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THE ROYAL
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The radular apparatus of cephalopods

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CONTENTS

This paper describes the ontogeny, breakdown and absorption of the radular teeth of cephalopods and, for the first time, considers the function of the 'bolsters' or radular support muscles.

The radular ribbon, which bears many regularly arranged transverse rows of teeth one behind the other, lies in a radular canal that emerges from the radular sac. Here the radular teeth are formed by a set of elongate cells with microvilli, the odontoblasts. These are organized into two layers, the outer producing the radular membrane and the bases of the teeth, the inner producing the cusps. The odontoblasts also secrete the hyaline shield and the teeth on the lateral buccal palps, when these are present. At the front end of the radular ribbon the teeth become worn in feeding and are replaced from behind by new ones formed continuously in the radular sac, so that the whole ribbon moves forward during ontogeny. Removal of the old teeth is achieved by cells in the radular organs; these cells, which are formed from modified odontoblasts ('odontoclasts'), dissolve the teeth and membranes and absorb them. There is a subradular organ in all cephalopods. In *Octopus vulgaris*, which bores into mollusc shells and crustacean carapaces, it is especially well developed and there is also a supraradular organ.

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A characteristic feature of the cephalopod radular apparatus is the pair of large radular support muscles or 'bolsters'. Their function seems never to have been investigated, but experiments reported here show that when they elongate, the radular teeth become erect at the bending plane and splayed, presumably enhancing their ability to rake food particles into the pharynx. The bolsters of *Octopus* function as muscular hydrostats: because their volume is fixed, contraction of their powerful transverse muscles causes them to elongate. In decapods and in nautiloids each bolster contains a 'support rod' of semi-fluid material, as well as massive transverse musculature. This rod may elongate to erect the radular teeth. At the extreme front end of the bolsters in *Octopus* there are many nerve fibres that may constitute a receptor organ signalling the movements of the radula against hard material. Such nerves are absent from decapods and from octopods that do not bore holes.

The buccal mass of *Nautilus* is massive, with heavily calcified tips to the beaks and a wide radular ribbon, with 13 rather than nine elements in each row. Nevertheless all the usual coleoid features are present in the radular apparatus and the teeth are formed and broken down in the same way. However, *Nautilus* has a unique structure, the radular appendage. This comprises a papillate mass extending over the palate in the midline and forming paired lateral masses that are in part secretory. The organ is attached to the front of the radula by muscles and connective tissue. Its function is unknown.

Keywords: cephalopods; radula; bolsters; muscular hydrostats

1. INTRODUCTION

Cephalopods are highly evolved molluscs, active carnivorous animals that often pursue and capture prey considerably larger than themselves: crustaceans, fish or other cephalopods (Hanlon & Messenger 1996). Yet, despite having a lifestyle quite different from that of a chiton or a limpet, cephalopods are nonetheless molluscs and have retained many fundamental molluscan features in their organization. One such feature is an oesophagus that runs through the brain. Consequently, large prey captured by the suckered tentacles or arms cannot be swallowed whole but must be reduced to small fragments before it can pass through the brain. As a result, cephalopods have an elaborate set of structures inside the mouth (the so-called 'buccal mass'; Young 1965; Bidder 1966; Nixon 1988) comprising a pair of strong, chitinous beaks, with their intrinsic musculature and nerves, salivary glands and papilla and, another fundamental molluscan feature, a radula (figure 1).

The beaks are of prime importance in tearing large prey into manageable pieces, although the way they function is still far from clear (Altman & Nixon 1970). Equally important for the manipulation of food material in these animals, however, is the ancient molluscan feeding device, the radula, which has been conserved during the evolution of the modern cephalopods and whose function is considered here.

The radular apparatus of cephalopods, like that of other molluscs, is an extremely complex structure comprising a toothed ribbon with associated muscles, a hyaline shield and accessory structures that we shall term the radular organs. The ribbon lies in a canal, originating in a radular sac posteriorly, where the teeth arise. The ribbon passes forward and curves upward before turning sharply downwards and backwards over the bending plane anteriorly (figure 2). The teeth are worn away in feeding and are continually replaced by new ones formed at the posterior end of the ribbon, in the radular sac. Thus during ontogeny the whole ribbon gradually moves forward, although the exact mechanism for this is still in dispute (Runham 1963; Mischor & Märkel 1984; Mackenstedt & Märkel 1987).

During feeding the radular ribbon moves rhythmically backwards and forwards. The movement was compared by Huxley (1853) to that of a chain saw, but how it is achieved has never been fully understood. It is the backward movement of the radular teeth that propels food into the pharynx. This movement is produced by powerful retractor muscles attached to the radula by a hyaline shield (figure 3). The forward movement is produced by protractor muscles attached to the radula (figures 4 and 5). The radula and its canal lie in a closed space, the odontophore sac. Within this there is also a pair of large structures, termed the radular support muscles by Young (1965), but which are better referred to as 'bolsters', following Hyman (1967) (figures 6 and 28). Similar supporting structures for the radula are present in all molluscan radulae, but their function seems never to have been properly explored (Salvini-Plawen 1988). In this paper we show that in cephalopods they push up the radular ribbon at the bending plane to erect and splay the teeth during feeding. The bolsters are also shown in *Octopus* to function as simple muscular hydrostats (Kier 1982, 1988); in decapods and in *Nautilus*, where they act in conjunction with a radular rod, their mode of action is less clear.

2. MATERIALS AND METHODS

The species studied are listed in table 1. We studied the radulae of *Sepia*, *Loligo* and *Octopus* by dissecting fresh material, by examining serially sectioned material and by electrical stimulation experiments; in *Nautilus* fixed material was dissected and serial sections studied. The sectioned material had largely been fixed in formalin and stained with Cajal's silver method (Young 1971). This is excellent for nerve fibres and often for other tissues, but has been supplemented where necessary by other techniques. Sectioning is difficult because of splintering caused by the teeth so that we have relied heavily on sections of newly hatched and young individuals.

For the stimulation experiments we used a hand-held silver/silver chloride electrode; trains of square wave pulses, duration 0.1 ms, frequency 20–30 Hz, were delivered at just suprathreshold strength. Responses to stimulation were photographed on Zeiss or Nikon photomicroscopes using Kodacolor film.

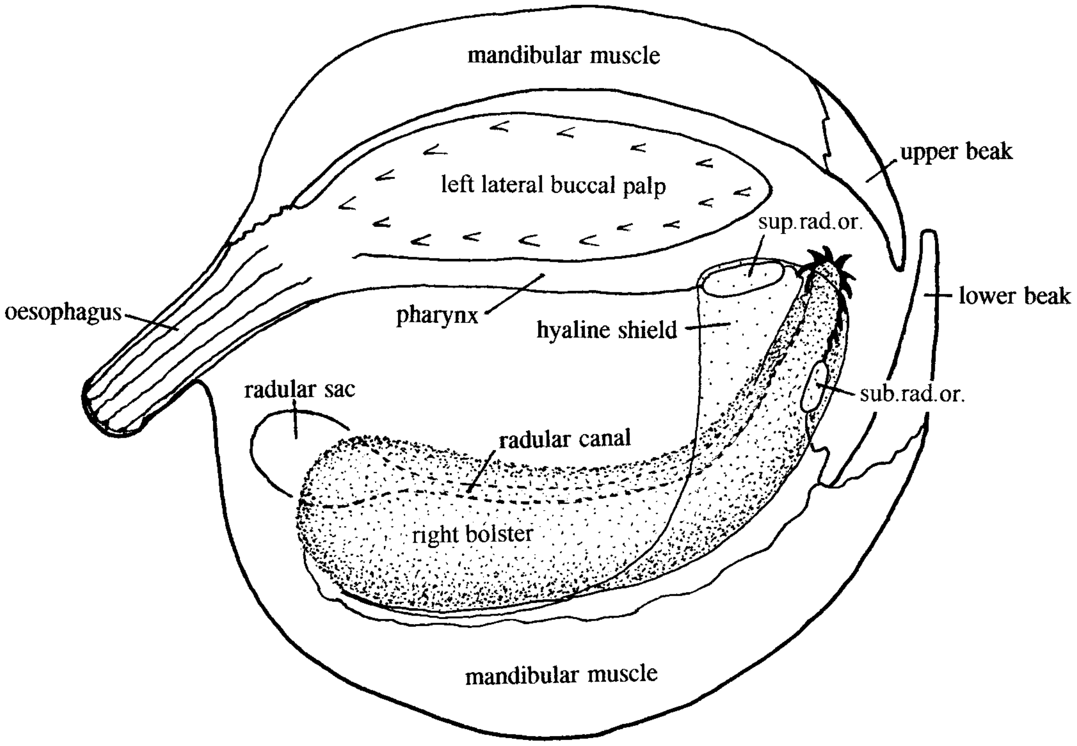


Figure 1. Generalized diagram of cephalopod buccal mass and radular apparatus, to show the main features described in the text. The beaks, the mandibular muscles and the lateral buccal palp have been cut away on the right side to reveal the pharynx, oesophagus and part of the radular sac in the midline. Only the right bolster is depicted, pushing up the radular teeth. The position of the supraradular (sup.rad.or.) and subradular organs (sub.rad.or.) in the midline is also indicated. Anterior is to the right.

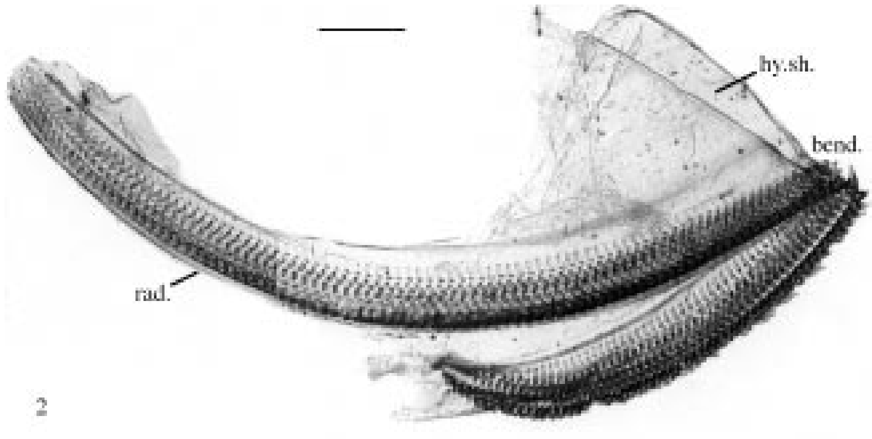


Figure 2. *Octopus* (adult, 5028 g). Whole radula from the right side, after maceration of tissues to show the hyaline shield. Scale bar, 0.5 mm. (From Nixon 1969.) Anterior is to the right; the youngest teeth lie to the left. For abbreviations, see Appendix A.

3. THE RADULAR APPARATUS OF *OCTOPUS*

(a) *The radular ribbon*

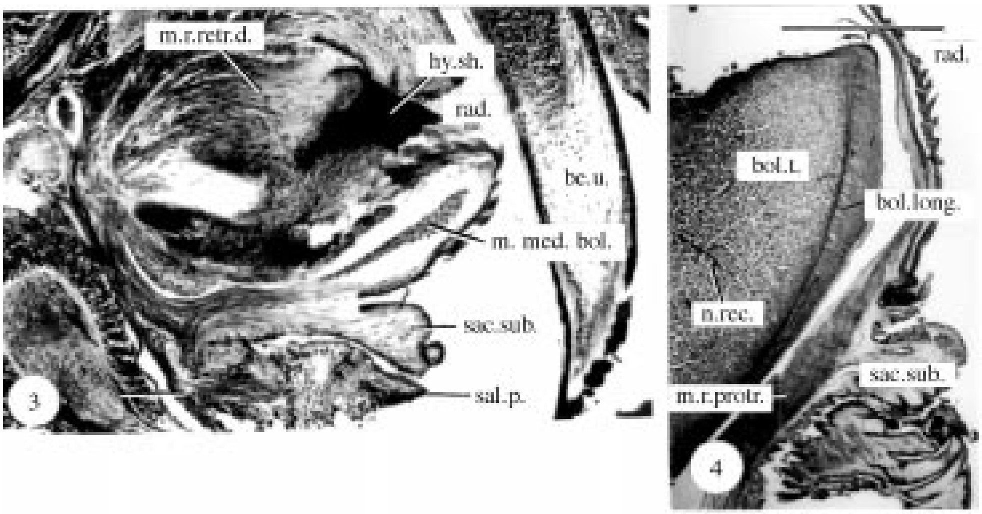
The radula consists of a radular membrane to which are attached teeth, regularly arranged in transverse rows one behind the other (figure 2) (Nixon 1995). The teeth point backwards for most of its length but anteriorly, where the ribbon turns downwards and backwards on the outside of the odontophore, they point forwards (figure 5). The radular ribbon lies in a radular canal, originating posteriorly in the radular sac: it is here that growth is initiated.

(b) *The odontophore sac*

This is a sac lying between the beaks and buccal palps, above the salivary papilla and below the pharynx (figure 6). The sac is closed except anteriorly where the radula emerges (figure 28). The radular canal divides the odontophore into paired compartments (figure 6). The posterior part of the canal is attached to the roof of the odontophore by a strand of muscle that we shall call the attachment strand (figure 7).

(c) *Formation of the radula*

The radula is produced by a set of cells lining the radular sac and canal. These odontoblasts form the radular teeth and membrane. Similar cells form the teeth on the lateral buccal palps (Young 1965) and the hyaline shield, which is attached to the front of the radula. Since new teeth develop continuously we have an excellent opportunity here to study all stages of their formation in a series of sections of a single animal.



Figures 3–4. For abbreviations, see Appendix A.
Figure 3. Sagittal section of the buccal mass of a small *Sepia* close to the midline, showing part of the radula. Anterior is to the right. Note the transverse muscle (m.med.bol.) linking the two bolsters (not visible because they lie laterally). Scale bar, 100 µm.
Figure 4. *Octopus* NPO. Lateral sagittal section showing the lateral part of the radular ribbon and the bolster. Note also the radular protractor muscle and subradular sac. Scale bar, 1 mm. (The letters and numbers in the captions (e.g. *Octopus* NPO, ZGA; *Nautilus* 467) refer to slide series in the former collection of J. Z. Young, now located in The Smithsonian Institute, Washington, DC)

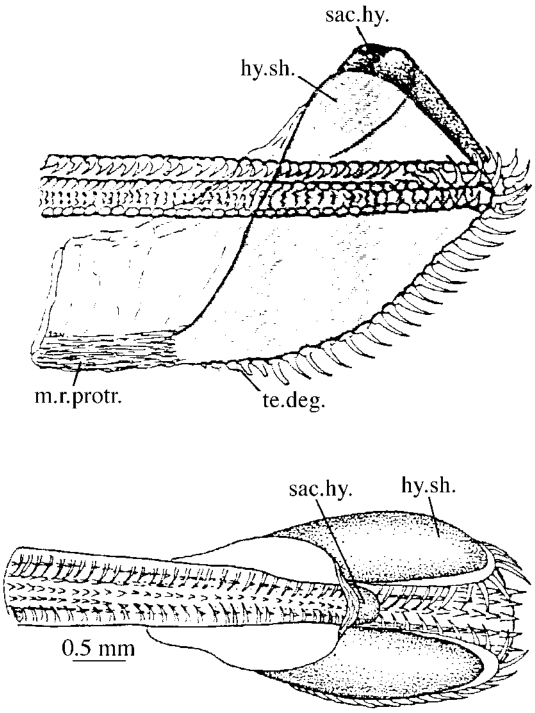


Figure 5. *Octopus*. The radula and hyaline shield, from the side and above. Anterior is to the right. For abbreviations, see Appendix A.

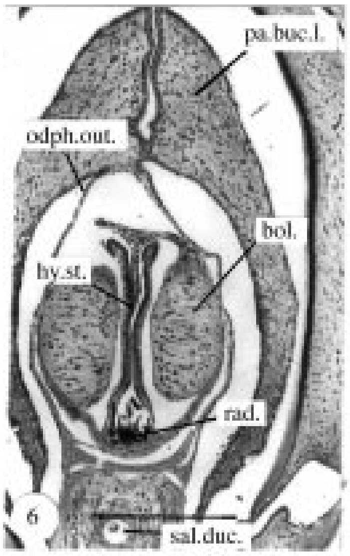
The odontoblasts are elongate cells with an oval nucleus and a large tuft of fibrils (figures 8 and 9). These are massed together to form the teeth, which move anteriorly. The remains of the odontophore fibrils can be seen in the young teeth (figure 10). At the posterior end the radula appears in cross-section as a solid mass of odontoblasts (figure 11). A little farther forward it has become a

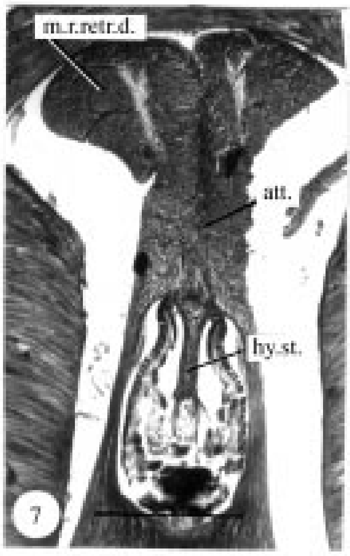
Table 1. *Genera and species studied*

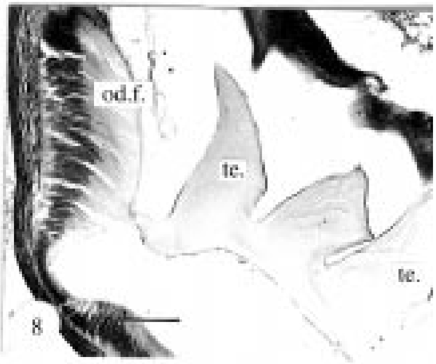
(Classification based on Clarke & Trueman (1988). For brevity generic names alone are used throughout the text and figure legends: the term *Sepia* refers to *S. officinalis*.)

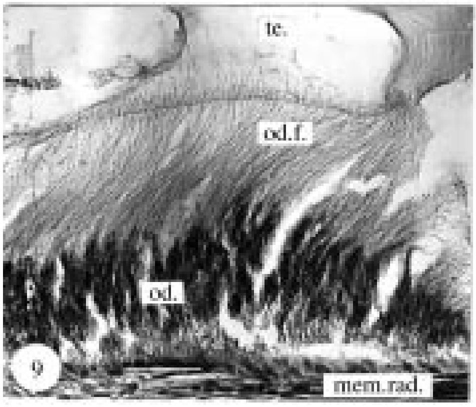
- Class Cephalopoda
  - Sub-Class Nautiloidea
    - Family Nautilidae
      - *Nautilus pompilius Linnaeus* 1758

  - Sub-Class Coleoidea
    - Order Sepiida
      - Family Sepiidae
        - *Sepia elegans* d'Orbigny, 1826
        - *Sepia officinalis* Linnaeus, 1758
    - Order Sepiolida
      - Family Sepiolidae
        - *Rossia macrosoma* delle Chiaje, 1829
        - *Sepiola robusta* Naef, 1912
    - Order Teuthida
      - Family Loliginidae
        - *Alloteuthis subulata* Lamarck, 1798
        - *Loligo vulgaris* Lamarck, 1788
        - *Lolliguncula brevis* Blainville, 1823
      - Family Mastigoteuthidae
        - *Mastigoteuthis* sp. Verrill, 1881
      - Family Cranchiidae
        - *Teuthowenia* sp. Chun, 1906
    - Order Vampyromorpha
      - Family Vampyroteuthidae
        - *Vampyroteuthis infernalis* Chun, 1903
    - Order Octopoda
      - Family Octopodidae
        - *Octopus vulgaris* Lamarck, 1798
        - *Pteroctopus tetracinus* delle Chiaje, 1830
      - Family Argonautidae
        - *Argonauta* sp. Linnaeus, 1758









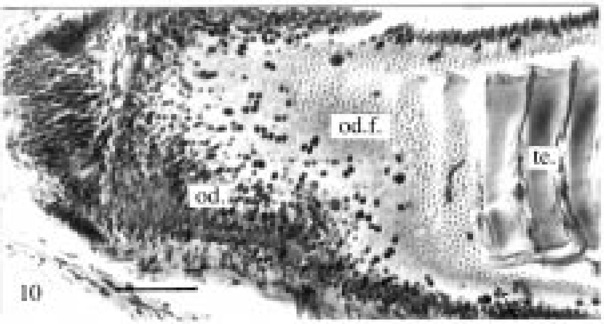


Figure 6–10. For abbreviations, see Appendix A.
Figure 6. *Octopus* ZGA. Transverse section (TS) showing labial palps, odontophore sac, and bolsters. Scale bar, 1 mm.
Figure 7. *Octopus* ZRC. TS to show the attachment strand and the dorsal retractor muscles of the radula. Scale bar, 1 mm.
Figure 8. *Octopus* 59. Developing teeth, sagittal. Scale bar, 40 µm.
Figure 9. *Octopus* 59. Odontoblasts. Scale bar, 40 µm.
Figure 10. *Octopus* RWH. Sagittal section of earliest teeth, showing the imprints of the villi of the odontoblasts. Scale bar, 50 µm.

sac with paired cavities, divided by a central partition (figure 12). The cavities are lined by odontoblasts, which form two layers on each side of a central mass that we shall term the radular core. The cells of the outer wall produce the radular membrane and the bases of the teeth; the cells of the median walls produce the cusps. The rhachidian tooth forms in the ventral midline (figure 14). The process of formation of the radula is similar in all the species studied.

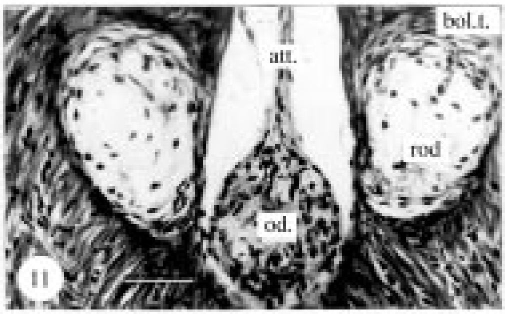
The radular canal is oval and projects dorsally into a strand of connective tissue and muscle, to which is inserted the large dorsal radular retractor muscle: this is therefore called the attachment strand (figures 7, 11 and 12). Rows of odontoblasts form vertically within the strand, dividing it into two parts with the radular core continuing between them (figure 13).

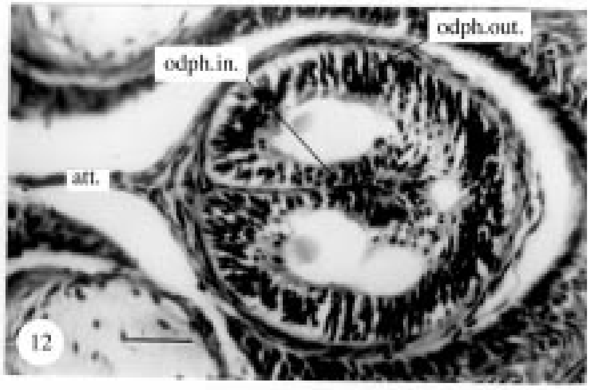
(d) *The hyaline shield*

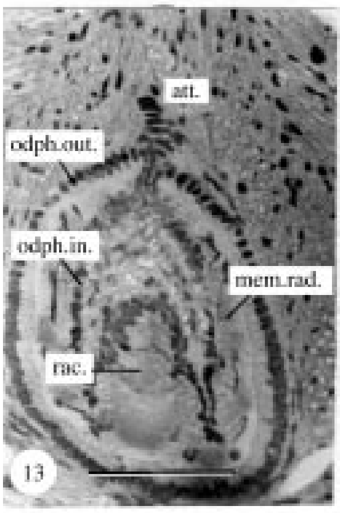
This is a rigid structure of chitinous material, attached to the radula and extending backwards from the bending plane (figures 2 and 3). To it are attached the dorsal radular retractor muscles, which serve to draw in the radular ribbon (figure 3). The shield is produced by layers of odontoblasts covering the attachment strand, which we therefore term the hyaline strand (figures 14 and 15). There is a small hyaline sac (figure 5), the walls of which join the medial walls of the lateral buccal palps. The odontoblasts also produce teeth on the palps.

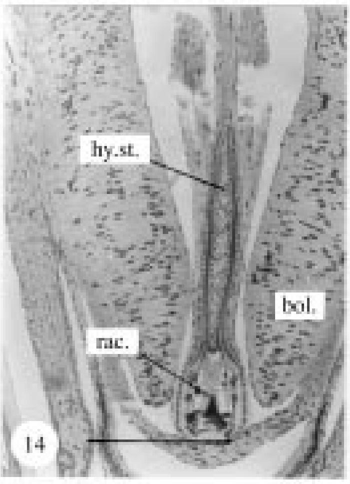
The layers of odontoblasts forming the wing on each side continue dorsally over the bolster (§ 3f; figure 16) and then down to form the outer wall of the odontophore. The two sides meet ventrally and support the radular membrane after it has turned outwards. The hyaline shield is contiguous with the radular membrane, which is drawn in by the retractor muscles.

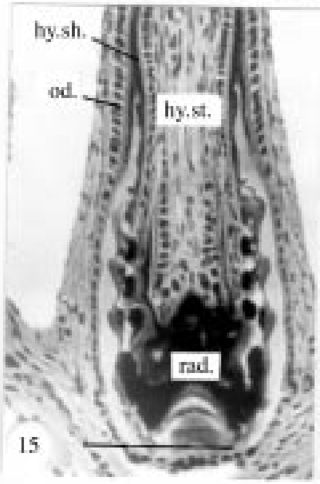
Sections in the sagittal plane show how the hyaline shield is attached to the muscles (figure 3). The hyaline shield is secreted by a series of pockets (figures 17 and 18). The secreted material forms strands that proceed to join the main shaft of the hyaline shield. The layers of odontoblasts continue upward over the top of the bolsters. Here they branch and carry many pockets and form a complex mass of tissue. Further material is added here to the shield (see also figure 38). The indentations separate the hyaline strand into several pieces anteriorly (figure 19).

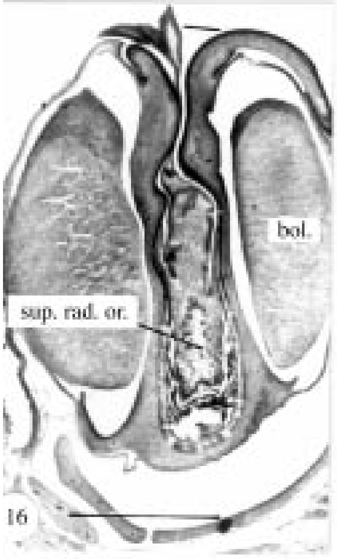


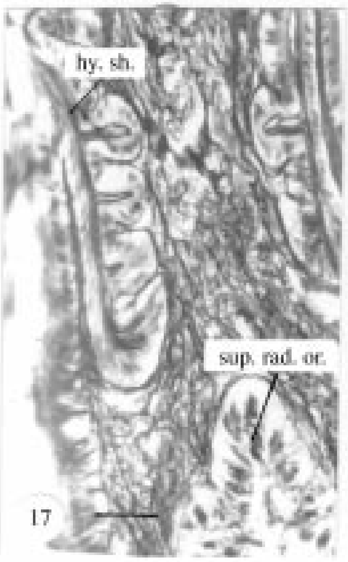












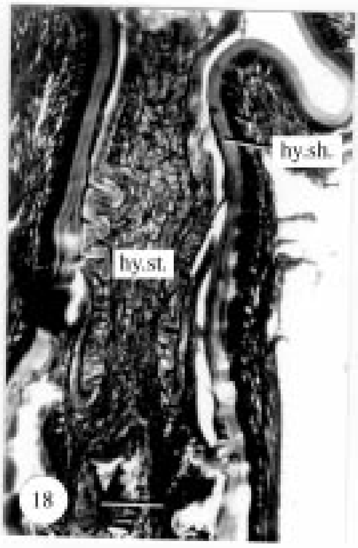


Figure 11–18. For abbreviations, see Appendix A.
Figure 11. *Sepia* B. TS posterior, showing the radular sac, part of the bolsters with some muscles dorsally, and the solid mass of odontoblasts centrally. Scale bar, 50 µm.
Figure 12. *Sepia* HC. TS showing the two layers of the odontophore. Dorsal is to the left. Scale bar, 40 µm.
Figure 13. *Octopus* ZGC. TS showing the outer sheath of the odontophore and early radula. Scale bar, 100 µm.
Figure 14. *Pteroctopus*. Horizontal section (HS) showing the hyaline strand and the front ends of the bolsters with the transverse muscle pressing against the odontophore sac. Scale bar, 1 mm.
Figure 15. *Octopus* ZGC. HS showing the layers of odontoblasts and formation of the wings of the hyaline shield. Scale bar, 100 µm.
Figure 16. *Octopus* LQY. TS showing the hyaline shield extending over the tops of the bolsters; note also the supraradular organ in the hyaline strand. Scale bar, 1 mm.
Figure 17. *Octopus* LRC. TS of hyaline strand showing formation of the wings of the hyaline shield, and part of the supraradular organ. Scale bar, 100 µm.
Figure 18. *Octopus* LRC. TS of hyaline strand, showing the series of sacs of odontoblasts that form the wings of the hyaline shield. Scale bar, 100 µm.

(e) *The radular organs*

The radular teeth are in continual use and the teeth and radular membrane are continually worn away and lost at the front end (figure 20), to be replaced from behind. The removal of teeth at the end of their life is achieved by the tissues of the subradular organ, which are formed from modified odontoblasts. These become converted into odontoclasts, whose secretions dissolve the teeth and membranes. In all cephalopods this occurs where the ribbon is drawn into a subradular sac by the protractor muscle (figure 21).

(i) *The subradular organ*

This lies at the distal (external) end of the radula, ventral to the bending plane (figure 22). Here, close to the point at which the protractor muscle is attached to the radular ribbon, the odontoblasts that secrete the membrane become modified (figures 4, 20 and 21). The cells become elongated and may be secretory as the membrane and teeth become detached at this point. The walls of the sac, which are highly folded, enclose the remains of the membrane and teeth, which then disappear, either by absorption or expulsion (figure 23). The cells of the organ contain granules of various sizes and shapes, staining black with silver. Passing backward along the pocket the granules become fewer until finally the cells form a simple epithelium covering the surface of the underlying salivary papilla (figure 24).

(ii) *The supraradular organ*

In cephalopods such as *Octopus*, the teeth may have to act on hard substances, for instance when boring into a shell (Arnold & Arnold 1969; Nixon 1969; Nixon & Maconnachie 1988; Wodinsky 1969), and there is, in addition to the subradular tissue, a region near the front end of the hyaline strand where the odontoblasts become modified and parts of the teeth and membranes are lost. We call this the supraradular organ.

This organ, which is associated with the removal of the layer of odontoblasts covering the cusps of the teeth, is barely evident in young octopuses (0.3 g and 5 g): groups of odontoblasts with black granules are absent. But at the front end of the radular core of a specimen of 46 g, there are many fragments with dark granules (figures 16, 17 and 25). They probably include portions of the cusps of the teeth, the radular membrane, as well as portions of the radular core (figures 17 and 26). The fragments are incorporated into invaginated pockets of odontoblasts and presumably absorbed. The whole front of the core is thus filled with columns of cells (figure 27). It looks like a gland, but there are no ducts. Proceeding dorsally in the strand there are groups of cells with fewer black granules, large and small and of various shapes.

(f) *The bolsters*

The two bolsters, as the name suggests, are roughly cylindrical masses of muscle, mainly transverse muscle, one on each side of the radula (figures 6, 16, 19 and 28). The bolsters lie in the odontophore sac, on either side of the radular canal. They are attached posteriorly and laterally to the wall of the odontophore but anteriorly they are free and press against the odontophore wall at the point where the radular ribbon turns outwards (figure 14). Thin layers of longitudinal muscle cover the transverse muscles and the whole bolster is wrapped in a sheath of connective tissue. It appears, then, that the volume of the bolster cannot change, so that contractions of the powerful transverse muscles must cause it to increase in length. The bolster thus functions as a muscular hydrostat, as do the arms, tentacles and fins of cephalopods (Kier 1982). In *Octopus* they do not contain any rods of 'chondroid tissue' such as occur in decapods and in *Nautilus* (see below).

(g) *Stimulation of the bolsters*

Electrical stimulation has confirmed that this is indeed the way the bolster acts. The dorsal radular muscles were first removed. Stimulation of the inferior buccal ganglion then caused the bolsters to elongate and come together. Direct stimulation of one bolster alone also caused it to elongate (figure 29): anteriorly the bolster became greatly narrowed, tapering to a point in the odontophore sac, immediately below the lateral part of the radular ribbon at the bending plane. Shortly behind and below the narrow front end the bolsters of the two sides are joined by a transverse band of muscle (figure 3). The transverse band thus supports the central part of the radular ribbon while the bolsters push up the sides. Retraction of the bolster is presumably produced by the thin layers of longitudinal muscles.

(h) *The radular receptor*

At the extreme anterior end of each bolster in the transverse muscle there are many nerve fibres. They are all connected with fine nerve trunks running along the outer sides of the bolsters and may constitute a receptor organ (figure 30). Some of these fibres end in bushes of fine fibres near the surface. It is not easy to decipher the dense plexus of fibres. Many of the branches end in knobs among the muscle (figure 31). Others end as fine twigs in the epithelium (figure 32). Dark masses that are probably nerve cells occur (figure 33) and some of these have many branched dendrites. These latter may be receptor cells like those in the mantle muscles described by Sereni & Young (1932) and by Alexandrowicz (1960), although we have not been able to identify the end organ with certainty.

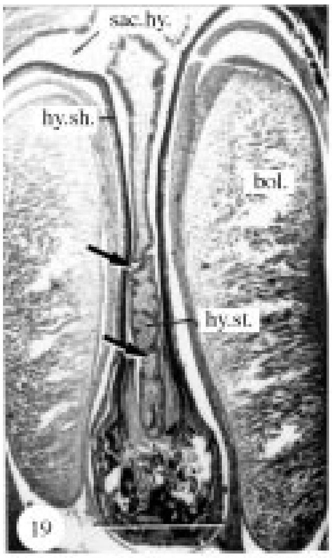
It is of interest that such nerve fibres are not seen in the bolster muscles of octopods that do not bore holes, nor in such decapods as *Sepia* or *Loligo*.

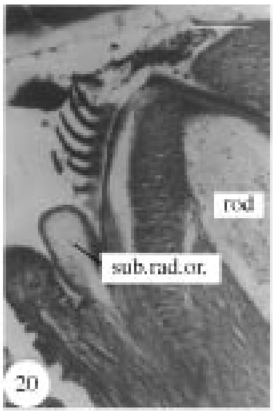
4. THE RADULAR APPARATUS OF DECAPODS

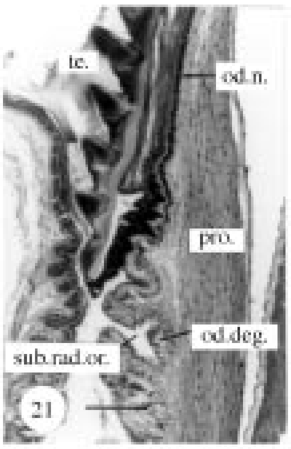
The organization of the buccal mass in *Sepia* and *Loligo* is broadly similar to that of *Octopus*, although the lateral buccal palps bear teeth (Bidder 1966). There are important differences in the radular apparatus however. First, the bolsters contain supporting rods, and second, there is no sign of a supraradular organ.

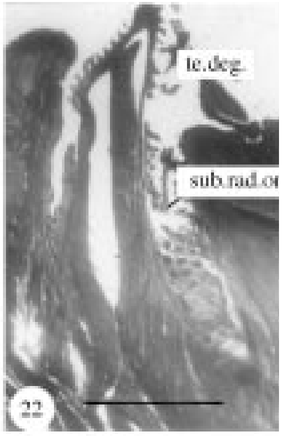
(a) *The bolster rods*

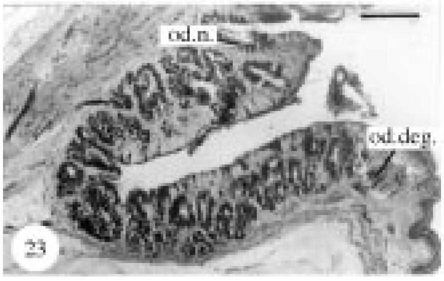
In most decapods (and in *Nautilus*) the bolsters each contain an elongate structure that we shall term the rod (figure 34). This probably corresponds to structures that occur in the bolsters of other molluscs (Salvini-Plawen 1988; see § 6) and which have been assumed to be skeletal

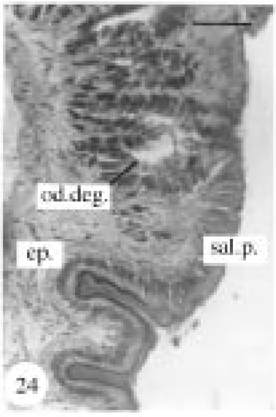


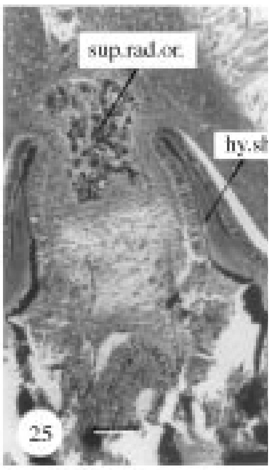


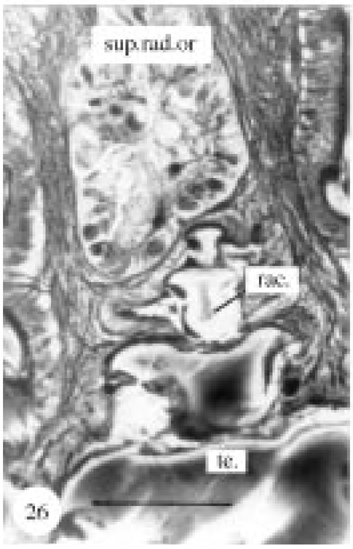


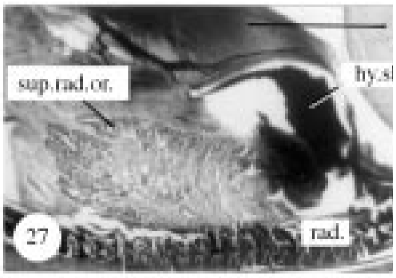












Figures 19–27. (*Opposite*) For abbreviations, see Appendix A.
Figure 19. *Pteroctopus* A. TS of hyaline strand showing break-up into fragments (arrows). The wings of the shield are continuous with the radular membrane. Scale bar, 1 mm.
Figure 20. *Sepiola* 74/8. Lateral sagittal section, showing rod, and teeth being absorbed in the subradular organ. Scale bar, 100 µm.
Figure 21. *Octopus* NOT. Sagittal section of subradular sac, showing break-up of the layers of odontoblasts and formation of the subradular organ. Note end of protractor muscle. Scale bar, 100 µm.
Figure 22. *Lolliguncula* B. Sagittal section, subradular organ, showing dissolution of teeth. Scale bar, 1 mm.
Figure 23. *Octopus* NPO. Sagittal section showing the subradular organ with a layer of normal odontoblasts folding up to form sacs of degenerating odontoblasts. Scale bar, 100 µm.
Figure 24. *Octopus* NPO. End of subradular organ where the degenerating odontoblasts are replaced by epithelial cells covering the salivary papilla. Scale bar, 10 µm.
Figure 25. *Pteroctopus* A. HS showing supraradular organ and layers of odontoblasts forming the wings of the hyaline shield. Scale bar, 100 µm.
Figure 26. *Octopus* LRC. TS part of radula, showing the supraradular organ newly formed from the odontoblasts of the cap over the rhachidian tooth. Scale bar, 100 µm.
Figure 27. *Octopus* NPO. Sagittal section to show front end of the radula, hyaline shield and supraradular organ. Scale bar, 1 mm.

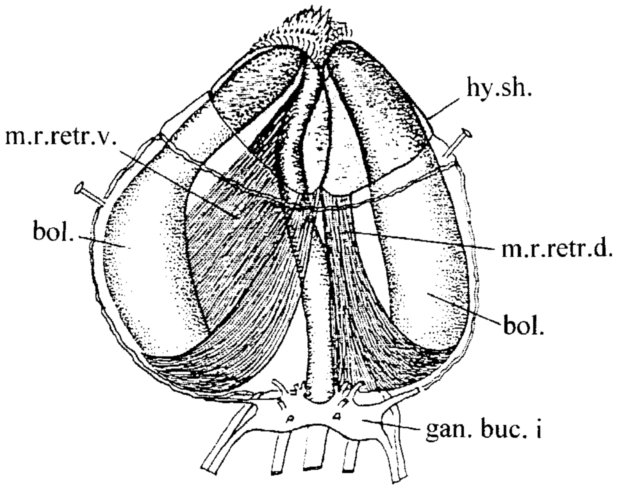


Figure 28. *Octopus*. Dissection showing the bolsters in the odontophore sac. For abbreviations, see Appendix A.

supports. In some molluscs they have been considered to consist of cartilage or to be 'chondroid'. In cephalopods they are not made of cartilage but appear to contain a semi-fluid, gelatinous substance, at least in *Sepia*, *Loligo* and *Nautilus* (see below). The term rod implies that under compression from the bolster muscles they become rigid.

In sepiolids and loliginids the rod is composed of large cells that fill the whole space, leaving no large cavities (figure 35). The cells lie in watery spaces separated by irregular fibrous material. They vary in size and shape. There are branching blood vessels within the rods. The rod has its own sheath of several layers, probably mainly connective tissue, with elongated nuclei (figure 36). The rod runs the whole length of the bolster ventrally, below the transverse muscles (figures 34, 37 and 38). It is of small diameter posteriorly and anteriorly (figure 37) but it is larger centrally. Anteriorly may extend beyond the leading edge of the main muscle of the bolster (figure 39). More ventrally the rod pushes against the transverse muscle connecting the two bolsters, which supports the centre of the radular ribbon as it passes over the bending plane.

When the bolster of a freshly killed *Sepia* or *Loligo* is cut transversely no fluid exudes from the cut rod. But if pressure is applied to the rod a viscid jelly can be expelled as in *Nautilus* (figure 56).

Direct electrical stimulation of the bolster in *Sepia* or *Loligo* causes the tip to curve up strongly. This lifts the transverse muscle, raising and splaying the radular teeth as in *Octopus*.

(b) ***The subradular organ***

We have studied this only in loliginids, *Sepia* and some sepiolids. In *Lolliguncula*, the subradular organ is a rather narrow strip above the salivary papilla (figure 22). There is no special development of the odontoblasts. The anterior end of the hyaline strand is broad. There are no cells filled with granules in the strand, which is filled by fibrous tissue containing scattered cells of various types. The hyaline shield is formed by odontoblasts. There is no sign of a supraradular organ.

In *Alloteuthis* and *Loligo*, the hyaline strand and absence of supraradular organ are strikingly like that of *Lolliguncula*. The broad hyaline strand contains no masses of cells with black granules. There is therefore no evidence for a dorsal region for removal of teeth in loliginids. Nor is there in *Sepiola*, *Rossia* or *Sepia*. Neither *Rossia* (figure 38) nor *Sepia* show any signs of accumulation of odontoblasts in the regions above the rhachidian tooth or elsewhere in the hyaline strand.

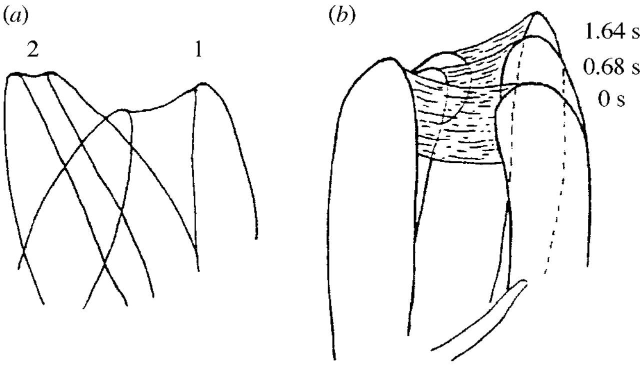


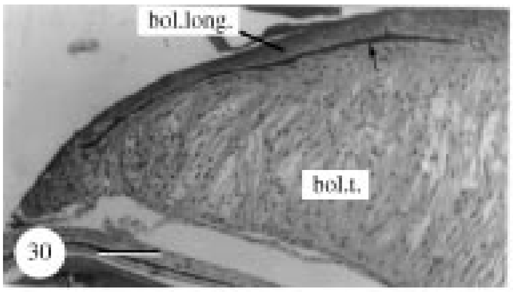
Figure 29. *Octopus*. Elongation of the bolsters, in isolated preparations, by electrically stimulating the inferior buccal ganglion (*a*) or the bolster directly (*b*). In (*a*) the effect has been to raise the bolsters from the resting position (1) and turn them to the left (2): in the intact animal this would raise the radular teeth at the bending plane and splay those on the left side of the ribbon. In (*b*) stimulation of the right bolster causes it to elongate and narrow (traced from videofilm: figures indicate time in seconds). Note, too, the effects on the contralateral bolster, via the median muscle linking the bolsters.

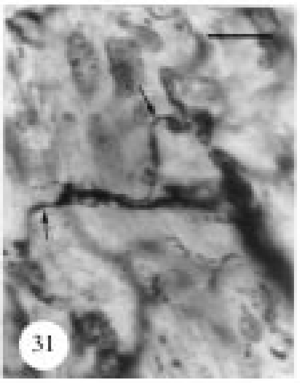
5. THE RADULAR APPARATUS OF *NAUTILUS*

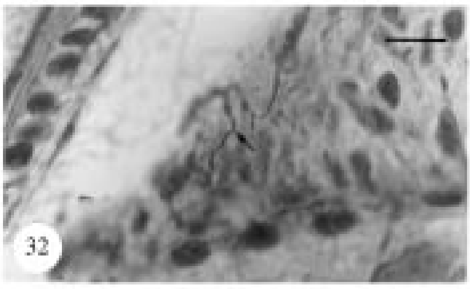
(a) ***The radular appendage***

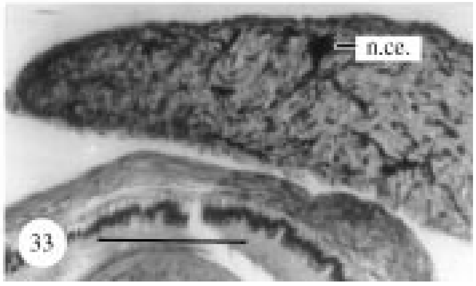
The radula has all the parts found in coleoids. There is, however, a unique addition we have called the radular appendage, which will be described first. After removing the upper beak the front of the radula appears as a broad, brownish band across the front of the pharynx (figure 40). The appendage is seen as pale feathery or papillate mass in the midline, on the floor of the pharynx, and on both sides (figures 41 and 42). This great mass of tissue is attached by muscles and connective tissue to the front of the radula at about the level of the supraradular organ in *Octopus* (figures 43–45). There are signs that the appendage may absorb the remains of the radula, but the lateral parts are also secretory.

The histology of the radular appendage is shown in figures 46–49. Branches radiate from the core, proceeding forwards and outwards (figures 46 and 47). Each branch carries a series of papillae, which carry closely packed elongated cells (figures 44 and 49). These are of three sorts. The first are numerous cells filled with a 'foamy' cytoplasm with a nucleus at the base (figure 49); some of these are much expanded. The second type of cell is also numerous and contains oval nuclei with dark granules. The third type of cell is very thin and elongated with a long nucleus and is perhaps a supporting cell. Cells of the first type are almost certainly secretory. They can be seen to open into the spaces between the papillae. The openings are often seen in transverse section surrounded by darkly stained rings. There are no signs of the accumulation of secretory products and no evidence of their function. Their









Figures 30–33. For abbreviations, see Appendix A.
Figure 30. *Octopus* MGX. Sagittal section of tip of bolster showing the nerve trunk that supplies the bolster receptor organ. Scale bar, 100 µm.
Figure 31. *Octopus* MGX. Nerve endings at the tip of the bolster. Scale bar, 10 µm.
Figure 32. *Octopus* RWI. Nerve plexus at the tip of a bolster. Scale bar, 10 µm.
Figure 33. *Octopus* MGX. Receptor cells of nerve plexus in the tip of a bolster. Scale bar, 100 µm.

secretion must pass into the pharynx and thence perhaps to the oesophagus.

(b) *Development of the teeth*

As in other molluscs (Rottmann 1901; Gabe & Prenant 1952; Fuchs 1973; Runham 1963; Mischor & Märkel 1984; Mackenstedt & Märkel 1987), the teeth originate at the posterior end, in open-ended sacs formed by material staining blue with Mallory's method, perhaps cartilage. There are irregular masses of rounded cells, presumably destined to be odontoblasts. A little farther forward these are aligned on the inside of the canals and form groups of cells within which the teeth develop. The cell groups join to form a single ring of teeth with a core at the centre (figure 50). This core is a characteristic feature of the *Nautilus* radula. It is formed of a matrix, perhaps collagenous, staining blue or green, with Mallory's containing a few muscle fibres (figure 51). Bundles of muscle fibres proceed upwards in the midline from the core, passing the bolsters (figure 45*a*). Some of the muscle fibres turn outwards from the core above the odontophore sacs and form the hyaline shield (figure 45*b*). Others are attached to a dorsal cartilage (figure 45*c*). This is a triangular plate, staining blue and containing many fibres and oval nuclei, stained red. This dorsal cartilage covers and proceeds some way down the sides of the odontophore sacs. Tissue of the radular appendage is embedded in its upper surface and many bundles of muscle fibres attach it to the surrounding tissue.

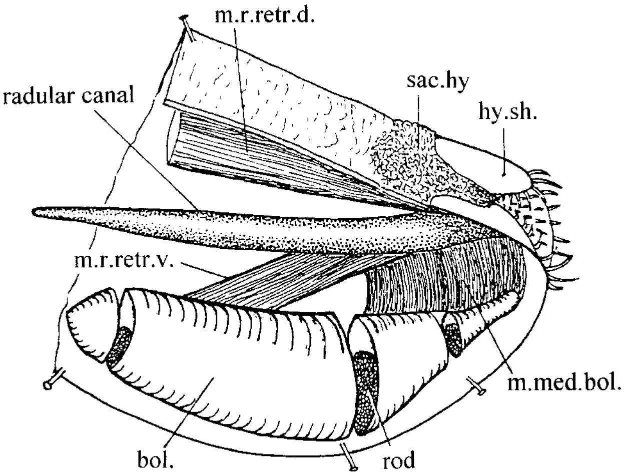


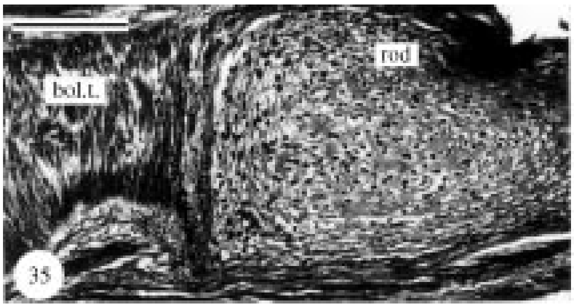
Figure 34. *Sepia*. Drawing showing a typical decapod bolster with its ventral rod. Anterior is to the right.

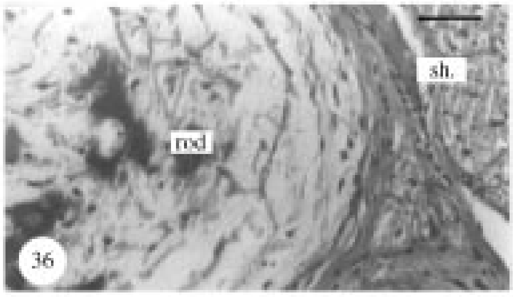
(c) *Maturation and breakdown of the teeth*

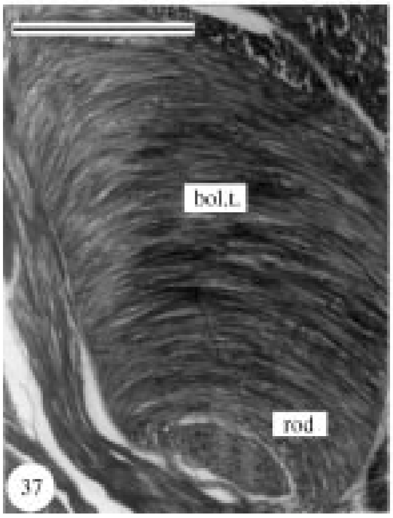
The youngest teeth are pale after Mallory's stain. As they pass forward in ontogeny they become brown and then black. From an early stage they have an internal structure of vertical columns that stain red (figure 52). These form overlapping plates on the surface of the teeth.

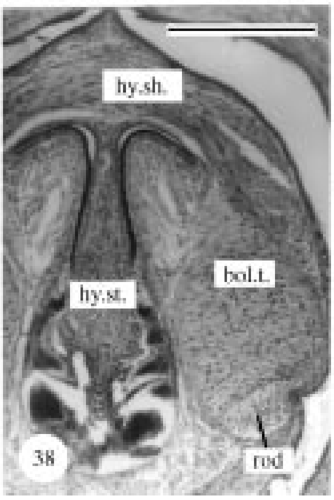
Many of the odontoblasts are elongated and set at right angles to the surface of the teeth. There is a nucleus at the outer side of each cell and villi at the other end, presumably adding more material to the teeth. Odontoblasts cover the inner surface of each tooth. There are also many masses of round cells, presumably odontoblasts, between the teeth (figure 53).

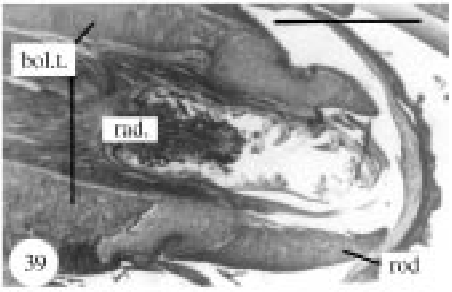
At the very front the teeth are 'cleaned' by contact with the front end of the radular core (figure 51). At the turn











Figures 35–39. For abbreviations, see Appendix A.
Figure 35. *Lolliguncula* G. HS anterior region of the bolster, showing the cellular nature of the rod and the transverse muscle. Scale bar, 100 µm.
Figure 36. *Sepia elegans* A. TS bolster rod, showing the sheath. Scale bar, 10 µm.
Figure 37. *Alloteuthis* AF. TS bolster, posterior region, showing the large mass of transverse muscle above the small rod ventrally. Scale bar, 200 µm.
Figure 38. *Rossia*. TS bolster muscle and rod. Scale bar, 1 mm.
Figure 39. *Lolliguncula* G. HS front of the radula showing the tips of the bolsters with the rods extending to the end of the odontophore sac. Scale bar, 1 mm.

they are therefore quite free of odontoblasts. The remains of the odontoblasts are somehow broken down and incorporated in the subradular sac and perhaps also the radular appendage, together with pieces broken off the tips of the teeth. As in coleoids, there is a well-defined subradular organ in the subradular pockets (figures 44 and 45).

(d) *The odontophore sac*

The odontophore sac lies below the pharynx (figure 45*b*). It contains the radula in its canal and above this and laterally the paired radular supports, each with its rod. The odontophore sac opens in front allowing passage of the radular ribbon.

The lateral walls of the odontophore sac are formed from thin membranes, with longitudinal muscles dorsally; the antero-ventral walls contain cartilage, which is joined to the front end of the bolster rod (figure 45*b*). This is the region in which the lateral part of the radular ribbon turns outwards and it thus receives here the support of the bolsters.

(e) *The hyaline shield*

Muscles attached to the radular core pass up between the sacs and over the odontophores and down the outside (figure 45*b*–*d*). The hyaline shield is formed by layers of odontoblasts continuous with those that form the teeth. These appear in our preparations as irregular layers of cells between the muscles. The layers of odontoblasts are carried on a series of projections on the sides of a cavity around the newly formed shield. The shield is thus formed over the sides and front of the odontophore. It continues ventrally, where it carries the teeth after they have been turned outwards. The shield stains very darkly.

(f) *The bolsters*

These are massive and extend over the whole length of the radular canal; they are attached to the back of the odontophore (figures 43–45). Each bolster consists of a dorsal muscular part and a ventral rod (figure 54). The muscle fibres lie in a matrix that stains green with Masson's stain and is probably collagen. The most dorsal fibres are longitudinal and some of them are attached to the back of the odontophore (figures 43 and 45*b*). At the hind end they are very loosely packed.

Most of the muscle fibres are transverse and run around the sides of the rod and compress it. The most ventral of these transverse fibres are very closely packed. The two bolsters are joined near the front part of their length by a

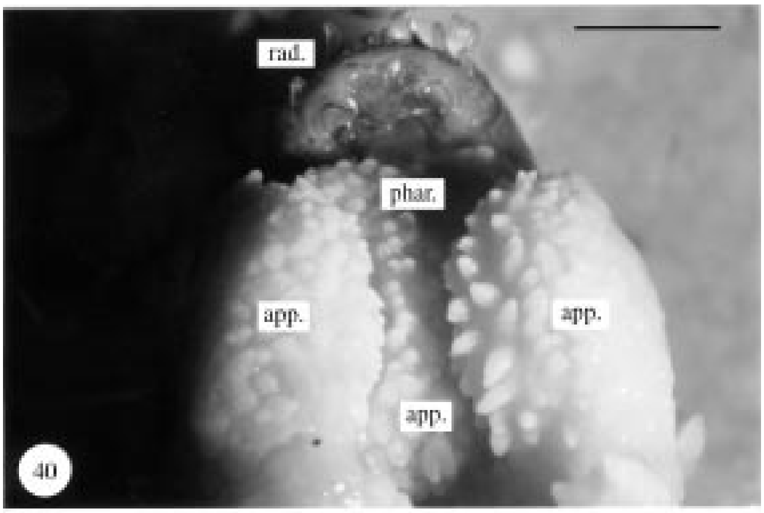


Figure 40. *Nautilus*. The front end of the pharynx seen from above after removal of the upper beak and its muscles. Note the lateral and medial parts of the radular appendage. Scale bar, 5 mm. For abbreviations, see Appendix A.

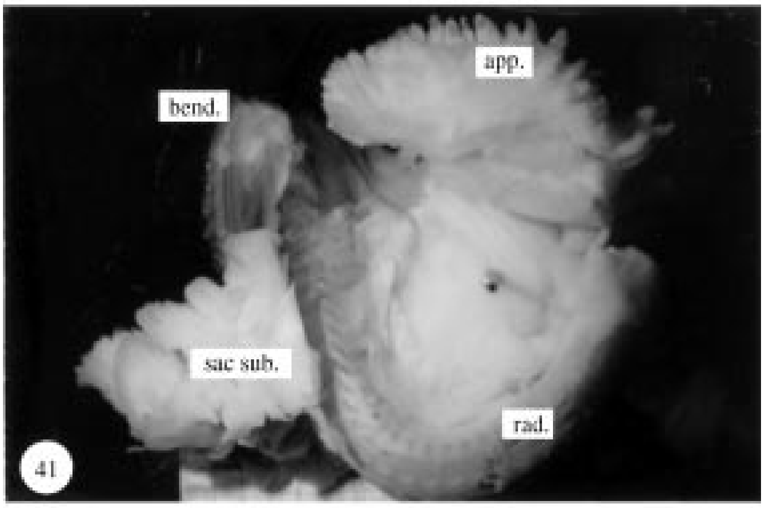


Figure 41. *Nautilus*. The entire radula dissected and seen from the side. Scale intervals in mm. For abbreviations, see Appendix A.

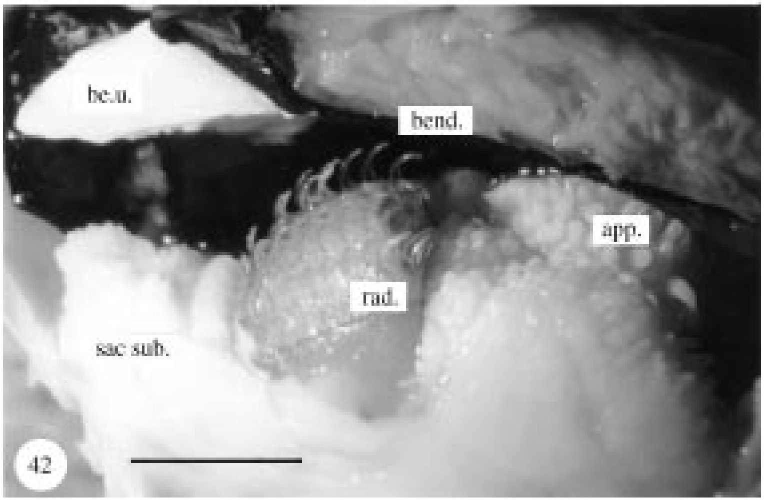


Figure 42. *Nautilus*. Front end of the radula showing its relations with the radular appendage and the subradular sac. Scale bar, 5 mm. For abbreviations, see Appendix A.

thin but strong band of transverse muscle fibres (figure 45*b*,*c*). These form a sling below the radula but are separated from it by longitudinal muscle at the sides.

(g) *The bolster rod*

This is very large in *Nautilus*, more than half of the cross-section of the bolster (figures 43, 44 and 55). At the front end the rod reaches into the lateral corner of the odontophore and is attached to the cartilage of its wall (figure 45*c*). This is the level at which the lateral part of the radular ribbon turns outwards. Presumably the bolster rod serves to transmit the force of the bolster muscles to support this turn and to push the teeth upwards. The junction sometimes has the appearance of a rather loose joint.

The whole rod is enclosed in a thin membrane and although embedded in the bolster muscle it is quite separate from it. If a (formol-fixed) bolster is cut transversely

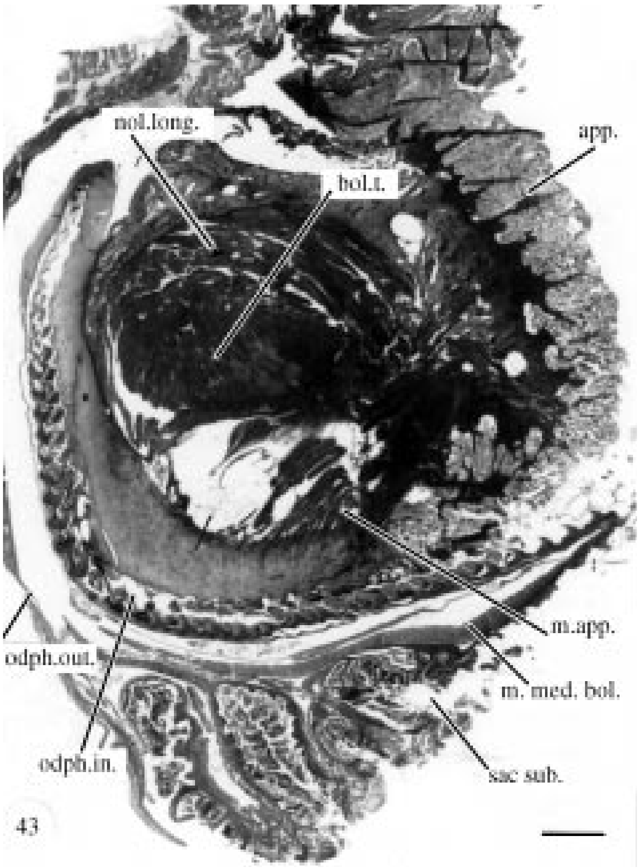


Figure 43. *Nautilus* 467. Midline sagittal section. Masson's stain. Scale bar, 2 mm. For abbreviations, see Appendix A.

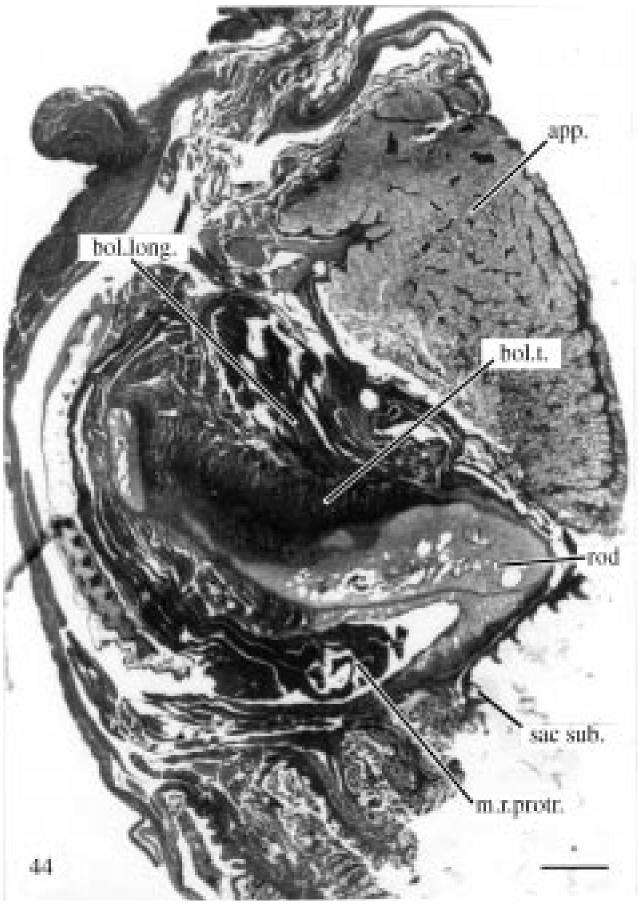


Figure 44. *Nautilus* 467. Lateral sagittal section. Masson's stain. Scale bar, 2 mm. For abbreviations, see Appendix A.

(figure 55) and a glass rod is pressed with moderate force against the rod, a jelly-like substance can be forced out of the cut face (figure 56). This is sufficiently viscous to retain its cylindrical cross-section (more or less) but not enough to prevent it from collapsing slightly and folding up on itself.

The rod is composed of material stained blue with Mallory's stain and not resembling cartilage. It is interrupted by very large spaces along the whole length. These are mostly empty. There are many large branched blood vessels in the matrix, stained red. Scattered throughout the matrix are many globules, stained red, of 1–10 μm diameter. They are especially dense around the blood vessels. They are mostly round, but some are elongated along the length of the rod (figure 57).

As in decapods the bolster and the rod appear to constitute a hydrostatic support system (Kier 1988). As the rod is enclosed by a membrane its volume must remain constant. Contractions of the transverse bolster muscles would, therefore, compress the jelly in the rod and cause it to elongate. The whole system serves to support the lips of the odontophore and perhaps to push the teeth upwards, as in *Octopus* or *Sepia*.

(h) *Final fate of the radular teeth*

There is no clearly defined supraradular organ in *Nautilus*. The appendage may serve to remove some of the remains of the teeth and membranes, leaving the teeth clean and ready for use. There is certainly a process of breaking up of the whole front end of the radular core, leaving a mass of debris consisting of the remains of the core, of the odontoblast coverings of the teeth and of the radular membrane (figure 58). Some of the contents of these rings of cells are stained red and seem to be the remains of teeth.

The lowest part of the appendage is thus made up of odontoblasts separated from the teeth, together with pieces of the core and radular membrane. These materials then probably move gradually upwards. Irregular pieces of material occur throughout the appendage (figure 59). They are probably the remains of pieces of basal radular membrane, taken in lower down. Some of these run along the outer edge of the appendage (figure 45*c*). Others run transversely and appear as stars in sagittal sections (figure 45*c*). Still others run antero-posteriorly (figure 45*a*,*b*). It is not clear how these differences come about.

The radular appendage appears to contain the remains of the radular core, the radular membrane, teeth and odontoblasts that have been swept upwards into the pharynx. The upper end of the appendage is in the pharynx, close to the oesophagus. It may be that the material is finally digested by the gut. The medial surface is composed of material like that of the whole organ (figure 45*a*–*e*). The lateral surface is much broken up and shows no trace of an outer membrane (figure 59).

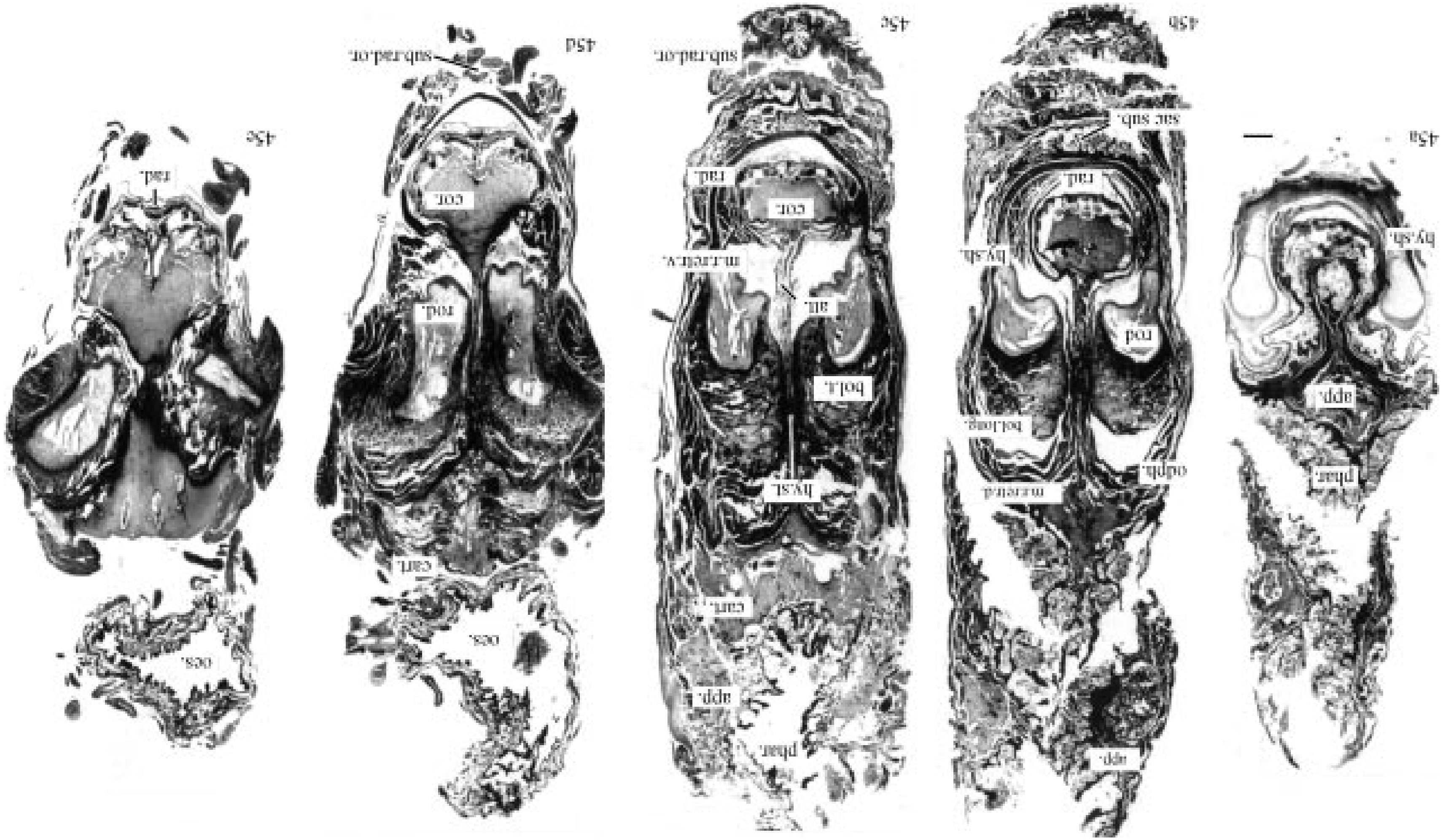


Figure 45. *Nautilus* 467. Series of transverse sections through the radular apparatus, proceeding from anterior (*a*) to posterior (*e*). Masson's stain. Scale bar, 1 mm. For abbreviations, see Appendix A.

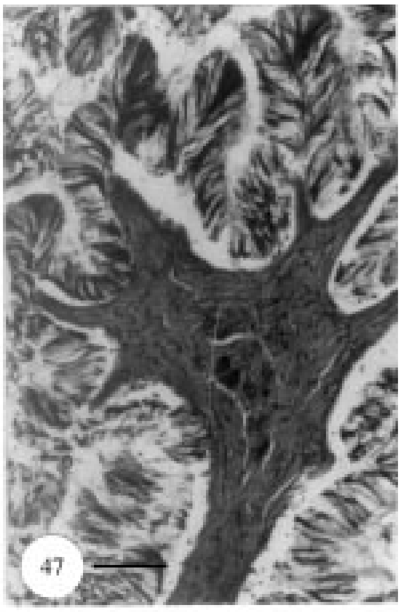
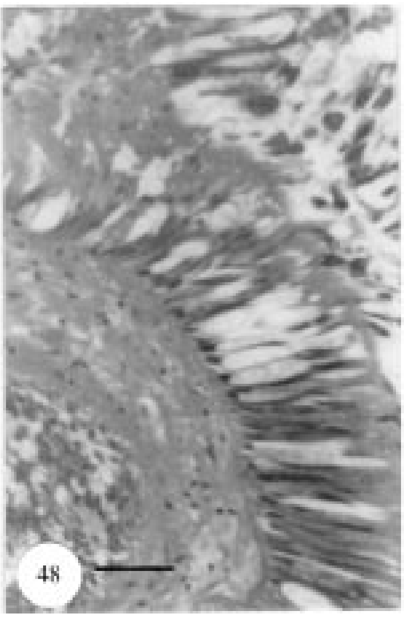


Figure 46. *Nautilus* AA. Section of radular appendage showing a single lobe with cells attached. Scale bar, 100 µm.

Figure 47. *Nautilus* AA. Section showing the axis of a lobule with cells attached. Scale bar, 100 µm.



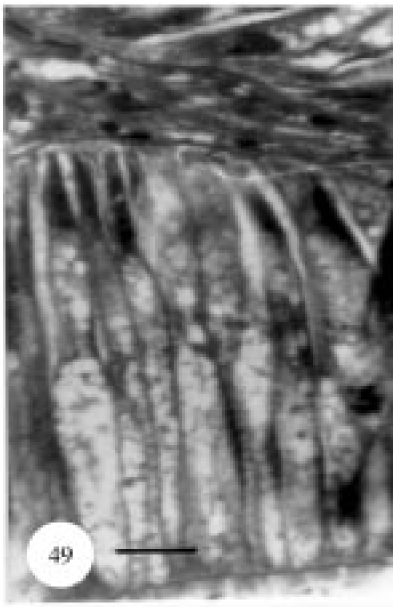


Figure 48. *Nautilus* AA. Row of cells of a lobule of the appendage apparently discharging material into the space between lobules. Scale bar, 40 µm.

Figure 49. *Nautilus* AA. Cells of lobule containing 'foamy' material. Scale bar, 10 µm.

It is not clear how the odontoblast cells come to adopt the regular arrangement in the appendage. Perhaps the majority of them are odontoblasts of the radular membrane, carried into the appendage as pieces come away from the core. We have not seen any process of digestion or dissolution of material in the appendage but this seems likely to occur. Some areas contain more darkly stained pieces than others but there is no progressive reduction passing dorsally.

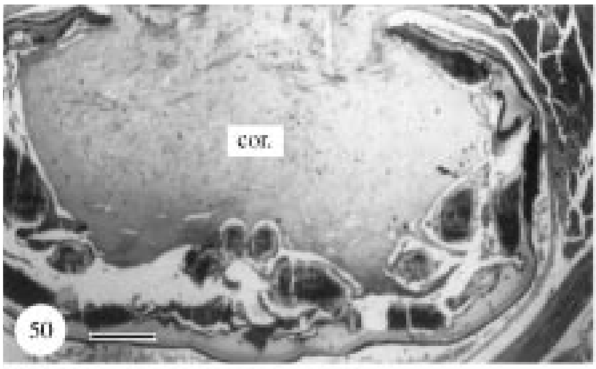
(i) ***The subradular organ***

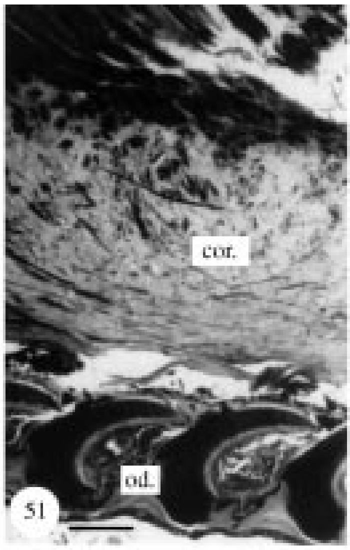
The extent of the radular ribbon that is pulled in and out during feeding includes only about six rows of teeth. Those farther back in the upper part are still accompanied by odontoblast sheaths. Those that have turned over the bending plane are often broken and have lost their tips. The protractor muscle extends nearly to the tip (figure 44). In the midline the bending plane consists of the walls of the odontophore, the hyaline shield and the radular membrane carrying the teeth. Laterally the lips are supported by the end of the bolster rod.

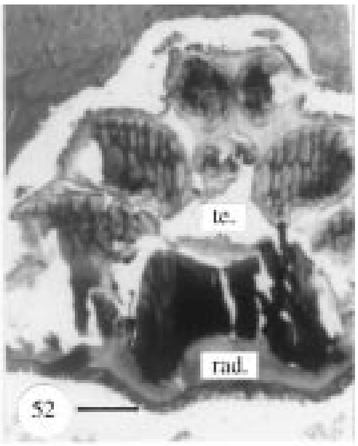
The protractor muscle raises up the radular membrane and draws it and the teeth into the subradular sac (figures 42 and 44). The remains of the teeth are accompanied here by masses of odontoblast cells. These are probably derived from the layer of odontoblasts that formed the radular membrane.

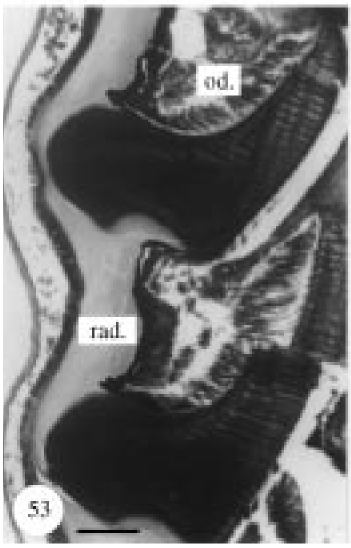
The subradular organ comprises four pockets, the first of which is the subradular sac (figure 43). The walls of the pockets are probably formed by the remains of the radular membrane, rolled up by the protractor muscle (figure 44). The partitions contain collagen. The pockets all contain masses of odontoblasts. In the most anterior one they are partly in well-orientated rows, perhaps the remains of pieces of radular membrane, with their attached odontoblasts. In the more posterior pockets the cells are generally less well orientated. The most posterior pocket has shrunken walls and a few bundles of disorientated cells (figure 60).

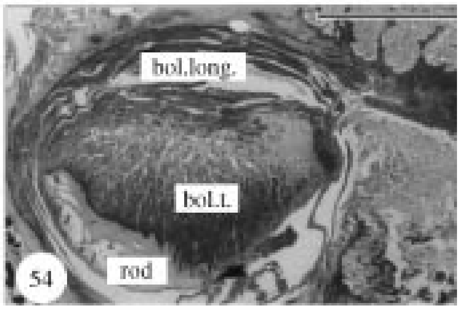
There is therefore evidence that in the subradular sac the teeth and radular membrane are actually dissolved as they are in coleoids. Presumably this is the action of the











Figures 50–54. For abbreviations, see Appendix A.
Figure 50. *Nautilus* 467. TS early teeth around central radular core. Scale bar, 400 μm.
Figure 51. *Nautilus* 467. Sagittal section of radular core and teeth. Scale bar, 400 μm.
Figure 52. *Nautilus* 468. TS early teeth, showing the internal columnar structure. Scale bar, 40 μm.
Figure 53. *Nautilus* 468. Sagittal section of maturing teeth, showing layers of odontoblasts with their villi. Scale bars, 40 μm.
Figure 54. *Nautilus* 467. Sagittal section of bolster showing longitudinal muscle fibres dorsally, scattered transverse fibres below and the rod ventrally. Scale bar, 1 mm.

odontoblast cells, converted into odontoclasts. We have not seen any other evidence of an absorptive process. There is no obvious increase in vascularity in the pockets.

6. DISCUSSION

(a) *The nature of the bolsters*

The radula is a characteristic molluscan feature: it is present in all classes of molluscs, apart from the filter-feeding bivalves (Salvini-Plawen 1988), and has been the subject of innumerable studies (e.g. Fretter & Graham 1962, 1994; Hyman 1967). Most of these have concentrated on the nature of radular ribbon, whose teeth are of taxonomic importance in some groups, on its development (Rottmann 1901; Gabe & Prenant 1952; Fuchs 1973) and on its regeneration and renewal (Runham 1963; Mischor & Märkel 1984; Mackenstedt & Märkel 1987).

Far less attention has been paid to radular-supporting structures and in cephalopods they seem never to have been described. The first difficulty in comparing them with similar structures in other molluscs is that there seems to be no agreement about terminology. Fretter & Graham (1962, 1994) always refer to them, in gastropods, as the 'radula support muscles'. Hyman (1967), however, prefers the term 'bolsters' for the 'firm internal supports' that stiffen 'the radula eminence, badly called tongue by some authors', and she uses it for Aplacophorans, Polyplacophorans, Monoplacophorans and Gastropods. She does not consider cephalopods but the name 'bolster' seems entirely appropriate for these animals too, because of their roughly cylindrical form (figure 28), and we have not hesitated to adopt it.

In his description of recent monoplacophorans, Wingstrand (1985) uses the term 'radula support', although he appears to equate this with 'odontophore' and 'tongue'. In *Neopilina*, Lemche & Wingstrand (1959) refer to paired 'radula vesicles', so called because they appeared as empty sacs in their histological sections (see below).

Another difficulty is the naming, and the nature, of one of the constituent parts of the bolster. Probably all authors would agree there is a muscular component but the non-muscular part has been described, in various molluscs, as comprising 'chondroid tissue', cartilage (several authors write of 'radula cartilages'), muscle, connective tissue, fluid or even gas. This last claim was made by Plate (1898), working with chitons, but Lemche & Wingstrand (1959) found that the freshly caught

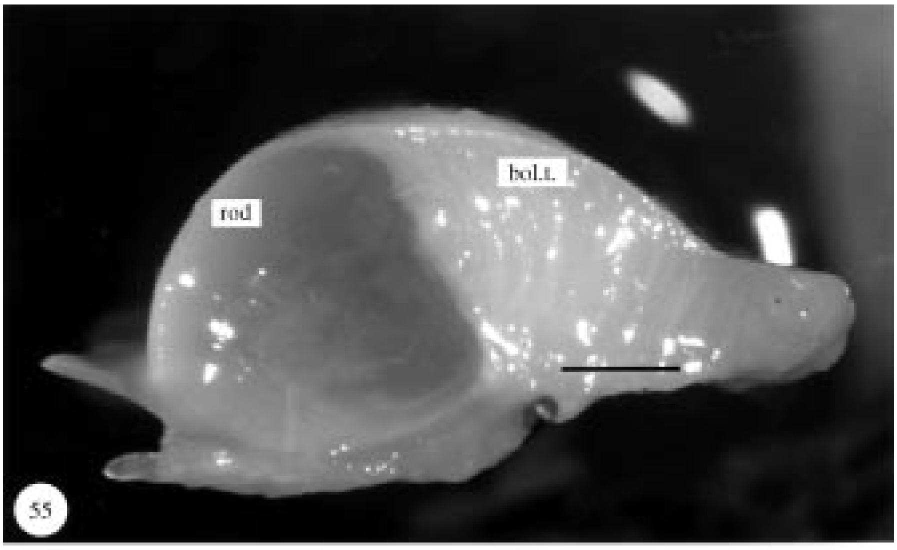


Figure 55. *Nautilus*. TS cut through an isolated bolster. Dorsal is to the right. Scale bar, 1 mm. For abbreviations, see Appendix A.

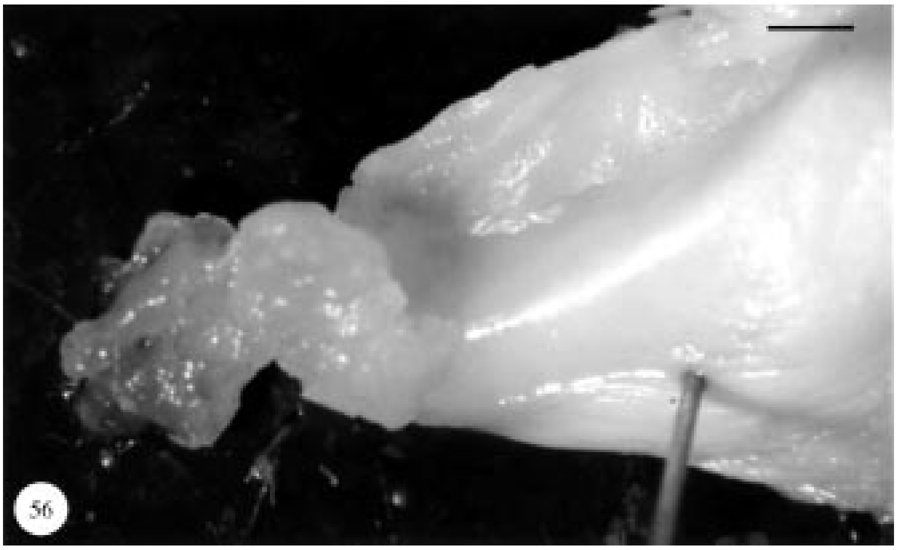


Figure 56. *Nautilus*. A whole bolster, lying on its medial aspect, after pressure had been applied to squeeze out the contents of the rod. Scale bar, 1 mm.

chiton, *Lepidopleurus*, had vesicles that had no gas but instead 'were hard and distended by their fluid contents', an interesting comment in view of our theory of bolster function (see below).

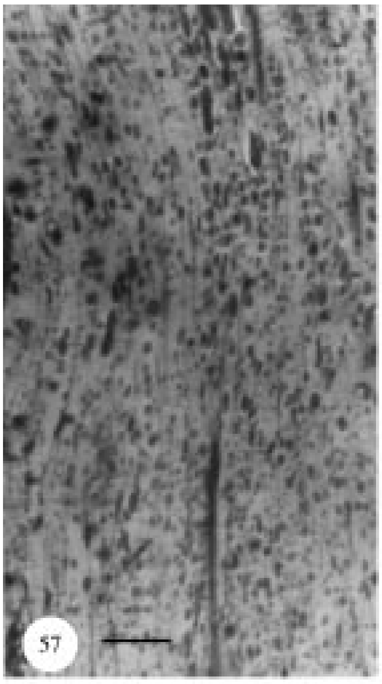
None of these authors describe the radular apparatus of cephalopods however. Here the bolsters comprise either muscles alone (as in octopods and vampyromorphs) or muscles closely associated with a semi-fluid 'rod' (as in decapods and *Nautilus*). The exact nature of the rod remains to be established: the histology reveals that it is definitely not cartilage, although there are sometimes a few cells present in a watery matrix. Dissection of the bolsters, whether of fresh *Loligo* or *Sepia* or of fixed *Nautilus*, shows the rod to contain a gelatinous, not fluid, substance, for when it is cut transversely no liquid runs out. There is certainly no evidence for a fluid under pressure as in the *Lepidopleurus* bolster (see above). The jelly can be extruded from the rod by squeezing it with a suitable instrument but only after the application of moderate force (figure 56).

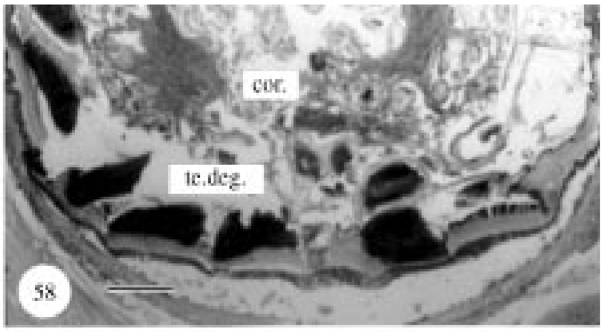
Despite the differences in bolster design in the different cephalopod groups they clearly share a common pattern, one distinct from those of other molluscs, suggesting that it must be of very ancient origin.

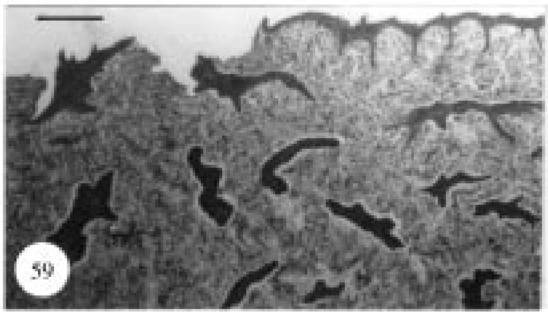
(b) *The function of the bolsters*

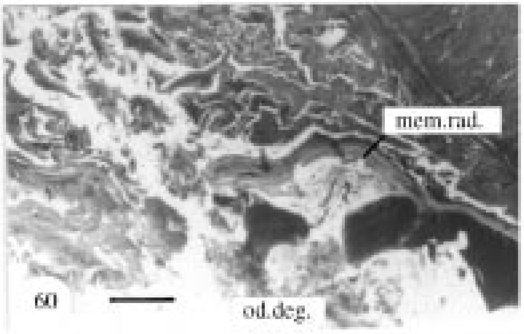
Although bolsters have been described in all molluscan classes with a radula, little attention seems to have been paid to their function. Only Hyman (1967), as far as we can ascertain, has even begun to address this problem. She points out that 'the radula is opened out flat only over the anterior ends of the bolsters', hinting at the thesis developed here that the bolsters function to extend the radula laterally and to raise the radular teeth at the bending plane. This presumably makes them more effective at bringing food on to the pharynx.

Our experiments with isolated bolsters in *Octopus*, *Sepia* and *Loligo* have shown that when the transverse muscles are electrically stimulated the bolsters elongate, the front ends moving freely within the odontophore sac. The bolsters are joined in front by the median transverse muscle, which contracts when the inferior buccal ganglion is stimulated, bringing the two bolsters together. The overall effect of this is to push up the radular ribbon at the bending plane, erecting a row of teeth, as the inner radular ribbon slides over the transverse muscle. At the same time the lateral teeth are raised, extending the ribbon to its maximum extent, and converting what was a U-shaped array of teeth (in the









Figures 57–60. For abbreviations, see Appendix A.

Figure 57. *Nautilus* 467. Section of a bolster, showing blood vessels (dark here, but red after Masson's stain). Scale bar, 40 µm.

Figure 58. *Nautilus* 468. TS extreme anterior part of the radula, showing the broken core and degenerating teeth. Scale bar, 400 µm.

Figure 59. *Nautilus* 467. Front of radular appendage, showing pieces of radular membrane scattered throughout the tissue and along the edge. Scale bar, 400 µm.

Figure 60. *Nautilus* 467. End of radular membrane being pulled into subradular sac, where teeth are associated with degenerating odontoblasts. Scale bar, 40 µm.

radular canal) into a linear one (over the bending plane).

There are important differences between the organization of the bolsters in *Octopus* and in cuttlefish and squid. In *Octopus* the transverse muscle linking the bolsters is small and the bolsters themselves lack a rod. When electrically stimulated in a dissected preparation, the bolsters appear to be capable of much greater independence and manoeuvrability than in either of the other species. It is simple to elicit extension of a single bolster, which erects and extends teeth only on that side of the ribbon. In *Sepia* or *Loligo*, the transverse linking muscle is more robust and each bolster contains a rod. It is this that transfers the force of contraction of the transverse bolster muscles to the radular teeth. Electrical stimulation leads to a curving upwards of the bolsters rather than elongation, but the effect is similar: the radular teeth are erected across the full width of the bending plane. It may be that the curving up of the bolster is brought about by an elongation of the rod but if so the increase in rod length is not obvious and further experiments, with careful measurements, are required. Although direct stimulation of a single bolster in *Loligo* has unilateral effects on the radular teeth, the effect is less marked than in *Octopus*.

It is not clear why decapods but not octopods need a rod in the bolster. The absence of a rod seems to confer greater flexibility on the octopod bolster and the difference may be related to diet. Octopuses are far more likely to take shelled prey than the common squid or cuttlefish and may need a more mobile radula action than those animals. The radula is undoubtedly involved in hole-drilling in mollusc shells (Arnold & Arnold 1969; Wodinsky 1969), although the process is completed by the action of a salivary papilla (Nixon 1979). There is also good evidence that *Octopus vulgaris* is extremely efficient at leaving crab exoskeletons free of tissues, certainly more so than the cuttlefish (Guerra *et al.* 1988). The rod is absent in all the other benthic octopods that we have examined and in the pelagic forms, such as *Argonauta*, whose ancestors were presumably also benthic; it is also absent in *Vampyroteuthis*.

The bolsters of *Nautilus* have a massive rod, the opposite extreme to *Octopus*. In this form the beak is massive and the radula very wide, with 13 elements rather than the nine found in coleoids (Nixon 1995); moulted crustacean carapaces constitute a substantial part of the diet (Saunders & Ward 1987), and large particles of food are bitten and swallowed. The radula seems to be mainly operated by the bolsters so that power rather than refinement may be required and the coarse hydrostatic skeletal system provided by the rod may be adequate for controlling the radula.

Unfortunately, we are still ignorant of the exact way in which cephalopods use the radula in feeding. Indeed even in gastropods, where there is an extensive literature on the radular ribbon and its teeth, far less attention has been paid until recently to the behaviour of the radula during feeding. However the studies of Carriker *et al.* (1974), Morris & Hickman (1981) and Smith (1988, 1990) have shown just how complex this behaviour is. Smith, who studied *Helisoma*, a freshwater pulmonate that feeds on algal scum, has recently made the important discovery that during feeding its radula does not simply move like a chainsaw (Huxley 1853). He showed that the radula and underlying cartilage move independently but concurrently, with the result that the two separate functions of a radula (food transport and what he terms 'excavation') are both optimized.

No such detailed study of radula behaviour during feeding has been attempted in a cephalopod and it is not easy to envisage how this could be done in these carnivorous animals. Future workers interested in this problem might consider experimenting with *Nautilus*, which could presumably be induced to scrape suitable nutritive substances from a glass plate that would allow the necessary filming (Smith 1988).

In summary, our thesis is that the bolsters perform the critical function of making a linear 'rake' of the radula at the bending plane, ensuring that it has a full transverse row of erect teeth. Other muscles produce the back-and-forth movement of the radula but such a 'rake' would be more effective at food transport and 'excavation'. To what extent this is true of other mollusc radulae remains to be investigated.

(c) *The mechanism of action of the bolsters: muscular hydrostats*

In *Octopus* we have shown that each bolster can be made to elongate, by electrically stimulating either the inferior buccal ganglion or the bolster itself. The bolster comprises mostly transverse muscle fibres with some longitudinal fibres and is contained within a connective tissue sheath. Its volume is therefore fixed, so that contraction of the transverse fibres inevitably leads to its elongation; contraction of the longitudinal fibres will restore the bolster to its original length.

The bolsters are thus a beautiful example of what Kier & Smith (1985) have termed a 'muscular hydrostat' (see also Kier 1988), a type of support system common in cephalopods (Kier 1982, 1989). They comprise two blocks of muscle fibres lying orthogonal to each other in a constant volume system; contraction of one set of muscles elongates the antagonistic set. Muscular hydrostats differ from classical hydrostatic skeletons only in that the muscles act directly on each other: there is no fluid-filled central cavity.

The cylindrical form of the bolster and its fairly high initial length–width ratio means that a small decrease in diameter will lead to a large increase in length (Kier 1988). This is ideally suited to its function of elevating the radular ribbon over the bending plane.

The way the bolsters with a rod function is not yet clear however (see above). In *Loligo*, *Sepia* and *Nautilus*, the rod is intimately associated with the bolster muscles, lying within a tough connective tissue sheath (figure 55). One hypothesis is that contraction of the powerful transverse muscles transmits a force to the semi-fluid cylindrical rod along its entire length, causing it to elongate and push up the radular ribbon. This assumes that the rod has a constant volume (which seems reasonable) and that the jelly within it is sufficiently fluid to transmit forces readily (which is difficult to reconcile with the very viscous nature of the jelly in fresh cuttlefish or squid). Further speculation seems pointless without more data and experiments, but if a bolster with rod does indeed function like this it is behaving more like a classical hydrostatic skeletal system, its muscles acting on a fluid-filled compartment.

The idea that the radula movement of cephalopods involves a hydrostatic system need not surprise us given that such a situation occurs in gastropods and, probably, in *Neopilina*. In *Monodonta*, the 'opening of the radula' during feeding depends on three separate factors, one of which is 'the hydrostatic pressure of the blood within the haemocoelic spaces of the odontophore creating turgor pressure' (Fretter & Graham 1962, 1994). Similarly, in *Helisoma*, changes in blood volume in the cephalic haemocoel have been recognized as important during some stages of the radula feeding cycle (Smith 1990). In *Neopilina*, Lemche & Wingstrand (1959) suggest that the radular vesicles 'must serve as a kind of skeleton . . . Since [they] are stiff and firmly connected with the radula cartilage, their movements will be transferred immediately to the transverse bar, thus assisting in the manipulation of the radula'.

(d) *The development of the radula and its degradation: the radular organs*

As we have noted, serial sections of the radula provide an excellent opportunity of studying the ontogeny of the radula in the individual. There is a moderately large literature on radula development in molluscs and there has been much controversy about how the odontoblasts secrete the teeth (see Fretter & Graham 1962 1994; Runham, 1963; Mischor & Märkel 1984; Mackenstedt & Märkel 1987). Although radula development has been studied in a few cephalopods (see Rössler 1885; Rottmann 1901; Gabe & Prenant 1952; Fuchs 1973), there have been no experimental studies using autoradiography such as those carried out on gastropods by Märkel and his associates.

Nevertheless, studying sections of buccal masses from different species suggests that the cephalopod radula develops like that of other molluscs. Teeth are formed in the radular sac from odontoblasts with long microvilli, the bases being produced by one epithelium and the cusps by another. As the teeth move forward they stain differently with trichrome stains and, as they approach the bending plane they become freed of any remaining odontoblasts to become fully functional.

As in all molluscs, the teeth wear as a result of use and as they approach the very front of the ribbon, below the bending plane, they must be broken down or resorbed in some way. In all cephalopods this occurs in the subradular organ, in the subradular sac, which contains modified odontoblasts (the odontoclasts) that somehow dissolve the teeth and membranes. In *Octopus* (and other benthic octopods), there is also a supraradular organ in adult animals, at the anterior of the hyaline strand, that is also involved in the removal of the radular teeth and membranes. The presence of this second region for degrading the radula may be associated with diet: mollusc shells and crustacean carapaces presumably cause much wear of the radular teeth. It is surely significant that pelagic octopods, which feed on small planktonic creatures (Nixon 1987; Nixon & Young 1999), lack a supraradular organ, as do decapods, whose diet is also much softer. Whether or not there is a supraradular organ in vampyromorphs remains to be established.

In *Nautilus* there is a very well-developed subradular organ and the radular teeth and membranes are degraded and dissolved in the four-pocketed subradular sac, whose size must reflect the magnitude of task of breaking down the large radula of this predominantly carapace feeder (Saunders & Ward 1987). However, our understanding of the fate of the radula in this form is complicated by the existence of the enigmatic radular appendage.

(e) *The radular appendage of* Nautilus

Although the radular apparatus of *Nautilus* is generally similar to that of coleoids, there are two major differences. The beaks are unusually massive, with calcareous tips, and there is an organ on the floor of the pharynx and extending up its sides that is absent from all other cephalopods. This structure corresponds to those labelled by Griffin (1900) as 'tongue' (for the median part) and 'salivary process' (for the lateral parts). Griffin, whose description of his dissection is excellent, but who did not cut sections of his material, found the nature of the radular apparatus of *Nautilus* 'problematical, if we do not use a still stronger term'. Having cut sections and studied them we fully concur with this view.

Histologically the median and lateral parts clearly constitute a single functional structure, although the lateral parts are partly secretory as noted by Griffin. It is possible, incidentally, that the presence of such secretory organs in *Nautilus* may be related to the absence of chitin in the oesophagus in this genus (Fukuda 1980). The nature of the median 'tongue' is especially difficult to interpret. It is not secretory and possibly plays a part in the breakdown of the radula: in our sections there are what appear to be odontoblasts as well as pieces of teeth. Another possibility is that it acts as some kind of toothbrush to keep clean radular teeth that, because of diet, would otherwise quickly become occluded and blunted. Only further investigations can resolve this.

(f) *The radular apparatus of decapods, octopods and vampyromorphs*

We have studied serial sections of the buccal masses of many other genera of coleoids and can make a few generalizations about the cephalopod radular apparatus.

It is at once apparent that the nautiloid condition is quite different from the coleoid; not only are there 13 teeth rather than nine in each row but there is the curious radular appendage, at least part of which is secretory but whose function remains obscure.

Among decapods the bolsters of sepioids, sepiolids and loliginids are very similar as are those of cranchiids, such as *Teuthowenia*; like *Nautilus* they all have a rod, although some details of its histology differ, and this is presumably the primitive condition in cephalopods. In *Mastigoteuthis*, the bolsters are large and are composed of transverse muscles, with many spaces, giving it a reticulate appearance (Dilly *et al.* 1977). In octopods, the bolsters lack a rod, even the secondarily pelagic forms, such as *Argonauta*; nor is there a rod in *Vampyroteuthis*. This relic genus has a number of octopod features and the lack of a rod in the bolster is another indication that the vampyromorphs may have diverged from the octopods after they had split off from decapods (Young 1977).

Another interesting feature of *Vampyroteuthis* is the presence of a supraradular organ. This is an organ absent from decapods but present in many benthic though not pelagic octopods. The suggestion has been made that this may be related to diet, yet *Vampyroteuthis* is not known to feed on shelled molluscs.

A paper giving some of the facts of the present paper was published by J.Z.Y. in the now defunct *Journal of Cephalopod Biology* **2**, 65–93, which had only an extremely limited circulation. This is a considerably enlarged version of the observations reported there, together with further observations and experiments. We are most grateful to those who supplied the fixed material upon which this study has been based, especially J. M. Arnold, B. U. Budelmann and M. R. Clarke. We are also indebted to Miss P. R. Stephens for her skill and patience in preparing long series of sections; and D. Hollingworth for his help with the photography. The stimulation experiments were carried out at the Naples Zoological Station and at the MBA Laboratory, Plymouth, and we thank the Directors of both those institutes for their hospitality. J.B.M. thanks Dr M. Nixon and an unknown referee for their many helpful comments on an earlier version of the manuscript. J.Z.Y. was supported in part by a grant from the Wellcome Trust and was most grateful to the Department of Experimental Psychology, Oxford, for accommodation.

APPENDIX A. ABBREVIATIONS

app.	radular appendage
att.	attachment of dorsal retractor muscle
be.u.	upper beak
bend.	bending plane
bol.	bolster
bol.long.	longitudinal fibres of bolster
bol.t.	transverse fibres of bolster
cart.	dorsal cartilage
cor.	core of radula
ep.	epithelial cells
gan.buc.i.	inferior buccal ganglion
hy. sh.	hyaline shield
hy.st.	hyaline strand
m.app.	muscle joining appendage to radula
m.c.	muscular core
m.med.bol.	median muscle linking bolsters
m.r.protr.	radular protractor muscle
m.r.retr.d.	dorsal radular retractor muscle

m.r.retr.v.	ventral radular retractor muscle
mem.rad.	radular membrane
n.ce.	nerve cell in plexus
n.rec.	nerve to receptor organ
od.	odontoblasts
od.deg.	degenerating odontoblasts
od.f.	fibres of odontoblasts
od.n.	normal odontoblasts
od.p.	pockets of odontophore
odph.	odontophore sac
odph.in.	inner layer of odontophore sac
odph.out.	outer layer of odontophore sac
oes.	oesophagus
pa.buc.l.	lateral buccal palp
phar.	pharynx
rac.	rhachidian tooth
rad.	radular ribbon
rod	radular support rod
rod.mem	membrane of rod
sac.hy.	hyaline sac
sac.sub.	subradular sac
sal.duc.	salivary duct
sal.p.	salivary papilla
sh.	sheath of rod
sub.rad.or.	subradular organ
sup.rad.or.	supraradular organ
te.	radular teeth/tooth
te.degen.	degenerating radular teeth

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