ant ([http://www.bioone.org/perlserv/doi=10.1672/1536-2442\(2004\)004\[0001:TNAOTF\]2.0.CO;2&request=get-document&ct=1#toclink6](http://www.bioone.org/perlserv/doi=10.1672/1536-2442(2004)004[0001:TNAOTF]2.0.CO;2&request=get-document&ct=1#toclink6))
  - Ant Hill Wood, a site about ants (<http://www.anthillwood.com/>)
  - Myrmecodrome, a realistic ant colony simulator (<http://www.not-equal.eu/myrmecodrome/>)

# Ant-fungus mutualism

**Ant-fungus mutualism** is a symbiosis seen in certain ant and fungal species, where ants actively cultivate fungus much like humans farm crops as a food source. In some species, the ants and fungi are dependent on each other for survival. The leafcutter ant is a well-known example of this symbiosis.<sup>[1]</sup> A mutualism with fungi is also noted in some species of termites in Africa.<sup>[1]</sup>

## General overview

Given the exclusive New World distribution of the >230 attine ant species,<sup>[1]</sup> this mutualism is thought to have originated in the basin of the Amazon rainforest some 50–65 million years ago. There are five main types of agriculture that the attine ants practice include:<sup>[1]</sup> lower, coral-fungus, yeast, generalized higher, and leafcutter agricultural systems. Lower agriculture was the first type of attine agricultural system and is currently practiced by 80 attini species in 10 genera.<sup>[1][2]</sup> Coral-fungus agriculture is practiced by 34 species by a single derived clade within the attine genus *Apterostigma*.<sup>[2]</sup> The coral fungus farmers underwent a switch of cultivars between 10 and 20 million years ago to a nonleucocoprineaceous fungus, which makes its choice of cultivar different from all other attines.<sup>[1][3]</sup> Yeast agriculture is practiced by 18 species of *Cyphomyrmex rimosus*. The *C. rimosus* group is hypothesized to have evolved growing fungus in a yeast form between 5 and 25 million years ago.<sup>[3]</sup> Generalized higher agriculture is practiced by 63 species in two genera and refers to the condition of highly domesticated fungus.<sup>[2]</sup> The fungi used in higher agriculture cannot survive without its agriculturalists to tend it and has phenotypic changes that allow for increased ease of ant harvesting.<sup>[3]</sup> Leafcutter agriculture, which is a more highly derived form of higher agriculture, is practiced by 40 species in two genera and has the most recent evolution, originating between 8 and 12 million years ago.<sup>[3]</sup> Leaf cutters use living biomass as the substrate to feed their fungi, whereas in all other types of agriculture, the fungus requires dead biomass.<sup>[3]</sup>

In all of these types of agriculture, the attine ants actively propagate, nurture and defend the basidiomycete cultivar.<sup>[1]</sup> In return, the fungus provides nutrients for the ants, which may accumulate in specialized hyphal-tips known as "gongylidia". In some advanced genera the queen ant may take a pellet of the fungus with her when she leaves to start a new colony.<sup>[4]</sup> While this vertical transmission of fungal cultivars<sup>[5]</sup> and strong host-symbiont specificity<sup>[1]</sup> might suggest a tight coevolutionary relationship, recent phylogenetic analyses suggest this is not the case. Multiple domestications of the same fungus, fungal escape from domestication, or cultivar switching could lead to the

observed diffuse coevolutionary pattern.<sup>[6]</sup>

This mutualism is further complicated by the introduction of two other organisms, a fungal parasite *Escovopsis* and *Pseudonocardia* bacterial species residing on the ants' integuments that assist in defending the fungus from this parasite through the production of secondary metabolites.<sup>[7]</sup> In fact, some species of ants have evolved exocrine glands that apparently nourish the antibiotic-producing bacteria inside them.<sup>[8]</sup> A black yeast has been recorded as a partner in the mutualism. The yeast has a negative effect on the bacteria that normally produce antibiotics to kill the parasitic fungus and so may affect the ants' health by allowing the parasite to spread.<sup>[9]</sup>

Whereas the ants are monophyletic, their symbionts are not. They fall roughly into three major groups, only G1 having evolved gongylidia. Some G2 species grow long hyphae that form a protective cover over the nest. Those in G3 are paraphyletic, the most heterogeneous, and form the most loose relationships with their cultivators.<sup>[1]</sup> Studies now show that the fungi themselves may not be completely dependent on the ants. The fungi were earlier thought to be propagated by ants purely through clonal (vegetative) means. However considerable genetic variation in the fungi suggests that this may not be the case.<sup>[1]</sup>

## References

- [2] Mehdiabdi and Schultz 2009
- [3] Schultz and Brady 2008

## External links

- Fungus-growing ants (<http://www.zi.ku.dk/personal/drash/atta/Pages/Leafcut.html>), Social Insect Research Group, Universities of Copenhagen and Aarhus.
- Ulrich G. Mueller: Publications (<http://www.sbs.utexas.edu/Muelleru/publications.html>) (Includes links several key papers on ant/fungal symbiosis)
- Mueller, Ulrich G.; Rabeling, Christian (April 8, 2008). "A breakthrough innovation in animal evolution" (<http://www.ncbi.nlm.nih.gov/pmc/articles/PMC2291106>). *Proceedings of the National Academy of Sciences* **105** (14): 5287–5288. Bibcode: 2008PNAS..105.5287M (<http://adsabs.harvard.edu/abs/2008PNAS..105.5287M>). doi: 10.1073/pnas.0801464105 (<http://dx.doi.org/10.1073/pnas.0801464105>). PMC 2291106 (<http://www.ncbi.nlm.nih.gov/pmc/articles/PMC2291106>). PMID 18385372 (<http://www.ncbi.nlm.nih.gov/pubmed/18385372>).

# Subfamilies

## Aenictogitoninae

<b><i>Aenictogiton</i></b>	
	
<b>Scientific classification</b>	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Family:	Formicidae
Subfamily:	<b>Aenictogitoninae</b>
Genus:	<b><i>Aenictogiton</i></b> Emery, 1901
<b>Species</b>	
7 species; see text.	

*Aenictogiton* is a genus of ants, comprising seven rarely collected species, and given its own subfamily, **Aenictogitoninae**.<sup>[1]</sup> All of the species are known only from males from Central Africa and show a morphological and phylogenetic affinity to the army ant genus *Dorylus*.<sup>[1]</sup> Nothing is known about the workers, queens<sup>[1]</sup> and behavior of these ants. A few undescribed species are known to exist in a few collections in the world.

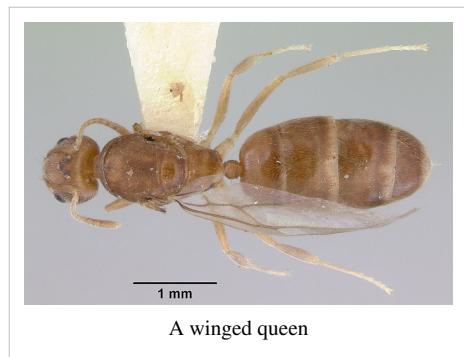
- *Aenictogiton attenuatus* - Santschi, 1919
- *Aenictogiton bequaerti* - Forel, 1913
- *Aenictogiton elongatus* - Santschi, 1919
- *Aenictogiton emeryi* - Forel, 1913
- *Aenictogiton fossiceps* - Emery, 1901 (type species)<sup>[1]</sup>
- *Aenictogiton schoutedeni* - Santschi, 1924
- *Aenictogiton sulcatus* - Santschi, 1919

## References

# Aneuretinae

<b>Sri Lankan relict ant</b>																				
 0.5 mm																				
<b>Conservation status</b>																				
<table style="width: 100%; text-align: center;"> <tr> <td style="width: 25%;">Extinct</td> <td style="width: 25%;">Threatened</td> <td style="width: 25%;">Lower Risk</td> </tr> <tr> <td>EX</td> <td>EW</td> <td>CR</td> </tr> <tr> <td>EN</td> <td>VU</td> <td>cd</td> </tr> <tr> <td>nt</td> <td></td> <td>Ic</td> </tr> </table>									Extinct	Threatened	Lower Risk	EX	EW	CR	EN	VU	cd	nt		Ic
Extinct	Threatened	Lower Risk																		
EX	EW	CR																		
EN	VU	cd																		
nt		Ic																		
Critically Endangered (IUCN 2.3) <sup>[1]</sup>																				
<b>Scientific classification</b>																				
Kingdom:	Animalia																			
Phylum:	Arthropoda																			
Class:	Insecta																			
Order:	Hymenoptera																			
Family:	Formicidae																			
Subfamily:	<b>Aneuretinae</b>																			
Genus:	<b><i>Aneuretus</i></b>																			
Species:	<b><i>A. simoni</i></b>																			
<b>Binomial name</b>																				
<b><i>Aneuretus simoni</i></b> Emery, 1893																				

The **Sri Lankan relict ant** (*Aneuretus simoni*) is a species of evolutionarily ancient ant that is placed in a separate tribe of its own within the Formicidae family. The genus is monotypic, with the only species endemic to Sri Lanka where it is known from just a few locations. It is one of the few ant species that are considered endangered.



The species is the only extant genus in the tribe Aneuretini (other members include the extinct *Protaneuretus*, *Paraneretus* and *Mianeuretus*). They are believed to be intermediate in their phylogenetic position between the Myrmeciinae-Ponerinae and the Dolichoderinae. The workers show very distinct dimorphism with "majors" being much larger than the "minors" and lacking few workers intermediate in size. The minor workers are found in the largest numbers within a nest and have a small compound eye having only about 30 ommatidia (units within the compound eye). The antennae have 12 segments with the segments increasing gradually in size from the base to the tip. The clypeus is broad and flat, lacking any central ridge. The mouthparts show Dolichoderine affinities.<sup>[1]</sup> There are outward facing spines on the propodeum. The petiole node is separated from the anterior peduncle by swellings on the sides and tops. They have a well-developed sting that is similar in structure to that of the Dolichoderinae.<sup>[2][3]</sup> Workers are yellow to orange coloured and the surface has striations running transversely.

The queen is larger than the major and has reduced propodeal spines and a much broader head than the major worker. The pupae are characteristic in being enclosed in cocoons. They are predatory and forage mainly on the ground in leaf-litter.<sup>[4]</sup> Major workers are rare and there are at the most two per colony. The social organization of the colony was found to be similar to that of the Dolichoderinae.<sup>[4]</sup>

They are known from only a few areas in central Sri Lanka. In Gilimale forest, E O Wilson and other researchers found that the colonies were mainly at the edge of forest clearings. The nests are small and have only a small number of individuals, ranging from two to a hundred. The nests are most often made mainly within rotting and crumbly wood pieces or logs fallen on the ground.<sup>[5]</sup> The few areas in which they live are often disturbed by humans. The species has not been recorded in many of the areas where it was formerly collected and it was recommended for conservation by E O Wilson.<sup>[5]</sup> A study in 1985 recorded the species at just one location, Gilimale.<sup>[6]</sup>

"Twenty years later one of my undergraduate students, Anula Jayasuriya, a native Sri Lankan, found the species rare or absent in the same localities. I recommended placement of *Aneuretus simoni* in the Red Data Book of the International Union for Conservation of Nature and Natural Resources, and in time it became one of the first of several ants to be officially classified as a threatened or endangered species."

— E O Wilson, 1994

## References

### External links

- Photographs (<http://www.antweb.org/fieldGuide.do?subfamily=aneuretinae&genus=aneuretus&species=simoni&project=worldants>)

# Brachymyrmex

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<b><i>Brachymyrmex</i></b>	
<i>Brachymyrmex aphidicola</i>	
<b>Scientific classification</b>	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Family:	Formicidae
Subfamily:	Formicinae
Genus:	<b><i>Brachymyrmex</i></b>

**Brachymyrmex** is a genus in the ant subfamily Formicinae. These ants are native to Northern Africa but several species have spread around the world with human commerce. The genus can be recognized by the combination of having nine antennal segments (fewer than most ants) and the petiole concealed by the gaster in dorsal view. They are sometimes called "rover ants".

- *Brachymyrmex coactus*
- *Brachymyrmex depilis*
- *Brachymyrmex obscurior*
- *Brachymyrmex patagonicus*

## External links

- *Brachymyrmex patagonicus*<sup>[1]</sup> on the UF / IFAS Featured Creatures Web site

## References

[1] [http://entnemdept.ifas.ufl.edu/creatures/urban/ants/dark\\_rover\\_ant.htm](http://entnemdept.ifas.ufl.edu/creatures/urban/ants/dark_rover_ant.htm)

# Cerapachyinae

Cerapachyinae	
	
<i>Cerapachys biroi</i>	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Family:	Formicidae
Subfamily:	<b>Cerapachyinae</b>
Genera	
5 extant genera, *217 extant species. <sup>[1]</sup>	

**Cerapachyinae** is a subfamily of ants of the Formicidae family. They are sometimes classified as a tribe of the Ponerinae subfamily.

They possess spines on the pygidium and short, thick antennae. They lack dorsal thoracic structures. They are predators of other ant species. There are about 200 species, distributed throughout the tropics.

## References

[1] Antweb.org (<http://www.antweb.org/description.do?name=cerapachyinae&project=calants&rank=subfamily>)

# Dolichoderinae

Dolichoderinae	
	
<i>Iridomyrmex purpureus</i> feeding on honey	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Family:	Formicidae
Subfamily:	<b>Dolichoderinae</b>
Diversity	
24 genera, hundreds of species.	

**Dolichoderinae** is a subfamily of ants, which includes species such as the Argentine ant (*Linepithema humile*), the erratic ant, the odorous house ant, and the cone ant. This subfamily is distinguished by having a single petiole (no post-petiole) and a slit-like orifice, from which chemical compounds are released, rather than the round acidopore encircled by hairs that typifies the family to which it belongs, Formicinae. Dolichoderine ants do not possess a sting, unlike ants in some other subfamilies, such as Ponerinae and Myrmicinae, instead relying on the chemical defensive compounds produced from the anal gland. <sup>[1]</sup>

Of the compounds produced by dolichoderinae ants, several terpenoids were identified including the previously unknown iridomyrmecin, iso-iridomyrmecin, and iridodial<sup>[2]</sup> Such compounds are responsible for the smell given off by ants of this subfamily when crushed or disturbed.

This subfamily is not currently divided into tribes, but there are 24 genera.

## Genera

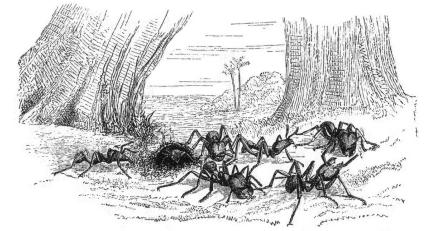
- *Amyrmex* (monotypic)
- *Anillidris* (monotypic)
- *Anonychomyrma* (27 species)
- *Axinidris*
- *Azteca*
- *Bothriomyrmex*
- *Doleromyrma* (monotypic)
- *Dolichoderus* (~140 species)
- *Dorymyrmex*
- *Ecphorella* (monotypic)
- *Forelius*
- *Froggattella*

- *Gracilidris*
- *Iridomyrmex*
- *Leptomyrmex*
- *Linepithema*
- *Liometopum*
- *Loweriella*
- *Ochetellus*
- *Papyrius*
- *Philidris*
- *Tapinoma*
- *Technomyrmex*
- *Turneria*

## References

- [1] Fisher, Brian L. and Stefan P. Cover (2007) Ants of North America: a guide to the genera
- [2] EDWARD O. WiLSON 2 AND MARIO PAVAN (1959) "Glandular sources and specificity of some chemical releasers of social behavior in dolichoderine ants." PSYCHE, Vol. 66, No. 4

# Ecitoninae

Ecitoninae	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Family:	Formicidae
Subfamily:	<b>Ecitoninae</b>
Tribes	
Cheliomyrmecini Dorylini (incl. Aenictini) Ecitonini	

Most New World army ants belong to the subfamily **Ecitoninae**. This subfamily is further broken into two groups in the New World, the tribes Cheliomyrmecini and Ecitonini. The former contains only the genus *Cheliomyrmex*, and the tribe Ecitonini contains four genera, *Neivamyrmex*, *Nomamyrmex*, *Labidus*, and *Eciton*, the genus after which the group is named.<sup>[1]</sup> The genus *Neivamyrmex* is the largest of all army ant genera, containing some 120 species, all in the United States. The most predominant species of *Eciton* is *E. burchellii*, whose common name is "army ant" and which is considered to be the archetypal species.

The Old World army ants are divided between the two tribes Aenictini and Dorylini (often treated as Dorylini alone), each of which is made up of a single genus; in the former case, *Aenictus*, that contains over 100 species of army ant, while the Dorylini contains the aggressive "driver ants" in the genus *Dorylus*, of which there are some 70 species known.

Army ant taxonomy remains ever-changing, and genetic analysis will continue to provide more information about the relatedness of the various species; many genera contain large numbers of taxa at the rank of subspecies (e.g., *Dorylus*, in which some 60 of roughly 130 named taxa are only considered subspecies at present).

## New World Army Ants

There are about 150 species of army ants in the New World (that is, North, South, and Central America), all in the tribe Ecitonini. Although these army ant species are found from Kansas to Argentina, few people in North America realize that there are plenty of army ants living in the United States, in part because the colonies are rarely very abundant, and because the United States species (mostly genus *Neivamyrmex*) are quite small (~5 mm), with small and generally unobtrusive raiding columns, most often active at night, and easily overlooked.

*E. burchellii* and *E. hamatum* are the most visible and best studied of the New World army ants because they forage above ground and during the day, in enormous raiding swarms. Their range stretches from southern Mexico to the northern part of South America.

## Old World Army Ants

There are over 100 species of army ants in the Old World, all in the tribe Dorylini (in some older classifications, also the tribe Aenictini), approximately equal numbers in the genera *Aenictus* and *Dorylus*. The latter group is by far the better-known, including the infamous "driver ants" (or "safari ants").

## Army ants in popular culture

Army ants was a toy line in the late 80s. They were portrayed as cartoonish ants crossed with gruff characteristics of the US army; helmets, rifles and so on.

## References

- O'Donnell, Sean; Kaspari, Michael; Lattke, John (21 Nov 2005). "Extraordinary Predation by the Neotropical Army Ant *Cheliomyrmex andicola*: Implications for the Evolution of the Army Ant Syndrome". *Biotropica* (Wiley InterScience) **37** (4): 706–709. doi: 10.1111/j.1744-7429.2005.00091.x (<http://dx.doi.org/10.1111/j.1744-7429.2005.00091.x>).
- Hölldobler, Bert; Wilson, Edward O. (1990). *The Ants*. Belknap Press of Harvard University Press. ISBN 0-674-04075-9.

## External links

- Current Debate in Army Ant Taxonomy (<http://www.armyants.org/>)
- Tree of Life - Ecitoninae pages (<http://tolweb.org/tree?group=Ecitoninae&contgroup=Dorylomorphs>), New World Army Ant phylogeny

# Formicinae

Formicinae	
	
<i>Camponotus fellah.</i>	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Family:	Formicidae
Subfamily:	<b>Formicinae</b> Lepeletier, 1836
Genera	
60, 59 extant (in 11 tribes). See text.	

The **Formicinae** are a subfamily within the Formicidae containing ants of moderate evolutionary development.

Formicinae retain some primitive features, such as the presence of cocoons around pupae, the presence of ocelli in workers, and little tendency toward reduction of palp or antennal segmentation in most species, except subterranean groups. Extreme modification of mandibles is rare, except in the genera *Myrmoteras* and *Polyergus*. On the other hand, some members show considerable evolutionary advancement in behaviors such as slave-making and symbiosis with root-feeding homopterans. Finally, all formicinae have very reduced stings and enlarged venom reservoirs, with the venom gland, specialized (uniquely among ants) for the production of formic acid.<sup>[citation needed]</sup>

All members of the Formicinae "have a one-segmented petiole in the form of a vertical scale".<sup>[1]</sup>



Carpenter ant

## Classification

The tribal structure of Formicinae is not completely understood. This list follows the scheme at antbase.org [2], but there are other schemes and names.

- Camponotini
  - *Calomyrmex*
  - *Camponotus* – carpenter ants (Global)
  - *Chaemeromyrma*
  - *Echinopla*
  - *Forelophilus*
  - *Opisthopsis*
  - *Overbeckia*
  - *Phasmomyrmex*
  - *Polyrhachis* (Asian, African tropics)
  - *Pseudocamponotus*
- Formicini
  - *Alloformica*
  - *Bajcaridris*
  - *Cataglyphis*
  - *Formica*
  - *Polyergus* – Amazon ants
  - *Proformica*
  - *Protoformica*
  - *Rossomyrmex*
- Gesomyrmecini
  - *Gesomyrmex*
  - *Prodromorphomyrmex*
  - *Santschiella*
  - *Sicilomyrmex*
- Gigantopini
  - *Gigantiops* (Neotropical)
- Lasiini
  - *Acanthomyops*
  - *Acropyga*
  - *Anoplolepis*
  - *Cladomyrma*
  - *Lasiophanes*
  - *Lasius*
  - *Myrmecocystus*
  - *Prolasius*
  - *Stigmacros*
  - *Teratomyrmex*
- Melophorini
  - *Melophorus* (Australian)
- Myrmecorhynchini
  - *Myrmecorhynchus*

- *Notoncus*
- *Pseudonotoncus*
- Myrmoteranini
  - *Myrmoteras*
- Notostigmatini
  - *Notostigma*
- Oecophyllini
  - *Oecophylla* – weaver ants
- Plagiolepidini
  - *Agraulomyrmex*
  - *Aphomomyrmex*
  - *Brachymyrmex*
  - *Bregmatomyrma*
  - *Euprenolepis*
  - *Myrmelachista*
  - *Nylanderia*
  - *Paraparatrechina*
  - *Paratrechina* – crazy ants
  - *Petalomyrmex*
  - *Plagiolepis*
  - *Pseudaphomomyrmex*
  - *Pseudolasius*
  - *Tapinolepis*
- *Incertae sedis*
  - *Eucharis*
  - *Imhoffia*
  - *Kyromyrmex* (fossil: Cretaceous)
  - *Leucotaphus*
  - *Protrechina*
  - *Tylolasius*

## References

### Notes

- [1] Klotz, 2008: p. 11 (<http://books.google.com/books?id=Q7T4gg6j7xUC&pg=PA11>)  
 [2] <http://antbase.org/>

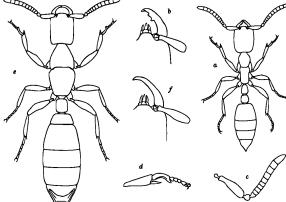
### Bibliography

- B. Bolton, *A new general catalogue of the ants of the world*, Harvard University Press, Cambridge, MA, 1995.
- Klotz, John H. (2008). "Formicinae" (<http://books.google.com/books?id=Q7T4gg6j7xUC&pg=PA11>). *Urban ants of North America and Europe: identification, biology, and management*. Cornell University Press.  
 ISBN 978-0-8014-7473-6.

## External links

- Formicinae ([http://atbi.biosci.ohio-state.edu:210/hymenoptera/nomenclator.name\\_entry?text\\_entry=formicinae&Submit=Submit+Query](http://atbi.biosci.ohio-state.edu:210/hymenoptera/nomenclator.name_entry?text_entry=formicinae&Submit=Submit+Query)) at antbase.org (<http://antbase.org/>)
- Kye S. Hedlund, Subfamily Formicinae (<http://www.cs.unc.edu/~hedlund/ants/SubfamilyPages/Formicinae-print>)

# Leptanillinae

Leptanillinae	
	
<i>Leptanilla swani</i> female and worker	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Family:	Formicidae
Subfamily:	<b>Leptanillinae</b>
Genera	
<i>Anomalomyrma</i> <i>Leptanilla</i> <i>Phaulomyrma</i> <i>Protanilla</i> <i>Yavnella</i>	
Diversity	
c. 50 species	

**Leptanillinae** is a subfamily of ants. They are further divided into the tribes Anomalomyrmini and Leptanillini.

In all Leptanillini the larva feed their hemolymph to the queen through specialized processes on their prothorax and third abdominal segment.<sup>[1]</sup> This behavior resembles that of the unrelated *Adetomyrma*, also called Dracula ants, which actually pierce their larvae to get at the body fluids.

At least *Leptanilla* and *Phaulomyrma* are minute, yellow, blind ants living below the surface.

## Systematics

- Anomalomyrmini
  - *Anomalomyrma* Taylor, 1990
    - *Anomalomyrma boltoni* Borowiec et al, 2011<sup>[2]</sup>
    - *Anomalomyrma helenae* Borowiec et al, 2011<sup>[2]</sup>
    - *Anomalomyrma taylori* Bolton, 1990
  - *Protanilla* Taylor, 1990
    - *Protanilla bicolor*
    - *Protanilla concolor*
    - *Protanilla furcomandibula*
    - *Protanilla rafflesii* Taylor, 1990

- Leptanillini
  - *Leptanilla* Emery, 1870
    - *Leptanilla africana* Baroni Urbani, 1977
    - *Leptanilla swani* Wheeler, 1932
    - *Leptanilla kubotai* Baroni Urbani, 1977
    - *Leptanilla palauensis* (Smith, 1953)
    - *Leptanilla santschii* Wheeler & Wheeler, 1930
    - *Leptanilla vaucherii* Emery, 1899
    - *Leptanilla theryi* Forel, 1903
    - *Leptanilla tenuis* Santschi, 1907
    - > 30 more species
  - *Phaulomyrma* G.C. Wheeler & E.W. Wheeler, 1930
    - *Phaulomyrma javana* Wheeler & Wheeler, 1930 — Java
  - *Yavnella* Kugler, 1987
    - *Yavnella argamani* Kugler, 1987
    - *Yavnella indica* Kugler, 1987

## Footnotes

[1] Tree of Life: Leptanillini

[2] Borowiec, M.L., Schulz, A., Alpert, G.D., & Banar, P. (2011). "Discovery of the worker caste and descriptions of two new species of *Anomalomyrma* (Hymenoptera: Formicidae: Leptanillinae) with unique abdominal morphology." *Zootaxa* 2810: 1-14.

## References

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# Martialinae

<i>Martialis heureka</i>	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Family:	Formicidae
Subfamily:	<b>Martialinae</b>
Genus:	<i>Martialis</i> Rabeling & Verhaagh, 2008
Species:	<i>M. heureka</i>
Binomial name	
<i>Martialis heureka</i> Rabeling & Verhaagh, 2008	
Diversity	
Sole species in subfamily	

*Martialis heureka* is a species of ant that was discovered in 2000 from the Amazon rainforest near Manaus, Brazil. It was described as a new species and placed as the sole member of a new subfamily (**Martialinae**). The generic name means "from Mars" and was given due to its unusual morphology, and the species epithet *heureka* indicates the surprising discovery. It is the oldest known species of ants currently in the wild.

## Description



Like all members of the family Formicidae these ants have the distinctive elbowed antennae, prominent metapleural glands and a distinctive petiole. The ants however lack compound eyes, are pale in colour, and lead a subterranean life preying on small litter organisms. The workers have unusual, elongated mandibles that are distinctly basal in their features.<sup>[1]</sup>

Based on the morphology the authors suggest that the ants lead an underground life, possibly foraging on the surface during the night. The first two specimens were found in soil core samples while another was found in leaf litter. They probably make use of pre-existing underground cavities as the legs do not show adaptations for digging.<sup>[1]</sup>

## Discovery

Two specimens were first discovered by Manfred Verhaagh of the Staatliches Museum für Naturkunde in Karlsruhe, Germany in 2000, but they were damaged and it was only in 2003 that a new specimen was collected by Christian Rabeling, a graduate student of the University of Texas at Austin.<sup>[1]</sup>

## Name

The aberrant features of this ant led Stefan P. Cover and Edward O. Wilson to comment that it was an ant that had to be from Mars. The genus name therefore refers to the planet Mars, alluding to the strange characteristics that seem to come out of nowhere, the species epithet is from Ancient Greek ηύρηκα "I found it", echoing Archimedes' famous exclamation was meant to epitomize the troubles involved in the rediscovery of the species after the first specimen discovered in a soil sample was lost.<sup>[1]</sup>

## References

# Myrmeciinae

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Myrmeciinae	
<i>Myrmecia gulosa</i>	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Suborder:	Apocrita
Superfamily:	Vespoidea
Family:	Formicidae
Subfamily:	<b>Myrmeciinae</b> Emery, 1877
tribes & species	
• see text	

The **Myrmeciinae** is a subfamily of the Formicidae that was once found worldwide but is now restricted to Australia and New Caledonia. This subfamily is one of several ant subfamilies which possess gamergates, female worker ants which are able to mate and reproduce, thus sustaining the colony after the loss of the queen.<sup>[1]</sup> The Myrmeciinae subfamily was formerly composed of only one genus, *Myrmecia*, however the subfamily was redescribed by Ward & Brady in 2003 to include two tribes and four genera:<sup>[2]</sup> An additional three genera, one form genus, and nine species were described in 2006 by Archibald, Cover and Moreau from the Early Eocene of Denmark Canada, and Washington.<sup>[3]</sup>

- Tribe Myrmeciini
  - *Myrmecia*
- Tribe Prionomyrmecini
  - †*Archimyrmex*
  - *Nothomyrmecia*
  - †*Prionomyrmex*
- Tribe *incertae sedis*
  - †*Avitomyrmex*
  - †*Macabeemyrma*
  - †*Ypresiomyrma*
- Form genus (for species belonging to the subfamily but not identifiable to current genera)
  - †*Myrmeciites*

## References

### External links

-  Media related to Myrmeciinae at Wikimedia Commons

# Myrmicinae

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Myrmicinae	
<i>Atta cephalotes</i> worker	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Suborder:	Apocrita
Superfamily:	Vespoidea
Family:	Formicidae
Subfamily:	<b>Myrmicinae</b>
Tribes	
<i>See text</i>	

**Myrmicinae** is a subfamily of ants. There are about 140 genera within the group, with the family being cosmopolitan. The pupae lack cocoons. Some species retain a functional sting. The petioles of Myrmicinae consist of two nodes. The nests are permanent and in soil, rotting wood, under stones or in trees.<sup>[1]</sup>

## Classification

The subfamily is divided into a number of tribes:

- Agroecomyrmecini
- Attini
- Basicerotini
- Blepharidattini
- Cataulacini
- Cephalotini
- Crematogastrini
- Dacetonini
- Formicoxenini
- Melissotarsini
- Meranoplini
- Metaponini
- Myrmecinini
- Myrmicariini
- Myrmicini
- Ochetomyrmecini
- Phalacromyrmecini
- Pheidolini
- Pheidologetonini
- Solenopsidini
- Stegomyrmecini

- Stenammini
- Tetramoriini

In addition, several living and fossil genera are not placed in tribes. Their position is either placed *incertae sedis* or, especially for fossil forms, too basal:

- *Archimyrmex* Cockerell, 1923
- *Attopsis* Heer, 1850
- *Cephalomyrmex* Carpenter, 1930
- *Electromyrmex* Wheeler, 1910
- *Eocenidris* Wilson, 1985
- *Eoformica* Cockerell, 1921
- *Eomyrmex* Hong, 1974
- *Lenomyrmex* Fernandez & Palacio G., 1999
- *Promyrmicium* Baroni Urbani, 1971
- *Tyrannomyrmex* Fernández, 2003

## References

- [1] Goulet, H & Huber, JT (eds.) (1993) Hymenoptera of the world: an identification guide to families. Agriculture Canada. p. 224

## External links

- *Pheidole megacephala*, bigheaded ant ([http://entomology.ifas.ufl.edu/creatures/urban/ants/bigheaded\\_ant.htm](http://entomology.ifas.ufl.edu/creatures/urban/ants/bigheaded_ant.htm)) on the UF / IFAS Featured Creatures Web site

# Paraponerinae

<i>Paraponera</i>	
	
Conservation status	
Extinct	Least Concern
EX	LC
EW	
CR	
EN	
VU	
NT	

Least Concern (IUCN 3.1)

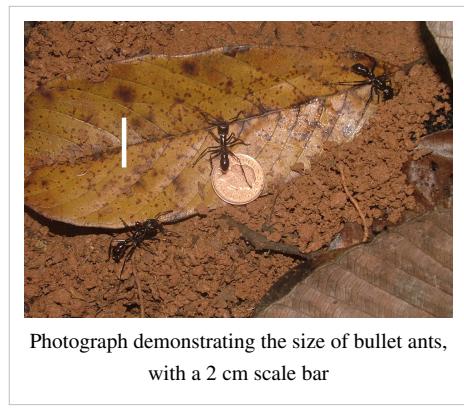
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Family:	Formicidae
Subfamily:	<b>Paraponerinae</b>
Genus:	<i>Paraponera</i> F. Smith, 1858
Species:	<i>P. clavata</i>

Binomial name	
<i>Paraponera clavata</i> (Fabricius, 1775)	

**Paraponera** is a genus of ant consisting of a single species, commonly known as the **lesser giant hunting ant**,<sup>[1]</sup> **conga ant**, or **bullet ant** (*Paraponera clavata*), named on account of its powerful and potent sting. It inhabits humid lowland rainforests from Nicaragua and the extreme east of Honduras south to Paraguay. The bullet ant is called "**Hormiga Veinticuatro**" or "24 (hour) ant" by the locals, referring to the 24 hours of pain that follow being stung.<sup>[2]</sup> The species epithet *clavata* means "club shaped".

## Description

Workers are 18–30 mm (0.7 to 1.2 inches) long<sup>[1]</sup> and resemble stout, reddish-black, wingless wasps. *Paraponera* is predaceous, and like all primitive poneromorphs does not display polymorphism in the worker caste. The queen is not much larger than the workers.<sup>[2]</sup>



## Sting

The pain caused by this insect's sting is purported to be greater than that of any other Hymenopteran, and is ranked as the most painful according to the Schmidt Sting Pain Index, given a "4+" rating, above the tarantula hawk wasp and, according to some victims, equal to being shot, hence the name of the insect. It is described as causing "waves of burning, throbbing, all-consuming pain that continues unabated for up to 24 hours". It is thought that the ant has evolved this way to ward off any predators who would normally unearth them.<sup>[1]</sup> A paralyzing neurotoxic peptide isolated from the venom is poneratoxin. It affects voltage-dependent sodium ion channels and blocks the synaptic transmission in the central nervous system. It is being investigated for possible medical applications.<sup>[3][4]</sup>

voltage-dependent sodium ion channels and blocks the synaptic transmission in the central nervous system. It is being investigated for possible medical applications.<sup>[3][4]</sup>

## Initiation rites

The Satere-Mawe people of Brazil use intentional bullet ant stings as part of their initiation rites to become a warrior.<sup>[5]</sup> The ants are first rendered unconscious by submerging them in a natural sedative and then hundreds of them are woven into a glove made out of leaves (which resembles a large oven mitt), stinger facing inward. When the ants regain consciousness, a boy slips the glove onto his hand. The goal of this initiation rite is to keep the glove on for a full ten minutes. When finished, the boy's hand and part of his arm are temporarily paralyzed because of the ant venom, and he may shake uncontrollably for days. The only "protection" provided is a coating of charcoal on the hands, supposedly to confuse the ants and inhibit their stinging. To fully complete the initiation, however, the boys must go through the ordeal a total of 20 times over the course of several months or even years.<sup>[6]</sup>

## Nest distribution

Colonies consist of several hundred individuals and are usually situated at the bases of trees. Workers forage arboreally in the area directly above the nest for small arthropods and nectar, often as far as the upper canopy; little foraging occurs on the forest floor. Nectar, carried between the mandibles, is the most common food that is taken back to the nest by foragers. Two studies in Costa Rica and on Barro Colorado Island (BCI), Panama, found that there are approximately four bullet ant nests per hectare of forest. On BCI the nests were found under 70 species of tree, 6 species of shrub, 2 species of liana and 1 species of palm. Nests were most common beneath the canopies of *Faramea occidentalis* and *Trichilia tuberculata* but these trees are also the most abundant in the forest. Nests were present more frequently than would be expected based on the abundance of the trees under *Alseis blackiana*, *Tabernaemontana arborea*, *Virola sebifera*, *Guaria guidonia* and *Oecocarpus mapoura*. The large number of nest plants suggests that there is little active selection of nest sites by bullet ants. Small shrubs however are under utilised, probably because they do not provide access to the forest canopy. The study on BCI concluded that trees with buttresses and extrafloral nectaries may be selected for by bullet ants.<sup>[7]</sup>

## Parasites

The small (1.5–2 mm long) phorid fly, *Apocephalus paraponerae*, is a parasite of injured workers of *P. clavata*, of which there is a constant supply because there are frequent aggressive encounters between neighbouring colonies resulting in maimed workers. They are able to parasitise healthy ants if they are artificially restrained, but this is thought to be rare in practice as healthy ants are agile and able to repel the flies. Both male and female flies are attracted by the scent of injured ants, the females to lay eggs as well as feed and the males to feed and possibly to mate with the females. The flies are attracted to a crushed ant within two to three minutes and ten or more flies may be attracted to each ant. Each ant can harbour 20 fly larvae. Carl Rettenmeyer observed *P. clavata* actively trying to attack *A. paraponerae* when they approached the entrance to their nest, but other authors have not observed similar behaviour.<sup>[8]</sup>

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- [2] The Natural History of Bullet Ants (<http://www.sasionline.org/antsfiles/pages/bullet/bulletbio.html>)
- [3] Eur. J. Biochem. 271, 2127–2136 (2004) (<http://content.febsjournal.org/cgi/reprint/271/11/2127.pdf>) *Poneratoxin, a neurotoxin from ant venom. Structure and expression in insect cells and construction of a bio-insecticide* (pdf)
- [4] Baillie Gerritsen, Vivienne. "Princess Bala's sting" ([http://us.expasy.org/spotlight/back\\_issues/sptlt014.shtml](http://us.expasy.org/spotlight/back_issues/sptlt014.shtml)). Protein Spotlight. Issue 14 September 2001.
- [6] "Incredible Ritual With Hundreds of Poisonous Bullet Ants" (<http://www.youtube.com/watch?v=9WQ6rFKhyn0>). YouTube. January 26, 2007. Retrieved June 13, 2012.

## Further reading

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## External links

- Brief article about *Paraponera clavata* (<http://www.antblog.co.uk/species/bulletants.htm>)
- Short article on the bullet ant and poneratoxin ([http://us.expasy.org/spotlight/back\\_issues/sptlt014.shtml](http://us.expasy.org/spotlight/back_issues/sptlt014.shtml))
- Giant tropical bullet ant, *Paraponera clavata*, natural history and captive management (<http://www.sasionline.org/antsfiles/pages/bullet/bulletbio.html>), article with images
- YouTube video of initiation ritual (<http://www.youtube.com/watch?v=ZGIZ-zUvotM&feature=related>)
- *Paraponera clavata* (<http://www.antweb.org/description.do?name=paraponera&rank=genus&project=worldants>) at AntWeb
- (<http://www.antweb.org/specimen.do?name=casent0612145>) data for specimens collected in Grace a Dios, Honduras, the northernmost extent of its range.

# Ponerinae

Ponerinae	
 fighting <i>Harpegnathos saltator</i>	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Family:	Formicidae
Subfamily:	<b>Ponerinae</b> Lepeletier, 1835
Genera	
See text	

**Ponerinae** is a subfamily of ants in the Poneromorph subfamilies group, with about 1,600 species in 28 extant genera, including *Dinoponera gigantea* - one of the world's largest species of ant.

They are most easily identified from other sub-families by a constricted gaster (abdomen). They are rare examples of stinging ants.<sup>[1]</sup>

## Tribes

- Platythyreini - only one genus *Platythreya*
- Ponerini
- Thaumatomyrmecini - *Thaumatomyrmex*



*Plectroctena* sp fighting.

## Genera

- *Afropone* (extinct)
- *Anochetus* (115 species)
- *Asphinctopone* (3 species)
- *Belonopelta* (3 species)
- *Boloponera* (1 species)
- *Centromyrmex* (18 species)
- *Cryptopone* (25 species)
- *Diacamma* (51 species)
- *Dinoponera* (6 species, 3 subspecies)
- *Dolioponera* (1 species)
- *Emeryopone* (5 species)
- *Eogorgites* (extinct)
- *Eoponerites* (extinct)
- *Feroponera* (1 species)
- *Furcisutura* (extinct)
- *Harpegnathos* (12 species)
- *Hypoponera* (343 species)
- *Leptoponera* (339 species)
- *Loboponera* (11 species)
- *Longicapitia* (extinct)
- *Myopias* (38 species)
- *Odontomachus* (66 species)
- *Odontoponera* (7 species)
- *Pachycondyla* (335 species)
- *Phrynoponera* (6 species)
- *Platythyrea* (50 species)
- *Plectroctena* (17 species)
- *Ponera* (57 species)
- *Promyopias* (1 species)
- *Psalidomyrmex* (6 species)
- *Simopelta* (29 species)
- *Strebognathus* (2 species)
- *Thaumatomyrmex* (19 species)

### Genera previously classified in Ponerinae subfamily but reclassified

- *Rhytidoponera* - subfamily Ectatomminae
- *Discothyrea* - subfamily Proceratinae
- *Probolomyrmex* - subfamily Proceratinae
- *Proceratium* - subfamily Proceratinae
- *Amblyopone* - subfamily Amblyoponinae
- *Onychomyrmex* - subfamily Amblyoponinae

## References

[1] Hoffman, Donald R. "Ant venoms" Current Opinion in Allergy and Clinical Immunology 2010, vol. 10, pages 342-346.

## External links

- Ponerinae at Antweb (<http://www.antweb.org/description.do?rank=subfamily&name=ponerinae&project=worldants>)

# Pseudomyrmecinae

Pseudomyrmecinae	
	
Pseudomyrmex acanthobius	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Suborder:	Apocrita
Superfamily:	Vespoidea
Family:	Formicidae
Subfamily:	<b>Pseudomyrmecinae</b>
Genera	
<ul style="list-style-type: none"> <li>• <i>Myrcidris</i></li> <li>• <i>Pseudomyrmex</i></li> <li>• <i>Tetraponera</i></li> </ul>	

The ant subfamily **Pseudomyrmecinae** is a small group, containing only three genera of generally slender, wasp-like forms that forage solitarily and sting readily.

## External links

- *Pseudomyrmex gracilis*, elongate twig ant <sup>[1]</sup> on the UF / IFAS Featured Creatures Web site

## References

[1] [http://entomology.ifas.ufl.edu/creatures/misc/ants/elongate\\_twig\\_ant.htm](http://entomology.ifas.ufl.edu/creatures/misc/ants/elongate_twig_ant.htm)

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