Form and Habit in Pinna carnea Gmelin

C. M. Yonge

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FORM AND HABIT IN *PINNA CARNEA* GMELIN

By C. M. YONGE, F.R.S.
University of Glasgow

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CONTENTS

The shell of the Pinnidae consists of characteristic fan-shaped valves united for their entire length dorsally by some form of ligament. The posterior and postero-ventral extensions of the valves are formed exclusively by the outer lobe of the mantle edge and so consist of the outer calcareous (prismatic) layer only. In the Pinnidae this layer has an exceptionally high organic content and so is flexible. The inner (nacreous) calcareous layer is thin and confined to the region occupied by the body, i.e. between the two adductors.

The ligament is composed of three layers (disregarding the outermost, but vestigial, periostracum). Anteriorly it consists of inner and outer layers; posterior to this for a short distance of outer layer, and for the remaining, and greatest, length it represents a fusion layer. This also continues forward over the middle region and traces persist still farther forward.

The inner ligament layer is secreted by the mantle isthmus, i.e. it corresponds to the inner calcareous layer of the valves; the outer ligament layer is secreted by the outer lobes of the mantle edge, i.e. it corresponds to the outer calcareous layer of the valves. The fusion layer represents the result of union posteriorly of the outer lobes of the mantle edge. That part of the ligament which is formed in the same way as the valves (all being constituents of the shell) is here termed the primary ligament, that part formed by fusion of the outer lobes of the mantle edge constituting the secondary ligament.

The mantle epithelium is divisible into proximal and distal regions, both containing mucous glands. The former, continuous with the mantle isthmus, secretes the inner calcareous layer; the latter is pigmented. Apart from the adductors, the mantle is attached only by the large anterior and posterior pallial retractors which subdivide within the mantle folds.

Posterior elongation of the mantle involves corresponding extension of the eulamellibranchiate ctenidia. All connexions between the two ctenidia and between ctenidia and mantle are by ciliary junctions. The ctenidia are very muscular; observations of Atkins on collection and sorting of particles are confirmed.

The unique gutter-like waste canals, originally described by Stenta, ensure that pseudofaeces and other waste from the inhalant chamber are continuously removed. A preoral, unpaired racemose gland opens into the inhalant chamber. Its most probable function is that of excretion; anything discharged from it will be removed by way of the waste canals. The pallial organ in the exhalant chamber is composed of a stalk and a more swollen head. It can be greatly distended and probably serves to clear away shell fragments. The projecting valves are subject to frequent damage.

The Pinnidae live vertically embedded in soft substrata into which they cannot withdraw. The animals burrow as they grow but only to the extent that the portion of the shell occupied by the body (i.e. as far as the position of the posterior adductor) is buried. The wide posterior region of the shell is always exposed. Water can thus be drawn in from well above the surface of the substratum. The waste canals in the inhalant chamber and the powerful exhalant current keep the cavity clear. The projecting valves can be rapidly repaired since they are composed exclusively of the outer calcareous layer. Such repair strengthens the valves. During repair new inner and outer ligament layers may be laid down beneath the previously formed primary ligament.

In the Lamellibranchia change in form and proportions of the body on the one hand, and of the mantle and shell on the other, are best discussed by reference to the two major axes in the sagittal plane, i.e. the antero-posterior and median axes of the body and the hinge and normal axes of the mantle and shell.

In their evolution the Pinnidae probably passed through a 'Modiolus stage' with the large posterior adductor close to the margin of the shell and little secondary extension of the ligament. Subsequently posterior extension of the mantle and so of the shell doubled the length of the animal and was accompanied by secondary extension of the ligament.

Such extensions of the mantle occur throughout the Anisomyaria (including the Pinnidae). They involve loss of the primitive pallial attachments apart from the adductors (the anterior of which is always reduced and often lost). The mantle becomes re-attached to the shell by secondary pallial retractors in the Pinnidae and also in *Malleus*, but along a new line peripherally in the Pectinacea and Ostreacea.

Existing data on development in the Pinnidae show that, with the formation of the dissoconch, new shell, secreted by the outer lobe of the mantle edge, is added to the posterior margin of the almost equilateral prodissoconch. The adult form is probably quickly acquired by the post-larva, the proportions of the different regions then remaining constant although with continual reduction anteriorly.

Success in the Pinnidae is due partly to characteristics shared with related families, partly to unique features. The former include great extension of mantle lobes without peripheral attachment, the latter include waste canals, pallial organ and pallial retractors. The rigid ligament only unites the valves; it has no opening thrust. The Pinnidae can survive loss of the anterior adductor or fusion of the ventral margins of the valves. It is only essential that the posterior adductor should be able when necessary to pull together the flexible posterior margins of the valves.

I. INTRODUCTION

The family Pinnidae consists of the single genus *Pinna* Linné, 1758 which comprises the two subgenera *Atrina* Gray, 1842 and *Pinna* s.s. (Thiele 1935). The family is of particular interest with many unique features of structure and habit. The shell is unmistakable; it is often very large but is always triangular in outline, tapering to a point anteriorly. All species have the same mode of life, living vertically embedded in a soft substratum of mud or muddy sand. They are attached by exceptionally long and numerous byssus threads to stones and gravel some distance below the surface of the substratum above which project the broad posterior regions of the shell. Movement being impossible, this part of the animal is fully exposed to the danger of damage from predators or other causes. It is significant that it represents extension of the mantle and shell *behind the posterior* *adductor*. As already noted by Grave (1911), the mantle lobes are here free from the shell. This makes possible repair of the damage frequently experienced. These adaptations are of great interest, and it is with their nature and, more especially, their possible origin that this paper is primarily concerned.

Work was carried out on *Pinna carnea* Gmelin, sometimes known as the sand or Spanish oyster or as the flesh pen, which is common in shallow water at Bermuda. Observations were made on living specimens and material was fixed in Bouin's fluid. This species attains a length of up to 30 cm and a breadth of some 16 cm and is found vertically embedded in fine calcareous sandy mud within sheltered areas usually among eel-grass. *P. carnea* is somewhat smaller than the British fan mussel, *P. fragilis* Pennant, and the still larger Mediterranean *P. nobilis* L., but it is more accessible than these species. The latter was originally described by Aristotle and has frequently excited comment because of its size and of the former commercial value of the long byssus* threads, but there is no adequate account of its structure. The very size of the shell, up to 60 cm long, presents difficulties. Milne-Edwards (1847) and Menegaux (1890) give some account of the circulatory system in species of *Pinna*, but the only general account of anatomy in any member of the Pinnidae would appear to be that of Grave (1911) on *Atrina rigida* (Dillwyn). Differences between species of the two subgenera of the Pinnidae are not great. In *Atrina* the mantle and shell do not extend to the same extent behind the posterior adductor. Nomenclature and classification within the Pinnidae are fully dealt with by Winckworth (1929, 1936).

II. Mantle/shell

(*a*) *General description*

Mantle and shell are co-extensive, the former secreting the latter; it is therefore logical to consider them together as mantle/shell (this matter is fully discussed elsewhere (Yonge 1953)). The remarkable form of the shell, shown in figure 1, is due to the great posterior extension of the mantle lobes, and the attachment of the two shell valves for their entire length dorsally is to an important degree the result of the fusion of the mantle edges. Structure will be described in this section of the paper, possible causes being discussed later.

The shell valves have the fan shape typical of all the Pinnidae and are longitudinally grooved with the well-marked keel which is characteristic of the subgenus *Pinna* but absent in *Atrina*. The colour, especially conspicuous in newly formed areas, is orange to reddish. The valves are thrown into a series of very low and broad ridges which radiate out from the narrow anterior tip towards the broad posterior margin. Few shells, however, are regular, the great majority showing frequent evidence of damage and repair (as in figure 1). The shell valves are almost straight dorsally and are united, in a manner which is described later, along the full length of this surface, from extreme anterior to extreme posterior end.

The shells of the Pinnidae are described as 'gaping posteriorly'. This certainly is the case when a dried shell is examined. For instance, a shell some 26 cm long gaped to a maximum width of 2 cm along the posterior margin and then, to a decreasing extent,

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* See Feen (1949) for a discussion on the origin of the term byssus, which was first used in descriptions of *Pinna nobilis* L.

ventrally to within 16 cm of the anterior end. Attempts to close the gape merely resulted in breaking the brittle shell. But in life, when the shell valves are in water, they are sufficiently flexible for the adductors (in effect the large posterior adductor) to pull them together and so completely to close the posterior gape. Noted by Winckworth (1929), this was here observed on many occasions in many animals. In the living animal there is *no* gape when the adductors contract, but this is due to the flexibility of the shell substance (described below) and *not* to any appreciable bending along the line of the ligament which represents a rigid attachment between the two valves.

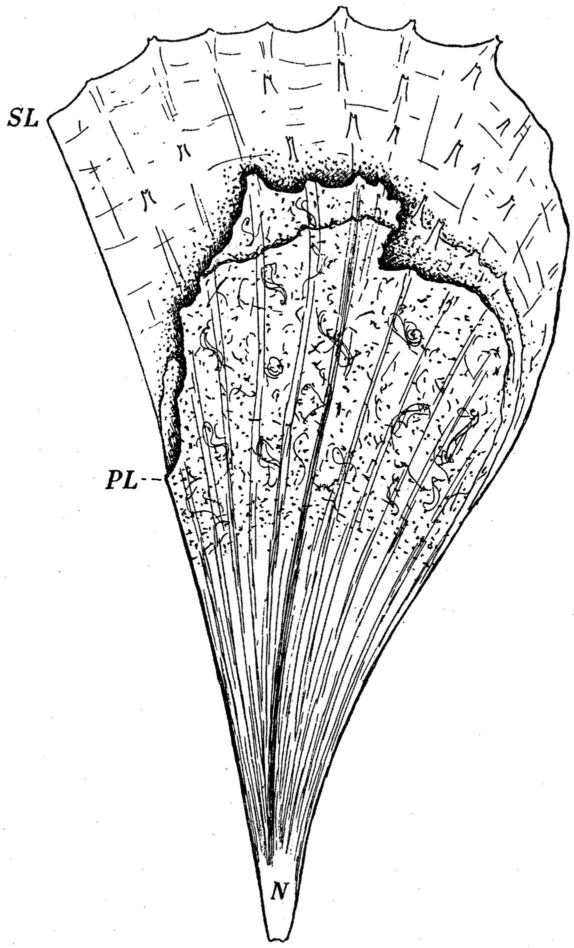


FIGURE 1. *Pinna carnea*. Outer surface of left valve, showing extensive repair. (Magn. × $\frac{2}{3}$.) *N*, inner nacreous shell layer exposed owing to abrasion of outer layer; *PL*, posterior end of primary ligament; *SL*, posterior end of secondary ligament.

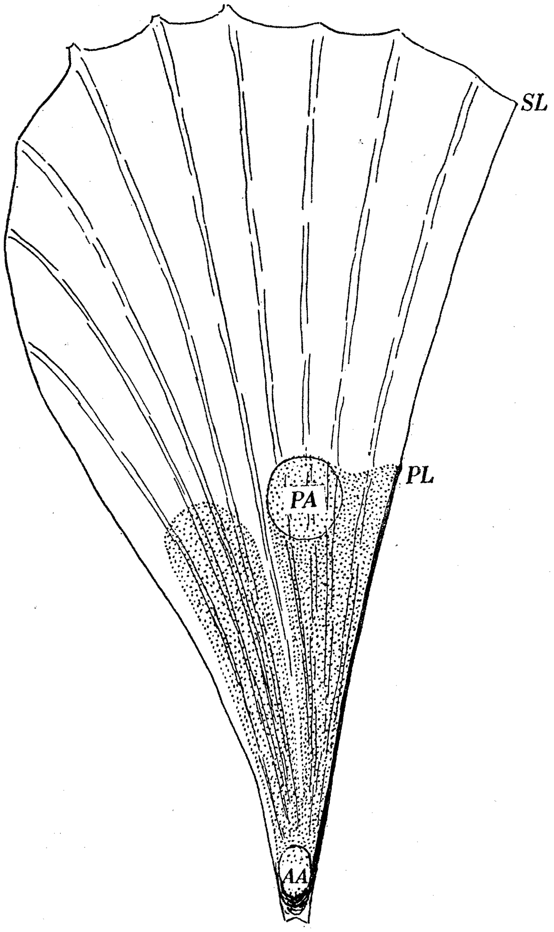


FIGURE 2. *Pinna carnea*. Inner surface of valve shown in figure 1, indicating extent of nacreous layer (stippled). (Magn. × $\frac{2}{3}$.) *AA*, *PA*, scars of anterior and posterior adductors. Other lettering as before.

The mantle extends to the margin of the shell valves when the animals are functioning normally in the sea. The inner lobes of the mantle edge are pigmented and fringed with a single row of fine and very short tentacles (figures 9, 12). The mantle can be drawn back to a remarkable extent. It contracts at the slightest stimulation, and when the shell is broken open the mantle tissues are found folded tightly against the posterior adductor, which is situated somewhat nearer to the anterior than to the posterior end of the shell, and also along the ventral surface of the visceral mass between the two adductors (see figure 15B).

As noted by Grave (1911) for *Atrina* and by many earlier workers on *Pinna*, the great part of the shell is composed of the outer, prismatic layer. As figured by Schmidt (1923) and Winckworth (1929) for various species and shown in figure 2 for *P. carnea*, the inner or nacreous layer is restricted in the Pinnidae to the anterior third of the internal surface, extending as far back as the posterior adductor. This layer is confined in area to that occupied by the adductors and the area between and dorsal to them. The extensive area of the shell behind the posterior adductor, which in life projects above the substratum in which the animal is embedded, is composed, apart from negligible amounts of periostracum, exclusively of the prismatic outer layer which is secreted by the outer lobe of the mantle edge.

(*b*) *Shell structure*

Fine strands of periostracum represent the only connexion between the margin of the mantle and that of the shell when the former is withdrawn. They are produced, as always in the periostracal groove which, as shown in figure 8A, remains closely associated with the outer lobe of the mantle edge. The periostracum (*P*) is extremely thin as well as discontinuous and must be worn away almost as soon as it is formed. Certainly in the adult Pinnidae it appears to be functionless. No trace of it can be detected on the outer surface of the shell. Bevelander & Benzer (1948) and Bevelander (1952) strangely suggest that the periostracal groove is the source of the organic matter *within* the outer calcareous layer of the shell.

Starting with the work of Carpenter (1845, 1848) the structure of the calcareous layers of the shell in the Pinnidae has probably been more thoroughly studied than that in any other group of Lamellibranchia, the most important later work being that of Schmidt (1923, 1925). The shell structure is unusually simple. As already noted, by far the greater part consists of the outer layer which is composed of polyhedral prisms formed, as in all lamellibranchs, by the outer lobe of the mantle edge. This layer attains a thickness in *P. carnea* of up to 1·5 mm and is correspondingly thicker in larger species. It consists of an organic framework within which crystals of calcite are deposited as described most recently by Bevelander & Benzer (1948) and Bevelander (1952). In the Pinnidae the ratio of organic conchyolin to inorganic salts is exceptionally high, so that after decalcification, to quote Carpenter (1845), 'a consistent and almost leathery membrane remains, which exhibits the prismatic structure just as perfectly as does the original shell; the hexagonal division being seen when either of its surfaces is examined, and the basaltiform appearance being evident on the inspection of its edge'. The high proportion of organic matter accounts for the unusual flexibility of the shell already noted. It also probably makes possible the remarkable speed with which the shell can be extended marginally in the course of normal growth and especially of repair. Initially the areas of shell so formed are extremely thin, but there is ample opportunity for thickening which can effectively continue until such time, should this occur, as the mantle epithelium secretes inner shell layers beneath it.

The inner calcareous layer, which consists of flat overlapping layers of nacreous material, is confined to the limited area shown in figure 2, being absent, it will be noted, along the line of the longitudinal groove within the keel on each valve. Descriptions of structure and formation are given by Schmidt (1923, 1925). In *P. carnea* this layer attains a maximum thickness of about 1 mm, but only anteriorly where it has been subject to increase for the longest time.

(*c*) *Mantle epithelium*

The outer epithelium of the mantle is divisible into a limited inner, or proximal, region and a much more extensive outer, or distal area. The latter only is pigmented so that, as shown in figure 7 (*pt*), there is a clear line of demarcation between the two when the shell valve is removed. These two regions of the pallial epithelium represent those that, in most Lamellibranchia, are separated by the line of attachment of the pallial muscles, the inner secreting the inner, often nacreous, calcareous layer of the valves, the outer forming the outer, prismatic layer. In the Pinnidae the latter area is enormously developed.

The epithelia of the two regions differ to some extent histologically, that of the inner area consisting of extremely flat cells, only some 5 μ deep and with the long axes of the nuclei usually parallel to the surface. Cell walls, though difficult to distinguish, probably exist; the contained protoplasm shows nothing but a faint reticular structure. The corresponding cells in the outer area may be as much as ten times deeper with more obvious cell boundaries and rather larger nuclei with prominent nucleoli. These cells are filled with fine granular inclusions some at least, containing pigment. These cells are bounded by a fine brush border 1 to 2 μ thick.

Two types of mucous gland cells occur in both areas. The commoner type contains a reticular secretion which stains a vivid blue-green with Alcian Blue (Steedman 1950). In the inner area these cells extend laterally for up to lengths of 30 μ, but also frequently bulge out greatly beyond the inner and outer boundaries of the epithelium. In the outer area these gland cells are broader but not deeper than the epithelial cells. Where visible the nuclei are usually irregular and elongated. A characteristic funnel-like aperture may open to the exterior. The less common gland cells have large granular or globular inclusions which stain, also intensely, with Orange G. They attain much the same size as the other cells and their nuclei appear similar. The reticular gland cells are some six times more abundant than the granular type.

Secretion of shell must be included in the functions of the epithelial cells; no attempt is here made to consider this problem, but the difference in thickness of the epithelia of inner and outer areas may well be correlated with the very much greater speed with which the outer layer of the shell is secreted. The presence of mucous gland cells, of the same type as those found in the epithelium which bounds the mantle cavity, is unusual. It is presumably connected with the almost complete freedom of the mantle from the shell. These glands will supply the necessary lubrication for the very extensive withdrawal and re-extension of the mantle.

(*d*) *Ligament*

This is of the greatest interest; the study of its structure has proved most illuminating and made possible generalizations of wide application to the Lamellibranchia, as already briefly outlined elsewhere (Owen, Trueman & Yonge 1953).

There are no hinge teeth, and the shell valves are rigidly united, as indicated in figure 4, for their entire length dorsally. It has been suggested (Owen *et al.* 1953) that the term ligament should be used to comprise *all* structures that unite the valves, irrespective of whether these are primary structures, i.e. a part of the original shell, or secondary structures. The latter represent extensions of the primary ligament formed by the fused outer lobes of the mantle edge. In the Pinnidae the ligament is actually composed of three portions, distinct in structure and origin, of which the secondary extension, posteriorly, is the longest.

(i) *Structure*

When viewed externally, the two valves of an intact shell appear to be united in the same manner along the entire dorsal surface. But examination of a separate valve reveals that the ligament is much thicker and is dark in colour for the anterior half of its length, up to a point in line with the hind surface of the posterior adductor (figures 1 and 2, *PL*). This also corresponds to the posterior boundary of the inner calcareous layer of the valves. The remainder of the ligament, up to its posterior extremity (*SL*), is thinner and almost colourless.

The anterior, and primary, half of the ligament is divided into two regions. The first, and much the longer, is composed of three layers of which the outermost is usually lost (figure 3B), while the second region, which occupies the middle of the ligament, is formed of two layers (figure 3C). The posterior, and secondary, half of the ligament consists of one layer only (figure 3D). The lengths of these three regions in a typical shell were 8·5, 1·2 and 11·8 cm respectively. Details of structure can best be given by reference to figure 3. Here (A) is shown the appearance of the central region of the ligament when viewed from the inside, i.e. from the ventral aspect. All the middle portion of the ligament is shown together with the hind end of the anterior portion and the front end of the posterior region. Transverse sections of the three regions, anterior (B), middle (C) and posterior (D), are also figured. The posterior portion consists solely of what, for reasons given below, may best be termed the fusion layer (*FL*). This unites the valves which here consist exclusively of the outer calcareous layer (*OC*). The middle region of the ligament consists of the fusion layer with beneath it a dense black layer which represents what is usually termed the 'outer' ligament (figure 3C, *FL*, *OL*). Although possibly containing a somewhat higher proportion of organic matter than the valves, this layer is highly calcified and is certainly non-elastic. In this region also thin sheets of the inner or nacrous layer (*IC*) are laid down on the inner surface of the valves. As shown in figure 3A, although this layer extends posteriorly on either side of the mid-dorsal line, it does *not* here stretch over the ligament itself.

At the posterior end of the anterior region of the ligament there is an obvious union, in the mid-dorsal line, of this layer. This is shown in figure 3A and also in section in figure 3B. The nature of the substance here secreted is modified to form the inner layer of the ligament (*IL*) which extends to the anterior end. As shown in figure 3B, the fusion layer usually breaks away in this region, the ligament thus consisting of 'outer' (*OL*) and inner (*IL*) layers only. The latter is no less calcified than the 'outer' layer but is lighter in colour. It is laid down in horizontal sheets, like the inner shell layer with which it is continuous. It is a part of the primary shell which, in the course of the evolution in the Lamellibranchia, has been modified to form two calcareous valves and a relatively less calcified ligament. The layers of secretion which form the inner ligament are influenced in form by the forces to which they are exposed along the mid-dorsal line of the shell where curvature is great. The pallial epithelium which secretes the inner ligament

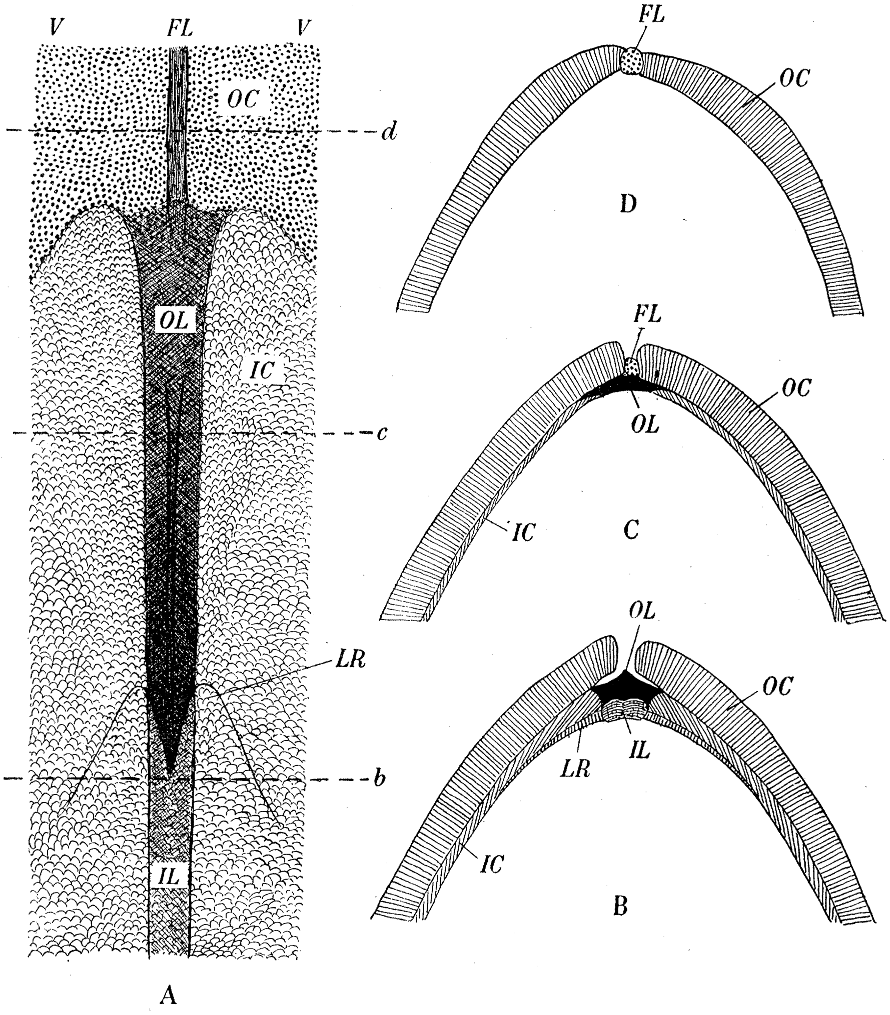


Figure 3. *Pinna carnea.* Structure of ligament. (Magn. × 5.) A, central region of ligament viewed from inner, i.e. ventral, surface; B, C, D, sections through ligament and adjacent regions of valves in region indicated by broken lines *b*, *c*, *d* in A. *FL*, fusion layer; *IC*, inner calcareous layer of valve; *IL*, inner layer of ligament; *LR*, ligament ridge; *OC*, outer calcareous layer of valve; *OL*, 'outer' layer of ligament; *V*, valve of shell.

extends laterally, where it is responsible for the formation of thin additional layers of inner calcareous layer over the previously secreted layers. This is best understood by reference to figure 3, where this layer is shown both superficially (A) and in section (B). It probably corresponds to what has elsewhere been described as the ligament ridge (see Trueman (1950) for description of this in *Mytilus*); it is convenient to retain the term, although in *Pinna* the structure is actually flat (figure 3B, *LR*).

(ii) *Formation*

Of the four possible constituents of a ligament (Owen *et al.* 1953), the periostracum is lacking in *Pinna*. The formation of the other three, however, is almost diagrammatically obvious owing to the characteristic form of the Pinnidae which involves great posterior extension of the mantle/shell accompanied by actual reduction at the anterior end (discussed later). To make matters as clear as possible, comparison is made in figure 4 between conditions in a diagrammatically equivalve dimyarian (A) and in the heteromyarian Pinnidae (B). In the former, the periostracum, which, unless worn away, forms the true outermost layer of the ligament, is omitted. The 'outer' layer of the ligament (*OL*) is shown to be produced by the outer lobe of the mantle edge in the depths of the anterior and posterior embayments in this, such secretion here replacing that of material composing the outer calcareous layer of the valves. It must be borne in mind that the primary ligament and valves together constitute the shell, all parts of which are secreted by the same agencies, although the two differ in proportions and physical properties of the substances of which they are composed. Along the mid-dorsal line, between the embayments, extends the mantle isthmus (defined by Owen *et al.* 1953) which secretes the inner layer (*IL*) of the ligament, i.e. corresponding to the inner calcareous layer of the valves. In both embayments some fusion of the outer mantle lobes (responsible for secretion of the outer layers of the shell, i.e. valves *and* ligament) is shown as having occurred with consequent formation of fusion layers (figure 4A, *FL*) which may correspond to the covers described by Trueman (1949, 1950, 1951). These

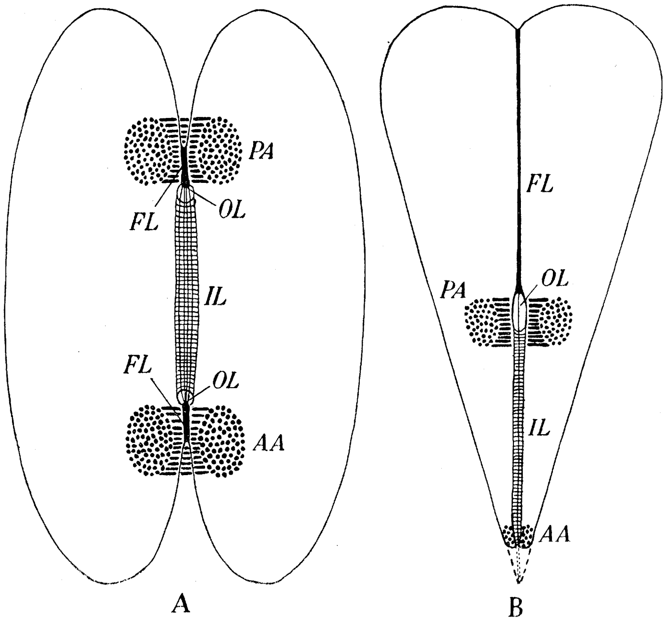


FIGURE 4. Diagrammatic comparison, showing shell (i.e. valves and ligament) spread out flat and viewed from above, between structure of the ligament in A, hypothetical dimyarian lamellibranch and B, heteromyarian Pinnidae. Primary ligament (omitting periostracum) shown as consisting of 'outer' layer (*OL*) formed by mantle edge in the depth of embayment, and inner layer (*IL*) formed by mantle isthmus beneath it. Secondary ligament consists of the fusion layer (*FL*). Other lettering as before.

layers, which represent the products of secretion by the fused outer lobes of the mantle edge, constitute secondary extensions of the primary ligament as shown diagrammatically in figure 4A. Such extensions may, of course, be absent or confined to one end.

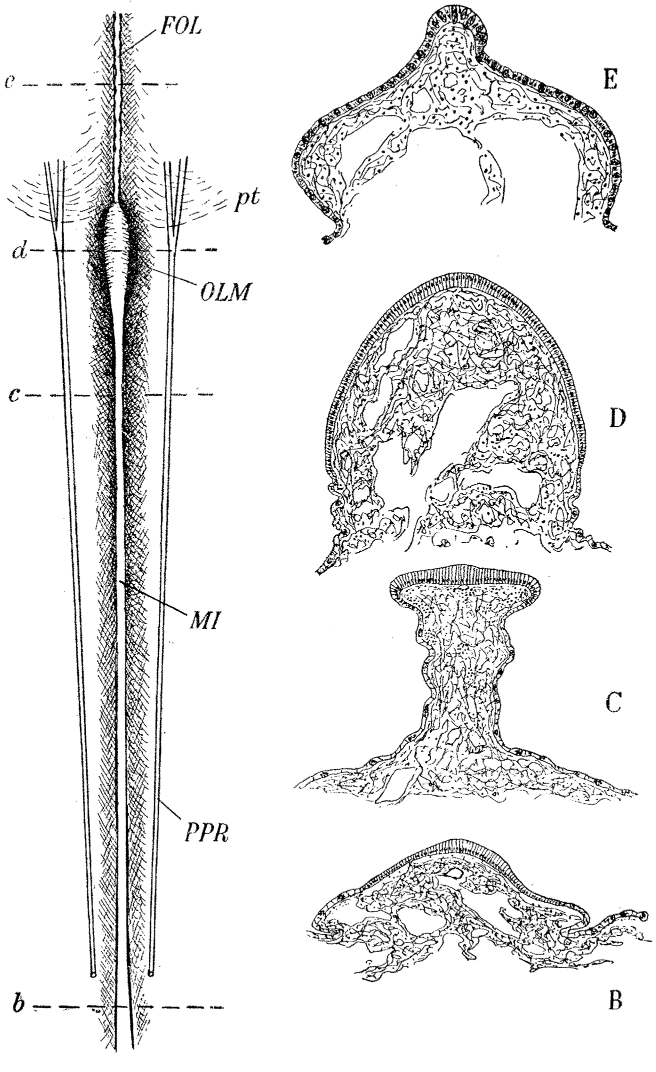
In the Pinnidae (B), as will be discussed at appropriate length later, growth of the mantle/shell is such that the dorsal and posterior margins become extended into what is effectively a straight line. In consequence, an exceptionally long ligament is formed. The anterior half of this is *primary* ligament and the posterior half *secondary* ligament. During growth the mantle retreats from the anterior end of the shell which is worn away. The anterior embayment (initially reduced as in all heteromyarians) is therefore obliterated. At the same time the mantle/shell extends far behind the posterior adductor and so makes possible the great extension of the fusion layer (figure 4B, *FL*) posterior to the primary ligament. As shown in figures 4B and 19, the anterior end of the ligament is constantly becoming reduced as the mantle tissues retreat. At the same time the mantle isthmus is growing in length posteriorly (see figure 19) with corresponding elongation of the inner layer of the ligament. The manner in which this spreads posteriorly is shown in figure 3A.

Secretion of the ‘outer’ ligament by the epithelium of the outer lobe of the mantle edge in the depth of the posterior embayment is shown with particular clarity in *Pinna* owing to the manner in which this epithelium also has been drawn out longitudinally. In the example quoted above this secreting surface extends for some 1·2 cm behind the mantle isthmus. In the life of the animal this is constantly secreting ‘outer’ ligament under which the inner ligament is later added by the epithelium of the mantle isthmus as, in the course of growth, this extends posteriorly. This is indicated diagrammatically in figures 6B and 19. Finally, there is the great length of the fusion layer due to closure of the once very deep posterior embayment by application and final fusion of the outer lobes of the mantle edge. These are the areas normally responsible for secretion of the outer calcareous layers of the valves, *not* of the ‘outer’ ligament. The product of secretion after the two unite constitutes the fusion layer (*FL*), or secondary ligament, by means of which the two valves are united for the posterior halves of their length. In the more anterior regions, where the two layers of the primary ligament are secreted beneath it, these tend to push the valves slightly apart with the result that the fusion layer usually breaks away as shown in figure 3B.

The appearance of the secretory surfaces when viewed laterally is shown in figure 7, as seen from the dorsal aspect together with their appearance in transverse section in figure 5, and the appearance in longitudinal section (for *P. nobilis*) in figure 6A. The long mantle isthmus (*MI*) forms a low elevation anteriorly (figure 5B), but behind the attachment of the posterior pallial retractor (*PPR*) this becomes an increasingly high ridge (figure 5C). In contrast to the low epithelium of the adjacent proximal mantle area, that of the isthmus consists of narrow and tall columnar cells up to 80 μ high. The nuclei lie in the basal half of the cells, the protoplasm of which contains very fine granules, largest and most numerous near the free margin where the cells are drawn out slightly, indicating their secretory function (figures 5B, 5C, 6A). There are no mucous glands.

The mantle isthmus is shown in figure 7 as being separated by a groove from the epithelium of the outer lobe of the mantle edge which secretes the ‘outer’ ligament.

This groove, however, is due to partial contraction of the tissues (here a consequence of fixation) and is *not* present when these are fully extended in life. This region is broader than the mantle isthmus. As shown in figure 5D it is rounded with the secreting epithelium almost semicircular in section. This epithelium is not unlike that of the mantle isthmus but the nuclei are situated in the centre of the cells. In *P. nobilis* (figure 6) the epithelial cells are taller than those of the mantle isthmus, and the free margins of the cells are drawn out to a much greater extent in connexion with secretion of the 'outer' ligament. These differences are not so conspicuous in *P. carnea*. In both, occasional mucous glands



A

FIGURE 5. *Pinna carnea.* A, central region of mid-dorsal line of body viewed from above after removal from shell; B, C, D, E, transverse sections through epithelia secreting layers of the primary and secondary ligament in regions indicated by broken lines *b*, *c*, *d*, *e* in A. (Magn. A, × 3; B–E, × 35.) *FOL*, fusion of outer lobes of mantle edge (shown in section in E) forming fusion layer; *MI*, mantle isthmus (in section in B and C) forming inner layer of primary ligament; *OLM*, outer lobe of mantle edge (in section in D) forming 'outer' layer of primary ligament; *PPR*, posterior pallial retractor muscle; *pt*, limit of pigment (see also figure 7) representing boundary between distal (pigmented) and proximal regions of mantle.

occur marginally and also posteriorly (figure 6A) where this epithelium begins to merge with that of the fused outer lobes (figure 6A, *OLM*, *FOL*). But there are no sharp distinctions between the epithelia of the three regions, and the one gradually passes into the other as indicated in figure 6A.

Another transverse groove appears, in figure 7, to separate this region from the long posterior extension consisting of the fused outer lobes of the mantle edge (figures 5 and 7, *FOL*). This groove also is due to contraction, indeed is absent in the longitudinal section of *P. nobilis* shown in figure 6. The epithelium here is strikingly different from that of the other two regions. In transverse section (figure 5E) it consists of a small rounded ridge which surmounts a larger elevation the epithelium of which is, however, identical with that of the rest of the distal mantle area (note boundary of this, represented by limit of pigmentation, shown in figure 5A, *pt*).

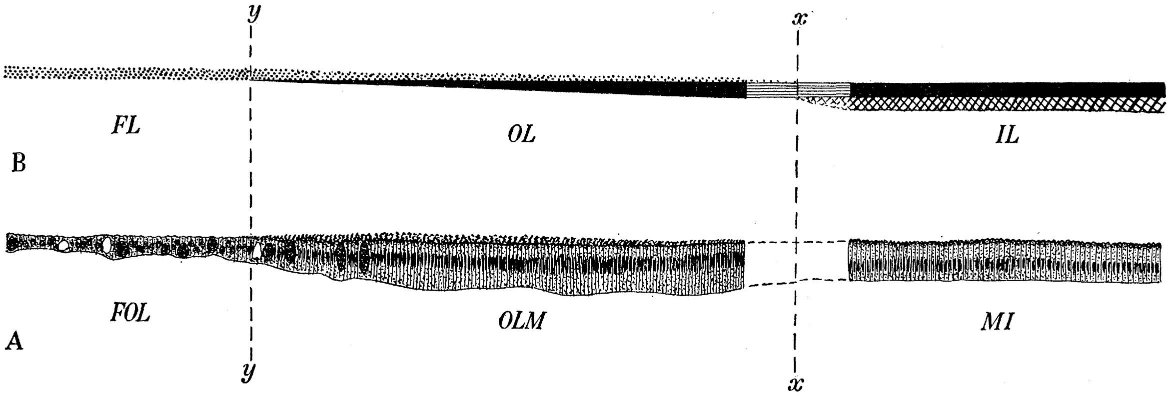


FIGURE 6. *Pinna nobilis*. A, sagittal section through mid-dorsal tissues, showing epithelia secreting three regions of ligament. (Magn. × 70.) B, diagrammatic longitudinal section through ligament. *x*, posterior end (approximate) of mantle isthmus and so of inner ligament; *y*, posterior end of epithelium secreting 'outer' ligament. Other lettering as before.

The epithelium of the ridge which secretes the fusion layer (figures 5, 6, *FOL*) consists of columnar cells of the same general type as those which form the epithelium of the distal regions of the mantle but they are somewhat taller. As shown in figure 5E, mucous glands occupy about one-half of this surface. Both types occur, the reticular (Alcian Blue staining) cells being the more numerous. The fusion layer is secreted by the columnar cells and consists of the same substance as the outer calcareous layer of the valves but differs in the absence of prismatic form. This is probably a consequence of the different manner in which the organic matrix is laid down. The presence of mucous glands can be associated here, as on the mantle surface generally, with the frequent withdrawal and re-extension of the tissues.

The epithelium forming the secondary ligament (i.e. fusion layer) represents a modification of that concerned with secretion of the outer calcareous layer of the valves. The epithelia forming the two layers (apart from periostracum) of the primary ligament are, as always, distinct histologically from those forming the corresponding layers of the valves (e.g. see description by Trueman (1949) of the ligament in *Tellina tenuis*). Although valves and ligament together constitute the shell, the ligament represents the greatly modified mid-dorsal region of this. In a typical lamellibranch it is lightly calcified and elastic, usually with a pronounced opening thrust (Trueman 1951). In *Pinna*, although the primary ligament is *not* elastic and has *no* opening thrust, yet the two layers continue to be secreted by epithelia distinct from those that secrete the layers of the valves. Moreover, these layers of the ligament remain themselves distinct in character, although no longer in function, from the rest of the shell.

(*e*) *Mantle attachments*

In typical dimyarian lamellibranchs the mantle is attached to the shell peripherally by pallial muscles which cross-fuse in the anterior and posterior embayments to form the two adductors. A consequence of change to the monomyarian condition is the initial reduction and loss of such attachments, e.g. in Anomiacea and Pteriacea, although secondary attachment may take place as in the Pectinidae (Yonge 1953). However, in the special conditions prevailing in the Pinnidae primary attachment is reduced to that represented by the large posterior and the small anterior adductor (see figure 7). There is no line of pallial attachment between these adductors as there is, for instance, in the heteromyarian Mytilidae. Secondary attachment is, however, present in the form of two muscles, not apparently previously described, here designated the anterior and posterior pallial retractors (figure 7, *APR*, *PPR*). Each consists of a paired muscle having a single insertion into each of the shell valves, but which divide up to spread widely throughout the substance of the mantle posterior and ventral to the posterior adductor. The anterior retractor is inserted a little distance anterior to the ventral margin of the posterior adductor. It divides up into some eighteen branches (there is probably variation here) which ramify through the greater part of the inhalant or infrabranchial region of the mantle and also along the ventral border of the exhalant region (figure 7). The insertion of the posterior retractor is actually much farther forward than that of the anterior retractor (figure 7). Nevertheless, it is morphologically posterior. As already noted, it is anterior to this insertion that the mantle isthmus becomes raised into a ridge. Immediately behind the end of the isthmus this muscle divides and subdivides, the branches spreading out through the substance of the exhalant or suprabranchial region of the mantle.

As examination of figure 7 will indicate, contraction of these muscles will pull back the mantle until it lies in tight folds against the ventral and posterior margins of the posterior adductor (figure 15B). At the same time contraction of the radial muscles which extend from the visceral mass into the mantle margins anteriorly will pull back the mantle between the two adductors. When so withdrawn the mantle tissues will occupy approximately the area covered by the inner, nacreous shell layer (figure 2). The extensive posterior and postero-ventral regions over which the mantle may extend and be drawn back are exclusively formed of outer, primatic shell layer. The great extent of this back and forward movement of the mantle within the shell provides explanation for the presence of the mucous glands in the epithelium, including that which secretes the fusion layer and to a much less extent that which forms the 'outer' ligament. The mantle may be so far withdrawn as to uncover the whole of the fusion layer which involves some movement of the epithelia secreting the layers of the primary ligament. Owing to the lack of hinge teeth the only restrictions on the movement of the tissues mid-dorsally are the attachments of the adductor and the posterior pallial retractor muscles.

Comparable pallial retractor muscles have been described in species of *Malleus* by Pelseneer (1911) and Kühnelt (1938). They consist of a single pair of muscles inserted near the posterior end of the elongated single adductor but morphologically dorsal to the ctenidia. The muscle extends postero-ventrally (i.e. into the handle of the 'hammer') to ramify terminally within the suprabranchial tissues (figure 17D, *pr*). In *Malleus*, as in *Pinna*, these extend far beyond the posterior adductor, and this region of the shell is similarly devoid of inner, nacreous shell layer. With the different form of the mantle/shell

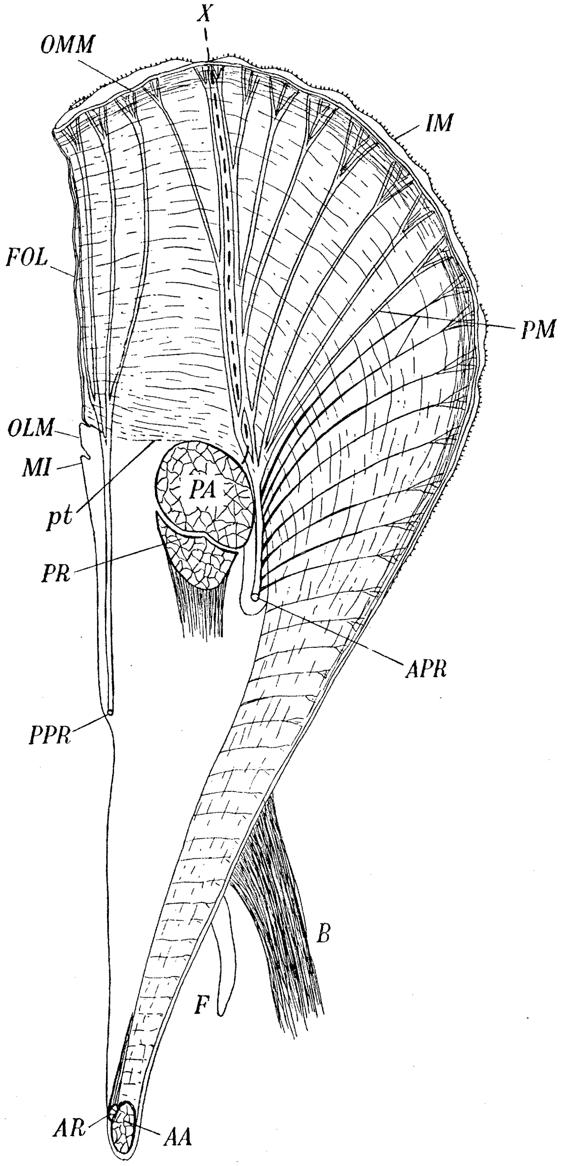


FIGURE 7. *Pinna carnea*. Animal removed from shell and viewed from left side, slightly contracted, especially postero-dorsally. (Magn. × ½.) *AR*, anterior pedal retractor; *APR*, anterior pallial retractor; *B*, byssus threads; *F*, foot; *IM*, inner lobe of mantle edge; *MI*, posterior end of mantle isthmus (groove due to contraction); *OMM*, outer and middle lobes of mantle edge; *PM*, pallial muscles extending through distal (i.e. retractile and pigmented) regions of mantle; *PR*, posterior pedal retractor; *PPR*, posterior pallial retractor; *X*, broken line indicating boundary between inhalant and exhalant chamber. Other lettering as before.

in *Malleus* a single pair of pallial retractors is adequate. The possible origin of these muscles is discussed later.

(*f*) *Mantle edge and inner epithelium*

The edge of the mantle is typical in general form although with interesting modifications in detail. When viewed in life from the inside, as represented in figure 9, the mantle appears to be bounded by a single lobe (*IM*) which is scalloped posteriorly where it also carries a single row of very small tentacles. This is the inner lobe of the mantle edge, and only when it is turned back are the much smaller middle and outer lobes revealed, with the periostracal groove between them. The middle lobe carries none of the sensory tentacles which it does in many other Lamellibranchia (e.g. the Pectinidae where it bears both tentacles and eyes). The outer lobe is responsible for the great marginal increase of the shell valves.

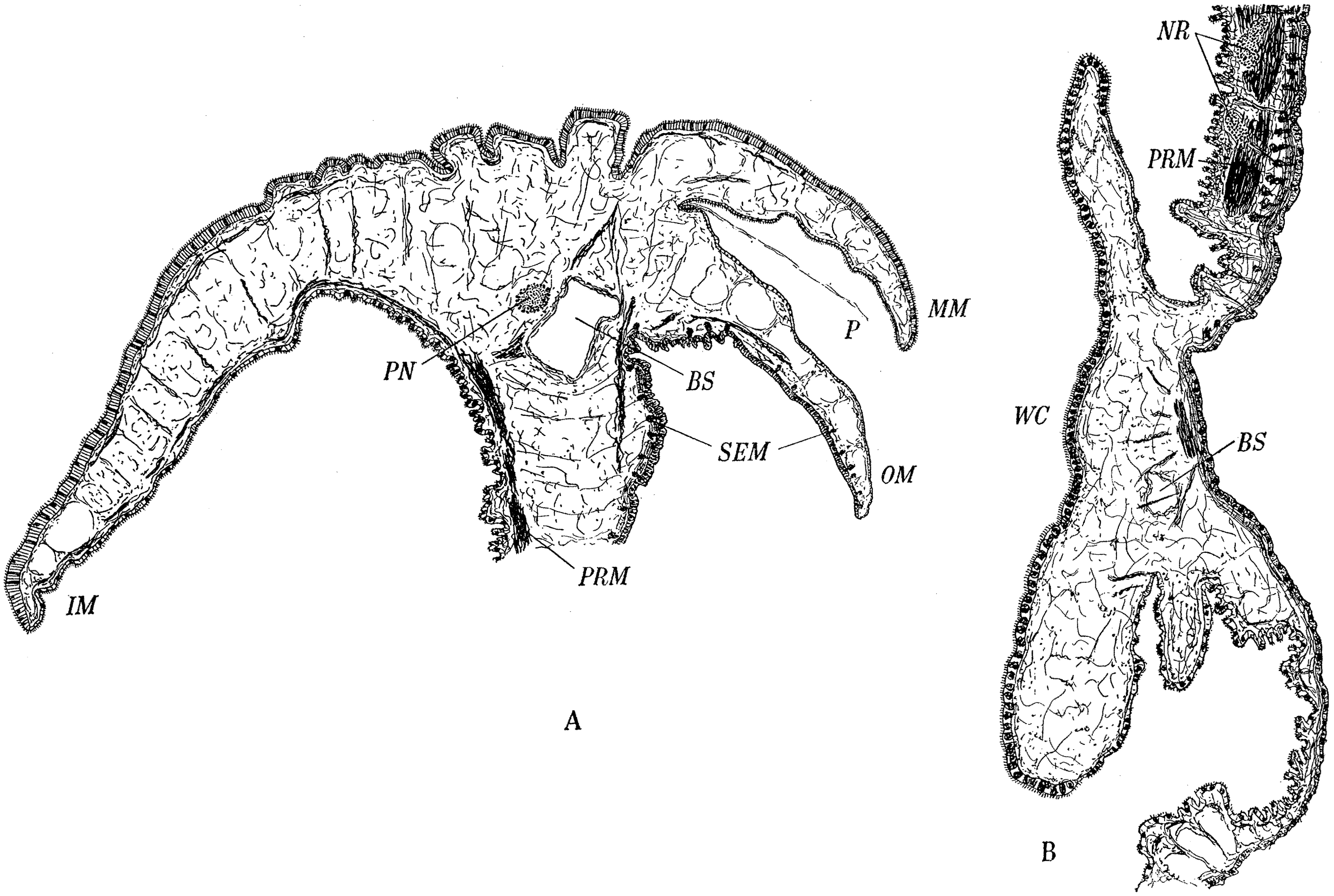


FIGURE 8. *Pinna carnea*. Transverse sections through mantle. A, mantle edge; B, region of waste canal. (Magn. × 25.) *BS*, blood sinus; *MM*, middle lobe of mantle edge; *NR*, nerve associated with pallial retractor muscle; *OM*, outer lobe of mantle edge; *P*, periostracal thread issuing from periostracal groove; *PN*, pallial nerve; *PRM*, pallial retractor muscles; *SEM*, subepithelial mucous glands; *WC*, waste canal, richly ciliated epithelium with great accumulation of mucous glands. Other lettering as before.

The mantle edge is shown in section in figure 8A. The inner lobe (*IM*), containing most muscle, is relatively more contracted than the middle (*MM*) and outer (*OM*) lobes. Between these two last lies the periostracal groove from which emerge thin strands of periostracum (*P*). Descriptions of the epithelia may suitably begin with that of the outer surface of the outer lobe (i.e. that applied to the shell). This generally resembles that of the distal, pigmented areas of the mantle but with fewer mucous glands and these largely Alcian Blue staining and sub-epithelial in position (*SEM*). It is as though every possible epithelial cell is here needed for secretion of shell, space being therefore not available within the epithelium for mucous glands. This epithelium blends imperceptibly with that of the adjacent mantle surface, all of which is probably concerned in some measure with secretion of the outer, prismatic layer of the shell valves.

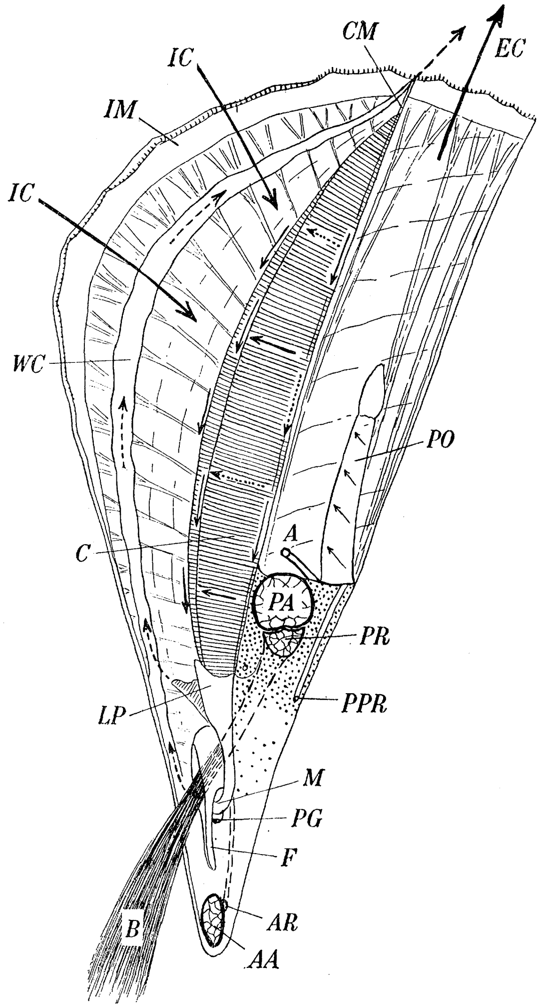


FIGURE 9. *Pinna carnea*. Organs and currents in mantle cavity, viewed from right side after removal of right valve and mantle lobe. (Magn. $\times \frac{1}{2}$.) *A*, anus; *C*, ctenidium; *CM*, ctenidial membrane; *EC*, *IC*, exhalant and inhalant currents; *LP*, labial palps; *M*, mouth; *PG*, pallial gland; *PO*, pallial organ; *WC*, waste canal. Other lettering as before. Entire arrows represent collecting currents on exposed surfaces of ctenidia, dotted arrows those on under surfaces; broken arrows indicate rejection or cleansing currents.

The epithelium of the inner side of the outer lobe is very low with occasional slight indications of sparse ciliation; there are a few scattered Alcian Blue staining mucous glands. In the depth of the groove, where the periostracum is secreted, the epithelium is locally somewhat deeper. The outer surface of the middle lobe is bounded by an almost equally flat but uniformly ciliated epithelium without mucous glands. The inner surface of this groove is continuous in character with the outer surface of the inner lobe (see figure 8A). The epithelium throughout consists of long, conspicuously ciliated cells, up to 60 μ in height. Among these are many equally elongated Alcian Blue staining mucous glands. But the epithelial cells are notable for the absence of stainable contents. The epithelium on the inner surface of the inner lobe is about half as high but otherwise not dissimilar. This in its turn merges with that which lines the mantle cavity generally. This is lower, with irregularly disposed patches of longer cells which alone appear to be ciliated. Alcian Blue mucous glands persist.

The one notable interruption in this epithelium is provided by the waste canal (figures 8B and 9, *WC*). The epithelium which bounds the surface of this channel is sharply distinguished from that of the rest of the mantle surface. It consists of long, densely ciliated cells with the highest possible concentration of mucous gland cells. A few of these stain with Alcian Blue but the majority with haemalum. This is the only place where glands of this type have been observed in *Pinna*; their possible function will be discussed later.

Within the substance of the mantle ramify the ultimate branches of the pallial retractor muscles (figure 8A, B, *PRM*). With each bundle is associated a nerve (*NR*) which runs through it in a manner similar to that described in the pearl oyster, *Margaritifera* (=*Pinctada*) by Herdman (1904). In the mantle edge, at the base of the three lobes, lies as always, the pallial nerve (*PN*). Menegaux (1890) describes in *Pinna nobilis* the large circumpallial blood sinus and this is seen in section in figure 8A (*BS*). He also described two other sinuses between this one and the efferent vessel that carries blood from the ctenidium to the auricle. The position in which he figures these sinuses coincides with that of the waste canal (which he does not mention). One such sinus was seen in all sections made of this region (e.g. that shown in figure 8B, *BS*), but no cavity sufficiently definite to constitute a second. This sinus is presumably concerned with dilation of the waste canal, strands of muscle which radiate within it (figure 8B) supplying the means of retraction.

III. Organs in the mantle cavity

(*a*) *General description*

The general appearance of the organs in the mantle cavity when viewed from the right side is shown in figure 9. The small anterior adductor (*AA*) is situated at the extreme anterior tip, and the much larger posterior adductor (*PA*) lies rather less than half-way back along the length of the shell. The body of the animal (i.e. apart from the mantle with associated structures including the ctenidia) is thus confined to the anterior two-fifths of the shell in length and very much less than this in area. The foot (*F*) lies about midway between the two muscles and has large posterior and small anterior retractors (*PR*, *AR*). The foot is elongated anteriorly with the byssal groove running along the posterior surface. Planting of the very long and numerous byssal threads must be its sole function, except in very early life. These threads (*B*) emerge from between the shell valves antero-ventrally. The large size of the posterior pedal retractor is clearly associated with the byssus, and by means of its contractions the animal will be enabled gradually to work its way into the substratum as it grows. The anterior end of the shell is very much worn, but this is partly the effect of abrasion and partly no doubt a result of the constant withdrawal of the mantle during growth (see discussion later) which makes internal repair impossible. But there is evidence that the action of the posterior retractor, or byssal, muscle must literally be to grind the anterior end of the shell into the deeper layers of gravel and stones which lie below the softer upper layers of the substratum in which attachment must initially be made. The tip of a large specimen of *P. carnea* may be some 15 cm below the surface (larger species correspondingly further) and will have penetrated to this depth as a result of successively deeper attachments of byssal threads (planted by the extended foot) followed by contractions of the byssal retractor.

The organs in the visceral mass call for little comment, the alimentary canal and the circulatory, renal and nervous systems are essentially similar to those described by Grave (1911) in *Atrina rigida*. The reproductive system is interesting because in *Pinna carnea* sections reveal the presence of both spermatozoa and ova in the gonad. Ripe spermatozoa occupy the centre of the tubules, ova developing around the walls. This species must therefore be added to the list of hermaphrodite lamellibranchs, although whether *P. carnea* is a protandrous or an alternating hermaphrodite remains to be determined. In view of the size, and presumed age, of the specimens examined, the latter alternative appears the more probable.

It is the widely extended mantle with its associated organs, some of which are unique, which is of particular interest in the Pinnidae. The ctenidia, which are primitively pallial outgrowths and only secondarily associated with the mouth for feeding (see Yonge 1947), are also affected by the great posterior extension of the mantle. It will be most convenient to consider them first.

(*b*) *Ctenidia and palps*

When the mantle is fully extended the ctenidia are drawn out, as shown in figure 9, with only the anterior quarter of their length within the confines of the body as delimited posteriorly by the posterior adductor. As noted by Grave (1911) in *Atrina*, the ctenidial axes, through which blood enters and leaves the gills, are attached by way of a suspensory membrane to the body, i.e. for only a limited extent anteriorly (figure 10A). Apart from this, all attachments of the ctenidia to the mantle and to one another are by way of broad and very firm ciliary junctions (figure 10A, B, *j*). This is probably true for all the Pinnidae judging from the work of Grobben (1900), Stenta (1903), Grave (1911) and Atkins (1938).

Thus the two ctenidia are united in this manner along the middle line by way of the dorsal extremities of the ascending lamellae of the inner demibranchs (figure 10B). Only anteriorly are they separated for a short distance by the foot. The extremities of the ascending lamellae of the outer demibranchs are similarly attached for their entire lengths to a low ridge on the mantle. In consequence of these two sets of ciliary junctions the mantle cavity is most effectively divided into inhalant and exhalant chambers (figure 10B, *I*, *E*). This condition is similar to that described by Grave in *Atrina*, but he failed to note conditions at the posterior end. There, in *Pinna carnea*, the pallial ridges become more pronounced and finally unite with one another, by way of a broad and very firm ciliary junction, in the mid-line behind the gills. This ctenidial membrane (figures 10 C, 12, *CM*) fuses posteriorly with the inner lobe of the mantle edge, so completing the separation of the two chambers; there is no actual fusion of any part of the mantle edge. Thus, despite the great posterior extension of the ctenidia, there is, as shown in figure 9, efficient division of the mantle cavity into a straight exhalant chamber, of the same depth as the body, and a larger inhalant chamber which, however, diminishes greatly in depth anteriorly. The appearance of these chambers when viewed looking down upon the opened shell valves of a living animal is shown in figure 12.

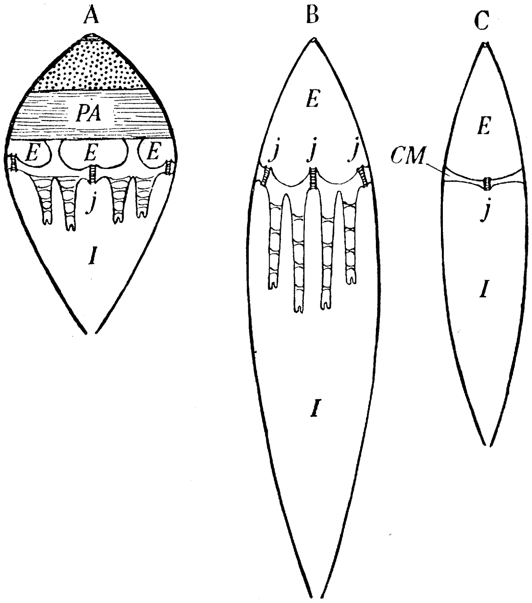


FIGURE 10. Pinnidae. Diagrammatic transverse sections through A, region of posterior adductor; B, middle of ctenidia; C, immediately posterior to ctenidia. *CM*, ctenidial membrane; *E*, *I*, exhalant and inhalant chambers; *PA*, posterior adductor; *j*, ciliary junctions uniting ctenidia in mid-line, ctenidia and mantle ridge laterally, also membranes posterior to ctenidia.

The inner demibranchs are slightly deeper than the outer ones, but this is the only difference between them. The structure of the ctenidia in species of the Pinnidae has been described in considerable detail by Stenta (1903), Ridewood (1903), Grave (1911) and Atkins (1937 *a*, *b*, 1943). They are eulamellibranchiate, very deeply plicate and heterorhabdic with deep marginal grooves along the free edges of the four demibranchs. The principal filament, which is grooved, occupies the depths between the plicae, the summits of which are formed by almost equally large apical filaments. There are fifteen ordinary filaments (including the apical filament) in the plicae. Conditions vary in other species, five of which are described by Ridewood (1903).

The observations of Atkins (1937*a*, *b*) on the ciliary currents on the ctenidia of *P. fragilis* were confirmed on those of *P. carnea*. On each ctenidium there are five oralward tracts, dorsally along the axis and along the summits of both ascending lamellae, and ventrally within the marginal grooves. All carry material towards the palps. Except for narrow regions adjacent to the dorsal oralward tracts, all frontal cilia beat ventrally on principal, ordinary and apical filaments. When the ctenidia are fully relaxed and extended, material passes freely from the frontal surfaces into the very deep marginal grooves. But the lamellae readily contract (down to as little as one-quarter the length when fully expanded), and this causes restriction of the grooves between adjacent plicae on the frontal surface and at the same time an overarching of the marginal groove by the ends of the plicae. Full description and figures are provided by Atkins (1937*a*) who has shown that plicae may be utilized for sorting in two ways. There is the *Pecten* type in which there is a difference in the direction of ciliary currents between the principal and ordinary filaments, and the *Pinna* type in which cilia beat in the same direction on both but where coarse material may be prevented from entering the marginal groove. Under these circumstances particles carried on the crests of the plicae reach the ventral margin only to be passed immediately on to the surface of the mantle. Only the very finest particles can now enter the restricted grooves between the plicae where, by the cilia on the principal filaments, they are carried between the overarching ends of the plicae and so into the marginal grooves. Within these now largely enclosed channels, material is conducted between the palps and so in most cases reaches the mouth. Thus when little material enters in suspension in the inhalant current the greater part of this should reach the palps. But when larger quantities enter, the ctenidial lamellae contract, by the agency of the vertical muscles described by Atkins (1943) and earlier workers, so that the selective mechanism is brought into play and most of the particles are passed on to the surface of the mantle. In both cases the dorsal oralward currents will operate, but, as material is carried into them solely from the closely adjacent frontal surfaces, only a small amount of food can reach the mouth by this route.

The ctenidia end anteriorly between the elongated palps (*LP*), the grooved inner surfaces of which carry out final selection of food particles in the usual manner. These are then carried forward in long oral grooves to the mouth (*M*) which, owing to the characteristic form of the Pinnidae, lies at an unusual distance posterior to the anterior adductor (figure 9).

(*c*) *Waste canal*

This paired structure, there is one in each mantle flap, occurs only in the Pinnidae. It was originally described in *Pinna nobilis* by Stenta (1901, 1903) and in *Atrina rigida* by Grave (1911). As shown by figures 8B and 9, it consists of a channel or gutter raised above the general surface of the mantle. It arises anteriorly near the mouth and terminates at the posterior end of the inhalant chamber where the ctenidial membrane unites with the inner lobe of the mantle edge to complete the division between the inhalant and exhalant chambers. The canal is widest in the middle of its course becoming very narrow posteriorly.

As already described, its internal surface is very richly ciliated and, as shown in figure 8B, the epithelium is largely occupied by mucous glands that stain with haemalum. All material that enters is carried rapidly back, i.e. in life vertically upward, and at the same time consolidated in mucus which is possibly more viscous than that produced by the Alcian Blue staining glands which appear largely confined to surfaces needing lubrication. The distinction is not absolute, however, because the mucous glands in the ctenidia are of the latter type; however, there is certainly not the same need here for a viscid secretion as there is in the waste canal. In that, particles of all sizes (see later) have to be consolidated into a firm string of pseudofaeces which must be carried vertically upward out of the mantle cavities of animals up to 30 cm high in this species and even higher in others.

(*d*) *Pallial gland*

Stenta (1906) described a pre-oral unpaired gland which opens into the mantle cavity in *Pinna nobilis*. He called it Poli's gland. Pelseneer (1911) and White (1942) have since noted its presence in some species but its absence, or at any rate slight development, in others. Grave (1911) makes no mention of such an organ in *Atrina rigida*, but he did not apparently seek for it as he makes no mention of Stenta's work. His failure to note what is externally never a conspicuous structure does not necessarily imply that the gland is absent.

The pallial gland is situated, as shown in figure 9 (*PG*), on a small papilla immediately anterior and dorsal to the mouth. It opens outside the oral groove so that its secretion cannot pass into the alimentary canal (unless, most improbably, it does so eventually by way of the ctenidia and palps). Stenta has described and figured it in full anatomical and histological detail, and the gland in *Pinna carnea* agrees with his description of that in *P. nobilis*. It is an elaborate racemose structure with a very extensive internal surface. Ducts, which lead to a common opening, are ciliated and contain Alcian Blue staining mucous glands. The tubules of the gland are composed of one type of cell. The nuclei are rounded and the cytoplasm has little structure or affinity for stains. The only contents are minute brown concretions, usually scattered throughout the cells but occasionally massed together, in which condition they appear to be expelled from the cells. There is a good blood supply, and the general impression gained is certainly that of an excretory organ.

Suggested functions of this gland are that it is salivary or else excretory. The fact that its products will inevitably be carried by ciliary action on the mantle into the waste canals for speedy removal really disposes of the first suggestion. Stenta thought the gland was excretory, partly, however, because he considered that pericardial glands were not present in the Pinnidae. White (1942) has since reported their presence in some, though absence in other, species of *Pinna*. But she also finds that the pallial gland is largest in species devoid of pericardial glands and therefore supports the theory that it is excretory in function. As noted above, this view is further strengthened by histological examination, although it would be most desirable to confirm this experimentally. If it is an excretory organ then it is unique in opening into the *inhalant* chamber, but it certainly does so in the one position, possibly confined to this one family of lamellibranchs, from which waste will be quickly and *continuously* removed from the mantle cavity. If this is an excretory organ then it is interesting to speculate why certain of the Pinnidae should need an additional organ with this function. Despite the great size of the shell, the animals themselves are not very large. However, they do produce an unusually massive byssus, the secretion of which presumably represents a considerable metabolic strain. Possibly there is need for additional excretory surface to dispose of the waste products of this metabolism.

(*e*) *Pallial organ in exhalant chamber*

A second organ, also confined to the Pinnidae, occurs in the exhalant chamber. As shown in figure 9 (*PO*), it consists of a large, unpaired tentacular body which projects posteriorly from the base of the exhalant chamber where it arises in the mid-line dorsa to the anus (*A*). Grave (1911) has described a similar organ in *Atrina rigida*, where, owing to the form of that species, it is relatively shorter and much stouter. He terms it the mantle gland, but it certainly cannot be so described in *Pinna carnea*, and in various respects his description does not agree with observations here recorded.

This pallial organ is divisible into a stalk and a more swollen head (described as a mucous gland by Grave). The former is faint brown in colour, the latter opaque white. Only the stalk is ciliated with scattered Alcian Blue staining mucous glands. As shown in figure 9, these cilia beat towards the mid-ventral line where material collects to be carried away in the exhalant current. In life the organ is very active, extending on occasion for the full length of the exhalant chamber. Thus in an animal 23 cm long, the pallial organ extended to a length of 10 cm with the head, which can stretch and become terminally very pointed, some 3·5 cm long.

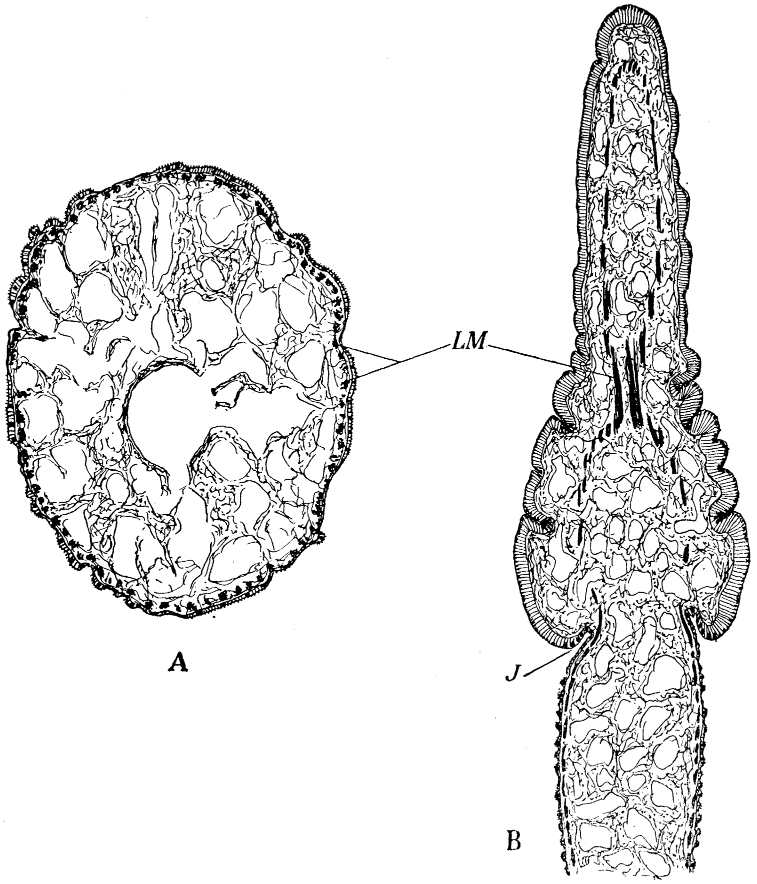


FIGURE 11. *Pinna carnea*. Pallial organ from exhalant chamber. A, transverse section through stalk. (Magn. × 20.) B, longitudinal section through head and part of stalk. (Magn. × 10.) *J*, junction between head and stalk; *LM*, longitudinal muscle. Description in text.

Transverse and longitudinal sections (figure 11A, B) reveal a marked distinction between the epithelium of the head and that of the stalk. The former is unciliated, consisting of very tall cells (up to 160μ) without stainable contents except terminally, where minute mucous glands, not more than 10μ long, occur between the ends of the epithelial cells. Most of these glands have granular contents staining with Orange G, a few stain with Alcian Blue. The epithelium of the stalk is ciliated and thrown into low folds owing to variation in the height of the cells. These are some 60μ high in the folds and often less than a quarter of this in the intervening furrows. Alcian Blue-staining mucous glands are common in the folds. Internally the organ is composed of open connective tissue with a conspicuous blood vessel, originally described by Milne-Edwards (1847) and Menegaux (1890), running up the centre. Strands of longitudinal muscle (*LM*) extend immediately under the epithelium of the stalk, but continue more centrally within the head where they reach to the tip. Structure could not be simpler to achieve the necessary result, extrusion by forcing in of blood, withdrawal by contraction of the one set of muscles which, by appropriate local action, will also cause the organ to bend in any direction.

(i) *Function of the pallial organ*

Grave, who regarded the head as a mucous gland, stated that the pallial organ seems 'to be a "swab" for the purpose of freeing the mantle of any foreign body which may lodge upon it'. He points out that much debris does enter the mantle cavity, and that this has to be raised vertically to the edge of the shell. He therefore concluded that 'structures especially adapted for this purpose are to be expected'.

Observations on *P. carnea* did not, however, suggest that the pallial organ is needed for cleansing the exhalant cavity. The exhalant current is extremely powerful (as it is also in *Atrina* according to Grave). When great quantities of sand are allowed to fall into the mantle cavity the tissues contract and the shell valves close (*no* gape being left). The accumulated sand is then gradually forced out by the action primarily of the adductor which relaxes and then contracts with sudden force. The mantle edges probably assist in this process, but there was *no* evidence that the pallial organ did so. A more probable explanation of its function has to do with repair after damage to the shell. This, as will be discussed more fully later, is a major danger to which all of the Pinnidae are exposed. When the shell is crushed, the pallial organ probably helps to clear away broken fragments of shell, sand and other debris which has fallen between the valves and lie above the withdrawn mantle and which may prevent the adductor from contracting. When the mantle is fully retracted, blood will be available for the extension of the pallial organ; conditions are comparable with those in the Tellinacea where blood can distend the long siphons *or* the large foot, but not both simultaneously (Yonge 1949). In *Pinna carnea* the pallial organ was observed to distend greatly *after the mantle had been withdrawn*, when it could, and did, range over the upper regions of the shell. When so expanded it was in a state of continual activity, and there seems no doubt that it can push fragments of broken shell from between the valves. This would enable the adductors to contract and so force out smaller fragments and permit the outer lobe of the mantle edge to start repair of the broken shell margins. When the mantle is withdrawn there will be adequate quantities of blood available to extend the pallial organ to its fullest extent and render it very turgid. Cleansing of this type, by direct pressure, not as the glandular 'swab' envisaged by Grave, seems the most probable function of this unusual organ.

(ii) *Origin of the pallial organ*

As noted by Grave, the organ 'appears from its connexions to have developed from the mantle'. It comes off at the base of the long line of pallial fusion dorsally. It could therefore represent a median unpaired posterior pallial tentacle which had migrated ventrally when the mantle edges posterior to it became fused. Such median, unpaired tentacles exist in certain Protobranchia such as *Malletia* or *Yoldia* (Yonge 1939). In structure, moreover, the epithelium of the stalk corresponds closely to that of the inner surface of the mantle, while the much taller cells without stainable contents composing the epithelium of the head are very like those of the opposed (and therefore outwardly or upwardly directed) surfaces of the middle and inner lobes of the mantle edge (see figure 8A). The major difference is the ciliation of the latter epithelium and the greater length of most (although not all) of the mucous glands which do, however, all stain with Alcian Blue. There is thus some indication that the stalk of the pallial organ represents an extension of the general surface of the mantle, but that the head is derived from the mantle edge.

IV. MODE OF LIFE

(*a*) *Habits*

The Pinnidae always live embedded vertically in soft substrata, although with enough underlying gravel to provide attachment for the byssus threads. They usually occur at some depth, but in sheltered areas, such as those between the islands of Bermuda, they may be found in shallow water, occasionally even intertidally. Little is known about development or how soon the post-larvae assume the form and habits of the adult. Certainly from the time when these are assumed the animal, if undisturbed, must remain in the same position, growing both down into the substratum and also upward into the water above. But the body itself, i.e. as distinct from the great posterior extension of the mantle/shell, will remain always embedded in the substratum. It seems unlikely that animals completely uprooted by storms can re-establish themselves. None of the animals observed at Bermuda made any attempt to do so when laid on a suitable substratum. Grave (1911) reports the same failure in the case of *Atrina rigida*, but he did find that if specimens of this species were removed and then partially reburied, anterior end downward, they were capable of burrowing. Under these circumstances water was expelled downward into the substratum from the *anterior* end of the mantle cavity, the posterior end being closed by apposition of the mantle edges. This process was repeated several times at intervals of a few seconds, and then, during a period of rest, sand and mud was removed from the mantle cavity by way of the waste canal. He reports that in this way one specimen sank to a depth of 3 or 4 in. in the course of 1 hr. Doubtless species of *Pinna* possess similar powers which will be used occasionally in the course of the normal growth and with greater force and urgency should the animal be partially dislodged by storms or perhaps by the action of other animals.

(*b*) *Feeding and respiration*

The projection of the posterior end high above the substratum, while it presents problems the solution of which is discussed later, does enable the animal to draw in clear water with little mud in suspension. This is a matter of considerable importance in view of the habitat. It also enables the powerful exhalant current to be expelled without disturbing the bottom deposits. This is shown in figure 15A. The Pinnidae are suspension feeders drawing in water over a wide area posteriorly and ventrally. The great extent of the fully extended ctenidia creates a very powerful current which, concentrated in the exhalant chamber, issues with considerable force from the exhalant aperture. The appearance when viewed from above of an animal with the valves and mantle margins fully open is shown in figure 12. The inner mantle lobe (*IM*), fringed with small tentacles, borders the margins of the inhalant (*I*) and exhalant (*E*) openings. By its extension or withdrawal the effective size of these openings can be controlled. The inhalant opening may, indeed, be completely closed by this means without the adductors contracting. This state of affairs may continue even after sand is dropped in and covers the exposed, i.e. outer, surfaces of these inner mantle lobes. Only after relatively prolonged or powerful stimuli do the adductors contract and then water, as always under such circumstances, is expelled with force through the inhalant aperture. The small size of the middle, typically sensory, lobe of the mantle edge would seem to be associated with this marked insensitiveness to external stimulation.

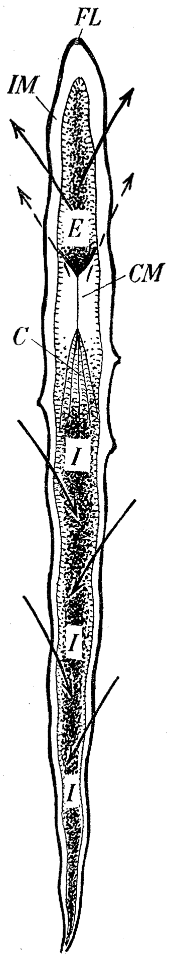


FIGURE 12. *Pinna carnea*. Viewed in life, looking down upon upwardly projecting posterior end of shell valves, animal vertically embedded in substratum. Ctenidial membrane (*CM*) seen separating inhalant (*I*) and exhalant (*E*) chambers. (Magn. × $\frac{3}{4}$.) All lettering as before.

Within the mantle cavity food particles are collected on the ctenidia in the manner already outlined and also described by Atkins (1937*a*, *b*). Apart from the extensive collecting surface and the mode of selection, also described by Atkins, there is little worthy of comment. The palps are of average size and normal in form and selective activity. The Pinnidae are able to pass great quantities of water through the mantle cavity and efficiently sieve this through the ctenidia, passing a continuous but never over-large stream of particles to the mouth. At the same time more than adequate supplies of oxygen are provided.

(*c*) *Cleansing*

This represents a major problem. The animals are vertically embedded, with the mantle lobes everywhere free from one another, and are yet incapable of avoiding adverse conditions, such as silting, by downward movement either of the entire body or of posterior siphons. Although the posterior end is raised well above the substratum this is frequently very soft, so that silt must frequently enter the mantle cavity. Moreover, as described by Grave for *Atrina*, 'burrowing' movements involve the passage of sediment into the anterior end of the mantle cavity.

The waste canal with its powerful ciliation and great concentration of mucous glands (possibly producing a very viscous mucus) certainly represents the major adaptation for cleansing. The epithelium lining the mantle cavity is seen in section to be sparsely and intermittently ciliated, but in life there is little evidence of ciliary action, and probably all particles that fall out of suspension in the inhalant current or are rejected from the surface of the ctenidia drop to the bottom (i.e. anterior end) of the inhalant chamber. There, presumably (for it is difficult to determine such matters after the mantle cavity has been opened), they accumulate to pass into the anterior end of the waste canal together with other excess material from the palps (figure 9). In the canal, mucous-laden strings are carried upwards (i.e. posteriorly) and so direct to the exterior, as shown by the broken arrows in figures 9 and 12. The pseudofaecal strings are conveyed to the end of the waste canals and so into the angle between the inner lobe of the mantle edge and the ctenidial membrane (figure 12), above which they are caught in the exhalant current and carried away.

In most bivalves, as described in a variety of cases by Kellogg (1915) and in the special case of certain Mactridae by Yonge (1948*a*), pseudofaeces are conveyed back along the ventral side of the inhalant chamber to accumulate in masses at the posterior end. Periodically such masses are ejected through the inhalant aperture or siphon following sudden contractions of the adductors. In *Pinna*, however, the process is *continuous*; there is no accumulation of pseudofaeces at the posterior, i.e. uppermost, end of the mantle cavity and cleansing contractions of the adductors are unnecessary. These do occur when great quantities of sand or mud are deliberately introduced into the mantle cavity, as they might occasionally enter in nature during local disturbance of the sea bottom. As already noted, Grave has described similar contractions in *Atrina* following the entrance of material anteriorly during 'burrowing'.

The waste canals represent specialization of a strip of pallial epithelium. No similar structures so large or of such obviously great importance to their possessors are found in other lamellibranchs, but there are various instances of mantle folds enclosing posteriorly directed ciliary currents, notably in the Mactridae (Kellogg 1915; Yonge 1948*a*), the Tellinacea (Kellogg 1915; Yonge 1949) and in *Siliqua patula* (Yonge 1952*a*). In the Pinnidae the canal consists of a double fold and is some distance removed from the ventral margin. In these respects it is unique, but not more so than are the needs for cleansing in the Pinnidae.

(*d*) *Repair of shell*

While projection of the posterior end of the mantle/shell above the soft substratum permits species of *Pinna* to draw in relatively clear water, it also exposes the stationary shell to constant risk of damage, more often probably from predatory fish than from water movements which must normally be slight in the silty areas where they live.

Repair of the shell is therefore a matter of prime importance, or, it is more correct to state, unusual powers of repairing the shell have made possible the adoption of this unusual mode of life.

In a typical lamellibranch, apart from purely marginal repair, damage to the shell can only be made good by the addition of inner shell layers secreted by the underlying surface of the mantle. In these animals the mantle margins are attached to the shell by pallial muscles and also frequently by a thick periostracum. The enormous posterior and ventral extension of the mantle in the Pinnidae, which stretches far beyond the limits set by the presence of the adductors and the former pallial attachments between these, together with the vestigial nature of the periostracum, produce a totally different condition. All the area outside that stippled in figure 2 is composed exclusively of outer, prismatic shell layer and all can be fully reformed by the mantle edge if it should be damaged. Such damage frequently occurs, and most shells, such as that shown in figure 1, show evidence of extensive repair.

Grave (1911) records that, following damage in *Atrina rigida*, strips of shell up to one-eighth of an inch wide may be added in 24 h. Repair is much quicker in *Pinna carnea* (where, incidentally, much more of the shell is exposed). Bevelander & Benzer (1948) and Bevelander (1952) note this and describe the process of shell formation. Unfortunately, no precise record was made during the short period spent at Bermuda, but certainly a strip of new shell, 3·5 cm wide, was added during the course of 3 days, and most of it may have been formed during a fraction of this time. There is no doubt that the mantle margin, i.e. the outer lobe of the mantle edge, initiates all repair as well as the addition of new shell during growth. Grave describes how in *Atrina rigida* the edge of the mantle is withdrawn and applied to the base of the notch formed by breaking the shell. Moreover, when holes were cut at some distance from the edge of the shell, the margin of the mantle was similarly withdrawn before repair began. It is the great extent to which the mantle can be withdrawn that makes this possible. What is also apparent is the capacity of the extensive area within the mantle edge (and having similar histological structure) to increase the thickness of the prismatic layer, a fact originally noted by Jackson (1890). Thus newly formed marginal shell is no more than some 130 μ thick, whereas it is at least ten times as thick in the regions where it becomes covered by the inner shell layer. Whereas in a typical lamellibranch, e.g. *Tivela* as described by Weymouth (1923), all the outer layers of the shell are laid down over a very limited area to be followed, almost immediately, by underlying layers of inner shell, in the Pinnidae this process takes place over a very wide area. The difference (and underlying similarity) between the two is shown in figure 13.

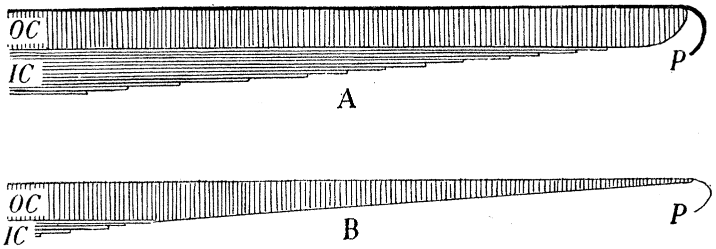


FIGURE 13. Diagrammatic radial sections from marginal regions of valves in A, typical lamellibranch; B, Pinnidae (and certain other Anisomyaria). Three constituents of valve shown, namely, periostracum (*P*) with inner (*IC*) and outer (*OC*) calcareous layers.

Shell growth in *Pinna* represents the most extreme example of what becomes possible after loss of the primary muscle (and to a greater or lesser extent also periostracal) attachments. All monomyarians belonging to the Anisomyaria have lost primary pallial attachments (apart from the posterior adductor) as described elsewhere (Yonge 1953), the Pinnidae being the one heteromyarian family to do likewise. The similar growth of the shell by periodic additions of broad, thin sheets or 'shoots' in *Margaritifera* (= *Pinctada*) *vulgaris* and in *Ostrea edulis* is described by Herdman (1903) and Orton (1928) respectively.

One probable, however incidental, effect of repeated repair of the shell is increase in strength because formation of new shell usually starts from a little distance interior to the broken edge. This eventually forms an irregular thickened and projecting ridge. Because the posterior regions of exclusively prismatic shell largely project above the substratum, they suffer little wear. Indeed, they often receive adventitious additions in the form of serpulid tubes or other calcareous encrustations. But anteriorly the shell is much abraded, especially when it is being pulled down into the substratum during growth by the action of the byssal muscles. Here the prismatic layer, originally thin because laid down when the animal was small, is often worn through to expose the underlying nacreous layer (figure 1, *N*). This is added to throughout life and so is in no danger of being perforated.

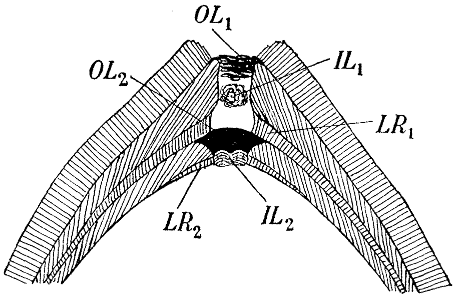


FIGURE 14. *Pinna carnea*. Transverse section through mid-dorsal region of shell showing effect of withdrawal of mantle due to injury (as in figure 15B) with consequent formation of an additional primary ligament under the original one. (Magn. × 5.) IL_1, OL_1, LR_1, inner and 'outer' layers and ligament ridge of original ligament; IL_2, OL_2, LR_2, similar constituents of second ligament.

A particularly interesting consequence of the withdrawal of the mantle when the shell is extensively damaged posteriorly is the frequent duplication, or even multiplication, of the layers of the ligament. As already noted, the absence of hinge teeth makes it possible for the mid-dorsal tissues to slide anteriorly for long distances, restrained only by the posterior adductor and the posterior pallial retractor. If such withdrawal is long continued, as it must be if the shell has been very extensively damaged, then secretion takes place under that portion of the ligament against which the tissues *now* lie. It is not uncommon among a collection of the shells of *Pinna carnea* to find the condition shown in figure 14. There, beneath a fully formed but somewhat eroded ligament composed—the fusion layer having been lost—of 'outer' (OL_1) and inner (IL_1) layers with ligamental ridge (LR_1), a new ligament composed of new 'outer' and inner layers with a new ligamental ridge (OL_2, IL_2, LR_2) has been laid down with new inner, nacreous shell layer adjacent to these. This is what must occur if the epithelium which secretes the 'outer' ligament (figures 5A and 6A, *OLM*) is drawn forward under the previously completed ligament. It will then proceed to secrete new 'outer' ligament under inner ligament formed by the epithelium of the mantle isthmus; later movement, due to regeneration of the shell posteriorly, will allow the mid-dorsal tissues to slide back again, and so the mantle isthmus will resume its former position with consequent secretion of new inner ligament. The condition at the anterior end of the shell, in the region of the anterior adductor, is usually most complex, showing indications of many series of such 'ligaments' due to repeated withdrawals of the secreting epithelia during early life.

It is interesting to note that Schmidt (1923) describes in three species of *Pinna* the presence of clear layers of shell which cover areas of the nacreous layer dorsally. He regards these as a result of degeneration of nacreous material due to the juxtaposition of the posterior adductor and representing a process of crystallization in the unorganized secretion *outside* the cells. He observed that the crystals were disposed perpendicular to the surface. In view of what is described above, there is no doubt that what Schmidt considered to be a fourth shell substance represents secretion of prismatic layer over nacreous material owing to enforced withdrawal of the distal mantle tissues. Such secretion may occur dorsally, on either side of the ligament, which is where it is figured by Schmidt.

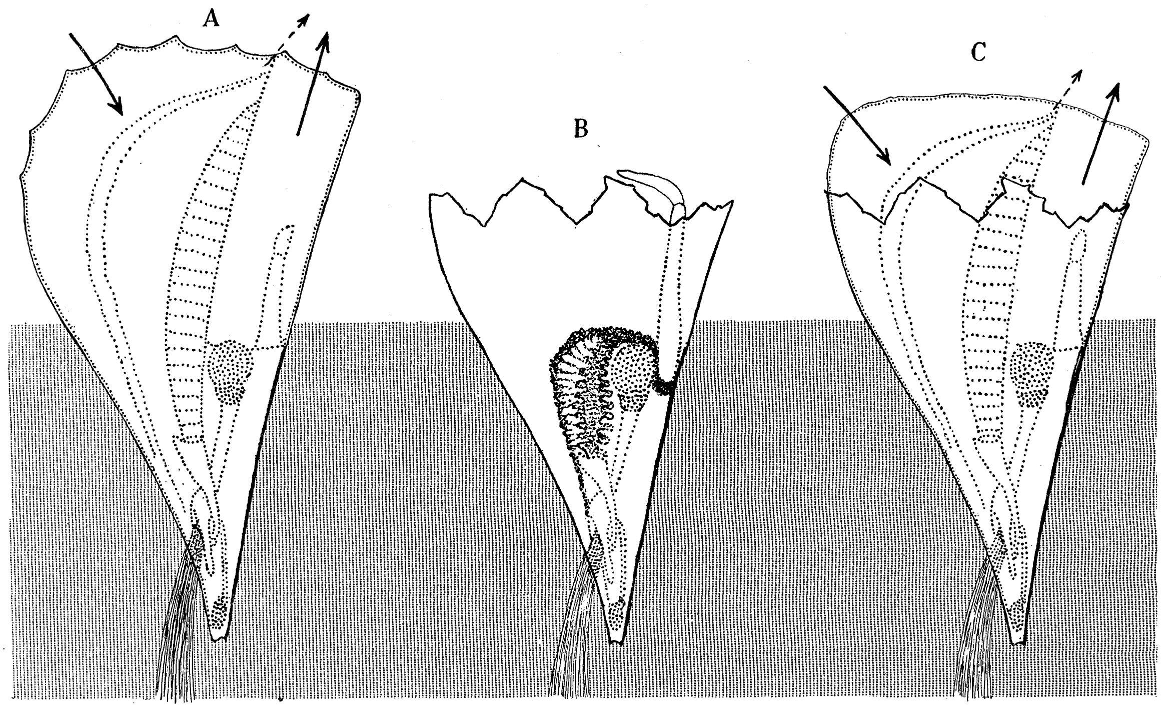


FIGURE 15. Pinnidae. Diagrams indicating effects of damage and mode of repair. A, animal *in situ* and functioning (chief organs within shell indicated by dotted outlines); B, immediate effects of extensive damage to protruding valves, i.e. mantle and ctenidia fully withdrawn due to contraction of anterior and posterior pallial retractors (shown in figure 7) while pallial organ distended and probably actively clearing away shell fragments, etc. from between valves; C, valves in process of repair by outer lobe of mantle edges, additional layers of primary ligament laid down under posterior end of primary ligament, mantle with attached ctenidia extended and animal already functioning normally. Soft substratum in which anterior end of animal embedded shown stippled.

A probably not infrequent sequence of events in the life of any species of the Pinnidae is indicated in figure 15A to C. An intact animal is shown in A, the body, it will be noted, being contained in the anterior half of the shell which is buried. Upward projection of the posterior half enables water and food to be drawn in freely, well clear of the bottom. The result of extensive damage to this region of the shell is shown in B. The mantle has withdrawn together with the posteriorly extended ctenidia which are attached to it. Possibly the only part of the body now active is the pallial organ in the exhalant chamber which does project under such conditions and can then range widely over the posterior surface, probably pushing away fragments of shell which have lodged between the valves. As soon as the mantle edges are able to extend again they will do so and bring about rapid reformation of the shell valves marginally, including reformation of the fusion layer. The latter process was actually observed to accompany that of shell formation and at the same speed. The mantle will extend posteriorly with the same rapidity that it reforms the shell. In turn this will permit the further extension of the ctenidia which can, however, presumably function even when not fully extended. The final and probably very speedy result will be complete reformation of the broken regions of the shell, although with the line of the fracture persisting in the form of an irregular, projecting ridge across the surface of each valve.

V. Discussion: form and evolution in the pinnidae

As the foregoing account has shown, the Pinnidae have many unique features of structure and have also a mode of life peculiar to themselves. In continuance of previous studies of a similar nature (Yonge 1952*a*, *b*, 1953), an attempt is here made to follow the possible course of evolution which has resulted in the present structure and made possible existing habits.

In the Lamellibranchia the laterally compressed mantle/shell completely encloses the body and assumes major responsibility for growth and form (Yonge 1953). Changes in the form of the mantle/shell, the result of alterations in the growth gradients around the margin of the mantle lobes, influence the arrangement, although not significantly the proportions, of the body. This is well exemplified in the Solenidae (Yonge 1952*a*, 1953). Changes in the proportions of the body are associated with the attachment of this to the substratum by means of a byssus, which is the primitive method of such attachment. Changes of this character have occurred throughout the Order Anisomyaria, all members of which are either heteromyarian or monomyarian (Thiele 1935). Here it is the proportions of the body which are primarily affected, the form of the mantle/shell being influenced, at any rate initially, as a secondary consequence.

Such changes in form and proportions are best discussed by reference to the two major axes in the sagittal plane, namely, the antero-posterior and median axes of the body (figure 16, *AX*, *MX*) and the hinge and normal axes of the mantle/shell (*HX*, *NX*). The antero-posterior axis (Jackson 1890) is represented by a line drawn between the mouth and the middle of the posterior adductor; the median axis (Yonge 1953) by a line running from the mid-dorsal point of the body through the middle of the base of the foot to the mid-point ventrally of the foot (or byssus). The hinge axis is described by Jackson (1890) as the axis of motion of the valves; the normal axis (Owen 1952; Yonge 1953) is represented by a line running from the umbones dorsally through 'the point where the greatest transverse diameter of the shell intersects the surface of the valves' (Owen 1952) to the normal zone of the mantle edge ventrally. This zone—which is not necessarily the region of greatest marginal increment—is that portion of the generative curve of the mantle/shell where the transverse, as contrasted to the radial, component of shell growth is the greatest. It should be noted that the mid-dorsal point of the body is considered to be the middle of the mantle isthmus, while that of each valve of the mantle/shell is the umbo. The two do not therefore necessarily coincide.

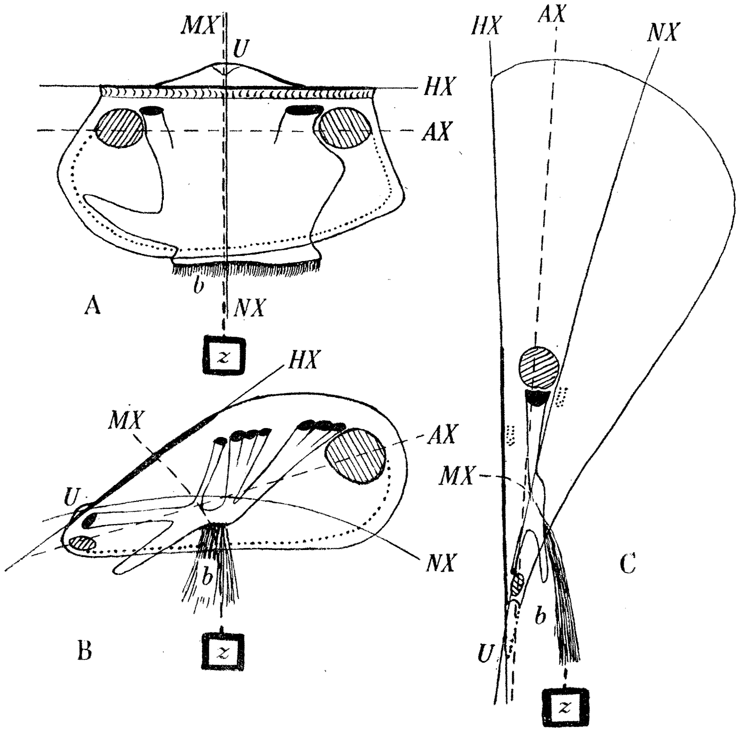


FIGURE 16. Comparison, in terms of major axes in the sagittal plane of both body and mantle/shell, between A, *Arca*; B, *Modiolus*; C, *Pinna*. All attached by byssus (*b*) to substratum (*z*) the foot therefore representing the one fixed, ventral, point. Axes of body represented by broken lines, *AX*, antero-posterior axis; *MX*, median axis. Axes of mantle/shell represented by complete lines, *HX*, hinge axis; *NX*, normal axis. Position of pallial attachments (other than anterior and posterior adductors) shown dotted.

On this basis it is possible, as shown in figure 16, to consider the form of *Pinna* (C) in comparison with that of two other bysally attached genera, the dimaryian *Arca* (A) and the heteromyarian *Modiolus* (B). In all three the foot with its associated byssus remains as a fixed point in relation to the substratum (*z*). In *Arca* original symmetry is unchanged, the antero-posterior axis of the body and the hinge axis of the mantle/shell retaining their normal relation, i.e. parallel to one another (Yonge 1953). The median axis of the body and the normal axis of the mantle/shell effectively coincide and are at right angles to the other two axes. In *Modiolus* the anterior half of the body is reduced, the median axis no longer dividing the animal into two very similar portions, while the antero-posterior axis is inclined to the substratum owing to reduction of the anterior half of the body. Secondary effects on the mantle/shell (fully analysed elsewhere, Yonge 1953) have as consequences an even greater tilting of the hinge axis, so that it is no longer parallel with the antero-posterior axis. Moreover, the normal axis diverges widely from the median axis which it crosses, both dorsal and ventral ends of these two axes being widely separate (figure 16B). The curvature ventrally of the normal axis is due to a tangential component in mantle/shell growth which is present in some genera (most obviously in *Glossus* (*Isocardia*) and *Chama*), in addition to the radial and transverse components (Owen 1952).

In *Pinna*, although contact with the substratum has been maintained by way of the unusually massive byssus, the position of the animal in relation to this has changed. It is now vertically disposed with the long, i.e. antero-posterior, axis of the body parallel to the direction of byssus threads instead of at right angles to these as in *Arca* or at an angle of about 75° as in *Modiolus*. This change is possible because the Pinnidae attach themselves not to hard but to soft substrata, in which the anterior part of the animal can and does become embedded. The form of the body (i.e. neglecting the great posterior extension of the mantle/shell) is not unlike that of *Modiolus*, the median axis (*MX*) dividing the body into very similar reduced anterior and enlarged posterior regions, and having very similar relations to the antero-posterior axis (cf. figures 16B and 16C).

It is in the form of the mantle/shell that these two heteromyarian genera differ. It appears reasonable to assume that during the course of evolution the Pinnidae passed through what may be described as a 'Modiolus stage'*, i.e. heteromyarian but with the posterior adductor near to the posterior margin of the shell and little secondary extension of the ligament posteriorly. Further evolutionary change would seem to have involved migration still further anteriorly of the umbones (cf. figures 16B and C, *U*) and a loss in shell growth of any tangential component (if such ever existed). Thus the normal axis, originally at right angles to the hinge axis (as in *Arca*) has swung round until it is now only separated from it by an angle of some 12° (figure 16C, *HX*, *NX*). Meanwhile great posterior extension of the mantle/shell doubled the length of the animal and made possible the great posterior extension of the secondary ligament formed by the fusion layer.

It would therefore appear that up to the 'Modiolus stage' the form of the animal is primarily influenced by changes in the proportions of the body associated with byssal attachment. Later the mantle/shell may be regarded as reassuming control of growth and form. Evolution within the Order Anisomyaria may be considered from this standpoint. Thiele (1935) divides this Order into five groups, the stirps Mytilacea, Pteriacea, Pectinacea, Anomiacea and Ostreacea. Of these the first is composed exclusively of heteromyarian genera, the second and third of monomyarian genera, except for *Pinna* and *Dimya* respectively, while the two last are exclusively monomyarian. The Mytilacea comprises animals in the 'Modiolus stage' or its further development into *Mytilus* where the umbones are terminal. In all the mantle is firmly attached to the shell both by pallial muscles (figure 17A) and by an extremely stout periostracum. In the other four groups the form of the animal has been profoundly altered by the agency of the mantle/shell. In the Pectinacea (except for *Dimya*), Anomiacea and Ostraecea, the body has been reorganized around the now solitary and central adductor, as outlined elsewhere (Yonge 1953). Secondary pallial attachments occur in the Pectinacea and the Ostreacea but not in the Anomiacea (*Anomia* and *Placenta*). In this respect the Anomiacea resemble the Pteriacea where the greatest variety of form exists. Some examples are shown in figure 17

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* But presumably *without* any tangential component in shell growth.

where *Pedalion* (*Perna*) (B), *Pteria* (*Avicula*) (C) and *Malleus** (D) are compared with *Pinna* (E) as well as with *Modiolus* (A). Pallial attachment is confined in *Pedalion* and *Pteria* to the adductor together with a series of individual muscle bundles anterior to this. In *Malleus* and *Pinna* it is confined to the one or two adductors respectively and also the single pallial retractor in *Malleus* (figure 17D, *pr*) and the pair in *Pinna* (see figure 7).

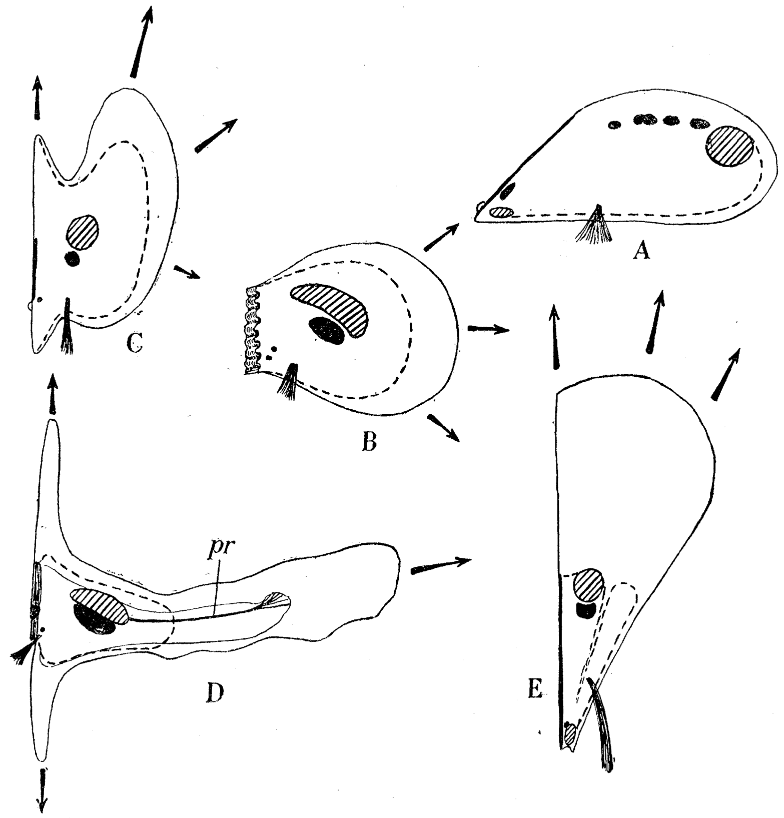

FIGURE 17. Examples of various types of shell form in the Pteriacea (Anisomyaria) due to different modes of growth of mantle/shell and associated with loss of pallial attachment (apart from adductors). Extent of inner, nacreous shell layer indicated by broken line, byssus indicated, also adductors (cross hatched) and pedal retractors (solid black). A, *Modiolus* (Mytilacea) for comparison; B, *Pedalion* (*Perna*); C, *Pteria* (*Avicula*); D, *Malleus*, *pr*, pallial retractor (after Kühnelt); E, *Pinna*. Arrows indicate regions of greatest growth around generative curve of mantle edges.

In all of these genera therefore (and this is generally true of the Pteriacea) the mantle may retreat far from the margin of the shell and periostracal strands are thin and discontinuous. In all, although most conspicuously so in *Malleus* and *Pinna*, the area of the valves covered by inner, nacreous shell layer is very limited (see broken lines in figure 17) being surrounded by a broad marginal area composed exclusively of outer shell layer. This is added to, as already noted, by the sudden addition of 'shoots'.

In *Pedalion* (B) the growth gradients around the margins of the mantle lobes are such as to produce a rounded shell valve. This is also true of the pearl oyster, *Pinctada*, but in

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* *Pedalion alata* was examined alive at Bermuda in 1951, preserved specimens of *Pteria hirundo* and of *Malleus albus* were obtained respectively from the Stazione Zoologica, Naples, and from the British Museum (Nat. Hist.), the latter through the kindness of Dr W. J. Rees.

the closely allied *Pteria* (C) the major effect is increase in length posteriorly. In some species elongation is much greater than in the species here figured (*P. hirundo*). In *Malleus* mantle growth proceeds in three directions, opposite to the hinge (not strictly ventral; the foot and byssus are ventral), and on either side of the hinge line, forming the ends of the 'hammer head', as shown in figure 17D. This is due to the presence of three growth centres around the mantle margins. Finally, in *Pinna* (E) extension of the mantle is exclusively posterior; there is actually a reduction of the anterior end during growth (figure 19).

What is known about development in *Pinna*, unfortunately but little, helps to substantiate these evolutionary speculations. Relationship to the Mytilacea is indicated in the larva followed by great posterior extension of the shell in the post-larva and adult. As most recently and fully described by Rees (1950), the veliconch shell (prodissoconch II) of the veliger larva is characteristically hinged in different groups of lamellibranchs. Bernard (1898) described the somewhat triangular shaped veliconch of *Pinna*. The hinge, i.e. ligament and dentition, is similar to that of the Mytilacea as described by both Bernard and Rees. Borisiak (1909), who appears to be the only worker to have examined a complete larva and not merely the shell, states that it is somewhat heteromyarian. Both Bernard and Borisiak regarded the triangular shell of the veliconch, as in some measure related to or influenced by the form of the future adult, but it is only slightly inequilateral. However, as shown clearly in figure 18, where figures by Lynge (1909) are reproduced, when the adult, or dissoconch, shell is formed the outline completely alters. New shell is added almost exclusively to the posterior margin, and the form of the adult shell appears to be attained very quickly in the post-larva. Both Bernard and Borisiak note that the dissoconch shell has a prismatic structure not present in the veliconch. This now actually invades the inner surface of the prodissoconch shell (Bernard). Thus there is an abrupt change at metamorphosis in both the form and structure of the shell valves. It is at this stage, one must assume, that the outer lobe of the mantle edge begins to secrete the outer calcareous layers of the valves of the adult.

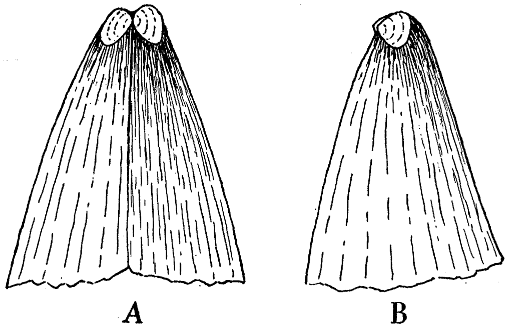

FIGURE 18. *Pinna* sp. Anterior end of young shell showing the veliconch and the great extension posteriorly of the dissoconch shell, the latter secreted by the outer lobe of the mantle edge. A, viewed from dorsal aspect; B, from right side. (Magn. × 5.) (After Lynge).

It follows that the form of the adult shell will depend on the manner of growth of the mantle margins, i.e. on the disposition of growth gradients around the generative curve. The eventual result of their activities, in the case of *Pinna*, is illustrated diagrammatically in figure 19. The normal axis has swung round so far posteriorly that growth may be considered in terms of length and is divisible into four regions. Anteriorly (figure 19, 1–2) there is progressive loss of shell, the mantle tissues retreating in a manner possibly only paralleled in the case of the 'fresh-water oyster', *Acostaea* (*Mulleria*), where, however, the anterior adductor itself is lost (see Yonge (1953) for description and references). The

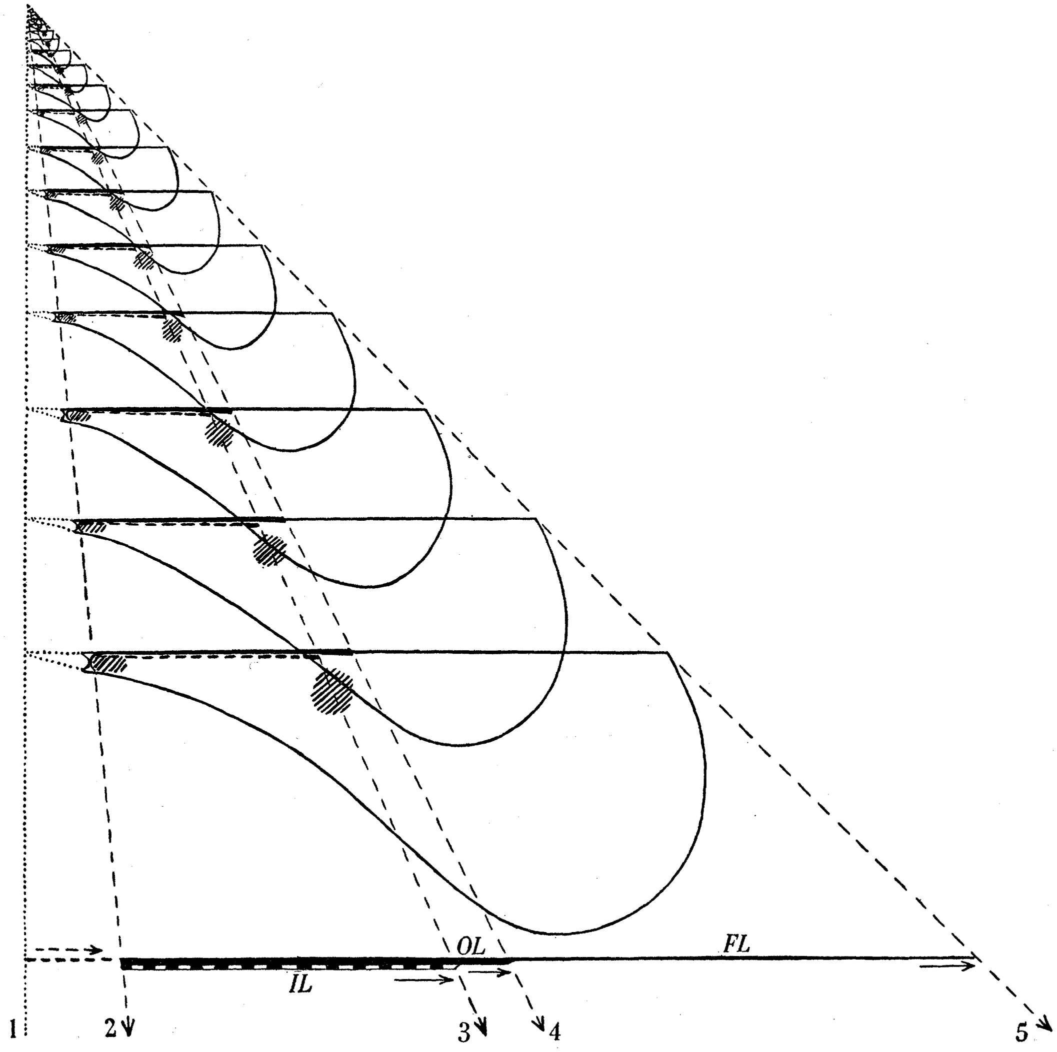

FIGURE 19. *Pinna*. Diagrammatic representation of growth after assumption of adult form in post-larva. 1, dotted line indicating original anterior end (and position of umbo); 2, broken line indicating actual position of anterior end, also beginning of ligament; 3, broken line indicating posterior end of mantle isthmus and inner ligament (*IL*); 4, broken line indicating posterior end of 'outer' ligament (*OL*) and so of primary ligament; 5, broken line indicating posterior end of fusion layer (*FL*) and so of secondary ligament. Thus, 1–2 = loss anteriorly during growth; 2–3 = increase in length of inner ligament; 3–4 = increase in length of 'outer' ligament; 4–5 = increase in length of secondary ligament. The continual extension posteriorly of the 'outer' ligament under the fusion layer and of the inner ligament beneath both is also shown.

second region (2–3) consists of the mantle isthmus which secretes the inner ligament (*IL*), the third region (3–4) is that of the outer mantle epithelium which secretes the 'outer' ligament (*OL*), and the fourth region (4–5) that of the fused outer lobes of the mantle edge which secrete the fusion layer (*FL*). The progressive stages in form during growth of the adult shell are shown in figure 19. This indicates no alteration other than in size, the proportions of the different regions probably remaining constant from very early age. The length of time taken for the adult form to be assumed by the post-larva, i.e. after the outer lobe of the mantle edge takes over responsibility for form, is unknown, but judging from what occurs in other bivalves the process may be quick, and the more unusual the form, and the habit, of the adult, the quicker would metamorphosis seem to be completed. This is well exemplified in the wood-boring Teredinidae. The young *Pinna* presumably make rapid change of habits as well as of form, but nothing appears to be known about early stages in the life history.

Winckworth (1929) refers to the posterior direction of growth with the prodissoconch initially at the apex as 'unique among bivalves' and 'as bound up with the peculiar character of the animal: the animal must move bodily upward in its shell as it grows, and with it both adductor muscles move onward posteriorly; the empty anterior end of the shell is soon worn away by friction as the growing shell burrows; the mantle produces new shell ends to protect the anterior adductor muscle at each growth stage, in consequence the anterior end of the shell shows a series of loculi formed by these temporary shell ends. The posterior adductor moves upward along a widening scar'. He adds that 'Such a top-heavy shell finds its best mechanical support in its embedded habitat'. This is certainly true; only in such a habitat could the Pinnidae exist. A few of the diverse forms assumed by members of the Pteriacea have already been mentioned and are shown in figure 17. All may best be regarded as consequences of different types of growth gradients around the generative curve of the mantle lobes. Each in its different way has proved successful, for attachment to various types of hard substrata in the cases of *Pedalion*, *Pteria* and *Malleus*, but to soft substrata only in the case of the Pinnidae.

The success of these animals is due in part to characteristics shared with other Pteriacea, in part to features unique to themselves. The former include great extension of the mantle lobes with freedom from pallial attachment. Shell can be added with spectacular rapidity. Jackson (1890) regarded the Pinnidae 'as a degradational group because of the great development of prismatic cellular tissue and loss of nacreous tissue (a weakening character), loss of teeth on the hinge line, and relatively large development of the anterior adductor muscle (a larval character, highly reduced or wanting in the ascendant series of related groups)'. However, so far from weakening, the exclusively prismatic character of the posterior half of the shell makes possible rapid and repeated repair which—although perhaps rather incidentally—actually increases the strength of the shell. Loss of teeth is due to the great posterior extension of the hinge line—to a greater extent only than in other Pteriacea—and this loss has made it possible for the mid-dorsal tissues to be withdrawn during repair. Retention of the anterior adductor is associated with vertical erection in a soft substratum; functionally it is of little or no value. Pallial extension also involves lengthening of the ctenidia and so creation of the necessary powerful water currents (the exhalant current is of unusual force in the Pinnidae). Ctenidia are so extended in all Pteriacea and are also characteristically muscular (Atkins 1943).

The features peculiar to the Pinnidae are especially, as noted by Winckworth (1929), the waste canal and the pallial organ. The former is an essential structure. The Pinnidae could not exist as they do without it. It does, however, represent the ventral rejection tracts present in the mantle cavity of other lamellibranchs; difference is in degree of development, involving continuous, instead of intermittent, rejection. The pallial organ is unique and possibly all-important. Its function, however, is certainly not clearance of sand and other fine particles from between the valves; this can be done by contraction of the adductors aided by the powerful exhalant current. But probably this organ is of supreme importance in shell repair when, the mantle being contracted, much of the blood can be transferred into the sinuses of the pallial organ rendering it long and relatively turgid. In origin it is possibly an enlarged median tentacle.

On the other hand, the pallial gland may not be present in all species and both its functions and importance remain uncertain. Its origin is obscure; only its position, in association with the base of the waste canals, is obviously advantageous. Finally, the pallial retractors demand mention. The posterior retractor is certainly a secondary structure and so probably is the anterior retractor. But similar muscles exist in other Anisomyaria. In *Malleus* (figure 17D, *pr*) one such retractor occurs. In the Pectinacea and Ostreacea the mantle is everywhere attached, near to its margins, by muscles which encircle, but are nowhere associated with, the solitary and centrally placed adductor which represents the posterior end of the primitive semicircle of pallial attachments. The presence of these secondary pallial attachments is associated with the great extension of the mantle/shell.

This extension has brought about a corresponding posterior extension of the ligament. Primary and secondary ligaments are in a straight line. Nevertheless, the Pinnidae have *functionally no ligament*, if by this is meant a structure capable of supplying an opening thrust which separates the valves. The latter gape posteriorly, but, owing to their high organic content, are sufficiently flexible to be drawn together when the adductors contract. The Pinnidae may be regarded as tapering funnels open, apart from the anterior extrusion of the byssus and occasionally of the foot, only at the posterior end. So long as attachment is maintained and the shell valves can gape posteriorly, the animals can withstand great damage. Thus Jackson (1890) described a specimen of *Atrina saccata* in which the ventral as well as the dorsal borders of the valves were united so that a tubular shell was produced resembling that of *Aspergillum*. Stenta (1927) has given a very full account of a specimen of *Pinna nobilis* in which the apex of the shell, including the anterior adductor, was destroyed. Lobes of the mantle secreted an effective partition of shell which closed the anterior end and, with no more serious consequences than in this case of *Atrina saccata*. Loss of the anterior adductor Stenta thought was made good by attachment of the byssus to the right valve. There is, however, nothing to prevent the animal functioning normally without this adductor so long as the body is not seriously mutilated and the valves can gape posteriorly and the normal feeding and respiratory currents be maintained. In a typical lamellibranch the hinge and the adductor apparatus must function efficiently or the animal will die; in the Pinnidae all that is necessary is that the posterior adductor should be able when necessary to pull together the posterior margins of the valves.

The Pinnidae are unique in form and habit, but their success in exploiting this habit can most reasonably be attributed to modifications in the form of the mantle/shell following byssal attachment in a 'Modiolus stage'. These modifications have taken various forms in the Pteriacea in particular and the Anisomyaria in general. They do *not* represent adaptation to environmental conditions but a series out of a wide variety of possible forms. These particular forms have been selected because each does permit of habits suitable for life in some particular existing environment. The Pinnidae have no more been adapted for life attached by byssus threads in a soft substratum than have, for instance, certain of the Pectinidae been specially adapted for swimming (Yonge 1936) or the Solenidae for vertical movements within unstable sands (Yonge 1952*a*). In all cases the form has made possible the habit and so the exploitation of the habitat.

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