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The Functional Anatomy of the Mantle Complex and Columellar Muscle of Tectibranch Molluscs (Gastropoda: Opisthobranchia), and its Bearing on the Evolution of Opisthobranch Organization

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[Plate 1]

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An account is given of the anatomy of a series of opisthobranch molluscs principally to assess the change in importance and functioning of the mantle cavity and columellar muscle throughout the transition from prosobranch to opisthobranch organization. Intermediate steps are represented by living tectibranchs, of which *Philine* and *Scaphander* are investigated in detail, *Acteon*, *Bulla*, *Haminoea*, *Akera*, *Aglaja* and *Gastropteron* more briefly. Though an opisthobranch, *Acteon* has an organization typical of a monotocardian prosobranch; the remainder show trends affecting the shell and visceral mass, mantle cavity and head-foot, which resulted finally in the production of nudibranch types.

It is confirmed that the adaptations exhibited by primitive tectibranchs relate to the assumption of a burrowing mode of life. Initial changes were the reduction of the nuchal area and sealing of the mantle cavity anteriorly so that it opened on the right, where it became restricted, the first perhaps prompting the sealing. A broadening and an anterior elongation of the head-foot produced a wedge to facilitate burrowing. Change in disposition of the mantle edge, incurred by differential growth, produced an involute shell with a large body whorl, alignment changing from erect to horizontal. The resultant streamlining eased infaunal progression; no vertical insinking of the viscera was involved. Subsequently the shell became reduced and finally lost.

A section of the mantle edge enlarged to produce a posterior mantle lobe upon which sit both the shell and viscera, and which later became redundant as posterior elongation of the head-foot produced a slug-like form, the viscera being incorporated within the head-foot. As the nuchal area became reduced, mechanical needs prompted alteration to both the form and attachment of the columellar muscle. In *Acteon* the muscle is like that of a prosobranch, but the proximal region has broadened, a change of proportion required by primitive tectibranchs in order to support the floor of the mantle cavity formed from the section of mantle skirt which in prosobranchs lies on the right. This was followed by reduction and re-alignment of the entire muscle along an anteroposterior axis as emphasis changed from the muscle effecting retraction into a shell to producing contorsions of the head-foot. The shell, similarly reduced, instead of providing anchorage, became itself anchored by additional anterior and posterior attachment zones with, in more advanced forms, dorsoventral muscles of the body wall rather than longitudinal muscles fastening to the former. Importance was placed on the mutual stabilization of constituent parts of the posterior body region.

Re-alignment of the muscle induced breaking up of the longitudinal muscle sheet of the head-foot to produce muscle tracts, best exhibited in those tectibranchs which swim; they are derived from both the columellar muscle and intrinsic body wall muscles. In advanced opisthobranchs, the importance of the columellar muscle progressively diminishes and it is finally lost in the adult.

The mantle cavity shallowed, partially due to lack of space on the right where the mantle abuts against the viscera, but principally to avoid instability of its walls. Without support the walls will, especially in larger animals, tend to collapse owing to the restricted inhalant flow of water caused by the absence of an effective siphon and the adverse infaunal conditions. The floor may tend perhaps to be pushed laterally by increases in pressure within underlying haemocoelic spaces. Tensor muscles arose to stabilize the floor, for this became distinct from the thickened mantle edge represented by the posterior mantle lobe, and viscera were interpolated between the inner surfaces of the two regions of this section of the mantle skirt. The separation of surfaces was a consequence of the creation of space posteriorly by reduction of the nuchal area, shell and proximal columellar muscle, all adaptations to produce a slug-like form; the first was the most important at an early stage in evolution, the latter two at a later stage. There is no evidence that any tensor muscle is derived from the columellar muscle.

It is suggested that the first opisthobranchs were small, a feature which almost certainly favoured colonization of the infaunal niche, and lacked a gill, water flow being produced by ciliated bands as in various small gastropods. Upon a subsequent increase in size, a gill of different pattern to the prosobranch ctenidium evolved which is not important in producing water flow. The pallial caecum is a further respiratory innovation to offset functional inefficiencies which might otherwise have been incurred upon the increase in size which was undertaken under conditions of poor ventilation. Respiratory exchange was also facilitated by fusion of the pallial caecum to the visceral mass (*Philine*, *Aglaja*, *Akera*), which also enabled tensor muscles to attach to and stabilize its floor. In *Philine*, the roof also is stabilized by areas which adhere to the shell thereby ensuring that this caecum is always fully open.

Discussion of both the mantle complex and columellar muscle indicates a high incidence of parallelism.

It is suggested that the term detorsion be discarded. No rotation of the mantle skirt took place, but differential growth followed by folding to which the term posterior migration has been applied. Discussion of developmental studies indicates that torsion in opisthobranchs is halted at a stage which approximately corresponds to the position of the mantle complex in the adult, and in more advanced forms torsion is essentially abolished.

The final changes leading to the assumption of the nudibranch condition, and the phylogenetic interrelations of the animals investigated are briefly discussed. It is concluded that the general pattern of opisthobranch evolution was one of initial assumption of infaunal life, followed, after varying intervals of time, by return to the surface; only a few groups, of which the Philinidae are a good example, have fully exploited the infaunal niche.

1. INTRODUCTION

Until recently it has been generally accepted that the major evolutionary trends exhibited by the opisthobranchs are established (Boettger 1954; Morton 1958, 1963; Fretter & Graham 1962; Minichev 1967), but despite this, no detailed analysis of the relevant anatomical changes is available. Changes relate primarily to (1) loss of the shell, (2) migration of the mantle complex from an anterior position, characteristic of prosobranchs, to the right and subsequently posteriorly (to which the term detorsion has previously been applied) and (3) the production of a slug-like form.

That the adaptations might primarily relate to the infaunal niche of primitive opisthobranchs is stressed only by Fretter & Graham (1954), Morton (1958) and Fretter (1960). Central to these adaptations are changes in form of the mantle complex and skirt and of the columellar muscle, all of which reflect and take part in the modification of gross external form, and these are examined in detail. Emphasis has been placed on the functional problems involved in these adaptations and how they were solved, not only to give rise to the nudibranch forms, but also to tectibranchs which proved successful in exploiting soft substrata. Intermediate evolutionary stages are well represented by living forms, and a series of animals has been examined: *Acteon tornatilis* (L.), *Bulla striata* (Bruguière), *Haminoea navicula* (da Costa), *Scaphander lignarius* (L.), *Akera bullata* Müller, *Philine aperta* (L.), *Aglaja depicta* Renier and *Gastropteron rubrum* (Rafinesque), with most attention focused on *Philine* and *Scaphander* which are treated first. Examination of *Philine* is considered especially important because Rudman (1972*a*) has pointed out that the genus *Philine* is a successful one with almost 100 living species.

It is accepted, in agreement with most malacologists, that the opisthobranchs evolved from monotocardian prosobranchs, so that in the consideration of the evolutionary change of the mantle complex, the starting point is envisaged as an anteriorly facing mantle cavity containing a single ctenidium. The general form of the prosobranch columellar muscle which similarly provides a starting point is that of a strong band of fibres which twists around and originates on the columella, with fibres spreading out distally to all parts of the head-foot.

Although many authors have dealt with the anatomy of some or all of the species investigated here, and give some details of either the columellar muscle or the mantle complex, or both, most studies are of a general nature only and do not facilitate the tracing of evolutionary changes as is possible for those relating to the prosobranch mantle complex (Yonge 1947). Of these, earlier contributions are faithfully documented by Hoffman (1932–39). Relevant papers are those by Cuvier (1810), Vayssière (1880, 1885), Gilchrist (1894), Pelseneer (1894), Bergh (1900, 1901) Guiart (1901), Tchang-Si (1931, 1934), Eales (1938) and Risbec (1951).

Important studies of the mantle complex are those by Perrier & Fischer (1911) which dealt in detail with *Acteon*, *Hydatina*, *Scaphander* and *Akera*, Brown (1934) on *Philine*, Fretter & Graham (1954) on *Acteon*, Marcus (1956) on *Haminoea*, Marcus (1957) on *Bulla*, Fretter (1960) on *Ringicula*, Rudman (1971*a*) on *Haminoea* and Morton (1972) on *Akera*. Descriptions of the columellar muscle have been provided for *Aglaja* and *Gastropteron* by Bergh (1893*a*, *b*) and for *Philine* by Hurst (1965). An important contribution on *Cylichna* was made by Lemche (1956), who also dealt with the mantle complex. Additional scattered details of the columellar muscle of opisthobranchs have been collated by Franc (1968).

In this work, orientation of structures within the posterior body region of tectibranchs, which comprises the shell, visceral mass and the mantle complex, is based on the anteroposterior axis of the head-foot.

2. Materials and methods

Philine aperta and *Scaphander lignarius* were obtained from Plymouth Sound, the former from sandy-mud substrata and the latter from mixed bottoms. *Haminoea navicula* was collected from the Salcombe Estuary, Devon, and Seafield Bay, Co. Mayo, Ireland. Small specimens of *Akera bullata* were obtained from the Fleet, Dorset, and *Acteon tornatilis* from Oxwich Beach, Gower

Peninsula, South Wales. For the remainder of the work preserved material of *Acteon tornatilis*, *Bulla striata*, *Akera bullata*, *Aglaja depicta* and *Gastropteron rubrum* was examined.

In the laboratory *Philine* and *Scaphander* were kept in well-aerated seawater tanks at 10 °C. For *Philine* its normal substratum was added to a depth of approximately 4 cm, and in this they survived for up to two weeks; *Scaphander* survived best in tanks devoid of substratum.

Ciliary tracts on the walls of the mantle cavity, and the presence of water currents, were elucidated by the addition of carmine. A variety of common fixatives and staining procedures were used (see Pantin 1946).

Photomicrographs were taken on a Zeiss photomicroscope.

3. ANATOMY OF *PHILINE APERTA* (L.)

(*a*) *Organization of the posterior body region*

The body of *Philine* is divisible into anterior and posterior regions (figure 1), the former consisting of a cephalic shield (csh), and a broad ventral foot produced laterally into parapodia

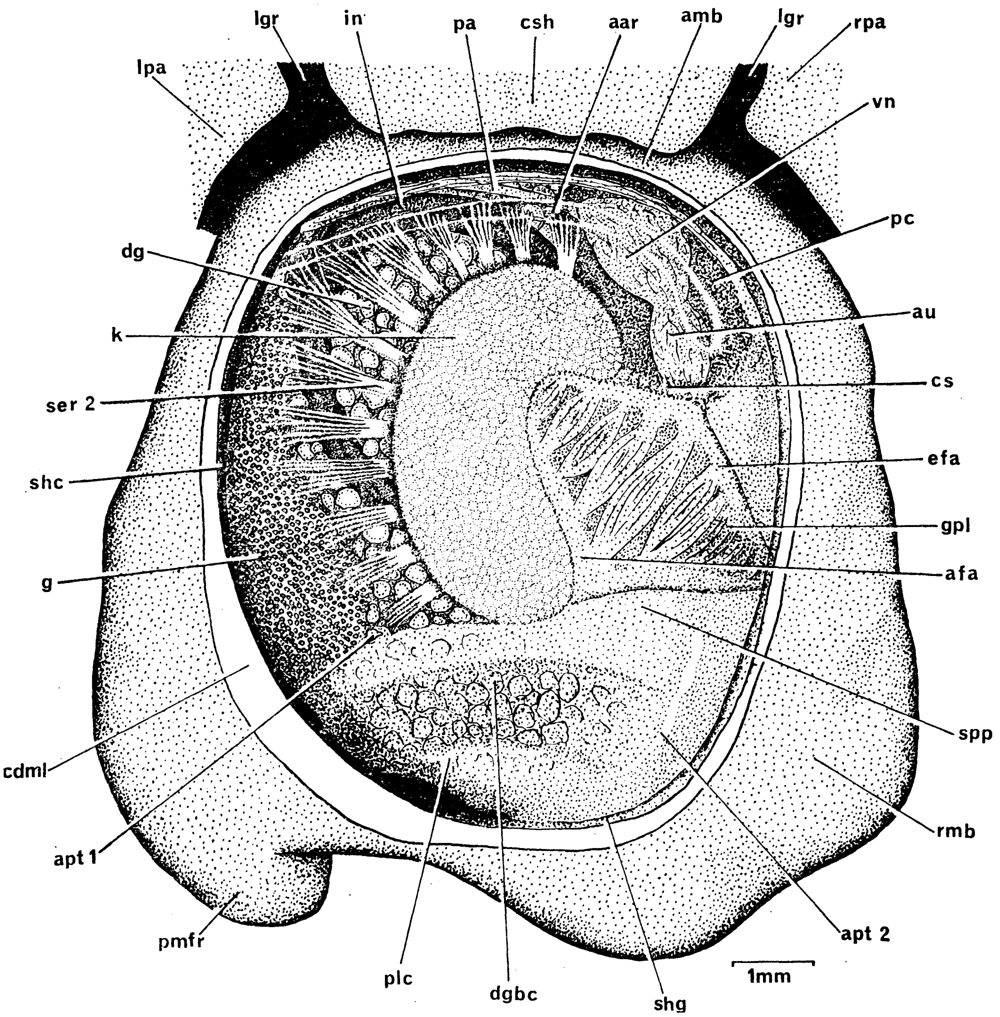

FIGURE 1. *Philine aperta*: dorsal view of the posterior body region with some structures seen by transparency; the shell and much of the dorsal mantle lobe have been removed.

(lpa, rpa). The posterior region comprises the visceral mass with mantle cavity and shell; its organization has been partially elucidated by Förster (1934) and Brown (1934).

The posterior region rests on a flattened posterior mantle lobe (pml, figures 2, 7*a*) (*lobe épicochléaire* of Perrier & Fischer 1911) continuous on the right with the floor of the mantle cavity, badly termed the infrapallium (ifp, figures 2, 5*b*). To its upper surface is fused the proximal portion of the columellar muscle (pcm, figures 6, 7*a*). Anteriorly it is joined to the foot by a narrower nuchal area marked by a gutter, the ventral nuchal groove (vncg, figure 2). The anterior limit of the infrapallium is difficult to define as it merges indistinctly with nuchal body wall. Certainly the genital opening (go) is surrounded by infrapallium; dorsally the 'osphradium' (os) is located in the roof of the mantle cavity or suprapallium (spp). The surface anterior to a line joining these two areas is taken as being nuchal.

Upon the posterior mantle lobe rests the visceral mass which has a swollen basal whorl, with its axis of coiling, as indicated by the reduced apical section, in an anteroposterior direction. The posterior mantle lobe to the left enlarges to produce a dorsal lobe (dml, figure 1) which encloses the shell. The later-formed section of the body whorl of the reduced involute shell takes the shape of a curved plate over the dorsal face of the visceral mass and suprapallium. The shell gland (shg) can be traced from a posterior limit (figures 1, 3*a*) on the right mantle border (rmb) anteriorly, and then left along the anterior mantle border (amb, figures 1, 7*d*). On the left it travels posteroventrally on to the posterior mantle lobe (figure 7*b*), but then becomes indistinct.

The anterior mantle border is fused to the dorsal nuchal area. It encloses beneath its free portion, a dorsal nuchal groove (dncg, figures 1, 7*d*).

The cephalic and visceral haemocoels are separated by a diaphragm (di, figures 5*a*, 7*d*) sloping obliquely backwards from a dorsal insertion to the nuchal area below the anterior mantle border, to a ventral insertion which, in the midline, is immediately anterior to the posterior edge of the foot. Its attachment to the foot on the left is closer to the midline than on the right (figure 6) due to a forward shift to allow for a sinking of the posterior body region into the anterior one.

The pericardial cavity (pc, figures 1, 7*c*, *d*) extends transversely across the most anterior section of the posterior body region, partly under the anterior mantle border to which its anterior wall is fused dorsally. The cavity is deep dorsoventrally on the right, but shallows on the left where also it does not extend so far back. Posteriorly the pericardium (prcd, figure 7*c*) bounds the digestive gland (dg); it extends anteroventrally over the reproductive structures to merge with the diaphragm and body wall (figure 7*d*).

Two blood vessels form important landmarks and their courses are described. The anterior aorta (aa), from its origin, runs to the right on the floor of the pericardial cavity, and then passes anteriorly, ventral to the duct of the bursa copulatrix. An anterior mantle vessel (amv) runs through the anterior mantle border to deliver blood to a collecting sinus (cs, figure 1), and thence to the heart.

Ventrally the visceral sac is filled with reproductive structures grouped around the genital opening, through both the bursa (bc, figure 7*d*) and the anterior lobe of the mucous gland (almg, figure 7*c*) are pressed against the diaphragm.

(*b*) *Organization and functioning of the pallial complex*

The mantle cavity opens along almost the entire length of the posterior body region on the right, though the opening is occluded laterally by the mantle border and the right parapodium (figure 2). The lateral cephalic groove (lgr, figures 1, 2) between the head-shield and foot allows the cavity to communicate freely with the exterior anteriorly. Posteriorly a gap occurs where the suprapallium and infrapallium meet; this is sometimes termed the cloacal sinus, but here will be called the exhalant aperture (exa, figure 2). It extends towards the midline because the junction of the outer lip with the shell apex is almost median.

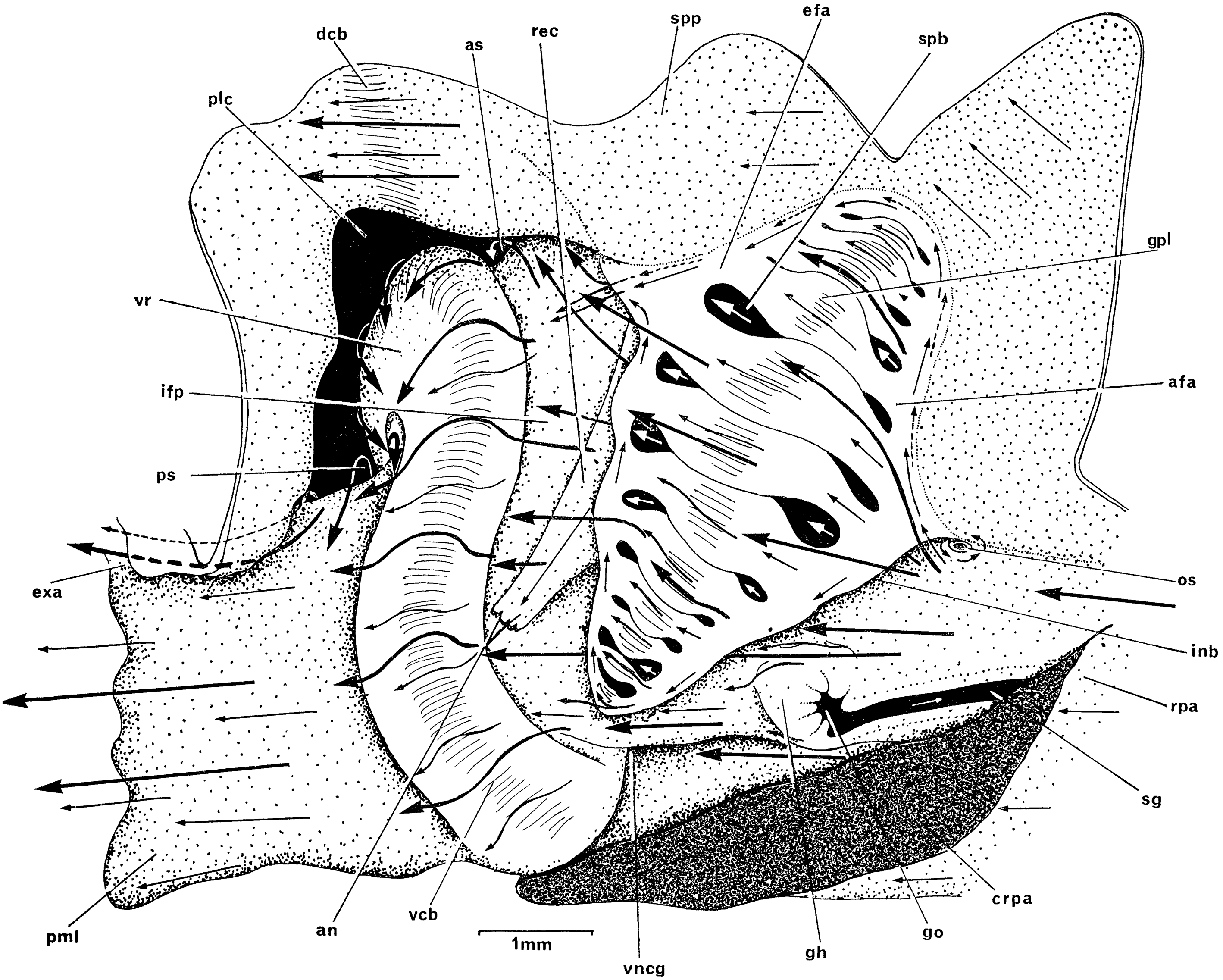

Figure 2. *Philine aperta*: diagrammatic lateral view of the mantle cavity from the right to show water currents and ciliary tracts; the suprapallium has been reflected dorsally. Large and small arrows denote, respectively, water currents and ciliary tracts; small broken arrowed lines indicate ciliary tracts on the ventral surfaces of the attached portions of the afferent and efferent gill axes, and on the medial face of the exhalant aperture.

The mantle cavity consists of two chambers which merge laterally. The anterior one is tongue-shaped and extends medially in an anterodorsal direction. It is largely bordered by the kidney (k, figure 1) and accommodates the lozenge-shaped plicate gill which lies horizontally between a posterior afferent axis (afa) and an anterior efferent axis (efa). The two medial edges of the gill attach to the wall of the chamber (figure 2), dividing it into suprabranchial (spb)

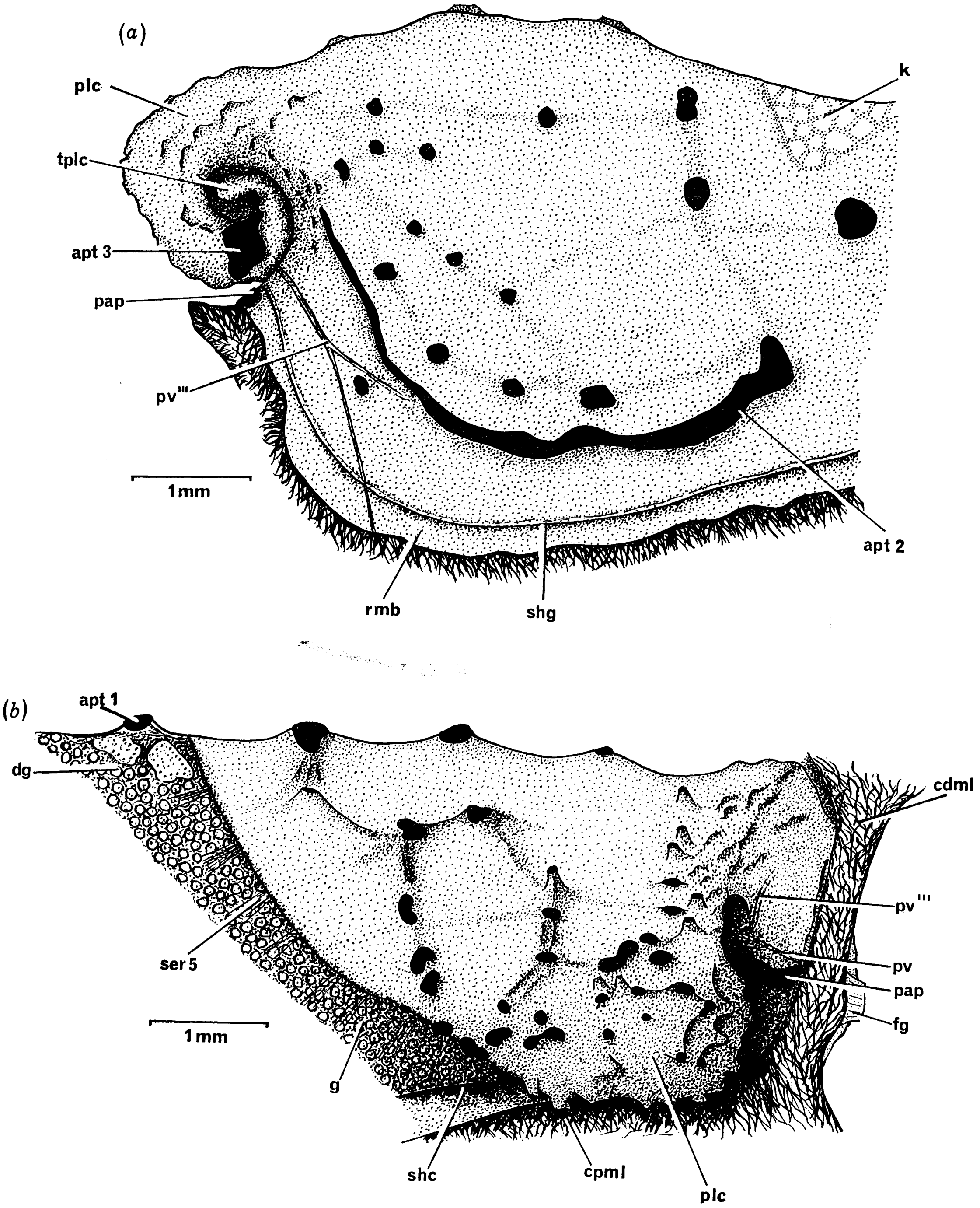

FIGURE 3. *Philine aperta*: to show the distribution of adhesive patches on the suprapallium. (*a*) Dorsolateral view from the right of the animal, to show the posterior section of the suprapallium; (*b*) lateral view from the left of the animal, to show the suprapallium of the pallial caecum. Adhesive patches are shown in black. The drawings are of material that has shrunk somewhat during fixation, thus emphasizing the locations of the patches.

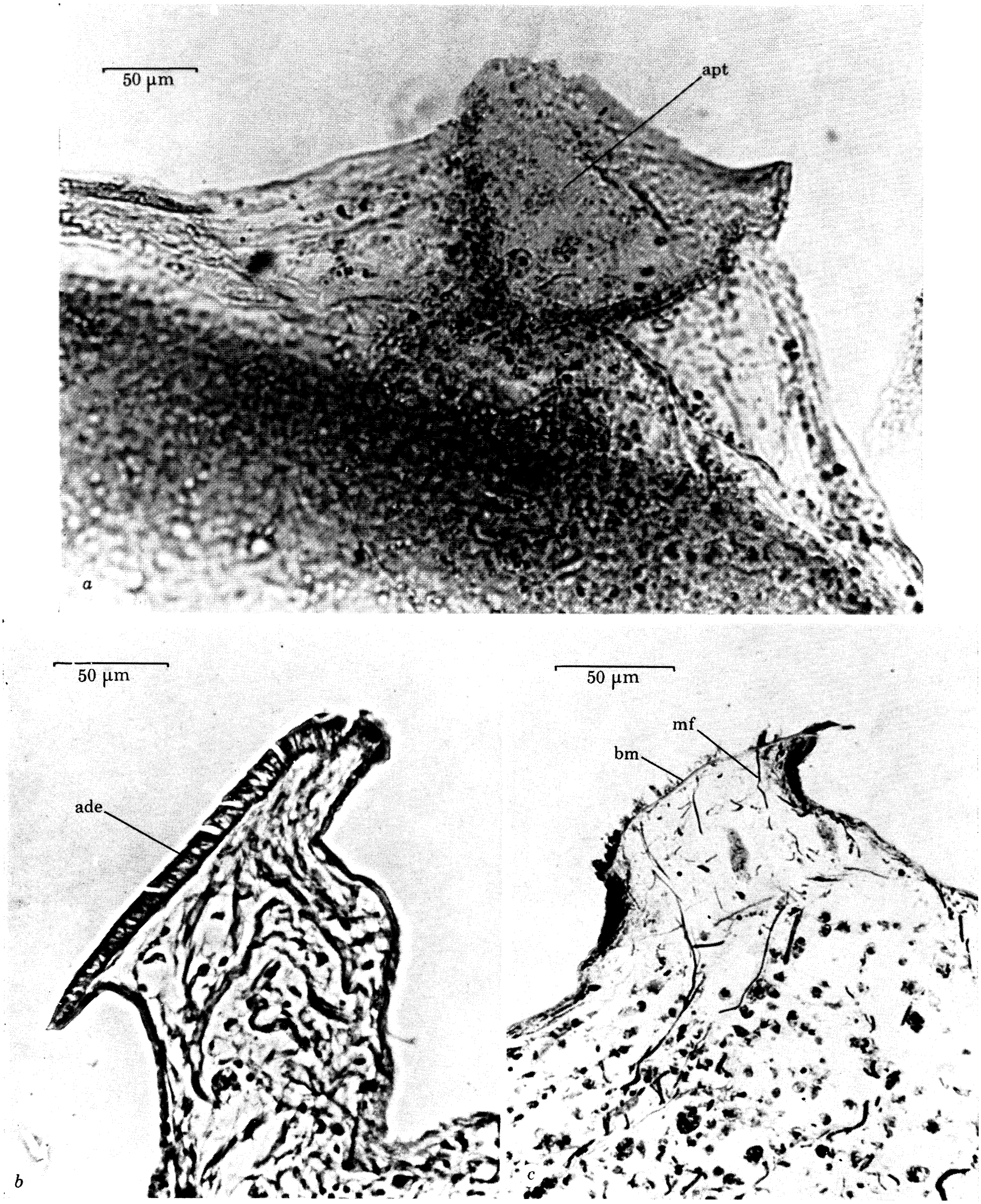

FIGURE 4. *Philine aperta*: raised adhesive patches. (*a*) Whole mount of one of the larger patches from the suprapallium of the pallial caecum (stained borax carmine); (*b*) transverse section of a patch to show the adhesive epithelium (stained Heidenhain's haematoxylin, phase contrast); (*c*) transverse section of a patch to show the basement membrane and muscle fibres attaching to it; the epithelium is largely torn away (stained Heidenhain's haematoxylin).

and infrabranchial (ifb) chambers. Underlying the infrapallium anteriorly is the genital mass which produces a large hump (gh). The rectum (rec) becomes attached to the infrapallium deep inside the infrabranchial chamber and runs posterolaterally to the anus (an.)

The posterior chamber or pallial caecum (plc, figures 2, 3, 5*b*) is a tapering tube, the anterior wall of which is attached to the visceral mass. It follows a vertical planospiral course for just over one turn, its tip (tplc, figure 3*a*) pointing posteriorly. Along its entire length run two bands of ciliated columnar cells which travel medially and slightly posteriorly from the mantle edges (figure 2) to the entrance of the pallial caecum. On entering it their relative positions alter so that the dorsal band (dcb) comes to lie posterodorsal to the ventral one (vcb), the latter sited on the prominent ventral ridge (vr). In cross-section (figure 5*c*) the cavity of the caecum is kidney-shaped owing to the ventral ridge which divides it into two chambers, the anterior (as) and posterior (ps) spaces. The rest of the epithelium of the caecum provides for an accumulation of mucous cells constituting the hypobranchial gland (hygl).

The suprapallium of the caecum is attached to the shell by adhesive epithelium which covers areas (apt) raised from surrounding tissue (figure 4*a*, plate 1). These patches pull away from the shell easily, but leave distinct scars on its surface. Their distribution has been determined; many of the larger ones (apt 1, figures 1, 3*b*; apt 2, figures 1, 3*a*; apt 3, figure 3*a*) have a constant position.

Few muscle fibres (mf) attach to the basement membrane (bm) of the adhesive epithelium (ade, figure 4*b*, *c*, plate 1); this is to be expected since their function is only to maintain the position of the suprapallium (see figure 5*c*).

Passage of water through the mantle cavity is from anterior to posterior (figure 2), first over the gill and then into the pallial caecum. It is caused, as in other tectibranchs, by the ciliated bands. The gill ciliation is weak and serves primarily to cleanse that organ; elsewhere ciliary activity keeps surfaces clear of particulate material (Brace 1974), although only a small amount enters the mantle cavity owing to the straining effect of a mucous veil over the entire external surface of the animal. The ciliated bands enable water to enter the anterior space of the pallial caecum by reducing pressure there, for the bands are in close approximation (figure 5*c*) allowing a pressure difference between compartments of the caecum to be utilized. This was ascertained by watching the path taken by fine suspended particles.

(*c*) *Extrinsic musculature of the mantle cavity floor*

A number of muscles called here tensor muscle strands stabilize the floor of the tectibranch mantle cavity.

(i) *Tensor muscle strands acting on the anterior region of the floor of the mantle cavity*

Three strands (tms 1, 2, 3, figure 5*a*) within the anterior body region attach to the median columellar muscle (mdcm, p. 12), and on the right fasten to nuchal body wall of the cavity floor. Strands 4 (tms 4, figure 5*a*), 5, 6 and 8 (tms 5, 6, 8, figure 5) have medial attachments on the proximal columellar muscle and pass to the right between viscera, the first attaching to the body wall and the remainder to the infrapallium of the anterior diverticulum. Fibres of strand 6, the major component, like those of strand 5, curve to run along the infrapallium, fanning out as they do so; the two strands, together with strand 7 cause a depression of the surface posterior to the genital hump. The attachments and course of strand 7 (figure 5*b*) are similar, though posterior to those of strand 6.

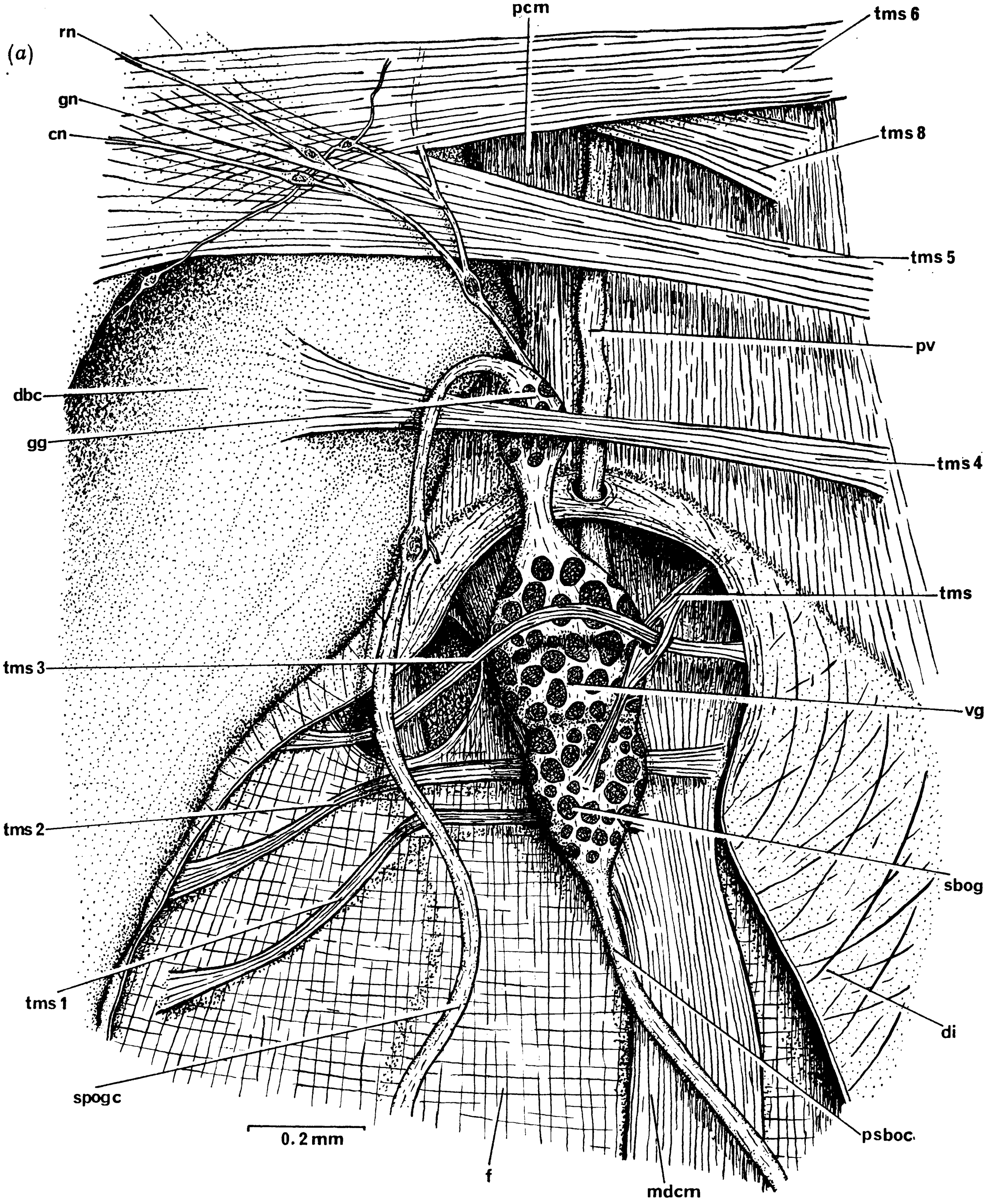

Figure 5. *Philine aperta*: dissections and diagram to show extrinsic muscles of the floor of the mantle cavity. (*a*) Dorsal dissection of the mid-body region; the viscera, anterior alimentary tract, and part of the diaphragm have been removed. Neurones within ganglia are represented semi-diagrammatically. (*b*) Dorsal dissection of posterior body region; the viscera have been removed. The infrapallium is reflected dorsally as is the pallium which lies immediately anterior to the pallial caecum which has been opened on the left side of the animal. The dissections are seen from an anterodorsal position. (*c*) Diagrammatic transverse section of the pallial section of the pallial caecum viewed from the left of the animal; the suprapallial adhesive patches and extrinsic muscles of the infrapallium are shown. Note the close apposition of the ciliated bands which is maintained by the muscles and adhesive areas.

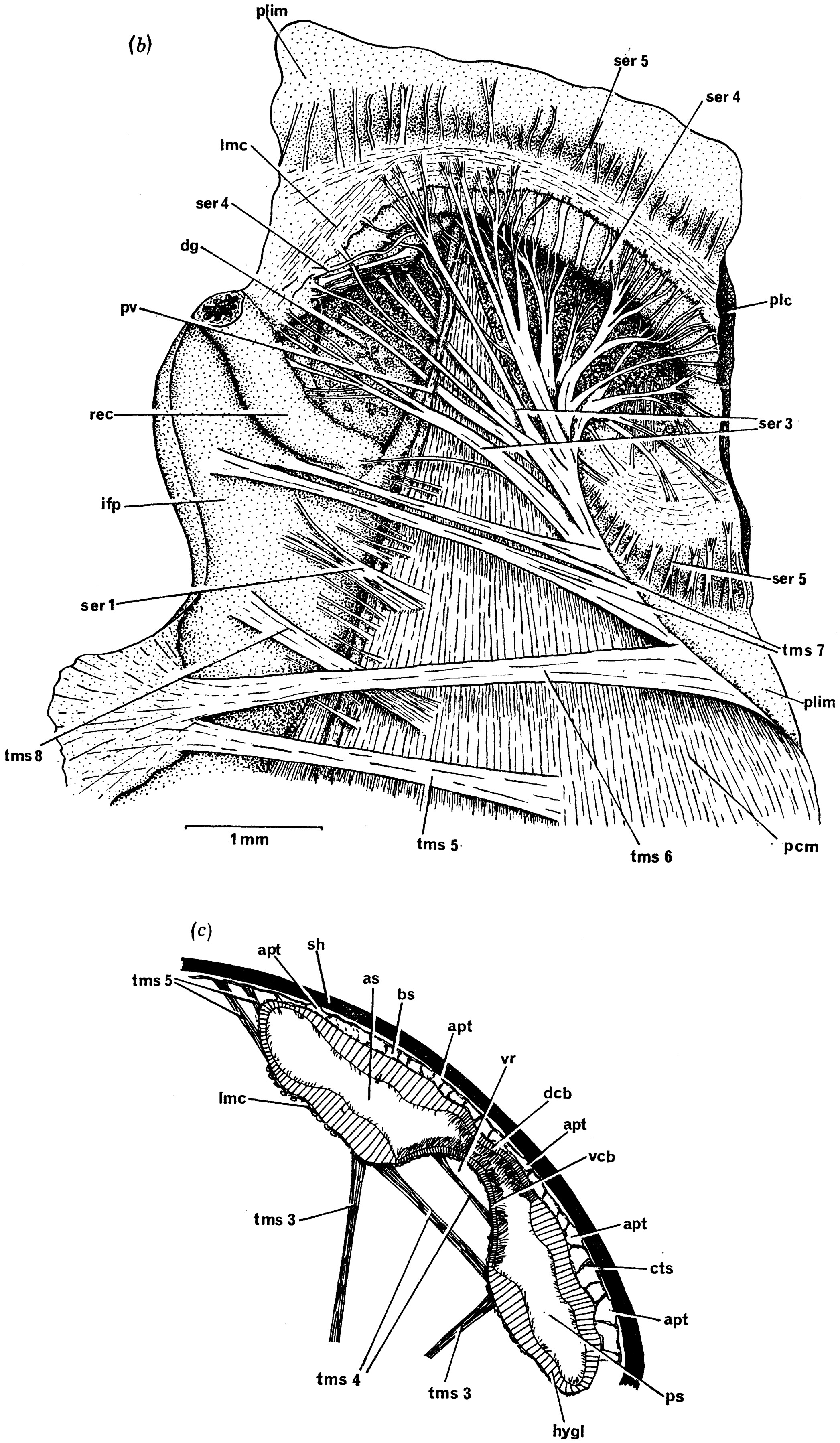

Figure 5 (*b*–*c*). For description see opposite.

In addition the floor of the gill chamber is anchored by a minor series of strands (ser. 1), and by a second series (ser. 2, figure 1) which consists of a radially arranged network ventral to the kidney, and attaches to the pallium and, anteriorly, also to the mantle border where many fibres fasten to the epithelium of the anterior adhesive ridge (aar, figure 7*d*).

All the major strands steadying the floor of the gill chamber act on one small area, where restraining forces are combined. Series 2 provides a force which acts in a dorsomedial direction, while forces imposed by strands 5, 6 and 7 act ventromedially. These groups of extrinsic components act simultaneously, but somewhat antagonistically. Similarly, if forces acting anteriorly and posteriorly are considered, the posterior members of series 2 partially antagonize the anterior ones dorsally, and strand 7 partially antagonizes strands 4 and 5 ventrally. The overall effect is that the infrapallium is kept taut and the gill chamber open.

(ii) *Tensor muscle strands acting on the anterior wall of the pallial caecum*

Three series serve the entire length of the attached region of the caecum. One (ser. 3, figure 5*b*) with ventral attachments continuous posteriorly with that of strand 7 is closely applied only to the columellar muscle, and largely attaches to the pallium (plim). Strands pass dorsally or posterodorsally between lobules of the digestive gland and gonad; near their ends they branch and attach to the ventral ridge, mostly at its sides (figure 5*c*). Another series (ser. 4, figure 5*b*, *c*), members of which are regularly spaced, traverses the ventral ridge, and the third (ser. 5) connects the dorsal region of the anterior wall of the pallial caecum to the dorsal face of the visceral mass. Series 3 and 4 sustain the shape of the ventral ridge, and thus aid the adhesive patches of the suprapallium (figure 5*c*) in maintaining the close apposition of the ciliated bands. Some muscles (lmc, figure 5*b*, *c*) run the length of the caecum in the anterior wall of the anterior space, their contraction tightening the infrapallium as it presses against parts of the visceral haemocoel.

(*d*) *Columellar and other muscles originating on the shell*

As the anterior insertions of the anterior columellar components have been fully described by Hurst (1965), detail given here is minimal and the reader is referred to figure 6.

The anterior part of the muscle consists of a median columellar muscle (mdcm) which runs freely through the cephalic haemocoel (cph) to insert on the anterior tip of the foot, and two lateral columellar muscles (lcm) each divisible into dorsal (dtr) and ventral (vtr) tracts, both situated within the body wall at a level externally marked by a lateral cephalic groove. Superficial longitudinal musculature (lccs) of the lateral areas of the cephalic shield is prominent and presumably of columellar origin (see p. 47).

Much of the superficial longitudinal muscle layer of the lateral regions of the foot is also probably constituted by columellar fibres, but discussion will show that the longitudinal fibres (dlmff) of the median region are not of columellar origin.

All columellar musculature in the foot emanates from the proximal columellar muscle. The origin of the median component (figures 5*a*, 6) is immediately anterior to the attachment of the diaphragm. The two tracts of the right lateral columellar muscle (figure 6) curve ventromedially as a strong bundle of fibres (ulm) which originates amongst fibres of the extreme right of the proximal mass. Posterior to the diaphragm, tracts of the left muscle similarly curve ventromedially, but the origin of this muscle is broader than that of the right since the two tracts do not converge.

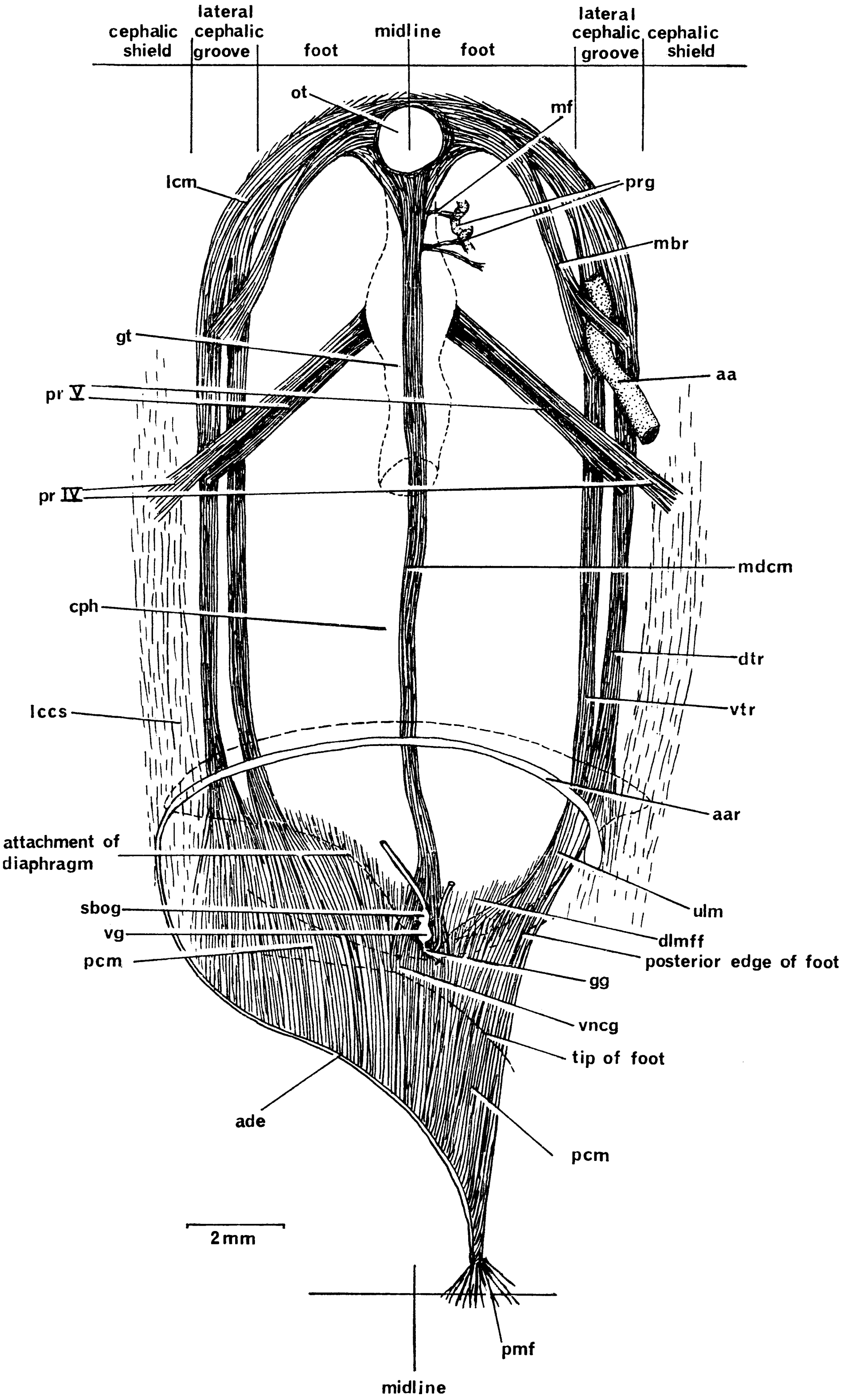

FIGURE 6. *Philine aperta*: semi-diagrammatical dorsal representation of the columellar muscle system and anterior adhesive ridge. The anterior, lateral columellar components are viewed as though laid flat; their proper positions can be ascertained by reference to locations provided at the top (anterior) of the figure. Both the anterior adhesive ridge and attachment of the diaphragm are drawn so as to accommodate for the flattening of the columellar components.

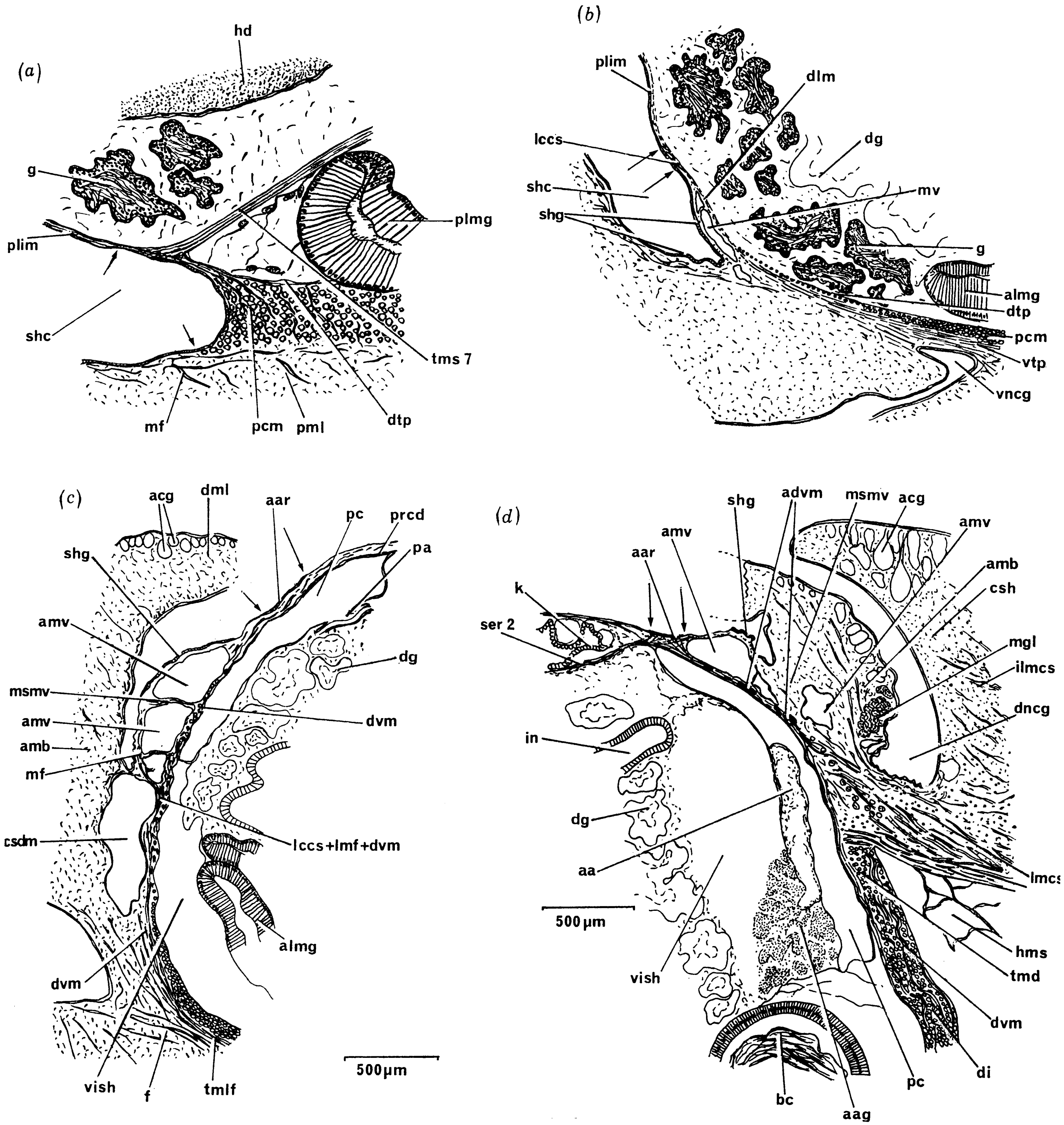

Figure 7. *Philine aperta.* (*a*–*c*) A series of progressively more anterior, semi-diagrammatic, transverse sections through parts of the posterior body region to show the shell attachment and associated muscles. (*a*) At the level of tensor muscle strand 7; (*b*) at a level a little posterior to the rear (vertical) edge of the foot; (*c*) at the level of commencement of the anterior adhesive ridge on the left. All sections are viewed from the posterior end of the animal. (*d*) Sagittal section of posterior body region to show the anterior adhesive ridge and muscles originating on it. Epithelium between members of each pair of arrow-heads is adhesive.

Fibres of the prominent musculature (lccs) on the right continue posteriorly through the nuchal area, with many of the medial ones terminating anterior to the attachment of the diaphragm. More lateral fibres curve ventromedially to terminate within the body wall more posteriorly. Other longitudinal fibres here, pass anteriorly into the diaphragm. The few columellar fibres in this region interweave with dorsoventral fibres. Many of the latter enter the mantle border, ventral to the mantle vessel, and some originate on the epithelium of the adhesive ridge. Insertions are to the foot and parapodium. The posterior course of columellar fibres (lccs) on the left is dealt with below, but many of the medially placed fibres, like those on the right, terminate anterior to the diaphragm.

The dorsoventrally flattened, proximal portion of the columellar muscle extends for almost the entire length of the posterior mantle lobe, and, as defined here, spans the ventral nuchal area also. Posteriorly it tapers to a point, right of the midline and ventral to the meeting of the suprapallium and infrapallium. Fibres run principally anteroposteriorly, though along the left margin they curve posterolaterally to the left where tapering, unlike the condition on the right, is not constant, for the narrow face follows the curvature of the shell to which attachment is made by an overlying adhesive epithelium. The fanning out of fibres which occurs on the right, is not seen on the left, for broadening is due to the addition of further fibres from a posterior origin on the shell.

To follow the course of the band of adhesive cells by which attachment is made to the shell, and to examine the muscles originating on it, it is convenient to start at the level where the proximal muscle has tapered somewhat, and adhesive epithelium overlies the whole of its lateral face and, in addition, extends dorsolaterally along the pallium, there providing stable attachment for tensor muscle strand 7 (figure 7*a*). The band will be followed posteriorly and then anteriorly.

Posteriorly adhesive epithelium extends well beyond the muscle not only to face ventrolaterally to the left, but also ventrally and then ventrolaterally to the right, providing anchorage for tensor muscle strands, some fibres of which attach to the epithelium, though most mix with other muscle fibres and connective tissue below it. The adhesive epithelium comes to overlie the suprapallium of the pallial caecum. A limited ventral extension anchors muscle fibres which attach to the infrapallium on the right. Remaining columellar fibres run posterodorsally to the left. Posteriorly, their attachment is to the first-formed section of the body whorl of the shell, to the later-formed section of the preceding whorl and then to the adapical umbilicus.

Numerous fibres (pmf, figure 6) fan out posteriorly and posterodorsally from the tip of the proximal muscle into the posterior and dorsal mantle lobes, below a raised adhesive patch (pap, figure 3) situated at the meeting of the two, the epithelium of which is continuous with that overlying the columellar muscle.

Anterior to the attachment of strand 7, the columellar muscle broadens rapidly, and its adhesive face becomes extremely concave, for here it attaches to the reduced columella. Initially the adhesive epithelium extends a short distance dorsolaterally along the pallium from the muscle, but then moves away from the proximal mass which assumes a shallow U-shape in cross-section, on to the anterior mantle border. There originate other muscles (dlm, figure 7*b*) which insert in a transverse muscle layer (vtp) ventral to the proximal columellar muscle, and to a less extent in a layer (dtp) overlying it. Not all the muscles fasten to the adhesive epithelium, for many merge with the pallium. Lateral fibres of the proximal muscle at this level overlie the dorsomedial edge of the mantle vessel (mv) and anteriorly are traceable into the lateral columellar muscle.

Anteriorly, the dorsolateral muscles assume a dorsoventral orientation (dvm, figure 7*c*) as the mantle moves dorsally, and ventrally reach into the transverse muscle layer (tmlf) of the foot (f). Many of these muscles, as more posteriorly, pass into the dorsal mantle lobe below the epithelium of the shell cavity (shc, figure 7*b*), while others penetrate the parapodium.

At this level, columellar fibres (lccs, figure 7*c*) on the left are present at a more dorsal level and pass, ventral to the anterior mantle vessel, through the nuchal area into the cephalic shield. Further longitudinal fibres (lmf) enter the diaphragm. Under the anterior mantle vessel are fibres (dvm) which form a continuation of dorsoventral muscles described above which, as the mantle border curves to the right, maintain the same relationship to it by, ventrally, being directed progressively more anteriorly. Some of these originate on the adhesive epithelium of the anterior ridge. Thus the situation on the left is similar to that on the right where the ridge forms the origin for dorsoventral muscles only, through towards its posterior limit on the left, as expected, columellar fibres (lccs) do originate there (figure 7*b*).

The anterior adhesive ridge (figures 1, 6) slightly raised, travels to the right, dorsal to the pericardial cavity and posterior to the shell gland from which it diverges somewhat on the right, to end in a boss. It adheres to the abapical shell margin, a little way in from the edge. To the ridge fasten some longitudinal muscles (lmcs) of the dorsal nuchal area and cephalic shield (figure 7*d*), and many aggregated fibres (advm). The latter form a criss-cross arrangement ventral to the mantle vessel, anteriorly enter the diaphragm, and stabilize the shell further by preventing lateral movements and uplifting. This is aided by the anterior members of series 2, for they act simultaneously, though somewhat antagonistically to the criss-cross arrangement.

4. ANATOMY OF *SCAPHANDER LIGNARIUS* (L.)

(*a*) *Organization of the posterior body region*

This is similar to that of *Philine* and only relevant differences between the two are enumerated.

The involute shell largely encloses the posterior body region, with the first formed part of the body whorl, in comparison to the later-formed section, larger than in *Philine*. The left face of the posterior mantle lobe, with the adhesive face of the columellar muscle (ade) form a concave surface (figure 12) on which the shell rests. Both the ventral nuchal area and rear edge of the foot are relatively better developed than in *Philine*, as is the rear extension of the foot, and consequently the anterior tip of the posterior mantle lobe is dorsal to the pedal sole (figure 9).

The attachment of the diaphragm (figures 10, 12) is symmetrical to the left and right, and dorsally, unlike *Philine*, lies below the attached portion of the anterior mantle border, for this is broadly fused to the nuchal area; ventrally the partition attaches to the nuchal area.

The pericardial cavity is extensive (figure 8). Anteriorly the pericardium lies against the dorsally sited bursa copulatrix, and there is extremely concave as the dorsal and ventral attachments to the pallium and diaphragm respectively, are placed along the long axis of the bursa. To the right, the pericardium meets the wall of the mantle cavity and anteroventrally fuses to the diaphragm, but becomes free at the level of the transversely running anterior aorta (figure 12) which is on the floor of the pericardial cavity, and extends dorsally to fuse with the pallium. Posteriorly on the right, it abuts against the kidney and overlies the albumen gland.

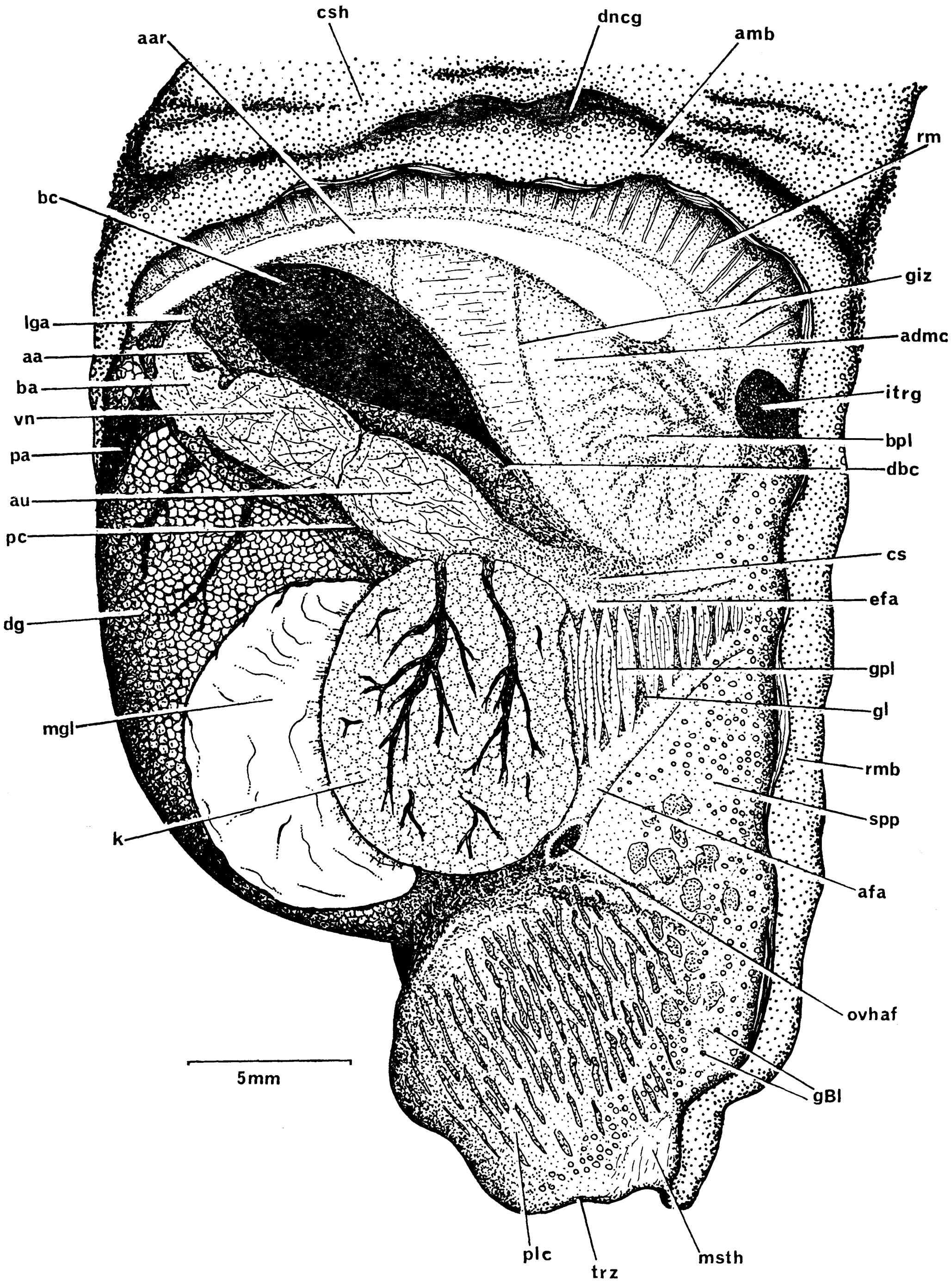

Figure 8. *Scaphander lignarius*: posterior body region in dorsal view; the shell has been removed and some structures seen by transparency.

(*b*) *Organization of the pallial complex*

The anterior diverticulum (admc, figures 8, 9, 12) of the mantle cavity, not present in *Philine*, is limited anteriorly by the mantle border and posteriorly by the bursa which lies between it and the pericardial cavity. It extends to a level two-thirds of the way along the long axis of the bursa to the left, with a posterior boundary below the midline of that axis. The infrapallium of

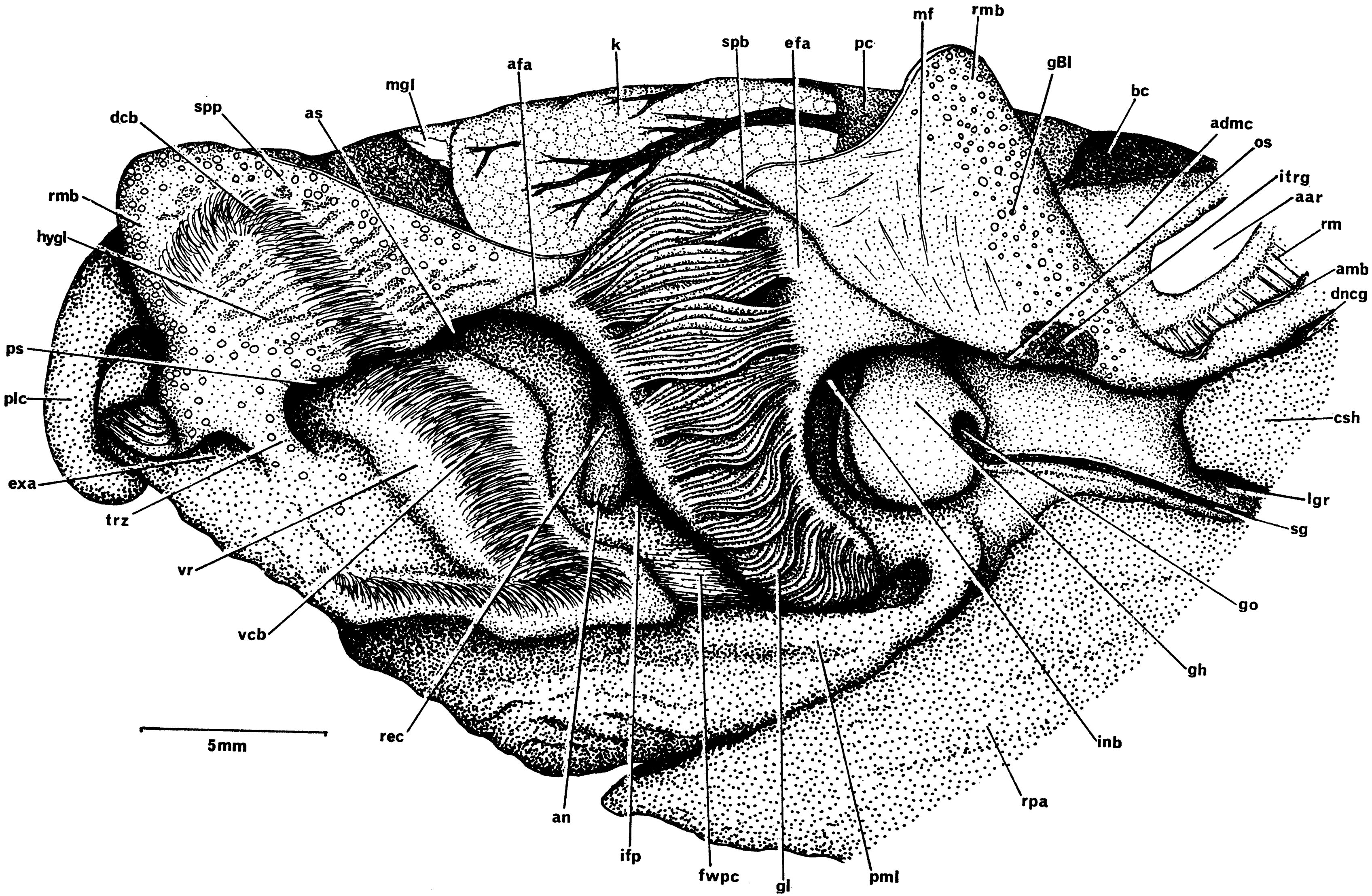

FIGURE 9. *Scaphander lignarius*: lateral view of the mantle cavity from the right; the shell has been removed and the suprapallium cut and reflected dorsally to expose fully the contents of the cavity.

the diverticulum is fused to the diaphragm. At the entrance to the chamber lies the 'osphradium' (figure 9) on the suprapallium, which also houses the kidney. The plicate gill (gl, figures 8, 9) is attached to the walls of the gill chamber by a short section of the afferent axis placed at the meeting point of the chamber and the pallial caecum, and by a somewhat longer section of the efferent axis. The most medial part is free, and thus the suprabranchial and infrabranchial chambers are not isolated from one another. The free distal section of the gill points laterally and is capable of considerable movement.

The pallial caecum (figures 8, 9) which in cross-section is similarly organized to that of *Philine*, coils independently of the visceral mass for approximately 45° against the adapical umbilicus, following a planospiral course and narrowing anteriorly to end bluntly. Unlike *Philine*, a distinct, dorsoventrally orientated section of the mantle skirt, called here the transitional zone (trz) connects the infrapallium and suprapallium medial to the exhalant aperture. This zone (pli sutural of Perrier & Fischer 1911) is lodged against the shell apex; immediately medial to the exhalant aperture it is thickened and muscular (msth, figures 8, 11*b*).

The mantle cavity is not cut off from the exterior to the same degree as in *Philine*, though most water enters anteriorly after passing along the lateral cephalic groove.

(*c*) *Columellar muscle and shell attachment*

Within the anterior body region the columellar muscle is not confined to discrete tracts as in *Philine*, and its fibres constitute much of the superficial longitudinal muscle layer of the body wall laterally (figures 10, 12), forming broad bands. Two obvious bands (lcb, figure 10), one on either side, run along the lateral areas of the cephalic shield, and at a level marked externally by the lateral cephalic grooves. The median regions of the foot, cephalic shield and dorsal nuchal area are virtually devoid of columellar fibres.

Posteriorly the muscle bands pass ventromedially through the nuchal area, converging to origins within the proximal mass, though this course of travel, as in *Philine*, is less noticeable on the left than on the right.

When viewed dorsally, the proximal mass is triangular with sides approximately twice the length of the base. Broadening on the left, as in *Philine*, occurs by the addition of further fibres originating on the shell, rather than by spreading as on the right. Posteriorly the muscle lies right of the midline, its tip at a level immediately anterior to the pallial caecum (figure 11*a*). The ventral face of the muscle is thus fused to the posterior mantle lobe for approximately two-thirds of that lobe's length (figure 10). Anteriorly the muscle has a shallow U-shaped outline in cross-section, replaced posteriorly by a roughly triangular one, concave on the left. To the right a few muscle bands (mbcm) diverge. Fused to the mantle lobe, these run posteriorly towards the ventral ciliated ridge at the point where it curves posteriorly.

The adhesive epithelium of the proximal columellar muscle faces ventrolaterally; a ventral extension occurs as in *Philine*, but not a dorsal one. At the rear of the proximal mass fibres fan dorsolaterally to the left, following the curvature of the shell, and there the adhesive face attaches to the outer surface of the later-formed section of the penultimate whorl. The adhesive epithelium continues beyond the posterior tip of the columellar muscle, below the proximal region of the caecum, as a narrow band of cells (ade, figure 11*a*) facing ventrally. Towards the rear of the animal the band broadens, moves slightly ventrolaterally to the right, and then narrows again to travel dorsally over the rear face of the transitional zone, where it attaches to the adapical umbilicus. The adhesive area terminates on the suprapallium (figure 11*b*), partially overlying the muscular thickening of the transitional zone, and fastens there to the inner face of the later-formed section of the body whorl. Attachment is also secured to the adapical umbilicus by raised patches along the rear edge of the caecum.

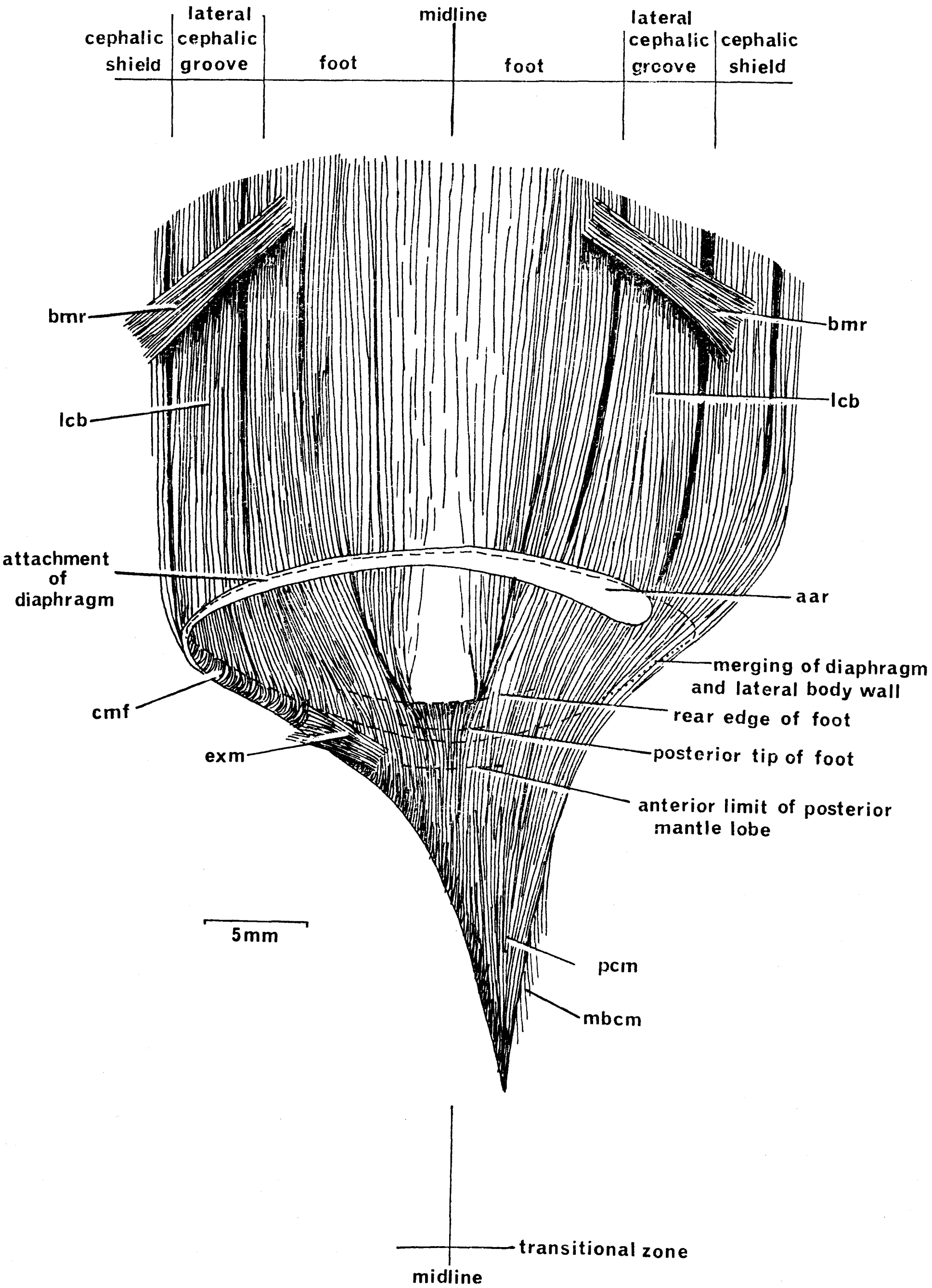

FIGURE 10. *Scaphander lignarius*: a semi-diagrammatic dorsal representation of the columellar muscle system and anterior adhesive ridge. The anterior, lateral columellar components are viewed as though laid flat; their proper positions can be ascertained by reference to locations provided at the top (anterior) of the figure. Both the anterior adhesive ridge and attachment of the diaphragm are drawn so as to accommodate for the flattening of the columellar components; the most anterior section of the columellar muscle is not depicted.

Within the muscular thickening, fibres run principally transversely, many originating on adhesive epithelium which faces ventrally, a few on that facing dorsally; to the right, fibres enter the suprapallium overlying the exhalant aperture. Certainly the muscle will, as Lemche (1956) has suggested for *Cylichna* (musculus retractor pallialis posterior), be capable of retracting the mantle, but it also presumably has, together with the overlying adhesive epithelium, the more important function of keeping the mantle rigidly in place against the shell. Some fibres continue along the rear edge of the caecum and fasten to the epithelium of the adhesive patches.

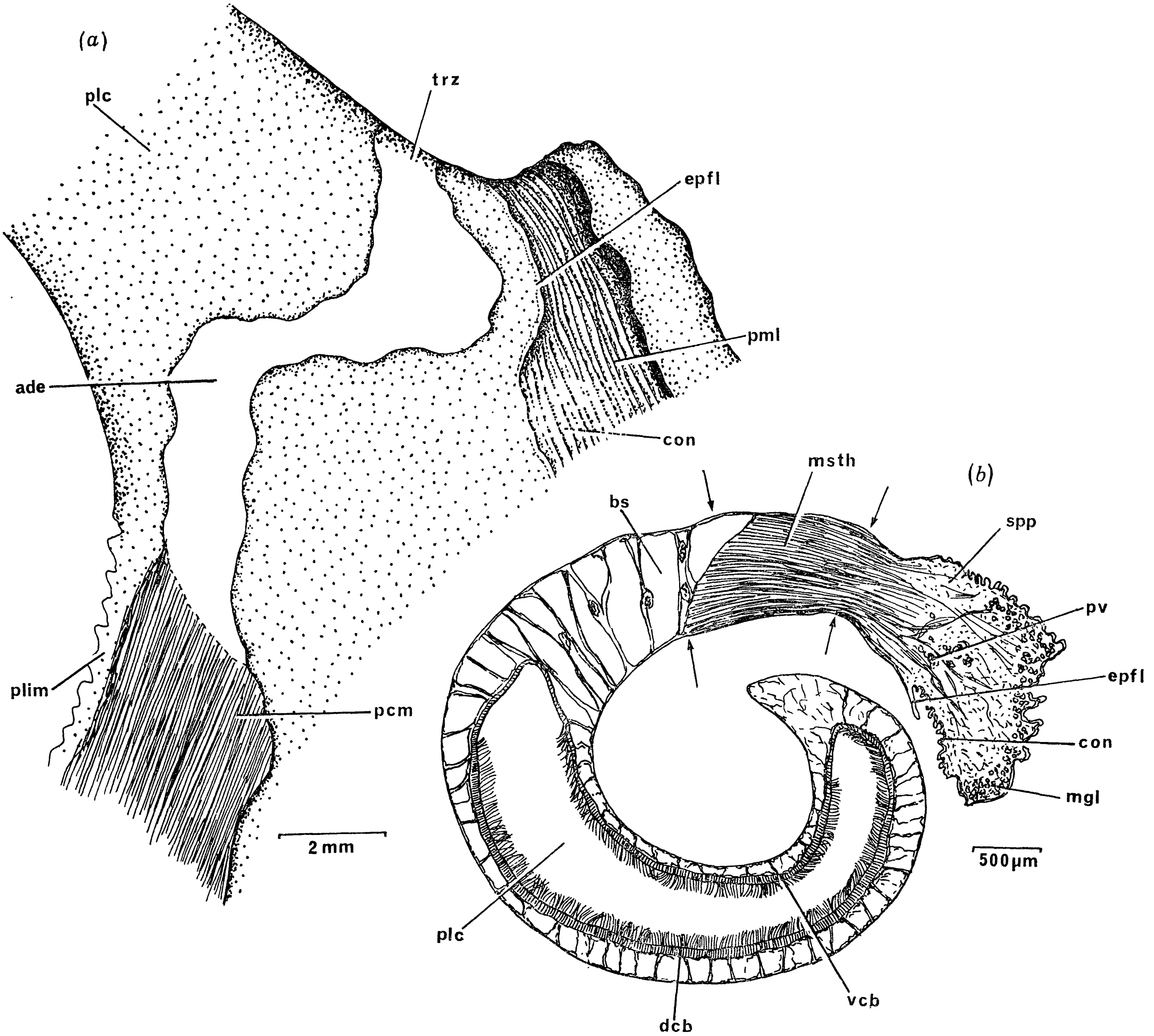

FIGURE 11. *Scaphander lignarius*: to show shell attachment areas. (*a*) The ventral surface of the base of the pallial caecum and concave face of the posterior mantle lobe which have been laid flat; note the band of adhesive epithelium linking that overlying the proximal columellar muscle and that overlying the posterior muscular thickening. (*b*) Transverse section through the pallial caecum posteriorly to show the posterior muscular thickening, viewed from the posterior end of the animal; epithelium between members of each pair of arrowheads is adhesive.

Anteriorly, the adhesive face becomes exceedingly concave, moves dorsally well left of the midline (figures 10, 12), and attaches to the columella. After passing posterior to the diaphragm and leaving the nuchal body wall, fibres (cmf) curve posteroventrally to the left and quickly find origins on the shell. Here, as in *Philine*, though not to the same degree, the proximal mass of fibres is not obvious. Fibres are traceable anteriorly into the body wall at the levels of the lateral cephalic groove and lateral region of the cephalic shield. Subsequently the band of adhesive cells travels dorsomedially, situated on the anterior adhesive ridge upon which originate fibres (lmcs, figure 12) which pass into the nuchal area and cephalic shield. Only a few fibres take this course in *Philine* as a consequence of the narrower width of fusion between the mantle border and body wall. In addition, some fibres (dvm) enter the diaphragm but, as the partition initially extends posteroventrally from its dorsal attachment rather than anteroventrally as in *Philine*, they are few in number and cannot stabilize the shell margin. In *Philine* in which only a few muscular ties are required to stabilize the reduced shell, emphasis has shifted

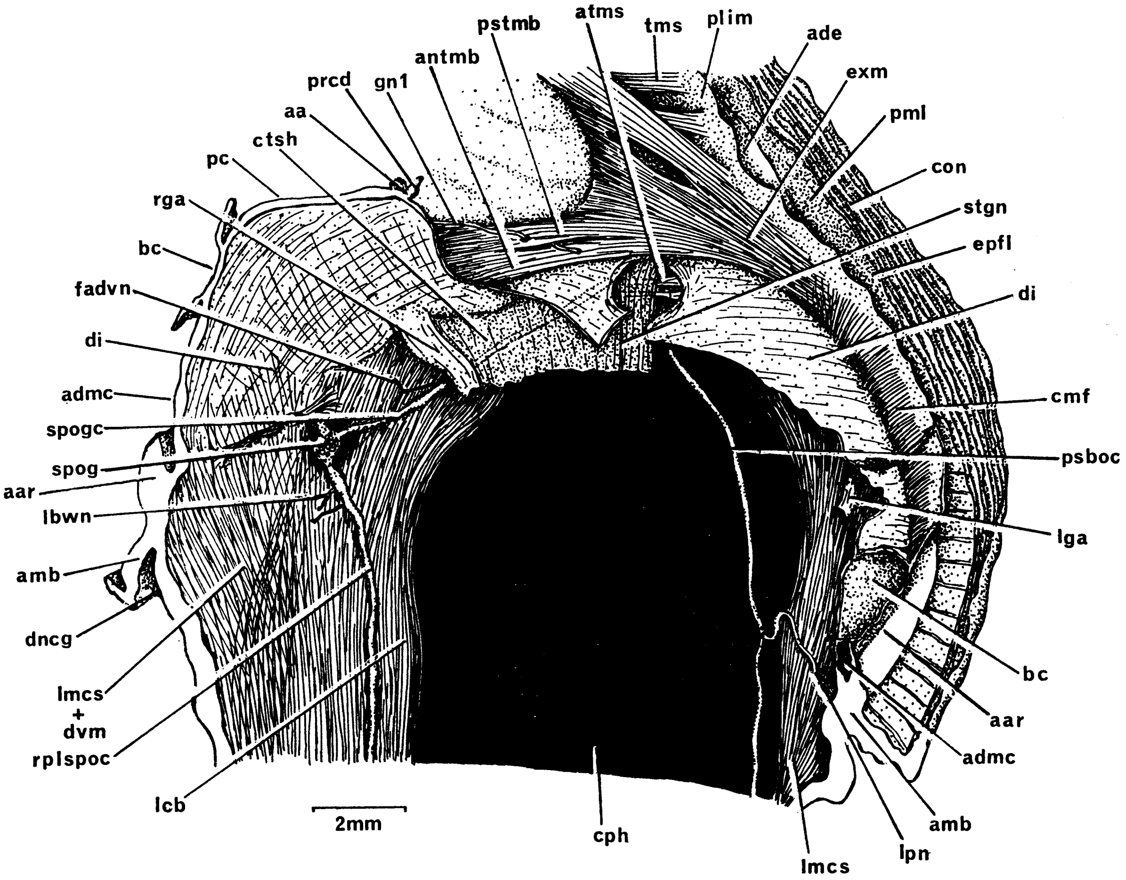

FIGURE 12. *Scaphander lignarius*: dorsal dissection of the mid-body region to show general anatomy, extrinsic muscles of the infrapallium, other musculature and part of the visceral loop; most of the viscera have been removed, and the infrapallium (not shown) reflected dorsally to the right of the animal. The anterior body region has been opened by a median, longitudinal incision in the cephalic shield and the two parts pulled laterally; the incision has been carried posteriorly to the anterior mantle border. The gut has been completely removed and the cephalic haemocoel is shown in black; the diaphragm has been cut and part of it reflected towards the right side of the animal. The anterior diverticulum of the mantle cavity has been opened by removal of the suprapallium; posterior is at the top of the figure.

from anchorage by fibres passing posteriorly from the cephalic shield to the adhesive ridge, to weak, but more effectively placed, dorsoventral muscles.

On the right, the ridge broadens and terminates a short distance medial to the lateral point of fusion of the mantle border to the body wall, where it overlies the anterior diverticulum of the mantle cavity and acts as origin to a few muscles which run anteroventrally and slightly laterally into the body wall, lateral to the columellar fibres there.

(*d*) *Extrinsic musculature of the mantle cavity floor*

Two tensor muscle strands (atms, figure 12) span the cephalic haemocoel, on the right attaching to the floor of the mantle cavity; they are comparable with the musculus transversus corporis inferior and the musculus transversus capitus inferior of *Cylichna* (Lemche 1956).

The major extrinsic components (exm, figures 10, 12) attach largely on the proximal columellar muscle to the left, stabilized there by its adhesive face, but some fasten to the pallium where no underlying adhesive epithelium occurs. They fan out laterally and posterolaterally to the right. Anterior muscles curve dorsally, splitting into two bands; fibres of the anterior one (antmb, figure 12) attach to the infrapallium, largely below the duct (dbc, figure 8) of the bursa copulatrix. Fibres of the posterior band (pstmb, figure 12) and remaining muscles fan out more posteriorly fastening to the floor of the gill chamber, keeping it depressed. All these muscles are comparable with the fascia genitale (Lemche 1956) of *Cylichna*.

Tensor muscle strands (tms) also fasten ventrally to the pallium or to the proximal muscle and dorsally to the infrapallium of the gill chamber. A series of minor strands connects the infrapallium and pallium dorsally.

5. ANATOMY OF *ACTEON TORNATILIS* (L.)

(*a*) *General organization, and anatomy of the nuchal region*

The proportions of the head-foot are similar to those of a coiled prosobranch (figure 13), but the nuchal area is less extensive and the head bears flattened labial (lt, figure 13*a*) and cephalic (cpt) tentacles. The operculum (opc) may completely seal the retracted animal within its shell. Details of the mantle complex have been covered by previous authors; it is necessary only to note that the pallial caecum is long, the infrapallium extensive, the mantle lobe incipient, and that the anterior mantle border is fused to the nuchal area left of the midline only.

Posteriorly the cephalic haemocoel is blocked by a septum (vs, figure 14*a*) at a level posterior to the anterior mantle border. It appears to be homologous with the vertical septum (Fretter & Graham 1962) of monotocardian prosobranchs which separates the cephalic and visceral haemocoels, but its position with respect to those animals is more anterior, and the body wall extends for some distance posterior to it. The visceral ganglia (vg, figure 24*b*) are similarly more anterior, for they lie at a level immediately posterior to the septum as in prosobranchs.

Anteriorly to the right, the floor of the mantle cavity, formed there by body wall, is anchored by ranks of oblique muscles (obl, figure 14*b*). Relationships of the vertical septum, visceral ganglia, oblique muscles and neighbouring blood spaces (Brace 1974) are as in monotocardian prosobranchs; the muscles are homologous to the transverse septum of those animals.

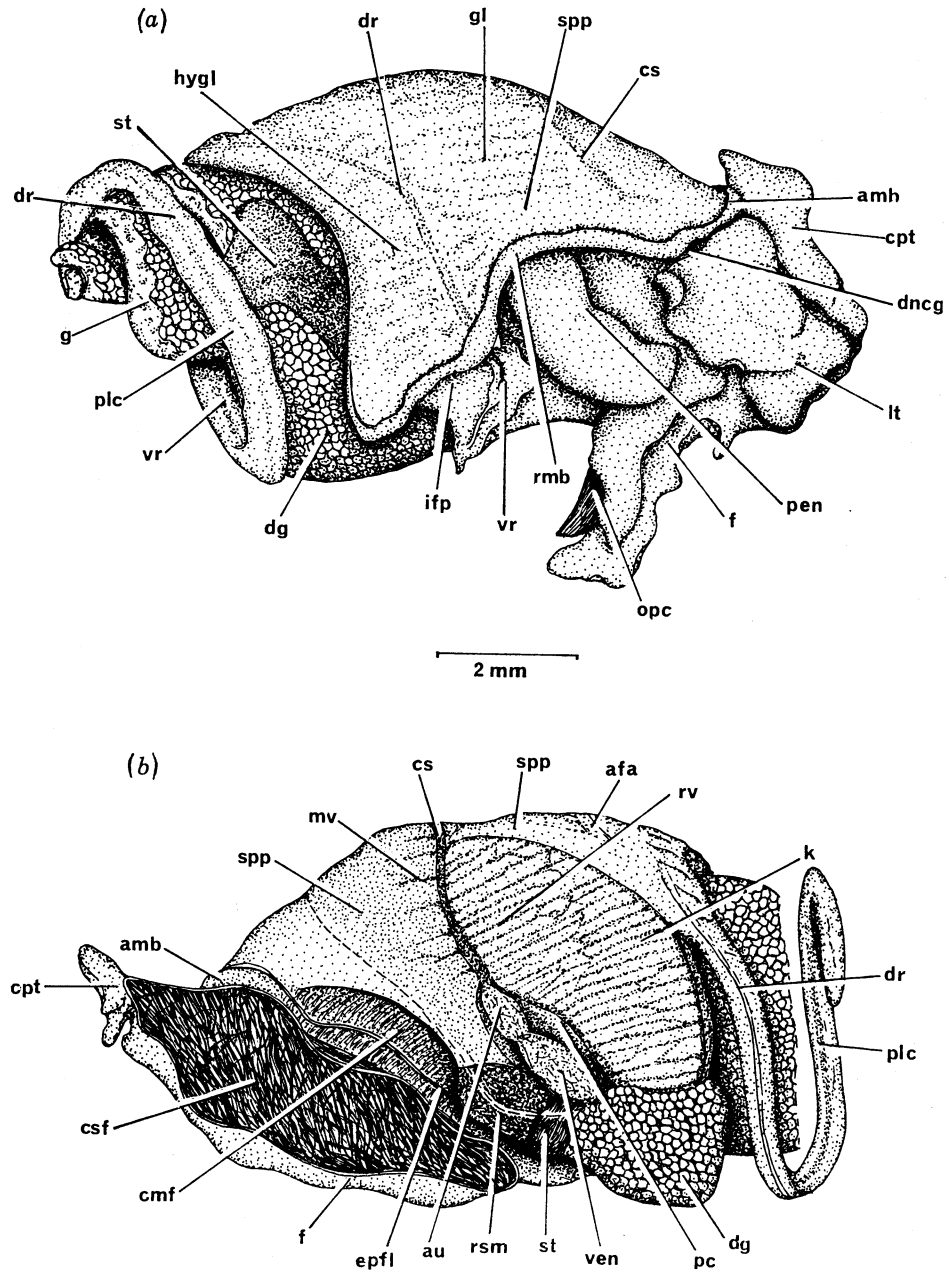

Figure 13. *Acteon tornatilis*: external features; the animal, which is not extended, has been removed from its shell. (*a*) Animal seen from the right; (*b*) in ventrolateral view from the left. The anterior margin and part of the medial margin of the mantle cavity are indicated by a broken line.

Figure 14. *Acteon tornatilis*. (*a*) Dorsal dissection from the right seen in anterolateral view to show the relationships of structures bordering the mantle cavity at the rear of the head-foot and base of the visceral hump; the suprapallium has been removed, though part of the pericardial cavity and heart remain. Much of the infrapallium and the genital mass have been taken away to expose the underlying nervous system and proximal columellar muscle. (*b*) Dissection to show the columellar and other muscles within the cephalopedal mass; a median dorsal, longitudinal incision has been made in the body wall and the two parts pulled laterally to expose the inner face of the body wall and contents of the cephalic haemocoel. The oesophagus has been cut through and part of it, together with the buccal mass, pinned anteriorly; all nerves emerging from the nerve ring, except the visceral loop, are omitted.

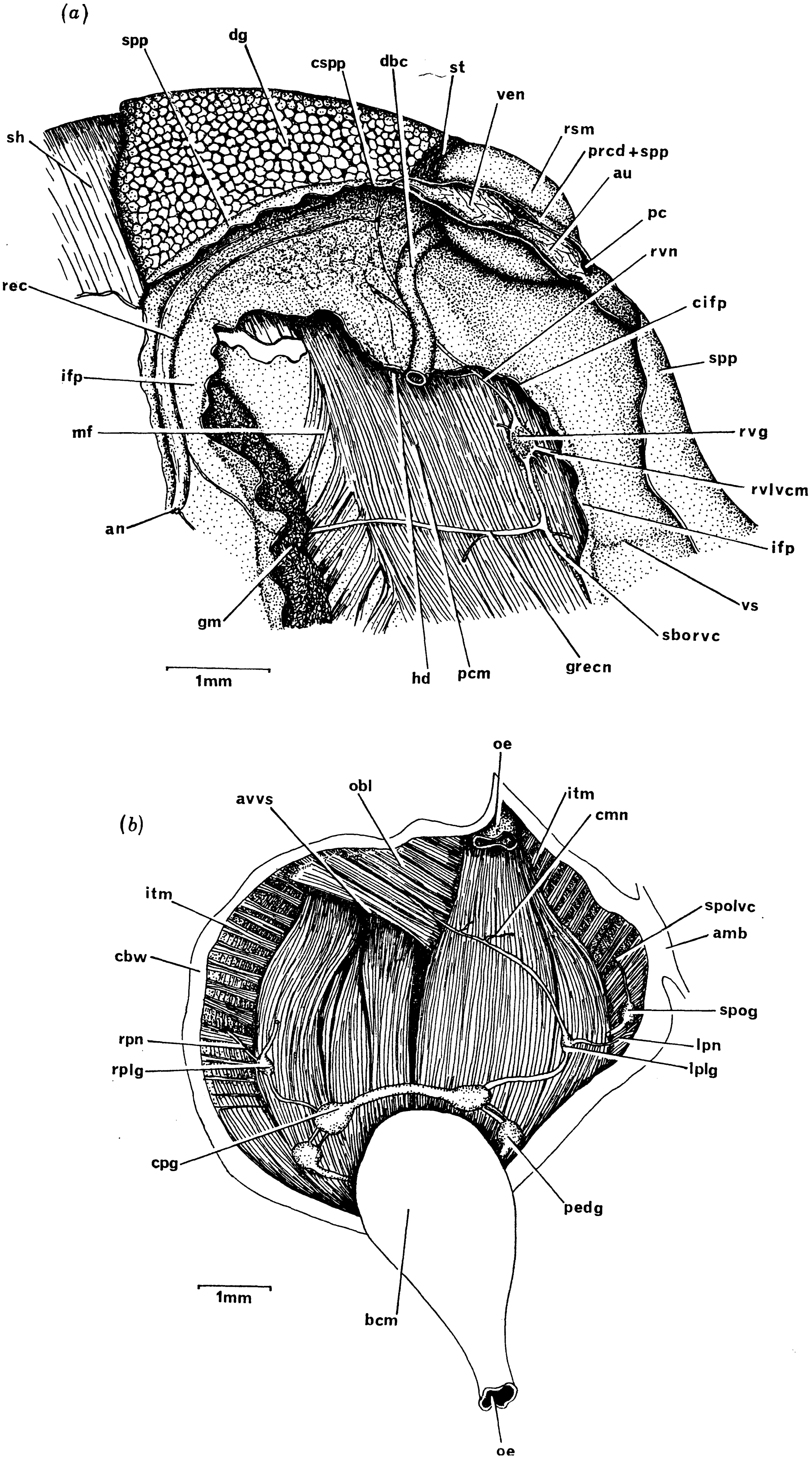

Figure 14. For description see opposite.

(*b*) *Columellar muscle*

The proximal section of the muscle (figure 14*a*) is broad and, when contracted, is coiled more tightly and to a greater degree than that of a typical prosobranch. The muscle originates on the columella with its upper part lying against the visceral hump; from its right edge diverge groups of fibres (mf) which attach to the infrapallium over the lateral face of the genital hump.

More anteriorly the muscle spreads out within the head-foot, but does not encroach upon the dorsal body wall posterior to the vertical septum, or for a short distance anterior to it. Many fibres (cmf, figure 13*b*) run within the posterior face of the neck to interweave anteriorly with muscles of the metapodium and insert on the operculum and ventral epithelium. Remaining fibres constitute most of the longitudinal muscle bands of the body wall (figure 14*b*), with some fibres fastening to the ventral epithelium.

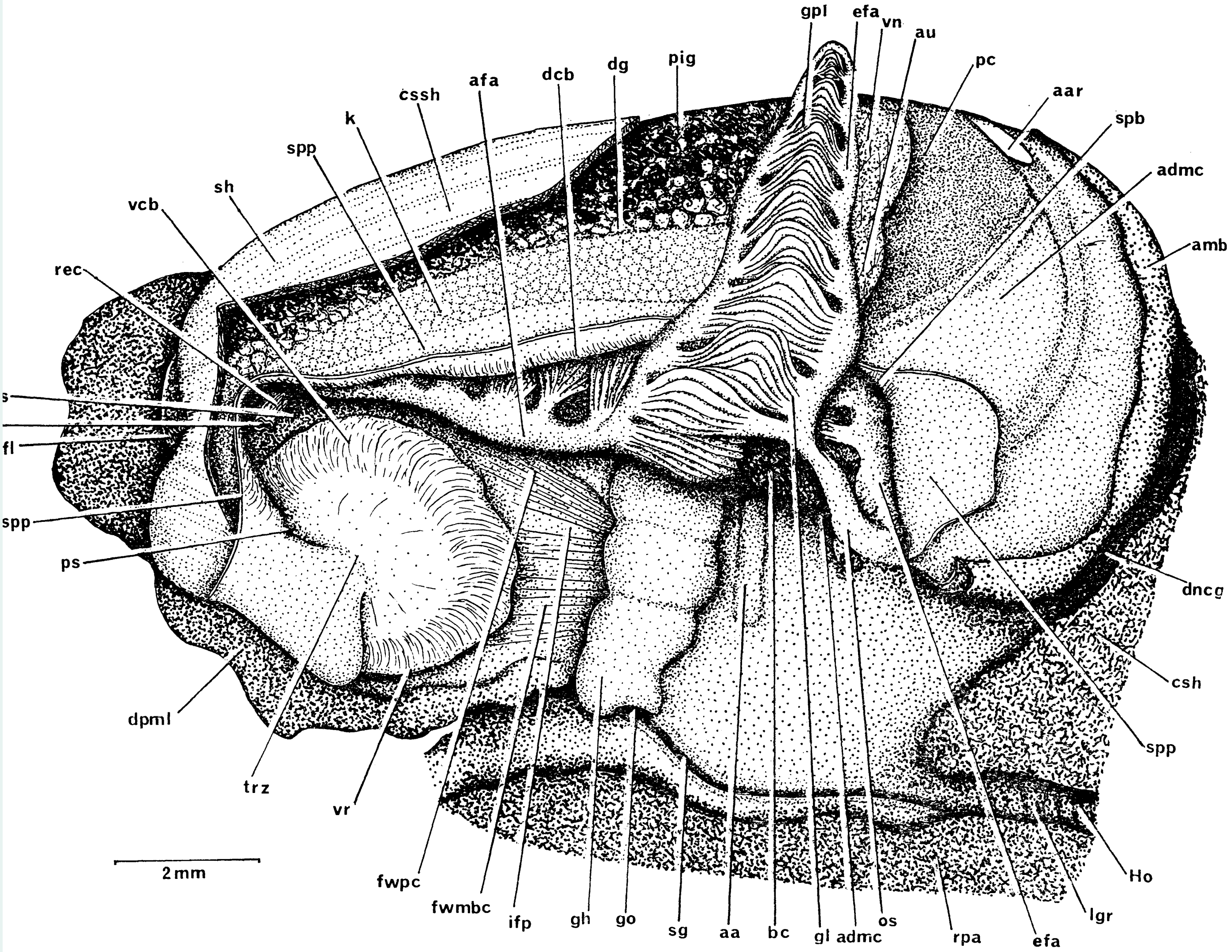

Figure 15. *Haminoea navicula*: dorsolateral view of the mantle cavity from the right; the right mantle border and parts of the suprapallium and shell have been removed to expose the contents of the cavity. The remaining suprapallium has been reflected dorsally; the dorsal extension of the posterior mantle lobe has been pulled ventrolaterally and the right parapodium pulled somewhat ventrally. The distal section of the gill is shown reflected dorsally to the left.

6. Anatomy of *Haminoea navicula* (da Costa) and *Bulla striata* (Bruguière)

(*a*) *Organization of the posterior body region*

Both animals have the body whorl of the involute shell well developed; it rests on the posterior mantle lobe which is similar in form (figure 16*e*) to that of *Scaphander*, but, in addition, projects dorsally on the right (dpml, figures 15, 16*a*, *e*), and, in *Haminoea*, reaches left of and posterior to the shell. A mantle flap (mfl, figures 15, 16*c*) from the transitional zone passes right of the apex to cover the adapical umbilicus.

The disposition of the mantle cavity and associated organs (figures 15, 16*a*) is almost identical in the two animals, though differences occur not previously appreciated. The anterior diverticulum, more spacious in *Bulla*, is limited anteriorly by the mantle border, and ventrally by the infrapallium which is fused to the diaphragm. In *Bulla* it reaches left of the midline, overlain there by the bursa copulatrix which is interposed between it and the pericardial cavity. The bursa of *Haminoea* is also associated with the rear wall of the diverticulum, but lies at the entrance to the former, which reaches to the midline only and almost completely undercuts the bursa. The pericardial cavity of *Haminoea* is spacious and the pericardium, to the left and anteriorly, is fused to the mantle border, and ventrally to the diaphragm, but at the level of the transverse anterior aorta separates to run over the digestive gland to fuse with the pallium dorsally.

The gill chamber and pallial caecum are not obviously separated from one another (figure 15), and the medial border of the mantle cavity, to which the rectum (figure 16*e*) is attached, sweeps uninterrupted from the posterior limit of the anterior diverticulum to the transitional zone. The pallial caecum (figures 15, 16*a*, *e*) coils horizontally, independently of the visceral mass. The area of the transitional zone acting as the medial border to the exhalant aperture is thickened, containing, in *Bulla*, numerous transverse muscle fibres (mf, figure 16*c*) and provides for an anterior projection whose medial face is indented. Within this indentation is the distal tip of the caecum from which the dorsal and ventral ciliated bands, the latter perched on a flattened ridge, extend towards the exhalant aperture, almost completely encircling the thickening (figures 15, 16*a*). Those parts of the mantle cavity roof and floor enclosed by the bands are occupied by the hypobranchial gland (figure 16*e*).

(*b*) *Columellar muscle*

Broad columellar bands (figure 16*b*) form much of the superficial longitudinal muscle of the head-foot.

The proximal muscle overlies the initial portion of the body whorl and, posteriorly, the later-formed section of the preceding whorl. It is thin dorsoventrally forming a curved plate, underlies the infrapallium and visceral mass, is both broader and longer in *Bulla* (figure 16*a*, *b*) than in *Haminoea* (figure 16*d*). In the former it is coiled to the extent of almost one turn ventral to the pericardial cavity. In *Bulla* the proximal mass reaches virtually to the transitional zone, remaining broad; on the right fibres pass beneath the ventral ridge. However, in *Haminoea* it tapers to a point at the level of the medial section of the ventral ridge. Muscle bands (mbcm, figure 16*a*, *b*, *d*) diverge from it and run below the lateral part of the ridge.

The anterior attachment of the proximal mass is to the columella, the posterior to the outer surface of the shell. Adhesive epithelium overlies much of the muscle, but not the muscle bands (figure 16*e*). In *Haminoea* the band of adhesive cells continues posteriorly from the muscle and, at the level of the anus, widens to overlie not only the infrapallium, but also the pallium,

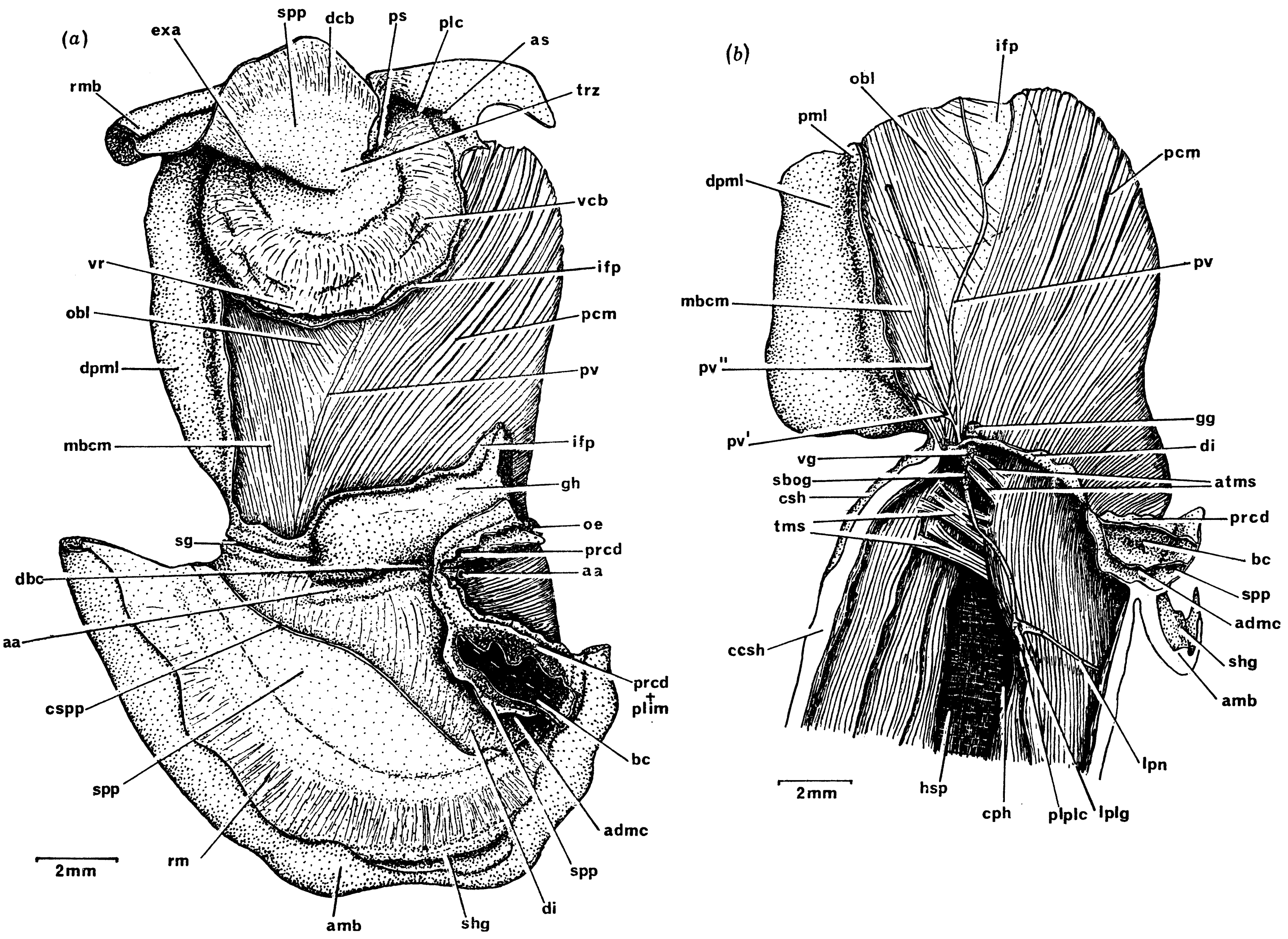

FIGURE 16 (*a*, *b*). For description see opposite.

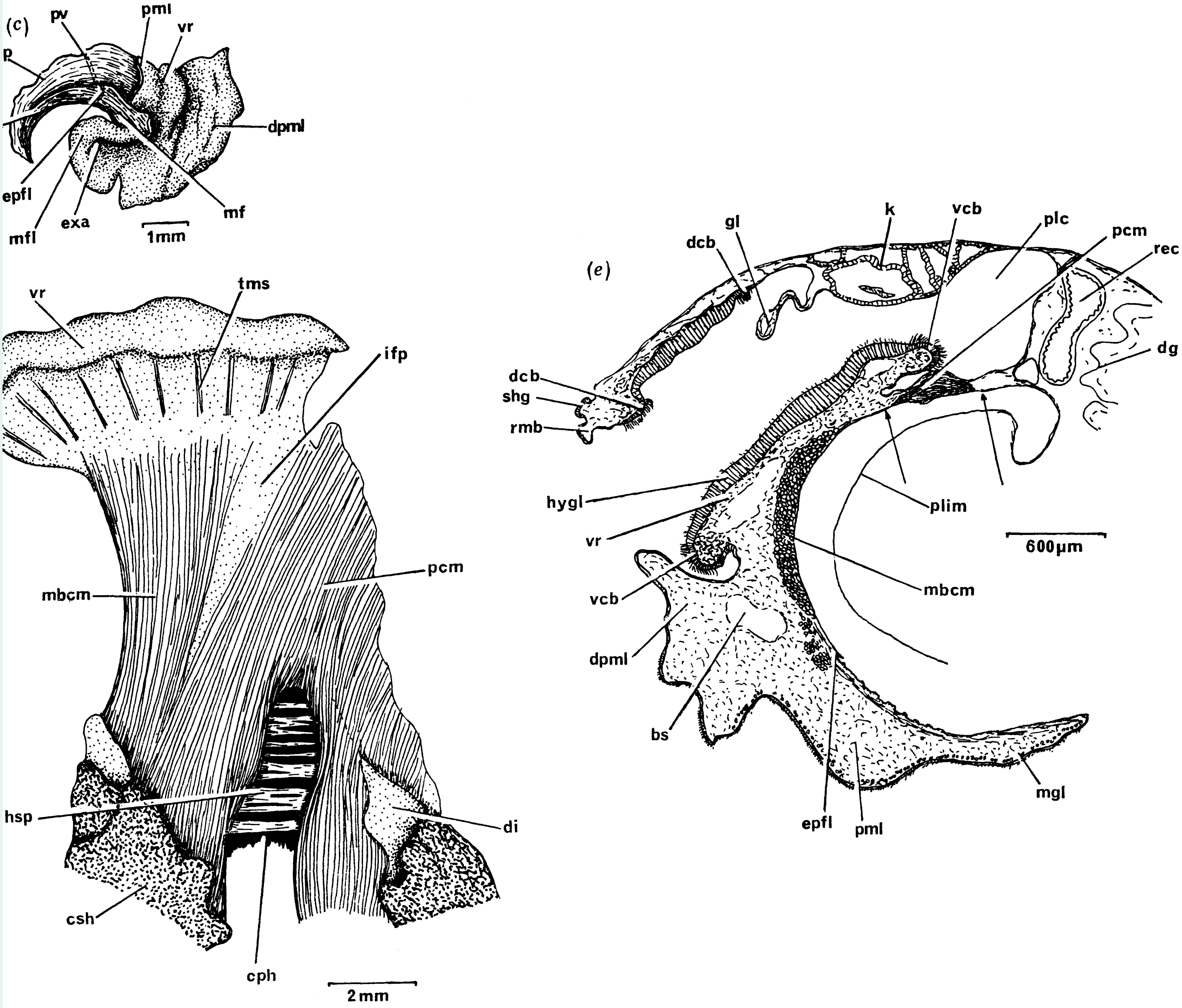

Figure 16. Dissections and a transverse section to show the columellar and other muscles of *Bulla striata* and *Haminoea navicula*. (*a*) Dorsal dissection of the posterior body region of *Bulla*; the visceral mass and shell have been removed. Most of the suprapallium and infrapallium have been cut away, though posteriorly the former has been reflected dorsally and the latter remains. Virtually the whole of the proximal columellar muscle has been exposed, the pericardial cavity and bursa copulatrix have been opened, and the auricle and ventricle have been removed. A broken line indicates the extent of the mantle cavity anteriorly. (*b*) Further dissection to show the muscles of the cephalopedal mass; note the tensor muscle strands. The cephalic haemocoel has been exposed by a median longitudinal incision made in the cephalic shield and the two parts pulled laterally; the gut has been removed and some nerves shown. (*c*) Posterodorsal view of the transitional zone of *Bulla*; the suprapallium has been completely removed. The mantle flap passes to the right of the shell apex. (*d*) Dorsal dissection of *Haminoea* to show the proximal columellar muscle and divergent columellar muscle bands; virtually all the posterior body region, including much of the infrapallium which overlies the proximal columellar muscle, has been removed. The cephalic haemocoel has been exposed by making a median longitudinal incision in the cephalic shield and pulling the two parts laterally which has necessitated cutting of the diaphragm also; posterior is at the top of the figure. (*e*) Semi-diagrammatic transverse section of *Haminoea* at the level of the posterior end of the mantle cavity; the visceral mass and shell are not depicted.

persisting to the transitional zone where it fastens to the adapical umbilicus. From the rear face of the zone, adhesive epithelium extends for a short distance along the rear face of the visceral mass, and occurs over the base of the mantle flap reaching almost on to the suprapallium.

An anterior adhesive ridge (figure 15) is present only in *Haminoea*; it is short, adheres to the columella, and acts as origin to the longitudinal muscles of the cephalic shield, but to few dorsoventral muscles.

(*c*) *Extrinsic musculature of the mantle cavity floor*

The infrapallium is only narrowly separated by blood spaces (bs) from the proximal columellar muscle (figure 16*e*), and is thus largely, though indirectly, supported by the shell. However, minor tensor muscle strands in *Haminoea* which pass from attachments on the proximal muscle, and more posteriorly from the pallium to its medial margin, help to stabilize it. Further strands pass ventrolaterally from the dorsal surface of the visceral mass to the infrapallium. Anteriorly the floor of the mantle cavity, constituted by the body wall, is anchored by strands (atms, figure 16*b*) which span the cephalic haemocoel. Strands (tms, figure 16*d*) embedded in the ventral ridge effect limited movement of the ridge and maintain its form.

7. Anatomy of *Akera bullata* Müller

(*a*) *Organization of the posterior body region*

The shell is similar to that of *Haminoea*. The cephalic shield (figure 17) is relatively narrower than that of *Scaphander*, but the dorsal and ventral nuchal areas, and the parapodia are more extensive. The greater extent of the former nuchal area is reflected in that between the levels of the rear edge of the cephalic shield and of the attachments of the diaphragm and the anterior mantle border to the nuchal area, the cephalic haemocoel outpockets dorsally (figure 18*a*).

The posterior mantle lobe is similar in shape to that of *Scaphander*. The anterior diverticulum of the mantle cavity is extensive (figures 17, 19) and is bounded ventrally by the diaphragm; within its roof to the right is the kidney which spreads into the roof of the gill chamber, and to the left is the spacious pericardial cavity. Anteriorly to the right, the pericardial cavity reaches to the medianly placed, anterior adductor muscle (aadd). More posteriorly to the right, the pericardium abuts both the kidney and the efferent gill axis, and posteriorly, at the levels of the transverse anterior aorta and posterior boundary of the anterior diverticulum, extends posterodorsally to fuse with the pallium.

The genital mass is largely situated below the infrapallium to which it is fused, and reaches anteriorly to the diaphragm. The duct of the bursa copulatrix, after diverging from the genital mass, runs medially, attached to the infrapallium. Fused to the rear wall of the anterior diverticulum and pericardium, it continues to the left to reach the bursa which sits in a concavity in the diaphragm ventral to it.

The spacious gill chamber is not appreciably divided off from the anterior diverticulum (figure 17) unlike *Scaphander* in which the pericardial cavity intervenes. The pallial caecum coils, attached to the visceral mass, for approximately 360° in a plane spiral. For much of its length, the ventral ridge is filled by the rectum. The anus opens within a depression in the mantle, posterior to the ventral ridge; thus the ciliated bands play no part in voiding faeces.

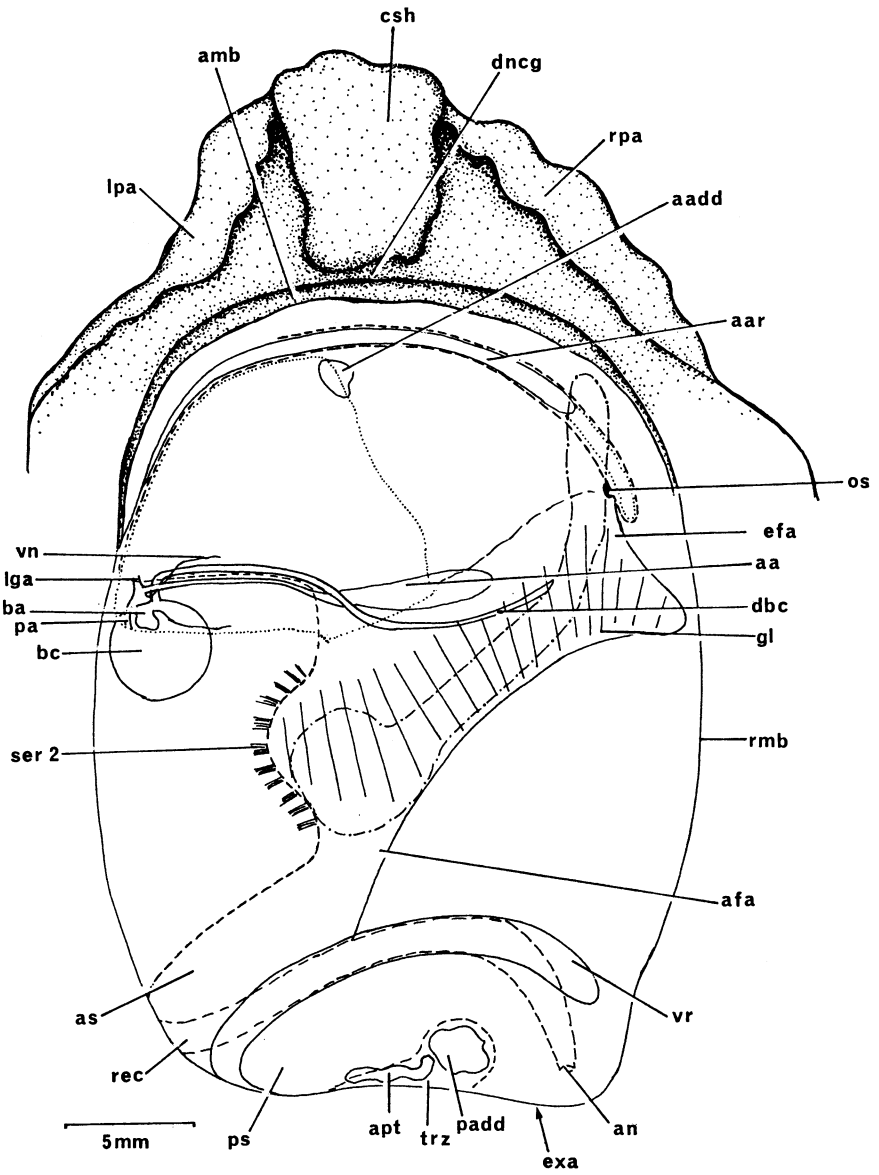

Figure 17. *Akera bullata*: diagram to show the general organization of the mantle complex and viscera from above; the medial limit of the mantle cavity is shown as a broken line, as is the position of the rectum. The genital structures (excluding the hermaphrodite duct and gonad) are outlined by a line composed of alternating dashes and dots; dotted line denotes the extent of the pericardial cavity and also the extent of fusion of the anterior mantle border to the nuchal area, to the right of the anterior adhesive ridge. Broken line running posteromedially from osphradium indicates the anterior boundary of the efferent gill attachment.

(*b*) *Columellar and other muscles originating on the shell*

Separate columellar tracts run along the foot and cephalic shield (figure 18*a*). Two broad muscles (lcm) sited within the lateral regions of the cephalic shield, one on either side, are each divisible into two narrowly separated tracts. The median region of the cephalic shield has many longitudinal muscles (lmcs) overlain by transverse muscles (tmcs); the latter, to either side, attach largely to the medial tract of the lateral columellar muscle.

The foot also has many longitudinal muscles (lmft) of which lateral components (lcmf) on each side merge posteriorly with the lateral columellar muscle, and thus are presumably of

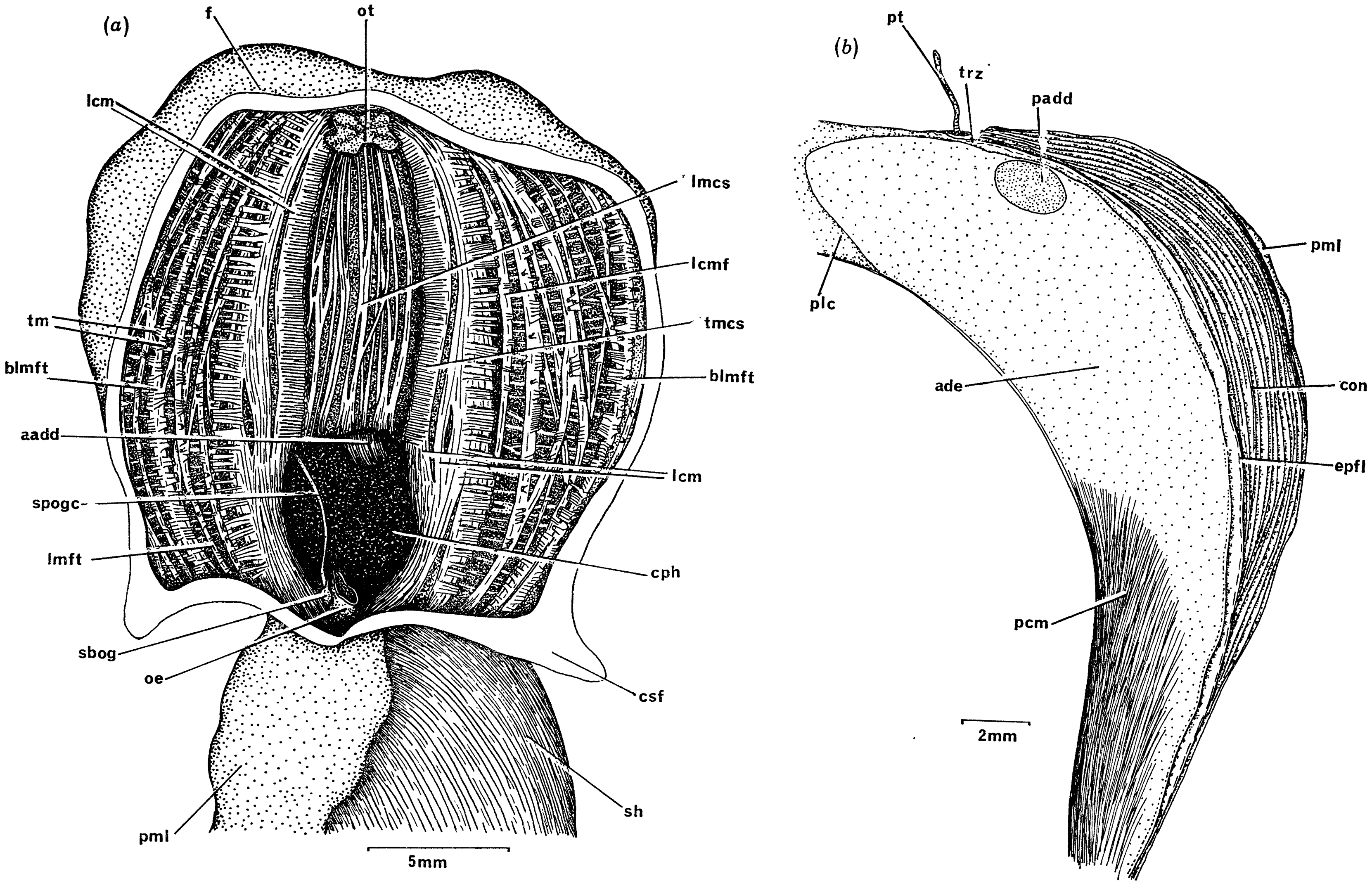

FIGURE 18. *Akera bullata*. (*a*) Ventral dissection to show the columellar and other muscle tracts of the anterior body region; the cephalopedal mass has been opened by a sagittal cut along the foot and the two parts pulled laterally. The alimentary tract has been removed, and the transverse muscles of the cephalic shield also largely cut away. (*b*) Concave face of the posterior mantle lobe and infrapallium of base of the pallial caecum laid flat, to show the posterior adhesive areas.

columellar origin; medially placed ones are clearly of pedal origin as they continue within the rear extension of the foot. United these muscles then travel posteroventrally through the nuchal area to merge within the proximal columellar muscle (figure 19) which is similar to that of *Scaphander*, though relatively shorter. To all these muscles attach transverse muscles (tm, figure 18*a*) which within the lateral parts of the foot progressively assume a dorsoventral orientation. Together with the transverse muscles (tmcs) of the cephalic shield they form an interrupted circular muscle layer.

Posteriorly, the longitudinal muscles of the cephalic shield enter the nuchal area; on the right, few of these originate on the anterior adhesive ridge. Those muscles which do, run dorsoventrally.

The anterior adductor muscle (figures 17, 19) extends anteroventrally from its origin on the shell, a little posterior to the attachment of the anterior adhesive ridge, in turn a short distance in from the abapical margin, initially to run separately, but subsequently to become fused to the longitudinal muscles of the dorsal nuchal area (figure 18*a*). More anteriorly its fibres fan out, and it is evident that the muscle is constituted by few fibres of the longitudinal muscles of the cephalic shield. Thus the muscle is comparable to the dorsoventral muscles (advm) of *Philine*. Many fibres of the longitudinal muscles (lmcs) originate on the anterior adhesive ridge. To the left, as in *Scaphander*, columellar musculature posterior to the diaphragm fans out to the nuchal area, but unlike *Scaphander* the adhesive ridge lies left of most muscles and overlies the fleshy section of the mantle border, though it does act as origin to some slender dorsoventral muscles.

More ventrally and posteriorly the band of adhesive cells broadens and comes to overlie the proximal muscle, and part of the concave face of the posterior mantle lobe (figures 18*b*, 19). Posteriorly attachment moves away from the columella on to the outside of the first-formed section of the body whorl, and then on to the later-formed section of the penultimate whorl. The band continues beyond the posterior tip of the columellar muscle (figure 18*b*), broadening further to cover virtually all the under surface of the infrapallium of the pallial caecum. Adhesive epithelium does not reach over the rear face of the transitional zone, though two adhesive patches occur dorsally (figure 17), one overlying the posterior adductor (padd), the second (apt) located a little to the left.

The posterior adductor muscle is comparable to the muscular thickening of *Scaphander*. Its fibres run dorsoventrally, and dorsally adhere to the outer lip of the shell. According to Perrier & Fischer (1911) their function, together with the anterior adductor, is to depress the outer lip of the shell, thus narrowing the aperture, presumably to prevent entry of material into the mantle cavity, or perhaps to aid replenishment of water; correlated with this is the flexible nature of the adapical umbilicus. This may be so, but conspicuous movements of the shell lip have not been noted. However, as already mentioned, the anterior adductor must also function to stabilize the abapical shell margin, and may be concerned in locomotion (p. 48).

(*c*) *Extrinsic musculature of the mantle cavity floor*

A horizontal septum (hsp, figure 19) traverses the cephalic haemocoel and posteriorly consists of muscle strands which to the right attach to the floor of the mantle cavity. Two stouter strands (atms) fasten dorsal to the genital mass. All these strands preserve the relatively narrow form of the nuchal area.

Strand 1 (tms) within the posterior body region, fastens ventrally to the pallium close to the

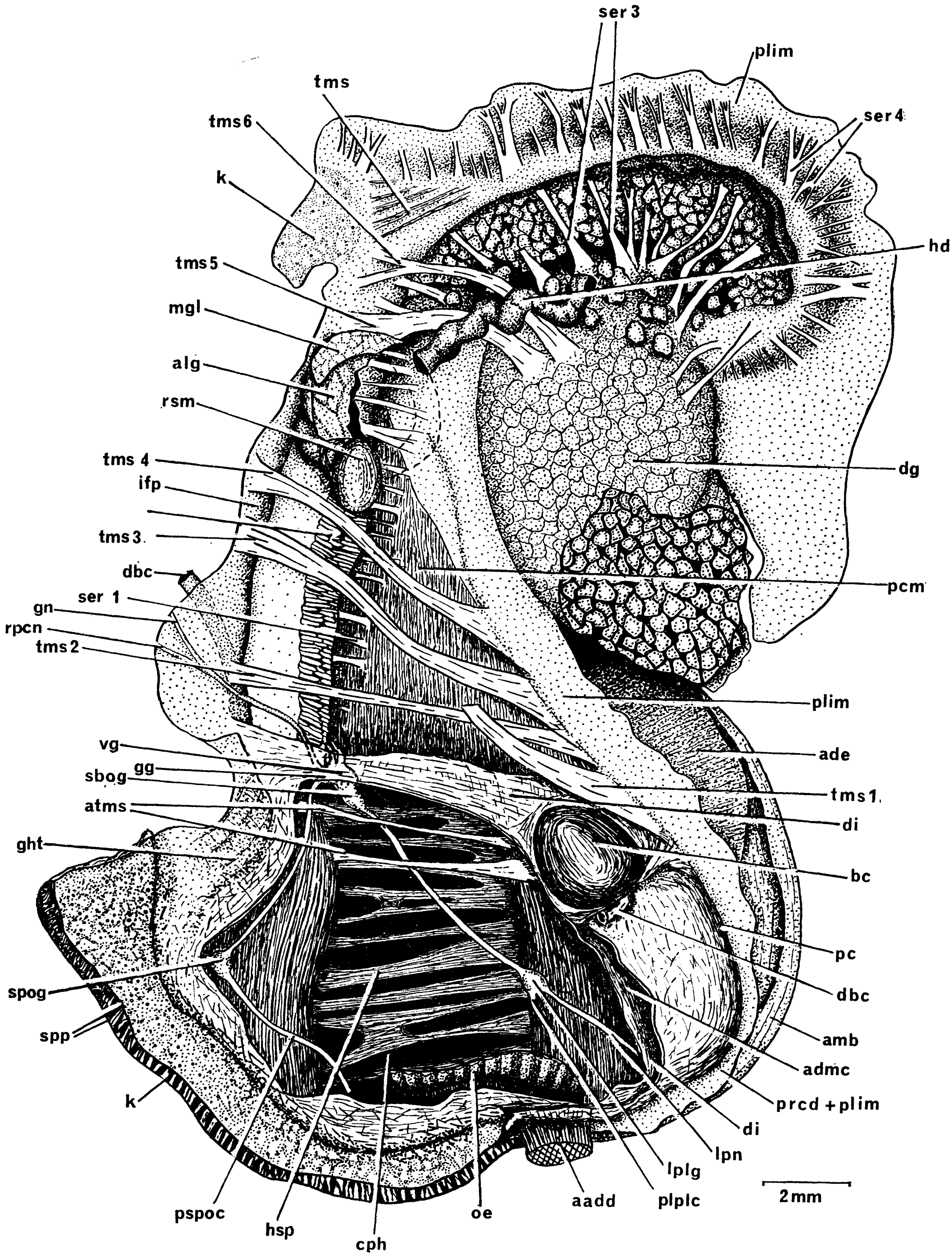

Figure 19. *Akera bullata*: dorsal dissection to show general anatomy, and extrinsic muscles of the mantle cavity floor; the shell and much of the visceral mass have been removed, though many genital structures remain. The remaining infrapallium has been reflected dorsally to expose muscles, as has the pallium immediately anterior to the pallial caecum; much of the suprapallium which incorporates the kidney and pericardial cavity has been removed. The floor of the latter, however, is still present on the left side of the animal; the diaphragm has been cut away to expose the contents of the cephalic haemocoel and the body wall on both sides pulled laterally. The anterior section of the gut has been removed; the haemocoel is shown in black.

transition between anterior mantle border and posterior mantle lobe and secured by adhesive epithelium. It passes dorsally to fasten to and stabilize the pericardium, posterior to the anterior aorta, which in turn will facilitate stabilization of the rear face of the anterior diverticulum. From ventral attachments posterior to that of strand 1, several components run dorsomedially to reach the infrapallium of the gill chamber, strand 2 (tms 2) where the duct of the bursa copulatrix diverges from the genital mass, strands 3 and 4 (tms 3, 4) at the level of the rear of the anterior diverticulum, and strands 5 and 6 (tms 5, 6) close to its junction within the anterior wall of the caecum. The infrapallium is also fastened to the columellar muscle by a series (ser. 1) of short ties, and to the pallium dorsally (ser. 2, figure 17).

The infrapallium of the caecum is stabilized by two series of strands (figure 19). One (ser. 3), comparable to series 3 of *Philine*, extends dorsally from ventral attachments similar to those of strands 5 and 6, between the lobules of the digestive gland and to either side of the rectum, to fasten to the sides of the ventral ridge. A second series (ser. 4), comparable to series 5 of *Philine*, connects the infrapallium to the dorsal surface of the visceral mass.

8. Anatomy of *Aglaja depicta* Renier and *Gastropteron rubrum* (Rafinesque)

(*a*) *Organization of the posterior body region*

Emphasis in this section lies on a comparison of certain features with those of *Philine*.

The foot of *Aglaja*, in respect to body length, is relatively longer than that of *Philine*. The increased length has been brought about partially by increase in size of the posterior free extension which, together with a shortening of the posterior mantle lobe, enables the foot to reach to the rear of the animal, and partially by elongation of the remainder, for on comparing the levels of the dorsal and ventral nuchal areas they are relatively further apart. The meeting of the anterior and posterior body regions, delimited by the diaphragm, is thus more oblique than in *Philine*, and an indication of insinking of the latter region into the former is seen dorsally where the visceral mass is under the rear of the cephalic shield. In *Gastropteron*, unlike *Aglaja* and *Philine*, the cephalic shield is small, the parapodia enormous and the ventral nuchal area extensive. Reduction of the posterior mantle lobe (figure 21*a*) has also taken place in *Gastropteron* with the result that, together with the dorsal lobe and infrapallium, there arises a smooth covering to the posterior body region. In comparison with *Philine*, both the dorsal mantle lobe and shell cavity are more extensive, as a consequence of the curious form of the posterior body region. *Aglaja*, on the other hand, has a much reduced shell cavity. This is due to fusion between the dorsal mantle lobe and the pallium which has occurred over a short distance behind the anterior mantle border, and also on the left where it is less noticeable posteriorly, where the cavity is over the suprapallium of the pallial caecum (figure 20*b*). Dorsally both the pallium and the inner face of the dorsal lobe have longitudinal muscles (lmf, figure 21*b*). In both species, the kidney (figure 21*a*) borders, but does not invade, the suprapallium.

In *Aglaja* the mantle cavity is sited posteroventrally (figure 20), unlike *Gastropteron* in which it lies on the right (figure 21*a*). It is extensive in *Aglaja*, though largely filled by the gill which, from short attachments on the right, sweeps ventrally to the left; there the cavity is large, for the posterior mantle lobe is deeply undercut. Posteriorly the right mantle border is much thickened, and not only encloses the cavity laterally, but also to a small extent ventrally, though this is achieved largely by the foot. The exhalant aperture is formed by a tucking in of the posteromedial tip of the mantle border immediately in front of the posterior extremity of the posterior mantle lobe, so as to leave a roughly circular aperture. The pallial caecum is organized similarly to that of *Philine*, but is smaller in cross-section; on the right, however, the ciliated bands and ventral ridge continue ventrally and then to the right so that before terminating the ventral band becomes dorsal to the dorsal one. The ventral ridge is largely filled with connective tissue in which are embedded numerous muscle strands, comparable with series 3 of *Philine*, which stabilize the ridge. Unlike *Philine*, the caecum is somewhat separated off from the visceral mass because digestive gland underlies the infrapallium of the anterior space only. The apex of the visceral mass which in *Philine* is shrouded by the caecum, is within a depression (ddml, figure 21*b*) in the dorsal mantle lobe.

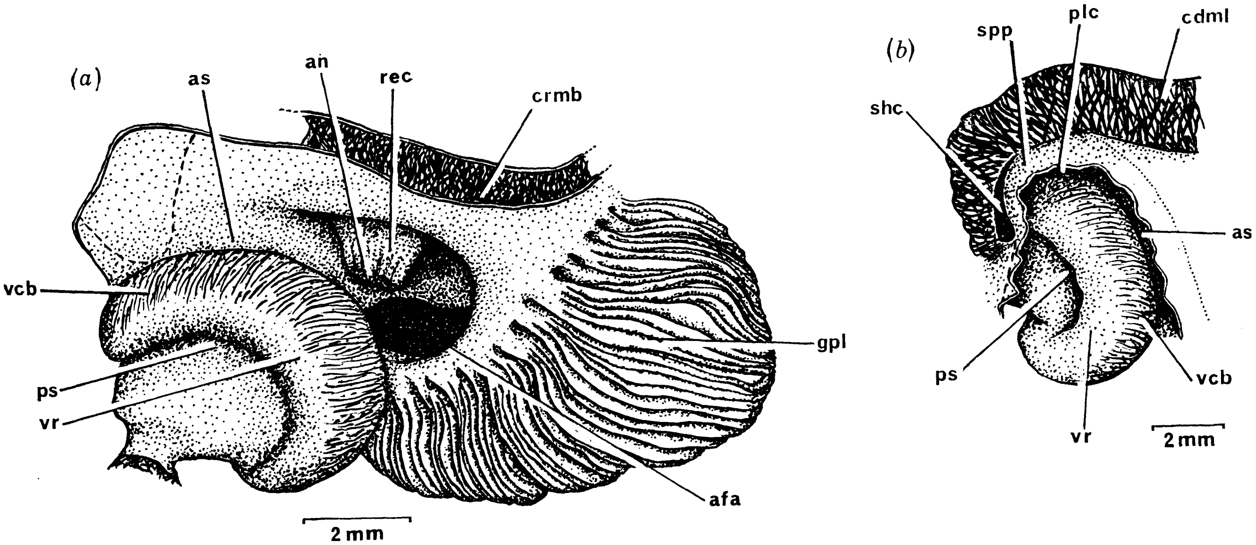

FIGURE 20. *Aglaja depicta*: features of the mantle complex. (*a*) Posterolateral view from the right to show the gill and ventral ridge; the right mantle border and suprapallium have been removed. The broken line signifies the depression in the inner face of the mantle into which the apex of the visceral mass inserts. (*b*) To show the pallial caecum; the dorsal mantle lobe has been partially removed and the shell taken from the shell cavity. Some of the suprapallium has been taken away to expose the caecum; the dotted line marks the anterior margin of the anterior space of the caecum dorsally.

The gill structure of *Gastropteron* (figure 21*a*) is complex in that each gill leaflet is comparable to the entire gill of *Philine* or *Aglaja*. An 'osphradium' is present in *Gastropteron* despite the exposed position of the gill, but genital hump and gill are absent. The anus faces posteriorly, in a more dorsal position than that in *Philine* or *Aglaja*.

(*b*) *Columellar muscle*

Within the cephalic haemocoel of both run columellar tracts fastened only at their ends; anteriorly they insert on body wall surrounding the oral tube (ot). In *Aglaja* a median columellar component (figure 22*a*) runs from an origin immediately in front of the attachment of the diaphragm to the foot. Its fibres originate within the proximal muscle (figure 21*b*) which is shorter than that of *Philine*.

The proximal muscle is not related to the shell attachment for the shell cavity terminates dorsal to it; to the left it is continuous with longitudinal muscles (lmf) of the dorsal mantle lobe. To either side of the median component are two pairs of lateral muscles (dlcm, vlcm, figure 22*a*);

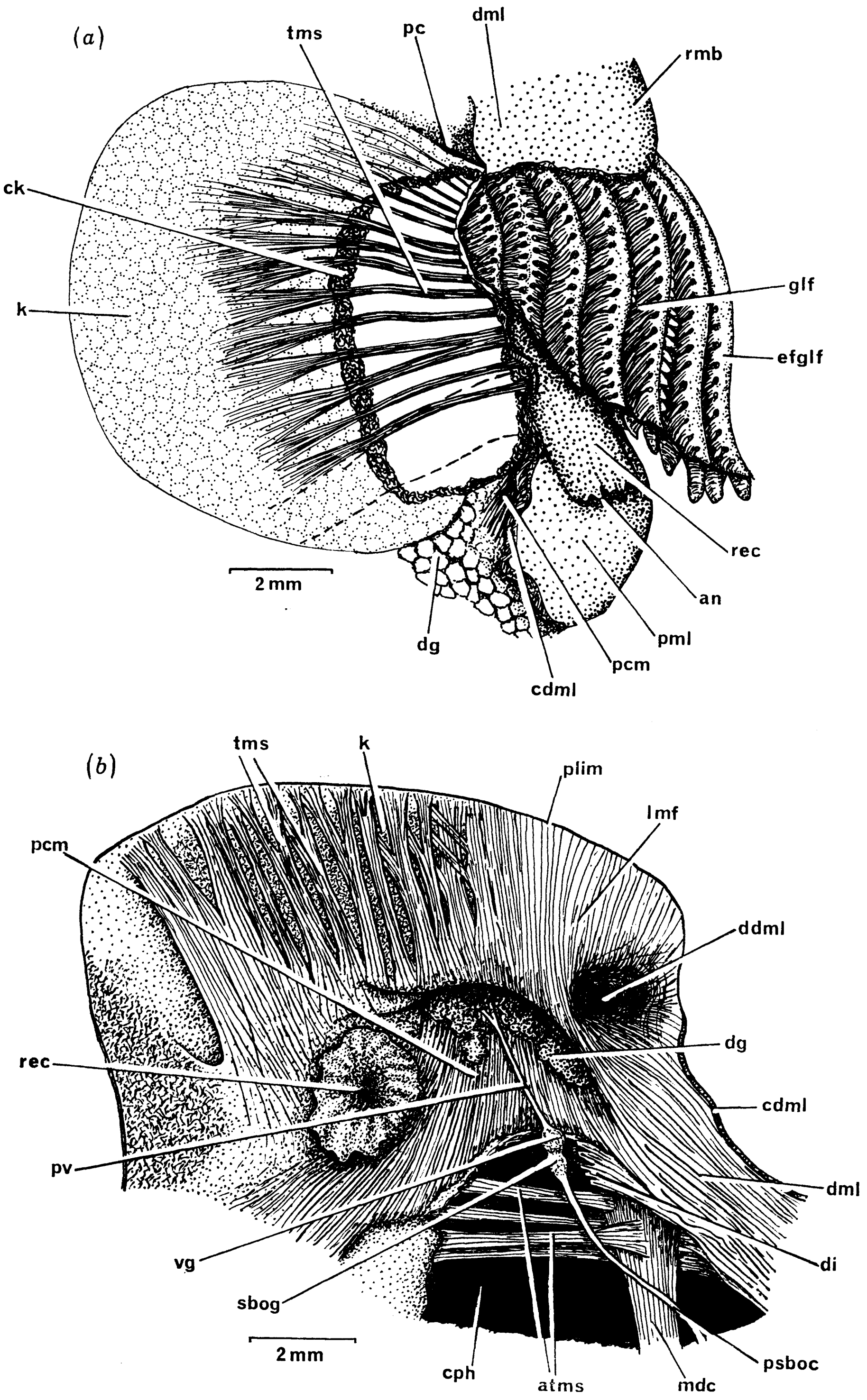

FIGURE 21. (*a*) Dorsal dissection of *Gastropteron rubrum* to show the gill and extrinsic muscles of the infrapallium; the dorsal mantle lobe has been largely removed, as has the shell. The right mantle border, dorsal to the mantle cavity, has been cut away to expose the gill; the lateral part of the kidney has been dissected away to show the path of extrinsic muscles which pass through the organ from the infrapallium to the pallium overlying the kidney. The broken line indicates the position of the rectum lying within the visceral haemocoel. (*b*) Dorsal dissection of *Aglaja depicta* to show the extrinsic muscles of the floor of the mantle and the median columellar muscle posteriorly; the viscera have been removed and the diaphragm cut away. The kidney and surrounding pallium have been reflected posterodorsally; the cephalic haemocoel is figured black. Note the depression in the mantle which accommodates the apex of the visceral mass.

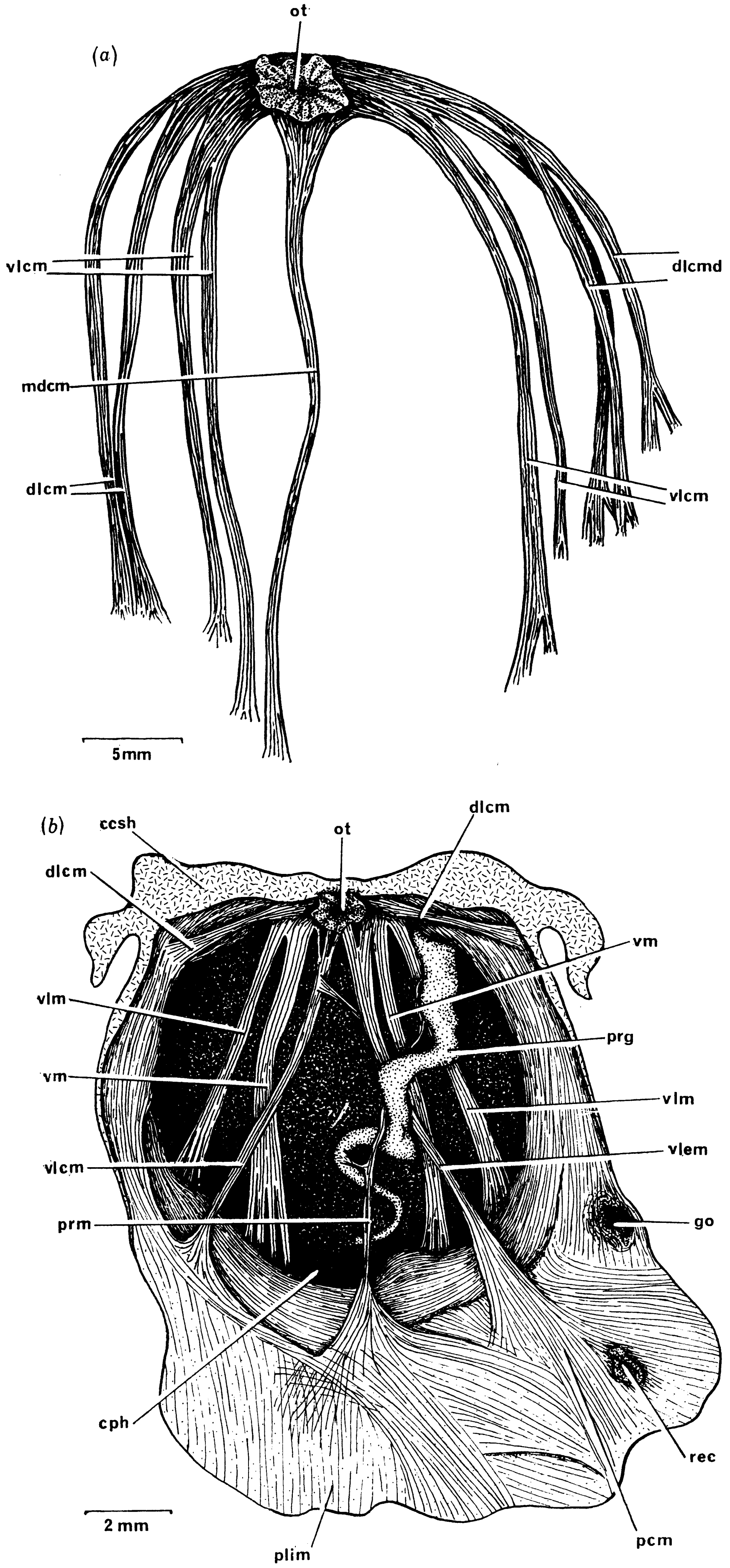

FIGURE 22. Columellar muscle systems. (*a*) *Aglaja depicta*: the muscle is shown in isolation, but the proximal columellar muscle is not figured. (*b*) *Gastropteron rubrum*: the columellar muscle has been exposed by making a median longitudinal incision in the cephalic shield and the two parts pulled laterally; the viscera and anterior portion of the alimentary tract have been removed. The pallium is reflected posterodorsally. Anterior in both figures is at the top of the figure.

in the animals observed the dorsal member (dlcmd) of the right dorsal pair was split into two for most of its length. The ventral pairs extend further posteriorly than the dorsal ones, and originate from fibres which themselves originate within the proximal mass. Fibres of the right dorsal pair run towards the infrapallium; those of the left, though becoming less discernable, also continue and are continuous with longitudinal fibres of the dorsal mantle lobe.

In *Gastropteron*, two components (vlcm, figure 22*b*) presumably of columellar nature, one either side of the midline, run somewhat dorsally to origins within the body wall, a little anterior to the diaphragm. Fibres of the left muscle subsequently curve somewhat to the right to enter the pallium, where they fan out. Fibres of the right muscle, considered homologous to the median columellar muscle of *Philine* and *Aglaja*, also spread out, with those to the right entering the infrapallium and the remainder forming a small proximal muscle, a little posterior and ventromedial to the anus. Some fibres run close to the shell cavity, but what their role is, if any, in shell attachment was not determined. Two shorter muscles (dlcm), not noted by Bergh (1839*b*), run, one either side of the midline, to origins within the posterolateral areas of the cephalic shield.

Two further pairs of muscles (vlm, vm), on either side of the midline, run, from anterior insertions, to the ventral nuchal area; they are probably of pedal origin, and comparable to those muscles (lmft, figure 18*a*) of *Akera* which run into the rear extension of the foot.

(*c*) *Extrinsic musculature of the mantle cavity floor*

Several tensor muscle strands (atms, figure 21*b*) in *Aglaja* run transversely from body wall to body wall and anchor the anterior mantle cavity floor; two, however, fasten instead to the median columellar muscle. A series of strands (tms), comparable to series 2 of *Philine*, radiates out beneath the kidney in *Aglaja* and through it in *Gastropteron* (figure 21*a*) to anchor the infrapallium to the pallium.

9. CHANGES IN BODILY ORGANIZATION DURING TECTIBRANCH EVOLUTION

The changes which call for comment are (*a*) those which relate to the gross body form, and to the mantle complex and skirt. In addition, further adaptations which accompanied the gross changes are described: (*b*) the evolution of the extrinsic muscles of the mantle cavity floor, (*c*) modification to the columellar muscle, and (*d*) changes within the nuchal area.

(*a*) *Gross organization, and the mantle skirt and complex*

The burrowing habit promoted a broadening (1) and an anterior elongation (2) of the cephalopedal mass (figures 23 and 24). Indications of this are shown by the separation of the pallial ganglia (lplg, rplg, figure 24*b*) from the pleurals (Brace 1974, and in preparation), and in *Acteocina canaliculata* Say (Scaphandridae) by a great increase in the size of the propodium at metamorphosis (Franz 1971). It also promoted the loss of the tentacles (3, figure 23).

In all, except *Acteon* (figure 24*b*), the nuchal area is much shortened (4, figure 23) and the dorsal nuchal area is anterior to the corresponding ventral region (figure 24*c*, *d*), a disposition most obvious in *Philine* and *Aglaja*. These relative placings are due to a concurrent elongation of the mesopodium (5, figure 23 and figure 24), though in part to the reduction of the nuchal area itself (see figure 23). A broadening of the nuchal area (6) also took place. Lengthening of the mesopodium, in turn, involved reduction or incorporation of the metapodium (7), perhaps explaining the absence of an operculum (8) in certain tectibranchs (Ringiculidae, Diaphanidae, Hydatinidae) which possess a shell into which they can retract fully. Its loss could, however, have been associated with other trends discussed below.

The mantle complex moved to the right and then posteriorly, achieved by a migration of the mantle skirt (see below). Movement along the left flank was not possible owing to the dextral coiling of the shell. Fusion of the mantle skirt to the dorsal nuchal area occurred anteriorly (figure 24). The formation of a head-shield does not seem to have been responsible for this migration as has been supposed, for the elongation of the body wall dorsally involved an anterior rather than posterior extension. However, broadening of the cephalopedal mass may have tended to occlude the aperture of an anterior mantle cavity, and it may be that the tendency for the cavity to clog is reduced when sited on the right. Whatever the contribution of these factors, it is clear that the major influence was the shortening of the nuchal area, for this reduced space anteriorly for the mantle complex.

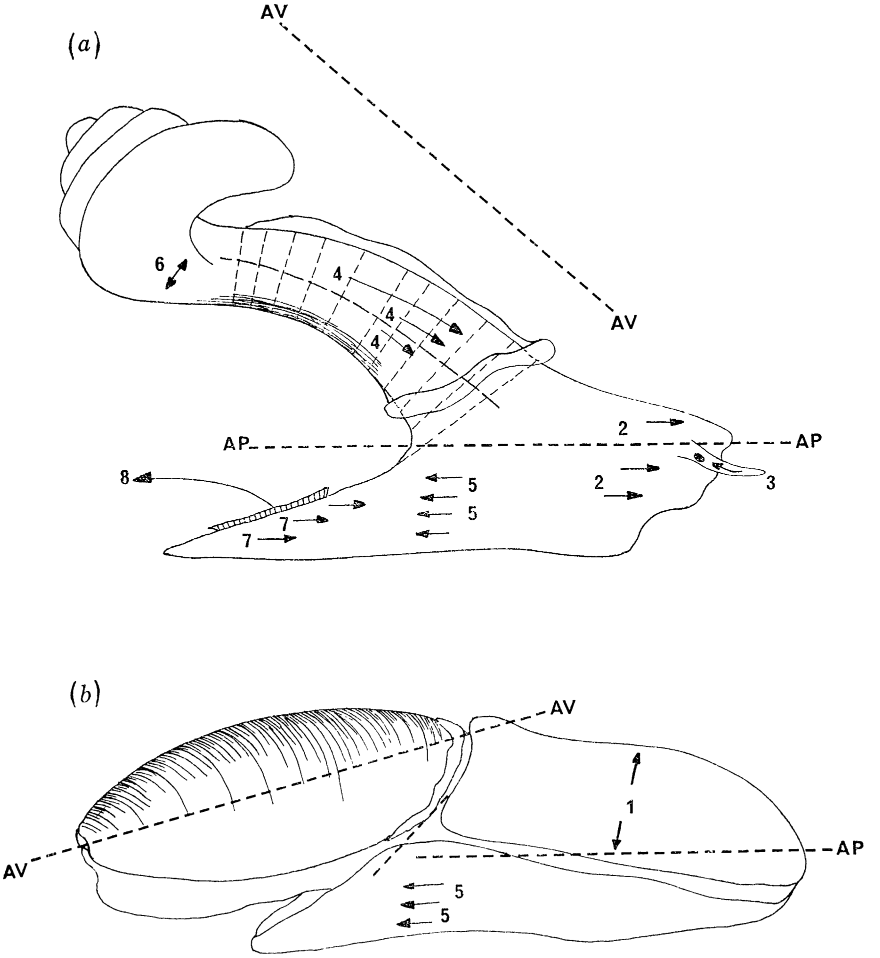

Figure 23. Comparative diagrams to show the changes in gross structure incurred during the the transition from prosobranch to opisthobranch organization. (*a*) A monotocardian prosobranch with a coiled visceral mass, viewed from the right; (*b*) *Scaphander* viewed from the right. Changes shown are (1) broadening of the head-foot, (2) elongation of the head-foot *anteriorly*, (3) loss of the tentacles, (4) shortening of the nuchal area, (5) elongation of the mesopodium *posteriorly*, (6) broadening of the nuchal area and of the base of the visceral mass, (7) reduction of the metapodium, and (8) loss of the operculum. Arrows signify the direction in which changes of proportion have occurred or, in the case of (8), removal of the operculum. See text for full details.

With migration of the mantle complex necessarily went a change in the disposition of the mantle skirt and shell gland (figure 25). This gave the shell a horizontal alignment (AV, figure 23), so producing the necessary streamlining of the body and prompting a different growth of the base of the visceral mass. No vertical sinking of the visceral hump into the head-foot was involved. In this change the body whorl and mouth of the shell enlarged, the spire becoming involute. The shell showed signs of being overgrown by the mantle, and ultimately the animal could no longer withdraw into it (*Scaphander*), and it became internal (*Philine*, *Aglaja*, *Gastropteron*). With these changes was lost the circular continuum of the shell gland typical of prosobranchs, and it occurs along the right and anterior mantle borders only; the columella became reduced.

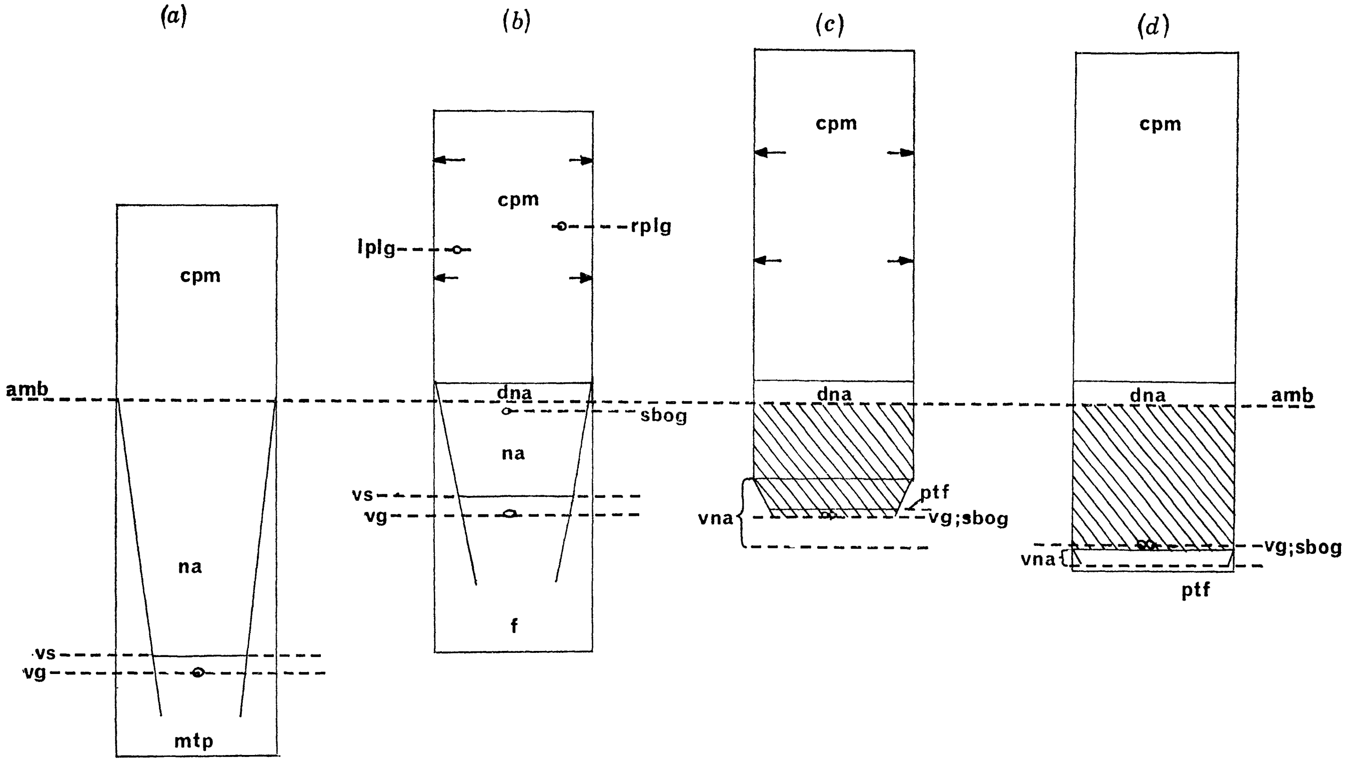

FIGURE 24. Comparative diagrams to show the changes in proportion of the body regions and changes in position of certain structures, incurred in the transition from prosobranch to opisthobranch organization. (*a*) A monotocardian prosobranch, (*b*) *Acteon*, (*c*) *Scaphander*, (*d*) *Philine*. Arrows in (*b*) and (*c*) indicate broadening of the head-foot which, however, is not indicated by a change of proportion in the diagrams; cross-hatched areas in (*c*) and (*d*) denote the diaphragm which is set more obliquely in *Philine* than in *Scaphander*. Levels of certain structures are shown by broken lines; animals are viewed dorsally and anterior is at the top of the figure. See text for full details.

Perrier & Fischer (1911), Fretter (1960) and Minichev (1967) examined this reorganization of the mantle skirt and agreed, as is accepted here, that a folding posteriorly produced a section running vertically. This links the infrapallium, derived from the skirt which in prosobranchs forms the right wall of the mantle cavity, to the suprapallium, derived from the left section. Fretter supposed that, in addition, the migration involved differential growth between the left and right halves, possibly a continuation of the process which brought the morphologically median rectum to a topographically right position. That differential growth between regions of the skirt was involved is not in doubt, but no reduction of the right side occurred for both sides increased in length. In later forms the 'osphradium', which may not be homologous to that of prosobranchs, is posterior, indicating that the greatest elongation concerned that section of mantle which in prosobranchs lies immediately left of the osphradium, a conclusion supported by its innervation (Brace 1974, and in preparation). Because of the need to communicate with the penis, the gonoduct (gd) retained its anterior position within the mantle skirt, but the rectum moved posteriorly.

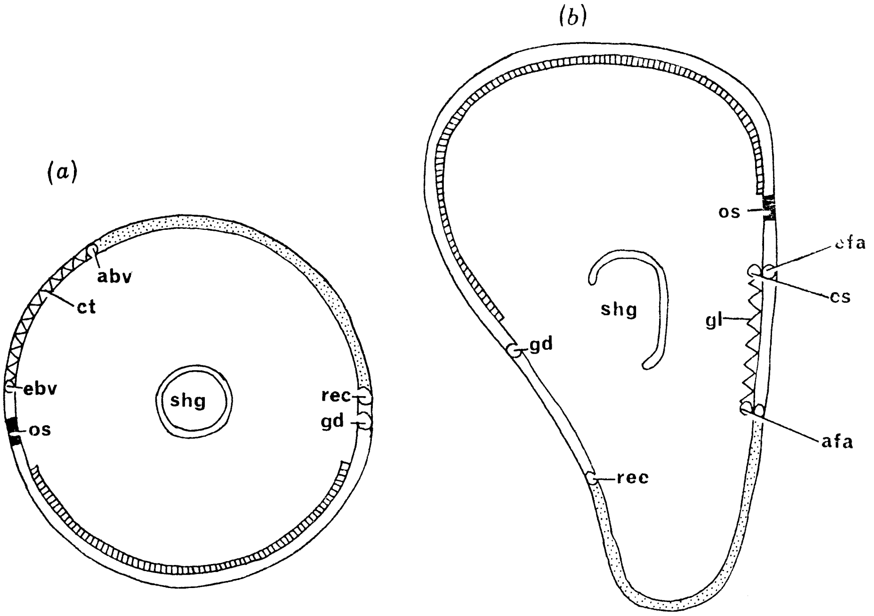

FIGURE 25. Comparative diagrams to show the changes in proportion and organization of the mantle skirt, incurred in the transition from prosobranch and opisthobranch organization. (*a*) A monotocardian prosobranch, (*b*) *Scaphander*. Stippled area shows the extent of the hypobranchial gland; hatched area shows that region of the mantle skirt which is fused to the nuchal region. The extent of the shell gland is also shown and anterior is at the top of the figure. See text for full details.

Reduction in the depth of the mantle cavity and skirt was a consequence of a number of factors of which reduction of the nuchal area has already been mentioned (p. 40). Even to the right space is limited for there, greater contact with the bulging viscera is made than in a a prosobranch, but the existence of tectibranchs with a relatively deep, lateral mantle cavity shows this cannot be the whole truth. Indeed, the principal factor is the problem of stabilization of the infrapallium for which tensor muscles have evolved (p. 44). Fretter (1960) supposed that shallowing of the mantle cavity was correlated with the development of sites of respiratory exchange elsewhere, but as is shown below, primitive opisthobranchs exhibit other adaptations which ensure an adequate uptake of oxygen. It is only to later stages in evolution that Fretter's suggestion may apply.

Features of the pallial caecum, including details of its vascular supply (Brace 1974), leave no doubt that this prolongation of mantle skirt bears the hypobranchial gland. Consolidation of particles which have entered the mantle cavity still devolves upon the gland as in prosobranchs, and its extension along the pallial caecum appears to emphasize its necessity.

The production of ciliated bands which produce a water flow through the mantle cavity appears to be correlated with small size and the loss of the ctenidium, for they occur in the minute animals described by Fretter (1948). The tectibranch gill is built on a different pattern to that of the prosobranch ctenidium, and it seems likely (Fretter & Graham 1962) that the ancestors of tectibranchs lacked a ctenidium and a new structure was redeveloped with a subsequent increase in size. Presumably the small size of these animals can be considered as a pre-adaptation for an infaunal mode of life.

The new gill is extremely muscular and contraction, both of the axes and plicae in *Scaphander*, aids circulation of blood (Brace 1974, and in preparation) as in *Aplysia californica* (Cooper) (Koester, Mayeri, Liebeswar & Kandel 1974). Its successful functioning is dependent on the quality and quantity of water entering the mantle cavity, both of which may be adversely affected by conditions in the substratum, especially the latter for burrowing forms need largely to isolate the cavity from the exterior. This has been achieved by a thickening of the mantle border (*Scaphander*, *Philine*, *Aglaja*), extension of the foot posteriorly (*Aglaja*), extension of the posterior mantle lobe dorsally (*Haminoea*, *Bulla*, *Akera*), or, as in all the above, by enclosure by the right parapodium. Inhalant and exhalant apertures have become restricted to anterior and posterior positions respectively.

In larger animals, the need for a greater uptake of oxygen is reflected in the evolution of the pallial caecum, and perhaps also in the loss of the shell, giving additional respiratory sites. That many small tectibranchs possess a gill and caecum, suggests the need for both under infaunal conditions. Circulation of water through the caecum depends on a reduction in pressure in its anterior space effected by the ciliated bands sucking water from it into the posterior space. However, their prolongation into a caecum does not improve flow through the remainder of the mantle cavity, so supporting the contention that the prime function of the caecum is to provide an additional respiratory surface, and that the evolution of the ciliated bands preceded the formation of the caecum.

In *Philine*, the caecum has fused to the rear face of the visceral mass, perhaps allowing for direct transport of oxygen to the viscera, but with more relevance to packing, and stabilization of its ventral wall (p. 44). The fused condition has been independently attained in *Akera*, indicating, as that species has a bulbous shell, that attachment does not primarily relate to shell reduction. *Bulla* and *Haminoea*, along with *Smaragdinella* (Bullacea) (Rudman 1972*b*), display a differently disposed pallial caecum, which, although attached, coils independently of the visceral mass. The caecum of *Phanerophthalmus* (Rudman 1972*b*), which is related to *Smaragdinella*, coils with the visceral mass, indicating that the change from coiling horizontally to coiling vertically is not a drastic one. It is difficult to understand why the caecum should be disposed horizontally, as in that situation it cannot be spacious. This can best be explained by noting that the gill of *Bulla* and *Haminoea* stretches virtually to the transitional zone and, in view of the reduced ventilation of the tectibranch mantle cavity, probably an early extension of that structure was favoured. Later changes whereby the mantle cavity became posterior, and the infrapallium and posterior mantle lobe reduced, entailed a convergent change to the organization of *Aglaja* in order to retain the pallial caecum.

In primitive tectibranchs the kidney lies within the suprapallium. This appears to have been a valuable feature, for its extensive capillary bed can act as a useful respiratory surface. Increasing efficiency of oxygen uptake elsewhere, and reduction in depth of the mantle skirt presumably account for its migration back into the visceral mass. Primitively the heart appears to also have resided within the suprapallium, a position no doubt connected with that of the kidney, the two being linked by the collecting sinus.

During the migration of the mantle complex, the margin of the infrapallium thickened to produce the posterior mantle lobe, which undercut and became fused to the proximal columellar muscle (figure 26), and upon which the shell came to lie. This lobe has been produced by enlargement of the mantle edge only, for in *Acteon* the rest of this section of the skirt forms the infrapallium which overlies the columellar muscle (figure 26*a*); this distinction is more obvious in the advanced tectibranch *Philine* (figure 26*d*).

The anterior diverticulum of the mantle cavity, present in *Bulla*, *Haminoea*, *Scaphander* and *Akera*, may be occluded by the gizzard pushing against its floor. It can have little functional significance except in *Akera* where it is spacious, and when the animal swims circulation of water within it must be greater, and its thin floor and vascularized roof then take up oxygen; it is lost in more advanced forms (*Philine*).

The mantle cavity of *Gastropteron* is lateral and shallow as in the Notaspidea. This may be due to a change from a strictly infaunal mode of life to one which includes swimming and locomotion over the substratum. In *Aglaja*, a secondary reduction of the posterior mantle lobe has allowed extension of the gill, but compelled reduction of the caecum. Thus a further indication (see above, *Haminoea*, *Bulla*) is given that enlargement of the gill proved valuable, despite a concomitant reduction of the caecum.

(*b*) *Tensor muscles and stabilization of the mantle skirt*

With the inability to retract within the shell, the function of the columellar muscle changed from retraction to stabilization of the mantle skirt. Unlike prosobranchs, few extrinsic muscles insert on the mantle skirt of *Acteon*, though much of the infrapallium is attached to the underlying proximal columellar muscle (figure 26*a*) by connective tissue strands. The sole extrinsic muscles run from the muscle to infrapallium over the lateral face of the genital mass. In prosobranchs, the mantle close to the 'osphradium' contains columellar fibres, but as this area shifted to the right in tectibranch evolution and fused to the nuchal area, corresponding connections were neither feasible nor necessary.

Evolution of the tensor muscles has been linked to the separation of the infrapallium from the proximal columellar muscle, and so to such factors as reduction of the spire of the shell, of the proximal muscle and of the nuchal area. In *Bulla* the proximal muscle still supports the infrapallium (figure 26*b*), and is itself supported by the shell, but in more advanced forms the muscle has narrowed. This has occurred to approximately the same extent in *Akera* and *Scaphander*, and has allowed separation of the infrapallium and posterior mantle lobe, and created space between them (figure 26*c*). The broadening of the nuchal area also created space behind the diaphragm, and although *Akera* still retains an extensive ventral nuchal area as in *Scaphander*, broader confluence between body regions occurs because of a secondary enlargement of the dorsal nuchal area (p. 47); consequently a greater array of tensors is present than in *Scaphander*.

In *Philine*, the factors which promoted more complexity in tensor musculature were the continuing shell reduction, and the dorsoventral flattening and broadening of the proximal columellar muscle (secondarily) and of the posterior mantle lobe (figure 26*d*).

The inhalant flow of water into the mantle cavity of prosobranchs helps to keep the cavity fully open, but the reduced flow of water through the tectibranch mantle cavity, under infaunal conditions and in the absence of an effective siphon, is not able to do so, emphasizing the need for tensor muscles. The muscles are termed tensors because their primary function is to stabilize the infrapallium and maintain it in position, pressing it against underlying blood spaces the contents of which can provide a skeletal cushion. They perhaps contract if extended beyond a certain limit. Ventral attachments of the muscles are effective only when made to stable points such as the proximal columellar muscle, or to areas of the pallium (see below) adhering to the shell (*Scaphander*, *Akera*, *Philine*). These connections may result in mutual stabilization of surfaces.

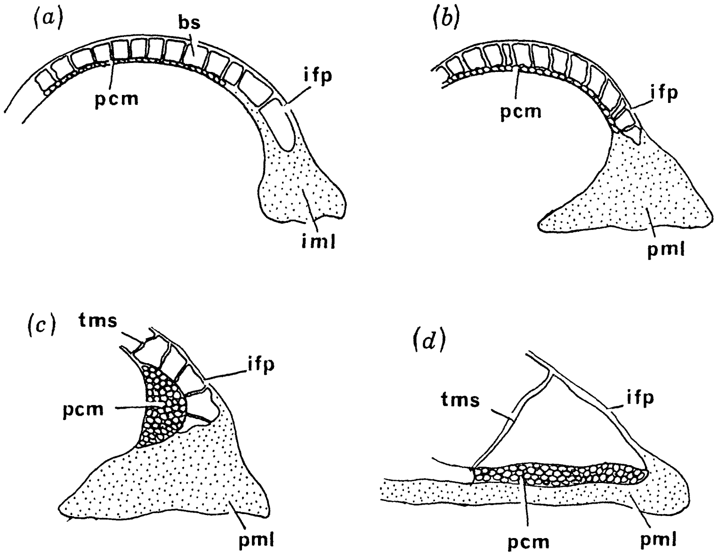

FIGURE 26. Comparative diagrams to show the evolution of the posterior mantle lobe and its relationships to the infrapallium and proximal columellar muscle. (*a*) *Acteon*, (*b*) *Bulla*, (*c*) *Scaphander*, (*d*) *Philine*. See text for full details.

Anteriorly the infrapallium of *Haminoea* is anchored by minor tensors which appear homologous with those muscles in *Acteon* mentioned above. Further development of the muscles is seen in *Scaphander*, *Akera* and *Philine*, but more posterior strands are comparable to the connective tissue ties in *Acteon*. Since *Acteon* possesses few extrinsic muscles of the infrapallium, it may not be valid to homologize any tensor muscle with those columellar strands of prosobranchs which run to the mantle skirt.

Horizontal alignment of the shell necessitated additional anterior and posterior attachments to stabilize it. Posteriorly these take the form of adhesive areas on or close to the transitional zone (*Haminoea*, *Scaphander*, *Akera*, *Philine*), which hold the mantle against the shell apex, and thus mutual stabilization of the two structures ensues. Anteriorly, attachment is provided by the adhesive ridge which prevents uplift of the shell.

(*c*) *Columellar muscle*

In monotocardian prosobranchs the proximal section of the columellar muscle is a flattened bundle below the nuchal area. Anteriorly, it divides to enter all part of the head-foot (figure 27*a*), and the mantle skirt near the 'osphradium', anus and genital opening. It arises from a larval retractor originating on the left posterior region of the shell (Crofts 1955; Fretter 1969, 1972), but in those diotocardians which have been studied (Crofts 1937, 1955; Smith 1935; Fretter 1969, 1972) it is the muscle attaching to the right which forms the more important adult retractor muscle. The musculature of veligers of both tectibranchs and nudibranchs (Saunders & Poole

1910; Brown 1934; Crofts 1955; Thompson 1958) agrees with that of monotocardian prosobranch veligers.

The course of the columellar muscle of the adult *Acteon* is similar to that of prosobranchs, though few fibres pass to the mantle skirt. The proximal portion, however, is broader since it supports the extensive infrapallium, and reaches, owing to the reduction of the nuchal area, further along the concave face of the visceral mass.

As might be expected, the broad proximal muscle of *Bulla* attaches to the outer surface of the shell in addition to the reduced columella. This reduced attachment of the columella is continued in more advanced forms despite a secondary narrowing of the proximal mass (*Haminoea*, *Scaphander*, *Akera*). It is partly due to the continued shortening of the muscle and

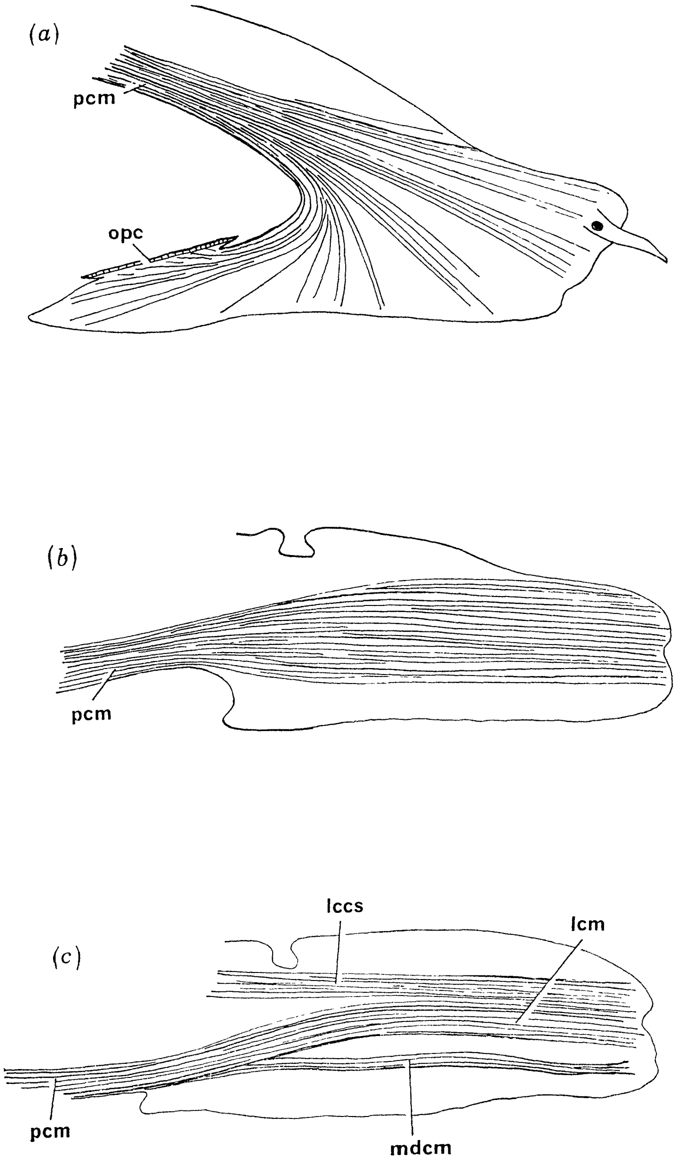

FIGURE 27. Comparative diagrams to show the reorganization of the columellar muscle system incurred in the transition from prosobranch to opisthobranch organization. (*a*) Prosobranch, (*b*) *Scaphander*, (*c*) *Philine*; note that the columellar muscle becomes strictly orientated along a horizontal (anteroposterior) axis, and that in *Philine* some fibres (lccs) no longer originate within the proximal columellar muscle. See text for full details.

further reduction of the columella. However, it is principally due to a re-alignment of fibres, concurrent with the assumption of slug-like form, such that they run anteroposteriorly and no longer twist around the columella (but see below). This is understandable for the proximal muscle no longer withdraws the head-foot within the shell, and is only concerned in uniting the two. This is reflected in that the form of the proximal mass, unlike that of a coiled prosobranch, is relatively unchanging, even in animals in which it is long and noticeably coiled (*Bulla*). Furthermore, most of the ventral face of the proximal mass in more advanced tectibranchs is secured to the shell by an overlying adhesive epithelium such that the shape of the muscle, even where coiled, is permanently maintained.

However, attachment to the columella is retained anteriorly (*Bulla*, *Haminoea*, *Scaphander*, *Akera*), where fibres, though progressively shorter through this series of animals, may still be noticeably coiled, and attachment to the shell extends to the abapical margin; these features are understandable when the horizontal alignment of the shell is taken into account. Fibres of the right side of the proximal mass remain long, and extend in a straight line towards the shell apex.

Reduction of the nuchal area in the assumption of a slug-like form brought about the situation whereby the proximal muscle and visceral mass came to lie horizontally at a level only a little above the pedal sole (figure 27*b*, *c*). This change made it increasingly difficult for fibres from the proximal mass, except those on the extreme left which are placed more dorsally, to enter the dorsal region of the cephalopedal mass.

On the left, the anterior adhesive ridge represents the reduced portion of the columellar fibres which enter the lateral region of the cephalic shield, but in *Philine* it is doubtful whether any columellar fibres either from the left or right, originate on the ridge. On both sides these terminate within the body wall, whereas in more primitive forms they converge to the proximal mass. Some intrinsic longitudinal muscles of the cephalic shield attach to the ridge in *Scaphander*, *Akera* and *Philine*, but in the last two, principally dorsoventral muscles which aid stabilization of the abapical shell lip.

In the nuchal area of *Akera* to the right, intrinsic longitudinal muscles of the cephalic shield fan dorsolaterally, and to the left, few attach to the adhesive ridge. These features suggest a secondary elongation of the dorsal nuchal area, apparently accompanying a decrease in size of the cephalic shield more anteriorly. This in turn was linked to the evolution of parapodia, which required lateral musculature to stabilize their bases during swimming.

Anteriorly, obvious changes in the columellar muscle were the separation of lateral and other tracts, and the restriction of fibres to the inner part of the body wall, for in advanced tectibranchs the muscle serves only to effect contorsions or shortening of the head-foot. The tracts in *Philine* closely resemble counterparts in *Cylichna* (Lemche 1956). There are few columellar fibres in the medial parts of the foot and cephalic shield of advanced tectibranchs, a feature largely explained by the broadening of the surfaces, but also due in part to the anteroposterior realignment. In *Philine* and *Aglaja*, however, a median muscle is present which has separated from the body wall.

The reduced proximal portion of *Aglaja* lacks an adhesive face, because fusion between the pallium and dorsal mantle lobe has occurred on the left. Its reduction in *Gastropteron* may be linked with the production of large parapodia for swimming.

Another swimmer, *Akera*, has a muscular lattice-work within the head-foot. Dorsoventral components presumably stabilize the parapodia, and together with the transverse components, tense the head-foot while the parapodia are flapping. Moreover, *Akera* is capable of extreme contorsions of the cephalopedal mass which aids movement over weed as well as through the substratum. These movements together with elongations of the head-foot, each followed by a rapid shortening which draws up the posterior region, are effected more readily by separate muscles than by a single thick sheet. The anterior adductor may also aid the longitudinal tracts in drawing up the posterior region, and may be of use during swimming when this part hangs below the head-foot (Morton & Holme 1955), with the adductor and longitudinal components acting. The musculature is similar to that of *Aplysia punctata* Cuvier (Eales 1921). *Gastropteron* is also a swimmer, but does not display such a complex array of muscles, presumably because, proximally, the parapodia are narrow; in *Akera* they are broad.

Anteriorly, in both *Scaphander* and *Philine*, strong buccal retractors link the columellar tracts to the buccal mass, muscles which do not occur in primitive tectibranchs (Hurst 1965; Rudman 1971*b*, 1972*c*, *d*, *e*), but which are present in prosobranchs (Graham 1973). Fretter (1969) has indicated that in *Lacuna vincta* (Montagu), bundles of the velar retractor appear to persist, with columellar connections, as median protractors of the subradular membrane. Graham (1973) suggests that the odontophoral protractors may also be derived from larval muscles. These facts indicate that the buccal mass retractors of opisthobranchs are derived from detached slips of body wall muscle.

(*d*) *Changes in organization of the nuchal area and of the base of the visceral mass*

Broadening of the nuchal area, which is exhibited during the development of *Onchidella celtica* (Forbes) (Fretter 1943), *Berthellina citrina* Rüppell & Leuchart (Gohar & Abul Ela 1957) and *Adalaria proxima* (Alder & Hancock) (Thompson 1958), allowed for many changes within this region.

The vertical septum of monotocardian prosobranchs (and *Acteon*) expanded in size to produce the diaphragm which still separates the cephalic and visceral haemocoels. Moreover, with the migration of the mantle complex posteriorly, the mantle cavity floor anteriorly could no longer be formed entirely by the body wall, and this was replaced by the infrapallium which became fused to the diaphragm (*Bulla*, *Haminoea*, *Scaphander*, *Akera*). Concurrent elongation of the mesopodium caused the diaphragm to slope increasingly backwards from its dorsal insertion (figure 24*c*, *d*). Movement of the infrapallium posteriorly drew the suboesophageal ganglion (sbog) posteromedially to lie adjacent to the visceral ganglion (vg, figure 24*b*, *c*).

Posteriorly in prosobranchs, the suboesophageal section of the visceral loop lies, to the right, within the body wall. In *Acteon*, it lies a little further right (figure 14*a*) below the infrapallium. In the other tectibranchs examined it has a different location and lies within the cephalic haemocoel, with both the suboesophageal ganglion, and the visceral ganglion (equivalent to the right visceral ganglion (rvg) of *Acteon* (Brace 1974) and prosobranchs), lying adjacent to or embedded in the diaphragm. In these animals, too, the supraoesophageal section of the loop passes through an aperture in the diaphragm whereas in *Acteon* the corresponding section passes, embedded in the body wall, on the left. It is apparent that the new course came about with migration of the connective to the right and, with enlargement of the vertical septum, ventrally also, to penetrate the enlarged aperture through which the oesophagus also passes.

Before travelling anteriorly, the anterior aorta in tectibranchs passes first to the right, attached to the diaphragm in all except *Bulla*. This course, which is different from that in *Acteon* where it immediately runs anteriorly, arose through posterior extension of the cephalopedal mass and reduction of the nuchal area.

The variable position of the bursa copulatrix indicates rearrangements at the base of the visceral mass. Its position in all can be easily derived from that occupied by the receptaculum seminis (Fretter & Graham 1954) of *Acteon* with which it is considered homologous (Brace 1974). However, its position on the left in *Akera* is not easily derivable from the site it occupies in *Haminoea*, *Bulla* and *Scaphander* (see page 51). In more advanced forms the bursa has sunk into the haemocoel, and this insinking of the reproductive organs is an important trend which allowed for their further elaboration (Lloyd 1952; Fretter 1960; Rigby 1965). It was largely permitted by the formation of large haemocoelic spaces between the viscera and the infrapallium.

In *Philine* and *Gastropteron* the disappearance of the anterior diverticulum of the mantle cavity allowed the pericardial cavity to move forwards, and the pericardium fused to the diaphragm anteriorly, rather than ventrally as in *Bulla* and *Scaphander*. The viscera forced the diaphragm on the left in *Philine*, forwards, and in *Aglaja* underlie the rear edge of the cephalic shield.

With increased length of the pedal sole, the mantle cavity moved to the posterior (*Aglaja*) and shallowed further (*Runcina*). The dorsal mantle lobe of *Aglaja*, and the pallium of *Gastropteron*, acquired longitudinal muscles. With the fusion of the two on the left in *Aglaja*, a body wall was formed here. With further extension of the pedal sole as in *Runcina*, the ventral portion of the cephalopedal mass, unlike *Aglaja*, stretched backwards. In *Runcina* the diaphragm appears to have been lost, the viscera anteriorly envelope the gizzard (personal observations), the body wall is relatively thin, and no columellar tracts, proximal columellar muscle or posterior mantle lobe are present.

10. DISCUSSION

Abundant evidence indicates that the migration of the mantle complex which produced an apparent detorsion accompanied the adaptation of a prosobranch stock to an infaunal mode of life. The term ‘detorsion’ should be discarded for the migration did not entail rotation of the mantle skirt as occurs during torsion, but differential growth followed by folding. Similarly no rotation of the visceral mass took place, though its orientation changed from erect to horizontal.

Whatever its original cause, nature and consequences, it is clear that torsion is now brought about by a larval mechanism, and, as discussed by Fretter (1969), has more relevance, like migration of the mantle complex, to the adult than to the larva as had been supposed by Garstang (1928). In opisthobranchs, both torsion and posterior migration of the mantle complex occur during early ontogeny, and it is apparent from investigations on *Acteocina canaliculata* (Franz 1971), *Philine aperta* (Brown 1934), *Aplysia punctata* (Saunders & Poole 1910), *Berthellina citrina* (Gohar & Abul-Ela 1957) and *Adalaria proxima* (Thompson 1958) that torsion is halted at a stage approximately corresponding to the position of the mantle complex in the adult. Thus migration becomes less noticeable in more advanced forms and, together with torsion, occurs during progressively earlier developmental stages. In *Adalaria*, the migration is represented only by a movement of the rectum from a posterolateral position to a median one, and organs, as soon as they are recognizable, are already in the post-torsional position. On the contrary, both torsion and anopedal flexure are clearly evident in *Aplysia*, and in *Onchidella celtica* (Fretter 1943) migration of the mantle complex is marked since the adult position of the mantle cavity in this euthyneuran is at the rear.

In those pulmonates investigated (Regondaud 1961, 1964; Ghose 1963), torsion is similarly halted at a stage corresponding to the position of the mantle complex of the adult, and the visceral loop remains uncrossed.

Whereas in prosobranchs the mantle cavity acts as a shelter for the veliger head-foot on retraction, the importance of an anterior mantle cavity to nudibranch veligers is diminished, for Thompson (1958) has shown that in many, the larva retracts not into the mantle cavity, but into the shell cavity. However, in *Acteocina* (Scaphandridae) (Franz 1971) mantle tissue remains at the shell edge, and the anterior mantle cavity affords protection to both the head-foot and velum upon retraction.

The possible origin of opisthobranchs and their relationships to the primitive pulmonates are discussed elsewhere (Fretter 1975; Brace, in preparation), but the marked anatomical similarity of *Acteon* and the pulmonate genus *Chilina* (Haeckel 1911) indicates that the connection is a close one. The structure of the nuchal area of *Acteon* shows that the Acteonidae can be derived only from a monotocardian and not a trochid stock.

The anterior expansion of the head-foot, reduction of the nuchal area to aid streamlining, and the migration of the mantle complex, the second perhaps influencing the last, were the prime adaptations for infaunal life. The extensive radiation which followed incorporated further adaptations which included the horizontal alignment of the visceral mass, loss of the shell, and modification to the columellar muscle.

The presence of ciliated bands within the mantle cavity in several prosobranchs (Fretter 1948; Fretter & Graham 1949, 1962) is correlated with small size. Their occurrence in opisthobranchs therefore suggests that the first tectibranchs were small, a fact borne out by further adaptations shown by their descendants which include, upon a subsequent increase in size, the redevelopment of a gill and evolution of the pallial caecum to offset respiratory inefficiencies which might otherwise have been incurred, especially in situations within the substratum where ventilation is difficult. The initial small body size presumably constituted a pre-adaptation to an infaunal mode of life.

With the assumption of a slug-like form the infrapallium separated from underlying muscle, and tensor muscles evolved in order to retain it in constant position. Without stabilization and with reduced ventilation of the mantle cavity it would tend, perhaps under pressure from the visceral haemocoel, to be forced laterally so that the cavity would be occluded, especially in larger animals. Furthermore, in some instances the suprapallium became fastened to the reduced shell.

Within the Opisthobranchia, as demonstrated by Morton (1958, 1963), there are many lines of descent from shelled to shell-less, and parallelism and convergence are common, for example, in the gut and reproductive system. Evolution of both the mantle complex and columellar muscle conform to this pattern.

The family Acteonidae is recognized as the most primitive living opisthobranch family (Boettger 1954; Fretter & Graham 1954). *Scaphander*, *Philine*, *Aglaja* and *Gastropteron* fall into one class, the Philinacea (Pelseneer 1894; Guiart 1901; Fretter 1939; Lloyd 1952; Boettger 1954; Ghiselin 1965), all derivable from an *Acteon*-like stock. *Gastropteron* cannot have arisen from the Philinidae as Boettger (1954) supposed, owing to the better developed ventral nuchal area and the curious construction of the posterior body region, but can be derived from a pre-*Philine* stock, as probably can *Aglaja*.

Akera is included in the Anaspidea by Morton & Holme (1955), but it has several general features which align it, as Pelseneer (1894) thought, with the Cephalaspidea. It is herbivorous, occurs in the same habitat as, for example, *Haminoea*, has a globose shell and an extensive ventral nuchal area, and the pericardial cavity is within the suprapallium which makes derivation from a *Haminoea*-like group impossible; it is to the primitive members of the Bullacea, or perhaps to an *Acteon*-like stock which showed adaptations towards herbivorous feeding, that we turn to find a likely ancestor. The production of large parapodia resulted in a taller body form and the partial separation of muscle tracts from the body wall, innovations which were carried through to the Aplysiidae. An early offshoot is indicated for *Akera* by the placing of the right pallial ganglion adjacent to the supraoesophageal ganglion, an arrangement which is, as Boettger (1954) mentioned, anomalous within most tectibranch groups, but is known within the pulmonate Chilinidae (Haeckel 1911). The alimentary tracts of *Akera* (Morton & Holme 1954), higher basammatophorans and *Succinea* (Rigby 1965), the Runcinidae (Burn 1963) and Atyidae (Fretter 1939) resemble each other, as do the reproductive systems (Ghiselin 1965). Therefore, considerable anatomical similarity links these herbivorous forms.

During tectibranch evolution there was a tendency for the production of dorsoventral muscles to stabilize the abapical shell margin (*Akera*, *Philine*) continued in *Aplysia* in which the shell, essentially a dorsal plate, is secured by a peripheral band of adhesive epithelium upon which fasten three mantle retractor muscles (Eales 1921) and other dorsoventral muscles (personal observation). This further attachment was possible only with an increase in the length of the cephalopedal mass so that it came to underlie the whole of the shell. Dorsoventral muscles are prominent also in the lateral body wall of *Berthella plumula* (Montagu) (personal observation), and the band of adhesive epithelium is virtually continuous as it is on the shell of *Tylodina corticalis* (Tate) (Burn 1960).

The body wall of burrowing tectibranchs is relatively thick; with emergence on to the surface thinning occurred, principally of the dorsal and lateral body walls. In the Sacoglossa, for example, which live on vegetation, the foot also is thin and possesses few longitudinal muscles which extend the length of the surface (*Elysia*, *Acteonia*; personal observation). Work on *Adalaria proxima* and *Tritonia hombergi* Cuvier (Thompson 1958, 1962) indicates that the larval retractor muscle is incorporated into the subepidermal complex of the adult; muscles with connections to the rhinophores and buccal mass arise later, and thus are not of columellar origin. This is supported by the conclusion reached here that the buccal mass retractors of cephalaspids are detached slips of body wall muscle. In view of the Anaspidea having prominent muscle tracts not of columellar origin, those of gymnosomatous pteropods, held to have arisen from the Anaspidea (Boettger 1954), are probably also not of columellar origin.

Attention is now turned to the position of the mantle complex and its bearing on the origins of the nudibranchs. Minichev (1970) grouped together the Eolidiacea, Dendronotacea and Arminacea, and separated off the Doridacea. In the last, the mantle complex (except for the genital opening) is posterodorsal and during development is displaced from a terminal position; in the remaining groups it is displaced from a lateral position. This argues for the derivation of nudibranchs from tectibranchs in which the mantle complex was either lateral or posterior in position. On the basis of gross morphology and the structure of the reproductive and vascular systems, Minichev suggested separate origins for dorids and the Pleurobranchidae from the Cephalaspidea. On this view, the dorids did not arise from the Notaspidea, as Boettger (1954) supposed. In this context, I fully agree with Minichev when he commented that dorids are not necessarily related to pleurobranchids because the mantle and rhinophores develop in the same manner in both, for there is essentially only one way of forming a dorsal mantle. Ghiselin (1965) suggested a similar division of nudibranchs, and supported a derivation of dorids from cephalaspids. Certainly the gill arrangements of the Runcinidae (Burn 1963) lend support to this idea, for in *Ildica nana* Bergh the gill is lateral and resembles that of the pleurobranchids, while in *Runcinella zelandica* Odhner the pinnules are separate from one another and encircle the anus, producing a doridiform pattern. Indeed Minichev (1970) noted that the gills of dorids are laid down as an unpaired group right of the anus followed by multiplication, and Evans (1914) indicated a similar innervation of the gill of dorids and cephalaspids, both supporting a derivation from cephalaspids.

Origins of the advanced groups of opisthobranchs cannot be determined until the anatomy of the lesser-known tectibranch groups is examined. However, this work has elucidated the pathway of change through the tectibranch series, and has briefly attempted to show how, with further modification, the nudibranch condition was assumed. Thiele (1931) listed a large number of tectibranch families, but in most only a few species are found, suggesting that in the evolutionary burst which produced opisthobranchs, many groups penetrated soft substrata which are widespread, but difficult environments to exploit; subsequently many came to the surface. The Philinacea, Acteonacea, and initially the Bullacea, remained below the surface successfully.

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List of abbreviations

aa	anterior aorta
aadd	anterior adductor muscle
aag	anterior aortic gland
aar	anterior adhesive ridge
abv	afferent branchial vessel
acg	acid gland
ade	adhesive epithelium
admc	anterior diverticulum of the mantle cavity
advm	aggregated anterior dorsoventral musculature
afa	afferent gill axis
alg	albumen gland
almg	anterior lobe of mucous gland
amb	anterior mantle border
amv	anterior mantle vessel
an	anus
antmb	anterior extrinsic muscle band
AP	anteroposterior axis
apt apt 1, 2, 3	adhesive patches
as	anterior space of pallial caecum
atms	anterior tensor muscle strand
au	auricle
AV	axis of volution
avvs	anterior ventral visceral sinus
ba	bulbous aorta
bc	bursa copulatrix
bcm	buccal mass
blmft	broad longitudinal muscle of foot
bm	basement membrane
bmr	buccal mass retractor muscle
bpl	blood plexus
bs	blood space
cbw	cut surface of body wall
cdml	cut surface of dorsal mantle lobe
cifp	cut surface of infrapallium
ck	cut surface of kidney
cmf	columellar muscle fibres
cmn	nerve to columellar muscle
cn	cardiac nerve
con	convolution
cpg	cerebropleural ganglion
cph	cephalic haemocoel
cpm	cephalopedal mass
cpml	cut surface of posterior mantle lobe
cpt	cephalic tentacle
crmb	cut surface of right mantle border
crpa	cut surface of right parapodium
cs	collecting sinus
ccsh	cut surface of cephalic shield
csdm	collecting sinus of dorsal mantle lobe
csf	cut surface of foot
csh	cephalic shield
cspp	cut surface of suprapallium
cssh	cut surface of shell
ct	ctenidium
cts	connective tissue strand
ctsh	connective tissue sheath
dbc	duct of bursa copulatrix
dcb	dorsal ciliated band
ddml	depression in dorsal mantle lobe
dg	digestive gland
dgbc	digestive gland below pallial caecum
di	diaphragm
dlcm	dorsal lateral columellar muscle
dlcmd	dorsal member of dorsal lateral columellar muscle
dlm	dorsolateral muscles
dlmff	dorsal longitudinal muscle fibres of foot
dm	dorsal muscle layer of foot
dml	dorsal mantle lobe
dna	dorsal nuchal area
dncg	dorsal nuchal groove
dpml	dorsal extension of posterior mantle lobe
dr	dorsal ridge
dtp	dorsal transverse muscle layer overlying the proximal columellar muscle
dtr	dorsal tract of lateral columellar muscle
dvm	dorsoventral muscles
ebv	efferent branchial vessel
efa	efferent gill axis
efglf	efferent vessel of gill leaflet
epfl	epichochlear fold
exa	exhalant aperture
exm	extrinsic muscles of infrapallium
f	foot
fadvn	nerve to floor of anterior diverticulum
fg	fossette glandulaire
fwmbc	fibrous whitening of divergent muscle bands of proximal columellar muscle
fwpc	fibrous whitening of proximal columellar muscle
g	gonad
gBl	gland of Blochmann
gd	genital duct
gg	genital ganglion
gh	genital hump
ght	genital hump (by transparency)
gl	gill
glf	gill leaflet
gm	genital mass
gn, gn 1	genital nerves
go	genital opening
gpl	gill plicae
grecn	genitorectal nerve
gt	gut
hd	hermaphrodite duct
hms	haemal sac
Ho	Hancock's organ
hsp	horizontal septum
hygl	hypobranchial gland
ifp	infrapallium
ilmcs	intrinsic longitudinal muscles of cephalic shield
iml	incipient mantle lobe
in	intestine
inb	infrabranchial chamber
itm	internal transverse muscle of body wall
itrg	intrapallial gland
k	kidney

lbwn	nerve to lateral body wall
lcb	lateral columellar muscle band
lccs	lateral columellar musculature of cephalic shield
lcm	lateral columellar muscle
lcmf	lateral columellar muscle of foot
lga	left gizzard artery
lgr	lateral cephalic groove
lmc	longitudinal muscles of anterior wall of anterior space of pallial caecum
lmcs	superficial longitudinal muscles of median region of cephalic shield
lmf	longitudinal muscle fibres
lmft	longitudinal muscle of foot
lpa	left parapodium
lplg	left pallial ganglion
lpn	left pallial nerve
lt	labial tentacle
mbcm	divergent muscle bands of proximal columellar muscle
mbr	medial branch of lateral columellar muscle
mdcm	median columellar muscle
mf	muscle fibres
mfl	mantle flap
mgl	mucous gland
msmv	main septum of anterior mantle vessel
msth	muscular thickening of transitional zone
mtp	metapodium
mv	mantle vessel
na	nuchal area
obl	oblique muscles
oe	oesophagus
opc	operculum
os	osphradium
ot	oral tube
ovhaf	opening of visceral haemocoel into afferent gill axis
pa	posterior aorta
padd	posterior adductor muscle
pap	posterior adhesive patch
pc	pericardial cavity
pcm	proximal columellar muscle
pdml	posterior extension of dorsal mantle lobe
pedg	pedal ganglion
pen	penis
pig	pigment
plc	pallial caecum
plim	pallium
plmg	posterior lobe of mucous gland
plplc	connective linking pleural ganglion and left pallial ganglion
pmf	posterior muscle fibres
pmfr	posterior frill of dorsal mantle lobe
pml	posterior mantle lobe
pr IV prV	buccal mass retractor muscles (pairs)
prcd	pericardium
prg	prostatic gland
prm	penis rectractor muscle
ps	posterior space of pallial caecum
psboc	connective linking pleural ganglion and suboesophageal ganglion
pspoc	connective linking pleural ganglion and supraoesophageal ganglion
pstmb	posterior extrinsic muscle band
pt	posterior tentacle
ptf	posterior limit of foot
pv	pallial nerve arising from visceral ganglion
pv′, pv″, pv‴	branches of pv
rec	rectum
rga	right gizzard artery
rm	radiating muscle
rmb	right mantle border
rn	renal nerve
rpa	right parapodium
rpcn	renopericardial nerve
rplg	right pallial ganglion
rplspoc	connective linking right pallial ganglion and supraoesophageal ganglion
rpn	right pallial nerve
rsm	receptaculum seminis
rv	renal vessel
rvg	right visceral ganglion
rvlvcm	commissure linking right visceral ganglion and left visceral ganglion
rvn	nerve arising from right visceral ganglion
sbog	suboesophageal ganglion
sborvc	connective linking suboesophageal ganglion and right visceral ganglion
ser. 1, 2, 3, 4, 5	tensor muscle strands (series)
sg	sperm groove
sh	shell
shc	shell cavity
shg	shell gland
spb	suprabranchial chamber
spog	supraoesophageal ganglion
spogc	connective linking supraoesophageal ganglion and genital ganglion
spolvc	connective linking supraoesophageal ganglion to left visceral ganglion
spp	suprapallium
st	stomach
stgn	stomatogastric nerve
tm	transverse muscles
tmcs	internal transverse muscle layer of cephalic shield
tmd	transverse muscles of diaphragm
tmlf	transverse muscle layer of foot
tms, tms 1, 2, 3, 4, 5, 6, 7, 8	tensor muscle strands
tplc	distal tip of pallial caecum
trz	transitional zone
ulm	unified lateral columellar muscle
vcb	ventral ciliated band
vg	visceral ganglion
vish	visceral haemocoel
vlcm	ventral lateral columellar muscle
vlm	ventrolateral longitudinal muscle
vm	ventral longitudinal muscle
vn	ventricle
vna	ventral nuchal area
vncg	ventral nuchal groove
vr	ventral ridge
vs	vertical septum
vtp	transverse muscle layer ventral to proximal columellar muscle
vtr	ventral tract of lateral columellar muscle

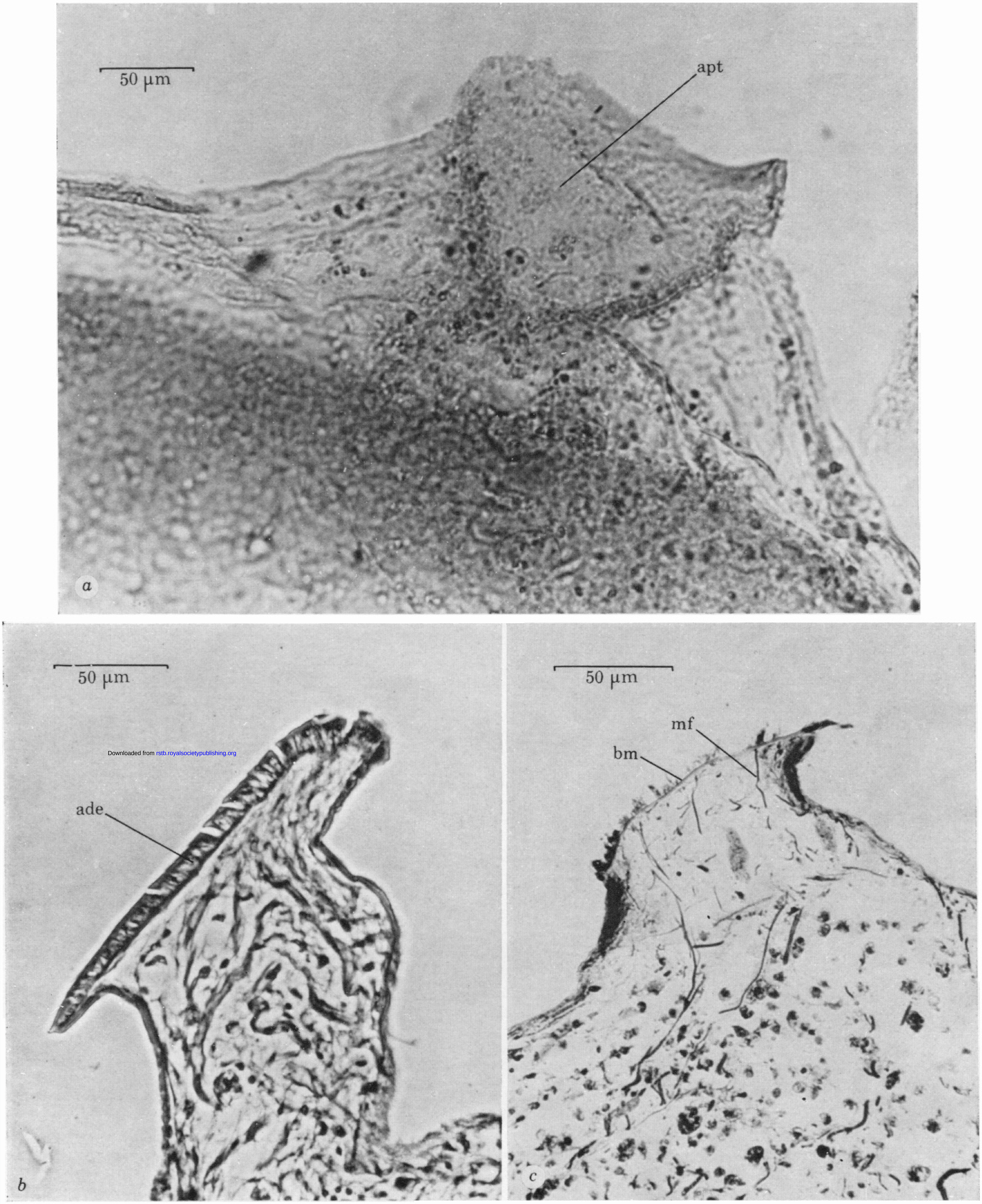

FIGURE 4. *Philine aperta:* raised adhesive patches. (*a*) Whole mount of one of the larger patches from the suprapallium of the pallial caecum (stained borax carmine); (*b*) transverse section of a patch to show the adhesive epithelium (stained Heidenhain's haematoxylin, phase contrast); (*c*) transverse section of a patch to show the basement membrane and muscle fibres attaching to it; the epithelium is largely torn away (stained Heidenhain's haematoxylin).