

PART H

BRACHIOPODA

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INTRODUCTION

By ALWYN WILLIAMS

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Brachiopods are solitary marine animals commonly anchored to the substratum by a fleshy stalk or pedicle. The soft parts are protected by a pair of valves of variable organic and mineral composition, that cover the ventral and dorsal surfaces and project forward to enclose a cavity in which is suspended a filamentar feeding organ or lopho-

phore. The body is regionated but the coelom indistinctly so and there is no real evidence of cephalization, so that only a small fold above the mouth can doubtfully be identified as the protosome, and the principal nerve center is located below the esophagus. The digestive tract is normally recurved and in articulate brachiopods it

terminates blindly; metanephridia and an open circulatory system are present.

More than 1,600 brachiopod genera have been described and, judging from current research, the number is likely to increase substantially during the next decade or so. This high taxonomic activity is mainly a measure of the long and rich history of a group of animals that is now in decline. About 70 genera are found in the seas today where they constitute a negligible part of Recent marine faunas compared with the dominance and diversity of their ancestors during, for example, Caradocian time when three times as many genera are known to have existed. Nonetheless, they are still as widely distributed as they have ever been, so that living and fossil species are available in every continent.

Such a profusion of brachiopod species in time and space inevitably led to an early appreciation of their distinctive morphology. MUIR-WOOD (19) has recorded that their fossil remains attracted attention even in the Middle Ages and that from the late 16th century onward, they were regularly figured by naturalists, like GESNER, FABIO COLONNA, PLOT, etc., under a variety of names, including the pre-Linnean designation of "Terebratula" by LLHYD. The term "lamp-shell" which alludes to a likeness between the lateral profile of the terebratulid shell and the outline of a Grecian lamp, although frequently cited today as an established nontechnical name for the phylum, does not seem to have been used until the latter part of the 18th century (19).

Despite this familiarity with brachiopod shells, the practice of indiscriminately grouping all bivalves together prevailed until the close of the 18th century. LINNÉ, for example, used the generic name "*Anomia*" for Recent and fossil species of brachiopods and pelecypods, and the first adequate illustrations of internal characteristics of Recent species were not published by PALLAS (21) until 1766, only a decade earlier than the founding by MÜLLER of the first valid brachiopod genus, *Terebratula*. Indeed, even when CUVIER (4), guided by his anatomical studies of *Lingula anatina*, proposed the familial group of "Brachiopodes" (formalized by DUMÉRIL, 5) for certain "acephalous Mollusca," he did so in the

belief that the uncoiled lophophore performed the same function as the molluscan foot, a fallacy that is unfortunately perpetuated in the collective name adopted by him for the group (*βραχιών*-arm, and *πούς*-foot).

During the 19th century, many aspects of brachiopod organization and history were rewardingly explored. OWEN, HUXLEY, HANCOCK, and BLOCHMANN carried out notable researches on the anatomy of brachiopods; LACAZE-DUTHIERS, KOVALEVSKIY, MORSE, MÜLLER, and SHIPLEY on their embryology, and DAVIDSON and HALL on their fossil record. Consequently by the time BEECHER (1) came to synthesize a classification for the phylum (1891), not only had many of the fundamental differences between the inarticulate and articulate brachiopods been discovered but many opinions had also been expressed on the status of the Brachiopoda within the animal kingdom.

It was inevitable that bivalved brachiopods should first be classified as mollusks. Such a procedure was adopted by CUVIER, LAMARCK, MENKE, and others early in the last century and although doubts about its merits were soon forthcoming, it persisted for many years even as an expression of affinity (8). Meanwhile, comparative studies carried out by HANCOCK (10) on the newly understood bryozoans, led him to believe that they were closely related to both tunicates and brachiopods, and prompted HUXLEY (12) to emend MILNE-EDWARDS' molluscan "subphylum" Molluscoidea to include not only bryozoans and tunicates but also brachiopods. In the course of reiterating the relationship implied in the recognition of the "Molluscoidea" ("Molluscoidea" had already been proposed in place of Molluscoidea and is the better-known formal version of this taxon), HUXLEY (13) rejected any suggestion of molluscan affinity for the group and later supported MORSE's contention (18) that the Brachiopoda should be grouped with the Annelida.

The debate over the molluscan or annelid affiliations of the Molluscoidea continued for some time but is really less important than the correct identification of those groups that are most closely related to

brachiopods. Following KOVALEVSKIY's demonstration (15, 16) of the chordate affinities of tunicates and the precise nature of phoronid development, and NITSCHKE's segregation (20) of ectoproct and entoproct bryozoans, CALDWELL (3) inferred that ectoprocts, phoronids, brachiopods, and sipunculoids were closely linked. BLOCHMANN (2) came to the same conclusion and HAECKEL (9) erected the phylum Prosopygia to accommodate all four groups. It was HATSCHKE (11), however, who expressed the relationships most satisfactorily when he excluded sipunculoids from a new phylum, Tentaculata, which embraced the Brachiopoda and two new classes, the Ectoprocta and Phoronida.

HATSCHKE's arrangement, usually with the classes elevated to phyla and grouped under the designations of Tentaculata, Lophophorata (14) or an emended Molluscoidea, has been generally adopted even in classifications of the animal kingdom that are basically different. Hence all three groups in close association have been assigned to the Protostomia by GROBEN (6), the Coelomata or Bilateria by MARCUS (17) and the Oligomeria by HADŽI (7). It is still, however, unresolved whether brachiopods are part of an evolutionary plexus leading to either arthropods and mollusks as postulated by GROBEN and MARCUS, or chordates as envisaged by HADŽI, or whether they and other lophophorates evolved independently of the remaining coelomates from the Protozoa.

The insignificance of brachiopods among modern marine faunas has undoubtedly been responsible for their neglect during the 20th century as living organisms worthy of intensive study. A glance at the bibliographies for the chapters on "Anatomy" and "Ecology" is alone sufficient to emphasize the need for a comprehensive reappraisal of their anatomy, function, and mode of life. Little is known about the nervous and circulatory systems, especially of articulate; while many basic histological and physiological problems on shell growth, for example, have yet to be solved. Adequate embryological studies are so few and even conflicting in certain fundamental matters, like the origin of the coelom, that they have tended to raise more questions than have

been answered. Even less information is available on the relationship between the living brachiopod and its environment. As is stated in the chapter on "Ecology," much more reliable data are required on such elementary aspects of brachiopod life as feeding habits, respiration, and population distributions and structures, before most of the fossil evidence can be interpreted with any confidence. Clearly such deficiencies as these preclude any definitive conclusions on the organization of living forms and reduce the prospects of significant advances in paleontological research.

The preponderance of paleontological data has had a profound effect on the mode of study and classification of the Brachiopoda in that variation in the exoskeleton has always been accepted as the chief gauge of diversity of the phylum and relationships within it. In some respects, this bias has its advantages since it ensures a similar systematic approach to both living and extinct forms. Less desirable features include the creation of a large and complicated terminology mainly to draw attention to minor differences in shell morphology. Altogether about 700 terms have been employed in past descriptions of brachiopods and despite the pruning indulged in during the compilation of the glossary, about 500 still survive. A number of the established terms are justifiable because each conveys through one word or phrase the subtle complexity of a particular characteristic which would otherwise have to be described at some length in a variety of languages. Others, however, are either synonyms in that they are used for structures of the same origin in different fossil groups or have been coined for unimportant growth variants of a well-known feature. Consequently in the chapter on "Morphology" and in the accompanying glossary, an attempt has been made to relate shell differences to processes of growth and to identify homologous features in unrelated groups, in the hope of achieving a consistent terminology of manageable proportions that will act as a deterrent to any further maintenance of elaborate private vocabularies.

All classifications of the Brachiopoda have been based on variation in the exoskeleton. In some, the type of lophophore support

is the prime factor in taxonomic segregation; in others, much more arbitrary differences, like the form of the shell, have served in this capacity. Even BEECHER's classification, exploiting the nature of the pedicle opening, which enjoyed so much popularity earlier in this century, was really an exercise in interpretative shell morphology. The chief merit of such classifications is their applicability to extinct as well as living groups: but since they are founded on changes in a few exoskeletal features that have all reappeared in independent stocks several times during brachiopod evolution, they neither epitomize phylogeny nor provide suitable morphological keys for generic dissociation.

In the classification adopted for the *Treatise*, great importance is still attached to the morphology of the shell. But the practice of using a few characters to subdivide the phylum has been discarded in favor of building up higher taxa from assemblages of related genera. This scheme not only accords more closely with known phylogenetic relationships, as is shown in the chapters on "Evolution and Phylogeny" and "Classification," but is also more adaptable for the accommodation of further discoveries.

The systematic sections of this volume include diagnoses of nearly 1,700 genera assembled in 202 families, 48 superfamilies, 11 orders, and 2 classes, all also requiring description and discussion. Such an undertaking could not have been completed without the cooperation of a large number of colleagues who readily gave contributors to this volume valuable information and access to brachiopod collections.

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BRACHIOPOD ANATOMY

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GENERAL CHARACTERS

The soft parts of all living brachiopods (21) are enclosed by a pair of valves which typically are bilaterally symmetrical but dissimilar in size, shape, and even ornamentation. Posteriorly the valves may be attached to the substratum by a variably developed stalk, the **pedicle**, which normally emerges from the ventral or **pedicle valve** (Fig. 1). The dorsal or **brachial valve** is generally smaller than the pedicle valve, both of which constitute the shell. The body occupies the posterior part of the space inside the shell and the body wall is prolonged forward and folded as a pair of **mantles** lining the anterior inner surfaces of the valves to enclose the brachial or **mantle cavity** (Fig. 2). The body space or **coelomic cavity** accommodates the digestive, excretory, and reproductive organs, as well as muscle systems, some of which are responsible for movements of the valves relative to each other, including open-

ing of the shell (gape). The mantle cavity is separated from the body by the **anterior body wall** and contains the feeding organ or **lophophore** (Fig. 1; 2,A). A nervous and a primitive circulatory system are present.

Despite the similarities outlined above, Recent Brachiopoda may be allocated to one of two clearly defined classes, the Inarticulata and Articulata. Modern representatives of these two groups are fundamentally different in certain aspects of their development and also in their gross morphology. Both valves of articulate brachiopods are invariably calcium carbonate and articulated by complementary teeth and sockets, while the brachial valve is commonly equipped with outgrowths forming **lophophore supports** (Fig. 2,B). The inorganic content of inarticulate valves, in contrast, is calcium phosphate and only exceptionally (Craniacea) calcium carbonate, and no outgrowths are developed for either articulation or lophophore support. This

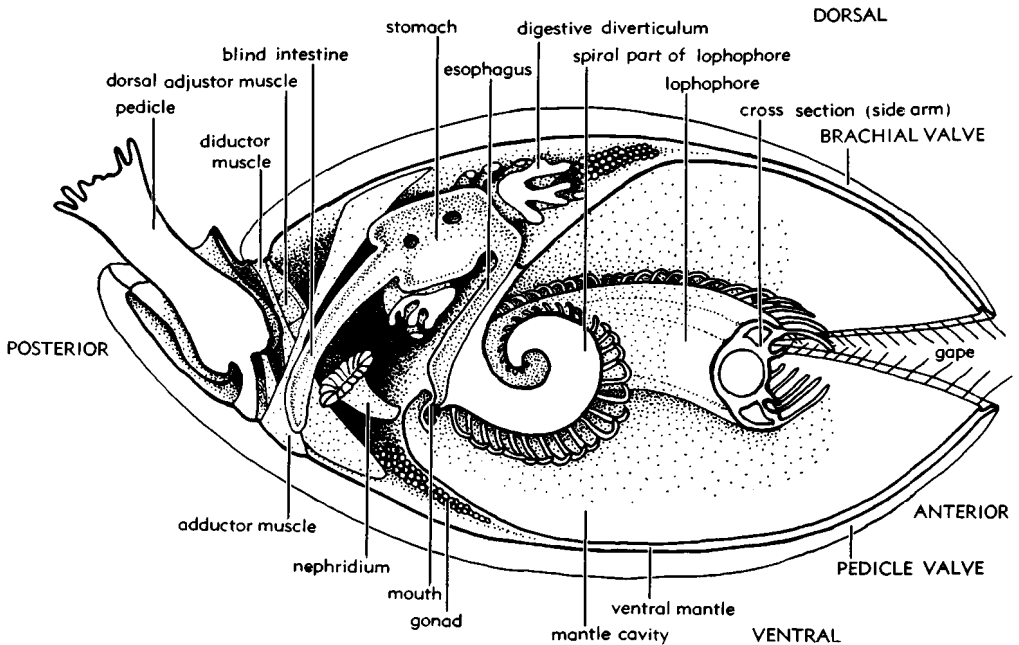


FIG. 1. Diagrammatic representation of principal organs of brachiopod typified by *Terebratulina* (48).

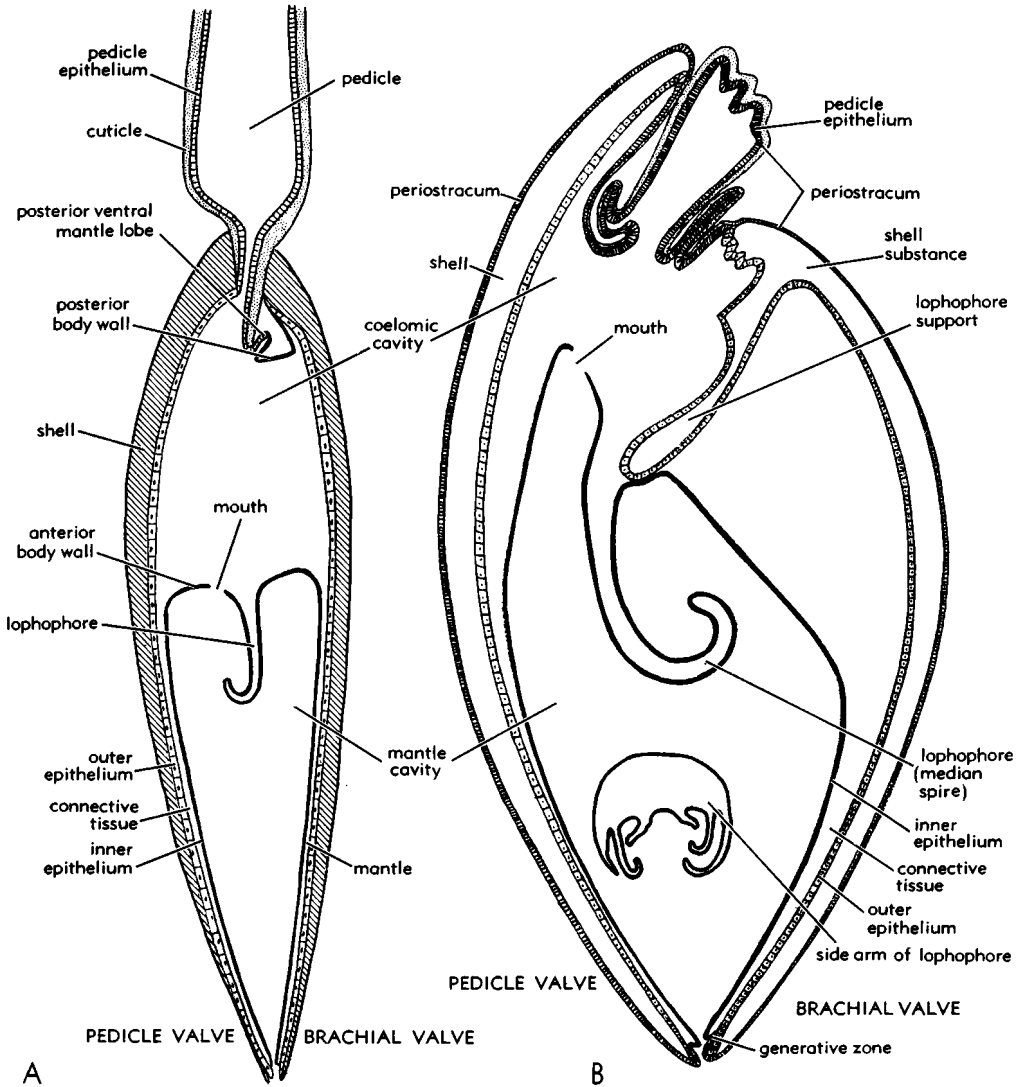


FIG. 2. Generalized representation of distribution of epithelium (A) in lingulids (47) and (B) terebratulids (44).

lack of articulation permits rotation in the plane of the margins or commissure of inarticulate valves, and consequently the musculature of the group is commonly more complex. Other internal differences are even more profound. The pedicle of articulate brachiopods develops from a primary segment of the larva, while that of the inarticulates arises from evagination of the inner surface of part of the ventral mantle. Finally, the alimentary canal of the articu-

lates ends blindly, while that of the inarticulates terminates in an anus.

In both groups, the body wall consists of an outer layer of ectodermal epithelium resting on a thin connective tissue layer and lined internally by a ciliated coelomic epithelium (peritoneum). In the mantles coelomic space is greatly reduced, being limited to a number of canals, and the coelomic epithelium is correspondingly restricted in distribution. The ectodermal epithelium is

responsible, among other things, for the secretion of the shell and its outgrowths, and since these are the sole remains of fos-

sil brachiopods, it seems appropriate to begin with an account of the morphology and function of this tissue.

The external epithelium is differentiated into four distinctive zones. Posteriorly, it underlies and secretes a cuticular cover for the pedicle and is known as **pedicle epithelium** (Fig. 2, *A,B*). Anteriorly, it forms the selectively ciliated surface to the lophophore and also the cuboidal epithelium, which constitutes the outer and inner layers of the mantles. The **outer epithelium** secretes the shell; the **inner epithelium**, which, as previously noted, is ciliated, lines the mantle

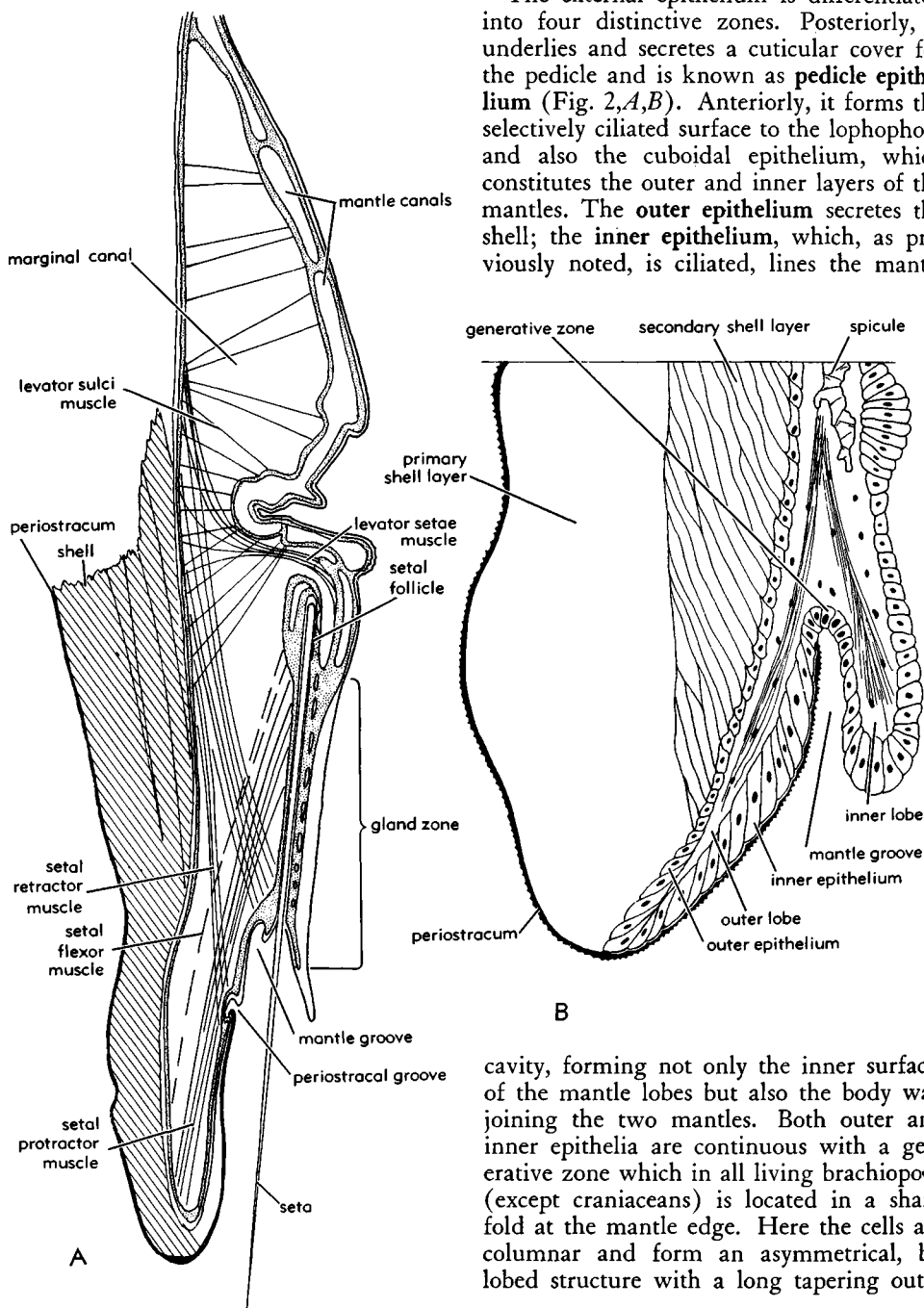


FIG. 3. Sections through anterior mantle margins of (A) *Lingula* (12) and (B) generalized articulate brachiopod (44).

cavity, forming not only the inner surfaces of the mantle lobes but also the body wall joining the two mantles. Both outer and inner epithelia are continuous with a generative zone which in all living brachiopods (except craniaceans) is located in a sharp fold at the mantle edge. Here the cells are columnar and form an asymmetrical, bilobed structure with a long tapering outer

lobe extending to the very edge of the shell and a more posteriorly situated, rounded inner lobe. The lobes are separated by a deep groove (**mantle groove**) from which arise the *setae*, the chief tactile organs of the brachiopod and a thin organic cover to the shell (**periostracum**) (Fig. 3).

The outer epithelium is therefore continuous posteriorly with the pedicle epithelium and anteriorly with the inner epithelium of the mantles. Nonetheless the boundaries of each are clearly defined and are important to an understanding of shell growth.

MANTLES

In inarticulates, the ventral and dorsal mantles are always discrete, even posteriorly about the pedicle, where a strip of body wall intervenes between the two mantle edges (Fig. 2,A). Over most of the area of the mantles, the inner and outer epithelium are separated only by a thin layer of connective tissue. The epithelium is typically cuboidal, and except for a peripheral zone usually occupied by the mantle groove, the inner epithelium is ciliated. Secretory cells are interspersed with cuboidal epithelium. In both mantles of the lingulids and discinids secretory cells are concentrated in a sub-peripheral zone roughly coincident with the base of the *setae* (Fig. 3,A).

Outgrowths of the mantle which pervade the inarticulate shell are entirely ectodermal in origin and develop at the margins of the mantles (Fig. 4,A). The protoplasmic strands seen as projections into the shell of *Lingula* and *Discinisca* are extremely fine and their detailed structure is still unknown. In contrast, the *caeca* of *Crania* are quite large and have a very characteristic arborescent appearance (Fig. 4,B), "branching" toward the outside of the shell. They arise from a peripheral zone of outer epithelium where the cells are larger than over the remainder of the mantle and strongly directed outward.

The mantle margin of *Crania* is relatively simple since the genus lacks the *setae*, mantle groove, and **marginal canal** found in lingulids and discinids (Fig. 3,A). However, a narrow peripheral zone of relatively high epithelial cells appears to secrete the periostracum on the mantle cavity or inner

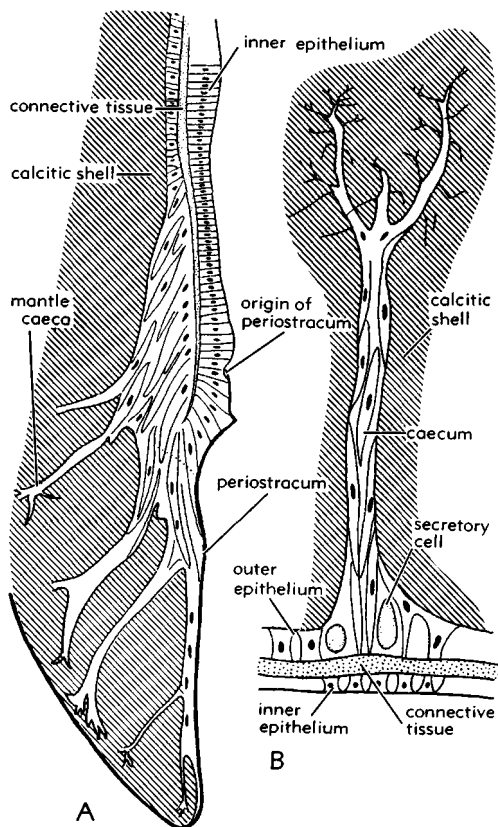


FIG. 4. Morphological features of *Crania*: (A), section through mantle margin; (B), mantle caecum (12).

side of the mantle (Fig. 4,A). The periostracum of lingulids and discinids arises in a similar position but is secreted by a limited number of cells in the **periostracal groove**, a narrow furrow situated on the outer lip of the mantle groove (Fig. 3,A).

The *setae* are developed peripherally in both valves and are only absent in the lingulids near the pedicle. Those of discinids are characteristically barbed, bearing numerous fine projections. Each seta arises from a tubelike invagination of epithelium into the connective tissue of the mantle groove and is secreted by one or more cells at the base of the follicle.

In the lingulids and discinids a large marginal canal is developed in the connective tissue of both mantles (Fig. 3,A). This runs peripherally around both mantle margins and is rather wider anteriorly than pos-

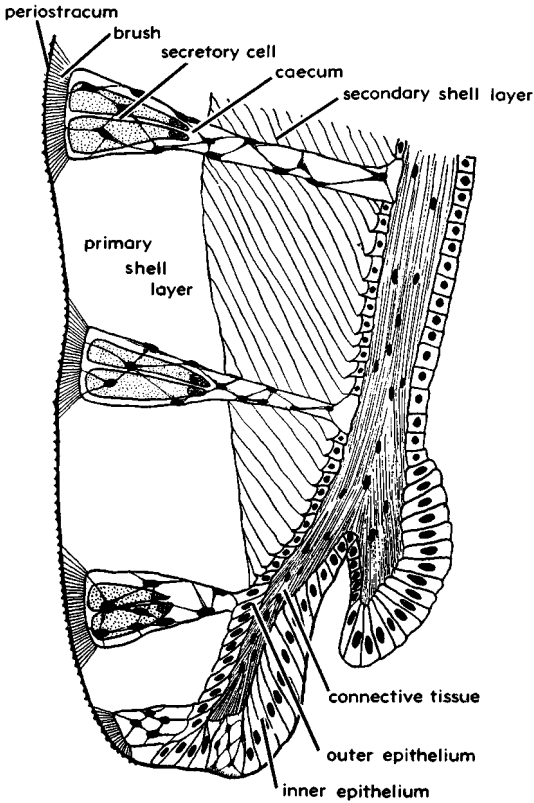


FIG. 5. Origin and growth of terebratulid caeca (44). [Noteworthy is absence of external openings to punctae (containing caeca) in shells of living terebratulids.]

teriorly. In both valves the marginal canals, which are particularly conspicuous in the lingulids, occur on the shell side of the mantle canals and setal follicles and are not in communication with the body cavity or its extensions (Fig. 3,A). They contain a well-developed musculature which controls movement of the setae and mantle margin. In *Discinisca* the musculature is relatively simple, consisting of radially arranged bundles of fibers attached to the base of the setal follicles peripherally and to the shell side of the marginal canal wall toward the center of the valve. The marginal musculature in *Lingula* is more complex. Five separate groups of muscles are present in the marginal canal (Fig. 3,A), and an additional three groups of muscles run through the connective tissue of the proximal end and inner side of the setal follicles. This elaborate musculature is undoubtedly used

in formation of the setal tubes during feeding.

The mantle edge of articulate brachiopods is always clearly differentiated into an outer and inner lobe separated by a mantle groove (Fig. 3,B). The periostracum is spun out from the closed end of the groove and remains adherent to the inner surface of the outer lobe as far as the tip; thereafter it becomes increasingly separated from the outer epithelium by the intercalation of the growing calcareous shell. The periostracum is not a uniformly thick sheet because commonly it is differentially thickened into bars arranged in a honeycomb pattern, as in *Macandrevia*, or rarely in a diamond pattern, as in *Terebratulina*.

A complication in the details of these relationships arises in portions of the mantle containing setae. Here, the mantle groove persists as a notch on the inner surface of the outer lobe and still gives rise to the periostracum; but it is no longer bounded by the inner lobe, which is separated from it by the seta and its follicle. Such an arrangement is very like that characteristic of the lingulids (compare, Figs. 3,A and 7). A difference is noted, however, in that the mantle groove of the lingulids appears to be always internal of the persistent periostracal groove, whereas the mantle groove of articulate brachiopods is coincident with the "periostracal notch" between the follicles. Whether this difference is really a reflection of the very much greater density of setae along the lingulid mantle edge remains to be seen.

The posterior migration of caecal outgrowths from the outer lobe of the mantle edge in punctate shells (Fig. 5) shows that the groove is an epithelial generative zone responsible for enlargement of the shell. The origin and disposition of the periostracum suggest that the actual generative zone is the closed end of the mantle groove (44). If this is so, the entire outer lobe is the region of proliferation and differentiation for the continuously migrating outer epithelial cells and the inner lobe serves a similar function for the inner epithelium.

At the tip of the outer lobe a physiological change¹ must occur within the migrating

¹ A comparable change, but generally involving the secretion of calcium phosphate, presumably also occurs at the tip of the outer lobe of inarticulate brachiopods.

columnar epithelial cells which had hitherto been secreting periostracum, because here they begin depositing a two-layered calcareous shell, an outer **primary layer** and an inner **secondary layer** (Fig. 3,B; 5). The primary layer is secreted only by those columnar cells forming the outer boundary of the outer lobe so that it is a continuous sheet, the thickness of which is related to the number of cells involved in its secretion. The layer has a finely fibrous texture with the long axes of the fibers coincident with their crystallographic *c*-axes and normal to the shell surface; it is entirely inorganic in composition and must have been deposited extracellularly. Immediately behind the primary layer the cells of the underlying epithelium become cuboidal and begin to secrete the secondary layer, which may continue over the entire surface of the outer epithelium within the peripheral outer lobe. The layer is therefore variable in thickness and consists of long, thin fibers of calcite disposed at low, oblique angles to the primary layer. Each fiber is well defined, for it is secreted by one cell only and is enclosed in a delicate cytoplasmic sheath which probably represents a greatly extended cell membrane so that deposition was intracellular. The *c*-axes of the secondary layer are

oblique to the long axes of the fibers but parallel with those of the primary layer, and the distinction between the two layers is due ultimately to the intracellular secretion of the former and the extracellular deposition of the latter.

All internal features of the brachiopod skeleton, like the articulatory devices of teeth and sockets, complex as well as simple supports for the lophophore, elaborate platforms for the insertion of muscle bases, etc., are composed of secondary shell, and their growth is due to accelerated secretion in localized zones of the outer epithelium (44). The only calcareous deposits not built up in this way are irregular bodies or spicules occurring within the connective tissue of the mantle and lophophore of some articulate brachiopods. They are secreted by mesenchymous cells, and although they are densely developed in certain brachiopods like *Terebratulina* and *Fallax* (Fig. 6), and have also rarely been found loose in fossil thecideaceans, they never contribute to the solid skeleton.

As in most inarticulates, follicles occur at regular intervals along the mantle edge of articulate brachiopods and bear one, or exceptionally two or more, ringed setae (Fig. 7). Movement of the setae is also controlled by muscles attached to the follicular bases which are served not by a marginal canal but by terminal branches of the mantle canal system.

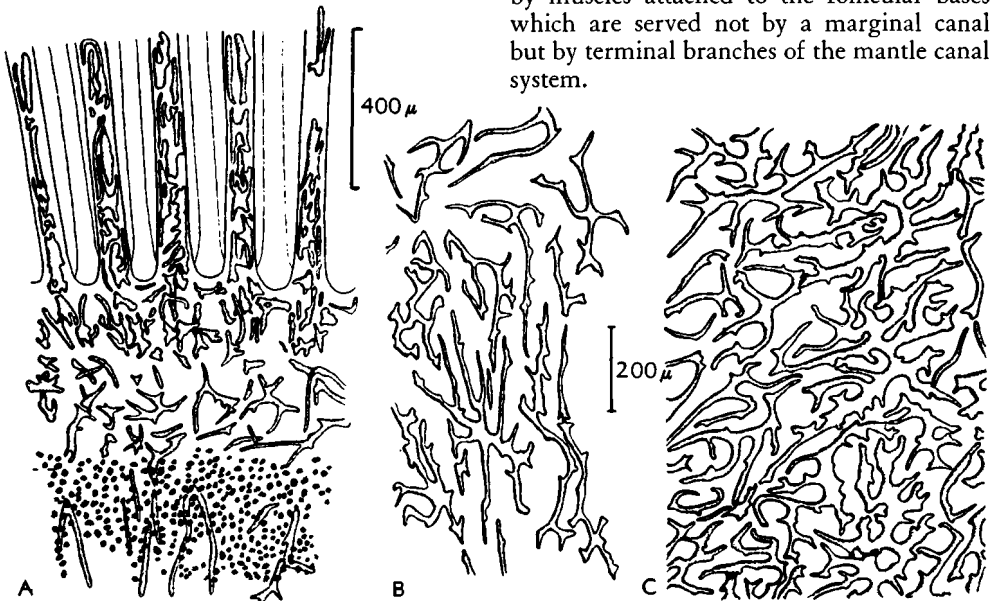


FIG. 6. Spiculation in *Fallax dalliniiformis* ATKINS: (A) of ablabial filaments and lophophore, (B) of body wall, and (C) of mantle over gonad (6).

The growth of the shell leading to a triple stratification of periostracum, primary layer of calcite, and secondary layer of calcite is typical of all living articulate brachiopods (Fig. 3,B; 5). But the terebratuloid shell is also characterized by the presence of numerous caecal evaginations of the mantle (**endopunctate** condition) (Fig. 5) in contrast to their absence in Recent rhynchonelloid¹ shells (**impunctate** condition) (Fig. 3,B). Each caecum first appears along the inner surface of the outer lobe as a small bud consisting of a few large cells but is not fully differentiated until it reaches the tip. At this stage it is cup-shaped and is connected with the periostracum by numerous fine cytoplasmic strands (**brush**) radiating from a membranous cover to a conical lumen. As the caecum migrates posteriorly along the outer lobe a few elongated mucus

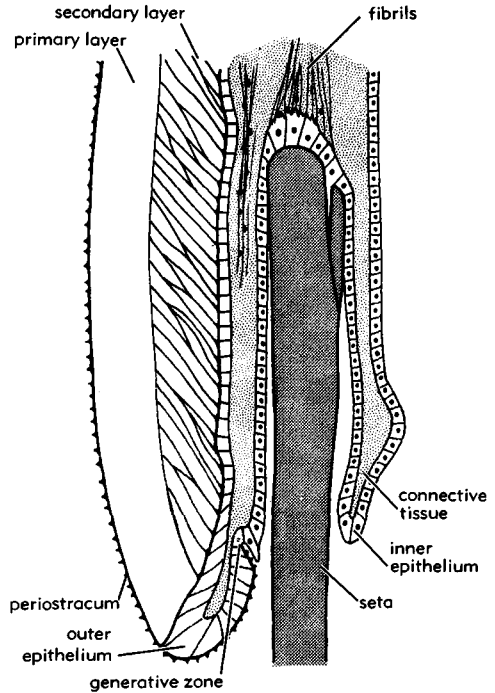


FIG. 7. Generalized diagram of mantle edge of *Terebratulina* showing follicle with seta (48).

gland cells appear within the lumen. The entire secretory portion of the caecum to the tips of its brush is completely encased in the calcite of the primary layer and at the junction of the primary and secondary layers a stalk, connecting the cup with the outer epithelium, is formed. As the valves expand peripherally, the caeca come to occupy an increasingly intramarginal position and may keep pace with the progressive thickening of the encasing secondary shell substance by convergence of adjacent stalks to give a branching effect, as in *Terebratulina*.

The growth of the valves outlined above is typical of any free mantle edge corresponding to the gape of articulate shells, but posteriorly around the pedicle and in the region where the valves articulate an important modification occurs.

The shell of an articulate brachiopod may be compared with a pair of very asymmetrical cones built up from the apices (umbones) by retardation of growth in a pair of short inner posterior sectors which are represented externally by triangular sur-

¹ Vernacular designations of brachiopods. It is a common and useful practice in writing about fossils to employ vernacular terms (common nouns, almost invariably in plural form, and adjectives) for assemblages of various taxonomic rank, but mostly suprageneric. Such terms appear in all *Treatise* volumes. In dealing with the Brachiopoda, however, problems have been encountered in this area, because no consistent procedure in anglicizing formal zoological names has been agreed on by authors and accepted editorially. Typescripts submitted for publication have referred to brachiopod groups called "rhynchonelloids," "rhynchonellaceids," "chonetids," "scaphelasmatinids" and numerous others. What are these? Should readers understand that "-oids" indicates a brachiopod group resembling and related to the genus from which the first part of the name is derived, without connotation of any particular taxonomic assemblage (order, suborder, superfamily, family, subfamily, genus)? Some authors are unconcerned about this, whereas others think that each particular taxonomic category needs to be specified. The termination "-aceans" (not "-aceids") is satisfactory for superfamilies, and "-ids" is appropriate for family-rank groups but in my opinion inappropriate for other assemblages.

Belatedly (that is, after very much *Treatise* typescript had been set in galleys) ROWELL & WILLIAMS have advocated rejection of "-oids" for vernacular names of brachiopod groups, despite general acceptance of them by paleontologists and despite their own usage of them in earlier-submitted typescripts. Their objection to "-oids" stemmed from asserted ambiguity of its taxonomic significance or at least its insufficient precision in referring to orders, suborders, superfamilies, or some other assemblage. As substitute they recommended that groups of ordinal rank (e.g., Orthida) should be referred to as "-ides" (e.g., orthides), and those of subordinal rank (e.g., Orthidina) as "-idines" (e.g., orthidines). Superfamilies (e.g., Orthacea) can be cited readily in vernacular terms with the termination "-aceans" (e.g., orthaceans) and families (e.g., Orthidae) with ending in "-ids" (e.g., orthids). For subfamily-rank groups they proposed adoption of anglicized names ending in "-ins" (e.g., Orthinae, orthins). Adjectival words for each of these categories are derived simply by dropping the "s" of plural nouns. This scheme has the merit of allowing precise taxonomic groups to be cited for reference but it is objected to by some highly qualified *Treatise* advisers as too technical and complicated, thus very unlikely to win acceptance by paleontologists, either specialists on brachiopods or others.

Editorial decision is to accept the anglicized designations of brachiopod taxonomic groups proposed by ROWELL & WILLIAMS wherever this can be accommodated without resetting of type but to retain such vernacular names as "orthooids," "strophomenoids," "productoids," and others where used by authors without (in editorial opinion) appreciable uncertainty of meaning.—R. C. MOORE.

faces (**cardinal areas**) rutt by transverse lines of interrupted growth (growth lines). Each cardinal area usually slopes anteriorly from the umbo toward that of the opposing valve and the two rarely match in size, for the dorsal cardinal area is commonly little more than a narrow ledge. The inner edges of cardinal areas (posterior margins) are always contiguous and are so maintained by a fusion of the mantle lobes (44). Thus at lateral limits of cardinal areas, the mantle edges come together so that the inner and outer lobes of the pedicle valve lie closely adjacent to their counterparts in the brachial valve. The effects of fusion may then be traced inwardly toward the median plane of the shell. The inner lobes lose their identity and fall away anteriorly to become the inner epithelium of the anterior body wall, while the outer lobes form a common generative zone in front of the posterior margin (Fig. 8). The fused outer lobes control growth of both cardinal areas, which are covered by a thick periostracal pad between the posterior margins and extending from the outer edge of one cardinal area to the other where it is continuous with the periostracal sheets secreted by the

free mantle edges of both valves. In this manner the hinge line is completely sealed by the periostracal pad, which is deeply inserted into growth lines of the cardinal areas. Lateral expansion of cardinal areas is apparently not due to a progressive fusion of free mantle lobes but to an actual growth expansion of the lateral edges of the initial area of mantle fusion. Medially, along a line which completely encircles the external base of the pedicle, the shell-secreting generative zone of the posterior margin is confluent with the principal growing edge of the pedicle epithelium. The changing relationships that occur between these two distinct epithelial zones during the growth of the animal are discussed below.

PEDICLE

The majority of Recent brachiopods are attached to the substratum during life by a pedicle. However, the pedicle of the Inarticulata is only analogous with that of articulate brachiopods because the origin and morphology of the organ is completely different in the two classes.

In both families of living inarticulate brachiopods possessing a pedicle, lingulids

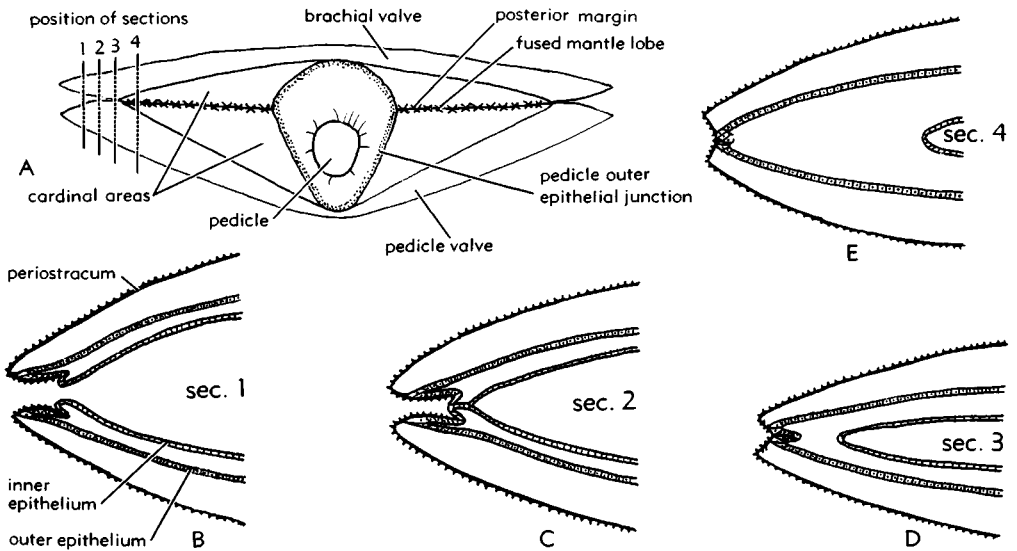


FIG. 8. Stylized sections showing relationship between dorsal and ventral mantle edges of articulate brachiopods along posterior end of gape and the posterior margin: (A) posterior view of shell showing location of sections; (B-E) successive sections 1-4 (48).

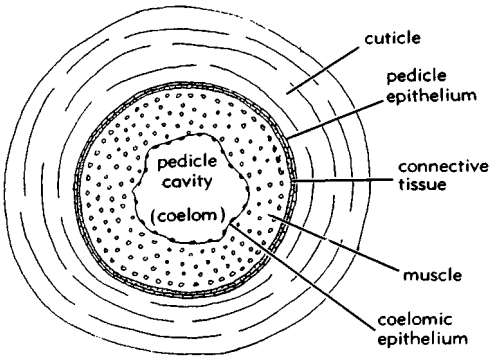


FIG. 9. Section through pedicle of *Lingula* (40).

and discinids, the organ arises as an outgrowth of the inner epithelium of the ventral mantle and is attached only to the pedicle valve (Fig. 2, A). Its epithelium is continuous with that of the ventral body wall and shows many similarities to it. The pedicle epithelium is covered externally by a thick layer of chitinous cuticle, continuous with the periostracum (Fig. 9). Internally it rests on a connective tissue layer which separates the pedicle epithelium from the coelomic epithelium lining the pedicle cavity (12).

In modern representatives of the lingulids and discinids a considerable difference is seen in the gross form and musculature of the pedicle, a difference that undoubtedly reflects the different mode of life of the two groups. The pedicle of the lingulids, which live in burrows, is invariably long and flexible, commonly several times the length of the shell. In the discinids, on the other hand, which live attached to a hard substratum, the pedicle is very short and the pedicle muscles are very strongly developed, permitting movement of the shell normal to the surface of attachment, as well as a variety of controlled rotational and tilting adjustments.

The thick cuticular layer ensheathing the pedicle of *Lingula* is transparent in life. Below this layer, the thin pedicle epithelium shows a marked thickening at the distal swelling (ampulla) of the pedicle. Underlying the pedicle epithelium a thin layer of connective tissue lies externally to a thick muscle layer. The individual muscle fibers are long and are attached at both ends to the

connective tissue. The fibers are arranged longitudinally along a helical spiral, two directions of coiling are present, clockwise and counterclockwise, and contraction of the fibers causes a reduction in length of the pedicle. Thin coelomic epithelium separates the muscle layer from the pedicle cavity (Fig. 9), which varies in width along its length, broadening gradually from a sharp contraction immediately in front of the distal ampulla. Where the pedicle enters the valves it is strongly flattened and the pedicle coelom is likewise constricted to form the narrow pedicle canal opening into the body cavity to the right of the umbonal muscle. Gland cells, which apparently supply the secretion used to bind grains of sand into the sand tube surrounding the pedicle, are located on the posterior lateral body walls.

In *Discinisca* the basic structure of the pedicle is the same, but the muscle layer in the wall of the pedicle is not as well developed. The principal pedicle muscles of *Discinisca* consist of three pairs located in the pedicle coelom which they nearly fill. A large pair of rectus muscles run dorsoventrally through the pedicle and are attached to its distal end and to the shell at the sides of the pedicle opening. Additional are two pairs of oblique muscles, the pedicle oblique median muscles and oblique external muscles (Fig. 10). At the proximal end of the pedicle the pedicle coelom is restricted to a narrow pedicle canal by a sphincter, which controls the opening into the body cavity.

Members of the only other inarticulate family represented in the seas today, the

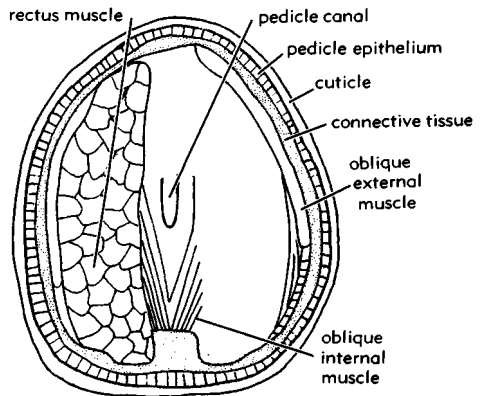


FIG. 10. Pedicle of *Discinisca* viewed ventrally, ventral surface and left rectus removed (12).

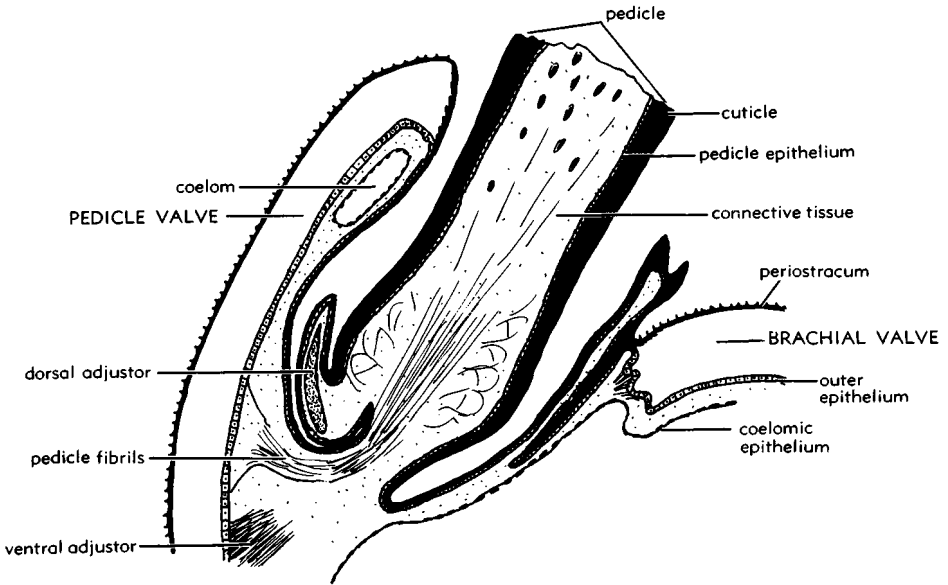


FIG. 11. Generalized diagram showing tissue distribution within pedicle of *Terebratulina* (48).

Craniidae, lack a pedicle at all known stages of development and are attached by cementation of all or part of the pedicle valve to foreign objects; the cementation seemingly is effected by adhesive properties of the periostracum.

The pedicle of the articulate brachiopods is essentially a solid cylinder of variable length and diameter with a core of connective tissue enveloped in pedicle epithelium and the outer chitinous cuticle. The proximal end tends to be bulbous and in Recent rhynchonelloids and terebratuloids is accommodated within the umbonal region of the pedicle valve in what is usually referred to as a capsule but which actually consists of a deep infold of pedicle epithelium and cuticle (Fig. 11). The distal end may also be bulbous or splayed with many rootlike extensions acting as adherent "hold-fasts" to the substratum; rarely, as in *Chlidonophora*, the pedicle is divided into a series of long, slender filaments. The connective tissue forming the pedicle axis is made up of longitudinal fibrils which may pass anteroventrally to the floor of the pedicle valve and form a small scar of attachment (the "median adjustor" or "pedicle muscle scar"). The tissue is not, however, part of the muscle system of the brachiopod, for the movement of the shell

about the pedicle is controlled by adjustor or pedicle muscles attached to the pedicle and the interiors of both valves. The adjustor muscles normally consist of two sets. The ventral pair arise from the dorsolateral surface of the pedicle and pass ventrally to become inserted on the floor of the pedicle valve lateral to the diductor muscles. The dorsal pair, arising ventrolaterally, are attached to either the hinge plate or socket plates of the brachial valve, as in *Hemithiris* and *Magellania* or, less commonly, anterior to the hinge plate on the floor of the valve, as in *Terebratulina*. In adult *Lacazella*, which is cemented to the substratum, neither the pedicle nor its muscle system is developed.

Since the pedicle of inarticulate brachiopods is exclusively an extension of the ventral body wall, the posterior part of the ventral mantle edge lies entirely outside the organ and never fuses with the part of the dorsal mantle edge, from which it is separated by the posterior body wall. The pedicle of articulate brachiopods, however, although largely accommodated by a median opening (delthyrium) in the ventral cardinal area, is confluent with the body wall of both valves and this leads to complications unknown in the inarticulates. The junction between the epithelia responsible

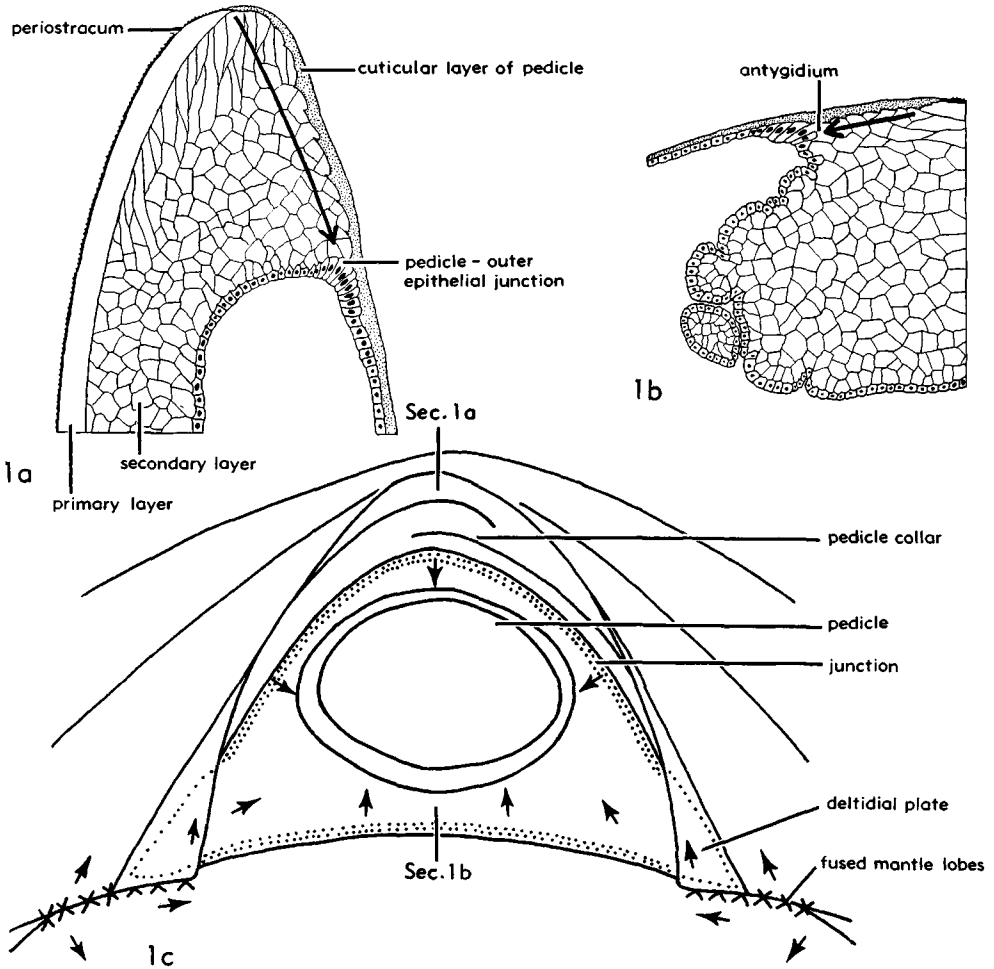


FIG. 12. Disposition and growth of outer-pedicle epithelial junction in articulate brachiopods; 1a,b, partial sections; 1c, posterior part of pedicle valve showing position of 1a,b (arrows indicate direction of migration of proliferated outer or pedicle epithelium) (48).

for the secretion of the shell and the pedicle cuticle is sharply defined throughout the life of an articulate brachiopod. In its unmodified form it is subcircular to suboval in outline and lies mainly within the pedicle valve, that is, ventral of its intersection with the fused mantles controlling the growth along the posterior margins. The junction is responsible for the proliferation of the pedicle epithelium but in a manner which suggests that it is not a generative zone along its entire length for two types of epithelium like the closed end of the mantle groove. Thus, as growth proceeds, the junction becomes a zone of excessive secretion in the

pedicle valve and here it retreats anteriorly, leaving behind a semicircular ridge of secondary calcite, the **pedicle collar**, coated on its inner side by a thick cuticle which is deeply inserted along irregular growth lines in the calcareous ridge. Along its dorsal edge, a very much slower retreat of the junction occurs, which is directed ventrally, not anteriorly, and leaves behind an external cuticle with insertions into a faint ridge of secondary calcite (**antygidium**) (Fig. 12). The most important aspect of this type of growth is the contrasting activities of the epithelia forming the junction. The secretion of primary shell substance takes place

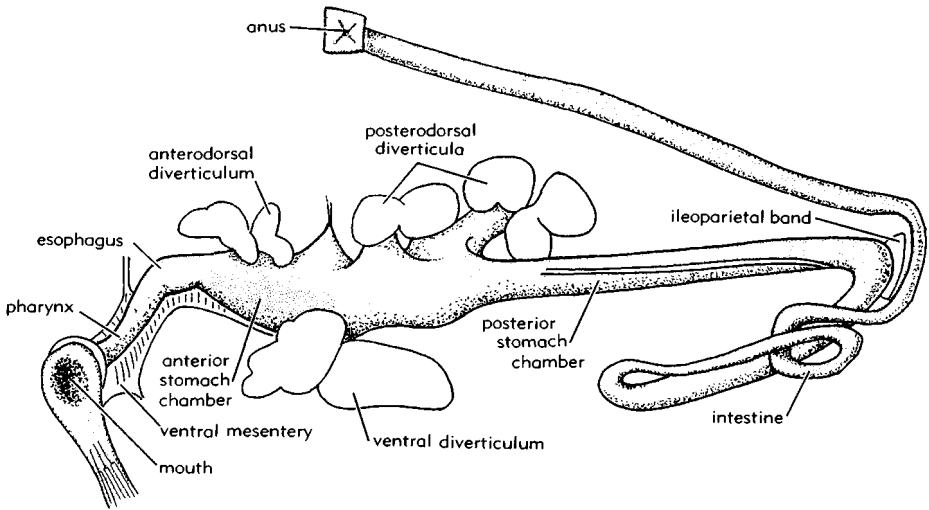


FIG. 13. Alimentary canal of *Lingula*, showing coiled anterior portion of intestine depressed and straight posterior portion elevated (17).

only along the posterior margin up to the intersection of the fused mantle lobes with the outer-pedicle epithelial junction. No primary shell is ever deposited at the junction within either the delthyrium or notothyrium, so that the outer epithelium encircling the pedicle is proliferated only by the fused mantle lobes at their two points of intersection with the pedicle epithelium. The pedicle epithelium, on the other hand, is responsible for the steady growth of the pedicle, including the deep infolds of cuticle and epithelium around the capsule. Hence, although circumferential enlargement is controlled at the posterior margin, the entire pedicle epithelium, at least along the junction, must continue to function as a generative zone (Fig. 12).

In most living brachiopods, the delthyrial opening of the adult shell is restricted by the growth of lateral plates (**deltidial plates**) so that the pedicle emerges through a variably placed foramen. Such modifications can involve complicated growth readjustments around the umbones of both valves and are more appropriately described in the chapter on shell morphology.

The shell growth of the thecideacean *Lacazella*, which lacks a pedicle, is not known in detail, but the arched, imperforate, triangular area of primary and secondary shell

(pseudodeltidium) lying between the teeth ridges was evidently secreted by outer epithelium; and along the entire width of the hinge line the mantle lobes of both valves are fused and produce a periostracal pad.

ALIMENTARY CANAL

All brachiopods possess a well-developed alimentary tract. In the inarticulates its length is considerably greater than the length of the body cavity and it is consequently folded to varying degree. In this class, in contrast to the articulate brachiopods, the alimentary canal terminates in an anus.

In all members of the phylum the mouth is a transverse slit situated medianly in the brachial groove where the two arms (brachia) of the lophophore unite. This opens into the pharynx, a short, dorsally curved, muscular tube, which is embedded in the bases of the brachia. Behind the anterior body wall, the gut is continued as the esophagus, a relatively short tube of uniform diameter, which leads into the stomach. The stomach varies in shape in different genera, but in all of them it is the most expanded part of the alimentary canal and is supported in varying degree by mesenteries, gastroparietal and ileoparietal bands.

The stomach of living inarticulates extends posteriorly along the median line and in *Glottidia*, *Lingula*, and *Discinisca* is attached by part of the ileoparietal band to

the posterior body wall. In *Crania*, however, it curves ventrally forward toward the left before reaching the extreme posterior end of the coelomic cavity (12). The

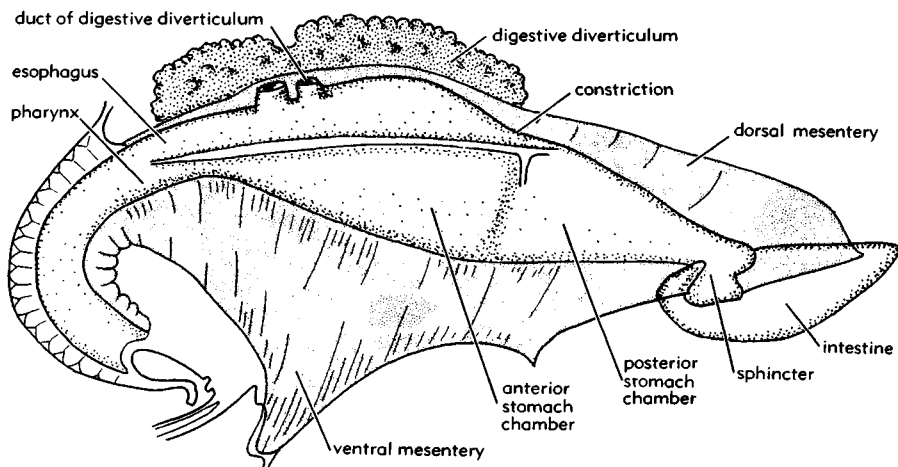


FIG. 14. Alimentary canal of *Crania* viewed from left side (left diverticulum removed) (18).

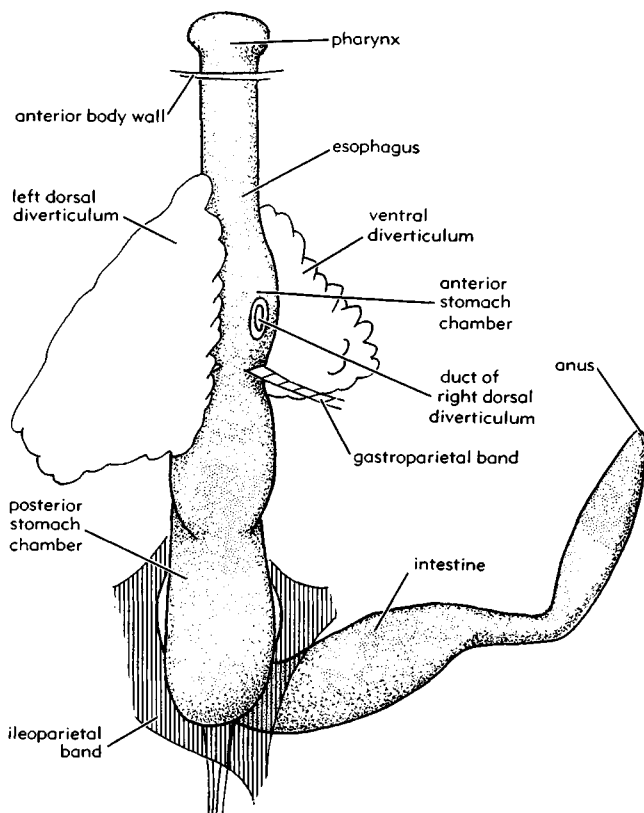


FIG. 15. Alimentary canal of *Discinisca* viewed dorsally (right diverticulum removed) (23).

stomach itself is divisible into an anterior and posterior chamber. This division is most marked in the lingulids where the anterior chamber is a thin-walled sac capable of considerable dilation in contrast to the thicker-walled, much narrower posterior chamber (Fig. 13). In *Crania* and the discinids the external difference between the two chambers is less conspicuous, but they are separated by a constriction (Fig. 14, 15).

Behind the sphincter, which limits the stomach posteriorly, is the intestine, the course of which differs considerably in the three inarticulate families with Recent representatives. The intestine of the lingulids is a slender thin-walled tube which bends to the left and forms a free loop before returning to the posterior end of the coelomic cavity. It then turns to the right and fol-

lows an oblique course anteriorly to open at an anus on the right body wall. Another sphincter controls the opening of the anus. In the discinids the course of the very much shorter intestine is somewhat similar. From the stomach it turns to the right toward the lateral body wall and then obliquely forward in a dorsal direction, to open at an anus on the right body wall. *Crania* differs considerably from the previous genera in that its intestine is capable of considerable dilation and its course is markedly different. It has the form of an inverted V with the apex directed anteriorly. From the sphincter at the end of the stomach it continues anteriorly and then bends back acutely to open at an anus medially placed on the posterior margin. Although the anus is on the mid-line, it lies to the right of the attachment of the ventral and dorsal mesenteries

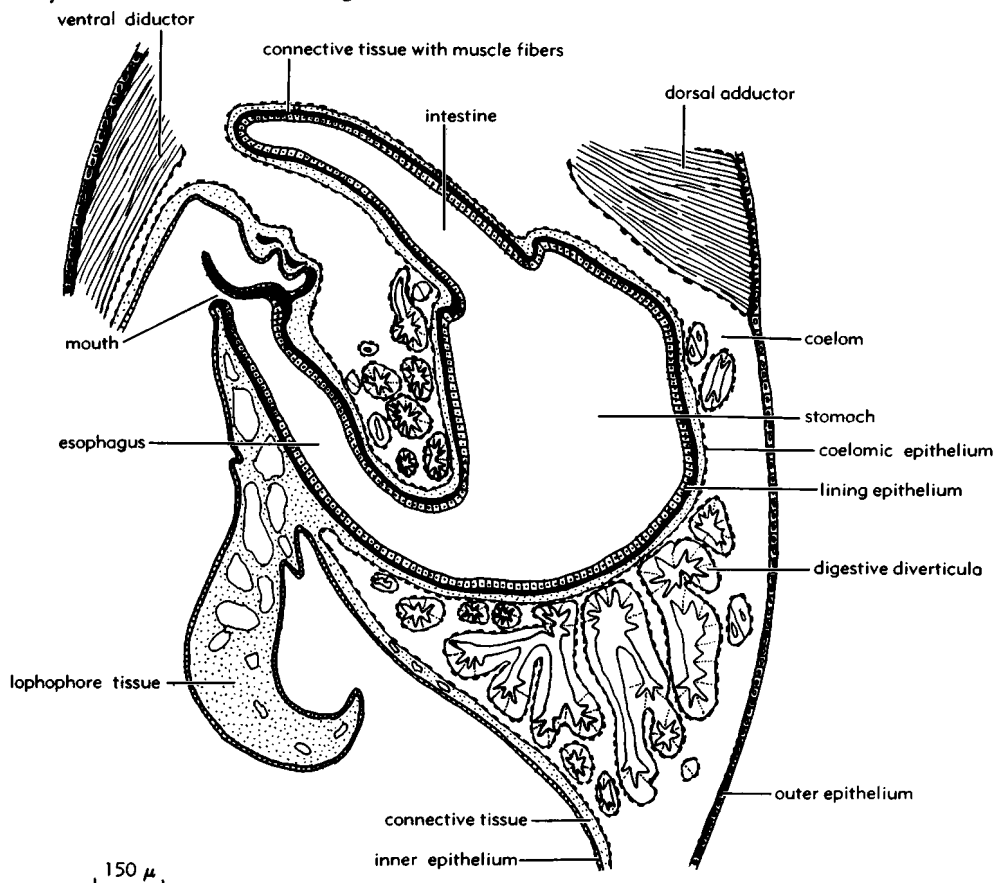


FIG. 16. Generalized longitudinal section of body of *Terebratulina* showing disposition of alimentary canal and diverticula relative to anterior body wall and brachial cavity (48).

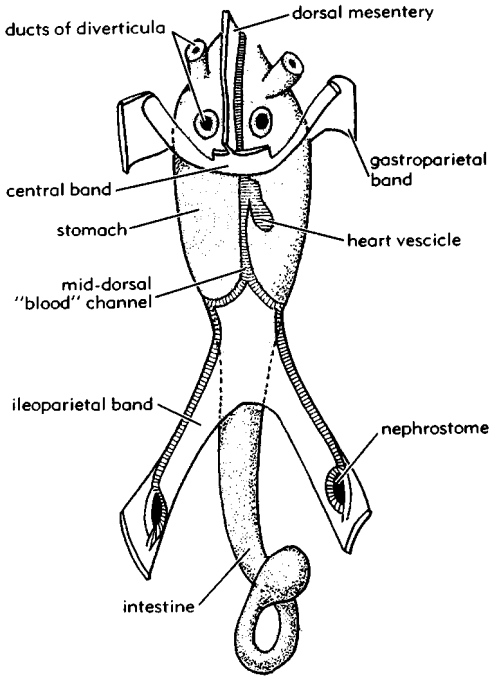


FIG. 17. View of part of alimentary canal of *Hemithiris psittacea* (GMELIN) showing distribution of main mesenteries (21).

to the intestine. In this respect the intestine may be thought of as opening on the right-hand side of the animal, as in other families of the inarticulates, although the anus is much more posteriorly placed in *Crania* than in the other genera (18).

Among articulate brachiopods the disposition of the alimentary canal is somewhat different in that the relatively longer esophagus is more strongly anterodorsally inclined before it bends abruptly into the relatively short stomach (Fig. 16). The stomach passes mid-dorsally into a tapering intestine directed posteroventrally and terminating blindly as either a blunt end supported by mesentery (Fig. 16) or exceptionally, as in *Hemithiris*, as a bulbous end twisted upon itself and hanging free (Fig. 17).

The digestive diverticula (or liver) open through ducts into the stomach, and are such conspicuous features of the coelomic cavity that they can almost conceal the stomach. Four diverticula are present in *Lingula*, three dorsal and one ventral, each

opening through a separate duct into the stomach. The three dorsal diverticula consist of a single anterior diverticulum on the mid-line and a posterior pair left and right of the axis of the stomach, slightly behind the place of attachment of the gastroparietal band. The diverticula are not all of the same size in the adult, the right posterior dorsal being the largest and the anterior dorsal the smallest, but they all have a similar structure. Each diverticulum consists of a fixed number of lobes, seven in the right posterodorsal, two in the left posterodorsal, and four lobes in both the ventral and anterodorsal diverticula. The main duct of each diverticulum bifurcates shortly after leaving the stomach and from the bifurcation a number of lobular ducts arise which serve the lobes. The lobes consist of repeatedly branching ducts terminating in bunches of blind sacs (acini) (17).

In *Crania* only a pair of diverticula are present, both dorsally placed and separated by the dorsal mesentery. Each diverticulum is divided into two lobes and their basic structure is similar to the lobes in *Lingula*.

Discinisca has three diverticula (23), all of them situated in front of the gastroparietal band, a dorsal pair and a single, unpaired ventral diverticulum. Their detailed structure is unknown. They open into the stomach through separate ducts, but apparently are not divided into lobes, their terminal portions being long tubules.

Crania and *Lingula* both have a ciliated epithelial groove running along the stomach (17, 18). In *Lingula* this arises in the right posterodorsal diverticulum, traverses all the lobes of this organ and emerges to run along the dorsal surface of the posterior stomach chamber. The epithelial groove in *Crania* lies longitudinally along the floor of the anterior chamber of the stomach and is continued into the posterior chamber, rising dorsally from the floor to the roof of the chamber by the right lateral wall.

The diverticula of articulate brachiopods are less well known. They commonly consist of a pair of posterior lobes and a pair of larger anterior lobes, symmetrically arranged about the dorsal mesentery, which communicate with the stomach through one to three pairs of ducts. In detail, such diverticula are apparently like those of

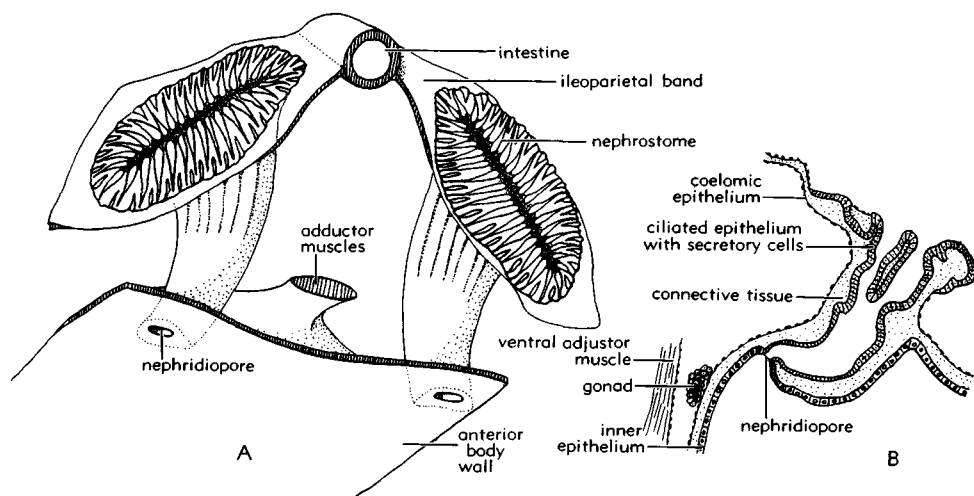


FIG. 18. Generalized diagrams showing (A) attitude of nephridia of *Terebratulina* relative to anterior body wall and (B) structure of nephridium as seen in longitudinal section (48).

Lingula, but differences are seen in at least *Argyrotheca* and *Lacazella*, where the diverticula consist respectively of six to eight pairs and 10 to 16 pairs of elongate tubules.

As far as is known, the histology of the gut of all living brachiopods is broadly similar (Fig. 16). The inner surface of the alimentary canal is lined with a simple columnar endodermal epithelium which rests on a basement membrane forming the inner surface of a connective tissue stroma. The epithelial cells are tall and slender in the pharynx and esophagus of *Crania* and are shorter elsewhere. They have a similar distribution in *Lingula*, but in this genus the epithelial lining of the posterior stomach also consists of tall cells. This epithelium is ciliated in all of the gut except the acini of the digestive diverticula. Interspersed between the normal epithelial cells are mucus cells and some wandering phagocytes. The latter also occur in the lumen of the stomach, digestive diverticula and intestine of *Lingula* (17).

Embedded in the outer part of the connective tissue stroma, which lies external to the basement membrane, are two sheets of muscle fibers. The fibers are arranged in an inner circular layer and an outer longitudinal sheet and are developed in the wall of all of the alimentary canal. They appear to be smooth in the stomach and intestine of all brachiopods, but the esophageal mus-

cles of certain rhynchonelloids and terebratuloids are known to be striated. Where it is free, the canal is lined externally by a thin ciliated coelomic epithelium.

EXCRETORY SYSTEM

The brachiopod excretory organs consist of one or exceptionally, as in rhynchonelloids, two pairs of metanephridia, which also serve as gonoducts in that sex cells are discharged through them from the body cavity.

Although there is some variation in detail, the shape of the nephridia is similar in all living brachiopods. The nephridial opening within the coelomic cavity consists of a broad funnel-shaped nephrostome with a ruffled inner surface. Each nephrostome is continued anteriorly by a narrow tube, usually ventrally placed against the lateral body wall and opening into the mantle cavity through a small nephridiopore on the anterior body wall, close to the mid-line and ventral to the mouth (Fig. 18). The posterior pair of nephrostomes of the rhynchonelloids and the nephrostomes of all other brachiopods are supported by the ileoparietal band and the anterior pair, when present, by the gastroparietal bands.

The nephridia of the lingulids are broad and relatively long and the nephrostomes are turned laterally, away from the mid-line,

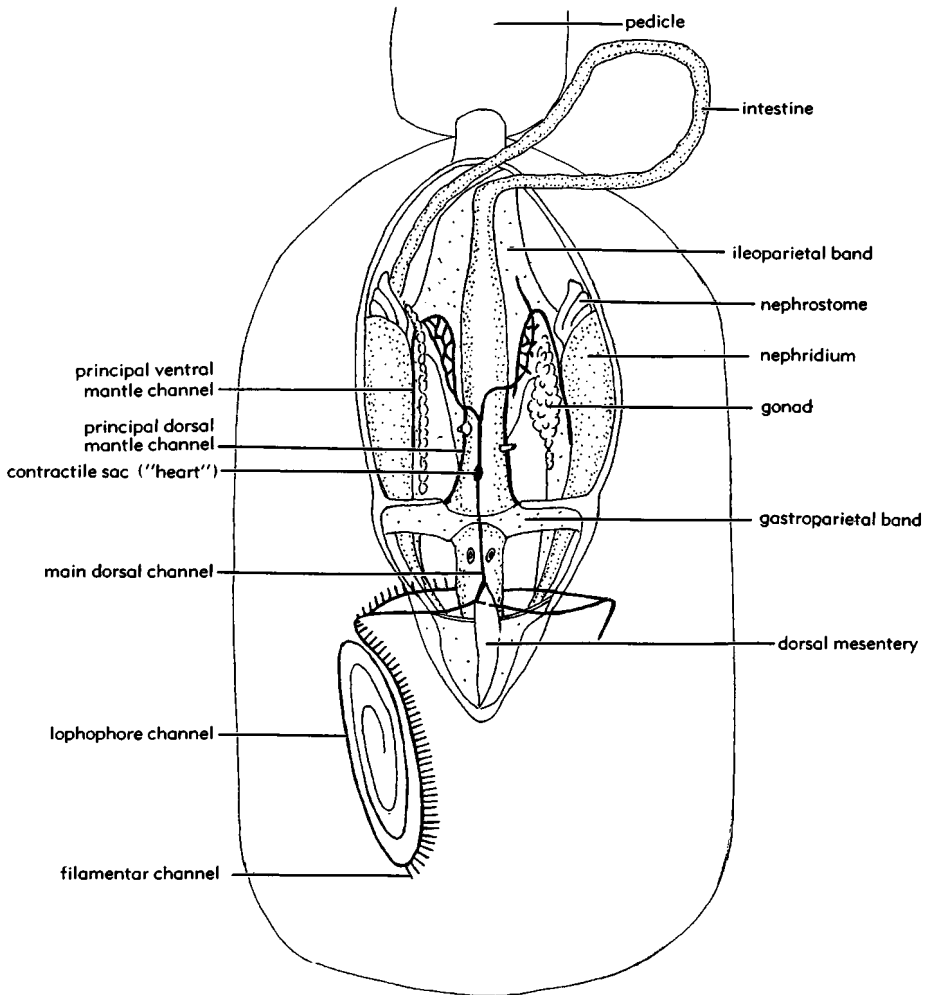


FIG. 19. Generalized diagram of circulatory system of *Lingula* (40).

to face the lateral body wall (Fig. 19). In the discinids and craniids, the nephridia are relatively shorter, the nephrostomes facing dorsally and slightly medially in the former family, while in the Craniidae they open medially. In the Articulata, the nephrostomes appear to be consistently oriented to face dorsally or dorsomedially.

Histologically, as far as is known, the structure of the nephridia is similar in all living brachiopods. The inner surface is covered by ciliated epithelium with interspersed secretory cells. This layer is separated from the outer layer of coelomic epithelium by a connective tissue, which is differentially thickened in the ruffled surface of the nephrostomes (Fig. 18).

COELOM

The muscles, alimentary canal, excretory organs and all or part of the sexual organs, constituting the "body" of the brachiopod, are lodged in the posterior part of the shell within a coelom which also contains a fluid and may be divided by vertical and transverse mesenteries. Other coelomic spaces exist within the lophophore and mantle lobes and also in the pedicle of inarticulate brachiopods and theoretically the entire coelom may be divided into proto-coel, meso-coel, and metacoel (22). These divisions are not very meaningful in that they have not been identified in embryological studies. But the coelomic spaces of the lophophore

have been recognized as possible representatives of the protocoel and mesocoel and the body cavity with its extensions into the mantles and pedicle as the metacoel. More often than not, however, there is communication between at least part of the lophophore coelom and the body cavity and it is not proposed to use the terminology of this hypothetical threefold division of the coelom in the subsequent account.

The coelom and the organs and connective tissue it contains, including muscle bands and the mesenteries, are lined with a flat, ciliated coelomic epithelium (Fig. 16).

All coelomic spaces of living brachiopods contain a fluid which, in the main body cavity and its extensions, is a coagulable liquid carrying a variety of free cells. These include spherical or slightly irregular coelomocytes, phagocytic amoebocytes, and the so-called spindle bodies that are known only in the lingulids. KAWAGUTI (24) has found that the coelomocytes of *Lingula* contain a red pigment, hemerythrin. This pigment has a limited ability to carry oxygen

which is released on the reduction of hemerythrin to a colorless form. The reaction is reversible and in all probability fulfills a respiratory function.

BODY CAVITY

The body cavity is normally traversed by a number of flat sheets of connective tissue (mesenteries) locally pervaded with fine muscle fibers. Dorsal and ventral mesenteries that run from the alimentary canal to the respective body walls are present in all living brachiopods but are incompletely developed, except in *Crania*, where the body cavity is divided into two separate compartments by them (12). In addition, two lateral pairs of mesenteric bands usually connect the alimentary canal to the body wall and give some support to it and other organs within the body cavity. The anterior pair, forming the gastroparietal band, which is absent in *Crania*, is relatively narrow and extends on both sides from the stomach, near the digestive diverticula, to the lateral

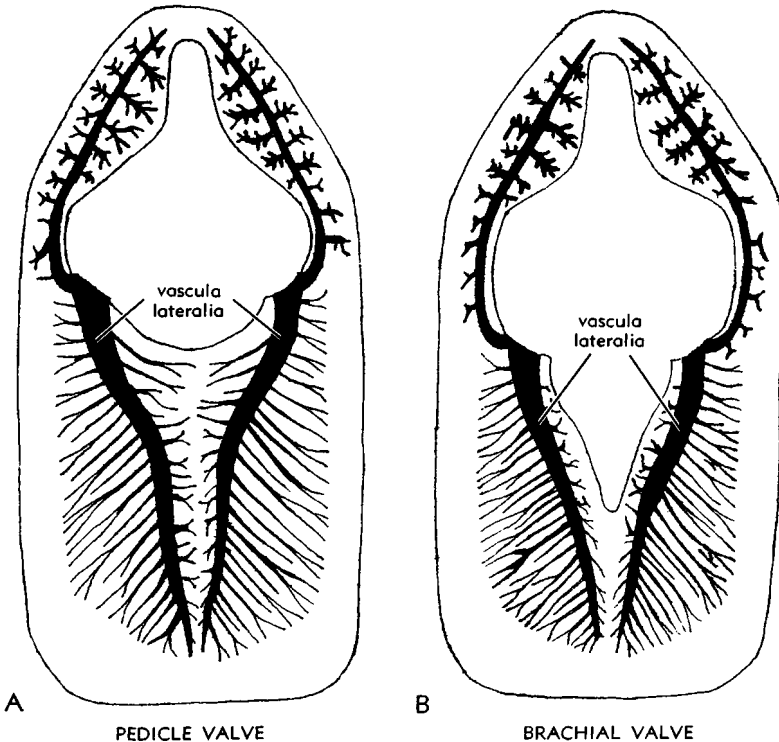
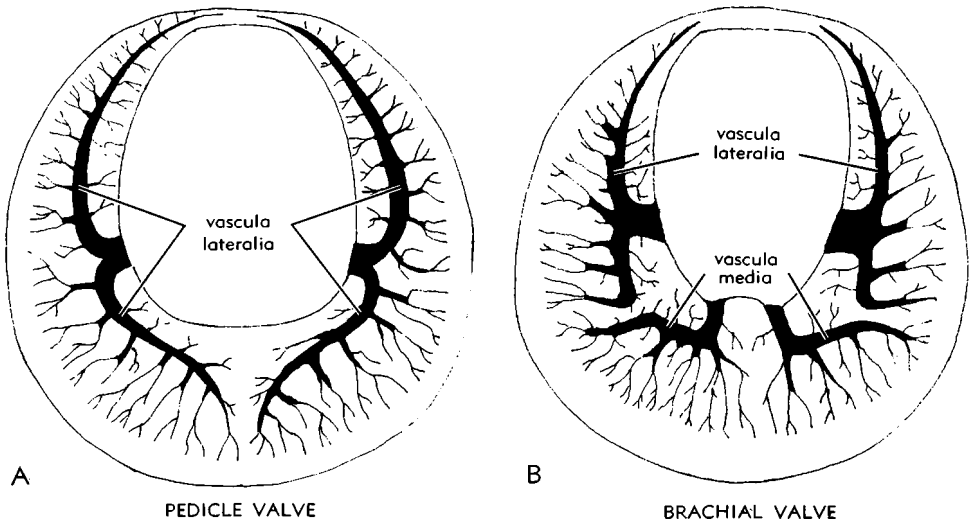


FIG. 20. Mantle canals of *Lingula* (12).

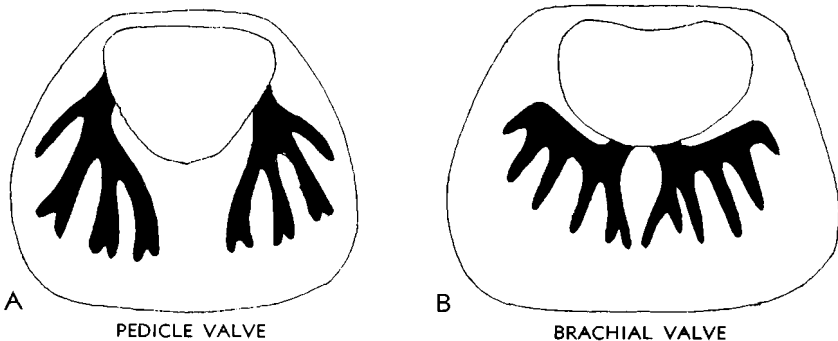
FIG. 21. Mantle canals of *Discinisca* (12).

body wall. The ileoparietal band has more complex ramifications but essentially it extends between the lateral body walls and the stomach, along which it may persist for some distance posterior to the gastroparietal band. In addition to affording support to the posterior ends of the excretory organs, it carries some or all of the gonads (Fig. 17, 19).

MANTLE CANALS

The mantle canals are long tubular extensions of the body cavity into the mantles. They are lined with ciliated coelomic epithelium and in the inarticulates at least a thin muscle layer underlies the epithelium on the side facing the mantle cavity.

In Recent inarticulates two main canals (*vascula lateralia*) enter each mantle from the body cavity. In *Discinisca*, two more main canals (*vascula media*) occur in the dorsal mantle. The principal canals of the lingulids and discinids open into the body cavity through muscular valves and branch repeatedly to produce a large number of minor canals which end blindly and are distributed throughout most of the mantles (Fig. 20; 21). In *Crania*, each principal canal gives rise to a small number of second- or exceptionally third-order branches and further differs from its counterpart in other living inarticulates not only in the absence of a muscular valve at its junction with the body cavity but also in containing part of the gonads (Fig. 22).

FIG. 22. Mantle canals of *Crania* (12).

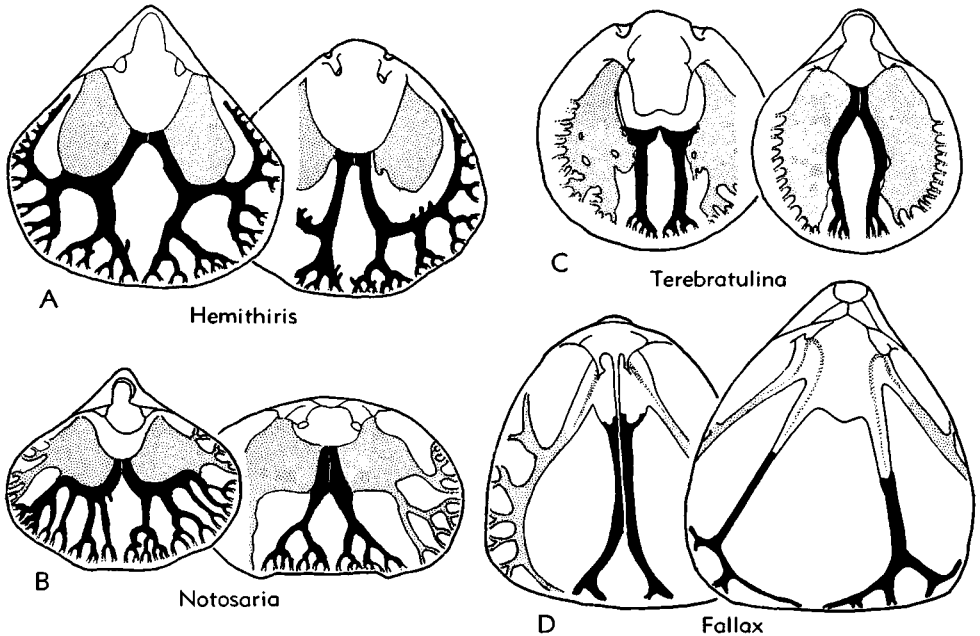


FIG. 23. Mantle canal systems of Recent rhynchonellids (A, B) and terebratulids (C, D); *vascula media* black, *vascula genitalia* and gonadal sacs stippled, A-C (44), D (6).

In Recent Rhynchonellida and Terebratulida, two pairs of principal canals occur in each mantle (44), but the patterns become complicated because some, but not all, invariably act as repositories for part of the gonads (Fig. 23). In the rhynchonellaceans, for example, each mantle contains a pair of submedian canals (*vascula media*) curving posterolaterally and branching repeatedly toward the mantle edge. In *Hemithiris* the *vascula media* are flanked by a pair of short broad canals (*vascula genitalia*) which are unbranched saclike extensions of the body cavity containing the gonads (Fig. 23,A). In *Notosaria* the pattern is identical except that the *vascula genitalia*, although still saclike proximally, branch repeatedly toward the mantle margin, and the *vascula media* are correspondingly abbreviated (Fig. 23,B). In all known terebratuloids the pattern is similar to that of *Notosaria* in that the *vascula genitalia* are branched and the *vascula media* restricted peripherally (Fig. 23,C); but in some genera, like *Macandrevia*, *Pumilus*, *Fallax* (Fig. 23,D), and *Magellania* gonads are also found in the *vascula media*.

The ciliated epithelium lining the canals is responsible for the circulation of coelomic fluid. In the lingulids, this is regular and controlled in that the ciliary beat aided by a median ridge apparently separates an outgoing current from a return flow in each canal (Fig. 24). A similar epithelial ridge also located medianly on the canal wall adjacent to the shell is known in *Discinisca* and *Terebratalia*, where it may perform the same task.

The principal function of the mantle canals is respiratory and an unusual adaptation is seen in the lingulid *Glottidia* (30). In this genus, the peripheral minor canals in the anterior part of the shell bear a number of projections (Fig. 24). These small, thin-walled, tubular saclike extensions (gill ampullae) project into the mantle cavity, thereby increasing the surface area of the mantle canal system.

MUSCULATURE

The main muscle system of living brachiopods is responsible for the movement of the brachial valve relative to the pedicle valve

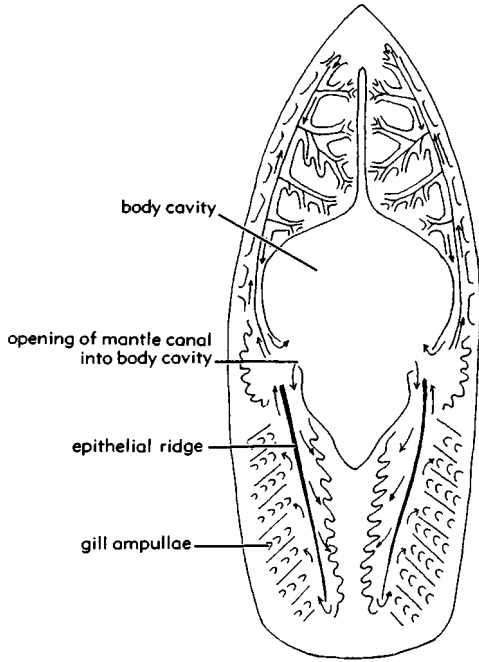


FIG. 24. Circulation in dorsal mantle canals of *Glotidia* (30).

and of the entire shell about the pedicle. The principal movement in both articulate and inarticulate shells is an opening and closing of the valves in the plane of bilateral symmetry. But the arrangement of muscle sets is fundamentally different in the two groups because the absence of a hinging device in the inarticulates permits rotation and even sliding of the valves in the plane of the commissure. The muscles are usually smooth (although the striated type is certainly known in the lophophore filaments and also the posterior adductors of some terebratuloids like *Pumilus*) and, within the body cavity, are encased in a thin sheath of coelomic epithelium. Where the muscles are attached to the shell the intervening outer epithelium becomes modified to a series of striated cells containing tonofibrils. Such areas of attachment are commonly seen on the inner surfaces of the valves as impressions (muscle scars) because of the significantly slower rate of secondary shell secretion by the modified epithelium.

In articulate brachiopods the muscle system responsible for the opening and closing

of the shell includes a set of adductors which pass from one valve to the other in front of the posterior margin and set of diductors which are typically inserted, at least in the brachial valve, posterior to the fulcrum (hinge axis) represented by articulating teeth and sockets (Fig. 25). The adductors arise from a pair of ventrally located scars placed postero-medially in the pedicle valve, but each bifurcates in its passage toward the

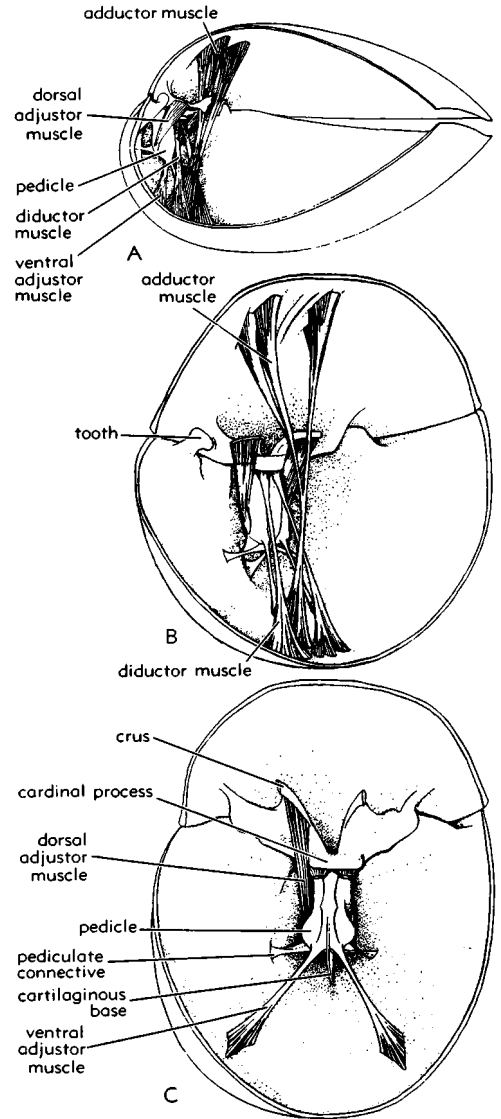


FIG. 25. Musculature of *Gryphus vitreus* (BORN), (A) lateral and (B) anterolateral views and (C) anterior view of pedicle with its musculature (20).

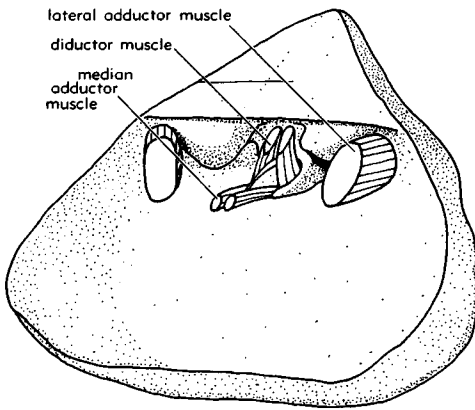


FIG. 26. Musculature of *Thecidellina*, brachial valve removed (47).

brachial valve so that four dorsal attachment scars are situated anteromedianly of the hinge region. In the thecideaceans a pair of adductors occupy the median position characteristic of other articulate brachiopods but do not divide dorsally; in addition, an extra pair of adductor muscles occupy posterolateral positions just in front of the hinge line and presumably prevent any lateral movements that might arise from an articulation which is sufficiently loose to allow the brachial valve to open at right angles to the canted pedicle valve (Fig. 26).

The diductor muscles are inserted immediately in front of the beak of the brachial valve, commonly in, or at the side of, a cardinal process, *i.e.*, posterior to the hinge axis of the shell. From this position they pass anteroventrally and splay out to occupy a pair of large attachment areas in the pedicle valve, commonly on either side of the adductor bases. The only exception to this relationship is found in certain terebratellaceans (e.g., *Platidia*) in which the dorsal umbo is resorbed to accommodate the pedicle (Fig. 27). In such shells the dorsal attachment areas are in front of the hinge axis and the ventral areas posterior, thus reversing the normal arrangement. A pair of slender accessory diductors are also usually present, passing from the cardinal process to become inserted on a small pair of attachment areas situated posteriorly to the ventral adductors.

The contrast between the sudden closure and gradual opening of a shell suggests that

the latter movement depends as much on the relaxation of the adductor muscles as on the contraction of the diductors. During a snap closure, the shell also rotates about, and moves backward along the pedicle, which thus seems to be shortened. This movement is brought about by contraction of the adjustors pulling the proximal end of the pedicle deep into the body cavity, but it is believed that, since the diductors are intimately associated with the connective tissue around the base of the pedicle, their contraction during the opening of the shell would assist in ejecting the pedicle, thus moving the shell forward to an erect position.

In addition to opening and closing the valves, rotation and sliding are possible in Recent inarticulates. The muscles that control these movements are necessarily more complex than those of the articulates. Basically they consist of two groups. The first group consists of two pairs of muscles that pass more or less directly dorsoventrally through the body cavity. They are usually the largest sets in the animal, and, although they are known under different names in different families, they are all concerned with the closure of the shell. The second group includes a variable number of oblique muscles controlling the rotational and longitudinal movements.

In *Lingula* the muscles responsible for the closure of the shell consist of a pair of central muscles near the middle of the valves and effectively an umbonal muscle, which is actually made up of two very unequal bundles of fibers (Fig. 28). The larger

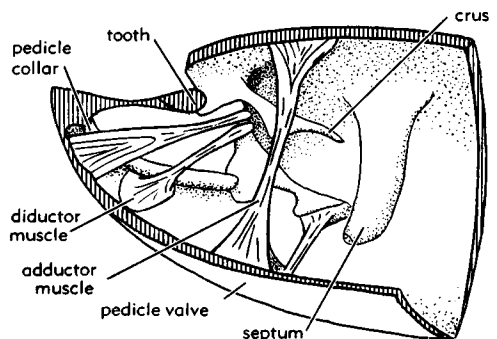


FIG. 27. Musculature of *Platidia annulata* ATKINS (48).

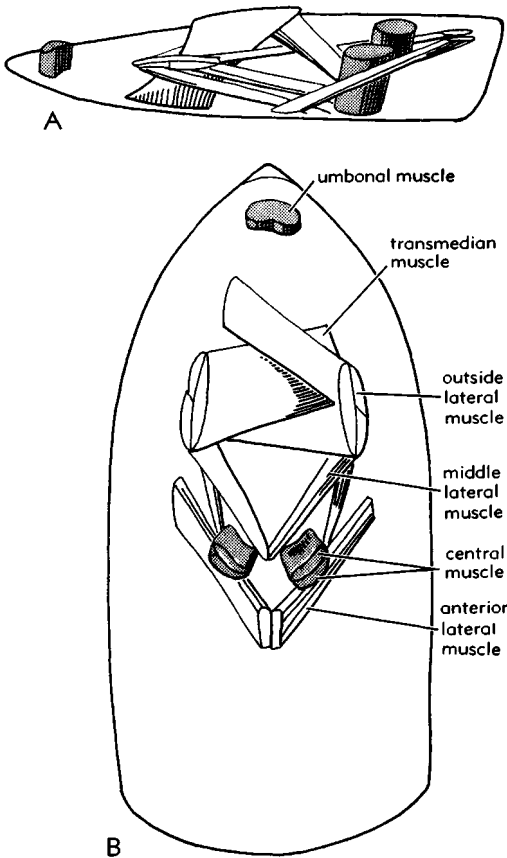


FIG. 28. Muscle system of *Lingula* viewed (A) laterally and (B) dorsally (14).

bundle of the umbonal muscle runs directly dorsoventrally; but the smaller, flat bundle which is inserted on the pedicle valve in front of the main bundle, spirals around the latter and is inserted on the brachial valve posterior to it (12). Both central muscles consist of a double bundle of fibers passing directly dorsoventrally. Four pairs of oblique muscles are present, three of which, the middle laterals, outside laterals, and transmedians, form a composite scar in the brachial valve. The middle laterals arise between the central muscles in the pedicle valve and pass obliquely backward to be inserted on the brachial valve, immediately in front of the scar of the outside laterals. These outside lateral muscles converge slightly anteriorly from the brachial valve and are inserted on the pedicle valve lateral of the centrals. The third pair of muscles,

the transmedians, are the largest of the oblique muscles and form the inner part of the composite scars. The right transmedian muscle runs ventrally from the brachial valve to become attached on the left side of the pedicle valve. The left transmedian splits just below its insertion on the brachial valve, and the two branches cross over the right transmedian to become fixed to the right side of the pedicle valve. This is the usual condition of the transmedians, but the left transmedian of a few brachiopods may be undivided (14). The fourth pair of muscles, with an oblique course, are the anterior laterals. These are inserted on the pedicle valve posterolateral of the outside lateral muscles and rise anteriorly to become attached to both the brachial valve and the anterior body wall near the mid-line of the valve.

The muscle system of *Glottidia* is basically similar to that of *Lingula* (30), but those of other Recent genera are somewhat simpler, since they have fewer oblique muscles.

In the discinids (Fig. 29, *1a,b*), two pairs of adductor muscles, a small posterior pair and a large anterior pair, run directly dorsoventrally between the valves. Each anterior adductor consists of a small median and a much larger lateral bundle of muscle fibers. Three pairs of oblique muscles occur, all of them relatively long and thin in comparison with adductors. The internal obliques arise from near the center of the pedicle valve and diverge posteriorly so as to become inserted on the brachial valve slightly anterolateral of the attachment of the posterior adductors. The oblique lateral muscles originate on the pedicle valve anterolaterally of the posterior adductors, near the side wall of the body, and run forward to be inserted on both the brachial valve and the anterior body wall close beside the main bundle of the anterior adductors. The third pair of oblique muscles, the posterior obliques, arise on the pedicle valve, slightly in front and median of the site of attachment of the oblique laterals. They pass dorsally and converge posteriorly, becoming inserted on the brachial valve close together near the mid-line, slightly in front of the posterior margin.

The principal muscles of *Crania* are similar to those of *Discinisca*, but rather simpler.

Two pairs of adductors occur, the anterior set consisting of two bundles of fibers. The oblique internals occupy a similar position to those of the discinids but follow a more S-shaped course. The oblique laterals originate on the pedicle valve at the side of the posterior adductors and are attached not to the brachial valve but to the anterior body wall (Fig. 29,2a,b).

The correlation of the muscles of the lingulids, discinids, and craniids is based on form, assumed function, and more fundamentally on their innervation (12). The posterior and anterior adductors of the craniids and discinids are considered to be the homologues of the lingulid umbonal and central muscles, respectively. The transmedian, outside, and middle lateral oblique muscles of the lingulids, which are attached only to the shell, may be correlated with discinid oblique posterior and oblique internal muscles and with the oblique internals of *Crania*, all of which are similarly attached.

The opening of the valve of all of these genera is thought to be effected by contraction of the posterior adductors or umbonal muscle and relaxation of the anterior adductors or their homologues. The action is probably assisted and partly controlled by the various oblique muscles and dermal muscles of the body wall.

LOPHOPHORE

The brachiopod feeding organ, the **lophophore**, which may also assist in respiration, is a filamentous appendage disposed symmetrically about the mouth and typically suspended from the anterior body wall, extending into the mantle cavity. The fully developed lophophore is essentially a variably disposed tube bearing a pair of ridges along its length bordering the brachial (or food) groove. The frontal ridge forms a flap, the brachial lip (or fold), which is actually a lateral extension of the preoral lobe in front of the slitlike mouth; the other (abfrontal ridge), forms a broad base to the filaments (Fig. 30). The entire surface of the lophophore consists of inner epithelium, with tall, slender, selectively ciliated cells and ciliated columnar cells forming the epidermis of the filaments and the lopho-

phore, respectively. Mucus-gland cells are usually more abundantly interspersed within the epithelium of the lophophore, but in *Lingula* at least, they are also arranged in definite longitudinal rows along the filaments (15).

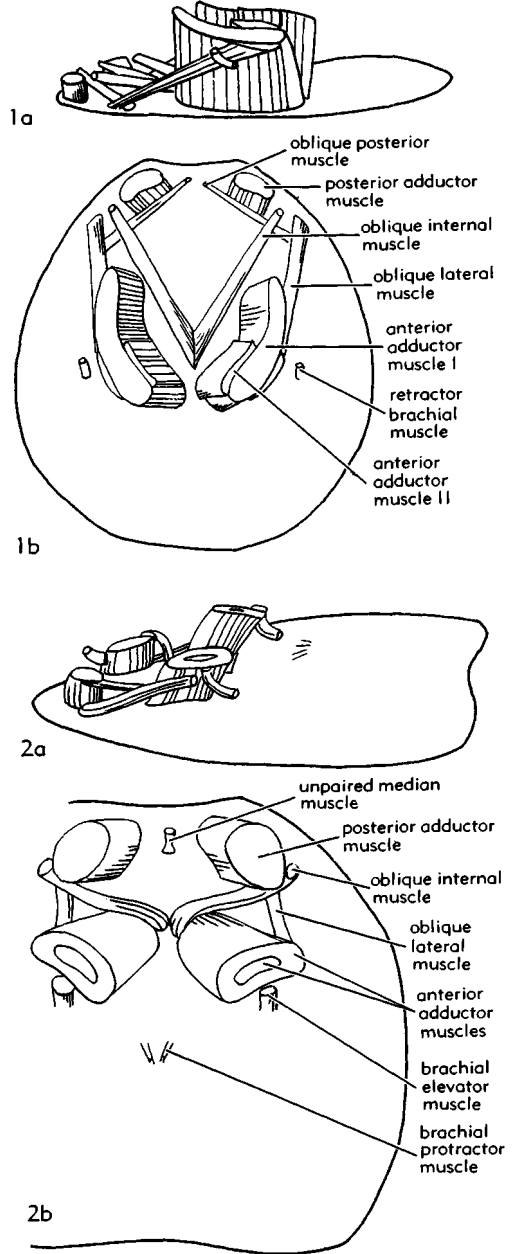


FIG. 29. Muscle systems of (1a,b) *Discinisca* viewed laterally and dorsally (14), and (2a,b) *Crania* viewed laterally and dorsally (14).

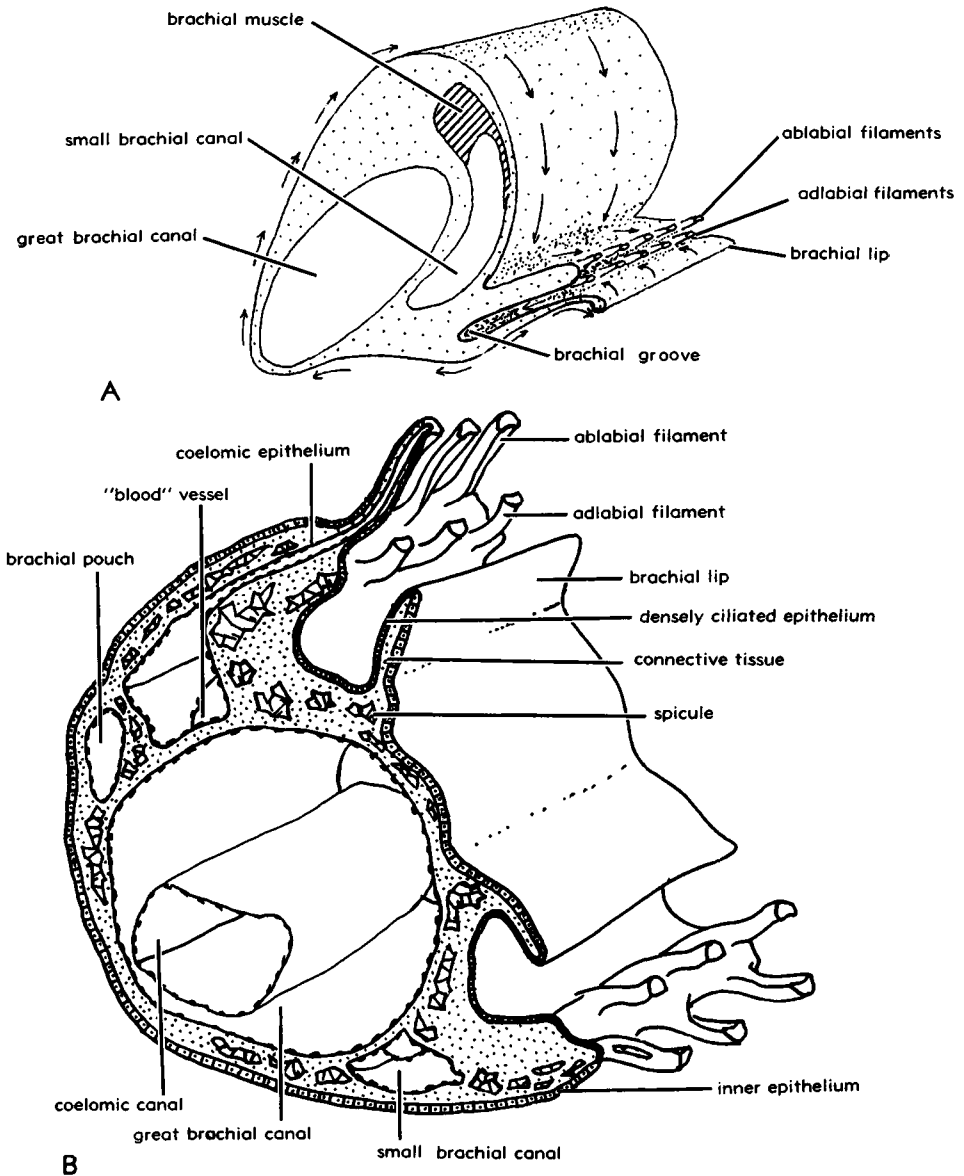


FIG. 30. Diagrammatic sections of (A) brachium of *Lingula* with arrows showing direction of ciliary beat (15), and (B) side arm of *Terebratulina* (48).

Two liquid-filled canal systems, lined by coelomic epithelium and embedded in a firm collagenous connective tissue, occupy the axes of the lophophore and the filamentous base. The former, the **great brachial canal**, is closed off from the body cavity, at least during the life of the adult, and in inarticulates it is also divided into two separate cavities symmetrically disposed about the

mid-line. The latter, the **small brachial canal**, gives off a branch into each filament (filamentar canal) and except in some inarticulates (craniids, discinids), opens into the body cavity around the esophagus. Although this generalized pattern is typical of all living brachiopods, a number of minor complications characterize the inarticulates. Thus, in *Lingula* and to a lesser extent in

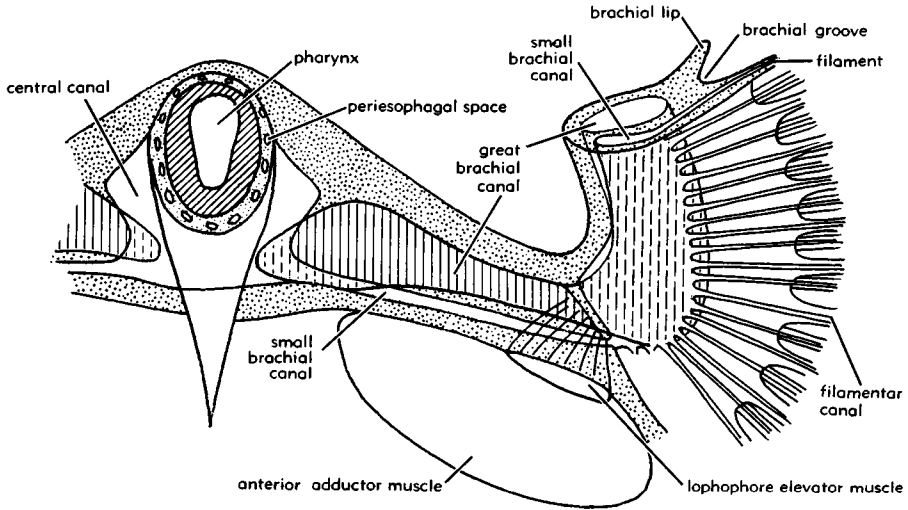


FIG. 31. Diagrammatic representation of canal systems in lophophore of *Crania* (12).

Discinisca, the proximal ends of the great brachial canals are divided into several lobes (12), and the course of the canals in the region of the esophagus is further complicated by infolding of narrow pouches of the main body cavity. Moreover, where the lophophore is attached to the anterior body wall of inarticulates, the small brachial canals contract abruptly (Fig. 31). They are then continued medially as narrow tubes, which in *Crania* and *Discinisca* open into a large median central canal developed in the supporting tissue of the lophophore, on the ventral side of the pharynx (Fig. 31, 32). In *Lingula*, although the two small brachial canals are connected medially, the central canal is poorly developed. In all inarticulate genera, the connective tissue surrounding the pharynx contains a number of small interconnected chambers, the **periesophageal spaces** which are in connection with the small brachial canals (Fig. 32) (12). In *Discinisca* and especially *Lingula* a further extension of the small brachial canal system is found in coelomic spaces of the **brachial lip**. Thus the small brachial canal system in inarticulates consists of interconnected elements which include the **filamentar canals**, small brachial canals, central canal, periesophageal spaces, and lacunae in the brachial lip.

No complications on this scale affect the cavity systems of the articulates. In tere-

bratellaceans like *Pumilus*, the small brachial canals arise laterally from pouchlike extensions of the main body cavity and although these have been called periesophageal sinuses (3), they are not infolded in the manner of the inarticulate periesophageal canals (Fig. 33). The body cavity is also prolonged as a pair of brachial pouches along the medianly facing surfaces of the terebratuloid side arms (Fig. 30). These pouches extend forward more or less to the same degree as the skeletal loop, so that they are only incipiently developed in the septate *Pumilus* but extend to the tip of the side arms of the long-looped *Macandrevia*.

The lophophore is apparently not capable of much extensible movement, even in the inarticulate brachiopods, which not only lack skeletal support for the organ but also have the best-developed musculature. Within the inarticulate lophophore, a pair of strongly developed brachial muscles arise from the connective tissue at the constricted proximal end of the small brachial canal and extend along the length of the canal in each brachium.

Some of the inarticulates have additional muscles attached to the lophophore, the apparent function of which is to control the position of the organ relative to the brachial valve and anterior body wall. Thus the discinids and craniids both possess a pair of small "brachial retractor muscles," which

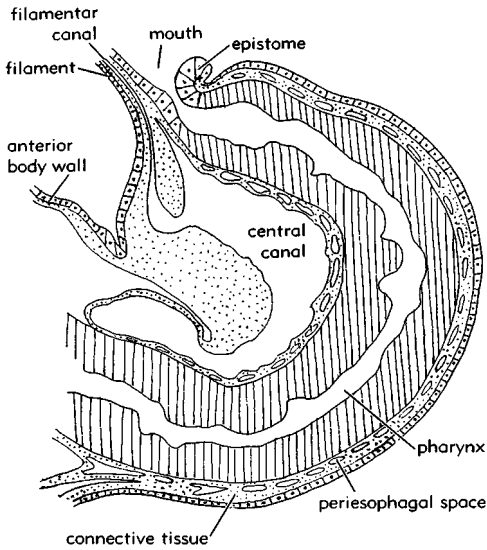


FIG. 32. Median section through lophophore and pharynx of *Crania* (12).

arise from the brachial valve lateral to the attachment of the anterior adductors. A further two pairs of muscles occur only in the craniids. A pair of stout brachial-elevator muscles inserted on the brachial valve anterolateral of the anterior adductors are attached at their other extremity to the connective tissue at the base of the brachial muscle. A pair of small brachial-protractor muscles placed anteromedially are also present (Fig. 29,2a,b).

In the supported lophophores of articulate brachiopods, the muscle fibers do not show the same degree of organization. They are

more numerous, however, in the spirally coiled free brachia (*spirolophe*) of the rynchonelloids than in lophophores associated with a complex skeletal support, which may be made even more rigid by the development of irregular plates of calcite (spicules) within the connective tissue (Fig. 6,A).

The filaments, which are responsible for activating water flow through the lophophoral apparatus and for diverting food particles into the brachial groove, whence they are conveyed to the mouth, are of two distinctive types in most adult brachiopods. On either side of the mouth are the first-formed filaments of the *trocholophe*, the ringlike lophophore that is attached to the anterior body wall and even part of the dorsal mantle of larvae and juvenile shells. The actual number of these filaments, which, except in lingulids and discinids, are arranged in a single row, varies at least from one genus to another according to the size of the fully developed trocholophe (45). Their frontal surface (facing the brachial lip) forms a broadly rounded ridge bearing cilia that beat with the length of the filament, in contrast to the two sets of longer lateral cilia that beat across the length of the filament from the frontal to the abfrontal surface. The abfrontal surface appears to be sparsely ciliated in all brachiopods, with exception of the lingulids, in which they are as densely distributed as on the frontal surface (Fig. 34).

In a minority of brachiopods like *Argyrotheca* and *Dyscolia*, this type of filament alone is also characteristic of adults. But with the transformation of the trocholophe

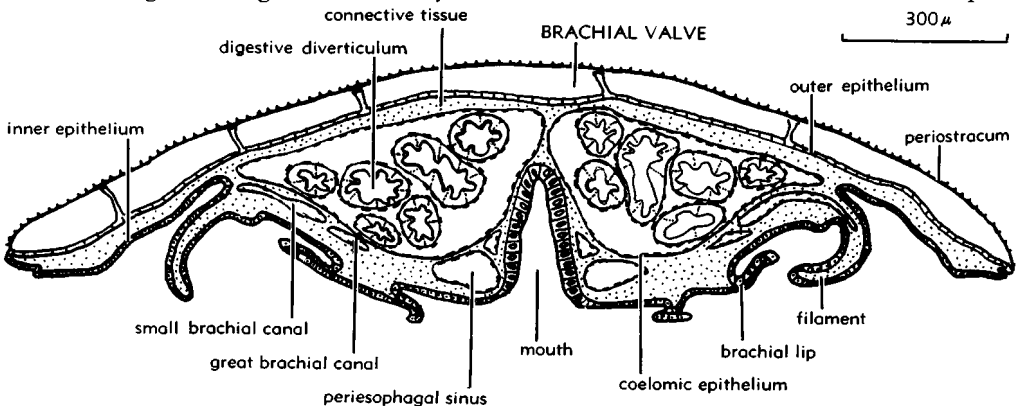


FIG. 33. Sections of brachial valve of *Pumilus antiquatus* ATKINS showing periesophageal sinuses (3).

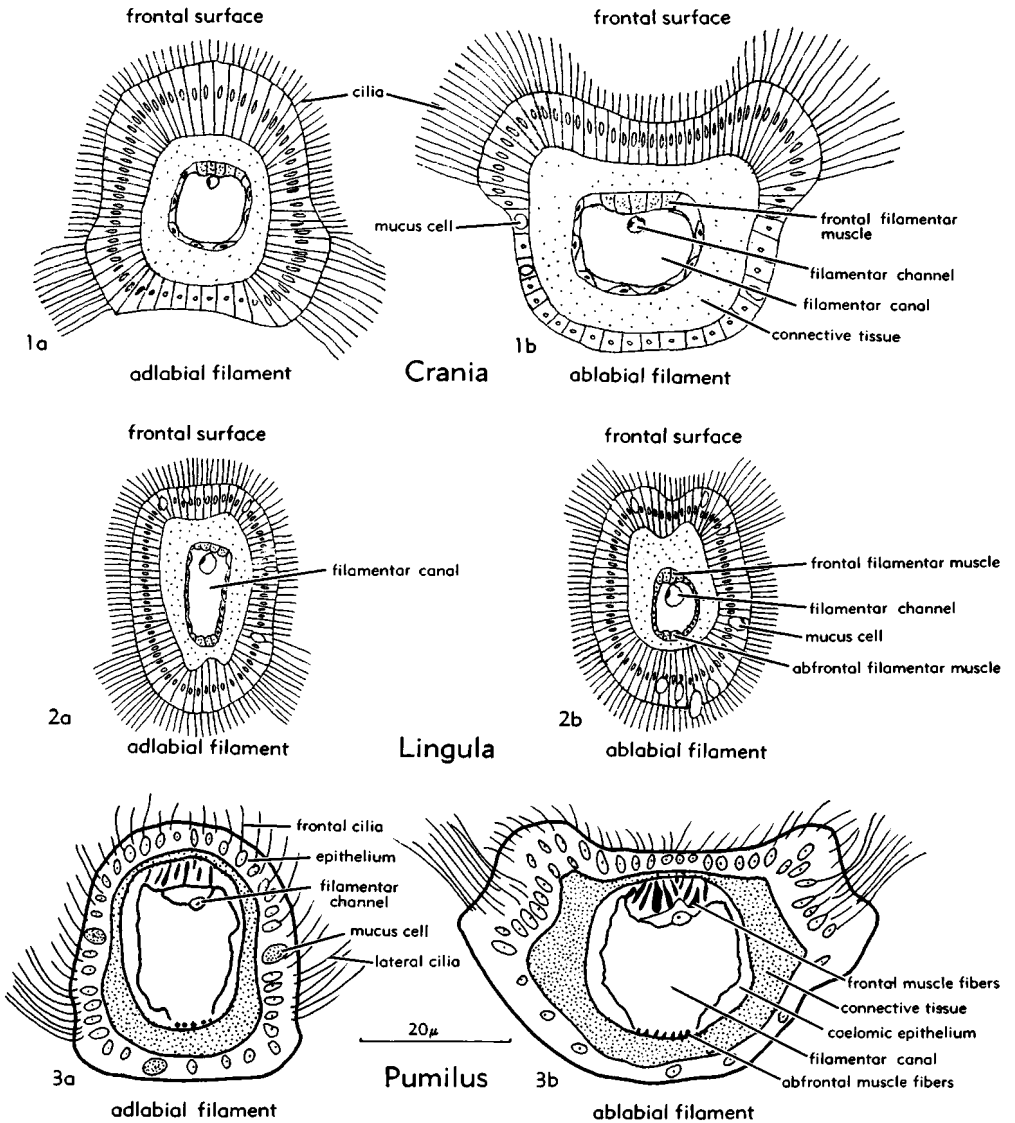


FIG. 34. Diagrammatic sections through adlabial and ablabial filaments of inarticulates (1a,b, *Crania*, 12; 2a,b, *Lingula*, 15) and a terebratellacean (3a,b, *Pumilus antiquatus* ATKINS, 3).

into the more complex attitudes found in most adult shells a second set of filaments appears and alternates with the ridged frontal types (adlabial filaments). Filaments of this second series (ablabial filaments) are longer and appear on the filamentous ridge at a greater distance from the brachial lip than those of the first series; and although they are ciliated in the manner of the ablabial filaments their frontal surface is a shallow groove (Fig. 34). In lingulids and

discinids all of the filaments are arranged in a double row; even those of the mouth segment are differentiated into ridged adlabial and grooved ablabial types and do not merely represent a post-larval crowding of trochlophous adlabial filaments.

The internal organization of both series is similar to a subepidermal layer of connective tissue and an inner layer of coelomic epithelium lining the filamentar canal. Throughout the length of the filament ex-

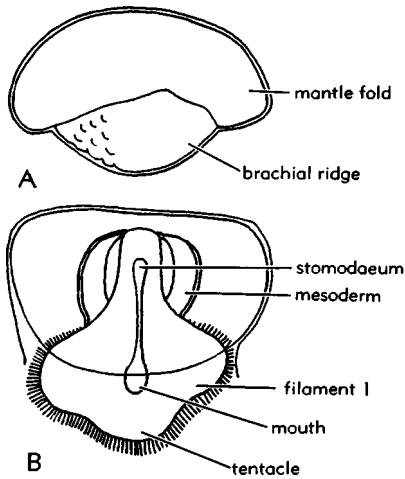


FIG. 35. *Lingula* embryo (A) with brachial ridge and mantle fold, and larva (B) with one pair of filaments (46).

tends the nerve lodged in the base of the epithelium of the frontal surface and frontal and abfrontal muscles within the coelomic epithelium; also a blood vessel (filament channel) occurs within the filamentar canal, commonly attached to the coelomic epithelium beneath the frontal surface (Fig. 34). All muscle fibers appear to be smooth in *Lingula*, but in *Crania*, *Notosaria*, and many terebratuloids, most if not all of the fibers in the more strongly developed group (concentrated beneath the frontal surface) are striated.

The disposition of the adult lophophore is so intimately related to its early growth that it is best described in relation to the development of that organ.

In all living inarticulates the lophophore is first differentiated in the free-swimming larval stage. Details of its earliest growth, however, are known only in *Lingula* although there is no reason why they should not be regarded as typical for the class (46). In *Lingula*, the lophophore develops from a moundlike, densely ciliated brachial ridge which initially is invaginated ventromedianly to form the rudimentary mouth (Fig. 35,A). The ridge then flattens ventrodorsally and assumes a triangular outline with the two posterior angles forming the first pair of rudimentary filaments and the anterior apex the earliest manifestation of the median tentacle (Fig. 35,B). The sec-

ond pair of filaments are added anteriorly on either side of the median tentacle. At the same time a part of the lophophore immediately posterior to the mouth becomes elevated ventrally so that the mouth is shifted to a central position, where it becomes flanked anteriorly by a transverse ridge, the preoral lobe or epistome. A third pair of filaments arises between the median tentacle and the second pair and proliferation of filaments continues from the generative zones on either side of the tentacle so that the lophophore assumes the form of a filamentous ring with the earliest filaments situated posteriorly (trocholophe). The trocholophous stage is known in craniids and discinids, as well as in the lingulids. At varying stages in the proliferation of filaments (four to five pairs in *Crania*, 15 pairs or more in *Lingula*) the median tentacle disappears and the two generative zones at the tips of a pair of brachia (or arms) gradually move apart to define a median indentation (schizolophous condition). At about this phase in growth of *Crania* the adlabial and ablabial filaments arise in alternating series. The preoral lobe is then undergoing lateral expansion concentric with the filament bases to form the juvenile brachial lip. Exceptionally, as in *Pelagodiscus*, the schizolophe is characteristic of the adult, but with further growth of the lophophore in other genera, the generative zones are pushed away as the apices of two ever-increasing spires (spirolophe) directed dorsally in the craniids, ventrally in the discinids, and medianly in the lingulids.

The best accounts of the origin of the lophophore in articulate brachiopods are those of PERCIVAL (35, 36) for *Notosaria nigricans* (SOWERBY) and *Terebratella inconspicua* (SOWERBY), but some inconsistencies appear, especially with regard to growth of the brachial lip, which, according to ATKINS (9), arise from misinterpretation of the development in the latter species.

As the larvae of *Notosaria* settle, the surface of the apical lobe becomes modified into a low central mound surrounded by a broad margin (Fig. 36,A). Two crescentic slits appear at the base of the mound (dorsal one first), and ultimately join as the central mound sinks from sight (Fig. 36,B,C). Concomitant with depression of the central

mound, the margin becomes broken by a gap on the dorsal side to form a horseshoe-shaped rim with two ends touching and with an outline becoming hexagonal as the

rudiments of the first three pairs of filaments become differentiated. The central mound now reappears as an azygous lobe which moves into the gap in the rim and

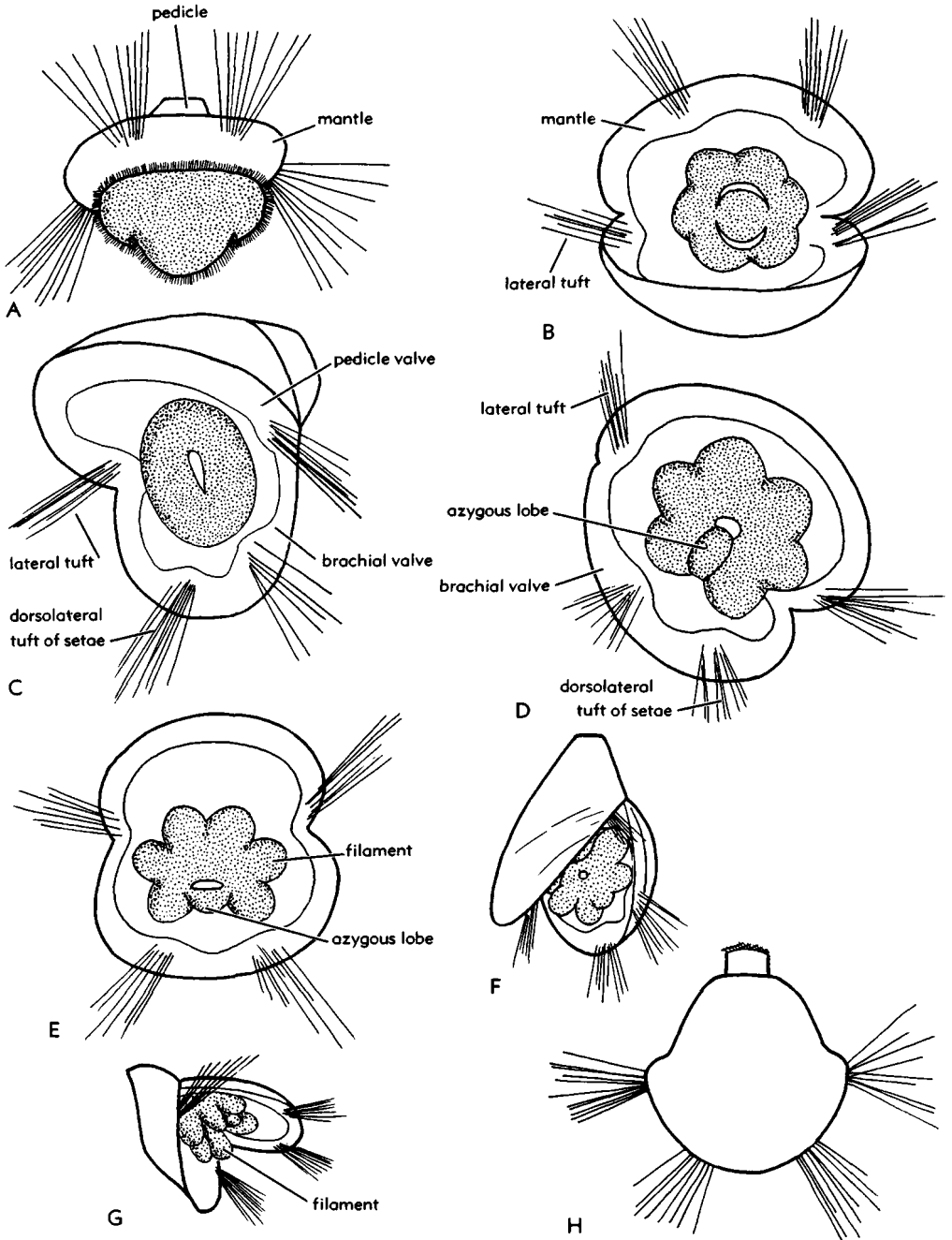


FIG. 36. A-H. Stages in development of lophophore of *Notosaria nigricans* (SOWERBY) showing differentiation and migration of azygous lobe (A-D), breakthrough of stomodaeum (C,D) and definition of filament rudiments (B, D, E-G); H, young adult viewed dorsally (36).

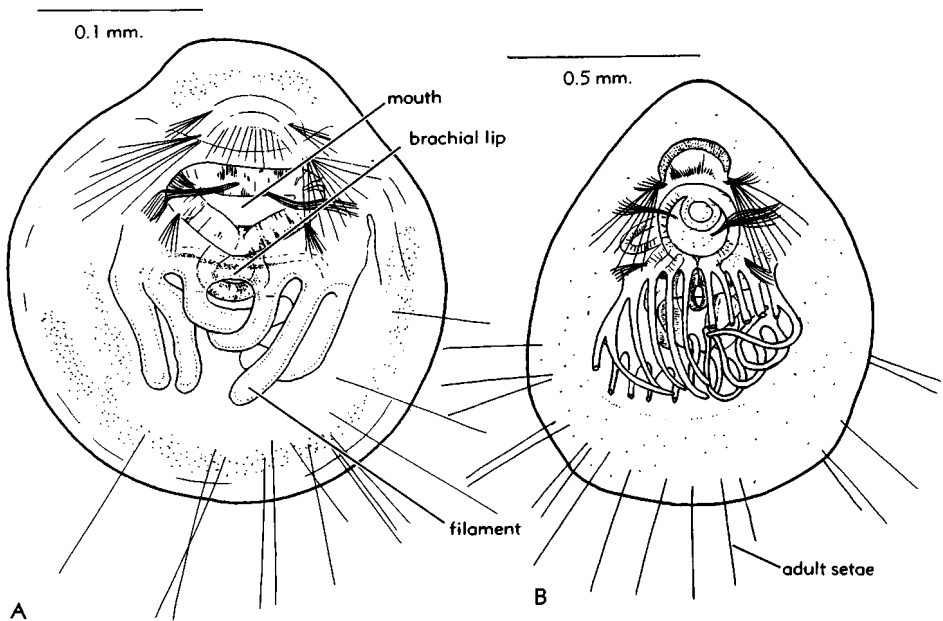


FIG. 37. Young adult of *Notosaria nigricans* (SOWERBY); A, with 6 filaments and brachial lip above mouth; B, with 10 pairs of filaments and well-developed brachial lip (36).

is the rudiment of the brachial lip (Fig. 36, D, E). The first-formed filaments continue to elongate and new ones are formed simultaneously at both ends of the arc on each side of the azygous lobe, which is modified into a thin hood projecting toward the middle of the oral field. When eight pairs of filaments have appeared, this brachial lip enlarges toward the filaments to form a crescentic flap concentric with their bases and partially covering the juvenile mouth (Fig. 37).

PERCIVAL's description (35) of the development of the lophophore of *Terebratella* differs from the process outlined above especially in formation of the brachial lip, which he claimed arises as a rapid posterior extension of the anterior border between the latest pair of filaments, when eight pairs have appeared (Fig. 38, A). ATKINS (9), however, maintained that the brachial lip of *Terebratella* and also of a number of terebratuloid (Fig. 39) and rhynchonelloid species, developed by anterolateral extension on either side of a small, preoral lobe in the manner of *Notosaria* (Fig. 38, B, C). Her material did not include early postlarval spats available to PERCIVAL, but her observations so endorse the differentiation of the

lophophore of *Notosaria* that this may be taken as the typical mode of development in articulate brachiopods. At this stage of development PERCIVAL also recorded that in *Terebratella* the rudiments of the first three pairs of filaments do not appear simultaneously, as in *Notosaria*, but in a definite order with the posterior pair arising first, followed by the lateral, then the anterior pair (Fig. 40). This suggests a migration of two generative zones, responsible for the proliferation of filaments toward a contiguous anteromedian position on the rudiment of the filamentous base. Whether PERCIVAL was mistaken in believing the lateral and anterior pair to be initially absent, as claimed by ATKINS, remains to be seen.

With the formation of about eight pairs of filaments the lophophore consists of a posteromedian mouth with a preoral brachial lip rapidly expanding anterolaterally, surrounded by a circular and expanding base bearing filaments that are being added in pairs from two contiguous generative zones situated anteromedianly in a position formerly occupied by the azygous lobe. This represents the **trocholophous stage** (Fig. 39). The lophophore base is attached to the dorsal mantle and anterior body wall and con-

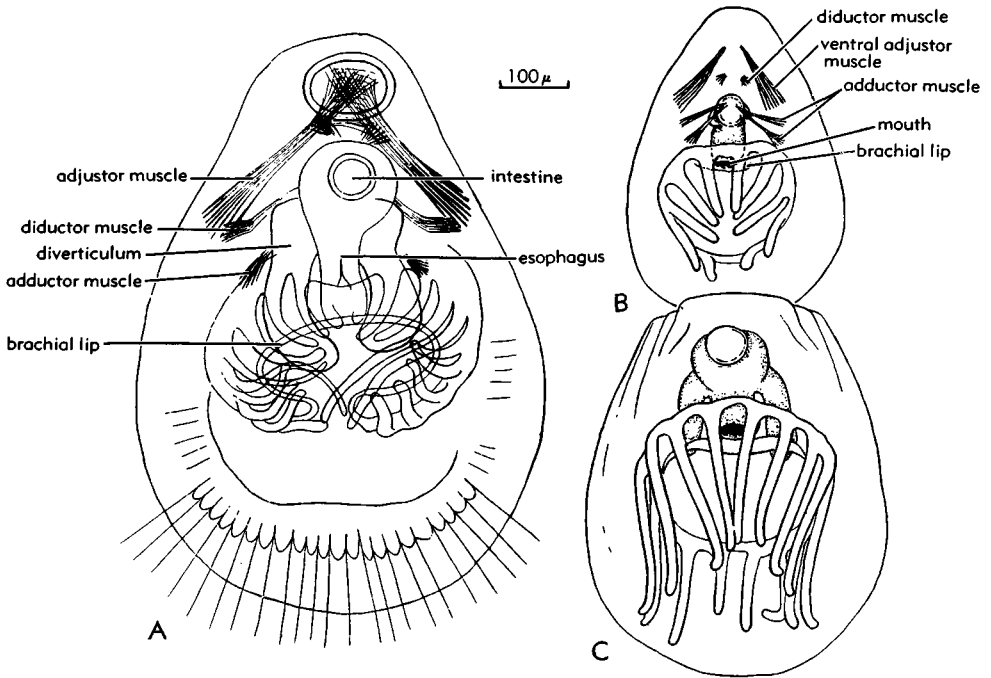


FIG. 38. Origin of brachial lip of *Terebratella inconspicua* (SOWERBY), (A) according to PERCIVAL (35) and (B, C) ATKINS (9).

tains only the small brachial canal, so that it is really the filamentar base. At this stage of development all filaments have ridged frontal surfaces and exceptionally, as in *Dyscolia* and probably *Gwynia*, the adult lophophore simply consists of an expanded

trocholophe equipped solely with adlabial filaments.

The lophophores of adult *Argyrotheca*, *Megathiris*, and *Thecidellina* also bear a single series of adlabial filaments, but they are folded into either two or four lobes,

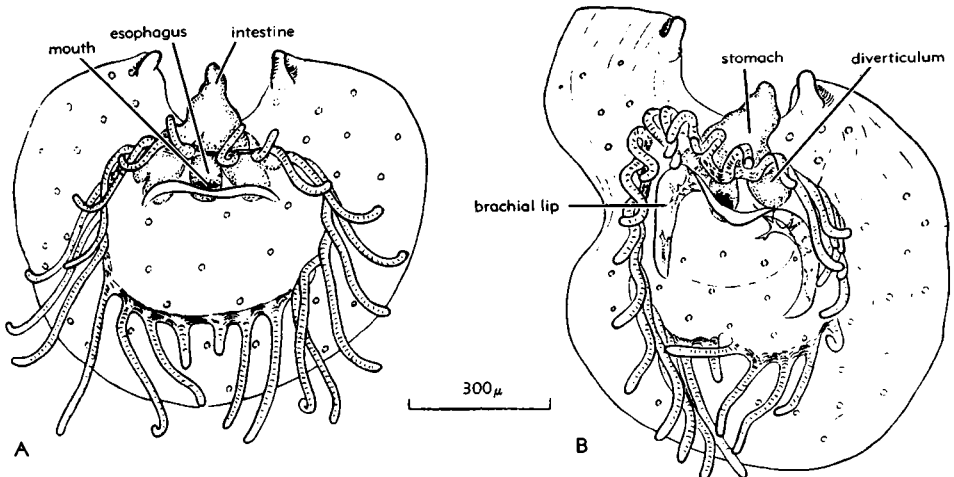


FIG. 39. Origin of brachial lip and disposition of trocholophe in *Platidia davidsoni* (DESLONGCHAMPS) (4).

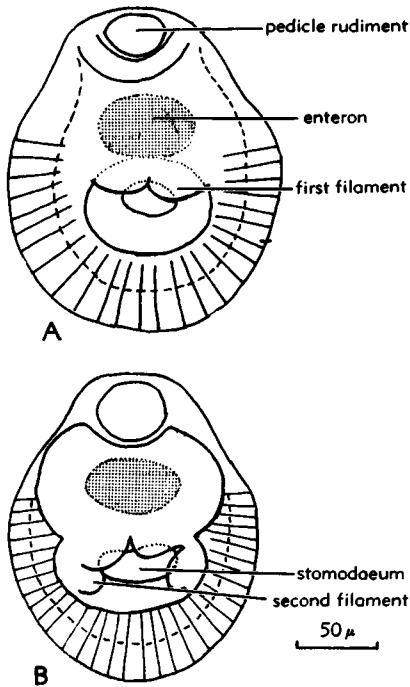


FIG. 40. Origin of filament rudiments during development of *Terebratella inconspicua* (SOWERBY) (35).

with the generative zone forming a continuous posterior tip across the median ridge. Despite some inconsistency in nomenclature, it seems better to refer to such structures as “bilobed” or “quadrilobed” trochophores in order to recognize their simple arrangement of filaments (Fig. 41, A, B; 42). For in most articulates as in the craniids, after the formation of a variable number of adlabial filaments, about eight pairs in *Terebratella inconspicua*, 18 pairs in *Platidia davidsoni* (DESLONGCHAMPS), an alternating series of ablabial filaments with grooved frontal surfaces is also proliferated. At the same time the generative zones may become separated by a median septum, as in the terebratellaceans, or directed posteriorly in such a way that the circular disposition of the trochophore is deformed by a median indentation. This is the **schizolophous stage** in which, as in the inarticulates, the lophophore is identified for the first time as consisting of a pair of brachia, each terminating in a medianly situated generative zone (Fig.

41, C). The schizolophe is characteristic of adult *Pumilus*. Both the trochophore and schizolophe are disposed more or less in the same plane and further lengthening of the brachia can continue only if subsidiary indentations of schizolophe take place (**ptycholophous stage**). Alternatively, the generative

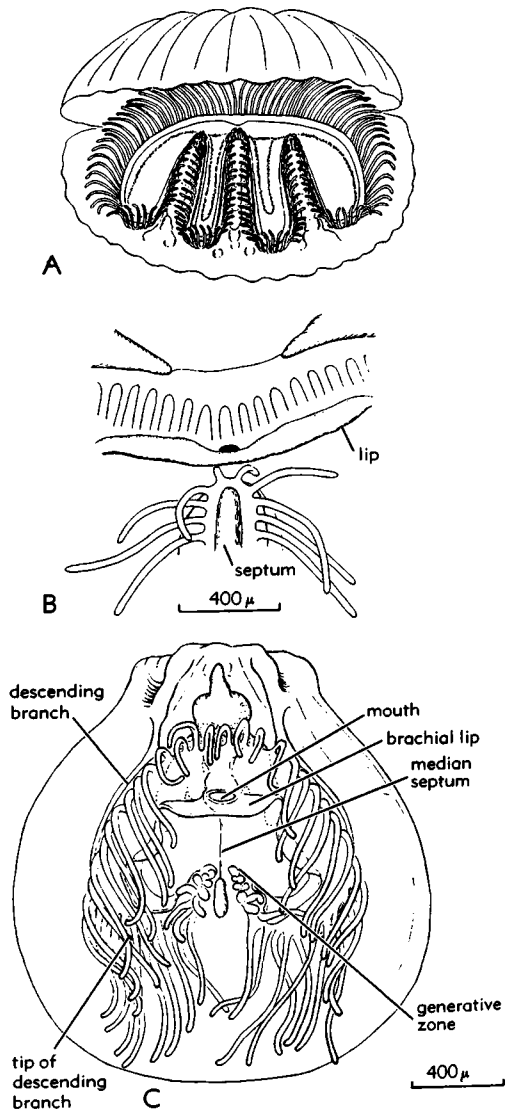


FIG. 41. A. Quadrilobed trochophore of *Megathiris detruncata* (GMELIN) (7).—B. Details of generative tip of *Agyrotheca cordata* (RISSE) (7).—C. Schizolophe of *Macandrevia cranium* (MÜLLER) (5).

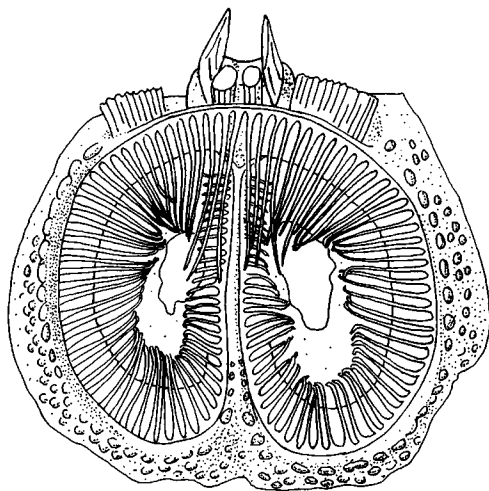


FIG. 42. Bilobed trochlophore of *Thecidellina* (47).

zones may move spirally away from their median position to form the dorsally directed spirolophes of the rhynchonelloids (Fig. 43,2a,b). In contrast, the generative zones of the terebratuloid lophophore remain in median position and increase in length of the brachia is initially accommodated by development of a pair of long loops (side arms) equivalent to the proximal whorls of the spirolophore but rotated to lie more or less parallel with the plane of shell symmetry (Fig. 43,1a,b). This is the **zygolphous stage** and is usually precursory to the ultimate **plectolophous stage**, so characteristic of most terebratuloids, in which the terminal portions of the brachia also move away from the anterior body wall by coiling in the median plane (Fig. 44).

NERVOUS SYSTEM

A central nervous system is present in all brachiopods. Among the articulates it is only well known in *Gryphus* (Fig. 45) although its ramifications are probably typical of the class. The system consists of a smaller, transverse supraenteric ganglion and a larger subenteric ganglion, lying respectively above and below the esophagus near its junction with the anterior body wall. The ganglia are joined by one or more circumenteric connectives. The subenteric ganglion and the connectives are responsible for the innervation of the lophophore, the

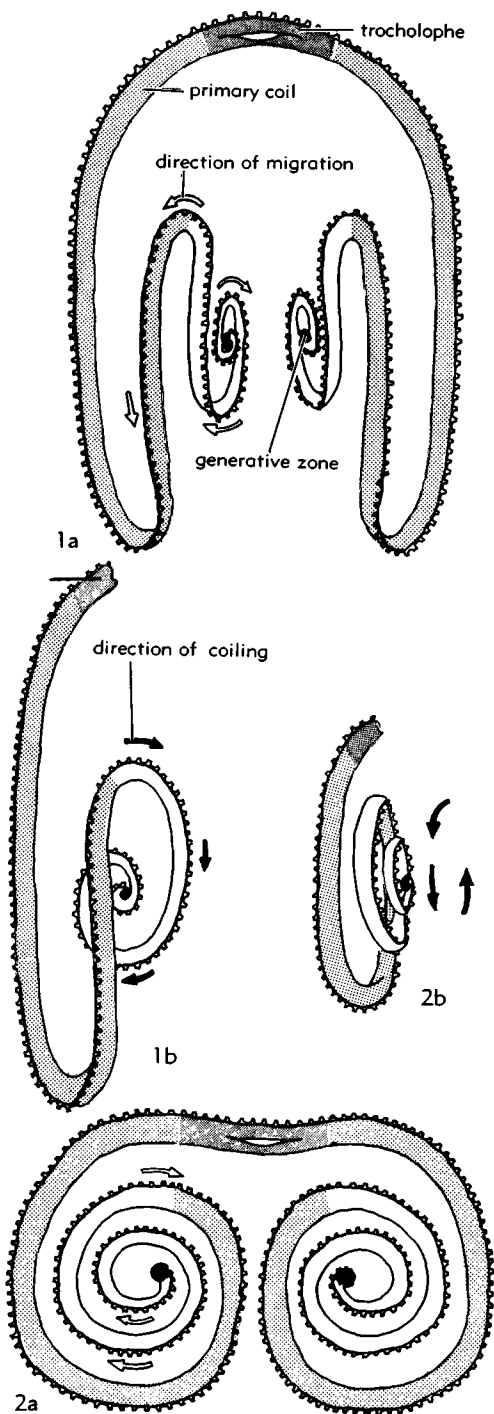


FIG. 43. Stylized ventral and lateral views of (1a,b) terebratulid plectolophe and (2a,b) rhynchonellid spirolophore, showing positions of original trochlophores, primary coils, and generative zones (45).

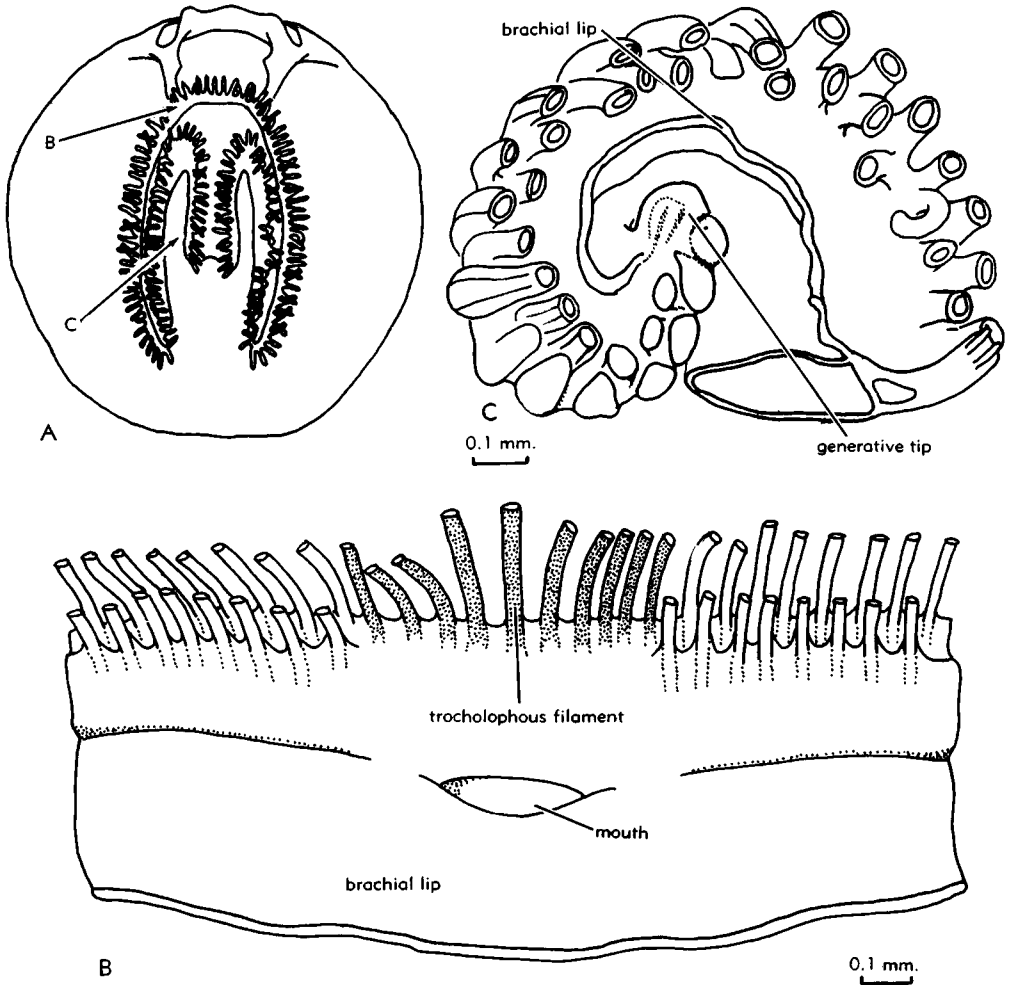


FIG. 44. Plectolophus of *Terebratulina* (A), with enlargements showing arrangement of trochophorous filaments behind mouth (B) and one of median generative zones (C) (45).

former giving rise laterally to a pair of nerves that activate the brachial lip and the latter forming branches (accessory and lower brachial nerves) that serve the brachia and filaments. A pair of main lateral and a number of ancillary branches arise from the subenteric ganglion to innervate the dorsal mantle lobe. The ventral mantle lobe, the adductor muscles, and the pedicle are served by a pair of thick, subparallel branches passing posteriorly from the same ganglion.

The nervous system of inarticulate brachiopods differs importantly from that of the articulates in the absence of a supraenteric

ganglion and also possibly in its location in the base of the epithelium, rather than in the connective tissue.

The principal nervous mass is the subenteric ganglion, which in the lingulids and *Discinisca* is medially placed, beneath the esophagus, in the epidermis of the anterior body wall. Two principal nerve trunks diverge laterally from the ganglion and give rise to the circumenteric connectives which pass in front of the esophagus to complete the circumenteric ring. In *Crania*, the subenteric ganglion is divided into two parts which occur in the epidermis of the lateral body wall, lateral to the anterior adductor

muscles; circumenteric connectives complete the circumenteric ring (Fig. 46-48).

The main brachial nerves for the lophophore branch laterally from the circumenteric connectives. They are developed in the epithelium near the base of the brachial lip and give rise to the filamentar nerves.

The nerves associated with the ventral and dorsal mantle arise from the subenteric ganglion and split into numerous fine branches. In *Discinisca* and *Lingula* the branches of the mantle nerves are joined at their distal end to form ventral and dorsal marginal mantle nerves. These are ring-like nerves following the periphery of the mantle and are found on the inner side of the follicles. In *Crania* both follicles and marginal nerves are absent.

The pedicle in *Discinisca* and *Lingula* is provided with a pair of nerves which branch from the subenteric ganglion or from ring-shaped lateral nerves located in the body wall. The course of the nerves to the various muscles is seen in diagrams (Fig. 46-48).

A nervous plexus in the base of the epithelium lining the alimentary canal has been detected by BLOCHMANN (12).

No special sensory cells have been observed in adult brachiopods. Statocysts containing small statoliths are present in larval *Lingula* and *Discinisca* and also in the juvenile forms after settling (46). They may persist in adult lingulids because MORSE (30) has recorded their presence in two species of *Lingula*, although it is noteworthy that he did not find them in *Glottidia*, and BLOCHMANN (12) was unable to confirm their existence in *Lingula*.

CIRCULATORY SYSTEM

An open circulatory system containing a coagulable colorless fluid free of cells is variably developed in all living brachiopods. It is imperfectly known, especially in the articulates, although throughout the phylum it appears to conform to a basic pattern best known in *Lingula* and *Crania*. Essentially the system is served by one or more contractile appendages ("heart") of a main mid-dorsal channel, which is supported by the dorsal mesentery in the vicinity of the stomach. The heart of *Lingula* and probably of other brachiopods is crudely differ-

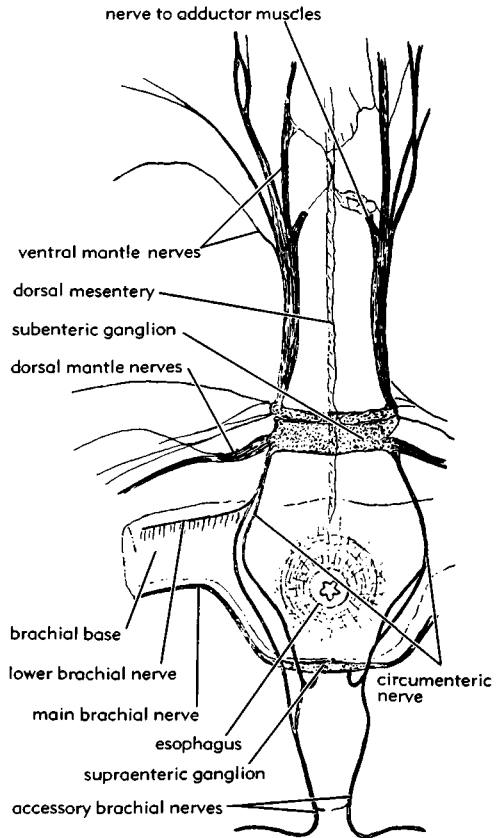


FIG. 45. Nervous system of *Gryphus vitreus* (BORN) (11).

entiated as a chamber with an outer layer of coelomic epithelium underlain by a thick layer of circularly disposed muscle fibers but without an inner endothelial lining. The main channel is similarly constructed, except that the muscle fibers are helicoidal, but all branches consist solely of continuous channels within the connective tissue.

The course of the principal channels is basically alike in *Crania* and *Lingula*, although in the former genus several contractile sacs fulfill the function of one, or rarely, more appendages in *Lingula* (Fig. 19). In front of the heart the main dorsal channel runs forward dorsal of the esophagus and bifurcates to serve each brachium of the lophophore. Inside the lophophore, the branch runs ventrally and laterally in the central canals to the entrance of the brachial canal. At this point another branch arises and runs medianly in the ventral part

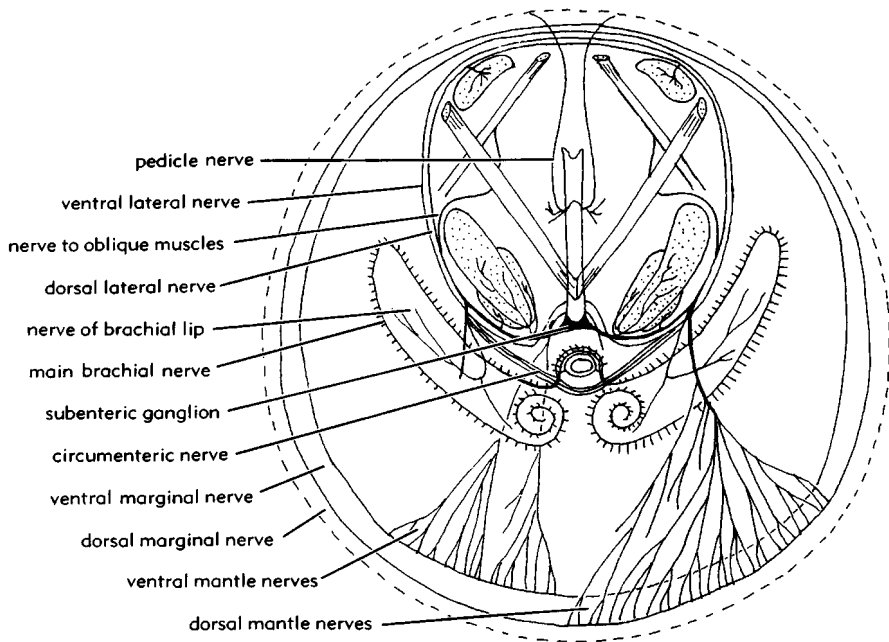


FIG. 46. Diagram of nervous system of *Disciniscia* (mantle nerves only shown anteriorly) (12).

of the central canal to connect with the corresponding branch in the other brachium. In this way the circulatory system of both brachia is joined by a connective blood channel ventral of the esophagus. The main branch in each brachium continues along the length of the small brachial canal. The lophophore circulatory system terminates as blind filamentar channels arising from the small brachial or ventral connective channels (12).

Behind the heart, the main dorsal channel splits into a left and right branch, each of which runs ventrally for a short distance before bifurcating into anterior and posterior branches; these two pairs of branches form the dorsal and ventral mantle channels, respectively. The two dorsal mantle channels pass to the anterior body wall along the outer surface of the alimentary canal, on either side of the mid-line. They are then inserted into the dorsal mantle canal and send a branch, which ends blindly in each branch of the mantle canal system.

The ventral mantle channels follow a more complex course before they reach the ventral mantle canals. The course of these channels is different in *Crania* and *Lingula*,

but in both genera, they, or their branches, supply the ileoparietal bands and associated gonads and form a network of small channels in this region. Both channels then run anteriorly along their respective nephridia and at the front turn laterally to be inserted in the ventral mantle canals, sending branches into the ramifications of the mantle canal system.

Disciniscia is apparently aberrant in the very poor development of its circulatory system (12). The channels in the lophophore are developed normally and are like those

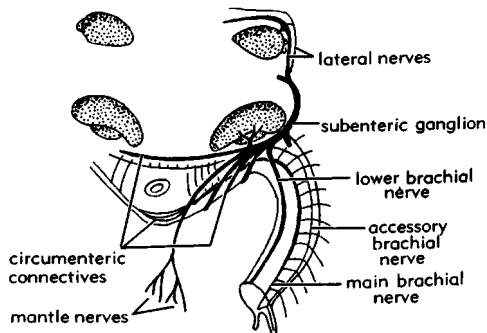


FIG. 47. Diagram of nervous system of *Crania* (mantle nerves only shown anteriorly) (12).

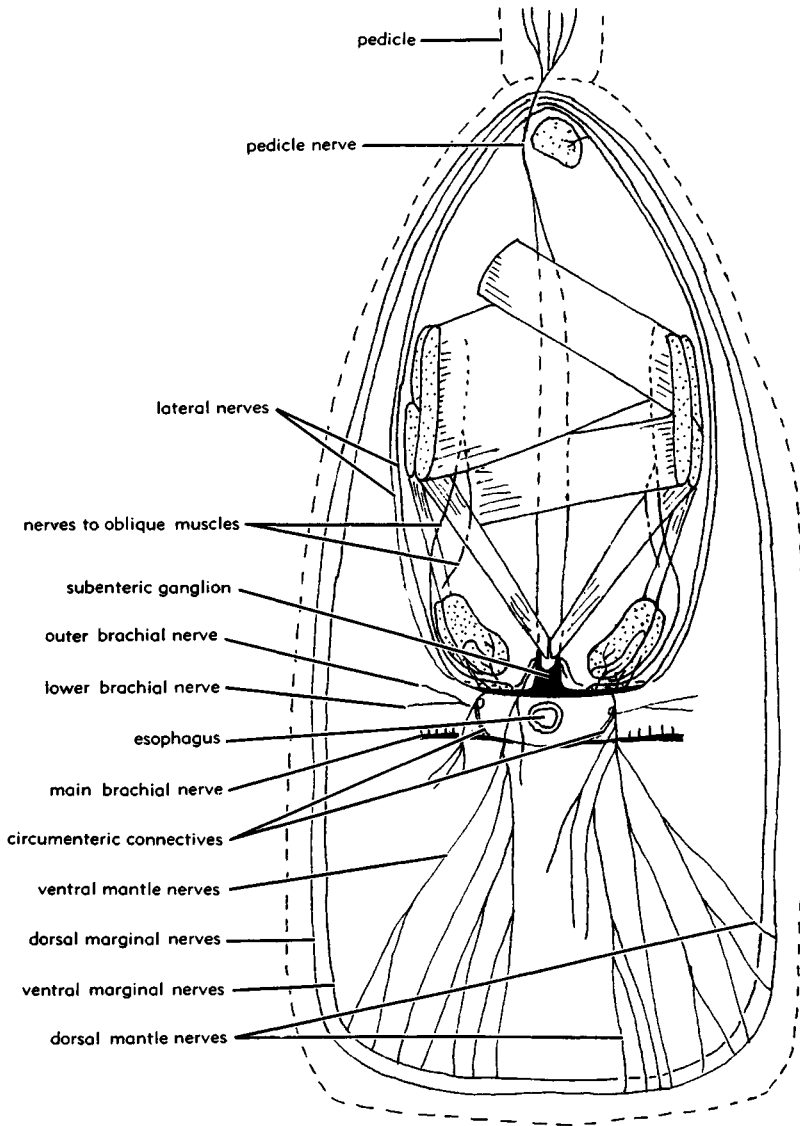


FIG. 48. Diagram of nervous system of *Lingula* (mantle nerves only shown anteriorly) (12).

in *Crania* and *Lingula*, but the remainder of the system appears to be absent.

REPRODUCTIVE SYSTEM

Most brachiopods are apparently dioecious, although some species of *Argyrotheca*, *Pumilus*, and *Platidia* are known to be hermaphroditic and it is also possible that an alternation occurs in the production of sex cells of *Fallax*. Sexual dimorphism is

known in *Lacazella*, but the sexes of other brachiopods are only distinguishable by color of the ripe gonads: the testes tend to be white or pale yellow and the ovaries deep yellow to red-brown.

The sex cells develop from folds of the coelomic epithelium, usually located in the body cavity of the inarticulates and mantle canals of the articulates. Two pairs of gonads are commonly present in all brachio-

Pods, but they show consistent differences in location and disposition.

Two pairs of gonads develop in the lingulids, confined to the ileoparietal band which ramifies and branches within them (40). The dorsal pair appears along the free edges of that part of the ileoparietal band running along the sides of the alimentary canal, while the ventral pair occurs on the section of the ileoparietal band supporting the nephridia. In the discinids, the gonads develop on the ileoparietal band but are also present on the free ventral edge of the gastroparietal band. The distribution of the gonads in the craniids, however, is like that of the articulate because, although gonads are found on the ileoparietal band, a conspicuous pair develops in the canals of both ventral and dorsal mantles; when ripe they completely fill the mantle canal systems (12).

The gonads of articulate brachiopods, like those of *Crania*, are mainly developed from the coelomic epithelium lining the inner sides of coelomic embayments and canals within the mantles. The organs may also extend into the body cavity, especially on the ventral side where they may reach posteriorly as far as the nephrostomes. In the rhynchonellaceans the gonads are contained in the *vascula genitalia* either as two pairs of sacs representing anterolateral extensions of the body cavity (e.g., *Hemithiris*) (Fig. 23,A), or as sacs that give off branching canals towards the mantle edges (e.g., *Notosaria*) (Fig. 23,B). Accommodation within greatly distended *vascula genitalia* are also characteristic of *Terebratulina* (Fig. 23,C), and *Megerlina*. But in the ventral mantles of *Macandrevia*, *Magellania*, *Fallax* (Fig. 23,D), etc., each gonad, which tends to be long and relatively thin, is doubled back upon itself to occupy the *vascula media*, as well as the *vascula genitalia*.

Two pairs of gonads are also found in *Pumilus* but are differently disposed within its limited canal system. The ventral pair develops within the *vascula media*, while the dorsal pair, which occurs mainly in the body cavity, extends anterolaterally into the short, saclike *vascula genitalia*. In contrast, only one pair of gonads develop in *Argyrotheca* and *Lacazella*, a dorsal pair in the former and a ventral pair in the latter.

BREEDING AND DEVELOPMENT

Information on the breeding season of brachiopods is still too scanty to permit any generalizations. The breeding habits of *Lingula* are best known, but even so, the data are inadequate to cover possible variations arising from its wide geographical distribution. In Japan, YATZU (46) concluded that *Lingula* spawns from mid-July to the end of August, with, according to more recent work, a peak in early August. *Lingula* off the south coast of Burma, however, spawns during December and February (42) while in the southern part of the Red Sea, ASHWORTH (2) found larvae whose stages of development indicated spawning in May and September, possibly as part of a continuous breeding season extending from early March to September. A detailed study of the breeding habits of *Lingula* from Singapore has been carried out by CHUANG (16), who presents very strong evidence for a succession of spawnings throughout the year. Larvae in growth stages with two or three pairs of lophophore filaments were taken during June to November inclusive as well as January and February; while some females in collections made during the remaining months had ripe ovaries. Breeding as continuous as this is probably due to the prevalence of optimum conditions, like constant sea temperatures, throughout the year.

Among other inarticulates the following information is noteworthy. PAINE (34) has recently published the results of a study on the larval and postlarval ecology of *Glottidia pyramidata*, in which he reports that in northern Florida breeding begins in the early spring at a water temperature of 20°C–22°C and lasts some nine months, whereas in southern Florida the evidence suggests that spawning occurs throughout most of the year. Larval *Pelagodiscus atlanticus* have been taken in the late summer or early autumn, suggesting a spawning during the summer months. There is also a shortage of information concerning the spawning season of *Crania*. ROWELL (38) considered that *Crania anomala* off the northwest coast of Scotland spawns in April and again in November, but that there was inadequate

information to decide whether there was a succession of spawnings in the summer. JOUBIN (23) found that the gonads in a Mediterranean species of this genus contained eggs in November but were most distended in May.

Among the articulate, it may be significant that in New Zealand, the only locality in the Southern Hemisphere for which reliable information is available, spawning takes place in the winter months. It is known to occur in *Notosaria* during May and June (36) and in *Terebratella* during April and May (35), and although it has not been observed in *Pumilus* the gonads of that genus are ripe in June and late May (3). In the Northern Hemisphere, however, the breeding season seems to vary greatly. *Terebratulina septentrionalis* from north-eastern United States certainly spawns during April to August inclusive, and MORSE (29) believed that this species breeds continuously throughout the year. Ripe gonads were found in *Platidia davidsoni* dredged off the coast of France during June and July (4). This condition suggests summer breeding in this species too, although ripe eggs have also been recorded in shells taken from the same area in February. The gonads of *Dallina septigera* collected from approximately the same area in November were ripe, as were those of *Gryphus vitreus* recovered from the Mediterranean in December (28). These two species, then, may possibly have a limited winter breeding season.

When ripe, the discharged sex cells leave the body cavity and the mantle canals to enter the mantle cavity through the nephridia, which in *Pumilus* are distensible and act as temporary stores (3). Only a minority of species brood the fertilized egg up to the free-swimming larval stage, either in the mantle cavity or even in specialized receptacles. The fertilized eggs of *Terebratella inconspicua* generally attach themselves, before final release, to the inner surfaces of the mantles (35). But in *Notosaria nigricans* (36) and *Liothyrella antarctica* (13) some of the lophophore filaments interweave to form a temporary brood basket. In *Lacazella* the fertilized eggs attach themselves to swollen portions near the ends of a pair of lophophore filaments that have been inserted into a median brood pouch occupying

a depression in the pedicle valves of females (27). Probably the most unusual specialization is found in *Argyrotheca* in which the nephridia become enlarged to act as brood pouches (41).

SPAWNING

Spawning has been observed only in *Lingula anatina* (46, 16), *Terebratulina septentrionalis* (29), and *Glottidia pyramidata* (34). In these species the eggs are ejected into the sea from the mantle cavity, through the median exhalant current and fertilization is external. If considerable numbers of eggs are released quickly, they are enveloped in mucus and form large clumps or sheets. Spawning is well known in *Lingula anatina* from Singapore (16), where the young females become capable of producing ova when they are a year to a year and a half old. They remain sexually mature throughout a considerable size range, for spawning has been observed in specimens with pedicle valve lengths varying between 14.3 and 46 mm. Any one individual does not release all of its ova during the initial burst of spawning, for the process extends over several months as subsidiary phases, separated by rest intervals. The number of ova shed is great; the maximum recorded for one female is 28,600 in 104 days, although the average for large adults is about two-thirds of this value. Individual females of *Glottidia pyramidata* likewise do not release all their eggs during the initial burst of spawning, for PAINE (34) considers that reproductive activity extends over a 3- or 4-month period. The number of ova released during a single burst of spawning varies greatly, but may be enormous, a maximum of 47,000 being recorded from one female. Seemingly the early and late phases of spawning are smaller, but PAINE (34) estimates that one female will shed in the order of 150,000 ova during her total spawning period. In contrast with *Lingula*, females commence spawning when 6 to 9 months old, but this early onset of sexual maturity is undoubtedly related to their much shorter life span.

Sexual maturity is not attained in *Terebratella* until individuals are more than one year old, and PERCIVAL (36) noted that both

sexes of *Notosaria* were capable of reproduction when they were between 9 and 20 mm. long and produced between 4,000 and 8,000 eggs in a season. Indeed, judging from various accounts, it seems likely that most brachiopods become sexually mature when they attain about one-third to one-half the size of an average adult.

DEVELOPMENT

The full development of the brachiopod from the fertilized egg is reliably known for *Lingula* (46), *Terebratella* (35), and *Notosaria* (36). Supplementary information is also available for the prelarval stages of *Terebratulina* (19), *Argyrotheca* (25, 26, 37), and *Lacazella* (27, 25, 26), and for the larval or early postlarval stages of *Glottidia*, *Discinisca*, *Pelagodiscus* (31, 32), and *Crania* (38). The scarcity of detailed records and the controversial nature of some that are available make it impossible to generalize on brachiopod ontogeny with certainty. Nonetheless, the fundamental differences between inarticulate and articulate brachiopods are nowhere better shown than in the contrasted development of representative species. Apart from the significantly greater duration of the free-swimming stage of the inarticulates, there are other, more important differences. Internally, the coelomic spaces of the inarticulates are said to be schizocoelic in that they arise by a hollowing-out of the mesoderm, whereas those of the articulates are enterocoelic, developing as pouches from the enteron. The articulate embryo is soon differentiated into an anterior lobe and rudiments of the pedicle and mantle, the latter subsequently undergoing reversal. In contrast, the inarticulate embryo consists simply of an apical brachial ridge and the mantle rudiment, which does not undergo reversal during growth; the pedicle arises much later as an evagination of the ventral mantle.

The development of *Lingula anatina* has been described in detail by YATSU (46), who reared early larvae to the stage where they possessed three pairs of lophophore filaments, and obtained later stages in plankton collections from Misaki Harbor. Some variation appears between YATSU's Japanese material and other scattered records of lar-

val *Lingula* as to the age, expressed in terms of the number of pairs of lophophore filaments, at which various structures and organs appear. The sequential pattern of development, however, is the same. YATSU found that after fertilization of the eggs a hollow blastula is formed by regular cleavage which at the 30- to 40-cell stage develops into a gastrula by invagination. The gastrula is subsequently flattened in an anterior-posterior direction and the external opening of the archenteron, the blastopore, is closed. A ringlike flap arises by outward growth of the ectoderm, which becomes partially divided into two by diametrically opposed depressions. This flap marks the first stage in development of the mantle. In front of the flap and partially covered by it is the brachial ridge from which the lophophore subsequently develops (Fig. 35, A). An invagination of the ventral median part of the brachial ridge gives rise to the stomodaeum, which soon communicates with the archenteron to form the larval alimentary canal. This phase coincides with the appearance of the first pair of rudimentary filaments on the brachial ridge, the subsequent growth of which has already been outlined in the section dealing with the lophophore. Shortly afterward the ringlike flap becomes completely divided into two mantles, which grow rapidly to assume a semicircular form and almost enclose the brachial ridge. The mantles now secrete a thin chitinous shell in one piece, folded across the posterior margin. Internally, the mesoderm, which has been proliferated by the endoderm, lies laterally to the alimentary canal. At this stage too, the young animal escapes by rupturing the egg membrane and becomes free-swimming, using the lophophore for propulsion (Fig. 35, B).

Subsequent development is most conveniently described in stages defined by the regular appearance of new lophophore filaments. Thus, by the time two pairs of filaments are present, the coelomic cavities have been hollowed out of the mesoderm and are developing as schizocoeloms. The anterior part of the mesoderm becomes mesenchymatous and migrates into the recently formed rudimentary lophophore canal system, which communicates with the body cavity.

At the stage defined by three pairs of

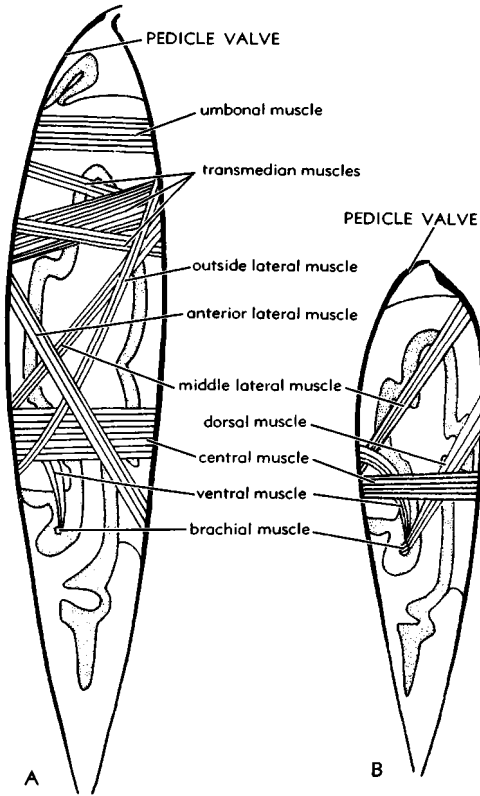


FIG. 49. Diagrammatic sections through *Lingula* larva showing muscle development (A) with eight pairs of filaments, (B) with five pairs of filaments (46).

filaments, the first pair of muscles appear, but they are characteristic only of the free-swimming stage, since they degenerate after the animal becomes attached. These ventral muscles arise from the ventral mantle and pass forward from the posterior end of the esophagus to the brachial canal at about the level of the mouth (Fig. 49,B). At this stage too, the filamentar muscles and the filamentar canals are present, the latter being diverticula of the lophophore canal system.

With the appearance of the fourth pair of filaments, the alimentary canal begins to differentiate into its adult components. The posterior dorsal digestive diverticula and intestine first appear together with the small ciliated mid-gut and by the time the ninth pair of filaments have arisen, the animal has a functional anus and rudiments of all the digestive diverticula.

The nephridia first appear as a pair of cell strands at the five-pair-filament stage. At the same time, the first adult muscles, the centrals and middle laterals, are formed along with another pair of larval muscles, which are located dorsally and degenerate before two more pairs of filaments are added. The remainder of the adult muscles develop before the ninth pair of filaments are added to the lophophore (Fig. 49,A), by which time the nephridia are already conspicuous (Fig. 50). Meanwhile, the mantle canals have developed as prolongations of the body cavity into the mantle when the lophophore possessed eight pairs of filaments.

The pedicle was first seen by YATSU at the six-pair-filament stage. It arises from the posterior end of the ventral mantle as a hollow hemispherical projection of the inner epithelium communicating through a narrow lumen with the body cavity. By the nine-pair-filament stage it has increased in length and is twisted but still totally enclosed by both valves. The pedicle of specimens examined by ASHWORTH (2) originated in the same way, but the organ did not appear until 11 pairs of filaments had developed.

In captivity, YATSU's specimens attached themselves to the substratum at the ten-pair-filament stage, when they were about 650μ long. Attachment does not always occur quite as early as this, for ASHWORTH observed free-swimming larvae with 15 pairs of filaments. This discrepancy may

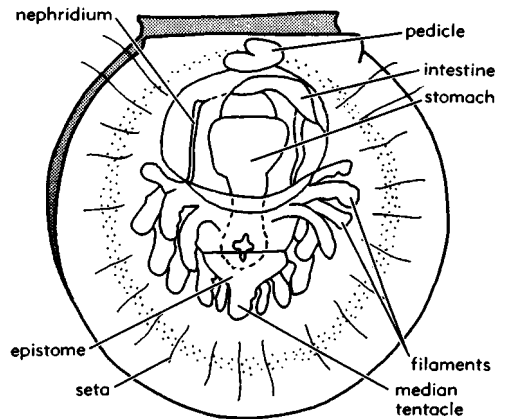


FIG. 50. Larval *Lingula* with eight pairs of filaments, viewed ventrally (musculature omitted) (46).

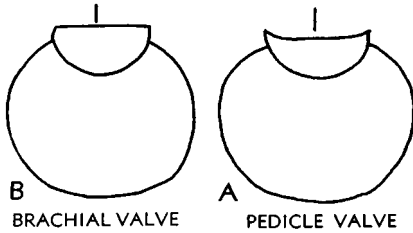


FIG. 51. Outline of shell of *Lingula* 0.5 mm. long (47).

be due to either specific differences or artificial conditions under which the Japanese larvae were reared—for example, differences in depth of water, for PAINE (34) considers that deeper water and lack of bottom contact tend to retard the age at which settling occurs. Immediately prior to attachment the pedicle is protruded and secretes a gelatinous substance which is viscous at first, but subsequently hardens.

On adopting the sedentary mode of life, the lophophore ceases to be a locomotory organ and by means of its cilia induces circulation of water in the mantle cavity. With this change in function, the more persistent, ventral pair of larval muscles degenerate. Considerable changes affect the lophophore itself, involving not only its transformation into a schizolophe but also the development of a partition which divides the brachial canal into two, the future great and small brachial canals.

Increase in the size of the mantle and shell is continuous throughout these early developmental stages. As has been noted, the shell first appears as a very thin cuticle over the entire external surface of the mantle when the animal has a single pair of filaments. At this stage, the shell is a circular lamella folded double along one of its diameters (the “hinge line”).

When three pairs of filaments are present, the two valves, still joined together, attain the protegulum stage of BEECHER. Each valve is almost a semicircle; the “hinge line” is about 280μ wide and does not increase with subsequent growth of the shell. The ends of the “hinge line” project laterally as a pair of small ears (termed “teeth” by YATSU).

Further growth of the shell is now confined to the anterior and lateral margins so

that the valves become almost circular in outline by the time the seventh pair of filaments appear on the lophophore (Fig. 51). Later growth is so much more rapid along the anterior margin that the shell quickly elongates and an elliptical outline is attained about the 15-pair-filament stage. The thin cuticle, which initially joins the valves, is ruptured along the “hinge line” before the appearance of the eighth pair of filaments. The break develops nearer the brachial valve, so that the pedicle valve ends posteriorly in a thin lamella, a remnant of the fold, which is bent dorsally to overlap the thickened margin of the other valve (Fig. 49, A). Concomitantly the shell, which at first is colorless and transparent, acquires a brownish tint along the margins. At the posterior end the superficial layers are bright green.

Setae first appear along the margin of the mantle during growth of the seventh pair of filaments. At first they are very short and by the time the next pair of filaments are added project beyond the edge of the shell only at the posterolateral corners. Subsequent to attachment of the animal, growth of the setae is very rapid and unequal, those along the anterior and anterolateral borders becoming relatively long (some 300μ) and assisting in producing currents of water within the mantle.

The rate of growth up to this stage of development when the animal has become attached to the substratum and has acquired all adult organs, is relatively fast when compared with articulate genera. PAINE (34) considers that the larval life of *Glottidia pyramidata*, living in shallow water, is about 20 days, but that settlement may be retarded for individuals which have drifted seaward over deeper water. YATSU found that *Lingula* has 15 pairs of filaments when it is about 800μ long and 630μ wide, some six weeks after the eggs have been fertilized. Subsequent growth is mainly concerned with increases in size and shell thickness and further elaboration of existing organs.

More than 30 discinid larvae have been described, the majority belonging to the cosmopolitan species *Pelagodiscus atlanticus*. All the larvae of this species have been found in approximately the same stage of development, with four pairs of lophophore

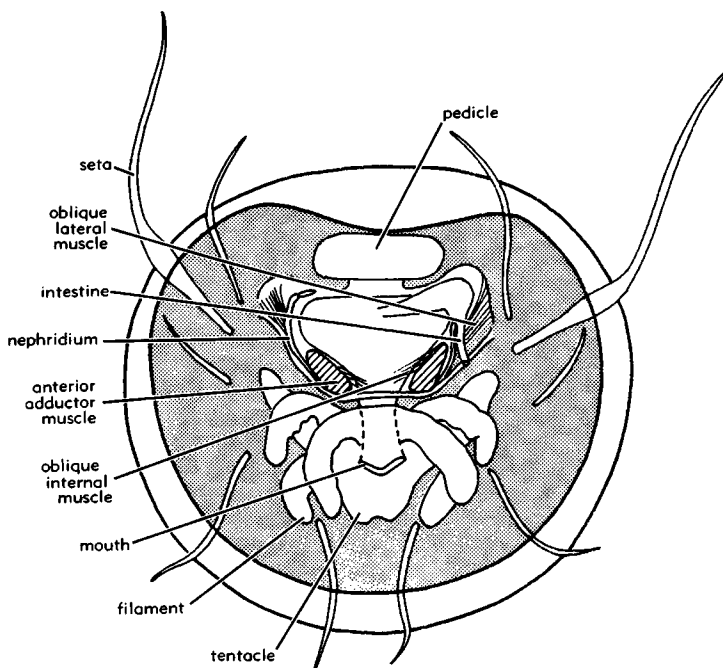


FIG. 52. Larval *Pelagodiscus* with four pairs of filaments, viewed ventrally (minor setae in dorsal valve omitted) (2).

filaments. They were all taken in shallow water (less than 200 m. deep), well above the known upper limit of the bathymetric range of adult *Pelagodiscus* and it is probable that earlier stages remain in the deeper water. Little information about settling is available but MÜLLER observed that larvae studied by him remained free-swimming for a maximum of five or six days. Presumably they became attached while still at the four-pair-filament stage.

The two thin valves of the larvae are roughly circular in outline, with a width of 400μ to 500μ , and are held together only by the body wall and muscles. Characteristically there are five pairs of principal setae (Fig. 52). The anterior four pairs are attached to the pedicle valve, those placed farthest back being much larger and broader than the others. The fifth pair of principal setae occur posteromedianly in the dorsal mantle where they are associated with about 30 pairs of minor setae developed along the lateral and anterior margins. The lophophore, which at this stage contains coelomic spaces and associated musculature, is basically similar to that of *Lingula*, but the filaments are relatively thicker and the median

tentacle is only a broad projection of the anterior margin. Within the body cavity, the alimentary canal is functional and the intestine opens on the right side of the body wall through an anus. The digestive diverticula are not developed, but the wall of the gut is already differentiated. Nephridia and statocysts are present and the musculature is well advanced, although the posterior adductor muscles are not yet formed. A pedicle rudiment occurs, confined within the valves, and as in *Lingula*, it is a projection from the inner surface of the ventral mantle (Fig. 53). A pair of larval sense organs, the so-called "eye spots," are developed on the lateral body walls.

On settling, the pedicle is protruded from the valves through the notch at the posterior margin of the pedicle valve. The eye spots are lost, larval setae replaced by adult ones, and the median tentacle reduced in size shortly after settling. Detailed information on the later growth of the animal is still unavailable.

Very little is known of the larval stages of other discinids and a few that have been taken as plankton cannot be specifically recognized with certainty. YATSU has ob-

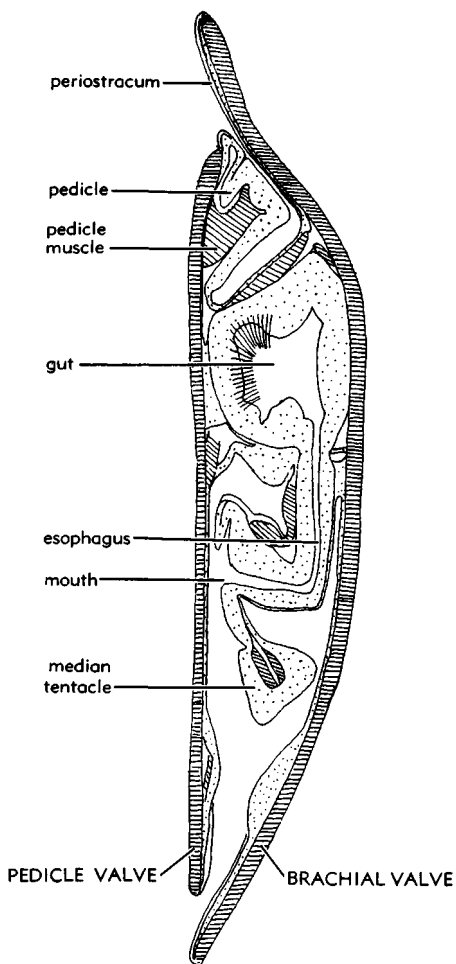


FIG. 53. Diagrammatic median longitudinal section of larval *Pelagodiscus* with four pairs of filaments (not shown because located laterally from mid-line) (2).

served young *Discinisca laevis* which were already attached at the six-pair-filament stage. Morphologically they are similar to *Pelagodiscus* that had recently settled.

Free-swimming stages of *Crania* are still completely unknown, but some of the early postlarval stages have been described for *Crania anomala* (38). The animal settles relatively early in its development, compared with other inarticulates, for it becomes attached during the stage of three pairs of lophophore filaments, when it is about 200 to 300 μ long (Fig. 54, A). At this size the dorsal mantle has already secreted a thin conical calcareous shell covered by

periostracum, but the ventral mantle is invested only in a periostracal layer, which apparently cements the animal to the substratum (Fig. 54, B).

No trace of a pedicle is known in attached *Crania* at any stage of development, although possibility exists that a pedicle is present in free-swimming forms. At the youngest stage known, the animal shows an early development of many adult features. With exception of the lophophore protractor and anal muscles, the adult muscle system is already present. The alimentary canal is developed, but ends blindly and lacks digestive diverticula, which first appear at about the ten-pair-filament stage as pouchlike outgrowths of the anterodorsal stomach wall. The anus originates rather earlier, when the animal has five pairs of filaments. The nephridia first occur at the nine-pair-filament stage as two rows of cells embedded in the connective tissue of the lateral body walls. They do not develop a lumen or become functional until the animal has acquired about 16 pairs of filaments. In the earlier stages of development, the lophophore possesses a median tentacle and is rather like that of *Lingula*, but loss of the median tentacle when the lophophore has four or five pairs of filaments and the onset of the schizolophous condition during pro-

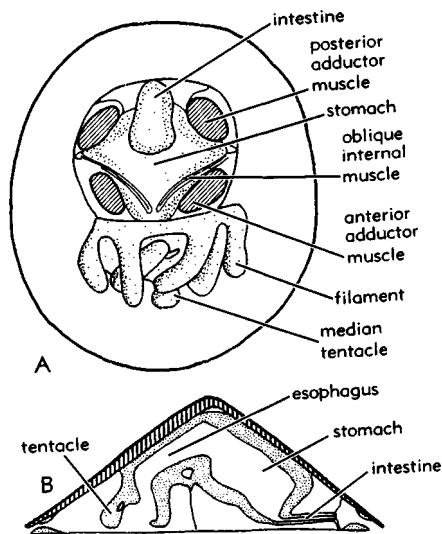


FIG. 54. Young *Crania*, recently attached, with three pairs of filaments, (A) viewed ventrally and (B) in diagrammatic median section (38).

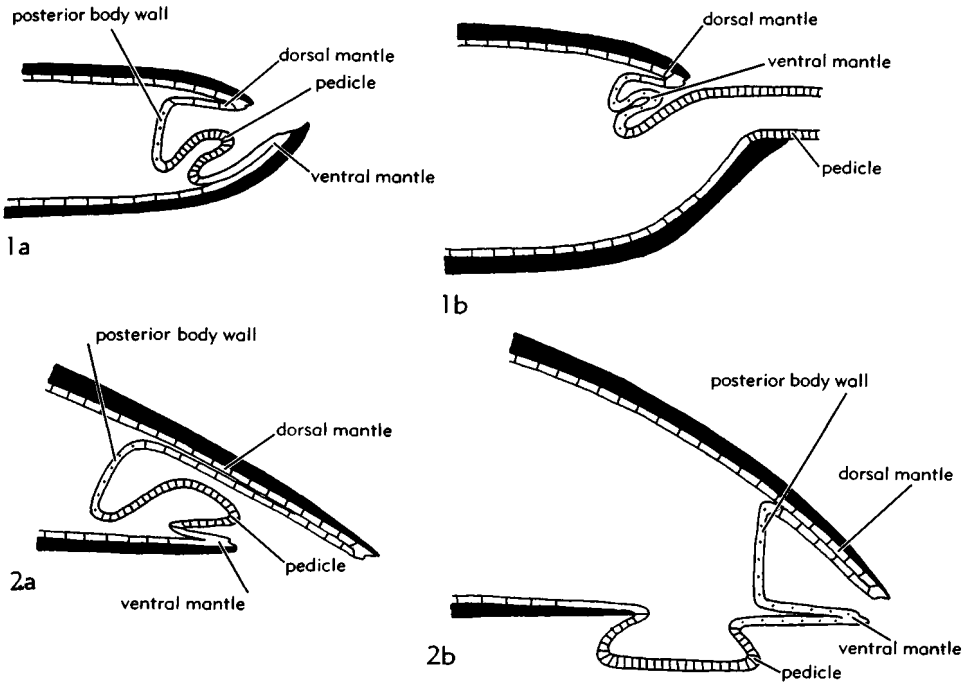


FIG. 55. Diagrammatic longitudinal median section through (1a) young lingulid prior to settling, (1b) adult lingulid, (2a) young discinid prior to settling, (2b) adult discinid (47).

liferation of the seventh pair of filaments occurs earlier in *Crania* than in *Lingula*.

Comparison of the morphology of the posterior region of adult lingulids and discinids with that of young forms which have not settled, but which have developed a pedicle enclosed between the valves, reveals considerable differences in the distribution of epithelium. These are important in a consideration of later shell growth.

In both families the pedicle is initiated as an evagination of the inner surface of the ventral mantle immediately behind the posterior body wall, the juvenile mantle continuing on the posterior side of the pedicle to the margin of the valve. At some later developmental stage prior to settling, probably closely associated with the protrusion of the pedicle, this organ comes to assume a position entirely posterior to the tissue which formed the posterior sector of the juvenile ventral mantle. The change in relative position must also be associated with transformation of the juvenile ventral mantle lobe, for in adults the tissue immediately in front of the pedicle comprises a single layer of outer epithelium lining the

body cavity. However, since the ventral mantle is intact in discinids and lingulids after settling, it follows that subsequent to, or possibly contemporaneously with, the loss of the posterior sector of the juvenile mantle, a flap of epithelium is developed which is continuous anterolaterally with the remainder of the ventral mantle. This sector of the adult mantle can only have developed from, or have been proliferated by, the tissues which initially formed the posterior body wall of the young animal prior to settling. It is separated by the pedicle from the tissue which was involved in the corresponding sector of the juvenile mantle (Fig. 55). The secretory behavior of this posterior sector of the adult ventral mantle and the extent to which it is integrated with the remainder of the mantle are of fundamental importance in determining the form of the adult shell, and as such they are better discussed in the section dealing with morphology of the shell.

The most comprehensive account of development among articulate brachiopods is that given by PERCIVAL (36) for *Notosaria nigricans*. A spherical blastula is developed

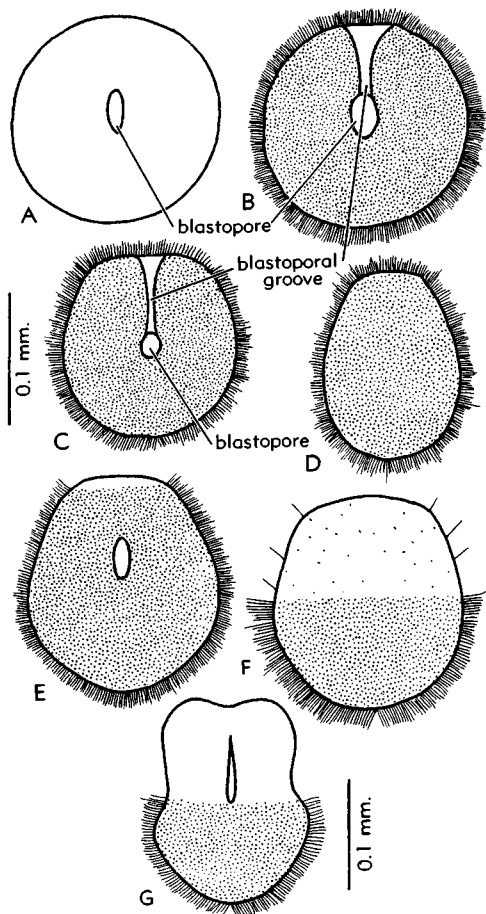


FIG. 56. A-G. Stages in the development of the gastrula of *Notosaria nigricans* (SOWERBY), showing closing of the blastopore, deepening of the blastoporal groove, loss of cilia posteriorly, and beginnings of body differentiation (D is side view of C) (36).

at the eight-cell stage and normally consists of subequal blastomeres which arise by a slightly oblique or, more rarely, a radial cleavage of the fertilized egg. Gastrulation is effected by invagination of the coeloblastula and the blastopore soon becomes oval within a wide depression, which is continued in the future posterior direction as a groove (Fig. 56, A-D). Quite early in the development of the gastrula its entire surface is ciliated, but as it assumes the shape of a blunt wedge, the cilia disappear from its flattened posterior end (Fig. 56, E, F). The rounded, ciliated anterior part may now be identified as the anterior lobe. The blastopore, which has meanwhile been reduced to

a small pit, is located in the base of the anterior lobe and the blastoporal groove still remains as a trace in the mid-line of the slightly narrower and bilobed posterior part (Fig. 56, G). But with the differentiation of the mantle rudiment, the blastopore closes and the groove disappears.

The mantle rudiment first appears as a transverse ridge on the dorsal side of the posterior part of the embryo, separated from the anterior lobe by a well-developed constriction (Fig. 57, A). The ridge is enlarged posteroventrally, ultimately to form a continuous mantle rudiment which is quite distinct from a posterior unciliated lobe (the pedicle rudiment) and bears two pairs of long setal tufts located dorsally and dorso-laterally. The anterior lobe is now separated from the rest of the body by the encircling constriction and is further characterized by the appearance of an apical tuft of long cilia and about 48 marginal "eye spots." The cilia disappear before settling, but the eye spots persist for some time after metamorphosis. The pedicle rudiment tends to be partially enclosed by a sheath of mantle rudiment, which at this stage grows posteriorly and becomes lobed along its posterior margin about each tuft of setae (Fig. 57, B-D). Cilia also appear on the ventral surface of the mantle rudiment and aid the embryo in its movement over the substratum, although the cilia of the anterior lobe are responsible for its gyrotory propulsion through the water prior to settling (Fig. 57, E, F).

Concurrently with these external changes, profound internal modifications occur (Fig. 58). The formation of the blastoporal groove results in the depression of its floor as a partition in contact with the ectoderm on the opposite surface of the gastrula. In this way the archenteron is divided into an anterior sac, "the enteron," penetrated by the blastopore, and a pair of posterolateral diverticula. The enteron lengthens with the long axis of the body and its endoderm remains temporarily in contact with the blastopore, now reduced to a pit. The diverticula grow forward on each side between the enteron and ectoderm as a pair of mesodermal bodies and then divide into posterior and anterior parts to occupy respectively the future pedicle and the remaining body regions. As the mantle grows, its meso-

derm is not easily distinguishable from the ectoderm, in contrast to the clarity of the two hollow mesodermal masses within the pedicle rudiment. At this stage of development, muscle fibers appear within these posterior mesodermal bodies which later become the adjustors and possibly also the diductors.

The larva of *Notosaria* remains free-swimming from two to seven days before it settles, attaching itself to the substratum by a secretion from the tip of the pedicle lobe. The mantle then shortens and thickens by rolling upward so that the setal tufts become directed first horizontally, then anteriorly (Fig. 36,A). Meanwhile, the apical lobe becomes contracted longitudinally to form a low central mound surrounded by a ring-like margin containing the "eye spots." The mound continues to subside and is eventually separated from the peripheral ring by a pair of growing crescentic slits (Fig. 36,B). With the union of these slits and the sinking of the central mound, the processes leading to the definition of the lophophore are initiated (Fig. 36,C-H); they are outlined in the description of the lophophore. The mantle rudiment, while still disposed as a short cone, secretes a protegulum as a pair of discrete, thin valves. A dorsoventral flattening then occurs accompanying the differentiation of a smaller brachial valve with the former dorsolateral tufts of setae, now located anteriorly, and a larger pedicle valve bearing the remaining pair of tufts posterolaterally. At first the valves lie well within the mantle edges but later growth reverses the relationship. This dorsal-ventral flattening also affects the apical lobe (now modified into a rudimentary ring, six filaments, and a brachial lip surrounding a stomodaeum) which spreads onto the inner surface of the brachial valve (Fig. 37,A,B).

The longitudinal contraction that follows the settling of the larva is accompanied by a dorsoventral reorientation of the long axis of the enteric mass, the rudiment of the alimentary canal (gut) (Fig. 58,E-F). In this position, it develops a lumen and makes contact with the stomodaeum along the ventral crescentic slit. However, before an open connection is established between the stomodaeum and the gut rudiment, two pairs of muscles are present in addition to the adjustor. They lie anterolaterally and pos-

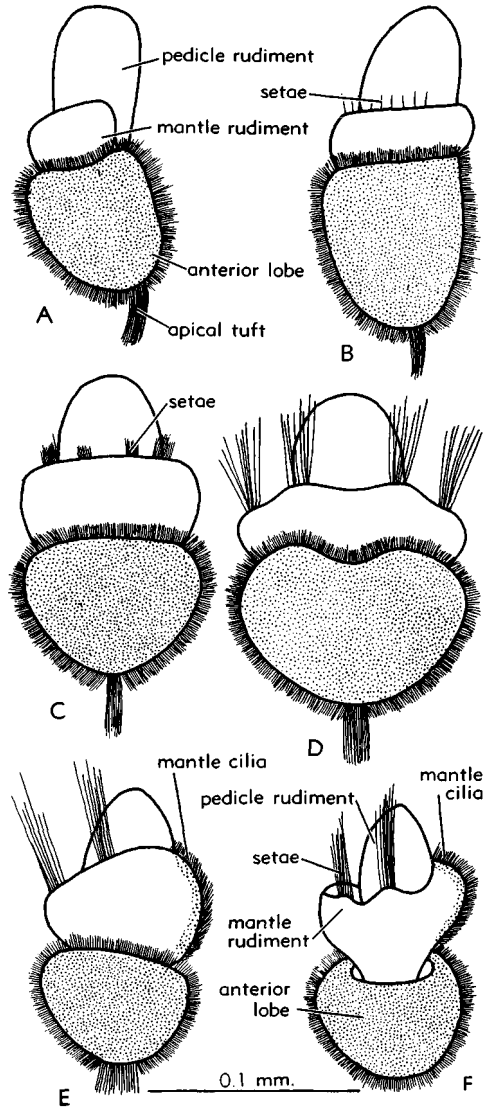


FIG. 57. A-F. Stages in differentiation of the anterior lobe, mantle, and pedicle rudiments of the larva of *Notosaria nigricans* (SOWERBY) (36).

teriorly to the mid-gut and are the adductors and diductors respectively. The muscles are at first unlined within the cavities that have reappeared in the mesoderm. But subsequent to opening of the stomodaeum into the mid-gut rudiment, an epithelial lining appears in the cavities between the gut and muscles. With the enlargement of these cavities toward each other, the dorsoventral mesenteries, which support the alimentary

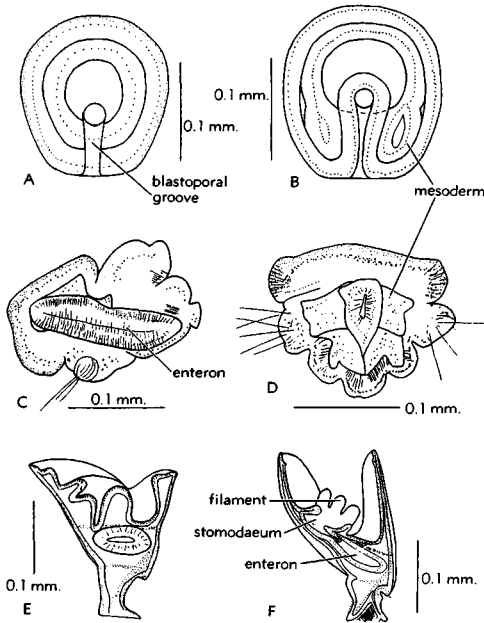


FIG. 58. *A-F*. Stages in internal development of *Notosaria nigricans* (SOWERBY), *A,B*, showing origin of mesodermal masses in late gastrula; *C,D*, longitudinal and horizontal sections of late embryo and larva showing enteron and two pairs of mesodermal masses; *E,F*, longitudinal sections of young adult before and after breakthrough of stomodaemum (36).

canal, are formed; and about the time that ten pairs of filaments are present on the lophophore, rudimentary digestive diverticula also project into the body cavity. A pair of ciliated ducts representing the anterior nephridia of adults first appear at the six-pair-filament stage; the posterior pair develop later.

Traces of filamentar canals are seen when three pairs of filaments are first differentiated, and by the time another pair have been added, circulatory canals continuous with the periesophageal canals are developed.

When allowance is made for a misidentification of the juvenile valves, which was later corrected, the development of *Terebratella* is similar to that of *Notosaria*. PERCIVAL (36) remarked on differences in development of the lophophore, notably those involving growth of the brachial lip and the first three pairs of filaments. But, as has been pointed out elsewhere, the differ-

ences may prove to be unimportant; the pattern of growth is more likely to be that seen in *Notosaria*. Other differences are mainly matters of timing. The free-swimming life of the *Terebratella* larva is variable but, with average duration of about 30 hours, is distinctly shorter than that of *Notosaria*. Indeed, it may be said that the entire development of *Terebratella* is accelerated, so that not only do the mesodermal cavities appear by the four-pair-filament stage but also the first outgrowths of the digestive diverticula.

In general, less satisfactory accounts describing the larval growth of other articulates confirm the pattern of development outlined above, although some noteworthy discrepancies may be due to faulty observation. CONKLIN (19) investigated the free-swimming stages of *Terebratulina septentrionalis* and reported that tufts of long setae are not developed along the edge of the mantle rudiment and that the diverticulum, which later forms the mesoderm, is partitioned off from the anterior (*not* posterior) end of the archenteron. This diverticulum is later constricted by the growth of the enteron into two lobes, which elongate but do not divide, as in *Notosaria*. The anomalous location of the enterocoelic sac when it first arises has been commented on by PERCIVAL (35), who pointed out that CONKLIN used preserved material and might have been mistaken in his orientation of specimens at this stage of development. In *Argyrotheca*, according to KOVALEVSKIY (25, 26), SHIPLEY (43), and PLENK (37), the diverticula arise as a pair of lateral pouches pinched off from the sides of the archenteron. They then spread along the sides of the enteron and meet ventral to it. Both KOVALEVSKIY and SHIPLEY also record that the first three pairs of filaments arise in the same way as those of *Terebratella*, by spreading around the oral disc from either side of the first-formed posterior pair.

The embryology of *Lacazella* is the most difficult of all to understand, mainly because it has only been sketchily outlined in a rarely seen paper by KOVALEVSKIY (25). According to this account, gastrulation is effected by delamination (*not* invagination) and the mantle lobes are defined before reversal takes place. This differentiation is

then followed by atrophy of the ventral mantle rudiments and the deposition of chitinous plates on both the inner surface of the dorsal mantle rudiment and the adjacent surface of the pedicle rudiment. The plates have been respectively identified as the beginnings of the brachial valve and a delthyrial cover; BEECHER (10) believed that the pedicle valve was formed later and subsequently ankylosed to this cover. Such interpretations cannot be accepted without further investigations. Admittedly important modifications of larval development are to be expected in cemented brachiopods, like *Lacazella*, that lack a pedicle. Nonetheless, it is important to note that KOVALEVSKIY's illustrations were not based upon prepared sections and the plate homologized by BEECHER with the delthyrial cover could well have been a stylized representation of a ring of chitin around a degenerating pedicle rudiment (1, 44).

LENGTH OF LIFE

Crania has survived in the laboratory for more than a year and its rate of growth suggests that its life span can be greatly in excess of a year. This is borne out by the size distribution within a sample of *C. anomala* off northwestern Scotland, which led ROWELL (38) to conclude that in this area the animals were capable of living for four or five years.

YATSU (46) found that in Misaki Bay (Japan) it took a year for *Lingula* to attain a shell length of 5 mm., and assuming that the rate of growth was constant, he concluded that maximum adult size indicated a life of five years or more. CHUANG (18a), however, working on *Lingula anatina* from Singapore, has found that although the rate of growth varies, in general it is inversely proportional to length of the individual. He obtained direct evidence that the animals live more than five years and considers that the life span varies probably between six and twelve years. The life span of *Glottidia pyramidata* off Florida is seemingly much shorter (34), with a maximum probably in the order of 20 months.

Very little information has been published on the life span of discinids. PAINE (33) found that size variation in a sample

of *Discinisca strigata* from Mexico was normally distributed, and thought it likely that these animals were annuals. Other interpretations of this curve are possible, however, and more data still are required.

Articulate brachiopods are known to be less hardy than inarticulates under laboratory conditions, but the only noteworthy comments on longevity are those for *Terebratella inconspicua*. From the size distributions of his samples, PERCIVAL (35) concluded that adults lived for about four years. RUDWICK's sampling (39) provided entirely different patterns of distribution with fewer peaks. Despite this difference, he maintained that since rate of growth decreases with increasing age, the life span of surviving individuals with the largest shells is probably much greater than four years.

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MORPHOLOGY

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SHELL FORM

The brachiopod shell which is normally bilaterally symmetrical about the longitudinal median plane (plane of symmetry) consists of two dissimilar valves and is oriented according to the growth and disposition of the soft parts. That region of the shell from which the pedicle emerges and which normally represents the first-formed part of each valve is posterior, so that the median portions at the opposite ends of the shell margin constitute the anterior (Fig. 59). The valve that accommodates most, if not all, of the pedicle is referred to as the **pedicle valve**; it is typically larger than the opposing **brachial valve**. The valves are also called ventral and dorsal respectively in recognition of their orientation relative to the body axis; and although these terms are less

meaningful in identification of the valves, they are nonetheless correct and may be retained for describing the disposition of various features. Dimensions measured to give some indication of shell size, outline and profile are conventionally taken in the manner shown in Figure 59.

The growth of the brachiopod valve subsequent to the secretion of the protégulum may proceed in three different ways (49) (Fig. 60). In certain inarticulates like the discinids, deposition by an expanding mantle edge continues around the entire margin of the protégulum which, as a result of this process of holoperipheral growth, migrates forward away from the posterior margin toward the center of the adult valve (Fig. 60, *1a, b*). In other inarticulates like the lingulids, although the posterior margins are thickened by some growth, nearly all the

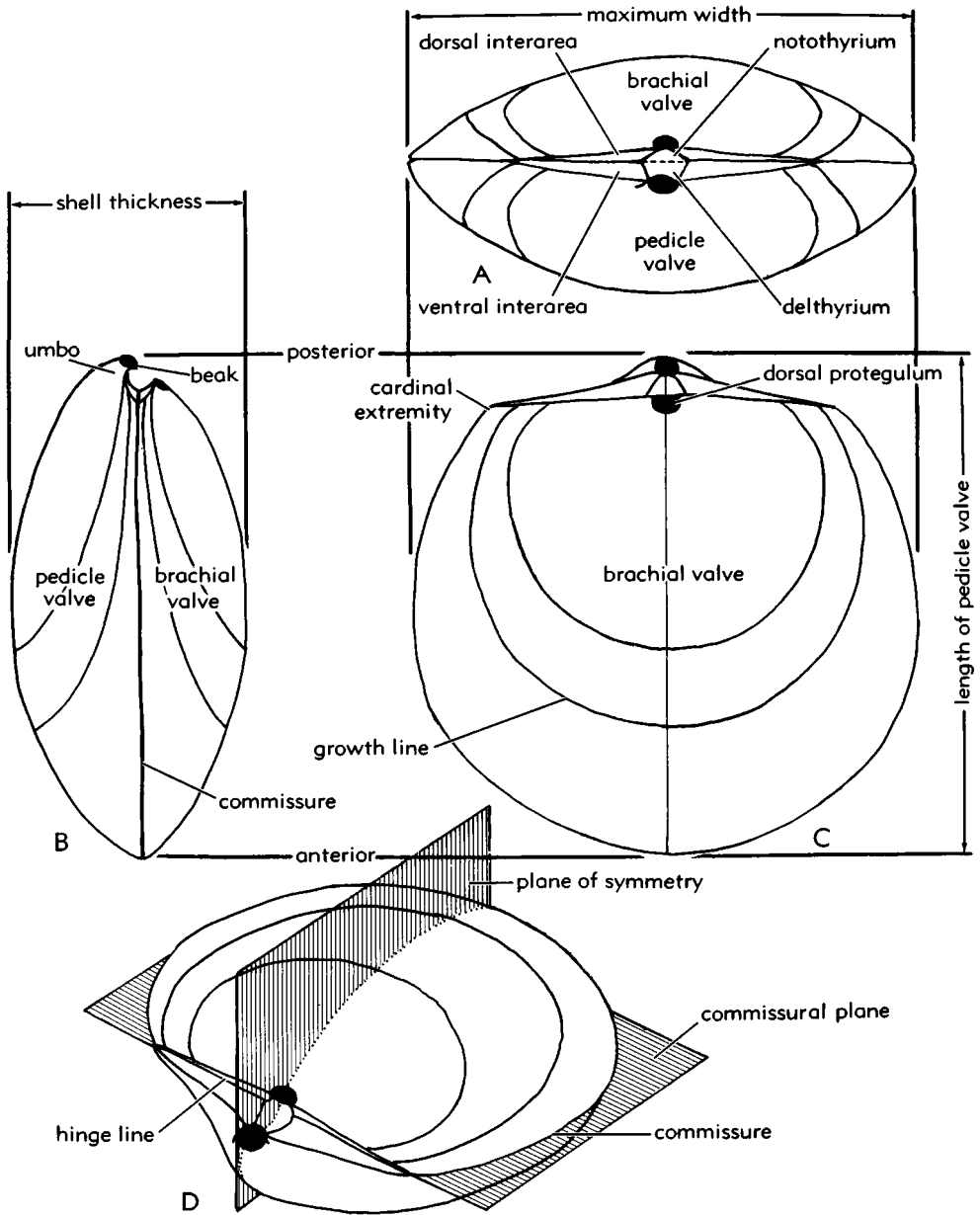


Fig. 59. External features of generalized enteletacean brachiopod seen in posterior (A), left lateral (B), dorsal (C), and dorsolateral (D) views (65).

new shell is added to the lateral and anterior margins (hemiperipheral growth) so that the protegulum remains in posteromedian position (Fig. 60,3a,b). The third type of growth affecting inarticulates (e.g., some acrotretaceans and paterinaceans), which is

known as mixoperipheral, is really a modification of holoperipheral growth in that the posterior surface of a valve is inclined anteriorly toward the other valve (Fig. 60,2a,b). Such a surface has been called a palintrope (49), but the term has limited use in this

context because changes in growth directions, involving transitions between holoperipheral and mixoperipheral patterns, are common among brachiopods. Mixoperipheral growth is pre-eminently characteristic of the articulate brachiopods (Fig. 60, 5a,b), especially in the definition in both valves of a planar or curved triangular shelf (cardinal area) subtended between each apex and the posterior ends of the lateral margins (cardinal extremities) (Fig. 59). The growth of the cardinal area is controlled at its free edge (posterior margin). In many genera the posterior margin is parallel to the hinge axis (i.e., the line about which the valves rotate during opening or closing of the shell) and forms a true hinge line, the growing edge of the posterior margin of

the two valves being identical in extent. Shells in which both conditions are fulfilled are referred to as strophic (40) (Fig. 61) and the cardinal areas of these shells as **interareas**. The ventral interarea of such shells is commonly larger than the dorsal and both may be variously inclined relative to the surface containing the boundary line (commis sure) between the anterior and lateral margins of the valves (Fig. 59). As can be seen in Figure 61,C, the disposition of interareas relative to the "plane" of commissure (the "normal plane" of RUDWICK) may vary by more than 180°. The commonest attitude adopted by the ventral and dorsal interareas is apsacline and anacline, respectively, and the rarest conditions are probably the procline and hypercline, which represent aspects

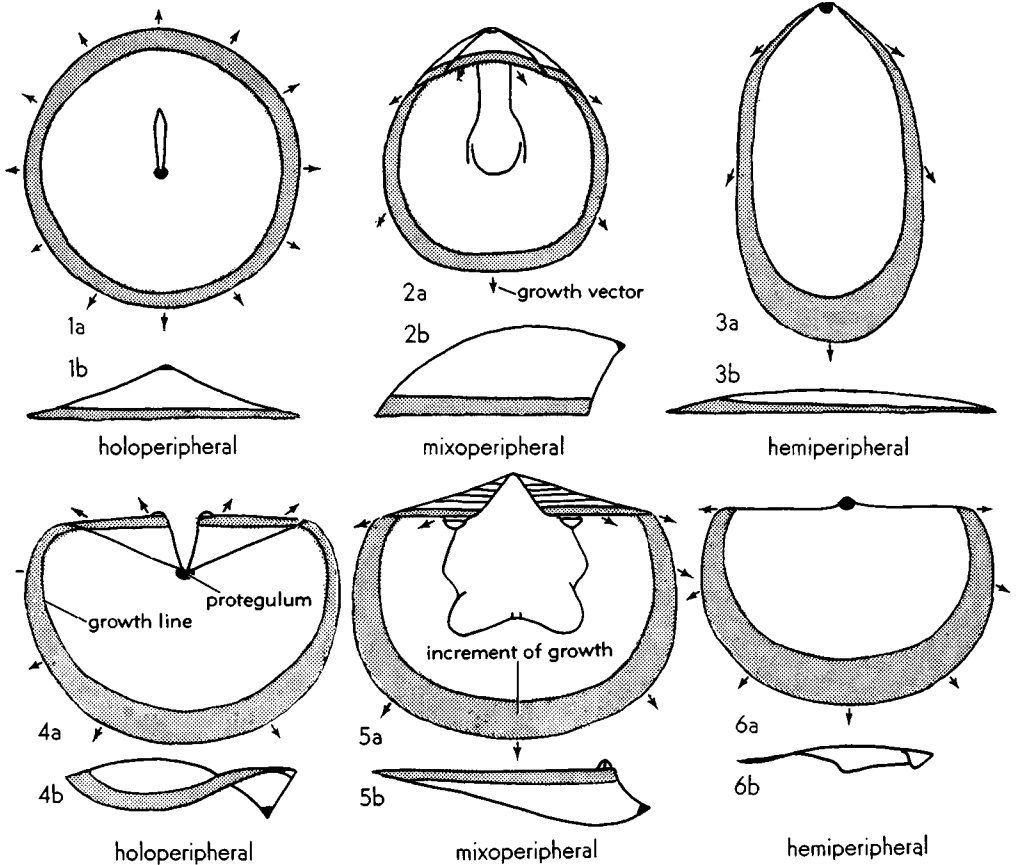


FIG. 60. Nature of shell growth as typified by holoperipheral increase in pedicle valves in ventral and lateral views of *Orbiculoidea* (1a,b) and *Plaesiomys* (4a,b); mixoperipheral increase in pedicle valves in dorsal and lateral views of *Apsotreta* (2a,b) and *Dinorthis* (5a,b); and hemiperipheral increase in brachial valves in dorsal and lateral views of *Lingula* (3a,b) and *Productus* (6a,b) (64).

of holoperipheral growth. Among wide-hinged orthoids, strophomenoids, and spiriferoids, the interareas form very obtuse-angled triangles, but extreme lateral reduc-

tion of the hinge line led to rostrate shells like *Perditocardinia* in which the apical angle of the interareas is narrowly acute. A conical pedicle valve, due to excessive for-

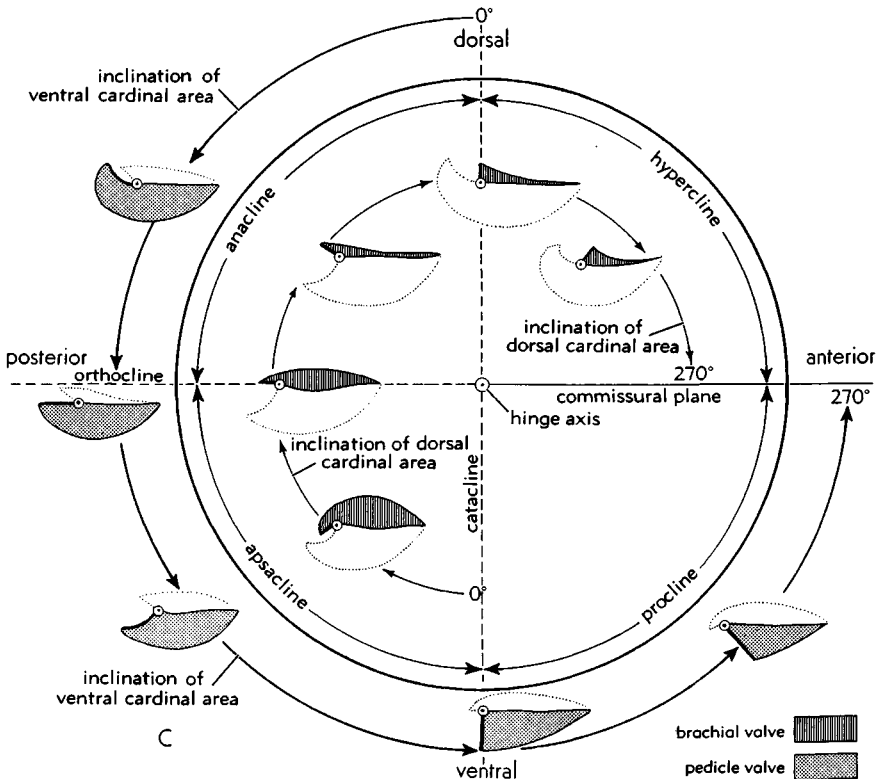
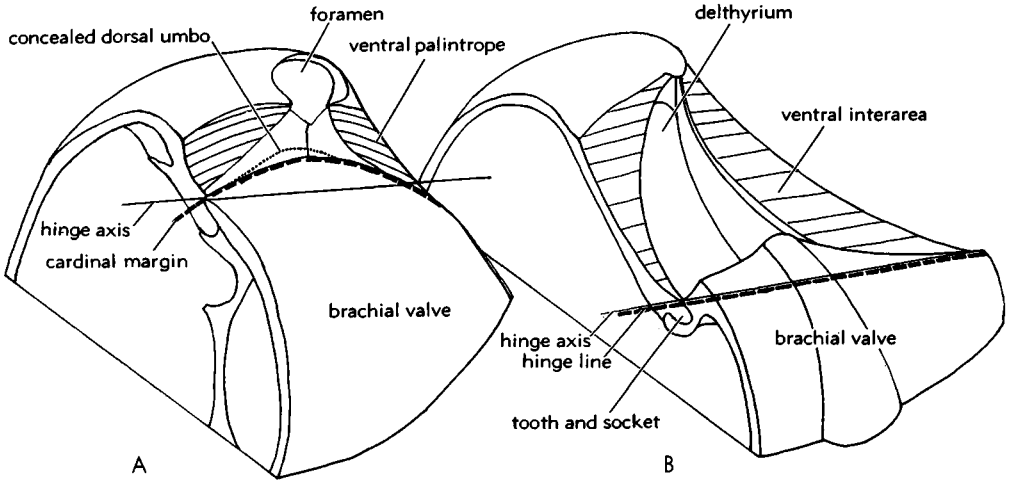


FIG. 61. Posteromedian regions of (A) nonstrophic and (B) strophic shells, with (C) a chart showing the various attitudes of cardinal areas about the hinge axis relative to the commissural plane (65).

ward growth of the ventral interarea, is characteristic of a number of genera (e.g., *Onychotreta*, *Scacchinella*, *Syringothyris*), whereas a suppression of forward growth, as in the majority of productoids, led to linear interareas and "hemiperipheral" expansion of the brachial valve.

Rostrate shells are also characteristic of nonstrophic terebratuloids, rhychonelloids, and atrypoids, in which homologues of the interareas are greatly reduced or absent and homologues of the hinge lines are short and curved, so that their traces only intersect the hinge axis (Fig. 61). RUDWICK (40) prefers to use the terms "palintrope" and "cardinal margin" to distinguish these vestiges from the well-developed interareas and hinge lines, respectively, of strophic shells. This distinction may seem academic, because the free edge of the dorsal umbo which protrudes into the delthyrial cavity of the pedicle valve of the nonstrophic shell (i.e., most of the cardinal margin as understood by RUDWICK) is no more an integral part of the hinge line than are the notothyrial edges of strophic brachial valves. However, if reference is made exclusively to those posterior surfaces and edges lateral of the points of articulation (i.e., to the arcs underlain by fused mantle lobes), the differences described by RUDWICK are valid.

Irrespective of the different types of growth, the protogula occupy the apices (or beaks) of the valves, and the shell region immediately around the apex is referred to as the umbo (Fig. 59). The attitude of the ventral beak can vary from being in the commissural plane (straight) to a dorsally directed inclination of up to 150° to that plane (strongly curved). Typically the cardinal areas of articulate brachiopods, immediately beneath apices of the valves, are notched by a pair of triangular openings—the delthyrium of the pedicle valve, which normally accommodates the pedicle, and the notothyrium of the brachial valve, which usually is filled with the attachment base (cardinal process) for the dorsal ends of the diductor muscles (Fig. 59). Both of these openings may be partially or completely covered by shell outgrowths described below.

The posterior surface of the inarticulate valve may be completely unmodified and

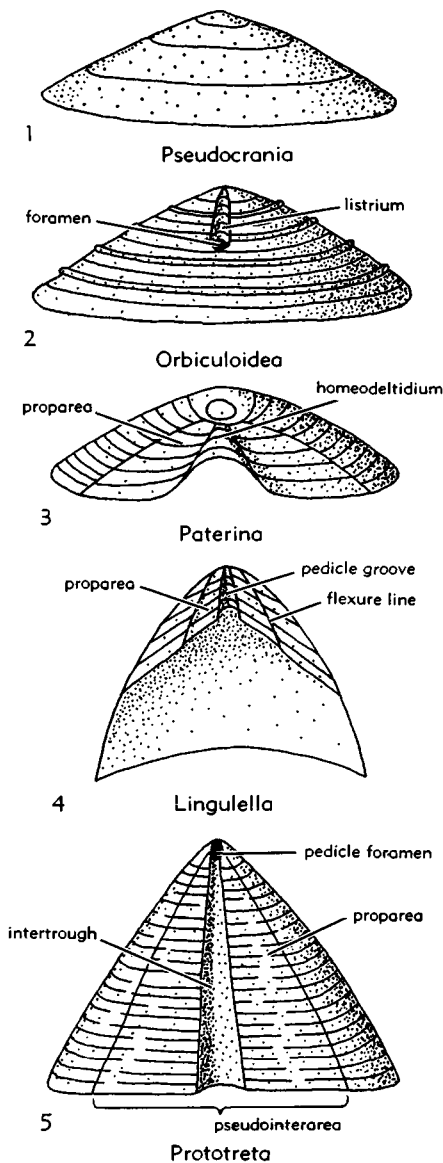


FIG. 62. Modifications of posterior sector of pedicle valve of some inarticulate brachiopods; 1, craniacean (*Pseudocrania*); 2, discinacean (*Orbiculoidea*); 3, paterinacean (*Paterina*); 4, lingulacean (*Lingulella*); 5, acrotretacean (*Prototreta*) (63).

comparable with the anterior and lateral slopes, as in the majority of craniaceans (Fig. 62,1). More commonly some differentiation occurs especially in the pedicle valve. The simplest modification is some form of opening such as a notch or a slit

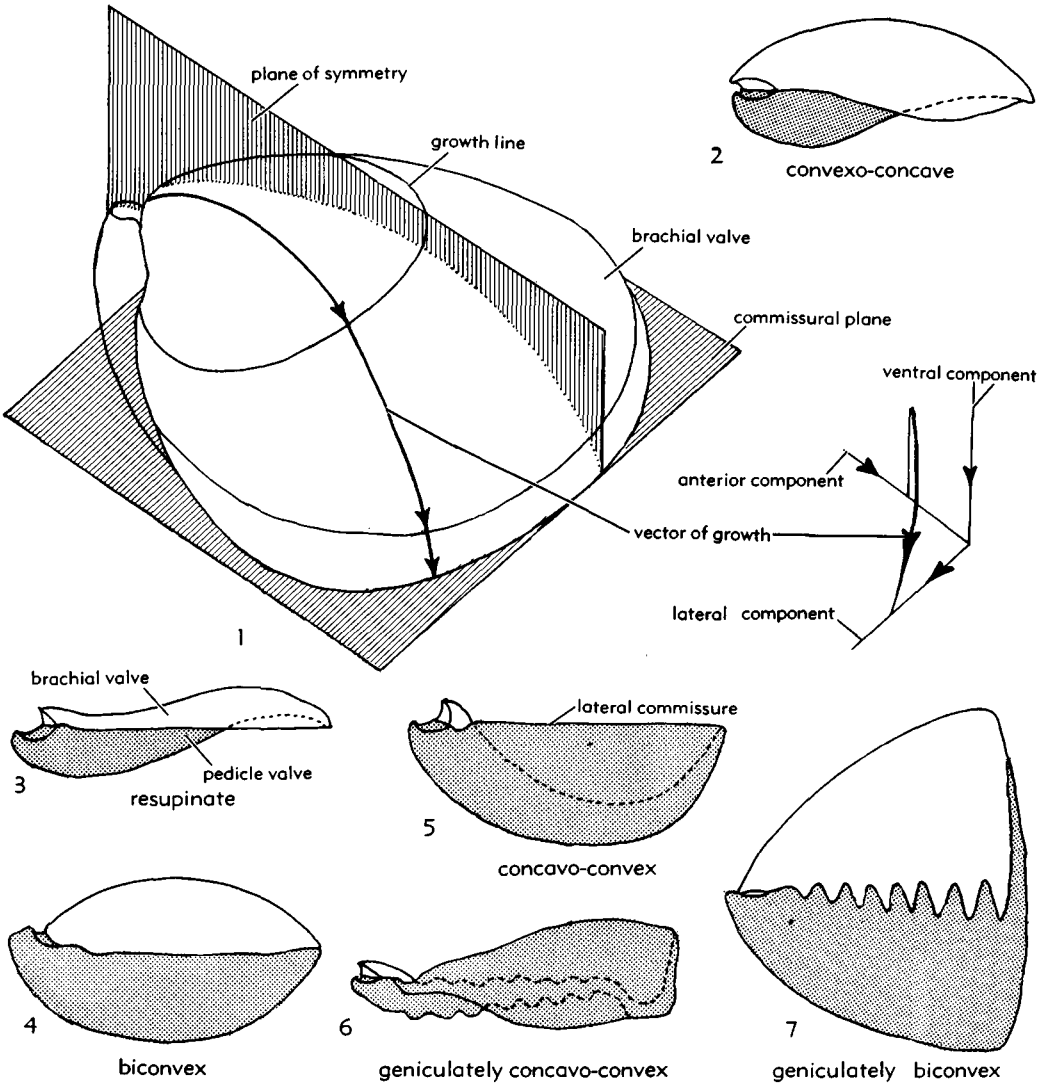


FIG. 63. Components of growth in brachiopod shells (1), with illustrations of various types of lateral profiles (2-7) (65).

for the pedicle (e.g., discinids) while a flattened surface (pseudointerarea) on the posterior margin of either valve is characteristic of many groups (Fig. 62,3-5). Thus, in the paterinaceans the pseudointerarea of the pedicle valve consists of a pair of flattened triangular areas (propareas) marked off from the posterolateral regions of the valve by a break in slope and separated by the delthyrium. The ventral pseudointerarea of lingulaceans, in contrast, is approximately orthocline in disposition and the two tri-

angular propareas flank a pedicle groove. These basic patterns, with minor modifications, also occur in other inarticulate groups and can involve the posterior margin of the brachial valves. An orthocline or anacline dorsal pseudointerarea, which may be divided medially as in many acrotretids, is commonly developed, although other less complex modifications may occur.

The protegula of living and extinct brachiopods suggest that in both transverse and longitudinal profiles, the unspecialized

shape of the adult shell is biconvex (Fig. 63). Ideally, then, three components of growth relative to the median and commissural planes of the shell may be recognized and vectors of growth, traced on the shell surface from the protegular node, may be resolved according to these axes. They are an anterior component parallel with the intersection of both planes, a ventral or dorsal one normal to the commissural plane, and a lateral one normal to the median plane. In general, the pedicle valve is not only larger in outline but deeper than the brachial valve, but every conceivable variation in this relationship was attained during brachiopod evolution. Thus among the strophomenoids, chonetoids, and productoids, the more usual adult profile was concavo-convex, that is, with a brachial valve becoming concave beyond the protogular node and the pedicle valve continuing its initial convexity (Fig. 63,5). A reversal in growth direction was also common, so that the biconvexity of the protogulum was modified to a concavo-convex relationship in young shells, which in turn gave way to a convexo-concave attitude during adult stages of growth. This type of growth is known as **resupination** (Fig. 63,2). Such reversals in direction of growth were also accentuated by an angular deflection of one or both valves (**geniculation**) due to a marked reduction or cessation of the radial components of growth. Such deflections are directed either toward the other valve (e.g., *Enantiosphen*, *Sphaerirhynchia*, Fig. 63, 6,7), or in the same direction to define a disc, commonly with an internal confining ridge (submarginal ridge) and a trail (Fig. 63,6). The disc corresponds more or less to that part of the shell occupied by the body and lophophore, and the trail may be directed dorsally or ventrally and may even reverse direction as in some leptaenids.

A common modification of the profile of inarticulate brachiopods is the development of a conical valve. Both valves of *Orbiculoidea* may be subconical but it is more usual for only one valve to become conical, such as the acrotretid pedicle valve and the discinid brachial valve. This profile is very much less common in the articulate brachiopods, the most spectacular being the cone-shaped pedicle valve of *Richthofenia*, which encloses a sunken subcircular brachial valve.

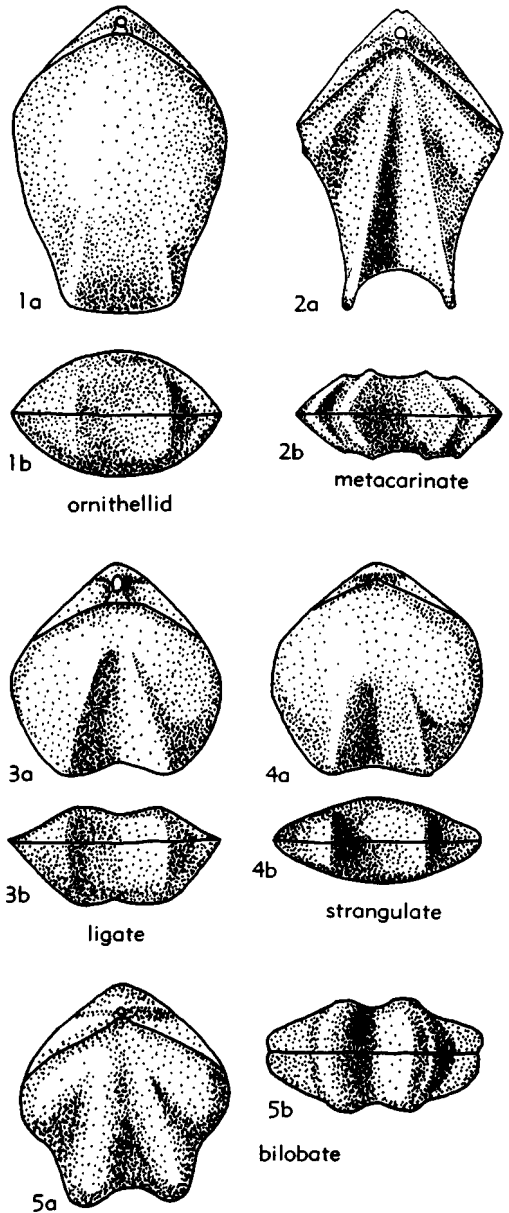


FIG. 64. Types of opposite folding; 1-5, dorsal and anterior views of indicated stages (63).

The brachiopod outline varies greatly, apart from the more orthodox transversely semioval, subcircular, elongately oval, and subtriangular appearance of wide- to short-hinged shells. Some of the more bizarre forms include the saucer-like, incurved, or conical pedicle valve of the oldhaminoids,

with highly lobed dorsal structure which may have consisted of a vestigial brachial valve and a large internal plate supporting the lophophore; the tubelike pedicle valve of the productoid *Proboscidella*; and the terebratuloid *Pygope*, pierced subcentrally by a hole which was sealed off by antero-median fusion of a deeply indented (emarginate) anterior margin. Both outline and profile of the shell may be considerably modified by radially disposed deformations which display a variety of form and amplitude. The major, radial elevations of the valve surface are **fold**s and the complementary major depressions are **sulci**. These broad deformations grade down into minor features (costae, costellae) which are produced in a comparable manner but are normally regarded as part of the ornament and as such are discussed in detail elsewhere.

In terms of their effect on the commissure, folds and sulci fall into two broad groups, and it is apparent that the deformations of these two groups arose in different ways (40). In one group, the folds and sulci are developed opposite each other in the two valves (**opposite folding**), a fold being opposed to a fold and the commissure remaining straight (rectimarginate) (Fig. 64). These deformations may be regarded as being produced by localized anomalies of the radial growth component, which is the vector sum of the anterior and lateral components; since the commissure is not deflected, they do not involve anomalies in the vertical component. Deformations produced in this way have their maximum expression when the valve is strongly convex.

In the second group, the folds and sulci are complementary to one another (**alternate folding**), a fold in one valve being opposed by a sulcus in the other, and the commissure becomes correspondingly undulated by deflections directed dorsally (**plicae**) and ventrally (**sinuses**). The commoner arrangements of this type are shown in Fig. 65, but these are not necessarily constant throughout ontogeny, because during growth a median sulcus may be replaced by a fold and vice versa. Deformations of the alternate type commonly involve localized anomalies of the vertical growth com-

ponent either acting alone or in conjunction with localized anomalies of the radial component. If the anomalies are entirely in the vertical component, the deformations will have their maximum expression on a plane valve and be less conspicuous on a highly convex one.

SHELL STRUCTURE AND ORNAMENTATION

The shell structure of living and extinct articulate brachiopods may be referred to one of three conditions: **impunctate**, **endopunctate**, and **pseudopunctate**. The triple stratification of the shell described in the chapter on "Anatomy" is known or presumed to be normally true of at least the first two types, although the periostracum is never preserved on fossil shells. The thin primary layer is difficult to detect except in well-preserved, unaltered specimens. It is, however, immediately recognizable in the spiriferoids, thecideaceans, pentameraceans, and at least the later porambonitaceans, *Anastrophia* and *Camarella*, as well as fossil terebratuloids and rhynchonelloids. In these groups it is always cryptocrystalline and fairly constant in thickness except for consistent variations related to the development of radial and concentric ornamentation as in the atrypoids (Fig. 66). The boundary between the primary and secondary layers is commonly so sharply defined that one can reasonably assume all obliquely disposed fibers of the inner secondary layer to have been enclosed in cytoplasmic sheaths. Variations do occur. In the thecideaceans and some terebratellaceans (56) the fibers of the secondary layer are disposed at high angles to the external shell surface in a series of bundles forming the cores of internal tubercles (Fig. 67). Among the spiriferoids and pentameroids, a third calcareous layer is commonly found (the prismatic layer of ALEXANDER, 1) which although distinct in appearance is simply a modification of the secondary layer (Fig. 66). It consists of coarse prisms of calcite in continuity with underlying, earlier formed, obliquely disposed fibers and is commonly well developed in those parts of the shell occupied by the muscle bases, which suggests that it

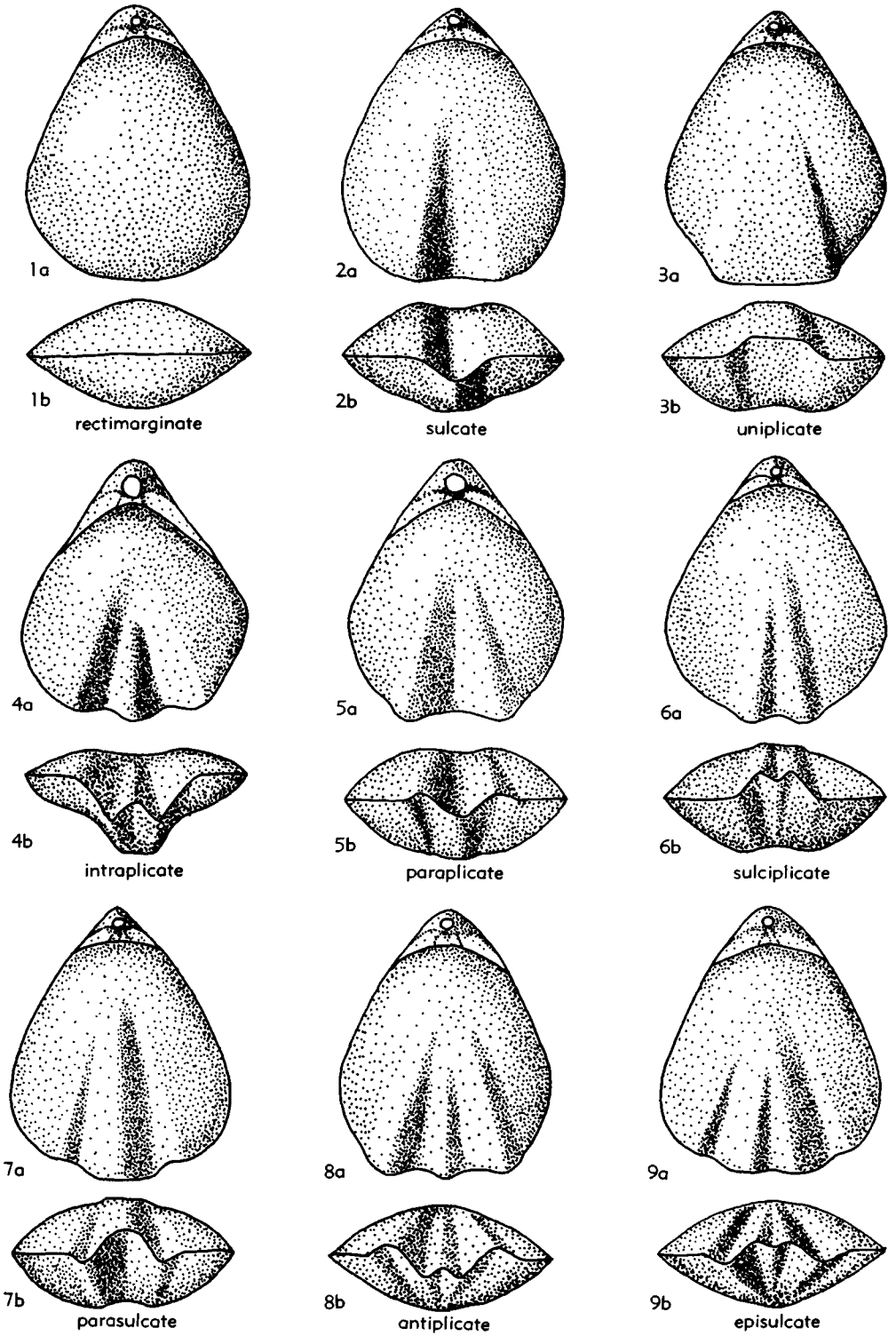


FIG. 65. Types of alternate folding; 1-9, dorsal and posterior views of indicated stages (63).

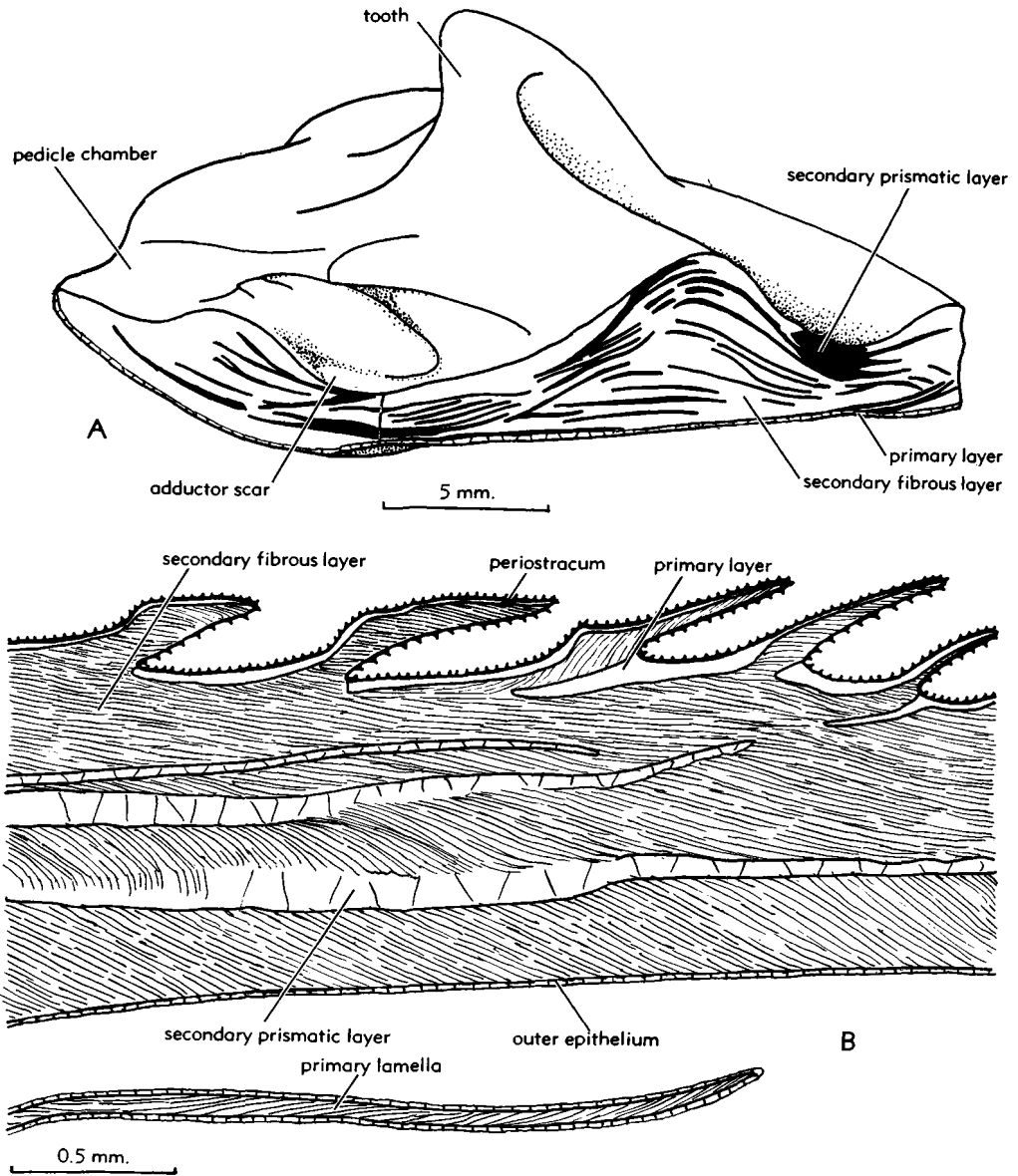


FIG. 66. Stylized sections showing (A) distribution of prismatic shell within secondary layer of posterior part of pedicle valve of *Atrypa* sp., M.Dev., USA, and (B) inferred relationships during life with periostracum and outer epithelium (65).

could be secreted extracellularly by adult outer epithelium associated with tonofibrils. In respect of surface detail, the exterior of the primary layer of well-preserved fossils is seen to be made up of slightly convex minute polygons like those associated with the periostracal net of living brachiopods (Fig. 68); and the internal surface of the

secondary layer is appropriately differentiated into a fine mosaic consisting of the ends of the fibers within their organic sheaths (Fig. 69). The dimensions of the bases of the fibers which make up the mosaic are supposedly sufficiently constant within a species to be used systematically (10).

The primary layer in its typical form is also found sporadically on the shell surface of orthoids and clitambonitoids. This impersistence is usually attributed to mechanical abrasion or solution during fossilization, but it may be that in these groups, the primary shell was very thin, although not invariably so, because exaggerated concentric ornamentation (as in *Glyptorthis*) consists mainly of primary shell substance.

The impunctate shell appears to be the most primitive, because, as yet, no endopunctate or pseudopunctate brachiopods have been recorded from strata older than the Ordovician, while the Cambrian articulate shell (as typified by *Nisusia*) is comparable in structure with that of the younger impunctate stocks and was presumably also deposited by the outer mantle lobe and the

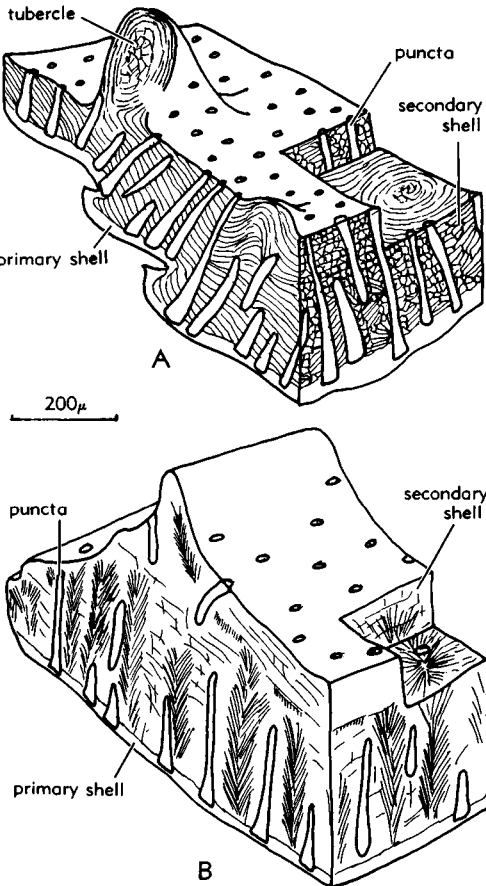


FIG. 67. Sections showing shell structure of *Megerlia truncata* (LINNÉ) (A), and *Lacazella mediterranea* (Risso) (B) (65).

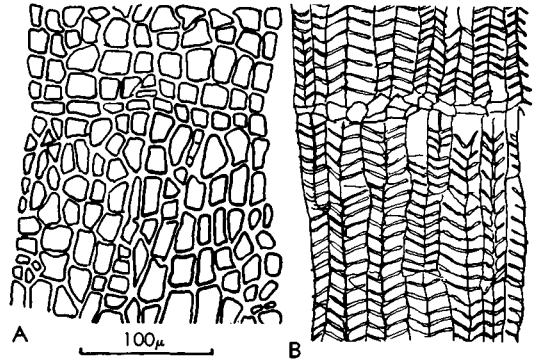


FIG. 68. Impressions of periostracal cover to exteriors of (A) *Hemithiris psittacea* (GMELIN) and (B) *Notosaria nigricans* (SOWERBY), prepared as cellulose acetate peels (65).

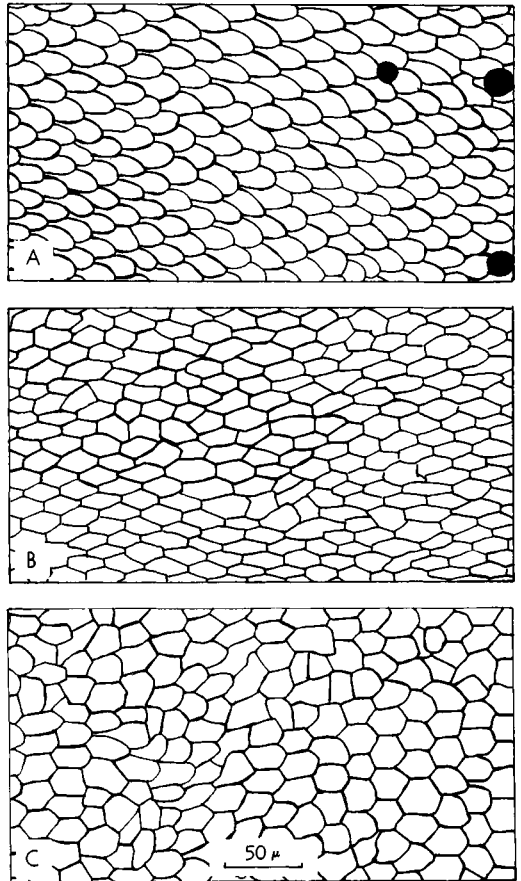


FIG. 69. Shell mosaic of (A) *Terebratulina caputserpentis* (LINNÉ) and (B) *Hemithiris psittacea* (GMELIN), with (C) impression of epithelium underlying muscle base of latter, all prepared as cellulose acetate peels (65).

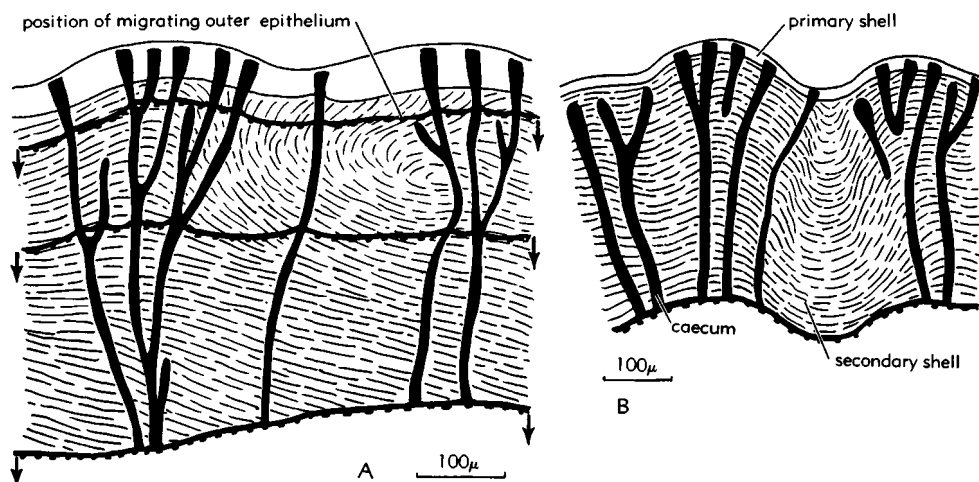


FIG. 70. Branching caeca seen in cross sections of (A) *Rhipidomella* sp., M.Dev., USA, and (B) *Terebratulina caputserpentis* (LINNÉ) (65).

outer epithelium. Indeed, so great is the time lag before the first appearance of endopunctate and pseudopunctate stocks that they were most probably derived from impunctate ancestors.

The shells of all extinct endopunctate brachiopods are comparable in morphological detail to those of living terebratuloids (Fig. 70). The punctae have the same kind of conical distal end and although canopies of calcite, which in living brachiopods lie penetrated by caecal brushes, are rarely seen, even in fossil terebratuloids, it is reasonable to assume that all punctae were occupied by caeca proliferated at the mantle edge. The punctae may be single or they may branch freely when the caecal cups bud off singly but come to share a common secondary stalk of outer epithelium which is pinched up from the mantle by deposition of the surrounding secondary shell (Fig. 70). The diameter of the cups varies greatly (although 30 to 50 μm seems to be representative), as does the density of their incidence (Fig. 71, A). In radially ornamented shells, punctuation is commonly concentrated in strips coincident with ornamentation (Fig. 71, C); it may also develop in distinct rows concentric with, or oblique to, the lines of growth (Fig. 71, B), or it may be sporadically or densely distributed with no apparent sense of pattern.

Punctuation is invariably characteristic of the enteletaceans and terebratuloids. It is al-

so known in the thecideaceans, certain spiriferoids, and exceptionally even in the rhynchonelloids (*Rhynchopora*). It is unlikely that this similarity in shell structure reflects any close relationship between the various groups; more probably the incorporation of secretory cells within the brachiopod shell, in the manner characteristic of living terebratuloids, occurred repeatedly during brachiopod evolution and became a persistent feature of independent stocks. Indeed, the only prerequisite for the initial development of caeca in impunctate shells, or their degeneration in endopunctate brachiopods to give rise to impunctate descendants, is the presence of secretory glands in the primary layer (57); and it is significant that superficial perforations (*exopunctae*) which might have accommodated the cups of impersistent caeca are preserved in fossil shells. Exopunctae, however, might have arisen in a number of ways. Those typical of the plaesiomyids and plectorthids seem to have represented the incipient development of hollow costellae (Fig. 72). They are formed by a regularly occurring inward sag of the mantle edge away from the sharply angular margins of the principal ribs while deposition continued and ultimately sealed off the re-entrant as a short, oblique cylindrical hollow. The exopunctae of *Crurithyris* are the bases of hollow spines (24) which almost certainly enclosed columnar epithelium sealed off from the mantle at the junction

of the primary and secondary layers, while others like those in the rhynchonellid *Porostictia* (12) are definite pits and must also have contained, temporarily at least, epithelium budded off from the mantle edge.

In most strophomenoids, productoids, chonetoids, and some clitambonitoids, the shell is penetrated by rods of calcite (*talectolae*) in a manner reminiscent of true punctation (57). The general shell condition is referred to as pseudopunctation.

The shell structure of strophomenoids differs from that of most articulate brachiopods in lacking a clearly differentiated primary layer over most of the shell surface and in being, with rare exceptions, pseudopunctate. Many references (e.g., 55) have

been made to the existence of an outer shell layer like that of the terebratuloid primary layer in members of this group, but its full and invariable development has always been inferred from the structure of the interareas and the origin of the pseudopuncta within the rest of the shell. Thus in strophomenoids and also chonetoids, the interareas are made up of inner fibrous layer and an outer layer, composed of either cryptocrystalline calcite or very fine calcite fibers disposed normal to the external surface, which thickens gradually toward the hinge line and which must have been secreted at the mantle edge in the manner of the true primary layer (see Fig. 116). This differentiation led to the assumption that a similar "pri-

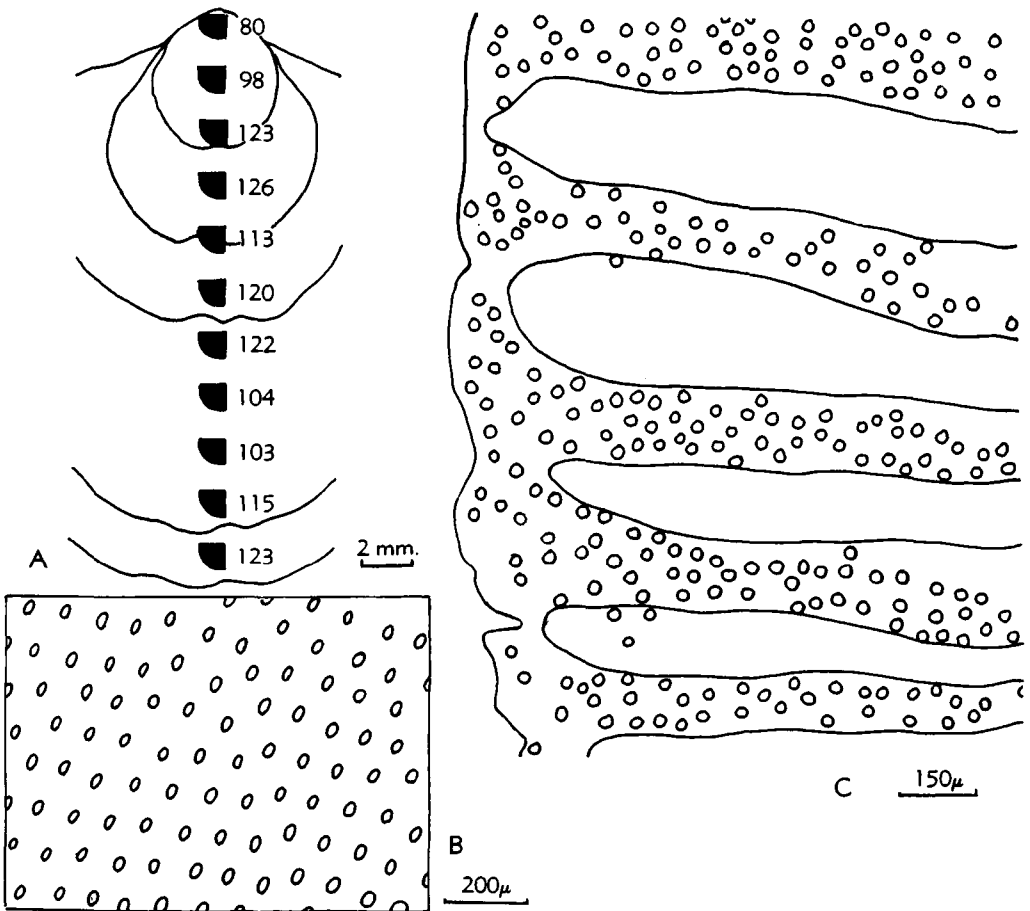


FIG. 71. Distribution of endopunctae showing (A) number of punctae occurring in sectors with radius of 1 mm. along mid-line of brachial valve of *Magellania flavescens* (LAMARCK) and (B) details of their arrangement; also (C) concentration of punctae in crests of costellae as seen along edge of brachial valve of *Terebratulina caputserpentis* (LINNÉ) (B, C, prepared as cellulose acetate peels of shell surfaces) (65).

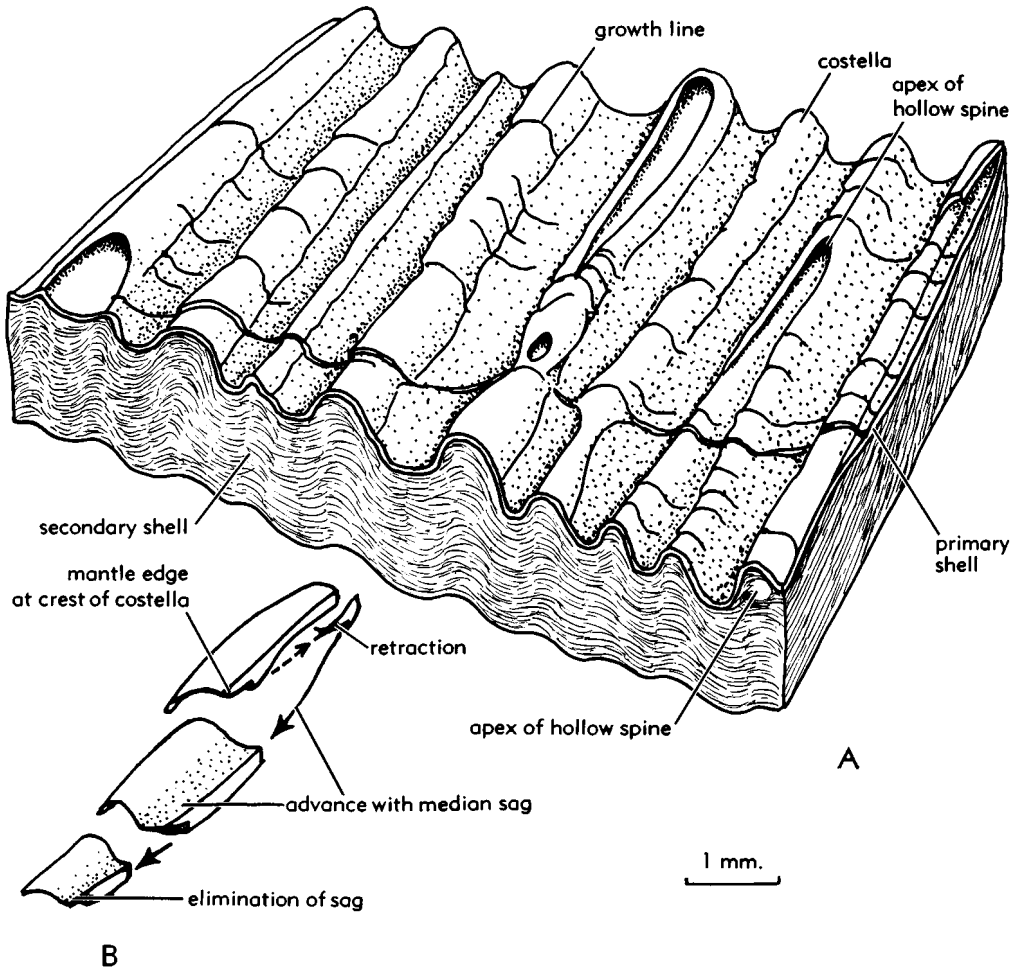


FIG. 72. Part of pedicle valve of *Plaesiomys subquadrata* (HALL), U.Ord., USA, showing (A) nature of hollow costellae and (B) inferred path of mantle edge during formation of hollow rib (65).

mary" layer was also deposited along the mantle edges responsible for the growth of the rest of the shell but was so thin as to have been dissolved away or recrystallized into an unrecognizable state during fossilization. Such modifications would account for its never having been positively identified over the remainder of the shell surface and also for the absence of pits corresponding to the pseudopunctae on the external surfaces of well-preserved shells.

Sections of Upper Silurian and Lower Carboniferous limestones, however, have shown skeletal remains of rhynchonelloids, spiriferoids, and terebratuloids, all with a nonfibrous primary layer, side by side

with those of leptaenids (and also stropheodontids in the older limestones), the shells of which were undifferentiated except along the interareas. This confirms the impression gained from a detailed study of about 40 strophomenoid genera that the homologue of the terebratuloid primary layer over much of the strophomenoid shell consists of the outermost layers of calcite fibers which are disposed parallel with the external surface and are indistinguishable from the inner secondary layer, except for a scattering of pseudopunctae throughout the latter.

The strophomenoid arrangement is also characteristic of at least some chonetoids, but in some productoids like *Dictyoclostus*

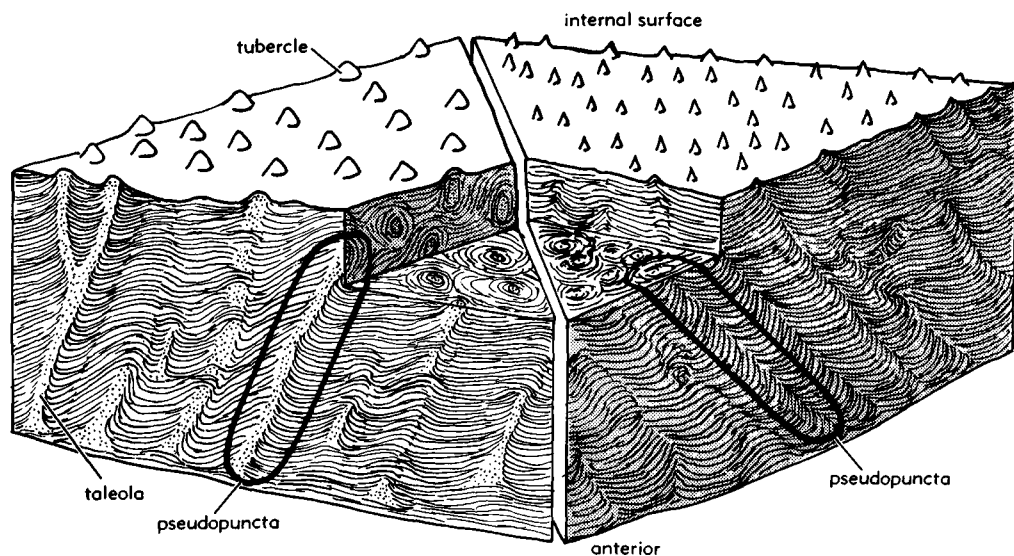


FIG. 73. Idealized sections of strophomenoid shell showing disposition and structure of pseudopunctae (65).

an identifiable primary layer is found, especially in the vicinity and along some of the external spines (see Fig. 88). It is significant that such spines occur in juxtaposition with others lacking any differentiation of an outer calcareous layer and that, unlike the terebratuloid primary layer, it is distinguishable from the underlying fibers, with which it is parallel, only in being uniformly thicker. Its differentiation, therefore, might have taken place in the productoids independently of other articulate brachiopods and even to a variable degree in different stocks because VEEVERS (52, 53) has reported its presence on both valves of *Productella* and on only the pedicle valve of *Avonia*.

Pseudopunctuation has been described in a number of conflicting ways, due mainly to either imperfect preservation and inadequate preparation of thin sections purporting to show its structure, or a too limited survey of the stocks that are characterized by this condition. It has been interpreted as a form of endopunctuation modified by a calcification of caecal outgrowths from the mantle (46); a series of conical puckerings of the inner shell layers (45, 48); and tubercles built up around rods of calcite (taleolae) (28, 57). Irrespective of origin, the fibers contributing to the formation of all pseudopunctae are buckled into a series

of superimposed cones and are commonly obtusely and acutely deflected along the respective posterior and anterior surfaces of the cones. The pseudopunctae are consequently markedly asymmetrical in longitudinal section with their apices directed inwardly and anteriorly to protrude from the internal surfaces of both valves as tubercles (Fig. 73). Among certain strophomenaceans (like *Strophomena*), gonambonitaceans, and many davidsoniaceans (*Derbyia*), the pseudopunctae are composed solely of fibrous cones one within another; but in leptaeonids, stropheodontids, productoids, and chonetoids, taleolae, as cleaved rods of granular calcite surrounded by deflected fibers, occupy the axial regions of pseudopunctae. The taleolae almost invariably occur singly and extend continuously throughout the pseudopunctae, although they are known to bifurcate in *Leptagonia* and may be superficially indented at their tuberculate ends, as in some leptaeonids and stropheodontids. There is, however, no conclusive evidence that the axes of taleolae were ever occupied by epithelial extensions from the mantle in the manner of caeca. Clay minerals have rarely been identified within taleolae of *Leptaena* (46), but their presence is more likely to reflect an accident of preservation than any deep invagination of the mantle. Indeed, the reflexed attitude

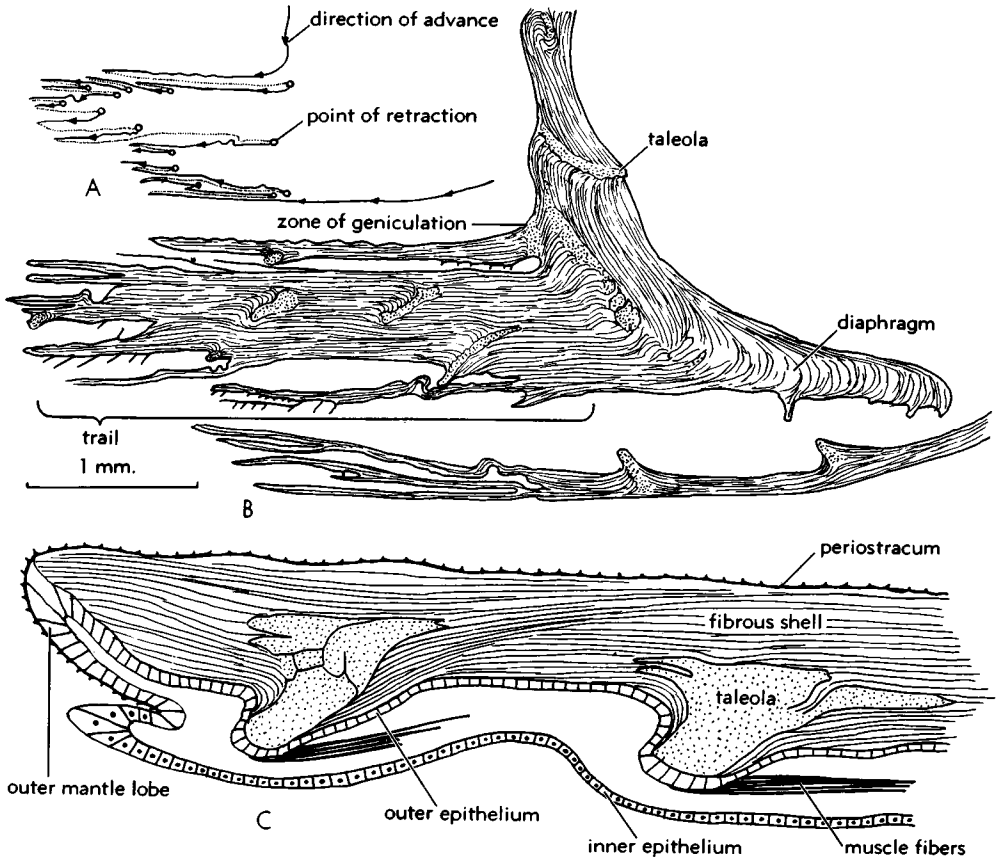


FIG. 74. Stylized sections through trail of *Leptaena* sp., U.Sil., USA, showing (A) inferred path of migration for mantle edge, (B) detail of mantle edge, and (C) inferred relationship between shell and mantle (65).

of the surrounding fibers are proof that the tubercles were contained in evaginated cups of outer epithelium and the only indication of endopunctation among the strophomenoids is found in *Streptorhynchus* as a series of penetrative canals occupying the axes of outwardly directed fibrous cones (48).

Clearly a close relationship exists between pseudopunctae with taleolae and those lacking them, for the presence of taleolae must ultimately have depended upon subtle histological differences within the outer epithelium. The taleolae are comparable in texture with both the terebratuloid primary layer and the areas of muscle attachment in strophomenoids, so that their growth was probably controlled by small islands, each of a few cells of either columnar epithelium or epithelium associated with tonofibrils, within the main spread of cuboidal epi-

thelium responsible for the secretion of the rest of the shell. Sections of the trail of *Leptaena* show that they arose early but behind the inferred position of the outer mantle lobe (Fig. 74). They are, therefore, unlikely to represent imperfectly developed primary shell secreted by persistent patches of columnar epithelium that survived from the tip of the outer mantle lobe, and were more probably the seats of tendonous attachments. This interpretation is consistent with the fact that the mantle edges must have been greatly retractable in many pseudopunctate brachiopods, although, as can be seen in *Leptaena*, incipiently developed pseudopunctae at least were not necessarily permanent sites for tendons.

Pseudopunctae without taleolae are less specialized than those possessing them, since only evaginations of an otherwise undiffer-

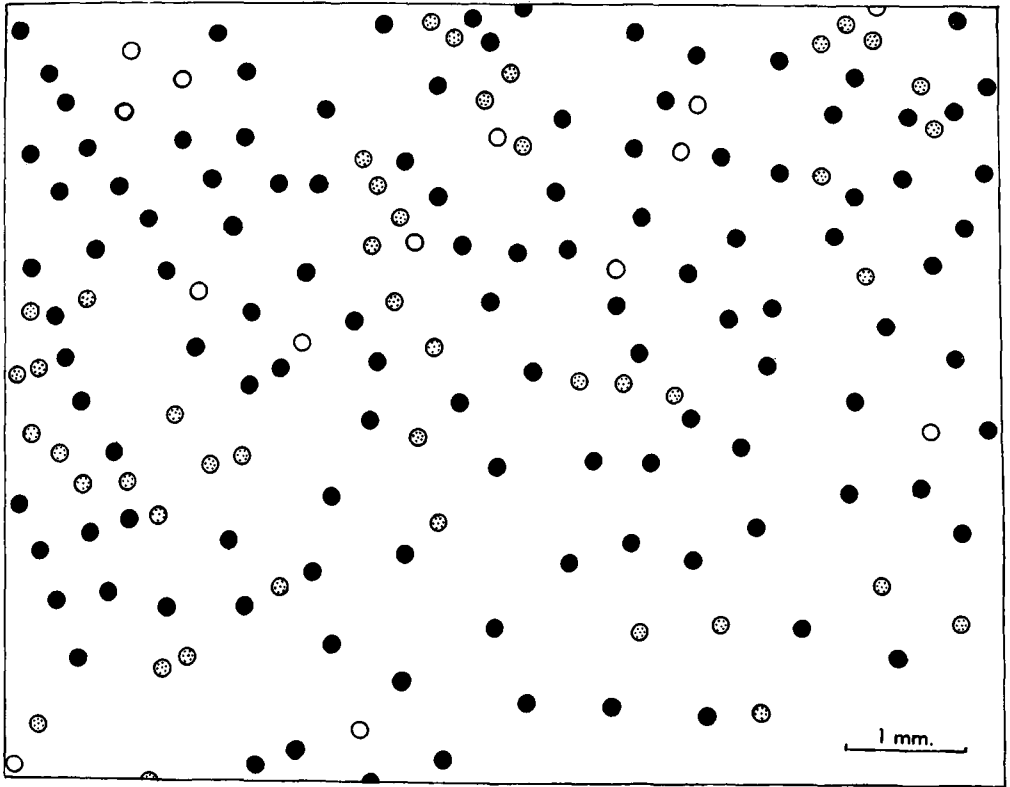
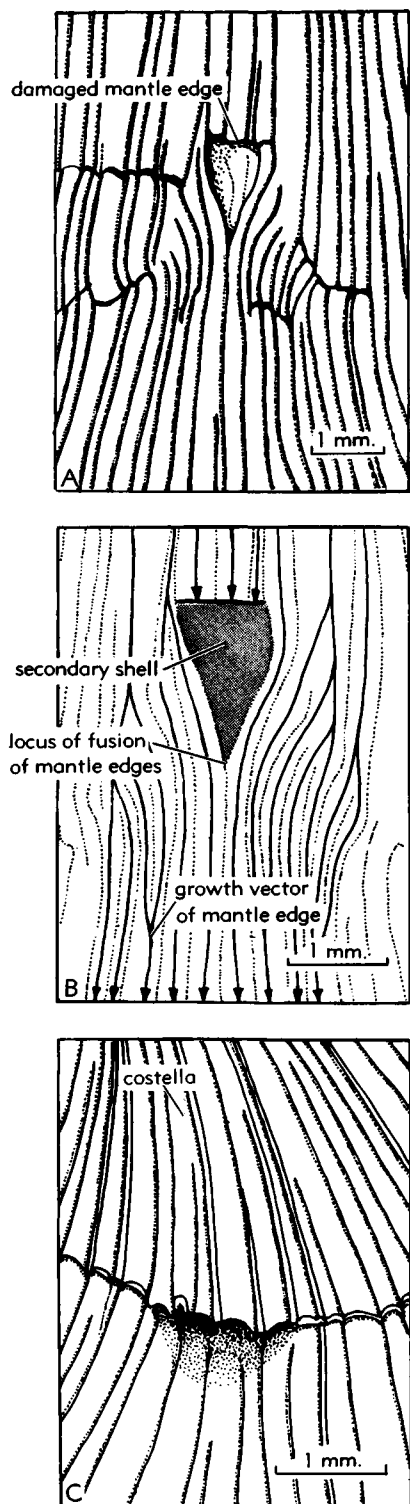


FIG. 75. Distribution of pseudopunctae within small portion of shell of brachial valve of *Rafinesquina nasuta* (CONRAD), U.Ord., USA (solid black circles representing persistent pseudopunctae, open circles impermanent pseudopunctae originating just within external shell surface, and dotted circles impermanent pseudopunctae originating well within secondary shell), prepared from tangential serial sections (65).

entiated cuboidal epithelium were necessary for growth of taleola-lacking pseudopunctae, which possibly supported too few mantle fibrils to promote the secretion of taleolae. It is likely, however, that both types of pseudopunctae are closely related and that taleolae were a later development; they are unknown in certain primitive stocks like the gonambonitaceans, stophomenids, and some of the early davidsoniaceans that must have descended from the impunctate *Fardenia* stocks. It is difficult to judge if both types occur together in the same shell because the disposition and impermanence of pseudopunctae with taleolae are such that random cuts of the pseudopunctae will be present in any section of the shell and will include lateral, tangential, and transverse portions of the reflected fibers simulating pseudopunctae without taleolae. For the same reason, sections normally show pseudopunctae

affecting only parts of the shell, as well as extending throughout the entire inner layer, giving an impression that the pseudopunctae are more commonly impermanent and that they arose anywhere during the growth of the shell (Fig. 73). It can be demonstrated, however, that the majority of pseudopunctae originated near the mantle edge and persisted throughout the growth of the shell (Fig. 75).

Traces of repair are found on the exterior of many brachiopod shells, and include especially those carried out subsequent to the malfunction or damage of the mantle edge. The commonest manifestation consists of a semiconical depression of the shell surface with a steep base more or less coincident with a growth line and a shallowing apex directed anteriorly (Fig. 76,C). It resulted from a localized and abrupt inward sag of the mantle edge and its gradual



elimination during the continued forward growth of the mantle edge. More spectacular malformations arose during temporary or permanent damage of the mantle edge and their origin is best understood in relation to the disruption of radial ornamentation in finely costellate shells (Fig. 76,A). When injury to part of the mantle edge was sufficiently severe to impede forward growth the space anterior to the zone of damage became constricted and ultimately sealed off by the encroachment and fusion of the flanking unaffected parts which thereby restored a fully functional and continuous mantle edge. Such encroachment involves an abnormal proliferation of tissue towards the area of injury, as is shown by the increased number of costellae given off to converge in that direction (Fig. 76,B). Concomitantly, the space immediately in front of the damaged part of the mantle edge became closed by outer epithelium which originated behind the flanking parts of the mantle edges as they moved forward, and was responsible for the deposition of a cover of secondary shell.

No triple stratification closely comparable with that of the articulate shells is known among either the calcareous or phosphatic shells of the inarticulate brachiopods. Intracellular deposition of inorganic shell material is very rare and seemingly occurs only in the Craniidae, and even in this family its secretion is localized, and it does not constitute the entire secondary layer similar to that of the articulates. The structure of the punctate, calcareous shell of the craniids is best known in the Recent *Crania anomala*, but this appears to be typical of the family (Fig. 77,1). Two layers may be recognized in the calcareous shell of the brachial valve, although the junction between them may be rather diffuse. Immediately beneath the periostracum is a thin outer layer within which the punctae "branch" arborescently. This layer varies somewhat in thickness and may be absent locally; it is commonly colored pale brown

FIG. 76. Shell repair in *Rafinesquina nasuta* (CONRAD), U.Ord., USA, showing (A) inferred relationships of area of repair with (B) undamaged growing mantle edges and (C) shell repair following sag of mantle edge in *Rhipidomella* sp., U.Sil., USA (65).

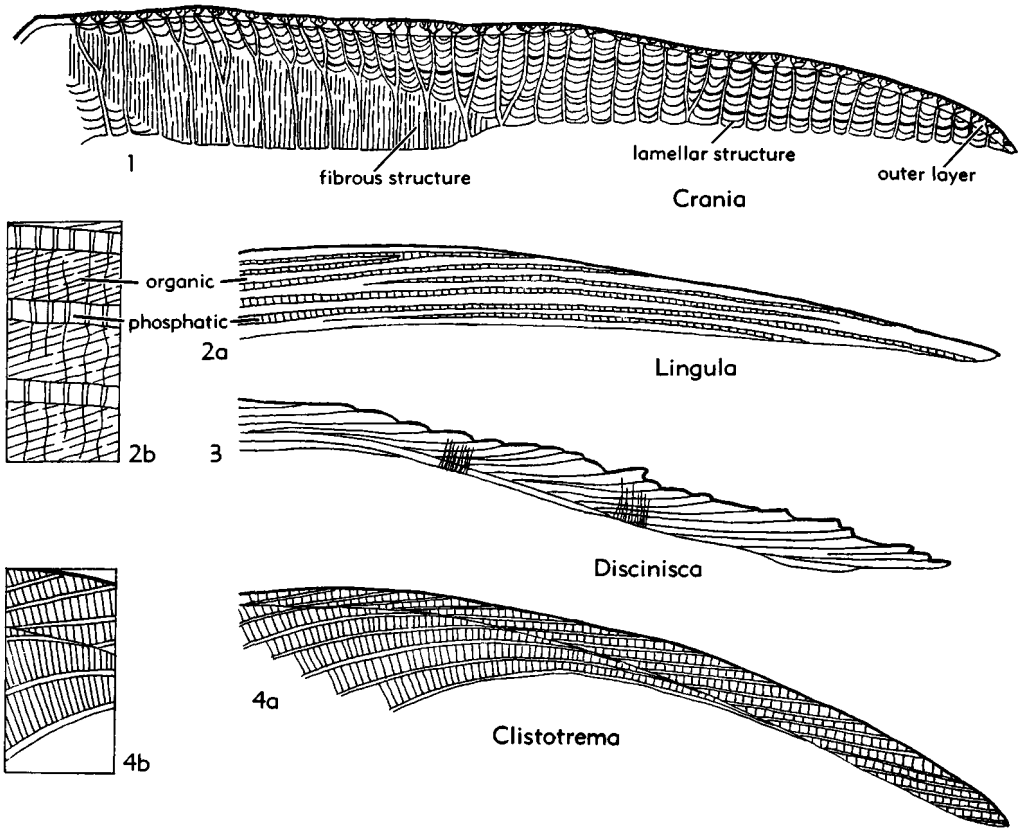


FIG. 77. Stylized thin sections of brachial valves of some inarticulate brachiopods with enlargements showing punctae in organic and phosphatic layers (2b) and disposition of fibers (4b) (63).

or yellow, but otherwise is relatively clear and apparently structureless. In young shells the calcite crystals forming the layer can be seen to be oriented at a high angle to the shell surface (38). Much of the remainder of the valve, comprising the inner layer, has a characteristically strong lamellar structure. The lamellae are oblique to the shell surface and are commonly thicker peripherally than toward the apex of the valve; they are not plane but are festooned between the punctae, sagging ventrally between adjacent perforations. Under high magnifications what appears to be a fibrous structure of the calcite runs parallel to the lamellae, but the more conspicuous breaks between the calcareous lamellae and also, according to BLOCHMANN (8), many of the finer ones, are formed by membranous sheets of organic material secreted between the calcite. This organic material is seemingly absent in the outer calcareous layer. A further

complication of the shell structure is associated with the site of attachment of the muscles, where the tonofibrils secrete fibrous calcite intracellularly (12). These patches of fibrous calcite, which are more sparsely punctate than the remainder of the valve, radiate obliquely outward and ventrally from the apex, marking the track of the muscle scars during progressive growth of the animal. The fibers, in contrast with those of the secondary layer of the articulate shell, are disposed approximately normal to the inner surface of the valve. The structure of the pedicle valve, which is commonly thinner, is basically similar to that of the brachial. In *Crania anomala* the most conspicuous differences between the two are the relatively poor development of the inner lamellar layer of the pedicle valve in addition to the reduced density of punctae, which rarely branch.

The complex craniid shell structure is

clearly a reflection of the varied physiological behavior of the outer epithelium. The cells of the mantle margin secrete only calcite and produce the thin outer layer. With increasing growth of the animal these cells move away from the periphery to occupy a more internal position and there develop a more complex secretory behavior, for the extracellular deposition of calcite of the outer epithelium (with exception of the peripheral zone) is commonly interrupted by the secretion of thin membranous sheets of organic material found in the inner layer of the shell. Thus, these cells are capable of secreting alternately either calcite or organic material. The continuity and disposition of these organic membranous sheets suggest that they are the simultaneous response of part of the outer epithelium to some physiological requirement of the animal. Superimposed upon this pattern is the additional modification of secretory behavior produced when normal outer epithelial cells acquire a tonofibril structure as they become associated with the muscle bases. The tonofibrils secrete calcite intracellularly, but they do not continuously alternate between the deposition of calcite and organic material, for in this part of the shell the organic lamellae are absent and organic material is restricted to what are presumably greatly extended cell walls bounding the fibrous prisms of calcite.

The shell structure of other calcareous-shelled inarticulate brachiopods, which are all impunctate, is not known in as much detail as the craniids, recrystallization proving a common obstacle, particularly in the Cambrian obolellids. The calcareous shell of the craniopsids, trimerellids and obolellids shows no trace of intracellularly secreted fibrous material, and similarly no thin outer layer deposited by peripherally placed cells and comparable with the craniid outer shell layer has been detected. All these shells show a crude layering, the lamellae making an oblique angle with the outer shell surface. It is probable that the calcite was secreted extracellularly, but it is not known whether the break between lamellae represents a small hiatus in secretion of calcite or whether, in life, it was occupied by a thin organic sheet homologous with those found in the craniid shell.

All Recent phosphatic inarticulate brachiopods have a shell consisting of a number of lamellae which are particularly conspicuous in the lingulids, where they are emphasized by their alternating composition (26). In *Lingula* itself, the lamellae are disposed subparallel with the surface of the valves, the phosphatic bands being commonly relatively thick in part of the shell covering the body cavity and thinning out laterally and anteriorly (Fig. 77,2). These phosphatic lamellae were described by GRATIOLET (26) as consisting of short prisms set normal to the shell surface, but this has not been confirmed, and it is possible that he confused some of the punctae with a prismatic structure. Each organic band itself consists of extremely fine lamellae sloping obliquely forward from the inside to the external side of the valve. The disposition of the phosphatic and organic bands relative to the outer surface of the valve and the outer epithelium which secretes them shows that although the adult shell consists of a large number of lamellae, only a few are being actively secreted at any particular stage in the growth of the animal (Fig. 77,2). The outer epithelium is divided into a number of zones which are arranged roughly subparallel with the margin of the valve, zones which secrete phosphatic material being interspaced between those which deposit organic matter. The position of these zones relative to the valve margin is not constant during growth, for the detailed structure of the shell shows that they have a tendency to migrate outward away from the body cavity toward the edge of the shell, and the outer epithelium at any point must alternate in its ability to secrete phosphatic and organic material.

The shell of *Discinisca* differs from that of *Lingula* both in the distribution of the organic material and in details of the shell structure (Fig. 77,3). Beneath the perostracum of *Discinisca* the shell is of uniform composition, the phosphatic material being dispersed in an organic groundmass (9). The shell is composed of a large number of lamellae, distribution of which tends to divide it rather crudely into two layers. The outer layer consists of oblique lamellae which crop out on the outer surface of the valve and are stacked one above the other,

so that in section they resemble tiles on a roof. In the brachial valve, the lamellae are commonly thickest submarginally, thinning and usually dying out before the apex is reached. They are commonly secreted by only the marginally placed cells of the outer epithelium, but in some the majority of the outer surface of the mantle is involved.

Their orientation suggests that, in contrast to the lingulids, significant increase in the size of the shell is invariably accompanied by the secretion of new lamellae in this layer. Although the more apically placed cells of the outer epithelium may be involved in the secretion of the lamellae of the outer layer of the shell, more commonly

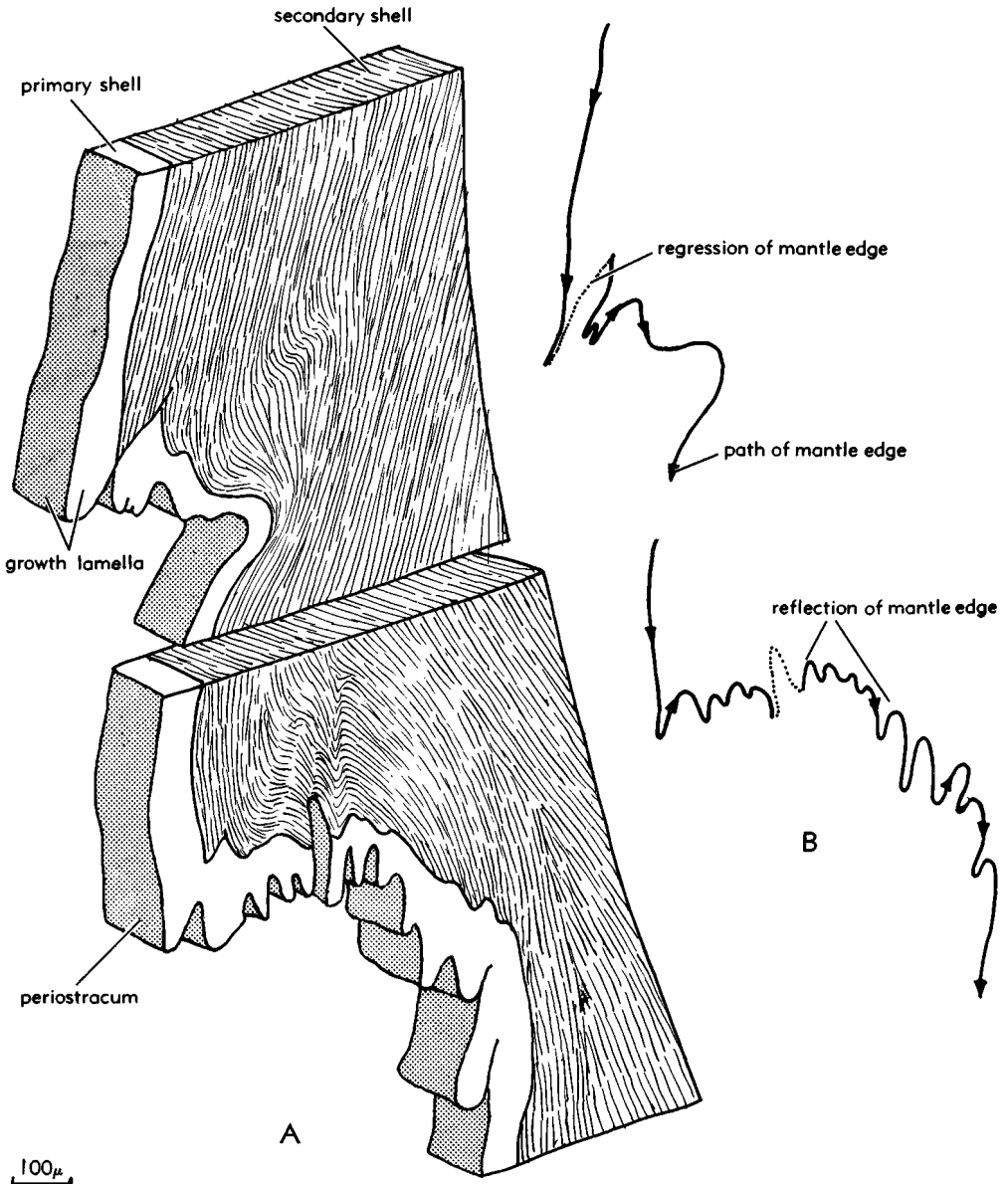


FIG. 78. Structure of portion of brachial valve of *Notosaria nigricans* (SOWERBY) showing (A) nature of lamellae and (B) inferred path of mantle edge responsible for the deposition of portion illustrated in A (65).

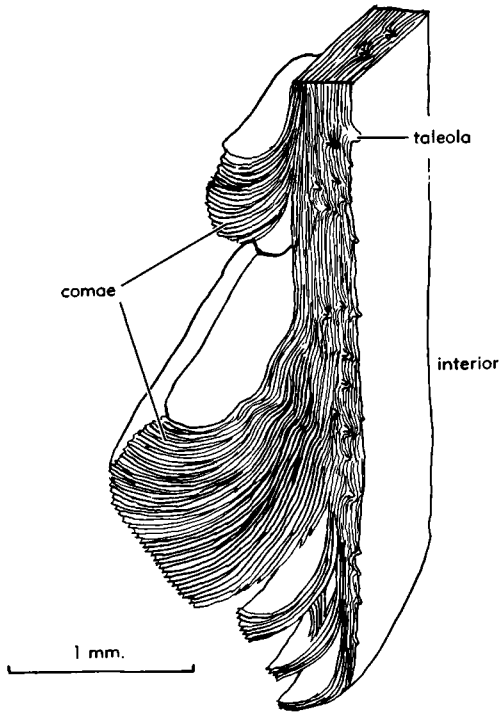


FIG. 79. Stylized section through brachial valve of *Bimuria* sp. cf. *B. buttsi* COOPER, M.Ord., Scot. (65).

they deposit lamellae subparallel with the inner surface of the valve which overstep the previously formed lamellae of the outer layer and form an inner shell layer.

The shell structure of fossil phosphatic-shelled inarticulate brachiopods is known for only a limited number of genera. The lingulaceans, with exception of the calcareous-shelled craniopsids, apparently have a shell structure closely resembling that of living *Lingula* and *Glottidia*. Similarly the shell structure of *Discinisca* appears to be typical of the discinaceans.

In the acrotretid shell the distribution of lamellae shows some similarity with the discinid pattern; an outer layer which consists of relatively short lamellae strongly oblique to the shell surface and secreted by only the periphery of the mantle and an inner layer secreted subsequently by the remainder of the outer epithelium (Fig. 77, 4). Although the shell is now seemingly made up mainly of calcium phosphate, both shell layers include two distinctly different types of lamellae which alternate with each other. The thicker lamellae, forming the

bulk of the shell, have a strongly fibrous structure, the fibers being arranged normal to the lamellae. The thinner intervening bands lack the conspicuous fibrous structure and may represent material of organic origin that has been phosphatized during diagenesis of the enclosing sediments. The shell structure of the paterinaceans is poorly known. Their valves consist of a number of lamellae disposed subparallel with the shell surface and some specimens show a suggestion of the discinid pattern with the shell divided into two layers by differing orientation of the lamellae.

The punctuation of Recent *Crania* is known to be due to the development of caecal evaginations from the outer epithelium (see Fig. 4), and since this condition is typical of all known species of fossil craniids it is probable that the shell was always permeated by branching caeca. It is feasible to assume that projections from the mantle occupied the coarse apertures in the phosphatic meshwork of *Dictyonites*, since no inner shell layer is known, but it is impossible to determine whether these projections were caeca. The extensions of the mantle into the shell of other living inarticulates like *Lingula* and *Discinisca* are extremely fine, and although BLOCHMANN (9) has recorded projections of the mantle epithelium into the shell of *Lingula* it is probable that many of these are cytoplasmic strands, rather than caeca. CHAPMAN (13) has reported the existence of fine perforations within the shell of Silurian lingulids which may have accommodated similar strands. In the lingulids, the punctae are consistently coarser in the phosphatic layers and may be virtually invisible in the organic lamellae of dried shells. The punctae of *Discinisca* are unusual in branching toward the inner surface of the valves (9).

The external surfaces of the protegulum are smooth, but a variety of distinctive features, usually arranged concentrically and radially, may develop during postlarval growth and are referred to as ornamentation. In many species the shells remain smooth except for the sporadic occurrence of concentric lines which are commonly more conspicuous and more closely spaced toward the periphery of gerontic specimens. These are known as **growth lines**, although they do in fact represent periods of shell

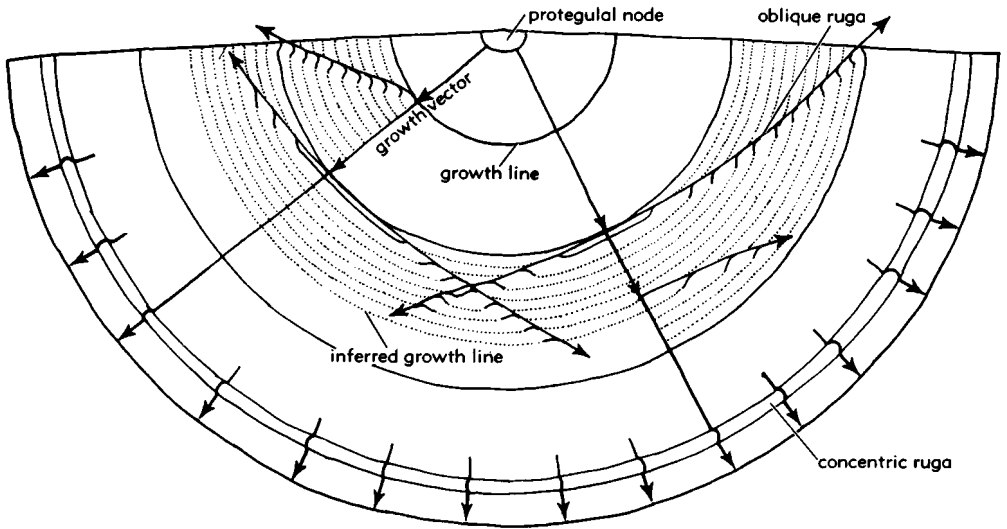


FIG. 80. Diagrammatic illustration of nature and origin of oblique and concentric rugae (65).

deposition when forward growth was in abeyance, so that their occurrence is controlled by environmental factors such as temperature (Fig. 59). Regularly spaced concentric outgrowths (lamellose or imbricate condition) which may be made up of secondary as well as primary shell are also characteristic of many genera (Fig. 78). These lamellose extensions may also be prolonged as spines (e.g., *Tegulorhynchia*) or may be so thickened as to form knobby protuberances (comae) that give the shell a gnarled appearance (e.g., *Bimuria*) (Fig. 79). Irrespective of the unusualness of these various features, however, they were all covered by adherent periostracum and deposited by a retractible mantle edge involved in a gradual retreat when the primary layer is doubled back or reflected upon itself or in a sudden regression when no duplication of primary shell is evident. The growth of lamellose skirts in several inarticulate genera was probably controlled by similar contractions of the mantle margins.

Another form of oblique or concentric ornamentation is the wrinkling of the shell surface (rugation) which is especially characteristic of the strophomenoids, productoids, and chonetoids but is also known rarely in other groups (e.g., *Kulumbella*, *Iru*). The rugae may be continuous and concentric, as in *Leptaena*, where they are

precursory to formation of the trail, which may be regarded, in that genus, as an indefinite continuation of the anterior face of the last-formed ruga; or impersistent and oblique, like those of *Sowerbyella* (Fig. 80). Rarely, as in *Ptychoglyptus*, the rugae are concentrically disposed but so interrupted at their junctions with the more accentuated elements of radial ornamentation that they are broken up into a series of chevron-like or oblique strips. Exceptionally also, two or more sets of oblique rugae may develop, intersecting at obtuse or acute angles (e.g., *Bellimurina*, *Kulumbella*).

Rugae were formed by a deflection of the mantle edge through an arc of 180 degrees along an axis which was disposed in any direction except that of the radial vector relative to the mantle periphery (deflections normal to the mantle margin giving rise to radially disposed features like ribs, folds, etc.). The concentric arrangement of *Leptaena* was the simplest condition in that it involved a simultaneous deflection of the growing mantle edges along the entire commissure anterior to the hinge line. An obliquely disposed ruga arose through a localized deflection of the mantle edges at any point along the margins and during subsequent growth the deflection was transmitted laterally either in one or both directions along an axis traced out by the rugae in a full-grown shell. In this manner two

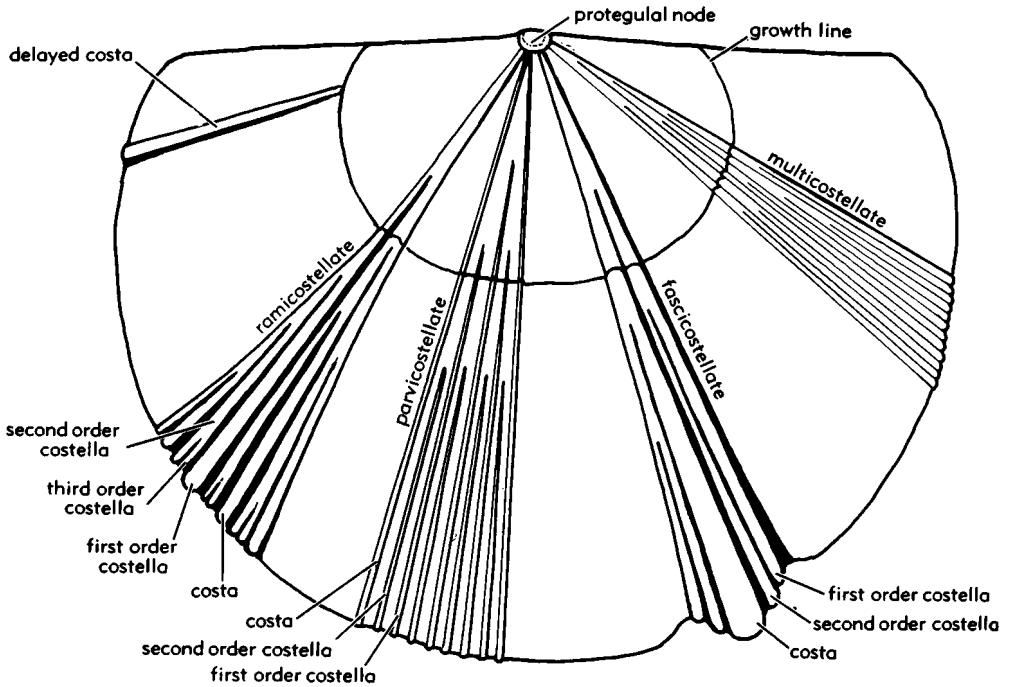


FIG. 81. Diagrammatic illustration of more important types of brachiopod radial ornamentation (65).

or more sets of rugae may have developed a complicated pattern of intersections (Fig. 80).

The raised concentric ridges or threadlike lines (*fila*) ornamenting the valves of some inarticulates, like *Schizotreta* and *Rhyso-treta*, must have formed in the manner of small scale rugae by the periodic deflection of part or all of the mantle edge into a wave.

All radial ornamentation (*ribs*) is due to a persistent or impermanent deflection of the mantle edges along vectors radiating from the protegular nodes, so that every variety in size and shape can be found (Fig. 81). The basic element is a well-defined elevation of the shell surface, triangular to rounded in transverse section and of variable amplitude and wave length, which arises at the protegular node and almost invariably extends to the margins of adult shells. Such a feature is known as a *costa*, whereas a *costella*, which may be of comparable thickness and shape, does not arise at the margin of the brephic shell but by branching from or intercalation between costae at any stage during subsequent growth. Defined in this way according to

the point of origin of the features, the terms have a different meaning from that understood by many students who have used them in a necessarily arbitrary manner to imply a relative coarseness in texture, which is better expressed as a frequency count for a standard arc at a stipulated distance from the beak. In a few species (e.g., triplesia-ceans, rhynchonelloids, etc.), the radial ornamentation may first appear along an arc of growth well beyond the protegular node and it is suggested that this pattern be called delayed costation or delayed costellation if first or higher orders of costellae are involved. Certain brachiopods, especially the strophomenoids, are characterized by a finely textured ornamentation consisting of costae and several orders of costellae, all of which arise by intercalation. This pattern is usually referred to as *parvicostellate* (as opposed to *ramicostellate*, which implies an origin solely by branching, as in most orthoids); and when the costae and certain costellae are accentuated to segregate the ornamentation into a series of sectors, the condition is referred to as *unequally parvicostellate*. When the costellate and rami-

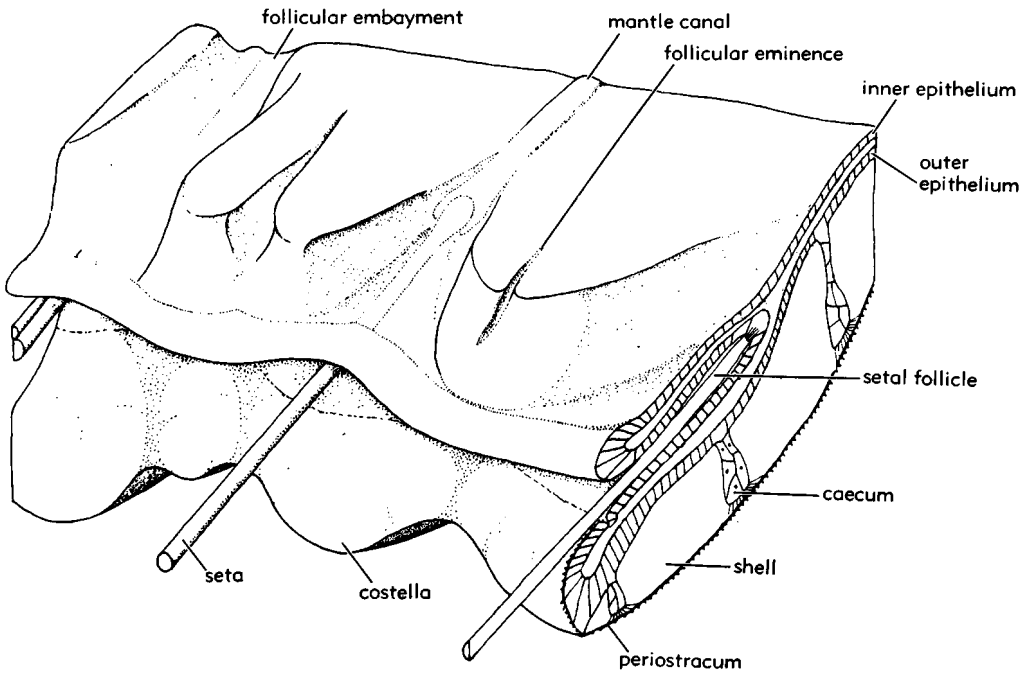


FIG. 82. Inferred relationships between mantle edge and shell margin in typical enteletacean (65).

costellate patterns are so evenly divided as to give an appearance of a uniformly fine ornamentation they are referred to as **multicostellate** (e.g., *Schizophoria*), whereas the segregation of these patterns into conspicuous bundles is called **fascicostellation** (e.g., *Fascicostella*).

The costellate radial ornamentation of some extinct brachiopods is probably related to the distribution of setae along the mantle edge in the style characteristic of Recent *Terebratulina* (compare Fig. 82). Along the edge of the *Terebratulina* valve, the secondary shell layer is not uniformly distributed, for it is indented by a series of V-shaped embayments, underlying the crests of fully formed ribs and pointing posteriorly. Each embayment accommodates a follicle containing one or two setae or, very rarely, two follicles separated by a narrow ridge. The interspace of two adjacent ribs mutually coincides with a V-shaped eminence on the internal surface of the valve, pointing anteriorly but ending abruptly just inside the zone of the valve edge which is occupied by the mantle lobes. As the shell grows, each eminence develops a slight median furrow

which begins to widen and deepen into an embayment, later to be occupied by a new follicle. Fully developed follicles appear relatively suddenly along the mantle edges of dissected specimens, but it is likely that they are first differentiated within the mantle groove when the eminence, corresponding to the intercostellate spaces on the outer surface, is first indented by a median furrow, that is just before a new costella, containing the developing embayment, branches off from its parent (61). When the *Terebratulina* shell is closed, the crenulated commissures of the valves interlock in such a way that the eminences of one valve fit into the embayments of the other valve. The edges of both valves, corresponding to the zone of the mantle lobes, remain slightly parted and parallel to each other and thus facilitate the continuous deposition of the shell, as well as the movements of the setae which protrude between each costella and the complementary eminence of the other valve.

The setal arrangement in *Terebratulina* with its well-developed incostellate spaces is quite distinct from that of *Hemithiris*,

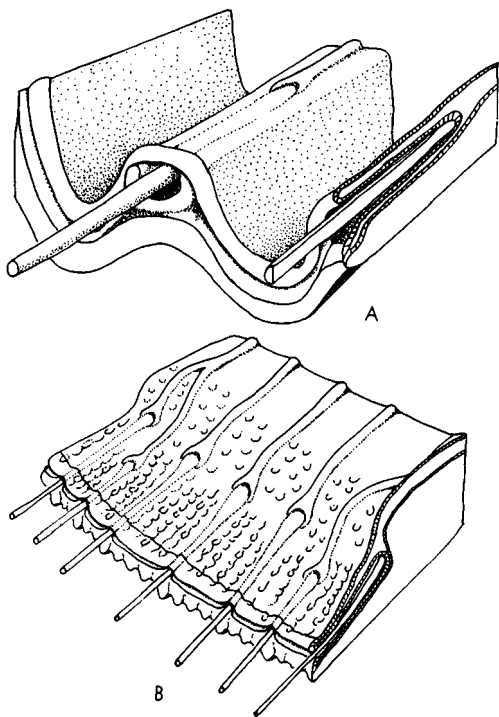


FIG. 83. Inferred relationships between mantle edge and shell margin in *Hesperorthis* (A) and *Sowerbyella* (B) (65).

which is ornamented by low-rounded ribs separated by linear interspaces. In the latter genus the follicles occur at regular intervals along the mantle edge, irrespective of external ornamentation, and apart from a marginal occurrence of slight ridges corresponding with the interspaces there is no differentiation of the internal edges of the shell. This lack of indication of setae on the internal surfaces is also true of smooth shells like *Macandrevia* and of the coarsely costellate *Terebratalia* in which the radial ornamentation may be regarded as a superimposed crenulation of the commissure not affecting the distribution of setae.

The morphology of the inner marginal edge of costellate fossil shells like those of the enteletaceans is so like that of *Terebratulina* that a similar arrangement of setae probably obtained (Fig. 82). A comparable pattern was also characteristic of costate shells (e.g., *Hesperorthis*, *Plaesiomys*, *Orthambonites*) (Fig. 83,A). In such stocks as these, the costae are represented internally by grooves, and the interspaces by V-shaped

or bluntly rounded eminences indented by a median furrow which is shallower than the groove but about as long. Judging from comparisons with living brachiopods and the impressions of peripheral branches of the mantle canals on the interiors of fossil shells like *Cyrtonotella* (37), it is feasible to assume that follicles occupied at least the median furrows. The arrangements in other costellate orthoids and cliambonitoids seem to have been more primitive in that no well-differentiated eminences, coincident with the intercostellate spaces, were developed and it seems likely that the follicles occupied short grooves corresponding to the crests of the costellae. The absence of distinct grooving at the inner margins of adult shells of *Atrypa* suggests that as in *Hemitheir*, there was no relationship between the incidence of setae and costellae in fossil species with this style of radial ornamentation. *Enteletes*, *Meekella*, and other brachiopods with strong costae superimposed upon a finely costellate ornamentation probably possessed a follicle distribution unaffected by the coarser ribbing, as in *Terebratalia*. The parvicostellate ornamentation of the strophomenoids may well have reflected a high density of setae at the shell margin. In *Sowerbyella*, for example, deeply incised, short grooves, each ending posteriorly as a pit in the peripheral rims of secondary shell, occur at regular intervals along the lateral and anterior margins (Fig. 83,B). These grooves probably contained follicles. They underlie the crests of all costae and older generations of costellae and are separated from each other by low, flat, rectangular-ended eminences that correspond to as many as 5 or 6 younger costellae. Here and there slight pits and furrows indent the eminences and probably represent the early development of follicular grooves. Thus, at any one stage of growth, setae protruded from beneath about one-quarter of the costellae.

Some rhynchonelloids (e.g., *Sphaerirhynchia*) which are highly globose when adult and which develop a vertical zone formed when anterior and lateral growth is in abeyance show an unusual modification of the anterior and lateral margins of the valves. The interspaces between costae or costellae are elongated to form long, slender marginal spines which lie against the inner surface

of the costae or costellae involved in the vertical zone of the opposing valve. Conceivably, these spines had some protective function when the shell was open, as they form a regular grille across the gape (44) (Fig. 84).

The valve margins of Recent setae-bearing inarticulate brachiopods, lingulids, and discinids are smooth, and it is only in the craniids, which lack setae, that modifications

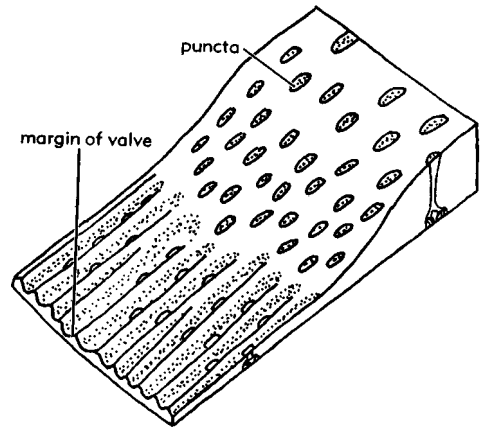


FIG. 85. Small segment of posterior margin of brachial valve of *Crania anomala* viewed internally, punctae initially located in grooves separated by low ridges (63).

of the periphery of the valves occur. In *Crania anomala*, the modifications in the brachial valve are superficially similar to the eminences and furrows of *Terebratulina* but are very much finer and associated with the development of the punctae. A narrow peripheral zone bears numerous, very fine, radially disposed ridges separated by narrow grooves in which the punctae are located. With growth of the shell, the ridges increase in number by bifurcation, but apically they are buried by the later-formed lamellae of the secondary shell layer (Fig. 85). The margin of the pedicle valve of this species, as in many post-Paleozoic craniids, is minutely pustulose, and the punctae are not regularly arranged but are grouped in the depressions of the shell between the pustules (8).

The brachiopod shell may also be finely to coarsely ornamented by a series of outgrowths on the inner, as well as the outer, surfaces, generally cylindroid to conical in habit and referred to as granules, tubercles, or spines. In terms of growth, two distinct categories may be recognized. The fine granules of *Platystrophia* and *Lingulasma*, the tear-shaped tubercles of *Spinocyrtia*, and the spines along the ribs of *Dictyothyris* (Fig. 86) represent solid excrescences on the external surface of the valves fashioned out of primary shell at the tip of the outer mantle lobe. The spines of *Tegulorhynchia*, *Spinilingula*, etc., normally represent curved, triangular prolongations of the lamellae, but

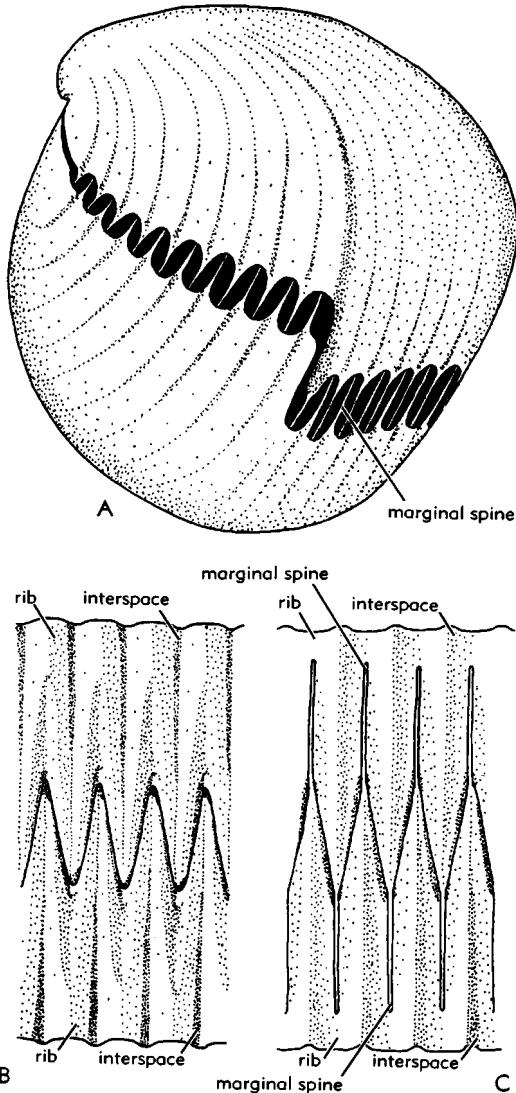


FIG. 84. Marginal spines of *Sphaerirhynchia*; A, oblique anterolateral view of open shell showing grille formed by spines; B, detail of part of anterior commissure, viewed externally; C, detail of part of anterior commissure, viewed internally, showing relation of spines and interspaces (63).

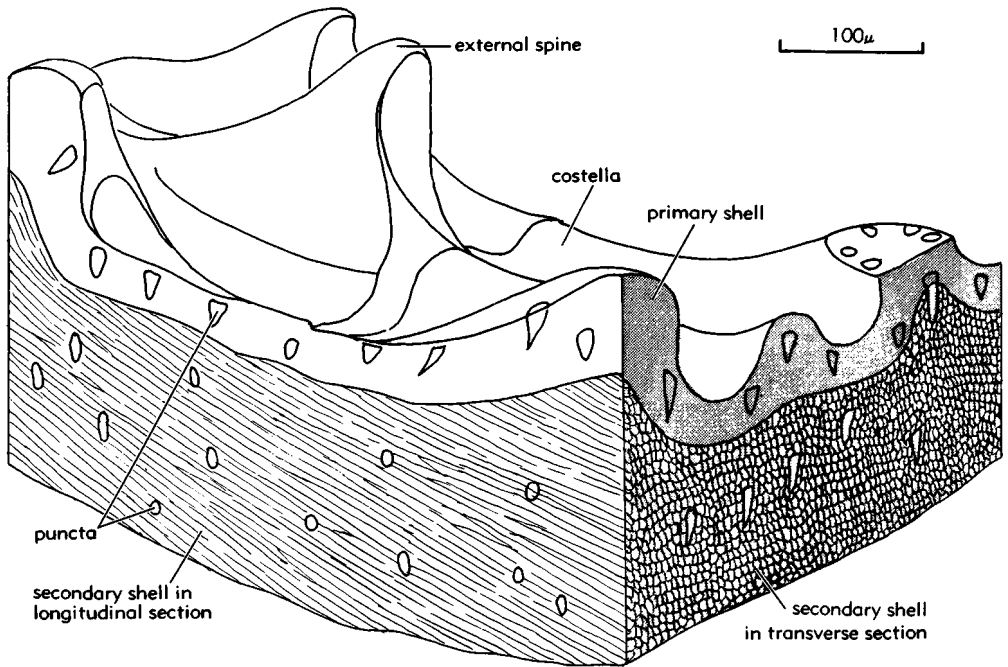


FIG. 86. Section of pedicle valve of *Dictyothyris coarctata* (PARKINSON), M. Jur., Eng., showing relationships of external spines with primary and secondary shell layers (65).

may also develop into hollow cylinders which must have been secreted around retractable epithelial outgrowths from the tips of the outer lobes and which were subsequently sealed off by deposition of the secondary shell layer. The double-barreled spines of *Phricodothyris* were probably formed in the same way by pairs of adjacent epithelial outgrowths (25) (Fig. 87).

The hollow productoid, chonetoid, rhynchonelloid, and siphonoretacean spines that also open into the shell interior were formed in a different way (Fig. 88). Many of these spines must have continued to increase in length throughout life of the animal. But increments could only have been added at the distal ends which must have been occupied by persistent generative tips capable of proliferating outer epithelium to line the lengthening axial canals and thereby maintain the processes of shell secretion (57). Since all spines were first differentiated at the shell margin, it is likely that the tips were actually isolated bits of the outer epithelial lobes that simply retained the generative properties of that part of the mantle. In all probability, continuity of the perio-

stracal layer was maintained by the activity of the apical cells making up these generative tips and it is feasible that, in some spines, these were responsible for the secretion of a chitinous pad by which they became attached to the substratum. These epithelial evaginations were commonly sealed off by later deposition, especially in the body cavity, in which event growth of the spines ceased and the axial canals end blindly within the secondary shell layer.

Striking color patterns are rarely developed in the Brachiopoda. The presence of periostracum usually imparts a brown tinge to shells, but the underlying calcareous or chitinophosphatic material commonly provides the basic colors of the brachiopods. In inarticulate brachiopods, browns, or more rarely, green or cream colors predominate, while among the articulate brachiopods creams to pinks are common, especially among the terebratuloids, although whites and blue grays (e.g., *Hemithiris*) are also known. Original color variations are less certainly diagnosed in fossil groups because even consistently variegated patterns may be related to post-mortem differential stain-

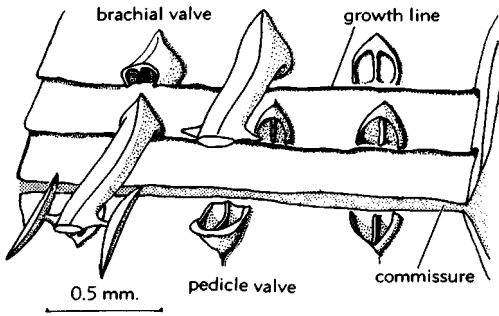


FIG. 87. Double-barreled spines of *Phricodothyris* sp., L.Carb., N.Ire. (65).

ing particularly of punctate shells that were subjected to selective penetration. A small number of species (23), however, show variations in light and dark grays or browns that evidently arose during shell growth. They are first found in Devonian shells and are indeed best known in terebratuloid species of that period. The variations include concentric alternations of light and dark hues as in *Cranaena*, *Hamburgia*, and *Subrensselandia*, as well as radial alternations and spotted patterns in members of the first two genera (14). CLOUD has remarked that concentric changes could have resulted during phases of slower shell growth involving a relative concentration of color-inducing compounds which are more diffuse in the more quickly growing bands. He also noted that the radial bands of *Cranaena* coincided with the principal canals of the mantle lobes, although this coincidence is not true for the numerous, somewhat irregular, radial bands of *Coenothyris vulgaris* (SCHLOTHEIM).

MODIFICATIONS OF PEDICLE OPENING

The pedicle of young Recent articulate brachiopods protrudes posteriorly through the delthyrial opening, which, during further growth, is generally restricted by the development of lateral deltidial plates defining the foramen. The relationship between the unmodified delthyrium and the pedicle-outer epithelial junction has already been discussed, and the growth of coverings to the delthyrium has to be reviewed in this context. The delthyrium is bounded by a pair of progressively divergent ridges

representing the continuously growing teeth. That part of the pedicle epithelium initially attached to the apices of both valves

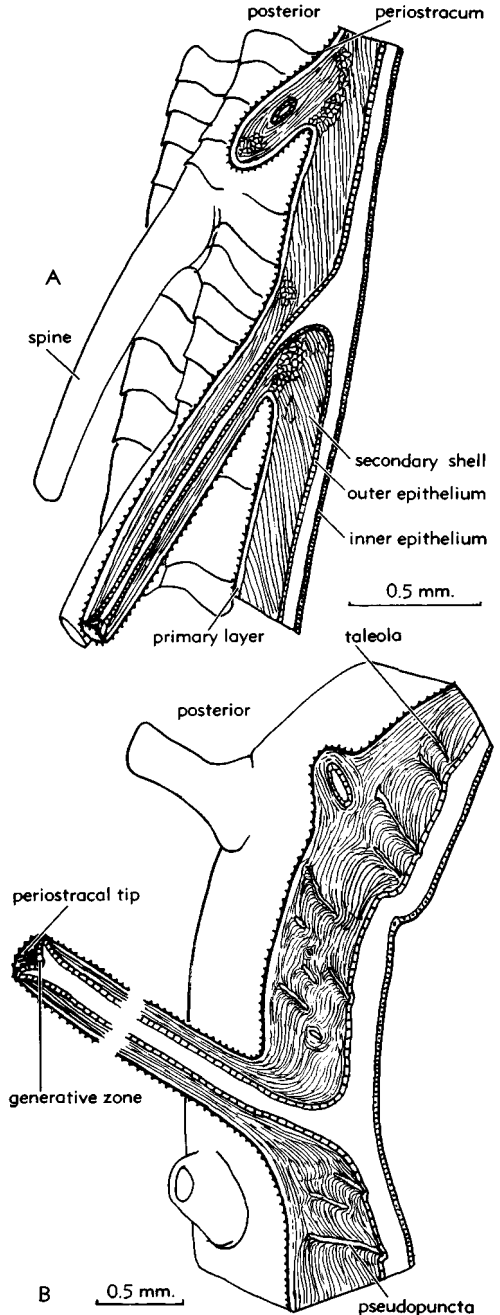


FIG. 88. Reconstructions showing inferred relationships between mantle and shell spines (A) in *Acanthothyris spinosa* (LINNÉ), M.Jur., Eng., and (B) in *Productella* sp., U.Dev., USA (65).

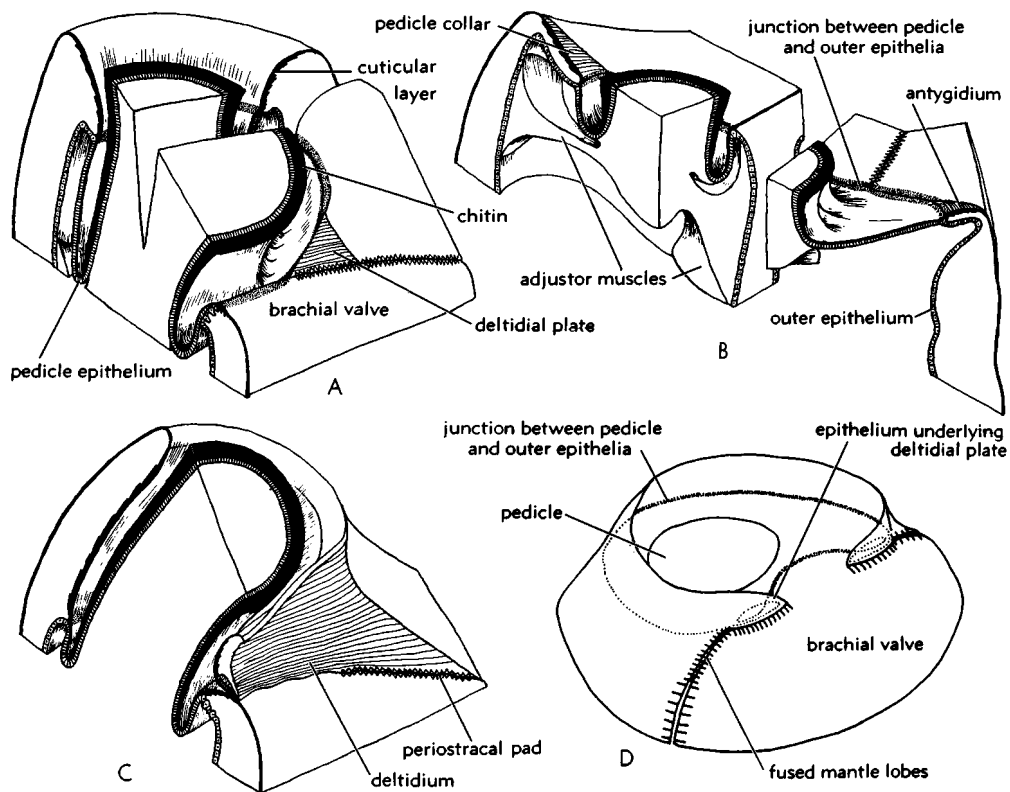


FIG. 89. Relationships between pedicle and shell in (A) *Terebratulina* and (C) *Laqueus*, with (B) inferred restoration of them in *Hesperorthis australis* COOPER, M.Ord., USA, and (D) diagrammatic representation of course of junction between pedicle and outer epithelia in *Laqueus* prior to fusion of epithelium underlying deltidial plates (A-C, 57; D, 65).

is fixed; but lateral expansion along the posterior margin during the growth of the ventral cardinal area causes the epithelial junction to assume an oval outline, with an increasing proportion of the circumference within the pedicle valve (compare Fig. 89,D). It is this widening gap between the diverging teeth ridges and the boundary of the pedicle epithelium which is filled by deltidial plates. The inner surfaces of the deltidial plates are necessarily continuous laterally with the pedicle collar, but the outer surfaces are made up of primary shell. They are therefore deposited by outer lobes of outer epithelium, continuous at least with the ventral part of the fused mantle lobes at the posterior margin (57) and are like a pair of triangular flaps, posterior to the dorsal beak, with their bases expanding toward the median plane. In rostrate brachiopods with the dorsal pedicle zone not projecting beyond the hinge axis

(e.g., *Terebratulina*), the plates remain discrete, flanking the dorsal sheet of pedicle epithelium (Fig. 89,A). In other living brachiopods, however (e.g., *Magellania*, *Laqueus*), the growth of the dorsal umbo well into the pedicle valve shifts the dorsal pedicle boundary anteroventrally from the expanding bases of the deltidial plates, which, continuing to grow toward each other, ultimately meet medially to form a single structure (deltidium). If the outer epithelial sheets underlying the deltidial plates fuse medially, the line of junction on the deltidium is lost and a **symphytium** results (Fig. 89,C). The edge of the pedicle capsule now appears to be restricted to the foramen of the pedicle valve, although a dorsomedian strip of pedicle epithelium is still connected with the posterior edge of the brachial valve (Fig. 89,D). The position of the foramen relative to the deltidium and the ventral beak can vary through migra-

tion and resorption, and a number of terms are in general use to indicate its location (Fig. 90).

The open delthyrium and its dorsal counterpart, the notothyrium, are typical of the great majority of orthacean, enteletecan, and pentameroid brachiopods, and it is safe to assume that the junction between the pedicle and outer epithelia in such forms as these coincided with the boundaries of the diamond-shaped aperture made up of both notches (Fig. 89,B). Some modification did occur. The pedicle collar (pedicle or apical plate) was quite commonly developed by retreat of the ventral edge of the junction, and deltidial plates fusing to form either a deltidium or notodeltidium (16) are known to have developed independently in *Barbarorthis* and *Phragmophora*. The unmodified notothyrial edges acted as attachment surfaces for the pedicle junction in precisely the same way as those of the delthyrium, so that lateral or apical extensions of them (the so-called "chilidial plates" and "chilidium" of *Hesperorthis*, *Nicolella*, *Valcourea*, etc.) arose in exactly the same manner as the deltidia. The spiriferoids display a greater variation in delthyrial modification owing to repeated atrophy of the pedicle and the common, extravagant development of the ventral interarea. The sunken delthyrial plate of *Syringospira*, *Syringothyris*, etc., is the homologue of the elevated pedicle collar of the living terebratulacean *Agulhasia*. In *Syringospira* (Fig. 91), the gap between the delthyrial plate and the brachial valve was closed by the deposition of a series of concentric layers (the largest basal layer overlapping the posterior surface of the delthyrial plate) secreted by the ventral and lateral edges of the outer epithelium of the junction moving posterodorsally. This abnormal structure (stegidium of COOPER, 15) was clearly related to a dorsal migration and ultimate atrophy of the pedicle and a similarly induced condition is known in stocks like *Mucrospirifer* which lacked delthyrial plates. An apically situated, imperforate delthyrial cover is found in some spiriferoids like *Eospirifer* and also rarely in the pentameroids (14) and was deposited by outer epithelium at the ventral edge of a pedicle undergoing atrophy. The delthyrial cover

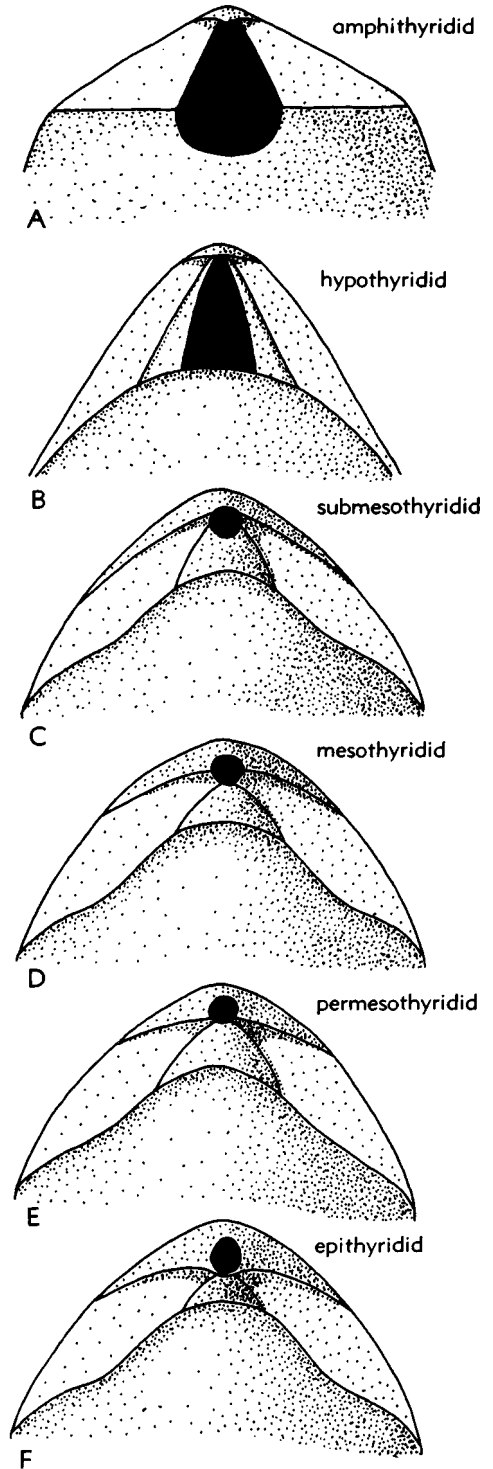
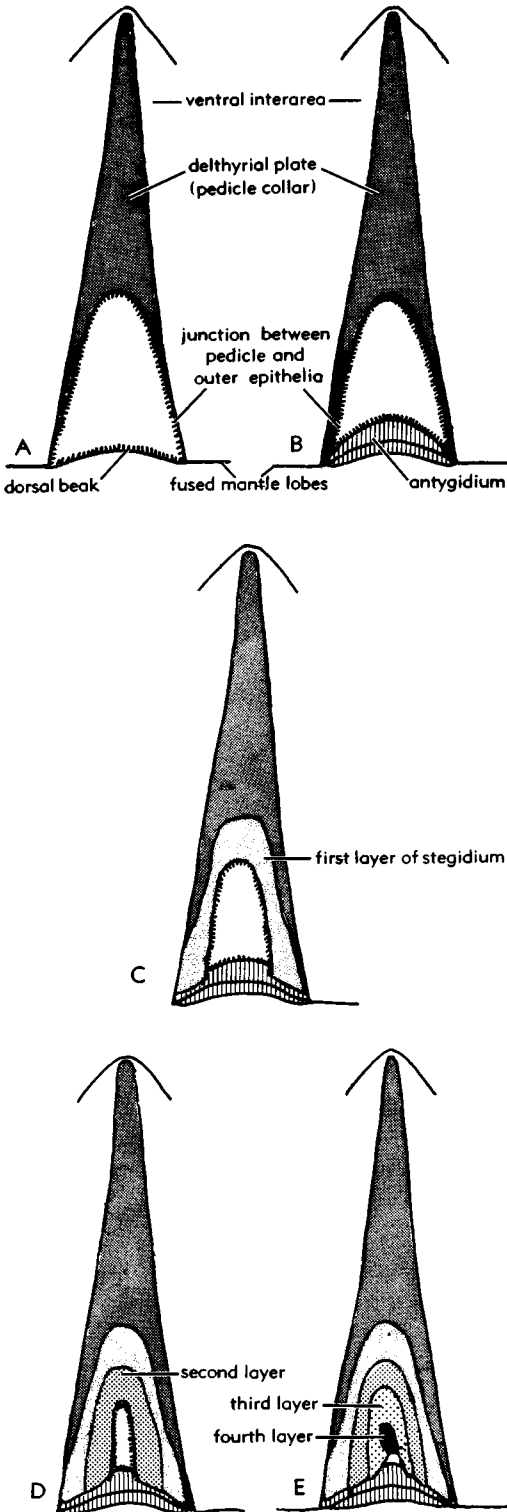


FIG. 90. Classification of some articulate brachiopods based on position of pedicle opening relative to beak ridges (63).



of *Cyrtina*, with its subcentrally placed foramen (see Fig. 120), was probably formed by a similar secretion of the apical portion of the cover, combined with deposition of a symphytium dorsal of the foramen.

The covers to the delthyrium and notothyrium of the strophomenoids, referred to respectively as **pseudodeltidium** and **chilidium**, were deposited in an entirely different way. The young shells of a sufficient number of independent stocks are now known to suggest that the junction between the outer and pedicle epithelia was restricted, throughout growth, to the pedicle valve. In such first-formed shells the pedicle opening occurs supra-apically (3) within the pedicle valve and is commonly enclosed in a high calcareous ring (pedicle sheath) (Fig. 92,B). The pedicle junction, therefore, must have lain within the edge of the ring, so that the pseudodeltidium lying dorsal of it was an integral part of the interarea, and its development was in no way dependent upon the presence of the pedicle but on secretion of its dorsal edge by an outer lobe of outer epithelium (57) (Fig. 92,A). The deposition of the chilidium must have been controlled in exactly the same way by outer epithelium as were the entire margins of both valves, a condition comparable with that involving the growth of the inarticulate shell. In early strophomenoids, as well as the billingsellaceans and kutorginaceans, which also possess such covers, the dorsal edge of the pseudodeltidium is not flush with the hinge line but concave to it; and although the chilidium may protrude into the gap, it is not entirely filled, so that a well-defined posteromedian gape commonly is found. The gape may have been bridged by periostracum secreted by an isthmus of outer epithelium homologous with the zone of fused mantle lobes (Fig. 92,C); alternatively it may have been closed by an inner epithelial strip homologous with part of the posterior body wall of the inarticulate brachiopods (Fig. 92,D).

Despite the lack of information about development of the delthyrial covers in the clitambonitoids and triplesiaceans, it is likely that they too were homologous with the strophomenoid pseudodeltidia, and the

FIG. 91. Stages in deposition of the stegidium of *Syringospira prima* KINDLE, U.Dev., USA (65).

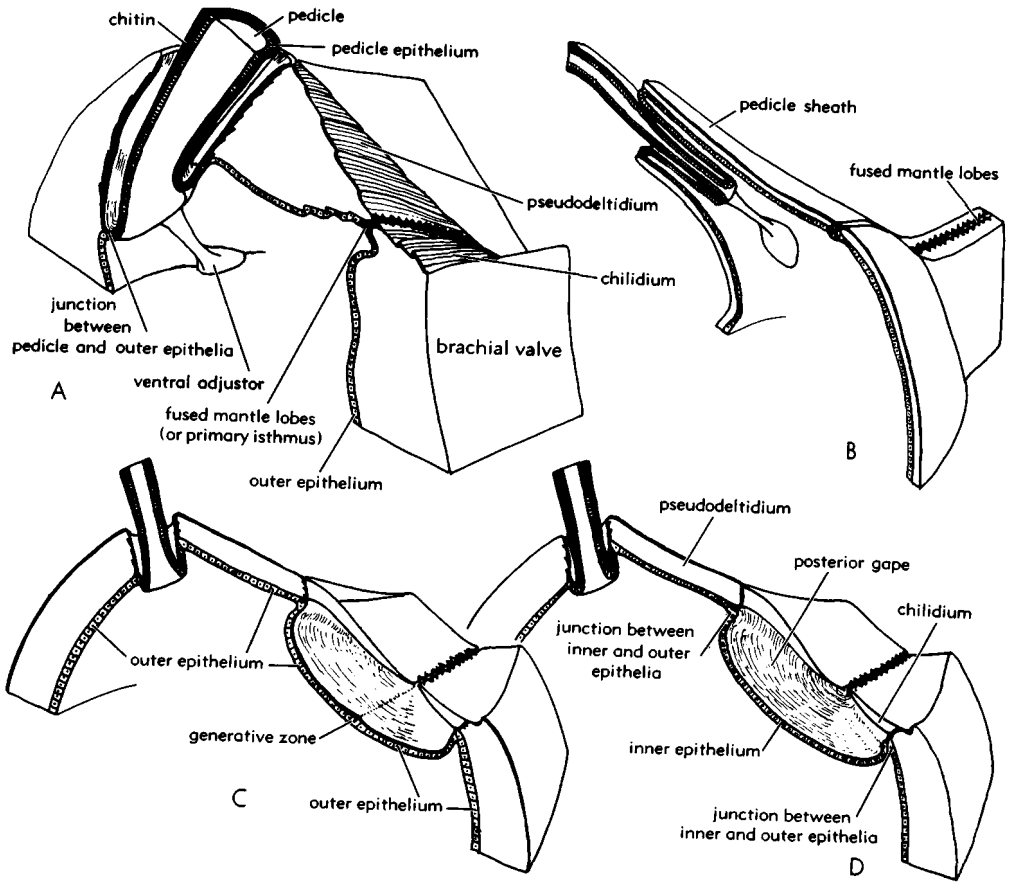


FIG. 92. Inferred relationships between the pedicle and pedicle opening (A) in adult *Leptaena*, (B) young *Fardenia*, (C) adult *Nisusia* on assumption that the posterior gape was closed by a primary isthmus of outer epithelium or an extension of fused mantle lobes, and (D) adult *Nisusia* on assumption that the posterior gape was closed by a posterior body wall of inner epithelium (65).

presence of an inner calcareous pedicle tube in the triplesiaceans can only be explained on this assumption (62). The pseudodeltidium may be resorbed along with the beak of the pedicle valve, as in *Leptaena*, *Macrocoelia*, etc., and if the cover in the clitambonitoids has been correctly homologized it may not develop at all (e.g., *Apomotella*). A loss of pedicle occurred in the majority of the strophomenoids and all productoids and chonetoids, the pedicle valves of which were commonly cemented to the substratum, probably by a sticky periostreal pad that gave rise to a cicatrix of attachment.

Among the inarticulates, *Paterina* and its allies alone have features recalling the

articulate pattern. In these stocks, the arrangement of structures that are assumed to have been associated with a pedicle is reminiscent of certain strophomenoids in that all or part of the delthyrium and notothyrium are covered by externally convex plates (*homeodeltidium* and *homeochilidium*, respectively). However, no indication is found that an apical or supra-apical foramen ever existed, and it is usually supposed that the pedicle emerged between the two plates (Fig. 93, A). If this were so, the plates would be the homologues of the pedicle collar and orthacean "chilidium." Alternatively, it is possible that no pedicle developed in postlarval stages, at least, and that the gape was underlain by inner epithelium of

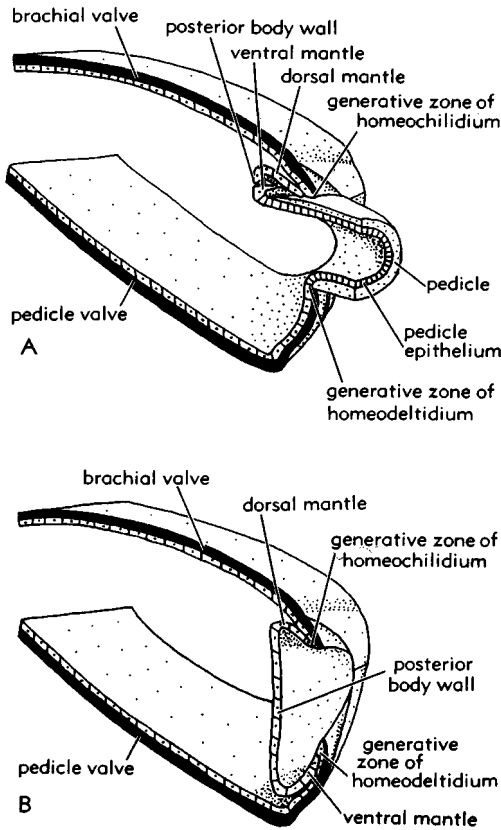


FIG. 93. Stylized reconstruction (with median longitudinal section) of posterior part of paterinid showing alternative interpretations of epithelium-and-shell relations (anterior body wall omitted): (A) inferred to possess pedicle, (B) inferred to lack pedicle (63).

the posterior body wall in the inferred manner of the gape between the true pseudo-deltidium and chilidium (Fig. 93,B).

There is less uncertainty about the presence or absence of a pedicle in the remainder of the Inarticulata, although considerable variation is observed in form of the posterior sector of the shell and nature of the pedicle opening. Much of this variation is controlled by the secretory behavior of a narrow posteromedian strip of the ventral mantle which lies posterior or dorsal of the pedicle of the attached animal. This sector of the mantle is seemingly developed later than the remainder, after the formation of the pedicle rudiment, and its appearance is probably associated closely with protrusion of the pedicle between the valves prior to settling (p. H51).

The ventral pseudointerareas of most Lingulida are indented medially by a pedicle groove which is homologous with the pedicle collar of the articulate brachio-

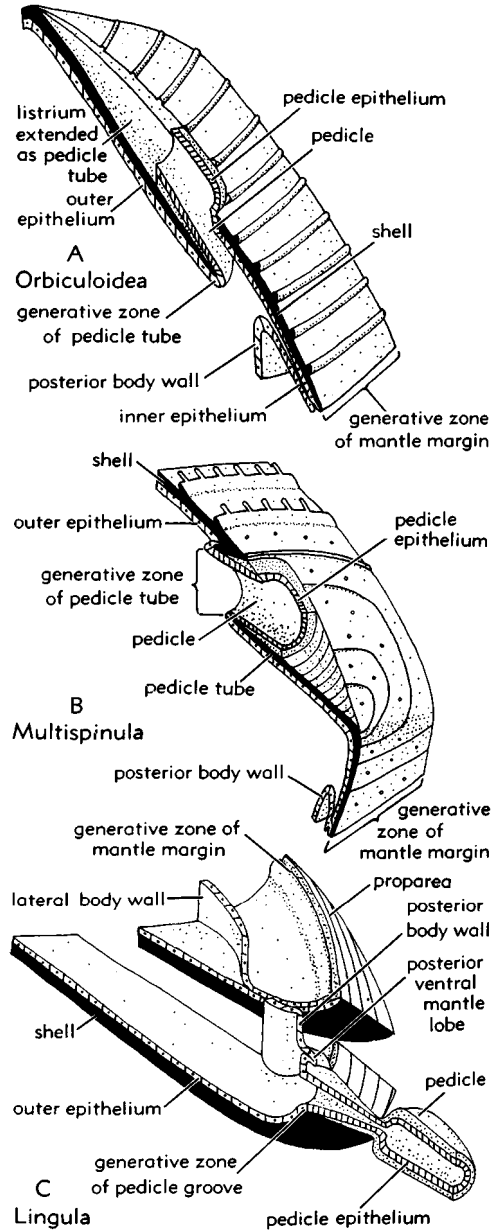


FIG. 94. Stylized reconstruction of posterior part of pedicle valve with longitudinal section showing inferred epithelium-and-shell relations in (A) *Orbiculoidea*, (B) *Multispinula*, both viewed externally, (C) observed epithelium-and-shell relations in *Lingula*, viewed internally (63).

pois, for it is secreted by outer epithelium at its junction with the pedicle epithelium. The flanking propleas and the entire pseudointerarea of the brachial valve are secreted independently by the outer lobes along the posterior segments of the ventral and dorsal mantles, respectively. In these forms the posteromedian sector of the ventral mantle is greatly reduced in size and takes no part in the secretion of the shell (Fig. 94,C).

In some modern discinaceans (e.g., *Discinisca*) the homologous posterior sector of the ventral mantle, although oriented differently to lie posterior of the pedicle, also plays no part in the secretion of the mineralized shell; but in contrast to the Lingu-*lida*, it does secrete the outer, chitinous periostracal layer. The same relationship probably existed in the trematids, for in this family, although growth of the pedicle valve was essentially holoperipheral, the posterior margin of the valve is broken by a variably shaped opening which extends radially from the apex. The secretory behavior of the posterior sector of the ventral mantle of many young discinids was probably similar, for their triangular pedicle opening, breaching the posterior margin of the valve, is broadly comparable with the pedicle opening of adult trematids; during later life in many genera, however, this sector of the mantle acquired the ability to secrete shell material in continuity with that deposited by the remainder of the ventral mantle, and the posterior margin of the adult shell is entire (e.g., *Orbiculoidea*, *Discina*) (Fig. 94,A). In the discinaceans, posterior migration of the pedicle tends to enlarge the triangular opening between it and the apex of the valve, which is commonly filled by a plate (*listrium*), growing posteriorly and secreted by the anterior part of the junction of the pedicle and outer epithelia (Fig. 94). The free margin of the *listrium* in the *Orbiculoideinae* projects internally, posterior of the external pedicle foramen, as a distinct pedicle tube lying against the previously formed shell of the

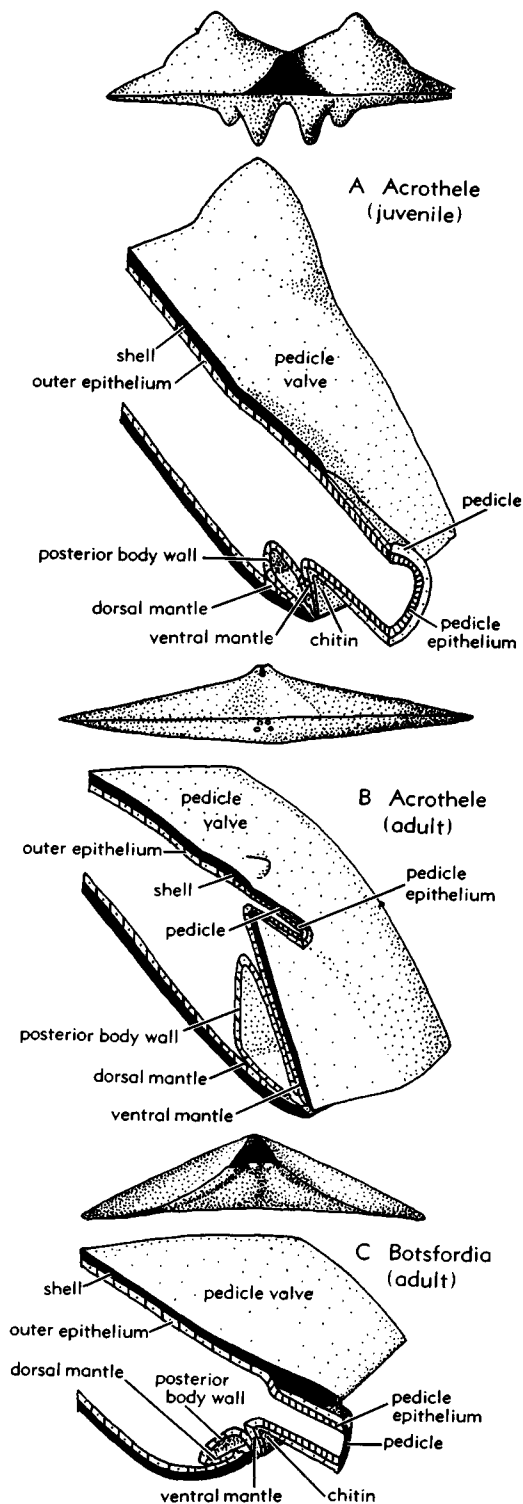


FIG. 95. Posterior views of shell and stylized reconstructions with longitudinal median section of posterior part of shell showing inferred epithelium-and-shell relations of (A) young *Acrothele*, (B) adult *Acrothele*, (C) adult *Botsfordia* (anterior body wall omitted in A-C) (63).

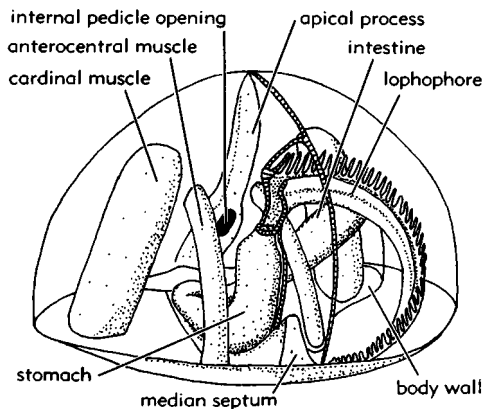


FIG. 96. Stylized reconstruction of *Ceratreta* with inferred location of musculature, lophophore and alimentary canal, shell treated as transparent (63).

posteromedian part of the pedicle valve. In older animals the pedicle tube may be almost completely buried by the deposition of later secondary shell. The pedicle opening of some living and many extinct discinaceans is contained within an elongately oval depression of the shell to which the expanded pedicle is attached externally.

In the majority of adult acrotretaceans the posterior margin of the pedicle valve is entire and is commonly flattened to produce a strongly developed pseudointerarea, but it is presumed that in their very earliest stages, generally unknown, the pedicle opening intersects the posterior margin of the valve. This is true in *Acrothele* (Fig. 95), but in this genus and probably most acrotretaceans, the posterior sector of the mantle rapidly begins to secrete shell material to produce the entire ventral pseudointerarea. The posterior slope of the acrotretid pedicle valve is usually slightly indented or raised along a median sector (intertrough, deltoid

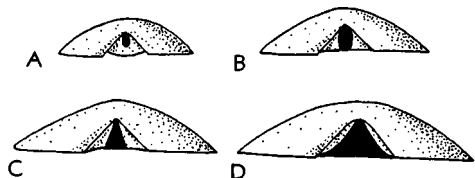


FIG. 97. Development of pedicle opening of *Curticia minuta*, posterior view of pedicle valve: A, youngest stage known, 1.1 mm. wide; B, dorsally directed resorption causes pedicle opening to breach posterior margin of shell; C, D, pedicle opening more widely triangular, with increasing size of shell (39).

pseudointerarea) (Fig. 62). These features seem to have had nothing to do with the development or disposition of the pedicle which lay ventral of their growing edge, although they may conceivably reflect the later-formed posteromedian sector of the ventral mantle. In the majority of acrotretaceans there is a very limited posterior migration of the pedicle opening, which is usually located near the apex of the valve and which may be prolonged internally by a differential thickening (apical process) secreted by outer epithelium around the

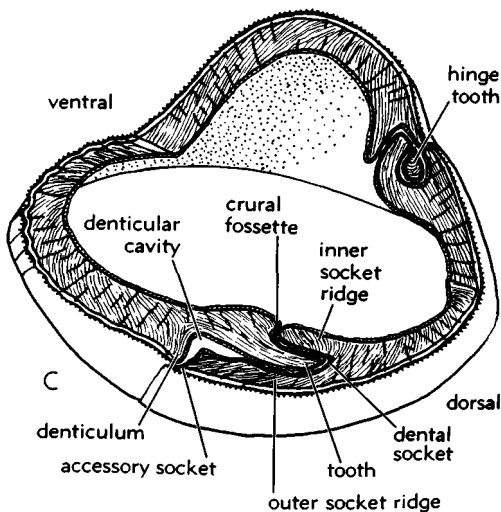
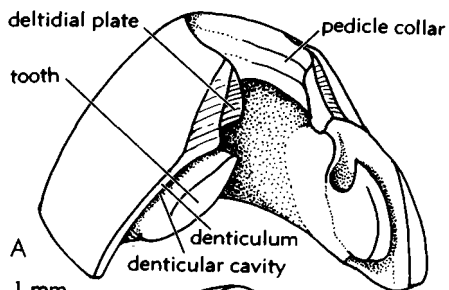


FIG. 98. Articulatory features of (A) pedicle valve and (B) brachial valve of *Terebratulina caputserpentis* (LINNÉ), also (C) as seen in transverse and submedian sections (65).

junction (Fig. 96). Rarely, as in the curticiids, the pedicle migrated posterodorsally and the posterior margin of the valve was breached by resorption to produce a triangular pedicle opening (Fig. 97) (39).

The botsfordiids also have a triangular pedicle opening that breaches the posterior margin of the valve. This could have been formed in a comparable manner to that of the curticiids or, alternatively, it may have been produced by an adult perpetuation of the arrangement found in young *Acrothele*, with secretory failure of the posteriomedian sector of the ventral mantle. Although quite small specimens of *Botsfordia* are known, the form of the pedicle opening is always comparable to that of the adult, with no indications of any resorption on the curticiid pattern, and in this family failure to secrete (rather than migration of the pedicle) appears to be the more likely explanation for the unusual pedicle opening (Fig. 95). The acrotretacean anacline to orthocline dorsal pseudointerarea, although differing in details of form, is homologous with that of the lingulaceans, being secreted by the posterior sector of the outer lobe of the dorsal mantle.

In the siphonotretaceans, the ventral pseudointerarea is entire, and the arrangement of the pedicle junction relative to the ventral mantle edge is like that inferred for the triplésiaceans. The pedicle opening of adult siphonotretaceans lies well forward of the ventral beak and its position is due to an anterior migration by resorption. The posterior part of the track is restricted by a superficial plate or an internally protruding tube secreted by the junction of the outer and pedicle epithelia migrating anteriorly or anterodorsally (Fig. 94,B).

Neither pedicle nor pedicle opening is known in the craniaceans, which either lived free on the sea floor or, more commonly, attached themselves to the substratum by cementation of all or part of the pedicle valve, the ventral periostracum seemingly functioning as the cementing medium.

ARTICULATION

The articulate brachiopods are pre-eminently characterized by a pair of teeth in the pedicle valve which fit into a pair of depressions or sockets in the brachial valve

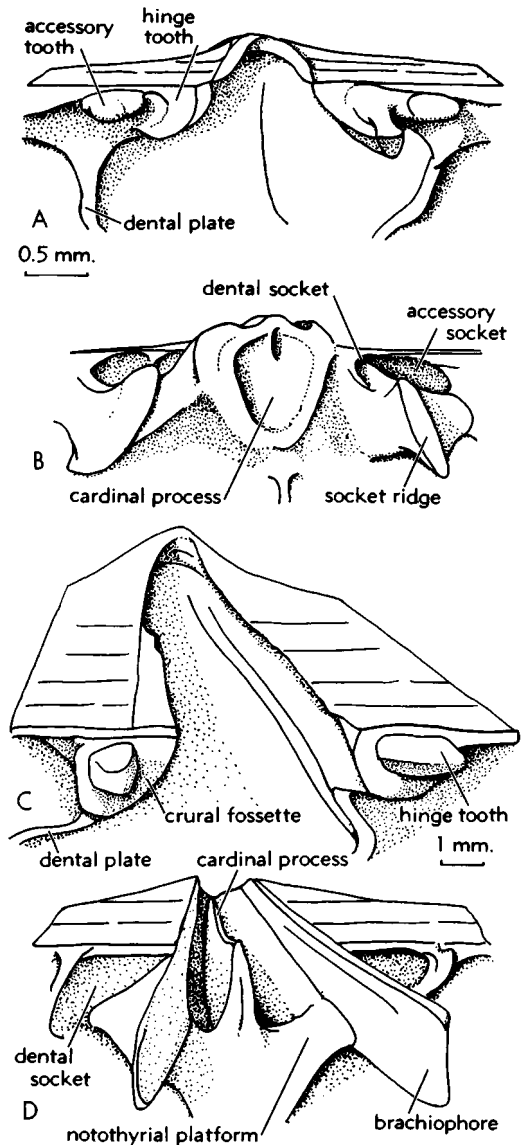


FIG. 99. Articulating outgrowths of (A, B) *Leptellina tennesseensis* ULRICH & COOPER and (C, D) *Hesperorthis australis* COOPER, M.Ord., USA (65).

(Fig. 98). The teeth are composed entirely of secondary shell deposited within invaginations of outer epithelium. The track of their growth invariably defines the margins of the delthyrium, so that they protrude from beneath the ventral cardinal area on either side of the delthyrium or its cover. The teeth may be circular to triangular in cross section and are commonly supported by a pair of variably disposed

plates, also built up exclusively of secondary shell and known as **dental plates** (Fig. 99, *A,C*). The dorsal surfaces of the teeth may be blunt or sharp, smooth or crenulated, and further complicated by minor grooves and

apophyses, which fit snugly with complementary features associated with the socket. The **crural fossette** is perhaps the commonest of these minor modifications (Fig. 99, *C*). It consists of a groove located on the

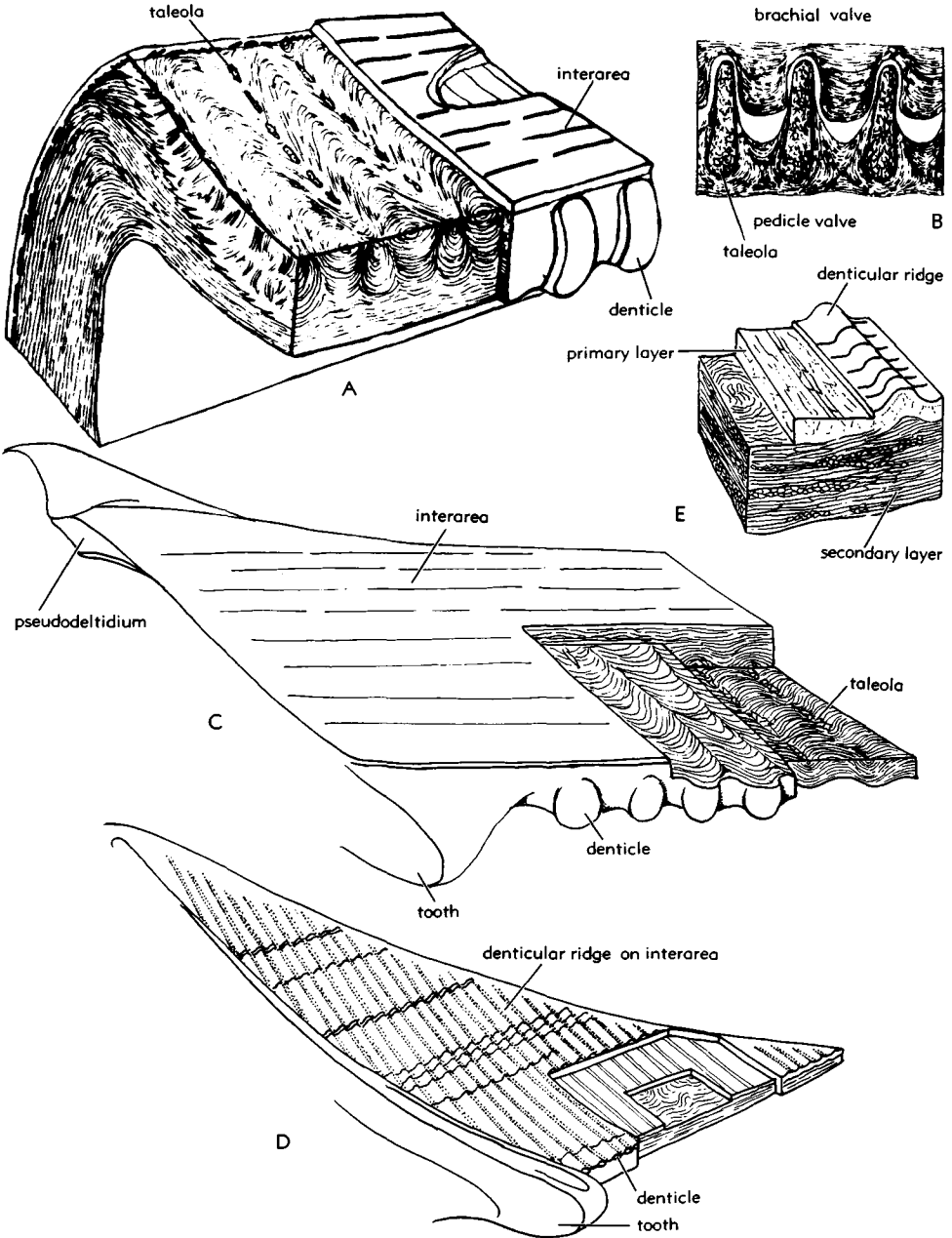


FIG. 100. Denticular structures of stropheodontids (idealized): *A*, *Pholidostrophia* sp., M.Dev., USA; *B*, *Plectodonta transversalis* WAHLENBERG, M.Sil., Eng.; *C-E*, *Tenticospirifer* sp., U.Dev., USA (*A, B*, 55; *C-E*, 65).

inner (anteromedian) side of the tooth and accommodates the posterolateral edge of the ventral wall of the brachiophore (43). A more unusual arrangement, which is especially characteristic of the plectambonitaceans, involves the growth of a pair of accessory teeth lateral to the teeth bordering the delthyrium and separated by a pair of deep grooves (35) (Fig. 99,A). Two pairs of sockets are found in the brachial valve, one on either side of the socket ridges, the posterior surfaces of which fit into the grooves between the teeth.

It is inevitable that, since the tooth and socket are fashioned from secondary shell, the former is commonly separated from the valve margin by a groove that receives the variably thickened or undercut dorsal margin forming the posterior edge of the socket. A number of conflicting terms have been used to describe this relationship, but the following selections seem to be the most appropriate, although they do not necessarily have historical precedence. Thus **denticulum** (31) may be used for the posterior edge of the pedicle valve margin (e.g., *Digonella*) or of the symphytium (e.g., *Laqueus*). For the prominence of secondary shell along the posterior edge of the socket, **outer socket ridge** affords the best description; while the grooves accommodating the denticulum and outer socket ridge are best referred to as **accessory socket** and **denticular cavity** (Fig. 98).

The teeth may be supplemented or, rarely, replaced by a series of smaller protuberances extending lateral to the teeth and in a complementary arrangement along the posterior margin of both valves. In spiriferoids, such denticles are small crenulations of primary and adjacent secondary shell underlying the interareas (Fig. 100,D,E), as are the denticles found in many plectambonitaceans except that each of them appears to have been built up around a taleola (Fig. 100,C). The stropheodontid denticulation, in contrast, only arises after the fusion of widely divergent, platelike teeth and dental plates, following the posterior migration of the latter, although in this group too, the denticles contain taleolae (55) (Fig. 100,A,B). The denticulation of the chonetoid *Eodevonaria* and the productoid *Ctenalosis* appears to be most close-

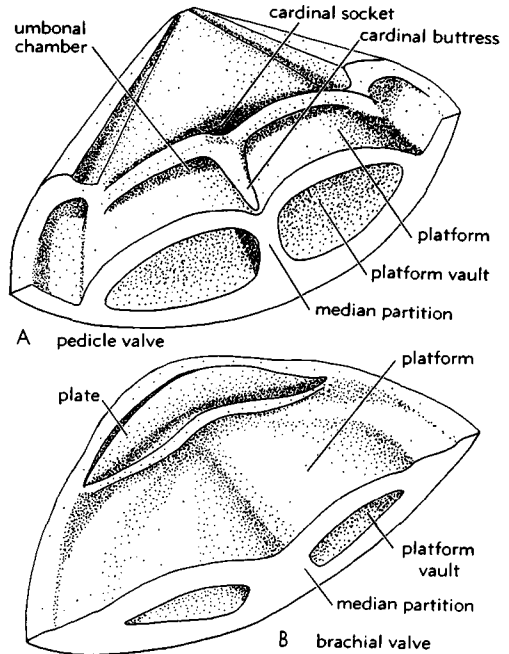


FIG. 101. Morphology of posterior region of (A) pedicle valve and (B) brachial valve of *Dinobolus* (63).

ly related in development to that of the stropheodontids (33).

Although the majority of inarticulate brachiopods lack any form of articulation between the valves, which are merely held together by muscles, aided by the body wall, hinge structures are known in a few genera. An unusual type of articulation occurs in *Dinobolus* and probably in other genera of the Trimerellacea (51). On the posterior margin of the brachial valve is a single, medially placed plate which fits into a corresponding cardinal socket in the pedicle valve (Fig. 101). These structures probably contributed little toward holding the valves together, but they would have inhibited any relative rotational or sliding movements between the valves. What is probably another form of primitive articulation, which developed quite independently of that of the Trimerellacea, occurs in the acrotretid genus *Linnarssonella* (7). In this genus the typical acrotretid dorsal pseudo-interarea is modified by the development of a groove on both propleas, which are elevated ventrally immediately in front of

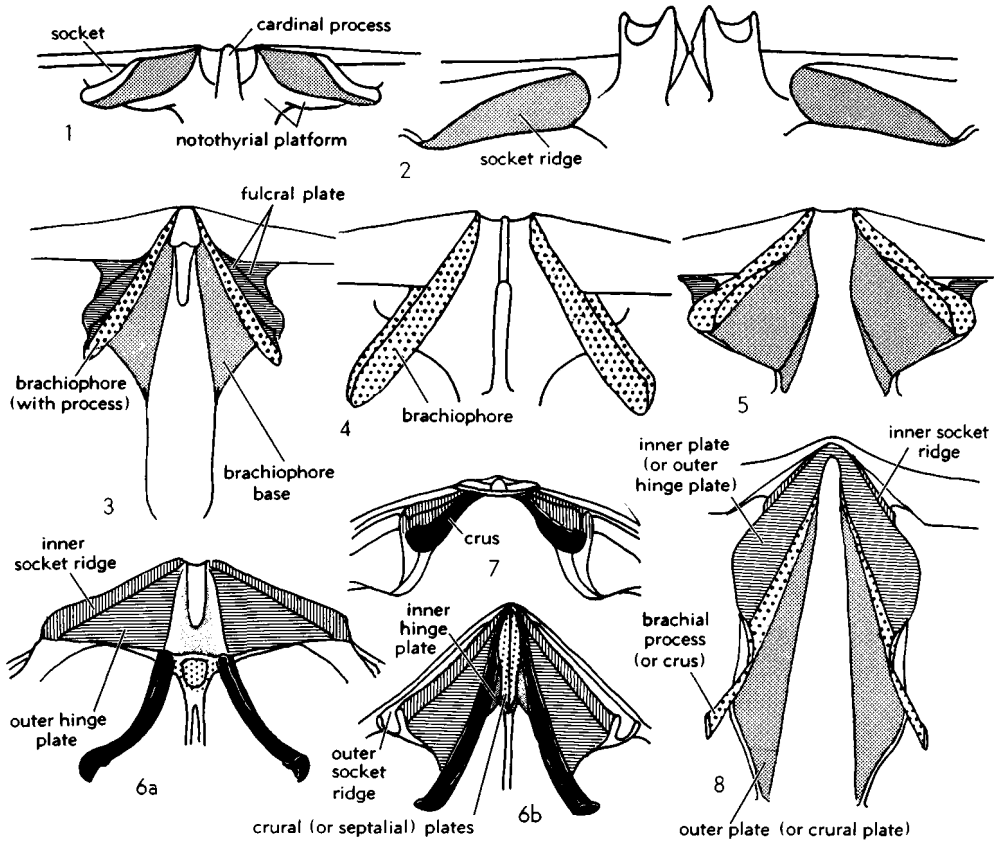


FIG. 102. Cardinalia of (1) *Billingsella*, (2) *Strophomena*, (3) *Dalmanella*, (4) *Hesperorthis*, (5) *Imbricata*, (6a,b) a camarotoechiid, (7) *Notosavia*, and (8) *Gypidula*, all ventral views (65).

the grooves. The grooves may have functioned as sockets receiving the dorsal edge of the pedicle valve, but the latter bears no distinct structures or thickenings interpretable as teeth, and it is possible that the elevated propareas may only have restricted relative rotational and sliding movements of the valves without occurrence of any positive articulation. A similar form of constraining mechanism, or possibly full articulation, is also present in the obolid *Dicellomus* (6), for the posterolateral margins of the brachial valve bear conspicuous grooves, but details of the corresponding margin of the pedicle valve are unknown. In *Linnarssonella* and *Dicellomus* the supposed sockets can, of course, be only analogous with true sockets, because they were developed on the shell surface and not as modifications of inner layers of the shell.

The plates or ridges defining the sockets

in the brachial valves of articulate brachiopods are part of structural modifications of varying complexity found in the dorsal umbo and collectively referred to as the **cardinalia**. The several pieces comprising the cardinalia are composed of secondary shell and, apart from defining the sockets, afford attachment areas for musculature and even include the bases of processes giving support to the lophophore. This diversity of function has naturally given rise to a wide variety of features (Figs. 102, 103), and since combinations of them tend to be characteristic of major taxa, a complicated terminology, frequently incompatible with that employed for other groups, has grown up for each taxon. An important element of the cardinalia is a medially situated out-growth(s) (**cardinal process**), which is commonly developed as an attachment area for the dorsal ends of the diductors. This fea-

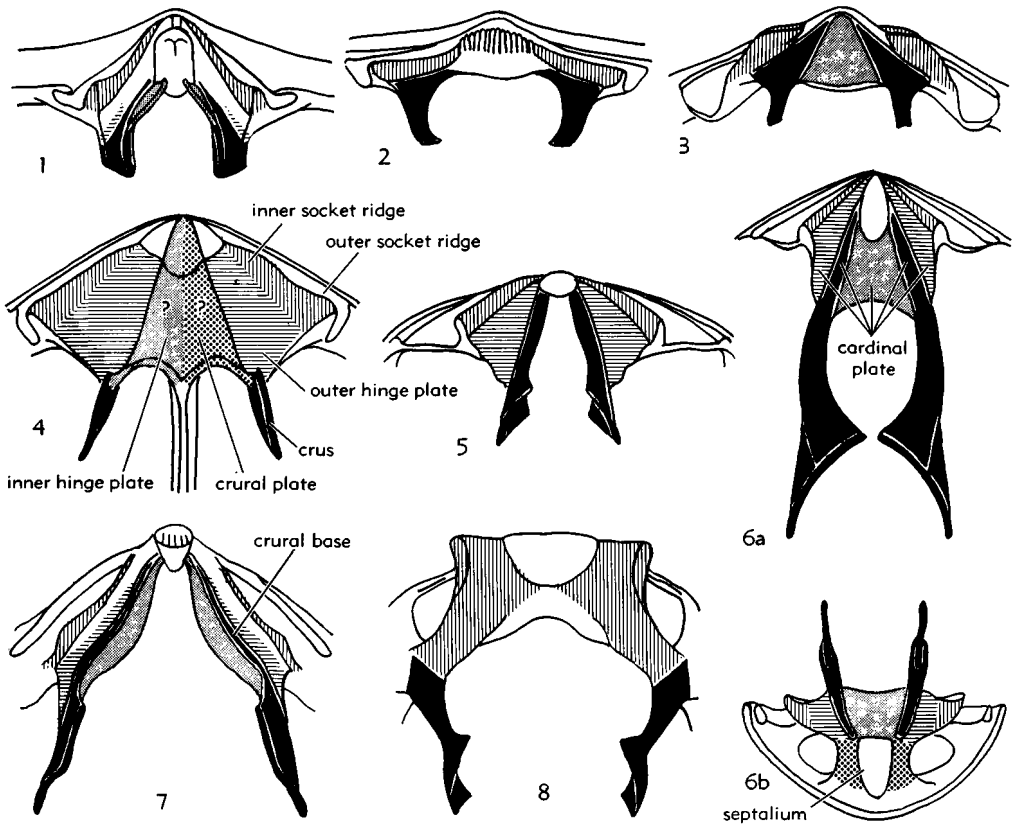


FIG. 103. Cardinalia of (1) *Crenispirifer*, (2) *Neospirifer*, (3) young *Cleiothyridina*, (4) *Laqueus*, (5) *Dallithyris*, (6a,b) *Nanothyris*, (7) *Terebratulula*, and (8) *Terebratulina*, all ventral views except 6b, which is posterior (65).

ture is more conveniently dealt with when considering the shell modifications due to the insertion of muscles concerned with relative movements of valves.

The most primitive arrangement is found in the billingsellaceans (Fig. 102,1), where a pair of widely divergent plates bound the notothyrium and also act as inner walls to sockets which are excavated within the secondary shell uniting the plates with the edge of dorsal interarea. Medially, the proximal ends of the plates may be encased by lateral extensions of a low-lying deposit of secondary shell which forms the floor of the notothyrium (**notothyrial platform**). These plates have been called brachiophores in the belief that prolongations of their ventroposterior edges gave support to the lophophore. Such processes however, are unknown in the billingsella-

ceans, in which the plates do not extend beyond the lateral edges of the sockets, and are only rarely developed incipiently among the strophomenoids and clitambonitoids; and even in later orthoids they rarely extended sufficiently anteroventrally to reach the inferred position of the anterior body wall. In all, it seems preferable to use the term **socket ridge** for widely divergent structures of limited extension like those of the billingsellaceans, strophomenoids, etc. (Fig. 102,2) (55). Certainly an exclusive function of articulation may be inferred for the socket ridges of stropheodontids which became vestigial or even disappeared subsequent to the loss of teeth in members of that family (55).

The orthacean arrangement represents a significant advance in that the shell outgrowths (**brachiophores**) that serve to de-

fine the ventral limits of the sockets were rotated to point anterolaterally and were also prolonged as blade-shaped or rodlike processes beyond the limits of the sockets (43). Disposed in this manner, the brachiophores are free of the posterior margin and in many orthids (e.g., *Hesperorthis*) are supported by a well-developed notothyrial platform (Fig. 102,4). The sockets are excavated in secondary shell deposited between the brachiophores and the posterior margin but in other orthoids their anterolateral limits may be defined by concave plates (fulcral plates), which are partially or completely elevated above the valve floor (Fig. 102,3). The forward growth of the brachiophores and their processes, as in most enteletaceans and many orthaceans, was accompanied by the forward growth of connections between the brachiophores and the floor of the brachial valve, as a pair of plates supporting the upper part of the brachiophore. These plates may be disposed at varying angles to the median plane of symmetry and have generally been called "supporting plates" only when they converge towards the dorsal median ridge. It seems best, however, to refer to them as **brachiophore bases**, irrespective of inclination (61).

It is significant that the ventral adjustor scars are first indisputably identified in the orthaceans and enteletaceans, and judging from anatomical reconstruction, the only sites for the attachment of the dorsal adjustor muscles were the inner faces of their well-developed brachiophores (61).

The cardinalia of early porambonitaceans consist essentially of fulcral plates and brachiophores (50) with bases variably convergent onto the floor of the valve (Fig. 102,5). The brachiophore processes may be negligible in the older stocks but were very well developed in some younger forms like *Camerella*. Furthermore, a raised ridge is commonly found standing above the posterior edge of the brachiophore, but intervening between it and the concave socket of the fulcral plate. Theoretically, at least, this ridge could have arisen either as an upgrowth along the contact between the fulcral plate and the brachiophore or within the fulcral plate as an inner restriction to a small posterolateral socket. These arrangements are reminiscent of the patterns

characteristic of many spiriferoids and rhynchonelloids, respectively. In both conditions, the raised ridge is at least analogous with the rhynchonelloid "inner socket ridge" and that part of the fulcral plate, which now intervenes between the inner socket ridge and the brachiophore, is homologous with the outer hinge plate (Fig. 102,6,7). One other modification is noteworthy. In camerellids, for example, the brachiophore bases converge toward the floor of the valves, either uniting with or fusing to form a median septum. This structure is usually referred to as a cruralium, but since it did not contain the dorsal ends of the adductor muscles, it is more correctly spoken of as a **septalium** (see Fig. 128).

The use of an entirely different terminology for the pentameracean cardinalia is not a reflection of any radical departure from porambonitacean morphology but of historical precedent. In general, the cardinalia are only better developed, or, as with the homologues of the brachiophore bases, are only differently disposed. Nonetheless the extended brachiophore of the pentameraceans is known as the brachial process (*crus*); the brachiophore base as the outer plate; and the fulcral plate, with or without modification like the inner socket ridge, as the inner plate (42) (Fig. 102,8). Such terminology is so divorced from that employed for other groups that it may be worthwhile discarding it in favor of the terminology for either the porambonitacean or, preferably, the rhynchonellacean cardinalia.

In the remaining groups of articulate brachiopods, some sort of calcareous support to the lophophore was almost invariably developed, so that greatly prolonged homologues of the brachiophores and their processes, the *crura*, are the dominant element of the cardinalia. The *crura*, which are commonly strongly curved, divergent apophyses extending anteroventrally, are known in living brachiopods to pass forward on either side of the esophagus to make contact with the anterior body wall and posterior part of the lophophore on either side of the mouth; and it is highly probable that all processes so named in fossil rhynchonelloids, terebratuloids, and spiriferoids performed a similar function.

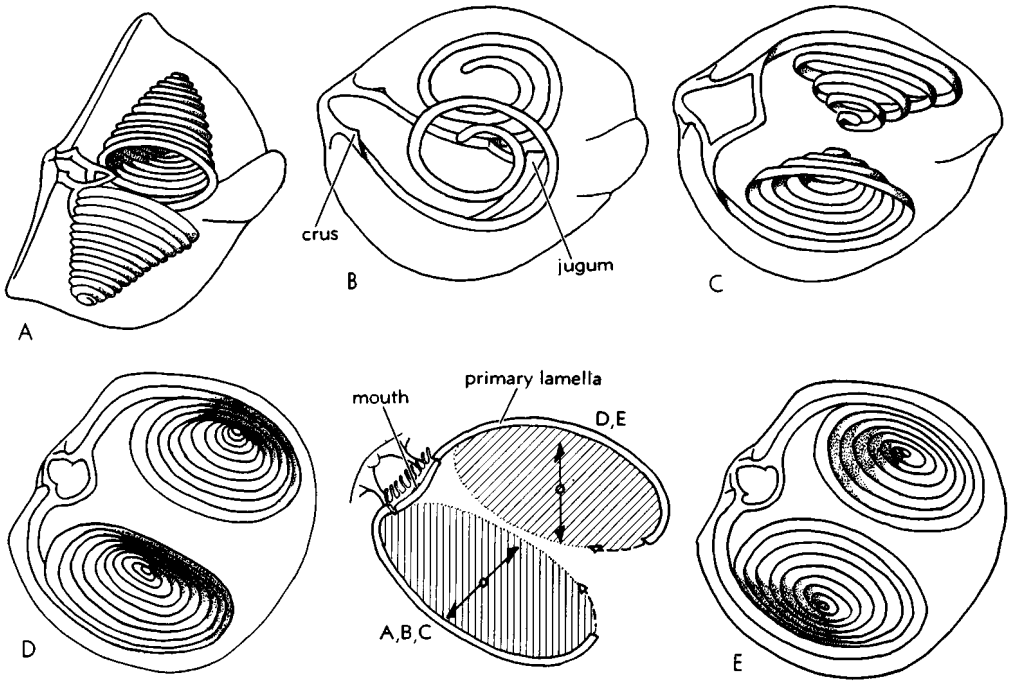


FIG. 104. Stylized representation of various attitudes adopted by primary lamellae of the spiralia relative to planes parallel with the plane of symmetry (as in A,B,C) and parallel with the commissural plane (as in D, E) (65).

Only rarely, as in *Enteleles* and *Skenidioides*, were the brachiophores sufficiently prolonged and suitably disposed to give support to the lophophore (57). The crura, therefore, represent an important advance in brachiopod organization and are associated with other features of the cardinalia that are distinctive enough to warrant a different terminology from that used for the more primitive groups. Apart from the replacement of the fulcral plate by a fully differentiated inner socket ridge and outer hinge plate, the rhynchonelloid crura were commonly underlain by a pair of plates (crural plates) that converged to form a septalium (Fig. 102,6), but these could also have arisen from the sides of the crura rather than from their anterior margin. Another pair of plates (inner hinge plates) could also have grown from the sides of the crura to meet medially as a cover to the septalium (Fig. 102,6b).

The cardinalia of Paleozoic terebratuloids (14) are very like those of the rhynchonelloids, although the crural plates, defining the septalium, may be subparallel, as in

Nanothyris (Fig. 103,6), or convergent, as in *Globithyris*. The inner hinge plates are normally well developed, and together with the posterior faces of the crura and the outer hinge plates, constitute the cardinal plate (Fig. 103,6a). The median elements of the cardinalia of Mesozoic and Recent terebratuloids (49) are commonly greatly modified or incomplete so that it is difficult to be certain about their relationships with similarly disposed structures of older groups. The simplest arrangement is that of *Terebratulina* (Fig. 103,8) which consists of crura springing directly from high inner socket ridges. In other terebratuloids, like *Dallithyris*, outer hinge plates are differentiated (Fig. 103,5); and in a minority like *Terebratula* a pair of discrete inner hinge plates were also developed (Fig. 103,7). The cardinalia of *Laqueus*, in contrast, include a pair of plates, arising at sides of the crura and converging on to the dorsal median septum, which have been called both inner hinge plates and crural plates (Fig. 103,4). But until more is known about their origin, it seems preferable to refer to

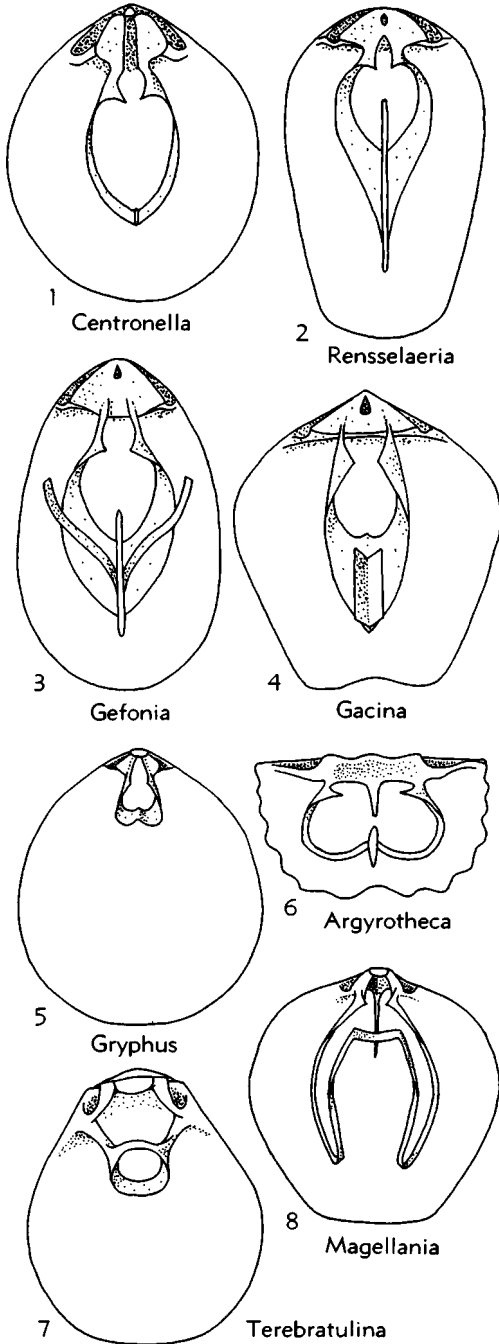


FIG. 105. Some loop forms in the Terebratulida: 1, *Centronella*; 2, *Rensselaeria*; 3, *Gefonia*; 4, *Gacina*; 5, *Gryphus*; 6, *Argyrotheca*; 7, *Terebratulina*; 8, *Magellania* (1, 2, Cloud; 3, 4, Stehli; 5, 7, 8, Rowell, n; 6, Thomson).

them as crural plates, which at least reflects their disposition relative to the rest of the cardinalia and the floor of the brachial valve.

The cardinalia of many spiriferoid brachiopods, especially the spiriferacean and atrypacean stocks, are reminiscent of *Terebratulina* in that the crura arose directly from well-developed inner socket ridges (e.g., *Neospirifer*) (Fig. 103,2). Less commonly, thin strips representing outer hinge plates (e.g., *Plectatrypa*), crural bases and inner hinge plates (e.g., *Crenispirifer*) were developed (Fig. 103,1). Among *Athyris* and its allies (like *Cleiothyridina*), the fusion of the inner hinge plates to form a median horizontal plate, subtended between the inner surfaces of the crura or the inner socket ridges, commonly took place (Fig. 103,3).

The cardinalia of many articulate brachiopods are also connected with spirally coiled, calcareous ribbons (*spiralia*) or calcareous loops (Figs. 104, 105). The spiralia and loops are greatly variable in form and attitude and, indeed, may have arisen in different ways. Nonetheless, two aspects of their growth and disposition seem to have been common to them all. First, they represent outgrowths from the crura, extending well into the brachial cavity and, like the crura, were contained in sheaths of outer epithelium responsible for their growth and enlargement by controlled processes of secretion and resorption (57). (The only exception seems to have been the spiralia of *Thecospira* which were connected by short apophyses to the cardinal process, although they were probably deposited in a like fashion.) Secondly, although the loops grew independently of the lophophores, in living terebratuloids they are intimately associated with that organ and the disposition of both loops and spires in extinct stocks suggests that they performed a similar function of support.

As far as is known from the development of spiralia in a few species (5), the first structure formed was an elongately oval loop (centronelliform loop) by the anteromedian fusion of a pair of curved prongs extending from the crura. The small size of the shell at this stage in growth suggests that the loop supported a trocho-

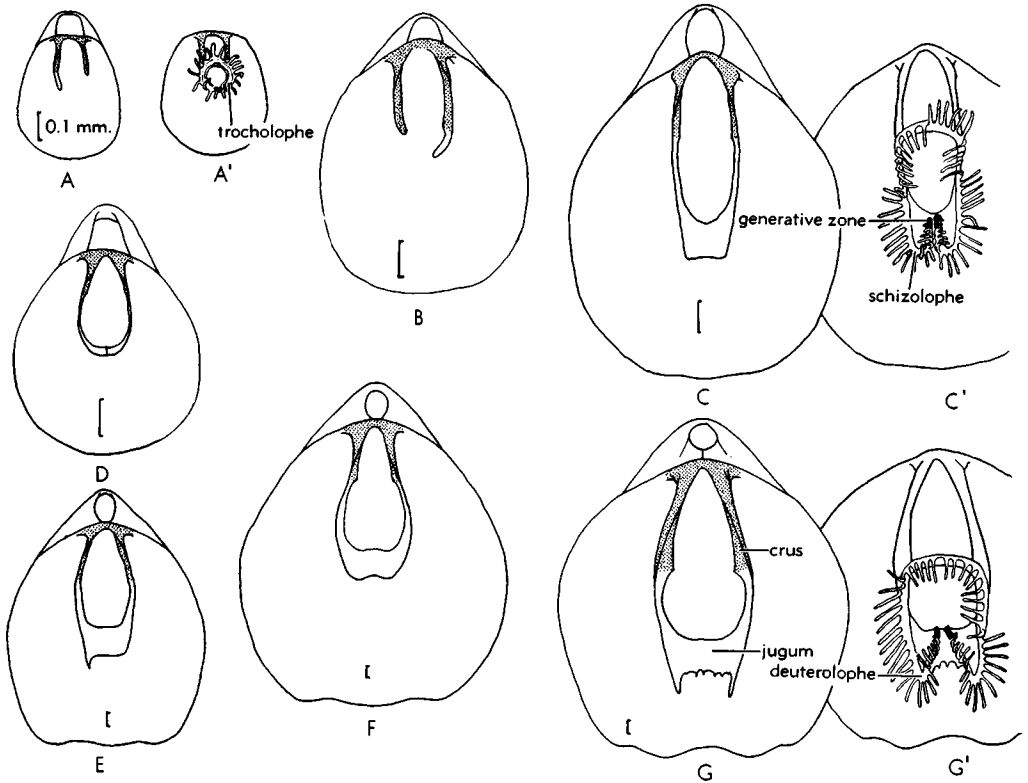


FIG. 106. A-G. Growth of the brachidial apparatus of *Protozyga elongata* COOPER, with reconstructions of the trocholophe (A') and the schizolophe (C', G') (60).

lophous or schizolophous lophophore (Fig. 106). During subsequent enlargement, differential resorption took place, so that the transverse part of the loop became truncated anteriorly to form a band (**jugum**) with a pair of short apophyses at the anterolateral corners. These prolongations represent the beginnings of the first pair of coils (**primary lamellae**) of the spiralia. But the inferred arrangement of the lophophore may *not* be a simple spirolophe coincident with the calcareous ribbons of the spiralia (41), for, if the paired generative zones of the early schizolophe were retained medially on the jugum, which must have been the original position, the growth of the primary lamellae would have been accompanied by an anterolateral lobation of the lophophore to fit around the peripheries of the calcareous ribbons (57). In these circumstances the doubled lophophore (deuterolophe) borne by the spiralia would have been homologous with the side arms of *Terebratulina* (Fig.

107, B, D). Moreover, the elaboration of the jugum in some spire-bearing brachiopods, which must also have been due to secretion and resorption by ensheathing outer epithelium, may indicate the retention of the generative zones of the lophophore in a median position on the jugum. In a number of genera this structure developed into a spinose platform and also gave rise to a posteriorly directed process (jugal stem) which bifurcated in a number of stocks (e.g., *Athyris*) to form a pair of arcs (arms of jugum) lateral to the primary lamellae; and in certain unrelated genera (e.g., *Kayseria*, *Diplospirella*) the arms continued to grow into a pair of spires (**accessory lamellae**) coextensive with the primary spiralia (Fig. 108). If the generative zones of the lophophore moved away from the jugum at all, it is at least as likely that they did so posteriorly along the jugal stem and then laterally in association with the accessory lamellae; and if this is so, it is these single

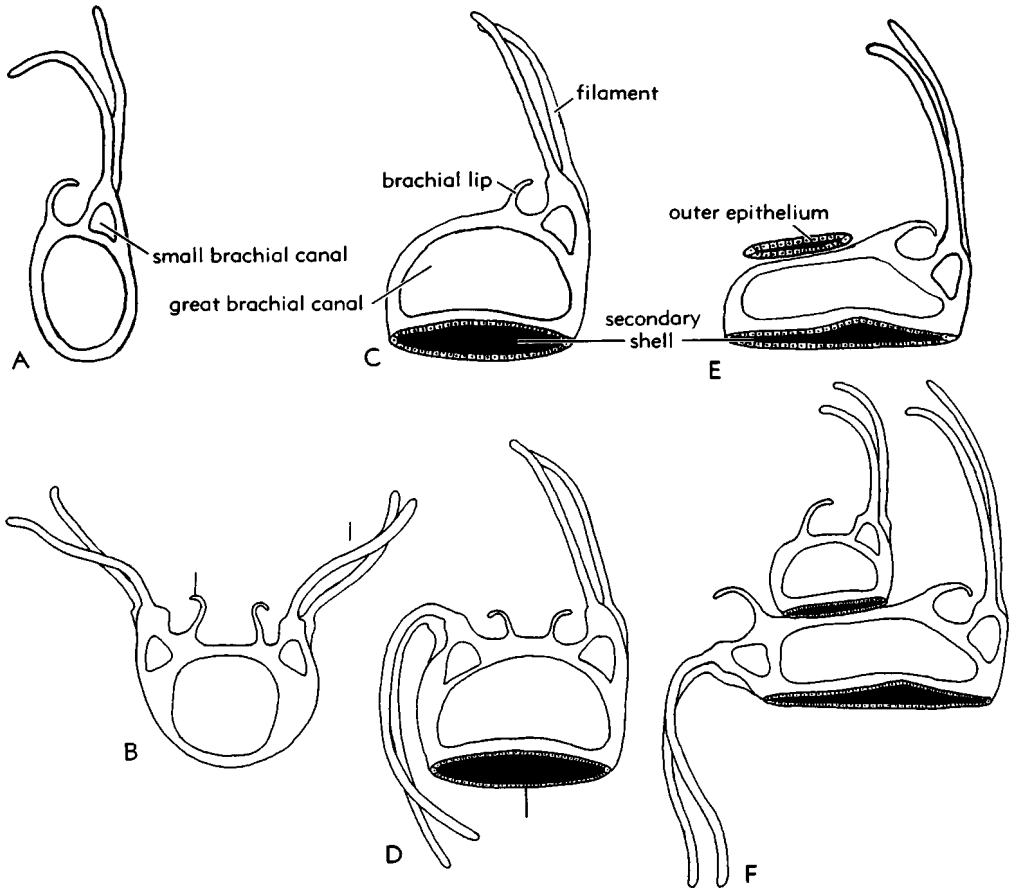


FIG. 107. Diagrammatic cross sections of (A) brachium of *Notosaria* and (B) side arm of *Terebratulina* with inferred lophophore restorations of (C, D) spiriferoids and (E, F) athyridaceans according to whether they should be homologized with A (as in C and E) or with B (as in D and F) (65).

elements of the lophophore which are to be homologized with the rhynchonelloid spirolophe, not the deuterolophe, which is really equivalent to the side arms of the terebratuloid (Fig. 107,F).

The jugum is unknown in a number of spire-bearing brachiopods. In many poorly investigated stocks, the absence could well be ascribed to the breakage of such a delicate structure during burial of the shell. In others, its absence may have been due to resorption, which is known partially to have affected the juga of certain adult spiriferoids and atrypoids. But in a few stocks like *Cyclospira*, no jugum has been found in well-preserved adult shells and if it proves that the spiralia developed directly from the crura and not by modification of a lophophore, it is more likely that the spiralia gave

support to a spirolophe, rather than a deuterolophe (compare Fig. 107,A,C).

The calcareous ribbons of the spiralia are commonly wafer-like but they may be differentially thickened or impermissibly spinose (fimbriate) along one side or the other; or folded upon themselves to a varying degree, to give a V-shaped cross section (e.g., *Thecospira*). The spiralia may be oriented to take up almost any attitude within the mantle cavity, but all of them are variants of five basic dispositions (Fig. 104). The simplest arrangement (e.g., *Protozyga*) consists of a pair of planospiral calcareous ribbons, parallel with the longitudinal median plane of symmetry of the shell. This attitude is essentially adopted by the primary lamellae of *Spirifer* and *Zygospira*, but the ribbons are drawn out into spires with apices di-

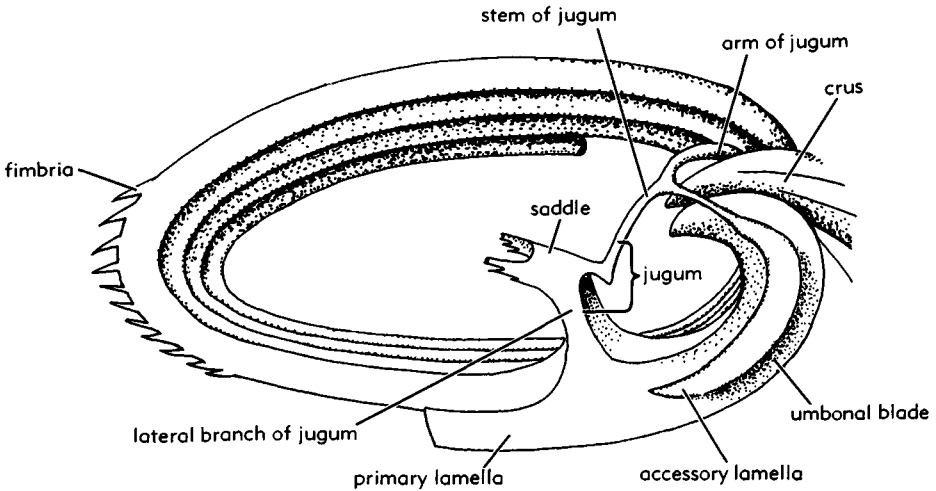


FIG. 108. Structure of spiridium in *Athyris* (27).

rected laterally and centrally, respectively. The primary lamellae of *Atrypa* and *Cyrtina*, on the other hand, are more or less normal to the plane of symmetry, with apices of the spiralia directed dorsally and ventrally, respectively. Judging from the inferred disposition of the lophophore between the ends of the crura and along the calcareous ribbons, the zygospirid pattern could have been derived from the protozygid by extension of the apices of the spiralia toward the center, and the atrypid and cyrtinids by rotation of the primary lamellae through 90°, accompanied by apical extensions dorsally or ventrally. The spiriferid arrangement, however, is quite different, for it involved an eversion of the lophophore as well as a rotation relative to the mouth segment (41).

Calcareous ribbons composed of secondary shell may also extend from the distal ends of the crura to form a closed structure known as the loop, which is especially characteristic of the terebratuloids. The loop varies greatly, not only in form but also in its origin and growth; yet it gives support to a plectolophous lophophore in the great majority of adult living terebratuloids, an association that probably also obtained for most fossil members of the group.

The simplest arrangement is found in Paleozoic terebratuloids like *Centronella* and consists of a band suspended between the crura; the band is lanceolate anteriorly

where it tends to form a broad pointed blade (*echmidium*). This is the centronelliform loop (50) (Fig. 105,1), which was probably associated with a trocholophe or early schizolophe. Such a loop persisted in some adult shells with little modification, apart from enlargement of the outer edge and resorption along the inner edge, as in *Rensselandia*, with or without peripheral spines (e.g., *Stringocephalus*). In other stocks a median plate (*vertical plate*) normal to the anterior blade of the loop developed (e.g., *Rensselaeria*, Fig. 105,2) which may further divide (e.g., *Gacina*, Fig. 105,4) or give rise to a pair of bands diverging posterolaterally (e.g., *Gefonia*, Fig. 105,3) in a manner which suggests that the generative tips of a highly modified schizolophous lophophore moved out in the same direction (Fig. 105,4). More important modifications included the development of short and long loops morphologically like those of living terebratuloids. Thus in *Cranaena*, median resorption and deposition accompanied by lateral enlargement of a centronelliform loop gave rise to a short truncate loop in which a pair of descending branches are clearly identifiable, in the manner of modern *Terebratulina*, and must also have supported a plectolophe (Fig. 105,7). In *Cryptacanthia* (19) and related stocks, however, resorption and deposition were accompanied by an accelerated forward growth of the anterolateral corners of the loop to

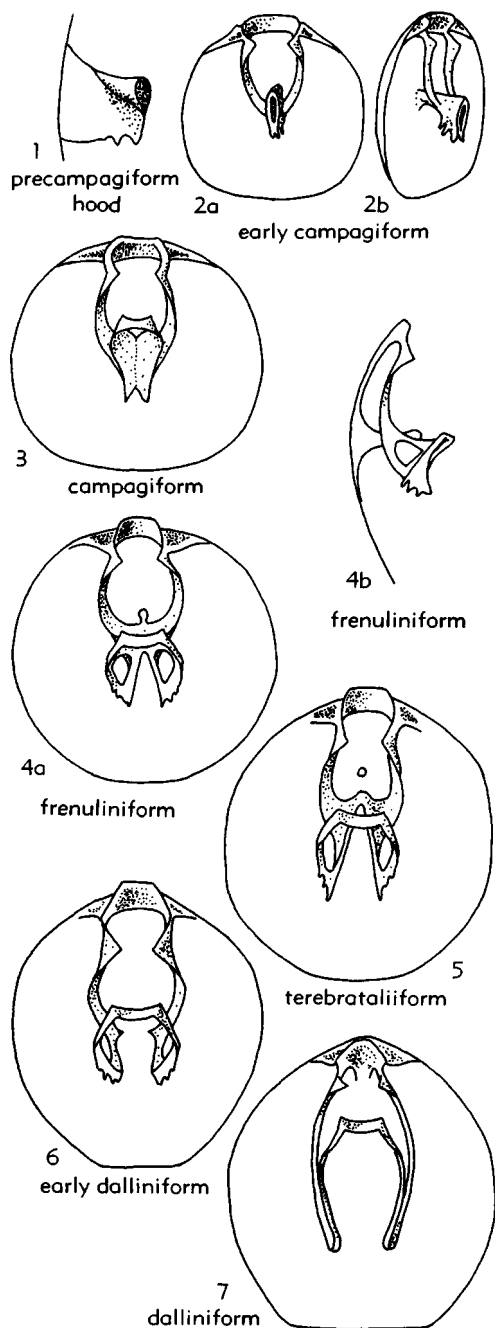


FIG. 109. Stages in loop development of *Cryptacanthia prolifica*: 1, ventral view of precentronelliform stage; 2, ventral view of centronelliform stage with development of echmidium; 3a,b, ventral and oblique lateral views of early cryptacanthiiform stage showing development of hood on anterior tip

define a pair of ascending branches connected by a transverse band, as well as the descending branches. The resulting glossothyropsiform loop is similar to the long loops of some living terebratellaceans, which are fashioned, however, in an entirely different way (Fig. 109).

The growth of the terebratellacean loop (22) is linked with the development of a dorsal median septum (or septal pillar), which first makes its appearance as a high platelike outgrowth of secondary shell inserted in the posterior indentation of the schizolophe (Fig. 110). A ring or cone (hood) of secondary shell is then secreted along the posterior face of the septum and by enlargement and modification may be transformed into the ascending branches and transverse band. At about the same time as the appearance of the hood, descending branches appear as prolongations growing anteriorly from the crura to meet and fuse with either the septum or a pair of posteriorly directed upgrowths from it. Further growth and modification by resorption may ultimately give rise to a long recurved loop entirely free of septal support (e.g., *Macandrevia*) in which the descending and ascending branches form the dorsal and ventral boundaries, respectively, of the side arms; and the transverse band joining the ascending branches gives support to the medially coiled spirolophe (Fig. 110). Alternatively the resorption of the median septum and the anteromedian surface of the hood may be arrested so as to leave connections (connecting bands) between the descending branches and remnants of the median septum (e.g., *Terebratella*) (Fig. 111).

The development of the terebratellacean free loop, therefore, involves a complex series of metamorphoses; and since the adult loops of living and extinct terebratellacean stocks together typify nearly all possible variations within such a series, distinctive stages in development have been named after genera. In this way an extensive terminology indicating the nature of the loop

of echmidium; 4a,b, ventral and lateral views of cryptacanthiiform stage, descending branches still joined medially with remnant of echmidium intact posteriorly; 5, ventral view of early glossothyropsiform stage, descending branches separate (19).

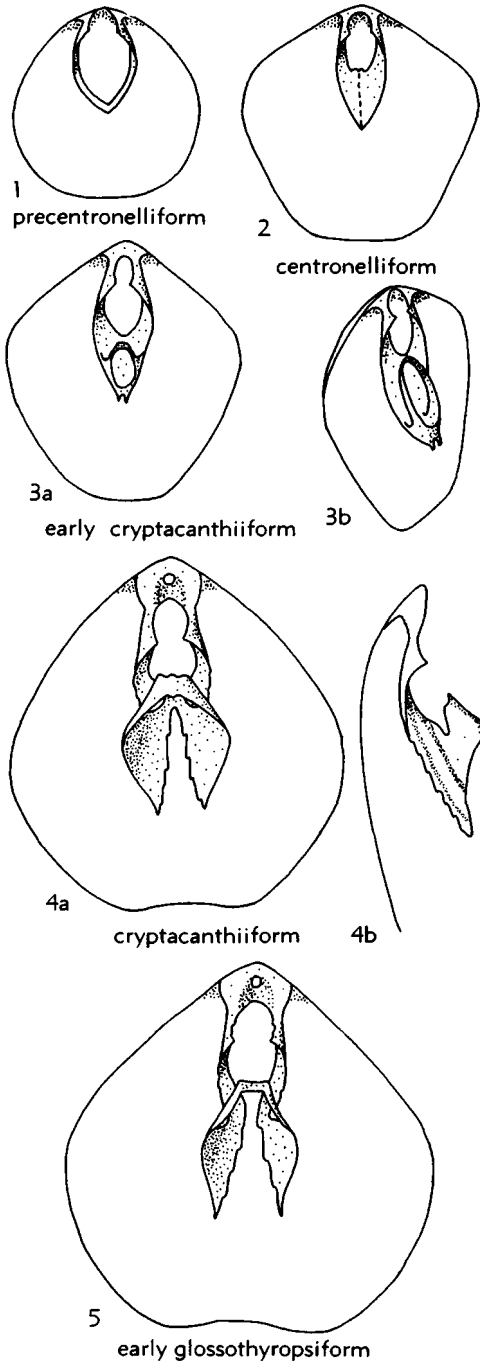


FIG. 110. Growth stages in development of dalliniform loop: 1, lateral view of precampagiform hood; 2a,b, ventral and oblique lateral views of early campagiform growth stage; 3, ventral view of campagiform growth stage; 4a,b, ventral and lateral views of frenuliform growth stage; 5, ventral view of terebrataliiform growth stage; 6, ventral view of early dalliniform growth stage, 7, ventral view of dalliniform growth stage (Rowell, after 49).

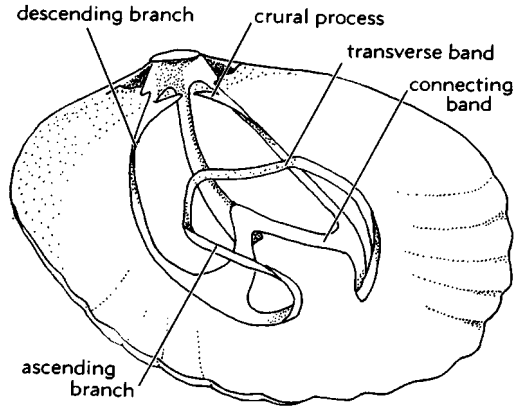


FIG. 111. Morphology of terebratellid loop (early terebratelliform growth stage) (63).

has been built up and is fully illustrated in the systematic section dealing with the terebratuloids. In the meantime it is worth noting that in the kraussinids, structures associated with the septa are the first to appear, and the descending branches appear later or not at all (22). In *Argyrotheca* (Fig. 105,6), the descending branches unite with an undifferentiated median septum to support a trocholophe (4).

Apart from the terebratuloids and immature spiriferoids, loops are found in only the pentameracean *Enantiosphen* and the enteleteacean *Tropidoleptus* (Fig. 112). The bilobate loop of the former seems to have developed by accelerated anterolateral growth as well as general enlargement (with resorption) from a young subcircular structure and may have supported a modified schizolophe. The growth of the *Tropidoleptus* loop, on the other hand, was dependent on the development of a dorsal median septum and the inferred arrangement seems to have been like that of terebratellaceans, although the lophophore it supported was much more likely to have been spirolophous in the plane of commissure rather than plectolophous (60).

Despite the lack of structures comparable with crura, certain internal features of the brachial valves of strophomenoids, chonetoids, and productoids seem also to have functioned as supports to the lophophore (57). Among the plectambonitaceans, a variably elevated, semicircular, medially cleft disc (**lophophore platform**), like that of *Leptellina*, is commonly found and may

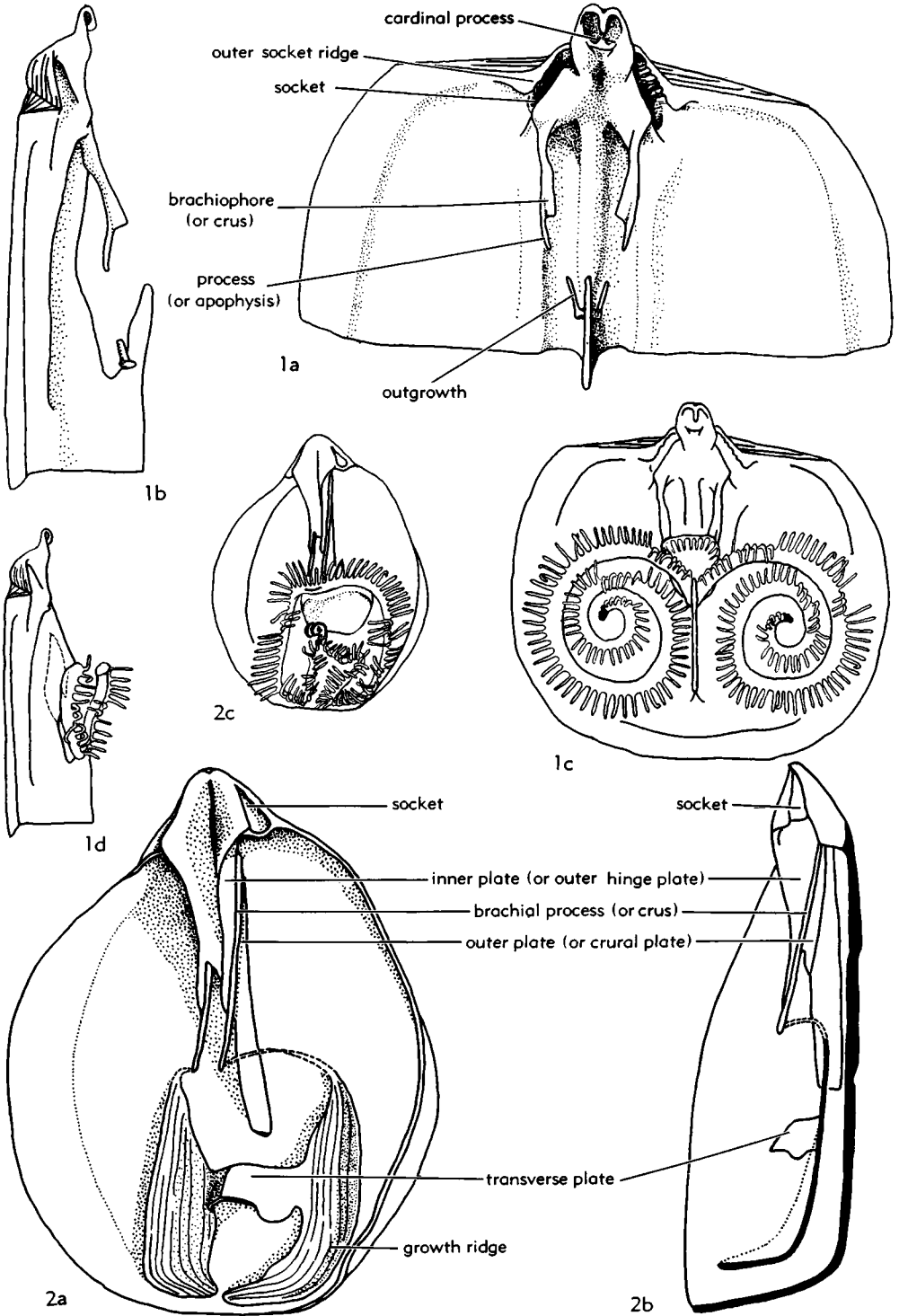


FIG. 112. Internal morphology of brachial valve in (1a) ventral and (1b) lateral views of *Tropidoleptus carinatus* CONRAD, M.Dev., USA, with (1c,d) inferred restoration of lophophore in ventral and lateral views; and of brachial valve in (2a) ventral and (2b) lateral views of *Enantiosphen vicaryi* (DAVIDSON), M.Dev., Eng., with (2c) inferred restoration of lophophore in ventral view (60).

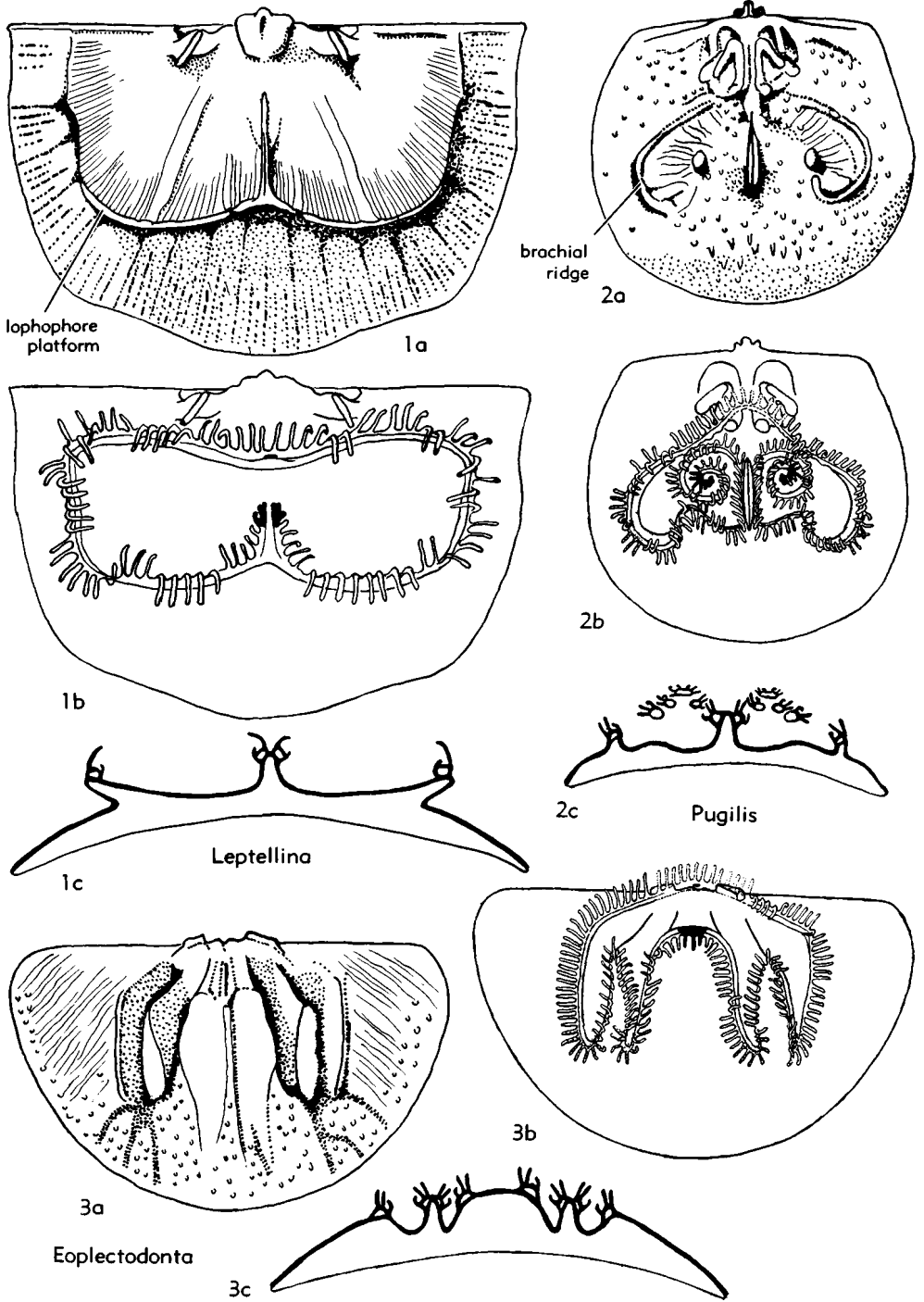


FIG. 113. Internal features of brachial valves of *Leptellina* (1a-c) and inferred restorations of the lophophore viewed ventrally and in transverse section, also of *Pugilis* (2a-c) and *Eoplectodonta* (3a-c) (65).

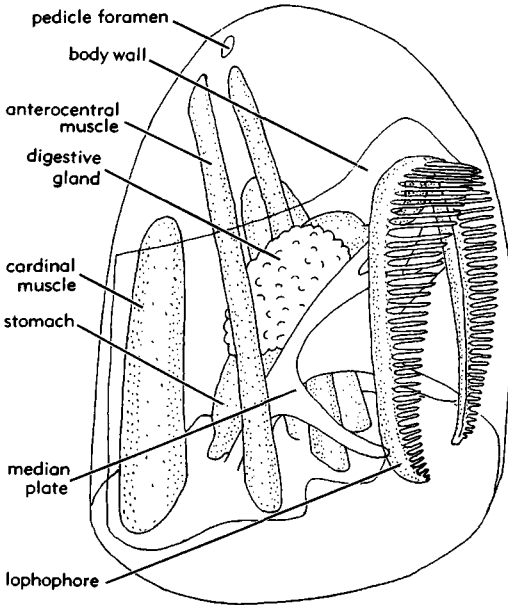


FIG. 114. Stylized reconstruction of *Ehippelasma* with inferred location of lophophore, musculature, and alimentary canal, shell treated as transparent (63).

be interpreted as having borne a schizolophous lophophore (Fig. 113,1a-c). The deeply divided, elongately oval platform of *Bimuria* or the pair of long, U-shaped sets of ridges of the strophomenacean *Christiania* must have functioned in a similar way; although like the divergent oval areas of the sowerbyellids, which are not only bounded submedially by ridges but also divided by a pair of divergent lateral septa, the structures may have supported a lobate trochlophore rather than a ptychlophore (Fig. 113,3a-c). Indeed, attached and modified trochlophores or schizolophes seem to have been the more likely kind of plectambonitacean lophophore, although spiral impressions in *Leptestia jukei* (DAVIDSON) suggest that in this stock, at least, the development was not arrested in the schizolophous stage but continued to the spirolophous climax.

Most strophomenaceans and davidsoniaceans were probably equipped with unsupported low spirolophes directed ventrally or dorsally and rarely, as in *Leptaena* and *Davidsonia*, an accommodating differential thickening of the shell has left impressions of spiral coils on the floor of the valves.

The productoids, however, together with later chonetoids and rare strophomenaceans (e.g., *Leptaenisca*, *Leptodonta*), are characterized by a pair of ridges arising between the posterior and anterior pair of dorsal adductor scars and recurring to define a pair of anterolateral areas commonly occupied by a smooth raised mound of secondary shell, or even twisted into two or three convolutions (e.g., *Leptaenisca*). These features are called **brachial ridges**, in the belief that they gave support to the lophophore. They are exceptionally associated with subconical impressions directed ventrally, which might represent differential thickening to accommodate the spirolophous part of a lophophore (e.g., *Levitusia*, *Gigantoproductus*). The ensemble suggests a plectolophous arrangement but with the side arms remaining adnate to the brachial valve and the spirolophes disposed as a pair of low spires in the same plane, so that both parts were aligned normal to their attitude in terebratuloids (Fig. 113,2a-c).

It has also been suggested that the brachial ridges may represent traces of the mantle canal system, such as sites of gonocoels, mainly because they commonly arise from the dorsal muscle field in a position occupied by the *vascula myaria* of orthoids and strophomenoids (33). The mantle canal systems of the productoids are unknown, but traces of radiating peripheral canals seen in *Peniculauris* terminate abruptly against the well-developed brachial ridges. This dissociation is even better seen in *Leptaenisca* and *Leptodonta*, both of which belong to groups that are known not to possess any feature like brachial ridges in the mantle canal system. Indeed, the elongately oval platforms of *Stipulina*, which are clearly elevated structures incorporating the brachial ridges, are so like the lophophore platforms of the plectambonitaceans that any function other than support to the feeding organ is difficult to imagine.

Among inarticulate brachiopods there are no prolongations of the shell which indisputably functioned as lophophore supports; but projections from the brachial valve of a few acrotetid genera may have given support to the lophophore and anterior body wall. This would appear to be the most probable function of the saddle-shaped plate of *Ehippelasma* (18), which arises from a

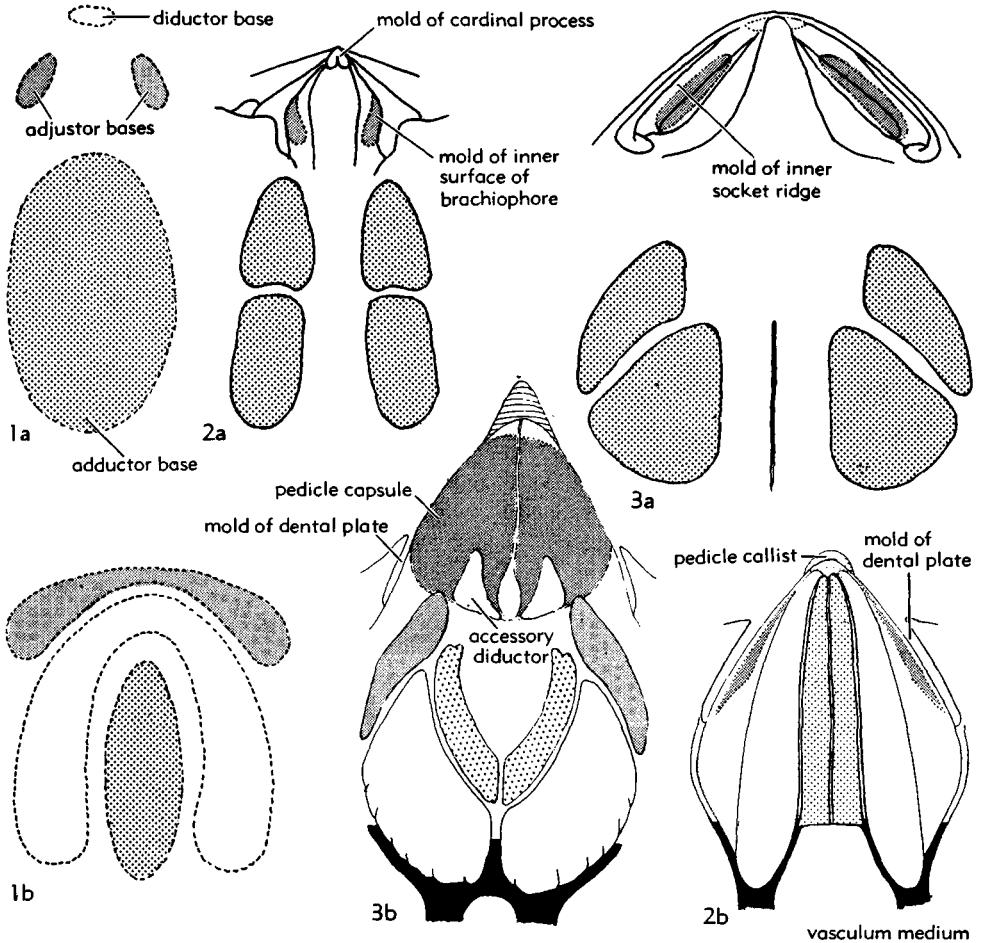


FIG. 115. Diagrammatic representation of principal muscle marks in (1a) dorsal and (1b) ventral interiors with examples of corresponding actual scars seen in *Dalmanella wattsi* (BANCROFT), M.Ord., Eng. (2a,b) and *Hemithiris psittacea* (GMELIN) (3a,b) (65).

relatively narrow base slightly behind the center of the valve and expands ventrally and anteriorly to terminate in a number of slender projections (Fig. 114). These projections are disposed with a crude symmetry about the median plane and their tips roughly fall on an imaginary surface which is inclined posteroventrally to make a high angle with the plane of commissure. The mouth in *Ephippelasma* presumably lay in the plane of symmetry, as in all Recent brachiopods, and must have opened along the crest line of the median plate or ventrally of this line. All adult individuals of *Ephippelasma* are small enough to suggest that their lophophores were probably trocholophous or schizolophous; and if the tips of the projec-

tions from the median plate touched the anterior part of the body wall, the limited brachial cavity could conveniently have accommodated a trochlophore (or schizolophore) only when the organ was oriented approximately parallel with the plane defined by the tips of the projections. In this attitude, the median projection could have supported the lophophore immediately dorsal of the mouth, with the laterally placed prongs embedded in the posterior arcs of the trochlophous ring on either side of the mouth.

Many other acrotretid genera have a thin bladeliike median septum, usually subtriangular in lateral profile and attached basally along its length to the brachial valve. The posteroventral edge of the median sep-

tum is commonly unmodified, but it may bear a slender triangular plate (e.g., in *Torynelasma*) or it may be narrowly expanded and digitate in a plane more or less normal to the septum (e.g., in *Angulotreta*, *Prototreta*). In all these forms, the medially situated mouth must have lain on, or ventral of, the free edge of the septum, which dorsally may have supported the generative tips of a trochlophore or schizolophore. The modifications on the posteroventral edge of the septum, however, are generally too narrow to have given much support to the lophophoral arcs lateral of the mouth.

MUSCULATURE

The muscles of most articulate brachiopods that leave their impressions (**muscle marks**) on the shell interior consist of two sets passing between the valves (**diductors**, **adductors**) and another two sets controlling the pedicle (**ventral** and **dorsal adjustors**). In the pedicle valve, all muscle marks tend to be grouped together to form a muscle field, which is ideally differentiated into a median adductor muscle mark contained posteriorly by two incomplete arcs of inner diductors and outer adjustors (Fig. 115, *1b*, *2b,3b*). The attachments areas in the brachial valve, however, are generally much more scattered (Fig. 115, *1a,2a,3a*). The adductor field commonly consists of an anterior and a posterior pair of marks, with one of each pair discernible on either side of the median line and well forward of the cardinalia, which accommodated both the dorsal adjustors and dorsal ends of the diductors, usually along the inner faces of the hinge plates (or brachiophores) and on a posteromedian outgrowth of secondary shell (cardinal process), respectively.

The muscle marks can vary not only in their relative position but also in the clarity of their impression. They may be deeply inserted or raised above the general level of the valve floor, or even greatly elevated on elaborate platforms. The definition of muscle marks in brachiopod shells is normally a function of age, so that the ultimate area of attachment attained in adult stages of growth (**muscle scars**) is much more easily seen than the impressions in young or immature valves. This clarity is due mainly to differential secretion but can also

result from a change in the texture of that part of the secondary layer affording attachment. Deposition by the modified epithelium underlying the muscle bases is commonly slower than elsewhere, so that the muscle marks are sunk below the level of adjacent shell. Indeed, even when the entire muscle field is raised above the valve floor on thick deposits of secondary shell, the marks themselves may be deeply impressed on the platform. Such impressions usually include a variable number of strip-like indentations (**muscle tracks**) disposed parallel with the adjacent boundaries of the muscle scars, which represent the course of migration for the muscle bases during shell growth.

The migration of muscle bases can involve two aspects of growth. First, the proportions of the field relative to those of the valve may remain constant, or they may undergo changes at any stage in growth by an accelerated expansion in size of either the valve or the muscle field. Greatly extended and splayed impressions (**flabellate muscle scars**) are commonly found in the adult pedicle valves of many stocks and usually result from an acceleration in the spread of the muscle bases. Secondly, irrespective of any changes in relative growth rates, there is always an absolute increase in the area occupied by the muscle bases, which may be greater along some vectors than others, so that the outline of the muscle marks may change significantly during growth.

The histological changes that make possible this increase in size are well seen in *Terebratulina* (Fig. 116, *A*), and were probably also typical of extinct groups. Fibers, together with an intervening sheet of connective tissue, are proliferated along the anterior and lateral boundaries of the muscles and spread over the inner surface of outer epithelium. As they become incorporated into the main mass of muscle, both connective tissue and associated outer epithelium become modified by the passage through them of tonofibrils. The muscle marks probably correspond to the area of modified epithelium and it is evident from the existence of muscle tracks that, like growth of the shell, distinct pauses occur in expansion of the muscle fields. Physiological changes within the modified outer epithe-

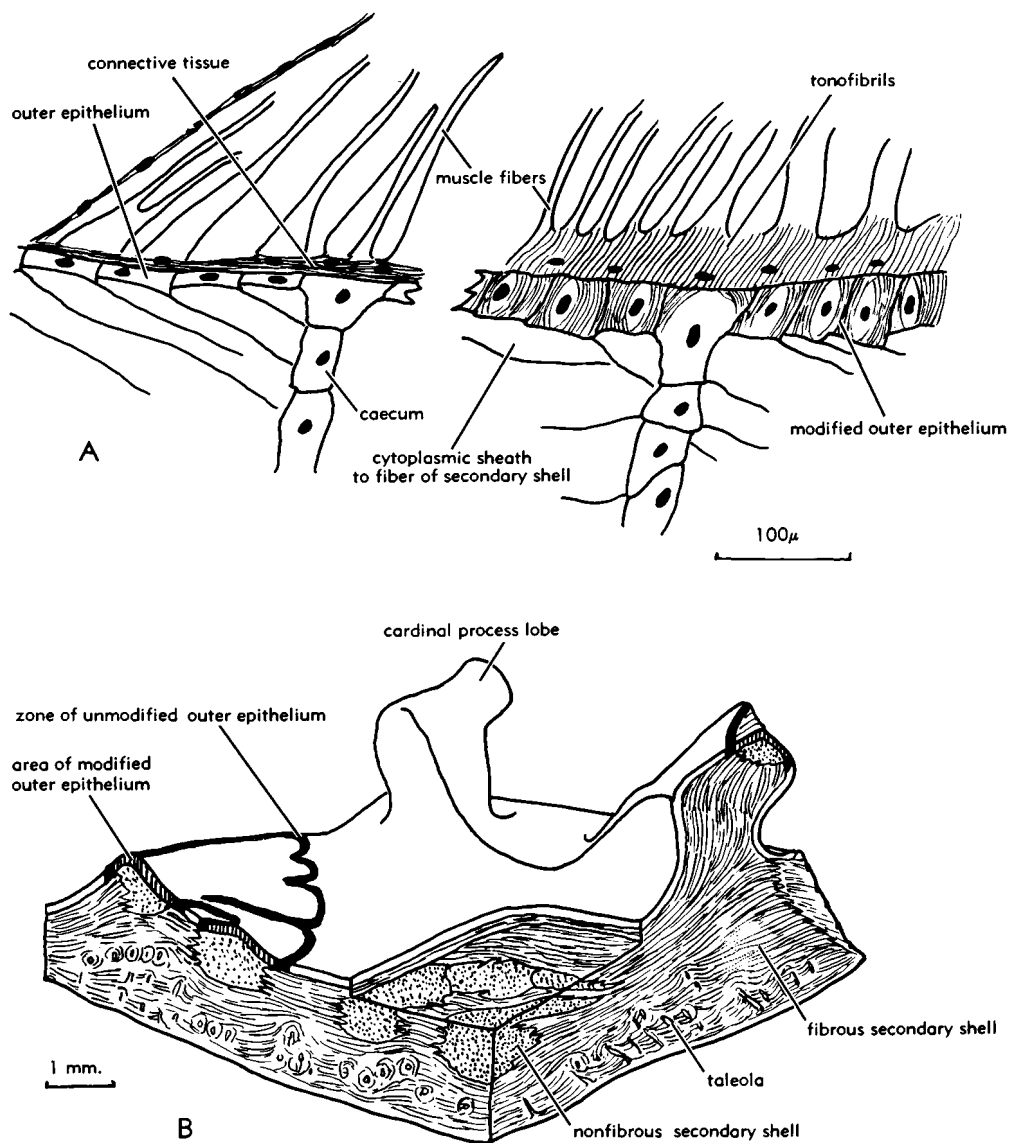


FIG. 116. Relationship (A) between diductor muscle base and shell of *Terebratulina caputserpentis* (LINNÉ) as seen at, and well within, the muscle boundary (to left and right respectively); and inferred relationship (B) between outer epithelium and muscle fields of *Strophonelloides* sp., U.Dev., USA (65).

lium underlying the muscle bases were probably responsible for differences in shell deposition that commonly characterize the muscle scars of later strophomenoids and productoids which are usually convoluted (dendritic impressions) in a manner that reflected the intricate lobation of the muscle bases. In these stocks, the shell making up the attachment areas for the muscles consists of cryptocrystalline calcite (55), which

was probably deposited extracellularly by modified epithelium, inserted deeply within and encroaching anteriorly over the fibrous layers (Fig. 116,B). Differences in texture may also be found in other articulate groups but are usually related to re-orientations of fibers within the secondary shell as in *Schizophoria* (52); or to concentrations of prismatic secondary shell, as in some spire-bearing brachiopods and pentameroids (42),

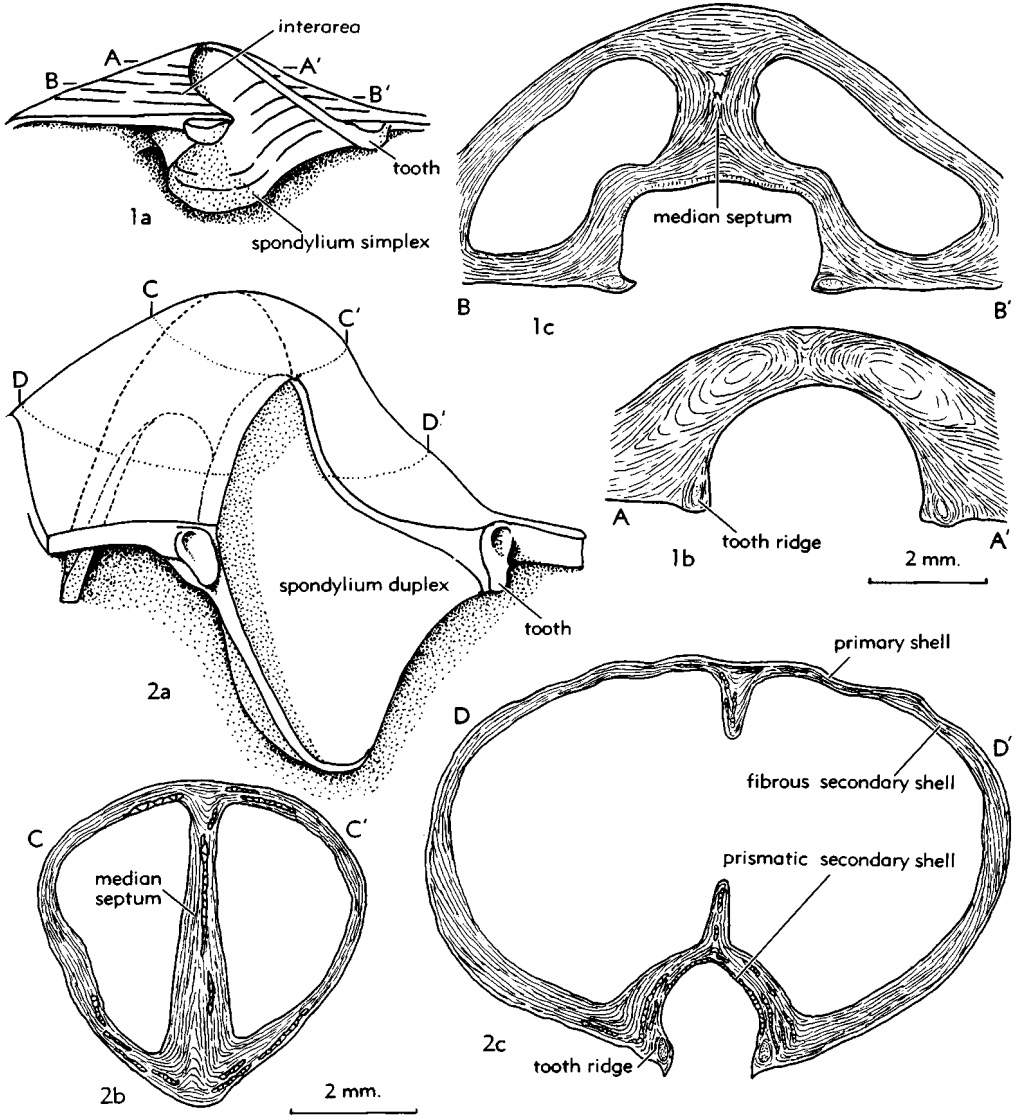


FIG. 117. Pedicle valves showing (1) spondylium simplex of *Skenidioides craigensis* REED, M.Ord., Scot., and (2) spondylium duplex of *Gypidula dudleyensis* SCHUCHERT, U.Sil. (Wenlock.), Eng.; 1a, oblique view showing location of transverse sections, 1b,c; 2a, oblique view showing location of transverse sections, 2b,c (65).

which, however, is not restricted exclusively to the main muscle-bearing bases (21).

The growth and distribution of platforms and apophyses to accommodate the various sets of muscles controlling shell movement are related to both the function and grouping of the muscles. The ventral muscle field tends to be located posteriorly of the transverse mid-line and, apart from details of

outline, its relative size probably does not vary greatly throughout the majority of articulate brachiopods. An important difference, however, is noted in location of the field within the valve, since those of rynchonelloids, spiriferoids, and terebratuloids are well forward of the umbonal chamber which accommodated the pedicle base, whereas the orthoid, strophomenoid, and

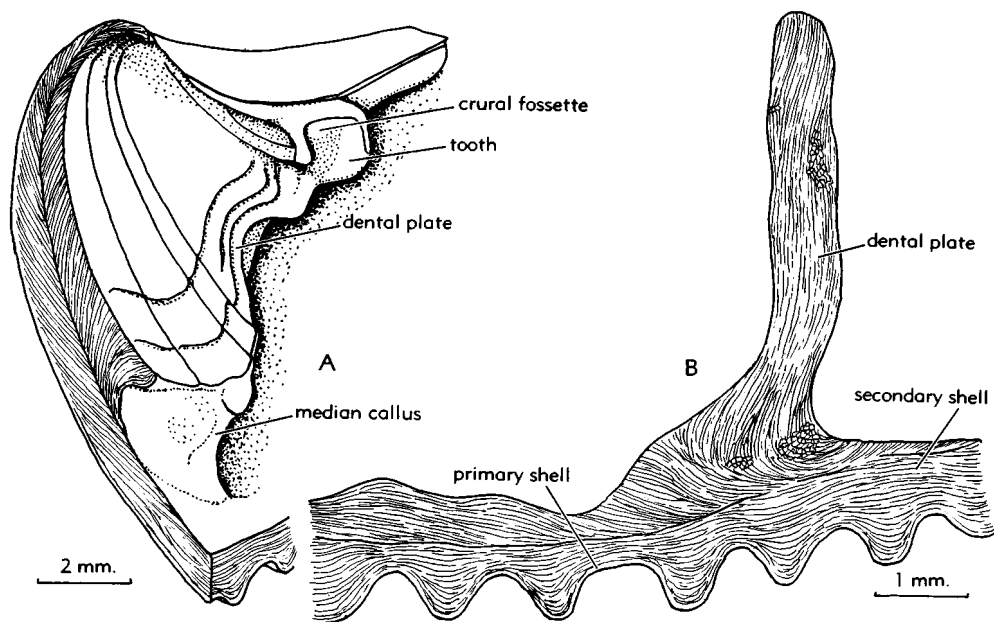


FIG. 118. *A*, Structure of pseudospondylium of *Glossorthis tacens* ÖRIK, M.Ord., USSR, with (*B*) transverse section showing relationship between dental plate and floor of pedicle valve (65).

porambonitacean fields typically occupied all available wall space within the delthyrial chamber, and usually did not extend very much forward of it (61) (Fig. 115,2*b*,3*b*). One of the consequences of this posterior location in the older brachiopods is that the dental plates commonly afforded attachment for the ventral adjusters and, by convergence toward each other, for an increasing area of the ventral diductor and adductor bases as well. Convergent dental plates that united with each other in such a way as to elevate the entire ventral muscle field above the floor of the pedicle valve constitute a **spondylium** (Fig. 117).

The spondylium is pre-eminently characteristic of the clitambonitoids, pentameroids, and stenocismataceans, but it is also found in other unrelated stocks such as the orthacean *Skenidioides*, the davidsoniacean *Ombonia*, and the stringocephalacean *Amphigenia*; and a complicated terminology, partly reflecting this diversity of origin, is now used to indicate various stages in spondylium development. KOZŁOWSKI (28) named the slightly convergent dental plates that grew directly from the floor of the pedicle valves of certain porambonitaceans like *Huenella*,

the **spondylium discretum**. This arrangement is, however, identical with that of most orthaceans and the term is acceptable only where clear evidence indicates that such a disposition was precursory to growth of a spondylium. Structures involving discrete dental plates are also known as **pseudospondylia** (43) if the anterior part of the ventral muscle field is elevated on an undercut callosity which may be prolonged anteromedianly as a ridge (Fig. 118). Pseudospondylia have frequently been designated sessile spondylia, but it is preferable to restrict the use of this latter term, with its implications of a true spondylium relationship, to structures formed by dental plates that unite with each other on the floor of the pedicle valve (e.g., *Sicelia*).

Spondylia formed by the convergence of dental plates above the floors of adult valves may be free of septal support, as in *Protorthis* and *Holorhynchus*, and presumably represent an anteromedian growth from a juvenile sessile spondylium. More commonly the spondylium is supported by a median septum or ridge of variable length. KOZŁOWSKI (28) distinguished between two types of septal support. In the **spondylium sim-**

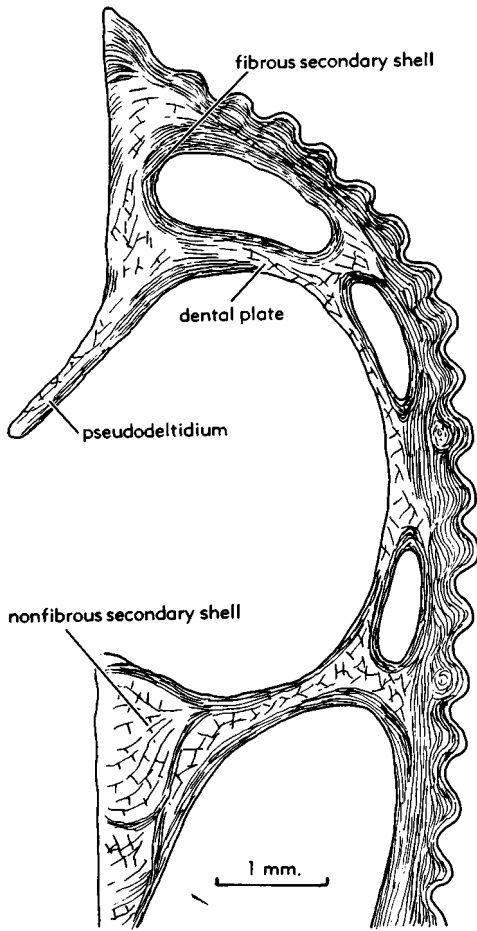


FIG. 119. Section through spondylium triplex of pedicle valve of *Antigonambonites planus* (PANDER), L.Ord., Baltic (65).

plex of *Skenidioides*, for example, the median septum consists of secondary calcite disposed in such a way as to suggest the incremental growth of a single structure. A low elevation of secondary shell commonly trailed anteriorly from the septum along the floor of the valve and became buried during the subsequent thickening and forward growth of the entire apparatus so that anterior sections of the adult spondylium simplex appear to show a dichotomy in the ventral end of the septum (Fig. 117,1a-c). KOZŁOWSKI believed that this kind of arrangement evolved by the elevation of the entire pseudospondylium above the floor of the valve, rather than by a convergence of dental plates. In contrast, a thin plate of prismatic calcite (intra-septal lamella) ap-

peared invariably to occupy the median plane of the septum supporting the pentameracean spondylium duplex; and its presence led KOZŁOWSKI to conclude that such a septum was formed by the incomplete fusion of the dental plates (Fig. 117,2a-c). He also assumed that the spondylium duplex was derived from the spondylium discretum by the convergence of the ventral parts of the dental plates toward each other.

The differences between the spondylia simplex and duplex may not be as fundamental as is generally believed (60). The intra-septal lamella has been described as having an enlarged base at the junction of the septum with the spondylium and as thinning out toward the floor of the valve, a disposition that is compatible with the prevalent interpretation of its origin. But ST. JOSEPH (42) and AMSDEN (2) have observed that the dorsal end of the intra-septal lamella can be continuous with extensive deposits of prismatic calcite lining the spondylium. Moreover, serial sections show that in at least some pentameracean genera (e.g., *Antirhynchonella*, *Pentamerella*, *Gypidula*) the prismatic calcite along the median plane of the septum is disposed more like a series of disconnected lenticles than a continuous sheet and in some planes of section is no more concentrated medially than elsewhere throughout the septum or spondylium (Fig. 117,2b). The distinctiveness of the spondylium duplex may therefore have resulted from the secretory activities of the outer epithelium of the pentameraceans, which, unlike that of the skenidiids, was capable of depositing prismatic calcite (57); and not from an imperfect fusion of dental plates. This interpretation would account for a more random distribution of the two different types of spondylia than was formerly believed possible. For a spondylium simplex has been identified in the syntrophiids and a spondylium duplex in the stenoscismataceans and camerellids; the spondylium of *Amphigenia* is truly duplex in that the dental plates are seen to unite into a median "septum" (11).

Complications also arise in the use of the term spondylium triplex (37) for an apparatus with a variably developed tri-septate support which is especially characteristic of certain gonambonitaceans (Fig. 119). In the genera described by ÖRİK, the

median and lateral (or accessory) septa underlying the spondylium were fashioned during early stages of growth by a pair of subconical hollows that developed between the floor of the valve and a sessile spondylium as it diverged in an anterolateral direction. In *Antigonambonites*, at least, the lateral septa acted as posterior partitions between the *vascula media* and *vascula genitalia* of the ventral mantle so that their growth may have been conditioned by the relationship between the ventral mantle canals and the body cavity. The term may therefore be used for the spondylia of some porambonitaceans, like *Tetralobula*, in which accessory septa, posteriorly underlying the spondylium, are also lateral boundaries to the ventral *vascula media*. It has been used, but is less appropriate, except in a strictly morphological sense, for the structure found in *Polytoecchia*, which appears to consist of a pair of subparallel dental plates containing a pseudospondylial platform elevated on a median septum.

The apparatus found in the pedicle valve of *Cyrtina* (Fig. 120) is not a spondylium in the sense that its posterior elements gave support to the entire ventral muscle field. It consists of a long, high, bladeliike, median septum to which the short, convergent, dental plates are ankylosed just below the posterior edge. A pair of lateral struts are subtended between the inner surfaces of the dental plates and the posteriorly protruding part of the median septum to define a small chamber (tichorhinum), suboval in section and extending from the umbo to the dorsal edge of the median septum. The tichorhinum is actually a chamber within a larger one bounded by an arched deltidium and the dental plates which must have contained the pedicle. Within such an arrangement, the tichorhinum, which may be incompletely partitioned (28), probably accommodated the base of the pedicle (the so-called unpaired median pedicle muscle) with the ventral adjustors attached to the anterolateral surface of the dental plates; and the ventral ends of the adductor and diductor muscles inserted on either side of the median septum anterior to its junction with the dental plates. In respect of their convergence into a median septum well posterior of the ventral muscle field, the dental plates are like the short dental ridges

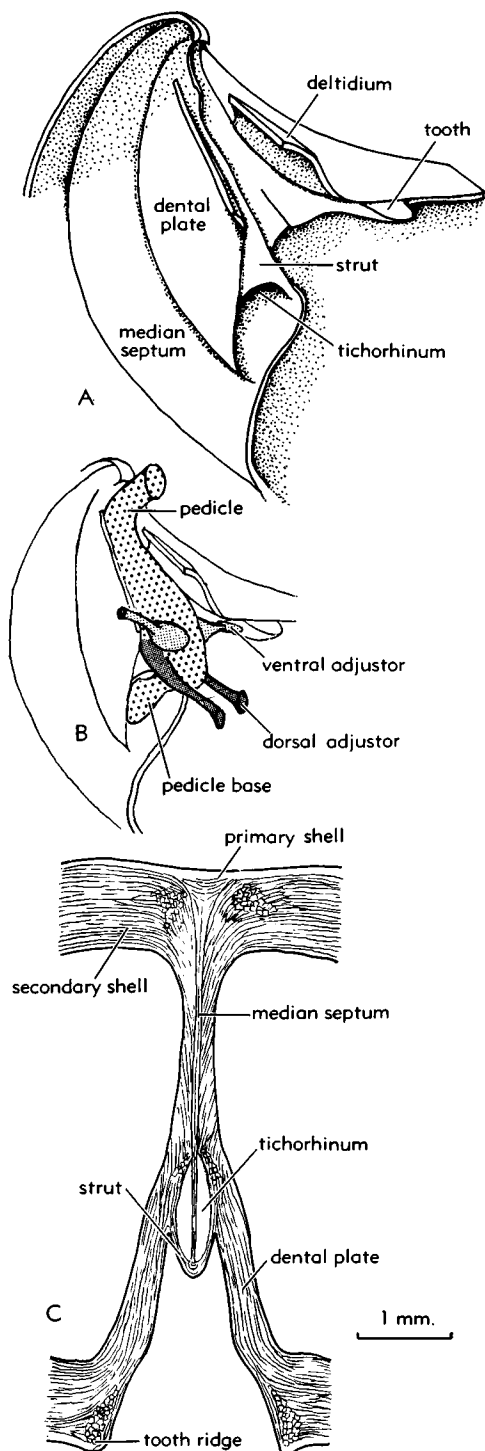


FIG. 120. A, Tichorhinum of *Cyrtina* sp., L.Carb., N.Ire., with (B) inferred disposition of the pedicle and its muscles, and (C) section showing tichorhinum of *Cyrtina* sp., M.Dev., USA (65).

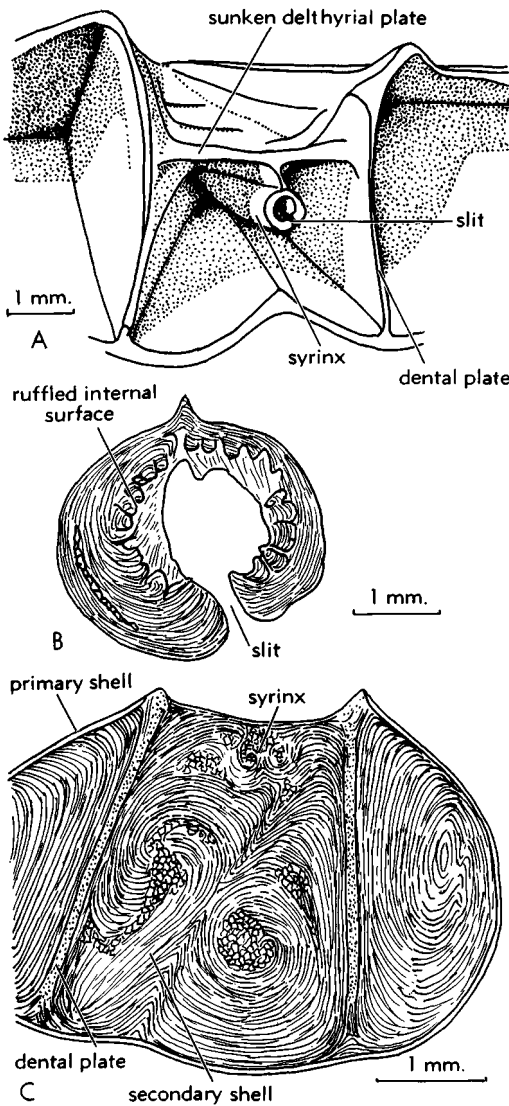


FIG. 121. *A*, Ventral interior of *Syringothyris cuspidata exoleta* NORTON, L.Carb., Eng., with (*B*) transverse sections of free dorsal end of syrx and (*C*) of apex (65).

of certain davidsoniaceans (e.g., *Orthotetes*), which also form a small chamber that has been incorrectly called a spondylium. Contrary to general opinion, the syrx of *Syringothyris* (Fig. 121) may have performed same functions as the tichorhinum. The sunken plate (delthyrial plate) within the delthyrium, to which the syrx is attached, is probably homologous with the pedicle collar and would thus have lain

anteroventrally to the pedicle or its remnant. If this were so, the syrx would have been deposited by outer epithelium around the attached end of the pedicle base which also

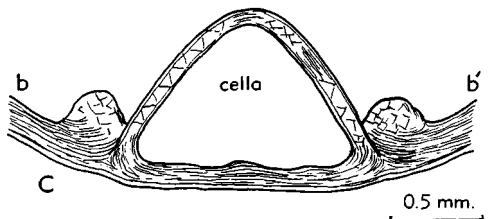
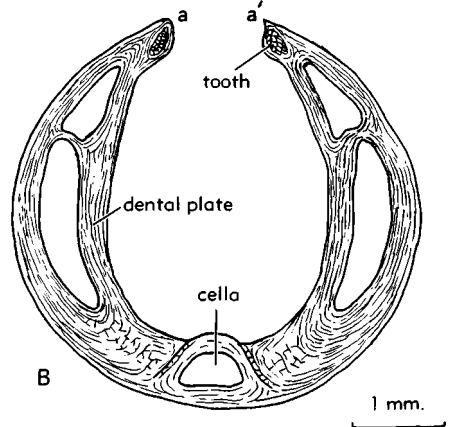
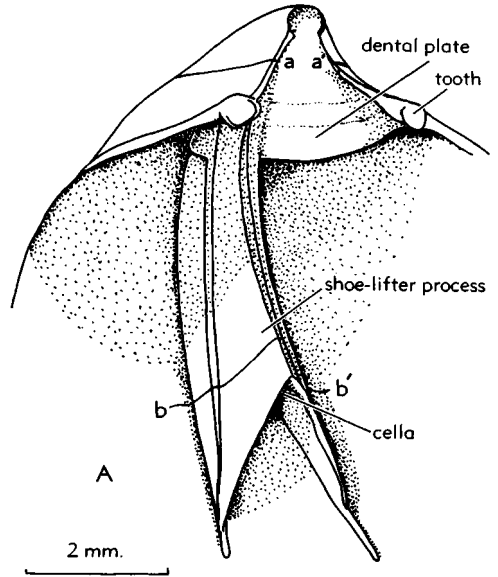


FIG. 122. Pedicle valve of *Merista tennesseensis* HALL & CLARKE, M.Sil., USA, showing shoe-lifter process; *A*, oblique view showing location of transverse sections, *B*, *C* (65).

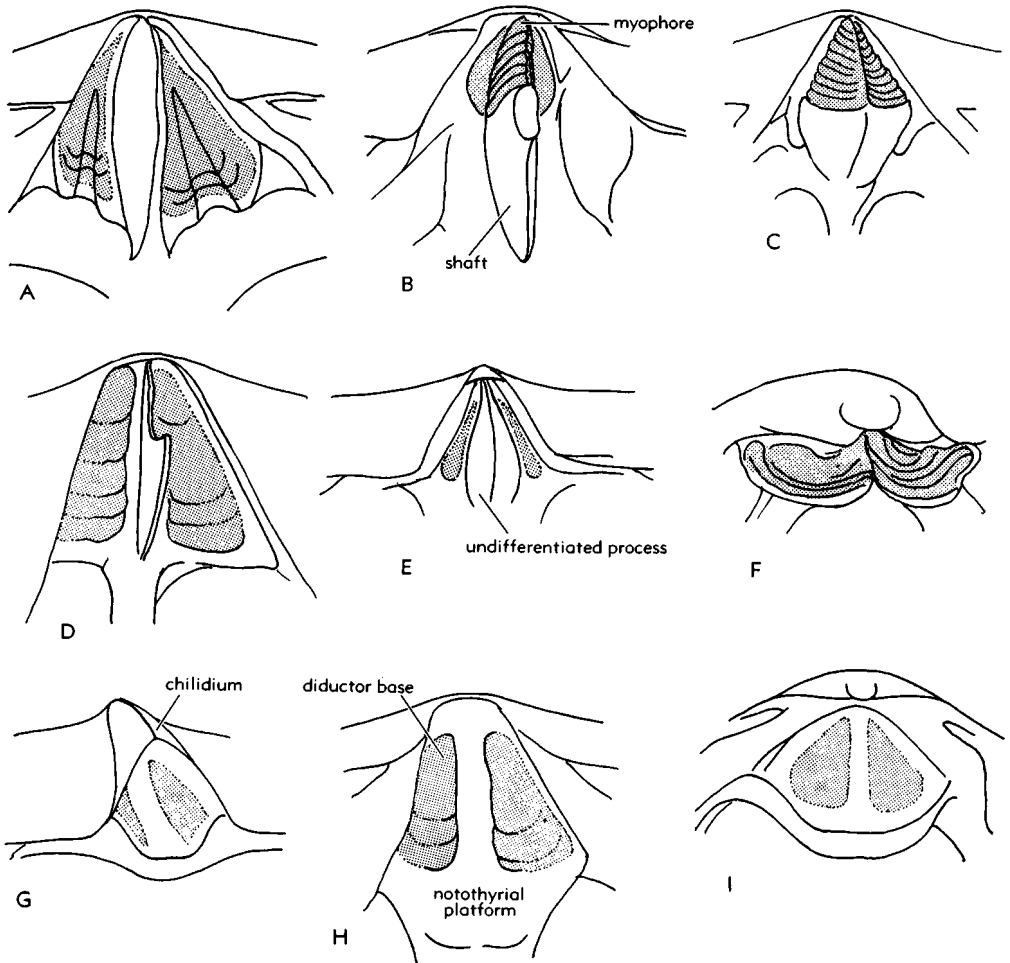
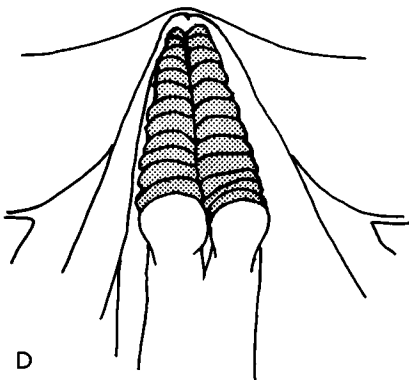
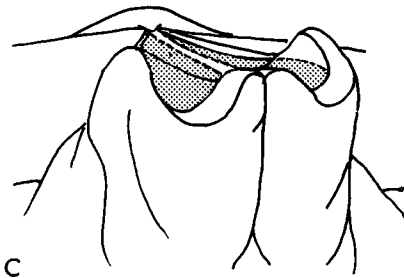
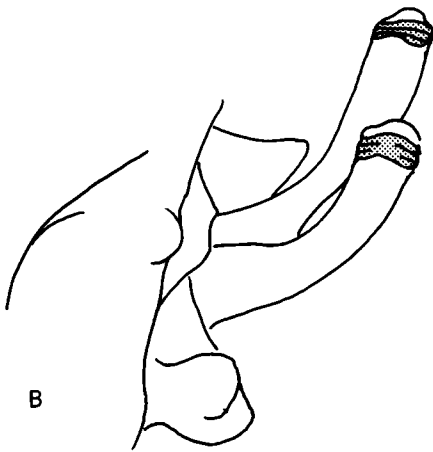
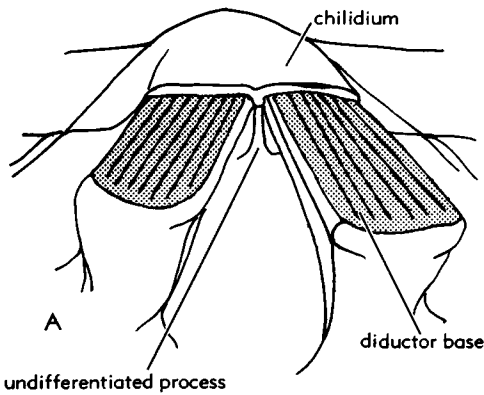


FIG. 123. Various types of cardinal processes: (A) development of subsidiary ridges flanking median septum of *Glossorthis*, with (B, C) differentiation of myophore and shaft in *Hebertella* and *Dinorthis*; (D, E) simple partition of *Glyptorthis* and *Bimuria* and (F) transverse area of muscle insertion of *Notosaria*; (G-I) undifferentiated areas for dorsal diductor attachment of *Leptella*, *Nothorthis*, and *Terebratulina* (65).

protruded anteriorly through the split on the syrninx. This interpretation is consistent with the pattern of muscle impressions on the floor of the pedicle valve, the closed ventral end of the syrninx and the sporadic development of a deltidium or stegidium posterior of the sunken plate. One other type of muscle platform was developed among certain spire-bearing brachiopods (27) such as *Merista* and its allies (Fig. 122). It consists of a transverse partition (**shoe-lifter process**) extending across the posterior part of the pedicle valve to define an open, hemipyramidal chamber (**cella**). The process was formed by deposition of

secondary shell within an infold of outer epithelium elevated above the floor of the pedicle valve even in early stages of growth so that in some genera (e.g., *Aulidospira*), the dental plates encroached forward over the inner surfaces of the partitions. A similar structure, which bears a strong median septum, is found in *Parenteletes*.

The dispersion of the attachment areas of the diductor and adductor muscles within the brachial valve has led to independently derived modifications of the dorsal interior. In general, the former are inserted near or at the notothyrial apex and posterior of the articular fulcral



points to provide a third order lever; and the latter submedially on the valve floor and well forward of the hinging mechanism. Ideally, both muscle sets are attached symmetrically about the median plane, the diductors to a pair of small bases, the adductors to two pairs of relatively large scars (Fig. 115, 1a, 2a, 3a); and this symmetry of insertion has led to many morphological changes especially around the dorsal beak.

In primitive articulate brachiopods, the dorsal ends of the diductor muscles were implanted on the notothyrial platform or, if this infilling was absent, on the inner sides of the brachiophores where they meet to define the notothyrial apex (Fig. 123, G, H). Accelerated deposition of secondary calcite by the strip of outer epithelium between the discrete muscle bases commonly led to the outgrowth of a variably defined median partition as in the orthaceans, plectambonitaceans, and even a few parambonitaceans (e.g., *Diaphelasma*). Such an outgrowth is referred to as a cardinal process, irrespective of whether it separated the areas for muscle insertion or whether it served as a surface for attachment (Fig. 123, D, E). Thus, in some orthaceans, most enteleteaceans and early rhynchonelloids (like *Orthorhynchula*), the muscle bases migrated medially to occupy the lateral and posterior surfaces of the partition (Fig. 123, B, C). Concomitant with this specialization, the median process became enlarged and differentiated into a shaft surmounted by a swollen head (**myophore**) which was crenulated by a series of thin plates of secondary calcite, thereby increasing the area for muscle attachment (Fig. 123, B, C). In many enteleteaceans (e.g., *Dalmanella*) the discrete nature of the muscle bases gave rise to a bilobed cardinal process by the development of a cleft on the posterior face of the myophore during its ventral growth (Fig. 124, D). In *Resserella*, each lobe of the divided myophore is bordered ventrally and laterally by a narrow, smooth ridge of secondary shell, which acted as a boundary to the central crenulated faces of muscle attachment (differentiated bilobed process)

FIG. 124. Various types of bilobed cardinal processes: A, *Rafinesquina*, with vestige of median undifferentiated process; B, *Oxoplectia*; C, *Resserella*; D, *Dalmanella* (65).

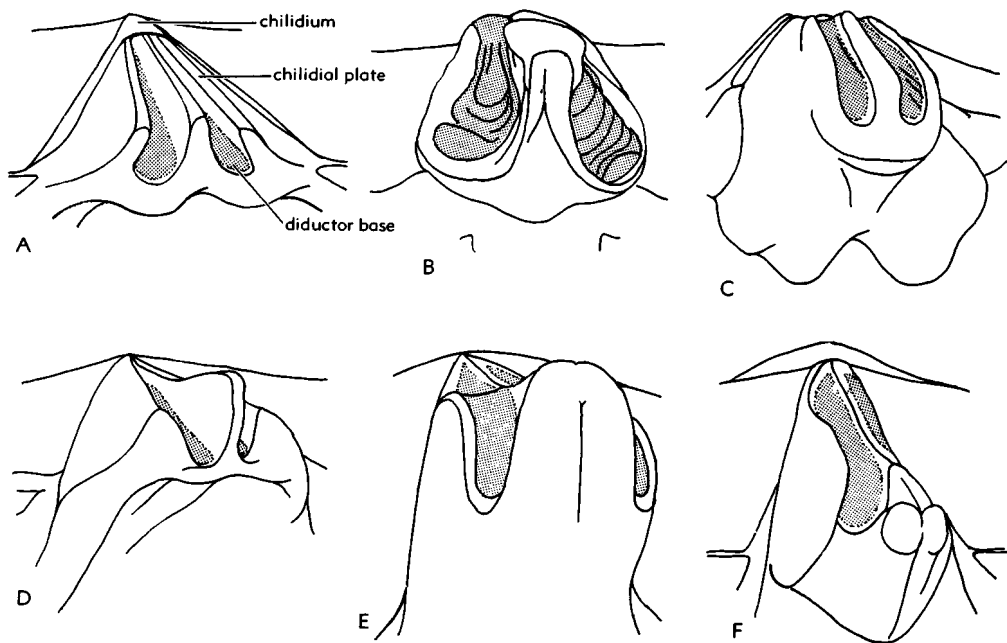


FIG. 125. Various types of trilobed cardinal processes: *A*, *Sowerbyella*; *B*, *Pugilis*; *C*, *Prionothisyris*; *D*, *Orthidiella*; *E*, *Resserella*; *F*, *Paucicrura* (65).

(Fig. 124,C); and in some species, the two inner adjacent boundary ridges also became ankylated and expanded posteriorly to simulate a trilobed myophore (Fig. 125,E). Alternatively, as in *Paucicrura*, the ventro-posterior edge of the myophore expanded at a greater rate than the crenulated areas to form a high median crest and with the development of smooth lateral and ventral boundaries to the attachment areas, a differentiated trilobed process came into being (Fig. 125,F), which is a reversion to the condition that prevailed in stocks with a simple median partition except, of course, for elevation of the entire arrangement above the floor of the notothyrium (61).

This pattern of elaboration, related to the posteroventral growth of the cardinal process and a migration of the muscle bases onto its distal surfaces, was repeated again and again during evolution of the articulate brachiopods and can be illustrated by a brief consideration of Paleozoic stocks.

Apart from unusual orthoids, like the triplesiaceans with their grotesquely exaggerated bilobed processes (Fig. 124,B), and the orthidiellids with their trilobed structures formed by the outgrowth of lateral

ridges that supported the muscle bases (Fig. 125,D), the plectambonitaceans show some resemblances to the enteleteacean elaboration. A trilobed condition, for example, was attained among the sowerbyellids (Fig. 125,A) by the posteroventral growth of the median partition and a pair of lateral plates bounding the notothyrium elevated as a single element above the hinge line. In the brachial valve of *Bilobia*, on the other hand, a basically trilobed arrangement became bilobed by the development of a cleft in the high median crest (36); and in *Anoptambonites*, the cardinal process consists of a median ridge and up to six lower lateral ridges simulating the transverse "comb" of many spiriferoids (58).

Among the strophomenaceans, davidsoniaceans, productoids, and chonetoids, variation in the morphology of the cardinal process was ultimately related to modifications of a bilobed structure (Fig. 124,A). This bilobation, however, did not result from a dichotomy of the median partition as in the enteleteaceans but to the posteroventral growth of flanking lateral ridges (compare Fig. 123,A). Such ridges supported the muscle bases and are found in a few clitam-

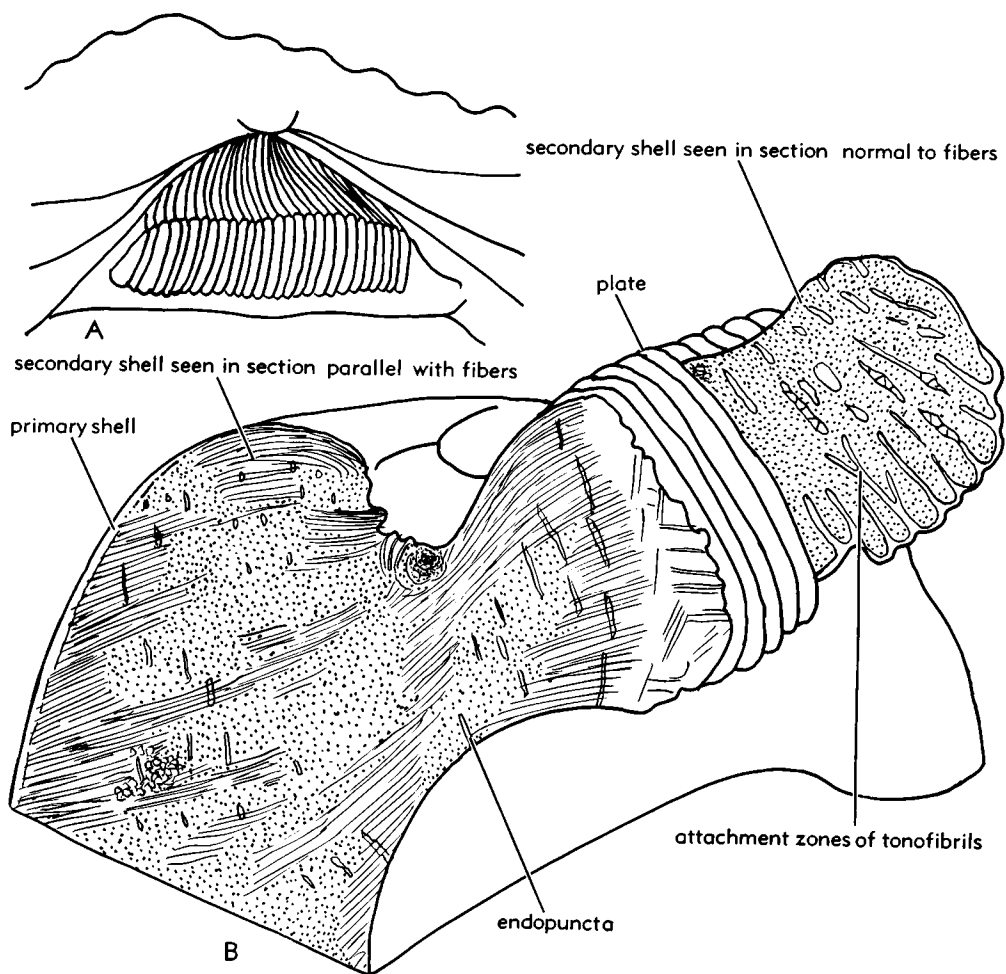


FIG. 126. Cardinal process of (A) *Neospirifer* and (B) *Terebratalia transversa* (SOWERBY) in median and tangential sections showing associated shell structure (65).

bonitoids (e.g., *Clinambon*) and especially in the orthidiellids (50). But their development in the strophomenaceans was accompanied by an atrophy of the median ridge and the differentiation of the greatly expanded posterior surfaces into crenulated zones with smooth boundaries (Fig. 124,A). In many chonetoids and productoids, the cardinal process lobes are slightly divergent and their boundaries are so exaggerated that they have a quadrilobed appearance. In other genera, the inner boundaries are more or less ankylosed to each other and the entire process is referred to as trilobed (Fig. 125,B); and in a few genera (e.g., *Titanaria*), the cardinal process consists simply

of a median lobe with a crenulated dorso-posterior face, a reversion that may have resulted from the atrophy of the lateral boundaries. Other modifications (33) that recall those of earlier independent stocks include the bilobed cardinal process of *Scacchinella*, which is as long and deeply forked as that of any triplesiacean, and the tendency for the productoid processes to overhang a conical hollow (*alveolus*) in a manner reminiscent of the undercut cardinal process of the sowerbyellids.

No elaborate cardinal process ever developed among the pentameraceans. It was also less prevalent among the rhynchonelloids, spiriferoids, and terebratuloids than

among the orthoids or strophomenoids, so that even in many Recent articulate brachiopods (e.g., *Hispanirhynchia*, *Dallina*), the attachment areas for the dorsal ends of the diductor muscles are nothing more than roughened surfaces beneath the beak. Modifications similar to those already discussed do occur, however. A simple, elongate, or transverse surface which is slightly elevated and tuberculate or crenulated is fairly common (Fig. 123,I) (e.g., *Rhynchotrema*, *Emanuella*, *Terebratulina*). A bilobed cardinal process comparable with the enteletacean structure is known in such genera as *Cryptopora*, *Ambocoelia*, and *Agulhasia*. Unusual variants include the forked, triplesiid-like process of *Stringocephalus* and the bilobed transverse outgrowth of *Notosaria*, with its transversely crenulated posterior face overhung by the dorsal beak (Fig. 123,F). A trilobed process like that of *Paucicrura* is also found in *Meganteris* and *Prionothyris* (Fig. 125,C); and a quadrilobate structure, reminiscent in section of the productoid arrangement, in *Eucharitina*. But perhaps the most novel kind of cardinal process developed in the rhynchonelloids, spiriferoids, and terebratuloids is a transverse ridge with a ventral face composed of thin plates aligned normal to the long axis of the ridge which, in thin section, give the cardinal process the appearance of a comb (Fig. 126).

The attachment areas for the dorsal ends of the adductor muscles normally consist of four scars impressed on the floor of the brachial valve at a variable distance anterior of the cardinalia. The scars may differ in size and arrangement, but they are commonly disposed in the median area of the valve with the posterior pair flanking the more closely placed anterior pair (Fig. 115, 3a). Modification by differential secretion of secondary calcite is minor except for the deposition of a median ridge that normally extends anteriorly from the vicinity of the cardinalia to separate the right and left set of adductor impressions (*myophragm*). The muscle field may, however, be raised above the floor of the valve in a number of different ways which deserve a brief review.

The best-known elevated structure for the reception of the dorsal adductor bases is the cruralium which, like its ventral counterpart, the spondylium, is especially char-

acteristic of the pentameraceans (28). It was formed by the forward growth of the outer plates underlying the base of the brachial

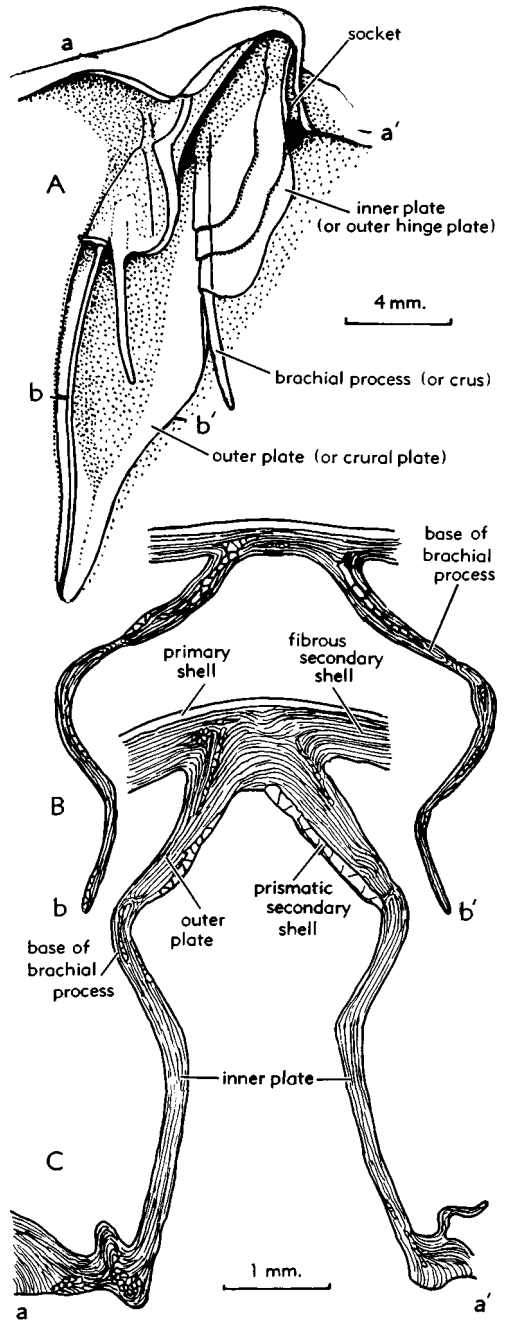


FIG. 127. Parts of brachial valves of *Gypidula*: A, *G. sp.*, M.Dev., USA, with convergent outer plates simulating sessile cruralium; B, C, transverse sections of *G. dudleyensis* SCHUCHERT, U.Sil. (Wenlock.), Eng., in planes indicated as A (65).

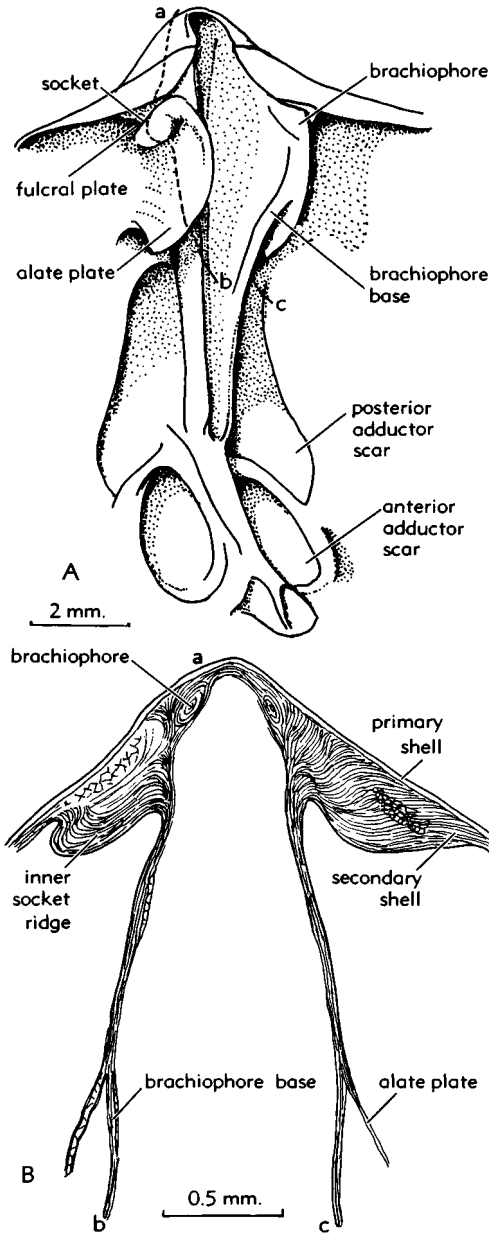


FIG. 128. Part of brachial valve of *Anastrophia* sp., M.Sil., Eng., showing (A) cardinalia relative to dorsal adductor field, and (B) oblique section along line indicated in A (65).

processes to receive part or all of the adductor muscle field. The plates may be subparallel to divergent (e.g., *Pentamerus*) or variably convergent (e.g., *Gypidula*, Fig. 127) so that they grow forward along the floor of the valve independently of each other to enclose a strip of the valve floor.

Alternatively, they may converge to unite with each other at their junction with the valve floor, the sessile cruralium of *Barrandella*, or above the valve floor to which they are joined by a median septum. The median septum of *Sieberella* is reported to have been developed independently of the

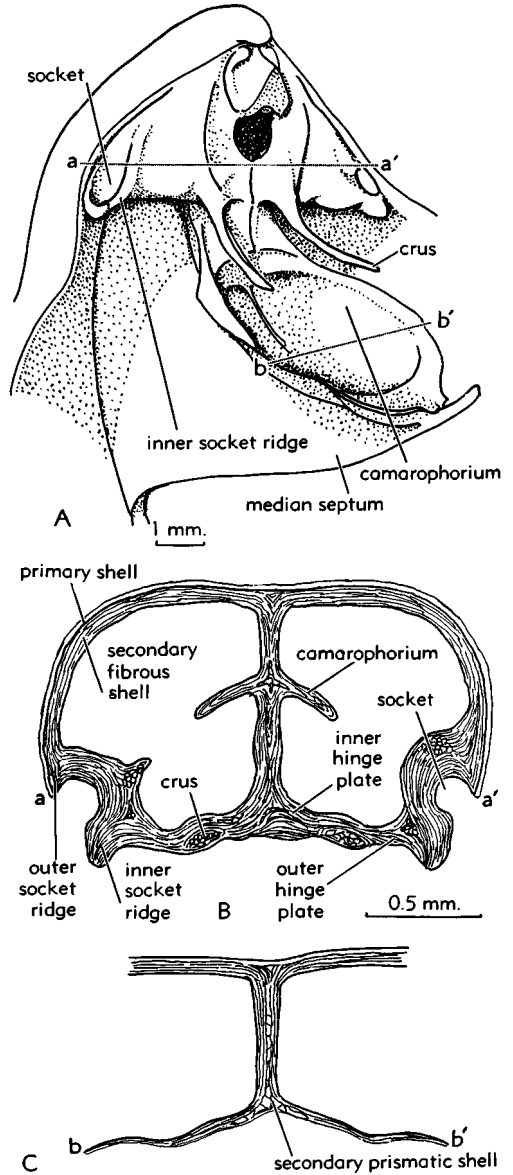


FIG. 129. A, Camarophorium of *Camerophoria* sp., M.Perm., USA; B, C, transverse sections of camarophorium of *Camerophoria* sp., U.Dev., USA, with approximate location of cuts indicated on A (65).

plates; but in some species of *Pentamerella* it is known to have been formed by the ankylosis of the converging plates.

The term cruralium has been used for structures which may have originated in the same way as that characteristic of the pentameraceans but which could not have given support to the dorsal adductor field. The elevated troughs found in the brachial valves of the syntrophiids and parastrophinids (Fig. 128) or of the skenidiids and *Kaysarella*, for example, were formed by the convergence of the brachiophore bases onto the valve floor or a median septum, but they all lie well posterior of the adductor scars and are more like septalia than cruralia, as originally understood by HALL & CLARKE (27). Moreover, although the spoonlike apparatus in the brachial valve of stenoscismataceans gives support to the dorsal adductor muscles, its growth around a high median septum was independent of the crura and it is more appropriately called a **camarophorium** or torynidium (17) (Fig. 129). The spiridium of *Spyridiophora* (20) and some aulostegids also supported the dorsal adductor muscles but on the transversely flattened posteroventral surfaces of a pair of subparallel plates that grew vertically from the floor of the brachial valve on either side of a low median septum (Fig. 130, A). These plates are quite different in disposition from the braceplates (55) of stropheodontids like *Douvillina* (Fig. 130, B), which grew anteromedially of the adductor field and are more likely to have given support to the median segment of the lophophore on either side of the mouth. In contrast, the apparatus subtended between the brachiophores and median septum of *Mystrophora* (16) did accommodate the dorsal adductor bases and is correctly called a cruralium.

In some genera (e.g., *Hypsomyonia*), the growth of a high median septum was accompanied by the elevation of the anterior boundaries to the dorsal adductor field above the floor of the valve. KOZŁOWSKI (28) has proposed the term pseudocruralium for this kind of structure, but it hardly seems necessary so to distinguish it from raised callus rims of secondary calcite that commonly defined the limits of the scars.

Apart from septa that clearly played a part in accommodating muscle bases (myo-

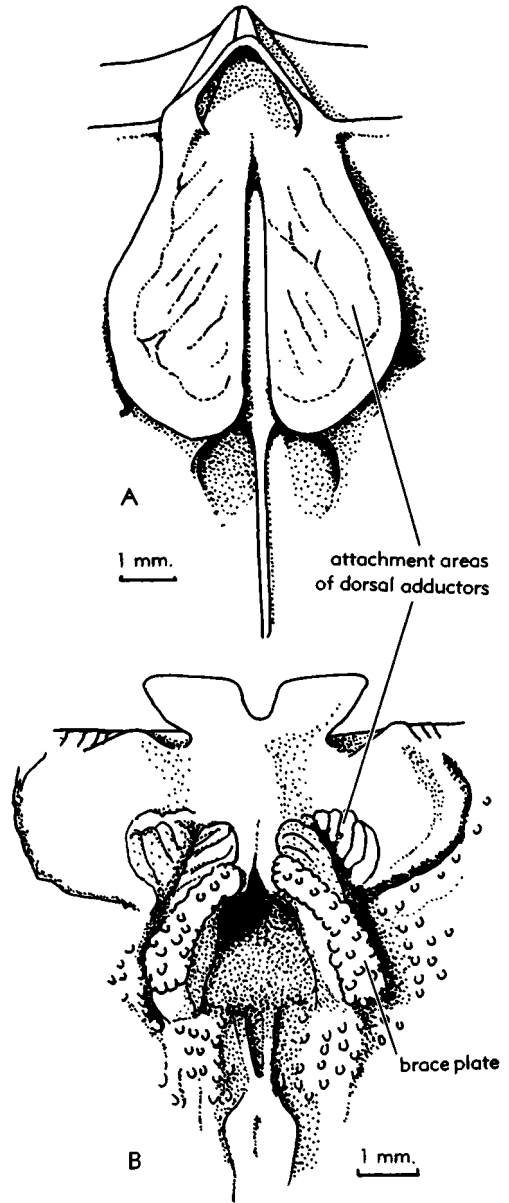


FIG. 130. Stylized representations of (A) subduced spiridium of *Echinosteges*, based on *E. tuberculatus* (R. E. KING), M. Perm., USA, and (B) braceplates of *Douvillina*, based on *D. arcuata* (HALL), U. Dev., USA (65).

phragms), found in either valve, a minority of articulate brachiopods (e.g., *Phragmorthis*, *Skenidioides*, *Mystrophora*, etc.) were equipped with septa that stood so high above the floor of the brachial valve as to divide the mantle cavity into two

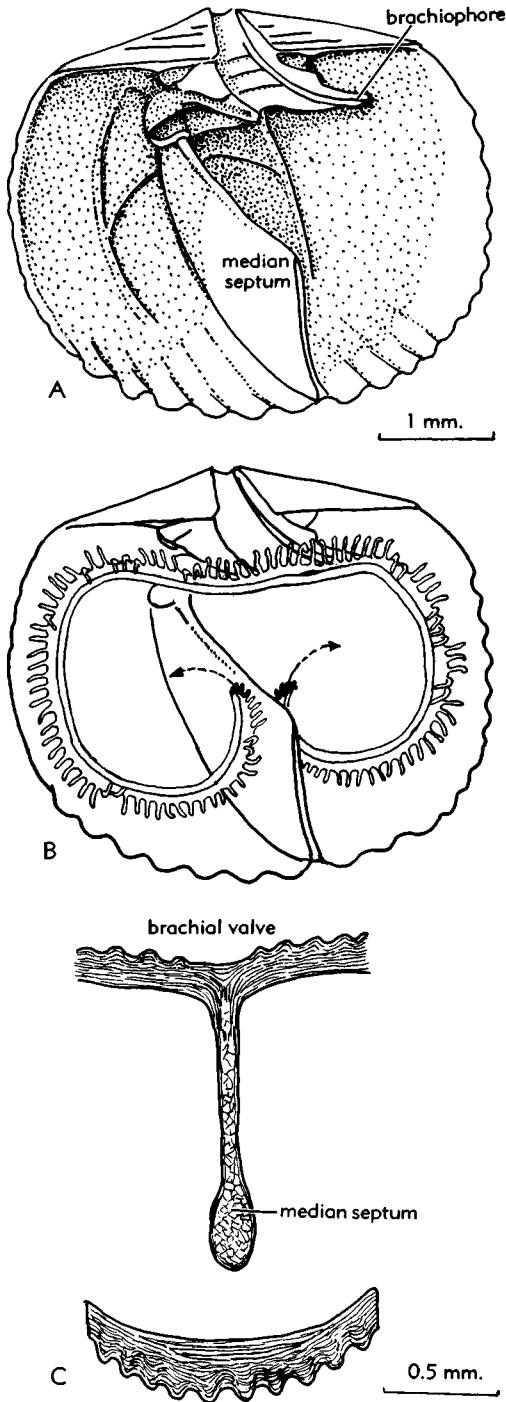


FIG. 131. *A*, Dorsal interior of *Phragmorthis* sp. cf. *P. butsi* COOPER, M.Ord., Scot., with (*B*) inferred disposition of lophophore about median septum and (*C*) transverse mid-section through shell to show relationship of septum to pedicle valve (65).

compartments (Fig. 131). A septum of this kind usually rises steeply to its apex along its posterior edge, whereas the anteroventral edge tends to fall away more gently, in a curve conforming to the anteromedian longitudinal profile of the pedicle valve. This characteristic profile and the closeness of the fit with the pedicle valve, when the shell was closed, suggest that the septum was associated with the lophophore. It is unlikely, however, that the septum gave support to the lophophore, although it may have assisted in the separation of the left and right halves of that organ during its schizolophous growth, in a manner reminiscent of comparable outgrowths in the brachial valves of terebratellaceans. Transverse partitions, again unrelated to the insertion of muscle bases, are also found in the pedicle valves of such independent stocks as richthofeniids (33), scacchinellids (54), and *Syringospira* (15) (in which they are known as blisters). All shells so equipped have very deep conical or subpyramidal pedicle valves which must have grown at such a faster rate than the enlargement of the contained soft parts that the viscera migrated continually in a dorsal direction, thereby creating space between the internal surface of the valve and the outer epithelium, which was then sealed off by deposition of a partition of secondary calcite (Fig. 132).

Muscle scars and, more rarely, muscle tracks are developed in the inarticulate brachiopods and are impressed on the inner surface of the valves by differential secretion of the outer epithelium associated with the muscle bases, and in this sense they are closely comparable with the scars and tracks of the articulate brachiopods. Commonly this differential secretion merely involves a reduced rate of deposition of shell material, the shell underlying the muscle scars being similar in structure and composition to the remainder of the valve. The physiological changes of the epithelium at the base of the muscles may, however, be more marked, as in *Crania*, where the modified epithelium is responsible for the deposition of calcite intracellularly, in marked contrast to the extracellular secretion which characterizes the remainder of the outer epithelium.

Within any Recent inarticulate genus the

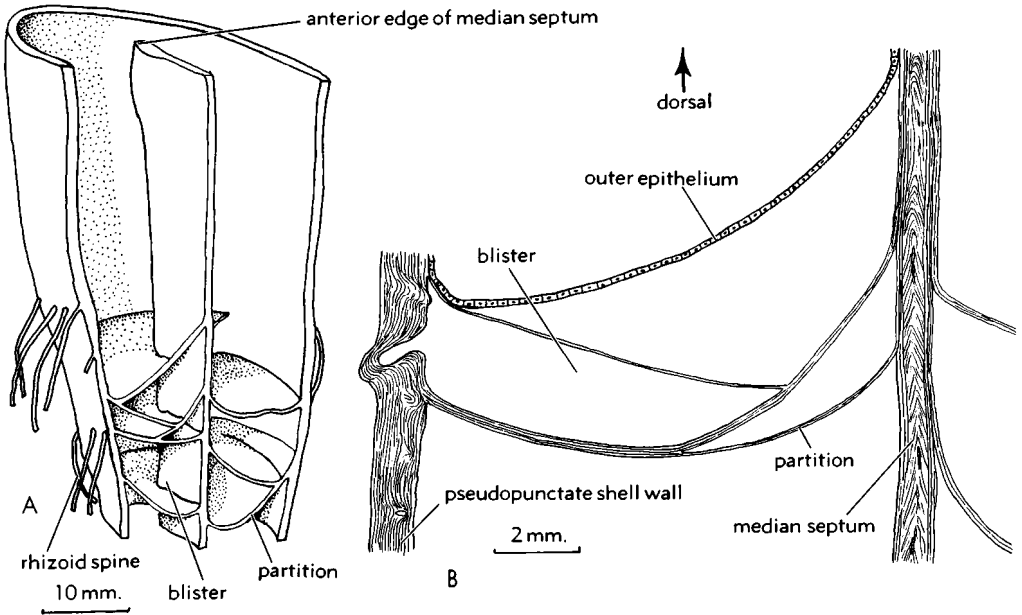


FIG. 132. A, Pedicle valve of *Scacchinella americana* STEHLI, L. Perm., USA, cut parallel with and anterior to interarea, with (B) section showing inferred relationship between transverse partitions and outer epithelium (65).

muscles fall into two groups, the adductors and the oblique muscles (see Figs. 28-29). Basically there are two pairs of adductors, the muscles of each pair being symmetrically disposed relative to the median line of the valve; the posterior pair are situated close to the posterolateral boundary of the body wall, while the anterior pair are placed well forward in the body cavity. Both pairs pass more or less directly dorsoventrally between the valves. The homologue of the posterior pair of adductors is strongly modified in Recent lingulids to form a single umbonal muscle consisting of two very unequal bundles of fibers (p. H27), but the homologues of the anterior adductor muscles, known as the central muscles in this family, do not deviate from the basic pattern. The oblique muscles are usually more slender than the adductors and are commonly longer; as their name implies, they traverse the body cavity obliquely, either in a dominantly anteroposterior direction or laterally. Although the number of oblique muscles is constant within any of the families of Recent inarticulate brachiopods, considerable variation exists between the families, the lingulids having four pairs, the discinids three, and the craniids only two

pairs. In all families, the function of the oblique muscles appears to be similar, to assist the adductors in opening and closing the valves and to control the relative longitudinal and lateral displacements of them.

Compared with the articulate brachiopods, the muscles of the inarticulates differ, not only in their function, but also in their distribution. The muscle bases of the inarticulates are commonly more peripherally placed within the body cavity and they are not grouped to form a well-defined muscle field in either valve. There is also another important difference. With a few exceptions (e.g., thecideaceans), the number of shell muscles is constant within the Articulata, in contrast to the variable number of oblique muscles found among inarticulates. This variation of the oblique muscles, combined with the delicacy of the impression of their attachment surface to the shell, makes it extremely difficult, and in some instances impossible, to reconstruct the entire muscle system for extinct stocks.

Within any one superfamily, the scattered evidence suggests that although the relative position of individual muscles is variable, the number of muscles is commonly constant. Thus, among the Lingulacea, with

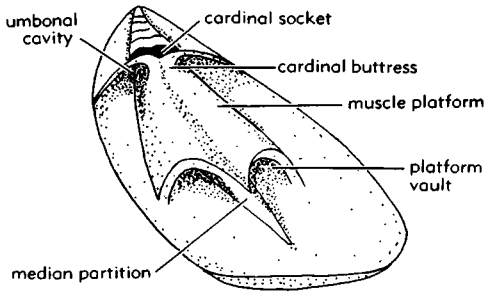


FIG. 133. Morphology of pedicle valve of *Trimerella* (63).

the possible exception of some of the paterulids and craniopsids, the basic muscle pattern appears to have been comparable with that of *Lingula*. The development of transmedian muscles, which cross the body cavity laterally as they pass from pedicle to brachial valve, is unknown outside the superfamily, although they may have occurred also in the trimerellaceans. Some variation in the relative positions of the muscles does occur and is seen for example in *Obolus* and *Pseudolingula* (29, 30). In the former genus, the transmedians do not form composite scars with the middle and outside lateral muscles on the brachial valve as they do in *Lingula* and the umbonal muscle consists of two subequal bundles of fibers which form separate scars on the pedicle valve and which unite to form a single scar on the brachial valve. In *Pseudolingula*, the umbonal muscle of *Lingula* is represented by two separate bundles of fibers which form a pair of posteriorly placed scars in both valves. Unfortunately, it is not known how persistent or widespread are these deviations from the *Lingula* pattern within the superfamily.

The details of the muscle system of the trimerellaceans (which, together with the lingulaceans, constitute the Lingulida) are still inadequately known. Within this superfamily there is a marked tendency for the development of muscle platforms in both valves. In the older genera (e.g., *Eodobolus*), these are poorly developed and are little more than a thickening of the posterior part of the valve, but they are extravagantly developed in younger forms like *Trimerella*. In *Trimerella* (Fig. 133) the platforms are hollow anteriorly and are elevated high above the valve floor, being supported medially by a median partition,

which projects in front of the platform and divides the cavity beneath it into two sub-tubular vaults. The entire platform was invested in and secreted by outer epithelium. During the earlier stages of growth of the animal, the front edge of the platform and the median partition grew anteriorly and the posterior ends of the vaults were progressively infilled with shell material secreted by the infolds of epithelium lining them. There are at least two and possibly three pairs of scars on the muscle platforms of both valves, with an additional minimum of at least two pairs of rather elongated scars on the floor of both valves, lateral to the platforms, forming the sides and ends of the so-called "crescent." The overall distribution of the scars suggests that the muscle system may have been of the *Lingula* type, but more information is required to confirm this hypothesis. Muscle platforms occur in other Lingulida stocks. Low platforms occur in *Lingulops* and most of the craniopsids, usually in both valves, but they may be restricted to the ventral one. These platforms are developed as low thickenings of the valve floor, their anterior margin may be slightly excavated and is always abruptly flexed above the inner surface of the valve. As in the trimerellids, they carried some of the musculature, but more laterally placed muscles were commonly inserted in the floor of the valve, lateral of the platform. Higher platforms are developed in *Lingulasma* and *Andobolus*. In the former genus, the platforms are broadly comparable to the trimerellacean development; they are internally gently concave and that of the brachial valve is hollow anteriorly and is supported by a median septum. In *Andobolus* the muscle platform, which is present only in the brachial valve, is strongly bifid, with a deep median groove separating the two halves; in transverse cross section the platform has the appearance of a pair of rabbit ears. The distribution of muscle scars on the platform of this rare genus is unknown.

Among the Obolellida the muscle scars are commonly only lightly impressed and the full complement of muscles is probably still unknown. Two pairs of scars are usually seen in the pedicle valve, one pair (the larger), posterolaterally placed, and a second pair, close together, near the middle of

the valve. Judging from the distribution of the muscle scars of other inarticulate brachiopods these are possibly the homologues of the posterior and anterior adductors. In the brachial valve three pairs of scars are commonly recognizable, two pairs close together, posterolaterally located in front of the pseudointerarea, with a third pair situated near the center of the valve. Additional muscles probably existed, however, for there are indications of a third pair of muscle scars in the pedicle valve of *Bicia*, situated in front of the better-impressed, medianly placed pair. Similarly, there are indications of a fourth pair of scars in the brachial valve of *Trematobolus*, in a position which would agree with that of the anterior lateral muscles of *Lingula*. These scars have not been identified in other genera referred to the order, however, and at present the muscle system cannot be reconstructed confidently.

In the Acrotretida, the complement of shell muscles of the craniids has seemingly been constant throughout the history of the stock. There is some variation in the relative size and position of the anterior and posterior adductors, but both pairs of muscles undoubtedly existed. The scars of the oblique muscles are not known in all genera referred to the family, but traces of them are frequently preserved and it appears probable that they possessed two pairs of oblique muscles similar to those of Recent *Crania*.

Only the adductor muscle scars are known in fossil discinaceans and extinct representatives of this superfamily possessed two pairs of these muscles, located in a broadly comparable position to those of modern *Discina* and *Discinisca*. It is not known whether, like these genera, they also possessed three pairs of oblique muscles; even in Recent shells, the impressions of these muscles are exceedingly faint.

Among the Acrotretacea, particularly the acrotretids, two pairs of muscle scars are commonly fairly conspicuous in both valves. The pedicle valve bears a pair of large cardinal muscle scars on the posterolateral or posterior slopes of the valve and a much smaller pair of apical pits, usually located near its apex. The brachial valve has a complementary pair of large cardinal scars posterolaterally placed and a small pair

of scars near the center of the valve. A further unpaired scar, the posteromedian, situated on the posterior end of the median septum of the acrotretids has been described, but its existence is doubtful. A number of reconstructions of the muscle system are possible, but the one here illustrated (Fig. 96, 114) is based on the assumption that the posteromedian muscle, if it exists, is a body muscle not attached to the pedicle valve. The principal muscle scars are all assumed to be sites of attachment of single muscles, because no specimen shows evidence suggesting that they are composite. It is difficult to homologize acrotretacean muscles with those of other members of the Acrotretida, but it appears possible that the cardinal muscles are equivalent to the posterior adductors of the discinaceans and craniaceans, and the antero-central muscles, which form the apical pits in the pedicle valve and the small, centrally placed scars in the brachial valve, are the homologues of the anterior adductors. Additional scars which could be referred to oblique muscles have not been observed and these muscles may not have been present in this group. The form of the posterior margin of the brachial valve in many genera suggests that oblique movement would have been restricted if not entirely inhibited. Opening of the valves in the group was probably largely controlled by dermal muscles in the body wall. Another interpretation of these muscles, which cannot be entirely dismissed, is that the cardinal muscles are homologues of both the posterior and anterior adductors and that the antero-central muscles are oblique muscles.

The muscles of the remaining superfamily of the Acrotretida, the Siphonotretacea, are poorly known. Only one pair of relatively large scars may be definitely recognized in each valve, and these possibly may be homologues of the acrotretacean cardinal muscle scars.

The internal morphology of the Paterinida, unfortunately, is only imperfectly known for a limited number of genera. Impressions on the internal surface of the shell are very delicate and it is difficult to be confident of their origin, but what are seemingly muscle tracks suggest that the musculature of this order differed considerably from that of the remainder of the inarticu-

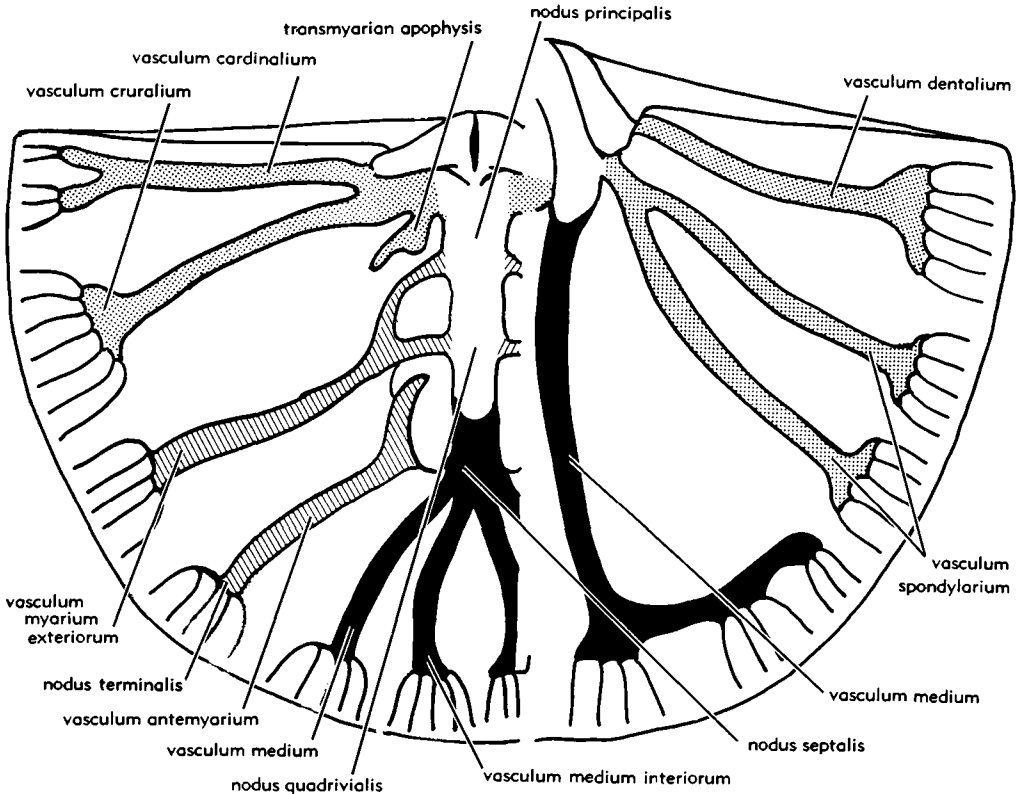


FIG. 134. Idealized canal systems in brachial (to left) and pedicle (to right) valves of primitive articulate brachiopod to illustrate terminology used by ÖRİK (37) (65).

late brachiopods. All of the scars recognized produce narrowly triangular tracks radiating from the apex. In the pedicle valve two such tracks diverge slightly anteriorly, terminating near the center of the valve, whereas in the brachial valve there are seemingly two pairs of tracks, one pair diverging anterolaterally and a second pair forming a single medianly located depression. The location of these tracks, if they are correctly interpreted as muscular in origin, in some ways is more reminiscent of the muscle system of the articulate brachiopods than the Inarticulata.

MANTLE CANAL SYSTEMS

The system of canals that pervaded the mantles of fossil brachiopods may be reconstructed by deciphering a series of impressions on the interiors of both valves. These impressions consist of a number of grooves or ridges, more or less symmetrical-

ly disposed on either side of the longitudinal mid-line, which are commonly seen to emanate from the vicinity of the muscle scars. They arose by differential deposition of secondary shell because these strips of outer epithelium arching the canals secreted shell material at a slower or, less commonly, faster rate than over the mantle generally.

The fine distal branches of all canals that terminate just within the shell margins are known to connect with the setal follicles in living articulate brachiopods. The disposition of impressions of terminal branches relative to the grooves and eminences along the internal margins of fossil shells suggest that this relationship always has obtained.

Interpretable patterns are rare and in general are more likely to be found not only in gerontic specimens but also, for some obscure reason, in older stocks (e.g., orthoids, strophomenoids, porambonitaceans), and it is symptomatic of this geological circumstance that the first analytical study of the patterns

was prepared by ÖRİK (37). He showed that arrangements deduced from a study of the clitambonitoids were sufficiently consistent to merit special terminology (Fig.

134). Some of the terms have been proposed for details of canal intersection or location within what must have been the body cavity and are not important in any

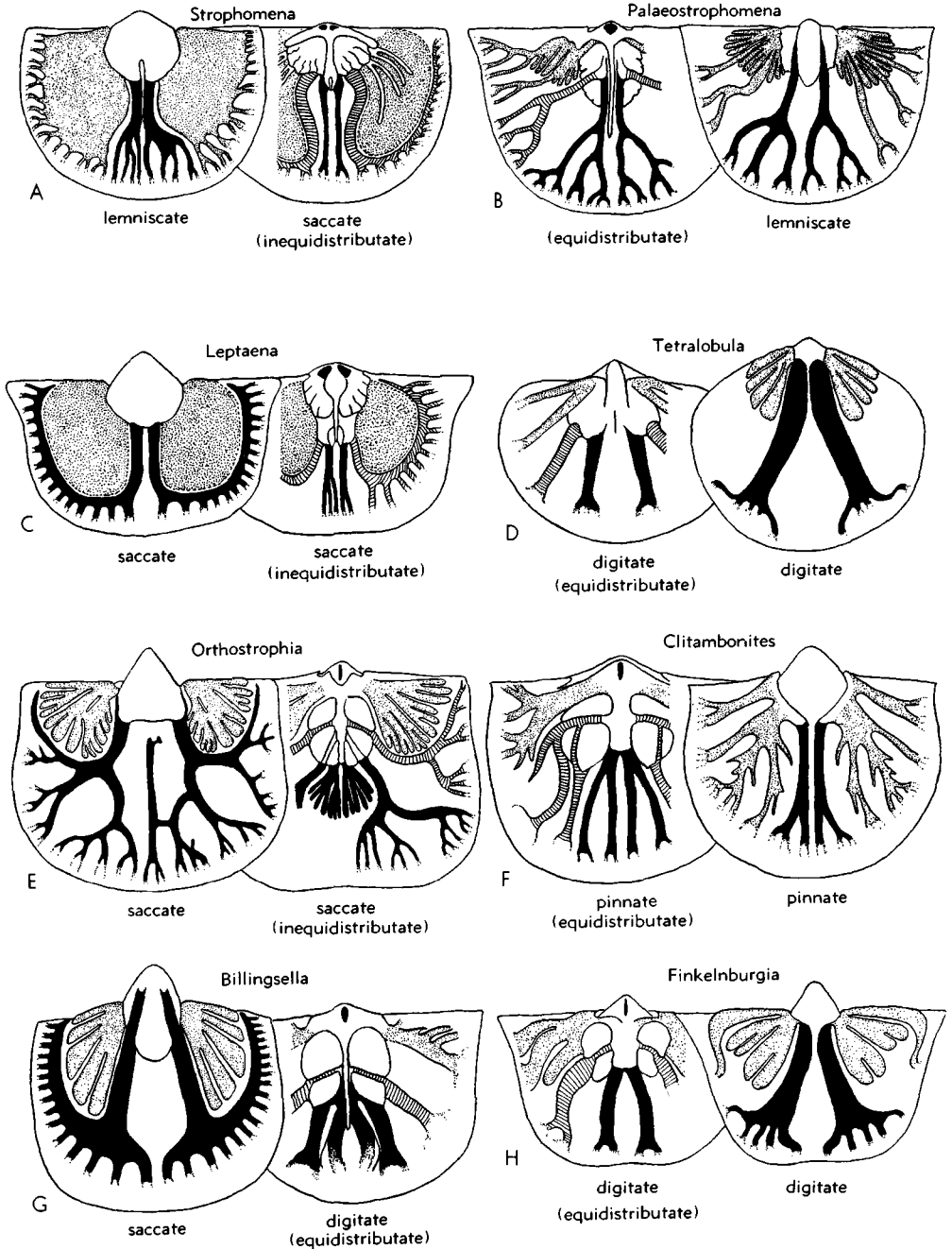


FIG. 135. Mantle canal systems of selected brachiopods; in each example brachial valve is inner figure and pedicle valve outer (*vascula media* in solid black, gonadal sacs and *vascula genitalia* stippled, *vascula myaria* ornamented by closely spaced lines) (57).

comparative survey. But having regard for what is now known of the patterns in fossil and living shells, all canals can ultimately be related to three principal pairs of extensions of the body cavity into the mantles (57). They are the *vascula media*, which arise anteromedially of the muscle fields; the *vascula myaria*, which originate between or within muscle bases and which are unequivocally identifiable mainly in brachial valves with their widely separated posterior and anterior adductor attachments; and the *vascula genitalia*, which normally occupy the posterolateral areas of the mantles. These last vary from peripheral branches given off from pouches within the mantles that contain the gonads (gonocoels) to a complex of branches (including, according to Öpik's terminology, combinations of *vascula dentalia* and *myaria* and of *vascula cardinalia* and *cruralia* in the ventral and dorsal mantles, respectively). In adult shells, however, they are always associated with the gonads, which may occur elsewhere within mantle canals but are invariably present in the posterolateral areas.

A survey of the known patterns of articulate brachiopods shows that they can be assigned to a few standard types, which were probably derived from those characteristic of Cambrian shells. Thus, in *Billingsella* (Fig. 135,G), circulation within the ventral mantle was apparently effected by a pair of *vascula media* which curved arcuately within the shell margin and presumably served the peripheral mantle lobes with their setae. This arrangement is not far removed from that of certain living inarticulates (e.g., *Lingula*). But the ventral mantle of *Billingsella* also contained a pair of pouchlike sinuses lying wholly posterior to the arcuate *vascula media*, which were probably homologous with similarly disposed gonocoels of *Hemithiris* (see Fig. 23,A); and this entire pattern is referred to as the saccate condition (57). The projection of the gonads into the mantle is rare among inarticulate brachiopods but was always characteristic of the articulate brachiopods and was, in fact, the main source of subsequent development.

The beginning of a profound modification of the saccate condition is seen in impressions on the ventral interior of *Finkelnburgia* (Fig. 135,H). The gonocoels pro-

jected laterally almost as far as the mantle edge (digitate condition) and must have served not only as sexual receptacles but also as circulatory channels because the lateral arcs of the *vascula media* were correspondingly reduced. In most younger stocks, this tendency is carried to conclusion. The *vascula media* became greatly abbreviated, although never entirely suppressed, while the *vascula genitalia*, which originated as a pair of gonocoels, also became the dominant circulatory canals. In *Palaeostrophomena* the gonocoels are still pouchlike but gave rise to a series of canals (lemniscate condition) (Fig. 135,B); and in *Clitambonites* the pouches were entirely replaced by radially disposed *vascula genitalia* (pinnate condition) that presumably contained gonadal cords (Fig. 135,F).

The dorsal mantle canal systems, despite a basic difference in arrangement, underwent the same kind of changes as those described for the ventral mantle. In *Billingsella* and *Finkelnburgia*, digitate gonocoels were developed but the *vascula media* far less so than those of the ventral mantle because a third pair of primary canals appeared laterally between the posterior and anterior adductors (*vascula myaria*) (Fig. 135,G,H). These are probably best interpreted as principal branches of the *vascula media* with which they enveloped the submedian anterior adductor scars in such a way as to suggest that the muscles were responsible for a premature branching of what were really a pair of median canals.

Such digitate patterns as these did not represent the most primitive grade of differentiation. The dorsal mantle of some Cambrian forms, possibly stocks like *Eoorthis*, in which the patterns were not impressed on the shells, must have been saccate because a pair of pouchlike gonocoels were certainly typical of many Ordovician brachiopods (e.g., *Orthostrophia*, *Strophomena*, *Leptaena*, etc.) (Fig. 135,A,C,E), and the peripheral extensions of the other canals, especially the *vascula myaria* to cover the entire margin, suggest that they alone were responsible for circulation in the mantle (inequidistributate condition). More commonly, the digitate, lemniscate (e.g., *Palaeostrophomena*), or pinnate (e.g., *Clitambonites*) patterns prevailed, and the *vascula genitalia* also assisted in circulation

(equidistributate condition). ÖRIK (37) figured a very instructive variation within the species *Cyrtototella kükersiana*. In one

specimen, the entire posterolateral periphery of the mantle was served by arcuate *vascula myaria*, while the lemniscate *vascula*

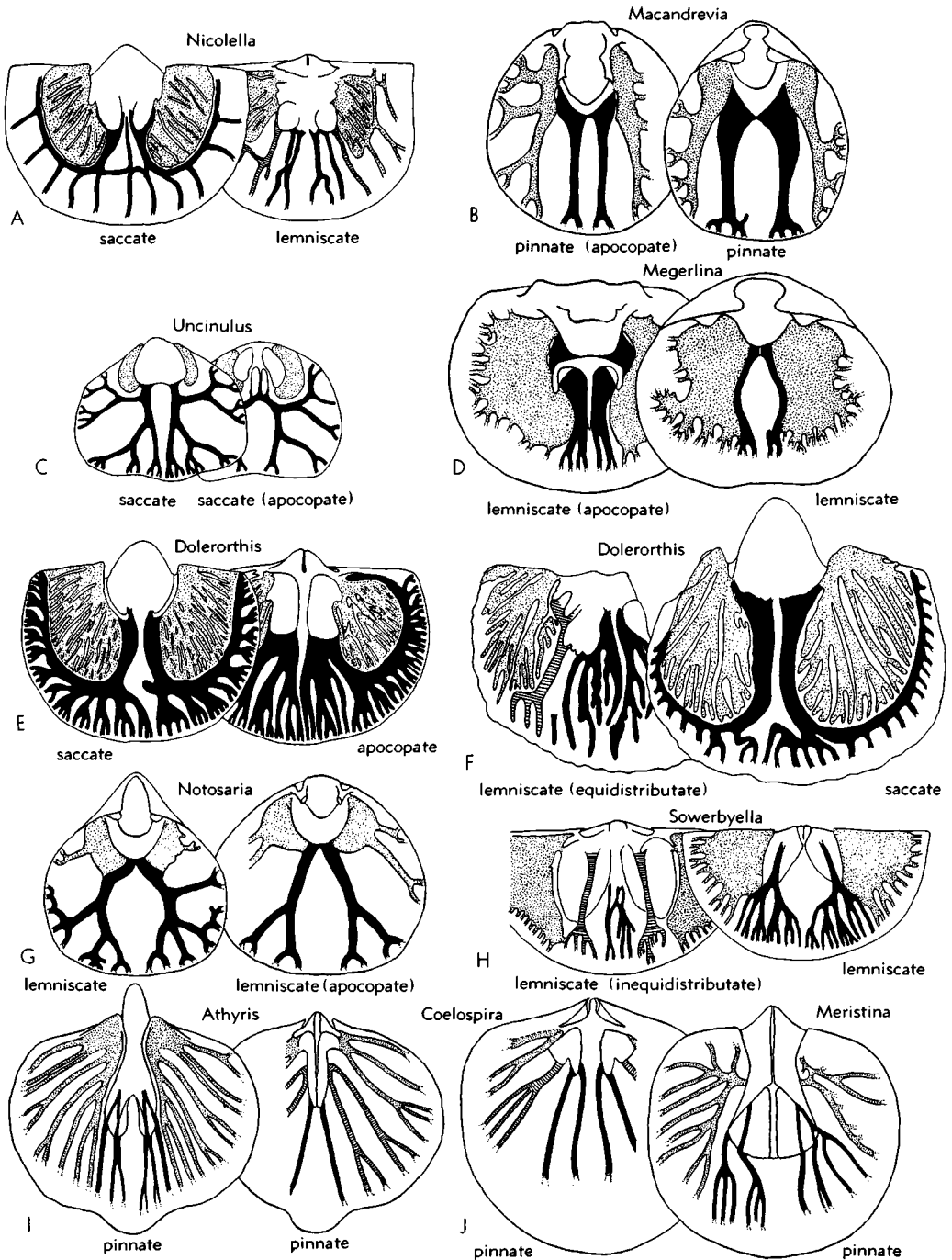


FIG. 136. Mantle canal systems of selected brachiopods, arrangement and shading as in FIG. 135 (A,F,H, 59; C, 52; E, 37; remainder, 57).

genitalia were limited within the arc. In another, the peripheral arcs of the *vascula myaria* were abbreviated and the posterolateral mantle margin, for about one-third its length, was pervaded by *vascula genitalia*. The same degree of variation probably obtained in the basically saccate to lemniscate dorsal mantle of *Nicolella actoniae* (59) (Fig. 136,A).

It is now evident that, although these different patterns are well defined, they really constitute morphological grades which were attained during the development of several independent stocks. The post-Cambrian orthaceans tended to retain a saccate ventral mantle, although, as in the orthids, plaesiomyids, and plectorthids, the arcs to the *vascula media* developed in the posterior part of the mantle and served the mantle edge by giving rise to a series of long radiating branches, while the small posterolateral gonocoels were supplemented by subsidiary median ones. The most radical departure from this condition is found in *Dolerorthis*. In later species of this genus, the ventral pattern was orthodoxly saccate, but that of the dorsal mantle consisted of greatly branched *vascula media* with complete lateral arcs and pouchlike gonocoels; the *vascula myaria* do not appear to have developed (apocopate condition) (Fig. 136, E). This simple arrangement seems to represent a degeneration from an equidistributate lemniscate pattern, as is seen in some Ordovician species (Fig. 136,F).

The triplesiaceans and clitambonitoids, which are contemporaries of the orthaceans, are decisively lemniscate and pinnate, respectively. The enteleteaceans are also predominantly lemniscate in both valves, but the saccate condition was characteristic of the ventral mantle of *Paurorthis*.

Reconstructions of the strophomenacean and plectambonitacean mantles show a similar drift away from the primitive saccate condition. A few genera (e.g., *Titanambonites*) possessed saccate ventral mantles, but in both superfamilies the lemniscate or pinnate condition was more usual (e.g., *Strophomena*, *Strophonelloides*, *Plectodonta*, *Palaeostrophomena*) (Fig. 135, A,B; 136,H). The effects of sexual maturity can be seen in species of *Leptellina*. The basic ventral pattern is saccate, but the distension of the gonocoels became so great

in some valves that they became amalgamated with the lateral arcs of the *vascula media* to simulate a lemniscate condition; and indeed, this process of "capture" may have been the chief process of development. The dorsal mantle systems of these groups are not well known. Among plectambonitaceans, the lemniscate equidistributate pattern of *Palaeostrophomena* and the pinnate inequidistributate patterns of *Plectodonia* and *Sampo* seem to be dominant, and this conclusion may also be true for the strophomenaceans, although in *Leptaena* and *Strophomena* the dorsal mantles were essentially saccate (Fig. 135,A,C).

The patterns of other groups (e.g., davidsoniaceans, spiriferoids, pentameroids) are rarely preserved and those of the chonetoids and productoids entirely unknown except for traces of *vascula media* belonging to what was possibly a lemniscate ventral mantle of *Rugosochonetes* (32). The davidsoniacean *Davidsonia* clearly had a saccate ventral mantle, but species of *Schuchertella* rarely show impressions of patterns more suggestive of expanded lemniscate (or pinnate) *vascula genitalia* and abbreviated median and submedian canals in both valves.

The patterns of atrypaeans are indifferently preserved but if *Atrypa* is representative, the mantle canal systems developed in members of the superfamily constituted an interesting modification (Fig. 137). Judging from the distribution of impressions of muscle ties found in the shell interior, the gonads occupied most of the disrupted mantles of both valves in adult specimens, although the courses of the principal canals can still be made out. VANDERCAMMEN & LAMBIOTTE (51) have plotted these for *Atrypa reticularis* but have also included patterns within the body cavity which were not canals but were produced by strips of unmodified outer epithelium within the muscle fields, etc. Ignoring these, however, one may see that the *vascula media* were poorly developed in the ventral mantle to give a modified saccate condition and were equally reduced in the dorsal mantle where also the *vascula myaria* and *vascula genitalia* were about equally developed (modified digitate condition). In contrast, a pinnate condition with destructive narrow radiating primary canals was probably the prevalent type of the atyridaceans (Fig. 136, I,J), and

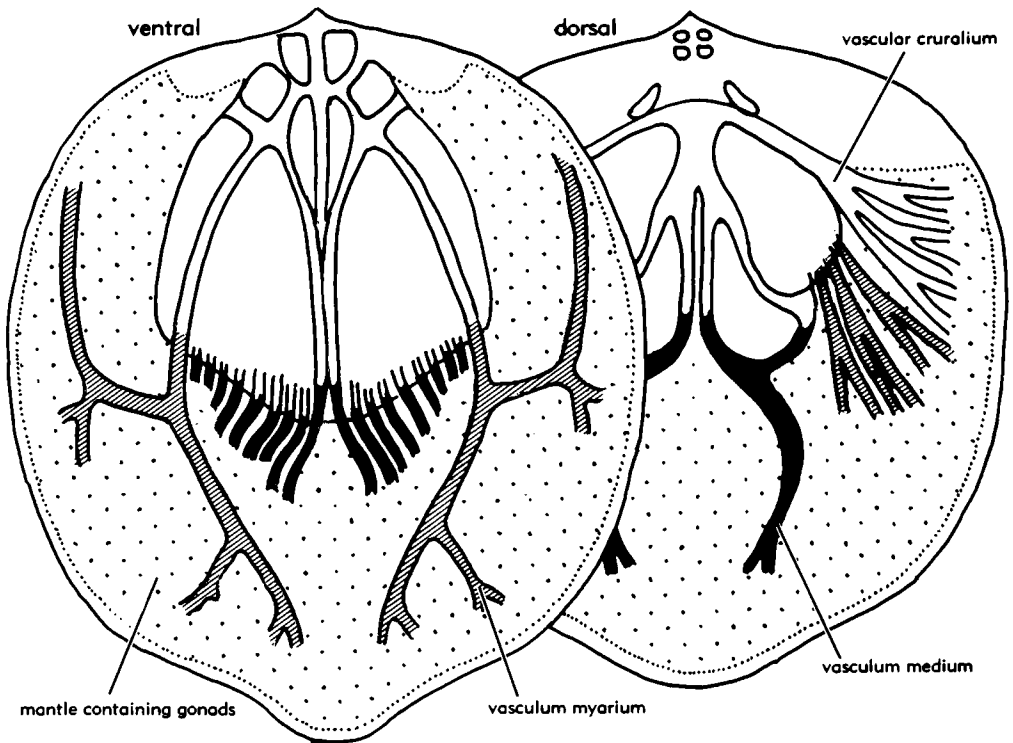


FIG. 137. Mantle canal system of sexually mature *Atrypa* (Williams, after 51).

was also possibly the representative pattern of the spiriferoids among which traces of a pinnate arrangement can rarely be found especially as impressions of the ventral mantle.

The two remaining major groups, the rhynchonelloids and terebratuloids, are represented by living species, the canal systems of which can be studied by injection preparations of the mantles. Both are unusual in that the pattern for the dorsal mantle is, and almost invariably was, apocopate. Yet it is fairly certain that the rhynchonelloid arrangement was independently derived from a saccate or lemniscate condition and the terebratuloids from a radial pinnate pattern.

Two contrasting patterns exist among Recent rhynchonelloids. The gonocoels in both mantles of *Hemithiris* are pouchlike and conform to the saccate condition, while those of *Notosaria* give off branches peripherally in the lemniscate manner (Fig. 136, G). Both these patterns occur in fossil forms. *Sphaerirhynchia*, *Fitzroyella*, and *Uncinulus* (Fig. 136, C) are saccate and

Leiorhynchus lemniscate, but whether they constitute two persistently independent groups or whether the saccate stocks continually replenished the lemniscate ones is unknown. The latter conclusion is the more likely, because impressions on the interiors of *Pugnax* may show a saccate condition or one in which the gonocoels may have enlarged sufficiently to rupture into the lateral arcs of the *vascula media* and capture them.

In modern terebratuloids, the *vascula media* are subordinate to the lemniscate or pinnate *vascula genitalia*, and this relationship seems not to have varied greatly throughout their history. Even in Devonian times, when the terebratuloids first emerged as significant members of the brachiopod phylum, the pattern of some living terebratuloids like *Macandrevia* (Fig. 136, B) was already characteristic of stringocephalaceans (14). A few stocks (e.g., *Meganteris*, *Cranaena*) displayed the impressions of three or even four pairs of narrow sinuses radiating from the muscle scars of each

valve in a manner reminiscent of the athyridaceans. It is possible, then, that the characteristic dorsal pattern was derived from a pinnate condition by atrophy of the *vascula myaria*. In some modern terebratulaceans (e.g., *Laqueus*, *Macandrevia*, *Pumilus*) gonadal cords also occur in the *vascula media*, and in some respects this development may be regarded as the climax of anatomical reorganization that began with the formation of the gonocoel in the mantle. It is not unique, however; the ventral mantle of *Plaesiomys* and the dorsal mantle of *Orthostrophia* possessed a pair of subsidiary saccate gonocoels situated antero-medially between the *vascula media*, and in view of the poor data on mantle canal systems generally, it may well have been characteristic of other groups unrelated to the terebratuloids.

The mantle canal pattern of the inarticulate brachiopods is basically simpler than that of the articulate. Commonly, there is also some difference in function of the canals, for only in the Craniidae are the gonads known to be partially inserted into them; in all other Recent inarticulates the gonads are confined to the body cavity, and the canals have primarily a respiratory function.

The majority of inarticulates have a single pair of main trunks in the ventral mantle (*vascula lateralia*) and two pairs in the dorsal mantle, one pair (*vascula lateralia*) occupying a similar position to the single pair in the ventral mantle and a second pair projecting from the body cavity near the mid-line of the valve. For convenience, this latter pair may be termed the *vascula media*, but whether they are strictly homologous with the *vascula media* of the articulate brachiopods is difficult to determine. Similarly, it is impossible to be certain that the *vascula lateralia* are the homologues of the *vascula genitalia* of the articulate, although they do arise in a comparable position.

The basic pattern of one ventral and two dorsal pairs of canals is commonly developed in the lower Paleozoic Lingulida, the ventral *vascula lateralia* curve forward from a lateral position on the anterior body wall, subparallel with the shell margin; the dorsal *vascula lateralia* are similarly disposed and the *vascula media* diverge anteriorly

from near the anterior lateral muscles. In *Broeggeria* and *Obolus* (Fig. 138,B,C) numerous minor canals branch off from either side of the main trunks and they and their ramifications permeate much of the mantle. These small branches are rarely seen in fossil forms, but it appears reasonable to suggest that they are probably present in the majority of the Lingulacea. The branches from the principal canals are relatively minor and in particular, the *vascula lateralia* extend forward without any major dichotomy or bifurcation (baculate condition).

The seemingly fundamental pattern of a pair of baculate *vascula lateralia* in each valve with a pair of *vascula media* in the dorsal mantle occurs in a number of stocks. In the siphonotretacean *Schizambon* and in *Obolella* (Fig. 138,G,H) the major canals are arranged similarly to those of *Obolus*, but minor branches from them are unknown. Among the acrotretaceans, although the slender principal canals of *Acrothele* give off delicate branches, the majority of the acrotretids appear to lack the fine ramifications of the vascular system (Fig. 138,D,F). In this family, a modification of the mantle canal system occurs, well displayed by *Conotreta*, in which the *vascula lateralia* rapidly branch into a number of subequal, radially disposed canals (pinnate condition) (Fig. 138,E). Although this branching commonly produces medially situated canals in the ventral mantle, whose position is similar to that of the dorsal *vascula media*, they are probably best regarded merely as branches of the *vascula lateralia*, since true *vascula media* are otherwise unknown in the pedicle valve of inarticulate brachiopods.

The ventral *vascula lateralia* of the craniids exhibit a modified form of the pinnate condition in which the branching is delayed. The same type of branching affects the single pair of principal canals in the dorsal mantle; these are probably the *vascula lateralia*, which in Recent *Crania* occupy a rather median position. The distribution of the canals in older genera of the family (e.g., *Petrocrania*, Fig. 138,I) suggests that the *vascula media* are absent in this family.

In the Recent lingulids, *Glottidia* and *Lingula*, and possibly in many closely re-

lated fossil representatives of the family, other modifications of the mantle canal system occur. The dorsal *vascula media* are not developed and the *vascula lateralia* in both valves divide immediately after leaving the body cavity (bifurcate condition), the smaller branch of each main canal extending posteriorly to supply the mantle

lateral of the lateral body wall and the larger branch passing anteriorly and converging toward the mid-line of the valve. From these principal branches minor canals are given off comparable to those of *Broeggeria* and *Obolus*. The bifurcation of each of the *vascula lateralia* into anterior and posterior branches is not solely a function of

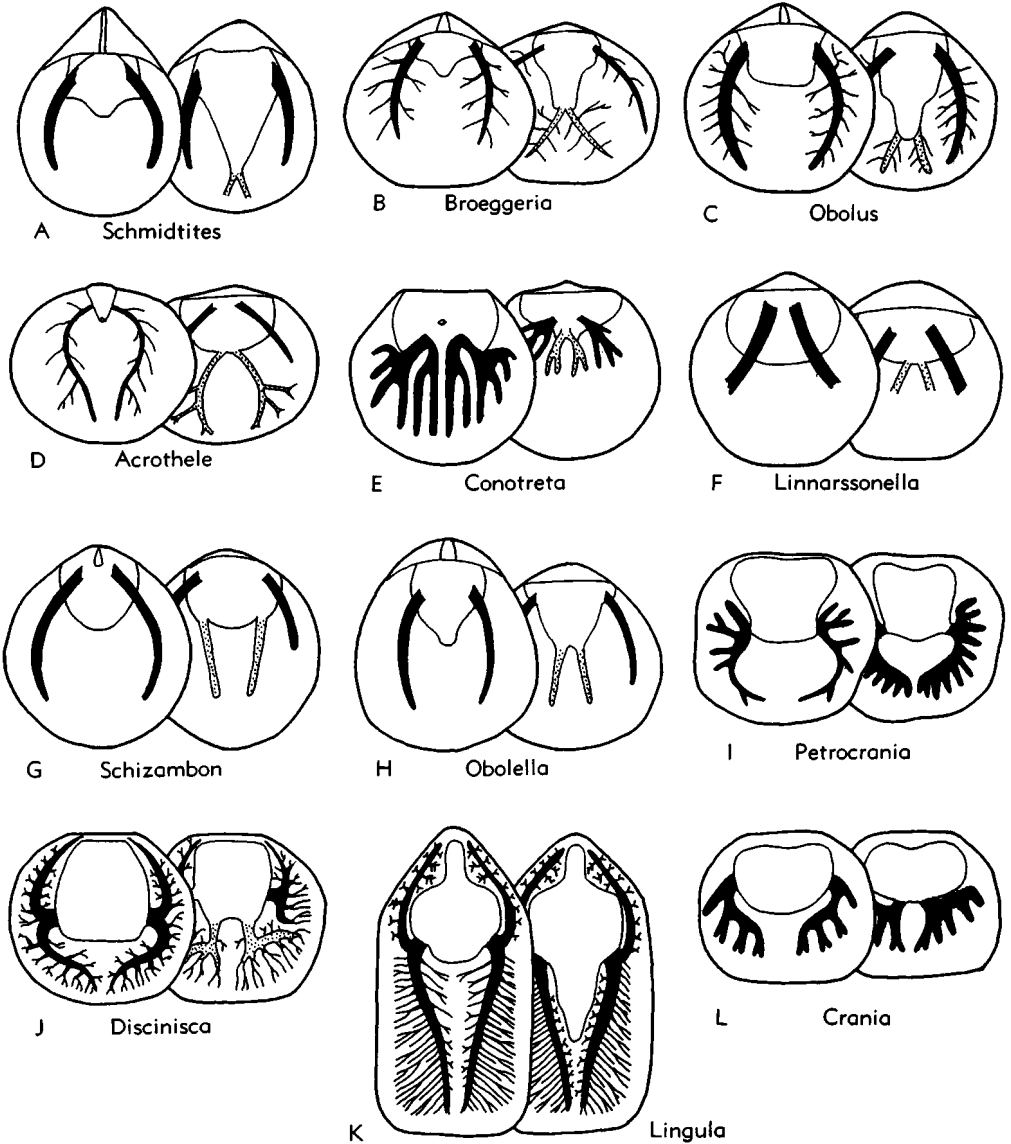


FIG. 138. Mantle canal patterns of some inarticulate brachiopods, pedicle valve on left, brachial valve on right, *vascula lateralia* in black, *vascula media* stippled: A, *Schmidtites* (bifurcate condition); B, *Broeggeria* (baculate condition); C, *Obolus* (baculate condition); D, *Acrothele* (baculate condition); E, *Conotreta* (pinnate condition); F, *Linnarssonella* (baculate condition); G, *Schizambon* (baculate condition); H, *Obolella* (baculate condition); I, *Petrocrania* (pinnate condition); J, *Discinisca* (bifurcate condition); K, *Lingula* (bifurcate condition); L, *Crania* (pinnate condition) (63).

the form of the shell, for in *Barroisella* and *Langella*, genera very similar in outline to some Recent *Lingula*, the *vascula lateralia* arise in a similar position and are comparable in form to those of *Obolus*. The bifurcation of these canals in the Recent lingulids appears to be more closely related to their relatively anterior origin and to the attenuated outline of the posterior part of the body cavity. Both these factors combine to produce a comparatively large area of mantle, posterolateral of the body cavity, which if it is to be supplied by the existing vascular system necessitates a relatively large, posteriorly directed branch from the *vascula lateralia*. The absence of the dorsal *vascula media* is more difficult to explain. It is not directly a consequence of the considerable forward extension of the body cavity, for in several Paleozoic Lingulida, particularly *Schmidtites*, the limit of the anterior body wall is placed relatively farther forward than that of *Lingula*, yet they still develop *vascula media*. The respiratory function of the *vascula media* of Paleozoic lingulaceans is performed in modern lingulids by the anterior branches of the *vascula lateralia* which converge medially.

A similar bifurcate condition of the *vascula lateralia* has also arisen independently in the Discinidae (Fig. 138, J), but in contrast to the lingulids, the dorsal *vascula media* are well developed. On phylogenetic grounds it is probable that the bifurcate *vascula lateralia* in this family were developed from the baculate condition of the acrothelids, but the condition of the *vascula lateralia* of the early discinaceans is quite unknown. In this family the mantle canal system is only known from Recent species, for the epithelium beneath the canals secretes at the same rate as the adjacent outer epithelium of the remainder of the mantle, and consequently the canals leave little or no trace of their position on the shell.

The mantle canal system of the Paterinida is unfortunately still unknown and a similar lack of differential secretion appears to have occurred in these forms, although it is possible that some of the scars, provisionally regarded as being associated with the muscles, may ultimately prove to be vascular in origin.

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MORPHOLOGICAL TERMS APPLIED TO BRACHIOPODS

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The following glossary has been compiled to include terms used in descriptions of brachiopod shells, together with anatomical definitions necessary for understanding shell morphology. Terms most commonly used are in capitals (as **ADDUCTOR MUSCLES**); less important terms are printed in uncapitalized letters (as **accessory adductor scars**). Terms printed in italics are considered by some or all of the contributors to be superfluous or obsolete and therefore continued use of them by brachiopod workers is not recommended.

Glossary of Morphological Terms

accessory adductor scars. Pair of muscle scars in pedicle valve of daviesiellids lying anterior to principal adductor impressions; interpreted by WAAGEN (1884) as ancillary adductor bases.

accessory denticles. See denticles.

accessory dental socket (of Orthidina). See denticular cavity.

accessory diductor muscles. Pair of muscles branching posteroventrally from main diductor muscles and inserted in pedicle valve posterior to adductor bases (Fig. 115).

accessory lamellae. Pair of lamellae developed from arms of jugum and coiled parallel to main lamellae of spiralia (Fig. 108).

accessory septa. Two septa in brachial valve of some chonetoids situated between median septum and lateral septa. [Muir-Wood]

accessory socket. Depression in outer socket ridge articulating with denticulum (Fig. 98,C). [Muir-Wood] Also used for outer part of divided dental socket of plectambonitaceans (Fig. 99,B).

accessory tooth. Articulating process flanking hinge tooth of plectambonitaceans and fitting into accessory socket in brachial valve (Fig. 99,A).

ADDUCTOR MUSCLES. Muscles which contract to close shell. Two adductor muscles, each dividing dorsally, are commonly present in articulate brachiopods to produce single pair of scars located between diductor impressions in pedicle valve and 2 pairs (anterior, posterior) in brachial valve. Two pairs of adductor muscles (anterior, posterior) are commonly present in inarticulate brachiopods, passing almost directly dorsoventrally between valves (Fig. 1, 25, 115). (See central and umbonal muscles.)

adductor pits. Pair of depressions indenting anterior face of notothyrial platform of some orthoids for attachment of posterior adductor muscles.

ADJUSTOR MUSCLES. Two pairs of muscles in many articulate brachiopods branching from pedicle and responsible for moving shell relative to it; ventral pair attached posterolaterally from diductors, dorsal pair on hinge plates or floor of brachial valve behind posterior adductors (Fig. 1, 25, 29, 115).

admiculum. See dorsal and ventral admiculum.

alae. Winglike ears or cardinal extremities. [Muir-Wood]

alate plate. Flaplike extension of secondary shell arising from lateral surface of brachiophore base in porambonitaceans (Fig. 128).

alternate folding. Deflection of shell surface in which fold of one valve is opposed by sulcus of other (Fig. 65).

alveolus. Pit anterior to internal face of cardinal process. [Muir-Wood]

amphithyridid (foramen). Pedicle opening shared by delthyrium and groove in beak of brachial valve (Fig. 90,A).

anacline. See inclination of cardinal area or pseudo-interarea (Fig. 61,C).

ancillary strut. Secondary shell material deposited between brachiophore base and median ridge in some orthoids.

angle of spines. External angle subtended by chonetoid external hinge spines with posterior margin of pedicle valve, measured in plane parallel with plane of commissure.

ANTERIOR. Direction in plane of symmetry or parallel to it away from pedicle and toward mantle cavity (Fig. 59,B).

anterior commissure. Anterior part of line of junction between valves.

anterior margin. Anterior edge of valve.

anterior lateral muscles. Pair of muscles in some Lingulida originating on pedicle valve posterolateral to central muscles, converging dorsally to their insertions anteriorly on brachial valve (Fig. 28).

anterolateral commissure. Anterolateral parts of line of junction between valves.

antiplicate (folding). Similar to paraplication but with fold developed along mid-line of median sulcus (reverse of episulcate) (Fig. 65). [Muir-Wood]

antron. Triangular gap due to incomplete fusion of cardinal process, buttress plates, and brevi-septum in some productoids. [Muir-Wood]

antygidium. Low ridge of secondary shell near beak of brachial valve, covered externally by cuticle and deposited during ventral migration of junction of pedicle epithelium with outer epithelium (Fig. 12, 89).

apex. First-formed part of valve around which

- shell has grown subsequently (term usually restricted to valves having this point placed centrally or subcentrally).
- apical angle.** Angle subtended by umbonal slopes at umbo.
- apical callosity.** See pedicle callist; for inarticulate brachiopods, see apical process.
- apical cavity.** Undivided space beneath umbo in either valve.
- apical plate.** Dorsally enlarged pedicle collar partly closing apex of delthyrium.
- apical process.** Variably shaped protuberance in umbonal region of pedicle valve of some acrotretaceans which may contain pedicle tube (Fig. 96).
- apocopate** (mantle canal). Dorsal mantle-canal system with single pair of canals in addition to *vascula genitalia* (Fig. 136).
- apsaline.** See inclination of cardinal area or pseudointerarea (Fig. 61,C).
- arcuifer** (crura). Crura hammer-shaped in cross section, with arcuate heads concave toward each other (Fig. 1, 7,4). [Ager]
- area.** See cardinal area.
- areola.** See planarea.
- arms.** See brachia.
- arms of jugum.** Processes arising by bifurcation of distal end of jugal stem, which may become extended into accessory lamellae (Fig. 108).
- ARTICULATION.** Interlocking of 2 valves by projections along their posterior margins, commonly effected in Articulata by 2 ventral teeth fitting sockets of brachial valve but may be assisted or replaced by other projections and complementary pits (Fig. 98).
- ascending branches** (of loop). Two ventral elements of loop continuous anteriorly with ventrally recurved descending branches and joined posteriorly by transverse band (Fig. 111).
- atrite** (foramen). Opposite of telate, when ends of beak ridges are worn away. [Muir-Wood]
- aulacoterma.** Thickening on inside wall of richthofeniid pedicle valve against which brachial valve rests when shell is closed. [Muir-Wood]
- auriculate** (foramen). Opening bounded by deltoidal plates bearing external rims or winglike extensions.
- baculate condition** (mantle canal). *Vascula lateralia* lacking major dichotomy or bifurcation (Fig. 138).
- band.** See connecting band and transverse band.
- base of brachial process.** Proximal part of pentameracean brachial process attached dorsally to outer plate and ventrally to inner plate (Fig. 127).
- BEAK.** Extremity of umbo, commonly pointed (Fig. 59,B). [Muir-Wood]
- beak angle.** Angle subtended between commissural plane and line bisecting beak of nonstrophic pedicle valve as seen in lateral profile, defined as straight (beak angle, 0-20°), nearly straight (20-30°), suberect (30-70°), erect (70-90°), incurved (more than 90°), corresponds to ortho-
- cline-anacline condition of strophic shells (Fig. 61).
- beak ridges.** More or less angular linear shell elevations extending from each side of umbo so as to delimit all or most of cardinal area. [Muir-Wood]
- biconvex.** Both valves convex (Fig. 63).
- bifurcate condition** (mantle canal). *Vascula lateralia* split into anterior and posterior branches immediately beyond point of leaving body cavity (Fig. 138).
- bilobate** (folding). Similar to strangulate stage but with sulci and folds both well developed (Fig. 63, 64). [Muir-Wood]
- biplicate** (folding). Alternate folding with 2 submedian folds in brachial valve separated by median sulcus; includes sulcificate and episcutate conditions (Fig. 65).
- bisepium.** Double septum in pedicle valve formed by union of dental plates.
- blister.** Vesicles of secondary shell in umbonal and delthyrial chambers of some spiriferoids and productids (Fig. 132).
- BODY CAVITY.** Principal part of coelomic space, situated posteriorly, bounded by body wall and containing alimentary tract, nephridia, etc. (Fig. 1, 2).
- brace plates.** Narrowly diverging septa extending anteriorly of adductor muscle scars in some stropheodontids (Fig. 130).
- BRACHIA.** Two armlike projections from either side of mouth segment of lophophore, variably disposed but symmetrically placed about mouth (Fig. 1).
- brachial bases.** See inner socket ridge.
- brachial branches.** Narrow elevations of secondary shell contained within brachial ridge and converging anteromedially.
- brachial cavity.** See mantle cavity.
- brachial lamellae.** See lophophore platform.
- brachial loop.** See loop.
- brachial muscles.** Muscles in small brachial canal of inarticulate genera, arising from connective tissue at proximal ends of canals and extending along their length (Fig. 30).
- brachial plate.** One of pair of subvertical plates constituting pentameracean cardinalia and including inner plate, base of brachial process, and outer plate.
- brachial process.** Anteriorly directed blade or rodlike projection from pentameracean cardinalia (Fig. 102-107).
- brachial protractor muscles.** Pair of muscles in craniids which assist movements of lophophore, located anteromedially on brachial valve.
- brachial retractor muscles.** Pair of small muscles in brachial valve of discinids and craniids, located lateral to anterior adductor muscles.
- brachial ridges.** Narrow elevations of secondary shell extending laterally or anteriorly as open loop from

- dorsal adductor muscle field of some articulate brachiopods (Fig. 113,2).
- BRACHIAL VALVE.** Valve that invariably contains any skeletal support for lophophore and never wholly accommodates pedicle, commonly smaller than pedicle valve and having distinctive muscle-scar pattern (Fig. 59).
- brachidium.** Calcareous support for lophophore in form of loop or spires.
- BRACHIOPHORES.** Blades of secondary shell projecting from either side of notothyrium and forming anteromedian boundaries of sockets in orthoid, enteletecean, and porambonitacean brachial valves (Fig. 102).
- brachiophore base.** Basal (dorsal) part of brachiophore which joins floor of valve (Fig. 102,3).
- brachiophore plate.* See brachiophore base.
- brachiophore process.** Distal rodlike extension of brachiophore that possibly supported lophophore in some genera (Fig. 102,8).
- brachiophore support.* See brachiophore base.
- breadth.* See width.
- brephic.** Juvenile stage in shell development following secretion of protogulum, best seen on ribbed valves where it can be distinguished from protogulum by presence of growth lines and from neanic shells by absence of radial ornament.
- brevisseptum.** Dorsal median septum not extending posteriorly to fuse with cardinal process. [Muir-Wood]
- bridge.** Posteromedian part of marginal flange of thecideacean brachial valve free of valve floor.
- brush.** Numerous fine cytoplasmic strands radiating from distal end of caecum and connected to periostracum of punctate shells of Articulata (Fig. 5).
- butress plates.* See cardinal process buttress plates.
- caecum.** Evagination of outer epithelium projecting into endopuncta of shell (Fig. 5).
- calcareoconeous.* See chitinophosphatic.
- calcarifer (crura).** Crura said to be characterized by dorsally directed process at distal end of each crus (Fig. 1, 2,2). [Ager]
- callist.* See pedicle callist.
- callus.** Any excessive thickening secondary shell located on valve floor (Fig. 118).
- camera.* See cella.
- camarophorium.** Spoon-shaped, adductor-bearing platform in stenoscismatacean brachial valve supported by median septum and derived independently of cardinalia (Fig. 129).
- campagiform (loop).** Term for growth stage of the loop of dallinids marked by proportionally large hood without lateral lacunae, position of attachment of descending branches to septum and hood varying in different genera (Fig. 110,2,3). [Elliott]
- campagiform hood.** Large, commonly funnel-shaped structure without lateral lacunae, with descending branches attached to median septum by transverse processes.
- canalifer (crura).** Variant of radulifer type, folded longitudinally in form of dorsally facing channel or gutter (Fig. 20,11). [Ager]
- capilla.** Very fine radial ridge on outer surface of shell. See costa.
- capillate.** Ornamented by capillae.
- capsular muscles.* Longitudinal fibers in connective tissue of pedicle of articulate brachiopods, may be attached to floor of pedicle valve.
- cardinal angle.** Angle between hinge line and posterolateral margins of shell.
- cardinal area.** Posterior sector of articulate valve exclusive of delthyrium or notothyrium (may be interarea, planarea, or palintrope) (Fig. 61,A,B).
- cardinal buttress.** Vertical plate or ridge supporting cardinal socket in some trimerellids, dividing cavity beneath beak into 2 umbonal chambers (Fig. 101).
- cardinal extension.* Thecideacean cardinal process.
- cardinal extremities.** Terminations of posterior margin (Fig. 59,C).
- cardinal facet.* See cardinal socket.
- cardinal margin.** Curved posterior margin of shell, homologous with hinge line of strophic shells but not parallel with hinge axis (Fig. 61,A).
- cardinal muscle scar.** Posterolaterally placed muscle scars in acrotretaceans and obolellaceans (Fig. 96).
- cardinal plate.** Plate extending across posterior end of brachial valve, consisting laterally of outer hinge plates and medially of either conjunct inner hinge plates or single plate, commonly perforated posteriorly (Fig. 103,6).
- CARDINAL PROCESS.** Blade or variably shaped boss of secondary shell situated medially in posterior end of brachial valve and serving for separation or attachment of diductor muscles (Fig. 99, 123-125).
- cardinal process buttress plates.** Two vertical converging or diverging plates which extend anteriorly from cardinal process and in some shells unite with brevisseptum. [Muir-Wood]
- cardinal process lobes.** Projections forming all or part of cardinal process and bearing muscle bases (Fig. 116).
- cardinal process shaft.** Ridge- or stalklike proximal part of cardinal process which supports myophore (Fig. 123).
- cardinal socket.** Transverse depression on posterior margin of trimerellacean pedicle valve which receives plate or tooth of brachial valve (Fig. 101).
- CARDINALIA.** Outgrowths of secondary shell in posteromedian region of brachial valve, associated with articulation, support of lophophore, and muscle attachment; include, for example, cardinal process, socket ridges, crural bases and their accessory plates (Fig. 102).
- carina.** Major angular elevation of valve surface, externally convex in transverse profile and radial from umbo.
- catacline.** See inclination of cardinal area or pseudo-interarea (Fig. 61,C).

- cella.** Any chamber contained between floor of valve and elevated muscle-bearing platform, best known as inverted V-shaped chamber beneath shoe-lifter process (Fig. 122).
- central muscles.** Anteriorly or medially placed pair of muscles in Lingulida, originating on pedicle valve and passing anterodorsally to brachial valve (Fig. 28).
- centronellid stage** (of folding). Terebratuloid brachial valve sulcate umbonally.
- centronelliform** (loop). Simple lanceolate loop suspended free of valve floor, commonly bearing median vertical plate in addition to echmidium (Fig. 105,1,2; 109,2).
- cheniothyridid stage** (of folding). See ligate stage.
- CHILIDIAL PLATES.** Pair of posterior platelike extensions of notothyrial walls, commonly forming lateral boundaries of cardinal process (Fig. 125).
- CHILIDIUM.** Triangular plate covering apex of notothyrium, commonly convex externally and extending for variable distance ventrally over proximal end of cardinal process (Fig. 92,A; 124).
- chitinophosphatic** (shell). Consisting dominantly of some form of calcium phosphate and chitin.
- chlidonophorid** (loop). Short loop with converging but not fused crural processes, and transverse band not well differentiated from descending branches. [Muir-Wood]
- ciatrix of attachment.** Flattening of pedicle valve umbo, representing place of cementation of shell to foreign object. [Muir-Wood]
- clifer** (crura). Variant of radulifer type, flattened in plane of commissure, forming direct prolongations of horizontal hinge plates, then turning parallel to plane of symmetry as slightly crescentic blades. [Ager]
- cinctid stage** (of folding). See opposite folding.
- cincture.** External concentric incision in either valve of some productoids, corresponding to internal ridge or diaphragm. [Muir-Wood]
- circinate** (lophophore). Consisting of 2 elongate diverging brachia coiled distally into short laterally directed spires, as in cryptoporids.
- cirri socles.** Obsolete term for spicules at base of filamentar appendages to lophophore. See spicules.
- coma** (pl., comae). Concentrically disposed imper-sistent and irregular protuberances composed of primary and secondary shell on external shell surface of some plectambonitaceans (Fig. 79).
- COMMISSURE.** Line of junction between edges or margins of valves (Fig. 59, B,D).
- commissural plane.** Plane containing cardinal margin and either commissure of rectimarginate shell or points on anterior commissure midway between crests of folds in both valves (Fig. 59,D).
- concavo-convex** (shell). Brachial valve concave, pedicle valve convex (Fig. 63).
- conjunct deltidial plates.** Deltidial plates in contact anterodorsally of pedicle.
- connecting bands** (of loop). Parts of terebratellacean loop that join descending branches to median septum (e.g., terebratelliform, terebrataliiform loops) or ascending and descending branches posterior to their anterior curvature (e.g., laqueiform loops) (Fig. 111). [Elliott]
- convexo-concave** (shell). Brachial valve convex, pedicle valve concave (Fig. 63).
- convexo-plane** (shell). Brachial valve convex, pedicle valve plane.
- COSTA.** Radial ridge on external surface of shell originating at margin of protegular node (Fig. 81). Also, any coarse rib, without reference to origin. [In this context, which is the commoner usage, *costella* is a fine rib, and *capilla* a very fine rib; and among productoids and chonetoids the term "costate" is used when there are fewer than 15 ribs in a width of 10 mm., "costellate" for 15 to 25 ribs per 10 mm., and "capillate" for more than 25 ribs per 10 mm. (Muir-Wood). This usage gives no indication of the nature of radial ornamentation and any quantitative definitions related to the incidence of ribs at the shell margins are necessarily arbitrary. Thus, in brachiopods ornamented by ribs which increase in wave length during growth, shells of the same species could be described as capillate, costellate, or costate according to their size.]
- costate.** Shell radially ornamented exclusively by costae.
- COSTELLA.** Radial ridge on external surface of shell not extending to margin of protegular node but arising by bifurcation of existing costae or costellae or by intercalation between them. Also used for a fine rib irrespective of origin. See *costa*.
- costellate.** Shell radially ornamented by costae and costellae.
- crenulations.** See denticles.
- crescent.** Submarginal feature in trimerellids consisting of posteromedian raised "crown" and anterolateral depressions comprising "sides" and "ends"; crown occurs on site of cardinal socket in pedicle valve, whereas sides and ends are possibly muscle scars.
- crown of crescent.** See *crescent*.
- CRURA** (sing., crus). Two processes which extend from cardinalia or septum to give support to posterior end of lophophore; distal ends may also be prolonged into primary lamellae of spire or descending branches of loop (Fig. 103).
- crural band.** Ribbon of secondary shell joining crural processes ventrally.
- crural bases.** Parts of crura united to hinge plates and separating inner and outer hinge plates when present (Fig. 103,7).
- crural fossette.** Cavity on inner face of tooth receiving posteroventral edge of brachiophore or

- crural plate when valves are closed (Fig. 99,C; 118).
- crural keel*. Dorsal extension of crus beyond junction with flange.
- crural lobe**. Strongly developed, posteroventrally elevated inner socket ridge in atrypaeans.
- crural pit**. Cavity near floor of valve separating brachiophore base and fulcral plate in some orthoids.
- crural plate**. Plate extending from inner edge of outer hinge plate or crural base to floor of brachial valve, may fuse medially with counterpart to form septalium; *see* septalium plate (Fig. 102,6). Rejected as general term for platelike structures of orthoid cardinalia (Bancroft, 1928). For pentameroids, *see* brachial plate.
- crural point*. *See* crural process.
- crural process**. Pointed portion of crus directed obliquely inward and ventrally (Fig. 111). [Elliott]
- crural trough*. *See* septalium.
- cruralium**. Spoon-shaped structure of brachial valve formed by dorsal union of pentameracean outer plates (or homologues) and bearing adductor muscles.
- cruralium discretum*. Outer plates attached independently of each other to floor of pentameracean brachial valve to enclose dorsal adductor field.
- cryptacanthiiform** (loop). Loop composed of descending branches fused distally to form echmidium, which bears hood on ventral anterior end; with continued growth echmidium becomes deeply cleft anteriorly but still connected with descending branches (Fig. 109,3,4).
- cryptonelliform** (loop). Long loop unsupported in adults by median septum and having narrow transverse band. [Stehli]
- curvature of beak**. Curvature of ventral beak toward brachial valve; *see* beak angle.
- cuticle**. Chitinous cover of pedicle.
- cyclothyridid* (foramen). *See* auriculate.
- cynocephalous* (folding). Having exaggerated, very sharp fold in brachial valve, especially in rynchonelloids (e.g., *Homoeorhynchia*), supposedly resembling dog's head (Fig. 15). [Ager]
- cystose** (shell). Vesicles of secondary shell deposited in deep pedicle valves by dorsally migrating outer epithelium.
- dalliniform** (loop). Dallinid loop arrangement in which long descending branches recurve into ascending branches which meet in transverse band, all free of valve floor, morphologically similar to magellaniform and cryptonelliform loop (Fig. 110,6,7). [Elliott]
- delayed costation** (or **costellation**). Ribs first appearing at some distance outside of protogeval node (Fig. 81).
- deltarium discretum*. Impersistent thickening along posterolateral edges of delthyrium.
- delthyrial angle**. Angle subtended by margins of delthyrium.
- delthyrial callosity*. *See* apical callosity.
- delthyrial carinae*. *See* teeth ridges.
- delthyrial cavity*. *See* delthyrial chamber.
- delthyrial chamber**. Cavity beneath umbo of pedicle valve bounded by dental plates, if present, or by posterolateral shell walls, if dental plates absent.
- delthyrial foramen*. Relatively large aperture for emergence of pedicle through open delthyrium unmodified by plates; occurs in earliest growth stages, rare in adults.
- delthyrial plate**. Plate within delthyrial chamber of some spiriferoids, extending variable distance from apex between dental plates (probably homologue of pedicle collar) (Fig. 91, 121).
- delthyrial supporting plate*. *See* dental plate.
- DELTHYRIUM**. Median triangular or subtriangular aperture bisecting ventral cardinal area or pseudo-interarea, commonly serving as pedicle opening (Fig. 61,B).
- deltidial cover**. Externally concave plate in some pentameraceans closing posterior end of delthyrium (probably homologue of pedicle collar).
- deltidial grooves**. Lines delimiting thecideacean pseudodeltidium in species with this structure not flush with ventral area. [Elliott]
- DELTIDIAL PLATES**. Two plates growing medially from margins of delthyrium, partly or completely closing it (Fig. 89,A; 98,A).
- deltidial ridges**. Two narrowly triangular ridges reputed to separate homeodeltidium and propleareas of trimerellids.
- deltidium**. Cover of delthyrium formed by conjunct deltidial plates, line of junction of plates visible (Fig. 89,C).
- dental lamellae*. *See* dental plates.
- DENTAL PLATES**. Variably disposed plates of secondary shell underlying hinge teeth and extending to floor of pedicle valve (Fig. 99, 119).
- dental ridges*. *See* teeth ridges.
- DENTAL SOCKETS**. Excavations in posterior margin of brachial valve for reception of hinge teeth (Fig. 98,B,C).
- dental valve*. *See* pedicle valve.
- denticles**. Small, sharp, protruding ridges that alternate with complementary sockets located along cardinal margin or hinge line of both valves (Fig. 100); for denticles of orthoid cardinalia *see* outer socket ridge.
- denticular cavity**. Groove on outer side of teeth which receives projection from outer socket ridge (Fig. 98). [Muir-Wood]
- denticular plate**. Obtusely triangular plate lateral to delthyrium, bearing denticles and fused with dental plate, developed in stropheodontids.
- denticulated cardinal margin**. Posterior margin of both valves bearing denticles, fitting into complementary sockets.
- denticulated commissure**. Zigzag commissure due to interfingering of angular ribs.

- denticulum** (pl., *denticula*). Small toothlike termination of cardinal area, usually in pedicle valve, commonly articulating with accessory socket in outer socket ridge (Fig. 98). [Muir-Wood]
- depth**. See thickness.
- descending branches**. Two dorsal elements of loop extending distally from crura and recurved ventrally at anterior ends (Fig. 111).
- descending lamellae**. See descending branches.
- deuterolophe**. Spirally coiled part of lophophore bearing double brachial fold and double row of paired filamentar appendages, homologous with side arms of plectolophe (Fig. 106,G').
- deuterolophous** (adj.). Pertaining to deuterolophe.
- diaphragm**. Thin crescentic plate of secondary shell developed around visceral disc of brachial valve and restricting gap between brachial valve and trail of pedicle valve (Fig. 74). [Muir-Wood]
- dictyothyridid stage** (of folding). See pliciligate.
- DIDUCTOR MUSCLES**. Muscles serving to open valves of articulate brachiopods, commonly consisting of 2 pairs attached to brachial valve immediately anterior to beak, usually to cardinal process; principal pair commonly inserted in pedicle valve on either side of adductor muscles and accessory pair posterior to them (Fig. 115).
- digitate** (brachidium). Thecideacean brachidium with brachial branches extending inward from marginal flange. [Elliott]
- digitate** (mantle canal). Posterior part of *vascula genitalia* projecting laterally nearly to mantle margin, with corresponding abbreviation of *vascula media* or *vascula myaria* (Fig. 135).
- disjunct deltidial plates**. Plates not in contact anterodorsally of pedicle.
- divaricator muscles**. See diductor muscles.
- divided hinge plates**. Plates not united medially.
- dorsal**. Direction toward brachial valve from pedicle valve.
- dorsal adjustor muscles**. See adjustor muscles.
- dorsal adminiculum**. Dorsal part of dental plate.
- dorsal denticulum**. See outer socket ridge.
- dorsal foramen**. Posteriorly located perforation of cardinal plate which may encroach on beak of brachial valve; also used for so-called "perforation" of brachial valve representing passage between bases of cardinal-process lobes in some strophomenoids.
- dorsal valve**. See brachial valve.
- dorsibiconvex**. Brachial valve more convex than pedicle valve.
- dorsiconvex**. See dorsibiconvex.
- dotted brachial ridges**. Ridges of thecideacean brachidium represented by rows of small separate pustules. [Elliott]
- double-barrelled spines**. External spines of primary shell having oval cross section and commonly barbed, bearing fine longitudinal furrow on posterior surface and partially enveloping anterior chamber which is incompletely divided by median partition (Fig. 87).
- double deltidial plates**. Pair of deltidial plates, each of which is seen in certain transverse sections to consist either of 2 parallel plates or of one plate nearest hinge line buttressed by another disposed at angle to it (e.g., *Cirpa*, Fig. 11,2). [Ager]
- double median septum**. More or less elevated median plate in pentameroid brachial valve formed by union of 2 septal plates.
- dyscoliid stage** (of lophophore). Details unknown but probably trocholophe.
- ear**. Flattened or pointed extremity of shell subtended between hinge-line and lateral commissure.
- ear baffle**. Extension of lateral ridge across ear inside some productoids. [Muir-Wood]
- echmidium**. Spear-shaped plate formed during ontogeny of loop by fusion of anterior ends of descending branches (Fig. 109,2).
- elytridium**. Convex puckered cover of delthyrium in aulostegids. [Muir-Wood]
- emarginate**. Median segment of anterior commissure deflected posteriorly.
- endopuncta** (pl., *endopunctae*). Perforation of shell not extending to its external surface, occupied by caecal prolongation of outer epithelium (Fig. 5, 126).
- endopunctum** (pl., *endopuncta*). See endopuncta.
- endospines**. Fine, solid or hollow spines on interior of shell.
- entering valve**. See brachial valve.
- ephebic**. Mature.
- episulcate** (folding). Resembling parasulcate but with median fold of brachial valve indented by median sulcus (Fig. 65,9).
- epithyridid** (foramen). Pedicle opening wholly within ventral umbo and ventral from beak ridges (Fig. 90,E).
- equidistribute** (mantle canal). *Vascula genitalia*, *vascula myaria*, and *vascula media* all well developed and contributing to mantle canal circulation (Fig. 135).
- erect beak**. See beak angle.
- erect spines**. Spines projecting at high angle (75–90°) from shell surface. [Muir-Wood]
- euseptoidum**. See myophragm.
- euseptum**. Primary septum; see septum.
- everted stage** (of folding). See uniplicate.
- exopuncta** (pl., *exopunctae*). Perforation of external shell surface commonly restricted to primary layer and never penetrating to internal surface.
- exopunctum** (pl., *exopuncta*). See exopuncta.
- extremities**. See cardinal extremities.
- falcifer** (crura). Crura arising on dorsal side of hinge plates and projecting into brachial valve as broad bladelikey processes (Fig. 1, 14). [Ager]
- false cardinal area**. See cardinal area or pseudo-interarea; term previously used for any poorly defined cardinal area or pseudointerarea.
- false pedicle groove**. See intertrough.

- fascicostellate.** Ornament of costae and costellae bundled into fascicles (Fig. 81).
- fibrous layer.** See secondary layer; term commonly used as alternative in articulate brachiopods in which the secondary layer is exclusively fibrous.
- filum** (pl., *fila*). Fine concentric ridge on external surface of shell.
- fimbria** (pl., *fimbriae*). Spinellike projection from spiralia or jugum; also used for spinose projection on margin of growth lamella, as in *Spinilingula* (Fig. 108).
- flange** (of crus). Lateral projection from crus formed by anterior extension of part of outer hinge plate adjacent to crural base.
- flange** (dyscoliid). Incurved lateral and anterior margins of both valves. [Muir-Wood]
- flanks.** See lateral slopes.
- flap.** See posterior flap.
- flexure line.** Line extending from beak to anterior border of both ventral propleas in some lingu-laceans, marked by deflection of growth lines (Fig. 62,4).
- FOLD.** Major elevation of valve surface, externally convex in transverse profile and radial from umbo.
- foramen.** See pedicle foramen; term commonly used with this meaning (Fig. 61,A).
- foraminal sheath.** See pedicle sheath.
- foraminal tube.** See pedicle tube.
- free.** Animal not attached to substratum.
- free spondylium.** Spondylium unsupported by septum.
- frenuliniform lacuna.** Lateral hole in hood produced by resorption during dallinid loop development subsequent to campagiform growth stage. [Elliott]
- frenuliniform** (loop). Term for growth stage in dalliniform loop development when lateral resorption gaps occur in hood and before resorption of shell occurs posterior to gaps (Fig. 110,4). [Elliott]
- frill.** Relatively large lamella projecting well beyond general contour of valve, deposited by margin of highly retractile mantle.
- fulcral plate.** Small plate raised above floor of brachial valve extending between posterior margin and brachiophore base and bounding socket anterolaterally (Fig. 102,3).
- furrow.** See interspace.
- fused hinge plates.** Hinge plates joined together along mid-line as far as hinge line or in front of it, with no development of septalium (e.g., *Cirpa*). [Ager]
- gape.** Anterior and lateral opening of shell.
- gastrothyridid** (foramen). Pedicle opening limited to pedicle valve.
- geniculate.** Abrupt and more or less persistent change in direction of valve growth producing angular bend in lateral profile (Fig. 63).
- genital area.** Part of shell underlain by saccate gonocoel or posterior part of digitate or lemniscate gonocoel.
- genital markings.** Radial ridges or pits on inside of shell within genital area.
- ginglymus.** Secondary interarea in pedicle valve of some productoids serving to close gap between valves and to assist in articulation. [Muir-Wood]
- glossothyropsiform** (loop). Loop developed from cryptacanthiiform stage by final resorption of posterior part of echmidium and consisting of 2 descending branches unconnected posteriorly, bearing 2 broad ascending elements joined by wide transverse band (Fig. 109,5).
- granule.** See tubercle.
- growth lamella.** Concentric outgrowth of shell deposited by retractile mantle margin, smaller than frill (Fig. 78).
- growth line.** Concentric line on outer surface of shell formed when anterior and lateral growth of shell temporarily was in abeyance (Fig. 80).
- gutter.** Anterior recurvature of trail of one or both valves, possibly serving as strainer or stabilizer. [Muir-Wood]
- haemal valve.** See brachial valve.
- halteroid spines.** Long external hollow spines, commonly 4 to 6, symmetrically placed, acting as strutlike supports. [Muir-Wood]
- height.** In biconvex, plano-convex, and convexo-plane shells height equals thickness, being maximum dimension normal to length and width; in concavo-convex and convexo-concave shells height is maximum distance measured normal to length in plane of symmetry between shell and line joining beak and anterior margin (Fig. 59).
- hemiperipheral growth.** New shell material added anteriorly and laterally but not posteriorly (Fig. 60).
- hemispondylium.** Two small plates within thecideacean ventral umbo, usually free of valve floor and side walls but commonly supported by median septum and bearing median adductor muscles. [Elliott]
- hemisyrix.** Conical chamber extending medially along floor of clitambonitoid spondylium and delineated posteriorly by pair of discrete lateral ridges.
- hemisyrix ridge.** Ridge forming posterolateral boundary of hemisyrix.
- hemithyridid stage** (of shell structure). See impunctate shell.
- henidium.** Conjoint deltidial plates that lose line of junction during late stages of growth.
- hinge.** Often used loosely for either hinge line or cardinal margin.
- hinge area.** See cardinal area.
- hinge axis.** Line joining points of articulation about which valves rotate when opening and closing (Fig. 61,A,B).
- hinge line.** Straight posterior margin of shell parallel with hinge axis; also used as synonym of cardinal margin (Fig. 61,B).
- hinge plate.** See inner hinge plate, outer hinge plate.

- hinge platform.** Solid secondary shell platform extending between socket ridges of terebratellacean cardinalia. [Elliott]
- hinge projections.** Projections of fused inner socket ridges and crural bases, visible externally posterior to dorsal umbo. [Elliott]
- hinge socket.** See dental socket.
- hinge spines.** Hollow spines developed in chonetoids in row along posterior margin of ventral interarea on either side of umbo and continuous with cylindrical hollow, commonly deflected passages through interarea, often called roots of spines. [Muir-Wood]
- HINGE TEETH.** Two principal articulating processes situated at anterolateral margins of delthyrium and articulating with dental sockets in brachial valve (Fig. 98).
- hinge trough.** V- or U-shaped depression formed by fusion of bifurcated median septum with combined socket ridges and crural bases of some terebratellaceans. [Elliott]
- hinge width.** Lateral extent of hinge line.
- holcothyridid stage** (of folding). See paraplicate.
- holoperipheral growth.** Increase in valve size all around margins, in posterior as well as anterior and lateral directions (Fig. 60).
- HOMEOCHILIDIUM.** Externally convex triangular plate closing almost all or only apical part of notothyrium in Paterinida; spelled homoeochilidium by some authors (Fig. 93).
- HOMEODELTIDIUM.** Externally convex triangular plate closing almost all or only apical part of delthyrium in Paterinida; spelled homoeodeltidium by some authors (Fig. 62,3; 93).
- hood.** Arched plate of secondary shell arising from echmidium of *Cryptacanthia* or median septum of dallinids. See campagiform hood (Fig. 109, 110).
- hypercline.** See inclination of cardinal area or pseudointerarea (Fig. 61,C).
- hypothyridid** (foramen). Pedicle opening located below or on dorsal side of beak ridges with umbo intact (Fig. 90,B). [Muir-Wood]
- imbricate** (ornament). See lamellose.
- impunctate** (shell). Shell lacking endopunctae or pseudopunctae.
- inclination of cardinal area or pseudointerarea.** Commonly used terms for inclination of cardinal area or pseudointerarea in either valve based on convention of viewing specimen in lateral profile with beaks to left and brachial valve uppermost, referring cardinal area to its position within one of 4 quadrants defined by commissure plane and plane normal to it and symmetry plane, touching base of cardinal areas (Fig. 61). Cardinal area lying on continuation of commissure plane is **orthocline**. Moving clockwise, cardinal area in first quadrant (top left) is weakly to strongly **anacline**; in second quadrant (top right) weakly to strongly **hypercline**. Moving counter-clockwise from orthocline position, cardinal area lying in bottom left quadrant is weakly to strongly **apsac-line**; at 90° to orthocline it is **catacline**; and continuing counter-clockwise into bottom right quadrant cardinal area is weakly to strongly **procline** (Fig. 61,C).
- incurved beak.** See beak angle.
- inequidistribute** (mantle canal). *Vascula genitalia* of dorsal mantle saccate and contributing little to canal circulation (Fig. 135).
- inner carbonate layer.** See secondary layer.
- inner hinge plates.** Pair of subhorizontal plates in cardinalia of some rhynchonelloids, spiriferoids and terebratuloids located median of crural bases and fused laterally with them (Fig. 102,6).
- inner plates.** Pair of subvertical plates in cardinalia of some pentameraceans lying on ventral side of base of brachial process and fused dorsally with it; see brachiophore base for orthoids (Fig. 102,8).
- inner socket ridge.** Ridge of secondary shell commonly overhanging dental socket and forming its inner or anterior margin (Fig. 98; 102,6).
- interarea.** Posterior sector of shell with growing edge at hinge line; also, more commonly used for any plane or curved surface lying between beak and posterior margin of valve and bisected by delthyrium or notothyrium (Fig. 61,B).
- intercalary lamellae.** See accessory lamellae.
- intercalation.** Costella arising by insertion between costae or costellae, not by bifurcation of existing costa or costella (Fig. 81).
- intercamarophorial plate.** Short, low median septum on posterior mid-line of camarophorium in stenoscismataceans, extending to underside of hinge plate but independent of median septum duplex. [Grant]
- interconnecting bands.** See connecting bands.
- intercostal sulci.** See interspace.
- internal oblique muscles.** Pair of muscles in some inarticulates, originating on pedicle valve between anterior adductors and passing posterolaterally to insertions on brachial valve located anterolaterally from posterior adductor muscles (Fig. 29).
- interspace.** Flat or externally concave sectors of shell between adjacent costae or costellae (Fig. 84).
- intertext** (folding). Alternate folding with opposed sulci and carinae equal in amplitude.
- intertrough.** Median, narrowly triangular furrow dividing pseudointerarea of pedicle valve of some acrotretaceans (Fig. 62,5).
- intraplicate** (folding). Form of alternate folding with pedicle valve bearing median fold indented by shallower median sulcus (Fig. 65,4).
- intraseptal lamella.** Sheet of prismatic calcite of varying persistency found in median septum of spondylium duplex.
- inverted stage** (of folding). See sulcate.
- isemeniform** (loop). See campagiform loop.
- jugal processes.** Pair of ventromedially directed outgrowths from primary lamellae of spiralia which do not coalesce.
- jugal stem.** Ventroposteriorly directed continuation

- of jugum which by bifurcation may give rise to accessory lamellae posteriorly.
- JUGUM.** Medially placed connection of secondary shell between 2 primary lamellae of spiralia (Fig. 108).
- kingeniform** (loop). Adult dallinid loop in which tendency to retain campagiform hood during development leads to broad sheetlike transverse band with connecting bands leading to septum in addition to normal ones joining descending branches with septum. [Elliott]
- labiate** (foramen). Exaggerated marginate foramen in which dorsal edge is prolonged liplike. [Stehli]
- lacuna.** See frenuliniform lacuna.
- lamella.** Sheetlike extension of primary and even underlying secondary shell deposited by retractile mantle margin on external shell surface; also used for calcareous ribbon comprising spirulum and coiled extension from arm of jugum.
- lamellar layer.** See primary layer.
- lamellose.** Ornament consisting of overlapping growth lamellae.
- laqueiform** (loop). Dallinid loop pattern in which posterior connecting bands from ascending to descending branches are retained during enlargement and proportional thinning during change from frenuliniform to terebrataliiform loop. [Elliott]
- lateral areas.** General term for portions of ventral palintrope to left and right of delthyrial structures. [Elliott]
- lateral branch** (of jugum). Part of jugum continuous with primary lamella (Fig. 108).
- lateral cavities.** See umbonal cavities.
- lateral commissure.** Lateral part of line of junction of valves.
- lateral margin.** Lateral edge of valve.
- lateral oblique muscles.** Pair of muscles in some inarticulates, originating on pedicle valve anterolaterally from posterior adductor muscles and passing anterodorsally to insertions either on brachial valve and anterior body wall against anterior adductors (Discinidae) or entirely on anterior body wall (Craniidae) (Fig. 29).
- lateral slopes.** Valve surfaces on either side of median sector of shell.
- leiolophid stage** (of lophophore). Obsolete term for embryonic brachial structure before appearance of filamentar appendages of lophophore.
- lemniscate** (mantle canal). Gonocoel still saclike but giving rise to branches that extend to posterolateral margins with corresponding peripheral reduction of *vascula media* and *vascula myaria* (Fig. 136).
- LENGTH** (of valve). Distance from most posterior point of valve, normally umbo, to farthest point on anterior margin measured on commissural plane in plane of symmetry or parallel with it (Fig. 59,C).
- lenticular stage** (of folding). Both valves gently and subequally biconvex, anterior margin rectimarginate.
- ligate stage** (of folding). Opposite folding with single sulcus in one valve opposed by single sulcus in other, commissure rectimarginate (Fig. 64, 3). [Elliott]
- limbus.** Flattened inner margin of inarticulate valve.
- lingual extension.** See linguiform extension.
- linguiform extension.** Anterior tongue-shaped extension of either valve. [Muir-Wood]
- liothyrid stage** (of folding). See lenticular stage.
- lirae.** Fine ridges and grooves.
- LISTRUM.** Plate in some discinaceans closing anterior end of pedicle opening which has migrated posteriorly (Fig. 62,2; 94,A).
- longitudinal axis.** Intersection of planes of commissure and symmetry.
- LOOP.** Support for lophophore composed of secondary shell and extending anteriorly from crura as closed apparatus, variably disposed and generally ribbon-like with or without supporting septum from floor of brachial valve (Fig. 105).
- lophidium.** Inverted V-shaped projection of median posterior part of brachial valve or of external face of cardinal process, helping to close gap in delthyrium in some productoids. [Muir-Wood]
- LOPHOPHORE.** Feeding organ with filamentar appendages, symmetrically disposed about mouth, typically suspended from anterior body wall but may be attached to dorsal mantle; occupies mantle cavity (Fig. 1).
- lophophore platform.** Bilobed or U-shaped disc of secondary shell with anterior edge elevated above floor of plectambonitacean brachial valve; probably supported lophophore (Fig. 113,I).
- lophrothyridid stage** (of folding). See uniplicate.
- magadiform** (loop). See campagiform loop.
- magadiniform** (loop). Type of terebratellid loop or loop growth stage marked by completed descending branches from cardinalia to median septum, with ringlike structure on septum representing early ascending portion of loop. [Elliott]
- magaselliform** (loop). See magelliform loop.
- magellanian stage** (shell). See punctate (shell).
- magellaniform** (loop). Type of free terebratellid loop consisting of long descending branches recurved into ascending branches which meet in transverse band; morphologically similar to dalliniform loop. [Elliott]
- magelliform** (loop). Type of terebratellid loop or loop growth stage, in which bases of septal ring on median septum meet and fuse with attachments of completed descending branches. [Elliott]
- main flanks.** See lateral slopes.
- maniculifer** (crura). Derived from radulifer type, with handlike processes at end of straight, ventrally directed crura (Fig. 1, 25,2). [Ager]
- MANTLE.** Prolongation of body wall as fold of ectodermal epithelium (Fig. 1,2).
- MANTLE CANALS.** Flattened, tubelike extensions of body cavity into mantle.

- MANTLE CAVITY.** Anterior space between valves bounded by mantle and anterior body wall and containing lophophore (Fig. 1,2).
- mantle papilla.** See caecum.
- mantle sinus.** See mantle canal.
- margin** (of valve). Edge of valve.
- marginal flange** (of shell). See geniculation.
- marginal flange** (of thecideacean brachial valve). See subperipheral rim.
- marginal ridge.** Thickening along internal lateral and anterior margin of visceral disc of some productoids, usually in brachial valve. [Muir-Wood]
- marginal spines.** Long, slender prolongations of interspaces between ribs lying against inner surface of opposing valve when shell is shut and forming grille when shell is open (Fig. 84).
- marginate** (foramen). Pedicle foramen with thickened margin. [Stehli]
- marisupal notch.** Small double notch or perforation in ventral edge of brachial bridge in some adult female thecideaceans marking passage of 2 specialized posteriorly directed filaments to which embryos are attached. [Elliott]
- median.** In plane of shell symmetry.
- median partition.** Median septum supporting anterior part or trimerellacean muscle platform and dividing cavity beneath platform into 2 vaults (Fig. 101).
- median plane.** See plane of symmetry.
- megathyridid** (posterior margin). Posterior margin long and straight.
- megerliiform** (loop). Terabratellacean loop with descending branches joining anterior projections from large ring on low median septum; differs from similar dallinid and terebratellid loops by appearance of well-developed ring before growth of descending branches. [Elliott]
- mergifer** (crura). Variant of radulifer crura, long, close together, parallel, arising directly from swollen edge of high dorsal median septum (Fig. 1, 8,3). [Ager]
- mesothyridid** (foramen). Pedicle opening located partly in ventral umbo and partly in delthyrium, beak ridges appearing to bisect foramen (Fig. 90,D). [Muir-Wood]
- metacarinat stage** (of folding). Opposite folding, carinae continuous and strongly developed (Fig. 64,2).
- middle lateral muscles.** Pair of muscles in some Lingulida originating on pedicle valve between central muscles and diverging slightly posteriorly before insertion on brachial valve (Fig. 28).
- mixoperipheral growth.** Differs from holoperipheral growth in that posterior sector of valve increases in size anteriorly and toward other valve (Fig. 60).
- monticules.** Small rounded nodes, commonly bearing spines. [Muir-Wood]
- mosaic.** Pattern on interior of valve formed by outlines of adjacent fibers of secondary shell layer (Fig. 69).
- mouth segment** (of lophophore). Median part of lophophore containing mouth, attached to anterior body wall and bearing single row of paired or unpaired filamentar appendages.
- mucronate** (cardinal margin). Cardinal extremities extended into sharp points.
- muehlfeldtiiform** (loop). See megerliiform.
- multicostellate.** Costellae increasing in number by bifurcation or intercalation but not varying greatly in size (Fig. 81).
- muscle area.** See muscle field.
- muscle-bounding ridge.** Elevation composed of secondary shell bounding part of muscle field.
- muscle field.** Area of valve in which muscle scars are concentrated.
- muscle impression.** Marks of muscle attachment.
- muscle platform.** Solid or undercut elevation of shell to which muscles are attached (Fig. 122, 133).
- MUSCLE SCAR.** More or less well-defined impression or elevation on valve representing final site of attachment of muscle (Fig. 115).
- muscle track.** Path of successive muscle impressions formed by migration of muscle base during growth.
- myocoelidium.** Chamber similar to spondylium but not formed by dental plates, serving for attachment of muscles (e.g., Richthofeniidae). [Muir-Wood]
- myophore.** Distal expanded part of differentiated cardinal process to which diductor muscles were attached (Fig. 123).
- myophragm.** Median ridge of secondary shell secreted between muscles and not extending beyond muscle field. [Muir-Wood]
- mystrochial plates.** Pair of small plates buttressing spondylium posterolaterally, as in *Amphigenia*.
- neanic.** Youthful stage at which generic characters of shell begin to be apparent.
- nearly straight beak.** See beak angle.
- nepionic.** See brephic.
- neural valve.** See pedicle valve.
- nodus principalis.** Point from which *vascula cruralia* or *vascula cardinalia* (or both) diverge in mantle canal system of brachial valve (Fig. 134).
- nodus quadrivalis.** Point from which *vascula intermyaria* diverge in mantle canal system of brachial valve (Fig. 134).
- nodus septalis.** Point from which *vascula media* diverge in mantle canal system of brachial valve (Fig. 134).
- nodus terminalis.** Point of origin of *vascula terminalia* in mantle canal systems (Fig. 134).
- nonintertext** (folding). Type of folding in which sulcus or carina of one valve is opposed by plane valve. [Elliott]
- nonstrophic** (shell). Shell with posterior margin not parallel with hinge axis (Fig. 61,A).
- norellid stage** (of folding). See sulcate.
- notodeltidium.** Plate completely filling delthyrium, formed by fusion of deltidial plates with eventual plugging of pedicle foramen by posterior retreat

- of junction between pedicle epithelium and outer epithelium.
- notothyrial cavity*. See notothyrial chamber.
- notothyrial chamber**. Cavity in umbo of brachial valve corresponding to delthyrial chamber of pedicle valve, bounded laterally by brachiophore bases (or homologues) or by posterolateral shell walls if brachiophore bases absent.
- notothyrial platform**. Umbonal thickening of floor of brachial valve between brachiophore bases (or homologues) (Fig. 99,D).
- notothyridid** (foramen). Pedicle opening in brachial valve, condition never completely attained.
- NOTOTHYRIUM**. Median subtriangular opening bisecting dorsal cardinal area or pseudointerarea (Fig. 59,A).
- occluser muscle*. See adductor muscle.
- oligopalmate**. Mantle canal system with 2 pairs of principal canals in each mantle.
- opercular**. Lidlike, referring to brachial valve in some genera. [Muir-Wood]
- opposite folding**. Folding in which fold or sulcus in one valve is opposed by fold or sulcus in other, commissure remaining rectimarginate (Fig. 64).
- ornament**. Any outgrowth, minor deflection or non-pathological interruption in growth found on outer shell surface.
- ornithellid stage** (of folding). Characterized by presence of lateral carinae but without median sulci. (Fig. 64,I). [Muir-Wood]
- orthocline**. See inclination of cardinal area or pseudointerarea (Fig. 61,C).
- orthoconate*. Brachia coiled parallel with plane of commissure.
- outer carbonate layer*. See primary layer.
- outer epithelium**. Ectodermal epithelium adjacent to shell and responsible for its secretion (Fig. 2,3, 16).
- outer hinge plates**. Pair of concave or subhorizontal plates in cardinalia separating inner socket ridges and crural bases (Fig. 102,6).
- outer mantle lobe**. Outer peripheral part of mantle, separated by mantle groove from inner lobe, in articulate brachiopods responsible for secretion of primary shell layer (Fig. 3, 74).
- outer plates**. Pair of subvertical plates in pentameracean cardinalia with ventral surface fused to base of brachial process and dorsal edge attached to floor of valve or rarely septal plate (Fig. 102,8).
- outer socket ridge**. Low ridge bounding dental socket on outer lateral or posterior side (Fig. 98; 102,6).
- outside lateral muscles**. Pair of muscles in some Lingulida which originate on pedicle valve lateral to centrals and extend posteriorly to insertions behind middle lateral muscles on brachial valve (Fig. 28).
- ovarian impression*. See genital marking.
- ovarian marking*. See genital marking.
- palintrope**. Initially used for morphologically posterior sector of either valve which was reflexed to grow anteriorly (mixoperipheral growth); more recently used for curved surface of shell, bounded by beak ridges and cardinal margin of nonstrophic shells (differs from planarea in being curved in all directions) (Fig. 61,A).
- pallial caecum*. See caecum.
- pallial lobe*. See mantle.
- pallial markings*. See vascular markings.
- pallial sinus*. See mantle canal.
- pallium*. See mantle.
- papillae**. Regularly arranged endospines.
- paradental lamella*. See muscle-bounding ridge.
- paraplicate** (folding). Produced from sulcate stage by development of 2 folds in brachial valve bounding dorsal sulcus (Fig. 65,5).
- parasulcate** (folding). Form of alternate folding with brachial valve bearing sulcus on either side of median fold (Fig. 65,7).
- parathyridium**. Deep indentation of shell on either side of beak, formed by medially directed depression or flexure of posterolateral shell surface of both valves, particularly brachial (e.g., *Cardiarina*).
- parvicostellate**. Costellae numerous, arising entirely by intercalation between widely spaced costae (Fig. 81).
- paucicostate**. Costae distant and few.
- paucicostellate**. Costae and costellae distant and few.
- paucispinose**. With few spines.
- PEDICLE**. Variably developed, cuticle-covered appendage, commonly protruding from pedicle valve and responsible for attachment of animal to substratum (Fig. 1, 2).
- pedicle callist**. Localized thickening of secondary shell layer in apex of pedicle valve representing track of anterior migration of junction between pedicle epithelium and outer epithelium (Fig. 115).
- pedicle collar**. Complete or partial ringlike thickening of inner surface of ventral beak, continuous laterally with internal surface of deltidial plates, sessile, with septal support, or free anteriorly and secreted by anteriorly migrating outer epithelium at its junction with pedicle epithelium (Fig. 98, A).
- pedicle epithelium**. Ectodermal epithelium investing pedicle (Fig. 2).
- PEDICLE FORAMEN**. Subcircular to circular perforation of shell through which pedicle passes (Fig. 61,A).
- pedicle furrow*. External plate extending anteriorly from beak to pedicle foramen in some siphonotretaceans and obolellaceans (use not recommended because plate not invariably concave externally).
- PEDICLE GROOVE**. Commonly subtriangular groove dividing ventral pseudointerarea medially and affording passage for pedicle in many Lingulida (Fig. 62,4).

- pedicle muscle scar.** Scar of attachment on pedicle valve of longitudinal fibrils in connective tissue of pedicle of articulate brachiopods.
- pedicle muscles.** Any muscles associated with pedicle; in articulate brachiopods mostly synonymous with adjector muscles and may include longitudinal fibrils in connective tissue of pedicle; in inarticulate brachiopods includes muscles developed within wall and coelom of pedicle (Fig. 25).
- pedicle notch.** Small subtriangular depression, posteromedially placed on limbus of paterulids, probably functioning as pedicle groove.
- pedicle opening.** Variably shaped aperture in shell through which pedicle emerges.
- pedicle plate.** Tongue-shaped shelly deposit inside labium of labiate foramen.
- pedicle sheath.** Externally directed tube projecting posteroventrally from ventral umbo, probably enclosing pedicle in young stages of development of some shells with supra-apical pedicle opening (Fig. 92,B).
- pedicle tube.** Internally directed tube of secondary shell continuous with margin of pedicle foramen and enclosing proximal part of pedicle (Fig. 94,B).
- PEDICLE VALVE.** Valve through which pedicle commonly emerges, usually larger than brachial valve (Fig. 1, 59).
- peduncle.** See pedicle.
- perideltidial area.** Discrete part of perideltidium.
- perideltidial line.** Break of slope marking outer boundary of perideltidial area.
- perideltidium.** Pair of slightly raised triangular parts of interarea flanking pseudodeltidium or lateral to it and characterized by vertical striae in addition to horizontal growth lines parallel to posterior margin.
- periostracal pad.** Thickened band of periostracum covering cardinal areas and spun out by fused mantle lobes along posterior margin of some articulate brachiopods (Fig. 89,C).
- periostracum.** Thin, organic external layer of shell (Fig. 74).
- permesothyridid (foramen).** Pedicle opening located mostly within ventral umbo (Fig. 90,E). [Muir-Wood]
- pinnate (mantle canal).** *Vascula genitalia* or *vascula lateralia* consisting exclusively of radially disposed canals (Fig. 135).
- planareas.** Two flattened areas developed, one on either side of posterior part of shell in place of more common single median interarea. [Ager]
- plane commissure.** See rectimarginate.
- plane of symmetry.** Plane bisecting shell symmetrically (Fig. 59,D).
- plano-convex.** Brachial valve flat, pedicle valve convex.
- plate (of trimerellids).** Single transverse, platelike projection from cardinal margin of brachial valve articulating with cardinal socket of pedicle valve (Fig. 101).
- platform.** Relatively broad solid or undercut elevation of inner surface of valve, commonly bearing muscles (Fig. 101).
- platform (of Orthidina).** See notothyrial platform and chamber.
- platform line.** Side bounding notothyrial chamber.
- platform vaults.** Two cavities beneath platform in some trimerellids, separated by median partition (Fig. 101).
- platiidiform (loop).** Loop consisting of descending branches from cardinalia to median septum, with only rudimentary prongs on septum representing ascending part of loop. [Elliott]
- plectolophe.** Lophophore in which each brachium consists of U-shaped side arm bearing double row of paired filamentar appendages but terminating distally in medially placed plano-spire normal to commissural plane and bearing single row of paired appendages.
- plectolophous (adj.).** Pertaining to plectolophe.
- plectolophus (noun).** See plectolophe.
- pleuromal plates.** Pair of "plates" in posterior part of delthyrial cavity of some spiriferoids immediately internal to dental plates, probably merely later infilling of delthyrial cavity.
- plica.** Major undulation of commissure with crest directed dorsally, commonly but not invariably associated with dorsal fold and ventral sulcus; also used, irrespective of commissure, as small carina or fold.
- plication.** See plica.
- plicilligiate stage (of folding).** Having deep median ventral sulcus with strong bounding folds opposite low median dorsal fold bordered by shallow sulci. [Muir-Wood]
- polypalmate.** Mantle canal system with more than 4 principal canals in each mantle.
- pore.** See puncta.
- POSTERIOR.** Direction in plane of symmetry or parallel to it toward pedicle and away from mantle cavity (Fig. 59,B).
- posterior flap.** Reflexed to anteriorly directed extension of oldhaminoid pedicle valve lying dorsal to at least posteromedian part of brachial valve.
- posterior margin.** Posterior part of junction between edges of valves, may be hinge line or cardinal margin (Fig. 61).
- posterior oblique muscles.** Pair of muscles in discinaceans originating posterolaterally on pedicle valve and converging dorsally to insertions on brachial valve between posterior adductors (Fig. 29).
- posterolateral commissure.** Posterolateral parts of line of junction between edges of valves.
- precampagiform flange.** Lateral projections from early septal hood in loop development of some dallinids; may survive in later growth stages as small accessory structures on loop. [Elliott]
- precampagiform hood.** Tubular cone on posterior face of septal pillar, not fused with descending branches (Fig. 110,I).

- prefalcifer** (crura). Crura straight, in plane of commissure and slightly compressed, variant of falcifer crura (Fig. 1). [Ager]
- pre-ismeniform** (loop). See campagiform loop.
- premagadiniform** (loop). One of the early stages in terebratulid loop development marked by growth of descending branches from both cardinalia and median septum and their completion, and appearance of tiny hood developing into ring on septum. [Elliott]
- prepygites stage** (of folding). See intraplicate.
- presocket line**. Anterior or anterolateral side of triangular slot produced by brachiophore base (and fulcral plate if present) in internal mold of Orthidina.
- primary lamella**. First half whorl of each spirulum distal from its attachment to crus (Fig. 108).
- PRIMARY LAYER** (of shell). Outer shell layer immediately beneath periostracum deposited extracellularly by columnar outer epithelium of outer mantle lobe; in most articulate brachiopods forms well-defined calcareous layer devoid of cytoplasmic strands (Fig. 3, 78).
- prismatic layer**. See secondary layer.
- procline**. See inclination of cardinal area or pseudointerarea (Fig. 61,C).
- prodeltidium**. So-called "third plate" at one time thought to be developed in earlier embryonic growth of "atrematous," "neotrematous," and "protrematous" species, subsequently becoming more or less attached to either brachial atrematous) or pedicle valve.
- PROPAREAS**. Pair of subtriangular halves of pseudointerarea divided medially by various structures (e.g., homeodeltidium, intertrough, pedicle groove, etc.) (Fig. 62).
- prosocket ridge**. See socket ridge.
- prostrate spines**. Usually straight spines that lie prone on shell surface of some productoids. [Muir-Wood]
- protegular node**. Apical portion of adult shell, commonly raised, representing site of protegulum and later growth up to brephic stage (Fig. 80).
- protegulum**. First-formed shell of organic material (chitin or protein), secreted simultaneously by both mantles (Fig. 60).
- protractor muscle**. See outside and middle lateral muscles in articulates; also used in articulate brachiopods for longitudinal fibrils in connective tissue of pedicle (see pedicle muscle scar).
- pseudoarea**. See pseudointerarea.
- pseudobrache plate**. Tuberculate ridges bearing dorsal adductor muscles.
- pseudochilidium**. See chilidium.
- pseudocruralium**. Callus of secondary shell bearing dorsal adductor impressions and elevated anteriorly above floor of valve.
- PSEUDODELTIDIUM**. Single, convex or flat plate affording variably complete cover of delthyrium but invariably closing apical angle when foramen is supra-apical or absent and always dorsally enclosing apical foramen (Fig. 92,A).
- PSEUDOINTERAREA**. Somewhat flattened, posterior sector of shell of some inarticulate brachiopods secreted by posterior sector of mantle not fused with that of opposite valve (Fig. 62).
- pseudopedicle collar**. Sessile pedicle collar.
- pseudopedicle groove**. See intertrough.
- pseudopuncta** (pl., **pseudopunctae**). Conical deflection of secondary shell, with or without taleola, pointing inwardly and commonly anteriorly to appear on internal surface of valve as tubercle (Fig. 73).
- pseudopunctate** (shell). Possessing pseudopunctae.
- pseudopunctum** (pl., **pseudopuncta**). See pseudopuncta.
- pseudoresupinate**. Convexo-concave shells (Fig. 63, 2).
- pseudosockets**. See secondary sockets.
- pseudospondylium**. Cup-shaped chamber accommodating ventral muscle field and comprising undercut callus of secondary shell contained between discrete dental plates (Fig. 118).
- pseudoteeth**. See secondary teeth.
- pseudotelae**. Pair of external projections resembling telae but produced by dorsal migration of pedicle cutting labiate foramen, not beak ridges.
- ptycholophe**. Lophophore with brachia folded into one or more lobes in addition to median indentation (Fig. 113,3).
- ptycholophous** (adj.). Pertaining to ptycholophe.
- ptycholophus** (noun). See ptycholophe.
- puncta** (pl., **punctae**). See endopuncta.
- punctate** (shell). Commonly used to describe shell possessing endopunctae.
- punctum** (pl., **puncta**). See endopunctum.
- pygopid** (loop). Short ringlike loop with slightly arched transverse band. [Muir-Wood]
- quadruplicate** (folding). Having 4 anterior folds and 3 intervening sulci. [Muir-Wood]
- radulifer** (crura). Hook-shaped or rodlike crura which arise on ventral side of hinge plate and project toward pedicle valve (Fig. 1). [Ager]
- ramicostellate**. Costellae numerous, arising entirely by branching (Fig. 81).
- receiving valve**. See pedicle valve.
- rectimarginate**. Having plane anterior commissure (Fig. 65,1).
- recumbent spines**. Slightly curved spines extending at angle of less than 45° to shell surface. [Muir-Wood]
- reflexed interarea**. Dorsal interarea hypercline.
- remigrant** (foramen). Pedicle opening which tends to move dorsally after initially migrating toward ventral beak.
- resupinate**. Reversal in relative convexity of post-brephic shells with convex pedicle valve which becomes concave and with concave brachial valve which becomes convex during successive adult stages of growth (Fig. 63).
- reticulate** (ornament). Subrectangular patterns on

- shell exterior, commonly involving nodelike enlargements, formed by intersection of concentric and radial elements of ornament.
- retractor muscles.* See anterior lateral muscles.
- rhizoid spines.** Spines resembling rootlets, serving for attachment either by entanglement or by extending along and cementing themselves to foreign surface (Fig. 132). [Muir-Wood]
- rhynchonellid stage* (of folding). See uniplicate.
- ribs.** Any radial ornament.
- ridge.** Relatively long narrow elevation of secondary shell, indicated in articulates to variable depth within underlying floor of valve by low, wide deflections of fibrous calcite normal to long axis of ridge, and in inarticulates by comparable deflections of shell lamellae.
- rimmed** (foramen). See auriculate.
- ring.** Precursor to ascending branches of terebratellid loop in premagadiniform growth stage, consisting of thin circular ribbon, narrow ventrally and broadening dorsally to its attachment on median septum.
- rostellum.** Low projection between anterior adductor muscle scars of pedicle valve of some craniaceans to which internal oblique muscles are attached.
- rostral callosity.* See delthyrial plate.
- rostrate.** With prominent beak of pedicle valve projecting over narrow cardinal margin.
- rostrum.* Beak of articulate brachiopods (see beak).
- rostrum.** Elevation of secondary shell on inner surface of brachial valve of some craniaceans in front of anterior adductor muscles, consisting of pair of low club-shaped protuberances forming seat of attachment for brachial protractor muscles.
- RUGA** (pl., *rugae*). Concentric or oblique wrinkling of external shell surface (Fig. 80).
- saccate** (mantle canal). *Vascula genitalia* pouchlike, without terminal branches, not extending to anterolateral periphery of mantle, functioning primarily as gonocoels (Fig. 135).
- saddle.** Median arched part of jugum between stem and lateral branches (Fig. 108).
- scar.** See muscle scar.
- scar of pedicle attachment.* See pedicle muscle scar.
- schizolophe.** Lophophore indented anteromedially to define pair of brachia which bear row of paired filamentary appendages, at least distally (Fig. 106, C').
- schizolophous** (adj.). Pertaining to schizolophe.
- schizolophus* (noun). See schizolophe.
- SECONDARY LAYER** (of shell). Shell deposited by outer epithelium median of outer mantle lobes; in articulate brachiopods, layer secreted intracellularly as fibers bounded by cytoplasmic sheaths, or, less commonly, extracellularly as prismatic calcite (Fig. 5, 78, 117).
- secondary sockets.** Pair of small depressions immediately posterodorsal of cardinal process lobes receiving secondary teeth.
- secondary teeth.** Pair of dorsally directed projections from ventral process fitting into secondary sockets of stropheodontid brachial valve.
- septal pillar.** High dorsal septum anterior to cardinalia, formed early in development of terebratellacean loop.
- septal plates.** Two plates which fuse to form duplex median septum in brachial valve of some pentameroids and bearing outer plates on their ventral surfaces.
- septal plates.* Various parts of cardinalia; see crural plates, hinge plates.
- septalial plates.** Crural plates forming floor of septalium and united with earlier-formed part of median septum (Fig. 102, 6).
- septalium.** Troughlike structure of brachial valve between hinge plates (or homologues), consisting of septalial plates (or homologues) enveloping and buttressed by median septum; does not carry adductor muscles (Fig. 103, 6).
- septifer crura.** Crura having form of septa that descend directly from dorsal side of hinge plates to floor of brachial valve (Fig. 1, 6, I). [Ager]
- septum.** Relatively long, narrow elevation of secondary shell, commonly bladellike; indicated in articulates within underlying floor of valve by persistent high, narrow deflections of fibrous calcite originating near primary layer, and in inarticulates by comparable deflections of shell lamellae (Fig. 120).
- sessile cruralium.** Cruralium united with floor of brachial valve without intervention of supporting median septum.
- sessile spondylium.** Spondylium united with floor of pedicle valve without intervention of supporting median septum.
- seta** (pl., *setae*). Chitinous bristle arising from invagination of mantle groove (Fig. 82).
- shaft.** See cardinal process shaft.
- shell mosaic.** See mosaic.
- shell space.** Cavity enclosed by conjoined valves.
- shoe-lifter process.** Arched platform of secondary shell attached posteriorly and laterally to floor of pedicle valve but sharply elevated and free medially, bearing part of ventral muscle field and lying between or supporting dental plates (Fig. 122).
- sinus.** Major undulation of commissure with crest directed ventrally, commonly but not invariably associated with ventral fold and dorsal sulcus; also used irrespective of commissure, as a synonym of sulcus.
- siphonothyridid* (foramen). Pedicle foramen continued internally as tube made up of exaggerated pedicle collar.
- socket line.* Posterior side of triangular slot in internal molds of orthoid and enteletecean brachiopods produced by brachiophore base (and fulcral plate, if present) and bounding impression of socket.
- socket plate* (of orthoids). See fulcral plate.
- socket plate** (of davidsoniaceans). Pair of plates sup-

- porting socket ridges, attached to cardinal process and resting on floor of brachial valve.
- socket ridges.** Linear elevations of secondary shell extending laterally from cardinal process and bounding margin of dental sockets; *see* also inner socket ridge and outer socket ridge (Fig. 99,B; 102,2).
- socket valve.* *See* brachial valve.
- sockets.** *See* dental sockets.
- spinules.** Small, irregular bodies of calcite which may be secreted within connective tissue of body wall, mantle, and lophophore (Fig. 3,B, 6).
- spine.** Solid or hollow, cylindrical or, less commonly, elongate triangular projections from external shell surface (Fig. 72,A; 86-88).
- spine apertures.** Internal opening of spine bases.
- spine ridge.** Posterior trace of prostrate spine on shell exterior.
- spinule bases or apertures.** Small oval perforations in some chonetoids representing bases of spinules usually seen on summit of radial ornament and only penetrating external shell layer; possibly homologous with hollow ribs of some orthoids and enteletaceans. [Muir-Wood]
- spinules.** Spines of small diameter and approximately 1 or 2 mm. in length in chonetoids. [Muir-Wood]
- spinulifer (crura).** Variant of radulifer type, but with crura laterally compressed (Fig. 1). [Ager]
- SPIRALIA** (sing., *spirali*um). Pair of spirally coiled supports for deuterolophe or spirolophe, composed of secondary shell (Fig. 104).
- spires.** *See* spiralia.
- spiriferid stage** (of posterior margin). Shell very transverse, posterior margin long and straight.
- spirolophe.** Lophophore in which brachia are spirally coiled and bear single row of paired filamentar appendages (Fig. 43).
- splanchnocoel.* *See* body cavity.
- spondylial cavity.** Space enclosed by posterior part of spondylium and purported to be bounded by spondylial lining.
- spondylial lining.** Thin prismatic layer of secondary shell forming more or less continuous veneer on dorsal surface of pentameracean spondylium and entire deltidial cover (Fig. 117,2).
- spondylium.** Trough-shaped or spoonlike apparatus composed of dental plates in various stages of coalescence, usually with median septum, accommodating ventral muscle field (Fig. 117, 119).
- spondylium discretum.** Muscle-bearing chamber formed by slight convergence of dental plates which are attached separately to floor of valve.
- spondylium duplex.** Spondylium formed by convergence of dental plates and supported by variably developed median septum arising from floor of pedicle valve, septum supporting platform and attached to pedicle valve (Fig. 117,2).
- spondylium pseudotriplex.** *See* spondylium triplex.
- spondylium simplex.** Spondylium formed by convergence of dental plates and supported ventrally by variably developed simple median septum or ridge (Fig. 117,1).
- spondylium triplex.** Spondylium supported by median septum and 2 lateral septa (e.g., *Polytoechia*) (Fig. 119).
- spondyloid** (dental plates). Basal inner surfaces of dental plates thickened and coalesced to simulate spondylium.
- spyridium.** Cuplike apparatus affording attachment for dorsal adductor field and consisting of variably fused pair of subtriangular platforms elevated on subjacent ridges (Fig. 130). [Muir-Wood]
- squamose.** Having irregular and ragged margin to concentric growth lamellae. [Muir-Wood]
- stalk.* *See* pedicle.
- stegidium.** Convex plate closing gap between delthyrial plate and spiriferoid brachial valve consisting of series of concentric layers deposited by outer epithelium associated with atrophying pedicle migrating dorsally (Fig. 91).
- stolidium.** Thin marginal extension of one or both valves forming narrow to broad frill protruding at distinct angle to main contour of shell, as in stenoscismataceans. [Grant]
- straight beak.** *See* beak angle.
- strainer spines.* *See* endospines.
- strangulate stage** (of folding). Form of opposite folding, sulcus in each valve with incipient carinae (Fig. 64,4).
- striae.** Fine grooves or incisions.
- trophic (shell).** Shell with true hinge line parallel to hinge axis (Fig. 61,B).
- suberect beak.** *See* beak angle.
- suberect spines.** Spines inclined to shell surface at angles between 45°-75°. [Muir-Wood]
- subintertext folding.** Alternate folding with opposing sulci and carinae of unequal amplitude.
- submarginal ridge** (of productoids). Thickening of interior of either valve parallel to anterior margin of visceral disc. [Muir-Wood]
- submegathyridid** (posterior margin). Posterior margin approximately straight and slightly less than maximum width of shell.
- submesothyridid** (foramen). Pedicle opening located partly in ventral umbo, but mainly in delthyrium (Fig. 90,C).
- subperipheral rim.** Elevation of secondary shell concentric to margin of valve and just within it.
- subplectolophous** (lophophore). Plectalophous lophophore in which there is an incipient median coil. [Muir-Wood]
- subspondylial chamber.* *See* umbonal cavity.
- subterebratulid** (posterior margin). Posterior margin considerably less than maximum width of shell, but not strongly curved.
- sulcate** (folding). Form of alternate folding with brachial valve bearing median sulcus and anterior commissure median sinus (preferably not termed inverted stage) (Fig. 65,2).
- sulcificate** (folding). Form of alternate folding

- with brachial valve bearing median fold indented by shallower median sulcus (Fig. 65,6).
- SULCUS.** Major depression of valve surface, externally concave in transverse profile and radial from umbo.
- supporting plates* (of orthoids). See brachiophore bases.
- supporting septum** (of hemispondylium). Median septum attached to floor of thecideacean pedicle valve and supporting concave plates of hemispondylium.
- supra-apical foramen.** Pedicle foramen initially located in ventral umbo away from apex of delthyrium.
- symbolothyridid** (pedicle opening). Pedicle opening shared by both valves.
- symphytium.** Deltidial plates fused dorsally or anteriorly from pedicle foramen and lacking median line of junction.
- syndeltarium.* See deltidial cover.
- syrinx.** Tube of secondary shell medially located on ventral side of delthyrial plate and split along its ventro-anterior surface (Fig. 121).
- taleola** (pl., *taleolae*). Cylinder of granular calcite in axial region of some pseudopunctae (Fig. 73).
- taxolophous lophophore.* Rudimentary lophophore with filamentar appendages not completely encircling mouth.
- teeth.** See hinge teeth.
- teeth ridges.** Linear elevations bounding delthyrium laterally, representing growth track of hinge teeth and commonly forming low elevations on internal surface of cardinal area in absence of dental plates.
- telae** (sing., *tela*). Pair of pointed terminations of beak ridges projecting into and beyond pedicle opening, formed by apical migration of pedicle.
- terebrataliiform** (loop). Type of dallinid loop or growth stage consisting of long descending branches with connecting bands to median septum, then recurving into ascending branches which meet in transverse band; morphologically similar to terebratelliform loop (Fig. 110,5). [Elliott]
- terebratelliform** (loop). Type of terebratellid loop or growth stage consisting of long descending branches with connecting bands to median septum, then recurving into ascending branches which meet in transverse band; morphologically similar to the terebrataliiform loop (Fig. 111). [Elliott]
- terebratulid stage* (of folding). See sulcificate.
- terebratulid* (posterior margin). Strongly curved posterior margin much less than maximum width of shell.
- terebratuliform** (loop). Short, typically U- or W-shaped loop found in most terebratulaceans (Fig. 105,5).
- terebratuliniiform** (loop). Short loop in which crural processes are fused medially to complete ring or boxlike apparatus (Fig. 105,7).
- THICKNESS.** Maximum dimension normal to length and width (Fig. 59,B).
- tichorhinum.** Small, suboval chamber, with or without median partition, formed by medially directed struts arising from dental plates converged on to median septum in spiriferoid pedicle valve; probably accommodated base of pedicle (Fig. 120).
- tongue.* See linguiform extension.
- torynidium.* See camarophorium.
- track.** See muscle track.
- trail.** Extensions of shell in either valve anterior to visceral disc (Fig. 74). [Muir-Wood]
- transmedian muscles.** Pair of muscles in some Lingulida anterior to umbonal muscle; one muscle originating on left side of pedicle valve rising dorsally to be inserted on right side of brachial valve, second muscle originating on right side of pedicle valve and inserted on left side of brachial (Fig. 28).
- transmuscle septa.** Assemblage of narrow elevations comprising one median and 2 pairs of diverging laterals associated with strophomenacean dorsal adductor field.
- transverse band.** Connecting lamella joining posterior ends of ascending branches of loop (Fig. 111).
- transverse delthyrial plate.* See delthyrial plate.
- transverse plate* (of spiriferoids). See delthyrial plate.
- transverse plate* (of stringocephalacean loop). See echmidium.
- trocholophe.** Lophophore disposed as ring surrounding mouth, bearing either single row of unpaired (or more rarely double row of paired) filamentar appendages (Fig. 106,A').
- trocholophous** (adj.). Pertaining to trocholophe.
- trocholophus* (noun). See trocholophe.
- troccoconate.* Brachia coiled parallel with plane of symmetry.
- trough.* See hinge trough.
- tubercle.** Any fine, low, rounded protuberance on either surface of valve, irrespective of origin (Fig. 73).
- UMBO.** Apical portion of either valve containing beak (Fig. 59,B).
- umbonal angle.** See apical angle.
- umbonal blade.** Part of primary lamella of spirulum extending between lateral branch of jugum and distal end of crus (Fig. 108).
- umbonal chambers.** Pair of posterolaterally located cavities in either valve; in pedicle valve bounded by dental plates (cardinal buttress in trimerellids) and shell walls; in brachial valve limited medially by crural plates (or homologues) and shell walls (Fig. 101).
- umbonal muscle.** Single muscle occurring in some Lingulida, thought to be homologous with posterior adductors; consists of 2 bundles of fibers, posteriorly and slightly asymmetrically placed (Fig. 28).

- umbonal slopes.** Region of shell surface adjacent to umbo. [Muir-Wood]
- uniplicate** (folding). Form of alternate folding with pedicle valve bearing median sulcus and anterior commissure median plica (Fig. 65,3).
- uniseptum.** *See* septum.
- unisulcate.** *See* sulcate.
- unpaired median muscle scar.** Scar of attachment of base of pedicle to ventral floor; *see* pedicle muscle scar.
- varix** (pl., *varices*). *See* growth line.
- vascula** (sing., *vasculum*). Any identifiable branches of mantle canal system.
- vascula antemyaria.** Pair of mantle canals in brachial valve located between *vascula media exteriora* and *vascula myaria exteriora* (Fig. 134).
- vascula arcuata.** Any mantle canals which are curved subparallel with lateral or anterior margin of shell and which peripherally give off *vascula terminalia*.
- vascula cardinalia.** Posterior branches, subparallel with posterior margin of reduced *vascula cruralia*, commonly in digitate condition (Fig. 134).
- vascula cruralia.** Posterolaterally located pair of mantle canals in dorsal mantle of articulate brachiopods, into which gonads were inserted; varying from saccate to pinnate in outline (Fig. 134).
- vascula dentalia.** Pair of posteriorly located mantle canals in pedicle valve of articulate brachiopods into which gonads were inserted (Fig. 134).
- vascula genitalia.** Mantle canals of articulate brachiopods which contain gonads; may consist of *vascula dentalia* and *vascula spondyliaria* in pedicle valve and *vascula cruralia* and *vascula cardinalia*, if developed, in brachial valve.
- vascula intermyaria.** Posteromedian parts of *vascula myaria*, segments passing between anterior and posterior adductor scars, distal continuations of which form *vascula myaria exteriora*.
- vascula lateralia.** Laterally located pair of mantle canals developed in both valves of inarticulate brachiopods (Fig. 21, 138).
- vascula media.** Pair of mantle canals in either valve, medially located, projecting anteriorly from body wall (Fig. 134).
- vascula media exteriora.** Lateral branches from bifurcated *vascula media*.
- vascula media interiora.** Inner, medianly located branches of bifurcated *vascula media* (Fig. 134).
- vascula myaria.** Simple or branched pair of mantle canals arising between anterior and posterior adductor muscle scars of brachial valve of some articulate brachiopods (Fig. 134).
- vascula myaria exteriora.** Anterior continuations of *vascula intermyaria* outside adductor muscle scars (Fig. 134).
- vascula myaria ventri.** *See* *vascula spondyliaria*.
- vascula spondyliaria.** Pair of mantle canals located between *vascula media* and *vascula dentalia* of pedicle valve, receiving gonads (Fig. 134).
- vascula terminalia.** Terminal branches of mantle canals of articulate brachiopods, supplying setae (Fig. 134).
- vascular markings.** Impressions of mantle canals on shell interior.
- vascular sinus.** *See* mantle canal.
- vascular trunk(s).** Any major branches of mantle canal system.
- venter.** Median region of productoid shell between lateral slopes. [Muir-Wood]
- ventral.** Direction toward pedicle valve from brachial valve.
- ventral adjustor muscles.** *See* adjustor muscles.
- ventral adminiculum.** Ventral part of dental plate.
- ventral dental socket.** *See* denticular cavity.
- ventral process.** Median callus of secondary shell underlying pseudodeltidium and projecting dorsally to fit between lobes of cardinal process.
- ventral valve.** *See* pedicle valve.
- ventrally biplicate** (folding). *See* antiplicate.
- ventribiconvex.** Both valves convex, pedicle valve more strongly so than brachial.
- vertical plate** (of stringocephalaceans). Plate of secondary shell more or less in plane of symmetry and borne on echmidium.
- vertical zone.** Part of valve secreted normal to commissure plane.
- vestibule.** Subcylindrical prolongation of pedicle valve dorsal of brachial valve.
- virgate** (hinge plates or crural bases). Straight and erect. [Muir-Wood]
- visceral area.** Part of shell enclosing body cavity.
- visceral cavity.** *See* body cavity, also used to include both true body cavity and mantle cavity of productoids.
- visceral disc.** Part of shell posterior to geniculation.
- visceral foramen.** *See* dorsal foramen.
- WIDTH.** Maximum dimension normal to plane of symmetry (Fig. 59,A).
- xenidium.** *See* pseudodeltidium.
- zeilleriid stage** (of folding). *See* bilobate stage.
- zeilleriid** (loop). Having long loop, not attached to dorsal septum in adult. [Muir-Wood]
- zygidium.** Collar-like structure uniting lateral ridges on dorsal side of cardinal process and functioning like lophidium in some productoids. [Muir-Wood]
- zygophe.** Lophophore in which each brachium consists of straight or crescentic side arm bearing 2 rows of paired filamentar appendages.
- zygolphous** (adj.). Pertaining to zygophe.
- zygolphus** (noun). *See* zygophe.