The oculomotor system of decapod cephalopods: eye muscles, eye muscle nerves, and the oculomotor neurons in the central nervous system

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CONTENTS

SUMMARY

Fourteen extraocular eye muscles are described in the decapods *Loligo* and *Sepioteuthis*, and thirteen in *Sepia*; they are supplied by four eye muscle nerves. The main action of most of the muscles is a linear movement of the eyeball, only three muscles produce strong rotations.

The arrangement, innervation and action of the decapod eye muscles are compared with those of the seven eye muscles and seven eye muscle nerves in *Octopus*. The extra muscles in decapods are attached to the anterior and superior faces of the eyes. At least the anterior muscles, and presumably also the superior muscles, are concerned with convergent eye movements for binocular vision during fixation and capture of prey by the tentacles. The remaining muscles are rather similar in the two cephalopod groups.

In decapods, the anterior muscles include conjunctive muscles; these cross the midline and each presumably moves both eyes at the same time during fixation. In the squids *Loligo* and *Sepioteuthis* there is an additional superior conjunctive muscle of perhaps similar function. Some of the anterior muscles are associated with a narrow moveable plate, the trochlear cartilage; it is attached to the eyeball by trochlear membranes.

Centripetal cobalt fillings showed that all four eye muscle nerves have fibres that originate from somata in the ipsilateral anterior lateral pedal lobe, which is the oculomotor centre. The somata of the individual nerves show different but overlapping distributions. Bundles of small presumably afferent fibres were seen in two of the four nerves. They do not enter the anterior lateral pedal lobe but run to the ventral magnocellular lobe; some afferent fibres enter the brachio-pallioviscera connective and run perhaps as far as the pallioviscera lobe.

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1. INTRODUCTION

Most cephalopods are fast moving predators with a highly developed visual system. They show pronounced linear and rotatory eye movements that serve to compensate the retinal image motion during head movements (Wells 1960; Dijkgraaf 1961; Budelmann 1970, 1975; Collewijn 1970; Messenger 1970, 1977; Hartline *et al.* 1979). Not surprisingly, there are differences between the oculomotor systems of octopods and decapods. Octopods (except of juvenile stages) fix objects monocularly and have very little, or no, overlap of their visual fields (Wells 1978). Decapods, in contrast, fix objects binocularly to move to the proper distance for the capture of the prey with their tentacles (Messenger 1977).

The octopus oculomotor system, which has recently been described in detail, comprises seven extraocular muscles, seven eye muscle nerves (some innervating more than one muscle), and motoneurons in the oculomotor centre, which receive direct input from the statocysts and indirect input from the visual system (Budelmann & Young 1984). The decapod oculomotor system, however, is less well described. There are thirteen (*Sepia*) or fourteen (*Loligo*) extraocular muscles and these are innervated by only four eye muscle nerves (table 1; Hillig 1912; Glockauer 1915; Thore 1939; Tompsett 1939; Young 1976). The greater number of eye muscles is due to the presence of additional anterior and superior muscles for turning the eyes medially forwards and upwards, respectively, presumably for binocular vision. The remaining superior, posterior and inferior eye muscles are rather similar to those of octopods.

An especially interesting feature of the anterior muscles is that some of them are connected across the midline, so that contraction on either side presumably moves both eyes (Owen 1835; Glockauer 1915; Tompsett 1939). Associated with the anterior muscles and the front of the eyeball is a trochlear cartilage, which probably moves to some extent with the eyeball (Glockauer 1915). The trochlear cartilages of the left and right eye are attached to the cranial cartilage in the midline. They are certainly involved in convergent eye movements but their function is unclear.

The arrangement and innervation of the decapod eye muscles have never been described in detail and there is confusion about the terminology of the various muscles and nerves (to some extent perhaps because of species-specific differences; table 1). The aim of this present work is to describe and illustrate the arrangement of the muscles and their innervation in more detail, as well as to localize the eye muscle motoneurons in the oculomotor centre. The work is part of a more detailed study of the decapod statocyst–oculomotor system.

2. MATERIALS AND METHODS

Several dissections were made of the extraocular eye muscles of specimens of various sizes of the following species: *Loligo pealei, L. vulgaris, L. forbesi,* and *L. plei* (all from the collection of fixed specimens at the Marine Biomedical Institute in Galveston), *Lolligun-*

Table 1. *The extraocular eye muscles of Loligo, Sepioteuthis and Sepia and the nerves by which they are innervated (data from Tompsett (1939) and this study)*

(The columns to the right compare the different terminology that has been used for the decapod eye muscle nerves. No data are available on the innervation of the superior conjunctive muscle of squids; as it is most likely, however, that this muscle is innervated by a branch of the anterior superior ophthalmic nerve, it is attributed to this nerve. Note that the anterior and posterior inferior ophthalmic nerves are not included in this table since they do not innervate extraocular eye muscles.)

extraocular eye muscles		nerves		
Loligo, Sepioteuthis	*Sepia*	*Sepia* Hillig (1912) Tompsett (1939)	*Sepia* (Thore 1939)	*Loligo* (Young 1976)
m.ant.I	m.ant.I			
m.ant.II	—			
m.tr.I.	m.tr.I			
m.tr.II.	m.tr.II	n.oc.ant.	n.oc.ant.	n.oc.inf.ant.
—	m.tr.III			
m.ant.conj.I	m.ant.conj.I			
m.ant.conj.II	m.ant.conj.II			
m.inf.II	m.inf.II			
m.inf.I	m.inf.I	n.oc.post	n.oc.post.	n.oc.inf.post
m.sup.conj.	—			
m.sup.I	m.sup.I	n.oph.sup.ant.	n.oph.sup.post.	n.oc.sup.ant.
m.sup.II	m.sup.II			
m.sup.III	m.sup.III			
m.post.I	m.post.I	n.oph.sup.post.	n.oph.sup.post.rad.post.	n.oc.sup.post
m.post.II	m.post.II			

cula brevis (from the Gulf of Mexico), *Sepioteuthis lessoniana* (bred in Galveston from eggs from Japan), and *Sepia officinalis* (bred in Galveston from eggs from the Mediterranean Sea). For details of the dissection method and histological treatments of the eye muscle tissue, see Budelmann & Young (1984).

Histological sections were from brain series in the collection of J.Z.Y., many with Cajal's silver staining. Sections of juveniles were found to be particularly useful. The material was collected at Woods Hole (*Loligo pealei*), Plymouth (*Loligo forbesi*), Naples (*Loligo vulgaris*), and Bermuda (*Sepioteuthis sepioidea*).

Centripetal cobalt fillings of the eye muscle nerves of *Sepia officinalis* were done in six animals (mantle length between 75 and 90 mm) obtained from the Mediterranean Sea. The fillings were done from the orbital cavity, without opening the brain capsule. For the method of filling the eye muscle nerves with Co^{2+} ions, see Budelmann & Young (1984). After filling, the brain was not removed from its brain capsule to avoid damage. Instead, most of the cranial cartilage surrounding the brain was trimmed. For the precipitation of the Co^{2+} ions and subsequent treatment of the brain sections, see Budelmann & Young (1984, 1985).

To follow the course of the eye muscle nerves in the periphery and to compare the results with the histological findings, centrifugal cobalt fillings of the eye muscle nerves were done in four *Sepia officinalis* (mantle length between 75 and 95 mm) obtained from the Mediterranean Sea. The fillings were done from the neuropil of the anterior lateral pedal lobe (the oculomotor centre) after a midline cut of isolated head (brain and eyes) preparations. For the application of Co^{2+} ions into the neuropil of a brain region, see Novicki *et al.* (1990).

3. RESULTS

Following the descriptions of Glockauer (1915) and Tompsett (1939), the extraocular eye muscles are named 'anterior', 'posterior', 'superior', and 'inferior' according to their attachment sites at the cranial cartilage. The eye movements are suggested from the course of the muscles relative to the eye and their attachment sites at the orbital cartilage and the cartilaginous ring around the equator of the eyeball. A more precise description of the eye movements will be given below for each individual muscle. To indicate the position of the muscles relative to each other when they cross or overlap, the term 'inside' is used for muscles that run closer to the surface of the eyeball, and 'outside' for those that run closer to the orbit.

The experiments were performed with both the right and the left eyes, but to compare the results more easily, especially when describing the direction of eye movements, all results are reported as being from the *left* eye, throughout the text, diagrams and figures.

Note: In the vertebrate and invertebrate literature the terminology of eye movements is somewhat inconsistent and confusing, partly due to the fact that in some animals the eyes are situated laterally and in others frontally. In almost all cephalopods the eyes are situated *laterally*. In this paper, for simplicity and easier comparison with the earlier paper on *Octopus* eye movements (Budelmann & Young 1984), all straight eye movements produced by 'recti' muscles (i.e. during roll and yaw of the head) will be called *linear* eye movements, and all eye movements produced by 'oblique' muscles (i.e. during pitch of the head) will be called *rotations*. Linear eye movements, therefore, will be used for all horizontal and vertical movements (which cause a shift of the visual axis relative to the axes of the head), and rotations will be used for torsions (i.e. movements of the eye around its visual [antero-posterior] axis). More specifically, the terms for the various movements of the left (!) eye will be as follows (the equivalent terms used in ophthalmology are given in parentheses): *linear forwards* (for adduction), *linear backwards* (for abduction), *linear upwards* (for sursumduction or elevation), *linear downwards* (for deorsumduction or depression), *clockwise rotation* (for exocycloduction, or torsion with the upper pole of the eye templewards), and *anticlockwise rotation* (for incycloduction, or torsion with the upper pole of the eye nasalwards).

(a) The eye muscles of Loligo and Sepioteuthis

There are fourteen extraocular muscles attached to each eye (figure 1). Six muscles are mainly concerned with turning the eye(s) medially forwards (anterior muscles I and II, trochlear muscles I and II, and anterior conjunctive muscles I and II), one muscle turns the eye backwards (posterior muscle II), one downwards (inferior muscle I), and three upwards (superior muscle II, posterior muscle I, and superior conjunctive muscle I); the remaining three muscles act mainly to produce rotations (superior muscles I and III, and inferior muscle II).

(i) *The main eye muscles (figures 1, 2 and 3, for an overview)*

Anterior muscle I (m. anterior I). This is a strong muscle with a broad attachment to the base of the cranium. Its fibres run inside the trochlear cartilage, spreading gradually to insert at the equatorial ring of the eye. It is also attached to the inner surface of the trochlear cartilage. Its action is to turn the eye medially forwards and perhaps to hold the trochlear cartilage against the eyeball. It is innervated by the anterior oculomotor nerve (figure 4).

Anterior muscle II (m. anterior II). This muscle is large and strong. It arises from the base of the cranium and runs out obliquely downwards inside the anterior muscle I to insert on the equatorial ring ventrally almost as far as inferior muscle I, whose fibres it slightly overlaps. Its action is to turn the eye medially forwards and downwards and to rotate it clockwise. It receives a branch of the anterior oculomotor nerve.

Trochlear muscle I (m. trochlearis I). This is a strong muscle arising from the dorsal edge of the proximal part of the trochlear cartilage. It fans out inside the superior muscle III. It turns the eyeball medially forwards, with probably some anticlockwise rotation.

Trochlear muscle II (m. trochlearis II). This is a thin

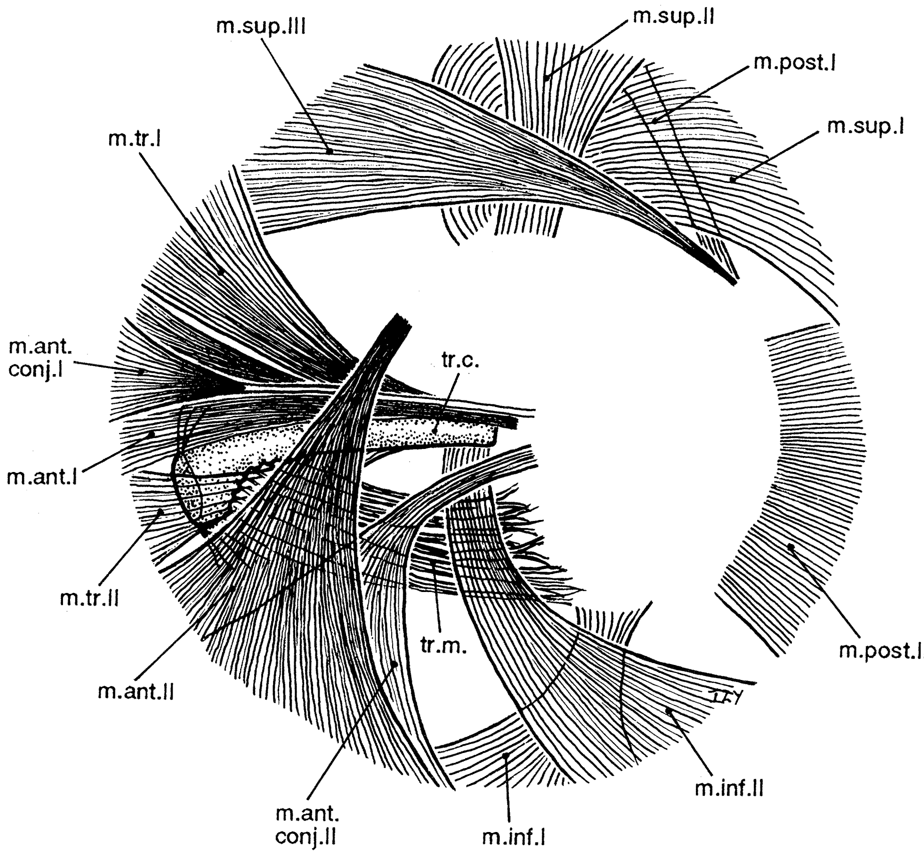


Figure 1. Ring of extraocular eye muscles of the left eye of *Loligo pealei*, seen laterally as a flattened preparation after removal of the eyeball. Note: for clarity the anterior conjunctive muscle I is shown inside anterior muscle I, although it really lies outside.

muscle with fibres that arise along the ventral edge of the trochlear cartilage, more distally than trochlear muscle I, fanning out only a little to overlap anterior muscle II but not anterior muscle I. It turns the eye medially forwards.

Superior muscle I (m. superior I). This muscle is a thin sheet of fibres that arises dorsally from the orbital cartilage and runs backwards around the dorsal and posterior surfaces. It is the most superficial of the superior muscles, but runs inside posterior muscle I. It rotates the eye anticlockwise, with some upwards movement.

Superior muscle II (m. superior II). This muscle is narrower and stronger than superior muscle I and lies inside the latter. It has a similar origin at the orbital cartilage but runs straight dorsally. It turns the eye upwards.

Superior muscle III (m. superior III). This is the strongest of the three superior muscles. It lies inside superior muscles I and II. It arises from the orbital cartilage posteriorly and runs forward to insert on the equatorial ring along the upper anterior surface of the eye. It rotates the eye clockwise.

Posterior muscle I (m. posterior I). This muscle consists of a narrow band of parallel fibres that arise dorso-posteriorly from the orbital cartilage and run obliquely forwards to insert at the dorsal equatorial ring. The muscle turns the eye upwards and rotates it clockwise.

Posterior muscle II (m. posterior II). This muscle has a long series of parallel fibres arising from the back of the orbital cartilage and running straight outwards. The muscle turns the eye backwards.

Inferior muscle I (m. inferior I). This is a strong muscle that arises low down on the ventral orbital cartilage and runs obliquely forwards. It narrows to a waist and then fans out to a broad insertion on the equatorial ring. It contains two distinct sets of fibres, which cross at the waist. The muscle turns the eye downwards, with probably some anticlockwise rotation.

Inferior muscle II (m. inferior II). This muscle arises from the extreme base of the trochlear cartilage and the floor of the cranium, close to the origin of anterior muscle I. It passes immediately across conjunctive muscle II and proceeds downwards and backwards (figure 10), spreading out inside inferior muscle I to insert along the ventral equatorial ring. Its action is to rotate the eye clockwise, with some downwards movement.

(ii) *The conjunctive eye muscles (figures 1, 2 and 3, for an overview)*

In loliginids there are three muscles that have been called *conjunctive muscles* (Glockauer 1915) because the corresponding muscles of the left and right eye are connected with each other across the midline, or have a joint attachment to the cartilage in the midline (figure 6). The anterior conjunctive muscles I and II

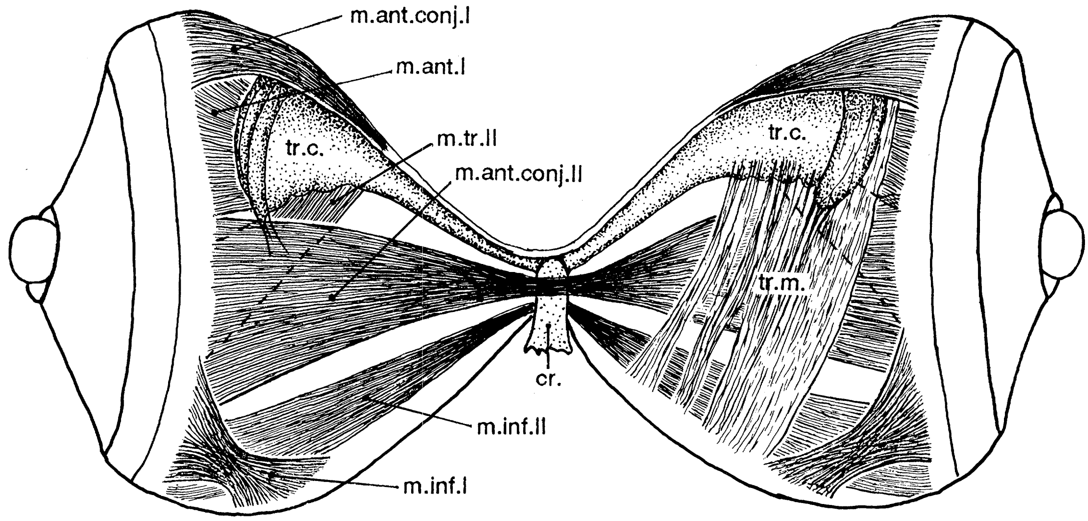


Figure 2. Arrangement of the extraocular eye muscles and trochlear cartilages on the anterior surface of the eyeballs of *Sepioteuthis lessoniana*. The trochlear membranes have been removed from the right eye.

are connected with their contralateral peers below the brain and presumably each moves both eyes at once. For the superior conjunctive muscle we have unfortunately only one specimen each of *Loligo pealei* and *Loligo forbesi* and they show different conditions. In the former the muscle joins its peer via a continuous tendon above the brain. In the specimen of *Loligo forbesi* it is attached by its tendon to the cartilage in the midline. In this species the muscle is not 'conjunctive' and moves only its own eye.

The two anterior conjunctive muscles are very unlike in structure and form (figures 1 and 2). The more dorsal anterior conjunctive muscles I of the left and right eye are united by a tendon in the midline. The more ventral anterior conjunctive muscle II, however, has no tendon but has muscle fibres that cross the midline to join the fibres of its contralateral peer. It is not certain whether individual bundles of muscle fibres run the whole course from the ipsi- to the contralateral eye.

Anterior conjunctive muscle I (m. conjunctus anterior I). This muscle consists of a rather short fan of fibres spreading widely to be attached to the equatorial ring (figures 3, 5 and 10). The fibres converge to a strong tendon, which runs in a groove along the length of the trochlear cartilage into which it is held by a covering sheath (figures 4 and 17). It joins the tendon of the corresponding muscle of the contralateral eye in the midline (figure 9); there the tendons pass through a tunnel, which is lined by the thin covering membrane (figure 8). The tendon is composed of long nucleated cells with fibres between (figure 11). There is a core of cells near the centre. The surface of the tendon is covered by a thin epithelium and a similar layer lines the sheath. The crossing tendon lies in a sling composed of the membranes that surround it (figure 7). This crossing lies immediately below the connectives that join the brachial and pedal lobes of the brain. There is no cushion or pad above the tendon, as there is in *Sepia*. This arrangement forms a pulley, as the name 'trochlear' suggests. Pulling on the tendon on one side turns the opposite eye medially forwards. Thus contraction of either muscle turns both eyes.

Anterior conjunctive muscle II (m. conjunctus anterior II). The fibres of this muscle do not join to form a tendon.

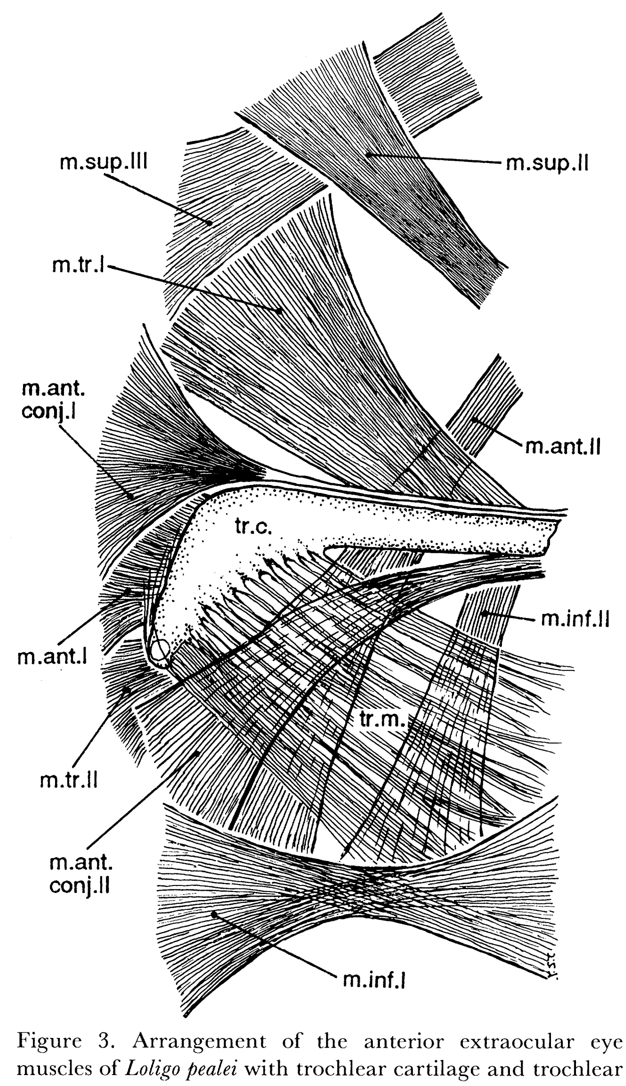
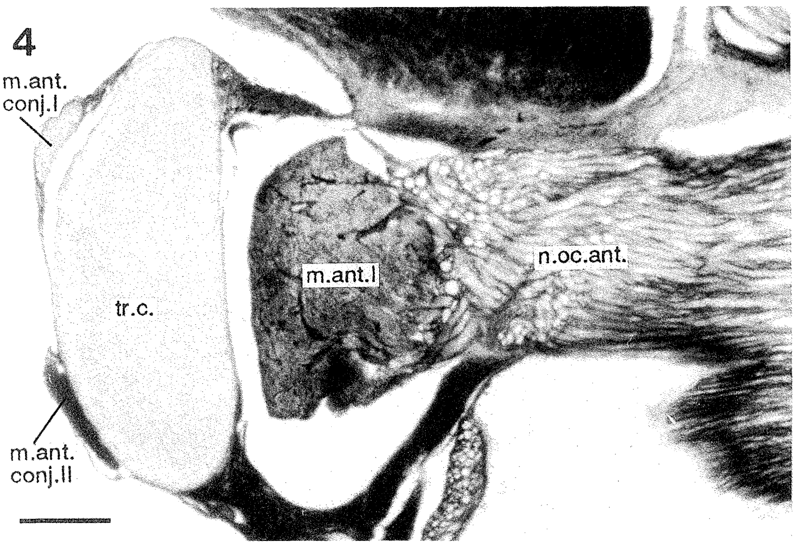
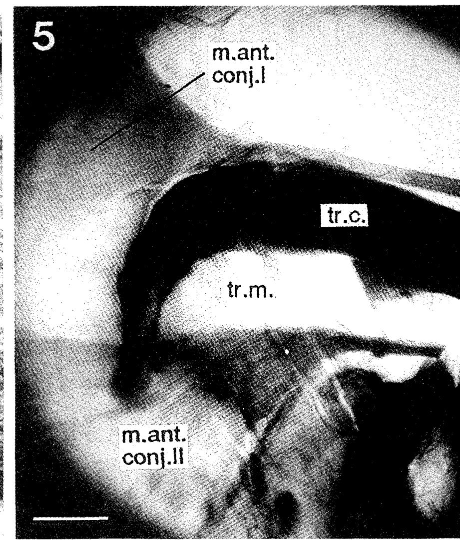
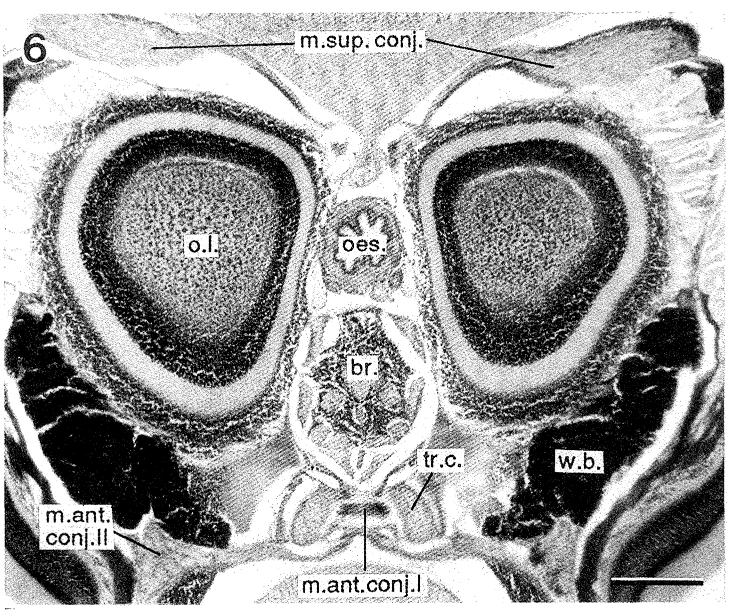


Figure 3. Arrangement of the anterior extraocular eye muscles of *Loligo pealei* with trochlear cartilage and trochlear membrane, seen from the outside of the eyeball.







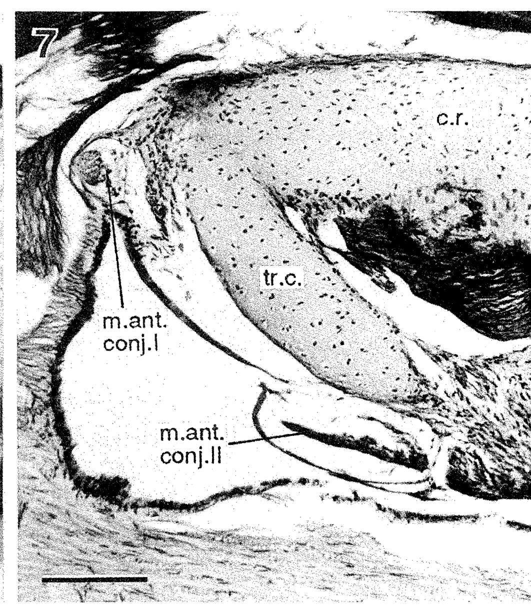


Figure 4. The anterior conjunctive muscles and anterior oculomotor nerve at the base of the trochlear cartilage. *Sepioteuthis sepioidea*. Horizontal section (compare figure 17). Cajal stain. Scale bar is 300 μm.

Figure 5. Preparation of some of the anterior eye muscles, showing the trochlear cartilage, the trochlear membrane and the two anterior conjunctive muscles. *Loligo pealei*. Mayer's haemalum stain. Scale bar is 500 μm.

Figure 6. The superior and two anterior conjunctive muscles crossing the midline. *Loligo pealei*. Transverse section. Haematoxylin and eosin stain. Scale bar is 500 μm.

Figure 7. Crossing of the two anterior conjunctive muscles. *Loligo vulgaris*. Sagittal section. Cajal stain. Scale bar is 200 μm.

They converge towards the midline to make a single bundle, which crosses to insert on the contralateral eye (figures 12 and 14). The crossing fibres are undoubtedly muscular and are accompanied by nerve fibres (figures 13 and 15). The crossing lies ventral to the bases of the trochlear cartilages (figure 12). Above the centre of the crossing there is a pad of connective tissue with some large veins. Lateral to the crossing the muscle fibres spread broadly and are interspersed with fibres of the trochlear membrane. This makes it difficult to follow the course of the muscle fibres and to decide whether they pass inside or outside the membrane.

The course of the muscles fibres has been most clearly seen in sections of *Sepioteuthis* (figures 16–21). The fibres spread out immediately lateral to the trochlear cartilage and separate into many small bundles interspersed by strands of connective tissue (figures 16 and 17). Sections at this level show irregular bundles embedded in a network of connective tissue. It is possible that some of the muscle fibres are attached to the strands that penetrate the bundles, but some of the bundles proceed outwards from the midline without interruption. The more dorsal of the bundles run close to the trochlear cartilage but separated from it by thick strands of connective tissue

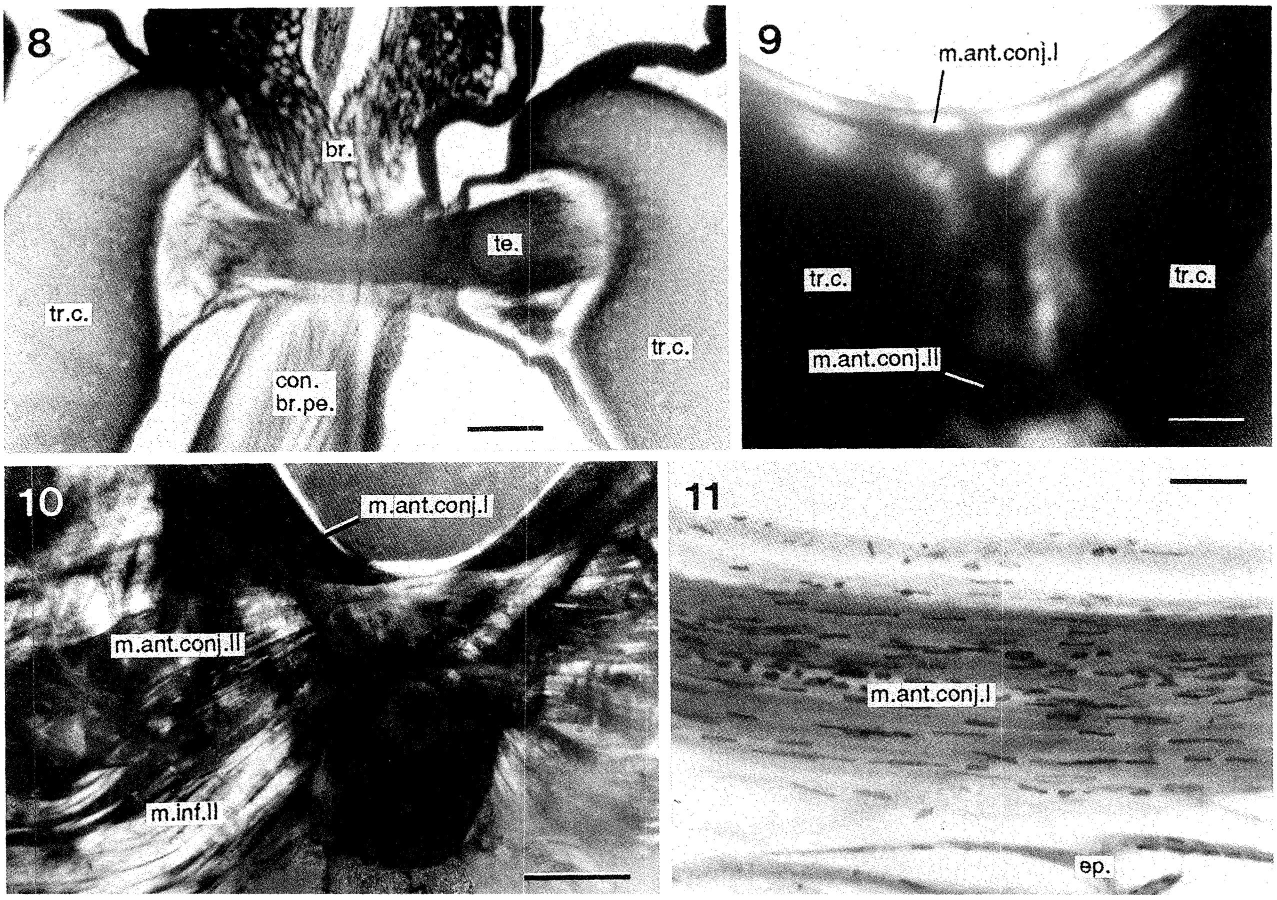


Figure 8. Crossing tendon of the anterior conjunctive muscle I. *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 100 μm.

Figure 9. Preparation of the crossing tendon of anterior conjunctive muscle I. The crossing of the anterior conjunctive muscle II is seen out of focus. *Loligo plei*. Scale bar is 400 μm.

Figure 10. Preparation of the two anterior conjunctive muscles crossing the midline, and the inferior muscle II, seen in polarized light. *Sepioteuthis lessoniana*. Mayer's haemalum stain. Scale bar is 2 mm.

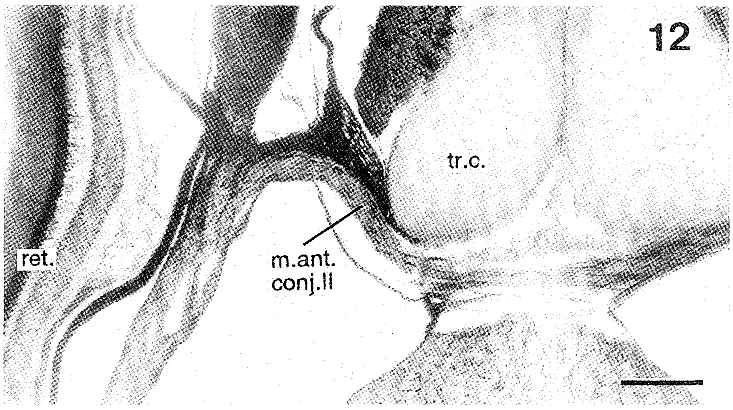
Figure 11. Crossing tendon of anterior conjunctive muscle I. *Sepioteuthis sepioidea*. Transverse section. Cajal stain. Scale bar is 30 μm.

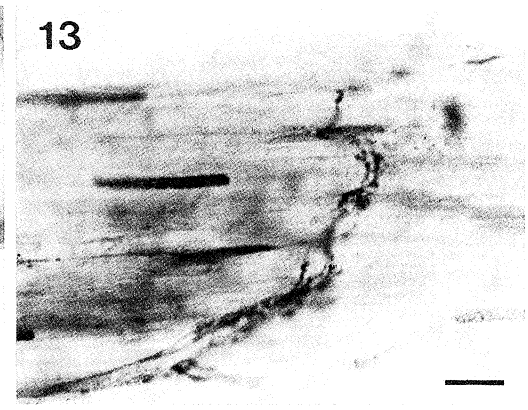
(figure 18). The muscular strands are so irregular and mixed with the connective tissue that the length of each bundle is uncertain. In *Sepioteuthis* some of the bundles are attached to the distal end of the cartilage (figures 19–21). Other bundles of the muscle fan out and run in an anterior and somewhat ventral direction; their exact sites of attachment to the eyeball are uncertain. In *Loligo* no fibres of the anterior conjunctive muscle II have been seen attached to the trochlear cartilage; their attachment to the eyeball is at its antero-ventral face. In both genera contraction of the muscle turns the eye medially forwards and downwards; presumably either muscle turns both eyes.

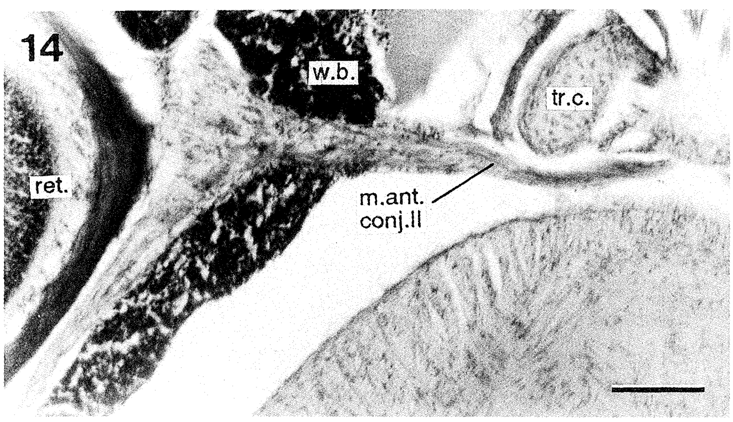
Superior conjunctive muscle (m. conjunctus superior). This muscle is attached to the upper surface of the eyeball at the level of the equatorial ring (figure 6) and turns the eye upwards. Its long tendon runs above the optic lobe to the midline. In juvenile *Loligo pealei* the tendons of the left and right muscle join in a tunnel beneath the cartilage at the extreme front end of the cranium, above the inferior frontal lobe (figure 22). At this juvenile stage, contraction of the muscle on either side presumably moves both eyes. In sections of *Loligo vulgaris* of 5 cm mantle length the situation appears to be different. The tendons of the two superior conjunctive muscles are inserted away from each other onto a cartilaginous knob, and are not joined (figure 23). Each muscle, therefore, moves only its own eye. The knob is attached to the front end of the cranium, which is called 'the cephalic process' (Williams 1909). The long, thin tendon proceeds outwards above the optic lobe and its muscle fibres are inserted along the dorsal border of the equatorial ring of the eyeball.

(iii) *The trochlear cartilage and trochlear membrane*

The trochlear cartilage is a narrow plate attached to the antero-medial surface of the eyeball. It differs in shape in various decapod species (Glockauer 1915). Its narrow base is attached to the floor of the cranium (figure 24). The attachment is narrow and allows for some movement of the trochlear cartilage with the







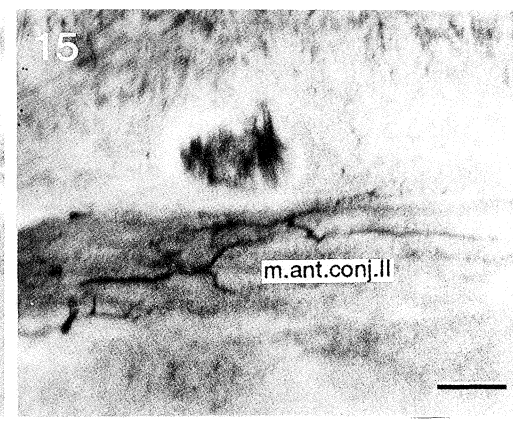


Figure 12. Bases of the two trochlear cartilages and the crossing of the anterior conjunctive muscle II. *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 150 μm.

Figure 13. Nerve fibres running across anterior conjunctive muscle II at its crossing. *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 10 μm.

Figure 14. Anterior conjunctive muscle II. Juvenile *Loligo pealei*. Transverse section. Haematoxylin and eosin stain. Scale bar is 500 μm.

Figure 15. Nerve fibres running along anterior conjunctive muscle II at its crossing. *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 30 μm.

eyeball. The shaft of the cartilage expands passing outwards and is grooved for the tendon of anterior conjunctive muscle I.

In *Loligo* the axis of the trochlear cartilage turns ventrally, giving it the form of a hockey stick (figures 1, 3, 5, and 28). The distal end of the cartilage is thicker than the rest and is composed of a complex of layers with clefts between them (figure 25). The end of the cartilage stains more darkly than the rest with haematoxylin, showing a complex internal structure (figure 27). The distal end of the cartilage is not smooth but frays out into a number of fibrous extensions (figure 28). These continue as a series of strands, which we shall call the 'trochlear membrane' (figure 32). The edges of the cartilage taper off gradually into these strands of trochlear membrane tissue. The typical cartilage tissue becomes gradually modified, thinner and more cellular towards the edge and changes into that of the membrane (figure 26). The trochlear membrane then forms sheets extending from the trochlear cartilage dorsally and ventrally, apparently serving to hold the cartilage against the eyeball. Proceeding away from the trochlear cartilage the fibres of the trochlear membrane join to form larger strands, which pass ventrally to be attached to the wall of the orbit (figure 33). In the main body of the cartilage are rounded cells scattered at intervals in an apparently structureless matrix. Towards the periphery the cells become arranged in rows and fibres can be seen in the matrix that are perhaps collagenous. The trochlear membrane is made up of strands of rounded cells in which fibres form serial thickenings; some of these may run in spirals (figure 29). The trochlear cartilage and membrane and the anterior conjunctive muscles are covered externally by sheets of epithelial cells with irregular nuclei and much pigment (figure 30). This layer becomes thinner where the tendon and muscle cross the midline.

In *Sepioteuthis* the trochlear cartilage is a broad plate, but its outer end is even more complex than in *Loligo*. At the base it is attached only by a narrow band of cartilage, which probably allows considerable movement (figures 20 and 24). The distal end differs from that of *Loligo* in that there is some expansion dorsally as well as ventrally (figures 31 and 33). The extent of expansion, however, differs between individuals, and sometimes even between the left and the right cartilage of the same individual. The expansion

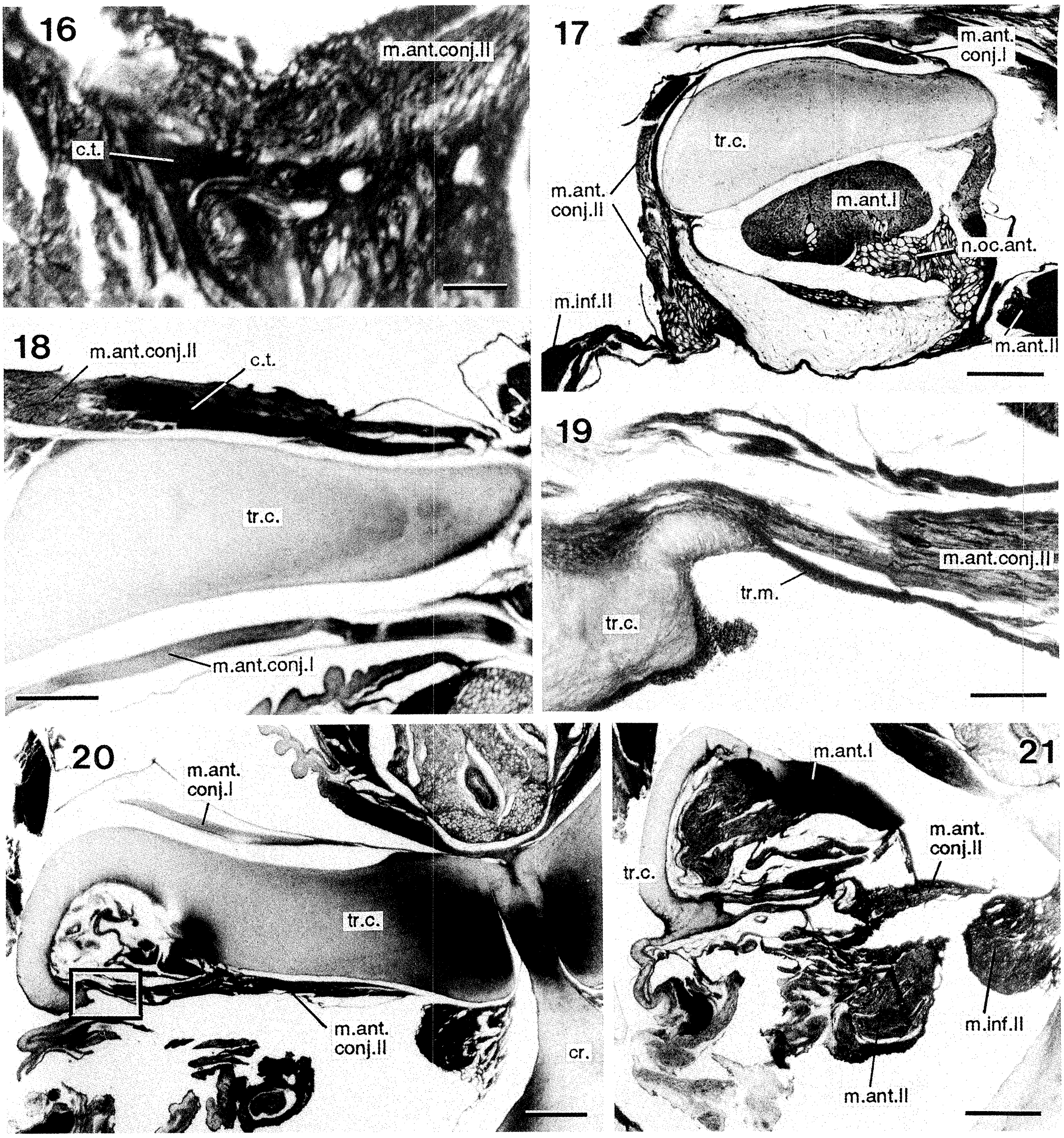


Figure 16. Enlarged view of anterior conjunctive muscle II where it breaks up into small bundles among dense connective tissue. *Sepioteuthis sepioidea*. Cajal stain. Scale bar is 50 μm.

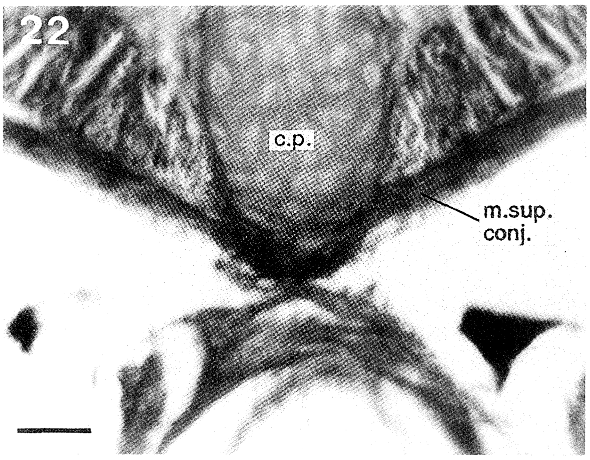
Figure 17. Anterior conjunctive muscle II divided into several branches. *Sepioteuthis sepioidea*. Horizontal section, slightly dorsal to figure 4. Cajal stain. Scale bar is 300 μm.

Figure 18. Trochlear cartilage and the two anterior conjunctive muscles. Note interruption of anterior conjunctive muscle II by connective tissue. *Sepioteuthis sepioidea*. Transverse section. Cajal stain. Scale bar is 500 μm.

Figure 19. Enlarged view of area outlined in figure 20 to show the attachment of the muscle to the cartilage. *Sepioteuthis sepioidea*. Transverse section. Cajal stain. Scale bar is 100 μm.

Figure 20. Trochlear cartilage and its attachment to the cranium. Part of the anterior conjunctive muscle II is attached to the tip of the trochlear cartilage. *Sepioteuthis sepioidea*. Transverse section. Cajal stain. Scale bar is 500 μm.

Figure 21. Anterior conjunctive muscle II and anterior muscle I attached to the tip of the trochlear cartilage. *Sepioteuthis sepioidea*. Transverse section, posterior to figure 20. Cajal stain. Scale bar is 400 μm.



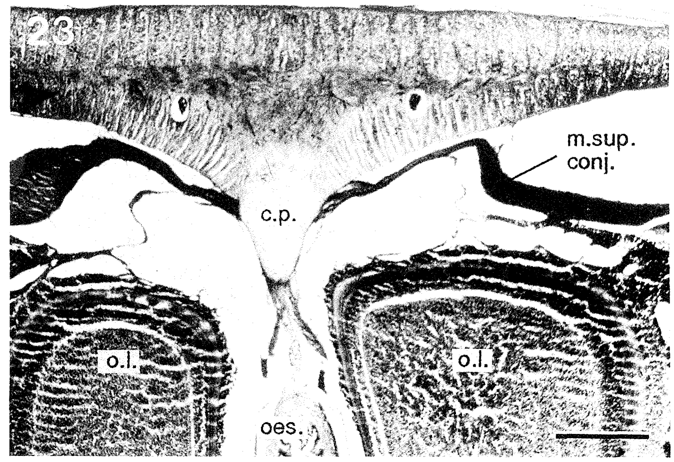


Figure 22. Crossing of tendons of the superior conjunctive muscles. Small juvenile of *Loligo pealei*. Transverse section. Haematoxylin and eosin stain. Scale bar is 40 μm.

Figure 23. Superior conjunctive muscles and their tendons attached to cartilage in the midline. Small specimen of *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 500 μm.

increases with age and/or size of the animal. In small animals (figure 33*a*) the end of the cartilage is hardly expanded dorsally or ventrally. It is crossed by a sheet of fine fibres. In larger animals (figures 33*b–d*) the end of the cartilage expands dorsally and especially ventrally into several projections to which fibres of the trochlear membrane are attached. The outline of the end of the cartilage is thus sometimes not clearly visible and the membrane appears to provide a continuation of the substance of the cartilage (figure 31). The more rigid ends of the cartilage remain, however, beneath this sheet (figure 33*d*). The complex nature of the end of the trochlear cartilage is well seen in sections (figures 19–21). The distal end is concave and encloses a cavity, within which lies the origin of the trochlear muscle II and some of the finer branches of anterior muscle I and anterior conjunctive muscle II (figure 34). Some branches of both of these muscles are attached to the cartilage, sometimes to special prolongations (figures 19–21). At the extreme tip the upper and lower edges of the cartilage come together to enclose a cavity (figures 34–36).

(iv) *The nerve fibres associated with the eye muscles and the trochlear cartilage and trochlear membrane*

In the sections of material stained with Cajal's method the nerve fibres of the eye muscles are well stained even to their finer branches (figures 13 and 15). The anterior oculomotor nerve divides near the base of the trochlear cartilage into branches for the anterior and trochlear muscles. The fibres are all large, up to 40 μm in diameter (figure 4) and remain large within the muscles until close to their terminations (figure 37). The nerve fibres extend either along or across the muscle fibres, often with occasional swellings. Bundles of nerves fibres pass among the eye muscle fibres, sometimes running across them or obliquely. In this situation it sometimes appears as if the nerve fibres were running spirally around the muscle fibres (figure 38). The nerve fibres in the bundles may be quite thick, as in figure 39, but others are very fine.

Bundles of fine nerve fibres are also common among the complex layers of the outer end of the trochlear cartilage. The finer branches of the fibres penetrate into the crannies between the layers (figure 40). Many of these nerve fibres accompany bundles of muscle fibres as they proceed to their attachments to the cartilage (figure 41). However, some of the finest nerve fibres run singly very close to the epithelial cells that cover the cartilage (figure 42). It seems likely that some of these fibres would be stimulated by movements of the cartilage, and may act as proprioceptors. If any of these are receptor systems, they should be associated with nerve cell bodies. Some large cells are indeed seen within the trochlear membrane, but it is not certain that they are neurons (figure 43).

(*b*) *The eye muscles of Sepia*

There is a total of twelve extraocular muscles attached to each eye of *Sepia* and an additional muscle passes between the two trochlear cartilages (figures 44–47). Five muscles, all innervated by the anterior oculomotor nerve, are mainly concerned with turning the eye(s) medially forwards (anterior muscle I, trochlear muscles I, II and III, and anterior conjunctive muscle I). One muscle turns the eye backwards (posterior muscle II), one downwards (inferior muscle I), and two upwards (superior muscle II and posterior muscle I). The remaining three muscles act mainly to produce rotations (superior muscles I and III and inferior muscle II). The anterior conjunctive muscle II is attached to the trochlear cartilage but not to the eyeball.

The *Sepia* eye muscle system thus differs in four ways from that of loliginids: (i) it has only one anterior muscle (anterior muscle II is absent); (ii) there is no superior conjunctive muscle; (iii) the location and form

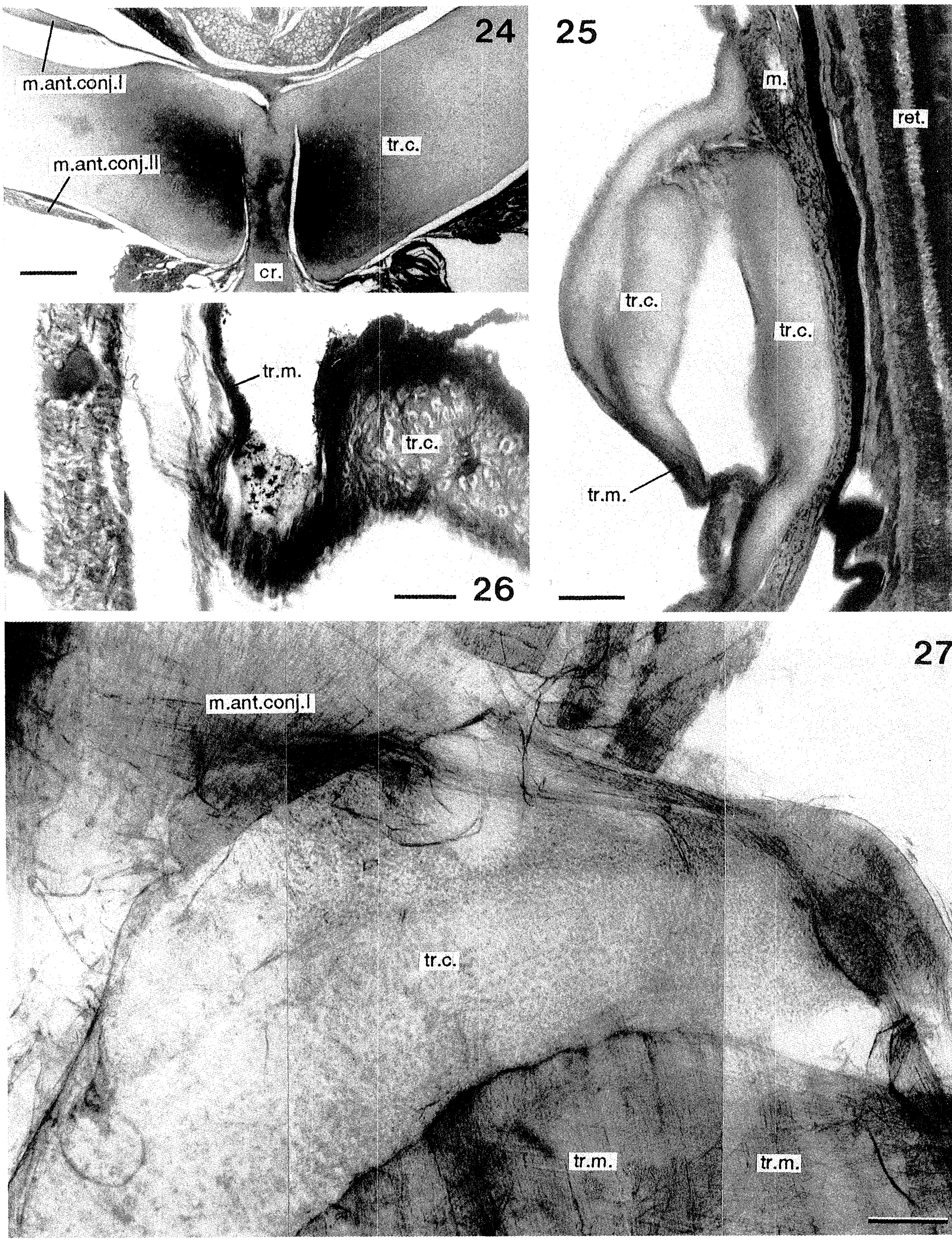


Figure 24. Narrow attachments of the trochlear cartilages to the base of the cranium. *Sepioteuthis sepioidea*. Transverse section. Cajal stain. Scale bar is 300 μm.

Figure 25. Distal end of the trochlear cartilage pressed against the eyeball. Note several layers and extensions to form the trochlear membrane. *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 150 μm.

Figure 26. The transition between trochlear cartilage and trochlear membrane. *Sepioteuthis sepioidea*. Cajal stain. Scale bar is 50 μm.

Figure 27. Tip of the trochlear cartilage showing the complex head and the attached strands of the trochlear membrane. *Loligo pealei*. Mayer's haemalum stain. Scale bar is 500 μm.

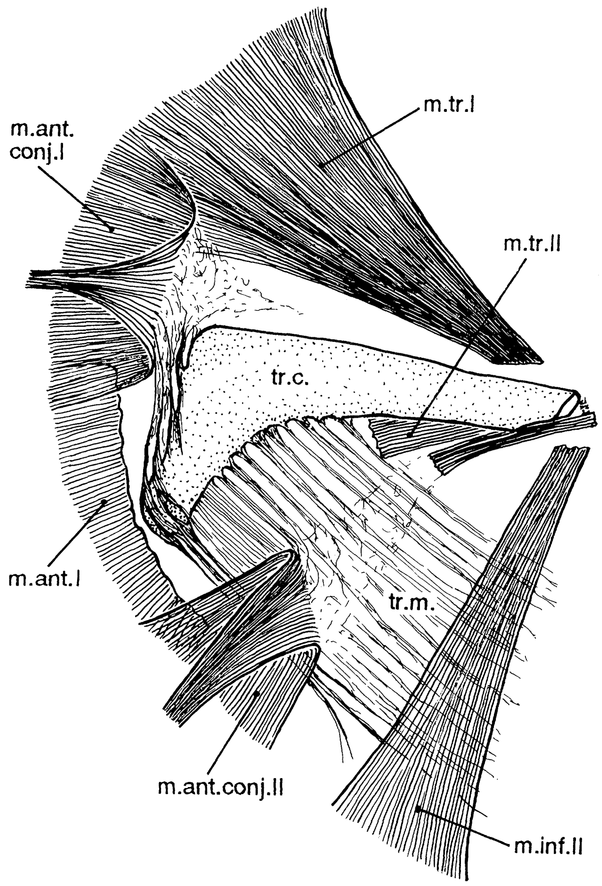


Figure 28. Arrangement of the anterior extraocular eye muscles of *Loligo pealei* with trochlear cartilage and trochlear membrane, seen from the outside of the eyeball. The two anterior conjunctive muscles have been cut and are turned back to show their attachments.

of anterior conjunctive muscle II is very different; and (iv) it has a third trochlear muscle.

(i) *The main eye muscles*

Anterior muscle I (m. anterior I). This muscle originates on the inner side of the base of the trochlear cartilage close to the origin of inferior muscle II. Its fibres run in parallel inside the trochlear cartilage, spreading peripherally to insertion on the equatorial cartilage (figures 45–47). Here it overlaps slightly the insertion of trochlear muscle II and anterior conjunctive muscle I. Anterior muscle I is a powerful muscle and turns the eye medially forwards. It is innervated by the anterior oculomotor nerve. In *Sepia,* there is no anterior muscle II; the muscle given that name by Glockauer (1915) is here called, in agreement with Tompsett (1939), trochlear muscle III (see below).

Trochlear muscle I (m. trochlearis I). This muscle has a broad origin on the dorsal edge of the trochlear cartilage along the middle part of its length (figure 46). The fibres proceed outwards in parallel, with little fanning except at the periphery. Their insertion overlaps that of anterior conjunctive muscle I and superior muscle III. The trochlear muscle I turns the eye medially forwards (with perhaps some anticlockwise rotation). It is innervated by a branch of the anterior oculomotor nerve.

Trochlear muscle II (m. trochlearis II). This muscle has a long origin along the ventral edge of the trochlear cartilage (figures 46, 47 and 49). Its fibres diverge slightly from the start and some may separate from the rest to run around the origin of trochlear muscle III (figure 46). The bundles reunite peripherally and all fan out to insert on the equatorial cartilage antero-ventrally, overlapping the insertion of inferior muscle I. The trochlear muscle II is strong and turns the eye forwards and downwards. The muscle is innervated by the anterior oculomotor nerve.

Trochlear muscle III (m. trochlearis III). This curious muscle arises on the inner surface of the distal end of the trochlear cartilage and passes inwards either between the two bundles of trochlear muscle II (figure 46) or between anterior muscle I and trochlear muscle II (figure 47). Its parallel fibres run to insertion on the scleral cartilage, close to the passages of the optic nerves. This course is unlike that of any other eye muscle in cephalopods and its significance is quite obscure. The muscle presumably exerts a strong pull holding the trochlear cartilage against the eyeball. The muscle is innervated by a long, distinct branch of the anterior oculomotor nerve (figure 45).

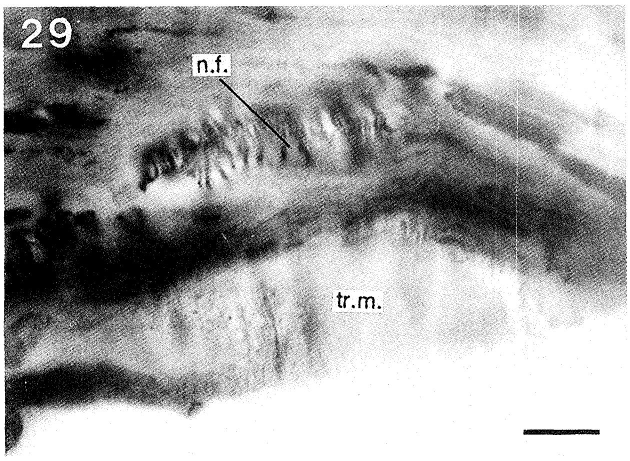
Superior muscle I (m. superior I). This muscle is a long, broad, thin sheet, extending half way around the circumference of the eyeball (figure 45). Its fibres arise along the dorsal wall of the orbital cartilage. The anterior fibres run straight, but the more posterior ones run obliquely backwards to insertion on the equatorial cartilage along the whole posterior extent of the eyeball, lying inside the fibres of posterior muscle II. The superior muscle I turns the eye upwards and rotates it anticlockwise. The muscle is innervated by a branch of the anterior superior ophthalmic nerve.

Superior muscle II (m. superior II). This muscle is a band of nearly parallel fibres. It arises from the anterior dorsal edge of the orbital cartilage inside superior muscle I; it proceeds dorsally to fan out slightly along the equatorial cartilage (figures 45 and 48). It turns the eye upwards. The muscle is innervated by a branch of the anterior superior ophthalmic nerve.

Superior muscle III (m. superior III). This muscle arises from the back of the orbital cartilage and runs obliquely forwards and laterally to be inserted on the eyeball far anteriorly outside trochlear muscle I (figure 45 and 48). It is a strong muscle that rotates the eye clockwise. The muscle is innervated by a branch of the anterior superior ophthalmic nerve.

Posterior muscle I (m. posterior I). This muscle is a thin narrow band passing from the postero-dorsal orbital cartilage upwards to insert on the equatorial cartilage (figures 45 and 48). It turns the eye upwards and rotates it a little clockwise. The muscle is innervated by fibres of the posterior superior ophthalmic nerve. The iris artery runs in front of this muscle.

Posterior muscle II (m. posterior II). This muscle consists of a long series of short bundles of fibres arising along the posterior edge of the orbital cartilage (figures 45 and 48). They all serve to turn the eye



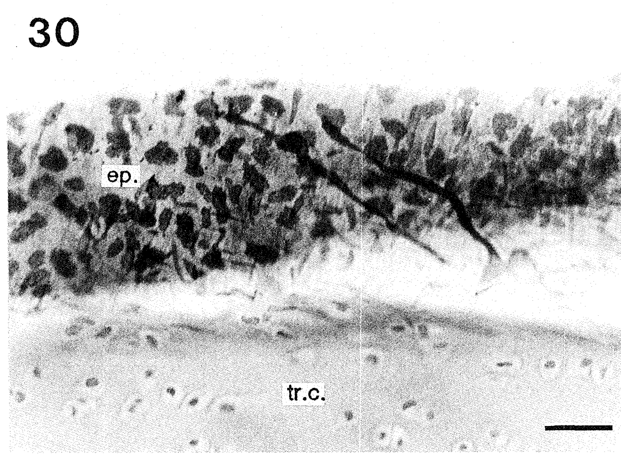


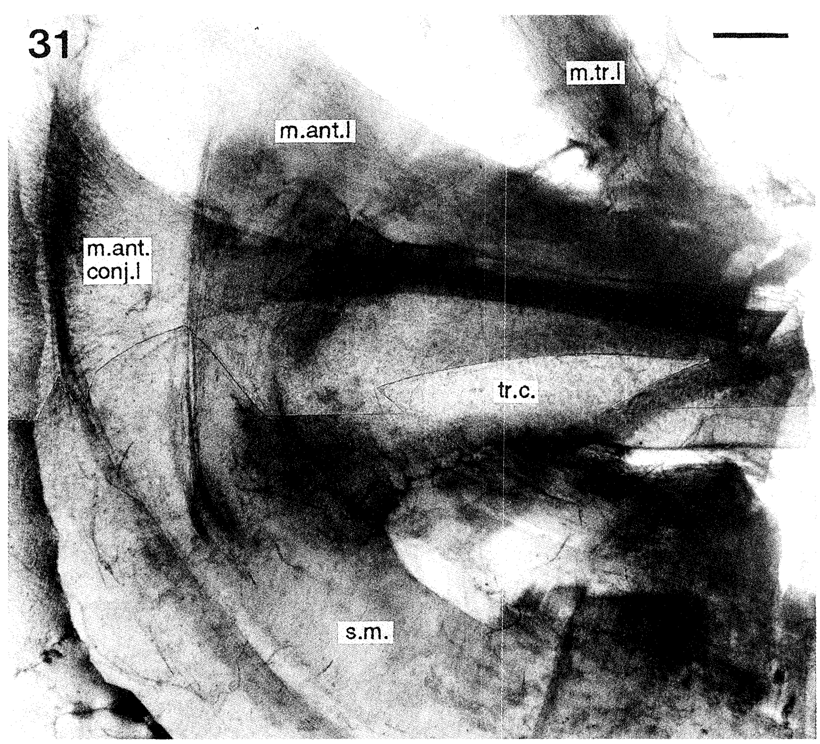
Figure 29. Anterior conjunctive muscle II with a bundle of small nerve fibres and a portion of the trochlear membrane with transverse banding. *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 10 μm.

Figure 30. Epithelium covering the trochlear cartilage. The nature of the two elongated fibres is uncertain. *Sepioteuthis sepioidea*. Transverse section. Cajal stain. Scale bar is 40 μm.

backwards. The muscle is innervated by several branches of the posterior superior ophthalmic nerve.

Inferior muscle I (m. inferior I). This muscle originates in a broad attachment to the orbital cartilage and runs almost straight to its insertion at the equator of the eyeball (figures 45 and 49). The muscle lies outside inferior muscle II. It is wide at its origin, then narrows to a waist and spreads out to its insertion. It is a strong muscle whose action is to turn the eye downwards, with probably some anticlockwise rotation. It is composed of two sets of fibres running in different directions and crossing, as can be seen in polarized light. The muscle is innervated by the posterior oculomotor nerve.

Inferior muscle II (m. inferior II). This muscle originates by a tendon inside the base of the trochlear cartilage and runs downwards to insert on the equatorial cartilage inside inferior muscle I (figures 44, 45 and 49). The muscle turns the eye downwards and rotates it clockwise. The muscle is innervated by a separate branch of the anterior oculomotor nerve.



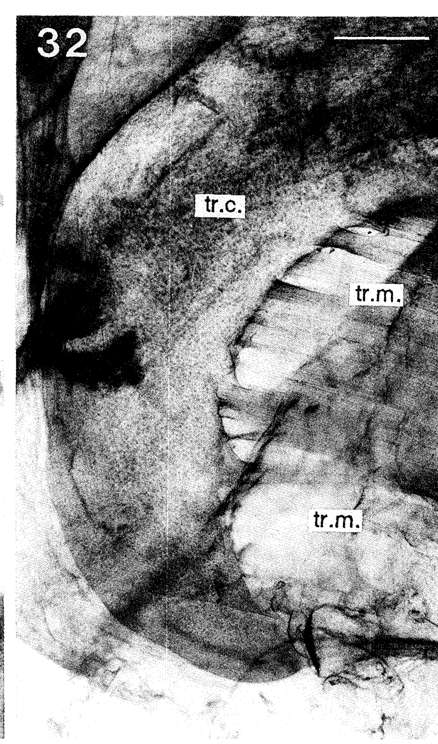


Figure 31. Tip of trochlear cartilage showing the trochlear membrane and smooth sheath. *Sepioteuthis lessoniana*. Mayer's haemalum stain. Scale bar is 500 μm.

Figure 32. Tip of trochlear cartilage with origin the trochlear membrane. *Loligo pealei*. Mayer's haemalum stain. Scale bar is 500 μm.

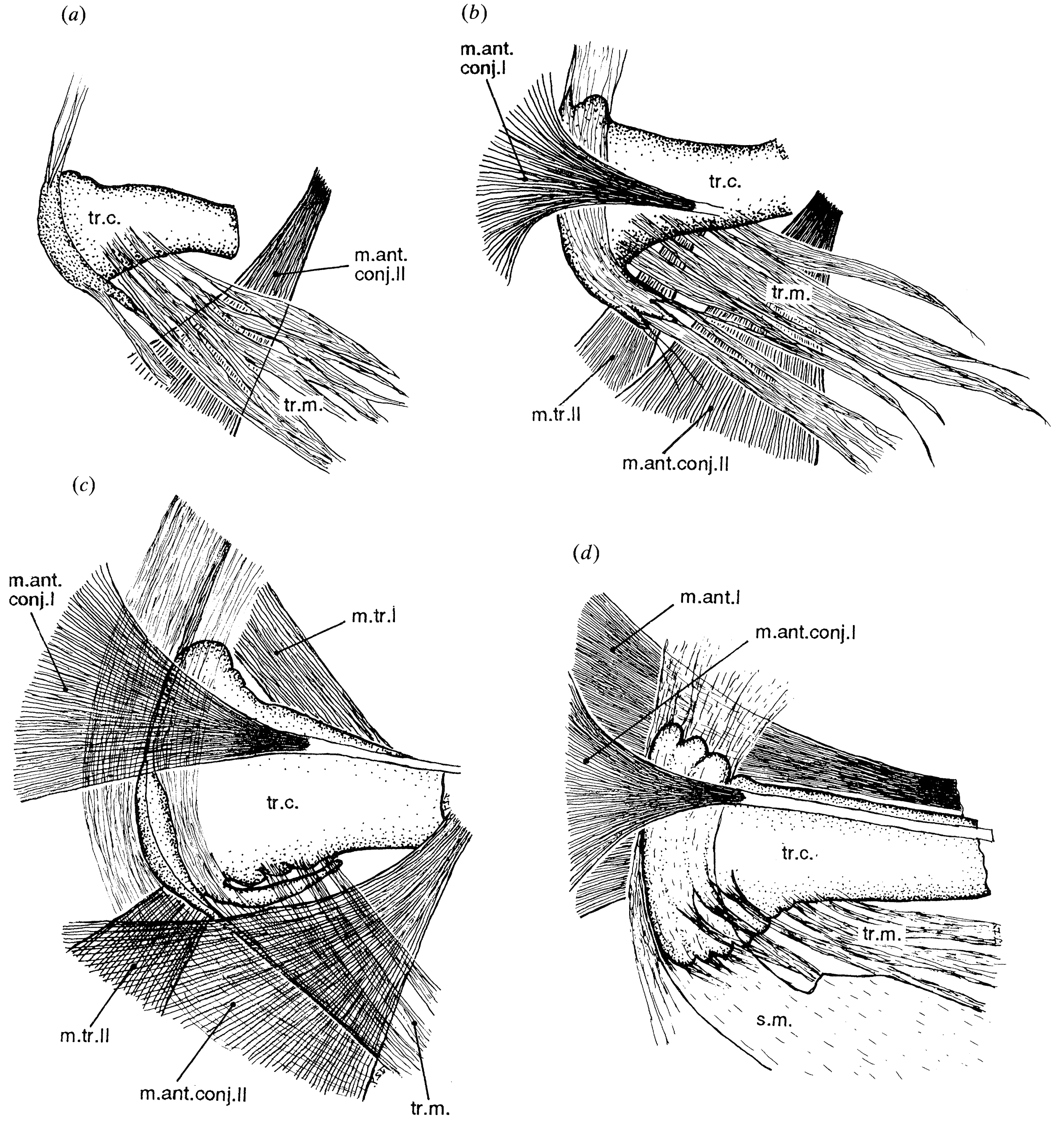


Figure 33. Changes of form of the distal end of the trochlear cartilage with increasing size of the animal. The diameter of the trunk of the cartilage indicates the increase in animal size from (*a*) to (*d*). Note that the anterior conjunctive muscles are shown somewhat displaced (during the preparation). In (*d*) part of the covering membranous sheet of the trochlear membrane have been cut away. *Sepioteuthis lessoniana.*

(ii) *The conjunctive muscles*

Anterior conjunctive muscle I (m. conjunctus anterior I). This muscle is similar to the anterior conjunctive muscle I of *Loligo*. Its tendon joins that of the corresponding muscle of the contralateral eye. The muscle consists of a small fan of fibres attached to the equatorial ring outside the trochlear cartilage and innervated by a branch of the anterior oculomotor nerve. Its tendon runs along the trochlear cartilage and across in front of the point at which the two cartilages come together and are attached to the base of the cranium (figures 50, 52 and 53). The conjoint tendon is enclosed in a fibrous sheath where it crosses the midline (figures 50 and 51). Its dorsal surface is smooth and presses against a pad of folded epithelium lying beneath the brain (figure 55). The ventral surface of the tendon carries a series of loose fibres, occupying an enclosed space. These conditions presumably provide for freedom of movement of the tendon, allowing either muscle to turn both eyes medially forwards.

Anterior conjunctive muscle II (m. conjunctus anterior II). This muscle runs between the two trochlear cartilages

Figures 34–36. Tip of the trochlear cartilage in progressively forward sections to show how the edges of the cartilage join to enclose a cavity. *Sepioteuthis sepioidea*. Transverse sections. Cajal stains. Scale bars are 300 μm.

in front of the point where they join the cranium (figures 44 and 51). The muscle probably represents the anterior conjunctive muscle II of loliginids. According to Glockauer (1915) that muscle has undergone reduction. Tompsett (1939) describes it as a 'tough little tendon passing from the other eye across the anterior surface of the bridge of the orbital cartilage'. He labels a tendon close to the base of the inferior muscle II. In fact it is doubtful whether this anterior conjunctive muscle II is a true eye muscle, that is to say one that is attached to the eyeball. The 'tendon' in the position described by Tompsett (1939) is the *outer* end of a muscle that runs between the two trochlear cartilages (figures 51–53). Most of the fibres of the muscle are inserted on the cartilage but some extend laterally over its base and may be attached to the tendon of inferior muscle II (figures 56–59). It is therefore possible that the anterior conjunctive muscle II has some influence on the eyeball through the action of inferior muscle II. Sections of a juvenile *Sepia* show that the muscle spans the two trochlear cartilages ahead of their junction with the cranial cartilage (figures 59–61). The anterior conjunctive muscle II is short but powerful and moves the two trochlear cartilages together, perhaps with some medially forwards movement of both eyes. The muscle is richly innervated (figure 54), probably by the anterior oculomotor nerve.

(iii) *The trochlear cartilage and trochlear membrane*

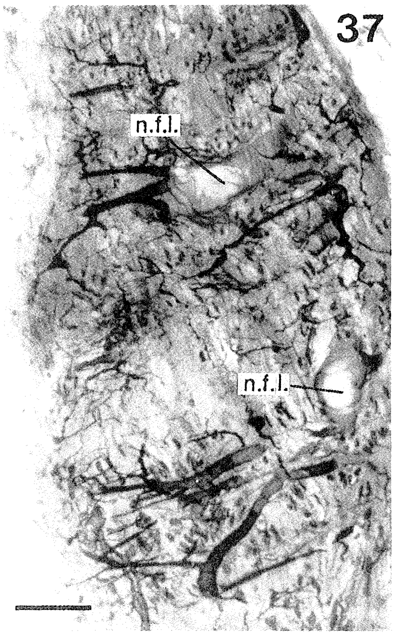
The trochlear cartilage of *Sepia* is a thin flat plate shaped like a banana, curved ventrally (figures 44 and 47). It narrows medially to a stalk, and the cartilage is here continuous with that of the floor of the cranium (figure 61). The outer end of the trochlear cartilage is held against the eyeball by dorsal and ventral membranes inserted on the tip of the cartilage and along its dorsal and ventral edges (figures 47 and 62–64). These trochlear membranes consist of thick and thin strands. They are similar to those of loliginids. At the outer ends these sheets are attached to the margins of the orbit. These membranes hold the cartilage firmly against the eyeball and provide the basis for the action of the three eye muscles that run from the trochlear cartilage to the eyeball. Trochlear muscles I and II are inserted on the equatorial cartilage and presumably serve to turn the eyes forwards. They depend for their action on the stiffness of the cartilage. Trochlear muscle III, however, runs from the scleral cartilage to the inner surface of the trochlear cartilage and may serve, like the trochlear membranes, to hold this latter pressed against the eyeball.

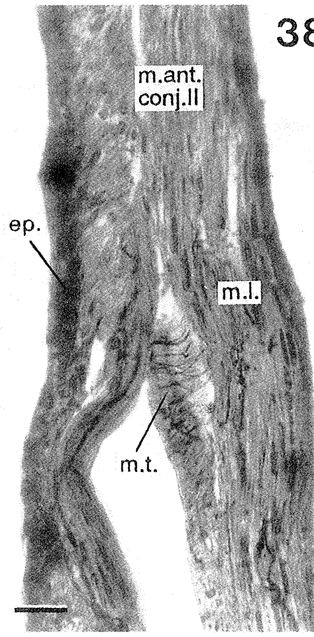
(c) The eye muscles of other decapods

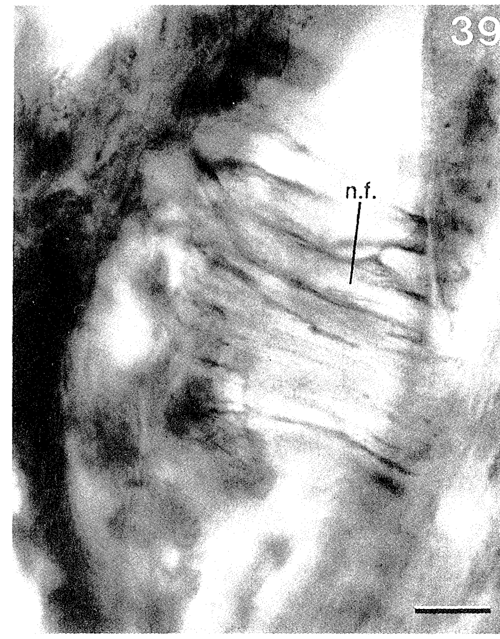
The presence of a trochlear cartilage and conjunctive muscles presumably indicates that the eyes are used for binocular vision for capture of prey by the tentacles. It would therefore be of interest to know how widely this condition is to be found among decapods. Since some deep-sea species are said not to have a trochlear cartilage (Glockauer 1915), we have looked for the cartilage and conjunctive muscles in *Spirula* and checked whether *Sepiola* is similar to *Sepia*.

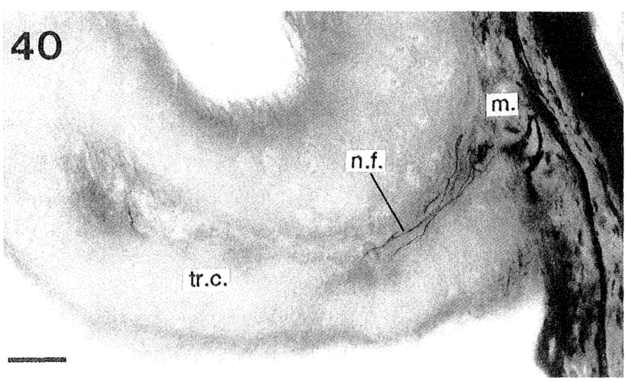
In *Sepiola* anterior conjunctive muscles I and II are present and resemble those of *Loligo*, rather than *Sepia* (figures 65 and 66). The anterior conjunctive muscle II appears as a continuous band of probably muscular fibres. It has no attachment to the basis of the trochlear cartilage.

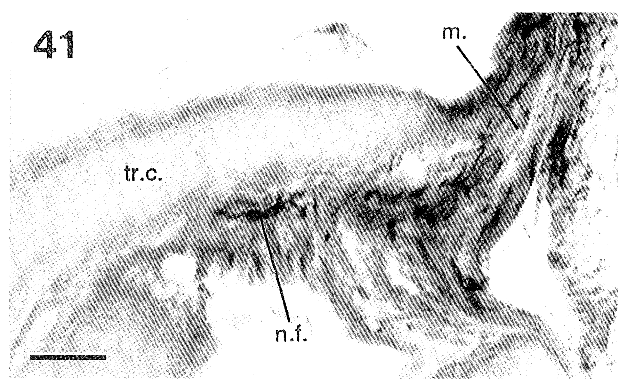
In *Spirula* also, in spite of its wide differences from other decapods, there are trochlear cartilages and two anterior conjunctive muscles that cross the midline (figures 67 and 68). It is not possible from our sections











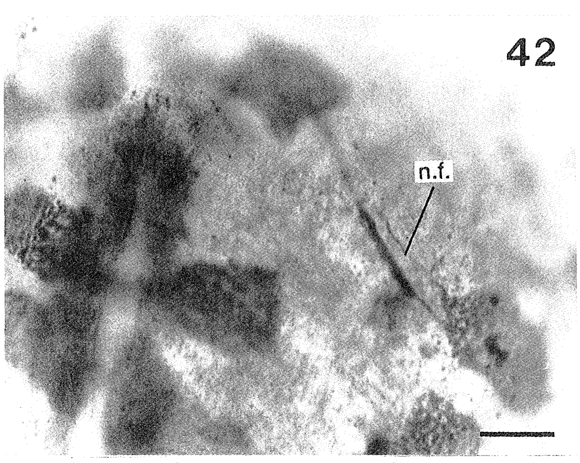


Figure 37. Anterior muscle I with large nerve fibres branching within the muscle. *Sepioteuthis sepioidea*. Transverse section. Cajal stain. Scale bar is 50 μm.

Figure 38. Nerve fibres in anterior conjunctive muscle II. When the muscle fibres are cut transversely or obliquely, the nerve fibre bundles give the appearance of spirals. *Sepioteuthis sepioidea*. Transverse section. Cajal stain. Scale bar is 20 μm.

Figure 39. Large bundle of nerve fibres (one branching) in anterior conjunctive muscle II. *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 10 μm.

Figure 40. Tip of trochlear cartilage showing folding and nerve fibres in the groove. *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 30 μm.

Figure 41. Tip of trochlear cartilage with muscle and nerve fibres in the groove. *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 40 μm.

Figure 42. Tip of trochlear cartilage with nerve fibres running among epithelial cells. *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 10 μm.

Figure 43. Soma of large cell in epithelium covering the trochlear membrane. *Sepioteuthis sepioidea*. Cajal stain. Scale bar is 20 μm.

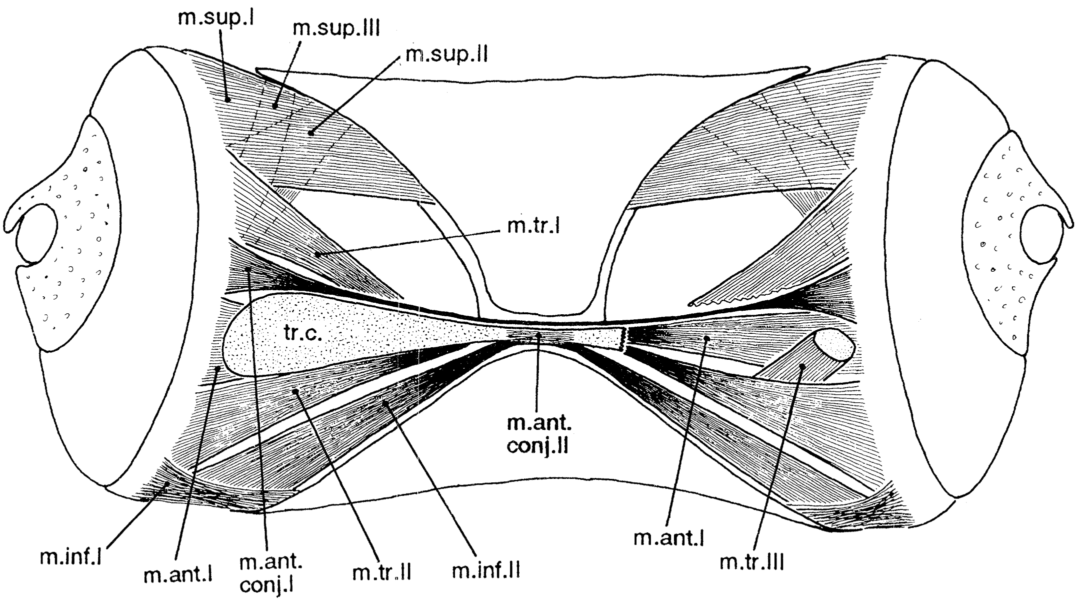


Figure 44. Arrangement of the extraocular eye muscles on the anterior surface of the eyeballs of *Sepia officinalis*, showing the conjoint anterior conjunctive muscles.

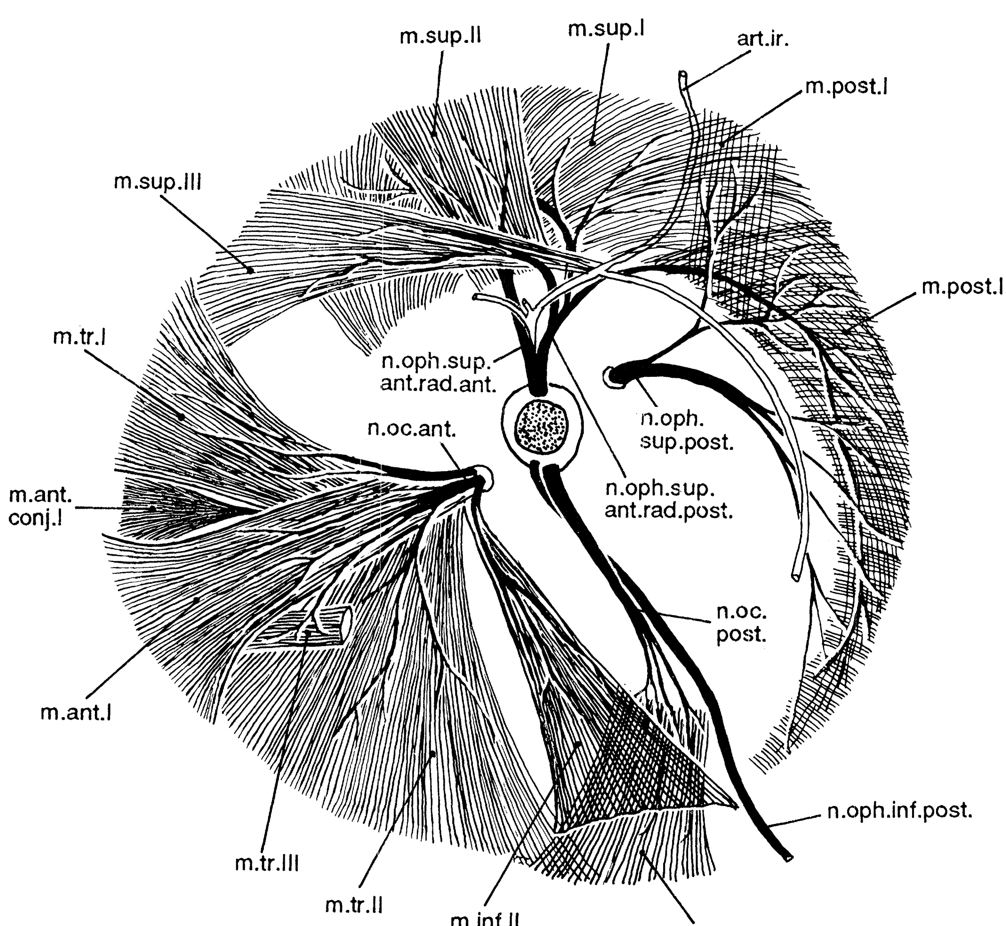


Figure 45. Ring of extraocular eye muscles of the left eye of *Sepia officinalis*, seen laterally as flattened preparation after removal of the eyeball.

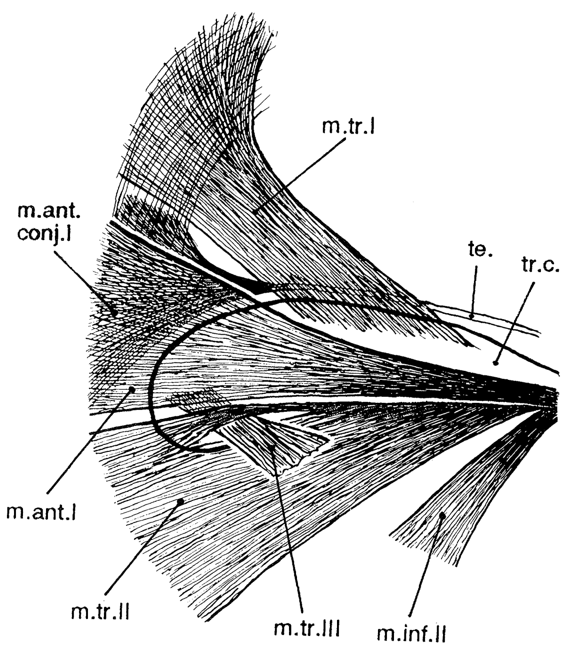


Figure 46. Trochlear cartilage and extraocular eye muscles of *Sepia officinalis* seen from the inside.

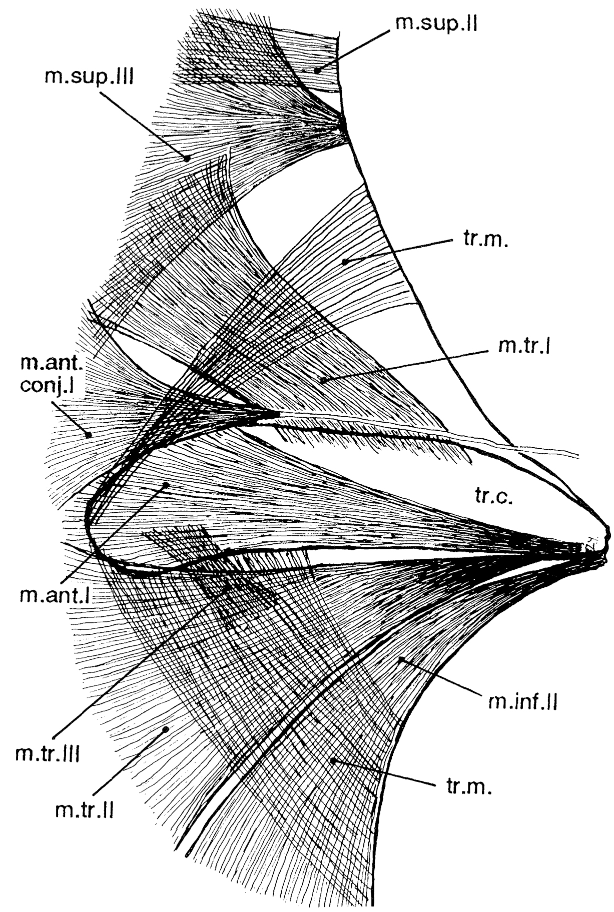


Figure 47. Trochlear cartilage and extraocular eye muscles of *Sepia officinalis* seen from the outside.

to decide whether there are muscle fibres in the strand of fibres of anterior conjunctive muscle II as it crosses the midline.

(*d*) *The innervation of the eye muscles of Sepia (figure 45 and table 1)*

Anterior oculomotor nerve (n. oculomotorius anterior). This nerve divides at entry to the orbit into three main branches. The dorsal branch innervates trochlear muscle I, the middle branch innervates anterior muscle I, with two long separate branches to trochlear muscles II and III, respectively; the ventral branch of the anterior oculomotor nerve innervates inferior muscle II. The anterior oculomotor nerve also sends branches to the anterior conjunctive muscles I and II (not shown in figure 45).

The anterior oculomotor nerve consists of fibres of varying diameter from 30 μm in diameter downwards (figures 69 and 70). The distribution of fibre sizes is not uniform. There is one large area without any fibres above 10 μm in diameter (figure 69). Small and very small fibres are distributed in small patches in all parts of the nerve. The smallest are less than 1 μm in diameter but there do not appear to be any areas composed of numerous very small fibres. A count of the number of fibres gave a total of 1100. This includes all detectable individual fibres down to the smallest, but many of the smaller are certainly not resolved. The area of the nerve with no fibres above 10 μm in diameter has 280 fibres.

Anterior superior ophthalmic nerve (n. ophthalmicus superior anterior). This nerve emerges with the optic tract and has two main branches. The anterior branch innervates superior muscle II, and the posterior branch innervates the superior muscles I and III.

Posterior superior ophthalmic nerve (n. ophthalmicus superior posterior). This nerve emerges by a distinct foramen, posterior to the optic tract foramen. It has two main branches. The dorsal branch innervates posterior muscle I and also the dorsal fibres of posterior muscle II. The much thicker ventral branch passes backwards around the origin of posterior muscle I, whose postero-ventral and ventral fibres it innervates.

Posterior oculomotor nerve (n. oculomotorius posterior). This nerve arises high up in the pedal lobe. It enters the orbit with the optic tract near to the posterior inferior ophthalmic nerve. It runs across the floor of the orbit to innervate inferior muscle I.

Note: The anterior and posterior inferior ophthalmic nerves innervate the muscular eyelid, but no extraocular muscles (Tompsett 1939). Therefore, they can not be considered as eye muscle nerves.

(*e*) *The oculomotor neurons of Sepia*

The origins of the efferent fibres, that is the location of the somata of the eye muscle motoneurons, and the course and destination of the afferent fibres, which are present in two eye muscle nerves (anterior oculomotor nerve and anterior branch of the anterior superior

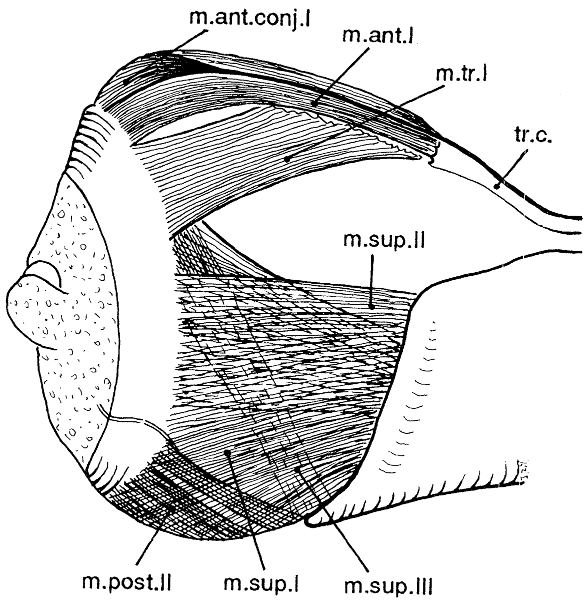


Figure 48. Arrangement of the extraocular eye muscles of the dorsal part of the left eye of *Sepia officinalis*.

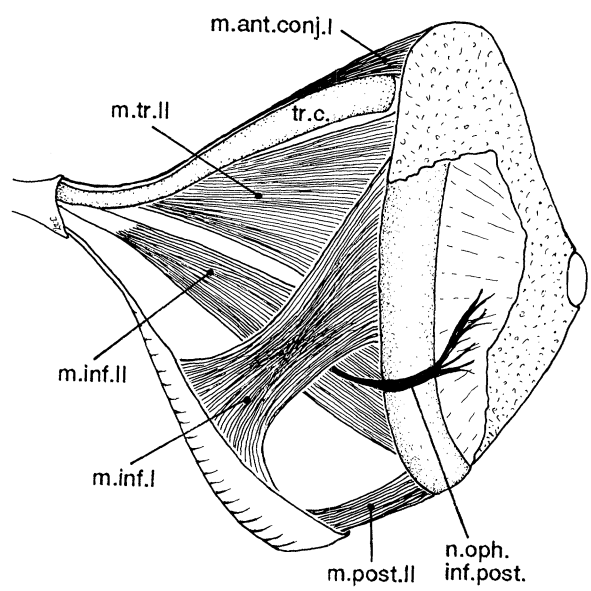


Figure 49. Arrangement of the extraocular eye muscles of the ventral part of the left eye of *Sepia officinalis*.

preparation (figures 71 and 72), the somata are distributed evenly over the lobe. Anteriorly, they are mostly of small and medium size (figure 73), whereas further posterior large and a few very large somata are filled in the outer perikaryal layer (figure 74). A few somata are seen medially of the continuous neuropil of the anterior pedal-median basal lobes, close to the oesophagus (figure 75). A single soma is filled medially to the brachial-palliovisceral lobe connective.

The larger of the two presumably afferent fibre bundles joins the brachial-palliovisceral lobe connective to run in a posterior direction, perhaps as far as the palliovisceral lobe. The smaller afferent bundle joins the brachial-magnocellular lobe tract and runs to the ventral magnocellular lobe. Its fibres run straight and are larger in diameter than typical varicose afferent fibres (but somata were not seen). A single large presumably afferent fibre crosses through the commissure to the contralateral side; it is unclear where it ends.

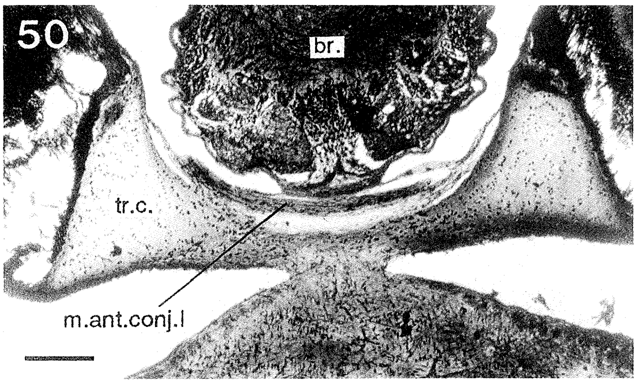
Anterior superior ophthalmic nerve (n. ophthalmicus superior anterior). This nerve has two branches in the orbital cavity, which have been filled separately, the 'anterior branch' and the 'posterior branch'. The two branches enter the cranial cavity together dorso-posteriorly to the optic tract and run down behind the optic tract to enter the suboesophageal brain posteriorly at the back of the posterior pedal and median basal lobes.

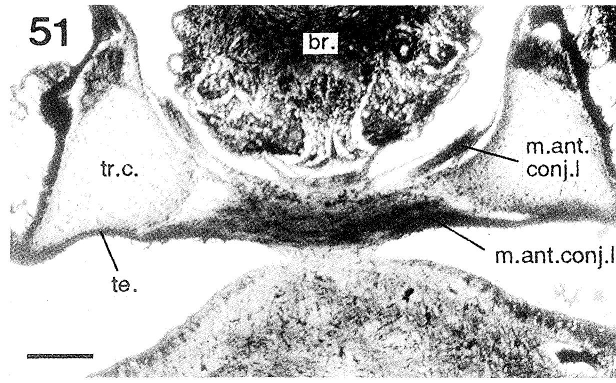
Anterior branch of the anterior superior ophthalmic nerve. After entry into the brain, the fibres of the anterior branch separate into two bundles: a large bundle of efferent fibres continues anteriorly to enter the anterior lateral pedal lobe, and a small bundle of presumably afferent fibres runs down laterally around the brachial-palliovisceral lobe connective to enter the ventral magnocellular lobe. The efferent fibres originate from about 60 mostly large and very large somata in the outer and middle perikaryal layers of the anterior lateral pedal lobe (figure 78). As seen in the whole ophthalmic nerve), were analyzed by centripetal cobalt staining. The terminology of the *Sepia* central nervous system is based on Boycott (1961) and Young (1976).

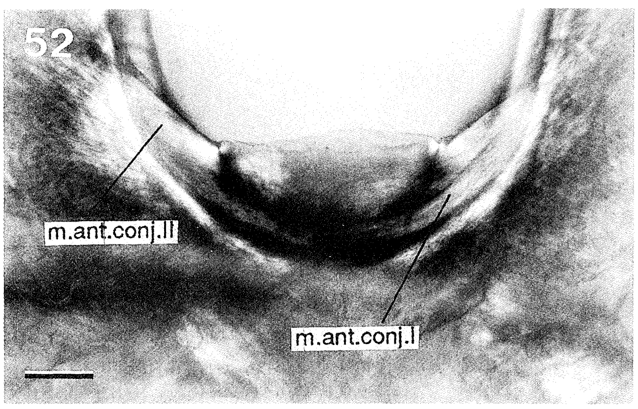
All four eye muscle nerves originate in the ipsilateral anterior lateral pedal lobe of the middle suboesophageal mass of the brain (figures 71, 76, 82, 87 and 89). The stained somata have different distributions within the lobe and vary in diameter from about 10 to 100 μm. They will be called according to their diameter: small (10–20 μm), medium (20–40 μm), large (40–60 μm) and very large (60–100 μm). All somata were found in the outer and middle perikaryal layers, none in the inner layer close to the neuropil.

Anterior oculomotor nerve (n. oculomotorius anterior). This nerve enters the suboesophageal mass of the brain anteriorly. After entry it splits into three bundles: a larger dorsal bundle of efferent fibres, and two smaller ventral bundles of presumably afferent fibres. The efferent fibres run to the anterior lateral pedal lobe. There they originate from 200–250 small, medium, large and few very large somata in the outer and middle perikaryal layers. As seen in the whole mount mount preparation (figures 76 and 77), the somata are not evenly distributed over the lobe. In the anterior part of the lobe, there are only a few somata filled dorsally below the median basal lobe and close to the oesophagus (figure 79); no somata are filled medially and ventrally in the anterior part of the lobe. Also, no somata were filled in the very posterior part of the anterior lateral pedal lobe. Two large somata were filled medial to the brachial-palliovisceral lobe connective (figure 80). Most of the afferent fibres enter the ventral magnocellular lobe. They are fine and varicose and end ipsilaterally; a few fine and medium afferent fibres cross through the ventral magnocellular commissure and end in the neuropil of the contralateral ventral magnocellular lobe (figure 81).

Posterior branch of the anterior superior ophthalmic nerve.







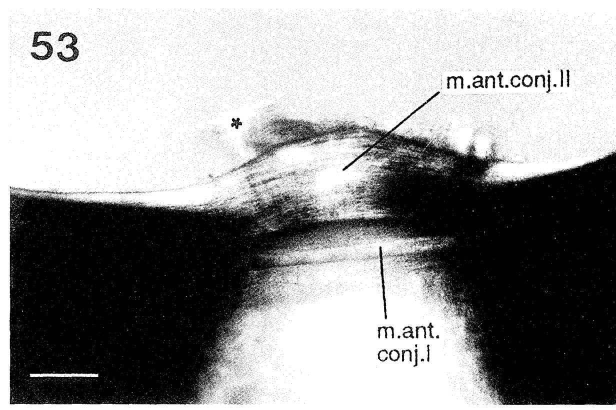


Figure 50. Bases of trochlear cartilages with conjoint tendons of anterior conjunctive muscles I. *Sepia officinalis*. Transverse section. Haematoxylin and eosin stain. Scale bar is 150 μm.

Figure 51. Crossing tendon of anterior conjunctive muscles I and crossing muscles of anterior conjunctive muscles II. *Sepia officinalis*. Transverse section, slightly posterior to section of figure 50. Haematoxylin and eosin stain. Scale bar is 150 μm.

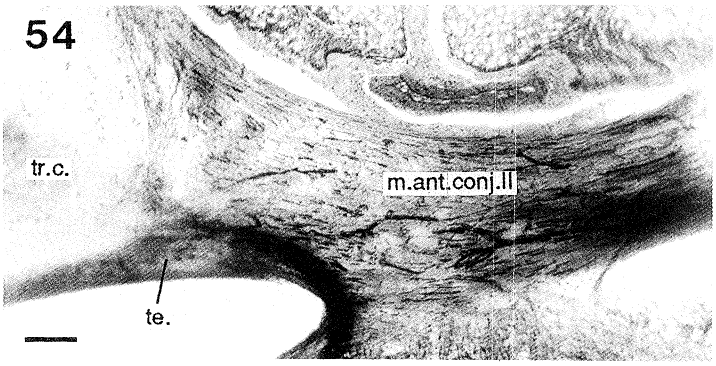
Figure 52. Preparation of the two anterior conjunctive muscles crossing the midline through a fibrous sheath, seen in polarized light. *Sepia officinalis*. Mayer's haemalum stain. Scale bar is 300 μm.

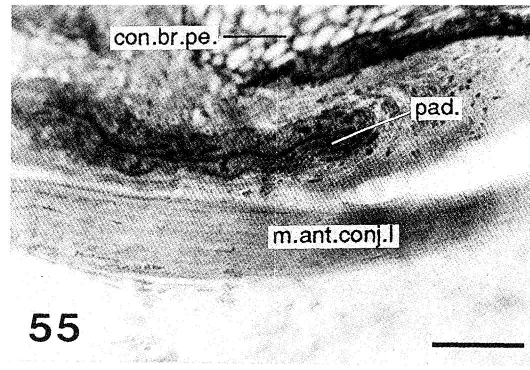
Figure 53. Preparation of the two anterior conjunctive muscles after removal of the fibrous sheath in the midline, seen in polarized light (asterix shows remnants of the sheath). *Sepia officinalis*. Mayer's haemalum stain. Scale bar is 300 μm.

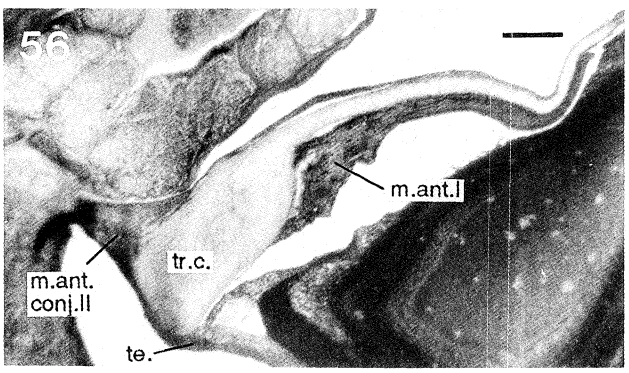
After entry into the brain, the fibres of the posterior branch do not separate into bundles, as those of the anterior branch, but all run to the anterior lateral pedal lobe. There they originate from about 90 somata of all sizes in the outer and middle perikaryal layers (figures 84 and 85). As seen in the whole mount preparation (figures 82 and 83), the distribution of the somata within the lobe is basically similar to that of the somata of the anterior branch of the nerve. An obvious difference, however, is that there are some small and medium somata filled in the anterior part of the lobe, as well as ventrally in the middle part of the lobe. Again, no filled somata were seen in the centre of the middle and in the very posterior part of the lobe (figure 83, compare also figure 77). The trunks of the neurons filled via this nerve (or via the other three oculomotor nerves) run straight and deep into the neuropil of the anterior lateral pedal lobe (figure 85). Some give off primary, secondary and tertiary collaterals with end 'bushes' that may be the sites of synaptic transmission (figure 86). Three large somata were filled medial to the brachial-palliovisceral lobe connective (figure 85). No afferent fibres have bee seen associated with the posterior branch of the nerve.

Posterior superior ophthalmic nerve (n. ophthalmicus superior posterior). This nerve passes through a hole in the cranial cartilage behind the optic tract and runs down to the suboesophageal mass of the brain to enter dorsally the front of the posterior lateral pedal lobe. After entry it turns forwards as a distinct bundle to enter the anterior lateral pedal lobe. All fibres of this nerve are efferent and originate from about 130 small, medium, large and very large somata in the middle and outer perikaryal layers (figure 91). As seen in the whole mount preparation (figures 87 and 88), somata were filled all over the lobe, with a concentration of small and medium somata in the middle perikaryal layers of the anterior half of the lobe. No somata were stained medially of the brachial-palliovisceral lobe connective.

Posterior oculomotor nerve (n. oculomotorius posterior). This nerve enters the cranial cavity below the optic







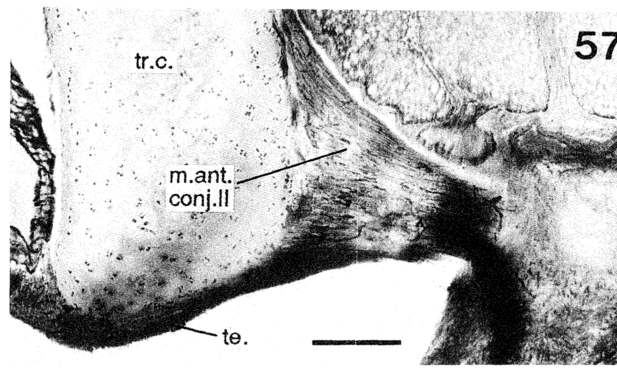
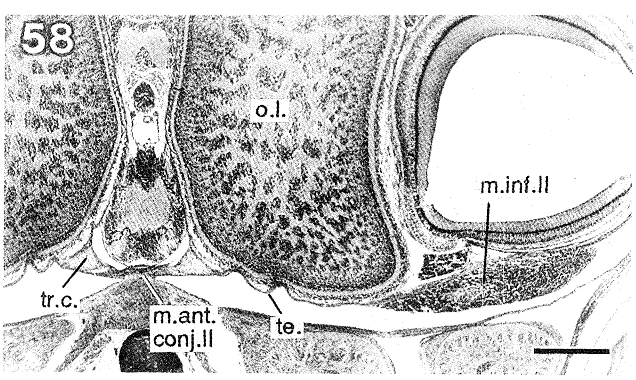


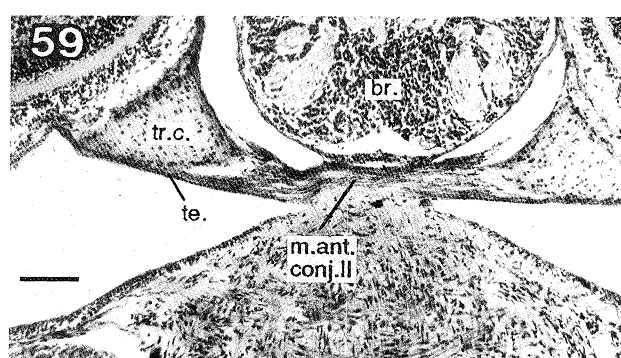
Figure 54. Anterior conjunctive muscle II with nerve fibres and attachment of the tendon to the trochlear cartilage. *Sepia officinalis*. Transverse section. Cajal stain. Scale bar is 100 μm.

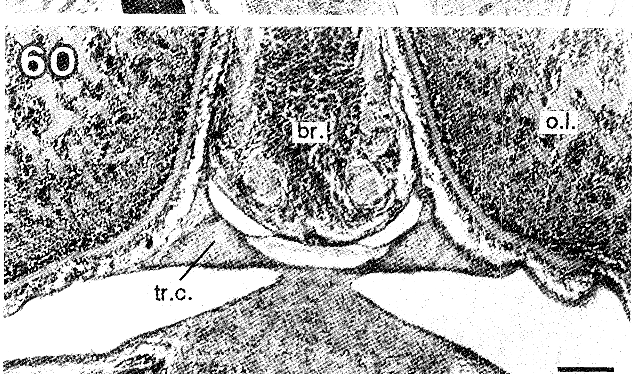
Figure 55. Pad above anterior conjunctive muscle I. *Sepia officinalis*. Transverse section. Cajal stain. Scale bar is 50 μm.

Figure 56. Trochlear cartilage with anterior conjunctive muscle II attached to its base. *Sepia officinalis*. Oblique transverse section. Cajal stain. Scale bar is 500 μm.

Figure 57. Attachment of the tendon. *Sepia officinalis*. Oblique transverse section. Cajal stain. Scale bar is 200 μm.







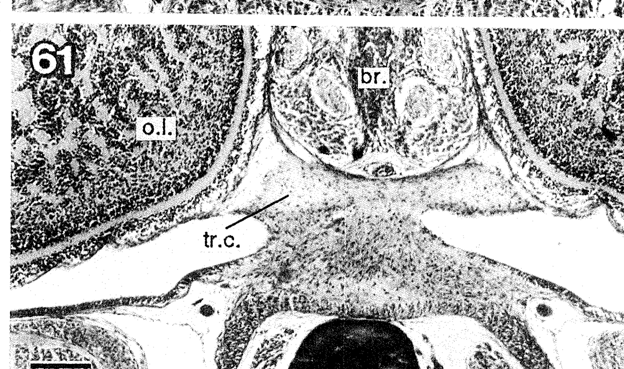
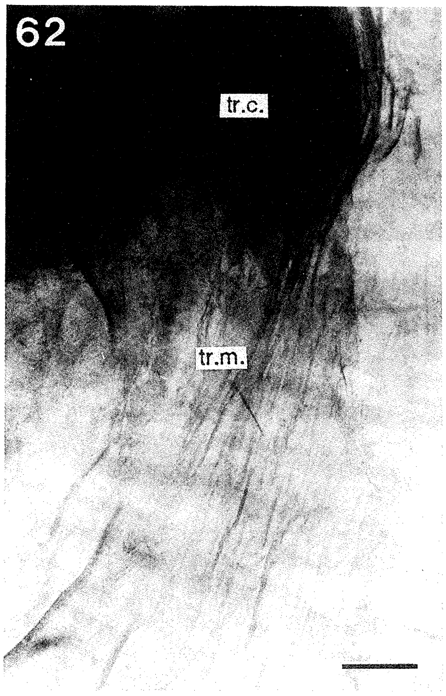
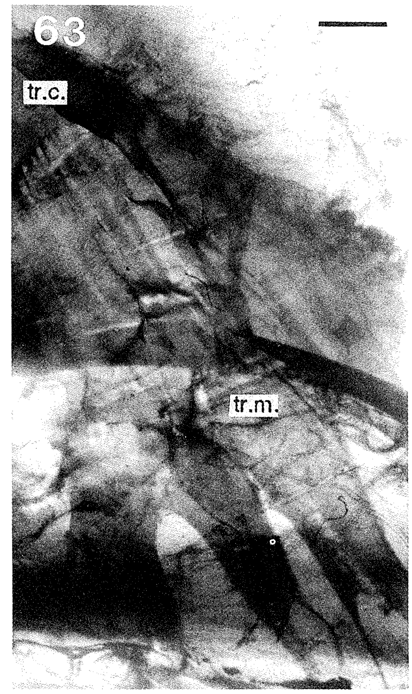


Figure 58. Inferior muscle II and the relationship of its tendon to anterior conjunctive muscle II. Juvenile *Sepia officinalis*. Transverse section. Cajal stain. Scale bar is 500 μm.

Figures 59–61. Three sections (60 μm apart) passing backwards to show that behind anterior conjunctive muscle II the trochlear cartilages are attached only by ligaments. Further back they are fused to the base of the cranium. Juvenile *Sepia officinalis*. Transverse sections. Cajal stains. Scale bars are 300 μm.





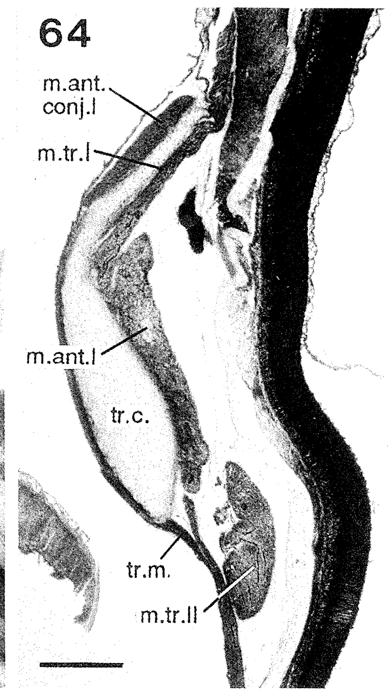


Figure 62. Distal tip of trochlear cartilage with fibres of the trochlear membrane. *Sepia officinalis*. Mayer's haemalum stain. Scale bar is 400 μm.

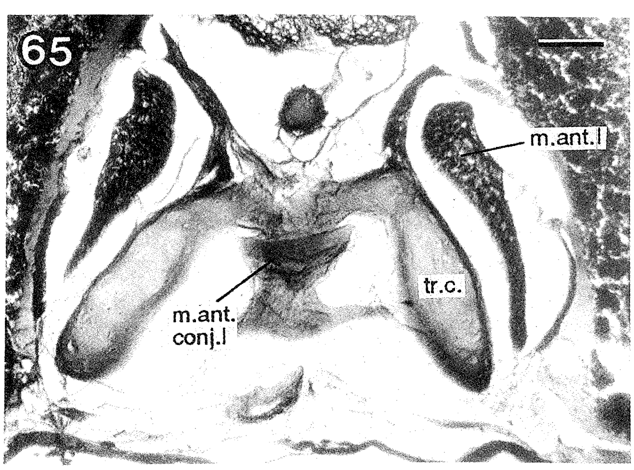
Figure 63. Fibres of trochlear membrane. *Sepia officinalis*. Mayer's haemalum stain. Scale bar is 500 μm.

Figure 64. Tip of trochlear cartilage with anterior conjunctive muscle I on the outside and two trochlear muscles inside. *Sepia officinalis*. Transverse section. Cajal stain. Scale bar is 400 μm.

tract together with the posterior inferior ophthalmic nerve, which does not innervate extraocular muscles. Just behind the level of the middle pedal commissure it enters the brain and continues to the anterior lateral pedal lobe. All its fibres are efferent and originate from about 70 mostly large and very large somata in the middle and outer perikaryal layers (figure 92). The trunks of most neurons run straight and deep into the neuropil of the lobe and give off many collaterals. As shown in the whole mount preparations (figures 89 and 90), no somata were filled in the anterior part of the lobe, except a few in the most dorsal region. Some lie close to the oesophagus (figure 93). Again, no filled somata were seen medial to the brachial-palliovisceral lobe connective.

4. DISCUSSION

The extraocular eye muscles in cephalopods were described as early as 1835 (Krohn 1835; Owen 1835) and a first comparative description of the eye muscles



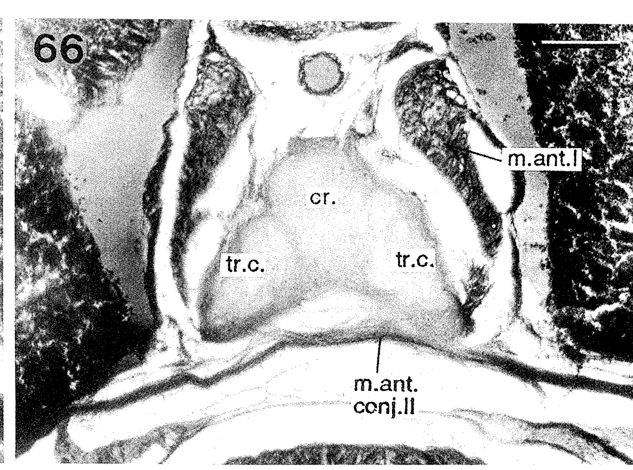
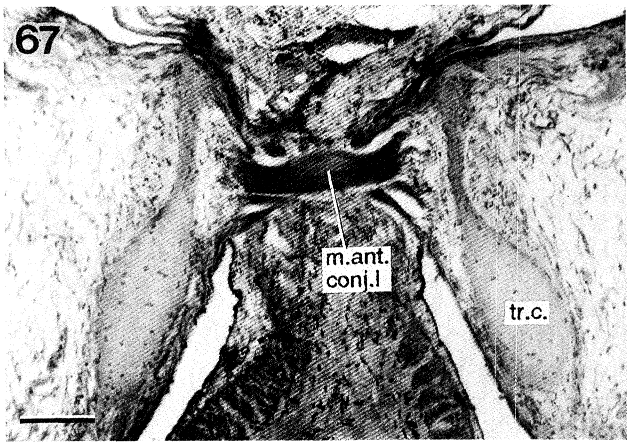


Figure 65. Trochlear cartilages and crossing tendons of anterior conjunctive muscles I. *Sepiola*. Transverse section. Haematoxylin and eosin stain. Scale bar is 100 μm.

Figure 66. Crossing anterior conjunctive muscles II; they are not attached to the trochlear cartilages. *Sepiola*. Transverse section. Haematoxylin and eosin stain. Scale bar is 150 μm.



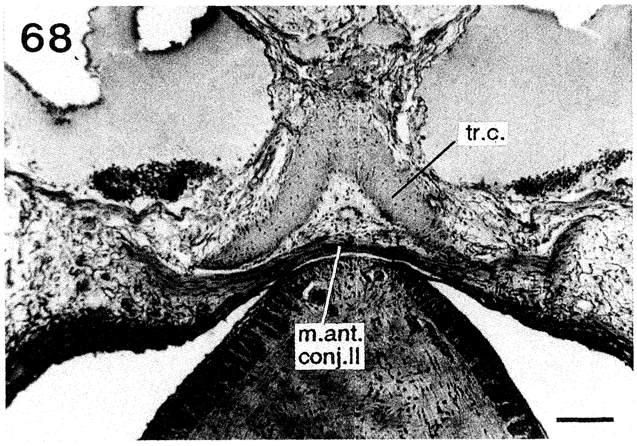


Figure 67. Crossing of anterior conjunctive muscles I. *Spirula*. Transverse section. Cajal stain. Scale bar is 100 μm.

Figure 68. Crossing of anterior conjunctive muscles II. *Spirula*. Transverse section. Cajal stain. Scale bar is 100 μm.

of different species is given by Glockauer (1915). To date the most comprehensive study is on the *Octopus* eye muscle system (Budelmann & Young 1984).

This present study describes the arrangement, innervation and actions of the extraocular eye muscles in some decapod cephalopods. As in all animals, extraocular eye muscles produce various eye movements, including compensatory reflexes necessary to stabilize the visual image on the retina and fixation movements, for example, for the capture of prey.

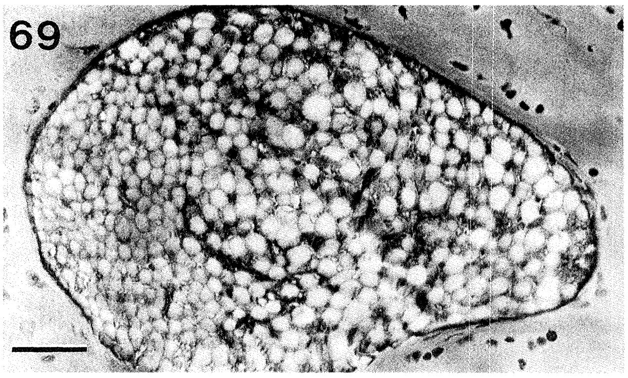
Differences in the complexity of the eye muscle systems of different decapods, and of decapods and octopods, almost certainly reflect differences in the animals' eye movements and their visually guided behaviour. Caution is necessary, therefore, when generalizing or extending the present data to other genera of decapod cephalopods. Considerable differences, for example, may be found in deep-sea forms, in animals that live in habitats where vision is greatly restricted, or in closely related species that display marked differences in their visually oriented behaviour.

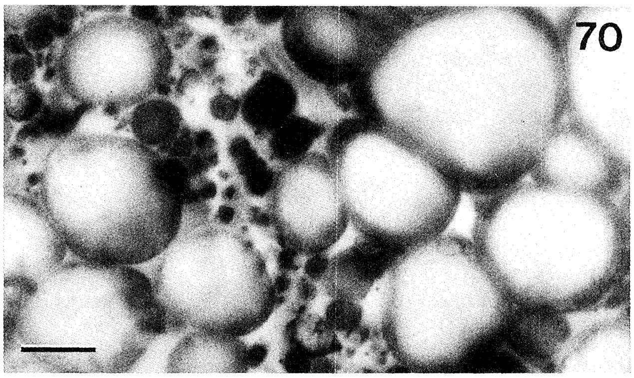
The most unusual feature of the decapod eye muscle system is the presence of conjunctive muscles running from one eye to the other. Such muscles are not found in any other animal group. In jumping spiders, though, one of the six extraocular muscles that move the antero-median eye crosses the midline; but this is for attachment only at the floor of the head capsule on the contralateral side, not for attachment at the contralateral eye (Land 1969). The muscle, therfore, is not a 'conjunctive' muscle.

(*a*) *Differences between the extraocular eye muscles of squids (Loligo, Sepioteuthis) and cuttlefish (Sepia)*

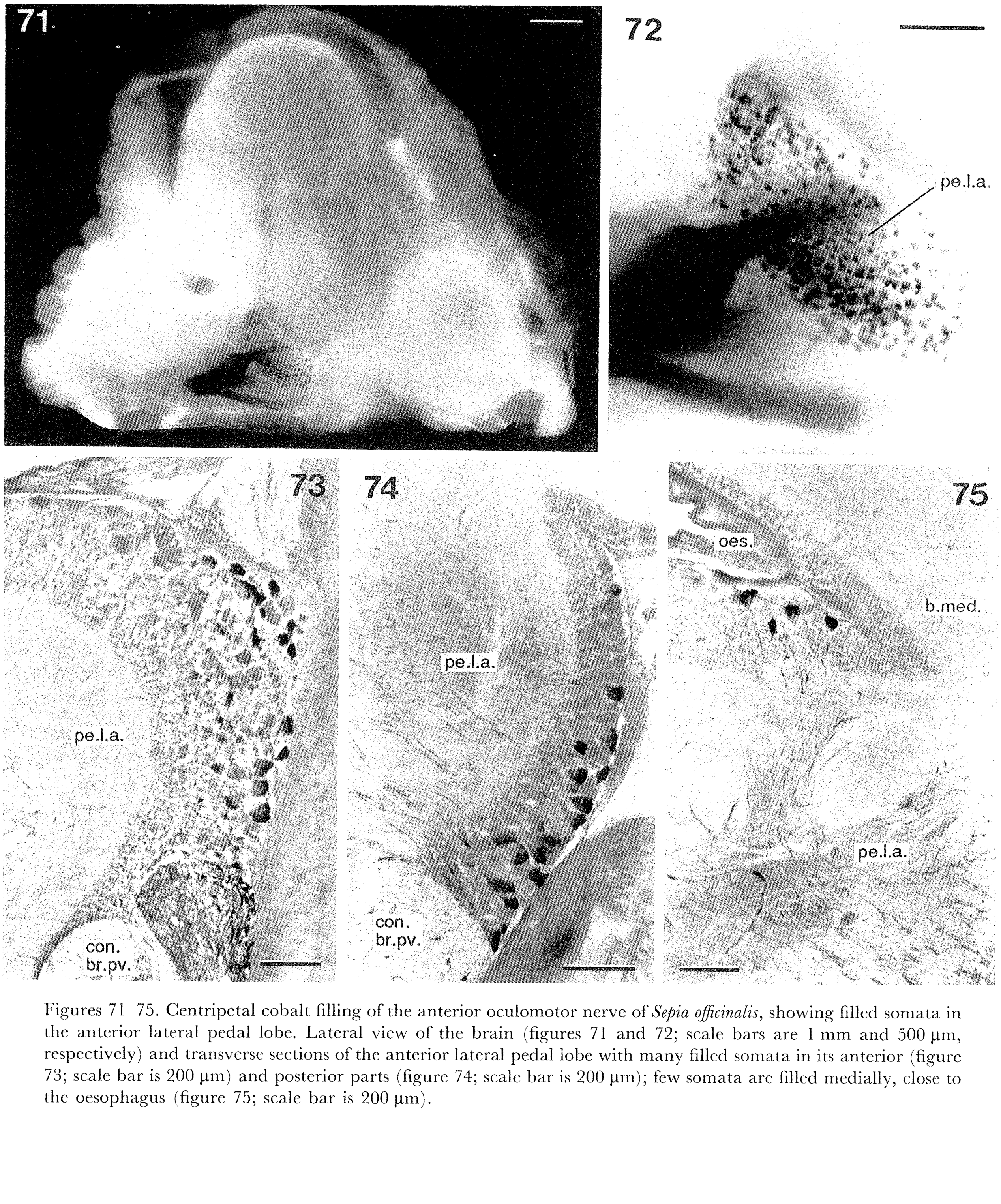
The basic organization of the eye muscle systems is rather similar in squids and cuttlefish but there are some marked differences. These concern the following muscles: anterior muscle II, trochlear muscle III, anterior conjunctive muscle II, and the superior conjunctive muscle (see tables 1 and 2).

In *Loligo* and *Sepioteuthis* there is a large and powerful anterior muscle II, of which there is no sign in *Sepia*. This muscle moves the eye downwards and





Figures 69 and 70. Cross-sections of the anterior oculomotor nerve. *Sepia officinalis*. Cajal stains. Scale bars are 100 μm and 10 μm, respectively.

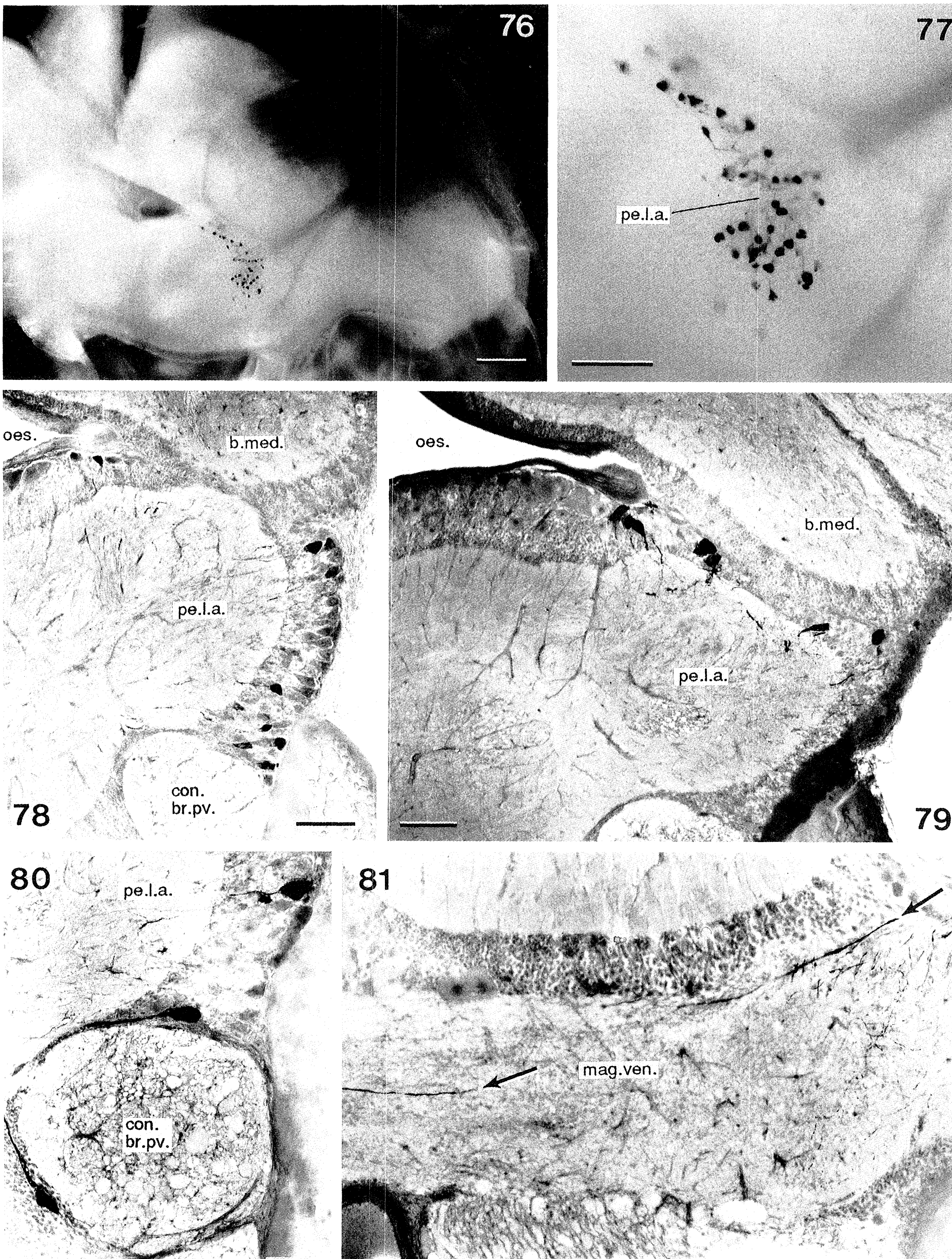


Figures 71–75. Centripetal cobalt filling of the anterior oculomotor nerve of *Sepia officinalis*, showing filled somata in the anterior lateral pedal lobe. Lateral view of the brain (figures 71 and 72; scale bars are 1 mm and 500 μm, respectively) and transverse sections of the anterior lateral pedal lobe with many filled somata in its anterior (figure 73; scale bar is 200 μm) and posterior parts (figure 74; scale bar is 200 μm); few somata are filled medially, close to the oesophagus (figure 75; scale bar is 200 μm).

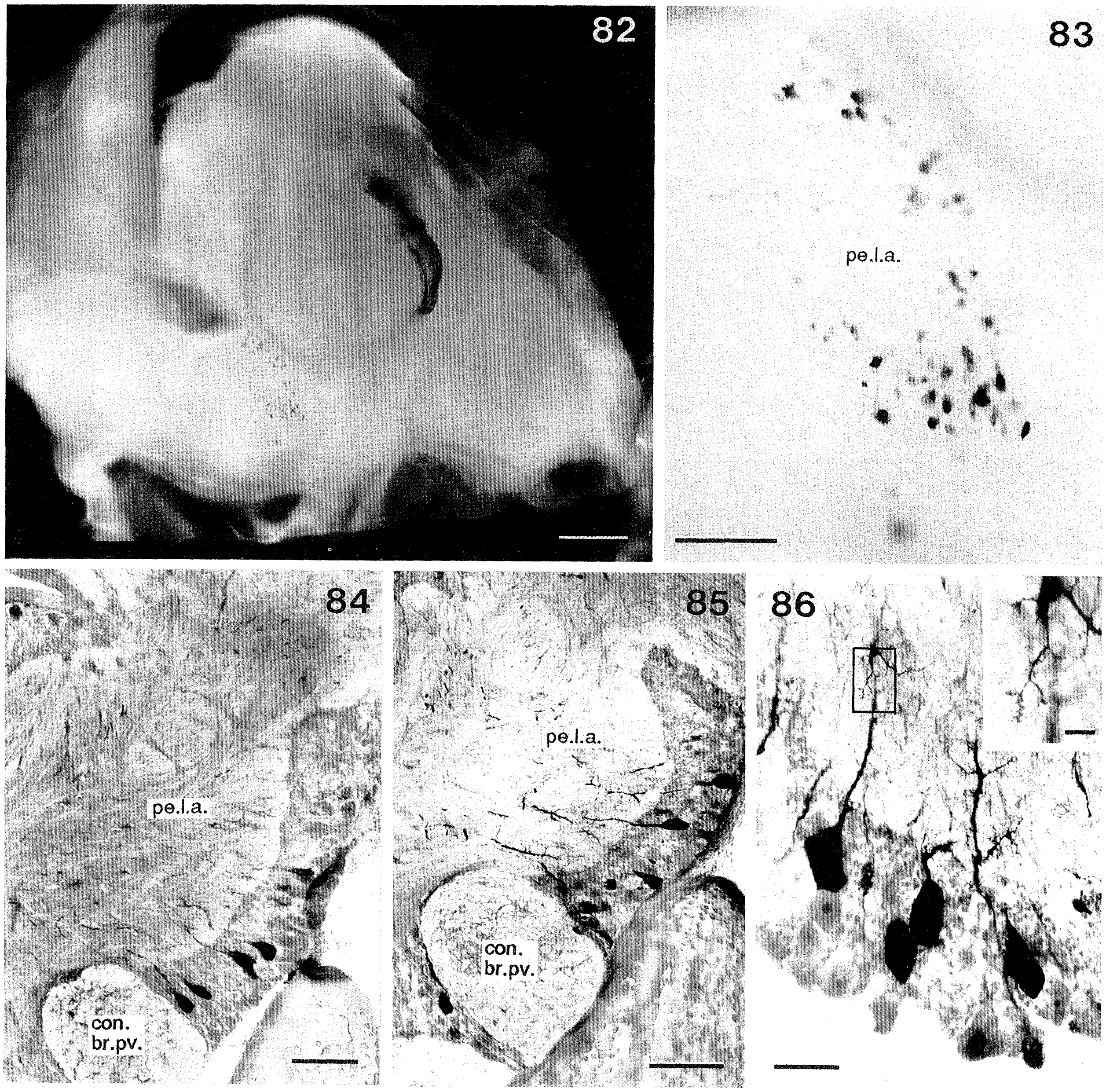
forwards and its long posterior fibres provide clockwise rotation. In *Sepia*, but not in *Loligo* and *Sepioteuthis*, there is a curious trochlear muscle III, running from the trochlear cartilage into the orbit. This muscle was called 'anterior muscle II' by Glockauer (1915), presumably to resolve the difference between the species; however, its position, attachments and possible function are quite different from those of the anterior muscle II of *Loligo* and *Sepioteuthis*.

The muscle here called 'anterior conjunctive muscle II' of *Sepia* runs between the bases of the trochlear cartilages of the left and right eye. This arrangement is peculiar to *Sepia*; it is not present in *Sepiola* or *Spirula*. When contracting, the muscle certainly moves the two cartilages together, but it needs to be seen whether this produces a medially forward movement of the eyes as well. In contrast, the muscle called 'anterior conjunctive muscle II' of *Loligo* and *Sepioteuthis* is much larger, does not span between the two cartilages and presumably moves both eyes at once in a forwards and downwards direction.

The superior conjunctive muscle is present in *Loligo*



Figures 76–81. Centripetal cobalt filling of the anterior root of the anterior superior ophthalmic nerve of *Sepia officinalis*, showing filled somata in the anterior lateral pedal lobe. Lateral view of the brain (figures 76 and 77; scale bars are 1 mm and 500 μm, respectively) and transverse sections of the anterior lateral pedal lobe with many filled somata laterally (figure 78; scale bar is 200 μm), some dorsally and medially close to the oesophagus (figures 78 and 79; scale bars are 200 μm) and one medially beside the brachial-palliovisceral lobe connective (figure 80; scale bar is 100 μm); afferent fibres (arrows) enter the ventral magnocellular lobe, with single fibres crossing to the contralateral side (figure 81; scale bar is 100 μm).



Figures 82–86. Centripetal cobalt filling of the posterior root of the anterior superior ophthalmic nerve of *Sepia officinalis*, showing filled somata in the anterior lateral pedal lobe. Lateral view of the brain (figures 82 and 83; scale bars are 1 mm and 400 μm, respectively) and transverse sections of the anterior lateral pedal lobe with many filled somata laterally in the middle and outer perikaryal layers (figures 84 and 85; scale bars are 200 μm) and a single soma filled medially beside the brachial-palliovisceral lobe connective (figure 85; scale bar is 200 μm). The trunks of the oculomotor neurons give off primary, secondary and tertiary collaterals with end bushes (figure 86, scale bar is 80 μm); inset upper right shows enlarged area as indicated (scale bar is 20 μm).

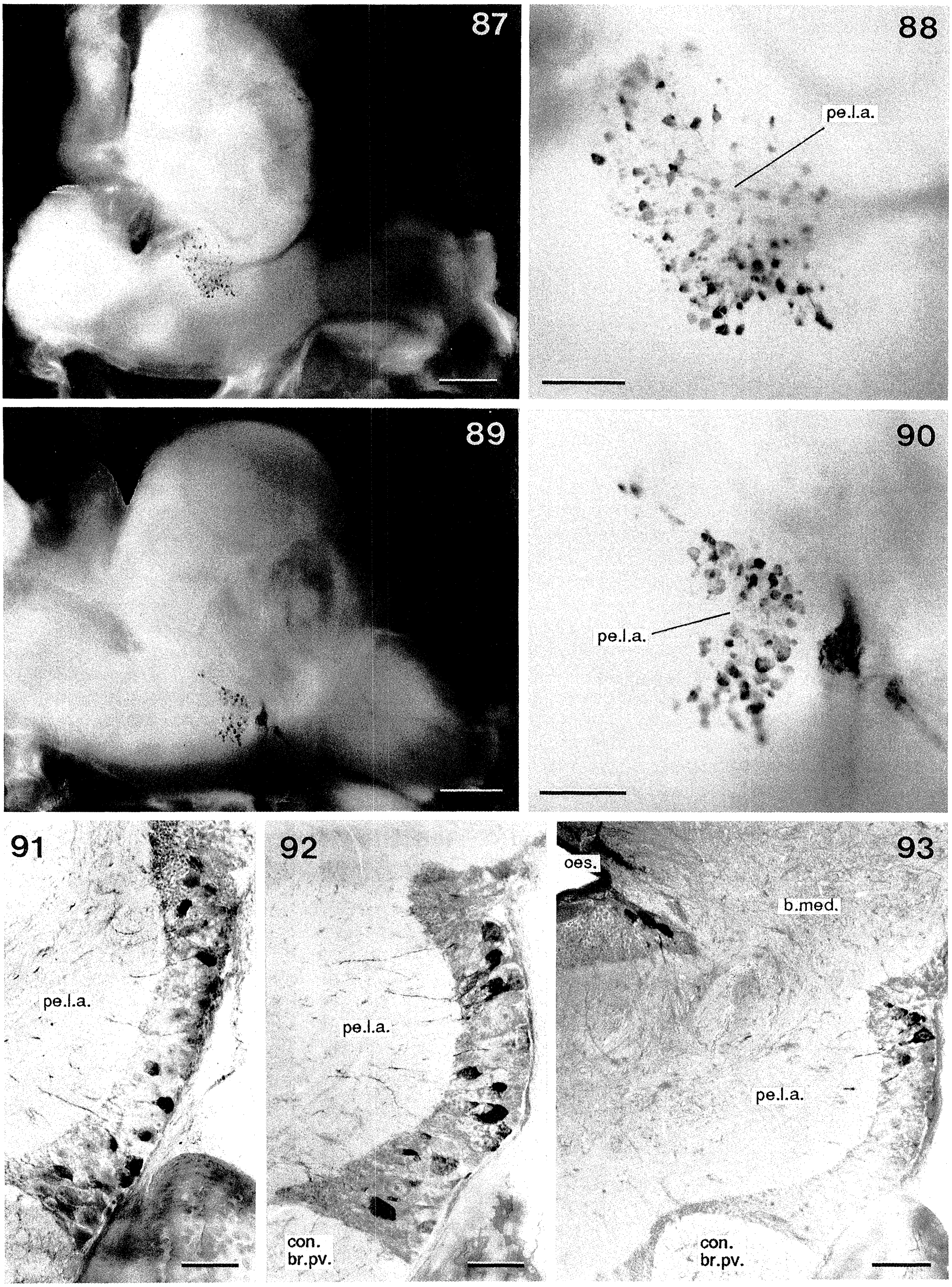
but not in *Sepia*. It moves the eye in an upwards direction, as do three other muscles on the superior face of the eye (figure 94). See below for further discussion.

(*b*) *Comparison of the eye muscle system of decapods and octopods*

The arrangement, function and innervation of the decapod extraocular eye muscles show both similarity and difference from those of octopods (see Budelmann & Young (1984) for data on the octopod eye muscles). There are thirteen eye muscles in *Sepia* and fourteen in *Loligo* and *Sepioteuthis*, as against seven in *Octopus*. The extra eye muscles in decapods are attached to the anterior and superior faces of the eye (figure 94) and are mainly concerned with convergent linear eye movements. The remaining muscles are rather similar to those of octopods; unfortunately the different names (see table 2) obscure these similarities.

(i) *The eye muscles with mainly linear action (table 2)*

Decapods and octopods have four eye muscles with



Figures 87, 88 and 91. Centripetal cobalt filling of the posterior superior ophthalmic nerve of *Sepia officinalis*, showing filled somata in the anterior lateral pedal lobe. Lateral view of the brain (figures 87 and 88; scale bars are 1 mm and 400 μm, respectively) and transverse section of the anterior lateral pedal lobe with many filled somata laterally in the lobe (figure 91; scale bar is 200 μm).

Figures 89, 90, 92 and 93. Centripetal cobalt filling of the posterior oculomotor nerve of *Sepia officinalis*, showing filled somata in the anterior lateral pedal lobe. Lateral view of the brain (figures 89 and 90; scale bars are 1 mm and 300 μm, respectively) and transverse sections of the anterior lateral pedal lobe with many filled somata laterally in the lobe (figure 92; scale bar is 200 μm) and a few medially close to the oesophagus (figure 93; scale bar is 200 μm).

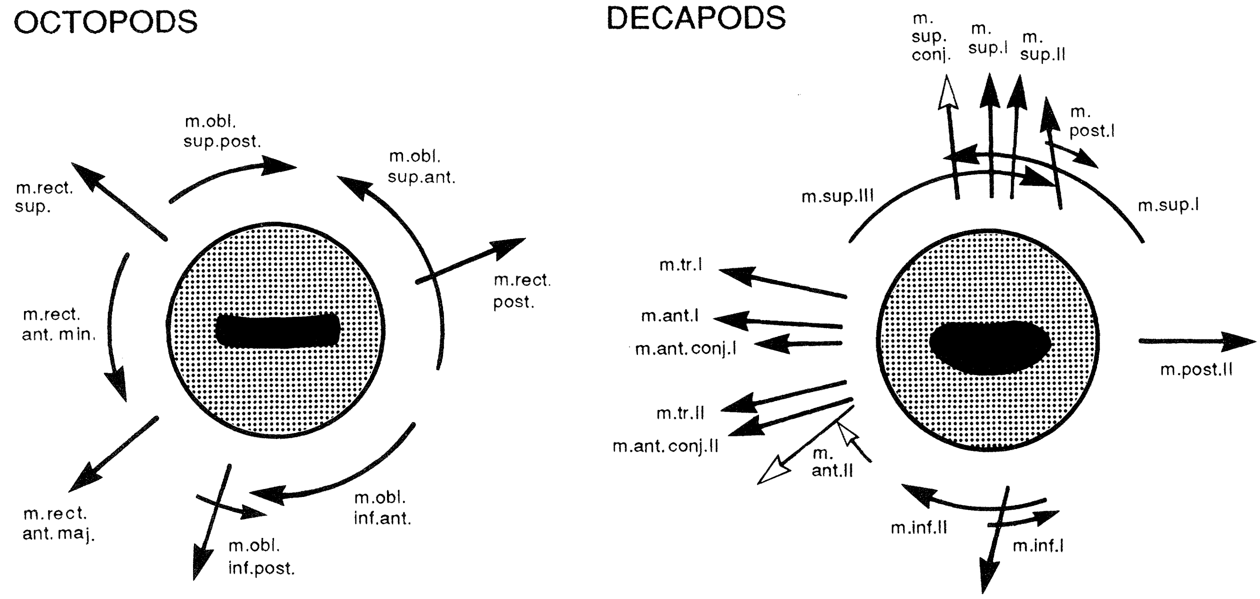


Figure 94. Diagrams to show the presumed linear and rotatory movements (arrows) of the left eye of the octopod *Octopus* (left; based on Budelmann & Young (1984)) and the decapods *Loligo*, *Sepioteuthis* and *Sepia* (right). The different lengths of the 'rotatory' arrows indicate the degree of rotation the muscles can produce. Note: (i) that the action of m.tr.III of *Sepia* is not shown as it is doubtful; and (ii) that m.ant.II and m.sup.conj. (open arrows) are absent in *Sepia*.

mainly linear action that can be compared, one each on the anterior, superior, posterior and inferior face of the eye. On the anterior face, a strong muscle in decapods and octopods turns the eye medially forwards; in decapods this is *anterior muscle I* and in octopods the *major anterior rectus muscle*. On the superior face of the eye, the anterior fibres of the decapod *superior muscle I* and the octopod *superior rectus muscle* turn the eye upwards. On the posterior face of the eye, a broad muscle with a series of parallel fibres turns the eye backwards; in decapods it is called *posterior muscle II* and in octopods *posterior rectus muscle*. On the inferior face of the eye, a conspicuous muscle, remarkably similar in the two groups, has a narrow waist and crossing fibres and turns the eye forwards and downwards; in decapods it is called *inferior muscle I* and in octopods *posterior inferior oblique muscle*. In both animal groups the latter muscles are innervated by their own nerve and both have rotatory functions as well (see below).

Decapods have several additional muscles (nine in *Loligo* and *Sepioteuthis*, and seven in *Sepia*) with linear action, most of which produce convergent eye movements; there are no equivalents for these muscles in octopods. The biological significance of this difference is certainly due to the fact that octopods fixate objects, such as prey, monocularly, whereas decapods do it binocularly. For decapods binocular vision, and thus precise convergent eye movements, are necessary to determine the proper distance to a prey before they shoot out their tentacles for its capture.

(ii) *The eye muscles with rotatory action (table 2)*

Decapods and octopods have four muscles with rotatory function that can be compared; two are on the superior and two on the inferior face of the eye. The decapod *superior muscle III* and the octopod *posterior superior oblique muscle* turn the eye clockwise, whereas the posterior fibres of the decapod *superior muscle I* and the octopod *anterior superior oblique muscle* turn the eye anticlockwise. The oblique fibres of the octopod *anterior superior oblique muscle* are continuous with the straight fibres of the *superior rectus muscle* and these octopod muscles together are the likely equivalent of the *superior muscle I* of decapods. On the inferior face of the eye, the decapod *inferior muscle II* and the octopod *anterior inferior oblique muscle* turn the eye clockwise. The anticlockwise rotation is produced by the conspicuous narrow-waisted muscles, the decapod *inferior muscle I* and the octopod *posterior inferior oblique muscle*.

In addition to the above muscles a large rotatory action is produced in *Octopus* by the minor anterior rectus muscle, which runs from the anterior to the superior face of the eye. This muscle has no equivalent in decapods, though decapods have other rotatory muscles with no equivalents in octopods. These are the trochlear muscle I and posterior muscle I in *Sepia*, and anterior muscle II, trochlear muscle I and posterior muscle I in *Loligo* and *Sepioteuthis*. The rotations that these muscles produce, however, are only small.

It is quite striking that the muscles that produce eye rotations in octopods are much longer than in decapods; three run almost halfway round the eyeball. An explanation for this might be that the range of normal positions of octopods around their transverse (pitch) body axes are much larger than in the more 'stable' decapods and thus require a much larger degree of

Table 2. *Comparison of the eye muscles and presumed main eye muscle actions of octopods (Octopus) and decapods (Loligo, Sepioteuthis and Sepia)*

(The *Octopus* data are from Budelmann & Young (1984). Eye movements given in brackets indicate small eye movements, lines indicate that there is no such eye movement or equivalent eye muscle. Question marks are included when the type of eye movement is uncertain. For the terminology of the eye movements, see the definitions given at the beginning of § 3.)

main eye movements (as referred to the left eye)		octopods	decapods		main eye movements (as referred to the left eye)	
linear	rotation	*Octopus*	*Sepioteuthis Loligo*	*Sepia*	linear	rotation
forwards–downwards	anticlockwise	m.rect.ant.	m.ant.I	m.ant.I	forwards	—
		—	m.ant.II	—	downwards–forwards	clockwise
		—	m.tr.I	m.tr.I	forwards	(anticlockwise)
		—	m.tr.II		forwards	—
				m.tr.II	forwards–downwards	—
		—	—	m.tr.III	forwards?	anticlockwise?
forwards–upwards	—	m.rect.sup.	m.sup.I	m.sup.I	upwards	anticlockwise
—	anticlockwise	m.obl.sup.ant.				
		—	m.sup.II	m.sup.II	upwards	—
—	clockwise	m.obl.sup.post.	m.sup.III	m.sup.III	—	clockwise
		—	m.post.I	m.post.I	upwards	clockwise
backwards–(upwards)	—	m.rect.post.	m.post.II	m.post.II	backwards	—
downwards–(forwards)	anticlockwise	m.obl.inf.post.	m.inf.I	m.inf.I	downwards	(anticlockwise)
—	clockwise	m.obl.inf.ant.	m.inf.II	m.inf.II	downwards	clockwise
		—	m.ant.conj.I	m.ant.conj.I	forwards	—
		—	m.ant.conj.II		forwards–downwards	—
				m.ant.conj.II	???	???
		—	m.sup.conj.	—	upwards	—

compensatory counterrolling of the eyes. In *Octopus* these eye movements can be as large as 60–80° in either direction (Budelmann 1970).

(iii) *The innervation of the eye muscles (table 2)*

The pattern of arrangement of the eye muscle nerves in decapods and octopods is also similar. This is despite the fact that only four named nerves innervate the thirteen eye muscles in *Sepia*, whereas seven nerves innervate the seven eye muscles in *Octopus* (although not in a 1:1 relationship). The additional nerves in *Octopus* are all dorsal and are likely to be equivalent to a single large nerve in *Sepia* (the anterior superior ophthalmic nerve), which has anterior and posterior branches.

In summary, most of the additional eye muscles in decapods produce linear eye movements forwards, forwards–downwards and upwards, and some of them are 'conjunctive' muscles, which probably move the left and the right eye at the same time. All the additional muscles are probably involved in binocular vision for prey fixation and capture by the tentacles.

The general pattern of arrangement, innervation and function of the decapod and octopod eye muscles are basically similar and some of the individual muscles can clearly be recognized in both groups. This is in spite of the long evolutionary separation of the two groups (Donovan 1977). The situation present in octopods has probably been evolved by a loss of anterior muscles that were present in their common ancestors.

(*c*) *The conjunctive eye muscles*

A muscle with a common tendon crossing the midline was first described by Owen (1835) as 'superior rectus muscle' and Williams mentions 'a digastric muscle in *Loligo pealei* that, passing through a pulley, extends from eye to eye'. More details on all three conjunctive muscles are given in Glockauer (1915).

These conjunctive muscles are unique in the animal kingdom. Contraction of such muscle on either side must converge both eyes simultaneously. This can be shown by pulling on the tendon on one side. Such convergent eye movements are necessary for binocular vision. It is difficult, however, to understand why conjunctive muscles are present in addition to 'non-conjunctive' muscles that produce eye movements in exactly the same directions. A hypothesis is that the conjunctive muscles are used for precise positioning of the eyes and head during prey capture by the tentacles. To hit a prey successfully decapods not only have to be at the appropriate distance but they also have to position their head symmetrically to the target, i.e. the head's longitudinal midline has to aim precisely at the prey (Messenger 1977). Such precise head positioning can be achieved in two ways, by symmetric convergent eye movements of the aiming left and right eye produced by conjunctive muscles, or by identical motor commands from the left and right oculomotor centre to 'non-conjunctive' muscles of each eye. The use of conjunctive muscles has the advantage that it assures symmetric eye movements, and thus the precise head positioning, even if the motor commands to the left and right eye muscles differ. This may be important since cephalopods are able to move their left and right eye independently (*Sepia*, *Sepioteuthis*; B. U. Budelmann & J. Z. Young, personal observation).

That a superior conjunctive muscle exists in squids, but not in cuttlefish, could be explained by the fact that the prey capture behaviour in squids includes attacks at prey from below (Moynihan & Rodaniche 1982). There is, however, confusion whether the superior conjunctive muscle is a true 'conjunctive' muscle in all squid species. There may well be species-specific differences and it would be interesting to see whether these correlate with specific visually oriented behaviours.

This hypothesis of the significance of the conjunctive muscles cannot explain the striking differences between the two anterior conjunctive muscles in squids. Anterior conjunctive muscle I is a very short and narrow fan with a long tendon; it moves the eye medially forwards. In contrast, anterior conjunctive muscle II is a much larger and broader fan which has no tendon but muscle fibres that cross to the contralateral side; in *Loligo* it moves the eye forwards–downwards, whereas in *Sepioteuthis*, which lives in more shallow waters, it seems to move the eye in a more anterior direction. The degree of contraction that the anterior conjunctive muscle I can produce is certainly much smaller than that of anterior conjunctive muscle II. This could mean that the anterior conjunctive muscles II are used for initial convergent eye movements during aiming at objects such as prey, and the anterior conjunctive muscles I for a more precise fine-tuning of the eye movements, e.g. during the final steps of aiming at the prey before the tentacles are shot out.

The hypothesis also fails to explain why in *Sepia* there are two so very different anterior conjunctive muscles. Anterior conjunctive muscle I presumably has a fine-tuning effect as in *Loligo*, but the function of the anterior conjunctive muscle II is puzzling since it is very short and primarily moves the trochlear cartilages together and not, or only indirectly via the trochlear cartilage, the eyeballs.

(*d*) *The trochlear cartilage and trochlear membrane*

A narrow plate of cartilage at the antero-medial surface of the eye has been known since Owen (1835) and Krohn (1835). Williams (1909) describes it as 'preorbital cartilage' in *Loligo*. It was first called 'trochlear cartilage' by Hensen (1865). The cartilage is associated with the two anterior conjunctive muscles and therefore with the use of the eyes for binocular fixation. It is certainly interesting to know in which other decapod species it occurs. Glockauer (1915) has already shown that the cartilage is present in several ommastrephid species but absent from the meso-bathypelagic *Abraliopsis* and *Chiroteuthis*. Our serial sections show that *Spirula* has both the trochlear cartilage and the crossing muscles and therefore presumably uses the eyes for binocular vision. The condition in *Sepiola* is more like that of *Loligo* than that of *Sepia*.

Sections of other squids confirmed that the cartilage is absent from *Abraliopsis* and also from *Histioteuthis*, *Pyroteuthis* and *Pterygioteuthis*. Surprisingly, in *Bathyteuthis* the full apparatus of cartilage and muscles is present. This animal lives in mostly very deep water and is also unique in having a fovea (Chun 1910). The condition in this and other genera will be described in detail elsewhere. (See note added in proof.)

The trochlear cartilage is not rigidly attached to the base of the cranium. In *Sepioteuthis* the attachment is very narrow (figure 24). The cartilage probably moves to some extent together with the eyeball. Such movement would limit its function as origin of the trochlear muscles. The cartilage, however, gets some restraint by the trochlear membrane. This elaborate set of fibres is attached especially to the distal end of the cartilage, with which its fibres are continuous. The thickening at the end of the cartilage proceeds progressively with the age, and thus the size, of the animal, so that eventually a cap composed of several layers of tissue appears at the distal end of the cartilage. The expansion of the cartilage is more pronounced ventrally than dorsally and the ventral trochlear membrane is thicker.

In addition to its function as the origin of the trochlear muscles, the trochlear cartilage, including the trochlear membrane, probably gives some retaining support for the eyeball. This might be of special importance since the eyeball does not get much support anteriorly from the orbital cartilage which is 'open' at this part of the eye. But further research is certainly necessary to better understand the functioning of the combination of the trochlear cartilage and muscles.

(*e*) *The nerve fibres associated with the eye muscles*

(i) *The efferent oculomotor fibres*

The eye muscles are richly innervated by a relatively small number of rather large nerve fibres. A count of the anterior oculomotor nerve of *Sepia* gave only 1100 fibres between about 1 μm and 30 μm in diameter; which innervate six muscles. The majority of the fibres are rather small and there may be even more of a diameter below 1 μm, which cannot be seen at light microscopical level.

The relatively low number of larger fibres (figure 69) correlates roughly with the 200–250 somata that have been filled in the anterior lateral pedal lobe (the oculomotor centre) via the anterior oculomotor nerve.

A similar situation most probably exists in the posterior oculomotor nerve, which innervates only one muscle. As seen in a cross-section of the nerve in *Loligo vulgaris* (see figure 41 of Young (1976); but note that the nerve has been incorrectly labelled), there are only about 70–80 fibres of 10–30 μm in diameter. This number correlates with the about 70 somata that have been filled, though in a different species (*Sepia*), via this nerve.

The large oculomotor fibres remain unbranched after entering the muscles and then divide rapidly (figure 37). This presumably ensures near simultaneous contraction of the muscle fibres. The silver preparations show rapid division down to fibres of less than 1 μm in diameter, running along and across the muscle fibres. Swellings along their course may be synaptic (figure 13). No other motor nerve endings were seen.

(ii) *The afferent fibres*

The nature of the many small fibres in the eye muscle nerves is uncertain. Small bundles of fine fibres are seen among the muscle fibres but with no definite end organs. Nerve fibres occur where the trochlear muscles are attached to the trochlear cartilage and in crevices in the latter. These might be proprioceptors. No peripheral receptors like those in the mantle and fin muscles were seen (Sereni & Young 1932; Alexandrowicz 1960; Kier *et al.* 1985).

Many fine fibres have been filled via two eye muscle nerves (anterior oculomotor nerve, anterior branch of the anterior superior ophthalmic nerve). They do not originate from somata in the anterior lateral pedal lobe but are afferent fibres that project to the ventral magnocellular lobe and via the brachial-palliovisceral connective probably as far as the palliovisceral lobe. Their significance is not clear; some may originate from the skin dorsal to the eye, the surface of the eyeball and/or the cornea and iris (Thore 1939; Young 1976). Afferent fibres of uncertain origin have also been found associated with two eye muscle nerves of *Octopus* (Budelmann & Young 1984). There, however, the distribution of the filled fibres in the brain is more complex than in *Sepia*, but the projections include fibres to the ventral magnocellular lobe and perhaps to the palliovisceral lobe.

In decapods, there is some confusion about the presence of a small ganglion associated with the anterior superior ophthalmic nerve. The ganglion is present in some species, but may be missing in others. It has been reported in *Sepia officinalis* and *(Eu)Sepiola robusta* (Hillig 1912; Thore 1939), but it has not been found in *Illex coindeti, Alloteuthis subulata* or in *Loligo vulgaris, L. pealei* and *L. forbesi* (Thore 1939, Young 1976). In octopods, two such ganglia exist on two different eye muscle nerves of *Octopus vulgaris* and *Eledone moschata* (Thore 1939; Young 1971; Budelmann & Young 1984). The significance of the ganglia is not clear, either in octopods or in decapods. In *Octopus* the ganglion includes somata that send fibres to the iris presumably for control of the pupil (Budelmann & Young 1984; Plän, unpublished results).

(f) **The oculomotor centre**

In *Sepia* the efferent oculomotor fibres of all four eye muscle nerves arise from somata in the anterior lateral pedal lobe, which therefore is the oculomotor centre, as in *Loligo* and *Octopus* (Young 1976; Budelmann & Young 1984). The filling of neurons close to the oesophagus shows that the posterior border of the anterior lateral pedal lobe reaches far medially.

The somata of the eye muscle nerves have characteristic, non-uniform distributions in the lobe. There is some overlap between the neurons of the different nerves. This was also seen in *Octopus* (Budelmann & Young 1984), but with less marked differences than in *Sepia*. The difference in distribution indicates that the input to the anterior lateral pedal lobe is organized around pools of motoneurons. As in *Octopus*, none of the very small somata in the inner perikaryal layers of the lobe was filled. Some are certainly efferents to the statocysts (H. Neumeister & B. U. Budelmann, unpublished results), as has been shown in *Octopus* (Budelmann & Young 1984); others may be local interneurons.

In *Loligo* input to the oculomotor centre is from the statocysts and the anterior and median basal and the peduncle lobes (Young 1976). All those lobes, in turn, receive input from the statocysts and from the optic lobes. In *Sepia* there is said to be an additional direct connection from the optic lobes (Boycott 1961).

Thus, the connections of the oculomotor centre are similar to those in *Octopus*. It is most likely, therefore, that the statocyst-oculomotor system in *Sepia* and in other decapods is organized in a similar way and is analogous in many details to the vestibulo-oculomotor system of vertebrates (see, for example, Precht (1978); Palay & Chan-Palay (1982); Budelmann & Young (1984)).

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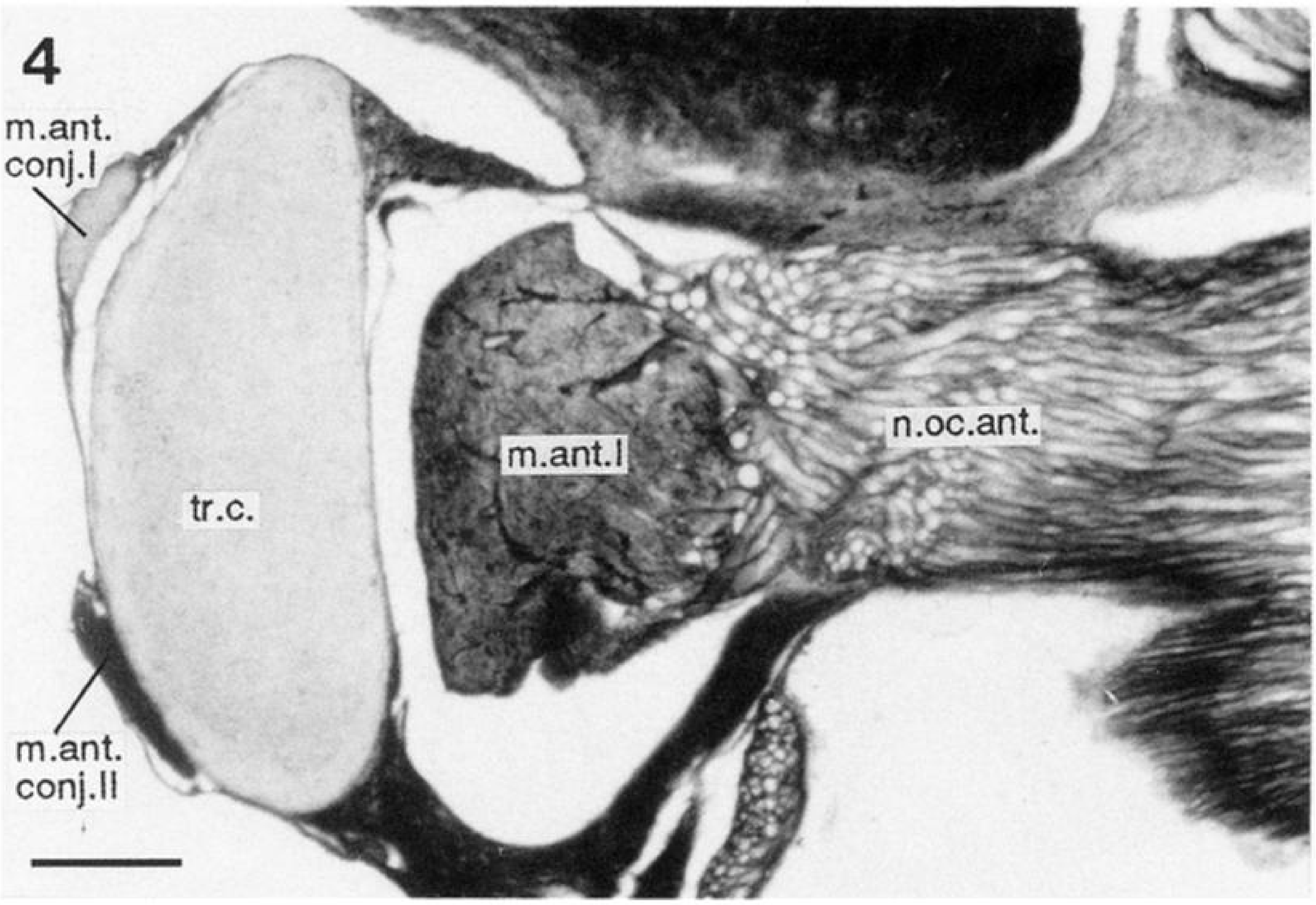
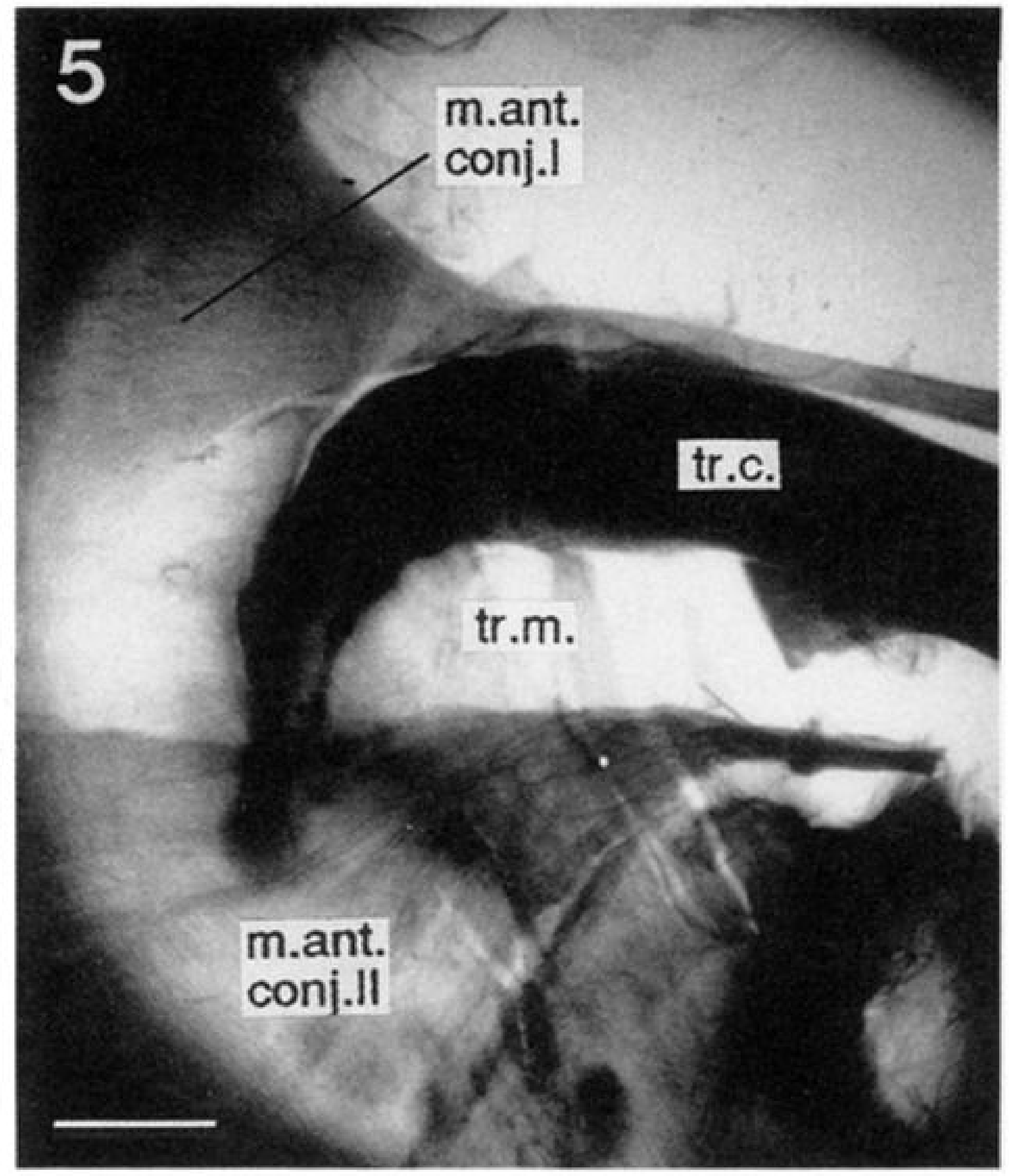
ABBREVIATIONS USED IN THE TEXT AND ON TABLES AND FIGURES

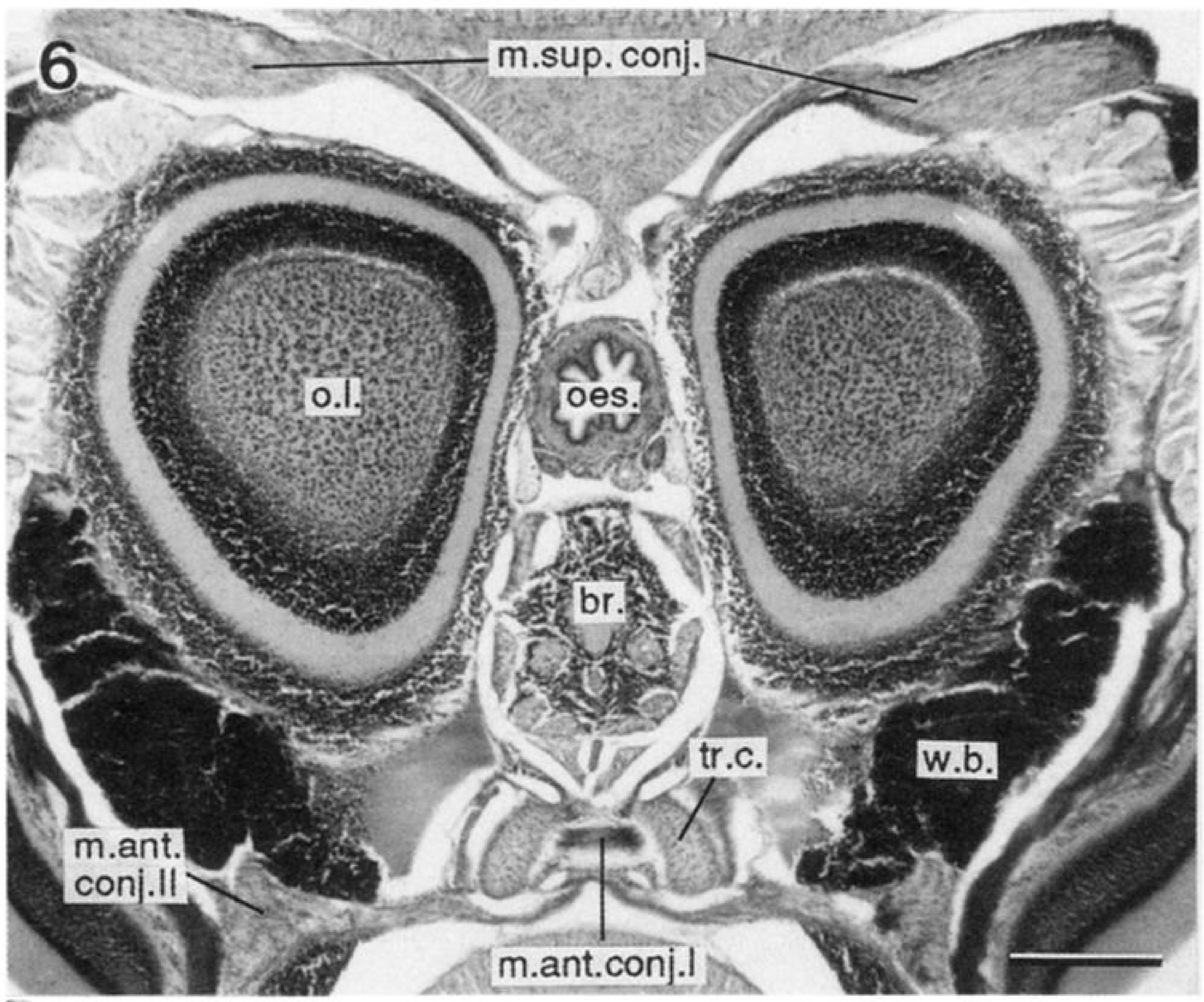
art.ir.	artery of the iris
b.med.	median basal lobe
br.	brachial lobe
con.br.pe.	brachial-pedal lobe connective
con.br.pv.	brachial-palliovisceral lobe connective
c.p.	cartilaginous process of cranium
cr.	cranium
c.t.	connective tissue
ep.	epithelium
m.	muscle (fibres)
mag.ven.	ventral magnocellular lobe
m.ant.I	anterior muscle I
m.ant.II	anterior muscle II
m.ant.conj.I	anterior conjunctive muscle I
m.ant.conj.II	anterior conjunctive muscle II
m.inf.I	inferior muscle I
m.inf.II	inferior muscle II
m.l.	muscle (fibres) cut longitudinally
m.obl.inf.ant.	anterior inferior oblique muscle
m.obl.inf.post.	posterior inferior oblique muscle
m.obl.sup.ant.	anterior superior oblique muscle
m.obl.sup.post.	posterior superior oblique muscle
m.post.I	posterior muscle I
m.post.II	posterior muscle II
m.rect.ant.	anterior rectus muscle
m.rect.post.	posterior rectus muscle
m.rect.sup.	superior rectus muscle
m.sup.I	superior muscle I
m.sup.II	superior muscle II
m.sup.III	superior muscle III
m.sup.conj.	superior conjunctive muscle
m.t.	muscle (fibres) cut transversely
m.tr.I	trochlear muscle I
m.tr.II	trochlear muscle II
m.tr.III	trochlear muscle III
n.f.	nerve fibre(s)
n.f.l.	large nerve fibre
n.oc.ant.	anterior oculomotor nerve
n.oc.inf.ant.	anterior inferior oculomotor nerve
n.oc.inf.post.	posterior inferior oculomotor nerve
n.oc.sup.ant.	anterior superior oculomotor nerve
n.oc.sup.post.	posterior superior oculomotor nerve
n.oc.post.	posterior oculomotor nerve

n.oph.inf.post.	posterior inferior ophthalmic nerve
n.oph.sup.ant.	anterior superior ophthalmic nerve
n.oph.sup.post.	posterior superior ophthalmic nerve
n.oph.sup.ant.rad.ant.	anterior root of the anterior superior ophthalmic nerve
n.oph.sup.ant.rad.post.	posterior root of the anterior superior ophthalmic nerve
n.oph.sup.post.rad.post.	posterior root of the posterior superior ophthalmic nerve
oes.	oesophagus
o.l.	optic lobe
pad.	pad above tendon/muscle
pe.l.a.	anterior lateral pedal lobe
ret.	retina
s.	soma of large cell
s.m.	membranous sheet
te.	tendon
tr.c.	trochlear cartilage
tr.m.	trochlear membrane
w.b.	white body

Note added in proof (3 February 1993): Sections have also shown the presence of trochlear cartilages and two anterior conjunctive muscles in other oegopsids, including *Gonatus*, *Joubiniteuthis*, *Mastigoteuthis* and the cranchiids: *Sandalops*, *Taonius* and *Cranchia*. Presumably all these animals use binocular vision to catch prey, although they live at great depths and have very long tentacles.







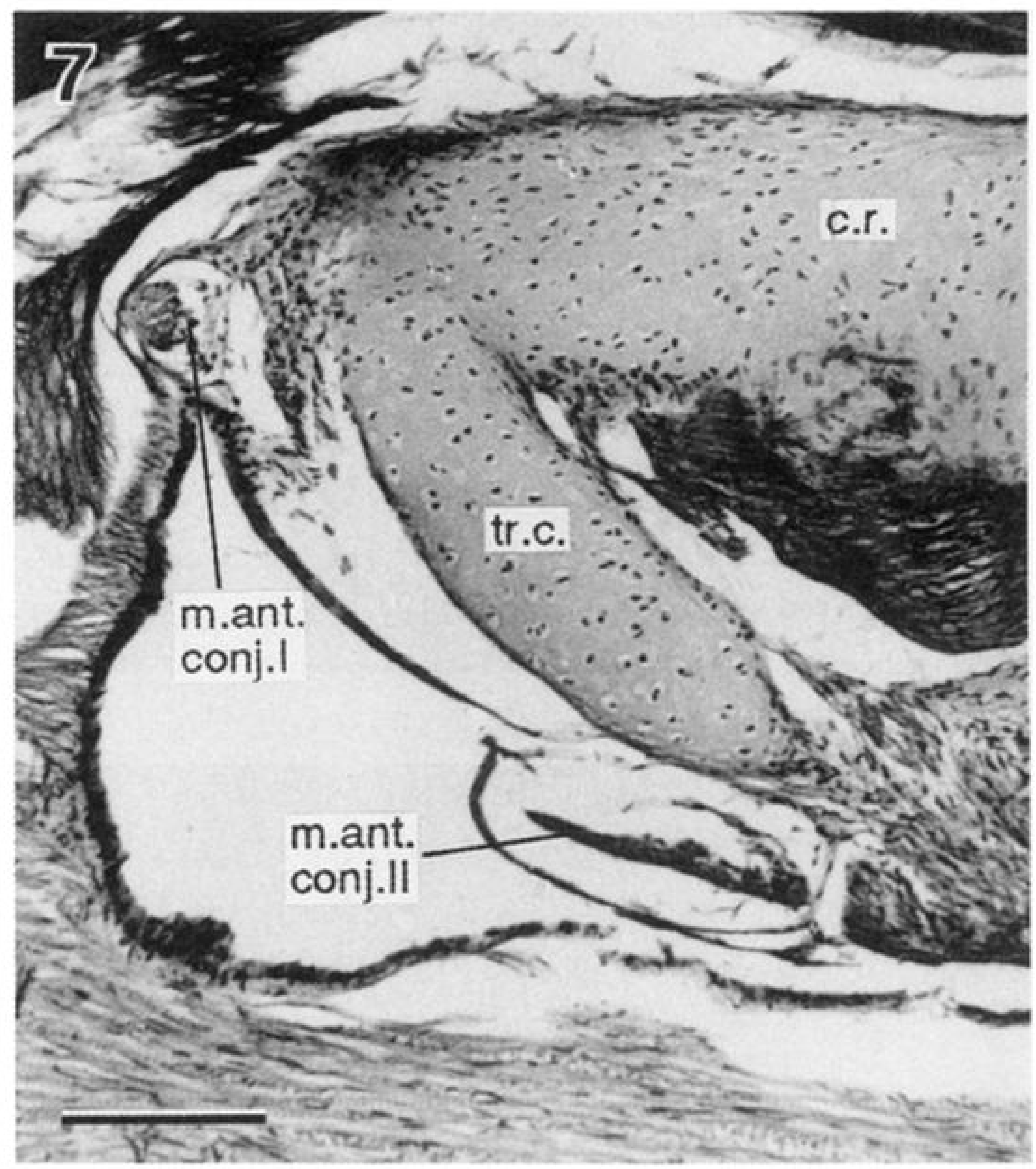


Figure 4. The anterior conjunctive muscles and anterior oculomotor nerve at the base of the trochlear cartilage. *Sepioteuthis sepioidea*. Horizontal section (compare figure 17). Cajal stain. Scale bar is 300 μm.

Figure 5. Preparation of some of the anterior eye muscles, showing the trochlear cartilage, the trochlear membrane and the two anterior conjunctive muscles. *Loligo pealei*. Mayer's haemalum stain. Scale bar is 500 μm.

Figure 6. The superior and two anterior conjunctive muscles crossing the midline. *Loligo pealei*. Transverse section. Haematoxylin and eosin stain. Scale bar is 500 μm.

Figure 7. Crossing of the two anterior conjunctive muscles. *Loligo vulgaris*. Sagittal section. Cajal stain. Scale bar is 200 μm.

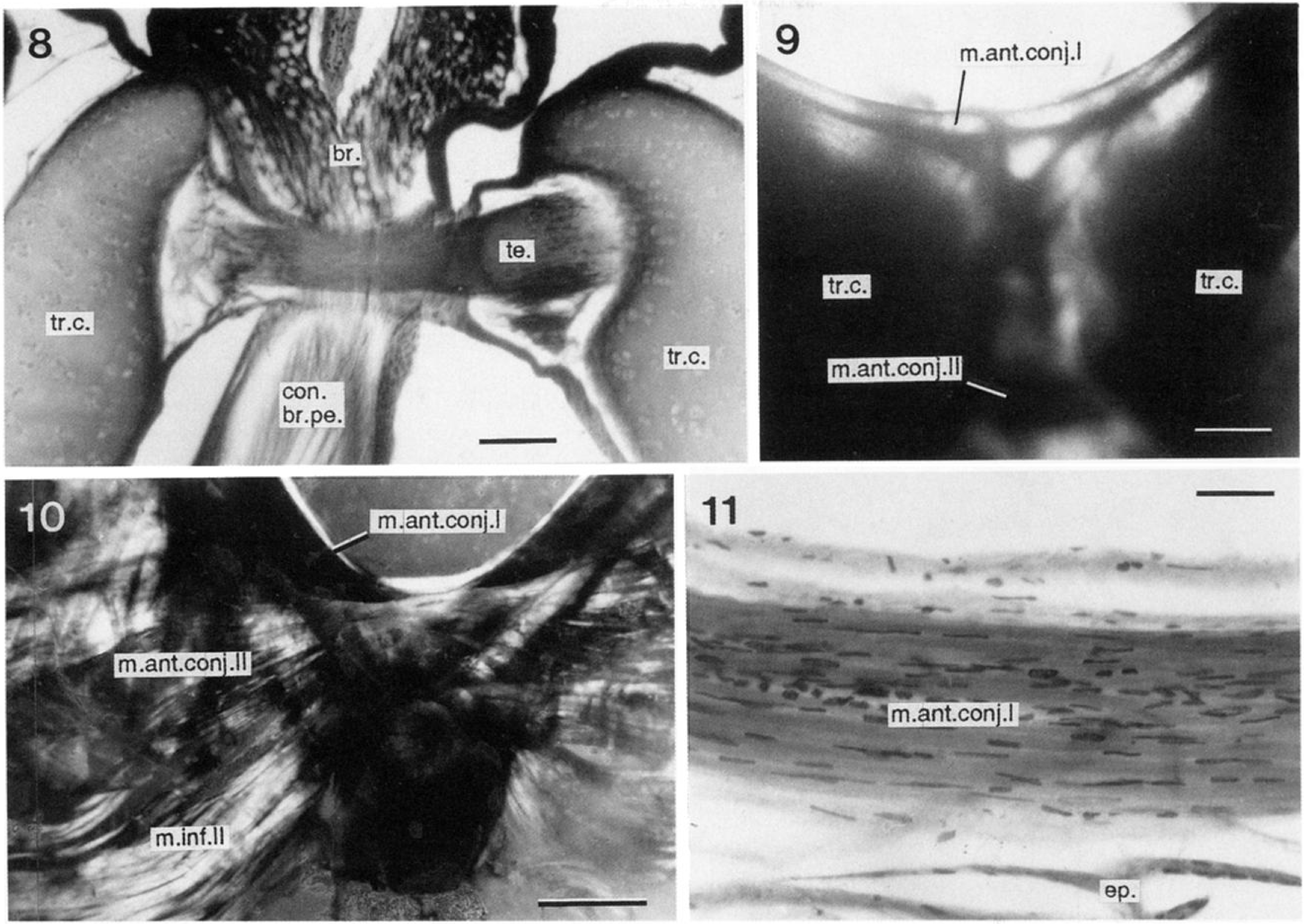
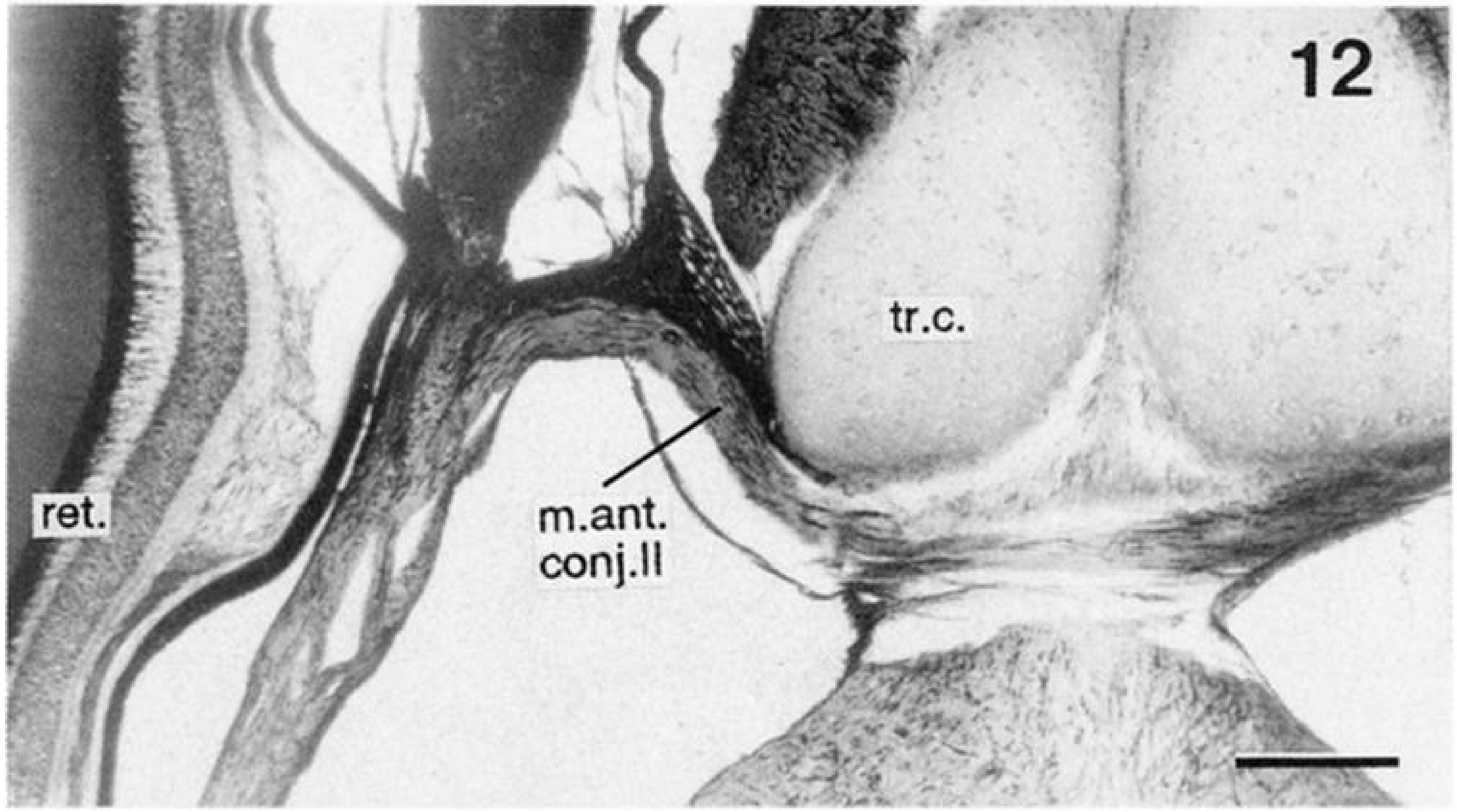


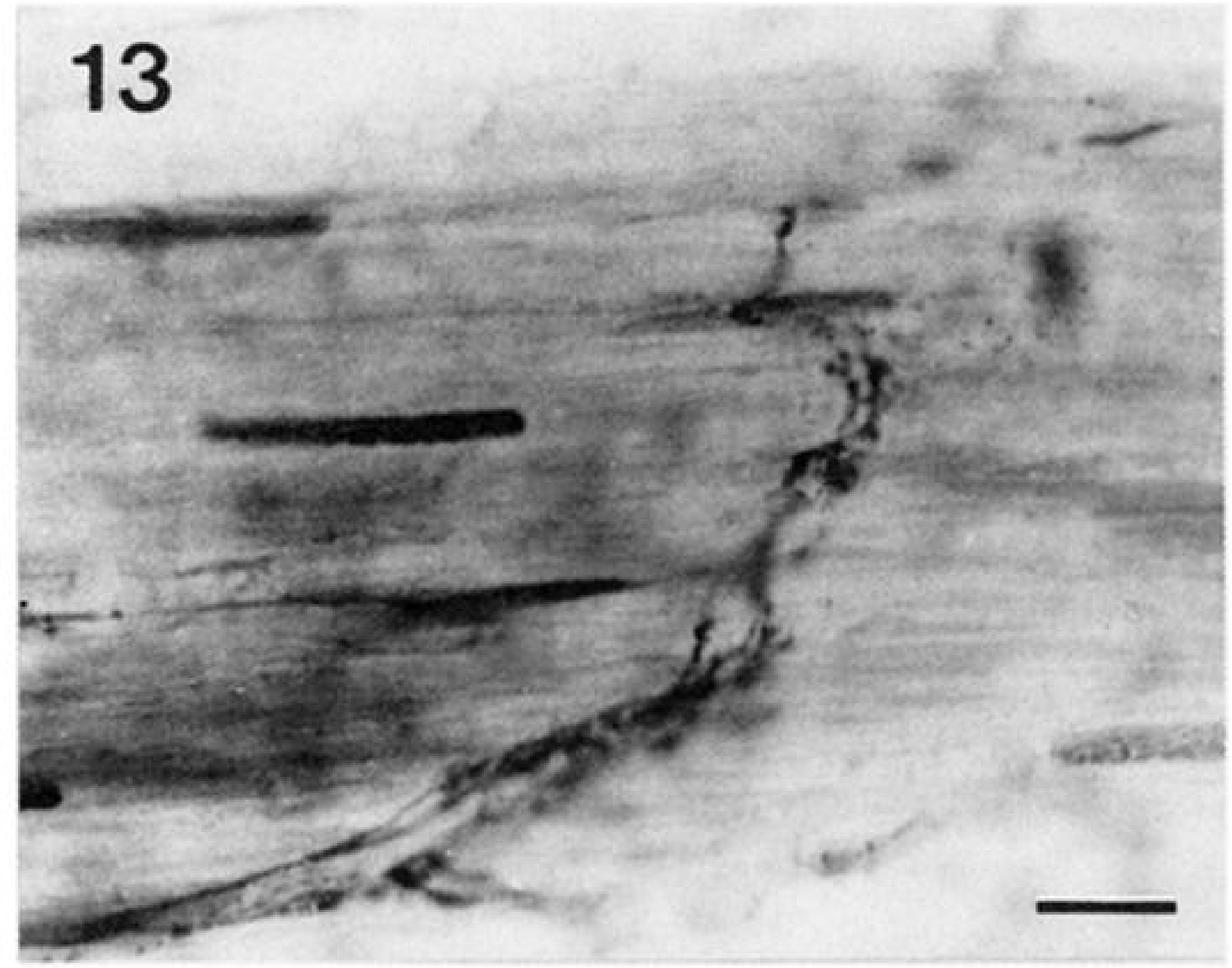
Figure 8. Crossing tendon of the anterior conjunctive muscle I. *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 100 μm.

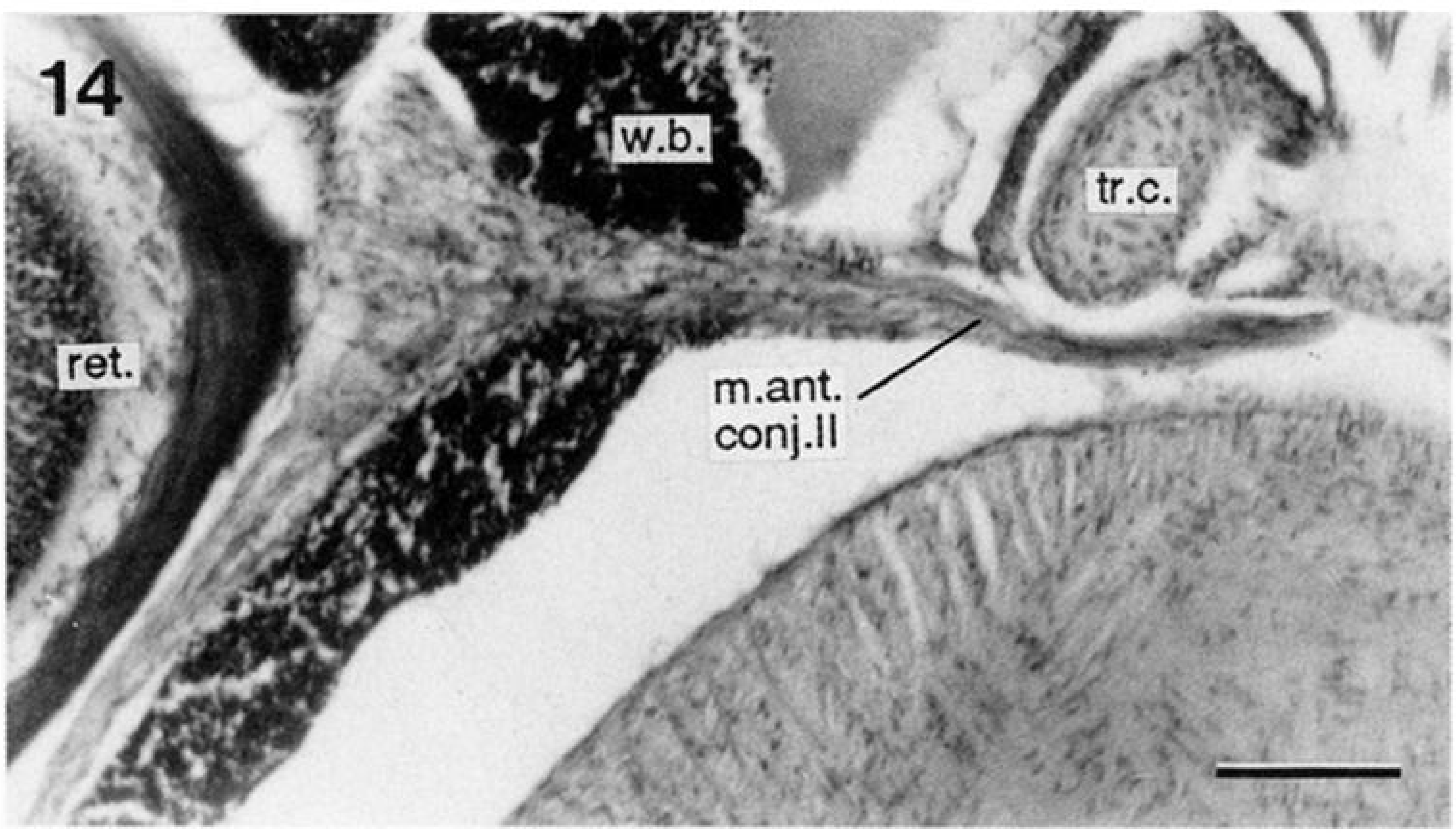
Figure 9. Preparation of the crossing tendon of anterior conjunctive muscle I. The crossing of the anterior conjunctive muscle II is seen out of focus. *Loligo plei*. Scale bar is 400 μm.

Figure 10. Preparation of the two anterior conjunctive muscles crossing the midline, and the inferior muscle II, seen in polarized light. *Sepioteuthis lessoniana*. Mayer's haemalum stain. Scale bar is 2 mm.

Figure 11. Crossing tendon of anterior conjunctive muscle I. *Sepioteuthis sepioidea*. Transverse section. Cajal stain. Scale bar is 30 μm.







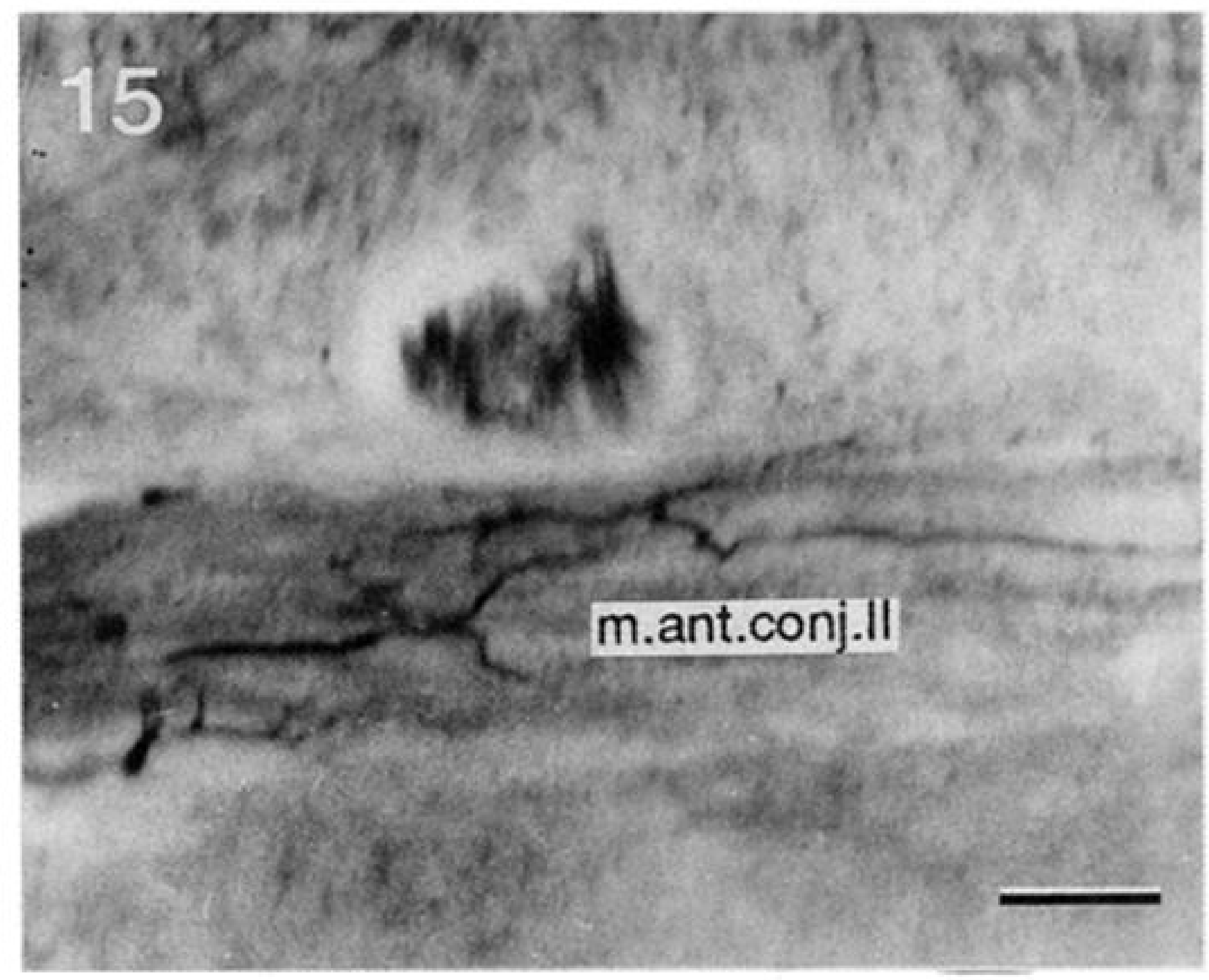


Figure 12. Bases of the two trochlear cartilages and the crossing of the anterior conjunctive muscle II. *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 150 μm.

Figure 13. Nerve fibres running across anterior conjunctive muscle II at its crossing. *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 10 μm.

Figure 14. Anterior conjunctive muscle II. Juvenile *Loligo pealei*. Transverse section. Haematoxylin and eosin stain. Scale bar is 500 μm.

Figure 15. Nerve fibres running along anterior conjunctive muscle II at its crossing. *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 30 μm.

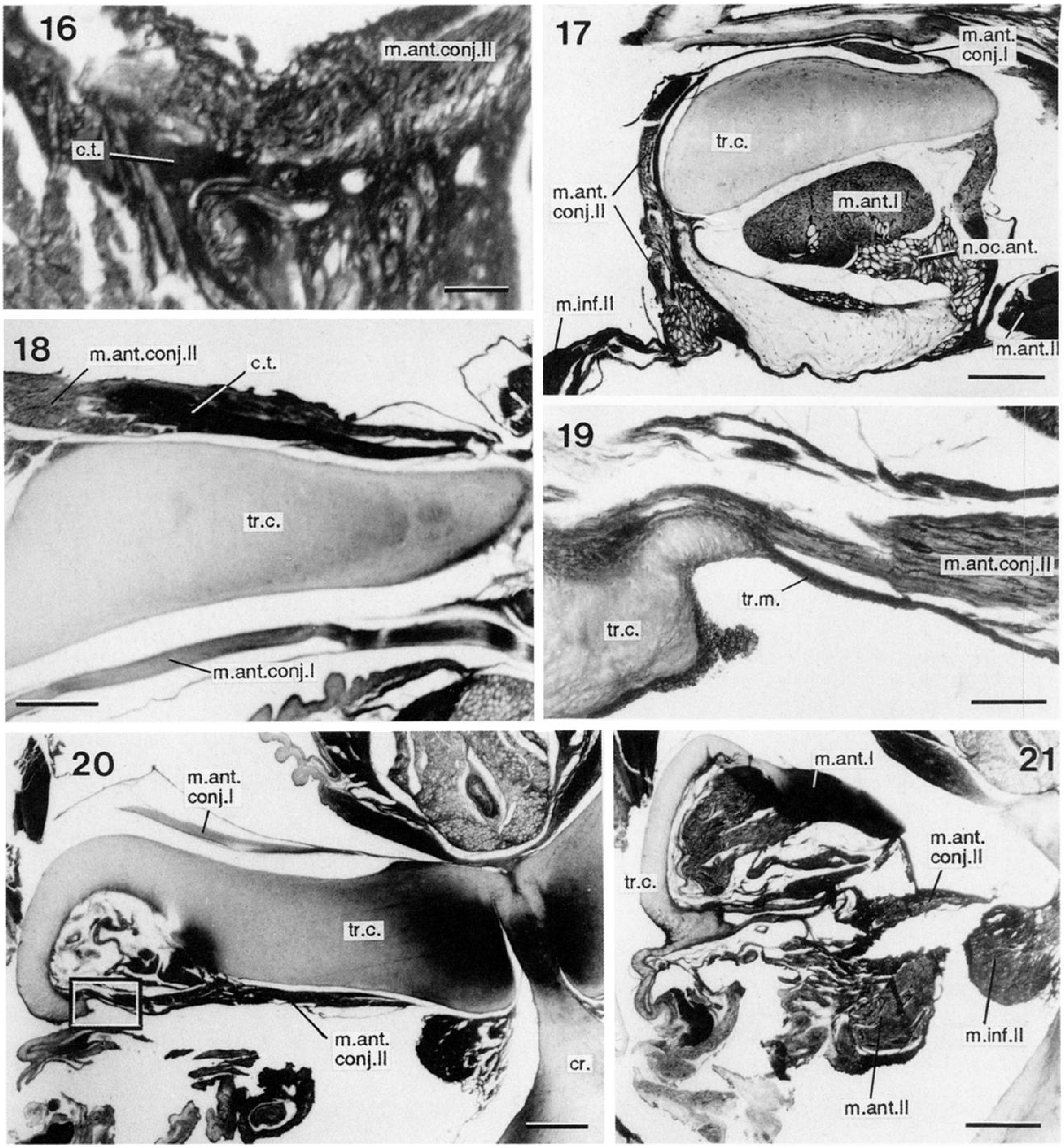


Figure 16. Enlarged view of anterior conjunctive muscle II where it breaks up into small bundles among dense connective tissue. *Sepioteuthis sepioidea*. Cajal stain. Scale bar is 50 μm.

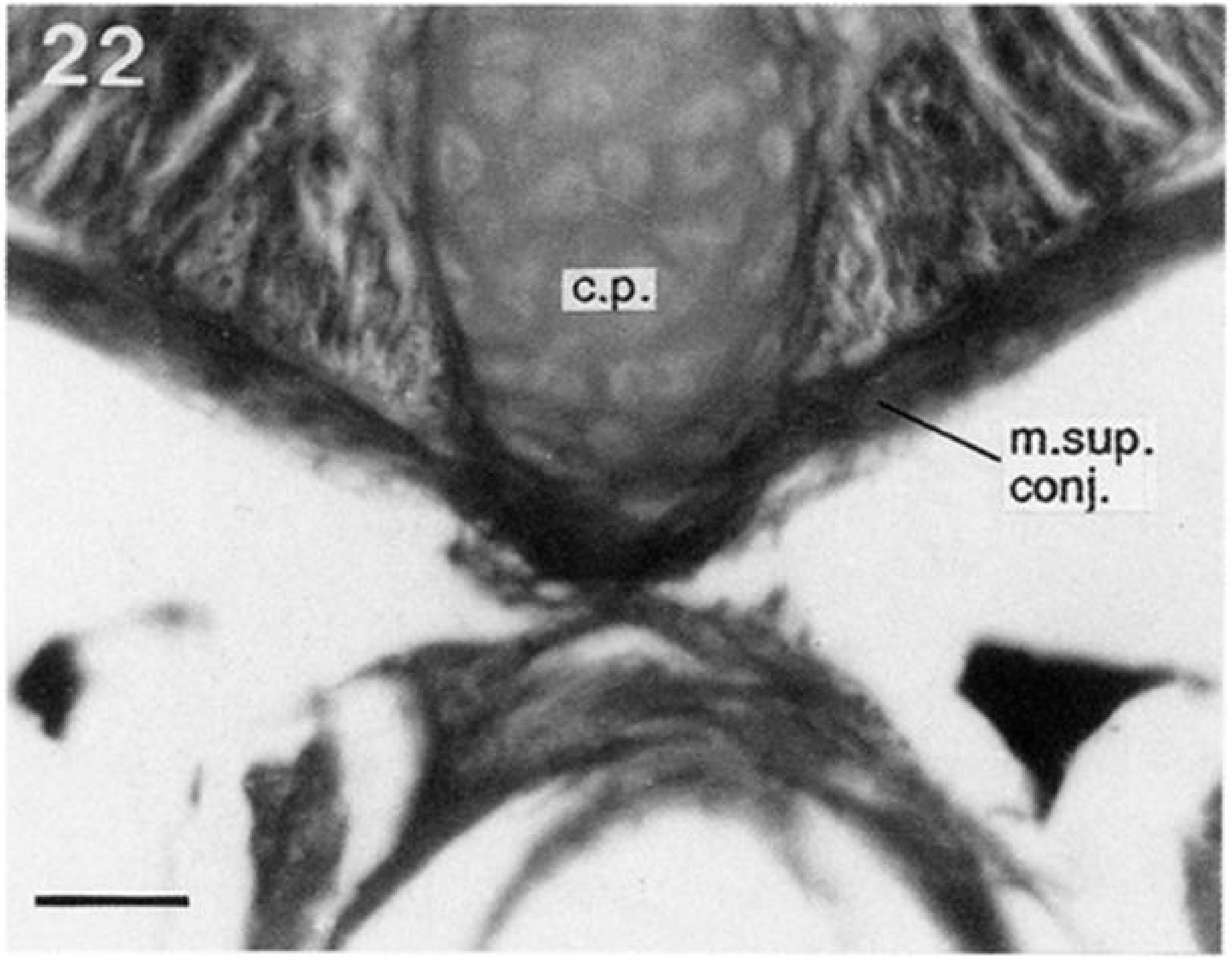
Figure 17. Anterior conjunctive muscle II divided into several branches. *Sepioteuthis sepioidea*. Horizontal section, slightly dorsal to figure 4. Cajal stain. Scale bar is 300 μm.

Figure 18. Trochlear cartilage and the two anterior conjunctive muscles. Note interruption of anterior conjunctive muscle II by connective tissue. *Sepioteuthis sepioidea*. Transverse section. Cajal stain. Scale bar is 500 μm.

Figure 19. Enlarged view of area outlined in figure 20 to show the attachment of the muscle to the cartilage. *Sepioteuthis sepioidea*. Transverse section. Cajal stain. Scale bar is 100 μm.

Figure 20. Trochlear cartilage and its attachment to the cranium. Part of the anterior conjunctive muscle II is attached to the tip of the trochlear cartilage. *Sepioteuthis sepioidea*. Transverse section. Cajal stain. Scale bar is 500 μm.

Figure 21. Anterior conjunctive muscle II and anterior muscle I attached to the tip of the trochlear cartilage. *Sepioteuthis sepioidea*. Transverse section, posterior to figure 20. Cajal stain. Scale bar is 400 μm.



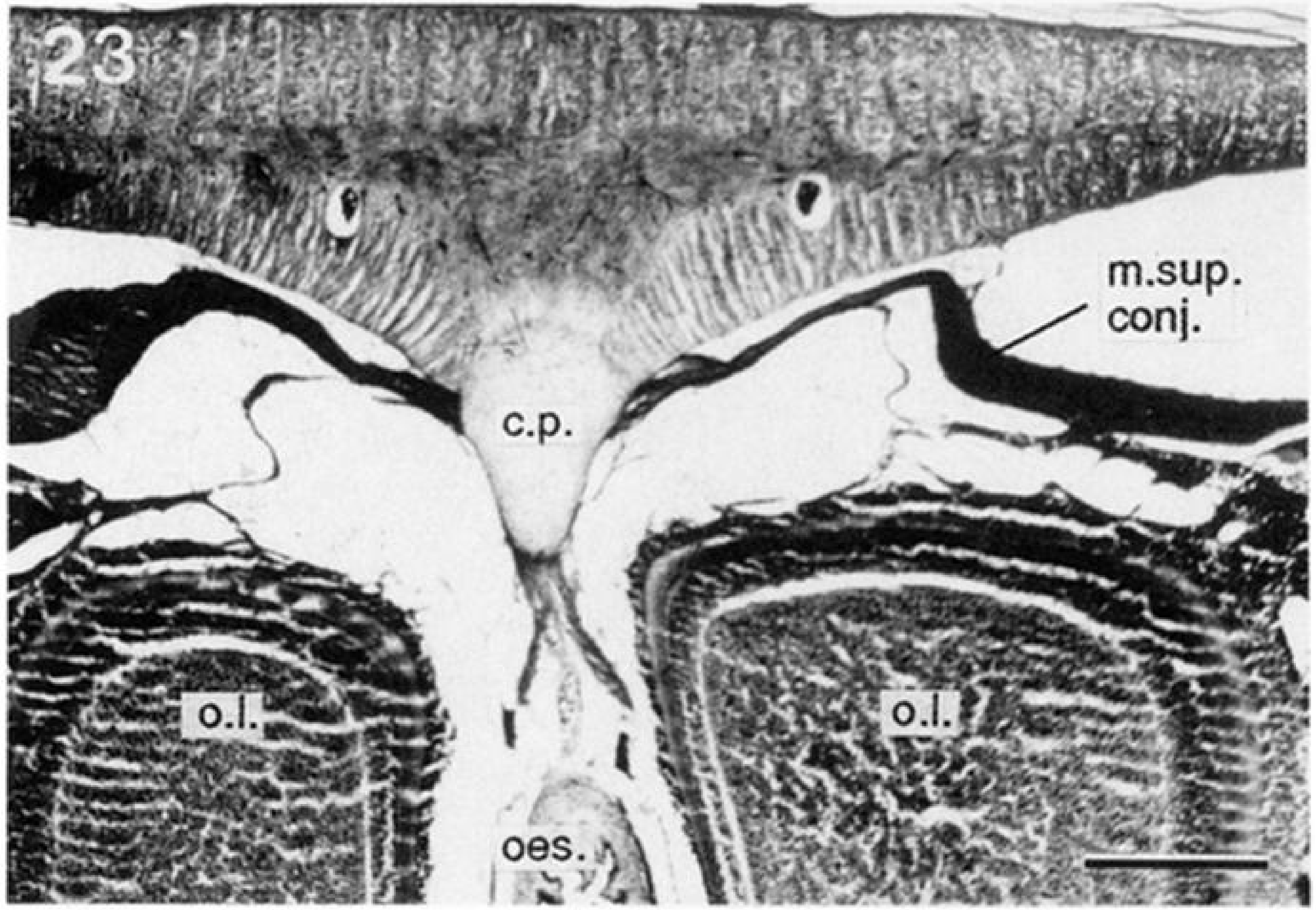
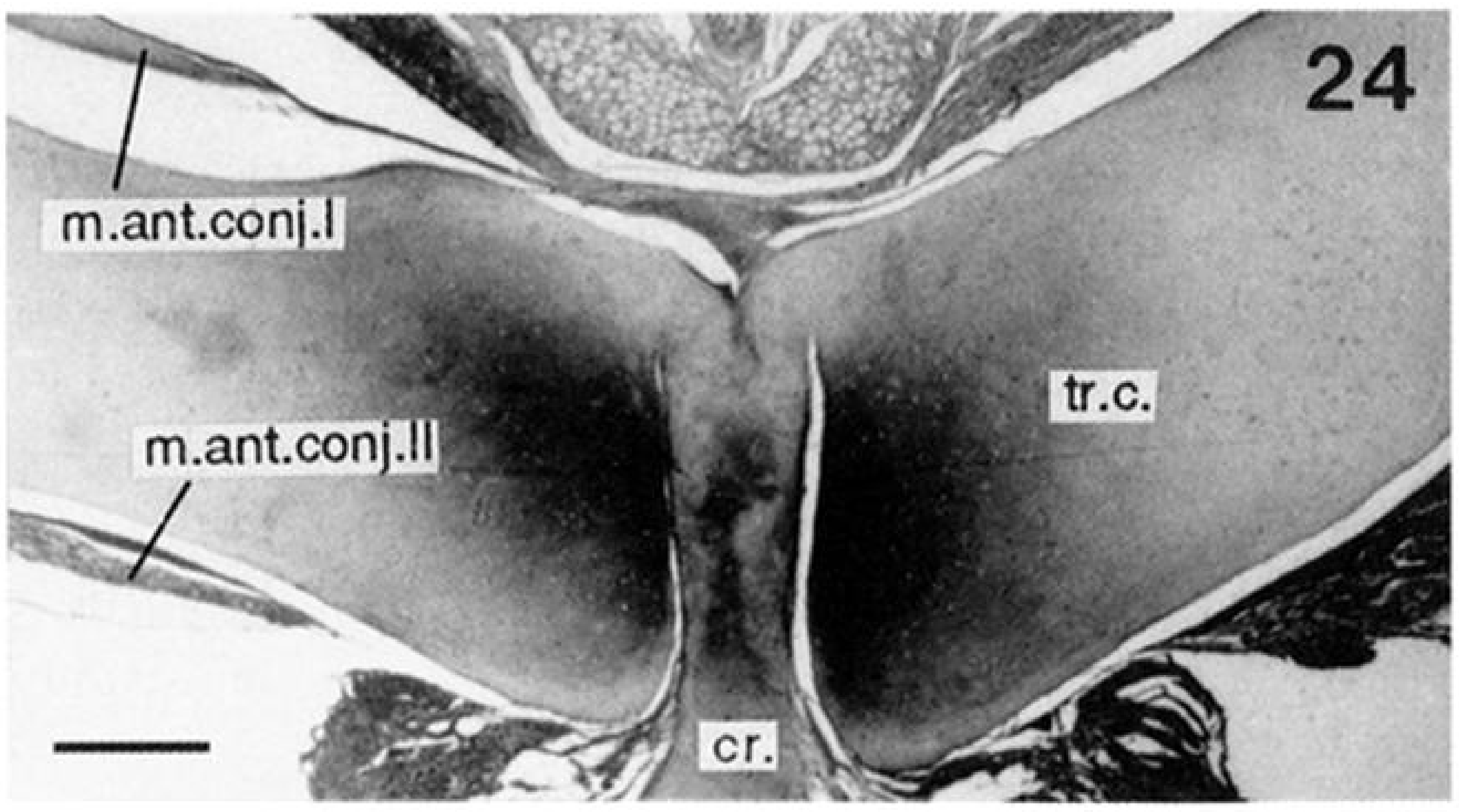
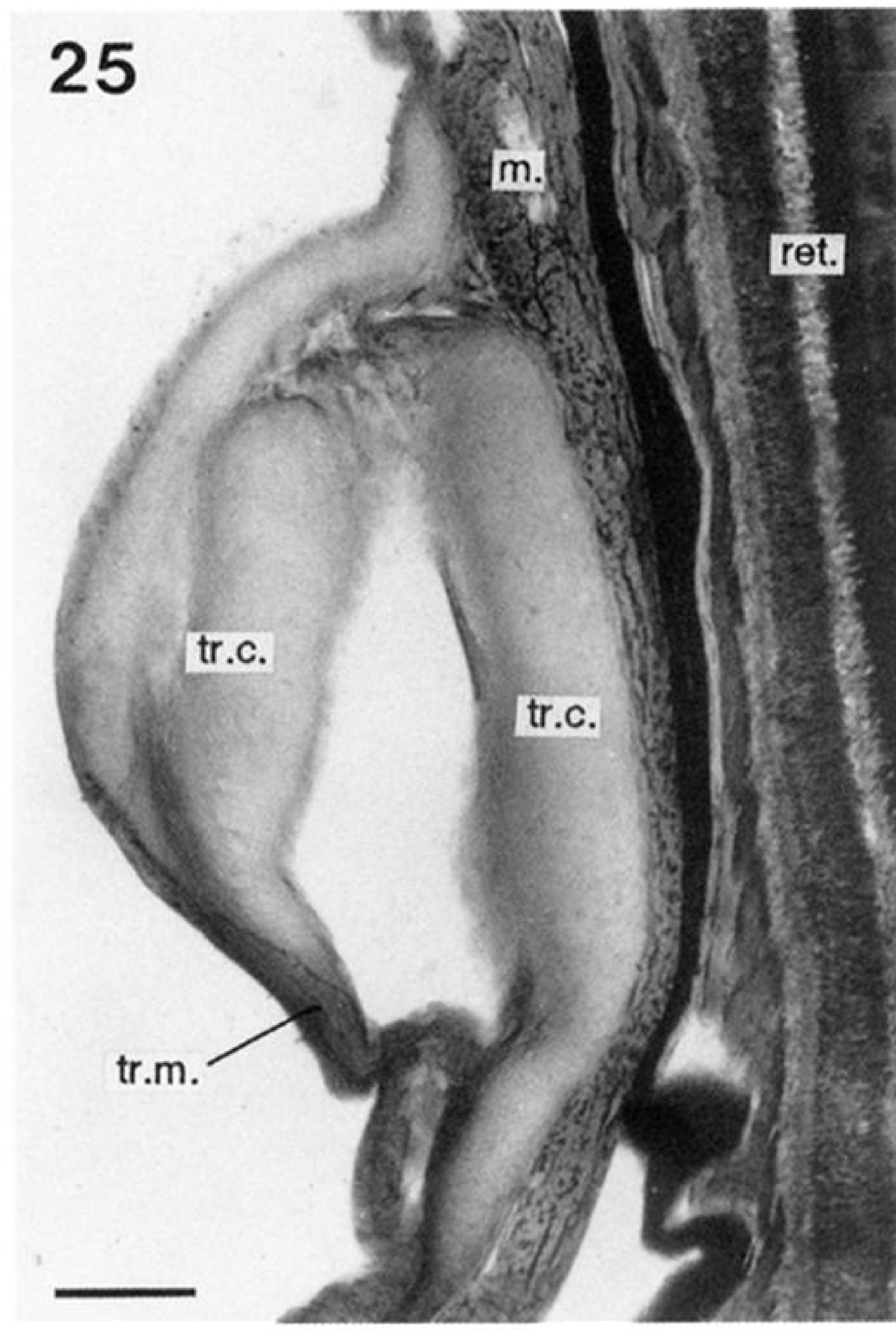
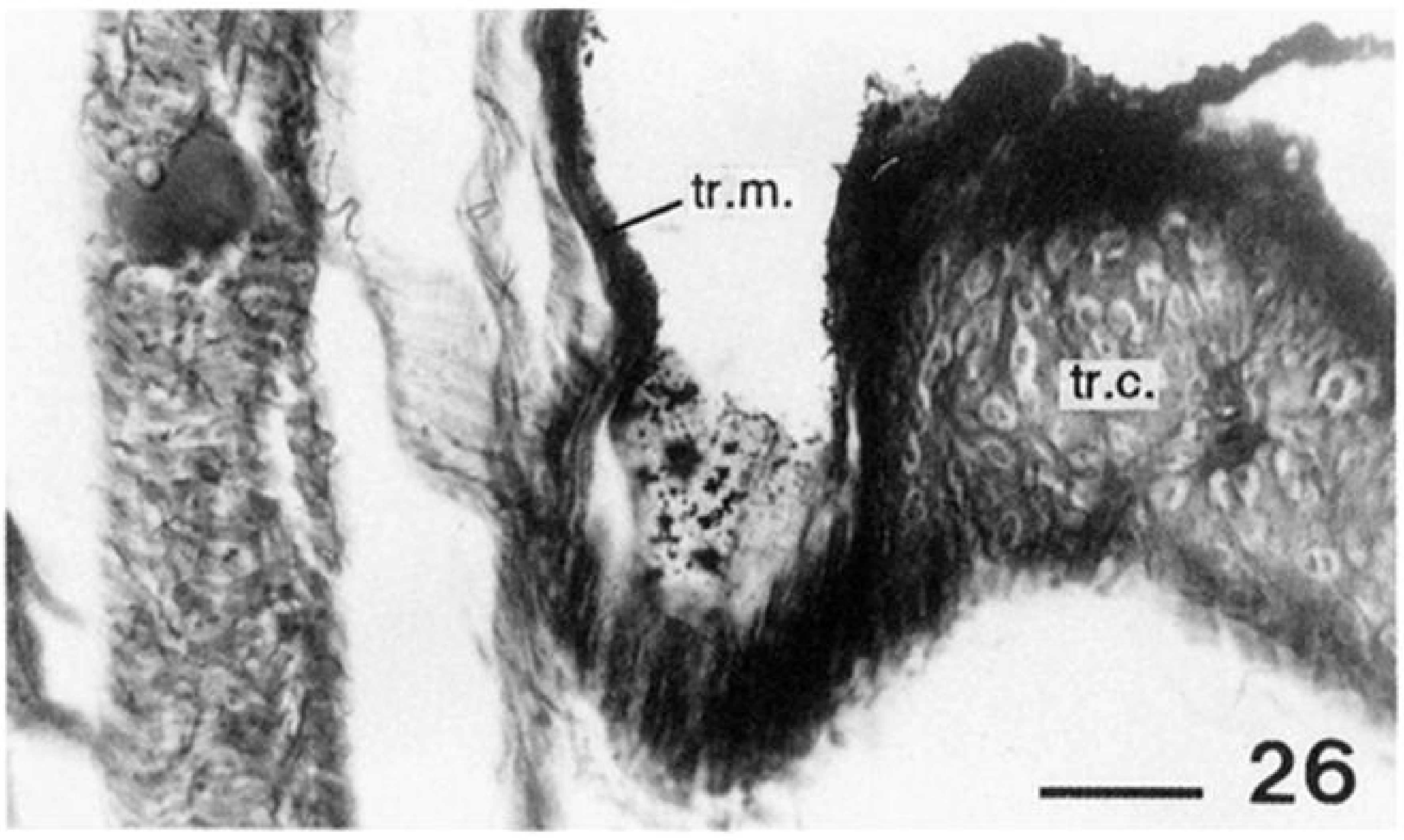


Figure 22. Crossing of tendons of the superior conjunctive muscles. Small juvenile of *Loligo pealei*. Transverse section. Haematoxylin and eosin stain. Scale bar is 40 µm.

Figure 23. Superior conjunctive muscles and their tendons attached to cartilage in the midline. Small specimen of *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 500 µm.







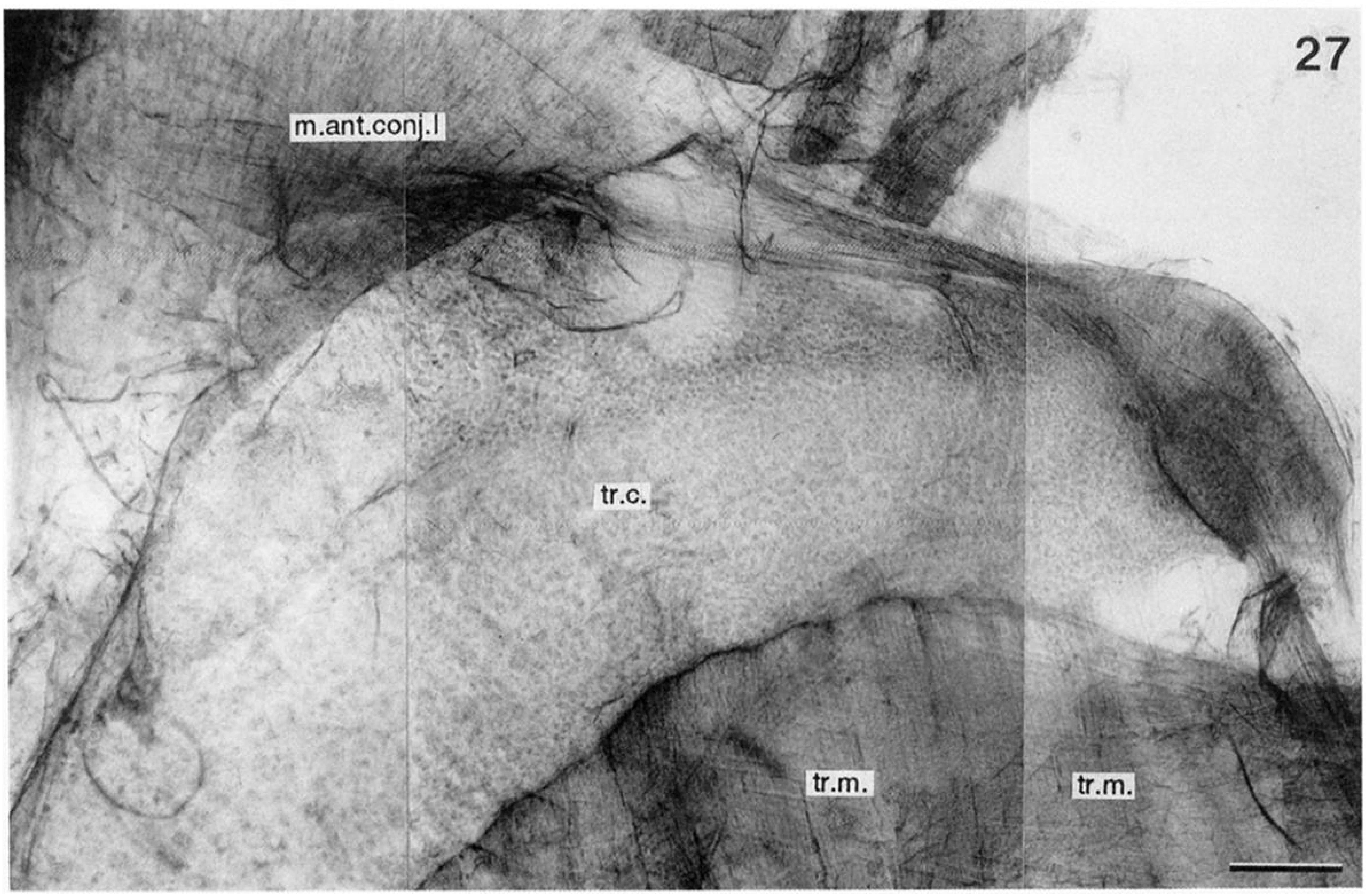
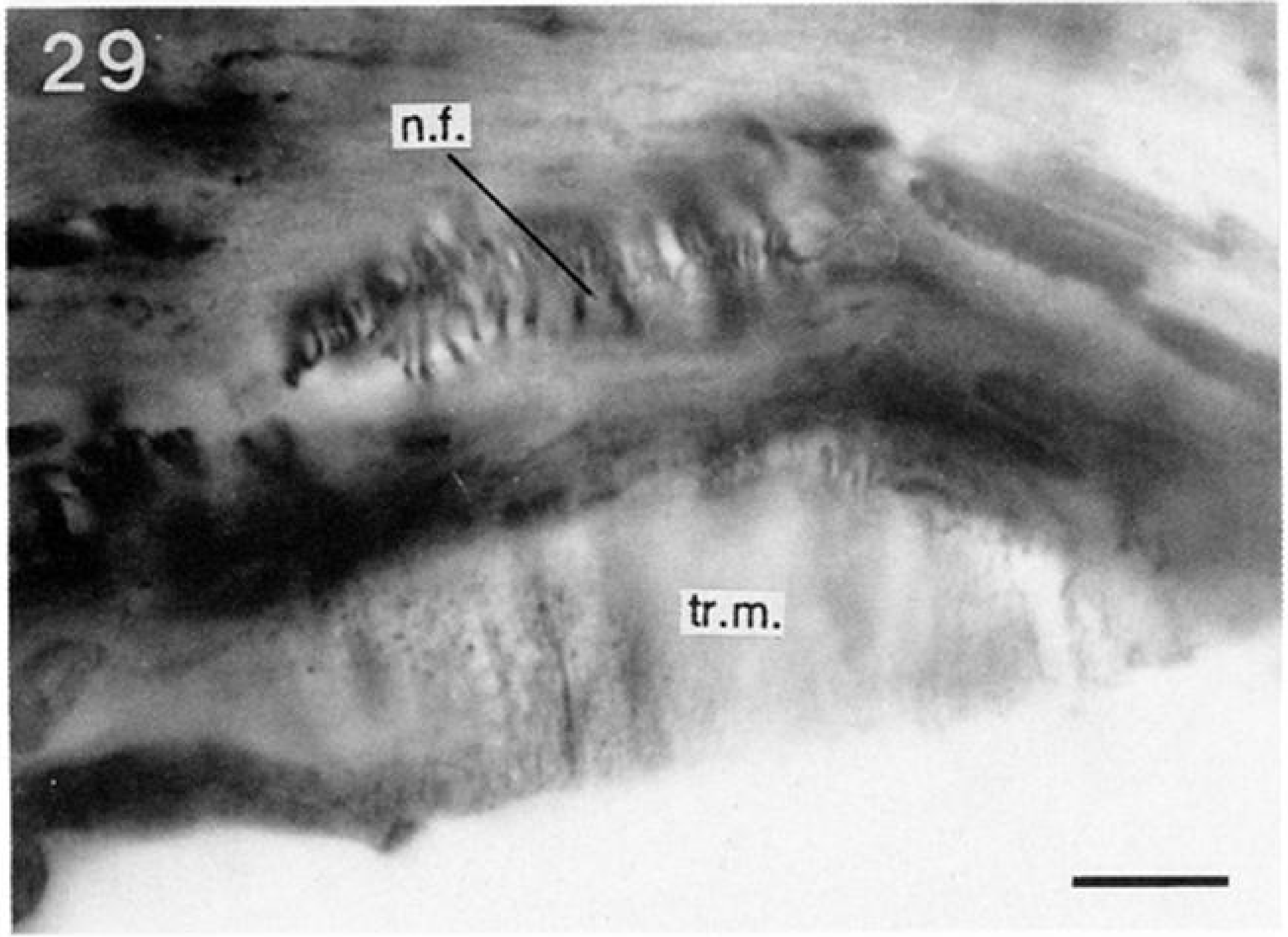


Figure 24. Narrow attachments of the trochlear cartilages to the base of the cranium. *Sepioteuthis sepioidea*. Transverse section. Cajal stain. Scale bar is 300 µm.

Figure 25. Distal end of the trochlear cartilage pressed against the eyeball. Note several layers and extensions to form the trochlear membrane. *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 150 µm.

Figure 26. The transition between trochlear cartilage and trochlear membrane. *Sepioteuthis sepioidea*. Cajal stain. Scale bar is 50 µm.

Figure 27. Tip of the trochlear cartilage showing the complex head and the attached strands of the trochlear membrane. *Loligo pealei*. Mayer's haemalum stain. Scale bar is 500 µm.



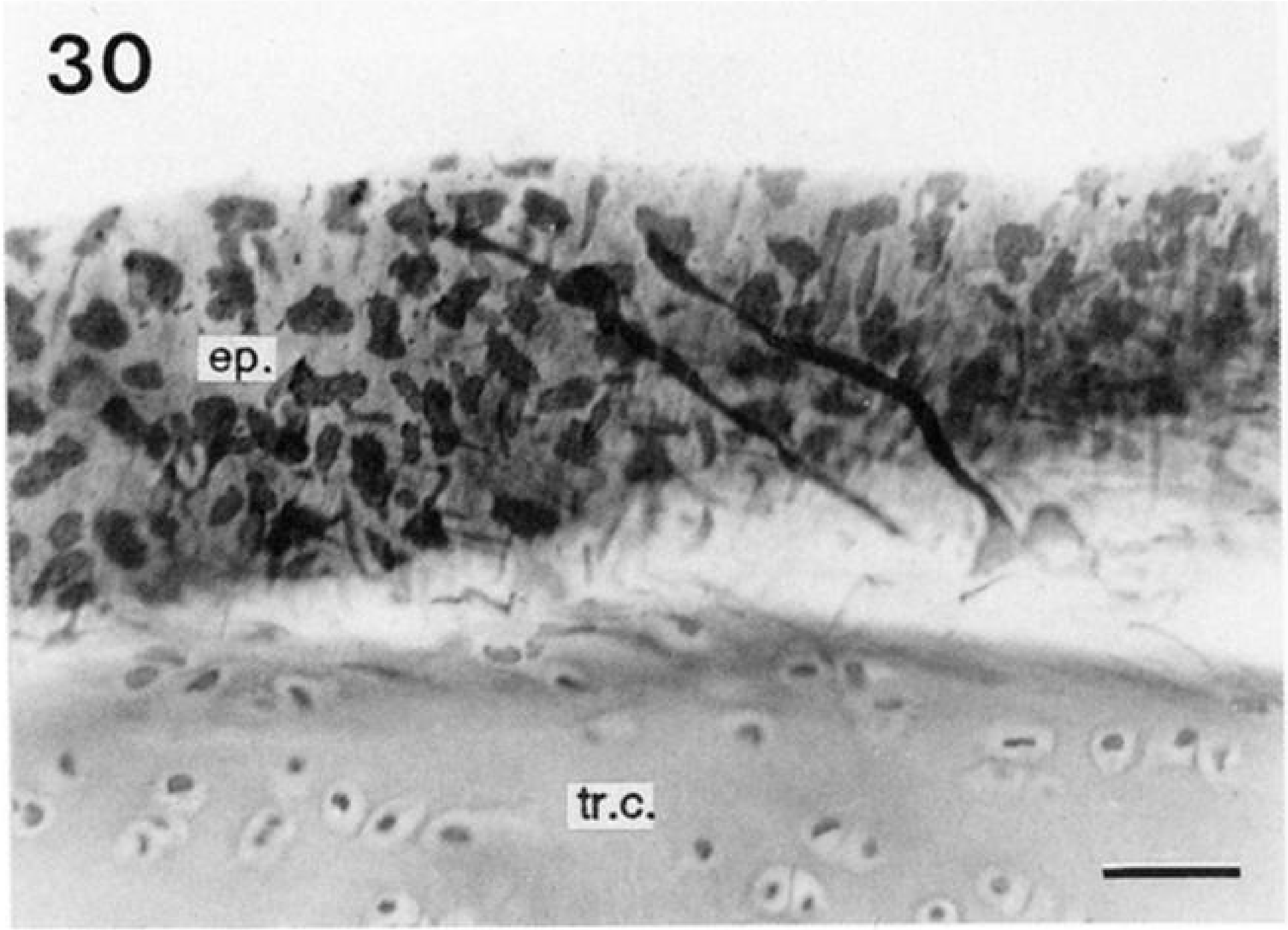
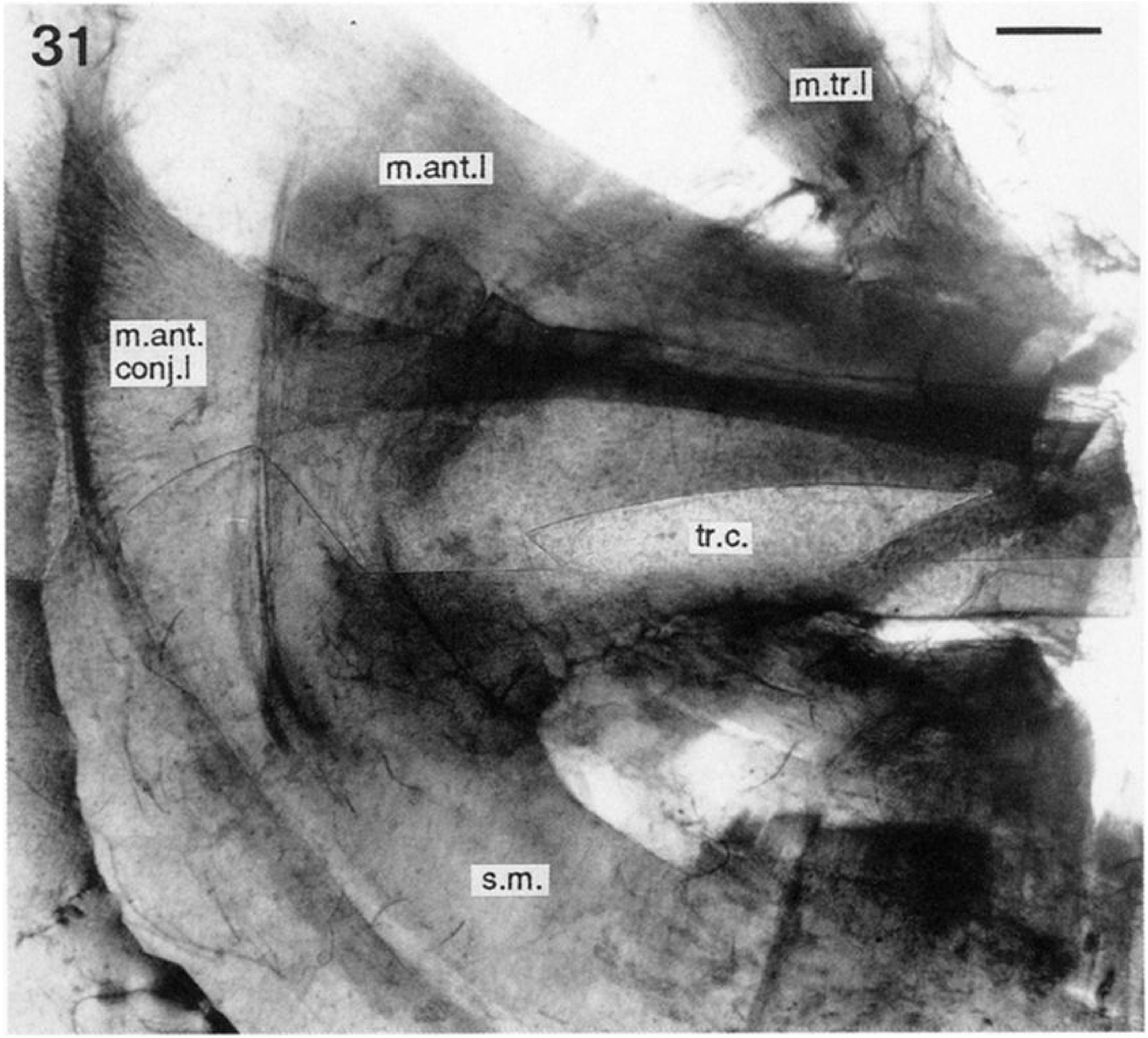


Figure 29. Anterior conjunctive muscle II with a bundle of small nerve fibres and a portion of the trochlear membrane with transverse banding. *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 10 µm.

Figure 30. Epithelium covering the trochlear cartilage. The nature of the two elongated fibres is uncertain. *Sepioteuthis sepioidea*. Transverse section. Cajal stain. Scale bar is 40 µm.



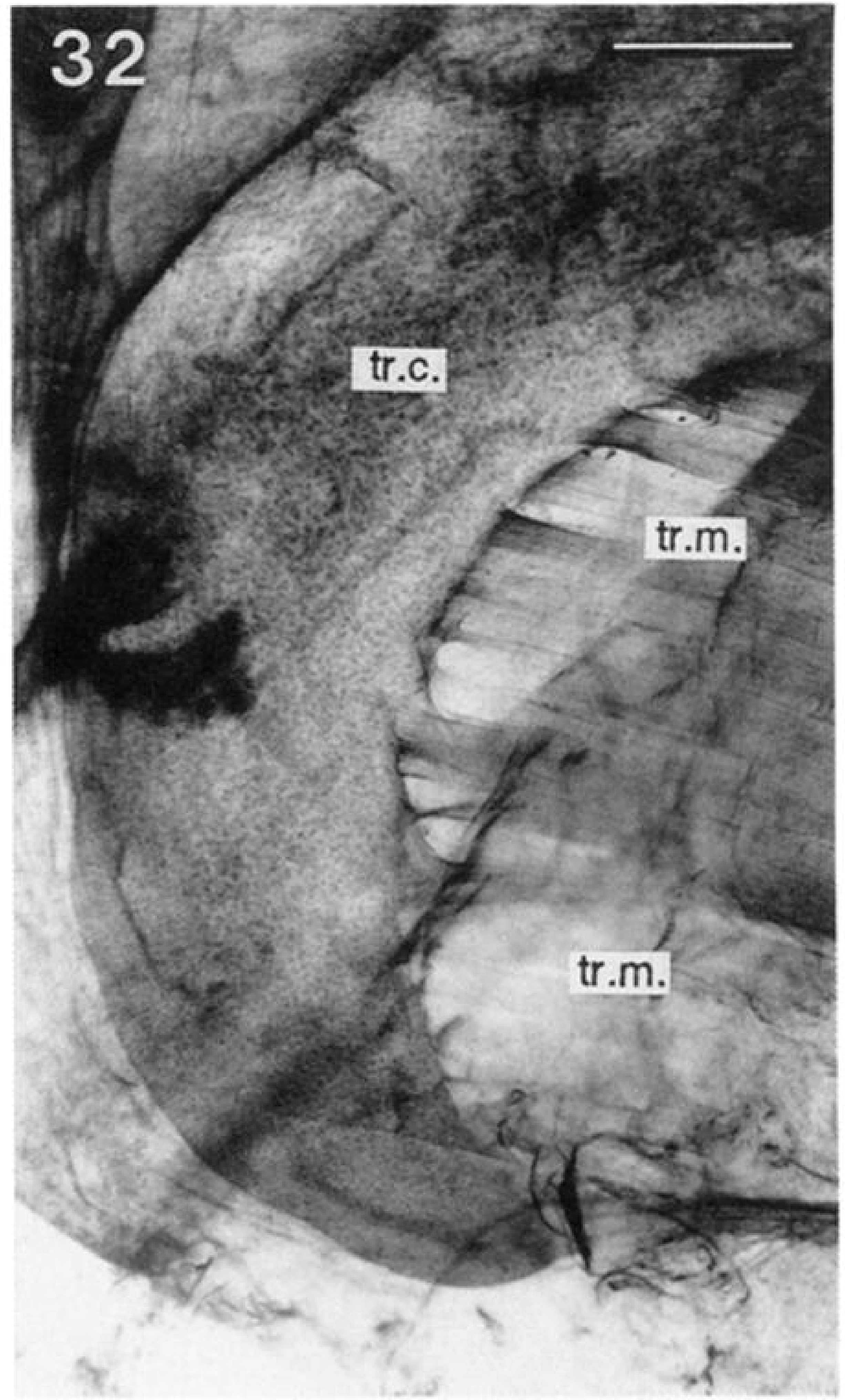
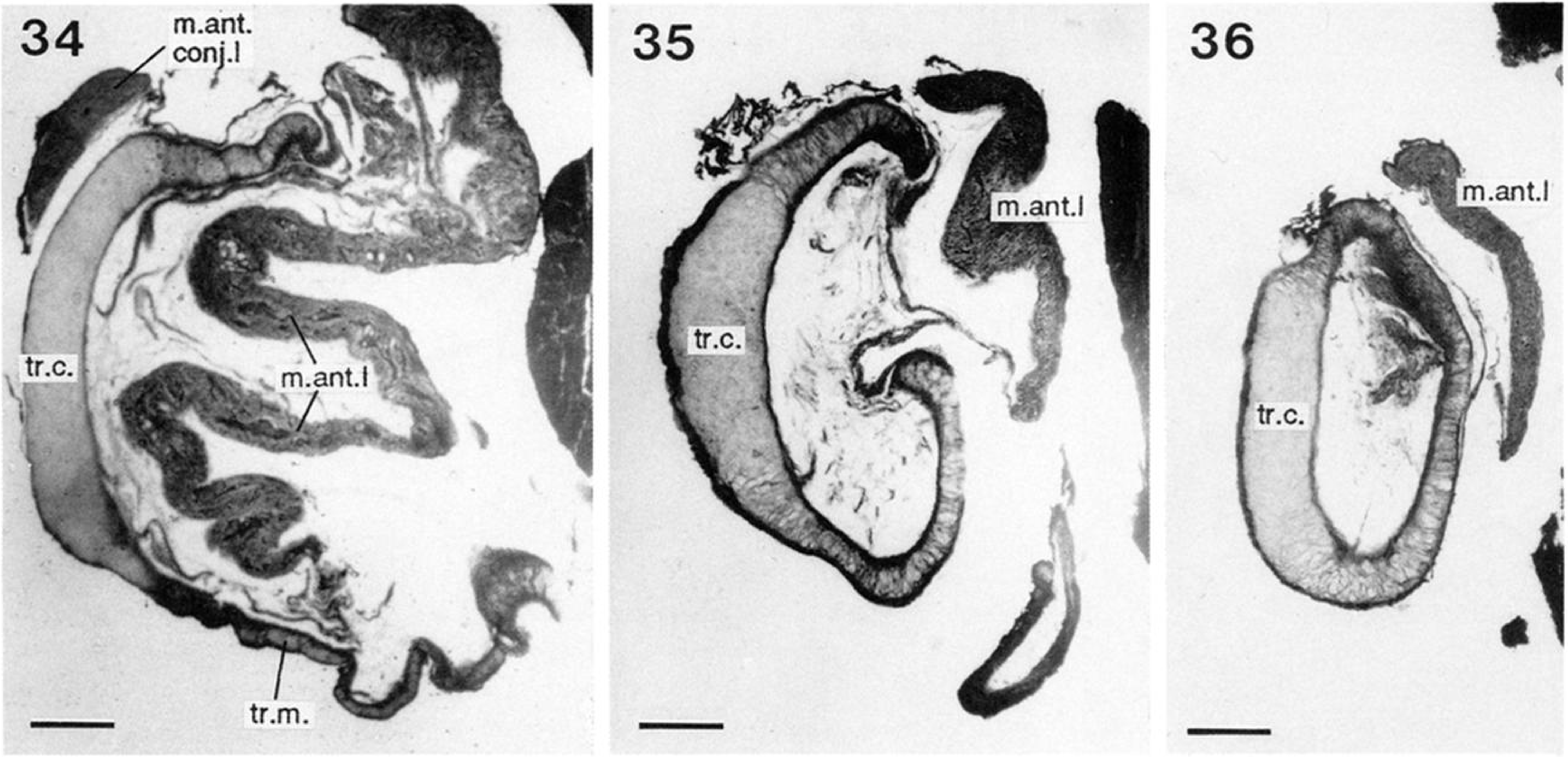
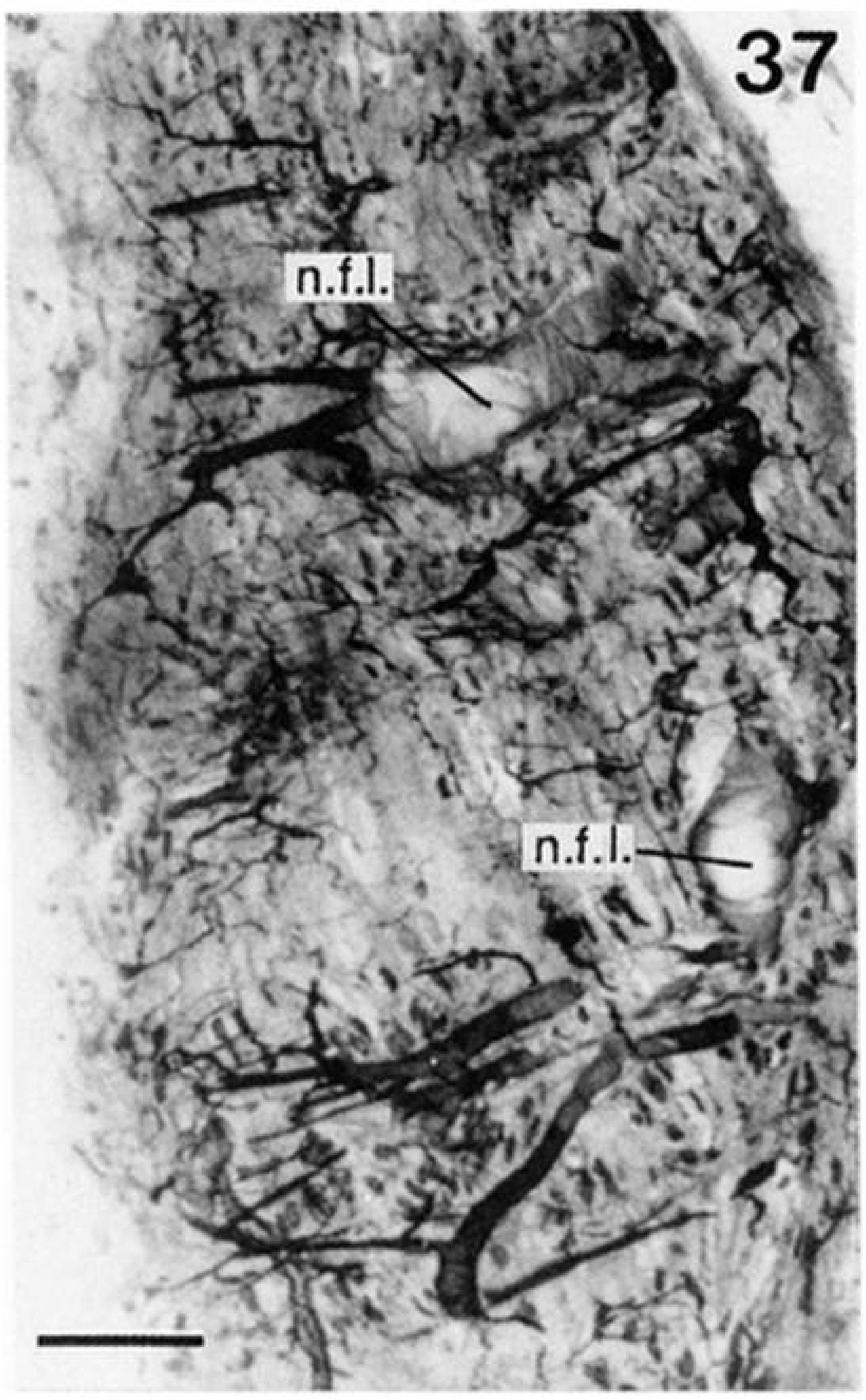


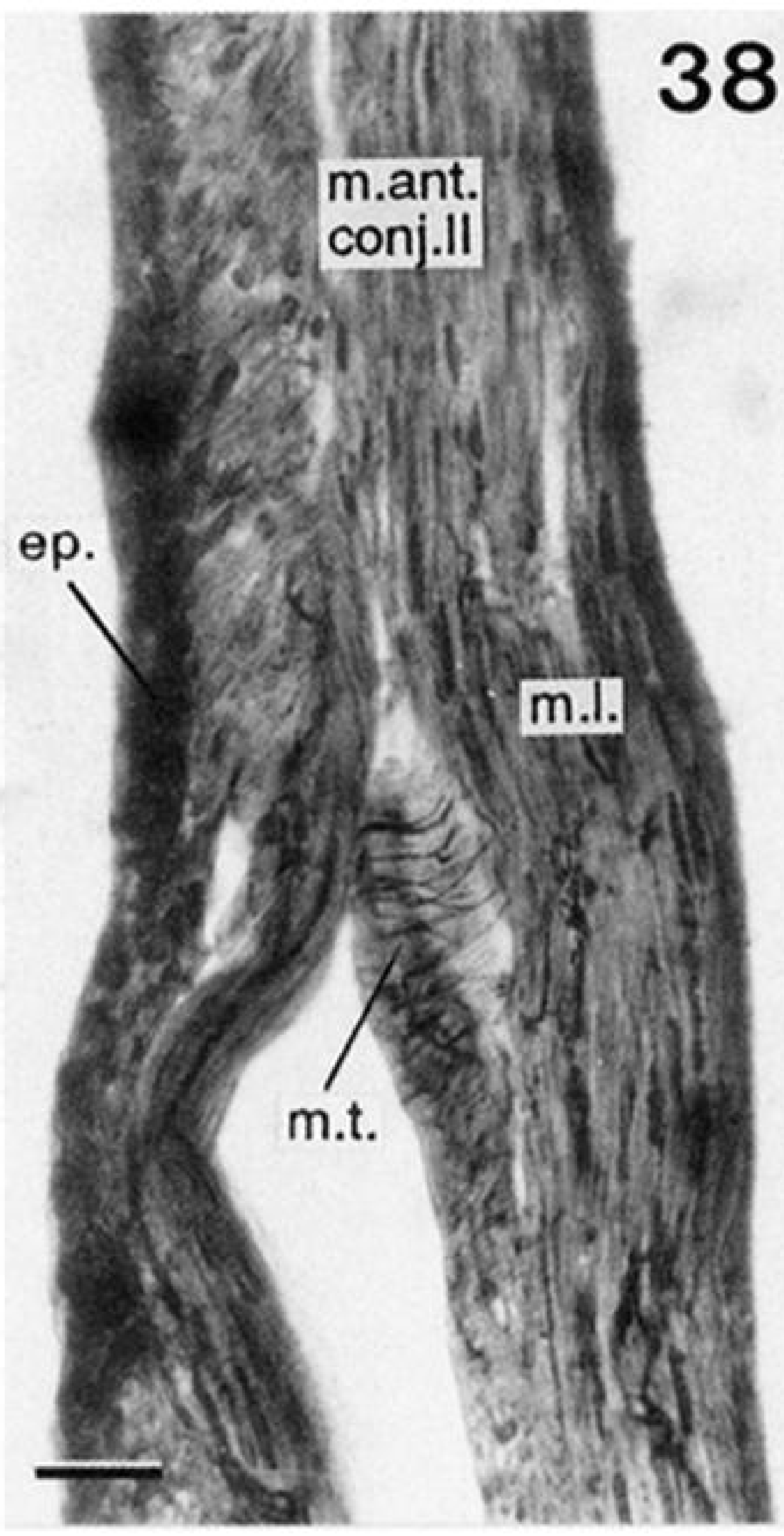
Figure 31. Tip of trochlear cartilage showing the trochlear membrane and smooth sheath. *Sepioteuthis lessoniana*. Mayer's haemalum stain. Scale bar is 500 µm.

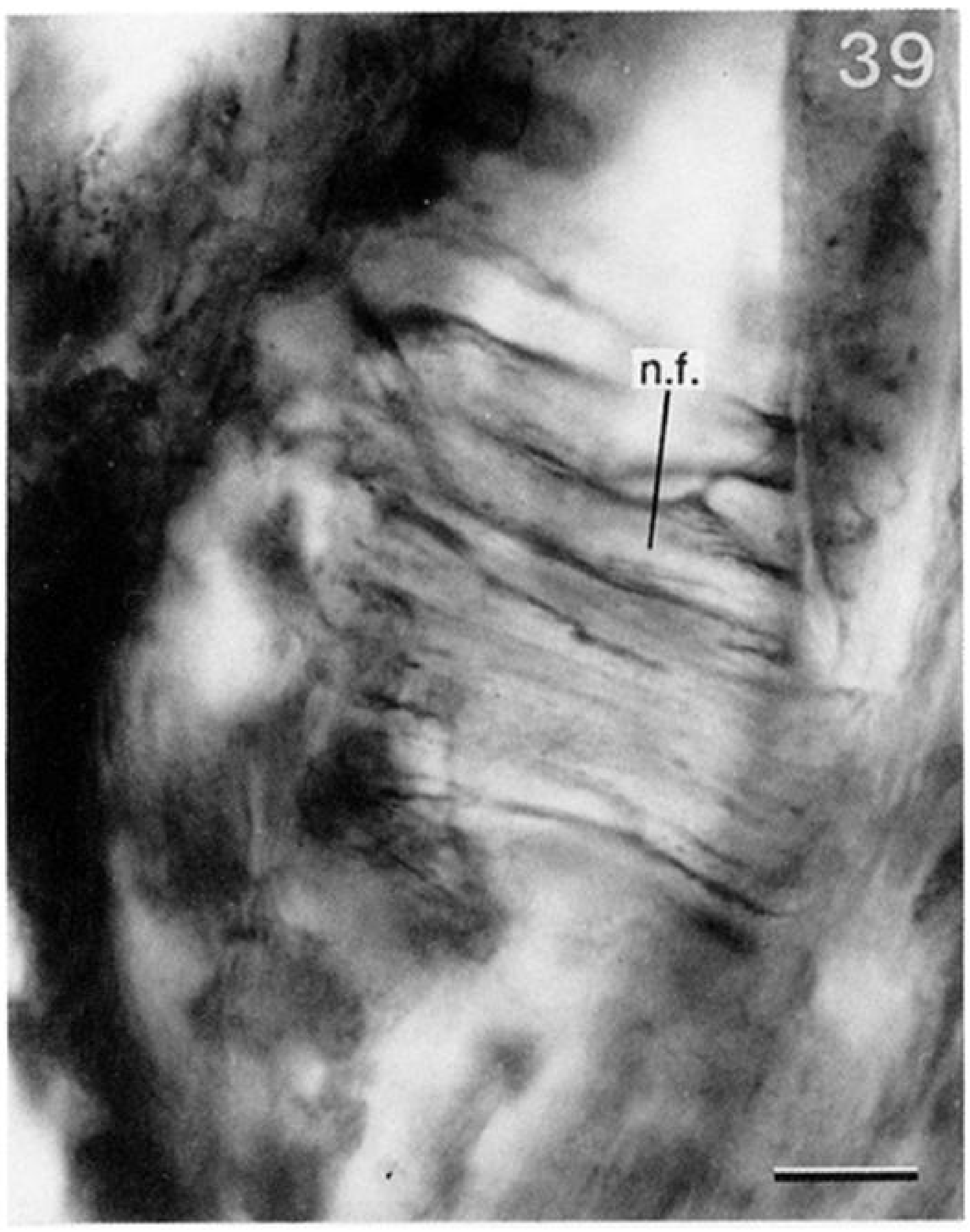
Figure 32. Tip of trochlear cartilage with origin the trochlear membrane. *Loligo pealei*. Mayer's haemalum stain. Scale bar is 500 µm.

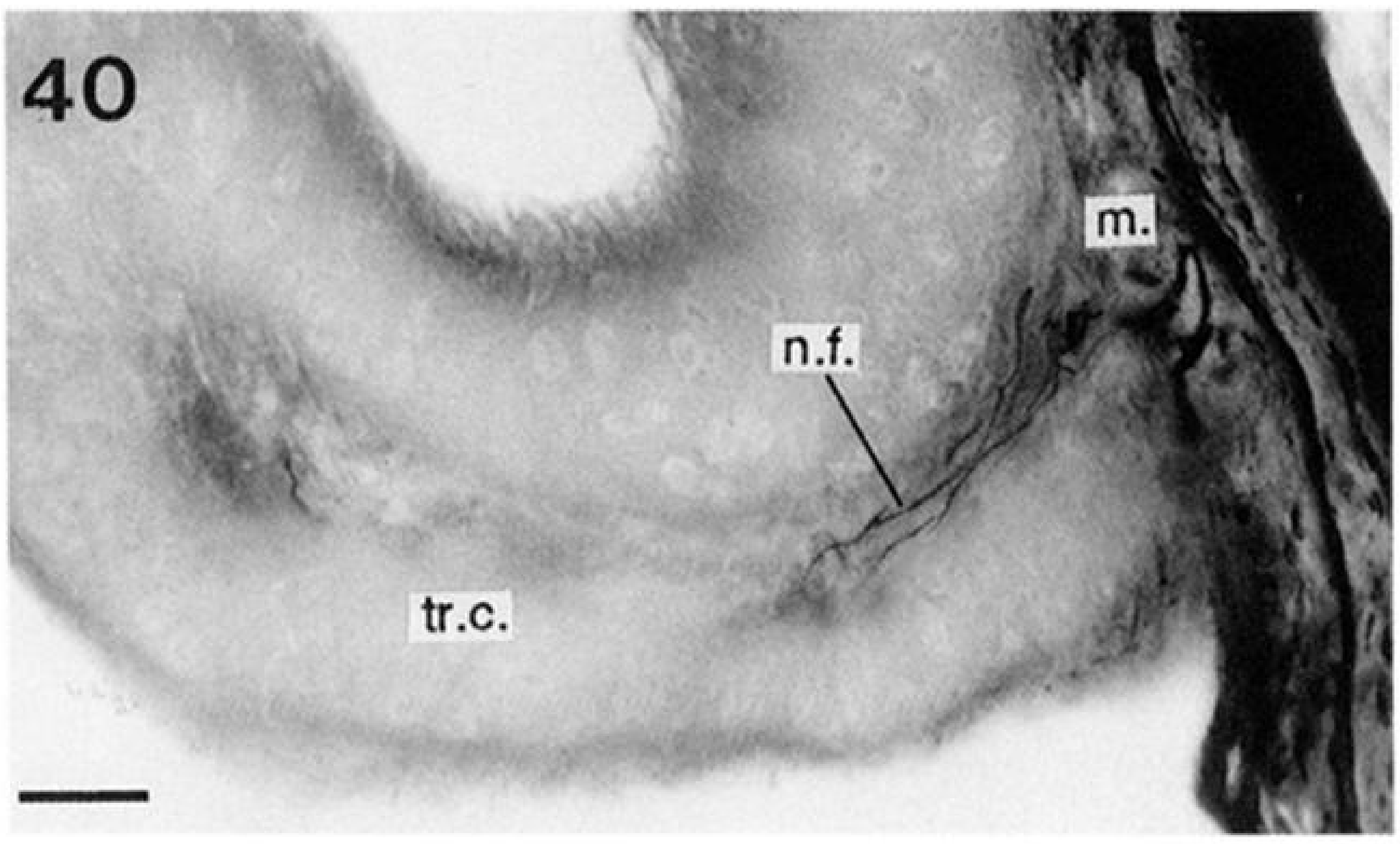


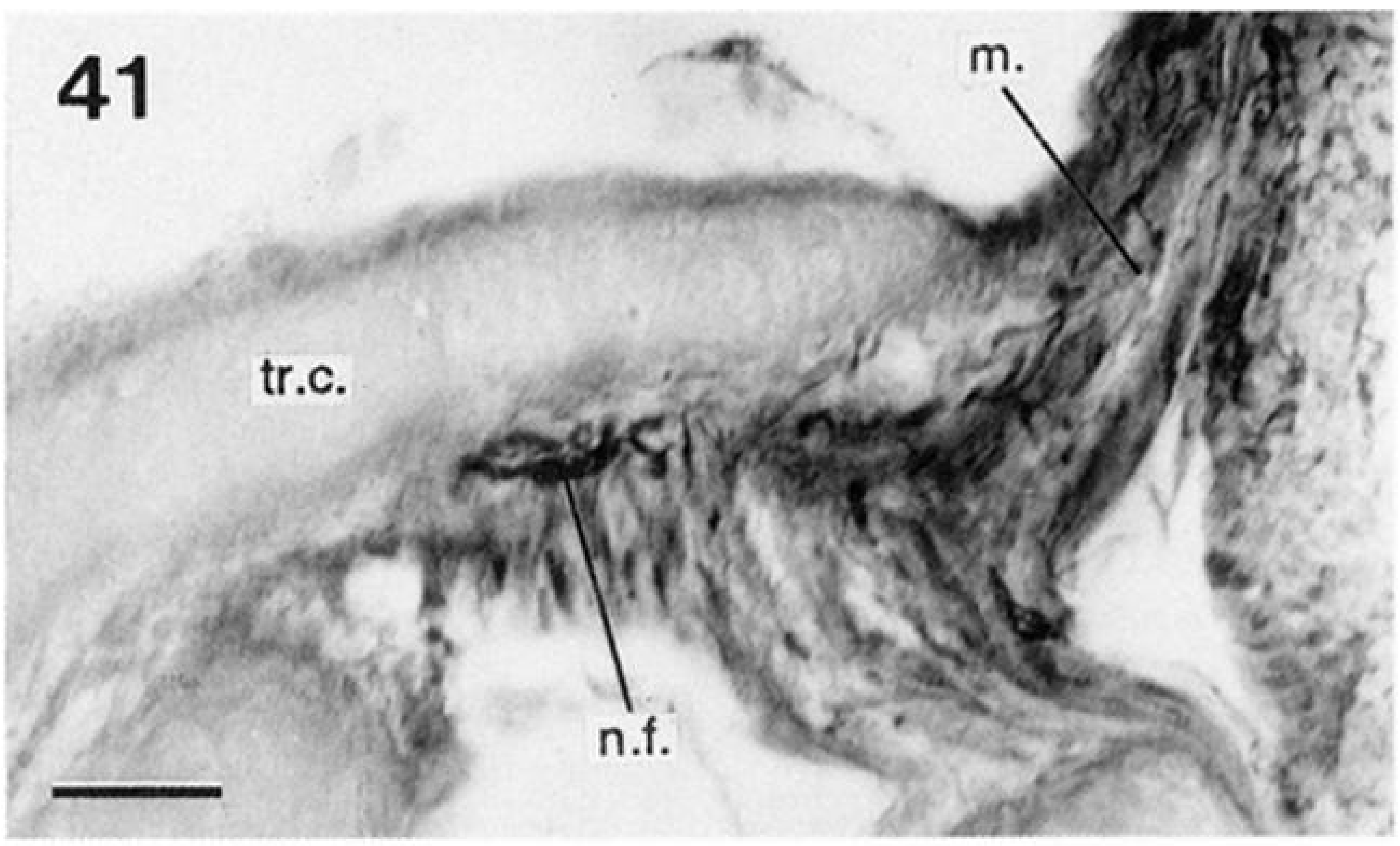
Figures 34–36. Tip of the trochlear cartilage in progressively forward sections to show how the edges of the cartilage join to enclose a cavity. *Sepioteuthis sepioidea*. Transverse sections. Cajal stains. Scale bars are 300 μm.

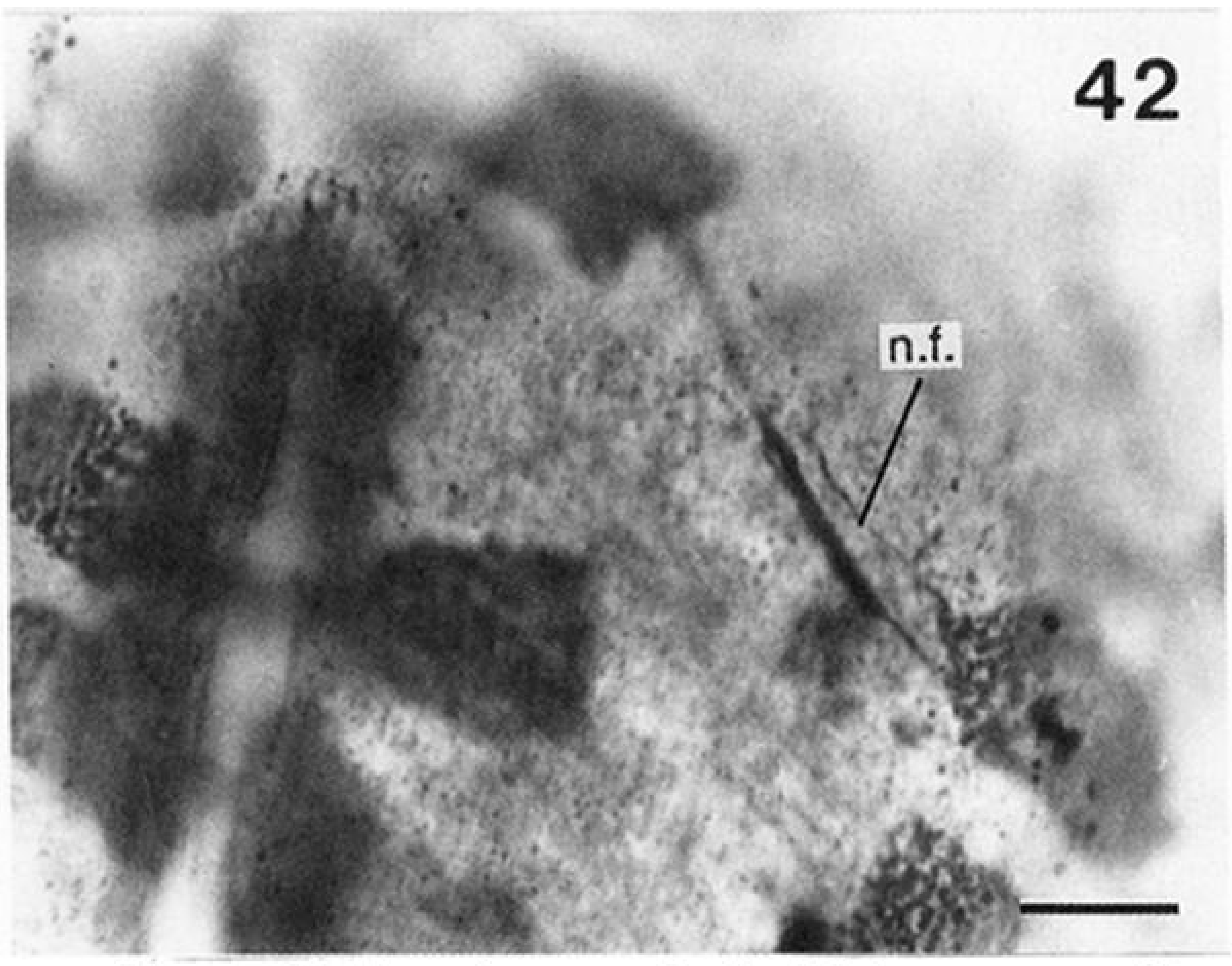












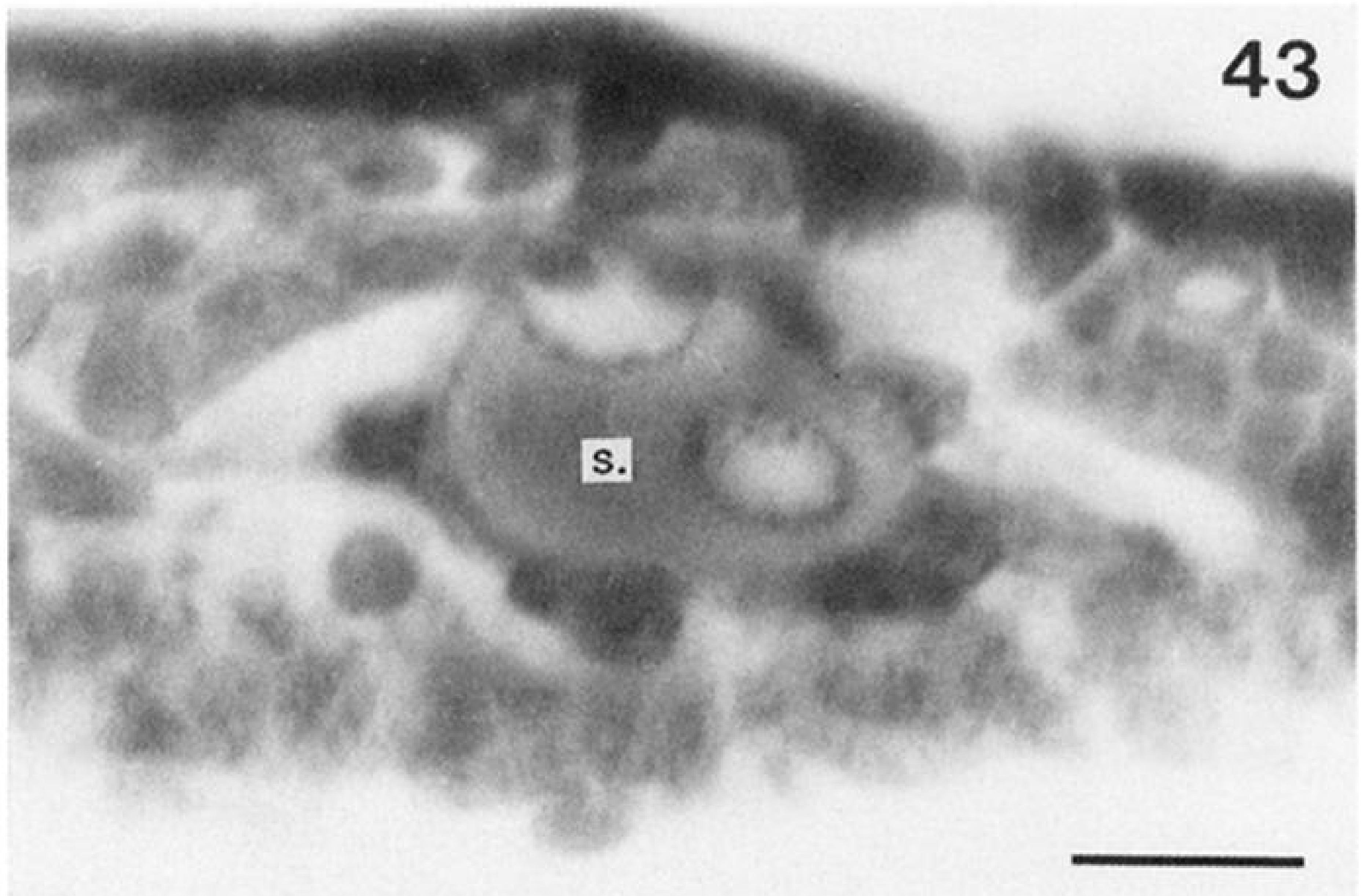


Figure 37. Anterior muscle I with large nerve fibres branching within the muscle. *Sepioteuthis sepioidea*. Transverse section. Cajal stain. Scale bar is 50 μm.

Figure 38. Nerve fibres in anterior conjunctive muscle II. When the muscle fibres are cut transversely or obliquely, the nerve fibre bundles give the appearance of spirals. *Sepioteuthis sepioidea*. Transverse section. Cajal stain. Scale bar is 20 μm.

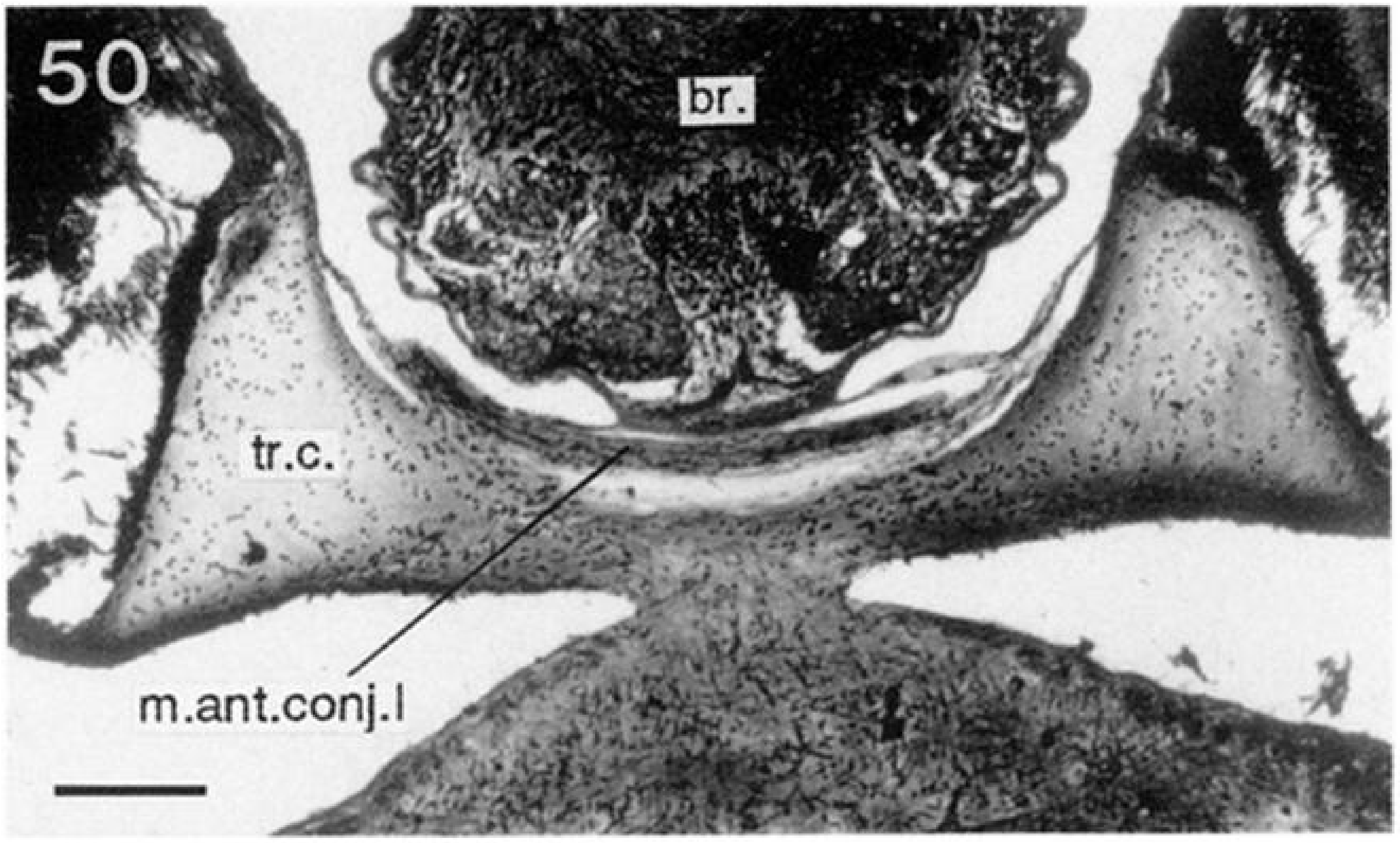
Figure 39. Large bundle of nerve fibres (one branching) in anterior conjunctive muscle II. *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 10 μm.

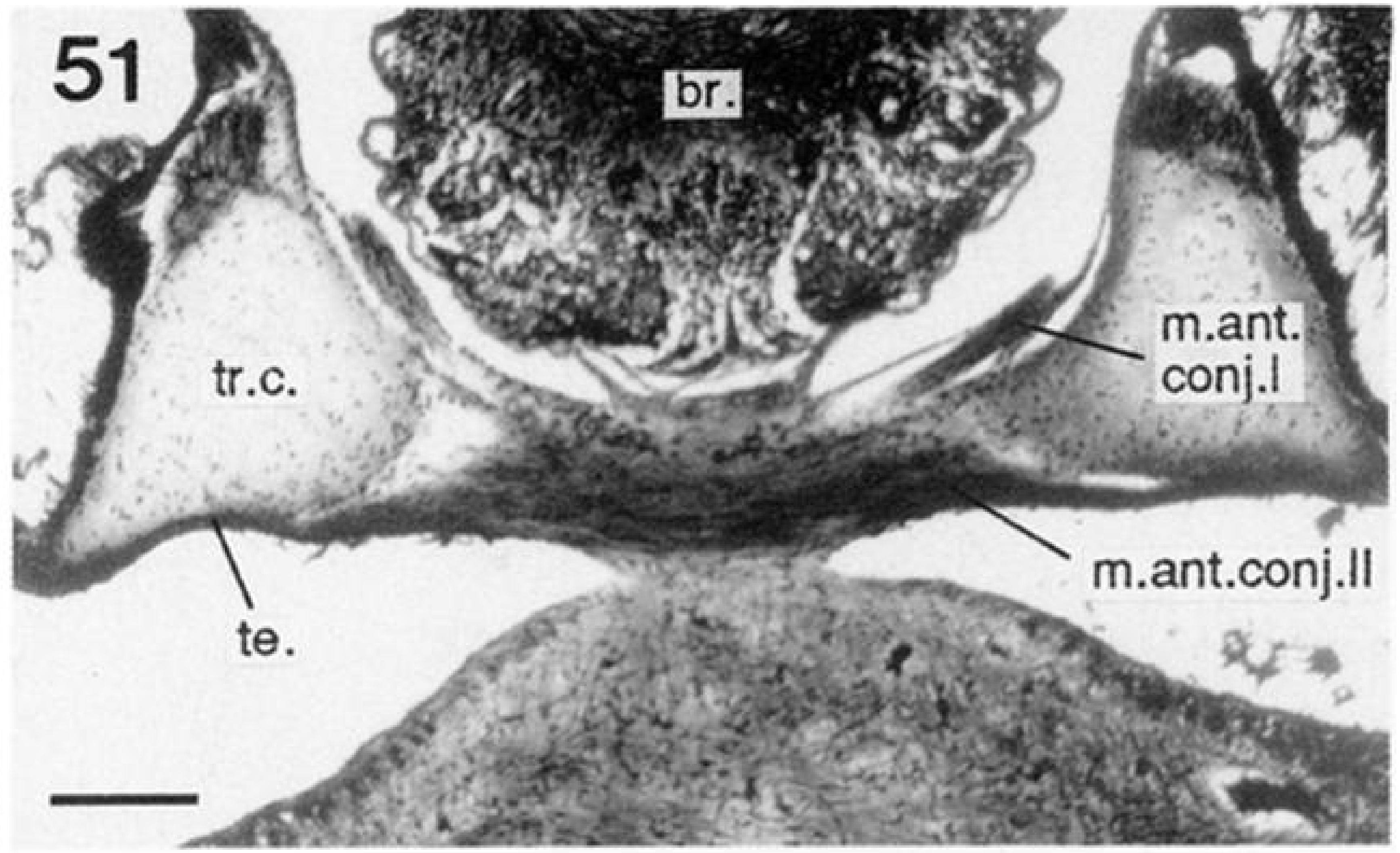
Figure 40. Tip of trochlear cartilage showing folding and nerve fibres in the groove. *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 30 μm.

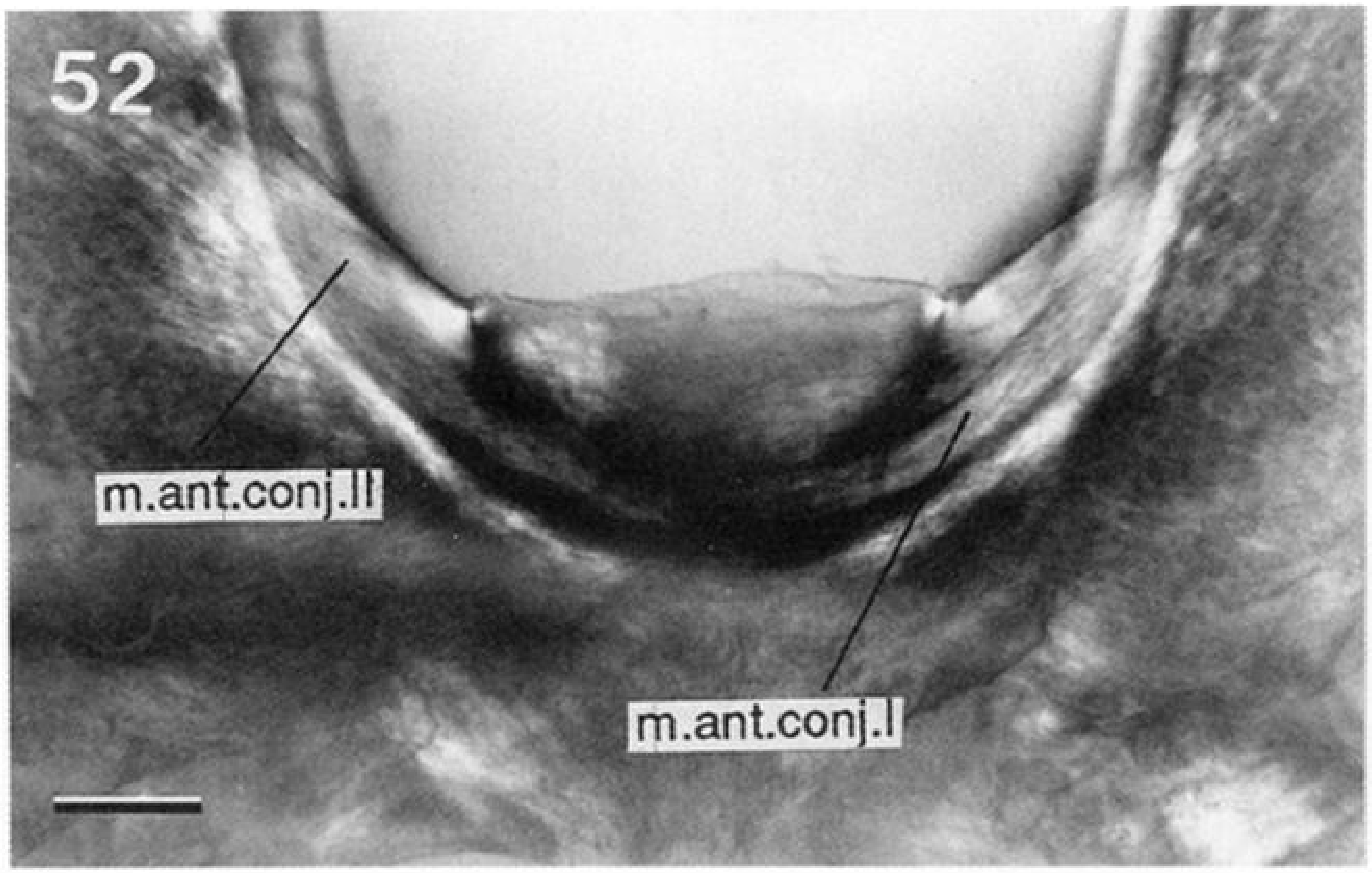
Figure 41. Tip of trochlear cartilage with muscle and nerve fibres in the groove. *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 40 μm.

Figure 42. Tip of trochlear cartilage with nerve fibres running among epithelial cells. *Loligo vulgaris*. Transverse section. Cajal stain. Scale bar is 10 μm.

Figure 43. Soma of large cell in epithelium covering the trochlear membrane. *Sepioteuthis sepioidea*. Cajal stain. Scale bar is 20 μm.







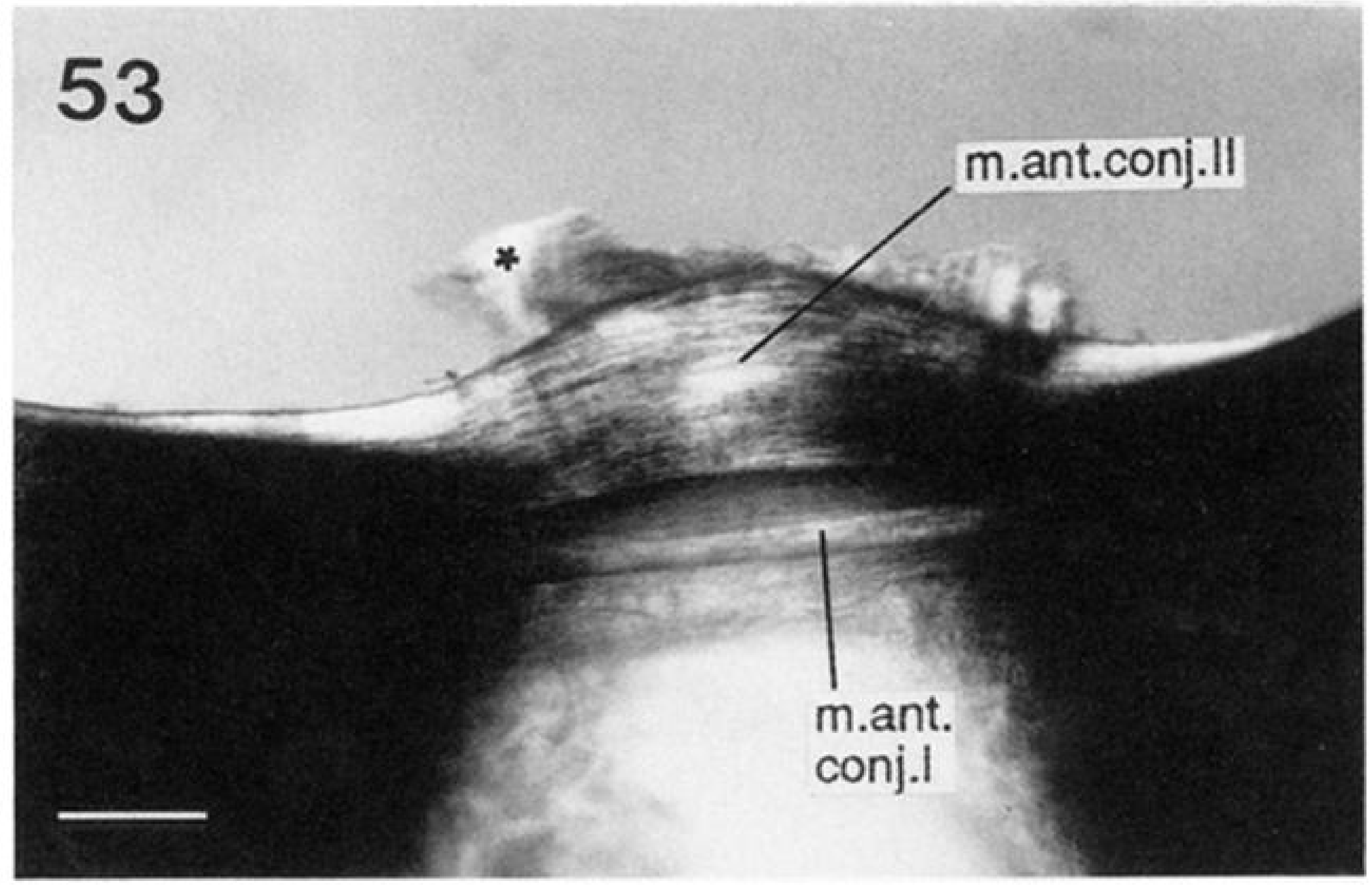
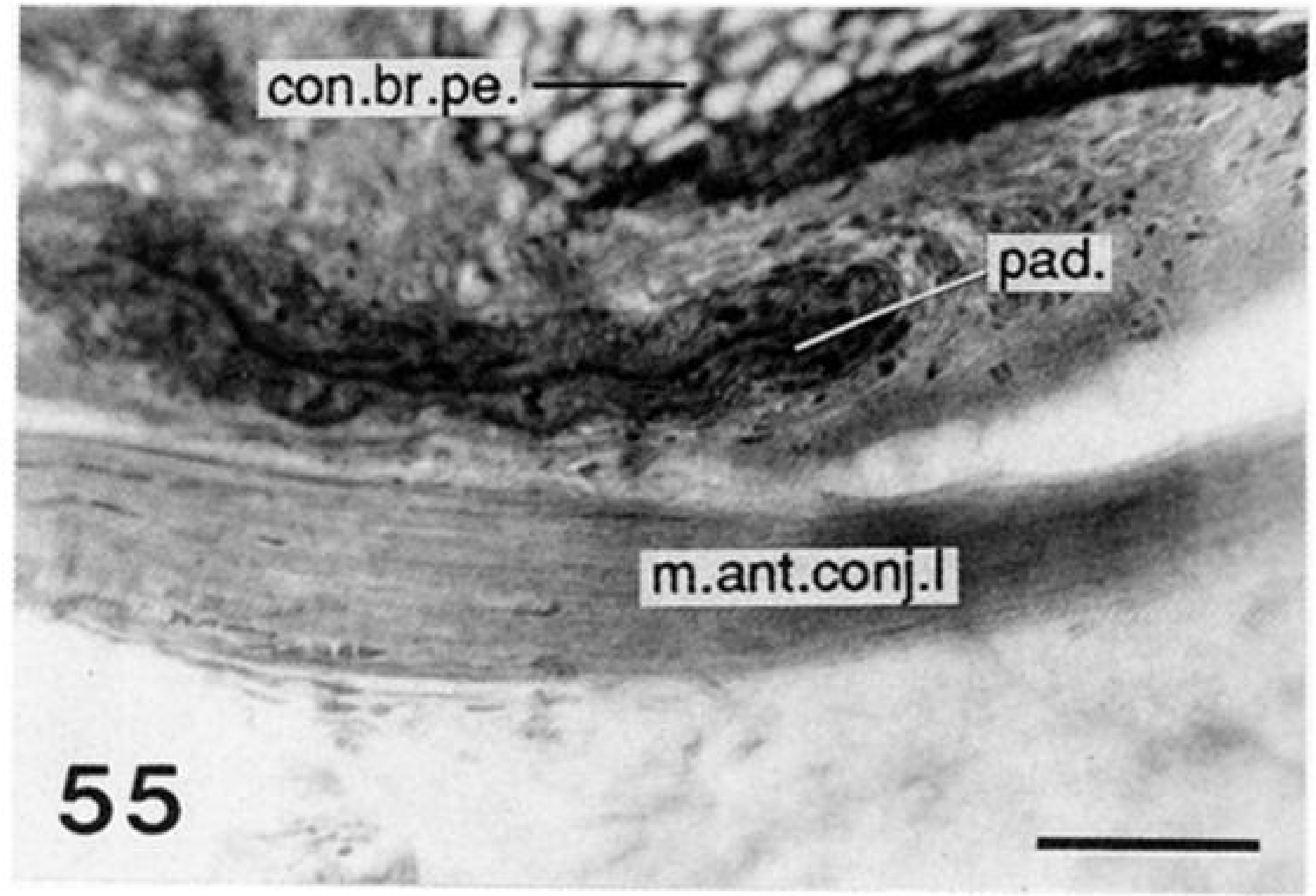


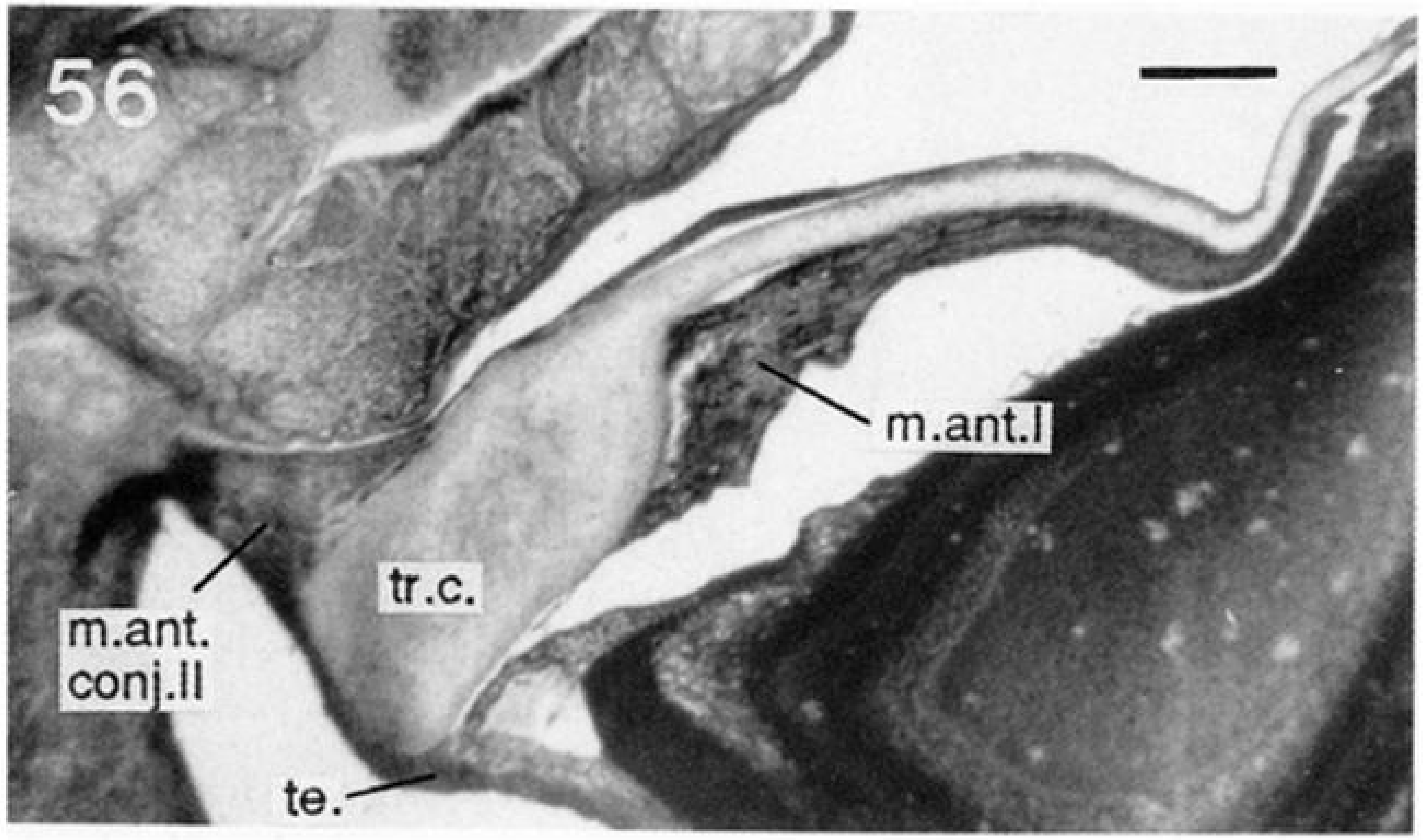
Figure 50. Bases of trochlear cartilages with conjoint tendons of anterior conjunctive muscles I. *Sepia officinalis*. Transverse section. Haematoxylin and eosin stain. Scale bar is 150 μm.

Figure 51. Crossing tendon of anterior conjunctive muscles I and crossing muscles of anterior conjunctive muscles II. *Sepia officinalis*. Transverse section, slightly posterior to section of figure 50. Haematoxylin and eosin stain. Scale bar is 150 μm.

Figure 52. Preparation of the two anterior conjunctive muscles crossing the midline through a fibrous sheath, seen in polarized light. *Sepia officinalis*. Mayer's haemalum stain. Scale bar is 300 μm.

Figure 53. Preparation of the two anterior conjunctive muscles after removal of the fibrous sheath in the midline, seen in polarized light (asterix shows remnants of the sheath). *Sepia officinalis*. Mayer's haemalum stain. Scale bar is 300 μm.





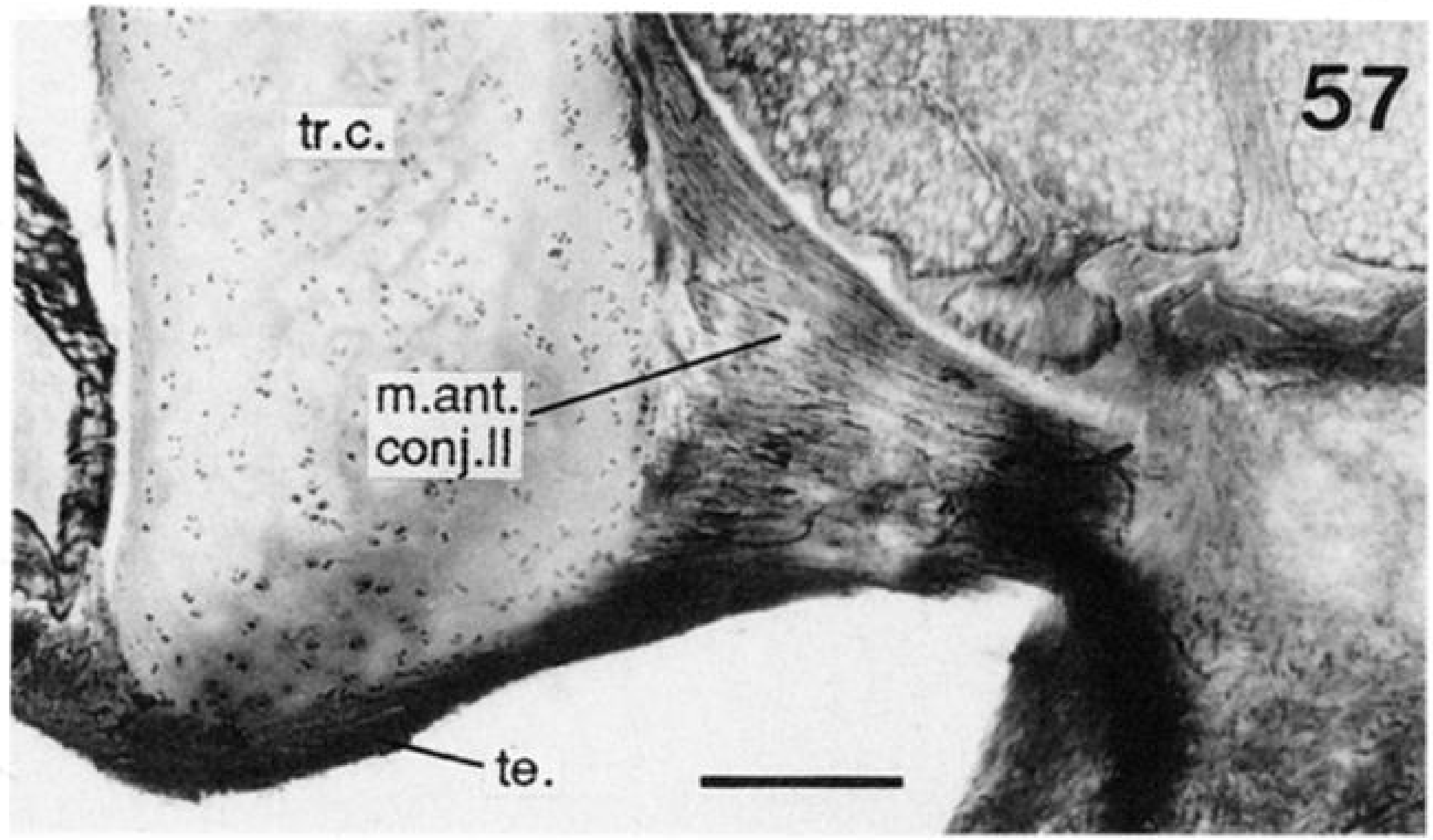
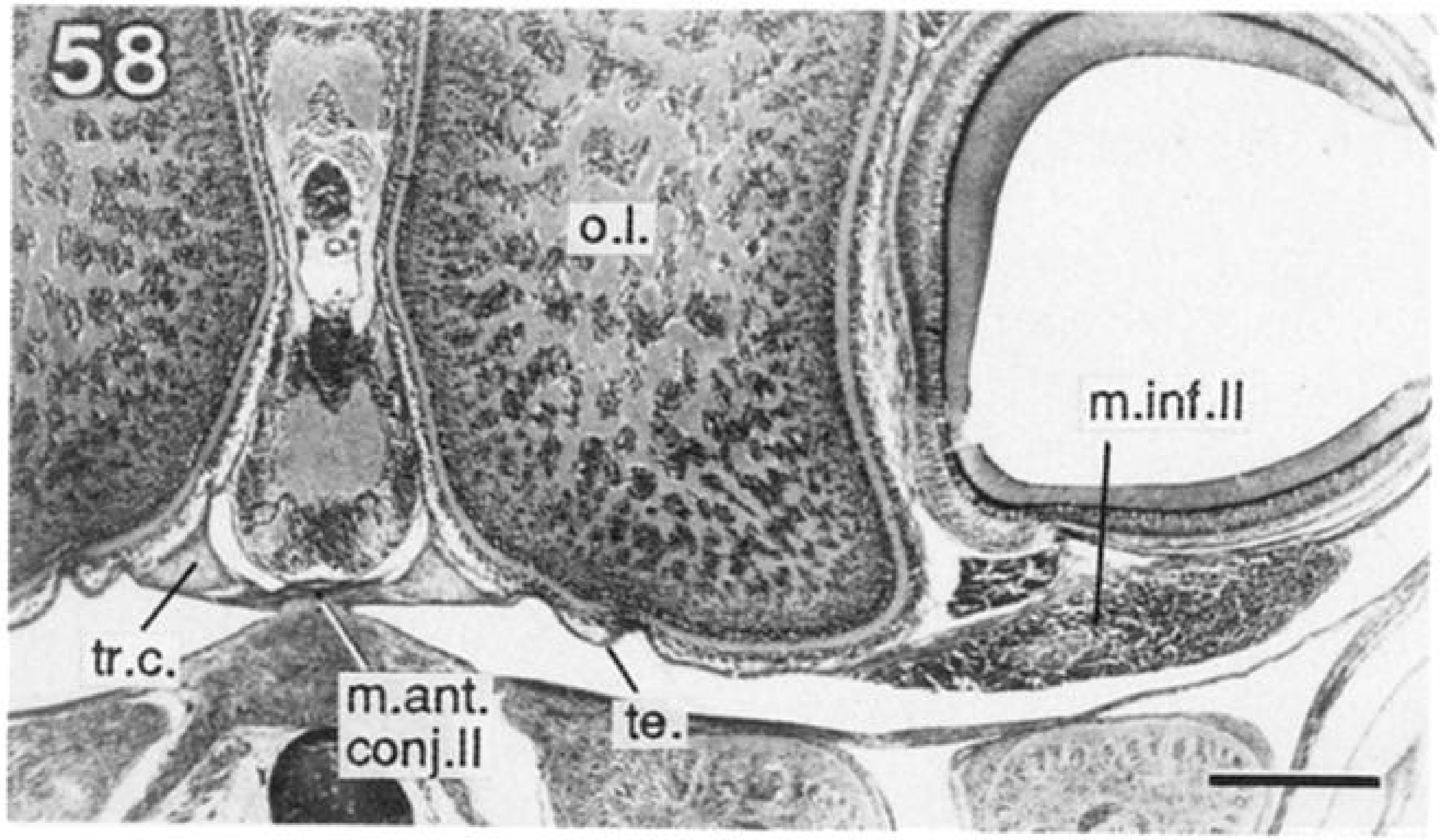


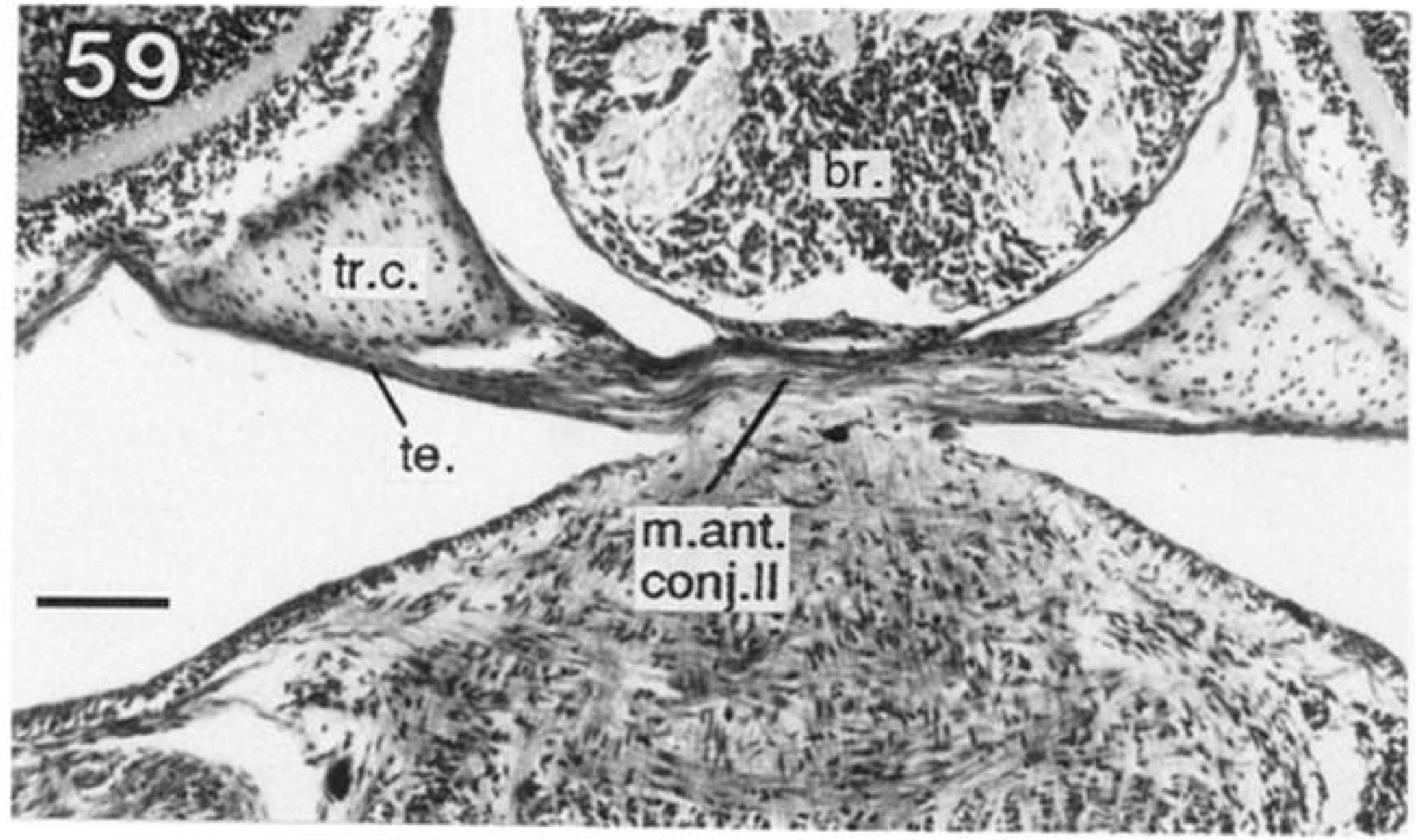
Figure 54. Anterior conjunctive muscle II with nerve fibres and attachment of the tendon to the trochlear cartilage. *Sepia officinalis*. Transverse section. Cajal stain. Scale bar is 100 μm.

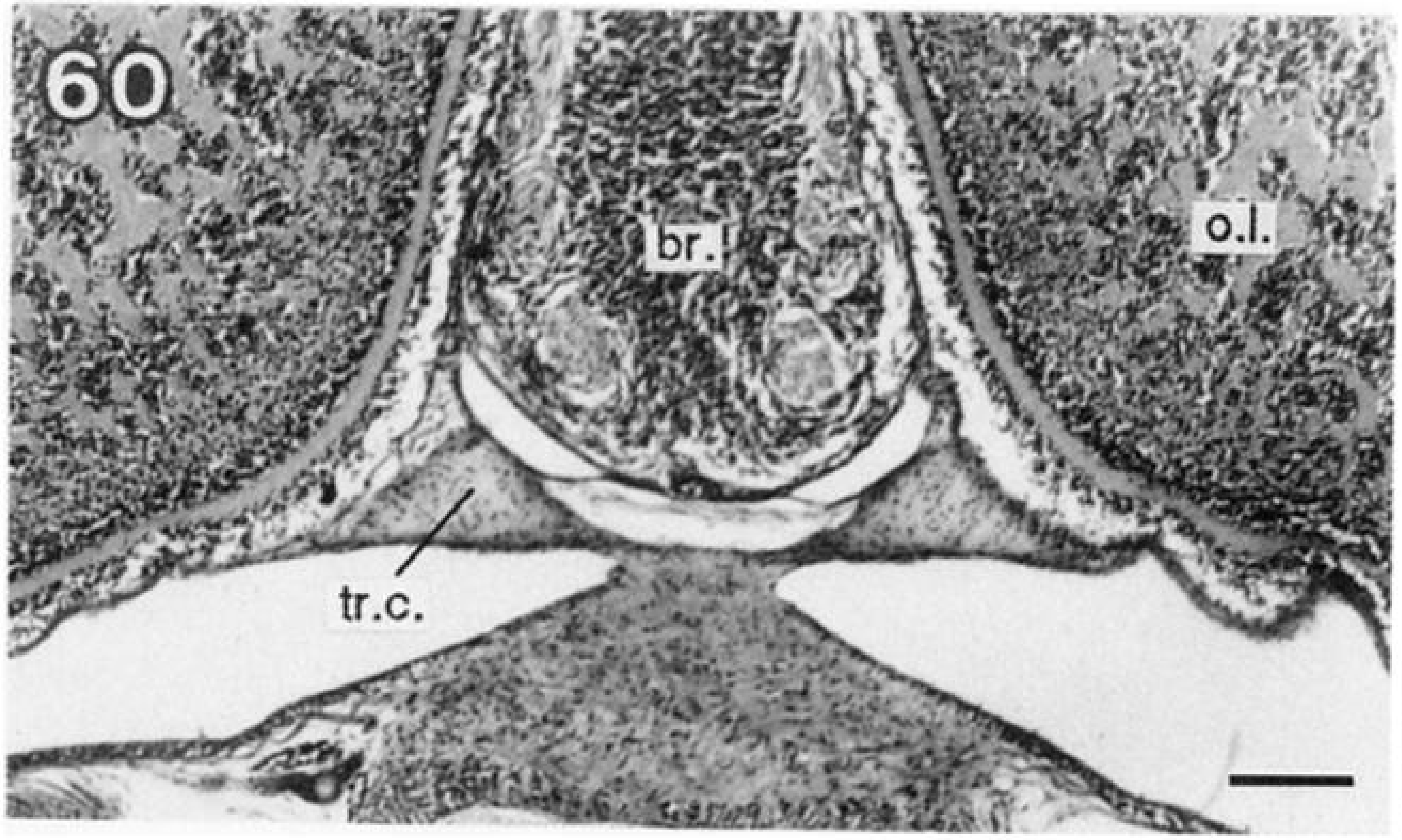
Figure 55. Pad above anterior conjunctive muscle I. *Sepia officinalis*. Transverse section. Cajal stain. Scale bar is 50 μm.

Figure 56. Trochlear cartilage with anterior conjunctive muscle II attached to its base. *Sepia officinalis*. Oblique transverse section. Cajal stain. Scale bar is 500 μm.

Figure 57. Attachment of the tendon. *Sepia officinalis*. Oblique transverse section. Cajal stain. Scale bar is 200 μm.







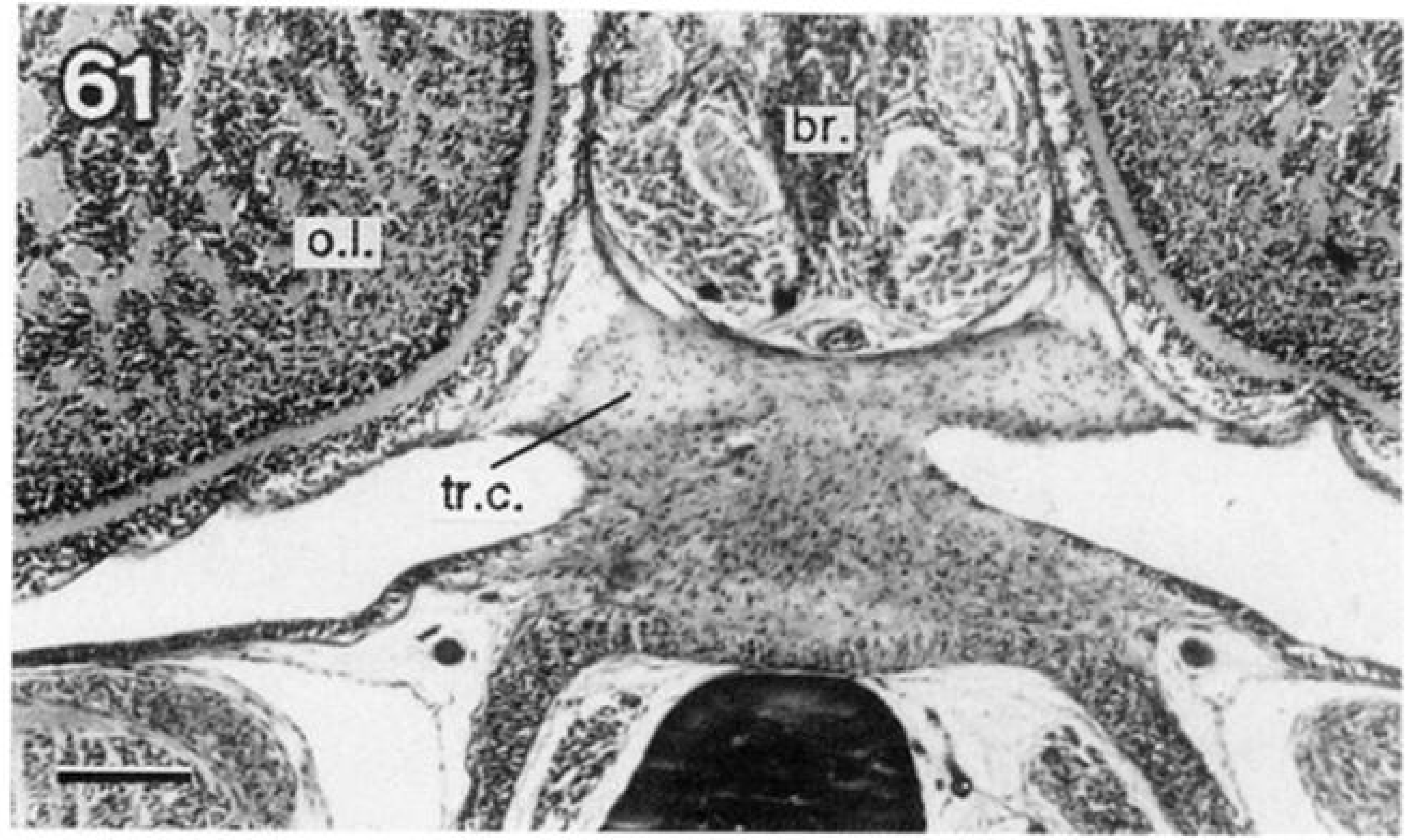
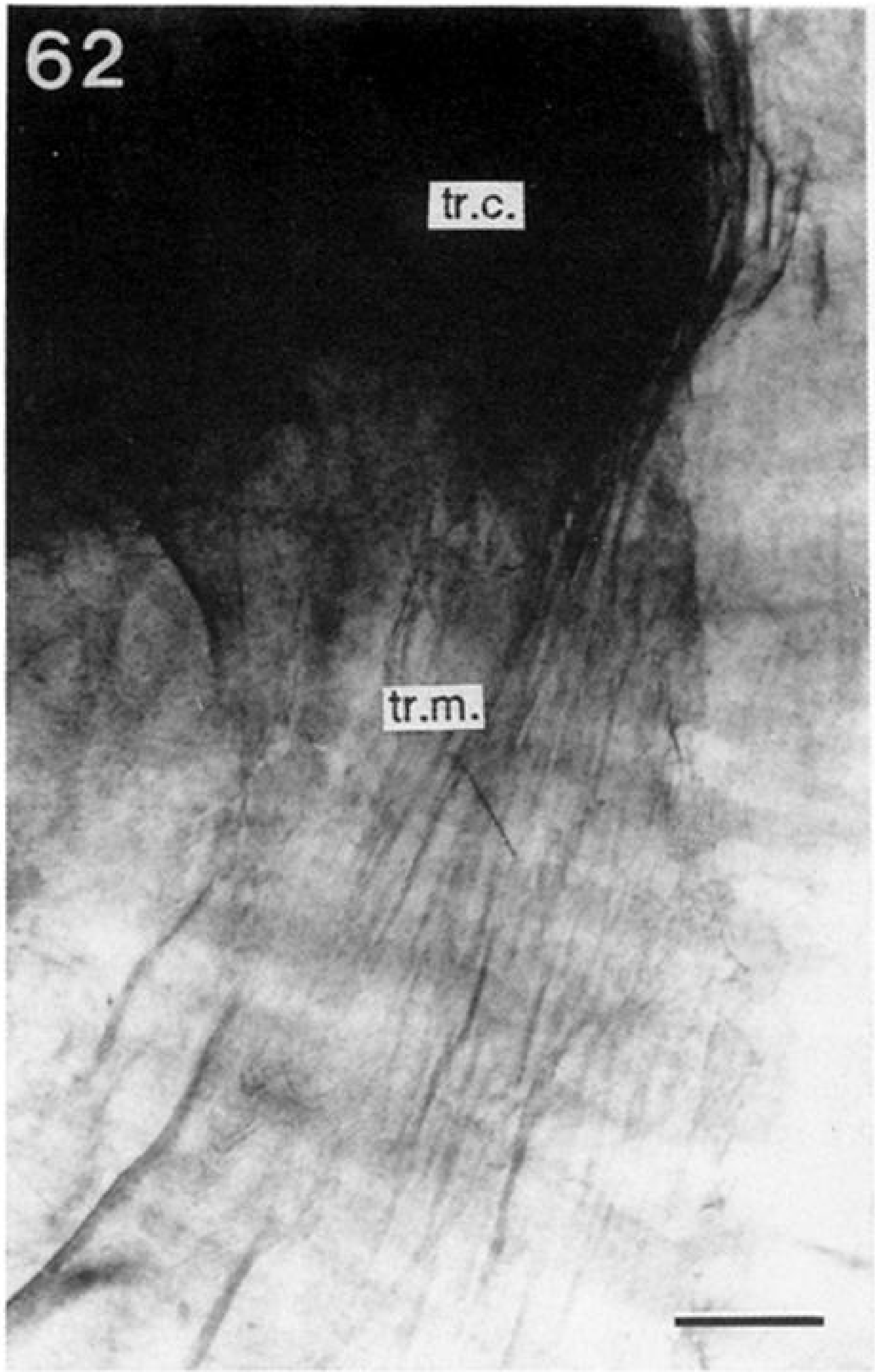
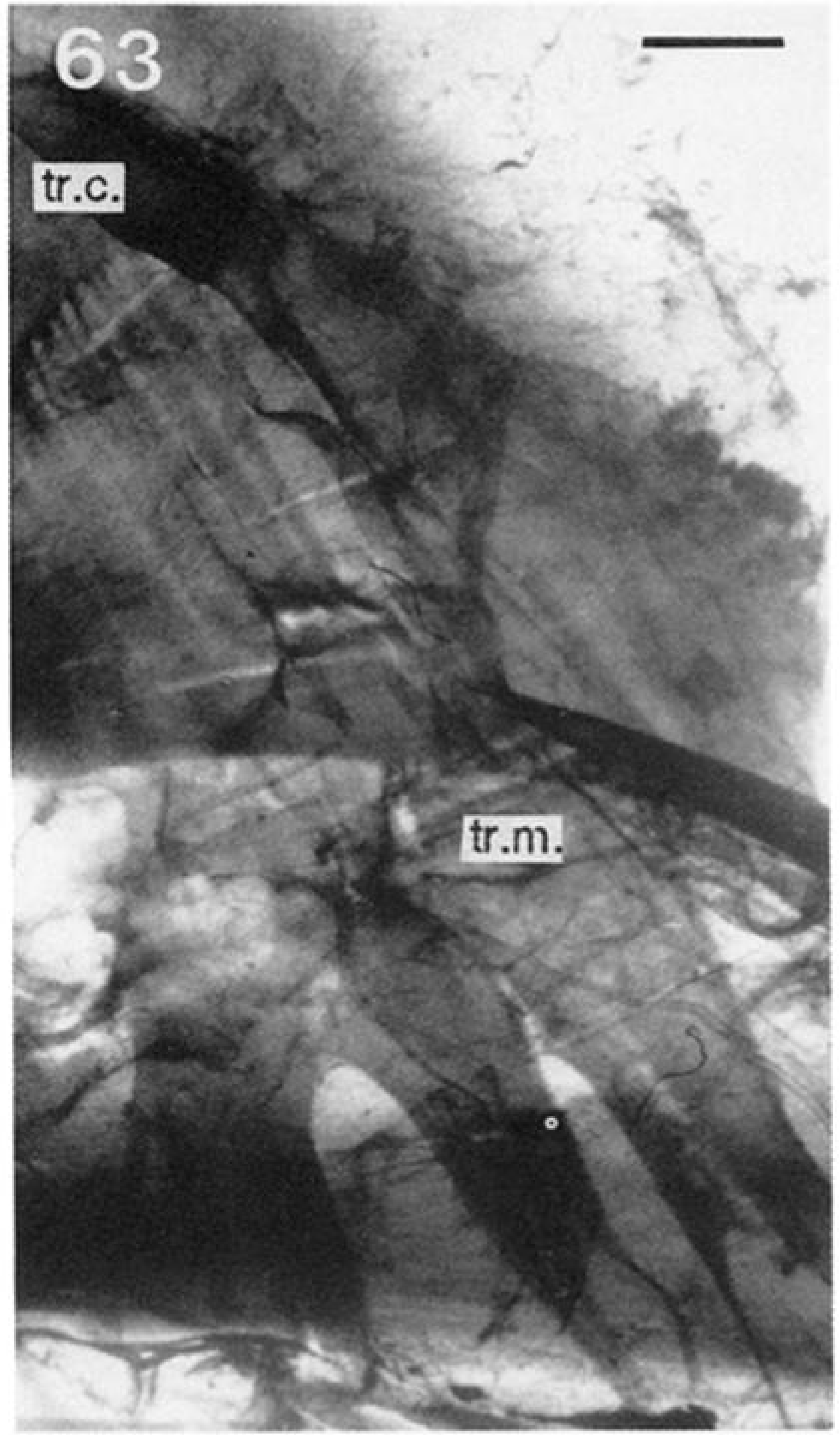


Figure 58. Inferior muscle II and the relationship of its tendon to anterior conjunctive muscle II. Juvenile *Sepia officinalis*. Transverse section. Cajal stain. Scale bar is 500 μm.

Figures 59–61. Three sections (60 μm apart) passing backwards to show that behind anterior conjunctive muscle II the trochlear cartilages are attached only by ligaments. Further back they are fused to the base of the cranium. Juvenile *Sepia officinalis*. Transverse sections. Cajal stains. Scale bars are 300 μm.





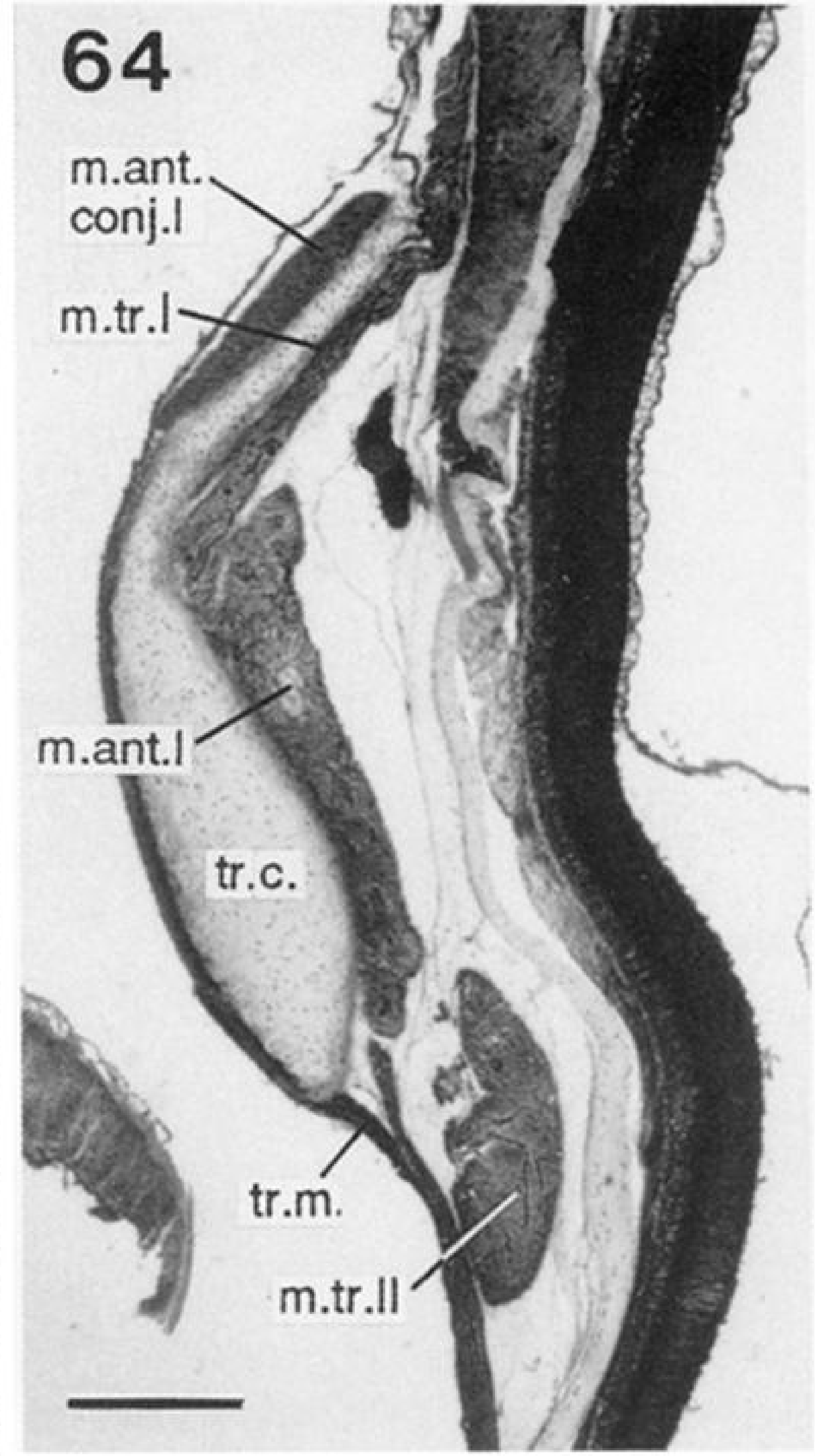


Figure 62. Distal tip of trochlear cartilage with fibres of the trochlear membrane. *Sepia officinalis*. Mayer's haemalum stain. Scale bar is 400 μm.

Figure 63. Fibres of trochlear membrane. *Sepia officinalis*. Mayer's haemalum stain. Scale bar is 500 μm.

Figure 64. Tip of trochlear cartilage with anterior conjunctive muscle I on the outside and two trochlear muscles inside. *Sepia officinalis*. Transverse section. Cajal stain. Scale bar is 400 μm.

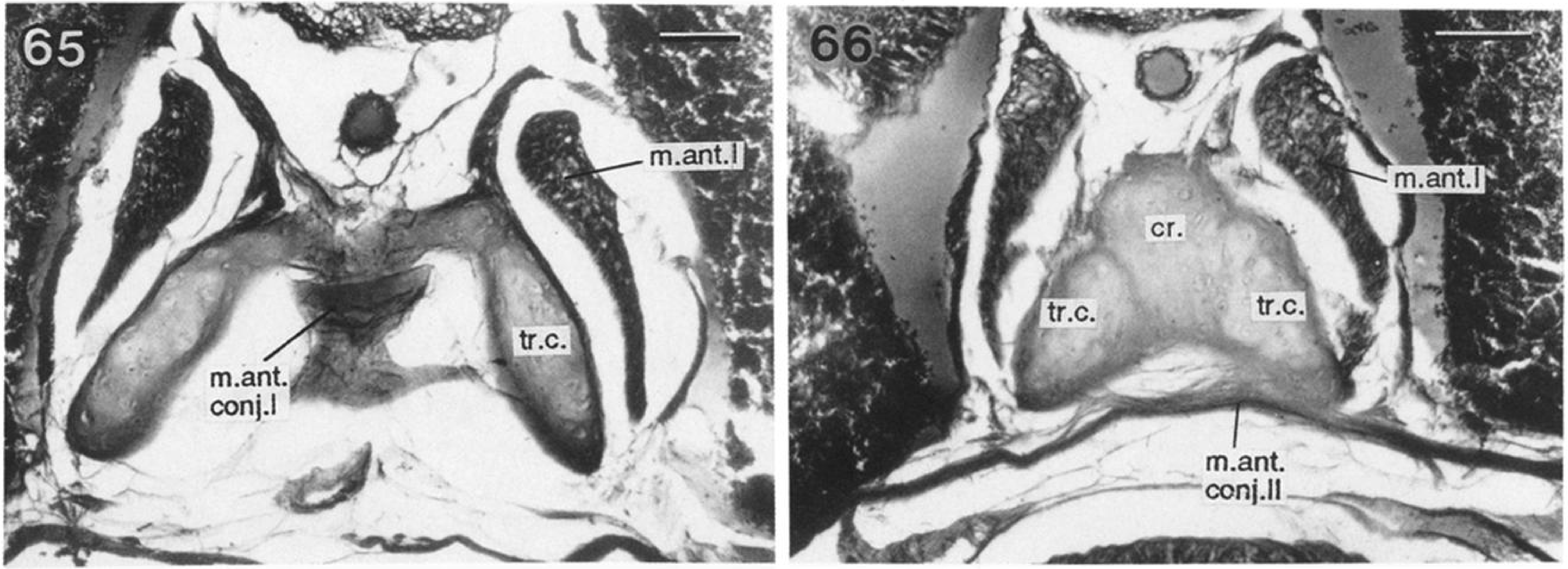
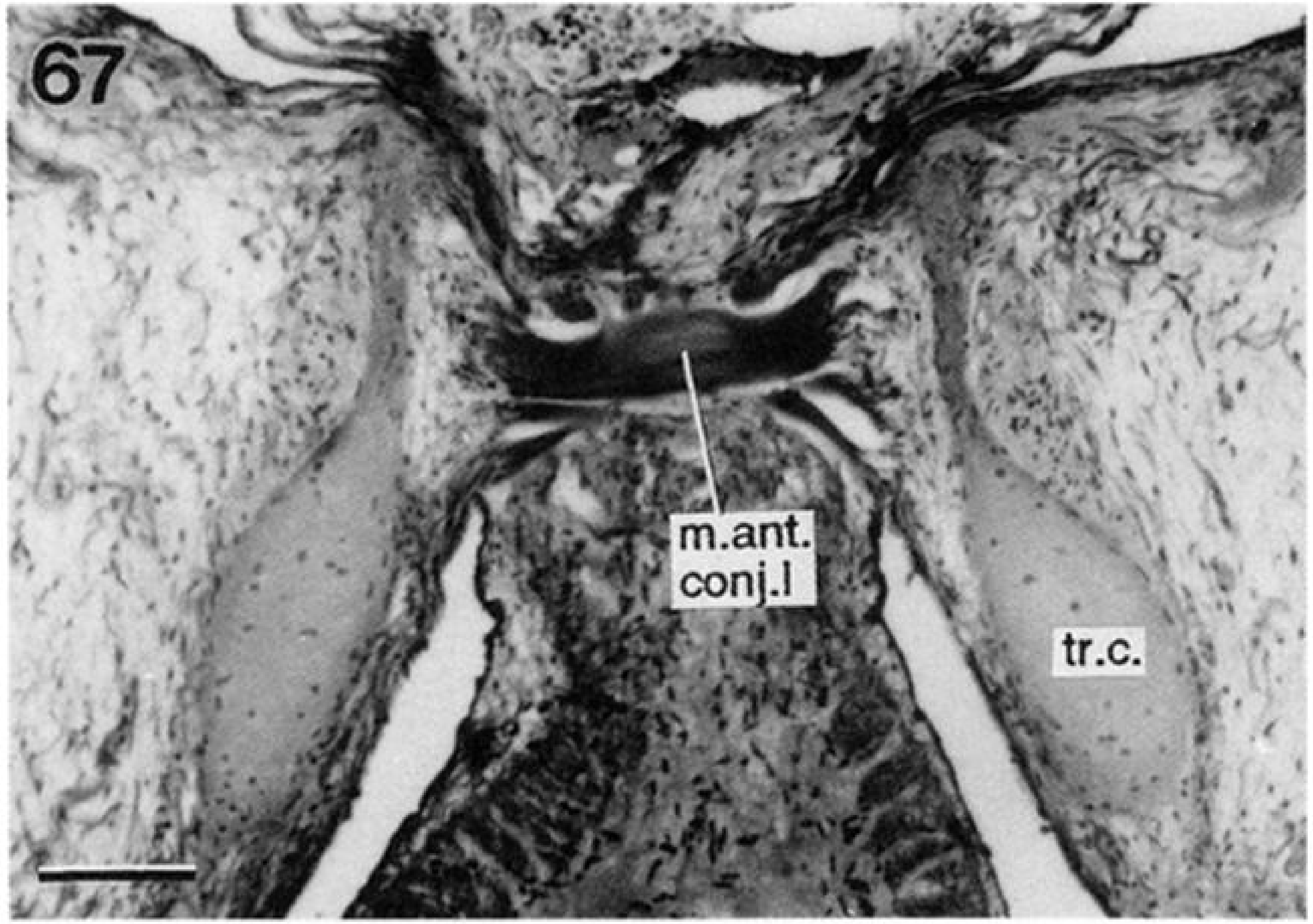


Figure 65. Trochlear cartilages and crossing tendons of anterior conjunctive muscles I. *Sepiola*. Transverse section. Haematoxylin and eosin stain. Scale bar is 100 μm.

Figure 66. Crossing anterior conjunctive muscles II; they are not attached to the trochlear cartilages. *Sepiola*. Transverse section. Haematoxylin and eosin stain. Scale bar is 150 μm.



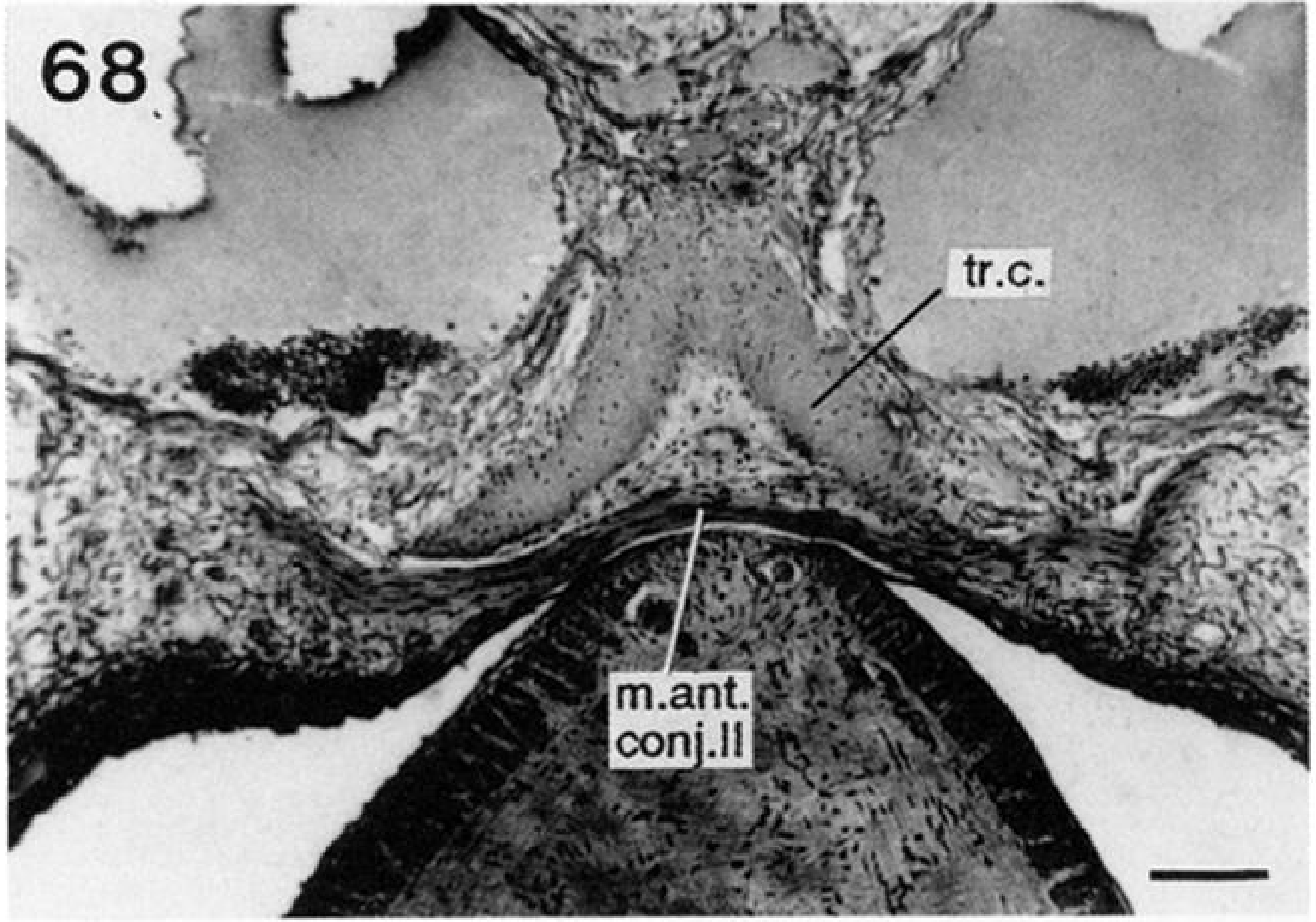
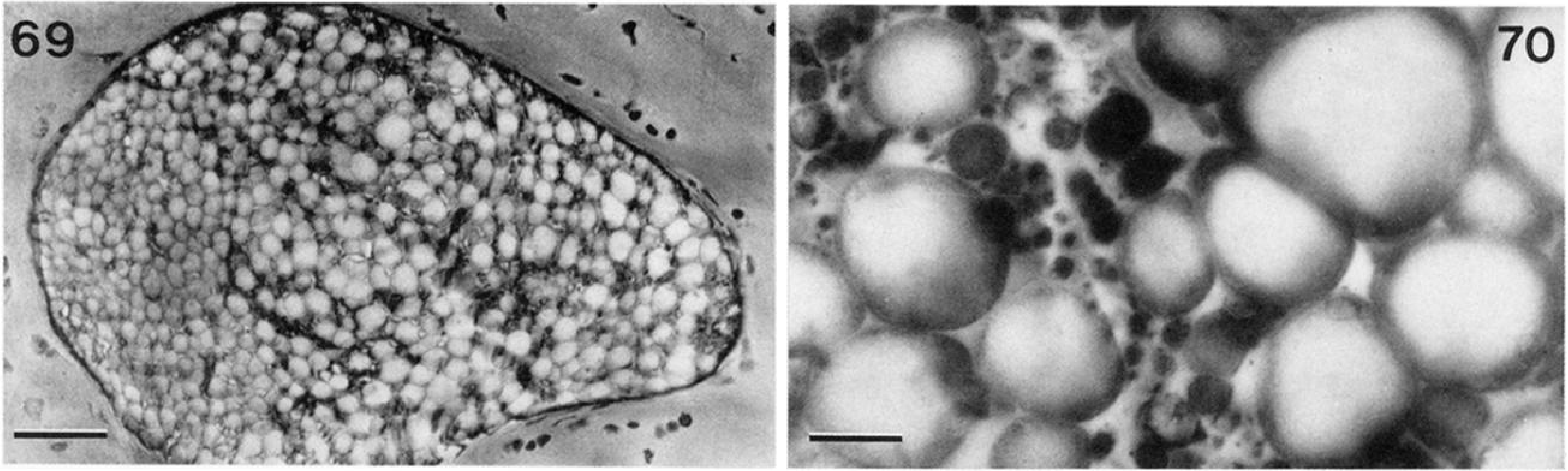
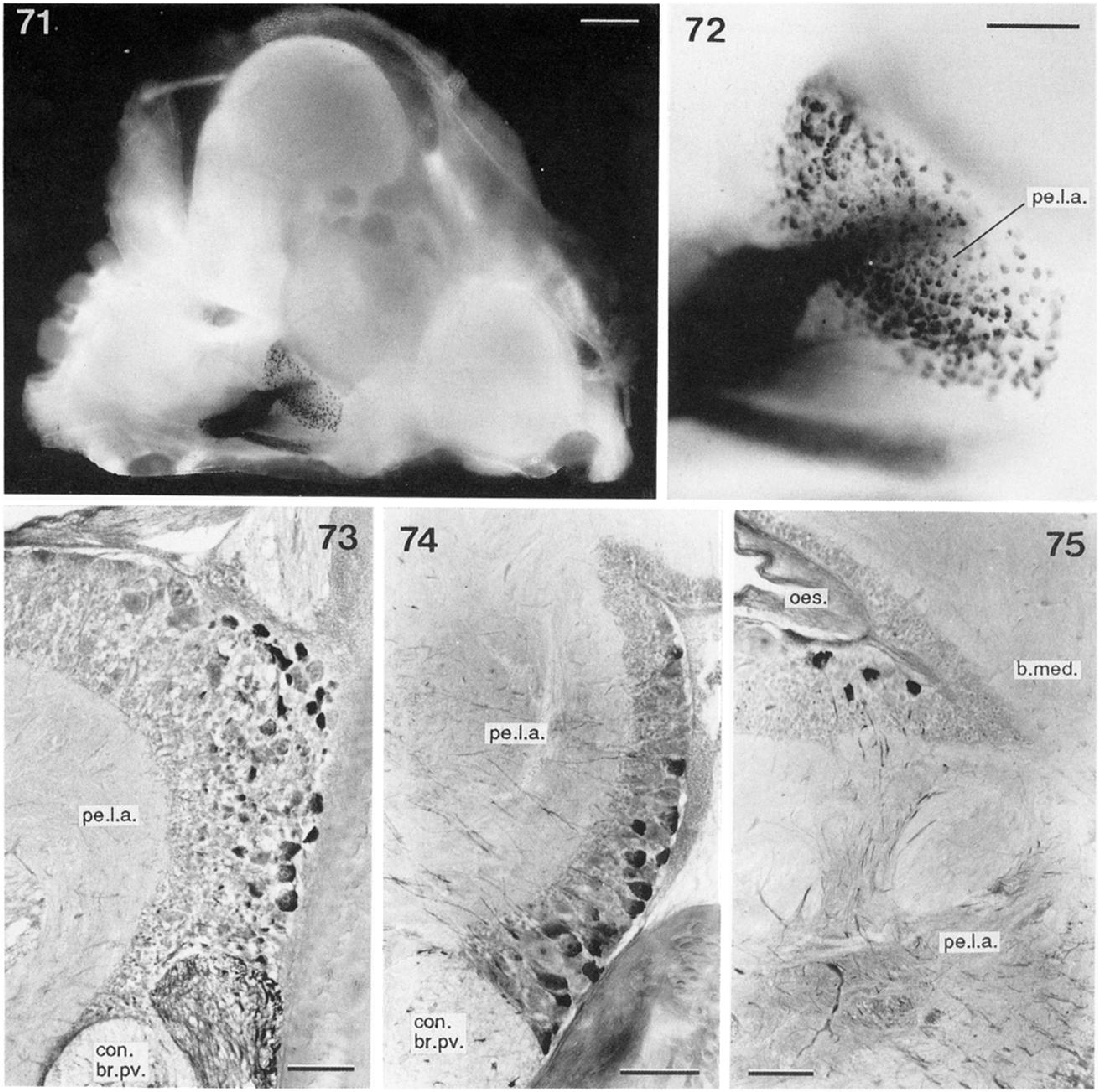


Figure 67. Crossing of anterior conjunctive muscles I. *Spirula*. Transverse section. Cajal stain. Scale bar is 100 µm.

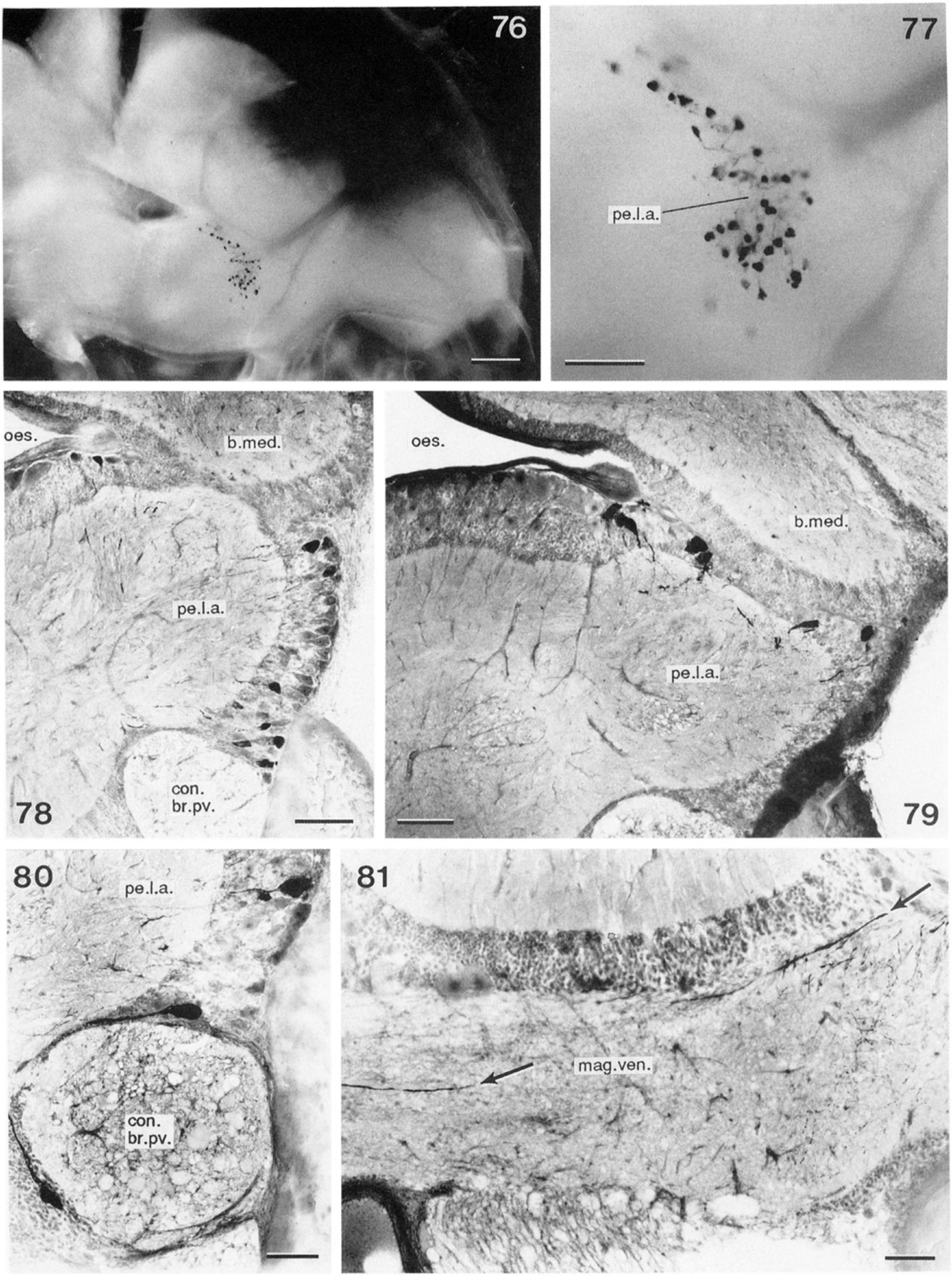
Figure 68. Crossing of anterior conjunctive muscles II. *Spirula*. Transverse section. Cajal stain. Scale bar is 100 µm.



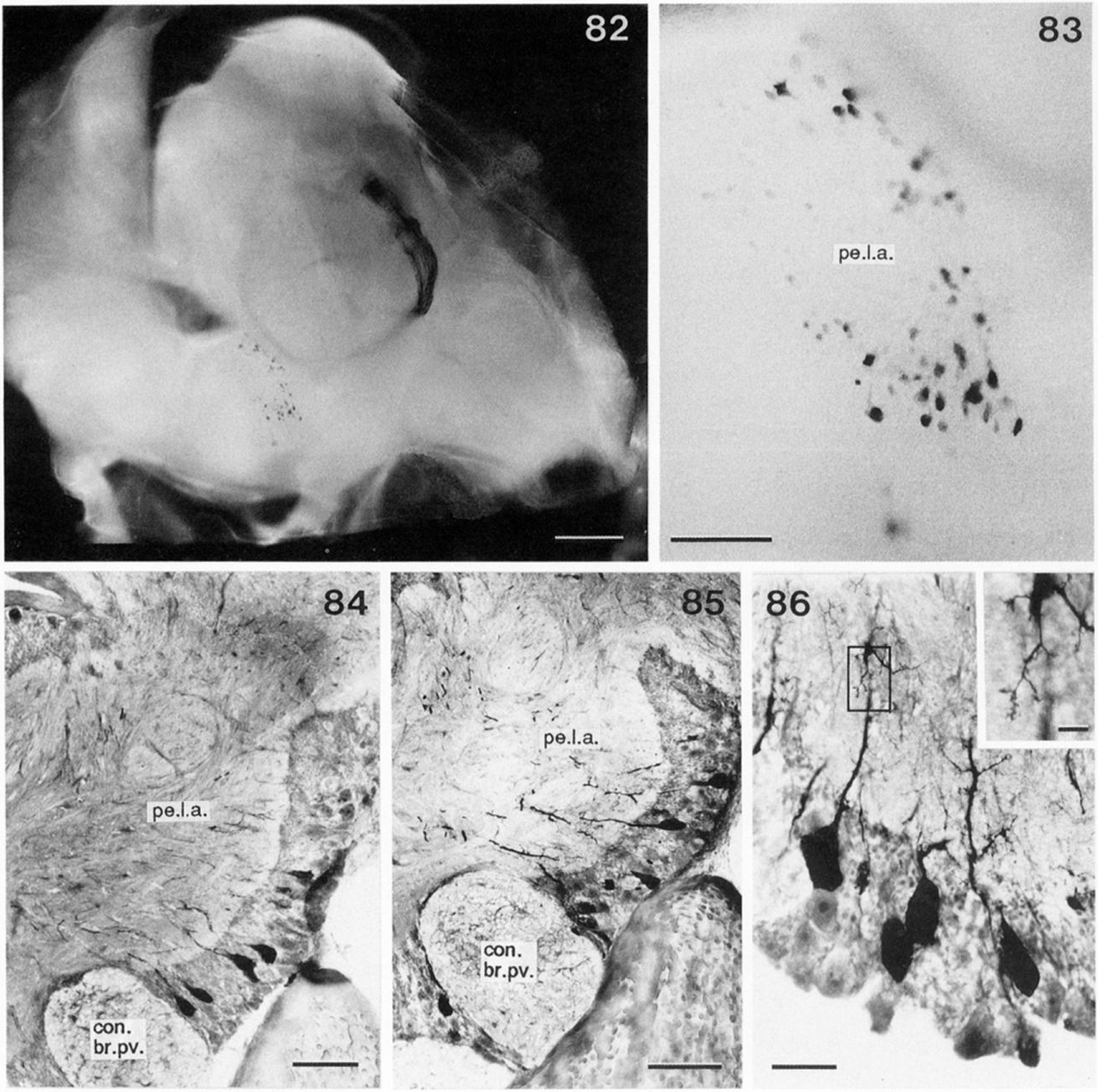
Figures 69 and 70. Cross-sections of the anterior oculomotor nerve. *Sepia officinalis*. Cajal stains. Scale bars are 100 μm and 10 μm, respectively.



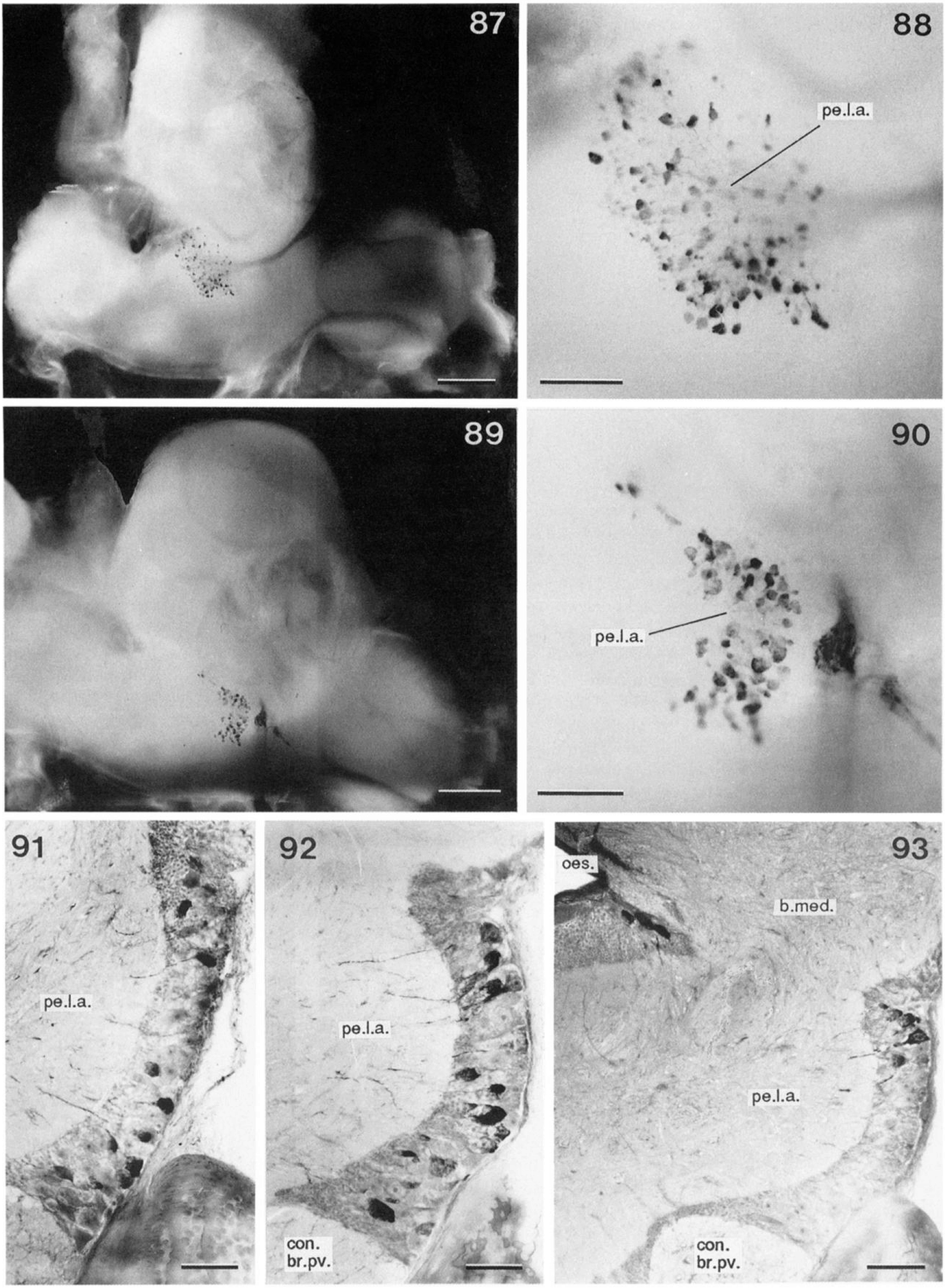
Figures 71–75. Centripetal cobalt filling of the anterior oculomotor nerve of *Sepia officinalis*, showing filled somata in the anterior lateral pedal lobe. Lateral view of the brain (figures 71 and 72; scale bars are 1 mm and 500 μm, respectively) and transverse sections of the anterior lateral pedal lobe with many filled somata in its anterior (figure 73; scale bar is 200 μm) and posterior parts (figure 74; scale bar is 200 μm); few somata are filled medially, close to the oesophagus (figure 75; scale bar is 200 μm).



Figures 76–81. Centripetal cobalt filling of the anterior root of the anterior superior ophthalmic nerve of *Sepia officinalis*, showing filled somata in the anterior lateral pedal lobe. Lateral view of the brain (figures 76 and 77; scale bars are 1 mm and 500 μm, respectively) and transverse sections of the anterior lateral pedal lobe with many filled somata laterally (figure 78; scale bar is 200 μm), some dorsally and medially close to the oesophagus (figures 78 and 79; scale bars are 200 μm) and one medially beside the brachial-palliovisceral lobe connective (figure 80; scale bar is 100 μm); afferent fibres (arrows) enter the ventral magnocellular lobe, with single fibres crossing to the contralateral side (figure 81; scale bar is 100 μm).



Figures 82–86. Centripetal cobalt filling of the posterior root of the anterior superior ophthalmic nerve of *Sepia officinalis*, showing filled somata in the anterior lateral pedal lobe. Lateral view of the brain (figures 82 and 83; scale bars are 1 mm and 400 μm, respectively) and transverse sections of the anterior lateral pedal lobe with many filled somata laterally in the middle and outer perikaryal layers (figures 84 and 85; scale bars are 200 μm) and a single soma filled medially beside the brachial-palliovisceral lobe connective (figure 85; scale bar is 200 μm). The trunks of the oculomotor neurons give off primary, secondary and tertiary collaterals with end bushes (figure 86, scale bar is 80 μm); inset upper right shows enlarged area as indicated (scale bar is 20 μm).



Figures 87, 88 and 91. Centripetal cobalt filling of the posterior superior ophthalmic nerve of *Sepia officinalis*, showing filled somata in the anterior lateral pedal lobe. Lateral view of the brain (figures 87 and 88; scale bars are 1 mm and 400 μm, respectively) and transverse section of the anterior lateral pedal lobe with many filled somata laterally in the lobe (figure 91; scale bar is 200 μm).

Figures 89, 90, 92 and 93. Centripetal cobalt filling of the posterior oculomotor nerve of *Sepia officinalis*, showing filled somata in the anterior lateral pedal lobe. Lateral view of the brain (figures 89 and 90; scale bars are 1 mm and 300 μm, respectively) and transverse sections of the anterior lateral pedal lobe with many filled somata laterally in the lobe (figure 92; scale bar is 200 μm) and a few medially close to the oesophagus (figure 93; scale bar is 200 μm).