Bollettino Malacologico, Supplemento 4, Roma, Dicembre 2002, 51-78 - Società Italiana di Malacologia

Foregut ontogeny of the Neogastropoda: comparison of development in *Nucella lapillus* and *Conus anemone*

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KEY WORDS: Gastropoda, Neogastropoda, Muricoidea, Conoidea, Development, Ontogeny.

ABSTRACT Characters of the foregut organs of neogastropods have been widely used in phylogenetic analyses. These include, especially, the two pairs of salivary glands, the radula, the valve and gland of Leiblein in muricids and the venom apparatus of conoideans. Assumptions and hypotheses concerning the homologies of these organs both within the Neogastropoda and with other gastropods can be tested by ontogenetic studies. Developmental stages of *Nucella lapillus* (Muricoidea) and *Conus anemone* (Conoidea) were studied through reconstruction of 1µm resin-embedded sections, light and scanning electron microscopy.

In both *Nucella* and *Conus* the buccal mass is derived from a ventral evagination of the oesophagus. An anterior portion forms the sub-lingual pouch in *Nucella* and the radular caecum in *Conus*, whilst the posterior portion forms the radular sac. The acinous salivary glands are derived as lateral evaginations of the wall of the buccal cavity. This region moves dorsally in *Nucella* and the salivary gland ducts grow posteriorly attached to the anterior oesophageal wall. In *Conus*, the buccal cavity is separated from the oesophagus by the buccal sac. The acinous salivary glands initially grow laterally from its walls and then dorsally as the secretory regions expand. They do not become associated with the oesophageal walls. The accessory salivary glands in both species arise as paired evaginations of the ventral lip, the ducts grow posteriorly and terminate in secretory areas. During the development of *Nucella* the ducts fuse, but terminate in paired, secretory regions. In *Conus*, the paired glands fuse completely during development, leaving a single tubular gland. The valve of Leiblein in *Nucella* is derived from the dorsal folds and dorsal wall of the mid-oesophagus. This region differentiates prior to proboscis elongation and passes through the circum-oesophageal nerve ring (together with the acinous salivary glands and radular sac) during development. The glandular folds (=glande framboisée) and rudimentary gland of Leiblein remain posterior to the nerve ring. The glandular folds are derived from the dorsal folds and the gland of Leiblein from the ventral strip which is rotated into a dorsal position by torsion. A finger-like evagination is formed which expands to form the gland and its duct.

Tracing the complete development of the venom gland in *Conus* was not possible, but early stages suggest a secretory region develops from the ventral strip and dorsal folds. In *Nucella* the same regions form the glandular oesophageal folds and the gland of Leiblein and these are believed to be the homologue of the venom gland and muscular bulb of the Conoidea. Both species exhibit striking developmental similarities. Features which are markedly different in their definitive state have identical ontogenetic origins and heterochrony of foregut development may explain the major differences observed in adult morphology.

RIASSUNTO I caratteri dell'apparato alimentare anteriore dei neogasteropodi sono stati ampiamente usati in analisi filogenetiche. Questi comprendono in particolare: le due paia di ghiandole salivari, la radula, la ghiandola e la valvola di Leiblein nei muricidi e l'apparato velenifero dei conoidei. Ipotesi e assunzioni sull'omologia di questi organi sia tra i Neogastropoda sia con altri gasteropodi possono essere verificate con studi ontogenetici.

Stadi di sviluppo in *Nucella lapillus* (Muricoidea) e *Conus anemone* (Conoidea) sono stati studiati con la ricostruzione di sezioni seriali (1µm - resin-embedded), microscopia ottica ed elettronica a scansione.

Sia in *Nucella* sia in *Conus* la massa boccale deriva da un'evaginazione ventrale dell'esofago. Una porzione anteriore forma la sacca sottolinguale in *Nucella* e il ceco radulare in *Conus*, mentre la porzione posteriore forma il sacco radulare. Le ghiandole salivari acinose, derivano come evaginazioni laterali della parete della cavità boccale. Questa regione si sposta dorsalmente in *Nucella* ed i dotti delle ghiandole salivari si accrescono posteriormente attaccati alla parete esofagea anteriore. In *Conus*, la cavità boccale è separata dall'esofago per mezzo del sacco boccale. Le ghiandole salivari acinose inizialmente si accrescono lateralmente dalla parete, quindi dorsalmente quando la regione secretoria si espande. I questo caso non divengono associate alla parete esofagea. Le ghiandole salivarie accessorie in entrambe le specie appaiono come evaginazioni appaiate del labbro ventrale, i dotti si accrescono posteriormente e terminano in aree secretorie. Durante lo sviluppo di *Nucella* i dotti si fondono, ma terminano in regioni secretorie appaiate. In *Conus*, le ghiandole appaiate si fondono completamente durante lo sviluppo, lasciando una singola ghiandola tubulare. La valvola di Leiblein in *Nucella* deriva dalle pieghe dorsali e dalla parete dorsale dell'esofago medio. Questa regione si differenzia prima dell'allungamento della proboscide e durante lo sviluppo passa attraverso l'anello nervoso circum-esofageo (assieme alle ghiandole acinose salivari e al sacco radulare). Le pieghe ghiandolari (=glande framboisée) e la rudimentale ghiandola di Leiblein rimangono posteriori all'anello nervoso. Le pieghe ghiandolari derivano dalle pieghe dorsali e la ghiandola di Leiblein dalla striscia ventrale che è ruotata per torsione in posizione dorsale. Si forma un'evaginazione digitiforme, che si espande a formare la ghiandola ed il suo dotto.

Tracciare il completo sviluppo della ghiandola del veleno in *Conus* non è stato possibile, ma gli stadi precoci suggeriscono che una regione secretoria si sviluppi dalla striscia ventrale e dalle pieghe dorsali. In *Nucella* le stesse regioni formano le pieghe ghiandolare esofagee e la ghiandola di Leiblein e queste sono ritenute essere omologhe alla ghiandola del veleno e al bulbo muscolare dei Conoidea. Entrambe le specie studiate mostrano rimarchevoli similarità nello sviluppo. Caratteristiche che sono marcatamente differenti nel loro stato definitivo hanno identiche origini ontogenetiche e fenomeni di eterocronia nello sviluppo dell'apparato alimentare anteriore possono spiegare le maggiori differenze nella morfologia adulta.

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INTRODUCTION

The Neogastropoda are generally regarded as monophyletic (PONDER 1973; TAYLOR & MORRIS 1988; KANTOR 1996), but their relationships to other gastropods and relationships of the family groups within the order are highly uncertain (PONDER & LINDBERG 1997).

The most important characters for phylogenetic studies of neogastropods are located in the alimentary system, particularly the foregut. PONDER (1973), defined four synapomorphies — two pairs of histologically distinct salivary glands located in front of the nerve ring, the mid-oesophageal valve of Leiblein, the mid-oesophageal gland and an anal gland - which he used to

divide the Neogastropoda into three superfamilies: the Muricoidea, Conoidea and Cancellarioidea. Recent studies have revealed a greater disparity in foregut anatomy (KANTOR 1991; TAYLOR, KANTOR & SYSOEV 1993) and KANTOR (1996) divided the Order into five suborders, three of these equivalent to PONDER's (1973) superfamilies, with the addition of the Olivelloidei and Pseudolivoidei.

The Neogastropoda have proven particularly intractable to phylogenetic analysis by either morphological or molecular methods. A recent cladistic analysis by PONDER and LINDBERG (1997) using only three neogastropod taxa, placed the Buccinidae as basal to the Muricoidea and Conoidea, which contradicts KANTOR (1996; this volume) who places Conoidea as basal to the Neogastropoda. HARASEWYCH, ADAMKEWICZ, BLAKE, SAUDECK, SPRIGGS, and BULT (1997) found that 18S rDNA sequences of taxa from about half the neogastropod families gave little resolution and whilst cytochrome C oxidase 1 sequence data produced resolved trees, these were characterised by low character indices and a high degree of homoplasy. Results so far however, reveal a lack of congruence with the morphological analyses.

One limitation for phylogenetic analysis of neogastropods is that little is known of the derivation and homologies of some foregut structures as related to other gastropods. Heterochrony was recently stressed as an important influence on the evolution of morphological trends in gastropods (PONDER and LINDBERG 1997) and ontogenetic studies are crucial for testing these ideas.

The present study is an attempt to bring together the results of work on two very different neogastropods; one, a muricoidean, relatively conservative in its foregut arrangement (*Nucella lapillus*), corresponding closely to the archetypal neogastropod form described by PONDER (1973), and the other a highly derived conoidean neogastropod with a foregut which exhibits extensive modifications from the archetypal state (*Conus anemone*). The aim is to determine whether common patterns exist in the development of key organ systems, and how the ontogeny of these organs produces the very different definitive morphologies found in these two species.

Nucella lapillus (Linnaeus, 1758), and *Conus anemone* Lamarck, 1810 are carnivorous species; *N. lapillus* is common on the Atlantic coasts of Europe and North America where it preys on sedentary bivalves and barnacles, whilst *C. anemone* lives on the intertidal reef platforms of the Indian Ocean shorelines of Western and South Western Australia (see RÖCKEL, KORN and KOHN, 1995 for details) and feeds on polychaetes.

The organogenesis of *N. lapillus* has been described by several authors (PORTMANN, 1925; PORTMANN and SANDMEIER, 1965), most notably STÖCKMANN-BOSBACH (1988, 1991) and STÖCKMANN-BOSBACH and FIORONI (1988) who investigated the pretorsional developmental stages. Post-torsional development, including organogenesis of the foregut, has been described by BALL (1994), BALL, TAYLOR and ANDREWS (1997) and BALL, ANDREWS and TAYLOR (1997).

There are only fragmentary accounts of the development of any members of the Conoidea. FIORONI (1965) described embryonic development of *Philbertia purpurea* (Montagu) (Conidae: Raphitominae) and there is an unpublished account of the development of *Conus mediterraneus* Bruguières by FRANC (1943) which includes some description of the development of the foregut and venom gland. Both accounts are, however, only sparsely illustrated. The larval development of *C. anemone* has also been studied using scanning electron microscopy to describe some of the external developmental features and to compare them with *N. lapillus* and *Conus dorreensis* Péron (BALL, 1999). The present paper expands on the latter work by investigating the internal anatomy through light microscopy of serial sections and computer-aided reconstructions.

METHODS

Collection of embryos

Nucella lapillus egg capsules were collected at Hayle Bay (Cornwall, U.K.). Identification was based on COSTELLO, DAVIDSON, EGGERS, FOX and HENLEY (1957) and on the presence of breeding females with the egg capsules.

Conus anemone egg capsules and adults were collected on Rottnest Island (near Perth, Western Australia) and identification was based on KOHN (1993) and SMITH, BLACK and SHEPHERD (1989).

After removal from the egg capsules using iridectomy scissors and pipettes, the embryos were examined to determine the approximate stage of development, narcotised and then fixed.

Specimen preparation

N. lapillus embryos were relaxed using 1% propylene phenoxytol in seawater. For *C. anemone* embryos, propylene phenoxytol was added in stages until relaxation was achieved. The amounts used varied with the stage of development. After relaxation, embryos were fixed using buffered glutaraldehyde and post-fixed for 1 hour in 1% osmium tetroxide.

Embryos were decalcified using saturated aqueous EDTA (disodium ethylene diamine tetra-acetic acid) to remove the larval shells and then dehydrated through ascending graded ethanol (acetone for *C. anemone*) prior to final preparation for electron microscopy or light microscopy.

Specimens for light microscopy (LM) were embedded in medium grade TAAB resin, re-orientated to give transverse sections and sectioned at 1µm intervals using an ultramicrotome. Slides were stained with toluidine blue in borax.

3D reconstruction

Transverse orientations were found to give the best results and serial sections were drawn using a *camera lucida*, and transferred to Jandell Scientific's PC3D computer program. This package was used to reconstruct the lateral viewpoints which were later redrawn by hand.

Scanning Electron Microscopy (SEM)

SEM specimens were critical point dried after dehydration and sputter coated with gold palladium. Philips XL30 FEG, Hitachi S800 and S2500 SEMs were used to examine the specimens.

Additional LM of adult *C. anemone* was carried out using 8µm wax-embedded serial sections stained with Haematoxylin and Eosin. Throughout the results, observations on adult anatomy are a combination of my own and Yuri Kantor's notes (Kantor, personal communication).

RESULTS

The anatomy of the adult *Conus anemone* is described and its development has been divided into 4 post-torsional stages (Stages I-III) summarised in two normal tables (Tables 1A and 1B).

Adult *Nucella lapillus* anatomy is not detailed here, since it has already been described by GRAHAM (1941) and MARTOJA (1971). Development has been described by STÖCKMANN-BOSBACH (1988; 1991); BALL (1994) and BALL *et al.* (1997a; 1997b). 11 developmental stages were recognised; 5 pre-torsional, 6 post-torsional. The post-torsional stages have been summarised here and compared to *C. anemone* in Table 2.

The developmental period described for *C. anemone* corresponds approximately to Stages 6-8 of *N. lapillus*. A different numbering system has been used for *C. anemone* to avoid confusion. Stages IA and IB can be regarded as early and late phases of Stage I, the differences are subtle and are based on observations of numerous specimens. There are however clear differences between Stages I and II and II and III.

Conus anemone

Adult proboscis

The proboscis is long and thin-walled with a basal rhynchodeal septum (Figure 1). The walls are formed from a layer of radial

Table 1A. Normal table for the development of *Conus anemone*.

External morphology

Stage / Feature	Stage IA	Stage IB	Stage II	Stage III
Protoconch	Small, 1 whorl, symmetrical aperture	Small, 1 whorl, symmetrical aperture	1_ whorls, asymmetrical aperture	1_ whorls, asymmetrical aperture
Velum	Bilobate, blunt, rounded lobes	Bilobate, blunt, rounded lobes	Bilobate, deeply notched	Collapsed against side of head
Propodium	Tiny/absent	Poorly-developed, finely ciliated	Well-developed, finely ciliated	Well-developed, finely ciliated
Metapodium	Well-developed, covered in ciliated papillae	Well-developed, covered in ciliated papillae	Elongate, waisted and pointed at posterior end, finely ciliated	Elongate, waisted and pointed at posterior end, finely ciliated
Operculum	Small, rounded	Small, rounded	Lens-shaped, elongate	Lens-shaped, elongate
Siphonal notch	Absent	Absent	Present	Present
Cephalocyst	Large, 2 cell types	Large, 2 cell types	Large, 2 cell types	Large, 2 cell types
Tentacles	Short, symmetrical in length, tipped with elongate cilia	Equal in length, longer than stage IA, tipped with elongate cilia	Elongate, narrow	Elongate, narrow
Tentacle bases	Small	Slightly enlarged	Bulbous, enlarged	Bulbous, enlarged
Anterior pedal mucus gland	Absent	Absent	Present	Present
Appearance of mouth	Narrow slit	Dorsal lips present, slightly enlarged	Dorsal lips enlarged to form buccal tube	Dorsal lips enlarged to form short proboscis
Proboscis sheath present?	No	No	Slight overgrowth dorsally	Dorsal overgrowth, ventral invagination
Behavioural development	Veliger	Veliger	Pediveliger	Hatchling

muscle fibres overlying a layer of longitudinal fibres. The proboscis retractor muscles occupy almost the whole volume of the proboscis. A snout gland is present on the right side of the rhynchodaeum in the form of a rounded sac filled with tall columnar cells which opens to the proboscis base via a wide duct. The rhynchodaeum is lined with a tall glandular epithelium.

Proboscis development

Proboscis development was not complete by the time of hatching and consequently could not be traced fully. Observations using SEM (Table 1A) showed that the initial elongation is due to the enlargement of the buccal lips to form a short snout (Figure 2A-C) (Stages I and II). This is followed by anterior growth of the body wall combined with dorsal and ventral invaginations to form the beginnings of a rhynchocoel (Figure 2D-E) (Stages II and III). The rhynchocoelic invaginations appear to be paired dorsally when they first appear and then fuse mid-dorsally to form a single curved dorsal invagination (Figure 3). Ventrally the invaginations are not so clearly defined but they are present in the later developmental stages (Stages II and III). The proboscis sheath continues to grow anteriorly as the tentacle bases fuse and begin to overgrow the proboscis base (Stage III). In sections (Table 1B), a fold near the base of the proboscis begins to develop and this is consistent with the rhynchodeal septum

Table 1B. Normal table for the development of *Conus anemone*.

Internal morphology

Stage/Feature	Stage IA	Stage IB	Stage II	Stage III
Position of buccal mass relative to cerebral commissure	Buccal mass posterior to cerebral commissure	Buccal mass posterior to cerebral commissure	Buccal mass level with cerebral commissure	Buccal mass anterior to cerebral commissure
Radular sac orientation relative to oesophagus	Radular sac short, lies ventral and parallel to oesophagus	Lies parallel to oesophagus, but alongside	Radular sac arches over cerebral commissure and tip lies anterior to cerebral ganglia	Radular sac penetrates nerve ring, lies approximately parallel with oesophagus
Radular teeth present?	Absent	Absent	Present	Present
Characteristics of radular sac	Flattened, posteriorly directed tube	Odontoblast nest appears	Odontoblast nest divided into two lateral regions by central ridge	Odontoblast nest divided into two lateral regions by central ridge, radular caecum present
Position of acinous salivary glands	Acinous salivary glands tubular, small and posteriorly directed	Start to point in opposite directions, still tubular, but lead to larger secretory areas	Point in opposite directions, left gland is anterior to nerve ring right gland penetrates it	Salivary glands prominent, tubular and anterior to nerve ring, ducts directed dorsally
Appearance of oesophagus posterior to buccal mass	Oesophagus short, before leading to stomach. Ventral and dorsal regions different	Oesophagus short, before leading to stomach. Ventral and dorsal regions different	Elongated, ventral region expanded, greenish granules present in cells	Elongated, thrown into longitudinal folds, venom gland separation begins. ventral part greatly expanded into W shaped lumen secretory granules shed into lumen
Appearance of accessory salivary glands	Accessory salivary glands short paired ducts	Difficult to determine if 2 ducts or one	Only one gland present, lumen is empty, no secretory cells	Lumen empty, no secretory granules, only one gland
Proboscis sheath present in sections?	No	Dorsal portion present	Dorsal and ventral components present	Dorsal and ventral components present
Proboscis present in sections?	No	No	Snout developing, with shallow sheath	Short proboscis present with dorsal sheath and ventral invagination

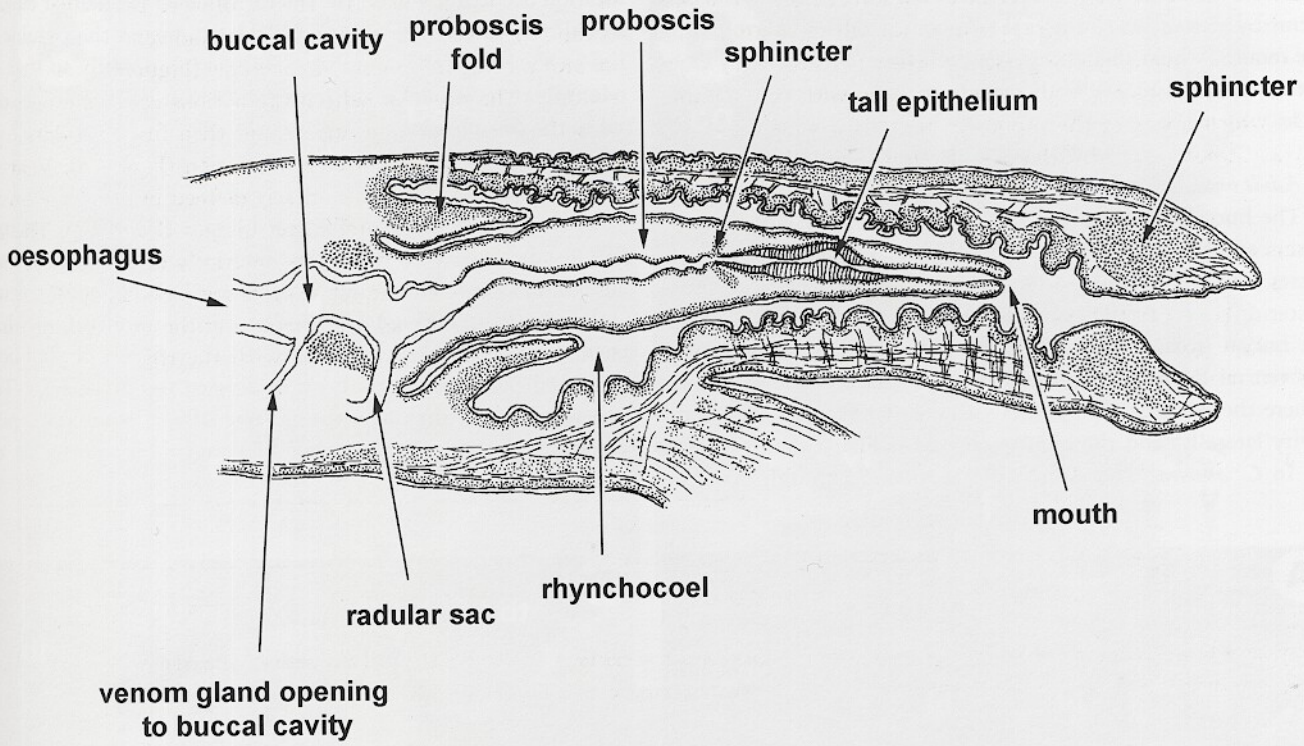


Figure 1. Longitudinal section through the proboscis and buccal mass of *Conus anemone*.

Table 2. Combined normal table comparing the development of *Nucella lapillus* with that of *Conus anemone*.

Nucella lapillus developmental stage	*Conus anemone* developmental stage
Stage 6 Post-torsional veliger	Stages IA and IB
Visceral mass rounded	Visceral mass rounded
Foot much smaller than visceral mass	Foot smaller than visceral mass
Shell covers visceral mass	Shell covers visceral mass
Tentacle rudiments appear	Tentacles present
Velar lobes simple and rounded	Velar lobes present, bilobed
Velum large relative to visceral mass	Velum large relative to visceral mass
Post-torsional	Post-torsional
Stage 7 Early pediveliger (veliconcha)	Stage II
Visceral mass begins to coil	Foot larger than visceral mass
Foot larger than visceral mass	Foot functional, pediveliger
Foot functional, pediveliger	Enlarged propodium
Enlarged propodium	Velum still relatively large
Velum much smaller than visceral mass	
Pallial organs begin to develop	Siphonal notch present
Siphonal notch present	First stages of proboscis development
Early stages of proboscis development	
Stage 8 First crawling stage	Stage III
Shell calcified	Velar lobes partially or wholly resorbed
Velar lobes resorbed	Early proboscis development
Proboscis develops	

found in the adult (compare Figs. 1 and 3). Thus the proboscis forms by elongation of the oral tube and body wall surrounding the mouth, whilst the proboscis sheath appears to grow by elongation of the body wall both anterior to and posterior to the tentacles.

Adult buccal mass

The buccal mass is muscular and lies at the base of the proboscis anterior to the nerve ring (Figure 1). The buccal tube passes from the mouth to the buccal mass and then continues posteriorly into the oesophagus whilst the venom gland enters the buccal mass ventrally on the right side. The buccal cavity lies ventral to the oesophagus and is composed of the buccal sac (where the ducts of the acinous salivary glands enter the buccal cavity laterally) and the radular sac and radular caecum (Figure 4). In *C. anemone*, the radular sac is rotated through 90° (the rotation occurring within the buccal sac) and the radular caecum lies almost directly below the buccal sac, whilst the radular sac lies to the left of the oesophagus and arches dorsally so that the odontoblast nest lies on the left extremity of the haemocoel dorsal to the oesophagus.

Buccal mass development

In the earliest embryos examined (Stage IA), the buccal mass lies just behind the level of the statocysts, posterior to the circum-oesophageal nerve ring (composed of the cerebral, pleural and pedal ganglia)(Figure 5A). The buccal commissure, which passes between the radular sac and the ventral part of the buccal mass and oesophagus, is also posterior to the nerve ring. This *embryological* condition is the reverse of adult neogastropods where the buccal mass and buccal ganglia lie anterior to the nerve ring (Ponder, 1973).

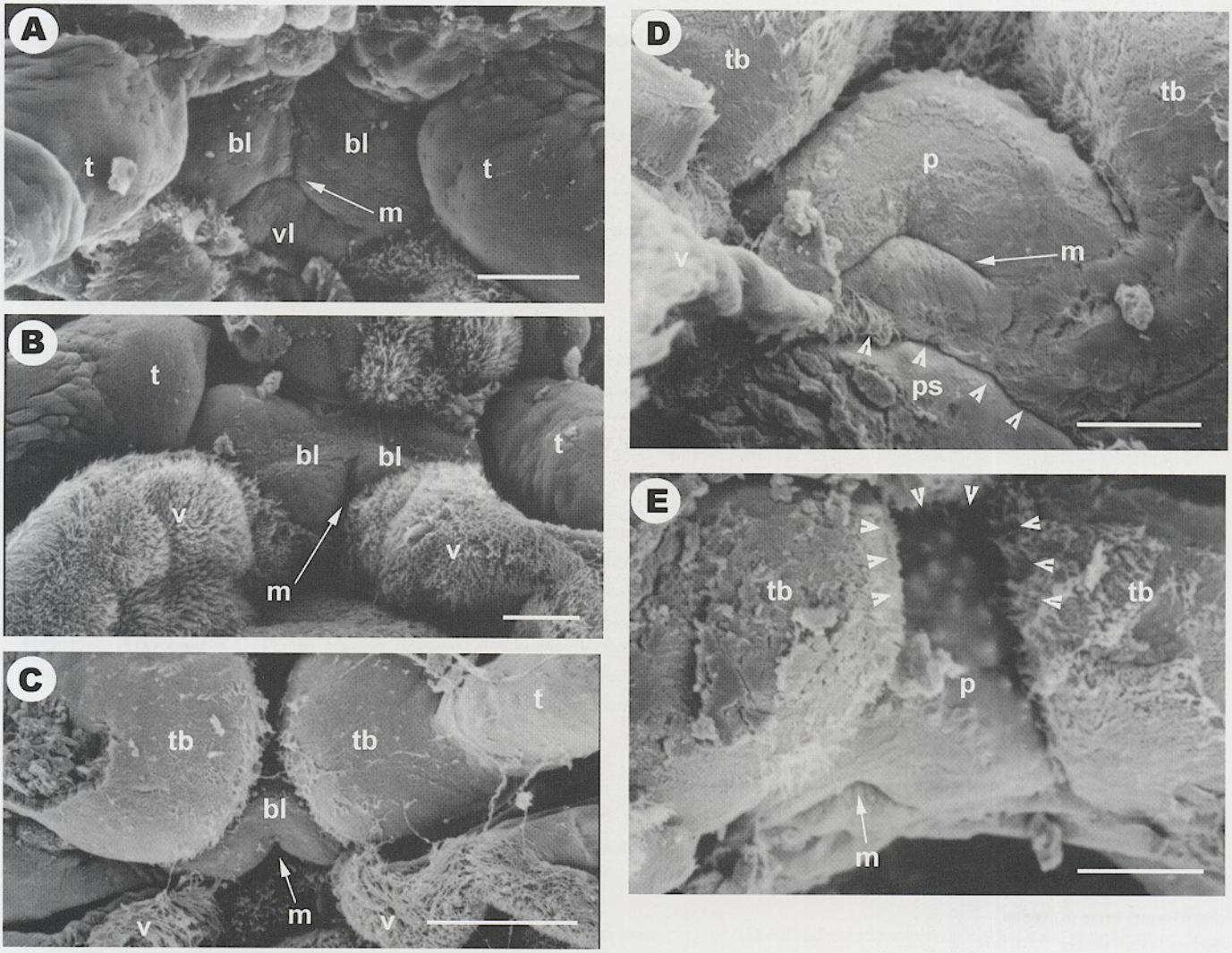


Figure 2. Development of the proboscis in *Conus anemone* observed using SEM. **A.** Stage IA. Buccal and ventral lips discernible, but not enlarged. Scale bar 25µm. **B.** Stage IB. Enlargement of buccal lips. Scale bar 30µm. **C.** Stage II. Buccal lips form distinct fold. Tentacle bases overgrow developing snout. Scale bar 50µm. **D.** Stage III. Oral tube and buccal lips form proboscis rudiment. Tentacle bases cover lateral and dorsal surfaces of proboscis. Lateral proboscis sheath absent due to presence of velar lobes. Ventral invagination present below mouth (arrow heads). Scale bar 20µm. **E.** Stage III, dorsal view. Tentacle bases overgrow proboscis. Growth direction indicated by arrowheads. Scale bar 20µm. (Key to lettering: bl-buccal lips; m-mouth; p-proboscis rudiment; ps-proboscis sheath; t-tentacle; tb-tentacle bases; v-velum; vl-ventral lip).

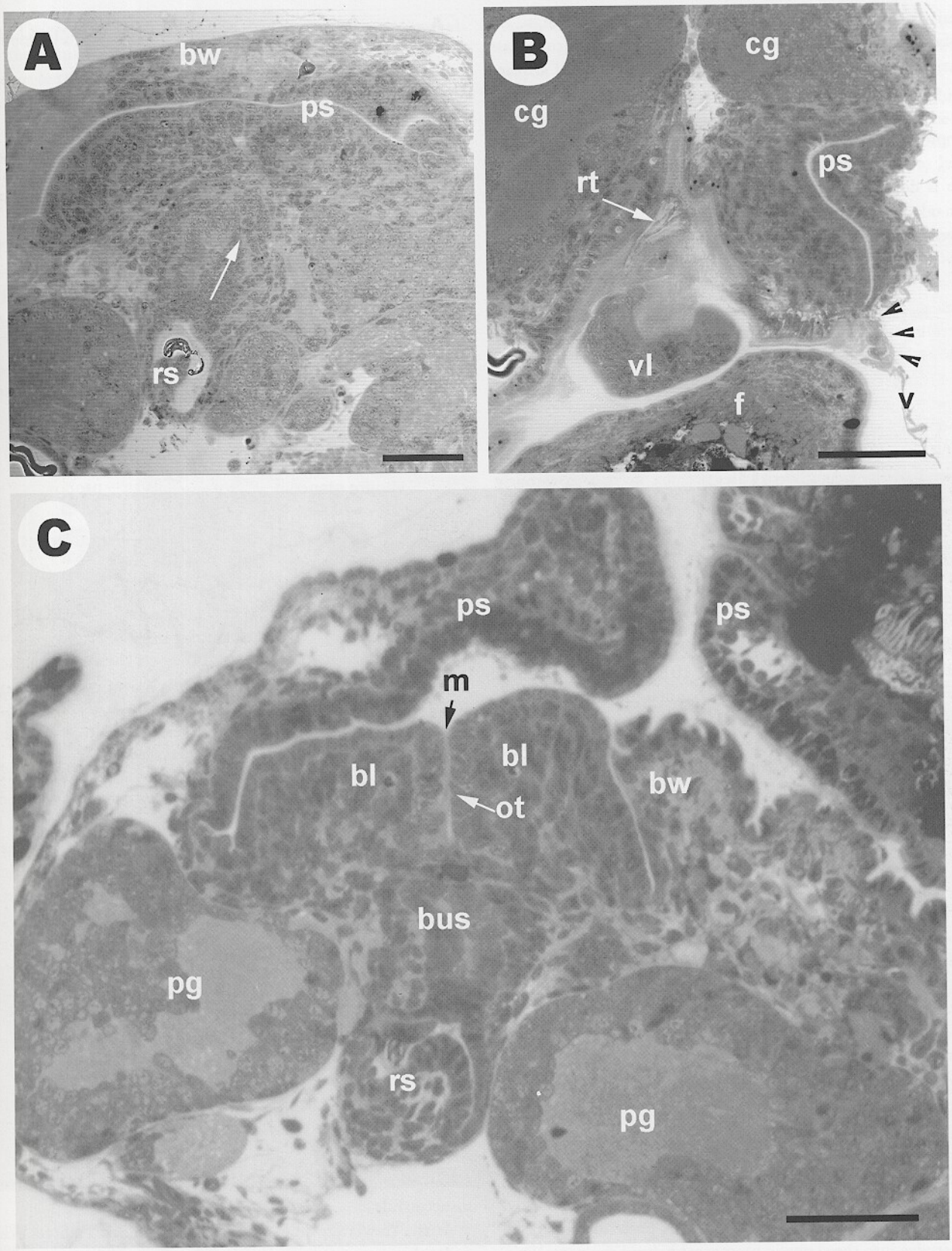


Figure 3. Development of the proboscis and proboscis sheath in *Conus anemone* observed using light microscopy. **A.** Stage II, oblique-transverse section through head. Arrow indicates path of oesophagus towards mouth. Scale bar 50µm. **B.** Stage III, transverse section level with mouth. Arrowheads mark point where invaginations interrupted by velum. Note radular tooth held at ventral lip. Scale bar 50µm. **C.** Stage III, horizontal longitudinal section. Proboscis viewed from above. Proboscis sheath covers developing proboscis. Scale bar 50µm. (Key to lettering: bl-buccal lip; bus-buccal sac; bw-body wall; cg-cerebral ganglion; f-foot; m-mouth; ot-oral tube; pg-pedal ganglion; ps-proboscis sheath; rs-radular sac; rt-radular tooth; v-velum; vl-ventral lip)

Four distinct stages of development of the buccal mass are described (Table 1B). Embryos at stage IA have a buccal mass consisting of a shallow buccal cavity, with short, paired salivary ducts, and a radular diverticulum (Figs. 5A and 6A). The radular sac, which has already formed in a previous, but unobserved, developmental stage, is short and poorly differentiated and lies parallel to the oesophagus pointing posteriorly (Figure 6A). Its lumen is dorso-ventrally flattened and lacks both radular teeth and an odontoblast nest.

In transverse section, the oesophagus at the level of the buccal mass is clearly divisible into a dorsal strip, composed of ciliated and mucus-secreting cells, and the ventral buccal cavity whose cells stain more densely and appear to be unciliated (Figure 5A). These cells form the lateral and ventral walls of the buccal cavity and also pass posteriorly into the next part of the oesophagus. The ventral part of the buccal cavity is dorso-ventrally flattened and towards the posterior of the cavity, paired lateral evaginations, which are the ducts of the acinous salivary glands, arise from the lateral walls (Figure 5A).

Ventral to the buccal cavity lies a thick mass of apparently undifferentiated tissue, this corresponds to the buccal musculature in other gastropod embryos (Figure 5A). There is a clearly defined muscle which originates within this mass and passes anteriorly through the nerve ring above the pedal commissure and merges with the floor of the haemocoel. Similarly, a posteriorly-directed muscle leaves this mass and merges with the pedal musculature posterior to the nerve ring (Figure 5D).

As the radular sac elongates (Stage IB), it remains approximately parallel to the path of the oesophagus, although it is deflected to the left and its posterior limit lies slightly dorsal to the oesophagus (Figs. 5B and 6B). The buccal mass still lies ventral to the oesophagus but has become slightly deflected to the left and twisted clockwise (when viewed from above) (Figure 5B). The twisting motion of the radular sac affects the lower part of the buccal cavity where the ducts of the salivary glands arise. As a result, the ducts no longer emerge at right angles to the oesophagus. This is seen to a greater degree in the next stage of development (Stage II)(Figure 6C).

The specialised characters of the conoidean buccal mass begin to appear in stage II. The buccal sac extends ventrally, further separating the radular sac from the oesophagus. As a consequence, the part of the buccal wall which includes the salivary gland ducts becomes recognisable as the buccal sac and the region postero-ventral to it becomes the definitive radular sac (sometimes referred to as the "long arm" of the radular sac) (Figure 5B). The radular sac rotates through approximately 90° with respect to the oesophagus and undergoes considerable growth. The salivary gland ducts show the effects of rotation as they now exit the buccal wall parallel to the oesophagus, but in opposite directions to each other (Figure 6C). This process is much more pronounced than in stage I. The right salivary gland is posteriorly directed and protrudes into the cephalic haemocoel behind the nerve ring, whilst the left salivary gland passes around the left side of the oesophagus and then anteriorly so that its tip lies within the nerve ring just anterior to the cerebro-pleural commissures.

The anterior portion of the radular sac has not yet become differentiated to form the radular caecum (= "short arm", the homologue of the sub-lingual pouch). However, the radular sac has grown in length so that it passes from behind the nerve ring arches dorsally above the oesophagus and circum-oesophageal nerve ring. Its tip passes between the cerebral ganglia and over the cerebral commissure and lies anterior to the nerve ring (Figure 5C-D).

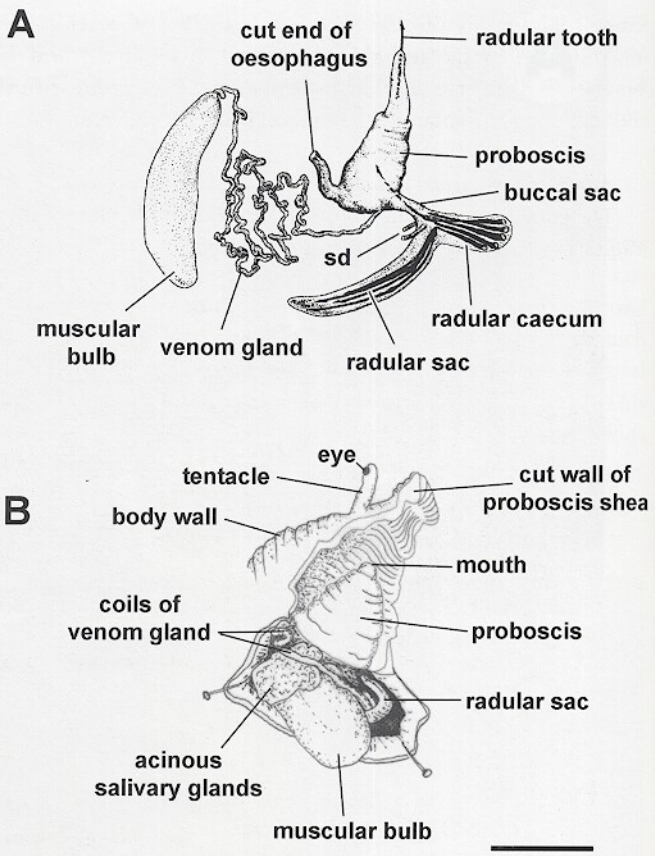


Figure 4. A. Diagrammatic view of generalised *Conus* foregut (modified after Wilson and Gillet 1979, Figure 4). B. Sketch diagram of dissection of adult *Conus anemone*. Scale bar 5mm. (Key to lettering: sd-salivary gland ducts (cut)).

During stage II, the internal structure of the radular sac also undergoes structural changes; the odontoblast nest (which first appears at Stage IB) has differentiated to form two distinct lateral regions separated by a low ridge. This arrangement seems to have formed through lateral expansion of the walls of the radular sac (Figure 5D). The radular sac now contains numerous radular teeth which are produced in two rows from the separate left and right portions of the odontoblast nest (Figure 5D). Each enrolled tooth is formed around a single cell. The teeth have recognisable barbs and are present within the whole length of the radular sac. Attempts to isolate larval teeth for SEM examination were unsuccessful.

At the crawlaway stage (Stage III - the oldest embryos examined), the anterior portion of the radular sac has expanded and differentiated to form the radular caecum (Figure 6C). Radular teeth stored within it are present in a distinctly different orientation from those remaining in the radular sac and appear to have undergone a 180° rotation from the radular sac to the cae-

cum. The most significant point is that the buccal mass (including the radular sac and the acinous salivary glands) now lies anterior to the nerve ring. This displacement coincides with the elongation of the snout as the proboscis begins to form

Adult acinous salivary glands

The paired acinous salivary glands form a single mass of interdigitating secretory tissue in the dorsal portion of the cephalic haemocoel anterior to the nerve ring. The glands are acinous in nature each consisting of a branching alveolar-like network leading to a single duct. A pair of ciliated ducts pass from the ventral surface of each gland to the buccal sac where they merge with the wall of the buccal cavity. Since the ventral part of the buccal mass in *C. anemone* is orientated at 90° to the long axis of the oesophagus the ducts enter the buccal cavity anteriorly and posteriorly with respect to the long axis of the animal.

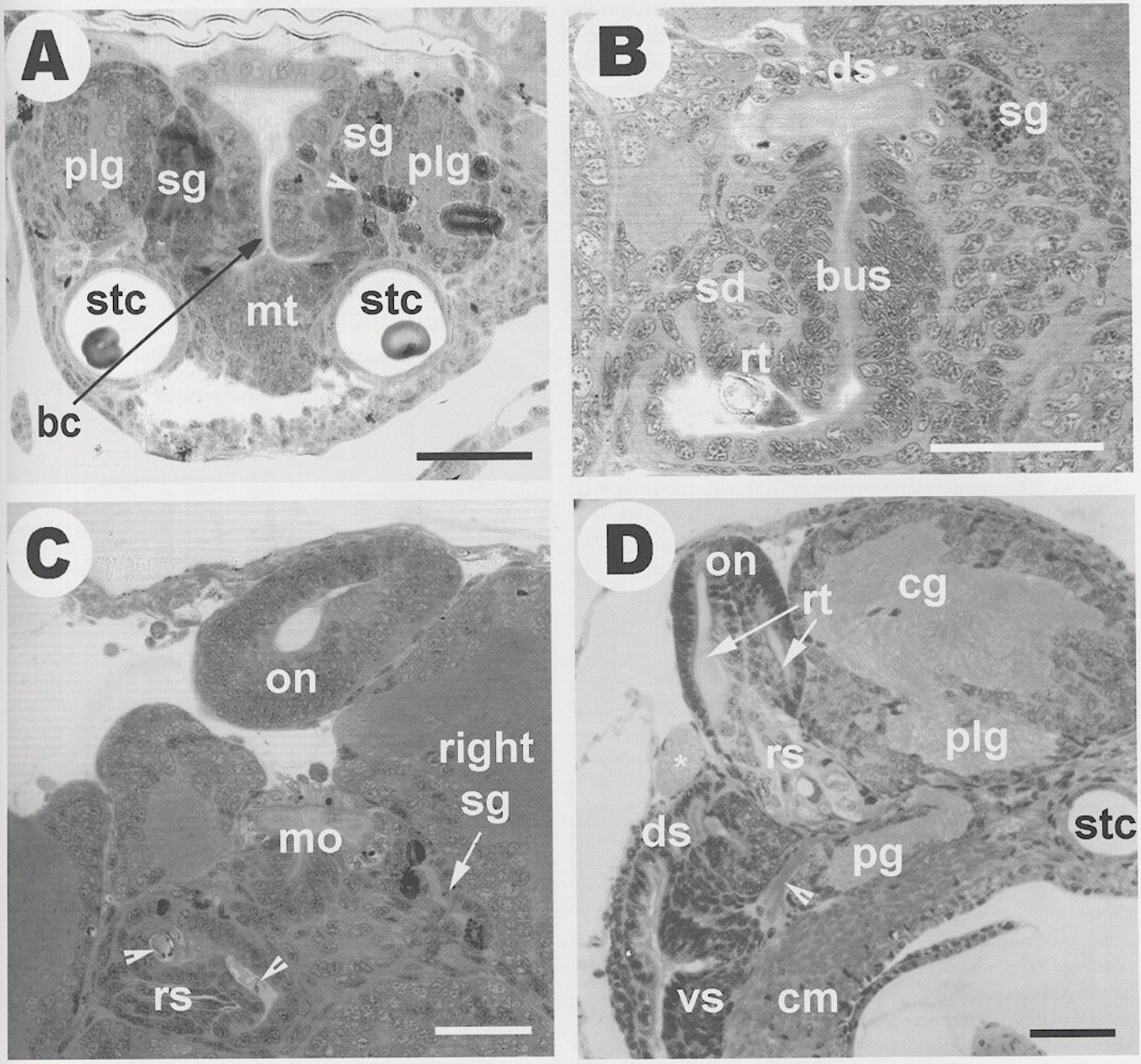


Figure 5. Development of the buccal mass in *Conus anemone* observed using light microscopy. **A.** Stage I, transverse section. Buccal cavity and acinous salivary glands, lying parallel to oesophagus are visible. Buccal mass posterior to nerve ring. Scale bar 50µm. **B.** Stage II, transverse section. Buccal sac and deflection of radular sac. Only right acinous salivary gland visible with left duct. Scale bar 50µm. **C.** Stage II, transverse section. Section posterior to buccal mass showing odontoblast nest and posteriorly directed right acinous salivary gland. Scale bar 50µm. **D.** Stage II, longitudinal section. Radular sac and odontoblast nest. Mid-oesophagus shows ciliated dorsal strip and secretory ventral strip. Buccal mass lies anterior to nerve ring, but is not visible in this plane of section. Arrow indicates retractor muscle passing through nerve ring. Star indicates supra-oesophageal connective. Scale bar 50µm. (Key to lettering: bus-buccal sac; cg-cerebral ganglion; cm-columellar muscle; ds-dorsal strip; mo-mid-oesophagus; mt-mesodermal tissue; on-odontoblast nest; pg-pedal ganglion; plg-pleural ganglion; rs-radular sac; rt-radular tooth; sd-acinous salivary gland duct; sg-acinous salivary gland; stc-statocyst; vs-ventral strip)

Acinous salivary gland development

The acinous salivary glands arise from dorso-lateral evaginations of the wall of the buccal mass (Table 1B; Stage IA) and their initial growth is directed posteriorly parallel to the oesophagus mid-line (Figure 5A).

The ventral growth of the buccal mass and its subsequent rotation during development (stages IB-II) means that the ducts no longer both grow posteriorly, but instead the left duct grows anteriorly and the right duct grows posteriorly (Figure 5B-C). Since the ducts are not associated with the walls of the oesophagus the glands are free to grow into the space available to them between the circum-oesophageal ganglia (nerve ring) and the oesophagus (Figure 5B-C). The growth of the left gland is constricted by the posterior wall of the rhynchodaeum and becomes folded over; the right gland is obstructed by the ganglia of the nerve ring and is also folded. Dark-blue staining granules begin to appear in the cytoplasm of the cells forming the terminal secretory regions which surround the ciliated, tubular ducts (Figure 5B).

This pattern of growth continues in the next developmental stage (Stage II); the anteriorly directed left salivary gland is compressed against the body wall, whilst the right salivary gland penetrates the nerve ring and expands posterior to it. In stage III, the glands lay anterior to the nerve ring, were clearly tubular and not yet strongly arborescent.

Adult accessory salivary glands

Only a single accessory salivary gland and its duct were observed. The duct could not be traced through the thick wax sections, but is presumed to open to the ventral lip as is the case in other neogastropods. Its appearance was similar to that described in *Conus flavidus* and *Conus vexillum* by Schultz (1983) and to adult *N. lapillus* (*see* Andrews 1981), a thin muscle layer lay between two layers of secretory cells which form a pseudostratified epithelium.

Accessory salivary gland development

The first developmental stage shows that the accessory salivary glands arise as paired evaginations of the ventral lip of the mouth (Stage IA)(Figure 7C). This region is recognisable since it has smaller, more densely staining cells than those of the oral tube or oesophagus (Figure 7D). The unciliated ducts appear to be filled with microvilli and are 60-100µm long. They can be traced for a short distance posteriorly along the ventral surface of the oral tube, before they terminate.

In subsequent stages only a single duct could be traced. The opening to the ventral lip appeared wider in stage IB than in the previous stage and it is likely the two ducts have fused. The single duct has a length of approximately 100µm and the termination is distinctly rounded at 30µm in diameter compared to a duct diameter of 10µm.

In stage III the gland is larger and has a defined sub-epithelial layer with a gap and then a layer of epithelial cells (Figure 7E). The necks of some epithelial cells can be seen to pass the gap and open to the lumen. Muscle cells which fill the gap in the adult are not distinguishable in the embryonic stages. The gland cells have a finely granular cytoplasm, but no secretory granules.

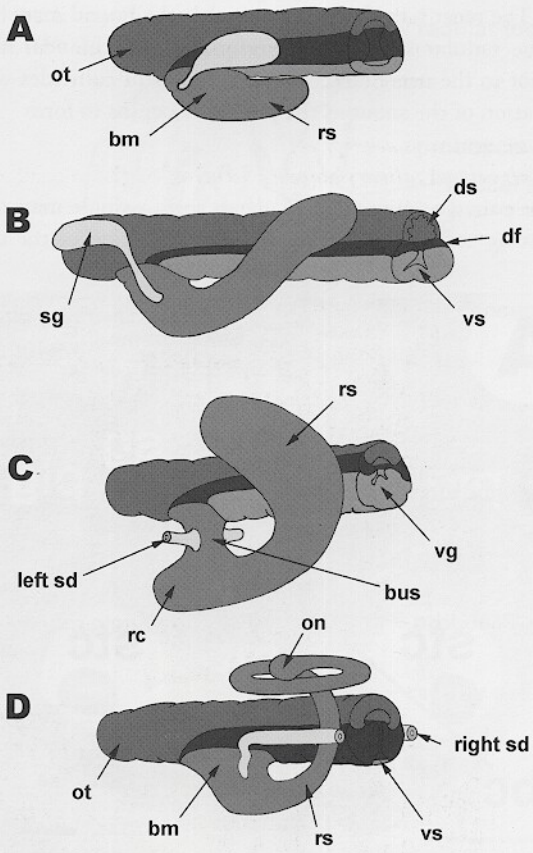


Figure 6. Diagrams comparing the development of the buccal mass and radular sac in *Conus anemone* with *Nucella lapillus*. **A.** *C. anemone* stage IA. Buccal mass and radular sac present. Acinous salivary glands and radular sac lie parallel to oesophagus. Ventral strip poorly developed. **B.** *C. anemone* stage IB. Radular sac has grown dorsally and twisted to the left. Left acinous salivary gland grows anteriorly, right (not shown) grows posteriorly. Dorsal strip has numerous longitudinal folds, ventral strip highly glandular. **C.** *C. anemone* stage III. Radular sac arches dorsally, anterior portion lies anterior to nerve ring (not shown). Buccal sac and radular caecum formed. Separation of venom gland from ventral strip has begun. **D.** *N. lapillus*, stage 10. Radular sac grows around left side of oesophagus and curves dorsally. Acinous salivary gland ducts pass posteriorly parallel to oesophagus. Ventral strip undifferentiated. (Key to lettering: bm-buccal mass; bus-buccal sac; df-dorsal fold; ds-dorsal strip; on-odontoblast nest; ot-oral tube; rc-radular caecum; rs-radular sac; sd-acinous salivary gland duct; sg-acinous salivary gland; vg-venom gland rudiment; vs-ventral strip)

Adult venom apparatus and mid-oesophagus

The mid-oesophagus commences just posterior to the buccal mass where a muscular sphincter is located. Just posterior to this sphincter the venom gland opens to the posterior right side of the oesophagus (Figure 1). The venom apparatus is well-developed with a highly coiled venom gland and a large oval, muscular bulb lying at the extreme posterior of the haemocoel with the anterior portion (leading to the venom gland) pointing ventrally (Figure 4). The bulb is large, occupying approximately half of the haemocoel and has two longitudinal muscle layers divided by a thin layer of connective tissue. In dissected anaesthetised

specimens, the bulb could be observed to pulse as it contracted. Each contraction drew the distal portion of the venom gland into the bulb as the bulb contracted longitudinally.

Venom apparatus development

In stage I the oesophagus posterior to the buccal mass is divisible into a ciliated dorsal strip and a ventral region composed of dense unciliated cells (Figure 8). This part of the oesophagus is short and at this stage leads to the stomach with little other differentiation.

In stage II, the anterior part of the oesophagus, near to the buccal mass, is tubular and divisible dorso-ventrally into a dorsal strip comprising mucous-secreting goblet and ciliated cells, and a ventral region of undifferentiated, unciliated cells (Figure

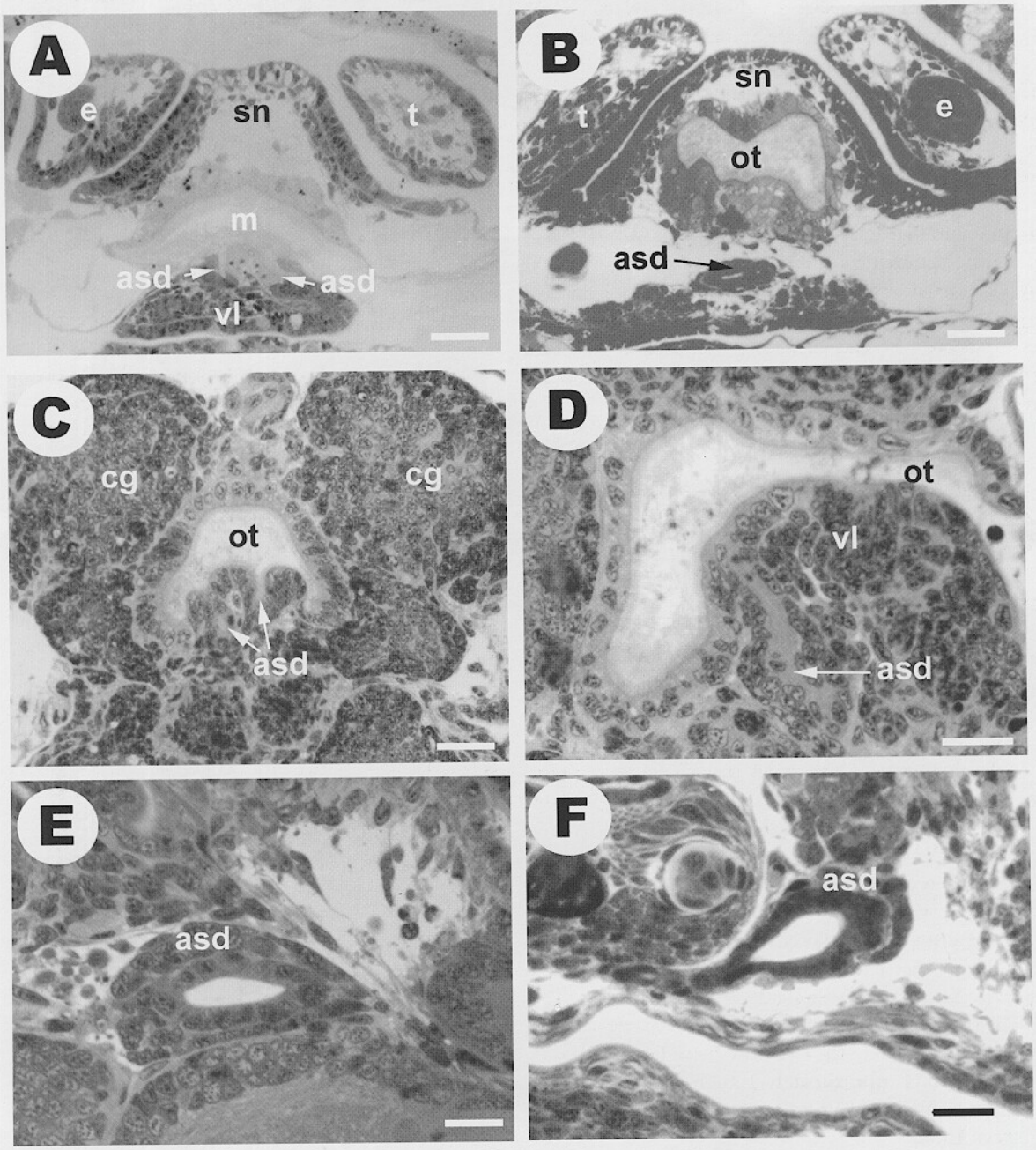


Figure 7. Development of the accessory salivary glands in *Conus anemone* and *Nucella lapillus* observed using light microscopy. **A.** *N. lapillus,* stage 7. Transverse section level with mouth. Note paired invaginations of accessory salivary gland ducts (arrowed). Scale bar 20µm. **B.** *N. lapillus*, stage 7. Transverse section posterior to mouth. Accessory salivary gland ducts fused, but lumen still paired. Scale bar 20µm. **C.** *C. anemone*, stage IA. Transverse section through oral tube. Note paired accessory salivary gland ducts. Scale bar 20µm. **D.** *C. anemone*, stage IB. Longitudinal section through oral tube. Accessory salivary gland duct lies further from mouth than *N. lapillus*. Scale bar 20µm. **E.** *C. anemone*, stage III. Accessory salivary gland showing two cell layers, muscle cells form central layer. Scale bar 10µm. **F.** *N. lapillus,* stage 7. Accessory salivary gland showing two secretory cell layers. Muscle cells appear between them. Scale bar 15µm. (Key to lettering: asd-accessory salivary gland duct; cg-cerebral ganglion; e-eye; m-mouth; ot-oral tube; sn-snout; t-tentacle; vl-ventral lip).

8). Posterior to this region, level with the oesophageal ganglia, the pleuro-visceral connectives cross over the oesophagus and the anterior aorta passes below it. These features would normally define it as the mid-oesophagus in adult neogastropods. At this point the oesophagus has three distinct dorso-ventral divisions; the dorsal strip is present dorsally, ventral to it on either side lie densely staining, ciliated cells which are probably homologous to the dorsal folds of the Muricoidea (Figure 8). The ventral region is glandular, unciliated and consists of tall cells containing fine green granules. This ventral region is

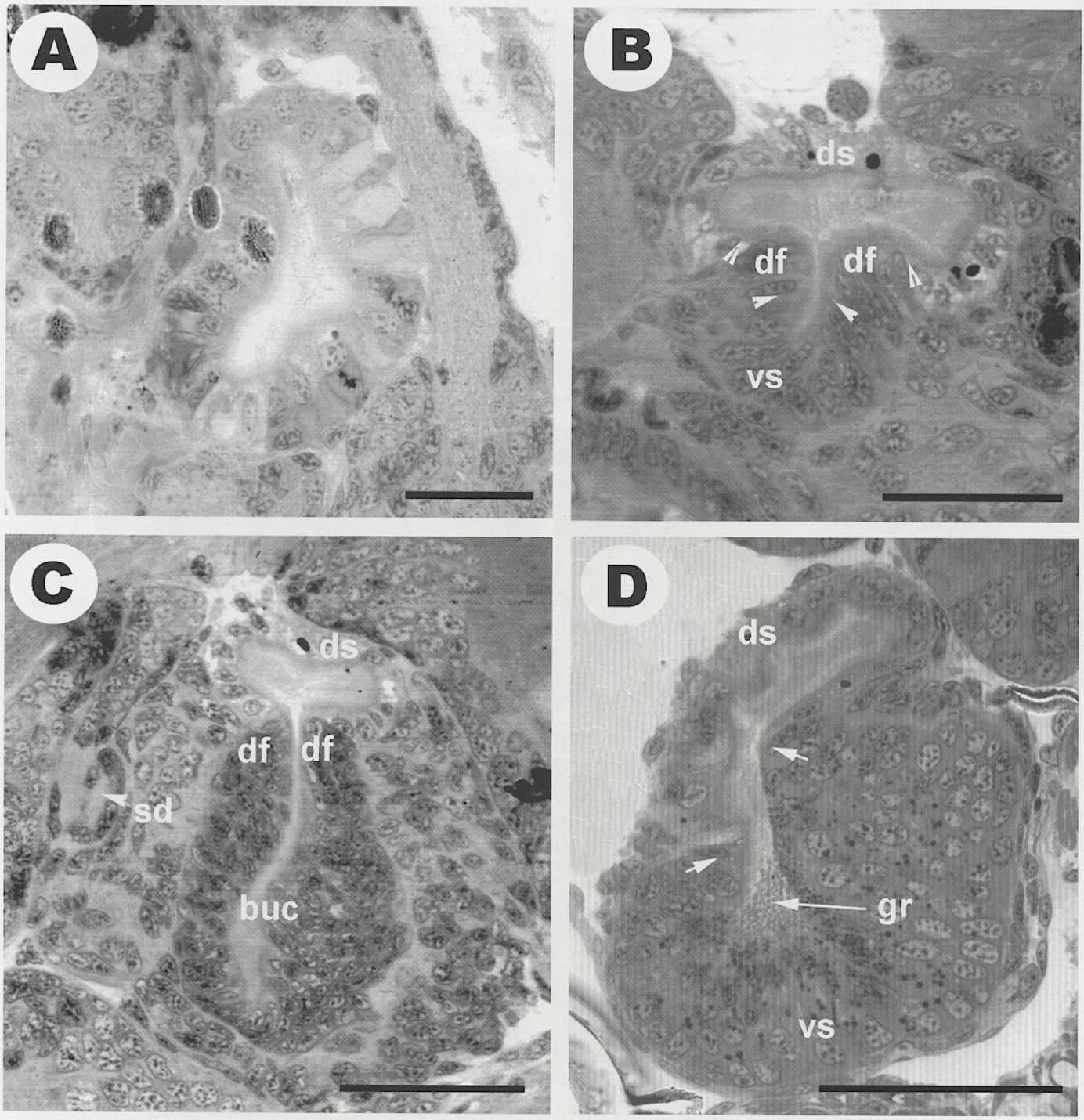
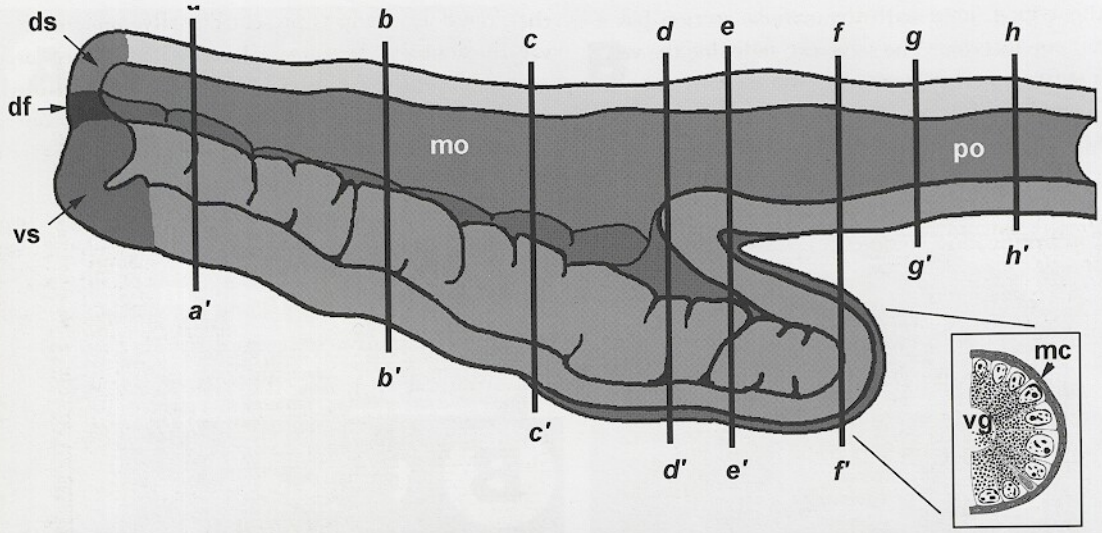


Figure 8. Development of *Conus anemone* mid-oesophagus observed using light microscopy. **A.** Stage IA, transverse section. Showing undifferentiated mid-oesophagus composed of ciliated and mucous-secreting cells. Scale bar 25µm. **B.** Stage IB, transverse section. Mid-oesophagus has differentiated close to buccal mass to form dorsal strip, ciliated dorsal folds (arrows indicate limits) and unciliated ventral strip. Scale bar 25µm. **C.** Stage II, transverse section. Ciliated dorsal folds close to unciliated buccal sac. Scale bar 50µm. **D.** Stage III, transverse section. Highly glandular ventral strip posterior to buccal mass. Dorsal folds reduced (arrowed), and ventral to dorsal strip. Note granules shed into oesophageal lumen. Scale bar 50µm. (Key to lettering: buc-buccal sac; df-dorsal folds; ds-dorsal strip; gr-secretory granules; vs-ventral strip)



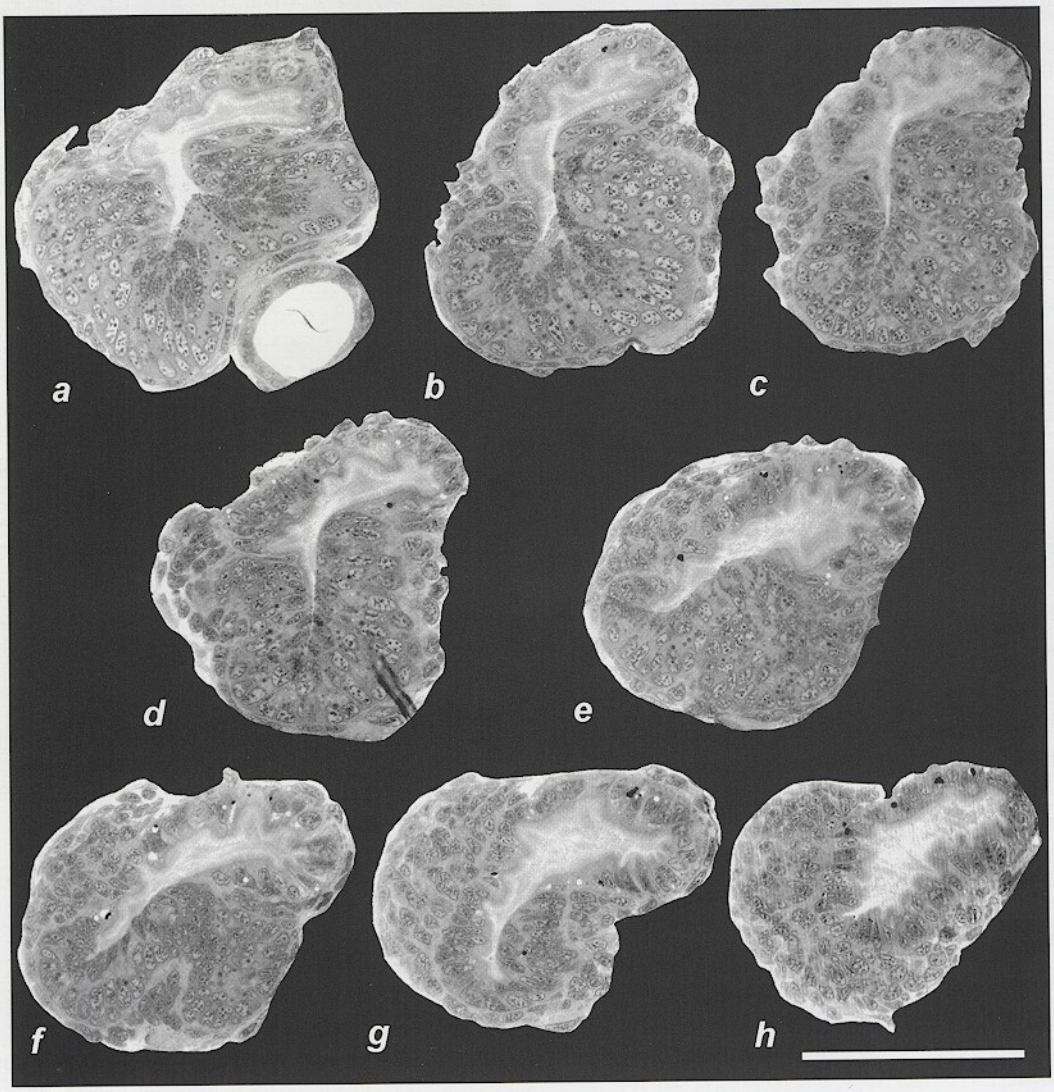


Figure 9. Reconstruction of the development of the venom gland in *Conus*, observed using light microscopy. Sections a-h transverse sections through mid-oesophagus at positions shown (a-a' to h-h') in diagrammatic reconstruction. Sections a-d show height increase in lumen. Sections e and f show dorsal portion of the oesophagus separated to form an outpushing containing secretory cells. Sections g and h show secretory cells absent from posterior oesophagus. Boxed diagram shows detailed reconstruction of tip of outpushing. Sections e and f show mixture of granules and nuclei in glancing section through base of columnar cells. Scale bar 50µm. (Key to lettering: df-dorsal folds; ds-dorsal strip; mc-muscle cells; mo-mid-oesophagus; po-posterior oesophagus; vg-venom gland; vs-ventral strip)

thrown into longitudinal folds and in transverse section has a shallow, w-shaped cross section. The secretory cells line the ventral side of the oesophagus and terminate at a point near to where the oesophagus enters the stomach (Figure 8). At this stage in development, the oesophagus has undergone a little over 90° of torsion and has become longitudinally folded and thrown into deep lateral folds. The glandular region lies entirely posterior to the nerve ring, and commences immediately posterior to the buccal mass (Figure 5D).

By stage III, the unciliated ventral glandular region has expanded and the ciliated cells (dorsal fold homologue) between the dorsal strip and the ventral glandular region have largely vanished. The secretory cells have begun to shed large, greenish granules into the lumen (Figure 8). This is particularly apparent towards the posterior limit of this part of the oesophagus. Granules fill the lumen of the dorsal part of the oesophagus.

Within the glandular region, the ventral secretory region bulges conspicuously and a finger-like projection is formed from the ventral wall of the oesophagus. Posteriorly, the oesophagus narrows again, but the ventral secretory cells are largely absent from the oesophagus walls (Figure 9). Detailed inspection of transverse sections reveals that at the end of the

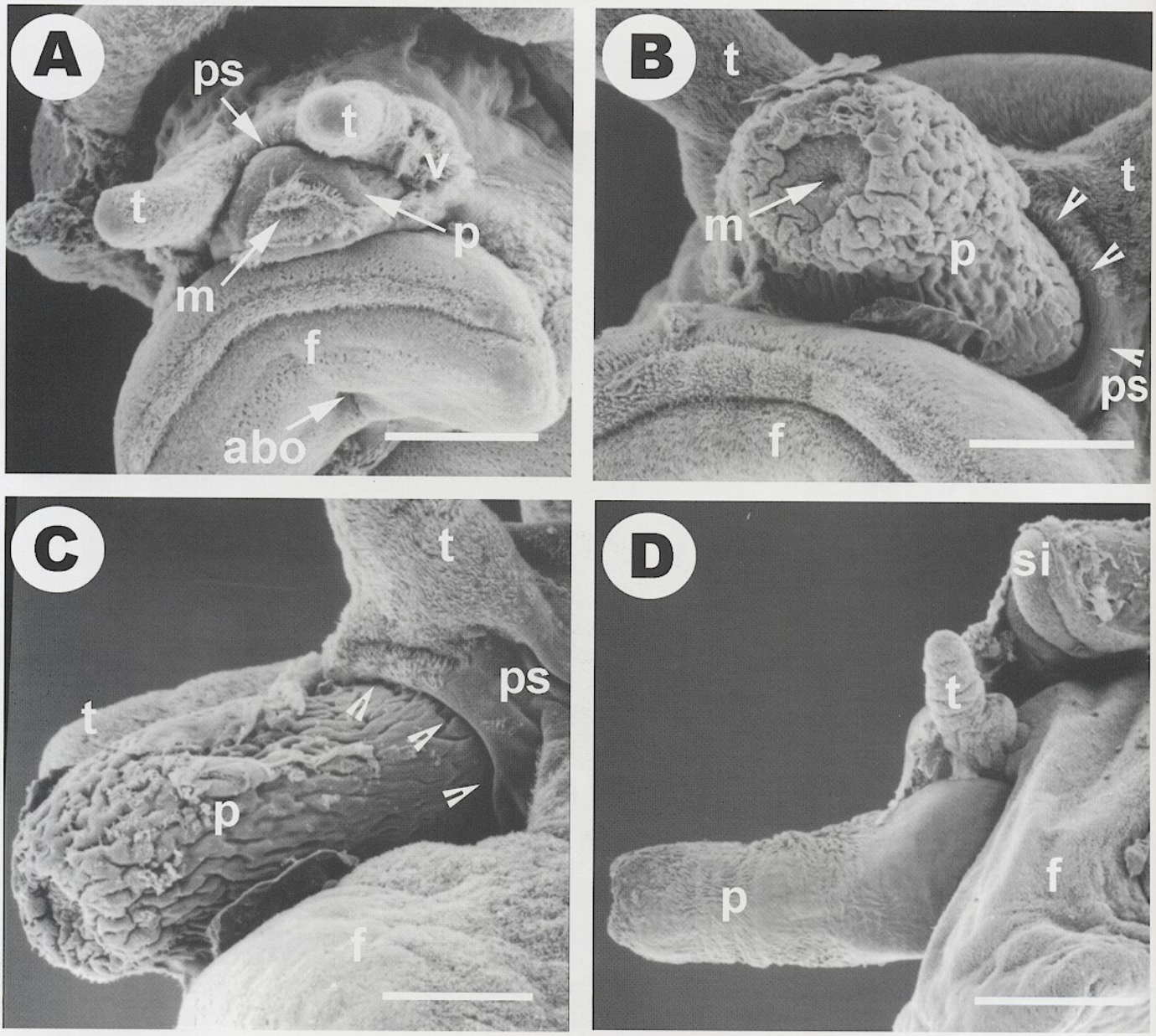


Figure 10. Proboscis development in *Nucella lapillus* observed using SEM. **A.** Stage 7, veliger. Proboscis rudiment overgrown by tentacle bases and proboscis sheath. No lateral proboscis sheath due to presence of velar lobes. Scale bar 100µm. **B.** Stage 8, post-veliger. Proboscis capable of limited extension. Base surrounded by proboscis sheath (indicated by arrowheads). Scale bar 75µm. **C.** Stage 8 post veliger, lateral view. Proboscis sheath indicated by arrowheads. Note smooth epithelium at th base of proboscis. Scale bar 75µm. **D.** Crawlaway stage. Note long proboscis, with smooth base and relatively smaller tentacles. Oesophageal loop well formed at this stage. Scale bar 200µm. (Key to lettering: abo-accessory boring organ; f-foot; m-mouth; p-proboscis; ps-proboscis sheath; si-siphon; t-tentacle)

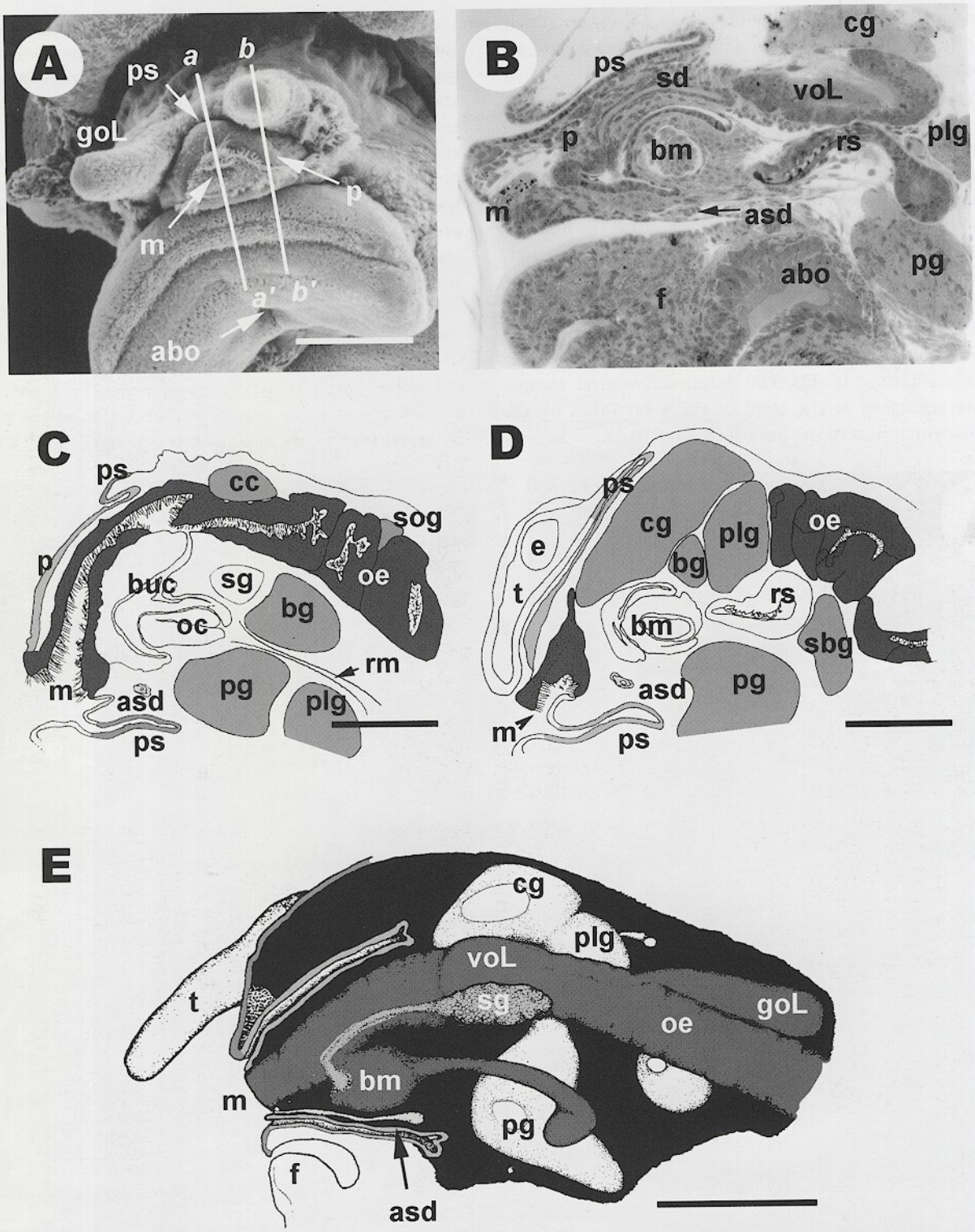


Figure 11. Proboscis development in *Nucella lapillus*, observed using SEM and light microscopy. **A.** Stage 7, frontal view. Showing well-developed proboscis rudiment overgrown by tentacle bases and proboscis sheath. Lines a-a' and b-b' refer to longitudinal sections C and D respectively. Scale bar 100µm. **B.** Stage 8, post veliger, longitudinal section, retracted proboscis. Note proboscis sheath formed by thinner infolded body wall. No oesophageal loop present at this stage. Scale bar 75µm. **C.** Stage 7, diagrammatic section through line a-a'. Exposed dorsal wall of proboscis rudiment covered at base by developing proboscis sheath. Oesophagus folded, but does not form loop. Note odontophoral retractor muscle passing through nerve ring. Scale bar 50µm. **D.** Stage 7, diagrammatic section through line b-b'. Showing lateral portions of proboscis rudiment covered by tentacle bases forming lateral proboscis sheath. Note radular sac penetrates nerve ring. Scale bar 50µm. **E.** Stage 8, longitudinal reconstruction. Note valve of Leiblein lies anterior to nerve ring. Gland of Leiblein has begun to separate from mid-oesophagus. Scale bar 75µm. (Key to lettering: abo-accessory boring organ; asd-accessory salivary gland duct; bg-buccal ganglion; bm-buccal mass; buc-buccal cavity; cc-cerebral commissure; cg-cerebral ganglion; e-eye; f-foot; goL-gland of Leiblein; m-mouth; oc-odontophoral cartilage; oe-oesophagus; p-proboscis; pg-pedal ganglion; plg-pleural ganglion; ps-proboscis sheath; rm-odontophoral retractor muscle; rs-radular sac; sbg-sub-oesophageal ganglion; sd-acinous salivary gland duct; sg-acinous salivary gland; t-tentacle; voL-valve of Leiblein)

evagination, the cells are predominantly in TS and the nuclei are wholly surrounded by granules. This suggests that the evagination terminates as a blunt tube (Figure 9).

Nucella lapillus

Proboscis development

The pleurembolic proboscis begins its development as an enlargement of the pre-tentacular region of the head, forming a short snout (Figure 10A). At this stage the reduced velar lobes are still present (Stage 7). Dorsal and ventral invaginations anterior to the tentacles form the first stages of the rhynchocoelic cavity. These invaginations are initially paired dorso-laterally and ventro-laterally but link at their dorsal mid-line to form an invaginated arc which divides posteriorly (Figure 11C-D). The dorsal and ventral components are separated at the level of the velar lobes by the velar cilia which pass to the mouth (Figure 10A).

Progressive increase in the length of the snout, to form the proboscis, accompanied by resorption of the velum and increase in the depth of the rhynchocoel forms the proboscis and its sheath (Stage 8)(Figure 10B-C). As the snout grows, an important factor in proboscis sheath formation is the anterior growth of the pre-tentacular epithelium which grows anteriorly to cover the developing proboscis, and the fusion of the tentacle bases along their mid-dorsal line (Figure 11). By stage 8, and well in advance of the hatching stage 11, the proboscis is capable of protrusion and at this stage in development profound internal changes are noted as the whole of the anterior oesophagus and the first part of the mid-oesophagus (valve of Leiblein) is drawn anteriorly through the nerve ring - presumably as a result of traction exerted by the growing proboscis since there is no oesophageal loop to allow for protraction of the proboscis without affecting the oesophagus (Figs. 10 and 11).

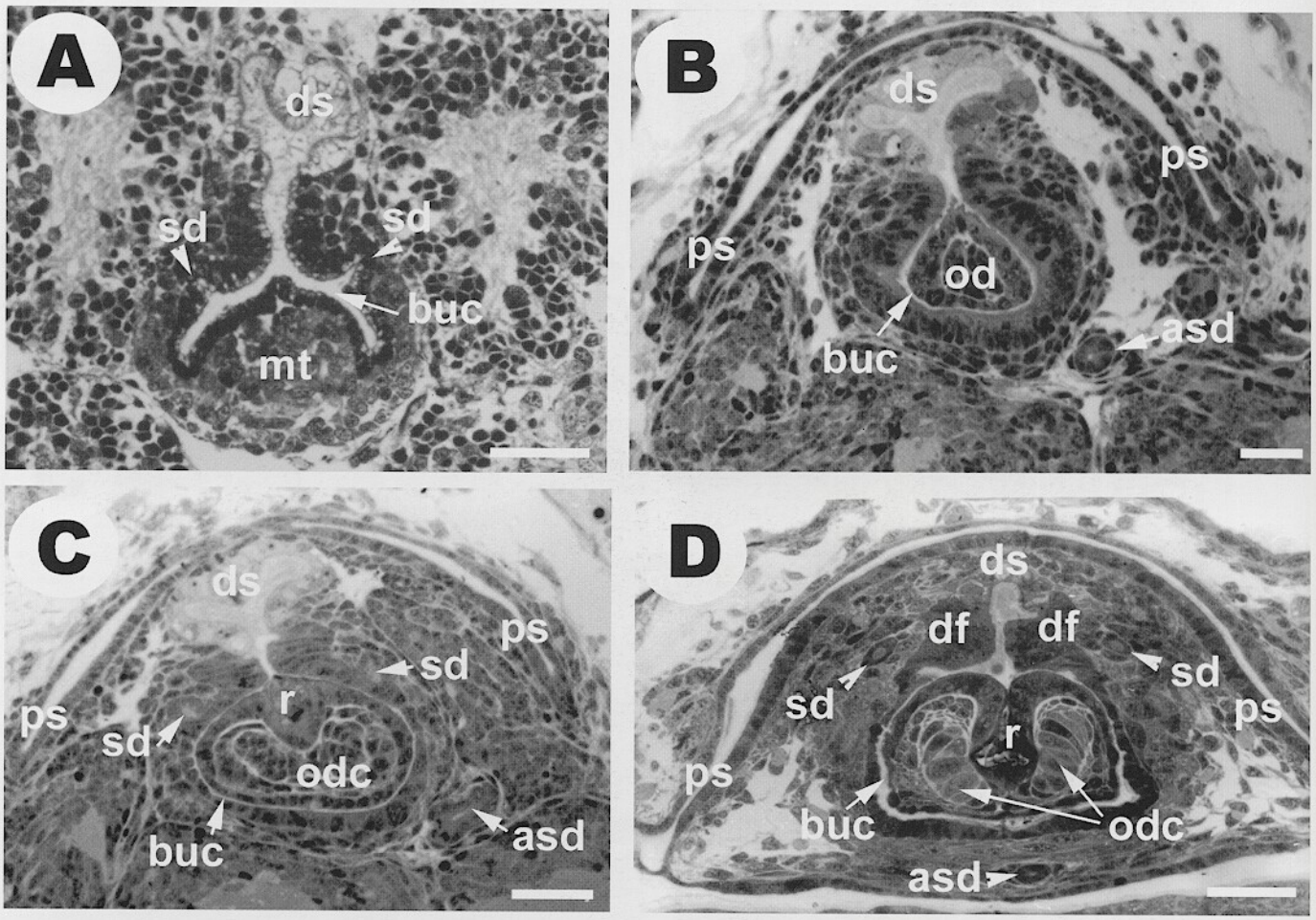


Figure 12. Buccal mass development in *Nucella lapillus* observed using light microscopy. **A.** Late stage 6, transverse section. Buccal mass lies level with nerve ring. Acinous salivary glands evaginate from buccal wall (arrowed). Scale bar 20µm. **B.** Late stage 7, transverse section - anterior portion. Buccal mass well formed, odontophore protrudes into buccal cavity, but radular does not yet wrap over anterior end. Proboscis sheath forms arc over dorsal wall of the snout. Scale bar 20µm. **C.** Late stage 7, transverse section - posterior portion. Acinous salivary gland ducts merge with wall of the buccal cavity. Single accessory salivary gland duct present. Radular protrudes into posterior portion of buccal cavity anterior to nerve ring. Proboscis sheath divided into two invaginations. Scale bar 20µm. **D.** Stage 10, transverse section. Proboscis sheath surrounds proboscis. Dorsal folds lie between buccal cavity and oesophagus. Acinous salivary gland ducts pass posteriorly ventro-lateral to dorsal folds. Radular passes into buccal cavity between odontophoral cartilages and well-developed musculature. Scale bar 20µm. (Key to lettering: asd-accessory salivary gland ducts; buc-buccal cavity; df-dorsal folds; ds-dorsal strip; mt-mesodermal tissue; od-odontophore; odc-odontophoral cartilages; ps-proboscis sheath; r-radular; sd-acinous salivary gland ducts)

By the time they hatch, the crawlaways have a long, relatively thin proboscis (Figure 10). A loop in the anterior oesophagus allows for protraction and retraction without exerting strain on the oesophagus.

Buccal mass development

In *Nucella*, the buccal cavity is derived from a pair of evaginations of the floor of the oesophagus (stage 6)(Figure 13A-B). The anterior-most cavity becomes the sub-lingual pouch, whilst the posterior cavity is the radular sac. Between the two invaginations, the floor of the oesophagus covers mesodermal tissue which later differentiates to become the odontophore and its associated musculature.

As the buccal cavity enlarges, the odontophore forms by differentiation of the underlying tissue and the musculature which operates the buccal mass forms around it and subse-

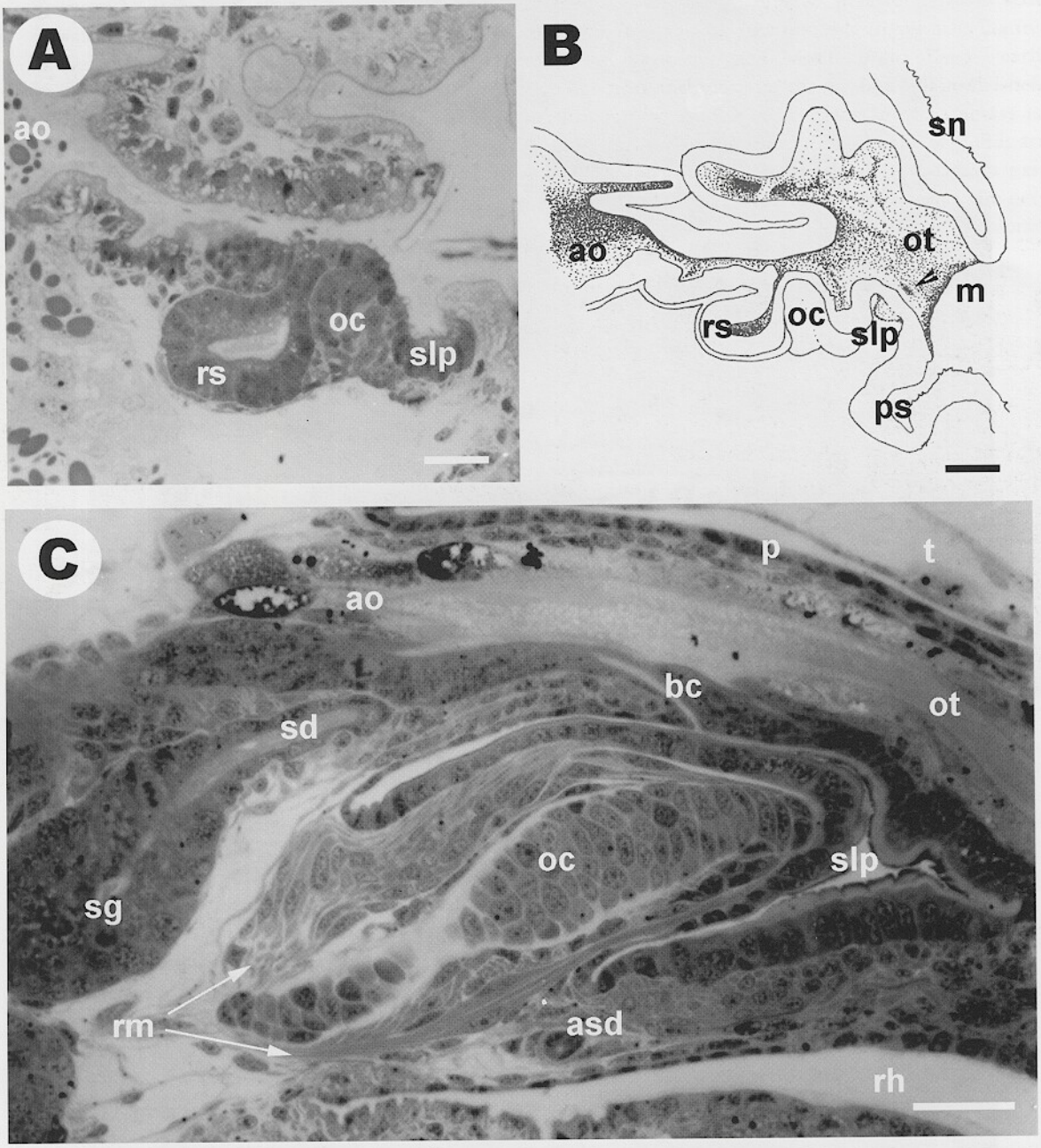


Figure 13. Buccal mass development in *Nucella lapillus* observed using light microscopy. **A.** Stage 6, longitudinal section. Radular sac and sub-lingual pouch evaginated. Odontophoral cartilages and musculature differentiate in gap between invaginations. Scale bar 20µm. **B.** Stage 6, lateral reconstruction showing the relationship between buccal cavity, mouth and oesophagus. Note first stages of ventral proboscis sheath and position of the accessory salivary gland duct on ventral lip (arrowed). Scale bar 40µm. **C.** Stage 8, longitudinal section. Opening between buccal cavity and oesophagus very narrow. Sub-lingual pouch undercuts oral tube and odontophore. Musculature highly developed. Scale bar 25µm. (Key to lettering: ao-anterior oesophagus; asd-accessory salivary gland duct; m-mouth; oc-odontophoral cartilage; ot-oral tube; p-proboscis; ps-proboscis sheath; rh-rhynchocoel; rm-odontophoral retractor muscles; rs-radular sac; sd-acinous salivary gland ducts; sg-acinous salivary glands; slp-sub-lingual pouch; sn-snout; t-tentacles)

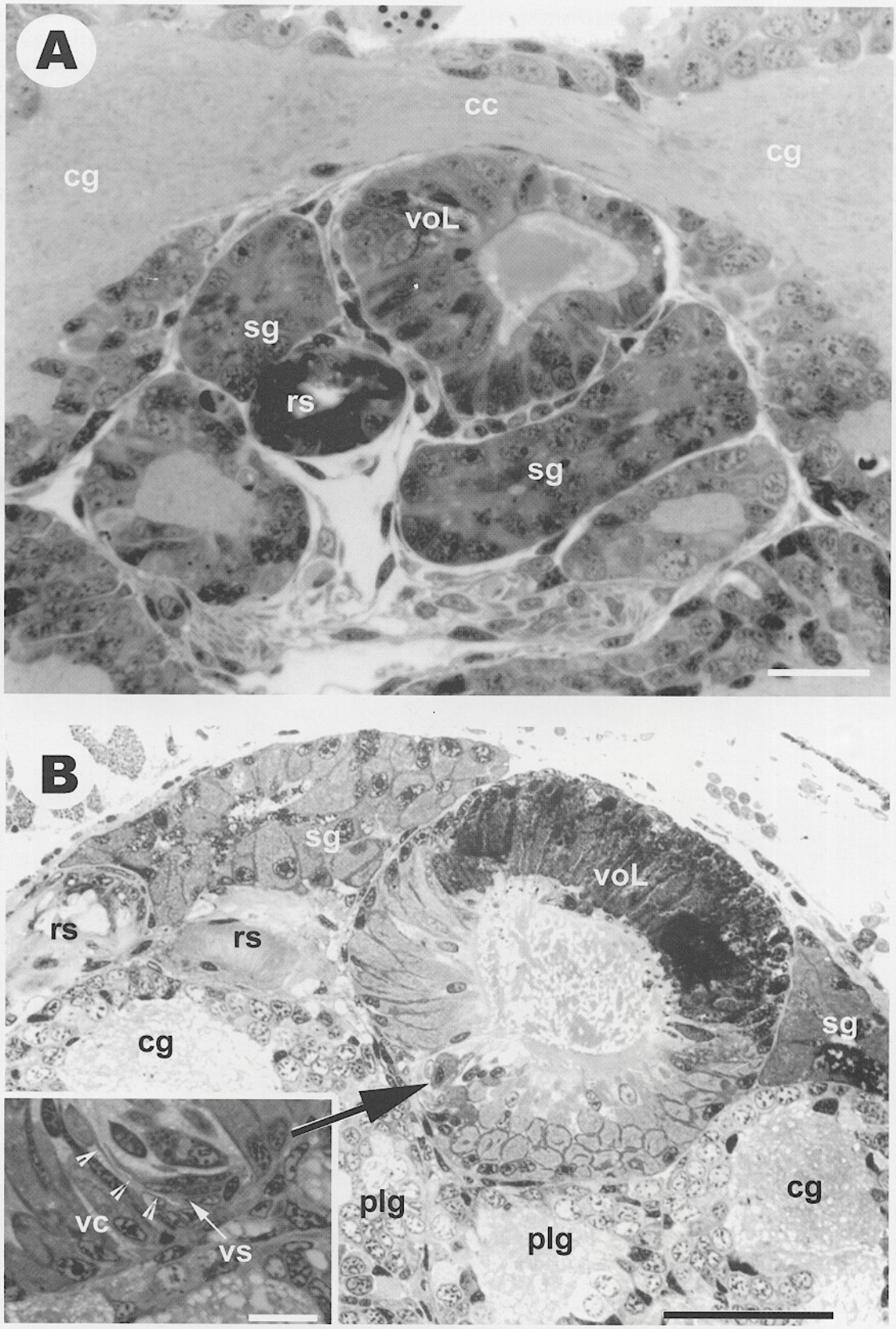


Figure 14. Relative positions of the valve of Leiblein and nerve ring in *Nucella lapillus* observed using light microscopy. **A.** Stage 7, transverse section. Valve of Leiblein, acinous salivary glands and radular sac lie within nerve ring (cg-cc-cg marks the cerebral commissure). Scale bar 10μm. **B.** Stage 10, transverse section. Valve of Leiblein, acinous salivary glands and radular sac now dorsal to nerve ring (cg-plg, plg-cg). Scale bar 25μm. Inset box shows undifferentiated ventral strip and ventral cleft (arrowed) overgrown by morphologically dorsal tissue. Scale bar 10μm. (Key to lettering: cc-cerebral commissure; cg-cerebral ganglion; rs-radular sac; plg-pleural ganglion; sg-acinous salivary glands; vc-ventral channel; voL-valve of Leiblein; vs-ventral strip)

quently becomes functional (stage 7)(Figure 11). The radular sac in *Nucella* is long, relatively thin walled and terminates in the odontoblast nest where the teeth are produced. The paired odontophoral cartilages form either side of the radular sac and as the radular is secreted by the odontoblast nest it passes into the buccal cavity and wraps over the anterior end of the odontophore (Figure 12 C-D).

The buccal mass lies within the circum-oesophageal nerve ring when it first appears and the radular sac grows posteriorly during development and initially penetrates the nerve ring (stage 7)(Figure 11C). However, during proboscis development, the buccal mass, radular sac and acinous salivary glands are all drawn anteriorly and come to lie in front of the nerve ring (stage 8). As the buccal mass moves anteriorly, the radular sac grows dorsally up the left side of the oesophagus where it is thrown into a flat spiral, dorsal to the oesophagus with the odontoblast nest at its centre (Figure 6D). During the anterior movement of the buccal mass, the radular sac is pulled through the nerve ring and consequently does not penetrate it in the adult.

Acinous salivary gland development

In *Nucella* the acinous salivary glands arise from dorso-lateral evaginations of the wall of the buccal cavity (Figure 12). They become associated with the walls of the oesophagus and lie level with the dorsal oesophageal folds, parallel to the oesophagus. At the anterior limit of the mid-oesophagus, the acinous salivary gland ducts separate from the wall of the oesophagus and the secretory regions develop, lying free in the haemocoelic cavity (Figs. 13C and 14A). During early development they grow posteriorly into the haemocoel behind the nerve ring (stages 6 and 7). As the buccal mass is drawn through the nerve ring (stage 8), the salivary glands are pulled anteriorly and come to lie wholly in the anterior part of the haemocoel. The ducts no longer pass through the nerve ring. As the glands continue to enlarge, they become dorsal to the

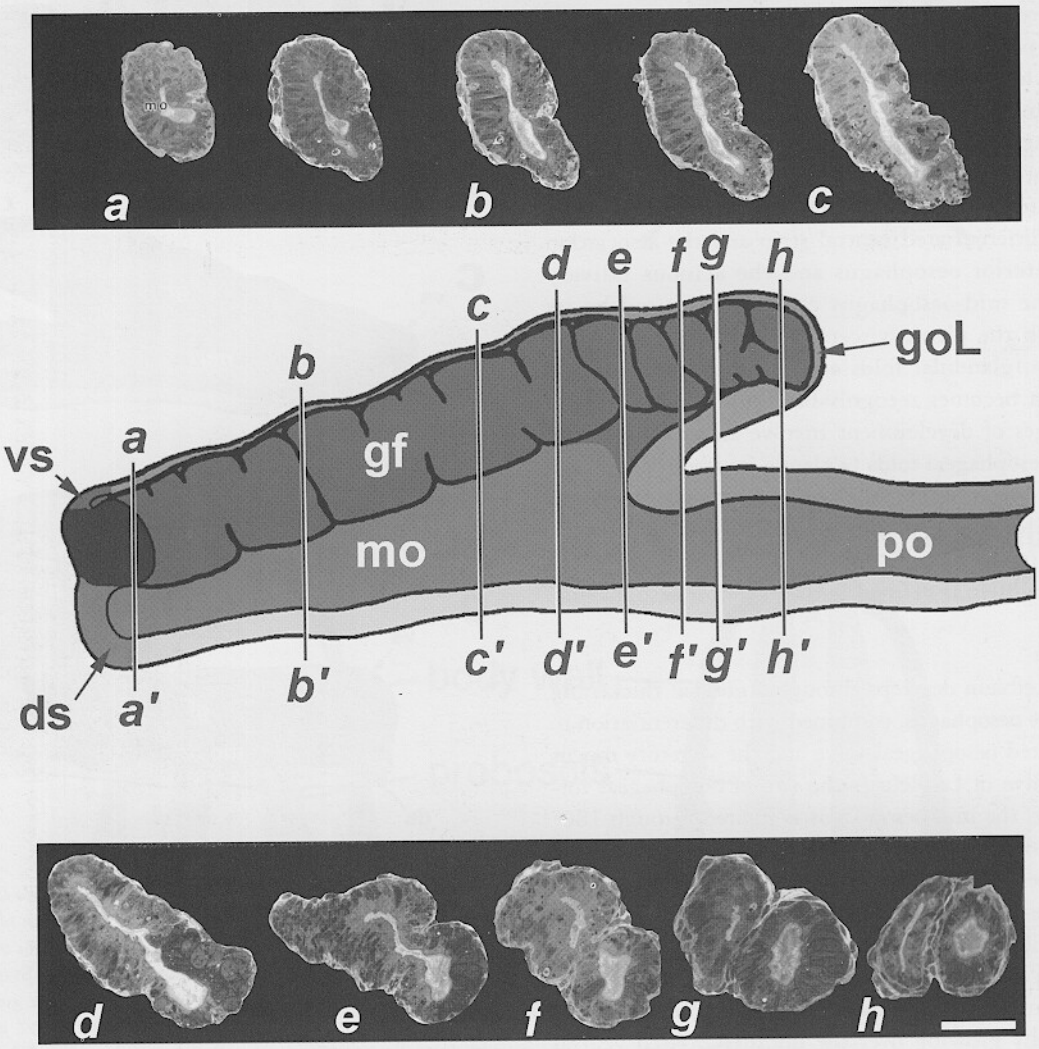


Figure 15. Reconstructions of the development of the gland of Leiblein in *Nucella lapillus* observed using light microscopy. Sections a-h transverse sections through mid-oesophagus of late stage 7 embryo at positions shown (a-a' to h-h') in diagrammatic reconstruction. Sections a-e show progressive height increase in lumen as gland of Leiblein evaginates. Sections f-h show gland of Leiblein (dorsal) and posterior oesophagus (ventral). Posterior oesophagus composed primarily of mucus secreting and ciliated cells. Scale bar 50µm. Diagrammatic reconstruction shows evagination dominated by dorsal folds and ventral strip undifferentiated. (Key to lettering: ds-dorsal strip; gf-glandular dorsal folds; goL-gland of Leiblein; mo-mid-oesophagus; po-posterior oesophagus; vs-ventral strip)

oesophagus, eventually lying above the valve of Leiblein and occupying much of the dorsal part of the anterior cephalic haemocoel (Figure 14). The radular sac passes between the two glands and the coiled radular ribbon lies above the mass of acinous secretory tissue.

Accessory salivary glands

These glands originate as a pair of ducts which arise on the ventral lip and open to the mouth (Figs. 7A and 13B). The two ducts grow posteriorly, ventral to the oral tube, and terminate just level with the buccal mass. During development, the ducts fuse along their length, first forming a single duct with paired openings to the lip and paired lumina leading to separate glands (stages 7 and 8)(Figure 7B). Finally they fuse along the length of the duct, whilst the glandular regions differentiate but remain separate. In the adult the accessory salivary glands are paired, but share a single duct which opens to the ventral lip of the mouth.

Oesophageal development

The anterior portion of the oesophagus in *Nucella* becomes differentiated relatively early in development. The oral tube consists of a simple ciliated, mucous secreting epithelium, leading from the mouth to the buccal cavity. From stage 7 onwards, the anterior oesophagus is recognisable due to the presence of ciliated dorsal folds, the ciliated, mucus secreting dorsal strip, undifferentiated ventral strip and the association between the anterior oesophagus and the acinous salivary gland ducts. The mid-oesophagus can be recognised by its relationship with the pleuro-visceral connectives and by the valve of Leiblein, glandular folds and gland of Leiblein. The valve of Leiblein becomes recognisable from stage 7 (Figure 14A). Later stages of development involve elaboration of the glandular mid-oesophageal folds (=glande framboisée) and the gland of Leiblein (from stage 8). The posterior oesophagus can only be defined once the gland of Leiblein has developed. From this point in time, the region lying posterior to the duct of the gland of Leiblein is defined as the posterior oesophagus.

Mid-oesophagus

The valve of Leiblein develops through a gradual thickening of the walls of the oesophagus, combined with differentiation to produce the ciliated oesophageal valve and the secretory mucus pad cells. The valve of Leiblein is the site of oesophageal torsion. In the adult, the mid-oesophagus is rotated through 180° relative to the anterior oesophagus. Thus the dorsal strip lies on the floor of the oesophagus and the ventral strip runs along the mid-dorsal centre-line of the roof of the oesophagus. Posterior to the valve of Leiblein, the epithelium differentiates to produce a secretory region derived from the dorsal folds. These glandular dorsal folds become very large and fill the dorsal region of the mid-oesophagus by growing over the undifferentiated ventral strip (Figure 14B, insert).

The gland of Leiblein develops at the posterior end of the mid-oesophagus and is derived from an evagination of the morphologically ventral wall of the oesophagus (Figure 15). This evagination is composed of tissue containing the undifferentiated ventral strip and the dorsal oesophageal folds. The first steps in its formation are an increase in the height of the oesophagus as the dorsal region expands, the lumen becomes taller. At the posterior limit a finger-like tubular evagination is formed which gradually enlarges and expands through later developmental steps (Figure 16).

The gland of Leiblein gradually separates from the oesophagus and a duct is formed from tissue drawn from the oesophagus anterior and posterior to the gland. The anterior face of the duct

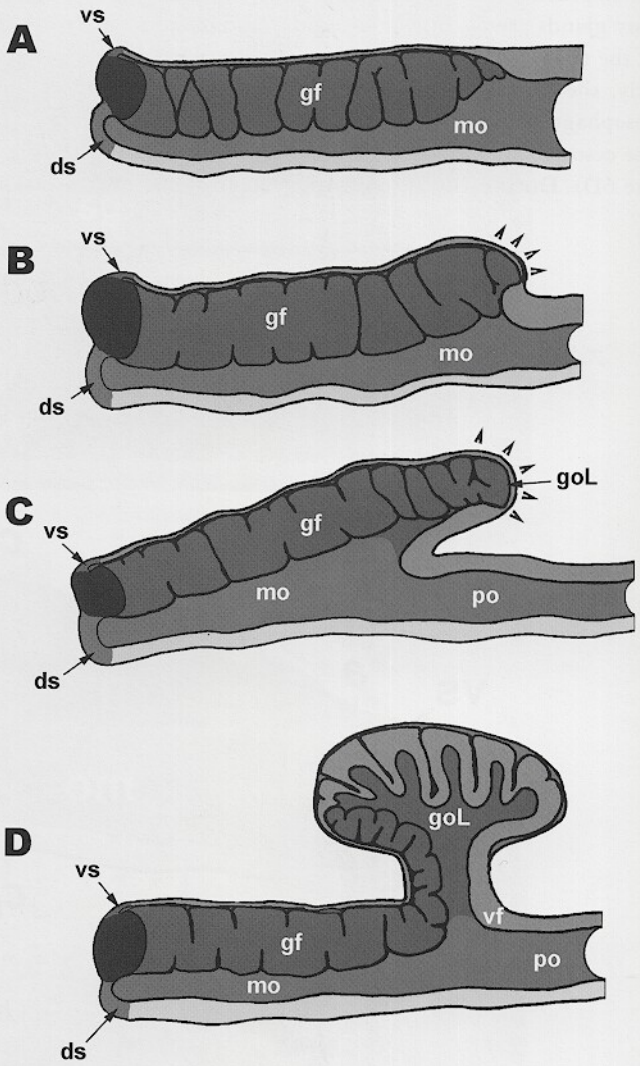


Figure 16. Development of the gland of Leiblein in *Nucella lapillus*. **A.** Differentiation of glandular folds in mid-oesophagus. **B.** Growth of glandular folds at posterior end of mid-oesophagus leads to increase in height of lumen and beginning of evagination (arrows mark growth direction). **C.** Evagination grows and outpushing develops into gland of Leiblein (arrows show growth direction). **D.** Differentiation of glandular strip produces highly folded glandular columnar epithelium, limited to anterior wall of duct and portion of floor of gland anterior to duct. Ventral strip in anterior portion of mid-oesophagus remains undifferentiated and squamous. Ventral folds differentiate and can be traced from floor of gland down posterior wall of duct into posterior oesophagus. (Key to lettering: ds-dorsal sheath; gf-glandular mid-oesophageal folds; goL-gland of Leiblein; mo-mid-oesophagus; po-posterior oesophagus; vf-ventral folds; vs-ventral strip)

bears the ventral strip flanked by the dorsal folds which form the lateral walls of the duct. The dorsal folds penetrate a short distance into the anterior portion of the gland and retain their discrete dense staining and are recognisable throughout development and into the adult. The ventral strip passes along the anterior wall of the duct, between the dorsal folds, and into the gland where it spreads and differentiates to form the glandular walls of the gland. The posterior face of the duct bears a pair of ventral folds in the adult which merge with the posterior oesophagus, but these are absent from the encapsulated developmental stages.

The gland of Leiblein is therefore morphologically ventral and rapidly becomes the most voluminous gland in the cephalic haemocoel, filling the space above the oesophagus and pressing the nerve ring and valve of Leiblein ventrally. The only other dorsally placed glands are the acinous salivary glands which lie anterior to the gland of Leiblein.

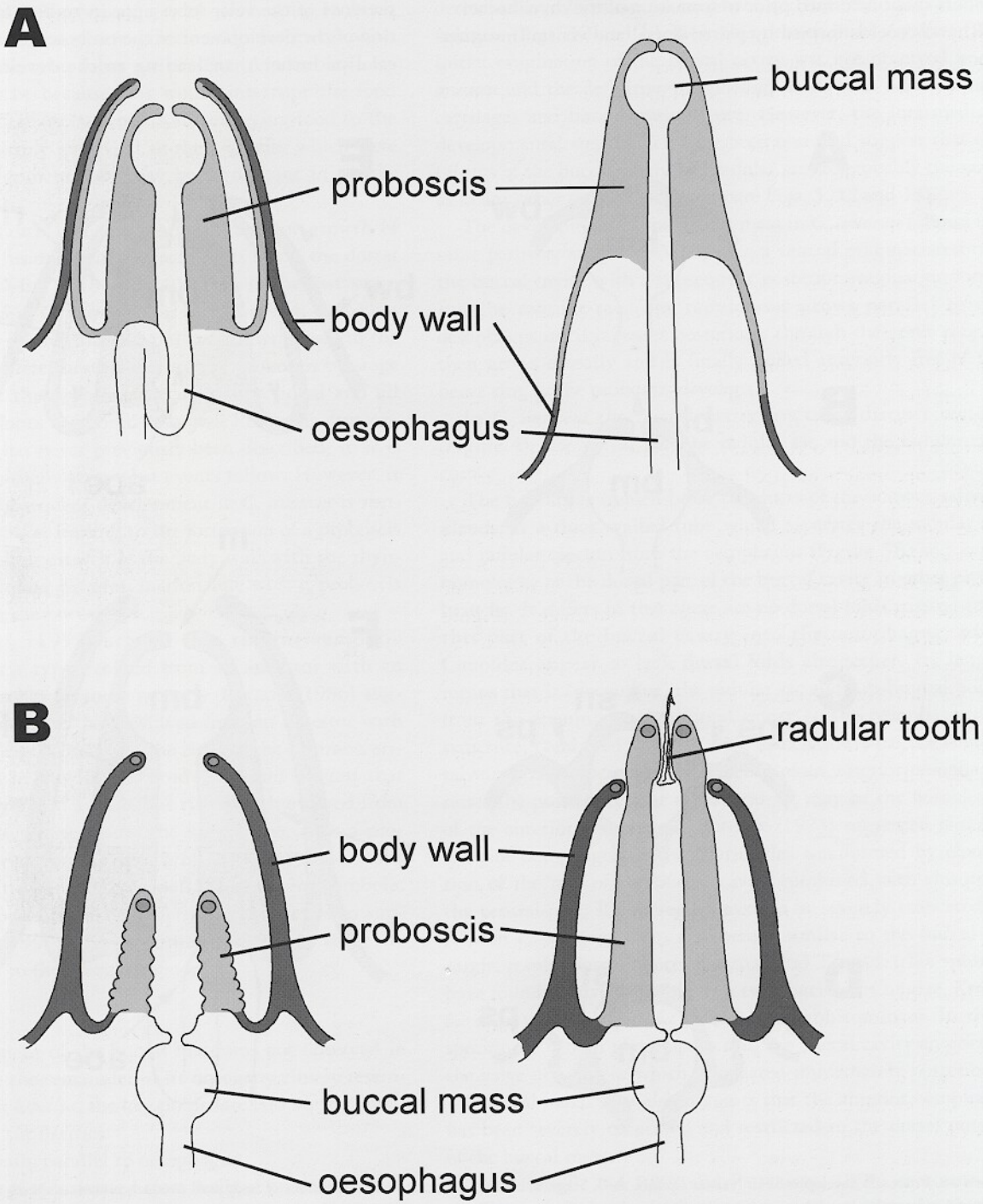


Figure 17. Proboscis types. **A.** Pleurembolic type proboscis found in *Nucella lapillus* and other Muricoidea shown in retracted and extended positions. Buccal mass is near proboscis tip and oesophagus forms a loop when proboscis is retracted. **B.** Intraembolic proboscis found in *Conus anemone* and other Conoidea. Buccal mass lies at proboscis base and extension of proboscis does not affect buccal mass or oesophagus.

DISCUSSION

Proboscis

Adult Conoidea and Muricoidea possess proboscides which have fundamental anatomical differences. In developmental terms however, both proboscis types appear to have common origins which later diverge to give radically different definitive morphologies (compare Figs. 2 and 10).

Common ontogenetic points:

- Initial growth involves the oral tube or buccal lips
- Short snout is formed prior to formation of the rhynchocoel
- Rhynchocoel is formed by paired dorsal and ventral invaginations
- All proboscis development is pre-tentacular
- Proboscis growth leads to anterior displacement of buccal mass, salivary glands and radular sac

In both species, the proboscis initially appears as an enlargement of the tissue surrounding the mouth. In *Conus anemone* the oral lips grow to form a short buccal tube which is later transformed into a short snout. In *Nucella lapillus* the initial developmental step leads directly to the formation of the snout. The presence of the velar lobes appears to be a factor in the restriction of the development of the proboscis *C. anemone* to the buccal lips rather than leading to the development of a larger

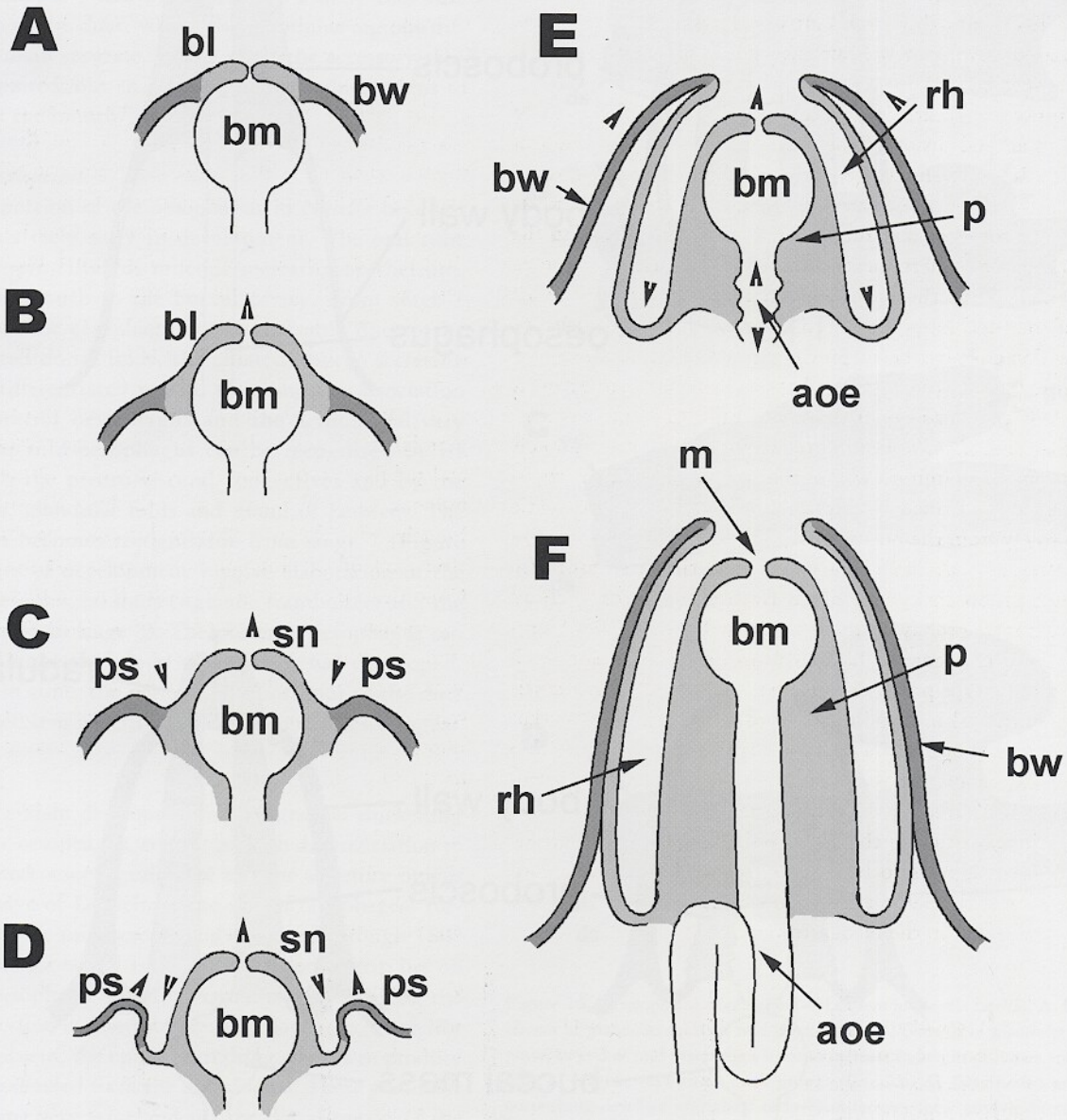


Figure 18. Proboscis development in *Nucella lapillus*. **A-C.** Stage 6, buccal lips elongate invaginations of body wall produce proboscis sheath rudiments. **D.** Stage 7. Proboscis rudiment forms buccal mass moves into proboscis. **E.** Stage 8. Proboscis elongation draws buccal mass anteriorly. Velum lost so proboscis sheath entirely surrounds proboscis. Body wall grows to cover proboscis when retracted. Folds in oesophagus allow proboscis extension, but no oesophageal loop present. **F.** Definitive state (Stage 10 onwards). Proboscis fully functional, oesophageal loop present in retracted specimens. (Key to lettering: aoe-anterior oesophagus; bm-buccal mass; bl-buccal lip; bw-buccal wall; m-mouth; p-proboscis; ps-proboscis sheath; rh-rhynchocoel; sn-snout)

snout. Velar lobes are present in *N. lapillus*, but they are very small in comparison to those of *C. anemone* (Figure 10A).
The rhynchocoel (or proboscis sheath) is a permanent cavity in adult *C. anemone*, but in *N. lapillus* the rhynchocoel is a temporary cavity formed from the proboscis wall when the proboscis is retracted. Despite these differences in the adult, the rynchocoel is derived from dorso-lateral and ventro-lateral invaginations of the body wall in both species. These invaginations eventually merge to completely surround the snout, which then begins to grow, becoming a true proboscis. In both species the dorsal and ventral invaginations do not merge with each other whilst the velar lobes are present. A possible functional cause might be because this would interrupt the food groove and prevent ciliary currents from conveying food to the mouth. This is probably irrelevant in these species which have encapsulated development, but may be significant in planktotrophic species.

The proboscis sheath is formed through anterior growth of the body wall and fusion of the tentacle bases along the dorsal mid-line (Figs. 2D-E;11; 18 and 19). This is the last stage which was observed in *C. anemone*, but in *N. lapillus*, continuation of this process of invagination and overgrowth leads to the formation of a complete sheath covering the proboscis by stage 8, by which point the proboscis becomes functional and all traces of the velar lobes have been resorbed. Proboscis development in Conoidea has never previously been described, so it is impossible to definitively state what events follow. However, it seems likely that subsequent development in *C. anemone* is similar to that of *N. lapillus* leading to the formation of a proboscis sheath formed through growth of the body wall with the rhynchocoelic cavity formed by invagination but with a proboscis derived solely from the buccal lips.

SHERIDAN *et al.* (1973) argued that the intraembolic conoidean proboscis type evolved from an ancestor with an acrembolic type proboscis; more recently TAYLOR (1986) suggested that it may equally have evolved from an ancestor with a pleurembolic type proboscis. On the basis of the common origins demonstrated in this limited study, I would suggest that the common ancestor had a proboscis type which evolved from an elongated snout, derived from the buccal lips, with a proboscis sheath derived by overgrowth of the snout rather than extensive invagination of the body wall. Thus the intraembolic type proboscis appears to be least derived. This tends to support KANTOR's (1996; this volume) viewpoint that the Conoidea are basal to the Neogastropoda.

Buccal mass

Initial development of the buccal mass was not observed in *Conus anemone*, but the remainder of its ontogeny closely resembles that of *Nucella lapillus*, the key points are laid out below.

Developmental similarities:
- Radular sac initially parallel to oesophagus
- Acinous salivary glands derived from walls of buccal mass
- Radular sac rotates with respect to oesophagus
- Radular sac and acinous salivary glands penetrate nerve ring
- Buccal mass is displaced anteriorly

Key differences:
- Loss of buccal musculature in *C. anemone*
- Acinous salivary glands free in body cavity

The buccal mass in prosobranchs appears to develop via a common mechanism, through evagination of the floor of the oesophagus to form the initial buccal cavity, followed by evagination of the radular sac and then elaboration of the buccal cavity and proliferation and differentiation of the underlying mesodermal cells to form the odontophoral cartilages and buccal musculature (Figs. 12 and 13 show this process in *N. lapillus*). The initial evagination of the buccal cavity was not observed in *C. anemone* and the definitive morphology lacks both odontophoral cartilages and buccal musculature. However, the intermediate developmental steps which have been observed suggest that the origins of the buccal cavity and radular sac are probably the same as in any other prosobranch (compare Figs. 5, 12 and 13).

The development of the buccal mass in *C. anemone* follows the same pathway as that of *N. lapillus*; a ventral evagination forms the buccal cavity with a subsequent posterior evagination forming the radular sac. The radular sac grows parallel to the oesophagus until it passes posteriorly through the nerve ring, it then grows dorsally and is finally pulled anteriorly free of the nerve ring as the proboscis develops.

In *C. anemone* the buccal cavity has three distinct regions (Figure 4); the buccal sac, the radular sac and the radular caecum.

The buccal sac (which bears the ducts of the acinous salivary glands) is a thick-walled tube which separates the radular sac and radular caecum from the oesophagus (Figure 5B) and is the homologue of the dorsal part of the buccal cavity in other prosobranchs. It differs in that there are no dorsal folds passing from this part of the buccal cavity into the oesophagus, adult Conoidea appear to lack dorsal folds altogether. Its length means that it "decouples" the radular sac and sub-lingual pouch from the opening of the buccal cavity to the oesophagus. Its structure, combined with its close association with the acinous salivary gland ducts and the absence of an anterior oesophagus raises the possibility that the buccal sac may be the homologue of the anterior oesophagus. PONDER (1973) suggested that the anterior oesophagus in the Muricoidea was formed by elongation of the roof of the buccal cavity combined with closure of the ventral part. If this region were to be severely truncated, as it is in *C. anemone*, then a structure similar to the buccal sac might result. Furthermore, KANTOR and TAYLOR (this volume) have found a valve of Leiblein in two species of Conidae, *Kermia barnadi* and *Paramontana rufozonata* (Raphitominae). In these species the venom gland opens into the buccal cavity anterior to the valve of Leiblein which is situated immediately posterior to the buccal mass. This also suggests that the anterior oesophagus has been severely truncated and restricted to the dorsal portion of the buccal mass.

PAGE (2000, and PAGE and PEDERSON, 1998) demonstrated that the anterior oesophagus in *Euspira lewisii* (Gould) (Neotaenioglossa: Naticoidea) and *Nassarius mendicus* (Neogastropoda: Muricoidea) is derived from the dorsal portion of the buccal cav-

ity during development. Through elongation, the buccal cavity becomes semi-isolated from the oesophagus and eventually forms a new link to the oesophagus at its anterior limit. Thus the larval mouth and adult mouth have different origins and a section of larval oesophagus dorsal to the buccal mass and anterior oesophagus is isolated and later destroyed. *E. lewisii* and *N. mendicus* both undergo planktotrophic development and it is likely that this mode of buccal mass development, first described by FRETTER (1969), enables the buccal mass to develop without interfering with the larval ability to feed on the plankton. *N. lapillus* and *C. anemone* both undergo encapsulated non-planktotrophic development and do not show this developmental pathway, but *N. lapillus* does exhibit an analogous transient narrowing of the connection between buccal cavity and oesophagus (Figs. 12B and 13C) and the opening in *C. anemone* is also narrow.

During the course of development in both *N. lapillus* and *C. anemone* anticlockwise rotation of the radular sac (when viewed from above) takes place. In *N. lapillus* the radular sac is thin walled and flexible and its rotation is less pronounced and has no effect on the walls of the buccal mass. In *C. anemone* however, the radular sac is thick walled and rigid and the buccal sac is twisted through 90° as the radular sac rotates. Whilst this is the same rotational direction as oesophageal torsion, the radular sac

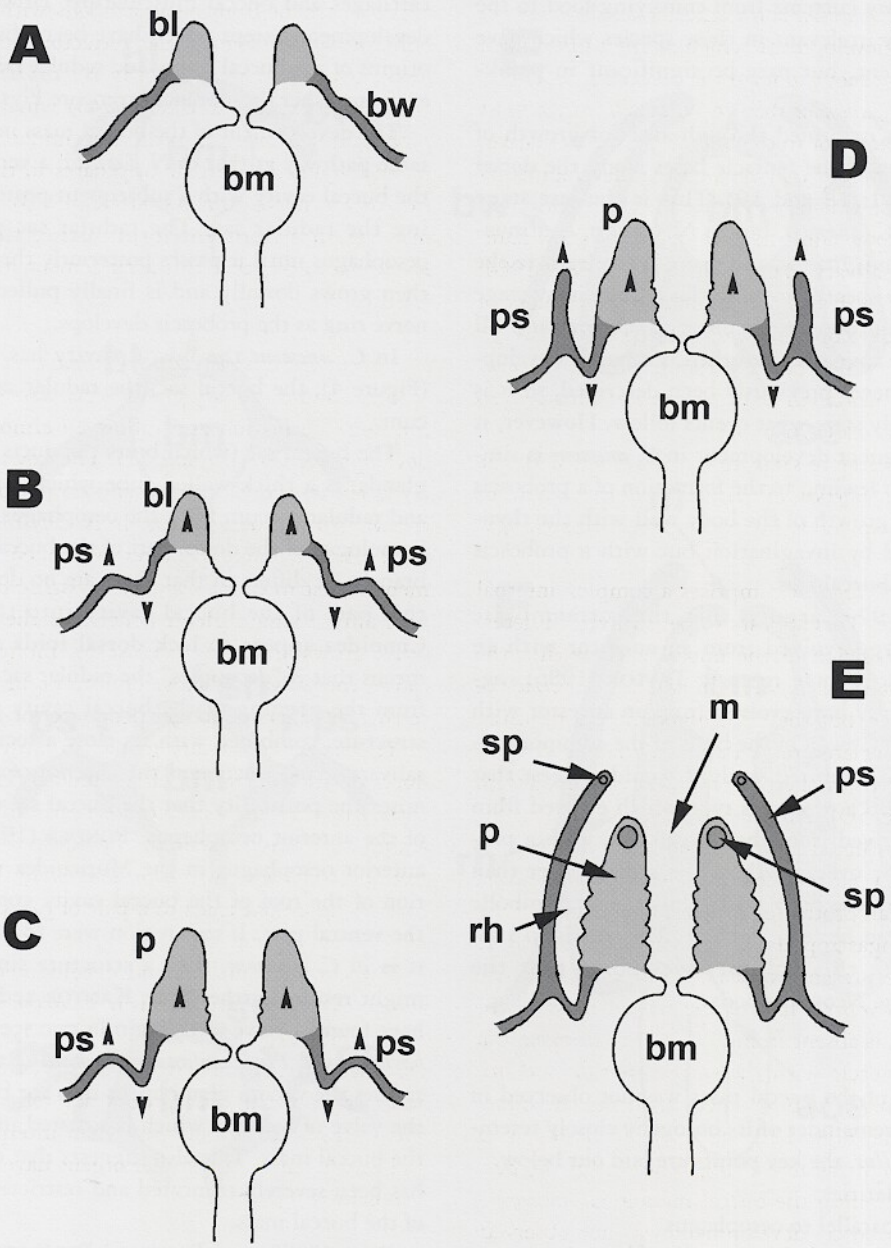


Figure 19. Proboscis development in *Conus anemone*. **A.** Stage IB. Buccal lips and oral tube elongate. **B.** Stage II. Elongated buccal lips form short tube with dorsal and ventral invaginations forming beginnings of proboscis sheath. **C-D.** Stage III. The proboscis begins to elongate and is overgrown by body wall and tentacle bases to form partial proboscis sheath. **E.** Definitive state. Proboscis lies within rhynchocoel. (Key to lettering: bm-buccal mass; bl-buccal lips; bw-body wall; m-mouth; p-proboscis; ps-proboscis sheath; rh-rhynchocoel; sp-sphincter muscles)

lies perpendicular to the oesophagus and the buccal mass lies anterior to the point of torsion in *N. lapillus* (the point of torsion in *C. anemone* has not been described), so the rotation is presumably not due to the buccal mass being dragged in one direction leading to the radular sac adopting the opposite orientation. At present the significance (if any) of this observation is unclear.

The radular caecum forms from the anterior limit of the ventral buccal cavity and is probably the homologue of the sub-lingual pouch. In other prosobranchs this would be the point where worn teeth would break free of the radular ribbon. In the Conoidea it is the site where detached radular teeth are stored prior to their utilisation for envenomation.

Both *N. lapillus* and *C. anemone* show anterior displacement of the buccal mass during development which seems to be linked with the elongation of the snout to form the proboscis. Its effects are less pronounced in *C. anemone* than in *N. lapillus* since most proboscis growth occurs anterior to the buccal mass. Alternatively, reorganisation of the foregut may be a normal developmental process in Neotaenioglossa which has received little attention up to this point. Certainly some adult neotaenioglossans show anteriorly displaced acinous salivary glands (HOUBRICK 1980; 1984; 1993; TAYLOR and MORRIS 1988) and an anterior movement of the buccal mass during development was reported in the *Lacuna vincta* (Neotaenioglossa) (which has no proboscis) and *Nassarius incrassatus* and *Nassarius reticulatus* (Neogastropoda: Muricoidea) by ABRO (1969) and FRETTER (1969).

This process would therefore seem to be connected with the elongation of the anterior portion of the head to form a snout or proboscis and is less conspicuous in species where this elongation is less pronounced.

The buccal mass in *N. lapillus* comprises a complex internal and external musculature. This appears to be involved in determining the definitive position of the buccal mass within the proboscis to some extent in *N. lapillus*. In adult *C. anemone* the buccal walls are muscular, but there are no odontophoral cartilages and none of the associated musculature. However, early in the development of *C. anemone* there are muscles associated with the buccal mass (Figure 5D). An anterior muscle linking the anterior part of the sub-lingual pouch to the body wall near to the mouth is probably a velar retractor muscle. These have been shown to form the median protractor muscles of the sub-radular membrane in other neogastropods (GRAHAM, 1973). Perhaps more significant, is the presence of a posterior muscle which passes from the postero-ventral face of the buccal mass to the pedal musculature. This is absent from the adult *C. anemone*, but the development of a muscle with the same insertion and origins can be observed in *N. lapillus* where it forms the odontophoral retractor muscle (Figs. 12B and 13C). In both species this muscle passes through the nerve ring. The role of the buccal musculature in positioning the buccal mass in *C. anemone* is uncertain, since late proboscis development was not observed. However, the loss of the buccal musculature in *C. anemone* is probably a derived feature since it appears to begin to develop ventral to the radular sac in a developmental stage analogous to *N. lapillus* stage 6, (stage II) but later degenerates.

The basal buccal mass found in the Conoidea has been described by KANTOR (1996; this volume) as a primitive feature. KANTOR suggests that a hypothetical neogastropod archetype might have a basal buccal mass and a short proboscis and that the neogastropods diversified from this point prior to the evolution of the various proboscis types now present in the order. A few other neogastropods are known to have a basal buccal mass; *Benthobia tryoni* (Pseudolividae) and *Olivella borealis* (Olivellidae) were described by KANTOR (1991; 1996). KANTOR (1991; 1996; this volume) suggested that the possession of radular retractor muscles which pass through the nerve ring, as seen in some species of the turrid subfamily Drillinae, in *Benthobia* and in most lower caenogastropods is also a primitive feature which is absent from neogastropods with an elongate pleurembolic proboscis. The radular retractor muscles pass through the nerve ring in the muricids *N. lapillus* (Ball, 1994) and *Urosalpinx cinerea* (Carriker, 1943) which have relatively short proboscides. However, in the Buccinidae, where the proboscis is much longer, this muscle originates in the proboscis wall anterior to the nerve ring (GRAHAM, 1973). The presence of these muscles in a transient form during the development of *C. anemone* suggests that this arrangement may well be a conserved feature.

Acinous and accessory salivary glands

The acinous salivary glands in *C. anemone* and *N. lapillus* have the same derivation and follow an almost identical pattern of development (Figs. 5 and 11). The key differences are that the ducts are free in *C. anemone* and do not become associated with the walls of the oesophagus. In *N. lapillus* both ducts of the acinous salivary glands penetrate the nerve ring early in development whilst in *C. anemone*, the twisting of the buccal sac means that only a single gland penetrates the nerve ring whilst the other grows anteriorly (Figure 5). Elongation of the proboscis causes the salivary glands come to lie in front of the nerve ring so that the ducts no longer penetrate the nerve ring.

The accessory salivary glands in both species arise as paired ducts on the ventral lip of the mouth (Figure 7). In *C. anemone* these paired ducts appear to fuse early in development and only a single duct is present in the adult. In *N. lapillus* the ducts have been shown to fuse progressively during development so that a single duct leads to a pair of glands (BALL, 1994; BALL *et al.* 1997b) (Figure 7B).

The common origins and developmental pattern of acinous and accessory salivary glands in *C. anemone* and *N. lapillus* is further proof of the homology of these glands within the Neogastropoda. Furthermore, it can be seen from this study that the adult state of the glands does not reflect the whole story and this could be of importance when interpreting character states and in determining whether organs have been lost or secondarily regained.

Mid-oesophageal gland

In *C. anemone* the mid-oesophageal gland is composed of a long, coiled tubular duct (the venom gland) terminating in a muscular bulb (Figure 4). In *N. lapillus* the mid-oesophageal

gland consists of a bulbous gland (the gland of Leiblein) connected to the oesophagus by a short duct. PONDER (1970) speculated that the venom gland in cones is homologous with the glandular mid-oesophageal folds (=glande framboisée, *sensu* AMAUDRUT, 1898) of the Muricoidea and that the conoidean muscular bulb is the homologue of the gland of Leiblein. In *N. lapillus* the glandular mid-oesophageal folds are derived directly through differentiation of the dorsal folds whilst the gland of Leiblein develops from the morphologically ventral strip. The gland of Leiblein is therefore derived from tissue which is predominantly morphologically ventral in origin and the morphologically dorsal glandular folds do not contribute to the secretory portion of the gland, although they are present in part of the duct in the adult (Figure 16).

In the developing *C. anemone* embryos a blunt, finger-like outpushing at the posterior limit of the oesophagus forms during stage III (Figure 9). This is composed predominantly of the glandular ventral tissue and might represent the first stage in the development of the venom apparatus. However, since no subsequent developmental stages could be examined, later events are still unknown. The only author to have described *Conus* development (Franc, 1943) simply stated (translated from the original French - p.122) that "in the larvae of *C. mediterraneus*, [the venom apparatus] is composed of, as in the adult, an elongated bulb, placed against the stomach at the posterior part of the oesophagus, whose anterior extremity extends via a long and contorted tube, which, later, occupies a large part of the free space in the cephalic cavity." His illustration of the developing venom gland (FRANC, 1943; Figure 73, page 122), shows a cross section of the duct with a diameter of approximately 50µm composed of perhaps a dozen secretory cells with basal nuclei and apical secretory granules. These cells have the same appearance as secretory cells found in the ventral mid-oesophagus of *C. anemone* (Figure 8). FRANC (1943 - p.123) found that the venom apparatus in *C. mediterraneus* was "clearly differentiated by the time of hatching", but he did not describe the appearance of the larvae at various developmental stages and does not show or discuss the development of any other part of the foregut or its glands.

The similarity of the cells illustrated by FRANC (1943) and those of the out-pushing in *C. anemone* suggests that the evagination, which starts close to the mouth and terminates near the posterior limit of the secretory portion of the oesophagus, is the origin of the venom gland. The muscular bulb presumably forms at the termination of the out-pushing, perhaps by proliferation and differentiation of the mesodermal cells which form a thin coat over the length of the oesophagus (Figure 9).

Although it is disappointing to be unable to examine the final stages in development, the possibility that the venom gland forms through evagination in a manner similar to the formation of the muricid gland of Leiblein is further evidence for the homology of this gland throughout the Neogastropoda. Furthermore the ventral origins of the secretory cells of this putative venom gland rule out any possibility of homology between the conoidean venom gland and the muricoidean glandular dorsal folds.

Competence of hatchlings

N. lapillus hatches as miniature, sexually immature adults which possess all of the definitive foregut features together with a functional proboscis and radula. Examination of bivalve shells kept with emergent crawlaways shows that many of them were drilled. GOSSELIN and CHIA (1994) also showed that *Nucella emarginata* crawlaways were able to feed three days after hatching.

C. anemone emerges at the pediveliger stage. The hatchlings have a large foot and crawl actively, but the velar lobes are still present, albeit shrunken in some individuals and the animals are no longer able to swim. At this stage the acinous and accessory salivary glands are well formed, but proboscis and venom gland development are incomplete, this would suggest that they would be unable to feed. However, in one larval specimen a radular tooth was found at the mouth suggesting that teeth can be detached and transported from the radular sac by this stage in development (Figure 3). Thus the emergent *C. anemone* larvae may not have a fully functional complement of foregut glands, but may nevertheless still be able to envenomate prey. Neither can the possible use of accessory salivary gland secretions be ruled out. However, they probably suffer limitations in their prey handling ability due to the lack of a fully formed proboscis and this probably means that the juvenile and adult diets are necessarily different, although this could only be confirmed by behavioural studies.

CONCLUSIONS

In general *Conus anemone* follows a similar developmental pattern to *Nucella lapillus*. This suggests that the autapomorphic features of the neogastropod foregut are homologous in both superfamilies and supports the monophyly of the Neogastropoda.

Retardation in the developmental process, perhaps due to the presence of redundant planktotrophic feeding structures, lack of true adaptation to encapsulated development (lack of food eggs) and limited protolecith reserves may explain the comparatively early developmental stage at which *C. anemone* hatches from the egg capsule.

Detailed examination of the post-hatching stages of *C. anemone* development, either in *C. anemone* or another suitable species, is necessary to determine the latter stages of proboscis and venom apparatus development. However, it is apparent that many of the specialised features of the conoidean foregut have common origins with the less specialised muricid foregut.

Heterochrony has been suggested as an evolutionary mechanism for generating morphological diversity amongst the Neogastropoda (BALL, 1994). It is clear that there is considerable plasticity in the neogastropod foregut as evidenced by the high diversity in foregut types (see TAYLOR, KANTOR and SYSOEV, 1993; KANTOR, Medinskaya and TAYLOR, 1997, for example). Changes in the rate of development in certain key organ systems could be responsible for major differences in adult morphology.

ACKNOWLEDGEMENTS

This research was funded by a Natural History Museum Research Fellowship. I would like to thank John Taylor for the loan of the adult *C. anemone* slides and Yuri Kantor for permission to use his

drawing for Figure 1. I am also grateful to John Taylor and Peter Mordan for their help in preparing this manuscript.

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Lavoro accettato il 27 Giugno 2001