The evolution and functional morphology of trap-jaw ants (Hymenoptera: Formicidae)

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Abstract

We review the biology of trap-jaw ants whose highly specialized mandibles generate extreme speeds and forces for predation and defense. Trap-jaw ants are characterized by elongated, power-amplified mandibles and use a combination of latches and springs to generate some of the fastest animal movements ever recorded. Remarkably, trap jaws have evolved at least four times in three subfamilies of ants. In this review, we discuss what is currently known about the evolution, morphology, kinematics, and behavior of trap-jaw ants, with special attention to the similarities and key differences among the independent lineages. We also highlight gaps in our knowledge and provide suggestions for future research on this notable group of ants.

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Introduction

Mandibles are critical to the biology of ants, being the primary structures they use to physically interact with their environment during activities like foraging, predation, food processing, defense, nest excavation, and brood care (HÖLLDOBLER & WILSON 1990, LACH & al. 2009). Although these essential functions constrain their morphology, ant mandibles display a remarkable amount of diversity, with elaborate examples of specialization including the pitchforks of *Thaumatomyrmex*, the sickles of *Polyergus*, the hooks of *Eciton* soldiers, and the vampiric fangs of *Amblyopone* (see WHEELER 1927, GOTWALD 1969, HÖLLDOBLER & WILSON 1990). One of the most extreme specializations of ant mandibles can be found among trap-jaw ants, whose long, linear, spring-loaded mandibles snap shut at some of the fastest speeds ever recorded for an animal movement (PATEK & al. 2006). Remarkably, the trap-jaw morphology has independently evolved at least four times across the ant tree of life. Each lineage of trap-jaw ant has converged on a common catapult mechanism for mandible closure, but collectively they display a great amount of diversity in body size, diet, nesting habits, and foraging strategies (Fig. 1).

While trap-jaw ants are frequently cited in reviews on animal speed or ant predation (PATEK & al. 2011, CERDÁ & DEJEAN 2011, HIGHAM & IRSCHICK 2013), there has never been an attempt to summarize their overall biology. The purpose of this review is to synthesize the literature on trap-jaw ant biology, especially focusing on their evolution and biomechanics, and the behavioral consequences of having trap jaws. We limit our discussion to those ants whose mandibles insert close to the midline of the head and use a catapult mechanism to shut their mandibles from an open position. Consequently, we exclude from this review "snapping ants" (for example the genera *Mystrium* and *Plectroctena*), which also have power-amplified mandibles but shut their widely set mandibles from a closed position, snapping them past each other (MOFFETT 1986a, GRONENBERG & al. 1998, DEJEAN & al. 2002). We also omit discussion of ants with linear mandibles that are not power-amplified, such as the genera *Harpegnathos* or *Myrmecia*, because their rapid mandible movements are the result of direct muscle action (PAUL 2001). Because of their small size and cryptic habits, less is known about the biology of trap-jaw ants from the Myrmicinae and Formicinae relative to the larger species in the subfamily Ponerinae. Consequently, much of this review will focus on the genus *Odontomachus*, where more information is available on their functional morphology, foraging behavior, and systematics.

Taxonomy and systematics

The term "trap-jaw ant" does not describe a monophyletic taxon. CREIGHTON (1930) used it to discuss how several distantly related lineages of ants have converged to possess long, linear mandibles whose rapid closure results from the

release of a latch mechanism and is triggered by long hair-like cuticular mechanoreceptors ("trigger hairs"). This trap-jaw condition has evolved once each in the subfamilies Ponerinae (*Anochetus* and *Odontomachus*) and Formicinae (*Myrmoteras*), and at least twice in the subfamily Myrmicinae (tribe Dacetini) (Fig. 2). Trap jaws may have also evolved in other lineages, including *Protalaridris armata* in the myrmicine tribe Basicerotini and the fossil genus *Haidomyrmex* (see BARDEN & GRIMALDI 2012). Without detailed studies of their functional morphology or behavior, however, it is difficult to confidently define these groups as trap-jaw ants, and so we do not include them in this review.

Subfamily Ponerinae: Two ponerine genera possess trap-jaw mandibles: *Anochetus* and *Odontomachus*, containing 110 and 69 extant species, respectively (BOLTON 2013). These genera are distributed worldwide in the tropics and subtropics but are most diverse in the Neotropics and South East Asia (BROWN 1976). The last worldwide revision was by BROWN (1976, 1977, 1978), but a number of recent studies have described new species and clarified the taxonomy of these genera in specific regions (DEYRUP & al. 1985, DEYRUP & COVER 2004, FISHER & SMITH 2008, SORGER & ZETTEL 2011, SHATTUCK & SLIPINSKA 2012, ZETTEL 2012). Like other ponerines (PEETERS 1997, SCHMIDT 2013), they display a suite of characteristics that are often considered ancestral in ants, including small colony size, monomorphic workers, little differentiation between the workers and queen, and solitary foraging (BROWN 1976, 1978). The body size of *Anochetus* is generally much smaller than *Odontomachus*, although there is some overlap. Within and between genera, nesting preferences vary widely, including soil, leaf litter, rotten logs, and even the canopy (RAIMUNDO & al. 2009, CERQUERA & TSCHINKEL 2010, SHATTUCK & SLIPINSKA 2012, CARMAGO & OLIVEIRA 2012).

Molecular phylogenetics strongly supports grouping the clade containing *Odontomachus* and *Anochetus* in the *Odontomachus* genus group, one of several large multi-generic clades found in the Ponerinae (SCHMIDT 2013). Other genera in the group include *Leptogenys*, *Odontoponera*, *Phrynoponera*, and a number of *Pachycondyla* "subgenera", but it is still unclear which of these is sister to the ponerine trap-jaw ants. Molecular divergence dating estimated that the *Odontomachus* group rapidly radiated between 50 and 45 million years ago, with the trap-jaw clade arising somewhat more recently (approximately 30 million years ago). Nine fossil species of *Anochetus* and three of *Odontomachus* have been described, mostly from Dominican Amber (but one compression fossil of *Odontomachus* from the Most Basin, WAPPLER & al. 2013), with ages ranging between 23 and 19 million years (BARONI URBANI 1980, MACKAY 1991, DE ANDRADE 1994).

Most recent morphological and molecular phylogenetic studies have strongly supported monophyly for the clade containing *Anochetus* and *Odontomachus* (see BRADY & al. 2006, MOREAU & al. 2006, SPAGNA & al. 2008, KELLER 2011, MOREAU & BELL 2013, SCHMIDT 2013), but whether they are monophyletic sister groups is still unclear. From the morphology of male genitalia and petiole, BROWN (1978) hypothesized that *Odontomachus* arose from within a paraphyletic *Anochetus*. Data from karyotypes (SANTOS & al. 2010) and adductor muscle morphology (GRONENBERG & EHMER 1996) corroborate this scenario, with *Anochetus* possessing ancestral states of both characters. However, preliminary molecular phylogenetic analyses have been hampered by small and unequal taxon sampling and have been unable to reject alternative relationships, including the two genera being exclusive sister groups, or *Odontomachus* being paraphyletic with respect to *Anochetus* (see SPAGNA & al. 2008, SCHMIDT 2009).

Subfamily Myrmicinae: The subfamily Myrmicinae has, by far, the most species of trap-jaw ants, all currently classified as members of the tribe Dacetini (which includes over 900 described species) (BOLTON 2013). Although not all dacetine species are trap-jaw ants, a large portion of the genus *Strumigenys* and all members of the genera *Acanthognathus*, *Daceton*, *Epopostruma*, *Microdaceton*, and *Orectognathus* display a trap-jaw morphology. Most of these genera are predominantly tropical or subtropical with the genus *Strumigenys* being found worldwide, *Acanthognathus* and *Daceton* limited to the Neotropics, *Microdaceton* only found in the Afrotropics, and *Epopostruma* and *Orectognathus* limited to Australasia (BOLTON 1999, 2000). Dacetine mandibles are remarkably variable, with some species clearly displaying long linear trap-jaw mandibles that open at least 180° (kinetic mandibles sensu BOLTON 1999), whereas others (many *Strumigenys*, and all *Colobostruma* and *Mesostruma*) have triangular (long or short), forcep-like, or plier-like mandibles that can not open beyond 60 - 90° (static mandibles sensu BOLTON 1999). Each mandibular form is correlated with discrete predatory modes of action (use of sting and speed of attack) (BOLTON 1999). Despite the variation in mandible morphology, body size, and foraging behavior, most dacetines are relatively small bodied and form small colonies in leaf litter or rotten logs (WILSON 1953, BOLTON 1999, DEYRUP & COVER 2009). They can often be locally abundant and it is difficult to find a Berlese or Winkler sample of tropical forest leaf litter that does not contain at least one dacetine species (WARD 2000).

It is beyond the scope of this review to thoroughly cover the taxonomic history of the Dacetini, but to say that the generic classification of the tribe is unstable is an understatement (BARONI URBANI & DE ANDRADE 2006a, b, BOLTON 2006a, b). Early generic and species-level revisions were conducted by BROWN (1948, 1953, 1961, 1962, and containing references) and BROWN & KEMPF (1969). More recent studies by BARONI URBANI & DE ANDRADE (1994, 2007) and BOLTON (1983, 1998, 1999, 2000), based on extensive comparative morphology, attempted to bring order to the tribe and resulted in major, and sometimes contradictory, rearrangements of genus- and tribe-level groups. Due to the quality of morphological characters used in

Fig. 1: Representative trap-jaw ant species. (a) Two species illustrating the extremes of size variation among different lineages: *Odontomachus chelifer*, in the subfamily Ponerinae, is one of the largest trap-jaw ant species, whereas *Strumigenys* sp., in the subfamily Myrmicinae, is one of the smallest. (b) *Anochetus faurei*. (c) *Odontomachus latidens*. (d) *Myrmoteras iriodum*. (e) *Strumigenys rogeri*. (f) *Microdaceton* sp. (g) *Acanthognathus ocellatus*. Images (b - g) © Alex Wild, used by permission.
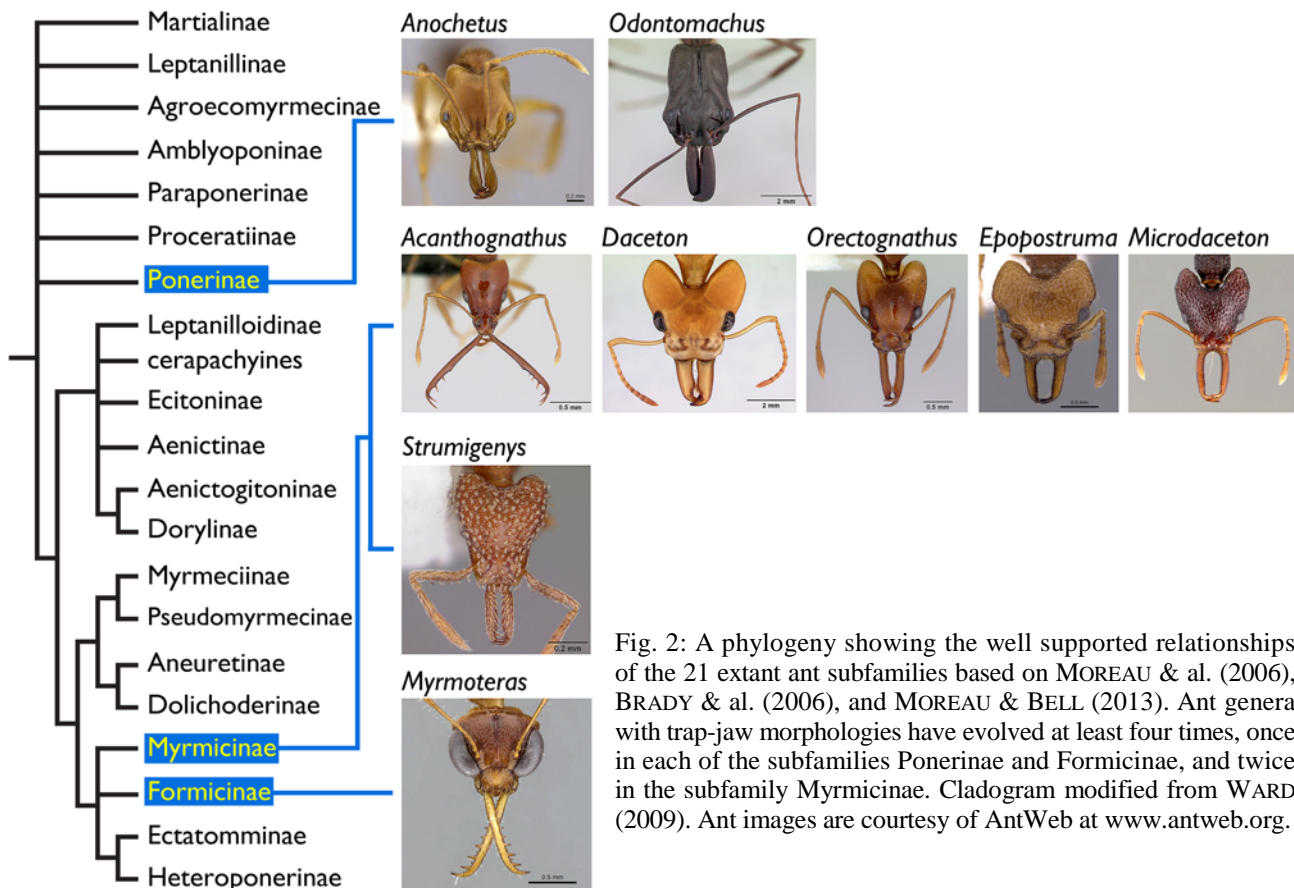
Fig. 2: A phylogeny showing the well supported relationships of the 21 extant ant subfamilies based on MOREAU & al. (2006), BRADY & al. (2006), and MOREAU & BELL (2013). Ant genera with trap-jaw morphologies have evolved at least four times, once in each of the subfamilies Ponerinae and Formicinae, and twice in the subfamily Myrmicinae. Cladogram modified from WARD (2009). Ant images are courtesy of AntWeb at www.antweb.org.

many of these studies, many questions remain about the classification of dacetines and the relationships between genera.

Given the uncertainty of Dacetini classification, it is not surprising that the evolutionary origin of the trap-jaw morphology within the tribe is also unclear. One possible scenario is that the common ancestor of all dacetines was an epigaeic trap-jaw ant from which hypogaeic short-mandible forms have been derived multiple times (BROWN & WILSON 1959). Despite some support for this scenario from a cladistic analysis of dacetine morphology (BOLTON 1999), most recent studies favor the alternative hypothesis that the trap-jaw morphology has evolved multiple times from a short-mandible non-trap-jaw ancestor (BOLTON 1999, BARONI URBANI & DE ANDRADE 2007). A recent comprehensive molecular phylogenetic analysis of the subfamily Myrmicinae by Ward and colleagues strongly supports *Strumigenys* (sensu BARONI URBANI & DE ANDRADE 2007) as sister to the Phalacromyrmecini, rendering the tribe Dacetini (sensu BOLTON 2000) paraphyletic (P.S. Ward, pers. comm.). This would reinforce the hypothesis that the trap-jaw morphology has evolved at least two times within the subfamily: once in *Strumigenys* and at least once in the remaining dacetine genera.

Subfamily Formicinae: The least species-rich trap-jaw ant group is the genus *Myrmoteras*, with only 34 described extant species (BOLTON 2013). A recurring theme in the *Myrmoteras* literature is how rarely workers are collected and how little is known about their general biology. The paucity of *Myrmoteras* collections may partially be explained by their relatively limited distribution (South East

Asia) (AGOSTI 1992) and small nests that are primarily located in leaf litter (MOFFETT 1986b). The majority of *Myrmoteras* species (> 20) have been described over the last three decades (MOFFETT 1985, ZETTEL & SORGER 2011, BUI & al. 2013), as standardized methods for sampling leaf litter arthropods have become the primary tool used to quantify ant biodiversity (AGOSTI & al. 2000). With continued efforts to intensively sample leaf litter worldwide, the likelihood of additional species discoveries and the opportunity to study their ecology and behavior will increase.

The morphology of *Myrmoteras* is exceptional even among trap-jaw ants, with long, slender, and dentate mandibles, large eyes, and a small head relative to other trap-jaw ants (AGOSTI 1992). The genus is divided into two subgenera based on the presence of trigger hairs: *Myrmoteras* and *Myagroteras* (see MOFFETT 1985). The subgenus *Myagroteras* lacks trigger hairs on the labrum, which may have interesting implications for its trap-jaw mechanism and foraging behavior (see below). Early myrmecologists easily placed *Myrmoteras* in its own tribe (Myrmoteratini) (WHEELER 1922), but a combination of ancestral and derived traits made the relationship of *Myrmoteras* to other genera within Formicinae more difficult. Based on their large eyes (WHEELER 1922) and simplified proventriculus (GREGG 1954), the genus had been thought to be the remnant of an early branch of the formicine tree. More recently, AGOSTI (1992) placed them in the *Formica* genus-group based on the simple form of the helcium, and molecular phylogenetic studies have suggested they are sister to the tribe Camponotini (BRADY & al. 2006, MOREAU & al. 2006, MOREAU & BELL 2013).

Tab. 1: Summary information on four independent origins of "trap-jaw" power amplified mandibles in ants. Each origin is listed under the subfamily heading. See text for more information.

Subfamily	Genera	Number of species	Distribution	Lock	Spring	Trigger muscle
Ponerinae	*Odontomachus* *Anochetus*	183	New and Old World tropics	Mandible joint	Adductor apodeme?	Mandible adductor
Formicinae	*Myrmoteras*	39	South East Asia	?	?	?
Myrmicinae	*Acanthognathus*	7	New World tropics	Mandibular processes	Adductor apodeme?	Mandible adductor
	Daceton	2	New World tropics	Labrum	Adductor apodeme?	Labral adductor
	Orectognathus *Epopostruma* *Microdaceton*	51	Old World tropics	?	?	?
	Strumigenys	834	Temperate and tropics worldwide	Labrum	Adductor apodeme?	Labral adductor

Biomechanics

Animals have repeatedly evolved suites of morphological and behavioral traits that allow them to overcome the physical and biological constraints of muscle speed. The record-breaking jumps of froghoppers (BURROWS 2003, 2006), the rapid predatory strikes of stomatopods (PATEK & al. 2004, 2007), and the ballistic tongues of chameleons (DE GROOT & VAN LEEUWEN 2004) all display movements that are many times faster than the maximum contraction speed of most skeletal muscles (JAMES & al. 2007). Like each of these cases, trap-jaw ants utilize a catapult mechanism that uses latches and elastic elements to amplify the speed and power of appendage movement. In this section, we will survey the functional morphology and kinematics of trap-jaw ants, with an emphasis on the independently derived strategies each lineage uses to amplify speed.

Morphology: Like in most other insects, two muscles are primarily responsible for "normal" mandible movement in ants: the mandible opener (abductor) and the mandible closer (adductor) muscles (SNODGRASS 1928, CHAPMAN 1995). The mandible moves as a simple hinge, with the closer and opener muscle attaching, respectively, to the medial and lateral portion of the mandible base. The closer muscle is the largest muscle found in ant workers and is composed of fast (but weak) and slow (but forceful) muscle fibers arranged in discrete bundles of a single fiber type (GRONENBERG & al. 1997). Species have varying absolute and relative amounts of each fiber type with varying angles of attachment to the mandible via an apodeme, and these species-specific traits often correlate with the ecological use of the mandible (GRONENBERG & al. 1997, PAUL & GRONENBERG 1999, PAUL 2001). In contrast, the mandible opener muscle is much smaller and usually consists of just a single fiber type.

Trap-jaw ants have modified the basic ant mandible plan by inserting specialized latch, spring and trigger structures that together enable the catapult mechanism. This mechanism allows muscles to build up power over the course of seconds and then release it in less than a millisecond (GRONENBERG 1996a, PATEK & al. 2011). A latch keeps the mandibles open even when the mandible closer muscle contracts (GRONENBERG 1995a, JUST & GRONENBERG 1999), allowing potential energy to slowly be stored in a spring until a specialized "trigger muscle" releases the latch and the man-

dibles shut nearly instantaneously (GRONENBERG 1995b, JUST & GRONENBERG 1999). All trap-jaw ants use this same basic mechanism, but the structures that comprise the individual components (the latch, spring, and trigger) vary between lineages. An initial mechanism was proposed by BARTH (1960) for the mandible snap of *Odontomachus chelifer*, but most of the details of trap-jaw functional morphology and neurophysiology were described by GRONENBERG in the 1990s (GRONENBERG & al. 1993, GRONENBERG & TAUTZ 1994, GRONENBERG 1995a, b, GRONENBERG & EHMER 1996).

In the genera *Odontomachus* and *Anochetus* the latch, spring and trigger all derive from modifications of the mandible joint and closer muscle (GRONENBERG 1995a, GRONENBERG & EHMER 1996). Contraction of the mandible opener muscle moves the ventral base of the mandible into a notch at the base of the mandible joint. This notch acts as the latch, keeping the mandibles securely open even when the relatively large mandible closer muscle contracts. Contraction of the mandible closer muscle builds up potential energy in a spring (GRONENBERG 1995a, b). The anatomical structures that serve as the spring have not yet been definitively described but are likely heavily sclerotized cuticular elements of the mandible, apodeme and anterior head capsule (GRONENBERG 1995a). To release a strike, the small trigger muscle attached to the closer apodeme pulls the mandible laterally out of the notch and allows the mandibles to snap shut. A comparison of *Anochetus* and *Odontomachus* trigger muscle morphology led GRONENBERG & EHMER (1996) to conclude that the trigger muscle is derived from the mandible closer muscle. As already noted, *Anochetus* are, on average, smaller than *Odontomachus* which may significantly affect the speed and acceleration of their mandible strikes (see below). Other notable differences between these two genera include the maximum mandible gape in *Anochetus* often surpasses 180°, in *Anochetus* the trigger and mandible closer muscles are attached to their apodemes via fibers, but in *Odontomachus* they are directly attached.

Reflecting their complex evolutionary history (BOLTON 2000, BARONI URBANI & DE ANDRADE 2007; P.S. Ward, pers. comm.), dacetine trap-jaw ants display multiple power amplification mechanisms. In *Daceton armigerum* and at least some *Strumigenys* species, the latch and trigger are formed by modifications of the labrum (GRONENBERG

1996b). Lateral projections of the "T-shaped" labrum engage with basimandibular processes, locking the mandibles open even when the large mandible closer muscle contracts. Potential energy is likely stored in cuticular elements of the head, but, like the ponerine trap-jaw ants, the spring has not yet been identified. The strike is released when the trigger muscle, derived from the labral adductor, pulls the labrum inward, disengaging from the basimandibular process and allowing the mandibles to close (GRONENBERG 1996b).

Ants in the genus *Acanthognathus* have an extremely reduced labrum (BOLTON 1999, 2000) and their mandible-locking mechanism is completely different from other dacetine trap-jaw ants (DIETZ & BRANDÃO 1993, GRONENBERG & al. 1998). In this genus, the latch is formed by long, curved basimandibular processes. As the mandibles open, they rotate about their longitudinal axis, which positions the processes so that their forked apices interlock with each other. In this position, and like in all other trap-jaw ants, the mandible closer muscles can contract without closing the mandibles. The trigger muscle is a distinct group of fibers derived from the mandible closer muscle that attach only on the dorsal and lateral sides of the "Y-shaped" mandible closer apodeme. Because of their asymmetrical position, contraction of the trigger muscles applies a torque to the heavily sclerotized arm of the mandible closer apodeme. This reverses the rotation of the mandibles, frees the basal processes, and allows the mandibles to snap shut. Until more information on the evolutionary history of dacetine ants is available, it is unclear if the morphology of *Acanthognathus* is derived from another trap-jaw mechanism like that in *Daceton* or if it is an independent origin from a short-mandible ancestor.

The mandibles of dacetine trap-jaw ants are dramatically different from those of non-trap-jaw dacetines, like some species of *Strumigenys* that were formerly in the genus *Pyramica*, and all species of *Colobostruma*, and *Mesostruma* (see BOLTON 2000, BARONI URBANI & DE ANDRADE 2007). Short-mandible static-pressure dacetines are also specialized predators, with large muscle-filled heads and fast mandible strikes (see below) (MASUKO 1985), but the functional morphology of their mandibles and muscles has not been studied in any detail. It is unclear if they use a power amplification mechanism different from the mechanism employed by trap-jaw ants, or if, like *Myrmecia*, *Harpegnathos*, and other predatory ants with rapid mandibles, they rely on the direct action of fast-contracting mandible closer muscles alone (GRONENBERG & al. 1997, PAUL & GRONENBERG 1999).

The convergence among trap-jaw ants extends beyond the morphological structures forming the latches, springs, and triggers. There is also convergence in the physiology of the trap-jaw mechanism, especially in the muscles and neurons controlling the reflex. In every group studied, these muscles and neurons show similar strategies for maximizing the speed of the mandible strike. The large mandible closer muscle that directly powers the trap-jaw is made up of tubular fibers with very long sarcomeres (5 - 11.4 μm), which characterize slowly contracting muscles. In contrast, the trigger muscle is composed of fibers with many short sarcomeres (1.8 - 3.0 μm) with large core diameters (2.4 - 8 μm), evidence of fast muscles (GRONENBERG &. al 1997). Likewise, the sensory neurons that receive stimuli from the trigger hairs and the motor neurons that innervate the trigger muscle have some of largest diameters among insects, (GRONENBERG & TAUTZ 1994, GRONENBERG 1996b, GRONENBERG & al. 1998), which reflect the incredibly fast speed of the trap-jaw reflex.

Despite what their name implies, trigger hairs are not solely responsible for eliciting mandible strikes. They clearly serve a sensory function; they are physically associated with giant sensory cells in the mandible or labrum (depending on lineage), and mechanical stimulation of the trigger hair results in electrophysiological signals in these sensilla (GRONENBERG & TAUTZ 1994, GRONENBERG 1995b, 1996b, GRONENBERG & al. 1998). However workers will often touch nestmates with their trigger hairs without eliciting a strike, and ablation of the hairs does not prevent *Odontomachus* workers from releasing strikes (CARLIN & GLADSTEIN 1989, unpubl.). Indeed, the *Myrmoteras* subgenus *Myagroteras* is defined by the complete absence of trigger hairs, and they might use visual cues to release the strike (MOFFETT 1985). Given the correlation between trigger hair and mandible length (BOLTON 2000) and observations of workers waiting until prey touch the trigger hairs (DEJEAN & BASHINGWA 1985, DEJEAN 1986, GRONENBERG & al. 1998), it is likely that the ants use trigger hairs to judge the distance of the target. A combination of factors, including tactile and chemical signals and even the "motivational state" of the ant together probably determines when a strike will be released.

Kinematics: The speed of trap-jaw ants has been noted by myrmecologists for decades, but it has only been recently that researchers have been able to accurately measure the mandible strike speed. Early investigations relied on phototransducers or high-speed videography (~ 400 frames per second (fps)) that could only estimate minimum strike duration (< 0.3 ms - 2.5 ms) because the mandibles would often shut between frames (GRONENBERG 1995a, GRONENBERG 1996b, GRONENBERG & al. 1998). With recent advances in videography, PATEK & al. (2006) were able to film mandible strikes of *O. bauri* at frame rates of 50,000 fps and showed that an entire mandible snap occurs within 0.13 ms (fastest 0.06 ms). These snaps had a mean linear velocity at the tip of the mandible of 38 m·s^{-1} (maximum 64.3 m·s^{-1}) and an angular velocity ranging from 2.85×10^4 to 4.73×10^4 rad·s^{-1}. These results rank the mandible strikes of trap-jaw ants as one of the fastest animal movements ever recorded, comparable to the velocity attained by the mandibles of snapping termites (*Termes panamaensis*), albeit through a different mechanism (SEID & al. 2008).

There is significant variation in mandible strike performance among species, which is not surprising considering their morphological and ecological diversity. A comparative study of eight species of *Odontomachus*, covering much of the range in body size displayed by the genus, found that average maximum strike speed ranged from 36 m·s^{-1} to 49 m·s^{-1} and average maximum angular acceleration ranged from 1.3×10^9 radians / s^2 to 3.9×10^9 radians / s^2 (SPAGNA & al. 2008). Strike acceleration and the estimated resulting strike force scaled negatively and positively with body size, respectively, even when accounting for the effects of shared ancestry. The head geometry (head width, head length, and mandible length) of the included species scaled isometrically with body size, provid-

ing the basis for predictive model of strike force based on body size. Based on this model, large trap-jaw ants are predicted to have slow but more forceful mandible strikes compared with smaller ants (SPAGNA & al. 2008). Other morphological features, more directly related to mandible function like muscle volume, angle of muscle attachment, or spring characteristics, may more accurately predict strike performance. Considering the tremendous amount of morphological diversity within and between lineages, additional comparative studies could help generate a mathematical model relating head and mandible morphology to strike performance and contribute to understanding the patterns of trap-jaw morphological evolution.

Predation and other behavioral consequences of trap jaws

The relative speed of predators and prey often determines the outcome of their interactions. Consequently, many predators have specialized morphologies and behaviors that increase their speed during prey capture or handling, while many prey have evolved rapid escape mechanisms to evade predators (ALEXANDER 2003, PATEK & al. 2011). The unique morphology and record-breaking speed of trap-jaw ant mandibles clearly mark these ants as specialized predators (WHEELER 1900, CREIGHTON 1930), and numerous studies have confirmed that trap jaws are fast enough to capture insects with rapid predator escape mechanisms or chemical defenses. However, trap-jaw mandibles can also be used in defense or escape during interactions with competitors or predators (CARLIN & GLADSTEIN 1989, PATEK & al. 2006). In this section we summarize what is known about the predatory behavior of trap-jaw ants and also discuss how their mandibles are used in defense.

Foraging and predation: Some aspects of foraging behavior and predation sequence display similarities across all trap-jaw ant lineages and these may reflect further layers of convergence beyond just the morphology of the trap-jaw. With the exception of *Daceton armigerum* (see HÖLL-DOBLER & al. 1990, DEJEAN & al. 2012), workers are not known to recruit nestmates to food sources, but some species of *Odontomachus* display a simple recruitment behavior, increasing forager activity when food is successfully returned to the nest (EHMER & HÖLLDOBLER 1995, MOF-FETT 1986b). With the high speed and force generated by their mandibles, foragers of all trap-jaw species are efficient, if solitary, predators. Foragers search for prey haphazardly on the forest floor, in leaf-litter, in rotting wood, or even in the canopy (WILSON 1953, WILSON 1962, EHMER & HÖLLDOBLER 1995, RAIMUNDO & al. 2009, CARMARGO & OLIVEIRA 2012, DEJEAN & al. 2012), usually with their mandibles in an open position, presumably in anticipation of striking prey. After detecting prey with their antennae, foragers approach with varying speed, depending on species, but all trap-jaw species appear to use their trigger hairs to position their prey in striking range of the apical teeth of their mandibles. After striking, often multiple times, foragers may also sting struggling prey before carrying it back to the nest (DE LA MORA & al. 2008, SPAGNA & al. 2009).

The role vision plays in the predation sequence varies among trap-jaw ant lineages. Many of the dacetines, for example, are cryptobiotic and have reduced or missing eyes, instead relying on olfactory and tactile cues to find prey (DEJEAN 1986, GRONENBERG 1996b). There is some evi-

dence that larger species, however, have a great deal of visual acuity. Workers of *Odontomachus ruginodis* use their eyes to detect prey from a distance, but rely on their antennae and trigger hairs to successfully aim strikes at nearby prey items (CARLIN & GLADSTEIN 1989). With their relatively large eyes, *Myrmoteras* workers likely use visual cues to detect, localize and catch prey, but their visual abilities have not been studied in detail (MOFFETT 1986b). Interestingly, the subgenus *Myrmoteras* (*Myagroteras*) lacks trigger hairs, and may use their eyes for detection, localization, and even for release of the strike. These ants were found to most commonly catch small non-springtail arthropods, which may indicate that relying solely on vision may limit the speed of prey that they can catch (MOFFETT 1986b).

There is considerable variation in prey type captured and degree of diet specialization displayed among trap-jaw ant genera. The mandibles of small trap-jaw ants (dacetines and formicines) are fast enough to capture springtails (Collembola), minute leaf-litter dwelling hexapods whose rapid predator escape jumps can occur in less than a millisecond (CHRISTIAN 1978). Field observations and cafeteria experiments have demonstrated that many species of *Strumigenys*, *Myrmoteras*, *Microdaceton*, and, possibly *Acanthognathus* feed mainly on entomobryid and isotomid springtails; however, these and other dacetine species will also accept other small-bodied litter arthropods (WILSON 1953, BROWN & WILSON 1959, BROWN & KEMPF 1969, MOFFETT 1986b, DIETZ & BRANDÃO 1993, BOLTON 1999, BOLTON 2000). The arboreal *Daceton armigerum*, which is much larger than other myrmicine trap-jaw ants, feeds on a variety of arthropods and will also tend honeydew-excreting insects (BROWN & WILSON 1959, WILSON 1962, DEJEAN & al. 2012). Foragers of the polymorphic myrmicine *Orectognathus versicolor* will also accept a wide variety of food items (CARLIN 1981).

The larger ponerine trap-jaw species are also active predators, however there are several differences in their predation sequence and prey preferences relative to smaller trap-jaw ants. In general, *Odontomachus* foragers do not approach prey as slowly as smaller species (CREIGTON 1937), in some species forgoing antennation of the prey prior to the strike (DEJEAN & BASHINGWA 1985, DE LA MORA & al. 2008). Foragers may strike prey items multiple times, using their strikes to break up large items into more manageable fragments (personal observation in *Odontomachus*). Across species, use of the sting may be related to the size of the worker relative to the prey item, with smaller individuals stinging more frequently than larger individuals (BROWN 1976, DEJEAN & BASHINGWA 1985, SPAGNA & al. 2009). In quantitative studies of foraging preference, *Odontomachus chelifer* and *O. bauri* foragers were found to significantly prefer termites, including chemically defended species of *Nasutitermes* (see FOWLER 1980, EHMER & HÖLLDOBLER 1995, RAIMUNDO & al. 2009). In the arboreal species *Odontomachus hastatus*, workers collected termites much less frequently, instead returning with dipterans, lepidopterans, and other ants (CARMAGO & OLI-VEIRA 2012). However, foragers of *Odontomachus* accept a wide variety of food including other ants and insects (WHEELER 1900, BROWN 1976, FOWLER 1980, EHMER & HÖLLDOBLER 1995, DE LA MORA & al. 2008, RAIMUNDO & al. 2009), insect frass (CERQUERA & TSCHINKEL 2010, author's unpubl. observ.), plant material (PIZO & OLIVEIRA

2001, PASSOS & OLIVEIRA 2004), honey-dew from tending hemipterans (EVANS & LESTON 1971), and even juvenile vertebrates (FACURE & GIARETTA 2009). Very little is known about *Anochetus* prey preferences, but at least one species, *Anochetus traegordhi*, is a specialist on *Nasutitermes* termites. This species is found nesting in the same rotten logs as termite colonies, and even retrieves termite worker prey in preference over soldier caste prey (SCHATZ & al. 1999). The colonies of several other *Anochetus* species are also found in termite nests (BROWN 1976, SHATTUCK 1999), but they will accept many different arthropods in the lab, including termites, fruit flies, and springtails (GRONENBERG & EHMER 1996, author's unpubl. observ.).

Trap-jaw ants are not unique among insects that specialize on fast or chemically defended prey. Workers of *Myrmica rubra*, for example, actively catch springtails without use of a trap-jaw, instead using a stereotypical jumping attack (REZNIKOVA & PANTELEEVA 2001). Likewise several species of beetles are springtail specialists. The carabid *Notiophilus biguttatus* is a visual hunter that relies on the accuracy of judging the distance and direction of prey to successfully capture springtails (BAUER 1981). The diverse genus *Stenus* (Coleoptera: Staphylinidae) comprises specialized collembolan predators that use an adhesive secretion on the distal end of their elongated labium to capture their prey. These beetles also employ a power amplification mechanism to rapidly (3 - 5 ms) extend their labium before a springtail can escape (BETZ & KÖLSCH 2004). No studies have been conducted on the relative capture efficiency or prey preference of these specialized predators compared with trap-jaw ants, and so it is unclear what their competitive interactions would be in areas where their distributions overlap.

Defensive behaviors: Just as the sting and other predatory weapons can be used in both predation and defense, the mandible strike of trap-jaw ants can also be used for colony or individual defense. The major workers in the polymorphic *Orectognathus versicolor* (see CARLIN 1981) as well as workers in the monomorphic *Odontomachus ruginodis* (see CARLIN & GLADSTEIN 1989) and *Myrmoteras* spp. (MOFFETT 1986b) wait at nest entrances with open mandibles and act as "bouncers", snapping their mandibles at would-be invaders and pushing them away. Additional observations have been made of trap-jaw ants attacking predators or potential competitors with their mandible strikes, often dismembering them without bringing them back to the nest as food (CREIGHTON 1937, MOFFETT 1986b, EHMER & HÖLLDOBLER 1995, SPAGNA & al. 2009).

One consequence of producing such large forces and snapping at prey, predators, and competitors is that, occasionally, individuals strike something much larger than themselves, resulting in the trap-jaw ant itself being launched into the air. This behavior was defined as "retrosalience" (backward jumping) by WHEELER (1900, 1922) who reviewed the natural history literature of a number of jumping *Odontomachus* species from the late 1800s and early 1900s. Later authors documented retrosalience in a number of other lineages including *Anochetus*, *Orectognathus*, *Strumigenys*, *Myrmoteras* and largely concluded that this behavior was an accidental by-product of striking a hard surface with high force (CREIGHTON 1930, 1937, BROWN 1953, CARLIN & GLADSTEIN 1989). The reported distance travelled by the ants as a consequence of their mandible strikes can be quite large ranging from 20 - 25 cm in a dacetine ant (WHEELER 1922) to over 40 cm in *Odontomachus bauri* (see PATEK & al. 2006). The escape jumps powered by trap-jaw ant mandibles are comparable to the record-breaking jumps of froghoppers, fleas and other jumping arthropods that use modified legs (BURROWS 2006, SUTTON & BURROWS 2011).

Recent research suggests that, in some instances, jumping may be an intentional predator avoidance behavior (PATEK & al. 2006, SPAGNA & al. 2009). PATEK & al. (2006) distinguished two different jumping behaviors in *Odontomachus bauri* based on their trajectory: horizontal "bouncer" jumps (not to be confused with bouncer behavior sensu CARLIN 1981) resulting from striking a large object and vertical "escape" jumps, resulting from striking the substrate. Using four species of *Odontomachus*, SPAGNA & al. (2009) demonstrated that escape jumps rarely occurred during interaction with prey but were more likely when a focal ant was surrounded by heterospecifics. Predators that *Odontomachus* workers may use the escape jump against include, but are not limited to, a number of specialist or generalist predatory ants. For example, *Formica archboldi* is thought to be a specialist on *Odontomachus brunneus* (see DEYRUP & COVER 2004), and the diurnal forager *Pachycondyla striata* occasionally takes as prey or even robs the prey of *Odontomachus chelifer* (see RAIMUNDO & al. 2009). More research is still needed, however, to examine how often escape jumps are used in natural contexts and whether the behavior actually improves individual survival.

Trap jaws as key morphological innovation

The trap-jaw apparatus is a dramatic example of morphological innovation, where a structural novelty (latch and trigger muscle) has facilitated the evolution of a completely new function (power amplification), but it is still unclear why this morphology would evolve convergently so many times in a single insect family. It is possible that trap jaws enable their owners to catch fast or dangerous prey that are largely inaccessible to other predators. If so, power-amplified mandibles may have facilitated access to a previously untapped dietary source and caused an increase in speciation and morphological evolution (HEARD & HAUSER 1995, HUNTER 1998a) and would fit the definition of a key morphological innovation: traits that allow organisms to interact with their environment in a new way.

Two recent studies provide some evidence that the lineages that contain the ponerine and myrmicine trap-jaw ants are each associated with significant increases in diversification rate (PIE & TSCHÁ 2009, MOREAU & BELL 2013), consistent with the hypothesis that the trap-jaw is a key innovation. Key innovations have been used to explain patterns of diversity in many animal groups (HUNTER 1998a, PRICE & al. 2010, DUMONT & al. 2012), but establishing causality of proposed key innovations can be difficult (HUNTER 1998b, MASTERS & RAYNER 1998). In addition to demonstrating a shift in diversification rate, linking trap jaws to patterns of species diversity will require showing that trap-jaw ants have entered new adaptive zones compared to closely related non-trap-jaw ant species and that trap jaws quantitatively improve the ecological performance of lineages that have them. For example, *Odontomachus bauri* has been shown to be quantitatively better at disabling *Nasutitermes* soldiers than other ants by using a "strike and re-

coil" strategy (TRANIELLO 1981). However little is known about predation efficiency for the majority of trap-jaw ant species. More research is needed on the diet, ecology, and macroevolution of trap-jaw ants before any conclusions can be drawn about their importance in trap-jaw ant diversification.

Conclusions

With so much of their biology still unknown, trap-jaw ants should serve as excellent study organisms for future students of functional morphology, behavior, evolution, and development. In many cases, we still know very little about basic natural history and functional morphology, especially in the genus *Myrmoteras*. Accurate estimates of the kinematic capabilities (speed, acceleration, and force) for the vast majority of trap-jaw ants are still unavailable. Paired with mandible performance data, dietary preferences could provide insights into predator-prey arms races. Future efforts should also focus on identifying what structure act as a spring and stores the elastic strain energy that makes power amplified mandibles possible. Only with this information we will be able to derive a predictive model that relates morphology to strike performance.

Beyond stabilizing their classification, working out the phylogenetic relationships among trap-jaw ant genera and their closest non-trap-jaw relatives, especially in the subfamilies Ponerinae and Myrmicinae, will be critical for correctly understanding the evolution of this extreme condition. The tribe Dacetini, as currently defined, is ideal for a careful synthesis of systematics, morphology, and behavior to understand the transition from short, muscle driven mandibles to the power-amplified mandibles of true trap-jaw ants.

Finally, modern genomic and evolutionary development tools will enable research on the developmental patterning of trap-jaw mandibles and insights into the comparative morphology of ant mouthparts. Recent research has provided insight into the genetics and development of insect mouthparts (ANGELINI & KAUFMAN 2005) and established a foundation for studying the mechanisms responsible for producing morphologically specialized structures like trap-jaw mandibles. Combined with careful phylogenetic methods, future research will be able to reveal the homology of trap-jaw mandibles across each lineage and study the convergent evolution of morphological innovations at the levels of genetics and development.

Acknowledgments

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