

SYMMETRIES AND THE ROLE OF THE MANTLE MARGINS
IN THE BIVALVE MOLLUSCA

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ABSTRACT

Evolution throughout the Mollusca is explicable as the consequence of diverse interactions between the bilaterally symmetrical visceropedal mass and the radially symmetrical mantle/shell, which gives protection and overlaps the respiratory ctenidia. Following lateral compression, the Bivalvia become enclosed within calcified valves and a mid-dorsal, uncalcified ligament. Further evolution is controlled by the mantle/shell by way of the middle and inner marginal folds. The middle marginal folds usually carry receptors, and in some bivalves the middle folds emerge to assist — even replace — the valves in penetration of calcareous rock. In other bivalves, the middle folds completely enclose the valves. The inner folds control water flow, their radial muscles attached along the pallial line, cross fusing at both ends forming adductors, pallial like the ligament they work against. Fusion of mantle margins in the Mesozoic produced increasingly complex siphons, giving wider range of habit. Fusion of periostracal grooves (or of their secretions) extended the primary ligament, leading to formation of a secondary, more dorsal ligament. Control of form and habit also is shown by the effects of a tangential growth component in the Chamacea and in *Cleidothaerus* (Pandoracea) and by those of cementation in the Etheriidae (Unionacea).

Descending possibly from turbellarian-like ancestors, the first molluscs basically consisted of ventral foot and dorsal mantle with intervening viscera (Stasek, 1972). Paired ctenidia with central axis and lateral filaments bearing cilia for current production and for cleansing appeared laterally beneath an overhanging mantle that secreted an initially non-calcareous shell. Various modified (multiplied, reduced or hypertrophied), these structures continue to meet the respiratory needs of all marine molluscs apart from the Scaphopoda and the opisthobranchiate Gastropoda but including the Cephalopoda (Yonge, 1947). In the Bivalvia, the single pair of ctenidia enlarge to form elaborate, highly efficient ciliary feeding mechanisms.

Thus, bilaterally symmetrical animals with laterally projecting gills and associated organs came under the protection of a radially symmetrical mantle/shell, the two united by paired pedal, or shell, muscles. Evolution in the Mollusca is explicable only as the outcome of the diverse interactions between these symmetries. Its understanding, therefore, demands acquaintance with the separately originating, and still frequently independently studied, subject matters of malacology and conchology.

Retention of the primitive crawling habit, the elongate mantle secreting an articulating shell with multiplied ctenidia occupying narrow pallial grooves (Yonge, 1939a), produced the Amphineura adapted for life on irregular hard surfaces. Dorsal extension with resultant coiling led, if followed by torsion, to the epifaunal and secondarily infaunal or pelagic Gastropoda; if followed by separation of apical, gas-filled chambers, they led to the pelagic Cephalopoda. In the former, with anterior mantle cavity, apotheosis is attained in neogastropods, where prey is detected in the respiratory current entering through an exploratory pallial siphon and tested by a probably originally sediment-detecting osphradium (Yonge, 1947). In the predatory decapod Cephalopoda with internal shell, the mantle cavity (still the respiratory chamber, although with reversed, muscle-created current passing between complexly folded ctenidial filaments; Yonge, 1947) becomes the means of jet propulsion.

In the Amphineura, form and habit are dominated by the mantle; in the Gastropoda,

conditions range from complete mantle domination, as in the cemented, worm-like vermetids, to loss of the mantle/shell and reversion to almost complete bilateral symmetry in the nudibranchs. In the Cephalopoda, symmetries blend; mantle cavity and head both face anteriorly, while the ventral foot becomes a mobile funnel directing the jet stream.

In the Bivalvia, the animal becomes enclosed within its respiratory cavity, the visceropodal mass profoundly and irrevocably affected. The head is lost, while the compressed, terminably distended foot with paired retractors pulls the animal through the soft substrates it now inhabits (Trueman, 1968). The bivalve form is here considered to have evolved *prior* to calcification (Yonge, 1953a), the mantle consisting of lateral lobes with a uniting mid-dorsal isthmus (Owen et al., 1953). The lobes secrete the valves, the isthmus the inner layer of the *primary ligament*. The outer layers of both, as noted below, are formed by the outer marginal folds.

Beneath the mantle isthmus, the mantle lobes unite to form the pallial crest which, creating teeth on one side and sockets on the other, produces the hinge plate with its characteristic dentition (Fig. 5C). The hinge, therefore, consists of a ligament producing the opening moment (Trueman 1964) and the teeth which ensure valve alignment after adduction. In the boring Adesmacea, this no longer applies, the separated valves rock on the dorso-ventral axis. Form in the Bivalvia is dominated by the mantle/shell, the valves adapted as a means of rock or wood boring in some or all members of six superfamilies and also of swimming in some Pectinidae and Limidae.

The early Cambrian Rostronchia are claimed as ancestral to the Bivalvia (Runnegar, 1978), but the compressed, presumably infaunal, shell lacks ligament and adductors and so could neither open nor close. The Rostroconchidae appear to have calcified prematurely to be ousted by the possibly related but better adapted Bivalvia where calcification followed complete lateral compression.

Pallial enclosure involved withdrawal of the mouth and loss of cephalic sense organs. Food presumably initially consisted of organic detritus collected by protruding lip appendages, as in the modern protobranch Nuculacea, with later evolution in the Nuculanacea of pumping ctenidia (Yonge, 1939b) and extensive exploitation of the abyssal environment (Allen, 1979). The lamellibranch ctenidium ensured increased water flow with highly efficient filtration of suspended material, especially phytoplankton. Accompanying sediment — always a problem in gill chambers — together with particles rejected by the now solely sorting labial palps, was collected in the ciliary rejection tracts (first fully described by Kellogg, 1915). These aptly designated pseudofaeces (Dodgson, 1928) were rejected from the inhalant chamber, sometimes, as in the Tellinacea, finally through overhung channels, by sudden contractions of the striated “quick” muscle, which came to occupy distal areas in both adductors.

Sensory contact with the environment had to be re-established and control imposed on the greatly increased water flow. Development of additional folds around the mantle margins solved both problems and also was to be the means of acquiring new habits and exploiting fresh environments. Their potential was responsible for the striking success, despite enclosure within the mantle/shell, of the Bivalvia.

Throughout this class, with the recently established exception of some Arcoida (see below), the mantle is fringed by three folds (Fig. 1). The outermost is a basic molluscan structure (Stasek & McWilliams, 1973) forming the outer shell layers. It is bounded internally by a groove from which emerges the non-calcareous periostracum, which initially covers the entire surface of the shell. Within the pallial space below this, the outer surface of this fold secretes the outer (prismatic or crossed-lamellar) layer of the valves (Taylor et al., 1969) and, at each end of the mantle isthmus, the anterior and posterior outer (lamellar) ligament layers (Yonge, 1978a).

Although additional folds appear in other molluscs, the middle and inner folds in the Bivalvia meet the particular needs imposed by compression and enclosure. With distal surfaces covered by periostracum, the middle folds, first in contact with the environment, assume

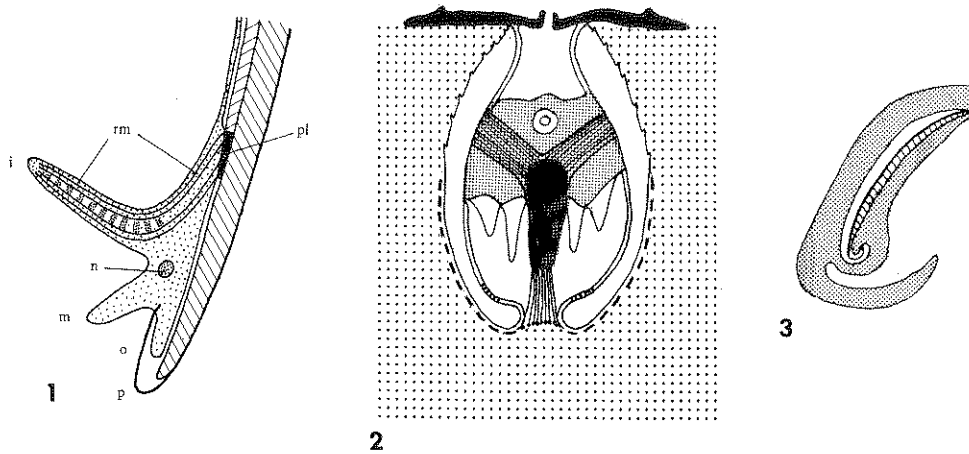


FIG. 1. Formal transverse section through margin of mantle lobe and valve of typical bivalve, outer fold (o) secreting outer calcareous layer of valve with superficial periostracum (p) issuing from groove at base, middle (sensory) fold (m) with nerve (n), inner fold (i) with radial muscles (rm) attached to valve along pallial line (pl). FIG. 2. *Tridacna crocea*, semi-diagrammatic transverse section of animal *in situ* byssally attached within coral rock, exhalant siphon above, gape with emerging byssus below, also paired byssal (pedal) retractors. Hypertrophied inner mantle folds (black) above exposing contained zooxanthellae to light; equally hypertrophied middle mantle folds (broken lines) below, extended to provide chemical assistance in boring (based on Yonge, 1981a). FIG. 3. Semi-diagrammatic section through valve of leptonacean *Phlyctenachlamys* showing its enclosure within the extruded middle mantle fold, inner fold also enlarged (after Popham, 1939).

the sensory functions of a head by way of chemoreceptive or tactile tentacles and also eyes in the Pectinacea and Limacea, with greatest complexity in the anomalodesmatan *Laternula* (Adal & Morton, 1973). The exception, discussed later, is in the Cardicea, where eyes occur on the inner folds.

In various bivalves, the middle folds extend outside the shell, causing major changes in habit. They may hypertrophy to assist the valves in rock boring. All species of *Lithophaga* (Mytilacea) penetrate calcareous rock, culminating in those species that bore into living corals (Morton & Scott, 1980). Although the boring is shaped by the byssally attached shell, the rock is initially softened by anteriorly protruding middle folds (*not* inner as earlier stated (Yonge, 1955)) which secrete a presumably calcium-chelating mucus (Jaccarini et al., 1968). Species boring into living coral also possess posterior glandular areas, their secretion considered to prevent overgrowth of the boring by the coral (Morton & Scott, 1980).

The Tridacnidae (Cardicea) demand special attention. During evolution (*not* during development, when of necessity the final form is quickly attained) the mantle/shell turned through an angle of some 180° in the sagittal plane in relation to the byssally attached visceropedal mass (Yonge, 1953b). The umbones are thus situated midventrally, immediately anterior to the enlarged byssal gape (Fig. 2). The anterior adductor is lost. The siphons, solely composed of inner folds bearing modified eyes (Stasek, 1966), occupy the entire upper surface and are enormously enlarged to house and expose to the light a vast population of endosymbiotic dinoflagellate zooxanthellae. On the under surface, the middle folds are enlarged and protrude to assist by chemical means the mechanical action of the massive valves in excavating a shallow depression in the invariable substrate of dead coral rock. Together with adventitious additions to the rim of the byssal gape by the outer folds, this excavation ensures intimate contact between shell and substrate so preventing any entrance of even the smallest predators which could destroy the delicate pallial organs (Yonge, 1981a).

Such is the condition in *Tridacna maxima* and *T. squamosa*, while in the smaller *T. crocea* the ventral middle folds and the posterior pedal (byssal) muscles (rocking the downward grinding valves) are further enlarged to achieve full penetration. Massively attached below, the richly pigmented inner folds spread widely over the rock surface above. In the "giant" species (*T. gigas*, *T. derasa* and the related *Hippopus hippopus*), byssal apparatus and gape are lost during growth, with posture finally maintained by virtue of the weight of the enormously thickened umbonal region of the valves (Yonge, 1981a).

Fungiacava eilatensis (Mytilacea) penetrates, pedal side uppermost, into the skeleton of the hermatypic coral, *Fungia scutaria* (Goreau et al., 1969). The enlarged inhalant siphon opens into the coelenteron, the two animals with the zooxanthellae in the coral living in three-way symbiosis (Goreau et al., 1970). The middle folds protrude and unite, entirely enclosing the very delicate shell. Penetration of the calcareous skeleton can only be by the agency of this pallial covering (Goreau et al., 1972).

Similar partial or total enclosure of the valves by the united middle folds (Fig. 3) occurs in the largely commensal Leptonacea (Erycinacea), particularly in the Galeommatidae, with progressive reduction of the shell (but *not* of the mantle) in the series *Galeomma/Ephippodonta/Phlyctaenachlamys/Chlamydoconcha* (Morton, 1981b). Forming the outer covering of these delicate animals, the middle folds have acquired a protective role, some carrying autotomizing and probably poison-containing tentacles, while in *Galeomma polita* (Morton, 1973a) large tentacles project in an apparent dynamic display. In *G. takii* (Morton, 1973b), the young are protected among defensive papillae dorsally.

In *Lima hians* (Limacea), the long, bright yellow and non-retractile middle fold tentacles assist by "rowing" the swimming movements, which Gilmour (1967) associates with nest-formation in these unusual bivalves. The flexibility needed in these movements explains their uniquely complex structure. Each tentacle is subdivided by septa at the level of any one of which it may autotomize. Again protection is chemical, a distasteful mucus produced by epidermal glands.

The sand grains which encrust the shell surface in various of the Anomalodesmata are attached by secretions from arenophilic glands. In *Periploma*, these originate in the middle folds (Morton, 1981a) but, in *Entodesma*, Prezant (1981) stated that they open under the periostracum, i.e., on the outer lobe, through which the secretion passes. But it seems probable that all such glands originate in the middle folds. In the Veneracea the middle folds are duplicated (Ansell, 1961).

The inner folds are muscular and they control the increased water flow. Their radial muscles (Fig. 1) are attached to the valves along the pallial line so that lateral compression inevitably produced cross-fusion at each end with creation of the adductor muscles. Like the ligament which opens the valves, these are of pallial origin; they are *not* modified shell muscles.

Apart from the uniquely specialized Tridacnidae, inner folds are most enlarged in the Pectinacea, forming the velum or pallial curtains. Their local apposition separates inhalant and exhalant regions. Areas of separation direct the jets produced by contractions of the enlarged region of quick muscle in the solitary adductor. This enlargement was initially due to the need for cleansing the under (right) half of the mantle cavity in these pleurothetic bivalves (Yonge, 1936). With loss of byssal attachment, these sudden ejections came to produce the "escape" and "swimming" movements exhibited by the stream-lined scallops, species of *Chlamys* (Moore & Trueman, 1971), *Pecten* (Thayer, 1972) and *Amusium* (Morton, 1980). Pallial curtains are largest in the abyssal, possibly carnivorous, Propeamussidae (Knudsen, 1970). All have a filtering fringe of "guard" tentacles distinct from the longer and extensile "exploratory" tentacles which, with eyes (except in the Propeamussidae), surmount the middle folds (Waller, 1972).

Conditions differ in the Arcoida. As shown in a variety of species by Morton (1978, 1982) and Waller (1980), there are *two* outer folds, the more distal one secretory, the other one

carrying simple photoreceptors beneath the periostracum. Waller considered that a middle fold is lacking with the inner fold sometimes duplicated, but Morton (1982) thought that both are present with the middle fold (devoid of sensory functions) often reduced. Waller found evidence here against the existence of a basic three-fold pattern in the Bivalvia but, as noted elsewhere (Yonge, 1982b), duplication of the outer folds further emphasizes the distinctive characters of the Arcoida.

Early evolution involved conquest, by the Bivalvia, of the superficial infaunal habitat. Neotenic retention of the larval byssal apparatus next permitted epifaunal exploitation (Yonge, 1962b). One result of byssal attachment was anterior reduction (of positive advantage by raising the posterior inhalant opening higher above the substrate), with change from the original isomyarian to a heteromyarian condition (as in the Mytilacea (Yonge & Campbell, 1968)) leading on to pleurothetic monomyarians (Yonge, 1953a). These had a secondary amphidetic ligament and the viscera were reorganized in the sagittal (now horizontal) plane around the central pallial pillar of the adductor.

In the Pectinacea, with right valve undermost, byssal (i.e., pedal) attachment either is retained – even enlarged in species associated with corals (Yonge, 1981b) – or, in scallops, gives place to freedom, or else to cementation (pallial attachment) in *Hinnites* and *Spondylus* (Yonge, 1979). Although viscera and foot are very similar in these genera, hinge and ligament are totally dissimilar (Yonge, 1973), providing further convincing evidence of the separate identities of the visceropedal mass and mantle/shell. Throughout, the foot persists as a means of cleansing. In the byssally cemented Anomiacea, it regains its primary function in the crawling *Enigmonia* (Fig. 4) although not in the also unattached, although immobile, *Placuna* (Yonge, 1977). In the Ostreacea, cemented by the left valve, the foot is lost as it is in the very different Plicatulidae and Dimyidae, both attached by the right valve (Yonge, 1978c).

These major changes were unaccompanied by any attachment between opposing mantle margins, which remained free as in modern Nuculacea, Arcoida and Pterioda. Union was delayed until the Mesozoic when, as emphasized by Stanley (1968, 1970), there was a second evolutionary radiation, notably of deep burrowing bivalves. Fusion involved successively that of inner, middle and then the inner surface of outer folds, with accompanying formation of different types of siphons (Yonge, 1957).

The originally suggested categories have now been simplified (Yonge, 1982b) to cover (A) union of inner folds only with separate siphons; (A+) the special case of the Cardacea where sense organs are carried on the inner folds, the middle folds usually greatly reduced; (B) addition of the middle folds, this now including the Pholadidae; (C) also including the periostracal groove. Previously suggested fusion involving the outer surface of the outer folds and thus union of the outer calcareous layer only occurs “supradorsal” to the ligament in the upper (left) valve of the Anomiidae, most strikingly in the bivalve “limpet” *Enigmonia* (Fig. 4).

Fusion involving the periostracal grooves, or certainly of their secretions, has a major effect on the primary ligament, which in many superfamilies is secondarily extended by fused periostracum (initially misleadingly termed “fusion layer”). This may occur at one end (normally posterior as in *Pinna* where first described (Yonge, 1953c)) or at both ends (Fig. 5B). This provides greater attachment between the valves with reduction in the now less needed teeth (e.g., in Saxicavacea (Yonge, 1971)), but the primary ligament remains solely responsible for valve separation.

A major contribution to bivalve success was the move from anterior to posterior end of the inhalant aperture to be sited ventral to the exhalant opening where, in the septibranch Cuspidariidae, its siphon even becomes adapted for sizing animal prey (Reid & Reid, 1974). This posterior enlargement led to the originally antero-posteriorly symmetrical amphidetic ligament (Fig. 5A) becoming opisthodontic, the posterior outer layer enlarged, the anterior one reduced or lost (Fig. 5B, C). Such ligaments are “external”, arching dorsally with the pivotal axis running along the plane of contact between the inner layer and outer posterior

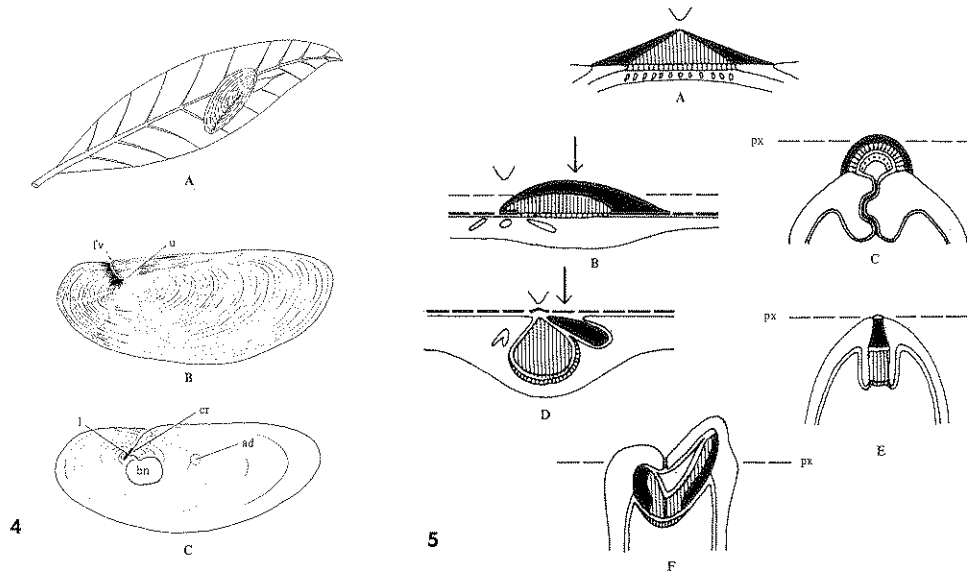


FIG. 4. *Enigmonia aenigmatica* (ca. 30 mm long). A, *In situ* on mangrove leaf showing extended foot; B, upper (left) valve showing position, at apex, of umbo (u) separated from margin by length of fused "supradorsal" valve (fv), ligament lies beneath umbo; C, upper surface of under valve showing position of ligament (l) at end of jutting crurum (cr) posterior to the deep byssal notch (bn), also of reduced adductor (ad) (from Yonge, 1977). FIG. 5. Diagrams of ligamental structure, inner layer with underlying mantle isthmus indicated by vertical lines, outer layers black, periostracal extensions and secondary ligament by thick broken lines. A, "Ideal" amphidetic ligament with taxodont dentition; B, opisthodetic ligament with secondary extensions and heterodont dentition; C, transverse section at arrow in B, hinge plate with tooth (t) and socket (s); D, "internal" ligament (e.g., Mactracea), condensed primary ligament and hinge plate extended ventrally, anterior outer layer lost, secondary ligament occupying pivotal axis (px); E, transverse section at arrow in D; F, transverse section showing separate primary and secondary ligaments in *Plicatula* (after Yonge, 1978a).

layer (Fig. 5C). When the adductors contract, the former layer is compressed with the latter suffering tensile stress, the one a resilium, the other a tensilium.

In various superfamilies, the hinge plate and condensed primary ligament extend ventrally displacing the reduced cardinal teeth, while above the anterior and posterior periostracal extensions unite between the umbones. The valves are now completely united dorsally by the periostracum, which forms a *secondary ligament* (Fig. 1D,E) (Yonge, 1978a). Centrally, this may consist solely of periostracum, the secreting epithelia not united, and primary and secondary ligaments joined dorsally. This is the case in the Lyonsiidae and related Pandoracea (Yonge & Morton, 1980), and also in the Mactracea (Fig. 1C) and Myacea (Yonge, 1982a). Where these epithelia *do* overarch the primary ligament, the secondary ligament is separate as in *Placuna* (originating from byssally cemented Anomiacea), in *Plicatula* (Fig. 1F) and the Dimyidae (Yonge, 1973, 1977, 1978c). In all, the primary ligament forms a resilium, the secondary ligament, attached along the pivotal axis, ensuring valve alignment and possibly providing some tensile force.

The "inner" and "outer" ligaments of conchology are often the inner and the outer (usually posterior) ligament *layers*. The differences between "external" ligaments (as in Veneracea and Cardiacea) and the "internal" ligaments described above are due to ventral extension of the hinge plate and primary ligament with periostracal union dorsally.

The mantle margins may split the primary ligament with major effects on both form and habit. In most bivalves, form is the resultant of radial and transverse growth components, the former radiating out from the umbones and acting in the plane of the generative curve, the latter at right angles to this. As shown by Owen (1953) in *Glossus (Isocardia)*, the former may be deflected anteriorly by a third, tangential, component. Dorsally, this acts in a posterior direction so splitting the entirely primary ligament, with separation of the anterior-facing (prosogyral) umbones and conversion of each valve from a logarithmic planospiral into a corresponding turbinate spiral. Separation of the umbones is accompanied by division of the epithelium secreting the anterior outer ligament layer and anterior regions of the mantle isthmus. The ligament is correspondingly extended at the posterior end.

In the similarly growing, but cemented, *Chamaea* (Yonge, 1967), where the attached valve (right or left) has a large transverse component but the upper one none, the tangential component produces an inverted "gastropod" with deep half turbinate under valves and flat "opercular" upper ones. In striking evidence of the different symmetries involved, although species (possibly individuals) cement by either side, the hinge is that of an upper or lower valve; irrespective of whether this be right or left, the one is the mirror image of the other (Fig. 6), this an apparent result of cementation (Yonge, 1979).

Presence of a tangential component explains the diversity of form displayed in the similarly cemented and normal or inverse Mesozoic Hippuritacea (Yonge, 1967), culminating in the Hippuritidae and Radiolithidae with massive cone-shaped under valves and flat upper ones. All trace of coiling is lost, the completely divided, now vertical, ligament is functionless. Such rudists formed reefs, their height probably lifting them clear of sediment but also ensuring their later destruction.

The effect of a tangential component where a secondary ligament is present in *Cleidothaerus* (Yonge & Morton, 1980) is to obliterate anterior and posterior outer ligament layers and so separate an external (secondary) ligament from an internal (primary) one, here reduced to the inner layer secreted by an isolated island of mantle isthmus. The calcareous lithodesma which in related bivalves occupies the central area of the inner layer, offsetting the effects on this of diverging chondrophores, is, in further consequence of the tangential component, here wrapped around this layer.

In the cemented, freshwater Etheriidae (Unionacea) (Anthony, 1907; Yonge, 1962a), the mantle plays a no less impressive role in the control of form and habit, the animals adapted for life in rushing waters and most strikingly in the South American (Colombian) *Acostae*

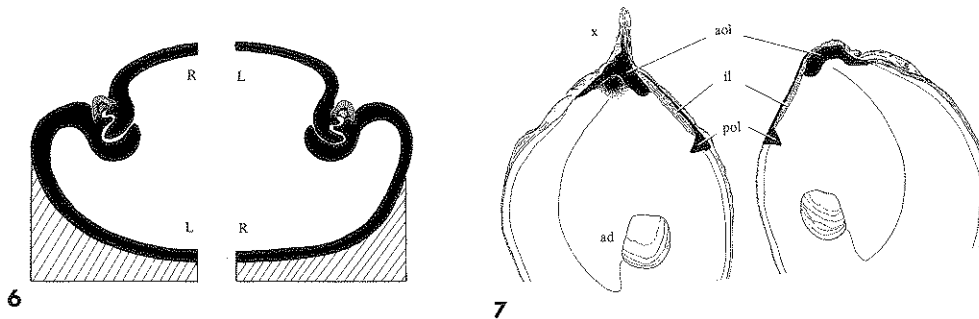


FIG. 6. *Chamaea*. Hinges (ligament and teeth) of shells attached by right and left valves, mirror images the one of the other, i.e., under and upper, *not* right and left, valves resembling each other (from Yonge, 1967). FIG. 7. *Acostaea rivoli*, inner surface of valves, cemented (here right) valve on left with attached first-formed regions (x) of both valves including original ligament. Final position of three layers of typically unionid primary ligament (aoi, il, pol) shown, also solitary adductor scar (ad) (from Yonge, 1978b).

(Yonge, 1978b). The post-larva apparently attaches laterally in rock depressions, anterior end downward. Later growth can be only in a posterior, initially upward, direction. Conformity with the substrate then demands a bending in the long axis of the valves which necessitates formation of a new hinge. This is accomplished by movement of the epithelia secreting the typically unionid primary ligament and loss of the most anterior regions, especially of the mantle/shell. The animal becomes monomyarian in a unique manner. The foot is lost in all Etheriidae.

The under, cemented valve incorporates the anterior regions of *both* post-larval valves (Fig. 7). Here, as in the related isomyarian *Etheria*, cementation with its subsequent major effects is entirely a matter of the individual. Settlement is indifferently right or left, solely dependent on which side the post-larva chances to come to rest and then cement itself. What may happen in some Chamacea invariably happens in all Etheriidae: pallial asymmetry is dependent on ontogeny.

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LITERATURE CITED

- ADAL, M.N. & MORTON, B. 1973. The fine structure of the pallial eyes of *Laternula truncata* (Bivalvia: Anomalodesmata: Pandoracea). *J. Zool. Lond.*, 171: 535-556.
- ALLEN, J.A. 1979. The adaptations and radiation of deep-sea bivalves. *Sarsia*, 64: 19-27.
- ANSELL, A.D. 1961. The functional morphology of the British species of Veneracea (Eulamellibranchia). *J. mar. biol. Assoc. U.K.*, 41: 489-517.
- ANTHONY, R. 1907. Étude monographique des Aetheriidae (Anatomie, Morphogénie, Systématique). *Ann. Soc. R. Zool. Malacol. Belg.*, 41: 322-430.
- DODGSON, R.W. 1928. Report on mussel purification. *Fish. Invest.*, ser II, 10: 1-498.
- GILMOUR, T.H.J. 1967. The defensive adaptations of *Lima hians* (Mollusca, Bivalvia). *J. mar. biol. Assoc. U.K.*, 47: 209-221.
- GOREAU, T.F., GOREAU, N.I., SOOT-RYEN, T. & YONGE, C.M. 1969. On a new commensal mytilid (Mollusca: Bivalvia) opening into the coelenteron of *Fungia scutaria* (Coelenterata). *J. Zool. Lond.*, 158: 171-195.
- GOREAU, T.F., GOREAU, N.I. & YONGE, C.M. 1972. On the mode of boring in *Fungiacava eilatensis* (Bivalvia: Mytilidae). *J. Zool. Lond.*, 166: 55-60.
- GOREAU, T.F., GOREAU, N.I., YONGE, C.M. & NEUMANN, Y. 1970. On feeding and nutrition in *Fungiacava eilatensis* (Bivalvia: Mytilidae), a commensal living in fungid corals. *J. Zool. Lond.*, 160: 159-172.
- JACCARINI, V., BANNISTER, W.H. & MICALEF, H. 1968. The pallial glands and rock boring in *Lithophaga lithophaga* (Lamellibranchia, Mytilidae). *J. Zool. Lond.*, 154: 397-401.
- KELLOGG, J.L. 1915. Ciliary mechanisms of lamellibranchs with descriptions of anatomy. *J. Morphol.*, 26: 625-701.
- KNUDSEN, J. 1970. The systematics and biology of abyssal and hadal Bivalvia. *Galathea Rep.*, 11: 1-241.
- MOORE, J.D. & TRUEMAN, E.R. 1971. Swimming of the scallop, *Chlamys opercularis* (L.). *J. exp. mar. Biol. Ecol.*, 6: 179-185.
- MORTON, B. 1973a. Dymantic display in *Galeomma polita* Deshayes (Bivalvia: Leptonacea). *J. Conchol.*, 28: 365-369.
- MORTON, B. 1973b. The biology and functional morphology of *Galeomma (Paralepida) takii* (Bivalvia: Leptonacea). *J. Zool. Lond.*, 169: 133-150.
- MORTON, B. 1978. The biology and functional morphology of *Philobrya munita* (Bivalvia: Philobryidae). *J. Zool. Lond.*, 185: 173-196.
- MORTON, B. 1980. Swimming in *Amusium pleuronectes* (Bivalvia: Pectinidae). *J. Zool. Lond.*, 190: 375-404.
- MORTON, B. 1981a. The biology and functional morphology of *Periploma angasai* (Bivalvia: Anomalodesmata: Periplomatidae). *J. Zool. Lond.*, 193: 39-70.

- MORTON, B. 1981b. The biology and functional morphology of *Chlamydoconcha orcutti* with a discussion on the taxonomic status of Chlamydoconchacea (Mollusca: Bivalvia). *J. Zool. Lond.*, 195: 81-121.
- MORTON, B. 1982. The biology and functional morphology of the twisted ark *Trisidos semitorta* (Bivalvia: Arcacea) with a discussion on shell 'torsion' in the genus. *Malacologia*, in press.
- MORTON, B. & SCOTT, P.J.B. 1980. Morphological and functional specializations of the shell, musculature and pallial glands in the Lithophaginae (Mollusca: Bivalvia). *J. Zool. Lond.*, 192: 179-203.
- OWEN, G. 1953. On the biology of *Glossus humanus* (L.) (*Isocardia cor.* Lam.). *J. mar. biol. Assoc. U.K.*, 32: 85-106.
- OWEN, G., TRUEMAN, E.R. & YONGE, C.M. 1953. The ligament in the Lamellibranchia. *Nature, Lond.*, 171: 173.
- POPHAM, M.L. 1939. On *Phlyctaenachlamys lysiosquillina* gen. and sp. nov. a lamellibranch commensal in the burrows of *Lysiosquillina maculata*. *Sci. Rep. Gr. Barrier Reef Exped. (1928-29), Br. Mus. (nat. Hist.)*, 3: 247-272.
- PREZANT, R.S. 1981. The arenophilic radial mantle glands of the Lyonsiidae (Bivalvia: Anomalodesmata) with notes on lyonsiid evolution. *Malacologia*, 20: 267-289.
- REID, R.G.B. & REID, A.M. 1974. The carnivorous habit of members of the septibranch genus *Cuspidaria* (Mollusca: Bivalvia). *Sarsia*, 56: 47-56.
- RUNNEGAR, B. 1978. Origin and evolution of the class Rostroconchia. *Philos. Trans. R. Soc. Lond.*, B, 284: 319-333.
- STANLEY, S.M. 1968. Post-paleozoic adaptive radiation of infaunal bivalve molluscs - a consequence of mantle fusion and siphon formation. *J. Paleontol.*, 42: 214-229.
- STANLEY, S.M. 1970. *Relation of shell form to life habits in the Bivalvia (Mollusca)*. Mem. 125, Geol. Soc. Am., Boulder, Colorado, U.S.A. 296 pp.
- STASEK, C.R. 1966. The eye of the giant clam (*Tridacna maxima*). *Occas. Pap. Calif. Acad. Sci.*, (58): 9 pp.
- STASEK, C.R. 1972. The molluscan framework. In: Florkin, M. & Scheer, B.T. (Eds.), *Chemical zoology*. Vol. VII, Mollusca. Academic Press, New York. 567 pp [p 1-44].
- STASEK, C.R. & McWILLIAMS, W.R. 1973. The comparative morphology of the molluscan mantle edge. *Veliger*, 16: 1-19.
- TAYLOR, J.D., KENNEDY, W.J. & HALL, A. 1969. The shell structure and mineralogy of the Bivalvia. *Bull. Br. Mus. (nat. Hist.) Zool.*, suppl. 3: 1-125.
- THAYER, C.W. 1972. Adaptive features of swimming monomyarian bivalves (Mollusca). *Forma Functio*, 5: 1-32.
- TRUEMAN, E.R. 1964. Adaptive morphology in paleoecological interpretation. In: Imbrie, J. & Newell, N.D. (Eds.), *Approaches to paleoecology*. Wiley. 432 pp. [p. 45-74].
- TRUEMAN, E.R. 1968. The burrowing activities of bivalves. *Symp. Zool. Soc. Lond.*, 22: 167-186.
- WALLER, T.R. 1972. The Pectinidae (Mollusca: Bivalvia) of Eniwetok Atoll, Marshall Islands. *Veliger*, 14: 221-264.
- WALLER, T.R. 1980. Scanning electron microscopy of shell and mantle in the order Arcoida (Mollusca: Bivalvia). *Smithson. Contrib. Zool.*, (313): 58 pp.
- YONGE, C.M. 1936. The evolution of the swimming habit in the Lamellibranchia. *Mem. Mus. R. Hist. nat. Belg.*, (2), 3: 77-100.
- YONGE, C.M. 1939a. On the mantle cavity and its contained organs in the Loricata (Placophora). *Q. J. microsc. Sci.*, 81: 367-380.
- YONGE, C.M. 1939b. The protobranchiate Mollusca; a functional interpretation of their structure and evolution. *Philos. Trans. R. Soc. Lond.*, B, 230: 79-147.
- YONGE, C.M. 1947. The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca. *Philos. Trans. R. Soc. Lond.*, B, 232: 443-518.
- YONGE, C.M. 1953a. The monomyarian condition in the Lamellibranchia. *Trans. R. Soc. Edinb.*, 62: 443-478.
- YONGE, C.M. 1953b. Mantle chambers and water circulation in the Tridacnidae. *Proc. zool. Soc. Lond.*, 123: 551-561.
- YONGE, C.M. 1953c. Form and habit in *Pinna carnea* Gmelin. *Philos. Trans. R. Soc. Lond.*, B, 237: 335-374.
- YONGE, C.M. 1955. Adaptation to rock boring in *Botula* and *Lithophaga* (Lamellibranchia, Mytilidae) with a discussion on the evolution of this habit. *Q. J. microsc. Sci.*, 96: 383-410.
- YONGE, C.M. 1957. Mantle fusion in the Lamellibranchia. *Pubbl. Stn. zool. Napoli*, 29: 151-171.
- YONGE, C.M. 1962a. On *Etheria elliptica* Lam. and the course of evolution, including the assumption of monomyarianism, in the family Etheriidae (Bivalvia: Unionacea). *Philos. Trans. R. Soc. Lond.*, B, 244: 423-458.
- YONGE, C.M. 1962b. On the primitive significance of the byssus in the Bivalvia and its effect on evolution. *J. mar. biol. Assoc. U.K.*, 42: 113-125.

- YONGE, C.M. 1967. Form, habit and evolution in the Chamidae (Bivalvia) with reference to conditions in the rudists (Hippuritacea). *Philos. Trans. R. Soc. Lond.*, B, 252: 49-105.
- YONGE, C.M. 1971. On the functional morphology and adaptive radiation in the bivalve superfamily Saxicavacea (*Hiatella (Saxicava)*, *Saxicavella*, *Panomya*, *Panope*, *Cyrtodaria*). *Malacologia*, 11: 1-44.
- YONGE, C.M. 1973. Functional morphology with particular reference to hinge and ligament in *Spondylus* and *Plicatula* with a discussion on relations within the superfamily Pectinacea (Mollusca: Bivalvia). *Philos. Trans. R. Soc. Lond.*, B, 267: 173-208.
- YONGE, C.M. 1977. Form and evolution in the Anomiacea — *Pododesmus (Monia)*, *Anomia*, *Patro*, *Enigmonia* (Anomiidae); *Placunanomia*, *Placuna* (Placunidae fam. nov.). *Philos. Trans. R. Soc. Lond.*, B, 276: 453-523.
- YONGE, C.M. 1978a. Significance of the ligament in the classification of the Bivalvia. *Proc. R. Soc. Lond.*, B, 202: 231-248.
- YONGE, C.M. 1978b. On the monomyarian *Acostaea rivoli* (Desh.) and evolution in the family Etheriidae (Bivalvia: Unionacea). *J. Zool. Lond.*, 184: 429-448.
- YONGE, C.M. 1978c. On the Dimyidae (Mollusca: Bivalvia) with special reference to *Dimya corrugata* Hedley and *Basiliomya goreau* Bayer. *J. moll. Stud.*, 44: 357-375.
- YONGE, C.M. 1979. Cementation in bivalves. In: van der Spoel, S., van Brugen, A.C. & Lever, J. (Eds.), *Pathways in malacology*. Bohn, Scheffers & Holkema, Utrecht, and Junk, The Hague. 295 pp. [p. 83-106].
- YONGE, C.M. 1981a. Functional morphology and evolution in the Tridacnidae (Mollusca: Bivalvia: Cardiacea). *Rec. Aust. Mus.*, 33: 735-777.
- YONGE, C.M. 1981b. On adaptive radiation in the Pectinacea with a description of *Hemipecten forbesianus*. *Malacologia*, 21: 23-34.
- YONGE, C.M. 1982a. Ligamental structure in Mactracea and Myacea (Mollusca: Bivalvia). *J. mar. biol. Assoc. U.K.*, 62: 171-186.
- YONGE, C.M. 1982b. Mantle margins with a revision of siphonal types in the Bivalvia. *J. moll. Stud.*, 48: 102-103.
- YONGE, C.M. & CAMPBELL, J.I. 1968. On the heteromyarian condition in the Bivalvia with special reference to *Dreissena polymorpha* and certain Mytilacea. *Trans. R. Soc. Edinb.*, 68: 21-43.
- YONGE, C.M. & MORTON, B. 1980. Ligament and lithodesma in the Pandoracea and Poromyacea with a discussion on evolutionary history in the Anomalodesmata (Mollusca: Bivalvia). *J. Zool. Lond.*, 191: 263-292.

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