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► To cite this version:

Alain Dejean, Xim Cerdá, Jérôme Orivel, Frédéric Azémar, Alexander L Wild, et al.. The predatory behavior of ants: an impressive panoply of morphological adaptations. *Insect Science*, 2025, <10.1111/1744-7917.70088>. <hal-05468495>

HAL Id: hal-05468495

<https://hal.science/hal-05468495v1>

Submitted on 20 Jan 2026

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REVIEW ARTICLE

The predatory behavior of ants: an impressive panoply of morphological adaptations

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Abstract Ants are typically omnivorous insects with ovoid heads equipped with short mandibles, but there is great diversity in both the adaptations of their morphological and behavioral traits, as well as their dietary habits. Here, we review the variety of form and function in ant predation. Predation and scavenging were likely the plesiomorphic modes, with Cretaceous ants evolving mandibles well-suited to prey capture. In contemporary ground-dwelling species, mandible morphology can vary with adaptations to capturing particular prey as they may possess trap-jaw, snapping, or falciform mandibles characterized by their high closure speed. To capture termites or other ants, specialized ants may eliminate guards to prey on workers and brood or use allomones that cause the workers of raided nests to flee, providing access to the brood. Among arboreal ants, many species rely on vision to detect flying insects that land on their host trees. In tropical rainforests, territorially dominant arboreal ants (TDAAs) often hunt in groups, spreadeagling their prey, while venom use is noted in only a few species. Some obligate plant-ant species have developed ambush strategies for prey capture, building traps or hiding in shelters. Consequently, ants, due to their large number, their species diversity, and their capacity to live from the ground to tree crowns, regulate all kinds of arthropods through their predation. Ground-dwelling ants impact arthropods in the leaf-litter or provide biotic protection on small plants, but rarely on trees, while the TDAAs that occupy tree crowns protect their host trees from defoliating insects.

Key words arboreal and terrestrial ants; behavioral adaptations; generalist predators; mandible shape; olfaction and vision; traps

Introduction

Among aculeate hymenopterans, ants (Formicidae) are eusocial insects forming colonies whose sizes range from 5 to 10 workers in *Thaumatomyrmex* to \approx 300 million in *Linepithema humile* supercolonies (Giraud *et al.*,

2002; D'Esquivel *et al.*, 2017). Ubiquitous, they are present from the equator to subpolar regions, occurring in deserts, grasslands, and forests; they are involved in a number of key ecological processes and, frequently, they are ecologically dominant. Diverse, they belong to 16 subfamilies, 344 genera, and 14 456 species representing \approx 12 million tons of dry biomass on Earth, so more than both wild birds and mammals combined (Borowiec *et al.*, 2021; Camacho *et al.*, 2022; Schultheiss *et al.*, 2022; Antwiki, 2025).

Ants appeared during the beginning of the Cretaceous (145 to 66 million years ago [Mya]) and were initially

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predators before diversifying alongside the rise of the angiosperms, which generated the proliferation and diversification of herbivorous insects and decomposers so that potential ant prey became abundant and diverse (Chouvenc *et al.*, 2021; Benton *et al.*, 2022). Recent phylogenomic analyses show that the Leptanillinae and the Martialinae (the latter represented by 1 Neotropical species) are ancestral to other ants that are characterized by 2 clades: the Poneroids with 6 subfamilies (i.e. the Ponerinae, Amblyoponinae, Apomyrminae, Paraponerinae, Proceratiinae, and Agroecomyrmecinae) and the Formicoids with 8 subfamilies (i.e. the Dorylinae, Formicinae, Myrmicinae, Ectatomminae, Dolichoderinae, Aneuretinae, Pseudomyrmecinae, and Myrmeciinae) (Romiguier *et al.*, 2022; Borowiec *et al.*, 2025).

Angiosperms also permitted ants to evolve mutualisms with plants to feed on extrafloral nectar, food bodies, or seed elaiosomes, or to become granivorous (Moreau *et al.*, 2006; Nelsen *et al.*, 2018; Romiguier *et al.*, 2022; Jouault *et al.*, 2024). However, ant abundance in many ecosystems is only possible thanks to their relationships with sap-sucking hemipterans that provide them with honeydew (Davidson *et al.*, 2003). In natural conditions, these hemipterans are regulated by the ants that prey on them (Styrsky & Eubanks, 2007; Pringle, 2021; Nelson & Mooney, 2022). This relationship permitted canopy-dwelling ants, particularly the territorially dominant species of the Myrmicinae, Formicinae, and Dolichoderinae, to comprise one of the largest components of the animal biomass in this habitat as these ants are omnivorous (Davidson *et al.*, 2003; Basset *et al.*, 2015; Leponce *et al.*, 2021). Consequently, many ant species are used as biological control agents because of their predatory activity (Dejean *et al.*, 2007a; Diamé *et al.*, 2018; Anjos *et al.*, 2022; Jensen *et al.*, 2023; Sankovitz *et al.*, 2024), whereas certain species serve as ecological indicators (Lawes *et al.*, 2017; Zina *et al.*, 2021).

Generally, predator–prey interactions are body-size dependent. Small prey are less valuable due to their low energy content, whereas the capture of large prey requires an excessive energy expense. A predator will try to select prey with the highest energy ratio between benefits (i.e. prey size or a large group of prey) and costs (i.e. pursuit, capture, handling, and transport) to maximize the rate of energy gain at the lowest cost based on its hunting mode. In this context, pursuit predators need to be faster or more aggressive than their prey, or form well-organized groups, whereas ambush predators can sit-and-wait, hiding in holes or mimicking the substrate; they can also stalk stealthily to approach prey undetected before triggering their attack (Moore & Biewener, 2015; Schmitz,

2017). They also need to avoid being injured by their prey (Frank *et al.*, 2024). Consequently, to capture large prey, predatory arthropods have evolved hypertrophied prehensile organs (i.e. raptorial forelegs; mandibles; extensible labium) and venoms (i.e. to paralyze or kill prey) in addition to the construction of traps and the use of group hunting in predation (Curio, 1976; Krebs & Davies, 1981; Nentwig, 1985; Bauer & Pfeiffer, 1991; Nakazawa *et al.*, 2013; Aili *et al.*, 2014; Touchard *et al.*, 2016a).

Ants seem to be particularly well adapted to predation, as $\approx 70\%$ of the species have a stinger to inject a cocktail of venom peptides to paralyze their prey (Aili *et al.*, 2014). These peptides are often cytotoxic with insecticidal, hemolytic, and/or antimicrobial properties, although several neurotoxic peptides have also been identified. The remaining $\approx 30\%$ include Formicinae that spray a defensive venom composed mostly of formic acid, while the Dolichoderinae spray ketones and iridoids secreted by their pygidial glands (Touchard *et al.*, 2016b; Barassé *et al.*, 2023; Koch *et al.*, 2025). Due to their eusociality, ants can recruit nestmates to kill and retrieve large prey or hunt in groups (army-ant-like behavior) (Sudd & Franks, 1987; O'Donnell *et al.*, 2005; Peeters & de Greef, 2015). Furthermore, certain species have hypertrophied trap-jaw mandibles able to strike prey by releasing stored energy to close astonishingly swiftly (a movement lasting only 0.13 ms in *Odontomachus*), or an even quicker snapping motion to strike large prey or termites in *Myrmium* (Patek *et al.*, 2006; Larabee *et al.*, 2017; Larabee *et al.*, 2018). All these features were likely present early in the evolution of ants, as reflected in the specialized mandibles preserved in amber from the Cretaceous period (Barden & Grimaldi, 2012; Barden *et al.*, 2020) and the army-ant-like group hunting behavior noted in the Leptanillinae (Romiguier *et al.*, 2022). Hence, ants that are specialized in predation have evolved morpho-physiological adaptations permitting them to reduce the time and energy needed to capture their prey, particularly oligophagous species as they evolved ways to counter their prey's defenses or means of escape. These prey are frequently involved in the degradation of wood and the leaf litter, and include earthworms, isopods, myriapods, collembolans and, among social insects, termites and other ants. As we already noted, sap-sucking hemipterans are regulated by ant predation, whereas the Diaspididae that exceptionally do not produce honeydew, are preyed upon by myrmicine ants of the genus *Melissotarsus* (Delabie, 2001; Styrsky & Eubanks, 2007).

In this review, which corresponds to an updated version on ant predation and follows a paper dealing with foraging behavior (Cerdá & Dejean, 2011; Dejean *et al.*, 2025),

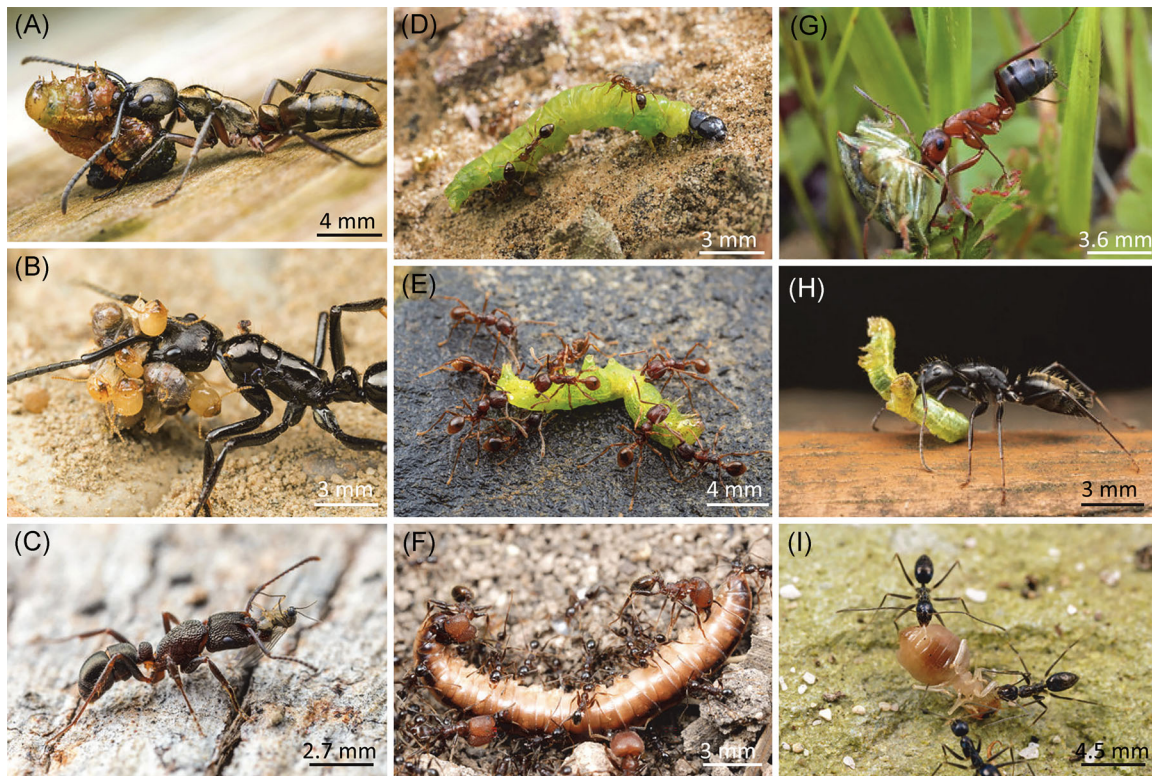


Fig. 1 Predation by ants with a typical head shape. (A) *Neoponera villosa* worker (Ponerinae) retrieving a caterpillar. (B) *Neoponera commutata* worker (Ponerinae) gathered several termite prey before retrieving them. (C) *Rhytidoponera tasmaniensis* worker (Ecitoninae) transporting a freshly captured fungus gnat (Diptera). (D) Beginning of the attack of a caterpillar by *Solenopsis invicta* workers (Myrmicinae). (E) Capture of a caterpillar by numerous *Pheidole fimbriata* workers (Myrmicinae). (F) Diplopod mastered by numerous *Pheidole obscurithorax*; here we can see recruited soldiers as the prey is difficult for the smaller workers to process. (G) *Formica moki* worker (Formicinae) retrieving a heteropteran. (H) *Camponotus pennsylvanicus* worker (Formicinae) transporting a caterpillar. (I) Three *Paratrechina longicornis* workers (Formicinae) capturing a termite (photos A. Wild).

we have gathered information on the different modes of prey capture by ants.

Generalist predator species with typical head shape

Typically, ants have spherical, quadrate, or ovoid heads equipped with mandibles considerably shorter than the head length and bearing small numbers of teeth, regardless of their predatory habits (Wilson & Hölldobler, 2005).

Ground-dwelling ants capture a large number of prey because of their abundance. For example, wood ants of the genus *Formica* have a daily intake of up to 100 000 caterpillars (Stradling, 1978; Fig. 1). In one instance, the presence of *Formica* reduced the leaf scab *Venturia inaequalis* by 34% on apple trees (Jensen *et al.*, 2023). Ants (e.g. genera *Labidus*, *Paratrechina*, *Crematogaster*,

Pheidole, *Solenopsis*, *Iridomyrmex*, and *Tapinoma*) also prey on lepidopteran eggs and emerging larvae (Mansfield *et al.*, 2003; Ramos *et al.*, 2012; Schifani *et al.*, 2023).

Indeed, across both ground-dwelling and arboreal ant species, 7 genera were recorded as beneficial because of their predation on pests: *Formica* in temperate regions, *Solenopsis* in the subtropics, and *Anoplolepis*, *Oecophylla*, *Dolichoderus*, *Azteca*, and *Wasmannia* in the tropics and equatorial regions (Way & Khoo, 1992). These generalist ants are efficacious because of their abundance, and can respond quickly to changes in prey densities: when prey abound, they can store them for a short time; when prey become scarce, they target their attended hemipterans (Fig. 1). They are also able to deter agile or very large arthropods (Rico-Gray & Oliveira, 2007; Thurman *et al.*, 2019; Anjos *et al.*, 2022; Despland & Lessard, 2022). The myrmicine *Pogonomyrmex rugosus*, although granivorous, add beneficial proteins to their

diet by exhibiting a “pulse” of predation in response to a strong increase in populations of grass cicadas (Whitford & Jackson, 2007).

Although ground-dwelling, the formicine *Gigantiops destructor* hunt solitarily during the daytime mostly on trees where, thanks to large eyes (4000 ommatidies per eye), they easily detect prey (Macquart *et al.*, 2008). Able to make detours to place themselves behind the prey, they can jump up to 30 cm, their good vision permitting them to promptly seize the prey between their mandibles; then, they generally bend their gaster to project venom that rapidly numbs the prey. They can capture several prey successively that they hold between their rather short mandibles and retrieve them all at once. When a flying insect approaches a hunting worker, she is able to jump vertically to catch it (Beugnon *et al.*, 2001).

Mandibles and head of ant species specialized in predation

Among species specialized in predation, the head shape evolved to contain large adductor muscles permitting the quick closing of their elongated mandibles (Table S1; Avila-Núñez *et al.*, 2011; Gibson *et al.*, 2018; Lattke *et al.*, 2018; see also Klunk *et al.*, 2023, for the mechanical performance of ant mandibles).

Fossil ants

Today, Hydroporinae larvae (Dytiscidae) have characteristically grooved mandibles to suck up the liquefied contents of their prey. Yet, their mandibles do not move horizontally, close to one another as do those of most insects, but vertically, permitting them to squeeze their prey against a protruding part of their head, a modified clypeus with a frontal horn called the nasale (Friis *et al.*, 2006; Hayashi & Ohba, 2018).

This is to say that among the stem ants (late Albian to Campanian ages of the Cretaceous, ≈ 100 –79 Mya), predatory “hell ants” (Haidomyrmecinae) evolved mandibles that likely moved vertically in conjunction with the horn on their modified clypeus. Phylogenetic analyses suggest the early radiation of these characteristics in 2 monophyletic stem groups that were probably extinct before the Cretaceous–Paleogene extinction event (66 Mya). Hell ants likely captured prey by positioning their mandibles forward, the movement of which was controlled by specialized setae functioning as trigger hairs (see below). The capture of a nymph of an extinct dictyopteran (e.g. resembling a termite) by *Ceratomyrmex ellenbergeri* was preserved in Burmese amber

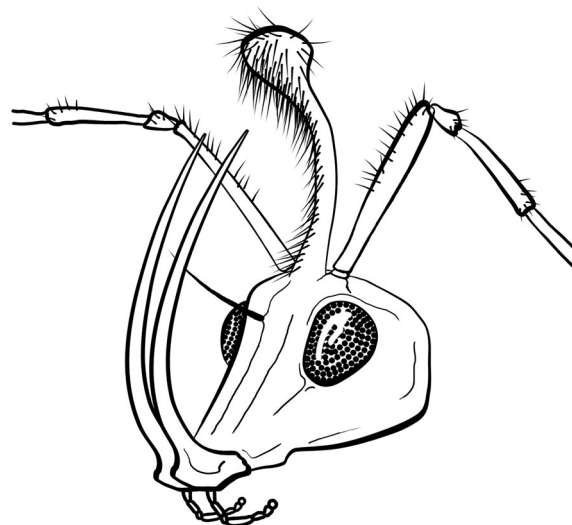


Fig. 2 Schema representing the head of a *Ceratomyrmex* (Haidomyrmecinae) with its characteristic mandibles and the trigger hairs permitting control of the closure of these mandibles against the cephalic horn corresponding to a modification of the clypeus (illustration by F. Azémar).

(Fig. 2). Hence, the Haidomyrmecinae had a mandible characteristic that has been definitively lost in living ants (Perrichot *et al.*, 2016; Barden *et al.*, 2020).

Trap-jaw mandibles

Trap-jaw-mandibled species have convergently evolved in 3 ant subfamilies: the Ponerinae (tribe Odontomachini), Formicinae (tribe Myrmoteratini), and Myrmicinae (some Attini belonging to the former tribes Basicerotini and Dacetini) (Larabee & Suarez, 2014; Larabee *et al.*, 2017; Gibson *et al.*, 2018; Booher *et al.*, 2021; Fig. 3). Such a mechanism is also suspected in *Protanilla lini* (belongs to the Leptanillinae), whose mandibles open to an angle of 180° and can close quickly, resembling those of the Attini of the genus *Strumigenys* (see below) (Hsu *et al.*, 2017; Richter *et al.*, 2021).

In long-mandibled species, such as *Odontomachus* spp., trap-jaws are a power-amplified structure in which hyper-developed adductor (closing) muscles, which take up most of the head capsule volume, are contracted while their “condyles” situated at the bases of the mandibles serve as a latch, locking the mandibles in an open position at $\approx 180^\circ$ (Fig. 3B). The bases of the mandibles are equipped with trigger hairs connected to large-diameter nerves (i.e. representing a high conduction velocity) with the abductor (opening) muscles permitting them

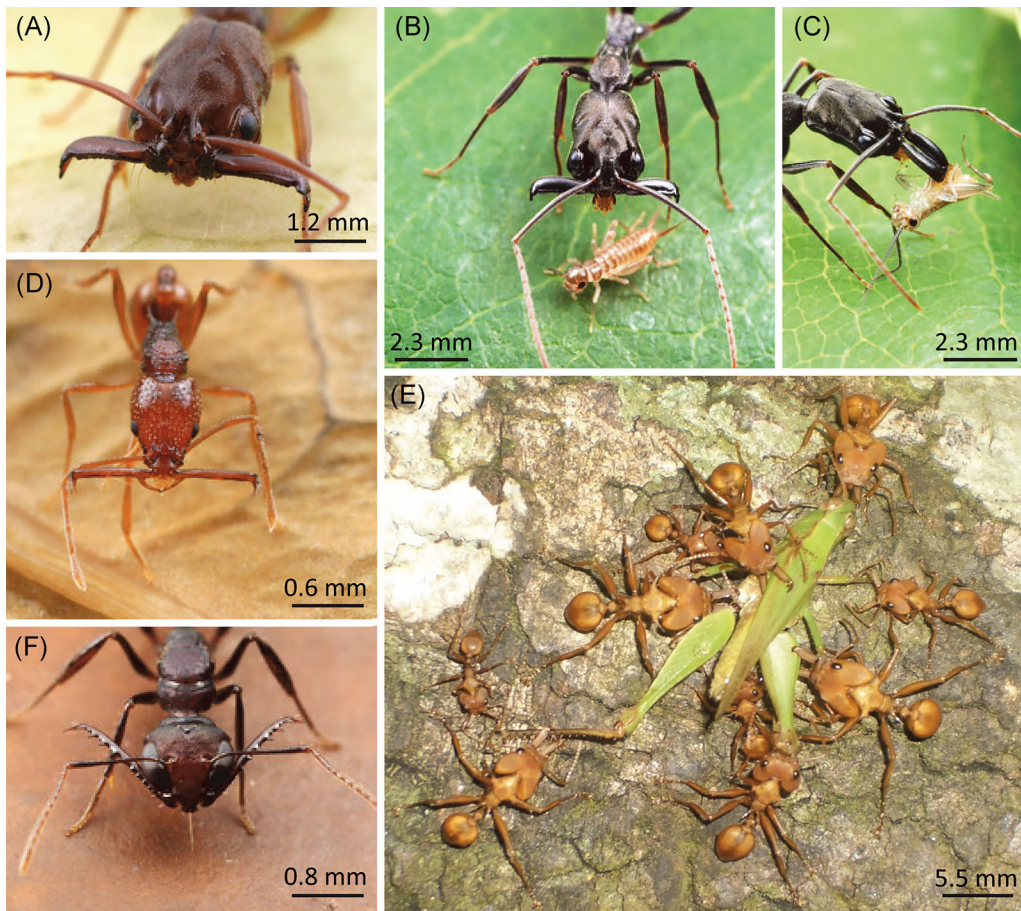


Fig. 3 Predation by ants equipped with trap-jaw mandibles. (A) *Odontomachus meinerti* worker (Ponerinae) with its mandibles opened to 180°. (B, C) Capture of a cricket by *Odontomachus bauri*. (D) *Acanthognathus ocellatus* worker (Myrmicinae) foraging with its mandibles opened to 180°. We can see the “accessory mandibular processes” situated at the bases of the mandibles; they form the latch permitting the mandibles to strike (photos A. Wild). (E) Ambushing *Daceton armigerum* worker (Myrmicinae) has successfully positioned itself to strike the head of a landing locust, its nestmates hunting in close vicinity begin to attack this numbed prey (photo A. Dejean). (F) Mandibles of the *Myrmoterus iriodum* worker (Formicinae) opened to $\approx 208^\circ$; we can see the trigger hairs (photo A. Wild).

to unlock the latch, and, so, cause the instant closing of the mandibles whose bases correspond to a simple joint. Note that both small opening muscles and fast hypertrophied closing muscles also permit the slow opening and closing of the mandibles (Gronenberg *et al.*, 1993; Gronenberg, 1995a; Gronenberg, 1995b; Just & Gronenberg, 1999; Larabee & Suarez, 2014; Hao *et al.*, 2018; Aonuma *et al.*, 2023).

The trap-jaw mechanism corresponds to a “latch-mediated spring actuation” known for devices that use stored elastic energy mediated by a latch. However, in this mechanism, 2 springs are at work. (1) The exoskeleton of the head capsule can become deformed under the contraction of the adductor muscles of the mandibles. It

can recoil quickly when the latch becomes unlocked due to the contraction of the opening muscles controlled by trigger hairs. (2) When the latch is unlocked, the long apodemes of the closing muscles also recoil (apodemes are highly sclerotized tissues that act like vertebrate tendons). The whole constitutes a “dual spring force couple” as 2 springs work in coordination to create torque while greatly reducing the stress on the joints. Consequently, an estimate of the muscle mass-specific power during a mandible strike corresponds to 396 000 W/kg to be compared with the 100–400 W/kg in normal muscle contraction (Sutton *et al.*, 2022).

In the monophyletic tribe Odontomachini of the Ponerinae, the genera *Odontomachus* and *Anochetus* comprise

3 and 4 clades, respectively, that evolved during the mid-Eocene in Southeast Asia and the Neotropics and expanded later throughout all tropical and subtropical regions (Larabee *et al.*, 2016). In the genus *Odontomachus*, different jaw forces were registered based on worker size. As a defensive behavior, their trap-jaw mandibles can also permit them to jump when they strike a substrate (De la Mora *et al.*, 2008; Spagna *et al.*, 2008; Spagna *et al.*, 2009; Larabee & Suarez, 2015). In the genus *Anochetus*, some species have mandible strikes comparable to *Odontomachus*, but the strikes are slower in *Anochetus horridus* and *Anochetus emarginatus* (Gronenberg & Ehmer, 1996; Gibson *et al.*, 2018).

When foraging, *Odontomachus* and *Anochetus* workers open their mandibles as they leave their nests, permitting them to react quickly in the event they encounter prey (Fig. 3B). Although generalist predators, they capture mostly termites and many species exploit extrafloral nectar or attend honeydew-producing Hemipterans (Fowler, 1980; Dejean & Bashingwa, 1985; Dejean, 1988a; Ehmer & Hölldobler, 1995; Schatz *et al.*, 1999; De La Mora *et al.*, 2008).

Among the Myrmicinae, the Attini *Daceton armigerum* (Fig. 3A), and long-mandibled *Strumigenys*, the base of the trigger hairs is located on the labrum, which here corresponds to the latch (Gronenberg, 1996). In the genus *Strumigenys*, some species have typical short, gripping mandibles, while others have trap-jaw mandibles that can either be short or long (i.e. mandible opening to 60–90° versus 180°); still other species evolved short mandibles from long-mandibled ones (Booher *et al.*, 2021). In the very long-mandibled *Acanthognathus*, the trigger hairs are located on the middle part of the mandibles. Two protuberances, the “accessory mandibular processes”, situated at the bases of the mandibles form the latch (i.e. in place of the labrum; Fig. 3C). The tip of the right one has 3 asperities forming a hole into which the rounded extremity of the left one can be inserted when the mandibles are opened to $\approx 180^\circ$. Hence, the interlocked mandibles are maintained in this position when the closing muscles contract. The strike results from the stimulation of the trigger hairs permitting the lateral arms of the closing muscle apodemes to provoke a slight rotation of the mandibles that then unlocks the latch (i.e. the “accessory mandibular processes”) that slide on each other during mandible closure (Gronenberg *et al.*, 1998a).

In the tribe Myrmoteratini of the Formicinae, 2 subgenera have been distinguished: *Myrmoteras* (e.g. *Myrmoteras barbouri*) and *Myagroteras* (e.g. *Myrmoteras toro*, which lack trigger hairs so that prey capture is only

generated visually). In both cases, the mandibles can open up to 208° (Moffett, 1985; Moffett, 1986a; Fig. 3D). The latch results from the antagonistic contraction of the opening muscles and the “slow closing” muscles. In *My. barbouri*, the contraction of the powerful “quick closing muscles”, which are stimulated by the trigger hairs, provokes the relaxation of the opening muscles. This triggers the strike which likely results from (1) the spring effect of the recoil of the head capsule, which recovers its shape after being deformed by the quick closing muscles, and (2) the recoil of the apodemes of both types of closing muscles (Larabee *et al.*, 2017).

Note that, except for the visually hunting *Myagroteras* that lacks trigger hairs, all other trap-jawed ants forage mostly inside the leaf litter or in rotten logs to capture small-bodied arthropods or termites (Masuko, 1984; Moffett, 1985; Moffett, 1986a; Masuko, 2009a; Masuko, 2009b; Larabee & Suarez, 2014).

Mandibles that snap

Rather than having devices permitting the mandibles to close quickly, as for trap-jaw mandibles, some species such as *Mystrium* (Amblyoponinae) and *Plectroctena* (Ponerinae) similarly evolved a power-amplified mechanism called “snapping” used to capture large prey and termites, particularly soldiers, or used against competitors (Fig. 4) (Moffett, 1986b; Dejean *et al.*, 2002). Several termite genera also use snapping for defense (Kuan *et al.*, 2020).

Detailed information is provided for *Mystrium* for which the bases of the mandibles are set widely apart because of a broad head capsule in the area where they are anchored. This permits their slender, long mandibles with rounded tips to be placed face to face when closed (Fig. 4A). They then are submitted to a strong pressure due to the contraction of 3 closing muscles (i.e. 2 with slow and 1 with quick fibers). When under tension, the 2 tips can slide on each other due to the slight rotation of 1 mandible around its axis, permitting a sudden crossing of the mandibles to an angle of 40°: this is the snap (Gronenberg *et al.*, 1998b). As the tips of the mandibles are opposite one another and the closing muscles are loaded, the long mandibles flex. During the snap, they recoil like a spring, permitting their quick crossing with strong linear velocities (i.e. ≈ 90 m/s) and accelerations, as 1 mandible, known as the “strike mandible” slides across the other (Larabee *et al.*, 2018; Divi *et al.*, 2020; see the video: <https://www.youtube.com/watch?v=v9dsINb64Q0>).

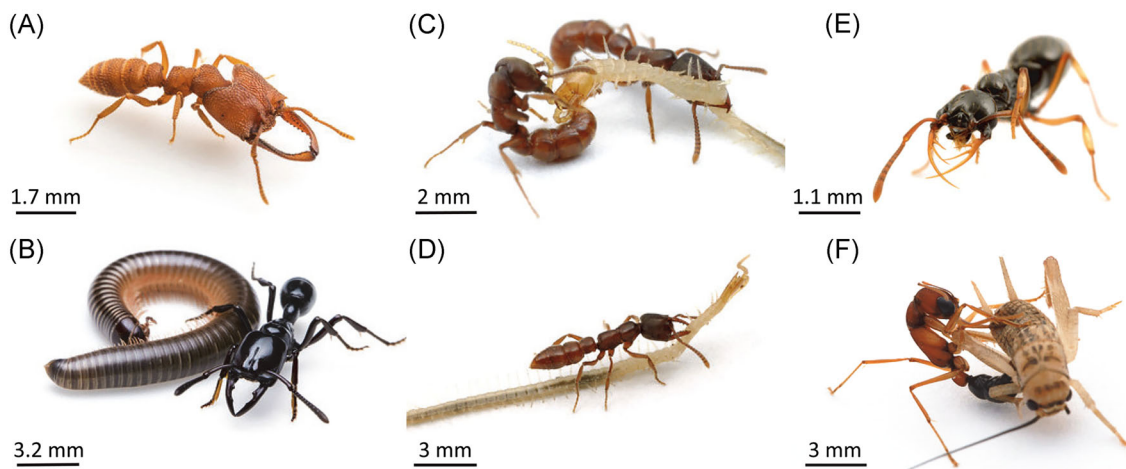


Fig. 4 Mandibles that snap (A) *Myrmiromyrmex camillae* (Amblyoponae). (B) *Plectroctena cristata* worker (Ponerinae) and a diplopod, its main prey. (C, D) Mandibles adapted to long-bodied prey, a *Stigmatomma oregonensis* worker (Amblyoponae) capturing, then retrieving a geophilomorph centipede. (E) Pitchfork-shaped mandibles in *Thaumatomyrmex* sp. (Ponerinae). (F) *Harpegnathos saltator* (Ponerinae) have long mandibles and good vision; here a worker has seized a cricket and stung it on the ventral face (photos A. Wild).

Mandibles adapted to capturing long-shaped prey

Nutcracker mandibles correspond *de facto* to ponerines of the genus *Plectroctena* specialized in the capture of millipedes (Fig. 4B; their mandibles can also snap, see above). They seize these long-bodied arthropods by their anterior part with their very powerful mandibles, close them tightly so that they slip on the exoskeletal coils, separating 2 segments, and exposing the soft intersegmentary membrane. This allows the ant to sting the ventral part of this membrane, which is near the ventral nerve chain and so paralyze the distal parts of the millipedes. Then, the prey is easily retrieved (Schatz *et al.*, 2001). When found in galleries, large-bodied millipedes (e.g. 95–105 mm long; \approx 8 mm in diameter; the diameter of the galleries being 15 mm or more) can be captured during head-on encounters. The workers grip an antenna or a mandible, flex their gaster under their thorax and head to extend their stingers toward the millipede heads so that the venom acts on the intersegmentary membranes situated around the mouth, paralyzing these prey quickly. The worker tries to pull the prey to retrieve it, but generally fails and recruits nestmates. For workers that successfully retrieve these millipedes alone, their prey/predator body weight ratio of 94 to 117 is very high (Dejean *et al.*, 2001).

The predation of long millipedes was recorded in a few ant genera with species having long mandibles, including the Ectatomminae *Gnamptogenys* (Brown Jr, 1992; Wang *et al.*, 2021) and, among the Ponerinae, *Leptogenys* (Ito & Ohkawara, 2000; Peeters & De Greef, 2015; Mizuno

et al., 2022), *Myopias* (Ito *et al.*, 2020), and *Plectroctena* (Dejean *et al.*, 2002).

By extension, this predatory technique may also be the case for several stenophagous Amblyoponinae of the genera *Amblyopone*, *Myopopone*, *Myrmiromyrmex*, *Prionopelta*, and *Stigmatomma*, which have long mandibles emerging from the extreme corners of the frontal part of the head capsule (Fig. 4C, D). This permits them to easily seize long-bodied prey with a relatively large diameter (e.g. centipede geophilomorphs, their principal prey) (Brown Jr, 1960; Gotwald Jr & Léviéux, 1972; Traniello, 1982; Moffett, 1986b; Yoshimura & Fisher, 2014; Ladino & Feitosa, 2020). The detailed capture of centipedes was described for *Stigmatomma silvestrii* workers equipped with 2 trigger hairs that emerge from the clypeus, enabling them to adjust mandible closure as for trap-jaw-mandibled species. These workers detect centipedes from a distance, approach cautiously to place themselves over the prey body, seize it, and bend their gaster to sting the ventral face where the neural chain passes. The behavior can be repeated if the prey is large (Masuko, 1993; Wild, 2005).

In humid areas, long-bodied lumbricid earthworms are among the most frequent ground-dwelling invertebrates. When attacked by a predator, they lose their distal part through autotomy. The African ponerine *Psalidomyrmex procerus*, equipped with long mandibles, is specialized in their capture. When confronted with a relatively small earthworm, a worker concomitantly seizes its anterior part and stings; the paralyzing effect is so rapid that the distal part is not detached through autotomy, enabling

the ant to retrieve the entire prey. Large earthworms are seized by the part that workers first encounter. If this is the anterior part, the process is similar to that for small earthworms; if not, due to autotomy, the workers retrieve only the part they seized (Dejean *et al.*, 1999b).

Thaumatomyrmex: pitchfork-shaped mandibles

Colonies of the Neotropical ponerine genus *Thaumatomyrmex* contain only a few workers equipped with slightly asymmetric, pitchfork-shaped mandibles each with 3 long tines joined at their bases (Fig. 4E). They prey specifically on Polyxenidae (Diplopoda), which are known to project detachable barbed trichomes as an anti-predator strategy (Eisner *et al.*, 1996). Encountered polyxenids are antennated, seized and then stung on an intersegmentary membrane, resulting in their rapid immobilization. The worker then seizes the prey at the base of the head to place it over its own head, thus avoiding contact with the barbed trichomes. Upon reaching the nest, the worker grasps the polyxenids with its mandibles to strip the barbed trichomes using the short, stout setae situated on the tarsi of its forelegs. The workers can also feed on the hemolymph of partly stripped polyxenids, even just after their capture in the field, while they thoroughly depilate those given to their larvae, probably to protect them from the irritating trichomes (Brandão *et al.*, 1991; Rabeling *et al.*, 2012).

Workers of the Asian ant proceratiine *Probolomyrmex dammermani* are also specialized in hunting polyxenids and strip them of their barbed trichomes inside their nest, but they do not have pitchfork-shaped mandibles (Ito, 1998).

Harpegnathos: long mandibles, detection by sight and jumping

Among the Ponerinae, the workers of the Asian species *Harpegnathos saltator* and *Harpegnathos venator* forage solitarily and can jump using their median and hindlegs (Fig. 4F). Generalist predators, they detect their prey by sight thanks to large compound eyes (i.e. ≈ 1600 ommatidies per eye) permitting the detection of prey from long distances (up to 10 cm). After seizing their prey with their long mandibles, they use their stinger to paralyze it (Maschwitz *et al.*, 1979; Mustahk Ali *et al.*, 1992; Baroni-Urbani *et al.*, 1994; Crosland, 1995).

Although predation by a solitary forager is the general rule, foragers occasionally hunt collectively. A detailed study on their predatory behavior showed that workers are sensitive to mobile prey that they can capture by jumping at them, seizing them between their large mandibles and

stinging them before retrieving them to the nest. Among prey, they rather select active locusts and cockroaches for which they prefer nymphs over adults (Nie *et al.*, 2022).

Myrmecia: a genus from Australian regions with long mandibles and good vision

Workers of this diverse (≈ 90 species) lineage forage diurnally on trees and the ground, acquiring sugary substances from flowers and the honeydew of hemipterans. *Myrmecia varians*, *Myrmecia comata*, and *Myrmecia desertorum* workers are generalist predators that remain immobile, mandibles open, crouched on trees, as do ambush predators of landing insects such as flies or cicadas (Fig. 5A, B). These workers are able to jump and quickly seize the prey head and sting it; their venom is peptidic (Gray, 1971; Gray, 1974; Robinson *et al.*, 2018). Due to their orientation capabilities, they then let themselves fall from their trees to retrieve the prey directly to their nest. In woodland, *Myrmecia croslandi* workers can acquire sufficient navigational information to permit them to determine their nest direction from anywhere up to 15 m (Narendra *et al.*, 2013a; Jayatilaka *et al.*, 2014; Islam *et al.*, 2023).

Myrmecia dispar is mainly a predator of other ants (Gray, 1971). *Myrmecia gulosa* also preys mostly on other ants, particularly *Camponotus* species, which they hunt close to their nest entrance, stinging or decapitating them after perceiving their presence via their odor (Haskins *et al.*, 1973). The use of vision as a starting point during predation was noted for *Myrmecia gulosa* and *Myrmecia nigriceps* workers, which obtain information on targets using movement parallax (Via, 1977; Erikson, 1985). Among active nocturnal foragers, *Myrmecia pyriformis* workers are generalist predators (Reid *et al.*, 2013) that also have the means of easily finding their nest thanks to navigation as they have good nocturnal vision (Greiner *et al.*, 2007; Narendra *et al.*, 2013b; Freas *et al.*, 2018; Ogawa *et al.*, 2022).

Leptogenys: falciform mandibles

The genus *Leptogenys*, with more than 300 species, is widespread throughout the tropics and subtropics and shows diverse life histories (Hoenle, 2021; Mizuno *et al.*, 2022). Most *Leptogenys* have small colonies whose workers have long, thin, curved mandibles articulated at the extreme corners of the anterior margin of the head and are specialized in hunting oniscoid isopods solitarily (Lattke, 2011; Schmidt, 2013; Fig. 5C). This trait is likely plesiomorphic, as noted in all regions where *Leptogenys*

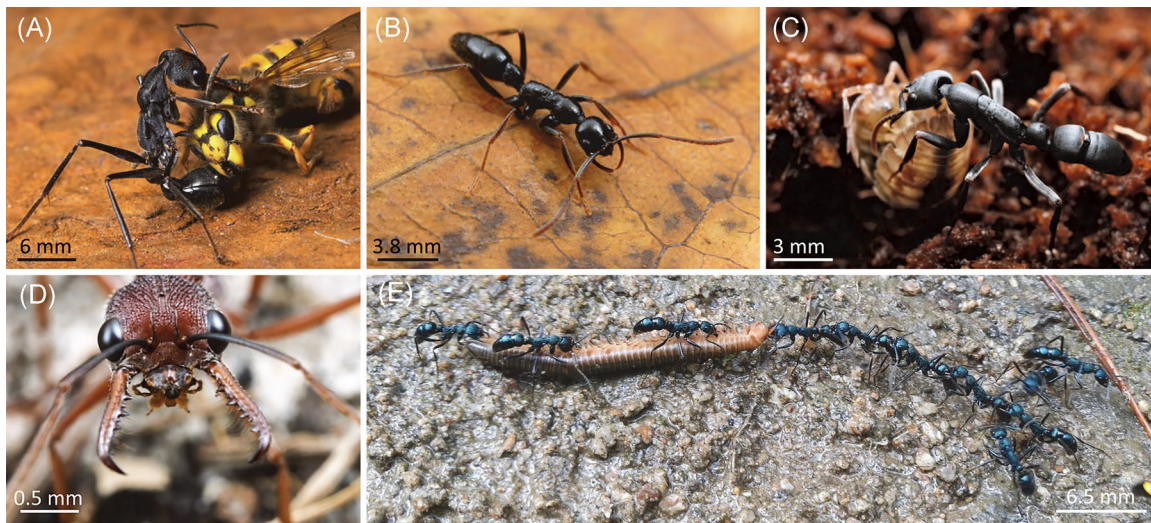


Fig. 5 (A) *Myrmecia pyriformis* (Myrmeciinae) capturing a social wasp. (B) Falciform mandibles of *Leptogenys* sp. (Ponerinae). (C) *Leptogenys falcigera* retrieving an isopod, their main prey (photos A. Wild). (D) *Myrmecia nigricapae* showing the long mandibles and good vision (eyes with numerous ommatidies). (E) *Leptogenys cyanicatena* forming chain to retrieve a diplopod (photo C. Peeters).

has been recorded (Lattke, 2011; Schmidt & Shattuck, 2014).

All oniscoid isopods are protected by a shell and tegumental gland secretions, but have different morphological and behavioral defenses. “Rollers” are well known as they roll into a ball when attacked. *Leptogenys* workers can seize them by their body whether or not they are rolled up. There is a relationship between prey size and the length of ant mandibles; the longer the mandibles, the larger the prey that can be easily captured. In this case, there is no stinging and the prey is retrieved alive. When the isopod is too large, the ant seizes it by the edge of the shell, turns it over and immediately stings it on its ventral face, which is not sclerotized, facilitating the penetration of the stinger; we assume that the venom quickly reaches the ventral neural chain, hastening paralysis (Fig. 5D). This behavior is used systematically in the 2 other cases. “Spiny forms” have long spines that stick out when they roll into a ball as an antipredator defense, but *Leptogenys* workers skirt this defense by seizing the edge of the shell. “Runners” can escape swiftly from antennal contact, but are pursued, seized by the edge of the shell, turned over and immediately stung on the ventral surface. When an isopod escapes, the ant workers, very excited, generally find it again through a fast and sinuous searching path, seizing the edge of the prey shell and stinging; this local searching is called “reserve” behavior (Dejean & Evraerts, 1997).

In the flooded lowland forest (i.e. 20–60 cm of water) on the Yucatan peninsula, Mexico, 4 *Leptogenys* species nest arboreally in the suspended soils where epiphytic

bromeliads and orchids grow. They prey on the numerous isopods sharing this humid environment (Dejean *et al.*, 1995). Among them, entire colonies of *Leptogenys sianka* (identified as *Leptogenys mexicana*) attract Bathytropidae isopods, so that foraging is unnecessary (Dejean & Evraerts, 1997).

Among other *Leptogenys* species with solitary hunters, *Leptogenys binghami* is specialized in the capture of termites (Maschwitz & Mühlenberg, 1975) and *Leptogenys* sp. 13 is an earwig predator (Steghaus-Kovac & Maschwitz, 1993).

Among species with larger colonies, “*Megaponera*-like” foraging was noted when a scout, having successfully discovered a group of prey, lays a recruitment trail while returning to the nest (mass recruitment). For *Leptogenys chinensis*, this trail is then used by a group of nestmates to raid termites (Maschwitz & Schönegege, 1983), whereas *Leptogenys diminuta* preys on millipedes (Ito & Ohkawara, 2000). In mainland Southeast Asia *Leptogenys cyanicatena* is also specialized in the capture of millipedes. When encountering large individuals during their foraging, the workers sting them and, after paralysis, retrieve them by forming chains where each worker seizes a nestmate by the abdomen and walks backward, so that the millipedes are pulled toward their nest (Peeters & De Greef, 2015; Mizuno *et al.*, 2022; Fig. 5E).

Large *Leptogenys* colonies with several thousand individuals were recorded having true group raiding species with an army-ant-like mass foraging behavior including *Leptogenys processionalis distinguenda* in Asia, which raids mostly termites and *Leptogenys intermedia*

(= *Leptogenys nitida*), a generalist predator in South Africa (Maschwitz et al., 1989; Duncan & Crewe, 1994; Witte & Maschwitz, 2000).

An indirect way to obtain prey: Melissotarsus and Rhopalomastix (Myrmicinae) whose mandibles dig galleries in sapwood permitting them to breed hemipterans for their “meat”

We saw above that many ants can prey on the hemipterans they attend, preventing uncontrolled proliferation in natural conditions (Styrsky & Eubanks, 2007; Pringle, 2021; Nelson & Mooney, 2022). However, the closely related genera *Melissotarsus* and *Rhopalomastix* attend in their galleries armored Diaspididae scale insects (Hemiptera; Sternorrhyncha) that do not produce honeydew, so that they are bred for their “meat” and so are used as “domestic cattle.” This association represents a case of “predatory mutualism” as the diaspidids are well protected from enemies and desiccation (Delage-Darchen et al., 1972; Ben-Dov, 1978; Mony et al., 2002; Ben-Dov & Fisher, 2010; Schneider et al., 2013). However, *Melissotarsus emeryi* workers obtain a few liquid substances representing a basic form of trophobiosis by licking gland secretions, the excretions from the Malpighian tubules, and the liquid obtained by squeezing adult female diaspidids (Schneider et al., 2013; Peeters et al., 2017).

All 6 *Melissotarsus* species, 1 from Madagascar and 5 from the Afrotropical regions are small (2.75–3.5 mm in length) (Bolton, 2003). They are all adapted to living in tunnels that they dig in the sapwood (or living wood) of different tree species, and they are able to digest plant polysaccharides (Mony et al., 2013). Their closing and opening muscles occupy a large part of the head capsule whose force is concentrated toward the tips of their short mandibles, which are hardened with zinc (Khalife et al., 2018). Yet, old workers have worn mandibles (Mony et al., 2007). Their aberrant midlegs are pointed upward, so that the workers walk with the fore- and hindlegs on the floor and the midlegs on the ceiling of their calibrated galleries (Delage-Darchen, 1972; Khalife et al., 2018).

In Southeast Asia, *Rhopalomastix* is a sister genus to *Melissotarsus* with which it shares a similar ecological niche as they dig galleries in sapwood where they attend diaspidids; the adult workers also secrete silk, but their midlegs are not highly specialized (Yong et al., 2019; Billen & Peeters, 2020).

Behavioral adaptations permitting capture of specific prey

We saw above that most prey captured by ground-dwelling species equipped with specialized mandibles

participate in the comminution of dead plant material (e.g. leaf litter and wood), feces, and dead animals, a first step in the decomposition of organic material into water, carbon dioxide, and simpler compounds containing nitrogen, phosphorus, and calcium (Culliney, 2013). Here, we will see new cases of prey capture, including species with “typical” mandibles.

Egg predators

Arthropod eggs are generally clumped together and easily preyed upon by many predators, particularly when they are not defended by their parents. This includes generalist-feeding ants whose workers frequently retrieve arthropod eggs among other prey (Kar et al., 2022; Schifani et al., 2023).

Specialized egg predators were first noted in the proceratiine *Proceratium* and *Discothyrea* and the myrmicine *Carebara* (formerly *Erebomyrma*) (Brown Jr, 1957; Brown Jr, 1979; Wilson, 1986). Among the Myrmicinae, *Stegomyrmex vizottoi* prey on millipede eggs (Diniz & Brandão, 1993) and *Calyptomyrmex rectopilosus* prey on cricket eggs (Ito et al., 2023).

Proceratium spp. are generalist egg predators, preying on chilopod, spider, opilone, and hemipteran eggs (Brown Jr, 1979; Masuko, 2019). All *Discothyrea* species are likely spider egg predators (Hölldobler & Wilson, 1990; Dejean et al., 1999a; Katayama, 2013; Masuko, 2020; Fig. 6). In Africa, both the founding queens and workers of *Discothyrea oculata* are able to open the oothecas of various spider species. They can also manipulate the crimped silk that protects the oothecas using their forelegs equipped with parallel claws and a comb-shaped tibial spur opposite a brush-like zone on the first article of the tarsi. These apparatuses permit them to open the oothecas and to line and obstruct cavities where the colonies settle. Founding queens and adult colonies can occupy the spider oothecas, finding there both shelter and food. Spiderlings emerging from eggs are stung and eaten (Dejean et al., 1999a; see also Masuko, 2020, for the Asian *Discothyrea sauteri*).

Myriapod predators

We already saw that the workers of different taxa use their specialized mandibles to capture myriapods.

The workers of the short-mandibled, trap-jawed myrmicine *Strumigenys hexamera* hunt in galleries or crevices where they crouch and remain immobile when encountering a centipede. As the centipede moves forward, it steps on these workers' heads, these then attack from below in an upward strike of their mandibles,



Fig. 6 *Discothyrea mixta* (Proceratiinae), a predator of spider eggs (photo A. Wild).

impaling the centipede on their long apical teeth (Masuko, 1984).

Among species with typical mandibles, the ponerine *Pachycondyla pachyderma* is a semi-specialized centipede predator that can also attack termites. Whatever their size, centipedes are mostly seized by the anterior part of their body and are stung ventrally, large individuals being retrieved thanks to long-range recruitment (Dejean & Lachaud, 2011).

Collembolan predators

Among the hexapoda, collembolans are abundant and small (i.e. most are 3–4 mm in length) so that their predators are small in turn because of body-size dependency. Generalist feeders contributing to the comminution of organic material, they are characterized by their colophore, a tubular-shaped appendage likely serving for fluid uptake and excretion, and as a stabilizer when jumping. Indeed, most species have a furca, a catapult-like appendage situated under the abdomen permitting them to jump. The retinaculum triggers the furca, which then snaps on the

substrate, enabling the collembolans to spring upward in less than 20 ms, hence their second name “springtails” (Kriska, 2022; Oliveira, 2022).

As collembolans are able to jump very quickly, their predators have evolved specific means of capturing them. For instance, individuals of the staphylinid coleopteran *Stenus comma* have a labium that can be projected in 4–5 ms (Bauer & Pfeiffer, 1991).

Among ants, this is the case for small species equipped with trap-jaw mandibles such as workers of the formicine *Myrmoteras barbouri* (Moffett, 1986a) and the long-mandibled, trap-jawed myrmicine *Strumigenys*, for which details have been provided. These species detect a collembolan from a few millimeters, stop and open their mandibles to 180° exposing their forward-leaning trigger hairs. The labrum keeps the bases of the mandibles open, while the adductor muscles tense. As the workers begin to approach the prey, the trigger hairs touch its body and so the labrum drops, producing a violent strike. As the collembolan is impaled on the mandibles’ apical teeth, the ant does not need to sting it (Brown Jr & Wilson, 1959; Masuko, 1984; Dejean, 1986).

In medium-mandibled, trap-jawed *Strumigenys* the mandibles open only to 90° so that the collembolans are seized by an appendage and must be stung (Dejean, 1980a).

Short-mandibled, trap-jaw *Strumigenys* halt when detecting collembolans, crouch on the substrate folding their antennae into their scrobe and opening their mandibles to $\approx 60^\circ$. They approach the prey collembolan very slowly, placing their mandibles on both sides of one leg and seizing it when the trigger hairs are contacted. Here, too, stinging is necessary (Dejean, 1985b). To better approach the prey, the workers of the Asian short-mandibled, trap-jawed species, *Strumigenys bentenm*, gather organic material from the ground and use their forelegs to spread it on the dorsum of their head and thorax (Masuko, 2009a). The workers of African species even attract collembolans thanks to secretions from the labrum and likely from the spongiform appendages of the petiole (Dejean, 1985a).

A study of predation by short-mandibled, trap-jaw *Strumigenys* also showed that when a collembolan escapes during an attempt at capture, the worker seems excited and engages in a form of intensive search (i.e. greater sinuosity and velocity) that facilitates the recapture of the prey. If the escaping collembolan (or another one) is encountered, it is immediately attacked and stung (Dejean, 1988b). This “reserve behavior” also exists in other ground-hunting ant species (Dejean, 1991; Schatz *et al.*, 1997; De la Mora *et al.*, 2008).

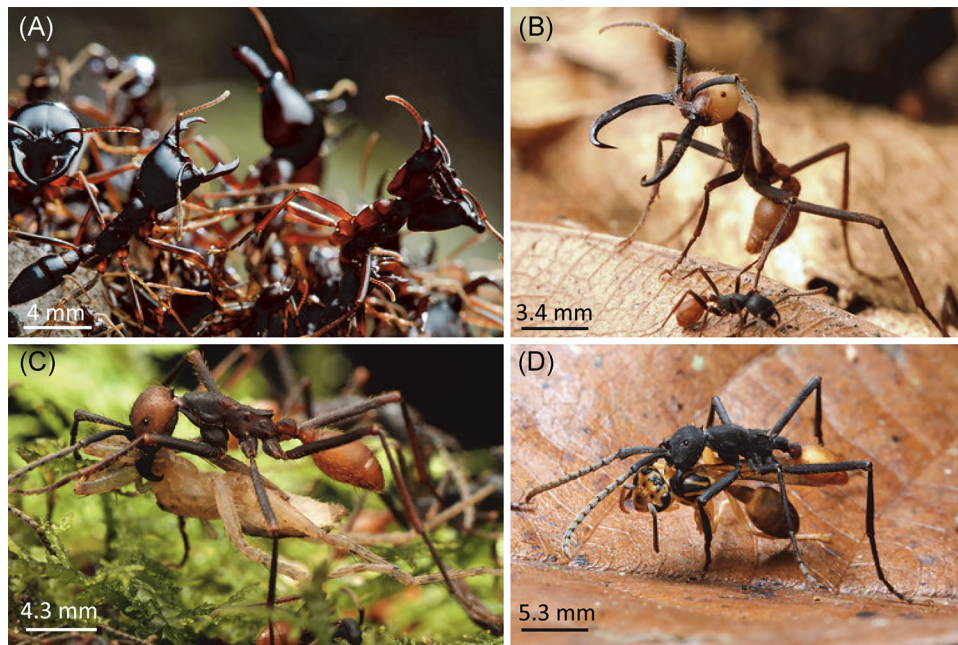


Fig. 7 Dorylinae. (A) Part of a column of *Dorylus* sp. (Dorylinae of the Old World) with major workers protecting a column. (B) *Eciton burchellii*, major worker of the New World Dorylinae with hypertrophied mandibles. (C) An *E. burchellii* worker retrieving a spider. (D) *Eciton rapax* worker retrieving a social wasp (photos A. Wild).

Building a trap to attract prey

The nest of the ground-dwelling myrmicine *Pheidole oxyops* acts as a pitfall trap: the nest entrance is ringed with excavated soil; this structure coupled with worker ant behavior converts the entrance into a very efficient pitfall trap, which plays a role in prey capture (Forti *et al.*, 2007). This trap design is even more effective when the workers of *Pheidole oxyops* place feathers around their nest entrance to attract prey (e.g. mites, springtails, other ants) that then fall into the slippery vertical main gallery of the nest. The falling prey are then easy to subdue as the major workers wait inside the nest near this vertical gallery, ready to restrain or catch the prey after it falls (Gomes *et al.*, 2019).

Preying on other ants or termites: the theory

Franks & Partridge (1993) proposed “The Lanchester theory of combat” to clarify combat between ants. The Square law predicts that numerical superiority is the deciding factor when combatants can mix freely, whereas the Linear Law predicts that fighting ability contributes more to victory than does the number of combatants when, in a restricted combat area, the individuals are forced to engage in a series of duels.

Hence, the Square law applies when army ants of the genus *Dorylus* and *Eciton* with large colonies (i.e. ≈ 20 million and $\approx 600\,000$ workers, respectively) attack other ants whose colonies comprise only a few thousand workers (Fig. 7). For instance, the swarm front of these army ants contains many thousands of individuals per square meter, so that the number of fighters is fundamental to the fate of the combats.

The Linear Law in ants corresponds to cases where the ability to fight depends on several chemical strategies that can be used to facilitate predation. This includes (1) chemical insignificance or the very slight production of cuticular hydrocarbons (CHCs) serving as recognition cues; (2) camouflage through the acquisition of CHCs; (3) mimicry through the production of CHCs matching the other species; and (4) weaponry through chemicals that cause panic (i.e. propaganda), confuse, or appease the host species. For example, weaponry is used by slave-making ants that secrete propaganda (Franks & Partridge, 1993; see also Champer & Schlenoff, 2024, for different cases concerning ant aggressiveness and predation).

Termite predators

Due to termite abundance, particularly in the tropics, the workers of many ant species occasionally prey on

termites. The ants' foraging strategy is related to termite sociality as finding one individual generally indicates the presence of siblings in the vicinity. Also, detecting a termite track can be enough. Hence, the ants engage in concentrated searching where greater sinuosity and lower speed permit the capture of several termites, something limited by the length of the ant mandibles. Then, these ants will recruit nestmates (Hölldobler & Wilson, 1990; see Tuma *et al.*, 2020, for general information on ant–termite interactions).

The Linear Law of the Lanchester theory of combat comes into play when hunting ants use chemical mimicry to prey on termites as do the myrmicine *Crematogaster* sp. and *Tetramorium uelense* (Longhurst *et al.*, 1979a). Also, the CHC profiles of a Mexican *Anochetus* are similar to those of *Nasutitermes* sp. soldiers permitting these ponerine ants to approach the termite columns undetected and capture termite workers unmolested (Bagnères & Lorenzi, 2010). A similar situation likely existed between the African *Anochetus traegaordhi* and *Nasutitermes* spp. (Schatz *et al.*, 1999). Another strategy noted for *Crematogaster striatula* workers is based on a venom able to act from a distance. Recruited individuals point their protruded stinger toward the termite prey until it is numbed and killed, so that these ants are not injured by the termite defenses (Rifflet *et al.*, 2011).

Among specialized termite predators, the workers of the Australian formicine *Melophorus potteri* prey on termites individually using their mandibles equipped with a large apical tooth that facilitates this task (Andersen, 2000). Also, the workers of the short-mandibled myrmicine *Eurhopalothrix heliscata* ambush solitarily in rotting wood to capture termite workers, seizing them by an appendage and stinging them in a behavior very similar to that described for short-mandibled, trap-jawed *Strumigenys* with regard to collembolans (Wilson & Brown Jr, 1984).

The defense mechanisms of termites are efficacious against most army ants, including Old World ones that are generalist predators (see “Army ant behavior” in Dejean *et al.*, 2025), but some subterranean African *Dorylus* are specialized in termite predation, including the epigaeic *Dorylus nigricans rubellus* (Gotwald Jr, 1995; Schöning & Moffett, 2007).

The scouts of the African ponerine *Megaponera analis* are major workers looking for Macrotermitinae foraging sites or their termitaries (there is a monophasic allometry in worker sizes in this species). The foraging distance around their nest varies between 48 and 95 m. These scout ants, whose number varies between 10 and 50 individuals, detect their termite prey thanks to odors issuing from the galleries (Yusuf *et al.*, 2014). Then, they return

to their own nests laying a scent trail with their stinger and recruit 50 to 800 nestmates, mostly minors, that form a column guided by the scouts that follow the trail. All the workers of the column reinforce this scent trail and stridulate. Upon reaching the targeted foraging sites of the termites or a termitary, the major workers break open the galleries to permit the minors to enter and attack the termites for ≈ 9 min, during which time they create piles of paralyzed prey around the gallery entrances. Then the majors gather ≈ 10 termites between their mandibles, the minors only a few or none, before the returning column is formed, led by the majors that followed the scent trails (Longhurst *et al.*, 1978; Longhurst & Howse, 1979; Corbara & Dejean, 2000; Yusuf *et al.*, 2014; Frank & Linsenmair, 2017a; Frank & Linsenmair, 2017b).

The elimination of soldiers in order to gain access to termite workers and the brood is a challenge because Macrotermitinae soldiers guard galleries with their large sclerotized head aided by powerful mandibles that can snap and can also produce defensive anti-ant chemicals (Prestwich, 1979).

Attacks on *Macrotermes* by *Megaponera analis* were observed under laboratory conditions using large pieces of termitaries whose galleries, connected to chambers, were opened laterally to provide a narrow window permitting direct observation (Corbara & Dejean, 2000). Minor *Megaponera analis* workers that enter the galleries detect termite guards from a distance, and so flex their gasters under their thoraces and heads to extend their stingers toward these snapping termites. The guards' mandibles slip on the tip of the fusiform, sclerotized gasters of the ants. Yet, after snapping, the termite mandibles remain closed due to the tetany of its adductor muscles to permit the secretion of chemical defenses, an effective behavior *vis-à-vis* non-specialized predators. Because the *Megaponera analis* minors are apparently immune to these secretions, their stingers extruded, they deposit venom on the mouthparts of the now inoffensive termite soldiers. This venom has a rapid topical effect due to numerous thin intersegmental membranes surrounding the mouthparts. The minors pull the paralyzed termite soldier backward and then can prey upon the termite workers (Corbara & Dejean, 2000).

This type of behavior is called “*Megaponera*-like foraging behavior”. Some variants were noted in the myrmicine ant *Tetramorium uelense* preying mostly on *Microtermes*, the ponerine ants *Leptogenys chinensis* on *Odontotermes* or *Hypotermes*, *Neoponera commutata* and *Neoponera laevigata* on *Syntermes*, and *Neoponera marginata* on *Neocapritermes* (Longhurst *et al.*, 1979b; Maschwitz & Schönegege, 1983; Leal & Oliveira, 1995; Troya & Latke, 2022).

Note that the termite guards can cut off the extremity of some *Megaponera analis* minors' legs. These minors are rescued by nestmates that carry them back to their nest. There, they are treated by other workers using the antibacterial secretions of their mandibular gland (Frank et al., 2017; Frank et al., 2023; Frank et al., 2024 for amputations in *Camponotus floridanus*).

Ant predators

Here, too, we can see that the Linear Law applies for the myrmicine *Megalomyrmex* spp., which, at the beginning of their attack, use an alkaloid venom triggering panic in the workers of the fungus-growing Attini *Sericomyrmex* or *Cyphomyrmex*. Then, they use chemical insignificance, permitting them to be accepted by their host and so to feed on its fungal garden and brood. *Megalomyrmex symmetochus*, however, defend their host *Sericomyrmex* colonies from *Gnamptogenys* raids thanks to their venom (Adams et al., 2013; Adams et al., 2015; Neupert et al., 2018). Indeed, fungus-growing *Sericomyrmex* and *Trachymyrmex* can also be attacked by the ectatommine *Gnamptogenys hartmani*, which also uses propaganda to cause panic among the raided workers that leave their nest, which is then usurped by the raiders that feed on the fungus and brood before raiding another nest (Dijkstra & Boomsma, 2003).

Foragers from the dolichoderine *Iridomyrmex sanguineus* cower when encountering individuals of the formicine *Melophorus anderseni*, permitting the latter to rub their bodies against the *Iridomyrmex* and so to acquire their colony odor. Then, these *Melophorus* can safely enter the *Iridomyrmex* nests to rob larvae (Agosti, 1997).

New World army ants of the Dorylinae have a behavior dictated by their biology (Fig. 7B–D). During a nomadic phase, the colonies of *Eciton burchellii* emigrate daily (≈ 14.3 d), the queen does not lay eggs so that her gaster is contracted, while the larvae develop as they are fed with prey captured by the workers. This is followed by a stary phase (≈ 20.4 d) as the larvae pupate. The prey are mostly fed to the queen which, becoming physogastric, lays thousands of eggs. The colony remains in the same bivouac, organizing daily raids separated by $\approx 123^\circ$ corresponding to the spokes of a wheel radiating from its center (Kronauer, 2009; Kronauer, 2021). This maximizes the efficiency of the foraging paths, the raiding workers following the path up to the front of the swarm (≈ 5 m in width) where they can capture prey, return to the bivouac (those with prey leave them) and return to

the front of the swarm. Other *Eciton* species are called “column raiders” as they forage along narrower columns (Willson et al., 2011; Chandra et al., 2021).

Most New World army ants are ant predators with different levels of specialization with some species even adapted to preying on a particular genus (Perfecto, 1992; Gotwald Jr, 1995; LaPolla et al., 2002; Powell & Clark, 2004; O'Donnell et al., 2005; Le Breton et al., 2007; Souza & Moura, 2008; Hoenle et al., 2019; Manubay & Powell, 2020; Pérez-Espona, 2021). Despite their large number, they illustrate the Linear Law of the Lanchester theory of combat as they release an allomone that triggers panic among the raided workers that leave their nests, some of them carrying brood (Perfecto, 1992; Gotwald Jr, 1995; LaPolla et al., 2002; Le Breton et al., 2007). New World army ants sharing a geographical area show a certain specialization between prey ant species, particularly among the same genera (i.e. *Neivamyrmex*, *Eciton*, and *Nomamyrmex*), limiting competition between them. It was confirmed that their booty is mostly represented by ants (98.37%), particularly pupae and larvae (86.45%), a few eggs (0.89%), and adult ants (11.03%) (Hoenle et al., 2019). Hence, most fights are avoided because the raided queen(s) is/are spared and the panicked workers return to their nest after the attack, permitting the raided colonies to reconstitute themselves (Gotwald Jr, 1995; Dejean et al., 2014).

Still among New World army ants, *Nomamyrmex esenbeckii* workers exceptionally use their stinger during predation (e.g. *Eciton* workers only sting defensively). Their large colonies (i.e. more than 1 million workers) hunt day and night for mostly leaf-cutting, fungus-growing ants, but *Odontomachus*, *Camponotus*, and *Nasutitermes* termites can also be attacked (Rettenmeyer, 1963; Souza & Moura, 2008; O'Donnell et al., 2020). Although they mostly raid immature *Atta* colonies with only a few majors, they also raid mature colonies with more than 1 million workers including large-headed majors with large mandibles and good fighting abilities. Using both their mandibles and their venom, *Nomamyrmex* soldiers attempt to penetrate the targeted colonies whose gallery entrances are defended by *Atta* majors. When *Nomamyrmex* soldiers are successful, all other kinds of workers can enter the *Atta* nest, permitting the capture of one-third to one-half of the brood plus the numerous killed workers. In extreme cases, the *Atta* colony can die (Powell & Clark, 2004).

Most Old World army ants are generalist predators with some *Dorylus* that exceptionally prey on termites; occasionally they can eat palm nuts. The Asian *Dorylus orientalis* can strongly attack the roots of plants, although it

preys on other ants (Schöning, 2008; Devi *et al.*, 2022). *Aenictus* spp. mostly prey on other ants, social wasps, and termites (Gotwald Jr, 1995; Chandra *et al.*, 2021).

Preying on ant and termite brood: lestopiosis and termitolesty

The myrmicine *Solenopsis* of the former genus *Diplorhoptrum* nest close to or in the walls of the large nests of other ants that belong to several subfamilies. Their very tiny workers dig small-diameter galleries connecting their nest to that of their host ants. *Solenopsis* workers avoid contact with the host during encounters and discretely rob brood from the colonies they infiltrate (Pacheco & Mackay, 2013). Yet, *Solenopsis fugax* workers produce a long-lasting repellent venom permitting them to enter the host colony unmolested (Hölldobler, 1973). A field experiment revealed that their host ant abundance was particularly lowered by these thief ants, to the point that their impact was compared to that of New World army ants (Ohyama *et al.*, 2020).

Termitolesty was noted in the myrmicine genera *Carebara*, *Liomyrmex*, and *Solenopsis*, which nest close to termite mounds or in their walls and rob mostly termite eggs, sometimes larvae (Hölldobler & Wilson, 1990). *Tetramorium termitobium* lives in the mounds of different Macrotermitinae species. The mandibular glands of the workers produce aliphatic alcohols that do not trigger alarm among termites, so that they are not attacked by their termite prey (Longhurst *et al.*, 1980). The colonies of the ponerine *Hypoponera eduardi* develop in *Reticulitermes* termitaries. Their workers use a chemical camouflage as their cuticular hydrocarbons are very similar to those of the termite host (Bagnères & Lorenzi, 2010).

A behavior relatively similar to termitolesty was noted in the African ponerine *Centromyrmex bequaerti*, whose workers are large compared with their diverse Termitinae and Macrotermitinae prey. Colonies of these ants lodge in certain termitary chambers free of termites and interconnected by galleries. The workers are blind and polymorphic with a strong dimorphism between them and the large queens (oligogyny in this species, each queen is isolated in a chamber), these traits being rare in the Ponerinae. Generally, media workers hunt termites, while majors act as guards blocking the gallery entrances, and minors care for the brood (Dejean & Féron, 1999).

Arboreal ants

For ants, the main adaptations to arboreal life are seen in well-developed claws and tarsi equipped with adhe-

sive pads. Most arboreal ants have spherical or ovoid heads and short mandibles with small numbers of teeth, with some exceptions, such as the myrmicine *Daceton* equipped with trap-jaw mandibles (Federle *et al.*, 2002; Wilson & Hölldobler, 2005).

Arboreal ants are scarce in temperate to cold climates, although the colonies of the dolichoderine *Dolichoderus quadripunctatus* can be very large in Europe (Stukalyuk, 2018). On the contrary, arboreal ants dominate the canopy fauna in tropical rainforests, representing 86% of the arthropod biomass and up to 94% of arthropod individuals, and they are key predators (Rico-Gray & Oliveira, 2007; Dejean *et al.*, 2007a). This high ant abundance in tropical rainforests is possible thanks to liquid sugary sources such as extrafloral nectaries and Hemipteran honeydew that fuel costly prey-hunting activities by arboreal ants (Davidson, 1997; Davidson *et al.*, 2003).

Among plants, “myrmecophytes” or “ant-plants” have obligate, symbiotic interactions with specific “plant-ants” where, in exchange for a nesting place in cavities called domatia, the colonies of these ants protect their host from phytophagous insects, competitors, and pathogens. This relationship is enhanced when the myrmecophytes also provide their guest plant-ants with extrafloral nectar and/or food bodies; these ants can sometimes attend hemipterans for their honeydew particularly when the myrmecophyte does not produce sugary food (Rico-Gray & Oliveira, 2007; González-Teuber & Heil, 2015).

Predatory behavior in tropical rainforest canopies

The canopies of tropical forests and tree crop plantations shelter “territorially dominant arboreal ants” (TDAAs) characterized by large colonies with several hundred thousand to several million individuals and the ability to build large and/or polydomous nests (e.g. carton builders, carpenter ants, and weaver ants). TDAAs show a highly developed intra- and inter-specific territoriality, so that their territories are distributed in a mosaic pattern (Blüthgen & Stork, 2007; Dejean *et al.*, 2007a). Workers of these species deposit persistent landmarks lasting for several years and recognized by other ants that avoid them and so conflicts, particularly between TDAAs (Dejean & Beugnon, 1991; Offenber, 2007; Dejean *et al.*, 2007a; Offenber *et al.*, 2013).

Arboreal ants have evolved predatory behaviors adapted to hunting on tree foliage thanks to very good vision and by optimizing their predatory ability in this 3-dimensional space, permitting them to capture insects that can escape by flying away, jumping, or dropping. For

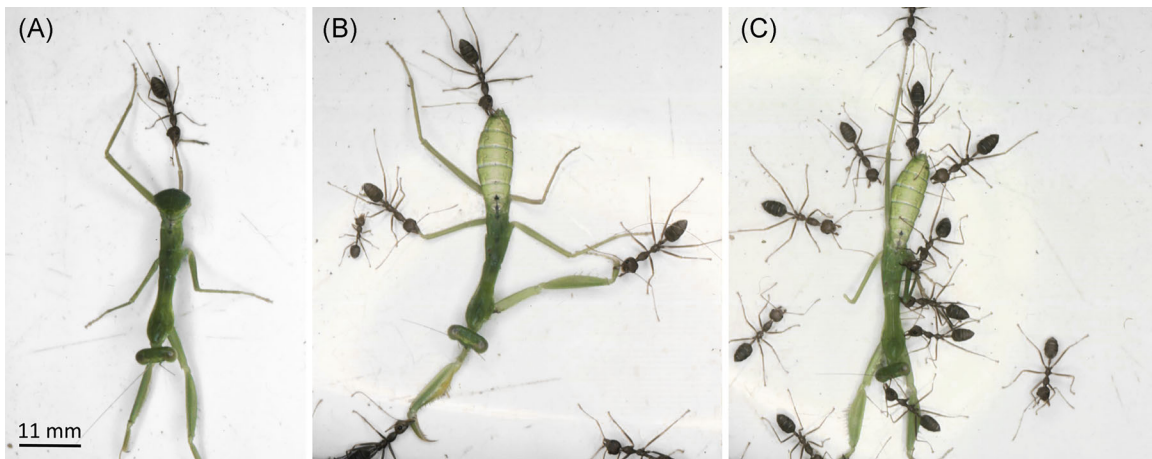


Fig. 8 Sequence of predation by *Oecophylla longinoda* workers (Formicinae). (A) One worker seizes a mantis by the extremity of a hind leg. (B) Nestmates situated in the proximity begin to arrive and spreadeagle the prey. (C) Later, they also bite the prey in different places but never use their venom (photos A. Dejean).

example, workers of the African formicine weaver ant, *Oecophylla longinoda*, the first species studied in this situation, hunt diurnally in groups. Prey are detected visually from a distance, seized by an appendage by 1 individual that then releases a pheromone to attract nestmates. These recruited workers immediately seize in turn a prey appendage and pull backward, spreadeagling the prey (Fig. 8). This behavior, used even for relatively small prey, also permits them to capture large insects and other animals that are cooperatively retrieved whole (Dejean, 1990a; Dejean, 1990b; Wojtusiak *et al.*, 1995).

Other TDAAs (e.g. the African myrmicine *Atopomyrmex mocquersyi*, *Crematogaster* spp., *Tetramorium aculeatum*, and the Neotropical dolichoderine *Azteca chartifex*) exhibit only some variations of this behavior based on spreadeagling the prey. Rarely, detection may occur from a short distance. Venom is frequently used to paralyze the prey, and the prey can be cut into pieces that are each retrieved by one or a few workers (Djiéto-Lordon *et al.*, 2001; Richard *et al.*, 2001; Dejean *et al.*, 2009; Kenne *et al.*, 2009).

Predatory plant-ants that generally spreadeagle insect prey, as do TDAAs, can be alerted when an insect lands on their host myrmecophyte (Dejean *et al.*, 2009). Even the African pseudomyrmecine *Tetraponera aethiops* and the Neotropical dolichoderine *Azteca bequaerti*, hidden in their host plant domatia, react to the vibrations transmitted by an insect landing on a leaf or a twig and immediately attack them. This avoids the need to forage for prey (Dejean *et al.*, 2008a; Dejean *et al.*, 2009).

The workers of 2 Neotropical *Azteca* ants, *Azteca lanuginosa* and the plant-ant *Azteca andreae*, ambush un-



Fig. 9 *Azteca andreae* workers (Dolichoderinae) ambushing side-by-side under the edges of the leaves of their host *Cecropia* tree, while a group of nestmates have captured a sphingid moth (photo A. Dejean).

der the edges of the leaves of their host tree side-by-side (Fig. 9). When a flying insect lands on that leaf, some workers rush to capture it (Morais, 1994; Dejean *et al.*, 2010). The prey is then transported over the edge of the leaves where numerous workers spreadeagle them on the underside of these leaves. Indeed, the ants' very large claws adhere particularly well there, illustrating the use of the "Velcro principle" to capture prey (Dejean *et al.*, 2010).

Although rarely noted on canopy trees (Campbell, 1994; Warner & Scheffrahn, 2007), *Pheidole megacephala* is a ground-nesting species that immobilizes

prey by sporedeagling it, dominating other ants through exploitative competition: raiding nests, capturing the queens and the brood, and finally occupying their territories (Dejean *et al.*, 2007b; Dejean *et al.*, 2008b; Sarnat *et al.*, 2015; Kamaru *et al.*, 2024). This strategy is enabled by huge unicolonial colonies with multiple nests (polydomy) and multiple queens per nest (polygyny), so that this species, native to tropical Africa, is one of the most destructive and widespread invaders throughout the tropics (Sarnat *et al.*, 2015).

Noted mostly in the Neotropics and Southeast Asia, mutualistic interactions also occur between ants and some epiphytes that form so-called “ant gardens” (Orivel & Leroy, 2011). Among the ant species associated with these epiphytes, 2 TDAs, namely *Camponotus femoratus* and *Crematogaster levior*, can live in parabiocotic association (i.e. they share the same nest inside the roots of the epiphytes, but each live in different cavities). In this mutualistic association, *Crematogaster levior* benefits from nest building and protection by *Camponotus femoratus*, which in turn benefits from the better ability of *Crematogaster levior* to discover food sources, including prey. Yet, prey discovered by the tiny *Crematogaster levior* workers can be robbed by the larger *Camponotus femoratus* workers (Orivel & Leroy, 2011).

In the rainforests of West and Central Africa, the ponerine *Platythyrea conradti* colonies live in association with the epiphytic fern *Platycerium stemaria*. The workers hunt solitarily nightly to capture diurnal insects that are made torpid by the colder air at that time of day. Their venom has an instant effect whatever the prey size, but small prey are not stung. Then the workers single-handedly retrieve their prey, even large items. These workers also hunt termites. To eliminate the termite soldiers that defend the entrances to the termitaries, the *Platythyrea conradti* workers crouch, folding their antennae backward, and stay immobile. Consequently, the termite soldiers end up by rolling onto their backs, their legs batting the air, something likely due to volatile secretions produced by the ants’ mandibular gland. This behavior was also noted against competing ants (Dejean, 2011). Note that *Platythyrea conradti* share their nests with the tiny myrmicine *Strumigenys maynei* that rather defend their nest against different intruders (Parmentier *et al.*, 2017).

Ambushing inside domatia pierced by small holes or building traps to ambush prey

In the understory of Neotropical rainforests, we noted two interesting cases among myrmecophytes. The walls

of the leaf domatia of *Clidemia killipii* and *Tococa spadiceiflora* (Melastomataceae) form small protuberances that are likely pierced by their associate plant-ants, the myrmicine *Pheidole* sp. or the formicine *Brachymyrmex heeri*. The workers of these ants hide under the holes to prey on insects that land or walk on these domatia, thus serving as a trap (Alvarez *et al.*, 2001; Vogel, 2012).

The myrmicines *Allomerus decemarticulatus* and *Allomerus octoarticulatus* build gallery-shaped traps on the branches of the myrmecophytes *Hirtella physophora* (Chrysobalanaceae) and *Cordia nodosa* (Boraginaceae). To build these traps, they first use intact host-plant trichomes as pillars and severed trichomes to constitute the vault of the gallery, the whole reinforced by the hyphae of Chaetothyriales fungi to create a composite material. The ants leave numerous holes in the surface of the traps, permitting workers to ambush insects walking or landing on the gallery. Indeed, several workers waiting under nearby holes seize different appendages of these prey and pull backward, moving deeper into the trap (Fig. 10). Then, as the prey is immobilized, new workers are recruited to sting it repeatedly before the entire prey is little by little retrieved toward a domatia. There, it will be cut into pieces (Dejean *et al.*, 2005; Dejean *et al.*, 2024).

A relatively similar situation was noted in the dolichoderine *Azteca brevis*. This species builds gallery-shaped traps formed by masticated plant material, reinforced by Chaetothyrlean hyphae, along the stems of the myrmecophyte *Tetrathylacium macrophyllum* (Salicaceae) and on canopy trees (Schmidt & Dejean, 2018).

Discussion and conclusion

Aware that most ants are generalist feeders, we limited this study to their predatory behavior, providing a detailed survey across species, from ground-dwelling to arboreal ants.

Strictly predatory species specialized in the capture of only one prey taxa are noted especially for ground-nesting species. Several have derived mandibles adapted to these situations, a characteristic that appeared in ants as early as the Cretaceous (Barden *et al.*, 2020). Predation by ground-dwelling ants has a significant ecological impact, regulating earthworms and other animals, particularly arthropods living in the ground and leaf litter, including detritivorous and some herbivorous taxa. Many are termite predators, particularly in intertropical areas (Hölldobler & Wilson, 1990).

Among ground-dwelling ants, the Dorylinae stand out for often having very large colonies, functioning as keystone species in tropical ecosystems by regulating the



Fig. 10 On the myrmecophytic treelet *Hirtella physophora* (Chrysobalanaceae), the plant-ant *Allomerus decemarticulatus* has captured a green locust, as well as a Reduviidae (here we see only its leg) thanks to their gallery-shaped trap made with their host plant trichomes and fungi they manipulated leaving small holes permitting them to catch the extremity of the prey legs. (A) A social wasp, *Agelaija cajenensis*, attracted by the captured locust begins to rob a part of its abdomen (cleptobiosis). (B) Because the wasp also put 2 legs on the trap, and then all legs while trying to free itself, it was captured in turn. We can also see the captured Reduviid. (C) Later the wasp was captured, stung by numerous *Allomerus* workers and died. (D) The captured worker was then transported, little by little from hole to hole, toward the closest leaf pouches located at the base of the lamina. Meanwhile, another social wasp, *Agelaija pallipes pallipes*, has begun to rob several parts of the locust but was captured in turn, unable to fly away. Consequently, the *Allomerus* lost a large part of their first prey, the locust, but captured 2 social wasps. Arrow: leaf pouches situated at the base of the laminas where ants lodge (photos A. Dejean).

populations of their prey. In addition, many invertebrates are commensals that follow their trails, and vertebrates, especially birds, follow their raids to benefit from the spoils (Gotwald Jr, 1995). Except for *Aenictus*, which prey on ants, social wasps, and termites, army ants from the Old World are mostly generalist predators (Gotwald Jr, 1995), while New World species more typically prey on ants and other social insects (Hoenle et al., 2024) with certain *Eciton* and *Neivamyrmex* species able to climb canopy trees (Fig. 7).

Plants also participate in feeding ants via extrafloral nectar, food bodies and indirectly via the honeydew of the hemipterans they attend. In exchange, the predatory behavior of ants provides good protection from defoliators (Davidson et al., 2003; Styrsky & Eubanks, 2007; Pringle, 2021; Nelson & Mooney, 2022). Indeed, defoliating insects can develop means to subvert plants' chemical defenses, but they rarely successfully circumvent ant presence (Coley & Kursar, 1996). This concerns ground-nesting ant species able to forage arboreally in temperate areas (Clark et al., 2016; Stockan & Robinson, 2016; Despland & Lessard, 2022). In intertropical areas, territorially dominant arboreal ant species

dominate the canopy of forests where, via their predatory activity and/or their territoriality, they greatly reduce herbivory and increase plant fitness (Dejean et al., 2007a; Trager et al., 2010; Thurman et al., 2019). Hence, they are used in tree crop plantations as biological control agents (Peng et al., 2014; Diamé et al., 2018; Anjos et al., 2022; Vayssières et al., 2022; see also the review by Sankovitz et al., 2024). Because some trees develop protein-rich food bodies, rendering hunting optional or even unnecessary, their associate ants nevertheless protect their host-tree foliage from defoliating insects via territorial aggressiveness (Janzen, 1966; Fiala et al., 1994).

Moreover, some arboreal species, including some associated with understory myrmecophytes, show ingenuity in ambushing ants from inside their domatia pierced with holes or, even by building gallery-shaped traps on their host tree branches, indicating that ant predatory behavior includes a wide array of possibilities.

To conclude, it is often thought that predatory ants mainly rely on their stinger (and therefore venom) to capture their prey (e.g. Casadei-Ferreira et al., 2025); but here we have shown that there are morphological (Table

S1) and behavioral traits that also influence their ability to capture prey. Morphology works closely with behavior to shape phenotypic evolution (Keller *et al.*, 2014), and morphological traits can reflect a species' habitat preferences or functional role within an ecosystem (Sosiak & Barden, 2021). For example, a recent review explored the relative roles of diet and colony size and brain structure in order to understand adaptive brain mosaicism and the neuronal regulation of predatory behavior (Azorsa *et al.*, 2022). These authors discussed the socioecology of predatory ants and its influence on neuroanatomy. Future studies should necessarily explore the evolutionary changes in both morphological and behavioral predatory traits using a phylogenetic approach.

Acknowledgments

Research funding was provided by the French *Agence Nationale de la Recherche*, grant number: ANR-10-LABX-25-01. We would like to thank Andrea Yockey for proof-reading the manuscript and Kamil Stajniak for providing photos.

Disclosure

The authors declare that they have no conflicts of interest associated with this work.

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Manuscript received February 16, 2025

Accepted May 6, 2025

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 Ant predator genera or species with a short description of their morphological or behavioral adaptations for predation.