MORPHOLOGY

ALWYN WILLIAMS[1], C. HOWARD C. BRUNTON[2], and DAVID I. MACKINNON[3]
[[1]University of Glasgow; [2]The Natural History Museum, London; [3]University of Canterbury, New Zealand]

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. 283). The valve that accommodates most, if not all, of the pedicle is referred to as the **ventral valve;** it is typically larger than the opposing **dorsal valve.** These terms are preferred to pedicle and brachial respectively as they describe the orientation of the shell relative to the body axis and facilitate reference to the disposition of its various features. Dimensions indicating shell size, outline, and profile are conventionally taken in the manner shown in Figure 283.

The growth of the brachiopod valve, subsequent to the secretion of the protegulum, may proceed in three different ways (Fig. 284; THOMSON, 1927). In such inarticulated brachiopods as discinids, deposition continues around the entire margin of the protegulum, which, as a result of this holoperipheral growth, maintains a position more or less at the center of the adult valve (Fig. 284.1a–b). In other inarticulated species like the lingulids, although the posterior margin is thickened by some growth, nearly all the new shell is added to the lateral and anterior margins (hemiperipheral growth) so that the protegulum remains in a posteromedian position (Fig. 284.3a–b). The third type of growth affecting inarticulated forms (e.g., some acrotretoids), mixoperipheral, is a variant of holoperipheral growth in which the posterior surface of a valve is inclined anteriorly toward the other valve (Fig. 284.2a–b). Such a surface has been called a palintrope (THOMSON, 1927), 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 preeminently characteristic of articulated brachiopods (Fig. 284.2a–b), especially in the definition in both valves of a planar or curved triangular area (**cardinal area**) subtended between each apex and the posterior ends of the lateral margins (cardinal extremities) (Fig. 283). 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 (Fig. 285; RUDWICK, 1959) and the cardinal areas of these shells are referred to 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 (commissure) between the anterior and lateral margins of the valves (Fig. 283). As can be seen in Figure 285.3, the disposition of interareas relative to the plane of commissure (the normal plane of RUDWICK, 1959) may vary by more than 180°. The most common 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 of holoperipheral growth. Among wide-hinged orthides, strophomenides, and spiriferides, the interareas form obtuse-angled triangles; but extreme lateral reduction of the hinge

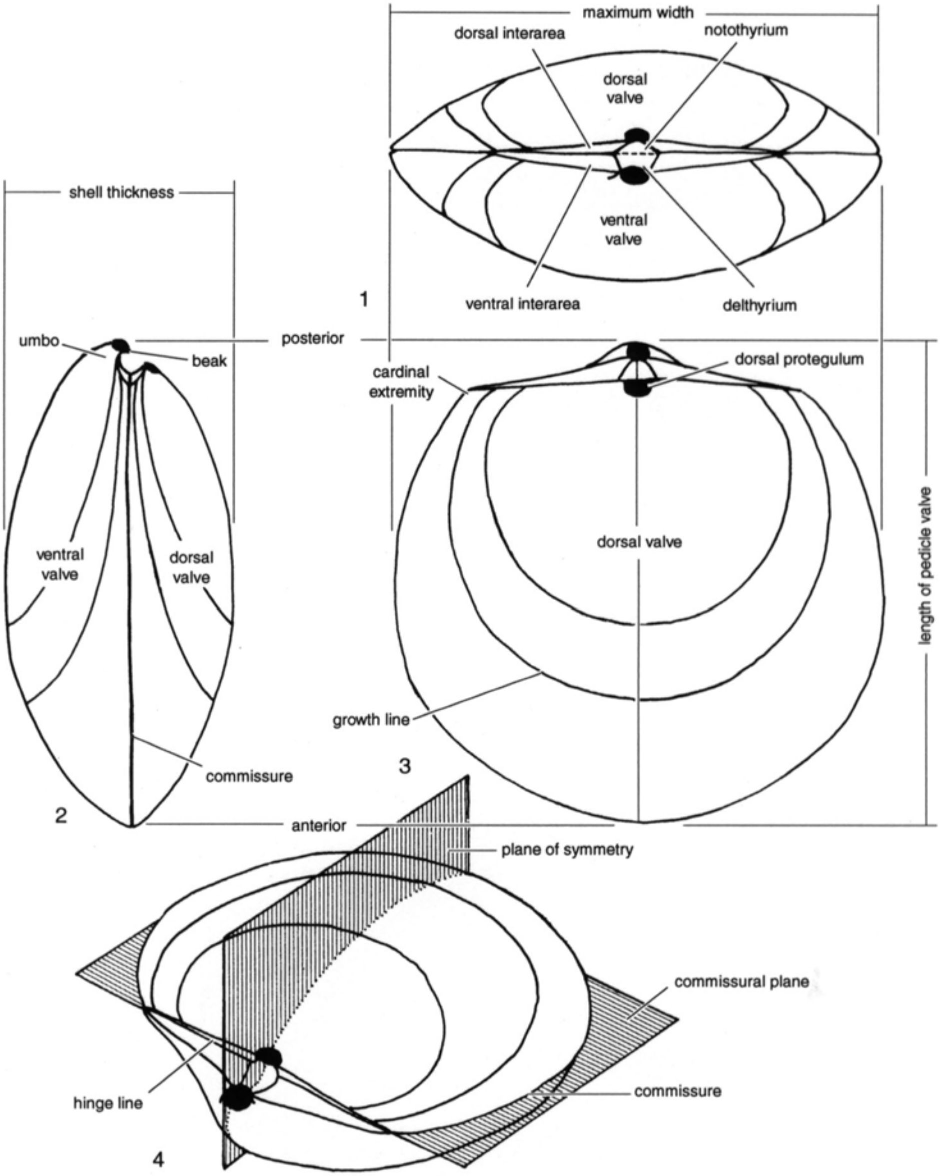

FIG. 283. External features of generalized enteletoid brachiopod seen in *1,* posterior, *2,* left lateral, *3,* dorsal, and *4,* dorsolateral views (Williams & Rowell, 1965b).

line led to rostrate shells like *Perditocardinia,* in which the apical angle of the interareas is narrowly acute. A conical ventral valve, due to excessive forward growth of its interarea, is characteristic of a number of genera (e.g., *Onychotreta, Scacchinella, Syringothyris*), whereas a suppression of forward growth, as in productoids, led to linear interareas and hemiperipheral expansion of the dorsal valve.

Rostrate shells are also characteristic of astrophic (nonstrophic) terebratulides, rhynchonellides, and atrypoids, in which homologues of the interareas are greatly reduced or absent and homologues of the hinge lines are

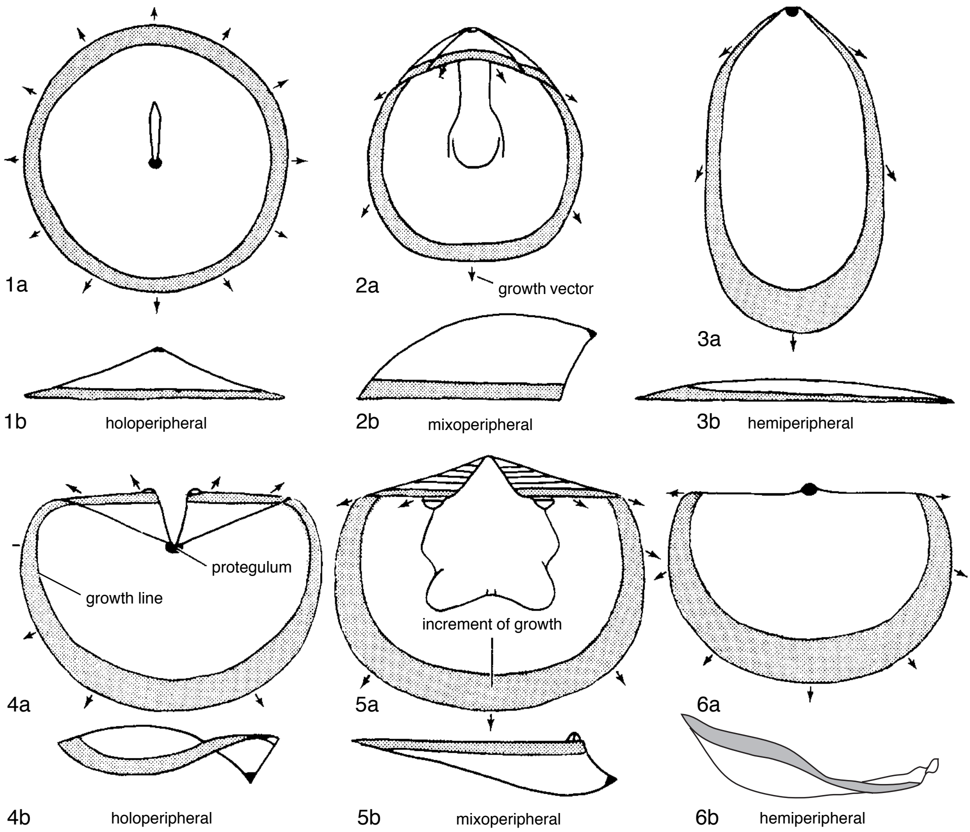

Fig. 284. Nature of shell growth as typified by holoperipheral increase in ventral valves in ventral and lateral views of *1, Orbiculoidea* and *4, Plaesiomys;* mixoperipheral increase in ventral valves in dorsal and lateral views of *2, Apsotreta* and *5, Dinorthis;* and hemiperipheral increase in dorsal valves in dorsal and lateral views of *3, Lingula* and *6, Productus* (adapted from Williams & Rowell, 1965b).

short and curved, so that their traces intersect only the hinge axis (Fig. 285). Rudwick (1959) used 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 ventral valve of the astrophic shell (i.e., most of the cardinal margin as understood by Rudwick, 1959), is no more an integral part of the hinge line than are the notothyrial edges of a strophic dorsal valve. 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 (1959) are valid.

Irrespective of the different types of growth, the protegula and larval shells occupy the apices (or beaks) of the valves, and the region immediately around the apex is referred to as the **umbo** (Fig. 283). 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 articulated brachiopods, immediately beneath apices of the valves, are notched by a pair of triangular openings—the **delthyrium** of the ventral valve, which

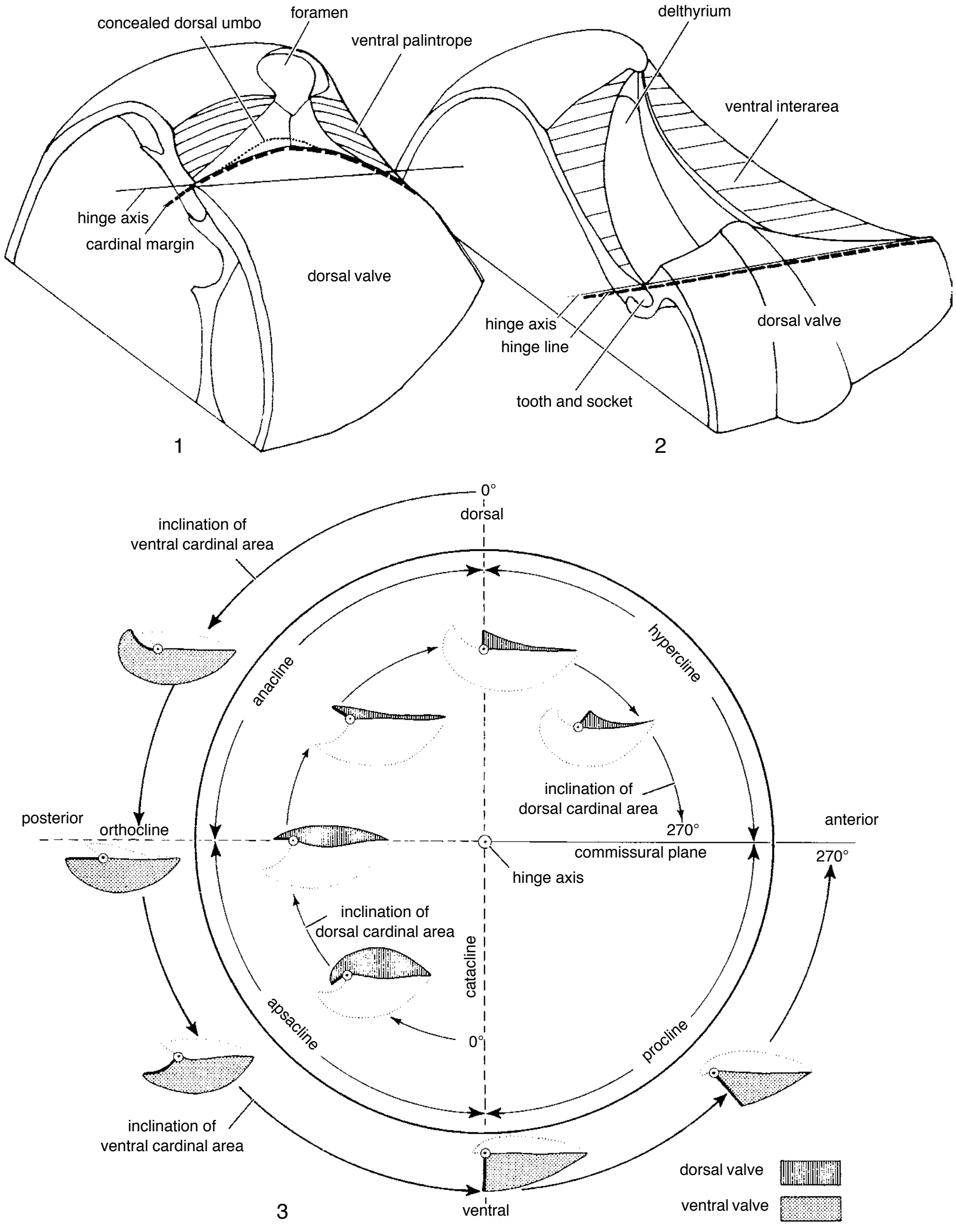

FIG. 285. Posteromedian regions of *1,* astrophic (nonstrophic) and *2,* strophic shells, with *3,* a chart showing the various attitudes of cardinal areas about the hinge axis relative to the commissural plane (Williams & Rowell, 1965b).

normally accommodates the pedicle, and the **notothyrium** of the dorsal valve, which usually is filled with the attachment base (cardinal process) for the dorsal ends of the diductor muscles (Fig. 283). Both of these openings may be partially or completely covered by shell outgrowths, as described below.

The posterior surface of the inarticulated valve may be completely unmodified and comparable with the anterior and lateral slopes, as in the majority of cranioids (Fig. 286.1). More commonly some differentiation occurs, especially in the ventral valve. The simplest modification is some form of opening such as a notch or a slit for the pedicle as in discinids (Fig. 286.2), while a flattened surface (**pseudointerarea**) on the posterior margin of either valve is characteristic of many groups (Fig. 286.3–286.5). Thus, in the paterinides the pseudointerarea of the ventral 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 partly covered by a homeodeltidium. The ventral pseudointerarea of linguloids, in contrast, is approximately orthocline in disposition and the two triangular propareas flank a pedicle groove. These basic patterns, with minor modifications, also occur in other inarticulated groups and can involve the posterior margin of the dorsal valve. An orthocline or anacline dorsal pseudointerarea, which may be divided medially as in many acrotretoids, 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. 287). Ideally, then, there are three components of growth relative to the median and commissural planes of the shell, and vectors of growth, traced on the shell surface from the protegulal 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 ventral valve is not only larger in outline but also deeper than the dorsal valve, although every conceivable variation in this relationship was attained during brachiopod evolution. Thus among the strophomenidines, chonetidines, and productidines, the more usual adult profile was concavoconvex, that is, with a dorsal valve becoming concave beyond the protegulal node and the ventral valve continuing its initial convexity (Fig. 287.5). A reversal in growth direction was also common, so that the biconvexity of the protegulum was modified to a concavoconvex relationship in young shells, which in turn gave way to a convexoconcave attitude

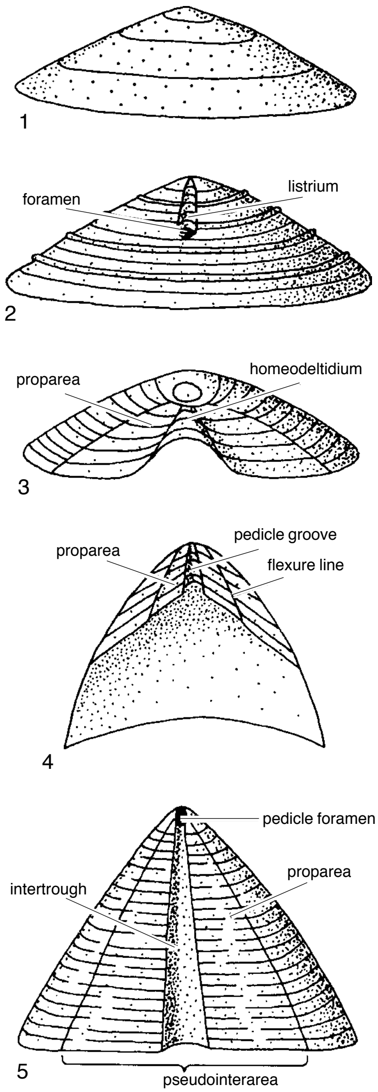

FIG. 286. Modifications of posterior sector of ventral valve of some inarticulated brachiopods; *1,* cranioid (*Pseudocrania*); *2,* discinoid (*Orbiculoidea*); *3,* paterinide (*Paterina*); *4,* linguloid (*Lingulella*); *5,* acrotretoid (*Prototreta*) (Williams & Rowell, 1965b).

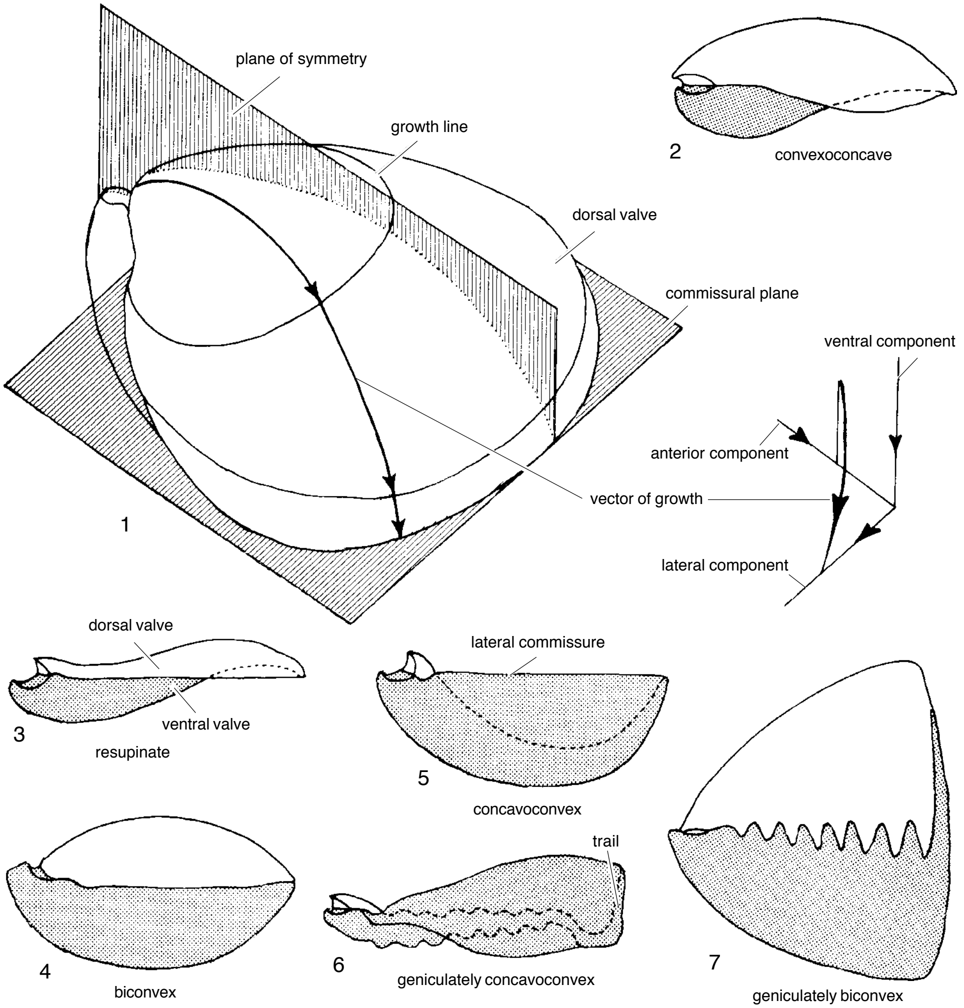

FIG. 287. *1,* Components of growth in brachiopod shells, with *2–7,* illustrations of various types of lateral profiles; the growth line marks the course of a growth band; the vector of growth traces a growth zone (Williams & Rowell, 1965b).

during adult stages of growth. This type of growth is known as **resupination** (Fig. 287.3). 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. 287.7), or in the same direction to define a corpus, commonly with an internal confining ridge (submarginal ridge) and a trail (Fig. 287.6). The corpus is that part of the shell occupied by the body and lophophore; it does not include narrowly separated peripheral areas such as the ears and trails of many strophomenides or the flanges of many athyridines. Trails may be directed dorsally or ventrally and may even reverse direction as in leptaenids and some productidines.

A common modification of the profile of inarticulated 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 in the acrotretid ventral valve and the discinid dorsal valve. This profile is very much less common in the articulated brachiopods, the most spectacular being the cone-shaped ventral valve of *Richthofenia,* which encloses a sunken, subcircular dorsal valve.

The brachiopod outline varies greatly, apart from the more orthodox transversely semi-oval, subcircular, elongately oval, and subtriangular appearance of wide- to short-hinged shells. Some of the more bizarre forms include the saucerlike, incurved, or conical ventral valve of the oldhaminidines, with a highly lobed dorsal structure that may have consisted of a vestigial dorsal valve and a large internal plate supporting the lophophore, and the tubelike ventral valve of the productidine *Proboscidella* and the terebratulide *Pygope,* pierced subcentrally by a hole that was sealed off by anteromedian fusion of a deeply indented (emarginate) anterior margin. Both outline and profile of the shell may be considerably modified by radially disposed deformations that display a variety of form and amplitude. The major, radial elevations of the valve surface are **folds** and the complementary major depressions are **sulci**. These broad deformations grade down into minor features (costae, costellae) that are produced in a comparable manner but are normally regarded as part of the ornament and as such are discussed in detail below.

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 (Rudwick, 1959). 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. 288). 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, such deformations do not involve anomalies in the vertical component. Deformations produced in this way have their maximum expression when the valve is strongly convex.

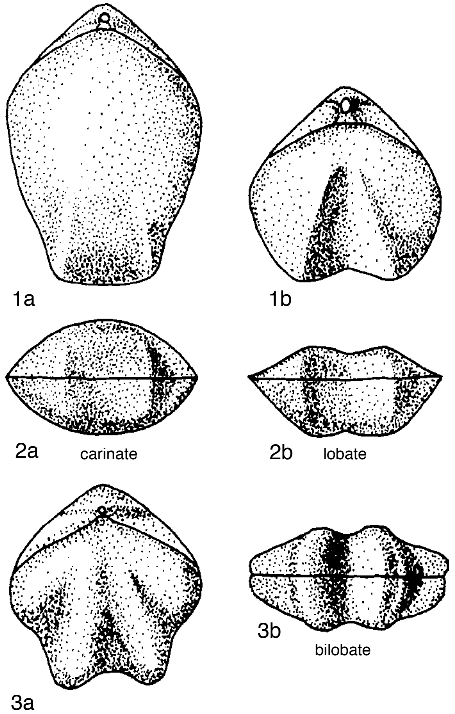

Fig. 288. Opposite folding; *1–3,* dorsal and anterior views of designated types (adapted from Williams & Rowell, 1965b).

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 (sulci). The more common commissural shapes are shown in Figure 289; 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 component either acting alone or in conjunction with localized anomalies of the radial component. If the anomalies are entirely in the vertical

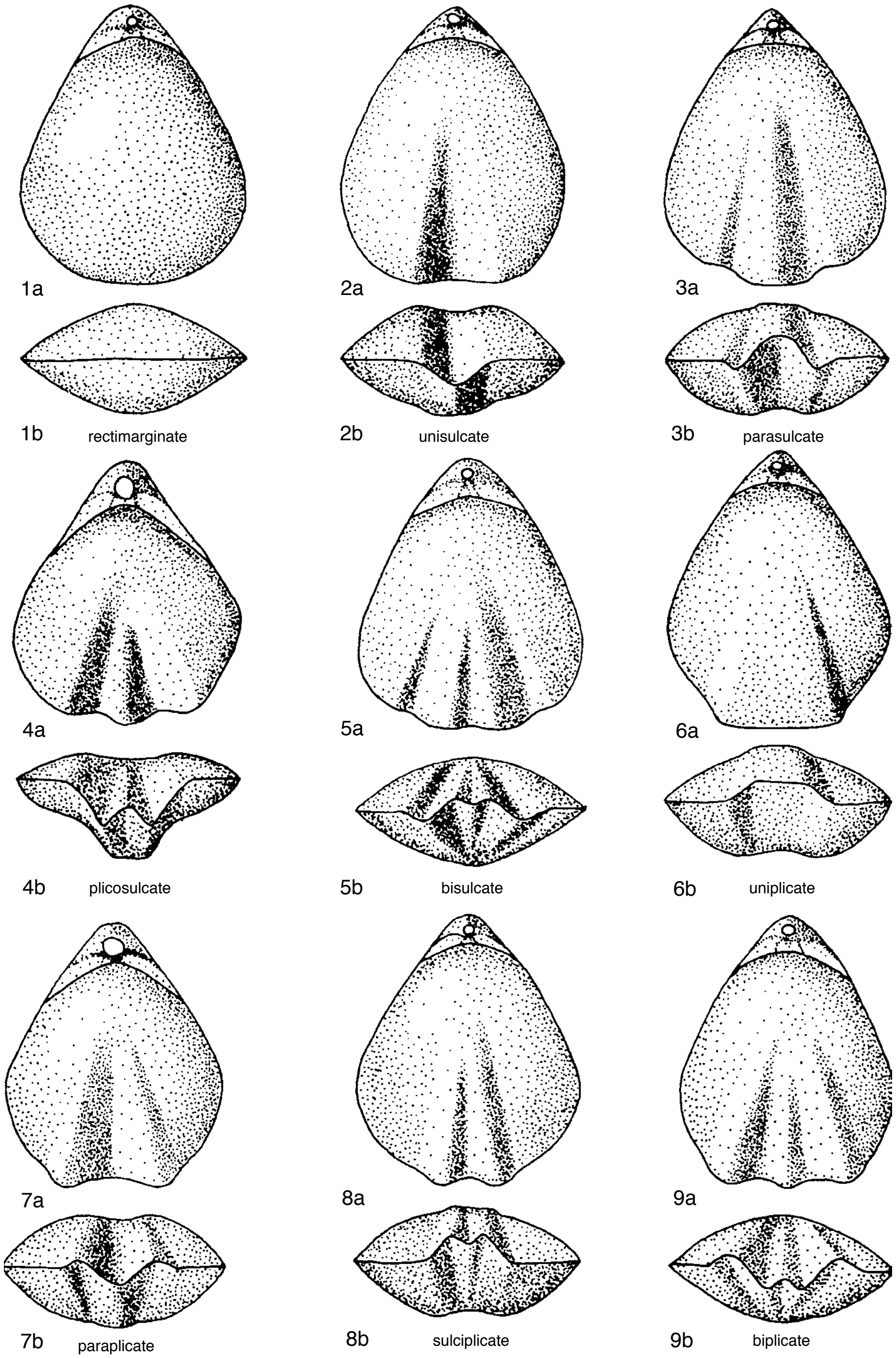

FIG. 289. Types of alternate folding; *1,* rectimarginate; *2–5,* forms of folding that are basically sulcate; *6–9,* forms of folding that are basically plicate (adapted from Williams & Rowell, 1965b). [Note: this figure was corrected from version in Volume 1.]

component, the deformations will have their maximum expression on a plane valve and be less conspicuous on a highly convex one.

ORNAMENTATION

The ornamentation of the brachiopod shell has been defined as any regularly occurring outgrowth, deflection, or nonpathological interruption in growth found on the outer shell surface (Williams & Rowell, 1965b; Williams & others, 1965). This definition covers most of the so-called growth lines on the shell surface even though they generally represent phenotypically controlled changes or breaks in secretion. Such growth lines are not always easily distinguishable from some variants of concentric ornamentation, which are genetically controlled. In effect there are several kinds of breaks or gradient changes posing as growth lines in the conventional sense on the surfaces of brachiopod shells (Hiller, 1988; Gaspard, 1989), and distinguishing them from one another largely depends on being able to gauge their effects on the fabric of the host integument.

Changes in the shell fabric of these concentric microstructures are determined by the mobility of the outer mantle lobe as well as the specificity of its secretory regime. Any temporary retraction or advance of the lobe that does not lead to permanent impairment of shell growth has to satisfy two criteria: no surface of shell accretion is ever exposed by mantle retraction, and organic substrates are always available for biomineral deposition during mantle advance. In typical sequences, illustrated by the impunctate rhynchonellide *Notosaria,* a smooth retraction of the outer mantle lobe does not inhibit continuing secretion so that, for example, a resultant ledge of primary shell is covered by a folded sheet of entire periostracum (reflection). A rapid retraction of the outer mantle lobe, on the other hand, is accompanied by the simultaneous secretion of a new outer bounding membrane, which acts as a wrapping to the inner edge of the primary layer (regression) (Fig. 290). The wrapping is probably proteinaceous and acts as a sealant as well as an organic slide for the regression. When readvance of the outer lobe takes place (transgression), the wrapping serves as a substrate on which cells apparently restart secretion at that phase of the regime where they left off. Accordingly new primary shell is seeded on that part of the wrapping covering the old layer, the inner bounding membrane of the periostracum on that part of the wrapping coating the inner zones of the periostracum, and so on (Williams, 1971a).

The distinctiveness of the fabric associated with mantle reflection, regression, and transgression helps to identify three different kinds of growth lines. Growth banding, which is measured in nanometers, may be seen on external shell surfaces (Fig. 291.1) but is as clearly and, indeed, more frequently displayed in sections of the shell (Fig. 291.2–291.4). Banding represents rhythmic, usually diurnal, changes in the rate of shell secretion (or in the proportion of biomineral and organic constituents) and is an expression of momentary growth (Rudwick, 1959; Westbroek, 1967). Any surface relief caused by growth banding is never more than small changes in gradient.

Growth banding may be interspersed with periodic sets of accentuated growth lines consisting of undercut microscopic ridges, which are usually measured in microns. Their inner sides (as well as their outer ones) are covered by an entire periostracum, which has been smoothly retracted. These concentric microstructures may even have been secreted slowly enough to be isoclinal folds (with cores of primary shell about axial planes inclined posteromedially). Such growth reflections are likely to represent seasonal changes in the environment.

Growth disturbances are induced by a sudden, traumatic interference with shell growth, which stimulates a rapid retraction of the lobe and even of the contiguous zone of the mantle proper so that the proteinaceous sheet secreted during regression may

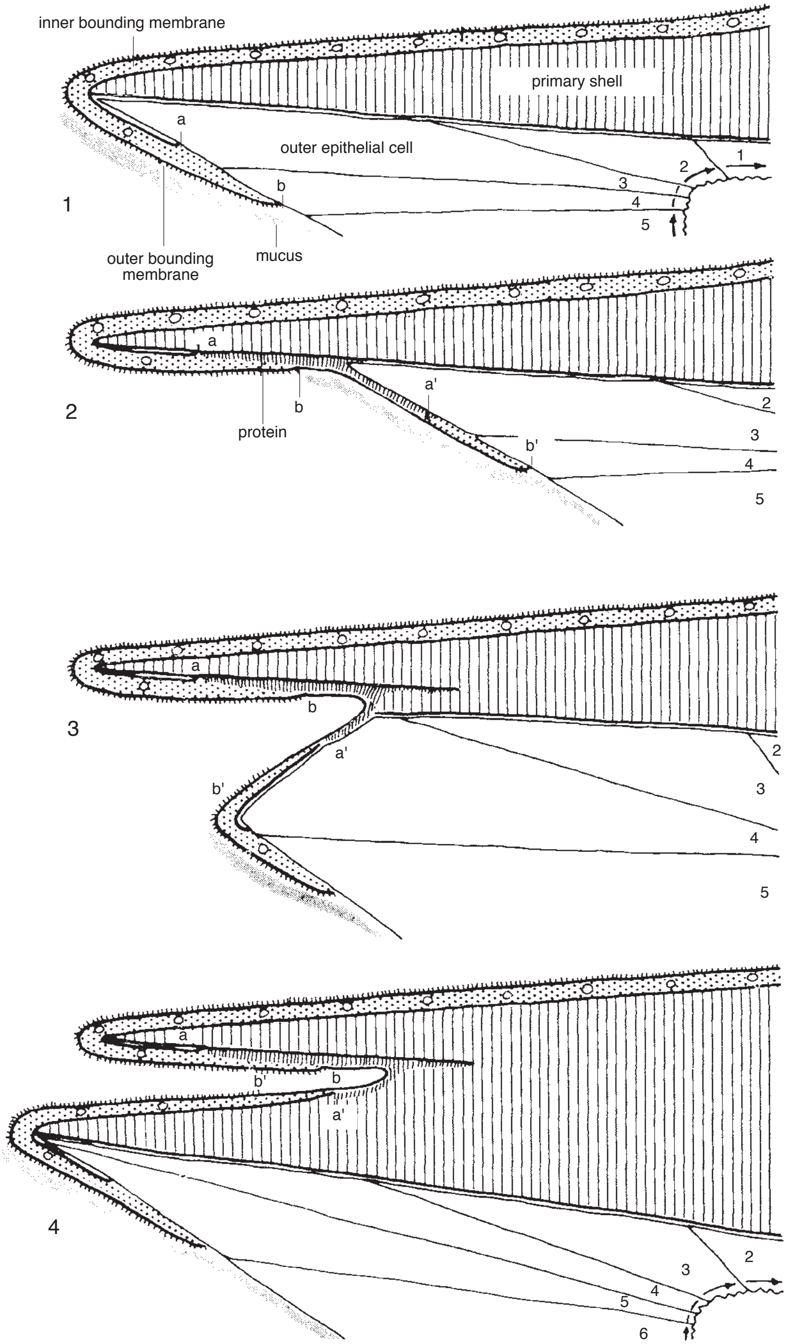

FIG. 290. Formation of a regression (a–a') in the periostracum of recent *Notosaria nigricans* (SOWERBY), shown embedded in primary shell in *4; 1,* sudden retraction of the outer mantle lobe from its normal depositional attitude and *2,* the concomitant secretion of the outer bounding membrane and a sealing proteinaceous layer before *3,* forward movement of the lobe and the resumption of normal deposition (Williams, 1971a).

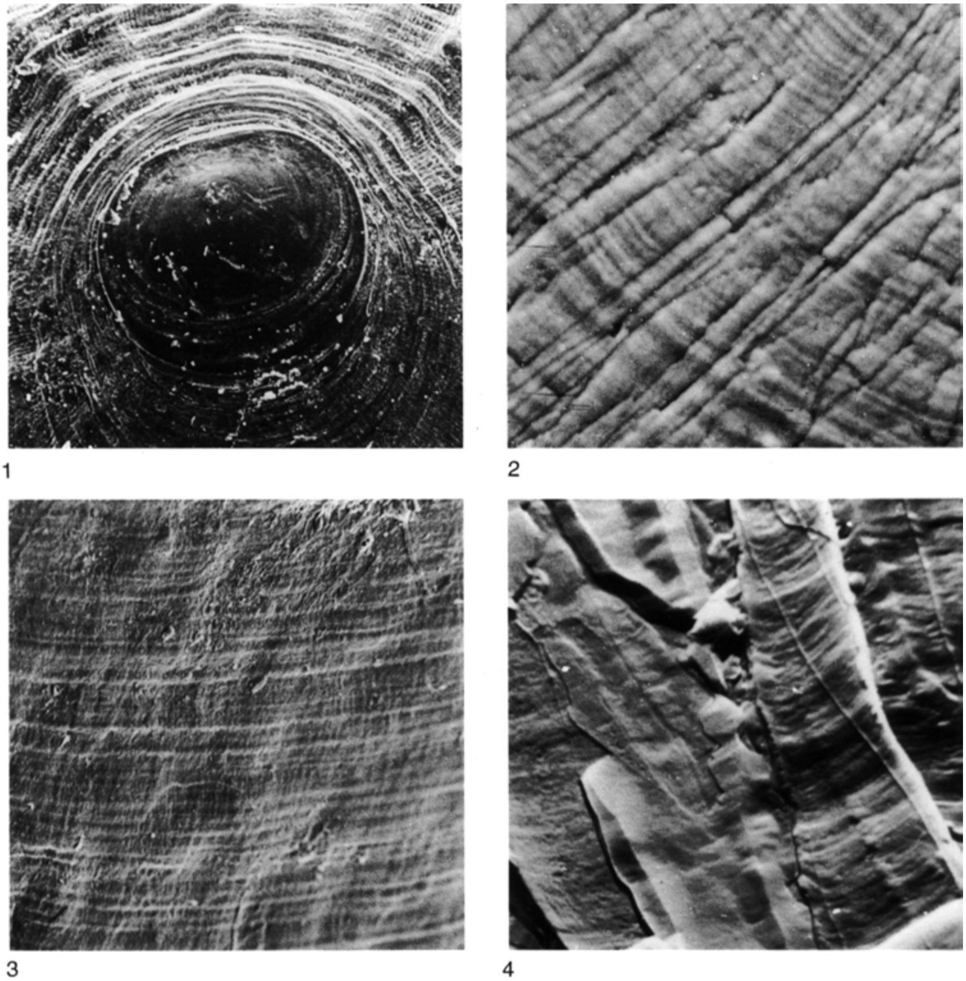

FIG. 291. Features of incremental growth; *1,* growth disturbance marking the junction of the central, dark, larval shell and surrounding juvenile shell (with growth banding) of the dorsal valve of recent *Discina striata* (SCHUMACHER), ×80; *2,* etched section showing growth banding in the primary shell of recent *Lacazella mediterranea* (RISSO), ×2,600; *3,* growth banding on exterior of recent *Calloria inconspicua* (SOWERBY), ×235; *4,* growth banding on the laminar laths of the Ordovician *Strophomena oklahomensis* COOPER, ×2,600 (new).

intrude deeply into the secondary shell. These concentric growth disturbances are randomly distributed on the shell surface as they are the effects of such haphazard extraneous factors as predatory attacks and storms.

All three kinds of growth lines are frequently seen on the surfaces of mature shells and may be confused with genetically controlled, concentric microstructures. Thus the junctions between juvenile and larval or protegular shells on the external surfaces of organophosphatic and articulated brachiopods respectively are normally marked by gradient changes and undercut ledges. In living discinids, the larval shell is bounded by a concentric, low, rounded ridge, the rim of the larval halo (CHUANG, 1977). A similar, raised rim commonly delineates the larval shells of fossil lingulides and acrotretides

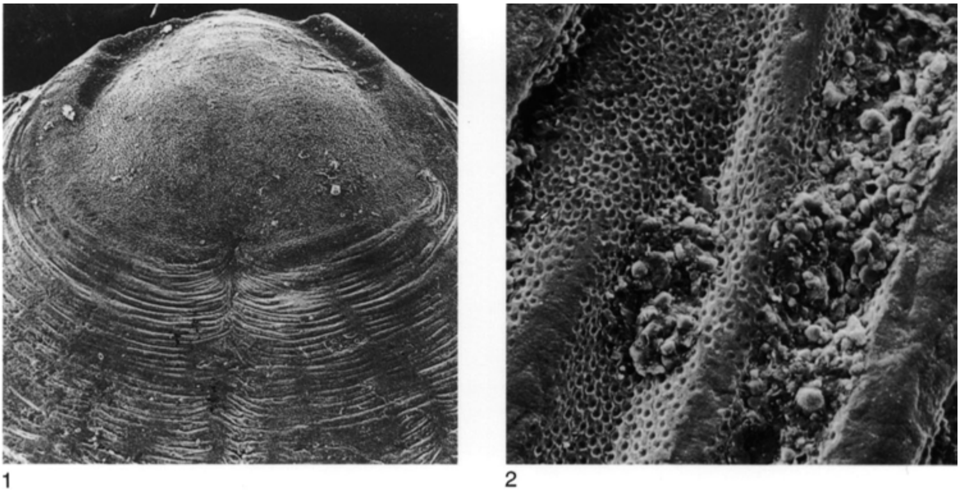

Fig. 292. Concentric microornamentation; *1,* fila deformed into sets of discrete, outwardly convex arcs, and separated from the larval shell by a zone of disturbance on the dorsal valve of an Ordovician acrotretoid sp., ×180 (Williams & Holmer, 1992); *2,* detail of fila bearing the cast of a vesicular periostracum on the dorsal valve of the Carboniferous *Orbiculoidea nitida* (Phillips), ×420 (new).

(Holmer, 1989; Williams & Holmer, 1992), and a change of gradient also occurs at the junction between the protegulum and juvenile shell of articulated brachiopods (Stricker & Reed, 1985b). These raised rims are frequently thrown into relief by the outer perimeter of undercut ledges representing growth disturbances (Fig. 291.1). The rims have been attributed to changes in the rate of shell secretion of differing components (and a consequential imperfect amalgamation of fabric) attending the change to a sedentary mode of life.

Periodically occurring ridges of a comparable nature to the raised rim of the larval shell form a fine concentric ornament (fila), especially on organophosphatic shells (Fig. 292). In acrotretoids, for example, fila resemble parallel-sided anticlines with rounded crests overturned toward the valve margin and may be up to 8 µm or more in wavelength (Williams & Holmer, 1992). In fossil discinids, like *Orbiculoidea,* fila commonly have a greater wavelength (up to 30 µm) but are similar in structure.

All such fila have been deformed by stresses demonstrably set up within the periostracum. They must, therefore, have originated as regular folds in a periostracum being secreted on the outer mantle lobe. These would have been homologous with the impersistent periclines (Fig. 293) developed around the hinge of the marginal fold of the shell of living *Lingula* (Williams, Cusack, & Mackay, 1994). Such folds are filled in by the primary layer and do not affect the secondary shell. The infill of fila would also have been part of the primary layer but with a particular consistency. It would have been sufficiently fine to act as a mold mixture for structures smaller than one micron and, when first secreted, sufficiently plastic to register small-scale folding, presumably preserved by polymerization of the infill. These criteria suggest that the first-formed biomineral coat was a cohesive paste of fine apatitic crystals suspended in a glycosaminoglycans (GAGs) matrix (Williams & Curry, 1991).

Acrotretoid fila anastomose and may become isolated as impersistent undulations. These are indistinguishable from a much coarser, oblique, or concentric wrinkling of the shell surface (rugation) (Fig. 294). **Rugae** are especially characteristic of the strophomenides (*s.l.*) with wavelengths varying from

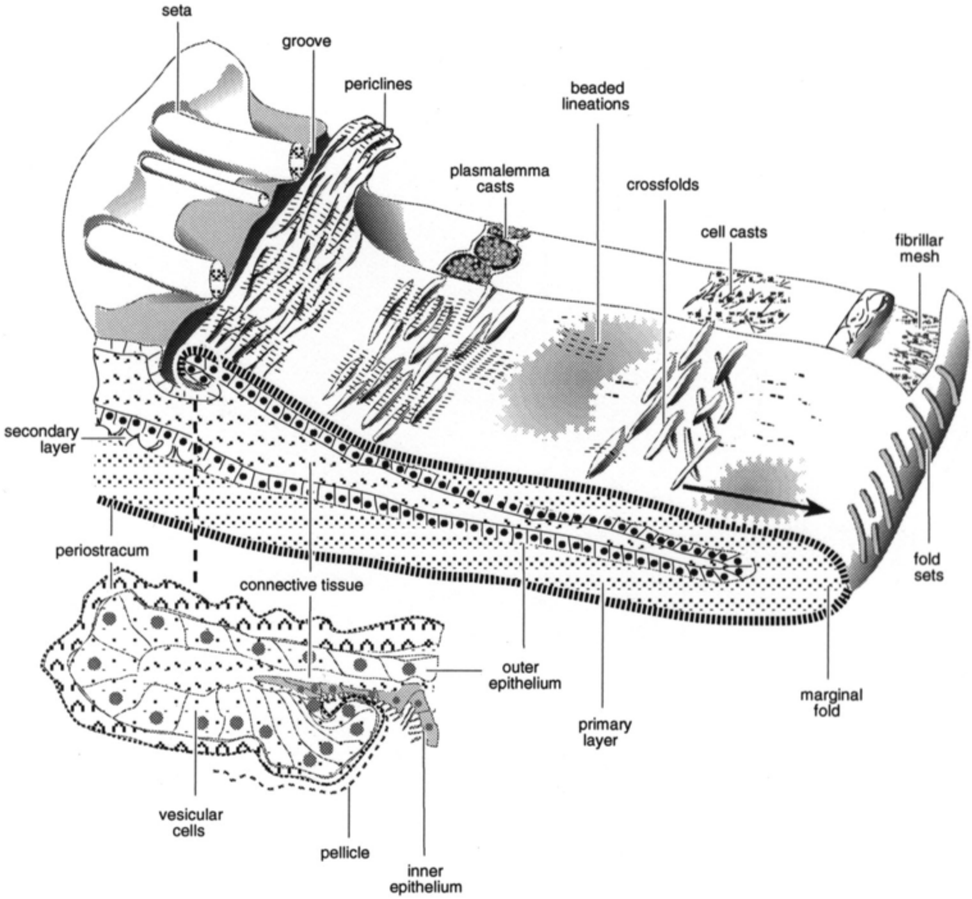

FIG. 293. Stylized block section of the marginal fold of *Lingula anatina* LAMARCK showing the relationship of an expanding mantle and a variously folded integument, unrolling in the direction of the *arrow;* enlargement of the periostracal lobe in the bottom left hand corner (Williams, Cusack, & Mackay, 1994).

about 100 µm (in plectambonitoids) to more than 3 mm in some productoids. Rugae of the coarser range of wavelength are also known rarely in other groups like pentamerides (*Kulumbella*). Rugae may be continuous and concentric, as in *Leptaena,* where they are precursory to the formation of the trail, which may be regarded, in that genus, as an indefinite continuation of the outer face of the last-formed ruga. Rugae may also be impersistent and oblique as in those of *Sowerbyella.* 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 chevronlike or oblique strips. Exceptionally, two or more sets of oblique rugae may develop, intersecting at obtuse or acute angles (e.g., *Bellimurina, Kulumbella*).

Rugae were probably formed by deflection of the mantle edge through an arc of 180° along an axis that was disposed in any direction except that of the radial vector relative to the mantle margin (radial deflections give rise to such features as ribs and folds). The concentric arrangement of *Leptaena* was the simplest condition as 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

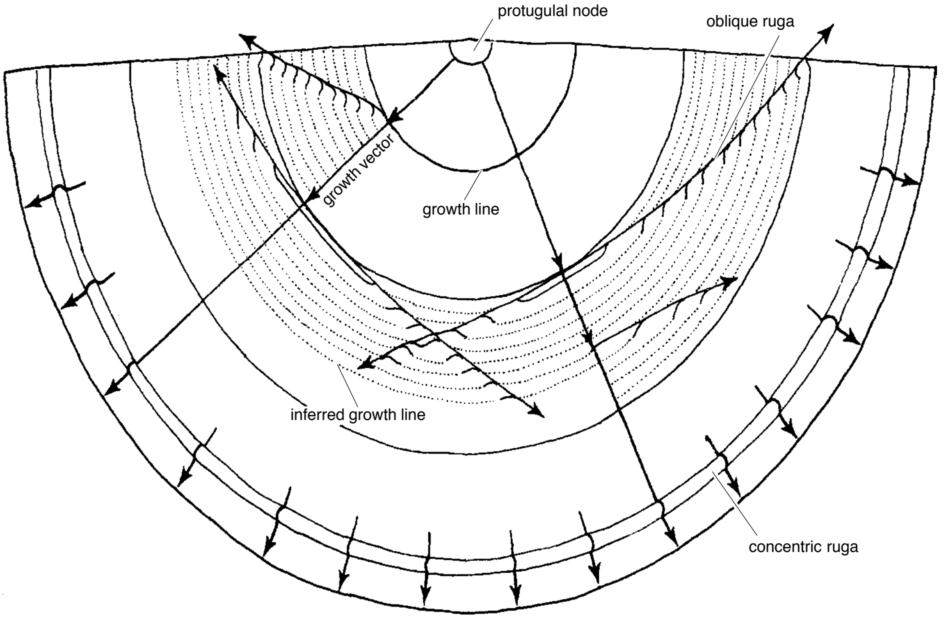

FIG. 294. Diagrammatic illustration of the nature and origin of oblique and concentric rugation (adapted from Williams & Rowell, 1965b).

edges at any point along the margins; and during subsequent growth the deflection was transmitted laterally either in one or both directions along axes traced out by the rugae in a full-grown shell. In the Carboniferous productidine *Vitiliproductus,* a quincuncial cross-rugation arose from a bilaterally symmetrical intersection of rugae, obtusely disposed in more or less paired sets along the hinge line on either side of the umbonal region (BRUNTON & MUNDY, 1988). In either manner, two or more sets of rugae may have developed a complicated pattern of intersections.

An interesting aspect of the assumed homology between rugae and fila is that rugae would have originated as folds of the periostracum around the outer mantle lobe. The folds would have been filled with secreted materials containing enough GAGs to polymerize into perfect casts. This mainly organic subperiostracal infill would have been unlike the almost pure calcitic composition of the primary layer of other articulated brachiopods, which may account for the difficulty in identifying a primary layer in strophomenide shells.

Other kinds of regularly spaced, concentric outgrowths on the shell exterior (lamellae and imbricae) may be composed of secondary as well as primary shell but invariably involve periodic buckling or retraction of the outer mantle lobe. The fine lamellae of many strophomenides (Fig. 295) are regularly spaced overfolds (at intervals of 80 µm to 100 µm and with wavelengths of about 20 µm in the orthotetidine *Xystostrophia*). In most other brachiopod groups (including productidines), lamellae can be extravagantly developed as variably inclined, skirtlike sheets that may be differentially extended as spinose, open tubes along the crests of ribs as in *Glyptorthis* and *Acanthobasiliola* (HILLER, 1988). Regularly spaced lamellae of *Athyris* can extend forward as recurved microfrills more than 300 µm long (Fig. 296.1). They are composed of secondary as well as primary shell and are associated with strongly developed regression surfaces. It is believed that microfrills, when newly formed at the shell margin, acted as baffle chambers for excess detritus in the feeding currents of the mantle cavities of living specimens (ALVAREZ, BRIME, & CURRY, 1987). Other athyridines, like *Pachyplax* (ALVAREZ & BRUNTON, 1990), are ornamented by very coarse lamellae that are composed of a succession of flattened secondary fibers underlying a granular primary layer and are two to four times as thick as the principal secondary succession of the shell (Fig. 296.2). These thick lamellae are homologous with the concentric, knobby protuberances (comae) that give *Bimuria* its gnarled appearance (Fig. 296.3). Regression surfaces are well developed, and the backward-curving comae secreted on them are composed of fibers that become flattened distally into laths forming laminar sheets, which presumably represent an extensively developed primary layer (WILLIAMS, 1970a).

All radial ornamentation (ribs) is due to a persistent or impersistent deflection of the mantle edges along vectors radiating from the junction between the neanic and brephic shell (protegulal node) or the margin of the larval shell, so that every variety of size and shape can be found (Fig. 297). 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 normally arises at the protegulal 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 intercalating between costae at any state during subsequent growth. Defining the terms according to the point of origin of the features precludes their arbitrary use 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 some species (e.g., triplesoids and rhynchonellides), the radial ornamentation may first appear along an arc of growth well beyond the protegulal node, and this pattern is referred to as delayed costation or delayed costellation if first or higher orders of costellae are involved. Certain brachiopods, especially strophomenides, 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 ramicostellate 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*).

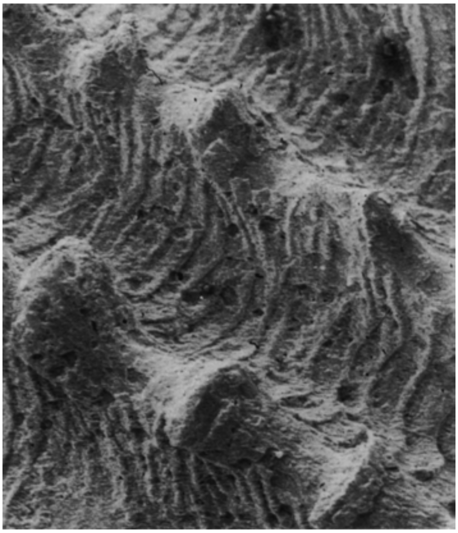

FIG. 295. Finely lamellose, parvicostellate exterior of the Middle Devonian *Xystostrophia umbulacrum* (SCHLOTHEIM) with shell margin to the right of the micrograph, ×55 (new).

The relative origins of costellae in ramicostellate patterns are stable enough to be used for taxonomic purposes. Several attempts have been made to devise a reliable notation. The most effective is that of

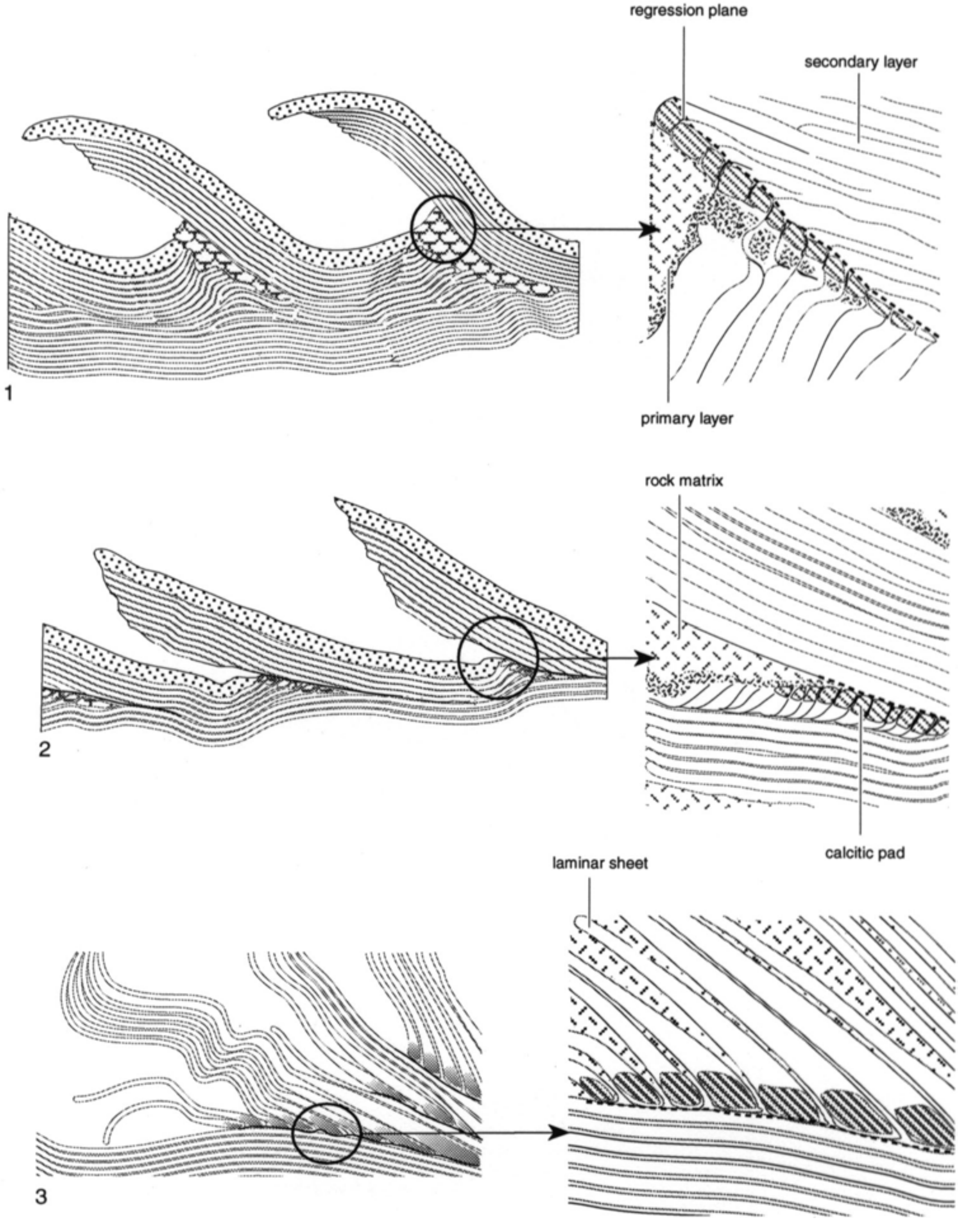

FIG. 296. Stylized structure of the lamellae of Devonian athyrids; *1, Athyris campomanesi* (VERNEUIL & ARCHIAC) (adapted from Alvarez, Brime, & Curry, 1987); *2, Pachyplax elongata* ALVAREZ & BRUNTON (Alvarez & Brunton, 1990); *3,* comae of the Ordovician plectambonitoid *Bimuria* cf. *buttsi* COOPER. Detailed drawings to the right approximately ×500, ×200, and ×400 respectively (new).

BANCROFT (1945). Costae originating at the protegulal node of the right half of the dorsal valve are termed primaries (Fig. 297) and are numbered *1, 2, 3,* and so on, primary *1* (which in the enteletoids arises from the very tip of primary *2*) being nearest the median line and primary *4* farthest away. Secondary costellae, which split off from the primaries,

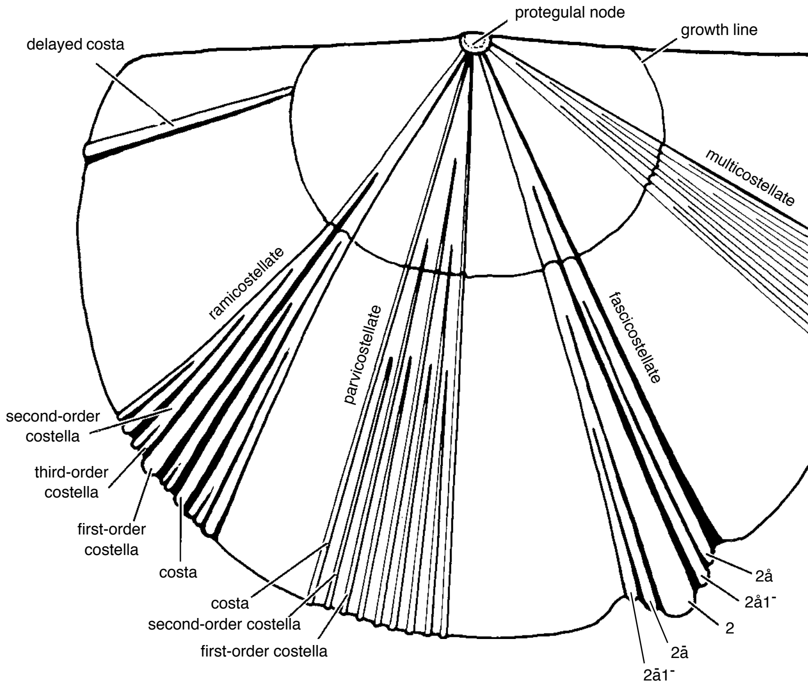

FIG. 297. Diagrammatic illustration of the more important types of brachiopod radial ornamentation; the notation for the order and direction of rib branching in the fascicostellate pattern is explained in the text (adapted from Williams & Rowell, 1965b).

are labelled *a, b, c,* and so on, *a* being the earliest to split off, *b* the next, and so on. Tertiary costellae, which branch from secondaries, are numbered in the same manner as the primaries; and for ribs of higher orders the numerals continue to alternate with the letters so that *1a1a* represents the earliest costella on the earliest tertiary on the earliest secondary on the first primary. Whether a costella branches toward the inside (i.e., toward the median line) or toward the outside of the parent is also important, and the superscript symbols "-" and "o" are used to denote inner and outer branches, respectively, so that $2\mathring{a}1^{-}$ represents a costella arising on the inner side of the first outer branch of the second primary.

There is a correlation between the profile of a valve and the branching of costellae in that ribs tend to split off downslope (WILLIAMS & WRIGHT, 1963). Yet the variability of a complex ramicostellate pattern can be expressed in terms of the earlier branching of about 10 costellae relative to 10 others (WILLIAMS, 1974) and appears to have the statistical validity of a genotypic character facies. The Bancroft notation has also been used to characterize the ribbing patterns of the Upper Ordovician *Diceromyonia* simply in terms of modal sectors (MACOMBER & MACOMBER, 1983). These sectors are composed of all ribs occurring in more than 50 percent of the valves irrespective of their order of branching from primary costae. This method is an alternative approach but is deficient in not taking into account valve size and in eschewing statistical controls. Other ribbing systems used to delineate suprageneric groupings of ramicostellate brachiopods, such as that used by KEMEZYS (1968) for enteletidines, have yet to be subjected to rigorous statistical controls.

The costellate radial ornamentation of some extinct brachiopods is probably related to the distribution of setae along the mantle edge (see chapter on shell structure, p. 272)

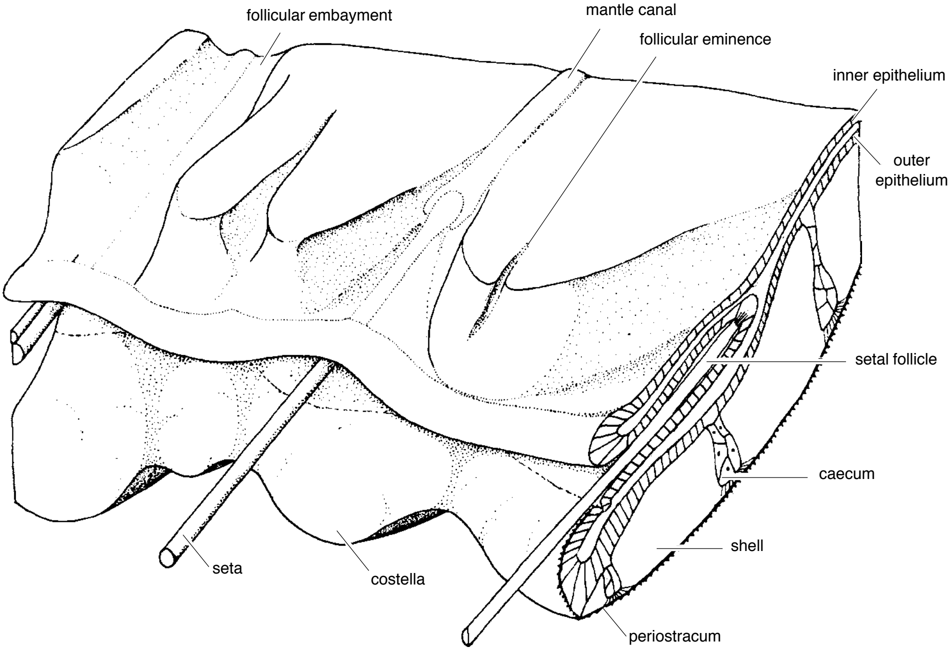

FIG. 298. Inferred relationship between the mantle edge and the shell margin of a typical, finely costellate, endopunctate articulated brachiopod (Williams & Rowell, 1965b).

as is characteristic of such living brachiopods as *Terebratulina* (compare Fig. 298). 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, more 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 outwardly 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 that 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. However, the morphology of the shell margin suggests 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. This occurs just before a new costella, containing the developing embayment, branches off from its parent. 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 intercostellate spaces is quite distinct from that of *Hemithiris,* 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 setal indentations 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, such as those of enteletoids, is so like that of *Terebratulina* that a similar arrangement of setae probably obtained (Fig. 298). A comparable pattern was also characteristic of costate orthidines (*Hesperorthis, Plaesiomys,* and *Orthambonites*) (Fig. 299.1). 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 that is shallower than the groove but almost 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 *Cyrtonella* (Öpik, 1934), it is feasible to assume that follicles occupied at least the median furrows. The arrangements in other costellate orthidines and clitambonitidines seem to have been more primitive in that no well-differentiated eminences, coincident with intercostellate spaces, were developed; and it seems likely that 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 *Hemithiris,* 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 follicular distribution unaffected by the coarser ribbing, as in *Terebratalia.*

In contrast, the parvicostellate ornamentation of the strophomenides 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. 299.2). 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 five or six 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.

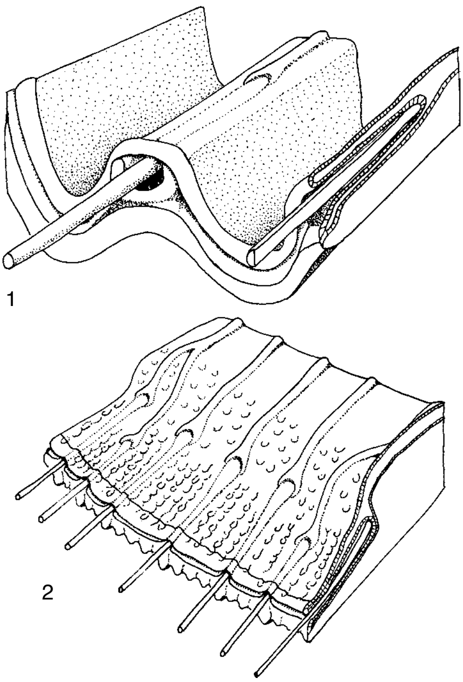

Fig. 299. Inferred relationship between the mantle edge and the shell margin of *1, Hesperorthis* and *2, Sowerbyella* (Williams & Rowell, 1965b).

Some rhynchonellides (*Sphaerirhynchia*), which are highly globose as adults and develop a vertical zone formed when anterior and lateral growth is in abeyance, show an

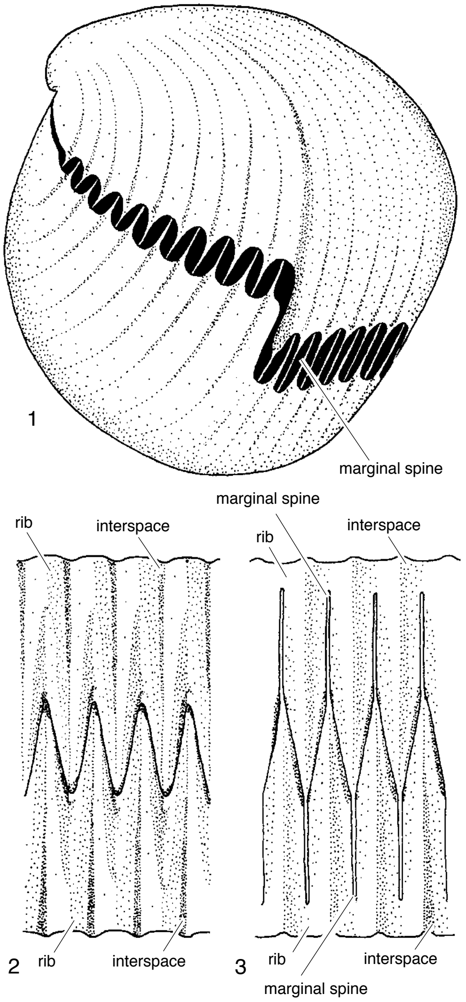

FIG. 300. Marginal spines forming a denticulate commissure of *Sphaerirhynchia; 1,* oblique anterolateral view of open shell showing grille formed by spines; *2,* detail of part of anterior commissure, viewed externally; *3,* detail of part of anterior commissure, viewed internally, showing relationship of spines and interspaces (Williams & Rowell, 1965b).

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 that 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 (Fig. 300; SCHMIDT, 1937).

The postlarval shell of *Discina* is parvicostellate but the valve margins, as those of other recent organophosphatic discinids and lingulids, are free of any grooves to accommodate setae, which are strongly developed in all stocks. In these brachiopods, the edge of a valve is a relatively wide marginal fold (see Fig. 293) of periostracum and a mainly organic primary layer, which together form an elastic cushion for the setae. Even in extinct organophosphatic species, the only traces yet found of a radial ornamentation, which may have been related to setal fringes, are those characteristic of some Paleozoic acrotretides and paterinides. As has been shown in the section on the shell structure of the brachiopod (p. 272), the impersistent radial distributions of dichotomizing arrays of surface pits in *Orbiculoidea* and of sets of nickpoints interrupting the fila of acrotretoids could have been induced by sets of muscles controlling marginal setae (WILLIAMS & HOLMER, 1992). Only the cranioids, which actually lack setae, have grooved internal valve margins (Fig. 301). In the dorsal valve of *Neocrania,* radial grooves and ridges, superficially similar to the eminences and furrows of *Terebratulina* but very much finer (with wavelengths of about 20 µm), are associated with the development of punctation. The punctae are located in the grooves, which increase in number distally by dichotomy of the ridges and become buried proximally in thickened concentric bands of secondary shell. This grooved margin corresponds to the gentler outer slope of the tuberculate subperipheral rim of the ventral valve, which is irregularly channelled. The apposition of these fine structures along the shell margins probably provides *Neocrania* with a crude sieve leading into the mantle cavity.

The brachiopod shell may also be finely to coarsely ornamented by superficial pits (exopunctae) or by outgrowths generally referred to as granules, tubercles, or spines. Superficial perforations are normally limited

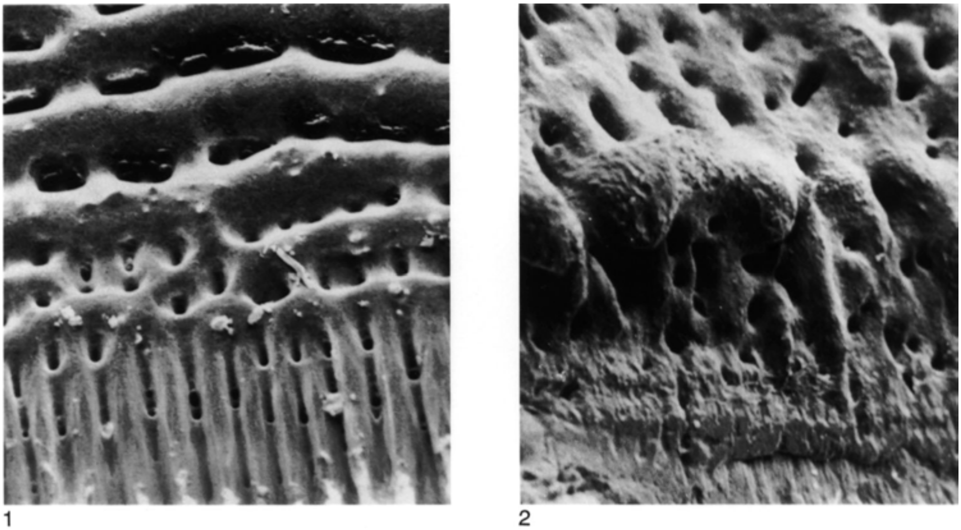

FIG. 301. The internal shell margins (along lower edges of micrographs) of recent *Neocrania anomala* (MÜLLER) showing *1,* the radial grooves of the dorsal valve, ×140, and *2,* the channelled subperipheral rim of the ventral valve, ×70 (new).

to the primary layer and, even when extending into the secondary layer, never penetrate the entire shell. WRIGHT (1981) has distinguished several types of superficial pits, although not all of them are distinctive enough to merit terminological recognition.

Shallow pits are found in widely different brachiopods. They are usually arranged radially as in the enteletoid *Saukrodictya* or in offsetting radiating rows culminating in hexagonal close packing (*Dictyonella*). In general, they tend to be symmetrical and evenly developed, as in the discinoid *Trematis;* but the outer rim may be subdued to give parabolic structures as in the rhynchonellide *Porostictia.*

Even more distinctive pits are relatively deep cylindroid perforations, which give rise to the hollow costellae (**aditicules**) of orthides, as in the impunctate orthoids (*Doleroides, Plaesiomys*) and punctate enteletoids (*Rhipidomella*). Hollow costellae have been interpreted (WILLIAMS & ROWELL, 1965b; WILLIAMS & others, 1965) as incipient spines that were formed by a regularly occurring, inward sag of the mantle edge away from the sharply rounded arches of the principal ribs, while deposition continued and ultimately sealed off the reentrant as a short, oblique cylindrical hollow (Fig. 302). More recently, it has been shown that the sequence of sealing off hollow costellae can be followed at the internal margins of valves where they start as embayments, as in those widely interpreted to be sites of setal follicles (WRIGHT, 1981). It is, therefore, likely that hollow costellae housed setae in their early stages of formation. It is unlikely, however, that the setae persisted to become encased in shell, as they are an integral part of the inner epithelium; and it seems topologically impossible for setae and their lubricating and secreting coats of inner and follicular epithelium to become embedded in a continuously advancing outer mantle lobe without causing major aberrations in shell secretion. The hollow costellae are, therefore, best interpreted as temporary containers of setae that migrated with the advancing mantle edges.

Other smaller, highly inclined pits found perforating the ribs of such orthides as *Plectorthis* and *Paurorthis* are true exopunctae in probably having contained isolated bits of vesicular cells or periostracal plugs as

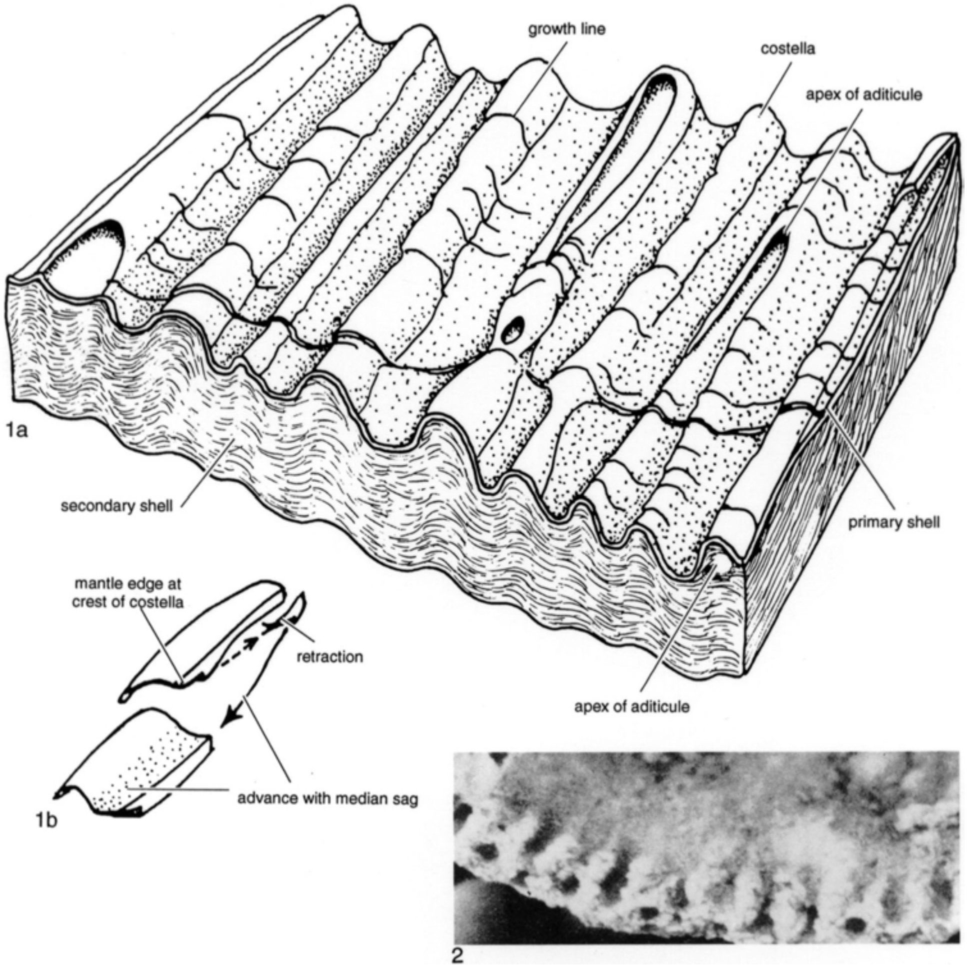

FIG. 302. Growth of hollow costellae (aditicules); *1a,* part of ventral valve of Ordovician *Plaesiomys subquadrata* (HALL) showing the nature of hollow costellae and *1b,* the inferred path of the mantle edge during the formation of an aditicule (Williams & Rowell, 1965b); *2,* internal margin of dorsal valve of Permian *Rhipidomella hessensis* KING showing stages in the sealing off of follicular embayments to form aditicules, ×15 (Wright, 1981).

envisaged in *Punctatrypa* (Fig. 260). There is little possibility of these perforations having accommodated sensory bristles as such structures would have to have been secreted by lobate cells on the basal layer of the periostracum.

The ornamental outgrowths on the external surfaces of brachiopod valves may be nothing more than nodes of excessive shell secretion in the form of fine granules and larger tubercles at the intersections of concentric fila or lamellae and rib crests (see Fig. 297). These range from the solid hooked spines of the terebratulide *Dictyothyris* (Fig. 303) to the densely distributed granules of the orthide *Platystrophia* and the lingulide *Lingulasma.*

Such excrescences are especially characteristic of many spire bearers, and recent studies (GOURVENNEC, 1987, 1989) have shown that their formation involves a distinctive secretory regime (Fig. 304). In such groups the fine ornamentation consists of capillae, which are disposed radially (the eospirifid

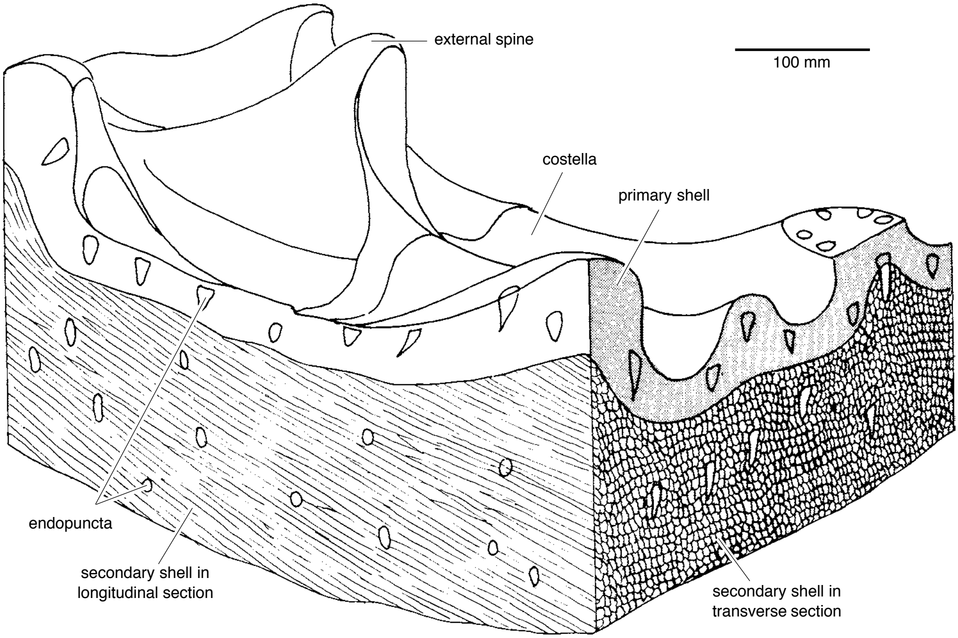

FIG. 303. Block section of ventral valve of Jurassic *Dictyothyris coarctata* (PARKINSON) showing the relationships of external spines with primary and secondary shell layers (Williams & Rowell, 1965b).

type) or pseudoradially (the delthyrid type) when they arise by intercalation in intercostal grooves and diverge onto the flanking costal crests (Fig. 305). Pseudoradial capillae may be superficial (*Maurispirifer*) or variably embedded in the lamellae of the primary layer and can be prolonged as spines (*Paraspirifer*). The spines can be quadrangular in transverse section and deeply grooved (*Elisia*) and are feasibly interpreted as having been secreted by fingerlike extensions of the outer mantle lobe (GOURVENNEC, 1987).

The microscopic spines of ambocoeliids are also outgrowths of the primary layer (BALINSKI, 1975) and can be exaggerated by differential weathering. They may contain impersistent canals like the **double-barrelled spines** of *Phricodothyris* (GEORGE, 1932a), but they are not continuous with perforations of the secondary shell (Fig. 306).

GOURVENNEC and MÉLOU (1990) have recently claimed that the microspinose frills of the well-developed lamellae of such orthides as *Ptychopleurella* are proof of the descent of the microspinose spiriferides from such stocks. The development of frilled lamellae, however, probably in relation to marginal setae, is likely to be as recurrent a theme in brachiopod evolution as any other morphological feature.

The hollow productidine, chonetidine, rhynchonellide, and siphonotretoid spines, which also opened into the shell interior, were formed in a different way from spiriferide spines. Many of these spines must have continued to increase in length throughout the life of the animal and bear growth banding consistent with deposition by discrete generative zones (RACHEBOEUF, 1973). Such increments, however, could have been added only at the distal ends (intussusceptive growth), 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 (WILLIAMS, 1956). Since all spines were first differentiated at the shell margin, it is likely

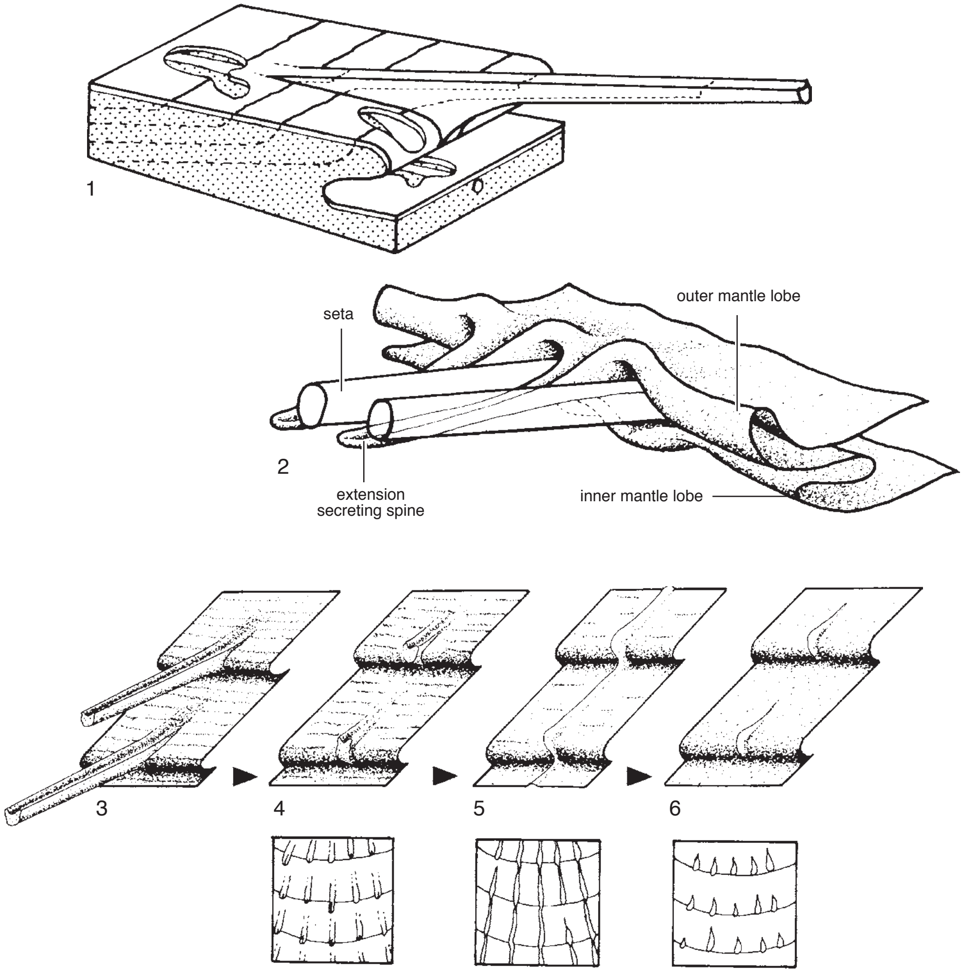

FIG. 304. Growth of delthyrid spines; *1,* stages in the emergence of a spine (shown by *dotted lines* within the stippled layer of secondary shell) and *2,* idealized reconstruction of the secreting mantle (shell and spines removed); *3–6,* stages in the weathering of the shell surface, leading to the development of teardrop-shaped granules on worn fila (Gourvennec, 1987).

that the tips were actually isolated bits of the vesicular cells of outer mantle lobes that retained the generative properties of that part of the mantle. Such vesicular cells would continue to secrete the basal layer (and any infrastructure) of the periostracum; and it is feasible that the periostracal caps of some kinds of spines remained sufficiently sticky to attach the animal to the substrate. 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.

The simplest hollow spines (Fig. 307) are those of the rhynchonellide *Acanthothiris* (RUDWICK, 1965b) and the finer of two distinct sets of the siphonotretide *Siphonotreta* (BIERNAT & WILLIAMS, 1971). These prostrate or tangential spines, which can be many millimeters long, are radially disposed and variously arranged in concentric zones of high density. Inward of the valve margin, they invariably become sealed by secondary

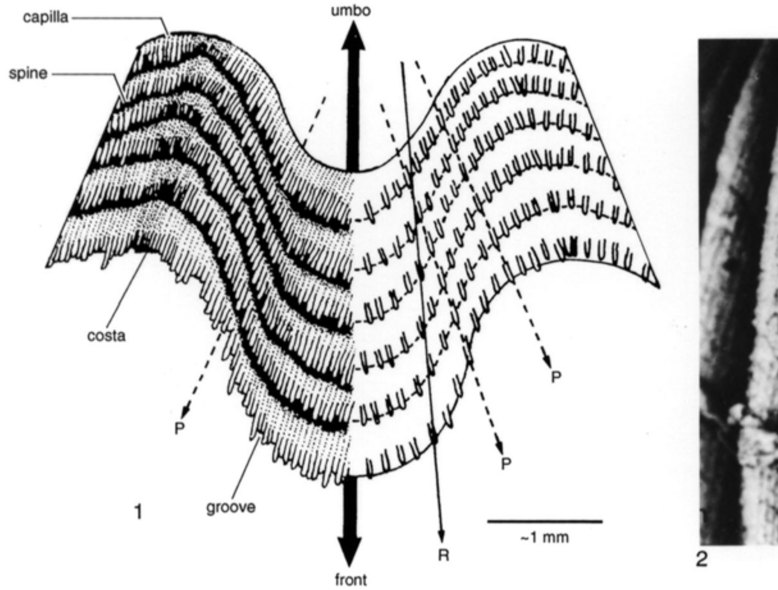

FIG. 305. Orientation of delthyrid-type, pseudoradial capillae; *1,* capillae diverge from the bottom of the intercostal grooves toward the costal crests in line with a pseudoradial direction (*P with dashed line*) and not a radial one (*R with solid line*); *2,* shell surface of Devonian *Adolfia* sp. showing the pseudoradial disposition of capillae, magnification about twice that of diagram (Gourvennec, 1989).

shell (unlike the coarser set in *Siphonotreta,* which remained open throughout life). Around the valve margins the fine spines interdigitate to form a grille that probably protected the commissural gape from extraneous objects (RUDWICK, 1965b; BIERNAT & WILLIAMS, 1971) and the shell surface from widespread colonization by cementing benthos. RUDWICK also concluded that such spines acted as sensory mechanisms, which hardly seems possible for mantle extensions that were completely enclosed in calcitic tubes with periostracal caps.

The spines of productidine brachiopods, which exceptionally exceed 20 cm in length, are much more diversified in form and function, even on individual shells. Some sets of spines (including arrays of strainer endospines on subperipheral rims) acted as external and internal grilles (Fig. 308; SHIELLS, 1968); others formed prostrate mats over external surfaces and probabaly protected the animals against predators as well as infestation by cementing benthos. Shells were also supported by symmetrically placed, strutlike, halteroid spines; but the most spectacular kind of support was that afforded by dense entanglements of rhizoid spines and clasping or attachment spines. The ability of these spines to converge and encircle cylindroid objects suggests a cementing capability like that of the craniid ventral valve. It is, therefore, possible that the generative tips of

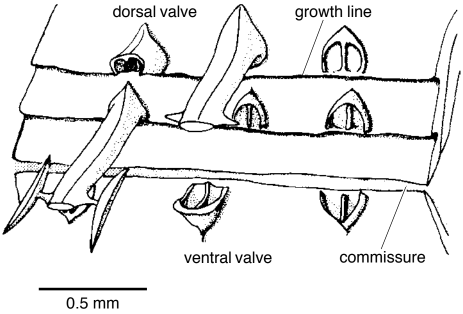

FIG. 306. Double-barreled spines of Carboniferous *Phricodothyris* sp. (Williams & Rowell, 1965b).

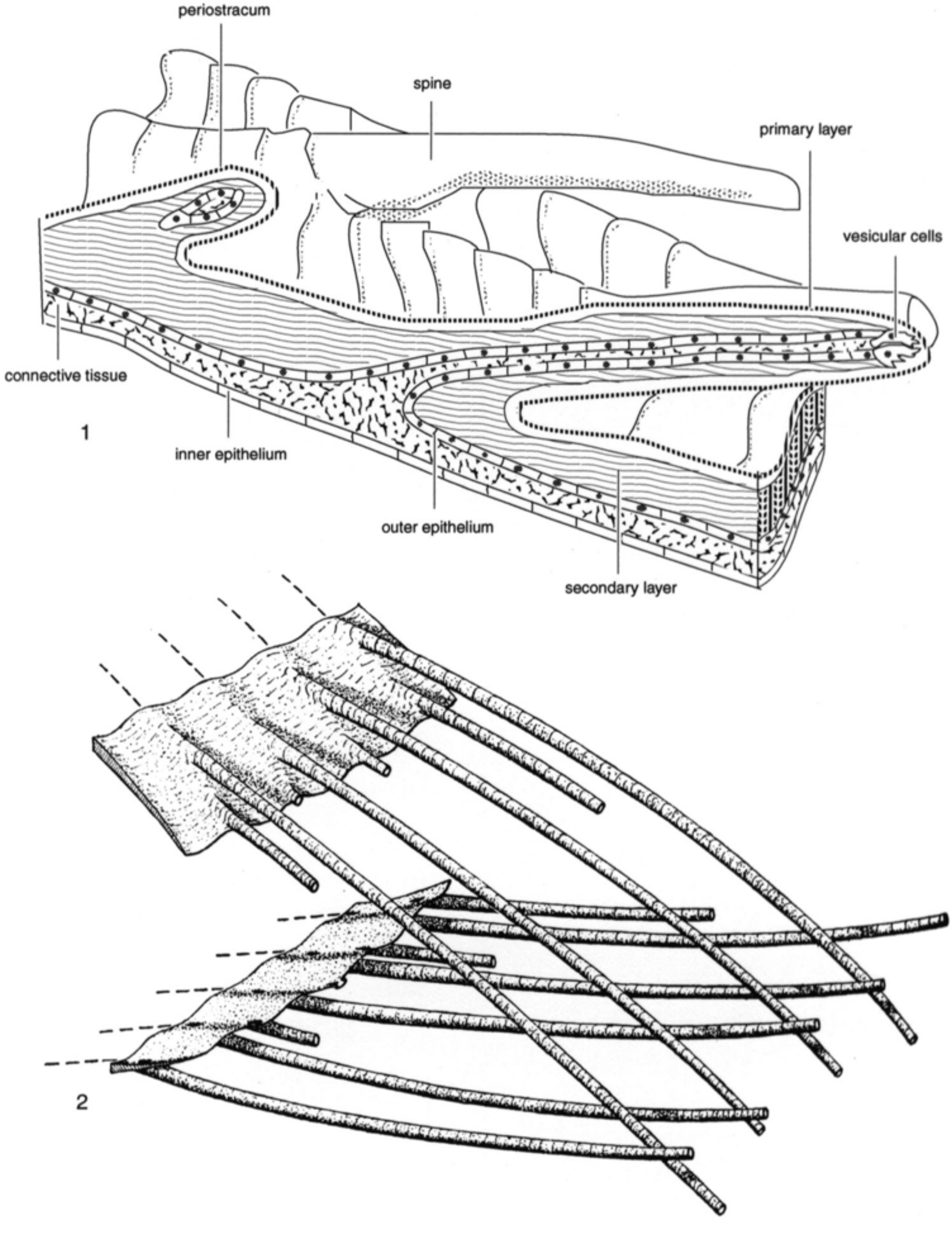

FIG. 307. The spines of Jurassic *Acanthothiris spinosa* (LINNÉ); *1,* reconstruction showing relationship between mantle and calcareous spines (Williams & Rowell, 1965b); *2,* reconstruction of parts of the valve edges, gaping as in life and showing how a grille of spines forms across the aperture (adapted from Rudwick, 1965b).

rhizoid and clasping spines exuded copious quantities of GAGs that cemented the periostracal coats of the spines to any contiguous object (Fig. 309). The first-formed biomineralized layers lining the extending periostracal sheaths would also have been secreted as a mixture of GAGs and calcitic granules, which polymerized as a plastic layer

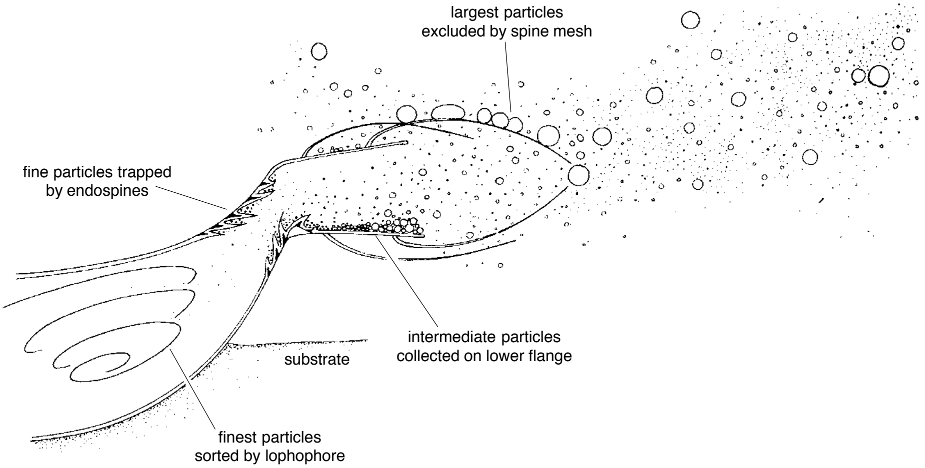

FIG. 308. The inferred filtering system of Carboniferous *Kochiproductus coronus* SHIELLS; the shell is shown partly buried in substrate with the gape of the valves facing a cross flow of detritus of various sizes; the productide lophophore was probably more like a schizolophe than a spirolophe (Shiells, 1968).

to account for the molding of spines to the contours of their substrates.

MODIFICATIONS OF PEDICLE OPENING

The anatomy of the pedicle and its cytological relationship with the mantle have been described, but its nature and disposition (as well as its absence) profoundly affect shell morphology in many ways. In particular, the opening in the shell for the emergence of the pedicle can vary greatly and is best described according to the degree of specialization of the organ during brachiopod evolution.

The simplest pedicle openings are found in organophosphatic brachiopods. In living lingulids the ventral pseudointerarea is indented medially by a pedicle groove that is lined by a strip of ventral outer epithelium sharing an arcuate junction with the circular base of pedicle epithelium (Fig. 310.3). The flanking propareas and the entire pseudointerarea of the dorsal valve are secreted by the outer lobes along the posterior segments of the ventral and dorsal mantles respectively. This relationship was typical of lingulides throughout the geological record although the pseudointerareas of early Paleozoic forms were better developed and the grooves more deeply indented (ROWELL, 1977).

The larval pedicle of the living discinoid *Pelagodiscus* (ASHWORTH, 1915) appears to develop, like that of *Lingula,* from the inner epithelial layer of the posteromedian sector of the ventral mantle (Fig. 39). However, a section of the mature pedicle of *Discinisca,* figured by BLOCHMANN (1900), showed a setal groove separating the inner epithelium of the posterior body wall from an outer mantle lobe, which secretes the posterior arc of the pedicle cuticle (Fig. 311). Accordingly, if this setal groove is the circumferential boundary between the ventral mantle and the body wall, the discinoid pedicle lies wholly within the outer layer of the ventral mantle and not just contiguous with it as in *Lingula.* Even so, this posteromedial strip of ventral outer mantle lobe seems never to have developed into an active site of integumental secretion during discinoid evolution. The postlarval, ventral valve of the early Paleozoic *Trematis,* which grew holoperipherally, was indented by a variably shaped pedicle notch so that no shell was secreted on the dorsal side of the pedicle along the mantle edge flanking the setal groove. In

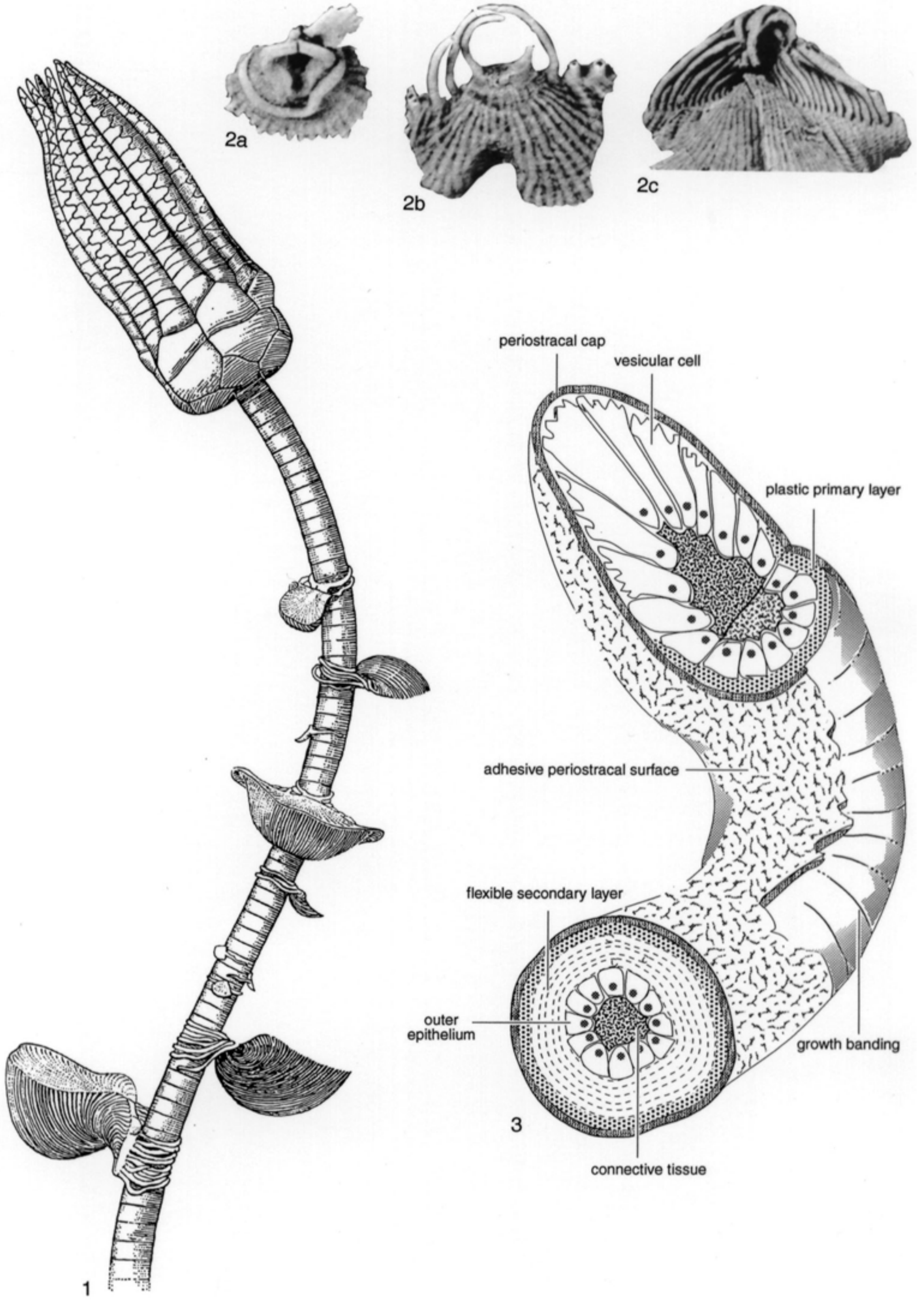

FIG. 309. Attachment spines of the Permian *Linoproductus; 1,* reconstruction of generalized crinoid and attached shells of *Linoproductus angustus* KING in various stages of growth; *2a–c,* three stages in the development of the attaching cardinal spines of *L. angustus,* ×3, ×3, ×1 (Grant, 1963); *3,* inferred structure and composition of an attaching spine in relation to the mantle of living *Linoproductus* (new).

other mature discinoids, this notch is closed toward the valve margin by a strip of periostracum in living *Discinisca* or by a fully developed shell succession as in recent *Discina* and Paleozoic *Orbiculoidea* (Fig. 310.1). Such closure, however, is effected by the convergent growth of the posterolateral sectors of the ventral outer mantle lobe, which surround the pedicle base and fuse dorsomedially in the manner of deltidial plates of articulated brachiopods.

In some discinoids, migration of the pedicle has led to the enlargement of the opening toward 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. The free margin of the listrium in *Orbiculoidea* projects internally as a pedicle tube lying against the previously formed shell of the posteromedian part of the ventral valve (Fig. 310.1). The discinoid pedicle also leaves traces of its presence on the external surface of the ventral valve. The pedicle opening of some living and many extinct discinoids is contained within an elongately oval depression marking the external attachment area of an expanded pedicle.

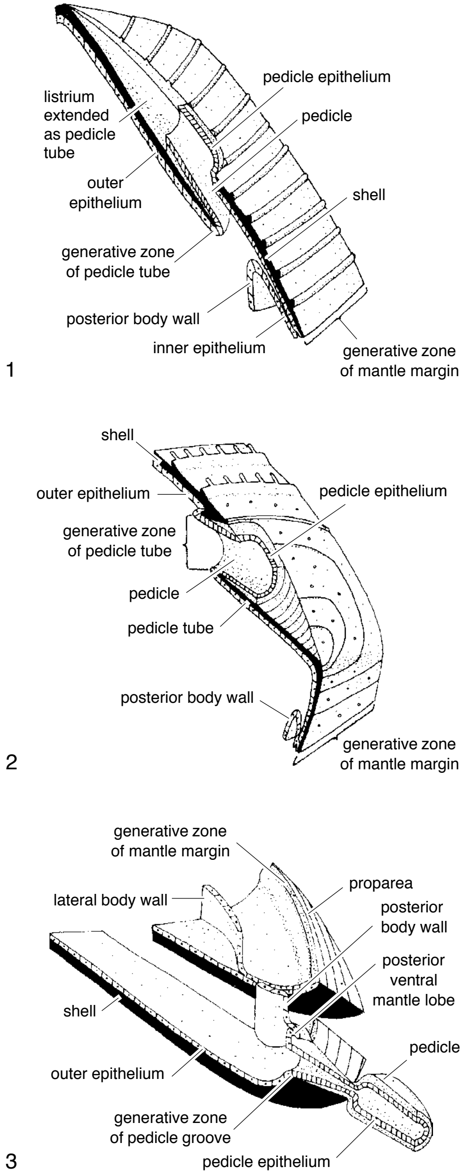

FIG. 310. Stylized reconstruction of posterior part of ventral valve with longitudinal section showing inferred epithelium-and-shell relations in *1, Orbiculoidea* and *2, Multispinula,* both viewed externally; *3,* observed epithelium-and-shell relations in *Lingula,* viewed internally (Williams & Rowell, 1965b).

The relationship of the pedicle to its putative opening in the remaining, wholly extinct organophosphatic brachiopods, the acrotretides and siphonotretides, is speculative. The pedicle openings of these groups are usually identified and interpreted in terms of the differentiation of the pedicle of living organophosphatic species, but there is a fundamental difference in the origin of the organ, at least compared with that of *Lingula.* In all siphonotretides and most acrotretides, the larval ventral valve, normally between 100 and 300 µm in length, is pierced more or less centrally by a foramen that is widely accepted as having accommodated the larval pedicle (Fig. 312). This suggests that the pedicle of these extinct organophosphatic stocks was an evagination of ectoderm that became the outer epithelium responsible for the secretion of the shell, and not an evagination of the inner epithelium as in *Lingula.* The pedicle of acrotretides and siphonotretides, therefore, could have been very different in its morphology and function from that of lingulides. In particular the pedicle of these extinct groups was probably a variably developed organ of adhesion with

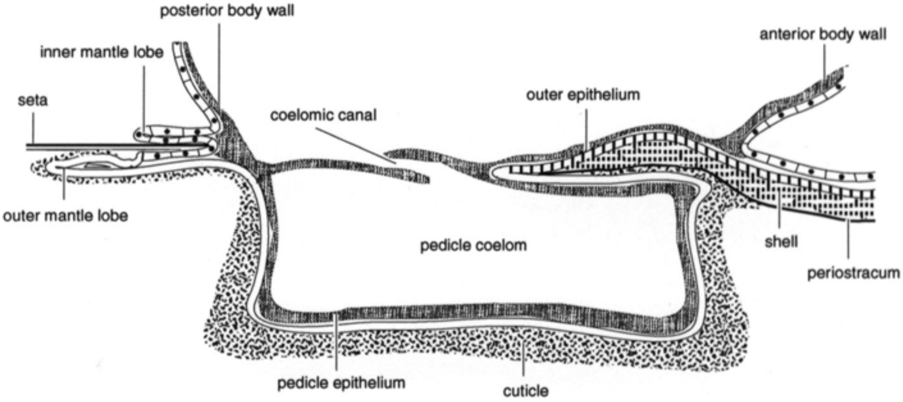

FIG. 311. Differentiation of epithelia associated with the pedicle of recent *Discinisca lamellosa* (BRODERIP) (adapted from Blochmann, 1900).

a cuticle closely related in composition to the periostracum and with a potential for atrophy as well as resorption of an organophosphatic shell. Whether such a pedicle was homologous with that of living discinids is presently undeterminable. On the basis of BLOCHMANN's (1900) interpretation of the mature discinid pedicle, it is possible that it, too, arose by differentiation of larval outer epithelium, although by changes in the vesicular cells of the outer mantle lobe.

Among the siphonotretides, the ventral pseudointerarea is always entire, and the foramen can be minute and plugged in maturity as in *Acanthambonia* or greatly enlarged anteriorly by resorption as a narrowly triangular opening restricted posteriorly by a plate (*Schizambon*) or pedicle tube (*Multispinula*) (Fig. 310.2). CHUANG (1971) has contended that the perforate valves of *Schizambon* and acrotretides are dorsal and that the foramina were for exhalant currents. This interpretation is contrary to brachiopod functional morphology in general and is untenable (ROWELL, 1977).

In most adult acrotretoids, the posterior margins of the ventral valves are entire and commonly flattened to produce strongly developed pseudointerareas. Entirely biomineralized posterior margins are also characteristic of their perforate larval valves except in two groups within this superfamily (Fig. 313). In maturing *Curticia,* the pedicle migrated posterodorsally and the posterior margin of the ventral valve was breached by resorption to form a triangular pedicle opening. In *Scaphelasma,* however, the larval ventral valve was not perforated by a foramen; instead the posteromedian margin was indented by a pedicle notch, and shell secretion did not delineate a foramen until the brephic or neanic growth stages (HOLMER, 1989). In contrast, the related, cemented acrotretoid *Eoconulus* has a swelling (bulla) that is perforated by a pair of lateral aper-

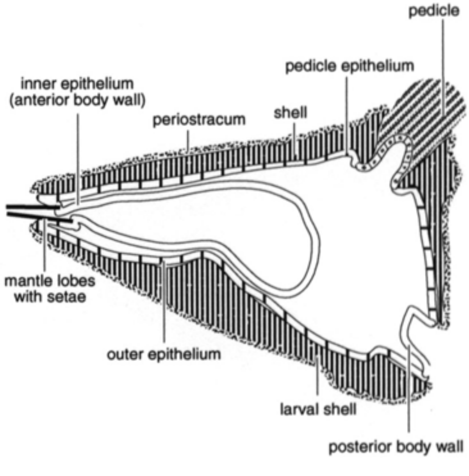

FIG. 312. Inferred distribution of the inner, outer, and pedicle epithelia in a longitudinal section of a typical juvenile acrotretoid (*Torynelasma*) shell, about ×150 (new).

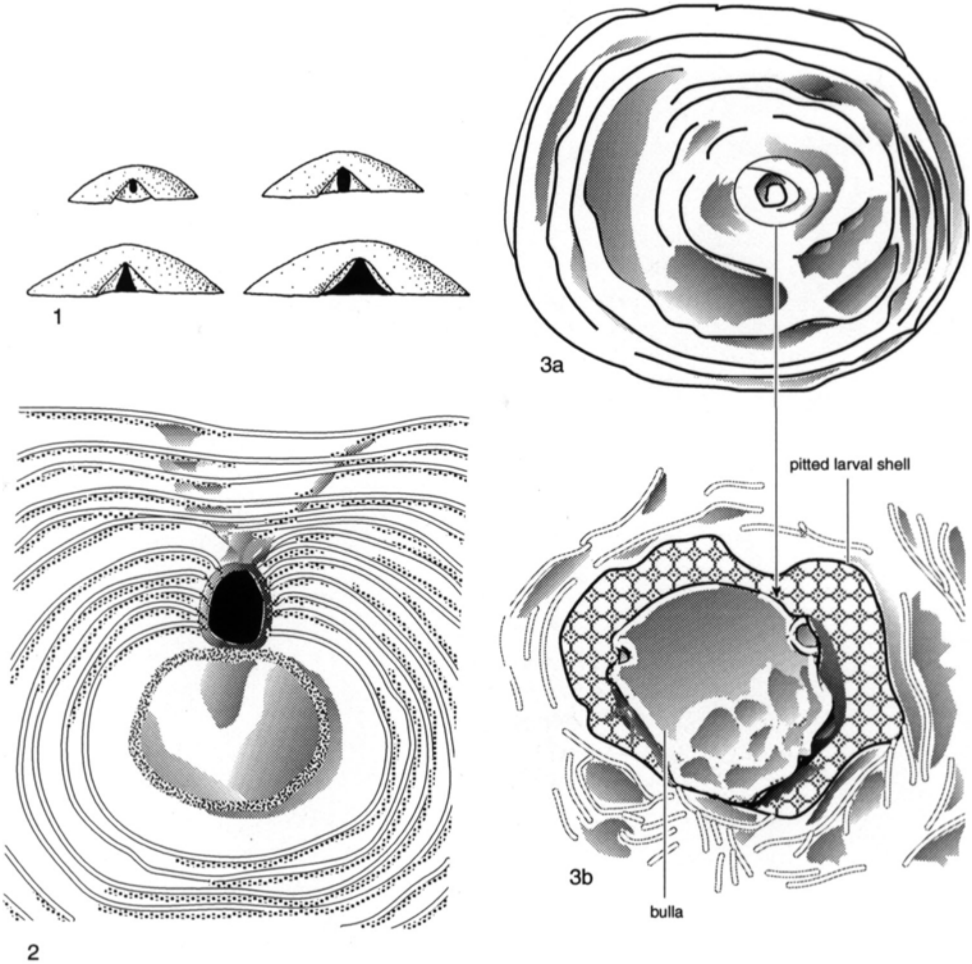

FIG. 313. Acrotretoid pedicle openings; *1,* growth series of the Cambrian *Curticia minuta* BELL (beginning with the youngest ventral valve known, 1.1 mm wide, in the top left-hand corner) showing an increasingly triangular pedicle opening breaching the posterior margin of the enlarging ventral valve (Williams & Rowell, 1965b); *2,* the closure of the pedicle opening during the growth of the Ordovician *Scaphelasma* sp., ×125; *3a,* external view of the ventral valve of the Ordovician *Eoconulus* cf. *semiregularis* BIERNAT, ×125, and *3b,* a detail of the central region of the valve showing the bulla in relation to the pitted larval shell, ×700 (adapted from Holmer, 1989).

tures and that generally has the appearance of having been a cast of sporadic clusters of vesicles; it is connected to the pitted larval plate by a constricted neck. The bulla has been interpreted as a protegulum (HOLMER, 1989); and this is borne out by the fact that similar swellings, in various stages of collapse, occur at the centers of the larval valves of living *Discinisca.*

The pedicle opening of the related botsfordioids is also fashioned differently from the typical acrotretoid foramen. In *Botsfordia,* the posterior margin of the larval ventral valve is indented by a triangular pedicle notch that persisted in maturity (Fig. 314.3), while in *Acrothele* rapid secretion along the posteromedian sector of the mantle gave rise to an entire ventral pseudointerarea restricting the foramen (Fig. 314.1–314.2). It is not known whether the growth of an entire pseudointerarea in such botsfordioids as *Acrothele* is homologous with the mineralized dorsal margins closing discinoid pedicle openings.

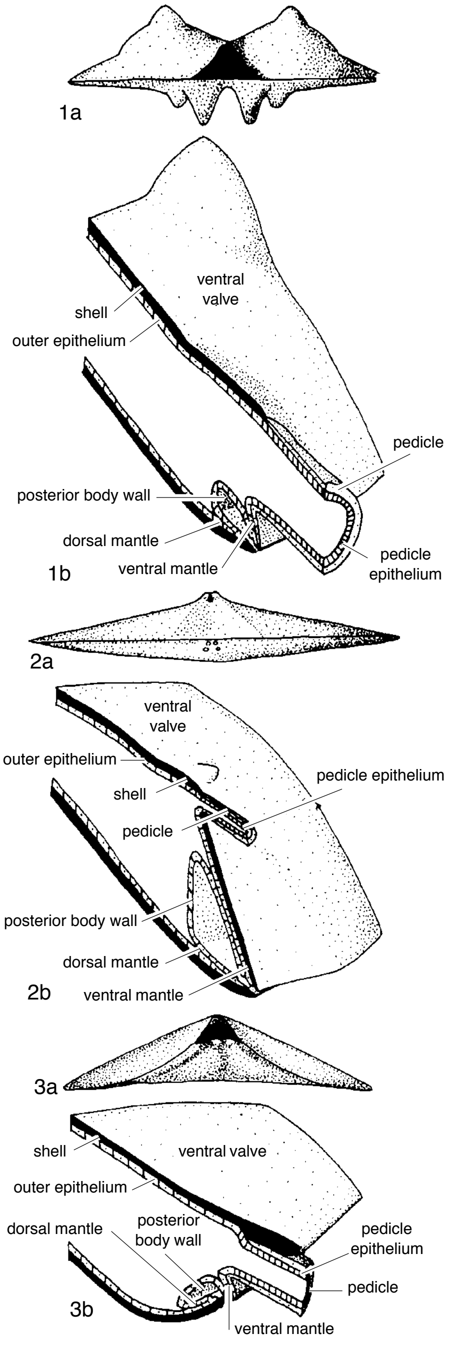

FIG. 314. Posterior views of shell and stylized reconstructions with longitudinal median section of posterior part of shell showing inferred eptihelium-and-shell relations of *1,* young *Acrothele, 2,* adult *Acrothele,* and *3,* adult *Botsfordia* (anterior body wall omitted) (Williams & Rowell, 1965b).

In retrospect, the inferred shift in the acrotretide larval pedicle from its presumed normal position at the center of a shell undergoing holoperipheral growth is greater than that of the pedicle rudiment of articulated brachiopods, but it affects only a minority of species. The posterior slope of the acrotretide ventral valve is usually slightly indented or raised medially (intertrough, deltoid pseudointerarea). These features seem not to have reflected the disposition of the pedicle, which lay ventral of their growing edge. Indeed in most acrotretides, there was 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 at its junction with pedicle epithelium.

The remaining organophosphatic brachiopods, the paterinides, are unique in having an imperforate shell with features normally associated with a supra-apical foramen as in the articulated strophomenides. These structures are the posteromedian, externally convex **homeodeltidium,** and **homeochilidium** of the ventral and dorsal valves respectively. It is usually supposed that the pedicle emerged between these two plates, which would then be the homologues of the pedicle collar and an exaggerated antigydium of living rhynchonellides. It is less likely that no pedicle developed, at least in postlarval stages, and that the median gape between the plates was underlain by inner epithelium of the posterior body wall (Fig. 315; WILLIAMS & ROWELL, 1965b, p. 90).

The variability in the position of the pedicle opening is also characteristic of the oldest, carbonate-shelled, inarticulated obolellides. The opening may be represented by a posteromedian groove in the ventral pseudointerarea (*Obolella*), an apical foramen, or a triangular resorption slot well forward of the beak of the ventral valve (*Trematobolus*). The remaining inarticulated, carbonate-shelled brachiopods lacked pedicles, and the only evident morphological effects are the absence of perforations and the distortion of the shell dependent on whether the animal was free-living or cemented. The development of living *Neocrania,* however, has some bearing on the nature of the acrotretide pedicle. The attachment area of a fully grown larva of *Neocrania* is a relatively thin patch of epithelium charged with electron-dense material (Nielsen, 1991). This patch is central to a shell that is secreted holoperipherally during postlarval growth and probably had as its plesiomorphy an atrophied holdfast acting as a pedicle such as one would expect to have existed in the earliest craniides, as in the free-living *Pseudocrania.*

The morphological relationship between the pedicle and shell of living articulated rhynchonellides and terebratulides is superficially reminiscent of that of inarticulated species, but the development and role of both hard and soft parts are fundamentally different. The manner in which the subcircular junction between the outer and pedicle epithelia is shared by the unmodified pedicle openings (the ventral **delthyrium** and the dorsal **notothyrium**) has already been described in the section on anatomy (p. 49), as has the replacement of the posterior body wall in these astrophic, tightly articulated shells by a strip of fused ventral and dorsal mantle lobes (p. 47). This basic arrangement is usually modified by the growth of plates that further confines the pedicle, as is well shown in mature *Notosaria* and *Liothyrella* (Williams & Hewitt, 1977).

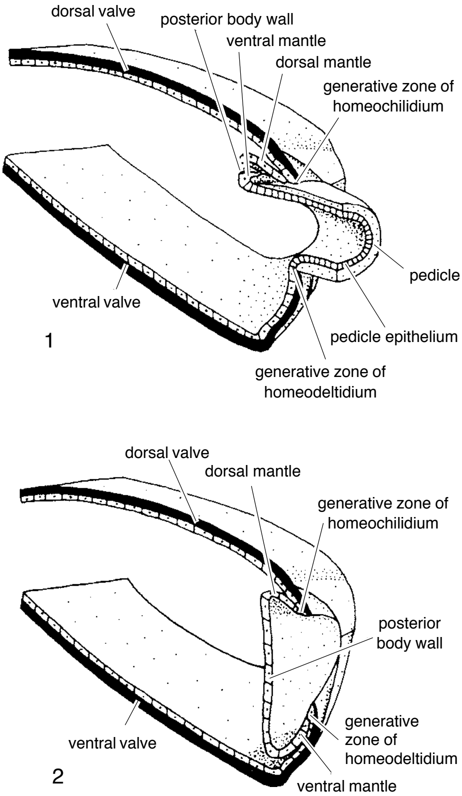

Fig. 315. Stylized reconstruction (with median longitudinal section) of posterior part of paterinide showing alternative interpretations of epithelium-and-shell relations (anterior body wall omitted); *1,* inferred to possess pedicle; *2,* inferred to lack pedicle (Williams & Rowell, 1965b).

The circumferential expansion of the junction occurs only at its intersection with the strip of fused mantle lobes, which are responsible for the growth of the cardinal margins of both valves (Fig. 316). As expansion takes place with a simultaneous increase in length, especially of the ventral cardinal margin, the junction migrates into the delthyrial cavity across the secondary fibers, which become realigned. This surface of inward migration is normally coated with a thin carbonate film and sealed by a proteinaceous membrane, both being secreted by the retreating outer epithelium forming the outer rim of the junction. The membrane acts as a bonding sheet for a cuticular fold secreted by the pedicle epithelium at the inner rim of the junction. This entire zone constitutes the **pedicle collar** of the ventral valve. A similar succession, on a more modest scale, usually marks the retreat of the junction across the antigydium within the notothyrium of the dorsal valve. With further expansion of the apertures, the ventral outer mantle lobes begin to grow posteromedially away from the fused strip at its two intersections with the pedicle-outer epithelial junction and secrete a pair of tetrahedral

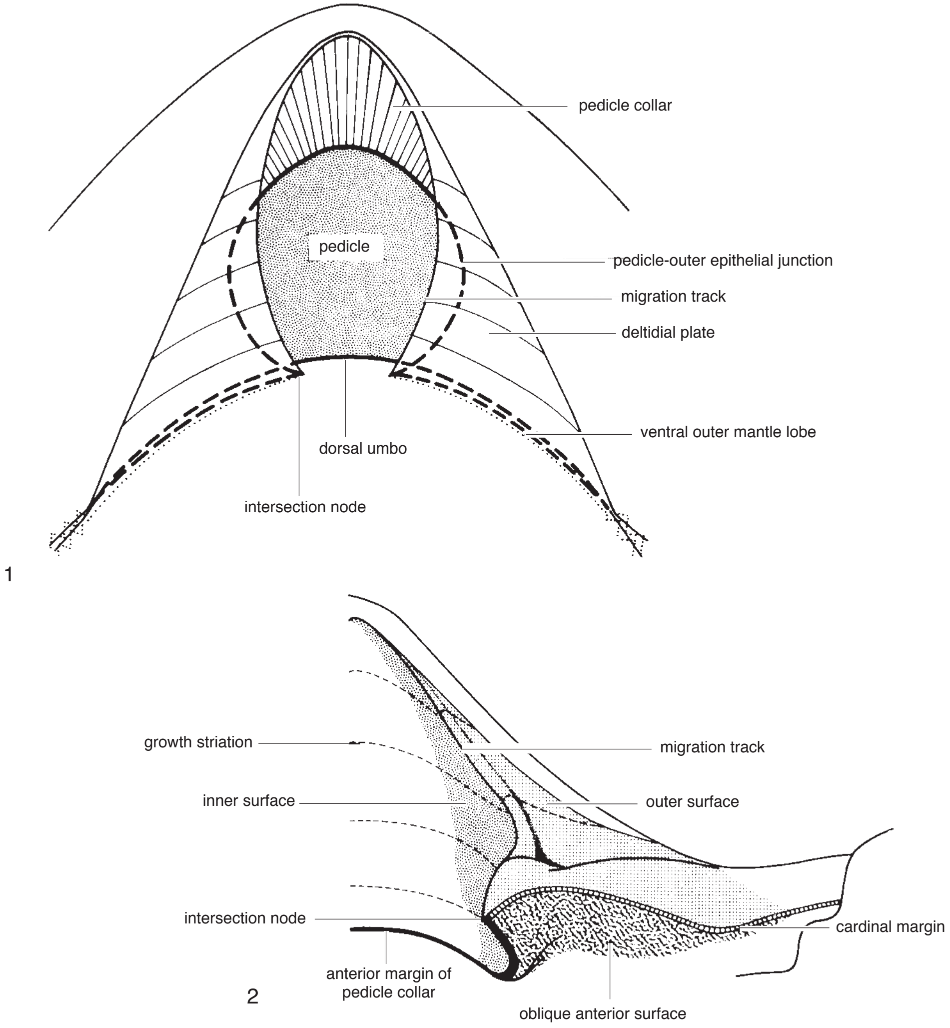

FIG. 316. Diagrammatic dorsal view of the pedicle opening of a mature *Notosaria nigricans* (SOWERBY) showing the relationship of the deltidial plates to *1,* the pedicle-outer epithelial junction and *2,* the surfaces defining a deltidial plate (Williams & Hewitt, 1977).

structures, the deltidial plates. Each plate is bounded by an outer surface of primary shell, an inner surface of pedicle collar, and an oblique anterior surface of secondary fibers.

The deltidial plates can extend medially only because they grow dorsally above the umbo of the dorsal valve. Further growth leads to a median conjunction of deltidial plates (deltidium). In such stocks as *Liothyrella,* a median fusion of the paired ventral mantle lobes then takes place to form a continuous structure (symphytium) across the dorsal edge of the delthyrial area (Fig. 317). The term henidium has been coined for a symphytium that bears no sign of a median fusion of deltidial plates.

Within the limits imposed by this sequence of growth of delthyrial and notothyrial biomineralized parts, the morphology of the pedicle opening in astrophic shells can vary. In rostrate shells with the dorsal sectors

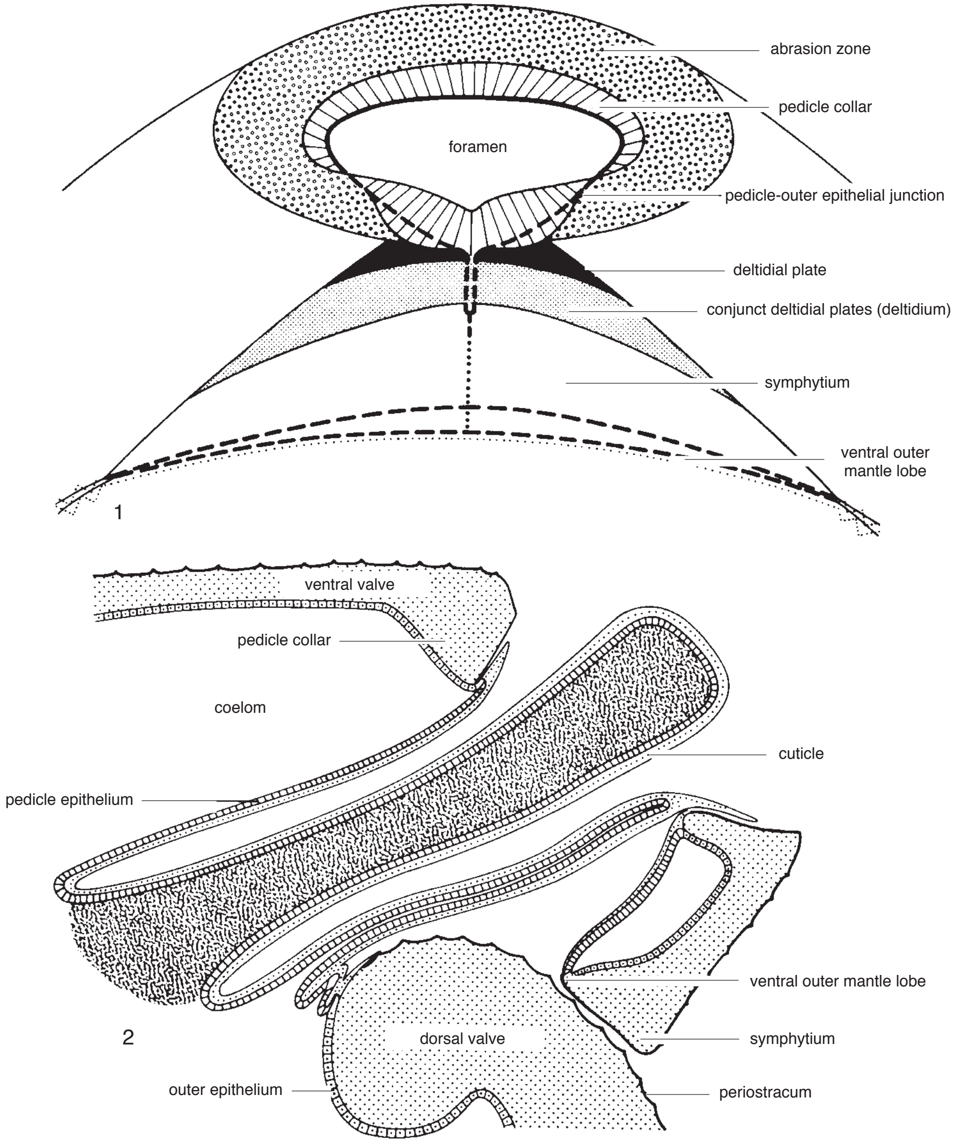

FIG. 317. *1,* Diagrammatic dorsal view and *2,* section of the symphytium with pedicle of a mature *Liothyrella uva* (BRODERIP) showing the relationship of the symphytium with the deltidium composed of conjunct deltidial plates (Williams & Hewitt, 1977).

of the pedicle zone not projecting beyond the hinge axis (e.g., *Terebratulina*), the plates remain discrete, flanking the dorsal sheet of pedicle epithelium. In other species, the growth of the dorsal umbo into the ventral valve facilitates the development of deltidia and symphytia. The position of the foramen relative to the deltidium and ventral beak can also vary through migration, and a number of terms are in general use to indicate its location (Fig. 318).

The open delthyrium and notothyrium are typical of most orthidines, enteletidines, and pentamerides (Fig. 319.3); and it is

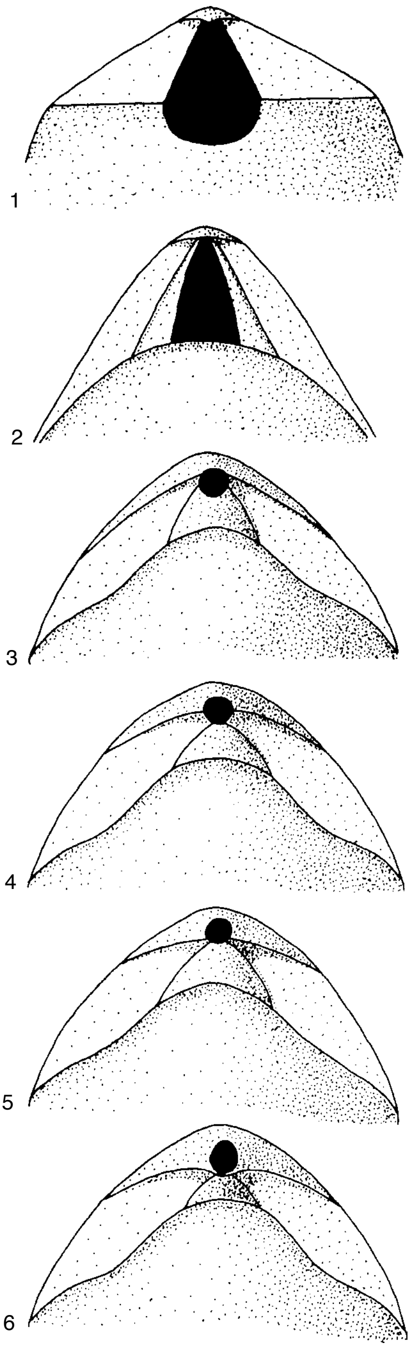

Fig. 318. Position of the pedicle opening relative to the beak ridges of some articulated brachiopods; *1,* amphithyrid; *2,* hypothyrid; *3,* submesothyrid; *4,* mesothyrid; *5,* permesothrid; *6,* epithyrid (adapted from Williams & Rowell, 1965b).

likely that the junction between the pedicle and outer epithelia in these groups coincided with the boundaries of the diamond-shaped aperture subtended by these structures. Some modifications did occur. The pedicle collar (also known as the pedicle or apical plate) was commonly but variably developed by retreat of the ventral edge of the junction. Deltidial plates, fusing to form a deltidium or **notodeltidium** (Cooper, 1955), developed independently in *Barbarorthis* and *Phragmophora.* The unmodified notothyrial edges must also have acted as attachment surfaces for the pedicle-outer epithelial junction, in 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,* and other genera) would have been secreted like deltidia. It is, however, probable that the pedicle apparatus of these Paleozoic groups differed from that of the rhynchonellides, spire-bearers, and terebratulides in lacking any well-developed pedicle capsule. As will be discussed later, this assumption is based on differences in the distribution of ventral muscle fields.

Spire-bearing brachiopods display a greater variation in delthyrial modification as a result of repeated atrophy of the pedicle and the common, extravagant development of the ventral interarea. Cementation of the ventral valve occurred in such widely differing stocks as *Davidsonia* and *Thecospira* (and also in the presumed direct descendants, the thecideidines). In these forms the delthyrial cover is a solid structure as it is in species that lost their pedicles early in ontogeny. This was so in *Bittnerula,* which additionally developed attachment or stabilizing spines on the deltidium within 5 mm of the beak (Cowen & Rudwick, 1970). Deltidial plates and conjunct deltidia are also found. The subcentrally developed foramen in the delthyrial cover of *Cyrtina,* for example, was probably formed by the secretion of an apically situated deltidial arch, like that found in *Eospirifer,* and a dorsally located symphytium homologous with that of *Liothyrella.*

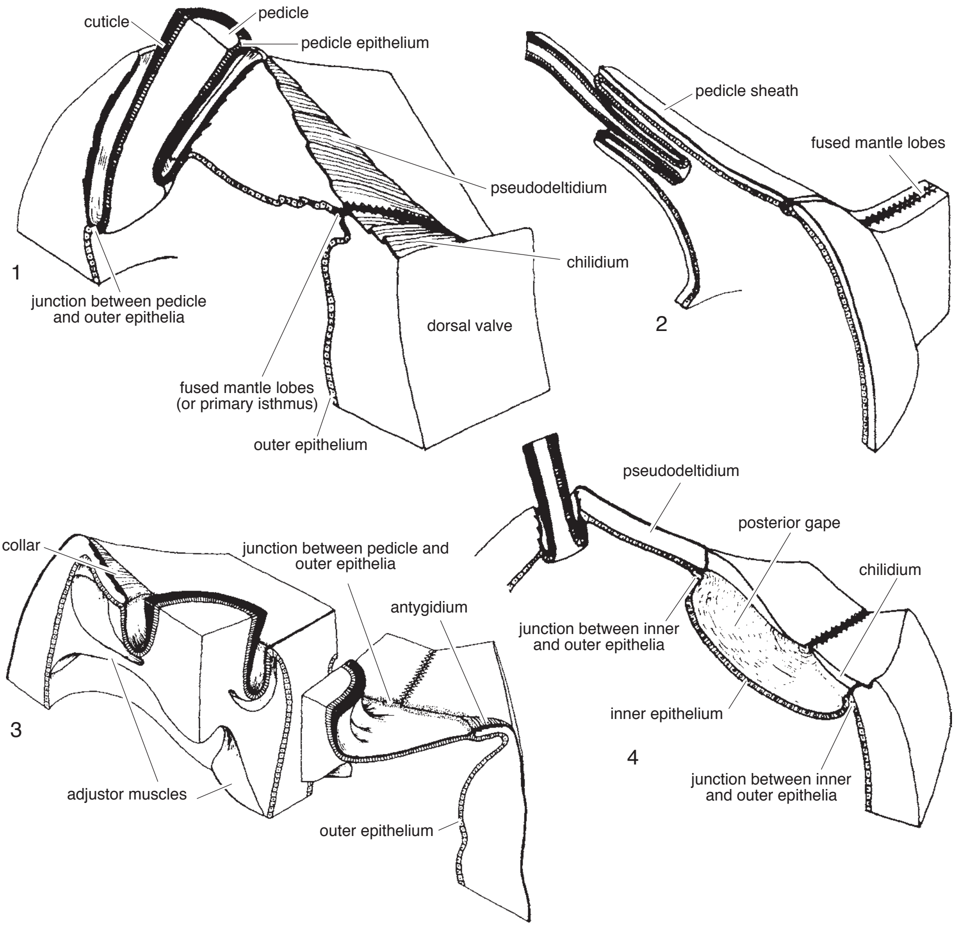

FIG. 319. Inferred relationships between the pedicle and pedicle opening; *1,* adult *Leptaena; 2,* young *Coolina; 3,* adult *Hesperorthis;* and *4,* adult *Nisusia* (adapted from Williams & Rowell, 1965b).

The most intriguing structures found in the spiriferides, however, are the **stegidia** of the pyramidal *Syringothyris* and *Sphenothyris* (COOPER, 1954) and the stegidial plates of the alate *Mucrospirifer* (COWEN, 1968).

In *Mucrospirifer,* the delthyrium is filled by two discrete mineralized plates (Fig. 320.2–320.3). The ventral plate fits into the apical part of the delthyrium and consists of a succession of laminae such that the first formed is the smallest, external unit and the last to be secreted is the largest, innermost unit. It is assumed that these laminae were initially deposited around a pedicle that had more or less atrophied when the innermost layer was secreted. The more dorsal plate fits into the open end of the delthyrium and overlaps onto the notothyrial sector of the dorsal valve. It, too, consists of a succession of thin laminae that are not single units but medially conjunct above the cardinal process.

The syringothyrid stegidium is essentially the same as the ventral stegidial plates of *Mucrospirifer;* and a rarely preserved set of laminae, fitting into the dorsal concavity of the stegidium and capping the cardinal process of *Syringospira* (COOPER, 1954), could well be homologized with the mucrospiriferid dorsal plates (Fig. 320.1). These

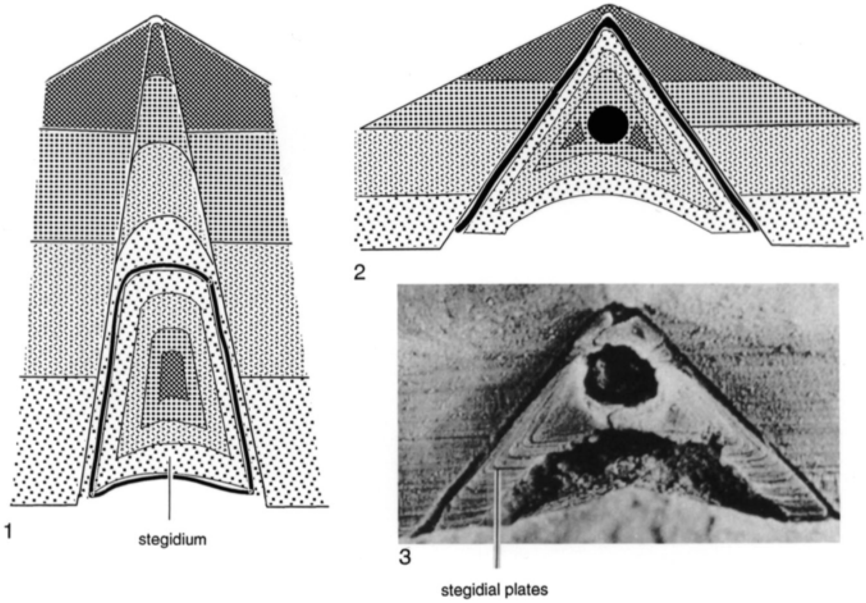

FIG. 320. Inferred growth of the stegidium of a *1,* Devonian *Syringospira* and *2–3,* Devonian *Mucrospirifer* with the first-formed layers of these structures and the apical regions of the ventral areas, into which they originally fitted, shown in the *darkest shade* of ornamentation to indicate successive growth stages (*3,* ×15) (adapted from Cowen, 1968).

structures, however, have been differently interpreted as having been secreted in stages by the outer epithelium forming the rim of the junction with pedicle epithelium, which decreased in circumference concomitant with the atrophy of the pedicle.

The mode of secretion described here for the stegidial plates is now preferred for two reasons (COWEN, 1968). First, stegidial plates are complete; and second, they consist of stacked laminae composed exclusively of secondary shell. Neither criterion would hold if the plates had been deposited by outer epithelium peripheral to a reducing junction with pedicle epithelium. COWEN's interpretation, however, poses a formidable problem in attempting to explain biomineral deposition at the sites postulated by him, without invoking a new secretory regime. A third kind of shell has been reported only once during embryological studies of brachiopods. Interestingly, this was in reference to the presence of a chitinous plate on the caudal segment of the embryo of the thecideidine *Lacazella,* which is assumed to have had a spire-bearing ancestor (KOVALEVSKIY, 1874).

The covers of the delthyrium and notothyrium of the strophomenides, referred to respectively as **pseudodeltidium** and chilidium, were deposited in a fundamentally different way (Fig. 319.1–319.2). The larval shells of a sufficient number and variety of species are now well enough known to conclude that the junction between the outer and pedicle epithelia was restricted throughout growth to the ventral valve. In such larval shells the pedicle opening occurs supra-apically (ARBER, 1942) within the ventral valve and is commonly enclosed in a high calcitic ring (pedicle sheath). The pedicle junction, therefore, must have lain within the edge of the sheath, so that the pseudodeltidium, lying dorsal of it, was an integral part of the interarea; and its development was not dependent upon the presence of the pedicle but on secretion of its dorsal edge by an outer lobe of outer epithelium. The deposition of the chilidium must have been controlled in the same manner by outer epithelium as were the entire margins of both valves, a condition comparable with that determining the growth of some inarticulated shells (acrotretides).

In early strophomenides, as well as billingselloids and kutorginides, which also possess pseudodeltidia and variably developed chilidia, the pseudodeltidium is not flush with the hinge line but concave to it; and, although the chilidium may protrude into this space, it is not entirely filled so that a well-defined posteromedian gap commonly persists. Previously it has been contended that the gap could have been closed internally by either a strip of periostracum secreted by a zone of fused mantle lobes, as in living articulated brachiopods, or a strip of inner epithelium homologous with the posterior body wall of inarticulated species (WILLIAMS & ROWELL, 1965b, p. 88). The first explanation, however, is unlikely for two reasons. First, the phylogeny of the strophomenides (*s.l.*) appears generally to preclude fusion of the mantle lobes along the cardinal margins; indeed, in some of the more aberrant groups, as the richthofenioids and the lyttoniioids, such a fusion would have been impossible. Second, there is good reason for believing that the anus opened into the postromedian gap of the *Nisusia* shell (ROWELL & CARUSO, 1985) and could only have perforated a posterior body wall (Fig. 319.4).

As to the nature of the pedicle itself, it was seldom strongly developed. In many leptaenids, for example, the foramen may be enlarged by resorption or completely plugged with secondary shell in adults from the same population. Indeed the pedicle atrophied at some time or other in most stocks during their evolution. It must, therefore, have been more akin, in its embryonic differentiation, to the attachment area of *Neocrania* than to the organ rudiments of living organophosphatic and articulated brachiopods. In particular, it was primarily differentiated as an adhesive pad, around which the larval ventral valve was secreted holoperipherally as a funnel-shaped receptacle closed by a lidlike dorsal valve. This structural relationship was especially characteristic of the ventral valve of productidines and strophalosiidines, which frequently bore a cicatrix of attachment.

Despite the lack of information about the development of the delthyrial cover in triplesiidines, it is likely that it, too, was homologous with the strophomenide pseudodeltidium, for the presence of an inner calcareous pedicle tube can only be explained on this assumption. The evidence for a close affinity between the strophomenides and the clitambonitidines is equivocal. The so-called pseudodeltidium of the latter is frequently pierced by an apical rather than a supra-apical foramen and did not develop at all in some forms such as *Apatomella.*

Finally, the elongate, subtriangular apertures perforating the ventral valves of a few extinct obscure groups, as the dictyonellidines and chileoids, have no parallel among better-known stocks, extinct or living; and the nature of their organic cover is entirely conjectural. The apertural boundaries are not smooth (YOUNG, 1884), as they would have been had they been fashioned along a persistent epithelial junction. One can, therefore, assume that they are roughened as a result of resorption and postmortem fracture. The aperture is overlain by an internal plate (colleplax), from which it is separated by a narrow space. The external surface of the colleplax, that seen through the aperture, is relatively smooth, while its internal surface bears scars and evidently served as a platform for the attachment of the adductor muscles as it is flanked by flabellate diductor scars on the valve floor (COOPER, 1952).

This kind of aperture has been variously described, mainly as pedicle openings (COOPER & GRANT, 1974) or even for the intake and expulsion of seawater (POPOV & TIKHONOV, 1990). The most feasible interpretation, however, is that the aperture was covered by a tissue coated with adhesive polymers (WRIGHT, 1981). The structure would not have been a pedicle in the sense of

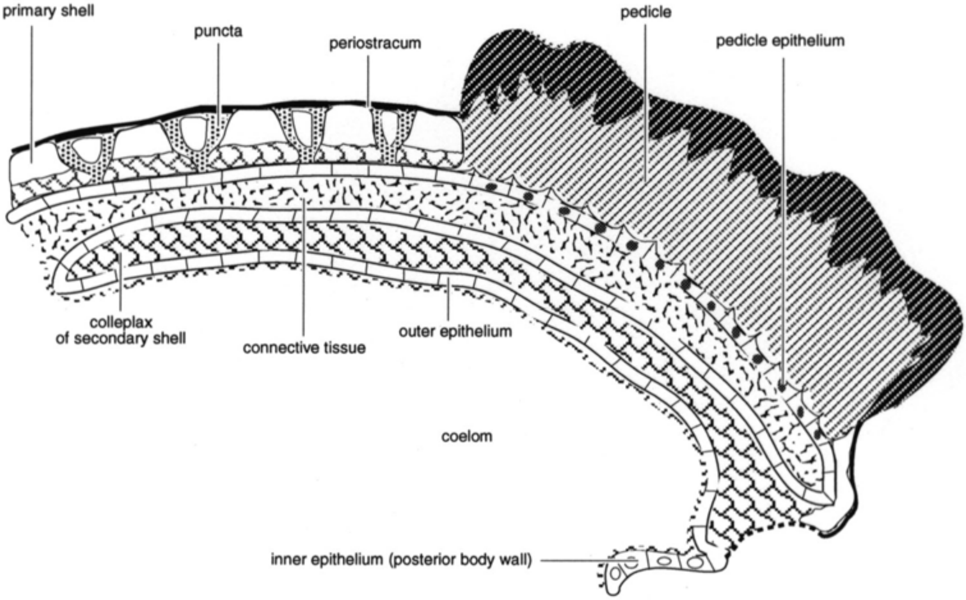

FIG. 321. Inferred relationship of the pedicle of the Silurian *Dictyonella* to the mantle lining the shell and investing the colleplax (adapted from Wright, 1981).

having afforded the animal an axis on which to rotate (Fig. 321). There are no markings that could reasonably represent the bases of adjustor muscles focused on the space between the aperture and the **colleplax,** while the narrowness of the space itself indicated that the adhering structure was essentially superficial. It must have been relatively large, however, and high enough to fill the aperture and to maintain distortion-free shells well above the substrate. In effect the structure could have been a cuticular pad, thick enough to persist some time after death and to have broken free of the shell by volumetric change.

ARTICULATION

The articulated brachiopods are preeminently characterized by a pair of hinge **teeth** in the ventral valve that fit into a pair of **dental sockets** in the dorsal valve (Fig. 322). In four-day-old specimens of *Terebratalia transversa,* STRICKER and REED (1985b) reported the initial appearance of teeth composed of finely granular calcite, with the differentiation of sockets evident in eleven-day-old specimens. After growth for 23 days each tooth had become transformed into a tight cluster of secondary layer fibers, similar in appearance, but much less numerous than in adults. The growth tracks of the teeth invariably define the margins of the delthyrium, so that they protrude from beneath the ventral cardinal area on either side of the delthyrium or its cover. Two distinct kinds of teeth have been described in articulated brachiopods (Fig. 322.1–322.2; JAANUSSON, 1971). They are either simple, knoblike **deltidiodont teeth**, which grew solely by shell accretion, or they are hook-shaped **cyrtomatodont** teeth whose more elaborate curved form involved partial posterior resorption of earlier formed shell. Deltidiodont teeth had their origin in the mid-Cambrian and are generally characteristic of extinct, strophic-hinged groups, but the latter occur in some spire-bearers and in fossil and living rhynchonellides, terebratulides, and thecideidines. JAANUSSON (1971) drew a clear taxonomic distinction between these two types of dentition. The cyrtomatodont style, which holds the two valves together while modifying its detailed morphology during growth, allows greater variability

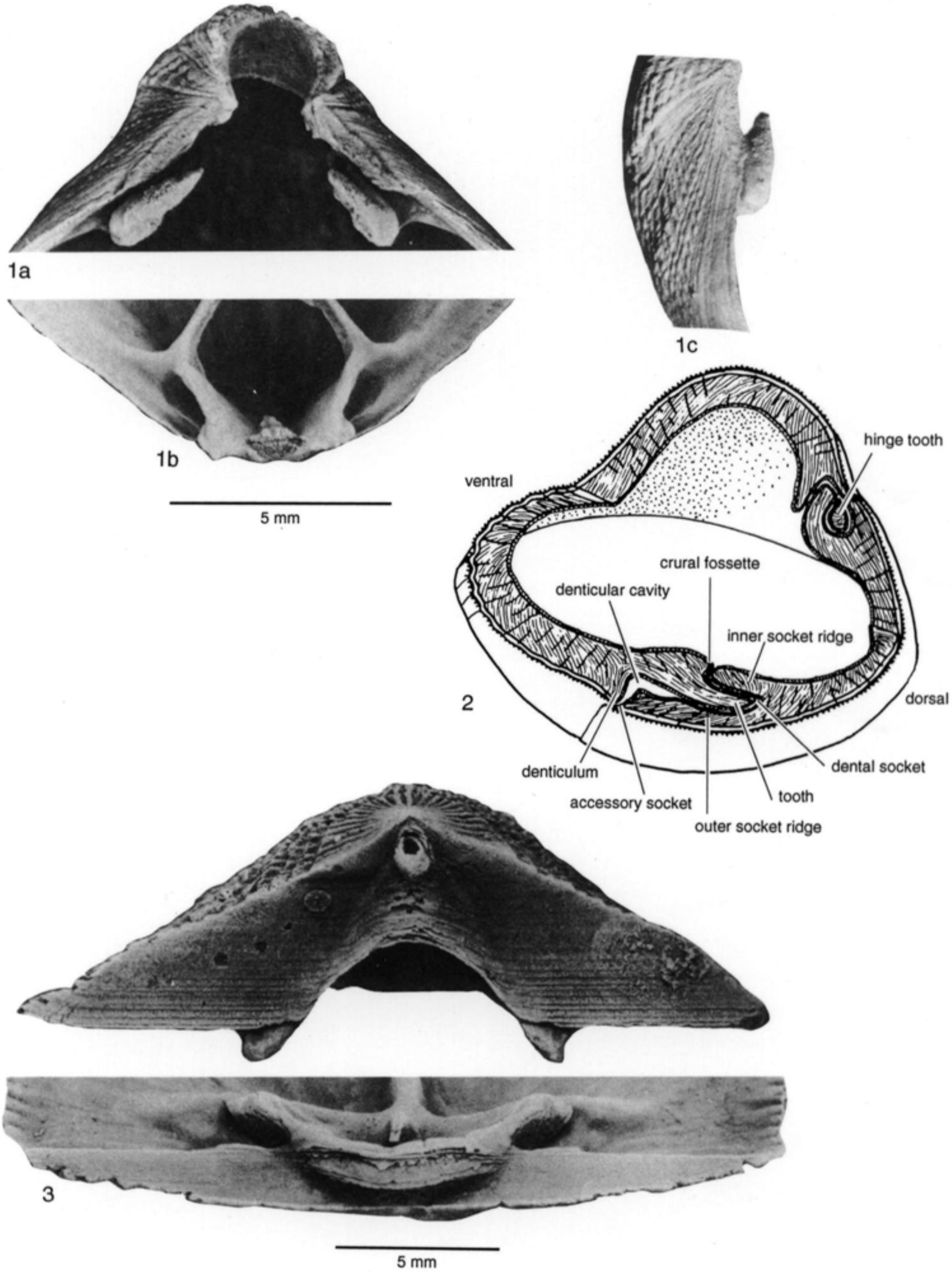

FIG. 322. *1–3.* Articulatory features; *1a–c,* cyrtomatodont *Terebratulina retusa* (LINNAEUS), recent, showing separated ventral and dorsal valves and a lateral view (Jaanusson, 1971); *2, T. retusa* umbonal region seen in transverse and submedian sections (Williams & Rowell, 1965b)*; 3,* deltidiodont *Clitambonites squamatus* (PAHLEN), Middle Ordovician, Estonia, showing separated ventral and dorsal valves (Jaanusson, 1971).

in hinge shape and function. A clear transformation, however, from deltidiodont to cyrtomatodont, possibly seen in the pentamerides, is not evident in the view of CARLSON (1993b). Although she demonstrated (1989) that the ability of brachiopods

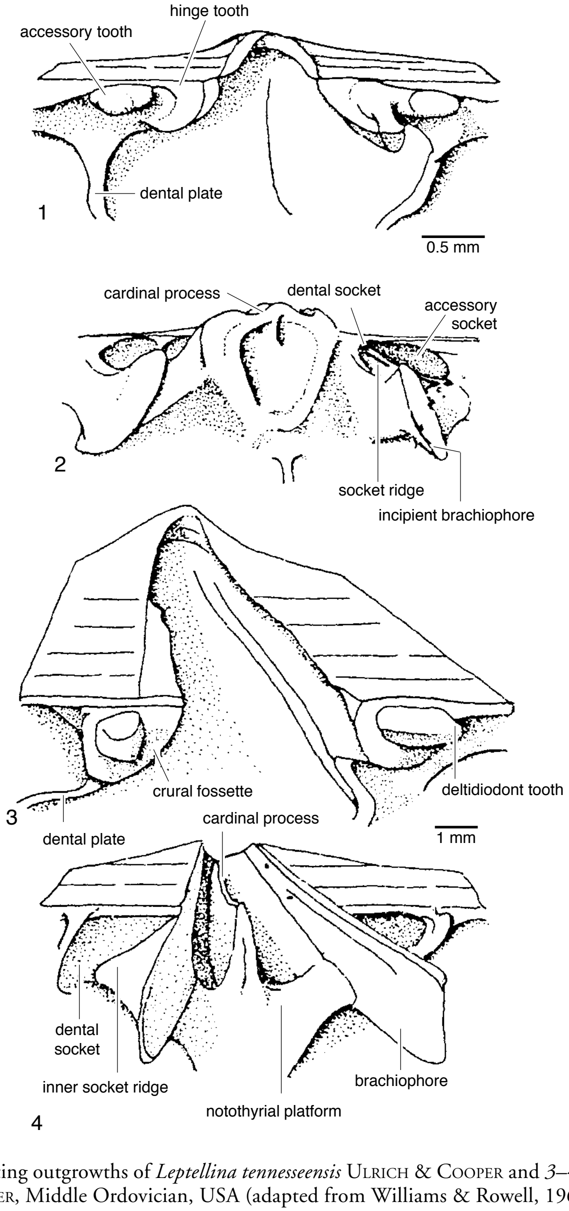

FIG. 323. *1–2,* Articulating outgrowths of *Leptellina tennesseensis* ULRICH & COOPER and *3–4, Hesperorthis australis* COOPER, Middle Ordovician, USA (adapted from Williams & Rowell, 1965b).

to resorb shell was not a prerequisite of cyrtomatodont articulation, it is undeniable that cyrtomatodont teeth are typical of the major groups in which shell resorption also plays important roles in the growth of spiral and loop-shaped brachia.

Teeth are varied 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. 323.1, 323.3). Dental plates in some spiriferides have been differentiated into two parts: **dental flanges,** which directly support the teeth, and ventral **adminicula** (BROWN, 1953) that connect these to the valve floor. Some authors follow BROWN (1953) in also recognizing dorsal adminicula, which connect crural bases to the dorsal valve floor, as

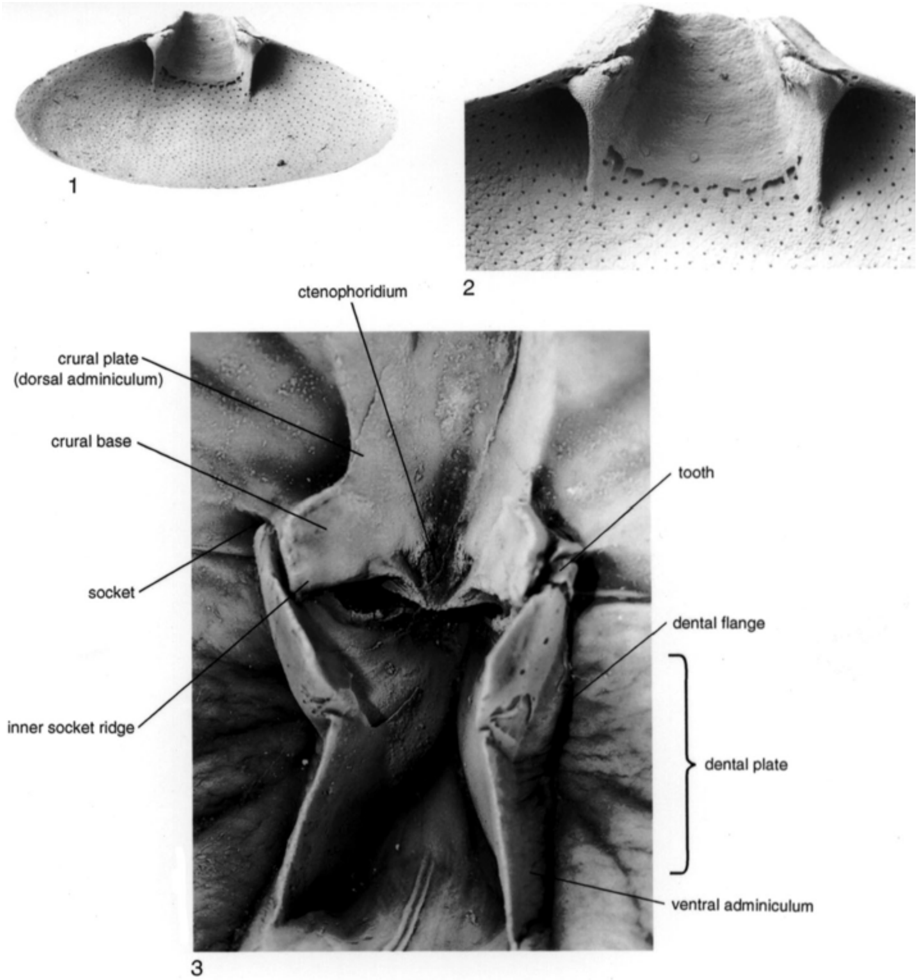

FIG. 324. Dental plates in *Fallax dalliniformis* ATKINS; *1,* general view, SEM, ×12.5; *2,* detail of dental plates and pedicle collar, SEM, ×30 (new); *3,* latex replica of articulatory structures in *Tomiopsis,* Permian, Australia, showing the relationships between the supporting structures for teeth and crura, ×3 (new).

do the better-known crural plates (Fig. 324). The dorsal surface of the tooth 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 most common of these minor modifications (Fig. 323.3). It consists of a groove located on the inner (anteromedian) side of the tooth and accommodates the ventral surface of the inner socket ridge. A more unusual arrangement, which is especially characteristic of the plectambonitoids, involves the growth of a pair of **accessory teeth** lateral to the teeth bordering the delthyrium and separated by a pair of deep grooves (Fig. 323.1; ÖPIK, 1930). Two pairs of sockets are found in the ventral 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** (Muir-Wood, 1934) may be used for the posterior edge of the ventral 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, the term 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. 322.2).

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 spiriferides, such **denticles** are small crenulations of primary and adjacent secondary shell underlying the interareas (Fig. 325.4–325.5), as are the denticles found in many plectambonitoids except that each of them appears to have been built up around a taleola (Fig. 325.3). The strophodontoid denticulation, in contrast, arises only 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 (Fig. 325.1–325.2; Williams, 1953). The denticulation of the chonetoid *Eodevonaria* and the strophalosioid *Ctenalosia* appears to be most closely related in development to that of the strophodontoids (Muir-Wood & Cooper, 1960).

Although all Early to Late Devonian productides have teeth and sockets, the productidines lost them entirely after the late Famennian. Articulation for most productidines relied upon the large, posteriorly projecting cardinal process extending into the confined ventral umbonal cavity. Not only did the cardinal process provide the simple lever system and muscle attachment necessary to open the shell, but also the location pin preventing lateral or rotational movement between the valves. Location and articulation of the valves was further aided by ridges close to the hinge lines fitting against slight depressions on the opposite valve (Fig. 326.1) and by the close fit of most dorsal valves within the more strongly convex ventral valve. By contrast, the articulation of many richthofeniids was by knobs (or **tegula**) at the positions of the ears on a narrow dorsal hinge fitting into weak pits in the ventral valve (Fig. 326.2).

Systems of articulation using thickened surfaces at the posterior margins are seen in such Lower Cambrian brachiopods as *Nisusia,* in which a thickened edge of the pseudodeltidium fits against shallow grooves in the dorsal valve, which can be identified as sockets and inner socket ridges; but no true teeth are present.

Early Cambrian calcareous-shelled brachiopods usually have strophic shells with a variety of articulatory structures (Popov, 1992); only chileides and some of the earliest Cambrian obolellides lack any form of articulation. The posterior margin of such early obolellides as *Obolella* and *Magnicanalis* is similar to that of chileides, with a ventral interarea and narrow delthyrium, but with a narrower and low dorsal pseudointerarea. In other Early Cambrian obolellides such as *Bicea, Alisina, Siberia,* or *Trematobolus* (Fig. 327.3), however, there are small teeth on the lateral sides of the delthyrium and shallow sockets on the posterolateral sides of the low notothyrial platform. In *Bicia* the teeth are composed partly of primary shell (Ushatinskaya, 1988), but in other obolellide genera they are composed entirely of secondary shell, lack supporting structures, and have no inner socket ridges. In the obolellide suborder Naukatidina the teeth are situated on an **anteris** (Fig. 327.4), forming an arcuate thickening of secondary shell anterior to the delthyrium.

A different pattern of articulation is known in the Kutorginida, including nisusiids, all of which have strophic shells and well-defined interareas on both valves. In the Lower Cambrian *Kutorgina* there are deep

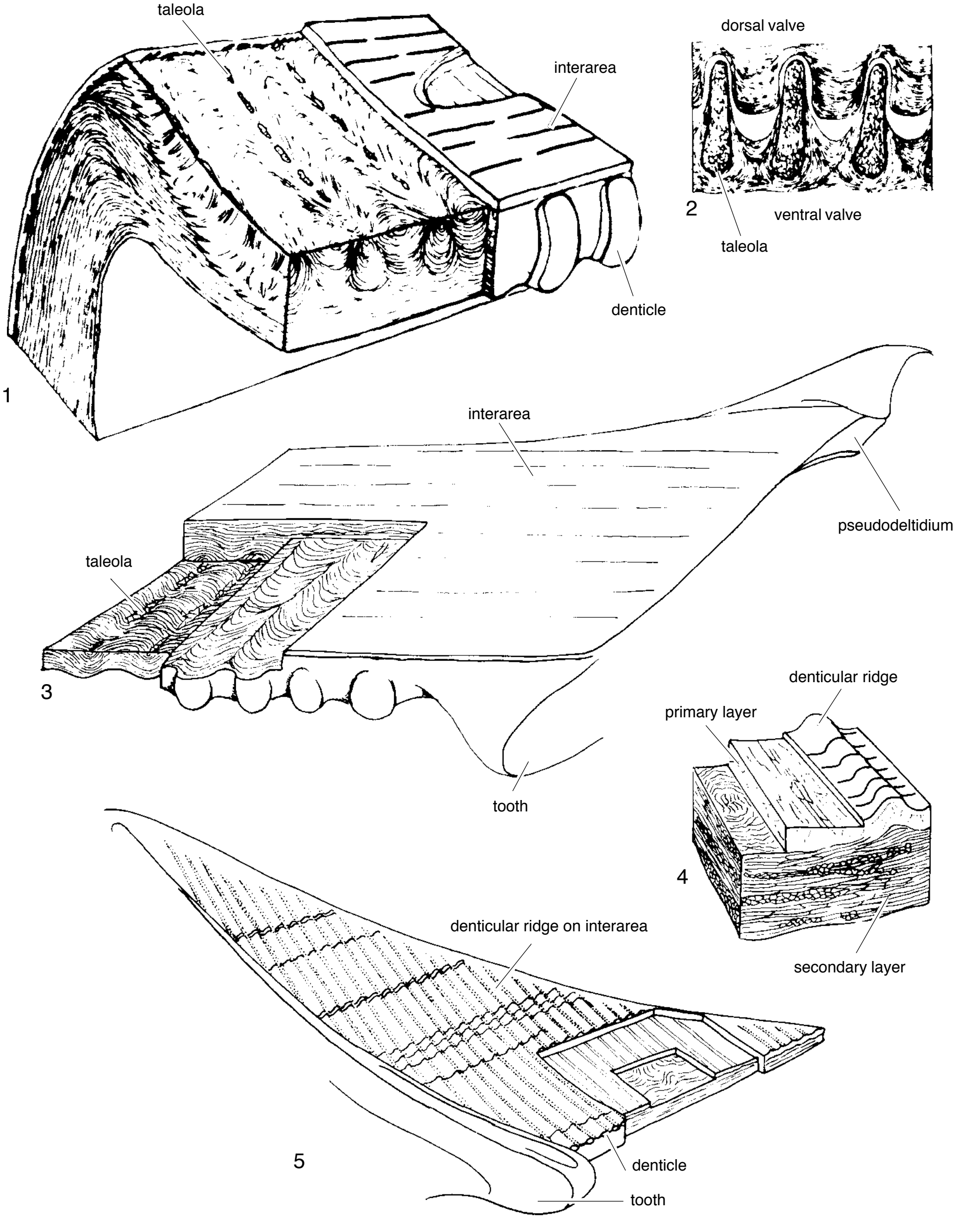

Fig. 325. Stylized denticular structures in *1, Pholidostrophia* sp., Middle Devonian, USA; *2, Plectodonta transversalis* Wahlenberg, Middle Silurian, England (adapted from Williams, 1953); *3,* a plectambonitacean; and *4–5,* a spiriferid (adapted from Williams & Rowell, 1965b).

furrows lateral to a broad pseudodeltidium and triangular dorsal propareas that fit into the furrows (Fig. 327.1; Popov & Tikhonov, 1990). This pattern of articulation is modified in nisusiids, as in *Nisusia* and *Narynella,* in which furrows and ridges are present along the inner sides of the ventral propareas, lateral to the pseudodeltidium,

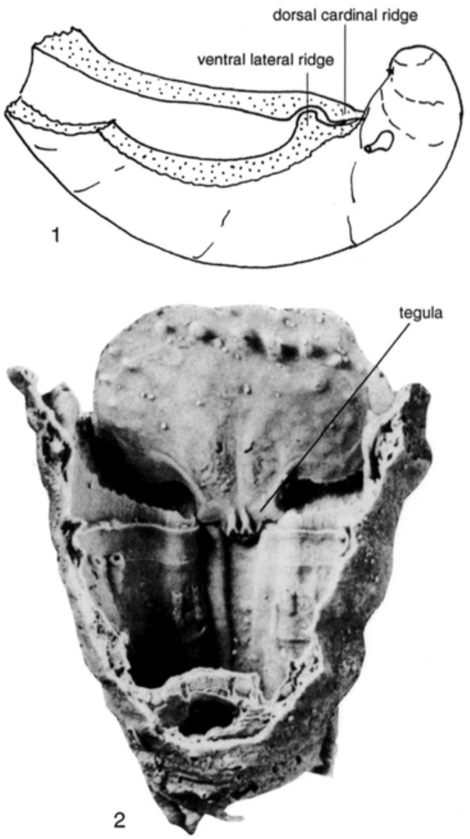

FIG. 326. *1,* Articulating hinge ridges in oblique lateral view of a submedian section of *Argentiproductus margaritaceus* (PHILLIPS), Lower Carboniferous, northern Wales (new); *2, Cyclacantharia kingorum* COOPER & GRANT, in the open position showing the articulating tegula on the dorsal valve hinge line fitting depressions at the hinge line of the ventral corpus, Upper Permian, Texas, ×2 (adapted from Cooper & Grant, 1975) .

which articulate with sockets, bounded by inner socket ridges originating on the inner sides of the dorsal propareas (Fig. 327.2). These paired sockets and ridges are functionally comparable with those of orthides but are probably not homologous and differ in being formed of primary plus secondary shell (ROWELL & CARUSO, 1985).

A similar type of articulation developed independently in the craniformean trimerellides (NORFORD & STEELE, 1969; GORJANSKY & POPOV, 1985, 1986). Most trimerellide genera, such as *Dinobolus, Eodinobolus, Monomerella,* and *Trimerella,* have cardinalia with a median hinge plate that fits into the cardinal socket of the ventral valve (Fig. 328). The axis of rotation is along the outer sides of the ventral propareas. The concave **homeodeltidium** of trimerellides did not originate only as a cover to the pedicle opening but also as a means of restricting lateral movement of the dorsal valve.

A simple articulatory structure occurs in some lingulates. For example, in the Late Cambrian acrotretid genus *Linnarssonella* the dorsal pseudointerarea has distinctive grooves that may have functioned as simple sockets fitting with ridges on the ventral pseudointerarea and may have restricted relative movement and sliding of the valves. There are similar structures on the dorsal propareas of some acrotretides within the Torynelasmatinae, and a similar feature is present in the obolid *Dicellomus.* All these articulatory structures in lingulides and acrotretides, however, are only analogous to true sockets because they developed on the shell surface and not as modifications of the inner shell layers.

The ridges defining the sockets in the dorsal valve of toothed articulated 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 provide vital structures, even from the earliest growth stages. Apart from defining the sockets (allowing articulation between the valves), the cardinalia 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 (Fig. 329–330), and since combinations of them tend to be characteristic of major taxa, complicated terminologies, frequently incompatible with one another, have grown up for each taxon. In living brachiopods the importance of articulation is clearly expressed by the presence of well-differentiated teeth and sockets, even

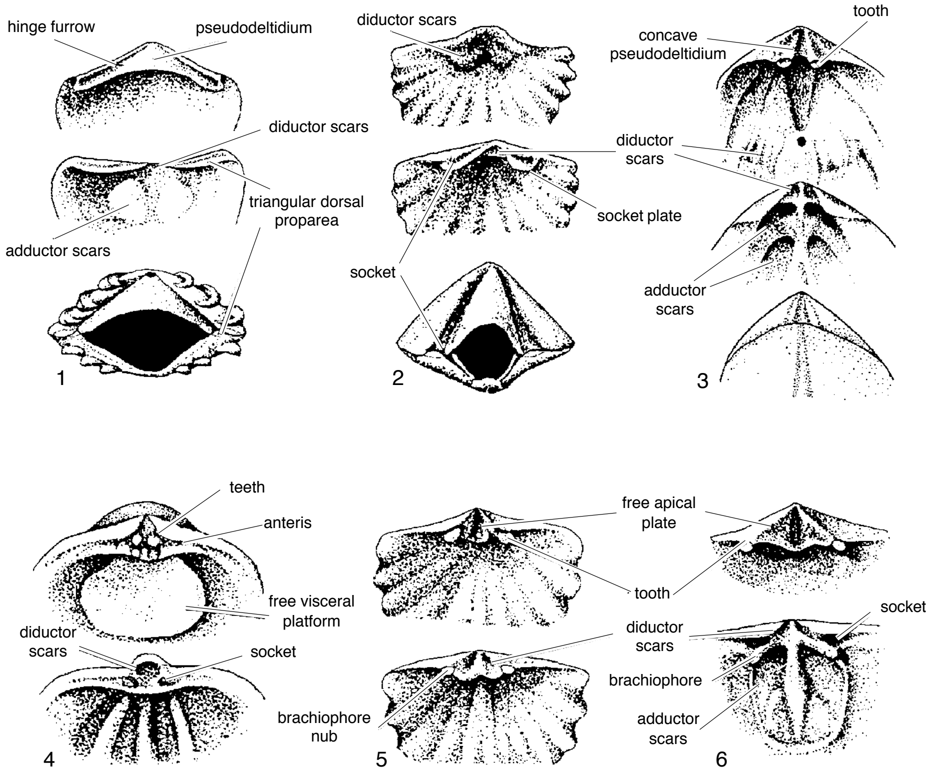

FIG. 327. Articulation of various groups of brachiopods lacking a well-developed tooth-and-socket hinge mechanism; *1, Kutorgina; 2, Nisusia; 3, Trematobolus; 4, Oina; 5, Glyptoria; 6, Arctohedra* (adapted from Popov, 1992).

in the smallest of shells (Stricker & Reed, 1985b). When shells are still only a few millimeters long, crura start to grow from the prominent, inner socket ridges and soon support the body wall in the mouth region of the lophophore. Thus in the ontogeny of living specimens as well as in the evolution of articulated brachiopods, the lophophore-support structures had origins intimately associated with the inner socket ridges.

Another generality in the emended terminology is that a structure connecting some part of the cardinalia to the valve floor, with cavities remaining between it and the valve wall, is called a plate, while a shell thickening, representing the growth trace of a structures, is called a base (as in crural bases). In view of the above the terminology of the cardinalia has been rationalized as compared to that of the 1965 edition (Fig. 331). Previously used, but discarded, terms are listed as synonyms in the glossary of morphological terms (p. 423–440).

An important element in the dorsal valve cardinalia is a medially situated structure (**cardinal process**), which is developed as the attachment area for the dorsal ends of the diductor muscles. This feature is more conveniently dealt with when considering the shell modifications resulting from the insertion of muscles concerned with relative movements of valves (see section on musculature, p. 385).

True deltidiodont teeth fitting well-developed sockets with inner ridges first appeared in the mid-Cambrian orthides and pentamerides (Popov, 1992). In mid-Cambrian and later orthides (Fig. 329.1),

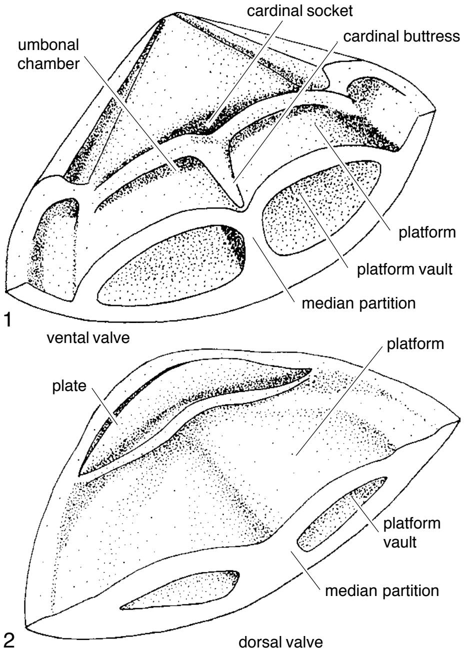

FIG. 328. Morphology of posterior region of *1,* ventral valve and *2,* dorsal valve of *Dinobolus* (Williams & Rowell, 1965b).

a pair of widely divergent ridges act as inner walls to sockets that are excavated within the secondary shell, uniting the ridges with the edge of the dorsal interarea. Medially, the proximal ends of these socket ridges may be encased by lateral extensions of a low-lying deposit of secondary shell that forms the floor of the notothyrium (**notothyrial platform**). These socket ridges have been called **brachiophores** in the belief that prolongations of their distal (anteroventral) edges gave support to the lophophore. Such processes, however, are unknown in early protorthoids, 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 it is questionable whether they extend sufficiently anteroventrally to reach the inferred position of the anterior body wall. In all, it seems preferable to use the term **inner socket ridge** for widely divergent structures of limited extension like those of the billingselloids, strophomenoids, as well as in all other groups (Fig. 329.2; WILLIAMS, 1953). Certainly an exclusive function of articulation may be inferred for the socket ridges of strophodontids although they became vestigial or even disappeared subsequent to the loss of teeth in members of that family (WILLIAMS, 1953).

The orthoid arrangement represents a significant advance in that the shell outgrowths (commonly in the past called brachiophores) associated with the ventromedian limits of the socket ridges were rotated to point anterolaterally and were also prolonged as blade-shaped or rodlike processes beyond the limits of the sockets (SCHUCHERT & COOPER, 1932). Thus disposed, they probably performed the function of the crura in more recent groups. However, in view of the functional uncertainty of these structures in stratigraphically older taxa, the term brachiophore remains appropriate in those species. Disposed as previously described, the brachiophores are free of the posterior margin and in many orthoids (e.g., *Hesperorthis*) are supported by a well-developed notothyrial platform (Fig. 329.4). The sockets are grooves in a thick, secondary shell deposit between the socket ridges and the posterior margin; but in other orthoids the development of a pair of lateral umbonal cavities within the shell thickening underlying the sockets may lead to the differentiation ventrally and medially of **fulcral** and **socket plates** respectively (Fig. 332). The forward growth of brachiophores (or **crural bases**) and their anterior processes, as in most enteletoids and many orthoids, was accompanied by the forward growth of support plates reaching the floor of the dorsal valve. These plates, which can include those called socket plates, may be disposed at varying angles to the median plane of symmetry and have been called supporting plates only when they converge toward the dorsal median ridge. It seems best, however, to refer to them as **brachiophore plates,** irrespective of

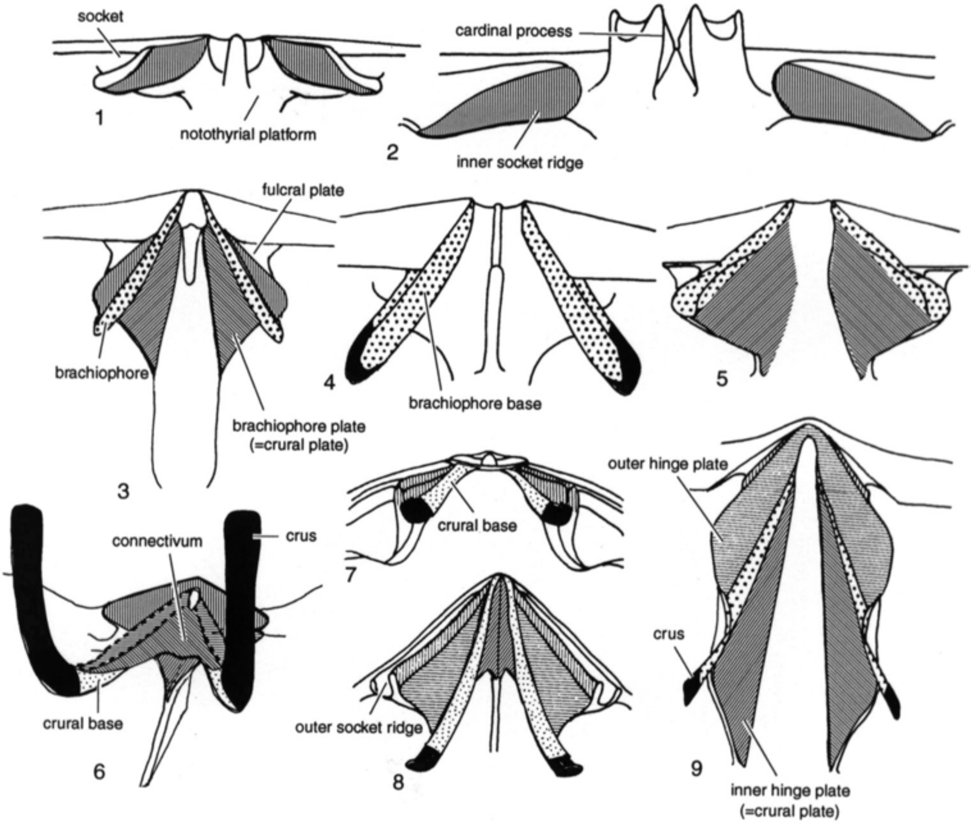

FIG. 329. Cardinalia of *1, Billingsella; 2, Strophomena; 3, Dalmanella; 4, Hesperorthis; 5, Imbricatia* (adapted from Williams & Rowell, 1965b); *6,* a Devonian rhynchonellid (adapted from Johnson & Westbroek, 1971); *7, Notosaria; 8,* a camarotoechiid; and *9, Gypidula,* all ventral views; *vertical lines,* inner socket ridge; *horizontal lines,* outer hinge plate; *diagonal lines,* inner hinge plate, brachiophore plate, or crural plate; *dots,* brachiophore or crural base; *solid black,* crus (adapted from Williams & Rowell, 1965b).

inclination (WILLIAMS & WRIGHT, 1963) and to think of them as homologues of crural plates in more recent taxa.

It is significant that the ventral adjustor scars are first indisputably identified in the orthoids and enteletoids, 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 (WILLIAMS & WRIGHT, 1963). This is exactly the situation seen in living species, where pedicle adjustor muscle scars are distinguished before diductor muscle scars. Initially, dorsal adjustor muscles are situated between the inner socket ridges, but commonly they spread during ontogeny onto variously disposed hinge plates as these grew.

The cardinalia of early porambonitoids consist essentially of socket ridges and brachiophores (ULRICH & COOPER, 1938) with plates variably convergent onto the floor of the valve (Fig. 329.5). The protruding brachiophores (called brachiophore processes in some literature) may be negligible in the older stocks but were very well developed in such younger forms as *Camerella,* where they deserve the name crura. Furthermore, a raised ridge is commonly found standing above the posterior edge of the

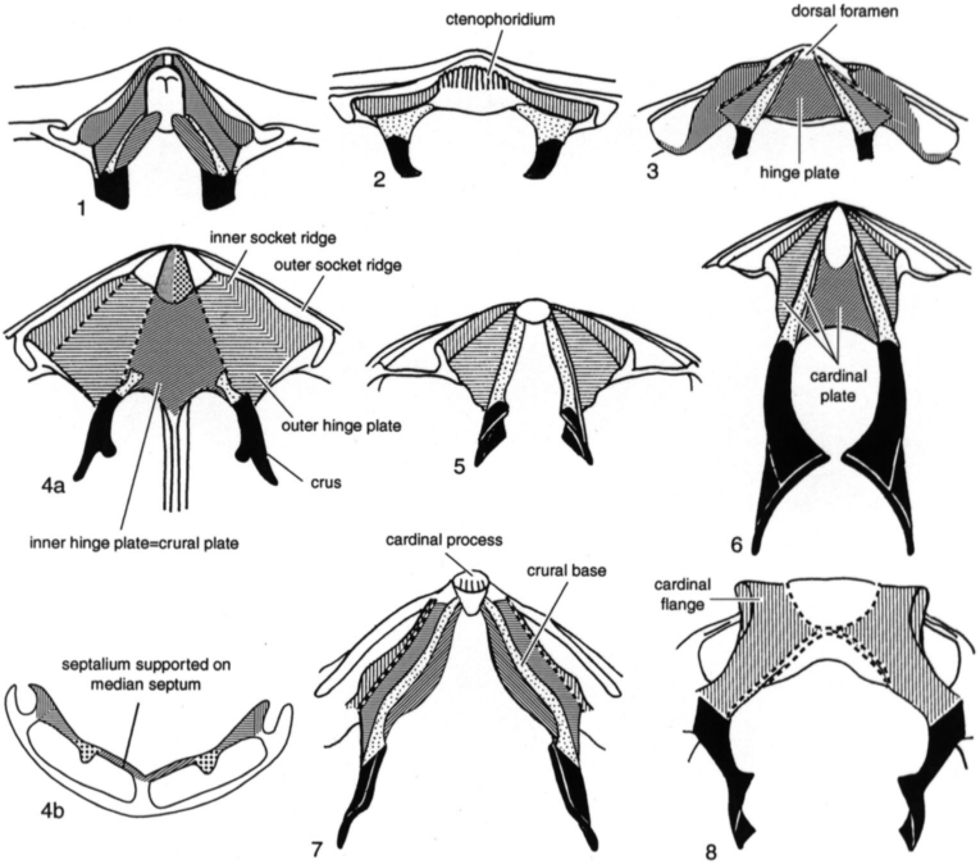

FIG. 330. Cardinalia of *1, Crenispirifer; 2, Neospirifer; 3,* young *Cleiothyridina; 4a,b, Laqueus; 5, Dallithyris; 6, Nanothyris; 7, Terebratula;* and *8, Terebratulina;* all ventral views except 4b (new), which is a transverse section showing the septalium; *vertical lines,* inner socket ridge; *horizontal lines,* outer hinge plate; *diagonal lines,* inner hinge plate, brachiophore plate, or crural plate; *dots,* brachiophore or crural base; *solid black,* crus (adapted from Williams & Rowell, 1965b).

brachiophore (or crural base) but intervening between it and the concave socket floor or 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 crural base) or within the fulcral plate as an inner restriction to a small posterolateral socket. These arrangements, however, 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 socket, which now intervenes between the inner socket ridge and the brachiophore, is homologous with the outer hinge plate, thus justifying the term crural base for the brachiophore (Fig. 329.6–329.7). One other modification is noteworthy. In camerellids, for example, the brachiophore plates converge toward the floor of the valves, either uniting with or fusing to form a median septum. This structure has been referred to as a cruralium, but since it did not contain the dorsal ends of the adductor muscles, it is more correctly termed a **septalium** (Fig. 330).

The use of an entirely different terminology for the pentameroid cardinalia is not a reflection of any radical departure from the

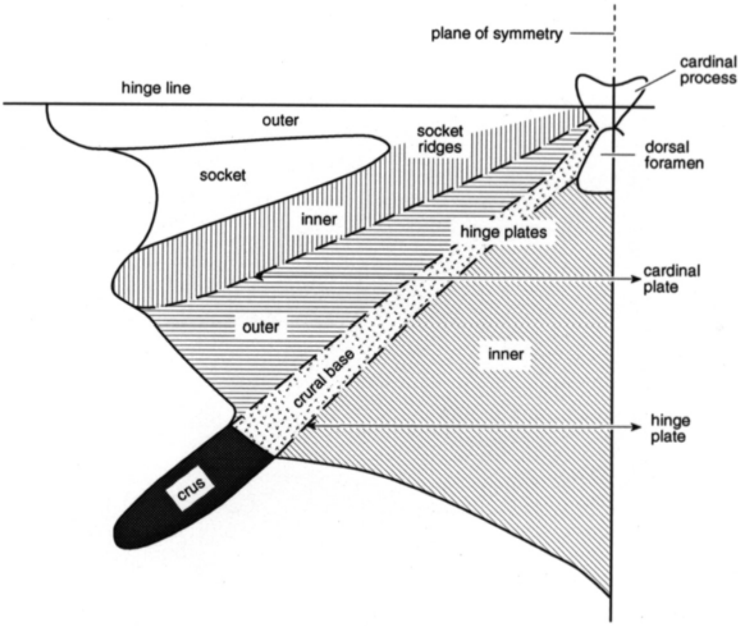

FIG. 331. Schematic view showing relationships of structures within the cardinalia of articulated brachiopods (new).

morphology of ancestral groups but of historical precedent. In general, the cardinalia are only better developed, or, as with the homologues of the brachiophore plates, are only differently disposed. Nonetheless the extended crus of the pentameroids has been known as the brachial process, the brachiophore plate or crural plate as the outer plate, and the outer hinge plate (with or without modification like the inner socket ridge) as the inner plate (Fig. 329.9; ST. JOSEPH, 1938). Such terminology is so divorced from that employed for other groups that it should be discarded in favor of the more unified terminology presented here and seen, for example, in the rhynchonelloid cardinalia.

In the remaining groups of articulated brachiopods some sort of calcareous support to the lophophore was almost invariably developed, so that greatly prolonged homologues of the brachiophores and their processes of the early Paleozoic brachiopods are the **crura,** which form important elements 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 rhynchonellides, in terebratulides, and in many spire-bearing brachiopods performed a similar function. Only rarely, as in *Enteletes* and *Skenidioides,* were brachiophores known to be sufficiently prolonged and suitably disposed to give support to the lophophore (WILLIAMS, 1956). 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 an elaboration of the terminology used for the more primitive groups. The rhynchonellide crura were commonly supported by a pair of plates (**crural plates**) that converged to form a septalium (Fig. 329.6–329.7). In some Paleozoic rhynchonelloids another pair of plates grew from the median sides of the crural bases to fully or partially cover the septalium ventrally. These have been called inner hinge plates or the **connectivum**

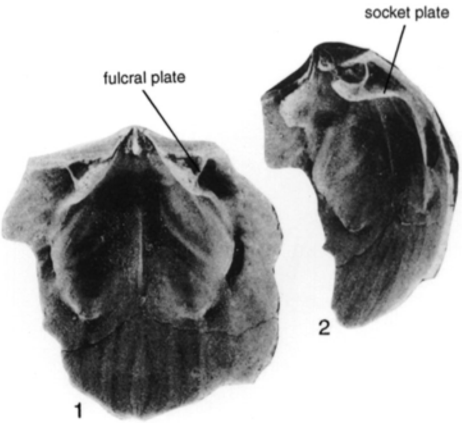

FIG. 332. Dorsal valve interior views of *Schizophoria iowensis* (HALL), Upper Devonian, Iowa, USA, showing socket structures, ×2 (Schuchert & Cooper, 1932).

(HAVLIČEK, 1961), but the former have well-defined different positions in Mesozoic and recent terebratulides, so it is recommended that the description cover plates or term connectivum be used (Fig. 329.6).

The cardinalia of Paleozoic terebratulides (CLOUD, 1942) are very much like those of the rhynchonellides, although the crural plates defining the septalium may be subparallel, as in *Nanothyris* (Fig. 330.6), 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. 330.6). The simplest arrangement found in post-Paleozoic terebratulides is that found in *Terebratulina* (Fig. 330.8), which consists of crura arising directly from high inner socket ridges. In other terebratulides like *Dallithyris,* outer hinge plates are differentiated (Fig. 330.5); and in a minority like *Terebratula,* a pair of discrete inner hinge plates were also developed (Fig. 330.7). The cardinalia of *Laqueus,* in contrast, include a pair of plates arising inside the crural bases and converging on to the dorsal median septum, forming a septalium. In the past, these have been called inner hinge plates, crural plates, or septalial plates. However, new studies of the early ontogenetic development of the cardinalia in very young *Laqueus* clearly indicate that the inner plates appear initially prior to the crura in association with the dorsal pedicle adjustor musculature and thus are more appropriately referred to as inner hinge plates.

The cardinalia of many spire-bearing brachiopods, especially the spiriferide and atrypide stocks, are reminiscent of *Terebratulina* in that the crura arose directly from well-developed inner socket ridges (e.g., *Neospirifer,* Fig. 330.2). Less commonly, thin strips representing outer hinge plates (e.g., *Plectatrypa*), crural bases, and inner hinge plates (e.g., *Crenispirifer,* Fig. 330.1) were developed. Among *Athyris* and its allies (like *Cleiothyridina*), the inner hinge plates are commonly fused to form a median horizontal **hinge plate,** subtended between the inner sides of the crural bases or a **cardinal plate** between prominent inner socket ridges (Fig. 330.3). In earlier athyridides these undifferentiated hinge or cardinal plates are commonly penetrated posteromedially by a canal, the **dorsal foramen**, connecting the dorsal umbonal cavity to the ventral surface of the plate (see Fig. 359.1). In more recent examples this foramen is absent, and the cardinal plate is bounded posteromedially by ridges that, in some genera, aided articulation by curving posteroventrally into the ventral umbo. In still younger athyridides these ridges, called **cardinal flanges**, became serrated by diductor myophores, simulating, in some genera, a true cardinal process (see section on musculature, p. 396).

BRACHIDIA

The cardinalia of many articulated brachiopods are also connected with spirally coiled ribbons (**spiralia**) or calcareous **loops** (Fig. 333–334). 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 all. First, they represent outgrowths from the crura, extending well into the mantle cavity and, like the crura, were contained in sheaths of outer epithelium responsible for their

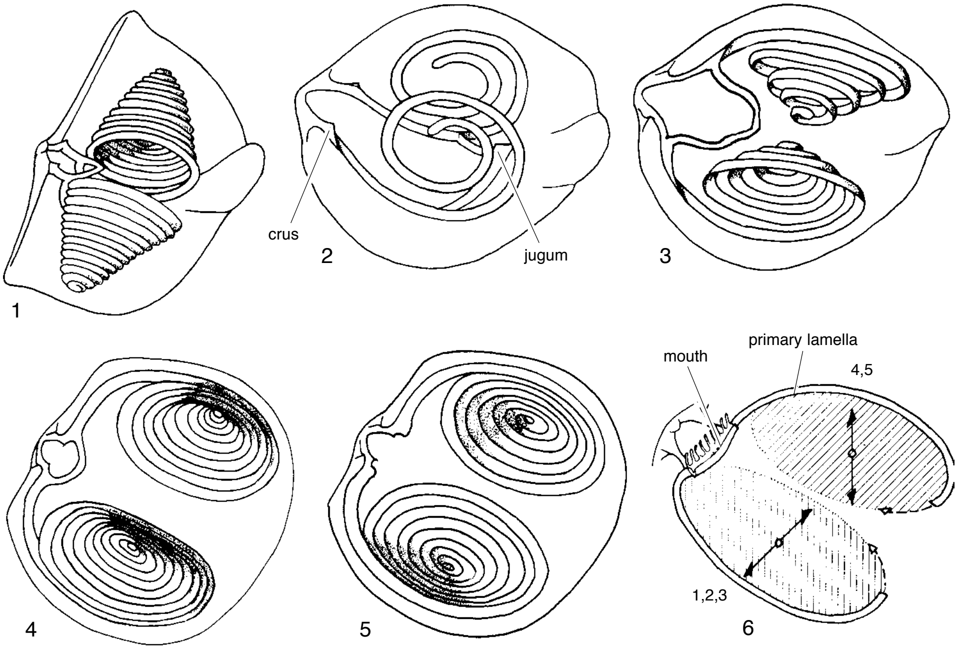

FIG. 333. Stylized representation of various attitudes adopted by primary lamellae of the spiralia relative to planes parallel with the plane of symmetry, as in *1,* a spiriferid, *2, Protozyga, 3,* a zygospirid; or parallel with the commissural plane (with apices of spiralium directed ventrally) as in *4,* a koninckinid, or *5,* an atrypid (with apices dorsally directed); 6, general diagram of the crus and primary lamellae showing the orientations of the previous representations (adapted from Williams & Rowell, 1965b).

growth and enlargement by controlled processes of secretion and resorption (WILLIAMS, 1956, 1968a; MACKINNON, 1991; MACKAY & others, 1994). Second, although the loops grew independently of the lophophores, in living terebratulides 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 (BEECHER & CLARKE, 1889), the first structure was an elongately oval loop formed by the anteromedian fusion of a pair of curved prongs extending from the crura. Thereafter, through a process of differential secretion and resorption, the anterior part of the loop became truncated to form a band (**jugum**) with a pair of short projections at the anterolateral corners (Fig. 335). These prolongations represent the beginnings of the first pair of coils (**primary lamellae**) of the spiralia.

Succeeding coils of the spiralia may be oriented to take up almost any attitude within the mantle cavity, but all of them are variations of five basic dispositions (Fig. 333). In most Atrypida, which include the geologically oldest spire bearers, the apices of spiralia were directed medially or dorsomedially but occasionally were planispiral parallel to the median plane. In most Spiriferida and Athyridida, the apices of the spiralia were laterally directed, but in Suessioidea and Koninckinoidea they were ventrally directed. Although laterally directed spiralia predominate in both the Spiriferida and Athyridida, the angular relationships between the crura and primary lamellae are markedly different in the two orders. In spiriferides, as well as in early atrypides such as *Protozyga,* the primary lamellae grew as direct extensions of the

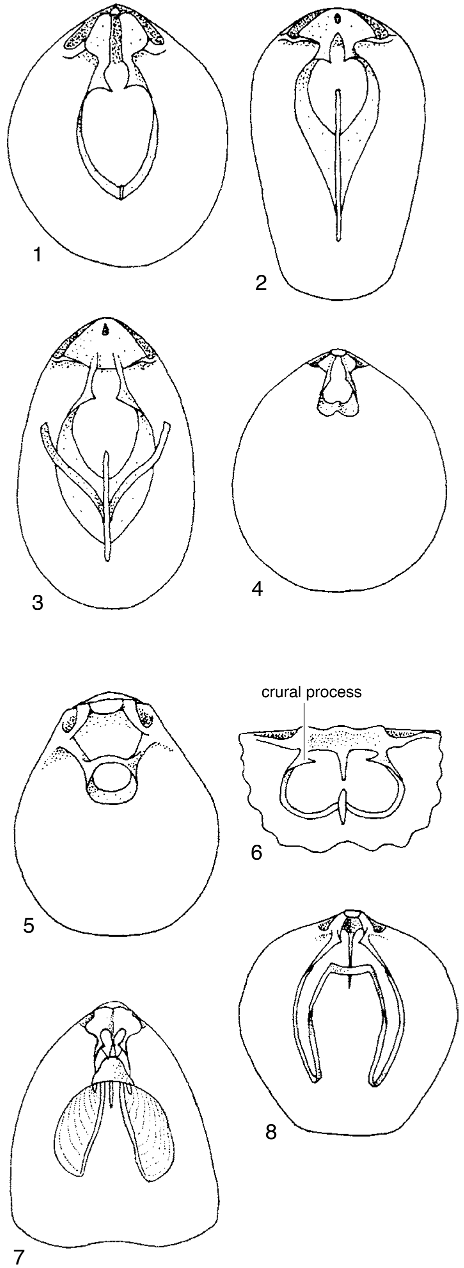

Fig. 334. Some loop forms in the Terebratulida; *1, Centronella; 2, Rensselaeria* (Cloud, 1942); *3, Gefonia* (Stehli, 1956); *4, Gryphus; 5, Terebratulina* (Williams & Rowell, 1965b); *6, Argyrotheca; 7, Campages* (adapted from Thomson, 1927); *8, Magellania* (Williams & Rowell, 1965b).

anteriorly directed crura (Fig. 333.2); in athyridides the initial growth direction of primary lamellae was posterior (Fig. 336), in precisely the opposite direction from that of the crura.

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 some adult Spiriferida and Atrypida. In a few stocks, like *Cyclospira,* however, no jugum has been found in well-preserved adult shells, suggesting that the spiralia developed directly from the crura and not by modification of a loop (Copper, 1965, 1986). Furthermore, Copper (1986) has argued that in the earliest atrypides of Late Ordovician age, the spiralia evolved without the development of a jugum and that this structure is only found in some later stocks. By the Silurian, the **jugal processes** in many atrypoids became divided. The relationship of the spiralia to the crura in atrypides may also differ from other spire bearers. Copper (1986) suggested, for atrypides, that the lack of continuous skeletal connection between crura and spiralia allowed the spiralia some freedom of movement within the mantle cavity. Copper's contention (1965) that generation of the spiralia may have occurred at this proximal position of the crura has been contested by MacKinnon (1991), who advocated expansion of the spiralia by generative zones at the leading edges of each spiralium. In Athyridida, by contrast, development and elaboration of the jugum was widespread. Here the jugum consists of a pair of **lateral jugal branches** that arose near the middle of the dorsal limb of the primary lamella and extend ventromedially or anteromedially, until they unite in a V- or U-shaped jugal arch (Alvarez, 1990). Commonly the leading edge of the jugal arch is extended anteriorly as a prominent, anteriorly spinose jugal saddle, while the posterior

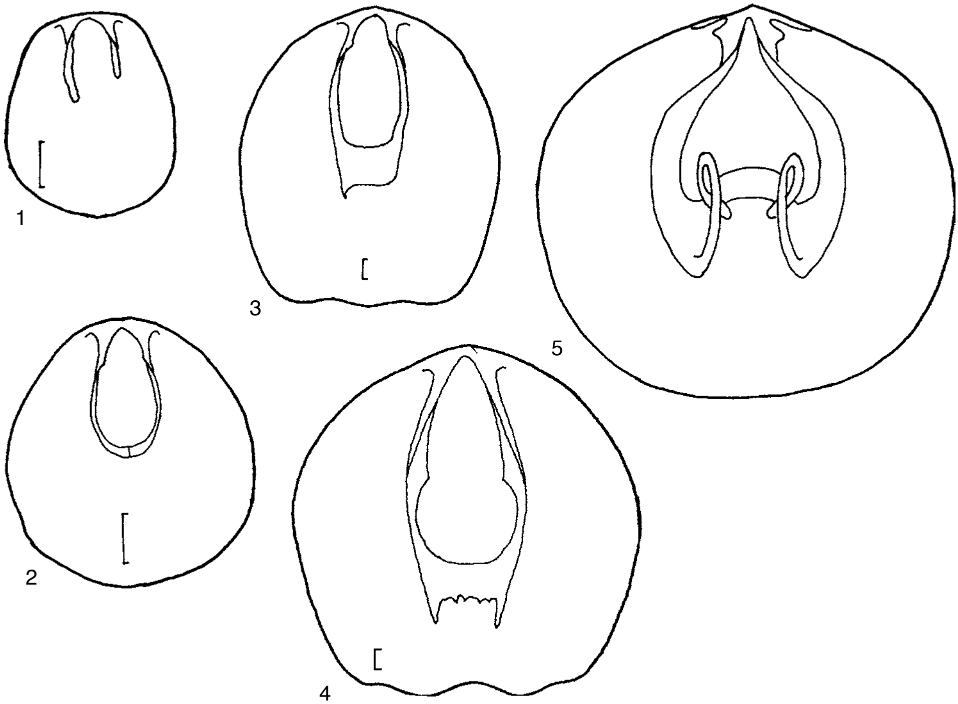

FIG. 335. Growth of the brachidial apparatus of *Protozyga; 1–4, P. elongata* COOPER; scale bars: 0.1 mm (adapted from Williams & Wright, 1961); *5, P. exigua* (HALL) with adult loop (adapted from Copper, 1986).

edge of the jugal arch tapers and bends sharply to become a thin, posteromedially directed process, the **jugal stem**. In a number of stocks bifurcation of the jugal stem gave rise to a pair of arcs (**arms of the jugum**) lateral to the primarly lamellae. In some Meristellidae, strongly arcuate jugal bifurcations became reunited with either the jugum or jugal stem to form a pair of jugal loops. In *Athyris* and related genera, the arms of the jugum were further extended as narrow curved blades (**accessory lamellae**) running adjacent to the primary lamellae for about half a coil (Fig. 336). In certain other, unrelated genera (e.g., *Kayseria, Diplospirella,* and *Koninckina*) the accessory lamellae continued to grow into a pair of spires coextensive with the entire primary spiralium.

The relationship of the inferred lophophore to the calcareous spiralium and its functional morphology have been the subject of debate. The simple spirolophe coincident with the spiralia, as advocated by RUDWICK (1960), may not be true for all genera. If the paired generative zones of the early schizolophe were retained medially on the jugum, which must have been their 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 (WILLIAMS, 1956). In these circumstances the double lophophore (**deuterolophe**) borne by the spiralia would have been homologous with the side arm of *Terebratulina* (Fig. 337.4; WILLIAMS & WRIGHT, 1961). In the athyridides ALVAREZ and BRUNTON (1990) suggested that the migration of the generative zones from the jugum posterolaterally formed the accessory lamellae while, anteriorly, the deuterolophe continued to grow on the apical sides of the

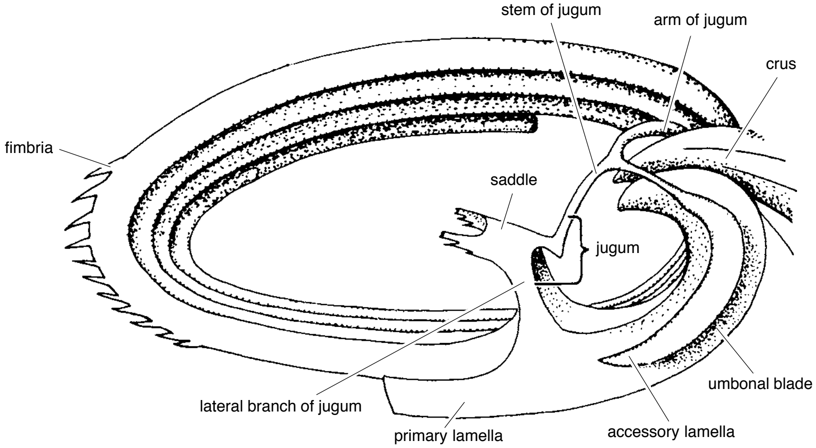

FIG. 336. Structure of spiralium in an athyridid (Hall & Clarke, 1894–1895).

developing spiralium. The demonstration by MacKinnon (1974, 1991) that the shell structure of spiralia in many spiriferides and atrypides differs from that of athyridides indicates that there may well have been fundamental differences in the dispositions of their lophophores. Campbell and Chatterton (1979) reviewed the discussion on spiralia and their inferred lophophore reconstructions in a detailed study of *Coelospira.* Its double spires, which do not connect with the crura, and unusual jugal apparatus were thought to have supported a double lophophore with the jugum secreted by epithelium from both valves, allowing some adjustment of the lophophore position while the shell was open.

Calcareous ribbons composed of secondary shell and brachiotest (Mackay and others, 1994) may also extend from the distal ends of crura to form a closed structure known as the **loop**, which is especially characteristic of the Terebratulida. The loop varies greatly, not only in form but also in origin and growth; yet it gives support to a plectolophous lophophore in the great majority of living adult terebratulides, an association that also probably applied to most fossil members of the group. Depending on whether support for both the side arms and the central coil of the plectolophe is provided by a narrow and twisted calcareous ribbon (Mackay and others, 1994) or by a spicular meshwork, the terebratulide brachidium may be broadly categorized as either long-looped or short-looped. In the past, it was customary to apply to mainly long-looped terebratulides an extensive loop terminology based on genera considered to be closely related phylogenetically that purported to illustrate various stages of loop development in particular stocks (e.g., Thomson, 1927; Muir-Wood, 1934; Elliott, 1953; Cooper, 1956; Stehli, 1956). By the mid-1970s at least ten stocks had been given their own set of terms (Dagys, 1974). In order to overcome the difficulties in dealing with the plethora of taxon-based terminology, which has, at times, been based on incomplete sequences of loop development, a more recently proposed descriptive scheme (Richardson, 1975), somewhat emended and expanded, is introduced herein.

The simplest loop arrangement is found in Paleozoic terebratulides such as *Centronella* (Fig. 334.1) and consists of a pair of gently curved **descending lamellae** that unite anteriorly and tend to form a broad-pointed blade, the **echmidium.** This is the **acuminate loop,** 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 *Rensellandia,* with or without peripheral spines (e.g., *Stringocephalus*); how-

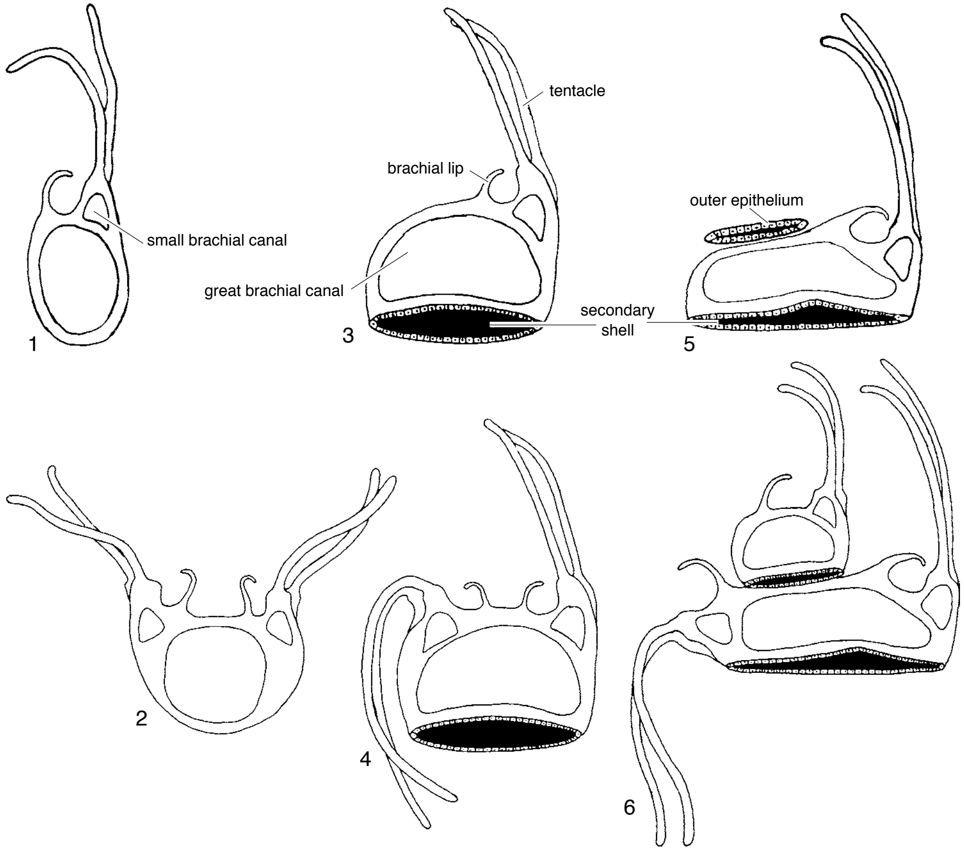

FIG. 337. Diagrammatic cross sections of lophophore of *1, Notosaria* and *2,* side arm of *Terebratulina* with inferred lophophore restorations of *3–4,* spiriferoids and *5–6,* athyridoids, according to whether they should be homologized with *1* (as in *3* and *5*) or with *2* (as in *4* and *6*) (adapted from Williams & Rowell, 1965b).

ever, in a number of Paleozoic and Mesozoic terebratulides, a ventrally projecting median plate (vertical plate) developed normal to the echmidium (e.g., *Rensselaeria,* Fig. 334.2). Accelerated growth in the anterolateral parts of a juvenile, acuminate loop (with or without a vertical plate) gave rise, in the adult stage of many Paleozoic terebratulides (e.g., *Dielasma* and *Cranaena*), to a **deltiform loop** (Fig. 338). This subtriangular form of loop, consisting of two short, divergent descending lamellae with distal extremities united by an undulating transverse band, is typical also of many post-Paleozoic, short-looped brachiopods and is very similar to that partly supporting a plectolophous lophophore in living *Gryphus.* In such late Paleozoic dielasmatoids as *Labaia* and *Gefonia,* the ventral edge of the vertical plate split into a pair of slender, sharply recurved lamellae that, unlike the **ascending lamellae** of post-Paleozoic, long-looped forms, were not posteriorly united by a transverse band. In *Cryptacanthia* and related stocks (COOPER, 1957; COOPER & GRANT, 1976), however, the echmidium (without a vertical plate) was the site of differential secretion and resorption of a juvenile acuminate loop that gave rise, ultimately, to a **teloform** loop (Fig. 338) consisting of long, gently curved descending lamellae and reflected ascending lamellae united by a transverse band. The teloform loop of *Cryptacanthia* and its allies is comparable to that supporting a plectolophous lophophore of many recent terebratellidines but fashioned in an entirely different way.

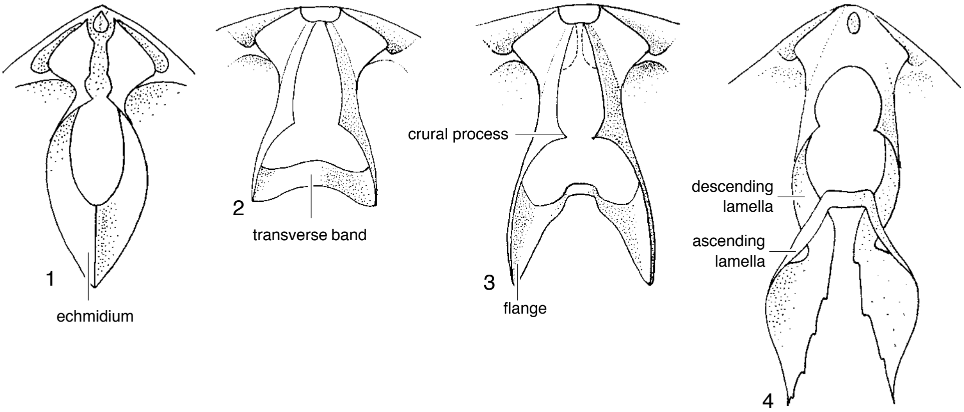

FIG. 338. Terebratulide loop types; *1,* acuminate loop of *Centronella* (adapted from Stehli, 1965); *2,* deltiform loop typical of many short-looped Terebratuloidea; *3,* long-flanged deltiform loop typical of Lobothyroidea (adapted from Cooper, 1983); *4,* teloform loop of *Cryptacanthia* (adapted from Cooper, 1957).

Unlike their Paleozoic antecedents, growth of a teloform loop in most post-Paleozoic terebratulides is linked with the development of a **septal pillar**, which first makes its appearance as a high columnar or platelike outgrowth from the dorsal valve floor. During the ontogeny of many long-looped taxa, the ventral or posteroventral edge of the septal pillar undergoes cleavage to form first a shallow groove and then an inverted, variably compressed cone or hood. By means of localized resorption in the vicinity of the dorsally directed apex of the hood and secretion of new shell around its ventrally facing rim, the hood is transformed into a ring, representing the rudiments of the ascending lamellae 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 septal pillar or a pair of posteriorly directed outgrowths. From such beginnings, the development of a teloform loop may involve any one of a number of complex series of metamorphoses; these are more fully discussed and illustrated in the systematic volume dealing with the terebratulides (Part H(R), vol. 4, in preparation).

Although many long-looped taxa utilize a septal pillar during various complex loop metamorphoses, similarly complex loop sequences have been recorded in several species of Mesozoic Loboidothyroidea that, as adults, exhibit essentially a deltiform loop with extremely prominent, long-flanged, anterolateral extremities (Fig. 338). In forms such as *Viligothyris* and *Taimyrothyris,* juvenile phases of loop development involve the growth of ascending elements such as a hood and ring, not on a septal pillar but on a vertical plate supported only by descending lamellae (DAGYS, 1968, 1972). In many-short looped terebratuloids, support for the side arms and central coil of the plectolophe is provided by a dense, interlocking

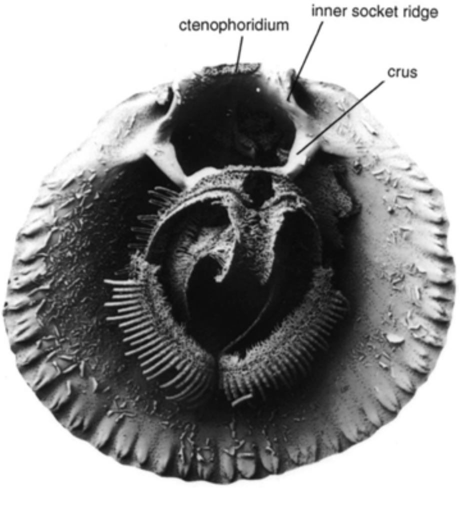

FIG. 339. *Terebratulina unguicula* (CARPENTER), recent, Puget Sound, USA, showing the nearly complete spiculation of the lophophore, SEM, ×7.5 (new).

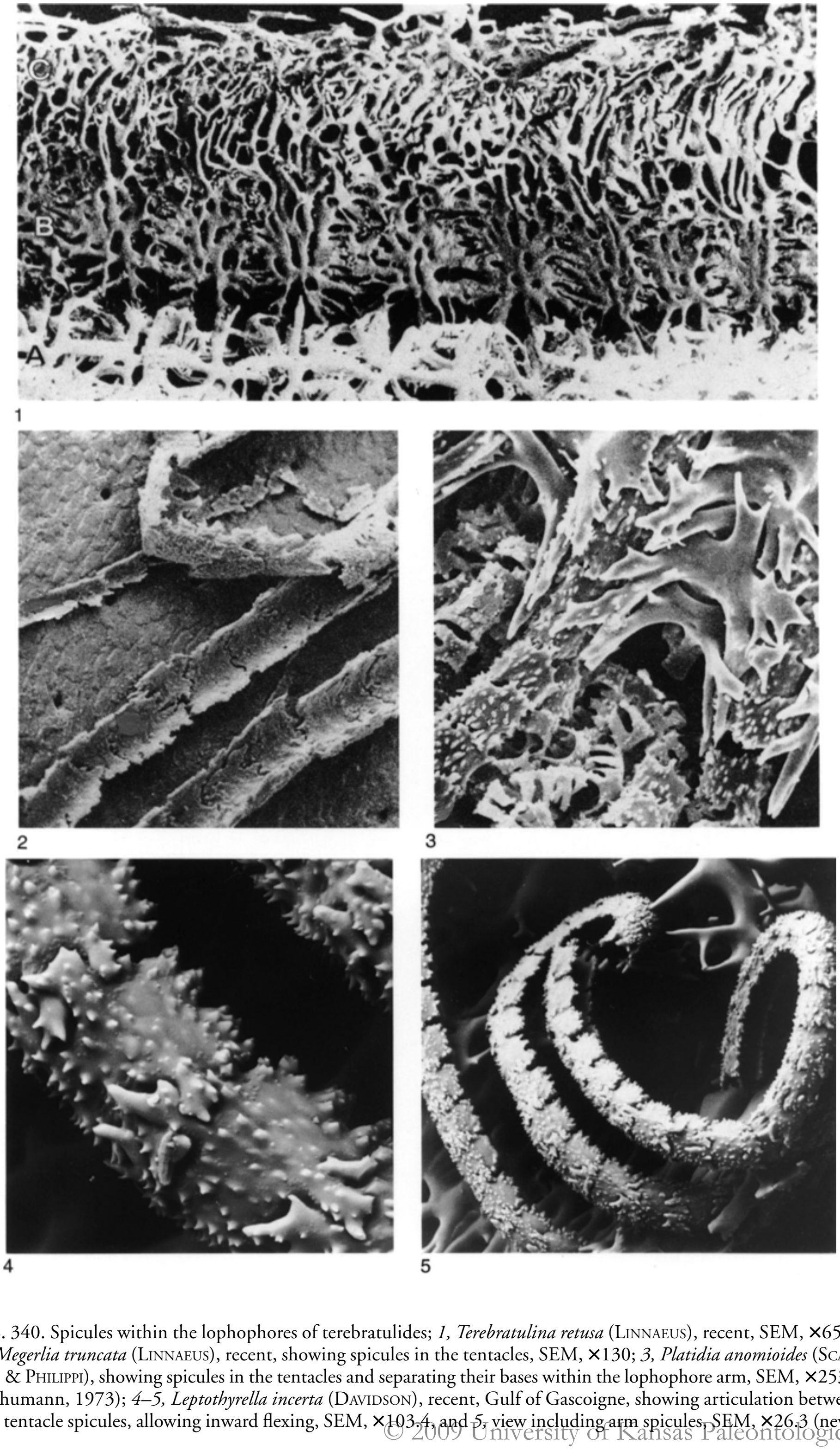

Fig. 340. Spicules within the lophophores of terebratulides; *1, Terebratulina retusa* (Linnaeus), recent, SEM, ×65.8; *2, Megerlia truncata* (Linnaeus), recent, showing spicules in the tentacles, SEM, ×130; *3, Platidia anomioides* (Scacchi & Philippi), showing spicules in the tentacles and separating their bases within the lophophore arm, SEM, ×253.8 (Schumann, 1973); *4–5, Leptothyrella incerta* (Davidson), recent, Gulf of Gascoigne, showing articulation between the tentacle spicules, allowing inward flexing, SEM, ×103.4, and *5,* view including arm spicules, SEM, ×26.3 (new).

FIG. 341. Dorsal valve interior of *Spondylospira lewesensis* (LEES), Triassic, central Peru, showing the brachidial net. A broken crus shows on the right, ×7 (Sandy, 1994).

meshwork of **spicules** (e.g., *Terebratulina,* Fig. 339), which is only rarely preserved in fossils (STEINICH, 1965; SURLYK, 1972; BRUNTON & HILLER, 1990). Spicules are highly variable in form and size and in some genera (e.g., *Terebratulina, Platidia,* and *Megerlia*) extend into the brachial tentacles (Fig. 340; SCHUMANN, 1973). Body wall and brachial arm spiculation is particularly strongly developed in platidioids and cancellothyridids but meager or absent in zeillerioids, laqueoids, and some terebratelloids. There is, however, insufficient information on the distribution, nature, and growth of spiculation in living genera.

A structure loosely connected with the lophophore is the **brachidial net** (SANDY & LANGENKAMP, 1992), first noted by COOPER (1942) in the Late Triassic *Spondylospira,* and well illustrated by SANDY (1994; Fig. 341). This calcareous netlike structure unites the crura and crural processes (or jugum) to the dorsal valve floor, in so doing surrounding the inferred body cavity, as if by a heavily mineralized, body-wall spiculation. Anteromedially and ventrally, between the crural processes, a gap probably accommodated the mouth and esophagus leading posteriorly from the lophophore. Another structure in a similar but median position in several genera of the Neospiriferinae has been described by COOPER and GRANT (1976) as a **buccal plate.** This is a bilaterally symmetrical, stellate, concave posterodorsally, five- to seven-rayed, perforate plate medially positioned between the spiralia (Fig. 342). These plates were commonly lost from the insides of silicified specimens as they were digested by acid from the rock, and it seems, therefore, they were not fixed in place; in consequence their true position is conjectural. The nature of the plates is indicative of their being formed within the anterior body wall, and thus they may have aided support of the lophophore in the mouth region.

Apart from the terebratuloids and immature spiriferoids, loops are found only in the somewhat problematical pentameroid? *Enantiosphen* and the enteletoid? *Tropidoleptus* (Fig. 343; WILLIAMS & WRIGHT, 1961). 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. The inferred arrangement seems to have been like that of terebratelloids, and it may have supported a plectolophe, especially if spirolophes were restricted to the spiriferides (*s.l.*), as seems likely.

The interiors of the dorsal valves of many thecideidines exhibit a variety of patterns of grooves, ridges, and tubercles that correspond with the configuration of an associated **schizolophous** or **ptycholophous** lophophore (BAKER, 1990). During the early phases of thecideidine evolution in the Triassic Period, some particularly novel forms of brachidial structures have been recorded (DAGYS, 1974). Spiralia with V-shaped cross sections and ventrally directed apices, found in *Thecospira* and *Thecospiropsis,* provide undisputable evidence of spirolophous lophophores in those genera. On the other hand, the disposition of lamellar and septal outgrowths in the dorsal valves of *Pamirotheca, Hungaritheca,* and *Thecospirella* suggest that in those taxa a plain or modified schizolophe prevailed (DAGYS, 1974). Brachidial development in post-Triassic thecideidines seems to have proceeded along

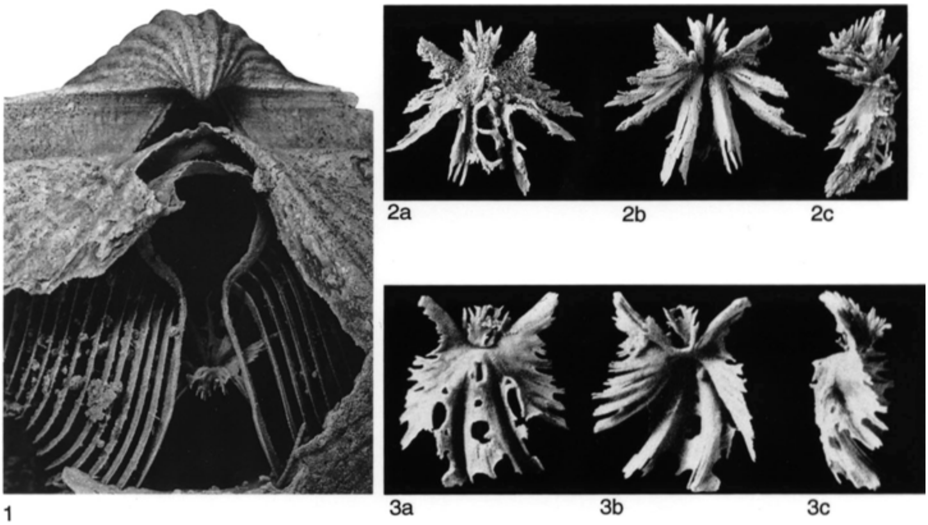

FIG. 342. *1,* Buccal plate, possibly *in situ* between the spiralia of a *Neospirifer* species, Permian, Texas, USA, ×2.5; *2a–c,* anterior, posterior, and lateral views of isolated plates, ×3; *3a–c,* anterior, posterior, and lateral views of isolated plates, ×3 (Cooper & Grant, 1976).

two main lines, reflecting differentiation of schizolophous and ptycholophous stocks (BAKER, 1990).

Despite the lack of structures comparable with crura, some internal features of the dorsal valves of plectambonitoids, strophomenides, chonetidines, productines, and strophalosiidines seem also to have functioned as supports to the lophophore (WILLIAMS, 1956). Among the plectambonitoids, a variably elevated, semicircular, medially divided disc (**brachial platform**), like that of *Leptellina,* is commonly present and may be interpreted as having borne a schizolophous lophophore (Fig. 344.1). The deeply divided, elongately oval platform of *Bimuria* or the pair of long, U-shaped sets of ridges of the strophomenoid *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 (**bema**) may have supported a lobate trocholophe rather than a ptycholophe (Fig. 344.2). Indeed, attached and modified trocholophes or schizolophes seem to have been the more likely kind of plectambonitoid lophophore. Some strophomenoids, most chonetidines, and other early productides are characterized by a pair of ridges arising between the posterior and anterior pair of dorsal adductor scars (**anderidia**) while in other productides recurring ridges define a pair of anterolateral areas commonly occupied by a smooth, raised mound of secondary shell. These features are called **brachial ridges** in the belief that they gave support to the dorsal epithelium, from which hung the lophophore. They are exceptionally associated with subconical impressions directed ventrally, which might represent differential thickening to accommodate the median parts of the lophophore (e.g., *Levitusia, Gigantoproductus*). The evidence indicates a schizolophe or simple ptycholophe for most taxa in these groups (Fig. 345). There is evidence in the Permian among some aulostegids, however, for a calcified falafer brachidium (GRANT, 1972) supporting a multilobed ptycholophe (Fig. 345.2) of the type suggested by GRANT (1972) as being typical of all productides having a deep **corpus** cavity (see also the section on Productida in the systematic volume Part H(R), volume 2, in preparation). The extreme lobate brachiophore of lyttoniids can be seen as an exaggerated growth and reorientation of the above falafer type in response to their

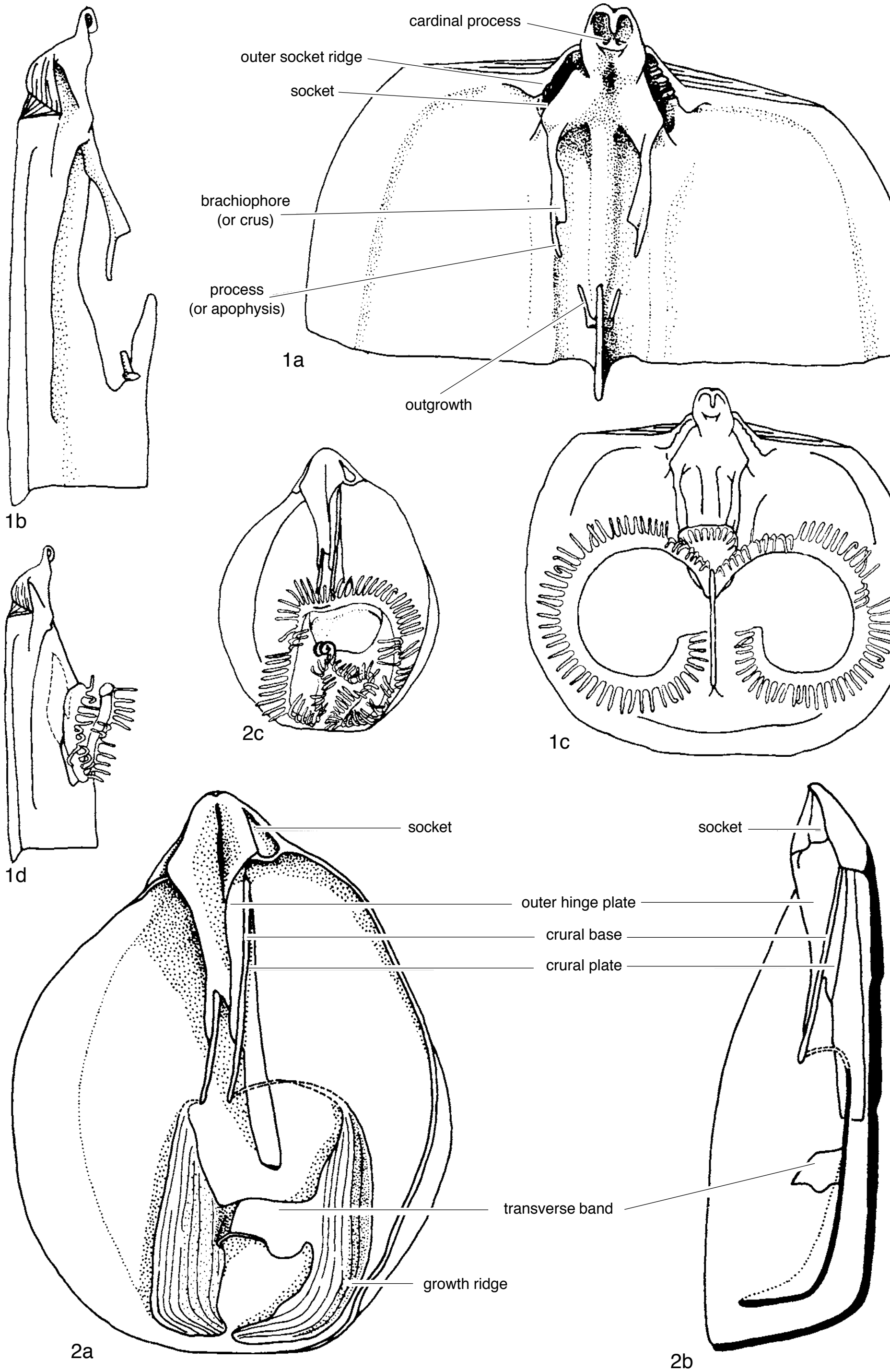

FIG. 343. Internal morphology of dorsal valve in *1a,* ventral and *1b,* lateral views of *Tropidoleptus carinatus* CONRAD, Middle Devonian, USA with *1c–d,* inferred restoration of lophophore in ventral and lateral views; and of dorsal valve in *2a,* ventral and *2b,* lateral views of *Enantiosphen vicaryi* (DAVIDSON), Middle Devonian, England, with *2c,* inferred restoration of lophophore in ventral view (adapted from Williams & Wright, 1961).

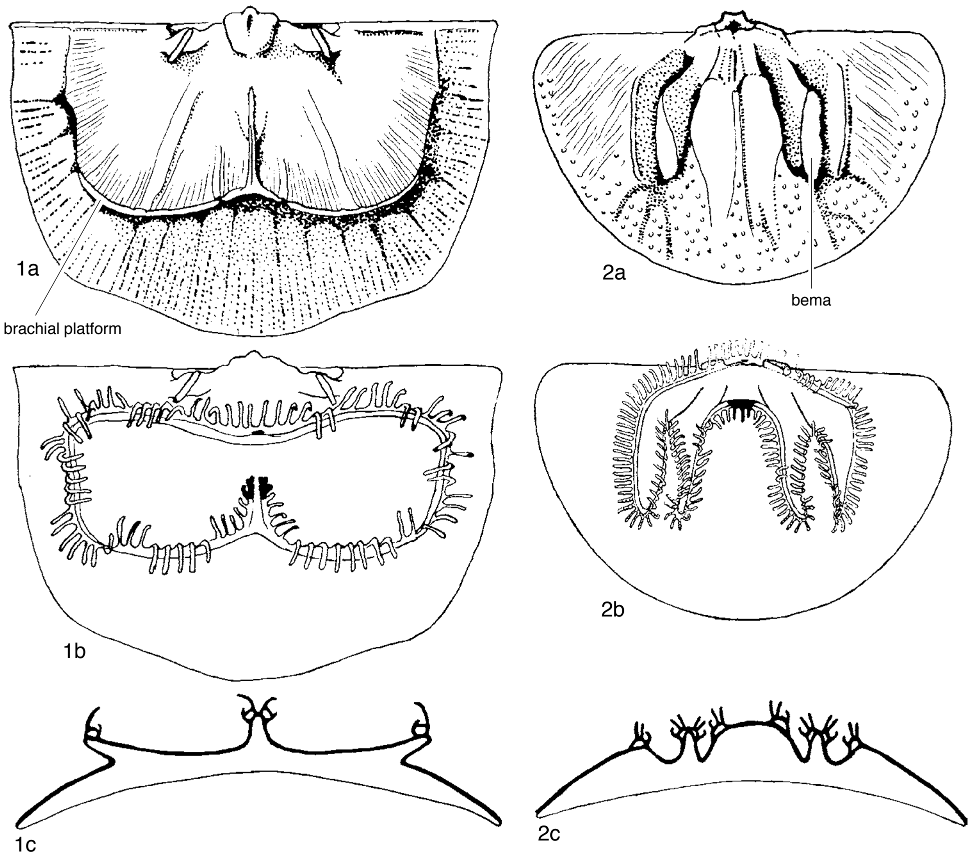

Fig. 344. Internal morphology of the dorsal valve in the plectambonitoids *1, Leptellina* and *2, Eoplectodonta; 1a, 2a,* internal view, with an internal reconstruction of the lophophore in *1b, 2b,* ventral, and *1c, 2c,* transverse sectional views; *dotted* segments of lophophore are inferred as raised above the valve floor; generative regions are in *black* (adapted from Williams & Rowell, 1965b).

oysterlike life habit (Grant, 1972). A variation on the usual schizolophous situation in chonetidines was suggested by Racheboeuf and Copper (1990) in a Late Ordovician example of *Archeochonetes* in which they found a gamma-shaped structure with a median lobe arching anteriorly around the dorsal median septum. They interpreted this as a remnant indication of the lophophore, which they termed a mesolophe, and suggested it might have been present in many chonetidines; but its growth remains difficult to envisage.

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 orthoides and strophomenoides (Muir-Wood & Cooper, 1960). The mantle canal systems of the productines are unknown, but traces of radiating peripheral canals seen in *Peniculauris* terminate abruptly against the well-developed brachial ridges. Generally the role of brachial ridges as part of the mantle canal system is now rejected.

Among inarticulated brachiopods there are no prolongations of the shell that indisputably functioned as lophophore supports, but projections from the dorsal valves of acrotetide genera may have given support to the lophophore and anterior body wall. This would appear to be the most probable

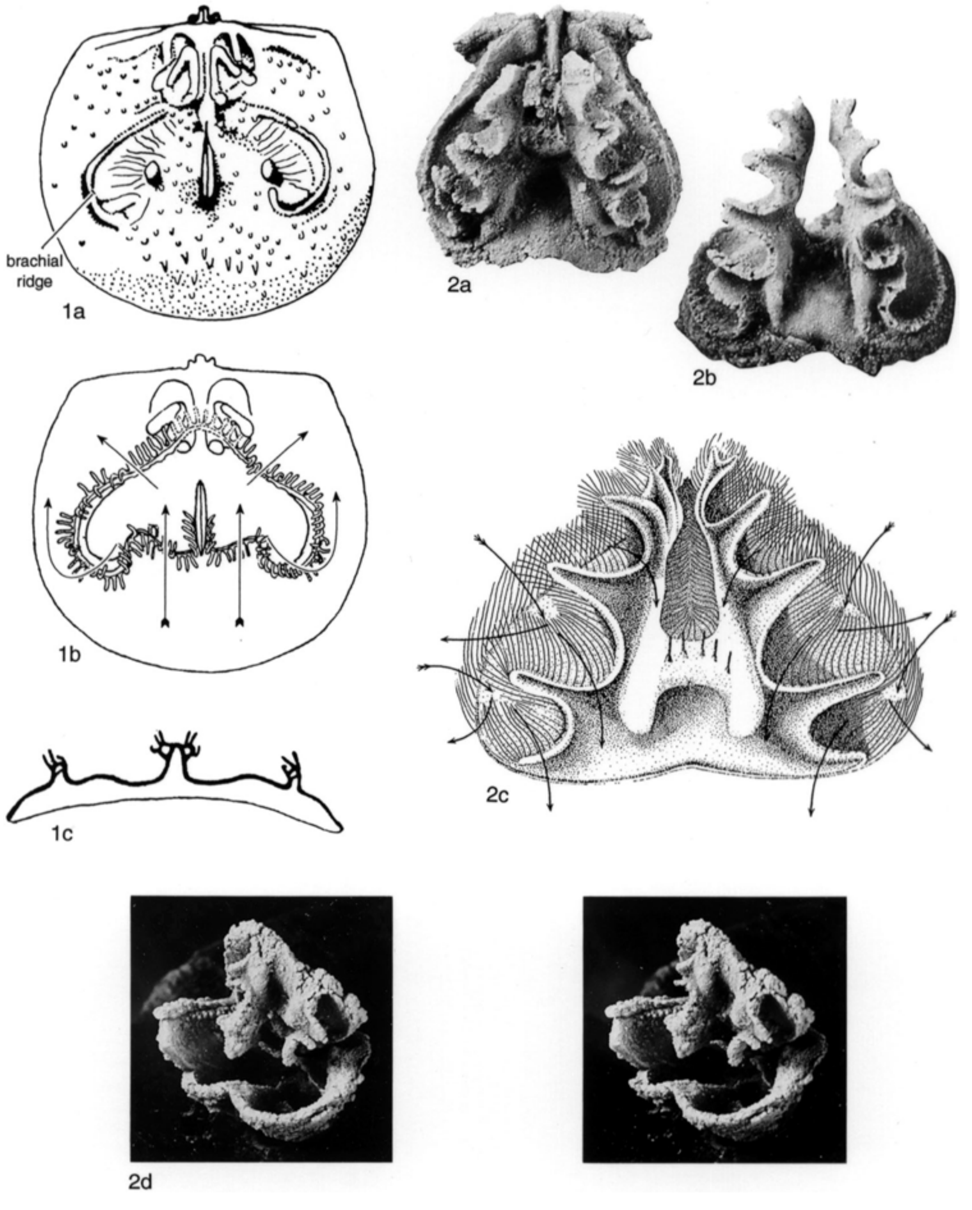

FIG. 345. Inferred dorsal features in productides; *1a–c,* productidine *Pugilis* with the inferred lophophore viewed ventrally and in transverse sections (adapted from Williams & Rowell, 1965b); *2a–d,* the aulostegoid *Falafer epidelus* GRANT, Permian, Greece, viewed *2a,* ventrally, ×8; *2b,* anteroventrally, ×8; *2c,* inferred ptycholophe reconstruction; *feathered arrows* indicate incurrents; and *2d,* complete shell widely open, stereopair, ×6 (Grant, 1972).

function of these saddle-shaped plates of *Ephippelasma* (COOPER, 1956) and *Numericoma* (see HOLMER, 1989), which arise from a relatively narrow base slightly behind the center of the valve and expand ventrally and anteriorly to terminate in a number of slender projections (Fig. 346). These projections are disposed with a crude symmetry about the median plane, and their tips roughly fall on an imaginary surface that

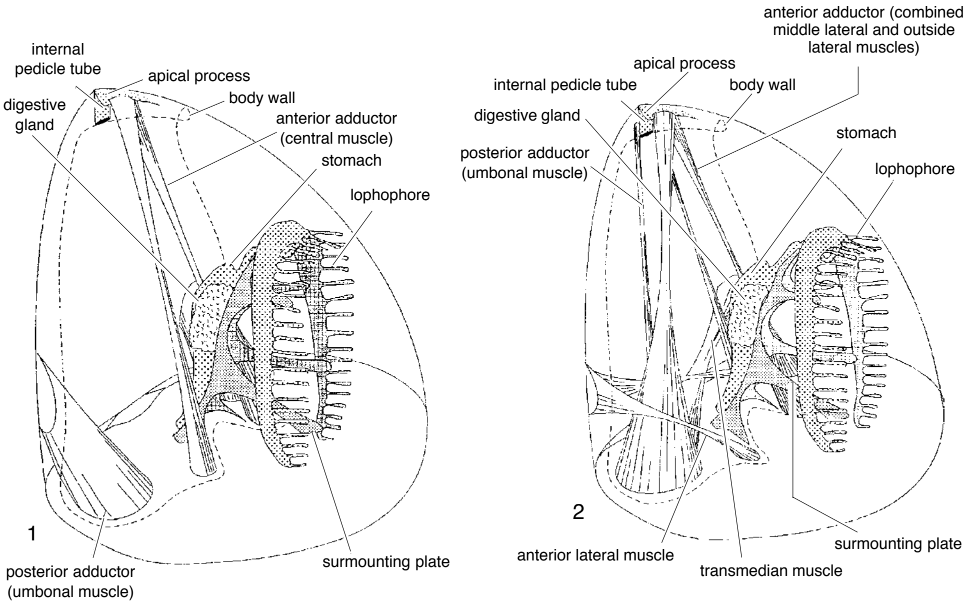

FIG. 346. Stylized reconstructions of *Ephippelasma* with inferred location of lophophore, muscles, and alimentary canal; shell treated as transparent; *1,* adapted from Williams and Rowell (1965b) assuming a cranioid relationship; *2,* with the lingulide relationship of POPOV, 1992 (new).

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 projections from the median plate touched the anterior part of the body wall, the limited mantle cavity could conveniently have accommodated a trocholophe (or schizolophe) 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 trocholophous ring on either side of the mouth.

Many other acrotretid genera have a thin, bladelike median septum, usually subtriangular in lateral profile and attached basally along its length to the dorsal valve. The posteroventral edge of the median septum is commonly unmodified, but it may bear variously disposed transverse plates (the **surmounting plate**). In *Torynelasma* this is a slender, ventrally concave, triangular plate; in *Biernatia* it is a ventrally convex plate (Fig. 347), or it may be narrowly expanded and digitate in a plane more or less normal to the septum as in *Angulotreta* or *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 trocholophe or schizolophe. 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 articulated brachiopods consist of two sets passing between the valves (**diductors, adductors**) and another two sets controlling the pedicle (**ventral** and **dorsal adjustors**). Distinct impressions

FIG. 347. Dorsal valve interior of the acrotretide *Biernatia holmi* HOLMER, Middle Ordovician, Sweden, showing the median septum with its posteroventrally convex surmounting plate in *1,* oblique anterior (SEM, ×105), and *2,* lateral (SEM, ×70) views (Holmer, 1989).

(**muscle scars**) commonly mark the sites of muscle bases on the interiors of both valves. Such impressions are formed as a result of modifications in the fine structure and secretory behavior of localized areas of shell-secreting outer epithelium to which the muscles became attached (WILLIAMS, 1968a; WILLIAMS & WRIGHT, 1970; MACKINNON, 1977). The microscopic shell structure of muscle scars is commonly so distinct that it is best regarded as a localized development of an additional shell layer, for which KRANS (1965) introduced the term **myotest**. During ontogeny, muscle bases (with the exception of the posteromedially located dorsal diductor attachment scar) generally migrate anteriorly more rapidly than the underlying epithelium. Thus, in radial section, myotest can be traced posteriorly, becoming buried by the overlap of normal secondary shell more recently secreted in that part of the shell located behind the muscle field. In the ventral valve, all muscle scars tend to be grouped together to form a muscle field, which is ideally differentiated into a median adductor muscle scar contained posteriorly by two incomplete arcs of inner diductors and outer adjustors (Fig. 348.1b, 2b, 3b). The attachment areas in the dorsal valve, however, are generally much more scattered (Fig. 348.1a, 2a, 3a). The adductor field commonly consists of an anterior and a posterior pair of scars, 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 (Fig. 349), usually along the inner faces of the hinge plates (or brachiophores) and on a posteromedian outgrowth of secondary shell (cardinal process), respectively.

Muscle scars can vary not only in their relative position but also in the clarity of their impression. They may be deeply inserted, raised above the general level of the valve floor, or even greatly elevated on elaborate platforms. The definition of muscle scars in brachiopod shells is normally a function of age, so that the ultimate area of attachment attained in adult stages of growth is much more easily seen than the impressions in young or immature valves. This clarity is due mainly to differential secretion involving greater organic and less mineral secretion, which results in a change in the texture of that part of the secondary layer affording attachment (Fig. 350; MACKINNON, 1977). As a consequence, muscle marks are commonly 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 included a variable number of striplike indentations or **muscle tracks** disposed parallel with the adjacent boundaries of the muscle scars, which represent the course of migration for the muscle bases during growth of the shell.

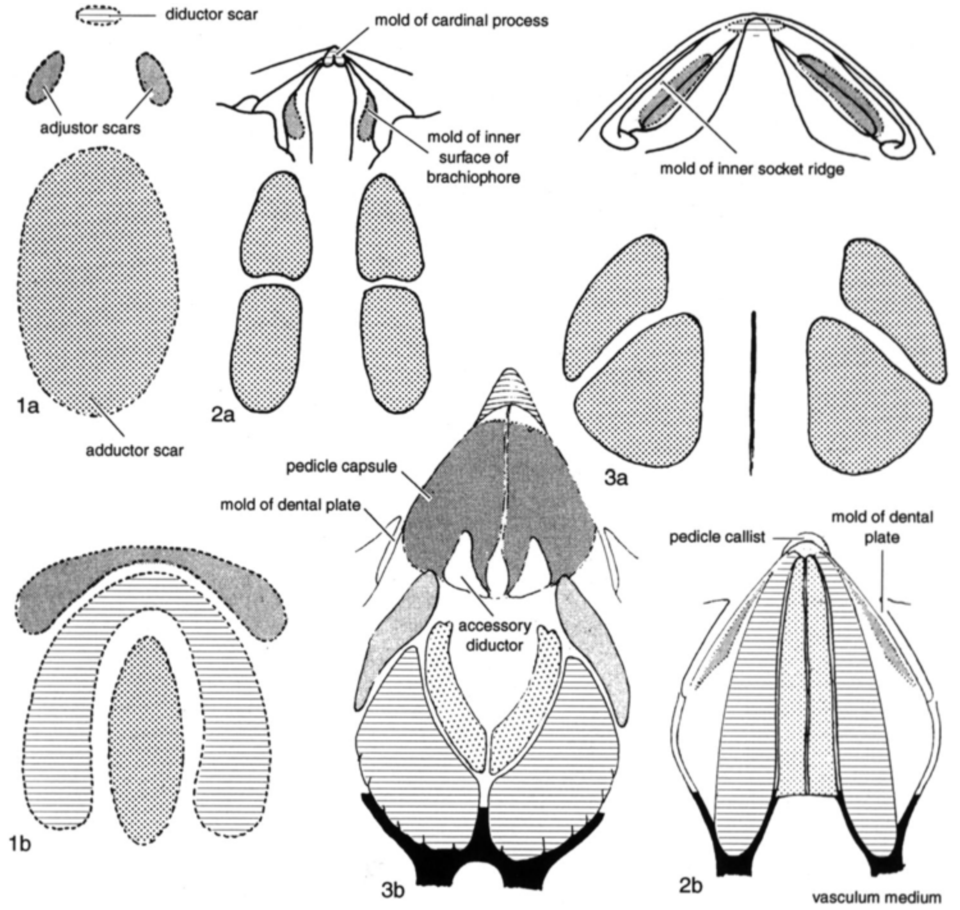

FIG. 348. Diagrammatic representation of principal muscle marks in *1a,* dorsal and *1b,* ventral interiors with examples of corresponding actual scars seen in *2a–b, Dalmanella wattsi* (BANCROFT), Middle Ordovician, England, and *3a–b, Hemithiris psittacea* (GMELIN), recent (adapted from Williams & Rowell, 1965b).

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 ventral valves of many stocks and usually result from an acceleration in the spread of the muscle bases. Second, 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. Even examination of muscle scars with a relatively low-powered microscope can reveal the type of modifications to the shell mosaic described by WILLIAMS and WRIGHT (1970), MACKINNON and WILLIAMS (1974) or MACKINNON (1977).

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 midline and, apart from details of outline, its relative size probably does not vary greatly throughout most articulated

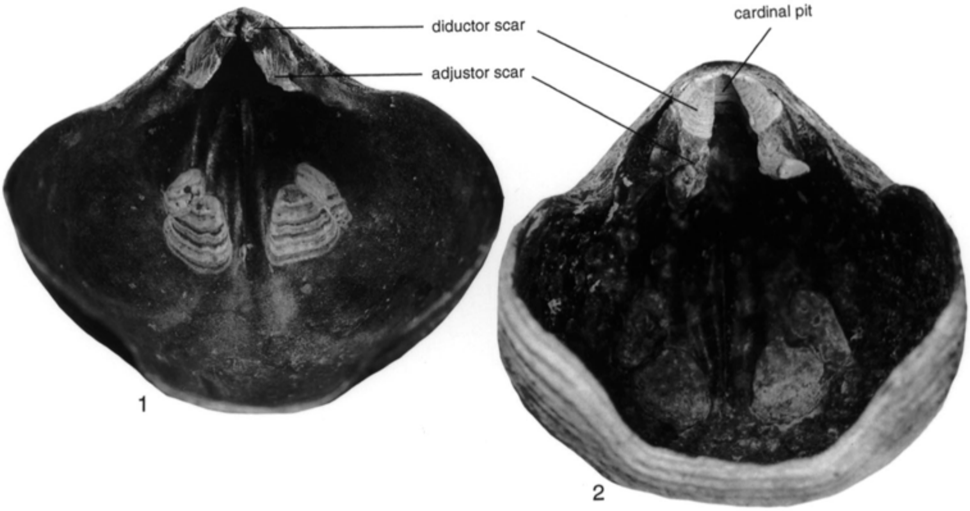

FIG. 349. Dorsal valve interiors of *Hemithiris psittacea* (GMELIN), recent, Tromso and Labrador, showing divided pair of adductor scars on valve floor; diductor scars posteromedially (especially in *2*) and dorsal adjustor scars on the crural bases, ×3 (new).

brachiopods. An important difference, however, is noted in location of the field within the valve, since those of rhynchonelloids, spiriferoids, and terebratuloids are well forward of the umbonal chamber that accommodated the pedicle base, whereas the orthoid, strophomenoid, and porambonitoid fields typically occupied all available wall space within the delthyrial chamber and usually did not extend very much forward of it (Fig. 348.2b,3b; WILLIAMS & WRIGHT, 1963). One of the consequences of this posterior location in the older brachiopods is that the dental plates commonly afforded attachment for the ventral adjustors 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. 351).

The spondylium is preeminently characteristic of the clitambonitoids, pentameroids, and stenoscismatoids; but it is also found in other unrelated stocks such as the orthoid *Skenidioides,* some orthotetoids, for example, *Ombonia,* and the stringocephaloid *Amphigenia.* A complicated terminology, partly reflecting this diversity of origin, is now used to indicate various stages in spondylial development. KOZLOWSKI (1929) named the slightly convergent dental plates that grew directly from the floor of the ventral valves of some porambonitaceans, like *Huenella,* the **spondylium discretum**. This arrangement is, however, identical with that of most orthoids, 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** (SCHUCHERT & COOPER, 1932) if the anterior part of the ventral muscle field is elevated on an undercut callosity, which may be prolonged anteromedially as a ridge (Fig. 352). 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 spondylial relationship, to structures formed by dental plates that unite with each other on the floor of the ventral 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. KOZLOWSKI (1929) distinguished between two types of septal support. In the **spondylium simplex** 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. 351.1). KOZLOWSKI (1929) 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 (intraseptal lamella) appeared invariably to occupy the median plane of the septum supporting the pentameroid **spondylium duplex.** Its presence led KOZLOWSKI (1929) to conclude that such a septum was formed by the incomplete fusion of the dental plates (Fig. 351.2). 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.

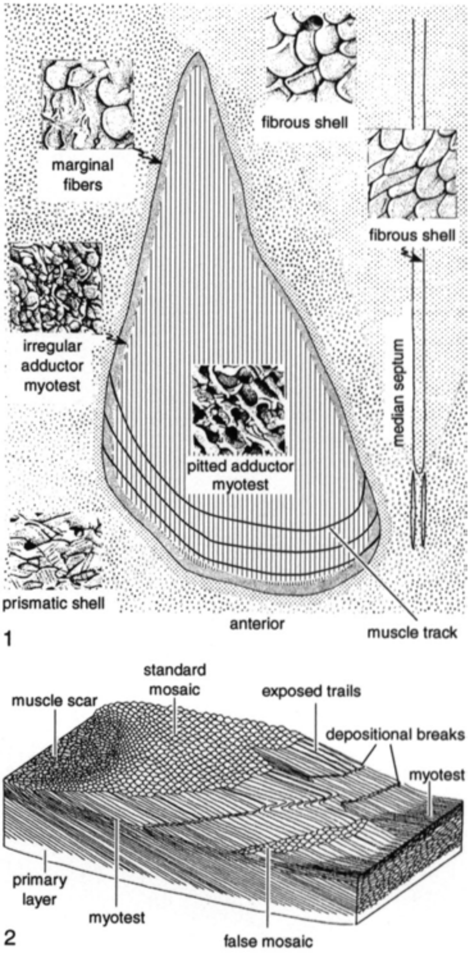

FIG. 350. Muscle scar morphology; *1,* diagrammatic representation of a dorsal adductor muscle scar in *Liothyrella* showing variations in the shell fabrics of the myotest and surrounding mosaic. In this genus secondary shell built the median septum on the right and tertiary prismatic shell surrounds the scar (MacKinnon & Williams, 1974); *2,* stylized block diagram of part of a dorsal valve of *Notosaria* exfoliated posterior to the adductor muscle scar (on left) and sectioned radially (adapted from MacKinnon, 1977).

The differences between the spondylia simplex and duplex may not be as fundamental as is generally believed (WILLIAMS & WRIGHT, 1961). The intraseptal lamella has been described as having an enlarged base at the junction of the septum with the spondylium and as thinning toward the floor of the valve, a disposition that is compatible with the prevalent interpretation of its origin. But ST. JOSEPH (1938) and AMSDEN (1953) have observed that the dorsal end of the intraseptal lamella can be continuous with extensive deposits of prismatic calcite lining the spondylium. Moreover, serial sections show that in at least some pentameroid genera (e.g., *Pentamerella* and *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. 351.2b). The distinctiveness of the spondylium duplex may therefore have resulted

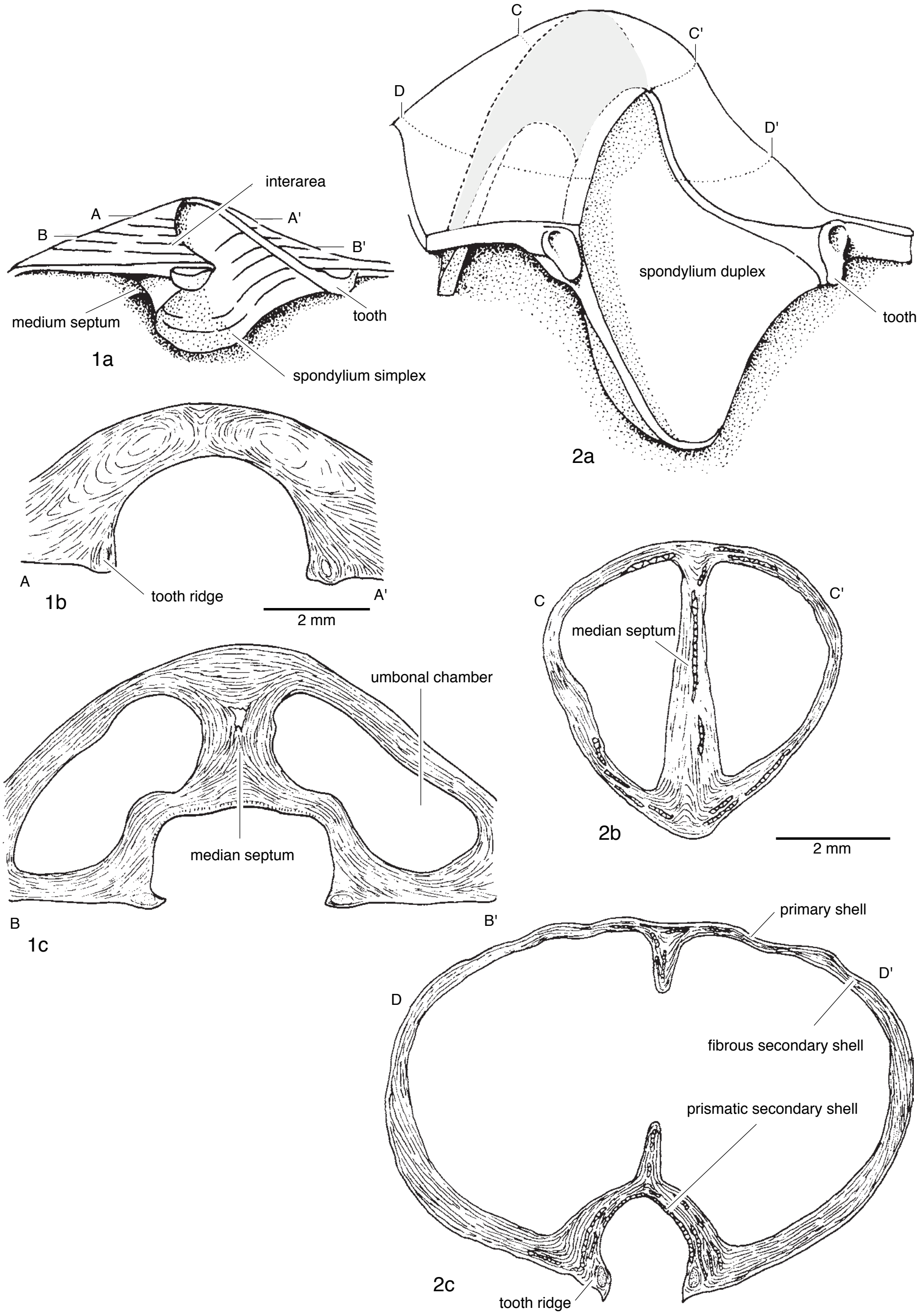

FIG. 351. Ventral valve showing *1,* spondylium simplex of *Skenidioides craigensis* REED, Middle Ordovician, Scotland, and *2,* spondylium duplex of *Gypidula dudleyensis* SCHUCHERT, Upper Silurian (Wenlock), England; *1a,* oblique view showing location of transverse sections (*1b–c*); *2a,* oblique transparent view showing position of median septum and location of transverse sections (*2b–c*) (adapted from Williams & Rowell, 1965b).

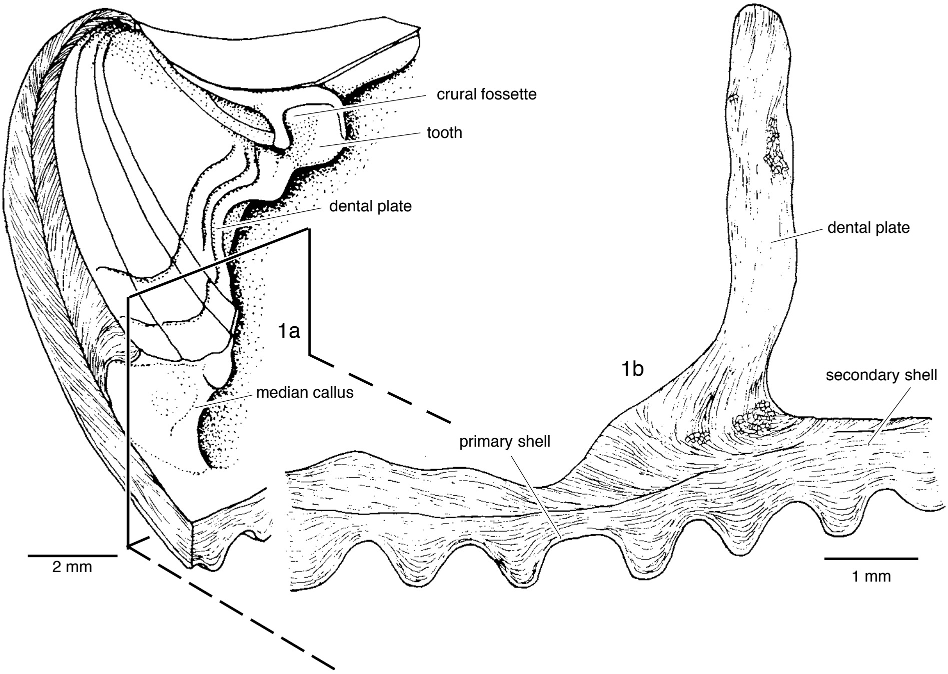

FIG. 352. *1a,* Structure of pseudospondylium of *Glossorthis tacens* ÖPIK, Middle Ordovician, USSR, with plane of transverse section showing *1b,* relationship between dental plate and floor of ventral valve (adapted from Williams & Rowell, 1965b).

from the secretory activities of the outer epithelium of the pentameroids, which, unlike that of the skenidiids, was capable of depositing prismatic calcite (WILLIAMS, 1956), 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 stenoscismatoids and camerellids. The spondylium of *Amphigenia* is truly duplex in that the dental plates are seen to unite into a median septum (BOUCOT, 1959).

Complications also arise in the use of the term **spondylium triplex** (ÖPIK, 1934) for an apparatus with a variably developed triseptate support that is especially characteristic of some gonambonitoids (Fig. 353). In some genera the underlying median and lateral (or accessory) septa 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 porambonitoids, as for *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 *Polytoechia,* 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. 354) is not a spondylium in the sense that its posterior elements gave

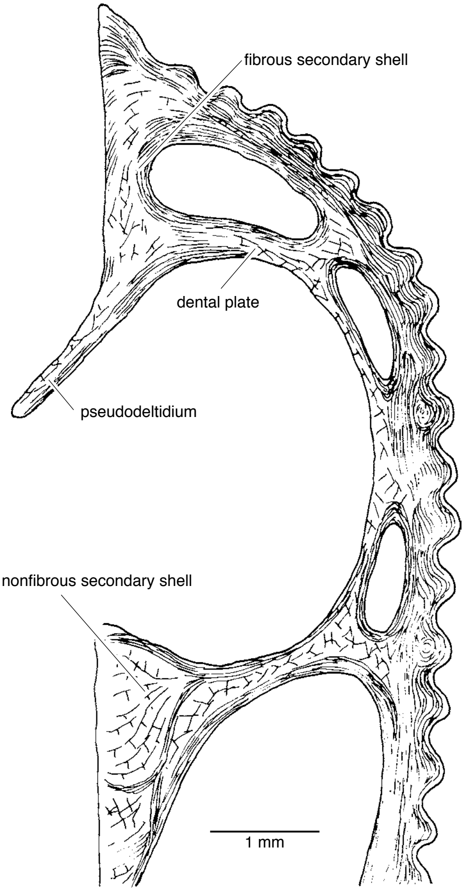

FIG. 353. Section through spondylium triplex of ventral valve of *Antigonambonites planus* (PANDER), Lower Ordovician, Baltic (Williams & Rowell, 1965b).

support to the entire ventral muscle field. It consists of a long, high, bladelike median septum to which the short, convergent, dental plates are ankylosed just below the posterior edge. A pair of lateral struts is subtended between the inner surfaces of the dental plates and the posteriorly protruding part of the median septum to define an anteriorly widening, medially positioned tube (**tichorhinum**) that is suboval in section and extends 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 that must have contained the pedicle. Given this likely location for the pedicle, the ventral adjustor muscles would have attached to the troughlike dental plates and the dorsal adjustor muscles to the crural bases. Most probably the main adductor muscles would have attached to the anterior part of the tichorhinum and the diductors to the lower anteroventral sides of the median septum (Fig. 354.2), where MACKINNON (1974) recognized the presence of myotest (Fig. 354.3). This interpretation does, however, raise a possible functional problem because the adductor and diductor muscle would have crossed close together. With respect to their convergence into a median septum well posterior of the ventral muscle field, the dental plates are like the short, dental ridges of some orthotetoids (e.g., *Orthotetes*), which also form a small chamber that has been incorrectly called a spondylium.

Quite possibly, the **syrinx** of *Syringothyris* (Fig. 355) may have performed the same function as the tichorhinum, that is, as the attachment site of the ventral adductor muscles, except that the tubular syrinx was attached to the ventral surface of a sunken delthyrial plate rather than to the posterodorsal edge of a median septum, as is the tichorhinum of *Cyrtina.* The sunken plate (**delthyrial plate**) within the delthyrium to which the syrinx is attached is probably homologous with the pedicle collar and would thus have lain anteroventrally to the pedicle or its remnant. This interpretation is consistent with the pattern of paired diductor muscle impressions only on the floor of the ventral valve, the closed ventral end of the syrinx, and the sporadic development of a deltidium or stegidium posterior of the sunken plate.

One other type of muscle platform developed among such spire-bearing brachiopods (HALL & CLARKE, 1894–1895) as *Merista* and its allies (Fig. 356). It consists of a transverse partition (**shoe-lifter process**) extending across the posterior part of the ventral 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 ventral 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 term has also been extended to similarly shaped structures in dorsal valves, where it is bisected by the dorsal median septum, as in the meristellid *Rowleyella.*

The dispersion of the attachment areas of the diductor and adductor muscles within the dorsal 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 articulatory fulcral points to provide a third-order lever, and the latter are positioned 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 and the adductors to two pairs of relatively large scars (Fig. 348.1a,2a,3a); this symmetry of insertion has led to many morphological changes, especially around the dorsal beak.

The dorsal attachment of the diductor muscles was commonly onto some form of boss or projection from the inside of the dorsal valve beak. Since DAVIDSON's use of the term in 1853, these structures have generally been called the **cardinal process** in whatever groups of brachiopods they occur, and the term remains in general use. Recent studies indicate, however, that there are at least two different forms of cardinal processes. The first and geologically earlier, seen typically in orthides and strophomenides *s.l.,* is a structure with radially disposed ridges bordering and separating a pair of laterally adjacent diductor scars. In more advanced forms the diductor attachment sites became raised on a **shaft** with the muscles inserted into crenulated grooves (**myophores**) at the distally lobed head of the cardinal process (e.g., *Dalmanella,* Fig. 357.4). The second style of cardinal process growth is seen in

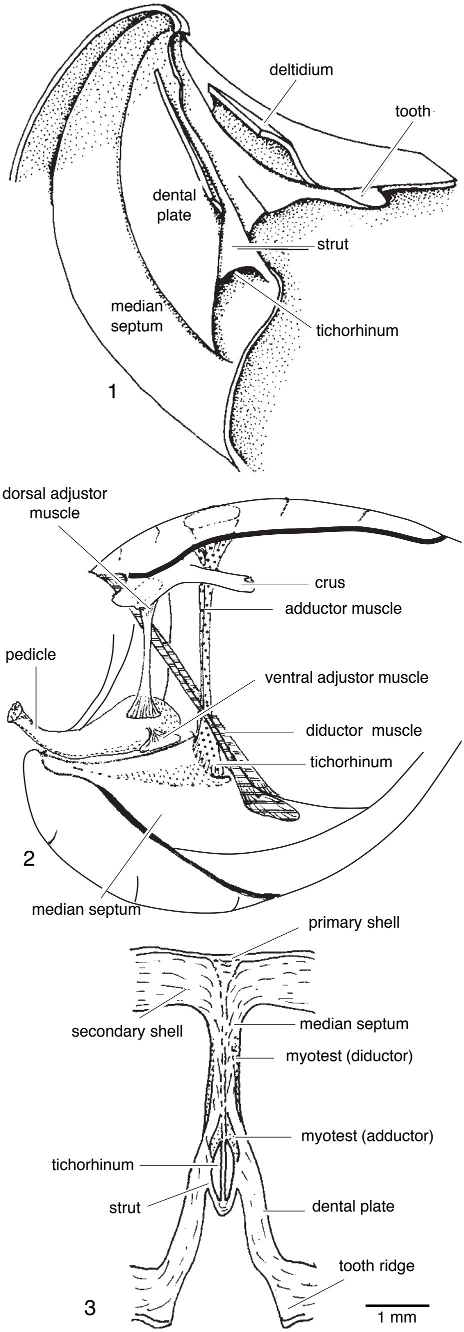

FIG. 354. *1,* Tichorhinum in the spondylium of *Cyrtina hibernica* BRUNTON, Lower Carboniferous, north Ireland (Williams & Rowell, 1965b); *2,* inferred disposition of the pedicle and muscles (new); *3,* transverse section showing tichorhinum of *Cyrtina* sp., Middle Devonian, USA (adapted from Williams & Rowell, 1965b).

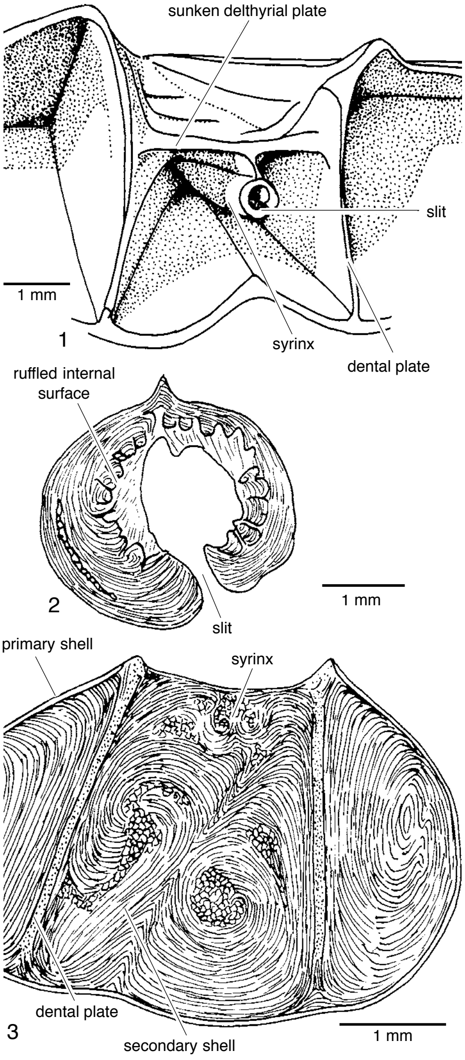

FIG. 355. *1,* Ventral interior of *Syringothyris cuspidata exoleta* NORTH, Lower Carboniferous, England, with *2,* transverse sections of free dorsal end of syrinx and *3,* of apex (Williams & Rowell, 1965b).

many spiriferides, athyrididines, atrypides, rhynchonellides, and terebratulides and includes the **ctenophoridium** (Fig. 358) and **cardinal flanges** (Fig. 359). The former may be within the dorsal beak or, as is common with the latter, elevated above the valve floor on ridges or plates, dorsal to which are cavities, and attached laterally to the inner socket ridges. They are discussed further below.

Orthides and strophomenides have cardinal processes in which the dorsal diductor bases commonly remain separated so that the muscle scars are paired and bordered laterally and medially by ridges. Throughout life the muscle bases remained in a posteromedian position and tended to become elevated onto protruding structures that became bilobed in many groups. There is considerable variation in these cardinal processes, depending on the degree of development of the ridges bordering the paired muscle bases and the elevation of the bases above the valve floor. In early orthoids the notothyrial platform thickened to raise the diductor muscles above the valve floor, and accelerated deposition of fibrous secondary layer by the outer epithelium between the paired muscle bases commonly produced variably defined median ridges separating the two scars. In some the median ridge itself became the seat of muscle attachment, as in some orthoids, enteletoids, and some early rhynchonellides (e.g., *Orthorhynchula;* Fig. 360.2–360.3). In others this median ridge or the closely positioned muscle scars themselves became elevated and differentiated into a proximal shaft and distal lobed head, which was crenulated to increase the areas of muscle attachment at the myophores, as in many productides (Fig. 361.2). In *Resserella* each of the two myophore lobes is bordered by low ridges of smooth shell, acting as boundaries to the crenulated muscle scars (Fig. 357.3). The development of cardinal process shafts and bilobed myophores is most prominently seen in strophomenates, especially some orthotetidines and the Productida, in which there is great variation. In some strophomenates, in which there is a dorsal interarea and a well-separated bilobed cardinal process, the median ridge on the notothyrial platform was retained in support of the chilidium, as in the orthotetidine *Schuchertella.* The diversity of form results from differences in the extent of growth of the shaft and from the growth or absence of the ridges separating the muscle bases medially or enclosing them laterally. To differentiate the main bilobed structure from these ridges, the latter have been designated by the suffix -fid. A single median ridge on the cardinal process, normally separating the muscles, is termed unifid, a pair of lateral bounding ridges is termed bifid, a median ridge plus paired bounding ridges is termed trifid, and paired median ridges plus paired lateral bounding ridges is termed quadrifid (Brunton, 1966). Ontogenetic and evolutionary changes from one condition to another led to adults of some species having a bilobed, trifid cardinal process through the median fusion of the paired median ridges of an earlier quadrifid stage of development, as in *Pugilis* (361.2). In other productides, such as *Echinoconchus,* and in the enteletoid *Paucicrura* (Fig. 361.5) the muscles spread medially onto the ridge and almost united into a single myophore, but commonly in productides the diductor bases were confined within myophore clefts with roughened surfaces.

Apart from unusual orthides, or in the triplesioids with their grotesquely exaggerated bilobed processes (Fig. 357.2) and the orthidiellids with their trifid structures formed by the outgrowth of high inner socket ridges with diductor scars between them and separated by a median ridge (Fig. 361.4), the plectambonitoids display an unusual variation on the cardinal process theme. Some of these genera have rudimentary diductor attachment structures with the scars on a slightly elevated notothyrial platform; some developed simple ridges separating the diductor muscle bases, while others developed a raised notothyrium with a small cavity below creating an overhung cardinal process, which was characteristically trifid, as in some sowerbyellids (Fig. 361.1). In the dorsal valve of *Bilobia,* on the other hand, a basically trifid arrangement became secondarily bilobed by the development of a cleft in the high median crest (Öpik, 1933); 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 (Williams, 1962). Although the cardinal processes of many plectambonitoids resemble, to some extent, the elevated diductor attachments of the cardinal flange condition, their paired diductor

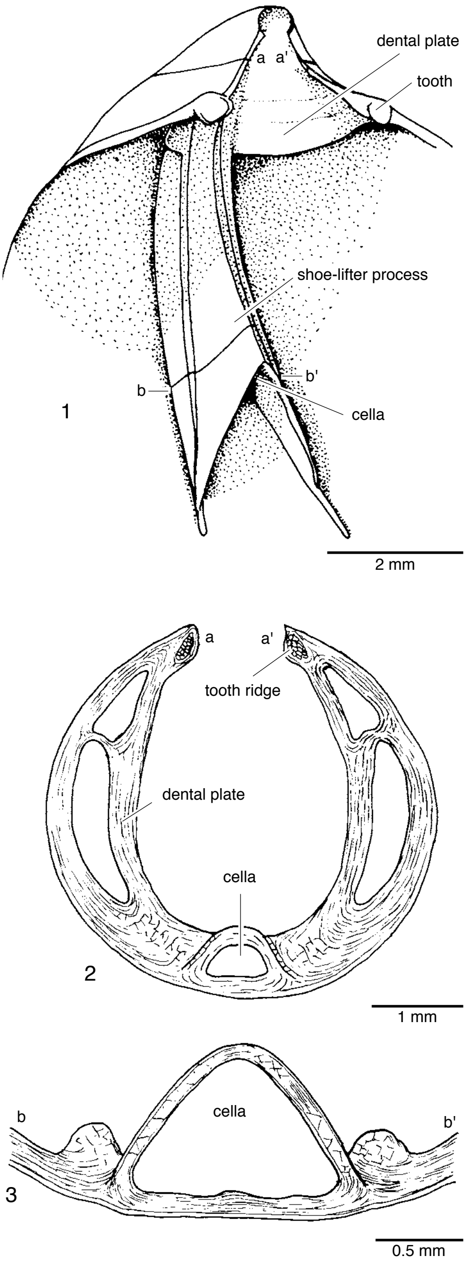

Fig. 356. Ventral valve of *Merista tennesseensis* Hall & Clarke, Middle Silurian, USA, showing shoe-lifter process; *1,* oblique view showing location of *2–3,* transverse sections (adapted from Williams & Rowell, 1965b).

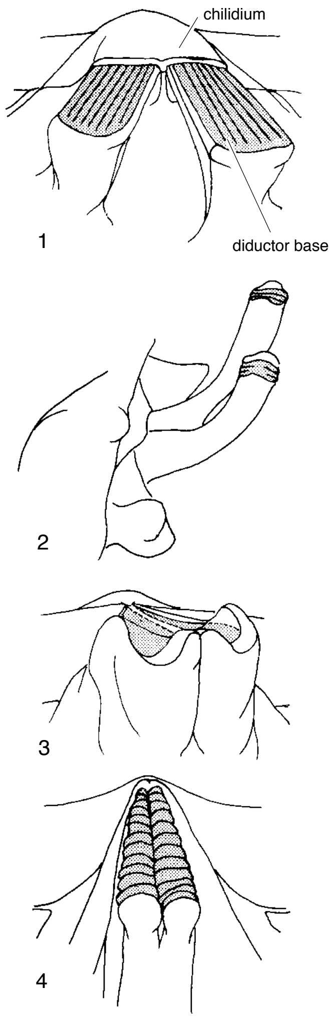

FIG. 357. Various types of bilobed cardinal processes; *1, Rafinesquina; 2, Oxoplica; 3, Resserella* (weakly fused bilobed producing a trifid cardinal process); *4, Dalmanella* (adapted from Williams & Rowell, 1965b).

scars and traces of their myophores from their origins close to the ventral beak and anteriorly across the cardinal process confirms their basic style of cardinal processes.

Another style of cardinal process, seen in many spire bearers, rhynchonellides, and terebratulides, is where the dorsal ends of the diductor muscles commonly produce a single attachment scar with no median separating structure. In the least elaborate taxa, the site of dorsal diductor muscle attachment occupies a shallow posteromedian depression or shallow **cardinal pit** at the dorsal umbo, but in others the muscle bases tend to encroach more widely onto a variety of structures in the cardinalia, such as the posteromedian ends of the inner socket ridges or the crural bases, as in *Hemithiris* (Fig. 349). In some fossil taxa an undifferentiated horizontal plate, the **cardinal plate**, extended between the inner socket ridges; in others a more restricted **hinge plate** partly or completely filled the gap between the crural bases. To maintain posteromedian attachment of the dorsal diductors on the valve floor, both types of plates incorporated a hole or **dorsal foramen** (Fig. 362) that would have allowed the muscles to pass from the dorsal beak to the ventral valve floor. In others the muscle bases spread onto prominent ridges at the beak, such as the ctenophoridium of many spiriferides or onto reduced cardinal plates, in some producing structures resembling a bilobed style of cardinal process, as in the cardinal flanges of athyridids (Fig. 359.2). Cardinal flanges are best seen in athyridids where the dorsal ends of the diductor muscles in juvenile and stratigraphically older species were inserted onto the beak floor. In stratigraphically younger species the dorsal foramen, which earlier was functional, became blocked by secondary shell, and the muscles became attached to the posterior edge of the cardinal plate. Here exaggerated growth of the posterior ends of the inner socket ridges gave rise to more substantial cardinal flanges, to which the diductor muscles became attached. These flanges, well developed in the genus *Pachyplax* (Fig. 359.1), were serrated in a manner characteristic of a myophore. In other athyridids, such as *Cleiothyridina* or Permian *Composita* (Fig. 359.2), the muscle bases spread onto reduced and much thickened cardinal plates, while in others the diductor scars produced shallow serrated pits on the cardinal plate. ALVAREZ and BRUNTON (1990) pointed out that this growth in athyridids was similar to that seen during the ontogeny of the recent *Eohemithiris* in which the diductor muscles spread from the juvenile median position onto the posterior ends of the crural bases and reduced inner hinge plates.

In some retzioids (e.g., *Nucleospira*), a juvenile median ridge grew ventroposteriorly into a hooklike structure extending into the ventral umbo (Fig. 363.1). This resembles a small version of the bilobed cardinal process of orthotetidine meekellids, but is built of medially united cardinal flanges. Unlike the bilobed cardinal process of strophomenates, which preserves growth traces of the myophores on the external (posterior) surfaces (Fig. 364), th 5 e retzioid structure is smooth as if secreted by conventional epithelium during growth. The myophores, being restricted to the distal tips, leave no growth traces (Fig. 363.2). This exaggerated cardinal flange has been called a cardinal process by some and a cardinal plate by others, but it cannot be the latter because the myophores, being distally positioned, would be in an impossible position at the anterior end of a more normally disposed cardinal plate.

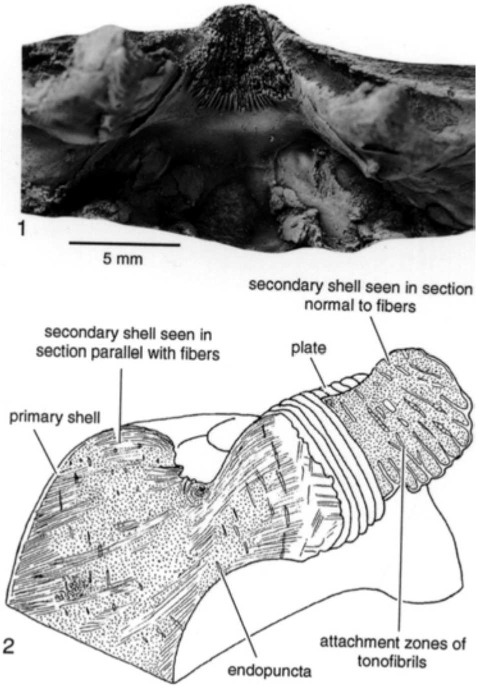

FIG. 358. Cardinal process, of ctenophoridium type; *1, Fusispirifer* sp., Permian, Tasmania, with a sessile cardinal process (new); *2, Terebratalia transversa* (SOWERBY) in median and tangential sections showing associated shell structure (Williams & Rowell, 1965b).

No elaborate dorsal diductor attachment structure is known among the Pentamerida. In some Cambrian genera there is a small median ridge, probably separating the diductor bases; in later genera there is a lack of any positive structure, and the diductor bases probably formed a single median scar, as seen in more recent rhynchonellides. In early rhynchonellides there is no elaborate diductor attachment structure, but in some a median ridge became enlarged into a bosslike structure, as in *Clarkeia,* and some genera developed a posterior, transverse structure resembling the ctenophoridium of some spiriferides (e.g., *Hypothyridina*).

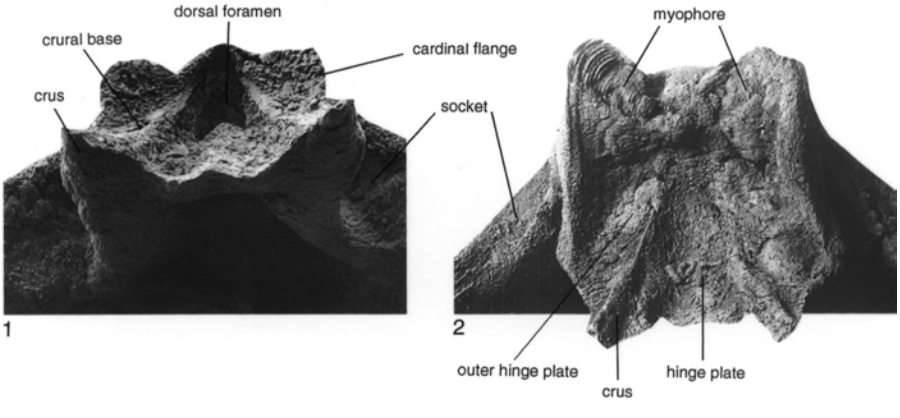

FIG. 359. Internal views of cardinalia in *1, Pachyplax gyralea* ALVAREZ & BRUNTON, Lower Devonian, Spain, ×30 (Alvarez & Brunton, 1990) and *2, Composita crassa* COOPER & GRANT, Middle Permian, Texas, USA, ×10 (new).

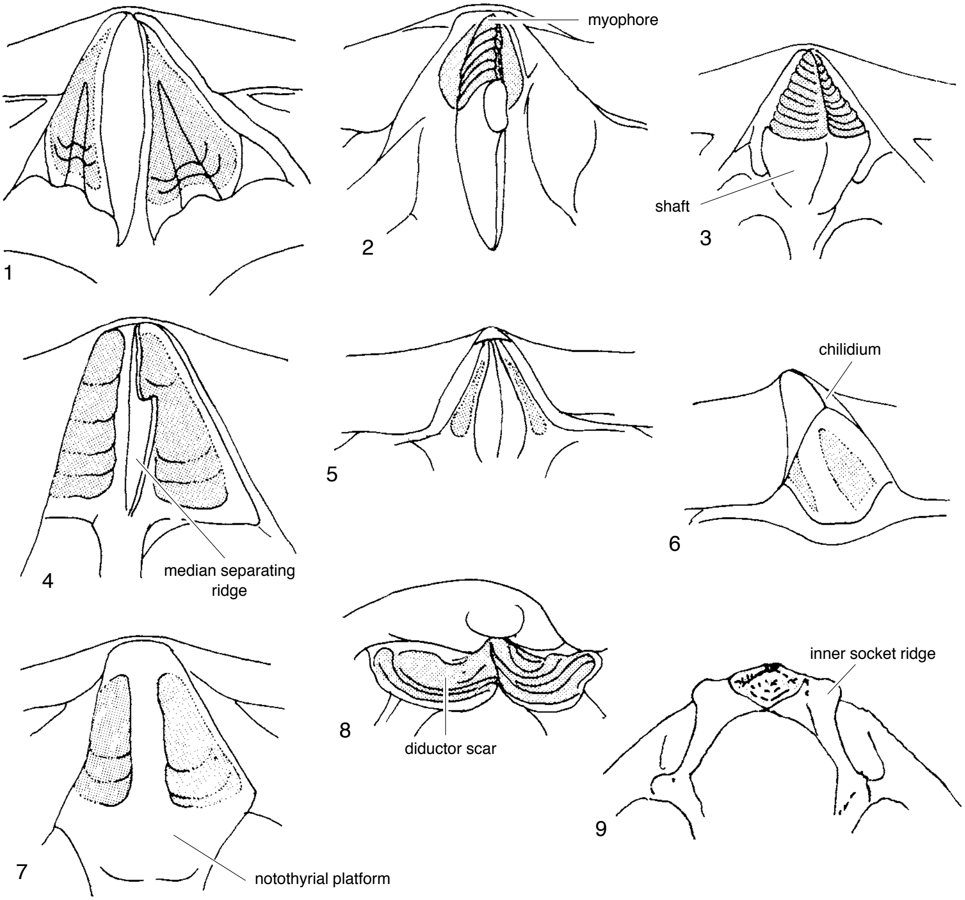

FIG. 360. Various types of cardinal processes; *1,* development of subsidiary ridges flanking median ridge of *Glossorthis;* differentiation of myophore and shaft in *2, Hebertella* and *3, Dinorthis;* simple partition of *4, Glyptorthis* and *5, Bimuria;* diductor scars on notothyrial platform with no enclosing ridges of *6, Leptella* and *7, Nothorthis;* and transverse and elevated muscle scars utilizing crural bases and inner socket ridges in *8, Notosaria* (adapted from Williams & Rowell, 1965b) and *9, Terebratulina* (new).

During the Mesozoic and up to recent times rhynchonellides generally failed to develop strong diductor attachments, retaining a median diductor pit flanked by scars extending onto the crural bases (Fig. 349).

The early terebratulides tend to display diductor attachment characters similar to those of athyridides with a dorsal foramen, and in stringocephaloid genera, with strongly developed ventral umbones, the cardinal process grew posteroventrally in an exaggerated fashion like those of some retzioids. Because of the ventral median septum in these terebratulides, however, the myophores divided so as to simulate the bilobed cardinal process of triplesioids. Genera with hinge plates bearing a dorsal foramen continued to the close of the Paleozoic after which the dorsal diductor scars were commonly spread onto the more median structures of the cardinalia. The distinctly knoblike structures associated with the cardinal processes of many adult species, such as *Chatwinothyris* or *Neothyris,* result from differential, posterior, shell thickening and weighting that accompanied a tendency to a

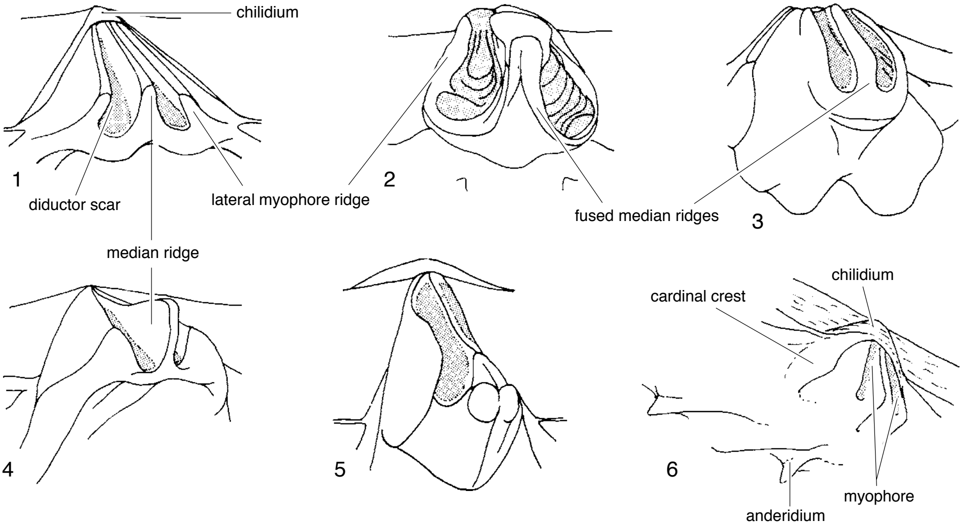

FIG. 361. Various types of trifid cardinal processes; *1, Sowerbyella; 2, Pugilis* viewed posteriorly; *3, Prionothyris; 4, Orthidiella; 5, Paucicrura* (Williams & Rowell, 1965b); *6,* a chonetoid (new).

freeliving mode of life. Again, in genera with elongate or strongly inflated ventral umbos the cardinal process extended posteriorly carrying the diductor bases into the ventral valve, but in no instance did these structures preserve the trace of the myophores on their dorsal surfaces as they would have if originating like the cardinal processes of strophomenides. The same is true of recent thecideioids, in which the diductors attached to the inner surface of ventrally or posteriorly facing distal ends of enlarged and unified cardinal flanges, lying between the inner socket ridges. Again this structure resembles a strophomenate cardinal process from the inner side, but externally it is smooth, and the muscle bases leave no scars on the external surface of the structure.

The attachment areas of the dorsal ends of the adductor muscles normally consist of two pairs of scars impressed on the floor of the dorsal 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. 348.3a). 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 that deserve a brief review.

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

FIG. 362. Cardinalia of *Cleiothyridina seriata* GRANT, Permian, Thailand, showing exaggerated inner socket ridges and dorsal foramen enlarged posteriorly by action of diductor muscles, ×7 (new).

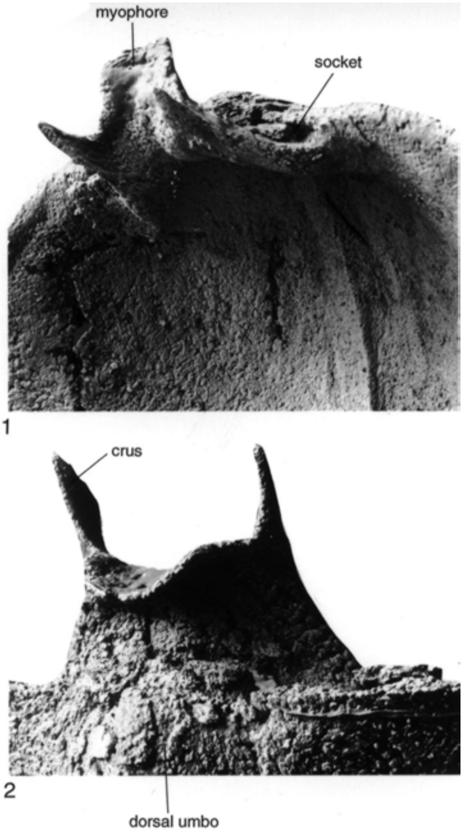

FIG. 363. Cardinalia of *Nucleospira carlukensis* (DAVIDSON), Lower Carboniferous, Ireland, viewed *1,* internally (SEM, ×27) and *2,* externally (SEM, ×34). The myophore is confined to the cardinal process tip and leaves no trace externally (new).

counterpart, the spondylium, is especially characteristic of the pentameroids (KOZLOWSKI, 1929). It was formed by the forward growth of the inner hinge plates underlying the base of the brachiophores 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. 365) so that they grew 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, with 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 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 that may have originated in the same way as those characteristic of the pentameroids but that could not have given support to the dorsal adductor field. The elevated troughs found in the dorsal valves of the syntrophiids and parastrophinids (Fig. 366) or of the skenidiids and *Kayserella,* 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 and CLARKE (1894–1895). Moreover, although the spoonlike apparatus in the dorsal valve of stenoscismatoids 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 (Fig. 367; COOPER, 1956). The **spyridium** of *Spyridiophora* (COOPER & STEHLI, 1955) and some aulostegids also supported the dorsal adductor muscles but did so on the transversely flattened posteroventral surfaces of a pair of subparallel plates that grew vertically from the floor of the

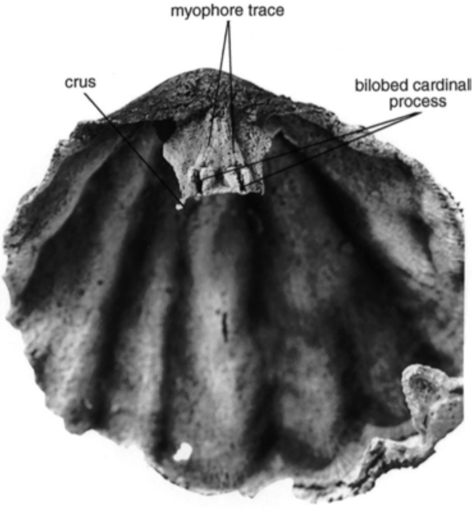

FIG. 364. Cardinalia of *Meekella,* Permian, Texas, viewed posteroventrally showing growth traces of myophores on cardinal process shaft, ×2.6 (new).

dorsal valve on either side of a low median septum (Fig. 368.1). These plates are quite different in disposition from the **braceplates** (Williams, 1953) of such strophodontids as *Douvillina* (Fig. 369), 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* (Cooper, 1955) accommodated the dorsal adductor bases and is correctly called a cruralium.

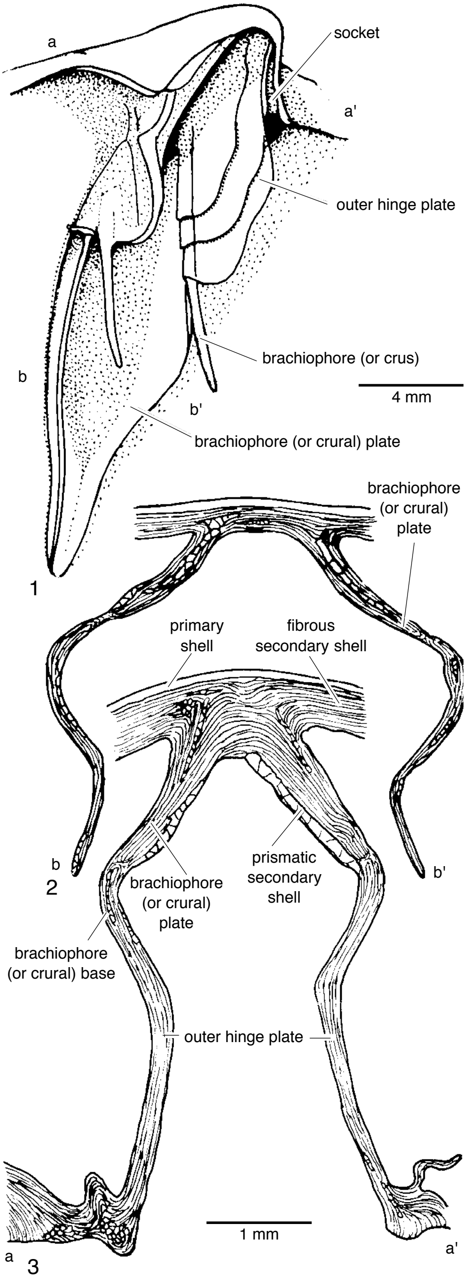

Fig. 365. Parts of dorsal valves of *Gypidula; 1, G.* sp., Middle Devonian, USA, with convergent brachiophore plates simulating sessile cruralium; *2–3,* transverse sections of *G. dudleyensis* Schuchert, Upper Silurian (Wenlock), England, in planes indicated on *1* (adapted from Williams & Rowell, 1965b).

Articulated brachiopods developed pedicle adjustor muscles from an early age, commonly producing scars that were visible before the scars of the diductor muscles. The dorsal adjustor muscles are situated on the posterior ends of the crural bases or on the inner hinge plates. During growth these scars moved forward so that in adult specimens they occupy the anterior regions of the inner hinge plates. The muscles commonly acted to rotate the shell relative to the attached pedicle. In some genera these plates united medially, forming a troughlike **septalium** that, in some, is supported on a median septum (Fig. 330.4), while in others it is sessile, resting directly on the valve floor, and in some it is unsupported. If the united inner hinge plates are unsupported, flat and medially undifferentiated between the crural bases, they are called a hinge plate (Fig. 330.3). Although the septalium commonly accommodated adjustor muscles and provided the base from which the cardinal process developed, it did not accommodate dorsal adductor muscles. For this reason septalia generally do not extend forward of crural bases, as do cruralia. A distinctive functional variation in the positioning and style of dorsal adjustor muscle scars has been described by Mineur and Richardson (1984) and Richardson (1991). Posteriorly thick-shelled terebratulides, such as the Anakineticinae, living in shallow-water sands, have long, thin, and mobile pedicles to which the dorsal adjustor muscles tend to be attached close to the cardinal process, leaving small, distinctive scars. This relatively posterior position allows the pedicle the maximum extension and withdrawal movement, which aids the specimen in shifting its position in coarse sediment.

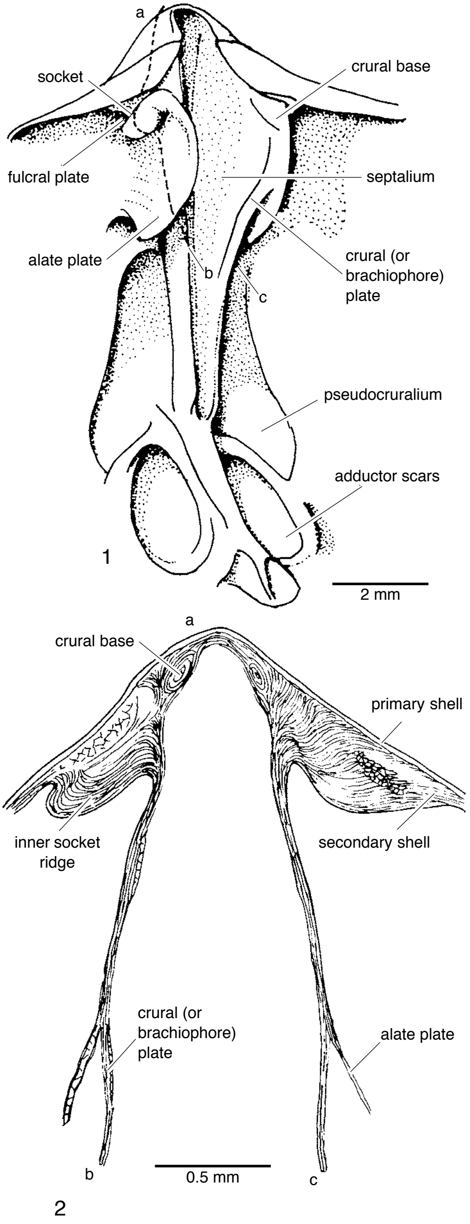

FIG. 366. Part of dorsal valve of *Anastrophia* sp., Middle Silurian, England, showing *1,* cardinalia relative to dorsal adductor field, and *2,* oblique section along line indicated in *1* (adapted from Williams & Rowell, 1965b).

In the ecologically similar Tertiary to recent terebratulide subfamily, the Bouchardiinae, the living type genus, *Bouchardia,* has been recognized as distinctive since being established by DAVIDSON in 1850. They also live in shallow water on coarse-grained sediments off the southeastern coast of South America (MANCENIDO & GRIFFIN, 1988). These shells are unique in having such highly and extensively thickened valves posteriorly, especially the cardinalia, that they completely fill the posterior internal space other than for muscle grooves and a central tunnel accommodating the pedicle (Fig. 370.3–370.4). Despite the high-energy environment of this genus, the pedicle adjustor muscles are reduced to a small, ventral pair attached immediately posterior to the ventral, centrally placed adductor scars. This reduction is related to the trend, suggested by RUDWICK (1970) and RICHARDSON (1973), of the activity of the reduced pedicle being correlated with increased weight of the posterior portion of the shell. The most obvious feature of *Bouchardia* is the dorsal, inverted V-shaped muscle scar. This represents the apical area of true muscle attachment (cardinal process) plus paired anterior grooves, in which the muscles were confined as they traversed the thickened posterior region. Anteriorly these grooves project from the anterior face of the massive cardinalia (**hinge platform**) (Fig. 370.2, 370.4). The diductor muscles become fan-shaped anteriorly and attached ventrally to poorly differentiated, widespread scars anterolateral to the adductor scars (Fig. 370.1).

In some genera (e.g., *Hypsomyonia*), the growth of a high, dorsal median septum was accompanied by the elevation of the anterior boundaries to the dorsal adductor field above the floor of the valve. KOZLOWSKI (1929) has proposed the term pseudocruralium for this kind of structure, but it hardly seems necessary to distinguish it from raised, callus rims of secondary calcite that commonly define the limits of the scars. In other genera, high median septa, commonly in ventral valves, include areas of **myotest**, as in *Cyrtina,* indicating that muscles attached to their sides (Fig. 354.3). The term myophragm has been used in these situations as well as for low ridges dividing muscle scars.

Apart from septa that clearly played a part in accommodating muscle bases, found in either valve, a few articulated brachiopods (e.g., *Phragmorthis, Skenidioides,* and *Mystrophora*) were equipped with septa that stood so high above the floor of the dorsal valve as to divide the mantle cavity into two compartments (Fig. 371). 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 ventral 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 dorsal valves of terebratelloids. Transverse partitions, again unrelated to the insertion of muscle bases, are also found in the ventral valves of such independent stocks as richthofeniids (Muir-Wood & Cooper, 1960), scacchinellids (Williams, 1953), and *Syringospira* (Cooper, 1954) (in which they are known as **blisters**). All shells with these **cystose** structures have deep, conical or subpyramidal ventral valves that must have grown at a faster rate than the enlargement of the contained soft parts so that the viscera migrated continually dorsally (Fig. 372). The formation of these blisters must have involved the movement of the brachiopod's body away from its shelly floor, aided by the secretion of a thin organic layer allowing uncoupling of the epithelium from the skeletal material, as in the process of mantle regression. This movement left a space across which the outer epithelium secreted a new organic membrane that acted as the seeding surface for a new shell partition and creation of a new blister (Fig. 372).

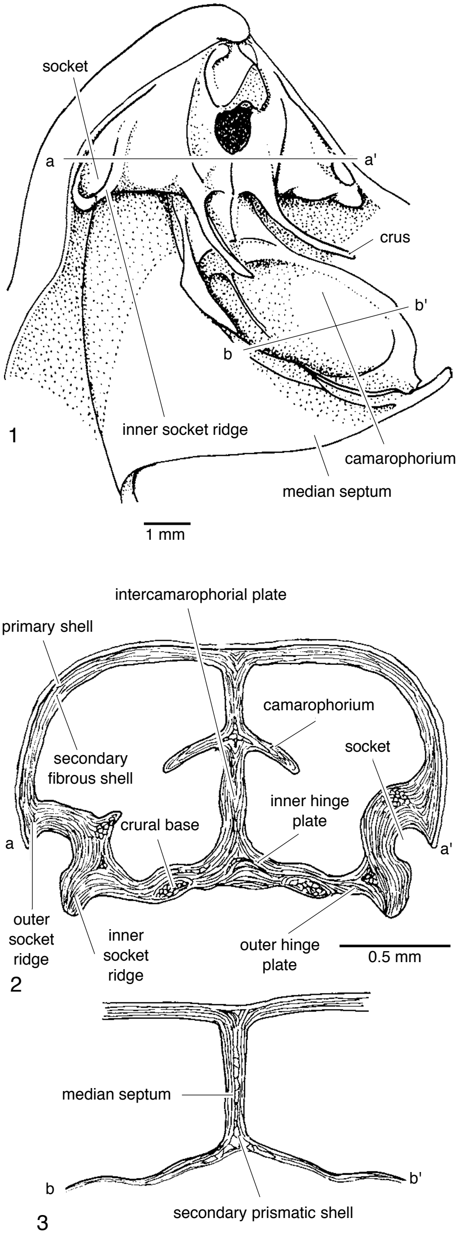

Fig. 367. *1,* Camarophorium of *Stenoscisma* sp., Middle Permian, USA; *2–3,* transverse sections of camarophorium of *Stenoscisma* sp., Upper Devonian, USA, with approximate location of cuts indicated on *1* (adapted from Williams & Rowell, 1965b).

Muscle scars and, more rarely, muscle tracks are developed in the inarticulated 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

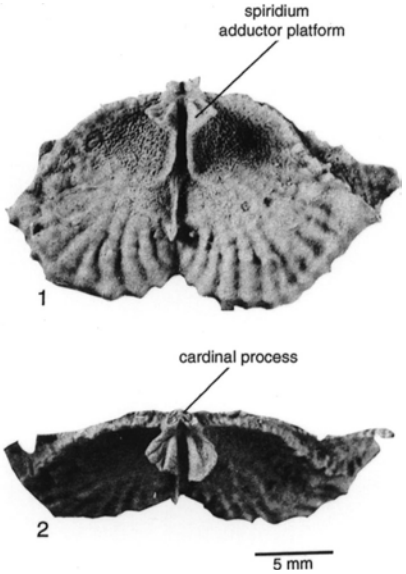

FIG. 368. *Spyridiophora reticulata* (R. E. KING), Lower Permian, Texas, USA, showing the spyridium viewed *1,* ventrally and *2,* posteroventrally (Cooper & Grant, 1975).

closely comparable with the scars and tracks of the articulated 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. Within the inarticulated brachiopod groups the numbers of muscles and their scars are variable, unlike the regularity of scars in the articulated groups.

Physiological changes of the epithelium at the base of the muscles may, however, be pronounced, as in *Neocrania,* where the modified epithelium is responsible for the deposition of calcite intracellularly, in marked contrast to the extracellular secretion that characterizes the rest of the outer epithelium. In fossil craniides, from the time of *Pseudocrania* in the Early Ordovician, muscle scars are commonly well preserved and similar to those of recent *Neocrania* (Fig. 373) in being distributed peripherally within the body cavity as two paired muscle fields in each valve. In recent species the paired adductors pass more or less directly between the valves, and they have been considered homologous with the adductor muscles of discinids and lingulids. Indeed it is possible that their musculature represents the primitive state for all stocks, the earliest known craniopsid-like brachiopod, *Heliomedusa* from the Early Cambrian apparently having a similar muscle pattern (JIN & WANG, 1992). Other aspects of craniid musculature are more unusual; the **oblique lateral** muscles in *Neocrania* are attached close to the posterior adductors in the ventral valve, but they are not attached to the dorsal valve but to the anterior body wall (see section on anatomy, Fig. 84). All known fossil craniids have similar oblique lateral muscle scars, unique to the group. GORJANSKY and POPOV (1986) suggested they might have acted as a type of diductor muscle by creating hydrostatic pressure in the body cavity; unlike recent lingulids, *Neocrania* does not have a well-developed musculature in the body wall and thus probably cannot open its shell as described by TRUEMAN and WONG (1987). The **internal oblique** muscles of craniids are

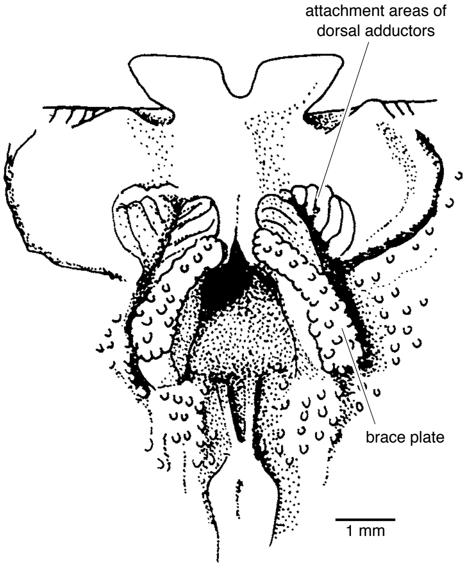

FIG. 369. Representation of brace plates in *Douvillina,* based on *D. arcuata* (HALL), Upper Devonian, USA (Williams & Rowell, 1965b).

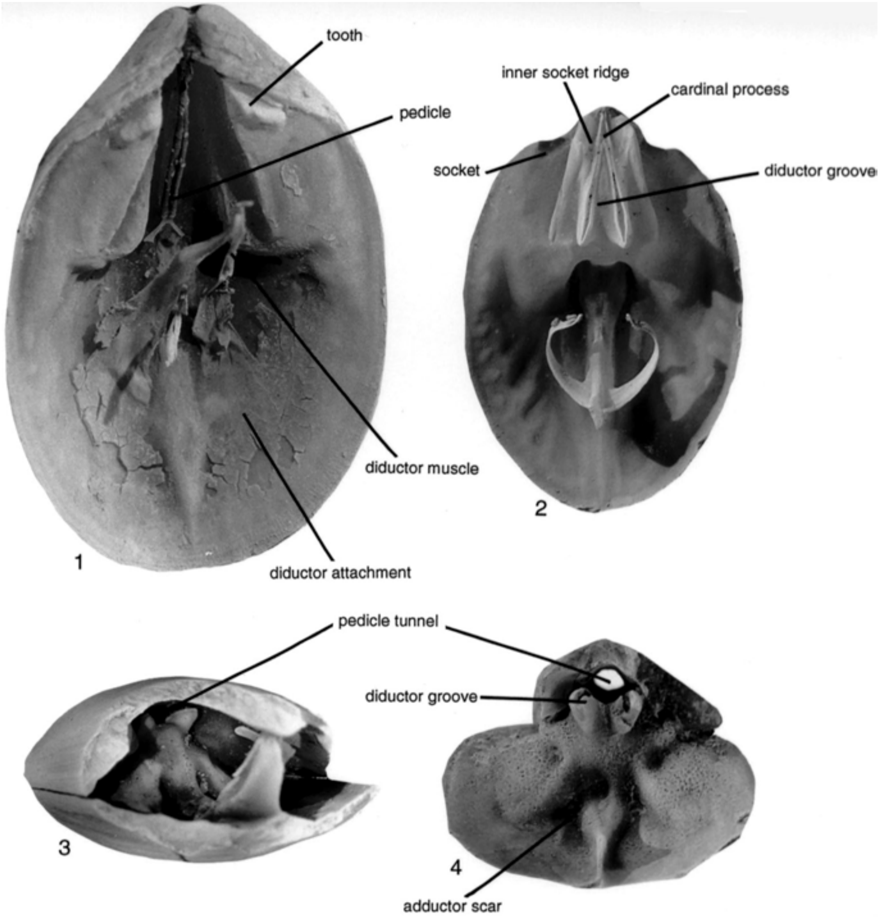

FIG. 370. *Bouchardia* specimens; *1–3, B. rosea* (MAWE), recent, Rio de Janeiro; *4, B. antarctica* BUCKMAN, Eocene, Seymour Island, Antarctica; *1,* ventral valve interior of a dry specimen retaining muscles, ×5; *2,* dorsal valve interior of a cleaned specimen, ×4; *3,* oblique anterior view of a cleaned, articulated specimen showing the massively thickened cardinalia, ×4; *4,* anterior view of the posterior region of an articulated specimen, ×3 (new).

the only oblique muscles comparable with those of lingulids and discinids; they are attached to the anteromedian region of ventral valves and close to the posterior adductors in the posterolateral region of the dorsal valve. Craniids also have a unique, unpaired **median muscle** controlling the position of the anus and several other muscles associated with the lophophore, all of which are also commonly preserved as scars in fossils.

The musculature of the extinct craniopsids and trimerellids has commonly been compared with that of lingulids, but GORJANSKY and POPOV (1985) interpreted the preserved muscle scars in these two groups by comparison with the craniids. Craniopsids (Fig. 374.1) have an unpaired median muscle scar posteriorly in both valves, comparable to that of craniids. In addition there are three paired dorsal and four ventral muscle scars comparable with the anterior and posterior adductors, oblique lateral, and the **brachial protractor muscles** of craniids (Fig. 374).

Muscle scars of trimerellids are more unusual, being different from those of lingulids (NORFORD & STEELE, 1969). All trimerellids

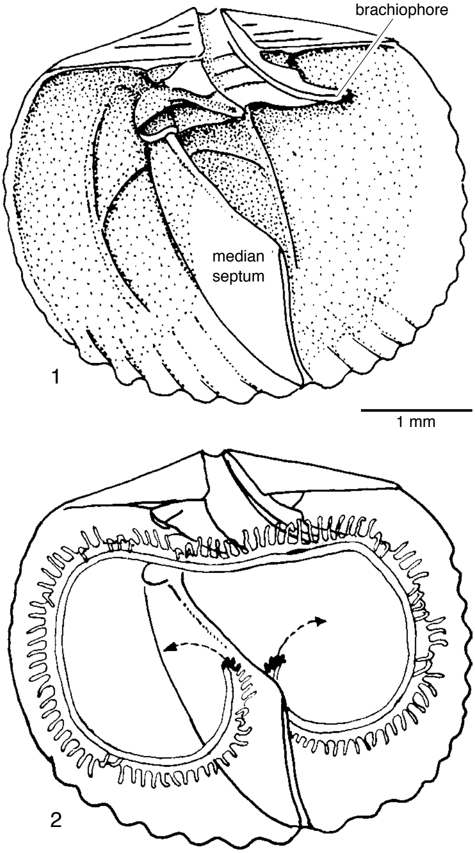

FIG. 371. *1,* Dorsal interior of *Phragmorthis* sp. cf. *P. buttsi* COOPER, Middle Ordovician, Scotland, with *2,* inferred disposition of lophophore about median septum (adapted from Williams & Rowell, 1965b).

have scars of two paired adductors, but some genera (*Palaeotrimerella* and *Eodinobolus*) have posterior diductor scars that might have worked posterior to the axis of rotation (Fig. 374; NORFORD & STEELE, 1969; GORJANSKY & POPOV, 1985, 1986), more as in the articulated brachiopods. In younger forms like *Trimerella* (Fig. 375), muscle platforms are hollow anteriorly and are elevated high above the valve floor, being supported medially by a **median partition** that projects in front of the platform and divides the cavity beneath it into two subtubular 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.

Calcareous-shelled members of the Obolellida include genera lacking articulatory structures (*Obolella*) as well as those with primitive structures (*Alisina, Trematobolus,* and *Oina*), but the muscle scars are invariably comparable to those of true articulated brachiopods (Fig. 376); they preserve scars of paired anterior and posterior adductors commonly forming a quadripartite muscle field in the dorsal valve.

In phosphatic-shelled brachiopods muscle scars are also produced by differential secretion of the outer epithelium between the muscle bases and the shell. This process includes not only differential rates of deposition but also changes in the relative amounts of organic and mineral components in the shell material underlying the muscles. The muscles in the two recent groups, the Linguloida and the Discinoida, can be divided into **dermal**, adductor, and oblique muscles (see section on anatomy, p. 83). The dermal muscles in both groups are probably responsible for the hydraulic opening of the shell, although this is only confirmed experimentally in the lingulids (TRUEMAN & WONG, 1987). Recent discinids have paired posterior adductors, which are probable homologues of the unpaired umbonal muscle in recent lingulids, and paired anterior adductors are apparently the equivalent of lingulid central muscles (see section on anatomy, Fig. 83). The scars of these muscles are commonly well preserved, even in their earliest known fossils, but in the early Paleozoic Obolellidae the scars of the umbonal muscles are paired (MICKWITZ, 1896; POPOV, 1992), which indicates that this type of musculature is primitive for lingulids and discinids, while the unpaired umbonal muscles appeared comparatively late in lingulide evolution, in the late Paleozoic and only in the Lingulidae.

In recent lingulids and discinids the oblique muscles control rotation and sliding of the valves; there are four pairs of these

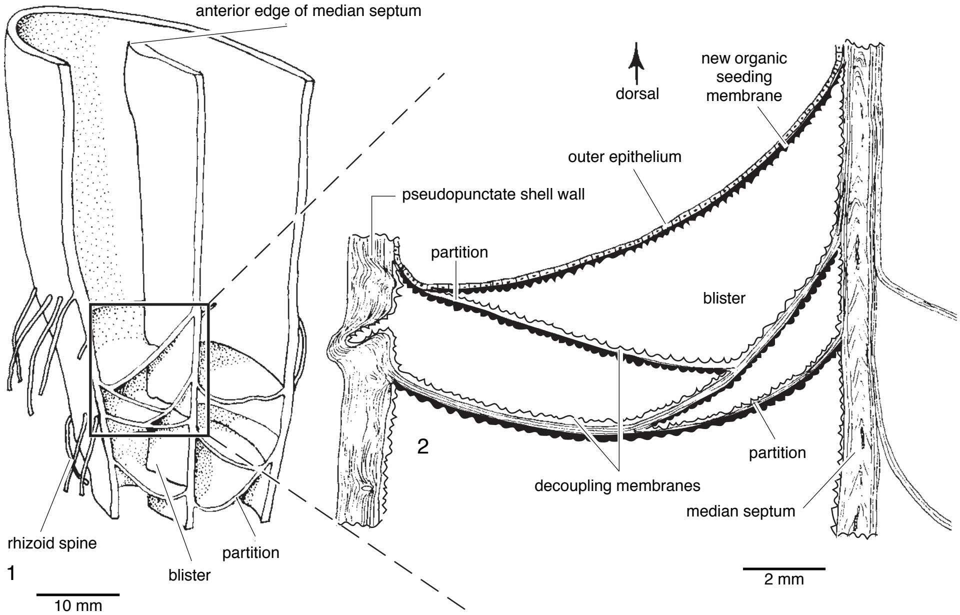

FIG. 372. *1,* Ventral valve of *Scacchinella americana* STEHLI, Lower Permian, USA, cut parallel with and anterior to interarea; *2,* section showing inferred relationship between transverse partitions and outer epithelium (adapted from Williams & Rowell, 1965b).

muscles in the Lingulida and three in the Discinida. The largest oblique muscles, the **transmedian,** are asymmetrically situated in recent Lingulidae, a position unique to this family. Scars indicating an identical type of asymmetry are recorded in Lingulidae as old as the Mesozoic (EGOROV & POPOV, 1990; BIERNAT & EMIG, 1993), and this type of musculature may be an adaptation to a more active, burrowing mode of life. In general oblique muscles are poorly defined in fossil representatives.

Apart from the Lingulidae, all known lingulides had symmetrical musculature that appears to have been conservative and almost identical to the pattern in obolides like *Oepikites, Obolus,* and *Ungula* (POPOV, 1992); it consists of four, major muscle fields (Fig. 377): (1) an umbonal field with paired **umbonal muscle** scars in both valves; (2) ventral **transmedian** and **anterior lateral** scars and dorsal transmedian, **outside lateral** and **middle lateral** scars in posterolateral muscle fields invariably placed posterolateral to the *vascula lateralia* in both valves; (3) ventral middle lateral and **central muscle scars** and dorsal central scars anterocentral to the *vascula lateralia* in both valves; and (4) the dorsal **anterior lateral muscle** field situated in the narrow, central, anterior projection of the dorsal body cavity.

The acrotretoid muscle system is reduced, as compared to the lingulides, and each valve of most species (including *Acrotreta*) has the following three muscle fields (Fig. 378): (1) a thickened field (**median buttress**) with one or two scars posteromedially in the dorsal valve and a field with two small scars (apical pits) directly lateral to the pedicle opening in the ventral valve; (2) a large, usually thickened, posterolateral field (**cardinal muscle** scars) in both valves; and (3) a small dorsal field with **anterocentral** scars placed directly lateral to the median septum and an equally small, but strongly raised scar on the **apical process**, just anterior to the pedicle opening.

The muscle system of actrotretides has been poorly understood, and it is difficult to homologize their muscles with lingulides. WILLIAMS and ROWELL (1965b) compared

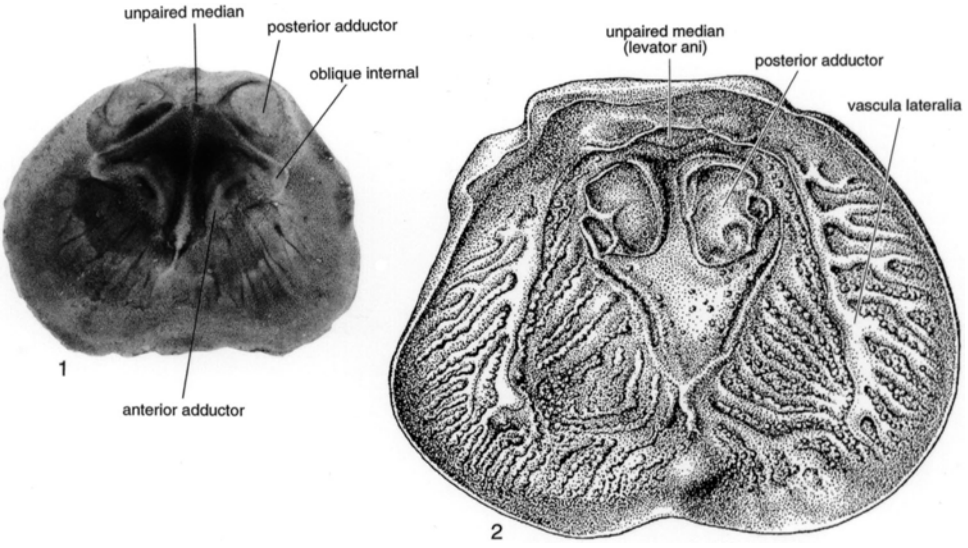

FIG. 373. *1, Neocrania anomala* (MÜLLER); dorsal valve interior showing main muscle scars, recent, west coast of Sweden, ×6; *2, Petrocrania* sp.; dorsal valve interior (anterior adductor scars are not preserved), Silurian (Wenlock), Gotland, Sweden, ×6 (new).

the inferred muscle system with discinioid or cranioid systems, suggesting that the large, posteriormost scars in each valve accommodated a pair of cardinal (umbonal) muscles; that the apical process, near the pedicle foramen, was the attachment for a pair of anterocentral muscles that attached dorsally close to the median septum (surmounting plate); and that these were equivalent to the posterior and anterior adductors respectively of cranioids (Fig. 346.1). POPOV (1992), however, has shown that the musculature is closer to that of lingulids (Fig. 346.2), the group from which he thought the acrotretides were derived. POPOV's (1992) interpretation necessitates the attachment of muscles within the apical pit and on the apical process of the ventral valve and the attachment of several muscles to some of the dorsal scars (Fig. 346.2).

The siphonotretoid muscle system is not well studied, although one pair of relatively large scars may be definitely recognized in each valve. According to HAVLIČÉK (1982), some well-preserved *Siphonobolus* specimens have a full set of scars closely similar to those of Paleozoic obolides.

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

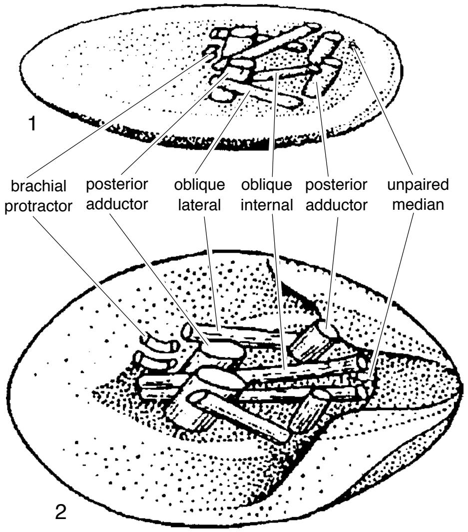

FIG. 374. Stylized reconstructions of muscle systems of *1, Craniops* and *2, Eodinobolus* (adapted from Gorjansky & Popov, 1985).

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 inarticulated brachiopods (see Fig. 383). All of the scars recognized produce narrowly triangular tracks radiating from the apex. In the ventral valve two such tracks diverge slightly anteriorly, terminating near the center of the valve, whereas in the dorsal valve there are seemingly two pairs of tracks, one pair diverging anterolaterally and a second pair forming a single, medially 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 articulated brachiopods.

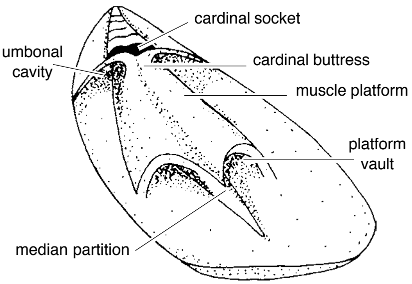

FIG. 375. Morphology of ventral valve of *Trimerella* (Williams & Rowell, 1965b).

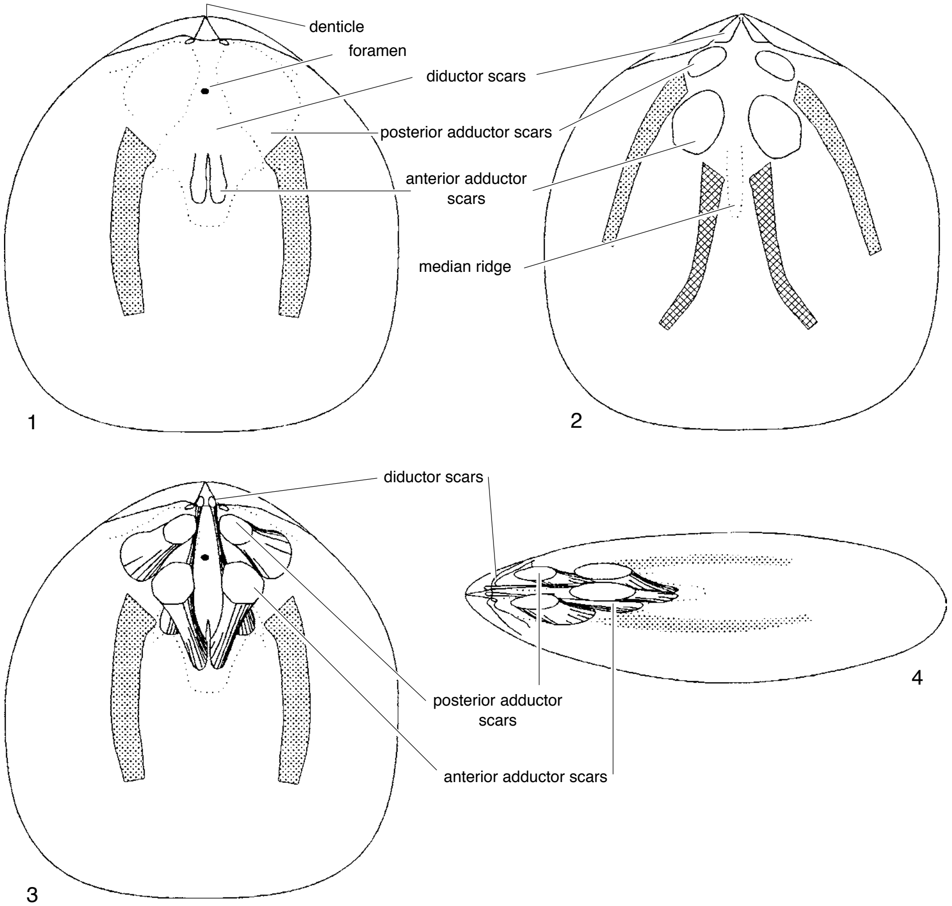

FIG. 376. *1–2,* Muscle scars and *3–4,* inferred musculature in the obolellide *Trematobolus,* based on *T. pristinus bicostatus* GORJANSKY, Lower Cambrian, north-central Siberia; *1,* ventral valve interior; *2,* dorsal valve interior; *3–4,* inferred musculature viewed dorsally and laterally (new).

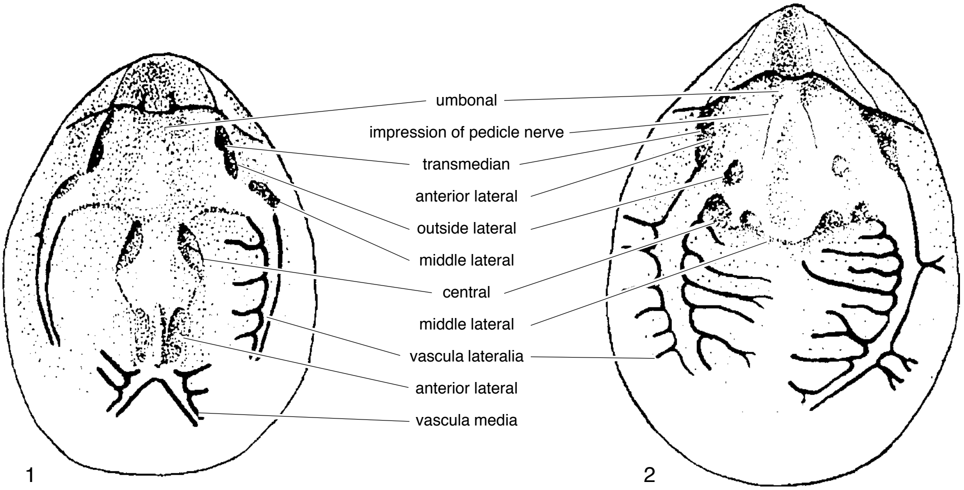

FIG. 377. Morphology of dorsal and ventral valves of *Oepikites,* showing muscle scars and mantle canals (new).

MANTLE CANAL SYSTEMS

The system of canals that pervaded the mantles of fossil brachiopods may be reconstructed by deciphering impressions on the interiors of both valves. These impressions consist of grooves or ridges, more or less symmetrically disposed on either side of the longitudinal midline, which are commonly seen to originate in the vicinity of the muscle scars. Many were differentially secreted by strips of outer epithelium, arching the canals, which deposited shell at a slower or, less commonly, faster rate than over the mantle generally. Larger, canal-like grooves may also truncate smaller ones, suggesting that they were caused by resorption (ROBERTS, 1968).

The fine distal branches of all canals, terminating just within the shell margins, are known to connect with setal follicles in living brachiopods. The disposition of impressions of terminal branches relative to grooves and eminences along the internal margins of fossil shells suggests that this arrangement 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., orthides, strophomenides, and porambonitoids); and it is symptomatic of this geological circumstance that the first analytic study of the patterns was prepared by ÖPIK (1934). He showed that arrangements deduced from a

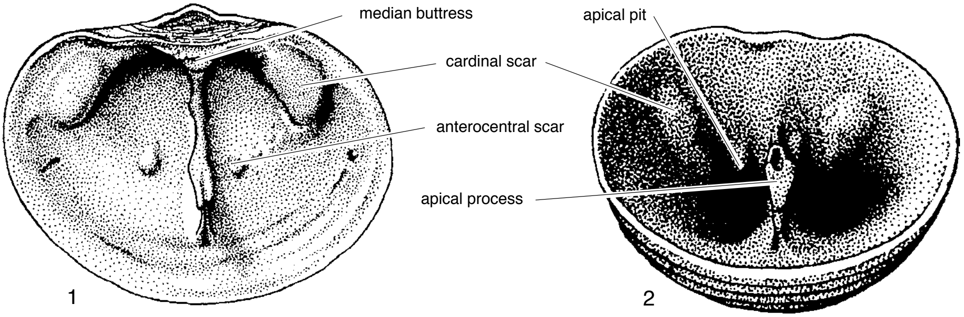

FIG. 378. Morphology of dorsal and ventral valves of *Ceratreta* (Holmer & Popov, 1990).

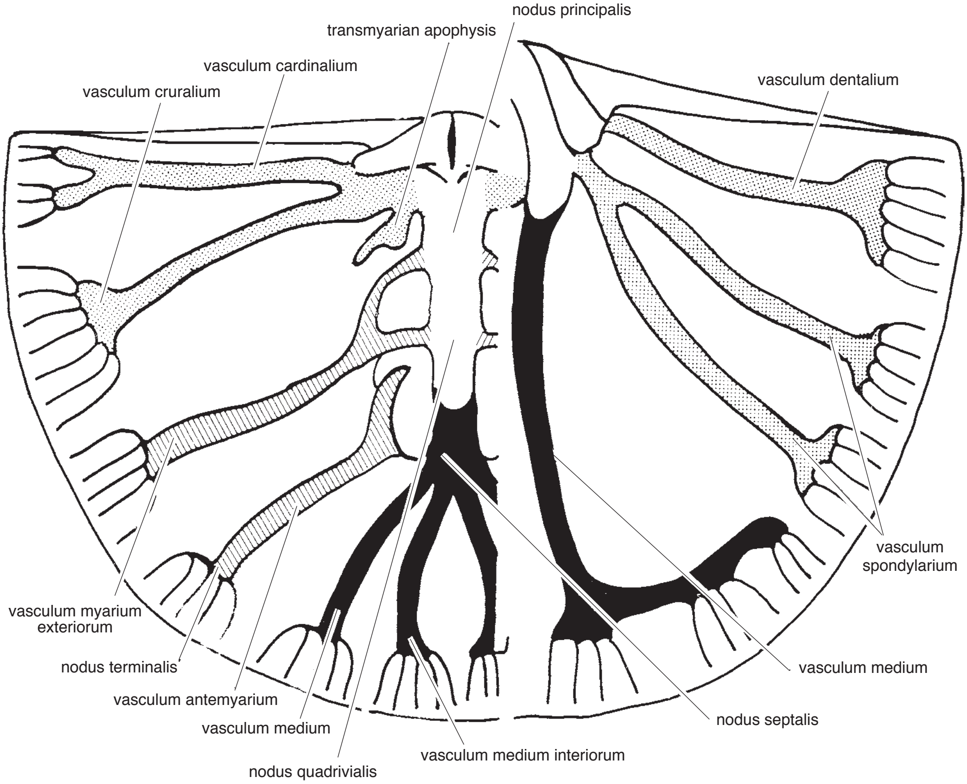

FIG. 379. Idealized canal systems in dorsal (to left) and ventral (to right) valves of primitive articulated brachiopod, especially to illustrate terminology used by ÖPIK (1934) (Williams & Rowell, 1965b).

study of the clitambonitoids were sufficiently consistent to merit a special terminology (Fig. 379). Some of the terms have been proposed for details of canal intersections or locations within what must have been the body cavity and the terms are not important in any 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 (WILLIAMS, 1956). 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 association with the dorsal adductor scars; 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* (or *spondylaria*) and of *vascula cardinalia* and *cruralia* in the ventral and dorsal mantles, respectively. In shells of adults, 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 articulated 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. 380.7), circulation within the ventral mantle was apparently effected by a pair of *vascula media* that curved arcuately within the shell margin and presumably served the peripheral mantle lobes and their setae. After allowing for the different distributions of muscle bases, this arrangement is not far removed from that of living *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;* this entire pattern is referred to as the saccate condition (Williams, 1956). The projection of the gonads into the mantle is rare among inarticulated brachiopods but has always been characteristic of the articulated brachiopods.

The beginning of a profound modification of the saccate condition is seen in impressions on the ventral interior of *Finkelnburgia* (Fig. 380.8). The gonocoels projected 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. 380.2); and in *Clitambonites* the pouches were entirely replaced by radially disposed *vascula genitalia* (pinnate condition) that presumably contained gonadal cords (Fig. 380.6).

Despite a basic difference in arrangement, the dorsal mantle canal systems underwent the same kind of changes as those described for the ventral mantle. In *Billingsella* and *Finkelnburgia,* digitate gonocoels were well 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. 380.7–380.8). 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 system. 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., *Strophomena, Leptaena,* and *Orthostrophia*) (Fig. 380.1, 380.3, 380.5), while 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). Öpik (1934) figured a very instructive variation within the species *Cyrtonotella kukersiania.* In one specimen, the entire posterolateral periphery of the mantle was served by arcuate *vascula myaria,* while the lemniscate *vascula 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* (Fig. 381.1; Williams, 1963).

It is now evident that, although these different patterns are well defined, they constitute morphological grades that were attained during the development of many independent stocks. The post-Cambrian orthoids tended to retain a saccate ventral mantle, although, as in the orthids, plaesiomyids, and plectorthids, the arcs to the *vascula media*

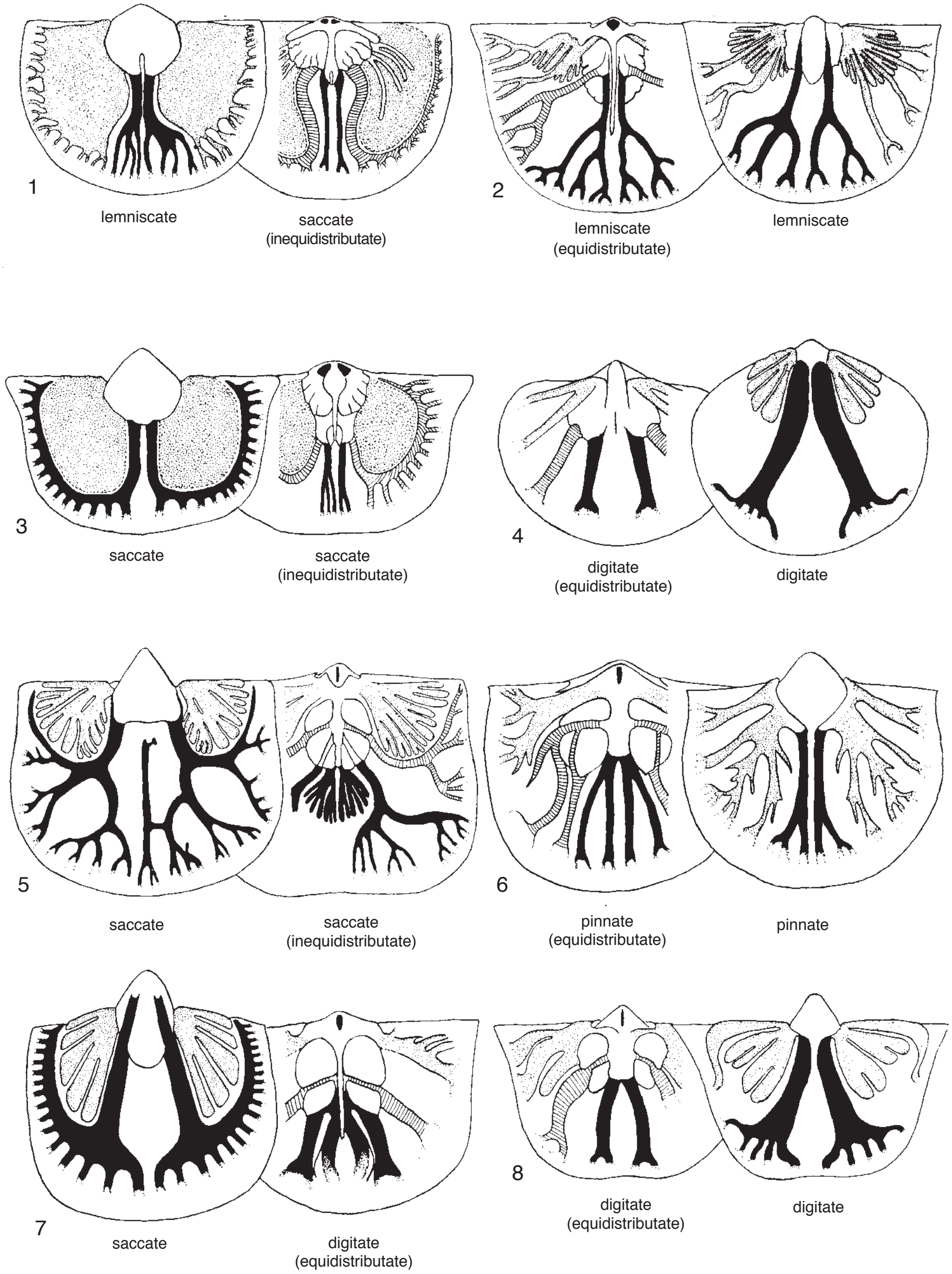

FIG. 380. Mantle canal systems of *1, Strophomena; 2, Palaeostrophomena; 3, Leptaena; 4, Tetralobula; 5, Orthostrophia; 6, Clitambonites; 7, Billingsella; 8, Finkelnburgia;* in each example dorsal valve is inner figure and ventral valve is outer; *vascula media* in *solid black;* gonadal sacs and *vascula genitalia stippled; vascula myaria* ornamented by *closely spaced lines* (Williams, 1956).

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. 381.5). This simple arrangement seems to represent a degeneration from an equidistributate lemniscate pattern, as is seen in some Ordovician species (Fig. 381.6).

The triplesioids and clitambonitoids, which are contemporaries of the orthoids, are lemniscate and pinnate, respectively. The enteletoids are also predominantly lemniscate in both valves, but the saccate condition was characteristic of the ventral mantle of *Paurorthis.* Roberts (1968) has shown that, during the ontogeny of the lemniscate mantle canal system of *Schizophoria,* the *vascula genitalia* became interconnected by small branches with *vascula media* and *vascula myaria* in the manner described for the orthoids *Cyrtonotella* and *Nicolella.*

Reconstructions of the strophomenoid and plectambonitoid mantles show a similar drift away from the primitive saccate condition. A few genera (e.g., *Titanambonites*) possessed saccate ventral mantles, but in both groups the lemniscate (or pinnate) condition was more usual (e.g., *Strophomena, Palaeostrophomena, Sowerbyella*) (Fig. 380.1–380.2; 381.8). 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. Indeed, this process of capture, presumably involving replacement of connective tissue by embayments of ciliated epithelium, may have been the main mode of development.

The dorsal mantle systems of these groups are not well known. Among plectambonitoids, the lemniscate equidistributate pattern of *Palaeostrophomena* and the pinnate inequidistributate patterns of *Plectodonta* and *Sampo* seem to be dominant; and this conclusion may also be true for the strophomenoids, although in *Leptaena* and *Strophomena* the dorsal mantles were essentially saccate (Fig. 380.1, 380.3).

The pattern of other groups (e.g., orthotetoids, spiriferides, and pentameroids) is rarely preserved, and those of the chonetoids and productoids is largely unknown except for traces of *vascula media* belonging to what was possibly a lemniscate ventral mantle of *Rugosochonetes* (Muir-Wood, 1962). The orthotetidine *Floweria* rarely shows impressions of patterns suggestive of expanded lemniscate (or pinnate) *vascula genitalia* and abbreviated median and submedian canals in both valves.

The patterns of atrypoids are indifferently preserved, but if *Atrypa* is representative, the mantle canal systems developed in members of the superfamily constituted an interesting modification (Fig. 382). The distribution of impressions of discrete muscle attachments in the shell interior suggests that 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 and Lambiotte (1962) have plotted these for *Desquamatia* but have also included patterns within the body cavity that were not canals but sites of unmodified outer epithelium within the muscle fields and sporadically on the valve floor (P. Copper, personal communication, 1993). Ignoring these, the *vascula media* were poorly developed in the ventral mantle to give a modified saccate condition and were somewhat reduced in the dorsal mantle where 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 athyroids (Fig. 381.9–381.10) and

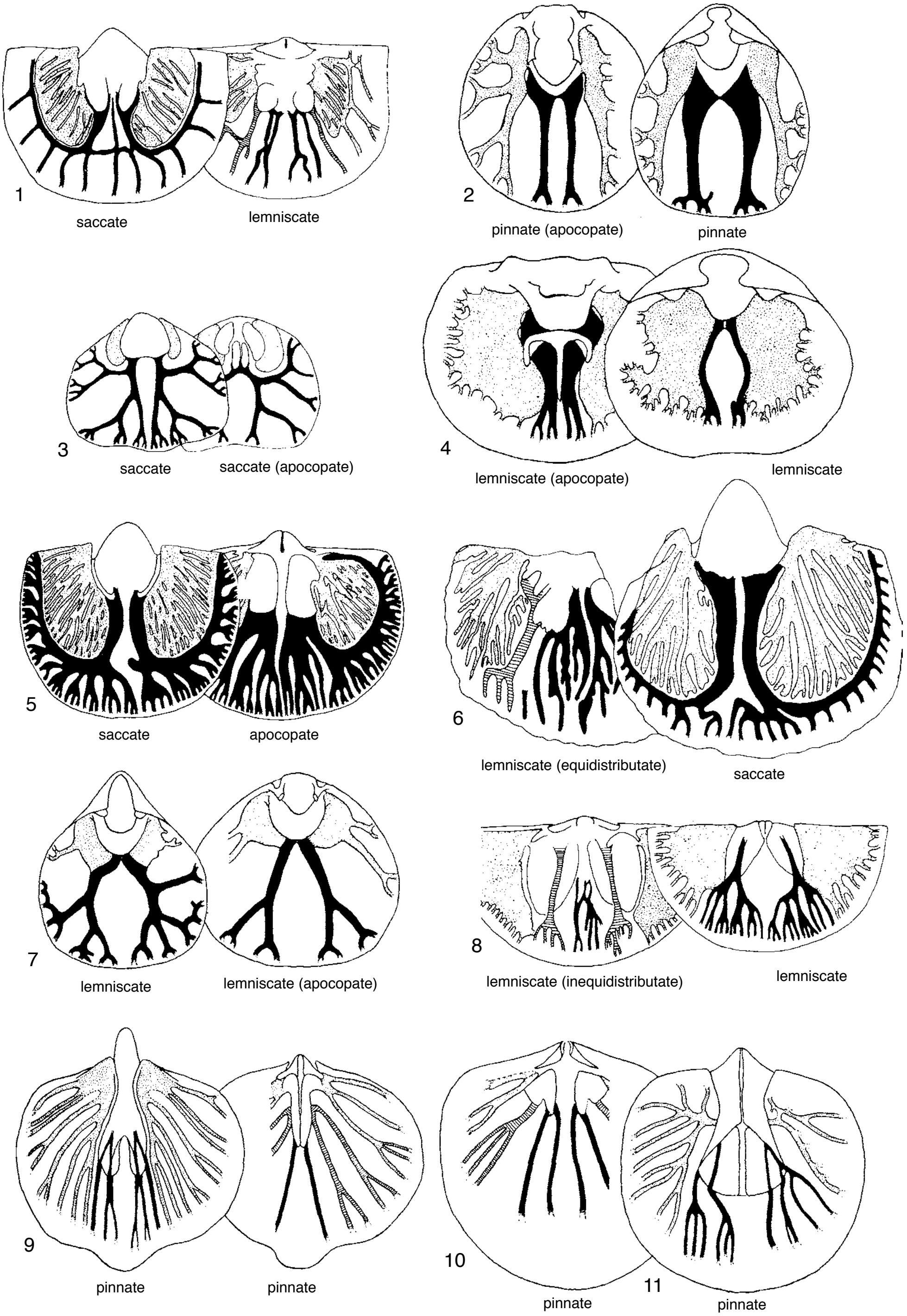

FIG. 381. Mantle canal systems of *1, Nicolella; 2, Macandrevia; 3, Uncinulus; 4, Megerlina; 5–6, Dolerorthis; 7, Notosaria; 8, Sowerbyella; 9, Athyris; 10, Coelospira; 11, Meristina;* arrangement and shading as in Figure 380 (Williams & Rowell, 1965b).

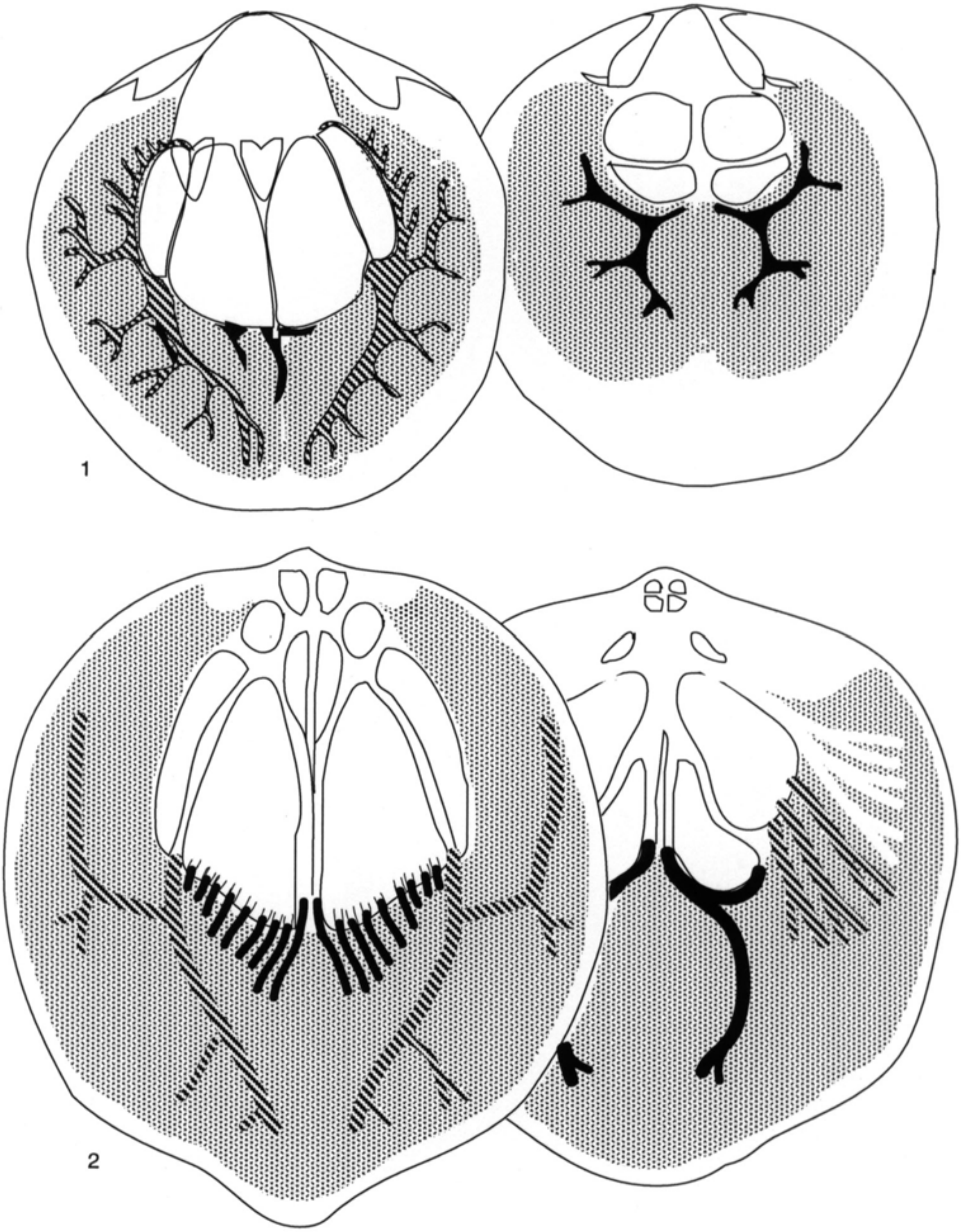

FIG. 382. Mantle canal systems of sexually mature atrypidines, as typified by *1, Atrypa reticularis* LINNÉ and *2, Desquamatia* sp. (original drawing by P. Copper and Vandercammen & Lambiotte, 1962).

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 rhynchonellides and terebratulides, 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 apocapate. Yet it is fairly certain that the rhynchonellide arrangement was independently derived from a saccate or lemniscate condition and the terebratulide from a radial pinnate pattern.

Two contrasting patterns exist among recent rhynchonellides. 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. 381.7). Both of these patterns occur in fossil forms. *Sphaerirhynchia, Fitzroyella,* and *Uncinulus* (Fig. 381.3) are saccate and *Leiorhynchus* is 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 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 terebratulides, 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 terebratulides first emerged as significant members of the brachiopod phylum, the pattern of such living stocks as *Macandrevia* (Fig. 381.2) was already characteristic of stringocephaloids (Cloud, 1942). A few genera (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 athyridoids. It is possible, then, that the characteristic dorsal pattern was derived from a pinnate condition by atrophy of the *vascula myaria.* In some modern terebratelloids (e.g., *Laqueus, Macandrevia,* and *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 anteromedially 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 terebratulides.

The mantle canal pattern of inarticulated brachiopods is basically simpler than that of articulated species. Commonly, there is also some difference in function of the canals, for only in the Craniidae (see Fig. 387) are the gonads known to be partially inserted into them; in all other recent inarticulated brachiopods the gonads are confined to the body cavity, and the canals have primarily a circulatory function.

There is, however, a striking anomaly in the mantle canal systems (and musculature) of the early Paleozoic organophosphatic Paterinida (Fig. 383). Laurie (1987) has shown that arcuate *vascula media* were present in the mantles of both valves as were pouchlike *vascula genitalia,* especially in the ventral valve. Such patterns are indeed best described as either saccate or saccate (possible apocapate) for the ventral and dorsal valves respectively and are orthide rather than lingulide in arrangement.

The mantle canal system of most of the organophosphate-shelled species consists of 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 midline of the valve. This latter pair may be termed the *vascula media,* but whether they are strictly homologous with the *vascula media* of articulated brachiopods is a matter of opinion. It is also impossible to assert that the *vascula lateralia* are the homologues of the *vascula myaria* or *genitalia* of articulated species, although they are likely to be so as they arise in a comparable position.

This basic pattern of one ventral and two dorsal pairs of canals is commonly developed

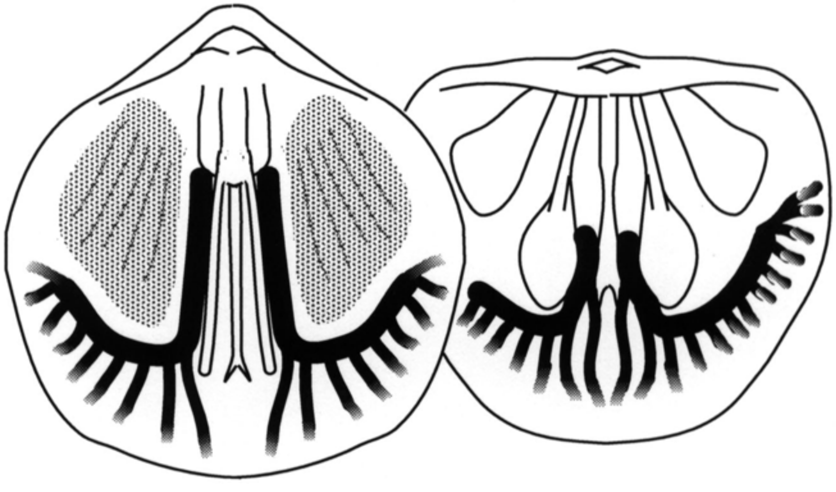

FIG. 383. Mantle canal systems of *Paterina* with ventral valve on the left and dorsal valve on the right; *vascula media* in *black*; gonadal sacs *stippled* (adapted from Laurie, 1987).

in lower Paleozoic lingulides. 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 obolids (*Oepikites*) and elkaniids (*Broeggeria*) (Fig. 384.1, 384.5) numerous minor canals branch from either side of the main trunks, and they and their distributaries permeate much of the mantle. These small branches are rarely seen in fossil forms, but it is reasonable to assume their presence in most lingulides. The branches from the principal canals are relatively minor; the *vascula lateralia,* in particular, 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 is also characteristic of many of the older lingulides including the paterulids (*Paterula*) and zhanatellids (*Zhanatella*) (Fig. 384.3–384.4) as well as the elkaniids and obolids.

In the lingulids and pseudolingulids (*Pseudolingula*), however, the mantle canal systems are fundamentally different (Fig. 384.2, 384.6) as is well shown in recent *Glottidia* and *Lingula.* In these groups, the dorsal *vascula media* are not developed and the *vascula lateralia* in both valves divide immediately after leaving the body cavity (bifurcate condition) or could well have done so as in *Pseudolingula.* Thereafter, the smaller branch of each main canal extends posteriorly to supply the mantle lateral of the lateral body wall, while the larger branches pass anteriorly and converge toward the midline of the valve. From these principal branches minor canals are given off comparable to those of elkaniids and obolids. The bifurcation of each of the *vascula lateralia* into anterior and posterior branches is not solely a function of the form of the shell, for in the obolids *Barroisella* and *Langella,* genera very similar in outline to recent *Lingula,* the *vascula lateralia* arise in a similar position but are comparable in form to those of other obolids. The bifurcation of these canals in recent lingulids appears to be more closely related to their relatively anterior origin and

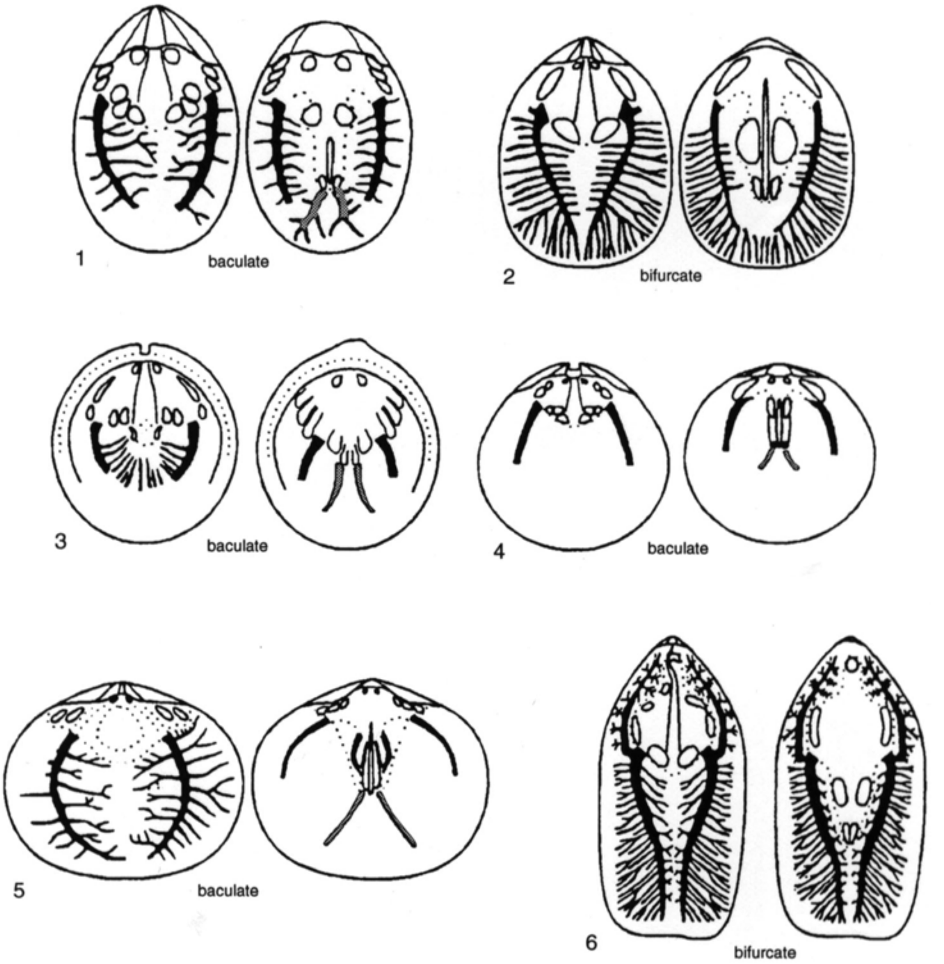

FIG. 384. Mantle canal systems of representative organophosphatic inarticulated brachiopods (lingulides); *1, Oepikites; 2, Pseudolingula; 3, Paterula; 4, Zhanatella; 5, Broeggeria; 6, Lingula;* ventral valve on left, dorsal valve on right; *vascula lateralia* in *black; vascula media* in *gray* (original drawings by L. E. Holmer & L. Popov).

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 lingulides, particularly the obolid *Schmidtites,* the limit of the anterior body wall was placed relatively farther forward than that of *Lingula,* yet they still developed *vascula media.* The respiratory function of the dorsal *vascula media* of Paleozoic lingulides is performed in modern lingulids by the anterior branches of the *vascula lateralia,* which converge medially.

A similar bifurcate condition of the ventral *vascula lateralia* has also arisen

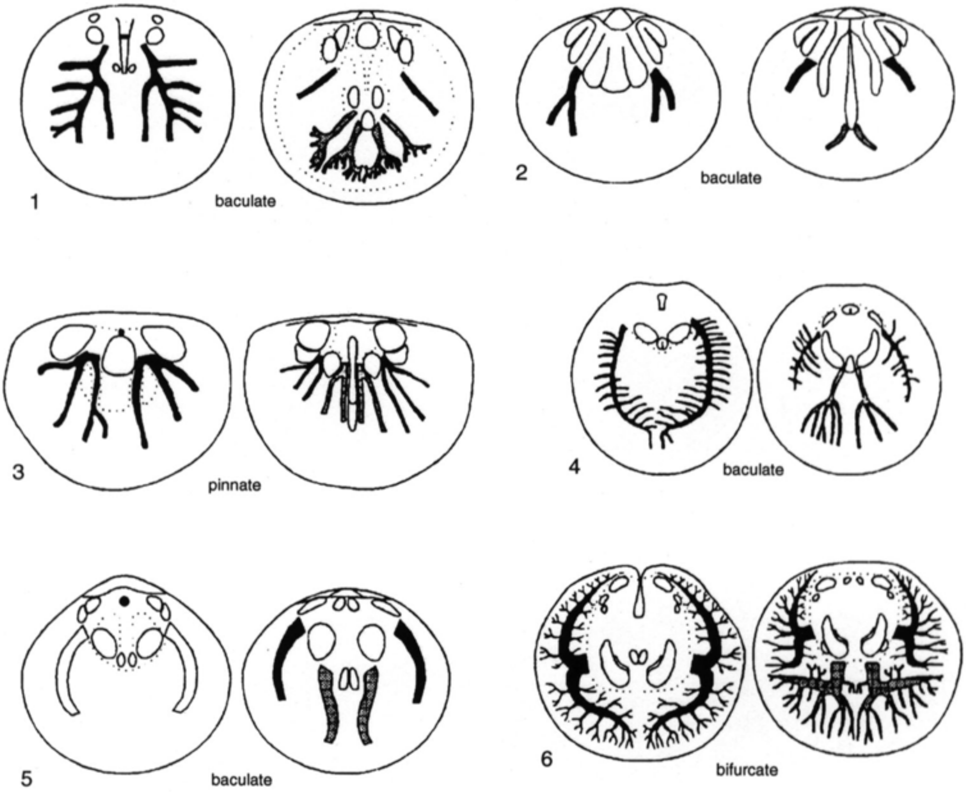

FIG. 385. Mantle canal systems of representative organophosphatic inarticulated brachiopods (discinides, siphonotretides, and acrotretides); *1, Orbithele; 2, Botsfordia; 3, Cyrtonotreta; 4, Lochkothele; 5, Schizambon; 6, Discinisca;* ventral valve on left, dorsal valve on right; *vascula lateralia* in *black; vascula media* in *gray* (original drawings by L. E. Holmer & L. Popov).

independently in living discinides but with the dorsal *vascula media* expanded to serve the anterior half of the dorsal mantle (Fig. 385). The older Paleozoic discinides, as the orbiculoid *Lochkothele,* had baculate mantle systems (Fig. 385.4) that, however, could easily have been transformed into the bifurcate condition. The dorsal *vascula media* were also relatively more important among acrotretides, especially the later botsfordiids (*Orbithele*). Indeed in acrotretoids (*Cyrtonotreta*), the *vascula lateralia* of both valves rapidly branch into a number of subequal, radially disposed canals (pinnate condition) (Fig. 385.3). Although this branching commonly produced in the ventral mantle medially situated canals whose position is similar to that of the dorsal *vascula media,* they may be regarded as branches of the *vascula lateralia,* since true *vascula media* are otherwise unknown in the pedicle valve of inarticulated brachiopods.

The mantle canal systems of the carbonate-shelled inarticulated brachiopods show some interesting variations (Fig. 386–387). The baculate condition (Fig. 386.3–386.4) seems to have been wholly characteristic of the Cambrian obolellides (*Obolella, Trematobolus*) and of the oldest craniide, the Ordovician *Pseudocrania* (Fig. 387.3) although, with the main branches of both the *vascula media* and *lateralia* giving rise to second-order distributaries marginally, the craniide canal systems simulate the pinnate condition. Subsequently, however, the canals of the dorsal mantle seem to have undergone extreme changes with the suppression of the *vascula lateralia* in living *Neocrania* and of

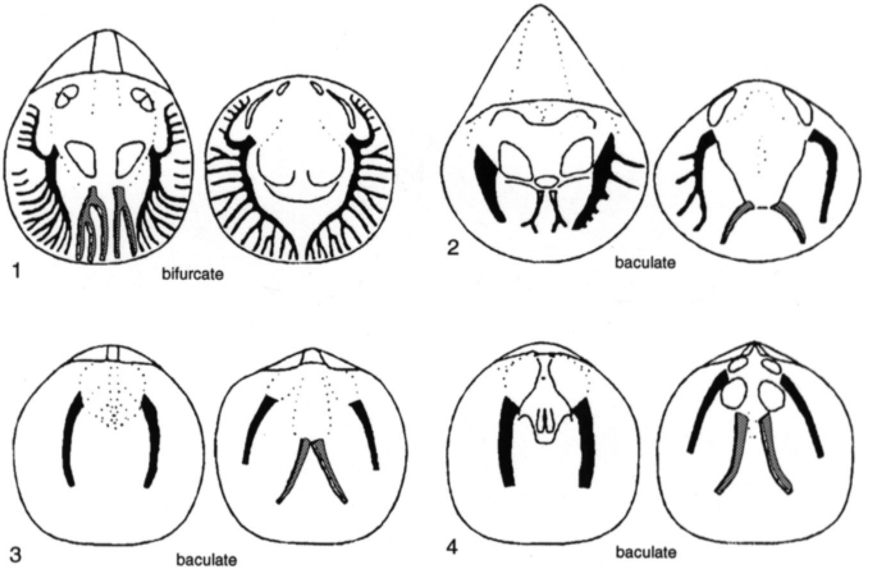

FIG. 386. Mantle canal systems of representative carbonate-shelled inarticulated brachiopods (obolellides, trimerellides); *1, Palaeotrimerella; 2, Monomerella; 3, Obolella; 4, Trematobolus;* ventral valve on left, dorsal valve on right; *vascula lateralia* in *black; vascula media* in *gray* (original drawings by L. E. Holmer & L. Popov).

the *vascula media* in *Petrocrania;* these atrophies were accompanied by a compensatory enlargement of the remaining network of canals (Fig. 387.1–387.2). Yet the mantle canal system that most diverged from the basic baculate condition of inarticulated brachiopods is that of the carbonate-shelled trimerellides (Fig. 386.1–386.2). In this

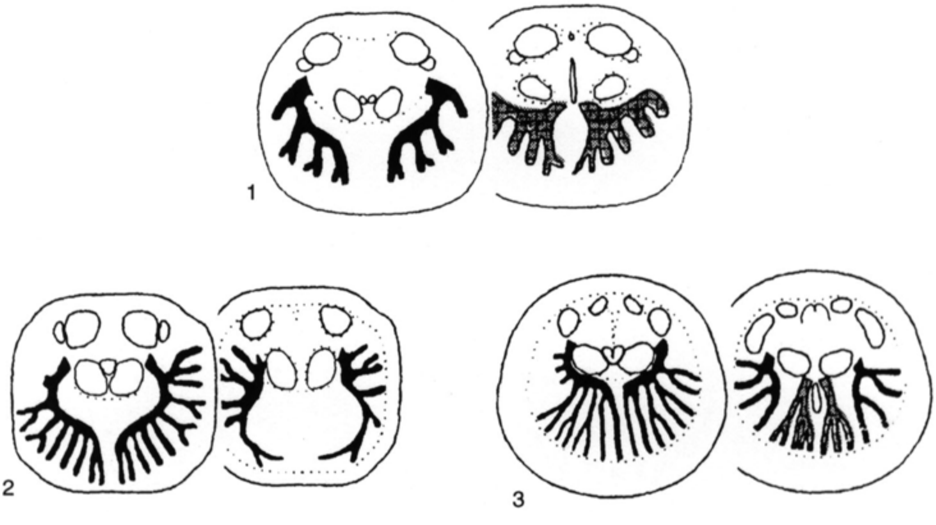

FIG. 387. Mantle canal systems of three genera selected to show the diversity attained during the evolution of craniide brachiopods; *1, Neocrania; 2, Petrocrania; 3, Pseudocrania;* ventral valve on left, dorsal valve on right; *vascula lateralia* in *black; vascula media* in *gray* (original drawings by L. E. Holmer & L. Popov).

lower Paleozoic group the main submedial trunks of the *vascula media* were fully developed in the ventral mantle but only variably so in the dorsal one. Moreover, both main mantle canal patterns characterizing inarticulated brachiopods as a whole are found in this order: the baculate condition in such forms as *Monomerella* and *Gasconsia* and the bifurcate condition in *Palaeotrimerella.*

MORPHOLOGICAL AND ANATOMICAL TERMS APPLIED TO BRACHIOPODS

Alwyn Williams[1] and C. Howard C. Brunton[2]

with contributions from other contributors to this revision of Part H, Brachiopoda

[[1]University of Glasgow; [2]The Natural History Museum, London]

The following glossary consists of terms used in a distinctive way to describe brachiopod shells and to define the biology of the phylum as a whole. Anatomical terms defined herein are restricted to those used for soft parts that directly affect shell morphology.

All terms given in boldface in the glossary are used throughout the text in the way they have been defined. Those that can normally be used for any taxon, at least to class level within the phylum, are printed in capitals (for example, ADDUCTOR MUSCLES). Those that describe a feature generally specific to a particular taxonomic group(s) are printed in lower case letters (for example, accessory adductor scars).

Terms printed in plain style do not merit formal recognition that would restrict their use to a singular feature, for example, flange (of a crus); the term flange is currently used in morphological descriptions of several unrelated features.

Terms in italics (for example, *accessory denticles*) are considered by most or all of the contributors to be obsolete. They have been listed and, where necessary, defined so that future researchers with the aid of the glossary can consult older literature without being misled by outmoded terminology. Their continued use by brachiopod workers is not recommended.

GLOSSARY OF MORPHOLOGICAL AND SELECTED ANATOMICAL TERMS

accessory adductor scars. Pair of muscle scars in ventral valve of daviesiellids lying anterior to principal adductor impressions, interpreted as ancillary adductor bases.

accessory dental sockets (of orthidines). See denticular cavities.

accessory denticles. See denticles.

accessory diductor muscles. Pair of muscles branching posteroventrally from main diductor muscles and inserted in ventral valve posterior to adductor bases (Fig. 348).

accessory lamellae. Pair of lamellae developed from arms of jugum and coiled parallel to main lamellae of spiralia (Fig. 336).

accessory septum. Used informally for any septum ancillary to others. See anderidia.

accessory socket. Outer part of divided dental socket of plectambonitoids (Fig. 322–323); also used for depression in outer socket ridge.

accessory tooth. Articulating process flanking hinge tooth of plectambonitoids and fitting into accessory socket in dorsal valve (Fig. 323).

acuminate (loop). Phase in loop development with laterally bowed, descending lamellae extending from crura but otherwise unsupported and uniting anteromedially to form an echmidium (Fig. 334.1, 338.1).

adductor dividing ridges. See anderidia.

ADDUCTOR MUSCLES. Muscles that contract to close shell. In articulated brachiopods two adductor muscles, each divided dorsally, are commonly present to produce single pair of scars located between diductor impressions in ventral valve and two pairs (anterior, posterior) in dorsal valve. In inarticulated brachiopods two pairs of adductor muscles (anterior, posterior) are commonly present, passing almost directly dorsoventrally between valves (Fig. 348). See central muscles, umbonal muscles.

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

aditicule. Gently inclined, coarse exopuncta; allegedly contained seta (Fig. 302).

ADJUSTOR MUSCLES. Two pairs of muscles in many articulated brachiopods moving pedicle or shell and arising from proximal end of pedicle to attach posterolaterally of diductors in the ventral valve (pedicle adjustors) and on hinge plates or floor of dorsal valve behind posterior adductors (brachial adjustors) (Fig. 348–349).

adminicula (sing., **adminiculum**). Paired subvertical plates situated umbonally in either valve and extending from valve floor to ventral edges of dental flanges (ventral adminicula) or to dorsal edges of crural bases (dorsal adminicula; however, see crural plates) (Fig. 324.3).

alae. Winglike extensions at cardinal extremities. See ears.

alate plate. Flaplike extension of secondary shell arising from lateral surface of brachiophore plate in porambonitoids (Fig. 366).

alternate folding. Deflection of shell surface in which fold of one valve is opposed by sulcus of other (Fig. 289).

alveolus. See cardinal process pit.

amphithyrid (foramen). Pedicle opening shared by delthyrium and notch in beak of dorsal valve (Fig. 318).

anacline. See inclination of cardinal area or of pseudointerarea (Fig. 285).

ancilliary strut. Secondary shell material deposited between brachiophore base and median ridge in some orthides.

anderidia (sing., **anderidium**). Paired ridges in some strophomenides, situated posterolaterally of median plane of dorsal valve, of increasing elevation or projecting anterolaterally (Fig. 361).

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

annular (loop). Phase of loop development with a ring formed by resorption of the posterior apex of the hood. The attachments of the ring and descending lamellae are separate and the descending lamellae are usually complete.

ANTERIOR. Direction in plane of symmetry or parallel to it away from pedicle and toward mantle cavity (Fig. 283).

anterior lateral (oblique) muscles. Pair of muscles in some lingulids originating on ventral valve posterolateral to central muscles, converging dorsally to their insertions anteriorly on dorsal valve (Fig. 346.2).

anteris. Arcuate plate of secondary shell underlying hinge teeth in some Early Cambrian articulated brachiopods (Fig. 327.4).

antiplicate (folding). See biplicate.

antron. Triangular to elongate groove variably developed between cardinal process buttress plates and breviseptum in some productides. See cardinal process buttress plates.

antygidium. Low, platelike ridge of shell near beak of dorsal valve, covered externally by cuticle and deposited during ventral migration of junction of pedicle epithelium with outer epithelium (Fig. 319.3).

anvil-type fiber. A fiber of the secondary shell with the convex surfaces of the anvil-like cross section facing the valve interior (Fig. 242).

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 inarticulated brachiopods, see apical process.

apical cavity. Undivided space beneath umbo in either valve. See delthyrial chamber, notothyrial chamber.

apical plate. Dorsally enlarged pedicle collar partly closing apex of delthyrium.

apical process. Variably shaped protuberance in umbonal region of ventral valve of some acrotretoids, which probably served as a muscle platform and may have contained a pedicle tube (Fig. 346, 378).

apicate (beak). Beak of ventral valve with a subapical hypothyrid or amphithyrid foramen.

apocopate (mantle canal). Dorsal, mantle-canal system with single pair of canals in addition to *vascula genitalia* (Fig. 381).

apsacline. See inclination of cardinal area or of pseudointerarea (Fig. 285).

arcuiform (crura). Crura hammer shaped in cross section, with arcuate heads concave toward each other.

area. See cardinal area.

areola. See planareas.

arms. See brachia.

arms of jugum. Processes arising by bifurcation of distal end of jugal stem, which may become extended into accessory lamellae (Fig. 336). See jugal stem, jugal processes.

arrugia. Highly inclined, fine exopuncta; allegedly contained chitinous bristle.

ARTICULATION. Interlocking of two valves by projections along their posterior margins; commonly effected in articulated brachiopods by two ventral teeth fitting sockets of dorsal valve but may be assisted or replaced by other projections and complementary pits (Fig. 322).

ascending lamellae (of loop). Paired ventral elements of long terebratelloid loop continuous anteriorly with ventrally recurved descending lamellae and joined posteriorly by transverse band (Fig. 338).

astrophic. Shell with posterior margin not parallel with hinge axis (Fig. 285).

attrite (foramen). Ends of beak ridges worn away.

aulacoterma. Thickening on inside wall of richthofeniid ventral valve against which dorsal valve rests when shell is closed.

auriculate (foramen). Opening bounded by deltidial plates bearing external rims or winglike extensions.

axial (loop). Phase of loop development with a vertical plate (Paleozoic forms) or septal pillar (post-Paleozoic forms); descending lamellae complete in Paleozoic forms, rudimentary in most post-Paleozoic forms.

baculi (sing., baculum). Microscopic apatitic rods forming a criss-cross array in an organic matrix in linguloid and discinoid shells (Fig. 238).

baculate condition (mantle canal). *Vascula lateralia* lacking major dichotomy or bifurcation (Fig. 384).

band. A distinguishable increment of growth on a shell. See transverse band.

base of brachial process. Proximal part of pentameroid brachial process attached dorsally to outer plate and ventrally to inner plate; homologue of base of brachiophore crus (Fig. 365).

BEAK. Extremity of umbo, commonly pointed (Fig. 283).

beak angle. Angle subtended between commissural plane at the hinge axis and line bisecting beak of astrophic ventral valve as seen in lateral profile; defined as straight (beak angle, 0 to 20°), inclined (20° to 30°), suberect (30° to 70°), erect (70° to 90°), incurved (more than 90°); corresponds to orthocline-anacline condition of strophic shells (Fig. 285).

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.

bema. Raised area of secondary shell originating near anterior ends of inner socket ridges in some plectambonitoids; may be elevated marginally or divided by radial ridges (Fig. 344.2).

biconvex. Both valves convex (Fig. 283).

bifurcate (loop). Lophophore support in form of Y-shaped median septum (characteristic of Kraussinidae).

bifurcate condition (mantle canal). *Vascula lateralia* split into anterior and posterior branches immediately beyond point of leaving body cavity.

bilacunar (loop). Long reflected loop, typical of adult *Kingena* and related genera, with a lacuna in the dorsal segment of each ascending lamellae defining a pair of mediovertical connecting bands extending between the median septum and transverse band; descending lamellae still united to the median septum.

bilateral (loop). Long reflected loop, typical of adult *Laqueus* and related genera, with two pairs of connecting bands, lateral and laterovertical.

bilobate (folding). Opposite folding with well-developed median sulci flanked by variably developed carinae (Fig. 288.3).

biplicate (folding). Alternate folding with pair of submedian folds in dorsal valve separated by sulcus containing smaller median fold (Fig. 289).

biseptum. Double septum in ventral valve formed by union of dental plates.

bisulcate. Alternate folding resembling parasulcate condition but with median fold of dorsal valve indented by median sulcus (Fig. 289).

blister. Space and enclosing curved partition of secondary shell in umbonal and delthyrial chambers of some spiriferides, productides, and pentamerides; formed by sporadically migrating outer epithelium (Fig. 372).

BODY CAVITY. Principal part of coelomic space, situated posteriorly, bounded by body wall and containing alimentary tract, nephridia, and other organs (Fig. 1).

braceplates. Narrowly diverging septa extending anteriorly of dorsal adductor muscle scars in some strophodontids (Fig. 369).

BRACHIA (sing., BRACHIUM). Two armlike projections from either side of mouth segment of lophophore, variably disposed but symmetrically placed about mouth (Fig. 1).

brachial base. See inner socket ridge.

brachial branches. Narrow elevations of secondary shell within brachial ridges and converging anteromedially.

brachial cavity. See mantle cavity.

brachial lamellae. Calcareous support for lophophore. See brachidium and brachial platform.

brachial loop. See loop.

brachial muscles. Muscles in small brachial canal of inarticulate genera, arising from connective tissue at proximal ends of canals extending along their length.

brachial plate. One of pair of subvertical plates constituting pentameroid cardinalia and including inner plate, base of brachial process, and outer plate.

brachial platform. Raised area of secondary shell originating near alae in dorsal valves of some plectambonitoids that may be elevated marginally (Fig. 344).

brachial process. Anteriorly directed blade or rodlike projection from pentameroid cardinalia; comparable with crus.

brachial protractor muscles. Pair of muscles in craniids that assists movements of lophophore, located anteromedially on dorsal valve (Fig. 374).

brachial retractor muscles. Pair of small muscles in dorsal valve of discinids and craniids, located lateral to anterior adductor muscles.

brachial ridges. Paired narrow elevations of secondary shell extending laterally or anteriorly as open loops from dorsal adductor muscle field of some articulated brachiopods (Fig. 345).

brachial valve. See dorsal valve.

brachidial net. Calcareous netlike structure uniting the crura and jugum to the floor of the dorsal valve (Fig. 341).

brachidium. Calcareous support for lophophore in form of loop or spires.

BRACHIOPHORES. Blades of secondary shell projecting from either side of notothyrium and forming or in close association with inner socket ridges (Fig. 329).

brachiophore bases. See brachiophore plate.

brachiophore plates. Basal (dorsal) parts of brachiophores that join floor of valve (Fig. 329, 365).

brachiophore process. See brachiophore.

brachiophore support. See brachiophore plates.

brachiotest. Thin, granular layer overlain by secondary fibers in calcareous ribbons (lamella) of loops and spiralia; secreted by densely filamentar, outer epithelium (Fig. 29).

breadth. See width.

brephic. Juvenile stage in shell development following secretion of protegulum; best seen on ribbed valves where it can be distinguished from protegulum by presence of growth lines and from neanic shells by absence of radial ornament.

breviseptum. Dorsal median septum not fused posteriorly with cardinal process.

bridge. Posteromedian part of marginal flange of thecideoid dorsal valve free of valve floor.

brush. Many fine radiating tubular extensions of proteinaceous membrane, which permeate a thin canopy of primary shell separating periostracum from distal head of caecum of terebratulides, thecideidines, and spiriferides (Fig. 31).

buccal plate. Small, variously shaped, but bilaterally symmetrical, posteriorly concave plates, normally loose within complete shells of spiriferids, but exceptionally placed posteromedially between spiralia and close to jugal processes; possibly discrete supporting piece for the mouth region of the lophophore (Fig. 342).

buttress plates. See cardinal process buttress plates.

caecum (pl., caeca). Papillose outgrowth of mantle occupying a puncta and connecting with periostracum either by a brush as in articulated brachiopods or by fibrillar strands as in cranioids (Fig. 31).

calcareocorneous. See chitinophosphatic.

calcariform (crura). Falciform crura said to be distinguishable by dorsally directed process at distal end of each crus.

callist. See pedicle callist.

callus. Any excessive thickening of shell located on valve floor (Fig. 352).

camarophorium. Spoon-shaped, adductor-bearing platform in stenoscismatoid dorsal valve supported by median septum (Fig. 367).

camerate. Acrotretoid shell fabric of discrete apatitic lamellae connected by perpendicular walls forming polygonal chambers (Fig. 241).

campagiform (loop). Growth stage of loop of certain terebratulides marked by proportionally large funnel-shaped ascending elements without lateral lacunae. See diploform.

campagiform hood. Large, commonly funnel-shaped structure without lateral lacunae, with descending branches attached to median septum by transverse processes.

canal (shell). Fine perforation of organophosphatic shell not penetrating primary layer and partly occupied by secreting plasmalemma (and exuded bodies) of outer epithelium (Fig. 261).

canaliform (crura). Variant of raduliform type, folded longitudinally in form of dorsally facing channel or gutter.

capilla (pl., capillae). Very fine radial ridge on outer surface of shell. See costa.

capsular muscles. Longitudinal fibers in connective tissue of pedicle of articulated brachiopods; may be attached to floor of ventral valve.

cardinal angle. Angle between hinge line and posterolateral margins of shell.

cardinal area. Posterior sector of valve of articulated brachiopods exclusive of delthyrium or notothyrium (may be interarea, planarea, or palintrope) (Fig. 285).

cardinal buttress. Vertical plate or ridge supporting cardinal socket in some trimerelloids dividing cavity beneath beak into two umbonal chambers (Fig. 375).

cardinal crests. Paired ridges originating near apex of notothyrium, below chilidium and flanking cardinal process of chonetidines (equivalent to the chilidial crests of some authors) (Fig. 361).

cardinal extension. Thecideidine cardinal process.

cardinal extremities. Lateral terminations of posterior margin (Fig. 283).

cardinal facet. See cardinal socket.

cardinal flanges. Variably disposed posteroventral extensions of inner socket ridges or cardinal plate protruding into ventral umbo; in some taxa becoming thickened and serrated ventrally to accommodate diductor muscle bases (Fig. 359).

CARDINALIA. Structures of secondary shell in posteromedian region of dorsal valve, associated with articulation, support of lophophore, and muscle attachment; include, for example, cardinal process, socket ridges, crural bases, and their accessory plates (Fig. 329–331, 359).

cardinal margin. Curved posterior margin of shell, homologous with hinge line of strophic shells but not coincident with hinge axis (Fig. 285).

cardinal muscle scar. Posterolaterally placed muscle scars in acrotretoids and obolellides (Fig. 378).

cardinal pit. Depression between inner socket ridges accommodating cardinal process and diductor muscle bases as in some rhynchonellides (Fig. 349).

cardinal plate. Plate extending across posterior end of dorsal valve, consisting laterally of outer hinge plates and medially of either conjunct inner hinge plates or single plate, commonly perforated posteriorly by dorsal foramen (Fig. 331, 362).

CARDINAL PROCESS. Blade or variably shaped boss of secondary shell situated medially in posterior end of dorsal valve and serving for separation or attachment of paired diductor muscles (Fig. 357–364). See also cardinal flanges, ctenophoridium, myophore.

cardinal process buttress plates. Two vertical converging, parallel, or diverging plates extending anteriorly from cardinal process to enclose space and, in some productidines, uniting with breviseptum.

cardinal process cowl. Proximal cover directed umbonally on triplesioid cardinal process.

cardinal process hood. See cardinal process cowl.

cardinal process lobes. Projections forming all or part of cardinal process and bearing muscle bases or myophore (Fig. 357, 360).

cardinal process pit. Pit at internal base of cardinal process in some plectambonitoids, chonetoids, and productoids.

cardinal process shaft. Ridge- or stalklike proximal part of cardinal process (Fig. 360).

cardinal ridge. Thickened ridge confined to hinge lines of some productidines, aiding in articulation of shell (Fig. 326).

cardinal socket. Transverse depression on posterior margin of trimerelloid ventral valve that receives plate or tooth of dorsal valve (Fig. 375).

carina. Major angular elevation of valve surface, externally convex in transverse profile and radial in disposition.

carinate (of folding). Opposite folding characterized by incipient lateral carinae but without median sulci (Fig. 288). See also rectimarginate.

catacline. See inclination of cardinal area or of pseudointerarea (Fig. 285).

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. 356).

central muscles. Anteriorly or medially placed pair of muscles in lingulides, originating on ventral valve and passing anterodorsally to dorsal valve (Fig. 346.1).

centronellid stage (of folding). See unisulcate.

centronelliform (loop). Simple lanceolate loop suspended free of valve floor, commonly bearing vertical median plate in addition to echmidium. See acuminate and axial.

cheniothyrid stage (of folding). See lobate stage.

chilidial crests. See cardinal crests.

CHILIDIAL PLATES. Pair of posterior platelike extensions of notothyrial walls, commonly forming lateral boundaries of cardinal process.

CHILIDIUM. Crescentic plate covering apex of notothyrium, commonly convex externally and extending for variable distances ventrally over proximal end of cardinal process and chilidial plates when present (Fig. 319, 357, 361).

chilidonophorid (loop). Short loop with converging but not fused crural processes, and transverse band not well differentiated from descending branches.

chitinophosphatic (shell). Consisting dominantly of some form of calcium phosphate and chitin (hexosamine) with various proteins.

cicatrix (of attachment). Scar on ventral umbo or umbonal region, representing place of cementation of shell to substrate.

ciliform (crura). Variant of raduliform type; flattened in plane of commissure, forming direct prolongations of horizontal hinge plates, then turning parallel to plane of symmetry as slightly crescentic blades.

cinctid stage (of folding). See opposite folding.

cincture. External concentric furrow in either valve of some productoids, corresponding to internal shell deflection or thickening.

circinate (lophophore). Distally coiling spirolophe.

cirri socles. See spicules.

clavicular plates. See cardinal crests.

colleplax. Triangular umbonal plate in dictyonellidines exposed externally by resorption of ventral umbo (Fig. 321).

columnar (shell). Acrotretoid shell fabric of discrete apatitic lamellae connected by microscopic perpendicular columns (Fig. 240).

coma (pl., **comae**). Concentrically disposed impersistent and irregular protuberance composed of primary and secondary shell on external shell surface of some plectambonitoids (Fig. 295).

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. 283).

COMMISSURE. Line of junction between edges or margins of valves (Fig. 283).

concavoconvex (shell). Dorsal valve concave; ventral valve convex (Fig. 287).

conjunct deltidial plates. Deltidial plates in contact anterodorsally of pedicle.

connecting band (of loop). Band of terebratellide long loop connecting ascending lamellae to each other (transverse band), descending lamellae to median septum (lateral connecting band), and descending lamellae to ascending lamellae (vertical connecting band) (Fig. 338).

connectivum. Medially united plates extending from crural bases to cover septalium ventrally (Fig. 329).

convexoconcave (shell). Dorsal valve convex; ventral valve concave (Fig. 287.2).

convexoplane (shell). Dorsal valve convex; ventral valve plane.

corpus. Shell enclosing principal part of body cavity and mantle cavity, excluding peripheral extensions of shell such as trails or flanges (see section on Productida in systematic volume Part H(R), volume 2, in preparation).

coscinidium. Reticulate extension of inner secondary shell over aperture of conicoventral valve of richthofenioids (Fig. 273).

COSTA (pl., **COSTAE**). First-formed radial ridge on external surface of shell most commonly originating at the junction between the brephic and neanic shell (Fig. 297). [Also but ambiguously used for any coarse rib, without reference to origin. **Costella** is a fine rib, and **capilla** a very fine rib. This usage gives no indication of the nature of radial ornamentation and any quantitative definitions, related to the incidence of ribs at the margins of shell irrespective of their sizes, are of no value. Thus in brachiopods ornamented by ribs that 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 (pl., **COSTELLAE**). Radial ridge on external surface of shell originating later than costa by bifurcation of existing costa or costella or by intercalation between earlier-formed ribs (Fig. 297).

costellate. Shell radially ornamented by costae and costellae.

cowl. Anterodorsally growing shell producing conical shape of holoperipheral ventral valve of lyttoniids.

crenulations. See denticles.

crescent. Site of cardinal socket of trimerelloids.

cristae. See socket ridges.

crossed-bladed structure. Sheets of parallel aggregations of laths or blades oriented in different directions in adjacent sheets and in parts of same sheet of a laminar shell succession, for example, secondary layer of most strophomenides (Fig. 251).

crown of crescent. See crescent.

CRURA (sing., **CRUS**). Paired processes extending 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 lamellae of loop (Fig. 329–331).

crural band. Ribbon of secondary shell joining crural processes ventrally.

crural bases. Parts of crura united to hinge plates or socket plates and separating inner and outer hinge plates when present (Fig. 329–331).

crural fossette. Cavity on inner face of tooth receiving posteroventral edge of brachiophore or crural plate when valves are closed (Fig. 322).

crural hooks. Hooklike ends of crura facing a matching set of curved primary lamellae of the spiralium.

cruralium. Spoon-shaped structure of dorsal valve formed by dorsal union of pentameroid, ambocoeliidid, or some meristellid brachiophore plates (or homologues) and bearing adductor muscles (Fig. 365).

cruralium discretum. Paired outer plates attached independently of each other to floor of pentameroid dorsal valve to enclose dorsal adductor field.

crural keel. Dorsal extension of crus beyond junction with flange.

crural lobe. Strongly developed, posteroventrally elevated inner socket ridge in atrypoids and some athyroids.

crural plate. Plate extending from inner edge of outer hinge plate or crural base to floor of dorsal valve; may fuse medially with counterpart to form septalium. See septalial plate (Fig. 329–330).

crural pit. Cavity near floor of dorsal valve separating brachiophore plate and fulcral plate in some orthides.

crural point. See crural process.

crural process. Pointed part of crus directed obliquely inward and ventrally (Fig. 334).

crural trough. See septalium.

CRUS. See CRURA.

cryptacanthiiform (loop). Long, reflected loop unsupported by median septum with descending lamellae anterolaterally divergent but still fused posteromedially. See diploform.

cryptonelliform (loop). Long, reflected loop unsupported in adults by median septum and having narrow transverse band. See teloform.

ctenophoridium. Cardinal process with radially striated myophore not elevated on a shaft but commonly on an elevated transverse ridge (Fig. 358).

cucullate (loop). Phase of loop development with a hood on either vertical plate or septal pillar. Descending lamellae complete in Paleozoic forms, commonly incomplete in post-Paleozoic forms.

curvature of beak. Curvature of beak toward the opposing valve. See beak angle.

curvilinear (length or width). A dimension measured along the external curvature of a valve.

cuticle. Organic cover of pedicle; secreted by pedicle epithelium.

cyclothyrid (foramen). See auriculate.

cynocephalous (folding). Sharply folded dorsal valve.

cyrtomatodont. Knoblike or hook-shaped hinge teeth developed by differential secretion and resorption of secondary shell (Fig. 322.1).

cyrtomorph. Chonetid hinge spines curving medially or laterally but remaining close to commissural plane.

cystose (shell). Valves containing blisters of secondary shell (Fig. 372).

dalliniform (loop). Loop arrangement typical of adult *Dallina* in which long descending lamellae recurve into ascending lamellae that meet in transverse band, all free of the valve floor. See teloform.

delayed costation (or **costellation**). Ribbing that first arises in postneanic stages of shell growth. See costa (or costella) (Fig. 297).

deltarium discretum. Thickened edge of delthyrium.

delthyrial angle. Angle subtended by margins of delthyrium.

delthyrial callosity. See pedicle callist.

delthyrial carinae. See teeth ridges.

delthyrial cavity. See delthyrial chamber.

delthyrial chamber. Cavity beneath umbo of ventral valve bounded by dental plates, if present, or by posterolateral shell walls, if dental plates absent.

delthyrial foramen. Foramen in young shells.

delthyrial plate. Plate within delthyrial chamber of some spiriferides, extending variable distance from apex between dental plates (probably homologue of pedicle collar) (Fig. 355.1).

DELTHYRIUM. Median triangular or subtriangular aperture bisecting ventral cardinal area or pseudointerarea, commonly serving as pedicle opening (Fig. 283).

deltidial cover. Externally concave plate in some pentameroids closing posterior end of delthyrium (probably homologue of pedicle collar).

deltidial grooves. Lines delimiting thecideidine pseudodeltidium in species with this structure not flush with ventral area.

DELTIDIAL PLATES. Two plates growing medially from margins of delthyrium, partly or completely closing it (Fig. 316).

deltidial ridges. Two narrowly triangular ridges separating homeodeltidium and propareas of trimerelloids.

deltidiodont. Simple hinge teeth developed by distal accretion of secondary shell (Fig. 322).

deltidium. Cover of delthyrium formed by conjunct deltidial plates; line of junction of plates visible (Fig. 317).

deltiform (loop). Terminal loop phase typical of many short-looped terebratulides with a variably disposed transverse band extending between the distal ends of two relatively short, divergent, descending lamellae.

dental cavity. Anteriorly expanding cavity, presumably occupied by evagination of outer epithelium secreting the tooth of some atrypoids.

dental flange. Internal border and buttress to delthyrium and teeth in spiriferides, not extending to valve floor (Fig. 324). See adminicula.

dental lamellae. See dental plates.

DENTAL PLATES. Variably disposed plates of secondary shell underlying hinge teeth and extending to floor of ventral valve (Fig. 323).

DENTAL SOCKETS. Excavations in posterior margin of dorsal valve for reception of hinge teeth (Fig. 323).

dental valve. See ventral valve.

denticles. Small, protruding ridges that alternate with complementary sockets located along cardinal margin or hinge line of both valves; also small processes on posterior surfaces of dental sockets fitting into accessory sockets in hinge teeth (Fig. 325).

denticular cavities. Pair of grooves on outer side of teeth that receives projections from outer socket ridges (Fig. 322).

denticular plates. Pair of obtusely triangular plates lateral to delthyrium, bearing denticles and fused with dental plates, developed in strophodontids.

denticulated cardinal margin. Posterior margin of both valves bearing denticles, fitting into complementary sockets.

denticulated commissure. Zigzag commissure due to interfingering of angular ribs (Fig. 300).

denticulum (pl., denticula). Small toothlike termination of cardinal area, usually in ventral valve, commonly articulating with accessory socket in outer socket ridge (Fig. 322).

dentifer. Vestigial brachiophore in some orthotetidines. See brachiophore.

depth. See thickness.

descending branches. See descending lamellae.

descending lamellae. Paired dorsal elements of loop extending anteriorly from crura and recurved ventrally at anterior ends (Fig. 338).

deuterolophe. Spirally coiled part of lophophore bearing double brachial fold and double row of paired tentacular appendages, homologous with side arms of plectolophe (Fig. 337.2, 337.4–337.6).

diaphragm. Extension of visceral disk, commonly as marginal ridge, of productide and strophomenide dorsal valve maintaining a close fit with ventral valve and usually associated with trails.

dictyothridid stage (of folding). See parasulcate.

DIDUCTOR MUSCLES. Muscles serving to open valves of articulated brachiopods, commonly consisting of two pairs attached to dorsal valve immediately anterior to beak, usually to cardinal process; principal pair commonly inserted in ventral valve on either side of adductor muscles and accessory pair posterior to them (Fig. 348).

digitate (brachidium). Thecideoid brachidium with brachial branches extending inward from marginal flange.

digitate (mantle canal). Posterior part of *vascula genitalia* projecting laterally nearly to mantle margin, with corresponding abbreviation of *vascula myaria* (Fig. 379–380).

diploform (loop). Phase of loop development, typical of adult *Campages,* with adjacent ascending and descending elements fused, well developed, and free of the septum except at their posterior extremities (Fig. 334).

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 dorsal valve.

dorsal adjustor muscles. See adjustor muscles.

dorsal adminicula. See adminicula.

dorsal denticulum. See outer socket ridge.

dorsal foramen. Posteriorly located perforation of cardinal plate which may encroach on beak of dorsal valve (Fig. 359).

DORSAL VALVE. Valve that invariably contains any skeletal support for lophophore and never wholly accommodates pedicle; commonly smaller than ventral valve and with distinctive muscle-scar pattern (Fig. 283).

dorsibiconvex. Dorsal valve more convex than ventral valve.

dorsiconvex. See dorsibiconvex.

dotted brachial ridges. Ridges of thecideoid brachidium represented by rows of small, separate pustules.

double-barrelled spine. External spine of primary shell having oval to subquadrangular cross section and commonly barbed, bearing variably closed suture on commissural surface and, at least proximally, a median partition so that spine scars are bipartite (Fig. 306).

double deltidial plates. Pair of deltidial plates, each of which is seen in certain transverse sections to consist either of two parallel plates or of one plate nearer hinge line, buttressed by another disposed at angle to it.

double median septum. More or less elevated median plate in pentameride dorsal valve formed by union of two septal plates.

dyscoliid stage (of lophophore). Probably a trocholophe.

ear. Flattened or pointed cardinal extremity of shell subtended between hinge line and lateral commissure usually distinct from corpus (Fig. 283).

ear baffle. Ridge differentiating ear from corpus in some productides.

echmidium. Spear-shaped plate formed during ontogeny of loop of Paleozoic terebratulides by fusion of anterior ends of descending lamellae (Fig. 338).

elytridium. Narrowly convex, puckered cover of delthyrium in aulostegids. See pseudodeltidium.

emarginate. Median segment of anterior commissure deflected posteriorly (Fig. 288.2a, 288.3a).

emarginatura. Median semicircular opening bisecting apical region of the ventral valve of some oboloids.

endopuncta (pl., **endopunctae**). Perforation of shell separated from periostracum on external surface by sievelike canopy of primary shell; occupied by caecum as in terebratulides, thecideidines, and spiriferides; also used for perforations ending within the primary layer of some rhynchonellides (Fig. 31).

endopunctum (pl., *endopuncta*). See endopuncta.

endospines. Fine, solid or hollow, short spines on interior of shell.

entering valve. See dorsal valve.

ephebic. Mature.

episculate (folding). See bisulcate.

epithyrid (foramen). Pedicle opening wholly within ventral umbo and ventral from beak ridges (Fig. 318).

equidistribute (mantle canal). *Vascula genitalia, vascula myaria,* and *vascula media* all well developed and contributing to mantle canal circulation (Fig. 381).

erect beak. See beak angle.

erect spines. Spines projecting at high angle (more than 70°) from shell surface.

erisma (pl., *erismata*). Plate supporting cardinal process and brachiophore of orthotetidines. See socket plates.

euseptoidum. See myophragm.

euseptum. 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.

extropuncta (pl., **extropunctae**). Microscopic, asymmetrical, conical deflection of laminae of secondary shell invariably pointing externally, characteristic of orthotetidine schuchertellids (Fig. 271).

falciform (crura). Crura arising on dorsal side of hinge plates and projecting into dorsal valve as broad, bladelike processes.

false cardinal area. Previously used for any poorly defined cardinal area or pseudointerarea.

false pedicle groove. See intertrough.

fascicostellate. Ornament of costae and costellae arranged into bundles (Fig. 297).

fastigium. Dorsal radial fold resulting from commissural flexure in many spiriferides.

fenestrae (sing., **fenestra**). Concentrically aligned, orthogonal openings in anterior part of punctatrypid shells, extending from interior through primary layer to exterior; closed posteriorly by shell secretion (Fig. 259–260).

fibrous layer. See secondary layer; term commonly used as alternative for secondary layer of articulated brachiopods when exclusively composed of calcitic rods (fibers) with lenticular or anvil-like cross sections (Fig. 242).

filum (pl., **fila**). Fine concentric ridge of variable persistence ornamenting external surface of shell (Fig. 292).

fimbria (pl., **fimbriae**). Spinelike projection from spiralia or jugum; also used for spinose projection on margin of growth lamella, as in *Spinilingula* (Fig. 336).

flange (of cardinal plate). See cardinal flange.

flange (of corpus). Peripheral shell beyond corpus as trails in productids or shell extensions in athyrids. See frill.

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.

flanges (septal, of loop). Pair of small, laterally projecting flanges that appears very early in loop ontogeny on the posteroventral edge of the septal pillar of laqueoids and some platidioids.

flanks. See lateral slopes.

flap. See posterior flap.

flexure line. Line extending from beak to anterior border of both ventral propareas in some linguloids, marked by deflection of growth lines (Fig. 286).

FOLD. Major elevation of valve surface, externally convex in transverse profile and radial from umbo (Fig. 288–289).

foramen. See pedicle foramen; term commonly used with this meaning (Fig. 285).

foraminal sheath. See pedicle sheath.

foraminal tube. See pedicle tube.

free (brachiopod). Animal not attached to substrate.

free spondylium. Spondylium unsupported by septum.

frenuliniform (loop). Growth stage of loop characterized by a lacuna in each ascending lamella. See bilacunar.

frill. Relatively large growth lamella projecting well beyond general contour of valve, deposited by margin of highly retractile mantle.

fulcral plate. Small plate raised above floor of dorsal valve extending between posterior margin and brachiophore plate or inner socket ridge and socket plate and forming floor of socket (Fig. 332).

furrow. See interspace.

fused hinge plates. Hinge plates joined together along midline with no development of septalium (Fig. 330.3).

gape. Anterior and lateral opening of shell (Fig. 1).

gastrothyrid (foramen). Pedicle opening limited to ventral valve.

geniculate. Abrupt and more or less persistent change in direction of valve growth producing angular to sharply rounded bend in lateral profile (Fig. 287).

geniculated spines. Chonetid hinge spines, commonly cyrtomorph, bending along their length.

genital area. Part of shell known to be or inferred to have been overlain by gonocoel.

genital markings. Radial ridges or pits on inside of shell within genital area.

ginglymus. Secondarily developed, heavily thickened hinge line especially characteristic of ventral valves of some productides, externally resembling interarea.

glossothyropsiform (glossothyropsidiform) (loop). Long reflected loop, unsupported by median septum, bearing two broad ascending elements joined by wide transverse band. See teloform.

glotta (pl., glottae). See squama.

granule. See tubercle.

growth lamella. Concentric outgrowth of shell deposited by retractile mantle margin; smaller than frill (Fig. 295–296).

growth line. Concentric line on outer surface of shell formed when forward growth of shell temporarily ceased (Fig. 290–291, 294).

gusset. Plate uniting brachiophore to cardinal process shaft of orthotetidines; homologue of inner hinge plate.

gutter. Marginal anteroventral recurvature of trail of one or both valves.

halteroid spines. Long, straight, external hollow spines, symmetrically developed as strutlike supports on productide ventral valve.

hamiform (crura). Crura straight, in plane of commissure and slightly compressed; variant of falciform crura.

haptoid (loop). Phase of loop development with anterior fusion of ascending and descending elements and their accompanying separation from the vertical plate or septal pillar. Posterior sections of the ascending and descending elements still separately attached to vertical plate or septal pillar.

HEIGHT. In biconvex, planoconvex, and convexoplane shells, height equals thickness, being the maximum dimension normal to length and width; in concavoconvex and convexoconcave shells, height is maximum distance measured normal to length in plane of symmetry between shell and line joining beak and anterior margin (Fig. 283).

helicophores. See crura.

hemiperipheral growth. New shell material added anteriorly and laterally but not posteriorly (Fig. 284).

hemispondylium. Two small plates within thecideoid ventral umbo, usually free of valve floor and side walls but commonly supported by median septum and bearing median adductor muscles.

hemisyrinx. Conical chamber extending medially along floor of clitambonitoid spondylium and delineated posteriorly by pair of discrete lateral ridges.

hemisyrinx ridge. Ridge forming posterolateral boundary of hemisyrinx.

hemithyrid stage (of shell structure). See impunctate.

henidium. Symphytium that loses 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. 285).

hinge line. Straight posterior margin of shell parallel with hinge axis; previously used as synonym of cardinal margin (Fig. 285).

hinge notch. Notch at lateral margin of pentameroid delthyrium accommodating posterior side only of hinge tooth.

hinge plate. Medially undifferentiated plate between crural bases. See inner hinge plates, outer hinge plates (Fig. 331).

hinge platform. Solid secondary shell platform extending between socket ridges of terebratellide cardinalia (Fig. 370).

hinge projections. Projections of fused inner socket ridges and crural bases, visible externally posterior to dorsal umbo. See cardinal flanges.

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 passageways through interarea, often called roots of spines. Also used for spines at hinge line in productidines.

HINGE TEETH. Two principal articulating processes situated at anterolateral margins of delthyrium and articulating with dental sockets in dorsal valve (Fig. 322). See cyrtomatodont and deltidiodont.

hinge trough. See septalium (in sessile form).

hinge width. Lateral extent of hinge line.

holcothyrid stage (of folding). See paraplicate.

hollow ribs. Marginally facing openings on ribs of some orthides and strophomenides (Fig. 302).

holoperipheral growth. Increase in valve size all around margins, in posterior as well as anterior and lateral directions (Fig. 284).

homeochilidium. Externally convex triangular plate closing almost all or only apical part of notothyrium in paterinides; spelled homoeochilidium by some authors (Fig. 315).

homeodeltidium. Externally convex triangular plate closing almost all or only apical part of delthyrium in paterinides; spelled homoeodeltidium by some authors (Fig. 286).

hood. Conical structure arising at posteroventral edge of septal pillar, or vertical plate on echmidium, representing rudiment of ascending elements of loop.

hypercline. See inclination of cardinal area or of pseudointerarea (Fig. 285).

hypothyrid (foramen). Pedicle opening located below or on dorsal side of beak ridges with umbo intact (Fig. 318).

imbricate (ornament). Strong, regular, overlapping growth lamellae.

impunctate (shell). Shell lacking punctae, pseudopunctae, or canals of any kind.

inclination of cardinal area or of pseudointerarea. Commonly used terms to describe the condition of either valve based on convention of viewing specimen in lateral profile with beaks to left and dorsal valve uppermost, referring cardinal area to its position within one of four quadrants defined by commissure plane and plane normal to it and symmetry plane, touching base of cardinal areas (Fig. 285). 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 counterclockwise from orthocline position, cardinal area lying in bottom left quadrant is weakly to strongly **apsacline;** at 90° to orthocline it is **catacline;** and continuing counterclockwise into bottom right quadrant cardinal area is weakly to strongly **procline** (Fig. 285).

inclined beak. See beak angle.

incurved beak. See beak angle.

inequidistribute (mantle canal). *Vascula genitalia* of dorsal mantle saccate and contributing little to canal circulation (Fig. 380).

inner carbonate layer. See secondary layer.

inner hinge plates. Pair of subhorizontal or concave plates in cardinalia located medially of crural bases and fused laterally with them (Fig. 330–331). See cardinal plate, hinge plate, crural plate.

inner plates. Pair of subvertical plates in cardinalia of some pentameroids lying on ventral side of base of brachial process and fused dorsally with it; homologue of outer hinge plates. See brachiophore plates for orthides.

inner socket ridge. Ridge of secondary shell commonly overhanging dental socket and forming its inner or anterior margin (Fig. 329–331).

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. 285).

intercalary lamellae. See accessory lamellae.

intercalation. Costella arising by insertion between costae or costellae, not by bifurcation of existing costa or costella (Fig. 297).

intercamarophorial plate. Short, low median septum on posterior midline of camarophorium in stenoscismatoids, extending to underside of hinge plate but independent of median septum duplex (Fig. 367).

interconnecting bands. See connecting bands.

intercostal sulci. See interspace.

internal oblique muscles. Pair of muscles in some inarticulated brachiopods originating on ventral valve between anterior adductors and passing posterolaterally to insertions on dorsal valve located anterolaterally of posterior adductor muscles (Fig. 374).

interridge. Median external ridge in pedicle pseudointerarea of some acrotretoids.

interspace. Flat or externally concave sectors of shell between adjacent costae or costellae (Fig. 298, 300).

intertext (folding). See alternate folding.

intertrough. Median, narrowly triangular furrow dividing pseudointerarea of ventral valve of some acrotretoids (Fig. 286).

intraplicate (folding). See plicosulcate.

intraseptal lamella. Sheet of prismatic calcite of varying persistency found in median septum of spondylium duplex (Fig. 351.2b).

inverted stage (of folding). See sulcate.

ismeniform (loop). See diploform.

jugal processes. Pair of discrete, ventromedially directed lamellae arising from primary lamellae of spiralia.

jugal stem. Ventroposteriorly directed continuation of jugum which, by bifurcation, may give rise to accessory lamellae posteriorly (Fig. 336).

JUGUM. Medially placed structure of secondary shell connecting two primary lamellae of spiralia; also junction between descending lamellae in loop of *Cryptacanthia* (Fig. 336).

kingeniform (loop). Long reflected loop, typical of adult *Kingena* and related genera, with descending lamellae united to median septum, and ascending lamellae supported by mediovertical connecting bands also converging on median septum. See bilacunar.

koskinoid perforations. Clusters of fine perforations penetrating the ventral valves, especially in the beak region, of many orthotetoids and *Uncites* (Fig. 282).

labiate (foramen). Exaggerated marginate foramen in which dorsal edge is prolonged and liplike.

lacuna. Aperture in hood.

lamella. Sheetlike extension of primary and even underlying secondary shell deposited by retractile mantle margin on external shell surface (see growth lamella); also used for calcareous ribbon comprising spiralium and coiled extension from arm of jugum.

lamellar layer. See primary layer, secondary layer.

lamina. Parallel-sided, thin mineral constituents of a shell succession, normally ensheathed in membranes and consisting of tablets, plates, or blades in various stages of amalgamation (Fig. 247).

laqueiform (loop). Long reflected loop with laterovertical connecting bands connecting ascending and descending lamellae, and lateral connecting bands extending between descending lamellae and median septum. See bilateral.

lateral adductor muscles. Paired muscles in thecideidines attached posterolaterally in ventral valve and on either side of cardinal process of brachial valves.

lateral areas. Ventral palintrope on either side of delthyrial structures.

lateral branch (of jugum). Part of jugum continuous with primary lamella (Fig. 336).

lateral cavities. See umbonal chambers.

lateral connecting bands. See connecting bands.

lateral oblique muscles, also **oblique lateral muscles.** Paired muscles in some inarticulated brachiopods, originating on ventral valve anterolaterally of posterior adductor muscles and passing anterodorsally to insertions either on dorsal valve and anterior body wall against anterior adductors (discinids) or entirely on anterior body wall (craniids) (Fig. 374).

lateral ridges. Ridges of secondary shell common in productines, extending laterally from cardinal process or ventral beak, diverging from posterior margin toward ears or lateral margins.

lateral septa. See anderidia.

lateral slopes. Valve surfaces on either side of median sector of shell.

laterovertical (loop). Long reflected loop, typical of adult *Pictothyris,* with laterovertical connecting bands only.

leiolophid stage (of lophophore). Rudimentary lophophore ring, before development of tentacular appendages.

lemniscate (mantle canal). Saclike gonocoel giving rise to branches that extend to posterolateral margins with corresponding peripheral reduction of *vascula media* and *vascula myaria* (Fig. 380).

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. 283).

lenticular stage (of folding). Both valves gently and subequally biconvex, anterior margin rectimarginate.

ligate stage (of folding). See lobate.

limbus. Flattened inner margin of inarticulate valve.

linguiform extension. Anterior tongue-shaped extension of either valve.

liothyrinid stage (of folding). See lenticular stage.

lirae. Fine concentric or radial ridges and grooves.

listrium. Plate in some discinids closing anterior end of pedicle opening that has migrated posteriorly (Fig. 286).

lobate (of folding). Opposite folding with single sinus in one valve opposed by single sulcus in other; commissure rectimarginate (Fig. 288).

longitudinal axis. Intersection of planes of commissure and symmetry (Fig. 283).

long loop. See loop.

LOOP. Support for lophophore composed of secondary shell and brachiotest extending anteriorly from crura as closed apparatus that may be short (centronellidines, terebratulidines) or long (terebratellidines) or a derivative of one of these forms (Fig. 338).

lophidium. Inverted V-shaped projection of median posterior part of dorsal valve or of external face of cardinal process, helping to close gap in delthyrium in some aulostegoids.

LOPHOPHORE. Feeding and respiratory organ with tentacles, symmetrically disposed around mouth, typically suspended from anterior body wall but may be attached to dorsal mantle; occupies mantle cavity (Fig. 1).

lophophore platform. See brachial platform.

lophrothyrid stage (of folding). See uniplicate.

magadiform (loop). See diploform.

magadiniform (loop). See annular.

magaselliform (loop). See haptoid.

magellanian stage (of shell). See endopuncta.

magellaniform (loop). Type of free terebratellide loop consisting of long descending lamellae recurved into ascending lamellae that meet in transverse band. See teloform.

magelliform (loop). See haptoid.

main flanks. See lateral slopes.

maniculiform (crura). Derived from raduliform type, with handlike processes at end of straight, ventrally directed crura.

MANTLE. Prolongation of body wall as fold of ectodermal epithelium (Fig. 1).

MANTLE CANALS. Flattened, tubelike extensions of body cavity into mantle (Fig. 379).

MANTLE CAVITY. Anterior space between valves bounded by mantle and anterior body wall and containing lophophore (Fig. 1).

mantle papilla. See caecum.

mantle sinus. See mantle canal.

margin (of valve). Edge of valve.

marginal flange (of shell). See geniculate.

marginal flange (of thecideoid dorsal valve). See subperipheral rim.

marginal ridge. See subperipheral rim.

marginal spines. Long, slender prolongations of interspaces between ribs of rhynchonellides lying against inner surface of opposing valve when shell is shut and forming grille when shell is open (Fig. 300); also used for spinose extensions of growth lamellae.

marginate (foramen). Pedicle foramen with thickened margin.

marsupial notch. Small double notch or perforation in ventral edge of brachial bridge in some adult female thecideoids marking passage of two specialized posteriorly directed filaments to which embryos are attached.

median. In plane of shell symmetry (Fig. 283).

median buttress. Knoblike projection at posterior end of dorsal median septum in some acrotretoids, which may have been the site of attachment of umbonal muscle (Fig. 378).

median partition. Median septum supporting anterior part of trimerelloid muscle platform and dividing cavity beneath platform into two vaults (Fig. 375).

median plane. See plane of symmetry (Fig. 283).

mediotest. Variably persistent, granular sheet occurring medially in platelike structures of fibrous secondary shell.

mediovertical (loop). Long reflected loop, typical of adult *Ecnomiosa* with a pair of mediovertical connecting bands extending from the median septum to the transverse band.

megathyrid (posterior margin). Posterior margin long and straight.

megerliiform (loop). Loop of kraussinids with descending lamellae united to anterior projections of Y-shaped median septum; extremities of median septum also united by narrow transverse band. See mediovertical.

mergiform (crura). Variant of raduliform type with long, closely parallel crura arising directly from swollen edge of dorsal median septum.

mesothyrid (foramen). Pedicle opening located partly in ventral umbo and partly in delthyrium; beak ridges appearing to bisect foramen (Fig. 318).

metacarinate stage (of folding). See bilobate.

micropuncta (pl., **micropunctae**). Perforation of calcitic shell, too fine to contain caecum but possibly extension of secreting plasmalemma (Fig. 265).

middle lateral muscles. Pair of muscles in some lingulides originating on ventral valve between central muscles and diverging slightly posteriorly before insertion on dorsal valve (Fig. 377).

mixoperipheral growth. Differs from holoperipheral growth in that posterior sector of valve increases in size anteriorly and toward other valve (Fig. 284).

monticules. See tubercle.

monticulus. Narrow median fold of the pseudodeltidium of orthotetidines and triplesiidines.

mosaic. Pattern on interior of valve formed by outlines of adjacent fibers of secondary shell layer (Fig. 242).

mouth segment (of lophophore). Median part of lophophore containing mouth; attached to anterior body wall and bearing single row of paired or unpaired tentacles.

mucronate (cardinal margin). Cardinal extremities extended into sharp points.

muehlfeldtiform (loop). See mediovertical.

multicostellate. Costellae increasing in number by bifurcation or intercalation but not varying greatly in size (Fig. 297).

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. 375).

MUSCLE SCAR. More or less well-defined impression or elevation on valve representing final site of attachment of muscle (Fig. 350).

muscle track. Path of successive muscle impressions formed by migration of muscle base during growth (Fig. 350).

myocoelidium. Chamber similar to spondylium but not formed by dental plates, serving for attachment of muscles as in richthofeniids.

myophore. Differentiated site of diductor muscle attachment on cardinal process, consisting of ridged myotest (Fig. 357, 360).

myophragm. Ridge or septum of secondary shell dividing paired muscle scars that may encroach on its sides.

myotest. Muscle scar shell usually bearing impressions of the secretory cuboidal epithelium associated with the attached bases of muscle systems; commonly granular in texture and pitted by resorption in carbonate shells (Fig. 350).

mystrochial plates. Pair of small plates buttressing spondylium posterolaterally, as in *Amphigenia* and some meristids.

neanic. Youthful phase, immediately following brephic stage of shell development, at which generic characters of shell begin to be apparent.

nearly straight beak. See beak angles.

nepionic. See brephic.

neural valve. See ventral valve.

node. Thickened junction of rib and lamella, frequently accentuated by growth line. Any thickening at a junction between converging apophyses.

nodus (*principalis, quadrivialis, septalis, terminalis*). Point of divergence of branches in mantle canal system (Fig. 379).

nonintertext (folding). Type of folding in which sulcus or carina of one valve is opposed by plane valve.

nonstrophic (shell). See astrophic.

norellid stage (of folding). See unisulcate.

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 dorsal valve corresponding to delthyrial chamber of ventral valve, bounded laterally by inner socket ridges, brachiophore plates (or homologues), or by posterolateral shell walls if brachiophore bases absent.

notothyrial platform. Umbonal thickening of floor of dorsal valve between inner socket ridges, brachiophore, or crural plates (Fig. 323.4, 329).

notothyrid (foramen). Pedicle opening in dorsal valve, a condition never completely attained.

NOTOTHYRIUM. Median subtriangular opening bisecting dorsal cardinal area or pseudointerarea (Fig. 283).

oblique lateral muscles. See lateral oblique muscles.

oblique muscles. Variable sets of muscles in inarticulated brachiopods responsible for rotational and longitudinal movements of valves (Fig. 374).

occlusor muscle. See adductor muscle.

oligopalmate. Mantle canal system with two pairs of principal canals in each mantle.

opercular. Lidlike valve.

opposite folding. Folding in which fold or sulcus in one valve is opposed by fold or sulcus in other; commissure remaining rectimarginate (Fig. 288).

ornament. Any regularly occurring outgrowth, deflection or nonpathological interruption in growth (other than growth lines) found on outer shell surface.

ornithellid stage (of folding). See carinate.

orthocline. See inclination of cardinal area or of pseudointerarea (Fig. 285).

orthoconate. Brachia coiled parallel with plane of commissure.

orthomorph. Chonetoid hinge spines remaining straight, perpendicular, oblique, or parallel to hinge line.

outer carbonate layer. See primary layer.

outer epithelium. Ectodermal epithelium underlying shell and responsible for its secretion (Fig. 3).

outer hinge plates. Pair of concave or subhorizontal plates in cardinalia separating inner socket ridges and crural bases (Fig. 329–331).

outer mantle lobe. Outer peripheral part of mantle, separated by mantle groove from inner lobe; in articulated brachiopods responsible for secretion of periostracum and part or all of primary shell layer (Fig. 3).

outer plates. Pair of subvertical plates in pentameroid cardinalia with ventral surface fused to base of brachial process and dorsal edge attached to floor of valve or rarely, septal plate; homologue of crural plates or inner hinge plates (Fig. 329.9).

outer socket ridge. Low ridge bounding dental socket on outer lateral or posterior side of dorsal valve (Fig. 322, 331).

outside lateral muscles. Pair of muscles in some lingulides that originates on ventral valve lateral of centrals and extends posteriorly to insertions behind middle lateral muscles on dorsal valve (Fig. 377).

ovarian impression. See genital marking.

ovarian marking. See genital marking.

palintrope. Originally used for morphologically posterior sector of either valve that was reflexed to grow anteriorly (mixoperipheral growth); more recently used for curved surface of shell, bounded by beak ridges and cardinal margin of astrophic shells (differs from planarea in being curved in all directions) (Fig. 285).

pallial caecum. See caecum.

pallial lobe. See mantle.

pallial markings. See vascular markings.

pallial sinus. See mantle canal.

pallium. See mantle.

papillae. See endospines.

paraendopunctae. See extropunctae.

parallel. Hinge spines of chonetoids bending sharply laterally to become parallel with posterior margin of ventral valve.

paraplicate (folding). Alternate folding in which two folds in dorsal valve bound median sulcus (Fig. 289).

parasulcate (folding). Alternate folding in which dorsal sulcus bears strong median fold (Fig. 289).

parathyridium. Deep, pouchlike indentation of shell on either side of beak, formed by medially directed depression or flexure of posterolateral shell surface of both valves, particularly dorsal (e.g., *Cardinarina*).

parvicostellate. Costellae numerous, arising entirely by intercalation between widely spaced costae (Fig. 297).

paucicostate. Costae distant from umbo and few.

paucicostellate. Costae and costellae distant and few.

paucispinose. Very few spines.

PEDICLE. Variably developed, cuticle-covered, stalklike appendage commonly protruding from ventral valve that adjusts position of shell relative to external environment (Fig. 1).

pedicle callist. Localized thickening of secondary shell layer in apex of ventral valve representing track of anterior migration of junction between pedicle epithelium and outer epithelium (Fig. 348).

pedicle capsule. Cylindroid infold of pedicle epithelium and cuticle accommodating the proximal bulbous end of the pedicle of articulated brachiopods (Fig. 1).

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. 316).

pedicle epithelium. Ectodermal epithelium investing pedicle (Fig. 2).

PEDICLE FORAMEN. Subcircular to circular perforation of shell through which pedicle passes (Fig. 317).

pedicle fulcrum. Pair of subparallel plates median to dental plates in ventral umbo of some early athyridines.

pedicle furrow. External plate extending anteriorly from beak to pedicle foramen in some siphonotretoids and obolellides.

pedicle groove. Subtriangular groove dividing ventral pseudointerarea medially and affording passage for pedicle in many lingulides (Fig. 286).

pedicle muscles. Muscles associated with pedicle; external to pedicle in articulated brachiopods (adjustor and median pedicle muscles); internal in inarticulated brachiopods.

pedicle muscle scar. Scar of attachment on ventral valve of longitudinal fibrils in connective tissue of pedicle of articulated brachiopods.

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 labiate foramen.

pedicle sheath. Externally directed tube projecting posteroventrally from pedicle umbo, probably enclosing pedicle in young stages of development of some shells with supra-apical pedicle opening (Fig. 319).

pedicle tube. Internally directed tube of secondary shell continuous with margin of pedicle foramen and enclosing proximal part of pedicle (Fig. 310).

pedicle valve. See ventral valve.

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; characteristic of orthotetidines.

periostracal pad. Thickened band of periostracum covering cardinal areas and spun out by fused mantle lobes along posterior margin of some articulated brachiopods (Fig. 44).

periostracum. Organic external layer of shell secreted by the outer mantle lobe beneath an impersistent film of glycosaminoglycans and acting as the seeding sheet for the primary mineralized shell (Fig. 2).

permesothyrid (foramen). Pedicle opening located mostly within ventral umbo (Fig. 318).

pinnate (mantle canal). *Vascula genitalia* or *vascula lateralia* consisting exclusively of radially disposed canals (Fig. 381).

planareas. Two flattened areas developed, one on either side of posterior part of shell, more or less perpendicular to commissural plane; single median interarea may be much reduced or absent.

plane commissure. See rectimarginate.

plane of symmetry. Plane bisecting shell symmetrically (Fig. 283).

planoconvex. Dorsal valve flat; ventral valve convex.

plate (trimerellids). Single transverse, platelike projection from cardinal margin of dorsal valve articulating with cardinal socket of ventral valve (Fig. 375).

platform. Relatively broad, solid, or undercut elevation of inner surface of valve, commonly bearing muscles (Fig. 368, 375).

platform (of Orthidina). See notothyrial platform, notothyrial chamber.

platform line. Side bounding notothyrial chamber.

platform vaults. Two cavities beneath platform in some trimerelloids, separated by median partition (Fig. 375).

platidiiform (loop). Loop consisting of descending lamellae from cardinalia to median septum occasionally with only rudimentary outgrowths from distal end of septum analogous to ascending lamellae. See axial.

plectolophe. Lophophore in which each brachium consists of U-shaped side arm bearing double row of paired tentacles but terminating distally in medially placed planospire normal to commissural plane and bearing single row of paired tentacles (Fig. 114).

plectolophus (noun). See plectolophe.

pleuromal plates. Pair of plates in posterior part of delthyrial cavity of some spiriferides immediately internal to dental plates; probably merely later infilling of delthyrial cavity.

plica. Major undulation of commissure, reflected on shell interior, with crest directed dorsally; commonly but not invariably associated with dorsal fold and ventral sulcus.

plication. See plica.

pliciligate stage (of folding). See parasulcate.

plicosulcate. Alternate folding in which dorsal sulcus bears small median fold (Fig. 289).

polypalmate. Mantle canal system with more than four 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. 283).

posterior flap. Reflexed to anteriorly directed extension of lyttoniid ventral valve lying dorsal to at least posteromedian part of dorsal valve.

posterior margin. Posterior part of junction between edges of valves; may be hinge line or cardinal margin (Fig. 285).

posterior oblique muscles. Pair of muscles in discinoids originating posterolaterally on ventral valve and converging dorsally to insertions on dorsal valve between posterior adductors; equivalent to oblique internals (Fig. 374).

precampagiform flange. See septal flange.

precampagiform hood. See hood.

prefalcifer (crura). See hamiform.

pre-ismeniform (loop). See diploform.

premagadiniform (loop). One of the early stages of terebratellide loop development marked by growth of descending branches from both cardinalia and median septum and their completion and by the appearance of tiny hood developing into ring on septum. See cucullate and annular.

prepygites stages (of folding). See plicosulcate.

presocket line. Anterior or anterolateral side of triangular slot produced by brachiophore plate (and fulcral plate if present) in internal mold of orthides.

primary lamella. First half whorl of each spiralium distal from its attachment to crus (Fig. 336).

PRIMARY LAYER (of shell). Outer, mineralized shell layer immediately beneath periostracum, deposited by vesicular cells of outer mantle lobe (Fig. 11).

prismatic shell. Band or continuous layer of polygonal columns of calcite disposed normal to the shell surface. See tertiary layer.

procline. See inclination of cardinal area or of pseudointerarea (Fig. 285).

prodeltidium. So-called third plate; at one time thought to be developed in earlier embryonic growth of atrematous, neotrematous, and protrematous species (Beecher, 1891, 1892), subsequently becoming more or less attached to either dorsal (atrematous) or ventral valve.

promontorium (pl., **promontoria**). Shelflike structure extending laterally from lateral sloping face of cardinal process; homologue of inner socket ridges in some orthotetidines.

PROPAREAS. Pair of subtriangular halves of pseudointerarea divided medially by various structures (e.g., homeodeltidium, intertrough, and pedicle groove) of inarticulated brachiopods (Fig. 286, 327.1).

propuncta (pl., *propunctae*). See pseudopunctum (proposed for deflections without taleolae).

prosocket ridge. See socket ridge.

prostrate spines. Usually straight spines that lie prone on shell surface of some productides.

protegulal node. Apical portion of adult shell, commonly raised, representing site of protegulum and later growth up to neanic stage (Fig. 297).

protegulum. First-formed shell of periostracum and mineralized lining secreted simultaneously by both mantles (Fig. 283).

protractor muscles. See outside lateral muscles, middle lateral muscles in inarticulated brachiopods; also used for longitudinal fibrils attached to setae and those in the connective tissue of pedicle of articulated brachiopods. See pedicle muscle scar.

pseudoarea. See pseudointerarea.

pseudobrace 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 (Fig. 366).

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. 319; 327.1, 327.3; 353).

PSEUDOINTERAREA. Somewhat flattened, posterior sector of shell of some inarticulated brachiopods secreted by posterior sector of mantle not fused with that of opposite valve (Fig. 286).

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. 267–269).

pseudopunctum (pl., pseudopuncta). See pseudopuncta.

pseudoresupinate. Convexoconcave shell.

pseudosocket. See secondary sockets.

pseudospondylium. Cup-shaped chamber accommodating ventral muscle field and comprising undercut callus of secondary shell contained between discrete dental plates (Fig. 352).

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. 115).

ptycholophus (noun). See ptycholophe.

puncta (pl., **punctae**). Perforation penetrating shell to connect with periostracum and occupied by caecum as in cranioids; any perforation apparently penetrating fossil shell and large enough to accommodate caecum (Fig. 261).

punctum (pl., puncta). See puncta.

pygopid (loop). Short, ringlike loop with slightly arched transverse band. See deltiform.

quadriplicate (folding). Having four anterior folds and three intervening sulci.

raduliform (crura). Hook-shaped or rodlike crura that arise on ventral side of hinge plate and project toward ventral valve.

ramicostellate. Costellae numerous, arising entirely by branching (Fig. 297).

ramulus (pl., ramuli). Folds developed on lateral walls of longitudinally divided dorsal median septum in thecideids.

receiving valve. See ventral valve.

rectimarginate. Having planar anterior commissure (Fig. 289).

recumbent spines. Slightly curved spines extending at angle of less than 45° to shell surface.

reflexed interarea. Hypercline dorsal interarea.

remigrant (foramen). Pedicle opening that tends to move dorsally after initially migrating toward ventral beak.

resupinate. Reversal in relative convexity of postbrephic shells with convex ventral valve that becomes concave and with concave dorsal valve that becomes convex during successive adult stages of growth (Fig. 287).

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 oblique muscles.

rhizoid spines. Spines of productides resembling rootlets, serving for attachment either by cementation to substrate or by entanglement.

rhynchonellid stage (of folding). See uniplicate.

ribs. Any ornament of radial ridges.

ridge. Relatively long narrow elevation of secondary shell, indicated to variable depth within underlying floor of valve by low, wide deflections of the skeletal fabric normal to long axis of ridge.

rimmed (foramen). See auriculate.

ring. Precursor to ascending elements of terebratellide loop arising from resorption of hood apex, consisting of thin circular ribbon; narrow ventrally and broadening dorsally to its attachment on septal pillar.

rostellum. Low projection between anterior adductor muscle scars of ventral valve of some cranioids to which internal oblique muscles are attached.

rostral callosity. See delthyrial plate.

rostrate. With prominent beak of ventral valve projecting over narrow cardinal margin.

rostrum. Beak of articulated brachiopods. See beak.

rostrum. Elevation of secondary shell on inner surface of dorsal valve of some cranioids in front of anterior adductor muscles, consisting of pair of low clubshaped protuberances forming seat of attachment for brachial protractor muscles.

RUGA (pl., **RUGAE**). Concentric or oblique wrinkling of external shell surface (Fig. 294).

saccate (mantle canal). *Vascula genitalia* pouchlike, without terminal branches, not extending to anterolateral periphery of mantle, functioning primarily as gonocoels (Fig. 381).

saddle. Median arched part of jugum between stem and lateral branches (Fig. 336).

scar. See muscle scar (Fig. 348–350).

scar of pedicle attachment. See pedicle muscle scar.

schizolophe. Lophophore indented anteromedially to define pair of brachia, each bearing row of paired tentacles, at least distally (Fig. 112–114).

schizolophus (noun). See schizolophe.

SECONDARY LAYER (of shell). Shell deposited by a layer of outer epithelium within the circumferential lobes of the mantle and consisting of fibers or laminae ensheathed in interconnecting membranes (Fig. 5, 222).

secondary pseudointerea. Flat, undivided pseudointerarea, lacking flexure lines and developing after origin of pedicle foramen in some lingulides.

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 strophodontid dorsal valve.

septal pillar. High, brachial septum anterior to cardinalia, formed early in development of terebratelloid loop.

septal plates. Two plates that fuse to form duplex median septum in dorsal valve of some pentamerides and bearing outer plates on their ventral surfaces. See also septal plates, below.

septal plates. Various parts of cardinalia. See crural plates, hinge plates. See also septal plates, above.

septalial plates. Crural plates forming floor of septalium and united with earlier formed part of median septum.

septalium. Troughlike structure of dorsal valve between crural bases, consisting of crural plates (or homologues) fused medially and usually supported by median septum, but may be unsupported or sessile; does not carry adductor muscles (Fig. 330.4). See crural plates.

septiform (crura). Crura having form of septa that descend directly from brachial side of hinge plates to floor of dorsal valve.

septule. Small elongate tubercle within strophomenide valves. See also accessory septa.

septum (pl., **septa**). Relatively long, narrow elevation of secondary shell, commonly bladelike; indicated within underlying floor of valve by persistent high, narrow deflections of shell fabric originating near primary layer (Fig. 354).

sessile cruralium. Cruralium united with floor of dorsal valve without intervention of supporting median septum.

sessile spondylium. Spondylium united with floor of ventral valve without intervention of supporting medium septum.

seta (pl., **setae**). Chitinous bristle arising from invaginated follicle along mantle grooves and commonly protruded beyond shell margin (Fig. 48).

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 either valve but sharply elevated and free medially; in ventral valve, bearing part of ventral muscle field and lying between or supporting dental plates; in dorsal valve bisected by median septum (Fig. 356).

short loop. See loop.

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.

siphonothyrid (foramen). Pedicle foramen continued internally as tube made up of exaggerated pedicle collar.

socket line. Posterior side of triangular slot in internal molds of orthide brachiopods produced by brachiophore base (and fulcral plates if present) and bounding impression of socket.

socket plate (of orthides). See fulcral plate.

socket plates. Pair of plates supporting inner socket ridges, attached to cardinal process, and resting on floor of dorsal valve of orthotetoids and some orthoids; also pair of plates defining sockets of atrypid dorsal valve, confined by inner socket ridges medially and normally supported by thickened shell deposit (Fig. 332).

socket ridges. Linear elevations of secondary shell extending laterally from cardinal process and bounding anteromedian margin of dental sockets. See also inner socket ridge and outer socket ridge (Fig. 323, 331).

sockets. See dental sockets.

socket valve. See dorsal valve.

spicules. Small irregular bodies of calcite secreted by scleroblasts within connective tissue of mantle and lophophore (Fig. 53, 339–340).

spine. Solid or hollow, cylindrical, parallelepipedic, or, less commonly, elongate triangular projections from external shell surface or anterior margin (Fig. 304, 307).

spine apertures. Internal opening of spine bases.

spine ridge. Ridgelike radial trace of prostrate spine on shell exterior.

spinule bases or apertures. See hollow ribs.

spinules. Spines of small diameter and approximately 1 or 2 mm in length in chonetoids.

spinuliform (crura). Variant of raduliform type, but with crura laterally compressed.

SPIRALIA (sing., **SPIRALIUM**). Pair of spirally coiled lamellae composed of secondary shell and supporting lophophore (Fig. 333, 336).

spires. See spiralia.

spiriferid stage (of posterior margin). Long, straight posterior margin.

spirolophe. Lophophore in which brachia are spirally coiled and bear single row of paired tentacles (Fig. 113).

splanchnocoele. 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 tertiary shell forming more or less continuous veneer on dorsal surface of pentameroid spondylium and entire deltidial cover.

spondylium. Trough-shaped or spoonlike apparatus composed of dental plates in various stages of coalescence, usually with median septum, accommodating ventral muscle field (Fig. 354).

spondylium discretum. Muscle-bearing chamber formed by slight convergence of dental plates that 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 ventral valve (Fig. 351.2).

spondylium pseudotriplex. See spondylium triplex.

spondylium simplex. Spondylium formed by convergence and growth of dental plates and supported by variably developed simple ventral median septum or ridge (Fig. 351.1).

spondylium triplex. Spondylium supported by median septum and two lateral septa as in *Polytoechia* (Fig. 353).

spondyloid (dental plates). Basal inner surfaces of dental plates thickened and coalesced to simulate spondylium.

spyridium. Cuplike apparatus affording attachment for dorsal adductors and consisting of variably fused pair of subtriangular platforms elevated on subjacent ridges (Fig. 368).

squama (pl., **squamae**). Small arc of posterolateral margin of dorsal valve, especially of rhynchonellides, overlapping complementary arc (glotta) of ventral margin.

squamose. Growth lamellae having irregular and ragged margin.

stalk. See pedicle.

stegidium. Convex plate or series of imbricate concentric plates closing gap between delthyrial plate and spiriferide dorsal valve consisting of series of concentric layers deposited by outer epithelium associated with atrophying pedicle migrating dorsally (Fig. 320).

stolidium. Thin, marginal, short to long frill protruding at distinct angle to main contour of one or both valves of adult stenoscismatoids.

straight beak. See beak angle.

strainer spines. See endospines.

strangulate (of folding). See lobate.

striae. Fine grooves or incisions.

strophic (shell). Shell with true hinge line coincident with hinge axis (Fig. 285).

subdelthyrial plate. See delthyrial plate.

suberect (beak). See beak angle.

suberect spines. Spines inclined to shell surface at angles between 45° to 75°.

subhypothyrid (foramen). Foramen occupying apex of delthyrium as in atrypids.

subintertext folding. See alternate folding.

submarginal ridge (of productids). Thickening of either valve anterolaterally bordering corpus cavity.

submegathyrid (posterior margin). Posterior margin approximately straight and slightly less than maximum width of shell.

submesothyrid (foramen). Pedicle opening located partly in ventral umbo but mainly in delthyrium (Fig. 318).

subperipheral rim. Elevation of secondary shell concentric to and within margin of valve.

subplectolophous (lophophore). See plectolophe.

subspondylial chambers. See umbonal chambers.

subterebratulid (posterior margin). Posterior margin considerably less than maximum width of shell but not strongly curved.

sulcate (folding). See unisulcate.

sulciplicate (folding). Form of alternate folding with dorsal valve bearing median fold indented by shallow median sulcus (Fig. 289).

SULCUS. Major depression of valve surface, externally concave in transverse profile and radial from umbo.

supporting plates. See brachiophore plates.

supporting septum (of hemispondylium). Median septum attached to floor of thecideoid ventral valve and supporting concave plates of hemispondylium.

supra-apical foramen. Pedicle foramen initially located in ventral umbo away from apex of delthyrium (Fig. 319.2).

surmounting plate. Variably developed platform along posteroventral margin of dorsal median septum of some acrotretoids (Fig. 346–347).

symbolothyrid (pedicle opening). Pedicle opening shared by both valves.

symphytium. Deltidial plates fused dorsally or anteriorly from pedicle foramen and retaining only weak median line of junction (Fig. 317).

syndeltarium. See deltidial cover.

syrinx. Tube of secondary shell medially located on ventral side of delthyrial plate and split along its ventroanterior surface (Fig. 355).

tabella (pl., *tabellae*). See adminicula.

taleola (pl., taleolae). Porous cylinder of granular calcite in axial region of many pseudopunctae (Fig. 269–270).

taxolophous lophophore. Rudimentary lophophore with tentacles 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 (Fig. 351.1b,2c).

tegula. Articulating knobs on dorsal hinge line of richthofeniids (Fig. 326.2).

telae (sing., **tela**). Pair of pointed terminations of beak ridges projecting into and beyond pedicle opening, formed by apical migration of pedicle.

teloform (loop). Long reflected loop, typical of adult stage of various remotely related long-looped stocks (e.g., *Macandrevia, Magellania*), with loop free of septum (Fig. 338.4).

terebrataliiform (loop). Long reflected loop typical of *Terebratalia* and related genera, with lateral connecting bands extending between descending lamellae and median septum. See trabecular.

terebratelliform (loop). Long reflected terebratellide loop with lateral connecting bands uniting descending lamellae to median septum; morphologically similar to terebrataliiform loop, but deriving from dissimilar loop ontogeny. See trabecular.

terebratulid (posterior margin). Strongly curved posterior margin much less than maximum width of shell.

terebratulid stage (of folding). See sulciplicate.

terebratuliform (loop). Short, typically U- or W-shaped loop found in most terebratuloids. See deltiform.

terebratuliniform (loop). Short (deltiform) loop in which crural processes are fused medially to complete ringlike structure.

TERTIARY LAYER (of shell). Continuous layer of prismatic shell secreted by outer epithelium within margin of secondary layer and in internal succession to that layer (Fig. 254–255).

THICKNESS. Maximum dimension between valve exteriors normal to length and width (Fig. 283).

tichorhinum. Small, suboval chamber, with or without median partition, formed by medially directed struts arising from dental plates converging onto median septum in spiriferide ventral valve; possibly accommodated base of adductor muscles (Fig. 354).

tongue. See linguiform extension.

torynidium. See camarophorium.

trabecular (loop). Long reflected loop, typical of adult state of several remotely related long looped stocks (e.g., *Terebratalia, Calloria*), with lateral connecting bands extending between descending lamellae and median septum.

track. See muscle track.

trail. Subparallel extensions normally of both valves anterior to corpus and commonly resulting in a geniculate shell profile (Fig. 287.6).

transmedian muscles. Pair of muscles in some lingulides anterior to umbonal muscle; one muscle originating on left side of ventral valve rising dorsally to be inserted on right side of dorsal valve; second muscle originating on right side of ventral valve and inserted on left side of dorsal (Fig. 346.2, 377).

transmuscle septa. Assemblage of narrow elevations comprising one median and two pairs of diverging laterals associated with strophomenoid dorsal adductor field.

transverse band. Lamella joining posterior ends of ascending lamella of loop (Fig. 338).

transverse delthyrial plate. See delthyrial plate.

transverse plate (of spiriferides). See delthyrial plate.

transverse plate (of stringocephaloid loop). See echmidium.

trocholophe. Lophophore disposed as ring surrounding mouth, bearing either single row of unpaired (or more rarely double row of paired) tentacles (Fig. 112–114).

trocholophus (noun). See trocholophe.

tropoconate. Brachia coiled parallel with plane of symmetry.

trough. See septalium.

truncate (beak). Ventral umbo of articulated brachiopods with beak abraded due to pedicle movement and foramen in transapical position (submesothyrid, mesothyrid, permesothyrid, and epithyrid).

tubercle. Any fine, low, rounded protuberance on either surface of valve, irrespective of origin (Fig. 274).

UMBO (pl., **UMBONES**). Apical portion of either valve containing beak (Fig. 283).

umbonal angle. See apical angle.

umbonal blade. Part of primary lamella of spiralium extending from lateral branch of jugum to distal end of crus (Fig. 336).

umbonal chambers. Pair of posterolaterally located cavities in either valve; in ventral valve bounded by dental plates (cardinal buttresses in trimerelloids) and shell walls; in dorsal valve limited medially by crural plates (or homologues) and shell walls (Fig. 351).

umbonal muscle. Single muscle occurring in some lingulides, thought to be homologous with posterior adductors; consists of two bundles of fibers posteriorly and slightly asymmetrically placed (Fig. 346.1).

umbonal slopes. Region of shell surface adjacent to umbo.

uniplicate (folding). Form of alternate folding with ventral valve bearing median sulcus and anterior commissure median plica (Fig. 289).

uniseptum. See septum.

unisulcate (folding). Form of alternate folding with dorsal valve bearing median sulcus and anterior commissure median sinus (Fig. 289).

unpaired median muscle scar. See pedicle muscle scar.

vallum. Wall of secondary shell surrounding body and mantle cavities in lyttoniid valves.

varix (pl., varices). See growth line.

vascula (sing., vasculum). Any identifiable branches of mantle canal system (Fig. 379).

vascula - antemyaria, arcuata, cardinalia, cruralia, dentalia, media exteriora, media interiora, myaria ventri, spondyliaria, terminalia. Finely divided components of mantle canal.

vascula genitalia. Mantle canals of articulated brachiopods that contain gonads; may consist of *vascula dentalia* and *vascula spondyliaria* in ventral valve and *vascula cruralia* and *vascula cardinalia,* if developed, in dorsal valve (Fig. 379).

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 inarticulated brachiopods (Fig. 384).

vascula media. Pair of mantle canals in either valve, medially located, projecting anteriorly from body wall (Fig. 379).

vascula myaria. Simple or branched pair of mantle canals arising between anterior and posterior adductor muscle scars of dorsal valve of some articulated brachiopods (Fig. 379).

vascular markings. Impressions of mantle canals on shell interior.

vascular ridges. See vascular markings.

vascular sinus. See mantle canal.

vascular trunk. Any major branch of mantle canal system.

venter. Median region of productoid shell between lateral slopes.

VENTRAL. Direction toward ventral valve from dorsal valve.

ventral adjustor muscles. See adjustor muscles.

ventral adminicula. See adminicula.

ventral biplicate (folding). See biplicate.

ventral dental socket. See denticular cavities.

ventral process. Median callus of secondary shell underlying pseudodeltidium and projecting dorsally to fit between lobes of cardinal process.

VENTRAL VALVE. Valve through which pedicle commonly emerges, usually larger than dorsal valve and invariably containing teeth when present (Fig. 283).

ventribiconvex. Both valves convex, ventral valve more strongly so than dorsal.

vertical connecting bands. See connecting bands.

vertical plate (of terebratulides). 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 ventral valve dorsal of dorsal valve.

virgate. Straight and erect.

visceral area. Part of shell enclosing body cavity.

visceral cavity. See body cavity.

visceral disk. Part of shell posterior to origin of trails.

visceral foramen. See dorsal foramen.

WIDTH. Maximum dimension normal to plane of symmetry (Fig. 283).

xenidium. See pseudodeltidium.

zeilleriid (loop). Long reflected loop, not attached to dorsal septum in adult. See teloform.

zeilleriid stage (of folding). See bilobate.

zygidium. Collarlike structure uniting lateral ridges on posterodorsal side of cardinal process and fitting within ventral umbo of some productides.

zygolophe. Lophophore in which each brachium consists of straight or crescentic side arm bearing two rows of paired tentacles (Fig. 114).

zygolophus (noun). See zygolophe.