# PART N
# MOLLUSCA 6
# BIVALVIA

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## VOLUME 1

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## DEDICATION

By Raymond C. Moore and Norman D. Newell

Part N of the *Treatise on Invertebrate Paleontology,* devoted to the great group of mollusks named Bivalvia, here is dedicated to the memory of Leslie Reginald Cox, one of the chief contributing authors both to this and other *Treatise* volumes concerned with the Mollusca. He died quite unexpectedly on August 5, 1965, at the age of 67 just after completion of a typescript draft of his chapter on General Characters of Bivalvia, which follows, but before illustrations planned by him had been organized. He had already finished work on many bivalve families, including preparation of figures for genera included in them. The magnitude of loss to paleontology and especially to the *Treatise* caused by his death goes without saying. Whereas no previously published unit of this series has been designated to honor an individual paleontologist, it seems highly appropriate that Part N on Bivalvia should be dedicated to Dr. Cox.

Except to record that Dr. Cox's scientific career is almost entirely linked with the British Museum (Natural History), where in later years he was Deputy Keeper of the Palaeontology Department, and that his research activities broadly and mainly embraced groups of post-Paleozoic Mollusca represented by fossils from all parts of the world, the scope and importance of his very numerous published contributions are not pertinent for review by us here. Rather, it is desirable to stress the extraordinary degree of Dr. Cox's dedication to objectives of the *Treatise,* for without any financial remuneration to him or even financial assistance from *Treatise* sources, he not only labored indefatigably to achieve utmost quality of his own chapters in this collaborative project but unstintingly furnished aid to other *Treatise* workers. The wisdom of his counsel and generosity in drawing on his time and accumulated knowledge for the benefit of others, including both of us in disposing of editorial and organizational problems, are irreplaceable assets. In short, without trace of provincial outlook, scientifically or politically, LESLIE R. COX epitomizes the able, energetic, best possible *Treatise* collaborator, who is indispensable for achieving the high aims of leadership in authoritative, comprehensive presentation of present-day knowledge of invertebrate fossils, both for understanding of them as remains of once-living animals and for practical use of them in solving geologic problems.

Acknowledgment of work done by Mr. C. P. NUTTALL, British Museum (Natural History), in revising parts of the text, in completing illustrations, and in adding to literature references, deserves record. This help has been extremely valuable, and because of his substituting as far as possible for Dr. Cox, special appreciation is expressed to Mr. NUTTALL.

# GENERAL FEATURES OF BIVALVIA

By †L. R. COX (with additions by C. P. NUTTALL and E. R. TRUEMAN)
[British Museum (Natural History), London]

## CONTENTS

# NAME AND CHARACTERS OF CLASS

## NAME BIVALVIA

Probably more disagreement on the name to be applied to this class has arisen than in the case of any other major taxon. Of some 13 names for the bivalve mollusks which have been introduced in the literature, those of Pelecypoda GOLDFUSS and Lamellibranchia (or Lamellibranchiata) DE BLAINVILLE were preferred (to an almost equal extent) by malacologists for many years. Until fairly recently, in fact, it is only in occasional works that we find the Linnean name Bivalvia, and in still fewer do other names appear, such as Conchifera LAMARCK and Acephala CUVIER. The designation Bivalvia, however, has now been revived in several major works of reference, notably F. HAAS's monumental contribution to the revised edition of BRONN's *Klassen und Ordnungen des Tierreichs* (1929-56), J. THIELE's *Handbuch der systematischen Weichtierkunde* (1934-35) and the Russian *Osnovy Paleontologii* (1960). It has thus become increasingly familiar to the present generation of workers, and has been accepted for use in the present *Treatise*

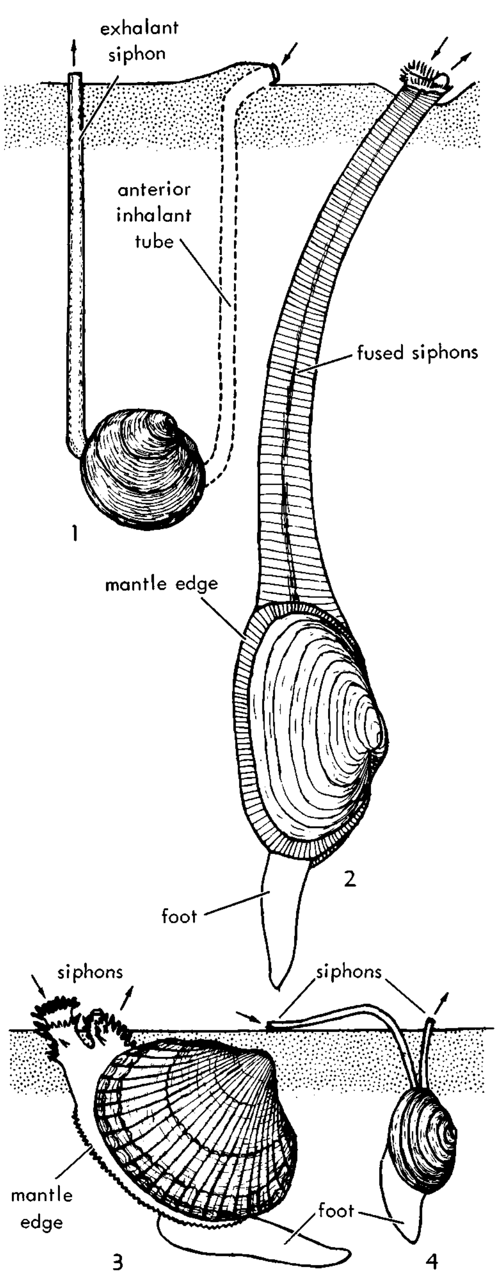

FIG. 1. Habitat of bivalves—burrowing types (Cox, n).——*1. Loripes lucinalis* (LAMARCK), suspension-feeder with anterior inhalant tube punched through sediment by foot, ×1.——*2. Mya arenaria* LINNÉ, deep-burrowing suspension-feeder with fused siphons, ×0.4.——*3. Cardium edule* LINNÉ, shallow-burrowing suspension-feeder with short siphons, ×0.7.——*4. Tellina tenuis* DA COSTA, shallow-burrowing deposit-feeder with long unconnected siphons, ×0.6.

in the hope that this course will promote stability and uniformity in nomenclature.

Used by various early workers from the time of BUONANNI (1681) onward, the name Bivalvia was adopted by LINNÉ in 1758 in the 10th edition of the *Systema Naturae* (p. 645) for a subdivision of the group Testacea of the class Vermes; no diagnosis was given, the subdivision being defined by listing the genera included in it. In fact, these consisted of all the Linnean genera of the class as still understood, with the exception of *Teredo,* which was included in the group Intestina. Among the Linnean species of *Anomia* were certain forms now classified as Brachiopoda, but otherwise the Bivalvia included no non-molluscan elements. If objections to the name are raised on the ground that there are other groups of invertebrates protected by tests with two valves (e.g., Brachiopoda, some Crustacea, and even certain Mollusca recently recognized to be Gastropoda), it may be answered that a name is merely a name, and neither a key to recognition nor a definition. This consideration apart, it can at least be said that all Bivalvia have tests with two valves, whereas not all have an axelike foot[1] or platelike gills.[2]

## MAIN CHARACTERS OF BIVALVIA

The Bivalvia are aquatic mollusks which fundamentally are bilaterally symmetrical and laterally compressed, and very commonly are elongated in an anteroposterior direction. They invariably are provided with a shell consisting of two wholly or partly calcified valves lying on left and right sides of the body. The shell is external except in a few forms. Typically, the two valves are of equal convexity; but in some forms bilateral symmetry has been lost, usually as the result of cementation of one valve to the substrate, and the valves differ in size to a varying extent. The valves (except in some aberrant genera) are connected dorsally by an only partially calcified, elastic structure (**ligament**), and open and close by hinging along an axis

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[1] The name Pelecypoda was derived from the Greek words πέλεκυς, axe, and πούς, ποδός, foot.

[2] The name Lamellibranchia was derived from the Latin words *lamella,* thin plate, and *branchiae,* gills.

which passes through or close to this. Typically, the hinge axis has an approximately anteroposterior direction. The two valves thus open along their anterior, posterior, and ventral margins, most widely along the last. The valves are closed by the action of muscles **(adductor muscles)**, two or one in number, attached to the inner face of each; these muscles, by drawing the valves together, oppose the action of the ligament, which acts as a spring tending to open them.

The mantle consists of two lobes, one lining each valve. These lobes are joined dorsally, but elsewhere their edges are either completely free or joined only along part of their length. The body of the mollusk normally occupies a dorsal position within the shell and mantle, to the latter of which it is fused. Ventrally, the mantle encloses a relatively large space (**mantle cavity**).

The animal lacks a head, radula, and jaws. Cephalic sensory organs (eyes, tentacles, etc.) found in other mollusks are thus absent, but in many Bivalvia they are replaced by organs with similar functions located mainly along the periphery of the mantle. The **mouth** and **anus** are usually at opposite ends of the body and the intestine is convoluted to a varying extent. The mouth lies between two pairs of ciliated, flaplike structures known as **labial palps**, which assist in conducting food to it. The stomach contains a peculiar structure, the crystalline style (present also in certain gastropods), which aids the digestion of carbohydrates.

A **foot** present in most Bivalvia is an extensile structure which most commonly serves mainly for burrowing. Most forms have a pair of **gills** or ctenidia which are suspended within the mantle cavity from the body and are arranged symmetrically with regard to the median plane of the mollusk. Their detailed structure varies considerably. The nervous system includes visceral and pedal ganglia, together with cerebral and pleural ganglia which are fused in most forms but separate in some. A pedovisceral commissure is lacking. Reproduction is without copulation. Most marine Bivalvia pass through a pelagic larval stage.

# BIOLOGY OF BIVALVIA

## HABITATS AND FOOD

The Bivalvia are essentially aquatic animals. No members of the class can respire, feed, or remain active except in an aqueous medium. The period for which any species can survive, inactive, when removed from such an environment depends largely on its capacity to close its two valves hermetically so that loss of moisture is reduced to a minimum. Of marine forms, those accustomed to life attached to rocks and other objects in the intertidal zone, where they may be exposed for several hours daily, are most tenacious of life. Specimens of the oyster *Crassostrea virginica* (GMELIN) are said to have revived after being kept for as long as ten weeks out of water and specimens of *Mytilus* can survive for a month or more under such conditions. Most marine forms, however, remain alive only for a few days out of water. Some fresh-water bivalves that live in pools which dry up periodically, particularly in hot climates, are the most retentive of life of all bivalves. Usually for aestivation they burrow more deeply into the muddy bottom before it becomes dry, but at times they merely lie loose on the floor of the former pool. Some Unionidae and Sphaeriidae are known to be dormant for as much as six months in every year, and are probably capable of survival for even longer periods. A case is on record of an Australian unionid, probably *Velesunio ambiguus* (PHILIPPI), which made a full recovery on reimmersion after being kept out of water (for much of the period in a dry drawer) for as long as 498 days.

The laterally compressed form characteristic of the great majority of bivalves renders them well adapted for burrowing in sandy or muddy substrates, a process accomplished with the aid of their extensile foot. Many burrowers ascend toward the

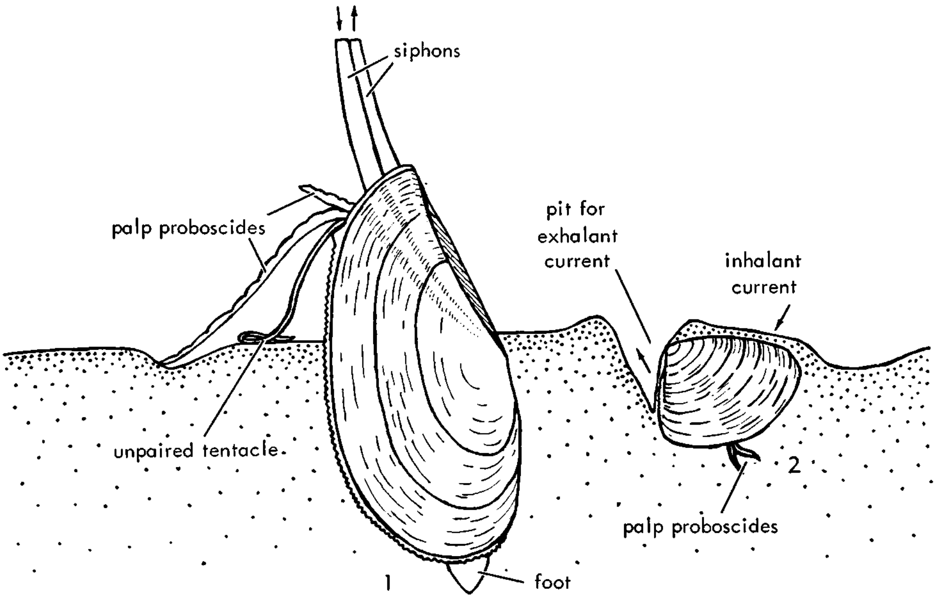

FIG. 2. Habitat of bivalves—nuculacean shallow-burrowing deposit-feeder groping for food by means of palp proboscides *(43)*.——*1. Yoldia limatula* (SAY), form with posterior siphons, ×2.5.——*2. Nucula nucleus* (LINNÉ), showing posterior pitlike opening forced through sediment for exhalant stream, inhalant stream being drawn in anteriorly between shallowly buried shell margins, ×1 *(189)*.

sea floor in order to feed, withdrawing to a greater depth when this activity ceases, as when the bottom is uncovered between tides. Some can burrow rapidly when attacked by an enemy (Fig. 1). Many shallow burrowers, such as *Cardium,* emerge to the surface of the sea floor from time to time and can migrate laterally, again with aid of their foot. The movement of such forms is not, however, a gentle creeping. *Cardium,* for example, moves by a series of jerks or even leaps resulting from the sudden straightening of its bent foot.

Some of the deeper burrowers lead a more or less sedentary life. Usually it is necessary for some communication to be established, either continuously or at frequent intervals, with the relatively clear bottom water. Most bivalves accomplish this with the aid of their two siphons, inhalant and exhalant, and as these structures constitute posterior extensions of the mantle, the usual position occupied by the deeper burrowers is with the anteroposterior axis of the mollusk almost vertical, the anterior end of the shell facing downward and the siphons extending upward from the other end. The deepest burrowers are thus those with the longest siphons, and some species of such genera as *Mya* and *Lutraria* live permanently buried to a depth of as much as 30 cm. in the bottom sediment. It is not, however, to be assumed that the normal position of life of all burrowers is with the plane of the valve margins vertical or almost so; evidence has been found recently that some Tellinidae lie below the surface with the commissure horizontal and right valve uppermost. The Lucinidae have no inhalant siphon, but draw in a current through an inhalant tube which is driven through the sediment by an up-and-down motion of the end of an extensile vermiform foot, and is lined with hardened mucus. This tube projects from the shell at its anterior end, which points obliquely upward, buried perhaps to a depth of 6 to 8 cm.

In *Nucula,* which is without siphons, the shell is buried so shallowly that it is possible for the inhalant current to be drawn in between its anterior margins; at the same time, a passage is maintained for the exhalant current, which passes between the more deeply buried posterior margins, by repeated extrusions of water expelled from the mantle cavity by sudden contractions of the adductor muscles (Fig. 2). *Solemya* is thought to be able to exist for considerable periods buried in soft sediment without any communication with the clear water above, but is exceptional if not unique in this respect.

While great numbers of Bivalvia are thus burrowers in unconsolidated sediment, others have become borers in solid rock (Fig. 3). *Hiatella* is able to bore into relatively soft rock by the mechanical action of the two valves of the shell, which are forced apart repeatedly by sudden pressure of water expelled from the siphons after their partial withdrawal into the borehole (Fig. 3,*2*). In this case, however, individuals unable to find a suitable spot for penetration can exist just as well without boring.

The genus *Pholas* can penetrate harder types of rock. Its shell, the surface of which bears rows of toothlike protrusions, rasps its way forward by a rocking motion of its valves produced by the two adductor muscles acting alternately. The foot forms a sucker which grips the end of the burrow, changing position frequently, with the result that a hole circular in cross section is bored (Fig. 3,*5*).

*Lithophaga* bores into calcareous formations, including coral rock, with the aid of an acid secretion from which its own shell is protected by a thick periostracum. The mollusk is held in position by byssal threads attached to the side of the burrow (Fig. 3,*1*). In all these cases the cavity widens inward, the shell growing as it bores; the mollusk, therefore, can never emerge from the cavity. The siphons, however, must always be capable of becoming extended as far as the opening, and the depth of penetration is limited by this factor. Some of the smaller species of *Tridacna* can bore mechanically obliquely downward

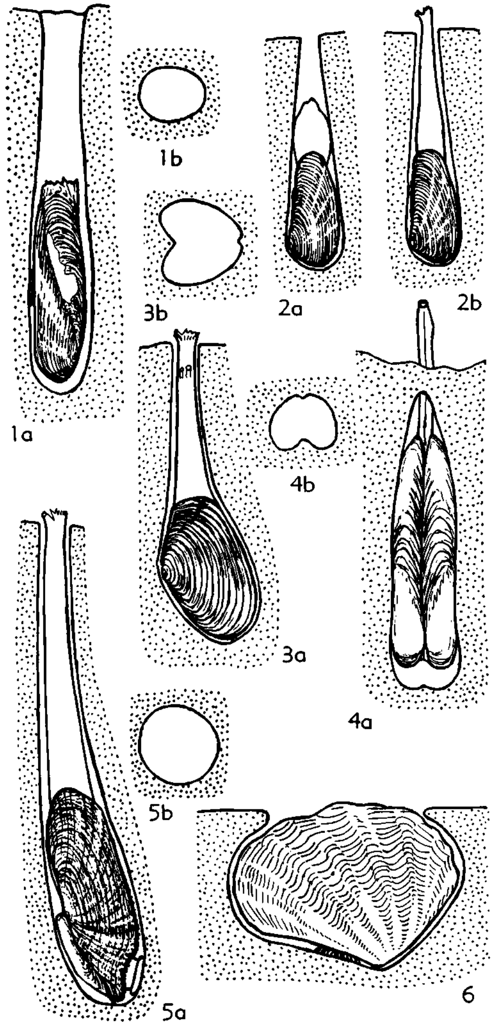

FIG. 3. Habitat of bivalves—rock-borers (surface of rock directed upward) showing relations to their crypts (Cox, n).——*1. Lithophaga cumingiana* (REEVE); *1a,* longitudinal section of crypt with animal attached to its wall by byssus threads; *1b,* transverse section of crypt showing oval shape; both ×0.4.——*2. Hiatella gallicana* (LAMARCK), longitudinal sections of crypt with animal in place; *2a,* siphons withdrawn, gripping walls of crypt; *2b,* siphons extended; both ×0.3.——*3. Platyodon cancellatus* (CONRAD); *3a,* longitudinal section of mechanically bored crypt without rotation of animal; *3b,* cross section of crypt with shape like that of shell; both ×0.2.——*4. Adula californiensis* (PHILIPPI); *4a,* longitudinal section of crypt enclosing animal with extruded siphons seen from dorsal side, umbones of shell abraded by mechanical action in boring; *4b,* transverse section of crypt; both ×0.7.——*5. Pholas dactylus* LINNÉ; *5a,* longitudinal section of crypt with side view of animal attached by sucker-like foot while boring; *6b,* cross section of crypt; both ×0.3.——*6. Tridacna crocea* LAMARCK, side view of animal in cavity bored obliquely downward in coral rock, at first held in place by byssus thread, ×0.3.

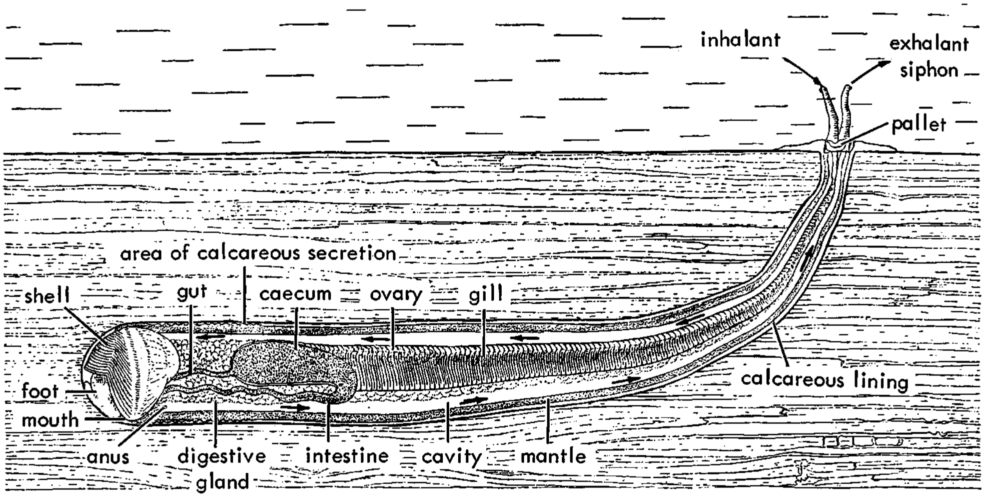

FIG. 4. Habitat of bivalves—wood-borer *Teredo,* side view of animal with posterior extremity permanently fixed to burrow entrance, boring effected by rasplike bivalve shell with wood particles broken down by enzyme in capacious caecum and waste thrown off through anus and carried away by exhalant-siphon stream, ×1 (Lane, 1961).

into coral rock. During the process the mollusk is oriented with its hinge margins facing downward. The byssus, which in this peculiar genus projects through a gap between these margins, pulls the shell against the rock and facilitates its penetration. The process stops when the opposite margins of the valves, which must remain capable of opening, are almost flush with the surface of the rock (Fig. 3,6).

The wood-boring Teredinidae ("shipworms") are the most highly specialized boring bivalves (Fig. 4). As in the case of *Pholas,* the anterior end of the valves of the shell has a rasplike surface and penetration is mechanical. The wood particles are, however, ingested by the animal, which is not, therefore, completely dependent on the outside water for food. The valves are much reduced in size and cover only a small part of the animal, which is wormlike and extends along the whole length of the boring. The latter, which is lined with calcium carbonate, and therefore the mollusk itself, may be of very considerable length (up to 1.2 m. in some species of the genus *Bankia*). Its opening can be closed by two calcareous paddle-shaped structures known as **pallets,** so that (unlike the rock-borers) the animal can seal itself off from the exterior.

Bivalves form an important element of the benthonic epifauna. Some rely on the weight or shape of their shell to maintain their position on the sea floor. Others, which live on rocky or coarse bottoms, attach themselves to stationary objects by one of two methods. The first is by means of their **byssus,** and the second is by **cementation** of one of the valves of the shell. The byssus, well developed, for example, in *Mytilus, Arca,* and *Pinctada* (pearl oyster), is typically a bunch of threads, secreted by glands at the posterior end of the foot and projecting through a gap between the valve margins (Fig. 5). In *Anomia,* however, it consists of a rigid calcareous plug which passes through a foramen in one of the valves. The Ostreidae, Spondylidae, and Chamidae are examples of living families in which attachment of one valve to some solid object is effected by a calcareous cement secreted by the equivalent of the byssal glands. The rudists of the Cretaceous Period are the most notable example of this mode of life provided by the fossil record.

The genus *Pinna* combines byssal attachment with a burrowing mode of life. The shell is conical or fan-shaped and lives half or more buried in the muddy sea floor with its pointed (anterior) end lowermost and its broader end projecting into the relatively clear water above. The byssus, by which *Pinna* is attached to buried stones or other objects, emerges from between the valve margins close to the anterior end of the shell (Fig. 6). Some species of the Limidae and of the genus *Musculus* (family Mytilidae) construct quite elaborate nests from byssus threads. When the mollusk has surrounded itself by one of these structures, which usually occupy holes in rocks or similar positions, its vulnerable trailing tentacles are protected from predators.

The most active living Bivalvia belong to the family Pectinidae. Many species of this group can swim near the sea bottom, propelled by sudden expulsions of water from the mantle cavity, produced by clapping their valves together. When not active in this manner the mollusk rests on one valve on the sea floor (Fig. 7). Some Limidae can also swim in a similar manner. In this family the valve margins remain more or less vertical during the process, whereas their position remains nearly horizontal in the Pectinidae.

No living Bivalvia are pelagic except in the larval state. It has, however, been suggested that *Bositra*, a Jurassic genus which until recently was not considered distinct from *Posidonia* of the Carboniferous, led a pelagic existence. The evidence for this conclusion has been summarized by JEFFERIES & MINTON *(78)*, who postulate that the means of propulsion was similar to that employed in the Pectinidae.

Bivalves are most abundant in the sublittoral zone, but some forms have been dredged from very deep sea floors. The deepest record for a member of the class is of an unnamed species of *Axinulus* (family Thyasiridae) from 10,415-10,687 m. in the Tonga Trench *(185)*. CLARKE *(22,23)* has listed three species as occurring off Bermuda at a depth of 5,199 m. (2,843 fathoms) and six species as having been found in the South Atlantic at depths exceeding 4,572 m. (2,500 fathoms). The Nuculacea are well represented in the abyssal bivalve fauna, and other forms include certain thin-shelled Pectinacea (e.g., *Pseudamussium, Propeamussium*) and the septibranch genera *Poromya* and *Cuspidaria*.

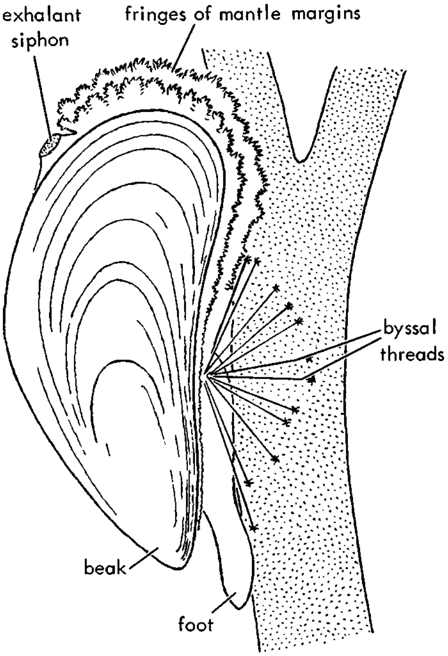

FIG. 5. Habitat of bivalves—*Mytilus edulis* LINNÉ, Rec., cosmop, side view of animal with extruded foot attached by byssus threads to branching object, fringes of mantle and exhalant siphon seen at posterior extremity, ×1 (Cox, n).

From a purely marine environment, bivalves pass into less saline waters of landlocked seas such as the Baltic, parts of the Caspian, and into estuaries. Some marine forms (e.g., *Mytilus, Cardium, Macoma*) are notably tolerant of brackish-water conditions, and other genera exist only in such environments. Bivalves confined to fresh water include the Unionacea and the family Etheriidae, in which one valve of the oyster-like shell is cemented to stones. The genus *Dreissena,* while probably unrelated to the marine mussel *Mytilus,* resembles it both in shape and in its byssal attachment.

The great majority of Bivalvia have been divided, according to their feeding habits, into suspension-feeders and deposit-feeders. Those of the first group feed on phytoplankton, relying for their supply on the inhalant current in which large numbers of microscopic protists (chiefly diatoms and dinoflag-

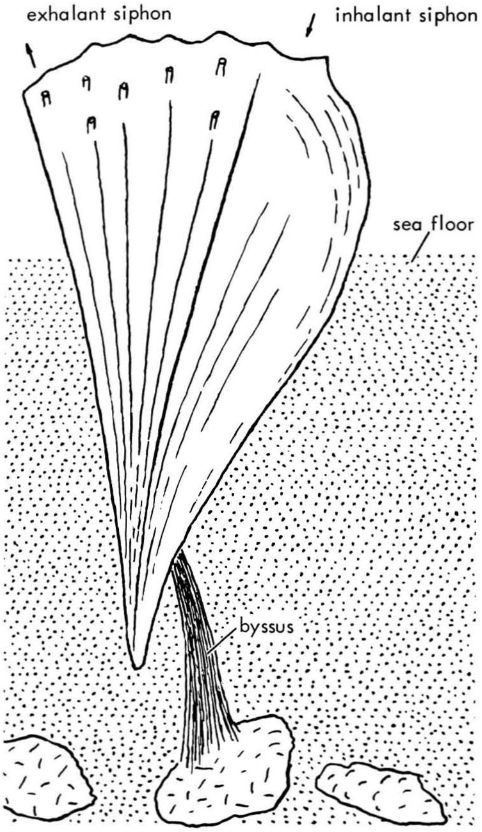

FIG. 6. Habitat of bivalves—*Pinna* sp. in living position partly buried in sea bottom with pointed anterior end lowermost, attached by byssus to stones or other objects in sediment, ×0.5 (Cox, n).

ellates) are suspended. These are strained off by the ctenidia of the mollusk and conveyed to the mouth by a process to be described in a later section (p. *N*16). Deposit-feeders live on organic debris and bottom-living diatoms contained in the mud or sand of the sea floor into which they burrow. The organ used to collect the food is usually the inhalant siphon. In most such forms this is long and slender and not attached to the exhalant siphon, and its tip ranges over the surface of the sediment in search of food. In the Nuculacea, however, the collection of food-bearing sediment is the function of the two palp proboscides, appendages of the labial palps. Only one small group of Bivalvia, the septibranchs (Poromyacea), has acquired a carnivorous habit. The branchial apparatus is here converted into a mechanism for trapping small

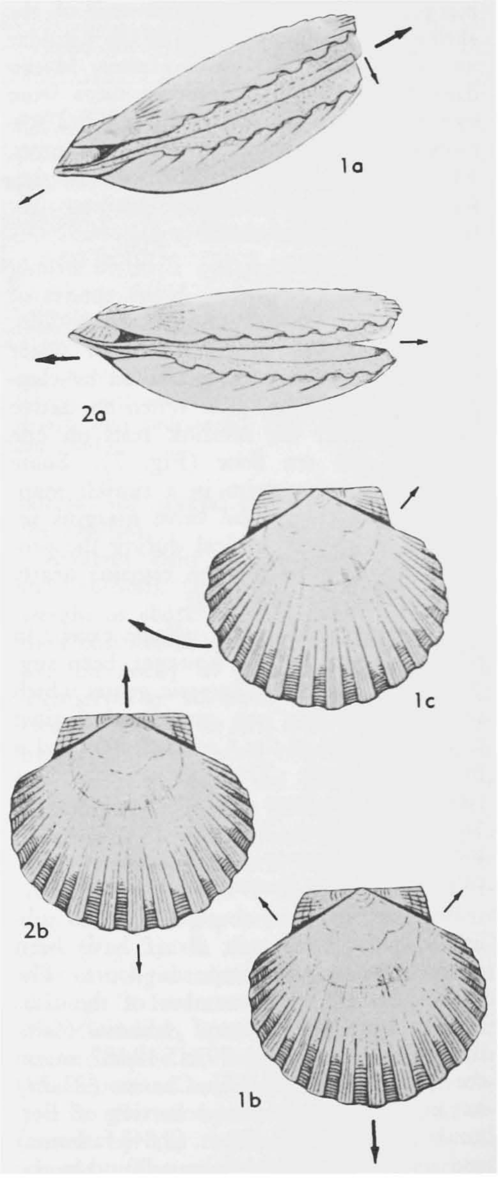

FIG. 7. Habitat of bivalves—free-swimming scallop *Pecten* sp., edge and lateral views showing *(1a-c)* forward swimming and *(2a,b)* "escape" movement, direction of movement indicated by larger arrows and that of propelling water jets by smaller arrows, ×0.25 *(142)*.

worms and crustaceans drawn into the mantle cavity.

Reference has already been made to the ingestion of wood particles by the shipworms (Teredinidae). Some small bivalves of the superfamilies Cyamiacea and Erycinacea are commensal with echinoderms, crustaceans, and other invertebrates, while *Entovalva* is parasitic in the esophagus of holothuroids. *Vulsella* lives commensally in sponges.

## DURATION OF LIFE

Direct observations on the duration of life in Bivalvia in their natural habitats obviously present considerable difficulty, and much of the available information on longevity in this group, summarized by COMFORT (1957), is based on the counting of growth rings or rugae and the assumption that these are annual. As might be expected, some of the smaller bivalves are the shortest-lived. A life span of less than one year is reported for one species of *Sphaerium* and of less than two years for a second species of this genus. The duration of life of marine bivalves varies greatly. A few examples are as follows: *Tellina tenuis* DA COSTA, 5 years; *Mya arenaria* LINNÉ, <8 years; *Mytilus edulis* LINNÉ, 8 to 10 years; *Ostrea edulis* LINNÉ, >12 years; *Cardium (Cerastoderma) edule* LINNÉ, 14 years; *Pecten maximus* (LINNÉ), 22 years; *Mercenaria mercenaria* (LINNÉ), 25 to 40 years.

No reliable observations seem to have been made on the life span of the largest living bivalve, the "giant clam" *Tridacna gigas* (LINNÉ), statements that this species can live to an age of 100, 200, or even 300 years being based on conjecture. There is good evidence, however, that some of the larger fresh-water mussels live to a considerable age. Specimens of *Margaritifera margaritifera* (LINNÉ) 100 years and 70 to 80 years in age have been mentioned in the literature.

# MORPHOLOGY OF BIVALVIA SOFT PARTS

## MANTLE AND SIPHONS

The **mantle** is the name given to the integument which surrounds the vital organs of the mollusk and which secretes and then forms the lining of the shell. It consists of two **lobes**, one corresponding to each valve, which are joined along their mid-dorsal margin. Dorsally the mantle lobes enclose the **body** or **visceral mass**, to which they are fused, but ventrally they surround a relatively large space, the **mantle cavity**. This plays a fundamental part in the life of the mollusk. Not only does it form a respiratory chamber and an enclosure through which all foods must pass to reach the mouth, but it is also the receptacle into which excreta and genital products are discharged before being expelled into the surrounding medium. Interchange of water between the mantle cavity and the exterior is maintained by two currents, an **inhalant current**, oxygenated and food-bearing, and the other an **exhalant current**, which removes the deoxygenated water and with it the waste products of metabolism and, usually, the genital products. The exhalant current invariably leaves the mantle cavity at its posterior end; the inhalant current enters posteriorly in the great majority of bivalves, but anteriorly and to some extent ventrally in some forms (Fig. 8). An extensile muscular organ, the **foot**, projects from the body of the mollusk into the mantle cavity along the median plane in an anteroventral direction, and can be protruded beyond the margins of the shell. This structure is discussed later (p. *N*14).

The margins of the mantle have three folds (Fig. 9), each with a definite function. The outer fold secretes the **outer calcareous layer** of the shell and the **periostracum.** The middle fold usually bears tentacles or other sensory organs. The inner fold contains radial muscles (**pallial muscles**) which are attached to the interior of the shell along a well-defined line (**pallial line**), more or less parallel to the margin. They control the flow of water into and out of the mantle cavity.

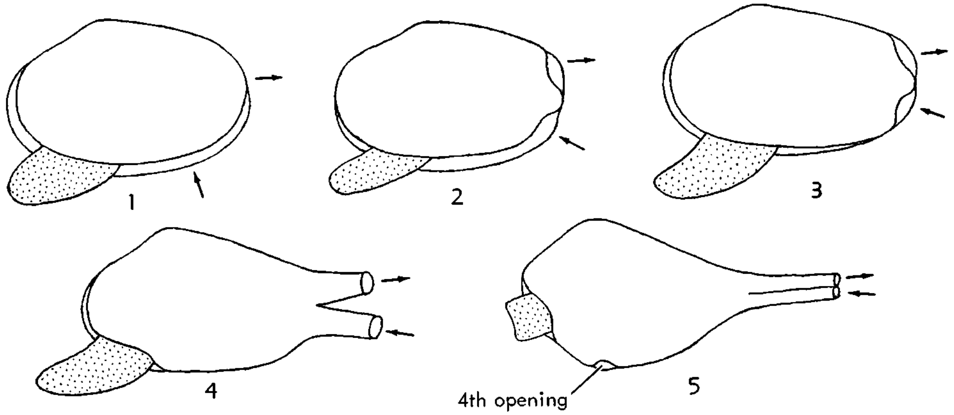

FIG. 8. Bivalve mantle and siphons—diagrams showing degrees of closure of mantle margins, foot (stippled) protruding anteroventrally and shell supposedly removed with mantle margins represented as confluent where fused together (arrows indicate direction of inhalant and exhalant currents) (Cox from Hescheler).——*1*. Margins completely open, unfused.——*2*. Margins fused only at single posterior place between exhalant and main openings.——*3*. Margins fused only at two posterior points so as to define exhalant and inhalant openings and separate these from main opening.——*4*. Margins fused except at openings for siphons and at anterior pedal opening.——*5*. Margins fused all around except for openings indicated in *4* and an additional opening of uncertain function.

In some bivalves the mantle cavity is completely open along its anterior, ventral, and posterior margins, although the inhalant and exhalant streams are localized. Such forms include the Nuculidae, Glycymerididae, Anomiidae, Arcidae, Trigoniidae, Pectinidae, Spondylidae, Plicatulidae, Limidae and Dimyidae, together with certain species of *Crassatella*. The Pteriidae and related families, together with the Pinnidae and the Ostreidae, may be considered to belong to the same group, as there is no direct fusion of the mantle margins, although in each lobe the margin is joined to the adjacent gill demibranch.

In most members of the Bivalvia the mantle-lobe margins are fused along some part or parts of their length, in varying degrees of intimacy *(195)*. Fusion may affect the inner of the three folds only, both inner and middle folds, or all three folds, and in the case of the middle and outer folds the inner surface only, or both surfaces, may be involved. In each case, moreover, attachment may be by ciliary junctions only, by adherence between the cuticular boundaries of epithelial cells, or by actual union of the tissues. Without entering into details regarding the intimacy of fusion, we may review the remaining bivalves according to the positions where fusion occurs.

In some forms the lobe margins are fused at a single place at the posterior end of the mantle cavity, a relatively small opening, through which the exhalant current passes, being thus separated from the main opening, through parts of which the foot can be extruded and the inhalant current can pass. Bivalves in which this condition exists include Mytilidae, Carditidae, Astartidae, most Lucinidae, and Crassatellidae, some Unionidae, and the genus *Pisidium*. In *Solemya* a more extended line of fusion separates the two openings, reaching halfway along the ventral margin. In some species with a single place of fusion the part of the mantle ending in the exhalant opening can be extended beyond the margin of the shell to form a tubelike projection (**siphon**), although a relatively short one. The entry of the inhalant current tends to be localized close to the point of fusion, indicating an approach to the condition found in the next group.

In another group of Bivalvia the mantle margins are fused in two places, leaving two more or less contiguous posterior openings, the upper (more dorsal) one for the exhalant current, and the lower for the inhalant current, together with a third opening for the foot. The marginal region of the mantle is usually extensible at the two posterior openings to form siphons of varying length. The pedal opening occupies the whole length of the ventral and anterior margins in most bivalves belonging to this group (e.g., *Malletia, Yoldia,* most *Nuculana,* many Lucinidae, most Corbiculidae, Mutelidae, Donacidae, Psammobiidae, Tellinidae, Scrobiculariidae, Veneridae, Cardiidae, Mactridae, Mesodesmatidae, Poromyidae, Cuspidariidae, and some other forms). It is somewhat reduced, by further fusion of the ventral margins in the Chamidae and Tridacnidae and becomes a small anterior orifice in *Modiolarca, Dreissena,* the Pholadidae, Teredinidae, Verticordiidae, Lyonsiidae, and a few other forms.

Finally, in a few bivalves there are three places of fusion of the lobe margins, leaving four openings. The fourth opening lies between the pedal and inhalant ones and is usually small. Its function is uncertain. Forms with four mantle openings include the Pholadomyidae and Clavagellidae, *Solen, Lutraria, Panopea, Thracia, Myochama,* and *Chamostrea.*

The siphons, which are contractile, can be withdrawn partly or wholly between the two valves of the shell by means of **siphonal retractor muscles,** which are local modifications of the pallial muscles. To provide space for the withdrawal of the siphons the line of insertion of these muscles recedes inward in many forms to give rise to an embayment in the pallial line, known as the **pallial sinus** (Fig. 10). The length of the siphons varies considerably, being greatest in the more deeply burrowing forms. They are separated along their whole length in the Donacidae, Psammobiidae, Tellinidae, Scrobiculariidae, Mesodesmatidae, and some other forms, all of which are deposit-feeders. In other groups (e.g., Mactridae, Pholadidae, Clavagellidae, many Laternulidae, *Solen, Lutraria,* and some Veneracea) they are fused along their entire length, forming a single tubelike projection from the shell. In a few forms, including *Petricola* and *Teredo,* they are united at their base but free and divergent distally. When united and not completely retractable into the shell the siphons may be protected by a special coating of epidermis. The degree of intimacy of fusion of the margins of the mantle lobes where these are extended to form the siphons varies in the same way as elsewhere, as described above. Details have been given by Yonge *(195).*

The foregoing account applies to the great majority of siphonate bivalves, in which two siphons occur, both posterior in position. In a few genera (e.g., *Kellia* and *Lasaea,* both belonging to the Erycinidae), however, the inhalant siphon is anterior and the exhalant one posterior; and in some

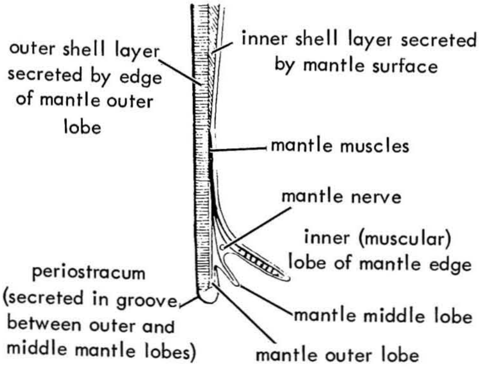

Fig. 9. Bivalve mantle and siphons—section of mantle edge and associated shell and periostracal layers (Yonge, 1953).

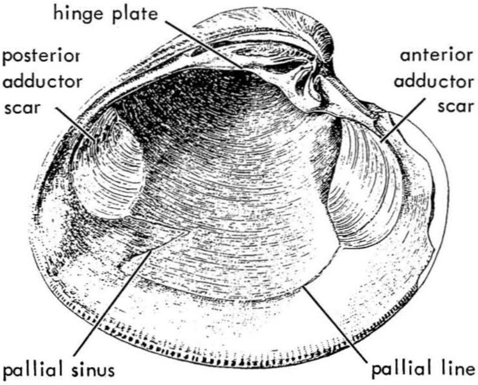

Fig. 10. Bivalve mantle and siphons—interior of shell of *Venus campichiensis mortoni* (Conrad) from Miocene of Maryland showing attachment impression of mantle (pallial line and sinus), ×1 (Dall, 1904).

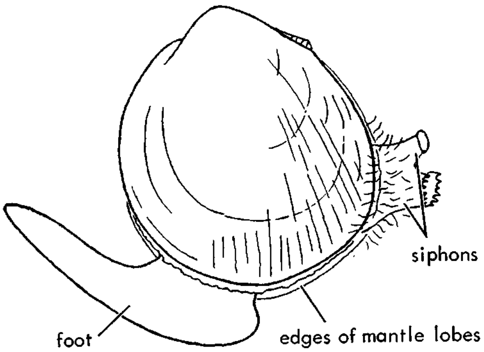

FIG. 11. Bivalve foot and siphons—*Cardium (Laevicardium) crassum* GMELIN, Recent, British Isles, with foot and siphons protruded, ×0.7 (Cox, mod. from Forbes & Hanley).

(e.g., Lucinidae) only one siphon, a posterior exhalant one, is present. In the Lucinidae this siphon is unique in that it is reversible, contracting into the mantle cavity by turning itself inside out.

When the mollusk is respiring and feeding, the valves of the shell are opened slightly and the mantle edge with its tentacles is protruded slightly beyond the margins. In a number of genera belonging to the superfamily Leptonacea, in all of which the shell is quite small, the mantle is reflected to a varying extent over its exterior, until in such forms as *Chlamydoconcha, Entovalva, Ephippodonta,* and *Scioberetia* the shell is completely internal.

Dorsally, the two mantle lobes are united along a line of primary continuity, the **mantle isthmus**, and from either end of this their margins may be joined for some distance by secondary fusion in one of the ways already described. Thin projections of the mantle extend between the hinge teeth of the two valves, which thus do not fit together so very closely, as is commonly supposed.

## FOOT AND BYSSUS

The **foot**, which in the typical bivalve is an anteroventrally directed extensile muscular process projecting from the body of the mollusk into the mantle cavity, is primarily an organ for burrowing and locomotion, although it may have secondary uses (Fig. 11). It can be extruded beyond the valve margins when the animal is active and is of various shapes, depending to some extent

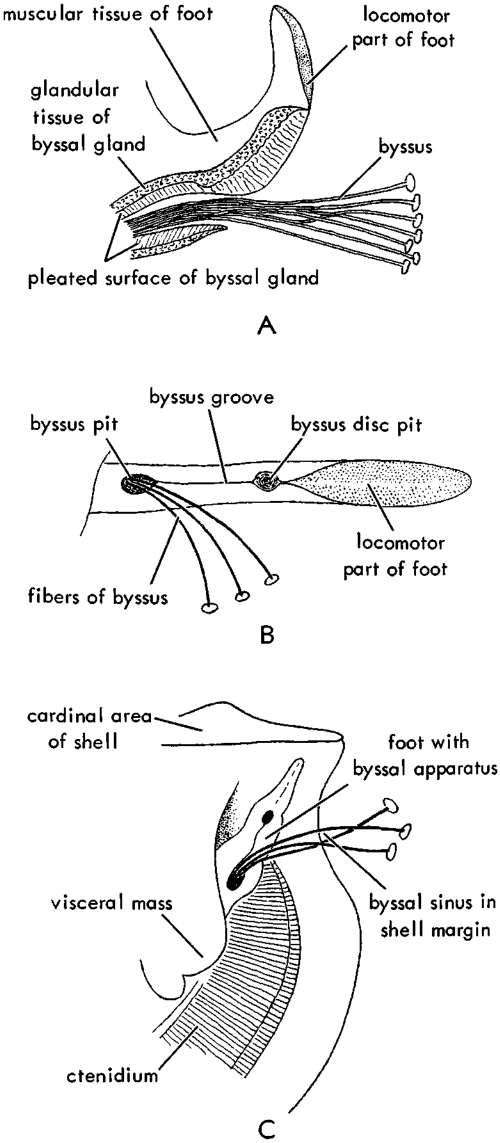

FIG. 12. Foot and byssus of Ceylon pearl oyster *Pinctada vulgaris* (SCHUMACHER), Recent, south Asia, enl. (Cox from Herdman, 1904).——*A.* Sagittal section.——*B.* Ventral surface of foot attached by three byssal fibers, foot elongated for making fourth byssal fiber.——*C.* Anterior part of animal, foot resting in mantle cavity and three byssal fibers projecting through byssal sinus of shell margins.

on the mode of life of the bivalve. The **byssus**, an important structure associated with the foot and secreted by the byssal gland or glands, is typically a bundle of hairlike threads by means of which the mollusk can attach itself to other objects, such as rocks and seaweed (Fig. 12). Attachment may be throughout life (as in genera such as *Mytilus* and *Pteria*), or only during a particular phase in the animal's existence. In many bivalves the byssus is absent or merely vestigial in the adult stage, but is present (if only as a single thread) in the early postlarval ontogeny of a great many forms and has a definite function. In *Mya,* for example, it enables the young animal to anchor itself temporarily to sand grains and other objects, pending the development of structures essential to its adult burrowing mode of life (Fig. 13). YONGE *(196),* therefore, has suggested that the byssus is essentially an early postlarval structure retained, by neoteny, in those adult bivalves in which it is present. Most byssiferous species can cast off the byssal threads and replace them by new ones, and some, including *Mytilus,* can move over a vertical surface by planting a succession of such threads and hauling themselves along, leaving a trail of disused threads attached to the surface over which they are moving. Among bivalves in which the adult has a well-developed byssus the foot has usually lost its function as an organ of locomotion, although there are exceptions. Such forms belong largely to the Pteriomorphia, but also include representatives of other groups widely scattered taxonomically. Their foot is commonly a slender, finger-like or tonguelike structure, possibly with a ventral keel.

The structures associated with formation of the byssus consist (where fully developed) of the **byssal pit**, a cavity at the posterior end of the foot; the **byssal gland** or **glands**, situated around the byssal pit and along the foot; and the **byssal groove**, which starts from the byssal pit, runs along the underside of the foot, and ends in a small depression (byssus disc-pit) forming a sucker. The byssal glands secrete a sticky fluid which accumulates in the byssal pit and along the byssal groove, and solidifies immediately on contact with water to form each byssal thread. The end of the foot plants the distal end of the thread on the object of attachment, while the proximal end remains attached within the byssal pit. Chemically, the material of the typical byssus consists of a protein of the albuminoid group, and its composition is similar to that of the organic material present in the molluscan shell.

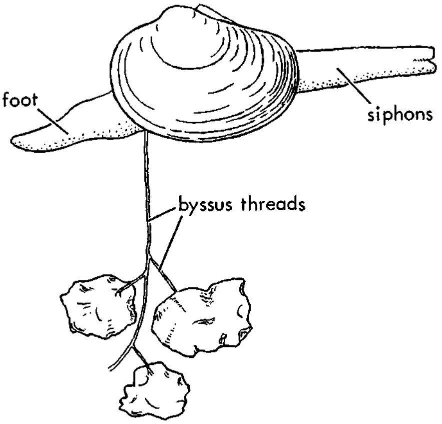

FIG. 13. Bivalve foot and byssus—*Mya arenaria* LINNÉ, Recent, juvenile specimen (length, 2.3 mm.) showing byssus attached to sand grains prior to adoption of burrowing existence (Cox, mod. from Yonge).

Byssally attached Pteriomorphia include most Mytilacea, Pteriacea, Anomiacea, the Pinnacea, and many Pectinacea and Limacea. In the Anomiacea the byssus, where present, is a rigid calcified structure, projecting through a foramen in the lower (right) valve, but in the Eocene genus *Carolia* it became obsolete during growth and the foramen gradually sealed up; in *Placuna* (Upper Tertiary-Recent) the calcified byssus is present only in very early stages of ontogeny. The Pinnacea differ from most byssiferous forms in their burrowing mode of life. The animal lives almost completely buried in the muddy substrate, with the pointed anterior end of the shell directed downward; the well-developed byssus, consisting of numerous silklike strands, emerges from the ventral margin close to this end and is attached to buried stones. As already mentioned, the genus *Musculus* [Mytilidae] and some Limidae construct protective nests from strands of the byssus. In the Ostreacea and in Pectinacea having one valve cemented to the substrate, cementation is effected by the foot, the cementing calcium carbonate originating in the byssal gland. In the Ostreidae the foot then atrophies; it becomes merely vestigial in the Plicatulidae and Dimyidae, but remains better developed, although reduced, in adult *Spondylus* and in *Hinnites*. A byssus is absent in highly mobile members of the Pectinidae.

In the Nuculacea, the superfamily commonly thought to retain the greatest number of primitive features, the foot is a relatively large but not greatly elongated organ broadening distally (when expanded) to a flat, disclike "sole" with marginal crenulations. It has been variously regarded as a primitive structure retaining a creeping sole comparable to that of many gastropods, or as a highly specialized structure adapted for rapid burrowing in soft substrates. The former interpretation seems to be refuted by our knowledge that members of this group do not creep about on a hard sea bottom but are shallow burrowers. A small byssal gland has been observed in a number of species of the superfamily, but it is functionless in the adult stage. A massive byssus is present in those Arcacea (e.g., *Arca* itself, typified by *A. noae* LINNÉ) which grow attached to rock surfaces, but it is absent in burrowing members of the family.

In more advanced bivalve groups also retention of the byssal gland in the adult mollusk depends largely upon the mode of life. The gland is absent in adult Unionacea, Arcticacea, Lucinacea, Mactracea, Tellinacea, Solenacea, Pholadacea, Clavagellacea, and Poromyacea, all of which are burrowing or boring forms. A byssus is also absent in the Chamacea, a group in which one valve of the shell is cemented to the substrate. On the other hand, it is well developed in the mussel-like Dreissenacea, in the Tridacnacea, and in some Lyonsiidae. A small byssal gland is found in adult Trigoniacea, Crassatellacea, Corbiculacea, and Cyamiacea, and in some Carditacea, Glossacea, Leptonacea, Carditacea, Veneracea, and Myacea. Many Leptonacea show a marked tendency to attach themselves by means of a few byssal threads. Some live commensally in the burrows of other invertebrates, attaching themselves to the walls.

The foot itself is of various shapes in the groups just mentioned, hatchet-like, tongue-like or even wormlike. In some forms, such as the Cardiidae and Arcidae, it has a pronounced knee-shaped bend. A broad sole, used for burrowing and not for creeping, is developed in a number of genera, particularly in the families Veneridae and Tellinidae. In a few small forms belonging to the Leptonacea, on the other hand, a broad, flat-soled foot is actually used for creeping over solid surfaces.

## CTENIDIA AND LABIAL PALPS

The conversion of the well-developed gills or **ctenidia** from organs of respiration into an apparatus concerned largely with the collection of food in most forms is among the most characteristic features of the Bivalvia. The extension of the mantle cavity in an anteroposterior direction along the whole length of the shell has provided space for enlargement of the two ctenidia. Attached by membranes to the body of the mollusk, these lie on each side of the cavity, with their front end to the left and right of the foot, if they are not completely posterior or dorsal to the latter. They converge in a posterior direction and in many forms are connected together at their posterior end. Each ctenidium consists of a hollow, longitudinally directed **axis** and of a series of thin leaflike or lathlike hollow structures (**filaments**) attached to it, usually on both sides. The structures on each side of the axis constitute a **demibranch**, and in many bivalves the two demibranchs are more or less symmetrical with regard to the axis. The demibranchs may be described as **inner** and **outer** according to their position, closer to the sagittal plane of the mollusk or to the mantle. The outer demibranch is absent in the Lucinidae (see Fig. 20,*J*). In most bivalves both demibranchs extend in a ventral direction from the axis, but in some forms the outer demibranch

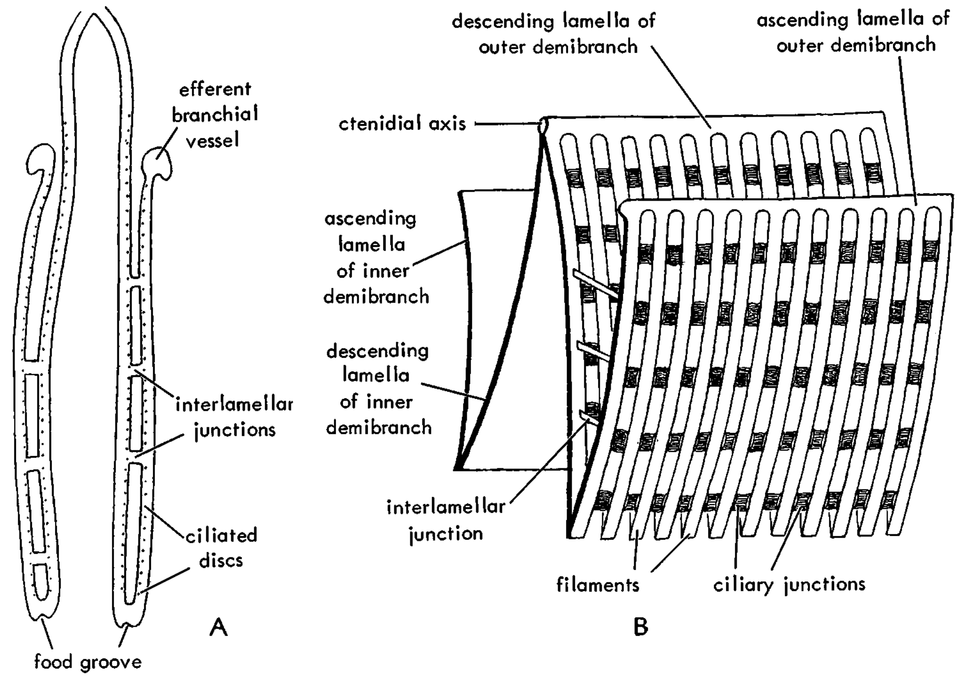

FIG. 14. Filibranch ctenidium of *Mytilus edulis* LINNÉ (Cox, n).——*A*. Side view of corresponding filaments of two demibranchs showing interlamellar junctions and positions of ciliated discs, ×40.——*B*. Part of ctenidium viewed obliquely, nearer demibranch with 12 filaments joined by ciliary junctions (not to scale and thickness of filaments not indicated, ciliary junctions far fewer than in nature).

extends either wholly or partly in a dorsal direction (Fig. 14,*A*). The structure of the ctenidia varies considerably in complexity and has served as the basis of a system of classification of the Bivalvia, associated with the name of PELSENEER, which has been widely used by students of living Mollusca.

The simplest and presumably most primitive type of ctenidium found in the Bivalvia is comparable to the bipectinate ctenidium of the Archaeogastropoda, the demibranchs being symmetrical or slightly asymmetrical and formed of simple, broad, leaflike filaments. Adjacent filaments are unconnected or have at the most only loose and sparse ciliary attachments. Bivalves with this type of ctenidium, consisting of the superfamilies Nuculacea and Solemyacea among Recent forms, have been grouped together under the name Protobranchia.

In most other bivalves the filaments constituting the demibranchs are narrow, elongated, lathlike structures, and, except in a few forms (Fig. 14,*B*), each is bent back upon itself so as to have a reflected (usually ascending) limb, as well as the proximal (usually descending) limb which is attached to the axis. Each series of filament limbs forms a sheet or **lamella**, so that a typical ctenidium consists of four lamellae, a descending and ascending one in each demibranch. The lamellae are flat in some forms and thrown into folds or **plicae** in others. Adjacent filaments in a lamella may be attached in two ways. Each filament may bear on its sides small brushlike patches of cilia (**ciliated discs**) which merely interlock with those of the next filament and can be separated from them without much difficulty; or else adjacent filaments may be connected at regular intervals by strands of cellular organic tissue, so that they cannot be separated. The two lamellae of a demibranch may be joined at intervals back to back in a similar manner. In many forms such junctions are so exten-

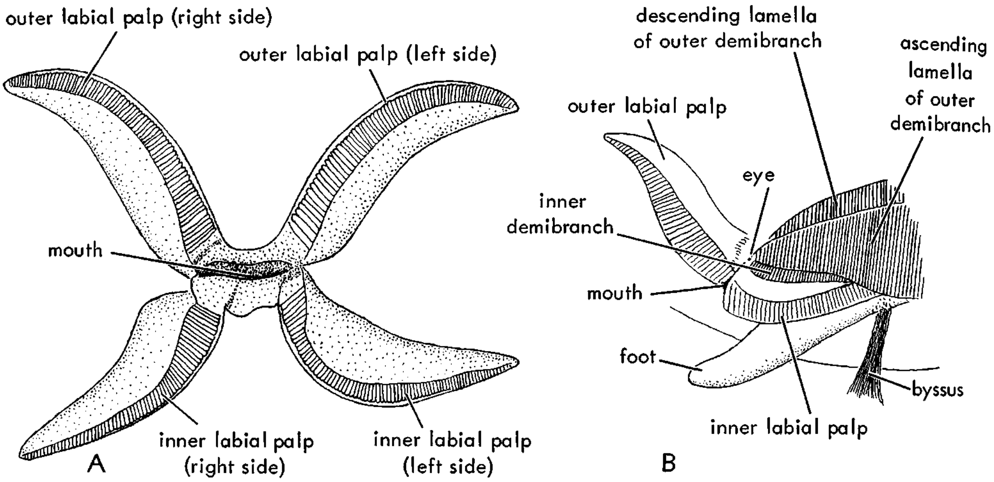

FIG. 15. Labial palps of *Mytilus edulis* LINNÉ, enl. (Cox, n).——*A*. Anterior view of mouth and lips showing their relation to palps, outer ones (normally contiguous to lower) reflected upward and all four palps turned into transverse plane.——*B*. Left-side view of palps, outer one (cut at base and turned away) normally contiguous to inner palp with anterior end of ctenidium between them.

sive that the faces of the demibranchs are interrupted only by series of transversely aligned pores (**water pores** or **ostia**), while the space between the two lamellae of the same demibranch is reduced to a series of transverse tubular cavities.

Bivalves with ciliary interfilamental junctions constitute the group Filibranchia of PELSENEER, and form the superfamilies Arcacea, Trigoniacea, Anomiacea, Mytilacea, Pteriacea, and Pectinacea. Interlamellar junctions are absent in the first three of these groups but present in the last three. Bivalves with interfilamental and interlamellar junctions formed of organic tissue constitute the Eulamellibranchia of the same author, and comprise all other living superfamilies except those already mentioned as forming the Protobranchia, and the Poromyacea, referred to below. It is to be noted that in this classification the Ostreacea, Limacea, and Pinnacea are included in the Eulamellibranchia and thus separated taxonomically from superfamilies of the Filibranchia, to which all other evidence suggests they are most closely related.

Ctenidia are absent in one superfamily, the Poromyacea, which constitute the Septibranchia of PELSENEER's classification. They are replaced by a horizonal longitudinal muscular septum dividing the mantle cavity into dorsal and ventral chambers, which communiciate only by narrow slits in the septum. This is the superfamily already mentioned as consisting of carnivorous feeders.

The **labial palps** are structures in the mantle cavity which belong to the same physiological system as the ctenidia (Fig. 15). They consist of two pairs (right and left) of usually acutely triangular, leaflike, contiguous flaps or **lamellae** forming prolongations of the upper and lower lips of the mouth but extending posteriorly. When they occupy their normal positions the lamellae belonging to the upper lip fold down so that their joined proximal ends are in front of the mouth, and in each pair (right or left) the one belonging to the upper lip lies on the outer side of the one belonging to the lower lip; for this reason they are termed **outer** and **inner lamellae,** respectively.

The labial palps of the Nuculacea are remarkable both for their large size and for the presence of **palp proboscides**, extensile tentacle-like processes attached to the posterodorsal corner of the outer of each pair of lamellae. When the animal is feeding, the proboscides are extruded between the

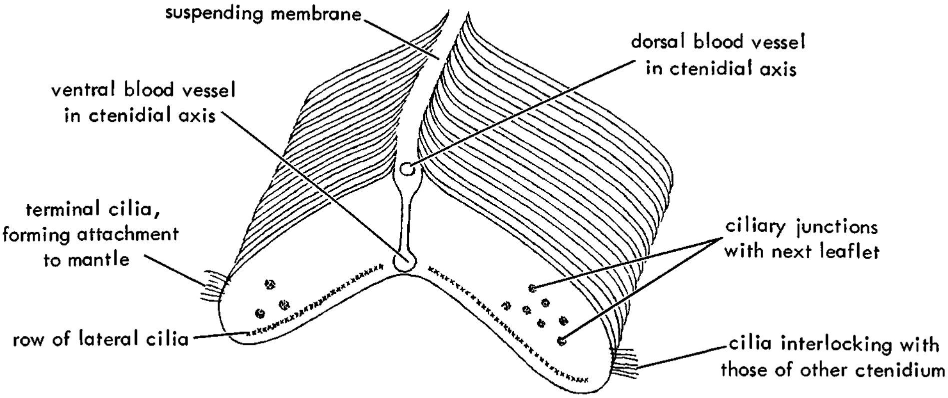

FIG. 16. Protobranchiate ctenidium of *Nucula* sp., diagrammatic oblique view of region from just in front of posterior adductor muscle to well behind foot, showing ten pairs of leaflets or filaments with cilia indicated only on nearest ones (Cox, n).

opened valve margins of the shell just behind the foot and function as food collectors in much the same manner as the inhalant siphon of other deposit-feeders. The material collected is conveyed along a ciliated groove to the **palp pouch**, at the proximal end of the pair of palp lamellae; the latter then proceed to sort it by a complicated process, with the ultimate result that the part finally accepted reaches the animal's mouth.

It is only in the Nuculacea that the ctenidia function mainly as respiratory organs. Their role in suspension-feeders may now be briefly described. The surfaces of the gill lamellae bear innumerable minute cilia, the beating of which creates a complicated series of currents within the mantle cavity, details of which vary in different genera (Fig. 16). Water from the surrounding medium, oxygenated and bearing food and other particles in suspension, is drawn in through the inhalant opening or siphon. When the inhalant current has entered the mantle cavity its velocity is at first checked, with the result that heavier particles, inorganic or otherwise, sink to the ventral edge of the mantle; together with later rejected material, these are carried by movements of cilia on the mantle, to be discharged (as the result of sudden contractions of the adductor muscles) as **pseudofeces**. They are most commonly ejected

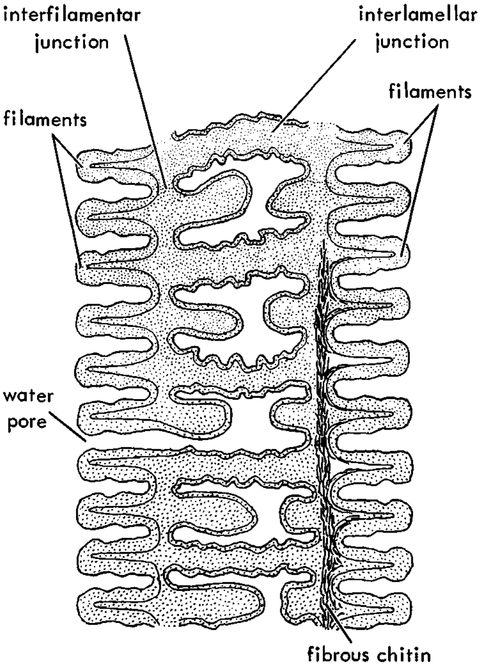

FIG. 17. "Eulamellibranch" type of gill structure in *Tellina nitida* PERRY indicated by horizontal section through outer demibranch passing through ten filaments of each lamella with illustration of interlamellar and interfilamentar junctions of organic tissue, much enl. (Cox, n, after *143*).

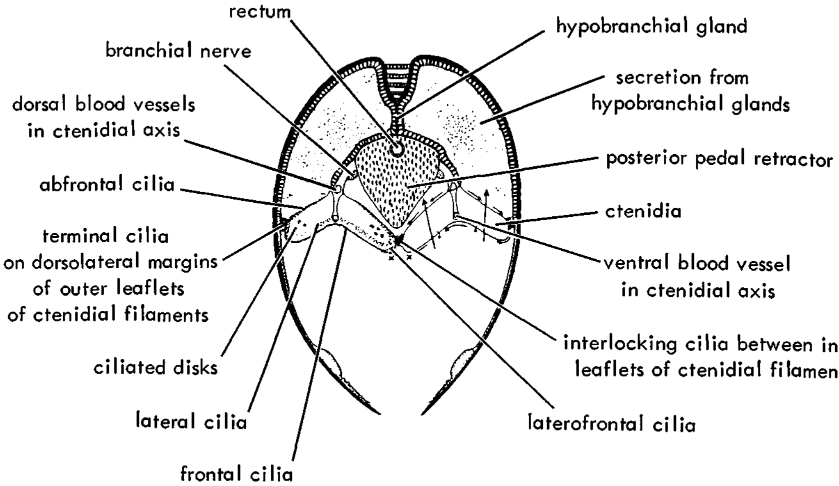

Fig. 18. Semidiagrammatic transverse section of *Nucula turgida* Leckenby & Marshall, Recent, northern Europe, showing relations of organs in region immediately in front of posterior adductor muscle, arrows on ctenidial filaments indicating direction of beat of abfrontal lateral, laterofrontal, and frontal cilia, ×20 *(189)*.

through the pedal and inhalant openings. The inhalant current then impinges on one of the ctenidia, where the remaining suspended particles or organisms are strained off, entangled in mucus, and carried by ciliary movements along the ventral parts of the ctenidium to the corresponding labial palp, between the lamellae of which the anterior end of the inner demibranch of the ctenidium commonly terminates (Fig. 17). Further sorting and partial rejection takes place between the palp lamellae, the opposed inner surfaces of which bear ciliated ridges and grooves. The accepted lighter material passes along the **food groove**, at the angular junction of the two lamellae (Fig. 18), eventually reaching the animal's mouth.

In most bivalves the inner demibranchs of the two ctenidia are joined to the foot where this lies between them and to one another posterior to it (Fig. 18-20). At the same time the outer demibranchs are joined to the mantle. In the protobranchs and many filibranchs the junctions, if present, are by interlocking cilia, but in other forms they are by vascular tissue. As a result, a space (**epibranchial chamber**) dorsal to the ctenidia is partitioned off from the re-

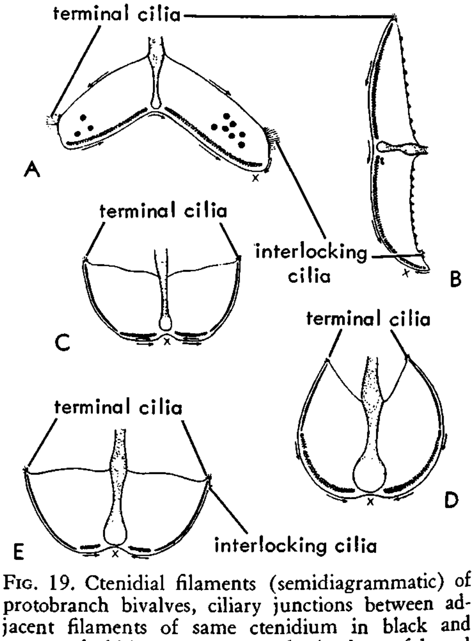

Fig. 19. Ctenidial filaments (semidiagrammatic) of protobranch bivalves, ciliary junctions between adjacent filaments of same ctenidium in black and extent of chitinous support rods (and so of lateral cilia) shown by cross hatching; arrows indicate beat of frontal cilia (and abfrontals in *Nucula*) and crosses show position of anteriorly directed ciliary currents *(189)*.——*A. Nucula*.——*B. Solenomya*.——*C. Lembulus*.——*D. Yoldia*.——*E. Malletia*.

mainder of the mantle cavity. This space is continuous with the exhalant opening or siphon at the posterior end of the cavity. The water from which suspended particles have been strained off by the ctenidia passes through the ostia, or spaces between the filaments, and then is directed dorsally into the epibranchial chamber, along which it passes posteriorly to form the exhalant current.

It would hardly be expected that traces of such soft organs as ctenidia would be preserved in fossils. There is, however, an interesting record of the discovery of specimens of *Laevitrigonia* in the Portland Beds (Upper Jurassic) of Wiltshire, England, in which the ctenidia and some other organs were thought to be preserved in a silicified state. The discovery was mentioned and the identity of the preserved structures accepted by so competent a malacologist as S. P. Woodward, as well as by some of his contemporaries; a plate illustrating the remains was, moreover, prepared for a London journal which, unfortunately, ceased publication before the plate could appear. The present writer (who possesses a copy of the plate) has made unsuccessful attempts to trace the specimens, which originally belonged to the amateur geologist Etheldreda Benett and were apparently taken to Philadelphia by Thomas Wilson, who acquired her collection. Judging by the illustrations, the identification as filibranch ctenidia of the preserved structures seems plausible.

## DIGESTIVE SYSTEM

A bivalve has no head and its **mouth** (Fig. 21,*2,3*) is a small orifice situated in a median position at the anterior end of the body, above the front of the foot. In dimyarian forms it lies just behind the anterior adductor muscle. The mouth is continued on each side by a groove (**oral groove**) along which food passes to it from the corresponding labial palp and ctenidium. Above and below the mouth and the adjacent part of each oral groove are the two **lips**, which are usually merely raised folds of the epithelium covering the body. As already seen, the labial palps are expanded continuations of these lips.

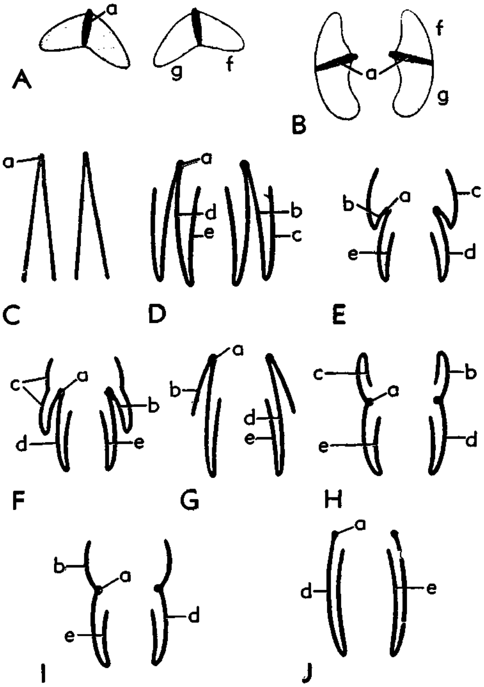

Fig. 20. Diagrammatic transverse sections of bivalve gills *(143)*.——*A. Nucula.*——*B. Solenomya.*——*C. Dimya, Anomia aculeata.*——*D.* Most Bivalvia.——*E. Donax faba.*——*F. Donax variabilis, Corbicula, Tapes, Venus, Isocardia.*——*G. Lasaea.*——*H. Tellina* (posterior part of gills).——*I. Lyonsia, Pandora, Scrobicularia.*——*J. Lucina, Montacuta.* [Explanation: *a,* axis; *b,* direct (usually descending) lamella of outer demibranch; *c,* reflected (usually ascending) lamella of outer demibranch; *d,* direct or descending lamella of inner demibranch; *e,* reflected or ascending lamella of inner demibranch; *f,* leaflets of outer demibranch; *g,* leaflets of inner demibranch.]

Jaws and a radula are absent, and a short **esophagus** leads from the mouth to the stomach, into which ducts open from the surrounding **digestive gland** or **liver**. The function of the **stomach** is to sort out and to pass on to the intestine such indigestible matter as has not already been rejected by the ctenidia and labial palps and discharged from the mantle cavity, and to carry out preliminary digestion of nutritive matter. In the latter process an important part is played by the **crystalline style**, a rodlike structure of hyaline mucroprotein which is secreted in the **style sac**, a posterior diverticu-

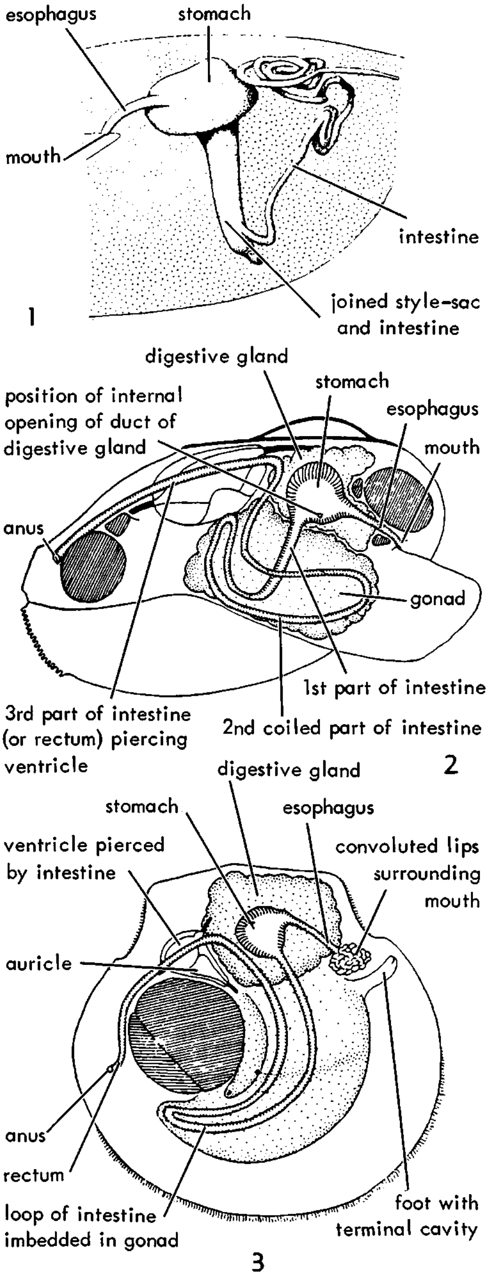

FIG. 21. Digestive systems of bivalves.——*1. Macoma balthica* (LINNÉ), ×4 *(55)*.——*2. Anodonta, ca.* ×1 (Bullough, 1958).——*3. Pecten, ca.* ×1 (Bullough, 1958).

lum of the stomach (Fig. 21,*1*). The style rotates continuously as the result of ciliary action, with its distal end projecting into the stomach and its head bearing against a hardened patch of the stomach wall (**gastric shield**). Its head is thus gradually worn away and the enzyme which it contains is stirred up with the contents of the stomach, acting as a ferment for the digestion of carbohydrates. The partially digested food then passes into the digestive gland, in the diverticula of which intracellular digestion and absorption occur. In the protobranchs, however, the crystalline style is absent, its place being taken by a rotating rod of fecal matter, the **protostyle;** the soluble products of digestion are absorbed in the stomach and intestine, and there is no intracellular absorption in the digestive gland. The style is much reduced in the septibranchs, a carnivorous group.

From the stomach the fecal matter passes posteriorly into the **intestine**, which either emerges from the style sac or forms a separate tube close to it. The intestine first takes a ventral course and then forms from one to several coils which invade the upper part of the foot; it next ascends dorsally and turns in a posterior direction, to form the **rectum,** which passes over the posterior adductor and ends on the posterodorsal side of the latter, in the **anus**. This lies near the exhalant opening or the proximal end of the exhalant siphon, and the exhalant current carries the feces away.

Before reaching the posterior adductor, the rectum passes through the **pericardial cavity** (space surrounding the heart), within which is the ventricle which in most forms is wrapped round and appears to be pierced by it. The fecal matter carried by the intestine forms a string of mucus-bound material, which is naturally more compact in deposit-feeders than in suspension-feeders. This is discharged at the anus as a series of **fecal pellets**, which may be oval, rodlike, or ribbon-like and commonly have a series of longitudinal grooves corresponding to ridges (**typhlosoles**) on the interior of the intestine. In *Nucula* the pellets are rodlike, with a varying number of grooves. In the Pectinidae they are usually rodlike and tri-

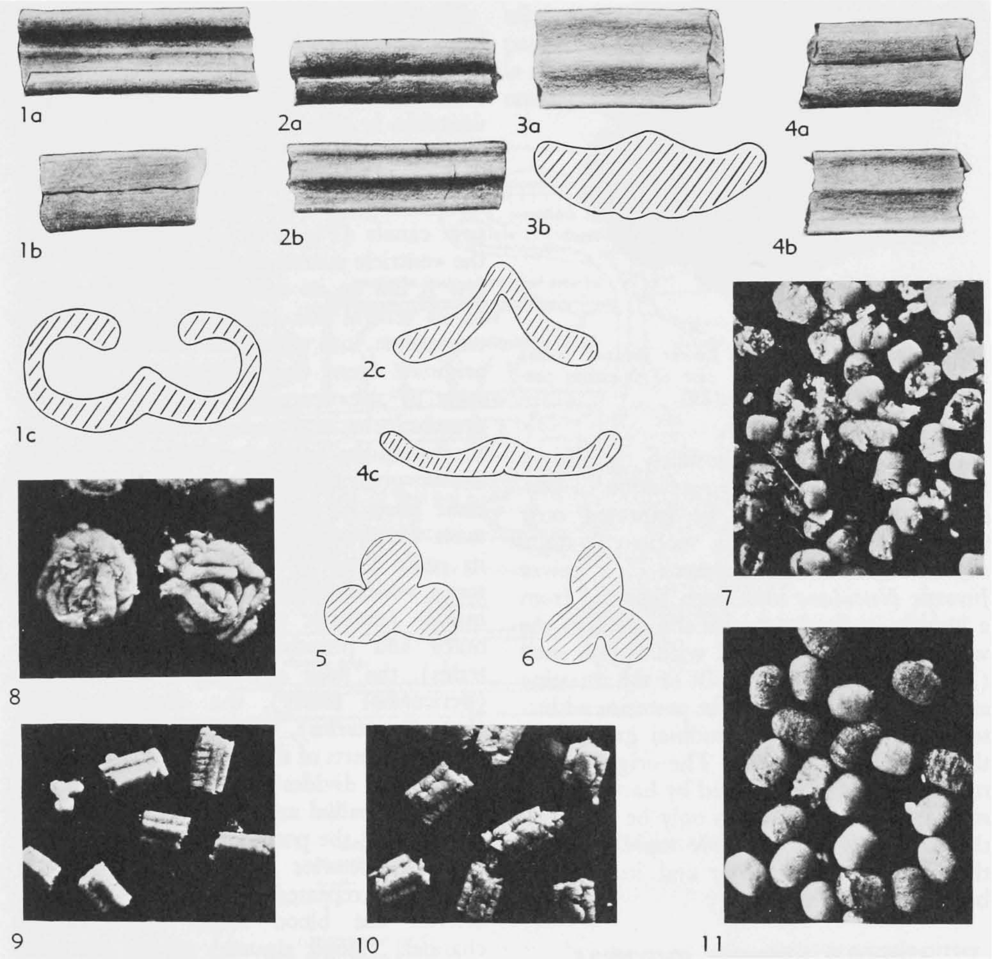

FIG. 22. Bivalve fecal pellets (various magnifications, not to scale) *(106)*.——*1. Mytilus edulis* LINNÉ; *1a,b,* side views; *1c,* cross section.——*2. Modiolus modiolus* LINNÉ; *2a,b,* side views; *2c,* cross section.——*3. Musculus marmoratus* (FORBES); *3a,* side view; *3b,* cross section.——*4. Modiolus phaseolinus* (PHILIPPI); *4a,b,* side views; *4c,* cross section.——*5. Chlamys varia* (LINNÉ), cross section.——*6. Chlamys opercularis* (LINNÉ), cross section.—— *7. Moerella donacina* (LINNÉ).——*8. Pecten maximus* (LINNÉ).——*9. Chlamys tigerina*( MÜLLER).——*10. Chlamys varia* (LINNÉ).——*11. Arcopagia crassa* (PENNANT).

angular or trefoil-shaped in cross section, although in *Pecten maximus* (LINNÉ) the rod becomes wound into a mucus-bound ball (Fig. 22,*7-11*). In the Mytilidae they are ribbon-like and fragile, with cross sections of various shapes (Fig. 22,*1-6*). In the Tellinidae they are ovate-cylindrical and smooth. The pellets from a specimen of *Mytilus edulis* LINNÉ about 8 cm. long are about 1.5 mm. wide and may be up to 5 cm. long, although usually they are broken up into shorter lengths. From a specimen of *Moerella donacina* (LINNÉ) 1.5 cm. long the pellets average 0.36 mm. in diameter and nearly four-thirds of that amount in length. The diameter of the pellets from a specimen of *Nucula* 1 cm. long is about 1.5 mm. and their length is up to about 1 mm. Each species in any community has its characteristic pellets.

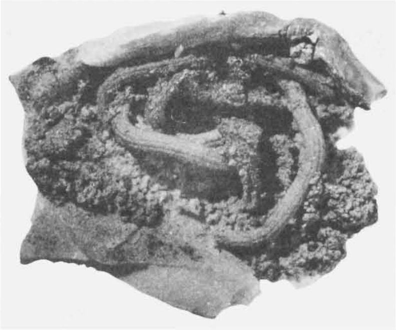

FIG. 23. *Nuculana* sp., from Lower Jurassic (Lias) of England, specimen with cast of intestine preserved, ×6 *(28)*.

Fecal pellets disintegrate fairly quickly on the sea floor, and their preservation in geological deposits would be expected only when consolidation has occurred quite rapidly. Interesting specimens of a Lower Jurassic *Nuculana* have been reported from a locality in England with the mold of the whole intestine preserved within each shell (Fig. 23). The several coils of the intestine and its termination near the posterior adductor, as well as the longitudinal grooves on the molds, are well seen. The original fecal matter has become replaced by hard ferruginous material, and it can only be supposed that this change took place rapidly, before the intestine could decay and its contents become dispersed.

## CIRCULATORY SYSTEM

The blood of the Bivalvia is a clear, transparent fluid in which are suspended colorless amoebocytes which can pervade all tissues of the mollusk, assisting in the transport and assimilation of food, in excretion, and in conveyance of calcium carbonate for shell formation. In most forms it contains no special oxygen-carrier like the haemocyanin of gastropods and cephalopods, but merely bears oxygen in solution; hemoglobin, however, is present in some species. Circulation is maintained by regular pulsations of the heart, and during its circuit the blood at first becomes deoxygenated and contaminated with waste products of metabolism, and is then reoxygenated and purified.

The heart, which lies within the fluid-filled **pericardial cavity** situated in the mid-dorsal region of the body, consists of the **ventricle** and of two **auricles** or **atria.** The ventricle is elliptical in form and extends along the whole length of the cavity, and the auricles are large sacs which lie on its left and right sides and open into it by narrow canals (Fig. 24,*2*). In most bivalves the ventricle surrounds the rectum, but in a few it lies on its dorsal side and in others on its ventral side. In the majority of forms two aortae, into which the blood is pumped, originate from the anterior and posterior ends of the ventricle respectively; in the protobranchs and many filibranchs, however, only the anterior aorta is present, but it soon gives off an artery which serves the same parts of the animal as the posterior aorta when present. The anterior aorta (or its main branch) divides into various arteries, which supply the anterior part of the mantle (**anterior pallial arteries**), the stomach and intestines (**gastro-intestinal arteries**), the floor of the pericardial cavity (**pericardial artery**), the digestive gland (**hepatic arteries**), the foot (**pedal artery**), and other parts of the animal. The posterior aorta soon divides into two large arteries (**posterior pallial arteries**) which supply the two sides of the posterior part of the mantle and the posterior adductor muscle. After traversing repeated subdivisions of these arteries the blood seeps into irregular channels (**blood sinuses**) which permeate the connective tissue of the animal. It is within these sinuses, in the epithelium of the mantle and body of the mollusk, that reoxygenation of the blood from water drawn into the mantle cavity largely takes place, although, as seen below, some part of the blood undergoes this process on its passage through the ctenidia.

The **venous system**, consisting of various veins and sinuses, collects the blood thus distributed by the arterial system, and conveys it back to the heart. Most of the blood from the stomach, digestive gland, and intestines is conveyed, by the visceral veins, to the **kidneys** (or **nephridia**), a pair of organs situated one on each side of the body. Each kidney has more or less the form of a U-shaped tube, the lower limb of the U being oriented longitudinally. This lower limb, traversed by a **longitudinal vein,** has glandular walls penetrated by narrow diverticula, and in it the waste products of metabolism are removed from the blood during its passage along the vein. The upper limb is a thin-walled **bladder** from which the excretory products are discharged into the

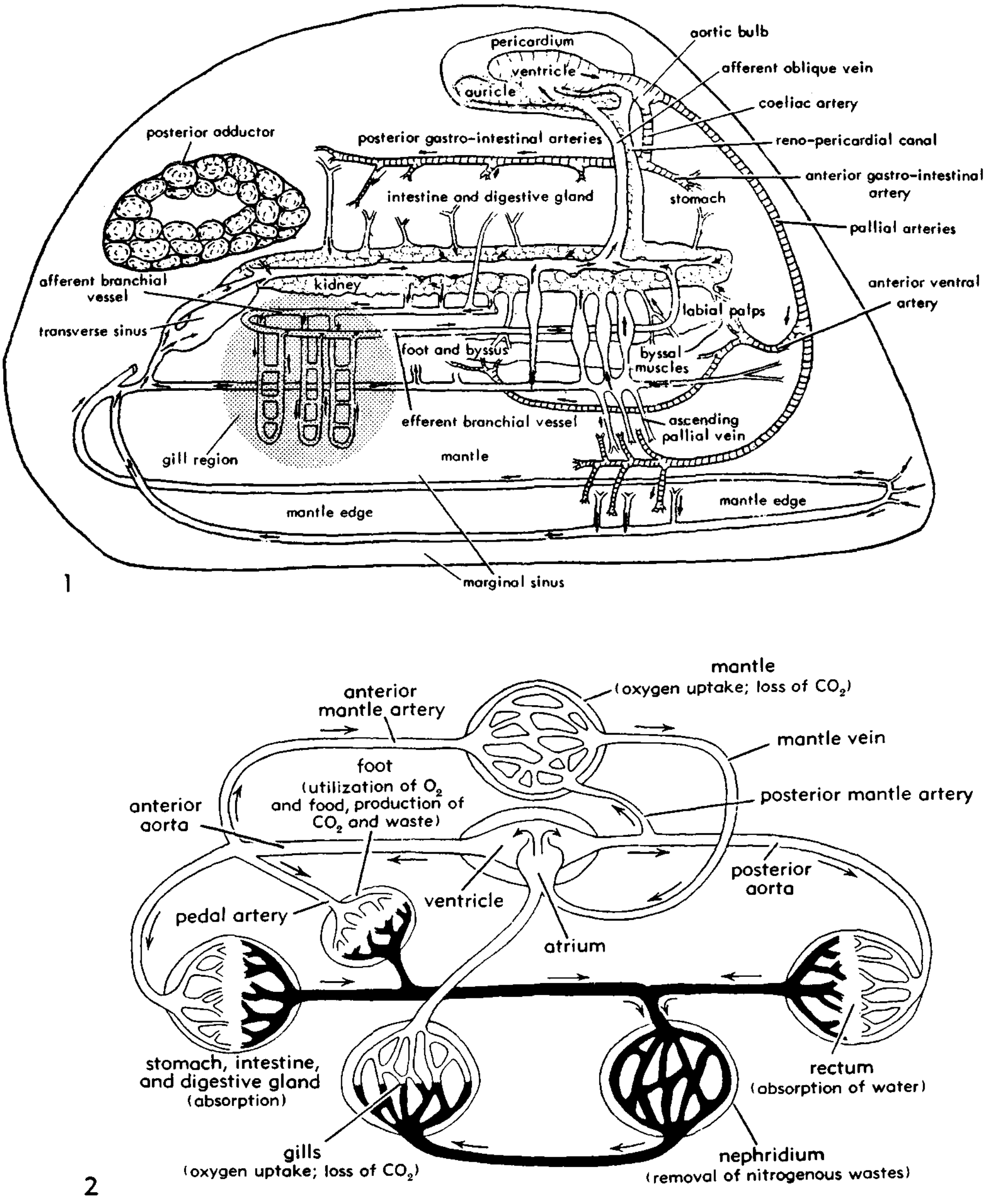

FIG. 24. Circulatory systems of bivalves shown diagrammatically.——*1. Mytilus edulis* LINNÉ, enl. arterial system hatched, venous system clear *(181)*.——*2.* Generalized bivalve, oxygenated blood clear, deoxygenated blood black *(62)*.

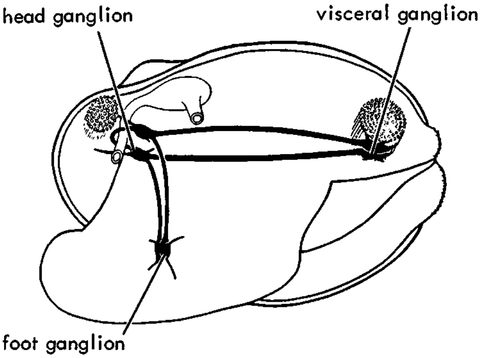

Fig. 25. Nervous system of bivalve, diagrammatic *(18)*.

mantle cavity at a point near the genital opening.

In some bivalves the venous blood from the mantle is conveyed direct to the auricles, bypassing the kidneys. In some forms, including *Mytilus,* it passes to the kidneys through ribbon-like passages known as **plicate canals,** in which further oxygenation occurs (Fig. 24,*1*). A varying proportion of the blood stream is conveyed by a vein direct from each kidney to the corresponding auricle. Part, however, completes its return journey to the heart by a longer course, as it circulates first through one of the ctenidia, passing thence to the auricle either by a direct vein or (as in *Mytilus*) via the anterior end of the kidney.

Special devices are incorporated in the circulatory system of many bivalves to allow the foot or siphons to be extended by flooding with blood.

## NERVOUS SYSTEM AND SENSE ORGANS

The nervous system in most Bivalvia consists of three pairs of **ganglia,** symmetrically arranged except in inequivalve forms (Fig. 25). The ganglia on each side (left and right) are generally widely separated and joined by long connectives. The **cerebropleural ganglia** lie in an anterior position not far behind the anterior adductor (when this is present) and close to the esophagus, above which the commissure joining them passes. They innervate the labial palps, the anterior adductor, and the anterior part of the mantle. The **pedal ganglia** lie close together in the foot and are joined by connectives to the ganglia already mentioned. The **visceral ganglia** lie below the rectum, behind the foot and close to the posterior adductor, and are also joined by connectives to the cerebropleural ganglia. They innervate the ctenidia, heart, pericardium, posterior part of the mantle, siphons, and posterior adductor. A nerve (**pallial nerve**)

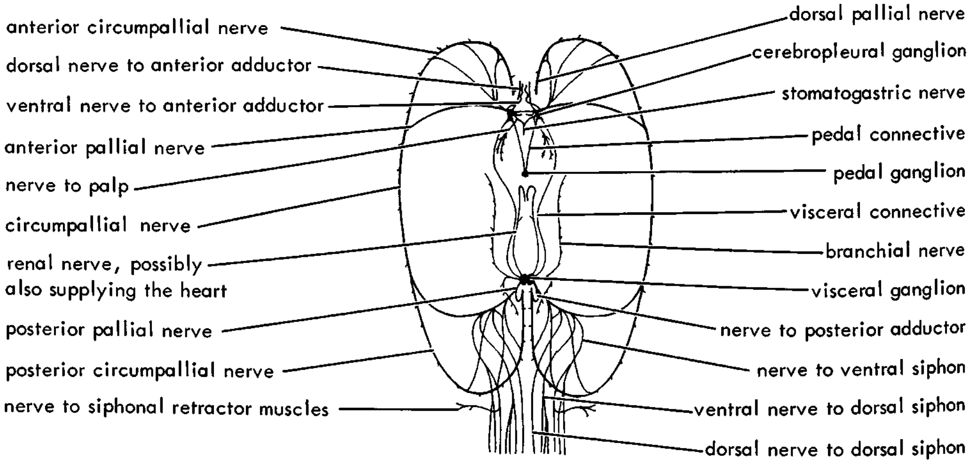

Fig. 26. Nervous system of *Psammocola (Psammobella) tellinella* (Lamarck), Recent, northern Europe *(55)*.

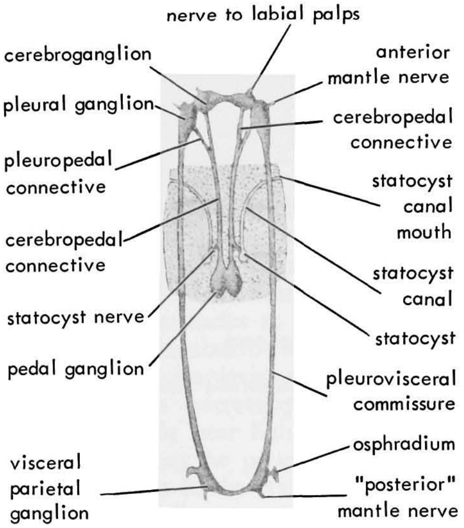

FIG. 27. Nervous system of *Nucula (69)*.

runs close to and more or less parallel to the mantle margin on each side, and is connected anteriorly with the cerebropleural ganglion and posteriorly with the visceral ganglion (Fig. 26).

Only in certain protobranchs (e.g., *Nucula*) are there distinct cerebral and pleural ganglia, the latter lying behind the former at the beginning of the visceral connectives. Other protobranchs show successive stages in the fusion of these two ganglia, and in *Yoldia* they are completely united. In the Ostreidae, in consequence of the disappearance of the foot, the pedal ganglia are absent or almost so (Fig. 27).

As there is no head, anteriorly situated sense organs have virtually disappeared in the Bivalvia, although two vestigial eyes are found in the Mytilidae and Pteriidae. In the former family these are small dark spots at the proximal end of the most anterior filament of each inner demibranch. Many bivalves possess a pair of **otocysts** in the foot, above the pedal ganglia. They are minute hollow, oval bodies which lie just below the epithelium and open into the mantle cavity by a small canal. They are thought to be organs of orientation. Two **osphradia**, pigmented sensory patches of the epithelium, are present on the wall of the mantle cavity close to the attachment of the gills. They are probably chemoreceptors, their function being to test the quality of the incurrent water.

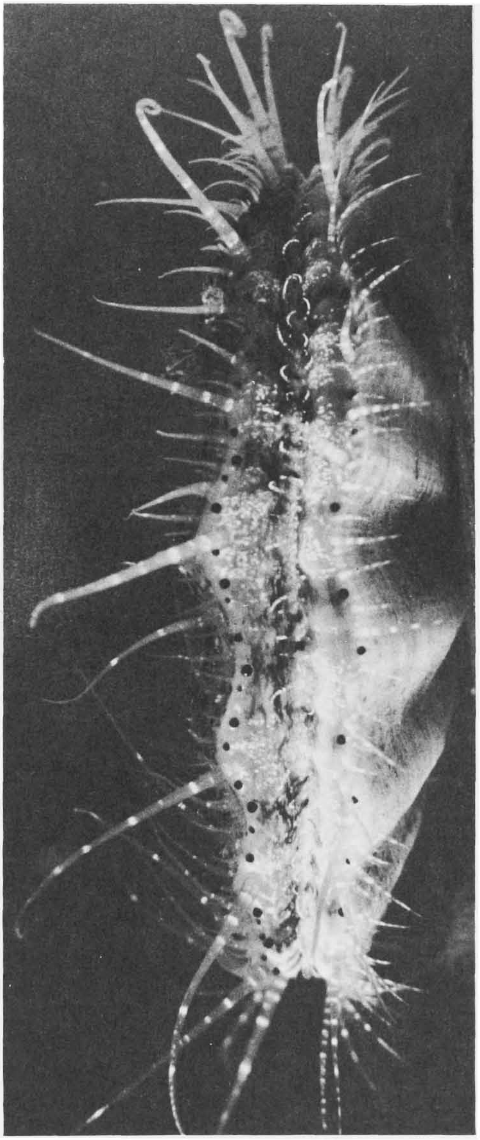

FIG. 28. Sense organs of *Chlamys (Pseudamussium) septemradiatus* (MÜLLER), Recent, northern Europe; anterior view showing tentacles and eye spots along mantle margin, ×3 (photo by W. J. Rees, published by permission).

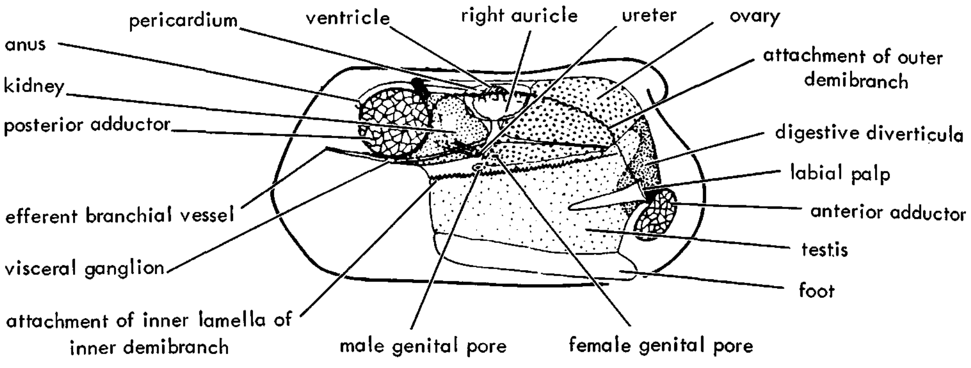

FIG. 29. Reproductive system of *Entodesma saxicola* (BAIRD), Recent, California; visceral mass viewed from right side after removal of right ctenidium, ×2 *(191)*.

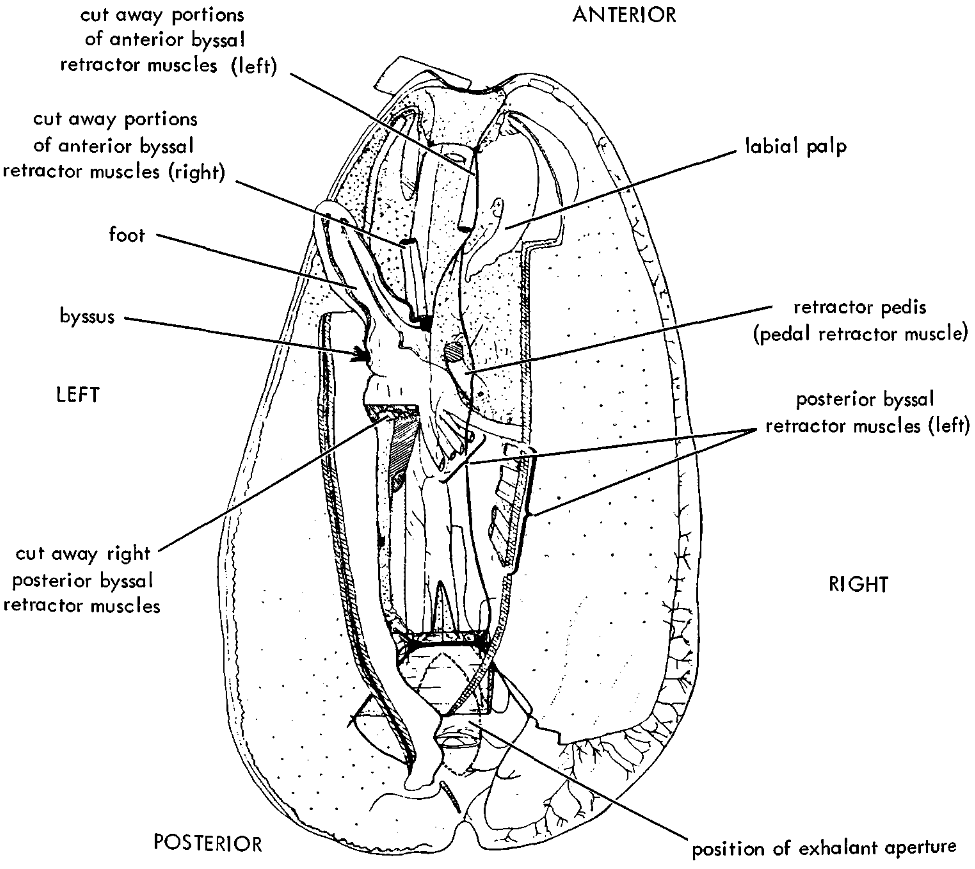

FIG. 30. Dissection showing soft parts of *Mytilus edulis* LINNÉ, ×1.3 *(181)*.

The unfused parts of the mantle edges and the extremities of the siphons are the regions where sensory organs have mainly developed. **Sensory tentacles** occur along the mantle edge in many bivalves and are highly developed in the Limidae and the swimming Pectinidae. In some genera (e.g., *Pecten, Spondylus*) the mantle edge between these tentacles bears small but quite elaborate, irregularly distributed **eyes** (Fig. 28), while in *Cardium* fairly complex eyes are carried by tentacles at the ends of the siphons. Many nonburrowing bivalves have eyes of varying complexity along the mantle edges, while in burrowing forms the siphons commonly bear light-sensitive spots. Sensory cells may be present singly or as scattered groups in the wall of the mantle cavity. In *Mytilus* a pair of abdominal sense organs lie on the ventral side of the posterior adductor muscle and may serve to detect vibrations of the sea water.

## REPRODUCTIVE ORGANS AND SEXUALITY

Reproductive organs in the Bivalvia are relatively simple. They consist of a pair of **gonads** which are usually placed symmetrically on the two sides of the visceral mass, each forming a branching system of follicles surrounding the intestine (Fig. 29). In *Mytilus* the gonads extend into the mantle cavity of both valves and in *Anomia* into the mantle cavity on the right side of the body only. According to Coe *(24)*, 96 percent of species in which sexual conditions have been investigated are unisexual (or dioecious), the remainder exhibiting various grades of ambisexuality. In some the ovary and testis are distinct glands, discharging their products through separate ducts, but in others different parts of the same gonad, or even the same parts, may function as ovary and testis, and then there is only one duct. In some of the more primitive genera the ducts open into the kidneys and the genital products reach the mantle cavity through the same outlet (**renogenital pore**) as the renal excreta. In other forms the efferent ducts lead direct to the mantle cavity, ending on the same papillae as the renal openings, or else discharging through distinct pores. The genital ducts are short and devoid of glands. Their outlets lie along the dorsal gill passage, so that the genital products are usually caught up by the exhalant stream.

In many species fertilization takes place in the surrounding water, between ova and spermatozoa which have been discharged from the mantle cavities of the parent animals. In others fertilization takes place in the mantle cavity. In many such cases one of the gametes (usually the spermatozoan) is drawn in with the inhalant current, but self-fertilization is known to occur in hermaphrodite species. The larvae are usually soon expelled from the mantle cavity, but some species incubate their young in a **brood chamber**, usually between the lamellae of the gill demibranchs.

Of the approximately 10,000 described species of living Bivalvia, about 400 are known to be ambisexual—that is, their individuals do not function solely as males or as females during their lifetime. Coe has distinguished four grades of ambisexuality, the differences between which, however, are not altogether clear-cut. They are as follows:

1) *Functional hermaphroditism.* Both ova and spermatozoa are produced simultaneously for a period by the same individual, although there may be a brief initial period of unisexuality, usually male (**protandrous hermaphroditism**).

2) *Consecutive sexuality.* In this type there is a single reversal of sex during the lifetime of the mollusk, usually from male to female.

3) *Rhythmic consecutive sexuality.* A series of alternating male and female phases occurs during life. A well-known example is that of *Ostrea edulis* Linné, in which each adult oyster passes through one male and one female phase each year. In any interbreeding population roughly one-half of the individuals start as males each season and change to females while the other half undergoes the reverse change, so that both sexual types are always present.

4) *Alternative sexuality.* In every season the sex of each adult remains unchanged, but in successive seasons changes of sex, affecting part of the population only, occur.

This type of sexuality has been observed mainly in certain oysters, among them *Ostrea virginica* Gmelin.

## MUSCULATURE

Many of the muscles in the Bivalvia are attached to the interior of the shell and leave on it a series of scars, some well impressed, others superficial and seen only in very well-preserved fossils (Fig. 30). A description of the arrangement of the shell-attached muscles will, therefore, appropriately form a link between the foregoing account of the soft parts and a

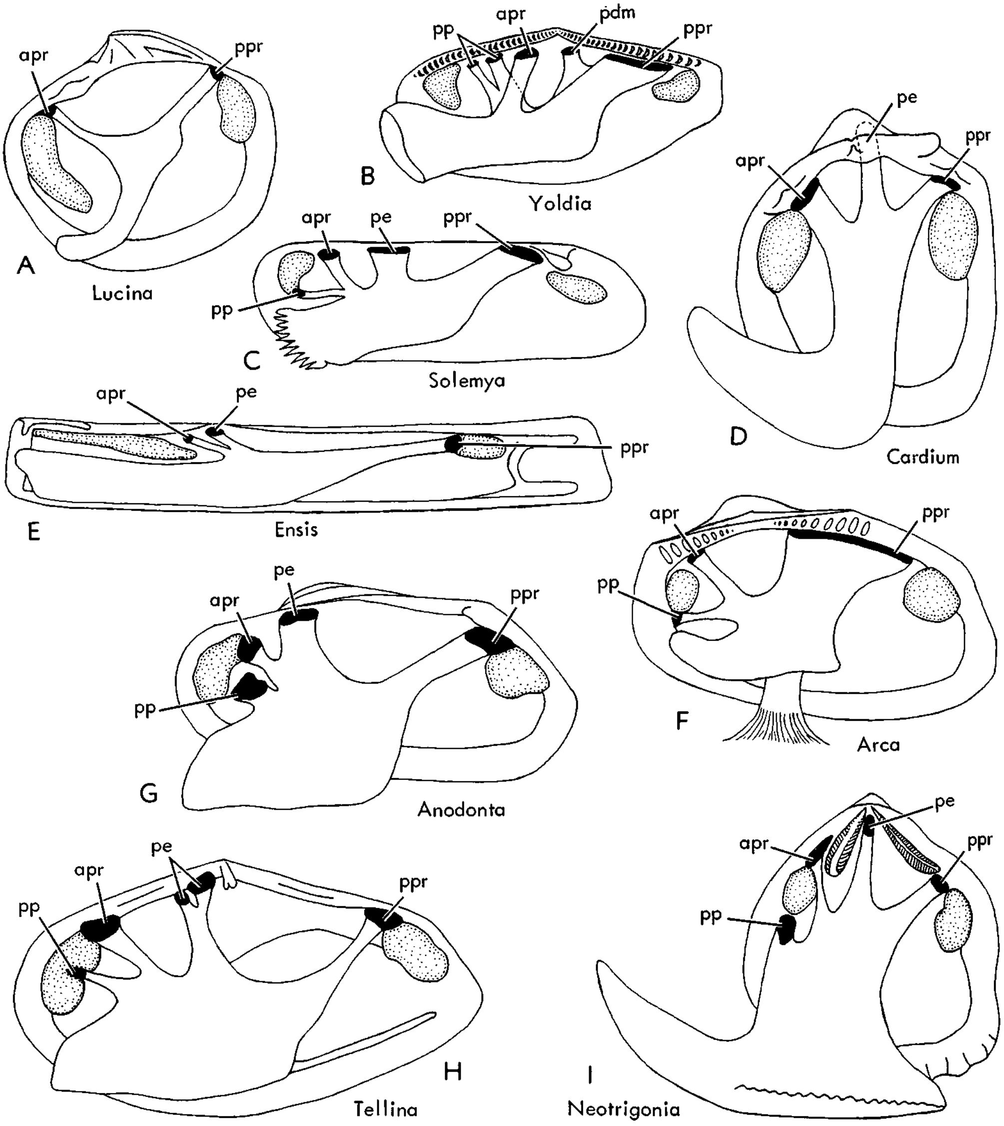

Fig. 31. Diagrams showing pedal musculature in dimyarian bivalves, illustrated by right valves viewed from inside (adductor scars stippled, pedal scars black, except in pedal elevator of *Cardium* which is attached in umbonal cavity under hinge plate), not to scale (all modified from Pelseneer, 1911, except *B, C, E, G,* and *I*.——*A. Lucina*.——*B. Yoldia (66)*.——*C. Solemya* (Pelseneer, 1891).——*D. Cardium*.——*E. Ensis (126)*.——*F. Arca*.——*G. Anodonta* (Brück, 1914).——*H. Tellina*.——*I. Neotrigonia* (Pelseneer, 1891). [Explanation: *apr,* anterior pedal retractor; *pdm,* dorsomedian pedal muscles; *pe,* pedal elevator; *pp,* pedal protractor; *ppr,* posterior pedal retractor].

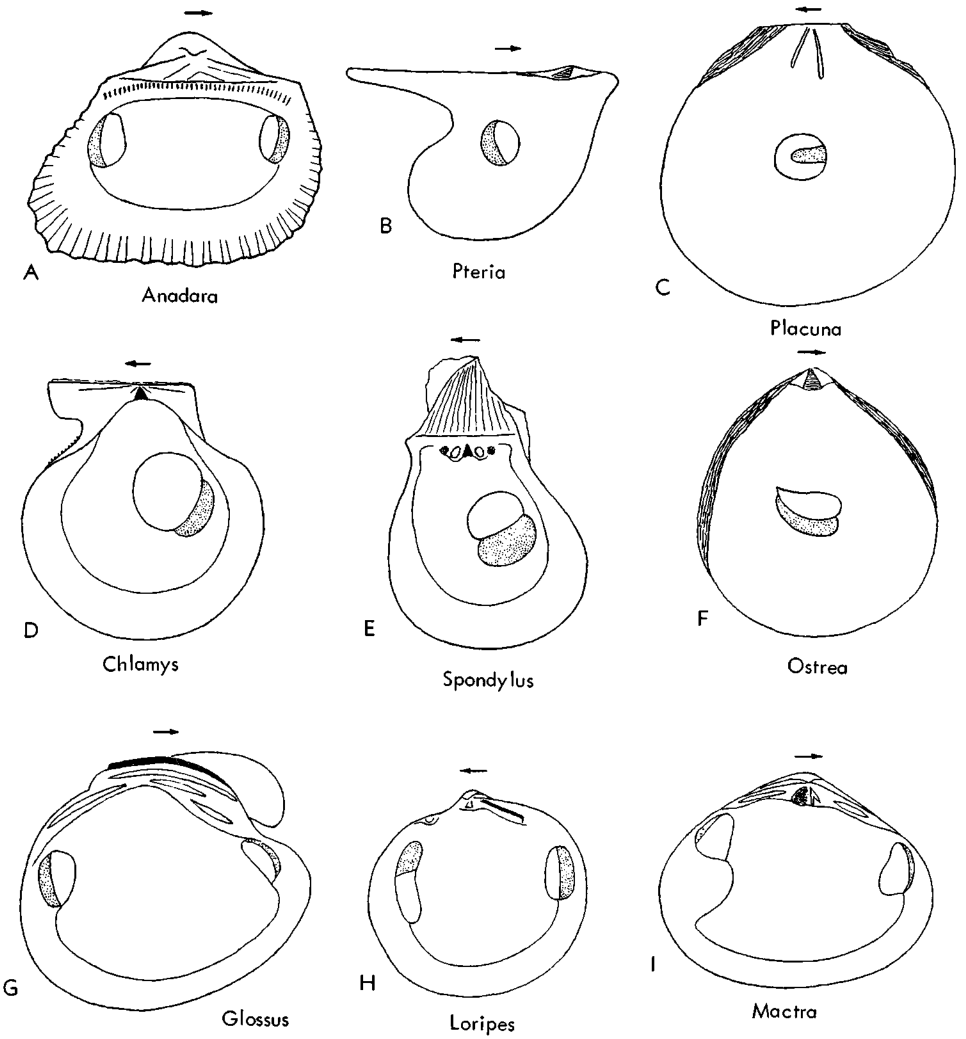

FIG. 32. Adductor-muscle scars in selected bivalve genera, not to scale (arrows directed anteriorly), showing attachment areas of striated or "quick" muscle (unshaded) and smooth or "catch" muscle (stippled) (Cox, n).

discussion of the general features of the shell. For treatment here they may be classified as the adductor muscles, the pallial muscles, the muscles of attachment of the foot and byssus, and a miscellaneous group. No account will be given of muscles which lie entirely within the soft parts of the mollusk, such as the intrinsic muscles of the foot, ctenidial muscles, and muscles of the auricles and ventricle (cardiac muscles).

## ADDUCTOR MUSCLES

The **adductors**, the largest and strongest muscles found in the Bivalvia, extend between the two valves and serve to draw them together, opposing the tendency of the ligament (p. *N*58) to open them. Fundamentally they are two in number and are designated, according to their positions, as the **anterior** and **posterior adductors.** Their

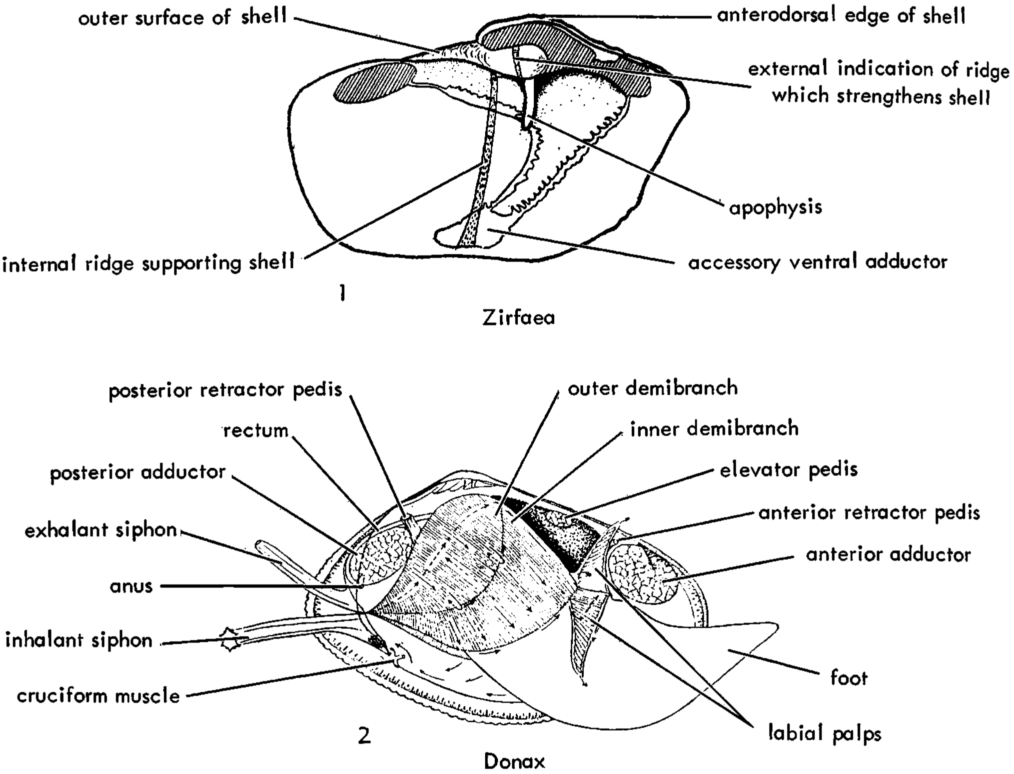

FIG. 33. Bivalve musculature.——*1. Zirfaea crispata* (LINNÉ) showing attachments of anterior adductor and accessory muscles, ×1.5 (Purchon, 1955).——*2. Donax vittatus* (DA COSTA) showing cruciform and other muscles in relation to various anatomical features, ×2 *(190)*.

scars of attachment are usually circular or oval in shape and in many forms do not differ greatly in size. Bivalvia in which two adductor muscles are present are described as **dimyarian** (Fig. 31), and dimyarian forms in which the two muscles do not differ greatly in size are called **isomyarian** or **homomyarian**. Use of these last two terms is usually extended to apply to such genera as *Lucina,* in which the anterior adductor is larger than the posterior one and dorsoventrally elongated, and *Ensis* and *Pharus,* in which the anterior adductor, like the shell itself, is greatly elongated in an anteroposterior direction.

The scars of the two adductors usually lie within the dorsal half of the shell, but well below the axis about which the two valves hinge (Fig. 32). In the genus *Cucullaea* one scar is located on a raised platform on the interior of the shell; in the mussel-like genera *Septifer* and *Dreissena* the anterior scar occupies a septum in the umbonal angle. In some genera of the rudists the scars are borne by processes protruding prominently into the cavity of the shell. Such muscle-bearing structures are known as **myophores.** In the great majority of forms, however, the adductor scars are flush with or form shallow depressions of the general inner surface of the shell. In the Pholadacea (Fig. 33) the anterodorsal part of the shell is broadened and reflected dorsally over the umbo and the anterior adductor is attached to the reflected part, thus lying on the dorsal side of the hinge axis. Usually the two adductors contract or relax in union, but in a few genera (e.g., *Solecurtus, Hiatella,* and members of the Pholadidae) they are capable of contracting alternately, so that the valves can rock about a transverse axis.

Among numerous representatives of the Bivalvia, however, we find all stages in the progressive diminution of the anterior adductor, and in many genera this muscle is absent, at least in the adult stage. Forms in which it is small or absent are termed **ani-**

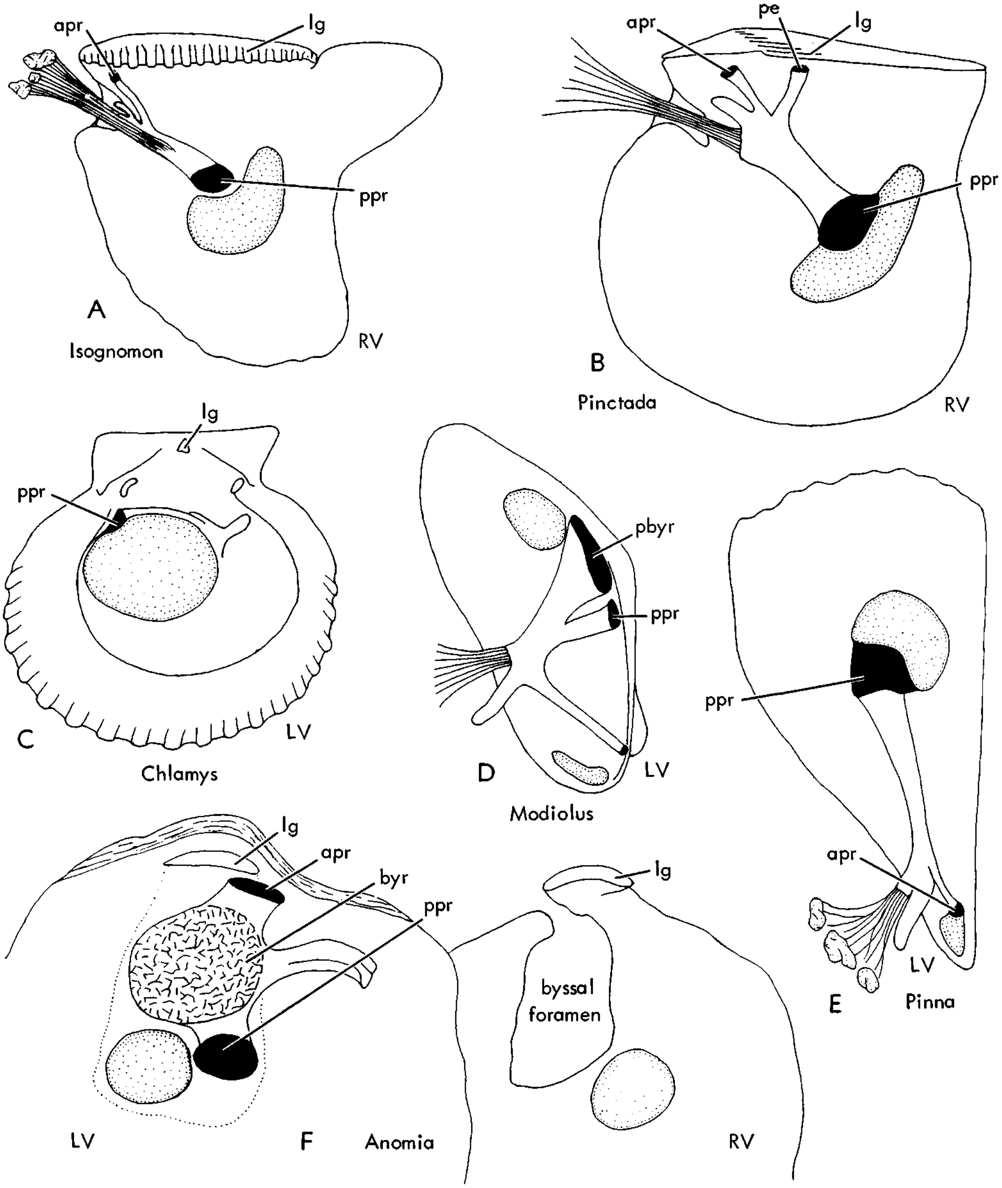

FIG. 34. Diagrams showing pedal musculature in heteromyarian and monomyarian bivalves, illustrated by valves viewed from inside (adductor scars stippled, pedal scars black), not to scale (all modified from *132*, except *B* and *E*).——*A. Isognomon.*——*B. Pinctada (113).*——*C. Chlamys.*——*D. Modiolus.*——*E. Pinna* (Rosewater, 1961).——*F. Anomia.* [Explanation: abbreviates as for Fig. 31 and, in addition, *byr,* byssal retractor; *lg,* ligament; *LV,* left valve; *pbyr,* posterior byssal retractor; *RV,* right valve.] [Note that pedal and byssal muscles are attached only to left valves in *Chlamys* and *Anomia.*]

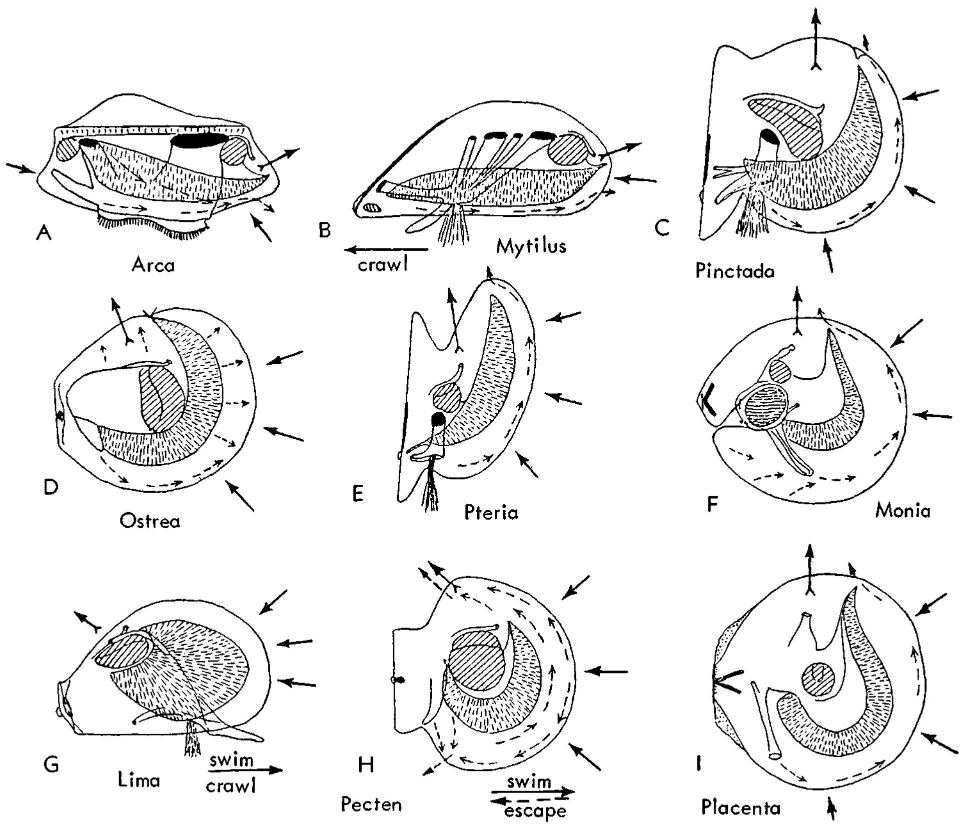

FIG. 35. Bivalve musculature in dimyarian *(A)*, heteromyarian *(B)* and monomyarian *(C-I)* genera (with left valve and mantle removed) showing adductors (oblique ruled), pedal muscles (left-valve attachments in black) in relation to ctenidia (broken-line pattern), plain arrows indicating inhalant currents, feathered arrows exhalant currents, and broken arrows cleansing currents in mantle cavity (diagrammatic, not to scale) (*193*, from various sources). [*A, B, G,* viewed from left side; *C-F, H,* viewed from above; *I,* viewed from underside (animal lies on concave right valve in life).]

**somyarian,**[1] and among them we may distinguish those that are **heteromyarian** (anterior adductor much reduced) and those that are **monomyarian** (only posterior adductor present) (Fig. 34, 35). Under certain earlier taxonomic schemes such names as Anisomyaria and Dimyaria were considered to designate major taxa of the Bivalvia, but it is now realized that the degree of reduction of the anterior adductor is not a satisfactory criterion in classification. Thus *Tridacna,* although now thought to be fairly closely related to the Cardiidae, a typical homomyarian family, possesses only one adductor, while on the other hand *Dimya,* considered to be close to the monomyarian family Plicatulidae, has two well-defined although small adductors. Stages in the disappearance of the anterior adductor are well shown in the Mytilidae. In some species of *Botula* the two muscles differ very little in size; in *Modiolus* the anterior adductor, although still well developed, is considerably the smaller of the two; in *Mytilus* it is very small, and in *Choromytilus* it is absent. In many of the earlier Pteriacea a small anterior adductor is present, whereas in modern forms this muscle is absent in the adult stage. When the anterior ad-

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[1] Some authors use "anisomyarian" as a synonym of "heteromyarian."

ductor is absent or much diminished in size there is a general tendency for the posterior adductor to assume a more central position, as it is then best able to perform its function of drawing the valves together when so located.

In most bivalves the adductors are formed of two distinct bundles of muscle fibers, each attached to its own part of the complete adductor scar. These two types of muscle have been termed "nacreous" and "vitreous"; the fibers of the former type are smooth and those of the latter type striated, either transversely or obliquely. The "vitreous" or striated muscle (termed "quick" muscle by some workers) is believed to function during the rapid closing of the two valves, whereas the "nacreous" muscle (also termed "catch" muscle) acts more slowly and serves to hold the two valves of the shell closed for considerable periods. In dimyarian forms the "nacreous" muscle generally occupies the more peripheral part of the scar (anterior or posterior as the case may be) and the "vitreous" muscle the part closer to the middle of the shell, but in the anterior adductor of the Lucinidae the former type occupies the dorsal half of the muscle. The distinctions between the types are particularly well defined, and the two parts of the adductor scar are commonly distinguishable in monomyarian families (e.g., Pectinidae, Spondylidae, Plicatulidae, Ostreidae). In the Pectinidae (in swimming representatives of which the striated muscle functions during the rapid opening and closing of the valve) the attachment area of this part of the muscle forms the anterior three-quarters of the scar, whereas in *Plicatula* it forms only its anterior quarter. In the Ostreidae there is less difference in the size of the two areas, that belonging to the striated muscle occupying the dorsal half of the whole scar.

## PALLIAL MUSCLES

The muscles of the mantle are known collectively as **pallial muscles**. Radially directed muscle fibers are present within the entire mantle, but are strongest near its periphery and attached to the interior of the shell along a line or narrow band (**pallial line**) which for all or part of its length is parallel and fairly close to the margin (Fig. 36). The function of these marginal radial muscles is to withdraw the mantle edge well within the valves of the shell before they are closed. Concentrically directed muscles also extend round the margin of the mantle close to its free edge. The pallial line is distinctly impressed on the interior of the shell in most homomyarian and some heteromyarian forms, running from the lower margin of one adductor scar to that of the other.

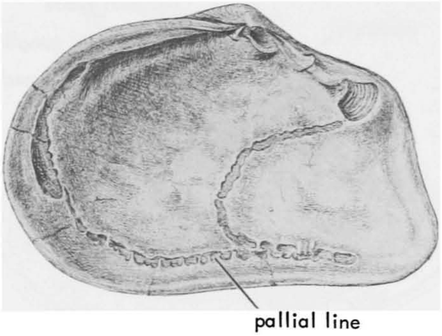


FIG. 36. *Mya truncata* LINNÉ, interior of right valve showing muscle attachments of mantle along pallial line, ×0.7. Pallial sinus at right (Wood, 1857).

In most forms in which the anterior adductor has been completely lost, a line of mantle attachment representing the original pallial line stretches from the posterior adductor towards the hinge line, following a direction more or less parallel to the anterior margin of the shell, but it is shorter than in most dimyarian forms owing to displacement of the remaining adductor towards the center of the shell. In the Pteriidae a continuous pallial line is replaced by a series of irregularly spaced pits, each marking the insertion of fanlike muscles for the retraction of the mantle margin. In the Pinnacea, a heteromyarian group, primary mantle attachment exists only along the two adductor muscle insertions and there is no pallial line like that present in the Mytilidae, another heteromyarian group. In the Pteriacea and Anomiacea the considerable area of the mantle posterior to the single adductor is unattached to the shell near its margin, and the unattached area is even more extensive in

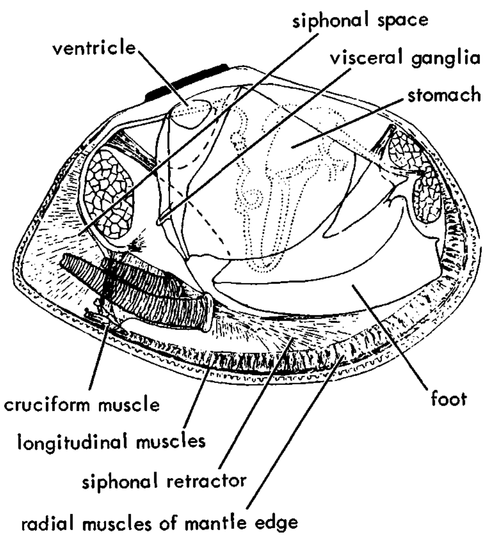


FIG. 37. *Tellina tenuis* DA COSTA showing mantle muscles, cruciform and siphonal retractor muscles, ×3 *(190)*.

the Pinnacea, for the reason just stated. Special **pallial retractor muscles** (posterior only in the first two superfamilies, posterior and anterior in the third) exist, however, in these groups, and serve to withdraw these parts of the mantle far within the shell when stimulated. In the Pectinacea, Limacea, and Ostreacea a secondary line of posterior pallial attachment has become developed, passing around the adductor scar on its posterior side and upward towards the hinge line. Except in the Limidae this line of secondary pallial attachment is less distinct than the true pallial line, and in the Ostreidae even the latter cannot be clearly seen in many species.

In the dimyarian family Solenidae, in which the shell is much elongated in an anteroposterior direction, a line of pallial attachment runs along the dorsal margin from the posterior adductor (Fig. 36).

JAWORSKI *(77)* has interpreted the fine radial ridges seen on the interior of the shells of some members of the Ostreidae and Chamidae, particularly near the margin, as reflecting the radial musculature of the mantle, suggesting that where there has been particular pressure on the mantle the musculature has affected the secretion of shelly matter. He has thus dismissed the theory of some other workers that these ridges, seen also on the lip of the lower valve of many hippurites, are impressions of the cirri (tentacles) of the mantle edge. In some species, particularly of the family Lucinidae, the musculature of the general surface of the mantle leaves numerous small attachment scars, in the form of pits or furrows, on the interior of the shell.

In siphonate forms, with the exception of the Lucinidae (in which the single siphon, the exhalant one, is invaginable), **siphonal retractor muscles** are present as modifications of the radial muscles of the mantle margin, and serve to withdraw the siphons partly or wholly within the shell (Fig. 37). Except when the siphons are short, these muscles are attached to the interior of the shell along an embayment of the pallial line known as the **pallial** sinus, the space within the embayment accommodating the retracted siphons. Bivalves with a simple pallial line are described as **integripalliate** and those with an embayed pallial line as **sinupalliate**, but the distinction between these two types is not of fundamental significance. In forms with a deep pallial sinus (e.g., Tellinidae) the lower border of the sinus may coincide with the marginal part of the pallial line for a considerable distance, and in the Solenidae, in which the pallial line bends back close to the dorsal margin before joining the dorsally and relatively anteriorly placed posterior adductor scar, the upper border of the sinus may also coincide with part of it (Fig. 36).

The Pholadidae are remarkable for the development of an **accessory ventral adductor**, the insertion of which in each of the two valves forms an irregularly shaped area at the posterior angle of the pallial line, where it bends back to form the sinus. This muscle must be interpreted as having arisen from pallial muscles at this point by the fusion of those on the two sides across the shell. The **cruciform muscle** found in the Tellinacea and some Solenidae occupies a very similar position. Located just below the base of the siphons, it consists of two bundles of muscle fibers running transversely from one valve to the other and intersecting at an acute angle, so as to form a cross

(Fig. 33,37). In many Recent specimens their small circular scars of attachment are just visible near the posterior angle of the pallial line. YONGE has suggested that their function is to take the strains that occur during the extrusion and retraction of the siphons (Fig. 38).

## ATTACHMENT MUSCLES OF FOOT AND BYSSUS

The number and positions of attachment of the various pedal muscles vary in different genera. Such muscles have almost completely disappeared in the Plicatulidae, Chamidae, and Laternulidae, and are absent in the Spondylidae and Ostreidae, in the last of which families the foot itself has atrophied. In equivalve genera the pedal muscle scars are equal in number and similarly arranged in the two valves, but this may not be the case in inequivalve forms.

The **anterior pedal retractor** is usually attached on the posterodorsal or posterior side of the anterior adductor scar. In some forms (e.g., *Ensis*) the muscle divides into two bundles, each with its area of attachment. In others there is a tendency for the attachment of this muscle to migrate ventrally along the posterior margin of the adductor scar. The anterior retractor is absent in most monomyarian forms, such as the Pectinidae, and small dorsally placed muscles formerly identified as such in *Pteria* and some species of *Lima* are now regarded as elevator muscles. The anterior retractor is present in the heteromyarian families Pinnidae and Mytilidae. In *Mytilus* this muscle arises from the base of the byssus and is attached to the shell very close to the umbo, but in the related genus *Choromytilus* it is attached in a much more posterior position. In the Pholadidae the anterior pedal retractor is attached to a process or **apophysis**, usually narrow and spoonlike, which projects into the interior of the shell from under the beak.

The attachment of the **posterior pedal retractor** is usually on the dorsal side of the posterior adductor scar, but in some forms it has migrated to the ventral side of this muscle and when present in the Limidae it is on its posteroventral side. In byssiferous forms the posterior retractor is joined to the byssus and forms its retractor as well as that of the foot. In the Mytilidae and Arcidae this muscle tends to become extended in a direction parallel to the dorsal margin. Actually, in *Mytilus edulis* LINNÉ it is split up into three to six bundles, the most anterior of which arises from the base of the foot itself and constitutes the pedal retractor, while the others form byssal retractors. On the shell, however, the scars of the individual bundles are merged together. In *Anomia* the posterior retractor is modified to form the byssal muscle or muscles, developed on the left side only, its commonly duplicated scars occupying a position which is anterior and slightly dorsal to median, facing the foramen in the right valve through which the calcified byssus passes. In the Pectinidae also the posterior retractor (if developed at all) is present only on the left side, its scar being situated along the dorsal margin of the adductor scar. In the Pteriidae a posterior retractor is present on both left and right sides, its scar in each valve lying on the antero-

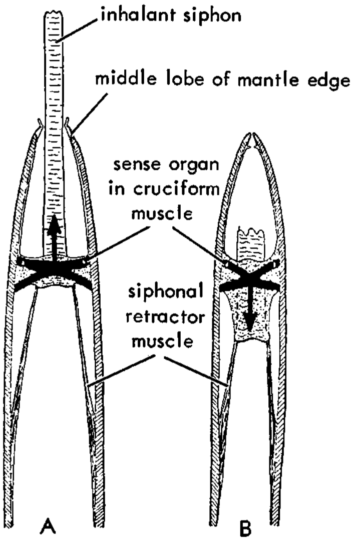


FIG. 38. Bivalve musculature—semidiagrammatic ventral views of inhalant siphon attachments in Tellinidae and Semelidae showing how cruciform muscle acts as tie taking backward strain when siphon is extruded *(A)* and forward strain when it is withdrawn *(B) (190)*.

dorsal side of the adductor scar. In both cases the line of junction of the scars is indistinct. In *Isognomon,* on the other hand, the adductor scar is crescentic, with its hollow side facing dorsalward, and the pedal retractor lies within the concavity, well separated from the adductor. In nonbyssiferous members of the Pectinidae and Limidae and in the Vulsellidae the posterior retractor, like the anterior one, has disappeared, although a small foot is present.

A **pedal protractor muscle**, serving to extend the foot, is fairly widespread in the Bivalvia, although it has not been observed in some families. In some genera (e.g., *Pleiodon*) its place of insertion in the shell is on the posterior side of that of the anterior retractor, or it may migrate anteriorly so as to encroach on the anterior adductor scar, in some (e.g., *Tellina, Donax, Montacuta*) almost dividing it in two; or it may lie on the ventral side of that adductor (e.g., *Glycymeris, Limopsis, Arca, Trigonia, Cardium,* and other forms). In some Nuculacea there are two **anterior protractors**, inserted close to the dorsal margin just posterior to the top of the anterior adductor scar, and in front of the anterior retractor scar.

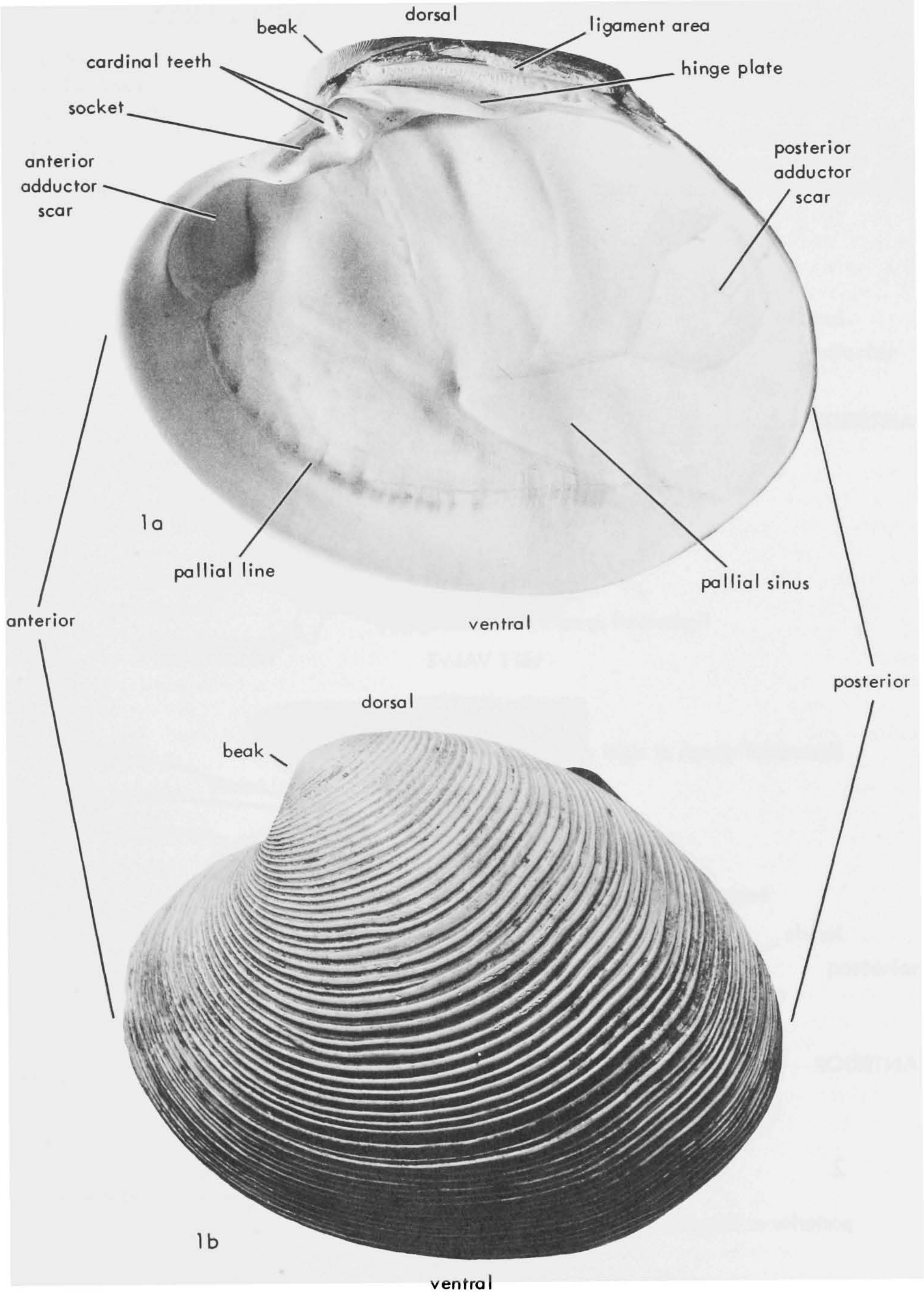
A **pedal elevator muscle**, best developed in the Cardiidae, Tellinidae, Psammobiidae, and Unionidae, among living families, is a thin bundle of muscle fibers attached to the shell very commonly in the umbonal cavity, in which case its scar is represented by an umbonal protuberance in fossil specimens which are internal molds. Small paired or single pedal elevator muscles are present near the hinge margin in *Pinctada, Pteria, Isognomon, Malleus,* and some species of *Lima.*

## MISCELLANEOUS SHELL-ATTACHED MUSCLES

The visceral mass is secured in place by muscles which leave attachment scars on the interior of the shell in some species. Thus in some Unionacea (e.g., *Spatha*) visceral attachment muscles leave two impressions, a rather large, crescentic one behind the anterior adductor and a smaller, more elongated one in a mediodorsal position. In the Pholadidae an **anterior retractor muscle of the visceral mass** is inserted in each valve a little behind the anterior adductor scar, while the **posterior retractor of the visceral mass** is inserted within or close to the posterior adductor, first dividing into two bundles in some species. In *Solemya* a narrow band on the interior of the shell ascends obliquely from the posteroventral corner of the anterior adductor scar towards the dorsal margin, where it broadens out to merge with the pedal retractor scars. It marks the attachment of muscles of the integument of the visceral mass.

A small **gill retractor** muscle exists in *Anomia,* some Ostreidae, Pectinidae and Solenidae, and probably in other forms. In *Hemipecten* its attachment is just in front of the middle of the valve. NEWELL *(113)* has recorded that areas of attachment of two gill muscles can be detected on the interior of the right valve of *Chlamys islandica* (MÜLLER), a large crescentic one below the adductor scar and a small one above it.

Not all the scars visible on the interior of bivalve shells are definitely assignable to muscles of known function, and some have been alluded to merely as "accessory muscle scars." Several such scars are well seen in some modern species of the Nuculacea, particularly on the dorsal part of the surface. SCHENCK *(146)* has applied such noncommittal terms as "median muscle scar" and "punctiform scars" to them, while HEATH *(66)* has termed two of them the "dorsomedian" and "ventromedian" scars. Such scars are numerous and conspicuous on some of the Paleozoic nuculaceans. The Ordovician *Babinka* has radially directed pyriform scars between its adductor scars, with smaller and less conspicuous scars below them. STENZEL *(154)* has called attention to a small scar, which he terms that of "Quenstedt muscle," a short distance below the center of the ligamental area in all species of Ostreidae. As no foot is present in this family, the muscle in question cannot function as a pedal muscle, although it may have arisen as a modification of one.



Amiantis

FIG. 39. Bivalve shell morphology.——*1. Amiantis (Amiantis) callosa* (CONRAD), Recent, California, equivalve, inequilateral shell of venerid; *1a,* right valve interior; *1b,* left valve exterior, both ×0.7 (Keen, n, from Stanford Univ. Coll.).

# MORPHOLOGY OF BIVALVIA HARD PARTS

## GENERAL EXTERNAL FEATURES OF SHELL

In the class Bivalvia the shell consists of two usually convex, calcareous structures (**valves**) of various shapes which open and close by hinging along an imaginary straight line (**hinge axis** or **cardinal axis**) that coincides with or is close to one margin (**hinge margin**) (Fig. 39-42). The structures belonging to this part of the shell (ligament, hinge teeth, hinge plate, etc.,

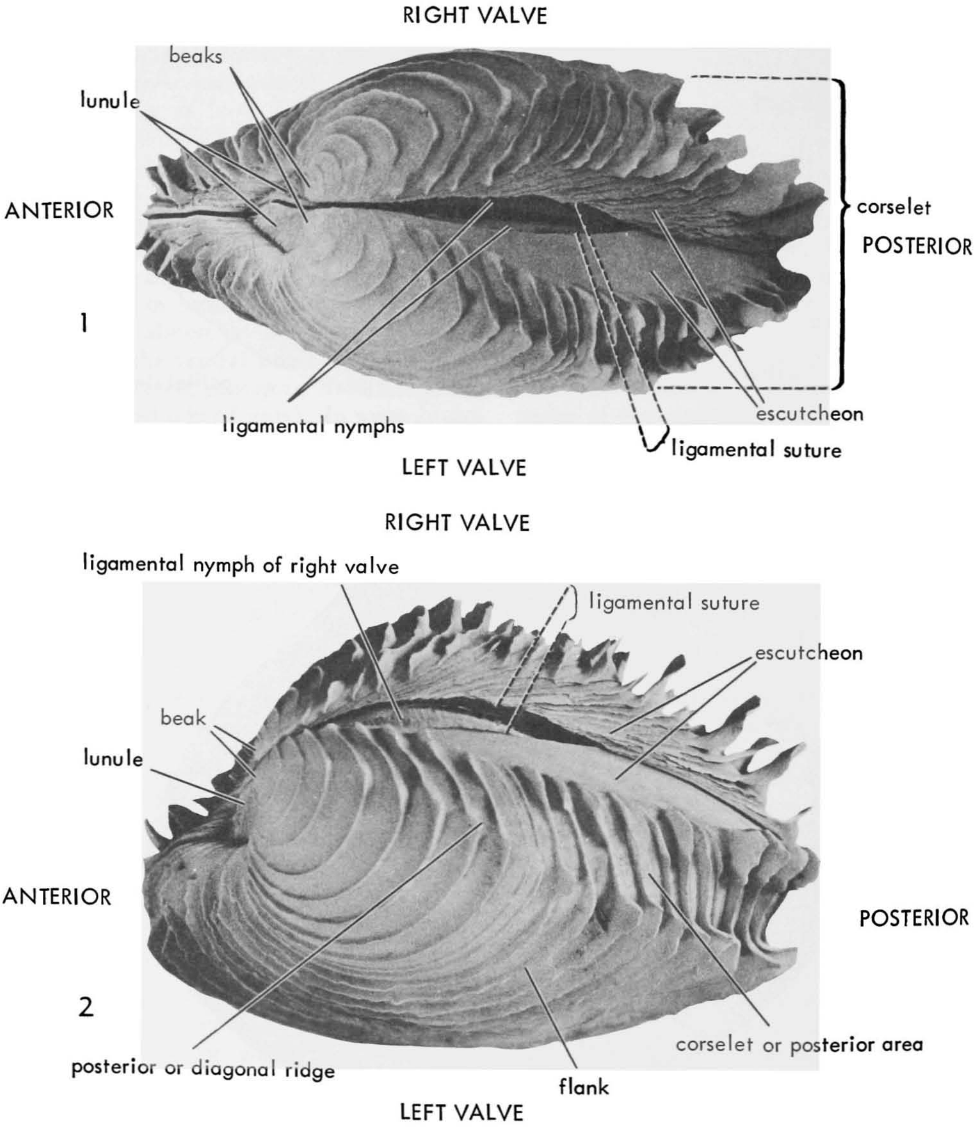


FIG. 40. General external features of shell—*Circomphalus foliaceolamellosa* (DILLWYN), Neog., Medit., Rec., W.Afr.——*1*. Dorsal view.——*2*. Specimen viewed obliquely from above left. Note slight size difference between LV and RV lunules and escutcheons, ×1.4 (Nuttall, n).

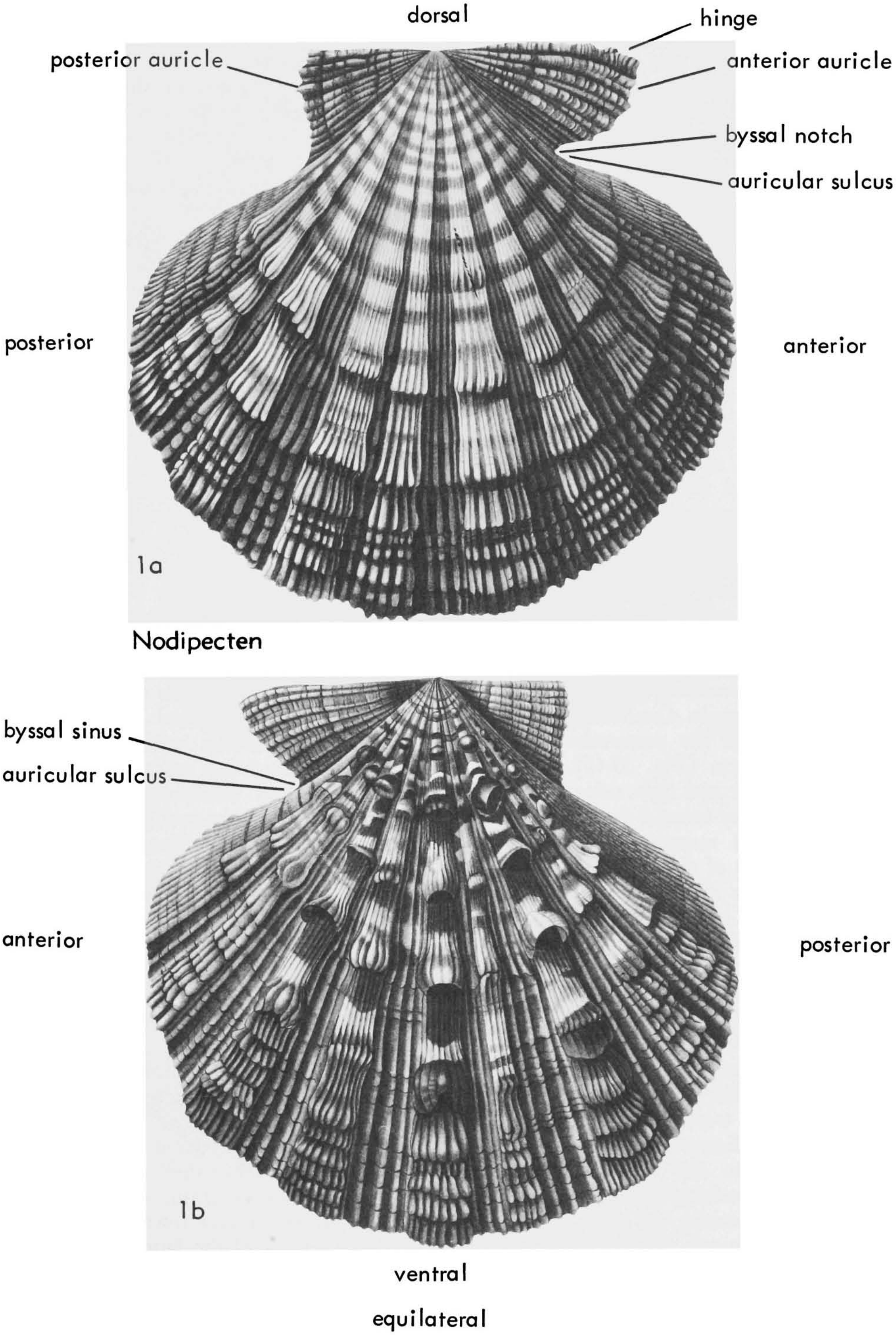


FIG. 41. Bivalve shell morphology.——*1. Chlamys (Nodipecten) nodosa* (LINNÉ), Recent, off Florida, equivalve, equilateral pectinid; *1a,b,* right and left valve exteriors, ×0.5 (Chenu, 1844).

described later) which function during opening and closing of the valves are collectively known as the **hinge**. In typical homomyarian bivalves the hinge occupies a strictly **dorsal** position in relation to the soft parts; on the opposite margin (along which the valves open most widely), is **ventral;** one end of the shell is **anterior,** as it lies relatively close to the mouth of the animal, and the other end is **posterior**, as it lies relatively close to the anus (Fig. 39). In heteromyarian bivalves the corresponding parts of the shell do not occupy similar positions in relation to the soft parts.

The point is discussed later (p. *N*78) and the conclusion is reached that, for lack of any alternative directional terminology, it is desirable to regard the hinge in all Bivalvia as dorsal and to designate the other three "points of the compass" as ventral, anterior, and posterior, although the oro-anal axis may, in fact, diverge widely from the antero-posterior direction taken as parallel to the cardinal axis. The various parts of the margin of the shell may thus be termed the **dorsal, anterior, ventral,** and **posterior margins**, the dorsal margin in many forms consisting of two parts, the **anterodorsal margin** anterior to the beaks (see below) and the **posterodorsal margin** posterior to them (Fig. 39-42). The two valves lie on left and right sides of the body and are therefore termed the **left valve** and the **right valve** respectively. In most bivalves these are of equal size, and in some although not in all respects mirror images of one another; but in some forms they are unequal. Usually the line of junction of the two valves (**commissure**) lies within a single plane, and in equivalve forms this coincides with the **sagittal plane** of the animal (Fig. 42).

The measurement of length and height in bivalve shells poses certain problems. Some workers would wish to define the **length** as the distance between two planes perpendicular to the cardinal and hinge axes and just touching both the anterior and posterior extremities of the shell. The **height** is measured perpendicular to the length.

Most experienced workers achieve a certain consistency in deciding on the cardinal axes of bivalves and one particularly useful aid is that this axis normally lies parallel to a line through the adductor scars of many dimyarian shells. In some forms, including many species of *Donax* and *Macoma,* the ligament is set at a noticeable angle to this imaginary axis and acts as a hinge about which the valves turn when opening and closing.

It must therefore be stressed that the axes can only be determined with certainty in genera with cardinal areas (e.g., *Arca, Gervillia, Malleus, Pinctada, Pteria, Lima, Pecten*). In dealing with other genera it is often safer, especially when measurements are made for statistical purposes, to take the maximum shell length and then the maximum height perpendicular to it. The **inflation** of bivalve shells may be defined as the distance between two planes parallel to the plane of the commissure which touch the outermost parts of the two valves. [The term thickness is not recommended for use in this connection, as it is also commonly applied to the calcareous wall of the shell.]

When describing the outline of a bivalve (i.e., as seen in lateral view), recourse is usually made to such terms as suboval, subtrigonal, suborbicular, and the like (Fig. 43). It is preferable wherever possible, however, to use terms such as mytiliform, pectiniform, and ensiform, which evoke the shapes of well-known genera. In the same way, species of *Pinna* are best described as either being wedge-shaped or ham-shaped, rather than trigonal. The geometrical terms mentioned above are mostly very imprecise and their main usefulness lies in comparisons; for instance, the statement that one species of *Dosinia* is more quadrate in outline than another is informative.

Starting with the larval shell or **prodissoconch** (p. *N*94), growth of a bivalve shell proceeds by successive increments along the margins of the two valves. The increments are broadest in a direction determined by the shape of the adult shell and are narrow close to the dorsal margin, where they converge from either end toward the prodissoconch. A valve of the latter is commonly preserved on each valve of the adult shell, forming a small, noselike angle termed the **beak** (Fig. 39), which adjoins the dorsal

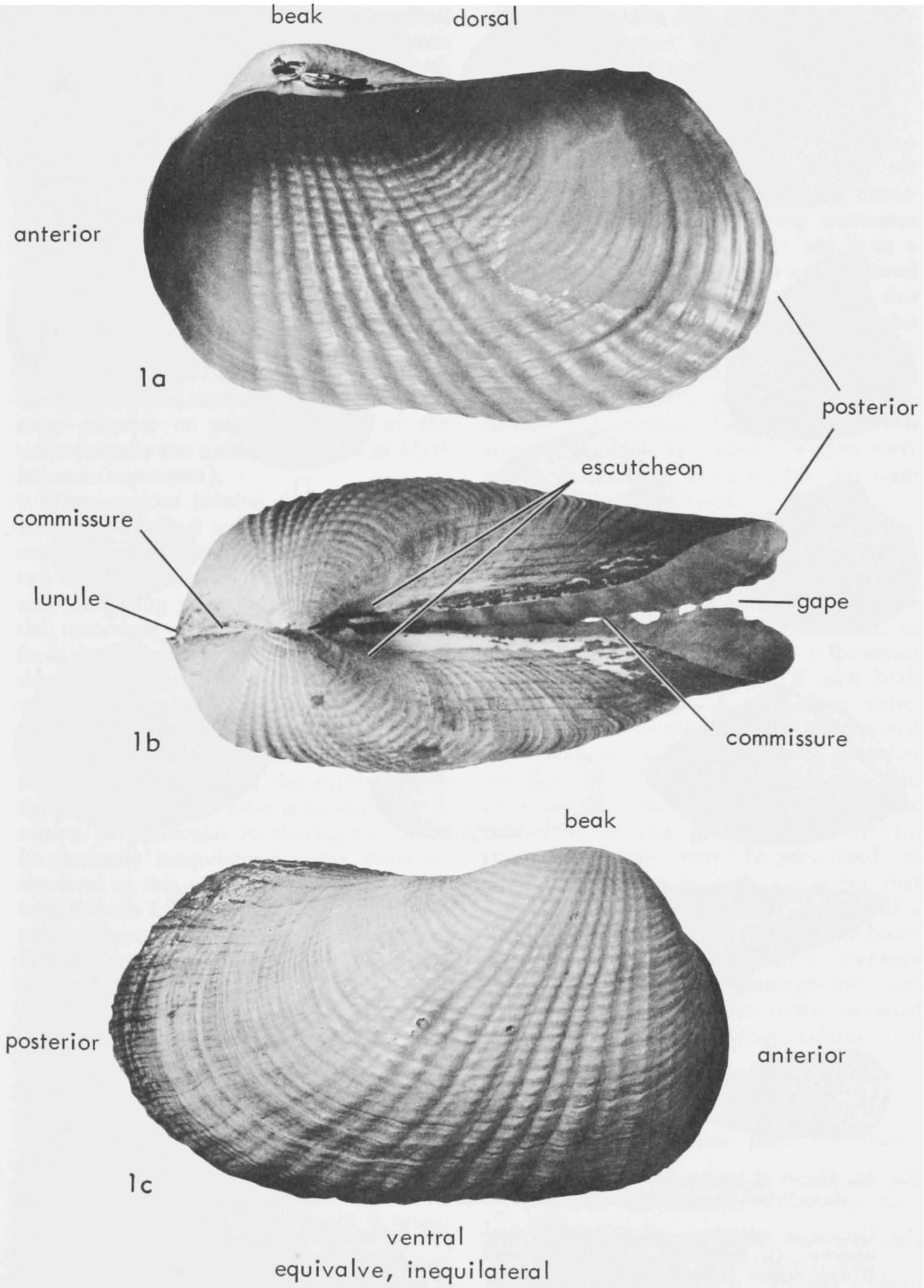


FIG. 42. Bivalve shell morphology.——*1. Pholadomya (Pholadomya) candida* G. B. SOWERBY, Recent, Caribbean, equivalve, inequilateral pholadomyid; *1a,b,* right valve interior and dorsal views of both valves; *1c,* right valve exterior; all ×0.7 (Cox, n).

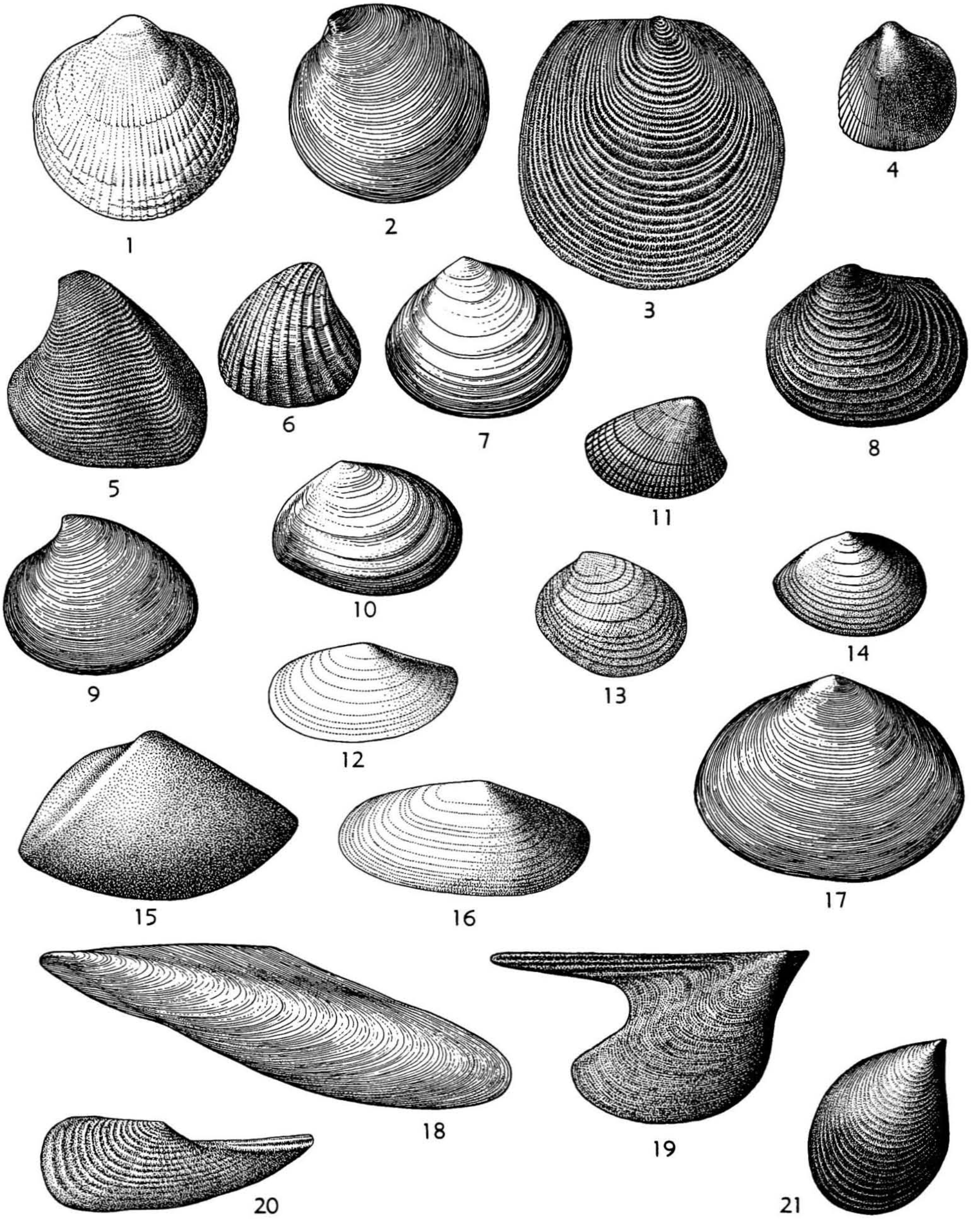


Fig. 43. Shapes of bivalve shells, illustrating terms commonly used to describe them, all ×1 except *14* (from British Museum (Natural History), *British Mesozoic Fossils, British Caenozoic Fossils*).

*1,2*. Circular or orbicular.——*1*. *Glycymeris plumstediensis* (J. Sowerby), L.Eoc., Eng.——*2*. *Dosinia exoleta* (Linné), Pleist.-Rec., N.Eu.

*3,7*. Subcircular or suborbicular.——*3*. *Steinmannia bronni* (Zieten), L.Jur.(U.Lias., Toarc.), N. Eu.——*7*. *Macoma obliqua* (J. Sowerby), Plio.-Pleist., Eng.

*4,8*. Subquadrate.——*4*. *Nemocardium nitens* (J. Sowerby), L.Eoc., Eng.——*8*. *Lucina concinna* (Damon), U.Jur.(Kimmeridg.), Eng.

*5,6*. Trigonal.——*5*. *Opis trigonalis* (J. de C. Sowerby), Jur.(U.Lias.-Bajoc.), Eng.——*6*. *Cardita deltoidea* (J. Sowerby), L.Oligo., Eng.

*9*. Trigonally suboval. *Astarte semisulcata* (Leach), Pleist., Eng., Rec., Arctic.

margin in most forms lacking a cardinal area (p. *N*103). Indications of the successive increments are preserved as growth lines on the surface of the shell. If, in the adult shell, the beak occupies a position close to the middle of the length, the shell is described as **equilateral** (Fig. 41), but if the beak lies closer to one end or the other the shell is described as **inequilateral** (Fig. 42). In the great majority of bivalves the beak lies anterior to mid-length, but in some genera the reverse is true. Its position is best described by citing the ratio between its distance from the anterior end of the shell and the total length of the latter. The beak is described as **terminal** if it forms the most anterior or posterior point of the valve (usually the most anterior, as in *Mytilus* and *Isognomon*).

When various bivalve shells are viewed along the cardinal axis from beyond their anterior or posterior end, it is seen that the two beaks only rarely form the most dorsally projecting parts of the shell. Usually the transverse profile of each valve rises from them to a point termed the **summit** of the valve before curving round towards the ventral margin. In more or less equilateral forms the summit usually coincides with the point of maximum curvature of the longitudinal dorsal profile of the valve; that is, the profile when the valve is viewed in a direction perpendicular to the sagittal plane. In markedly inequilateral forms, however, the level of this point of maximum curvature (which I propose to call the **umbonal pole** of the valve) lies nearer the beak than does the summit and occupies a less dorsal position than the latter.[1]

The term **umbo** (pl., **umbones**) has been used by different workers in different senses. As understood by MURRAY (1771) in his explanation of the terminology of LINNÉ, it is the point of the valve most distant from the sagittal plane. For many authors it is synonymous with "beak," for others with "summit" or else with the abovementioned point of maximum curvature (umbonal pole), while others use it in a rather indefinite sense to denote the general region of the valve which surrounds this point and extends to the beak. It is in this last sense that I recommend its employment, although in parts of the present *Treatise* it is probably used with a more restricted connotation. The umbones in this sense were called the *"nates"* by some early workers, including MURRAY, but this term has now been abandoned.

The **umbonal cavity** is the part of the interior of the valve that lies within the umbo. The umbones are described as **prosogyrate** if they curve in such a manner that the beaks point in an anterior direction, as **opisthogyrate** if they point in a posterior direction, and as **orthogyrate** if each beak points directly toward the other valve. Usually these conditions are determined by the position of the beaks, whether anterior to mid-length, posterior to it, or more or less median, but there are exceptions to this generalization. In addition, umbones may be described as **coiled** if incurved in such a manner that their transverse outline forms a spiral of a complete whorl or more. Coiled umbones are commonly prosogyrate (but in *Gryphaea* and *Exogyra* they are opisthogyrate), and in addition, they may be coiled outward from the sagittal plane (e.g., *Glossus, Di-*

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[1] In *Glossus* it actually faces ventralward.

FIG. 43. *(Continued from facing page).*

*10.* Suboval. *Macoma calcarea* (GMELIN), Pleist., Eng., Rec., Arctic.
*11.* Subtrigonal. *Nucula pectinata* J. SOWERBY, L.Cret.(Alb.), Eng.
*12.* Subelliptical. *Yoldia oblongoides* (S. V. WOOD), Pleist., Eng.
*13,14.* Oval.——*13. Acila cobboldiae* (J. SOWERBY), Pleist., Eng.——*14. Abra splendens* (J. DE C. SOWERBY), L.Eoc., Eng., ×3.
*15.* Donaciform or rhomboidal. *Tancredia donaciformis* LYCETT, Jur.(Toarc.-Bajoc.), Eng.
*16.* Elongate elliptical. *Gari edwardsi* (MORRIS), L.Eoc., Eng.
*17.* Elliptical. *Scrobicularia plana* (DA COSTA), Pleist.-Rec., N.Eu.
*18.* Lanceolate or modioliform. *Gervillella sublanceolata* (D'ORBIGNY), L.Cret.(Apt.-Alb.), N.Eu.
*19.* Alate (bialate) or pteriiform. *Pteroperna plana* MORRIS & LYCETT, M.Jur.(Bajoc.), Eng.
*20.* Rostrate or nuculaniform. *Cercomya undulata* (J. DE C. SOWERBY), Jur.(Bajoc.-Oxford.), Eng.
*21.* Mytiliform. *Inoceramus (Pseudomytiloides) dubius* J. DE C. SOWERBY, Jur.(U.Lias., Toarc.), Eng. (Nuttall, n).

*ceras*), in which case the term **spirogyrate** has been applied to them.

In many shells one or more ridges or carinae originate at the beaks. Most commonly such a ridge passes over the umbo on the posterior side of the umbonal pole and runs diagonally across the surface of the valve to (or toward) an angle in the outline of the latter which may be considered to separate the ventral from the posterior margin. This ridge is usually termed the **posterior ridge** or **diagonal ridge** (Fig. 40), but within the Trigoniacea, in many genera of which it is very pronounced, it has been designated as the **marginal carina.** This sector of the surface of a valve, running posteroventrally from the umbo, is commonly termed the **posterior slope**, irrespective of the presence or absence of a ridge. The diagonal ridge separates two parts of the surface of the valve which in some genera (most Trigoniacea, *Protocardia,* etc.) have a different type of ornamentation. The part posterior to the ridge is known as the **corselet** (or merely as the **area** in the Trigoniacea), while the median part, extending anteriorly from the ridge to an undefined limit, is known as the **flank** (Fig. 40,*2*). A broad radial depression (or **sulcus**) of the flank may lie on the anterior side of the diagonal ridge (e.g., some Trigoniacea, *Crassatella*). In some genera one or more radial sulci are present even when no diagonal ridge is developed.

In many bivalves, notably Veneridae and Lucinidae, a heart-shaped morphologically differentiated area occurs anterior to the umbones. This is termed the *lunule*[1] (Fig. 40, 42). The lunule corresponds to the track (on the outside of the shell) of growing anterodorsal hinge structures. An analogous structurally differentiated area behind the umbones is termed the **escutcheon** (Fig. 40, 42). The escutcheon sometimes is itself bounded by a ridge known as the **escutcheon ridge.** It may also fall within the further differentiated posterior area termed the corselet. The corselet may be bordered by the posterior ridge (or carina) or alternatively be circumscribed by a groove as in the Lucinidae. Both the lunule and the escutcheon are composed of the same shell layer as the dentition.

The ligament, the elastic structure by which the two valves are joined dorsally, is described in later sections of this introduction, but allusion may here be made to external features of the calcareous part of certain shells which are associated with it. The **nymphae** or **nymphs** are narrow lunate platforms (one in each valve) which in many bivalves extend from the beaks along part of the posterodorsal margin, lying at the bottom of the escutcheon when one is present (Fig. 40,*1*). Each has a more or less flattened side facing toward the opposite valve and a deep groove separating it from the posterodorsal margin. They serve for the attachment of the ligament, and when this has been removed they are just visible in dorsal view of the shell. The elongate space, with the nymphs inside, left on removal of the ligament is termed the **ligament suture.** In many Pteriomorphia the dorsal margin in both valves, or only in one, forms the base of a flat or slightly concave, commonly triangular area (**cardinal area**) which makes a well-marked angle with the plane of the commissure (Fig. 44). As the result of the presence of this area the two beaks are well separated. It may bear a single triangular transverse depression, a series of transverse depressions, chevron-like grooves, or longitudinal grooves, the relations of which to the ligament are explained later (p. *N*60-*N*62).

The Pectinacea, Pteriacea and, to a less marked extent, the Limacea, comprise shells in which part of the straight hinge margin lying on either side of the beak forms the margin of a triangular, relatively compressed part of the valve known as an **auricle** or **wing** according to its length (Fig. 41). The auricles and wings may be clearly delimited from the remainder of the valve (termed **body** of valve, or, in the Pectinidae, **disc**), or their lower border may be less distinct. In most Pteriacea the beaks lie close to the anterior end of the hinge margin so that the anterior auricle is small or even obsolete; the posterior wing is elongate and acutely pointed at its tip in some species.

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[1] H. Dodge (1950, *Jour. Paleontology*, v. 24, p. 500) has called attention to the inappropriateness of the terms "escutcheon" and "lunule" and has suggested their replacement by "vallis" and "sigilla," respectively, but they are now very firmly entrenched in the literature.

When the two valves are drawn together by the adductor muscles, many bivalve shells are completely closed along all margins. In some, however, these still remain open **(gape)** in one or more places (Fig. 42). Most commonly the gape affects the posterior margins. This condition is obviously essential in species with long siphons that cannot be completely retracted, but it also exists in some forms with relatively short siphons. A gape for the extrusion of the foot **(pedal gape)** may affect the anterior or anteroventral margins, and an opening for the passage of the byssus is found in all species firmly attached by this structure. In *Arca* the **byssal gape** is commonly broad and may give rise to much irregularity of the ventral margin, while in *Mytilus* it is a narrow cleft. In the Pectinacea, Limacea, and Pteriacea the byssal opening, when present, is close to the anterior auricle. In *Chlamys* and some other Pectinacea it is present in the right valve only and lies at the base of a deep notch **(byssal notch)** below the anterior auricle (Fig. 41). In *Tridacna* a broad, almost cordate byssal gape affects the hinge margin immediately in front of the beaks. In *Anomia* a deep embayment of the margin of the right valve or even an enclosed foramen connected to the margin only by a groove serves as the byssal opening.

## INTERNAL CALCAREOUS STRUCTURES OF HINGE

The hinge teeth, hinge plate, and structures serving for ligamental attachment will be discussed together, leaving the ligament to be dealt with by Dr. E. R. TRUEMAN in an ensuing part of this introduction. The ligament, composed of elastic horny material, connects the two valves dorsally, at the same time acting as a spring tending to open them. The function of the **hinge teeth,** which lie below the actual axis (usually passing through the ligament) about which the two valves hinge, is to guide them into the exact position in which they will fit tightly together when they are closed by the adductor muscles, and to interlock so that any rotational or shearing movements

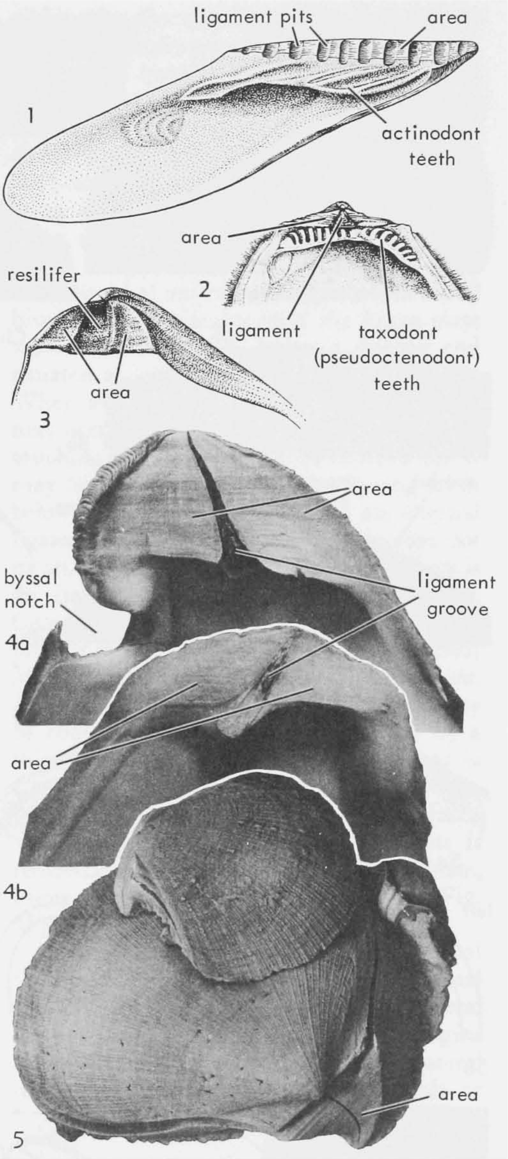

FIG. 44. General features of shells, with cardinal areas (Nuttall, n, except as stated otherwise).——*1. Gervillella sublanceolata* (D'ORBIGNY), L.Cret. (Apt.-Alb.), Eng., LV, ×0.3.——*2. Limopsis aurita* (BROCCHI), Mio.-Rec., Eu., Medit., RV, ×2.6 (from *157a*).——*3. Plagiostoma gigantea* J. SOWERBY, L. Lias., Eng., RV, ×0.5.——*4. Pedum spondyloideum* (GMELIN), Pleist.-Rec., Red Sea; *4a,* RV; *4b,* LV, ×1.3.——*5. Spondylus pacificus* REEVE, Rec., Pac., colony showing deep area on attached RV, much reduced in LV, ×1.

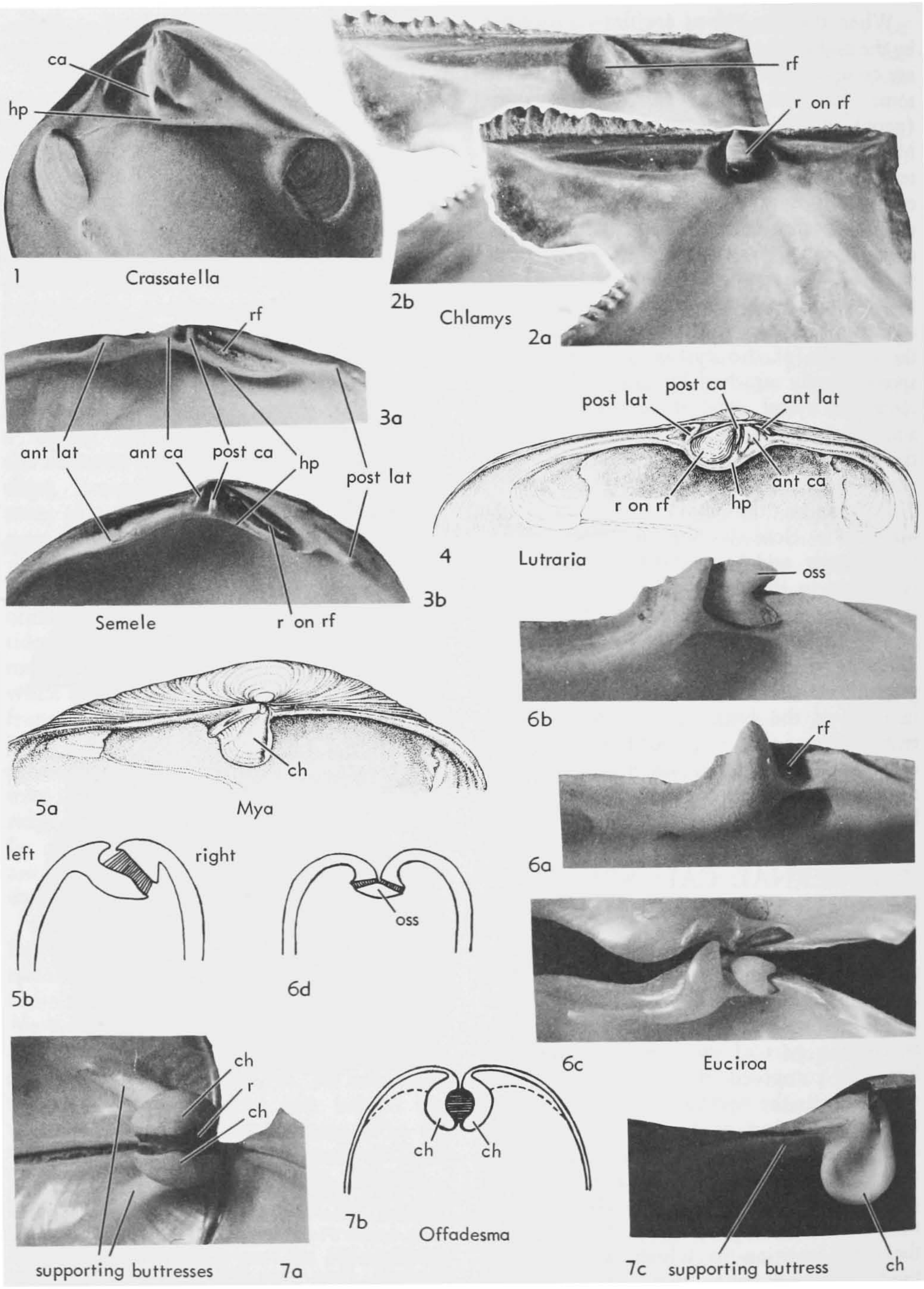

FIG. 45. Internal calcareous structures of the hinge (Nuttall, n, except as otherwise stated). Ligamental attachments.——*1.* RV of *Crassatella tumida* LAMARCK, Eoc.(Lutet.), France; resilium touching beak, ×1. ——*2. Chlamys* sp., Rec.; *2a,* RV showing partly calcified resilium; *2b,* after removal of resilium, ×2.——

of the valves are prevented (Fig. 45). It is clear that those bivalves, such as deep burrowers or rock-borers, that lead a relatively sheltered existence are less in need of a hinge apparatus that is thoroughly effective in performing these functions than those liable to be exposed to disturbed conditions. In *Spondylus,* which lives under such conditions, it is often impossible to separate the two valves of the shell without breaking the teeth. In most bivalves the two valves can be separated once the ligament is ruptured, some much more readily than others. It is evident from the way in which the teeth interlock that there will usually be a socket along the hinge of one valve for the reception of each tooth of the other valve, except perhaps for weak teeth which are merely projections of the dorsal margins. Thus, although a thin film of the mantle separates structures belonging to one valve from those of the other, an artificial mold of the dentition of one will reproduce the features of that of the other, apart from small details.

In the Bivalvia as a whole a great variety in the basic pattern of the structure of the hinge is observed, but in most forms striking homologies exist in arrangement of the teeth throughout any one major taxon. In addition, many show progressive changes in the dentition which can be shown to have occurred during the course of geological time. Thus the dentition constitutes the most satisfactory and practicable basis of classification within the class, while it is also an invaluable aid in evolutionary studies. Hinge teeth are found in the earliest known Bivalvia, and it seems scarcely necessary to indulge in speculations as to their origin. The suggestion that they arose from ribbing on the exterior of the shell has no supporting evidence.

In many forms some or all teeth in each valve are borne by a **hinge plate** (cardinal platform of some authors), an undercut shelly plate situated below the beak and the proximal parts of the dorsal margins and lying approximately in the plane of the valve margins (Fig. 45). The **nymph,** already mentioned (p. *N*46) as serving for attachment of an external ligament in many bivalves, is continuous with the hinge plate when this is present. It has a sloping end situated at some distance behind the beaks. When an internal ligament is present, this may occupy a depression in the hinge plate, touching the beak, as in *Crassatella,* or it may be borne by a process projecting from below the beak. DALL termed an internal ligament a **resilium** and any structure for its attachment a **resiliifer.**[1] **Chondrophore** is an alternative term for a projecting resiliifer. Commonly a spoonlike structure, this is present only in the left valve in the genus *Mya,* but in many genera (e.g., *Laternula, Periploma*) it occurs in both valves. It may be connected to the wall of the valve by a thin supporting buttress (or clavicle), as in *Laternula* and *Periploma.* In some genera, particularly in the superfamilies Pandoracea and Poromyacea, the internal ligament is reinforced by an accessory calcareous plate, known as the **lithodesma** or **ossiculum** (Fig. 45).

In many groups of the Bivalvia it is usual to refer to two categories of teeth, **cardinal teeth** lying just below the beaks and **lateral teeth** situated close to the dorsal margins at some distance from the beaks. Lateral teeth are described as **anterior laterals** or

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[1] Also known as *resilifer.*

FIG. 45. *(Continued from facing page).*

*3. Semele elliptica* (G. B. SOWERBY), Rec., Columbia; *3a,* RV hinge line viewed obliquely; *3b,* normal view, both showing weak external ligament and strong resilium in elongate sunken groove on hinge plate, ×1.——*4. Lutraria angustior* PHILIPPI, Rec., E.Atl. and Medit.; LV with resiliifer on prominent hinge plate, ×0.7 (from *157a*).——*5. Mya arenaria* LINNÉ, Pleist. and Rec., Arctic; N.Atl., N.Pac.; *5a,* oblique view of strong chondrophore of LV, ×0.5; *5b,* same, transverse section (from *157a*).——*6, Euciroa eburnea* (WOOD-MASON & ALCOCK), Rec., Ind.O.; *6a,b,* RVs, lithodesma or ossiculum missing and present, ×3.3; *6c,* both valves in juxtaposition, ×2.7; *6d,* transverse section.——*7. Offadesma angasi*-(CROSSE & FISCHER), Rec., N.Z., with spoon-shaped chondrophore mounted on strong posterior supporting buttress or clavicle; *7a,* both valves of broken specimen, ×2.3; *7b,* section; *7c,* LV, ×3. [Explanation: *ant,* anterior; *ca,* cardinal tooth; *ch,* chondrophore; *hp,* hinge plate; *lat,* lateral tooth; *oss,* ossiculum or lithodesma; *post,* posterior; *r,* resilium; *rf,* resiliifer.]

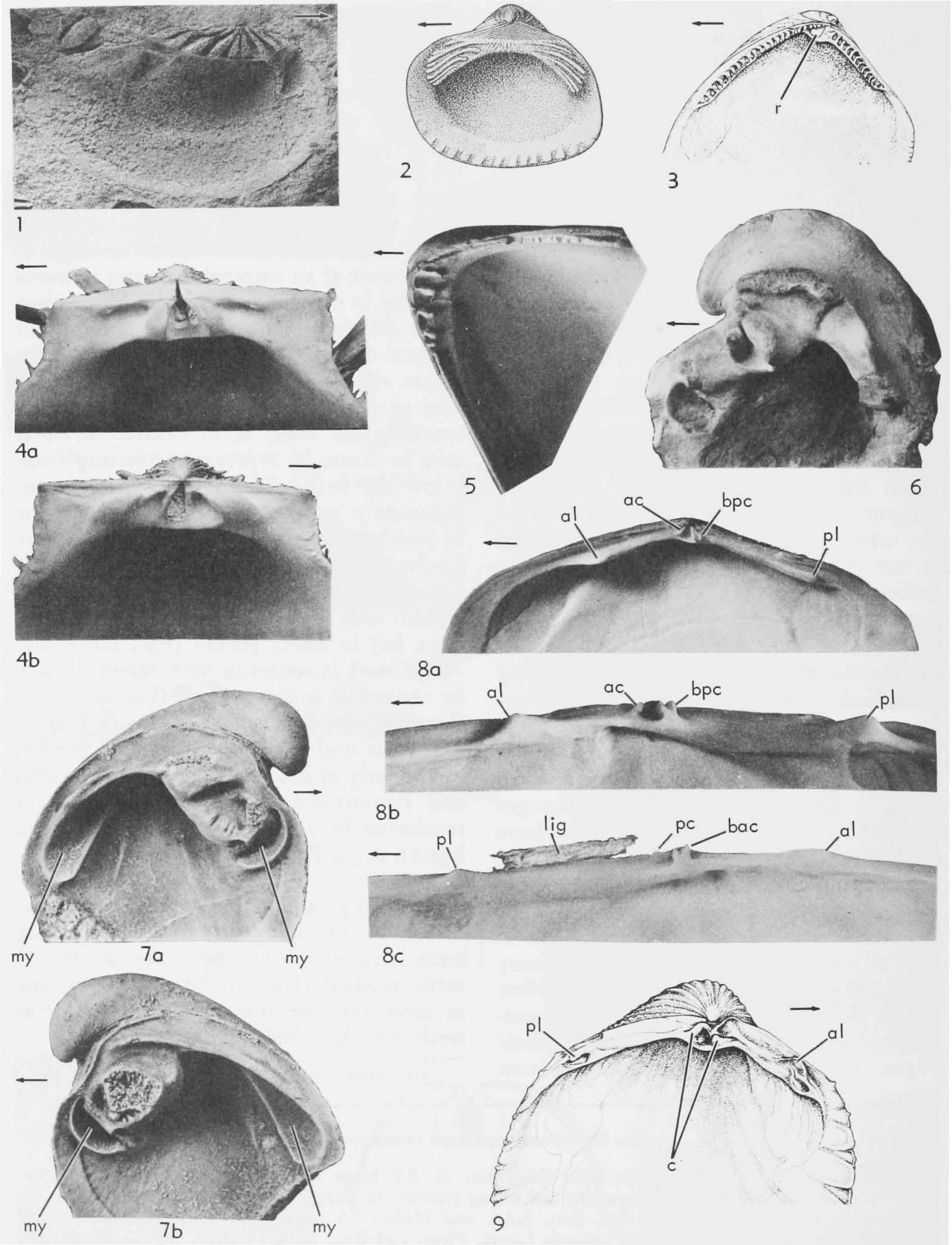

Fig. 46. Internal calcareous structures of the hinge—types of dentition (Nuttall, n, except *3* and *9,* from *157a*).——*1.* Actinodont, *Lyrodesma caelata* Salter, Ord.(Llandeil.), Eng., ×2.——*2.* Taxodont, *Cucullaea donningtonensis* (Keeping), Cret.(Neocom.-Apt.), Eng., ×0.5.——*3.* Taxodont, *Nucula turgida* Leckenby & Marshall, Rec., E.Atl.-Medit., ×3.——*4.* Isodont, *Spondylus imperialis* Chenu, Rec., China Sea; *4a,b,* ×1.——*5.* Dysodont, *Mytilus edulis* Linné, Rec., Eu.-E.N.Am.-W.N.Am.-Japan, ×3.——*6.* Pachyodont, *Pachyrisma grande* (Morris & Lycett), Jur.(Bathon.), Eng., ×0.4.——*7.* Pachyodont, *Mega-*

**posterior laterals** according to the end of the shell to which they are the more closely situated (Fig. 45). Cardinal teeth tend to radiate from the beaks, whereas lateral teeth commonly have a longitudinal orientation, parallel to the adjacent margin of the valve. There is some disagreement as to whether the term "lateral" should be restricted to teeth of which even the proximal end is well separated from the beaks, or if it should also refer to elongate longitudinal teeth (found, for example, in many Unionidae), although their proximal end is close to the beak. The term **pseudolateral** teeth has been applied to this latter category. Many authorities on the Unionidae apply the term **pseudocardinal** to teeth agreeing with the above definition of cardinals but differing from the cardinal teeth of other groups in their very irregular form. Cardinal teeth may be described as **prosocline or opisthocline** according to whether they slope (from their lower end) toward the anterior end of the shell or away from it, and as **orthocline** if they are almost perpendicular to the hinge axis. In view of the function of hinge teeth it is natural that their shape and development should depend to some extent on the shape of the shell within any major taxon. Thus in *Glossus,* a genus in which the umbones are placed very far forward and are strongly prosogyrous, anterior lateral teeth are absent and the much elongated cardinals are almost parallel to the dorsal margin instead of diverging radially, as in less inequilateral forms. Many such instances could be cited.

Hinge teeth are absent in some bivalves, including members of a number of families found in Paleozoic rocks; among these are the Solemyidae, which have survived to the present day. Such edentulous forms have been described as cryptodont (from the Greek κρυπτός, hidden, ὀδοντόω, to furnish with teeth). There are also edentulous (or anodont) genera belonging to families in which hinge teeth are usually well developed Examples are *Anodontia,* of the Lucinidae, and *Anodonta,* of the Unionidae. Several other terms including the letters "-odont" have been introduced in connection with hinge dentition, and it is important to distinguish their use as descriptive adjectives from those for names of taxonomic categories, in some cases with definitions extended beyond their literal meaning. In this section they are used in an adjectival sense; a number of "-odonta" names that have been proposed for major taxa are included in the list on p. *N*118.

One of the more simple types of dentition, described as **taxodont** (Greek τάξις, a single rank or line) consists of a series of short, straight or chevron-shaped teeth occupying the entire length of the dorsal margins (Fig. 44,*2;* 46,*2,3*), except that in some forms they are interrupted just below the beaks by a small triangular recess (resiliifer). Most commonly the teeth are not quite perpendicular to the hinge margin but slightly oblique, those on one side of the beak sloping inward so as to converge toward the series on the other side in a ventral direction. The taxodont type of hinge is met with very early in the geological history of the Bivalvia in representatives of the superfamily Nuculacea, but it has also arisen as a secondary development in the Arcacea. For this reason primary taxodont dentition has been described as **ctenodont** (Greek κτενίον, small comb) and the secondary type as **pseudoctenodont** (Fig. 44,*2*). An uneven series of small transverse teeth simulating taxodont teeth occurs in the nonmarine genera *Palaeomutela* of the Permian and *Pleiodon* of the present-day fauna. Such teeth have been termed **pseudotaxodont.**

**Actinodont** (Greek ἀκτίς, ray) dentition is another type that appeared very early in the history of the Bivalvia (Fig. 44,*1;* 46,*1*). The teeth radiate from the beak and the outer ones are more or less elongate, usually

Fig. 46. *(Continued from facing page).*

*lodon cucculatus* J. de C. Sowerby, Dev., Ger.; *7a,b,* ×1.3.——*8.* Heterodont, *Tellinella interrupta* (Wood), Rec., Carib.; *8a-c,* ×1.——*9.* Heterodont, *Acanthocardia echinata* (Linné), Rec., NE.Atl.-Medit., ×1. [Explanation: *ac,* anterior cardinal; *al,* anterior lateral; *bac,* bifid anterior cardinal; *bpc,* bifid posterior cardinal; *c,* cardinal teeth; *lig,* ligament; *my,* myophore; *pc,* posterior cardinal; *pl,* posterior lateral; *r,* resiliifer. Arrows indicate anterior of shell.]

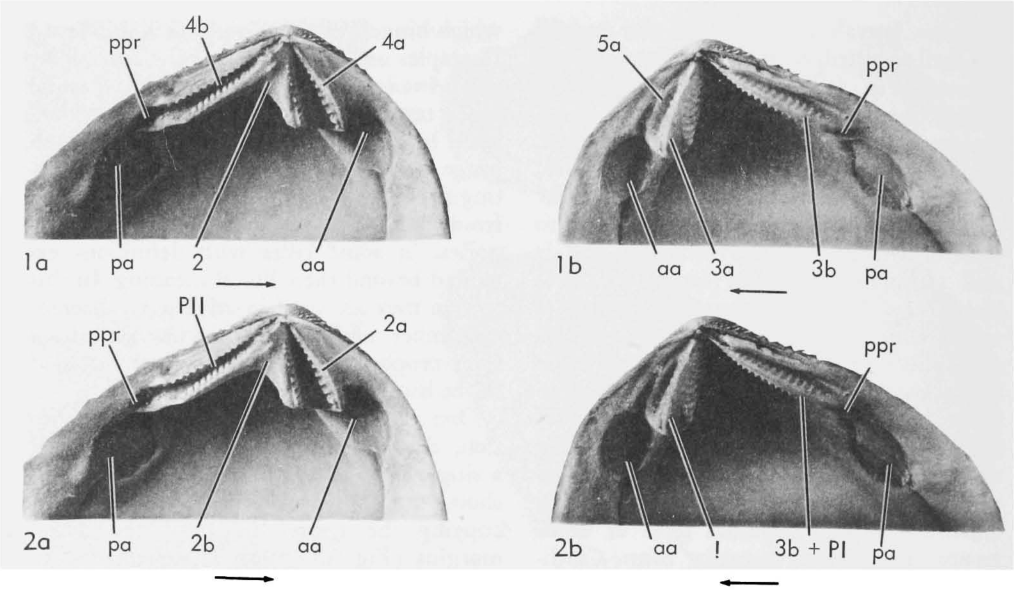

FIG. 47. *Neotrigonia margaritacea* (LAMARCK), Rec., Tasmania, ×1.3, showing notation for trigoniid dentition: *(1a,b)*, usual interpretation, and *(2c,d)* ODHNER's interpretation (mod. from Cox, 1952). [Explanation: *aa*, anterior adductor; *pa*, posterior adductor; ppr, posterior pedal retractor.]

diverging only slightly from the dorsal margin to which they are adjacent. In the lower Middle Cambrian genus *Lamellodonta* VOGEL the dentition approaches this pattern, but short subumbonal teeth are lacking, and the lamelliform teeth that are anterior and posterior to the beaks number only one or two on each side.

The term **schizodont** (Greek σχιζω, to split) has little value. It was originally applied primarily to the type of dentition found in the family Trigoniidae, in which the median tooth of the left valve, one of a small number radiating from the beaks, is broad and bifid (Fig. 47). This feature has no particular significance, as bifid teeth are found in other groups, including many heterodonts, discussed below. Forms belonging to the fresh-water superfamily Unionacea have been described as schizodont, as their dentition shows some similarity to that of the Trigoniacea, although not in this particular respect. The types of hinge found in these two superfamilies probably arose independently from the actinodont type. As already mentioned, there is no clear differentiation of the teeth into cardinals and laterals.

The **heterodont** (Greek ἕτερος, different) type of dentition was so termed because of the presence of distinctly differentiated cardinal and lateral teeth (Fig. 46,*8,9*). This condition is not, however, obvious in all bivalves to which the term is applied; in other words, use of the adjective is influenced to some extent by taxonomic considerations. The lateral teeth are obscure in many representatives of some heterodont families (e.g., Veneridae), and they are absent in other families (e.g., Thyasiridae, Psammobiidae, Solenidae, Hiatellidae). When laterals are present, they may belong to both anterior and posterior categories or only to one. Posterior laterals, when present in heterodont forms, lie entirely posterior to the ligament.

**Pachyodont** dentition (Greek παχυς, thick, stout) consists of heavy, blunt, amorphous teeth (Fig. 46,*6,7*). These mostly correspond to the definition of cardinals, but certain lamellar teeth present in some Megalodontidae (oldest family in which this type of dentition appears) could be termed laterals. In later groups (Diceratidae and rudists) there are two teeth in one valve and one tooth in the other. Some of these form elongate, projecting structures in many rudists, particularly the Hippuritidae and Radiolitidae, and are commonly associated with other heavy processes (**myophores**) for attachment of the "adductor" muscles (Fig. 46,7).

The typical **isodont** dentition (Greek ἴσος, equal) is that of the genera *Spondylus* and *Plicatula,* in which there are two equal teeth in each valve, placed symmetrically on either side of a triangular or rounded resilium pit and received in corresponding sockets in the other valve (Fig. 46,*4*). In the Pectinidae the hinge teeth are also symmetrically arranged with regard to the resiliifer but differ from those of the two genera just mentioned. Narrow, lamelliform teeth, one to three in number on each side and termed **cardinal crura** (sing., **crus**), radiate from the apex of the resiliifer, remaining close to the dorsal margin of each auricle. In some species of the family blunt ridges, each swelling out distally into a low tubercle, mark the lower boundary of the interior of the auricles; these ridges are termed **auricular crura.** The apparently feeble and relatively ineffective dentition found in some mytiliform shells, and consisting of small denticles situated close to the beak, is termed **dysodont** (Greek prefix δῦσ, badly, ineffectively) (Fig. 46,5).

For recording the hinge structure of any species there is no satisfactory substitute for clear illustrations. Formulae which have been devised to represent hinge dentition are unsatisfactory alone, as they do not indicate the shapes and relative sizes of the various teeth, their exact positions, or the angle that each forms with the adjacent dorsal margin. It is, however, an advantage to be able to letter the teeth in an illustration according to some standard notation. The earliest attempt to represent hinge teeth by a formula was that of STEINMANN, who designated each tooth by the numeral 1 and each socket by a cipher (0). Beginning at the anterior end of the hinge it was thus possible to represent the dentition of one valve by some such formula as 101010 and that of the opposite valve by reversing the 1's and the 0's. This crude method did not enable lateral teeth to be distinguished from cardinals, nor did it take into account teeth developed merely in a rudimentary form. DALL attempted to remedy such defects by introducing separate symbols for lateral teeth, by recording rudimentary teeth (by symbols placed in parentheses), and by adding a symbol for the resiliifer, but his system was rather confusing and was never widely adopted.

A system of hinge-tooth notation devised by BERNARD and MUNIER-CHALMAS has been much more widely accepted. It was based on ontogenetic studies carried out on heterodont bivalves and enables homologies between teeth of different genera to be indicated. To explain this system it is necessary to anticipate part of the section of this introduction dealing with ontogeny. The actual larval shell has small transverse crenulations rather like taxodont teeth along its hinge line. In the immediately ensuing postlarval stages of heterodonts these primitive crenulations are replaced by lamellae parallel to the dorsal margins (Fig. 48). There are usually two of these lamellae along the anterior part of the hinge in the right valve, one belonging to the left valve fitting between them; in addition, a further lamella may be developed as a projection of the hinge margin of the left valve. Similar lamellae may or may not be developed along the posterior part of the hinge. At this early stage the ligament is internal, separating the posterior lamellae from the anterior ones; in many genera it subsequently assumes an external position, but the effects of this original separation of the dental elements remain. The posterior lamellae give rise only to posterior lateral teeth, when these are present in the adult shell, but otherwise they disappear. The anterior lamellae, however, give rise to all the cardinal teeth, as well as to the anterior laterals, when present. The lamellae are assigned roman numerals, of which *I* and *III* (also, in some forms, *V*) represent those of the right valve, while *II* and *IV* (also, in some forms, *VI*) represent those of the left valve. The numbering is from the lowest (most ventral) tooth upward.

Cardinal teeth arise by the swelling out and detachment of the proximal ends of the

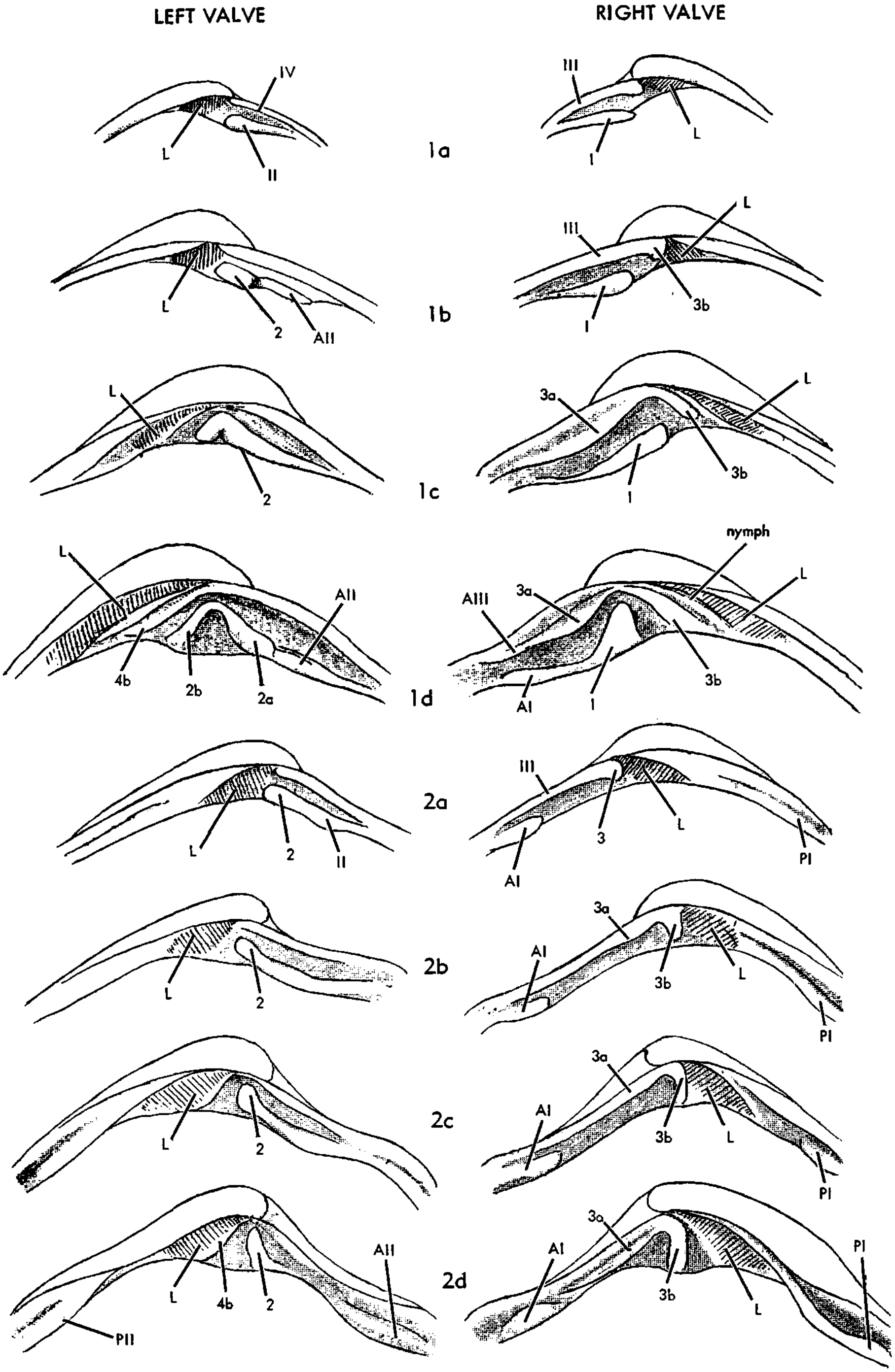

Fig. 48. Internal calcareous structures of hinge. Ontogenetic development of two species from lower Miocene of Bordeaux region, France (mod. from Bernard, 1895-97).——*1.* Corbiculoid (*ex* cyrenoid) type illustrated by *Gouldia deshayesiana* (Basterot); *1a,* at 0.4 mm.; *1b,* 0.64 mm.; *1c,* 0.96 mm.; *1d,* 1.2 mm.——*2.* Lucinoid type illustrated by *Loripes neglecta* (Defrance); *2a,* at 0.32 mm.; *2b,* 0.48 mm.; *2c,* 0.64 mm.; *2d,* 0.96 mm. [Explanation: *L,* ligament.]

lamellae, and are designated by arabic numerals corresponding to the roman numerals of the lamellae from which they are formed. The lamella *I* is not known to give rise to more than one cardinal, which receives the number *1,* and when its distal end persists as an anterior lateral tooth, this lamella is designated as *AI*[1] (Fig. 48, 49). The remaining lamellae have the potentiality for giving rise to two cardinals each. Thus, lamella *II* in some forms bends up to the beak as the juvenile shell grows and then bends down again, producing two cardinal teeth, to the posterior (downbent) one of which BERNARD assigned the number *2b* and to the anterior (upbent) one the number *2a;* but in some forms it merely bends up and gives rise to a single tooth which was designated as *2a* by BERNARD, merely as *2* by many authors, and as *2b* by DOUVILLÉ.[2] The proximal end of lamella *III* bends down to give rise to one cardinal tooth, designated as *3b,* while the same end of its unbent part swells out to form a cardinal designated as *3a;* both of these teeth are usually distinguishable. The proximal end of lamella *IV* may advance beyond the beak and above tooth *2,* to bend down next to the ligament to form a posterior cardinal tooth to which the number *4b* is assigned; more rarely, the same end of its unbent part may swell out to form a marginal cardinal tooth just in front of the beak, which is given the number *4a.* Usually only *4b* is present, but according to BERNARD, both *4a* and *4b* can be recognized in some species of *Corbula.* A tooth identified as *5b* is distinguishable in some species of *Astarte.* In all cases, when the primitive lamellae or their distal ends remain as lateral teeth, these receive the symbols, *AI, AII,* etc., and *PI, PII,* etc., *"A"* standing for anterior and *"P"* for posterior. The socket which receives any particular tooth is conveniently designated by the symbol for the tooth, to which is added an accent (for example, *AI′* is the socket that receives *AI*).

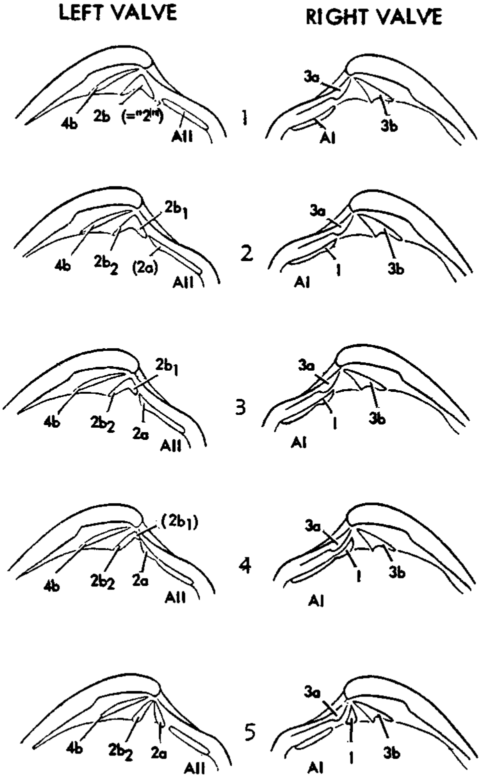

FIG. 49. Internal calcareous structures of the hinge. Generalized evolutionary changes between the Lower Jurassic and Lower Cretaceous (Lias to Neocomian) in members of the families Arcticidae and Veneridae. This shows (in LV) gradual production of *2a* as a swelling which eventually becomes separated at the rear of *AII;* simultaneously the anterior half of bifid *2b* atrophies. In RV, the median cardinal *1* can be seen separating from *AI* (Casey, 1952, fig. 1, p. 125).——*1.* Lucinoid type.——*2.* Arcticoid (*ex* cyprinoid) type.——*3.* Advanced arcticoid type.——*4.* Early corbiculoid (*ex* cyrenoid) type.——*5.* Corbiculoid type.

It follows from the above account that with the BERNARD notation all teeth in a right valve have odd numbers and all teeth in a left valve even numbers; also that, in a closed heterodont shell with every theoretically possible cardinal tooth developed, a series of pairs of teeth, diverging chevronlike and numbered upward, would be

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[1] BERNARD designated the lateral teeth as *LA I, LP I,* etc., but inclusion of the *"L"* makes hinge formulae unnecessarily long and might even cause confusion, as the same letter has also stood for "ligament" and for "left."

[2] This tooth commonly is bifid, however, its anterior and posterior branches being assigned the symbols $2b_1$ and $2b_2$ by CASEY, who has studied evolutionary changes in hinges of Mesozoic Arcticidae and Veneridae (see Fig. 49). CASEY, like DOUVILLÉ, has based his conclusions on historical rather than ontogenetic studies (such as employed by BERNARD). We must note yet again that the Theory of Recapitulation cannot fully explain their different observations.

stacked upon tooth *1,* the tooth designated by the letter *a* being the anterior one of each pair and that lettered *b* the posterior one. In almost every known hinge, however, one pair or another is incomplete.

In the construction of hinge formulae it is usual to follow STEINMANN's method of arranging the symbols for the teeth of each valve in alignment, starting with the anterior end of the hinge, but the symbols are separated by spaces instead of by ciphers. The whole hinge is usually represented by placing the formulae for the two valves one above the other, separated by a line (as numerator and denominator of a fraction). The symbol for each cardinal tooth is placed above or below the space representing its socket in the other valve. If a tooth is developed only in a rudimentary form its symbol is usually placed in parentheses.

BERNARD distinguished between two main types of heterodont dentition. In the first type, which he termed the **lucinoid type** (Fig. 48,*2;* 49,*1*), usually only two cardinal teeth occur in each valve, *3a* and *3b* in the right, and *"2"* (see above) and *4b* in the left, *"2"* occupying the so-called pivotal position immediately below the beaks. The chief families with dentition of this type are the Lucinidae, Cardiidae, Carditidae, Astartidae, and Crassatellidae, and the first four of these are among the earliest heterodont families to appear in the geological record. The hinge formula for bivalves with lucinoid dentition (omitting teeth *5b* and *6b,* recognizable in a few Astartidae) is as follows:

$$\frac{AI\quad AIII\quad 3a\quad 3b\quad PI\quad PIII}{AII\quad 2\quad 4b\quad PII\quad (PIV)}$$

(in single line this is given as *AI, AIII, 3a, 3b, PI, PIII / AII, 2, 4b, PII, (PIV).*

In the second type, which BERNARD termed the **cyrenoid type** (a name which must now presumably be emended to **corbiculoid** (Fig. 48,*1;* 49,*4,5*), there are usually three cardinal teeth in each valve, *3a, 1,* and *3b* in the right, and *2a, 2b,* and *4b* in the left, tooth *1* occupying the pivotal position below the beaks. The chief families in which this dental pattern is developed most typically are the Corbiculidae and Veneridae, and the hinge-formula reads as follows:

$$\frac{AI\quad AIII\quad 3a\quad 1\quad 3b\quad PI\quad PIII}{AII\quad 2a\quad 2b\quad 4b\quad PII\quad (PIV)}$$

or *AI, AIII, 3a, 1, 3b, PI, PIII/AII, 2a, 2b, 4b, PII (PIV).*

The **arcticoid** ("cyprinoid") (Fig. 49,*2,3*) type of dentition, introduced by CASEY, is more or less intermediate between the two just described. Tooth *1* is present at the posterior end of the anterior lateral *AI* and has not advanced to a pivotal position below the beak; *3b* is conspicuously bifid. Tooth *2b* is bifid in some but not in all forms, while *2a,* if distinguishable at all, is present only as a tubercle at the proximal end of *AII.* The hinge formula of a representative of the Arcticidae would thus read:

$$\frac{AI\quad AIII\quad 3a\quad (1)\quad 3b\quad (5b)\quad PI\quad (PIII)}{AII\quad (2a)\quad 2b\quad 4b\quad PII\quad (PIV)}$$

or *AI, AIII, 3a, (1), 3b, (5b), PI, (PIII) / AII, (2a), 2b, 4b, PII, (PIV).*

Attempts have been made by DOUVILLÉ and others to apply the BERNARD notation to several nonheterodont groups, in none of which has the early ontogeny of the shell been investigated adequately. It would certainly be useful to have an acceptable symbol for each hinge tooth in genera belonging to these groups, but not if this implies homologies which have not been proved to exist. Thus, four entirely different Bernardian hinge formulae have been suggested for the Trigoniacea (two shown in Fig. 47), three assuming that homologues of lateral teeth are present, the fourth that there are only cardinal teeth. DOUVILLÉ also considered that the two teeth in the rudist left valve were homologues of the laterals *AII* and *PII* (later reidentified as *AII* and *PIV*), whereas the single tooth in the right valve should be designated as *3b* (later *3*). The present *Treatise* designated the three teeth in question merely as *1, 3* and *2* respectively. DOUVILLÉ's application of cardinal hinge teeth notation to the Unionidae, (e.g., *5a, 3a, 3b/4a, 2a, 2b, 4b,* has not met with general acceptance. [See Addendum (p. *N*908) for more on bivalve dental notation.]

## TRANSPOSED HINGES

There are many recorded cases where certain hinge teeth of the two valves are transposed, those present in one valve corresponding in number and positions to those usually found in the other (Fig. 50). Such occurrences resemble sinistrality in gastropods in that they may constitute individual abnormalities in particular species, while in certain cases they have been considered to have greater taxonomic significance. There appears to be a particular tendency for abnormal transposition to occur in certain families, notably the Astartidae, Crassatellidae, and Unionidae. An investigation carried out by POPENOE & FINDLAY (1933) showed that in *Astarte* one specimen in 130 exhibited this phenomenon and in *Cardita* one specimen in 180, and these authors quote a statement by DALL that in one lot of *Goodallia* examined nearly one-third had the hinge reversed. They also found that transposition did not affect the complete hinge (that is, posterior laterals, cardinals, and anterior laterals) in any of the species studied. In some specimens the cardinals and anterior laterals were transposed while the posterior laterals were developed normally in the respective valves; in other specimens it was only the posterior laterals that were transposed. On the other hand, EGGLETON & DAVIS have recorded that in a living population of the freshwater genus *Sphaerium* there was a transposition rate of 12.1 percent, and of the transposed specimens 40.5 percent had the posterior laterals only reversed, 41.0 percent the anterior laterals and cardinals, and the remainder (18.5 percent) all the teeth. NEWELL found that all the teeth were transposed in a Permian specimen of *Permophorus albequus* (BEEDE), probably the geologically oldest shell in which the phenomenon has been observed.

The case of the Chamidae, a family in which one valve is cemented to the substrate, has attracted considerable attention because transposition of the hinge teeth goes hand-in-hand with reversal of the valve of fixation. The fixed valve invariably has two teeth and the free valve one tooth. The so-called "normal" condition is when fixation is by the left valve and the "inverse" condition when it is by the right valve; the two valves can be distinguished readily because the umbones are strongly prosogyrous in all specimens. ODHNER considered that "normal" and "inverse" specimens should be referred to different genera, *Chama* and *Pseudochama,* but not all authorities are in agreement with this conclusion, some believing that both types of shell could even belong to a single species.

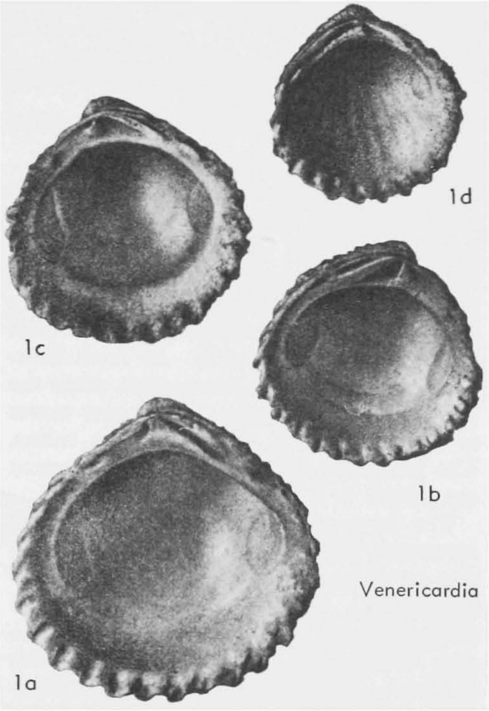

FIG. 50. Bivalve shells with transposed hinges.——*1. Venericardia parva* LEA, Eocene (Claiborne), Alabama; *1a,b,* normal right and left valves, ×14; *1c,d,* right and left valves having transposed cardinal and anterior lateral teeth, ×15 *(136).*

Some discussion has arisen as to how BERNARD's notation should be applied to specimens with transposed hinge teeth. While some authors have advocated interchanging the symbols between the two valves, others have maintained that the apparent transposition could have resulted from the suppression or accentuation of tooth elements belonging properly to the valves in which they are found so that symbols appropriate to that valve should be used. It seems advisable to refrain from applying any notation to transposed hinges, particularly as no observations have been made on the ontogeny of shells in which they occur.

## LIGAMENT

### By E. R. Trueman

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The shell in the Bivalvia consists characteristically of two lateral calcified valves joined by a horny ligament; being parts of the same structure, these are all formed in the same manner. The term **ligament** may be used to describe all parts of the shell joining the valves dorsally. Its main function is to cause the valves to open when the adductor muscles relax, and it also serves to unite the dorsal margins of the valves. The form and composition of the ligament are related to both of these functions.

The form of the ligament, which with reasonable probability represents the primitive condition, is termed the **primary ligament** *(127)*. Such a ligament consists of the superficial periostracum and the lamellar and fibrous layers (Fig. 51,*A*). This ligament somewhat resembles that of *Limopsis.* It is secreted respectively by the inner surface of the outer mantle fold (formerly termed the periostracal groove), the outer surface of the same fold, and a specialized region of the general outer surface of the mantle, the mantle isthmus. The primary ligament represents the basis of the ligament throughout the Bivalvia except where it is largely or completely lost, as in the Pholadacea.

Previous authors *(34, 76, 127)* have used different nomenclature in describing the principal layers of the ligament. For instance, the lamellar layer corresponds to the outer layer or to what Dall considered the ligament proper, while the fibrous layer has been variously referred to as the inner layer, cartilage, or resilium. But the terms **lamellar** and **fibrous layers**, first used by Newell *(113)*, are probably those most generally acceptable. The terms outer and inner layer are certainly confusing when used in combination with the terms internal or external to describe the location of the ligament on the valves. In the ligament of *Ostrea,* for example, both layers are situated internally, whereas in the Semelidae *(167)* the ligament is in two parts, along the valve margins and between the valves, and both parts contain lamellar and fibrous layers. The structure of these layers is generally quite distinct. The lamellar layer consists of nearly parallel lamellae of protein which lie parallel to the growth surface of the layer when they are being secreted but subsequently may lie obliquely (Fig. 51,*B,C*). This layer is characteristically dark brown in color and has undergone hardening by aromatic tanning. The fibrous layer shows growth lines, which may correspond to the laminations of the lamellar layer, so that both structures may be considered to represent phases of secretory activity of the mantle epithelium. The fibrous layer also shows a fibrous structure in which the long axis of each fiber is normal to the growth surface at the point of its secretion (Fig. 51). The horny organic material of the ligament, termed **conchiolin,** largely consists of protein material. In the periostracum and outer layers the conchiolin is hardened by quinone tanning and is not calcified, whereas the inner layer is calcified, though to a less extent than the inner layer of the valves (a notable exception to this being observed in the Pectinidae, where the main part of the inner layer is not calcified but is extensively tanned *(166)*.

The primary ligament appears to persist unmodified in some genera (e.g., *Monia,* Anomiidae; *Lima, 195,* Fig. 51,*A*), but usually some degree of secondary extension is provided at either end of the ligament or at both ends. The secondary ligament may consist of either periostracum (e.g., *Entodesma, Mytilimeria, 191,* and *Mytilus, 195,* Fig. 51,*B*), or of a fourth layer of the ligament, the **fusion layer** (e.g., in *Pinna, 192; Glossus (Isocardia), 123,* and *Tellina, 164,* Fig. 51,*C*). The fusion layer is secreted by the outer surface of the outer folds of the mantle edge after they have become fused in early postlarval life, and its appearance is somewhat intermediate between the periostracum and the lamellar layer. It generally plays only a minor role in the mechanical operation of the ligament, functioning simply as a union or cover between the dorsal margins of the valves as in *Pinna (192).* In *Tellina (164)* this layer forms a

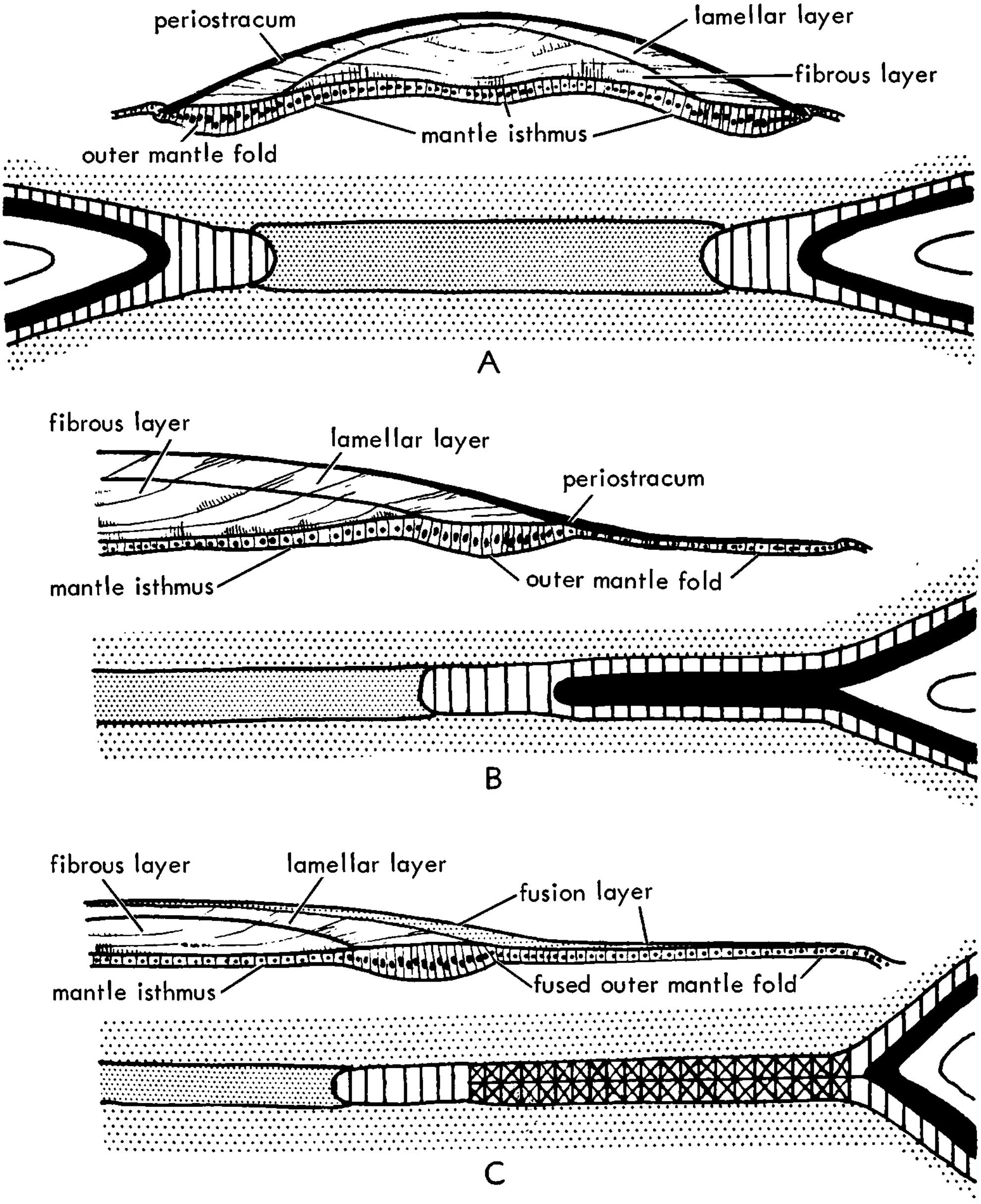

FIG. 51. Bivalve ligaments (diagrammatic) (Trueman, n).——*A*. Primary ligament.——*B*. Primary ligament with periostracal secondary extension (e.g., *Mytilus*).——*C*. Primary ligament with secondary extension produced by fusion layer (e.g., *Tellina*). [Explanation: Upper diagram of each pair represents median longitudinal section of ligament and lower diagram shows dorsal aspect of mantle tissues involved in its secretion. *Coarse stipple,* general outer surface of mantle secreting fibrous layer of valves; *fine stipple,* mantle isthmus secreting fibrous layer of ligament; *vertical rules,* outer surface of outer mantle fold secreting outer calcareous layer of valve and lamellar layer of ligament; *black,* inner surface of outer mantle fold secreting periostracum; *cross hatching,* fused outer mantle folds secreting fusion layer.]

relatively long posterior extension of the primary ligament and has been described as the posterior cover. The anterior cover appears to be formed by the anterior lamellar layer in this genus, but in the Solenidae the fusion layer extends both in front of and behind the primary ligament *(125)*. Discrimination between periostracum and the fusion layer depends on the degree of fusion of the mantle folds and the extent of the pallial muscles has been used to distingush between them *(124)*. Where the outer surfaces of the outer folds of the mantle are fused, leading to secretion of the fusion layer, pallial attachment is lost. Pallial muscle attachment is retained where the valves are joined by periostracum.

The ligament is formed in a characteristic manner in each group of bivalves, being situated either between the cardinal areas of the valves, as in *Ostrea* and *Mya,* or conspicuously along the valve margins, as in *Tellina* and *Cardium*. The ligament may be either elongated or condensed, with primary and secondary constituents variously developed. No general description will cover all cases but the terms **amphidetic** and **opisthodetic** *(112)* may be usefully employed to express the relation of the mantle isthmus to the umbones. Thus a symmetrical condition of the mantle isthmus between the umbones gives an amphidetic ligament, as in *Glycymeris* and *Pecten*. In an opisthodetic ligament, the mantle isthmus is mainly posterior to the umbones, as in *Mytilus* and *Tellina*. The terms **alivincular** and **parivincular** are used to describe the form of the ligament *(34)*, an alivincular ligament being a flattened structure situated between the cardinal areas of the valves with the lamellar layer both anterior and posterior to the fibrous layer, as in *Ostrea (165)* (Fig. 52,*A*). The parivincular ligament is usually conspicuous along the posterior margins of the valves and is cylindrical in shape, as in *Tellina (164)* (Fig. 52,*D*). It has probably evolved from an opisthodetic ligament situated between the valve margins, as in *Mytilus* or *Pinna* (52,*C*).

During growth of the bivalve shell the ligament elongates, and it is functionally essential that a straight longitudinal hinge axis be maintained. To lengthen a straight line on the border of a rounded body, either the axis of the ligament must descend or the outline of the body must be elongated. The method of growth of the postlarval ligament of most bivalves falls into these two broad categories. In some the hinge axis elongates largely by ventral growth of the ligament, as in *Ostrea (165)*. The early (and dorsal) part of these ligaments commonly becomes worn away and the inner layer exposed, replacement taking place by addition to the ventral surface, as most markedly occurs in *Hinnites*. This appears to be a modification associated with attachment by cementation, as has also been described for *Etheria (196)*. Indeed, alivincular ligaments of the general form of that of *Ostrea* commonly occur in cemented genera such as *Spondylus*. The ratio between anterior-posterior length and the dorsoventral thickness is usually of the order of not more than 3 or 4 : 1. Other bivalves, as in *Mytilus,* show extension of the dorsal valve margin, and the axis of the ligament exhibits little ventral migration but considerable posterior extension to form an opisthodetic ligament. For opisthodetic ligaments the length to thickness ratio is rarely less than 10 : 1.

The alivincular ligament may be oriented more or less symmetrically about the umbones (amphidetic), as in *Ostrea, Spondylus,* and *Limopsis* (Fig. 52,*A*), but in some genera, for example *Pteria* (Fig. 52,*B*), it is inclined from the umbones into a condition which appears to be somewhat intermediate between amphidetic and opisthodetic ligaments (Table 1). During growth an alivincular ligament becomes fractured dorsally, being replaced by ventral secretion *(165)*, while the cardinal area of an opisthodetic ligament is similarly changed because of the tangential growth of the valves. In the latter, replacement takes place by posterior growth of the anterior lamellar layer (Fig. 52,*D*), which occurs very markedly in *Glossus (123)*.

The principal exceptions to the above classification of the ligament are the **multivincular** and **duplivincular** ligaments. The multivincular ligament found in *Isognomon (76, 113, 114, 169)*, for example, develops from an alivincular ligament by the addition posteriorly of successive areas of fibrous layers **(resilia)**, which are completely isolated from each other by the lamellar layers (Fig. 52,*F*). The ligament of young *Isognomon* resembles that of *Pteria* (Fig. 52,*B*) *(76)*. The production of these successive resilia can only take place by the development of successive areas of

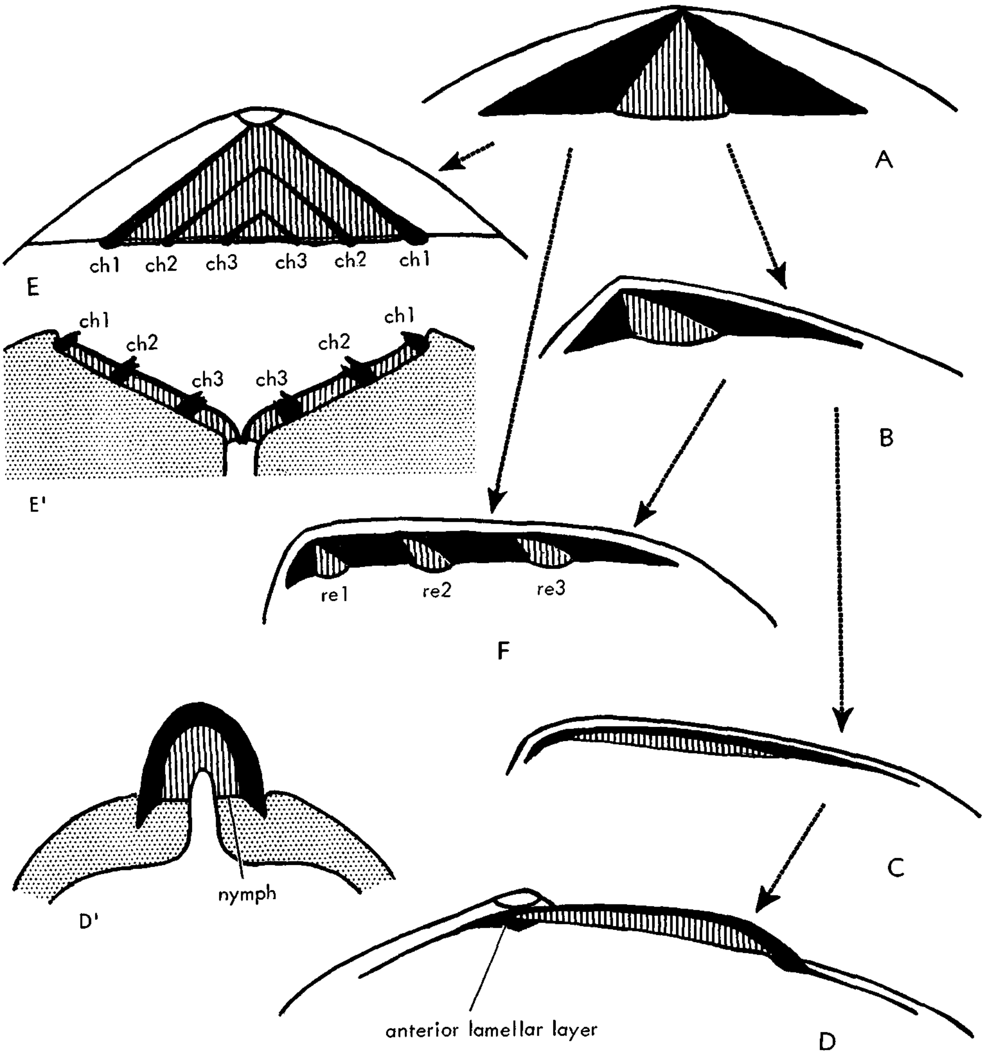

FIG. 52. Bivalve ligaments, diagrammatic sections showing location of ligament in relation to right valve (Trueman, n).——*A*. Alivincular amphidetic ligament comparable to primary ligament (e.g., *Limopsis*).——*B*. Alivincular ligament intermediate in form between amphidetic and opisthodetic.——*C*. Opisthodetic ligament placed directly between valve margins (e.g., *Mytilus*) (=*tr.*, Table I).——*D*. Opisthodetic parivincular ligament (e.g., *Cardium*) showing anterior lamellar layer with posterior growth below ligament in cardinal area, accompanying transverse section *(D')* showing C-spring shape of ligament and nymph.——*E*. Duplivincular ligament (e.g., *Arca*) with true lamellar layer *(ch1)* comparable to that of primary ligament and similar successive chevrons *(ch2, ch3)* shown in longitudinal *(E)* and transverse *(E')* sections.——*F*. Multivincular ligament (e.g., *Isognomon*) showing first-formed fibrous layer *(re1)* and successive resilia *(re2, re3)*. [Explanation: *Black*, lamellar and fusion layers of ligament; *vertical rules*, fibrous layer of ligament; *stippled pattern*, calcareous shell of valves in section. Arrows indicate inferred possible evolutionary relationships between different ligament types.]

secondary mantle isthmus epithelium *(169)*. The duplivincular ligament *(114)*, found, for example, in *Arca,* has bands of lamellar layer on the cardinal area of the valves, giving the appearance of a series of chevrons (Fig. 52,*E*). The ligament is amphidetic and new chevrons usually occur centrally and grow centrifugally. The fibrous layer runs continuously from end to end of the ligament, but it is usually partially (as in *Glycymeris*) or completely (as in *Arca noae*) divided into two lateral halves. It has been suggested *(126)* that the mantle in many of the Arcoida has divided, during ontogeny, into two lobes in the region of the mantle isthmus. Considerable interumbonal growth of the valves takes place in the cardinal area, and, as the umbones move apart in ontogeny, so, also, does the earliest formed ligament, producing a chevron effect. In its earliest ontogenetic stages this ligament is not unlike the primary ligament and, indeed, in the Limopsidae this condition persists.

The insertion of the ligament into the valves generally exhibits an arrangement characteristic of the form of the ligament, and it is often possible to infer the nature of the ligament from the valves even in Paleozoic shells. Many of these have ligament areas similar to those of modern shells *(76)*.

Table 1 shows the structure of the ligament in representative genera and indicates the form of attachment of the ligament, particularly the fibrous layer, to the valves. Distinction usually can be made between the chevron pattern of the duplivincular ligament and the insertion of the fibrous layer in a resiliifer or along the thickened margins of the valve (nymphs).

It is difficult to utilize the ligament as a factor of importance in classification of the Bivalvia because of its adaptive characters. It is notable that the form of the larval ligament shows little variation throughout the group and resembles the primary ligament. Differentiation takes place immediately following settlement, being closely related to the change in habitat and the increase in shape and size of the valves. The development of diverse forms of adult ligaments from a fundamentally similar larval ligament is largely dependent on the growth pattern of the mantle and shell complex, and the effect on this of selective processes.

However, Table 1 does show something of the phylogenetic distribution of the ligament. In the Palaeoheterodonta and Heterodonta opisthodetic and parivincular ligaments with a well-developed fusion layer commonly occur. The most obvious exceptions to this are clearly adaptive modifications, such as in *Mya* or *Lutraria* to deep burrowing *(171)*, the Pholadidae to rock-boring, and *Etheria* to cemented attachment *(196)*. The parivincular ligament, in the form of a C spring, reaches its maximum development in genera such as *Arctica, Cardium,* and *Tellina,* but, even so, in the Semelidae and Scrobiculariidae, closely related to the last genus, there is also an internal or cardinal ligament which functions as the only part of the ligament under compression when the valves are closed *(167)*. The parivincular ligament has probably evolved to its present form by the upward growth of a ligament situated transversely between the dorsal margin of the valves, somewhat resembling that of *Mytilus* (Fig. 52,*C*). An opisthodetic parivincular ligament also occurs in *Malletia,* but this cannot be taken as indicating close affinity between the Palaeotaxodonta and Heterodonta.

The Palaeotaxodonta and Cryptodonta have ligaments which are essentially the same as those of other bivalves. They are groups which have undergone a considerable degree of adaptive radiation, as is indicated by the diversity of their ligament form (Table 1). Quite distinct from the previous groups, the ligament in the Arcacea and Limopsacea is generally characterized by interumbonal growth and duplivincular structure, the major exception to this being *Limopsis* where the ligament resembles the primary ligament. The juvenile stage of the duplivincular ligament before the development of chevrons, represented in Figure 52,*E* by the ligament nearest the umbo, is comparable to the primary ligament. Bivalves with duplivincular ligaments could give rise to forms with alivincular ligaments by a neotenous retention of the primary ligament perhaps consequent on relatively less interumbonal growth of the valves.

TABLE 1. *Some Characteristics of Ligaments in Representative Genera of Bivalves.*

[Explanation: ab, absent; al, alivincular; am, amphidetic; ca, cardinal area (or subcardinal area); ch, chevron pattern; co, calcareous ossicle; du, duplivincular; mu, multivincular; ny, nymph; op, opisthodetic; pa, parivincular; pr, present; re, resilia (placed between resilifers); tr, transverse between dorsal valve margins; *Etheria ligament much modified subsequent on attachment by cementation.]

| | Placement | Type | Fusion layer | Lamellar layer | Fibrous layer | References |
|---|---|---|---|---|---|---|
| PALAEOTAXODONTA | | | | | | |
| Nuculacea--Nucula | am | al | ab | tr | re | TR |
| Nuculanacea--Nuculana | am | al | ab | tr | re | 127 |
| Malletia | op | pa | ? | | ny | TR |
| CRYPTODONTA | | | | | | |
| Solemyacea--Solemya | op | tr | ab | tr | re | 127 |
| PTERIOMORPHIA | | | | | | |
| Arcacea--Arca | am | du | ab | ch | ch | 127 |
| Limopsacea --Limopsis | am | al | ab | | re | 113 |
| Glycymeris | am | du | ab | ch | ch | TR |
| Mytilacea--Mytilus | op | tr | ab | tr | ny | TR |
| Pinnacea--Pinna | op | tr | pr | tr | ny | 192 |
| Ambonychiacea--Myalina | op | du | ? | ch | ch | 115 |
| Pteriacea--Pteria | am/op | al | ? | | re | TR |
| Isognomon | op | mu | ab | tr | re | 169 |
| Pectinacea--Pecten | am | al | ? | tr | re | 166 |
| Pterinopecten | am | du | ? | | | 113 |
| Spondylus | am | al | ? | | re | TR |
| Ostreacea--Ostrea | am | al | ab | | re | 165 |
| PALAEOHETERODONTA | | | | | | |
| Anthracosiacea--Anthracosia | op | pa | ? | | ny | TR |
| Unionacea-- | | | | | | |
| Anodonta | op | pa | pr | | ny | TR |
| PALAEOHETERODONTA (continued) | | | | | | |
| Unionacea--Etheria | op | al* | ab | | | 196 |
| Trigoniacea--Trigonia | op | pa | pr | | ny | TR |
| HETERODONTA | | | | | | |
| Lucinacea--Diplodonta | op | pa | pr | | ny | 2 |
| Crassatellacea--Astarte | op | pa | pr | | ny | TR |
| Cardiacea--Cardium | op | pa | pr | | ny | TR |
| Mactracea--Lutraria | op | ca | ab | ca | re | 171 |
| Solenacea--Ensis | op | pa | pr | | ny | 126 |
| Tellinacea--Tellina | op | pa | pr | | ny | 164 |
| Donax | op | pa | pr | | ny | TR |
| Abra | (pa+ca) | | pr | (re+ny) | | 167 |
| Dreissenacea--Dreissena | op | tr | ab | | ny | TR |
| Glossacea--Glossus | op | pa | pr | | ny | 124 |
| Veneracea--Venus | op | pa | pr | | ny | 126 |
| Petricola | op | pa | pr | | ny | 126 |
| Glauconome | op | pa | pr | | ny | 126 |
| Myacea--Mya | op | ca | ab | ca | re | 170 |
| Pholadacea--Zirfaea | ab | | | | | TR |
| ANOMALODESMATA | | | | | | |
| Pandoracea--Cochlodesma | op | ca | pr | | re | 3 |
| Lyonsia | op | ca | ? | re,co | | 191 |

Index numbers for references correspond to those in list at end of chapter; TR denotes observations by Trueman.

Although the duplivincular ligament has been shown to occur in the ancestry of pteriaceans, scallops, and marine mussels, in all but the Arcoida it was replaced before the Jurassic, the two former groups having followed similar evolutionary trends *(115)*. Attainment of the monomyarian condition may be followed by secondary symmetry of the valves and ligament as has occurred in the evolution of *Pecten (193)*. But in the Dysodonta, as in all other bivalves, the ligament shows adaptive radiation in forms as diverse as *Pecten, Pinna,* and *Isognomon,* so that while the structure of the ligament may provide additional clues to phylogeny this evidence should not be used independently.

In all Bivalvia closure of the valves causes a condition of stress in the ligament, the lamellar and fusion layers being stretched and the fibrous layer compressed. In the ligament of *Mytilus* (Fig. 53), which may be taken as a fairly generalized example, the neutral axis of the structure lies approximately between the fibrous and lamellar layers. The orientation of the molecules of the lamellar layer is such that the tensile stress is imposed along their principal axis, while the structure of the fibrous layer is more suited to compression. When the fibrous layer is subjected to tension it readily fractures, as in an alivincular ligament such as that of *Ostrea,* where during growth it comes to lie above the axis. Some measure of the efficiency of operation of the ligament has been obtained by a study of the mechanical properties of the intact and isolated ligament. The ligament of the Pectinidae, in which the main part of the inner layer is not calcified, has been

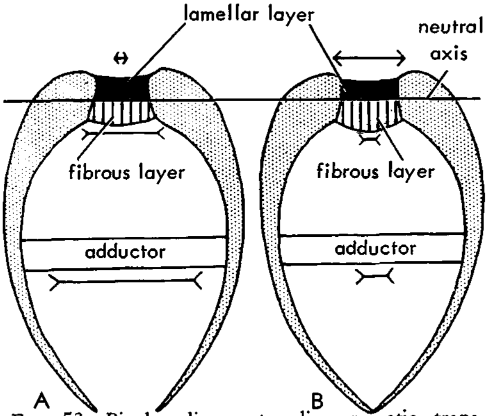

FIG. 53. Bivalve ligaments—diagrammatic transverse sections of *Mytilus* with valves gaping *(A)* and closed *(B)*, relative length of arrows adjacent to ligament layers and adductor muscle indicating change in their dimensions on closure of shell *(171)*. [Explanation: *Stippled pattern,* calcareous shell of valves in section; *black,* lamellar layer of ligament; *vertical rules,* fibrous layer of ligament; *horizontal line intersecting ligament,* approximate neutral axis of ligament.]

shown to be the most efficient mechanically *(168)*. It is notable that this family includes most of the few free-swimming bivalves. In few burrowing forms is the ligament strong enough to open the valves against resistance of the substratum, and it is usually supplemented either by the foot, as in *Tellina* and *Anodonta,* or by hydrostatic pressure of the water contained within the mantle cavity, as in *Mya (170)*.

The main ligament types may be briefly surveyed with regard to their design and to their mechanical efficiency of operation. The duplivincular ligament is a relatively ineffective structure. It provides a flexible attachment between the valves, acting more as a hinge than an opening mechanism, and the foot is probably used to push the valves open. The alivincular ligament, although it may be fractured dorsally, maintains an opening moment throughout the life of an individual bivalve. In certain genera, such as *Ostrea* and *Pecten,* where the foot is reduced or absent, it is the sole means of opening the valves and must maintain a sufficient opening moment. A somewhat similar condition must occur in *Mytilus,* where the long opisthodetic ligament is among the most powerful. The parivincular form probably represents the most highly evolved ligament mechanism and its mode of growth by posterior extension and replacement of the fractured umbonal region is both simple and efficient, more so than the repetition of duplivincular or ventral migration of the alivincular ligaments. It may be considered that an elongated opisthodetic ligament represents the most effective way that the bivalves have evolved of overcoming the allied problems of growth of an exoskeletal structure and its continued function, both as a means of uniting the valves dorsally and of causing the shell to gape ventrally. Perhaps this is the reason for the dominance of the opisthodetic ligament in the Heterodonta.

[*End of section by E. R. Trueman.*]

# SUPPLEMENTARY CALCAREOUS STRUCTURES

## PLATES ACCESSORY TO SHELL VALVES

In the Pholadidae the two valves of the shell are supplemented by plates located along the dorsal margin and, in some genera, along the ventral margin. These plates are of various shapes, and some are likely to be mistaken for gastropod shells of a simple type, such as *Scutum.* At the anterior end of the dorsal margin is the **protoplax,** an almost flat, longitudinally elongated, spearhead-like plate which is either in one piece or divided longitudinally into two; it may be chitinous or calcareous. Behind it is the **mesoplax,** a transversely elongated plate, commonly with infolded margins, which lies athwart the umbonal region of the shell and protects the posterior part of the anterior adductor muscle; this is always calcareous and may also consist either of one piece or of two. The **metaplax** is a long, narrow, usually calcareous plate which extends dorsally behind the umbones, covering the gap between the shell margins (Fig. 54). The **hypoplax,** also usually calcareous, is an elongate plate extending along the posterior end of the ven-

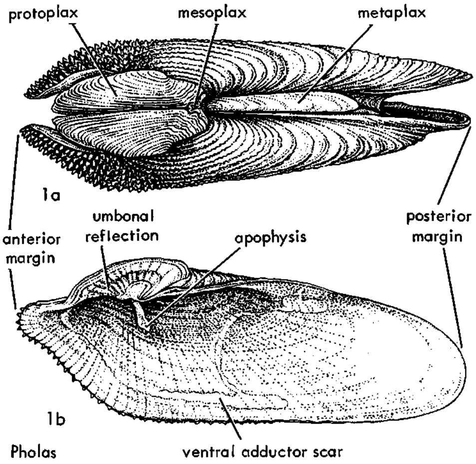

FIG. 54. Bivalve supplementary calcareous structures —*Pholas dactylus* LINNÉ, Recent, Europe, showing dorsal *(1a)* and interior lateral *(1b)* views, X0.8 *(157a)*.

tral margin, covering the gape of the two valves. The complete series of plates is not developed in any known species, the number present ranging from one to three (or four when one is divided). The mesoplax occurs most commonly; it is, however, absent in the genus *Barnea.*

Comparable to these structures is a small triangular plate present in the genus *Caestocorbula* (Corbulidae), occurring on the left side along the posterodorsal margin.

## PALLETS OF TEREDINIDAE

Pallets, which are peculiar to the Teredinidae, are small, paired calcareous structures that serve to close the end of borings when the siphons are retracted (Fig. 55). Each consists of a rodlike proximal part (**stalk**) and a broader distal part which may be bladelike or cuplike, or may consist of a series of funnel-shaped structures, each emerging from the one below it. The maximum length of the pallets of the shipworm *Teredo navalis* LINNÉ is about 5 mm., while that of a typical *Bankia capensis* (CALMAN) is about 30 mm. The stalk of the pallet fits into a groove between the siphons and the end of a duplication of the mantle (**collar**) that covers their proximal end. Fossil teredinid pallets are known from the Paleocene onward.

## SECONDARY ADDITIONS TO SHELL

In some Pholadidae an anterior (pedal) gape of the margins becomes closed after a certain stage of growth by an evenly rounded extension of the shell proper, known as the **callum.** In many of the Martesiinae this extends around the anterodorsal part of the shell and between the beaks, covering the anterior portion of the anterior adductors. In *Jouannetia* the presence of the callum gives the shell an almost spherical shape, the left valve partly covering the right valve; at the same time a tonguelike posterior secondary extension of the shell is present in the right valve only. In some Pholadidae a tubular secondary structure (**siphonoplax**) forms a continuation to the posterior end of the shell, protecting the proximal end of the siphons.

## TUBULAR PROTECTIVE STRUCTURES

Under this heading may be included the tubular structures built by certain bivalves

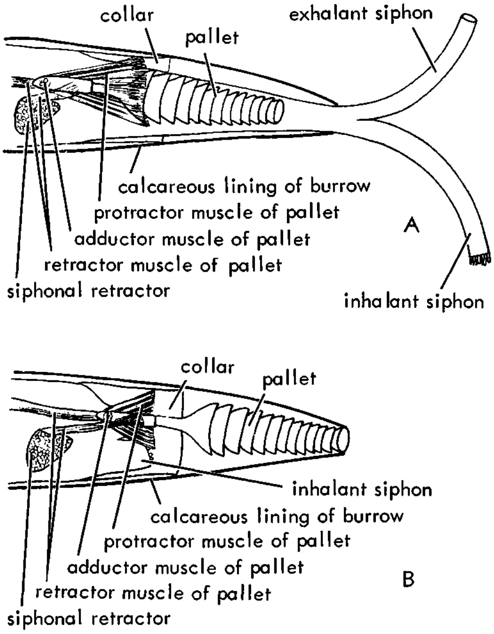

FIG. 55. Bivalve supplementary calcareous structures —*Xylotrea gouldi* JEFFREYS, Recent, Europe, posterior part of adult showing left side with siphons extended and pallets retracted *(A)* and with siphons contracted and pallets protracted *(B) (149)*.

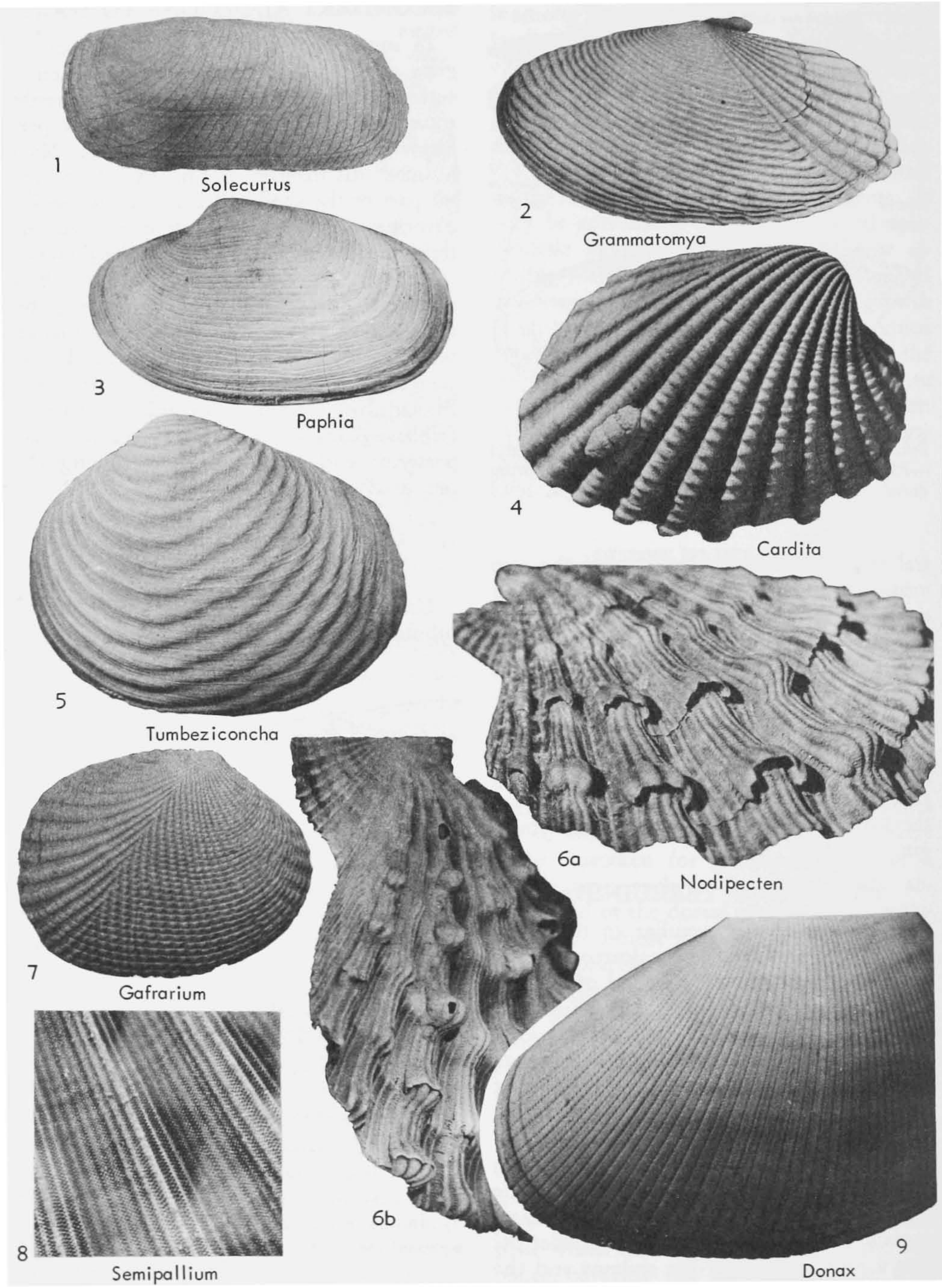

FIG. 56. Bivalve shell sculpture (Nuttall, n).——*1. Solecurtus philippinarum* (DUNKER), Recent, East Indies, imbricate surface, the unevenly grooved appearance given by overlapping lamellae with externally flush edges, ×1.——*2. Grammatomya pulcherrima* (DESHAYES), Recent, Indian Ocean, anterior part of shell with diagonal ribs and posterior part with radial ribs, ×1.7.——*3.Paphia neglecta* (MARTIN), Mio.-Plio., E.Indies, surface with basically concentric or commarginal grooves which are slightly undulating

for their encasement, usually when the two valves are so reduced as to form an inadequate protection for the soft parts. *Teredo,* the shipworm, secretes a constantly thickened calcareous lining to its borings into wood. The borings may twist about irregularly owing to the necessity of avoiding one another during penetration, and when further progress is impossible the animal secretes a calcareous wall at the innermost end of its tube and then ceases to grow. In places where the wood decays away the tube is left as the sole protection of the animal, and the thickness of its wall, usually not more than 0.5 mm., may be increased to as much as 2 mm. One teredinid, *Kuphus,* does not bore into wood, but burrows vertically into mud on the sea floor, lining its burrow with a calcareous tube with irregular growth rings; this tube may be a meter or more in length, up to 60 mm. in diameter, and 5 mm. or more thick. At its lower end the tube is sealed by one or more arched laminae, and at its upper end are two relatively small openings for the siphons, separated by a partition. Similar tubes are known as fossils from the Eocene onward and are particularly abundant in the lower Miocene in the Indian Ocean and Antillean regions, and elsewhere.

*Gastrochaena* may bore deeply enough into rock or other shells to render further protection unnecessary, but if penetration is only partial an "adventive" protective structure may be built over its shell. This commonly takes the form of a claviform tube or of an elongated botryoidal structure. *Fistulana,* which belongs to the same family, always secretes a rather fragile, straight, elongate, club-shaped tube, which is sealed at its anterior end and open at the other. In the position of life the tube is oriented vertically in sandy sediment; a partition divides it into two chambers, in the lower of which the animal lives, the upper serving to protect its siphons.

An elongate calcareous tube, smooth or with transverse fringes, is also secreted in the Clavagellidae. The much-reduced shell lies at its broader, anterior end, with the left valve merged in the wall of the tube in *Clavagella* and both valves in *Penicillus.* At the anterior end there is communication between the interior and exterior of the tube through a series of tubules, long and spinelike in some species, short in others. In *Penicillus* a convex, perforated disc recalling the rose of a watering can forms the anterior end of the tube, and above it is a tubule-bearing collar. Some Clavagellidae live in cavities in hard rock, but many live in a silty substrate with the tube vertical and its anterior end lowermost. It has been suggested that the mollusk can bury itself more deeply in the substrate by drawing silty water into the tube through the anterior perforations.

## SHELL SCULPTURE

Most bivalve shells retain on their surface, as irregularly spaced lines and coarser markings, a record of interruptions in secretion of the shell at its margins during growth or of changes in the rate of secretion (Fig. 56, 57). These markings, termed **growth lines** and **growth rugae**, form a series of conformable curves the course of which is commonly described as "concentric" by conchologists, although commarginal would be a more appropriate term.[1]

FIG. 56. *(Continued from facing page).*

and irregular, ×2.——*4. Cardita ovalis* (REEVE), Plio.-Rec., E.Indies, surface with strong radial rounded ribs and furrows, ribs bearing beadlike prominences in umbonal region and transverse bars toward shell margins, ×2.——*5. Mactra (Tumbeziconcha) thracioides* (ADAMS & REEVE), Rec., Peru, surface with excentric undulations, ×1.3.——*6. Chlamys (Nodipecten) nodosus* (LINNÉ), Rec., trop. W.Atl., oblique views *(6a,b)* showing strong radial ribs which bear secondary riblets and are crossed by concentric or commarginal growth rugae, tubercles hollow and not all of them entire, ×1.3.——*7. Gafrarium* sp., Pleist., E.Indies, surface with divaricate ribs interrupted by concentric or commarginal grooves, ×2.——*8. Semipallium tigris* (LAMARCK), Rec., E.Indies, with reticulate honeycombed surface on which main sculpture consists of radial ribs bearing secondary riblets, ×4.——*9. Donax punctatostriatus* HANLEY, Rec., trop.W.Am., showing pitted (punctate) radial grooves, ×2.

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[1] Compare *"collabral,"* introduced by the writer with a similar connotation in gastropod terminology.

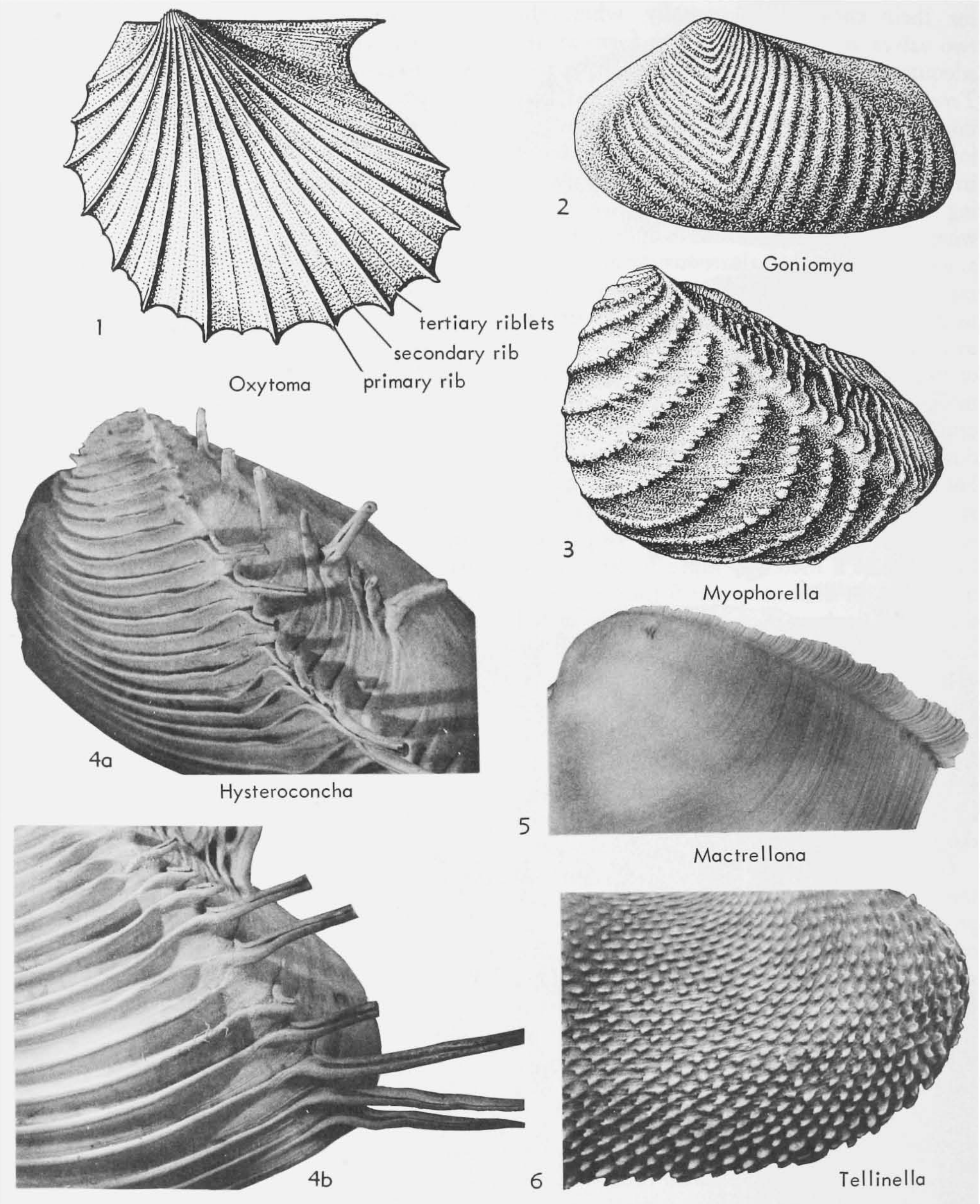


FIG. 57. Bivalve shell sculpture (Nuttall, n).——*1. Oxytoma inaequivalvis* (J. SOWERBY), L.Jur.(Lias.), Eng., surface with radial ribs of three size orders, ×1.3.——*2. Goniomya literata* (J. SOWERBY), M.Jur. (Bajoc.), Eng., with divaricate surface sculpture, ×1.——*3. Myophorella hudlestoni* (LYCETT), U.Jur. (Oxford.), Eng., surface with diagonally arranged pustules or nodes on anterior part of shell and irregular concentric lamellae on posterior slope, ×0.7.——*4. Pitar (Hysteroconcha) lupinaria multispinosa* (G. B. SOWERBY), Rec., Peru, with rows of spines on posterior slope, oppositely disposed to those of muricid gastropods, and remainder of shell surface marked by strong concentric lamellae (*4a,b,* different views of shell), ×2.——*5. Mactrellona alata* (SPENGLER), Rec., off S.Am.W.coast, surface marked by carina on posterior slope (at margin of corselet), ×1.——*6. Tellinella asperrima* (HANLEY), Rec., E.Indies, with hooked spines disposed concentrically or commarginally but also making diagonal patterns (divaricate), ×2.7.

Many bivalves have shells which are otherwise smooth, but a great number have a relief pattern, known as **sculpture** or **surface ornament**, which is of a more or less regular nature and (except for minor variations) is similar in all representatives of a species. The sculpture consists most commonly of one of two components or of a combination of these two. The first component is a **concentric** one and attributable to rhythmic changes in the rate of secretion of shelly matter along the mantle margins. The second component is a **radial** one and consists of elements diverging from the direction of the beak and crossing the concentric elements, although not at right angles except on one sector of the surface. Radial sculpture must result from the continuous enhanced secretion of shelly matter by particular groups of cells along the mantle margins during growth of the valve.

This analysis is oversimplified, however, as in many shells there are elements of sculpture crossing the directions just described obliquely at various angles. Thus in *Goniomya* there are steep, ventrally converging ribs which meet to form a series of downward pointing V's. In *Divaricella* and *Acila,* on the other hand, two series of parallel, oblique riblets meet in an obtuse angle to form chevrons pointing toward the summit of the shell. In the Trigoniidae oblique ribbing ranges from almost concentric to almost radial. Obliqueness of ornament is at the most a generic character found in families widely scattered taxonomically, and in some genera (e.g., *Ceratomya*) it is merely a specific character. Its existence shows that in some bivalves a condition associated with enhanced secretion of shelly matter shifts progressively along cells of the mantle margin during growth.

The various elements of ornament have been loosely classified into those projecting above the general level of the surface of the valve and those that are engraved into the surface, although, as protruding and engraved elements are obviously complementary, this distinction is not fundamental. According to their relative width and prominence, the projecting elements are termed **folds, undulations, costae** (or **ribs**), **costellae** (or **riblets**), **threads, lines,** etc., and the incised elements **grooves, striae,** etc. The terms **interval** and **interspace** are applied to the grooves separating two costae. Costae may be rounded or flat-topped and prominent or relatively depressed. When both radial and concentric components are present, one type may be confined to the intervals between the elements of the other, or the two may be superposed where they cross. Concentric threads may override radial costae, or, when both components are strong, **pustules, beads, tubercules,** transverse **bars** (as on the ribs of certain Arcidae), etc., may arise at the points of intersection. In some bivalves layers of growth project at intervals, forming lamellae, which extend in the direction of growth (**imbricate**) in many forms but are **erect** in others. Where they cross the ribs the imbricating lamellae may protrude prominently to form **scales,** as in *Tridacna* and many Pectinidae, or even sharp **spines.** In many Limidae concentric elements in the intervals between the ribs are small pinprick-like depressions or **puncta.** It is virtually impossible in a brief review to describe at all adequately the various ornamental patterns found on bivalve shells or to mention all the descriptive terms that have been employed in describing them.

In the majority of radially ornamented shells the radial elements remain constant in number after their first appearance, but in some they increase during growth, by bifurcation or by the intercalation of new elements in the intervals between the earlier formed ones. Some Pectinacea (e.g., *Oxytoma*) have a pattern of regularly arranged riblets of two or more orders of strength; the strongest **(primary)** ones are the first to appear. In some species the surface ornament of the two valves differs to a varying extent, not only when the valves are pronouncedly unequal (as in *Pecten s.str.*) but also (although more rarely) when they are of much the same size. The latter observation applies to some species of *Chlamys,* to representatives of the genera *Cucullaea* and *Indogrammatodon,* and to species of a number of other groups.

Mention must also be made of changes in sculptural pattern that take place during growth in some bivalves. Many Unionidae

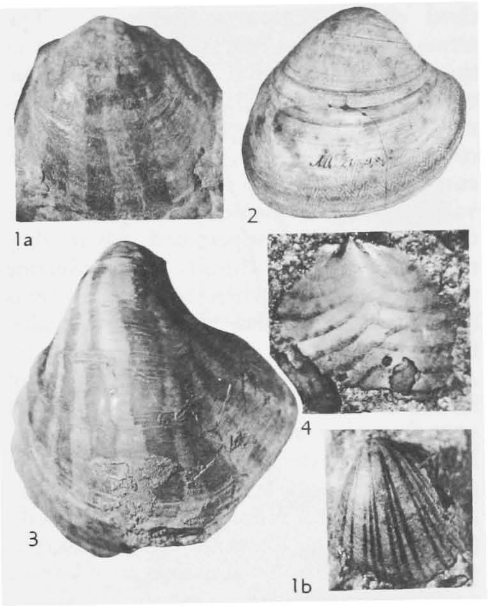


FIG. 58. Preservation of color patterns in fossils (Nuttall, n).——*1. ?Streblopteria sublobata* (PHILLIPS), L.Carb., Eng.; *1a,b,* ×2.5.——*2. Venilicardia lineolata* (J. SOWERBY), a silicified specimen from the Blackdown Greensand, Cret.(Alb.), Eng., ×1. ——*3. Exogyra columba* (LAMARCK), Cret. (Cenoman.), France, ×2.——*4. Pernopecten sowerbyi* (MCCOY), L.Carb., Ire., ×2. [Photographs by N. Tanti, B. M. (N. H.).]

are remarkable for the radial, wavy, or zigzag ribs which are present on their earlier-formed growth stages only. In some Trigoniidae the pattern of the ribbing in the neighborhood of the umbones is quite different from that on the later-formed part of the shell. In the Pteriidae, the left valve of *Pteroperna costatula* (EUDES-DESLONGCHAMPS), from the Bathonian, has radial ribs in the young state but is later devoid of ribbing. A great number of similar cases could be cited.

In strongly costate shells, such as *Tridacna, Lopha,* and many species of *Plicatula,* undulations of the whole ventral margin correspond to the external ribbing. In other bivalves with external costae the marginal region is **scalloped** internally; that is, it bears a series of regular flutings (each corresponding to an external costa), separated by flat or concave intervals with well-marked edges converging toward the actual shell margin. This type of internal marginal ornament is found, for example, in many Pectinidae, Cardiidae, Carditidae, and Arcidae. When the internal marginal ornament is still finer, it consists of what are usually called **denticles** or **denticulations.** Most commonly these also correspond to external radial ornament, but in some Nuculidae, Astartidae, and Crassatellidae they are present in shells which are apparently smooth externally. In such cases they correspond to radial structural elements belonging to an inner layer of the shell.

## COLORATION

[Revised by C. P. NUTTALL, British Museum (Natural History)]

Coloration can be correlated to a certain extent with the taxonomic arrangement of Bivalvia. In the first place, chemically dissimilar groups of pigments are found in different major taxa. In addition, certain types of color patterns, or even the absence of coloration, can be characteristic of particular families and genera. Coloration naturally was given considerable prominence in older conchological monographs; although it may be extremely constant within a species, a very large proportion of exceptions is found and unfortunately these lead to the creation of many synonyms.

While some bivalve shells are devoid of coloration, we find among the majority every gradation of color ornament from a slight uniform or irregular tinting to dense coloration, localized or otherwise, and to patterns of considerable complexity. When a definite pattern distinct from irregular mottling is present this may consist of radiating sectors or rays of various widths, of concentric bands, of series of spots or blotches, of chevrons or zigzagging lines and bands, or (as in certain Veneridae) of complicated mosaics composed of geometrical (commonly triangular) figures of various sizes. When zigzagging ornament is present, corresponding angles of successive zigzags tend to have a radial alignment *(188a)*.

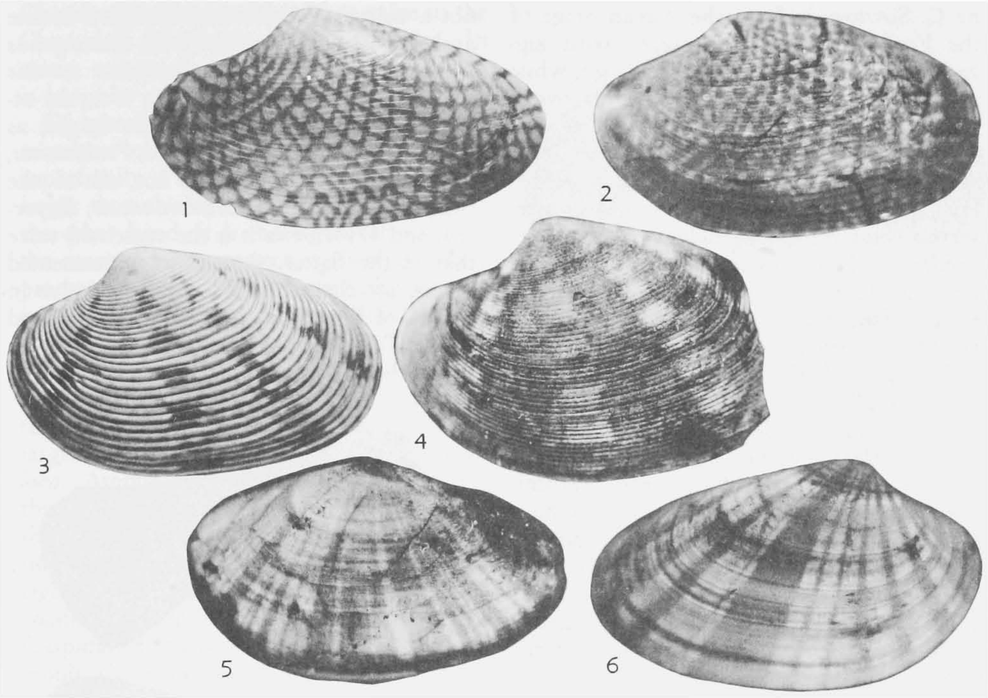


Fig. 59. Photography under ultraviolet light revealing negative or reversed color patterns. None of the fossils (except *Macrocallista,* fig. 6) showed any trace of color patterns when viewed in normal light, but fluoresced strongly under ultraviolet light. Under normal light *Macrocallista* shows concentric banding (Nuttall, n).——*1. Paphia undulata* (Born), IndoPac., Rec., ×2.——*2.* The closely related *Paphia neglecta* (Martin), Neog., Borneo, ×2.3 (see Fig. 56 for normal photo of same species).——*3. Paphia lirata* (Philippi), China Sea, Rec., ×1.2.——*4.* A similar pattern shown by *Paphia* sp., Neog., Borneo, ×2.3.——*5. Tellinella* sp., Neog., Borneo, ×2, showing patterns typical of the genus.——*6. Macrocallista laevigata* (Lamarck) from the Calcaire Grossière of Damery (Eoc., Lutet., France), ×2. [Photographs by N. Tanti, B. M. (N.H.).]

The coloration is not purely superficial, but may penetrate well into the calcareous test. The pigments are thought to be waste products of metabolism, derived from the diet or other sources, and secreted in the shell as a means of disposal *(24b)*. As in the gastropods, it is improbable that the color ornament can have any protective function in the great majority of bivalves which live buried in sediment. Some bottom-living forms, notably the pectinids, appear remarkably well camouflaged. In some evolutionally less advanced genera (e.g., *Pteria, Pinctada, Malleus, Pinna*), the pigments, notably porphyrins, are soluble in acid. In other forms the pigment is intimately associated with the conchiolin that forms the organic matrix of the shell and cannot be separated from it.

Traces of color ornament have been observed in fossil bivalves of various ages, although their preservation is less common than in gastropods (Fig. 58). Possibly the oldest of such bivalves on record is a specimen of *Leiopteria pseudolaevis* (Oehlert) from the Devonian of France, described by the author of the species as bearing dark, radially arranged specks. Both Newton and Brill have described a number of Carboniferous Pectinacea of various genera bearing colored spots, rays, concentric bands, or chevrons. Triassic species, specimens of which are recorded to have color ornament preserved, include the pectinacean *Pleuronectites laevigatus* (von Schlotheim), while Jurassic forms include representatives of *Entolium, Plagiostoma,* and *Plicatula.* A silicified specimen of *Venilicardia lineolata* (J.

DE C. SOWERBY), from the Albian Stage of the English Cretaceous, covered with zigzagging markings, has been described, while specimens of the Upper Cretaceous oyster *Exogyra columba* (LAMARCK) from various European localities not uncommonly bear wavy radial lines. Other Upper Cretaceous bivalves recorded as having traces of preserved color ornament include various Pectinidae and a specimen of *Inoceramus*. Among Tertiary bivalves the nonmarine genus *Congeria* seems to be particularly retentive of such ornament.

COMFORT (1950) has mentioned that certain mollusks containing porphyrin pigments fluoresce under ultraviolet light; but it is not clear whether this phenomenon is confined only to dyes of this type. Preliminary experiments with fossil bivalves have shown that fluorescence is widespread but of rather sporadic occurrence (Fig. 59). Good preservation seems essential and the shell must be cleaned, because the matrix itself usually fluoresces, thus obscuring the pattern. This phenomenon should prove a useful tool for paleontologists, particularly those working on Tertiary material, and has obvious applications as an aid in making identifications and in assessing the probable relationship of various species. It has also been found that the inside of a shell often will fluoresce, showing in strong relief the pallial line and muscle scars which are formed of prismatic aragonite.

[*End of section revised by C. P. Nuttall.*]

## INEQUIVALVE BIVALVES

The two valves of a bivalve shell may differ in convexity, shape, and ornament (Fig. 60,*1*). Such differences are pronounced in many forms in which one valve is cemented to the substrate, and they also exist in many species of certain byssally attached groups, such as the Pteriacea and Pectinacea. In addition, slightly to moderately strongly inequivalve forms are found in other groups well dispersed taxonomically. Whether it is the left or the right valve that is the more strongly convex is usually a generic or specific character and not a matter of individual variation in one and the same species. The fresh-water genus *Etheria*, however, is an exception to this statement. In cemented forms it is the attached valve that is usually the larger, as in most Ostreidae, Spondylidae, *Prohinnites*, Chamidae, and most but not all of the rudists, although in *Pseudomonotis, Eopecten*, and *Myochama* it is the cemented valve that is the flatter. Among these cemented forms, attachment is by the right valve in genera of Pectinacea in which it exists, and in the Terquemiidae and Myochamidae. It is by the left valve in the Ostreidae and

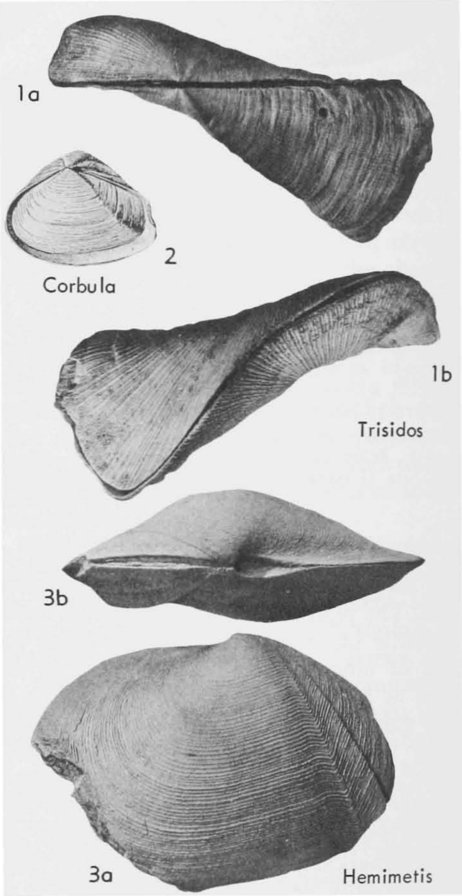


FIG. 60. Inequivalve bivalves (Nuttall, n).——*1. Trisidos tortuosa* LINNÉ, Rec., IndoPac., both strongly inequivalve and inequilateral; *1a,b*, ×0.5 (Nuttall, n).——*2. Corbula caloosae* DALL, Pleist. (Caloosahatchie), Florida (Dall).——*3. Hemimetis* sp. aff. *H. plicata* (VALENCIENNES), Neog., E.Indies; *3a,b*, ×1.

Chondrodontidae, and by either valve in the Chamidae, Diceratidae, and Etheriidae. In many cemented forms the attached valve is irregular and variable in shape.

Of byssally attached bivalves, inequivalve members of the large and long-ranging superfamily Pteriacea have the left valve larger than the right. In the Pectinidae, on the other hand, it is the right valve that is the more strongly convex if there is a very pronounced difference between the two, as in *Weyla* of the Lias, *Neithea* of the Cretaceous, and *Pecten s.str.* of the Tertiary. When, however, the difference is only slight, either valve may be the larger. In the superfamily Arcacea the left valve is larger than the right in the genus *Cucullaea*. Among burrowing bivalves in which the two valves are pronouncedly dissimilar, the Corbulidae and Thraciidae may be mentioned; in both of these families it is the right valve that is the larger. The same condition exists in some Myidae, but in the Cuspidariidae it is the left valve that is commonly the more convex. In the Tellinidae the two valves are dissimilar because their margins are sinuous, and the posterior end of the shell is commonly bent toward the right (Fig. 60,*3*). Slight differences between the two valves exist in certain species of other families, even the Veneridae.

Dissimilarity between the two valves is frequently accompanied by discordance of their margins. In *Oxytoma* the ventral margin of the left valve overlaps that of the right valve considerably, while in *Cucullaea* a similar but less pronounced overlap exists. In *Corbula,* on the other hand, the ventral margin of the right valve overlaps that of the left (Fig. 60,*2*).

## SEXUAL DIMORPHISM

In the Bivalvia sexual dimorphism is most evident in the Unionidae. In many species of this family the shell of the female tends to be shorter than that of the male but more gibbose posteriorly, where the gills are modified to form a brood chamber. The differences in shape of the shell are in some cases so marked that males and females have been described as different species. Sexual dimorphism is scarcely apparent in most marine species. Work on the pearl oysters *(Pinctada)* has now led to the conclusion that differences in shape formerly thought to be sexual have no such significance. A conjecture that in the species *Astarte sulcata* (DA COSTA) specimens with internal marginal crenulations are females and those devoid of them males has proved to be false, as crenulations are present in the majority of specimens of both sexes.

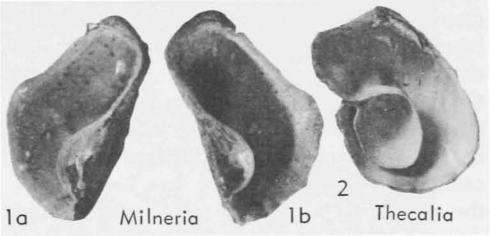


FIG. 61. Sexual dimorphism of bivalves (Cox, n). ——*1. Milneria minima* DALL, Rec., Calif.; *1a,b,* valves with brood pouches, ×6.7.——*2. Thecalia concamerata* (BRUGUIÈRE), Rec., S.Afr.(Capetown), right valve, ×2.

The only known cases in which the shell is very noticeably modified in the female are those of the genera *Thecalia* and *Milneria,* both of which belong to the family Carditidae. In *Thecalia* the ventral margins are infolded to form a shelly pocket serving as a brood chamber within the main shell (Fig. 61,*2*). In *Milneria* the corresponding margins are impressed to form a hemispherical indentation which serves the same purpose and can be covered by an extension of the mantle (Fig. 61,*1*). The males in both genera have only a narrow byssal gape of the corresponding part of the margins.

## STRUCTURE OF SHELL WALL

The wall of the shell consists, when complete, of a thin coat of dark flexible horny material (**periostracum**), secreted by the inner face of the outermost of the three lobes of the mantle edge, and of the main calcareous portion, of which the outermost layer is secreted by the outer face of the same lobe, and the inner part, which does not extend peripherally beyond the pallial line, by the general surface of the mantle (*see Treatise,* p. *I*22, Fig. 14). The outer layer thickens from the beak radially, as the shell was smaller when the part nearest the beak was secreted, whereas the inner part thickens in the reverse direction as it is secreted continually during growth. The calcareous part of the test has been called the **ostracum,** but as this term, as originally defined, was restricted to the outermost layer, secreted by the mantle edge, its use is best avoided.

Unlike the calcareous part of the shell, the periostracum is not interrupted along the dorsal margins, but shares with the ligament the role of connecting the two valves. It is particularly thick in many of the larger fresh-water mussels, serving to protect the calcareous part of the shell from acid corrosion. In many marine bivalves it is thin, and it has commonly been removed by erosion by the time the shell is full-grown. It is particularly well developed in *Solemya,* in which it is the only part of the shell present in later growth stages, forming a wide border (usually radially cracked in museum specimens) to the calcareous portion. The substance of which the periostracum consists long ago received the name **conchiolin.** It is now known to be a quinone-tanned protein (a scleroprotein) composed of a number of amino acids.

The more solid part of the shell consists mainly of aragonite, of calcite, or of both of these forms of calcium carbonate, but it may also contain very small quantities of other minerals. It is permeated by an extremely fine mesh of conchiolin very similar in composition to the material of which the periostracum is composed. The exact composition of this organic component has been found to differ in different species and also in calcitic and aragonitic layers when both are present in the same shell. It contains at least 11 amino acids, present in varying proportions.

Each distinguishable layer of the calcareous wall of the shell is composed of one of the two forms of calcium carbonate mentioned, but the structure varies and several types (some grading into others) can be recognized. These have been described by BØGGILD *(13).* **Nacreous structure,** confined to aragonite and never forming the outermost layer, consists of thin leaves of the mineral of the order of thickness of 1 micron, which are orientated almost parallel to the inner surface of the shell and are separated by very thin films of conchiolin, with the result that they tend to flake away. This structure, with its characteristic luster, is well displayed by mother-of-pearl, which forms the inner layer of the shell of *Pinctada,* the pearl oyster. The nacreous layers of some shells, such as *Mytilus,* are more compact and less lustrous.

**Prismatic structure** may occur both in calcitic and in aragonitic layers of the shell wall, but it is only when composed of calcite that the prisms may be aggregated together so regularly that the part of the test composed of them resembles inorganic mineral structures. The prisms may be single or branched, and their size differs considerably in different species. They are very commonly but not invariably oriented perpendicularly to the surface of the shell, so that sections of the prismatic layer parallel to the surface of the shell show a network of polygons. The prisms may be oblique to the surface, however, and their long axes may be radially or otherwise arranged. Their optic axes may be regularly or quite irregularly oriented. Most frequently each prism is a crystallographic entity, extinguishing as a whole under crossed nicols. In some cases, however, the mode of extinction shows that each is an aggregate of small, irregularly arranged crystals (*complex prismatic structure*). In other cases each large prism consists of numerous fine ones with a feather-like arrangement *(composite prismatic structure).*

Other types of structure give rise to the appearance of the shell commonly termed *porcelaneous.* **Crossed-lamellar structure** (confined to aragonite except in a few genera) is widespread in the Bivalvia (Fig. 62). It clearly gives much more strength to the shell than a nacreous or prismatic structure. The shell layer concerned consists of a series of more or less parallel rectangular lamellae which on the whole are perpendicular to its surface but tend to bend around close to the latter in some species until almost

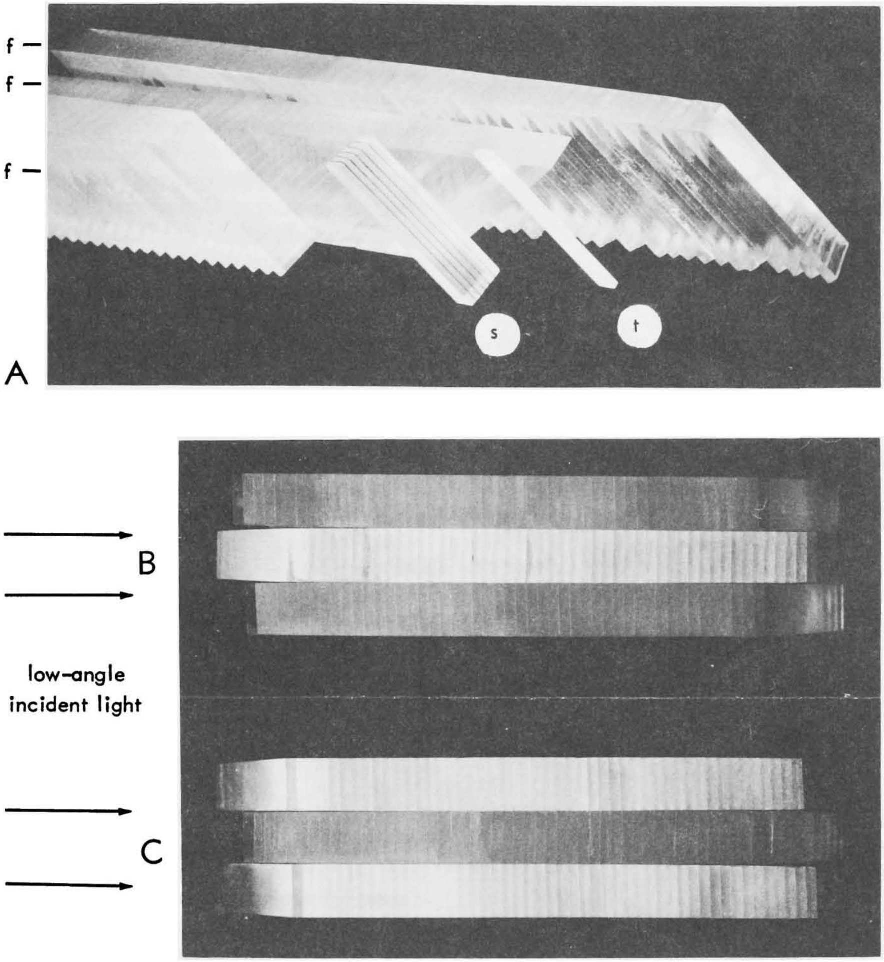


FIG. 62. Crossed-lamellar structure: parts of three first-order lamellae *(f)* each of which is about $15\mu$ wide.——*A*. Model showing the cross relationship of second-order lamellae within three adjacent first-order lamellae. Upper surfaces of first-order lamellae are parallel to growth surfaces within shell. Isolated second-order lamella *(s)* is shown to be composed of six third-order lamellae *(t)*. In each second-order lamella the "unit crystals" (third-order lamellae) are relatively much smaller and more numerous than shown in model.——*B*. Three first-order lamellae in plane of light source.——*C*. Same, rotated 180°. Alternation of light-dark pattern on adjacent first-order lamellae is a useful criterion for recognition of crossed-lamellar structure in shells partially recrystallized *in situ*. In the model used here, low-angle incident light on three adjacent first-order lamellae, viewed normal to growth surfaces, is reflected *up* by second-order lamellae dipping toward light, and *down* by second-order lamellae dipping away from light. Air spaces between second-order lamellae of model allow light to be reflected. (Model and photos by Copeland MacClintock, Yale University, n.)

tangential to it. The longer sides of the lamellae are parallel to the surface, and their direction is usually parallel to the growth lines, rather than radial. These primary lamellae, which mostly extend across the whole thickness of the shell layer, are about 0.02-0.04 mm. thick and up to several mm. in length, although in some forms they are short and branched. They thin out as a wedge between other lamellae at each end. They are themselves built up of transverse secondary lamellae less than 1 micron thick. These are inclined so as to form an angle of 41 degrees with the longer sides of the primary lamellae, adjacent series sloping in opposite directions. Notwithstanding its complex structure, each primary lamella extinguishes under crossed nicols as if it were a single crystal.

The **foliated structure** found in the calcite of some bivalve shells is similar to the aragonitic nacreous structure in that it consists of more or less parallel leaves of the mineral, but it is coarser, less regular, and without luster. The leaves may be parallel to the surface of the shell, oblique, or perpendicular to it. Two other types of structure found in bivalve shells have been described by BØGGILD. The first is the **complex structure,** confined to aragonite, and resembling crossed-lamellar structure except that it is more intricate. The second is the **homogeneous structure,** too fine for its details to be observable under the microscope, extinguishing in one direction over large parts of the shell under crossed nicols.

Apart from trace elements and organic constituents, the composition of bivalve shells ranges from entirely aragonitic to entirely calcitic, the latter being the rarer condition. Among Recent forms, those belonging to the Ostreidae and Anomiidae are almost wholly calcitic. Of extinct families, the Buchiidae and Oxytomidae are thought to have had entirely calcitic shells. Some calcite is present in almost all the Mytiloida and Pterioida, which together constitute the Anisomyaria of some older classifications, but only in a few other groups, which include the rudists. In the great majority of bivalve shells at least two calcareous layers are distinguishable and the number is greater in many species. Of the part of the shell not secreted by the mantle edge, particular reference must be made to that formed where the adductor muscle or muscles are attached. This commonly differs in structure from the surrounding material secreted by the general surface of the mantle and becomes buried under this material as the muscles migrate ventralward and the shell is thickened during growth. It has been called the hypostracum, but as this term was originally introduced with another meaning it seems preferable to adopt OBERLING's name **myostracum** for it. When there are more than two calcareous layers besides the myostracum, a transverse section must be cut through the shell if it is wished to determine which were secreted by the edge of the mantle and which by its general surface.

A nacreous layer is present in the Nuculacea, Mytilacea, Pteriacea, Pinnacea, Unionacea, Trigoniacea, Clavagellacea, and some Pholadomyidae, among Recent shells. Its presence is usually regarded as a primitive feature and it was probably more widespread in Paleozoic bivalves, in most of which, however, it has become transformed into calcite in the course of fossilization. It was present in Paleozoic Pectinacea, although it is wanting in later representatives of this superfamily.

Prismatic calcite forms the outer layer of the shell in the Pteriidae, Isognomonidae, Inoceramidae, Malleidae, Pinnidae, and Oxytomidae (right valves only). In *Trichites* (Pinnidae) and in many species of *Inoceramus* this layer is particularly thick. In *Hippurites* the thick outer layer of the shell is composed of compact prismatic calcite. Prismatic aragonite forms the outer layer of the shell in the Unionacea, Trigoniacea, Lucinidae, Donacidae, and in some Nuculidae, Veneridae, and Pholadomyidae. It forms the inner layer in the Limidae, Spondylidae, Astartidae, and Laternulidae, and in some Mactridae and Hiatellidae. Crossed lamellar calcite is rare, but forms the outer layer of the shell in the Buchiidae and at least some Oxytomidae, as well as in some Jurassic species of *Gryphaea.* Crossed lamellar aragonite is widespread, particularly in heterodont bivalves, in which it commonly forms the outer layer and less commonly a middle layer. Irregularly foliated calcite is characteristic of many Ostreidae and of the Anomiidae, forming almost the whole test. It also forms the outer layer of the shell in the Spondylidae and many Pectinidae. The "complex" and "homogeneous" types of aragonitic structure most commonly form the innermost layer of the shell, particularly in a number of heterodont genera, but both types form the outer layers in some species. Details and illustrations of the structure of the shell wall of many species have been published, notably in BØGGILD's monograph.

Investigations have been carried out by Lowenstam *(93, 94, 95)*, Dodd *(40)*, and others with the object of determining what factors govern the relative proportions of calcite and aragonite secreted in shells (such as some species of *Mytilus*) in which both minerals are present as interdigitating inner layers. The results have indicated that secretion of aragonite is favored by higher temperature of the sea water. Seasonal fluctuations in percentage of aragonite in the shell also have been observed. That changes in shell mineralogy can occur during ontogeny has been demonstrated by Stenzel *(155)*, who has found that the prodissoconch of the oyster *Crassostrea virginica* (Gmelin) is aragonitic, whereas the adult shell is mainly calcitic.

Molluscan shells contain, in addition to calcium carbonate and an organic constituent, minute quantities of trace elements, particularly magnesium, strontium and barium, the proportions of which can be determined by spectrographic techniques. According to Turekian & Armstrong *(172)*, the amounts, expressed in parts per million, present in various bivalve genera investigated are as follows:

*Trace Elements in Bivalve Shells*
(in parts per million)

| Element | Mg | Sr | Ba |
|---|---|---|---|
| *Arca* | 69-140 | 1200-2500 | 6-41 |
| *Glycymeris* | 140-220 | 1600-1900 | 6-29 |
| *Pecten* | 440-4700 | 660-1200 | 6-12 |
| *Lucina* | 53-89 | 1000-1500 | 6-7 |
| *Macoma* | 125-320 | 1400-1800 | 7-33 |
| *Tellina* | 59-180 | 1600-5000 | 6-17 |
| *Cardium* | 88-190 | 1200-1800 | 7-12 |
| *Chione* | 65-98 | 1100-1600 | 8-18 |
| Average[1] | 354 | 1570 | 12 |

[1] For all Bivalvia examined.

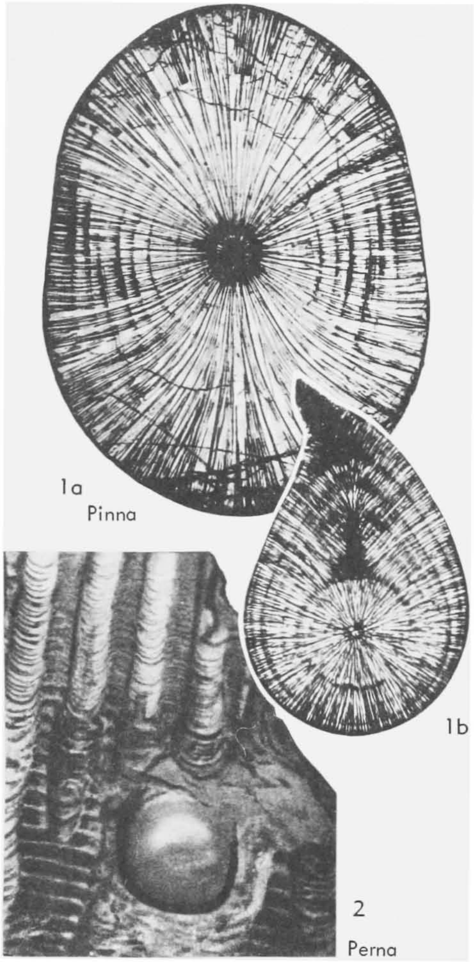


Fig. 63. Pearls in bivalves.——*1. Pinna nobilis* Linné, Rec., E.Atl.O.; *1a,b,* transverse sections through pearls composed of prismatic calcite, ×8 *(147)*.——*2. Perna oblonga* Römer-Büchner, U. Mio., Ger.(Mainz basin), attached "half pearl," ×3.5 (Zilch, 1936).

The results obtained by the authors cited and by other workers show that the trace element composition of the shell depends on a number of factors. Although the composition is related to that of the water in which the mollusk lives, there are noticeable discriminations against magnesium and strontium, less marked in the former than the latter, and a slight enrichment in barium. The concentrations of the trace elements also depend on the salinity and temperature of the water, on the ratio of calcite to aragonite in the shell, and on the species under consideration. Bivalvia are on the whole richer in strontium and barium than gastropods, while some analyses suggest that they are poorer in magnesium.

In some bivalves the wall of the shell is traversed by minute tubules, present only in its innermost layer, in its innermost and middle layers, or throughout its whole thickness. It is otherwise compact in most genera. Some of the rudists are a notable exception. In the Radiolitidae the wall of the shell is cellular, and in the Caprinidae it is traversed by longitudinal canals. In some species of the Ostreidae parts of the shell are cellular or cavernous.

## PEARLS

Pearls are calcareous growths formed within sacs in the tissues of the mantle of the mollusk or as blister-like excrescences (blister pearls) on the interior of the shell. Pearls of the first type may, however, become expelled from the soft tissues and cemented to the interior of the shell. The ultimate cause of the formation of pearls is irritation of the outer epithelium of the mantle arising from the presence of the larva of a parasite or of small extraneous objects such as sand grains, or from unknown causes. The formation of a pearl sac, lined with elongate epithelial cells, results from a series of changes set in motion when the outer epithelium is damaged by the intruding object or organism; this then usually acts as a nucleus around which the pearl is secreted. If, however, the extraneous object becomes lodged between the wall of the shell and the mantle epithelium without damaging the latter, a blister pearl may be the result.

The mineral constitution and structure of a pearl depend on the mineral-secreting tendency of the part of the mantle where it is formed. When this part of the mantle secretes nacreous aragonite, as in the pearl oyster *Pinctada* and the fresh-water clam *Margaritifera,* lustrous aragonitic pearls are formed. Such pearls are built up of concentric layers, consisting mainly of aragonite with a fibrous radial structure, separated by thin films of conchiolin; in some pearls a certain amount of calcite enters into their composition. In *Pinna* the inner nacreous layer of the shell is restricted to a relatively small part of the interior, the greater part of the test consisting of prismatic calcite (Fig. 63,*1*). Many *Pinna* pearls in consequence consist of radiating prisms of calcite. Pearls formed by *Ostrea* are also calcitic but have a less distinctly crystalline structure.

The geologically oldest reported traces of fossil pearls consist of rounded depressions on the surface of an internal mold of *Megalodon* from the Upper Triassic of Hungary. Pits on a number of similarly preserved specimens of *Inoceramus* from the Cretaceous also have been regarded as molds of pearls, although this interpretation has been queried. Pearls in the solid, attached to oyster shells, are known from the Jurassic. Isolated pearls of Cretaceous age have been found in several areas. Specimens from the Chico Formation of California are believed to have been formed by the species *Inoceramus subundatus* Meek; they now consist of concentric lamellae of calcite, but it is uncertain if they were originally aragonitic and have undergone subsequent change. Isolated small, lustrous, aragonitic pearls found in the London Clay (Lower Eocene) of southern England are believed to have been formed by a species of *Pinna.* Other pearls, some of them lustrous, have been found attached to specimens of *Isognomon* from Tertiary deposits at a number of European localities. Records of fossil pearls are, in fact, now fairly numerous (Fig. 63,*2*).

# ORIENTATION AND AXES

## RELATION TO BIOLOGIC FEATURES

A directional terminology is essential for morphological descriptive work in biology, and use of the six basic terms anterior, posterior, dorsal, ventral, left, and right was long ago extended from the vertebrate animals, to which they essentially refer, to invertebrates, with exception of the more primitive groups. In this process criteria other than the simple ones of the usual direction of the animal's movements and of the position of the various parts of its body in relation to gravity or to the supporting surface had to be considered and in certain cases (as in the application of "dorsal" and "ventral" to the Brachiopoda) somewhat arbitrary decisions made. The Bivalvia present no perplexing directional problems, although they are specialized for a sedentary or at least a relatively inactive life and have no head. When typical homomyarian forms move by ploughing their way through sediment with the aid of their foot their movement is usually more or less in the direction toward which one end of the shell points, and this is the end of the shell nearest the mouth. Added to these facts are their clear analogies with other and more active classes of the Mollusca, such as the Gastropoda and Polyplacophora, in which the application of the standard directional terms is obvious. If most importance should be attached to one particular feature in determining the basic directions it is here suggested that this feature should be the mantle isthmus, in all cases to be regarded as dorsal and extending anteroposteriorly. This would conform with the theory that the Bivalvia arose from a cap-shaped or low-conical, bilaterally symmetrical univalve mollusk by the shell bending and two embayments forming along a median line, giving rise to two valves hinging along the isthmus between the embayments (this *Treatise*, page *I*22). On the side of the body opposite the unmistakably dorsal shell was the broad foot by means of which this ancestral form crept over the substratum.

The basic directions, as so determined, agree with those as generally accepted for homomyarian bivalves, less attention being paid to the foot, which, no longer used for creeping, is to be accepted as commonly extending anteroventrally instead of indicating the exact ventral direction. Difficulties arise, however, when anisomyarian and monomyarian bivalves are considered. In these groups the anterior adductor tends to move to a position close to the anterior end of the hinge line before it disappears completely and the posterior adductor tends to assume a median position. The organs of the body are displaced accordingly; the mouth, followed by the adjacent end of each ctenidium, moves close to the dorsal margin, and is in turn followed by the much reduced foot. In consequence, if emphasis is placed on the positions of these organs, the conclusion is likely to be reached that the mantle isthmus, that is, the hinge, does not occupy a strictly dorsal position and may even be almost anterior.

YONGE has approached the subject by suggesting that the "mantle-and-shell" and the body may be considered as separate although interacting entities, each with certain definable axes, the mutual relationships of which afford a basis for comparison of the various bivalve groups. The cardinal axis or hinge axis, determined solely by the mantle-and-shell, is the only one which we have so far discussed. The term **anteroposterior axis** begs the question as to how exactly these basic directions are to be decided upon. FISCHER *(48)* defined the anteroposterior direction as that of a straight line touching the lower margins of the two adductors. This definition, of course, ignores monomyarian forms, and is, incidentally, based on structures belonging to the mantle-and-shell rather than to the body of the mollusk. JACKSON *(76)* considered the anteroposterior axis to be a straight line "passing through the mouth and middle of the posterior adductor muscle and nearly or quite coinciding with the termination of the intestine." This definition could be made to relate solely to the body by shortening it to "passing through the mouth and anus," and this axis whose direction will in some cases be rather different from JACKSON's "anteroposterior axis" would preferably be termed the "oro-anal axis."

The group of figures previously given (Fig. 35) compares the position of the cardinal or hinge axis with the oro-anal axis in several bivalves. It can be seen that it is dangerous to conclude too much from the fact that these axes tend to diverge as the monomyarian condition is reached. There are some homomyarian forms in which the oro-anal axis is by no means parallel to the cardinal axis (Fig. 64). The following figures were obtained: *Paphia,* 15°; *Lucina,* 0° to 15°; *Arca,* 25°; *Limopsis,* 35°. Moreover, variations of between 10° and 35° were found in diffierent species of *Modiolus.* In *Tridacna* the reorientation of the soft parts within the shell that has accompanied the loss of the anterior adductor is even more

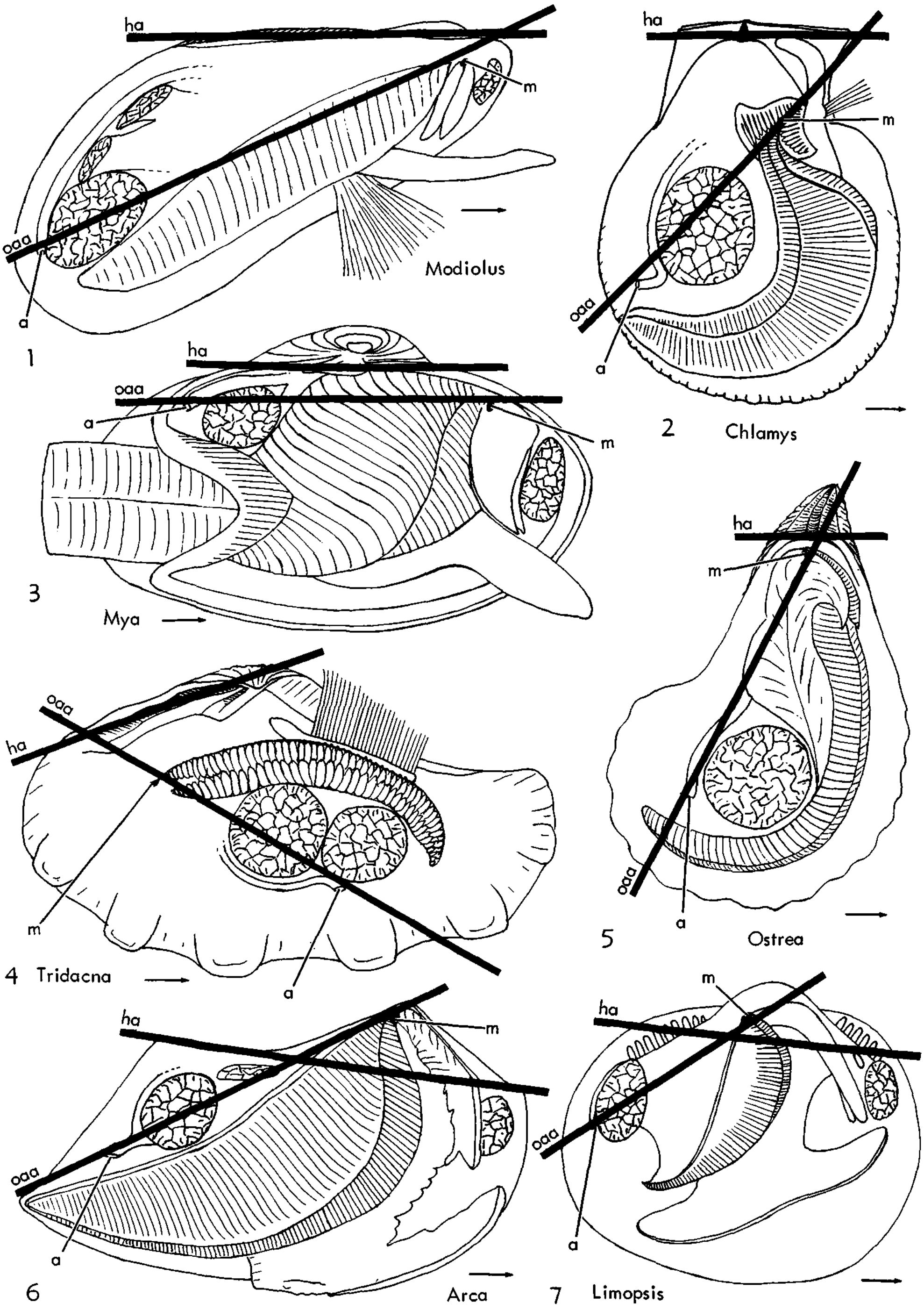


FIG. 64. Orientation and axes of bivalves showing relationship of oro-anal and hinge axes *(1, 3, 5,* after *76; 2, 4, 6,* after *150; 7* after *132).* [Explanation: *a,* anus; *ha,* hinge axis; *m,* mouth; *oaa,* oro-anal axis.]

remarkable (Fig. 64,*4*). The mouth lies close to the hinge line and on the same side of the beak as the ligament, and the byssus protrudes through a broad gape of the margins on the other side of the beak. The remaining adductor has moved to the opposite side of the shell to that in which it normally lies, with the anus just below and behind it. Thus the oro-anal axis forms an angle of about 120° with the cardinal axis. If use of the usual directional terms is to be based on a convention that the anteroposterior direction must be indicated by the oro-anal axis, it is clear that the paleontologist, dealing with many extinct genera in which the exact arrangement of the soft part is unknown, will find the terminology impracticable, and that even the student of Recent bivalves will find it most inconvenient. The only practicable course, apart from introducing a new series of directional terms, is to regard the cardinal axis as the criterion for determining the anteroposterior direction, and this, indeed, has long been the practice with the majority of workers. It has determined the traditional way of orienting bivalve shells with the cardinal axis horizontal for purposes of illustrating their side view.

While the direction of the cardinal axis is more easily ascertained in practice than that of any axis defined by reference to soft parts or even muscle scars, it must be admitted that it cannot always be determined with mathematical precision. When there is a long, straight hinge margin, as in the Arcacea, Pteriacea, and Pectinacea, the axis obviously almost coincides with this margin. When there is a ligamental nymph, its upper surface will usually indicate the direction of the axis. In many genera, however, it is necessary to determine this by trial with actual shells in which the valves open and close. Added to this is the fact that, as Anthony *(4)* showed by observation on living specimens, there is a slight vacillation of the hinge axis when the valves open and close in individual specimens of some species, particularly burrowing ones with a relatively simple hinge apparatus. Much statistical work has been based on measurements of the length and height of shells made in directions intended to be parallel and perpendicular to the hinge axis or "anteroposterior" axis. As these directions are usually determined by rapid inspection, it is to be suspected that the subjective element in posing each specimen for measurement may be so great as largely to vitiate the results. Measurements for statistical purposes should be of quantities ascertainable quite objectively, such as the maximum distance

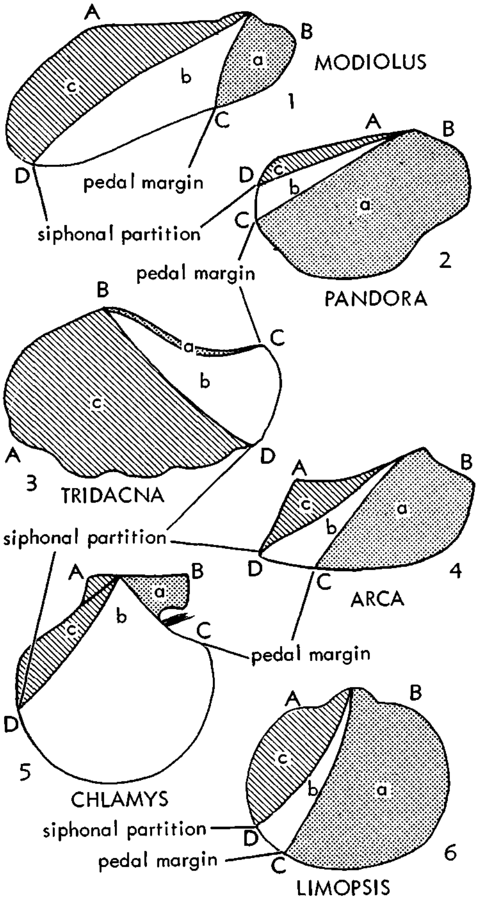


Fig. 65. Zonation of bivalve shell surfaces by interconnection of successive peripheral positions of pedal margin and siphonal partitions defining areas (a) with free borders at all growth stages adjacent to pedal margins, (b) with free borders adjacent to inhalant aperture, (c) with free borders next to exhalant region (*150,* mod.). [Explanation: A, B, upper limits of suprabranchial and infrabranchial chambers; D, C, outer limit of siphonal partition between these chambers; C, outer limit of inhalant region.]

between the anterior and posterior margins irrespective of the exact direction of the measurement.

The paleontologist will naturally ask to what extent the external features of the shell, apart from gapes of the margins already mentioned, indicate the positions of various soft organs. STASEK *(151)* recognized four particularly significant points on the margin (Fig. 65). Two *(A,B)* situated more or less dorsally, one posterior and the other anterior to the beak, represent respectively the upper limits of the suprabranchial and infrabranchial chambers. Of the other two, *D,* situated along or close to the posterior margin, represents the siphonal partition between these chambers, and *C,* the position of which varies greatly, represents the other limit of the inhalant aperture or region. Thus the pedal or byssal opening lies between *B* and *C.* Radial lines joining the points *C* and *D* to the beak separate three sectors of the surface of a valve which, although varying greatly in relative size in different genera, appear to correspond to functionally equivalent regions of the soft parts. It is usually difficult to distinguish these sectors using the shell alone except when, for instance, a pallial sinus enables us to position *D,* and the posterior end of the pedal gape reveals the approximate position of *C.* Nevertheless

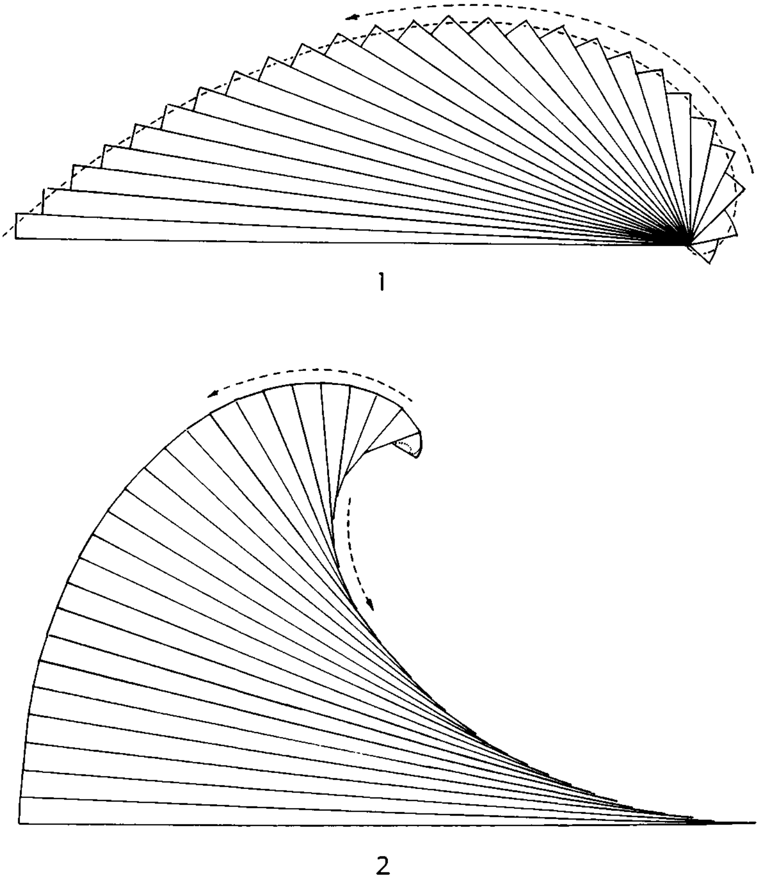


FIG. 66. Bivalve shell geometry—two constructions showing different methods of adding equal-arc increments resulting in gnomonic growth. In these examples secretion is shown decreasing uniformly from a maximum (lower left) to zero (lower right) *(92).*——*1.* Valve lacking cardinal area.——*2.* Cornucopia-like shell.

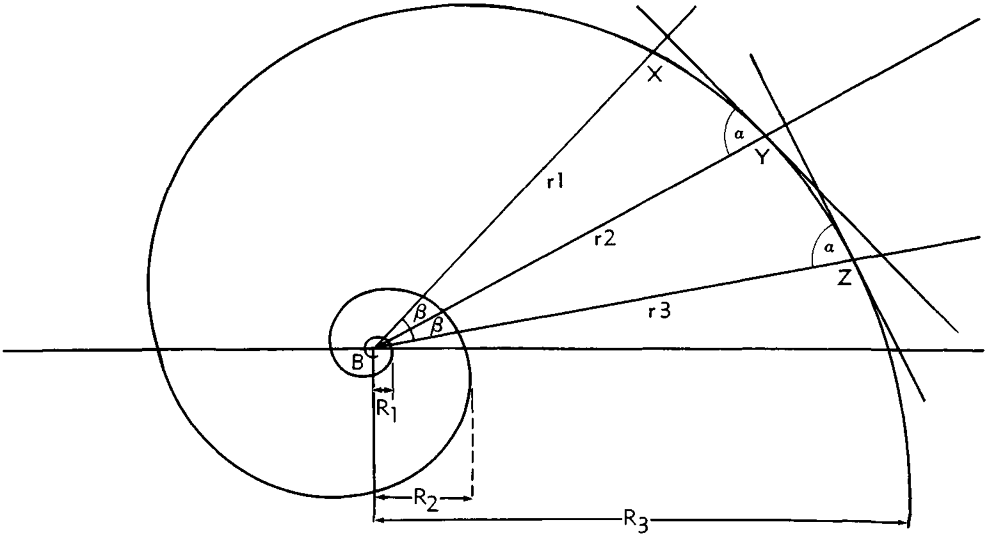


FIG. 67. Bivalve shell geometry—properties of the logarithmic or equiangular spiral. Triangles *BXY* and *BYZ,* in which the angle at *B* (β) is the same, are always similar. Angle (α) formed between tangent and radii *r1, r2, r3,* is always constant (Cox, n).

STASEK's approach should prove well worth pursuing by paleontologists.

In many shells there is a posterior area with ornament quite different from that on the flank of the valve; two parts of the valve are commonly separated by a carina. *Protocardia* and many Trigoniidae are well-known examples. Many authors, following HYATT *(73),* term this area the **siphonal area,** on the assumption that it is secreted by the part of the mantle edge that forms the exhalant and inhalant openings, protruded in many species to form siphons. Further observations, however, appear to be necessary before any generalizations can be made regarding the position of the boundary between the two types of ornament or of the diagonal carina in relation to these openings. From our knowledge of living representatives of the family, it appears that in the Trigoniidae, in which a posterior area is commonly particularly well differentiated, the mantle margins are completely open.

It will be seen that the review above does not give the paleontologist an easy answer to the problem of reconstructing the arrangement of soft parts in extinct genera. One constant connection between the body and the "mantle-shell" is that the rectum seems invariably to curl over the dorsal side of the posterior adductor. Other useful guides are given by general shell features such as gapes, and pedal and adductor scars, discussed in previous sections.

## RELATION TO SHELL CHARACTERS

With shells belonging to extinct families there may not be an infallible means of distinguishing between the left and right valves or (as amounts to the same thing) of deciding which are the anterior and posterior ends. The following general guidance may, however, be given.

1) When ligamental nymphs are present, these are invariably on the posterior side of the beaks.

2) If a pallial sinus is seen on the interior of the shell, this is invariably near the posterior end.

3) If only one adductor muscle scar is present, this lies posterior to the middle of the shell, although in some cases only slightly so; if one adductor scar is very much larger than the other, it is the posterior one.

4) If the beaks lie near one end of the

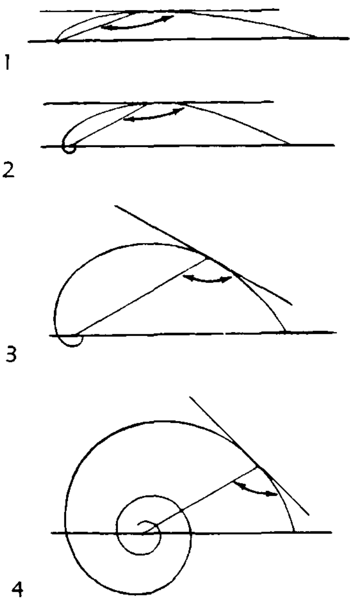


FIG. 68. Bivalve shell geometry.——*1-4*. Sections through beak and front edge of shell showing correlation between decrease in angle of equiangular spiral and increase of shell convexity *(92)*.

shell, the shorter end is very commonly the anterior end. It is always anterior in alate shells of the Pteriacea and in mytiliform shells, but there are some genera in which the beaks are posterior to mid-length, including *Nucula,* and various members of the Erycinacea, Mactracea, and Tellinacea.

5) If one end of the shell tapers to a narrow rostrum, this is usually the posterior end.

6) If there is a single diagonal umbonal ridge, this usually crosses the posterior part of the valve.

7) In the Nuculacea a careful study of the arrangement of the pedal retractor and protractor scars can indicate at which end of the shell the foot protruded; this end must have been anterior (DRISCOLL, *44*).

## GEOMETRY OF SHELL

By †L. R. COX and C. P. NUTTALL
[British Museum (Natural History)]

With many exceptions, which obviously include all cases of irregular growth arising from fixation to the substrate or other factors, bivalve shells may be regarded as geometrical structures which grow in accordance with definite laws. The fundamental observation that gives the clue to these laws is that from an early postlarval stage when the shell acquires definitive form its shape (in all three dimension) remains virtually unchanged as it continues to grow. Accordingly, fairly young shells can usually be identified specifically without great difficulty by comparing them with adult ones. Any addition to the shell during a period of growth thus forms what is termed a **gnomon** to the existing shell (Fig. 66); it increases its volume and surface area without changing its shape. The geometrical constructions explaining shell coiling in general have been based since the first part of the nineteenth century on the logarithmic or equiangular spiral, main properties of which are shown in the explanation of Figures 67 and 68. Our knowledge of bivalve shell geometry in particular is largely due to the work of THOMPSON (1942), LISON (1949), OWEN (1953), STASEK (1963), RAUP (1966), and CARTER (1967).

In the simplest case, the commissure may be considered to lie in a plane passing through the cardinal axis and to constitute the generating curve of the valve. During growth this plane may be imagined to rotate about an axis passing through the umbonal region, while the generating curve, without changing its shape, increases continuously from a negligibly small size to dimensions of the full-grown valve. The fact that growth of the generating curve is itself gnomonic means that, whatever its shape, every point along its margin (in other words, each shell-secreting cell or group of cells) is displaced outward continuously within its plane along a straight line radiating from the beak. However, on the three-dimensional surface traced out by the revolving, expanding generating curve, all such points will follow divergent spiral curves.

LISON *(92)* has explored the subject not only theoretically but also practically by observations on bivalves with radial ornament. He has shown that, if many radially ribbed valves are carefully examined, there is one rib, and one only, that lies entirely within a single plane, so that every part of it appears straight when viewed longitudinally. This rib is termed by him the **directive rib**, and the plane in which it lies the **directive plane** (Fig. 69). He also defines the angle between the directive plane and the plane of the commissure as the **angle of incidence** (Fig. 70). The course of this rib over the directive plane may be studied, either by cutting a transverse section through the valve along the rib or by turning the valve so that its transverse profile coincides with the whole length of the rib.

By making actual measurements on a number of different bivalves Lison was able to verify the conclusion that the directive rib forms a **logarithmic spiral**. He also

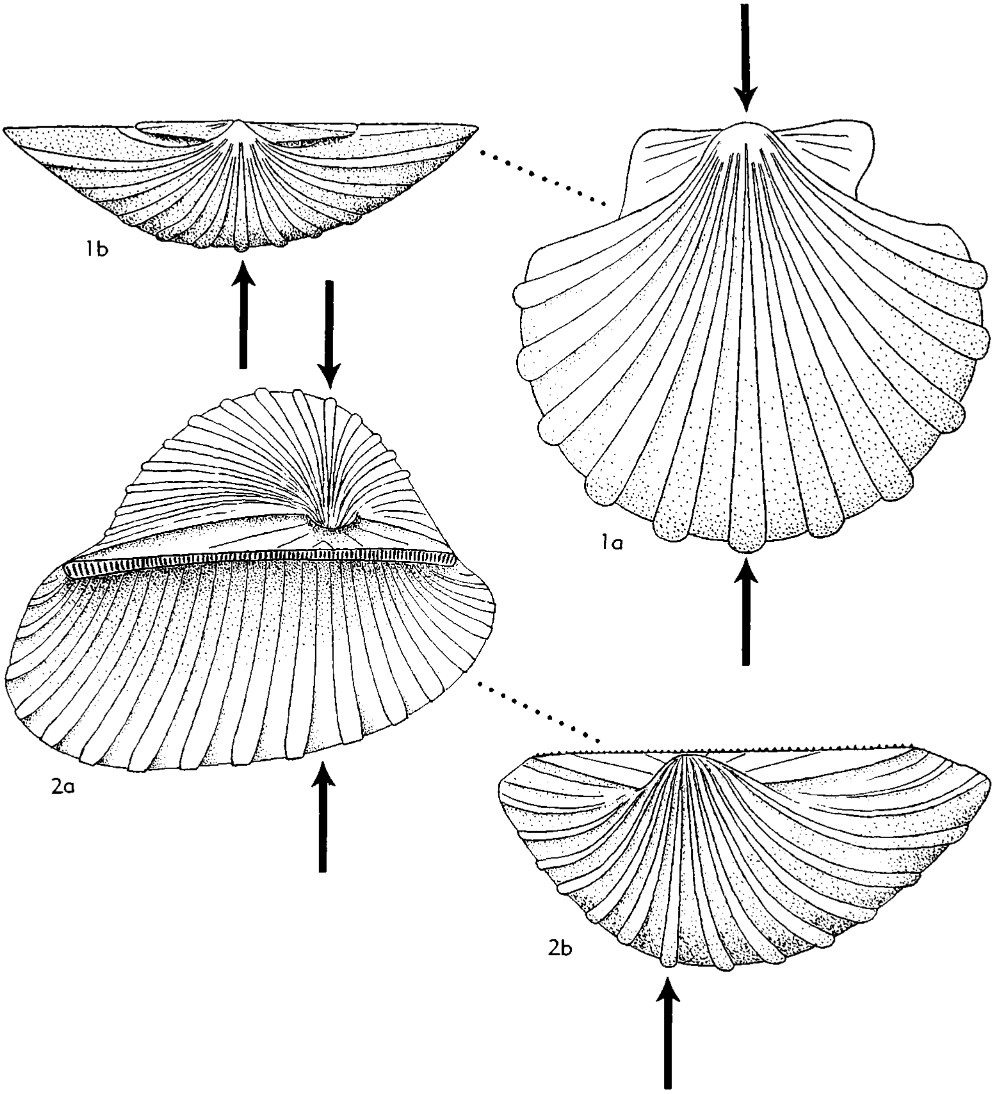


Fig. 69. Bivalve shell geometry—drawings of shells showing directive rib (Cox, n).——*1. Pecten; 1a,b,* views normal to plane of right valve and to beak.——*2. Anadara; 2a,b,* views oblique and normal to beak of left valve.

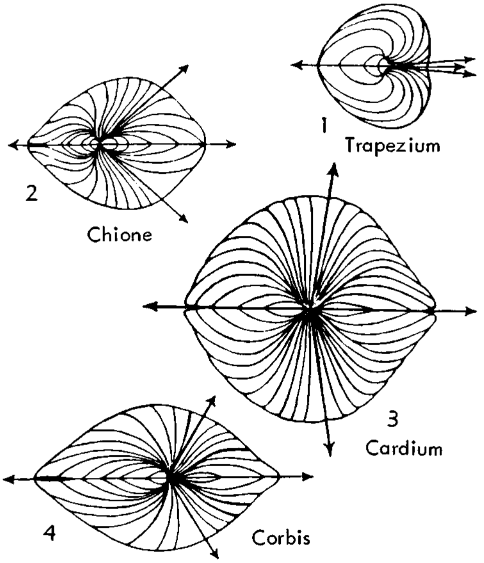


FIG. 70. Bivalve shell geometry—views of shells showing change in appearance with differing angles of incidence between directive plane and plane of commissure (arrows indicate position of these planes) *(92)*.——*1. Trapezium oblongum* (LINNÉ), Rec., E.Atl.——*2. Chione reticulata* (LINNÉ), Rec., E. Atl.——*3. Cardium orbita* G. B. SOWERBY, Rec., E. Atl.——*4. Corbis fimbriata* (LINNÉ), Rec., E.Atl.

showed, both theoretically and by measurement, that the other radial elements of the shell form three-dimensional (i.e., turbinate or gauche) logarithmic spirals (**helicospirals**), since their projections on the directive plane are logarithmic spirals (actually all with the same constant angle as the directive spiral), and the deviation of any point on them from the directive plane is proportional to its distance from the pole (i.e., beak of the valve) (Fig. 66,*1*). LISON also pointed out that in shells with a cardinal area, the area itself might form a spiral surface to which similar laws are applicable, both surfaces having the same directive plane. The hypothetical construction shown in Figure 66,*2* may well be applied to patelliform and bellerophontid gastropods and some spiriferid brachiopods with a high area may approach it. Bivalves such as *Arca* and *Spondylus* seem to represent a balance between Figure 66,*1* and *2* (i.e., secretion at lower right is more than zero).

In shells with almost orthogyrate umbones (e.g., *Pecten, Glycymeris*) the directive plane is nearly perpendicular to the plane of the generating curve (valve margins) and more or less bisects the valve, but in shells which have prosogyrate or opisthogyrate umbones and are commonly more or less inequilateral the angle of incidence may be much smaller (Fig. 67). For example, both in prosogyrate *Codakia* and opisthogyrate *Tellina* the angle of incidence is about 10°; but in the former the directive plane lies close to the commissure behind the umbo, and in the latter case the reverse is true.

LISON stated that the calculation of such quantities as the surface area or volume of a shell from a series of simple measurements presents mathematical problems of considerably complexity, but he showed that the form of a bivalve shell in which the valve

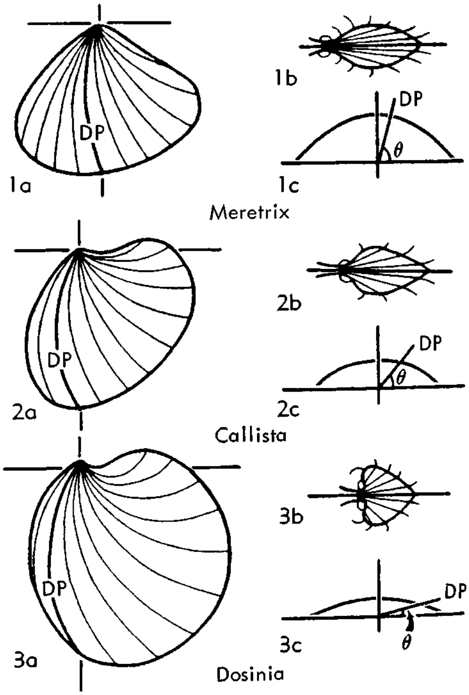


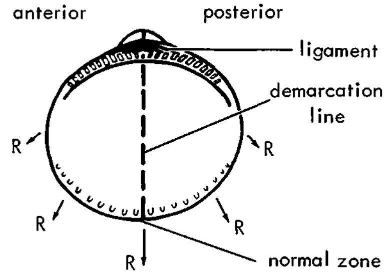
FIG. 71. Bivalve shell geometry—side and edge views of shells with sections showing relationship between directive plane *(DP)* and shape of lunule in some venerids with varying angle of incidence *(θ)* (Carter, 1967, *20a*).——*1. Meretrix,* with angle of incidence approximately 80°.——*2. Callista,* with angle of incidence approximately 50°.——*3. Dosinia,* with angle of incidence approximately 20°.

margins are plane can be fully defined mathematically, for purposes of comparison with other shells, in terms of the angle of the directive spiral, the angle of incidence of the directive plane, and three functions, obtained by a graphical method, expressing the shape of the generating curve.

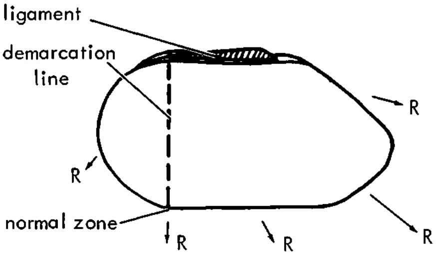
This approach to the subject cannot, of course, be demonstrated easily by visual inspection if the shell lacks radial ribbing, except in rare specimens with an umbonal ridge that proves to lie within the directive plane. The angle of incidence is clearly interdependent with several features of the shell, particularly convexity of the valve, position of the umbo, the extent to which it is prosogyrate or opisthogyrate, and relative development of the lunule and escutcheon (Fig. 71).

A rather different way of interpreting shell geometry in terms of three growth components has been developed by Owen *(121, 122, 124)* and Yonge (*194a* and this *Treatise,* p. *126*), who attached more importance to a line which was originally termed the normal axis (and now designated as demarcation line) than to the directive rib (Fig. 72). It originates at the beak and crosses the growth lines where they are most distant from the plane of the commissure. In radially ornamented shells it coincides with a rib or other element of sculpture, and it forms part of a logarithmic spiral of one of the types (planispiral, helicospiral) already discussed. It is identical with the directive spiral in equilateral shells like *Pecten* and *Glycymeris* (in which it coincides with the median rib or interspace).

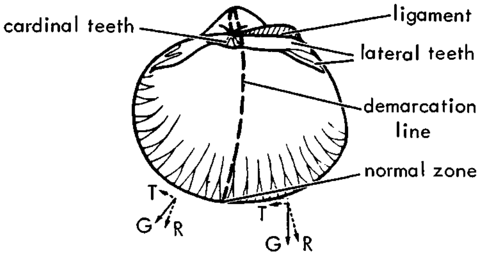
In such shells the direction of displacement in three-dimensional space of any point on the secreting edge of the mantle at any particular moment is considered to be the resultant of two components, a radial one (directed outward from the beak in the plane of the generating curve) and a transverse component (directed perpendicularly to this plane, to the rotation of which it is due). The normal axis or **demarcation line** therefore may be defined alternatively as the locus of points on the surface of the valve where the transverse component has its maximum effect.



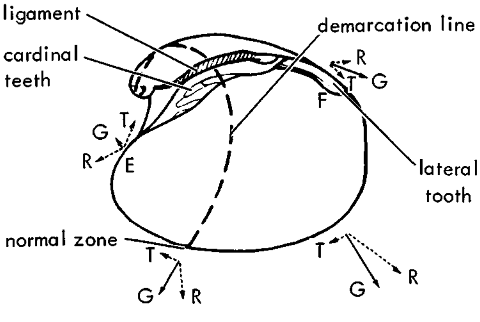
Glycymeris



Anodonta



Cardium



Glossus

Fig. 72. Bivalve shell geometry—diagrams showing growth components of valves radially *(R)* and tangentially *(T)* with resultant growth direction *(G) (122).*

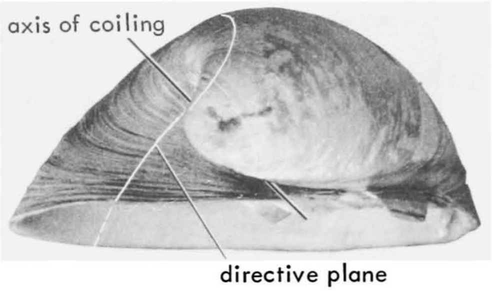


FIG. 73. *Glossus humanus* (LINNÉ), Neog.-Rec., Eu., slightly oblique view showing approximate position of axis of coiling and directive plane, ×0.78 (Nuttall, n).

In inequilateral forms the demarcation line diverges from the directive rib. Both OWEN and YONGE hold the view that in many bivalve shells a gradual twisting around of the generating curve occurs within its own plane, which is due to a third component, tangential to its margin. The effect of the tangential component would be, as it were, to "bow" all elements of radial ornament in the direction in which it acts. Thus, if this direction is toward the posterior end of the shell, the median rib, planar and "directive" in the absence of the tangential component, becomes bowed at right angles to its length so as to present a posteriorly facing convexity. If taken to a logical conclusion, it will be seen that some rib posterior to it, which would have had a posteriorly facing concavity in the absence of the tangential component, now becomes flattened out by virtue of the latter, becoming, in fact, the "directive" rib of LISON.

No mathematical calculations of the type made by LISON have been attempted to test the true relationship of the demarcation line in relation to the generating curve.

In addition, STASEK *(151)* has shown from careful measurements of certain inequilateral forms that considerable scope for disagreement in positioning of the demarcation line exists. For all these reasons, we agree with him that this term is too imprecise. STASEK also pointed out that confusion seems to have arisen from considering the three components of growth as forces acting to effect shell shape by a sort of vector addition. He rightly stressed that they simply describe the directions in which growth has occurred.

OWEN's rejection of the usefulness of LISON's concept of the directive plane cannot be accepted. He based his argument mainly on examples such as *Chama* and *Glossus* in which this plane apparently does not exist. In fact, it would seem that, apart from irregular forms such as oysters, all bivalves do possess a directive plane which is normal to the axis of coiling of the valve. Confusion may have arisen because in many cases it is impossible to find a straight or directive rib. In most species of *Chama,* all the ribs appear as turbinate spirals, because the directive plane is parallel, or almost so, to the valve surface. In the case of *Glossus* (Fig. 73) each valve grows in the same way as a virtually planispiral gastropod. To explain the form of *Glossus,* with its unusually coiled umbones, it is not necessary to postulate a gradual twisting round of the generating curve (and of the coiling axis) as growth proceeds. In multispiral genera such as *Diceras* the helicoid spiral stage, exhibited by most gastropods, is reached; the coiling axis passes through the nucleus and down through the "columella." In such cases no rib could be straight or "directive" and the directive plane (by definition perpendicular to the coiling axis) would merely touch the earliest part of the shell.

More recently RAUP (1966) has produced computer-constructed theoretical shell forms applicable to all of the important molluscan classes and to brachiopods. These are based on four parameters: 1) shape of the generating curve *(S)* which corresponds to the commissure in bivalves and brachiopods, and the aperture of ammonoids and gastropods; 2) rate at which the whorl expands *(W)*; 3) distance of the generating curve from the axis of coiling *(D)*; and 4) rate of whorl translation *(T)* (i.e., the rate at which the generating curve moves down the y-axis), to produce asymmetrical forms such as spired gastropods and inequilateral bivalves (Fig. 74,*1*). These parameters other than the shape of the generating curve (which is normally unrelated to any geometrically correct figure) may be altered to produce different shell forms (Fig. 74,*2*). These findings appear to be an amplification of LISON's work, and it seems likely that some mathematical relationship exists between angle of incidence and ratio of increase along the x-axis (*W* and *D*) compared with increase along the y-axis *(T)*.

So far, the exceptions to equiangular spiral growth and the problems associated with bivalvedness have been largely ignored. We may see that when the generating curve has turned through an angle greater than 180° from the definite beginning of the spiral course, the earlier part of the spiral (that is, part of the umbo of the valve) begins to project beyond the plane of the commissure (i.e., the generating curve at this later growth stage).

Both STASEK *(151)* and RAUP *(140b)* have explored some of the methods by which mutual interference of the umbones of the

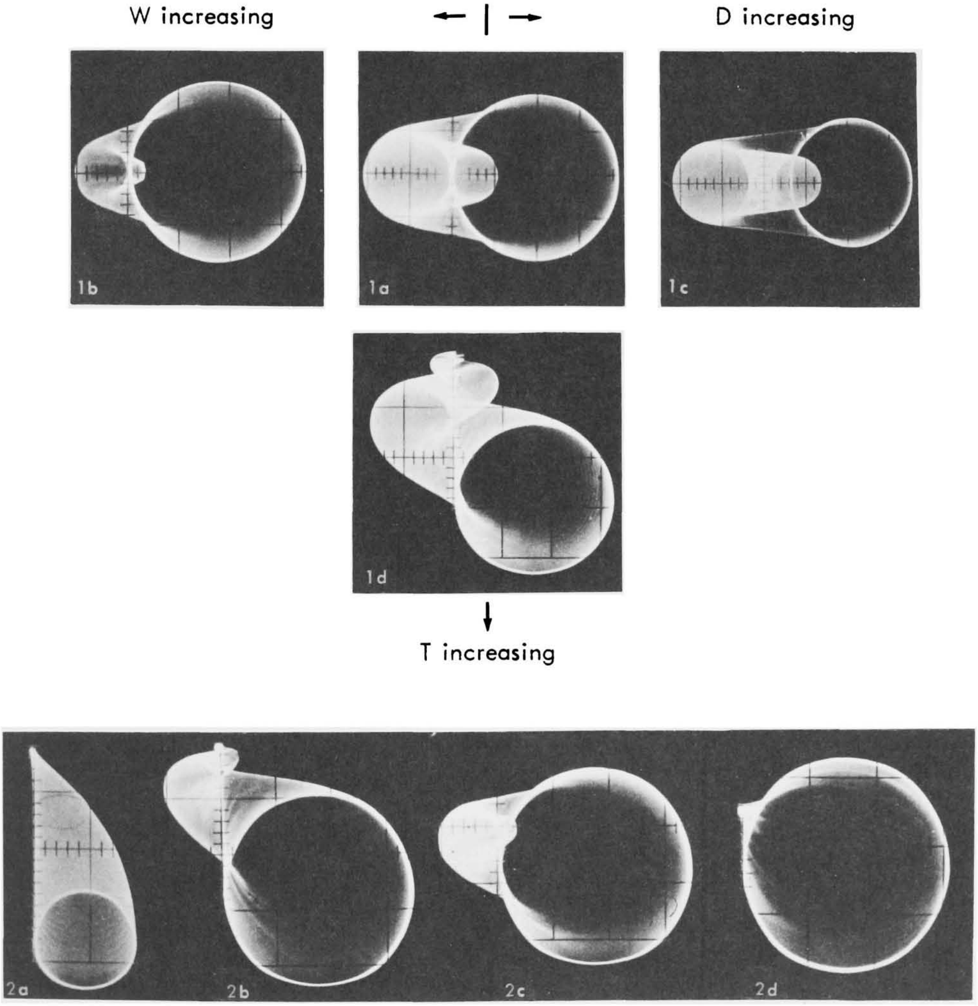


FIG. 74. Bivalve shell geometry—parameters and models of shell forms in mollusks *(140)*.——*1*. Explanation of parameters used in construction of theoretical shell forms (generating curve in all cases circular); *1a*, typical planispiral gastropod; *1b*, bellerophontid gastropod; *1c*, evolute ammonoid; *1d*, spired gastropod.——*2*. Models of shell forms found in Bivalvia; *2a*, typical rudist with high *W* and high *T*; *2b*, *Diceras*, with relatively low *W* and intermediate *T*; *2c*, *Gryphaea*, with relatively low *W* and low *T*; *2d*, slightly inequilateral shell of typical form with high *W* and low *T* (see p. *N*88).

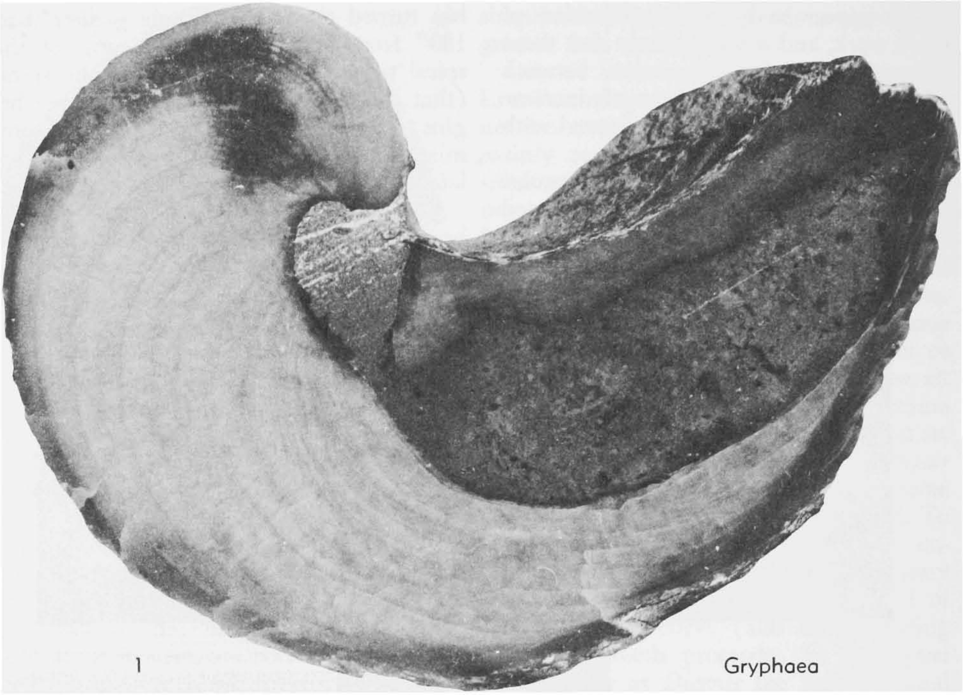


FIG. 75. Bivalve shell geometry—longitudinal section through *Gryphaea arcuata* LAMARCK, L.Jur.(Lias.), Eng., showing how mutual interference of umbones in growth of valves is avoided even when plane of generating curve is coiled through more than 180°, ×2 (Nuttall, n).

two valves is avoided. In the first place, the rate of whorl expansion is usually very high and the umbo does not project, because adult size is reached before the spiral has moved through half a whorl. Another important property of this rapidly expanding type of spiral shell is that it provides plenty of space for the attachment of adductor muscles in a mechanically advantageous position. Their strength will be in proportion to their cross-sectional area and in order for them to be effective this must be as large as possible in relation to the mass and volume of the shell. This problem is avoided by the possession of raised platforms or myophores, found in forms such as rudists which do not exhibit rapid whorl expansion.

In genera such as *Arca,* the umbones are separated by a broad cardinal area. In some shells (e.g., *Pecten, s.str.*) one valve is slightly concave and lies entirely below the projecting umbo of the convex valve. In *Gryphaea* the umbo and much of the earlier part of the left valve becomes infilled with callus which would serve to keep the shell balanced on the substrate (Fig. 75). As in many other oyster-like genera, the right valve is built up by the internal addition of successively larger lamellae. As interlocking teeth are absent, the valves are held together by the single adductor muscle and the ligament, the attachment of which must change position throughout growth. In this way the right valve is free to move away from the left umbo.

A high translation rate in genera such as *Diceras* and *Glossus* causes the umbones not only to be prosogyrate but also to coil outward from one another. In some shells (e.g., *Ceratomya, Corculum*) one umbo either lies slightly in front of the other or alternatively the valves rotate about slightly different axes, so that when the valves open the umbones pass sideways on to each other rather like the blades of a pair of scissors.

In a few shells (e.g., *Ensis ensis, Tellina (Peronaea) planata*) one umbo is known to penetrate the other. In any case, it is probable that in most bivalves, even when a cardinal area is absent, a certain amount of growth occurs along all parts of the dorsal margin of the two valves, as a result of which the umbones remain just sufficiently separated to allow the two valves to hinge freely along this margin.

It must be emphasized that the basis of the foregoing discussion, namely, that bivalve shells retain the same shape throughout growth, is only an approximation to the truth. The periodicity of elements of concentric ornament, in addition to irregularities resulting from pauses and accidents during growth, obviously must mean that every addition to the shell is not exactly gnomonic, and in many shells study of the growth lines will indicate a slight progressive change in shape as the valves grow. Nevertheless, the approach to study of the geometry of bivalve shells outlined above throws much light on its characteristics and provides a basis, not yet fully explored, for the comparison of shells of different species.

[*End of section by L. R. Cox and C. P. Nuttall.*]

# ONTOGENY

## EMBRYONIC AND LARVAL DEVELOPMENT IN MARINE BIVALVES

Three types of early development have been distinguished in marine Bivalvia. In the commonest (**planktotrophic**) mode of development the mollusk emerges from the egg early in ontogeny and passes through the full succession of swimming larval stages, leading a pelagic life and feeding on phytoplankton for a relatively long period before sinking to the bottom and undergoing metamorphosis (Fig. 76). A second type (**direct development**) involves the omission of any pelagic larval stage, the young bivalve hatching out only when sufficiently advanced for bottom life. The third type (**lecithotrophic larval development**) is more or less intermediate between the other two; the developing animal, when an embryo within the egg, derives sufficient nutrient matter from the relatively large yolk mass to sustain it during a definite but rather short ensuing larval life. It has no need to feed on phytoplankton before settling and undergoing metamorphosis. In such species as *Pandora inequivalvis* Linné the animal passes through the entire series of free-swimming larval stages, but very quickly. In other cases (*Ostrea chilensis* Philippi) the animal does not hatch out until it is a fairly advanced veliger (Fig. 77). **Brood protection,** by which the ova are retained and fertilized and the embryo undergoes a varying degree of development in a brood pouch, usually within the gills of the parent animal, may be associated with all three types of development, although it is most common in the second and third types. Even direct development, however, may occur in species that discharge their ova for external fertilization.

The embryology and larval history have been investigated under laboratory conditions in a number of species which undergo development of the first type. The quantity of eggs shed into the surrounding water by each spawning individual is enormous (5 to 12 million in the case of *Mytilus edulis* Linné), while spermatozoa are discharged in still greater and quite incalculable numbers. The diameter of the yolk-mass of ripe eggs is between 40 and 85$\mu$, the size (70 $\mu$ in *M. edulis* and 50$\mu$ in *Cardium edule* Linné) being fairly constant in any one species. In *M. edulis* the spermatozoa have a head 5$\mu$ long and a tail 35$\mu$ long. The ova are at first enclosed in a thin gelatinous membrane.

After fertilization, cleavage proceeds rapidly and the invagination process of gastrulation is complete within about 12 hours in a number of species in which it has been investigated. A circle of relatively large cilia forms at the front end of the larva, anterior to the mouth, and, in a period varying from 12 to 24 hours after fertilization, the young animal enters upon the **trochophore** stage of its existence. Beating of the cilia causes it to rotate, and as the result of this movement the enclosing membrane ruptures and the larva commences a swimming existence (Fig. 78). With rapid development of the

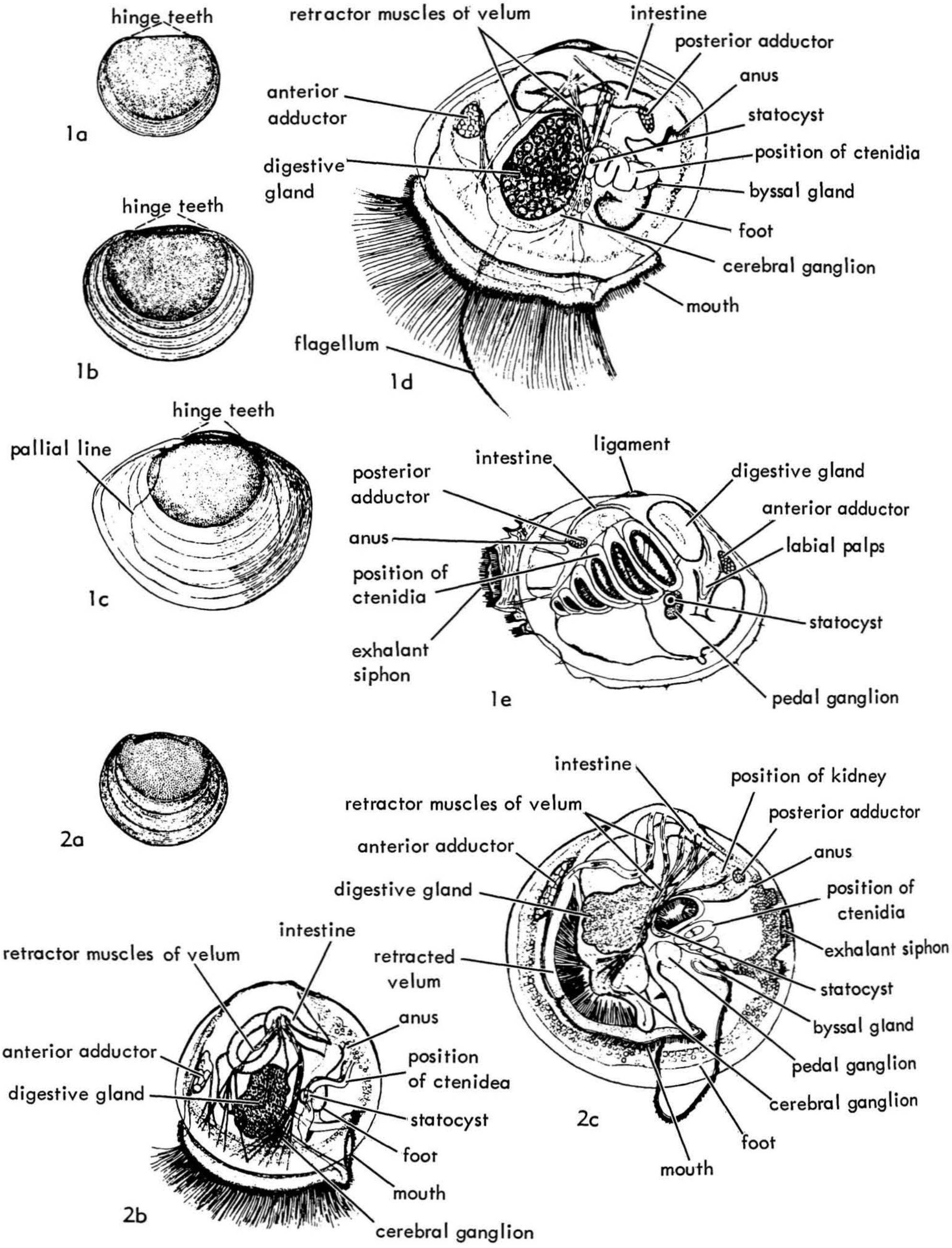


Fig. 76. Bivalve ontogeny—shells and anatomical features of larvae, all much enl. *(180)*.——*1. Cultellus pellucidus* (Pennant), Rec., E.Atl.; *1a,* prodissoconch I (=veliconch); *1b,c,* later larval growth stages of shell; *1d,e,* anatomy of larva and animal at early postlarval growth stage.——*2. Zirfaea crispata* Linné, Rec., E.Atl.; *2a,* prodissoconch and early subsequently formed shell; *2b,c,* anatomy at young and late larval stages.

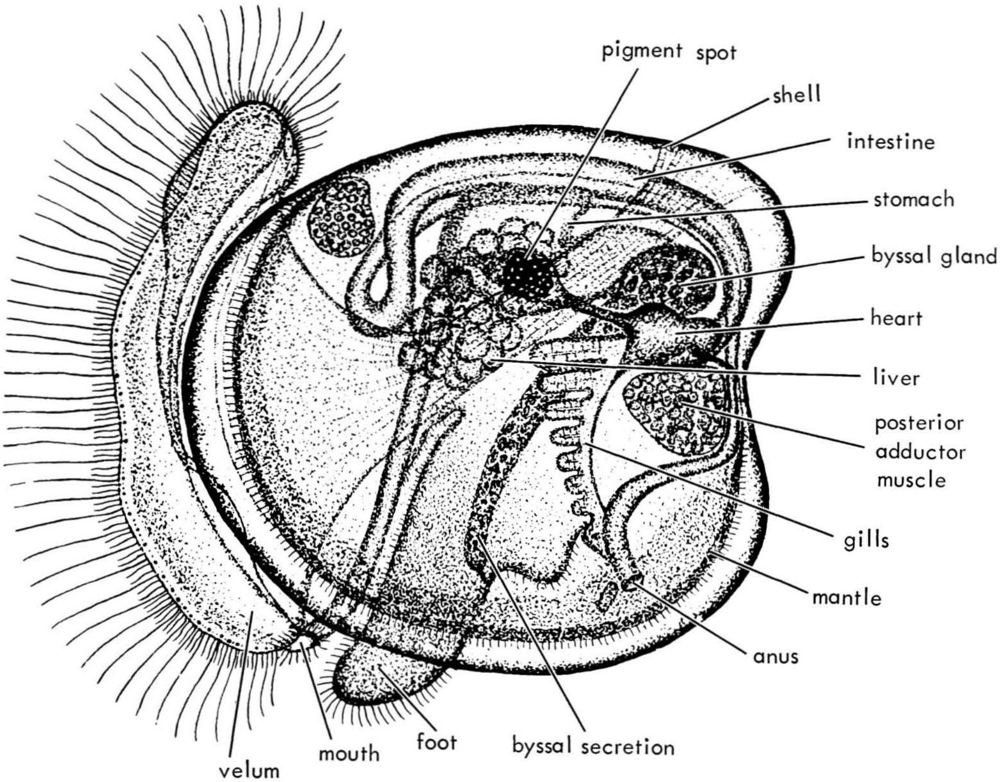


FIG. 77. Bivalve ontogeny—anatomy of veliger larva of *Ostrea virginica* GMELIN, Rec., W.Atl., much enl. (Prytherch, 1934).

**velum** (an anterior crownlike structure with long cilia) from the ciliated region already mentioned, the larva passes (17 to 48 hours after fertilization) into the **veliger** stage. Whereas trochophore larvae do not ascend into the plankton, velum-bearing larvae constitute one of its most important elements, and as such have been intensively studied in recent years.

The earliest-formed shell is secreted by the shell gland, which begins to appear on the posterodorsal part of the larva as soon as invagination has occurred. It is at first a patch of relatively large cells which form a thickened part of the ectoderm and begin to secrete a thin cuticle. The patch soon becomes divided into left and right halves along a median line (the future hinge line). In each half the cells become flattened and start secreting a calcareous shell valve. The two valves grow rapidly until, about three days after fertilization, they are large enough to cover the soft parts. At the same time larval retractor muscles, which serve to contract the whole body of the larva so that it can be withdrawn between the valves, have developed; in *Cardium edule* there are three pairs of these. Rudiments of the mantle have also arisen from the line of junction of shell gland tissue and ordinary epithelial cells, forming lateral folds that have begun to grow downward as left and right mantle lobes.

Whereas the term **veliger** was originally and is still commonly applied to the velum-bearing larva up to the time of metamorphosis, some authors, following WERNER (1937), now consider the veliger stage proper to end when secretion of the valves of the shell is taken over from the shell gland by the mantle. At this stage a primitive digestive system (esophagus, stomach,

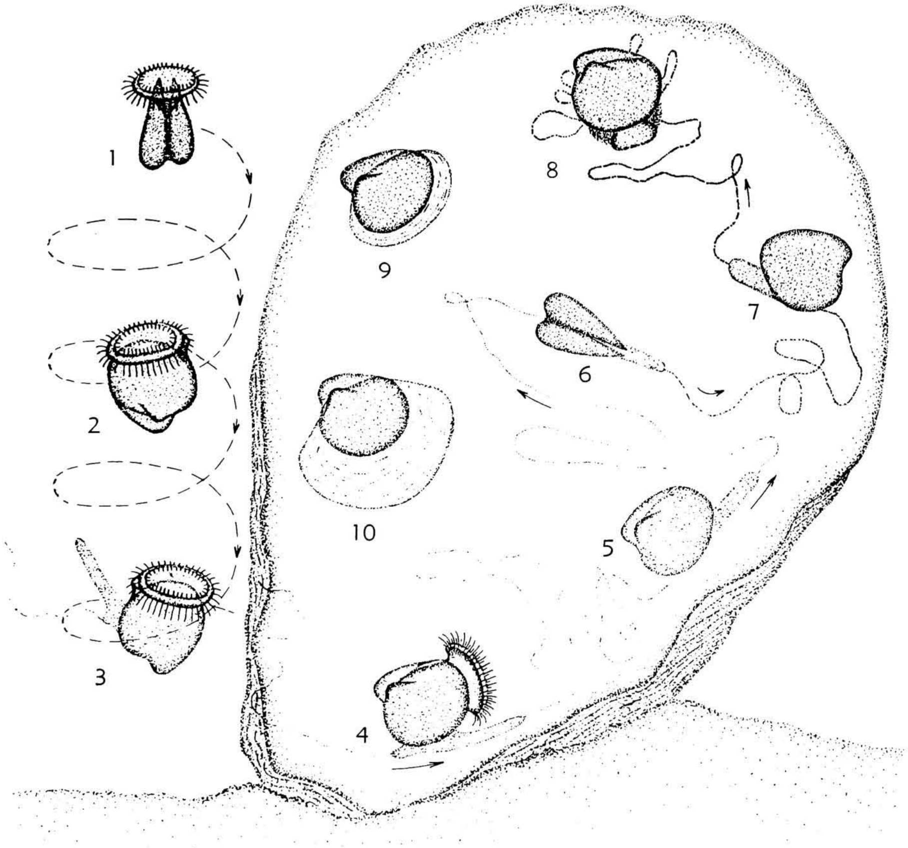


FIG. 78. Bivalve ontogeny—diagram of "settling" steps in development of *Ostrea virginica* GMELIN, Rec., W.Atl., much enl., with earlier stages proportionally most enl. (Prytherch, 1934).——*1,2*. Side and end views of swimming larvae.——*3,4*. Searching phase of larval growth.——*5-7*. Crawling phase of larval growth.——*8*. Fixation of larva to substrate.——*9,10*. One and two-day old spats.

intestine, and rectum) has appeared, together with a rudimentary anterior adductor in addition to the retractor muscles just mentioned. The two valves are D-shaped, hinging along a straight, toothless margin where they are joined by their outer cuticle, and are thin, translucent, and devoid of growth lines. The term prodissoconch having been originally applied to the complete larval shell, this earlier stage has been termed by WERNER (followed by other authors) the **prodissoconch I**, commonly abbreviated to "prod. I." It is virtually the same as the **protostracum** of BERNARD. The size of the prodissoconch I ranges from about 70 to 150 microns and is, again, fairly constant in any one species.

Secretion of the two valves is taken over by the mantle in an average period of about 10 days after fertilization, the total time elapsing before metamorphosis varying according to the species and temperature, and ranging perhaps from 2 to 6 weeks. The shell borne by the larva during the last and longest period of its existence is termed by WERNER the **veliconch.**[1] The veliconch consists of the prodissoconch I and of a newly added zone of mantle-secreted shelly matter, the **prodissoconch II**, on which distinct growth lines are visible. It slowly loses the D-like form of prodissoconch I and at the same time its convexity usually increases,

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[1] Originally, *veliconcha*, but better abbreviated to *veliconch* for uniformity with prodissoconch, etc.

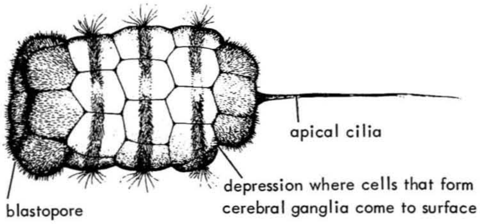


FIG. 79. Bivalve ontogeny—embryo of *Yoldia limatula* SAY, Rec., Atl., 45 hours old, much enl. *(43)*

distinct umbones commonly appear, and it acquires a variety of shapes—oval, trapeziform, or subtrigonal, according to the genus to which it belongs. A ligament and primitive hinge teeth, described more fully below, appear. The size of the velum increases and the digestive system becomes more elaborated, while further permanent soft organs (cerebral ganglia, gills, foot and byssal gland, siphons, posterior adductor) gradually become differentiated. The term **pediveliger stage** has been applied to a late larval stage marked by the coexistence of a velum and of a foot that has undergone rapid growth in preparation for a creeping existence. The length of prodissoconch II at metamorphosis ranges from about 0.2-0.6 mm. and may vary considerably in a single species.

Among bivalves that combine lecithotrophic development with a short free-swimming larval stage, the Nuculacea (several species of which have so far been investigated) are of particular interest. Instead of having a velum of the usual type, these forms develop a barrel-shaped structure, consisting of about five rows of large polygonal cells, which encases the growing larva and its shell (Fig. 79). About three of these rows bear cilia, the beating of which causes the larva to rotate and swim. The whole structure breaks up and is discarded at metamorphosis.

Prodissoconch II is ill-defined or absent in larval shells that have undergone lecithotrophic development, but stages I and II are both distinguishable on the prodissoconch of forms in which development to the bottom stage has been direct. They differ, however, in appearance from the corresponding stages of planktotrophic larval shells and can be distinguished by an experienced worker. It is believed that examination of the prodissoconchs of fossil bivalves, when well enough preserved, will throw light upon the mode of early development.

## EMBRYONIC AND LARVAL DEVELOPMENT IN FRESH-WATER BIVALVES

Fresh-water bivalves belonging to the family Dreissenidae have a free-swimming

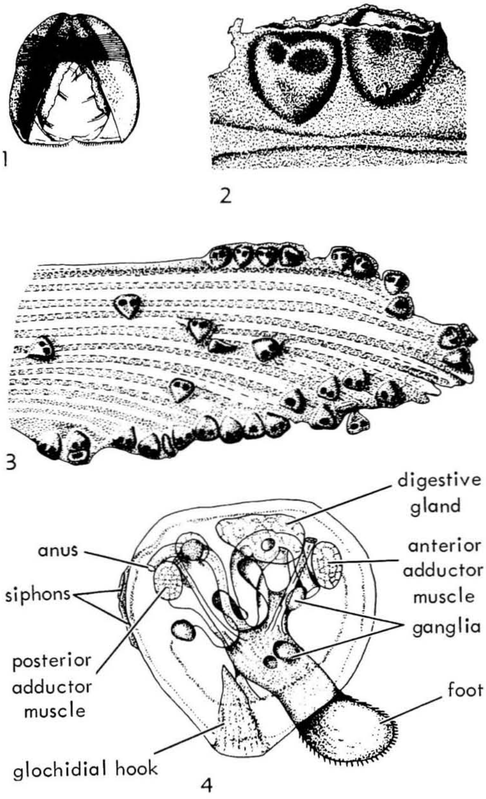


FIG. 80. Bivalve ontogeny—early growth stages of fresh-water mussels, much enl. (Guthrie & Anderson, from Lefevre & Curtis 1910 [1912]).——*1.* Hooked glochidium of *Symphynota* before attachment to fish.——*2.* Young glochidia of *Anodonta* 24 hours after attachment to fin of carp.——*3.* Same, 36 hours after attachment, glochidia well embedded in tissue of fin.——*4.* Juvenile *Symphynota* after end of parasitic phase, adult structures developed in association with persistent glochidial hook.

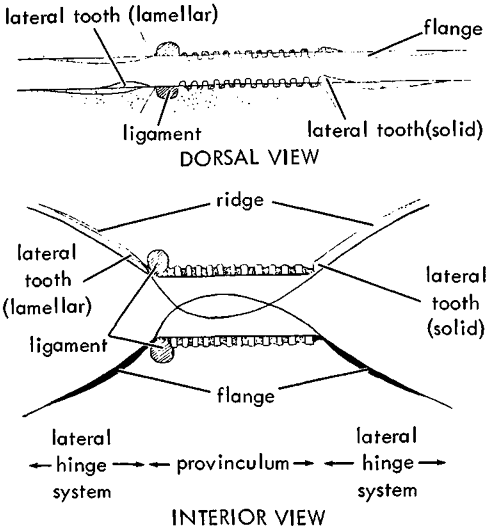


Fig. 81. Bivalve ontogeny—components of larval hinge showing terminology *(141)*.

larval life and pass through trochophore and veliger stages like most marine forms. The early development of *Dreissena* has been more thoroughly investigated in the laboratory than that of any other bivalve. Members of the families Corbiculidae and Pisidiidae undergo direct development in brood pouches within the mantle cavity of the mother, usually between the gill lamellae.

Many of the Unionacea are of particular interest in passing through a stage in which the larva is parasitic on fishes. In *Anodonta* and *Unio,* for example, the eggs are fertilized in the suprabranchial chamber of the parent mollusk and then pass to the interlamellar spaces of the gills, where development proceeds to a certain stage, when some stimulus (such as the movement of a passing fish) results in the expulsion of the larva into the surrounding water. This larva, termed the **glochidium**, already has a shell of two valves joined by a strong larval adductor muscle. There is no mouth or anus, a larval mantle serving as an organ of nutrition. A rudimentary foot is present, bearing a long filament. In the glochidium of *Anodonta* the margin of each valve opposite the hinge bears a barbed, hooklike projection; this is absent in that of *Unio,* but the corresponding part of the margin is extremely sharp. If the glochidium is successful in reaching a fish it attaches itself to a fin or gill by grasping it by means of the two valves of its shell, drawn together by the adductor (Fig. 80,*1-3*). A cyst soon forms in the tissues of the fish, and within this the larva completes its development, emerging when it is ready for bottom life (Fig. 80,*4*). The duration of the parasitic period depends to some extent on the temperature; for *Unio* it is usually 14 to 20 days but may be as long as 36 days; for *Anodonta* it is said to range from 12 to 80 days. The shell of the glochidium may remain as a prodissoconch at the umbo of the adult unionid, but it is usually removed by erosion.

The larval history of an African freshwater bivalve, *Mutela bourguignati* (Ancey), includes a parasitic stage which is quite unlike that of glochidium-producing unionids. The eggs first develop in the inner demibranchs of the gills into spherical larvae covered dorsally and laterally by a thin pellicle; anteriorly each larva bears a tentacle about 70 times its length. When about 0.2 mm. in diameter the larvae are discharged into the surrounding water and proceed to become parasitic on fish. Each one (termed the *haustorial larva* at this stage) develops into a bud which remains clear of the host and a stalk which penetrates into the latter and through which nourishment is conveyed from it. The two shell valves, enclosing the developing vital organs of the mollusk, originate within the bud. Eventually, when about 1 mm. long, the young bivalve is released to assume its bottom life, soon casting off the long stalk which it bears. Many South American unionids produce yet another type of larva, known as the *lasidium larva,* but their developmental history has yet to be worked out in detail.

A question which paleontologists still have to investigate is when the Unionacea first acquired a parasitic larval habit during their long geological history.

## HINGE STRUCTURES OF PRODISSOCONCH

No differentiated hinge structures are seen in the straight-hinged or D-shaped stage of the larval shell (prodissoconch I), but after the transition to the mantle-secreted prodissoconch II a larval ligament and a series of larval teeth appear (Fig. 81).

Rees *(141)*, after studying 77 types of bivalve pelagic larvae from the North Sea, was able to distinguish 18 basic types of larval hinge in this particular material. He

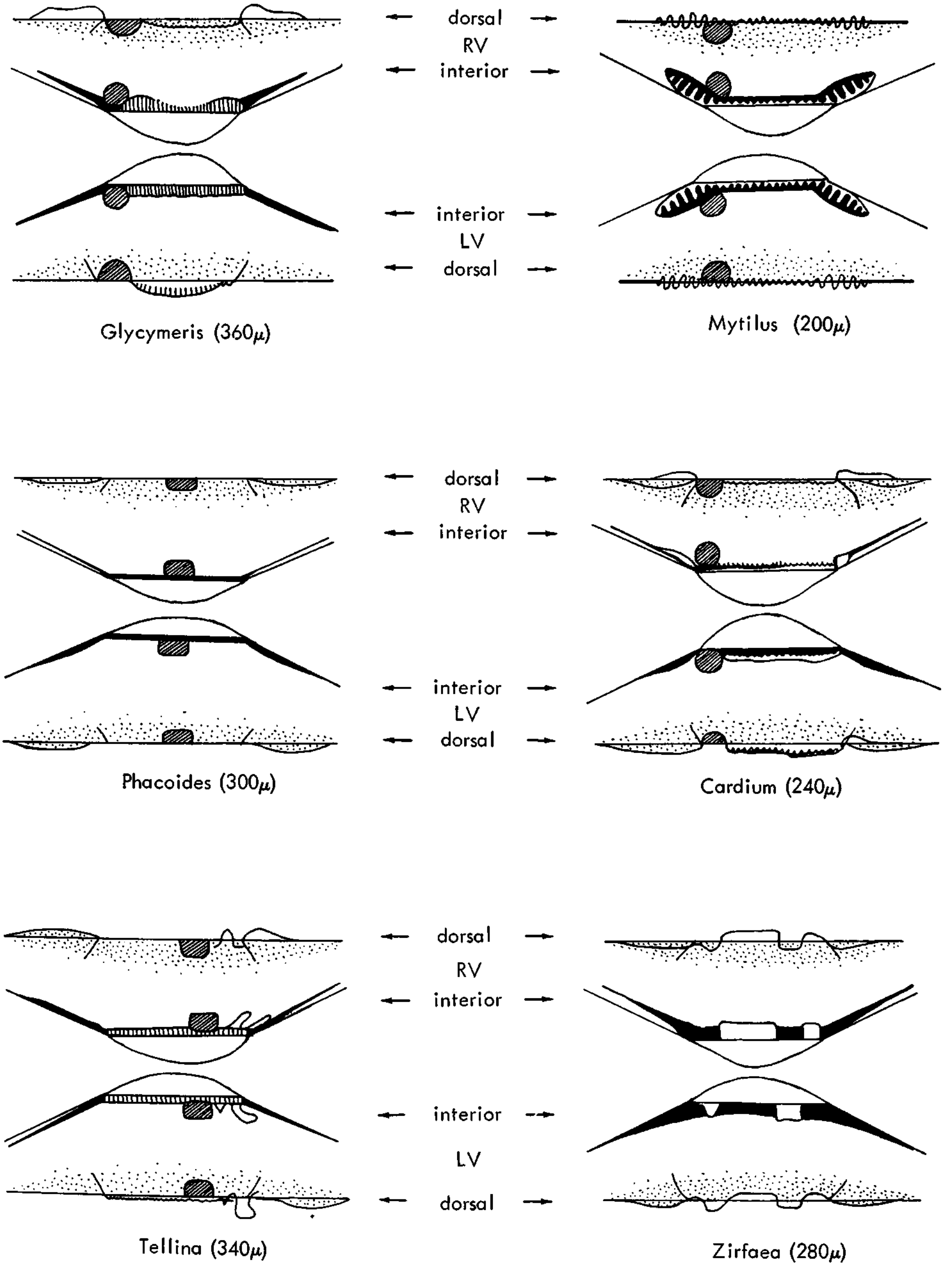


Fig. 82. Bivalve ontogeny—dentition of prodissoconch hinges in six North Sea genera, Rec. (diameter of larval shells in microns indicated) (Cox, from *141*).

found that these were characteristic of definite superfamilies, except that one type was common to the Pectinacea and Anomiacea, and another to the Ostreacea and Pteriacea. The straight median part of the hinge margin, termed the **provinculum**, bears the most obvious teeth, and REES recognized four main types of such dentition. In the first type each valve bears several or numerous small rectangular teeth or crenulations (recalling the taxodont teeth of the Nuculacea and Arcidae) arranged along a relatively thick provinculum; in the second type there are only one to three strong rectangular teeth along a relatively thick provinculum; in the third type the teeth form one or more elongated projections on a thin provinculum; and in the fourth type the right valve has a thin strip of small spiky provincular teeth. Teeth are entirely lacking on the provinculum in the Lucinacea and the Erycinacea.

Further structures, constituting the **lateral hinge system**, may be present along the valve margins anterior and posterior to the provinculum (Fig. 81, 82). In the left valve these parts of the margins have a projecting flange which is received in the right valve between the thin edge of the dorsal margin and an internal ridge. The proximal end of this ridge may bear a toothlike projection consisting either of a lamina underlying the marginal flange of the other valve or of a more solid tooth that comes into contact with the outer edge of the provinculum of the other valve when the shell is closed. Special teeth, variously shaped and commonly larger than those already mentioned, are also present in some species, usually at one end of the provinculum. The short transverse larval ligament is external in the Solenacea but internal in the other groups studied. When internal it occupies a recess interrupting the denticles of the provinculum, and its position is posterior except in the Lucinacea (in which it is median), in the Erycinacea and Tellinacea (in which it is anterior to mid-length), and in many Ostreidae.

RANSON's (1948) work on the prodissoconch in the Ostreidae is of interest as showing that its hinge structure may vary to some extent in the same family. He found that three different types of hinge are present and used them as a basis for generic classification. The types are *(a)* provinculum with five teeth, ligament just beyond anterior end of provinculum, further series of crenulations along anterodorsal margin; *(b)* provinculum with two teeth at each end and gap in middle, ligament well beyond anterior end of provinculum; *(c)* teeth as in *(b)* but ligament below provinculum, between its center and anterior end. The very anterior position of the ligament in the larva of many species of Ostreidae is an unusual feature, and was long ago commented upon by BERNARD.

## CHANGES DURING AND AFTER METAMORPHOSIS

When the larva assumes a bottom life (the episode of "spatfall" in the case of oysters) significant changes take place in its organization, the most important being the degeneration of the velum, which is no longer required as an organ for swimming and food collecting, and the loss of the larval retractor muscles. The byssus gland begins to function, for, as already seen, the byssus may play an important part in adaptation of the young mollusk to its new mode of life. At this stage the foot begins to grow rapidly when it is to function as an organ of locomotion and burrowing in the adult mollusk. In the Ostreidae, on the other hand, this organ performs its last function by holding the left valve in position while the fluid that cements it to the substrate is poured out by the byssal gland; this task accomplished, it quickly atrophies. In probably all bivalves the later larval stages have two equal adductor muscles, but in forms in which the adult is monomyarian the anterior of these dwindles away very rapidly after settlement. The loss is almost complete in about 90 hours in the case of *Ostrea edulis* LINNÉ, by which time the length of the shell has increased from 0.3 mm. at the time of spatfall to 0.6 mm. Loss of the anterior adductor is accompanied by migration of the posterior adductor and by changes in the positions of the internal organs, resulting in wide divergence between directions of the oro-anal and cardinal axes.

These changes are also almost completed within a few days after settlement. The gills continue to grow by increase in the number of filaments, and other soft organs which are to be retained in the adult mollusk continue to develop. Whereas the prodissoconch is devoid of ornament, the ribbing and other sculptural features characteristic of the adult shell commonly appear even on the earliest growth stages of the **dissoconch** (postlarval shell), which, except in attached forms, rapidly assumes the shape of the full-grown shell.

We are indebted to BERNARD and others for our knowledge of the earlier stages in the development of the hinge structures of the dissoconch. BERNARD made large collections of prodissoconchs and young dissoconchs, mainly from Recent shell sands and from various fossiliferous formations of Tertiary age, and was able to construct series showing successive ontogenetic stages in a number of species, in many cases confirming his identifications by examining prodissoconchs still preserved on the beaks of adult shells. His most important observations relate to the heterodonts and have been summarized when explaining the system of hinge notation which he devised in collaboration with MUNIER-CHALMAS. Similar work on some other important groups still living, such as the Unionacea and Trigoniacea, and on many extinct groups (if only the necessary material is obtainable) has yet to be accomplished, and should throw light on the relations of these groups to the heterodonts. His work on various Palaeotaxodonta and Pteriomorphia may be reviewed briefly.

In all the bivalves investigated the denticulations or crenulations of the provinculum persist in the earlier dissoconch stages and at first even increase in number and size, although they ultimately disappear. A hinge plate (if present in the adult shell) gradually becomes defined on the ventral side of the provinculum and extends beyond this anteriorly and posteriorly. The dissoconch teeth then appear on it in succession and the ligament undergoes a series of changes.

In Arcoida investigated by BERNARD the first two teeth (i.e., one in each valve) arise simultaneously on the posterior side of the beak below the provincular crenulations, to be followed very soon after by the first anterior pair. These earliest teeth (like the first few that succeed them) have a longitudinal orientation, and those in the right valve are dorsal to those in the left. Except for two small pairs that appear next in some species on the dorsal side of the earliest ones, the next few (but not necessarily all) subsequent teeth arise in order at the two extremities of the series, and not by intercalation between previously formed teeth at the middle of the hinge or elsewhere. (Investigations by subsequent workers suggest that this does not apply to all Arcoida.) In *Glycymeris obovata* (LAMARCK) the first two pairs of definitive teeth are present when the shell is 0.4 mm. long, and there are five pairs when the length is about 0.7 mm. The later-formed teeth have from the first the orientation (whether dorsoventral or longitudinal) they possess in the adult shell, and during growth the inner end of each of the earlier-formed, longitudinal teeth, occupying the middle of the hinge line, usually bends ventralward; the whole tooth eventually assumes a dorsoventral orientation. In *Nucula* and *Nuculana,* the development of the hinge teeth follows much the same course as in the Arcoida, but all teeth except the very first pair are chevron-shaped from the beginning, the downbending of the inner end of each being regarded by BERNARD as an "exaggeration and acceleration" of the process observed in the Arcoida. In *Malletia,* on the other hand, several of the earliest-formed teeth are at first straight and longitudinal. In *Nucula* and *Malletia* there is evidence of the obliteration by the ligament of some of the earlier-formed teeth, lying at the middle of the hinge, during growth of the shell.

In *Mytilus* a few small, almost longitudinal teeth develop along the posterodorsal margin some distance beyond the row of crenulations persisting from the prodissoconch, but are obliterated as the ligament extends posteriorly. Similar teeth appear along the margin anterior to the beak, also beyond the row of crenulations, and some of these persist to form the dysodont teeth of

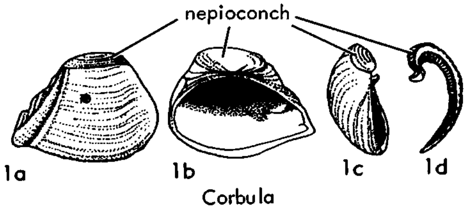


FIG. 83. Bivalve ontogeny—*Corbula costata* J. DE C. SOWERBY, U.Eoc.(Barton), Eng., showing change in valve shape from early form (nepioconch) as growth proceeds *(188)*.

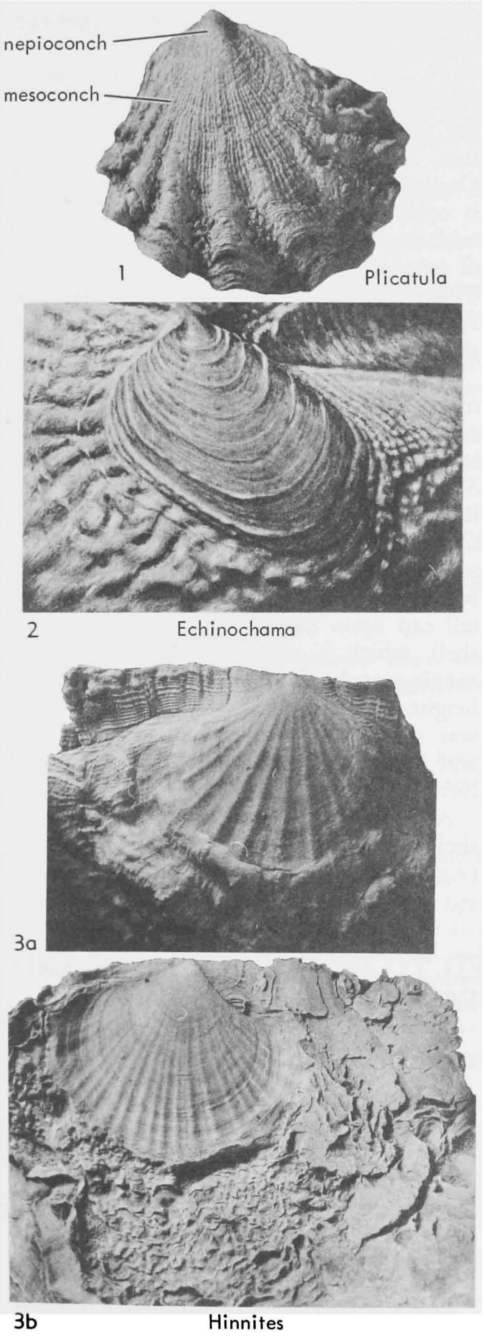
the adult mussel. In a species of *Pteria* it was found that definitive teeth do not make their appearance until a later stage in ontogeny than in the forms just mentioned. From the first these belong to two distinct series; the posterior teeth are elongate lamellae almost parallel to the hinge margin, the more ventral ones appearing first; the anterior teeth are short, and tuberculate or lunate in shape.

It is to be assumed that, as soon as secretion of the shell and ligament are taken over by the mantle with the resulting appearance of prodissoconch II, the ligament becomes differentiated into its fibrous, calcareous and its lamellar, noncalcareous parts. It would also be expected that the ligament of the adult shell would be derived from that of prodissoconch II. In the Nuculidae BERNARD observed that this early ligament expands in a ventral and anterior direction as the hinge plate develops and gives rise to the definitive ligament, which remains internal. In *Mytilus edulis,* on the other hand, he found that, at an early stage in the development of the dissoconch (length 0.6 mm.), a second ligamental depression appears a short distance posterior to the original depression. It is from this second center that the definitive ligament develops rapidly, until ultimately it extends along a considerable part of the posterodorsal margin; the original ligament apparently atrophies. The exact process involved in the lateral separation of the two constituents of the ligament in forms in which there is a cardinal area has yet to be observed. In the early ontogeny of members of the Arcoida it can be seen how the ligamental depression, at first internal, becomes marginal and then mainly external. Actual secretion of new ligament cannot, however, take place externally to the margin, since the mantle does not extend beyond the latter. In forms in which the lamellar ligament is inserted in grooves on the cardinal area, diverging to form the arms of chevrons, it is clear that the original center of secretion of lamellar ligament at the margin must divide into two, which draw apart and trace out divergent courses on the cardinal area as this increases in width and the hinge line in length. Further paired centers of secretion must then arise in turn at the middle of the hinge and separate in a similar manner. In the Noetiidae, however, there are no such paired centers of secretion, the ligamental grooves on the cardinal area being perpendicular to the hinge margin.

## ABRUPT POSTNEANIC CHANGES IN SHELL CHARACTERS

In addition to the changes in features of the shell corresponding to the transition from prodissoconch I to prodissoconch II and from the latter to the early dissoconch (the neanic shell of HYATT's terminology), a study of the ontogeny in some species shows that rather abrupt changes in shape and ornament may occur at later periods. In some instances the mollusk is apparently free-living for some time after metamorphosis and then becomes cemented; in other cases it is not at present possible to correlate the change in shell characters with a known episode in life history.

WRIGLEY *(188)* has called attention to several such cases of discontinuity. In some species of *Corbula* there is a distinct apical shell (much larger than the protoconch) which appears perched on top of the complete shell, from which it can be detached. In the Eocene species *Corbula costata* J. DE C. SOWERBY (Fig. 83) this apical shell, termed by WRIGLEY the nepioconch, is about 10 mm. long, ornamented with fine, regular concentric threads, and devoid of a carina, whereas immediately following the discontinuity in growth the ornament changes to irregular concentric rugae and



a posterior carina appears. Two such abrupt changes are observable in the Eocene species *Callocardia nitidula* (LAMARCK) and *Plicatula filamentosa* CONRAD, the first marking the transition from the nepioconch to the mesoconch (in WRIGLEY's terminology), and the second the change from the mesoconch to the part of the shell bearing the adult ornamental pattern. In *Plicatula* (Fig. 84,*1*) the nepioconch is smooth, the mesoconch is ornamented with fine radial threads, while the last-formed part of the shell bears broad radial ribs.

In the Chamidae the adult shell is inequivalve and rather irregular in form as the result of attachment by one valve, while the umbones are strongly prosogyrate and the hinge teeth (2 in the attached and 1 in the free valve) are thick, amorphous, and longitudinally elongate, as the result of the coiling of the valves that has taken place during growth. The early dissoconch, about 2.5 mm. in length, preserved at the umbo in some specimens, is, however, equivalve and very different from the adult shell in shape and appearance; it was obviously unattached. In the genus *Echinochama,* in which the change is strongly marked, this neanic shell is rectangular in outline, with anterior beaks and ornament of a few regularly spaced, thin concentric lamellae (Fig. 84,*2*). The dentition, consisting of two cardinal teeth and one elongate anterior lateral in each valve, is quite unlike that of the adult shell. It is difficult not to believe that this early, heterodont-like shell throws considerable light on the origin and affinities of the Chamidae. It may also be significant that no such neanic shell has ever been found in any of the Mesozoic rudists, some so similar to *Chama* in adult form and dentition.

In the family Pectinidae, those species which have been included in the genus *Hinnites* DEFRANCE resemble a typical *Chlamys* in shape and ornament until they become attached by the growing part of the

FIG. 84. Bivalve ontogeny—changes in shell characters during and after metamorphosis (Nuttall, n). ——*1. Plicatula filamentosa* CONRAD, Eoc.(Claiborn.), Ala., showing early (nepioconch) and intermediate (mesoconch) growth forms, ×2.——*2. Echinochama arcinella* (LINNÉ), Rec., E.Atl., umbo of left valve with preserved nepionic shell, ×17 (from Odhner, 1919).——*3. Hinnites crispus* (BROCCHI), Plio., Italy; *3a,b,* changes from early pectiniform to later oyster-like shape, ×1.

FIG. 85. Bivalve ontogeny—*Penicillus (Penicillus) pulcher fossile* (SIEVERTS), Mio., E.Indies(Brunei), showing changes in form subsequent to nepionic shell, ×4 (Sieverts, 1934).

surface of the right valve and develop an irregular form. The early shell is commonly preserved at the summit of both valves and its right valve has a well-defined anterior auricle and a byssal notch (Fig. 84,*3*). In the European Neogene species *Hinnites crispus* (BROCCHI) attachment may not occur until the shell is more than 20 mm. high. In *Prohinnites,* of the Lower Cretaceous, a juvenile shell, regular in form, is commonly preserved in the right valve, with its margin surrounded by the surface of attachment, but it lacks a byssal notch. This fact seems to afford evidence that *Prohinnites* and *Hinnites* arose by convergence from different stocks.

Among more ancient bivalves, a very remarkable instance of change in form and ornament at a moderately advanced stage in ontogeny is that observable in the genus *Slava* BARRANDE, from the Silurian of Bohemia. The earlier-formed shell, which is about 15 to 35 mm. in height, is elevated and subtrigonal in shape, with prominent but prosogyrous umbones, and sits like a tall cap upon the later-formed part of the shell, which is almost circular in outline, ranging up to about 55 mm. in length and height, and bears fine radial riblets. *Slava* was not attached at any stage in growth and reasons for the sudden change in the form of its shell are unknown.

A number of other striking changes in shell form during ontogeny could be cited (e.g., *Penicillus,* Fig. 85).

# MORPHOLOGICAL TERMS APPLIED TO BIVALVIA SHELLS AND SOFT PARTS AFFECTING SHELL

Terms considered most important are given in boldface type (as **accessory muscle**); use is not recommended of those printed in italics (as *epidermis*).

**accessory muscle.** Any muscle other than adductor and pallial muscles, with scar of attachment to shell (convenient noncommital term when referring to scars of muscles of uncertain function).

**acline.** Perpendicular to hinge axis or almost so (applied to hinge teeth or, in some genera, to direction of elongation of body of shell). Same as orthocline.

**actinodont.** With teeth radiating from beak, outer ones more or less elongate (applied to certain bivalves of early origin).

**adductor muscle.** Muscle, commonly one of 2, connecting 2 valves of shell, tending to draw them together.

**adductor scar.** Impression on interior of shell where adductor muscle was attached.

**alate.** With wings or auricles.

**alivincular.** Type of ligament not elongated in longitudinal direction nor necessarily situated entirely posterior to beaks, but located between cardinal areas (where present) of respective valves, with lamellar layer both anterior and posterior to fibrous layer; example, *Ostrea.*

*allomorphism. See* xenomorphism.

**amphidetic.** Extending on both anterior and posterior sides of beaks (applied to ligament or ligamental area); example, *Arca.*

**anachomata.** *See* chomata.

**anisomyarian.** With one adductor muscle (anterior) much reduced or absent.

**anodont.** Lacking hinge teeth. Same as edentulous.

**anterior.** Direction parallel to cardinal axis more nearly approximating to that in which mouth of animal faces.

**anterior lateral tooth.** Lateral tooth situated in front of beaks.

**anterodorsal margin.** Margin of dorsal part of shell in front of beaks.

**apophysis.** Projecting structure, such as that serving for attachment of pedal muscle in Pholadidae or adductor muscle in some rudists.

**arcticoid type.** Type of heterodont dentition intermediate between lucinoid and corbiculoid types; formerly termed cyprinoid type.

**auricle.** Earlike extension of dorsal region of shell, commonly separated from body of shell by notch or sinus.

**auricular crura** (sing., **crus**). Blunt internal ridges, swelling out distally as low tubercles, marking lower border of auricles in some Pectinidae.

**auricular sulcus.** External furrow at junction of auricle with body of shell.

**auriculate.** With auricles.

**basal margin.** Edge of shell opposite hinge, i.e., ventral margin according to terminology here adopted.

**bead.** Small rounded protuberance on rib.

**beak.** Noselike angle, located along or above hinge margin, marking point where growth of shell started.

**bialate.** With 2 wings or auricles.

**body of shell.** In alate or auriculate shells, entire shell with exception of wings or auricles.

**bourrelet.** Either of two portions of bivalve ligamental area flanking resilifer on its anterior and posterior sides; each comprises growth track and seat of the lamellar ligament. [The posterior bourrelet is flattish in all oysters except the Exogyrinae, in which it is a narrow sharp-crested spiral ridge on the LV and a corresponding groove on the RV.]

**branchitellum** (pl., **branchitella**). Point on posteroventral shell margin of oysters nearest to palliobranchial fusion, commonly forming conspicuously projected posteroventral tip on LV, especially in sickle-shaped oysters; aboral end of gills points toward it.

**buttress.** Internal projection from wall of shell supporting hinge plate or chondrophore.

**byssal foramen.** Opening in right valve in Anomiidae for passage of calcified byssus.

**byssal gape.** Opening between margins of shell for passage of byssus.

**byssal notch.** Indentation below anterior auricle of right valve in many Pectinacea for passage of byssus or protrusion of foot.

**byssal sinus.** Embayment of margin below anterior auricle of left valve in many Pectinacea, corresponding to byssal notch of right valve but usually shallower.

**byssiferous.** Possessing a byssus.

**byssus.** Bundle of hairlike strands by which temporary attachment of bivalve can be made to extraneous objects.

**callum.** Secondary calcareous structure present in some Pholadidae, forming anterior extension of shell proper and closing pedal gape in adult.

**cancellate.** Consisting of intersecting radial and commarginal threads.

**cardinal area.** Flat or slightly concave, commonly triangular surface extending between beak and hinge margin in many bivalves, and partly or wholly occupied by ligament.

**cardinal axis.** Imaginary straight line along which 2 valves of shell are hinged.

**cardinal costa.** Ridge or rib demarcating cardinal area from outer surface of shell.

**cardinal crura** (sing., **crus**). Narrow lamelliform teeth radiating from apex of ligament pit in Pectinacea.

**cardinal platform.** Shelly internal plate bearing hinge teeth, situated below beak and adjacent parts of dorsal margins and lying in plane parallel to that of commissure. Same as hinge plate.

**cardinal tooth.** Hinge tooth situated close to beak.

**carina.** Prominent keel-like ridge.

**carinate.** With carina or sharp angulation.

*cartilage.* Old term for internal ligament.

**catachomata.** *See* chomata.

**caudate.** With narrow, tail-like extremity.

**chevron groove.** V-shaped furrow on cardinal area in some Arcacea and early Pectinacea for insertion of ligament.

**chomata** (sing., **choma**). Collective term for anachomata, which are small tubercles or ridgelets on periphery of inner surface of RV, and catachomata, which are pits in LV for reception of anachomata; both generally restricted to vicinity of hinge, but may encircle whole valve.

**chondrophore.** Process with hollowed-out surface for attachment of internal ligament.

*cicatrix.* Scar (of muscle attachment).

**clavicle.** Shelly buttress supporting chondrophore in some genera.

**closed.** Not gaping anywhere along margins (applied to shell valves).

**commarginal.** With direction on part of surface of shell under consideration determined by former position of shell margin. (New term suggested for direction usually described as concentric.)

**commissure.** Line of junction of 2 valves.

**compressed.** Relatively flattened.

**concentric.** With direction coinciding with that of growth lines. (By no means concentric in literal and geometrical sense of term; *see* commarginal.)

**conchiolin.** Material (protein) of which periostracum and organic matrix of calcareous parts of shell are composed.

**convexity.** Degree of inflation.

**corbiculoid type.** Heterodont dentition with 3 cardinal teeth in each valve, middle one of RV occupying median position below beaks. Formerly termed cyrenoid type.

**corselet.** Differentiated posterior area.

**cordate.** Heart-shaped.

**costa.** Moderately broad and prominent elevation of surface of shell, directed radially or otherwise.

**costella.** Rather narrow linear elevation of surface of shell.

*costule.* Same as costella.

**crenate.** With notches along edge or crest (as of ribs).

**crossed-lamellar.** Type of shell structure composed of primary and secondary lamellae, latter inclined in alternate directions in successive primary lamellae.

**cruciform muscles.** Two bundles of muscle fibers present in Tellinacea and some Solenidae, joining valves posteroventrally and intersecting to form cross.

**cryptodont.** Lacking hinge teeth (applied to certain groups of early origin only).

**ctenodont.** With numerous short hinge teeth transverse to margin (applied to certain groups of early origin only).

**ctenolium.** Comblike row of small teeth on lower side of byssal notch in some Pectinacea.

**cuneiform.** Wedge-shaped.

**cyclodont.** With arched hinge teeth curving out from below hinge margin, hinge plate being small or absent.

*cyrenoid type. See* corbiculoid type.

**demarcation line.** Imaginary line on surface of valve originating at beak and marking locus of points on successive positions of margin where transverse growth component has had maximum effect. Forms dorsoventral profile when valve is viewed from one end.

**denticle.** Small rounded toothlike protuberance.

**denticulation.** Same as denticle.

**dentition.** Hinge teeth and sockets, considered collectively.

**diagenodont.** With differentiated cardinal and lateral teeth located on hinge plate, laterals not exceeding 2 or cardinals 3 in either valve; example, *Astarte.*

**diagonal ridge.** Ridge running diagonally from umbo toward posteroventral part of valve.

**dimyarian.** With 2 adductor muscles.

**directive rib.** Rib, forming part of surface ornament of shell, that lies entirely within single plane.

**directive spiral.** Spiral curve formed by directive rib within its own plane.

**disc.** In Pectinacea, whole of valve except auricles.

**discordant margins.** Margins of closed valves not in exact juxtaposition, but one overlapping other.

**dissoconch.** Postlarval shell.

**divaricate.** Type of ornament composed of pairs of rather widely divergent costules or other elements.

**dorsal.** Pertaining to region of shell where mantle isthmus was situated and valves are connected by ligament (i.e., to region of hinge).

**duplivincular.** Type of ligament with lamellar component repeated as series of bands, each with its 2 edges inserted in narrow grooves in cardinal areas of respective valves; example, *Arca.*

**dysodont.** With small weak teeth close to beaks (as in some Mytilacea).

**ear.** Small extension of dorsal region of shell, commonly separated from body by notch or sinus. Same as auricle.

**edentulous.** Lacking hinge teeth.

**emarginate.** With margin interrupted by notch or sinus.

**ensiform.** Shaped like genus *Ensis,* with outline resembling curved sword.

**entire.** Lacking sinus (applied to pallial line).

*epidermis.* Term used by some authors for periostracum.

**equilateral.** With parts of shell anterior and posterior to beaks equal in length or almost so.

**equivalve.** With 2 valves of same shape and size.

**escutcheon.** Typically lozenge-shaped dorsal differentiated area extending posteriorly from beaks and sometimes bordered by ridge in each valve.

**escutcheon ridge.** Ridge extending posteriorly from beak in each valve and forming border of escutcheon.

**excurrent.** Forming passage for current of water expelled from mantle cavity (applied to mantle opening or siphon).

**exhalant.** Same as excurrent.

**exogyrate.** Shaped like shell of *Exogyra,* that is, with left valve strongly convex and its dorsal part coiled in posterior direction, with right valve flat and spirally coiled.

**falciform.** Sickle-shaped.

**fascicle.** Small bunch (of ribs).

**fasciculated.** Arranged in small bunches.

**fibrous ligament.** Part of ligament characterized by fibrous structure and in which conchiolin is commonly impregnated with calcium carbonate; secreted by epithelium of mantle isthmus and elastic chiefly to compressional stresses.

**flabelliform.** Fan-shaped.

**flank.** Median part of surface of valve, limited posteriorly by posterior ridge where present.

**fluted.** With series of narrow parallel rounded excavations (like flutings of architectural column).

**fold.** Rather broad undulation of surface of shell, directed either radially or commarginally.

**foot.** Protrusible muscular structure extending from mid-line of body, anteroventrally in more typical bivalves, and used for burrowing or locomotion.

**foramen.** Opening, hole.

**fossette** (or fosset). Socket, as for cardinal tooth.

*fulcrum*. Old term for chondrophore.

**funnel plates.** Transverse laminae in wall of radiolitid lower valve, inclined downward funnel-wise toward axis and combining with radial laminae to produce cellular structure.

**fusion layer.** Part of ligament secreted where mantle edges are united dorsally by secondary fusion (i.e., anteriorly and posteriorly to mantle isthmus).

**gape.** Localized opening remaining between margins of shell when valves are drawn together by adductor muscles.

**gill retractor muscle.** Muscle present in a few Bivalvia attaching one of gills to shell.

**globose.** Tending toward spherical shape.

**growth line.** Line on surface of shell, one of usually irregularly arranged series, marking position of margin at some stage of growth.

**growth ruga.** Irregular wrinkle on surface of shell of similar origin to growth line but corresponding to more pronounced hiatus in growth.

**growth thread.** Threadlike elevation of surface of similar origin to growth line.

**gryphaeate.** Shaped like shell of *Gryphaea,* that is, with left valve strongly convex and its dorsal part incurved and with right valve flat.

**height.** Distance between 2 planes parallel to cardinal axis and perpendicular to plane of commissure, which just touch most dorsal and ventral parts of shell.

**heterodont.** With distinctly differentiated cardinal and lateral teeth.

**heteromyarian.** With one adductor muscle (anterior) much reduced.

**hinge.** Collective term for structures of dorsal region which function during opening and closing of valves.

**hinge axis.** Imaginary straight line about which 2 valves of shell are hinged.

**hinge line.** Term applied loosely by many authors to part of shell bordering dorsal margins and occupied by or close to hinge teeth and ligament; used by some in same sense as hinge axis.

**hinge margin.** Edge of shell that approximates most closely to hinge axis.

**hinge plate.** Shelly internal platform bearing hinge teeth, situated below beak and adjacent parts of dorsal margins, and lying in plane parallel to that of commissure.

**hinge tooth.** Shelly structure (usually one of a series) adjacent to dorsal margin and received in socket in opposite valve; hinge teeth serve to hold valves in position when closed.

**homomyarian.** With 2 adductor muscles equal in size or almost so.

**hyote spines.** Hollow, tubular and cylindrical shell outgrowths open distally at their tips as well as on their distal flanks, arising periodically from thin edges of shell margin of oysters. [The tip ends are rounded, ear-shaped openings, typically developed on *Hyotissa hyotis* (LINNÉ, 1758).]

**hypoplax.** Elongate accessory plate extending along posterior end of ventral margin in some Pholadidae.

**hypostracum.** Term used in 2 different senses: 1) inner layer of shell wall, secreted by entire epithelium of mantle (original sense); 2) part of shell wall secreted at attachments of adductor muscles (later sense: *see* myostracum).

**imbricate.** Overlapping like tiles or shingles on a roof.

*incremental line*. Same as growth line.

**incurrent.** Forming passage for current of water drawn into mantle cavity from medium (applied to mantle opening or siphon).

**inequilateral.** With parts of shell anterior and posterior to beaks differing appreciably in length.

**inequivalve.** With one valve larger than other.

**inflated.** Strongly convex.

**inflation.** Distance between 2 planes parallel to plane of commissure and touching outermost parts of 2 valves.

**inhalant.** Same as incurrent.

**inner** [layer of] **ligament.** Same as fibrous ligament.

**integripalliate.** With pallial line devoid of sinus.

**interband.** Longitudinal band on surface of lower valve of radiolitid rudist, separating 2 bands designated as siphonal bands.

**interdentum.** Shelly plate present in some Unionidae bridging space between pseudocardinal and lateral teeth.

**interspace.** Depression between adjacent costae or other linear surface elevations.

**interval.** Same as interspace when applied to surface ornament.

**inverse.** Term formerly applied to chamid in which attachment is by LV or rudist in which attachment is by RV.

**isodont.** With small number of symmetrically arranged hinge teeth; examples, *Spondylus, Plicatula.*

**isomyarian.** With 2 adductor muscles equal in size or almost so; same as homomyarian.

**keel.** Projecting ridge; same as carina.

**lamella.** Thin plate.

**lamellar ligament.** Part of ligament characterized by lamellar structure and containing no calcium carbonate; secreted at mantle edge and elastic to both compressional and tensional stresses.

**lamelliform.** Like thin elongate plate.

**lamina.** Thin plate.

**lanceolate.** Lance-shaped, i.e., tapering to point at one end, rounded at other.

**lateral hinge system.** Hinge structures present in some prodissoconchs anterior and posterior to provinculum.

**lateral tooth.** Hinge tooth partly or wholly located some distance from beaks.

**left valve.** Valve lying on left-hand side when shell is placed with anterior end pointing away from observer and commissure vertical, the hinge being uppermost.

**length.** Distance between 2 planes perpendicular to cardinal axis and just touching anterior and posterior extremities of shell.

**lenticular.** Shaped like biconvex lens.

**ligament.** Horny elastic structure or structures joining 2 valves of shell dorsally and acting as spring causing them to open when adductor muscles relax.

**ligament fulcrum.** Narrow lunate platform extending posteriorly from beak along dorsal margin and serving for attachment of ligament; same as nymph.

**ligament groove.** Narrow depression in cardinal area for attachment of fibers of ligament.

**ligament pit.** Relatively broad depression in cardinal area for attachment of ligament.

**ligament ridge.** Narrow ridge or lamina formed by projection of outer layer of shell wall into body cavity of many rudists (particularly hippuritids and radiolitids), thought to have served for attachment of ligament.

**ligament suture.** Elongated space behind umbones apparent after erosion of ligament.

**lithodesma.** Small calcareous plate reinforcing internal ligament in some genera; same as ossiculum.

**longitudinal.** Direction parallel to that of cardinal axis.

**lucinoid type.** Type of heterodont dentition with 2 cardinal teeth in each valve, anterior one in LV occupying median position below beaks.

**lunule.** Depression, commonly cordate in shape, present anterior to beaks in many bivalves.

**mantle.** Integument that surrounds vital organs of mollusk and secretes shell.

**marginal carina.** Ridge in Trigoniacea that runs from umbo to posteroventral angle of shell and delimits posterior area.

**mesoconch.** Part of dissoconch formed at an intermediate stage of growth and separated from earlier and later formed parts by pronounced discontinuities.

**mesoplax.** Transversely elongated accessory plate lying athwart umbonal region in some Pholadidae.

**metaplax.** Long narrow accessory plate covering gap between posterodorsal margins in some Pholadidae.

**modioliform.** Shaped like shell of *Modiolus;* differing from mytiliform in that beaks are not quite terminal and anteroventral region forms slight bulge.

**moniliform.** Composed of row of beads like a necklace.

**monomyarian.** With only 1 adductor muscle (posterior).

**multivincular.** Type of ligament consisting of serially repeated elements of alivincular type; example, *Isognomon.*

**muscle scar.** Impression on interior of shell marking former place of attachment of a muscle.

**myophore.** Process for attachment of muscle (usually adductor).

**myostracum.** Part of shell wall secreted at attachments of adductor muscles.

**mytiliform.** Shaped like shell of *Mytilus.*

**nacreous.** Type of shell structure consisting of thin leaves of aragonite parallel to inner surface of shell and exhibiting characteristic luster.

*nates.* Old name for umbones, as here defined.

**nepioconch.** Earliest formed part of dissoconch, when separated from later part by pronounced discontinuity.

**nepionic.** Earliest postlarval stage.

**nodose.** Bearing tubercles or knobs.

*normal.* Term formerly applied to chamid in which attachment is by RV or to rudist in which it is by LV.

**nymph.** Narrow lunate platform extending posteriorly from beak along dorsal margin and serving for attachment of ligament.

**oblique.** Most extended in direction neither parallel nor perpendicular to cardinal axis, but intermediate between these.

*obliquity.* Angle between straight dorsal margin and line bisecting umbonal angle (in terminology of some authors); or between dorsal margin and most distant point of ventral margin (in terminology of others).

**opisthocline.** Sloping (from lower end) in posterior direction (term applied to hinge teeth and, in some genera, to body of shell).

**opisthodetic.** Located wholly posterior to beaks (term applied to ligament).

**opisthogyrate.** Curved so that beaks point in posterior direction (term applied to umbones).

**orbicular.** Circular.

**orthocline.** Perpendicular to hinge axis or almost so (term applied to hinge teeth and, in some genera, to body of shell).

**orthodont.** Type of hinge in which direction of teeth is parallel to cardinal margin or almost so.

**orthogyrate.** Curved so that each beak points neither anteriorly nor posteriorly, but directly towards other valve (term applied to umbones).

**oscule.** Orifice in upper valve in some rudists, usually near margin.

**ossiculum.** Small calcareous plate reinforcing internal ligament in some genera; same as lithodesma.

**ostracum.** Term used in 2 senses: 1) outer part of calcareous wall of shell, secreted at mantle edge (original usage); 2) entire calcareous wall of shell (usage of some later authors).

outer [layer of] **ligament.** Same as lamellar ligament.

**ovate.** Shaped like longitudinal section of egg.

**override.** To pass over without interruption (commarginal over radial elements of ornament).

**pachyodont.** With heavy, blunt, amorphous teeth.

**pallet.** Small calcareous structure present in Teredinidae, one of pair closing end of boring when siphons are retracted.

**pallial.** Pertaining to the mantle.

**pallial line.** Line or narrow band on interior of valve close to margin, marking line of attachment of marginal muscles of mantle.

**pallial region.** Marginal region of shell interior adjacent to pallial line.

**pallial retractor muscles.** Muscles withdrawing marginal parts of mantle within shell where there is no distinct line of muscle attachment.

**pallial sinus.** Embayment of pallial line forming line of attachment of siphonal retractor muscles.

**parivincular.** Longitudinally elongated type of ligament, located posterior to beaks and comparable to cylinder split on one side with severed edges attached respectively along dorsal margin of 2 valves.

**pedal elevator muscle.** Thin bundle of muscle fibers attached to shell in umbonal cavity and serving to raise foot.

**pedal gape.** Opening between margins of shell for protrusion of foot.

**pedal levator muscle.** Same as pedal retractor muscle.

**pedal protractor muscle.** Muscle present in some genera, attached to shell interior and serving to extend foot.

**pedal retractor muscle.** Muscle attached to shell interior serving to retract foot.

**periostracum.** Thin coat of horny material covering calcareous part of shell.

**pillar.** Inward projection of outer shell layer extending longitudinally up lower valve in hippuritids.

**plica.** Fold or costa involving entire thickness of wall of shell.

**porcelaneous.** With translucent, porcelain-like appearance.

**posterior.** Direction parallel to cardinal axis more nearly approximating to that in which anus faces and exhalant current is discharged.

**posterior area.** Part of surface of valve posterior to posterior ridge.

**posterior lateral tooth.** Lateral tooth situated posteriorly to beaks and (in heterodonts) posteriorly to ligament.

**posterior ridge.** Ridge passing over or originating near umbo and running diagonally towards posteroventral part of valve.

**posterior slope.** Sector of surface of valve running posteroventrally from umbo.

**posterodorsal margin.** Margin of dorsal part of shell posterior to beaks.

**primary ligament.** Part of ligament representing original condition of structure, consisting of periostracum and lamellar and fibrous layers, but excluding secondary additions, notably fusion layer.

**primary riblet.** On shell with riblets of different orders of strength, riblet that appears early in ontogeny and remains stronger than those appearing later.

**prionodont.** Type of hinge in which teeth are developed in direction transverse to cardinal margin; virtually same as taxodont.

**prismatic.** Type of shell structure consisting of prisms of calcite or of aragonite.

**prodissoconch.** Shell secreted by the larva or embryo and preserved at beak of some adult shells.

**prodissoconch I.** Earlier-formed part of prodissoconch, secreted by shell gland of larva.

**prodissoconch II.** Later-formed part of prodissoconch, secreted by mantle edge.

**prosocline.** Sloping (from lower end) in anterior direction (term applied to hinge teeth and, in some genera, to body of shell).

**prosocoelous.** Same as prosogyrate.

**prosodetic.** Located anterior to beaks.

**prosogyrate.** Curved so that beaks point in anterior direction (term applied to umbones).

**prosopon.** Term recently proposed as suggested improvement on "surface ornament" or "sculpture."

**protoplax.** Flat, spearhead-like accessory plate, in 1 piece or divided longitudinally into 2, situated at anterior end of dorsal margin in some Pholadidae.

**protostracum.** Same as prodissoconch I.

**provinculum.** Median part of hinge margin of prodissoconch, usually bearing small teeth or crenulations.

**pseudocardinal.** Tooth irregular in form situated close to beak (as in some Unionacea).

**pseudoctenodont.** With numerous short teeth transverse to hinge margin, but descended from forms in which some teeth were longitudinally directed and more or less elongate.

**pseudolateral.** Lateral tooth (as here defined), proximal end of which is close to beak.

**pseudopillar.** Low, broad inward projection of shell wall present in some radiolitids.

**pseudotaxodont.** With numerous irregular short hinge teeth transverse to hinge margin and known to be unrelated to ctenodont and pseudoctenodont forms.

**punctate.** With pinprick-like depressions.

**punctum** (pl., **puncta**, never punctae). Pinprick-like depression of surface.

**quadrate.** Square, or almost so.

**Quenstedt muscle.** Small muscle of unknown function represented by scar below ligament area in Ostreidae.

**radial.** Direction of growth outward from beak at any point on surface of shell, commonly indicated by direction of costa or other element of ornament.

**resiliifer** (or **resilifer**). Recess or process for attachment of internal ligament.

**resilium.** Internal ligament, irrespective of composition.

**reticulate.** With network of oblique intersecting threads or other elements of ornament.

**rhomboidal.** Shaped like rhomb, figure with 4 equal sides and no right-angled corners.

**rib.** Moderately broad and prominent elevation of surface of shell, directed radially or otherwise; same as costa.

**riblet.** Rather narrow linear elevation of surface of shell; same as costella.

**right valve.** Valve lying on right-hand side when shell is placed with anterior end pointing away from observer and commissure vertical, the hinge being uppermost.

**rostrate.** With pointed, beaklike end.

**sagittal plane.** Anteroposteriorly directed plane of symmetry of shell and soft parts.

**scale.** Localized projection of outer layer of shell, commonly situated on a costa.

**scalloped.** With series of regular internal flutings corresponding to ends of external costae; term applied to shell margin.

**schizodont.** With 1 tooth (median of LV) broad and bifid.

**sculpture.** Regular relief pattern present on surface of many shells.

**secondary riblet.** On shell with riblets of different orders of strength, riblet that appears somewhat later in ontogeny than primary ones and remains weaker than these.

**sinupalliate.** Possessing pallial line with posterior embayment (or pallial sinus).

**sinus.** Indentation, embayment.

**siphon.** Tubelike extension of mantle for passage of inhalant or exhalant current.

**siphonal area.** Posterior sector of surface of shell, commonly demarcated anteriorly by umbonal ridge; secreted where mantle edge has openings or is produced to form siphons for passage of respiratory currents.

**siphonal band.** Longitudinal band (one of 2) on surface of some rudists (mainly radiolitids) differing in ornament from rest of surface and thought by some to have been secreted at part of mantle edge where respiratory current entered or left shell.

**siphonal retractor muscles.** Muscles serving to withdraw siphons partly or wholly within shell.

**siphonoplax.** Tubular secondary calcareous structure forming posterior extension of shell in some Pholadidae and protecting proximal end of siphons.

**socket.** Recess for reception of hinge tooth of opposite valve.

**spine.** Thornlike protuberance of surface of shell.

**spirogyrate.** Coiled outward from sagittal plane; term applied to umbones.

**squamose.** Bearing scales.

**stria.** Narrow linear furrow or raised line on surface of shell.

**submargin.** One of dorsal edges of disc or body of shell in Pectinacea, adjoining lower border of auricle.

**sulcus.** Radial depression of surface of shell.

**summit.** Most dorsal point of profile of valve when latter is viewed along cardinal axis or from side with cardinal axis horizontal.

**surface ornament.** Regular relief pattern present on surface of many shells.

**taxodont.** With numerous short hinge teeth, some or all transverse to hinge margin.

**teleodont.** With differentiated cardinal and lateral teeth, as in diagenodont forms, but with additional elements giving rise to more complicated hinge; example, *Venus*.

**terminal.** Forming most anterior or posterior point of valve; term applied to beak.

**thickness.** Used by some authors to denote the shell measurement here termed inflation, but also commonly applied to the distance between the inner and outer surfaces of wall of shell.

**thread.** Narrow elevation of surface of shell.

**transposed hinge.** Condition in which certain hinge teeth present in one valve occupy positions of teeth usually found in other.

**transverse.** Direction perpendicular to that of cardinal axis in plane of valve margins.

**trapeziform.** With 4 straight sides, only 2 of which are parallel.

**trapezoidal.** With 4 straight sides, no 2 of which are parallel.

**trigonal.** Three-cornered.

**truncate.** With curvature of outline interrupted by straight cut.

**tumid.** Strongly inflated.

**umbo.** Region of valve surrounding point of maximum curvature of longitudinal dorsal profile and extending to beak when not coinciding with it. (Many authors treat beak and umbo as synonymous, but with most shells two distinct terms are needed.)

**umbonal angle.** In pectinoid shells, angle of divergence of umbonal folds. In other shells, approximate angle of divergence of posterodorsal and anterodorsal parts of longitudinal profile.

**umbonal cavity.** Part of interior of valve that lies within umbo and under hinge plate (where present).

**umbonal depression.** Small depression at tip of umbo in some Arcacea.

**umbonal fold.** In pectinoid shell, ridge originating at umbo and setting off body of shell from auricle.

**umbonal pole.** Point of maximum curvature of longitudinal dorsal profile of valve.

**valve.** One of the calcareous structures (2 in most bivalves) of which shell consists.

**veliconch.** Shell borne by veliger larva; identical with prodissoconch when larva is pelagic.

**ventral.** Pertaining to or located relatively near to region of shell opposite hinge, where valves open most widely.

**ventricose.** Strongly inflated.

**vinculum.** Secondary shelly matter associated with basic dental structures; commonly takes form of bridge between two adjacent teeth, thus causing dentition to appear simpler than it is.

**wing.** More or less elongate, triangular, distally acute or obtuse, terminal part of dorsal region of shell in Pteriacea, Pectinacea, etc.

**xenomorphic** (adj.). Pertaining to xenomorphism.

**xenomorphism.** Special sculpture at the umbonal region of the unattached valve resembling the configuration of the substratum onto which the attached valve is or was originally fixed. Known in the Anomiidae, Gryphaeidae, Ostreidae and other pleurothetic and cemented families. It is on the right valves in oysters and on the left valves in *Anomia* (see STENZEL, KRAUSE & TWINING, 1957, p. 98-99). Erroneously called allomorphism by some authors.

# EVOLUTIONARY HISTORY OF BIVALVIA

The hypothesis that the Bivalvia were derived from a primitive univalve mollusk with a depressed uncoiled shell, perhaps numerous pedal muscles, and a line of pallial muscles close to the margin, has been expounded in Part I of this *Treatise* (p. *I*21-*I*22). Several authors have pointed out that the Monoplacophora, in which a whole series of shell-attached muscles is present, correspond better to the theoretical concept of the ancestral form than any other molluscan group at present known. Attention has, moreover, been called to the fact that the early Bivalvia include the genera *Babinka* and *Myoplusia,* both of which were characterized by multiple accessory muscles which may represent the retention of a primitive condition. The possibility of the derivation of a two-valved form from a group of univalve mollusks has, moreover, recently received unexpected confirmation by the discovery of two-valved opisthobranch gastropods and by observations on their ontogeny, although in this case the actual process of valve division is not in the manner postulated in the hypothesis mentioned.

Other interesting problems are connected with the origin of the class. Did the Bivalvia arise from a more primitive molluscan group as an adaptation to a particular environment and mode of life? Or, approaching the matter from a slightly different theoretical aspect, if they originated as chance mutations, were they successful in establishing themselves because they proved to be well suited to a particular environment and mode of life? Were the earliest bivalves epifaunal like the presumed ancestral form, or infaunal, adopting immediately a burrowing existence in the sea-floor sediment? Is there any evidence that the class arose polyphyletically? It is not proposed here to adopt any particular standpoint on these theoretical matters, but merely to record what is at present known of the earliest appearances of the various groups of Bivalvia in the fossil record.

Unfortunately difficulties arise at the outset owing to uncertainty as to whether some of the earlier forms with two-valved tests were Mollusca or Crustacea. The very earliest fossils which have been regarded by some workers as Bivalvia are two small species from the Lower Cambrian of New York State described by BARRANDE as *Fordilla troyensis* and by WALCOTT as *Modioloides* [originally *Modiolopsis*] *prisca,* both types of their respective genera. *F. troyensis* is about 4.5 mm. long, *M. prisca* only 2 mm. Both came from sequences of slates and shales with interbedded limestones and little at present can be said about their paleoecology. ULRICH & BASSLER, who have redescribed and refigured these remains, are of the opinion that both were Crustacea and not Bivalvia. Neither possessed features definitely identifiable as hinge teeth or as adductor muscle scars and, according to the authors cited, *Fordilla* had a test with a "calcareo-phosphatic structure."

Of equally doubtful affinities are some rather small internal molds, up to about 8 mm. in length, from the Lower Cambrian of eastern Portugal, first described by DELGADO. He considered these to represent nine species of Bivalvia, distributed among six previously known genera, including *Ctenodonta,* and details were given of the exact number of taxodont teeth seen in the specimen supposed to belong to this genus. In a revision of this assemblage by TEIXEIRA five of the species were considered identical and were referred to *Modiolopsis* (although on no certain evidence), while no conclusion was reached as to whether the remainder were Bivalvia or Crustacea. The supposed *Ctenodonta* has been refigured by VOGEL, who has recorded that its "taxodont teeth" were a product of the imagination. It does not, in fact, seem possible to say definitely if these Portuguese specimens are Bivalvia or Crustacea. The formation yielding them was a bluish-grey fine-textured shale containing siliceous concretions.

The problematic Ribeirioida [Tecnophoridae & Ribeiriidae], in which the two halves of the test are joined along the dorsal margin and hinge teeth are absent, first appeared in the late Lower Cambrian. Many authorities have referred this group to the Arthropoda, although not on altogether convincing grounds. Whether or not these forms are correctly placed here, they are morphologically intermediate between the Monoplacophora and undoubted Bivalvia.

The oldest species so far discovered that can be referred with confidence to the Bivalvia is *Lamellodonta simplex* VOGEL, described in 1962 from beds in the Zaragoza province of Spain dated by trilobites and brachiopods as lower Middle Cambrian. It is an oval, equilateral shell up to 18 mm. in height and 14 mm. in length, with well-developed hinge teeth, consisting of lamellae parallel to the adjacent dorsal margin and symmetrically arranged on the two sides of the beak, from below which corresponding pairs diverge at a very obtuse angle; two lamellae with an intervening socket are present on each side of the beak in some specimens, one lamella in others. Neither adductor scars nor the position of the ligament have been observed, but the ligament is thought to have been external. The matrix of the specimens is a very fine-grained quartzite. VOGEL concludes from the equilateral form of the shell that the mollusk crept about on the sea floor or possibly lived on seaweed. As, however, an equilateral shell is not a criterion of a nonburrowing mode of life, it is equally possible that *Lamellodonta* burrowed at least intermittently into the fine sandy substrate. While it would be rash to acclaim this form as the ancestor of all the Bivalvia (for earlier members of the class may yet be found), VOGEL's diagram (Fig. 86) suggesting its its relationship to main groups of the class found in later rocks deserves consideration. The discovery of this genus is of great interest, particularly as it does not support the theory, once widely accepted in consequence of R. T. JACKSON's demonstration of the presence of taxodont-like teeth on most prodissoconchs, that the most primitive bivalve was a form with taxodont dentition belonging to the Nuculacea.

Records of unmistakable Bivalvia from the later stages of the Cambrian (apart from the Tremadocian, included in the system by British but not by other authors) seem nonexistent. We find evidence in two widely separated areas, however, that diversification of the Bivalvia already had begun to take place in the Tremadocian, although (apart from the doubtful forms already mentioned) members of the class do not appear until a later stage of the Ordovician in most regions. Thus THORAL has reported the occurrence of the genus *Babinka,* as well as of a nuculacean bivalve in the Tremadocian of the Montagne Noire area of France. This discovery of *Babinka* is of interest, as in Bohemia, the part of Europe from which it was originally described, it does not appear until the Llanvirnian Stage. In both areas the genus occurs in siliceous nodules. Reference has already been made to the suggestion, based on the multiple muscle scars of this genus, of its possible derivation from the Monoplacophora. It has small but distinct cardinal hinge teeth, and a study of these and of its elongated anterior adductor scar has led McAlester to the conclusion that it was the ancestor of the heterodont superfamily Lucinacea. This author therefore considers that, like *Lucina* at the present day, it burrowed shallowly into sandy sediment, using a slender, wormlike foot to punch a tubular hole upward through this deposit for the passage of the inhalant current. From the Tremadocian of Argentina Harrington has described representatives of the three genera *Ctenodonta, Palaeoneilo,* and *Cosmogoniophorina.* The record of the first two, which belong to the Nuculacea, combined with Thoral's identification of a representative of this superfamily in French beds of the same stage, at least confirms the general view that the group is a very primitive one. On the other hand, an assumption that the Nuculacea arose more or less directly from *Lamellodonta* is not very plausible in view of the considerable modifications in the dentition and form of the shell that would have taken place in such a process. Still less acceptable would be a theory that *Babinka* arose from *Lamellodonta.* The problem of the original diversification of the Bivalvia is thus still unsolved.

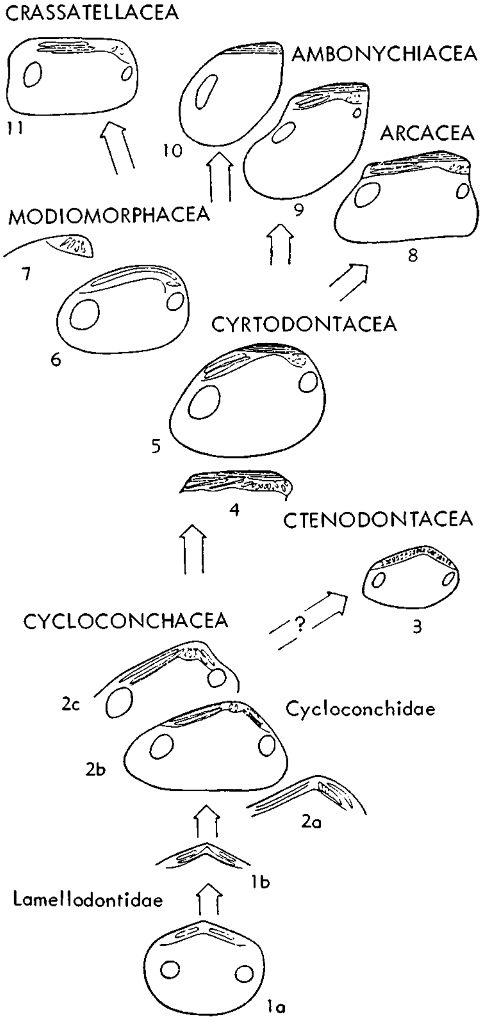


Fig. 86. Reconstruction of the phylogeny of early Paleozoic bivalves suggesting relationship of *Lamellodonta* to main groups (after Vogel, *176*). ——*1. Lamellodonta simplex* Vogel.——*2. Actinodonta* Phillips (*2a, A.* sp.; *2b, A. acuta* Douvillé; *2c, A. cuneata* Phillips).——*3. Ctenodonta planodorsata* Ulrich.——*4. Cyrtodonta gibbosa* Hind. ——*5. Cyrtodonta grandis* Ulrich.——*6. Redonia* Rouault.——*7. Modiolodon* Ulrich.——*8. Parallelodon* Meek & Worthen.——*9. Gosseletia* Barrois.——*10. Myalina* de Koninck.——*11. Cypricardinia* Hall.

*Cosmogoniophorina,* originally described from the Ordovician of Sweden, belongs to an important Paleozoic family, Modiomorphidae, the affinities of which have given rise to some disagreement. The shell in this group is rectangular or oval in shape, elongate, and strongly inequilateral, with the beaks near the anterior end. Hinge teeth are lacking in this particular subgenus, but in other members of the family they are of the actinodont type, consisting of lamellae radiating from the beak, the posterior ones commonly elongated and parallel to the adjacent margin. It is easier to conceive that the Modiomorphidae could have evolved from *Lamellodonta* than the other forms just mentioned, the symmetrically arranged hinge teeth of that genus giving rise to asymmetrical, actinodont dentition as the part of the shell anterior to the beaks became reduced in length; to attempt a functional interpretation of this change in shape would, however, be pure guess-work.

Unlike the later Mytilacea, which some of them resembled in shape, the Modiomorphidae do not appear to have been byssally attached.

It is in the succeeding Arenigian stage of the Ordovician that the Bivalvia, now still further diversified, can be said to have become successfully established. Even now, however, their distribution appears to have been restricted, and it seems that sandy sediments were their most favored environment. The Armorican Sandstone of northern France has yielded the most varied fauna of this stage, while a few further forms have been found in the Montagne Noire area, in southern France. In Wales the Abercastle and Porth Gain beds of St. Davids have yielded a small assemblage described in 1873 by HICKS, who dated the beds erroneously as Tremadocian, while in the USA the St. Peter Sandstone of Minnesota has yielded a few species described by SARDESON. Among these Arenigian bivalves the Nuculoida are represented by *Ctenodonta* and *Nuculites,* the Modiomorphidae by *Modiolopsis* and *Redonia,* and a further actinodont family, Cycloconchidae, by *Actinodonta.* The genus *Lyrodesma,* type of the family Lyrodesmatidae, which made its first appearance in the Armorican Sandstone, seems also to have been related to the actinodonts, although the posterior teeth of its radiating series are not greatly elongated. The Cyrtodontidae, represented in each of the areas mentioned by one or other of the genera *Cyrtodonta, Cypricardites,* and *Vanuxemia,* is of interest as being the earliest known group in which the ligament was placed on a distinct cardinal area. The hinge teeth in the Cyrtodontidae are arranged very similarly to those of the actinodonts, and derivation of the family from that group is a reasonable assumption. Although it is doubtful, in the absence of a distinct byssal gape, if the Cyrtodontidae were byssally attached, epifaunal mollusks, a very plausible tree of descent indicates that they could well have been the ancestors of the predominantly epifaunal bivalves here grouped in a subclass Pteriomorphia. A striking species from the Armorican Sandstone was classified by BARROIS as a *Parallelodon,* a genus of Arcoida otherwise not known until later in the geological record. It certainly has the shape and dentition of a *Parallelodon,* but it is not clear if it has a distinct cardinal area. Unfortunately, the specimen cannot be traced. The Montagne Noire has yielded a winged shell apparently belonging to the Pteriacea, referred by its describer, THORAL, to the genus *Pterinea* with a query.

Among the remaining Arenigian bivalves we may also note *Davidia* and *Sluzka.* These are two of several edentulous Paleozoic bivalves which, for lack of evidence as to their relationship to one another and (except for the long-ranging genus *Solemya,* mentioned again later) to post-Paleozoic taxa, are here grouped together as a subclass Cryptodonta (Palaeoconcha of an alternative nomenclature). Finally, *Coxiconcha* [*Sanguinolites*] *pellicoi* (DE VERNEUIL & BARRANDE) is an elongate form with cardinal teeth and a gaping posterior extremity, interpreted by DOUVILLÉ as an early permanent burrower, a forerunner of such families as the Pholadomyidae and Pleuromyidae, included in this *Treatise* in a subclass to which DALL's name Anomalodesmata is applied. This form does not, however, appear to have been sinupalliate, so that the depth to which it could burrow was probably restricted.

Passing, now, to the Llanvirnian and Llandeilian stages of the European Ordovician succession and their equivalent, the Chazyan stage of the USA, we find the Nuculacea, Modiomorphidae, and Cyrtodontidae still well represented. *Babinka* reappears in the Llanvirnian Stage of Bohemia, its type area, and is not met again. The cryptodont genera *Edmondia* and *Cardiomorpha* make their appearance in these stages, together with representatives of the mytiliform, byssiferous family Ambonychiidae (with little doubt an offshoot from the Cyrtodontidae), and a further early representative of the Pteriacea, described under the genus *Leptodesma.* The earliest known species of *Conocardium,* a very distinctive genus possibly related to the Ribeirioida, occur in Llandeilian beds in southern Scotland and in the Chazyan of the USA. Finally, beds of the same stage and area have yielded a form described as a *Cypricardinia;* if the generic reference is correct, this is the earliest known heterodont, unless *Babinka* is so regarded. *Lyrodesma,* of the Lyrodesmatidae is recorded also from the Lower Ordovician Armorican Sandstone of northern France.

Succeeding stages of the Ordovician, equivalents of the Caradocian and Ashgillian of the British succession, have yielded extensive bivalve faunas in a number of areas, particularly Sweden (*Leptaena* Limestone), Norway, France (Grès de May), southern Scotland, Bohemia, Kazakhstan, the USA (Minnesota, New York, Maryland, Ohio), and Canada. These faunas consist largely of groups encountered in earlier beds (Nuculacea, Cyrtodontidae, Ambonychiidae, Lyrodesmatidae, actinodonts [Modiomorphidae, with Allodesmatidae now added], *Conocardium* and various cryptodonts). Alone among these groups, the Nuculacea have persisted with only relatively slight changes to the present day, and further reference will not be made to them. The Pterineidae now begin to assume importance. Possible Myalinidae make their appearance. The earliest appearance of the Lucinacea (if we except the problematic *Babinka*) is marked by the presence of the genus *Paracyclas* in the Upper Ordovician of Scotland. Among the cryptodonts are some genera *(Rhytimya, Cuneamya, Sphenolium)* that give every appearance of having been permanent (although perhaps not very deep) burrowers and have been thought by some authorities to have been, like *Coxiconcha pellicoi* already mentioned, among ancestors of the Anomalodesmata. Upper Ordovician rocks have yielded the earliest Bivalvia which are thought to have bored into hard coral limestone. The genera in question are *Corallidomus* WHITFIELD and *Semicorallidomus* ISBERG, from Ohio and Sweden respectively, and both have been referred to the Modiomorphidae [Modiolopsidae].

In most areas the Silurian bivalve fauna differs very little in generic composition from that of the Ordovician, but the appearance of *Palaeopecten* WILLIAMS, found both in North America and in Wales, is to be noted. *Protopecten* HIND, from Scotland, also seems to have belonged to the Pectinacea. These forms, the earliest known representatives of this superfamily, differ from the Pteriacea from which they were presumably derived in their almost equilateral outline. *Palaeopecten,* like all Aviculopectinidae, had a distinct cardinal area with grooves corresponding to a duplivincular ligament. Bohemia is remarkable for its varied Silurian bivalve fauna described in a monumental monograph by BARRANDE. This fauna is particularly rich in members of the Cryptodonta, some *(Praecardium, Paracardium, Panenka)* with strong radial costation and much external resemblance to many Cardiidae found in much later formations. It is, however, highly improbable that these forms were ancestral to the Cardiidae, or that *Praelucina,* another cryptodont found with them, had any affinity with the Lucinidae. On the other hand, *Prolucina,* represented by large internal molds from the Silurian of Gotland, Sweden, clearly showing the impression of the characteristic elongated lucinoid anterior adductor scar, must undoubtedly belong to the Lucinacea. *Megalomoidea,* found in the Silurian (Guelph) of North America, marked (if the views here adopted are correct) the initiation of an important line of descent, the pachyodonts, that was to lead eventually to the remarkable sedentary bivalves, the rudists, of the Cretaceous.

During the Devonian Period the Bivalvia became very abundant and diversified. Faunas of this age, including numerous representatives of the class, have been described from every continent, particularly important monographs dealing with material from the USA, Germany, and Belgium. Some groups encountered in earlier rocks (including the Praecardiidae, Edmondiidae, Ambonychiidae, Modiomorphidae, and Conocardiidae) persist. Pectinacea and Myalinidae assume importance for the first time, the first group being represented by such genera as *Aviculopecten, Lyriopecten, Pterinopecten,* and *Posidonia.* The Pteriacea, with *Pterinea, Limoptera, Lepto-*

*desma,* and other genera, are abundant in some formations. *Parallelodon,* a possible member of which appeared, as already seen, in the Ordovician Armorican Sandstone, is represented by a number of typical species in the Devonian. *Carydium,* a new type of actinodont, also occurs. The earliest representatives of the Solemyidae, not separable more than subgenerically from the living genus *Solemya,* make their appearance. Although mytiliform shells referred by early authors to *Mytilus* or *"Modiola"* occur in earlier rocks, it is probable that these belonged to the Modiomorphidae and perhaps in some cases to the Myalinidae. True Mytilidae, belonging to the genus *Modiolus,* are, however, encountered in the Devonian. The Trigoniacea, very doubtful members of which have been reported from the Upper Ordovician and Silurian, are represented in the Devonian by several genera of Myophoriidae. The pachyodonts are represented by *Megalodon, Eomegalodon,* and *Prosocoelus.* Finally, certain genera which, like *Cypricardinia* and the lucinoids *(Paracyclas, Prolucina)* already mentioned as appearing in earlier rocks, and accepted as early heterodonts, are found in the marine Devonian; these are *Montanaria, Crassatellopsis, Cypricardella, Mecynodon,* and possibly others. The Devonian is the oldest fossiliferous system in which nonmarine formations are extensively developed, and it is interesting to note that fresh-water bivalves very similar in external appearance to some modern Unionidae are found in such rocks, both in Great Britain and in North America. They are referred to a genus *Archanodon.*

The marine faunas of the Carboniferous were marked by the dominance of most of the same groups as during the Devonian. New families to appear were the Pinnidae (including forms not separable generically from the modern *Pinna*) and the Limidae (*Palaeolima*). Among the Carboniferous Pectinacea were forms in which the ligament had advanced beyond the duplivincular stage of the Aviculopectinidae to the type found in modern members of the superfamily. These forms are referable to the genus *Pernopecten* (from which *Entolium* of the Mesozoic may not be separable). Among the Pectinacea there also arise what was probably the earliest bivalve genus to be cemented to the substratum, an oyster-like form described by DE KONINCK as *Pachypteria,* a genus united in the present *Treatise* with *Pseudomonotis,* based on a Permian species. This genus, in which fixation was usually by the right but occasionally by the left valve, has been regarded as a possible ancestor of the oysters. Among the Mytilidae we may note the appearance of elongate, cylindrical forms which have hitherto been included in the genus *Lithophaga,* although it has not been established that they bored into limestone, like modern representatives of this genus. The Carboniferous heterodonts include *Astartella,* in which the hinge teeth are very similar to those of modern members of the Astartidae. Finally, Carboniferous cryptodonts with the shell form of permanent burrowers, such as *Chaenomya, Solenomorpha, Wilkingia,* and *Sanguinolites,* approach some of the later Anomalodesmata very closely. *Wilkingia* and *Chaenomya* seem to be the earliest bivalves known to have been sinupalliate.

The Carboniferous system is particularly notable for the nonmarine bivalves which are locally abundant in the strata associated with coal seams and have been intensively studied in recent years because of their use in correlation. Among these forms, the genus *Naiadites* has close affinities with the marine *Myalina.* The origin of such genera as *Carbonicola, Anthracosia,* and *Anthraconaia* is puzzling, as it is doubtful if these relatively small bivalves were descendants of the large *Archanodon* of the Devonian.

In most areas the marine bivalve faunas of the Permian do not differ greatly in generic composition from those of the Carboniferous. New families to appear, however, were the Bakevelliidae (Pteriacea with a multivincular ligament) and the heterodont groups Myoconchidae, Permophoridae, and Crassatellidae. The Permian genera *Undulomya, Palaeocosmomya,* and *Praeundulomya* are here accepted as members of the Pholadomyidae, although it is not known if they were sinupalliate. The Australian Permian is noteworthy for the occurrence of *Megadesmus, Cleobis, Myonia,* and other genera united in the family Megadesmatidae. Many specimens attain a considerable size. These forms have been regarded as burrowers and early members of the Myacea, but they lack a posterior gape and pallial sinus and their systematic position may need reconsideration. Restricted to the Permian is the very characteristic genus *Eurydesma,* first described from Australia and since recorded from Pakistan, Kashmir, South Africa, and South America. Notwithstanding its globose shape, the general features of the shell indicate that this genus should be referred to the order Pterioida, but the relationship of the Eurydesmatidae, of which it is the type genus, to other families of this order has still to be established. The *Inoceramus*-like genus *Atomodesma,* found in the Permian of Timor and Pakistan, seems referable to the same family.

The successors of the small fresh-water bivalves of the Carboniferous, included with them in the family Anthracosiidae, are found in Permian nonmarine deposits in Russia, Africa, and elsewhere. Commonly occurring genera are *Palaeanodonta* and *Palaeomutela,* the latter characterized by its pseudotaxodont dentition. Reference must also be made to the very peculiar endemic fauna of the (probably) Permian Corumbatai Formation of Brazil and Uruguay, which includes such genera as *Plesiocyprinella, Terraia, Ferrazia, Pinzonella,* and *Cowperesia,* none obviously related to forms found in other areas. This assemblage is neither a typical fresh-water nor a marine one, but was possibly derived from a marine fauna which had become isolated in a large land-locked basin.

A few groups that had formed important constituents of the upper Paleozoic bivalve faunas lingered on and became extinct during the Triassic Period, but some had already died out. Of the cryptodonts, *Edmondia* and *Sanguinolites* are unrepresented in the Triassic; only one species of *Wilkingia* [*Allorisma*] has been described, and merely two or three of *Cardiomorpha.* The last known *Conocardium,* the only Triassic species of the genus recorded, occurs in the Rhaetic of Burma. *Myalina,* so common in the Carboniferous and Permian, is represented in the Triassic by only a few species. The Aviculopectinidae continued into and died out during this period, but, apart from *Aviculopecten* itself, the upper Paleozoic genera were replaced by others, such as *Eumorphotis, Claraia,* and *Leptochondria.* Certain pectinacean groups attained great importance, forming a very characteristic element of some of the bivalve faunas of the period. These were the Monotidae and the Halobiidae, the latter represented mainly by the genera *Halobia* and *Daonella.* Their thin, flattened, radially ribbed shells occur in enormous numbers in some deposits. Costate Pectinidae (*Chlamys* and other genera), the presence of which in earlier rocks is doubtful, became well established during the Triassic. Of the Pteriacea, the peculiar family Cassianellidae is virtually confined to this system. The genus *Bakevellia* persisted and was joined by other genera of the Bakevelliidae *(Hoernesia, Gervillia, Gervillella),* while the earliest representatives of the derivative family Isognomonidae (including *Isognomon* itself) appeared. The Triassic was also marked by the appearance of the families Plicatulidae and Ostreidae. Among the earliest representatives of the latter are small, smooth, gryphaeate forms found in the Upper Triassic of Sicily and the Bear Islands, while the plicated genus *Lopha* includes the species *L. montiscaprilis* (KLIPSTEIN), of the Carnian of the Alps. The relationship of these early Ostreidae to the plicated Triassic oyster-like forms included in the genus *Enantiostreon,* which were attached by the right valve and are here referred to the family Terquemiidae, has yet to be determined. Of the Limidae, *Mysidioptera,* in which anterior auricles are virtually lacking, was the most characteristic Triassic genus.

During the Triassic the Myophoriidae reached the acme of their development. In the preceding periods this family had been represented mainly by smooth-shelled genera such as *Schizodus,* but now many of its numerous representatives were quite elaborately ornamented. The first Trigoniidae, descendants of the Myophoriidae, are found in the Upper Triassic. This period was also marked by the reappearance of pachyodonts. *Megalodon,* which presumably had retreated during the Carboniferous and Permian to some region not yet located, flourished greatly in the calcareous sediments laid down towards the close of the Triassic and, like the related genus *Conchodus,* occurs in great number in the Rhaetic limestones of the Alps. Heterodonts were not very much in evidence during this period, but the appearance of the Carditidae (genus *Palaeocardita*) is to be particularly noted as it is not until the Cretaceous that comparable ribbed members of the family are to be found again. The genera *Protocardia* and *Eotrapezium,* the oldest known genera of the Cardiidae and Arcticidae respectively, appear at the very top of the Triassic, and *Corbula* a little lower. The Triassic Period also saw the incoming of some common Mesozoic genera of the Pholadomyidae (*Homomya, Pachymya (Arcomya),* and, more rarely, *Pholadomya*), and also of *Pleuromya.* Finally, fresh-water deposits of the period have yielded true Unionidae, very similar in appearance to modern representatives of the family.

The marine bivalve faunas of the Jurassic have quite a different aspect from those of the Triassic, owing largely to the abundance of Trigoniidae, Ostreidae, Limidae, and Pholadomyidae. Among the Arcoida the genus *Parallelodon* persists from the Paleozoic, and *Cucullaea* and *Grammatodon* from the Triassic. *Indogrammatodon,* a well-characterized subgenus of *Grammatodon,* is abundant in the Middle and Upper Jurassic in the area surrounding the Indian Ocean. *Eonavicula,* the obvious ancestor of the modern *Arca,* and *Barbatia* make their appearance. Mytilidae are usually abundant, and include radially ribbed forms *(Arcomytilus, Musculus),* although *Modiolus* is the commonest representative of the family. *Gervillella* assumes importance among the Bakevelliidae and *Isognomon* becomes more abundant. Among the Pectinacea, *Oxytoma,* which had appeared near the top of the Triassic, occurs commonly, especially in the Lias, while *Meleagrinella* is frequent at some horizons. The genus *Buchia,* particularly characteristic of boreal regions, makes its appearance in the Upper Jurassic. The Pectinacea include many species of modern aspect, some inseparable from the genus *Chlamys,* but a group of highly inequivalve forms, *Weyla,* occurs in the Lias of South America, North and East Africa, and elsewhere. The peculiar genus *Eopecten,* cemented to the substratum by the tip of its flat right valve, is reminiscent of the upper Paleozoic *Pseudomonotis* but has the hinge characters of a true pectinid. Most of the Jurassic Limidae differ very little from modern representatives of the family, but the genus *Ctenostreon,* with its thick shell and broad spinose ribs, was evidently adapted for life recumbent on the sea floor. Among the oysters, gryphaeate forms are abundant at many horizons of the Jurassic and their relationship to the flatter smooth oysters *(Liostrea)* has given rise to much speculation. Rather less frequent and virtually confined to post-Liassic beds are representatives of *Exogyra.* Ribbed oysters *(Lopha)* are common in the Middle and Upper Jurassic. The genus *Eligmus,* a ribbed, oyster-like form that was the earliest representative of the Malleidae, characterizes the Bathonian and Callovian of some areas.

*Hippopodium,* possibly the last survivor of the Modiomorphacea, is remarkable, not only for its thick, heavy shell, but also for its discontinuous range and localized distribution. Found in the Hettangian to Pliensbachian stages of the Lias in northwestern Europe, it is known otherwise only from the uppermost Jurassic of East Africa. *Megalodon* of the Trias was succeeded in the Jurassic by other pachyodont genera of the same family, notably *Pachyrisma* and *Pterocardia.* In the Oxfordian the genus *Diceras,* which is thought to have been derived from the Megalodontidae, acquired the habit of fixation by the tip of one valve and initiated lines of descent that led to the various rudistid groups of the Cretaceous. Throughout the Jurassic the commonest heterodont family was the Astartidae, represented by *Astarte* and other genera, among which *Opis* was remarkable for its strongly prosogyrate umbones. Of the Cardiniidae, a family that had appeared during the Triassic, the genus *Cardinia* was very abundant throughout the Lias and then died out. The Arcticidae increased greatly in importance during the Jurassic, newly appearing genera including *Isocyprina, Anisocardia, Pronoella,* and *Pseudotrapezium.* The Lucinidae, Cardiidae, and Corbulidae maintained their positions and the Fimbriidae made their appearance. Sinupalliate, presumably relatively deep-burrowing forms included *Pholadomya, Homomya, Goniomya, Pleuromya, Thracia,* and *Gresslya.* In addition to various Unionidae, Jurassic fresh-water deposits have yielded representatives of the heterodont genus *Neomiodon.* Those of central Asia contain a variety of rather small forms which have been referred to two families Ferganoconchidae and Pseudocardiniidae.

Many genera pass up from the Jurassic into the Cretaceous. The range of *Buchia* terminated in the Lower Cretaceous, while genera that did not continue into the Tertiary included *Oxytoma, Gervillia,* and *Opis.* The family Inoceramidae, which had existed but remained relatively unimportant during the Jurassic, burst forth into a great variety of species during the Cretaceous, some remarkable for their very large size and thick shells. Among the Pectinidae the genus *Neithea,* with one valve flat or concave and the other strongly convex, and with ornament of radial ribs usually of different orders of prominence, was particularly characteristic of the Cretaceous. Ostreidae occur in profusion and include many exogyrate as well as gryphaeate forms. The Trigoniidae are locally abundant and include a number of genera, such as *Pterotrigonia,* which are virtually although not in all cases strictly confined to the system. Among the heterodonts, the Arcticidae were still abundant and many attained a greater size than those of the Jurassic. The Veneridae gained steadily in importance. Radially ribbed genera of Carditidae, missing during the Jurassic, reappeared. Among the burrowers *Panopea* replaced the usually smaller *Pleuromya.*

The most notable of all Cretaceous bivalves were the rudists, particularly abundant in the Tethyan province although a few found their way to more northerly latitudes. The majority were cemented to the substratum and many lived gregariously, the lower valve acquiring a conical shape like some corals. Some rudists attained a very large size although in many cases they were not proportionately heavy owing to the cellular structure of their shells. None of the rudists survived beyond the Maastrichtian Stage. The Chamidae, the earliest members of which appeared in the Upper Cretaceous, resembled the rudists in their attachment by the tip of one valve and in the number of hinge teeth in the adult shell. It is, however, probable that they were of quite independent origin and derived from a heterodont family.

With the incoming of the Cenozoic Era bivalve faunas assumed a modern aspect, and many included a great number of species of all sizes. As Tertiary time advanced, marine geographical provinces become more strongly differentiated than during any other period. It is possible here to call attention to only a few points of particular interest relating to Cenozoic bivalves. During the Eocene a group of gryphaeate and exogyrate oysters, quite similar to those of the Cretaceous, made their appearance. Their geographical distribution, however, was very restricted, being virtually confined to central Asia and northern Africa. Pectinidae are abundant in many Tertiary formations and some genera, for example *Amussiopecten* of the Miocene, are of value as stratigraphical indices. The modern groups of highly inequivalve Pectinidae (genus *Pecten*) first appeared in the Oligocene, flourished in the Miocene, and still survives. During the Tertiary the once so abundant family Trigoniidae became restricted to Australasian seas and at the present day only one genus, living off eastern Australia, exists. The Cardiacea showed extraordinary potentialities for evolutionary diversification under the fresh-water and brackish conditions that prevailed during late Miocene and Pliocene times in southeastern Europe and adjacent parts of Asia. The great number of cardiid genera that existed in the area at that time constitute the family Lymnocardiidae. *Congeria,* a characteristic genus found in many of the same deposits, is referred to the family Dreissenidae, typified by the genus *Dreissena,* which, although so much like the marine *Mytilus* in external appearance, is believed to have been derived from some heterodont group. The marine genus *Tridacna,* commonly associated with coral formations, is notable, not only because it includes the largest bivalves still living, but also because of the extraordinary rotation that the soft parts have undergone in relation to the shell. It is thought to have been derived in Tertiary times from some genus of Cardiidae. Modern representatives of the freshwater superfamily Unionacea include, in Africa, India, and South America, genera of the remarkable family Etheriidae, in which one valve becomes cemented to other objects and the shell acquires an irregular, oyster-like appearance.

## SELECTION OF NAMES APPLIED TO HIGHER TAXONOMIC CATEGORIES OF BIVALVIA

[Names are listed in latinized form although some (as indicated) were originally introduced in vernacular; authors whose names are not included are GRAY *(56, 57),* LATREILLE *(88, 89),* DE BLAINVILLE *(12),* MENKE *(104),* M'COY *(148),* BRONN *(17),* FISCHER *(48),* HERTWIG *(68),* VON VEST *(175),* and LAMEERE *(87).* Most names based on those of genera are omitted.]

**Actinodonta** DOUVILLÉ, 1913 (*42,* p. 438, as "actinodontidés"). Introduced for group of lower Paleozoic bivalves of undefined taxonomic rank characterized by more or less longitundinally extended, divergent teeth on both sides of beaks. Accepted as suborder of order Taxodonta and scope extended by DECHASEAUX (*38,* p. 266).

**Adapedonta** COSSMANN & PEYROT, 1909 (*27,* p. 92). Proposed for 1 of 7 suborders of order Eulamellibranchia. Contents, Gastrochaenidae, Myacea, "Panopaeacea," Solenacea.

**Ambonodonta** GROBBEN, 1892 (*60,* p. 42). Proposed for 1 of 3 subclasses into which bivalves are divided. Contains (as orders) Eutaxodonta (=Arcidae), Heterodonta, Schizodonta, Anisomyaria.

**Ameodontida** STENZEL, KRAUSE & TWINING, 1957 (*156,* p. 43). Proposed for 1 of 8 orders into which bivalves are divided. Contents, Nuculacea, Nuculanacea.

**Anisomyaria** NEUMAYR, 1883 (*111,* p. 393, 412, as Anisomyarier). Proposed for 1 of 5 orders into which bivalves are divided; unites Monomyaria and Heteromyaria. Latinized by STEINMANN (1888).

**Anomalodesmacea** DALL, 1889 (*32,* p. 452, 460). Proposed for 1 of 3 orders into which bivalves are divided, in which "archaic anodontism still persists as the characteristic of chief importance." Original contents, Solemyacea, "Anatinacea," Myacea, Clavagellacea, Pholadacea. Name changed to "Anomalodesmata" by some authors.

**Asiphonida** FLEMING, 1828 (*50,* p. 381). One of 2 major subdivisions of the bivalves, characterized by complete openness of mantle margins.

**Astartedonta** KOROBKOV, 1954 (*85,* p. 56, 134). Proposed as 1 of 3 suborders of order Heterodonta. Contents, Astartacea, Crassatellacea.

**Asthenodonta** DALL, 1895 (*34,* p. 557). Proposed for a group of order Teleodesmacea with hinge "usually degenerate or obsolete, owing to modifications due to the burrowing habit." Contents, Myacea, Adesmacea [=Pholadacea].

**Autolamellibranchiata** GROBBEN, 1894 (*61,* p. 73). Proposed for 1 of 2 orders into which bivalves are divided and consisting of all members of class except Protobranchia.

**Colloconchida** COX, 1960 (*29,* p. 85). Proposed for 1 of 5 orders of subclass Pteriomorphia and consisting only of the Ostreacea.

**Cryptodonta** NEUMAYR, 1883 (*111,* p. 393, as "Cryptodonten"). Order of thin-shelled, toothless Paleozoic bivalves, many of which had been described by BARRANDE from Bohemia. Name latinized by FISCHER (1886). Same as "Palaeoconchae."

**Ctenodonta** DECHASEAUX, 1952 (*38,* p. 262); attributed by this author to DOUVILLÉ (1912), who, however, had merely cited the generic name *Ctenodonta* SALTER. Adopted for suborder of order Taxodonta to include Nuculacea and the cryptodonts.

**Cyclodonta** DALL, 1895 (*33,* p. 548). Proposed for group with "teeth arched, springing from below hinge margin, with hinge plate obscure or absent." Contents, Cardiacea, Tridacnacea, Isocardiacea.

**Cyrenina** STENZEL, KRAUSE & TWINING, 1957 (*156,* p. 133). Proposed for 1 of 2 suborders of order Heterodontida. Equivalent to "cyrenoid type" of BERNARD.

**Cyrenodonta** KOROBKOV, 1954 (*85,* p. 56, 141). Proposed for 1 of 3 suborders of order Heterodonta. Equivalent to "cyrenoid type" of BERNARD.

**Desmodonta** NEUMAYR, 1883 (*111*, p. 388, 411, as "Desmodonten"). Proposed for order in which 2 equal muscle scars and pallial sinus are present and in which hinge teeth are lacking or irregular and intimately connected with chondrophore. Contents, Pholadomyidae, Corbulidae, "Anatinidae," Mactridae, "Paphidae" [Mesodesmatidae], "Glycimeridae," ?Solenidae. Name latinized by FISCHER (1886).

**Dimyaria** LAMARCK, 1812 (*86*, p. 105, as "acéphalés dimyaires"). Proposed for 1 of 2 major taxa of bivalves; characterized by 2 adductor muscles. Name latinized by HERRMANNSEN (1846).

**Diogenodonta** DALL, 1895 (*34*, p. 538). Proposed for group of order Teleodesmacea defined as "laterals usually 1 or 2, and cardinals 3 or less." Contents, Cypricardiacea, Astartacea, Cyrenacea, Carditacea, Chamacea, Rudistae, Lucinacea, Leptonacea.

**Dysodonta** NEUMAYR, 1883 (*111*, p. 393, 412, as "Dysodonten"). Proposed for order of bivalves in which hinge teeth are wanting or irregular and 1 adductor only or 2 very unequal adductors are present; as originally proposed, identical with "Anisomyaria" of same author. Name latinized by FISCHER (1886).

**Eleutherorhabda** RIDEWOOD, 1903 (*143*, p. 185). Proposed for 1 of 3 orders of Bivalvia; characterized by ciliated discs forming only means of adherence of adjacent gill filaments. Contents, Dimyidae, Anomiidae, Arcidae, Trigoniidae, Mytilidae, "Melinidae," Spondylidae, Pectinidae, "Aviculidae."

**Eudesmodontida** COX, 1960 (29, p. 85). Proposed for 1 of 8 orders of subclass Heteroconchia. Contents, Allorismacea, Laternulacea, Clavagellacea, Pholadacea.

**Eulamellibranchia** PELSENEER, 1889 (*129*, p. 52, as "eulamellibranchiés"). Proposed for 1 of 5 subclasses of bivalves distinguished on basis of gill characters; in this group branchial lamellae are intimately connected by organic tissue. Contents, "Submytilacea," "Conchacea," Myacea, Pholadacea, "Anatinacea." Name latinized by COOKE (1895).

**Eutaxodonta** GROBBEN, 1892 (*60*, p. 42). Proposed for 1 of 4 orders of subclass Ambonodonta; hinge taxodont. Contents, Arcidae.

**Filibranchia** PELSENEER, 1889 (*129*, p. 52, as "filibranchiés"). Proposed for 1 of 5 subclasses of bivalves distinguished on basis of gill characters; in this group the 2 branches of same filament have no cross connections. Contents, Arcidae, Trigoniidae. Name latinized by COOKE (1895).

**Foliobranchia** MENEGAUX, 1889 (*103*, p. 142, as "foliobranches"). Proposed for 1 of 4 major taxa into which bivalves are divided on basis of gill characters; in this group (same as "protobranchiés" of PELSENEER) each demibranch consists of row of simple flattened leaflets. Contents, Nuculacea, Solemyacea. Name latinized by PERRIER (1897).

**Gastrodeuteia** PURCHON, 1959 (*138*, p. 225). One of 5 stomach types in Bivalvia; equated with Septibranchia, 1 of 3 orders into which class is divided.

**Gastropempta** PURCHON, 1959 (*138*, p. 228). One of 5 stomach types in Bivalvia, regarded as 1 of 3 suborders of 3rd order into which class is divided. Consists of many Eulamellibranchia.

**Gastroproteia** PURCHON, 1959 (*138*, p. 225). One of 5 stomach types in Bivalvia; equated with Protobranchia, 1 of 3 orders into which class is divided.

**Gastrotetartika** PURCHON, 1959 (*138*, p. 226). One of 5 stomach types in Bivalvia, regarded as 1 of 3 suborders of 3rd order into which class is divided. Consists of some Filibranchia and many Eulamellibranchia.

**Gastrotriteia** PURCHON, 1959 (*138*, p. 226). One of 5 stomach types in Bivalvia, regarded as 1 of 3 suborders of 3rd order into which class is divided. Consists of most of Filibranchia.

**Hemibranchia** PERRIER, 1897 (*133*, p. 2121). Proposed for 1 of 6 orders of bivalves. Contents, Septibranchia, Anatinacea, Tellinacea.

**Hemidapedonta** COSSMANN & PEYROT, 1909 (*27*, p. 92). Proposed for 1 of 7 suborders of order Eulamellibranchia. Contents, Tellinacea, Psammobiidae, Donacidae.

**Heterodonta** NEUMAYR, 1883 (*111*, p. 388, 412, as "Heterodonten"). Proposed for order of bivalves in which hinge teeth are clearly differentiated into cardinals and laterals. Name latinized by FISCHER (1886).

**Heteromyaria** PHILIPPI, 1853 (*134*, p. 361). One of 3 orders into which bivalves are divided, characterized by 2 very unequal adductor muscles.

**Homomyaria** ZITTEL, 1881 (*197*, p. 17). One of 3 subdivisions of order Asiphonida; hence definable as siphonless bivalves with 2 equal adductor muscles.

**Integripalliata** D'ORBIGNY, 1843 (*120*, p. 14, as "intégropaléales"). One of 2 suborders into which order "orthoconques" is divided. Name latinized as "Integropallialia" by WOODWARD (1854) and as "Integripalliata" by ZITTEL (1881).

**Isodonta** DALL, 1895 (*34*, p. 524). Proposed for group in order Prionodesmacea to include Pectinacea and Anomiacea. Name based on adjective "isodonte" introduced by FISCHER (1886, p. 936).

**Isofilibranchia** IREDALE, 1939 (*74*, p. 230, 409). One of 7 orders into which subclass Prionodesmacea is divided. Contents, Mytilidae.

**Lipodonta** IREDALE, 1939 (74, p. 229). One of 7 orders into which subclass Prionodesmacea is divided (given as alternative name for Palaeobranchia). Contents, Solemyidae.

**Lucinina** STENZEL, KRAUSE & TWINING, 1957 (*156*, p. 101). Proposed for 1 of 2 suborders of order Heterodontida. Equivalent to "lucinoid type" of BERNARD.

**Lucinodonta** Korobkov, 1954 (*85,* p. 56, 81). Proposed for 1 of 3 suborders of order Heterodonta. This and the Astartedonta correspond to the "lucinoid type" of Bernard.

**Macrociliobranchia** Atkins, 1938 (*5,* p. 425). One of 2 major groups into which bivalves are divided on basis of cilia of laterofrontal tracts of gill filaments. Contents, Protobranchia, Filibranchia (emend.), Eulamellibranchia, Septibranchia.

**Microciliobranchia** Atkins, 1938 (*5,* p. 426). One of 2 major groups into which bivalves are divided on basis of cilia of laterofrontal tracts of gill filaments. Consists of Pseudolamellibranchia as emended to include certain groups formerly classified as Filibranchia.

**Monomyaria** Lamarck, 1812 (*86,* p. 104, as "acéphalés monomyaires"). Proposed for 1 of 2 major taxa of bivalves, characterized by single adductor muscle. Name latinized by Herrmannsen (1847).

**Naiadacea** White, 1942 (*182,* p. 59). Cited as suborder, consisting of Unionacea. The earliest work traced in which this very old name is applied to a taxon ranking higher than those of family group.

**Neotaxodonta** Korobkov, 1954 (*85,* p. 56, 170). Proposed as 1 of 6 orders into which Bivalvia are divided. Contents, Arcacea.

**Oligodonta** March, 1912 (*101,* p. 113). Proposed for 1 of 2 divisions of order Heterodonta and consisting of forms with Bernard's "lucinoid type" of dentition.

**Orthoconchae** d'Orbigny, 1843 (*120,* p. 14, as "orthoconques"). Proposed for 1 of 2 orders into which bivalves are divided, characterized by symmetry of shell and soft parts and by vertical position of plane of valve margins during life. Name latinized by Geinitz (1845).

**Pachyodonta** Steinmann, 1903 (*152,* p. 242). Proposed for a division of the Heterodonta consisting of *Megalodon, Diceras,* and the rudists.

**Palaeobranchia** Iredale, 1939 (*74,* p. 232). One of 7 orders into which subclass Prionodesmacea is divided and consisting of Solemyidae. *See* also Lipodonta.

**Palaeoconchae** Neumayr, 1883 (*111,* p. 392). Proposed for order of thin-shelled, toothless bivalves, many of which had been described by Barrande from the Paleozoic of Bohemia. *See* also Cryptodonta.

**Palaeoheterodonta** Newell, 1965 (*116,* p. 16). Proposed for 1 of 6 subclasses into which Bivalvia are divided. Contents, Modiomorphacea, Unionacea, Trigoniacea.

**Palaeolamellibranchia** Iredale, 1939 (*74,* p. 229, 305). Proposed for 1 of 7 orders into which subclass Prionodesmacea is divided and consisting of Trigoniidae. Identical with Schizodonta.

**Palaeotaxodonta** Korobkov, 1954 (*85,* p. 55, 72). Proposed for 1 of 6 orders of Bivalvia. Contents, Nuculidae, Nuculanidae, Malletiidae.

**Pantodonta** Dall, 1895 (*34,* p. 537). Proposed for a group belonging to order Teleodesmacea defined as "laterals exceeding 2 in any one group." Contents, Allodesmatidae.

**Parafilibranchia** Iredale, 1939 (*74,* p. 230, 403). Proposed for 1 of 7 orders into which subclass Prionodesmacea is divided. Contents, Anomiidae, Placunidae.

**Pleuroconchae** d'Orbigny, 1843 (*120,* p. 15, as "pleuroconches"). Proposed for 1 of 2 orders of bivalves, characterized by asymmetry of shell and soft parts; normal position resting on one valve with plane of valve margins horizontal. Latinized by Geinitz (1846).

**Pleurodonta** March, 1912 (*101,* p. 112). Proposed for 1 of 2 orders of bivalves; main characteristic stated to be presence of embryonic teeth as crenulations on prodissoconch. Unites Dysodonta and Taxodonta as suborders.

**Pliodonta** March, 1912 (*101,* p. 113). Proposed for 1 of 2 divisions of order Heterodonta and consisting of forms with Bernard's "cyrenoid type" of dentition.

**Praeheterodonta** Douvillé, 1912 (*41,* p. 1680, as "préhéterodontes"). Proposed for a group of undefined taxonomic status, consisting of myophoriids, trigoniids and "préastartidés" (*Prosocoelus, Desertella, Megalodon, Palaeocardita,* etc.). Accepted as order and name latinized by Davies (1935).

**Prionodesmacea** Dall, 1889 (*32,* p. 453, 460). Proposed for 1 of 3 orders of bivalves; chief characteristic stated to be "transverse plication of hinge." Contents, Nuculacea, Arcacea, Naiadacea, Trigoniacea, Mytilacea, Pectinacea, Anomiacea, Ostreacea.

**Prionodonta** MacNeil, 1937 (*98,* p. 457). Proposed as suborder of order Filibranchia, to include Cyrtodontacea, Parallelodontacea, Glycymeracea, and Arcacea. Dall (*32, 34*) had introduced term "prionodont" in same sense as "taxodont" but had not given it Latin form or systematic status.

**Protobranchia** Pelseneer, 1889 (*129,* p. 52, as "protobranchiés"). Proposed for 1 of 5 subclasses into which bivalves are divided, to include forms with primitive gills. Name latinized by Grobben (1892).

**Pseudoctenodonta** Dechaseaux, 1952 (*38,* p. 267). Proposed for 1 of 3 suborders of order Taxodonta. Contents, Arcidae, Parallelodontidae.

**Pseudolamellibranchia** Pelseneer, 1889 (*129,* p. 52, as "pseudolamellibranchiés"). Proposed for 1 of 5 subclasses into which bivalves are divided, to include forms with filamentous gills in which connections exist between adjacent filaments and two branches of same filament. Name latinized by Cooke (1895).

**Pteriomorphia** Beurlen, 1944 (*10,* p. 144). Proposed for an order of bivalves to include the Pteriacea, Pectinacea, Ostreacea, Anomiacea, Mytilacea, and Arcacea.

**Pteroconchida** Cox, 1960 (29, p. 853). Proposed for 1 of 5 orders of subclass Pteriomorphia. Contents, Pteriacea, Pinnacea, Pectinacea, Limacea, Anomiacea.

**Rostroconchida** Cox, 1960 (*29*, p. 85). Proposed for 1 of 5 orders of subclass Pteriomorpha. Contents, Conocardiacea.

**Rudista** DE BLAINVILLE, 1825 (*12*, p. 516). Proposed as 1 of 4 orders of class Acephalophora. (LAMARCK had previously treated "les rudistes" as a family.)

**Schizodonta** STEINMANN, 1888 (*153*, p. 238, 250). Proposed as 1 of 6 orders of bivalves, to include only the Trigoniidae.

**Septibranchia** PELSENEER, 1888 (*128*, p. 1031). Proposed for a "sub-group" of bivalves in which gills are transformed into muscular partition dividing pallial cavity into 2 chambers.

**Sinupalliata** D'ORBIGNY, 1843 (*120*, p. 14, as "sinupaléales"). Proposed for 1 of 2 suborders of order "orthoconques." Name latinized as "Sinupallialia" by WOODWARD (1854) and as "Sinupalliata" by ZITTEL (1881).

**Siphonida** FLEMING, 1828 (*50*, p. 408). One of 2 major subdivisions of the bivalves, characterized by fusion of mantle margins in 1 or more places.

**Subfilibranchiata** COSSMANN & PEYROT, 1909 (*27*, p. 92). Proposed for suborder of order Anisomyaria. Contents, Mytilacea, Anomiacea.

**Synaptorhabda** RIDEWOOD, 1903 (*143*, p. 186). Proposed for 1 of 3 orders into which bivalves are divided; characterized by cellular tissue forming junctions between gill lamellae and between gill filaments.

**Taxodonta** NEUMAYR, 1883 (*111*, p. 388, 412, as "Taxodonten"). Proposed for 1 of 5 orders into which bivalves are divided; characterized by presence of numerous hinge teeth, undifferentiated into cardinals and laterals, arranged in row. Name latinized by FISCHER (1886).

**Teleodesmacea** DALL, 1889 (*32*, p. 453, 460). Proposed for 1 of 3 orders into which bivalves are divided; in this group the "various types of hinge have been harmoniously combined." Contents, Tellinacea, Solenacea, Mactracea, Carditacea, Cardiacea, Chamacea, Tridacnacea, Leptonacea?, Lucinacea, Isocardiacea?, Veneracea, Rudista?.

**Teleodonta** DALL, 1895 (*34*, p. 551). Proposed for group belonging to order Teleodesmacea characterized by "most perfected type of modern teeth." Contents, Veneracea, Tellinacea, Solenacea, Mactracea.

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# FORM, FUNCTION, AND EVOLUTION

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