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# 1 | WHAT IS AN ANT?

# ANT ANATOMY

ANTS CAN BE CHARACTERIZED BY a combination of three unique physical features: a distinct one- or two-segmented waist, elbowed antennae, and a metapleural gland. They follow a basic insect body plan. This includes six legs, two pairs of wings (which are absent in workers), and division into three main body sections. As invertebrates they have no spine or internal skeleton, instead relying on a hard, waterproof exoskeleton made of chitin to give their body rigidity and protection. The exoskeleton is punctuated with spiracles, small breathing holes that allow the uptake of oxygen into the body. Beyond this superficially simple anatomical outline, ants exhibit a wondrous range of physical adaptations. It is this specialization of form and function that has allowed ants to flourish in virtually every terrestrial habitat on Earth.

## BODY PLAN

Insects have three body regions: the head, thorax, and abdomen, whereas ants have differently named sections: the head, mesosoma, and gaster. The mesosoma is the middle body section, formed as the first abdominal segment (the propodeum) is fused to the thorax. The next one or two abdominal segments are much reduced in size to become small nodes. They form a distinctive waist known as the petiole and (if present) postpetiole, which is a defining characteristic of ants. These waist segments are useful to prevent misidentification where ants might be confused with small wasps or the erroneously named Velvet Ants, which are not in fact ants at all. The first step in identifying an ant to subfamily is to count the number of waist segments. Subfamilies including the Dolichoderinae, Formicinae, and Ponerinae have one waist segment, while the Myrmicinae and Pseudomyrmecinae have two waist segments. Following the petiolar nodes is the gaster, composed of the remaining abdominal segments.

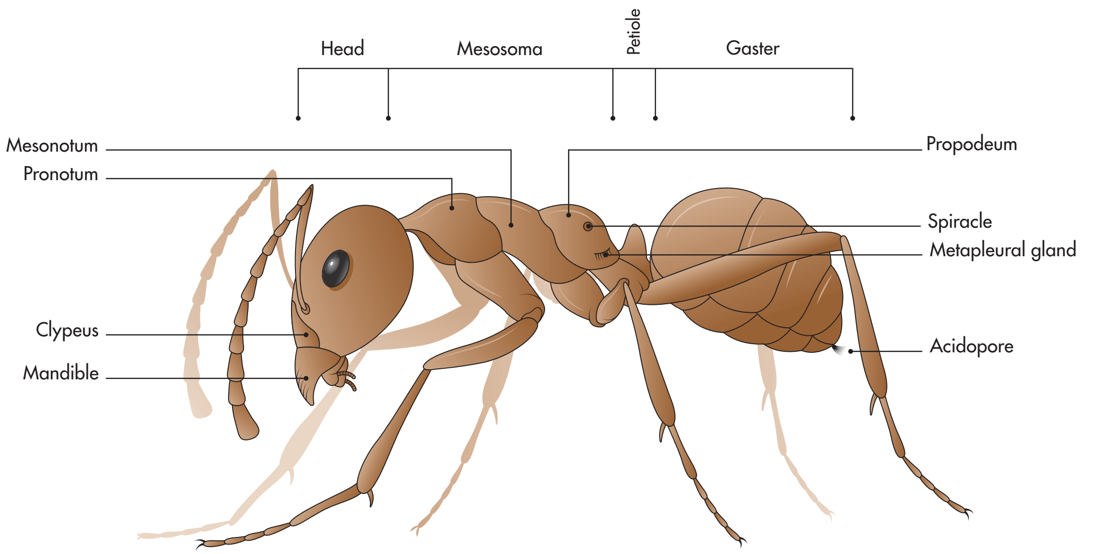
## MESOSOMA

The size of the mesosoma relative to the rest of the body is a good indicator of whether an ant will have wings and fly at any stage of its life cycle. In the case of males and reproductive females, queens, the thorax is enlarged to allow space for the flight muscles. Where present, ants possess two pairs of membranous wings. Wingless ants may be queens who have lost their wings after use—who are dealate. Alternatively, they may be female workers who never possess them to begin with. They are generally easy to tell apart as dealate queens are larger than workers and possess wing scars where wings have been bitten or rubbed off.

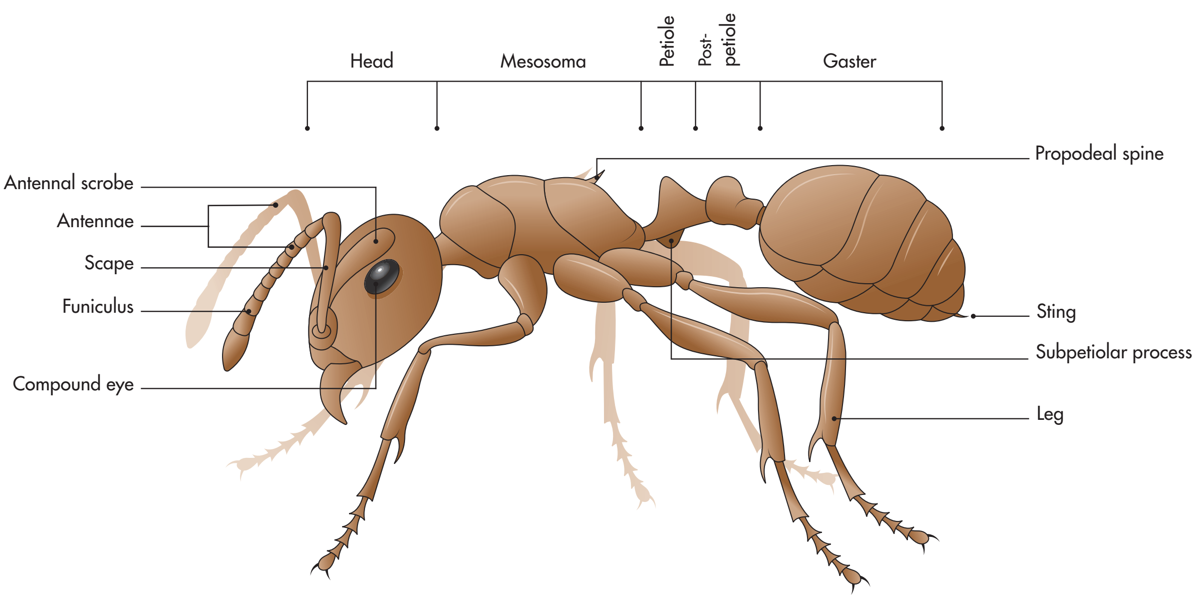
## GASTER

When it comes to organs, the ant brain and associated nervous system, along with the heart, run longitudinally through the mesosoma and gaster. Within the gaster, ants house their digestive and reproductive organs. They have two stomachs, one for their own digestion and the other a social stomach for sharing food in the colony. At the tip of the gaster, external evidence of defensive structures can be seen. Depending on the ant subfamily, they may possess a sting, a formic acid–spraying funnel of hairs known as an acidopore, or a simple slit. A unique identifying character of ants is the presence of the metapleural gland, although it has been lost in some subfamilies. This slit or round-shaped opening in the exoskeleton is a secretory gland found at the base of the propodeum. Its full significance is not understood. It could be for odor recognition or territorial marking but is most likely used in sanitation and chemical defense.

All the structures mentioned in this overview are elaborated on in the sections that follow. The different subfamilies are treated in more detail in Chapter 2.




**ABOVE:** As shown here a single waist segment, the petiole, is typical of subfamilies including the Dolichoderinae, Formicinae, and Ponerinae. Another notable feature includes the presence of a metapleural gland, a unique structure found only in ants.




**ABOVE:** The presence of antennal scrobes allows an ant to retract its antennae to be flush with its face. The two-segmented waist, comprised of a petiole and postpetiole, is indicative of ants belonging to subfamilies such as the Myrmicinae and Pseudomyrmecinae.

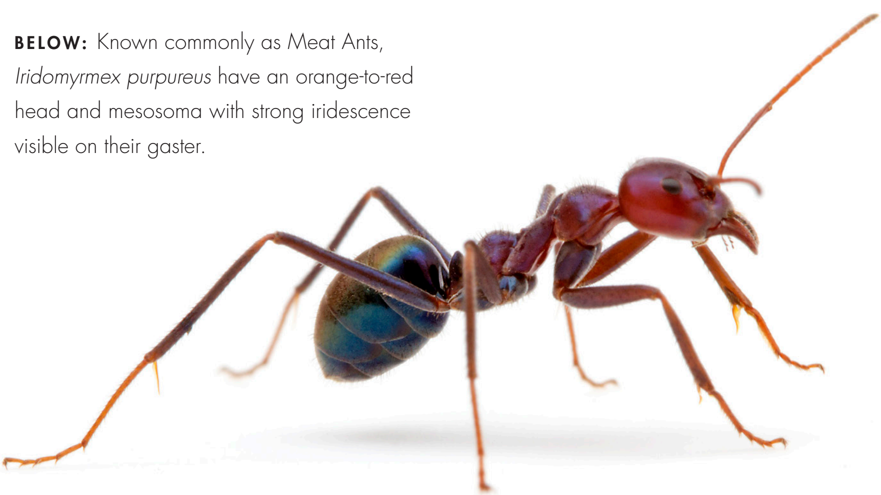
# WHEN FORM MEETS FUNCTION

MANY ASPECTS OF AN ANT'S appearance have likely evolved to meet a specific lifestyle requirement, although the extent to which this is true has not been fully explored for all aspects of anatomy. Adaptations could be due to environment, available food, or predators. Long legs and large eyes are commonly seen in ground-foraging ants that need to move quickly to avoid predators in open ground or be the first to acquire a food resource. In contrast, ants that forage and nest in leaf litter have shorter legs and antennae, alongside small eyes. This makes sense in the dark environment of leaf litter where moving through small spaces is easier with a compact body plan. Based on the unique combination of body size measurements, scientists can predict where an ant nests and forages or even what kind of food it eats. Predators have longer, flatter mandibles, while omnivores—those eating a diverse range of foods—have shorter, curved mandibles.

Size and shape alone are not the only ways in which ants vary in appearance. After seeing them under a microscope, the idea of ants as uniform specks of red or black quickly evaporates. While they may not compare with the gaudy splendor of multicolored butterfly wings, they do exhibit a range of hues in blacks, browns, reds, oranges, and yellows. Australia is home to ants in an even wider array of colors: *Rhytidoponera metallica* is more commonly known as the Green-Headed Ant for its green-blue metallic appearance, while ants in the genus *Iridomyrmex,* meaning Rainbow Ant, often possess blue, green, or purple iridescence. The most dazzling of all ants are those covered in a fine layer of golden hairs, such as the spectacular Golden Carpenter Ant, *Camponotus sericeiventris*, found in forests across Central and South America.

The thick cuticle that forms the ant exoskeleton can be highly patterned and covered in hairs. In fact, the terminology alone to describe "sculpturation"—the depressions and ridges of the cuticle—requires a 31-page guide. Ants range from having unsculptured, smooth, or glossy surfaces free of marks, to superficial wrinkles and bumps, through to deep corrugations and dense punctuations. The surface landscape of an ant sees sculpturing combined with "pilosity," the density of rigid hairs (setae) on the body, and "pubescence," the shorter fine hairs elsewhere. Hairs on ants come in many different shapes, including clavate (club-shaped), ovate (egg-shaped), reniform (kidney-shaped), and spatulate (spatula-shaped). Specialized hairs may help defend ants against predators, while certain

**BELOW:** Known commonly as Meat Ants, *Iridomyrmex purpureus* have an orange-to-red head and mesosoma with strong iridescence visible on their gaster.



**BELOW:** *Calyptomyrmex piripilis* is found across the Afrotropics from Sudan to South Africa. It has small eyes and characteristic scale-shaped hairs of unknown function.

patterns of sculpturing can create a stronger cuticle, another line of defense. Being hairy and having a thicker, more sculptured cuticle can also help avoid desiccation through water loss. It is even likely that these properties assist in thermoregulation, as hair thickness and reflectivity may help control body temperature and provide UV resistance.

**LEFT:** The widespread Australian genus *Rhytidoponera* exhibits a range of metallic colors from green and blue through purple.

**BELOW LEFT:** Arboreal *Cataulacus* ants have thick, highly sculptured exoskeletons, often with protective teeth or spines on their thorax and propodeum.

**BELOW:** Found in Neotropical rainforests, Golden Carpenter Ants are covered in a layer of long, dense golden (or sometimes silver) hair.

# ATTACK AND DEFENSE

ANTS ARE NOTORIOUS TO GARDENERS and outdoors folk alike for their ability to bite or sting at an unexpected moment. They have an extensive arsenal of physical and chemical defenses at their disposal. Ants use hairs, spines, and teeth for attack and defense, yet their most lethal weapon is located at the pointy end of the body. The subfamily Formicinae have an acidopore, a conical structure surrounded by hairs that squirts formic acid at any would-be attackers. In contrast, the subfamily Dolichoderinae have a slit-like opening with no hairs or sting. Other major subfamilies possess a venom-delivering sting for subduing prey or defending themselves. An internal poison gland produces either formic acid (in the Formicinae) or venom.

Ants have dorsal spines, protrusions of the cuticle on the upper surface of the body. They usually extend from the propodeum, pronotum, or petiole. Spines range in length and curvature from small bumps to elaborate branched structures. Considering the impressive spinescence of ants, the function is not studied in many species. In contrast to other ornate structures, such as the horns of Stag Beetles, ant spines are not a product of sexual selection in males but are most strongly displayed in the female workers. Unlike close relatives such as bees and wasps, wingless ant workers cannot fly away. It is thought that ant spines make it harder for vertebrate predators to capture and eat ants as well as for other invertebrates to attack them. Spines have evolved

**BELOW LEFT:** This species of *Polyrhachis* has three separate pairs of defensive spines on their pronotum, propodeum, and petiole.

**BELOW:** *Acanthognathus ocellatus* is a Neotropical Trap-Jaw Ant that uses its rapidly closing mandibles to catch springtails and other small leaf-litter arthropods.

repeatedly in many different and unrelated species, being present in at least 79 of 346 genera, most commonly in the megadiverse subfamily Myrmicinae.

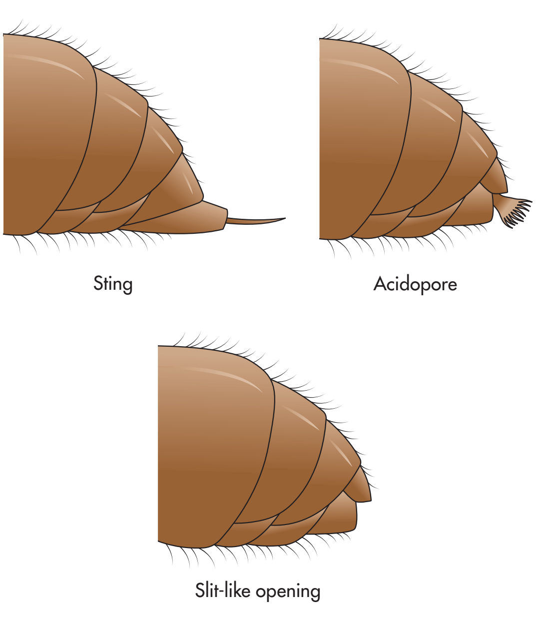
Jaws, or mandibles, are highly modified for feeding and in predatory species especially for hunting. As well as mandibles being used in direct attacks, they can be used to hold a prey item while a sting is deployed or to pin the prey in place while other workers dissect the unlucky individual. Trap-Jaw Ants have specialized mandibles that are held in an open position and have trigger hairs that, when tripped, cause the jaws to shut with extreme force. While these jaws are used mainly in hunting, they can also be co-opted as a defense mechanism to escape predators. Examples of Trap-Jaw Ants have evolved multiple times in different subfamilies, including in *Myrmoteras* within Formicinae, in the Myrmicinae subfamily for *Daceton* and *Strumigenys*, and in Ponerinae for *Anochetus* and *Odontomachus*.

Some species have different worker castes, with one specifically assigned a role in defense and usually referred to as soldier ants. These are often larger than other workers in the colony. Another physical defense strategy is phragmosis. Phragmotic species have truncated body structures that are used to block the entrance to their nests. This is most commonly seen in the head of ants from genera such as *Colobopsis*, *Cephalotes*, and *Pheidole*. *Cephalotes*, better known as Turtle Ants, have shield-like heads that can be used to plug the entrance to their nest without exposing the eyes or antennae. In *Cephalotes varians*, the head perfectly fits the nest entrance and the guard ant can allow other workers to enter and exit the nest while ensuring that any potential intruders are denied access.

**BELOW:** Major *Colobopsis etiolata* worker ants have an abruptly truncated phragmotic head. They use their head to block the entrance hole of nests in dead branches or oak galls.

**BELOW RIGHT:** Defensive structures include a sting (top left), an acidopore (top right), and a slit-like opening used to smear chemicals (bottom).

ANT DEFENSE



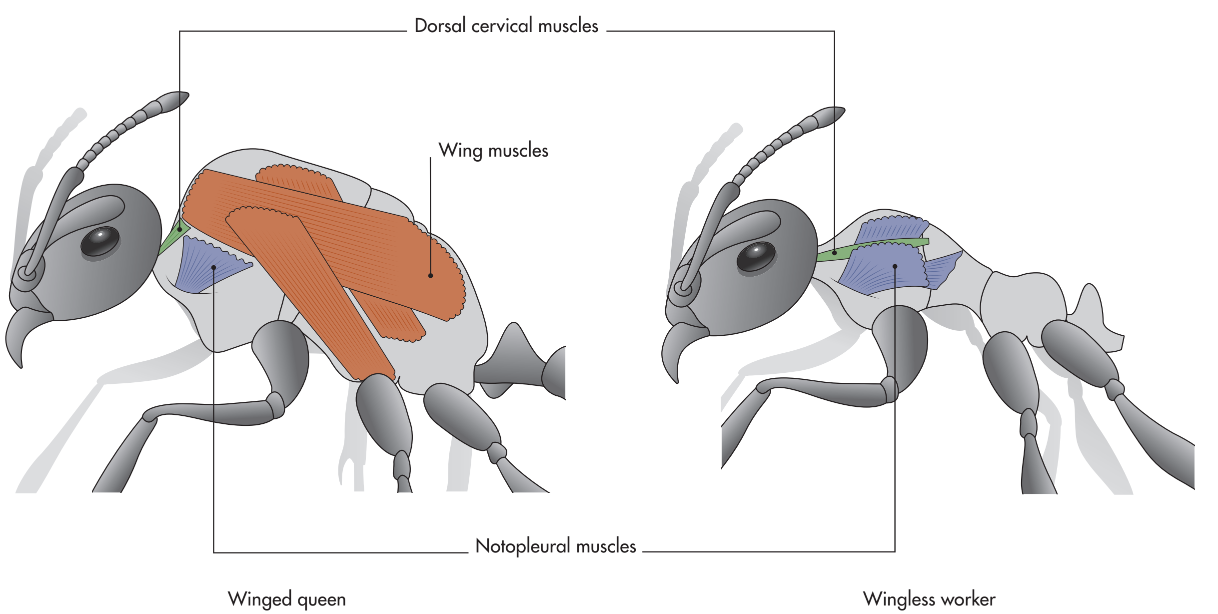
# LOCOMOTION

A RELATIVELY SMALL SUBSET of all ants use flight to get around, with wings mainly present in males and queens. Sometimes reproductive ants are wingless or show a reduction in wings (with short and long wings present in different morphs of the same species), but generally they have two pairs of soft membranous wings. The requirement for wings is because reproductives move much greater distances away from their birth nest in order to mate and in the case of queens to found a new colony. Workers move on foot, either to and from a central nest or with a colony in nomadic species. They usually move over the ground or vegetation, often through confined spaces, none of which would be feasible with two pairs of membranous wings. This means that the morphology of ants differs wildly depending on the caste of the individual being considered.

## MUSCLES

Queens have a morphology more typically seen of flying insects, with an enlarged thorax to carry the musculature required for wings. In most flying insects the first thoracic segment is small while the second and third are larger as each supports a pair of wings. The thorax arrangement for queens depends on their colony-founding strategy and therefore how they make use of their wings. Non-claustral species are those where the queen will actively hunt to feed the first generation of workers. Queens perform a high amount of foraging and their first thoracic segment is much closer in size to workers', with their wing and neck muscles more balanced in size. In contrast, claustral queens do not forage or go through a worker-like phase. They metabolize their own wing muscles to provide the energy needed for production of the first

THORACIC MUSCLE ARRANGEMENTS



generation of workers and therefore have a reduced neck segment while the wing muscles are enlarged. In contrast to the queens, worker ants show an enlarged first segment of the thorax and the muscles associated with it. This gives greater strength and mobility to the neck, which is in control of head movements.

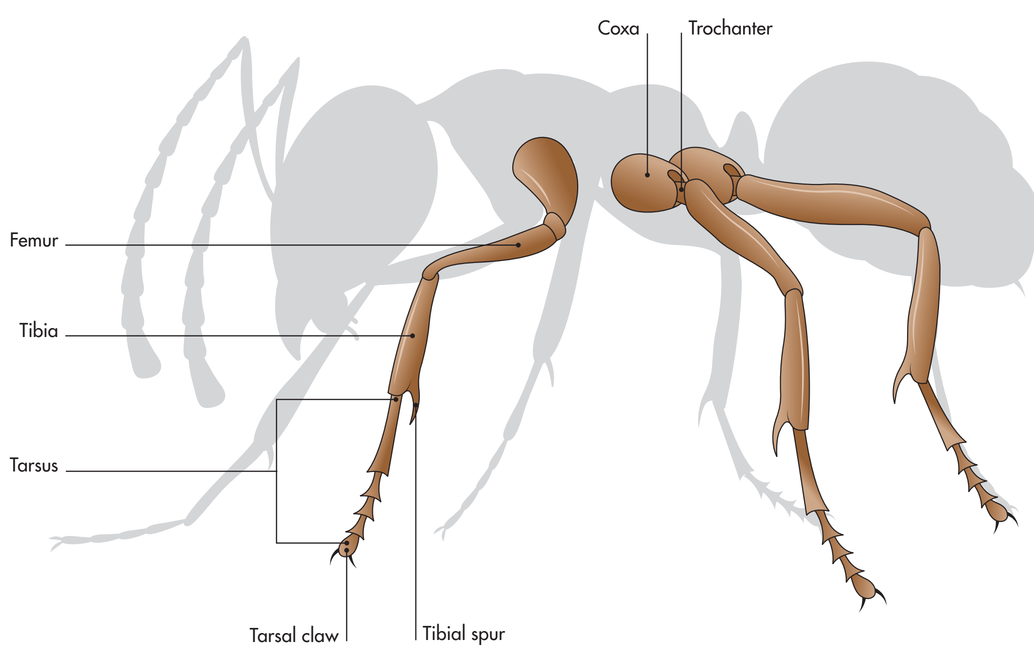
**OPPOSITE:** The structure of thoracic muscles is very different for winged queens (left) who have highly developed muscles for flight, unlike wingless workers (right).

**BELOW:** Ant legs can be highly modified depending on how and where a species lives and forages, but they all follow the same broad plan for each leg of coxa, trochanter, femur, tibia, and tarsus.

## LEGS

Ants have three pairs of legs that vary in size and shape to reflect the environment they occupy as well as their feeding habits. These legs are named according to where they attach to the body. They are pro-, meso-, and meta-, referring to the first, second, and third pairs of legs. The basal segment where the leg anchors to the body is the coxa. From there is found the trochanter, a relatively small segment, followed by the longer femur and tibia—equivalent to a human thigh and shin. The final section is the tarsus, which has five subsegments and terminates in a pair of claws—sometimes with a membranous lobe, the arolium, between the claws. The tibia sometimes possesses spurs that may be modified on the forelegs as a specialized device for cleaning the antennae.

LEG STRUCTURES



# SENSORY STRUCTURES

## EYES

Ants have two compound eyes composed of many facets known as ommatidia. Eyes have been lost completely or reduced in many subterranean species, contrasting with a number of predatory species that have extremely large eyes for hunting. The more ommatidia, the better the spatial resolution of the ant's vision. In ant species with large eyes, ommatidia numbers can be as high as 4,100 (in *Gigantiops*) and 3,200 (*Myrmecia*). Additionally, several species have ocelli on their forehead. These are light-sensitive eyespots that likely have a role in navigation. Ocelli are usually absent in workers and more commonly seen in queens and males. Ants are not primarily visual insects, and in ant brains the optic lobes are much smaller than are seen in close relatives such as wasps and bees. This may be because most ants do not fly and those that do spend only a small part of their life flying. Ants spend less time relying on visual sensory cues and are more heavily reliant on other senses such as chemicals. They can perceive UV light and have color vision, although this is likely limited to only a few colors. Ants also process other visual information about motion, patterns, directions (position of the sun, polarization pattern of the skylight), and landmarks.

## ANTENNAE

While ant reliance on visual cues varies across species, all ants rely heavily on chemical communication and use their antennae as their main sensory organs. The antennae are typically elbowed, consisting of 4 to 12 individual shorter segments called antennomeres. The base of the antenna is one long, single segment—the scape. This is followed by the funiculus, which is made up of multiple shorter segments. Segments in the funiculus may be of equal size or gradually increase in width. Occasionally a few of the end segments form a bulbous club. The scape and funiculus form an elbowed joint, a unique feature of the ants. The antennae nestle within a socket on the front of the head. Some species of ants have antennal scrobes—grooves on the sides of the head that the antennae can be retracted into.

Antennae are moved around by muscles inside the head as well as in the base of the antennae. These muscles are controlled by the dorsal lobe in the brain, which receives mechanical sensory information input from the antennae. Olfactory receptor neurons in the antennae are connected to the antennal lobe. Antennal lobes are large in ants relative to other insects because they rely more on smell than sight and because they use pheromones for communication. Antennal lobes can process ordinary smells as well as pheromones.

**LEFT:** Based on the number of ommatidia, *Gigantiops destructor* has the largest eyes of any ant, which it uses to locate prey while foraging in the forests of South America.

## MOUTHPARTS

Ants have biting and chewing mouthparts, often with distinctively shaped and well-developed mandibles. Ant mouthparts have an upper lip (labrum) and lower lip (labium). They also have a pair of mandibles and maxillae. The maxillae and labium each have sensory palps that can feel and smell food as it is being eaten. Mandibles are typically triangular in shape, with a smooth outer edge and a toothed inner masticatory margin. However, mandibles have evolved into a vast array of shapes and sizes, from toothless to double-forked teeth on the masticatory margin, to overall shapes that are variously short or elongated, straight or curved.

Mandibles are used by ants for a variety of tasks, including feeding, attacking, and defending, as well as handling and manipulating objects. Mandibles are used for excavation and construction of nests. Carrying behavior in ants requires a specialized skeletomuscular modification of the head and neck muscles. Some ants are known to carry prey between 30 to 90 times their own weight and perform delicate controlled head movements while carrying these objects. As well as food items, ants will also carry liquids suspended as a drop between their mandibles. Worker ants will carry brood (eggs, larvae, and pupae) to move them around different parts of the nest or to a new nest location. This requires a sensitive touch using mandibles in a careful and deliberate way so as not to damage the soft-bodied early life stages of the colony. Finally, ants are even known to carry each other.

**ABOVE LEFT:** Located above the eyes, the antennal scrobes of *Mycetomoellerius tucumanus* are visible as deep channels on the top of the head.

**ABOVE:** The trap-jaw mandibles of *Myrmoteras iriodum* have 12 teeth and are usually held open at 280 degrees. These, and large compound eyes, make these ants efficient hunters of small prey.

# INTERNAL ANATOMY

## NERVES

In the ant nervous system, bundles of nerve cells form ganglia that are connected by nerve cords to create the central nervous system. There is essentially one long nerve cord running from the brain through to the abdomen with branching nerves along it. Ant brains are like most insect brains, containing different regions that relate to various, often sensory, functions. The optic lobes are the visual centers, comprising the lamina, medulla, and lobula, while the antennal lobe is the primary olfactory center. There are also protocerebral lobes, the central body, and the mushroom body (made up of the calyx and the mushroom body lobes). Fused to the back of the brain is the subesophageal ganglion. This bundle of nerves branches into the mouthparts and acts in sensory detection and muscle movement. These nerves also control the head and neck movements. Following on from the subesophageal ganglion is the first thoracic ganglion. This then forms a chain of ganglia that run through the body as thoracic, petiolar, and gaster ganglia, although the numbers of ganglia are not well known in many ant species. The mushroom body may be involved in cognitive functions such as learning and memory. The role of the central body in ants is unknown but may be related to organizing behavior, for example in polarization vision or leg control. On average, larger ants have larger brains, with males having smaller brains than female queens and workers.

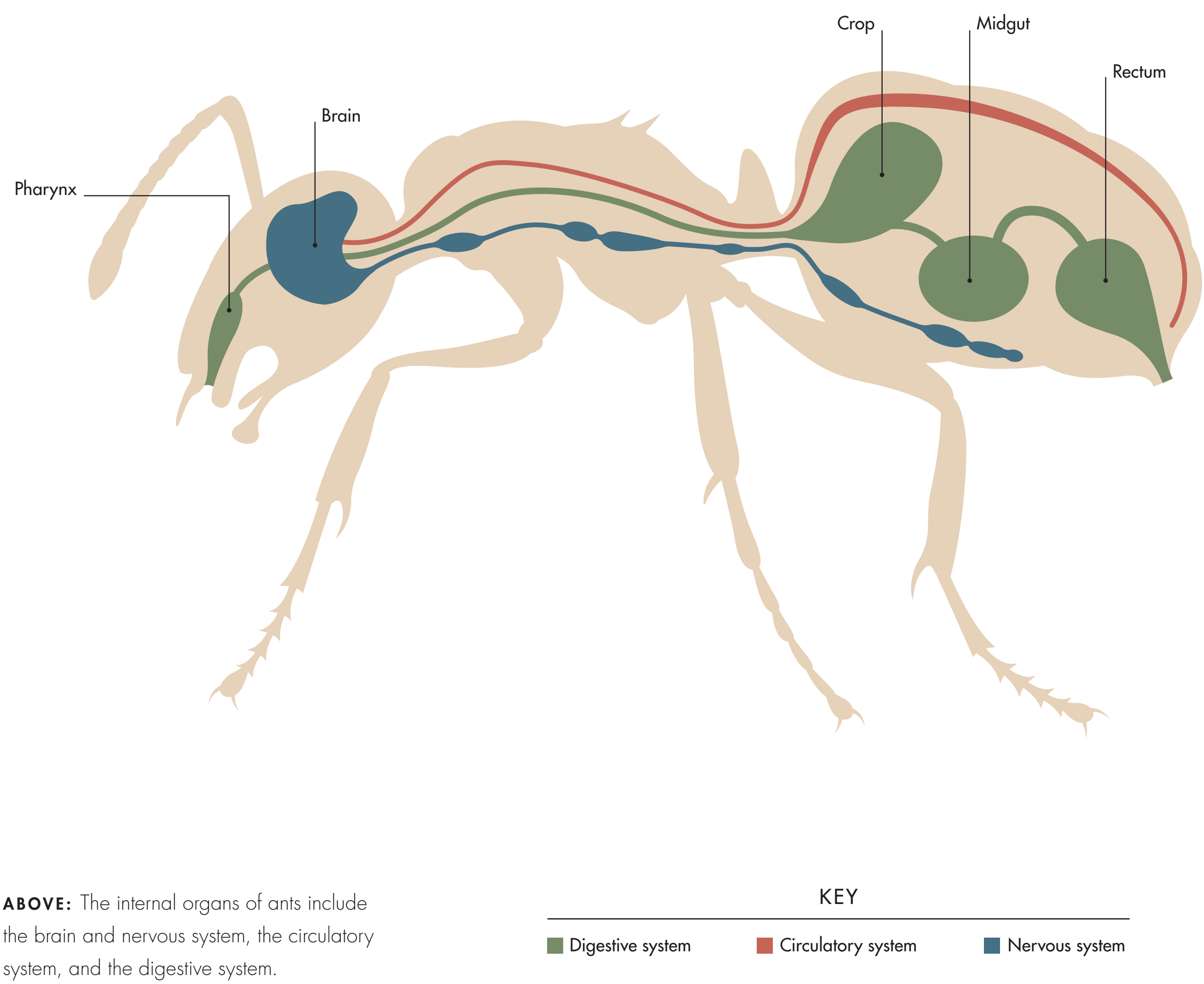
## CIRCULATION AND RESPIRATION

While an ant's respiration occurs in metabolically active tissue, the process of gas exchange (receiving oxygen and removing carbon dioxide) occurs through spiracles—tiny holes in the exoskeleton. Spiracles are connected to trachea, and these are connected to even finer branching tracheoles that perform gas exchange with cells throughout the body. Gas exchange can occur by diffusion of the gases through the tracheal system, where a continuous movement of oxygen and carbon dioxide occurs. Some ant species show discontinuous gas exchange, where there is a cyclical pattern created through the opening and closing of spiracles at different times, meaning that oxygen is taken in during activity and carbon dioxide is released during rest periods. The respiration system of ants delivers oxygen directly to tissues, reducing the requirement for a circulatory system to perform gas exchange. Ants have an open circulatory system with a single long tube running the length of the body that is equivalent to the heart. A pulsing movement moves hemolymph around the ant's body. Hemolymph is the ant equivalent of blood; it moves nutrients, hormones, and waste around the body while also circulating hemocytes—cells responsible for insect immunity.

## DIGESTION

Ants follow the same basic digestive system plan as most insects in that they possess a fore-, mid-, and hindgut. The foregut is the most complex, containing the oral cavity, followed by the pharynx, esophagus, crop, and proventriculus. The esophagus is a long tube that moves food through the insect body to the crop, a ball-shaped sac that acts as a food storage area and is located within the gaster. In ants the crop, often referred to as the "social stomach," is used by foraging worker ants to store liquid foods such as nectar or insect honeydew. In a process known as trophallaxis, this food is then regurgitated and shared out among other members of the colony. The proventriculus is a muscular valve that facilitates the process of trophallaxis. Any food allowed to pass into the midgut is digested by the ant, but food held in the crop due to the constriction of the proventriculus is part of the food supply for the colony's social stomach. The proventriculus also acts as a separation point to prevent digestive enzymes from the midgut flowing into the crop. Digestion occurs in the midgut, where absorption of nutrients takes place. The hindgut function is devoted to the process of reabsorption of water and salts.

INTERNAL BODY SYSTEMS




**ABOVE:** The internal organs of ants include the brain and nervous system, the circulatory system, and the digestive system.

# REPRODUCTION

RELATIVELY LITTLE IS KNOWN about ant copulation. It occurs with a male on top of, and facing the same direction as, a female, although exceptions are frequently observed. The male grasps a female by the legs and then probes with his genitalia before eventual penetration. The external genitalia are complex, with a large number of components serving different functions such as anchoring and clasping the male ant to the female. While internal reproductive organs are formed of soft tissue, the external genitalia are sclerotized. As well as being highly complex, the male genitalia exhibit a wide variety of different shapes across ant species.

Broadly, the external male genitalia comprise a ring of muscle at the base, known as the cupula, followed by three layers of paired valves: the outer parameres, the middle volsellae, and the inner penisvalvae. The outer parameres are used for grasping, while an inner serrated blade-like structure of the penisvalvae is thought to act as an anchor during copulation. Internally, male ants have testes as well as accessory testes and accessory glands. In the notorious Fire Ant, *Solenopsis invicta*, males have four testes that appear as four white lobes and are at a maximum size during a late pupal stage of development. They then turn amber and degenerate as the male reaches maturity. Hundreds of sperm are arranged with their heads oriented in one direction within sperm packets, of which there are many inside a follicle of the testes. The accessory testes comprise ejaculatory secretions and a sperm reservoir where sperm are kept in mature males. There is then an accessory gland that produces seminal fluid and this is attached to the external genitalia.

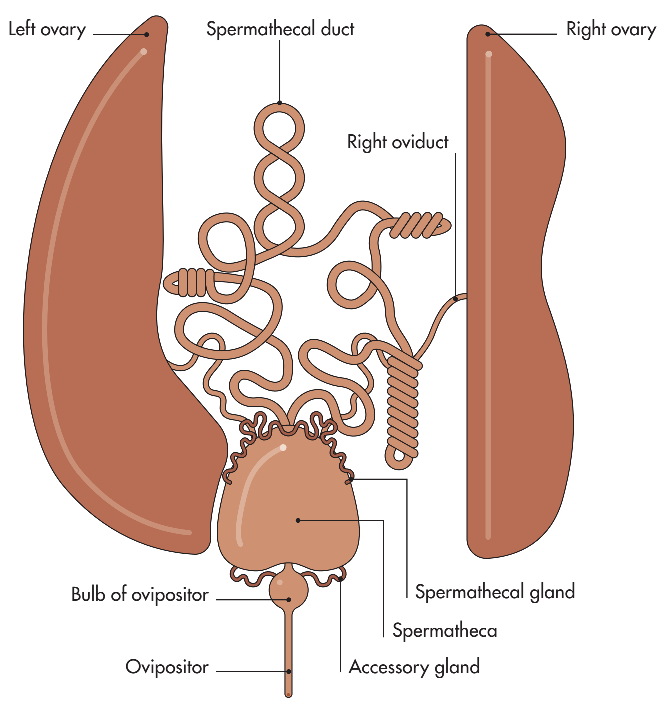
**RIGHT:** Mating of these *Brachymyrmex patagonicus* ants shows the relative size difference that occurs in some species between a smaller male and a much larger queen.

We know even less about female reproductive anatomy than we do for males. Females have two ovaries that are formed of several ovarioles. These have the appearance of strings of beads that are developing oocytes (eggs). The ovaries are connected to the uterus by the oviducts. As queen ants usually only mate at the beginning of their adult life, they need a way to store sperm. After mating with a male, a queen will store sperm inside a specialized structure called a spermatheca. This means sperm can be used as and when required to fertilize oocytes.

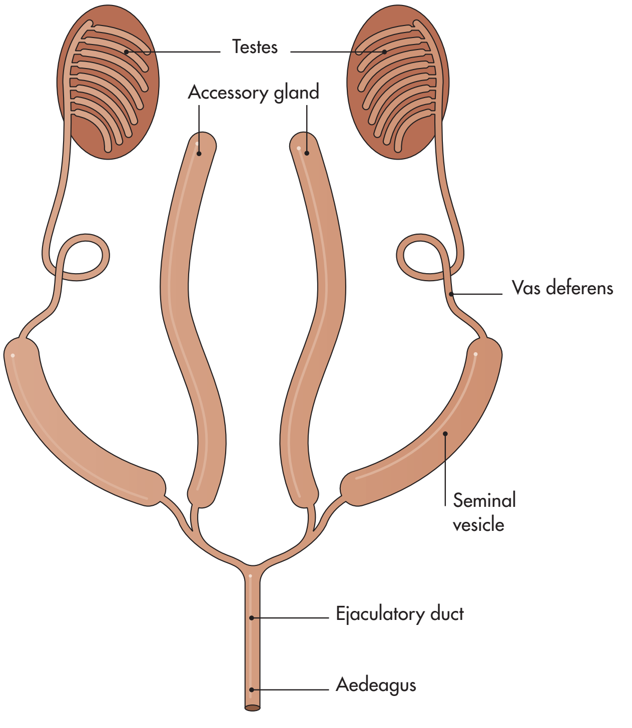
**BELOW LEFT:** A model of a female ant reproductive system based on images of *Eciton burchellii*, an Army Ant queen.

**BELOW RIGHT:** Ants follow an approximation of the same general model of the internal reproductive system for a male insect that can be seen here, although anatomical details vary between species.

FEMALE REPRODUCTIVE SYSTEM

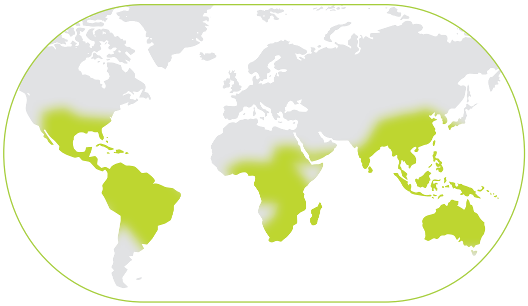



MALE REPRODUCTIVE SYSTEM



# ODONTOMACHUS

Trap-Jaw Ants



| | |
|---|---|
| **SUBFAMILY:** | Ponerinae |
| **DIVERSITY:** | 73 species |
| **DISTRIBUTION:** | Tropical and subtropical regions with highest diversity in the Neotropics and Asia |
| **HABITAT:** | Usually forest, sometimes scrub or estuarine |
| **NEST:** | Soil or rotting wood, abandoned termite nests, or trees |
| **DIET:** | Generalist predators, some omnivores |

*Odontomachus* are omnivores and generalist predators, feeding on invertebrates (especially termites), honeydew, nectar, fruits, and seeds. Their most distinctive feature is their long, straight mandibles, often held open at 180 degrees. They belong to a wider group of Trap-Jaw Ants who all have rapidly closing mandibles released by trigger hairs.

## FASTEST MANDIBLES

An ant's mandible is attached by a hinge with two muscles, an opener and a closer. The closer is the largest muscle ant workers have. Trap-Jaw Ants have modified this arrangement to include a latch, spring, and trigger mechanism. The latch holds the mandibles open at 180 degrees and the spring stores potential energy. When the trigger muscle is activated, the mandibles shut instantaneously. In *O. bauri* the mandibles close at a top speed of 210 ft (64 m) per second or 143 mi (230 km) per hour, making it one of the fastest animal movements ever recorded.

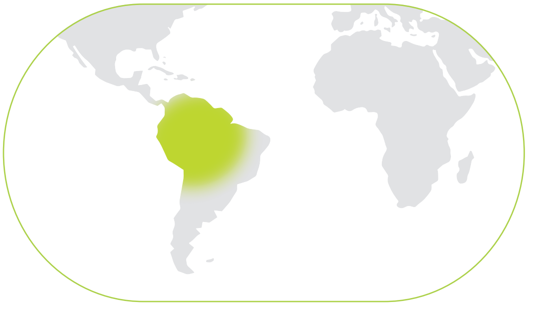
The trap-jaw mechanism is used in hunting and defense. Ants locate prey by sight until within striking distance and use their trap-jaws to complete the attack. Prey may be hit repeatedly with the mandibles to break it up. "Bouncer" ants at nest entrances will snap their jaws to push away intruders using a strike force 300 times greater than their own body weight. They are also known to escape from predators using the power generated by mandible closure to propel themselves backward to safety.

**HUNTING PROWESS**

As well as their formidably powerful jaws, *Odontomachus* ants use their large eyes and well developed sting for hunting prey.

# GIGANTIOPS

*Gigantiops destructor* is immediately recognizable from its enormous eyes, but spotting one in the first place may be difficult. These shy ants can identify humans from several feet away and will run and jump into a hiding spot. Colonies have several hundred individuals, yet workers are solitary foragers, collecting extrafloral nectar from plants and hunting various live arthropod prey (especially termites). They nest in cavities of fallen *Cecropia* trees, in the soil, under logs and stones, or in root cavities.



## FINDING YOUR WAY IN THE FOREST

Only one to three *Gigantiops* workers in a colony of a hundred will forage for prey items. Workers stack food in their mandibles, hunting up to eight small termites in a single trip. Prey are tracked visually from behind and pounced on, even flying prey. Workers in a colony will fight over food, sometimes snatching a captured prey item from the jaws of their nestmate, a behavior called cleptobiosis.

*Gigantiops* return to the same feeding spot for up to five weeks using an established route between the nest and food source. In the complex rainforest environment, they cannot employ the navigation methods commonly used by other species such as chemical trails, skyline panoramas, or canopy orientation. Instead, they navigate using known landmarks, relying especially on the first landmark near their nest to determine their direction, as well as final landmarks to confirm the location of their feeding site.

| | |
|---|---|
| **SUBFAMILY:** | Formicinae |
| **DIVERSITY:** | Monotypic (one species) |
| **DISTRIBUTION:** | Countries of northern South America |
| **HABITAT:** | Forest and savannah, usually rainforest |
| **NEST:** | Ground-nesting. Cavity-nesting. |
| **DIET:** | Omnivores |

**LONE FORAGER**

Although they are solitary foragers, *Gigantiops destructor* ants nest along rainforest edges in colonies with many hundreds of workers.

# *POLYRHACHIS*

Spiny Ants

| | |
|---|---|
| **SUBFAMILY:** | Formicinae |
| **DIVERSITY:** | Fourth-largest ant genus with over 700 species. Diversity hotspot is in Southeast Asia. |
| **DISTRIBUTION:** | Found throughout tropical and subtropical Africa, Asia, Australia, and the Pacific islands |
| **HABITAT:** | Forest, woodland, savannah |
| **NEST:** | Ground, leaf litter, and arboreal, including in carton nests or leaf structures woven together with larval silk |
| **DIET:** | Generally omnivorous, including scavenging for insects, tending aphid mutualists, and sucking excretions from plant wounds |

As one of the most diverse and conspicuous genera in the tropics, these ants exhibit stunning variation in morphological traits and ecological behavior. True to their name, most species sport varying numbers of spines, formed from pointy extensions of the cuticle on the dorsal surface of the body. As likely defenses against vertebrate predation, spine size and shape range from tiny needles to giant fishhook-shaped protrusions. The surface of many species are covered with tiny gold, silver, or white pubescence (hairs) that may serve as warnings to predators of the danger of their spines.

## NATURAL INNOVATORS

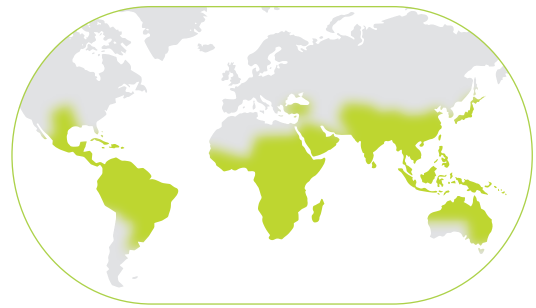
While best known for their spines, Spiny Ants have evolved a number of interesting responses to nature's challenges. Some arboreal species have abandoned more direct defenses altogether, losing their spines and instead relying on an unexpected behavioral defense: dropping off a leaf and plummeting down to the forest floor. These and most other arboreal species repurpose larval silk to bind leaves and other material together to form nest structures in the trees, with a few species even stealing spider silk for their constructions. When threatened with flooding, the mangrove forest-dwelling species *P. sokolova* can swim across the water with a dog paddle swimming stroke. As the tide rises and the subterranean nest is submerged, workers relocate the queen and brood to special air pocket chambers, allowing the colony to survive until the tide recedes.

**FINE GOLDEN HAIRS**

The unmistakable gold pubescence and hooked spines belong to *Polyrhachis ypsilon*, an ant species found in Brunei, Indonesia, Thailand, and Malaysia.

# CAREBARA

*Carebara* are ground-nesting ants found in many habitats of tropical or subtropical regions. They are a diverse genus that display distinct size patterns of workers relating to their roles inside the colony. *Carebara* ants show extreme size variation, with workers ranging in total length from $^{3}/_{64}$ in (1 mm) in the Neotropical *C. minuta* up to $^{5}/_{8}$ in (16 mm) in the Oriental *C. diversus*. Size divergence is exhibited for different worker castes—a large major may weigh up to 500 times as much as a small minor.



## MAJOR OR MINOR?

Division of tasks is related to size and age. Majors account for 10 percent of the colony's workers. They aid with dissecting and transporting larger prey as well as colony defense. A special subcaste of major workers are phragmotic—their heads are shaped into shields used to block nest entrances against attackers. Minor workers carry larvae while young but gain other responsibilities as they age.

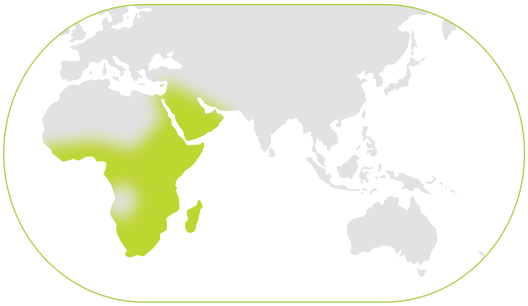
Whether workers vary in size depends on the individual species. Some species are all a similar size (monomorphic), while others have a distinct division into two size groups (dimorphic). Sometimes the size variation follows a gradual increase or is seen in more than two groupings (polymorphic). It is common to see multiple sizes in the major workers, which exhibit differences in head size, number of ocelli, and eye size. Some species like the Malagasy *C. jajoby* and *C. nosindambo* have up to four distinct-sized major workers.

| | |
|---|---|
| **SUBFAMILY:** | Myrmicinae |
| **DIVERSITY:** | 223 species |
| **DISTRIBUTION:** | Global distribution, concentrated primarily in the tropics and subtropics |
| **HABITAT:** | Multiple habitat types, often within forests |
| **NEST:** | Ground-nesting in rotten logs, leaf litter, under stones |
| **DIET:** | Specialized predators, including on mites, springtails, and arthropod eggs |

**FROM ONE EXTREME TO THE OTHER**

Minor *Carebara* workers are dwarfed by a single individual major worker who is many times their size.

# MELISSOTARSUS



| | |
|---|---|
| **SUBFAMILY:** | Myrmicinae |
| **DIVERSITY:** | 4 living species, 1 fossil species |
| **DISTRIBUTION:** | Mainland sub-Saharan Africa, Madagascar, and Saudi Arabia |
| **HABITAT:** | Forests, and infest orchards. Inhabit around 20 tree species. |
| **NEST:** | Arboreal. Tunnel nests under bark in live wood. |
| **DIET:** | Probably omnivore |

The tiny and rotund *Melissotarsus* ants live a secretive life contained entirely within their arboreal nest galleries under tree bark, where up to 1.5 million ants occupy a single tree. From head to tarsus they are perfectly adapted to a life of tunneling. They have zinc-reinforced chewing mandibles powered by well-muscled heads, meaning they can chew through live wood. Excavation tunnels are repaired and reinforced using silk secreted from the heads of workers—the only example of silk production known in adult ants. The front pair of legs is used to maneuver the silk into position. Oddly, the middle pair of legs faces upward, in the opposite direction of the front and back pairs, allowing ants to brace against tunnel walls. In fact, ants removed from their nests will often stagger and topple over.

## BUG FARMING

The diet of *Melissotarsus* is a mystery. They never forage outside their nest and live intimately with armored scale insects (Diaspididae) of 13 different species. Diaspids are a legless bug that inject enzymes into plants and then feed on the predigested plant material. *Melissotarsus* may feed directly on live diaspids, farming them like cattle, but it seems more likely they eat wax secretions produced by diaspids as well as dead or dying diaspids and the discarded skin of diaspid larvae. Workers may also be able to digest plant cytoplasm during their excavation of live-wood tunnels.

### GEOGRAPHICAL DISTRIBUTION

This species, *Melissotarsus weissi*, is found in mainland Africa along with *M. beccarii* and *M. emeryi*. The fourth species in the genus, *Melissotarsus insularis*, lives on Madagascar and nearby islands.

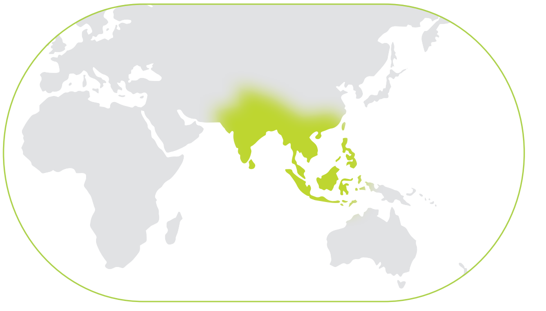
# *HARPEGNATHOS*

Jumping Ants

Jumping Ants are ferocious hunters of fast-moving or jumping prey including crickets, cockroaches, cicadas, flies, and spiders. They are large, up to $^{25}/_{32}$ in (2 cm) long, and possess huge forward-facing eyes, long legs, and scythe-shaped jaws with more than 50 sharp teeth. They are solitary crepuscular hunters that rely on visual hunting strategies and their excellent vision, thanks to having the largest number of ommatidia of any ant species. Their forceps-like mandibles have fast muscle fibers that ensure rapid closure on captured prey, which can then be subdued with a powerful sting that causes permanent paralysis.

## JUMP AROUND

As their common name suggests, *Harpegnathos* are best known for their jumping abilities. While Trap-Jaw Ants use their large mandibles to generate an explosive force for jumping, in *Harpegnathos* the jump is powered by their long legs. Jumping can form part of normal locomotion, but when under threat ants will perform an escape jump of up to 8 in (21 cm), sometimes repeatedly, until they reach safety. Shorter jumps are used in hunting fast-moving prey and sometimes to capture flying insects in mid-air. A fourth jumping behavior is "group jumping": an ant will jump around in a seemingly random fashion for no reason, and after a few minutes other worker ants will join in. Nobody knows why they perform this collective behavior, but it could be to flush out prey or prevent parasitoid attacks.



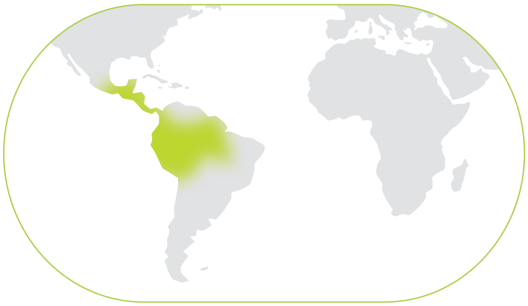
| | |
|---|---|
| **SUBFAMILY:** | Ponerinae |
| **DIVERSITY:** | 9 species, 4 subspecies |
| **DISTRIBUTION:** | India to Sri Lanka and Southeast Asia |
| **HABITAT:** | Forests and plantations |
| **NEST:** | Hypogaeic. Complex nest architecture in some species. |
| **DIET:** | Solitary predator. Hunts in leaf litter for fast-moving arthropod prey. |

**INSIDE THE NEST**

*Harpegnathos saltator* keep their flood-prone nest chambers dry by pasting the inner walls with debris including old cocoon, insect, and plant parts.

# *TATUIDRIS*

Armadillo Ants



| | |
|---|---|
| **SUBFAMILY:** | Agroecomyrmecinae |
| **DIVERSITY:** | Monotypic (one species) |
| **DISTRIBUTION:** | Neotropics |
| **HABITAT:** | Forest |
| **NEST:** | Ground-nesting |
| **DIET:** | Unknown, presumed to be predatory |

The rounded appearance of *Tatuidris tatusia* explains why its name means Armadillo Ant. It is not just the single representative of a species within its genus *Tatuidris*, but also one of only two species in its entire subfamily, the Agroecomyrmecinae. It is found in a range of forest types. Based on the small number of individuals collected at any one time, it is considered rare, yet it is locally abundant in mid-elevation premontane forest.

## DISCOVERING DIETS

Usually collected by leaf litter sifting and vegetation sweeping, no living *Tatuidris* ants were found until 2011. Seven individuals were discovered in a soil core taken in Ecuador and kept for 19 days to study their feeding behavior. In captivity, the Armadillo Ants would not accept any food, including live and dead prey, honey, or sugar water. This could be due to the stress of being in captivity or because they only feed after actively hunting their prey.

Given the lack of feeding behavior observed, scientists turned to other forms of evidence to understand their diet. Stable isotope analysis revealed that *Tatuidris* are predators at the top of the arthropod food chain. On the underside of their mandibles, *Tatuidris* have many long, stiff hairs—a mandibular brush. They also have stiff hairs on their front legs, in addition to a large sting and a rounded, smooth body. From this evidence, scientists believe Armadillo Ants are specialist predators of large, slippery arthropods.

**PATTERNS OF PILOSITY**

While *Tatuidris tatusia* is only a single species, it has four different morphs that all have distinct patterns of pilosity. Being relatively rare, most available images are of nonliving specimens.

# INDEX

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