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Form, Habit and Evolution in the Chamidae (Bivalvia) with Reference to Conditions in the Rudists (Hippuritacea)

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FORM, HABIT AND EVOLUTION IN THE CHAMIDAE (BIVALVIA) WITH REFERENCE TO CONDITIONS IN THE RUDISTS (HIPPURITACEA)

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CONTENTS

The Superfamily Chamacea contains the one Family Chamidae with free and attached species. Species of *Echinochama* are briefly attached by the right valve. Permanently attached individuals are cemented by one or other valve. Since some species may attach indifferently by either valve, separate genera cannot be erected on the basis of the valve of attachment, but it remains convenient to refer to '*Chama*' and '*Pseudochama*' denoting individuals attached by left and right valves respectively.

The tangential component in shell growth causes anterior separation of the umbones and splitting of the ligament, the valves becoming spirally coiled as in the unattached *Glossus* (*Isocardia*). Major bilateral asymmetry occurs in '*Chama*' and '*Pseudochama*', the under valves being the larger and deeper component. Since the work of Munier-Chalmas (1882) it has been known that dentition in the Chamidae is either normal (in '*Chama*') or inverse (in '*Pseudochama*'), i.e. that dentition on all attached and on all free valves is similar, conditions in '*Chama*' and '*Pseudochama*'

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being mirror images of one another. Right or left valves of the one cannot be compared with right or left valves of the other.

This research is based on study of two intertidal Californian species, *Chama pellucida* and *Pseudochama exogyra*, all individuals reported on having, respectively, normal and inverse dentition. The shell is particularly dense—in striking contrast to that of the extinct rudists. The primary ligament is greatly modified by the tangential component which anteriorly causes splitting and posteriorly overgrowth of the calcareous layers of the valves by the posterior outer, and the inner, ligament layers. Unlike an opisthodetic ligament, growth is exclusively in a posterior direction. It follows that growth represents a process of slow rotation on the substrate, in an anticlockwise direction in '*Chama*', clockwise in '*Pseudochama*'.

Posteriorly directed growth along the hinge line causes longitudinal extension of the two cardinal teeth present in each valve. Difficult to homologize, these teeth are designated a_1 and a_2 on the attached, and f_1 and f_2 on the free, valve. The first, and more ventrally situated, teeth which originate more anteriorly, are much the larger. Small posterior lateral teeth occur in each valve. The occurrence of inversion is undoubted and is fully illustrated.

The mantle on the under valve is the more extensive with umbonal regions curved anteriorly under the hinge plate. The mantle margins are united, by fusion of the inner folds exclusively, (Type A of Yonge 1957*a*) except for the pedal gape, through which the small foot occasionally protrudes, and inhalant and exhalant apertures. The latter are separately extended on short siphonal tubes. The adductors are large, in correlation with the habitat (exposure to the air and to violent water movements), and extended dorso-ventrally, the mouth being carried dorsally and the anus ventrally and the visceral mass extended dorso-ventrally.

The valves separate only slightly; pseudofaeces with much mucus are readily extruded by contraction of the 'quick' region of the adductors. The foot must assist in cleansing. The inner demibranchs of the dorso-ventrally extended ctenidia are much the larger. Elaborately plicate, the ctenidia furnish the maximum of current-producing and straining surface; consequent danger of blockage is countered by combined ciliary and muscular means. The pattern of ciliation is Type C (1) of Atkins (1937). The marginal groove along the inner demibranch is exceptionally deep and narrow and guarded by tufts of long cilia, only the finest particles enter. The small palps are asymmetrical with the longer proximal oral groove on the under side. Highly selective, they reject material from the anterior, instead of the usual posterior, end. Pseudofaeces collect at the base of the inhalant siphon.

The gut is very short, and, as in all Bivalvia, the stomach is highly asymmetrical; this is *not* influenced by inversion (e.g. it is the same on the right side in both '*Chama*' and '*Pseudochama*'). Inversion is thus revealed as affecting *only* pallial structures, i.e. dentition and the form of the mantle and valves. There are no unusual features of an internal anatomy already adequately described by earlier workers. Statocysts are retained. Sexes are separate and gonads penetrate the mantle. Nothing is known about development, although attachment is probably at the end of the dissoconch stage.

Bilateral asymmetry affects primarily the mantle/shell including the pallial organs (ctenidia and palps); a great part of the food collecting surface may lie in the larger mantle cavity on the under side. There are secondary effects on the visceral mass and on the pedal retractors.

Cementation in the Bivalvia is shown to occur at four stages in the life history in different groups. In the Anisomyaria the valve of attachment is predetermined by previous byssal fixation but not in the Chamidae. It was presumably always preceded by change from a vertical to a horizontal disposition, another probable preconditioning factor being absence of united siphons (and usually of teeth). The shell became inequivalve with the body bilaterally asymmetrical and rounded. The problem of growth when attached by one valve, usually solved by ventralward growth involving continual increase to the under side of the ligament, is met by rotation in the Chamidae. Mechanisms are developed for efficient cleansing of the horizontally fixed mantle cavity.

Form in the Chamidae is influenced by (1) the tangential component acting in the longitudinal vertical plane with the consequent separation and coiling of the umbonal regions modifying the transverse component dorsally, and (2) cementation causing bilateral asymmetry and so further modification of the transverse component. The effects of these on the median and antero-posterior axes of the body and the hinge and demarcation lines of the mantle/shell are discussed in relation to the longitudinal and transverse vertical planes.

The pattern of tooth and socket formation on either side of the crest of pallial epithelium ventral to the mantle isthmus, normally constant in relation to right and left valves, is related in the Chamidae to attached and free valves, i.e. is associated with cementation. This problem does not arise in edentulous cemented bivalves. Articulation between an upper opercular and a lower deeply concave valve involves a rolling back of the hinge plate on the former and corresponding over-arching of the latter. The hinge plate is always bounded ventrally by a tooth on the attached and by a socket on the free valve and this appears to be functionally necessary. Inversion would seem to be a consequence of cementation and to be the concern only of the mantle/shell.

Form in the extinct rudists (Hippuritacea) was basically similar to that in the Chamidae. Although attached by either valve (only the Diceratidae indifferently by either) inversion here appears to have been a phylogenetic not an ontological process. Comparisons are made between conditions in free *Glossus*, normal and inverse Chamidae and representatives of the rudist families Diceratidae, Requieniidae, Capulinidae, Hippuritidae and Radiolitidae. These exhibit full effects of the tangential component with often striking bilateral asymmetry, the umbones separated to maximum extent and the ligament consequently moved at right angles from the longitudinal to the transverse axis. The direction of the teeth is similarly changed, e.g. in the Hippuritidae and Radiolitidae those on the opercular upper valve become laterally (i.e. vertically) extended to fit into deep sockets on the cone-shaped under valve. Enormous shells of a unique cavernous character and consequently very light were rapidly secreted to raise these bivalves high above the rocky substrate; the rudists were the supremely adapted epifaunistic bivalves. Functional loss of the ligament must have preceded its final disappearance; the foot may then have raised the upper valve. It is suggested that the mantle lobes were united, as in the Chamidae, by the inner mantle margins with siphonal tubes at least as short.

Wide separation of the umbones would carry with them the anterior ends of the ctenidia with development of long proximal oral grooves; in cases of great asymmetry much the greater current producing and straining surface would be in the under mantle cavity. The general disposition of the body is deduced from the known association of the mouth with the anterior, and the anus with the posterior, adductor.

Pillars and oscules in the Hippuritidae could *not* have been 'siphonal'. The inhalant and exhalant openings were raised high by shell secretion. The pillars (and so the oscules) are here regarded as a consequence of the formation of pallial folds bounding a waste canal which, as in modern bivalves, would discharge through the inhalant opening. This would also explain the great antero-posterior asymmetry in the Hippuritidae. The greater symmetry of the Radiolitidae is suggested as due to the ventral displacement of the inhalant aperture with the waste canal bounded by pseudopillars. Cleansing of the deep under mantle cavity must have been of supreme importance.

The majority of rudists must have occupied very similar shallow and intertidal rocky areas as do the cemented Chamidae although often raised higher and becoming gregarious to form reefs. Especially in the Radiolitidae large species lost attachment to lie recumbent in deeper water with the posterior (siphonal) surface uppermost. The increase in numbers, size and elaboration of form throughout the Mesozoic indicates long continued stable conditions. Natural selection must then have favoured variations in these laterally extended rudists which raised them higher above the rocky substrate.

The final rudist forms, Caprinidae, Hippuritidae and Radiolitidae, represent a logical evolutionary consequence of the action of a tangential component in shell growth on cemented isomyarians, namely maximum separation of the umbones with eventual loss of spiral coiling and of the ligament. The effect was exaggerated by the exceptional powers of shell secretion. The results of lateral extension of the valves in the *absence* of a tangential component and of cementation is exhibited by the infaunal *Corculum* (Cardiacea). The antero-posteriorly flattened equivalve shell, almost circular in outline, lies on its anterior surface with the unseparated umbones overlapping. Change in shell form is here associated with the presence of symbiotic zooxanthellae.

INTRODUCTION

The evolution of form in the Chamidae, the sole family in the Chamacea as defined by Thiele (1935), is of unusual interest. The tangential component in shell growth is here more fully developed than in any other living Bivalvia apart from *Glossus* (*Isocardia*) as described by Owen (1953 *b*). Moreover, in the Chamidae this is associated with cementation (i.e. attachment by the mantle/shell) and hence, in the species where attachment persists throughout life, with consequent major bilateral asymmetry. The attached valve, right or left, is much the deeper with resultant effects on the form of the enclosed body. From conditions in these living bivalves, deductions may reasonably be drawn about evolution and possible mode of life in the remarkable series of largely Cretaceous fossils contained in the Hippuritacea or rudists. Starting from what would appear to be very similar beginnings, change in form was there carried much further, culminating in bilateral asymmetry so great that the free valve formed no more than an opercular cap closing the deep concavity formed by the attached valve, ligamental attachment being lost.

Despite their great inherent interest, little has previously been written about the Chamidae although species of the three genera are often very common, and sometimes very conspicuous, in warm temperate and especially in tropical seas. Knowledge has been almost entirely confined to shell characters and to the anatomy of preserved specimens. The observations of Kellogg (1915) on ciliary currents appear to be the only ones previously made on living animals. Little attempt has been made to analyse the causes of their unique structural features.

The observations here recorded were begun during 1949 while the author was Visiting Professor of Zoology in the University of California, Berkeley, and were carried out there and at the Hopkins Marine Station, Pacific Grove. Other species were briefly examined at Bermuda in the summer of 1951, while final observations were carried out at Pacific Grove between January and April 1960. The long period of preparation has been abundantly justified owing to the development and clarification over these years of ideas on such matters as the formation of the ligament, mantle fusion and the factors influencing form and evolution within the Bivalvia.

GENERAL CHARACTERS

In the Chamacea which consist, unless the extinct Hippuritacea be incorporated within this Superfamily, of the one family Chamidae, the valves are characteristically spirally coiled, the ligament and enrolled umbones separating widely at the anterior end. Shell characters generally have recently been well summarized by Nicol (1952 *a*, *b*). For reasons given later, it is most convenient to consider the family Chamidae as comprising only *two* genera but one of these containing individuals in one of two possible *conditions*. In *Echinochama* (figure 1 *A*) the shell has a lunule (LU) absent in the others; moreover attachment, by the right valve, is very brief. It is confined to the second of the three stages in shell growth—nepionic (dissoconch), neologic and ephebolic—described by Jackson (1890). Later in growth all species of this genus become free with the shell valves usually very similar (Nicol 1952 *c*, 1953), although with persistent evidence of attachment (AT) near the umbone of the right valve (R). But in '*Chama*' and '*Pseudochama*' (figure 1 *B*, *C*) the shell is permanently and extensively attached from the same stage (see figure 9*C*) and by the left and right valves respectively. These under, attached, valves are always the larger and much deeper components of the strikingly inequivalve shell.

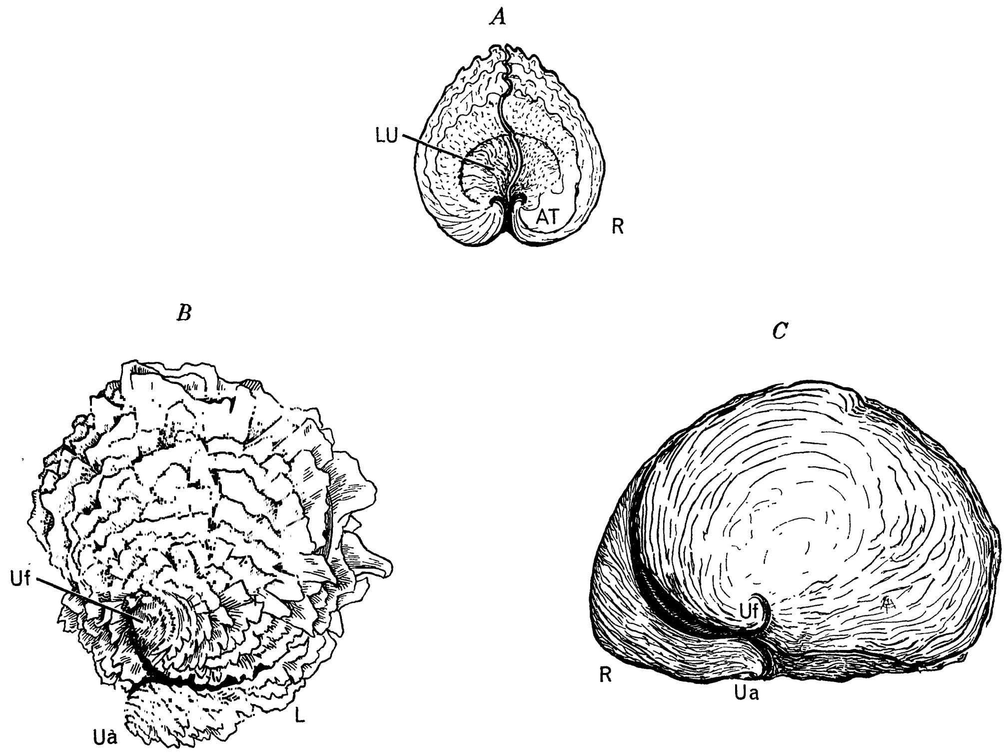

FIGURE 1. *A*, *Echinochama*, viewed from anterior; *B*, *Chama pellucida*, viewed from above, attached by left (L) valve; *C*, *Pseudochama exogyra*, viewed from above, attached by right (R) valve. About natural size. For key to the lettering on all figures see p. 105.

The key to the understanding of the highly characteristic organization of the Chamidae resides in the form and growth pattern of the mantle/shell with secondary effects on the contained body. Some initial appreciation of the position, so far as the growth of the ligament and hinge is concerned, is contained in the early work of Anthony (1905) but the whole matter demands drastic reconsideration in the light of recent advances in our understanding of the Bivalvia. It appears best to give initial description of conditions in the Chamidae in terms of this knowledge. The implications of this growth pattern on both mantle/shell and body and so on the form and habits of the animals will emerge later in detailed description and in discussion.

In the Bivalvia, growth of the shell—valves and ligament—is the result of secretion around the generating curve formed by the margins of the mantle lobes. Growth in any region of this may be resolved into three components, radial, transverse and tangential (Owen 1953*a*). Of these, the two first are always present, the third being often either absent or poorly developed. The radial component radiates out from the umbo and acts in the plane of the generating curve. With rare exceptions—*Anomia*, with the extensive embayment in the right (i.e. under) valve, is the most obvious—it is identical in the two valves, otherwise their margins would not coincide. This component does not further concern us.

The transverse component acts at right angles to the plane of the generating curve and so is responsible for the degree of internal concavity of the valves. In equivalve (i.e. bilaterally symmetrical) shells it is the same in the two valves; where it is different, e.g. in *Pecten*, *Ostrea* or the Etheriidae (Yonge 1962*a*), the two valves are dissimilar, the transverse component being largely or completely absent in the upper, flattened valve. In the Chamidae, *Echinochama* is effectively equivalve (figure 1*A*) with a pronounced and similar transverse component on each side. But in '*Chama*' and '*Pseudochama*', the under, attached, valves are deeply concave, i.e. with the transverse component pronounced, whereas the free valve is almost flat.

Before proceeding to discuss the tangential component, it is necessary to refer to the demarcation line (Yonge 1955*b*). Originally described by Owen (1953*a*, *b*) in *Glossus* as the 'normal axis', this represents the projection on to the sagittal plane of a line starting at the umbo and proceeding to the ventral margin by way of the region of greatest inflation of the valve, i.e. where the ratio of transverse to radial component is greatest. But, as recently indicated by Stasek (1963*a*, *b*), it does not invariably follow this course. He instances *Lithophaga lithophaga* and *Solen siliqua* and doubtless this will apply to other instances of markedly unequilateral shells, the form of which has been modified in relation to habitat. The demarcation line may therefore be more generally defined as a line drawn on a plane surface starting from the umbo and, except where it is influenced by a tangential component (see below), running at right angles to the hinge line. It thus cuts through the centre of the ligament where this is amphidetic (i.e. primitive) but through its anterior end in the more usual and modified opisthodetic condition (compare broken lines in figure 4*A*, *B*). The significance of the demarcation line is that it divides the mantle/shell into anterior and posterior *territories* which only in very primitive bivalves correspond to the anterior and posterior regions of the enclosed body. Often these territories, as in the Solenacea (Yonge 1952; Owen 1959*a*) may be strikingly dissimilar. The demarcation line is of the greatest value in any consideration of the course of evolution within the Bivalvia.

The third component of growth acts tangentially to, and in the same plane as, the generating curve. Although present in a variety of bivalves, e.g. *Astarte* and *Myadora* (Owen 1958), Lucinacea (Allen 1958) and Veneracea (Ansell 1961), it is immediately obvious in relatively few, notably the equivalve *Glossus humanus* (*Isocardia cor*) (where it was initially described by Owen (1953*b*)) and the inequivalve Chamidae which form the subject of this paper. It is also well developed in the Mytilidae where in *Botula* and *Lithophaga* it has the effect of counteracting the reduction of the anterior end associated with heteromyarianism (Yonge 1955*b*).

This tangetial component has the obvious effect of curving the demarcation line. With the possibly solitary exception of the extinct oyster, *Exogyra*, it is directed anteriorly. Except in a genus such as *Exogyra* where the mantle cavity is widely open, a posteriorly directed curvature would effectively obliterate the all-important inhalant and exhalant openings. In either case the effect of the tangential component is to cause the logarithmic spiral of growth to become turbinate.

The most striking effects of the tangential component are, however, on the ligament. Along the mid-dorsal line the resultant of the radial and tangential components is a marked posterior extension of the ligament, as demonstrated by Owen in *Glossus* and further described in the body of this paper (see figure 4*C*). An inevitable consequence, because the curved surface of the valves can only be in contact for a limited distance, is anterior splitting of the ligament, the separated portions curling forward beneath the umbones which are increasingly separated by the posteriorly directed wedge of shell secreted between them (see figure 1). This process, although without knowledge of the underlying factors concerned, was first noted by Anthony (1905).

Without personal investigation of the problem, Stasek (1963*b*) disputes the truth of this interpretation of the anterior splitting of the ligament. This he associates with the interumbonal growth characteristic of the Arcacea. But the formation and subsequent growth of the ligament in this family is totally distinct from that in all other Bivalvia, including—despite the contrary opinion based, however, on purely palaeontological evidence, of Newell (1937, 1942)—the Pectinacea and the Mytilacea. An initial statement of the problem involved is given by Owen (1959*b*). Stasek also regards as equivalent the dorsal splitting of the ligament found in *Ostrea* but also in all similarly cemented bivalves (e.g. *Spondylus Hinnites*, *Etheria*, etc.) and due to the necessary ventralward growth of the animal within its fixed shell. This has nothing whatever to do with the secreting surfaces and only by references to these can ligaments of at any rate living bivalves be understood.

Presumably because the commoner condition of attachment by the left valve (in *Chama*) was initially described, this has become known as the 'normal' condition in contrast to the 'inverse' condition found in the other genera. However, as will be described later, when the attached—or free—valves of normal and inverse shells are compared with one another, they are seen to be mirror images having the same components of teeth and sockets on the hinge plate. In terms of dentition and also of internal concavity, one must refer to *attached* and *free*, not to right and left, valves. This resemblance between the dentition of attached valves in the Chamidae was first noted by Munier-Chalmas (1882) in his pioneer studies on bivalve dentition and has been generally accepted by later workers with the notable exception of Odhner (1919) (who did not, however, accept the previous criticism of Bernard (1895)). Unable to accept inversion, Odhner postulated distinct dentitions in the two cases, writing that 'I tried to explain the dentition of both groups of Chamidae out of the general rule that a right valve is homologous with a right one only and that all parts of it must, and can be, homologized only with those of a right valve'. Correctly disposing of previously reported cases of inversion* attributed to species of *Astarte* and *Tellina*, he observed that 'Only among the Gastropods, where a twisted shell is present, have cases of inverted organization been observed', here referring to the sinistral or 'reversed' forms encountered either in whole genera or, either normally or abnormally, in species within a genus.

However, this argument cannot be applied to the Chamidae. The tangential component has the effect, already noted, of twisting growth in the sagittal plane with major effects on the ligament and also on the hinge plate below it. We are here therefore dealing with a coiled form of growth analogous, although in different planes, to that in the Gastropoda. Indeed in various of the Hippuritacea it had the same final effect, namely production of a deep, coiled shell with the aperture closed by a flat rounded opercular-like valve. There

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* Since, however, shown to occur in species of the Sphaeriidae, and in respect of either some or all teeth, by Eggleton & Davis (1961).

appears to be as great a probability for the production of inverse forms in the Chamidae—and in the Hippuritacea which were also divided into those with normal and those with inverse dentition—as there is for sinistral forms amongst certain Gastropoda such as *Busycon*. There seems no criterion for what is normal and what is inverted apart from the fact that the former is somewhat the more usual. What is interesting is the stimulus which causes, at some very early stage in development, attachment in some species or individuals by the right, and in others by the left, valve with a striking resultant bilateral asymmetry.

In the cemented Anisomyaria, e.g. *Spondylus*, *Hinnites* or *Ostrea*, previous byssal attachment predetermines the valve of attachment, invariably right in the Pectinacea and left in the Ostreacea (Yonge 1953*a*). In sharp contrast are conditions in the freshwater Etheriidae where cementation in any species (of three genera) although producing even greater asymmetry, is indifferently by either right or left valve (Yonge 1962*a*).

Conditions in the Chamidae are somewhat intermediate. While certain species do appear to be almost invariably attached by the one valve,* this is certainly not universally true. Bayer (1943) has shown that in the rare species, *Pseudochama inezae*, found off Florida, attachment is sometimes by the left valve (i.e. as in '*Chama*'). Two shells of *Chama radians* Lamarck from the British Museum kindly sent for inspection by Mr Norman Tebble are clearly attached, one by the right valve and the other by the left. They are undoubtedly of the same species, they are identical in shape, in superficial sculpturing of wavy growth lines and in possession of brown markings radiating from the umbones over the posterior half of both valves. Of the two species on which this research is based, *C. pellucida* was always found attached by the left valve but Palmer (1928) figures individuals attached by left *and* right valves. The great majority of *Pseudochama exogyra* (and all used in this work) were certainly attached by the right valve, but a small number were found which, while conforming to the general—rather indefinite—appearance of *P. exogyra*, were attached by the *left* valve.

While it is now clearly impossible to separate the cemented Chamidae into two genera on the basis of the valve by which they are attached, it remains convenient to use the accepted specific names, *Chama pellucida* and *Pseudochama exogyra* because all individuals studied and described in this paper were cemented by the left and right valves respectively. It is also convenient, regardless of species, to refer to '*Chama*' and '*Pseudochama*' thereby denoted individuals attached by these valves.

The characteristic features of the Chamidae are thus great development of the tangential component in growth and, apart from *Echinochama* where conditions must surely be secondary, permanent attachment by the left valve in '*Chama*' and by the right valve in '*Pseudochama*'. This is accompanied, as in other horizontally disposed and attached bivalves, such as the Anomiidae, various Pectinacea and, above all, the Etheriidae, by a notable degree of bilateral asymmetry. These features are illustrated in figure 1. Similar conditions probably represented the starting point for evolution in the Hippuritacea.

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* Out of 1000 specimens of *Echinochama arcinella*, Nicol (1952*c*) found only one that had been attached by the left valve.

SPECIES EXAMINED

This paper is based on the examination, largely in life, of two North Pacific species, *Chama pellucida* Broderip, the 'agate chama', and *Pseudochama exogyra* (Conrad), the 'reversed chama'. Both species (figure 1*B*, *C*) are extensively cemented to rocks or other hard substrate, even occasionally to floating timber, by the anterior half of the under valve the posterior end, with the small siphons, being raised well above the substrate. The upper valve is obliquely disposed facing to the left in *Chama* and to the right in *Pseudochama* (i.e. when viewed with the umbones directed towards the observer). Both species occur along the coast of California and extend as far north as Oregon; *C. pellucida*, which forms extensive reefs in southern California, ranging as far south as Chili, *P. exogyra* to Panama. Like all species of the attached Chamidae, they are admirably fitted for intertidal life under conditions of greatest exposure, in California often to the full force of the Pacific surf.

P. exogyra (figure 1*C*) has much the heavier shell and grows the larger, the upper valve (the best criterion of size) attaining a maximum diameter of 8 cm compared with some 5 cm for *C. pellucida*. It is typically found firmly cemented to thickly weed-covered rocks in mid to low intertidal levels so that, despite its size, it is often difficult to detect. Even when not overgrown by weed, the colour and texture of the shell closely resemble those of the underlying rock. One specimen was found which had become detached and with the surface of the shell rendered smooth by continual rolling amongst pebbles and rocks but with the contained animal alive.

C. pellucida (figure 1*B*), although smaller, is much more easily detected owing to the translucent wavy ridges which cover the white shell. Moreover, it usually occurs higher in the intertidal where there is little or no weed. It is commonest on under surfaces, many being uncovered at Point Cabrillo, Pacific Grove, following the great storm of 16 February 1960, when massive boulders were overturned (Yonge 1960). Like the pulmonate limpet *Trimusculus* (*Gadinia*) *reticulatus*, it was common also in the even greater shelter and the complete darkness of the sump at the entrance to the sea water circulation at the Hopkins Marine Station. McLean (1962) lists it among species encountered during diving off Carmel between 20 and 50 ft. below the surface, occurring 'in crevices and under sides of rocks'.

In both species the shell valves are invariably tightly closed when exposed and even when they are replaced in sea water they open most cautiously and close again on the slightest stimulus.

Other species examined provided no more than confirmatory evidence. They included individuals attached by the left valve but which otherwise closely resembled *P. exogyra* and might, as already noted, have been 'normal' individuals of that species. Both normal and inverse individuals were later examined at Bermuda.

SHELL AND MANTLE

Although the shell is formed by the mantle, it is more convenient to consider this product of secretion first. In doing so, however, it must be remembered that the shell consists of valves *and* ligament, each being formed of the same three constituents, (1) periostracum, (2) outer and (3) inner calcareous (or ligament) layers. These are secreted respectively by (1) the inner surface of the outer fold of the mantle edge, (2) the outer surface of this and (3) the general surface of the mantle which is modified along the mid-dorsal line to form the mantle isthmus which secretes the inner ligament layer (Yonge 1957*a*).

Valves

The external appearance of the asymmetrical valves with their pronounced tangential component has already been described. According to Bøggild (1930) the porcellanous shell is without calcite; he described the outer calcareous layer as composed of crossed lamellae with concentrical lamellae and the inner layer as being made up of very irregular alternation of prismatic and complex crossed lamellar structures. The end result is the formation of a particularly dense shell structure. The shell, especially in *P. exogyra*, is also unusually thick. In contrast, the non-calcareous periostracum is excessively thin and not to be detected on the outer surface. It is only visible, when the mantle margins are examined under the microscope, as a transparent film extending from the periostracal groove. Its function can be no more than the protection of the shell-secreting outer fold of the mantle edge (Yonge 1957*a*) except on the under valve where it must be concerned with at least the initial stages of cementation.

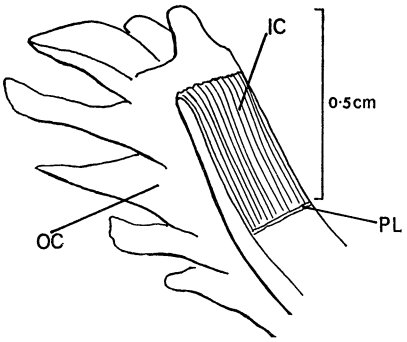

FIGURE 2. *Chama pellucida*, section through margin of shell.

The calcareous layers are both very thick. Conditions differ somewhat in the two species. In *C. pellucida* the outer layer, translucent and pinkish in colour, projects to form a series of wavy ridges (figure 2, OC) which are clearly formed, in the course of a series of 'shoots', by the outer surface of the outer fold of the mantle margin which, during periods of secretion, must be disposed almost at right angles to the outer surface of the valves. The inner layer (IC) is opaque white and, as in all Chamidae but unlike the majority of the bivalves, extends almost to the effective margin of the valves, i.e. for some distance peripheral to the pallial line (PL). In *P. exogyra* additions to the thick outer calcareous layer are also made discontinuously but they are closely applied to form, with the inner layer, an exceptionally thick and massive shell.

The general appearance of the interior of the attached and free valves and of the body, covered with the mantle including the associated adductor muscles in *P. exogyra*, is shown in figure 3*A* to *C*. Leaving detailed description of the body until later, attention must be drawn to the deeply concave attached (right) valve (*A*) and the flat free (left) valve (*B*).

The removed body (*C*) represents a cast of the interior of the shell with the enlarged umbonal region of the right side (UA) extending under the hinge plate (H) into the concavity, curved through an angle of about 90°, of the right valve. The umbonal region on the left side (UF) is greatly reduced to fit the shallow basin-like concavity in the almost flat upper valve.

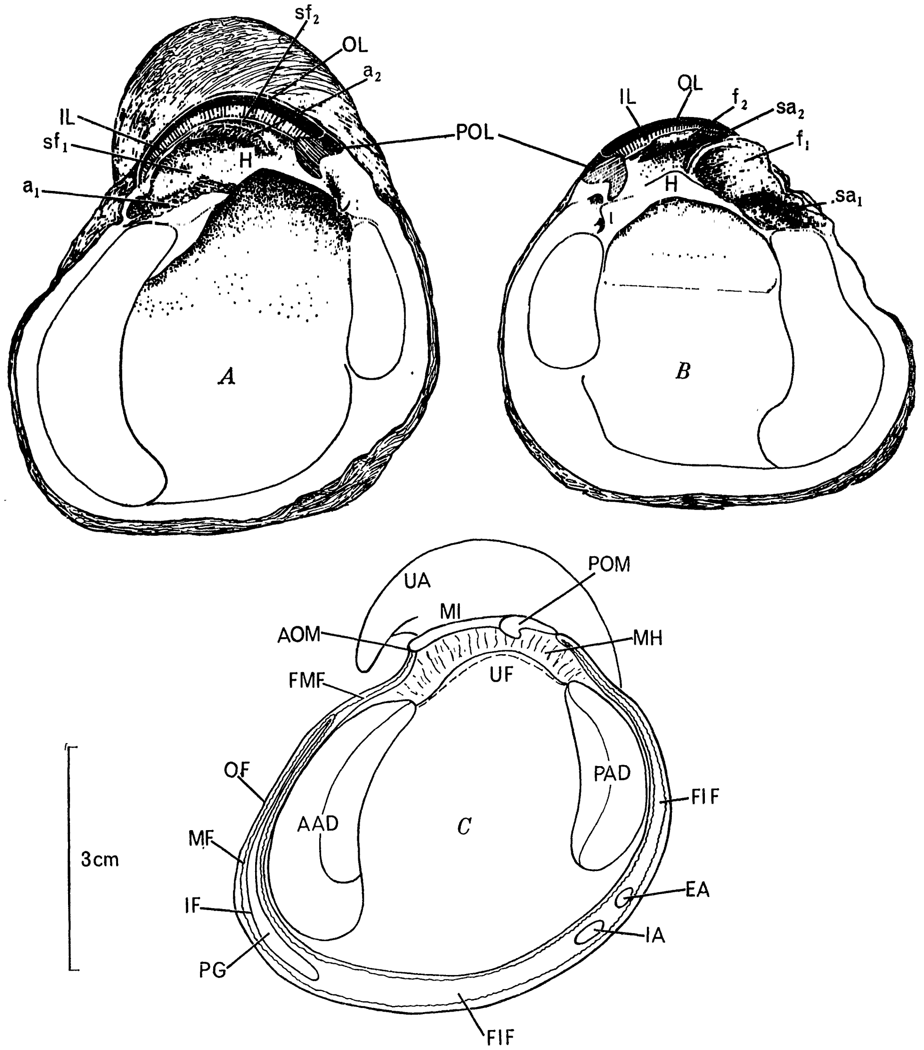

FIGURE 3. *Pseudochama exogyra*, inner surface of *A*, attached (right) and *B*, free (left) valves, with *C*, body of animal removed from the shell.

Ligament

This is a primary structure, i.e. without secondary extensions. The thin periostracum being almost immediately worn away, the ligament consists of inner ligament layer (figures 3 to 5, IL) formed by the mantle isthmus (MI) and outer ligament layer (AOL, POL) formed at both ends of this by the outer surface of the outer fold of the mantle margin (AOM, POM). The primitive condition (including periostracum) is shown diagrammatically in figure 4*A*. For reasons given below, in the Chamidae only the posterior portion of the outer ligament layer is functionally significant and it will be convenient to refer to that region of it which extends *over* the inner ligament as outer ligament (figures 3, 5, OL) reserving the term posterior outer ligament (POL) for the large region which stretches behind the inner ligament.

The primitive condition involving an antero-posteriorly symmetrical or equilateral, shell and so an amphidetic ligament (figure 4*A*) has been profoundly altered in the

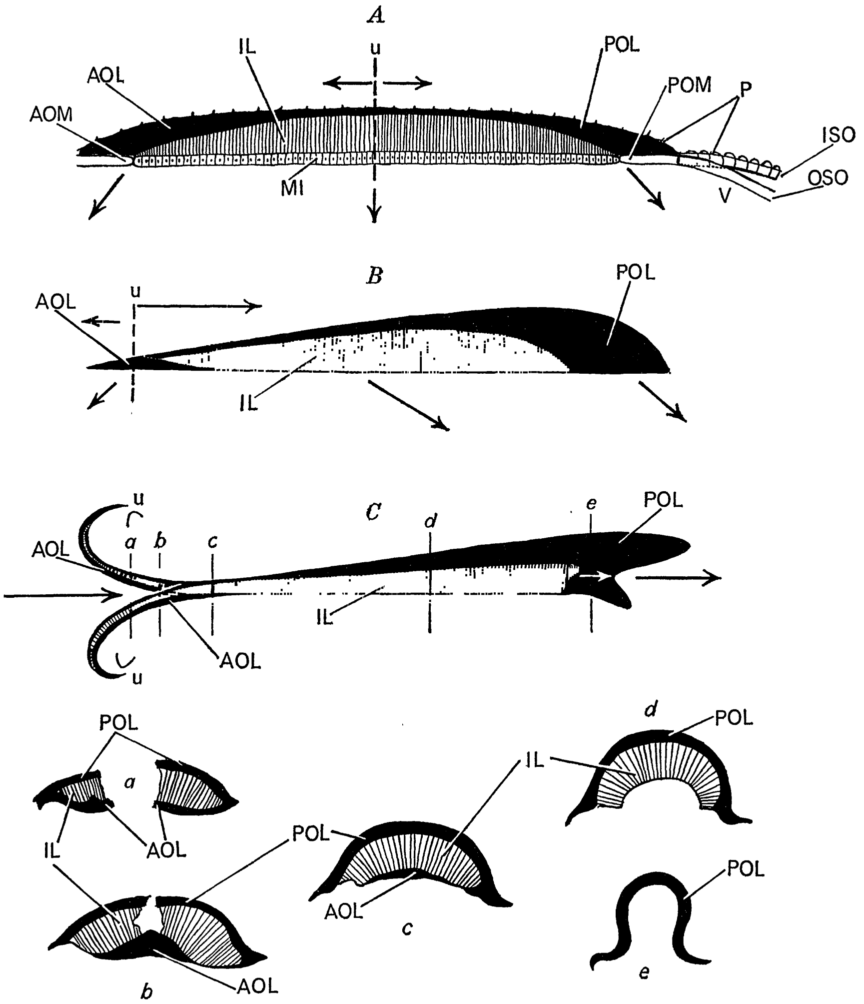

Figure 4. Diagrammatic longitudinal sections through *A*, primitive amphidetic ligament (showing secreting surfaces); *B*, opisthodetic ligament; *C*, 'tangential' ligament as in the Chamidae. *a–e*, transverse sections through 'tangential' ligament in regions indicated in *C*. Horizontal arrows above indicate direction of growth in relation to umbones (u); below (on right in *C*) direction of increase in thickness of ligament.

Chamidae. The ligament is here opisthodetic and has also been influenced to the greatest extent possible by the tangential component of shell growth. The structure of an opisthodetic ligament is shown in figure 4*B*. Here the whole structure is skewed in a posterior direction so that additional secretion causes extension in a postero-ventral direction, not just ventrally as in *A*, although, as in that case, the ligament grows at the same rate as do the valves. In these opisthodetic ligaments the posterior region of the anterior outer ligament layer (AOL) grows back *under* the inner ligament layer (IL) which in turn extends under the posterior outer layer (POL). Fusion layer (see comment at top of p. 64) is stated to occur above this in *Glauconema* (Veneracea) and *Pharella* (Solenacea) (Owen 1959*a*). If not worn away, periostracum (only indicated in figure 4*A*, P) lies above this. In the absence of the two latter layers, a transverse section through the middle of a more highly developed opisthodetic ligament, e.g. in *Bartlettia* (Yonge 1962*a*) shows posterior outer ligament layer above, inner ligament in the middle and anterior outer ligament below. The final effect is to produce a ligament of great strength.

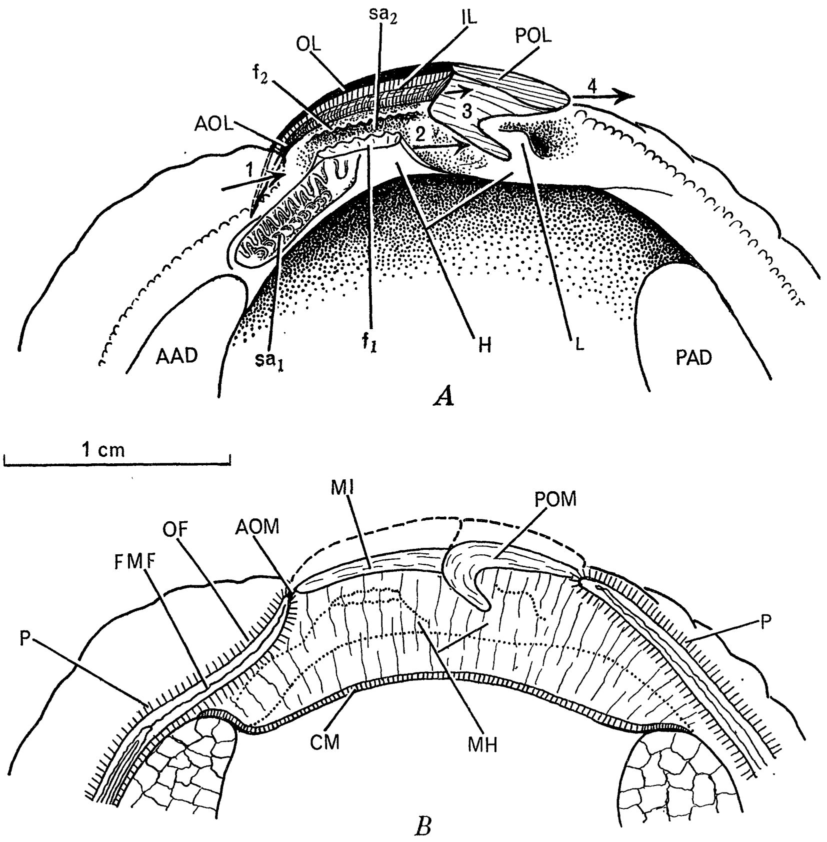

FIGURE 5. *C. pellucida*, *A*, dorsal region of free valve; *B*, dorsal region of animal with secreting surfaces (ligament indicated by broken lines). 1–4, direction of growth of ligament (see text).

The added influence of the tangential component, as first demonstrated by Owen (1953*b*) in *Glossus*, is to cause the ligament to grow in an almost exclusively posterior direction as indicated by the arrows in figure 4*C*. It therefore comes to exceed the rate of growth of the valves with consequent anterior splitting. As a result of this the anterior outer ligament layer ceases to have any functional significance.

This brief description of the manner in which the primitive ligament has been modified in the Chamidae renders easier description of the ligament in *C. pellucida* and *P. exogyra*. The appearance from above of this massive ‘external’ ligament with approximately the anterior third split and the halves curling back under the enrolled umbones is shown in figure 1. More can be seen from the ventral aspect and more easily in *C. pellucida*, as shown in figure 6. There, the abnormally wide separation of the valves has pulled the posterior outer ligament (POL) away from its attachment to the region of the valves marked X, but this is the only distortion. The inner ligament layer (IL), distinguished by its darker colour, represents the central region of the functional ligament. Anteriorly, the split is visible but further anterior extension of the halves is obscured by the growth beneath them of outer calcareous layer (OC) formed by the mantle margins. The thin anterior outer ligament layer (to be described later) cannot be distinguished against the dark mass of inner ligament. Posteriorly, however, the outer ligament layer (POL) extends beyond the inner ligament layer as a broad pointed median projection with wide lateral extensions into the two valves.

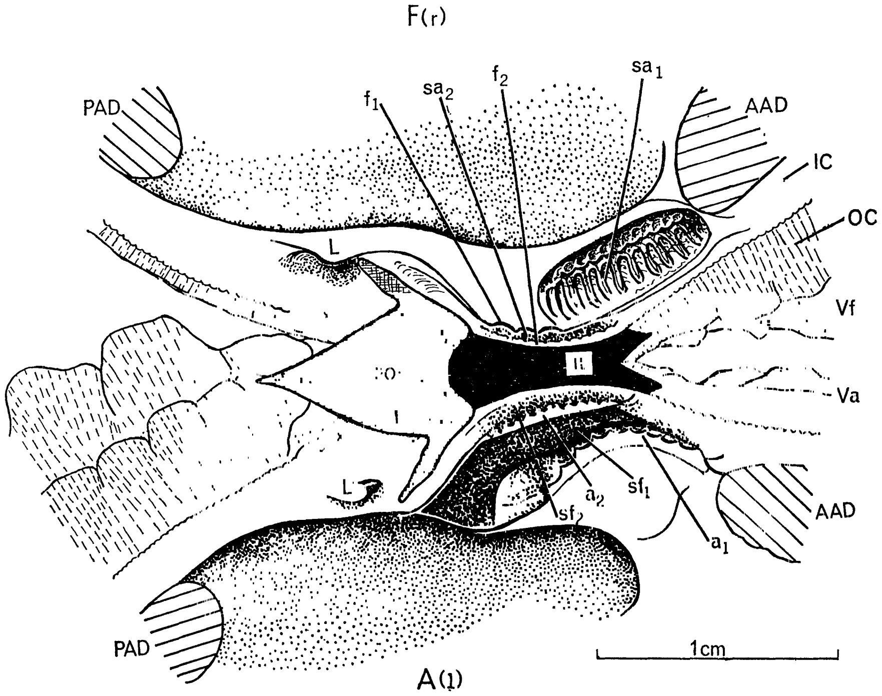

Figure 6. *C. pellucida*, hinge region, ligament and teeth viewed from ventral aspect, lateral wings of posterior outer ligament torn away from areas stippled and marked X. F(r), A(l), free (right) and attached (left) valves.

The appearance of the ligament in longitudinal section in both valves of *P. exogyra* is shown in figure 3*A*, *B*, and, in more detail, for the right valve of *C. pellucida*, in figure 5*A*. The great size of the ligament, especially in *P. exogyra*, is indicated in these figures. The thickness of the outer posterior ligament layer (POL), which stretches laterally beyond the margin of the inner ligament, is shown in section in figures 4*a* to *c* and 21. Except at the posterior end, it becomes covered over by the inner calcareous layer which forms the hinge plate (figures 3*A*, *B*; 5*A*, H). The position of the very small anterior ligament layer (AOL) is indicated in figure 5*A*. For reasons already noted, it extends beneath the inner ligament layer up to a point a little behind the position where the ligament splits (see figure 4*C*, *c*, AOL). For the greater part of its length it is therefore functionless and encased within the calcareous substance of the valves.

The mode of growth of the ligament is best described by reference to figure 5, showing in *A* the ligament (and teeth to be described later) and in *B* the pallial areas responsible for the formation of the various layers. As noted above, the obliquely posterior extension of an opisthodetic ligament is here reinforced by the full effect of the tangential component in shell growth. As a result, the growth of the ligament is effectively entirely in a posterior direction, the most significant areas of such growth being indicated by the arrows numbered 1 to 4 in figure 5*A*.

Beginning at the anterior end, there is first the posteriorly directed growth, already noted, of the outer calcareous layers of the valves (arrow 1) secreted by the outer surface of the outer folds of the mantle margin (figure 5*B*, OF). Extending between the diverging halves of the ligament (see figures 4, 5), this covers their under surfaces with increasingly thick calcareous layers (figure 7*A*, SL). Between the two surfaces responsible for this secretion, i.e. in the depth of the anterior embayment between the valves, lies the small area (figure 5*B*, AOM) responsible, as always, for the formation of the anterior outer ligament layer (AOL) which is here functionally negligible. On either side of the ligament, the inner mantle surface (figure 5*B*, MH) which secretes the hinge plate (H)—composed of inner calcareous layer—grows posteriorly over the lateral extensions of the outer ligament (arrow 2). These marginal areas of the outer ligament are thus laid down on the surface of the hinge plate and later covered over by the further secretion of calcareous matter upon them. This is shown in section in figure 7*B*, OL. The major growing surface of the inner ligament (IL) lies at the posterior end of the mantle isthmus (MI) where, as indicated by arrow 3, it grows under the broad backward and laterally extending posterior outer ligament (POL). Finally, extending in the same general direction (arrow 4) is the posterior region of the outer ligament (POL) secreted by the correspondingly extensive posterior outer mantle surface (figure 5*B*, POM). This is in striking contrast to the small surface (AOM) concerned with secretion of the anterior outer ligament layer. The extension of the posterior outer ligament layer unites the valves posteriorly (best indicated in figure 6, POL) at a somewhat greater speed than they are separated anteriorly. Like the rest of the shell, the functional ligament grows slowly in length and increasingly in breadth and thickness throughout life.

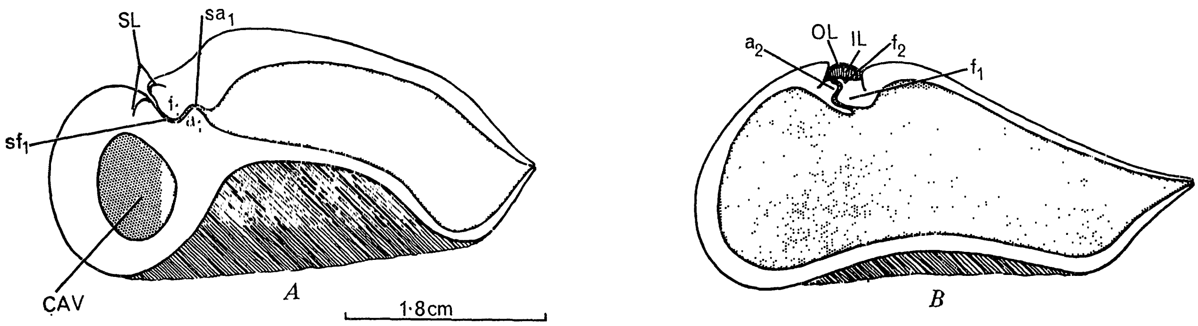

Figure 7. *P. exogyra*, transverse sections through shell, lower (right) valve shown cemented to substrate, internal cavity stippled. *A*, anterior, in region where ligament separated; *B*, through centre of functional ligament.

The first impression was to regard this broad and elongated posterior region of the ligament as largely composed of fusion layer, i.e. as formed by a fusion of the outer mantle margins posterior to those responsible for secretion of the posterior ligament layer. But such secondary extension of the primary ligament does now seem to be confined to genera such as *Pinna* (Yonge 1953*b*) and *Malleus* (unpublished observations) where the mantle margins are extensively withdrawn. In the Chamidae the broad secreting surface responsible for the posterior outer ligament represents hypertrophy of the outer surface of the outer fold of the mantle margin which borders the embayment between the valves posteriorly and is always responsible for the secretion of this ligament layer. Both anterior and posterior outer ligament layers are notably enlarged in this manner in the Etheriidae (Yonge 1962*a*).

Although this process of ligament formation proceeds throughout life (or as long as growth continues) with the anterior ends becoming, with the umbones, further and further separated, the final form of the shell must be established early in post-larval life. Shells of all sizes encountered, from about 8 mm diameter upwards, had the same proportions. Shells increase in size but not in the extent of coiling or in the relative, as distinct from the absolute, extent of anterior separation of the ligament. As in other much modified bivalves, metamorphosis must involve rapid and far-reaching changes in form with subsequent growth effectively representing no more than increase in size.

Dentition

As already stated, Munier-Chalmas (1882) first noted the 'normal' and 'inverse' conditions found in '*Chama*' and '*Pseudochama*' respectively. Attached valves in these are the mirror image the one of the other in respect of dentition—and also, with implications which will be discussed at length later, of internal concavity. It follows that the same is true of the flatter free valves. The conditions in the two genera are compared semi-diagrammatically in figure 8. Apart from the attempt by Odhner (1919) to deny that inversion has occurred, there has been considerable controversy about the precise dental formula as fully discussed by Odhner (1919, 1955) and Lamy (1927). So far as '*Chama*' is concerned, personal observations largely agree with those of Anthony (1905)—he did not see shells of '*Pseudochama*'. In young shells (figure 9*A*, *B*) Anthony shows two cardinals in each valve, 1 and 3 on the right (free) and 2 and 4 on the left with a posterior lateral (L) on each. In adult *C. lazarus* he considered that tooth 1 was lost. In an even younger *C. pellucida*, Dall (1903) figures two cardinals, radiating *not* parallel, in each valve and anterior as well as posterior laterals. A full study of early development in the Chamidae would be most illuminating.

However, as shown in figures 3, 5 and 6, there can be no doubt that adult Chamidae possess two cardinal teeth and one posterior lateral tooth in each valve. Nicol (1952*c*) states that there are two cardinal teeth in each valve of *Echinochama*. As a result of the posterior growth of the hinge line already discussed in connexion with the ligament, the cardinal teeth extend parallel to one another in an antero-posterior direction. In *C. pellucida* the dentition of the free valve is shown in figure 5*A* and, in both valves viewed ventrally, in figure 6. The dentition of the attached and free valves of *P. exogyra* is shown in figure 3*A* and *B*.

Owing to the impossibility, in this author's opinion, of homologizing the cardinal teeth, so greatly modified as a result of the tangential component in shell growth, with those of other Heterodonta, they are here designated a_1 and a_2 if on an attached, and f_1 and f_2 if on a free, valve. The first teeth, which are more ventrally placed and very much the larger, originate further to the anterior.

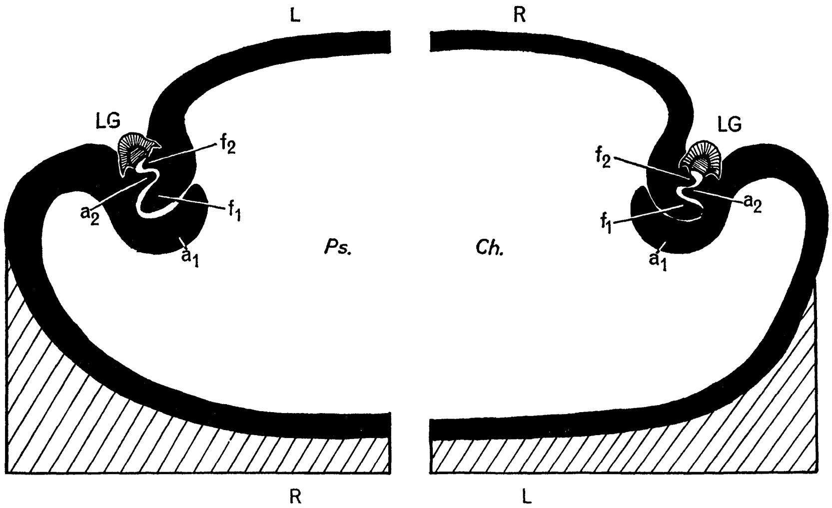

FIGURE 8. Diagrammatic representation of hinge region showing normal ('*Chama*') and reversed ('*Pseudochama*') dentition. L, R, left and right valves, under one attached to substrate.

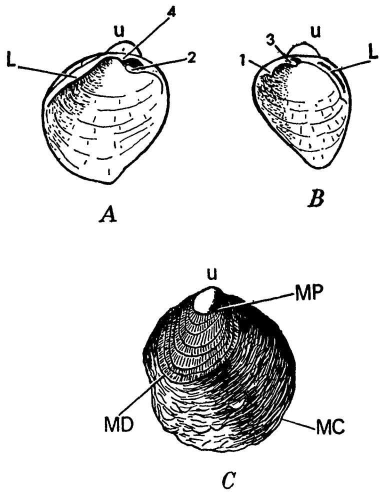

FIGURE 9. *Chama* sp., *A*, interior of left valve prior to cementation; *B*, interior of right valve (from different shell but about the same age); *C*, outer surface of right (free) valve shortly after cementation. 1–4, cardinal teeth; MC, margin of shell added after cementation; MD, margin of dissoconch (0·5 mm from umbo to MD); MP, margin of prodissoconch. (From Anthony 1905.)

In both *C. pellucida* (figures 5*A*, 6) and *P. exogyra* (figure 3*A*, *B*) the ventral teeth a_1 and f_1 are massive with strongly serrated margins which fit closely into similarly large and elaborately sculptured sockets (sa_1 and sf_1 respectively) in the opposite valve (figures 3, 6). This is also shown in section for *P. exogyra* in figure 7*A* and semi-diagrammatically for both conditions in figure 8. The much smaller dorsal cardinals, a_2 and f_2, which run closely parallel to the ligament, also have serrated margins. They fit into correspondingly small sockets, sa_2 and sf_2 (figures 3, 6). As shown in figures 3, 5 and 6, they originate posterior to the ventral cardinals. This is also apparent in figure 7; they only appear in the more posterior section (*B*). It is the small size of these teeth and sockets which has caused them to be overlooked by certain authors. In view of the elaborate structure of the large ventral cardinal in the free valve (f_1) Bernard (1895) considered that it represented (in '*Chama*' but it is no less obvious in '*Pseudochama*', cf. figures 5*A* and 3*B*) two teeth, 3a and 3b. But this conclusion, not accepted by Anthony, appears unjustified.

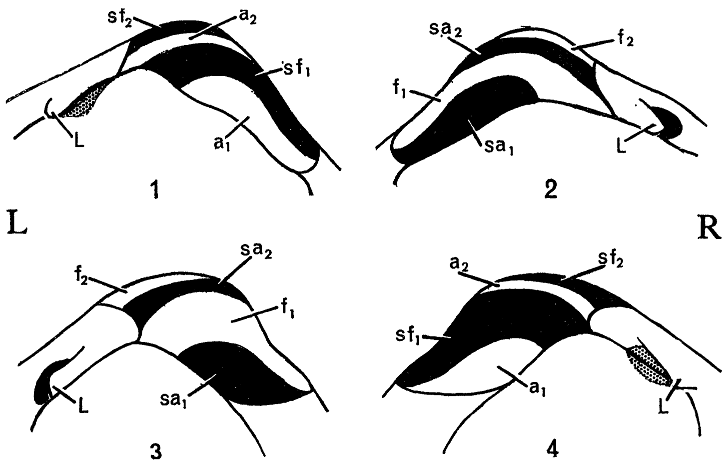

FIGURE 10. Semidiagrammatic representation of dentition in left (L) and right (R) valves of '*Chama*' (above) and '*Pseudochama*' (below) showing inversion. Teeth (a and f) shown white, sockets (sa and sf) black. Attached valves (1 and 4) have similar dentition so do free valves (2 and 3), *not* both left (1 and 3) and both right (2 and 4) valves.

Small posterior lateral teeth (figures 3, 5, 6, L) occur in both valves and fit into corresponding sockets in the opposite valve. Owing to the overgrowth of the hinge plate from the anterior end, any anterior laterals must early have disappeared in evolutionary history.

The dentition in the normal '*Chama*' and in the inverse '*Pseudochama*' and *Echinochama* may suitably be discussed by reference to figure 10. Here the upper figures (1 and 2) indicate the arrangement of teeth (white) and sockets (black) on the attached (left) and free valves of *C. pellucida*. The lower figures (3 and 4) refer to the teeth and sockets on the free and attached (right) valves in *P. exogyra*. It is at once apparent that left valves (1 and 3) do not correspond to one another, nor do right ones (2 and 4). Indeed the succession from ventral to dorsal of teeth and sockets (a_1, sf_1, a_2, sf_2) in 1 and 4 is the opposite to that in the valve of the same side in the other species (i.e. in 2 and 3). But when comparisons are made diagonally instead of vertically, it is seen that 1 and 4 and also 2 and 3 are mirror images, i.e. that attached valves (1 and 4) correspond and so do free valves (2 and 3). This is also shown in figure 8. There can be no question as to the presence of inversion in the dentition of '*Pseudochama*' and (also of *Echinochama*). This matter is more fully discussed later but it may be here noted that this inversion, which is associated with cementation, is of pallial, as distinct from bodily, origin.

Mantle

The form of this in *P. exogyra*, with enclosed viscero-pedal mass, is shown in figure 3*C* together with drawings of the inner surfaces of the valves which it secreted. The mantle isthmus (MI) is situated along the summit of the laterally compressed flap of tissue (rather like a cock's comb) which secretes on its two sides the massive hinge plate (H) with the teeth described above. It represents the morphological mid-dorsal region of the animal, here separated into two very dissimilar 'halves'. The umbonal area on the right, i.e. attached, side (UA) is very much larger than on the free side (UF) and extends dorsally and anteriorly into the deep and curved concavity within this attached valve (figure 3*A*). Mirror image conditions prevail in *C. pellucida*. A full account of this bilateral asymmetry is given later.

The mantle margin is bounded by the invariable three parallel folds, outer, middle and inner (figure 21, OF, MF, FIF). All are unusually small. Tentacles, more customarily found on the sensory middle fold, although sometimes also present on the muscular inner fold, are here very small and confined to the latter. The mantle margins are extensively fused leaving small inhalant and exhalant apertures (figures 3*C*, 11, 12, 13, 14, IA, EA) and an externally much larger and slit-like pedal gape (PG) much the greater part of which, as shown in figures 3*C*, 12, 13, 14, represents a dorsal extension around the anterior margin of the anterior adductor (AAD). The actual opening into the mantle cavity is very small although adequate for the occasional protrusion of the much reduced foot (figures 12, 13, 14, F).

Except at the extreme anterior end, i.e. between the dorsal surface of the anterior adductor and the mantle isthmus, fusion is exclusively by way of the inner mantle folds (figures 3*C*, 13, 14, 21, FIF), i.e. the simplest condition described elsewhere as Type A (Yonge 1957*a*). These regions of fusion which are pigmented are shown shaded in figures 13 and 14. The short inhalant and exhalant siphons (figure 11, IS, ES) represent extensions of this region. Dorsal to the pedal gape, fusion also involves the inner surface of the middle folds (i.e. Type B) as shown in figures 5*B* and 13 (FMF). Also indicated in the former figure are the limits of periostracal secretion (P) in the antero-dorsal and postero-dorsal extremities of the mantle margins; between these are the three epithelial surfaces (AOM, MI, POM) which secrete the ligament.

Pallial muscles

On the inner surfaces of the valves the thin line of attachment of the pallial muscles broadens out terminally into the extensive adductor scars, dorso-ventrally extended and roughly parallel (figure 3*A*, *B*). Both muscles are exceptionally large and clearly divisible into outer opaque ('catch') and inner and smaller clear ('quick') areas. The size of these muscles can be related to habitat, to the need for sustained closure during exposure to the air or to violent wave action to which they must frequently be exposed. Here, as elsewhere, the 'quick' muscle is an essential constituent in the cleansing mechanism, ejecting accumulations of pseudofaeces (figures 13, 14, PS) by occasional sudden contractions. While the tangential component of growth certainly influences the form of these muscles, the anterior adductor being extended dorsally and the posterior one ventrally, this effect is emphasized because, for functional reasons, these muscles are so enlarged. In *Glossus*, with an equal tangential component but living in still water on a mud bottom at some depth, the adductors are relatively small and only the anterior one somewhat elongated. Cleansing is there the prime function with the 'quick' area twice the size of the 'catch' area.

THE LIVING ANIMAL

Previous information about the morphology of the Chamidae derives largely from the work of Grieser (1913) on *Chama pellucida* and the very exhaustive studies of Odhner (1919) who is the major source of knowledge on the structure and taxonomy of the family. But these, and other authors to be later quoted with the solitary exception of Kellogg's observations on ciliary currents, dealt exclusively with preserved material. The major additional information here provided concerns the living animal.

A. EXTERNAL FEATURES

Until the upper shell valve has been removed, very little can be seen of the enclosed animal; even when fully relaxed the valves separate only slightly and this was only rarely observed. For a very large specimen of *P. exogyra* of greatest diameter 7·5 cm, the maximum observed gape was 5 mm, that of a much smaller *C. pellucida* of greatest diameter 1·2 cm was 2 mm. When the valves separate the short, well separated, siphonal tubes project from the ventral surface. In *P. exogyra* (figure 11), where the exposed mantle, including siphonal, tissues are orange coloured, the tentacles white, the inhalant siphon (IS) is directed ventrally and, in the case of the large specimen, to a length of 1·8 cm with a diameter of 0·7 cm. The opening is fringed, and the outer surface covered, with the minute tentacles which, as already noted, occur generally on the fused inner mantle folds. The exhalant siphon (ES) in this specimen was about 1 cm to the posterior and pointed obliquely back and slightly dorsalward. It was 1 cm long with the somewhat restricted opening 0·5 cm in diameter. This is not fringed with tentacles although these occur on the outer surface. Despite their small size, it will be noted how the relatively wide separation of the siphons (due to their origin exclusively from the inner mantle fold, i.e. with no common sheath of middle and possibly outer folds) and their divergence prevents any disturbance of the inhalant by the exhalant current.

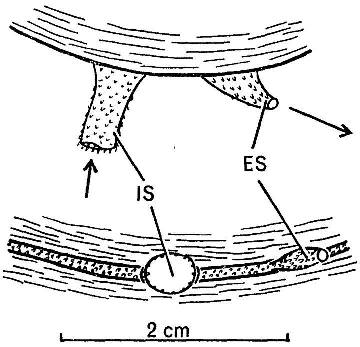

FIGURE 11. *P. exogyra*, showing appearance in life of inhalant and exhalant siphons, above in side view, below viewed facing margin of valves. Arrows indicate position of water currents.

When fully expanded, occasional sharp contractions of the adductors without withdrawal of the siphons were accompanied by extrusion of much flocculent pseudofaeces indicating considerable secretion of mucus in the mantle cavity. From time to time true faeces, in the form of very long strings, not pellets, passed out through the exhalant opening.

The appearance when viewed facing the free margin of the valves in an expanded *C. pellucida* is shown in figure 12. Apart from the reversed disposition, conditions are essentially similar. The mantle and siphons are white with a double row of yellow tentacles, more numerous on the siphons. Unlike *P. exogyra*, tentacles occur within the inhalant siphon. Basally on either side (not in the middle line) is a single row of nine rather staggered simple yellow tentacles; the interior of both siphons is pigmented, ranging from yellow basally to brown just within the opening. In this species the pedal opening—seldom visible in *P. exogyra*—opens relatively widely and the small foot may occasionally be seen curling around the ventral surface of the anterior adductor (figure 12, F).

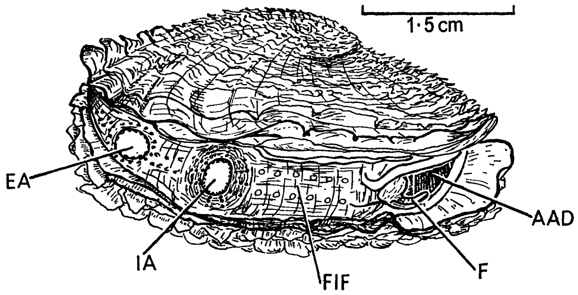

FIGURE 12. *C. pellucida*, viewed in life with valves fully open. Foot shown within pedal gape curling round outer side of anterior adductor.

Organs in the mantle cavity

The appearance after removal of the free valve and upper mantle lobe in *C. pellucida* and *P. exogyra* respectively is shown in figures 13 and 14. The effect on the body of the tangential component in the growth of the mantle/shell, combined, with that of cementation, is at once apparent. The visceral mass becomes extended dorso-ventrally instead of antero-posteriorly owing to the dorsalward movement of the anterior, and the ventralward movement of the posterior, adductor. The mouth (figure 17, M) and the anterior pedal retractors (APR) are carried far dorsally, while the anus (A) and the posterior attachment of the ctenidia move ventrally, associated with which is the ventral position of the siphonal openings. A very similar disposition of the adductors, visceral mass and ctenidia occurs in *Etheria elliptica* (Unionacea) but this is due to dorso-ventral extension of the mantle/shell; there is no tangential component in growth (Yonge 1962*a*).

Foot

Change in disposition of the visceral mass has led to posterior (topographically ventral) movement of the foot (figures 13, 14, F) which points anteriorly. It is small and very compressed but, in spite of the sessile habit, is not functionless. There are paired anterior and posterior retractors, the former, as shown in figure 19, being somewhat asymmetrical dorsally owing to the dissimilarity of the valves in the region of insertion. The posterior retractors (figure 17, PPR), also very small, extend posteriorly and dorsally, passing through the kidneys (K) to be inserted near the dorsal end of the adductor. Conditions are essentially similar in the two species. In *P. exogyra* the foot of a large specimen was observed to extend to a maximum length of 1·5 cm, the breadth being only 3·5 mm. It was thus long enough

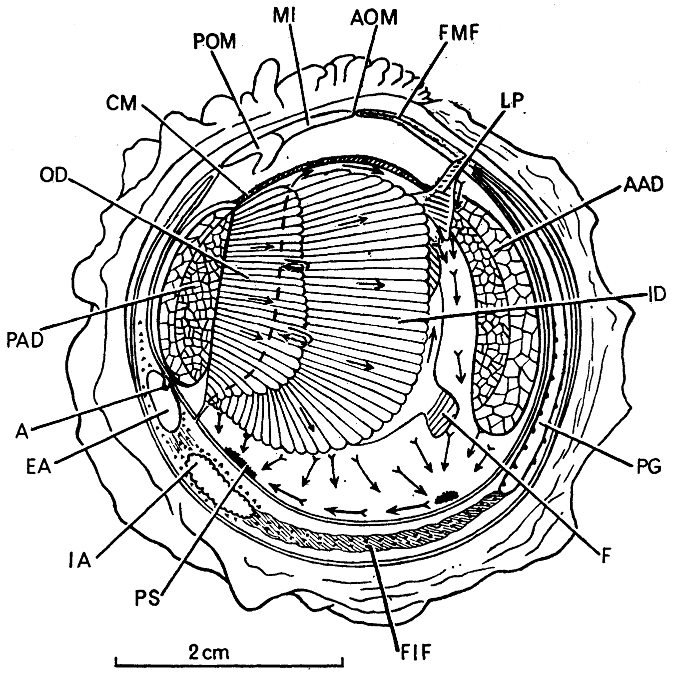

FIGURE 13. *C. pellucida*, animal lying in attached (left) valve, free valve and upper mantle lobe removed. Plain arrows indicate course of ciliary currents on the ctenidia, feathered arrows of cleansing currents in the mantle cavity.

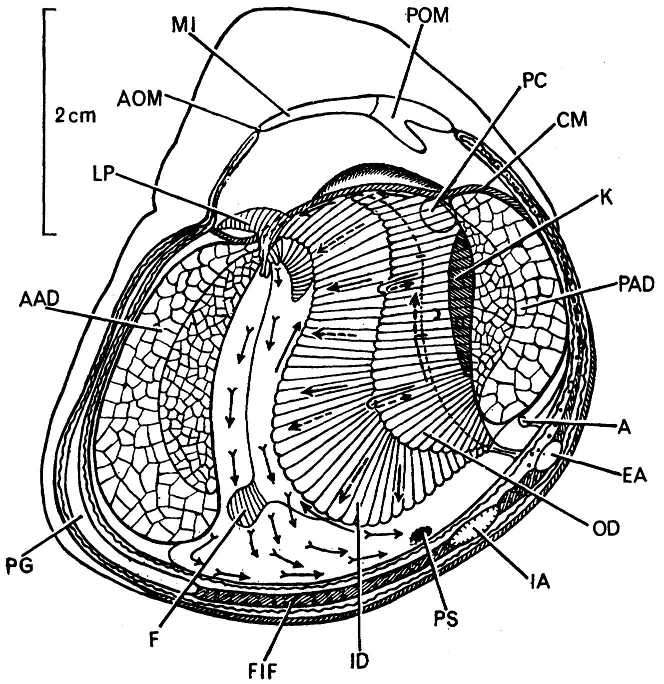

FIGURE 14. *P. exogyra*, animal lying in attached (right) valve, free valve and upper mantle lobe removed. Arrows as in figure 13.

to reach, but not to extend beyond, the pedal opening; but it was seen to extend and contract readily. In no other specimen was greater extension noted. In *C. pellucida*, as shown in figure 12, the thin and very pointed foot was seen to protrude, but only to the extent of moving dorsally along the outer surface of the anterior adductor. As in other attached genera where it is retained, such as *Spondylus*, *Hinnites* or *Anomia*, the foot probably assists in cleansing the mantle cavity and also the area, apparently unciliated, around the anterior face of the adductor.

Ctenidia

The inner demibranchs of the dorso-ventrally extended ctenidia are much the larger, the outer ones ending some distance short of the palps and mouth. Owing to a considerable supra-axial extension, the outer surface of the outer demibranch is considerably greater than the inner surface (the position of the ctenidial axis is indicated by a broken line in figures 13 and 14). Posteriorly the ends of both demibranchs are connected with the mantle margins immediately anterior to the exhalant opening. According to Odhner (1919) in some individuals of certain species they may be free but this condition was not seen in any living specimen examined. The ctenidial axis is free from the visceral mass for approximately the middle third of its length.

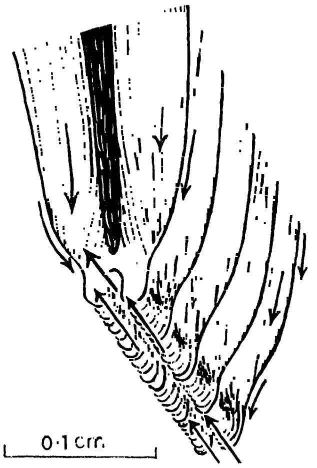

FIGURE 15. *P. exogyra*, portion of inner demibranch, showing pronounced plication and deep marginal groove. Arrows indicate direction of ciliary currents on frontal surfaces and within and alongside marginal groove.

The ctenidia of the Chamidae have been reported on by Ridewood (1903), Anthony (1905), Grieser (1913) and, in greatest detail, Odhner (1919). It is only necessary to note the leading characteristics and pass on to observations in life. As shown in figure 15, the ctenidia are markedly plicate, the numbers of filaments (up to 30 or over) in the plicae being variable. Principal filaments are broad. Adjacent filaments are united by interfilamentar junctions and principal filaments also by interlamellar junctions to those of the opposed lamella. Also, as observed by both Anthony (1905) and Grieser (1913), there are intraplicatural junctions between the bases of opposing filaments within the same plica. This condition was originally noted by Ridewood (1903) in other bivalves with very highly developed plicae. The probable course of blood flow within this complex ctenidium is discussed by Odhner (1919).

Ciliary currents

The only previous observations on ciliary currents in the Chamidae (indeed the only previous observations dealing with living Chamidae) are those of Kellogg (1915) on *Chama* (i.e. *Pseudochama*) *exogyra* in his classic paper on ciliary mechanisms in lamellibranchs. He found currents running to the free (here anterior) margin on both surfaces of the inner, and on the outer surface of the outer, demibranch but to the axis on the inner surface of the latter. Oralward currents run along the axis and the free margin of the inner demibranch which is grooved. Currents are similar of both ordinary and principal filaments. These general observations were confirmed and the same conditions found in *C. pellucida* (figures 13, 14). This pattern of gill ciliation, Type C (1) of Atkins (1937), is characteristic of many eulamellibranchs.

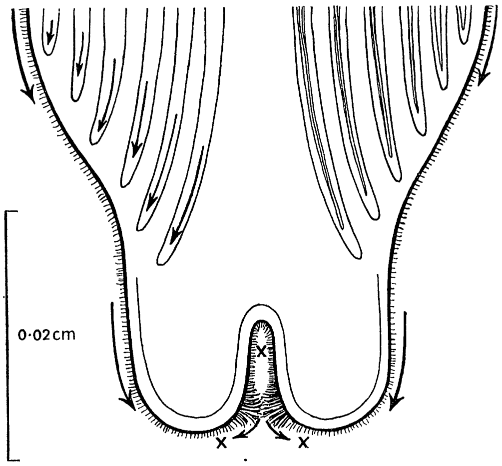

FIGURE 16. *C. pellucida*, section through margin of inner demibranch showing union of filaments marginally and details of marginal groove with zones of enlarged cilia guarding entrance. Arrows indicate ciliary currents in plane of drawing, crosses indicate oralward currents.

The marginal groove along the inner demibranch, the route whereby the greater part of collected particles must reach the mouth was further examined. In both species it is exceptionally narrow and deep (figures 15, 16). Owing to marginal fusion of filaments a plical length of some thirty-two filaments is bounded by usually only six ridges. The entrance to the groove is narrow and, as shown in figure 16, guarded by tufts of cilia somewhat longer than those of the surrounding frontal surfaces which average about 14 μm. But there are no conspicuous series of long guarding cilia such as those noted by Atkins (1937) in various species and by Yonge (1946) in *Aloidis gibba*. The presence of such cilia is generally correlated with the presence of much silt in the water. However, the effect in the Chamidae is much the same, only the most minute particles being able to enter the grove for certain transmission via the palps to the mouth. Larger particles or mucus-laden masses also proceed oralwards but along the free margin of the demibranch on either side of the groove. Much of this is transferred on to the surface of the mantle or of the visceral mass there to become incorporated in the pseudofaeces. The entrance into the marginal groove appears so narrow, and so well guarded, that by unaided ciliary means it is difficult to see how much material can enter but, as noted below, the ctenidia are very muscular and appropriate contractions may cause the groove to open. But undoubtedly the ctenidia are highly selective.

Muscular movements

These were constantly observed, are clearly of major importance in the functioning of the ctenidia and took the following three forms. (1) The narrow space between adjacent plicae intermittently opened and closed. (2) A slight but regular lengthening and shortening of the demibranchs, i.e. from axis to margins, probably due to rhythmical contraction of the axial musculature occurred. During relaxation, passage of water into the exhalant chamber would tend to lengthen the lamellae. Odhner (1919) has described the strong ctenidial musculature in the Chamidae. (3) Probably the most important movements were demonstrated after carmine was placed on the surface of the ctenidia when it was blown clear by expulsion of water from between the filaments, presumably owing to contraction of muscles within the lamellae or plicae. Unlike (2) this is a *local* reaction. The reduction in interlamellar space is accompanied by a wide opening between adjacent plicae. On relaxation, water is drawn with some force into the interlamellar space (which communicates with the exhalant chamber) and the space between plicae is reduced.

Functioning of ctenidia

The ctenidia are noteworthy on account of their complex folding with the elaborate system of internal cross connexions between lamellae, filaments and within the plicae, as described by Anthony (1905) and particularly by Odhner (1919) who was, however, particularly concerned with consequent complications in the circulatory system. Considered in relation to their prime function as feeding organs, the elaborate plication produces the maximum of current-producing and straining surface. This is clearly important to animals living attached to rocks, i.e. in water which carries very little suspended matter. At the same time the elaborate complexity of structure increases the danger of blockage by any excess of such matter and so may explain the presence of the series of mechanisms which ensure removal of all but the smallest particles or mucous masses from the surface. Removal (eventually within the pseudofaeces) is thus the work of both ciliary and muscular agencies. Only the finest particles and masses, notably those in the depth of the marginal grooves which may open to receive them, pass to the labial palps.

Labial palps

These are small (figures 13, 14) and, as shown in figure 19, are asymmetrical with the proximal oral groove (POG) on the under, and larger, side of the body much the longer. Material is carried between their opposed, ridged faces direct from the marginal groove on the inner demibranchs and by way of the axis from the outer demibranchs. Particles are then carried oralwards over the summits of the folds but these are small, whereas the intervening furrows are readily exposed and in them particles are carried to the ventral margins. There, as noted by Kellogg (1915), the direction of the currents is the reverse of what is normal. Instead of carrying material to the tip of the palps for disposal on to the visceral mass or mantle, they convey it anteriorly and so on to the mantle (figures 13, 14). As

Kellogg pointed out, rejected material carried to the tip of the palps in these modified animals would probably be caught in the gills and so returned. Material not rejected finally passes to the mouth in the depth of the long proximal oral groove (figure 19), although even there any excess is rejected by way of ciliary tracts running along the walls of the groove. Selection on the ctenidia is thus followed by equally rigorous selection on the palps and even in the proximal oral groove. Conditions are essentially similar in the two species.

Rejection currents in the mantle cavity

Material on the visceral mass is passed on to the mantle from a point just posterior to the foot (figures 14, 15). On the mantle surface, as noted by Kellogg in *P. exogyra*, all particles eventually accumulate in an area just within the inhalant opening forming a mass of pseudofaeces which is periodically expelled by sudden contractions of the 'quick' muscle. In *C. pellucida* there is prior collection of material from the anterior regions of the mantle cavity below the base of the anterior adductor and this is then conveyed in mid-ventral tracts to the inhalant opening (figure 14).

B. Internal anatomy

In view of the work of Anthony (1905), the detailed description of *C. pellucida* by Grieser (1913) and the wide comparative account of the Chamidae by Odhner (1919), little need be added about internal anatomy.

Gut

The anatomy and the histology of the gut of *C. pellucida* have been fully described by Grieser while Odhner has compared conditions in a variety of species. He does not support the view of Pelseneer (1911) that the mid-gut always extends into the topographically lower side of the visceral mass, i.e. to the left in *Chama* and to the right in *Pseudochama*. The significance of this is discussed later. As indicated in figure 17, the gut is unusually short. The elongation of the adductors has displaced the mouth (M) dorsally and the anus (A) ventrally. A somewhat compressed and internally ridged oesophagus (figure 18, O) leads into a capacious stomach with the associated mid-gut and style-sac (SS) leaving antero-ventrally. After termination of the style-sac, the gut proceeds, with only one anteriorly directed loop, dorsally to pass through the ventricle (VE) and, as the rectum (R), to run ventralward along the extended posterior surface of the posterior adductor. The anus (figures 13, 14, 17, A) lies just within the exhalant opening. The shortness of the gut is probably associated with the turbulence of the water in which these animals live. There is no need to compact the faeces into pellets.

The stomach was examined not in terms of its finely complicated structure of ciliated ridges and grooves and numerous openings into the digestive diverticula but as the one asymmetrical organ of the body (as distinct from the mantle/shell). In general form and mode of functioning, the stomach of neither species differs significantly from those of *C. multisquamosa* or *C. lazarus*, as described by Purchon (1958, 1960), or indeed of *Glossus* described, with a very convincing account of the probable manner in which it functions, by Owen (1953*b*). As in that genus, the stomach of the Chamidae is one admirably fitted for dealing with fine particles passed to it after much initial sorting on the ctenidia, palps and proximal oral grooves.

The appearance of the stomachs of *C. pellucida* and *P. exogyra* viewed in each case from the upper, i.e. free, surface is shown in figure 18*A* and *B* respectively. Apart from the brown voluminous mass of the surrounding digestive diverticula, the major associated structures, both without and within the cavity of the stomach are externally: (1) the oesophagus (O)

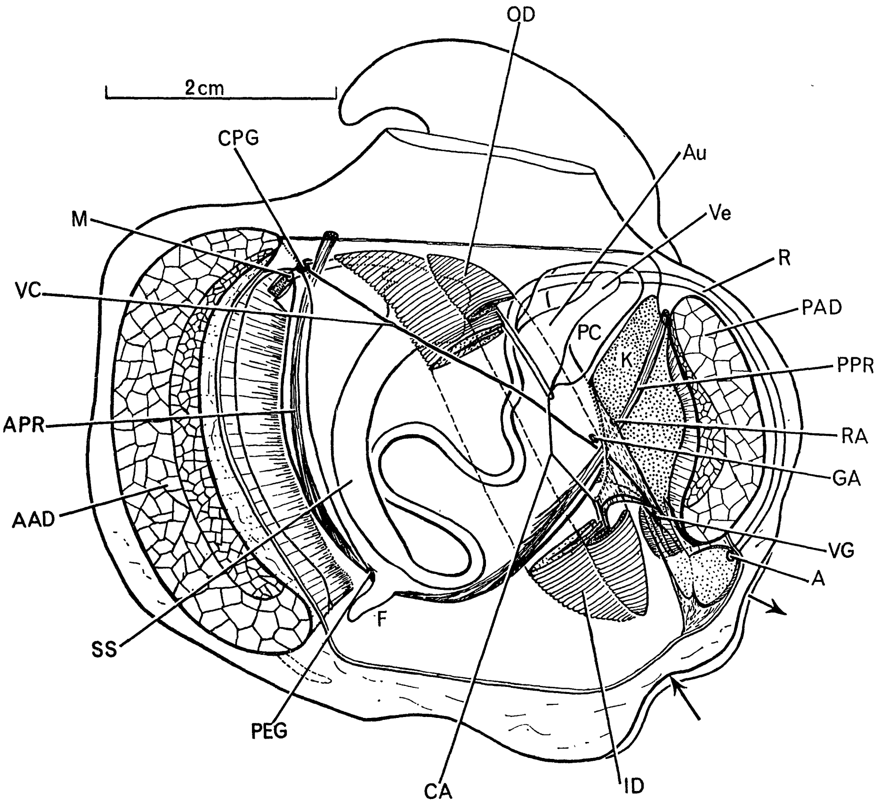

FIGURE 17. *P. exogyra*, dissection (of preserved specimen) showing major features of internal anatomy. Arrows indicate position of inhalant and exhalant currents.

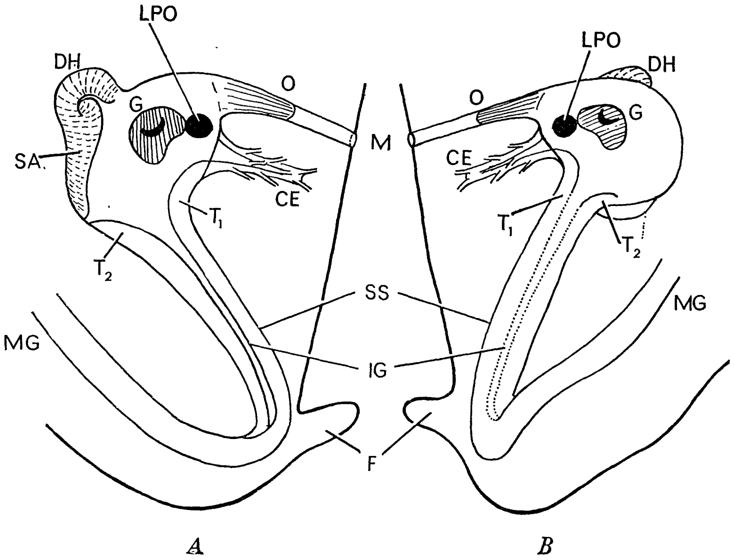

FIGURE 18. Upper views of stomach of *A*, *C. pellucida* (right side) and *B*, *P. exogyra* (left side) showing absence of inversion in this organ.

which opens antero-dorsally; (2) the anteriorly projecting caecum (CE) into which the major typhlosole (T_1) separating the mid-gut and style-sac extends and where the bulk of the numerous ducts from the digestive diverticula on both right and left sides open; (3) the style-sac (SS) with the mid-gut, or intestinal groove (IG) running along its right side, the two being separated by the major and minor typhlosoles (T_1, T_2); (4) the dorsal hood (DH), here somewhat posteriorly displaced owing to the alteration in the disposition of the visceral mass, which originates on the left side (see figure 18*B*) while the major sorting area (SA) associated with it extends along the right posterior wall of the stomach. Within the cavity of the stomach lie (5) the gastric shield (G) with single central tooth situated on the left side opposite the opening of the style-sac and (6) the opening, on the same side and in close association with the shield, of the left pouch (LPO).

These are among the major features in what in all Bivalvia, indeed in all Mollusca, is primitively a most asymmetrical organ as revealed in the exhaustive studies of Graham (1949) and Purchon (1957, 1958, 1960). Although the effect of torsion is to render it yet more complicated in the Gastropoda, in the Bivalvia it does not appear to be affected by either the bilateral asymmetry especially associated with cementation or the antero-posterior asymmetry associated with heteromyarianism and monomyarianism (Yonge 1953*a*, 1962*b*). The significant point in the Chamidae is that, as shown in figure 18, the form of the stomach is unaffected by the valve on which the animal rests and which has so profound an effect on dentition and on the form of the valves. Looking on the upper surface of the stomach of *Chama* as the animal lies attached by the left valve (*A*), we view the right side of the stomach, in the case of *Pseudochama*, lying on the right valve (*B*), we view the left side of what is, in all but the most minor details, an entirely similar organ. The implications of this are discussed later.

Heart and kidneys

The pericardium (figure 17, PC) is situated in the usual position, being uninfluenced by the change in disposition of the visceral mass. The heart in *C. pellucida* has been very fully described by Grieser, and the blood system generally by him and by Odhner who deals with a range of species in the Chamidae. As already noted, the gut passes through the ventricle (VE). White (1942) describes the anatomy of the heart and the presence of pericardial gland tissue on the surface of the auricles in *C. lazarus* and *C. broderipii*. The large and widely united kidneys (K) have been extended dorso-ventrally so that the posterior pedal retractors (PPR) have to pass through them to make attachment to the shell just within the upper margin of the posterior adductor. The kidneys open into the exhalant cavity by very inconspicuous pores (RA) situated at their anterior (morphologically ventral) margins and about half-way along the length of the ctenidia.

Nervous system

Full details of this have been given by Grieser for *C. pellucida* and confirmed and extended over a wide range of species by Odhner. The most interesting points are the unusual presence of small buccal ganglia and of a 'median commissure' which connects the two cerebro-visceral connectives a short distance anterior to the visceral ganglia. As shown in figure 17, these ganglia (VG) have moved ventrally with the extension in that direction of the posterior adductor and are now situated on the anterior instead of the ventral face of that muscle. Odhner notes that all Chamidae, despite their sessile habit, possess a pair of statocysts, each with one statolith, lying just within the pedal ganglia. However, this is also true of the Ostreidae where even the foot is lost.

Reproductive system

As noted by earlier workers, the sexes are separate. The gonopores (figure 17, GA) open into the exhalant chamber about midway along the length of the ctenidial axis and so opposite the region where this is free from attachment to the visceral mass. It is therefore possible, although certainly improbable, that eggs could, by appropriate muscular contractions, be forced into the inhalant chamber for incubation as—by different mechanisms in that case involving passage through the ostia in the ctenidia—they are in the genus *Ostrea*. But nothing appears to be known about development in the Chamidae or whether incubation occurs. Dall (1895) states that in the Chamidae the ovary extends into the mantle lobes. This was confirmed by White (1942). In large *P. exogyra* the gonads certainly extend into the mantle lobes when ripe; this was observed in two male specimens in March 1949.

Bilateral asymmetry

Both *C. pellucida* and *P. exogyra* are strikingly bilaterally asymmetrical. The under mantle lobe and so the attached valve which it secretes are much deeper then the upper lobe and valve. This has inevitable consequences on the form of the enclosed body. This is shown in figure 19 where, after removal of the mantle lobes (cut along CM) including the adductors, the bodies of *P. exogyra* (*A*) and *C. pellucida* (*B*), viewed from the anterior, are compared with that of a bilaterally symmetrical bivalve (*C*). As indicated in the last, the typical bivalve body is divisible into symmetrical right and left halves by a line running from the mantle isthmus (MI), through the mouth (M) to the middle of the foot (F). The palps (LP), ctenidia (CT) and attachments of the anterior pedal retractors (APR) are symmetrically disposed on either side. Although in *C. pellucida* and *P. exogyra* one effect of the tangential component is to move the posterior end of the ctenidia ventrally and the foot anteriorly (see figure 19; also 13, 14), this has no effect on bilateral symmetry. With the mantle isthmus and mouth, these remain in the mid-line (compare vertical lines in *A*, *B*, *C*). As also shown in figure 20, it is the umbonal regions which are bilaterally asymmetrical.

On the attached side, whichever that may be, the umbonal region (UA) is greatly inflated and also extended dorsal to the hinge plate as well as curved anteriorly as shown in figure 3*C*. The umbonal region of the free side (UF) is reduced (cf. UA and UF in figure 19*A* and *B*). There is some accompanying asymmetry in the anterior pedal retractors (APR) but to a much greater extent in the ctenidia (CT). These are notably elongated extending for a considerable distance dorsal to the mouth on the attached side. The difference between conditions on the two sides is shown in figure 20*A* and *B*. The palps (LP) are larger on the attached side and the proximal oral groove (POG) which runs from these to the mouth is longer. (In figures 13 and 14 only the smaller upper ctenidium and pair of palps with the shorter oral groove are shown.) Examination of figure 20 reveals that appreciably more than half the food collecting surface lies in the mantle cavity on the attached side; a corresponding proportion of the food will therefore be passed to the mouth from the ctenidium and palp of that side.

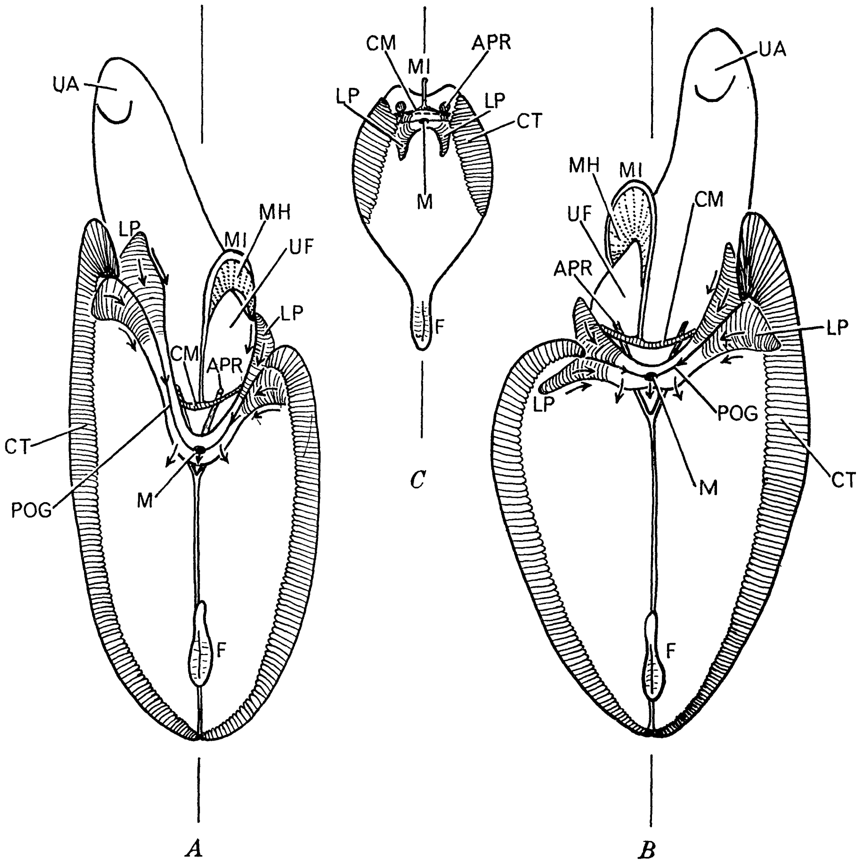

FIGURE 19. Anterior views of Chamidae removed from their shells and with mantle lobes, including adductors, removed. *A*, *P. exogyra*, with right side attached and so enlarged; *B*, *C. pellucida*, with left side enlarged; *C*, *Venus* as example of a free, bilaterally symmetrical bivalve. Vertical lines, passing through anterior end of the mantle isthmus, mouth and foot, indicate median vertical axis. Arrows indicate course of ciliary currents on palps and proximal oral grooves.

The great asymmetry of the mantle lobes is indicated in figure 20 and more clearly in the transverse section shown in figure 21. In the latter the mantle isthmus (MI) with the inner ligament (IL) secreted by it and the more laterally extending outer ligament (OL) represent the morphological mid-dorsal line. The mantle lobe on the attached side (A) contains a far larger cavity than that on the free side (F). Moreover, the mantle lobe on the attached side is much thicker (see figure 21 and also CM in figure 20*A* and *B*) with gonadial tissue extending into it from the viscera mass. The disparity between the ctenidia is clearly indicated in figure 20; only the inner demibranchs are cut in the posterior transverse section shown in figure 21.

CEMENTATION

The Chamidae are epifaunistic bivalves cemented by one valve to a hard substrate. Attachment of a diversity of adult bivalves by means of byssus threads secreted by a gland in the base of the foot is primitive to the extent that it probably represents the neotenous retention of a post-larval organ almost invariably present during development (Yonge 1962*b*). Cementation, on the other hand, probably comes later in evolutionary history; it is secondary and appears independently in a number of unrelated Superfamilies. The actual process is obscure. Although the very early attachment within the Ostreidae is due to secretion of a drop of cement from the modified byssal gland, subsequent attachment here and initial attachment in the majority of other cemented bivalves must come by way of the periostracum followed by that of the outer calcareous layer, i.e. be the concern of the inner and outer surfaces of the outer mantle fold.

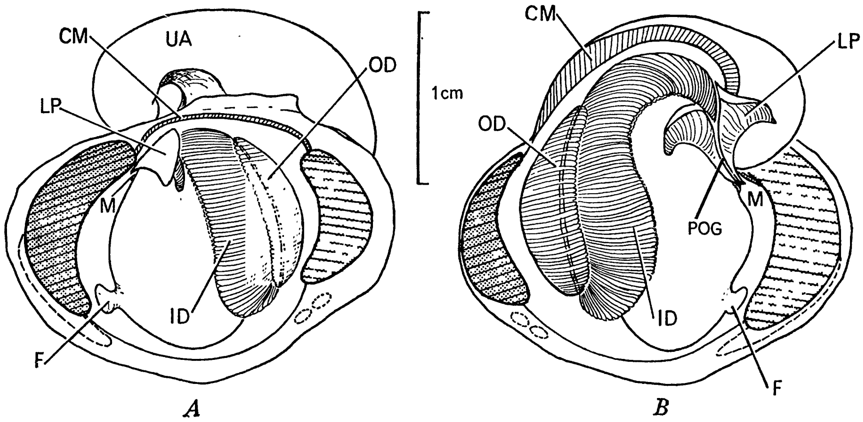

Figure 20. *P. exogyra*, animal (after fixation) removed from shell; *A*, lying on attached side with mantle lobe removed; *B*, on free side. The disparity in size between the mantle cavities is shown with the much larger ctenidium and palps on the attached side.

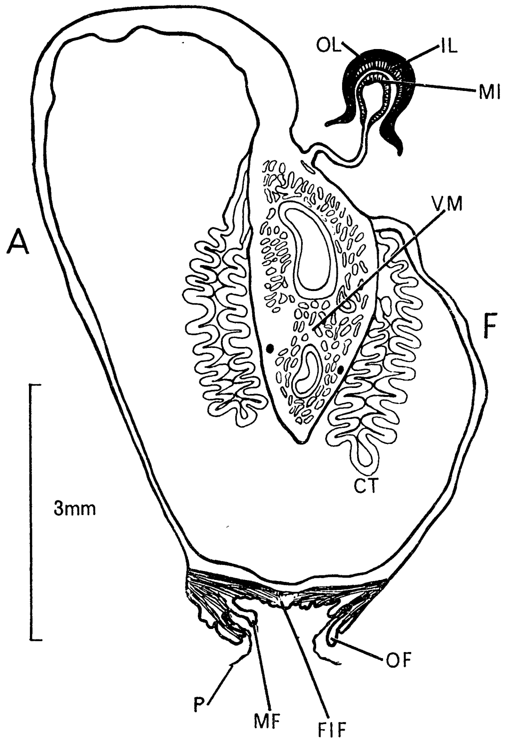

Figure 21. *C. pellucida*, transverse section through posterior region of body showing asymmetry of the mantle lobes on attached (A) and free (F) sides; to less extent of visceral mass. Median vertical axis runs between ligament dorsally and fused mantle margins ventrally.

Cementation occurs in both monomyarians and dimyarians. It has occurred most frequently in the Anisomyaria and there always, with the exception of *Dimya*, in monomyarians, namely the Ostreacea where its possibilities in the formation of massive 'reefs' have been exploited with unique success, and in *Plicatula*, *Spondylus* and *Hinnites* amongst the Pectinacea. Among the freshwater Etheriidae (Unionacea) it occurs in the dimyarian *Etheria* and the monomyarian *Acostaea* and *Pseudomulleria* (Yonge 1962*a*) and among the Pandoracea in the dimyarian *Cleidothaerus* (= *Chamostrea*) and *Myochama* (Hancock 1853*a*, *b*; Anthony 1905). Attachment occurs at various stages in the life history, at the beginning of the dissoconch stage (i.e. immediately on settlement from the plankton) in the Ostreidae and probably in *Dimya* and *Plicatula*; at the end of the dissoconch stage (as evidenced by the presence of a byssal notch in the post-larval shell) in *Spondylus*, or after full assumption of the equivalve adult shell form in the Etheriidae and even following a period of alternate byssal attachment and free-swimming freedom in *Hinnites* (Yonge 1951). The exact stage at which it occurs in the Pandoracea is unknown but is likely to be late; in the Chamidae, as indicated in figure 9*C*, it is almost certainly at the end of the dissoconch stage. Information about cementation is summarized in table 1.

TABLE 1. STAGE AT WHICH CEMENTATION OCCURS IN VARIOUS BIVALVIA

stage*	*Dimya* *Plicatula* Ostreidae	*Spondylus*	*Hinnites*	*Etheria* *Acostaea* *Pseudomulleria*	*Chama* *Pseudochama*	*Echinochama*	*Myochama* *Cleidothaerus*
prodissoconch veliconcha	free	free	free	free	free	free	free
dissoconch or nepionic	*attached*	free	free	free	free	free	free
neologic	*attached*	*attached*	free	free	*attached*	*attached*	free (?)
ephebic	*attached*	*attached*	*attached*	*attached*	*attached*	free	*attached*

* For definition of first three stages see Werner (1939); of three last see Jackson (1890).

Attachment is by way of the right valve in all the anisomyarians apart from the Ostreidae where it is always by the left. *Cleidothaerus* and *Myochama* are always cemented by the right valve and the etheriids quite indifferently by either valve while in the Chamidae, as we have seen, there is a greater although not invariable tendency for a species to be attached by a particular valve. Cementation would seem usually to have been preceded by structural change involving abandonment of a vertical for a horizontal disposition, i.e. lying on one valve. In the monomyarian Anisomyaria this is associated with byssal attachment (Yonge 1953*a*) but in the cemented Pandoracea possibly with freedom on the surface of sand as in the related *Myadora* and *Pandora* where the under (right) valve is deeply concave, the upper one flat (as in *Pecten*). How it arose in the initially equivalve Etheriidae is less obvious although the one genus which is free, *Barlettia*, has the unique habit of insinuating itself into crevices amongst rocks (Yonge 1962*a*). We can only speculate as to how it arose in the Chamacea; freedom in *Echinochama* would certainly appear to be secondary.

While certainly involving major changes in habit, cementation is of such restricted occurrence—especially when compared with byssal attachment (Yonge 1962*b*)—that other pre-conditioning factors may be sought. One of these appears to be absence of united siphons, i.e. of mantle fusion involving more than the inner lobes of the mantle margins (Type A, Yonge 1957*a*). This presumably has to do with the necessity for wide separation of inhalant and exhalant currents in cemented bivalves which normally live in turbulent water. In the cemented Anisomyaria siphons do not occur, the inhalant and exhalant regions are extensive and the currents more or less at right angles; the same is true of the eulamellibranch Etheriidae. Although siphons may be long in the Pandoracea, as in *Thracia* (Yonge 1937), there are always of Type A and so free. In the Chamacea we have seen that conditions are similar. Since in the majority of eulamellibranch Superfamilies the siphons are of Types B or C, i.e. with inhalant and exhalant siphons united, cementation is probably impossible. Nor does it occur in important Superfamilies with siphons of Type A, notably the deposit-feeding Tellinacea (Yonge 1949) which are very highly adapted burrowers, or, more surprisingly, in the surface attaching and sometimes commensal Erycinacea where the inhalant current is anterior (Popham 1940). The rarity of cementation outside the Anisomyaria may be connected with (*a*) the specialization of the majority of modern bivalves, and (*b*) the necessity for some preceding change in habit.

Bearing in mind the important pioneer studies of Anthony (1905) on 'pleurothetic' bivalves, the more important effects of cementation may be listed as follows:

(1) Assumption of a sedentary habit, horizontally disposed with inhalant and exhalant currents well separated. (Anthony refers to reduction of siphons, but this is hardly the point.)

(2) Whether or not this was previously so, the attached valve becomes concave,* the free valve flat (described by Anthony as respectively deeply cupped and opercular), i.e. the shell becomes inequivalve and the enclosed body bilaterally asymmetrical.

(3) With loss of movement, the mantle/shell alone becomes responsible for external form which becomes rounded. The enclosed animal is similarly affected. If isomyarian (e.g. *Dimya*, *Myochama*, *Cleidothaerus*, *Etheria*, Chamidae) it becomes antero-posteriorly symmetrical, if monomyarian (e.g. Ostreacea; Pectinacea; *Acostaea* and *Pseudomulleria* (Etheriidae)) it acquires a secondary symmetry around the central adductor (Yonge 1953*a*, 1962*a*). Anthony writes of a substitution of a primitive 'cephalic' by a secondary 'coronal' symmetry but the process is different in isomyarians and monomyarians.

(4) Cementation involves a 'ventralward' growth (not noted by Anthony) within the valves involving continual addition to the under surface of the ligament with consequent splitting of the upper surface. In monomyarians this is well shown in *Hinnites* (Yonge 1951) when compared with free *Pecten*, but also in *Spondylus* and the Ostreacea (very notably in elongated *Crassostrea gigas*). It leads in the dimyarian *Etheria* to the conditions in *E. elliptica* var. *cailliaudi* where the ligament elongates until it comes very greatly to exceed the length of the animal (Yonge 1962*a*). The problem is solved in the Chamidae by rotation during growth.

(5) Despite immobility, the foot, although, as noted by Anthony, reduced, is retained in all except those where cementation occurs immediately on settlement (in the first column in table 1), i.e. *Dimya*, *Plicatula* (Pectinacea) and all Ostreidae. In the others the reduced foot is probably of great assistance in cleansing the mantle cavity.

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* The exception to this is *Myochama* which attaches to the convex surface of the shells of other bivalves here the lower valve is thinner and smaller than the upper one.

(6) In more direct association with the horizontal disposition which accompanies cementation, there is (*a*) development of efficient means of cleansing the mantle cavity involving ciliary currents, foot and 'quick' adductor muscle, and (*b*) asymmetry of statocysts (at least in Pectinacea (Buddenbrock 1915)), the persistence of which even after loss of the foot still requires explanation.

As appears from consideration of the above, major features in the Chamidae, namely horizontal disposition, rounded shell with deeply concave attached valve, retention of the foot despite loss of mobility, separate siphons directing inhalant and exhalant currents at right angles to one another, may all be associated with cementation. Moreover, the presence of a 'tangential' ligament has solved the major problem of growth when attached by one valve. This will be realized by comparing figure 4*A* and *C*. The Chamidae were in this respect pre-adapted for a cemented habit. At the same time, unlike the Hippuritacea, the modern Chamidae have not become over-specialized. This is clearly indicated by the presence of *Echinochama* which is probably the only modern bivalve to resume freedom after cementation. According to Nicol (1952*c*), after losing attachment *E. arcinella* lies 'on the bottom on one valve, apparently kept in position by the long spines'. He adds that it appears to live on shell, gravel, *Lithothamnion*, or coral bottoms. The life history is surprisingly similar to that of the scleractinian coral *Manicina* (*Maeandra*) *areolata* (Yonge 1935).

Form in the Chamidae

Two major factors are responsible for the highly characteristic form. Acting in the longitudinal vertical plane, i.e. in that of the generating curve of the valves, is the tangential component in shell growth. By separation and consequent coiling of the umbonal regions this modifies the transverse component dorsally. The second effect is due to cementation with its invariable consequence of bilateral asymmetry which represents further modification of the transverse component.

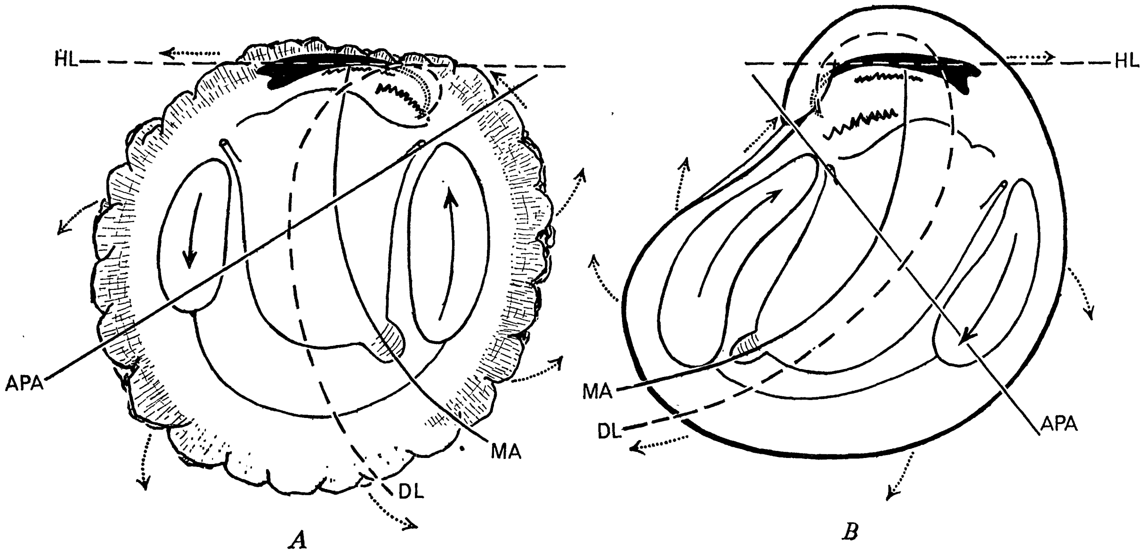

Figure 22. Diagrams showing the effect, in the longitudinal vertical plane, of the tangential component in shell growth on *A*, *C. pellucida*, *B*, *P. exogyra*.

Longitudinal vertical plane

The effects of the tangential component may be briefly recapitulated with reference to figure 22, in which the major features of '*Chama*' (*A*) and '*Pseudochama*' (*B*) are shown looking down on the attached valve. At this stage we are concerned solely with the radial and tangential components of shell growth which act in the longitudinal vertical plane. In the case of '*Pseudochama*' a somewhat elongate shell (frequently encountered) has been chosen, the better to emphasize the effects of the tangential component; *C. pellucida* is always rounded. The direction of growth at selected points around the generating curve of the mantle margin each representing, as shown by Owen (1953*b*) in his analysis of growth in *Glossus*, the resultant of the radial and tangential components, is indicated by the dotted arrows in figure 22. Presence of a tangential component (in association with cementation) has the following consequences:

(1) Dorsalward growth of the anterior region of the generating curve, so splitting the ligament anteriorly.

(2) Extension of the functional region of the ligament in a posterior direction.

(3) Extension in an antero-posterior direction of the cardinal teeth (a_1 and a_2 only being shown).

(4) Dorsalward extension of the anterior, and ventralward extension of the posterior, adductor (indicated by arrows), with consequent effects on the position of the mouth and anus respectively.

(5) Extension dorso-ventrally of the visceral mass (and ctenidia), the reduced foot, which is no longer in functional contact with the substrate, moving antero-ventrally. It should still, however, be regarded as the morphological mid-ventral region of the body.

The effects of this type of growth upon the major axes of the body, median (MA) and antero-posterior (APA), and on the demarcation (DL) and hinge (HL) lines of the mantle/shell are also shown in figure 22. The mantle/shell demands initial attention because, in the absence of freedom, this now assumes complete domination of form (the change from Anthony's designated 'cephalic' to his 'coronal' symmetry). The demarcation line, which does here follow the region of greatest concavity in the attached valve, is bent anteriorly. The hinge line is unaffected although not, of course, the direction of growth of the ligament and teeth which is now entirely posterior.

The axes of the body are profoundly influenced by change in form of the mantle/shell and by the consequences of cementation. Although within the equilateral shell the body is almost antero-posteriorly symmetrical, it has been twisted in the sagittal plane so that the median 'axis' (MA) (running from the middle of the mantle isthmus through the middle of the foot) is curved. Accepting the dictum of Pelseneer that the antero-posterior axis (APA) should run between mouth and anus, in the Chamidae this is no longer parallel to the hinge line (HL) as it is in primitive bivalves such as *Glycymeris* (Yonge 1952). This is due to the dorsalward displacement of the mouth and the ventralward displacement of the anus brought about by the elongation of the adductors. While the extension can be attributed to the tangential component, as indicated by the arrows in figure 22, the enlargement of the adductors is associated with the need in a cemented bivalve for rapid and often prolonged closure of the valves. In *Glossus*, where no such need exists, the adductors are not enlarged. The antero-posterior axis remains parallel to the hinge line.

Just as growth in the majority of cemented bivalves involves dorso-ventral elongation, in the cemented Chamidae it involves, as shown in figure 22, a continuous curling of the shell in an anticlockwise direction (when viewed from above) in '*Chama*' and in a clockwise direction in '*Pseudochama*'. The shell early assumes its final form, for instance, the proportions of the ligament which are split and attached must soon be established in post-larval development. But the presence of the tangential component involves continuous overgrowth of the constituents of the hinge plate from anterior to posterior as indicated by arrows 1 to 4 in figure 5*A*. It follows that as the animals grow the actual position, in relation to the rock surface to which they are attached, of the various regions of the mantle/shell and so of the enclosed body must alter in an anticlockwise or clockwise direction. This does not apply to *Echinochama* or to *Glossus* which are not cemented. In all these genera, in which the fullest effect of the tangential component is displayed, a consequence of the passage of zones of secretion across the hinge plate is a great thickening in this region of the inner calcareous layer of the shell.

Transverse vertical plane

Passing to bilateral asymmetry, initial concern is with the formation in an inequivalve shell, i.e. with the effect of differences in the transverse component of growth in the two valves. Where there is no tangential component such asymmetry lies entirely within the transverse vertical plane (now topographically horizontal) usually taking the form of a flat upper, and a deeply concave under, valve. The latter has an exaggerated, the former a much reduced, transverse component. The free-living *Pecten maximus* and cemented *Spondylus* spp. are good instances. In the Chamidae, however, the transverse component is influenced by the tangential component, growth taking place in an additional dimension and the valves assuming a spiral form with the umbones at the apex. The tangential component being necessarily the same in each valve, both assume the same spiral, but in the upper valve the spiral is almost flat, approaching a plano-spiral, while in the lower one it is pulled out to form a turbinate spiral. For *P. exogyra* this is shown in figure 3, the umbonal region of the attached valve extending beneath the hinge plate and then bending first anteriorly and then ventrally within the spiral cavity of the valve.

This bilateral asymmetry with its major effects on the pallial organs and smaller ones on those of the visceral mass has already been discussed with reference to figures 19, 20 and 21. It is further emphasized in the comparison, shown in figure 20, between the mantle cavity and the contained ctenidium and labial palps on the free (*A*) and attached (*B*) sides of a specimen of *P. exogyra*. Measured after preservation (as they are figured), the inner demibranchs (ID) are respectively 1·3 and 2·3 cm long and the outer (OD) ones 0·9 and 1·2 cm. In total length the ctenidium on the attached side is therefore some 75% longer than that on the free side. Moreover, the palps on that side (see also figure 19) are further removed from the mouth (M) to which they are connected by way of a long proximal oral groove (POG).

Inversion

The teeth of the bivalve hinge consist of inner calcareous layer secreted by the pallial epithelium on either side of and ventral to the mantle isthmus. These tissues (figure 3*C*, MH) extend as a film between the opposing hinge plates alternatively forming teeth on one side and sockets on the other. Apart from occasional abnormalities, the pattern of teeth and sockets on opposing right and left valves appears, apart from the Chamacea, to be constant. There alone is the pattern related not to right or left sides but to attached or free valves. Possible reasons for this have now to be considered.

Inversion of dentition appears to be associated with cementation. The great majority of cemented bivalves are edentulous, namely all species of Ostreidae, Pectinacea (the interlocking teeth in *Spondylus* and *Plicatula* are clearly secondary) and Etheriidae. The cemented Pandoracea possess a single tooth on the right (attached) valve. The Chamidae are alone in possessing well developed teeth on *both* valves.

It has been noted that in the absence of a tangential component cementation involves ventralward growth within the valves, the ligament being amphidetic. Absence of teeth appears to have been necessary before cementation could occur. The symmetrically disposed teeth of *Spondylus and Plicatula* which lock the valves must have been evolved subsequent to cementation and in relation to this new mode of life. But where there is a fully developed tangential component the ligament and hinge plate can extend posteriorly instead of ventrally. This is true of the Chamidae. It is possibly the case in the Pandoracea; Anthony (1905) indicates this possibility in his figure of *Chamostrea* (= *Cleidothaerus*) while Owen (1958) has demonstrated the presence of a tangential component in *Myodora*, closely related to the cemented *Myochama*.

In cemented bivalves the free valve forms an opercular lid to an often deeply concave lower valve. This frequently extends much further dorsally so that the hinge is no longer marginal (corresponding to dorsal in an unattached bivalve) but lies on the topographical upper surface as strikingly displayed in *Etheria elliptica* var. *cailliaudi* (Yonge 1962*a*) and also in *C. pellucida* and *P. exogyra* as shown in figure 1*B* and *C*. This presents no problem where teeth are absent as in *Etheria*, but in the Chamidae has involved a rolling back of the articulating surface on the free valve so that the teeth (f_1 and f_2) face dorsally to fit into the sockets in the overarching hinge plate of the attached valve. For *P. exogyra* this is shown in figure 7*B* and semi-diagrammatically for both '*Chama*' and '*Pseudochama*' in figure 8. In these cemented valves the hinge complex is topographically bounded above by the ligament and below by the large tooth, a_1, of the under valve which curls upward around the socket, sf_1, into which fits the corresponding tooth, f_1, of the upper valve. The tooth, a_1, and the posterior extension of the hinge plate also form the boundary to the deep concavity which extends beneath the hinge plate. This is best shown in figure 3*A*.

The bilateral asymmetry associated with cementation in the Chamidae involves the following differences between the valves: (1) much greater concavity within the attached valve, (2) hinge plate on the attached valve overarching, that on the free valve curled back, (3) hinge plate bounded ventrally by a tooth on the attached valve, by a socket on the free valve. These are all consequences of differences in the growth processes in the respective mantle lobes and may justifiably be regarded as correlated, cementation by either valve involving 1, 2 and 3. In other words, assuming the normal condition (in '*Chama*') to be primitive then the inverse condition came about *not* by 'a mere displacement of the hinge elements', as Odhner (1919) has postulated, but following mutation which made it possible for species of the Chamidae to attach by either valve with dentition associated with attached and free, *not* left and right, valves.

The bilateral asymmetry in normal and inverse Chamidae is due entirely to the mantle/shell. The visceral mass is certainly influenced because of the different amount of space available for its development on the two sides (see figures 19 and 20), but as was revealed by comparison of the stomachs in '*Chama*' and '*Pseudochama*' (figure 18) there is *no* inversion in the body. The independence of body* and mantle, which explains so much of the basic structure of the Mollusca, receives further and striking confirmation.

FORM AND HABIT IN THE RUDISTS

There is obvious bearing of the foregoing description and analysis of the form of the body and mantle/shell in the modern Chamidae upon any consideration of the extinct rudists of which over one hundred genera evolved during the Mesozoic. They were attached by one or other valve, a few attaining secondary freedom, and many assumed fantastic shapes with some reaching a size only exceeded in the Bivalvia by the subsequently evolved giant clam, *Tridacna gigas*. Although, following the advice of the late Dr L. R. Cox, the rudists will here be considered as constituting the separate Superfamily Hippuritacea, apart from the nature of the shell, relationship to the Chamacea is obviously close. A highly developed tangential component in shell growth and associated lateral extension and coiling of the umbonal regions of the shell with attachment leading to great bilateral asymmetry as well as dentition related to attachment of freedom of the valves, all of these are characteristic of the Hippuritacea as well as of the Chamacea.

It is not intended to do more here than emphasize these resemblances and, on the basis of the work done on the Chamidae, discuss the probable structure of the body in the rudists with speculations on their mode of life and on the course of evolution. Statements concerning the rudists are largely based on information obtained from Palmer (1928), Cox (1933)—to whom the author was also indebted for personal discussions—Chubb (1956) and especially Dechaseux (1948, 1952, 1960).

In the Hippuritacea attachment is by way of the left valve in *Heterodiceras* (Diceratidae) and throughout the Requieniidae. It is by the right valve in *Diceras* (Diceratidae) and in the families Monopleuridae, Caprotinidae, Caprinidae, Hippuritidae and Radiolitidae. In the Diceratidae no matter which valve is attached there is always a single tooth in the left, and two teeth in the right, valve. In the remaining rudists the free valve, right or left, carries two teeth, the attached valve one. Accepting the work of Munier-Chalmas on the Chamidae, it has been usual for palaeontologists to refer to 'normal' and 'inverse' dentition in the rudists. However, Dechaseux, on the basis of great experience, considers that the teeth in the two groups of rudists are *not* homologous and she prefers not to use these terms. In the Chamidae there is certainly an invariable association between the nature of the dentition and attachment or freedom of the valve. One might expect the same to be true of the rudists. However, in the Diceratidae dentition is *not* associated with

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* I.e. viscero-pedal mass.

attachment or freedom of the valves while throughout the Hippuritacea it does appear that attachment in any species is invariably by the same valve which is not true for the Chamidae. In other words, in any rudist attachment by one or other valve was predetermined which it is *not* in the Chamidae. It is possible to envisage a condition whereby, in the course of evolution, following cementation, the teeth on right and left *attached* valves came to resemble one another and those on left and right *free* valves did the same. What occurs in ontogeny in the Chamidae could have been a phylogenetic process in the Hippuritacea. In both cases there must have been some functional advantage, as postulated for the Chamidae, in the final arrangement of teeth and sockets on free and attached valves.

Comparisons are made in figure 23 between shell form in *Glossus*, free and bilaterally symmetrical and shown lying on left and right valves (A_1, A_2), '*Chama*' and '*Pseudochama*' (B_1, B_2) attached and so asymmetrical and with 'normal' and 'inverse' dentition respectively, and four genera of rudists, two (C, D) attached by the left and two (E, F) by the right valve. The effect of the tangential component of shell growth is apparent in all, causing anterior splitting of the ligament with accompanying lateral pulling out and coiling of the umbonal regions. In the rudists coiling of the umbonal regions is frequently much greater than in the Chamidae. The degree of asymmetry is also usually, although not invariably, greater. Thus for the four genera figured, in *Heterodiceras* (C) the valves are subequal but in each the umbonal region is twisted and pulled out laterally so that the shell is substantially wider than it is long. In *Requienia* (D) coiling is even greater but the valves could not be more dissimilar, that on the left being extremely deep while the free right valve forms a completely flat opercular plate. No bivalve has ever attained so complete a resemblance to a gastropod. In *Caprina* (E_2) asymmetry is also great but here the free left valve is much the larger and much the more coiled. The turbinate spiral of both valves in *Heterodiceras* and of the attached valve in *Requienia* has become a planospiral in *Caprina*, i.e. with coiling in the transverse vertical plane. Because of the origins of this coiling, namely the effect of the tangential component in shell growth accompanied by a great lateral pulling out of the umbonal regions, the assumption of the plano-spiral in the rudists must be secondary. It is unlike the Gastropoda where the appearance of a bilaterally symmetrical plano-spiral shell, as in the bellerophonts, must have preceded that of a turbinate spiral shell with the associated asymmetry in the mantle cavity which had such fundamental consequences in the subsequent evolution of the Gastropoda (Yonge 1947).

The ultimate modification in the rudists is represented by the Radiolitidae and the Hippuritidae (F_1, F_2) where the right valve is deep and cone-shaped with the left valve forming an unattached opercular cap. There is no trace of spiral coiling—at any rate in the adult: there may well have been in the young individual. The umbonal regions become centrally (or subcentrally) placed with the ligamental lines, almost at right angles to one another, running direct to the morphological mid-dorsal region of the shell. In both these families the now functionless and often atrophied ligament has become enclosed by overgrowth on either side by the calcareous layers of the shell. In the Hippuritidae (F_2) there are two further grooves (S, E) on the outer surface of the under valve which, to quote Cox (1933), 'correspond to projections of the outer shell-layer into the interior of the shell'. The significance of these 'siphonal pillars' is discussed below.

In all rudists with greatly elongated shells much of the internal cavity was occupied by shelly material containing many cavities so that the bulky shells must have been very light. Both inner and outer shell layers, secreted by the general mantle surface and the outer surface of the outer mantle fold respectively (Yonge 1957*a*) could be concerned (see figure 25). Particularly in the Caprinidae (which included the largest rudists), Hippuritidea and Radiolitidae the resultant condition in conical valves was rather like that in large vermetid gastropods, or indeed in cephalopods such as *Nautilus*, the animals occupying only relatively very small spaces within the massive shells. Only externally were even the largest rudists comparable in size with the modern *Tridacna gigas*.

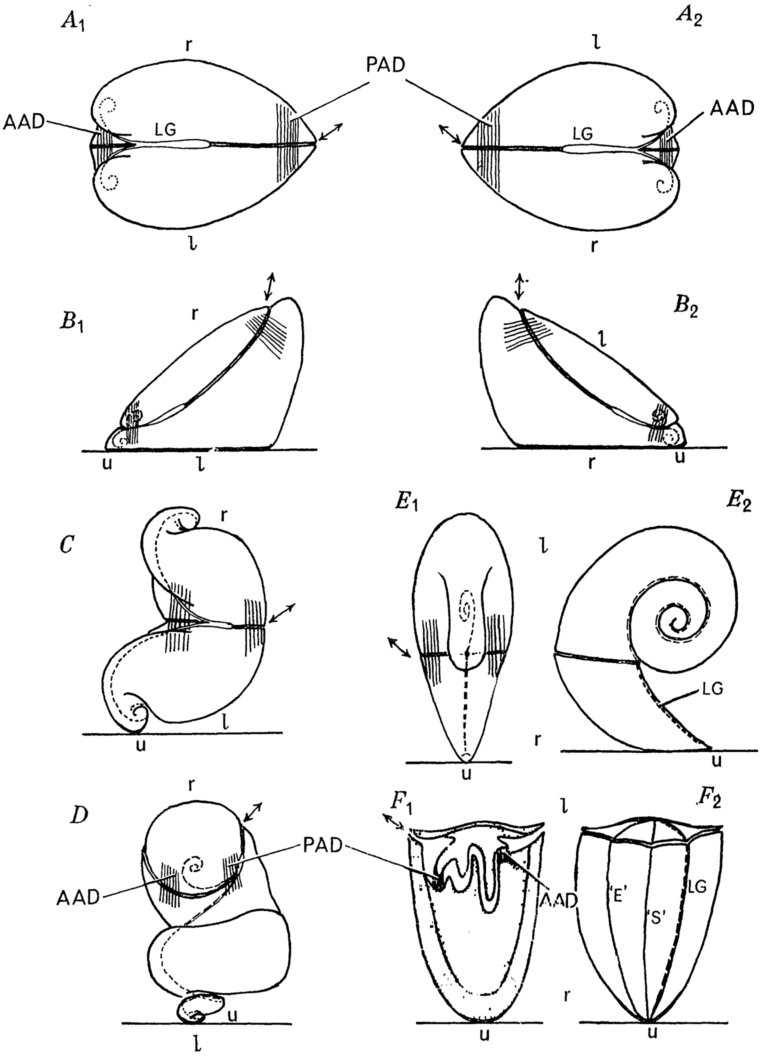

FIGURE 23. Semi-diagrammatic drawings showing the effects of the tangential component of growth on *A*, *Glossus*; *B*, Chamidae; *C* to *F*, Hippuritacea. Anterior and posterior adductors indicated throughout. On left side (lying on or attached by left valve): A_1, *Glossus* lying on left valve; B_1, normal '*Chama*' viewed from dorsal aspect; *C*, *Heterodiceras*; *D*, *Requienia* (two last both with 'normal' dentition and viewed from dorsal aspect). On right side (lying on or attached by right valve): A_2, *Glossus* lying on right side; B_2, inverse '*Pseudochama*'; E_1, *Caprina adversa* (with almost plano-spirally coiled upper valve) viewed from dorsal aspect, E_2, viewed from left side; F_1, *Hippurites* sp., longitudinal vertical section, F_2, shell viewed from postero-dorsal aspect, 'E', 'S' grooves external to 'siphonal' pillars. l, r, left and right; u, regions of umbonal attachment. Ligament shown plain where exposed, dotted where enclosed in shell. Arrows indicate positions of inhalant and exhalant apertures.

Ligament

It is only within the Diceratidae that the ligament runs parallel to the hinge line, i.e. as in the Chamidae, and is external. In all other rudists, as shown in figure 23 *E*, *F*, extension of the umbonal region, whether coiled or secondarily straightened, is so great that the ligament cuts the hinge line at right angles, i.e. is normal to the hinge line or commissure. This is the result of increased effect of the tangential component with consequent increased inter-umbonal growth. Various stages in this process are indicated diagrammatically in figure 24. At the same time overgrowth by the outer calcareous shell layers—precisely as in *C. pellucida* as shown in figure 6—leads to entire enclosure of the ligament which becomes sub-central in position well below the dorsal margin. The effect of this ultimate expression of the tangential component must have been complete separation of the anterior outer ligament region followed by that of the mantle isthmus with presumably some remaining effect of secretion by the mantle margins responsible for formation of the posterior outer ligament. But the functional significance of this transversely disposed ligament in opening the valves must have been very slight and the ligament atrophied in many of the Caprinidae and Radiolitidae and in all the Hippuritidae. Development of some accessory means of opening the valves must long have preceded the complete loss of the ligament. One can only speculate about the form this took, most probably involving hydrostatic pressure by inflation of sinuses within a foot which, as discussed below, could have become enlarged.

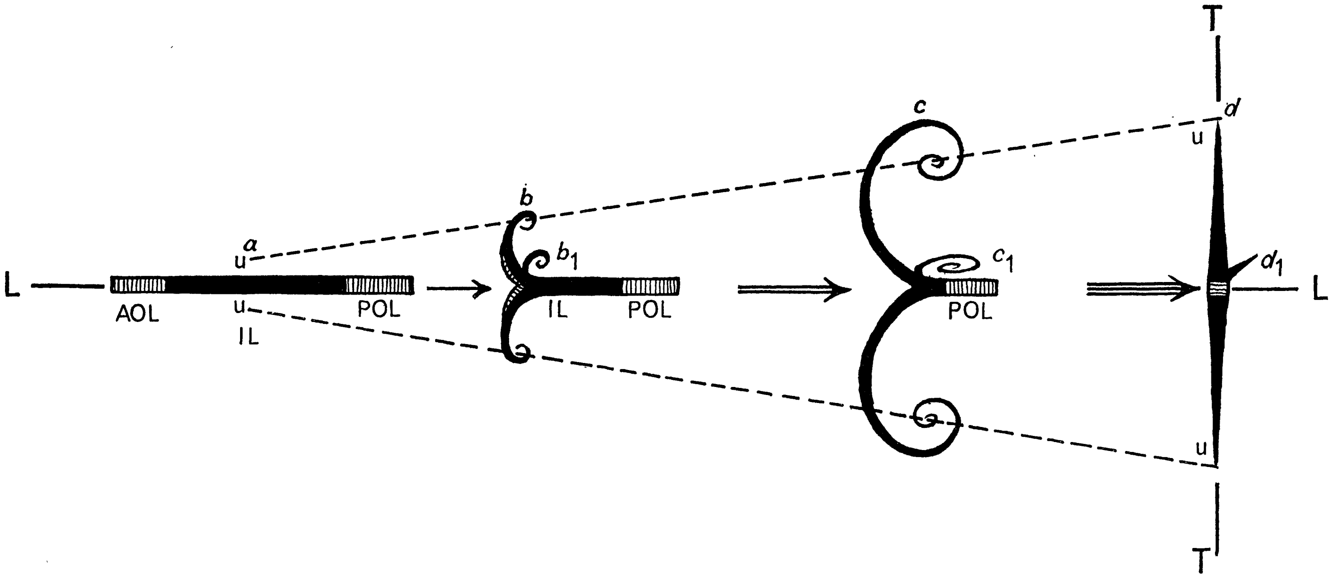

Figure 24. Diagram showing the effect of the tangential component on the ligament. Arrows indicate increasing effect. *a*, primitive amphidetic ligament (longitudinally disposed and antero-posteriorly symmetrical); *b*, anteriorly separated and coiled ligament in *Glossus* (bilaterally but not antero-posteriorly symmetrical), b_1, in Chamidae (bilaterally asymmetrical); *c*, further coiled ligament in Diceratidae (almost bilaterally symmetrical), c_1, in *Requienia* (bilaterally asymmetrical); *d*, secondarily straightened ligament in *Caprina* (functionless and now transversely disposed), d_1, in Hippuritidae and Radiolitidae (ligament bilaterally asymmetrical). L–L, longitudinal axis; T–T, transverse axis. Broken lines indicate divergence of the umbones due to interumbonal growth consequent on the increasing effect of the tangential component.

Mantle and shell secretion

In view of the many major resemblances between the recent Chamacea and the extinct Hippuritacea, it is reasonable to postulate basic similarities in the mantle cavity. Thus (as also in *Glossus*) fusion of the mantle margins could be exclusively by the inner folds (figure 25, FIF). In the absence of any involvement with the middle and outer folds, the inhalant and exhalant siphonal tubes would be separate (Yonge 1957*a*). In view of the height to which the openings were raised above the substrate (owing to shell secretion) the siphonal tubes could hardly have been longer than those in the Chamidae (figure 11). They may well indeed have been shorter than the inhalant siphon suggested for *Hippurites* in figure 25 (IS). Any suggestion of long siphons with which the pillars in the Hippuritidae and other rudists were associated receives no support from work on living bivalves. Siphons arise in association with burrowing or boring to give contact with the water above or outside the substrate. The rudists, on the contrary, raised themselves by shell secretion high above the substrate. For attachment this must have been hard and so in a region of considerable water movement and with a minimum of suspended material. The size, even the existence, of the pedal opening must be uncertain; it can hardly have been larger, and may well have been smaller, than that in the Chamidae. The reduction and final loss of the ligament would involve complete splitting of the mantle isthmus and the mantle margin responsible for secreting the posterior outer ligament. The mantle lobes would thus be separated as they are in Adesmacea (Pholadidae and Teredinidae), but there following reduction and loss of the ligament in association with rocking of the shell valves for boring.

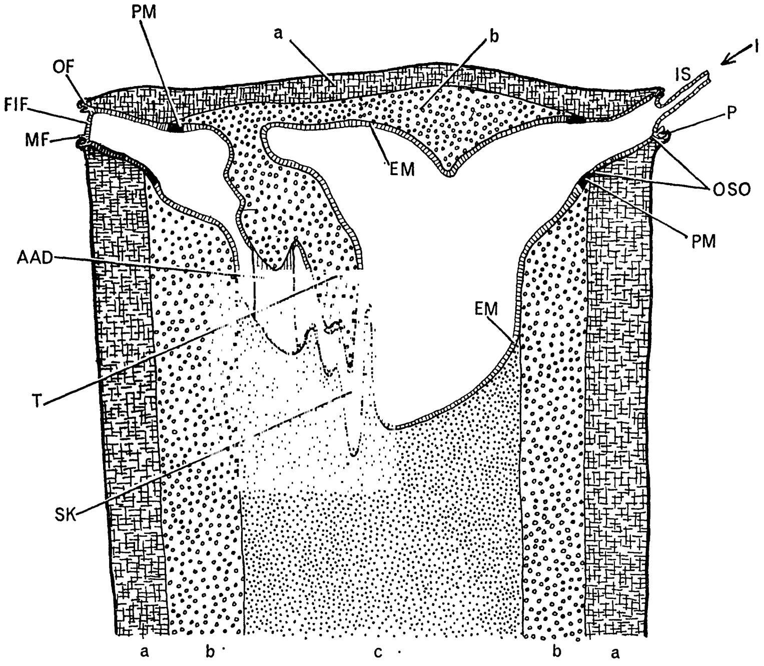

FIGURE 25. *Hippurites*, vertical (i.e. morphologically horizontal) section through free valve and upper region of attached valve between anterior adductor and anterior tooth (T) of upper valve and probable site of inhalant aperture (along line x–x shown in figure 28*B*). Layers of shell (a, b, c) with pallial secreting surfaces shown together with postulated fusion of inner folds of mantle margin.

Nevertheless, the two lobes could retain contact owing to fusion of the inner mantle folds which would be extended around the dorsal region as the ligament-secreting surfaces were increasingly separated and finally lost.

The two valves would thus retain connexion marginally by secondary attachment due to fusion of the inner mantle folds (figure 25, FIF) but also, of course, more centrally by the adductors (figure 23 F_1). As the effect of the tangential component was changed from the longitudinal vertical to the transverse vertical plane (as indicated by its effect on the ligament shown in figure 24) the hinge plate became more condensed. The attachments for the adductors, consisting of prominent myophores in the more complex rudists, were associated with the teeth which became vertically (i.e. *morphologically transversely*) instead of longitudinally disposed. Those of the upper valve in the Radiolitidae and Hippuritidae (figure 23 F_1) formed a clithrum fitting into deep sockets (SK) in the lower valve (figure 25) and permitting vertical movements of the opercular valve.

The calcareous layers of the shell in the rudists are characteristically thick with an extremely complex internal structure of cavities, tubes and both vertical and radial plates. All are very fully described and illustrated in palaeontological literature. The effect was to bring about the maximum of growth using the minimum of material and in the shortest possible time. As indicated for the Hippuritidae in figure 25, these calcareous layers would be produced from three sources. The greatly extended outer surface of the outer mantle folds (OSO)—the inner surface of which formed the periostracum (P) which would originally cover the surface of the shell—would be so disposed as to secrete the thick outer layer (a) equivalent to the dense calcareous layer in the Chamidae (figure 2, OC). Within the line of the pallial muscles (PM) the general surface of the mantle would secrete the inner calcareous layer (b). In the depth of the shell cavity additional substance (c)—like the 'chambering' and the chalky depositions often found in the under valves of *Ostrea edulis* (Korringa 1951) and other oysters—would be deposited by the topographically basal (actually umbonal) regions of the mantle surface.

The pallial surfaces (EM) of a relatively small animal were responsible for this great secretory activity, the difference between the valves being the consequence of differences in both the speed and the direction of secretion. It has been suggested by palaentologists that the cavities within the shell may in life have been occupied by extensions of the pallial secreting surfaces. Nothing of this sort occurs in any modern bivalve, but in none does the shell attain such a thickness or contain cavities. The precise manner in which the characteristic shell structure of the rudists was laid down must remain a matter of speculation.

Mantle cavity

The effects of bilateral asymmetry on the mantle cavity in the rudists must have been essentially similar to those already noted in the Chamidae. The mantle cavities on the two sides were presumably of much the same size in the Diceratidae and in many of the Caprinidae (although far smaller than the shell in the latter). In the Requieniidae, Radiolitidae and Hippuritidae the mantle cavity in the fixed valve would be further drawn out than in the Chamidae. In the first of these the umbonal region was more coiled than in the Chamidae but asymmetry was much greater. On the opercular side the mantle cavity and contained organs must have suffered maximum possible reduction. In the Hippuritidae and

Radiolitidae the mantle cavity on both sides was secondarily straightened. This final result of the process indicated in figure 24 is shown in the drawing of the fossil cast of the interior of a radiolite in figure 26. The upper (left) umbonal region which extends into a cavity topographically above the hinge plate on the opercular valve is less reduced than the external appearance of that valve would indicate. The same is true of the hippurites. The mantle cavity on the upper side would thus be appreciably larger than in *Requiena*.

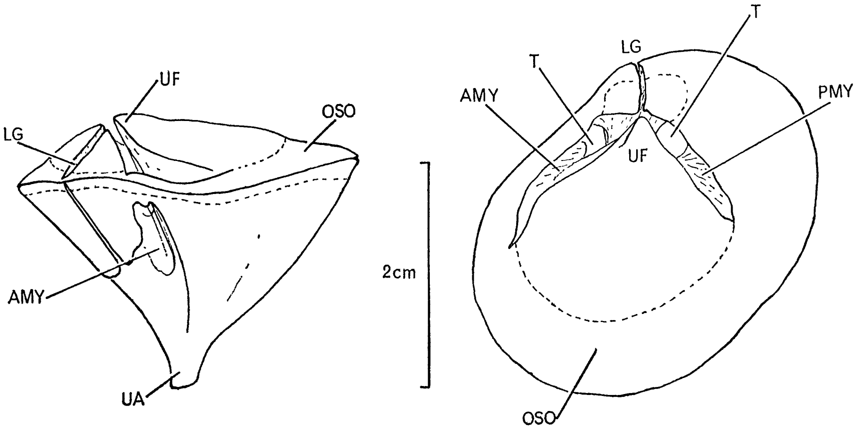

Figure 26. *Radiolites bournoni*, fossil cast of internal cavity viewed, *A*, from right side, *B*, from above. (British Museum specimen).

The result of umbonal separation, as shown for the Chamidae in figure 19, is to carry the anterior ends of the ctenidia (CT) away from the mouth (M). Functional connexion with the mouth involves extension of the lips, dilated on each side to form a pair of complex ridged palps (LP), and of the enclosed distal and proximal oral grooves (POG) along which material, collected on the ctenidia and sorted by the palps, passes to the mouth. The somewhat extended palps with the distal oral groove they enclose remain in contact with the ctenidia while the proximal oral groove appropriately elongates. The extent of this elongation depends on the degree of umbonal separation in the two valves. Precisely the same consequence follows separation of the umbones in the Arcacea due here to inter-umbonal growth along the hinge line without any tangential component and with no bilateral asymmetry. This is described and figured in *Glycymeris glycymeris* and *Arca tetragona* by Atkins (1936) and in *Arca* (*Senilia*) *senilis* by Yonge (1955*a*).

Conditions in 'normal' Diceratidae, as deduced from those in '*Chama*', are indicated in figure 27. The ctenidia and palps must have been of approximately the same size and functional capacity on the two sides. In the Requieniidae and Monopleuridae ('normal' and 'inverse' respectively) asymmetry was much greater than in the Chamidae and the ctenidium on the under side must have provided much the greater part of the current producing and feeding surfaces. The secondary change from turbinate to near plano-coiling of the umbonal regions in the Caprinidae (where the contained animal was less bilaterally asymmetrical than the shell it secreted) would produce conditions not unlike those in the Arcacea. The probable conditions in the lower mantle cavity of the Hippuritidae and Radiolitidae, with loss of umbonal coiling accompanied by great bilateral asymmetry, are indicated in figure 28*B* and *C*. The presence of very long proximal oral grooves (POG) is postulated. However, despite their wide departure from the primitive bivalve form there is no reason for assuming any significant difference between the pallial organs in these rudists and those in a typical bivalve (figure 28*A*). The position of the adductors gives that of the mouth—immediately posterior to the anterior muscle—and of the anus on the posterior side of the posterior muscle. The ctenidium must be in functional contact with the mouth by means already noted. The anus must open into the exhalant chamber

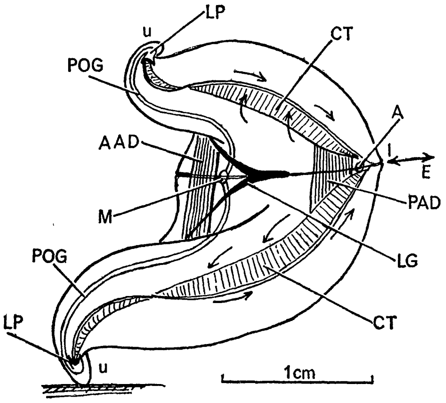

FIGURE 27. *Heterodiceras*, reconstruction of normal dicerid indicating disposition of adductors with mouth and anus, ctenidia diverging with the umbones but connected with the mouth by labial palps and greatly extended proximal oral grooves. Inhalant and exhalant currents (see arrows) situated at the posterior end. [Thickness of shell not indicated.]

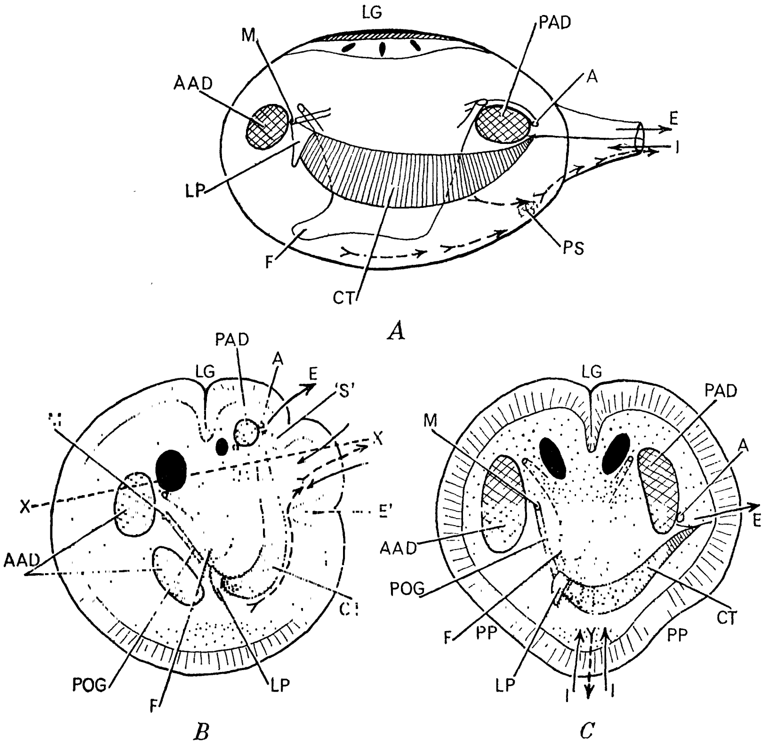

FIGURE 28. Left mantle cavity with contained organs in *A*, typical siphonate bivalve (vertically disposed in life); *B*, *Hippurites*; *C*, *Radiolites*. x–x, line of vertical section of *Hippurites* shown in figure 25. Plain arrows indicate water currents, broken arrows cleansing currents. Possible disposition of visceral mass and foot in *B* and *C* indicated by broken lines. Teeth sockets shown black.

above the ctenidium. In modern bivalves the posterior end of the ctenidium is invariably attached by a membrane to the under surface of the posterior adductor and, in eulamellibranchs, also to the inner fold of the mantle margin (as in the Chamidae, see figures 13 and 14). This conditions the equally invariable position of the exhalant opening above it (see arrows in figure 23*C* to *E*). With the probable exception of the Radiolitidae (see below) the inhalant opening in the rudists would occupy the usual (though not invariable) position immediately ventral to it, again as in the Chamidae.

Pillars and oscules

The 'siphonal' pillars characteristic of the Hippuritidae are due to shell secretion by two foldings of the mantle near the posterior end of the mantle cavity. The presence of these internal ridges (figure 28*B*, 'S', 'E') is indicated externally by grooves (figure 23F_2). Following Douvillé, who regarded them as structures associated with siphons, in palaeontological literature they are always designated 'E' (entrée) and 'S' (sortir) the latter being nearer the mid-dorsal ligamental groove (LG). The corresponding folding of the upper mantle lobe gives rise to the deep marginal embayments known as oscules. The Radiolitidae possess siphonal bands, in some forming more pronounced pseudopillars (figure 28*C*, PP) symmetrically situated mid-ventrally.

Views on the possible function of the pillars, 'siphonal bands' and pseudopillars have been well reviewed by Chubb (1956). Before Douvillé had suggested that they correspond with the siphons, the space between them had been regarded as the site of muscle attachment, or this confined to pillar 'S' with pillar 'E' representing the division between the siphons. Later Anthony (1924) considered that the exhalant aperture in the Hippuritidae was situated *between* the pillars with the inhalant opening ventral to the E pillar. Later workers even suggested the presence of siphonal tubes *within* the pillars or pseudopillars. Chubb has no difficulty in disposing of this morphological impossibility. Dechaseaux (1948, 1952, 1960) regards the pillars as functionless; whatever their origin they persisted, she considers, because they were not injurious to their possessors. Chubb himself inclines to this view regarding them as possibly 'a necessary consequence of the development of oscules'.

On the function of oscules he disagrees with Dechaseaux who points out that since these often close, at least partially, in old individuals they cannot have been of fundamental importance. Chubb considers that since they arose independently in members of three groups of rudists (Hippuritidae, Sauvagesinae and Radiolitinae) 'they must have fulfilled some vital function'. He draws attention to three specimens of the gregarious radiolite *Thyrastylon adherens* (Chubb 1956, pl. 7, figure 8) in which the disposition of the oscule E in the central individual is displaced so as to avoid obstruction by another shell. He considers this added evidence that 'the oscules fulfilled some useful purpose; they must surely have served to accommodate the siphonal orifices'. He further notes that nearly all rudists with oscules were gregarious.

Without the morphological evidence derived from the study of the modern Chamidae, Chubb considers that the mantle margins were united in the rudists. Primitively he thought there would be two posterior openings forming 'short, non-protuberant and non-retractile siphons'. The 'siphonal bands' on the shells of such individuals he thought represented evidence of the progressive sites of these short siphons. The formation of pillars and oscules he associates with a gregarious habit and the need for upward directed siphons, 'the margin of the mantle would', he considers, 'develop two indentations, separated by and bordered by rounded projections'. He makes the strange suggestion that the fused mantle lobes, acting 'like the leather of a bellows', would cause a current of water in and out of the mantle cavity by upward and downward movements of the opercular valve—oblivious of the fact that the gills must undoubtedly have been ciliated.

The immediate criticism of these ingenious views is that the oscules were *outside* the animal; they could not have communicated with the mantle cavity. Neither they nor the pillars could have had any direct connexion with the siphonal apertures. From consideration of the position of the posterior adductor and so of the anus, the exhalant opening must have been dorsal to the 'S' pillar and the inhalant aperture *between* the pillars (see figure 28*B*). It is difficult to understand Anthony's conclusions because he correctly figures the position of the anus, in association with the posterior adductor, and the exhalant opening must have been in a line with this. The effect of the mantle foldings which create the pillars is to create a deep canal between them which would lead to the inhalant opening. The corresponding folding of the mantle on the upper valve would produce the oscules. Any attempt to bring siphons upward through these openings would involve an upward and a *sideways* bending. Since the oscules would close down on top of the pillars when the adductors contracted the siphons would be in constant danger of being crushed. In any case there is the fact that oscules often close or greatly diminish with age. There could well have been short siphonal tubes as in the Chamidae (figure 11) which could have elongated and bent appropriately upward in gregarious species, but they would have been situated between, and dorsal to, the pillars (see I and E, figure 28*B*).

In contrast to the views of Chubb it is here suggested that the formation of oscules was an incidental consequence of the formation of pillars. It is now necessary to consider the possible function of the channel formed between the two folds in the mantle cavity.

Cleansing

Bivalves, like other sedentary organisms, are faced with the problem of aggregation and removal of silt and other suspended matter. Great quantities enter the mantle cavity in the powerful inhalant current created by the hypertrophied gills with their added function of food collection. The particles which fall out of suspension in the mantle cavity and the excess material rejected by the ctenidia and palps is mixed with mucus and carried in ciliary currents initially to the ventral margins whence, if the mantle margins are free, it may be expelled direct. More usually, because the margins are fused, it is then conveyed posteriorly by currents to collect as masses of pseudofaeces at the base of the inhalant aperture as in the Chamidae (figures 13, 14, PS). From time to time this material is expelled through the opening by sudden contractions of the 'quick' constituents of the adductor muscles. The evolution of this highly efficient method of cleansing the mantle cavity represents one of the major reasons for the supreme success of the Bivalvia.

The problem is clearly greatest in bivalves that are vertically disposed, e.g. in the byssally attached Pinnidae (Yonge 1953 *b*) where gutter-like waste canals (WC) are present on each mantle lobe (figure 29 *B*), and in deep burrowers with long siphons such as *Lutraria*

(Yonge 1948) with fused mantle margins where there is a single waste canal, also bounded by membranes, which opens posteriorly (i.e. above) by way of a fourth pallial aperture (figure 29*A*). In *Schizothaerus* (also Mactracea) and in *Mya* (Myacea) and *Panope* (Saxicavacea) pseudofaeces are expelled in long mucus-laden streams through the inhalant opening on to the surface of the substrate (unpublished observations).

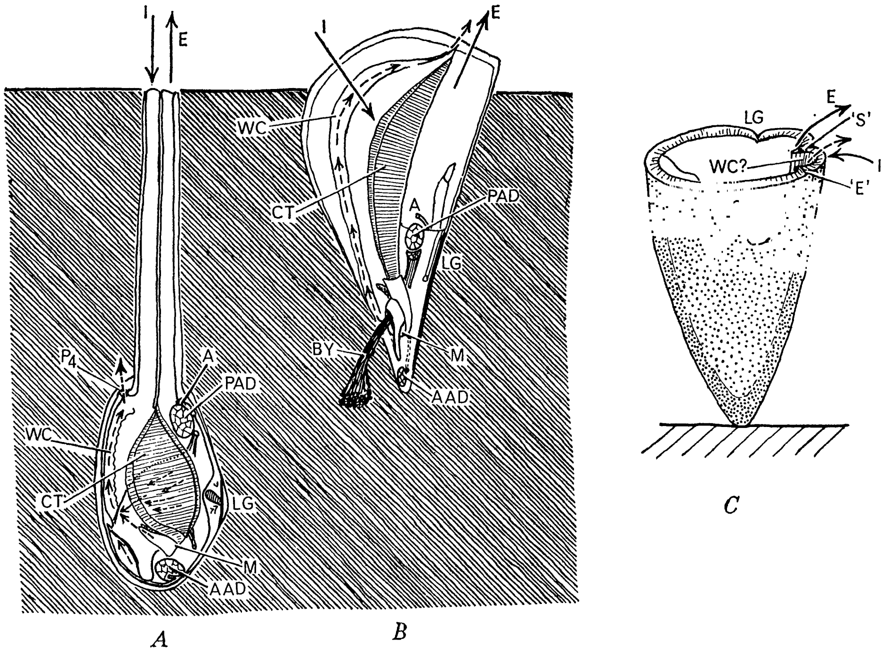

FIGURE 29. Cleansing mechanisms in bivalves. *A*, *Lutraria lutraria* (Mactracea), viewed from left side with left valve and mantle lobe removed but disposed as in nature, i.e. deeply buried in sandy substrate. Inhalant and exhalant currents shown with pseudofaeces carried along waste canal and ejected through fourth pallial aperture (after Yonge 1948); *B*, *Pinna carnea* (Anisomyaria), as in *A* but with waste canal on each mantle lobe opening at extreme dorsal side (i.e. topographically uppermost point) of wide inhalant opening (after Yonge 1953*b*); *C*, *Hippurites*, diagrammatic view indicating the postulated cleansing function of the groove between pillars 'S' and 'E'. The course, actual or postulated, of rejection currents shown throughout by broken arrows.

The same acute problem faced the rudists as the under valve became deeper, most obviously in the cone-shaped Hippuritidae and Radiolitidae. It concerned only the lower (right) mantle cavity and involved transport of pseudofaeces from the umbonal depths to the inhalant opening, i.e. morphologically almost at right angles to the direction taken in *Pinna* and *Lutraria* although, as there, upwards. This need could best have been met by a similar formation of waste canals which involved folding of the mantle surface with resultant secretion of pillars. These would therefore have been incidental and of exaggerated thickness owing to the exceptional powers of shell secretion possessed by the rudists. The suggested result is indicated in figure 28*B* with pseudofaeces carried up the waste canal between the pillars to be ejected through the inhalant opening as in all living Bivalvia. Comparison between conditions in *Lutraria* and *Pinna* and those postulated for the Hippuritidae is given in figure 29.

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Formation of the pillars by reducing space in the posterior half of the mantle cavity could well have been the cause of the antero-posterior asymmetry characteristic of the Hippuritidae with the posterior adductor and tooth socket much smaller than the anterior ones (see figure 28*B*). This asymmetry could be a direct consequence of the necessary formation of waste canals. The formation of oscules in the upper valve would then be a further consequence.

The Radiolitidae (figure 28*C*) show much less asymmetry. The anterior and posterior tooth sockets and adductor scars are very similar in size and disposition. But here a broader, shallower canal is created between the pseudopillars (PP) (with which shallow oscules in the upper valve are also associated) and this opens *mid-ventrally*. Because the pseudofaeces must be extruded through the *inhalant* aperture this must be displaced from a posterior to a mid-ventral position. There is nothing improbable about this. Although the exhalant aperture must, of strict functional necessity, always be posteriorly situated, this is not so with the inhalant opening. In the Bivalvia it is *primitively* anterior, i.e. in the protobranchiate Nuculidae and Solemyidae but not in the more highly modified Nuculanidae (Yonge 1939). It is also anterior in certain Arcacea (Atkins 1936; Yonge 1955*a*), in the Lucinacea (Allen 1958) and in the Erycinacea (Popham 1940). The advantage of a posterior inhalant opening is not greater respiratory or feeding efficiency but concentration at the one end of all necessary contacts with the environment enabling bivalves to burrow or bore deeply. It could have presented no advantage to these epifaunistic rudists raised high above the substrate.

The suggestion is therefore made, and it is surprising that it does not appear to have been made before, that the pillars and pseudopillars and associated oscules are the incidental consequence of folding the mantle to form waste canals along which pseudofaeces were conveyed for ejection through the inhalant opening. This is what would be expected of the existing Chamidae should they have evolved in the same direction as the Hippuritidae and Radiolitidae. Formation of pillars led to the characteristic antero-posterior asymmetry in the Hippuritidae but postulated displacement of the inhalant opening in the separately evolved Radiolitidae led to assumption of effective antero-posterior symmetry in that family.

Foot

The foot is the only organ suggested as being possibly responsible for opening of the valves after the disappearance (functionally if not always structurally) of the ligament. It may well have had that function. It is usually retained in cemented bivalves, having been lost only in the Ostreidae and in *Plicatula*. In a reduced form it becomes concerned with cleansing of the mantle cavity in Pectinacea such as *Spondylus* and in the Anomiidae. This would also seem to be its sole function in the Chamidae. Development of an organ capable by internal distension with blood of pushing up the opercular valve probably involved some enlargement to accommodate the necessary blood sinuses together with some valvular control of the blood which could have been forced into these by appropriate contractions of the pedal muscles. Moreover, such hypertrophy of a reduced foot is certainly possible as shown by conditions in *Enigmonia*. Species of this genus, clearly descended from anomids attached by a massive calcified byssus, have re-acquired capacity for movement by great enlargement of the foot with which they actively crawl, right valve undermost, like limpets (Yonge 1957*b*). The probable position of the foot in the Hippuritidae and Radiolitidae is indicated in figure 28*B*, *C* (F). As in the Chamidae it probably pointed somewhat anteriorly and possibly, owing to the bilateral asymmetry, also upwards. It could have been protruded through the pedal gape and around the outer surface of the anterior adductor (an action noted in *C. pellucida*) and so possibly gently pushed the opercular valve upward. The vertically extended teeth would keep this in position.

Mode of life

The rudists inhabited shallow tropical and subtropical waters largely around the margins of the former Tethys Sea. The great majority must have lived in a very similar manner to the cemented Chamidae although often raised much farther from the bottom. Certain of them lost attachment, either early in life like the modern *Echinochama*, or possibly because, in somewhat deeper water (where these occurred), they cemented themselves to small stones instead of to a rock surface as the permanently attached species did. Such unattached species included Radiolitidae such as *Bournonia*, which is obviously adapted for lying on one side and the enormous subequal *Titanosarcolites* over 5 ft. long with coiled shell, also the somewhat enigmatic *Immanites anahuanensis*, shown in figure 30, of which a single valve might be 25 in. long. These recumbent species occupied deeper, and so less water-scoured, bottoms although on account of the total immobility they must have lived on a relatively firm bottom, e.g. of stones or perhaps stiff gravel. They could not have lived on very soft substrates into which even the great size of their shells would not have prevented them sinking.

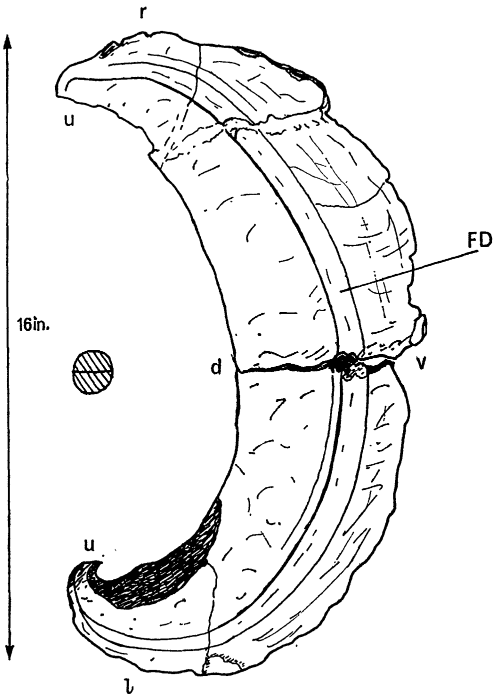

Figure 30. *Immanitas anahuacensis* Palmer, recumbent, possibly caprinid, rudist, upper (posterior) surface showing similar coiled valves with probably siphonal fold between two grooves; there is no ligament (after Palmer 1928). Circle on left indicates approximate size of contained animal.

The increasing abundance of rudists and the fantastic development in both size and form of the shell throughout the Mesozoic indicates the long persistence of very stable conditions. They must have been extensive shallow areas of very still and sediment-free water.

Considered ecologically the rudists may be regarded as *the* supremely adapted epifaunistic bivalves. Utterly immobile, they raised themselves clear of the bottom—for the better avoidance of sediment and better collection of phytoplankton—by development of a unique type of pallial secretion which produced shell of a character unlike that in any modern bivalve. These cavernous shells must have been extremely light (of help to the recumbent forms) and, especially in the warm waters the rudists inhabited, very quickly secreted. In the more highly evolved families the shell bore no relation to the size of the animal it contained (see figure 30). However, the mantle surface could well have been extended into diverticulae which passed into the canals and cavities which penetrate the shell substance, the complexities of which are the subject of a great palaeontological literature (see Dechaseaux 1952, 1960).

In some measure also upward growth must have been fostered by natural selection especially in the gregarious reef-building species among the hippurites and radiolites. In behaviour the rudists could well have resembled the modern Chamidae with the valves opening only slightly to permit entry of an inhalant current through a relatively small aperture, probably here also on a short separate siphonal tube. The ctenidia would need similar adaptations for collecting finely divided particles and the mantle cavity for ridding itself of accumulated sediment and material rejected by the ctenidia and palps. It appears completely reasonable to attribute the origin of the 'siphonate' pillars (and the oscules) in the Hippuritidae to development of a service of such supreme importance for cemented ciliary feeders.

The primitively infaunal bivalves probably initially exploited the possibilities of epifaunal life by byssal attachment, i.e. by way of the body (Yonge 1962*b*), and only secondarily by cementation, i.e. by way of the mantle/shell. The latter process involved change from a vertical to a horizontal posture, attached by one side or the other, a change which in some cases at least involved preliminary byssal attachment (Yonge 1953*a*). This new habitat has been exploited with immense success especially in the Mesozoic. Adaptation was assisted by the development of the capacity to secrete a cavernous shell which enabled its possessor to rise clear of the bottom and, in recumbent forms, to lie on the surface of non-solid substrates without danger of sinking into them. Such rudists must have lain with the siphon-bearing posterior surface uppermost. This is indicated in figure 30 where the conspicuous ridge with bounding grooves on the topographically upper surface of *Immanites* could well have been a true siphonal band.

With the extinction of the rudists, due doubtless to major climatic changes which brought heavy sedimentation as well as alteration in water movements and in temperature, their unique powers of shell secretion were lost. No existing bivalve possesses any corresponding facility, least of all in the Chamidae with their particularly dense shell and without even the degree of 'chambering' possible in similarly cemented Ostreidae. The epifaunal habit continues to be exploited by cemented bivalves, with supreme success in the Ostreidae, which also form (and have long formed) reefs, certain Pectinacea and in the freshwater Etheriidae, but without any attempt to raise themselves high above the rock to which they are attached. While the Ostreidae tend to inhabit quiet, often sediment-laden waters, other cemented bivalves, notably the Chamidae and pectinids such as *Spondylus* and *Hinnites*, live in very agitated seas while the etheriids are the one group of freshwater bivalves adapted, and very highly adapted, for life attached to the rocky floor of turbulently flowing rivers (Yonge 1962*a*).

Evolution of form

To the antero-posterior axis of the Bilateralia there has been added in the Mollusca a second growth axis due to the presence of the dorsal mantle/shell. This may be compared to a bell tent with the pole representing a central dorso-ventral axis and the skirts the mantle margin around which growth occurs. In the Bivalvia the mantle/shell becomes laterally compressed and the body, now completely enclosed, becomes acephalous and in consequence almost completely antero-posteriorly symmetrical. At the same time, some measure of bilateral symmetry has been imposed on the mantle/shell. Form is thus the resultant of the interaction of the growth axes of body and of mantle/shell (Yonge 1953*a*). Where the primitive mobile infaunal habit of the bivalves is retained, the mantle/shell may alter by changes in the growth gradients around the generating curve of the mantle margins. This may bring about changes in the extent of the anterior and posterior territories of the mantle/shell (separated by the demarcation line (Yonge 1955*b*)). The disposition but *not* the proportions (anterior and posterior regions) of the contained body are altered, as in the Solenacea (Yonge 1952; Owen 1959*a*). Following fixation of the body by a byssus the proportions of the body may be altered, the posterior half enlarging at the expense of the anterior half and with consequent effects on the mantle/shell. The isomyarian gives place to the heteromyarian condition, as in *Mytilus*, *Pinna*, *Dreissena*, etc. (Yonge 1953*a*, 1962*b*). Further change leads to loss of the anterior adductor and, as already noted, the body of this monomyarian becomes reorganized around the central adductor.

The presence of a significant tangential component in shell growth introduces a new factor into the control of form. The resultant anterior separation of the umbones affects the transverse component but, as long as the free infaunal habit is retained, as in *Glossus*, without effect on bilateral symmetry. But this is lost after cementation as described for the Chamidae. In the rudists this asymmetry was carried to unexpected extremes by a maximum separation of the umbones with an eventual loss of the initial turbinate coiling. The antero-posterior axis was reduced, the animals becoming circular in cross-section (figure 28*B*, *C*) and effectively re-organized around a transverse 'axis' (it may be curved in the lateral vertical plane in the Caprinidae). The animals became pulled out to the maximum extent laterally the effect of which is exaggerated owing to the exceptional powers of shell secretion. The final rudist form (Caprinidae, Hippuritidae, Radiolitidae) represents a logical evolutionary consequence of the action of a tangential component on a group of cemented bivalves. In the conditions prevailing in the Mesozoic the resultant changes in form and so habit were not rejected by natural selection.

It is worth comparing this with lateral extension of the mantle/shell in the Cardiacea which retain the infaunal habit. Such extension occurs in the tropical Indo-Pacific heart cockles of the genus *Corculum*. As shown for *C. cardissa* in figure 31, the somewhat globular cockle form is flattened antero-posteriorly with around the edges a slight upward, i.e. posterior, tilting. The viscera are accumulated centrally, accommodated within a bulging on both surfaces of the shell. The final form is not unlike that of a scallop of the genus *Chlamys* although with the valve margins vertically instead of horizontally disposed. The shell displays the effects of a maximum transverse component uninfluenced by any tangential component. So far from being separated, the umbones actually overlap (figure 31 *B*). The shell is almost circular in outline, the dorso-ventral and transverse axes being almost the same length and the antero-posterior axis extremely short. In the absence of cementation there is complete bilateral symmetry. To correspond to a rudist the shell would need to be upended, attached by one or other umbo.

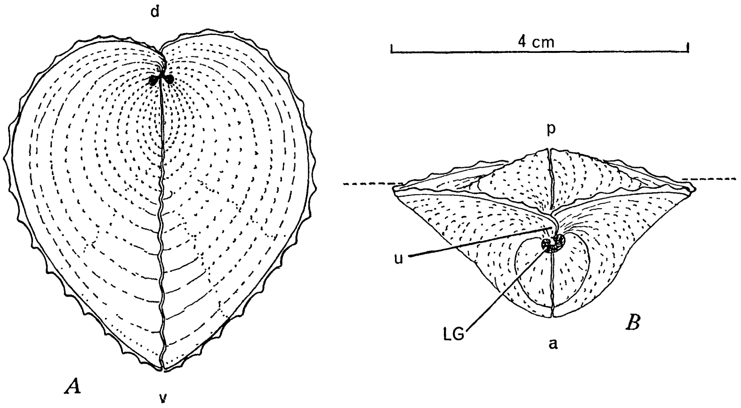

FIGURE 31. *Corculum cardissa*, lateral extension of valves in a cardiacean. *A*, shell viewed from posterior end; *B*, from dorsal surface showing overlapping of umbones and indicating disposition in life, on the surface of sand.

According to Kawaguti (1950) on whom our knowledge of the habits of this animal solely rests, *C. cardissa* lies on the surface of sand, occasionally attached by a few byssus threads, with the posterior surface uppermost, as indicated in figure 31 *B*. A short exhalant siphon projects upwards from the middle of the posterior surface but the inhalant siphon draws in water ventrally from the level of the sand. A great surface is thus exposed and this, with the thin translucent nature of the shell permits penetration of light adequate for the maintenance of zooxanthellae particularly within the ctenidia. There is here a biological 'reason' for the remarkable lateral extension of the shell because, as in the much more highly adapted Tridacnidae (also Cardiacea), the animals feed on these 'farmed' algae (Yonge 1936). It is illuminating to have for comparison with conditions in the rudists this example of the fullest effect of the transverse component, uninfluenced by any tangential component, on a bivalve which retains the primitive infaunal habit.

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Key to the lettering used in the figures

a	anterior
A	anus
a_1, a_2	outer and inner teeth of attached valve
AAD	anterior adductor
AMY	anterior myophore
AOL	anterior outer ligament
AOM	surface secreting anterior outer ligament
APA	anterior-posterior axis
APR	anterior pedal retractor
AT	attachment area
Au	auricle
BY	byssus
CA	ctenidial axis
CAV	cavity under hinge plate in attached valve
CE	caecum
CM	cut surface of mantle
CPG	cerebro-pleural ganglion
CT	ctenidium
d	dorsal
DH	dorsal hood
DL	demarcation line
E	exhalant current
'E'	'siphonal pillar' (entrée)
EA	exhalant aperture
EM	mantle epithelium
ES	exhalant siphon
F	foot
f_1, f_2	outer and inner teeth of free valve
FD	possible siphonal fold
FIF	fused inner mantle folds
FMF	fused middle mantle folds
G	gastric shield
GA	gonadial aperture
H	hinge plate
HL	hinge line
I	inhalant current
IA	inhalant aperture
IC	inner calcareous layer
ID	inner demibranch
IF	inner fold of mantle margin
IG	intestinal groove
IL	inner ligament
IS	inhalant siphon
ISO	inner surface of outer mantle fold
K	kidney
l	left
L	lateral tooth
LG	ligament
LP	labial palp
LPO	left pouch
LU	lunule
M	mouth
MA	median axis
MC	margin of shell after cementation
MD	margin of dissoconch
MF	middle fold of mantle margin
MG	midgut
MH	mantle crest secreting hinge plate
MI	mantle isthmus
MP	margin of prodissoconch
O	oesophagus
OC	outer calcareous layer
OD	outer demibranch
OF	outer fold of mantle margin
OL	outer ligament
OSO	outer surface of outer mantle fold (secreting outer calcareous layer)
p	posterior
P	periostracum
P_4	fourth pallial aperture
PAD	posterior adductor
PC	pericardium
PEG	pedal ganglia
PG	pedal gape
PL	pallial line
PM	pallial muscle
PMY	posterior myophore
POG	proximal oral groove
POL	posterior outer ligament
POM	surface secreting posterior outer ligament
PP	pseudopillars
PPR	posterior pedal retractor
PS	pseudofaeces
r	right
R	rectum
RA	renal aperture
'S'	'siphonal' pillar (sortir)
SA	sorting area
sa_1, sa_2	sockets on free valve for teeth on attached valve
sf_1, sf_2	sockets on attached valve for teeth on free valve
SK	socket for tooth
SL	separated region of ligament
SS	style sac
T	tooth
T_1, T_2	major and minor typhlosoles
u	umbo
UA	umbonal area of attached side
UF	umbonal area of free side
Uf	umbo of free valve
v	ventral
V	valve
Va	edge of attached valve
VC	visceral commissure
VE	ventricle
Vf	edge of free valve
VG	visceral ganglia
VM	visceral mass
WC	waste canal