Mandible muscle fibers in ants: fast or powerful?

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Abstract. Ants use their mandibles for catching prey, cracking seeds, cutting leaves, or for the construction of nests and the tender care of brood. The functional morphology of the mandibles reflect the species' adaptations to particular foraging habits and social life. The versatility and specialization of the mandibles depend directly on the design and physiology of the mandible closer muscles and their component fibers. A comparative video analysis of the closing movements of ant mandibles revealed that the maximal velocity varies considerably among species. The speed is correlated with the morphology of the mandible closer muscle, the largest muscle in ants. It is composed of two morphologically very distinct fiber types: long fibers with short sarcomeres (sarcomere length approximately 2 μm) showing all the structural attributes of fast muscle fibers, and shorter fibers with longer sarcomeres (sarcomere length approximately 5 μm) exhibiting the characteristics of slow and powerful fibers. Ants with fast-moving mandibles have a very high proportion of fast closer fibers, whereas the muscles of ants that cannot perform fast mandible movements have only a few or no fast fibers at all. Fast fibers always attach directly to the solid apodeme, while slow fibers often attach to thin apodeme threads. We suppose that the latter kind of fiber attachment is disadvantageous for fast contracting fibers but helps the ants to make better use of the space in the head capsule.

Key words: Mandibles – Muscle fibers – Fiber types – Contraction – Ant species (Insecta)

Introduction

Mandibles are to ants what hands are to humans – bodyparts highly adapted to master a diversity of tasks. Ants use their jaws for fighting and catching prey, for cracking seeds, cutting leaves, scarping wood, and moving soil, but they also employ them for the more delicate tasks of transporting liquid, tending the brood, and carrying nestmates. Predators often have long jaws equipped with piercing teeth and sharp edges (Fig. 1b, c), whereas herbivorous ants (Fig. 1a) have mandibles suited for the particular task of processing plant material (reviewed by Hölldobler and Wilson 1990). In many ant species, however, the mandibles resemble a general type found in many other insect groups: they are sturdy, shovel-like, unsegmented limbs (Fig. 1d) connected to the head capsule by a simple hinge and movable only in a single plane (inwards/outwards). Mandible specialization is not only based on shape but also depends on the speed of movement and on the force the jaws can generate. Obviously, catching elusive prey requires different velocity, power, and tactics than cracking seeds.

Mandibular velocity and force mainly depend on the muscles that control the mandible. While a few ant genera (the trap-jaw ants) have evolved a particular catapult mechanism (Gronenberg 1995, 1996c; Gronenberg and Ehmer 1996) to overcome the temporal limitations inherent to muscular contraction (Alexander 1988), other ants conform to the common mandible organization of other hymenopterans (Snodgrass 1942; Janet 1905): a hinge joint operated by only a single closer and opener muscle.

The key to the versatility of mandible functions is probably the mandible closer muscle. It is much larger than the opener muscle (Janet 1905) and generates all the fast, powerful, or delicate mandible movements. Assuming that different mandible functions require distinct properties of the closer muscle, we hypothesized that such functional differences are reflected in muscle morphology. A comparative approach seemed best suited to address this question. The parameters most indicative of
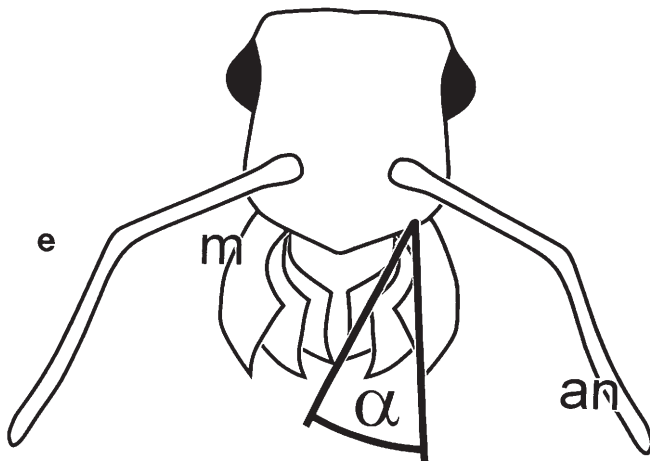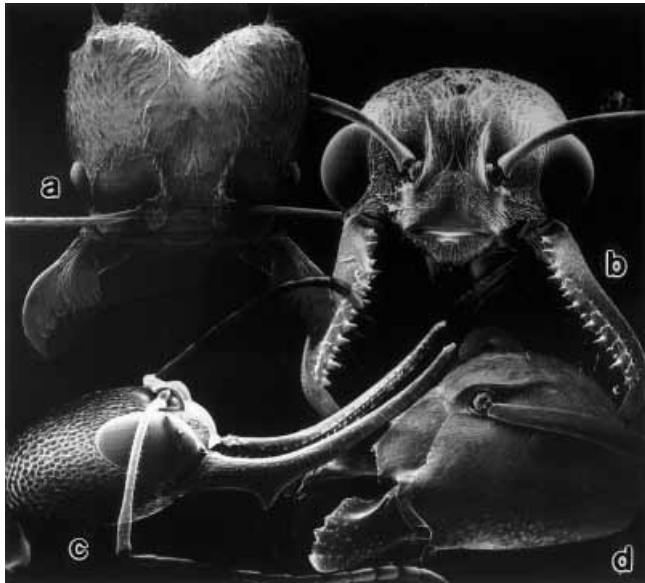
Fig. 1. Scanning electron micrographs (**a–d**) showing the heads of four ants (**a** *Atta sexdens*, **b** *Myrmecia* sp., **c** *Harpegnathos saltator*, **d** *Camponotus ligniperdus*) associated with different mandible functions (**a** leaf cutting; **b**, **c** predatory snapping; **d** less specialized 'all purpose' type). **e** Schematized superposition of three video images showing a closing movement of the mandibles (*m*) in the ant *Ectatomma ruidum*. Similar sketches were used to determine the mandible angle α and the duration of the movement (here: 3 frames at 20 ms/f together; 60 ms) in Table 1. Note that the fastest mandible closure measured for this ant occurred within only 2 frames (40 ms). *an*, Antenna

mandible function are their power and closing velocity. We chose to study the latter because mandible speed is easier to assess without restricting the animal. In the present study, we report mandible movement velocity for many ant species and correlate it with morphological features of the mandible closer muscle. By this approach we were able to appraise the function of different muscle fiber types and we gain a better understanding of the adaptive morphology of mixed muscle fibers.

Materials and methods

Experiments were carried out on the following ant species: *Anochetes gladiator*, *Diacamma* sp., *Ectatomma ruidum*, *Gnamptogenys* sp., *Harpegnathos saltator*, *Odontomachus bauri*, *O. clarus*, *O.*

troglodytes, *O. chelifer*, *Pachycondyla crenata*, *P. villosa* (Ponerinae); *Myrmecia* sp. (Myrmeciinae; preserved material only); *Cerapachys biroi* (Cerapachyinae); *Atta cephalotes*, *A. sexdens*, *Crematogaster lineolata*, *Daceton armigerum* (preserved material only), *Leptothorax gredleri*, *L. sordidulus*, *Pheidole* sp., *Pogonomyrmex badius*, *Strumigenys* sp. (Myrmicinae); *Tapinoma* sp., *Technomyrmex* sp. (Dolichoderinae); *Camponotus balzani*, *C. castaneus*, *C. floridanus*, *C. rufipes*, *C. sericeiventris*, *C. socius* (Formicinae). Examples of the different mandible shapes are demonstrated in Fig. 1a–d. Not all species were examined morphologically as well as behaviorally. All ants were kept in plaster of paris nests under a 12-h light/dark cycle at 25° C and 50% relative humidity. They were fed chopped cockroaches, crickets, or wingless *Drosophila* and honey water or (*Atta*) fresh leaves. For comparative reasons, we cursorily examined some other Hymenoptera: honeybees (*Apis mellifica*), social wasps (*Vespa saxonica*, *Paravespula germanica*, *Polistes* sp.), and the solitary digger wasp *Crabro* sp.

Behavior

The behavior of ants and particularly their mandible movements were videotaped at 50 frames/s or, if the mandible closure occurred within a single frame (20 ms), at 200 frames/s (5 ms resolution) using a high frequency NAC HSV 400 video system. As shown in Fig. 1e, consecutive frames were traced from the screen and mean angular velocities of the mandible movement calculated. Video sequences were taken from ants moving freely in small arenas or held by forceps at their thorax. In all ants examined, the fastest possible mandible closure could be provoked by teasing the ant's mandibles and antennae with a fine minuten pin. Supported in an 'uncomfortable' position (held between forceps), most ant species almost inevitably responded to the teasing with a defensive or aggressive snap or bite. We videotaped and evaluated 10–20 such fast mandible closures to determine the fastest movement (closing time and angular velocity) for each species.

Histology

To examine the organization of mandible muscles and apodemes within the head, ants were anesthetized with Enfluran (Abbot Ethrane) and decapitated. After fixation (buffered 4% formaldehyde or 2.5% glutaraldehyde), the tissue was stained either with 0.2% aqueous solution of methylene blue (1–6 h, fixation in 12% ammonium molybdate) or with osmium-ethyl gallate according to Gronenberg (1995). Alternatively, the heads were silver-impregnated (fixation in ammoniacal ethanol, impregnation in 4% aqueous silver nitrate solution for 6 days, development in 4% aqueous pyrogallol for 6 h). The heads were then dehydrated, embedded in Fluka Durcupan, and horizontally or vertically sectioned at 10–20 μm.

Electron microscopy

Transmission electron microscopy was performed on *Odontomachus bauri* and *Camponotus rufipes* to reveal ultrastructural differences between different muscle fiber types (fast and slow). Muscles were fixed in 0.1 M cacodylate buffer (pH 6.9) with 5% sucrose, 2% paraformaldehyde, and 2.5% glutaraldehyde, postfixed in 1% osmium tetroxide, plastic embedded, and sectioned at 30 μm on a sliding microtome. Appropriate sections containing the particular muscle fiber type were selected, re-embedded, sectioned at 60 nm (Reichert Ultracut), intensified in 5% ethanolic uranyl acetate, stained in 2.5% lead citrate, and examined under a Zeiss EM 900 electron microscope. For scanning electron microscopy, heads were air dried at 40° C for at least 8 h and, after gold-sputtering, examined with a Zeiss DSM 962 scanning electron microscope.

Morphometry

Light-microscopic images (Zeiss Axiophot) were vidoerecorded and digitally stored and evaluated with a computer equipped with a

Table 1. Mandible velocity

Subfamily	Species	Size[a]	Angle [°]	Duration [ms]	Velocity[b] [°/ms]
Ponerinae	*Diacamma* sp.	l	42	40	0.85
	Ectatomma ruidum	l	28	40	0.65
	Harpegnathos saltator	l	19	15	1.25
	Odontomachus chelifer	ll	26	120	0.15
	Pachycondyla crenata	l	25	40	0.73
	Pachycondyla villosa	l	25	40	0.63
Cerapachyinae	*Cerapachus biroi*	ss	43	80	0.53
Myrmicinae	*Atta cephalotes*	m	30	40	0.75
	Atta cephalotes	s	33	60	0.55
	Atta cephalotes	l	25	60	0.42
	Atta cephalotes	ll	33	50	0.83
	Atta cephalotes	lll	29	60	0.50
	Leptothorax gredleri	ss	26	80	0.33
	Pheidole sp.	s	27	80	0.34
	Pheidole sp.	ss	24	40	0.70
	Pogonomyrmex badius	l	31	60	0.52
Dolichoderinae	*Tapinoma* sp.	sss	30	30	1.00
	Technomyrmex sp.	ss	35	30	1.17
Formicinae	*C. balzani*	l	29	40	0.73
	C. castaneas	ll	17	20	0.85
	C. sericeiventris	ll	31	40	0.78
	C. floridanus	l	29	20	1.45
	C. rufipes	ll	19	40	0.48
	C. rufipes	l	28	40	0.70
	C. socius	l	31	40	0.78

[a] To indicate the size of each individual ant, the approximate head width is indicated as *lll*, 3–5 mm; *ll* 1.5–3.0 mm; *l* 1.0–1.5 mm; *m*, 0.7–1.0 mm; *s*, 0.5–0.7 mm; *ss*, 0.35–0.50 mm; *sss*, below 0.35 mm

[b] The highest angular velocity for mandible closure was calculated from the duration of movement and the angle moved

video card and appropriate software (Screen Machine, Fast Electronic) adapted for volume measurements (courtesy of Reinhard Wolf). From each microscopic slide, the outlines of the mandible closer muscle and of the different fiber groups composing the muscle were traced on the computer screen and the areas computed.

Three animals were analyzed per species (in *Atta sexdens* and *Camponotus rufipes*, which show pronounced size dimorphism, three minors and three majors were evaluated separately). In three species (*Pogonomyrmex badius*, *Pachycondyla villosa* and *Gnamptogenys* sp.), the relative muscle fiber volume was determined for only a single specimen and using a different method: each microscopic section was traced on paper, the outlines of the respective muscle fiber groups were cut out, and all the paper pieces representing a particular muscle fiber type were weighed on a balance. Likewise, the relative amount of myofilaments, sarcoplasmic reticulum, transverse (T)-tubuli, and mitochondria composing the different fiber types was determined from EM negatives projected onto and cut out from paper. Muscle volume was calculated considering the section thickness. Sarcomere length was established by counting all sarcomeres of an entire fiber (if possible, fibers were selected that could be traced within a single section) using a calibrated camera lucida attachment to the microscope, 10–60 fibers per type and species were thus measured.

Results

Mandible movements

All ants examined (including trap-jaw ants) are able to perform slow mandible movements. Slow opening or closing of the jaws may take several hundred milliseconds in any ant. Opening of the mandibles may be fast (when teased, some ants, such as *Camponotus florianus* or *Harpegnathos*, fling their jaws open in as little as 40 ms before attacking), but generally the opening of the mandibles is not a specialized movement and takes longer than 50 ms. Biologically, for almost any animal the closing movement is much more important than the opening movement. To assess specializations of mandible function, we have therefore focused on the fastest jaw-closing movement of the respective species. In most cases, this could be elicited by repeatedly touching the ant's mandibles and antennae with a pin. Only a few 'timid' ants, such as *Leptothorax*, needed additional coaxing (e.g., gentle squeezing with forceps) to provoke the defensive mandible movement. Those ants would rather back off than attack the pin and generally showed only slow mandible movements (see Table 1).

The angular velocity of the mandibles may be important for subtle manipulations such as brood care (low velocities allow for better feedback control of the force exerted), while in fast predatory or defensive mandible strikes, the absolute duration is crucial for the success of the action. For this reason, Table 1 lists both the duration of the fastest closing movements as well as the angular velocities. In principle, it takes longer to close wide gaping mandibles than only slightly open ones. In most cases, the ants were able to open their mandibles wider

than the angles listed in Table 1 and the fastest strikes were started from intermediate angles.

The shortest times required to close the mandibles ranged from 15 ms to 120 ms and the angular velocities were similarly divergent (0.15–1.45 °/ms). Preliminary experiments on only a few ant species suggested a correlation between body size and mandible velocity (the slow species *Leptothorax gredleri*, *Cerapachys biroi*, and *Pheidole* sp. are small ants), but this assumption turned out to be wrong (see Table 1).

The fastest strikes were performed by the relatively large *Harpegnathos* and *Camponotus floridanus* as well as by the tiny ant *Technomyrmex* sp. On the other hand, giant majors or medium-sized workers of *Atta sexdens* closed their mandibles almost as slowly as did the small *Pheidole* sp. or *Leptothorax gredleri* (Table 1). Hence, a correlation between mandible velocity and body size could not be established. Rather, foraging habits seem to correlate with mandible speed: the fastest movements were found in predators such as *Harpegnathos saltator*, whereas very slow mandible movements occurred in herbivorous ants (*Atta*, *Pogonomyrmex*) and in *Leptothorax*, a genus of slow-moving ants not known to be predatory.

The slowest mandible movements were found in *Odontomachus*; however, these ants are equipped with fast trap-jaws for predation and defense, and their fast mandible strike is described elsewhere (Gronenberg 1995). *Odontomachus* need their 'normal' repertoire of mandible movements (not engaging the trap-jaw mechanism) exclusively for slow activities. We did not determine mandible velocities for the bulldog ant *Myrmecia* because we had no live specimens. Yet it is known that *Myrmecia* are particularly fast predators that snap swift insects with their mandibles (Gray 1971). None of the other hymenopterans cursorily tested (bees and wasps) showed fast mandible movements (as compared to some of the ants). We could only elicit mandible closure movements taking 60 ms to more than 100 ms.

The mandible closer muscle

The aim of the present study was to examine a possible correlation between the velocity of the mandible-closing movement and the underlying structures. Therefore we examined the morphology of the mandible muscles that control the movement.

The mandible of hymenopterans is moved by two muscles. In ants (but not in the honey bee, which we will no longer consider in the current account), the smaller opener muscle resides ventralmost in the head capsule and its fibers project from the ventral midline towards the lateral side of the mandible base. The opener muscle corresponds to the unipinnate type of vertebrates (Lockhart 1972): all muscle fibers converge at the tip of the opener apodeme, a tendonlike structure attached to a small condyle of the mandible base situated laterally to the pivot. The apodeme may be sclerotized (hardened cuticle) in some ants. When the opener muscle contracts and pulls on its apodeme, the mandible is rotated outwards to the open position.

The closer muscle is much larger than the opener muscle. In all ant workers examined, it was by far the largest muscle of the body, taking up more than two-thirds of the entire head volume. This was not the case in male ants. Generally, these have small heads, of which the brain constitutes a substantial portion, and most head muscles are rather small. The reason is that most male ants are fed by workers and do not rely on powerful mandibles. In most males, the maxillary, labial, and antennal muscles are larger than the mandible muscles. Unlike many other ants, males of *Pogonomyrmex* use their strong mandibles to win access to females during mating (Hölldobler 1976). In addition, these males are not fed by workers and, thus, in order to be able to feed on seeds, have larger mandibles than other male ants. Accordingly, the present study revealed that the large heads of male *Pogonomyrmex* are equipped with powerful mandible adductor muscles that are substantially larger than those found in any other male ant examined in the present study, yet slightly smaller than those of female *Pogonomyrmex*.

The mandible closer-muscle fibers arise from lateral, ventral, dorsal, and posterior parts of the head capsule and project towards the large closer apodeme. Like most insect leg muscles, the mandible closer muscle of ants is a bipinnate muscle: at least one velumlike process of the closer apodeme reaches deep into the muscle and accepts muscle fibers on either side. This can be seen in Fig. 2c, f, and g, where muscle fibers attach to the thin part of the apodeme from either side. The angles of attachment vary between muscle fibers and also between species. We found the smallest angles in *Myrmecia* and *Harpegnathos* (about 20°; Fig. 2f, g), while some fibers in *Odontomachus* showed the largest angles of attachment (about 45°). These angles are of functional significance: the smaller the angle between muscle fiber and apodeme, the more effectively can the force generated by the fiber be employed with respect to the main direction of pull (towards the mandible base).

The main part of the closer apodeme has to funnel the force produced by all closer muscle fibers into the mandible base. Accordingly, it is very sturdy and even in small ants its cuticle is sclerotized (hardened) to withstand the forces acting on it. This principal part of the apodeme connects to the inner side of the mandible base via an unsclerotized (hence probably more flexible) thick ligament (Fig. 2a).

Fig. 2. Horizontal sections of heads (**a–c**) and mandible closer muscles of *Pogonomyrmex badius* (**a**), *Atta cephalotes* (**b, e**), *Myrmecia* sp. (**c, f–i**) and *Camponotus rufipes* (**d**) at different magnifications. *Rectangles* in **b** and **c** show approximate areas depicted in **e** and **f**, respectively; *rectangles* in **f** show muscle fibers enlarged in **g** and **h**. *ap*, Mandible closer apodeme, *br*, brain; *ey*, eye; *s*, short-sarcomere fibers; *l*, long sarcomere fibers; *m*, mandible; *sog*, suboesophageal ganglion. *Scale bars:* 250 μm in **a–c**, 100 μm in **d–f**, 20 μm in **g**, 15 μm in **h**, 25 μm in **i**
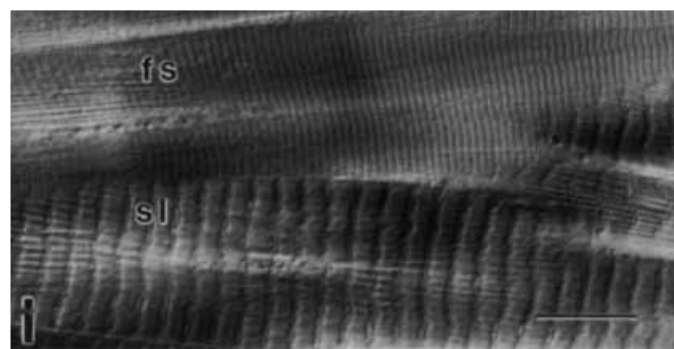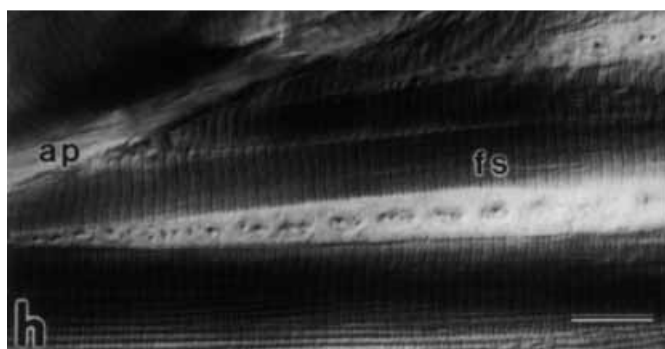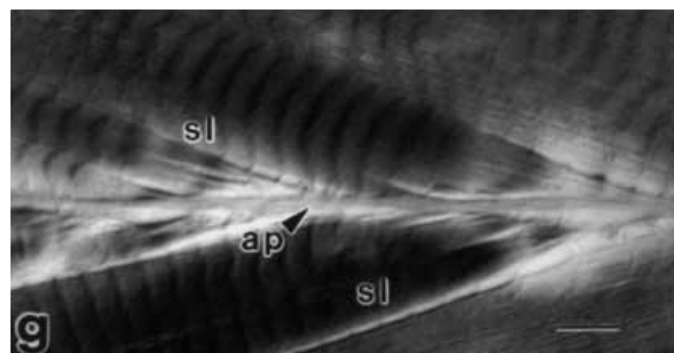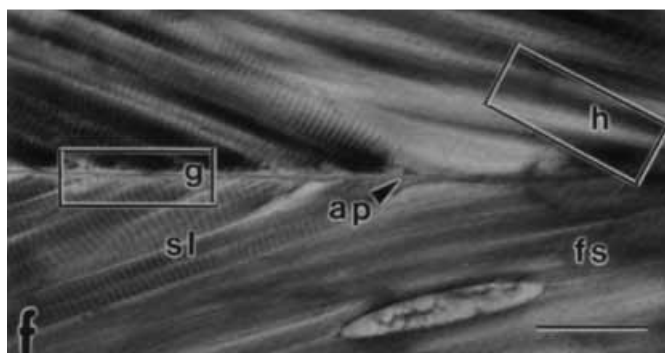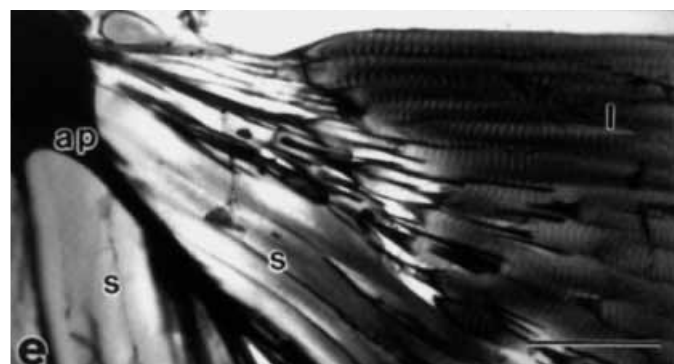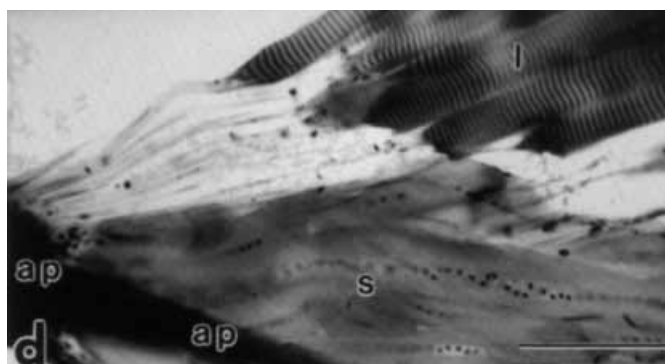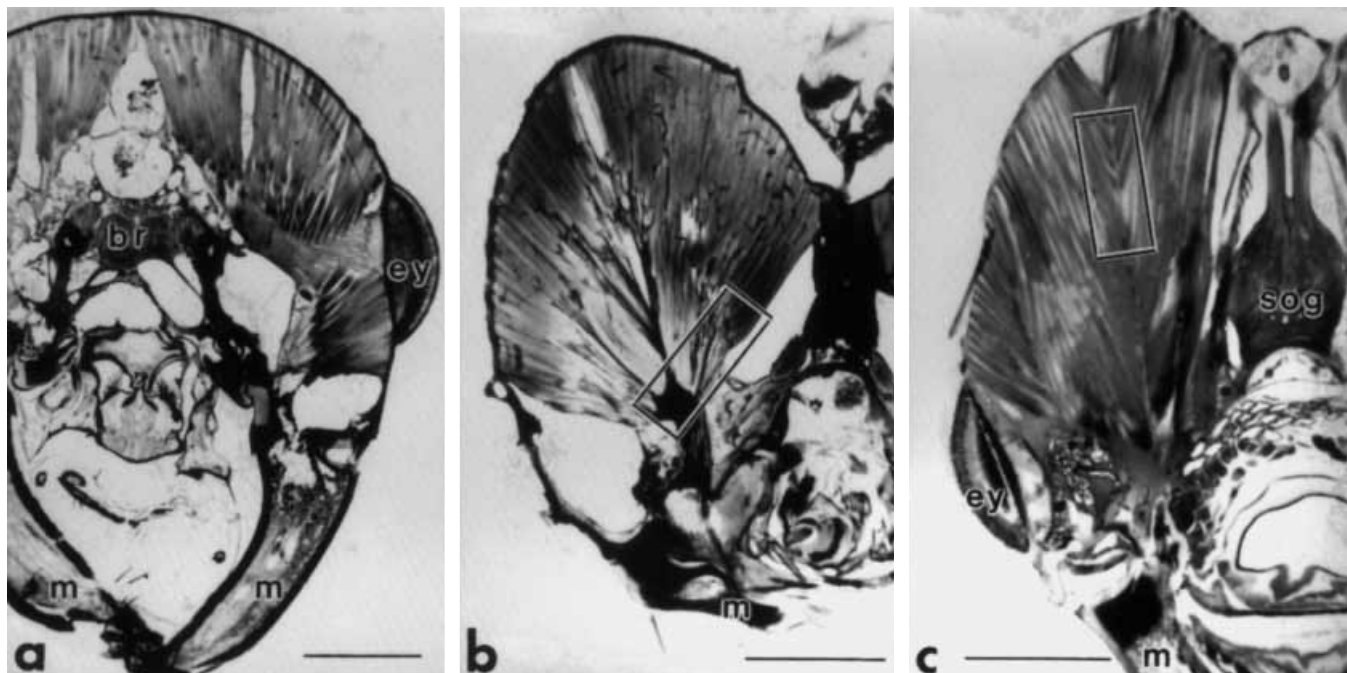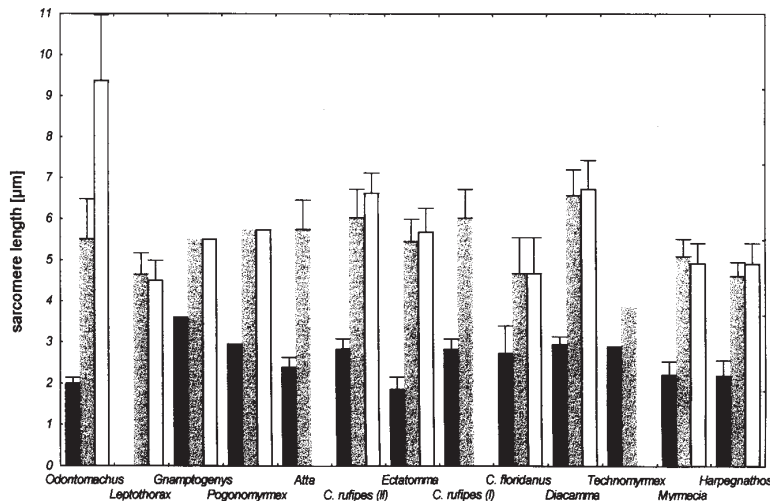
Fig. 3. Sarcomere length of the three different fiber types (*black bars*, direct with short sarcomeres; *open bars*, direct with long sarcomeres; *stippled bars*, thread-attached with long sarcomeres) in different ant species. Mean+standard deviation of 60 fibres (3 animals); bars without standard deviation: mean of 10 fibers (1 or 2 animals); *Camponotus*: *C. rufipes*, major II and minor I. Ant species are arranged according to the proportion of short sarcomere fibers; short fibers in *Odontomachus* refer to the trigger muscle

Closer-muscle fibers

Depending mainly on the size of the ant, the mandible closer muscle may be composed of as little as about 50 fibers (in small ants of the genus *Strumigenys*) or comprise more than 1000 fibers in large ants. While all these fibers connect to a single apodeme and thus belong to the same muscle, they are not morphologically identical. We found three distinct fiber types, all of which are present in most large ants (see below for distribution of fiber types among ant species). The three fiber types differ in their sarcomere length or their cuticular attachment.

The most obvious difference between closer fibers is that some attach directly to the apodeme (to its thick primary part or to the velumlike processes), whereas others attach to a filament originating from the apodeme. Both fiber types can be seen in Fig. 2a, b and, more clearly, in the enlarged photographs (Fig. 2d, e). We refer to the two fiber types as direct fibers and thread-attached fibers, respectively. The second apparent difference among fibers pertains to their sarcomere length.

"Normal" muscle fibers are of the directly attaching type in most animals. In ants and other Hymenoptera, too, most muscles are composed of this fiber type. Even in the mandible closer muscle of most ants, we found a substantial proportion of direct muscle fibers, particularly in some large ponerine ants (*Diacamma*, *Ectatomma*, *Pachycondyla*), where 60–90% of all fibers were of the direct type. They attach directly to the main apodeme or to its velumlike processes (Fig. 2h) without the interposition of cuticular threads.

The most differentiating light-microscopical feature of skeletal muscle fibers is their striation pattern. In any given muscle, the sarcomere length of its component fibers may vary. The sarcomere length is not only a dominant morphological feature, it also bears great functional significance. In general, short sarcomeres are associated with fast contraction, whereas long sarcomeres are associated with high force production.

Interestingly (in contrast to our preliminary findings in wasps and honey bees), we did not find a broad range of sarcomere lengths in ants. Rather, in any particular ant, the closer muscles featured two populations of direct fibers: fibers with short sarcomeres and fibers with long sarcomeres. The differences in sarcomere length can best be appreciated in Fig. 2f, i, where short and long sarcomere fibers ran next to each other. The difference is not always as striking as in this example taken from *Myrmecia* (where the short sarcomeres are less than one-third the length of the long ones), but the qualitative difference between long and short sarcomere fibers is always obvious. This is clearly demonstrated in Fig. 3. Among the species studied, the sarcomere lengths (mean values) of the short fibers range about 2–3 μm, while the long fibers range about 5–6 μm (the trap-jaw ant genus *Odontomachus* will be considered later). In contrast, in the bees and wasps superficially examined, we did not find evidence for two distinct fiber classes (see *Interspecific comparison*).

The two fiber types (short-sarcomere and long-sarcomere type) may also differ in diameter (fibers with short sarcomeres often are slightly thicker), but this difference is not very distinctive. Likewise, the diameter of the central core of the tubular muscle fiber is often larger in fibers with short sarcomeres, but this difference is less pronounced than in other tubular muscle fibers (see Gronenberg and Ehmer 1996).

Besides direct fibers with short or long sarcomeres, a third type is formed by thread-attached muscle fibers. Like the direct ones, thread-attached fibers are rooted in the cuticle of the head capsule. They project towards the

Fig. 4. Transmission electron micrographs of long-sarcomere (**a, c**) and short-sarcomere (**b, d**) muscle fibers of the mandible closer muscle in *Camponotus rufipes* and of the fast trigger muscle of *Odontomachus bauri* (**e, f**). Z-discs of long-sarcomere and short-sarcomere fibers are enlarged in **g** and **h**, respectively; **i** attachment of muscle fiber at the apodeme; **j** threadlike apodeme process. *ap*, Apodeme; *ep*, epidermis (attachment cell); *m,* mitochondria; *mf,* myofilaments; *n,* nucleus; *sr,* sarcoplasmic reticulum; *t,* transverse tubuli; *z,* Z-disc. **a, b, f** cross-sections; **c, d, e, g–j** longitudinal sections. *Scale bars:* 1 μm in **a–d, i, j** 0.25 μm in **e–h**
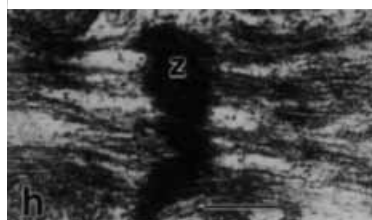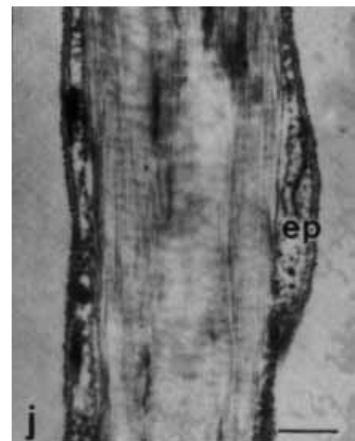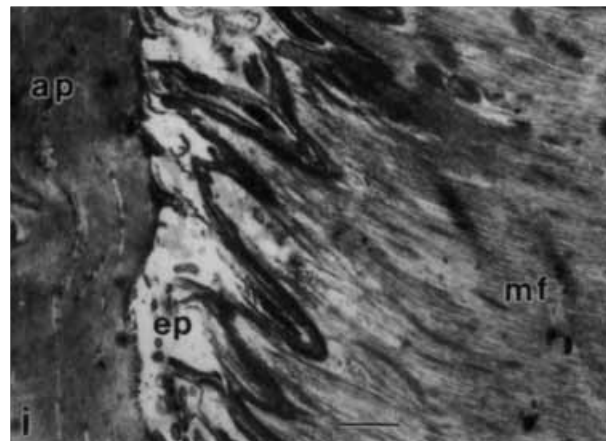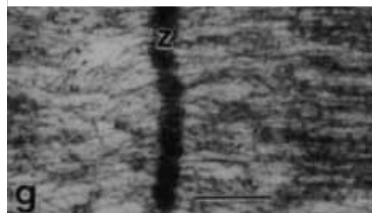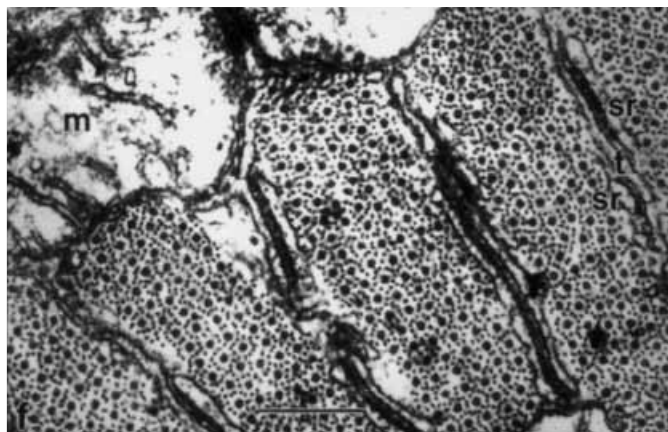
Table 2. Morphological and ultrastructural properties of mandible closer muscle fibers with long or short sarcomeres in the common (*Camponotus*) and a specialized (*Odontomachus*) case

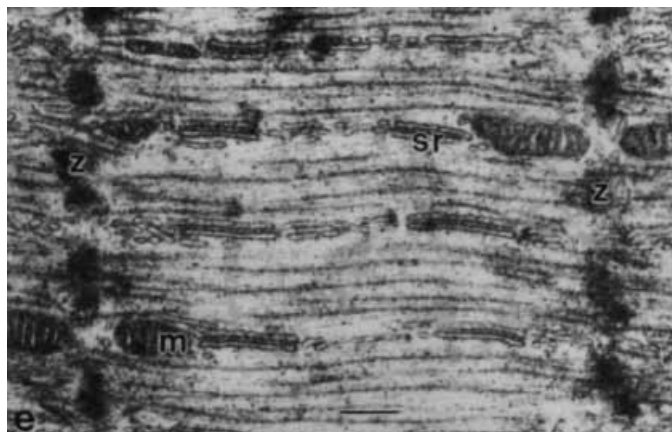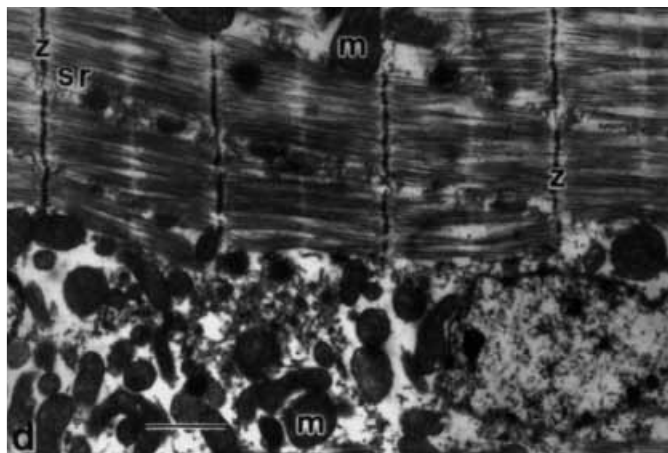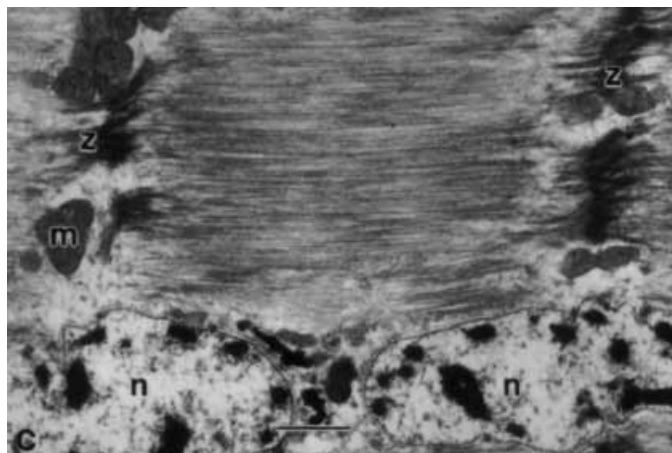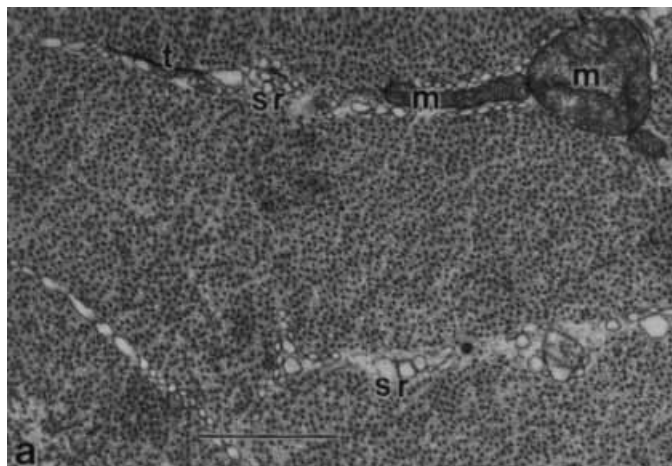|	*Odontomachus*		*Camponotus*	
	Long	Short[a]	Long	Short
Sarcomere length [μm][b]	9.4±1.6	2.0±0.14	5.7±0.6	2.2±1.1
Fiber diameter [μm][b]	35.5±5.4	19.4±2.3	35.2±5.4	49.8±9.5
Lumen diameter [μm][b]	4.5±1.3	9.4±1.1	4.1±0.9	5.9±2.2
Z-disc [μm][c]	0.18	0.11	0.20	0.07
Myofilaments [%][c]	89.0	75.3	83.9	76.1
Sarcoplasmic reticulum [%]	6.7	15.2	10.6	15.1
Mitochondria [%][c]	4.3	9.5	5.5	8.8

[a] Trigger muscle fibers
[b] Light-microscopical data from 30 typical muscle fibers from four animals
[c] Ultrastructural data from 4–7 fibers of a single animal

apodeme, but, before contacting it, they taper into a thread. This thread has a diameter of about 1–3 μm and varies considerably in length. It may only be a few microns long or, in large *Atta* or *Pogonomyrmex* ants, extend more than 500 μm before reaching the main apodeme. The length of the thread depends not only on the species (larger species or individuals in general have longer threads) but also on the position of the muscle fiber. While the two fiber types (direct and thread-attached) are generally clearly distinct, in some ants (e.g., in *Myremcia* and *Pogonomyrmex*), we found a transition between the two types. An example of intermediate fibers in *Myrmecia* is depicted in Fig. 2g: while the muscle fibers face the thin apoderme process, the actual attachment to the apodeme is made by short filaments. In contrast, in the direct fibers proper (Fig. 2h), no such filaments can be seen.

The thread-attached fibers are always of the long-sarcomere type. This can clearly be seen in Fig. 2e (in Fig. 2d only the long sarcomeres can be resolved), and Fig. 3 shows that this is the case in all species examined. With respect to other structural characteristics (diameter of the tubular fiber and of its central core), thread-attached fibers cannot be discriminated from direct fibers with long sarcomeres. At the light-microscopical level, we thus have three distinct closer-muscle fiber types: directly attaching fibers with either short or long sarcomeres and thread-attached fibers with long sarcomeres.

Ultrastructure

Light microscopy indicates that thread-attached muscle fibers and the direct-attaching fibers with long sarcomeres belong to the same fiber type. This is confirmed by electron microscopy. We found no differences between the two fiber classes with respect to their internal organization, sarcomere length, and amount of mitochondria and membrane systems. They differ only by their attachment to the main apodeme.

In arthropods, the epidermal attachment cells that line (and produce) the cuticle are equipped with specializations that ensure firm connection between muscle fibers and cuticle. Interdigitating cell invaginations increase the area of contact between muscle and epidermal cell membranes (Fig. 4i), and the dense intercellular matrix (basal lamina) forms the 'glue' between the adjacent membranes. Microtubules (in earlier literature referred to as 'tonofibrillae,' Richards 1951; not shown in Fig. 4) increase the tensile strength of the tissue, and hemidesmosomes anchor the microtubules to the membrane (Nakazawa 1992; reviewed by Neville 1975). We have not looked for such specializations in the attachment cells, but our low-magnification electron micrographs (Fig. 4i) look almost identical to those published by the aforementioned authors for other arthropods, indicating that the attachment of mandible muscle fibers corresponds to the general type of arthropod muscle attachment.

Longitudinal sections (Fig. 4j) and cross-sections through the attachment threads reveal that the threads are composed of chitin and wrapped by a thin layer of epidermal material. Hence the threads are thin protrusions of the apodeme rather than components of the muscle fiber proper. The muscle fibers connect to the cuticular threads in much the same way as direct-attached fibers are anchored to the apodeme (Fig. 4i) or to the head capsule. The only difference is that, in thread-attached fibers, the apodeme forms a thin thread before it merges with the main body of the apodeme.

We found prominent ultrastructural differences between the fibers with long sarcomeres (whether direct-attached or thread-attached) and those with short sarcomeres. The major fiber characteristics are illustrated in Fig. 4. They are compiled in Table 2 and summarized in the schematic drawing (Fig. 5). The most obvious difference is demonstrated by the cross-sections in Fig. 4. The fibers with long sarcomeres (Fig. 4a) appear less regularly organized, and, more importantly, they contain fewer transverse (T)-tubuli and less sarcoplasmic reticulum (SR). These canal systems separate and wrap around groups of myofilaments (actin and myosin), which can be resolved by the light microscope and are referred to as myofibrils. The myofibrils are much narrower in the short-sarcomere fibers than in those with long sarcomeres (compare Fig. 4a and b). The amount of the two membrane systems is tightly linked to the speed of muscle activation. T-tubuli propagate the electrical excitation of a muscle fiber and communicate with the SR in a still uncertain way [via mechanical or electrical
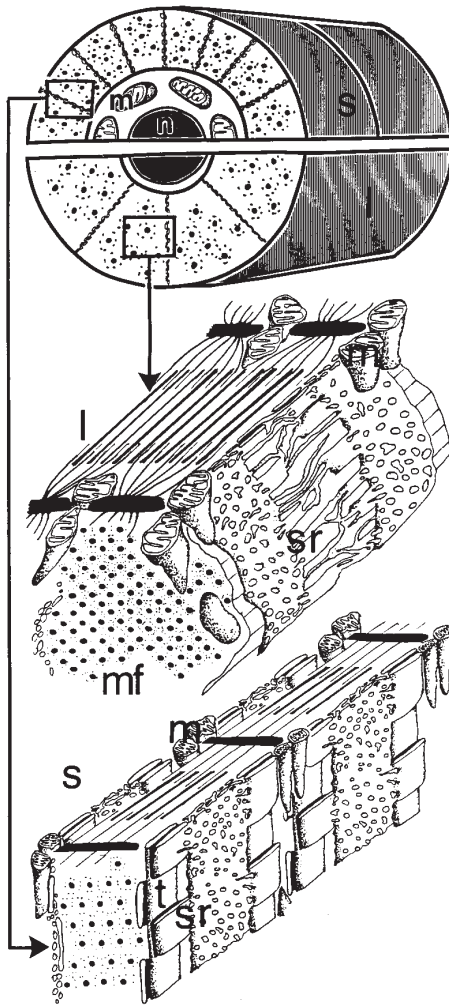
Fig. 5. Schematized drawing emphasizing the differences between mandible closer muscle fibers with short (*s*, upper half of top overview) and with long sarcomeres (*l*, lower half of top overview). *Insets* show details of the respective fiber types. *m*, Mitochondria; *mf*, myofilaments (actin and myosin); *n*, nucleus; *sr*, sarcoplasmic reticulum; *t*, transverse tubuli

calcium released by the bordering SR has to diffuse only about 150 nm from either side to reach (and activate) all myofilaments. In *Odontomachus*, the trigger muscle's specialization for speed coincides with an opposite specialization of the mandible closer muscle (Table 2). The closer muscle is composed entirely of fibers with particularly long sarcomeres containing a higher amount of myofilaments and less SR than any of the mandibular muscles examined. In this trap-jaw ant, we probably find the most advanced division of labor with respect to mandible muscle fiber function. Fibers with short or long sarcomeres are not only more distinct than in other ants, they even form two separate muscles.

Fig. 4f also nicely shows the regular organization of fast fibers: each T-tubule is flanked by a SR cistern either on its right or left side. The dark line between the two adjacent cisternae probably contains the proteins involved in SR activation. This arrangement, as seen in cross-section in Fig. 4e, is called a dyade (as opposed to the triade found in vertebrates; there, each T-tubule is lined by two SR cisternae). While the design is essentially the same in long-sarcomere fibers, their relative among of T-tubuli and SR is not only smaller, but they are also less regularly organized in these slower fibers (Fig. 4a).

In both fiber types, mitochondria are interspersed among the myofibrils, often (but not always) residing close to the Z-discs (Fig. 4c, e; 5). In addition, the "fast" fibers contain part of their mitochondria within the central lumen of the tubelike fibers together with the nuclei (Fig. 4d, 5). This is most conspicuous in the fast trigger-muscle fiber of *Odontomachus*, where more than two-thirds of all mitochondria are concentrated in the central fiber core. Another difference between long- and short sarcomere fibers is demonstrated by Fig. 4g and h. The Z-discs of the short-sarcomere fibers are thinner and more regular than those of the long-sarcomere fibers. This may affect the mechanical properties of the fibers. If the proteins composing the Z-discs are elastic (van Leeuwen 1991), thick Z-discs of the long-sarcomere fibers would function like serial springs and result in an (even) lower overall contraction of these fibers.

Interspecific comparison

Ants differ not only with respect to the sarcomere length of their mandible closer muscle fibers (Fig. 3) but also in the proportion of the different fiber types. Figure 6 shows a selection of schematized views of the heads of ants and their mandible closer muscles. These drawings represent sections in the mid-frontal plain and roughly reflect the distribution of the muscle fiber types. However, since the distribution is not homogeneous throughout the entire head (some fibers may be more abundant frontally, whereas others may reside in more caudal parts of the head), these drawings are not a quantitative rendering of the fiber distribution. Figure 6 also shows that the different fiber types do not occur randomly comingled but form homogeneous fiber groups.

mechanisms probably involving ryanodine or dihydropyridine-receptors or calcium gating (Iuni et al. 1987; Rios and Brum 1987; Block et al. 1988; Lai et al. 1988; Fleischer and Iuni 1989; Rios et al. 1991)]. The SR cisternae in turn control the myosin-actin interaction via the calcium concentration (Peachey 1985).

Sarcomere length and the high proportions of SR and T-tubuli both strongly suggest that the fibers with short sarcomeres are of a much faster-contracting type than the other fibers. The difference is particularly apparent when comparing long-sarcomere fibers (Fig. 4a, c) to those of the trigger muscle of the trap-jaw ant *Odontomachus* (Fig. 4e, f). The trigger muscle is known to be an unusually fast muscle (Gronenberg 1995), and the myofibrils composing its muscle fibers are narrower than those of any other mandibular muscle fiber (compare Fig. 4b and f; note the higher magnification of Fig. 4f). The trigger muscle myofibrils are only about six myofilaments (acto-myosin complexes) wide, so that
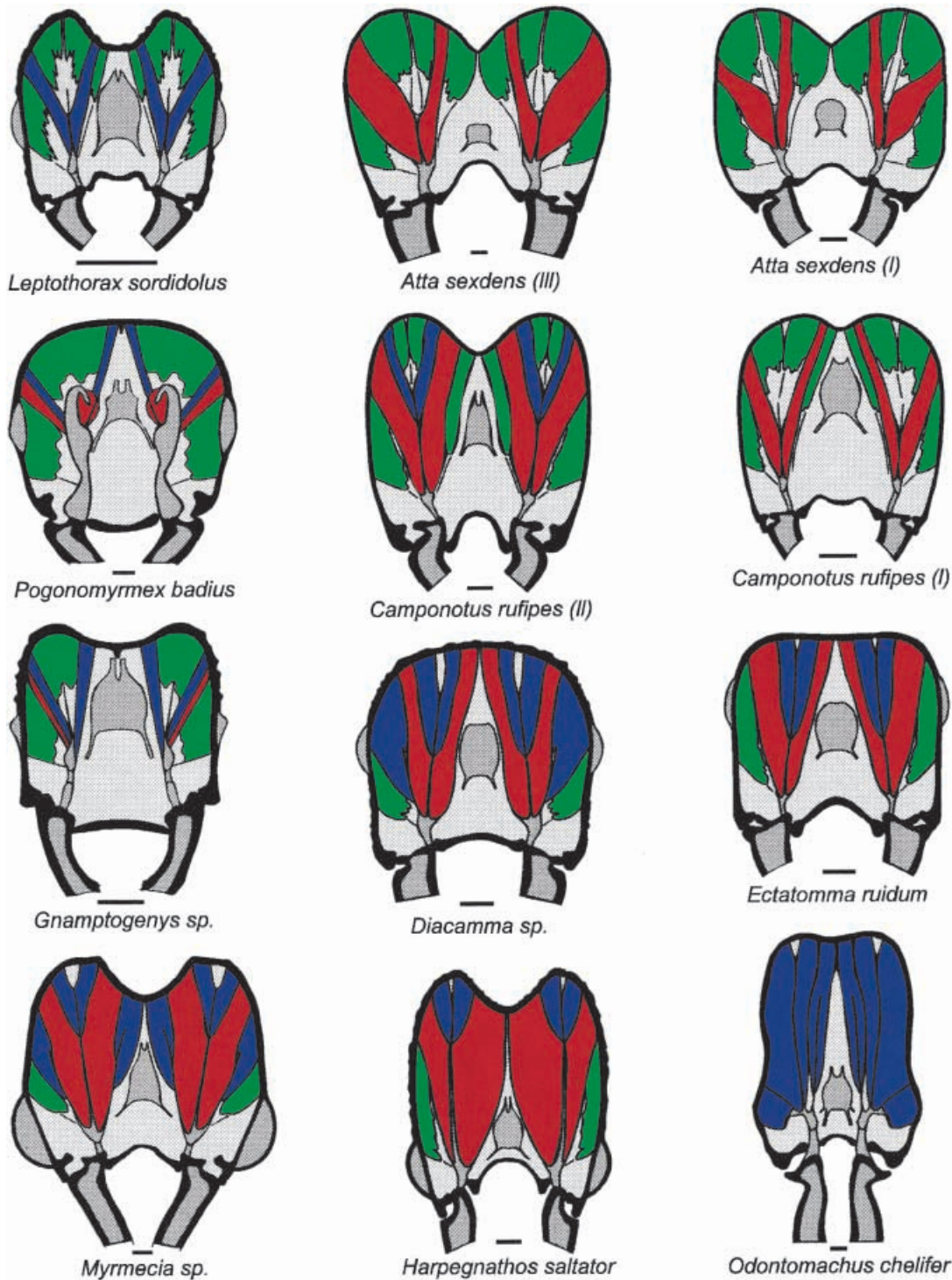
Fig. 6. Schematized drawings of mandible closer muscle fiber groups of selected ant species. Each drawing represents the fiber composition of several mid-frontal sections at the level of the suboesophageal ganglion (*crosshatched*), but does not reflect the amount of fibers located more frontally or more caudally in the head. Arrangement of ant species reflects the decreasing amount of thread-attached muscle fibers. *Solid black*, cuticle; *crosshatched* mandibles, eyes and closer apodermes; *green*, thread-attached muscle fibers with long sarcomeres; *red* direct fibers with short sarcomeres; *blue*, direct fibers with long sarcomeres; head width *lll*; 3–5 mm; *ll*, 1.5–3 mm; *l*, 1–1.5 mm. *Scale bar:* 250 μm

The drawings in Fig. 6 demonstrate the large variation in fiber composition. Most ants have all three fiber types in their closer muscle, but in the small *Leptothorax gredleri*, we found no fibers with short sarcomeres. In *Atta sexdens* and small individuals of *Camponotus rufi-* *pes* and of *c. floridanus* (not shown), all fibers with long sarcomeres are thread-attached. In the ponerine trap-jaw genera *Odontomachus* and *Anochetus* (not shown; see Gronenberg and Ehmer 1996), almost all fibers are of the direct type with long sarcomeres, whereas in the
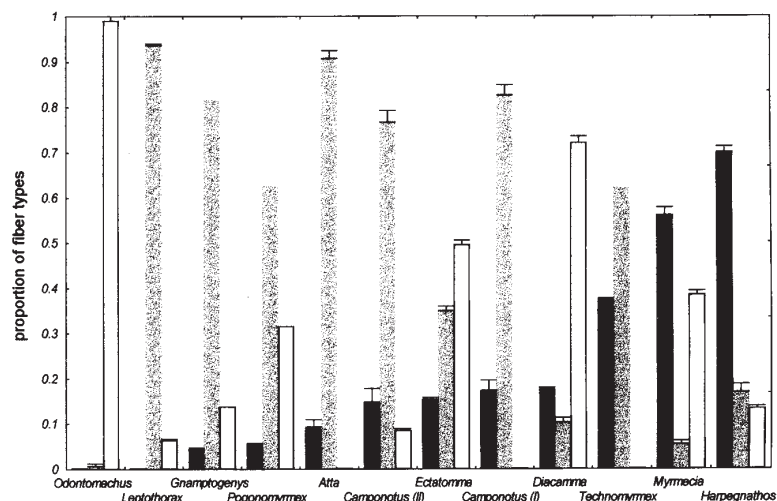
Fig. 7. Ratio of the three closer muscle fiber types (*black bars*, direct with short sarcomeres; *open bars*, direct with long sarcomeres; *stippled bars*, thread-attached with long sarcomeres) in different ant species. Mean+standard deviation (3 animals); bars without standard deviation: mean (1 or 2 animals); *Atta*: mean and standard deviation (2 majors and 2 minors); *Camponotus*: *C. rufipes*, 3 majors (*ll*) and 2 minors (*l*). The organization of ant species on the *abscissa* reflects the increasing proportion of short sarcomere fibers

myrmicine trap-jaw ants *Strumigenys* (not shown), almost all closer fibers are thread-attached (Gronenberg 1996c). Despite the large variability in fiber composition, Fig. 6 shows that one condition remains constant: the fibers with short sarcomeres (if present) always form two groups attached to the central part of the apodeme in a V-like fashion. These groups always comprise the longest fibers and have the most effective angle of attachment with respect to the resulting mandible movement (see Discussion). The short-sarcomere fibers are flanked by groups composed of shorter fibers with longer sarcomeres.

In Fig. 7, the ant species are arranged according to their proportion of short-sarcomere fibers, because the latter correlate with mandible velocity and are probably essential for fast movements (see Discussion). Regarding the long-sarcomere fiber types (direct and thread-attached), we found no general principle that would explain their occurrence and distribution. However, different trends may be involved in the dominance of one of the two fiber types:

In our sample of species, myrmicine (e.g., *Atta* or *Leptothorax*) and formicine ants (e.g., *Camponotus*) generally had more thread-attached fibers than ponerines (e.g., *Ectatomma* or *Diacamma*), indicating possible phylogenetic differences. Likewise, smaller ants appear to have a higher proportion of thread-attached fibers than larger ants (compare large and small individuals of *Camponotus rufipes* in Figs. 6 and 7), indicating a correlation of head size or head geometry with fiber distribution. In addition, dietary preferences seem to affect the fiber composition (compare seed-cracking *Pogonomyrmex* or leaf cutting *Atta* with predatory *Diacamma*, *Ectatomma*, or *Myrmecia* in Figs. 6 and 7). However, there are exceptions to all these trends and we will refer to this problem in the Discussion.

Thread-attached muscle fibers also occur in other hymenopterans. We found many such fibers in the digger wasp *Crabro* sp. but only very few in the honey-bee *Apis mellifica* or in *Vespa saxonica* and none in the wasps *Paravespula germanica* and *Polistes* sp. More significantly, we did not find two mandible closer-muscle

fiber types with distinct sarcomere lengths in any of these hymenopterans. Their closure-muscle sarcomeres are slightly shorter but well within the range found for the long sarcomeres of ants: *Apis mellifica* 3.95±1.5 μm (*n*=17), *Vespa saxonica* 4.2±0.7 μm (*n*=6), *Paravespula germanica* 4.7±0.6 μm (*n*=7), *Polistes* sp. 5.5±1.3 μm (*n*=17), *Crabro* sp. 4.4±0.7 μm (*n*=9). This systematic difference hints at phylogenetic origins of the dichotomy of ant mandible closer muscle fibers.

Discussion

Fast movements and fast-muscle fibers

We have shown that many ants are able to perform fast jaw movements. Particularly fast mandible closure movements were established in predatory ants such as *Myrmecia* or *Harpegnathos*. Obviously, the ability to perform fast movements is important for predators, because their prey will not stay put and wait for the mandibles to close upon them. Trap-jaw ants employ a catapult mechanism, which is even faster and does not rely on fast mandible closer muscles (Gronenberg 1995a, b, 1996a; Gronenberg and Ehmer 1996b). Interestingly, *Camponotus floridanus* was among the fastest ants of our sample with respect to mandible closure. *Camponotus floridanus* is not a specialized predator although it preys on insects, too. But fast jaws are not only prey-catching tools. Like the venomous stings or protective secretions found in most ant subfamilies (Hölldobler and Wilson 1990), fast mandibles make an excellent defensive device, which enables ants to protect themselves from other predators or to attack competitors.

The main question of the present study was whether there were any morphological specializations underlying the fast mandible movements of ants. Obviously, the large size of the mandible closer muscle is an indication for its functional significance in almost any ant worker. In the leaf-cutting ant *Atta sexdens*, the mandible closer muscle has a very high metabolic rate approaching that of insect flight muscle, and cutting leaves consumes al-
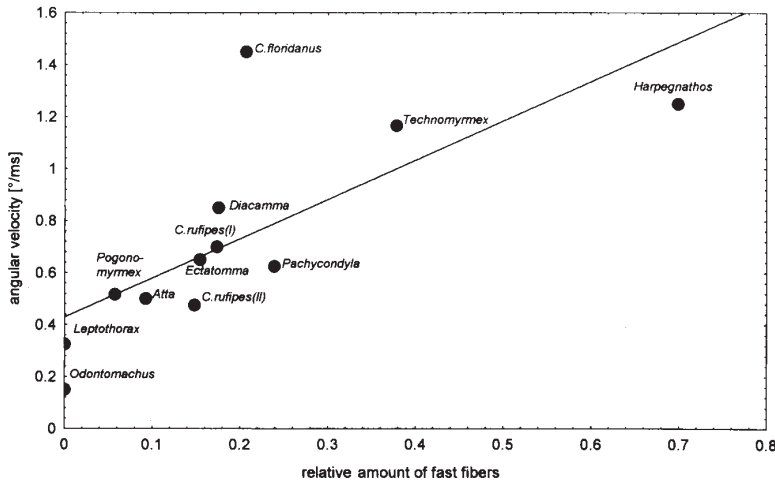
Fig. 8. Correlation between the angular mandible velocity (*ordinate*) and the amount of fast muscle fibers in the mandible closer muscle (*abscissa*) of different ant species. *l* and *ll* refer to the head width as defined in Fig. 6; linear regression: $y=0.43+1.51\ x$

most ten times as much energy as walking does (Roces and Lighton 1995). Based on the morphology, we think that activating the mandible muscle is energetically expensive in other ants, too. By the same token, ant males, which do not depend on their mandibles as much as workers, have very small mandible closer muscles. Likewise, our qualitative observations show that honey-bees have smaller closer muscles than ants (see also Snodgrass 1942), because, in bees, the mandibles do not need to be very powerful. But neither the size of a muscle nor its energy consumption reveals much about its velocity. Since almost all ants have large mandible muscles, the question of the differences between the mandible closer muscles of ant species with fast and slow jaws remains to be answered.

The sarcomere length may provide a clue to this question. In principle, muscle fibers with short sarcomeres can shorten faster than ones with long sarcomeres (O'Connor et al. 1982; Costello and Govind 1983; Stephens et al. 1984; Günzel et al. 1993), because the more sarcomeres that contract in series, the more the entire fiber will shorten in a given time (in addition, the molecular composition strongly determines a fiber's contraction velocity). Our ultrastructural findings confirm that the short-sarcomere fibers are of the fast contracting type (high amount of SR and T-tubuli). Additional factors that also control the contraction velocity of muscle fibers (e.g., enzymatic composition, glycogen content, or the kind and pattern of innervation, see Jahromi and Atwood 1969, Cochrane et al. 1972; Stokes et al. 1975; Govind and Atwood 1982; Josephson and Young 1987; Rathmeyer and Maier 1987; Müller et al. 1992) have not been examined in the present account. Previous studies show, however, that the characteristics of fast muscle fibers established for other arthropods apply to ants, too (Gronenberg and Ehmer 1995; Ehmer and Gronenberg 1996). Moreover, histochemistry suited to visualize myofibrillar ATPase activity revealed that the mandible closer muscle of *Camponotus rufipes* is composed of only two fiber types (Bonness 1995). The two mATPase-activity types coincide exactly with the short-sarcomere and long-sarcomere types, respectively, of the present study.

Taken together, there is convincing evidence that the short-sarcomere and the long-sarcomere fiber types in ant mandible muscles are distinctly specialized fast and slow fibers, respectively. While the absolute difference in sarcomere length between fast and slow fibers is apparent in all ants (except in *Technomyrmex*, where the slow fibers also have very short sarcomeres; see Fig. 3), we found no correlation between sarcomere length and movement velocity that would hold for all ant species examined. It appears that mandible muscles specialized for fast contraction (e.g., in *Harpegnathos*, *Myrmecia*, and *Camponotus floridanus* in Fig. 3) feature reduced sarcomere length in both fast and slow fibers, thus probably increasing overall contraction velocity. However, more species with different mandible movement velocities need to be examined to confirm this trend.

The major feature distinguishing ant species with fast or slow mandible movements is probably not the overall sarcomere length. Instead, we propose that the presence and quantity of fast muscle fibers determines the maximal velocity of a given species' mandible movement. Likewise, the peak velocity of antennal movements is correlated with the presence of a particularly fast fiber type in ants (Gronenberg and Ehmer 1995; Ehmer and Gronenberg 1996). In Fig. 8, the angular velocity of the mandible is plotted against the relative amount of fast (short-sarcomere) fibers in the closer muscle. Even though there is scatter around the regression line, we think that the trend is apparent: the higher the proportion of fast muscle fibers, the faster the mandible movement. The scatter in Fig. 8 can be explained by the fact that mandible velocity also depends on other factors besides muscle fiber composition:

1. Size and mass of the mandibles; obviously it takes more power to accelerate the long mandibles of *Myrmecia* and *Harpegnathos* than the smaller ones of *C. rufipes* (depicted in Fig. 1b, c, and d, respectively).
2. Overall size of the closer muscle significantly contributes to the acceleration; even if entirely composed of fast muscle fibers, a very small muscle could not move the mandible appropriately.

3. Mandible joint geometry and the lever arm of the closer muscle, which we have not examined, determine the resulting acceleration.

The fast mandible muscle fibers are grouped together and form a system separate from the 'normal' (slow) fibers and specifically designed for speed. We think that these specialized fast fibers are the origin of the trigger muscle of ponerine trap-jaw ants, in which these fibers form a separate, very fast muscle (Gronenberg 1995; Gronenberg and Ehmer 1996). In trap-jaw ants, the remaining closer muscle is devoid of any fast fibers (see *Odontomachus* in Fig. 6).

The fast fibers are the longest mandibular muscle fibers, which gives them an additional advantage with respect to speed of action: the absolute number of serial sarcomeres determines the resultant shortening. The absolute amount by which a muscle shortens per unit time determines the speed of the movement, hence the longer the fiber, the faster the movement it generates. Cuticular threads shorten the effective muscle fiber length and thus reduce the overall shortening of the fiber and the speed of the movement. In addition, the fast fibers always attach directly to or close to the most rigid part of the apodeme (see Fig. 6), ensuring good mechanical transmission of their fast contraction (thin elastic structures would diminish the temporal properties; see below). Moreover, the fast fibers' angle of attachment is optimized so that their energy can be employed most efficiently.

Slow movements

The mandible closer muscle is special in that it has only two distinct fiber types, even though it is the largest muscle in ants. In contrast, the muscles that move the extremities of other arthropods are commonly composed of morphologically, histochemically, and physiologically different fiber types (Hoyle 1974, 1978; Rathmayer and Maier 1987; Müller et al. 1992). The antennal muscles of ants agree with this type: they comprise different fibers ranging from very slow to very fast types (Gronenberg and Ehmer 1995; Ehmer and Gronenberg 1996).

Unlike antennae in ants or legs in insects in general, the mandibles of ants are primarily slow moving limbs. All the principal functions of ant mandibles, such as grinding wood, cutting prey or tough leaves, cracking seeds, or digging in the soil, require powerful muscular action but represent relatively slow activities. Likewise, food exchange, grooming, nursing, cleaning the antennae, or carrying eggs, pupae, or nestmates are delicate actions that require precise control and cannot be performed rapidly. Accordingly, the mandibles are controlled by essentially slow muscle fibers.

To this basic design (which we also found in the honey-bee and in the few wasp species examined), in many ants the set of fast muscle fibers described in the previous section is added to provide the means for additional fast movements. All the slow movements listed above are probably performed by the many slow fibers, which,

in all ants except *Harpegnathos* and *Myrmecia* (see Figs. 6, 7), are the major part of the mandible closer muscle.

Apart from their type of attachment (which will be discussed below) and in contrast to other large arthropod muscles, the slow mandible closer-muscle fibers form a homogeneous fiber group. This raises the question of how such a uniform fiber mass can generate so many nuances of force and movement. We think that the control of all slow mandible movements is based mainly on neuronal mechanisms rather than on muscle fiber characteristics. While the neuronal control is not the subject of the present account, we will briefly list some interesting observations that can explain the subtle control of the slow mandible closer-muscle fibers:

1. The ant mandible closer muscle is supplied by an unusually large number of motor neurons. Histological observations indicate that it is controlled by 6–10 motor neurons, depending on species (Bonness 1995; Gronenberg 1996a and unpublished). Irrespective of their precise number, the closer muscle is controlled by more motor neurons than other arthropod muscles. This set of motor neurons probably includes fast, slow, and inhibitory units and enables the central nervous system to finely tune its controls of the muscle.
2. This control is supported by sensory feedback to the central nervous system. Hairs and bristles (and probably also pressure-sensitive receptors; Gronenberg and Tautz 1994) located on the mandibles send their sensory afferents into the neuropile of the suboesophageal ganglion, which comprises the motor neuron dendrites. These sensory afferents most likely establish synaptic contact with the mandible motor neurons (which has been shown in *Odontomachus* for a particular subset of mandibular neurons by electron microscopy; Gronenberg 1996a). In addition, an internal muscle receptor organ analogous to the vertebrate muscle spindle seems to assess the tension of the mandible closer apodeme (W. Gronenberg, unpublished observation). All this sensory and proprioceptive information is integrated by the many motor neurons, which can thus adjust the muscle force output to meet the requirements for powerful bites as well as tender broodcare.
3. We have preliminary electrophysiological data suggesting that, during normal (slow) mandible operation, the mandible closer and opener muscles may be coactivated. Balancing the activity of the antagonistic muscles would result in yet another way of subtle control of the mandible force and velocity. In addition, the fast closer-muscle fibers may also be recruited during slow actions, e.g., if maximal mandibular strength is required.

Hence, it is evident that the mandibles can perform their wide range of activities even with a very limited set of muscle fiber types.

Thread-attached muscle fibers

Thread-attached fibers are not unique to ants. We found a few such fibers in the mandible closer muscle of the honey-bee and many more of them in the digger wasp

Crabro. It is well known (Gullan and Cranston 1994) that, in insects, muscle fibers may be attached to thread-like processes of the apodeme, sometimes referred to as apophyses. In ants, this fiber type has been morphologically described for the mandible closure muscle by Janet (1905, 1907a, b), but we are not aware of any discussions of the functional significance of these cuticular threads for any insect. Since we have looked at a broad sample of ants with widely varying numbers of thread-attached muscle fibers, it seems worthwhile to speculate about their function.

Our results indicate that only slow fibers are attached to the apodeme threads. Fibers with long sarcomeres (slow fibers) can produce higher forces (because more cross bridges are active in parallel; Huxley 1965; Huxley 1974), indicating that the cuticular threads are suited to withstand even the high strain acting on them when the slow fibers contract. However, these filaments are probably more elastic than the massive cuticle of the apodeme. They do not appear to be sclerotized (hardened) and, more significantly, due to their small diameter and their great length, the threads may be stretched considerably by the muscular force in the same way a rubber band is when loaded. Gullan and Cranston (1994) indicate that thin apodeme strands may even contain resilin, a rubberlike protein that would further increase the springiness of the threads. The supposed elasticity of the attachment threads would result in altered temporal properties, in which the threads could act like springs and delay the force transmission from fast muscle fibers into the mandible joint. This would destroy the advantage of fast muscle fibers. We think that, for the same reason, the Z-discs in the fast fibers are thinner (less elastic) than in the slow fibers (see Fig. 4g, h).

An elastic design would not, however, affect the properties of slow muscle fibers. For their function, a serial spring (the apodeme thread) could even be advantageous: the elasticity might protect the mandibles from damage when they snap shut on a very hard object. As the bumper in a car dissipates mechanical energy by deformation, the high power of the mandible muscle would stretch the apodeme threads rather than breaking the mandibular teeth.

Elastic properties of the thread and a slower movement resulting from a decrease in the effective muscle fiber length probably explain why only slow fibers are attached to cuticular threads. But why have such fibers evolved in the first place? Intuitively, it would appear more efficient to fill the entire head space with muscle fibers rather than to carry about inactive cuticular threads. But to use the head capsule volume most efficiently, ants are faced with a geometrical problem: muscle fibers need about the same attachment area at the apodeme as they need at the head capsule. Because of the curvature of the head, the apodeme surface is smaller than the head surface, hence fewer muscle fibers can attach directly to the apodeme than to the head capsule.

In elongate heads (Fig. 9a), head wall and apodeme run in parallel over longer distances, thus allowing for more muscle fibers to attach directly. Hence the elongation of the head appears to be an adaptation to accommo-
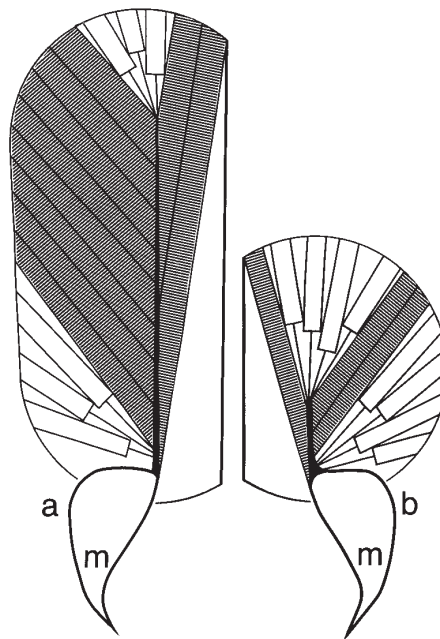

Fig. 9. Schematic drawing demonstrating how the best use can be made of the available space employing direct (*hatched*) and thread-attached fibers (*open profiles*) in **a** elongate heads and **b** broad heads; *m*, mandible

date direct attachment of muscle fibers. Still, at the rear of the head and beside the mandibles, not enough apodeme surface is available for the fibers to anchor. Some muscle fibers can only be attached via threads. Elongate heads are most often found in fast predators, such as *Harpegnathos* or *Odontomachus* in Fig. 6. Long heads minimize the need for thread-attached fibers and at the same time allow particularly long muscle fibers; both circumstances facilitate fast movements (see above).

When power, as opposed to speed, is the principal requirement of a muscle many muscle fibers should act in parallel. This requires a broad head such as sketched in Fig. 9b and exemplified by *Atta sexdens* in Fig. 6. These ants depend on powerful mandible action for cutting tough leaves and plant material but do not perform fast movements. Many other ants also have outward-bulging occipital heads to accommodate the many muscle fibers required. Most of their muscle fibers are thread-attached, because, in a short (or broad) head, the apodeme surface is much more limited than in elongate heads (compare Fig. 9a and b). Accordingly, only very few muscle fibers can attach directly at the relatively small apodeme; the vast majority has to be thread-attached (Figs. 6, 7), because all threads can radiate outwards from a single attachment point. The attachment threads may also have another advantage: they are more flexible and can easily follow movements of the apodeme in directions other than their own direction of pull. Such movements occur close to the mandible base when the apodeme is pulled inwards by the bulk of the other muscle fibers.

We conclude that thread-attached muscle fibers represent an adaptation to make the best use of the space available in the head capsule. Unlike direct fibers they are not suited for fast contraction. The mode of fiber at-

tachment is reflected by the head geometry and leads to a simple rule of thumb: ants with long and slender heads can move their mandibles fast (and are most often predatory), while ants with broad heads are able to develop higher mandibular forces.

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