Functional Morphology with Particular Reference to Hinge and Ligament in Spondylus and Plicatula and a Discussion on Relations within the Superfamily Pectinacea (Mollusca: Bivalvia)

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FUNCTIONAL MORPHOLOGY WITH PARTICULAR REFERENCE TO HINGE AND LIGAMENT IN *SPONDYLUS* AND *PLICATULA* AND A DISCUSSION ON RELATIONS WITHIN THE SUPERFAMILY PECTINACEA (MOLLUSCA: BIVALVIA)

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CONTENTS

Excluding the isomyarian family Dimyidae, the Pectinacea comprise the families Propeamussidae, Pectinidae, Spondylidae and Plicatulidae. Present investigations are primarily concerned with species of the last two, both of which are cemented by the right valve, with secondary teeth and sockets which form ball and socket joints between the valves. Neither has previously been examined in life or the hinge and ligament critically studied.

Comparing throughout with conditions in the Pectinidae, the ctenidia in *Plicatula* are simpler (like those of *Propeamussium*) but both here and in *Spondylus* the ciliary pattern (type B (1a)) is more primitive. *Spondylus* resembles the Pectinidae in that it has elaborate arborescent lips and pallial eyes; *Plicatula* (and *Propeamussium*) has neither, and the inner mantle folds (velum) are reduced (though enlarged in *Propeamussium*). The foot is lost in *Plicatula* and in *Spondylus* has solely to do with cleansing; the Pectinidae display a range of pedal form and function – from locomotion to byssal attachment and to cleansing.

The ratio of 'quick' to 'catch' muscle in the adductor is associated with habit, being greatest where need for rapid adduction is greatest, primarily in connexion with cleansing, a matter of particular urgency in horizontally disposed bivalves. Pallial eyes – as well developed in permanently attached as in swimming species – are most probably concerned with immediate response to predatory attack on pallial tissues widely exposed when the valves gape.

The ligament in both *Spondylus* and *Plicatula* is surprisingly different from that in the Pectinidae (and Propeamussidae). The long anterior and posterior outer ligament layers found in the two last which unite the valves at either end of the condensed rounded inner ligament layer are replaced in *Spondylus* by fused periostracum. The outer ligament layers have migrated inwards and, after dividing on either side of the unchanged inner ligament layer, unite (topographically) above and below it, forming morphologically left and right areas composed equally of anterior and posterior outer ligament layers. The inward extensions of the fused periostracal grooves which form the secondary extensions to the primary ligament may well be associated with the change in nature of the hinge plate (and thus of teeth and sockets) to crossed-lamellar aragonite instead of the foliated calcite present in the Pectinidae.

The combined inner and outer ligament layers produce the more powerful ligament demanded by the more massive valves; the secondary periostracal extensions serve only to unite the valves which are maintained in alinement by way of the secondary teeth and sockets. The conspicuous bilateral asymmetry in the hinge and ligament is a result of cementation; similar conditions exist in the cemented pectinid, *Hinnites*.

In *Plicatula* differences are much greater. Inward growth of the mantle margins results in union above the now submarginal ligament. This is extremely compressed in the transverse plane becoming hoop-like with the right limb the longer. Basally it fractures, although the two halves remain in contact and function is unaffected. As in *Spondylus*, the halves of the anterior and posterior ligament layers unite on the two sides of the inner ligament layer. Owing to dorsal overgrowth by the hinge plate, the epithelia secreting the outer ligament layers form the two sides and roof of a chamber the base of which is the mantle isthmus (forming the inner ligament layer). Contact with the valves is exclusively by way of the outer ligament layers.

The periostracum fuses in the mid-line dorsally and does not contribute to the ligament from which it is separated. Owing to the division of the inner ligament layer into right and left halves, union of the valves is effectively by way of the secondary teeth, here more dorsally extended than in *Spondylus* but, as there, composed of crossed-lamellar aragonite.

Evolution of these four families starts in Palaeozoic stocks with modifications of organs in the mantle cavity – ctenidia, lips, pallial eyes, etc. – proceeding along lines distinct from those involving modifications in the ligament. The former particularly concern the primitive Propeamussidae, largely confined to deep water, and the universally distributed Pectinidae, the latter the Spondylidae and the Plicatulidae. Modifications of the foot have to do with final habit which is invariable freedom in the Propeamussidae, byssal attachment, freedom or cementation in the Pectinidae, and invariable cementation in the Spondylidae and Plicatulidae, the process occurring earlier in the latter and involving loss of the foot. Separation of the Spondylidae from the Pectinidae is more fully established with the present demonstration of the totally different ligamental structure; the difference is so profound in the Plicatulidae as to raise the question of elevating this to superfamily status.

INTRODUCTION

The monogeneric families, Spondylidae and Plicatulidae, are usually closely associated with the Pectinidae in the superfamily Pectinacea. They possess a number of common features. Both are monomyarian and are cemented by way of the right valve, although settlement occurs at an earlier stage in *Plicatula*. In probable correlation, the foot is retained in *Spondylus* (as in all other Pectinacea), but *not* in *Plicatula* which in this respect resembles the Ostreacea. *Spondylus* and *Plicatula* are, however, unique among these edentulous monomyarians (i.e. all other Pectinacea with the Ostreacea, Pteriacea and Anomiacea) in possessing secondary teeth. The valves are attached by ball and socket joints so that they remain attached after disintegration of the ligament. They can only be separated by breaking either the teeth or the margins of the sockets into which they fit.

These teeth have no relation to the hinge teeth in other Bivalvia with which they are analogous, not homologous. As here demonstrated, their formation is associated with major changes in the formation, and in *Plicatula* also in the functioning, of the ligament which becomes transversely instead of longitudinally disposed. This is the first time that the ligament has been fully described and interpreted in either family. Moreover, the process – and end result – is distinct in the two. This has major implications for phylogeny and for classification.

As in previous studies on the Bivalvia, this one has involved initial examination of living animals, here of *Spondylus americanus* Hermann and *Plicatula gibbosa* Lam. Previous work on both had been exclusively on preserved material so that, before proceeding to major consideration of the hinge and ligament, knowledge was extended by observations largely on feeding and cleansing mechanisms. Both species were examined at the Discovery Bay Laboratory on the north coast of Jamaica during March and April 1970, with further confirmatory observations in 1972.
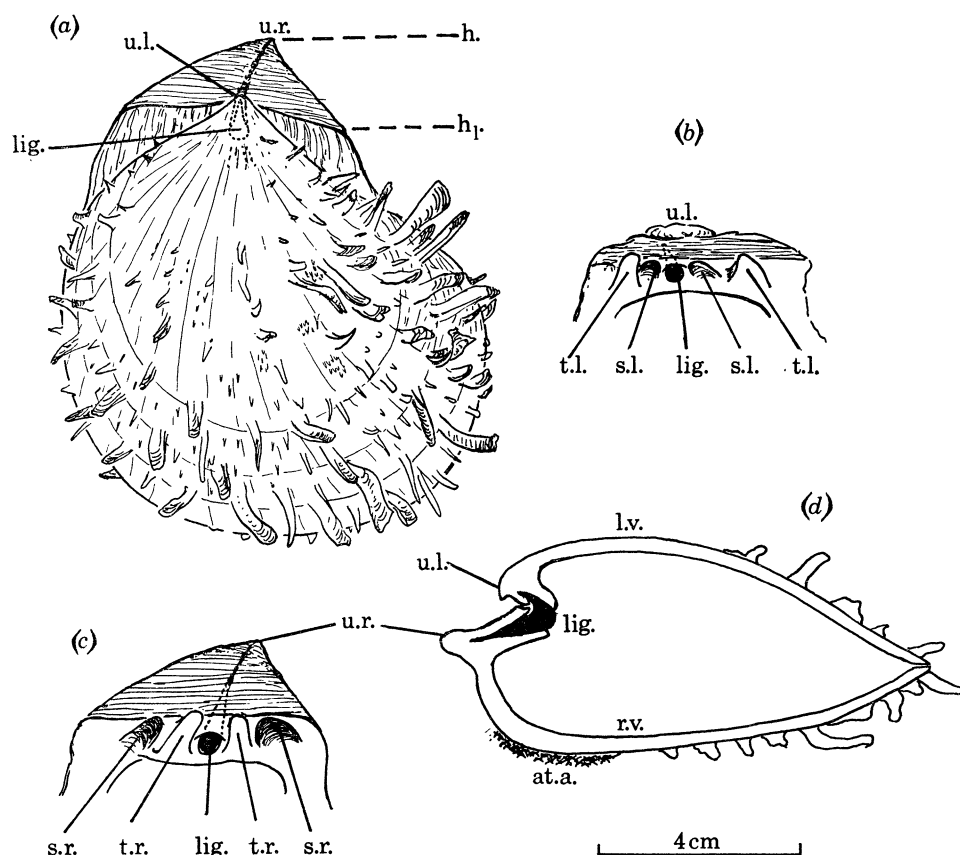

Figure 1. *Spondylus* sp., aspects of shell. (*a*) Intact viewed from above; (*b*) hinge area of upper (left) valve; (*c*) hinge area of lower valve; (*d*) transverse section through intact shell cutting through middle of ligament. For key to lettering on this and subsequent figures see p. 208.

SPONDYLIDAE

Species of the genus *Spondylus* occur widely in shallow tropical seas; they live cemented to hard surfaces and are characteristic members of the fauna of coral reefs. The thick shell is often conspicuously spiny and in some species brightly coloured. The larger species are among the most conspicuous tropical bivalves, the massive shells attaining maximum depths of over 12 cm. The majority are Indo-Pacific but the largest species, *S. americanus*, the Atlantic Thorny Oyster, occurs off the southern half of Florida and throughout the West Indies. It is common around Jamaica in depths of between 3 and 20 m usually.

The form of the inequivalve shell is shown in figure 1. Taylor, Kennedy & Hall (1969) find significant differences from the Pectinidae in shell structure, and these will be discussed later.

Cementation begins in a near umbonal area of the right valve (figure 1 d, at.a.). Its final extent depends on the length of time that the growing valve remains in contact with the substrate. Although settlement has never been followed, this certainly occurs at the postlarval stage when a byssal sinus (figure 25, b.s.) is present (Bernard 1896; Jackson 1890). The assumption is that (unlike the Ostreacea and also *Plicatula* which settle earlier) byssal attachment precedes cementation – as it does in the pectinid *Hinnites multirugosus* (Yonge 1951), although there for a much longer period and with frequent periods of freedom when the young swim. They are some 2 cm in diameter when they settle.
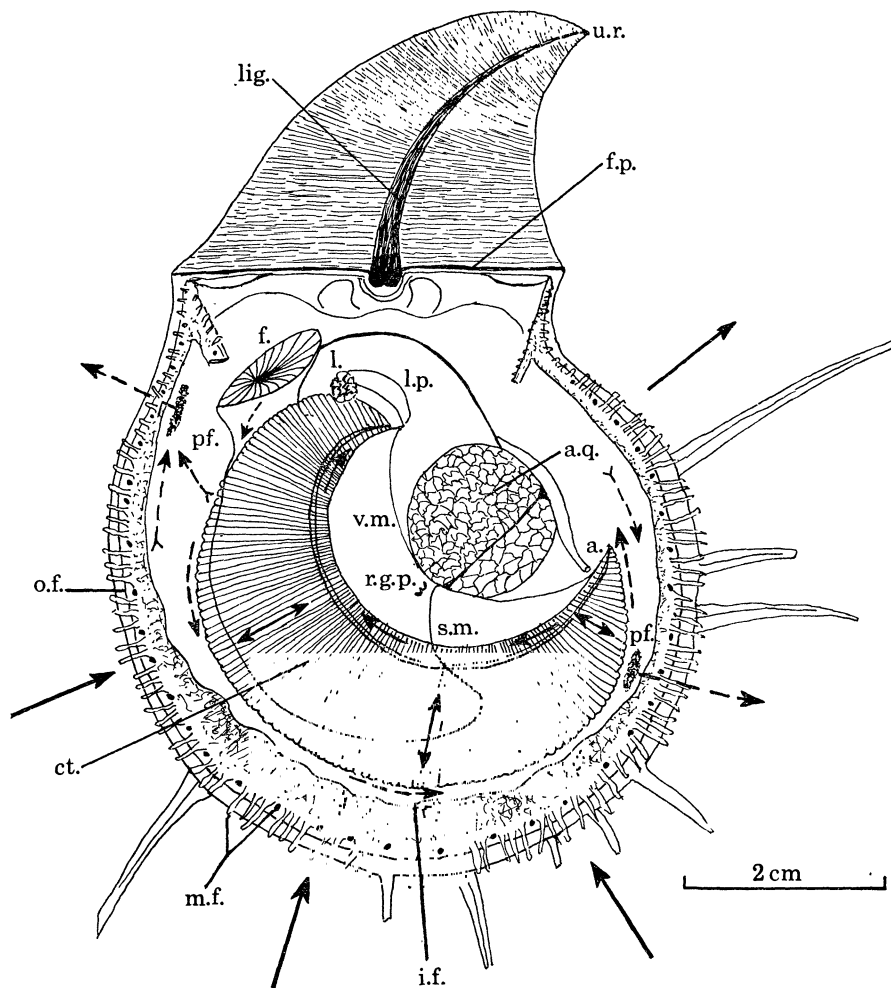

FIGURE 2. *S. americanus*, animal lying within right valve after removal of left valve and mantle lobe, arrows indicate direction of major water currents and of ciliary currents; broken arrows rejection currents, feathered arrows cleansing currents on mantle.

As in the Pectinidae, there is a long hinge line, the umbones, a little posterior to the centre, being flanked by large anterior and posterior auricles. Both valves are internally concave, the right valve in which the animal lies (figure 2) being the deeper, the more massive and notably longer from umbo to ventral margin. This is due to the extent of ventral migration of the hinge line (figure 1 a, h.–h_1.) on the fixed valve during growth forming 'interareas on the cardinal area' (Newell & Boyd 1970). This movement is associated with the need for adequate bilateral growth of the enclosed animal and occurs in all bivalves similarly constrained, most con-

spicuously in *Hinnites* (Yonge 1951), *Etheria elliptica* var. *cailliaudi* (Yonge 1962*a*) and in many *Ostreacea* (especially well shown in large shells of *Crassostrea gigas*). Where there is constraint on both sides, as there is in the byssally attached *Pedum spondyloideum* which lives in association with scleractinian corals, there is a similar movement of the hinge line in *both* valves (Yonge 1967). These movements involve separation of the umbones, that of the right valve (u.r.) remaining fixed in its original position while that of the left valve (u.l.) moves ventralward (figure 1*a*, *d*). In *Spondylus* there is some movement of the hinge line on the upper valve involving lateral (topographically upward) movement of the left umbo (u.l.). In transverse section, the area dorsal to the functional hinge line is thus V-shaped with the lower arm much the longer (figure 1*d*).

The hinge consists of a ligament (lig.) with two teeth (t.l., t.r.) and two sockets (s.l., s.r.) on each valve. For the greater part of their long dorsal surfaces the valves are attached by a thin membrane interrupted in the umbonal region by a rounded black 'internal ligament' or resilium (lig.) superficially like that of a typical pectinid, e.g. *Chlamys*. This massive structure is transversely compressed with a deeply sited attachment to the inner calcareous layer of the valves (figure 1*d*). The earlier positions of this ligament are indicated by a conspicuous groove on the V-shaped extension of the valves dorsal to the hinge line (figures 1*a*, 2). The teeth and sockets are symmetrically disposed on either side of the central ligament, the sockets being internal on the left valve (figure 1*b*) and the teeth on the right valve (figure 1*c*). Apart from the teeth, the hinge structure appears superficially identical with that in the Pectinidae but profound differences will be revealed.

Spondylus americanus

Mantle cavity

The disposition of the organs in this species after removal of the left valve and mantle lobe is shown in figure 2. The anatomy of related species has been described by Pelseneer (1911, 1931) and in more detail by Dakin (1928*a*), but their observations were on preserved material. Attention is here largely confined to features only apparent in life. The organs of the viscero-pedal mass will be discussed before consideration of the mantle/shell which involves analysis of the hinge mechanism.

In general arrangement (figure 2), the organs in the mantle cavity are typically pectinid. The solitary central adductor is largely composed of striated fibres forming the 'quick muscle'(a.q.) which is an essential part of the cleansing mechanism. Around this the semicircular visceral mass (v.m.) and ctenidia (c.t.) are disposed. The folds of the mantle margin are very well developed; the middle fold (m.f.) bears numerous tentacles and eyes, the inner fold ('velum') (i.f.) is deep and irregularly marked with brown. Conditions are essentially as in the Pectinidae. Pallial currents accumulate pseudofaeces (p.f.), both anteriorly and posteriorly (near the anus).

Ctenidia

These are attached to a suspensory membrane (s.m.) and entirely free from one another and from both visceral and mantle surfaces. They are typically filibranch with principal filaments cross-connected by interlameller septa, the filaments united by frequent rows of ciliated disks. The ascending filaments are a little shorter than the descending filaments and reflected terminally forming a narrow marginal gutter. Terminal attachment of filaments is by ciliary disks. In general structure, Ridewood (1903), who examined the ctenidia of five species of *Spondylus*, found only very minor differences between these ctenidia and those of species of the Pectinidae.

He failed to note that the latter have a groove along the ventral margin of the inner demibranch which is absent in *Spondylus* (cf. figure 3*a*, *b*).

There are, however, significant differences in the direction of the ciliary currents. Those on the frontal surfaces are the same as in all species examined by Atkins (1937) in the Arcacea, Anomiacea, Pteriacea, Pectinacea and Ostreacea, namely tracts of coarse cilia beating towards the free (ventral) margin and of fine cilia carrying smaller particles towards the axis or into the marginal gutters; only on the principal filaments do cilia beat exclusively towards the dorsal channels. In the last three of the superfamilies mentioned above, oralward currents are present along the free margins of the lamellae as well as along the axis and the marginal gutter (Atkins's current type B (1*b*)), but in *Spondylus* conditions resemble those in the Arcacea and Anomiacea (Atkins's type B (1*a*)), with currents along the free margins carrying particles *posteriorly*, oralward currents being confined to the three dorsal channels (see figure 3). This condition appears to be the more primitive. In *Spondylus* the coarser material tends to fall off the free margins of the demibranchs on to the mantle surface below; otherwise it is carried posteriorly. In either case it becomes incorporated in the pseudofaeces and is expelled.
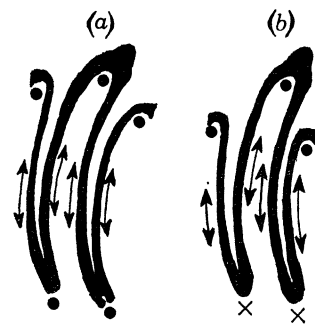

FIGURE 3. Diagrammatic sections through ctenidia of (*a*) *Pecten* (probably all Pectinidae); (*b*) *Spondylus* and *Plicatula*. Arrows show direction of beat of frontal cilia, oralward currents indicated by black circles, rejection (posteriorly directed) currents by crosses.

Palps and lips

The much greater transverse extent in *Spondylus* (with *both* valves deeply concave) compared with the Pectinidae influences the disposition of the elongate palps (figure 2, l.p.) which are transversely extended, and of the lips (l.) which are exceptionally wide. The palps function in the usual manner but rejected material, from both inner grooved and outer smooth surfaces, passes basally into a ciliary vortex from which mucus-laden masses pass on to the mantle or the visceral surface for incorporation into the pseudofaeces. Kellogg (1915) noted a similar condition in *Pecten irradians* and *P. tenuicostatus*.

The hypertrophied arborescent lips form an elaborate 'lip apparatus' even larger and more complex than that described in great detail by Gilmour (1964) in *Pecten maximus*. Arborescent lips are present throughout the families Limidae and Pectinidae but not in *Plicatula* or in *Propeamussium* (Bernard 1972). In those genera, as in bivalves generally, the lips are simple ridges bounding the proximal oral groove (Kellogg 1915) along which particles pass from the palps to the mouth. In *Pecten* (Dakin 1909, 1928*b*; Gilmour 1964) the lips are produced into elongate lobes, two on the upper, and three on the lower, side each being further subdivided into a complex series of lobules. These completely overarch the mouth region forming a functional tube by intimate interlocking, but *not* fusion, of the lobules. An only slightly simpler

condition prevails in *Pedum* (Yonge 1967). Structure is more complex in *Lima hians* where tissue fusion occurs, water escaping through minute pores; in *L. excavata* the system is almost as complex but without actual fusion (Gilmour 1964).

Pelseneer (1906, 1911, 1931), who first noted lip fusion in *Lima* with the formation effectively of separate right and left mouths, reported (1931) a similar condition in *Spondylus multisetosus*, although not in *S. gaederopus*, while Dakin (1928*a*) stated that in *S. americanus* 'The mouth opening is hidden in the characteristic manner seen in *Pecten*'. Personal examination confirmed this. Owing to the width of the animal, the lip apparatus is up to 2 cm long in a large *S. americanus* but with no increase in the number of lobes, only in their extent and degree of subdivision into closely interlocking lobules, but here also without tissue fusion. Membranes from the outer base of each lip extend over much of the surface but again without fusing. The mouth therefore lies at the centre of a tube up to 2 cm long with only minute openings to the exterior. In this respect, therefore, the condition in *Spondylus* is advanced. Bernard (1972) has suggested that particles are passed from the palps on to the surface of the lip apparatus the smallest ones to enter through the openings. But Gilmour has shown that water flows *out* through these. Selection is the function of the elaborate palps.

Food particles are certainly retained in the tube which Gilmour (1964) considered a means of combating the effects of the powerful water currents generated within the reduced anterior region of the mantle cavity in these monomyarians. However, as noted elsewhere (Yonge 1967), a better explanation may be the influence in both the Pectinidae and the Limidae (Gilmour 1967) of *anterior* as well as posterior rejection currents. The former are absent in the equally monomyarian Pteriacea (e.g. *Pinctada, Malleus, Isognomon* (Yonge 1968)) where the lips are un-modified. The presence of rejection currents on *both* sides of the hinge line also explains why species of both the Pectinidae and the Limidae can swim (Yonge 1936), whereas the still more flattened and equally free-living anomiid, *Placuna* which has *no* anterior rejection current cannot do so (personal observation).

Foot

As indicated by Pelseneer (1911), there is an evolutionary sequence in the form of the foot in the Pectinidae. In *Chlamys* (figure 4*a*) the well-developed foot has a terminal depression containing mucous glands (p.e.g.), a large byssal gland with a groove on the ventral side (b.g.), and a single but large posterior pedal (byssal) retractor (b.r.) attached to the upper (left) valve. In functional association with this asymmetry, the foot is twisted so that the byssal opening (b.g.) is on the under (morphologically right) side (figure 4*d*). Certain species, such as *C. varia* (and also *Pedum* where the byssal retractor is exceptionally large (Yonge 1967)), are byssally attached throughout life; after early life, others attach temporarily (see Waller 1972*a*). This attachment accounts for the size of the foot: the horizontal disposition for its asymmetry. The terminal depression, presumably represents the terminal 'sucker' in the foot which is an essential part of the locomotory apparatus in epifaunal bivalves such as *Mytilus* (Field 1922; White 1937); it could grip the substratum in young free *Hinnites* (Yonge 1951) although later it is probably concerned with cleansing of the mantle cavity. Thiesen (1972) has recently shown that in young *Mytilus* the outer surface of the shell is cleansed by the *dorsal* surface of the foot; clearly an independent mechanism.

The second condition is found in *Pecten* (figure 4*b*) all species of which are free and also inequivalve. Both byssal gland and the solitary retractor are reduced, asymmetry persists with the

opening of the byssal gland on the under side (figure 4*d*). There is a further increase in the now bifid terminal depression the epithelium of which is ciliated with both epithelial and sub-epithelial mucus glands. Conditions in *P. tenuicostatus* and *P. maximus* are described by Drew (1906) and Dakin (1909) respectively. Both noted the activity of the foot but Drew regarded it as largely degenerate whereas Dakin, who emphasized the amount of mucus secreted, thought
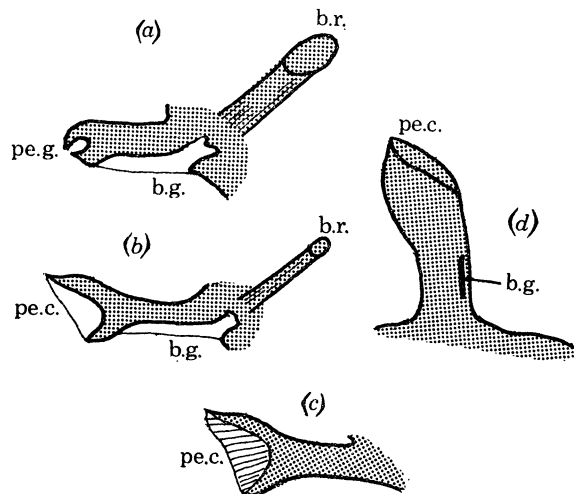

FIGURE 4. Diagrammatic representations of foot with byssal retractors in (*a*) byssally attached *Chlamys* (or *Pedum*); (*b*) *Pecten*; (*c*) *Spondylus*; (*d*) *Pecten* (showing byssal opening displaced to right (downwards). (*a–c*) after Pelseneer (1911); (*d*) after Dakin (1909)).
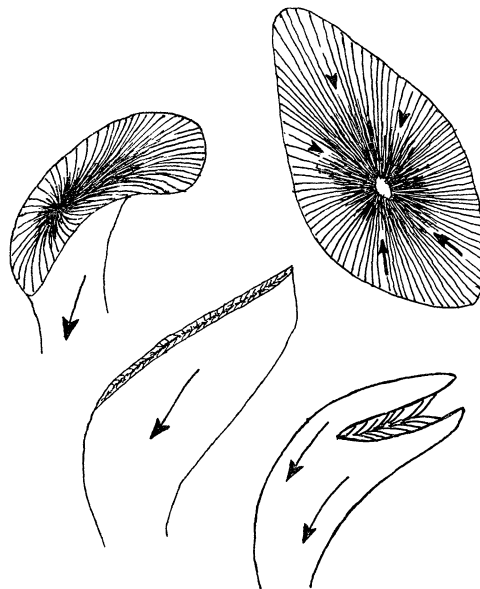

FIGURE 5. *S. americanus*, foot in life, viewed from various aspects showing twisting movements and closure of terminal funnel.

that the foot might be used 'for freeing the palps and gills of foreign matter'. Its undoubted cleansing function is wider than this with the increased size of the terminal depression correlated with the greater depth of the right (lower) valve and the consequent increased danger from accumulating sediment.

The final condition (described from the purely morphological aspect by Pelseneer) is found

in the cemented *Spondylus* but also in the free-living *Amusium* (figure 4*c*). There is no retractor and no byssal apparatus† but the terminal depression (pe.c.) is enlarged and impressively grooved. Observed in life, the foot constantly changes in shape (figure 5), bending from side to side and turning completely round, elongating as it does so. Thus it operates throughout the entire inhalant chamber. The terminal depression opens and closes; the lips are very sensitive and collect particles (as suggested by Dakin for *Pecten*) from the ctenidia and the mantle surface. Pedal distension will be due to blood pressure assisted by contraction of intrinsic circular muscles; retraction – in the absence of a retractor – by contraction of intrinsic longitudinal muscles. Both internal and external surfaces are ciliated; on the outer surface, particles are carried posteriorly and then basally on to the mantle surface. Within the depression they are conveyed along the converging series of ridges and grooves to the base of the funnel into which mucus is freely secreted. Gradually rounded masses of mucus-laden particles are built up. When they reach a certain size the funnel opens out widely and the waste mass is discharged, either on to the mantle surface or direct to the exterior. The anterior area of the foot originally concerned with locomotion has thus become involved in cleansing. Where the animals are motile, as in *Amusium* where the foot is identical with that of *Spondylus*, contractions of the quick muscle of the adductor are responsible for movement. The presence of this type of foot may be associated with turbidity over the mud bottoms on and above which *Amusium*, and also *Propeamussium* in greater depths, usually live.

In the Bivalvia the foot is initially concerned exclusively with locomotion – functioning in the manner described by Trueman, Brand & Davis (1966) – with the byssal apparatus functioning only during postlarval attachment. Where this is retained into adult life the bivalve becomes epifaunal with the foot a means of permanent attachment (Yonge 1962*b*). Such attachment leads to heteromyarianism (Yonge & Campbell 1968) – where, as in *Mytilus*, the foot retains powers of locomotion – and then to monomyarianism (Yonge 1953) which, apart from the Limidae, involves horizontal posture and increasing asymmetry. This is accompanied by loss of locomotory powers in the foot which finally becomes concerned exclusively with cleansing. Where the animals are free, locomotion is now by jet-propulsion.

Nervous system

No original observations appeared necessary, but the significant findings of Dakin (1928*a*) with later comments by Watson (1930*b*) and by Pelseneer (1931) must be noted. The nervous system in *Spondylus* is strikingly different from that in *Pecten*. In the former the pedal ganglia are connected with the fused viscerals, in the latter, as in the Bivalvia generally, with the cerebrals. The fused viscerals in *Spondylus* become even larger and more complex than in *Pecten* where already, with change to the monomyarian condition, this ganglionic mass represents the major nerve centre. Dakin explained the differences by postulating division of each cerebral ganglion in *Pecten*, the one part merging with the pedal ganglion, the other moving to the side of the mouth. The apparent pedo-visceral connectives would then represent a split part of the original cerebro-visceral connective. However, Watson (1930*b*) suggested the greater probability that the cerebral ganglia continued the movement towards the viscerals already apparent in *Pecten*,

† Connexion between persistence of the retractor and of the byssus is strikingly demonstrated in the life history of *Hinnites multirugosus*. While alternately free and byssally attached at a shell depth (hinge to free margin) of 0.8 cm, the cross-sectional area of the large retractor is about one third that of the adductor. Cementation occurs when the shell is about 2 cm deep and the retractor is still conspicuous after growth to 4 cm but has disappeared when the shell is 7 cm deep. (Personal observations on material supplied by Dr D. P. Abbott.)

finally merging with them. What appear as the cerebrals are actually, in his opinion, secondary enlargements at the base of the anterior pallial nerves. In the light of what occurs elsewhere in the Mollusca, e.g. in the pulmonate Gastropoda and in the Cephalopoda, this concentration of ganglia in one major centre – here visceral instead of cerebral – appears much the more probable explanation. Pelseneer (1931) describes precisely this condition in *S. multisetosus* where the cerebral ganglia, although in contact with the viscerals, do not fuse with them. The degree of concentration of nerve ganglia in the visceral region in *Spondylus* is much greater than in other pectinids being only equalled in the Limidae (Pelseneer 1907, 1911).
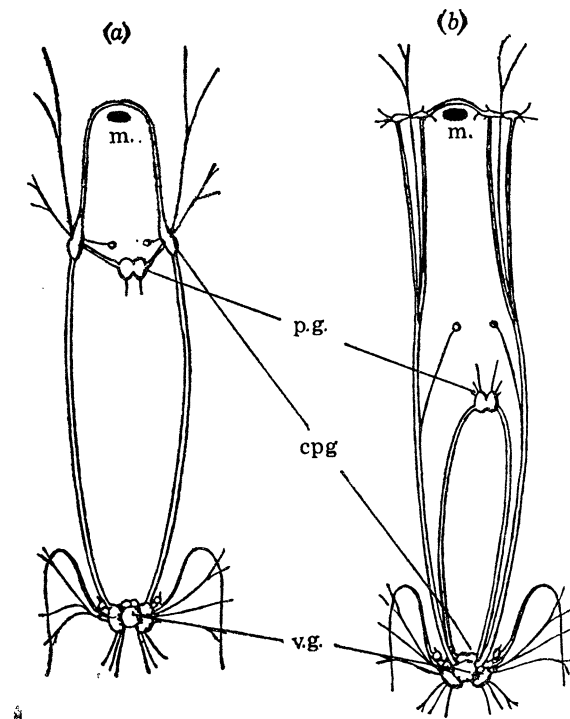

FIGURE 6. Central nervous system in (a) *Pecten* and (b) *Spondylus*, showing visceral migration of pedal and cerebro-pleural ganglia in the latter. (Modified after Watson 1930 b.)

Sense organs

Probably the most striking similarity between *Spondylus* and all genera of the Pectinidae resides in their common possession of numerous highly organized pallial eyes situated on the middle fold of the mantle margin. Such light receptors are absent in related families and superfamilies except for some species of *Lima* (although not in the swimming *L. hians*). Their presence in the cemented *Spondylus* (and the equally immobile *Hinnites* and *Pedum*) appears to be correlated with the need for rapid closure of the valves. This possibility is discussed later.

Hinge and ligament

The hinge clearly differs from that of all other bivalves (apart from that of *Plicatula* described later) by the presence of the conspicuous secondary teeth (figure 1 b, c) which fit within sockets in the opposite valve to form ball and socket joints. What is not immediately apparent is that the ligament has been profoundly modified. Adequate description of it demands preliminary mention of conditions in the Pectinidae, e.g. *Chlamys, Pecten, Pedum* and *Amusium*.

Here, as shown in figure 7, a central pear-shaped inner ligament layer (i.l.) forms a dark brown rubbery pad between the valves with which it is connected by way of deep resilifers (Trueman 1953a). It is flanked, up to the margins of a hinge line extended by long auricular surfaces, by stretches of anterior and posterior outer ligament layers (o.l.). These consist of a clear brown material usually forming a single arched sheet, although this is continually being replaced in cemented species such as *Hinnites multirugosus* (Yonge 1951) where the hinge line changes during growth as it does in *Spondylus*. The valves are thus closely united along the long hinge line.
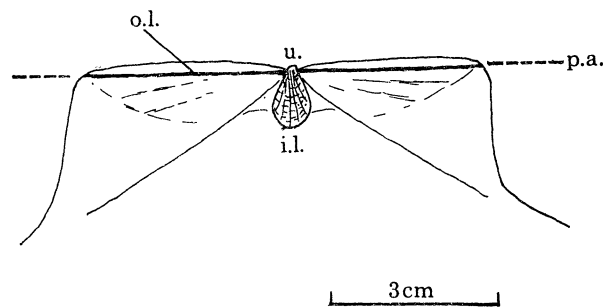

FIGURE 7. *Pecten maximus,* right valve showing hinge and ligament. (After Trueman 1953a.)

The inner ligament layer is secreted within a deep bowl-shaped mantle isthmus and is divisible into a central lamellar mass and fibrous regions containing aragonite adjacent to the resilifers (Taylor *et al.* 1969). The anterior and posterior inner ligament layers are formed by greatly elongated extensions of the epithelium of the outer surface of the outer mantle folds (figure 12a, o.s.o.f.) which bounds the margin of the embayments at either end of the ligament (Yonge 1957). Elsewhere this region of the mantle margin secretes the outer, here foliated calcitic, layer of the valves. The periostracal groove (p.g.) at the base of the inner surface of this outer mantle fold secretes the outermost shell layer, the periostracum (p). which, although here excessively thin and seldom, if ever, intact, completes the primary ligament. There is here no secondary extension involving fusion of the periostracum (Yonge 1957).
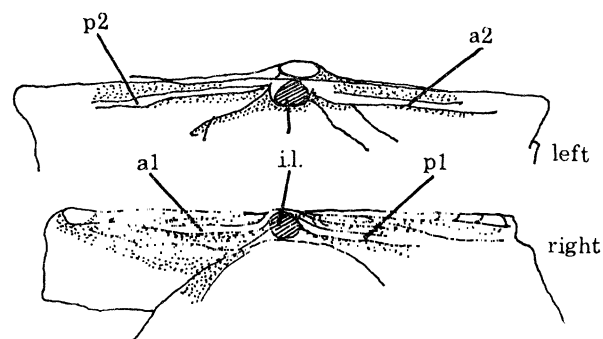

FIGURE 8. *Chlamys varia,* hinge and ligament in left and right valves in young individuals showing crura designated as lateral teeth (from Bernard 1896). *a,* anterior; *p,* posterior.

This ligament has been studied by Trueman (1953b). and Alexander (1966). Both layers are probably largely composed of a tanned protein complex with the central mass of inner ligament layer uncalcified and almost gelatinous. Contraction of the adductor causes compression of this while the outer layers are subject to tensile stress. The massive inner layer is solely responsible for the opening thrust, the outer layers being concerned with attachment only; cutting through

them results in misalinement of the valves (Trueman 1953 b). The relatively high efficiency of the inner ligament layer is associated by Trueman with the capacity for swimming. However, as already stressed, the basic need it serves is probably for frequent removal of sediment which collects in the horizontally disposed mantle cavity; it is just as well developed in permanently attached as in swimming species. The length of the outer ligament layers is associated with loss of interlocking teeth, traces of which appear, as described by Bernard (1896) in the dissoconch (figure 8). They may also be represented by the crura which extend parallel to the hinge line in the adult pectinid shell (Waller 1969, 1972 a).
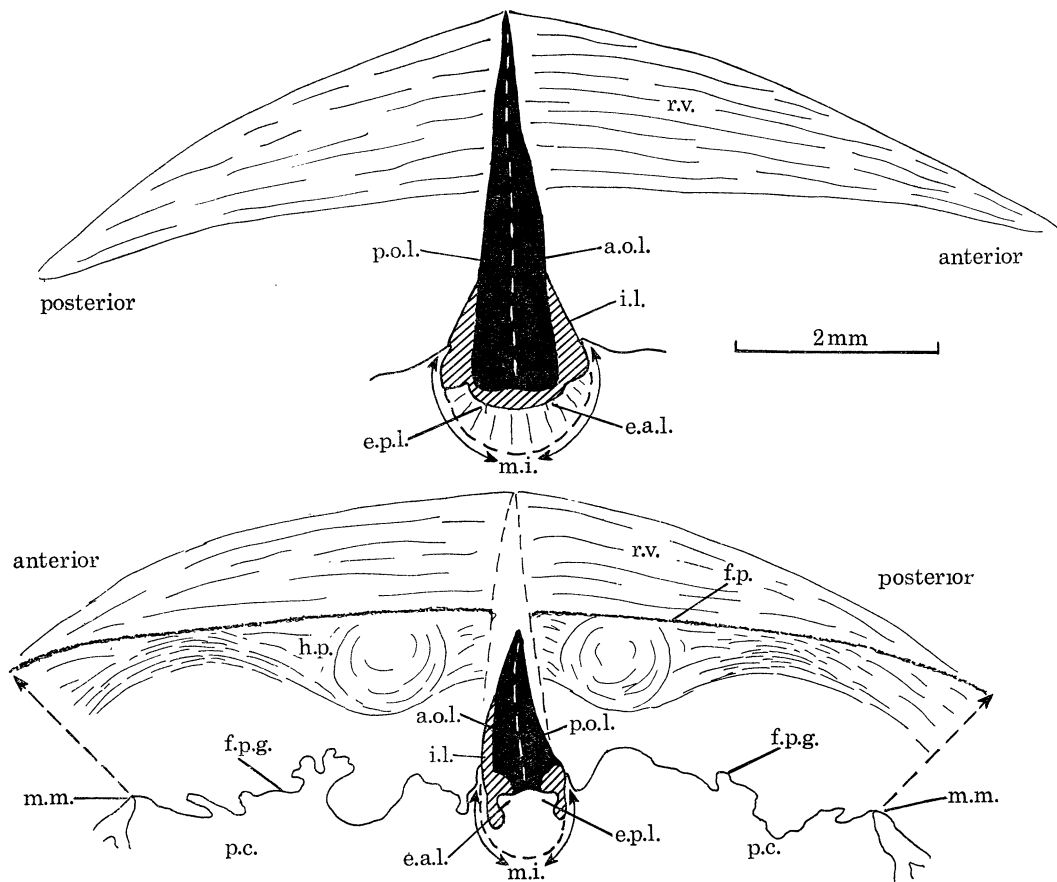

FIGURE 9. S. americanus, small specimen decalcified to show details of hinge and ligament; above, viewed from right (under) side, below, hinge plate and ligament viewed from left, broken lines indicating extent of ligament in right valve. Dorsal margin of tissues (f.p.g.) withdrawn from hinge line (f.p.) as shown by broken arrows; whole, curved, arrows indicate extent of (obscured) mantle isthmus. Here (and subsequently) outer ligament layers shown black, inner ligament layer by oblique lines.

Apart from the presence of the massive secondary teeth, the ligament in *Spondylus* appears, at first sight, to be very similar. However, the changes in the hinge plate (secreted by the pallial crest) which have involved the formation of these teeth would appear also to have been responsible for the inward movement of both anterior and posterior outer ligament layers which here come to lie on either side of (i.e. topographically above and below) the inner ligament layer, the three forming one massive central ligamental mass. The condition is shown in figures 9 and 10 in which, following decalcification, the ligament is viewed from left and from right sides
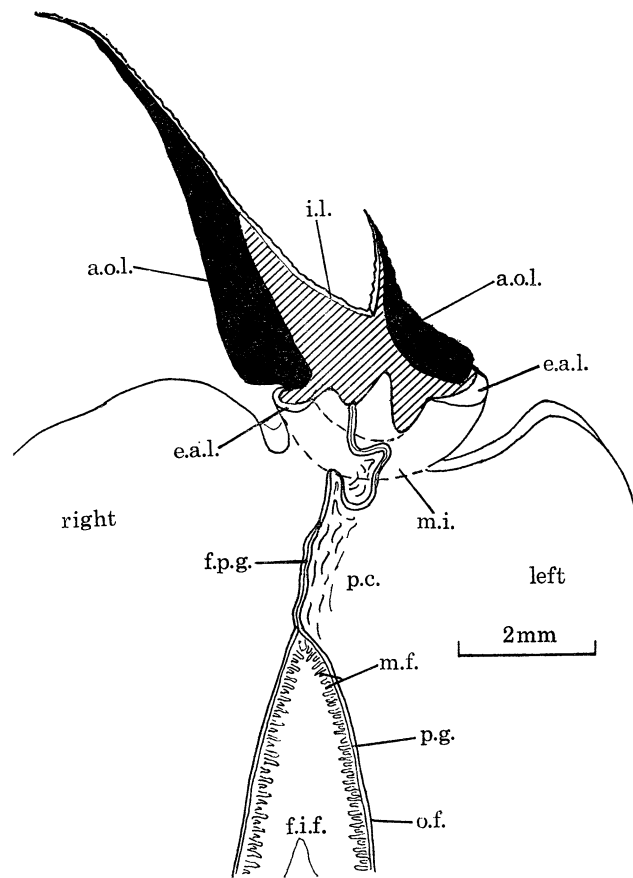
FIGURE 10. *S. americanus*, decalcified hinge region, ligament viewed from anterior end showing inner ligament layer flanked *laterally* by outer ligament layers, only anterior areas of which here visible. Right side of ligament notably the larger.
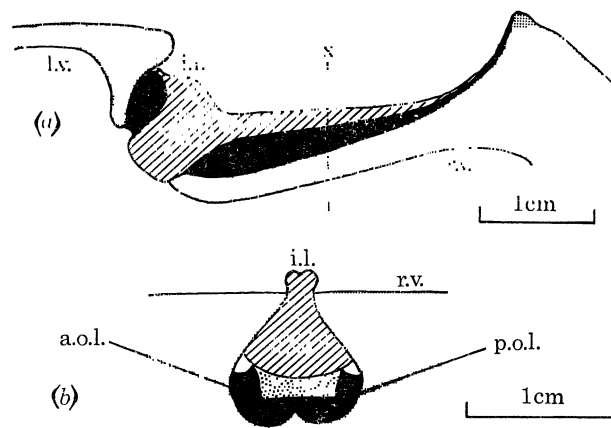

FIGURE 11. *S. americanus*, sections through ligament (obtained by grinding shell). (*a*) Transverse through centre showing bilateral asymmetry; (*b*) section at right angles to (*a*), made along line *x*, shows separation of outer ligament layer into anterior and posterior halves (a.o.l.; p.o.l.). Shell stippled.

(figure 9) and from the anterior end (figure 10). Conditions are somewhat complicated by the much greater length of the ligament attached to the right (under) valve as shown in transverse section in figure 11a.
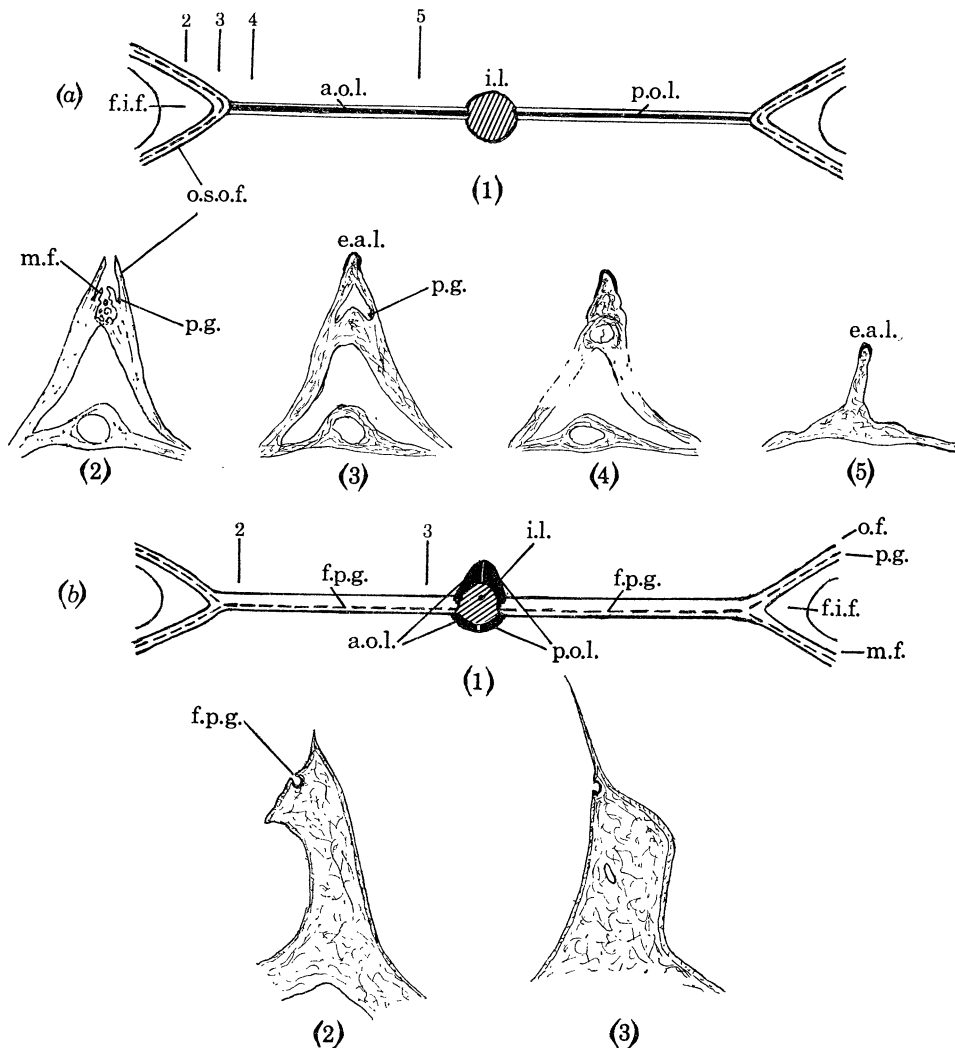

FIGURE 12. Comparison between structure of hinge and ligament in (a) Pectinidae; (b) Spondylidae. (a1) Diagram of conditions in Pectinidae showing ligament and mantle margins from above, periostracal groove indicated by broken lines, inner and outer ligament layers as before; (a2–5) transverse sections through mid-dorsal tissues of *Chlamys opercularis* ($\times 26$). (b1) Corresponding diagram of condition in Spondylidae showing fused periostracum replacing outer ligament layers; (b2, 3) transverse sections through mid-dorsal tissues of *S. americanus* showing lateral asymmetry and continuance of fused periostracal groove ($\times 26$).

The inner ligament layer (i.l.) is secreted, as in the Pectinidae, by the bowl-shaped mantle isthmus, but the anterior and posterior outer ligament layers have each become divided into topographically upper and lower sections, those from each end uniting (see broken white lines in figure 9) to form left and right, instead of the original anterior and posterior, outer ligament layers. The dual nature of these outer layers (a.o.l., p.o.l.) is well indicated in figure 11b which shows the composition of the ligament as revealed when cut at right angles (i.e. longitudinally in relation to the shell) near to its union with the lower valve (r.v.). As shown in figure 2 (lig.), there are well-defined anterior and posterior areas of attachment. In the larger

shells each area subdivides making four rounded areas. Attachment to the left valve is always single with no indication of the separate anterior and posterior components.

The inner ligament layer is little affected by these changes in the outer layers; it possesses the same rubbery, almost gelatinous, central consistency as in *Pecten* or *Chlamys*. This is in obvious contrast to the outer layers which consist of parallel fibres and which here take over the function of the lateral fibrous regions of the inner ligament layer in the Pectinidae. The properties of any part of the ligament are conditioned by its function, *not* by its origin. This is a highly significant point. All, however, are compressed when the adductor contracts so forming a functional unit. This greater ligamental mass can be functionally associated with the much thicker shell in the cemented Spondylidae.
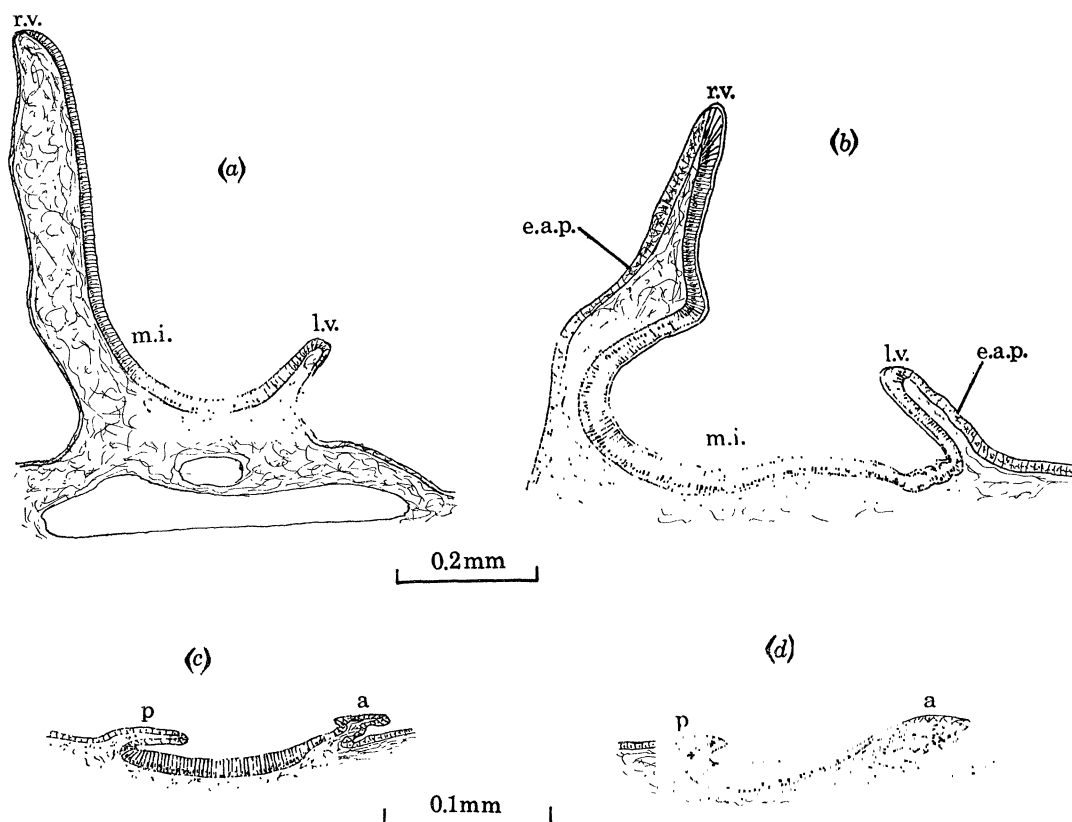

FIGURE 13. Sections through cup-shaped mantle isthmus (secreting inner ligament layer) and adjacent tissues. (*a*) *Pedum*, transverse section; (*b*) *Spondylus*, transverse section; (*c*, *d*) longitudinal sections. a, anterior; p, posterior.

The hinge line is effectively the same length as in the Pectinidae (cf. figures 12*a*, *b*) but here attachment, apart from centrally, is by way of a secondary extension of the ligament involving the periostracum as shown in figure 9 (f.p.) and diagrammatically in figure 12*b*, f.p.g. This consists of a softish green material which unites the valves without affecting the opening thrust. It has negligible strength, in no way comparable with that of the outer ligament layers in the Pectinidae, but this is of no significance because the valves are here maintained in particularly rigid alinement by way of the intimately interlocking secondary teeth. They take over the function of the outer ligament layers in the Pectinidae.

Adequate comparison of conditions in the Pectinidae and *Spondylus* involves that of the secreting surfaces involved. Diagrams and sections of significant areas are shown in figures 12 and 13, the former being concerned with the formation of the lateral regions of the ligament, the latter with the central mass of inner ligament layer (i.l.) exclusively in the Pectinidae (13*a*) and combined with anterior and posterior outer layers in *Spondylus* (13*b–d*). The conspicuously deep epithelium of the mantle isthmus which secretes the inner ligament layer (i.l.) is flanked by epithelia secreting outer ligament layers (a.o.l., p.o.l.) in the Pectinidae (figure 12*a*, 1) but by the inwardly extending fused periostracal grooves (f.p.g.) in *Spondylus* (figure 12*b*, 1), secretion of the outer ligament layers (a.o.l., p.o.l.) being there confined to regions on either side (*not* either end) of the inner ligament layer (figure 12*b*, 1). The hinge line is bilaterally symmetrical in *Pecten* or *Chlamys* (figure 12*a*), but asymmetrical in the permanently byssally attached pectinid, *Pedum* (figure 13*a*), and in *Spondylus* as indicated in transverse sections through both the secondary (periostracal) (figure 12*b*, 2, 3) and primary (central) regions of the ligament (figures 12*b*, 1 and 13*b*).

PLICATULIDAE

The single monomyarian genus *Plicatula* comprises the family Plicatulidae. All species are cemented by the right valve so resembling all related pleurothetic monomyarians apart from the Ostreacea which, however, they do resemble in the absence of a foot in the adult (the condition in the postlarva where it is there a highly significant organ is unknown in the Plicatulidae). Species are most numerous in the Pacific and within the tropics; Keen (1958) describes four species from the tropical north Pacific. Although the shell is well known both in recent and fossil species (it originates in the Middle Triassic), the sole descriptions of anatomy are those of Pelseneer (1911) and Watson (1930*a*). There is no previous account of the living animal, nor has the hinge region with the uniquely disposed ligament hitherto been described or interpreted. This is indeed so totally unlike that of the Ostreacea as to dispose completely of any tentative suggestion of relations with that superfamily (Newell & Boyd 1970).

Plicatula gibbosa

The sole representative of this genus in the North Atlantic is *P. gibbosa* Lam, 1801 (figure 14). According to Warmke & Abbott (1961), it occurs off the southeast United States, also off the Gulf States and in the West Indies. They continue, 'One inch in length, solid, shaped somewhat like a cat's paw. Usually light in colour and marked with red or brown. Sculptured with 5 to 9 radial ribs, which make the margins of the valves fluted. Hinge with two strong, equal-sized teeth. A common intertidal species found attached to stones, coral or dead shells. *P. spondyloidea* Menschen is this species.'

In Jamaica, Mr J. M. Humfrey, who collected the specimens examined at Discovery Bay, states that it is, or perhaps was, abundant in about 1 or 2 ft of water along the harbour side of the Palisados at Kingston, usually in Thalassia flats. It is usually very firmly and extensively cemented to some solid object, often a pebble smaller than itself so that, although completely immobile, it can be rolled about by water movements. Occasionally several individuals may attach to the same pebble with young specimens on the shells of adults. Dr Barry Wade (personal communication) has frequently found them on the shells of the sea-urchin, *Lytechinus*.

Jackson (1890) originally noted that, as in the Ostreacea, attachment occurs at the end of the prodissoconch stage. There is no byssal notch in the nepionic stage as there is in *Spondylus*.

Attachment is by a limited area on the right valve (figure 14) which, again unlike *Spondylus*, is flatter than the more concave upper valve. Ribbing does not start until shell growth extends beyond the limits of cementation. In life the valves separate only very slightly with a double row of small marginal tentacles barely exposed. After death the valves remain closely attached owing to the ball and socket hinge. Separation of the valves reveals details of the hinge with the same general arrangement of secondary teeth and sockets as in *Spondylu* but with the antero-posteriorly compressed ligament and disposition of the mantle margins widely dissimilar.
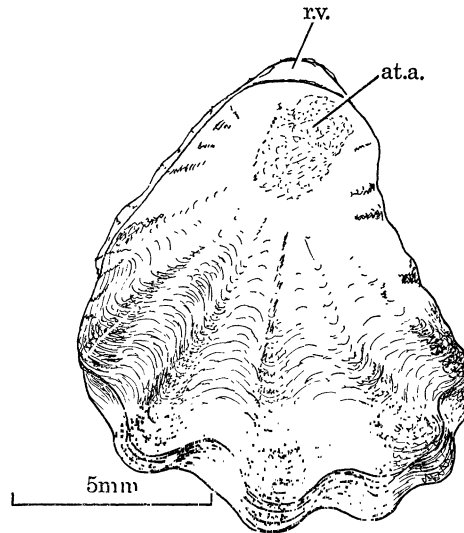

FIGURE 14. *Plicatula gibbosa*, viewed from above, area of attachment (on under, right, valve) indicated.

Mantle cavity

The general disposition of the organs in the mantle cavity viewed from the left side is shown in figure 15; representative transverse sections are shown in figure 16. As noted by Watson (1930a), who saw preserved specimens only, the folds of the mantle margin are poorly developed. The middle fold is without eyes and possesses only very short tentacles in two rows. The inner fold is a low ridge with a single row of short tentacles, unlike the deep inner mantle fold present in *Spondylus* and the Pectinidae. All of these gape widely but in *Plicatula* the valves separate only very slightly. When examined (at the end of March) both visceral mass and mantle lobes (figure 16a, g.) were distended with the gonad, in the latter respect resembling the Mytilacea. The animals, of separate sexes, were ready to spawn.

The single adductor, somewhat eccentrically situated towards the posterior, is relatively large with 'quick' and 'catch' muscle areas of approximately the same size indicating, in comparison with related monomyarians, a greater need for enduring contraction and a smaller one for frequent expulsion of pseudofaeces. However, Watson (1930a) states that in *P. australis*, the 'catch' muscle is the larger. The visceral mass is centrally placed and dorsoventrally extended. The gut is much as described by Watson (1930a) with the style-sac united with the mid-gut which then runs dorsally to pass ventrally through the large pericardium (pm.) and open at the anus (a.) on the mid-ventral surface of the adductor. The kidneys (k.) are large and unite posterior to the adductor (Pelseneer 1911; Watson 1930a). The reno-genital pores open on the under side of the adductor (figures 15, 16c, r.g.p.).
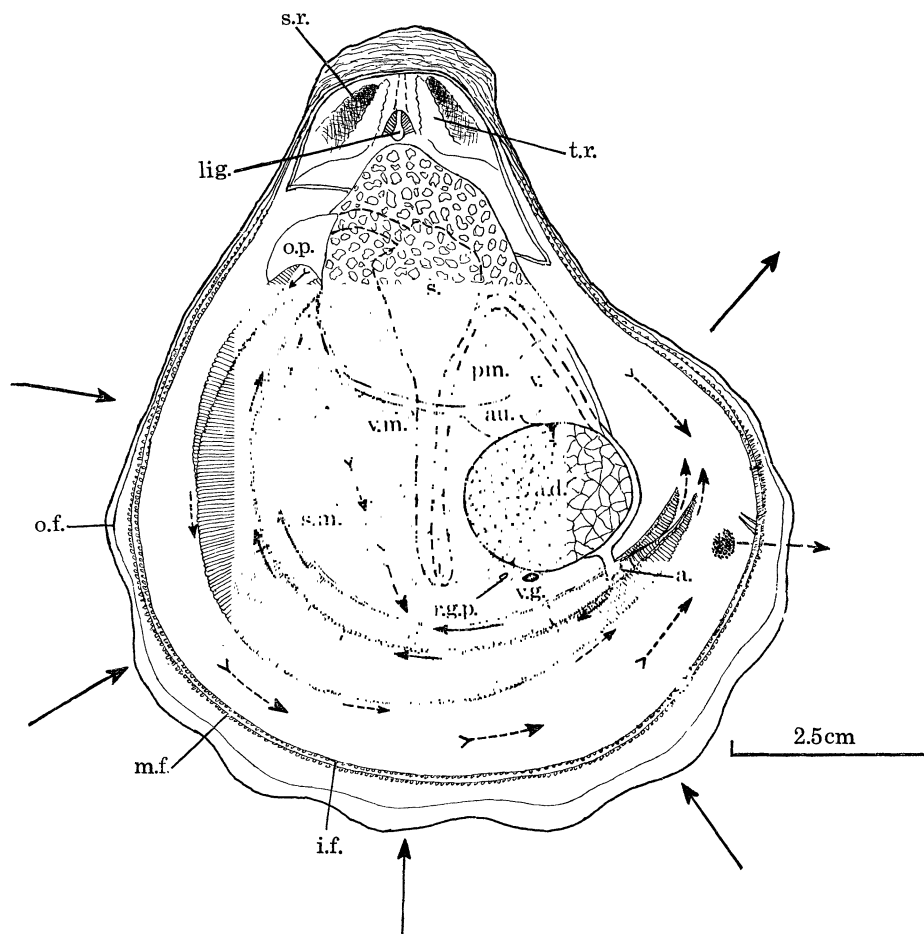
FIGURE 15. *P. gibbosa*, animal lying within right valve after removal of left valve and mantle lobe, arrows indicating major currents, broken arrows rejection currents (feathered on mantle and visceral surfaces, plain on ctenidia).
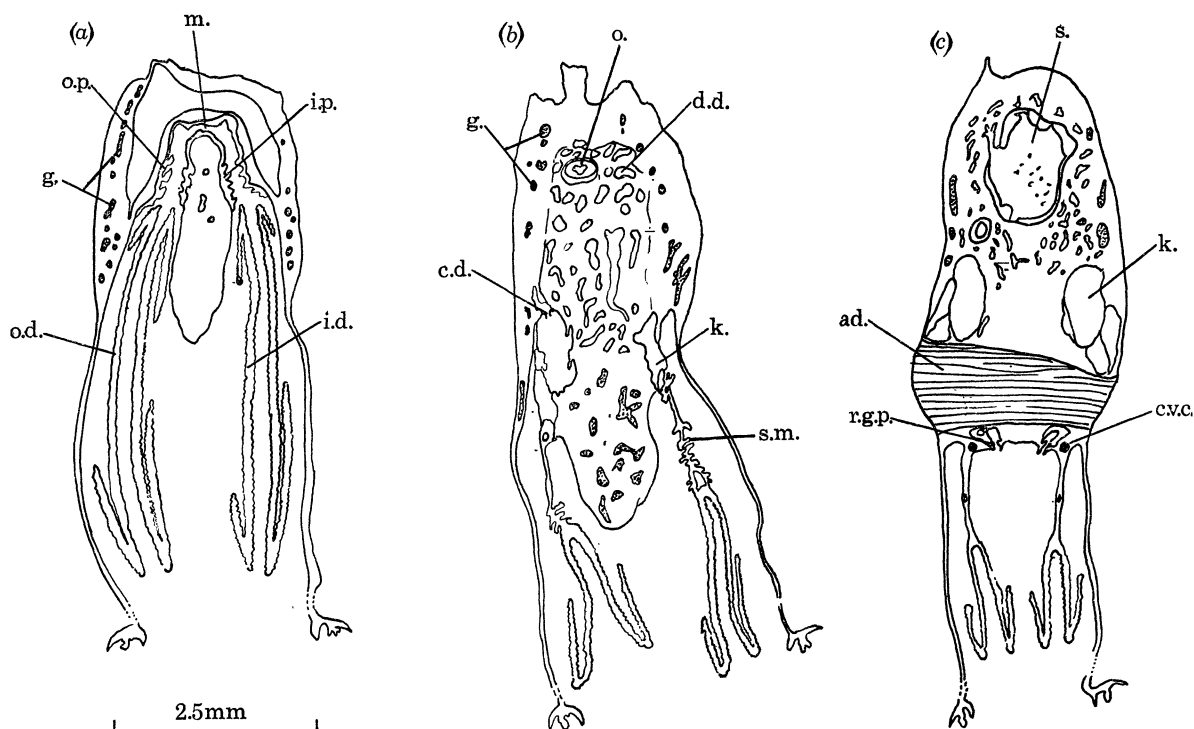

FIGURE 16. *P. gibbosa*, transverse sections: (*a*) in mouth region; (*b*) in middle of visceral region; (*c*) through adductor.

All ciliary currents on the mantle surface and visceral mass in the inhalant chamber and on the mantle surface in the exhalant chamber converge on the one area at the posterior end of the ctenidia. Here pseudofaeces accumulate and from here alone (unlike the Spondylidae and Pectinidae) are they ejected. Conditions here resemble those in the Pteriacea and Ostreacea where there is no anterior rejection of waste.

Ctenidia

Unlike the appearance after fixation when, as figured by Pelseneer (1911) and Watson (1930 *a*), they appear straight, in life the ctenidia, attached by a deep suspensory membrane (figures 15, 16 *b* s.m.), are disposed in a semicircle much as in *Spondylus*. But the lamellae are narrower with much simpler structure, not plicate, without interlamellar connexions and with adjacent filaments united only by two rows of ciliated disks, ventrally and terminally. The ascending filaments are short (figures 15, 16), the brief marginal gutter not apparent in sections. The ventral margins of the filaments are without grooves. Ridewood (1903) found identical conditions in *Amusium* but, as pointed out by Waller (1972 *b*), his species were all of *Propeamussium*, now placed in a separate family. Personal examination of the ctenidia of *Amusium pleuronectes* reveals that these *are* plicate and in all respects typically pectinid. Ciliation in *Plicatula* does resemble that in *Spondylus* with the same double series of frontal cilia (although here they are on *all* filaments), with rejection currents along the ventral margins and with three oralward currents dorsally (all as shown in figure 3).
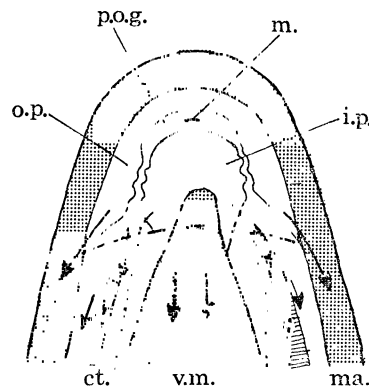
FIGURE 17. *P. gibbosa*, anterior end of visceral mass and mouth region viewed from anterior, semidiagrammatic view showing anterior end of ctenidia, with palps and mouth.

Palps and lips

There is a striking difference from *Spondylus* here, the palps being small and the lips short without trace of arborescent lobes. The ctenidia extend forward to within the opposing faces of the palps (figures 15, 17) which are thrown into a limited number of relatively large ridges (figure 17). The palps are fused in the midline forming a double hood over the mouth region; on the outer sides the outer palps are united to the mantle lobes and the inner ones to the visceral mass (all indicated in figure 17). Rejected matter is passed either into the posteriorly directed currents along the ventral margins of the lamellae or on to the mantle surface (see arrows in figure 17), in either case joining the pseudofaeces postero-ventrally. Apart from the unusual degree of fusion, the palps most closely resemble those of the Ostreacea.
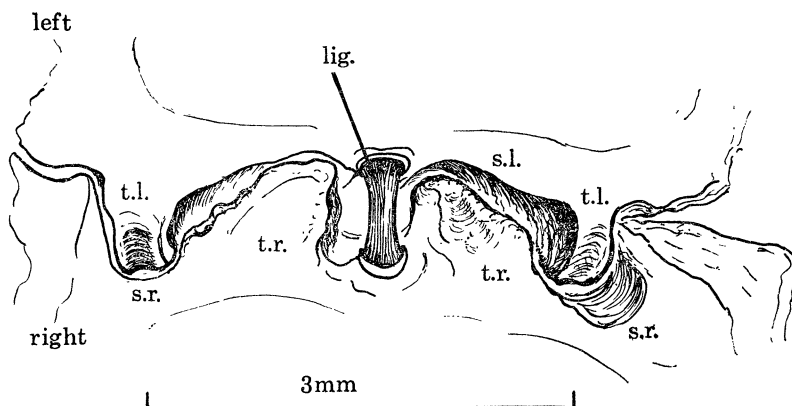
FIGURE 18. *P. gibbosa*, hinge and ligament viewed from within, i.e. ventrally.

Nervous system and sense organs

As noted by Watson (1930a) for *P. australis*, the visceral ganglia are united forming a small oblong mass 'very different from the highly complex visceral ganglia of *Spondylus*, *Pecten* and *Chlamys*'. There are no pallial eyes and this, as Watson thought, could explain the simplicity of the ganglia. Closed statocysts occur beneath the vestige of the foot (Watson 1930a). Probably the only significant receptive surfaces occur on the small marginal tentacles, but this immobile bivalve with unusually stout shell and slight gape would seem to have minimal need for exteroceptors.
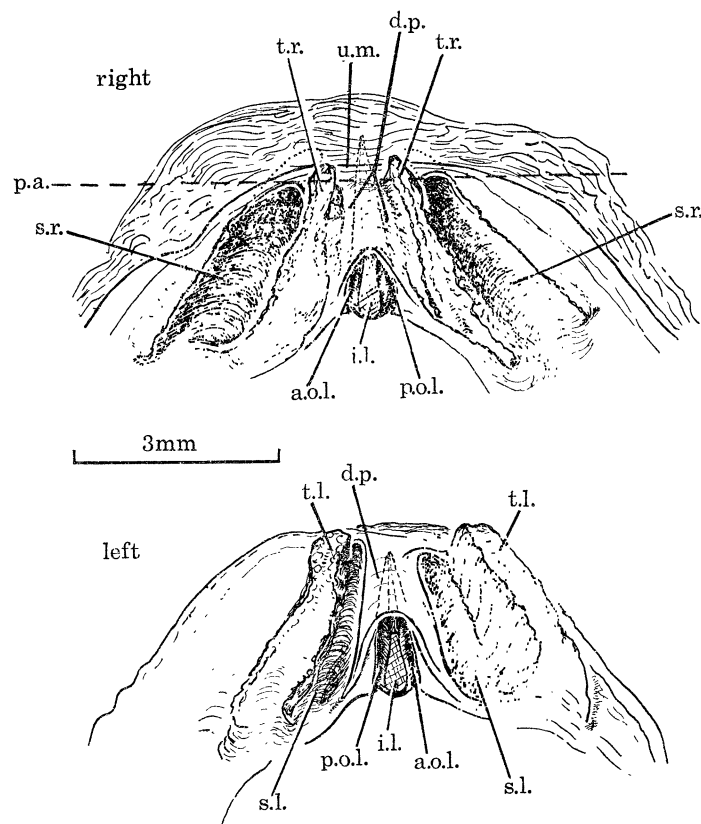
FIGURE 19. *P. gibbosa*, hinge plate and ligament, above of right valve, below of left valve.

Hinge and ligament

The immediate resemblance to conditions in *Spondylus* is indicated in figure 15 with the teeth on the fixed right valve (t.r.) flanking the central, antero-posteriorly greatly compressed ligament (lig.) with sockets (s.r.) peripheral to the teeth. Conditions in the intact hinge when viewed from the ventral aspect (the valves cut some distance ventrally) are shown in figure 18 with the narrow band of the centrally placed ligament (lig.) flanked by the teeth (t.r.) of the right (lower),
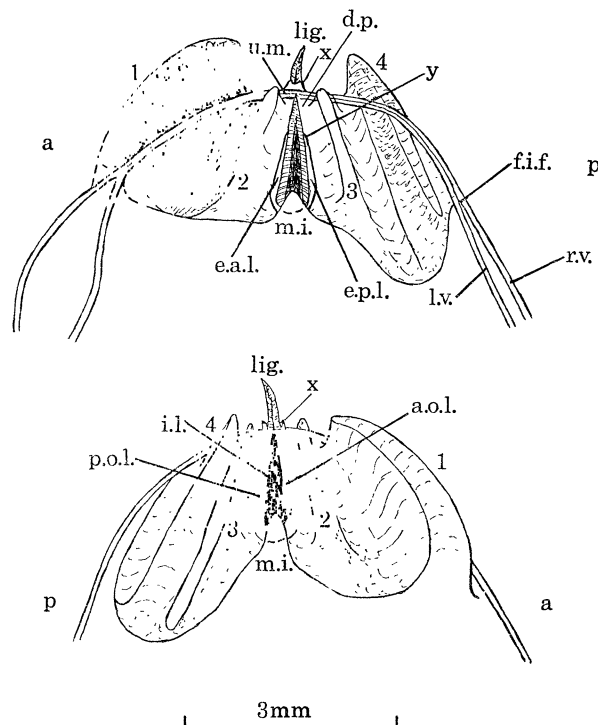

FIGURE 20. *P. gibbosa*, tissues, after decalcification, of pallial crest which secretes hinge plate showing disposition of secreting epithelia, upper from left, lower from right side, with (1–4) succession (from anterior) of teeth on the one side and sockets on the other. In centre, upper, mantle isthmus (m.i.) and tissues secreting outer ligament layers (e.a.l., e.p.l.), summits, x on right, y on left. a, anterior; p, posterior.

and sockets (s.l.) of the left, valve. More detailed representations of both sides of the hinge with the uniting ligament cut in the mid-line are shown in figure 19. The dispositions of the pallial crest (figure 20) which secretes the hinge plate with its teeth and sockets (figure 19), of the mantle isthmus (m.i.) and of the tissues secreting the outer ligament layers (e.a.l., e.p.l.), as all appear after decalcification with the ligament (i.l., a.o.l., p.o.l.) *in situ* when viewed from both upper and under sides are shown in figure 20. The deep foldings of the mantle crest indicate the areas where secretion (and resorption) are responsible for formation of teeth on one side and sockets on the other (1 to 4). Ground sections of valves and ligament appear in figure 21, (*a*) being transverse through the middle of the ligament and (*b*)–(*d*) horizontal sections at the levels indicated by arrows in (*a*). The detached ligament is shown in figure 22. These figures are an essential aid in describing the highly modified hinge plate and ligament in *Plicatula*.

The inward movements which in *Spondylus* bring the outer ligament layers into a central position on either *side* of the inner ligament layer and are also probably responsible for formation of the secondary teeth, are more far-reaching in *Plicatula*. As shown in figure 20, the mantle margins from the two ends of the hinge region are united (u.m.) dorsal to the ligament (lig.)
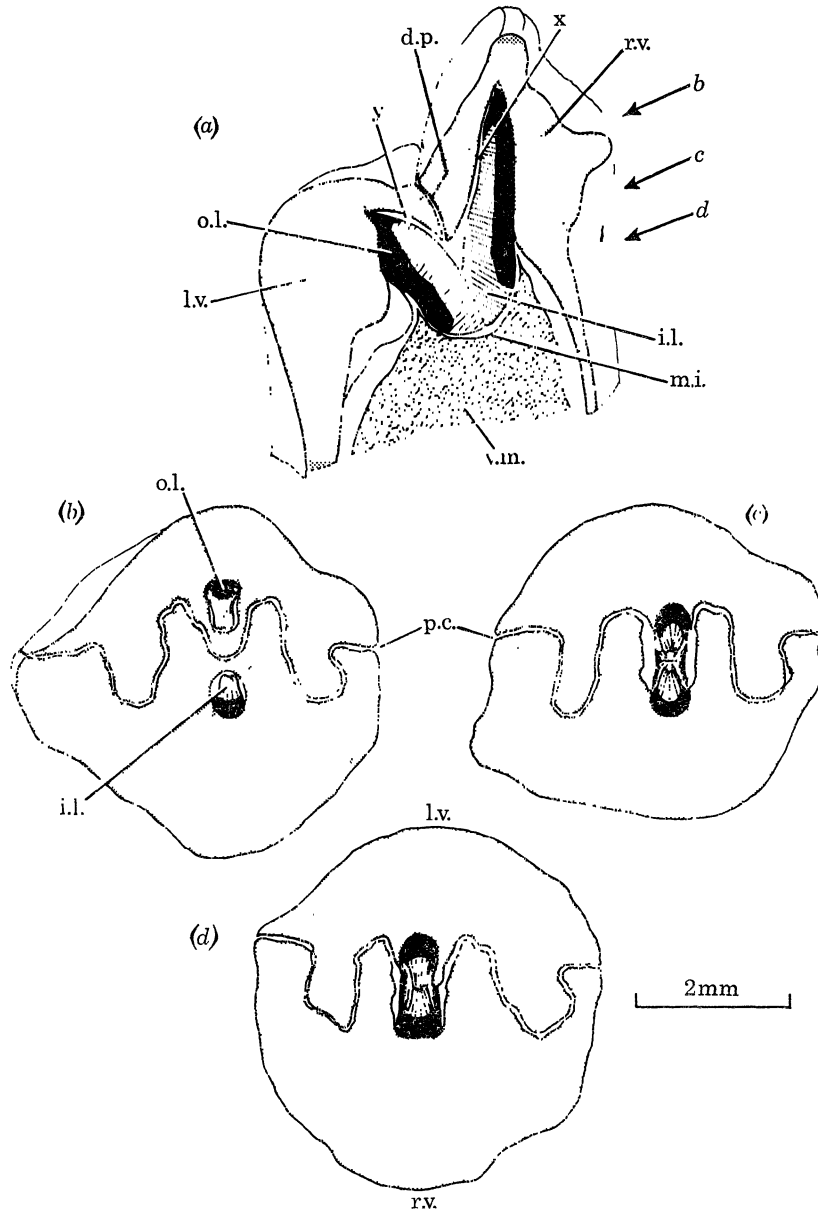
FIGURE 21. *P. gibbosa*, ground sections, slightly oblique, of hinge plate and ligament, inner and outer ligament layers indicated as before, valves stippled. (*a*) Transverse section, lower valve on right; (*b–d*) horizontal sections through lines indicated by *b–d* in (*a*), showing ligament at various levels and hinge plate secreted by pallial crest (p.c.) with interlocking teeth and sockets. *x*, *y*, as in preceding figure.

which thus ceases to be marginal. This mid-dorsal union is necessarily accompanied by that of the mantle crest (see arrows and broken lines in figure 22*c*) which on each side secretes shell which forms the dorsal extensions of the hinge plate (figures 19, 21, 22, d.p.). These separate the ligament from what has now become the dorsal margin of the valves (u.m.). In consequence of this overarching, the mantle isthmus (figures 20 to 22, m.i.) and the more dorsally extended regions on either side which secrete the outer ligament layers (figure 22*c*, e.a.l., e.p.l.) bound an island within the tissues of the pallial crest. A similar overarching of the ligament occurs in the Anomiacea but is there restricted to the upper (left) valve. This will be described in a forthcoming paper.

The overarching process indicated in figure 22 c will be discussed later in comparison with conditions in the Pectinidae and in *Spondylus*. Immediate concern is with its consequences, initially on the teeth and sockets. As shown in figure 19, these are not rounded as in *Spondylus*, but, as a result of overarching, are elongated dorsally and converge towards the mid-line. In figure 20 the tissues of the pallial crest which secrete teeth and sockets (1 to 4) and the mid-dorsal
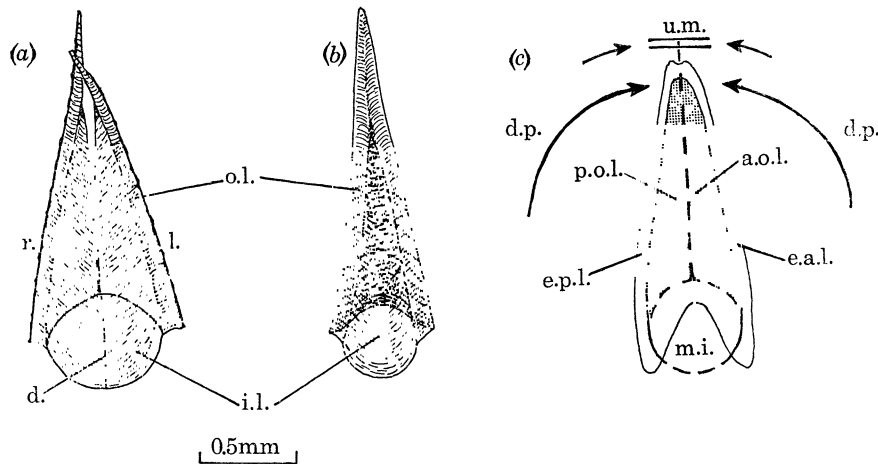

FIGURE 22. *P. gibbosa*, ligament. (*a*) Viewed from anterior, line of division (d.) between two halves of inner ligament layer indicated at base; (*b*) viewed from right, outer ligament layers obscuring inner layer; (*c*) diagram from this side showing the two areas of outer ligament layer, the stippled region (over inner ligament layer) indicating the area of ligamental attachment to the valve (inner ligament layer *not* attached). Arrows indicate overgrowth of mantle margins and pallial crest dorsally, line of union shown by broken line, secreting surfaces (e.a.l., m.i., e.p.l.) now forming island within mantle crest which secretes hinge plate.
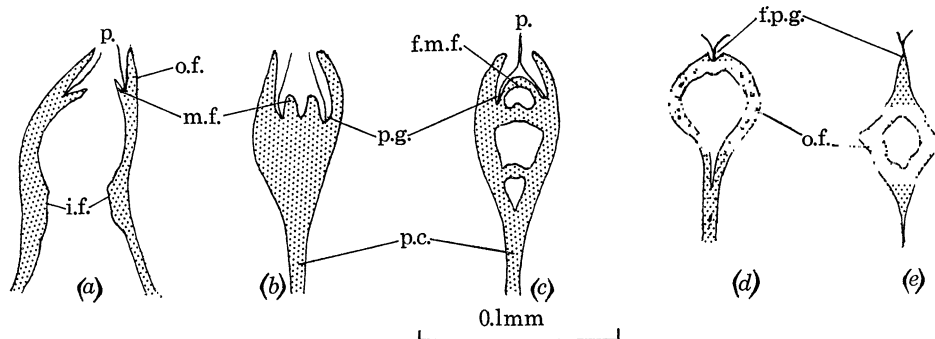
FIGURE 23. *P. gibbosa*. Transverse sections through mantle margins anterio-dorsally continuing to region of mid-dorsal fusion of two sides. (*a*) Mantle margins free; (*b*) fusion of inner folds; (*c*) fusion of middle folds; (*d,e*) fusion of periostracal grooves with outer mantle folds extending ventralwards.

extension of the hinge plate (d.p.) are shown, with the tissues responsible for formation of the ligament (m.i., e.a.l., e.p.l.). Owing to the greater extension dorsally of the attached valve, the sockets (s.l.) on that side extend beyond the area of contact of the two valves (see dotted lines in figure 19). Thus the conspicuously long teeth of the upper valve (t.l.) penetrate deep into the attached valve. This distal enlargement of teeth and sockets, ensures an even more rigid alinement of the valves than in *Spondylus* and their even more prolonged attachment after the death of the animal. Extensive collections of 'animals' may prove to consist exclusively of dead shells, the valves all intimately united. Secondary extension of the ligament by periostracum is

impossible because the secreting epithelium is separated from the ligamental region. It is also unnecessary.

Various stages in the fusion, at each end, of the three folds of the mantle margins leading to the final union mid-dorsally of the products of these fusions are shown in figure 23. The free mantle lobes (*a*) unite initially by fusion of the inner mantle folds (*b*) followed by that of the middle folds (*c*) at which stage the periostracal secretion also becomes fused. Later (*d*) the two periostracal grooves (at the base of the inner surface of the outer mantle folds) unite, the secretion separating to form a superficial sheet over each valve. In the mid-region, where the two ends unite (u.m.), this groove becomes a ridge (*e*). The outer surfaces of the outer mantle folds are no longer defined (they do not fuse or the periostracal region would be obliterated and the two valves become united), they tend to merge with the thin tissue of the pallial crest (p.c.).

Proceeding to the ligament, this is tightly compressed in the transverse plane and also extended dorsally to form, as indicated in figure 21*a*, a narrow hoop-shaped structure with the right arm longer than the left, the halves being separated dorsally by the extension of the hinge plate (d.p.). Inner and outer ligament layers are totally distinct, the former clear and yellowish, the latter silvery and opaque. On separation from the valves after decalcification the tips come together as indicated in figure 22*a*. The two halves very readily separate because the inner ligament layers of the two sides are only applied to each other (see d. in figure 22*a*), they are *not* structurally united. This is very apparent in paraffin sections. This division of the product of single secreting surface, namely the mantle isthmus, appears to be due to the unique transverse extension of this shown in figure 20 (m.i.). It does not, as explained below, affect function.

As appears in figures 20 to 22, the inner ligament layer (i.l.) is hemispherical at its base due to the curvature in the transverse plane of the mantle isthmus. It extends dorsally within the outer layers, although not to the tip of the ligament in either valve; the terminal third is composed exclusively of outer ligament layer.

The anterior and posterior outer ligament layers are secreted by epithelia which, as always, are in contact with the mantle isthmus but, owing to the dorsal overarching, have lost contact with the mantle margins. They extend up the anterior and posterior sides of the ligament (figures 20, 22*c*, e.a.l., e.p.l.) but, again owing to the effects of the overarching, only unite at the far dorsal extremity of the ligament as indicated in figure 22*c*. The condition is therefore very different from that in *Spondylus* where all ligament layers are secreted by epithelia at the base (figures 9, 10). These secreting surfaces are separated by the products of their secretion which are attached to the inner ligament layer internally and to the valves externally (see stippled area in figure 22*c* and entire ligamental surfaces shown in figure 20). The inner ligament layer is *not* attached directly to the valves, only by way of the outer ligament layers (this is the only bivalve where this has been observed). Secretion of outer ligament layers on the two sides is separated by the interposition of the dorsal extensions of the hinge plates as appears in figure 19 (d.p.) where the ligament, *in situ*, has been cut through in the mid-line. The secreting tissues extend further dorsally on the right side (cf. x and y in figures 20, 21); this is after fixation, in life they must extend into the tip of the cavities into which the ligament extends (see dotted lines, figure 19). This is in striking contrast to conditions in *Spondylus* (figures 9, 10), again a consequence of overarching.

As we have seen, the gape in *Plicatula* is exceptionally slight. This is due to the very restricted extent to which the teeth can move in the sockets. In *Plicatula* the pivotal axis is connected with the hinge, *not* with the ligament; it appears to run along the points of entrance of the teeth into

the enclosed dorsal end of the sockets in the attached valves, as indicated by the broken line, p.a., in figure 19. The rounded mass of the inner ligament layer (figure 22*a, b*) will be compressed when the adductor contracts and be responsible for the limited opening possible when the muscle relaxes. The lack of union between the two sides of the inner ligament layer is thus immaterial. The outer ligament layers are concerned primarily, perhaps exclusively, with attachment to the valves, i.e. with keeping the inner ligament layer in place. Unlike *Spondylus* the unity of the shell in *Plicatula* is broken by the separation of the two halves of the inner ligament although these remain applied. However, the valves are united functionally by way of the intimately interlocking teeth and sockets of the hinge plate.

DISCUSSION

Evolution of hinge and ligament

The most striking facts that have emerged from this investigation concern the hinge and ligament and reveal profound, hitherto unsuspected, differences between the Pectinidae, Spondylidae and Plicatulidae. These, with other features of structural or functional significance, are shown in table 1 which, together with *Spondylus* and *Plicatula*, covers a range of pectinid genera and also, for reasons that will become apparent, *Propeamussium*.

Starting with the amphidetic ligament of the primitive Bivalvia (Yonge 1957) with anterior and posterior outer ligament layers of equal extent and no secondary extension due to periostracal fusion, the attempt is made in figure 24 to indicate how this primitive ligament may have evolved to produce the conditions now existing in the Pectinidae, Spondylidae and Plicatulidae. However, it should be noted that these diagrams disregard the intervention of a heteromyarian condition (Yonge & Campbell 1968) involving change to an extreme form of opisthodetic ligament (although necessarily without complete loss of the anterior outer ligament layer) which must have occurred in the process from initial symmetry to the equally symmetrical but certainly secondary condition in the monomyarian Pectinacea. There the body is reorganized around the solitary adductor (Yonge 1953) and the inner ligament layer becomes highly concentrated.

Conditions in the equally monomyarian Pteriacea with the inner ligament layer less concentrated and the anterior shorter than the posterior outer ligament layer, as in *Pinctada*, represent a somewhat less evolved condition. This is associated with byssal attachment throughout life apart from *Malleus albus*, which lives free within sand, and species of *Crenatula* and *Vulsella* which inhabit sponges (Yonge 1968).

While byssal attachment is the basic habit in the Pectinacea, e.g. in many species of *Chlamys* and associated genera (see Waller 1969, 1972*a*), this has been lost in many adult genera or species which either become free (*Pecten, Chlamys* spp., *Amusium*) or cemented (*Hinnites, Spondylus, Plicatula*). In all cases change from the primitive isomyarian to the final monomyarian condition has involved loss of primitive hinge teeth although, as shown in figure 8, Bernard (1896) considered that the crura in *Pecten* (= *Chlamys*) *varia* represent a single pair of lateral teeth in each valve just as Jackson (1890) regarded the secondary teeth in *Spondylus* and *Plicatula* as modifications of the crura in the Pectinidae. Evidence here presented does not support these views.

Bearing in mind its evolution by way of an extreme opisthodetic condition, the structure of the pectinid hinge and ligament (figure 24*a*), well described by Trueman (1953*a, b*) raises no problems. Starting from a common ancestral stock, conditions in *Spondylus* (figure 24*b*) can be

attained by inward growth from each end of the fused periostracal groove (f.p.g.) with accompanying concentration of united areas of anterior and of posterior outer ligament layers *on each side of* (i.e. topographically above and below) the concentrated inner ligament layer. It appears reasonable to associate this with the presence in the hinge region of crossed-lamellar aragonite in place of the foliated calcite which forms corresponding regions in the Pectinidae (Taylor *et al.* 1969). It is from this aragonite that the secondary teeth are formed, whereas the pectinid crura are calcitic. Bernard (1896) shows how in the postlarval (nepionic) hinge plate,
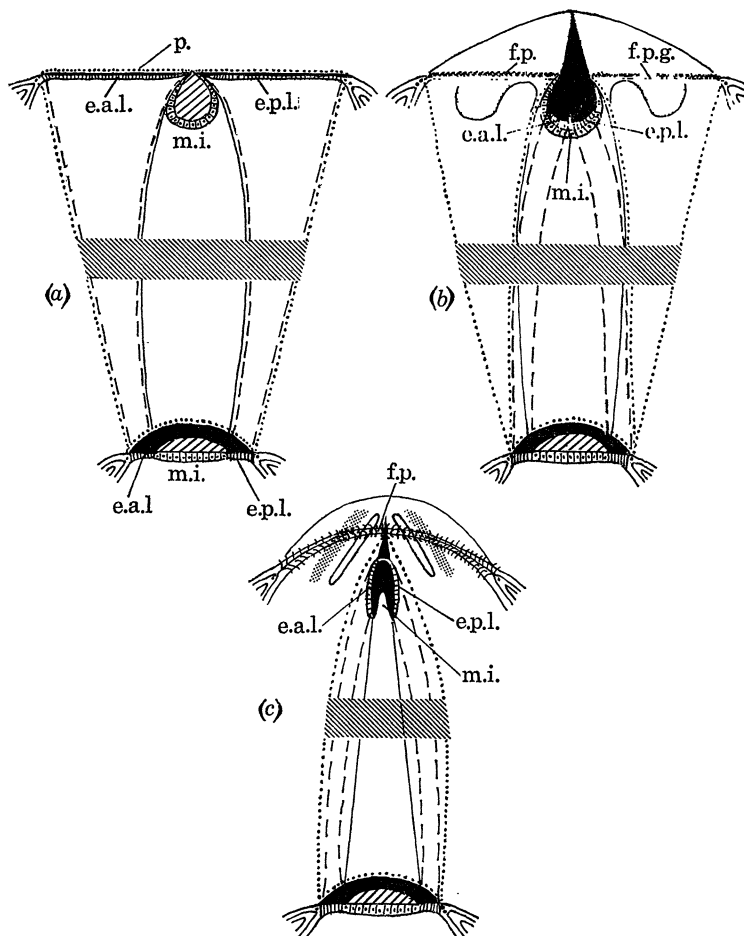
FIGURE 24. Diagrams of right hinge areas showing: (*a*) evolution of pectinid from primitive amphidetic ligament; (*b*) evolution of spondylid ligament; (*c*) evolution of plicatulid ligament. Interposition of the heteromyarian stage with opisthodetic ligament indicated by hatched areas. Teeth and sockets indicated in (*b*) and (*c*) but *not* inner ligament layer which in both is obscured by inward migration of outer ligament layers (black), ———, – – – –, ... respectively indicate boundaries of inner ligament layer, outer ligament layers and of extent of periostracal secretion (in (*c*) union of periostracal grooves of two ends).

formerly horizontally arranged crura (which he regarded as lateral teeth) have become vertically disposed (cf. figures 8 and 25) providing further indication of the inward pallial growth so evident in the adult hinge. The bilateral asymmetry in the hinge of *Spondylus* is associated with cementation and is paralleled by conditions in the pectinid *Hinnites*.

Both Jackson (1890) and Bernard (1896) stress the pectinid nature of the dissoconch in *Spondylus* (shown in figure 25, p.s.) with a byssal sinus (b.s.) which – like that of *Hinnites* at a much later stage in the life history – becomes overgrown following cementation. This would

TABLE 1. COMPARISON OF HABIT AND OF SIGNIFICANT STRUCTURES THROUGHOUT THE PECTINACEA

|	Spondylus	Plicatula	Pecten Chlamys	Chlamys Pedum	Hinnites	Amusium	Prope-amussium
				Pectinidae			
adult habit	cemented	cemented	free	byssally attached	cemented	free	free
hinge plate	crossed-lamellar aragonite		– – – – – foliated calcite – – – – –				crossed-lamellar aragonite
hinge teeth	secondary		– – – – – – – – absent			– – – – – – – –	
ligament							
inner layer	– – – – – – – – – – – –		massive, rounded			– – – – – – – – –	
outer layers	lateral to inner layer		– – – – – extended anterior and posterior to		inner layer	– – – – –	
ligament submarginal	no	yes	– – – – – – – – –		no	– – – – – – – –	
mantle margin							
inner fold ('velum')	broad	very narrow	– – – – – –	broad		– – – – – –	very broad
pallial eyes	yes	no	– – – – – – – –	yes		– – – – – – – –	no
ctenidia							
plicate	yes	no	– – – – – – – –	yes		– – – – – – – –	no
interlamellar junctions	yes	no	– – – – – – – –	yes		– – – – – – – –	no
ciliation; Atkins's type	B(1a)	B(1a)	– – – – – B(1b)		– – – – – – –	?	?
lips	arborescent	simple	– – – – – – arborescent			– – – – – –	simple
adductor							
approx. ratio of quick to catch muscle	1:1	1:4	3:1	2½:1	4:1	5:1	6:1 (most oblique)
foot (adult)	present	absent	– – – – – – – – –		present	– – – – – – – –	
byssal gland	no	—	reduced	large	no	no	no
retractor	no	—	small	large	no (finally)	no	no
cleansing funnel	large	—	small	small	small	large	? small
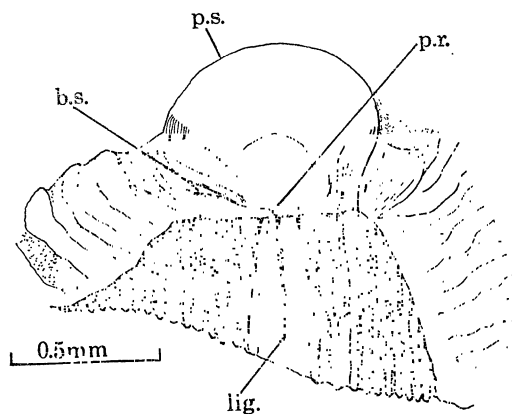
FIGURE 25. *S. gaedaeropus* (from Bernard 1896). Cardinal area in very young individual showing prodissoconch with later 'pecten' stage and byssal sinus with below this, on either side of ligament, vertically disposed 'crura' which Bernard considered equivalent to lateral teeth.

indicate descent from a common stock with the Pectinidae although retaining a more primitive type of gill ciliation – type B (1a) instead of B (1b). In other respects, for example ctenidial structure, presence of pallial eyes and of arborescent lips, conditions in the two families are largely identical indicating a long period of evolution before separation after which, as a possible consequence of cementation, there is greater visceral concentration of the nervous system in *Spondylus* (Dakin 1928a). As noted below, modification of the foot also appears to be connected with cementation.
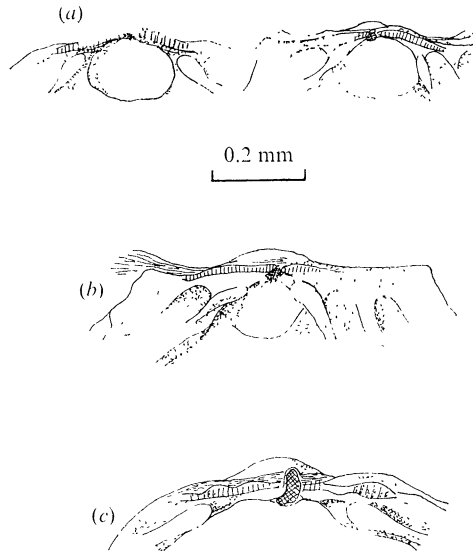

Figure 26. *P. ramosa*. Early stages in the development of the hinge (after Bernard 1896). (*a*) Left and right valves, prodissoconch teeth on either side of ligament and below them dissoconch teeth designated laterals by Bernard; (*b*) right valve showing later appearance of second 'lateral' on each side; (*c*) older left valve with teeth as in (*a*), prodissoconch teeth and 'laterals' persisting but ligament becoming constricted in transverse plane. No indication of enclosure of ligament dorsally.

Conditions in *Plicatula* indicate a much earlier separation from an original common stock (see table 2). In no larval stage is there evidence of a byssal sinus (Jackson 1890; Bernard 1896), while the adult foot is lost (although doubtless present in the as yet undescribed larva as it is in that of the Ostreacea). Bernard (1896) has described the early shell stages, first the prodissoconch with numerous fine 'teeth' on either side of the central ligament followed by the dissoconch (figure 26) where these are retained but, ventral to them, more definitive teeth appear. On the basis of these Bernard suggested the dental formula

right valve		II	L		II
left valve	I		L	III	I

But this cannot indicate more than a brief phase in development. In a later stage he indicated (figure 26c) that the prodissoconch dentition persists and although the constricted ligament is beginning to extend dorsally there is no sign of the overgrowth by the mantle margins which will later enclose the ligament dorsally. It is during this, as yet undescribed, stage that the definitive secondary teeth (designated as laterals by Bernard (1898)) presumably first appear.

The final condition is indicated diagrammatically in figure 24c. Although representing a more elaborate, more highly evolved, condition than that in *Spondylus*, it cannot have evolved from that. Putting aside loss of foot and of byssal apparatus, the ctenidial structure is less

complex, there are no pallial eyes, no anterior waste extrusion (like the Pteriacea) and the lips are simple. In all of these respects *Plicatula* is more primitive than is *Spondylus*. Only the hinge and ligament are more elaborately modified involving effective loss by the ligament of its basic role (as part of the complete shell) in uniting the two valves, this function being taken over by the interlocking secondary teeth. However the now transversely constricted hoop-like ligament continues to cause divarication of the valves. The comparative situation between the two is shown diagrammatically in table 2 and indicates early separation of *Plicatula* from generalized parental stock. Evolution of hinge and ligament is shown proceeding laterally while full development of pectinid characters is followed vertically.

Cleansing and the swimming habit

Cleansing of the mantle cavity, of profound importance to all bivalves, assumes even greater significance in those which are horizontally disposed. The relation between the processes involved and those concerned with swimming was first stressed by this author (1936). Conditions in *Lima hians*, where the animal swims vertically disposed, dorsalward expulsion of water at both ends of the hinge being aided by rowing movements by the greatly enlarged tentacles, have been fully analysed by Gilmour (1967) and need not detain us. The animal probably only swims when displaced from the elaborate byssally formed nest (Gilmour 1967). Otherwise swimming is confined to the horizontally disposed pectinids where movements of the secondarily symmetrical, almost spherical, shell valves are controlled by a centrally placed adductor and where pseudofaeces collect for subsequent ejection at *both* anterior and posterior ends of the mantle cavity. This is also true for the Limidae but *not* throughout the Pteriacea or Anomiacea where such accumulations and ejections are *exclusively posterior* (hence the unattached anomid *Placuna* cannot swim). Such ejections, powered by the striated, quick section of the adductor muscle, represent the means of jet propulsion which must attain the highest degree of efficiency in *Amusium* and *Propeamussium* where the internally ribbed valves are light and flattened and the auricles reduced. Sudden movement in the opposite direction is an escape reaction.

Comparisons of the cross-sectional areas of quick and smooth muscle in a variety of monomyarians have been made (Yonge 1936) and, over a somewhat wider range are expressed as very approximate ratios in table 1. Quick muscle preponderates in genera where the final stage in cleansing is accomplished by flapping of the valves. This also involves swimming in *Pecten*, some species of *Chlamys*, *Amusium* and *Propeamussium* but *not* in the attached *Pedum* and *Hinnites*. Quick muscle is relatively smaller in *Spondylus* where cleansing, involving the actual removal of collected sediment, is the sole function of the greatly modified foot (this is also true in *Amusium* and probably in *Propeamussium*). In *Plicatula*, where the valves separate so very slightly, reaction to stimuli is invariably prolonged closure; this is the function of the smooth muscle and here the catch muscle is small. These and related matters in these animals have recently been subjected to mathematical analysis by Gould (1971) and Thayer (1972).

Elaborate pallial eyes present on the middle fold of the mantle margins occur in all but some abyssal pectinids although they are reduced in species living in intermediate depths (Pelseneer 1911). In correlation with the habit of lying on the right valve, they are more numerous on the left side. They also occur in *Spondylus* and in some, but not all, species of *Lima* but never in *Plicatula* or *Propeamussium* (Waller 1971, 1972*b*). They have been considered to be receptors particularly concerned with swimming but this is improbable. They are just as numerous in the cemented *Hinnites* and *Spondylus* and in the byssally attached *Pedum* as they are in swimming

pectinids; in the Limidae the invariably byssally attached *L. excavata* has eyes, whereas the swimming *L. hians* has not. The Pectinidae are among the most successful of all bivalve families, a probable consequence of their high feeding capacity due to the wide gape and the associated hypertrophy of the inner fold of the mantle margin (velum). Waller (1972*b*) has also emphasized the importance of the foliated calcitic shell. But such wide display of usually brightly pigmented tissues involves danger from predators which is absent, for instance, in *Plicatula*, and against which immediate reaction is essential. Stimuli received by way of the pallial eyes are followed by sudden contractions which result in the escape reaction (*not* swimming movements) in the free species and firm closure of the shell in attached species. There appears no reason for thinking that the pallial eyes are of less importance to the latter than to the former.

The whole process of swimming in these animals has recently been most carefully analysed by Gould (1971), Moore & Trueman (1971) and Thayer (1972). The second named consider that the exceptionally high angle (20°) through which *Chlamys* closes its valves, so allowing more water to be expelled, does represent an adaptation to swimming; this may be true here and in the undoubtedly highly adapted *Amusium* and *Propeamussium*, but there is a relatively wide gape in both *Pedum* and *Spondylus*. The rubbery inner ligament layer is regarded by Trueman in the same light but it is even better developed in *Spondylus*. The original discovery by Buddenbrock (1911, 1915) that in *Pecten* all reflex movements associated with movement and orientation are initiated by the left statocyst with which the nerves of *both* mantle lobes exclusively communicate could represent a modification directly associated with swimming.*

The significance of the foot in cleansing demands comment. The increasing tendency towards an exclusively cleansing function in the Pectinidae has been noted (figure 4). This culminates in the greatly flattened *Amusium* but also in the cemented *Spondylus*. In the former, it is probably associated with life on muddy bottoms, in the latter with the deep concavity of the under valve which would be difficult to clear of sediment by collection in ciliary tracts followed by muscular expulsion. Waste masses need to be sought and further consolidated within the grooved funnel-shaped pedal depression. In *Hinnites* and *Pedum* the right valve is much less concave and the smaller, less modified foot is of minor significance in cleansing which is achieved by ciliary and muscular means. The position is less clear in *Propeamussium* where the foot has never been seen in life. After preservation it is very variable in size but with a bulbous tip (Pelseneer 1911; Knudsen 1967) and may well be capable of great dilation in life.

Relations

Spondylus and *Plicatula* were long associated in the same family (or subfamily) by Thiele (1935) owing to their common possession of secondary teeth. It was on the morphological findings of Watson (1930*a*) that Cox (1952) removed *Plicatula* into a family of its own, a division recognized in the *Treatise on invertebrate paleontology* by Newell (1969) who divides the superfamily Pectinacea into the families Pectinidae, Plicatulidae, Spondylidae and Dimyidae. But whereas Cox & Hertlein (1969), in their description of the family in the *Treatise*, state that the Plicatulidae are 'separated from the Spondylidae mainly on grounds of soft anatomy', the present study reveals the presence of fundamental dissimilarities in the hinge and ligament. It should be possible to detect and follow these in the palaeontological record. There are also far

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* So as emphasized by Thayer (1972), might reduction of body size in relation to shell and oblique positioning of the striated area of the adductor, the one reducing weight, the other increasing the rate of shell closure.

greater dissimilarities between the Spondylidae and the Pectinidae than have hitherto been recognized. The final section of this paper must therefore be devoted to a re-examination of relations within the Pectinacea (excluding the isomyarian Dimyidae).

This, however, would be inadequate without reference to the status within the superfamily of *Propeamussium*. On unspecified morphological grounds this genus was removed by Abbott (1954) from the Pectinidae into a family of its own. These grounds have recently been given substance by Waller (1971, 1972 b) who provides convincing evidence that the shells of this genus of delicate deep water scallops are significantly different from those of *Amusium*. The latter is an undoubted pectinid but with common possession of flattened, internally ribbed valves with reduced auricles the two genera have obvious superficial resemblances. The statement by Gould (1971), having particular reference to *Amusium balloti*, that 'I know of no actual observations, but every major feature of its design marks *Amusium* as the most accomplished bivalve swimmer' would apply to both genera.

In the Pectinidae, shell structure is dominated by foliated calcite, but Waller (1972 b) finds that, unlike *Amusium pleuronectes* (examined by Taylor *et al*. 1969) which possesses the same shell microstructure as *Pecten*, in *Propeamussium* the right valve is dominated by prismatic calcite with crossed-lamellar aragonite present in both valves. As Waller further points out, the species of the Propeamussidae inhabit deep water, the majority below 600 m, whereas the Pectinidae abound in all depths, a distinction he correlates with the presence in the latter of foliated calcite which permits formation of surface sculpture of high relief. The only other bivalves with shell structure similar to *Propeamussium* are the palaeozoic Pernopectinidae of which these deep-water species may well be the modern survivors.

Although he failed to notice differences in the lip apparatus, Verrill (1897) early pointed out the significance of morphological features in classification within the Pectinidae. Waller refers to certain of these including absence of pallial eyes (noted, however, by Pelseneer in 1911) and of tentacles on the margin of the inner mantle folds, although the absence he notes of a left pedal retractor is not unique to *Propeamussium*. Bernard (1972) has revealed the absence of the arborescent lips present in the Pectinidae and Spondylidae, although Pelseneer (1911) had noted this in '*Amussium marginatum*' and '*A. zonatum*'.

These differences, apart from shell structure, have all been checked by personal examination of preserved specimens obtained from the British Museum (Nat. Hist.) of *Amusium pleuronectes* (type species of the genus) and of *Propeamussium jeffreysi*, *P. meridionale*, *P. caducum* and *P. watsoni*. All came from the *John Murray* Expedition and were described by Knudsen (1967) but under the generic name of *Amusium* now known, from shell structure alone, to be incorrect.

A. pleuronectes has a stout, externally perfectly smooth, shell about 7 cm in diameter and with 14 pairs of internal ribs in each valve. Morphologically it is a typical pectinid with arborescent lips, pallial eyes, an inner mantle fold of pectinid dimensions fringed with tentacles and with typical pectinid ctenidia (unlike those attributed to this genus by Ridewood (1903)). On the other hand, species of *Propeamussium* are smaller with a delicately translucent shell with internal ribs and an unribbed marginal zone which continues the curvature of the upper valve. This must aid the downward expulsion of water needed to counteract the pull of gravity and so improve swimming efficiency. Although preservation in most cases was poor, the lips were invariably simple, pallial eyes were absent and the inner mantle lobe lacked fringing tentacles. Ventrally this lobe is far deeper than in any pectinid including *Amusium*. Mud was present in the mantle cavity of several species and this hypertrophy may well be associated with control of water in-

take in a muddy environment as well as with swimming. However, another function may well be involved.

In his report on bivalves taken at depths of between 390 and 1789 m on the *John Murray* Expedition, Knudsen (1967) describes the presence of crustaceans, foraminiferans and the remains of other animals in the stomachs of individuals of all species of *Propeamussium* and of *Amusium* (= *Propeamussium*) which he examined. He found similar evidence of a carnivorous habit in *P. meridionale* taken at depths of up to 4820 m during the *Galathea* Expedition (Knudsen 1970). He makes the point that such food could be captured by further development of the cleansing–swimming mechanisms in the Pectinidae (Yonge 1936). He noted the great efficiency

TABLE 2. POSSIBLE LINES OF EVOLUTION WITHIN THE PECTINACEA
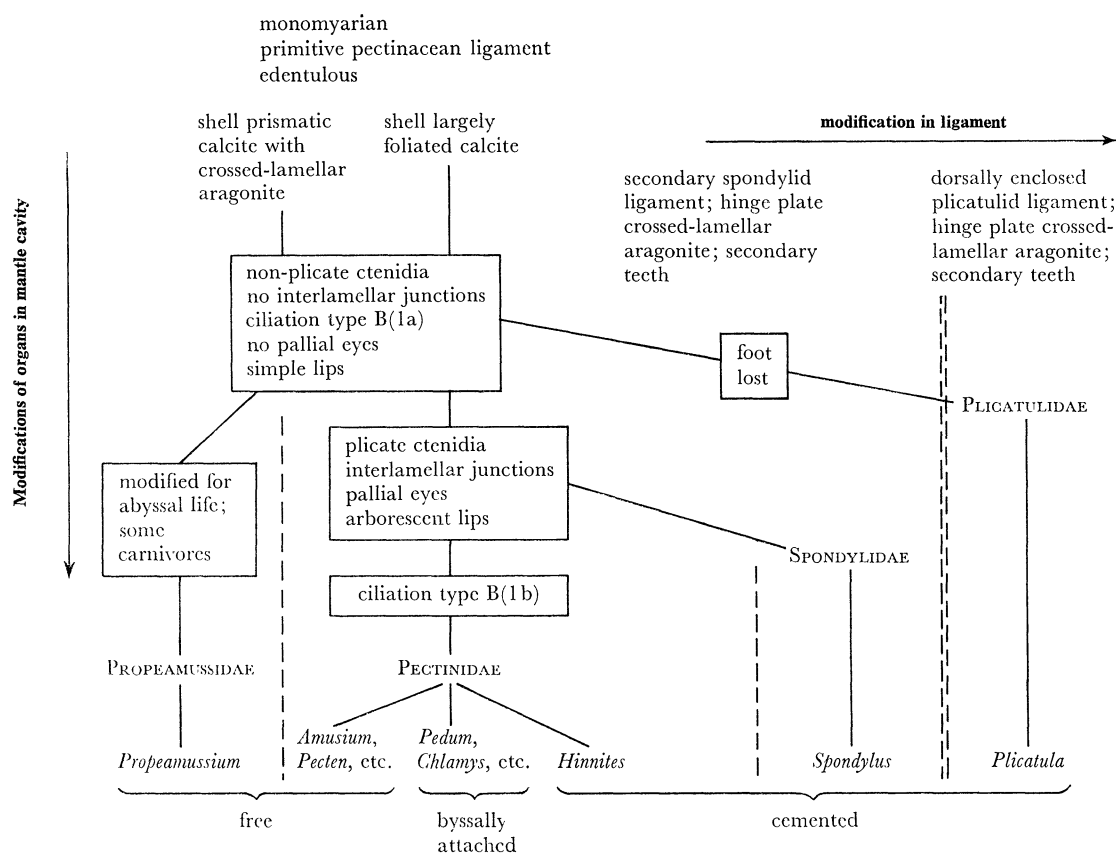
of the very obliquely disposed quick muscle, first described by Pelseneer (1911) the significance of which is stressed by Gould (1971) and Thayer (1972). The exceptional depth of the inner mantle fold in *Propeamussium*, not mentioned by Knudsen, could be concerned with food capture. What is however quite certain is that no bivalve could swallow such food if it possessed the arborescent lips present in *Amusium pleuronectes*. The absence of such lips – more probably because they never evolved rather than that they have been lost – in *Propeamussium* has made a carnivorous habit possible. The bulbous ended foot in *Propeamussium* can only be concerned with cleansing but its full significance in that capacity must await examination in life. As originally shown by Ridewood (1903), ctenidial structure is simple in this genus and this could also prove true of ciliary pattern. The Propeamussidae bear much evidence of primitive structure and seem to owe their survival to descent into deep water where they have become adapted in various ways, involving adductor, inner mantle lobes, possibly foot and certainly feeding, to abyssal and hadal life.

From consideration of the significant characters in the four monomyarian families of the Pectinacea (table 1) arises the question of the evolutionary processes involved. These are indicated in table 2 with the final habit attained shown on the bottom line. All probably originate about the Ordovician with monomyarians such as *Rhombopteria* (Jackson 1890; Newell 1937) somewhat intermediate between Pteriacea and Pectinacea. The later Aviculopectinidae and Terquemiidae respectively probably gave rise to the Pectinidae and Spondylidae (Newell & Boyd 1970). The Pernopectinidae which, retaining the calcitic prismatic layer, appear ancestral to the Propeamussidae (Waller 1971, 1972*b*) diverged as far back as the Devonian. The ancestry of the Plicatulidae is obscure; they appear earlier (Upper Triassic) than the Spondylidae (Jurassic) but shell structure indicates a relation.

In table 2, changes in the mode of formation of hinge and ligament are indicated horizontally while those concerned with structures in the mantle cavity, namely ctenidia and ciliary pattern (where known), presence of pallial eyes and nature of the lips, are indicated vertically. The inner fold of the mantle margin is largest in the Propeamussidae (left) and smallest in the Plicatulidae (right). Modifications in the foot, as we have seen, are largely correlated with habit. There are striking, but far from unique, differences in the extent to which changes in different characters have been associated with one another in the course of evolution. Thus the greatest change in hinge and ligament (in the Plicatulidae) is accompanied, apart from loss of the foot, by minimal changes in other characters. Maximal changes within the mantle cavity which have led to the striking success of the Pectinidae with their wide diversity of habit, have been accompanied by minimal changes in hinge and ligament. The Spondylidae lie somewhere in between, but in both families the foot as an organ of fixation and/or cleansing is of prime importance. Separated by significant differences in shell structure representing an earlier condition and also retaining simplicity in both the ctenidia and the lips, the Propeamussidae have become highly adapted for mobile life above and on the muddy substrates of abyssal depths. This has involved further elaboration of the adductor and of the inner mantle margins leading to greater mobility and cleansing efficiency (although the precise significance of the modified foot and hypertrophied inner mantle folds cannot be determined until examined in life) but also, on the evidence presented by Knudsen (1967, 1970), to the change to a carnivorous habit. In this they resemble other deep-sea invertebrates such as the septibranch Bivalvia (Yonge 1928) and ascidians such as *Octacnemus*, *Hexacrobylus* and *Gasterascidia* (Millar 1970) which have adapted mechanisms used for collecting phytoplankton in shallow water for the capture of small animals in abyssal depths.

The distinct identity of the Propeamussidae, Pectinidae, Spondylidae and Plicatulidae becomes apparent in table 2. They are separated by vertical broken lines. The one uncertainty is the status of the Plicatulidae where the hinge and ligament are unique. The presence of the double broken lines indicates a doubt as to whether this should not be raised from family to superfamily level.

Mr Norman Copland, Miss Eileen Graham and others who obtained, by diving, living specimens of *Spondylus americanus*. Preserved material of *Amusium pleuronectes*, of a variety of species of *Propeamussium* and of *Hinnites distorta* together with much helpful comment was supplied by Dr John Taylor of the British Museum (Nat. Hist.) and of *Hinnites multirugosus* in a necessary range of sizes by Dr D. P. Abbott of the Hopkins Marine Laboratory, Pacific Grove, California. Sections of both *Plicatula* and *Spondylus* were cut and many drawings made before I left Glasgow by my Research Assistant there, Miss J. I. Campbell, to whom I owe so much for expert help over a period of 10 years. Her salary was covered by a grant (B/SR/1835) from the Science Research Council and more recently I have been greatly helped by a personal grant (GR/3/ 1380) from the Natural Environment Research Council. The cost of one visit to Jamaica was paid for by the Browne Research Fund of the Royal Society. After unavoidable diversion to other research, this paper has been completed in the Department of Zoology, University of Edinburgh, and it is a pleasure to record thanks to Professor J. M. Mitchison for the facilities there provided.

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Key to the lettering used in the figures

a.	anus	m.	mouth
ad.	adductor	ma.	mantle
a.o.l.	anterior outer ligament layer	m.f.	middle fold of mantle margin
a.q.	'quick' muscle (adductor)	m.i.	mantle isthmus
at.a.	attachment area	m.m.	mantle margins
au.	auricle		
		o.	oesophagus
b.g.	byssal groove	o.d.	outer demibranch
b.r.	byssal retractor	o.f.	outer fold of mantle margin
b.s.	byssal sinus	o.l.	outer ligament layer
		o.p.	outer palp
c.d.	ciliated ducts into kidney	o.s.o.f.	outer surface of outer mantle folds
c.p.g.	cerebro-pleural ganglia		
ct.	ctenidia	p.	periostracum
c.v.c.	cerebro-visceral commissure	p.a.	pivotal axis
		p.c.	pallial crest
d.d.	digestive diverticula	pe.c.	pedal cone
d.p.	dorsal extension of hinge plate	pe.g.	pedal gland
		pe.r.	pedal retractor
e.a.l.	epithelium secreting anterior outer ligament layer	pf.	pseudofaeces
		p.g.	periostracal groove
e.a.p.	epithelium secreting anterior *and* posterior outer ligament layers	pm.	pericardium
		p.o.g.	proximal oral groove
e.p.l.	epithelium secreting posterior outer ligament layer	p.o.l.	posterior outer ligament layer
		pr.	protoconch
		p.s.	'pecten' stage
f.	foot	r.g.p.	reno-genital pore
f.i.f.	fused inner folds of mantle margin	r.v.	right valve
f.m.f.	fused middle folds of mantle margin		
f.p.	fused periostracum	s.	stomach
f.p.g.	fused periostracal grooves	s.l.	socket in left valve
		s.m.	suspensory membrane
g.	gonad	s.r.	socket in right valve
		s.s.	style sac
h.	initial hinge line		
h_l.	later hinge line	t.l.	tooth of left valve
h.p.	hinge plate	t.r.	tooth of right valve
i.d.	inner demibranch	u.	umbo
i.f.	inner fold of mantle margin	ud.l.	united anterior and posterior outer ligament layers
i.l.	inner ligament layer		
i.p.	inner palp	u.l.	umbo of left valve
		u.m.	mid-dorsal union of mantle margins
k.	kidney	u.r.	umbo of right valve
l.	lips	v.	ventricle
lig.	ligament	v.c.	vertically disposed crurae
l.p.	labial palp	v.g.	visceral ganglia
l.v.	left valve	v.m.	visceral mass