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Form and Evolution in the Anomiacea (Mollusca: Bivalvia)--Pododesmus, Anomia, Patro, Enigmonia (Anomiidae): Placunanomia, Placuna (Placunidae Fam. Nov.)

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FORM AND EVOLUTION IN THE ANOMIACEA (MOLLUSCA: BIVALVIA) – *PODODESMUS*, *ANOMIA*, *PATRO*, *ENIGMONIA* (ANOMIIDAE): *PLACUNANOMIA*, *PLACUNA* (PLACUNIDAE Fam. Nov.)

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A comprehensive survey of the superfamily Anomiacea is based on an initial study of *Pododesmus* which proves to be the most primitive living genus. Retention of the genus *Monia* cannot be justified, its species should be associated with those of *Pododesmus*.

The evolution of this highly specialized superfamily is traced by way of stages represented by 'anisomyarian' heteromyarians such as the modern Mytilacea and then monomyarians inclining to the right like the modern Pteriacea. Complete twisting of the hypertrophied byssal apparatus to the right accompanied by development of a deep byssal notch in that valve results in the assumption of a pleurothetic habit with intimate attachment by way of a calcified byssus. The left posterior byssal retractor displaces the original adductor which assumes a restricted role in shell closure.

The presence of the deep notch immediately anterior to the ligament (its position due to the monomyarian condition which involves loss of the anterior regions of the body) is responsible for major asymmetries in the ligamental region. The resilifer on the right valve becomes restricted to a stalked crurum, the corresponding surface on the other valve being sessile. So that it may extend over the smaller under valve, the left valve is increased dorsally as a result of supradorsal extensions of the mantle lobes at both ends of the ligament. An extent of fused shell displaces the umbo from its marginal position. Supradorsal shell secretion on the right valve does not extend that valve beyond the dorsal surface of the crurum. The final effect is the loss of a true marginal hinge, the left valve being pulled downward over the smaller right valve, the ligament vertically instead of laterally disposed.

This supradorsal extension involves the epithelia which secrete the anterior and posterior outer ligament layers which now curl back over the dorsal side of the inner ligament layer formed by the mantle isthmus. In *Pododesmus* there is no fusion of these supradorsal pallial extensions, although the shell they secrete *does* fuse. Later the tissues withdraw and the exposed upper surface of the ligament breaks down together with the supradorsal area of fused shell on the left valve. The manner in which the very dissimilar valves develop is followed.

Except in very young, unattached animals, the long, bulbous-ended and very mobile foot is exclusively concerned with cleansing. In addition to the hypertrophied left posterior retractor, there are small right and left anterior retractors, the former attached to a depression at the base of the somewhat convex crurum. Pallial tissue extends dorsally under this to form a characteristically upward pointing subcrural groove.

The pallial organs and ciliary currents are described. The ctenidia are separated anteriorly by the intervening mass of the byssal apparatus, the right proximal oral groove prolonged to pass round this to the mouth. There are very large hypobranchial glands.

Heteranomia is distinctive in the possession of unreflected ctenidial lamellae and in the complete fusion of the supradorsal pallial extensions. The reduction of the already small area of union between its mantle lobes involves the secondary extension of this by fusion of the inner folds of the mantle margins above the ligamental area and extending over much of the exhalant chamber. A subcrural groove is present but is usually reduced and rounded. There are no hypobranchial glands and no anterior right retractor, the crurum is horizontal.

Anomia resembles *Heteranomia* in the last respects, although there is no subcrural groove, and in complete supradorsal fusion. But the ctenidial lamellae are reflected and the ctenidia are asymmetrically divided anteriorly, three demibranchs being associated with the left pair of labial palps and only one with the other. Secondary pallial attachment dorsally is exclusively by way of the inner mantle fold of the right side which fuses with the mantle surface *within* the line of the corresponding folds on the left mantle lobe. *Patro*, of which shells only were available, appears very similar but has a smaller byssal notch and so a more restricted area of attachment probably projecting from the surface to which it is attached.

Enigmonia is a bivalve limpet which occurs on mangroves and other coastal vegetation in southeast Asia. It lives immobile on curved surfaces, such as stems, but also as flat mobile individuals on the lowest leaves of these trees. Only the latter were studied.

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This is a highly modified anomiid differing from *Anomia* in the elongate form and in the absence of calcification in the byssal secretion although this remains of supreme significance for 'temporary' attachment which may extend for periods of up to 10 days when some of these animals may be continuously exposed. The foot becomes again an organ of locomotion pulling the animal along, anterior end foremost, by means of a long creeping sole. It terminates in a unique, probably sensory, flagellum. The general surface (not the margin) of the left mantle lobe, covered by the thin, very translucent upper valve, carries a variable number of very simple 'eyes'.

The genera *Pododesmus*, *Heteranomia*, *Anomia* with *Patro* and probably allied genera not seen, together with *Enigmonia* are regarded as constituting the family Anomiidae, the contrasting characters of the genera being listed in table 1.

A small number of shells with only one small preserved specimen were all that were available for the study of the most interesting genus *Placunanomia* found exclusively off the Pacific coast of central America from Baja California to Equador. The typically plicated shell is much thicker than that of other Anomiacea. Cementation to the substrate must stop at a stage when the right valve ceases to be adpressed to the substrate and begins to assume the adult form. The walls of the opening into the byssal notch then unite and the calcareous byssal plug fuses with the surrounding margin of the byssal notch so that all is 'shell' and intimately united with the substrate. Associated with this, the crurum becomes sessile and the ligament more bilaterally symmetrical. Some initial supradorsal shell fusion is soon worn away during growth. Although in other ways so much more complex, *Placunanomia* retains primitive characters present in *Pododesmus*, notably hypobranchial glands and ctenidial characters including symmetrical separation of the demibranchs anteriorly.

In species of *Placuna*, the extremely flattened window pane shells that live unattached on the surface of mud flats, the byssal notch is only present in the post-larva. With the loss of the byssal apparatus, the pallial organs regain bilateral symmetry while the adductor moves back to a central position and resumes sole concern with closing the valves. There is a ∧-shaped primary ligament obviously similar to that in *Placunanomia*. This is *not* marginal and to meet the needs of a free-living bivalve, a new hinge line is created by extensive dorsal fusion of the mantle lobes to form a dorsal crest. This involves union of the periostracal grooves with formation of a secondary periostracal ligament which unites the valves dorsally and maintains them in alignment. The primary ligament provides a powerful opening thrust.

Although clearly the products of diverging lines of evolution, *Placunanomia* and *Placuna* have much in common. Although all members of the same superfamily, these two genera differ in notable respects from the Anomiidae, especially with regard to the byssal notch with resultant effects on the ligament and the crurum. In *Placuna* (conditions are unknown in *Placunanomia*) visceral asymmetry is also different. These two genera are here associated in the Family Placunidae, its major characteristics listed in table 2.

The extraordinary course of evolution within the superfamily Anomiacea is discussed and the applicability noted of Dollo's law of the irreversibility of evolutionary change. Basic anomiacean characters are listed stressing the unique capacity for byssal cementation. While this is retained in members of both diverging families, evolution in one leads to epifaunal mobility with loss of calcification in the byssus and the foot re-employed as an organ of locomotion permitting exploitation of a restricted and extreme environment. The other leads to complete freedom with secondarily almost symmetrical valves united by a new hinge line and a secondary, periostracal, ligament but completely without mobility, the foot remaining restricted to its cleansing functions within the mantle cavity. Nevertheless species of *Placuna* are extremely numerous on muddy substrates over wide areas of the tropical Indian Ocean. This is among the most successful of all bivalve genera.

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INTRODUCTION

In studies of bivalve superfamilies of which this paper is a continuation, attention has first been given to more generalized genera and then to those specifically adapted for particular habitats. Radiating adaptation, resulting in repeated instances of convergence with similarly adapted members of other superfamilies, occurs in all of the larger superfamilies. The very distinctive superfamily Anomiacea constitutes one of the five divisions of Thiele's (1935) Order Anisomyaria and of the four divisions in Newell's (1965) suborder Pteriina (he rightly excludes the Ostreacea).

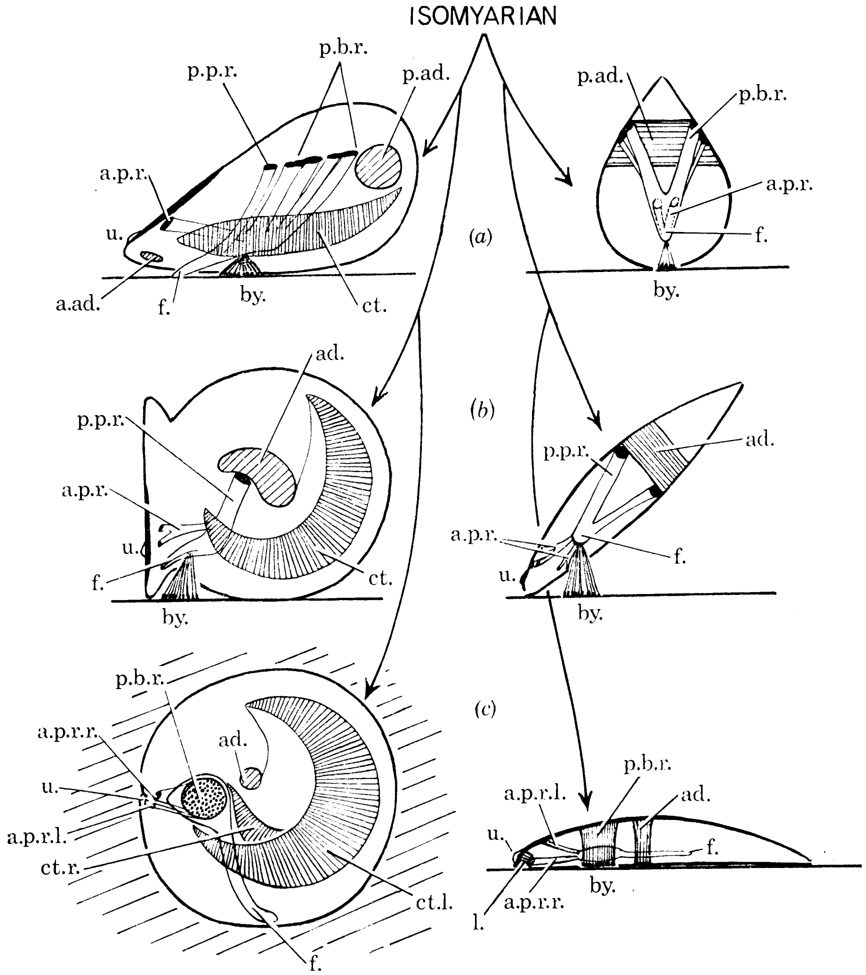

FIGURE 1. Evolution of monomyarianism in the 'Anisomyaria' leading to conditions in the Anomiacea. (*a*) Heteromyarian condition (vertically disposed, equivalve) as in Mytilacea; (*b*) initial monomyarian condition (inclined to right, slightly inequivalve) as in Pteriacea; (*c*) extreme monomyarian condition (right valve adpressed to substrate, cemented by calcified byssus, extremely inequivalved) in Anomiacea. Figures on *left* show animals viewed from left side, those on *right* viewed from posterior end. For key to lettering on this and on subsequent figures see p. 523.

While the degree of association between the superfamilies concerned is certainly not great, they do, as indicated in figure 1, represent a sequence. Certain early, and therefore isomyarian, bivalves in which the byssus had been neotenously retained (Yonge 1962) gave rise to heteromyarians such as the Mytilacea (figure 1*a*) where, as in *all* heteromyarians, prior byssal

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attachment was followed by enlargement of the posterior regions of both mantle/shell and enclosed visceropedal mass with corresponding reduction in the anterior regions (Yonge & Campbell 1968). Although so inequilateral, as indicated by the relative sizes of the anterior and posterior pedal (and byssal) retractors, these bivalves remain bilaterally symmetrical (i.e. equivalve) and vertically disposed.

Further evolution along these lines – of course from different origins – led to loss of the anterior adductor and reorganization of the visceropedal mass around the centrally placed posterior adductor. There was accompanying lateral compression, the animals tending to fall over on to the right side with the byssus emerging through a small embayment in that valve; the pedal retractors also becoming asymmetrical (cf. figures 1*a* and 1*b*), i.e. not only are the posterior pair the larger as in the Mytilacea, but the left members of each pair are larger than the right members. This is the general condition in the Pteriacea, as exemplified by the pearl oyster, *Pinctata*. This evolutionary trend is taken further in the Pectinacea (scallops) which are all horizontally disposed (pleurothetic), lying always on the right side, with resultant greater bilateral asymmetry. Both anterior pedal muscles are lost and also the right posterior retractor. All Pectinacea – now excluding *Plicatula* (Yonge 1975) – begin life byssally attached, some retain such attachment, some become free (e.g. *Pecten*, *Amussium*), others become cemented (*Hinnites*, *Spondylus*).

If the Pectinacea represent further evolution along the same lines as the Pteriacea, so do the Anomiacea (figure 1*c*) although here the basic habit (in the 'saddle oysters' or 'jingles') is a unique form of byssal cementation. The byssal embayment in the right valve extends towards the centre of the valve, the animals becoming adpressed to a hard surface to which they are permanently attached by way of a greatly enlarged and calcified byssus which emerges at right angles to the sagittal plane.† There is striking asymmetry of both mantle/shell and visceropedal mass. The massive posterior byssal (pedal) retractor (figure 1*c*, p.b.r.) takes over much of the function of the reduced adductor (ad.).

Such animals would appear just as much irrevocably committed to one highly specialized mode of epifaunistic life as are the Ostreacea or *Plicatula*. However, unlike those bivalves, the Anomiacea (like the also cemented *Hinnites* and *Spondylus*) retain the foot as a highly efficient organ for cleansing the mantle cavity. This, with the ability to reduce and eventually to lose byssal attachment with formation of a new, secondary, hinge line, is a crucial factor controlling adaptive radiation within this superfamily. Together these have been responsible for the evolution of the limpet-like and sometimes crawling *Enigmonia*, the relatively massive *Placunanomia* where, after initial secure cementation, further byssal secretion ceases to be applied to the substrate, and the somewhat related free, yet immobile, 'window pane' shells of the genus *Placuna*. This paper, based as far as possible on observations on *living* animals, represents an assessment of all information, the most significant of which revealed as concerned with the ligament, relevant to the elucidation of the modes of evolutionary change in the Anomiacea.

The saddle-oysters, characteristic members of the epifauna on rocky intertidal and shallow water surfaces in many parts of the world, belong to the genera *Pododesmus* (incorporating *Monia*) *Heteranomia*, *Anomia* and *Patro* with others not seen. Distinctions previously reported between them – here to be increased – are slight, largely a matter of the number of muscle scars on the upper valve although the ctenidia in *Heteranomia* are reduced to a single lamella in each demi-

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† Thus, unlike other byssally attached bivalves, detachment and later re-attachment are respectively unlikely and impossible.

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branch. All, including the highly adapted *Enigmonia*, have been included in the family Anomiidae in which both Thiele (1935) and Keen (1958) also place *Placunanomia* and *Placuna*. The inadvisability of so doing is discussed later. Basic structure and habit in the superfamily are undoubtedly those of the saddle oysters of which *Pododesmus* is here revealed as the most primitive. It is most fitting therefore to start this survey with a description of the large *Pododesmus cepio* of the north Pacific. Shells of the Caribbean *P. rudis* have also been available and also material of the large New Zealand *Monia zeylanica* (preserved only) and the smaller British *M. patelliformis*, without detection of any generic differences. *Pododesmus* is therefore considered to cover *Monia*.†

Pododesmus cepio (Gray, 1850)

This species, so designated by Keen (1958), was formerly known as *P. macroschisma* (Deshayes, 1839) but, as noted by McLean (1969), that is an Alaskan species. *P. cepio* is widely distributed on both sides of the north Pacific from low tide levels down to some 70 m. On the American side it occurs between 30 and 57 degrees latitude (Keen 1937). It was studied at the Friday Harbor Laboratory of the University of Washington, Seattle, during the summers of 1959 and 1969; finally at Pacific Grove in 1975.

Appearance and habits

P. cepio lives attached to rocks and stones or to the shells of other bivalves. In British Columbia, according to Quayle (1960), it attains a diameter of up to 12.5 cm but no specimen found at Friday Harbor was more than half of this size. The lower valve conforms to the substrate, the inner surface being concave, flat, convex or even irregular. On a flat substrate the upper valve is externally only gentle convex, the enclosed animal extremely flattened. Attachment by the calcified byssus which emerges through an oval shaped embayment (figure 2*c*) extending, in extreme cases, almost to the centre of the valve, is as secure as cementation (e.g. in *Hinnites*) although here accomplished by way of the visceropedal mass instead of the mantle/shell.

Valves

Dissimilarities between the mantle lobes produce corresponding differences between the secreted valves, the upper one both thicker and slightly larger, its margins overlapping those of the delicate under valve. Internally both have a characteristic lustre. An opaque white area occupies the centre of each valve delimited by the line of secondary pallial attachment marked b.w. in figure 2*d*. This indicates the extent to which the mantle lobes can be withdrawn, the area within being occupied by the visceropedal mass.

In various anomiids, Beu (1967) and Taylor, Kennedy & Hall (1969) have shown that the outer shell layer is of foliated calcitic structure, the inner layer (confined to this central area) being of aragonite with a complex crossed-lamellar structure; the muscle scars are prismatic aragonite. In *P. cepio* there are two such scars on the upper valve (figure 2*b*), those of the moderate sized adductor (ad.) and of the much larger posterior byssal retractor (p.b.r.). There is also a very small anterior pedal retractor scar (a.p.r.l.). The under valve (figure 2*d*) bears the scar of the adductor but also that of the right anterior pedal retractor (a.p.r.r.) which is situated in a depression on the ventral surface of the crurum (cr.) to which the ligament is attached. This muscle occurs only in *Pododesmus*.

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† In a somewhat different context, Keen (1959) has already suggested the merging of the two genera, *Pododesmus* Philippi, 1837 taking precedence over *Monia* Gray, 1850.

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Further and great dissimilarity between the mantle lobes is responsible in the right valve for the deep intrusion of the capacious byssal notch. Because these animals are monomyarian and so have lost the greater part of the original anterior regions of the body, this notch penetrates the valve immediately anterior to the ligament and has a profound influence on the nature of its attachments. As described later, the ligament is still more affected by the 'upward' growth of the mantle lobes at each end forming 'supradorsal' extensions only previously noted in *Plicatula* and in the Dimyidae (Yonge 1973, 1975). In *Pododesmus* these extensions affect the left valve because responsible for the secretion of a stretch of fused shell (figures 2, 3, 4, f.v.) which separates the umbo from the margin of the valve. Such fusion is *not* apparent on the right (under) valve where the secreting tissues tend to bend topographically downward, the umbo on that side obscured by overlaid secretion. The significant asymmetry is that the left valve extends dorsal to the upper surface of the ligament whereas the right valve does not (cf. figures 2*b* and 2*d*).

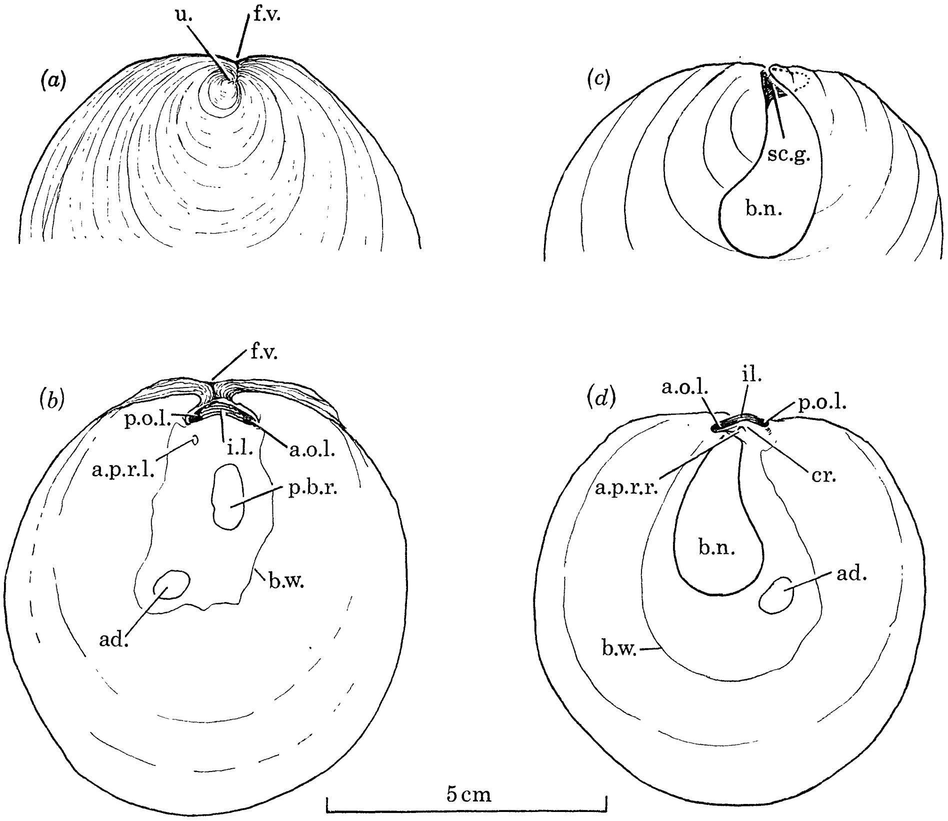

FIGURE 2. *Pododesmus cepio*, shell valves, (*a*) left valve, upper surface; (*b*) left valve, inner surface; (*c*) right valve, under surface; (*d*) right valve, inner surface showing byssal notch and crurum.

Within the byssal embayment the middle (sensory) fold of the mantle margin is greatly reduced but the inner (muscular) fold hypertrophies. The notch formed by the embayment undercuts the anterior end of the region of ligamental attachment or resilifer. It is thus responsible for the formation in the right valve of the somewhat mushroom-shaped crurum (cr.) as this characteristic anomiacean chondrophore is termed. In *Pododesmus* this is markedly convex. Viewed from the inner side (figure 2*d*), the anterior end of the crurum overlaps the antero-dorsal margin of the notch; this is also indicated by the dotted line in figure 2*c*. In older shells of

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Pododesmus, as illustrated in figure 3, these surfaces become so intimately related as to be separated by no more than a sinuous line of application. In some cases fusion eventually occurs converting the notch into a foramen. This was the case in all three specimens available of the Caribbean *P. rudis*.

The oval-shaped notch comes to a point dorsally where it is continued marginally into what is here termed a subcrural groove (figures 2, 3, 4, sc.g.) into which the byssal secretion extends so increasing the area of cemented attachment. This is a characteristic feature of *Pododesmus*. It is due to the presence of a dorsal pedal flap (p.f.) absent or much less developed in other genera.

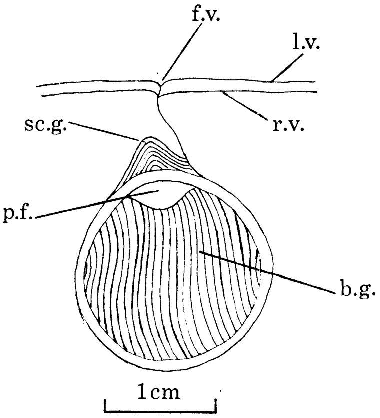

FIGURE 3. *P. cepio*, under surface of right valve showing ridged surface of byssal gland occupying byssal notch with dorsally extending subcrural groove with pedal fold (turned back), also overlapping margins of larger, left valve.

With displacement of the umbo of the left valve from its normal marginal position, there is the beginning of a new symmetry, the upper and larger valve assuming dominant significance. This process is carried further in other anomiids, notably in *Enigmonia*.

Ligament

This uncalcified constituent of the bivalve shell is primitively bilaterally symmetrical and so it very largely remains in the majority of the Bivalvia. A notable exception is provided by the Myacea where a massive chondrophore is present on the left side of the hinge although without significantly affecting the symmetrical opening of the valves. In anomiids such as *Pododesmus* conditions are very different. As shown in figures 4*a* and *b*, the overlap of the upper valve with its supradorsal extensions is so great that the ligament becomes *vertically* (topographically horizontally) instead of laterally disposed. The area of ligamental attachment (resilifer) on the left valve (figure 4*a*) is thus dorsal to that on the right valve the two being shown in their normal relation to one another in figures 4*a* and *b*. Thus when adduction ceases (more the concern of the posterior byssal retractor than of the much smaller adductor muscle), the upper valve moves more dorsally than laterally away from the under valve. No longer attached to the margin of the upper valve, the ligament cannot act as a true hinge. This fact was apparent to early workers such as Jackson (1890) who, with reference to *Anomia glabra*, wrote that 'it opens its shell by lifting of the upper valve alone and it has considerable forward and backward as well as lateral motion due to its peculiar method of attachment'.

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As part of the shell, the ligament is composed of inner and outer layers (apart from the periostracum). The inner layer (i.l.) is ventral and bent round this – a consequence of the supradorsal extensions of the mantle lobes – are anterior and posterior outer layers (a.o.l., p.o.l.) the former slightly the larger. The two layers are totally distinct, the inner dark brown and fibrous, the outer ones translucent green. A somewhat oblique ground section through approximately the middle of the intact ligament, i.e. cutting above the attachment of the crurum to the right valve, is shown in figure 5. The outer layers are cut at right angles but only adjacent areas of the inner layer. Owing to curvature, the middle region is occupied by inner and outer calcareous layers of the crurum (i.e. of the right valve) respectively above and below in the figure. The area between the former and the upper valve (l.v.) is occupied by the tissues, largely consisting of digestive diverticula (d.d.).

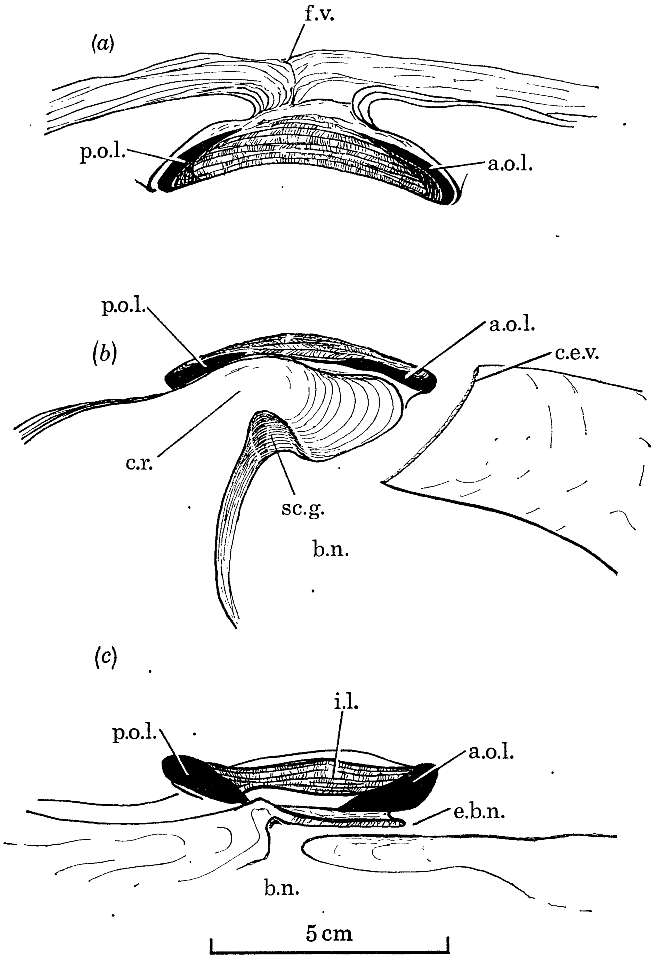

FIGURE 4. *P. cepio*, attachments of ligament, (*a*) to left valve; (*b*) to crurum in right valve, these two facing each other as in life, i.e. (*a*) dorsal (*not* lateral) to (*b*). (*c*) Dorsal view of crurum.

An understanding of this profoundly modified ligament involves discussion of the mode of origin. The primitive amphidetic ligament shown in figure 6*a* has a central inner ligament layer secreted by the mid-dorsally situated mantle isthmus (m.i.) flanked by approximately equal extents of anterior and posterior outer ligament layers secreted by the outer surfaces of the outer folds of the mantle margins (a.o.m., p.o.m.) in the depths of elongated embayments at

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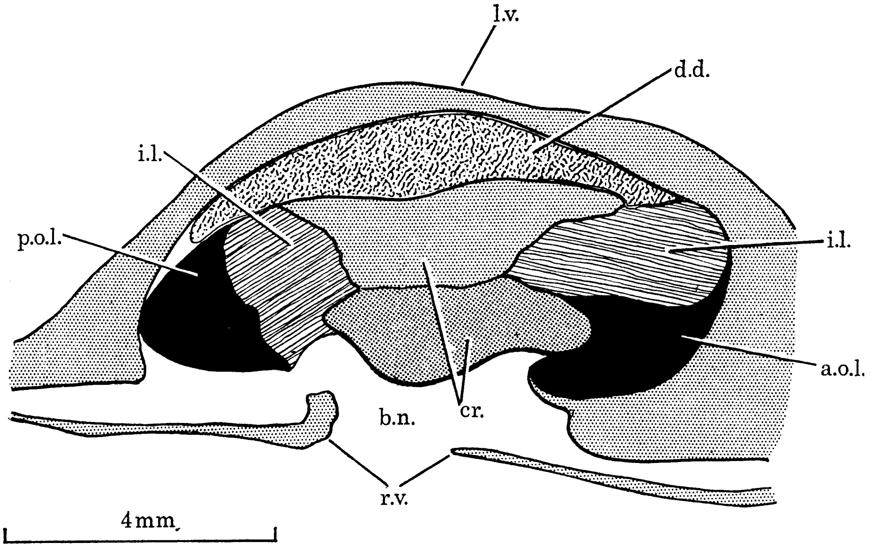

Figure 5. *P. cepio*, horizontal section through ligament in young specimen in dorsal region where at this stage the crurum is separated from the valve margin.

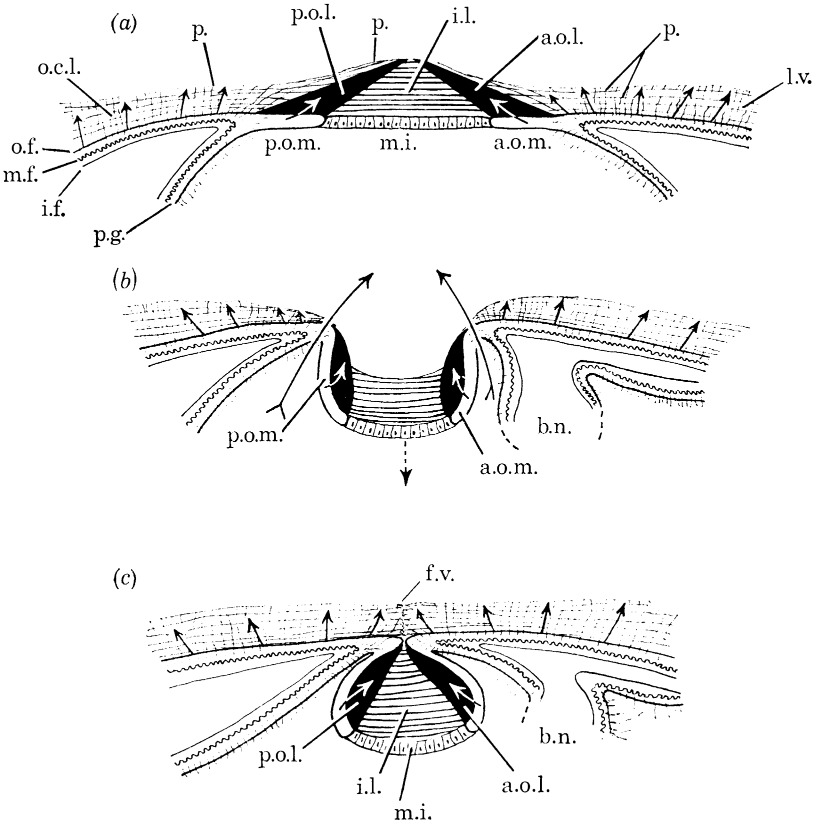

Figure 6. Anomiacea. Diagrams indicating probable mode of evolution of the ligament. (*a*) Primitive amphidetic ligament viewed from right (future under) side, bilaterally symmetrical; (*b*) hypothetical stage in evolution of asymmetrical ligament following deep extension of byssal notch in right valve with overarching dorsally of epithelia secreting outer ligament layers indicated by arrows, probably accompanying ventralward movement of mantle isthmus shown by broken arrow; (*c*) final condition reached in young *Pododesmus* with supradorsal fusion of shell but *not* of tissues.

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each end of the mantle isthmus. For the rest of their extent these outer folds secrete the outer calcareous layer of the valves. Like the rest of the shell, the ligament is initially covered by periostracum (p.) secreted in the groove at the base of the inner side of the outer folds.

The probable course of the changes which, in the course of evolution, led to the present conditions in *Pododesmus*, is indicated semi-diagrammatically in figure 6*a–c*. The mantle lobes became extended dorsally at both ends of the mantle isthmus (which may itself have moved ventrally – see complete and dotted arrows in figure 6). The former movement involved that of the epithelia secreting the outer ligament layers which became elongated and vertically disposed. Further changes (leading from the condition indicated in (*b*) to that in (*c*)) involved an inturning at each end with almost complete overarching of the mantle isthmus and the inner ligament layer it secretes. As already noted, the anterior and posterior secreting surfaces make contact but do *not* fuse, nor do the outer ligament layers which they secrete. On the other hand there *is* fusion of the inner calcareous layers of the valves supradorsally. This is not apparent in the right valve but in the left consists of an obviously fused extent of shell which separates the umbo (and the ligament below it) from the margin of that valve.

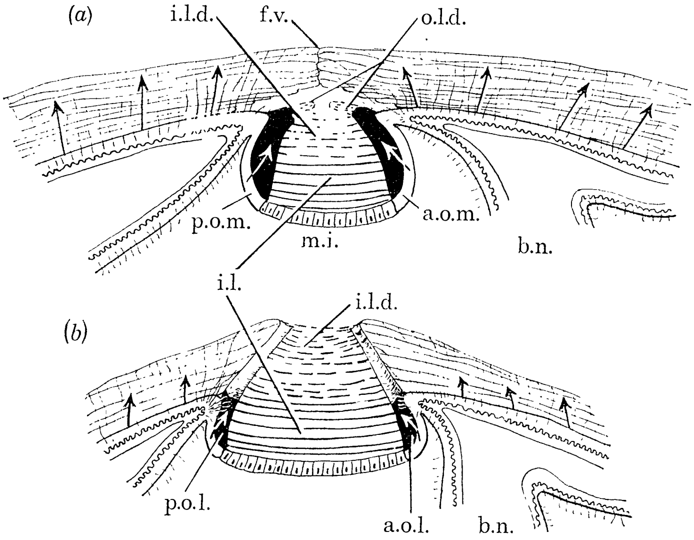

Figure 7. *P. cepio*, semi-diagrammatic representations of ligamental changes after its initial formation. (*a*) Outer calcareous layers of left valve still fused supradorsally, epithelia secreting outer ligament layers retreating and all layers (no longer covered by tissues) eroding dorsally; (*b*) later stage with supradorsally fused area broken down, extensive dorsal erosion of all ligament layers and further withdrawal of epithelia secreting outer layers.

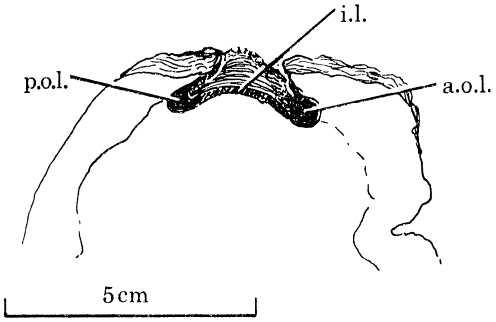

Figure 8. *P. cepio*, left valve of old individual viewed from within showing loss of supradorsal fusion and erosion of ligament.

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The condition, mantle margins just in contact dorsal to the ligament, is shown in figure 6*c*. The anterior and posterior outer ligament layers never entirely cover the dorsal surface of the inner layer. In older animals (figure 7) the regions of secretion separate, drawing back at each end, and the dorsal regions of all ligament layers become exposed and eroded (figure 7*a*). Mantle tissue no longer separates the inner (right) surface of the crurum from the dorsal surface of the valve. Finally, with the ligament farther eroded, the area of supradorsally fused valve may completely break down (Figure 7*b*) as indeed it does in all old shells (figure 8).

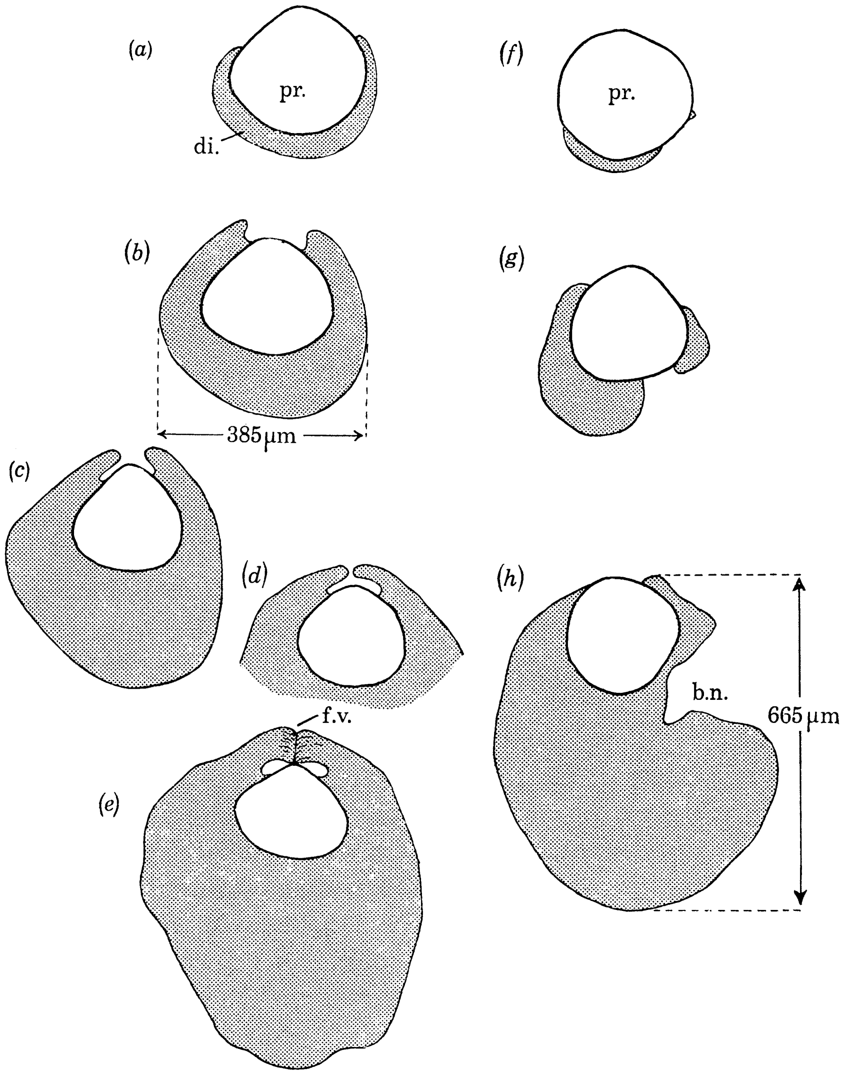

FIGURE 9. *P. cepio*, stages in development (based on sketches by D. B. Quayle). Prodissoconch shell shown white, addition of dissoconch shell stippled. (*a*)–(*e*) Left valve, stages in growth of dissoconch shell culminating in supradorsal fusion; (*f*)–(*h*) right valve, dissoconch shell appearing in two areas with final formation of byssal notch.

Development

The manner in which this striking asymmetry of valves and ligament is attained needs to be described. This involves reference to literature together with data and figures on the development of *Pododesmus* kindly made available by Dr D. B. Quayle working at Nanaimo, B.C., Canada.

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The valves appear to be completely symmetrical in the initial D-shaped or straight-hinged larva – the prodissoconch I of Werner (1939) – in which there is no differentiation along the hinge line (Rees 1950). Asymmetry begins with the addition of shell around this to form prodissoconch II which culminates in the formation of the veliconcha. The left valve now becomes more convex with the umbo protruding while the right, future under, valve becomes flat (Jackson 1890; Bernard 1896). A number of workers report the appearance at this stage of a notch on the anterior-ventral margin of the shell (e.g. in *Anomia ephippium* (Odhner 1914; Ranson & Desjardin 1941), in *A. patelliformis* (Bernard 1896), in *A. glabra* (Morse 1871; Jackson 1890), in *A. squamula* (Lebour 1938; Jørgenson 1946), in *A. lischkei* (Mizasaki 1935), in *A. aculeata* (Sullivan 1948). This has been claimed as representing the byssal notch (more accurately at this stage a pedal sinus). It coincides in position with the notch that so obviously appears in the dissoconch stage. Certainly in no other bivalves does this appear so early, on the other hand in no other bivalve is the fully formed notch so large and, very possibly, the foot appear so early. What, as Dr Quayle points out in correspondence, is unusual is that in the majority of reported cases the notch appears in *both* valves, only in *A. glabra* and *A. ephippium* does it appear to be confined to the right valve. In *Pododesmus* (figure 9) Quayle finds no trace of it in either valve. Finally Loosanoff, Davis & Chanley (1966) found that in *A. simplex* the notch was not always present. This lack of uniformity amongst such closely related species is surprising.

Major changes take place with the addition of the dissoconch shell. As shown in figure 9, prepared from sketches made by Dr Quayle, on the right valve new shell is added around all but the most dorsal regions of the veliconcha (figure 9*a*). This enlarges on either side dorsally, overarching the hinge and umbonal regions (*b*), (*c*), (*d*). The secreted shell layers (although as already noted, *not* the secreting tissues in *Pododesmus*) finally fuse dorsal to the umbo (*e*). Around the margin of the right valve the dissoconch shell first appears as very small anterior and much larger posterior regions (*f*), (*g*), these later unite (*h*) with the byssal notch lying between them. The larva is then about 665 μm deep, initial settlement having occurred when between 240 and 270 μm deep. During this period three gill filaments appear and also the red eye spots which are characteristic of all anomiid larvae. The foot is well developed. In *Heteranomia squamula*, Lebour (1938) figures it projecting from the larval shell, the tip bearing long cilia, and states that it aids swimming. After settlement with accompanying loss of the velum it becomes the sole organ of locomotion, 'very long and contractile', permitting the animal to crawl prior to fixation.

The hinge differentiates in prodissoconch II, the two sides being mirror images, with at each end a series of 4 or 5 teeth with the small ligament adjacent to the anterior group (Bernard 1896; Ranson & Desjardin 1941; Rees 1950). There is unfortunately little information about the manner in which this symmetrical larval structure is converted into the highly asymmetrical adult hinge. Bernard (1896) has described and figures how the ligament increases in extent during the growth of the dissoconch with final obliteration of the larval teeth. Ranson (1942) describes the hinge of the dissoconch in *Anomia ephippium* but, unfortunately, without figures; moreover he does little more than note the differences between the adult and larval hinge without following the process of change. All authors agree that, by its more vigorous growth, the left valve completely overlaps the right one while dorsally it comes to enclose the umbo on that side and so the hinge and ligament. Despite a statement, with two figures, to the contrary effect by Jackson (1890), no such overlap occurs, or can occur, on the right valve; Quayle (personal communication) writes that on the right valve 'the prodissoconch is retained at the edge of the dissoconch until it is worn away or sloughed off'. Indeed restriction of shell growth on the posterior side of

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the future byssal notch (figure 9*h*) has the eventual effect of producing the crurum on the summit of which the ligament is attached in this valve. Owing to overgrowth dorsally, the left side of the ligament comes to lie morphologically dorsal to, instead of lateral to, the right side.

As observed by Jackson (1890) for *A. glabra*, periods of crawling with an elongated foot and temporary byssal attachment precede permanent fixation when the byssus becomes calcified. This seems to occur at varying times in different species and under different conditions. Loosanoff (1961) states that in *A. simplex* metamorphosis with final attachment usually occurs when the post-larvae are about 200 μm long but that this may be delayed until they reach dimensions of 577 μm × 514 μm. These larvae had been kept in glass containers and Loosanoff attributes delay in settlement to lack of suitable surface. He writes of the foot being lost on settlement but this is not the case.

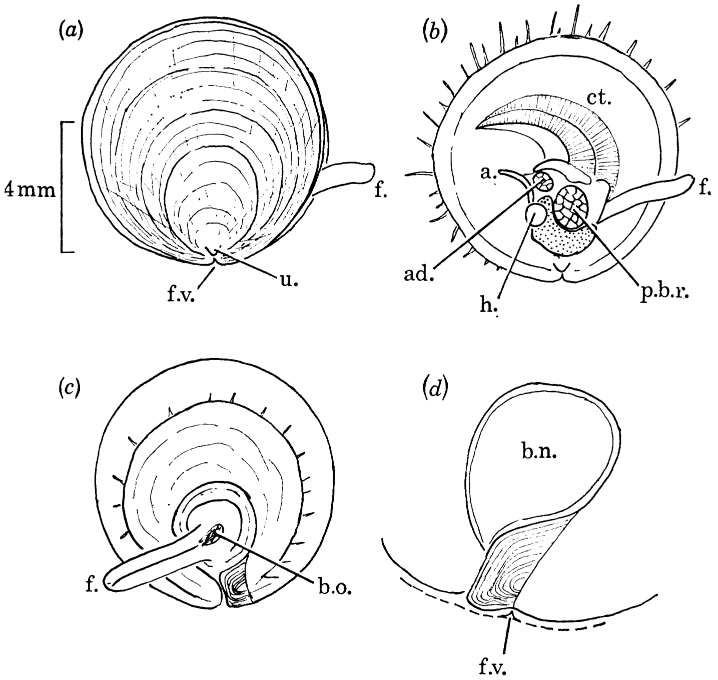

FIGURE 10. *P. cepio*, early (translucent) stages. (*a*) Intact, viewed from above, foot protruded; (*b*) showing major internal organs with marginal tentacles extended; (*c*) viewed from below showing locomotory foot with opening into byssal notch being reduced; (*d*) final application of margins to enclose notch.

Personal observations were made on young *Pododesmus* at the Shellfish Laboratory of the State of Washington at Point Whitney, Quilcene. All came from glass aquaria where they had settled from the plankton at periods of 5, 5½ and 11 months previously. They had reached maximum diameters of approximately 9, 11 and 8 mm respectively, indicating that growth is both slow and variable under these conditions. As shown in figures 10*a*, *b*, *c*, they had attained the appearance and major structure of adults but none was attached. All moved by means of the broad ended and ciliated foot (f.) which protruded anteriorly, the prehensile tip (Jackson 1890) gripping the surface, contraction of the retractors then pulling the animal along. Several were observed crawling up 45° slopes in glass dishes. Occasionally temporary attachment was made by blobs of transparent byssus. When not so attached the valves gaped widely. Sudden contractions of the adductor expelled pseudofaeces but the valves did not close for any appreciable time. Apparently the adductor can only very briefly

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overcome the opening thrust of the ligament; this is only achieved after attachment by contraction of the larger posterior byssal retractor (figure 10, cf. ad. and p.b.r.). This major disadvantage may explain the inability of these unattached animals to grow beyond a certain size. Internal movements could be viewed through the translucent shell. Contraction of the adductor is accompanied by withdrawal of the mantle lobes (figure 10*c*) due to contraction of muscles radiating from the region of the adductor. This is followed by their gradual extension to the margin of the valves and projection beyond this of the long pallial tentacles (figure 10*b*). The heart (h.) can be seen beating.

Byssal notch

The final stage in the enclosure of the notch or sinus in these unattached individuals (it must occur earlier and probably rather differently in normal development) is shown in drawings of their under surfaces (figure 10*c*, *d*). There is no fusion of shell surfaces but the byssal notch effectively becomes a closed foramen.

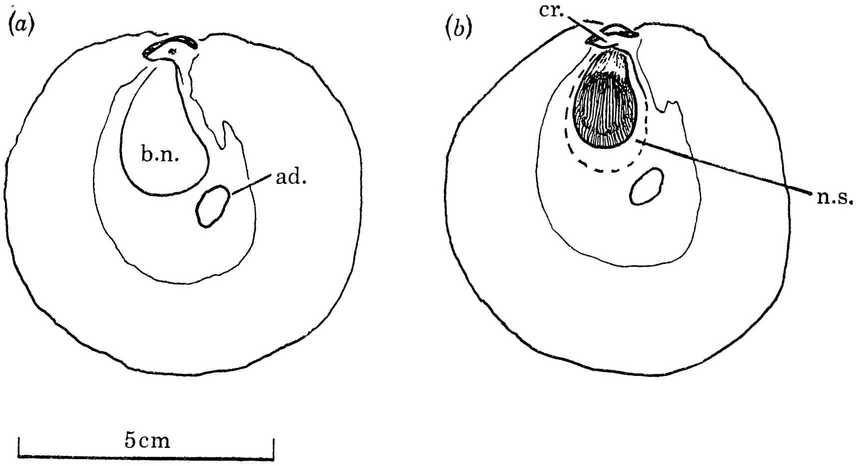

FIGURE 11. *P. cepio*, interior views of right valves. (*a*) Widely open byssal notch; (*b*) valve of similar size with byssal plug *in situ* and recently secreted shell uniting with this.

The inner surface of the under valve of a *Pododesmus* which had probably just attained its size of 7 cm × 6.5 cm is shown in figure 11*a*. The byssal sinus is pear-shaped, 2.5 mm long by 1.8 mm at the widest part. It has clearly enlarged during growth, i.e. resorption has occurred as well as some secretion which has thickened the ridge supporting the crurum. This is to be compared to the under valve of another animal (11*b*) found close to it on the same flat – actually plastic – dredged substrate. Although almost the same size, conditions are very different indicating what is probably the final stage in growth. The area occupied by the notch is oval-shaped and only 1 mm long, due to secretion of shell around all but its dorsal (crural) margins. This new shell (n.s.) is distinct, the earlier extent of the sinus, very similar to that in figure 11*a*, is indicated by the broken line.

At this final stage the now strongly calcified byssus fuses with the margins of the notch including the dorsally directed subcrural groove. The under valve is therefore attached to the byssal plug and so to the substrate. Only the upper valve can move with the left posterior byssal retractor now becoming a true adductor – a primitive function of the pallial musculature here taken over by a shell muscle (i.e. of the visceropedal mass).

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One can only speculate as to what brings about change from resorption which produces an enlarging notch (and must be characteristic of a growing animal) to the reduction in size by active marginal secretion. Detached specimens in the aquarium quickly add shell around the valve margins including those of the notch. When Manigault (1934) kept detached specimens of *A. ephippium* upside down he noted that the mantle margins around the notch grew rapidly inward and upward to secrete a calcareous tube perpendicular to the surface of the under valve; the process was so rapid that he postulated transference of calcium carbonate from the byssus where calcification was apparently reduced. The notch appears to be kept open by some restraint on secretion with accompanying powers of resorption. This restraint is obviously lost when the animal is detached when byssal secretion apparently ceases; the two processes may be connected.

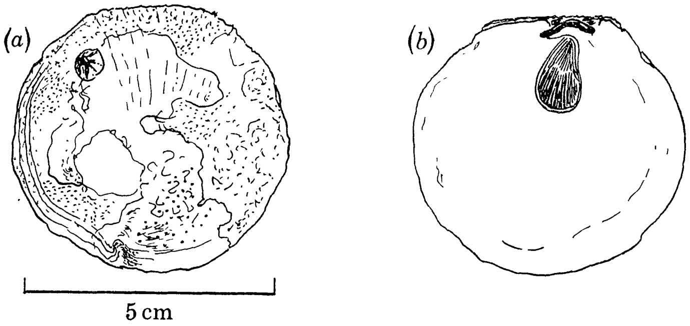

FIGURE 12. *P. cepio*, right valve of 'free' individual initially attached to shell of *Modiolus*. (*a*) Outer (now not necessarily under) surface covered with encrusting growths; (*b*) inner surface showing byssal plug and crurum.

An interesting final condition is found in specimens of *Pododesmus* which settle on the surface of other bivalves. This was particularly common in a bed largely of *Modiolus modiolus* near Friday Harbor at a depth of some 50 fathoms (1 fathom = 1.85 m). The mussel shells were on average some 9 cm long with specimens of *Pododesmus* often attached to the flattened posterior, but never to the very convex anterior, end. With growth the under valve of the anomiid conformed to the convex surface of the shell and then flattened out beyond this. After death the modiolid shell breaks up leaving a section attached to the byssal plug. The under surfaces of such, then free, *Pododesmus* were often covered with encrusting growth obscuring all trace of the byssus (figure 12). Many such individuals, resembling scallops or large *Pandora punctata* were collected, the apparent outer symmetry disguising a profound internal asymmetry; immobile with the major attachment between the valves provided by the posterior byssal retractor directly inserted into the left valve but attached to the right valve by way of the calcified byssus which has fused with this.

Mantle lobes

The highly asymmetrical mantle lobes (figures 13, 14) are bounded by the inner, muscular, fold which forms pallial curtains controlling water flow, the middle fold with numerous sensory tentacles and the outer, secretory, fold. The lobes are free throughout and can be deeply withdrawn by contraction of the contained radial muscles although always retaining contact with the valve margin by way of an excessively thin and extremely flexible sheet of periostracum.

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Musculature

In consequence of the double asymmetry (see figure 1), pedal retractors on the left consist of a small anterior and a hypertrophied posterior (byssal) muscle (a.p.r.l., p.b.r.) while – exclusively as we shall see to *Pododesmus* – there is an anterior retractor on the right (somewhat larger than the one on the left) which is inserted in a cleft on the ventral surface of the crurum (figures 1, 2*d*, a.p.r.r.).

Distinction between anomiid genera has largely been based on the attachment of the left posterior (byssal) retractor (Winckworth 1923). In *Pododesmus* this consists of a mass of fibres forming, by their attachment, a single rounded scar (figure 2*b*, p.b.r.) so that, with that of the adductor (ad.), there are *two* major scars on the left valve.[†] In the totally distinct *Heteranomia squamula* the two muscles are confluent so forming a *single* scar. In *Anomia* (e.g. *A. glabra* (Jackson 1890), *A. ephippium* (Winckworth 1923), *A. cytaeum* (Tanaka 1955) and *A. trigonopsis* (Beu 1967)) the byssal retractor is divided into two masses so that there are *three* scars. Although shells of *Anomia* spp. can be separated from those of other genera in this way, the present study has revealed other and more significant differences between the genera.

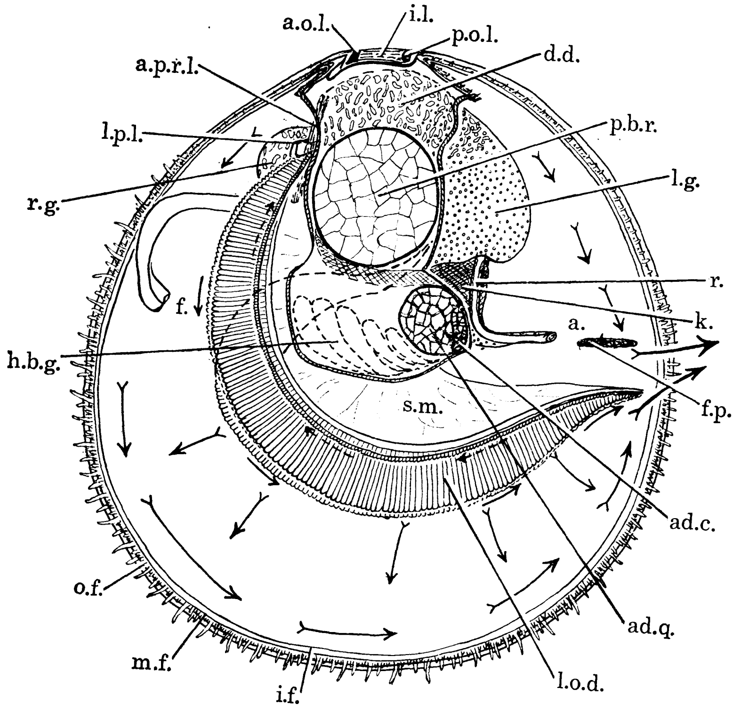

FIGURE 13. *P. cepio*, viewed lying within right valve (i.e. from above). Plain arrows indicate direction of ciliary currents on ctenidia, broken arrows along axis and feathered arrows on mantle surface. Anterior end of right ctenidium shown by broken lines.

Function of the muscles

The arrangement of the muscles in *Pododesmus* when viewed from the posterior end (in side view as they lie) is shown in figure 1. As appears from its size, the byssal retractor (p.b.r.) assumes major responsibility for adduction, pulling the left valve firmly down on to the substrate around

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[†] This is also true of *Pododesmus* (*Monia*) *patelliformis* but not of *P.* (*M.*) *squama* where the scars are confluent; this is the only, and very dubious, distinction between them.

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the margins of the smaller right valve. The adductor appears primarily concerned with producing the sudden contractions needed for expelling pseudofaeces, much the greater part of the muscle consisting of striated 'quick' fibres (figures 13, 14, ad.q.). The very small area of smooth 'catch' muscle in the adductors of anomiids was originally noted in '*Monia*' *patelliformis* (Yonge 1936).

Adduction also involves contraction of the anterior retractors present on both sides in *Pododesmus* although confined to the left in other anomiids. Contraction of the left muscle (a.p.r.l.) will help to pull the upper valve against the lower and to compress the ligament (the opening thrust of which is largely dorsoventral). The function of the larger anterior retractor (a.p.r.r.) in *Pododesmus* is uncertain but its contraction will tend to pull the ventral surface of the crurum firmly against the dorsally directed wedge of byssal threads that extends beneath the subcrural groove (see figure 11*b*). This ensures absolute closure of the opening.

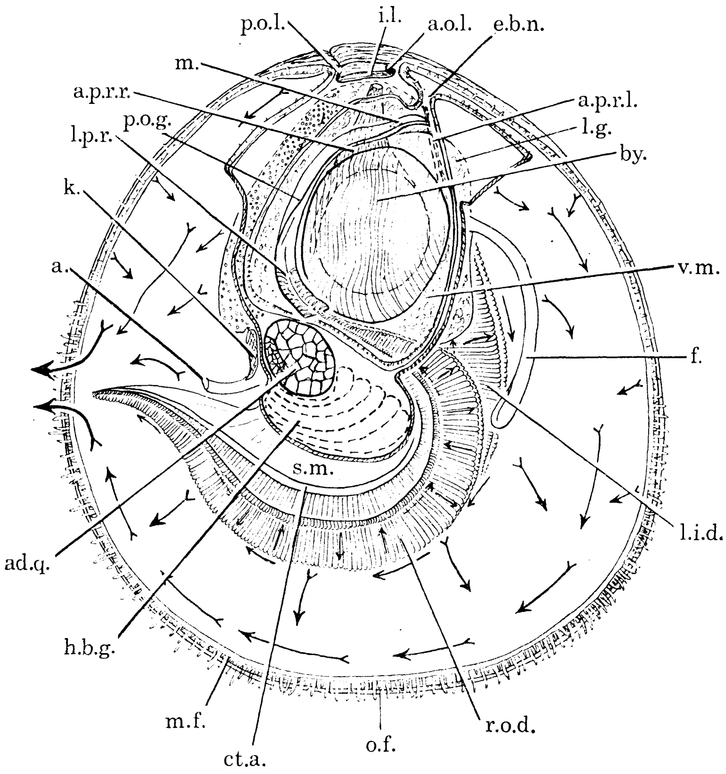

FIGURE 14. *P. cepio*, viewed lying within left valve (i.e. from below). Arrows as in figure 13.

Foot

Despite adult immobility, the foot is retained as in some other cemented Bivalvia, the pectinacid *Hinnites* and *Spondylus*, the Chamacea and also in *Cleidothaerus* (Anomalodesmata), but unlike the equally immobile Ostreacea and also *Plicatula* and the Dimyidae (Yonge 1975). In all it is probably present in the post-larvae where, certainly in the Ostreacea (Cranfield 1973*a–c*), it retains a brief but essential locomotory as well as attaching function. As already noted it may retain a locomotory function for months in *Pododesmus*. It is early concerned with byssal secretion, initially for temporary attachment – as in *Hinnites*, where permanent attachment is unusually long delayed (Yonge 1951) – but eventually for permanent fixation. In adult *Pododesmus*

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(and in all Anomiacea) the foot remains a conspicuous organ (figures 13, 14, 15); it is elongate, grooved on the ventral (under) side and ciliated. It is highly mobile, can be extended or withdrawn, turning and twisting within the mantle cavity collecting sediment which is carried into the groove or may drop off and enter the rejection tracts on the mantle surface as described by Atkins (1937) in '*Monia*': and *Heteranomia*. She noted how in the former the slightly spatulate tip would grip a relatively large particle and transfer it into a rejection current. Similar observations were made on *Pododesmus*.

The elongate pedal groove in the anomiids (figure 15) appears homologous with the terminal – and purely cleansing – pedal cone in the Pectinacea (Yonge 1973). The separate byssal groove present in all save the Spondylidae is here withdrawn within the relatively enormous rounded opening of the byssal gland at the base of the foot. From this byssal secretion is applied to the substrate, a process which was followed in young, still motile, animals but in more detail in *Enigmonia* (see later). The grooved and mobile regions of the foot are temporarily withdrawn.

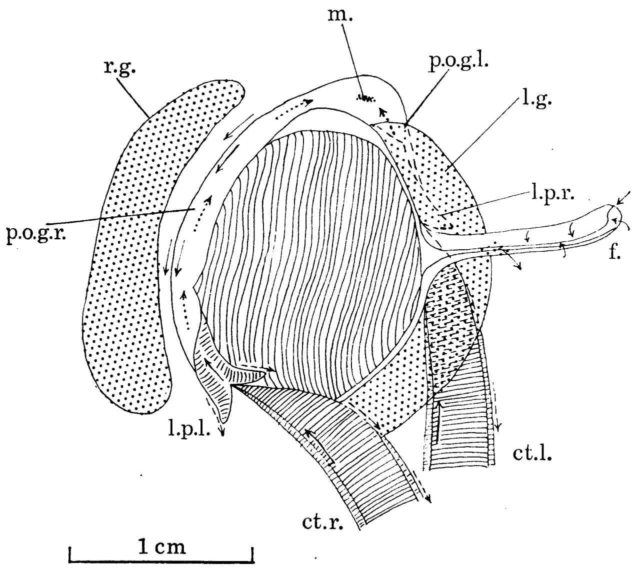

FIGURE 15. *P. cepio*, under surface showing parallel lamellae of enlarged byssal gland separating right and left gonads, ctenidia and palps with long proximal oral groove leading to mouth on right, very short one on left. Dotted arrows indicate direction of currents beneath overlapping outer lip; currents leading into pedal groove also shown.

Byssal apparatus (*figures* 13–15)

This is relatively larger than in any other bivalve with a unique calcified secretion (except in *Enigmonia*). The gland has been described by Seydel (1909). It consists of a rounded shallow cavity lined with the parallel lamellae characteristic of byssal glands but here exceptionally numerous and extending dorsally under the subcrural groove. The calcified byssal material is secreted by the opposing faces. The calcareous content accounts for 90 % of the weight of the byssus and is of aragonite with traces of calcite, there is some magnesium present. These facts with a full biochemical analysis are provided by Pujol *et al.* (1970).

Pallial organs

The appearance of the organs in the mantle cavity after removal of the appropriate valve and mantle lobe is shown from the upper side in figure 13 and from the under side in figure 14. The byssus and its major retractor separate the ctenidia anteriorly. Viewed from above, the left

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ctenidium (l.o.d.) and palp (l.p.l.) are disposed as in any pteriid or pectiniid. Viewed from below (figure 14), the anterior end of the right ctenidium (r.o.d.) and the right palp (l.p.r.) and long proximal oral groove (p.o.g.) are seen to have been pushed around to the posterior side of the byssal complex with the left palp and short proximal oral groove remaining in the normal anterior position. The mouth, obscured beneath the enlarged outer lip which encloses the oral grooves, is displaced somewhat to the right (figure 15). The anterior ends of the ctenidia with the palps are also twisted to the right, i.e. downwards. This raises further questions of symmetry.

The position of the major viscera is better viewed from above. The dark mass of the digestive diverticula (d.d.) is dorsal. The gonad (orange ovary or off-white testis) is asymmetrically divided, the left one (l.g.) extending on that side of the foot and into the mantle but the reduced right gonad (r.g.) displaced posteriorly (figure 15). The kidneys lie ventral to the left gonad. The anus (a.) projects posterior to the adductor depositing cigar-shaped faecal pellets on to the middle of the mantle surface.

Ctenidia

As shown in figures 13 and 14, these filibranch gills are large, the right one somewhat the smaller owing to the effect of the byssal apparatus. They are attached by way of deep suspensory membranes (s.m.) bearing conspicuous and elaborately ridged hypobranchial glands (h.b.g.) on their inner faces, but are free for the posterior third. The demibranchs have the usual form, the ascending filaments on the inner demibranchs being attached along the mid-line dorsally but only by *ciliary junctions* (figure 19*a*). Where the ctenidia are separated by the byssal complex the inner demibranchs make similar ciliary contact with the intervening surfaces. Each ctenidium makes full functional contact with the corresponding palps. This is true of all species of *Pododesmus*. Conditions are different in some other Anomiidae.

The dorsal margins of the outer demibranchs are somewhat reflected and successive filaments are terminally attached to one another by ciliary junctions, but there is no ciliary attachment to the mantle surface (figure 19). Throughout their length filaments are connected to one another by up to six rows of ciliary disks but interlamellar attachment is limited to an intrafilamentary septum within the angle of ventral reflexion.

The ctenidia in *Pododesmus* are essentially as described by Ridewood (1903) for those of '*Anomia* (*Monia*)' *patelliformis* and, in the greatest detail for that species and for '*Monia*' *squama*, by Atkins (1936). She also described the cilia, observing them in life. Laterals are normal, latero-frontals are small (micro-latero-frontals) with the frontals consisting of a major tract of coarse cilia along the posterior, and a narrow tract of fine cilia along the anterior, side of the frontal surface. There are no abfrontals. The presence of striated muscle in the axes and in the suspensory membrane with the very limited attachment between the filaments and the lamellae renders these ctenidia very mobile. The demibranchs dilate and contract and so do the entire ctenidia.

Ciliary currents

The course of the currents on the ctenidia and throughout the mantle cavity in *Pododesmus* was first described by Kellogg (1915) also working on specimens (designated *Monia machrochisma*) from Puget Sound. On all lamellae, material is carried to the ventral margins of the demibranchs where powerful currents carry it posteriorly for ejection from the mantle cavity (figures 13, 14). Kellogg regarded such aboral transport on the ctenidial margins as unique to the anomiids but it has since been noted in the Arcacea (Atkins 1936, 1937; Yonge 1955) and in *Spondylus* and *Plicatula* (Yonge 1973). All have the same combination of coarse and fine frontal

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cilia, their ctenidia constituting Atkin's Type B (1_a). The fine frontal cilia (not detected by Kellogg) beat dorsally where oralward currents run along the axes and the margins of the ascending filaments (see broken arrows in figures 13 and 14). There is therefore some selection of particles on the frontal surfaces but, as Atkins describes and figures, when the ctenidia are fully dilated a significant proportion of suspended matter will impinge directly on to the exposed surface of the ctenidial axes and so enter oralward currents. The exceptionally open character of these ctenidia and especially the retention of an exclusively cleansing function for the greater part of the frontal cilia are both highly primitive characters, this despite the very specialized structure and mode of life in the Anomiidae.

Palps, oral grooves and mouth

The very asymmetrical palps (figure 15), those of the left side short (l.p.l.), those on the right (l.p.r.) half encircling the protruding byssal mass, have the usual ridged inner and smooth outer surfaces and the customary selective function. Selected material passes into the proximal oral grooves (very long on the right (p.o.g.r.), very short on the left (p.o.g.l.)) and so the mouth. The outer bounding lip is enlarged so that it completely encloses the grooves and mouth on the under (right) side. Owing to the anterior twisting this is a necessary provision to prevent loss of food, corresponding to some extent to the elaborate arborescent 'lip apparatus' found in the Pectinidae, Spondylidae and Limidae (Gilmour 1964; Bernard 1972; Yonge 1973). Matter rejected by the palps is carried to their distal tips and so into the posteriorly running currents on the ventral margins of the gill lamellae. Gilmour (1974) has recently shown that water emerging from between the lips flows out through the opening of the byssal notch (figure 14, e.b.n.). All feeding processes are highly adapted for retention of only the finest particles.

Cleansing currents in the inhalant chamber

The general pattern of these is indicated by the feathered arrows in figures 13 and 14. They follow the same general course as those already described by Kellogg and by Atkins. Material from the mantle lobes, visceral mass and all exposed surfaces is carried to the margin of the lobes and there caught in powerful posteriorly directed currents. Without the usual preliminary aggregation into pseudofaecal masses, all is immediately expelled at the posterior end of the inhalant chamber. All cleansing currents are unusually powerful.

Exhalant chamber with hypobranchial glands

In this chamber particles are carried to the same region where they are expelled with the faecal pellets (figure 13). In *Pododesmus* (Kellogg 1915), as well as in '*Monia*' spp. (Atkins 1936), the mantle surface dorsal to the suspensory membranes is occupied by inwardly facing glandular masses forming a deep bag lying between the attachments of the ctenidia to the adductor and so forming a roof to the central part of the exhalant chamber. Secretion pours from the folded surface in a thick stream which becomes a dense obscuring white cloud. Powerful ciliary currents beat posteriorly along the line of folds. Kellogg thought these regions contained extensions of the gonads but, after histological examination, Atkins concluded that they were homologous with the hypobranchial glands in the Nuculidae (Protobranchia) (see Yonge 1939) and in most prosobranch Gastropoda the secretion of which entangles particles in the exhalant chamber. Their retention in *Pododesmus* and *Placunanomia* may be correlated with the more open, i.e. primitive, nature of their filibranch ctenidia, much material passing through these. The

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lamellae are presumably better compacted in other Anomiacea where these glands are absent. There is a similar difference between the Nuculidae and the related Nuculanidae, also without these glands but with firmly compacted, pumping ctenidia (Yonge 1939).

Sense organs in the exhalant chamber

Atkins (1936) states that in the two species of '*Monia*' osphradia are visible as yellow pigmented lines on the suspensory membranes running to the posterior extremity of the ctenidia. Obvious though their function is in the Gastropoda – probably initially tactile and then chemical receptors – their function in the Bivalvia remains obscure. They are certainly not obvious in *Pododesmus* which does, however, possess a pair of conspicuous yellow sense organs situated on the middle of short membranes attaching the base of the rectum (r.) to the adductor. Thus they lie in the middle of the restricted channel, interrupted in the middle by the rectum, leading from the bag-like cavity formed by the ctenidia and the hypobranchial glands into the posterior end of the mantle cavity. Both are long, slightly curved and covered with hair-like processes closely set and stiff (not vibratile) and up to 100 μm long. The sense organ on the right (i.e. lower) side is always about twice as large as that on the upper side, attaining, in an animal of shell diameter 4.5 cm, a length of 1.16 cm and a breadth of 0.3 mm. Nerves pass from each to the visceral ganglia.

Situated in the middle of the exhalant chamber these 'abdominal' sense organs cannot be concerned with any 'testing' of the inhalant water. But over them is carried all material which passes through the very loosely compacted ctenidia and then becomes aggregated in the hypobranchial secretion; i.e. they are in a position to estimate the sediment content of the ambient water. Accumulation will be greater on the under side, hence the larger organ on the right. Such sense organs appear to be confined to the filibranchs and the Ostreacea. They are paired in the bilaterally symmetrical Mytilidae (White 1937) and single and confined to the lower side in the asymmetrical monomyarian Pectinacea (e.g. *Pecten maximus*, Dakin 1909) and Ostreacea (e.g. *Crassostrea virginica*, Elsey 1935) i.e. on the right and left sides respectively. In this respect, therefore, these anomiids occupy an intermediate condition.

Viscera

Following the work of Lacaze-Duthiers (1854), who first demonstrated their true nature, various aspects of visceral and pedal anatomy in '*Monia*', *Anomia*, and *Heteranomia*, have been studied by Morse (1871), Jackson (1890), Pelseneer (1891, 1911), Sassi (1905) and Tanaka (1955). Apart from the significant retention of the right anterior byssal retractor, conditions in *Pododesmus* do not appear to differ appreciably.

The anatomy of these animals is basically primitive although profoundly modified by the effects of horizontal (pleurothetic) disposition and truly lateral (and permanent) byssal attachment. No other superfamily in the Bivalvia is more bilaterally asymmetrical and none more laterally compressed.

Gut

The alimentary canal is short with the uncoiled mid-gut running direct from the posterior side of the stomach to the anus, the rectum not passing through the ventricle. This may be primitive but could also be the result of extreme lateral compression. Purchon (1957) has described the stomach in *Anomia ephippium*. He assigns it, with that of *Placuna placenta* which is very similar, to his Type IV, the major typhlosole having no tongue. 'Being simple', he writes,

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'this is possibly a primitive feature.' A similar stomach type is present in the Limidae, Pectinidae and Trigonidae. Other filibranchs possess Type III. Despite its simplicity, Type IV is also present in a variety of eulamellibranchs. However the Anomiacea are unique among filibranchs in the separation of style-sac from mid-gut. This condition, which cannot be primitive, appears sporadically throughout the Bivalvia and has no phylogenetic significance. The style-sac is exceptionally long and delicate in all the Anomiacea and disposed asymmetrically on the right terminating in the mantle. The unusual length and firmness of the contained style could be functionally associated with an unusually rapid passage of material through the very short gut from which the largely unconsolidated faeces emerge as elongate pellets then rapidly removed from the mantle cavity (figure 13). Arakawa (1970) describes the pellets of *A. lischkei* as ungrooved ribbons including them in his Pellet-type III-10 together with those of most other filibranchs and the eulamellibranch Carditacea and Unionacea.

Circulatory system

The Anomiacea are unique among the Bivalvia in the absence of a pericardium, the ventricle (not penetrated by the rectum) projecting into the mantle cavity on the underside of the visceral mass. Seen through the translucent shell the pulsations of this exposed ventricle in *Anomia simplex* were used by Navez (1936) in work on the cardiac rhythm in bivalves. The auricles are asymmetrical in conformity with the different dispositions of the ctenidia. There is a single, anterior, aorta leaving the ventricle on the left. Loss of the pericardium is surely secondary, indeed Jackson states that it is present in young specimens of *A. glabra*.

Excretory and reproductive systems

As shown by Sassi (1905) in *A. ephippium* the kidneys in the Anomiidae are extremely asymmetrical, the left one much the larger. They are united with ciliated funnels that open into a small sac-like coelomic remnant. All this is clearly secondary and presumably a consequence of lateral compression together with the obstruction on the right side of the twisted and hypertrophied byssal apparatus. The gonads open into the kidneys at some distance from the renal pores. Here again the left gonad is much the larger. Sexes are separate. So far as could be determined conditions in *Pododesmus* are similar.

Nervous system

Due to the twisting that brings the mouth to face topographically downward, the cerebropleural ganglia lie in the sagittal instead of the transverse plane, with the right cerebro-pedal connective much longer than the left. The pedal ganglia are closely associated at the base of the foot and the visceral ganglia are on the anterior instead of the usual ventral side of the adductor. Eyes occur on the first gill filament on the left.

HETERANOMIA SQUAMULA (L.)

This common British species has been studied in life by Atkins (1936) and figured with her customary precision. Only significant facts with some additional observations need be recorded here. As noted by Ridewood (1903), '*Anomia aculeata*' is distinguished from all other anomiids, indeed from all other bivalves apart from the Dimyidae, because each demibranch (figure 19*c*) is restricted to a single (descending) lamella, Atkins (1937) placing it alone in her gill Type B (2).

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The outer lamellae are attached to the mantle surface by way of interlocking cilia and to each other by ciliary disks, the inner filaments united in the same way and to their fellows of the other side. The appearance in cross section is therefore that of an inverted W (figure 19*c*).The filaments are otherwise free. There is a single aboral current running along the united summits of the inner filaments with similar rejection currents along the mantle surface ventral to the outer filaments. As shown by Atkins there is the same arrangement of fine and coarse frontal with micro-lateral frontal cilia as in other anomiids. This is certainly *not* a primitive ctenidium. There are no hypobranchial glands.

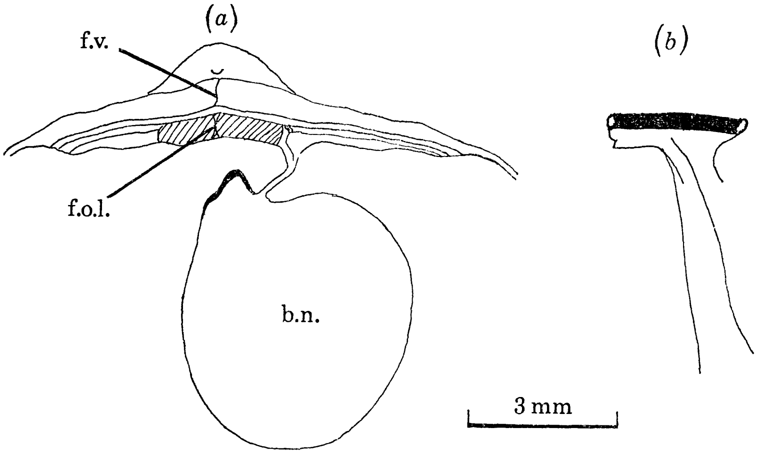

FIGURE 16. *Heteranomia squamula*. (*a*) Dorsal region of intact specimen viewed from right and slightly from 'above', showing fusion of epithelia (hatched) secreting outer ligament layers, also restricted subcrural 'groove' with thick lining periostracum. (*b*) Crurum viewed from inner side, horizontally disposed inner ligament layer and no anterior right pedal retractor.

Anteriorly the ctenidia are separated by the visceral mass before making functional contact with the palps. These are enclosed by a deep under fold which obscures the proximal oral grooves leading to the mouth. The palps have the usual selective function, the bulk of the rejected material emerging on the inner side to pass back along the tips of the inner filaments soon to unite in the middle line with those of the other side. Ejection of pseudofaeces and of faeces is at the base of the exhalant chamber; full details of ciliary currents are given by Atkins (1936).

In a variety of respects this genus is less primitive than *Pododesmus*. The mantle lobes which there extend dorsally on either side of the ligament (figures 6 and 7) without themselves ever fusing, do here actually *unite* supradorsally with the products of their secretion fusing to form a continuous outer ligament layer (figure 16*a*, f.o.l.) so that, uniting at each end with the inner ligament layer, the ligament becomes a continuous flattened oval structure. The outer ligament layer is yellow and opaque, the inner layer darker but clear and translucent. There is no evidence that even in the oldest animals the tissues ever break down or that the ligament becomes exposed and eroded during life as it does in *Pododesmus*. The crurum (figure 16*b*) is horizontal with no recess for insertion of a here non-existent right anterior retractor. The byssal notch is rounded with occasionally a subcrural groove resembling that of *Pododesmus* but more generally (figure 16*a*) consisting of a short, rounded depression edged with dark periostracum where the mantle margins extend over and may slightly resorb the under surface of the crurum.

The effect of supradorsal fusion of the mantle lobes has been to restrict the original mid-dorsal area of the mantle of which the two lobes are extensive marginal extensions; these are

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now united solely by the ring of tissue secreting the inner and outer ligament layers, i.e. the mantle isthmus with the marginal areas secreting the outer ligament layers. However the extent of connection is increased by some secondary union of mantle margins supradorsally. In *Heteranomia* this takes the form of a symmetrical union by way of the inner folds of the mantle margins (figure 17*a*), which represents the invariable first stage in the fusion of the mantle margins throughout the Bivalvia (Yonge 1957*a*). Atkins (1936) figured the union of these folds over a considerable extent of the exhalant region in this species. This now appears as a long posterior extension of the supradorsal union of the mantle lobes above the ligament. This mode of union is in striking contrast to the asymmetrical type of union (figure 17*b*) that will be shown to exist in *Anomia* and *Enigmonia* providing a further significant difference between *Heteranomia* and those genera, both again very different from *Pododesmus*. *Heteranomia* is a highly distinctive genus.

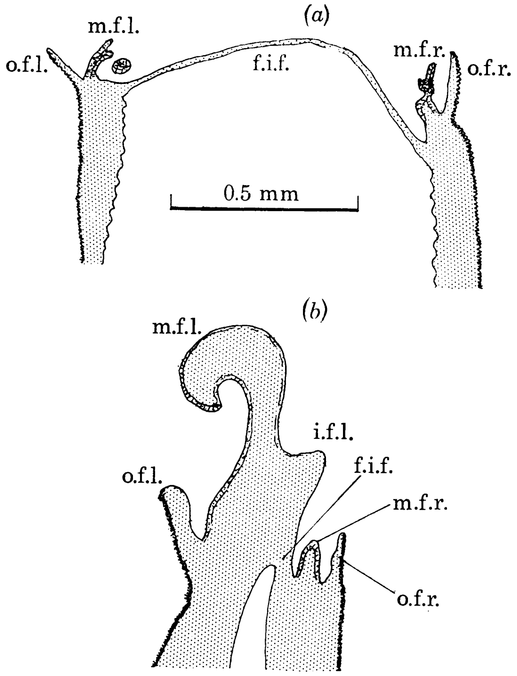

FIGURE 17. Supradorsal fusion of mantle margins in (*a*) *Heteranomia*, symmetrical condition with inner mantle folds uniting and (*b*) *Anomia ephippium*, asymmetrical condition with inner mantle fold of right lobe uniting with mantle surface *below* inner mantle fold of left lobe.

ANOMIA EPHIPPIUM L. AND *A. SIMPLEX* ORBIGNY, 1842

These two species, the one British and the second, larger, species from the Atlantic coast of N. America from Cape Cod to the Caribbean, were both studied. Apart from size, they are very similar. Unlike *Pododesmus*, the shell when not growing under restraint appears to be somewhat longer than it is deep (figure 18*b*) and there are three instead of a single muscle scar on the left valve. But there are further and much more significant differences between the genera. These particularly concern the extent of supradorsal fusion with details of the crurum and byssal notch together with major differences between the ctenidia.

As in *Heteranomia*, the mantle margins fuse completely dorsal to the ligament (figure 18*d*, f.m.m.). Even in the oldest shells this remains true with the upper surface never exposed and

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eroded. There is always tissue between the inner (under) surface of the crurum and the margin of the valve as indicated in figure 18*c*. The appearance of the ligamental region in *A. simplex* viewed from the under side is shown in figure 18*a*. Unlike *Heteranomia*, the anterior and posterior outer ligament layers, although approaching one another, do *not* actually meet (figure 18*c*) while supradorsal union of the mantle margins is restricted to the region immediately above the ligament. It is also asymmetrical (figure 17*b*), the inner mantle folds not uniting with each other, a condition more suitably described in *Enigmonia* (figures 28, 29) where, due to elongation, the region of secondary union is posteriorly extended.

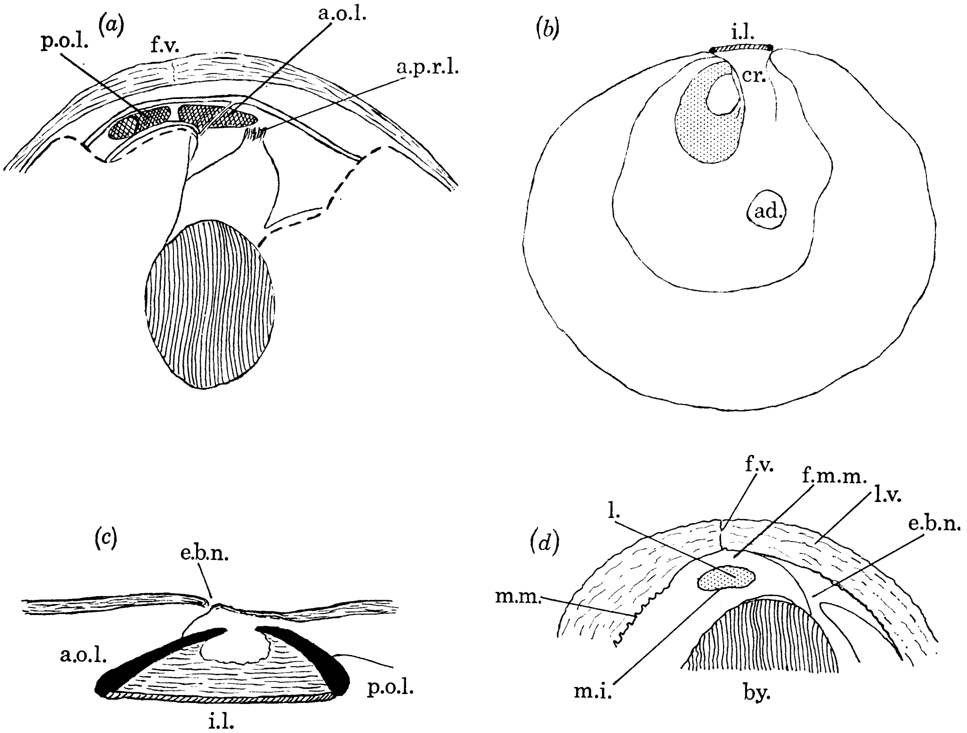

FIGURE 18. *Anomia simplex*. (*a*) Ligamental region viewed from right after removing shell around opening into byssal notch, outer ligament layers (cross hatched) shown *not* to be united (magn. × 4). (*b*) Inner surface of right valve showing horizontal crurum and filling in of byssal notch (stippled) (magn. × 2). (*c*) Ligament viewed from above (magn. × 6). (*d*) *A. ephippium*, ligamental region showing fusion of mantle margins above, i.e. supradorsally (magn. × 2).

The dorsal surface of the crurum is horizontal and lacks attachment for an anterior pedal retractor (cf. figures 2*d* and 18*b*). The byssal notch is small in an adult shell, only extending for about one fifth of the diameter of the valve; this is also (like that of *Heteranomia*) more rounded than in *Pododesmus* and never possesses a subcrural groove. This absence is a distinctive feature in anomiid shells.

Although the ctenidia resemble those of *Pododesmus* in possession of normally reflected demibranchs, they differ (Ridewood 1903; Atkins 1936) in having the summits of the ascending arms of the filaments united by tissue fusion (figure 19*b*). Those on the inner sides unite in the same way with each other, those on the outer sides, however, are not attached to the surface of the mantle although a blood vessel passes through their fused extremities which are reflected. There is no fusion or ciliary contact with the mantle surface. There are no ciliary disks along the course

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of the filaments. The differing conditions in the ctenidia of *Pododesmus*, *Anomia* and *Heteranomia* are shown semidiagrammatically in figure 19.

There is a notable degree of asymmetry in the ctenidia of *Anomia*. Anteriorly the inner demibranch of the right (under) side loses contact with the outer one to become associated with the left ctenidium (figure 19*e*). This condition, first noted and figured by Sassi (1905) in *A. ephippium*, represents a unique degree of ctenidial asymmetry in the Bivalvia. It is confined to *Anomia* (and presumably related genera such as *Patro*) with *Enigmonia* (figure 31). A comparison of conditions here and in *Pododesmus* and *Heteranomia* is shown in figure 19*d*, *e*, *f*. This asymmetry

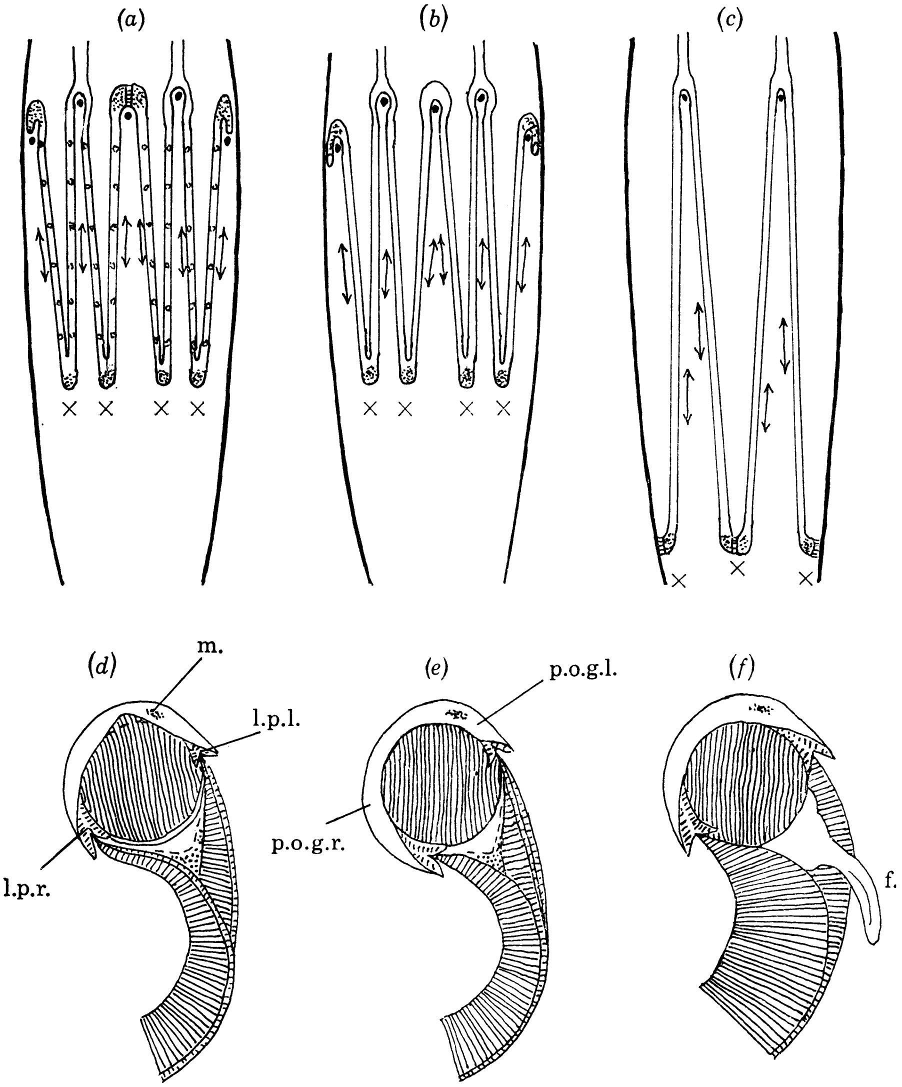

FIGURE 19. Anomiidae, ctenidial disposition and ciliation. *Above*, in transverse section, frontal currents on filaments indicated by arrows, circles oralward currents, crosses rejection currents. (*a*) *Pododesmus* showing ciliary attachments (see text); (*b*) *Anomia*, *Enigmonia*, ascending lamellae of inner demibranchs fused dorsally; (*c*) *Heteranomia*, lamellae not reflected, ciliary attachments as shown. *Below*, anterior end viewed from right side, ctenidia and palps of two sides separated by byssal apparatus, right proximal oral groove much the longer. (*d*) *Pododesmus*, ctenidia symmetrical; (*e*) *Anomia*, *Enigmonia*, three demibranchs associated with left palps; (*f*) *Heteranomia*, attached inner demibranchs alone shown, separated anteriorly by foot (not shown in (*d*) or (*e*)).

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represents a further consequence of lateral flattening in association with the protruding presence of the byssal complex and foot reducing the space on the right side.

There are also functional consequences. Three quarters of the material collected by the ctenidia and passed oralwards dorsally will now be conveyed to the left palps. These are particularly small with only some four folds and grooves on their inner faces compared with around 10 or 12 on the right palps (and around that number on both palps in *Pododesmus* and *Heteranomia*). The palps can have negligible selective capacity as observed by Morton (1976) in *Enigmonia*. Atkins (1936) illustrates how the ctenidia must be responsible for selection as well as for initial collection, material passing the palps to proceed directly to the mouth mainly by way of the very short proximal oral groove on the left side, only a third of this via the very long one on the right (figure 19*d*, *f*, p.o.g.l., p.o.g.r.). As further shown in this figure there is a greater twisting of this entire region in relation to the byssal apparatus in *Anomia* (*e*) than there is in *Pododesmus* or *Heteranomia* (*f*), a further instance of asymmetry in what was the horizontal, but has become the sagittal, plane.

Although hypobranchial glands are absent, Atkins (1936) did note the presence in the suspensory membranes of *A. ephippium* of 'small rounded groups of granular cells which are probably glandular'. These do not occur in *Heteranomia*.

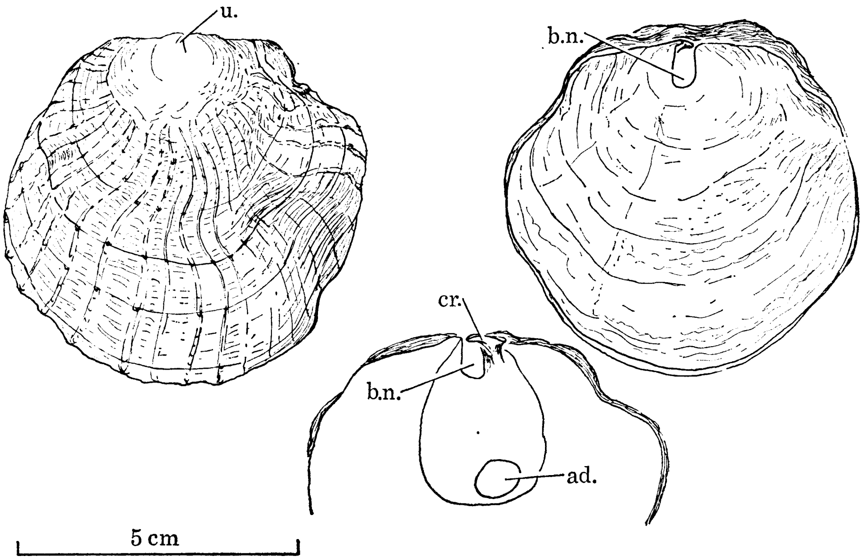

FIGURE 20. *Patro australis*. (*a*) Left valve, outer surface; (*b*) right valve, under surface showing restricted byssal notch; (*c*) right valve, inner surface.

Patro australis (Gray, 1847)

Shells of this interesting species were obtained from the British Museum (Natural History). The general appearance of the characteristically rounded and convex upper valve with radiating ribs and of the flat but regular under valve is shown in figure 20, the upward protrusion of the posterior regions in figure 21. Other details are supplied by Beu (1967) who also describes the shells of two other species. Although obviously resembling *Anomia*, differences appear great enough to justify separation as a distinct genus although it is unfortunate that only shells were available. The byssal notch is even smaller than in *Anomia*, its opening apparently wider and the

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crurum carried on a shorter 'stalk'. Moreover the two retractor scars on the upper valve (figured by Beu) are smaller than the adductor scar; all three are approximately in a straight line. The upper valve of species of *Anomia* reveals that the animals have grown, initially if not always in the peripheral regions, closely adpressed to the substrate. This is not so in *Patro* where all the surface of the under valve is sculptured and may also be covered with encrusting organisms. Little is known about *P. australis* which occurs around the northern coasts of Australia (Iredale 1939) or indeed about any species of *Patro* but the obviously small byssus is probably directed diagonally 'upward' so that the lower valve projects clear of the surface. Beu states that 'It appears that these forms occupy some situation where the shell is able to grow unrestricted'. The larger adductor scar indicates the greater size and significance of the adductor when the area of byssal attachment is reduced while the upward curvature of the posterior regions will carry the exhalant current with contained faeces and pseudofaeces well clear of the animal which may possibly inhabit more turbid water than other anomiids. Pending confirmation of these assumptions (including a study of the contained animal), there appears adequate reason for regarding *Patro* as a separate genus of somewhat different habits from *Anomia* where the very flattened valves are invariably closely adpressed to a clean rock surface.

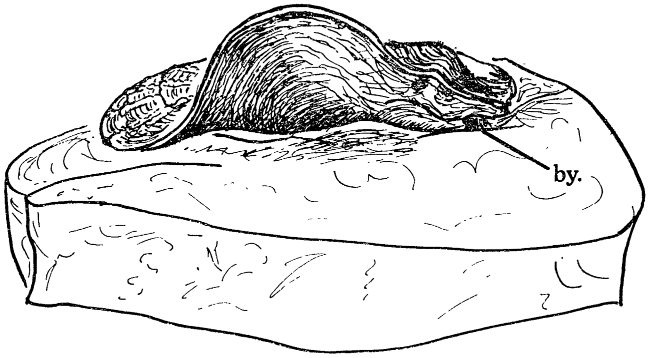

FIGURE 21. *P. australis*, probable posture in life with raised posterior surface where exhalant current and pseudofaeces discharged.

ENIGMONIA AENIGMATICA (IREDALE 1918)

This remarkable mollusc, a motile bivalve limpet, was first personally observed when living specimens were brought from Singapore by my then colleague, now Professor, Gareth Owen. A short note was written (Yonge 1957 *b*). The history of the genus, first described by Chemnitz in 1795, is outlined by Iredale (1939) who was responsible (1918) for the change from its former name of *Aenigma* Gray. Under that name Bourne (1907) produced a detailed account of structure although with little reference to other anomiaceans and without seeing the living animal. His specimens came from Shelford who later (1916) described them as occurring on the stems of Nipa-palms in Sarawak where they were found attached at levels above high water of neap tides.

Ample material was obtained for examination in life and for subsequent study intact and in sections during a visit to the Department of Zoology, University of Singapore in 1968. In the limited personal experience of the author, this species occurs very commonly on the main stems, branches and lowest leaves of the white mangrove, *Avicennia* from which it was collected at Kranje to the west of the Causeway, on the north side of Singapore Island. The highest sites

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were on leaves some 2 m (6 ft) above lowest tidal levels. It also occurs on *Rhizophora* and *Bruguiera* but fuller accounts of the habits and distribution of this species have come from the recent observations of Berry (1975) and Morton (1976) with personal communications from Dr Brian Bayne. It occurs widely throughout southeast Asian waters, always in association with mangrove formations. It can resist the effects of desiccation for altogether exceptionally long periods.

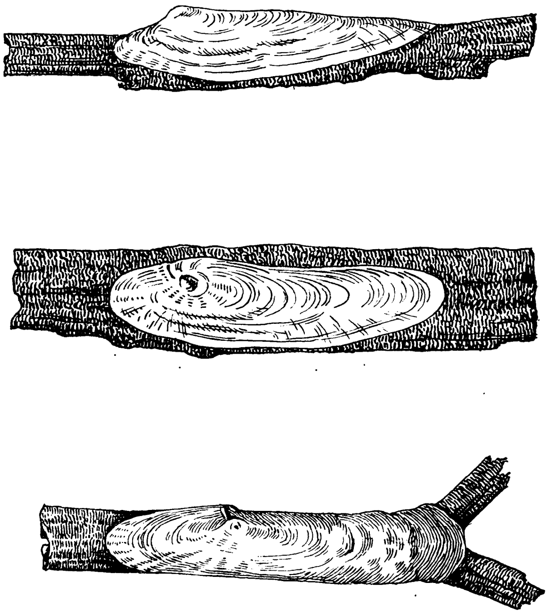

FIGURE 22. *Enigmonia aenigmatica*, drawings of specimens of '*E. rosea*' permanently attached to curved surface of mangrove branch. (Natural size.)

External form and habits

E. aenigmonia is extremely compressed, attaining a greatest length of up to 5 cm and being about half as broad as this. As originally described by Gray (1849), this is probably a polymorphic species consisting of four growth forms. This conclusion is strongly supported by Morton (1976) who relates each form to a distinct habitat. Some of the forms have been described as separate species notably, '*E. rosea*' which occurs on stems (figure 22). The validity of this species is accepted by Berry who examined animals which although 'certainly mobile during early growth' were always, even when only 6 mm long, attached to stems with the 'horny blades of byssus thickened distally to unite to a continuous byssal plate interdigitating with the bark of the tree'.

All specimens personally examined were completely flat, living on leaves (figure 23) on which they moved about when submerged, attaching only temporarily. When exposed they attached at any place on the leaf surface, there resisting the effect of desiccation until again covered with water. In contrast to the animals on stems which are dark reddish brown, the flat individuals are usually almost colourless with the organs visible through the translucent left valve. All other Anomiacea are rounded but, as Bourne (1907) pointed out, in *Enigmonia* the 'dorsal ventral axis' (the foot regarded as anterior) 'has been rotated through an angle of 40° in a posterior-anterior direction'. This is indicated by the direction of the umbo and the line of fused valve shown in figure 26. The effect, as already noted, is to produce a posteriorly extended shell twice

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as long as it is broad. No personal observations were made on orientation but Morton (1976) found that those attached to stems or strut roots always had the anterior end downward and that animals tended to be orientated in relation to the flow of water locally.

When placed in water these flat individuals almost immediately extend the foot. As shown in figure 23, this is a long, flat, somewhat ribbon-like organ with an attenuated terminal 'flagellum' which is constantly active apparently possessing tactile functions. The flattened region alone can extend for more than half the length of the shell and by its means animals crawl actively over the surface of mangrove leaves and with equal ease on the glass side of an aquarium. This is a crawling foot, with a sole like that of a typical gastropod or, among bivalves, of surface dwelling Erycinacea such as *Galeomma* (Popham 1940; Morton 1973). In movement the foot appears to flow, the distal region (excluding the flagellum) spreading out and acting as a sucker while the pedal retractors, visible through the translucent pedal tissues, contract and draw the animal along. The surface is ciliated with particles carried towards the base eventually to collect upon, and then be rejected from, the upper surface of the short 'heel'. Here the locomotory function in young *Pododesmus* (and doubtless other anomiids) is retained and developed with a new terminal addition in the probably sensory flagellum while the cleansing cavity subsequently developed in the foot of *Pododesmus* never appears.

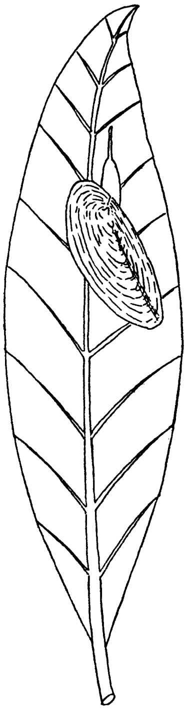

FIGURE 23. *E. aenigmatica*, motile individual crawling on surface of leaf of mangrove, *Avicenna* (half natural size).

When turned upside down (figure 24) the full length of the foot can be seen, some 2 cm (excluding the flagellum) in an animal with a shell 3.7 cm long. Under these conditions it emerges to its full extent initially groping for attachment, twisting round until it achieves this, the short heel turning upwards. When sure attachment is made, muscular contraction (according to Morton the concern solely of the adductor) rights the animal. The process is more fully

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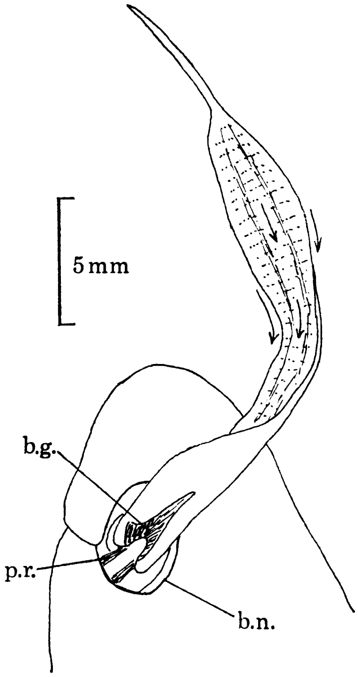

FIGURE 24. *E. aenigmatica*, under surface of anterior end of motile individual showing foot with terminal flagellum extending out of byssal notch with ciliated under surface forming 'sole'.

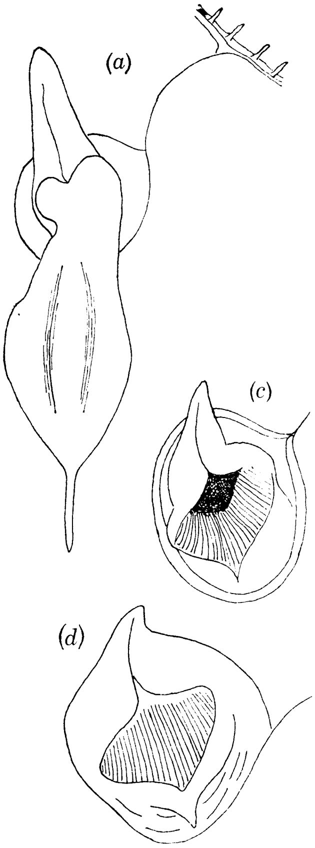

FIGURE 25. *E. aenigmatica*, (*a*)–(*d*) stages in withdrawal of foot with accompanying enclosure of the surface of the byssal gland (magn. × *ca.* 3).

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described by Morton (1976). Attached to coverslips, animals were viewed from the under side when the foot could be followed withdrawing in the stages shown in figure 25. The long distal region is first pulled in by contraction of the retractors to be eventually followed by the heel. This involves increasing exposure of the ridged surface of the byssal gland but without visible indication of the 'colourless parallel plates of byssus substance' (Bourne 1907) which were only apparent after detachment. These then appeared, transparent and superficially ridged, clearly the product of byssal secretion directly applied over a relatively wide area, i.e. *not* by the planting of individual threads. Doubtless this is much as it is in other anomiids but in *Enigmonia* the byssal secretion is *not* calcified. Certainly in these flat individuals it is used only for 'temporary' – although during periods of neap tides often extremely prolonged – attachment. Curved individuals (figure 22) are permanently attached by the same means.

The foot protrudes from the byssal notch in the region of the line of supradorsally fused upper valve and usually probes in various directions. It then proceeds to pull the animal with the pointed anterior end foremost (figure 23). The foot turns readily in any direction drawing the shell after it.

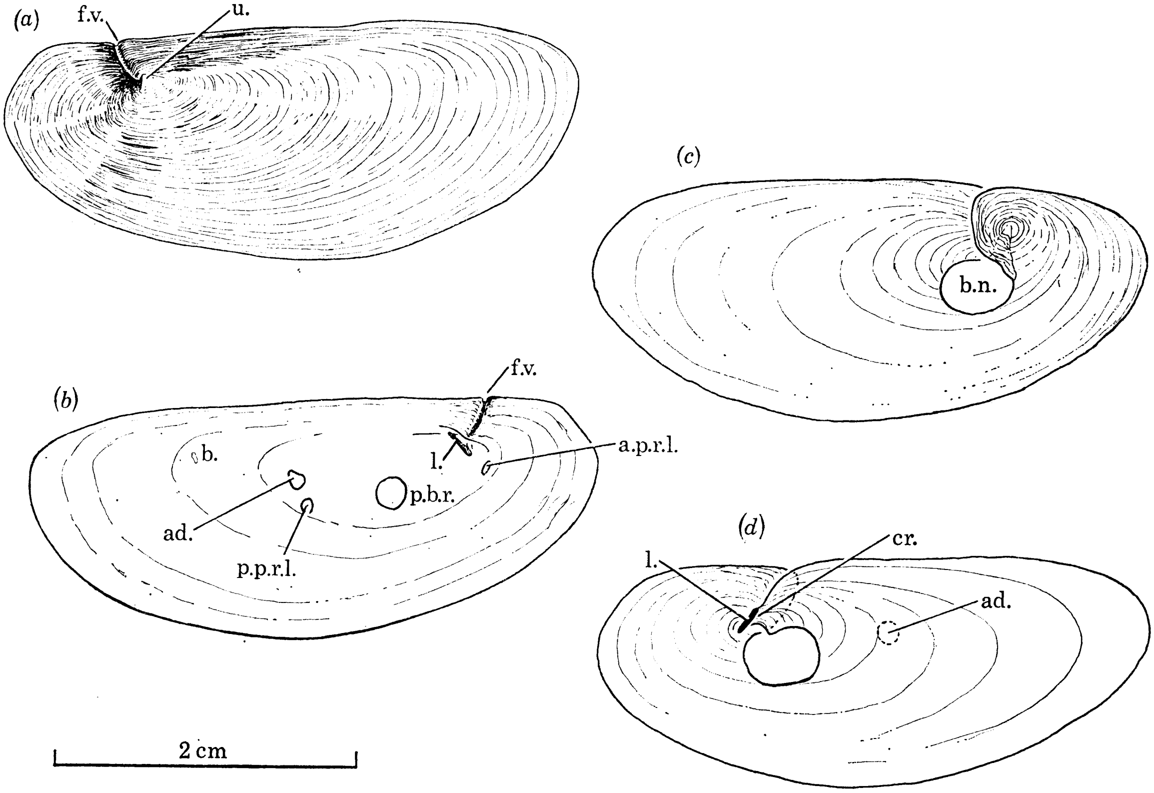

FIGURE 26. *E. aenigmatica*. (*a*) Left valve, upper surface; (*b*) left valve, inner surface; (*c*) right valve, under surface; (*d*) right valve, inner surface.

Shell

The appearance of the shell valves, the upper slightly convex, the lower completely flat, is shown in figure 26. Although very thin, the left valve (figure 26*a*) is substantially thicker than the excessively delicate right valve, it is also usually brown and glistening whereas the latter is colourless. Like all anomiids, the valves are composed, apart from the restricted central region,

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exclusively of outer, prismatic shell layer with a relatively thick periostracal covering. Many individuals show extensive evidence of repair, rapidly accomplished when only these layers are involved as strikingly demonstrated in *Pinna* (Yonge 1953). The conspicuous, diagonally pointing umbo on the left valve is subcentrally placed with a much longer extent of fused shell between it and the valve margin than in *Anomia*.

Viewed from above, *Enigmonia* appears as a very flattened and elongate, eccentrically spired, limpet. From the underside of the left valve (figure 26*b*), the ligament (described below) is now correspondingly far removed from the margin. There are widely separated small anterior and posterior retractor scars (a.p.r.l., p.p.r.l.) and midway between them the larger scar of the byssal retractor (p.b.r.). The adductor scar (ad.), situated in about the middle of the valve, is only some one third of this size. There is also, as noted by Bourne, the scar of a small branchial muscle (b.).

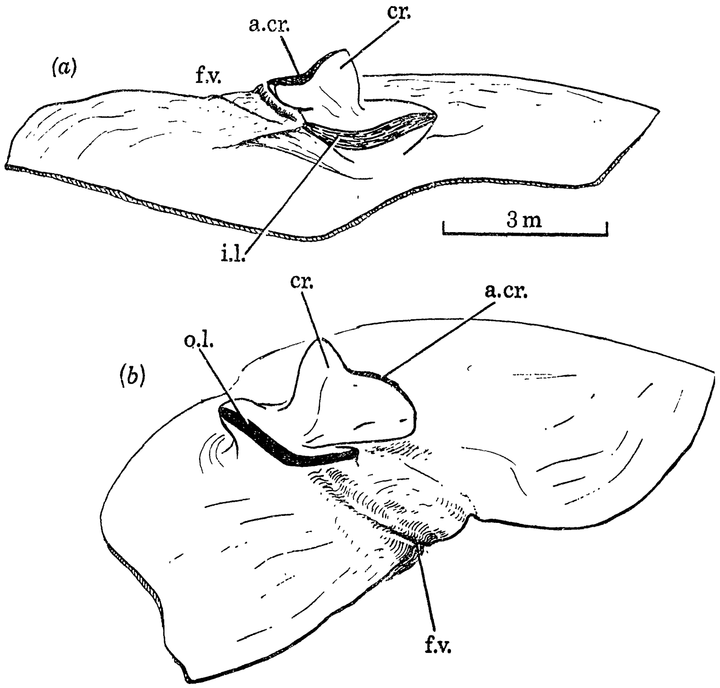

FIGURE 27. *E. aenigmatica*, ligamental region of left valve, crurum detached from right valve. (*a*) Ligament viewed from ventral surface, inner layer alone viewed; (*b*) viewed from dorsal aspect showing complete fusion of outer ligament layers, alone viewed on this side.

The right valve (figure 26*c*, *d*) is everywhere overlapped by the left one. Unlike *Anomia*, there is here very extensive supradorsal extension although no trace of an umbo. As a consequence of general posterior elongation, there is extensive underlap from the anterior of the posterior side of the entrance into the byssal notch so that the very rounded opening is completely enclosed. For reasons that become apparent later, the overlapping surfaces never fuse. Because the byssus is uncalcified, there can be no union of this with the margins of the notch. That of the adductor is the only muscle scar; there is no right anterior pedal retractor.

Crurum and ligament

The posterior extension of the shell affects the form of the crurum (figure 26*d*) which, in comparison with that of *Anomia* (figure 18) is slewed round from the horizontal to the diagonal,

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the anterior end pointed down with the basal region blade-like, unlike the rounded pillar on which the crurum in other anomiids is carried. Moreover, owing to the deep enclosure within the valves, the attaching ligamental surface on the right side points upwards the ligament extending vertically (in relation to the substrate) instead of horizontally as it does in *Pododesmus* or *Anomia*. In other words the ligament again connects the valves laterally although it can no longer serve as a hinge; it acts solely to provide an opening thrust whereby the upper valve rises clear of the under one when the byssal retractor and the adductor relax.

As in *Heteranomia* and *Anomia*, the ligament is completely enclosed within the secreting tissues but here, like *Heteranomia*, the anterior and posterior outer layers fuse to form a continuous layer dorsal to the inner layer. The lozenge-shaped ligament so formed is best displayed by cutting through the base of the crurum and viewing the intact ligament from both sides as shown in figure 27.

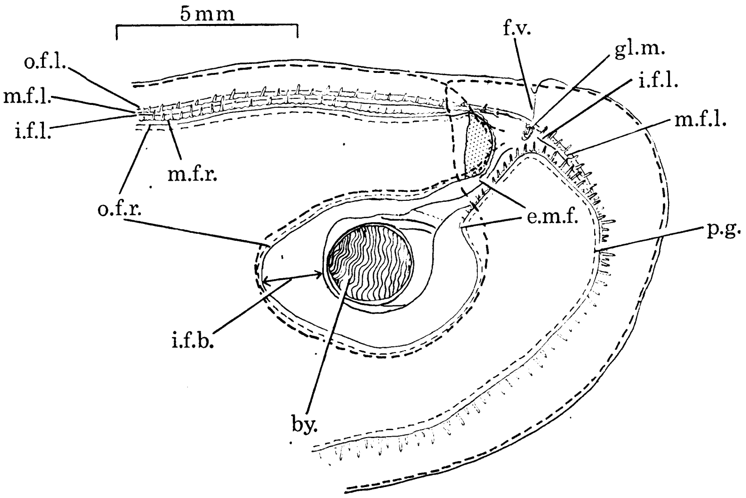

FIGURE 28. *E. aenigmatica*, anterior end viewed from under surface showing disposition of mantle margins around byssal notch and their secondary union dorsal to the ligament with overgrowth of mantle with periostracum on posterior side (stippled).

Mantle

As in *Anomia*, apart from the supradorsal regions (see below) the mantle lobes are free throughout. The marginal mantle folds have the usual structure, those of the upper valves notably the larger. In both there is conspicuous periostracal secretion; when valves are opened there is an obvious 'veil' of transparent periostracum stretching between the edge of the valves and the withdrawn margins of the mantle lobes. The periostracal layer of the shell is always intact and may well play an essential role in preventing loss of water through the otherwise almost entirely prismatic shell.

A single row of tentacles of very varying lengths arises from the middle fold, the longest, occurring at roughly regular intervals, extending for lengths of up to 3 mm beyond the margin of the shell. But sections indicate less sensory capacity than in *Pododesmus* where the tentacles are relatively larger with easily identified nerves. The inner mantle folds form pallial curtains up to 2 mm wide. These are very mobile in life when they may protrude beyond the valve margins. This fold enlarges around the byssal notch to widths of up to 4 mm in an animal 4 cm long (figure 28, i.f.b.). As appears in figure 28 it serves as a washer (width indicated by two-headed arrow), which will retain moisture in the mantle cavity during the long periods of exposure. The sensory middle fold is absent.

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The extent to which the supra-dorsal extensions of lower mantle lobe and valve overlap is shown in this figure (thicker broken lines) the anterior region lying beneath (above in the figure) the posterior region which carries the crurum and ligament (shown in figure 29). The mantle actually extends around the under surface of the end of this posterior region, as shown stippled in figure 28 which explains why the two shell lobes never fuse because separated in this way. The enclosed notch is rounded with a centrally placed byssus. The line of shell fusion on the under side of the upper valve is shown. There is no subcrural groove.

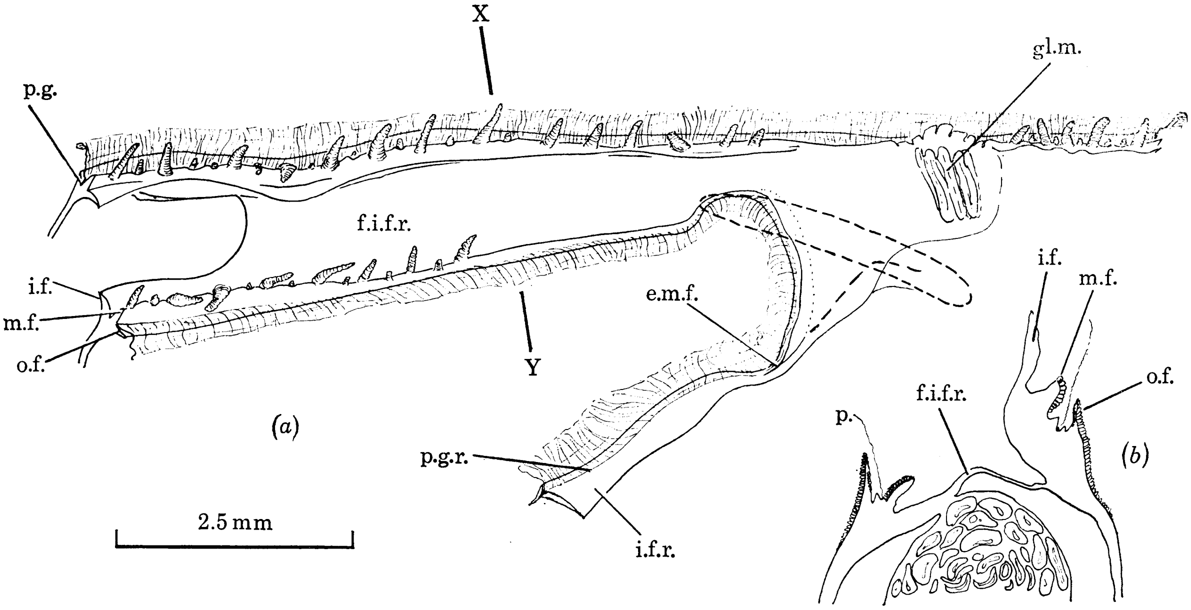

Figure 29. *E. aenigmatica*, mid-dorsal region viewed from below showing extent and nature of secondary attachment between mantle margins supradorsally. (*a*) Viewed somewhat from the dorsal aspect, outline of crurum indicated by broken lines; (*b*) transverse section along region X–Y in (*a*).

Supradorsal mantle fusion

The position reached as a result of supradorsal extension in *Pododesmus* with the ligament almost enclosed and the shell but *not* the mantle lobes fused in the upper valve is shown in figure 6, this later breaking down as shown in figure 7. This has led, apparently independently, in *Heteranomia* and *Anomia* to supradorsal fusion of the upper mantle lobes with complete enclosure of the ligament. This has further involved some cross connection between the mantle margins of the two valves, symmetrically in *Heteranomia* but asymmetrically in *Anomia*, both shown in figure 17. The region of attachment in the latter genus is very short so that it is only possible to study conditions in sections. Owing to the great elongation, this region is pulled out posteriorly in *Enigmonia* and so can be more explicitly described.

The three marginal folds of left and right mantle lobes are shown both in surface view and in section in figure 29, the outer (o.f.) with the periostracal sheet emerging from the groove on the inner side, the middle (m.f.) with a single row of here contracted tentacles and the inner (i.f.) forming the pallial curtains. Below the point of supradorsal fusion of the left valve lies a small but conspicuous swelling (gl.m.) revealed in sections (figure 30) as glandular and representing considerable inpushings at the base of the outer side of the middle fold, i.e. just within the periostracal groove. It is difficult to find a function for this gland any secretion from which will

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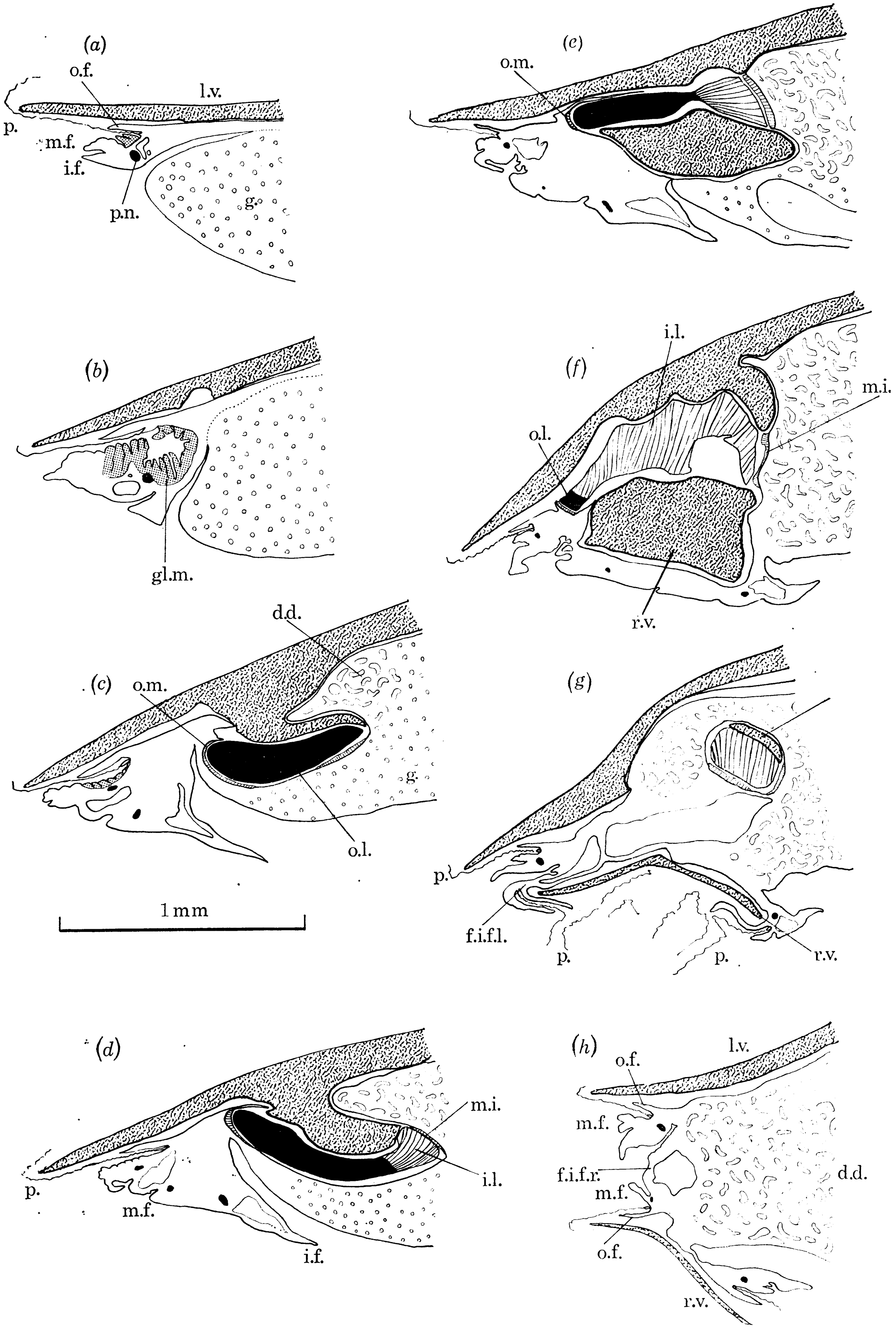

Figure 30. *E. aenigmatica*, transverse sections through dorsal regions of mantle lobes and valves starting anterior to glandular mass (gl.m. in figure 29). For details see text.

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flow *over* the periostracum. This is not a position in which mucous glands appear in other bivalves; just possibly this gland is in some way associated with permanent shell fusion.

The mantle margins of the two lobes are attached around the region of fusion and for some distance posterior to this. As in *Anomia*, this involves fusion of the inner fold of the right side (figure 29, f.i.f.r.) with the mantle surface below the corresponding fold on the left side. This is shown in the transverse section cut through the line X–Y shown in figures 29*a*, *b*. The area of fusion extends anteriorly to just within the byssal notch on the lower valve and enclosing the glandular region in the upper valve. It is shown in section in this region in figure 30*f*. This longer extent of attachment between the mantle lobes (indicated in figures 29 and 31) may be of significant value to this, at any rate occasionally, motile species, by keeping the two valves in greater contact.

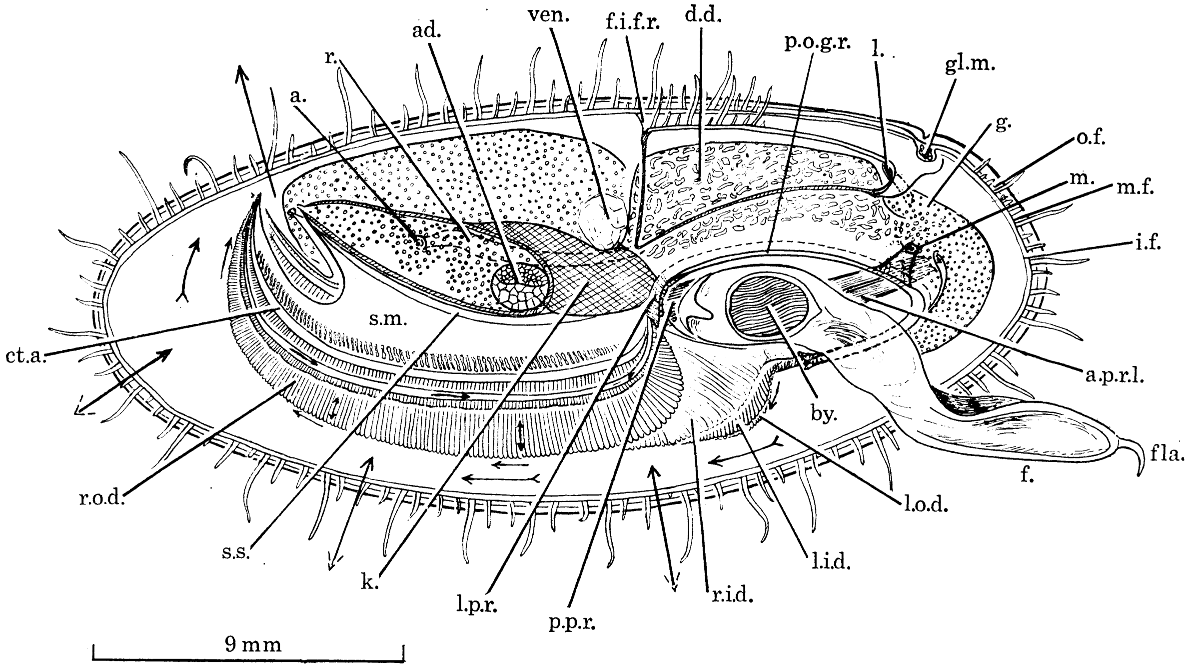

FIGURE 31. *E. aenigmatica*, animal viewed within left valve, i.e. from under side. A portion of the right mantle lobe is retained indicating the extent of secondary supradorsal union with left lobe.

Pallial organs

The appearance in life of these when viewed from the right side after removal of lower valve and mantle lobe is shown in figure 31. This may be compared with the figures of Bourne (1907) showing preserved specimens and those of Berry (1975) and of Morton (1976) of living but non-motile individuals. Conditions are fundamentally similar to those in *Anomia*, all the same features, such as the presence of hypobranchial glands and the more symmetrical ctenidia found in *Pododesmus*, are absent. The distinctive features are due to the greater flattening with the anterio-posterior extension and their effects on the form of the mantle/shell and so on that of the enclosed viscero-pedal mass. The mantle lobes with their single row of bounding tentacles and extent of supradorsal fusion are shown in figure 31, also the foot with its terminal flagellum and turned up heel and enclosed byssal apparatus. The foot is much larger and the byssus much smaller than in either *Pododesmus* or *Anomia*. Both anterior and posterior pedal retractors (a.p.r.,

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p.p.r.) are well developed, much of the latter obscured by the heel of the foot. The centrally placed adductor is small but the area of catch muscle is relatively much larger than in the other anomiids indicating a greater significance in adduction, probably in correlation with the small area of byssal attachment.

Ctenidia and palps

The ctenidia extend anterio-posteriorly only curling dorsally near the posterior end. For the greatest part of their length they are attached to an increasingly deep suspensory membrane (s.m.), much folded near the line of ctenidial attachment. These membranes contain branchial muscle fibres radiating from a point of attachment to the valve on the right side (figure 32, br.at.r) but to the mantle lobe only on the left. The anus (a.) opens at the end of a long papilla in the bay between these points of posterior attachment. In structure and function the ctenidia are essentially similar to those of *Anomia* (figure 19*b*) with the same double set of frontal cilia described by Atkins. There is also the same association of lengthened anterior filaments of the inner right demibranch (r.i.d.) with the two demibranchs of the left side (l.i.d., l.o.d.) (figure 19*e*).

Extension of the body (very pronounced on animals attached to stems) has pulled out the encircling series of palps and oral grooves into a long oval while greater bilateral asymmetry has carried the mouth (well covered by the deep upper lip) still further to the under side. The whole complex has now slewed so far around that the right palps (l.p.r.) are directly posterior to, and the left palps (l.p.l.) anterior to, the centre of the byssal mass. The proximal oral grooves on the two sides are even more asymmetrical than in *Anomia*. Morton (1976) has noted that the few very short folds carried on each pair of palps are non-selective, i.e. all cilia on both folds and grooves beat towards the mouth. This may well also be true of *Anomia*, in both cases correlated with the great selective capacity of the anomiid ctenidia as originally pointed out by Atkins (1936). However, as Morton points out, such reduced powers of selection may be of advantage to animals which can only feed over very limited periods of flood tides and then only on the very finely divided particles in still mangrove waters. A somewhat parallel condition occurs in the mytilid, *Fungiacava*, which lives symbiotically within the skeleton of fungid corals taking food from the coelenteron. Hence the ctenidia are enlarged but the palps reduced to the merest vestiges (Goreau, Goreau, Soot-Ryen & Yonge 1969).

Mantle circulation and cleansing currents

An inhalant current is drawn in over the entire under surface passing through the gill to emerge postero-dorsally above their free terminal regions. As the animals are normally disposed, anterior end upwards when on a vertical or a sloping surface (Morton 1976), this involves entrance of water above and to the one side and its emergence lower down and on the other side. Personal observations (all on flat individuals on leaf surfaces) revealed a constant inward and outward flow in the *inhalant* region (where the valves may gape as widely as 2 mm). This appeared to be a result of rhythmical pulsations of the conspicuous branchial muscles which appear of greater significance here than in other anomiids. Ciliary currents on the mantle surface were weak and pseudofaeces tended to collect in a line some distance within the mantle margins and to be ejected when the valves closed. Only weak currents carried material into the exhalant chamber where, however, currents were powerful on all surfaces including those of the prominent anal papilla. Long brown faecal strings joined pseudofaeces for expulsion here.

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Morton found powerful cleansing currents throughout the mantle cavity, similar to those described for *Pododesmus*. These differences are possibly correlated with habitat.

Visceral organs

No more need be noted than is required to emphasize or amplify the findings of Bourne with the recent functional studies of stomach, digestive diverticula and style sac by Morton (1976), all with reference to the primitive conditions in *Pododesmus*. Details of surface anatomy are given in figure 31 of internal anatomy, somewhat diagrammatically presented, in figure 32.

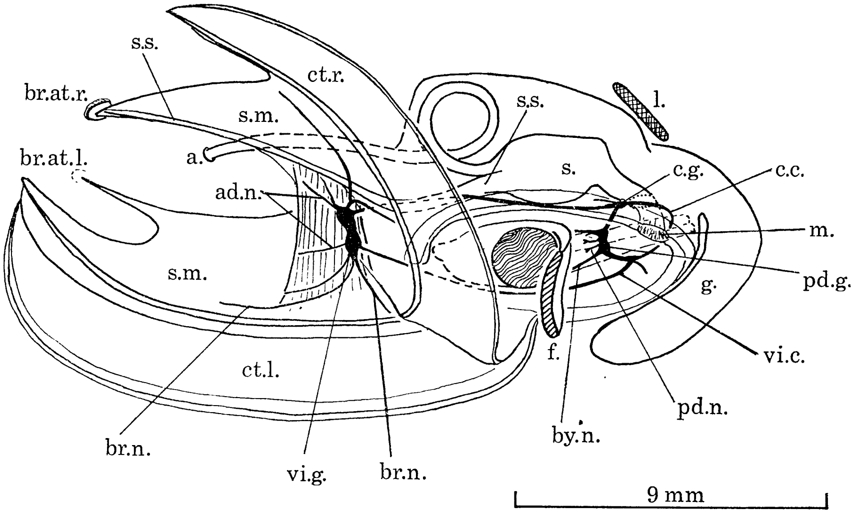

FIGURE 32. *E. aenigmatica*, dissection revealing course of gut and major nerves (right ctenidium raised to reveal visceral nerves).

Gut

The positions of mouth and anus are shown in both figures, of oesophagus and stomach, both elongated, with backward extended and single-coiled mid-gut, in figure 32. The characteristically long separate anomiacean style-sac (s.s.) is situated, as in *Pododesmus* and apparently all Anomiacea, well to the right where it extends above the suspensory membrane almost to the point of attachment to the mantle. Berry states that the style persists at all stages of the tide. Full details of internal structure and ciliary currents in the stomach and disposition of the openings into the digestive diverticula are given by Morton who also deseribes the histology of the style-sac. Differences from *Pododesmus* appear no more than those imposed by lengthening of the body. The stomach is of the same type.

Circulatory and excretory systems

The position of the large ventricle (ven.) is shown in figure 31, the rectum passes below it and between the auricles; there is no pericardium. The excretory system is fully described by Bourne who describes a pericardial gland absent in *Anomia*. In consequence of lengthening, the large left kidney (k.) no longer encircles the byssal muscle but stretches from in front of this muscle, passing between ventricle and adductor, almost to the anus. The right kidney is smaller.

Reproductive system

The gonads form conspicuous yellow masses, that on the left again much the larger with one lobe extending in a curved lobe around the extreme anterior end of the animal (figure 31, g.)

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while a posterior lobe penetrates the mantle lobe behind the black mass of the digestive diverticula. Berry found evidence of sex change.

Nervous system and sense organs

The dissection (figure 32) shows the distribution of major nerves and ganglia of which the visceral and the pedal (possibly receiving sensory impulses as in the equally modified *Fungiacava* (Goreau *et al.* 1969) are much the largest. Although more slewed to the right, there is less asymmetry in this nervous system than in that of *Pododesmus*. There is no attachment of the base of the ctenidial membranes to the rectum as there is in that genus with no abdominal sense organs – possibly unnecessary for life in still waters with little suspended matter. There is an elongate osphradium of doubtful function. Otoliths lie close to the pedal ganglia.

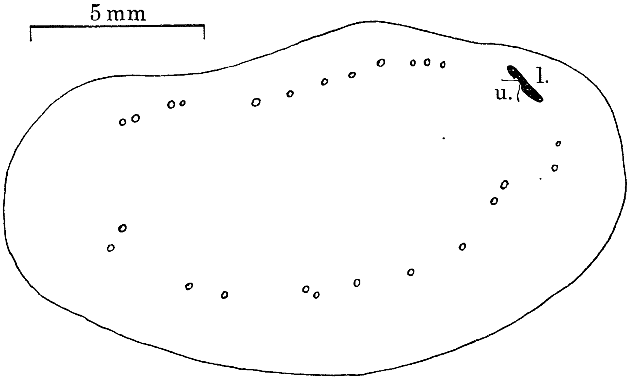

FIGURE 33. *E. aenigmatica*, upper view of flattened mobile individual showing distribution of pallial eyes.

Pallial eyes

Bourne noted the presence on the left mantle lobe of 'a number of deeply pigmented spots, arranged in an irregular oval at a considerable distance from the pallial margin' and which varied in number. In the specimen he figured there were 23, in the one shown in figure 33 there are 25. These structures have nothing to do with the mantle margins and so cannot be compared with the pallial eyes in Pectinacea and Cardiacea. They are formed by the inner and outer epithelia of the upper mantle lobe, each, as described and figured by Bourne, consisting of what he regarded as a cornea, a lens and a vitreous body together with a deep pigmented layer, this alone formed by the inner epithelial layer, to which he attributed retinal powers. However apart from the pigmented layer (obvious to the naked eye) these various structures are very simply developed, the whole structure sometimes no more than a flat plate, these 'eyes' being not comparable structurally with those in the Pectinidae or Cardidae.

Bourne regarded these as simple photo-receptors pointing out that the upper valve (certainly of flat individuals on leaves) is so thin and translucent that much light must penetrate. There can be no other bivalve that lives so high up as does *Enigmonia* and is so long exposed to air. Berry estimates that the highest specimens he observed must have been fully exposed for 245 days in the year, twelve of the continuous 'dry' periods lasting for 10 days or longer. Specimens he kept in the laboratory survived in air for 6 weeks. This is possible because they live in a damp still atmosphere with minimal evaporation. Bourne notes that some information about the presence or absence of light would enable such exposed animals to open the valves slightly in

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the dark so permitting some aeration of the water retained in the mantle cavity (his further statement that water is retained within mantle folds on the under surface of the mantle cavity was not confirmed). It would certainly appear that life in this, for a bivalve, unique habitat, has been accompanied by the appearance of no less unique photo-receptors under the upper valve. The only comparable molluscan structures are the more elaborate megaesthetes which penetrate the plates of certain chitons to be stimulated by the light which falls on the flat dorsal surface of these animals.

Table 1. Family Anomiidae

(Right valve always thinner)

	species examined				
characters	*Pododesmus cepio*	*Monia squama M. patelliformis*†	*Heteranomia squamula*	*Anomia simplex A. ephippium* ‡*Patro australis*	*Enigmonia aenigmatica*
general form	rounded	rounded	rounded	slightly longer than deep	elongate
muscle scars left valve	**2**	**2** or **1**	1	3	3
crurum	**convex**	**convex**	straight	straight	oblique
r. anterior retractor	**yes**	**yes**	no	no	no
subcrural groove	pointed	pointed	sometimes pointed	no	no
supradorsal fusion of:					
1. mantle lobes	**no**	**no**	yes	yes	yes
2. mantle margins	—	—	symmetrical	asymmetrical	asymmetrical
3. left valve	**temporary**	**temporary**	permanent	permanent	permanent
4. outer ligament layers	**not unite**	**not unite**	unite	not quite unite	unite
calcified byssus	**yes**	**yes**	**yes**	**yes**	no
hypobranchial gland	**yes**	**yes**	no	no	no
demibranchs, union ascending arms	**ciliary junctions**		—	tissue fusion	tissue fusion
anterior asymmetry of demibranchs	**no**	**no**	—	yes	yes
pallial eyes	**no**	**no**	**no**	**no**	yes
foot in adult	**cleansing**		**cleansing**	**cleansing**	**cleansing** locomotion
habit	**byssally cemented**		**byssally cemented**		temp. byssal attachment

Possession of primitive anomiacean characters indicated by bold type.

† Dubiously separate species. ‡ *Patro* similar for shell characters; others unknown.

Relations within the Anomiidae

The greater number of workers have regarded all the genera so far considered as belonging to the one family Anomiidae usually also incorporating the two further genera *Placunanomia* and *Placuna*. Beu (1967) considers the Anomiidae as divisible into the subfamilies Anomiinae (*Anomia*, *Patro*, *Enigmonia*) and Placunanomiinae (*Placunanomia*, *Pododesmus*, *Monia*). But, as appears later, *Placunanomia* is certainly to be associated with *Placuna* in a separate family while there appears no reason for separating *Pododesmus* (*Monia*) from the first three genera to which *Heteranomia* should be added. We are now in a position to consider interelationships within this family Anomiidae.

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To date, the distributions between these genera have been largely conchological, concerned with the number of muscle scars on the upper valve – single, double or treble. Other significant shell characters have emerged in the course of this research, namely the shape of the crurum with the presence or absence of an attaching anterior retractor and of a subcrural groove, the absence of these associated with a straight crurum and a more rounded byssal notch. Fusion of the byssal plug with the walls of the notch, although claimed as a significant character, appears (apart from *Enigmonia*) to occur in old individuals of many, if not all, species. The same applies, although certainly less frequently, to fusion across the opening of the notch to convert this into a foramen. The extent of supradorsal fusion of the ligament, itself dependent on the degree of union between the mantle folds that secrete the outer layers, is of the first importance.

Other anatomical features concern the hypobranchial glands and three features in the ctenidia, namely absence of reflexion of the demibranchs in *Heteranomia*, the degree of fusion of the ascending arms of the inner and outer demibranchs and anterior symmetry. There is also the question of the mode of secondary attachment between the mantle lobes following complete supradorsal fusion. All are listed and compared in table 1 with what are regarded as primitive characters shown in bold type.

It is apparent immediately that *Pododesmus* and *Monia* are identical, also that they possess the greatest number of primitive features. In *Heteranomia* primitive characters like hypobranchial glands have been lost, the demibranchs are uniquely extended as single unreflected lamellae while extended pallial attachment dorsally is by way of fused inner mantle folds. This is a very distinctive genus, evolving along different lines from *Anomia* and related genera.

Anomia also loses hypobranchial glands and the right anterior byssal retractor but the ctenidia differ in different ways from those of *Pododesmus*, by greater tissue fusion and particularly by the unusual anterior asymmetry which it shares with *Enigmonia*. *Patro* and other unexamined genera may be similar.

Enigmonia, at first sight, appears significantly removed from these other anomiids. It is certainly very greatly specialized, living exceptionally high up in an environment of still and damp air provided by mangroves and Nipa palms where it is exposed for exceptionally long periods. Remote from *Pododesmus*, it is a highly specialized *Anomia* this involving great elongation (with effects on crurum and byssal notch) and complete fusion of the outer ligament layers together with the same form of secondary pallial fusion dorsally. Apart from being more extended the ctenidia precisely resemble those of *Anomia*. The really distinctive features are (1) the supreme degree of flattening with assumption of a limpet form and habit (though *not* of feeding), (2) the absence of calcification in the byssus – although there cannot be certainty, the strong impression is of an animal which has evolved from byssally cemented ancestors, (3) the re-acquisition of mobility by way of the enlarged (previously exclusively cleansing) foot with its unique terminal, and possibly sensory, flagellum, (4) the appearance of a distinctive type of pallial eye, exclusively on the left (upper) surface and *not* along the mantle margins. This is to be associated with the thin translucent shell and the exceptionally high level at which the animals live exposed for long periods to relatively strong light.

Nevertheless *Enigmonia* is much closer to *Anomia* than that genus is to the undoubtedly most primitive anomiacean genus *Pododesmus* with all genera so far considered members of the one family Anomiidae.

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Placunanomia cumingii Broderip, 1832

The genus *Placunanomia* which consists, so far as is known, of the two species *P. cumingii* Broderip and *P. panamensis* Olsson, is confined to the tropical east Pacific the former extending from the Gulf of California to Ecuador and possibly further south (Keen 1958), the latter apparently confined to Panama (Olsson 1961). Only their shells have been described. The better known *P. cumingii* is exclusively dealt with here. It occurs (Keen 1958) 'in fairly shallow water intertidally or offshore in depths of up to 25 fathoms'. The valves, roughly circular in outline, are much thicker than those of any other anomiacean. Diameters of up to 8 cm are attained, the margins raised very characteristically into three very pronounced plications (figures 34 and 35) resembling a 'plicated oyster' (Olsson 1961). The two species are cemented by way of a limited basal region on the under valve (figure 34*c*), the interesting nature of which is discussed below.

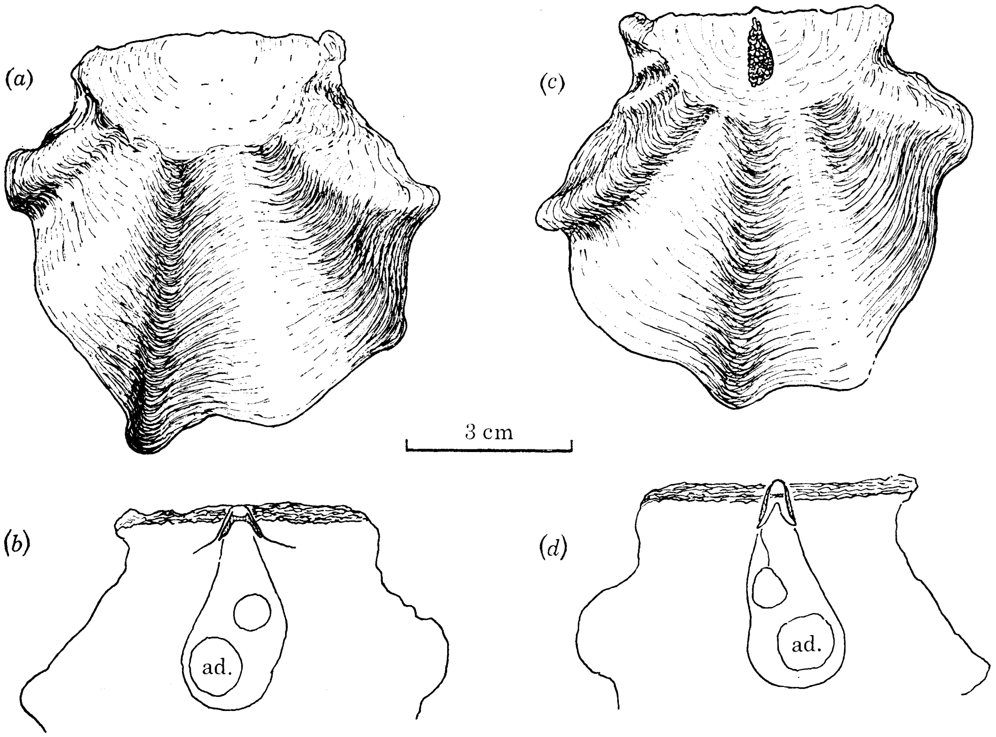

FIGURE 34. *Placunanomia cumingii*. (*a*) Left valve, upper surface; (*b*) left valve, inner view of dorsal half; (*c*) right valve, under surface showing area of byssal cementation; (*d*) right valve, inner view of dorsal half.

The probable posture in life is indicated in figure 35. It has unfortunately not been possible to examine living *Placunanomia*. This species occurs at some depth in the general vicinity of the marine laboratory of the Smithsonian Institution at Panama but enquiries there revealed no probability that specimens could be obtained. Fortunately three shells of very different sizes (figure 40) were obtained from the British Museum (Natural History) all originating in the Gulf of Dulse, Costa Rica. In addition a small upper valve with the preserved body of the contained animal (the only one personally examined) was received from Dr James H. McLean of the Los Angeles County Museum of Natural History and this has been extremely informative. This came from a depth of 20 fathoms in Francisquito Bay, Baja California.

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Shell

As appears in figure 34, during early growth both valves are flat and closely adpressed to the rocky substrate, later rising clear of this and being thrown into the characteristic plications. The shell is distinguished from that of all other anomiaceans owing to the thickness presumably of the outer calcareous layer of calcite foliated structure (Taylor, Kennedy & Hall 1969). The inner layer as usual is restricted to central regions. The umbo on the left valve, intact on the shell from Los Angeles (figure 36) is appreciably removed from the margin. This indicates a limited degree of supradorsal shell fusion although, as in *Pododesmus*, not of the mantle. As noted below, this region of purely shell fusion, together with the upper surface of the ligament, is eroded in older shells.

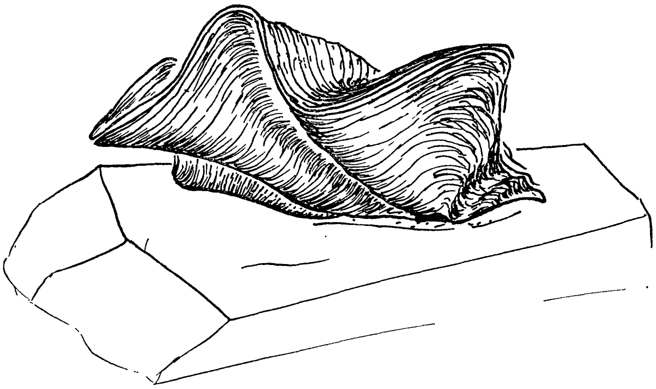

FIGURE 35. *P. cumingii*, probable posture of fully grown animal in life.

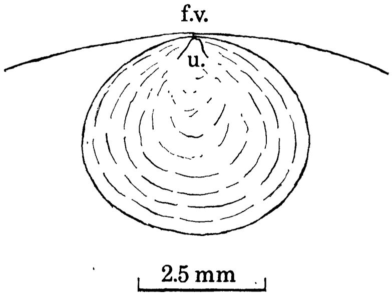

FIGURE 36. *P. cumingii*, umbonal region on left valve of young shell showing limited extent of supradorsal fusion.

There is no byssal notch – at any rate in shells within the size range available for examination – although a sinuous line (figure 34*d*) running from the dorsal margin to the area of byssal attachment does indicate its former site. It is not difficult to decide what must happen, namely initial attachment by way of a calcified byssus as in other genera with the area of such cementation increasing during this period while the right valve remains flat and adpressed. Three stages in this process are indicated in figure 40. Possibly about the time when the peripheral regions of the valves rise clear of the substrate, the result of a change in growth patterns around the mantle margins, the notch in the under valve closes. The sides certainly fuse in the region of the 'isthmus' (figure 34*d*) although the mantle tissues responsible for secretion are only *applied* (as shown from the under side in figure 37). Distally the margins of the notch become intimately fused with the calcareous byssal secretion. This builds up to form an upward projecting pillar.

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Later this secretion must be discharged upon and fuse with the inner calcareous layer of the valve; there is certainly a continuity of secretion as shown in the radial section (figure 38). The original area of calcified byssal attachment – a form of cementation to be distinguished from that produced (as in *Ostrea*, *Spondylus*, *Plicatula*, etc.) by pallial secretion – is large and intimate enough to secure the animal during subsequent growth. It certainly cannot be further extended. Meanwhile the area of byssal attachment – now within the under valve – becomes that of a

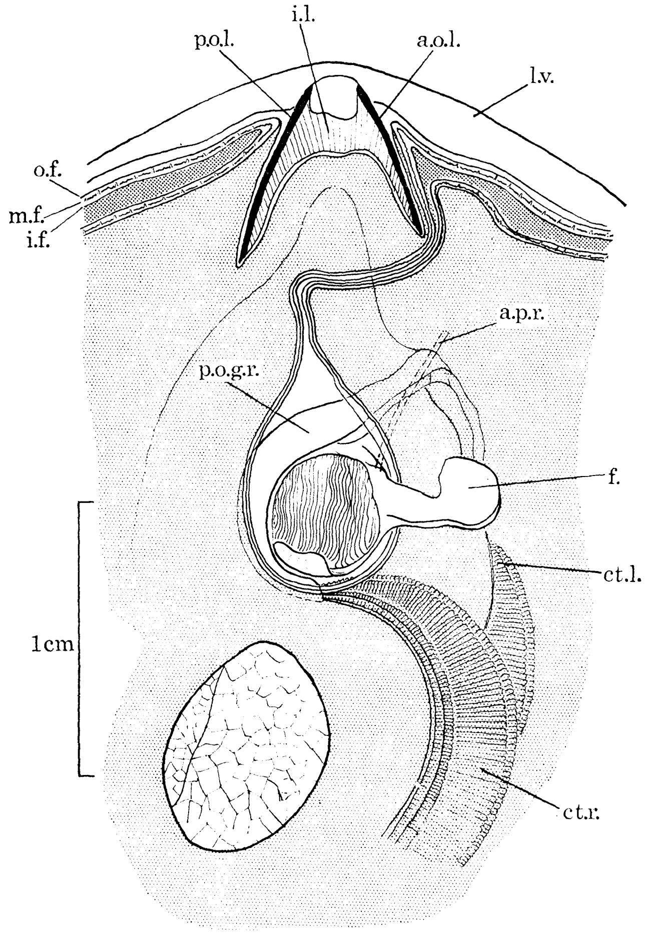

FIGURE 37. *P. cumingii*, under view of ligamental and byssal regions with right mantle lobe, byssal notch, ctenidia and adductor.

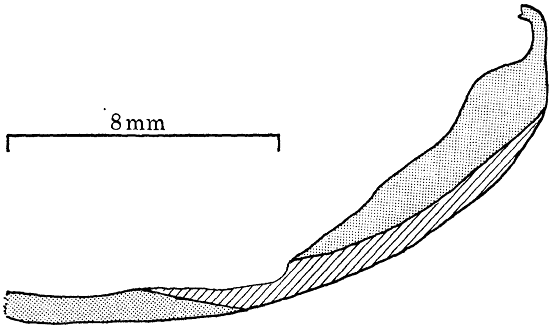

FIGURE 38. *P. cumingii*, radial section through right valve, hinge to right. Substance of valve stippled, extent of byssal secretion indicated by oblique lines.

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second and here somewhat *smaller* adductor, both valves having adductor *and* 'byssal retractor' scars (figures 34 *b*, *d*). The lower of the scars in (*d*) must represent the area of byssal attachment. It should be noted that whereas in the Anomiidae the position of the byssal retractor alters with change in that of the area of attachment to the substrate, this is *not* so in *Placunanomia*. After a certain stage in growth the area occupied by byssal attachment ceases to change, i.e. move further ventralward, but becomes intimately united marginally with the right valve fixing that firmly to the substrate. Meanwhile the position of the byssal retractor continues to move progressively further from the hinge and so obliquely away from the area of attachment.

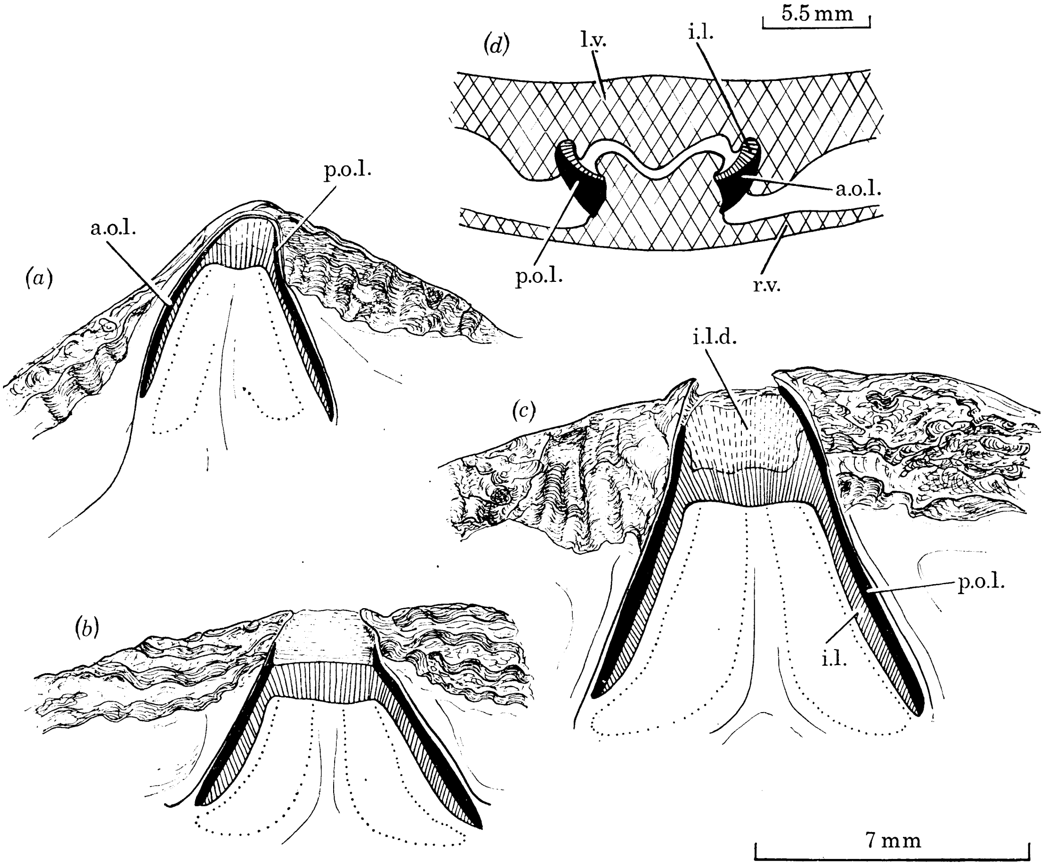

FIGURE 39. *P. cumingii*, ligament in right valves of (*a*) small, (*b*) medium, (*c*) large, shells. Dotted lines indicate the position of the crural ridges. (*d*) Transverse section showing crural ridges with attachments of ligament to both valves.

Ligament

The general appearance of the ligament in the two valves is indicated in figures 34 *b*, *d*. Owing to the absence of a byssal notch, ligamental asymmetry is largely lost and the general form of the deeply convex ligamental attachments with two ventrally descending arms is identical apart from the thickness of the ridges to which the ligament is attached. The convexity of the crurum in *Pododesmus* is here greatly exaggerated. Details appear in figure 39 showing ligamental attachment in the left valve in (*a*) small, (*b*) medium and (*c*) large shells. Initial supradorsal union (*a*) of anterior and posterior outer ligament layers (a.o.l., p.o.l.) is followed by ventral extension by both inner (yellow) and outer (greenish) ligament layers. As growth proceeds, in (*b*) and (*c*),

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the dorsal surface becomes extensively eroded very much as in *Pododesmus* (figure 8), the outer layers continuing to be added to at each side and basally while the inner layer thickens particularly mid-dorsally. At the same time, as indicated by the increasing extent of exposed valvular edges, the mantle margins are retreating on either side (cf. (*a*), (*b*), (*c*)) so that, as in other cemented bivalves, e.g. *Hinnites* and *Spondylus* (Yonge 1951, 1973), the hinge line moves ventralward during growth.

Attachment between the two valves is largely by way of the lateral ligament areas composed almost equally of inner and outer layers as shown in transverse section in (*d*). The area between is ridged, laterally in the lower and centrally in the upper, valve. The manner in which they interlock in the intact shell is indicated in (*d*).

Attachment

Unlike the other anomiaceans, the right valve in *Placunanomia* becomes literally cemented to the substrate. Other cemented bivalves, e.g. *Ostrea*, *Hinnites*, *Plicatula* or *Chama*, are attached by way of the superficial shell layer, the periostracum, on the under valve. Attachment occurs at various stages in the life history from earliest settlement in *Ostrea* to a late stage, after the animal has been swimming, in *Hinnites* (Yonge 1951). Byssal cementation in *Placunanomia* is confined to an area which enlarges and extends ventrally (figure 40) so long as the under valve remains adpressed to the substrate. It then becomes fixed, its margins intimately fused to those of the former byssal notch so uniting the under valve to the substrate. Examination of the one available animal (figure 37) reveals the typical anomiacean structure, namely an invagination of the right mantle lobe enclosing an hypertrophied byssal region with the typical anomiid foot.

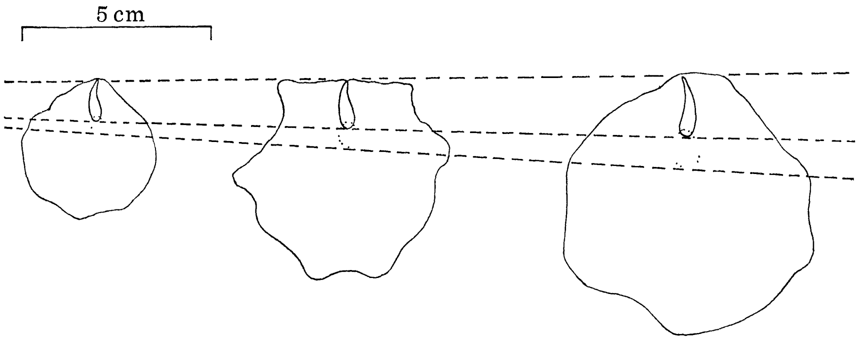

FIGURE 40. *P. cumingii*, under surfaces of small, medium and large shells showing movement ventrally of byssal gape (entirely filled with calcareous secretion) and of adductor (outline indicated by dotted line).

The exposed surface of the byssal gland has the usual appearance with its secretion now attached to the under valve, no longer direct to the substrate. Judging by the appearance in radial section (figure 38), this secretion appears to penetrate the substance of the right valve so retaining connection, although at an increasing distance, with the area of permanent cementation to the substrate. With growth the latter region becomes increasingly overlaid by inner shell layer, presumably of aragonite, complex crossed-lamellar structure, secreted by the mantle surface (Taylor *et al.* 1969). The mode of final attachment could be attained by a further development of conditions in the Anomiidae where the calcified byssal secretion eventually fuses with the margins of the byssal notch.

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Pallial organs

The general appearance from the under side of the one available specimen is shown in figure 37. The ctenidia are typically anomiid with two complete demibranchs, the outer lamellae slightly reflected, the filaments united by three rows of ciliated discs, without tissue fusion between the inner demibranchs or ciliary connections with the mantle and without anterior asymmetry. There is a very large hypobranchial gland on the inner surfaces of the suspensory membranes. In all these respects, *Placunanomia* resembles *Pododesmus*, not *Anomia* or *Enigmonia*. The palps with 10 or 12 ridges appear fully functional; the long right and the short left proximal oral grooves are enveloped by the long outer lips; the mouth is appreciably to the right.

Although so contracted here, the grooved foot is probably as well developed, for the same cleansing function, as in the Anomiidae. There is a small, essentially vestigial, left anterior pedal retractor (a.p.r.), too small to leave any scar, but, unlike *Pododesmus* and like *Anomia*, nothing on the right. By far the greater part of the enlarged adductor muscle (ad.) is composed of quick muscle, the smaller, although still sizable, byssal retractor possibly particularly concerned with prolonged closure of the valves. Shell closure in this genus has reverted to the primitive condition, the now marginal ligament extending between laterally opposed surfaces and opening in direct opposition to the combined adduction of large adductor and smaller, but still well developed, posterior byssal retractor.

General consideration of the characters of this genus are deferred so that they may be compared with those of *Placuna* which which *Placunanomia* is more closely associated, certainly in ligamental structure, than with the preceding genera.

Placuna placenta L.

This, the commonest species of its genus, is as well known as *Enigmonia* and *Placunanomia* are obscure. Specimens covering a wide range of size were most kindly sent from Singapore by Professor H. S. Chuang. Following their examination with preparation of sections of suitably fixed small individuals, living animals were later examined, obtained in 1969 from a sandy mud beach near to where *Enigmonia* was collected. Previous knowledge about this species was almost entirely based on the comprehensive and very beautifully illustrated paper by Hornell (1909). This was written before the full significance of ciliary currents was realized; however observations on these had been made by S. B. Yeo at Singapore and contained in an unpublished thesis available in the Department of Zoology, University of Singapore. The observations here recorded on respiratory, feeding and cleansing currents are very largely confirmations of those already made by Yeo.

The genus *Placuna* (established by Solander in 1786) consists of five species all widely distributed in the Indian Ocean. Both *P. placenta* and the more saddle-shaped *P. sella* (with which Yeo was particularly concerned) occur at Singapore. The different species would appear to differ primarily in shell characters (doubtless also in ecological preferences) and everything reported here concerns *P. placenta*, the window-pane shell, one of the best known of bivalve species. It occurs from the Gulf of Aden around India and the Malay Peninsula to the southern coasts of China and along the north coast of Borneo to the Philippines. It is extensively collected (often over-fished) and in places cultivated, originally as a substitute for glass in glazing, now

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(particularly in the Philippines) for the manufacture of trays, lamp-shades, etc. Its original use in glazing Hornell thinks may have begun in China and possibly then disseminated by the Portuguese from Macao. Medium-sized shells are best for this purpose, older shells becoming thicker and opaque.

An unquestioned anomiacean, *Placuna* differs from the other genera in its total freedom without trace of a byssus in adult life; Hornell speaks of this as being absent 'even in the very young' but evidence will be produced to the contrary. But the habits of the adult are in complete contrast to those of all other genera in the Anomiacea.

P. placenta lives unattached on the surface of mud flats. Hornell states that animals generally lie on the slightly more convex left valves, sometimes with the hinge sunk below the surface but personal observations indicated that they lie indifferently on either valve judging by the very similar number of acorn barnacles found attached to each of them. *Placuna* is certainly unable to move, even to turn over as *Pecten* and other scallops do when placed on the left valve – a capacity related to the functional dominance of the left statocyst (Buddenbrock 1911, 1915). Window pane shells appear to be totally at the mercy of wave action with young individuals possibly finding shelter among algal growths or eel grass. The larger ones, which attain diameters of up to 15 cm, are probably little disturbed by water movements, although they may possibly maintain position on the shore by expelling water 'forward' between the shell valves and moving with hinge foremost. This would be equivalent to the escape reaction of scallops; their swimming movements cannot be emulated because there is no discharge of water on either side of the hinge line, initially for cleansing (Yonge 1936). *P. placenta* occurs from mid tide levels to depths of up to 20 m but always on the same type of bottom, consequently it is often associated with a mangrove, but never a coral, coast.

Shell

No bivalve is more laterally flattened, the right valve externally very slightly concave, the other marginally more convex so that there seems inadequate space between them to accommodate the body. Hornell refers to shallow lateral depressions not infrequently present at the posterior end and less frequently at the anterior end, a tendency which culminates in the saddle shape of *P. sella*. But specimens of *P. placenta* from Singapore (the largest 90 mm in greatest diameter) were all very flat. The shell is sub-orbicular (figures 41, 43) with a straight hinge line the formation of which is discussed later. Hornell recorded an average shell length of 155 mm and a height of 142 mm in an extensive sample from the coast of what is now Pakistan. The outer surface, in his words, is 'marked by distinct concentric lines of growth, consisting of slightly projecting imbricate lamellae, the margins of which are rendered minutely uneven or roughly dentate by the presence of numbers of short, closely set and very delicate processes...'.

The thin valves carry at best an almost undectable covering of periostracum; internally there is no obviously distinct central layer such as there is in other anomiaceans. Taylor *et al.* report absence of the inner complex crossed-lamellar layer, 'the adductor myostracum is seen as aragonitic, prismatic myostracal trace, passing through the foliated layer'. This outer calcareous layer with, as they note, a high organic content, effectively forms the entire substance of the shell. The fact that it becomes exposed in older shells where the periostracum has worn away leads to the collection of mud on the rough surface. This was noted by Hornell who stated that the shell attains a final thickness of about 1 mm and 'losing its transparence becomes sub-opaque, white and somewhat friable, suggestive of dull white mica which has lost its

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transparency through weathering'. It is the medium sized shells that are best for glazing because they are transparent and usually colourless.

This extremely delicate shell, like that of *Pinna*, is very easily damaged but readily repaired as most old shells indicate. The valves are significantly less flexible than those of *Pinna*, indicating a relatively lower organic content (or higher degree of calcification in this) but they are notably thinner and much more translucent.

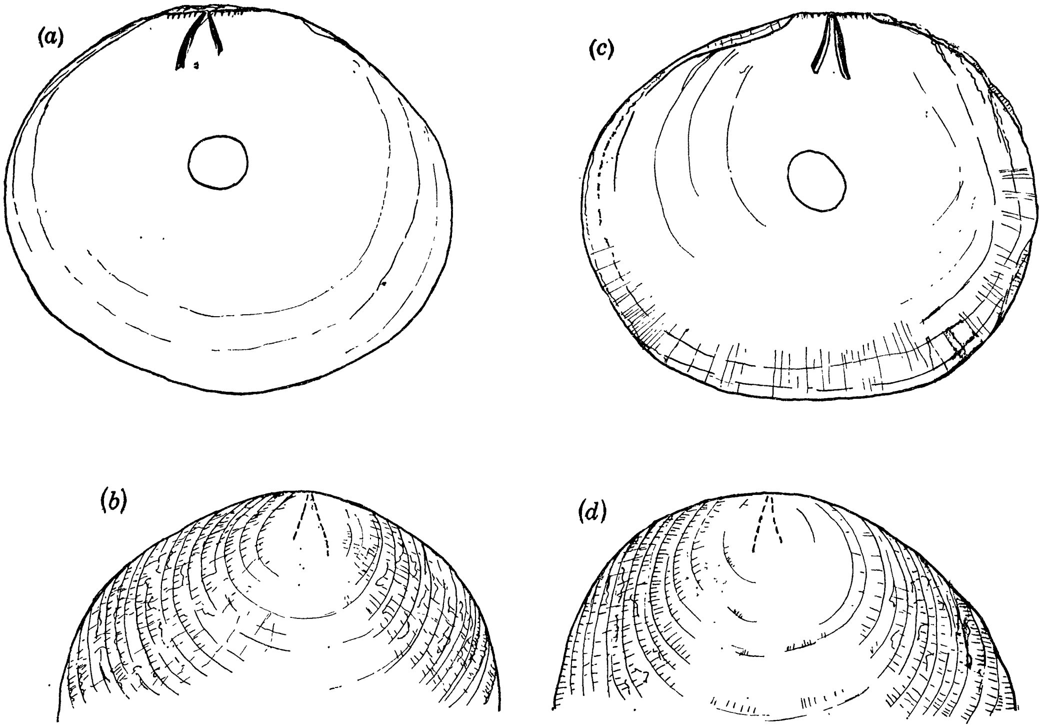

FIGURE 41. *Placuna placenta*. (*a*) Left valve, interior showing primary ligament with scars of adductor and anterior pedal retractor; (*b*) left valve, dorsal region of exterior surface; (*c*) right valve, interior; (*d*) right valve, dorsal region of outer surface. (Natural size.)

Muscles

Hornell noted the absence of a pallial line – *Placuna* here resembling all related (Anisomyarian) monomyarians – and the presence of a fan-like arrangement of muscles, radiating within fine grooves from the region of the adductor, responsible for deep withdrawal of the mantle lobes. Other muscle attachments are those of the enlarged, now centrally placed, adductor with the extremely small left anterior pedal retractor inserted just within the anterior arm of the Λ-shaped ligament (see figure 41). The still smaller left posterior retractor attached just within the adductor is too small to leave a visible scar. This almost complete suppression of the pedal retractors is associated with loss of the byssal apparatus. Comparison with conditions in *Pododesmus* and *Anomia* appears in figure 53.

There are obvious macroscopic differences in the adductor between an enveloping anterior and a smaller posterior region (figure 50) but, as noted by Hornell, little histological difference between the muscle fibres in the two regions. Previous views (Yonge 1936) that these represent regions of 'quick' and 'catch' muscle must, as pointed out by Thayer (1972), be withdrawn. All cleansing may well be the sole concern of the extremely mobile foot, the adductor exclusively concerned with prolonged contractions.

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Byssal notch

Hornell states that a byssus is absent 'even in the very young'; Taylor *et al.* also state that 'The byssal notch, byssal retractor and pedal muscles have disappeared'. This is *not* true for the notch or indeed, to the extent indicated above, for the muscles. A minute circular foramen with a short, completely fused, connection with the dorsal margin is present on the under side of the right valve (figure 42*a*), the opening initially situated just anterior to the summit of the Λ-shaped primary ligament (figure 46). But in the majority of even the very smallest available specimens, the internal opening has been overgrown by the inner regions of the ridge to which the anterior half of this ligament is attached (figure 42*b*). A byssal plug is retained in smaller shells but this has neither internal nor external attachments. The byssal gland can only be briefly functional during post-larval life.

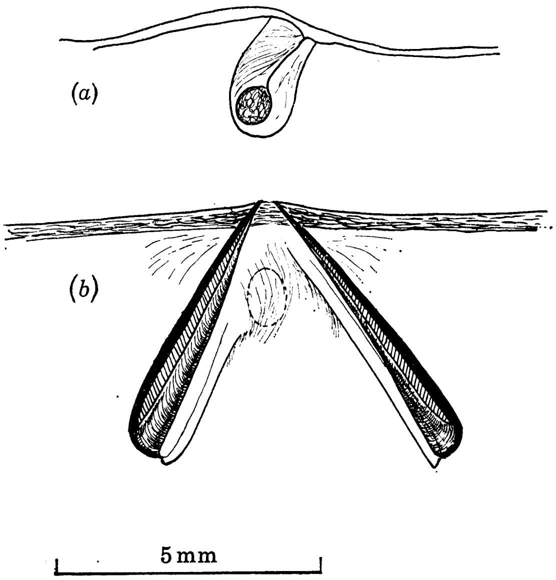

FIGURE 42. *P. placenta*, hinge region of right valve in very young specimen. (*a*) Outer surface showing closed byssal notch; (*b*) inner surface with position of byssal notch (overgrown by valve and anterior limb of ligamental ridge) indicated by broken line.

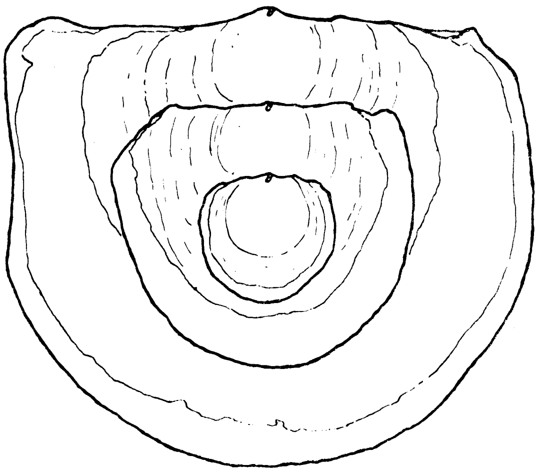

FIGURE 43. *P. placenta*, three shells of ascending sizes showing persistence of closed byssal notch, also straight, secondary, hinge line (natural size).

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Somewhat surprisingly in view of their economic importance, there is no knowledge about the life history of any species of *Placuna*, but the larvae must attach briefly, like all other metamorphosing bivalves, before becoming free. In some large shells the notch is lost due to wear along the hinge margin but in others, up to an observed maximum diameter of 14 cm (figure 43) it was retained although, as shown in figures 44 and 45, the internal hinge line does move ventralward during growth.

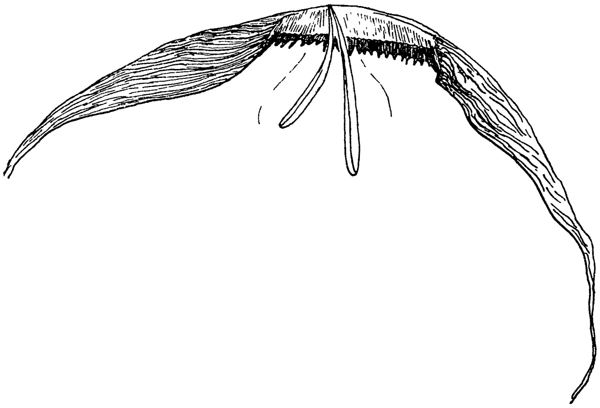

FIGURE 44. *P. placenta*, interior of dorsal region of right valve showing diverging arms of primary ligament, anterior the shorter, also secondary ligament with small 'periostracal' teeth along secondary hinge line (natural size).

Ligament

While an undoubted anomiacean ligament, this is more modified than that of *Placunanomia* although on basically similar lines. The significant point is that these now free living bivalves require a functional and so symmetrical *marginal hinge*. The attainment of this need demands attention.

The superficial appearance of the ligament, indicated in figures 44 and 45, is well described by Hornell as 'coincident with the greater part of the straight dorsal edge'. He continues that it is straight along the dorsal surface but ventrally consists of 'two very long linear projections and a number of short dentate ones 'corresponding in position and size with a similar number of projecting teeth arming the hinge line of the opposite valve'. The ligament is so strong that adjacent areas of the valves may break rather than the ligament when these are forcibly separated.

The 'teeth' have been regarded as equivalent to the hinge teeth in other bivalves but they are secondary (periostracal) and associated with the structure of the greatly modified ligament as, although in totally different manners, are the secondary teeth in *Spondylus* and *Plicatula* (Yonge 1973). The unique situation in *Placuna* becomes apparent in the following description.

The initial continuity between anterior and posterior arms of the primary ligament attached to what is an enlarged crurum – shown for *Placunanomia*, where continuity is maintained, in figure 39*a* – is only briefly maintained in *Placuna*. Continuity exists in the decalcified shell measuring 5 mm × 7 mm shown in figure 46. There is no evidence of any supradorsal fusion in the left valve (which does occur in *Placunanomia* (figure 36) but there is now an almost continuous straight stretch of fused periostracum (somewhat bent in figure 46 but only because of the effects of decalcification and mounting). This *secondary ligament* unites the dorsal valve margins formed by the hypertrophied dorsal mantle crest (d.c.). The lengths of fused periostral grooves at each end do not meet; they are separated by the dorsal extremity of the primary

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ligament. In *Placunanomia* the inner ligament layer continues intact throughout growth (figures 39*a*–*c*) but this is not so in *Placuna* (figure 45). As the summit of the mantle isthmus retreats from the peak of the Λ-shaped primary ligament (figure 46) it bends ventralward and, while continuing to secrete ligamental material, does so now in functional association with the secretion of fused periostracum anterior and posterior to it. There is thus functional continuity between these three secreting surfaces which nowhere fuse. The secondary ligament in *Placuna* is thus tripartite, the small central portion being of inner ligament layer.

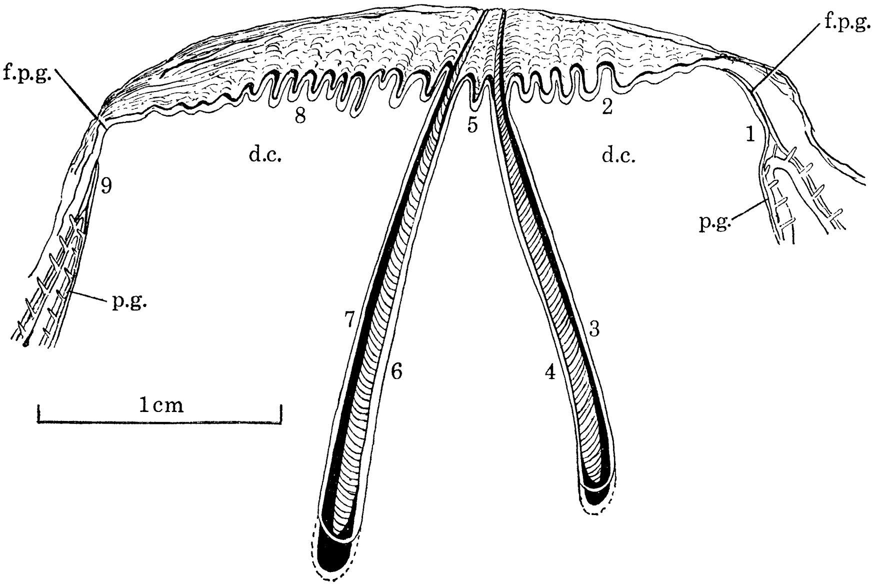

Figure 45. *P. placenta*, enlarged view of hinge region in left valve showing extensive fusion of the mantle lobes forming a dorsal crest on either side of the dorsal tip of the primary ligament. 1–9, regions of secretion of primary and secondary ligaments (explained in text).

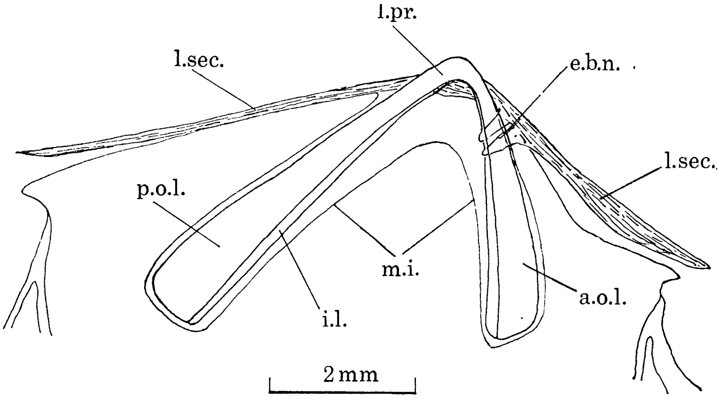

Figure 46. *P. placenta*, decalcified hinge region of very small shell showing primary ligament prior to its separation dorsally into separate arms, also entrance into byssal notch.

The disposition of the various secreting surfaces starting from the base of the dorsal crest anteriorly is thus (figure 45): (1) length of fused periostral grooves along the anterior margin of the crest (d.c.); (2) longer extent of similar surface secreting the anterior half of the secondary ligament; (3) the epithelium secreting the anterior outer ligament layer which extends obliquely anterio-ventrally; (4) the anterior limb of the mantle isthmus which runs parallel to (3) the two

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uniting in the formation of the anterior limb of the primary ligament; (5) the very short V-shaped area of mantle isthmus secreting the central region of the secondary ligament consisting of 'secondary' inner ligament layer; (6) the posterior arm of the mantle isthmus which, with (7) the epithelium forming the posterior outer ligament layer, produces the slightly longer posterior limb of the primary ligament; (8) the length of fused periostral grooves forming the posterior half of the secondary ligament; (9) the length of similar surface along the posterior margin of the dorsal crest. It is to be noted that 1, 2, 8, 9 represent a degree of dorsal (not supradorsal) extension of the fused mantle margins involving the periostracal grooves, 3 and 7 the ventralward extension of the embayments secreting the outer ligament layers (figure 6) and 4–6 the greatly modified mantle isthmus.

During growth the hinge line moves ventrally, the two arms of the primary ligament lengthening and thickening but also further separating dorsally where the central zone associated with formation of the secondary ligament widens. Meantime at either end the secondary ligament becomes thrown into the series of deep undulations that simulate teeth. Not covered dorsally by living tissue, the exposed surfaces of both primary and secondary ligaments erode.

The formation of the secondary ligament by three separate secreting surfaces which are not fused but only *applied* is of particular interest. It is by this unusual means that the highly modified anomiacean hinge has become adapted to fit the needs of unattached bivalve existence. Similar application of separate secreting epithelia to form a continuous ligamental structure has been observed in species of Carditacea and Astartacea (Yonge 1969), there between the mantle isthmus secreting the under surface of the primary ligament and epithelia forming a region of anterior† secondary ligament.

Thus the hinge of *Placuna* has become secondarily symmetrical, both laterally and anterior-posteriorly, with the primary and the secondary ligaments coming to possess completely separate functions. The former is concerned with separating the valves, the thick inner and outer ligament layers attached (figure 45) not to diverging 'cardinal teeth' but to calcareous ridges, similar to those in *Placunanomia* and representing greatly extended crural surfaces. In the absence of teeth, the valves are maintained in alignment by the long tripartite secondary ligament much as those of the equally edentulous Pectinidae are united by corresponding lengths of anterior and posterior outer ligament layers (Yonge 1973).

Conditions in *Placuna* represent a striking instance of secondary ligamental formation. The secondary ligament of fused periostracum was first identified in *Pinna* (there at the posterior end only) and later more comprehensively described (Yonge 1953, 1957). Its presence has subsequently been noted in various bivalves. It assumes major importance in *Spondylus* where, unlike other Pectinacea, the primary ligament becomes transversely disposed (Yonge 1973) and in *Plicatula* and the Dimyidae where the secondary ligament layers become fused supradorsally although in those cases over a transversely running primary ligament (Yonge 1975).

The primary ligament in *Placuna* demands some further description and analysis. The thick inner ligament layer faces inward while the thinner but longer outer layers curl round the inner layer ventrally (figure 45). As in *Placunanomia* the ligament is curved in transverse section (figure 47). When the adductor contracts the substance of the ligament will be compressed but the curvature will also be increased, so augmenting the opening thrust when the adductor relaxes. The ligament is yellow, the two layers absolutely distinct, the outer one translucent, the inner one opaque. Their staining reactions are totally different.

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† By an obvious error there stated to be posterior (Yonge 1969).

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Structural details are clarified by examination of a series of horizontal sections through a very small specimen starting dorsally and running to the ventral extremity (figure 48). Sections (*a*) first cut through the secondary ligament (staining red with Mallory as do the outer ligament layers) with only the two regions of the inner layer of the primary ligament (blue) distinct from this although the red staining area immediately lateral to these must be outer ligament layer.

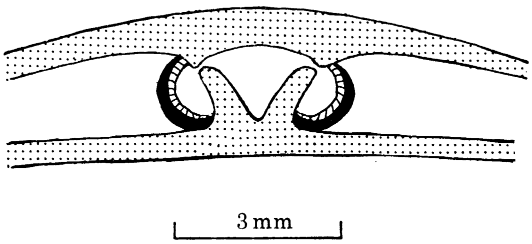

FIGURE 47. *P. placenta*, semi-diagrammatic transverse section through middle of primary ligament showing diverging crural ridges on under (right) valve, also attachments of ligament.

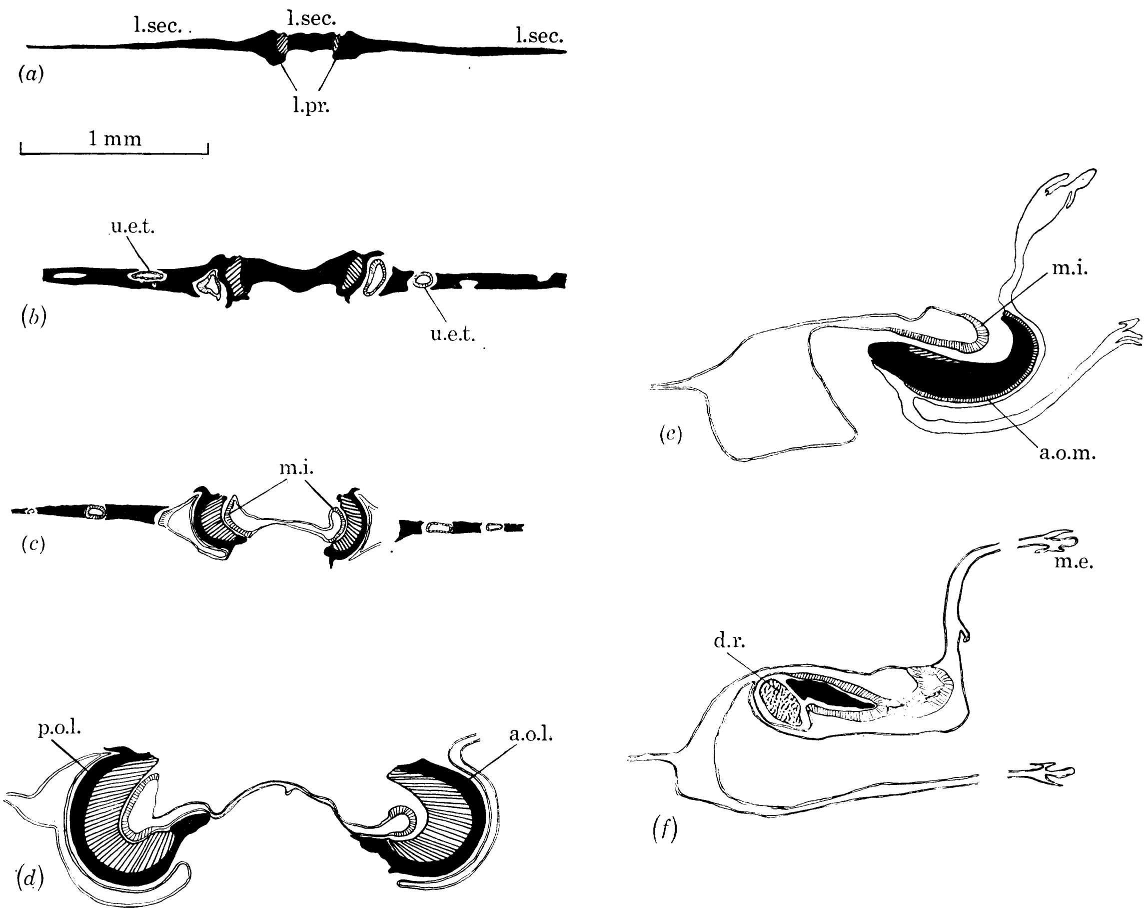

FIGURE 48. *P. placenta*, horizontal sections through both primary and secondary ligaments, i.e. cutting primary ligament in cross section (all sections) and secondary ligament, (*a*)–(*c*), longitudinally (see figure 45). (*e*) and (*f*), anterior half only.

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A little ventral to this (*b*, *c*) the undulating surface of the fused periostracal grooves (u.e.t.) (forming the 'teeth') is cut transversely in various places and, starting in (*c*) but very clearly in (*d*), the outer ligament layers separate from the fused periostracum. At the same time in (*c*) the two arms of the mantle isthmus (m.i.) appear. Each secretes a concavity of inner layer bounded by a thinner but over-arching extent of, on the one side anterior, and on the other posterior, outer layer. These layers thicken notably in (*d*) which is cut near the centre of the descending arms. The two final sections are cut through the base of the anterior arm, showing in (*e*) how the outer layer encloses the inner layer basally. Finally in (*f*) all trace of the latter has disappeared while an area of the decalcified ridge (d.r.) appears; in these small shells this is not apparent in more dorsal regions.

The anterior arm of the primary ligament is shown in longitudinal section (a transverse section through the animal) in figure 49. Dorsally the section cuts through the fused periostracum of the secondary ligament (l.sec.) with the epithelium secreting this (f.p.g.) and below this the lower half of the primary ligament, a gap of 3 mm between the two extremes is indicated. Again the clear distinction between the inner and outer ligament layers is revealed, also the disposition of the mantle isthmus (m.i.) and of the epithelium secreting the anterior outer ligament layer

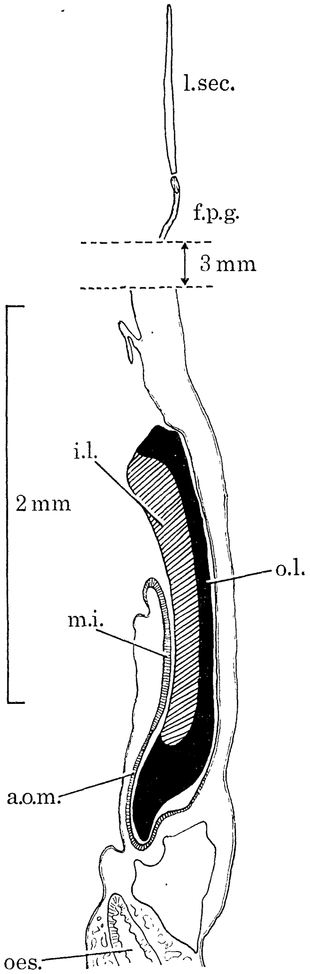

FIGURE 49. *P. placenta*, transverse section through hinge region comprising, *above*, transverse section through secondary ligament and, *below*, oblique section through ventral end of anterior limb of primary ligament (see figure 45).

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(a.o.m.) which is shown curling under the inner ligament layer at the ventral end. As the ligament grows, this region must elongate while the inner ligament layer will thicken. Further down appear the beginnings of the viscera with the cavity of the oesophagus (oes.).

Organs in the mantle cavity

The general appearance of the animal after removal of the left valve and mantle lobe is shown in figure 50. Apart from the arrows indicating ciliary currents (confirming the observations of Yeo) this closely follows the similar figure of Hornell who also provides illuminating outlines of the internal organs. The general appearance, apart from the strange ligament and absence of byssal notch, is that of a simple anomiid (e.g. *Pododesmus*, figure 13) but without ctenidial asymmetry and the muscles reduced to the very small anterior pedal retractor with the adductor reassuming its former size and reoccupying the centre of the valves. The original adducting function of prolonged contraction (of great significance to an intertidal animal) is here regained.

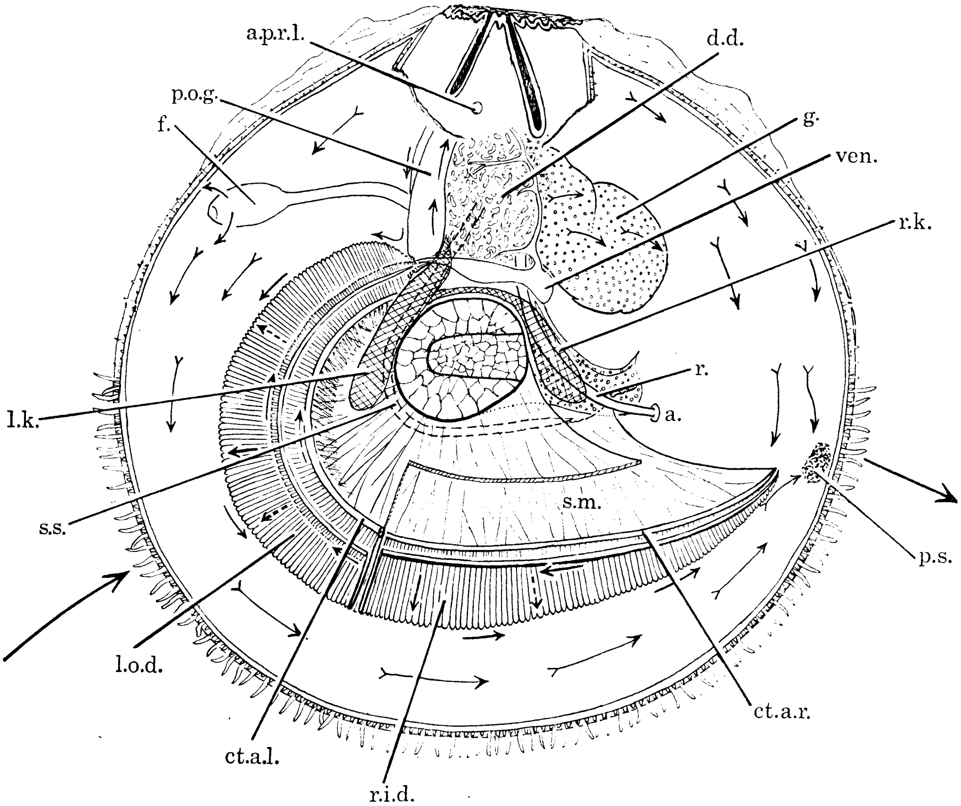

FIGURE 50. *P. placenta*, animal viewed lying within right valve with portion of left valve retained in hinge region and showing attachment of anterior pedal retractor. Arrows as before (natural size).

There is no fusion of the mantle margins; the middle mantle folds bear numerous tentacles, all short although larger around the ventral rim (figure 50), and the inner folds form only short curtains. The mantle margins are banded with dark pigment which also occurs generally over the mantle surface, but there are no eyes under the very translucent valves. But *Placuna* is exposed for very much shorter periods than *Enigmonia*.

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Foot

This is typically anomiid, long, highly contractile with a rounded and hollow barrel-like extremity. It is very active and material was observed being drawn, apparently by cilia, into the terminal cavity. It is a highly effective organ of cleansing. Hornell observed it with much care stating that it 'reaches a high degree of specialization; it is extremely mobile, and capable of great extension and equally great contractions...'. He considered that the apex formed a 'deep cup-shaped sucker with strongly developed muscles in the rim' but did not observe the cilia by means of which the cavity may become, as he puts it 'gorged with mud'. He realized that such an organ could not pull the animal along on the surface of mud flats and without knowledge of conditions in the anomiids, decided from observations in nature and in aquaria that 'the principal use – if indeed it be not the sole one – the foot subserves is that of a cleansing organ.' The presence of the anterior left pedal retractor and the still smaller posterior muscle have been noted; the main musculature is intrinsic, a network of fibres penetrated by blood vessels, the two jointly responsible for contraction and expansion and general mobility. Except in the very young stages, there is no trace of a byssal gland while Hornell notes the absence of an otolith. This could explain the indifference with which these animal lie on either valve.

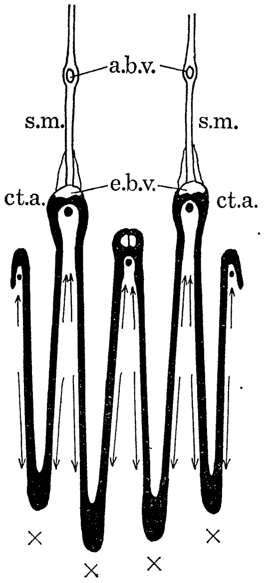

FIGURE 51. *P. placenta*, semi-diagrammatic transverse section through ctenidia, left one seen to be slightly the deeper, showing tissue fusion between ascending arms of inner lamellae, attachments between successive filaments confined to regions of reflexion. Arrows indicate directions of beat of frontal cilia, dots sites of oralward, and crosses of rejection, currents.

Ctenidia

The right ctenidium is slightly deeper than the left (figure 51) but this is the only asymmetry now that the ctenidia are no longer separated anteriorly by the byssal apparatus. Their general appearance is very similar to that in the Pectinacea. They have been described by Ridewood (1904) and in detail by Hornell. Structure is comparable to that in *Anomia* with the outer lamellae more deeply reflected (figure 51) but the same degree of organic fusion and absence of ciliary connections between filaments except at the angle of reflection where they are more extensively united than in *Anomia*. For a filibranch gill this is unusually coherent. The afferent

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branchial vessels (a.b.v.) are situated high above the efferent vessels (e.b.v.) within the exceptionally deep suspensory membrane.

There is the usual arrangement of ciliary currents but the disposition of the frontal ciliation appears to be unique. As already noted by Yeo (unpublished), cilia on the distal two thirds of the frontal surfaces beat towards the rejection tracts, those on the basal third in the opposite direction towards the oralward channels (figure 51). The only parallel condition is that in the Mytilidae and Pinnidae but there the basal zone of cilia is much narrower while both basal and summit tracts beat towards the mouth (Atkins 1937).

Major currents

The lateral cilia create a powerful flow of water usually concentrated by the inner mantle folds near the anterior end, although when these are fully withdrawn there is a gentle inflow around all the margins except posterior-ventrally where a powerful exhalant current emerges. Very active currents (see feathered arrows in figure 50) convey material from the surfaces of the mantle and visceral mass to a common point for accumulation of pseudofaeces opposite the tip of the ctenidia (which contribute to them) for expulsion in the exhalant current together with true faeces coming from the adjacent anus.

Palps

Like the ctenidia, these have resumed bilateral symmetry. They are relatively large with over 40 ridges on their opposed faces. They exercise the normal selective functions of these organs in the Bivalvia, finer particles passing to the mouth either over the summits or by way of the oral groove between the palps, larger ones rejected by way of grooves between the ridges and so via the margins on to the mantle surface. In this environment, the water so much richer in food particles than over rocky shores, a great deal of material must be collected by the gills to be sorted by the palps.

Viscera

The visceral organs have all been described and figured by Hornell, concern here is with the nature – and extent – of the asymmetry.

A trace of former asymmetry persists in the mouth which opens a little to the right of the median plane. The stomach (Purchon 1957) is very similar to that of *Anomia* while the style sac (s.s.) is characteristically long, extending again into the right mantle lobe to end near the anus (figure 50).

Hornell describes the kidneys as H-shaped, the two arms cross connected by a very short and wide channel but with the posterior portion of the left limb shorter than that of the right. He found evidence of the previous existence of reno-pericardial tubes. The gonad consists of a *single* yellowish coloured lobulated mass which encloses the greater part of the gut (figure 50, g.). It penetrates the right mantle lobes and opens into the channel between the kidneys, its products discharged by a single opening. Thus, although bilaterally asymmetrical like all anomiaceans, here the *right* kidney is the larger and the gonads reduced to a single one on that side (a small extension into the left mantle lobe suggesting a possible fusion with a gonad on that side). Hornell associates these developments with lying on the *left* side, a conclusion not accepted here. Unfortunately conditions in the one small specimen of the possibly related *Placunanomia* (which was possibly also immature) made it impossible to determine details of internal anatomy. Visceral asymmetry within the Anomiidae appears as a direct consequence of the twisting to the

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right of the byssal apparatus. *Placuna*, on the other hand, may be descended from ancestors in which the organs of the left instead of the right were reduced (although there is clear evidence that ancestral attachment was by way of the right side). Further information about conditions in mature *Placunanomia* is urgently needed.

Nervous system and sense organs

The cerebro-pleural and pedal ganglia are as close to one another as in other Anomiacea but, despite the loss of the intervening byssal apparatus, there is no movement towards the visceral ganglia as there is in the equally monomyarian *Spondylus* (Watson 1930). However, as in that genus, and in the Pectinacea generally, the visceral ganglia (or parietosplanchnic ganglion as Hornell terms them) become, in his words, 'the largest of the ganglionic centres' attaining 'relatively enormous proportions'. But the transfer of nervous dominance is less pronounced here than in the Pectinacea (and *not* solely a result of their mobility because *Spondylus*, where this condition is best developed, is cemented).

The absence of statocysts has been mentioned; Hornell found no sign of an osphradium and this is confirmed. He does, however, describe a pair of pallial sense organs on the inner side of each mantle lobe. Obscured in the figure by the terminal regions of the left ctenidium, these organs appear the same as those already described in *Pododesmus* and have presumably the same obscure function.

STATUS OF *PLACUNANOMIA* AND *PLACUNA* – FAMILY PLACUNIDAE

These genera unquestionably belong to the Anomiacea. In both the highly modified ligament can only be derived from conditions similar to those in *Pododesmus*. While ctenidia, palps and foot are essentially the same as in the Anomiidae, the asymmetry of kidney and gonads is certainly different in *Placuna* although conditions in *Placunanomia* are unfortunately unknown.

In many respects *Placunanomia* is the more primitive, resembling *Pododesmus* (and not *Anomia*) in possession of a hypobranchial gland, no association of the right inner demibranch with the left palps and without tissue fusion between the inner demibranchs or ciliary connection between the outer demibranchs and the mantle. In all these respects *Placuna* resembles the more highly evolved *Anomia*.

Both genera diverge very significantly from the Anomiidae in the character of the ligament. This is basically due to the closing of the byssal notch the great enlargement of which was a fundamental feature in the evolution of the Anomiidae. Just as this was responsible for the bilateral asymmetry of the hinge and formation of the crurum on the right valve, so the reduction and loss of the notch is followed by a secondary symmetry of the hinge.

In *Placunanomia* a deep notch with a calcified byssus (the primitive anomiacean condition) must be formed and enlarged up to the period when the lower valve ceases to be adpressed to the substrate (figure 34). This cementation persists after the byssal secretion, and by way of it the byssal retractor becomes attached to the *lower valve* coming to serve as an additional, but now subsidiary, adductor. Meanwhile the walls of the notch become fused to the calcified byssus distally and to each other proximally (figure 34). The sides of the notch in the mantle, although closely applied in this proximal region do not fuse (at any rate do not at the size of the single specimen examined). Although there is some initial supradorsal fusion on the left valve, the effects of the closure of the byssal notch are to extend the crurum into long, ventrally directed

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arms the only difference between the hinge regions in the two valves being the possession of much more pronounced ridges on the right valve.

In *Placuna*, byssal attachment is confined to a brief post-larval period, the small byssal notch being then filled in. The primary ligament is essentially similar to that in *Placunanomia* but, to fill the essential needs of an unattached bivalve, a straight hinge line has been formed by development of a prominent dorsal crest, its 'vertical' and 'horizontal' margins representing fusion of the mantle margins including the periostracal grooves (the final stage in the fusion of the mantle lobes (Yonge 1957)). This involves secretion of a single uniting sheet of periostracum forming a secondary ligament responsible for the dorsal attachment and alignment of the valves.

Placunanomia and *Placuna* certainly differ widely in habit, the one remaining byssally cemented but the other becoming free although incapable of self-generated movement either by way of the foot or, as in Pectinidae, by jet propulsion. With loss of the byssal apparatus, there is a striking degree of return to bilateral symmetry affecting the mantle lobes with secreted valves and ligament and also ctenidia and palps. The different asymmetry of the viscera compared with conditions in the Anomiidae may be associated with the exceptional degree of lateral compression. Although diverging instead of forming an evolutionary series as do *Pododesmus/Anomia/Enigmonia*, these two genera have much more in common with each other than either have with the Anomiidae.

On the basis of evidence here presented and summarized in table 2, it is proposed that these two genera be detached from the Anomiidae and be associated in a new proposed family

TABLE 2. FAMILY PLACUNIDAE

(Valves similar in thickness)

	species examined	
characters	*Placunanomia cumingii*	*Placuna placenta*
general form	rounded, plicate	rounded, greatly compressed
muscle scars left valve	**2**	1
crurum	not stalked, ∧-shaped sole ligamental attachment	not stalked, ∧-shaped primary ligament attached
secondary (periostracal) ligament	**no**	yes
byssal apparatus	**yes**	no
byssal notch	closes in adult	closes in post-larva
adductor	larger than byssal retractor	sole adducting muscle
hypobranchial gland	**yes**	no
demibranch, union ascending arms	**not fused**	tissue fusion
foot	**cleansing only**	**cleansing only**
supradorsal fusion:		
mantle lobes	**no**	hypertrophied mantle margins create new hinge line
valves	temporary	no
habit	**byssally cemented**	free: non-motile

Primitive characters indicated by bold type.

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Placunidae. *Placuna* Lightfoot, 1786 is older than *Placunanomia* Broderip, 1832. Beu's subfamily Placunanomiidae in which, without mention of *Placuna*, *Placunanomia* is associated with *Pododesmus* cannot be accepted. The main characteristics of the Placunidae are the form of the ligament, very convex with loss of the crural stalk, and increased bilateral symmetry with modification or loss of the byssal apparatus and notch. Comparison is made in figure 52 of these features in both Anomiidae (*a*–*c*) and Placunidae (*e*, *f*). The valves are of more equal thickness in the latter family, the adductor also comes to resume its former functions, in part in *Placunanomia* but fully in *Placuna* where there is only the solitary large muscle scar in each valve.

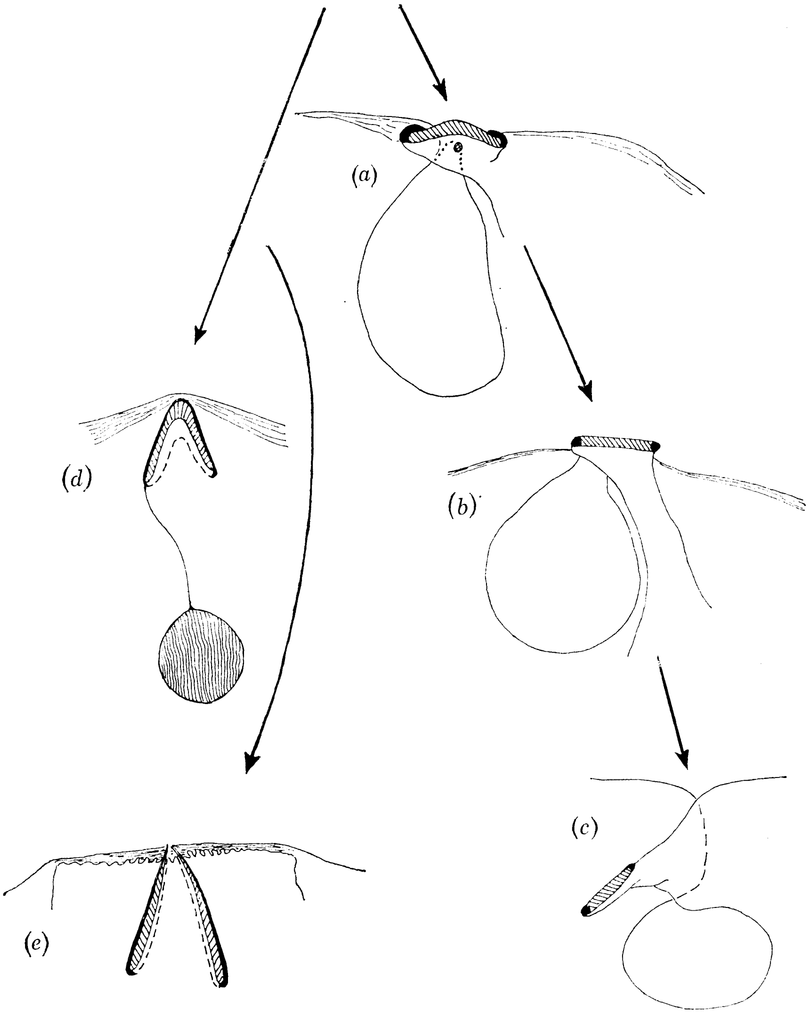

FIGURE 52. Anomiacea. Comparative views of crural regions in right valves of (*a*) *Pododesmus*, (*b*) *Anomia*, (*c*) *Enigmonia*, (*d*) *Placunanomia*, (*e*) *Placuna*. Arrows indicate possible lines of descent from primitive anomiacean stock.

DISCUSSION

The Anomiacea are unique among the superfamilies of the Bivalvia in a surprising number of inter-related ways. Here, alone, the pleurothetic habit is acquired by way of byssal, i.e. visceropedal, attachment involving a twisting at right angles of the hypertrophied byssal apparatus to open directly downward on the right side. This involves extension of the minor byssal notch on

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this side found in the Pteriacea (figure 1) to form a deep and terminally dilated cavity through which the massive byssus issues. In consequence of this and of the closely adpressed habit of life, the valves become highly dissimilar with major effects on the ligament and on its attachments. The presence of the deep byssal notch is responsible for the appearance of the stalked crurum on the right valve. The need for this valve to be overlapped by the upper, left, one appears responsible for the extension of that valve dorsal to the ligament, the umbo displaced from the margin. As a further result the anterior and posterior outer ligament layers come, at first partially but eventually completely, to enclose the inner layer dorsally. The calcification of the byssal secretion produces a unique mode of cementation; in all other bivalves so attached, by right or left valve, this is achieved by way of the mantle/shell.

A consequence of the extensive byssal cementation is the enlargement of the posterior byssal retractor which becomes the effective adductor, the reduced true adductor probably largely concerned with brief contractions for ejection of pseudofaeces. The foot is of supreme significance. Apart from the hypertrophy of the byssal apparatus, the elongated and highly mobile distal regions are concerned with the essential task of cleansing the mantle cavity, in this respect resembling the Pectinacea. Asymmetry of organs in the mantle cavity is a direct consequence of their displacement by the twisted byssal apparatus; that within the viscera – kidneys and gonads – is probably influenced by the great lateral flattening associated with the pleurothetic, closely adpressed, habit. Loss of the pericardium – also unique – may have a similar cause. In contrast to these numerous secondary characters are the filibranch gills and, above all, retention in both *Pododesmus* and *Placunanomia* of hypobranchial glands retained elsewhere in the Bivalvia only in the protobranch Nuculacea.

The essential characteristics of the superfamily Anomiacea may therefore be listed as follows:

monomyarian
pleurothetic, lying on right valve
hypertrophied, right twisted byssal apparatus, left posterior retractor acting as major adductor
calcified byssal secretion
asymmetrical crurum on right valve
Supradorsal extension, then fusion, of mantle lobes, umbo submarginally displaced on left valve
distal area of foot a mobile cleansing organ
no pericardium
asymmetrical kidneys and gonads
filibranch ctenidia
asymmetry of ctenidia, palps, proximal oral grooves, mouth displaced to right
hypobranchial glands

From animals possessing these initial characters both the Anomiidae with their increasing asymmetries and the Placunidae, culminating in the secondarily – superficially almost symmetrical – *Placuna*, may equally be derived. But basic similarities between *Pododesmus*, *Anomia* and *Placuna* are shown in figure 53. The Anomiidae certainly possess the more primitive characters although hypobranchial glands, ctenidial simplicity and incomplete dorsal fusion are retained in *Placunanomia* as well as in *Pododesmus*. The increasing degrees of specialization then found in *Anomia* and its highly derivative, *Enigmonia*, as well as in the very different *Heteranomia*, are indicated in table 1.

The Placunidae are undoubtedly less primitive, moreover, certainly in *Placuna*, the visceral asymmetry is different suggesting very early separation from the stock which gave rise to the Anomiidae. But the ligamental characters are fundamentally similar and can only have been

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derived from the same crural structure originally associated with a deep byssal notch and intimate byssal attachment. Certainly this genus can in no way be derived from *Placunanomia* which, despite its uniquely specialized mode of cemented byssal attachment, retains the hypobranchial glands, the simple ctenidial structure and symmetrical division of the demibranchs found in *Pododesmus*. Loss of the crural stalk with the great ventral extension of the two arms of the ligament do, however, give clear evidence of how the primary ligament in *Placuna* has evolved.

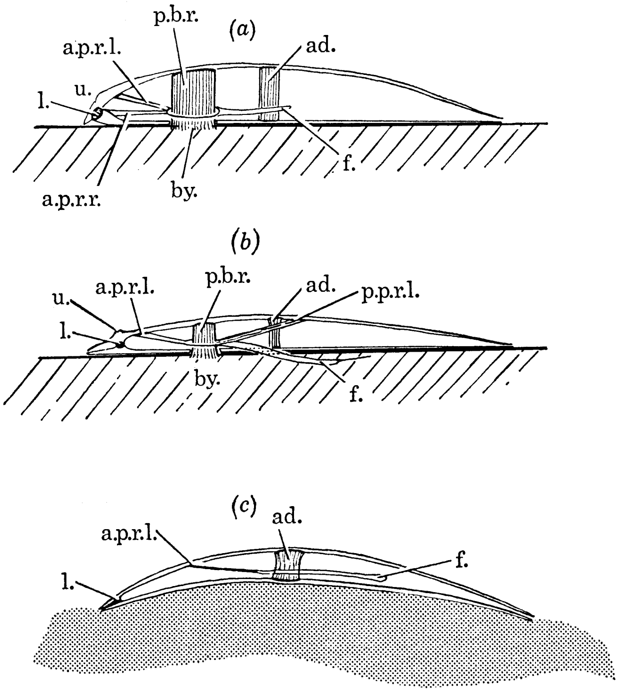

FIGURE 53. Anomiacea. Comparative lateral views, from anterior, showing disposition of foot and byssus with their muscle attachments and of the adductor in (*a*) *Pododesmus*, (*b*) *Enigmonia* (both attached, permanently or temporarily) and (*c*) *Placuna* (free on surface of sand).

Freedom here involves loss of the entire byssal apparatus (clearly persisting in the post-larva) the adductor regaining its original size and functional significance. Redevelopment of a functional hinge line has involved formation of a secondary, periostracal, ligament concerned solely with maintaining alignment of the valves, as in the Dimyidae (Yonge 1975), the primary ligament, as there, providing the opening thrust. Thus a genus of free living (although non-motile) bivalves has been evolved within a superfamily containing the most asymmetrical and intimately attached of pleurothetic bivalves.

This apparent return to conditions far more primitive than those in the ancestral anomiaceans involves some reference to Dollo's law of irreversibility in evolutionary change and the discussion that follows owes much to the recent clarification of Dollo's views by Gould (1970). Unrolled ammonites, Dollo stated 'have not reverted to the condition of the straight nautiloid'. Nor, despite superficial resemblance to other free living bivalves, does *Placuna* revert, for instance, to the ligamental conditions present in the equally monomyarian Pteriacea (figure 1). In the Anomiidae and in *Placunanomia* the valves are not hinged but the more extensive left valve is largely pulled down over the smaller right valve. In *Placuna* mantle growth produces a new hinge region with a straight dorsal line, its margins attached by fused periostracum forming a

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secondary ligament. There is absolutely no connection between the 'teeth' formed along the undulating dorsal margin or represented by the diverging ridges of the primary ligament and hinge teeth in other bivalves. The ctenidia and palps do regain almost complete bilateral symmetry with only the mouth remaining a little to the right side. But continued, indeed positively increased, lateral compression will retain visceral asymmetry. Moreover although possessing what initially appears to be a primitive bivalve form and living on a soft substrate, these window pane shells are epifaunal without means of moving over or into this. If it existed only in fossil form *Placuna* would surely be judged to have been infaunal.

Despite this inability to move, the foot remains a dominant organ. In the Bivalvia generally it has (1) a basic locomotory role, with (2) an added function as an organ of attachment by way of the byssal apparatus, probably always present in the post-larva and retained neotenously in various superfamilies, families, genera or even odd species (Yonge 1962). Finally, probably by modification of distal regions originally used for gripping a hard surface in epifaunal crawlers (as in the long exploring and byssal planting foot in the Mytilacea), it (3) becomes a cleansing organ. It acquires this function only in certain pleurothetic groups, notably in the Pectinacea (Yonge 1973) and possibly in the Chamidae (Yonge 1967) where the foot is retained for no other apparent reason. The sediment that inevitably collects within the deeper lower half of the horizontally disposed mantle cavity in such bivalves is collected and removed by such means. In the cemented Ostreacea and Plicatulacea (Yonge 1975), where the foot is lost, the under (left or right) valve is relatively shallow and cleansing is effected by ciliary means.

Pedal cleansing is employed throughout the Anomiacea. There the original pedal function of locomotion retained in the young (figure 10), has been lost in the adult except in *Enigmonia*. There it has been re-acquired with the under surface becoming a creeping sole rather like that of young mytilids. This could, therefore, represent the retention of post-larval capacities rather than a new development, were it not for the appearance of a terminal, probably sensory, flagellum which has no counterpart in any other bivalve.

Enigmonia remains a highly asymmetrical bivalve of limpet-like form and habit (apart from feeding). *Placuna*, however, has come again to reside upon soft substrates into which ancestral, infaunal bivalves burrowed. And it retains a very well developed, highly active, foot but, in justification of Dollo's law, this does not regain the primitive capacity for probing into such substrates and dilating terminally to produce the pedal anchor and so start the digging cycle described by Trueman (1968). This capacity is no longer latent. Moreover the foot in *Placuna* has, except in the post-larva, lost the byssal apparatus. But it has retained, possibly indeed increased, its efficiency as a means of cleansing which is essential to an animal living on a muddy substrate and entirely at the mercy of water movements.

This surprising evolutionary history involving no return to former structure or to a habit of life based on this, has nevertheless led to the appearance of one of the most numerous and successful of all bivalve genera. *Placuna* lies flat on the surface, like *Pecten* which avoids local problems by moving away, using jet propulsion, or *Pandora* which has some capacity for shallow burrowing. All three might be cited as instances of convergence (although far better examples can be selected from the variety of superfamilies giving rise to deep burrowers or to rock borers or to byssally attached heteromyarians). Dollo is quoted by Gould as stating that convergent species 'can be recognised by preservation of some ancestral structure (incomplete reversion)'. But Dollo was a palaeontologist dependent on structures that persist in fossil remains and so far as living molluscs are concerned members of all of these various converging groups can be

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distinguished on ligamental characters alone. Only if we restrict attention to external similarities can convergence fail to be recognized in the modern Bivalvia.

At the same time Dollo's law of the irreversibility in evolutionary change has received substantial confirmation in the course of this research. Basic conditions in the Anomiacea involve byssal cementation brought about by major modification in the shell (valves and ligament) and in the foot. These modifications are taken still further, within the same general habitat, in *Placunanomia* in the one family, in *Heteranomia* and *Anomia* in the other. But the two end points in evolution are, on the one hand, *Enigmonia* which achieves success in a most limited and extremely difficult environment, and *Placuna* which does so on a widely impressive scale occupying one of the most extensive of intertidal and shallow water habitats. In both cases degrees of freedom from the basic condition of byssal cementation have been achieved, in the one with retention of the byssal apparatus, although with loss of calcification, in the other with its complete suppression in the adult.

Acknowledgements are due to many. The initial work on *Pododesmus cepio*, undertaken at Friday Harbor in the summers of 1959 and 1969, owed much to the then Director, Dr R. L. Fernald and to Dr Paul Illg and Dr Dixy Lee Ray*; some final observations were made on this species at Pacific Grove in 1975 on specimens previously obtained by Dr D. P. Abbott. Work on *Enigmonia* and *Placuna* in the Department of Zoology, University of Singapore, during the summer of 1969 was made possible by the hospitality and help of the late Professor J. L. Harrison and of Dr (now Professor) S. H. Chuang, who had previously sent much material to Glasgow, with that of Dr C. F. Lim. Thanks are also due to Dr Brian Bayne for information about *Enigmonia* in Malaya.

The one small specimen of *Placunanomia cumingii* seen came from Dr James H. McLean of the Los Angeles County Museum of Natural History who obtained it from the Hancock Foundation through the good offices of Dr John S. Garth. Preserved material of *Anomia simplex* from the coast of New England was collected and preserved by Dr Robert Robertson of the Department of Malacology, Philadelphia Academy of Sciences who also provided specimens of the Caribbean *Pododesmus rudis*. Preserved '*Monia*' *zelandica* were received from Dr A. G. Beu of the Dominion Museum, Wellington, New Zealand.

In Great Britain, shells of *Placunanomia cumingii* and of *Patro australis* were obtained on loan from the British Museum (Natural History) by way of Dr John Taylor and preserved specimens of *Heteranomia squamula* were provided from the Royal Scottish Museum by Mr D. Heppel and Dr Shelagh M. Smith. Other material covering all British species was obtained from the Marine Laboratories at Plymouth, Dunstaffnage, Millport, Cullercoats and St Andrews.

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* Recently elected Governor of Washington State.

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KEY TO LETTERING USED IN THE FIGURES

a.	anus
a.ad.	anterior adductor
a.b.v.	afferent branchial vessel
a.cr.	cut attachment of crurum
ad.	adductor
ad.c.	'catch' muscle of adductor
ad.n.	nerves to adductor
ad.q.	'quick' muscle of adductor
a.o.l.	anterior outer ligament layer
a.o.m.	epithelium secreting anterior outer ligament layer
a.p.r.	anterior pedal retractor
a.p.r.l.	anterior pedal retractor of left side (or scar)
a.p.r.r.	anterior pedal retractor of right side (or scar)
b.	branchial muscle (or scar)
b.g.	byssal gland
b.n.	byssal notch
b.o.	opening of byssal gland
b.r.	byssal retractor
br.at.l.	attachment of left branchial muscle
br.at.r.	attachment of right branchial muscle
b.n.	branchial nerve
b.w.	boundary white shell area
by.	byssus
by.n.	byssal nerve
c.c.	cerebral connective
c.e.m.	cut edge of mantle
c.e.v.	cut edge of valve
c.g.	cerebro-pleural ganglion
cr.	crurum
ct.	ctenidium
ct.a.	ctenidial axis
ct.a.l.	ctenidial axis of left
ct.a.r.	ctenidial axis of right
ct.l.	left ctenidium
ct.r.	right ctenidium
d.	dissoconch shell
d.c.	dorsal crest
d.d.	digestive diverticula
d.r.	decalcified crural ridge
e.b.n.	entrance to byssal notch
e.b.v.	efferent branchial vessel
e.m.f.	end middle marginal folds (entrance byssal notch)
e.o.l.	epithelium secreting outer ligament layer
f.	foot
f.i.f.	fused inner folds of mantle margin
f.i.f.r.	fused inner fold, right side only
f.o.l.	fused outer ligament layers
fla.	pedal flagellum
f.m.m.	fusion (supradorsal) of mantle margins
f.p.	faecal pellet
f.p.g.	fused periostracal grooves
f.t.	fusion of epithelia secreting outer ligament layers
f.v.	supradorsal fusion of left valve
g.	gonad
gl.m.	glandular mass
h.	heart
h.b.g.	hypobranchial gland
i.f.	inner fold of mantle margin
i.f.b.	inner mantle fold hypertrophied around byssal notch
i.f.l.	inner marginal fold left side
i.f.r.	inner marginal fold right side
i.l.	inner ligament layer
i.l.d.	inner ligament layer degenerating
k.	kidney
l.	ligament
l.g.	left gonad
l.i.d.	left inner demibranch
l.k.	left kidney
l.o.	lines of growth of old ligament
l.o.d.	left outer demibranch
l.o.g.	lines of growth on inner ligament layer
l.p.l.	left labial palps
l.p.o.g.	left proximal oral groove
l.pr.	primitive ligament
l.p.r.	right labial palps
l.sec.	secondary ligament
l.v.	left valve
m.	mouth
m.e.	mantle edge
m.f.	middle fold of mantle margin
m.f.l.	middle mantle fold left side
m.f.r.	middle mantle fold right side
m.i.	mantle isthmus
n.s.	new shell within byssal notch
o.c.l.	outer calcareous layer of valve
oes.	oesophagus
o.f.	outer fold of mantle margin
o.f.l.	outer mantle fold left side
o.f.r.	outer mantle fold right side
o.l.	outer ligament layers (united)
o.l.d.	outer ligament layers degenerating
o.m.	epithelium secreting outer ligament layer
p.	periostracum
p.ad.	posterior adductor
p.b.r.	posterior byssal retractor (or scar)
pd.g.	pedal ganglion
pd.n.	pedal nerve
p.f.	pedal flap
p.g.	periostracal groove
p.g.l.	periostracal groove left side
p.g.r.	periostracal groove right side
p.n.	pallial nerve
p.o.g.	proximal oral groove
p.o.g.l.	proximal oral groove left side
p.o.g.r.	proximal oral groove right side
p.o.l.	posterior outer ligament layer
p.o.m.	epithelium secreting posterior outer ligament layer
p.p.r.	posterior pedal retractor
p.r.	pedal retractor
pr.	prodissoconch II
ps.	pseudofaeces
r.	rectum
r.g.	right gonad
r.i.d.	right inner demibranch
r.k.	right kidney
r.o.d.	right outer demibranch
r.p.o.g.	right proximal oral groove
r.v.	right valve
s.	stomach
sc.g.	subcrural groove
s.m.	suspensory membrane
s.s.	style sac
u.	umbo
u.e.t.	undulating epithelium secreting periostracal 'teeth and sockets'
ven.	ventricle
vi.c.	visceral connective
vi.g.	visceral ganglion
v.m.	visceral mass