

THE TRAP-JAW MECHANISM IN THE DACETINE ANTS *DACETON ARMIGERUM* AND *STRUMIGENYS* SP.

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Accepted 7 May 1996

Summary

Ants of three different subfamilies, among them the tribe Dacetini, have evolved very fast snapping mandibles called trap-jaws. The two dacetine genera examined, the large *Daceton* and the small *Strumigenys*, employ the same mechanism for their mandible strike. Video analysis reveals that, in *Strumigenys* sp., the strike takes less than 2.5 ms. It is released within 5 ms by contact of trigger hairs on the labrum. The ants employ a catapult mechanism to generate such a fast movement. Before the strike, the mandibles are opened wide and locked in the open position by the labrum, which functions as a latch. They stay open even when the large slow closer muscles contract. Upon trigger hair stimulation, the labrum is pulled backwards by

a small, fast trigger muscle. The mandibles are thus freed from the catch and close rapidly. This reflex is controlled by giant sensory and motor neurones in the labral neuromere that are probably monosynaptically coupled. The short latency of the reflex thus results from the combination of a catapult mechanism, fast trigger muscles, high neuronal conduction velocities and small synaptic delays. Comparison with the trap-jaw mechanism of the ant genus *Odontomachus* reveals a remarkable example of convergent evolution.

Key words: *Daceton armigerum*, *Strumigenys* sp., trap-jaw mechanism, ants, reflex pathway.

Introduction

Speed is a particularly significant factor in the evolutionary struggle for fitness. The ability to escape quickly from a predator is vital for most prey animals, while predators have obvious advantages if they are able to outrun fast prey and overpower it using even faster weapons. The speed of running, jumping, predatory strikes, etc. is generally correlated with the animal's size. In order to achieve velocities comparable to those of larger animals, small ones such as most arthropods have to rely on very high accelerations (Alexander, 1988). Therefore, in many insects, the speed of action reaches or even surpasses the velocity limitations inherent to muscle contraction. Irrespective of phylogenetic relationships, convergent evolution has resulted in special mechanical designs (e.g. springs or catapults; Alexander, 1995) that overcome the constraints of muscle action in many arthropods. In addition to fast mechanics, both prey and predators rely on rapid neuronal and muscular systems to initiate and control their swift escape or predatory actions.

Among the ants, several species employ particularly fast mandible strikes in order to catch swift prey or to defend themselves. This so-called trap-jaw mechanism (a mandible strike which far exceeds the speed allowed for by muscular contraction) has evolved independently in three ant subfamilies: the ponerine genera *Odontomachus* and *Anochetus*, the formicine genus *Myrmoteras*, and the

myrmicine tribe Dacetini comprising 24 genera, among them *Daceton* and *Strumigenys*. In the genus *Odontomachus*, the morphology, physiology and neuronal control of the trap-jaw mechanism have recently been examined in some detail (Gronenberg *et al.* 1993; Gronenberg and Tautz, 1994; Gronenberg, 1995*a,b*). These studies reveal that the fast strike results from energy storage in a catapult design, and its control relies on a monosynaptic pathway of giant neurones and on a trigger muscle specialized for high contraction velocity.

Likewise, many dacetine genera are able to close their long mandibles very rapidly. The similar trap-jaw action of *Odontomachus* and the dacetine genera *Daceton* and *Strumigenys* makes it worthwhile to look for functional similarities and equivalent structures between the dacetine and odontomachine trap-jaw mechanisms. In the genus *Odontomachus*, the system is composed of structures exclusively associated with the mandibles (mandibular muscles, sensilla and neuromeres of the central nervous system). For the dacetine genus *Strumigenys*, however, Brown and Wilson (1959) and Masuko (1984) have suggested a different mechanism involving the labrum as a catch mechanism and labral hairs as a trigger for the strike. For ants of another dacetine genus, *Acanthognathus*, Dietz and Brandao (1993) suggest yet another mechanism: the mandible strike might result from the contraction of the closer muscle alone.

In the present study, the mechanics and muscles involved in the trap-jaw action of two dacetine genera, *Daceton* and *Strumigenys*, are characterized in detail and the conclusions of Brown and Wilson (1959) and Masuko (1984) are corroborated. In addition, the neuronal network which controls the trap-jaw reflex in *Strumigenys* sp. is described and compared with that of the genus *Odontomachus*. This account demonstrates how different structures are employed for the same purpose: to generate and control a very fast and powerful mandible movement. It is the aim of the present study to show that, by convergent evolution, structures can be adapted to serve a particular function and that, during this process, they may become very similar irrespective of their independent origin.

Materials and methods

Strumigenys sp. were collected at Gigante, Lake Gatun, Panama, and on the Keys, Florida, USA. The colonies were fed on collembolans (springtails) and were kept in the laboratory according to Carlin (1981) and Hölldobler *et al.* (1990). Alcohol-preserved specimens (majors and minors) of *Daceton armigerum* Perti were provided by B. Hölldobler and were collected at the Imataca Forest Reserve, Venezuela (Hölldobler *et al.* 1990).

Prey-catching behaviour of unrestrained *Strumigenys* sp. was observed in a foraging arena with a high-frequency video camera and electronic strobe light (NAC HSV400) at 200 and 400 frames s⁻¹ (strobe exposure duration, 20 µs).

The external morphology of the head, mandible and mandible joint of *Daceton armigerum* and *Strumigenys* sp. was examined using scanning electron microscopy of critical-point-dried specimens using a Zeiss DSM 962 scanning electron microscope.

The organization of the muscles, apodemes and nerves within the head was studied from sectioned material (*Daceton armigerum*: 15–25 µm; *Strumigenys* sp. 5–10 µm) stained either with Methylene Blue (1–4 h in a 0.2 % aqueous solution of Methylene Blue, fixation in 12 % ammonium molybdate) or by block-silver impregnation (fixation in ammoniacal ethanol, impregnation in 4 % aqueous silver nitrate solution for 6 days, development in 4 % pyrogallol for 6 h). In *Strumigenys* sp., the neuroanatomy was further examined on aldehyde-fixed material stained with osmium-ethyl gallate (staining and sectioning techniques detailed in Gronenberg 1995a,b). In addition, sensory afferents originating from the labral trigger hairs of *Strumigenys* sp. were retrogradely labelled with a fluorescent dextran tracer (Fluoro Ruby; Molecular Probes). The dye was applied to the stumps of the cut sensilla and, after diffusion periods of 2–6 h, the heads were processed according to standard routines [paraformaldehyde fixation, ethanol dehydration, plastic embedding (Fluka Durcupan), sectioning at 5–10 µm, epifluorescence micrography; Gronenberg and Peeters (1993), Gronenberg and Tautz (1994)]. Graphical reconstructions were made either from colour slides

(fluorescent preparations) or using a *camera lucida* attachment to the microscope.

Results

Prey capture by Strumigenys sp.

In the foraging arena, *Strumigenys* sp. generally walk around slowly with closed mandibles. The scapes of their antennae are held perpendicularly to the body's long axis while the flagella point forwards (see Figs 1, 2E). These small ants (body length without mandibles, 1.2–1.5 mm) have to approach very close to the potential prey in order to initiate prey-capture behaviour. In the present experiments, most collembolan prey was smaller than the ants, but *Strumigenys* sp. also attacked prey of about their own size.

Upon brief antennal contact with the prey, the mandibles are opened completely (the angle between the mandibles is approximately 220°) and the ants move more slowly so as to avoid any disturbance of the prey. At the same time, they perform swaying search movements with the head and body in order to re-establish antennal contact with the prey (see detailed description by Dejean, 1986). Vision does not seem to be involved in this apparently chemosensory searching behaviour. In the absence of antennal contact, the springtails can literally step on the ants without releasing prey-catching behaviour. If, however, the collembolan's position is established by another antennal contact, *Strumigenys* sp. stalks the springtail until the forward-pointing trigger hairs on the labrum (see Fig. 2) contact the prey (schematized in Fig. 1E). The mandibles snap shut immediately after the prey touches the trigger hairs. As in other trap-jaw ants, the trigger hairs thus act as a rangefinder and trigger the strike when the prey is in the correct position between the mandibles. In the video sequence shown in Fig. 1A, the mandible strike occurs between the second and third frames (enlarged in Fig. 1C,D and explained in Fig. 1E,F), and hence within 2.5 ms. However, in several cases, prey catching was not successful: large collembolans may struggle free or, as in Fig. 1A, the strike may be triggered by a leg or antenna of the springtail. In this case, the ant clasps a limb of the prey rather than its body and the springtail may then be able to perform an escape jump. After a successful strike, when the prey is penetrated and firmly held by the mandibles, the ant immediately bends the gaster forwards and stings the prey to prevent further struggling.

The latency of the entire trap-jaw reflex (including trigger hair contact and mandible strike) could not accurately be assessed from the high-frequency video recordings because the hairs are too small to be resolved by the system. Only two video sequences allowed an approximation of the reflex latency (judging from the distance between the ant's head and the springtail). In both cases, the supposed trigger hair contact and the mandible strike occurred within two video frames (within 5 ms).

Morphology of the mechanism in Daceton armigerum

The basic design which allows for such a fast mandible

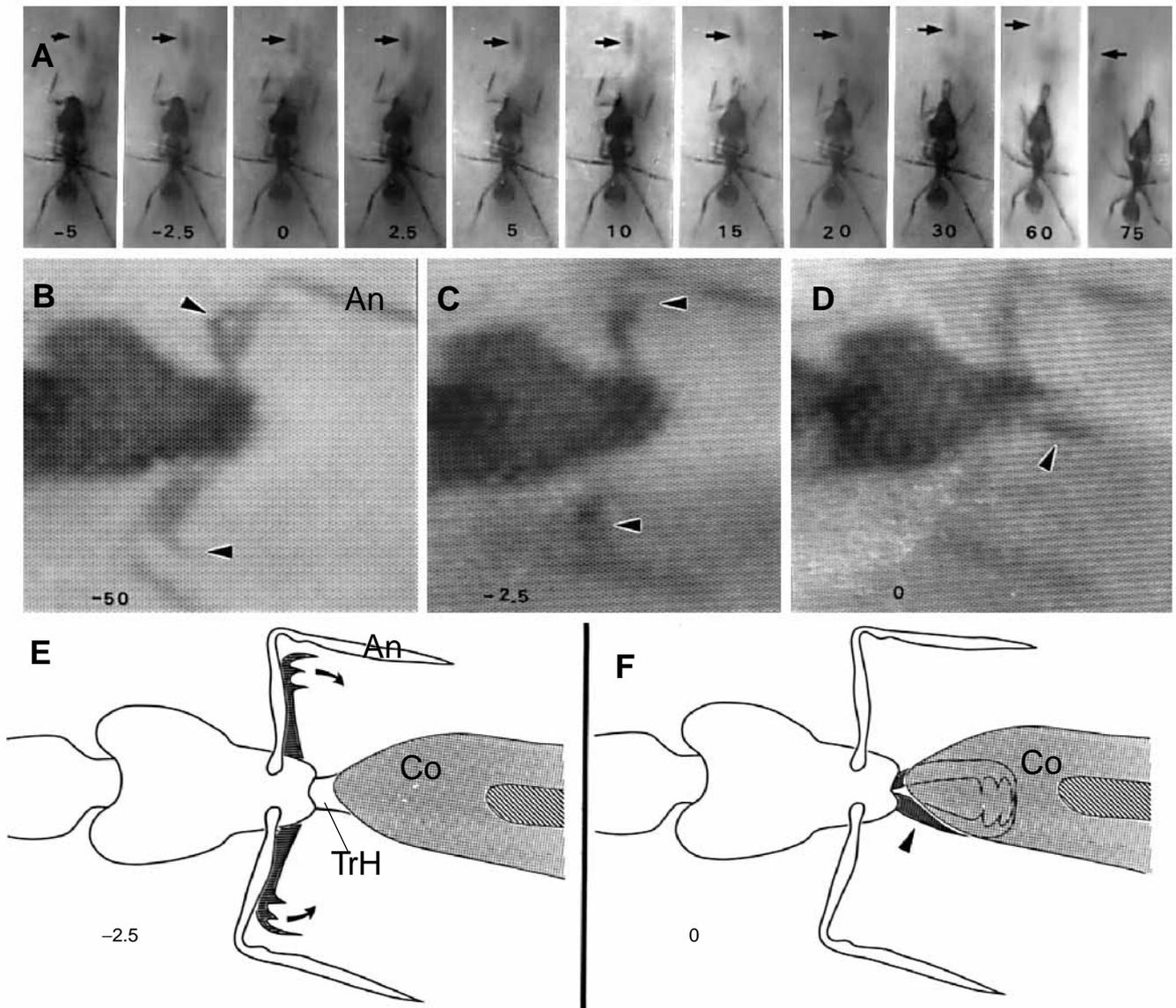


Fig. 1. Series of high-frequency videographs ($400 \text{ frames s}^{-1}$) showing (A) the mandible strike of *Strumigenys* sp.; time (in ms) before (-5 ms , -2.5 ms) and after the strike ($2.5\text{--}75 \text{ ms}$) is indicated at bottom of the respective image; the strike occurs at time 0, arrows indicate the gut of the collembolan prey. Note that the prey escapes (see last frame). As a consequence of the poor resolution of the video system, this sequence A requires some additional interpretation. The open mandibles (arrowheads in B, C) can barely be resolved because they are partly eclipsed by the antenna, as is more clearly shown in the magnified image (B; 50 ms before the strike). Immediately before the strike (C), the head and antennae have moved slightly and the blurred image almost entirely conceals the open mandibles (arrowheads). This image (C; 2.5 ms before the strike) is traced in E and interpreted by comparison with photographs and scanning electron micrographs (the trigger hairs TrH and the collembolan prey Co cannot be resolved from the video). Immediately after the strike (time 0 in A, enlarged in D and traced in F), both mandibles are concealed by the collembolan's head region (not resolved on the video). A dark spot (arrowhead in D and F) is all that is visible of the closed mandibles until 15 ms after the strike (see A) when the closed mandibles are revealed as the prey moves backwards; An, antenna.

strike is the same in *Strumigenys* sp. and *Daceton armigerum*: (i) long and slender mandibles that can be opened widely and that are equipped with apical teeth (Fig. 2A,D,E); (ii) oversized mandible closer muscles (Figs 2F, 3A,B,E, 4) accommodated by the outward-bulging rear lobes of the head capsules (Fig. 2A,D); (iii) a catapult-like energy storage system which involves a mandibular catch mechanism (Fig. 3C,D) that can be released by a set of specialized trigger muscles (Figs 3E,

4A,C) activated upon contact of particular trigger hairs situated on the labrum (Figs 1E, 2C, 3E, 4A).

This design will be described first for *Daceton armigerum* because these ants are much larger (the head width of the specimens studied was up to 4 mm) and some features of the mandible function can be assessed macroscopically (as has been done by Brown and Wilson, 1959). In contrast, the mandible function of *Strumigenys* sp. could only properly be

determined from sectioned material because of the minute size of these ants.

In *Daceton armigerum*, the mandible joints and associated

structures are covered by the rigid roof-like clypeus (Figs 2A, 3E), underneath which protrude the two long trigger hairs that originate from the anterior surface of the labrum (Fig. 2B,C).

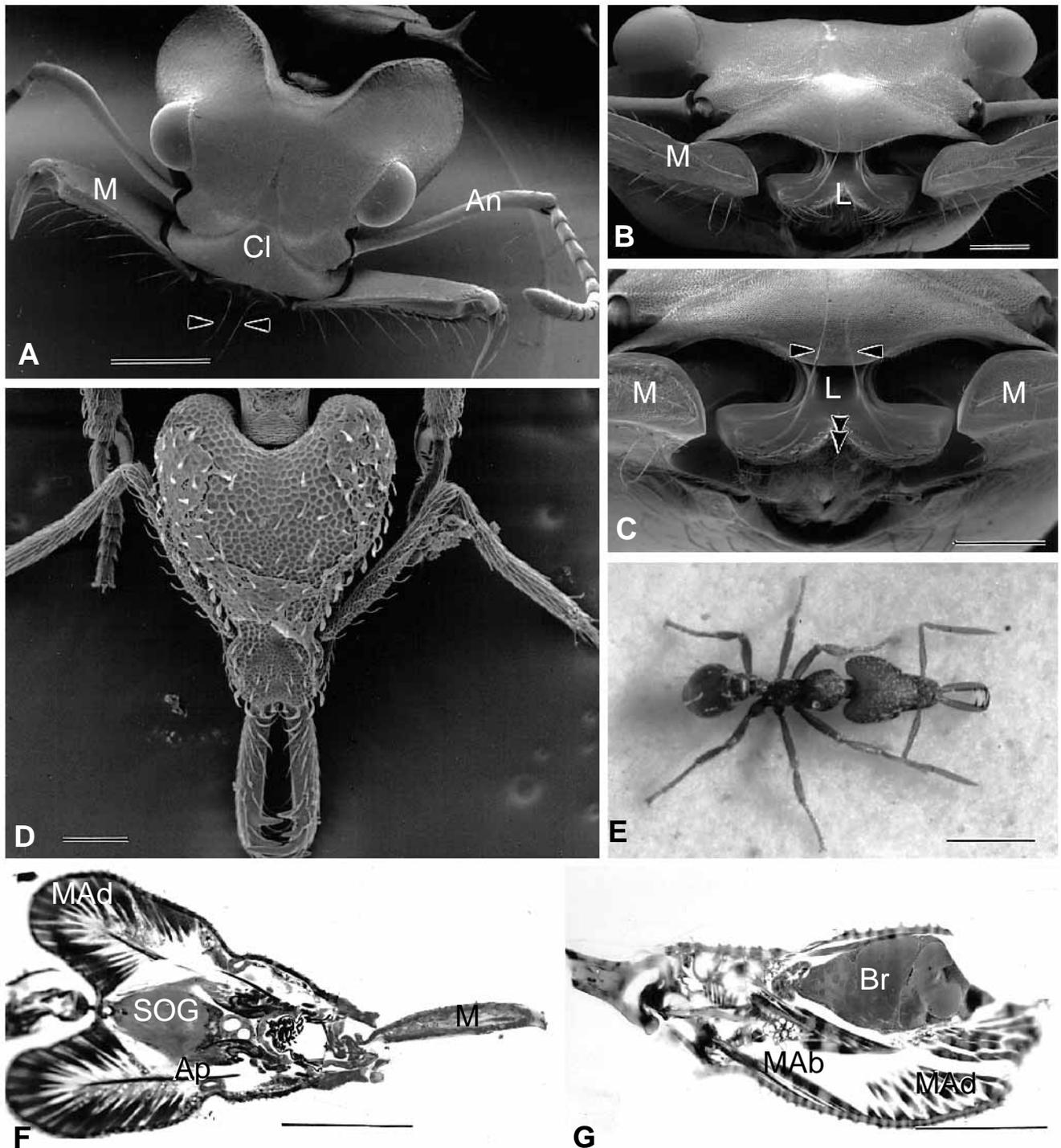


Fig. 2. Scanning electron micrographs (A–D) and photomicrographs (E–G) of *Daceton armigerum* (A–C) and *Strumigenys* sp. (D–G). (A) Dorsal and (B,C) frontal views of the head of *Daceton armigerum* at different magnifications. When positioned between the two mandible bases, the labrum L (hidden underneath the clypeus Cl in A) locks the mandibles M in the open position. After stimulation of the labral trigger hairs (arrowheads in A and C), the labrum clicks inwards (indicated by a double arrowhead) to release the strike. (D) Frontal and (E) dorsal views of *Strumigenys* sp. with closed mandibles. Horizontal (F) and sagittal (G) osmium-stained sections of the head of *Strumigenys* sp. show the small mandible abductor (opener) MAb (in G only) and the large adductor (closer) muscle MAAd and its apodeme Ap and the brain Br and suboesophageal ganglion SOG. An, antenna; scale bars, 500 μ m in A and E; 200 μ m in B, C, F and G; 100 μ m in D.

When the mandibles are closed, the labrum fits neatly into grooves formed by the two mandible bases (Fig. 3D). The mandibles are opened by the contraction of the mandible abductor (opener) muscles, which reside ventrally in the head capsule and project from the ventral midline of the head anterolaterally towards the lateral side of the respective mandible joint (Fig. 3B). During the process of opening the mandibles completely, a heavily sclerotized part of the labrum clicks between inward-pointing processes of the left and right mandible bases, thus effectively blocking the mandibles (Fig. 2C; redrawn from serial sections in Fig. 3C, which shows the labral structure situated between the two protrusions of the mandible bases). The part of the labrum which locks the mandibles extends dorso-ventrally and has long edges facing

(and locking) the protruding edge of each mandible base. Once the labrum has slipped between the mandible bases, the mandibles will stay open even when the mandibular adductor (closer) muscles contract.

These mandible closer muscles provide the energy for the powerful strike and they occupy about two-thirds of the total head volume (see Fig. 3A,B,E), thus representing the strongest muscle in *Daceton armigerum* workers. The adductor muscles originate from ventral, lateral and posterior parts of the head capsule. They are composed of from approximately 300 to more than 1000 tubular muscle fibres, depending on the size of the animal; there is considerable size dimorphism in *Daceton armigerum* and the heads examined ranged in width from 1.5 to 4 mm. The tubular muscle fibres have outer

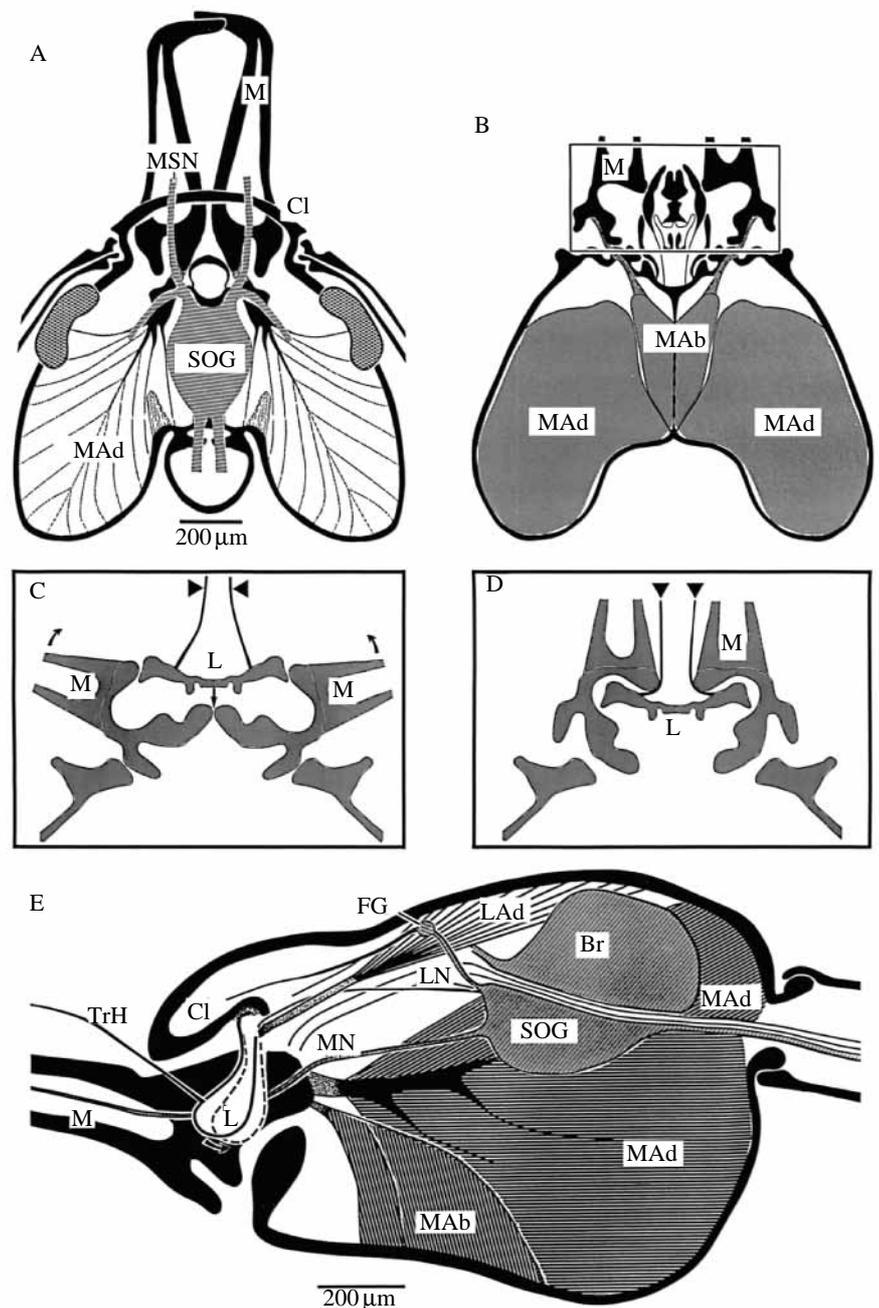


Fig. 3. Morphology of the head and mandible joint of *Daceton armigerum*. (A,B) Horizontal reconstructions of the head at two different depths (A, mid-horizontal plane; B, close to the ventral surface of the head) showing the mandible closer (adductor) muscles MAd, the mandible opener (abductor) muscles MAb (in B only) and their respective apodemes (tendons). The rectangle in B shows the approximate area enlarged in C and D. (C,D) The mandible joint and the locking mechanism of the labrum (mandibles open and locked in C, closed in D). Curved arrows in C indicate the trajectory of the closing mandibles; the small arrow in C indicates the direction in which the labrum L moves when the mandible strike is released; triangles indicate trigger hairs. (E) Schematic sagittal view of the head with the mandibular sensory nerve MSN and the frontal nerve which supplies the frontal ganglion FG and the trigger muscle (labral adductor muscle) LAd. Movement of the labrum L during mandible release is indicated by the curved arrow and broken line; Br, brain; Cl, clypeus; M, mandible; SOG, suboesophageal ganglion; TrH, trigger hair; LN, labral nerve (sensory); MN, mandibular nerve.

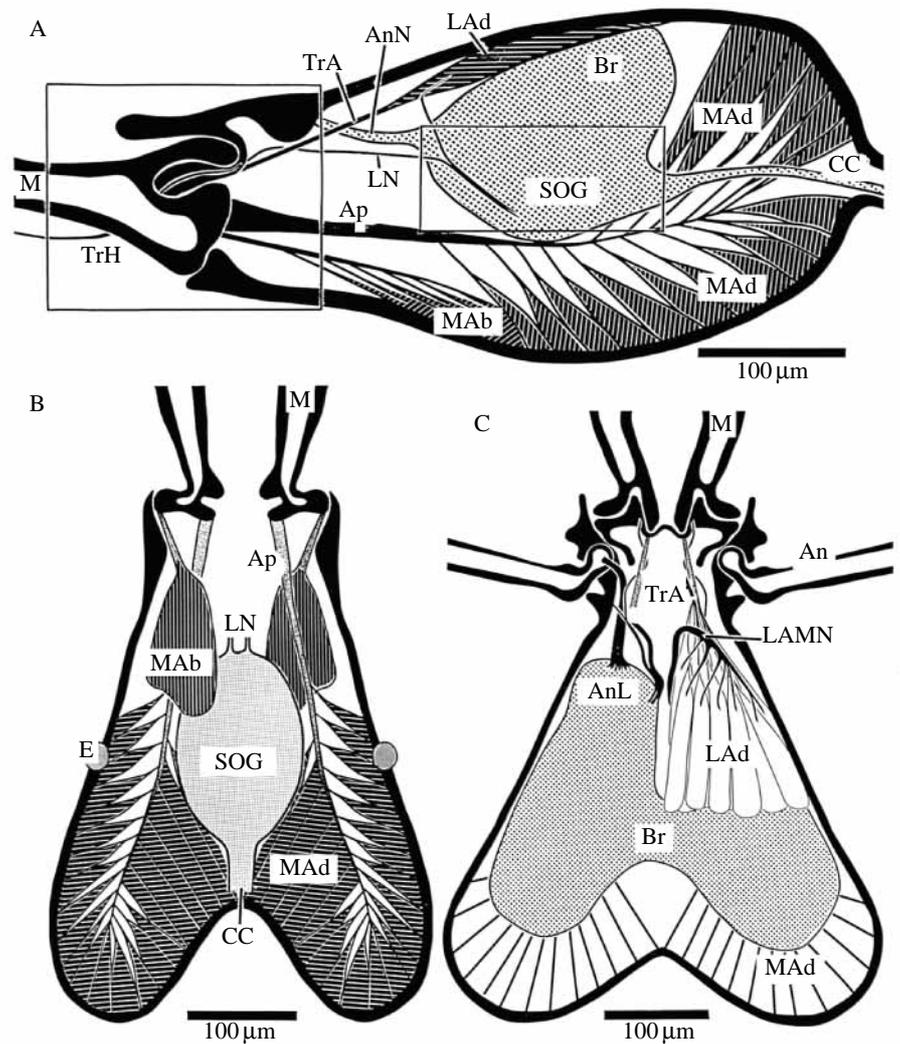


Fig. 4. Schematized sagittal (A) and dorsal (B,C) views of the head of *Strumigenys* sp. showing the antennae An, the antennal nerve AnN, the antennal lobe AnL, the brain Br and the suboesophageal ganglion SOG with labral sensory nerve LN and cervical connectives CC, the mandibles M with abductor (opener; left muscle exposed to show overall size) MAb and adductor (closer) muscle MAAd and its apodeme Ap, the labral trigger hairs TrH with their afferents in the labral nerve and the trigger muscle LAd (the labral adductor), its apodeme TrA and motor neurone LAMN. E, eye; rectangles in A show the approximate regions depicted in Fig. 5A,B.

diameters ranging from 13 to 25 μm (mean \pm S.D., $16 \pm 2.7 \mu\text{m}$; $N=150$ fibres, three animals). Their small inner core (diameter 1.5–2.5 μm) as well as their high sarcomere lengths (mean \pm S.D., $7.2 \pm 0.9 \mu\text{m}$; $N=150$, three animals) indicate that the fibres are of a slow-contracting type (see Discussion).

Each adductor muscle is attached to the mandible base by a massive apodeme (the arthropod analogue of vertebrate tendons). Anatomy suggests that, by analogy with the trap-jaw ant genus *Odontomachus*, the energy provided by contraction of the mandible closer muscle is stored mechanically until the mandibles are released from the catch. Elastic energy is thought to be stored in the large closer apodeme and particularly by deformation of the head capsule. These spring-like elements will then recoil instantaneously when the catch is released, delivering the stored elastic energy to accelerate the mandibles.

In order to release the mandibles from the catch, the labrum has to be removed from between the mandible bases. It is the labral adductor muscle which pulls the labrum inwards (Fig. 3E), and this muscle will be referred to as the trigger muscle. The trigger muscles are the dorsalmost muscles in the head. They are anchored dorsally to the head capsule and are

composed of about 40–50 muscle fibres (depending on head size). These comparatively thin tubular fibres are of relatively uniform outer diameter (10–12 μm) with large core diameters of 2.5–4 μm . Moreover, they feature the shortest sarcomeres found in the head of *Daceton armigerum* ($1.8 \pm 0.3 \mu\text{m}$, mean \pm S.D.; $N=40$ fibres, three animals). Core diameter and sarcomere length both indicate that the trigger muscle may be able to contract very fast (see Discussion).

The fibres of the trigger muscle are collected into a partly sclerotized apodeme which projects antero-ventrally towards the labrum (Fig. 3E). The labrum is hinged to the clypeus by elastic material in such a way that it will normally slip forward (solid labrum outline in Fig. 3E) between the two mandible bases without muscular action (no labral abductor muscle has been found in either *Daceton armigerum* or *Strumigenys* sp.). The labrum is U-shaped in cross section and the trigger muscle apodeme is attached to the rim of its inner flank (Fig. 3E). Accordingly, contraction of the trigger muscle results in an inward and upward pull, which lets the labrum flip inwards (adduction; indicated by arrow and broken labrum outlines in Fig. 3E), thus unblocking the mandible bases and releasing the strike.

The trigger muscle is supplied by a collateral of the frontal nerve, which connects to the frontal ganglion (Fig. 3E) and originates from the most anterior root of the suboesophageal ganglion (SOG). From this nerve originates the labral motor nerve (not shown in Fig. 3E) close to the frontal ganglion, which proceeds to the labral adductor muscle. This nerve carries one large axon (the trigger motor neurone; axon diameter approximately 8 μm), which is accompanied by a few other axons of much smaller diameter whose target has not been established.

The trigger hairs on the labrum which initiate the trap-jaw reflex send their afferent sensory projections through the labral sensory nerve. In contrast to *Strumigenys* sp., there are only two trigger hairs and accordingly two sensory trigger neurones in *Daceton armigerum*. The diameter of these trigger afferents is about 5 μm . The labral sensory nerve joins the SOG close to the nerve root of the frontal nerve and labral motor nerve. The basic trap-jaw reflex is thus controlled by only four large neurones (one sensory and one motor neurone on either side). The neuronal design is similar to that of *Strumigenys* sp. and will be described in more detail for the latter genus below.

Morphology of the mechanism in Strumigenys sp.

As mentioned above, the mechanism that leads to the fast mandible strike is the same in *Strumigenys* sp. and in *Daceton armigerum*. Accordingly, the structures involved (mandible joint, muscles, apodemes, neuronal supply) are organized in a very similar way (compare Fig. 3 with Fig. 4) and the dissimilarities mainly seem to result from size and geometry differences between the ants. I will therefore mainly focus on the differences between the genera.

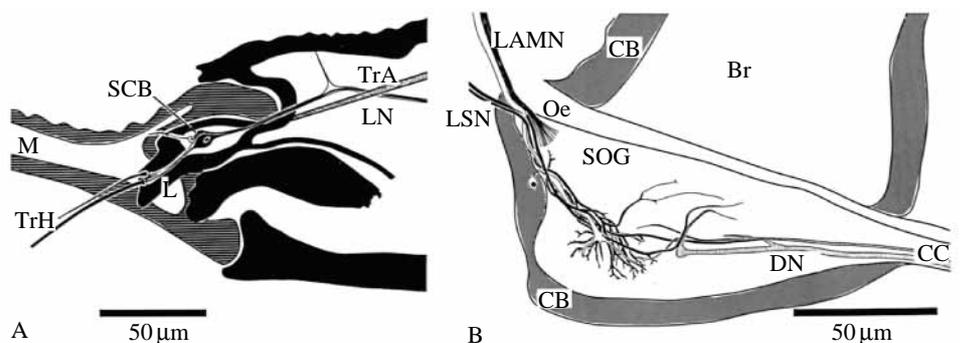
Strumigenys sp. has an elongate head with minute eyes (less than 20 ommatidia) and, accordingly, negligible optic lobes. However, compared with the large *Daceton armigerum*, *Strumigenys* sp. has a relatively large brain (Fig. 4C) which leaves less space for the muscles (it is well known that smaller insects often have relatively bigger brains than their larger relatives; Goossen, 1949; Rensch, 1956; Neder, 1959; Rossbach, 1962). The small overall size of *Strumigenys* sp. leads to a peculiar design: its head has a snout-like appearance (Fig. 2D) in which the ‘motor part’ (the bulk of the head

containing the brain and muscles) is separated from the moving parts (antennae, mandibles and other mouthparts). This design requires long apodemes that all funnel through the narrow front of the head (the ‘snout’). The sizes of these apodemes reflect the size of the attached muscles (the mandible closer apodeme is the thickest, while the trigger apodeme is slightly thinner than the mandible opener apodeme), and the relative sizes of the muscles are similar to those found in *Daceton armigerum*.

The mandible adductor muscle of *Strumigenys* sp. is composed of approximately 200–250 tubular fibres, most of which taper towards the partly sclerotized apodeme (diameter 7–10 μm ; Figs 2F, 4A) and attach to the main apodeme via thread-like processes (only some fibres originating from the rear of the head capsule attach directly to the apodeme; see Fig. 4B). The diameter of the closer muscle fibres varies from 10 to 15 μm at their base and the sarcomere length is about 4.9 μm [similar to that of the mandible opener muscles (4.7 μm), yet relatively long compared with other muscles in the head of *Strumigenys* sp.]. At their attachment points on the head capsule, strands of the cuticular filaments seems to extend into the closer muscle fibres, thus probably enhancing the attachment. Cross sections close to the attachment points of the fibres show a concentric fibre design. While they are indisputably striated muscle fibres, their pattern of striation appears less pronounced than in most other muscle fibres. This may result from a less precise alignment of the myofibrils. However, in the absence of electron microscopical evidence, nothing more decisive can be said about the nature of these fibres except that they look different from other muscle fibres in *Strumigenys* sp. or in larger ants.

As in *Daceton armigerum*, the trigger muscle pulls the labrum inwards via a long apodeme (Fig. 5A) and thus unlocks the mandibles. The trigger apodeme has a diameter of approximately 5 μm and is partly sclerotized, indicating its increased tensile strength, which probably makes it suited to convey fast twitches (except for the thick mandible closer apodeme, no other apodemes are sclerotized in *Strumigenys* sp.). The trigger muscle originates in the same location as that in *Daceton armigerum* (in the dorsal part of the head capsule above the brain) and is composed of only 9–12 tubular muscle fibres on either side. Unlike the mandible closer muscle, the

Fig. 5. Sagittal drawing of the mandible joint region (A) and the suboesophageal ganglion SOG (B) of *Strumigenys* sp. (A) When depressed by the trigger muscle via its apodeme TrA, the labrum L fits into a groove in the mandible M base (hatched). The sensory cell bodies SCB associated with the trigger hairs TrH send afferents through the labral nerve LN into the suboesophageal ganglion. (B) Giant neurones in the SOG of *Strumigenys* sp. reconstructed from osmium-stained material. Br, brain; CB, cell body layer around the brain and SOG; CC, cervical connectives; Oe, oesophagus; LAMN, labral adductor motor neurone (open profiles); and LSN sensory neurones (filled profiles) of the labrum; DN, descending neurones.



striation pattern is well expressed in the trigger muscle fibres (Fig. 6A). They have very short sarcomeres (approximately $1.8\mu\text{m}$) and large central cores ($3\text{--}5\mu\text{m}$; fibre diameter $9\text{--}13\mu\text{m}$). As in *Daceton armigerum*, this suggests a high contraction velocity for the trigger muscle in *Strumigenys* sp.

Neuronal control of the reflex

The basic arrangement of the reflex pathway (sensilla, muscles, nerves, ganglia) is the same in *Daceton armigerum* and *Strumigenys* sp. However, it was not possible to reveal the connectivity pattern within the ganglion from the preserved material of *Daceton armigerum*. Because of the availability of live specimens, the neuronal network controlling the trap-jaw reflex was examined in *Strumigenys* sp. in more detail.

The trigger hairs are mechanosensory bristles situated centrally on the labrum. Unlike *Daceton armigerum*, in *Strumigenys* sp. the two long thick bristles are accompanied by a second pair of smaller shorter hairs (Fig. 5A). The large sensory cells (one per bristle) reside in the lumen of the labrum. Their dendrites contact the hair bases and their axons project to the SOG within the left or right labral sensory nerve (Fig. 5A). In *Daceton armigerum* and *Strumigenys* sp. alike, these nerves, before approaching the ganglion, join another contributory nerve which supplies sensilla situated on the clypeus. The trigger hair afferents are the thickest axons in the labral sensory nerve. Close to the labral nerve root of the SOG, the afferents of the large and the smaller trigger hairs of *Strumigenys* sp. have diameters of $1.1\mu\text{m}$ and $1.5\mu\text{m}$, respectively. Within the SOG, they project ventrally (Figs 5B, 6B) and give rise to many collateral branches which are in close contact with collaterals of the trigger motor neurones (see below). Some of the trigger afferent collaterals reach far posteriorly and come into close contact with collaterals of very thick descending neurones (which proceed towards the thoracic ganglia; Fig. 5B).

The sensory afferents of *Strumigenys* sp. were stained using a fluorescent tracer and their reconstruction in a horizontal plane (Fig. 7A) reveals the massive overlap between the afferents of both sides. These collaterals coincide with motor neurone dendrites (reconstructed from osmium-ethylgallate-impregnated material in Fig. 7B) which supply the trigger muscles. Sensory collaterals and motor neurone dendrites are situated so close together that a monosynaptic connection is very likely (yet cannot be proved from light microscopy alone).

Further posterior, in a region not reached by motor neurone dendrites, the trigger hair sensory afferents overlap and are in close contact with dendritic branches of a giant descending neurone (Fig. 7C), again indicating (although not proving) a monosynaptic connection. These descending neurones have an axon diameter of $4\mu\text{m}$ and are thus the thickest neurones in the entire central nervous system of *Strumigenys* sp. They have not been reconstructed but are drawn schematically in Fig. 7C. In *Daceton armigerum*, no comparable giant descending neurones were found (despite the poor preservation of nervous tissue in the *Daceton armigerum* specimens, neurones of such a conspicuous size would have been resolved from the sections).

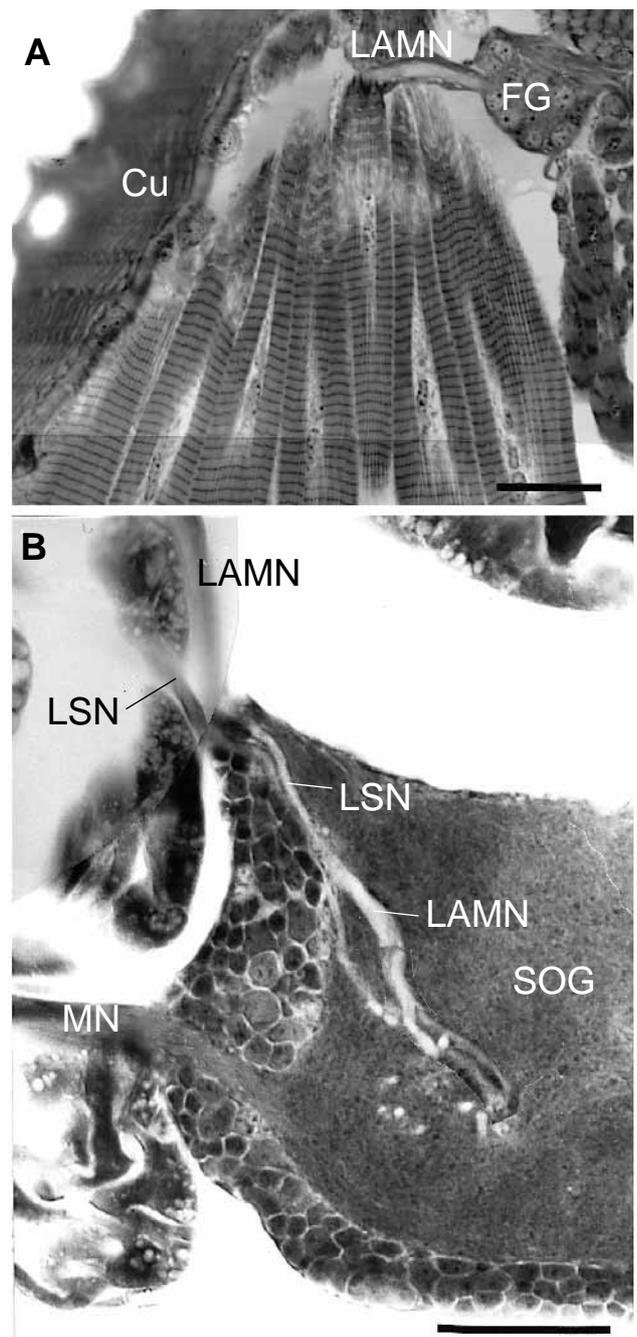


Fig. 6. Photomicrographs of (A) the trigger muscle (osmium-stained horizontal section) and (B) its motor neurone LAMN in the anterior half of the suboesophageal ganglion SOG (sagittal section) of *Strumigenys* sp. Cu, cuticle of the head capsule; FG, frontal ganglion; MN, mandibular nerve; LSN, sensory neurones (trigger hair afferents); scale bars, $20\mu\text{m}$.

As in *Daceton armigerum*, each labral adductor muscle is only supplied by a single motor neurone in *Strumigenys* sp. The diameter of this trigger muscle motor neurone is $2\mu\text{m}$ at the entrance into the ganglion and $4\mu\text{m}$ at the trigger muscle before its collaterals branch off to supply each muscle fibre (Fig. 4C). The trigger motor neurones thus constitute by far the

thickest axons in all the nerves of the brain and SOG (with the exception of the aforementioned giant descending neurone). The cell bodies of the trigger motor neurones are located medially in the anterior cell body layer which surrounds the SOG (Fig. 5B). Their dendrites are restricted to anterior neuropile of the SOG, where they overlap and intermingle profusely with the terminals of the trigger hair afferents (indicated in Figs 5B, 6B, 7B). As in *Daceton armigerum*, the trigger motor axon projects through the frontal nerve and enters the SOG together with many other, much thinner, axons which are indicated in Fig. 5B and which are thought to supply the frontal ganglion. Although in *Daceton armigerum* the labral adductor motor nerve separates from the frontal nerve before reaching the frontal ganglion, in *Strumigenys* sp., the trigger motor neurone actually projects through the rim of the frontal ganglion (Fig. 6A).

To summarize, in both ant genera, the trap-jaw reflex is controlled by a set of giant neurones: a sensory and a motor neurone on either side that may be monosynaptically coupled. In addition, in *Strumigenys* sp., a second (thinner) sensory axon

originating from an additional (smaller) trigger hair is also associated with the motor neurones. The sensory input of the trigger hairs appears to be relayed to the thoracic ganglia (which controls the legs) by a fast pathway (giant descending neurones).

Discussion

Convergent evolution of trap-jaws in ants

Many predatory ants depend on fast weapons to catch their swiftly moving prey. The primitive bulldog ants (*Myrmecia* sp.) or ants of the ponerine genus *Harpegnathos* are large visual hunters that jump and rapidly snap their mandibles at insect prey. This movement is not caused by a catapult mechanism but depends exclusively on the fast contraction of the mandible adductor muscles. While ant mandible closer muscles in general (and in trap-jaw ants in particular) are slow muscles, in *Myrmecia* and *Harpegnathos* sp. they are composed of fibres whose morphological characteristics indicate their high contraction velocity (W. Gronenberg, unpublished data). While the mandible closer muscles of both genera are very large (and hence expensive to build in evolutionary terms), it is likely that the mandible strike of *Myrmecia* or *Harpegnathos* sp. is not nearly as fast as that of trap-jaw ants.

To perform even faster strikes suited to cope with swiftly moving prey such as springtails or flies, a catapult mechanism has evolved repeatedly and independently in the Odontomachini, the Dacetini and the Myrmoteratini. The trap-jaw design thus provides a remarkable example of convergent evolution. Throughout this paper, reference has been made to the well-studied trap-jaw mechanism of the genus *Odontomachus*. Some of its features, together with those of the other trap-jaw ant genera, are listed in Table 1. The similarities in design and control of dacetine and odontomachine trap-jaws are remarkable (little is known about those of *Myrmoteras* sp.), but they are not homologous structures.

The present study has demonstrated that the major similarities (long mandibles, catch mechanisms, particularly large closer muscles, trigger hairs, fast trigger muscles, giant neurones probably monosynaptically coupled) between different trap-jaw ant genera result from a similar principal strategy to overcome slow muscle action (a catapult mechanism) and from the requirement for precise control of the release of the strike. Irrespective of their origin, these structures have been optimized to comply with these physical requirements, and the outcome of this evolutionary process is their striking resemblance.

The comparative approach used in the present study allows an explanation of the differences in the trap-jaw designs as either (a) arising from different evolutionary starting points (pre-adaptations) or (b) reflecting differences in prey type or hunting strategies. These are discussed below.

While in *Odontomachus* and *Anochetus* sp. only the mandibular head segment is involved in the strike, in dacetines the mechanical catch and the trigger mechanism are formed and controlled by the labrum and its associated muscles and

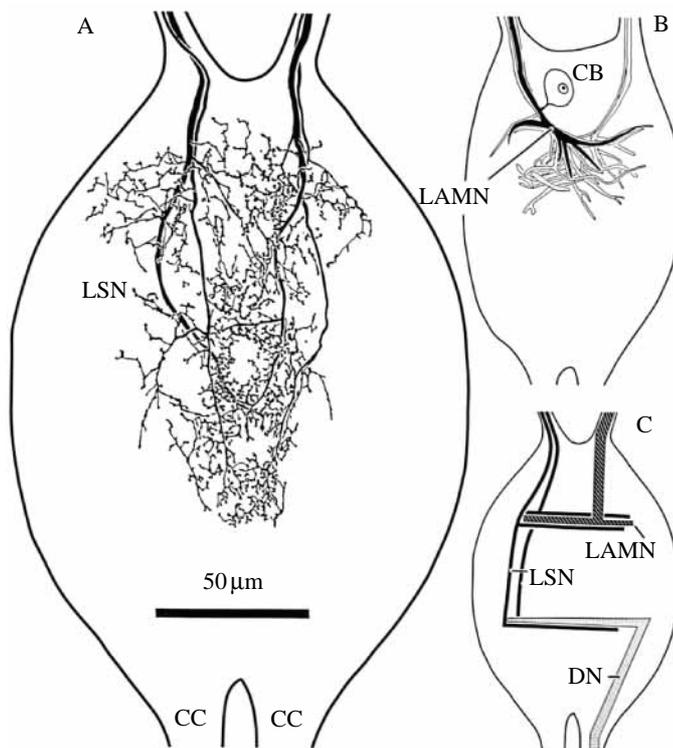


Fig. 7. Giant sensory neurones (LSN) (A) and motor neurones (LAMN) (solid profiles in B) serving the trap-jaw reflex in *Strumigenys* sp. and reconstructed from material retrogradely labelled with Fluoro Ruby (A) or from osmium-stained material (B). Open profiles in B depict sensory projections in close contact with the motor neurone dendrites. CB, cell body of the giant motor neurone. (C) Schematic diagram of the proposed information flow from labral sensory afferents LSN (solid) to the labral adductor motor neurone LAMN (hatched) and to the giant descending neurone DN (stippled). Note that the proposed connections are only based on the proximity of the processes as resolved by the light microscope; CC, cervical connectives.

Table 1. *Characteristics of trap-jaw mechanisms in ants*

	<i>Odontomachus</i> sp.	<i>Anochetus</i> sp.	<i>Daceton</i> <i>armigerum</i>	<i>Strumigenys</i> sp.	<i>Myrmoteras</i> sp.
Ant size	Large	Small–medium	Large	Small	Small
Prey type	Larger insects	Small insects (<i>Collembola</i>)	Larger insects	<i>Collembola</i>	<i>Collembola</i>
Rear head extended	Yes	Yes	Yes	Yes	Slightly
Mandibles	Blunt	Pointed	Pointed	Pointed	Pointed
Number of trigger hairs and sensory neurones	4 large	2 large, 2 slightly smaller	2 large	2 large, 2 small	None (visual)
Catch mechanism formed by	Mandible joint	Mandible joint	Labrum	Labrum	?
Power muscle	Mandible adductor	Mandible adductor	Mandible adductor	Mandible adductor	?
Sarcomere length (µm)	10	11.4	7.2	4.9	
Trigger muscle	Mandible adductor	Mandible adductor	Labral adductor	Labral adductor	?
Sarcomere length (µm)	2.7	2.9	1.8	1.8	
Number of trigger motor neurones	4	4	2	2	?
Giant descending neurone	No	No	No	Yes	?

Synopsis of major features underlying and determining the trap-jaw mechanisms in the three ant subfamilies Ponerinae (*Odontomachus* and *Anochetus* sp.), Myrmicinae (*Daceton armigerum* and *Strumigenys* sp.) and Formicinae (*Myrmoteras* sp.). Sarcomere length is given as an indication of the fast (trigger muscles) and slow (mandible closer muscles) nature of the respective muscle. Data from present study, Brown (1978) (*Anochetus*, *Odontomachus*), Moffett (1986) (*Myrmoteras*), Gronenberg (1995a,b) (*Odontomachus*) and W. Gronenberg, unpublished data (*Anochetus*).

neuromere (Table 1). Despite their different origin, both mechanisms provide a secure catch and withstand the power of the large contracting mandible closer muscles. Likewise, the existence or absence of a second set of trigger motor neurones seems to reflect the original innervation of the particular muscle (Table 1) and (provided that the axons are thick enough for the fast conduction required) may not be important for the functioning of the system.

In contrast, the shape and size of the mandibles and the presence of trigger hairs or of a fast descending pathway probably depend on the prey and the hunting strategies of the ant. *Strumigenys* sp. need to sting their struggling prey immediately after the strike, and success may thus depend on the presence of a fast descending neurone (see below). Like *Myrmoteras* sp., *Strumigenys* sp. need pointed or spiny mandibles that penetrate their soft-bodied prey and hold onto it. In contrast, most *Odontomachus* species have blunt mandible tips that stun their prey like a hammer (Brown, 1976). Sharply pointed teeth would break when they hit large solid prey such as termite soldiers. The mandible tips of *Daceton armigerum* (Fig. 2A) show intermediate (and less specialized) features: they are pointed and will penetrate tough cuticle of larger and armoured arthropod prey, but they will also stun and squeeze smaller and soft-bodied prey. Lacking slender spines, *Daceton armigerum* and *Odontomachus* sp. could not hold onto struggling springtails as do the more specialized collembolan hunters *Anochetus*, *Strumigenys* and *Myrmoteras* sp.

It would be interesting to examine further the mandible strike in the only formicine ant genus equipped with trap-jaws, *Myrmoteras*. These visual hunters with large eyes and fierce mandibles (Table 1) form two subgenera, one bearing prominent trigger hairs on their labrum and the other lacking trigger hairs (Moffett, 1985, 1986). The mandibles of *Myrmoteras* sp. open extremely wide (280°) and are locked in the open position (Moffett, 1986), but nothing is known about the nature of the catch mechanism. It would be very interesting to determine whether the catch mechanism is analogous to that of *Odontomachus* sp., to that of the dacetines or whether it represents a different design in the formicine ants. The triggering mechanism is expected to be different in the subgenus lacking trigger hairs; here, the strike is released by visual rather than mechanosensory input.

The trap-jaw design seems to be such an effective means for catching insect prey that it has evolved independently at least three times among the ants. Convergent evolution has modified different parts of the head and different neuronal elements to fit one function: a mandible strike of high speed and precision. However, despite this obvious specialization, the ants can also use their jaws in a 'normal' way: they groom themselves and their nestmates, carry and feed the brood and perform all the other normal chores that require the fine motor control involved in 'handling' delicate objects.

Dacetine foraging strategies

Dacetine ants are exclusively predacious. The size and

appearance of their mandibles give an indication of their foraging strategies: despite their differences in body size, *Daceton* and *Strumigenys* are both morphologically primitive genera which have long mandibles with which to strike at their prey. There exists an evolutionary tendency among dacetines to reduce the length of the mandibles and also a 'countercurrent' evolution from short-mandibulate forms back to long ones (Brown and Wilson, 1959). More advanced genera, such as *Neostruma* or *Smithistruma*, have retained the trap-jaw design, yet they have short mandibles and do not rely on a very powerful mandible strike. Instead, they have adopted a cryptic lifestyle and employ stealth hunting strategies (Brown and Wilson, 1959; Hölldobler and Wilson, 1990). They stalk their prey extremely slowly before they close their mandibles and then immediately sting the prey. Other short-mandibulate forms (e.g. in the genus *Pentastruma*) may have no labral catch mechanism (Masuko, 1984).

Large *Daceton armigerum* catch arthropods, including fast insects such as flies and grasshoppers (Brown, 1954), while many small dacetine species are specialized collembolan hunters (Wilson, 1953). *Strumigenys* sp. will also accept some other small insect species as food, although they prefer entomobryid *Collembola*. It is thus not surprising that they have evolved a mechanism that enables them to cope with the fast escape response of their prey. As documented previously, the mandible strike of most dacetine ants is very fast. In *Strumigenys* sp., the actual mandible movement may take much less than 2.5 ms, which was the temporal resolution limit of the video system used. The shortest strike duration recorded for *Odontomachus bauri* was 0.3 ms (Gronenberg, 1995a) and the strike might be comparatively fast in *Strumigenys* sp. While it was not possible to determine the exact latency of the entire reflex in the current study, two recorded sequences of unrestrained *Strumigenys* sp. suggest that the reflex can be performed in less than 5 ms (two video frames). This matches the fastest reflex recorded in the trap-jaw ant *Odontomachus bauri*: 4–10 ms (Gronenberg, 1995a; no data for *Daceton armigerum* are available).

Smaller prey items are stunned by the mandible strike of *Strumigenys* and *Daceton armigerum*. For *Strumigenys*, larger and struggling prey are stung immediately after the strike (Wilson, 1953; Dejean, 1986), thus reducing the prey's chances of escape. The present finding of a giant interneurone closely associated with the sensory trigger hairs may reflect the requirement for the fast stinging response of *Strumigenys* sp.: the same stimulus (trigger hair contact) may release the mandible strike as well as the leg and abdominal movements required for stinging after the strike. This may also explain a peculiar finding by Brown and Wilson (1959): several *Strumigenys* and other dacetine species will carry through their stinging movements to 'completion' once the behaviour is triggered even if the prey has been able to struggle free from the mandibles; hence, they will sting an imaginary prey.

Specialization for speed

Amazingly fast movements are performed by many insects,

e.g. the escape jumps of fleas, locusts, click beetles, flea beetles and springtails and the predatory strikes of the preying mantis, dragonfly larvae, some staphylinid beetles and beetle larvae, or of the ant *Odontomachus* sp. (all species reviewed in Gronenberg, 1996b). In order to move faster than synchronous muscles are able to contract, all these insects have evolved special devices; in particular, catapult mechanisms by which slowly generated muscular energy is stored as elastic strain energy which is then, very rapidly, converted into kinetic energy (Alexander, 1988; Alexander and Bennet-Clark, 1977; Gronenberg, 1996b).

The present study shows that such mechanisms are also employed by two dacetine ant genera, *Daceton armigerum* and *Strumigenys*: a catapult mechanism powered by the slow mandible closer muscles and equipped with a catch (the labrum) controlled by a fast muscle (the labral adductor). The contraction velocity of both muscle types has not been measured but is suggested by their morphology: the closer muscles have long sarcomeres and the central canal within each of their tubular fibres is very narrow. In contrast, the trigger muscles in both ant genera are composed of tubular fibres with much wider central cores and have very short sarcomeres (see Table 1). Sarcomere length generally correlates with contraction velocity [short sarcomeres cause fast contractions (O'Connor *et al.* 1982; Costello and Govind, 1983; Stephens *et al.* 1984; Günzel *et al.* 1993) because the more elements that contract in series, the faster the entire fibre will shorten] and, for reasons not yet entirely understood, the diameter of the central canal of tubular muscle fibres also correlates with contraction velocity (Gronenberg and Ehmer, 1995). It is thus reasonable to assume that, in dacetines, the mandible closer muscles which power the trap-jaw action are slow yet strong (as they are in other ants; Bonness *et al.* 1995), whereas the trigger muscles are very fast.

Dietz and Brandao (1993) suggest a different mechanism for the fast mandible strike of the dacetine genus *Acanthognathus*, which involves neither a click mechanism nor energy storage. Considering the massive changes dacetine ants have gone through during evolution, it seems possible that the trap-jaw mechanism has also been modified. However, from biomechanical considerations (Gronenberg, 1996b), it is very unlikely that the trap-jaws of *Acanthognathus* sp. can work without a catch mechanism and be accelerated solely by contraction of the mandible closer muscle. It may thus be worthwhile to reinvestigate the mandible strike of *Acanthognathus*.

To initiate and control particularly fast movements, the nervous system must be specialized for speed, in addition to the animal possessing specialized mechanical structures and muscles. Accordingly, most attack or escape systems throughout the animal kingdom contain giant neurones to increase conduction velocity and monosynaptic, often electrotonic, connections to reduce synaptic delays (e.g. fish, Eaton *et al.* 1981; squid, Young, 1939; earthworm, Günther, 1976; crayfish, Wiersma *et al.* 1953; Wine and Krasne, 1972; locust, Rowell and O'Shea, 1976; cockroach, Palka *et al.* 1977;

fly, Mulloney, 1969; Wyman *et al.* 1984; trap-jaw ant, *Odontomachus* sp., Gronenberg, 1995b).

The same design seems to operate in *Daceton* and *Strumigenys* species. In both genera, the trigger hair afferents contribute the thickest sensory axons and the trigger muscles are supplied by the thickest motor axons in the brain. The expense of producing such giant neurones is only justified (in evolutionary terms) if the speed of the behaviour controlled by these neurones is of vital importance for the animal. This is confirmed by the fact that the labral sensory afferents and adductor motor neurones are much thinner and the labral adductor muscle is smaller in other ants (Janet, 1905; W. Gronenberg, personal observations).

A second means of minimizing the delay required for neuronal processing, i.e. monosynaptic connections between sensory and motor neurones, also seems to be part of the dacetine trap-jaw design. While light microscopy alone cannot prove synaptic connectivity, the close juxtaposition of the giant sensory and motor neurones running in parallel over long distances and the tight intermingling of their finer processes are prerequisites and good indications for synaptic contacts between them. In *Odontomachus* sp., similar associations between the giant trigger and motor neurones have been found, and synaptic connections have subsequently been established by electron microscopy (Gronenberg, 1996a).

Few physical parameters are suited to increase nervous conduction velocity. When neuronal pathways are designed for ultimate speed of action, they will probably be composed of monosynaptically coupled giant neurones (in vertebrates they would, in addition, also feature a thick myelin sheath). It is thus not surprising that convergent evolution leads to a similar neuronal arrangement in all of the trap-jaw ants examined to date and in the fast sensory-motor systems of other insects as well.

I thank Birgit Ehmer, Jürgen Gadau and Klaus Schilder for collecting *Strumigenys*, Bert Hölldobler and Nicholas Strausfeld for providing specimens of *Daceton armigerum* and *Myrmecia*, respectively, and Birgit Ehmer (who also participated in videography) and Georg Krohne for expert help with scanning electron microscopy. I also thank Birgit Ehmer and Bert Hölldobler for helpful discussions and comments on the manuscript.

References

- ALEXANDER, R. MCN. (1988). *Elastic Mechanisms in Animal Movement*, pp. 81–90. Cambridge: Cambridge University Press.
- ALEXANDER, R. MCN. (1995). Leg design and jumping technique for humans, other vertebrates and insects. *Phil. Trans. R. Soc. Lond. B* **347**, 235–248.
- ALEXANDER, R. MCN. AND BENNET-CLARK, H. C. (1977). Storage of elastic strain energy in muscle and other tissues. *Nature* **265**, 114–117.
- BONNESS, V., JUST, S. AND GRONENBERG, W. (1995). The control of force production in ant mandibular muscles. In *Learning and Memory; Proceedings of the 23 Göttingen Neurobiology Conference* (ed. R. Menzel and N. Elsner), p. 213. Stuttgart, New York: Thieme.
- BROWN, W. L., JR (1954). A preliminary report on dacetine ant studies in Australia. *Ann. ent. Soc. Am.* **46**, 465–471.
- BROWN, W. L., JR (1976). Contributions toward a reclassification of the Formicidae. VI. Ponerinae, tribe Ponerini, subtribe Odontomachiti. Section A. Introduction, subtribal characters, genus *Odontomachus*. *Studia ent.* **19**, 67–171.
- BROWN, W. L., JR (1978). Contributions toward a reclassification of the Formicidae. VI. Ponerinae, tribe Ponerini, subtribe Odontomachiti. Section B. Genus *Anochetus* and bibliography. *Studia ent.* **20**, 549–652.
- BROWN, W. L., JR AND WILSON, E. O. (1959). The evolution of the dacetine ants. *Q. Rev. Biol.* **34**, 278–294.
- CARLIN, N. F. (1981). Polymorphism and division of labor in the dacetine ant *Orectognathus versicolor* (Hymenoptera: Formicidae). *Psyche* **88**, 231–244.
- COSTELLO, W. J. AND GOVIND, C. K. (1983). Contractile responses of single fibers in lobster claw closer muscles: correlation with structure, histochemistry and innervation. *J. exp. Zool.* **227**, 381–393.
- DEJEAN, A. (1986). Etude de comportement de predation dans le genre *Strumigenys* (Formicidae – Myrmicinae). *Insect Soc.* **33**, 388–405.
- DIETZ, B. H. AND BRANDAO, C. R. F. (1993). Comportamento de caca e dieta de *Acanthognathis rudis* Brown and Kempf, com comentarios sobre a evolucao da predacao em dacetini (Hymenoptera, Formicidae, Myrmicinae). *Revta. Bras. Ent.* **37**, 683–692.
- EATON, R. C., LAVENDER, W. A. AND WIELAND, C. M. (1981). Identification of the Mauthner-initiated response pattern in goldfish: evidence from simultaneous cinematographs and electrophysiology. *J. comp. Physiol.* **144**, 521–531.
- GOOSSEN, H. (1949). Untersuchungen an Gehirnen verschieden grosser, jeweils verwandter Coleopteren- und Hymenopteren-Arten. *Zool. Jb. Abt. Allg. Zool.* **62**, 1–64.
- GRONENBERG, W. (1995a). The fast mandible strike in the trap-jaw ant *Odontomachus*: temporal properties and morphological characteristics. *J. comp. Physiol. A* **176**, 391–398.
- GRONENBERG, W. (1995b). The fast mandible strike in the trap-jaw ant *Odontomachus*: motor control. *J. comp. Physiol. A* **176**, 398–408.
- GRONENBERG, W. (1996a). Neuroethology of ants. *Naturwissenschaften* **83**, 15–27.
- GRONENBERG, W. (1996b). Fast actions in small animals: springs and click mechanisms. *J. comp. Physiol. A* **178** (in press).
- GRONENBERG, W. AND EHMER, B. (1995). Tubular muscle fibers in ants and other insects. *Zoology* **99**, 68–80.
- GRONENBERG, W. AND PEETERS, C. (1993). Central projections of the sensory hairs on the gemma of the ant *Diacamma*: substrate for behavioral modulation? *Cell Tissue Res.* **273**, 401–415.
- GRONENBERG, W. AND TAUTZ, J. (1994). The sensory basis for the trap-jaw mechanism in the ant *Odontomachus bauri*. *J. comp. Physiol. A* **174**, 49–60.
- GRONENBERG, W., TAUTZ, J. AND HÖLLDOBLER, B. (1993). Fast trap jaws and giant neurons in the ant *Odontomachus*. *Science* **262**, 561–563.
- GÜNTHER, J. (1976). Impulse conduction in the myelinated giant fibers of the earthworm. Structure and function of the dorsal nodes in the median giant fiber. *J. comp. Neurol.* **168**, 505–532.
- GÜNZEL, D., GALLER, S. AND RATHMAYER, W. (1993). Fibre

- heterogeneity in the closer and opener muscles of crayfish walking legs. *J. exp. Biol.* **175**, 267–281.
- HÖLLDOBLER, B., PALMER, J. M. AND MOFFETT, M. W. (1990). Chemical communication in the dacetine ant *Daceton armigerum* (Hymenoptera: Formicidae). *J. chem. Ecol.* **16**, 1207–1219.
- HÖLLDOBLER, B. AND WILSON, E. O. (1990). *The Ants*. Cambridge MA: Belknap Press of Cambridge University Press.
- JANET, C. (1905). *Anatomie de la Tête du Lasius niger*. Paris: Limoges.
- MASUKO, K. (1984). Studies on the predatory biology of oriental dacetine ants (Hymenoptera: Formicidae). I. Some Japanese species of *Strumigenys*, *Pentastroma* and *Epitritus* and a Malaysian *Labidogermys*, with special reference to hunting tactics in short-mandibulate forms. *Insect Soc.* **31**, 429–451.
- MOFFETT, M. W. (1985). Revision of the genus *Myrmoteras* (Hymenoptera: Formicidae). *Bull. Mus. comp. Zool. Harv.* **151**, 1–53.
- MOFFETT, M. W. (1986). Trap-jaw predation and other observations on two species of *Myrmoteras* (Hymenoptera: Formicidae). *Insect Soc.* **33**, 85–99.
- MULLONEY, B. (1969). Interneurons in the central nervous system of flies and the start of flight. *Z. vergl. Physiol.* **64**, 243–253.
- NEDER, R. (1959). Allometrisches Wachstum von Hirnteilen bei drei verschieden großen Schabenarten. *Zool. Jb. Anat.* **77**, 411–464.
- O'CONNOR, K., STEPHENS, P. S. AND LEFEROVICH, J. M. (1982). Regional distribution of muscle fiber types in the asymmetric claws of Californian snapping shrimp. *Biol. Bull. mar. biol. Lab., Woods Hole* **163**, 329–336.
- PALKA, J., LEVINE, R. AND SCHUBIGER, M. (1977). The cercus-to-giant interneuron system of crickets. I. Some attributes of the sensory cells. *J. comp. Physiol. A* **119**, 267–283.
- RENSCH, B. (1956). Increase of learning capability with increase of brain size. *Am. Nat.* **90**, 81–95.
- ROSSBACH, W. (1962). Histologische Untersuchungen über die Hirne naheverwandter Rüsselkäfer (Curculionidae) mit unterschiedlichem Brutfürsorgeverhalten. *Z. Morph. ökol. Tiere* **50**, 616–650.
- ROWELL, C. H. F. AND O'SHEA, M. (1976). The neuronal basis of a sensory analyser, the acridid movement detector system. I. Effects of simple incremental and decremental stimuli in light and dark adapted animals. *J. exp. Biol.* **65**, 273–288.
- STEPHENS, P. J., LOFTON, L. M. AND KLAINER, P. (1984). The dimorphic claws of the hermit crab, *Pagurus pollicaris*: Properties of the closer muscle. *Biol. Bull. mar. biol. Lab., Woods Hole* **167**, 713–721.
- WIERSMA, C. A. G., FURSHPAN, E. AND FLOREY, E. (1953). Physiological and pharmacological observations on muscle receptor organs of the crayfish, *Cambarus clarkii* Girard. *J. exp. Biol.* **30**, 136–150.
- WILSON, E. O. (1953). The ecology of some north American dacetine ants. *Ann. ent. Soc. Am.* **46**, 479–495.
- WINE, J. J. AND KRASNE, R. B. (1972). The organization of escape behaviour in the crayfish. *J. exp. Biol.* **56**, 1–18.
- WYMAN, R. J., THOMAS, J. B., SALKOFF, L. AND KING, D. G. (1984). The *Drosophila* giant fiber system. In *Neural Mechanisms of Startle Behavior* (ed. R. Eaton), pp. 133–161. New York: Plenum.
- YOUNG, J. Z. (1939). Fused neurons and synaptic contacts in the giant nerve fibers of cephalopods. *Q. J. microsc. Sci.* **78**, 367–386.