# COMPOSITION OF BRACHIOPOD SHELL

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## INTRODUCTION

A study of shell structure and morphology, if it is to be used to understand evolutionary development, must be seen in relation to the fundamental biochemistry and metabolic processes of shell growth. Brachiopods must thus be considered as having exoskeletons similar in function to other invertebrate exoskeletons, with a general pattern underlying their structure and metabolic biochemistry, but with significant differences.

Shell growth is a chain of interlinked processes biochemically regulated so that the result is morphologically recognizable as producing heritable features; an understanding of its biochemistry may therefore contribute to classification on a rational basis. The adult shell is dead tissue which can have only repairs or additions to the inner layer, but during growth it takes an integral part in the basic metabolic processes of the animal. In assessing the relative phylogenetic or morphogenetic importance of the organic constituents, it is necessary to see them as interrelated parts of a functional system and to differentiate rejected or waste products from substances concerned in growth processes both structural and regulatory. There is an underlying homogeneity in biochemical processes of most living organisms and refined variants in the general pattern must be sought. There may nevertheless be some biochemical species variants such as in amino-acid constitution of specific proteins, which, if detected, may be a decisive factor in classification. Specific proteins may be specific by virtue of the order of array of amino acids, or of their actual amino-acid constitution; the latter holds promise of heritable characteristics potentially detectable even in fossil material. Functional variants of composition may occur, however (e.g., inner layer of the ligament of marine lamellibranchs has a different protein constitution from the remainder of the shell, thought to be correlated with its specialized function, 5). Sterols may be informative; in echinoderms and sponges the nature of the sterol present in different groups of the organism seems to have phylogenetic significance (6). Certain marine invertebrates (some anthozoans and sponges) are able to concentrate bromine and iodine and convert them into bromo- and iodoscleroproteins (24), in this respect differing greatly from their utilization of chloride, which has a role in controlling osmotic pressure. The bromoscleroproteins do not appear to have a definite composition but the iodoscleroproteins have this, and thus have contributed to a more precise definition of the systematic position of the Gerardiidae (Hexacorallia).

A start has been made toward understanding the biochemistry of morphogenesis, and compounds such as mucopolysaccharides are evidently involved. Neutral mucopolysaccharides (a class of compounds which includes chitin) and especially acid mucopolysaccharides are found in connective tissue where they probably play a part in the morphogenesis of the fibrous material (11). The shell mosaic of articulate brachiopods, for example, which is believed to be specifically diagnostic, is the pattern on the inside of the shell made by the ends of the calcite fibers and must be a reflection of the cross section of the cytoplasmic sheath within which they grow, and which is presumably genetically controlled.

The brachiopod shell resembles exoskeletons of arthropods and mollusks in consisting of proteinaceous layers secreted onto the outer surface of the body by a single layer of epidermal cells, strengthened by deposition of inorganic compounds (chiefly of calcium) and may contain much chitin. Exoskeletons of arthropods and mollusks contain also other organic constituents such as tanning agents and lipids, presumably equally essential in brachiopod shells. The periostracum is usually thin; it is mainly organic but may contain a relatively high proportion of iron (about 10 percent in some areas in *Lingula*) (17). It is resistant to abrasion and relatively impermeable to fluids though remaining elastic to some extent.

There are two main types of brachiopod shells, depending on whether the inorganic material is predominantly calcium phosphate or calcium carbonate. Phosphatic shells contain a high proportion of organic material, 25 to 52 percent (7, 28) (Table 1), which is mainly chitin and protein (Table 2). Carbonate shells contain a much lower proportion of organic material (0.93-4.7 percent) (7), largely protein, along with small amounts of material which is estimated as hexosamine but which could have been derived from some mucosubstance other than chitin. Organic substances such as lipids are present in both types of shells (17).

These major distinctions of composition provide a broad basis for classification of the organisms. The articulate shell is invariably carbonate, the inarticulate mainly phosphatic; the Craniidae have carbonate shells but are grouped with the inarticulates which they resemble anatomically. A number of forms are difficult to fit into either group: the Cambrian kutorginids, for example, are important in being among the most primitive brachiopods, but although their shell is calcareous, its true structure and detailed composition have yet to be determined. It would be valuable to know whether this shell had contained any chitin or significant amounts of phosphate.

## INORGANIC CONTENT

The main inorganic constituent of brachiopod shell structure is calcium phosphate in inarticulates (lingulids 74.7-93.7 percent, *Discinisca* 75.2 percent), and calcium carbonate in articulates (94.6-98.6 percent) and craniids (87.8-88.6 percent) (7,28) (Table 1). There are usually small amounts of phosphate in carbonate shells (e.g., about 0.5 percent in *Crania*), and carbonate in phosphatic shells (1-4 percent in lingulids;[1] 8.6 percent in *Discinisca*). $MgCO_3$ is almost always found in small amounts. It has not yet been shown whether these lesser constituents (or indeed others found in smaller amounts) are concentrated in specific locations or diffused generally through the shell structure. Small amounts of $Al_2O_3$, $Fe_2O_3$ and $SiO_2$ are found in all forms, and other elements have been shown in some species (Sr, which tends to follow Ca, in *Macandrevia* (26), *Hemithiris psittacea* (23), and *Lingula anatina* (28); $B_2O_3$ in *L. anatina* and *Terebratula vitrea* (14) and traces of Cu, Ba, Ti, and Zr in *L. anatina* (28). Lingulid shells have a high concentration of F, 1.6 percent (4), 1.91 percent (28), shown by McConnell (X-ray powder diffraction patterns, 21) to be present as carbonate fluorapatite (francolite). F is toxic to many biological systems, and such amounts in the shell may represent removal from the system by fixation. *Lingula anatina* has about 0.5 percent $Mn_3O_4$ (28).

Some of these elements are functional in brachiopods and are essential to the shell in so far as it is part of the living tissue of the animal; others are apparently merely ingested incidentally from the environment.

Ca, the major mineral constituent of shell structure, has also a physiological role in maintaining differential osmotic pressures and in stimulating muscular movement. Mg is variable; it is ingested from sea water and from green algae, and in traces it is needed for some enzyme systems; but the large amounts in *Crania anomala* and *Discinisca lamellosa* are probably incidental. Deposition of Mg by some marine invertebrates has been said to be greater in warm waters than in cold (7), but this is not so in brachiopods, since *Crania anomala* (Norway coast) with a cold-water habitat has a high proportion of $MgCO_3$ (Table 1). Part of the Fe is functional, in oxygen transporters and transfer; hemoglobin is the respiratory blood pigment in brachiopods (28), and hemerythrin has been found in *Lingula unguis* [=*L. anatina*] (18). Cu, Mn and perhaps other elements of variable valency are also essential in traces as components of specific enzyme systems. Si is sometimes found in exoskeletons and spicules (though not in brachiopods). On the other hand, Al and B have no known physiological function relevant here.

Analysis of fossil forms shows that while there may be secondary deposition of carbonate, sulfate, and fluoride, there need be little replacement of phosphate by carbonate, a concentration of 85.89 percent $Ca_3(PO_4)_2$ has been reported in the Ordovician *Obolus appollinis* Eichwald (22).

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[1] The high values for calcium carbonate in some lingulids in Table 1 may be due to inclusion of sulphate.

TABLE 1. *Inorganic Constituents of Recent Inarticulate and Articulate Brachiopoda*

| INDEX | Organic matter | Ash (a) | MgO | $FePO_4$ | $Ca_3P_2O_8$ | $CaSO_4$ | $CaCO_3$ | $MgCO_3$ | $(Al,Fe)_2O_3$ | $SiO_2$ | Other |
|---|---|---|---|---|---|---|---|---|---|---|---|
| A | 0.93 | 99.07 | --- | --- | tr. | 0.36 | 98.61 | 0.93 | 0.04 | 0.06 | --- |
| B | 1.00 | --- | --- | --- | 0.61 | --- | 98.39 | tr. | tr. | --- | --- |
| C | 4.73 | 95.27 | --- | --- | tr. | 1.18 | 96.78 | 1.37 | 0.15 | 0.52 | --- |
| D | 2.55 | --- | --- | --- | tr. | 2.40 | 94.60 | 1.05 | tr. | --- | --- |
| E | 1.55 | 98.45 | --- | --- | tr. | 0.36 | 98.30 | 0.68 | 0.48 | 0.18 | --- |
| F | 2.00 | --- | 0.60 | --- | 0.18 | 0.90 | 96.20 | --- | tr. | --- | 0.30(b) |
| G | 1.24 | --- | --- | --- | tr. | 0.85 | 96.20 | 1.20 | 0.40 | 0.60 | --- |
| H | 1.99 | --- | --- | --- | 0.12 | --- | 95.98 | 1.40 | 0.15 | --- | --- |
| I | 2.65 | 97.35 | --- | --- | 0.38 | 0.55 | 98.20 | 0.49 | 0.23 | 0.15 | --- |
| J | --- | --- | --- | --- | 0.27 | 0.75 | 98.06 | 0.92 | --- | --- | --- |
| K | --- | --- | --- | --- | --- | --- | --- | 0.45 | --- | --- | --- |
| L | 3.52 | 96.48 | --- | --- | 0.57 | 1.72 | 88.59 | 8.63 | 0.27 | 0.22 | --- |
| M | 4.30 | --- | 1.80 | --- | 0.28 | 2.15 | 87.80 | 3.40 | tr. | --- | --- |
| N | 40.00 | 60.00 | --- | --- | 91.74 | 2.93 | 1.18 | 2.70 | 0.54 | 0.91 | --- |
| O | 39.50 | 60.50 | --- | --- | 89.99 | 4.18 | 4.25 | 0.79 | 0.29 | 0.50 | --- |
| P | 42.60 | 57.40 | --- | 3.61 | 77.17 | --- | 12.19 | --- | --- | tr. | 7.03(c) |
| Q | 38.70 | 61.30 | 2.80 | --- | 85.79 | --- | 11.75 | --- | --- | --- | --- |
| R | --- | --- | --- | 0.77 | 84.94 | --- | 10.76 | 2.94 | --- | 0.18 | --- |
| S | 37.90 | 62.10 | --- | 0.76 | 85.32 | --- | 11.12 | 3.03 | --- | 0.17 | --- |
| T | 37.00 | 63.00 | --- | --- | 74.73 | --- | --- | 1.71 | 1.16 | 0.49 | --- |
| U | 25.00 | 75.00 | --- | --- | 75.17 | 8.37 | 8.35 | 6.68 | 0.58 | 0.85 | --- |
|  | Organic | Ash | $CaF_2$ | $Mn_3O_4$ | $P_2O_5$ | Indet. | CaO | MgO | $Fe_2O_3$ |  | Other |
| V | --- | --- | --- | --- | 23.20 | --- | 30.19 | --- | --- | --- | 1.52(d) |
| W | 52.10 | 47.90 | 3.93 | 0.46 | 42.99 | 1.44 | 50.66 | 0.30 | 0.22 | --- | --- |

(a) Per cent of dry matter. (b) CaO. (c) $Mg_3P_2O_8$. (d) F.

## NATURE OF ORGANIC CONTENT OF SHELLS

The chief organic constituents of brachiopod shells are protein and chitin. Protein is determined quantitatively by analysis of the amino-acid assemblage obtained on hydrolysis (Tables 2 and 3). Chitin is demonstrated qualitatively but specifically by the chitosan test and quantitatively by estimation of its breakdown product, glucosamine (Table 2). HYMAN (16), using the chitosan test, showed that the shell and pedicle cuticle of *Lingula* contained chitin, as did the shell of *Discinisca lamellosa* and the membrane covering the slot in its ventral valve but not the apex of its dorsal valve. *Crania anomala* gave a negative chitosan test. The shells of articulate forms (*Terebratulina retusa, T. transversa*, and *Laqueus californicus*) also gave negative chitosan tests, but the cuticle of the pedicle was chitinous.

Three main categories of organic components are distinguished within the brachiopod shell. They form the periostracum and any caecal strands which represent invaginations of the outer epithelium. They may also form part of the shell structure as cytoplasmic sheaths to calcite fibers.

Lingulid shells and the secondary layer of craniids have organic substances, including protein interleaved with the inorganic. In lingulids, chitin is present, as well as protein, possibly as alternating monolayers. FRAENKEL & RUDALL (13) from X-ray studies suggested this structure in insect cuticles. In craniids there is no chitin (17) (Table 2). *Discinisca* has both chitin and protein but distributed uniformly throughout the shell, not in layers.

The secondary layer of articulates and craniids at the muscle attachments have cell-wall material enclosing each calcite fiber, contributing phospholipids, steroids, proteins, and polysaccharides. Endopunctate forms have outer epithelium intruded as caeca into the shell structure. Their primary layer contains mucin-like material (possibly acid or neutral mucopolysaccharides) and strands of cytoplasm forming the brush, as well as epithelial cell material; their secondary layer contains epithelial cell wall and cell contents. Cells, while undergoing periodic mitosis during shell growth, would contain such substances as DNA of the nucleus, RNA, phospholipids, enzymes, and mucoprotein of the cytoplasm. The caeca of craniids are made up of epithelial cell material possibly containing mucus. Lingulid and discinid shells are traversed by fine cytoplasmic strands (mucoprotein possibly) which may contain intracellular fluid or mucus.

The periostracum of all shell types is mainly organic, in phosphatic shells chitin and protein, and in carbonate shells protein without chitin (17). The protein of all shells may be quinone tanned as in lamellibranch shells (5) and some arthropods (9). There may also be a lipid component, for in insect cuticles a sterol operates in the tanning and a straight chain paraffin forms the outermost layer (9, 10).

The dark brown color of the periostracum of *Lingula* is due to iron, probably as ferric hydroxide, in places forming about 10 percent of its weight. The iron tends to be distributed in bands following growth lines, the regions representing embryonic or young growth of the shell containing much

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Explanation of Table 1

[Specimens, localities, and index numbers for references given in list at end of this chapter are indicated by capital letters at left margin of table, as follows.——(A) *Gryphus cubensis* (POURTALÈS), Florida (7).——(B) *Gryphus* sp., Florida, Cuba (27).——(C) *Terebratulina septentrionalis* (GRAY), Maine (Eastport) (7).——(D) *T. caputserpentis* (LINNÉ),? (19).——(E) *Laqueus californicus* (KOCH), Calif. (Esteros Bay) (7).——(F) *Macandrevia cranium* (MÜLLER),? (19).——(G) *M. cranium* (MÜLLER), 68°12'N, 15°40'E (26).——(H) *M. cranium* (MÜLLER), Lofoten Is. (26).——(I) *Hemithiris psittacea* (GMELIN), Shetland Is. (7)——(J) *H. psittacea* (GMELIN), Barents Sea (25).——(K) *H. psittacea* (GMELIN), ?(12).——(L) *Crania anomala* (MÜLLER), Norway coast (7).——(M) *C. anomala* (MÜLLER), ?(19).——(N) *Lingula anatina* LAMARCK, Japan (Higo) (7).——(O) *L. anatina* LAMARCK, Philippine Is. (Iloilo) (7).——(P) *L. anatina* LAMARCK, ?(8).——(Q) *Lingula ovalis* REEVE, Sandwich Is. (20).——(R) *L. ovalis* REEVE, ?(15).——(S) *L. ovalis* REEVE, ?(15).——(T) *Glottidia pyramidata* (STIMPSON), North Carolina (7).——(U) *Discinisca lamellosa* (BRODERIP), Peru (7).——(V) *Lingula anatina* LAMARCK, Ceylon (3).——(W) *L. anatina* LAMARCK, Ceylon (28). (Question marks indicate no locality cited.)]

less proportion of iron than older regions. The iron, presumably taken in from the environment, becomes deposited in the periostracum as unused material. The young, fast-growing shell, therefore, receives a smaller proportion of iron than slow-growing parts of more mature growth. Brachiopods have iron-containing respiratory pigments (hemoglobin or hemerythrin): it is not yet clear whether their iron is drawn from this reserve in the periostracum or whether their breakdown products contribute thereto.

The periostracum of *Lingula* appears laminated in pigmented areas; the outermost layer may be very dark brown, the underlayer, amber-colored. Protein (67.9 percent) and chitin (10.6 percent) have been demonstrated from the periostracum. The protein contains most of the amino

TABLE 2. *Organic Content of Recent Brachiopod Shells*
[BV=brachial valve; P=pedicle; PV=pedicle valve]

| Specimen | Location of Sample | Chitin as Hexosamine (a) | Protein (a) |
|---|---|---|---|
| 1. Lingula sp. | PV, no periostracum | 18.0 | --- |
| | BV, no periostracum | 12.0 | --- |
| | PV, periostracum only | 8.2 | --- |
| | BV, periostracum only | 7.0 | --- |
| | P cuticle, inner layer | 26.2 | --- |
| | P cuticle, outer layer | 20.8 | --- |
| 2. Lingula sp. | BV, with periostracum | 20.3 | 22.0 |
| 3. Lingula sp. | PV+BV, periostracum only | 10.6 | 59.8 |
| 4. Glottidia pyramidata (Stimpson) | PV, with periostracum | 9.6 | --- |
| | BV, with periostracum | 9.6 | --- |
| | P cuticle, inner + outer | 19.6 | --- |
| 5. Discinisca lamellosa (Broderip) | PV, with periostracum | 4.5 | --- |
| | BV, with periostracum | 3.3 | 7.0 |
| | PV+BV, periostracum only | 3.2 | 10.9 |
| | PV+BV, with periostracum | 20.6(b,c) | --- |
| | PV+BV, with periostracum | 3.8(c,d) | --- |
| 6. Crania anomala (Müller) | BV, with periostracum | 0.09 | 0.54 |
| 7. Crania anomala (Müller) | BV, protegulum only | 0.0 | --- |
| 8. Notosaria nigricans (Sowerby) | PV, with periostracum | 0.05 | 0.16 |
| | BV, with periostracum | 0.02 | 1.7 |
| 9. Macandrevia cranium (Müller)<br>Magellania flavescens (Lamarck) | PV+BV, periostracum only | 0.0 | --- |
| 10. Macandrevia cranium (Müller) | PV+BV, with periostracum | 0.07 | 1.9 |
| 11. Laqueus californicus (Koch) | PV+BV, periostracum only | 0.4 | 21.1 |
| 12. Terebratalia transversa (Sow'by) | PV+BV, periostracum only | 0.5 | 10.6 |

(a) Percent of shell dry weight. (b) Percent of organic matter.
(c) C and H analysis by Mr. Dunn, Microanalysis Lab., Queen's University
(d) Percent of water.

acids of structural animal proteins with very high proportions of alanine, arginine, and proline. Cystine was not found, but there is a small amount of hydroxyproline (Tables 2, 3) (17). In *Discinisca lamellosa* the periostracum has been shown to have chitin (3.2 percent) and protein (14.3 percent), high arginine, alanine, glutamic acid and some hydroxyproline.

The periostracum of *Laqueus californicus*

TABLE 3. *Amino Acids in Brachiopod Shells*

| Amino acids | Specimens | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | A | B | C | D | E | F | G | H | I | J | K | L | M | N |
| Aspartic acid | + | + | 0 | - | + | 15.6 | 16.6 | 22.6 | 14.9 | 23.5 | + | + | + | - |
| Glutamic acid | + | + | 0 | - | + | 9.1 | 12.2 | 10.4 | 7.5 | 5.8 | + | + | + | + |
| Cystine | + | + | - | - | - | - | - | - | 0.3 | 0.3 | - | - | - | - |
| Serine | + | + | 0 | - | - | 8.9 | 4.7 | 9.3 | 9.7 | 7.0 | - | + | + | - |
| Threonine | 0 | 0 | 0 | - | - | 4.5 | 5.4 | 7.4 | 3.2 | 3.7 | - | + | + | - |
| Glycine | ++ | ++ | ++ | + | + | 7.2 | 29.1 | 16.5 | 31.5 | 32.4 | + | ++ | ++ | + |
| Alanine | ++ | + | + | - | - | 13.2 | 23.1 | 8.1 | 1.6 | 4.1 | + | + | + | + |
| Proline | ++ | 0 | - | - | - | 4.5 | 0.6 | 0.9 | 3.3 | 1.1 | + | + | 0 | - |
| Valine | + | + | 0 | - | - | 5.4 | 2.2 | 3.9 | 1.6 | 2.3 | + | + | 0 | + |
| Methionine | 0 | - | 0 | - | - | - | - | - | - | - | - | - | - | - |
| Leucine/isoleucine | + | + | 0 | - | - | 8.6 | 0.9 | 5.1 | 5.5 | 1.9 | + | + | 0 | + |
| Phenylalanine | ++ | + | + | + | + | 2.4 | 0.2 | 2.0 | 4.6 | 0.7 | - | ++ | ++ | - |
| Tryptophane | + | + | + | + | - | - | - | - | 0.9 | - | - | - | - | - |
| Tyrosine | + | + | + | + | - | 3.1 | 0.2 | 6.0 | 7.8 | 1.2 | - | - | 0 | - |
| Lysine | + | + | 0 | + | - | 2.7 | 0.4 | 0.7 | 0.8 | 0.7 | - | 0 | 0 | - |
| Histidine | + | + | + | + | - | 5.5 | 7.1 | 6.7 | 5.5 | 11.3 | - | ++ | ++ | - |
| Arginine | + | + | + | - | - | 7.3 | 3.3 | 0.5 | 1.2 | 3.9 | - | - | - | - |
| Hydroxyproline | + | 0 | 0 | - | - | 2.1 | 1.2 | - | - | - | - | - | - | - |
| µM amino acids per gram (fossil or matrix) | - | - | - | - | - | - | - | - | - | - | - | 0.5 | 0.3 | 0.5 |

[Explanation: O indicates no amino acid detected; +, amino acids present in small or moderate amounts; ++, amino acids present in high proportion; figures indicate percent of total amino acid residues present; µM (micromoles) denotes measure proportional to number of molecules per unit mass. Specimens analyzed are identified by letters, as follows: RECENT (whole shells):——(A) *Discinisca lamellosa* (BRODERIP).——(B) *Lingula* sp.——(C) *Crania anomala* (MÜLLER).——(D) *Notosaria nigricans* (SOWERBY).——(E) *Macandrevia cranium* (MÜLLER). RECENT (periostracum only, showing minimal number of amino acid residues):——(F) *Lingula* sp.——(G) *Discinisca lamellosa* (BRODERIP).——(H) *Crania anomala* (MÜLLER).——(I) *Laqueus californicus* (KOCH).——(J) *Terebratalia transversa* (SOWERBY). FOSSIL:——(K) *Spirifer* sp. (Carboniferous Ls.); *Atrypa* sp. (Wenlock Sh.); *Plectothyris fimbria* (SOWERBY), Jurassic.——(L) *Linoproductus* sp. (Carboniferous Ls.).——(M) Carboniferous Ls. matrix.——(N) *Plaesiomys (Dinorthis) subquadrata* HALL & CLARKE (Ordovician) (2). (Jope, n)] contains no chitin but yields about 0.4 percent hexosamine from some mucosubstance. Protein 21.8 percent was found, consisting of most of the usual structural animal amino acids including cystine but no hydroxyproline and high proportions of tyrosine, phenylalanine, proline, and glycine (Tables 2, 3) (17). As in *Lingula,* the periostracum of *Laqueus* contains iron in the form of ferric hydroxide, but in very much smaller amounts. The periostracum of *Terebratalia transversa* like that of *L. californicus* contains no chitin but 0.5 percent hexosamine; its protein (13.3 percent) has high arginine and glycine values.

The periostracum of the inarticulate *Crania* follows the pattern of the carbonate shells of the articulates in containing protein but no chitin. The formation of chitin is apparently associated with the presence of phosphate or its deposition, rather than carbonate, and is not a property of hingeless forms as such. The inarticulate *Crania,* anomalous with its carbonate shell and lack of chitin, may be seen as a transition between inarticulates and articulates.

Analysis of the organic content of impunctate articulate shells is without complications in that they contain structural material only; all other groups, however, contain some incorporated epithelial cell material in the form of caeca, and significant analytical data can only be obtained after differential micro dissections.

The organic content of the intrusive caeca differs only from that of impunctate shells (epithelial cell walls of cytoplasmic sheaths) in containing mucin-like material and cell contents: mucoprotein, DNA, and RNA, when the mantle cells are proliferating. The organic content of the primary layer alone (of endopunctate forms) will give data for caecal cup material (epithelial cell wall), mucus, and cell contents; that of the secondary layer will give data for the caecal stalks (epithelial cell wall and cell contents) along with material of the cytoplasmic sheaths.

Lingulid and discinid shells have fine cytoplasmic strands intruded into the shell structure. These shells, however, have a high organic content and the proportion from the cytoplasmic strands will be slight. *Crania* has punctae formed of epithelial cell material; these branch in the outer calcareous layer which otherwise contains no organic material. Analysis of the organic material of the outer layer will therefore give an estimate of the epithelial cell material which can be deducted from that found in the inner layer.

Carbonate shells contain small amounts of protein (about 0.5-2 percent) and very small amounts of hexosamine (<0.1 percent) derived more likely from a mucosubstance than from chitin, since hexosamine is a very common constituent of animal cell and connective tissue. Phosphatic shells contain relatively large amounts of chitin (*Lingula,* 20 percent, *Discinisca,* about 4 percent) and also protein (*Lingula,* 22 percent, *Discinisca,* 7 percent) (Table 2) (17). The chitin was estimated as hexosamine and so may contain small amounts of hexosamine from mucosubstances.

Impunctate articulate shells (e.g., *Notosaria nigricans*) contain about 1 percent of protein and about 0.05 percent hexosamine (Table 2) (17): material derived from the cell wall of the cytoplasmic sheaths. Lingulids have 22 percent protein and 20 percent chitin: material derived from the organic interleaves of the laminated shell structure, possibly alternating monolayers of chitin and protein. The "punctae" of lingulids are fine, and small amounts of protein and hexosamine from them will be included in the values given in Table 2. The protein from the whole shell of *Lingula* contains most of the common animal structural amino acids and is fairly rich in glycine; certain areas of the shell have also a green organic pigment. *Notosaria* contains the common amino acids of structural proteins but is not rich in glycine (Table 3) (17).

Endopunctate forms (e.g., *Macandrevia* and *Crania*) contain invaginated material from the epithelium. Their hexosamine content is a little higher than that of impunctate *Notosaria,* about 0.1 percent, and their protein content is low (0.5 percent in *Crania,* about 2 percent in *Macandrevia*) (Table 2) (17). In *Macandrevia* this material is derived from the cytoplasmic sheaths and caecal material including mucin, also from the thin periostracum. In *Crania,* the organic material comes from interleaves of the inner shell layer, cytoplasmic sheaths to calcite fibers at sites of muscle attachments, epithelial cell material forming the punctae and from the periostracum. The protein of *Crania* is rich in glycine and is unusual in containing little or no aspartic and glutamic acids.

Discinids contain smaller amounts of protein and chitin than lingulids (Table 2). Their protein is rich in glycine, alanine, proline, and phenylalanine, and like *Lingula,* contains hydroxyproline, characteristic of collagenous proteins.

## ORGANIC COMPOSITION OF FOSSILS

In fossil material, even of great age, recognizable fragments of these organic constituents are perserved. Proteins themselves may survive with their specific properties unchanged for 1,000 years (e.g., in the shell of *Mya arenaria*). In Pleistocene specimens of *Mercenaria mercenaria*, 1 to 5 percent of the peptide bonds are broken ($10^4$—$10^5$ years), giving more soluble protein fragments; in Miocene specimens all the peptide links are broken and only amino acids remain (1). Amino acids vary in their stability toward oxygen and temperature, only the more stable ones tending to be preserved in fossils. The more commonly found amino acids are alanine, glycine, glutamic acid, leucene, isoleucene, proline, valene, aspartic acid. These occur in *Atrypa reticularis* (LINNÉ) (Wenlock Sh.), *Spirifer* sp. (Carb. Ls.) and in *Plectothyris fimbria* (SOWERBY) (Jur.) (17), also (except proline) in *Plaesiomys (Dinorthis) subquadrata* (HALL & CLARKE (Ord.) (2) (Table 3).

Organic materials to some extent may accumulate in fossils by perfusion from the surrounding sedimentary rock. *Linoproductus* sp. contained all the amino acids that were present in its containing matrix of Carboniferous Limestone, but had a higher concentration of them and in addition contained several amino acids not found in the limestone matrix (17) (Table 3). The *Linoproductus* shell contained 0.5 micromoles ($\mu$M) amino acids per gram fossil; the limestone matrix contained 0.3 $\mu$M amino acids per gram.

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# EVOLUTION AND PHYLOGENY

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The chronology of morphological changes that represent evolution of the brachiopod shell can be really assessed only by comparative studies of continuous series of interrelated assemblages from given segments of the geological column. The opportunities for following the detailed course of even small skeletal alterations in this manner, however, are so reduced by the fortuitous nature of the geological record that nearly all statements on brachiopod evolution are inferential. They involve either deductive interpolations between the alleged end products of lineages (17, 46), or an inductive evaluation of the disparity between unrelated contemporary stocks (2). Both methods are attempts to estimate the drift away from common ancestry. The former approach is likely to lead to the identification of a more immediate relationship and tends to give a sense of continuous incremental change in features of minor taxonomic importance. The latter is generally concerned with more remote affinities and, more often than not, appears to reveal the sudden introduction or elimination of morphological features with great systematic weight. These apparent differences in the importance, as well as the pace, of morphological changes have led to a belief that they reflect varying scales of evolution. In fact, as the study of any well-documented group shows, the taxonomic importance of a feature is normally a function of the number of species to which it became common. Moreover, although no one doubts that evolution can proceed at greatly varying rates, all morphological discontinuities must ultimately be due to breaks in the geological record and are more likely to be met within the search for the common ancestry of independent stocks which, unlike the study of lineages, cannot be conducted selectively according to the completeness of the record.

Many fallacies can therefore arise from reviewing brachiopod evolution on such fragmentary evidence as we now have and within a classificatory framework which is at best an uneasy compromise with those evolutionary processes that are known to have affected the phylum. Nonetheless, it is still possible not only to demonstrate the repetitive nature of evolution but also to give some indication of the complex morphological and inferred anatomical changes that led to the emergence of the several major groups within the phylum.

It is symptomatic of the long and rich history of the brachiopods that few morphological features of the shell are unique to a particular stock. Such convergences vary from the repetition of one character, like the superposition of costation on finely costellate shells of *Orthis* and *Nikiforovaena*, to faithful mimicries of a complex of characters involving the entire external appearance of the shell (5, 7). Indeed, homeomorphy of this sort is so rife that when it is attended by a convergent likeness of internal characters as well, as in *Pionodema* and *Doleroides* (8), real difficulties are encountered in dissociating one stock from another. The repetitive appearance of internal features was also widespread throughout the phylum. Many of them are admittedly only analogous. The spread of denticles along the hinge lines of stropheodontids and possibly of the chonetacean *Eodevonaria*, for example, differs from that affecting the hinge lines of some plectambonitaceans in that it was preceded by fusion of the dental plates with the secondary shell of the interareas. In all three groups however, the denticles arose well within the secondary layer and were built up about taleolae, in contrast to those of the spiriferoids which were fashioned mainly from the primary shell layer. Other features are clearly homologous. Thus, no distinction can at present be drawn between the endopunctation of the enteletaceans and of the terebratulids, retziaceans, and many spiriferoids, which almost certainly arose in the last three groups independently of the first.

The extent to which the diversity of one group anticipated or repeated the trends in other groups is well illustrated by members of the Orthida. Insofar as the complex of stocks comprising this order probably was ancestral to all articulate brachiopods, some variation leading to morphological resemblances with the primitive antecedents of other later groups is to be expected. Yet the order also includes extinct lineages, clearly divorced from the main flow of descent, but foreshadowing to a remarkable degree many characteristics of the later phases in the evolution of the articulate brachiopods.

The modal orthoid shape includes a subquadrate outline, a biconvex profile, and a sulcate anterior commissure with well-developed interareas and hinge lines, but modifications in the first three attributes led to the strophomenacean appearance of *Cyrtonotella* and *Valcourea* and the spiriferacean habit of *Platystrophia*, while the pronounced emargination of *Dicoelosia* is suggestive of the trends that resulted in the emergence of the terebratulacean *Pygope*. The elongation of the ventral interarea is seen in the hesperorthids and skenidiids but was greatly exaggerated in the clitambonitaceans, which look like some later davidsoniaceans, and again in the triplesiacean *Onychotreta* which is very like the terebratuloid *Terebrirostra* (42). The interareas of *Productorthis*, in contrast, were sufficiently vestigial to persuade early students of the phylum, like Pander, that this lower Ordovician stock was a productid which, like its supposed relatives, also lacked a pedicle; whereas the reduction of both hinge lines and interareas, as in *Perditocardinia* and *Cyclocoelia*, anticipated the nonstrophic condition typical of the rostrate terebratuloids. Such trends were commonly accompanied by subtle changes in ornamentation that enhanced the homeomorphic properties of the stocks. The radial ornamentation of *Valcourea*, with its strong development of intercalated costellae, is fine enough to be mistaken for the parvicostellate condition of strophomenoids; and the lamellose and coarsely costellate condition of *Productorthis* recalls the exterior of *Reticulatia.* Strongly overlapping lamellae are especially characteristic of the glyptorthids and the spinose prolongations of *Spinorthis* are homologous with those of the atrypacean *Spinatrypa* and the rhynchonellacean *Tegulorhynchia.* Both the pseudodeltidium and the open delthyrium are typical of the orthids; but it is significant that, before the group became extinct, deltidial plates, which must have grown in the same way as those characteristic of rhynchonellid, terebratulid, and spiriferid shells, appeared independently in *Barbarorthis* and *Phragmophora.*

The internal characters also underwent changes that were echoed by contemporary or later stocks. The spondylia of the protorthids, skenidiids, and clitambonitaceans were developed independently of one another and of those diagnostic of the pentameraceans and later porambonitaceans; while the septate, muscle-bearing structure in the pedicle valve of *Parenteletes* is no different in function or origin from the meristinid shoe-lifter process. The pseudopunctate gonambonitaceans, which are only on balance assigned to the Orthida, include *Antigonambonites,* with a denticulate hinge line comparable with that of the spiriferids. The appearance of a cardinal process on the notothyrial platform, first as a median partition to segregate the dorsal ends of the diductor muscles which were later accommodated by the differentiation of the partition into a bilobed to trilobed myophore, with shaft, was a trend parallel with those that led to the elaboration and diversification of the strophomenoid cardinal processes. The orthid mantle canal systems show every conceivable variation achieved in later stocks, from the primitive saccate condition (e.g., *Billingsella*) to the advanced pinnate (e.g., *Clitambonites*) and apocopate (e.g., *Dolerorthis*) arrangements (Fig. 139). Finally, it is noteworthy that the brachiophores of a number of orthids were sufficiently prolonged to act as supports to the lophophore in the manner of crura. These processes are, for example, rodlike in *Skenidioides* and broad and bladelike in *Laticrura*, reminiscent respectively of the radulifer and falcifer crura of the rhynchonellaceans. In *Tropidoleptus*, apophyses from the brachiophores joined with outgrowths from a dorsal median septum to form a loop which, in certain aspects of growth, was like that of the terebratellaceans and must also have given support to the lophophore.

With the exception then of certain features, like the internally communicating hollow spines of productaceans and the rhynchonellacean *Acanthothiris,* or the calcareous spires of spiriferoids and the strophomenacean *Thecospira,* the morphological variability of the Orthida seems to have anticipated the diversity that arose during the subsequent evolution of the articulate brachiopods. There were, of course, recombinations of characters and changes in emphasis, both ontogenetic and phylogenetic, which produced new stocks. Such relationships are complex and the details of descent are still unknown, but the main paths of evolution can be traced with some confidence. Taxonomically the chief discontinuities in the morphological links from one group to another appear mostly at the superfamily or subordinal level. This classificatory aspect of evolutionary digression essentially reflects the systematic limit to which the procedure of assembling groups together by detailed morphological comparison can be taken. It may also have a more profound implication in being the taxonomic level at which successful neotenous changes become identifiable. Either way, it is convenient to take the superfamily as a basic unit for discussing the significance of evolutionary changes within the phylum.

One other aspect of evolution requires some comment before discussing the details of brachiopod phylogeny. It has long been known, if only through the remarkable geological record of *Lingula*, that some stocks are more persistent than others and that they are easily outnumbered by their short-lived relatives. This variability in longevity is, of course, a manifestation of the experimental nature of evolutionary processes and has been used by SIMPSON (35) as an index of evolutionary rates in the expectation that some quantitative comparisons can be made between phyla. Unfortunately, the raw data, whether they are species or genera, cannot be quantified with any degree of confidence (49). The known range of a stock is only as objective an estimate of its actual existence as hazards of the geological record will allow. Moreover, the subjective nature of taxonomic procedure frequently makes it difficult to distinguish "monographic" bursts (12) from real accelerations in evolutionary diversification. Consequently, no attempt has been made to calculate evolutionary rates for various brachiopod groups, although histograms (Fig. 140) have been prepared to show the incidence of extinct articulate and inarticulate genera according to their absolute ages in HOLMES' time scale (20). The details of these frequency distributions are obviously influenced by the estimated duration of systems and their major divisions, since generic ranges can only be expressed in terms of the grosser stratigraphic units. Nonetheless the distributions are of some value in that their positive skews reveal the clear preponderance of genera with relatively short ranges.

Representatives of all four orders of inarticulate brachiopods are present in the Lower Cambrian, but, as with the earliest known articulates, the Orthida, there is as yet inadequate information, on a worldwide basis, to comment on the sequence of appearance of the orders. Hence it is not known whether they were all independently derived from a remote common ancestor or whether there is a fundamental regularity in the succession of their appearance with one order arising from another. In the absence of chronological information, one is forced to rely solely on morphological comparison to assess affinities.

Two of the orders are represented in modern seas, the Lingulida by two and the Acrotretida by six or seven genera. Internally, these genera show many resemblances in their soft anatomy, as discussed elsewhere. In the musculature, for example, the posterior and anterior adductors of Recent Acrotretida may be homologized with the umbonal and central muscles of the lingulids. Indeed, there is more resemblance between the musculature in Recent members of these two orders (like *Lingula* and *Discinisca*) than between Cambrian representatives (e.g., *Linnarssonella* and *Lingulella*), an anomaly that must be a measure of convergence. Moreover, the known ontogenetic histories of living inarticulates are basically similar and probably the two orders were initially fairly closely related to each other, although no ancestral-descendent relationship between them can be postulated.

Less is known of the other two orders, Obolellida and Paterinida. The Obolellida had a relatively short existence, for they became extinct by the close of Middle Cambrian times. They differed from Cambrian members of the other three orders in having a calcareous shell. They also show a remarkable variation in the position of the pedicle opening, a character which is usually relatively stable within an order. In some genera, the pedicle either emerged between the valves or possibly atrophied; in others it passed through a foramen located apically or well forward of the apex of the pedicle valve (31). The musculature is not well known in detail, but seems to correspond with the basic pattern of the Lingulida and Acrotretida, with two sets of muscles so placed as to suggest homology with the posterior and anterior adductors. It appears probable that the Obolellida are related to these two orders, but all details of their phylogenetic position are quite unknown.

The Paterinida are even more problematic. They first appear in the Lower Cambrian and were long thought to be restricted to the Cambrian, but are now known to range as high as the Middle Ordovician (10). They resemble the majority of inarticulate brachiopods in having phosphatic shells and in lacking articulation between the valves; but what is considered to be the muscle pattern, although still incompletely known, is basically different from that of other inarticulates. All recognizable scars produce narrowly triangular tracks radiating from the beak of each valve, and it is not possible to homologize them with the anterior and posterior adductors of other inarticulate orders. The posterior margin of the Paterinida has some similarities with that of the kutorginaceans and the articulate billingsellaceans. In all three, a median gap separates the covers to the apical parts of the delthyrium and notothyrium, although this opening in the Paterinida may possibly be only analogous with that of the other two groups in which it definitely did not function as a pedicle foramen. The resemblance of *Paterina* to the protegulum of many brachiopods prompted several earlier writers (19, 34) to regard the stock as the an-

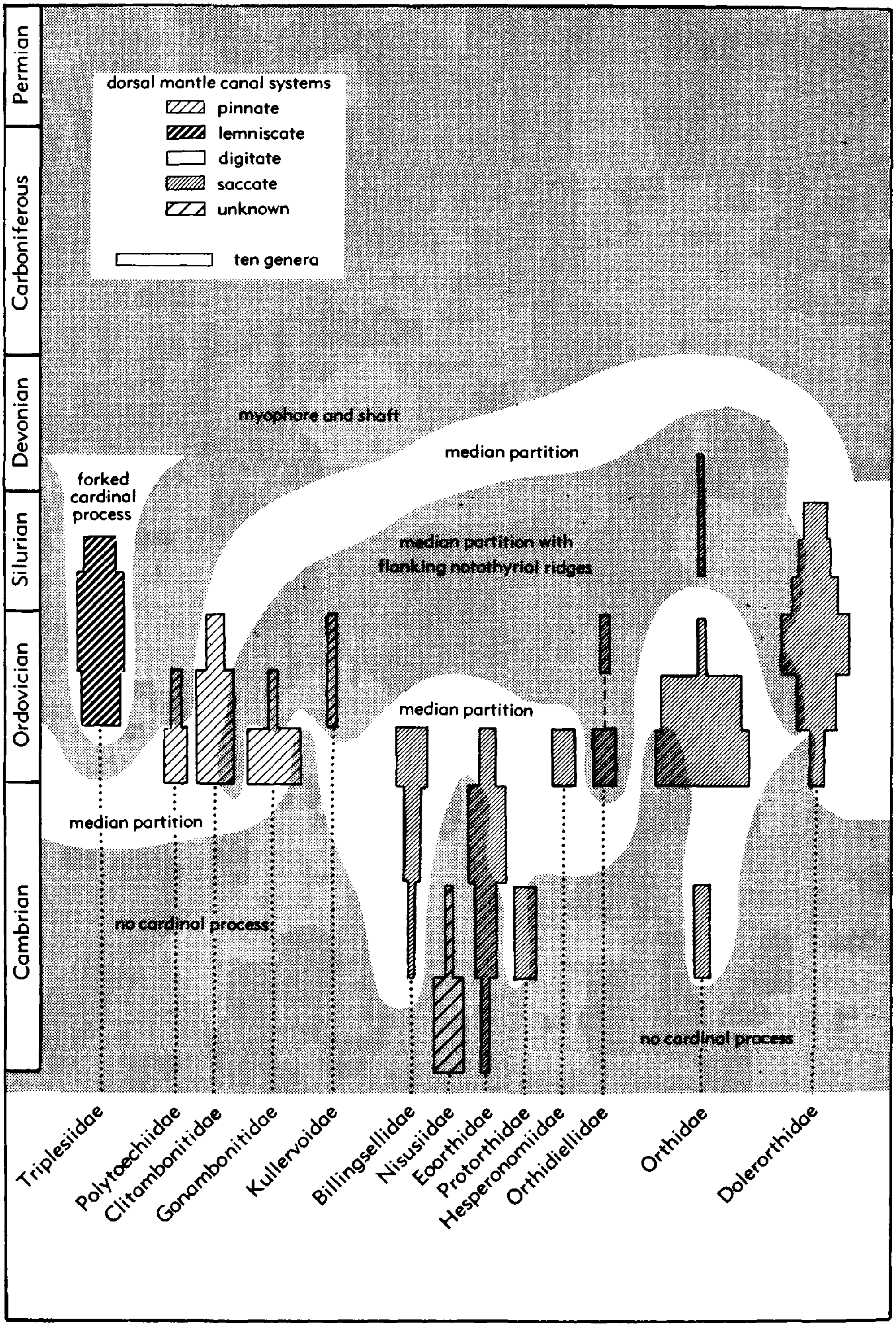

FIG. 139. Variation in cardinal process and dorsal mantle canal system in Orthida (54).

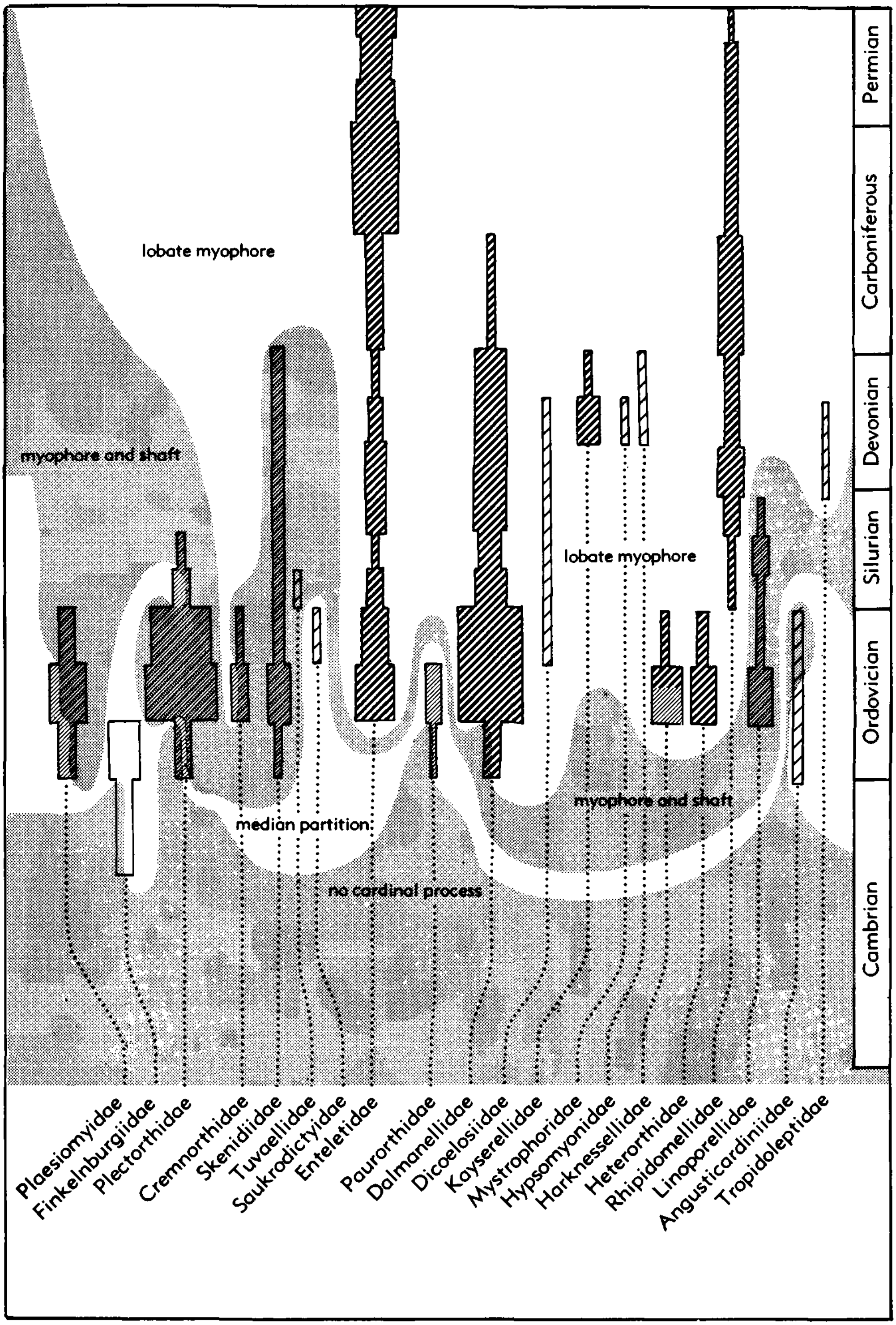

Fig. 139. *(Continued from facing page.)*

cestral radicle of the Brachiopoda. This relationship is unlikely because what is known of the paterinid internal markings precludes such a role.

The distinction between the Inarticulata and Articulata is also obscured by the existence of the Kutorginida, which, like the Paterinida, possess a conflicting assemblage of characters.

The kutorginaceans have been regarded as inarticulates by some students (18) and as early articulates by others (25), but on balance they do perhaps show greater similarities with the latter than the former. This likeness includes the calcareous nature of the shell, the variably developed cardinal areas, the pseudodeltidium with an apical or supra-apical foramen, and the postero-

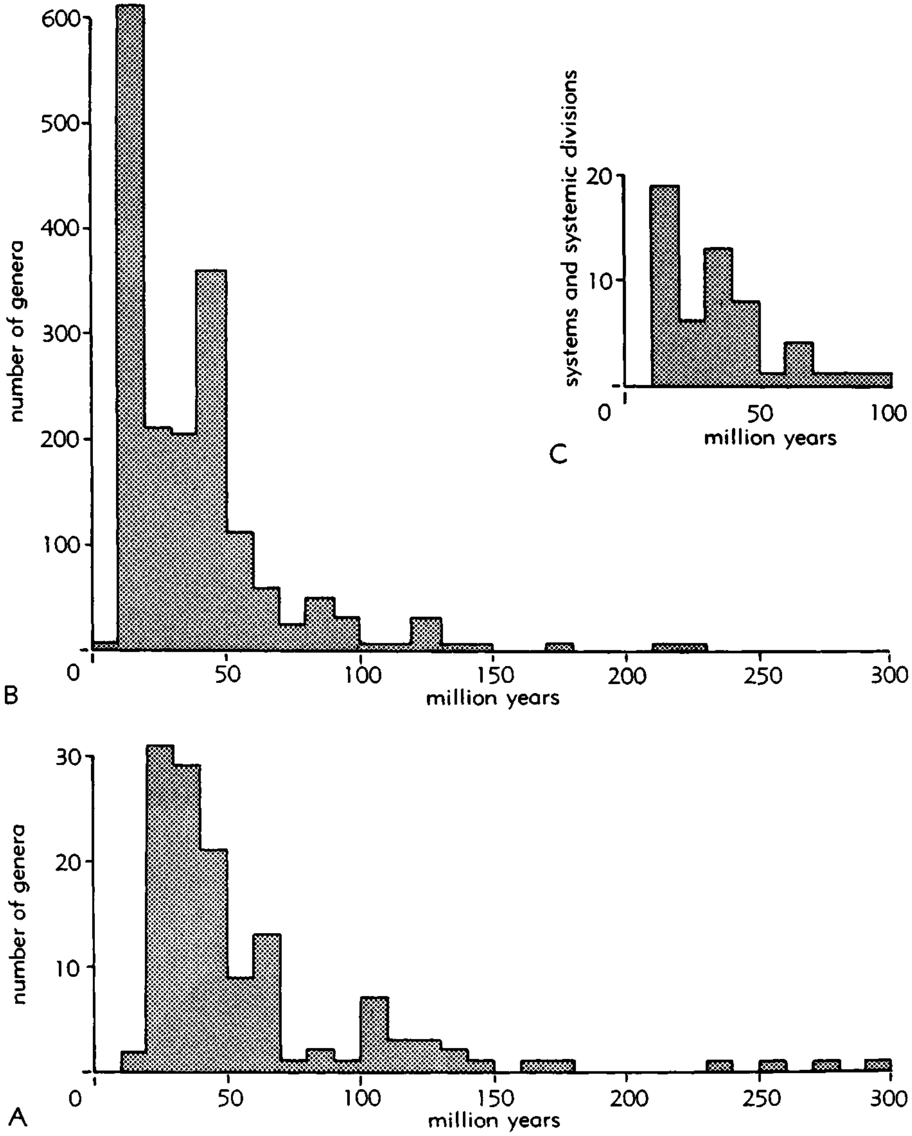

FIG. 140. Histograms representing frequency of *(A)* extinct inarticulate genera and *(B)* extinct articulate genera in stated segments of geologic time, and *(C)* absolute time-frequency distribution of post-Cambrian geologic periods and epoch divisions, showing that variations depicted in *A* and *B* mainly reflect estimated generic longevity in terms of geologic systems and series (54).

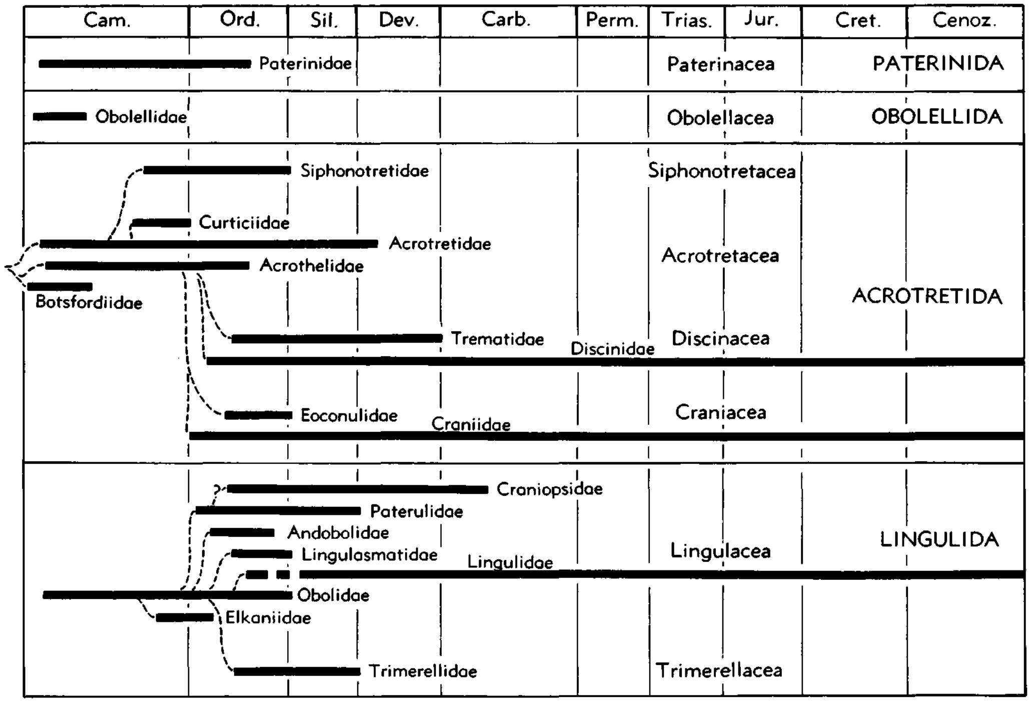

FIG. 141. Inferred relationships and approximate stratigraphic ranges of families in Inarticulata (53).

median location of the muscle scars. The inferred distribution of musculature and mantle canal systems, however, is difficult to reconcile with any categorical articulate organization.

An unusual modification of the pedicle valve characterizes the calcareous-shelled Dictyonellidina, a small group whose precise affinities are obscure and whose homogeneity is not beyond dispute. The group consists of the eichwaldiids and isogrammids, both of which bear a triangular opening extending anteriorly from the umbo of the pedicle valve. This opening is closed, except along the anterior side of the triangle, by a depressed plate fused with the remainder of the valve along the lateral margins of the triangular slot. The extreme similarity of this modification in both stocks suggests some degree of affinity between them rather than convergence. Although the eichwaldiids have been regarded as inarticulate brachiopods by some authors (18), the assemblage of characters possessed by the group, particularly by the later isogrammids [Dictyonellidina], which have a well-developed cardinal process and functional articulation, strongly suggests that they are articulate brachiopods with anomalous shell structure and pedicle opening.

Uncertainties, similar to those attending any inquiry into the affinities between inarticulate ordinal groups, also affect a review of evolutionary relationship within the groups, and are again due to significant gaps in the geological record, Indeed, so restricted are the obolellid and paterinid records that only the Acrotretida and the Lingulida afford any evidence of evolutionary processes (Fig. 141).

By early Cambrian times the Acrotretida were already represented by three well-established stocks, two of which (acrothelids and botsfordiids) are morphologically alike. The principal difference between these stocks is that the pedicle emerged through a triangular delthyrium which remained open in adult botsfordiids but, in adult acrothelids, was confined to a foramen at or slightly posterior of the apex by the growth of a pseudointerarea or an undifferentiated posterior margin. The fact that the botsfordiids are, on the whole, older suggests that they may have been the ancestral stock from which the acrothelids were derived by acquisition of an entire margin. Further, if the Lower Ordovician *Orbithele* is a true acrothelid, a convergence toward morphology of the Orbiculoideinae later took place in the development of a small pedicle tube.

The precise relationship between the third stock, the acrotretids, and the acrothelids or botsfordiids is unknown. Yet the number of features in common suggests that they are related, because the early acrotretids differ importantly only in having a median pit or groove dividing the variably developed dorsal pseudointerarea into two propareas, and in having an internal thickening near the beak of the pedicle valve (apical process). In the evolution of later acrotretids, changes in the apical process, position of the pedicle foramen, and form of the dorsal pseudointerarea and median septum played an important part.

The Linnarssoniinae [Acrotretidae] were the most conservative stock in that the dorsal pseudointerarea and median ridge remained weakly developed, although a secondary loss of the apical process also took place in later forms, like *Opisthotreta*. The dorsal pseudointerarea of their later contemporaries, the Acrotretinae, on the other hand, were well developed throughout stock history and the dorsal median ridge was commonly expanded into a bladelike septum independently in many members. In this stock, the foramen remained apical or immediately posterior of the apex and the apical process was commonly strong, although, as in the Linnarssoniinae it was secondarily lost in some later species.

Despite the gaps in the post-Cambrian record, it is likely that the Acrotretinae were ancestral to most of the later acrotretids. The Ceratretinae [Acrotretidae], for example, probably arose from them during Late Cambrian times by the elaboration of the apical process into a buttress bearing the internal pedicle opening, and a concomitant dorsoposterior migration of the external foramen. The Scaphelasmatinae [Acrotretidae], first known in the Middle Ordovician, may, in turn, have been derived from the Ceratretinae, to which they bear a strong external resemblance, by reduction and eventual loss of the apical process. Alternatively, the Scaphelasmatinae diverged from Ordovician acrotretids by adopting the external form of the Ceratretinae. The isolated occurrences of the Torynelasmatinae and Ephippelasmatinae [both Acrotretidae] present similar problems concerning descent. Their derivation from the Acrotretinae would have involved the loss of the apical process, a familiar theme in acrotretid history (Fig. 142), and the obsolescence of the dorsal pseudointerarea in the Ephippelasmatinae, a return to the condition typical of the Linnarssoniinae. The elaboration of the sporadically appearing acrotretid median septum reached its climax in the complex, saddle-shaped plate of the Ephippelasmatinae, which possibly represented the only successful trend towards a lophophore support among inarticulate brachiopods.

Curticiids, which are characterized by an open triangular delthyrium, show an interesting return to the botsfordiid condition. The musculature and pseudointerarea of young specimens, which have a closed pedicle foramen, are similar to those of the Acrotretinae, but during growth the constricting part of the ventral pseudointerarea was lost by dorsally directed resorption (32).

Relatively little is known about the origin of the siphonotretaceans. In this group, the pedicle foramen migrated anteriorly with growth of the shell and the track of the pedicle opening was closed to a variable extent by a plate or pedicle tube. Walcott (43) suggested that *Schizambon* developed from the obolellacean *Trematobolus*, but this appears most unlikely. Although the two genera are superficially alike, there are many differences, including shell composition, and it is probable that the elongate pedicle track, common to them both, is an example of homeomorphy (31). The majority of siphonotretaceans are spinose, but this feature probably developed subsequent to the emergence of the stock, because the Upper Cambrian *Dysoristus*, which in other respects seems to be closely related to *Schizambon*, is ornamented only by growth lines. The dorsal pseudointerarea of *Dysoristus* and the slightly younger *Helmersenia* shows some resemblance to the acrotretacean arrangement with a median pit separating the propareas; it is therefore possible that the

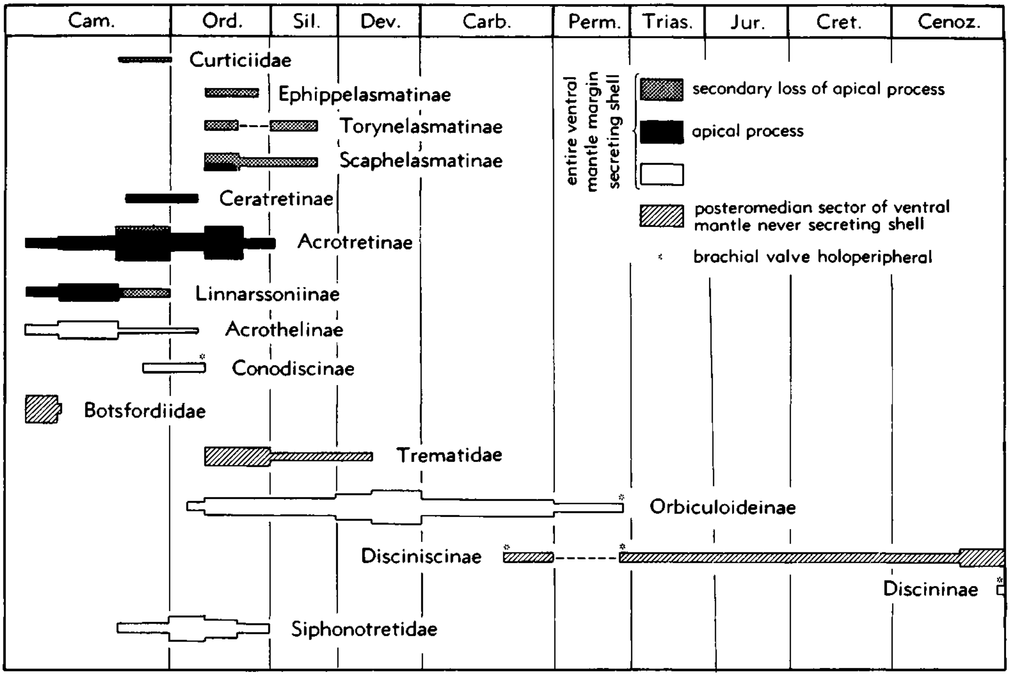

FIG. 142. Diagrammatic representation of evolutionary trends in Acrotretidina (53).

siphonotretaceans were derived from the acrotretaceans.

The discinaceans are first recorded from the Ordovician and, whereas it is almost certain that they arose from the acrotretaceans, it is also probable that the acrothelids were their ancestors (Fig. 141). Early in the history of the group two stocks were developed, which probably remained quite distinct from each other during their subsequent evolution. The trematids, in the manner of most acrotretaceans, retained a marginal beak in the brachial valve; but the pedicle emerged through a triangular opening which breached the posterior margin of the circular to subcircular pedicle valve in all stages of growth, and the only constriction of the opening resulted from the growth of the listrium at its apex (Fig. 142). In the discinids, which also appeared in the Ordovician, the dorsal marginal beak was lost, for the growth of the brachial valve was holoperipheral. Moreover, the pedicle opening of the earliest members, the Orbiculoideinae, became closed by an entire posterior margin in the adult shell, and the listrium was commonly elaborated to form a posterodorsally directed pedicle tube. Later discinids, the Disciniscinae, which must have descended from the Orbiculoideinae, show a reversion to the trematid condition in the pedicle valve because the pedicle opening intersected the posterior margin throughout life and a pedicle tube never developed from the listrium. Only living members of the third discinid stock, the Discininae, are known. The geological record indicates that they must have been derived from the Disciniscinae, with which they share an unmodified listrium, but they resemble the Orbiculoideinae in possessing a pedicle track that extends only a limited distance down the posterior slope of the pedicle valve.

The origin of the last group assigned to the Acrotretida, the Craniidina, is rather obscure; but it appears probable that they arose from either the acrothelids or the discinaceans, admittedly by fundamental changes in their physiology and soft anatomy. The majority of the craniaceans belong to a homogeneous stock, the craniids, characterized by calcareous, punctate shells and the lack of a pedicle in all known growth stages.

Apart from changes in surface ornament and the distribution of mantle canals and to a lesser extent musculature, the only common modification, which may have been repeated during stock history, was the development of the limbus in those forms which were free-living or attached only by the apical region of the pedicle valve. The phosphatic-shelled eoconulids resemble the craniids in the holoperipheral growth of the brachial valve, and the inferred cemented habit of the pedicle valve. Their shell composition suggests that they were more primitive than the craniids, although their rare occurrence at about the same time as early craniids may indicate an aberrant line of descent from a common ancestor.

The Lingulida, like the Acrotretida, were also represented in the Lower Cambrian by stocks that were sufficiently differentiated to imply either a substantial previous history or a rapid evolution. These early obolids possessed a deep pedicle groove separating the ventral propareas and a conspicuous dorsal pseudointerarea. They were probably ancestral to both the paterulids and the elkaniids. The latter stock developed a posteromedian thickening in both valves by the coalescence of oblique lamellae. The former was characterized by a limbus in both valves and a greatly reduced pedicle notch in the pedicle valve; exceptionally, as in *Lingulops*, a low muscle platform is found in both valves, a recurrent trend in many groups assigned to the order. It is possible that the craniopsids arose out of the paterulids especially by the acquisition of a calcareous shell. Three other small groups evolved from the main obolid stock during Ordovician times, the spinose *Acanthambonia*, *Andobolus* with its very high, bifid dorsal muscle platform valve, and *Lingulasma* which possessed a dorsal muscle platform supported by a high median septum as well as a ventral one.

The Lingulidae, which certainly occur in the Silurian but are also reported from the Ordovician, were derived from the Obolidae by the obsolescence of the pseudointerareas in both valves. It is, however, unknown whether they descended directly from the Lingulellinae [Obolidae], or whether the Glossellinae [Obolidae] constitute an intermediate stage in which only the dorsal pseudointerarea was reduced. The Lingulidae have been very stable throughout their history. Many Recent species show a remarkable resemblance to some of their Silurian ancestors, and the stock has formed the dominant element of post-Paleozoic inarticulate brachiopod faunas.

The trimerellaceans are first recorded from the Middle Ordovician and appear to have become extinct by the end of the Silurian. They display an unusual combination of important features in having a calcareous shell with a primitive form of articulation (29) and in probably lacking a pedicle. It is much more likely that they were descended from the main obolid stock than from other contemporary Lingulida, although it is evident that their emergence was due to major physiological and morphological changes. It is significant, for example, that early species had a typical obolid outline and profile, but low muscle platforms had already developed internally. During their subsequent history the shells commonly became obese and the muscle platforms, which were correspondingly high, became deeply excavated.

The earliest known articulate brachiopods are Lower Cambrian representatives of the billingsellaceans *(Nisusia, Eoconcha, Matutella)* and orthaceans *(Eoorthis)*. Allowing for the inadequacies of the geological record, it is a moot point which group is stratigraphically older. Much more important (9) is the undeniable evidence that the pseudodeltidium and chilidium are at least as old as the open delthyrium and notothyrium, and, from anatomical considerations, are even likely to have been the more primitive condition, so that initially it was the loss and *not* the growth of delthyrial and notothyrial covers that represented a significant evolutionary step away from the articulate ancestral archetype. These features, therefore, together with the impunctate shell, the flat-lying socket ridges and the variably developed cardinal process consisting of a median partition on the notothyrial platform, constituted the basic ingredients of billingsellacean morphology; and despite the lack of transitional forms, it is likely that six groups of Ordovician brachiopods, which were also equipped with a pseudodeltidium, were derived from such a radicle.

Two of these groups, the triplesiaceans

and clitambonitaceans, retained an impunctate shell but diverged principally by the acquisition of a forked cardinal process and a spondylium, respectively. The differentiation of the triplesiacean cardinal process was accompanied by a reduction of the dorsal interarea and some elaboration of the socket ridges (52) but without a rotation into the orthacean attitude, except in *Epacroplecia*. Some of the trends that affected the group before its extinction in Late Silurian times included an elongation of the ventral interarea *(Onychotreta)*, a reversal of the modal uniplicate condition *(Brachymimulus)*, and the development of an asymmetrical twist to the shell *(Streptis)*.

The clitambonitoids have been exhaustively studied by Öpik (30), and perhaps the most obvious general development in the clitambonitaceans, apart from the spondylium, was the pinnate mantle canal systems in both valves. One of the more tantalizing problems in reviewing clitambonitoid relationships is that of the affinities of the gonambonitaceans, which are regarded as being closely related to the clitambonitaceans. It is, however, significant that the shell substance is pseudopunctate and the spondylium a "triplex" rather than a "simplex" structure; and in view of certain other features, like the development of an incipient bilobed cardinal process in *Antigonambonites* and the impersistent rugation of *Raunites*, it may prove that the group was closer to the strophomenoids and only convergent toward the clitambonitaceans. One further comment remains to be made about the clitambonitoids. The delthyria and notothyria of the Atelelasmatinae [Clitambonitidae] and Anomalorthinae [Gonambonitidae] are open, but whether this lack of pseudodeltidium and chilidium involved any basic anatomical modification like that inferred for the orthaceans is unknown.

The three remaining Ordovician groups, which are assumed to have arisen from the billingsellaceans, also show a curious anomaly in shell composition. For two of them (plectambonitaceans, strophomenaceans) it is reasonable to visualize a common ancestor differing from the billingsellacean prototype in being concavo-convex and in possessing a parvicostellate ornamentation and a pseudopunctate shell. The earliest known davidsoniaceans (mid-Ordovician *Gacella* and *Fardenia*) are, however, impunctate and biconvex; and although they appear to have typical strophomenacean interiors, especially in the presence of a well-developed bilobed cardinal process, they could well represent an independent but convergent line of descent.

The divergence between the plectambonitaceans and strophomenaceans [Strophomenida] may be illustrated by differences in their cardinal processes. The plectambonitacean arrangement, stripped of its many variations, was essentially derived by an elaboration of the median partition on the notothyrial platform, whereas the bilobed strophomenacean process came into being by the forward and posterior growth of the areas flanking a median partition that underwent atrophy. Trends in both groups included the atrophy of the pedicle in adult shells of several stocks. This loss was precursory to cementation of the pedicle valve in the strophomenaceans *Liljevallia* and *Leptaenisca* and to the development of perforations through the ventral interarea of the plectambonitacean *Eochonetes*, which presumably contained anchoring strands of epithelium. Other trends among the plectambonitaceans include the spread of denticles along the hinge lines of independent stocks (e.g., Plectambonitinae, sowerbyellids) and the growth of lophophore platforms among the leptellinids and, later, among sowerbyellids by the coalescence and elevation of spinelike septules disposed in arcs. Indeed, the lophophore platform is so distinctively plectambonitacean that the similarly equipped *Christiania*, with its strophomenacean bilobed cardinal process, poses a systematic dilemma. It may well represent an aberrant line of descent independent of both groups, especially since the stock appears to have developed a pseudopunctate shell somewhat later than its inception (36).

The most widespread changes affecting the strophomenaceans involved repeated resupination and geniculation, and among the stropheodontids these were superimposed on a series of heterochronous parallel trends related to the loss of the pedicle and the spread of denticles along the hinge lines. Such trends included the fusion (and resultant loss of identity) of both the pseudodeltidium and chilidium with their containing interareas and the atrophy of the socket ridges or their realigned growth as ancillary struts to the cardinal process (46). As is to be expected in dorsoventrally compressed shells, elevations of secondary shell for the attachment of muscle bases were rarely developed (like the "pseudospondylium" of *Douvillina* and *Leptagonia*), and no true spondylium is known.

In spite of the problematic origin of the davidsoniaceans [Strophomenida], the group itself was sufficiently homogeneous to be traced without any profound break into the Permian. The earliest indications of pseudopunctation are at present found in some of the early Devonian stocks (e.g., *Schellwienella, Davidsonia*), and there seems to be little doubt that the condition was a late characteristic of the group (48). THOMAS (41) has also reported punctation in Permian species of *Streptorhynchus*, but it has yet to be confirmed whether this condition is strictly comparable with the endopunctation of the Enteletacea or Terebratulida. A few trends are noteworthy. The adult pedicle was lost and the foramen sealed before the end of the Ordovician, as in species of *Fardenia*. A secondary attachment by cementation of the ventral beak, however, became prevalent during the Devonian Period, and was later attended by a gross elongation of the pedicle valve in some forms like the Permian *Meekella*. Internally, the two most significant changes affected the dental plates which became either obsolescent and disappeared, as in the schuchertellids, or exaggerated and even convergent so as to form a spondylium *(Perigeyerella)*. In most stocks it seems unlikely that the socket plates were well enough developed to give support to the lophophore, although impressions of a spirolophe, disposed in the plane of commissure, are preserved in the shell of davidsoniids. In the Triassic stock *Thecospira,* however, a pair of calcareous spires gave support to the lophophore. Each apparently was suspended from the cardinal process by a short apophysis, an arrangement quite different from the crural support found in the Spiriferida, but one to be expected in an aberrant davidsoniacean.

The remaining post-Ordovician pseudopunctate groups, with exception of the oldhaminoids, appear to have identifiable antecedents. MUIR-WOOD (26), in reviewing origin of the chonetoids, has referred to the possibility that the group is polyphyletic. The bulk of the stocks are feasibly derived from a generalized form, in many respects comparable with the earliest known chonetoid *Strophochonetes*. Its basic characters probably included a smooth to costellate, concavo-convex shell with perforations along the ventral interarea, which may have been continuous with external spines, and a functional pedicle in at least the early growth stages. Internally there was a ventral median septum and a more variable dorsal one which may have been flanked by lateral septa; also present is a cardinal process variably lobate in ventral and posterior aspects, probably derived by longitudinal cleavage of an arched median outgrowth (comparable with the sowerbyellid arrangement) with or without lateral subsidiary ridges. All these attributes became manifest during plectambonitacean evolution. *Eochonetes*, for example, has a perforate ventral interarea, and although its decisively sowerbyelline interior militates against a role as an ancestral stock, it is highly likely that a paedomorphic introduction of such perforations in Aegiromeninae [Sowerbyellidae], such as in *Chonetoidea*, provided the link. The Devonian *Chonostrophia*, on the other hand, with a resupinate shell bearing an unequally parvicostellate ornamentation and distinctive musculature, may have been derived from the strophomenaceans (26).

Once established, the chonetoids did not undergo any spectacular change. The daviesiellids were affected by gross increases in size and thickness of the pedicle valve but the genera assigned to the family may represent the end products of a series of convergences rather than closely related stocks (26). Variation also occurred in the development of the dorsal septa and in the disposition and growth of the spines external to the ventral perforations; the repeated loss and acquisition of radial ornamentation are also noteworthy.

The origins of the productoids have been reviewed by MUIR-WOOD & COOPER (27). They concluded that the strophomenacean *Leptaenisca*, with cemented pedicle valve, simple teeth and socket ridges, bilobed cardinal process, and spirally disposed brachial ridges, conforms most satisfactorily to the inferred ancestral type. The two features indicative of a trend away from the orthodox strophomenoids toward the nascent productoids, are, of course, the ventral attachment of the shell by cementation and the brachial ridges, neither of which is unique to *Leptaenisca.* Brachial ridges occur in the Leptodontellinae [Stropheodontidae] and the problematic davidsoniacean *Irboskites*; and the cementing habit was achieved by the stropheodontid *Liljevallia* and contemporary davidsoniaceans (e.g., *Schuchertella, Irboskites*). These occurrences show how new characters can arise in a number of independent stocks and at opportune moments in evolution and in appropriate combinations can contribute toward the establishment of an entirely new group involving, in the case of productoids, the paedomorphic acquisition of spines.

Subsequent to their introduction, the productoids underwent what is probably the most prolific diversification in the brachiopod phylum, giving rise to an unprecedented number of bizarre stocks. By Early Devonian time the two principal antecedents to the strophalosiaceans and productaceans, *Devonalosia* and *Spinulicosta*, respectively, had appeared (27). Both are concavo-convex with small teeth and sockets and a modified bilobed cardinal process. But the spines, which are rare on the brachial valve of *Spinulicosta* and absent from that of *Devonalosia*, were already acquiring specialized functions, because, in addition to protective recumbent spines present in both, steadying spines were as characteristic of the former stock as were clasping spines of the latter. Both interareas (together with pseudodeltidium) were moreover present in *Devonalosia* but were obsolescent in *Spinulicosta.* These differences foreshadowed the divergent paths of strophalosiacean and productacean evolution.

Strophalosiaceans remained fixed throughout adult life by clasping and attachment spines, and they tended to retain primitive features like the interareas which were rarely absent from both valves, as in *Spyridiophora.* The teeth and sockets also persisted in the strophalosiids, and in *Ctenalosia,* a series of small cones with complementary sockets were proliferated along the hinge line to simulate denticulation.

The most spectacular trends within the strophalosiaceans [Productidina] were undoubtedly those involving the disproportionate growth of the pedicle valve. Umbonal lengthening was attended by a gross extension of the ventral interarea, as in the aulostegids with a medially raised elytridium simulating the pseudodeltidium, and in the scacchinellids, in which repeated deposition of cystose plates concomitantly reduced the shell space. Among teguliferinids and richthofeniaceans, the pedicle valves grew like cones which were attached apically, and the brachial valves relatively reduced to function as a lid commonly sunk well within the periphery of the pedicle valve.

Productaceans [Productidina] may have been fixed as spats by ringlike attachment spines or by cementation of the ventral beak but were detached for most of their lives. This free sedentary habit was successfully maintained by trends toward redistributions of spines into dense, symmetrical clusters (e.g., *Peniculauris*) or to their reduction to a few strong symmetrically placed ones (e.g., *Muirwoodia*). In respect of other features, the modifications of strophomenid morphology found in *Spinulicosta* were carried to a conclusion. Reduced interareas (with pseudodeltidium and chilidium) survived only in the Productellidae and Kansuellinae, although secondary structures simulating them (ginglymus) were rarely developed (e.g., *Reticulatia*). Similarly, teeth and sockets persisted only in the productellids, and even in that group were weak and not invariably present. The bilobed cardinal process, in contrast, underwent a series of changes that were convergent toward conditions prevalent in the chonetaceans. In general, as can be seen in the leioproductids, the submedian sides of the lobes became adjacent and incompletely fused to form a trilobed structure. Further modifications involved the lengthening or shortening of the shaft, and a dorsal rotation of the myophore, as well as an accentuation of the median crest, as in the dictyoclostids. The climax to this last trend is found in *Striatifera* and *Titanaria*, in which the lateral boundaries to the process atrophied, and the attachment areas were located on a median crest continuous with the dorsal median ridge, recalling the arrangement in certain orthoids.

The precise affinities of the oldhaminoids [Oldhaminidina], the last group which is inequivocally related to the pseudopunctate stocks just discussed, constitute a major problem in determining the pattern of descent among articulate brachiopods. Speculation on oldhaminoid ancestry is further complicated by the possibility that the dorsal part of the shell may have consisted of a vestigial brachial valve and a very much larger plate of secondary shell which acted as an internal supporting plate to a schizolophous or ptycholophous lophophore (38, 45). Assuming, however, that this condition, if it existed, arose paedomorphically, a number of features, other than pseudopunctation, indicate its strophomenid ancestry. Thus the earliest-recorded oldhaminoid, *Poikilosakos*, possesses a nonspinose cemented pedicle valve, which extends well beyond the limits of the "brachial valve" in all directions and lacks a true cardinal area, although secondary "teeth" are present and the weak cardinal process is distinctly bilobed. Taken in isolation, these characteristics are not conclusively diagnostic, but collectively they suggest a productoid ancestry in general and a richthofeniacean one in particular. The lack of spines does detract somewhat from this inferred derivation. But, when the unique growth relationships between the valves are considered, it can be appreciated that the stock came into being only after a fundamental anatomical reorganization had taken place in which the loss of spines would have been a minor event. FREDERIKS (16) believed that the oldhaminoids were descended from the marginiferids, but his chief reason for doing so was to account for the bilobation of the "brachial valve" which seems to be less important than other features.

During their brief recorded existence throughout Pennsylvanian and Permian times, many novel shapes were assumed by the oldhaminoids, dependent upon the extent to which the pedicle valve was attached. Internal changes involving the asymmetrical development of the ventral muscle impressions also took place. The most conspicuous trend, however, was an increase in the lobation of the "brachial valve," and a complementary development of ridges or septa in the pedicle valve, which were either normal to, and more or less symmetrical about the median plane, or less commonly subparallel with the median incision.

In comparison with the articulate brachiopods already discussed, the most important difference displayed by the earliest known eoorthids [Orthida], like *Wimanella*, is the open delthyrium. This condition was typical of all Cambrian and the great majority of younger orthaceans and enteletaceans, although, as in orthidiellid *Trematorthis*, dolerorthid *Barbarorthis*, plaesiomyids *Campylorthis* and *Valcaurea*, tuvaellid *Tuvaella*, and kayserellid *Phragmophora*, deltidial covers were secreted in a number of independent stocks. A further change, with implications of an equally profound anatomical reorganization, was introduced soon after the inception of the group. The ventral boundaries of the sockets in the eoorthids and *Protorthis* are flat-lying ridges; but by mid-Cambrian time, in the protorthid *Arctohedra* and the orthids *Bohemiella* and *Oligomys*, they had undergone a rotation toward the median plane. In this attitude, which is typical of the orthaceans and enteletaceans, the brachiophores became elongated in a ventral direction and were commonly equipped with processes. As unsupported rods or blades, like those of the orthids and dolerorthids respectively, it is unlikely that their functions were very different from those of the billingsellacean socket ridges. In Upper Cambrian finkelnburgiids, however, the brachiophores were supported by bases reaching to the floor of the valve, and the sockets were normally defined by fulcral plates. This arrangement is characteristic of the plectorthids, cremnorthids, skenidiids, and Evenkininae [Plaesiomyidae] (an independent derivation from the plaesiomyid pattern) and dominant in the enteletaceans. In some of these stocks the brachiophores were sufficiently prolonged to have acted as supports for the lophophore.

Such changes as these indicate the close affinities that existed between the orthaceans and enteletaceans and there seems little reason to doubt that the latter arose out of the former by the acquisition of an endopunctate shell. Indeed, judging from the many morphological differences between the orthid-like Paurorthidae, the nearly rostrate Angusticardiniidae, and the remaining endopunctate stocks with advanced cardinalia, it is possible that the enteletacean group was polyphyletic.

Other trends affecting the orthaceans and enteletaceans have been referred to in the introduction to this chapter; but those leading to the diversification of the cardinal process and mantle canal systems are noteworthy (Fig. 139).

The cardinal process is absent or rudimentary in the eoorthids and also in early members of many other stocks, including enteletaceans (e.g., *Paurorthis*), orthids (e.g., *Poramborthis*), dolerorthids (e.g., *Lepidorthis*) and finkelnburgiids (e.g., *Diparelasma*). Once established as a median partition, however, it became the seat of attachment for the medially migrating diductor muscle bases in the plectorthids and later plaesiomyids and thereby differentiated into myophore and shaft. Further elaboration occurred in the enteletaceans, which led, for example, to the formation of a trilobed process. The trilobed process is also found rarely among the orthaceans, but that of the orthidiellids at least was differently derived by the posterior growth of the notothyrial ridges flanking a high median plate, a style that is reminiscent of primitive strophomenaceans.

The basic patterns of the orthacean mantle canal systems are more primitive in some respects than those of the billingsellaceans because the saccate arrangement prevailed in both valves not only in the eoorthids but even in relatively late stocks such as the plaesiomyids, plectorthids, many orthids, and paurorthids. More advanced patterns, involving an enlargement of the gonocoels and a redistribution of the peripheral canals, were developed independently in many orthaceans. Thus the dorsal systems were digitate in the hesperonomiids and orthidiellids, and digitate to apocopate in the dolerorthids. In the finkelnburgiids both canal systems were digitate and in the enteletaceans dominantly lemniscate.

In summary, it may be remarked that the history of the orthaceans is sufficiently well known to illustrate the evolutionary processes of parallelism, convergence, and uneven progress of character changes within the group, so that advanced and primitive features combine to characterize various stocks (Fig. 139).

The Pentamerida form a homogeneous group of such modest variation and range that the main trends contributing to its evolution are obvious. Taxonomically, the principal feature for identification of the group is the spondylium, but this structure was a relatively late development. Indeed, judging from the Cambrian porambonitaceans (e.g., *Cambrotrophia*), the chief difference from orthacean contemporaries, with which they shared an open delthyrium, discrete dental plates, and rudimentary brachiophores, was the presence of a dorsal fold. Thereafter, a series of changes progressing at varying rates in different stocks became evident.

Discrete dental plates survive as a feature of some Ordovician stocks (e.g., *Xenelasma, Stenocamera*, *Lycophoria*, *Porambonites*). Yet by Late Cambrian time, every stage from a pseudospondylium to a spondylium simplex had been attained by the huenellids and clarkellids. The spondylium simplex was a dominant feature of many Ordovician porambonitaceans, as was the so-called "spondylium duplex" of the parastrophinids and the great majority of pentameraceans. Only the free spondylium of *Holorhynchus*, recalling that of the orthacean *Protorthis*, represented any noteworthy departure.

The rudimentary brachiophores of the ancestral stocks also underwent orderly transformation. By Late Cambrian time they had become well defined, flanked by small fulcral plates, and with their bases (brachiophore plates) reaching to the floor of the brachial valve, and disposed either divergently (e.g., *Mesonomia*, early clarkiids) or convergently (e.g., *Plectotrophia*). With rare exceptions (e.g., *Porambonites*), convergent brachiophore bases, either contributing to or associated with a dorsal median septum, became the dominant arrangement of the younger porambonitaceans. Such a structure has mistakenly been called a "cruralium" but it never enclosed the dorsal adductor bases of porambonitaceans. The pentameracean cardinalia in general differs from that of the porambonitaceans only in being better developed. Hence the homologues of the brachiophores probably gave support to the lophophore in all pentameracean stocks, compared with only a few late porambonitaceans (e.g., camerellids, parastrophinids). Moreover, although the homologues of the brachiophore bases were mainly discrete (e.g., *Pentamerus*), they also converged to form a true cruralium (e.g., *Pentameroides*), and even underwent atrophy as in the stricklandiids (4, 44) and the virgianids. The climax to this trend in improvement of the brachiophores as devices for the support of the lophophore is represented by the growth of a calcareous loop from the ends of the crura of *Enantiosphen* (50). This stock, which was without issue, did not contribute to the evolution of the articulate brachiopods, but the development of its loop was nonetheless a striking repetition of those processes that resulted in the establishment of the spiriferid and terebratulid calcareous supports.

Some of the changes that affected the pentamerid exterior also merit mention. The dorsal fold and ventral sulcus, although variably expressed, were always characteristic of the porambonitaceans but of only a minority of pentameraceans (e.g., *Barrandina*, *Clorinda*). Most pentameracean shells were either rectimarginate (e.g., Pentamerinae) or sulcate (e.g., *Gypidula*), and the difference between the two groups is an added reason for supposing that the Mid-Ordovician parallelelasmatids are really porambonitaceans and *not* early pentameraceans. The change in outline, arising from the reduction of both interareas and hinge lines were typical of the early porambonitaceans, was more uniform. Later, porambonitaceans (e.g., camerellids, parastrophinids) and most pentameraceans became nonstrophic, although the stricklandiids and the pentamerids *Aliconchidium* and *Pleurodium* were strophic, possibly through a secondary growth of the cardinal area.

Consideration of the origin and descent of the Rhynchonellida, Terebratulida, and Spiriferida is essential to any discussion of brachiopod evolution, because members of the first two orders, along with the problematic thecideids, constitute the only articulates surviving today. It is, moreover, appropriate to review them together because there are many indications that they were originally closely related to one another. In some respects this affinity isolates them from other extinct stocks and suggests that, with appearance of the rhynchonellids (oldest and least specialized of the groups) articulate brachiopods attained a third phase of anatomical modification as fundamental as that which is believed to have taken place during the derivation of the orthaceans from the billingsellaceans.

The oldest rhynchonellids yet recovered are the early Chazyan *Sphenorhynchia, Ancistrorhyncha, Dorytreta,* and *Rostricellula* (which is also known from the upper Llanvirn of Wales) and the late Chazyan *Oligorhynchia.* They are all sufficiently distinctive, not only from other contemporary groups but also from one another, to suggest that they had already diverged significantly from their presumed common ancestry. It is nonetheless profitable to enumerate the chief characteristics shared by this assorted lot. They include a rostrate impunctate shell with a vestigial to obsolescent ventral cardinal area, an open delthyrium which may be restricted by rudimentary deltidial plates, divergent dental plates supporting laterally set teeth, and sockets fashioned from fulcral plates and bounded by ridges which are separated from strong crura by outer hinge plates. The crural bases may be supported by plates convergent on to the floor of the brachial valve (e.g., *Oligorhynchia*) or on to a median septum (septalium of *Rostricellula*). In addition, *Rostricellula* is normally strongly uniplicate and *Ancistrorhyncha* less so, while *Dorytreta* and *Sphenotreta* are sulcate and *Oligorhynchia* intraplicate. Many of these features occur singly in contemporary orthaceans; but as a combination (excluding the sulcate anterior commissure and the rudimentary deltidial plates) they decisively reveal a porambonitacean ancestry. One can therefore think of the rhynchonellids as having been derived out of the porambonitaceans simply by a precocious development of crura and the elimination of any tendency to form a spondylium. The last factor may have been linked with a subtle but highly significant shift in the ventral seats of muscle attachment. For in *Rostricellula,* and all rhynchonellids, terebratulids, and spiriferids with well-preserved muscle impressions, the ventral adductor and diductor scars are well forward of the delthyrial cavity which accommodated the pedicle base. Such a redistribution distinguishes these three groups from all other articulate brachiopods. In Recent species it is an adult expression of mantle reversal which may therefore have become a feature of the embryonic development of articulate brachiopods only with the emergence of the rhynchonellids (51).

The Rhynchonellida are the most conservative group of articulate brachiopods, for they have survived to the present day with so few changes that the great majority of them, irrespective of their range, are instantly recognizable. Traces of cardinal areas persist only in certain Ordovician stocks (e.g., *Orthorhynchula, Orthorhynchuloides, Drepanorhyncha*), thereafter an exaggerated secondary expansion of posterior margins was confined to a few Triassic forms (e.g., *Dimerella, Halorella*). The most significant deviations were the appearance of endopunctation in the short-lived *Rhynchopora* and the acquisition of a spondylium "duplex" and a camarophorium by the stenoscismataceans. Neither of these is likely to signify polyphyly, and the only other indication of a disruptive change within the group seems to have been the neotenous advent of the dimerellids.

The essential stability of the group is reflected in both external and internal characteristics. A uniplicate commissure, normally associated with a well-developed dorsal fold and ventral sulcus, is the commonest condition of the shell, and its effects may be spectacularly exaggerated by a dimorphic segregation into high- and low-convexity species within closely related stocks, as in the Hebetoechiinae [Uncinulidae]. This arrangement, however, was repeatedly modified by reversals during growth, or by the retention or a later ventrally directed folding of the straight margins of the brephic shell. The rectimarginate commissure is found in some Orthorhynchulinae [Rhynchotrematidae], Uncinulidae (e.g., *Plethorhyncha, Uncinulus*), and Septalariinae [Camarotoechiidae] (e.g., *Pseudopugnax*). The sulcate condition is characteristic of *Sphenotreta* (a replacement of the dorsal sulcus by a fold took place in adult growth stages of *Dorytreta*), early Mesozoic dimerellids, and Recent Cryptoporidae and Basiolinae. An asymmetry in shell growth, like the more subdued manifestations in the triplesiaceans, also affected the stenoscismatacean *Camerisma* and some Mesozoic and Recent stock among the Dimerellidae, Cyclothyridinae, Basiolinae, and Erymnariidae.

Similarly, the fine to coarsely costate ornamentation, which is characteristic of the majority of rhynchonellids, was repeatedly suppressed at various stages of growth in a number of independent stocks. The commoner modifications entailed the persistence of the smooth condition of the brephic shell throughout adult growth as in the dimerellids *Rhynchonellina* and *Norella*, the basiliolid *Basiliola*, and some species of the camerophoriacean *Psilocamara*; or a variable delay in the onset of radial ornamentation during growth of the shell, which is especially characteristic of the Rhynchonellidae. More rarely, as in the Camarotoechiinae, the costae became obsolescent and died away in the late phases of shell enlargement.

The principal internal changes, apart from the growth of the stenoscismatacean spondylium and camarophorium, affected the cardinalia, because even the mantle canal systems seem to have been basically saccate with continual lemniscate elaborations (48). The crura certainly underwent a number of repeated modifications in their attitude and morphology, the historical consequences of which have still to be studied. The cardinal process was less important than in other groups, because it appeared only sporadically during rhynchonellid evolution, yet its appearance frequently involved morphological repetition—the bilobed process, for example, is known among Devonian eatoniids, Rhaetic austrirhynchids, and the Eocene to Recent *Cryptopora*.

The earliest known member of the Spiriferida, the mid-Ordovician *Protozyga*, is essentially a loop-bearer, because in the older species, the homologues of the distal parts of the primary lamellae are commonly only a pair of apophyses extending from the anterolateral corners of a closed calcareous ribbon. Such a structure was formed by the median fusion of a pair of prongs growing forward from well-developed crura and, at this juncture in brachiopod history, was entirely novel. The shape of the loop and the small size of the early spire-bearers in comparison with contemporary articulate brachiopods (Fig. 143) suggest that the loop functioned as a support to the ringlike trocholophe typical of living juveniles. Other features, like obsolescence of cardinal areas, presence of incipient deltidial plates, well-defined primary and secondary layers of the impunctate shell, and arrangement of the cardinalia, are diagnostic of ancestry. Thus, when all aspects of its morphology are considered, *Protozyga* is reasonably interpreted to have been derived paedomorphically out of the Rhynchonellida (50). This development seems to have been the source of most, if not all, spiriferoid and terebratuloid evolution. Other Ordovician spire-bearers (e.g., *Zygospira, Hallina, Catazyga*) can certainly be attributed to the same common ancestor, although the spiralium of *Cyclospira*, which lacks a jugum at least in adult shells, may have grown as discrete calcareous ribbons during post-trocholophous stages of lophophore development, to support a spirolophe (48).

From these beginnings the spire-bearing brachiopods proliferated along a number of independent lines of descent during the Paleozoic and early Mesozoic with important changes in form and internal organization.

One of the striking distinctions maintained throughout the history of the Spiriferida was the obsolescence of cardinal areas in the atrypoids, retzioids and athyridoids in contrast to their retention among spiriferoids. The rostrate shell was typical of even the oldest known atrypoids, because rarely did either traces of interareas survive, as in *Catazyga*, or secondary, straight hinge lines grow, as in some Carinatininae [Atrypidae] and koninckinaceans. Strongly developed interareas and wide hinge lines were nonetheless characteristic of the earliest known spiriferoids, the eospiriferids, and delthyridids; and since these stocks first appeared toward the end of the Early Silurian, it is probable that their strophic condition was acquired during their derivation from a rostrate atrypoid. Subsequently, some reduction took place as in the reticulariids, but, more commonly, the ventral interarea was repeatedly lengthened in the hemipyramidal pedicle valves of the cyrtiids, cyrtinids, syringothyridids, cyrtospiriferids (e.g., *Syringospira*), etc.

Another feature stabilized in the spiriferoids was the strong dorsal fold (with complementary ventral sulcus) which was almost invariably present. In only a few stocks, like some ambocoeliids, the brachythyridid *Palaeochoristites*, elythids, and martiniids, did the dorsal fold tend to become weak and disappear. It was also common enough in the remaining spire-bearers, but was never dominant to the same extent, so that even among the most primitive stock, the zygospirids, every condition, from sulcate to uniplicate, prevailed.

Radial ornamentation showed a similar variation in constancy. The atrypoids were normally devoid of radial ornamentation and persistently so in some stocks like the dayiids and lissatrypids, although others (e.g., atrypids) varied from smooth to costellate. Stabilization, however, took place in the retzioids, which were costate to costellate, and also in the athyridoids, which may have been coarsely plicate, as in *Tetractinella*, but almost invariably lacked radial ornamentation. At first sight, the spiriferoids appear to vary greatly, in much the same way as the atrypids, from smooth (elythids and many martiniids) to costellate (exceptionally in the cyrtinids, commonly in the cyrtospiriferids, brachythyridids, etc.). Yet the earliest stocks to some extent were all very finely costellate or capillate, and the fact that traces of this primitive ornamentation have been found in all stocks suggests that the more conspicuous ornamentation, or lack of it, is a secondarily imposed feature.

The shell structure of the Spiriferida is normally impunctate, but, as in the Orthida, the endopunctate condition was commonly attained. Indeed, the group provides very good evidence for both the acquisition and loss of caeca in independent stocks. Thus, the late Silurian to Permian retziaceans were persistently endopunctate, whereas the suessiaceans which first appeared in middle Silurian time, include certain early Mesozoic relatives (e.g., *Hirsutella, Suessia*) that are reputedly impunctate. Similarly the impunctate *Odontospirifer* and Licharewiinae [Syringothyrididae] appear to have arisen from the endopunctate spiriferinids and syringothyridids, respectively; and the su-

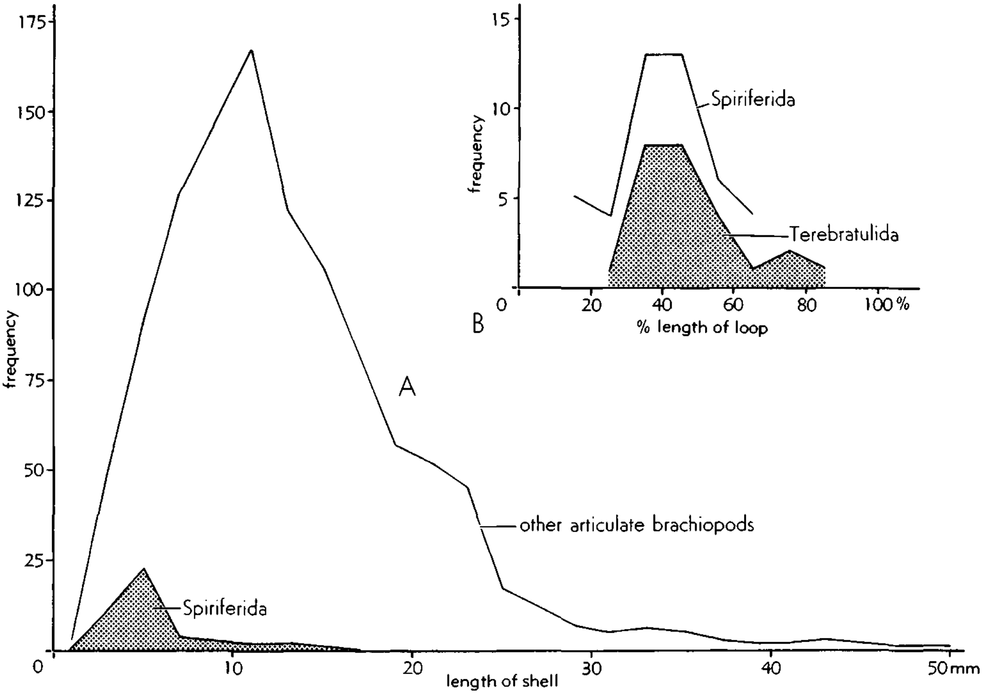

FIG. 143. *A*, Frequency distribution of longest pedicle valves recorded in type descriptions of 46 Ordovician spiriferid species (shaded area) and of 1, 113 other contemporary species of articulate brachiopods (unshaded area). *B*, Frequency distribution of lengths of "loops" (measured from dorsal umbones to posterior edges of transverse bands and juga) relative to length of brachial valves in Silurian and Devonian genera of terebratulids (25) (shaded area) and spiriferids (45) (unshaded area) (50).

perficial pits of the martiniids may be the relics of impersistent caeca.

The spiriferid interior is dominated by the spiralia, which may be disposed at any angle to the median plane of symmetry. Yet, as RUDWICK (33) has pointed out, there are actually a limited number of basic attitudes, only one of which tends to be consistently adopted within an established group, although, as one would expect, all are found in the earliest stocks. The orientations, assumed by the spiralia of *Protozyga* and *Zygospira*, for example, are different enough to have been the sources of all subsequent evolution. In the former, the umbonal blades and at least part of the primary lamellae were aligned parallel with the median plane; in the latter, they were deflected to be more or less normal to the median plane. The zygospirid pattern was probably the model from which all atrypid attitudes were derived by the dorsal or dorsomedian extension of the spires, and also the prototype for the dayiacean spires, which were elaborated by lateral or ventral extension. In most members of the retzioids, athyridoids, and spiriferoids, the umbonal blades and primary lamellae were retained more or less parallel with the median plane, as in *Protozyga*, and the spires extended laterally. Reversions toward the basic zygospirid condition did take place in some younger stocks (e.g., cyrtinids, koninckinaceans) by rotation of the umbonal blades toward the commissural plane. The continued growth of processes from the jugal stem also led to the development of accessory lamellae co-extensive with the primary spiralia in the Devonian Anoplothecinae [Anoplothecidae] (e.g., *Bifida*) and again in the Triassic Diplospirellinae [Athyrididae] and koninckinaceans. But the most astonishing change seems to have affected the leptocoeliids, because no spiralia have ever been seen in any member of this stock, not even in some 200 well-preserved specimens of *Eocoelia* sectioned by Nikiforova (28). Hence, it is possible that the lophophores of leptocoeliids were without the intricate calcareous support of other Spiriferida.

The cardinalia of the Spiriferida were only selectively modified during the evolution of the group. Among the more primitive atrypoid stocks, the cardinalia were usually divided or disjunct and consisted of socket ridges and variably disposed crural plates, which rarely converged to form a septalium in the Septatrypinae [Lissatrypidae], with or without intervening strips of outer hinge plates. Inner hinge plates, becoming conjunct, were developed in a number of independent stocks (e.g., the atrypids *Alispira* and *Gruenewaldtia,* some lissatrypids, and the early dayiacean *Cyclospira*). In most spiriferoids the unspecialized divided cardinalia prevailed, with repeated atrophy or forward growth of the crural plates, because only in spiriferaceans like *Dimegelasma* were the inner hinge plates conspicuously developed. Among the retzioids and athyridoids, on the other hand, the cardinalia not only included conjunct inner hinge plates, but were also consolidated to form a strong cardinal plate. This structure was supported by crural plates in the retzioids, while among the athyridoids it became imperforate (as in the meristellids) and was further elaborated by extravagant forward growth so that it varied from the enlarged concave trough, typical of the meristellids, to the high, recurved plate of the nucleospirids.

Other important internal changes, which were mainly concerned with accommodating the muscle bases, took place only sporadically but did result in the appearance of some unusual structures. The commonest was the growth of a ventral median septum, which was strongly developed in certain spiriferoids (e.g., delthyridids) and is known to have borne muscles in at least the spiriferinids. The tichorhinum of the cyrtinids and a transverse plate of the suessiids, each of which was an outgrowth along the posterior edge of a high median septum, probably received the bases and musculature of pedicles, as did the variably developed syrinx suspended beneath the delthyrial plate of the syringothyridids. True spondylia were rare and included the simplex type found in the reticulariid *Bojothyris* and a structure in *Camarophorella* which simulated the spondylium triplex. In general, the ventral muscle bases of the atrypoids and athyridoids were inserted on the floor of the valve, and any changes in this arrangement involved the secretion of a platform rather than a septum. Thus the muscle bases were accommodated on a solid platform in *Septatrypa* or on a platform supported by septa in *Gruenewaldtia*; but in the dayiacean *Aulidospira* and again in the meristinids, the shoe-lifter process appeared.

Elevated muscle-bearing structures were rarely secreted in the brachial valves. The crural plates were greatly extended in the ambocoeliids and provided a cruralium which was either sessile (e.g., *Metaplasia*) or elevated on a septum (e.g., *Prosserella*). Similar arrangements also occurred in the Meristellinae [Meristellidae] (e.g., *Charionoides*) and suessiaceans (e.g., *Suessia*), but the most unusual structures were the dorsal homologues of the shoe-lifter process which were developed in the brachial valves of the athyridaceans *Dicamara* and *Camarophorinella.*

The Terebratulida are the youngest ordinal group to emerge during evolution of the Brachiopoda, because the earliest known representatives like the stringocephalaceans *Podolella, Mutationella,* and *Brachyzyga* (22) do not appear until the end of Silurian times. In respect of their origin, their most important features include a rostrate, endopunctate shell with variably developed deltidial plates and hinge plates which may unite medially to complete a cardinal plate, well-defined crural processes, and a loop. The loops varied greatly in outline, even within a single species of *Mutationella,* and partly they anticipated the diversity of shapes that were ultimately characteristic of the younger, more stable, Devonian stocks (6). Despite the paucity of information on ontogenetic development of these loops, it can be safely assumed that they were formed by processes of secretion and resorption from a simple, lanceolate centronelliform loop, which is common to the early growth stages of *Cranaena* (37) and *Dielasma* (3). The centronelliform loop is identical with that found in young *Zygospira* shells (3) and is strictly homologous with the *Protozyga* apparatus. It must therefore have given support to a trocholophe or a schizolophe, with the generative zones disposed contiguously about a median plate whenever that structure developed (48). In adult *Rensselandia, Centronella*, and the majority of *Mutationella*, etc., this fundamental lanceolate pattern was retained. A more important modification, however, was manifest in many stocks like *Cranaena*, *Dielasma*, and a minority of adult *Mutationella.* It was brought about by resorption of the anteromedian part of the centronelliform loop and refashioning of the corroded connection into a transverse, posteriorly curved band making acute angles with the descending branches. This transformation must have been closely comparable with the definition of the spiriferid jugum, and there can be little doubt that those portions of the terebratulid and spiriferid apparatuses lying posteriorly to the band and jugum, respectively, were identical in origin. Even in adult shells the "loops" thus defined by transverse bands, and juga are similar in proportion (Fig. 143).

The terebratulid loop, then, was probably derived from the spiriferid brachial skeleton simply by a suppression of the growth of the calcareous spires. Moreover, since the development of spires was preceded by the secretion of a loop, it may be assumed that the earliest terebratulids were small generalized shells of pre-Ludlow age, barely distinguishable from the juveniles of contemporary, endopunctate, rostrate retzioids with cardinal plates, from which group they were probably neotenously descended (50).

The loop has so dominated the terebratulid interior and has undergone so many complex changes, ontogenetically as well as phylogenetically, that its modification has come to be regarded as the epitome of terebratulid evolution. Certainly the initial diversity and instability of primitive terebratulid loops and the ultimate survival of only the short, terebratulacean and the long, terebratellacean types are classic illustrations of radiation and selection (7). Thus it may be confidently inferred that the retention of an enlarged centronelliform loop which had undergone only minor alterations in shape (e.g., in adult *Rensselandia, Centronella*, etc.) signified the persistence of a trocholophe or early schizolophe, but that the differentiation of a transverse band in the dielasmatids, for example, indicated the beginnings of plectolophous side arms (48). Indeed, Stehli (37) has maintained that there is a direct line of descent from early Devonian, short-looped stocks, like the dielasmatids and cranaenids, to modern terebratulaceans. This phylogenetic link would have incurred little more than the suppression of the lanceolate shape of the first-formed loop of terebratulaceans and in later stocks (e.g., *Terebratulina*) an exaggerated growth of the crural processes so that they tended to meet medially, thereby completing a calcareous ring for lophophore support.

The development and disposition of the short loops characteristic of the terebratuloids have remained remarkably stable throughout time, although some gross changes did occur in the late Paleozoic. In *Centronelloidea* (40), for example, a pair of projections grew anteriorly from the junctions of the descending branches with the transverse band and presumably gave support to the side arms of a plectolophe, as did similar projections in the Lower Devonian stringocephalacean *Cimicinella.* A more profound change found in *Gefonia* and *Timorina* (37, 39) involved the retention in adult shells of a modified centronelliform loop bearing a pair of long divergent processes. The arrangement is unique and, if the generative tips of the lophophore had migrated out of the median plane along with the growing points of the calcareous processes, represented an unsuccessful trend towards the re-establishment of a spirolophous attitude by the lophophore.

The adult loop of a number of Triassic genera (e.g., *Cubanithyris, Nucleatula*) was also typically centronelliform with a ventrally directed plate medially disposed on the echmidium. In *Wittenburgella*, however, this plate extended both ventral and dorsal of the echmidium (12b): and in young *Rhaetina* the dorsal extension is known (12a, 12c) to have united with the floor of the brachial valve, although with further growth the entire vertical plate was resorbed and the echmidium transformed into the transverse band of the adult dielasmatid loop.

Long-looped terebratulids are also found in the Lower Devonian but their relationships with terebratellaceans are more controversial.

It is generally agreed that not all stringocephalaceans equipped with long loops that probably supported a plectolophe were directly related to the terebratellaceans. The side arms of *Cimicinella*, for example, must have been strengthened by a pair of long processes that grew in place of discrete descending and ascending branches, while the medially coiled part of the *Meganteris* lophophore must have been contained between slightly convergent processes originating from the crura. The long slender loop of *Cryptonella*, however, is strikingly like that of Recent terebratellaceans such as *Macandrevia*. Hence STEHLI (37) has concluded that the cryptonellids were the ultimate ancestors from which all zeilleriaceans and terebratellaceans were derived, and that the nature of the foramen tends to confirm these inferred relationships.

Further study of Paleozoic terebratulids is required to test the feasibility of this interpretation. As ELLIOTT (13, 15) has pointed out, the first-formed calcareous support for the terebratellacean lophophore has always included a dorsal median septum or pillar upon which the later development of other parts of the apparatus is dependent. Nothing is known of the ontogeny of the cryptonellid loop, although it may well have arisen simply by differential anterolateral growth of a short dielasma-like loop (48). In fact, COOPER (11) has shown that even growth of the loop of late Carboniferous *Cryptacanthia*, which included the differentiation of a hood, did not involve the secretion of any septal support. STEHLI (37) has invoked paedomorphism to account for the part played by the median septum in the growth of the terebratellacean loop, and has referred to the discovery by MUIR-WOOD (24) of a connecting band attached to the descending branch of a young *Digonella*, to support his thesis of the descent of the terebratellaceans from the cryptonellids through the zeilleriaceans. This band, however, was not attached to the median septum, and although it may have been a remnant of connections that existed in earlier growth stages, it does not necessarily indicate a metamorphosis related to that of the true terebratellacean loop. As for paedomorphism, it is well to remember that a plectolophe is normally developed in living terebratulides, irrespective of the nature of the supporting loop, because the generative tips are maintained in the median plane throughout growth (50). Hence, if a plectolophe were to develop, any elaboration of a calcareous apparatus following the insertion of a median septum between the contiguous tips of a trocholophe must include complex processes of differential growth and resorption similar to those affecting terebratellacean loops. Yet the earliest stages in the development of the descending branches up to their fusion with the median septum are the same for both terebratulaceans and terebratellaceans. It is, therefore, even possible that the terebratellaceans arose out of some short-looped stock which was characterized by a slight dorsal shift of the tropholophe and the early and accelerated growth of a median septum and the descending branches.

The phylogenetic importance of the zeilleriaceans has yet to be assessed because even the homogeneity of the group is not beyond dispute. Thus DAGIS (12a, 12c) in his study of the ontogeny of the Triassic *Zeilleria moisseievi* failed to find any connection between the loop and median septum, although the loop of the smallest specimen, about 5 mm. long, differed greatly from its adult form. It consisted of broad descending lamellae, fused together anteriorly and bearing a hood in which the elements of wide ascending branches, connected posteriorly by a narrower transverse band, were already discernible. The subsequent growth and resorption of the loop recall characters of *Cryptacanthia*, and earlier development of the loop leading to definition of the hood (although as yet unknown) may also have been comparable. Furthermore, BABANOVA (1a) has recently described some stages of loop development in three species which she has referred to *Aulacothyris*, a genus which is commonly placed in the zeilleriids. These specimens displayed the characteristic stages of dallinid loop ontogeny, however, and she concluded that *Aulacothyris* should be reassigned to this family. Until more is known of the loop development of genera placed in the Zeilleriidae, the possibility of incorrect familial assignments cannot be ignored and it may be premature to attach too much importance to the presence of connecting bands between the loop and median septum unless a substantial part of the ontogeny is also known.

Whatever the origin of the terebratellaceans, a series of distinct trends affected the metamorphoses and phylogeny of their loops and were due to variations in the rate of growth of the descending branches and in the style of supports arising from the median septum.

In the dallinids, which include the earliest terebratellaceans yet found, the descending branches have always developed early to unite with the sides of a septum that, even in this growth stage, normally bears a hood in the process of differentiation. In the later-appearing terebratellids, on the other hand, the descending branches become ankylosed to outgrowths from the septum and the crest of the ascending branches is fashioned out of a ring, not a hood. In both stocks, the culmination of a series of changes which involve the resorption of the septal support and connecting bands, gives freely hanging recurved loops, although during the proliferation of generic stocks, development was arrested at any stage to provide a variety of adult loops. The most interesting of such retardations were those that gave rise to late Cretaceous *Megathyris*, with its attached loop consisting exclusively of descending branches and supporting a lobate trocholophe, and post-Cretaceous *Platidia,* with its short loop and short discrete ascending branches supporting a schizolophe. Indeed, in both these stocks neotenous effects seem to become increasingly important in Recent times, because the trocholophe of the megathyridid *Gwynia* is unsupported and the brachial valve bears only traces of an attached loop, while the schizolophe of the platidiid *Amphithyris* is supported solely by a median septum.

Neotenous simplification of the adult brachial apparatus has also affected the kraussinids, which first appeared in early Tertiary time out of the terebratellids. In contrast to other terebratellaceans, the descending branches developed later than the septal ring to form an attached loop (as in *Megerlia*) or did not develop at all (as in Recent *Pumilus*), in which the schizolophe is supported by only a low septum bearing a pair of divergent projections. Clearly, the morphology of Recent stocks like *Gwynia, Amphithyris,* and *Pumilus* has become so generalized through neotenous influences that profound internal changes are possible in the future.

In respect of other features, the evolution of the Terebratulida seems to have been as conservative as that of the Rhynchonellida. Trends that led to gross changes in form of the shell of other groups also affected the terebratulids but were, on the whole, rare. The commonest were those that repeatedly gave rise to the intricate folding of the anterior commissure. Rarer changes include asymmetrical growth, which tended to be characteristic of the stringocephalids, deepening emargination that became incorporated as a subcentral hole through pygopid shells by anteromedian union of the shell lobes during subsequent growth; likewise rare is elongation of the ventral umbo (e.g., *Terebrirostra*) and growth of wide hinge lines (e.g., *Antigoniarcula, Megathiris*). Internally, the loss of dental plates in several independent lines of descent, such as later terebratulaceans and the terebratellids, and the less common elaboration of the cardinal process, as in *Stringocephalus* and *Eudesia*, are noteworthy. More important internal changes, however, which included some striking examples of similar, heterochronous trends (STELHI, 775, p. 196) affected the cardinalia; and, in general, led to the elimination of the cardinal and crural plates so typical of the older stocks.

Any discussion on the origin of the Thecideidina is, at present, compromised by an abundance of imperfectly known or understood facts about living, as well as extinct, species. From its first appearance in the Triassic, the group has been so distinctive morphologically that there has never been much doubt about its homogeneity, but a great deal about its relationship with other contemporary articulate brachiopods. Even more disconcerting are the inconsistencies and obscurities in the only detailed studies ever carried out on the development and anatomy of living *Lacazella* (21, 23). In all thecideaceans, the loss of the pedicle has been accompanied by a growth of the ventral interarea as one piece continuous across the delthyrial region. The median part between the teeth may be gently arched into what is described as a pseudodeltidium, although it is commonly nothing more than a bulge accommodating the high dorsal surface of the cardinal process. Yet nothing is known of the epithelial relationships along the hinge except those inferred by WILLIAMS (47).

KOVALEVSKIY's account of the development of *Lacazella mediterranea* is incomplete and ambiguous. It does indicate that a pedicle rudiment is formed in the larval stages but he asserts that the rudiment of the ventral mantle undergoes atrophy and that ventral shell is first secreted on the dorsal side of the thoracic segment. This is the "third shell" of BEECHER, which was believed by him to be a discrete piece, representing the adult pseudodeltidium and fusing only later with the true pedicle valve. KOVALEVSKIY's diagram showing this stage of development, however, is a longitudinal median profile and, as ARBER (1) has pointed out, does not preclude the so-called "third shell" from being simply a stage in the secretion of a pedicle valve that is continuous around a ringlike mantle rudiment without any ventral lobular extension. Indeed, the three most important facts to emerge from KOVALEVSKIY's description of *Lacazella* embryology are: first, the larval commissural plane divides the mantle rudiment so much more obliquely than in other modern articulates that its posterior trace is entirely dorsal of the pedicle rudiment. Secondly, the pedicle rudiment is supra-apical; and thirdly, only the dorsal segment of the original mantle rudiment undergoes reversal. Excluding the related *Thecidellina,* such characteristics as these are not manifest, as far as is known, in the development of any other living brachiopods; but they are reminiscent of certain phases in the inferred development of the Strophomenida (48). This similarity, however, is as likely to be an expression of convergence, due to independently attained obliquity of the commissural plane and loss of pedicle, as of affinity, and a survey of thecideacean morphology tends to promote the candidature of other groups as possible ancestors to the thecideaceans.

It is generally agreed that thecideacean antecedents are to be sought among articulate groups existing during Permo-Triassic times. Of these, only the Rhynchonellida and the last remnants of the Orthida can be immediately dismissed as unlikely sources, because the thecideaceans have much in common with members of the other orders then extant, *viz.*, the Strophomenida, Spiriferida, and Terebratulida. The loss of the pedicle, the acquisition of a cemented habit, and the development of a strong, wide ventral interarea continuous with the delthyrial cover, are recurrent themes in brachiopod history and are not only typical of late davidsoniaceans and chonetoids but also of some suessiaceans like *Thecocyrtella.* The thecideacean shell is well differentiated into primary and secondary layers, as in the Spiriferida and Terebratulida. It is also endopunctate (14), yet strongly tuberculate internally in a manner suggestive of pseudopunctation. The tubercles, however, also compare closely with those occurring sporadically in *Megerlina* (47), and, in general, the shell structure is more like that of the Spiriferida and Terebratulida than of the Strophomenida.

Internally, the development of posterolateral adductor muscles is unique, but the growth of ridges to support the lophophore has occurred repeatedly in the brachial valve of articulate brachiopods during their evolution. KOZLOWSKI (22) figured an instructive comparison between the arrangement of the lophophore supports of *Lacazella* and *Thecidella* and similarly disposed ridges in the plectambonitacean *Plectodonta.* The partially attached loop of *Megathyris* is another noteworthy homologue, which, moreover, bears an expanded trocholophe with a single row of filaments as in the lobate lophophore supported by the thecideacean apparatus. Such supports as these evidently arise paedomorphically and do not necessarily signify any close relationship. The cardinalia and associated structures, on the other hand, are less equivocal. The thecideacean cardinal process is not an independent outgrowth from the dorsal posterior margin but a single plate formed by the exaggerated posteromedian growth of the inner socket ridges; while the brachial bridge represents the median fusion of processes projecting inwardly from short crura that, in early growth stages at least, are seen to arise from the inner surfaces of the socket ridges. None of these features are found in the Strophomenida but all of them commonly occur together in the Spiriferida and Terebratulida.

The organization of the ventral interior is not very helpful in search for thecideacean antecedents, although the presence of strong teeth suggests that productoids and oldhaminoids need not be seriously considered. In all, even the remaining pseudopunctate groups, the chonetoids and davidsoniaceans, seem less likely to have been the source of the thecideaceans than the terebratelloids or suessiaceans.

The principal changes affecting thecideaceans during their existence led to the elaboration of the apparatus supporting the lophophore, which seems to have taken place independently and heterochronously in a number of stocks (14). The simplest arrangement involved the coalescence of submarginal tubercles and the growth of septa to form a strongly bilobed structure, commonly closed posteriorly by the median fusion of the crural processes. The development of brachial ridges was also common, as well as subsidiary infolds of each lobe, which were either aligned more or less with the median axis, as in *Lacazella* and *Eudesella*, or radially disposed (*Thecidiopsis*). This variation in pattern must have been accompanied by an identical infolding of a basically bilobed lophophore, which, despite such complications, probably never bore a double row of filaments.

The most significant aspect of any outline of brachiopod history, like the one given above, is the complexity of the inferred relationships within the phylum. Admittedly some complications are attributable to incompleteness of the geological record and an imperfect understanding of shell morphology. Yet the inescapable conclusion remains that the confusing intricacies of the general evolutionary design are mostly expressions of the repeated intervention of the same trends during the development of several stocks. The elaboration of muscle-bearing platforms is a good example of how progressive specialization of this sort contributed to the morphological diversity of many groups, because in varying degree it affected every articulate order, as well as the Lingulida. These recurrent trends, dramatic as they are, have nonetheless tended to obscure the more fundamental changes that contributed to the cumulative morphological drift away from the generalized organization of the earliest stocks. Indeed, when such trends are set aside, it appears that the most profound shifts were the consequence of changes in shell composition, pedicle accommodation, and muscle distribution, and of the introduction of articulation and skeletal supports for the lophophore.

The most important change in the shell composition of fossil brachiopods was that which led to the distinction between shells in which the inorganic content was dominantly either a calcium phosphate salt or calcium carbonate (Fig. 144). It is probably equally significant that the very much higher proportion of organic material in the phosphatic shells of living species contains chitin, which is absent even from the periostracum of modern calcareous shells, and it seems reasonable to assume that this relationship always obtained. Although both shell types occur together in the Lower Cambrian, the chitinophosphatic condition may well represent the more primitive state from which the earliest calcareous-shelled groups, the obolellaceans and billingsellaceans, evolved. This change, which seems to have been irreversible, certainly took place in several stocks during the Ordovician, because (like the relationship between the calcareous craniids and the chitinophosphatic Acrotretina) craniopsids and trimelleraceans can be accounted for only by assuming an independent derivation from the Lingulida.

Despite the polyphyletic origin of the calcareous shell, a subtle differentiation of its structure took place during derivation of the articulate brachiopods, which isolates them from other groups with a similar shell composition. The secondary layer of the articulates has always been secreted intracellularly, at least at the mantle edge, whereas a fibrous secondary shell is unknown among the inarticulates, except for the craniids, where it always has been impersistent and confined to the migratory regions of muscle attachment.

The differences between the endopunctate, pseudopunctate, and impunctate stocks are less important to the main progress of evolution than the attention they have attracted would suggest, because the first two were polyphyletically derived from impunctate ancestors. Indeed, the stabilization of

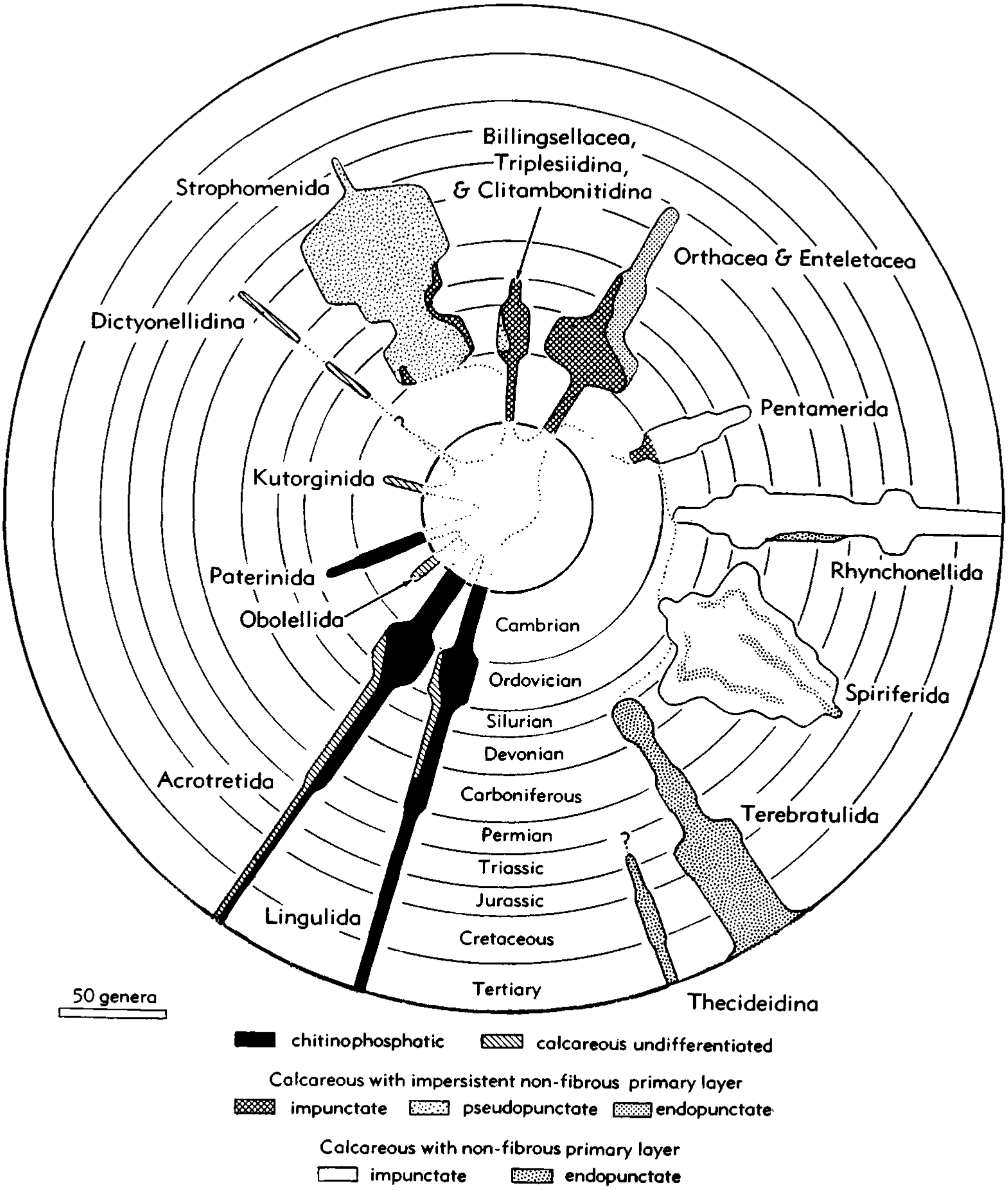

FIG. 144. Variation in shell composition and structure of brachiopod groups (thickness of plot for each group approximately proportional to average number of genera in each system) (54).

a well-differentiated nonfibrous primary layer was probably more significant. The layer seems to have occurred impersistently among the Strophomenida and Orthida; but in at least the later Pentamerida and in all the Rhynchonellida, Spiriferida, and Terebratulida it was invariably present and very well defined (Fig. 144). Hence, if the primary layer of the latter groups is regarded as an inorganic sheet deposited extracellularly to intervene between the periostracum and the secondary shell with its protein sheaths, the course of evolution in shell composition involved the progressive reduction of organic material in the exoskeleton.

In Recent species of the chitinophosphatic Lingulida and Acrotretida, and probably throughout the history of both groups, the

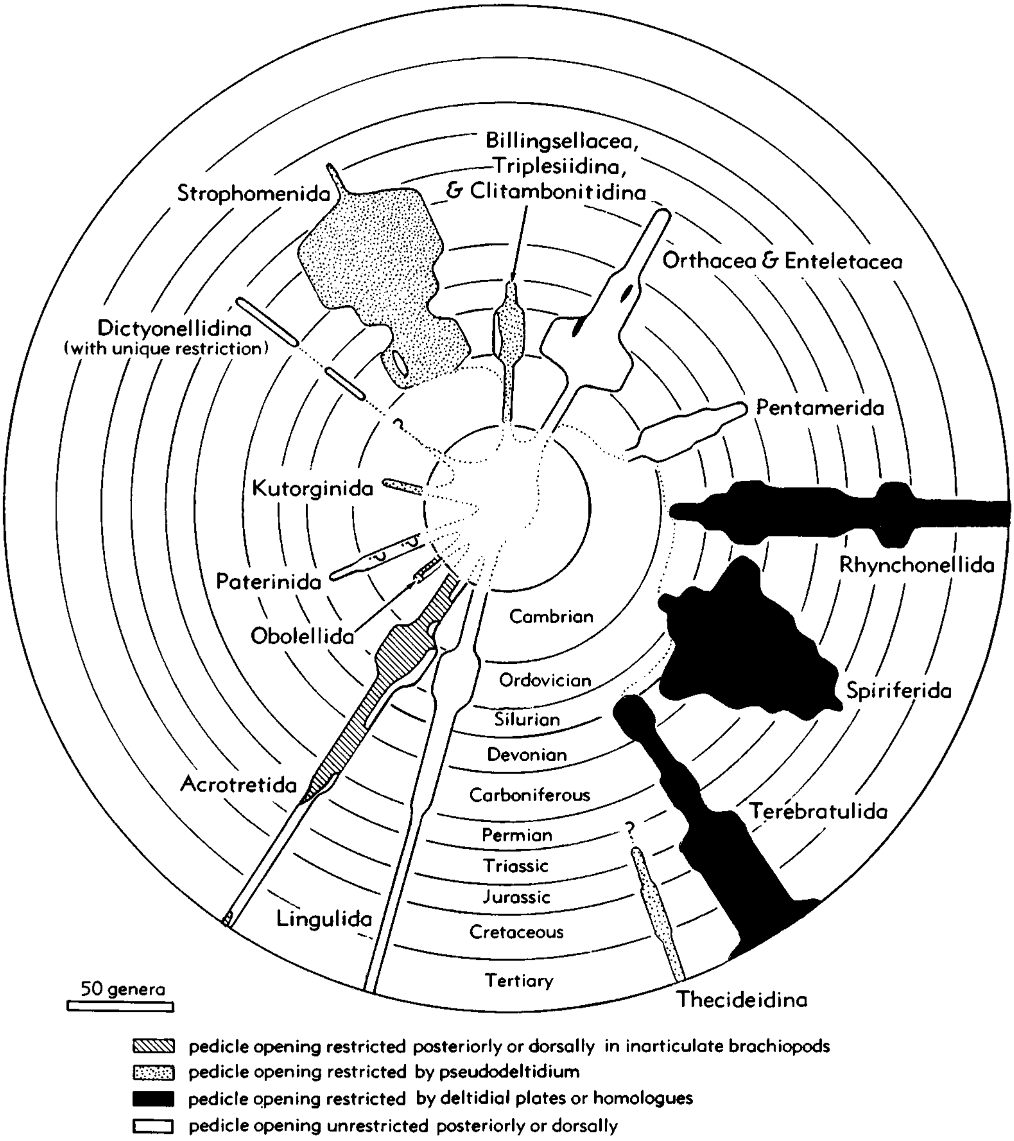

FIG. 145. Variation in structure of pedicle valve of brachiopods accommodating pedicle (thickness of plot for each group approximately proportional to average number of genera in each system) (54).

pedicle is merely an extension of the outer layer of the adult ventral body wall, invariably located within the ventral mantle margin. There is also good morphological evidence for assuming that both mantles were always separated, even posteromedially, by a variably developed body wall of inner epithelium. The mantle edges never fused, but from time to time in some Acrotretida the posteromedian margin of the ventral mantle secreted a strip of shell continuous with the rest of the valve, which restricted the pedicle opening to the apical region of the valve. The most important aspect of this variation is the persistence of the posterior body wall even in stocks having a physically restricted pedicle. The variable accommodation developed for the pedicle of the obolellaceans can be explained in the same way. The paterinaceans present a greater problem because their morphology offers no unique interpretation, but it is likely that they also had a posterior body wall.

The anatomy of living articulates is a less reliable guide to the distribution of soft parts in extinct ancestral stocks, because greater morphological changes took place during the evolution of the class than in the inarticulates (Fig. 145). The pseudodeltidium of the Strophomenida and certain Orthida, for example, cannot profitably be compared even with that of the problematic thecideids. Thus the development of the pseudodeltidium in extinct stocks provided with a functional pedicle must have entailed the existence of a continuous ventral mantle edge, which was responsible for the secretion of shell restricting the pedicle to one valve throughout all known growth stages. There is, moreover, a conspicuous median gap between the pseudodeltidium and chilidium of the billingsellaceans and other primitive stocks, which, since it led into the body cavity, must have been effectively sealed. It is possible that fused ventral and dorsal mantle lobes provided this cover, but in view of the size of the gap in early forms, it is more likely that the mantle edges were not fused, at least over this region, and that the cover consisted of a sheet of inner epithelium suspended between the mantle edges. According to this interpretation, certain primitive articulates may have possessed the homologue not only of the inarticulate posterior body wall but even of the inarticulate pedicle.

The disappearance of the median gap in later Strophomenida may have been associated, as in the tight fit of lingulid valves, with a reduction of the posterior body wall, and the absence of a pseudodeltidium in a few clitambonitoids may have represented a secretory failure of the posteromedian sector of the ventral mantle comparable with that observed in *Discinisca*.

The appearance of the eoorthids marked an important step toward the type of pedicle accommodation characteristic of living Rhynchonellida and Terebratulida. In all such articulates, the growth of restrictive plates and even entire covers to the delthyrium was common enough, but it occurred polyphyletically in several independent stocks and was always a later modification of an open delthyrium (Fig. 145). This homogeneity of basic pattern suggests that in all these groups (Orthacea, Enteletacea, Pentamerida, Rhynchonellida, Spiriferida, Terebratulida) the pedicle developed from a rudiment differentiated in the larval stage, and in absence of the posterior body wall was in contact with both mantle margins, which were fused along the posterior margins lateral of it. The only exception to this arrangement seems to have been the entire pseudodeltidium of the thecideaceans. The embryology of living species is poorly known, but undoubtedly there was an initial differentiation of a pedicle rudiment in the manner of rhynchonellids and terebratulids. The larval commissural plane, however, divides the mantle rudiment (prior to its reversal) so much more obliquely than in other modern articulates that its posterior trace is entirely dorsal of the pedicle rudiment. This rotation of the plane of mantle division and the alleged atrophy of the rudiment of the ventral mantle lobe may be responsible not only for the anomalous structure of the pedicle valve but also for the emergence of a stock bearing such ambiguous morphological evidence of its ancestors.

The acquisition of an efficient hinging device was the most consistent difference between the inarticulate and articulate brachiopods (Fig. 146). Other, cruder forms of pivoting one valve on the other are known among the inarticulates and an analogous modification was evolved in *Linnarssonella*. But unmistakable though weak teeth and sockets bordering the delthyrium and notothyrium, respectively, were developed by the billingsellaceans and persisted throughout the history of the articulate brachiopods with remarkably little replacement or obsolescence, except among the productoids.

In a way which illustrates the interdependence between morphological features, the development of lophophore supports as outgrowths from the dorsal posterior margin, which was exclusive to articulate brachiopods, was related to the stabilization of articulation (Fig. 146).

In the Billingsellacea, Strophomenida, Triplesiacea, Clitambonitidina, and early Orthacea (e.g., eoorthids) the dental sockets were bounded internally by ridges of secondary shell more or less parallel with the hinge line. In remaining articulates, the

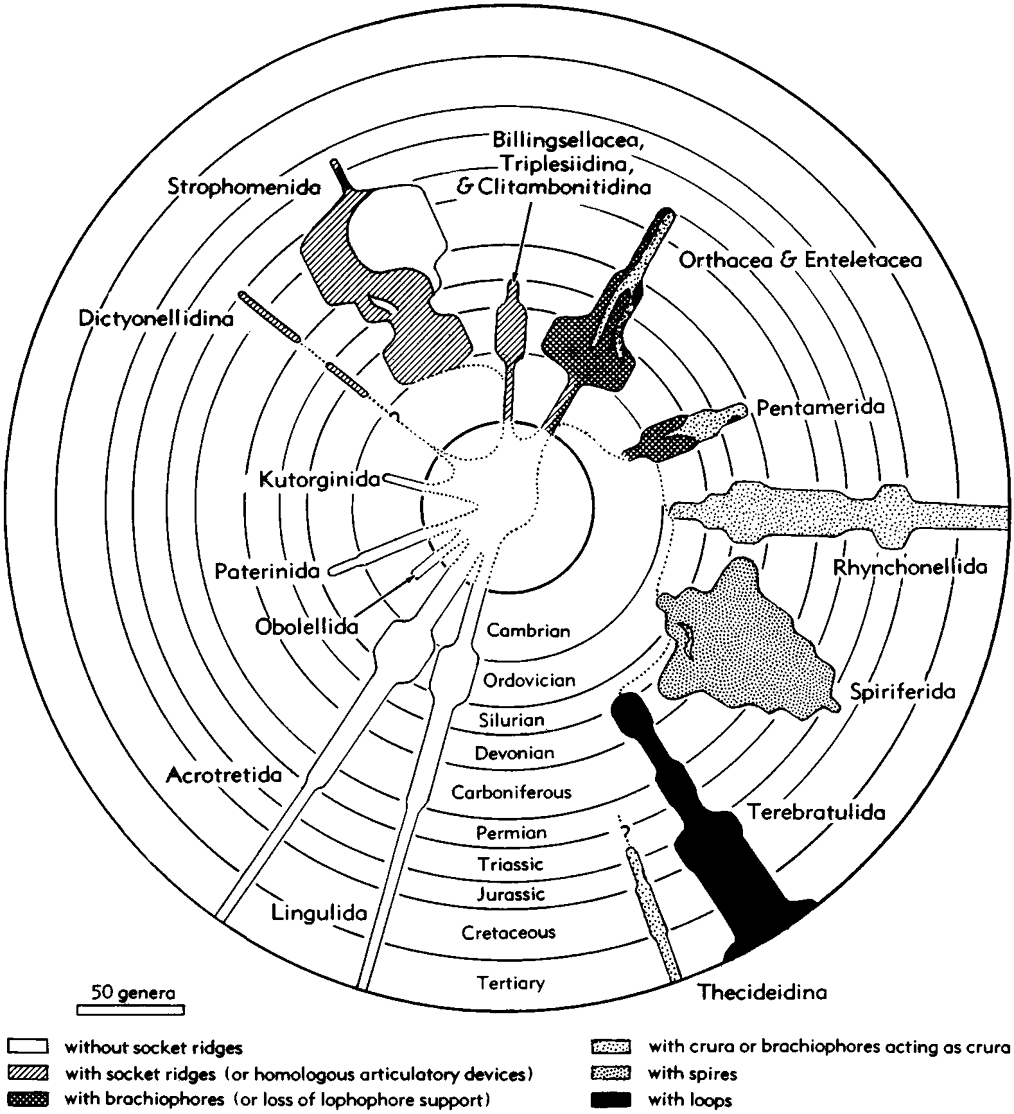

FIG. 146. Diversity of dorsal articulatory devices and associated supports for lophophore in brachiopod groups (thickness of plot for each group approximately proportional to average number of genera in each system) (54).

ridges became rotated toward the median plane and, in addition to functioning as socket boundaries, became extended toward the anterior body wall, where they gave support to the mouth segment of the lophophore. This elaboration of the socket ridges took place independently in some orthaceans and enteletaceans; but in later Pentamerida, Rhynchonellida, Spiriferida, and Terebratulida, it resulted in the appearance of the crura, which, in due course, became further extended into loops and spires. Nothing quite like this arrangement is known among either the inarticulates or the billingsellacean-like articulates in which all plates, platforms, or septa interpreted as lophophore supports grew directly from the floor of the brachial valve. Even the spiralia of the aberrant davidsoniacean *Thecospira* were not suspended from the socket ridges but from the base of the cardinal process. The growth of a dorsal septum to provide some lophophore support also took place in groups equipped with crura or their homologues. It is characteristic of the terebratelloids, for example, and the crura are lost in *Gwynia*, *Amphithyris*, and *Pumilus*, as well as the thecideaceans. In such stocks as these, however, vestiges of the loop or median septum or an elaborate platform, all attached to the floor of the brachial valve, represent only a reversion to the primitive condition.

One of the most interesting consequences of the development of articulation and the crural type of lophophore support was the anatomical reorganization that necessarily took place within the body cavity. Both the distribution and function of the muscle system were greatly affected. Its adaptation to opening and closing the valves exclusively on a lever system about a hinge axis led, in all articulate brachiopods, to the disappearance of the oblique muscles so characteristic of the inarticulates, and in turn to a more median concentration of the attachment bases. Further modification of the system also occurred with the development of a pedicle from a differentiated rudiment, which was accompanied by the attachment of its controlling adjustors not only to the pedicle valve but also to the brachial valve. These systems, whether they included adjustors or not, were initially grouped in such a way as to occupy the delthyrial cavity of the pedicle valve and the notothyrial cavity and posteromedian part of the floor of the brachial valve. This arrangement is typical of the Strophomenida, Orthida, and Pentamerida. The anterior extension of the ventral muscle field well beyond the limits of the delthyrial cavity occurred widely in all three groups, and the common presence of a pedicle callist indicated that the base of the pedicle was depressed relative to the apex of the pedicle valve. Any interpretive reconstructions of the disposition of the muscles in such shells, however, suggest that the base of the pedicle, even when it developed from a rudiment, was never more than a flat sheet extended into ventral and dorsal adjustors. The arrangement found in the Rhynchonellida, Spiriferida, and Terebratulida is strikingly different in that the delthyrial cavity was always occupied by the retractable base of the pedicle and, in consequence, the ventral muscle field was displaced anteriorly. It is significant that this considerable overlap between the posterior region of the shell and the proximal part of the pedicle is seen in young growth stages and represents an incomplete recovery of the mantle subsequent to its reversal. It is therefore feasible to assume that mantle reversal took place only in the Rhynchonellida, Spiriferida, and Terebratulida.

Little can be said about evolution involving anatomical changes apart from those that accompanied revelatory modifications of the shell. It is noteworthy, however, that some evidence concerning the redistribution of organs within the body cavity can be got from a study of the impressions of mantle canal systems, especially with regard to position of the gonads. Thus, it is significant that in living chitinophosphatic brachiopods the gonads are carried on the mesenteries well within the body cavity. Assuming this location to be the primitive one, the first important changes are seen to have occurred in the early articulate brachiopods, like the billingsellids and huenellids. In these, and apparently without exception in all articulate brachiopods, part or all of the gonads migrated out of the body cavity initially to occupy posterolateral pouches within the mantles. Already, as in the dorsal mantles of early stocks, the pouches were beginning to branch and subsequently they provided terminal canals for increasing arcs of the mantle edges, with a concomitant reduction of the principal circulatory canals. This change, therefore, which took place independently in most stocks, resulted in structures that performed the dual function of storing gonads and circulating the body fluid. Such economy was achieved independently in many groups (e.g., clitambonitoids, spiriferids, terebratulids) by total reduction of the primitive gonadal sacs to slender, radiating canals so well integrated with the mantle canal systems generally that, as in the terebratelloid *Fallax*, gonadal cords are also present in the *vascula media*. This series of changes did not, of course, take place uniformly. The primitive gonadal sacs, for example, are retained in living rhynchonellids, whereas the sex organs of the inarticulate craniids protrude into radiating canals within the mantles in the manner of more advanced articulates.

Two other important anatomical differences, seen in Recent brachiopods but unlikely ever to be confidently inferred from shell morphology, are worth a brief note.

It has been claimed that certain external openings, located posteromedially in the brachial valves of some Paleozoic articulate brachiopods, accommodated the anus in various stages of atrophy, thereby providing a link between living representatives of the two classes. The perforations may be either the median gap in a bilobed cardinal process or an imperfectly sealed cardinal plate. The impersistency of these holes, even in members of the same stock, and the secondary nature of their origin seems to preclude such a function. It is likely, therefore, that they were covered by periostracum or an extension of the pedicle cuticle.

The last important anatomical difference between living chitinophosphatic and calcareous-shelled brachiopods concerns the arrangement of the lophophore filaments. In the former group, both ablabial and adlabial filaments are present throughout all growth stages of the lophophore. In the latter, the ablabial set is absent in the trocholophe (the filaments of which are exclusively adlabial and disposed in a single row), appearing only with onset of the schizolophous condition. Assuming that the invariable presence of paired filaments is the more primitive condition, the arrangement characteristic of living articulates could have evolved by suppression of the outer ablabial filaments during the trocholophous stage of development. Such a trend is carried to its conclusion in the lophophores of living megathyridids and thecideids, which bear only adlabial filaments even in adult stages of growth. Nothing, of course, is known about the filament arrangement in extinct groups, but changes like those referred to must have occurred at least twice, because the filaments of the craniid trocholophe are also adlabial and disposed in a single row.

In summary, it may be said that four morphological characteristics, each really an assemblage of features, help to distinguish articulate from inarticulate brachiopods. They are (1) shell composition and structure, (2) articulation by teeth and sockets, (3) lophophore support from the posterior margin of the brachial valve, and (4) distribution of the musculature. Two inferences based on known anatomical distinctions may also be considered because they complete a gradient of change linking modern inarticulate and articulate brachiopods. They depend upon interpretations of the delthyrium and its various covers and on the location of muscle bases in extinct stocks. If they are correct, they give some indication of the nature of the pedicle and the occurrence of mantle reversal during early postlarval stages of growth.

The morphological differences do not coincide entirely with the conventional systematic boundaries between the two classes. The musculature of the Paterinida, for example, is not distributed peripherally within the inferred body cavity in the manner of orthodox inarticulates, and the typical articulate lophophore support is only rarely developed in the Orthida, Strophomenida, and early Pentamerida. The two inferences certainly conflict with present class groupings. They have led to the assumption that the pedicle of the Billingsellacea, Clitambonitidina, Triplesiacea, and Strophomenida arose from the ventral body wall in the inarticulate fashion. It is also believed that mantle reversal was first introduced into articulate ontogeny during the evolution of the Rhynchonellida (Fig. 147).

These conclusions emphasize the basic homogeneity of the phylum and show how living articulate species represent the culmination of divergence from ancestors close to primitive inarticulates. Hence, if the Cambrian chitinophosphatic forms were nearer the archetypal brachiopod than any other contemporary stocks, five structural grades may be distinguished as follows: (1) The first group comprises the Obolellida, Acrotretida, and Lingulida, which were involved only in the acquisition of a calcareous shell in some groups. (2) The Paterinida stand alone among the inarticulates in showing some regrouping of the muscle bases toward the median areas of the shell, although their scars are inadequately understood. (3) The Billingsellacea, Clitambonitidina, Triplesiacea, and Strophomenida make up a third group, which acquired a calcareous shell with an intercellularly se-

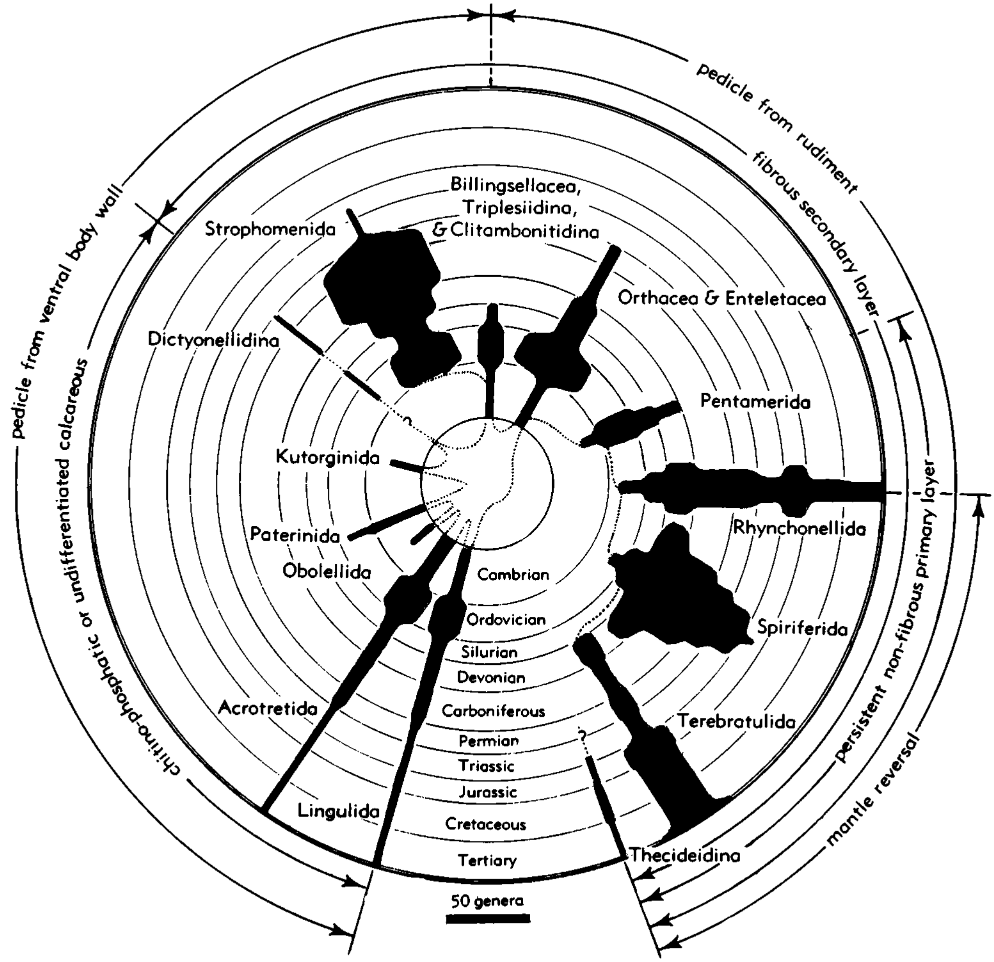

Fig. 147. Phylogeny of Brachiopoda with indications of some principal features developed during evolution (thickness of plot for each group approximately proportional to average number of genera in each system) (54).

creted secondary layer but a sporadically developed nonfibrous primary layer, teeth and sockets, and a medially arranged muscle system without obliques. (4) The fourth group includes the Orthacea, Enteletacea, and Pentamerida, with the pedicle originating from a differentiated rudiment of the larva; both a persistent primary layer and fully developed crura (or homologues) appeared in some of the later orthaceans and enteletaceans and all later Pentamerida. (5) Lastly, as a climax to all earlier changes, a persistent primary layer, functional lophophore supports (rarely secondarily lost) and mantle reversal became characteristic of all Rhynchonellida, Spiriferida, and Terebratulida.

In general, these grades can accommodate all members of the phylum, although there are three small stocks the precise affinities of which have yet to be decided. The Kutorginida include a few Cambrian genera with a superficial resemblance to the billingsellaceans; but teeth and sockets have never been identified positively in them, and the internal impressions, although including elements that are medially disposed, are unlike those of any articulate. They may have originated independently of all known articulate and inarticulate stocks. The Dictyonellidina are likely to have developed from some articulate ancestor, as yet unidentifiable, possibly through gross paedomorphic changes in the early eichwaldiids.

The origin of the thecideaceans presents a similar problem, mainly due to alleged anomalies in their development and to their cemented habit and supposed strophomenoid shell structure and pseudodeltidium. In fact, these features either have been mistakenly interpreted or are not as important in deciding the affinities of the group as they seem to be, and it is quite possible that the group was derived paedomorphically out of the suessiaceans or terebratuloids.

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# ECOLOGY AND PALEOECOLOGY

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## INTRODUCTION

Living brachiopods are comparatively rare and insignificant members of the faunas of the present day, and their study has therefore been neglected by zoologists. This neglect is especially serious in the field of ecology. Few Recent species have ever been observed alive, and fewer still have been the subject of any thorough ecological analysis. Most of our information is fragmentary, and comes from widely scattered sources, such as accounts of dredging operations, systematic descriptions of species, etc. In this chapter, therefore, all statements about the ecology of brachiopods include the implicit qualification that they are true only as far as our extremely imperfect information extends.

This neglect of brachiopod ecology is reflected in the poor quality and dubious validity of much published work on their paleoecology. Many conjectures about the paleoecology of brachiopods have been made in apparent ignorance of the physiology, life habits, etc., of living species, or even in ignorance of their basic anatomy. Other work purporting to deal with their paleoecology merely records characteristic assemblages of species, characteristic associations between species and their enclosing sediments, or characteristic patterns of geographical distribution. Without any truly ecological interpretation, such records cannot be regarded as more than raw material for future paleoecological work.

In these circumstances, a brief account of the ecology and paleoecology of brachiopods cannot hope to be definitive, and will necessarily be fragmentary and uneven in its coverage. Most generalizations about the ecology of the phylum will unavoidably represent no more than our knowledge of one or a few species. Even the limits of "ecology" are debatable. Here it is taken to include at least some aspects of the physiology and functional morphology of brachiopods (i.e., "autecology"). The relation of individual brachiopods to each other, to other organisms, and to the general inorganic environment (i.e., "synecology"), about which even less is known, is treated much more briefly.

Almost all living brachiopods are marine, benthonic, epifaunal, sessile suspension-feeders. This mode of life probably has been characteristic of the phylum as a whole throughout its history. A few brachiopods, however, seem to have modified it in one direction or another. A few were probably epiplanktonic and a few possibly nektobenthonic. Some may have become deposit-feeders or even in a limited sense carnivores. Some were virtually infaunal, and a few still are. Probably none has ever invaded any truly nonmarine habitat.

## RELATION TO SUBSTRATUM

Most brachiopods are and were sessile benthonic organisms. Their relation to the substratum is therefore of the greatest ecological importance and is reflected in many major features of morphology. All living brachiopods are permanently attached to the substratum, generally by a pedicle, more rarely by cementation of the ventral valve. Unlike byssally-attached bivalve mollusks, there is no evidence that any brachiopod (except possibly a lingulid) can change its position of attachment after the larval stage, or that if uprooted it can re-establish itself elsewhere.

The pedicles of inarticulates and articulates differ in structure and embryonic origin, and are evidently not homologous, but in most respects they are functionally equivalent.

The pedicle of an articulate develops from the caudal segment of the larva. It is a tough, solid, "cartilaginous" cylinder, covered with a thick chitinous cuticle. Its distal end is attached very firmly and rigidly to the material of the substratum, presumably by a sticky secretion. Its proximal end projects through the posterior body wall into the cœlom. Obliquely inserted pedicle muscles connect the pedicle to the inner surface of the valves. Their contraction enables the whole shell to be rotated laterally and to a lesser extent dorsoventrally around the immobile pedicle.

The pedicle of an inarticulate brachiopod develops from the posterior edge of the ventral mantle, the caudal segment being unrepresented in the larva. The inarticulate pedicle is a highly muscular cylinder with a central lumen connected to the cœlom. Its distal end is firmly attached to the substratum by a sticky secretion; proximally it remains intimately connected to the ventral mantle. There are no pedicle muscles external to the pedicle, but the muscle fibers within the pedicle serve the same function, enabling the shell to be rotated, elevated, or depressed relative to the substratum (the central lumen acting as a hydrostatic skeleton for extension of the pedicle).

In most living brachiopods, both inarticulate (e.g., *Discinisca*) and articulate (e.g., most Terebratulida), the pedicle is very short, and the shell is closely attached to some material on the substratum. The pedicle not only acts as an anchor, but also supports the weight of the shell and holds it in position relative to the substratum. The pedicle has this dual function even in the early growth stages, immediately after the larva has settled; and there is good reason to regard it as the "standard" mode of attachment to the substratum. Most living species seem to require, or at least to prefer, a hard material for attachment, such as a surface of rock, shell, or coral. Thus many species are most abundant on bottom environments such as boulders or stony gravel, coarse shell gravel, or coral debris. On bottoms of finer-grained sediments, such brachiopods would be restricted to sites of attachment such as shells or other fragments of hard material. It is possible that many fossil brachiopods were so restricted. Specimens are occasionally found in their position of life, with the pedicle foramen pressed closely against the surface of another shell (14), or lying in a cluster around an isolated pebble.

At least a few living brachiopods (e.g., *Kraussina*, *Terebratulina*, *Magasella*) are able to attach themselves to "soft" materials such as algal stems, ascidian tests and "horny" worm tubes. These and other organic materials would not normally be preserved in the fossil state; therefore, after death the brachiopod shells might be buried in a soft muddy sediment without preserving any trace of the original material of attachment. This probably accounts in part for the abundance of fossil brachiopods in fine-grained sediments.

Another explanation of the same fact is that the pedicles of many brachiopods may have been adapted to anchor the shell directly into the sediment itself. This is known in a few living species. The pedicle is relatively long, but like those of more normal brachiopods it serves to anchor the shell and hold it in position close to the surface of the substratum. In a few articulates (e.g., *Terebratulina*) the distal end of the pedicle is split into fine rootlets, which are apparently able to perforate calcareous material by means of an acid secretion. In *Terebratulina* the rootlets can penetrate the shell fragments in a fine shell gravel; in *Chlidonophora* the pedicle is even longer and more finely divided, and the rootlets penetrate the tests of *Globigerina* within a soft substratum of *Globigerina* ooze. Pedicles with branching rootlets leave no distinctive trace on the shells of brachiopods, and may have been much more abundant among fossil brachiopods than they are among living species.

The pedicles of living lingulids are also able to anchor the shell into soft sediment (e.g., sandy mud), not by divided rootlets but by a sticky secretion from the whole distal surface of the pedicle. Although at the present day this kind of pedicle is closely related to an aberrant infaunal mode of life, it is possible that some fossil lingulids (and perhaps other inarticulates) were attached epifaunally by similar pedicles.

It is possible that the pedicles of a few articulates and inarticulates were attached to "soft" materials not on the sea floor but in the surface waters. This epiplanktonic mode of life has been suggested principally for a few species (chiefly *Lingulida, Acrotretida, Rhynchonellida*) which are found in "black shale" and similar facies. They are accompanied by few if any other organisms that were certainly benthonic, and there is good evidence that the sediment accumulated in anaerobic conditions; they may have been attached to floating vegetation.

Any pedicle that actively supports the whole shell must be relatively stout, whether the attachment is to hard or soft materials. In a fossil shell this is shown by a relatively large pedicle foramen. On this criterion there is little doubt that the "standard" mode of attachment has been extremely common throughout the history of the phylum. Most other varieties of attachment or support seem to be derived from the standard mode, the pedicle being supplemented or replaced by other structures during ontogeny (13).

One very common derivative involves the use of shell material to weigh down the posterior end of the shell. In many living articulates (e.g., *Gryphus*, *Neothyris*) the shell is thickened internally in the umbonal region in such a way that it retains its orientation relative to the substratum even if the pedicle attachment is cut. The pedicle has thus lost much or all of its supporting function, but it retains its function of anchorage. Such shells are effectively tethered by the pedicle and cannot be swept away by currents or wave scour; yet the shell is maintained in its orientation without the tonic contraction of the pedicle muscles. In fossil shells this mode of support is shown not only in the posterior thickening of one or both valves, but also in the relatively small size of the pedicle foramen; in an ontogenetic series the foramen can be seen to have failed to enlarge in proportion to the growth of the whole shell.

In the ontogeny of many fossil brachiopods this process was carried to completion, and the pedicle finally atrophied. This is shown either by the gradual shrinking and final plugging of the foramen, or by a progressive incurving of the ventral umbo and final blocking of the foramen. After atrophy of the pedicle, the shell must have been maintained both in orientation and in position on the substratum purely by means of its weight. Such shells would be nominally "free" and unattached, but probably they lay immobile on the surface of the substratum or with the umbonal region slightly buried. With the posterior side downward, most of the commissure would have been held clear of the substratum in an oblique or even vertical plane.

Some brachiopods with reduced or atrophied pedicles seem to have developed other structures, in addition to or in place of shell thickening, as means of maintaining the position and orientation of the shell on a soft substratum. Thus the long lateral alae of some spiriferoids (e.g., *Mucrospirifer*) may have had a ski-like function, spreading the weight of the shell over a greater area of the substratum. In some other spiriferoids (e.g., *Cyrtia, Syringothyris*) the ventral cardinal area was modified into a broad flat base, which could have had the same function. In one genus *(Syringospira)* the area of this flat base was increased still further by the development of thin lateral frills. Frills that extend all around both valve edges (e.g., *Atrypa*) can also be interpreted, though perhaps with less confidence, as structures for supporting the shell on a soft substratum.

In most Strophomenida the pedicle (inferred from its foramen) ceased to grow or atrophied altogether at a very early stage in ontogeny, and the shell must have become free while still quite small. Generally there was a concurrent development of a gently concavo-convex shell form. This was probably an adaptation for lying freely on a soft substratum (24). By passing through the phase of pedicle attachment at an early stage of growth, even small fragments of shell, etc., would have been adequate as sites for initial settlement of the larvae; but thereafter the brachiopods would have been independent of any attachment materials whatever. With the shell lying on its convex valve, the commissure would have been held slightly above the surface of the substratum. If overturned by bottom currents, a vigorous "snapping" of the valves could have turned the shell back into its original orientation; if covered with sediment, a similar reaction would lift the shell off the substratum or at least shift it posteriorly into a different position. Such movements can be proved possible by experiments with working models, and they would be analogous to those known in living pectinid mollusks. It is even possible that, like some pectinids, various Strophomenida with gently concavo-convex shells may have been able to swim, if only as an occasional protective reaction to escape from potential predators.

But most Strophomenida passed during ontogeny from a gently to a strongly concavo-convex shell form (the change, if fairly sudden, being shown by geniculation of the shell). This probably represents a reversion to a sessile or immobile mode of life. The shell was probably large and heavy enough, commonly by great internal thickening of one or both valves, not to be overturned by any currents; the commissure could have been held slightly above the surface of the sediment, while allowing the convex valve to become quite deeply sunk within it. Some of the thinner and lighter shells may in effect have "floated" in a semiliquid sediment of very fine mud or ooze. Strongly concavo-convex shells are especially characteristic of the productoids, but they occur in many other Strophomenida, and occasionally are found in other articulate groups (e.g., *Koninckina, Amphiclina*). Some markedly plano-convex shells (e.g., *Productorthis, Ambocoelia*) may have had the same habit. The position of living productoids in particular has been the subject of much speculation (15, 21), since they differ from modern brachiopods perhaps more widely than any other extinct group. It is now fairly certain, however, that all strongly concavo-convex brachiopods must have lived in the manner described above; only by resting with the convex valve on or in the substratum, and with the commissure therefore held clear of the substratum, would they have been able to feed and to respire. At least some of them, as suggested above, may have adopted a virtually infaunal mode of life, with only the margins of the valves projecting above the surface, and perhaps with the concave valve itself filled with sediment. In such a position the brachiopod would have been well protected from predators.

The cemented brachiopods show a series of adaptations parallel to those found in pedicle-attached groups. Cemented brachiopods are represented today by both inarticulates (e.g., *Crania*) and articulates (e.g., *Lacazella*). The shell material secreted by the ventral mantle is laid down in intimate contact with a hard substratal material. In *Crania* the larva settles at an early stage of development, and becomes cemented immediately by the ventral protegulum; a pedicle is never developed. In *Lacazella* the larva settles by its caudal segment as in other articulates; the later stages of growth have not been fully described, but the larval pedicle must be replaced very soon by cementation of the ventral valve, for no trace of a pedicle foramen can be seen on the adult shell.

Initially, the ventral mantle edge remains in contact with the substratum, so that the whole surface of the ventral valve is cemented. In a few brachiopods (e.g., *Crania, Davidsonia, Poikilosakos, Leptalosia*) this simplest variety of cementation is or was retained throughout life. This undoubtedly provides the strongest form of attachment known in brachiopods (it is significant that *Crania* occurs in more strongly current-swept environments than any other living brachiopod). But such attachment is restricted, of course, to hard materials (generally rock surfaces or shells, but exceptionally stems of crinoids).

More usually the ventral mantle-and-valve edge rises away from the attachment surface at some stage in ontogeny, leaving an area of cementation around the ventral umbo. This may give a relatively weaker attachment than complete cementation, but it also raises the commissure away from the substratum. This variety of cemented attachment is common among the Craniacea, Thecideacea (including the living *Lacazella*), Davidsoniacea, and Lyttoniacea. In the Strophalosiacea the initial cemented attachment was generally supplemented by a series of struts or props, formed by tubular rhizoid spines (outgrowths of the ventral valve edge) which are themselves cemented distally to the substratum (e.g., *Aulosteges, Heteralosia*). This allowed the commissure to be raised from the substratum without sacrificing the strength of attachment.

The coralloid shell form can be regarded as an extreme development of this mode of attachment. The ventral valve became deeply conical in shape; it was cemented by its apex, and also (in Strophalosiacea) by a tangle of rhizoid spines. Occasionally these shells even formed reeflike masses. The dorsal valve was reduced to a lidlike operculum (e.g., *Scacchinella, Gemmellaroia*) or modified still more radically (e.g., *Teguliferina, Richthofenia*).

Many brachiopods passed through a cemented stage but later outgrew the cemented attachment and lay freely on or in the substratum. As in shells attached initially by a pedicle, this development is commonly associated with the concavo-convex shell form (e.g., *Oldhamina, Bactrynium*). The initial cementation is shown by an attachment area at the ventral umbo. In Strophalosiacea the rest of the ventral valve commonly bears spines of various kinds (e.g., *Strophalosia, Institella*). Some such spines, but not necessarily all, may have served to root the shell firmly into a soft substratum.

This habit was more characteristic of the Productacea. Their initial attachment by the ventral umbo was generally superseded at a very early stage, and in some may have been omitted altogether. In the next stage of growth they were commonly attached, by a ringlike pair of small clasping spines, to some slender cylindrical object (e.g., crinoid stem, spine of another productoid, or perhaps a plant stem or some other unpreserved object). But generally the shell seems to have outgrown even this attachment at a fairly early stage of growth, and thereafter it probably lay, like other concavo-convex shells, with the ventral valve resting on or floating in the soft or loose substratum. Its stability in this position was commonly aided by the development of rhizoid or halteroid spines, which probably penetrated the sediment or became entangled in it, or perhaps extended across its surface. The vermiform spines found in the concave dorsal valves of a few productoids (e.g., *Dasyalosia, Echinauris*) could have helped to retain sediment within the dorsal valve, so that only the valve edges projected visibly above the surface of the substratum.

This virtually infaunal mode of life is analogous to that of the only fully infaunal brachiopods, the lingulids. Although they are perhaps the most intensively studied living brachiopods, they are also some of the most aberrant of all brachiopods, living or fossil. Living lingulids build deep vertical burrows, generally in sandy mud, and are attached to the base of the burrow by the distal portion of the long muscular pedicle. The shell is held vertically within the burrow, with the anterior edge scarcely projecting above the surface of the substratum (3). When the lingulid is disturbed, contraction of the pedicle withdraws the shell into the deeper part of the burrow. Fossil lingulids preserved perpendicular to the bedding have been recorded from as far back as the Ordovician, and indicate the same highly aberrant mode of life (9). It is not certain, however, that all lingulids were infaunal burrowers; this mode of life is not reflected in any distinctive feature of the shell itself, and many fossil lingulids may have been epifaunal.

## SENSORY AND PROTECTIVE MECHANISMS

Living brachiopods have only one protective reaction in response to unfavorable circumstances in the external environment. The valves can be closed rapidly and tightly by contraction of the adductor muscles.

As in bivalve mollusks the adductors are differentiated into "quick" and "catch" portions; in at least some species these are composed of striated and unstriated muscle respectively. In inarticulates it is the anterior adductors that are divided into two portions; in articulates the anterior adductors are "quick," the posterior adductors "catch." The "quick" muscles snap the shell shut; the "catch" muscles, contracting more slowly, then hold the valves firmly together. When the shell is closed the valve edges fit tightly together along the commissure, sealing all the living tissues of the body (except the pedicle) from contact with the environment. The brachiopod can survive for periods of at least several hours with the shell tightly closed. It is significant that such tightly fitting valve edges have only rarely been abandoned in the history of the phylum (e.g., Teguliferinidae, Richthofeniidae, Oldhaminidina). The closure of the shell may be accompanied by a movement of the whole shell on the pedicle, drawing the shell nearer the substratum or (in lingulids) into its burrow, or merely rotating it into a different orientation.

This protective reaction is evoked by the stimulation of sensory mechanisms. In living brachiopods the sensory receptors seem to be confined to the extreme edges of the mantle lobes (and possibly also the pedicle). No special receptor organs have been discovered, but the mantle edges are sensitive to light, touch, and chemical stimuli. They are richly supplied with nerves leading to the central ganglia, through which there is a simple reflex circuit to the adductors. Under natural conditions a protective closure of the shell is produced, for example, in response to a shadow falling on the shell, or to a moving organism touching the shell. Clearly this serves to protect the brachiopod from potential predators or other organisms that might interfere with its delicate feeding mechanisms. In addition, the mantle edges seem to be able to detect water that is highly turbid, brackish, or poorly oxygenated.

These mechanisms are essentially uniform in all living brachiopods, and it is reasonable to infer that they were also common to all fossil brachiopods. The tightly fitting valve edges, and the scars of the adductors, are of course preserved. Among articulates the common twofold division of the adductor scars suggests that the muscles were differentiated into "quick" and "catch" portions as in living species. Many modifications of the valve edges of fossil brachiopods can be interpreted as adaptations of the sensory mechanisms at the mantle edges. In a few rhynchonelloids (e.g., *Uncinulus, Hypothyridina*) the valve edges are modified into uniformly spaced internal spines, which could have covered the apertures of the open shell with a sensitive "grille." In a much larger number of rhynchonelloids, but also in members of many other articulate groups, the valve edges are modified into distinctive zigzag forms; this could have reduced the distance between the sensitive mantle edges without any corresponding reduction in the area of the apertures (20). Although many varieties of tubular external spines were used for attachment and support, some others apparently were not, and may have functioned as sensitive "antennae," for at their open distal ends the sensitive mantle-edge tissue would have been extended outward from the rest of the shell. Examples of possibly sensory spines include the fine prostrate spines of many productoids, the posterior spines of most Chonetacea, and the tubular spines of a few other articulates (e.g., *Acanthothiris*). The long narrow extensions of the valve edges in the homeomorphic genera *Tetractinella* and *Cheirothyris* could have had a similar function.

The chitinous setae that project from the mantle edges of most living brachiopods serve to extend the tactile sensitivity outward from the mantle. Generally the setae are short, merely forming a fringe around the edges of the apertures. In a few genera (e.g., *Discinisca, Notosaria, Terebratulina*) the setae are much longer, and cover the apertures with a sensitive grille. The spacing of such setae determines the maximum size of objects that can approach the apertures without causing a protective closure of the shell. During growth of the brachiopod the spacing of the setae is kept fairly constant by intercalation of new setae. In *Terebratulina* the setae correspond in position to the growing edges of the external costellae. The spatial pattern of branching costellae on the valve surfaces therefore reflects precisely the temporal pattern of growth and intercalation of the array of setae. Similar patterns of branching costellae on the valves of many fossil articulates (especially Orthida and Strophomenida) probably reflect the existence of similar grilles of sensitive setae. But not all costellae in living brachiopods correspond in position to the setae (e.g., *Notosaria*). Other evidence of marginal setae in fossil brachiopods is shown occasionally by internal grooves shaped like the setal follicles of living brachiopods. In exceptional conditions the setae themselves have been preserved. A few living brachiopods (e.g., *Crania, Lacazella*) have no setae at all; they may have been lacking in earlier Craniacea and Thecideacea, and perhaps also in other groups. The setae of lingulids are highly specialized; not only are they sensitive, but they are also equipped with a complex musculature and are used in the maintenance of the burrow and to form siphon-like apertures (3).

## FEEDING AND DIGESTION

As in other sessile invertebrates, organs of feeding are elaborate and conspicuous parts of the body and are of great ecological importance. The lophophore is never preserved in fossil brachiopods, but indirect evidence of the feeding system is shown in many important features of morphology.

All living brachiopods are ciliary suspension-feeders. The lophophore acts as a combined pump and filter. Its ciliated filaments divide the mantle cavity into separate inhalant and exhalant chambers; when the shell is open they also divide the gape between the valve edges into separate inhalant and exhalant apertures. The lateral cilia on the filaments draw water from the inhalant into the exhalant chamber, and thus create a one-way circulation of water currents, the current system, through the mantle cavity (19). As the water passes between the filaments, many of the suspended particles collide with the filaments and are carried by frontal cilia to the food groove at the base of the filaments. Cilia in the food groove transport the particles along the brachium to the mouth. There is no qualitative sorting of the particles; the material reaching the mouth may therefore include a high proportion of silt or other material without food value. The food particles are chiefly diatoms and dinoflagellates.

The ingested material passes through the esophagus to the stomach. From here it is sucked by muscular action in and out of the diverticula ("liver"), where most of the digestion takes place (4). The digestion is mainly intracellular, though phagocytes may be important. Undigested material is returned to the stomach and passed on to the intestine, which contains a rotating thread of mucus (but not a crystalline style) and is probably concerned chiefly with the consolidation of rejected material into fecal pellets. In inarticulates the pellets are ejected from the anus by peristalsis in the intestine; in articulates they are returned through the stomach and ejected from the mouth by antiperistalsis in the esophagus. In either case they are then transported by mantle cilia to the edge of the mantle, and finally ejected from the shell by the periodic snapping of the valves.

Although no qualitative sorting of particles occurs during normal feeding, rejection mechanisms are highly developed (3). Occasional particles too large to be accepted within the food groove may be allowed to pass directly into the exhalant chamber by the contraction of one or more filaments. Such particles are then transported by mantle cilia to the mantle edge. More radical rejection mechanisms, which interrupt the feeding process on part or all of the lophophore, are evoked by the presence of unusually large quantities of suspended particles. The lateral cilia stop beating, so that the circulation of water currents ceases and no further particles enter the mantle cavity. The frontal cilia reverse their direction of beat (or, in *Lingula,* adjacent tracts of frontal cilia may begin beating away from the food groove); and mucus is secreted by the filaments. The particles are trapped in the mucus and swept by the reversed cilia to the tips of the filaments and then by mantle cilia to the edge of the mantle. The mass of pseudofeces which collects there is finally ejected from the shell by vigorous snapping of the valves. In natural conditions this rejection process serves to prevent the lophophore from becoming choked by a sudden influx of sediment. Very rarely, another rejection mechanism has been observed: the lateral cilia reverse their direction of beat, so that the whole current system is reversed in direction, and the particles are ejected from the mantle cavity through the inhalant apertures.

It is noteworthy that the snapping of the valves, though perhaps primarily a protective reaction, is also of great importance in the ejection of feces and pseudofeces. When the brachiopod is feeding undisturbed, the valves are snapped shut at fairly regular intervals, but they reopen immediately so that feeding is scarcely interrupted.

These mechanisms of feeding, digestion, and rejection are essentially uniform in living brachiopods of all groups, and may have been general in the past. Only in the form of the lophophore and the consequent current system is there much diversity, but even in this the basic structure and function of the lophophore remain constant. The lophophore always divides the mantle cavity into separate chambers and apertures, so that all the water is filtered once, but only once, during its passage through the mantle cavity. This accords with analogous enclosed suspension-feeding systems in other organisms (e.g., bivalve and some gastropod mollusks, ascidians, etc.).

The lophophore and current system become increasingly complex during the ontogeny of most species. This is related to increase in absolute size, and apparently reflects the increasing filtering capacity required by the metabolism of the growing animal (19). Thus, many species of unusually small size retain as adults the simpler forms of lophophore, which in larger species are confined to an early growth stage.

In brachiopods with trocholophes and schizolophes, the valves gape apart fairly widely and the filaments project forward like a bell. Water is drawn through a median inhalant aperture into the interior of the "bell" and after being filtered escapes laterally. In *Pumilus* the orientation of the inhalant aperture is shifted farther from the substratum by a ventral deflection in the commissure (i.e., ventral fold, dorsal sulcus). Trocholophes and schizolophes are almost invariably found in brachiopods of very small size, generally early growth stages. The only brachiopod with trocholophe in the adult stage is the very small *Gwynia*, which for long was thought to be the young of some other genus (the very large *Dyscolia* is also said to have a trocholophe, but has not been observed alive). Schizolophes are found in the adults of small thecideids (e.g., *Thecidellina*), megathyridids (e.g., *Argyrotheca*) and kraussinids (e.g., *Pumilus*). Small fossil species in these and other groups may also have had schizolophes, especially if their supporting structures (grooves, loops, etc.) can be shown to be comparable to those of living species. Other fossil structures alleged to have supported schizolophes (e.g., "lophophore platforms" of plectambonitaceans, "brachial ridges" of productoids) bear no close resemblance to the supports of schizolophes in living brachiopods, and their function is much more dubious.

The growth of a schizolophe into a ptychlophe increases the length of the rows of filaments and therefore the filtering capacity; but the current system is altered very little (it has only been studied fully in *Megathyris*, but *Lacazella* is probably similar). The valves continue to gape apart widely, and the water is drawn into the interior of the lophophore through a median inhalant aperture. Fossil megathyridids and thecideids have similar multilobed loops and grooves respectively, which probably supported similar ptycholophes. Some thecideaceans seem to have had ptycholophes of far greater complexity than any living species (e.g., *Vermiculothecidea, Bactrynium*). These have some resemblance to the multilobed plates (?dorsal valves) of Oldhaminidina, but interpretation of the latter is more problematic.

The growth of a schizolophe into a spirolophe also increases the size and filtering capacity of the lophophore, but it involves profound alterations of the current system. The brachia are coiled into conical spirals; according to the direction of coiling, the interiors of the spirals may form part of either the inhalant chamber (e.g., *Lingula, Crania, Notosaria*) or the exhalant chamber (e.g., *Discinisca*). The orientation of the spirals within the mantle cavity varies widely, but there is generally a median exhalant aperture flanked by paired inhalant apertures. This involves a complete reversal of the schizolophous arrangement of the apertures. During the early growth of the spirolophe the original median inhalant aperture is gradually split in two by a new exhalant aperture, while the original lateral exhalant apertures are shifted posteriorly and reduced in size or even lost.

Spirolophes are found at the present day without significant difference in both inarticulates and articulates, and they may also have been the most widespread form of lophophore among fossil brachiopods.

Spiral impressions are preserved on the inner surfaces of the valves of some Strophomenida (e.g., *Davidsonia, Gigantoproductus*), and these suggest spirolophes similar to those of living species.

The spiral brachidia of Spiriferida are more problematic. In general form they strongly resemble the spirolophes of living brachiopods. If interpreted as supports for spirolophes, their direction of coiling makes it possible to reconstruct their current systems (16). The interiors of the spirals would have formed part of either the inhalant chamber (most Atrypidina) or the exhalant chamber (all other Spiriferida). In either case there would have been a median exhalant aperture flanked by paired inhalant apertures. On an alternative interpretation (25), based on a different conception of the relation between lophophore and brachidium, the spiralia would have supported a deuterolophe with double rows of filaments; the median aperture would then have been inhalant and the lateral apertures exhalant. But this latter interpretation involves a current system in which the water would have been filtered twice during its passage through the mantle cavity; such a system is unknown not only in living brachiopods but also in living suspension-feeders of any phylum, and it would be highly inefficient.

The growth of a schizolophe through a zygolophe into a plectolophe involves changes analogous to those leading to a spirolophe. The inhalant chamber comprises the interior of the lateral arms of the zygolophe, supplemented in the plectolophe by the interior of the median coil; the rest of the mantle cavity is the exhalant chamber. The apertures are transformed during ontogeny as in the growth of a spirolophe; generally there is a median exhalant aperture flanked by paired inhalant apertures, with vestigial exhalant apertures posteriorly. The current systems of zygolophes and plectolophes depend for their efficacy on the development of the tissues flooring the lateral arms and median coil. They are affected very little by the great diversity in the nature of the supporting structures (short and long loops, etc.). Zygolophes and plectolophes are confined to living, and perhaps also to fossil, Terebratulida.

In many living articulates with spirolophes, zygolophes, and plectolophes, a gentle median deflection develops in the commissure during ontogeny. This invariably marks the position of the median exhalant aperture. Deflections may be either dorsal or ventral in direction (i.e., uniplicate or sulcate, respectively). They are never deep enough to isolate the median from the lateral apertures when the valves are gaping apart. Nor are they clearly related to the position of the shell on the substratum; they do not, for example, necessarily direct the filtered water away from the substratum. Similar weak median deflections are very common among fossil articulates of most groups; they too probably mark the positions of median apertures. In some species the median deflection became very deep in the later stages of ontogeny, and may then have served to separate the apertures from one another, or to direct the jet of filtered water well away from the inhalant apertures or the substratum. Among brachiopods, unlike bivalve mollusks, the apertures are never separated by means of erected or fused portions of the mantle edges, though exceptionally (lingulids) the setae are modified to serve this function.

It is possible that some fossil brachiopods may have abandoned the normal suspension-feeding found in all living species. For example, the peculiar morphology on one aberrant productoid *(Prorichthofenia)* can be interpreted in terms of a feeding mechanism analogous to that of the living septibranch mollusks (17). A rhythmic opening and closing of the highly modified dorsal valve could have sucked water in and out of the mantle cavity. As in septibranchs, the particles obtained in this way might have been much larger and more varied than those obtained by a ciliary suspension-feeder; and the animal might have been a deposit-feeder or even, in a limited sense, a carnivore. The lophophore, although thus losing its normal pumping function, might have retained its function of collecting captured particles and transporting them to the mouth. The morphology of richthofeniids can be interpreted as being especially well adapted to such a feeding mechanism; but a similar feeding process could have been utilized by many less aberrant productoids, and may even have been characteristic of the whole group.

The aberrant morphology of the Oldhaminidina, which has been the subject of much discussion (22), may also reflect some unusual mode of feeding. The "dorsal valve" (if such it is) is lobed in a manner that closely resembles the lobed ptycholophes of Thecideacea, though on a much larger scale. The hinge and musculature were apparently abnormal and commonly asymmetrical, but there is no reason to suppose that they were nonfunctional. When closed, the "dorsal valve" fits precisely on to the corresponding ridges on the ventral valve; and unless it was able to open, the "body" of the brachiopod would have been permanently sealed off from all contact with the environment.

## RESPIRATION, CIRCULATION, AND EXCRETION

Very little is known about the physiology of respiration and excretion in living brachiopods, or about the functions of the so-called blood vessels and the mantle canals. The lophophore was originally regarded as a respiratory organ, since it has an obvious superficial resemblance to the gills of many aquatic animals. Although it is now clear that it is primarily a feeding organ, its large surface area may be important for gaseous exchange, and the filaments are certainly supplied with a system of vessels (branches of the small brachial canal, and "blood vessels"). The thin body wall and mantle surfaces may also be important; in *Glottidia* the mantle surface is extended into thin-walled ampullae projecting into the mantle cavity. Most inarticulates have broad closely packed mantle canals, giving a large area for gaseous exchange; and the canals themselves have a crude ciliary circulation in communication with the coelom. Most articulates have much narrower mantle canals, which do not seem well adapted for respiration; as they are finely divided and terminate at the mantle edge, they may serve rather for the transport of metabolites to the growing tissues there. In any case, whatever the exact site of gaseous exchange, it is clear that the lophophore is important at least indirectly in respiration, in that it creates a flow of water through the mantle cavity. The function of the "blood vessels" is extremely uncertain; there is no respiratory pigment. The products of excretion are ingested by phagocytes in the coelom and drawn by ciliary currents into the nephridia, which perforate the body wall. They are ejected into the mantle cavity, and leave the shell in suspension in the exhalant currents.

## REPRODUCTION

The sexes are separate in almost all living brachiopods (*Argyrotheca* and possibly *Platidia* are hermaphrodite). The gonads are similar in size and position in both sexes; at maturity they extend from the coelom into the proximal parts of the mantle canals. Living brachiopods become sexually mature long before the average "adult" size is reached, i.e., morphologically "juvenile" individuals may be capable of reproduction.

Little thorough study has been made of the breeding seasons of living brachiopods. In tropical water *Lingula* seems to spawn at intervals throughout the year (5), but in temperate water it has a more limited breeding season. Scattered observations on the larvae of other temperate-water brachiopods suggests that they too probably have a limited breeding season in spring or summer.

Like other sessile invertebrates, brachiopods probably have some mechanism for ensuring a co-ordinated release of sperm and ova. When spawning occurs, the sperm and ova are released from the gonads and expelled through the nephridia (which thus act as gonoducts) into the mantle cavity. The sperm pass directly to the exterior in the exhalant current. The ova are yolky, relatively large and few. In most species they too pass out of the mantle cavity, and fertilization takes place externally. The larvae are then planktonic throughout their earlier stages of development.

In a few articulates the ova are retained in the mantle cavity of the female, and fertilization takes place there, the sperm entering with the inhalant current. The larvae are then released at a somewhat later stage of development, and probably settle on to the substratum after a very short planktonic phase. *Argyrotheca* and *Lacazella* have special brood pouches, formed by modification of the nephridia and the body wall, respectively. Traces of a brood pouch like that of *Lacazella* have been found in a fossil thecideid *(Bifolium)*. The pouches found in some specimens of *Uncites* were formed by invagination of the shell; they are closely analogous to the brood pouches of a living bivalve mollusk *(Thecalia)*. The female of the living *Gwynia,* like many other members of the interstitial fauna of marine sand, broods only a very small number of larvae.

Whether or not the larvae are brooded, successful reproduction clearly depends on the chances of fertilization, and hence, as in other sessile invertebrates, on a close proximity between the breeding individuals. This probably accounts for the fact that living brachiopods are almost always very patchy in distribution, dense colonies being separated from one another by areas of apparently similar environment in which brachiopods are rare or absent.

Another probable factor is the very short planktonic period of most brachiopods, for this limits their powers of dispersal. In most living species the larva is planktonic only for a few hours before settling permanently on the substratum. Some of the inarticulates (e.g., *Lingula* and *Discinisca,* but not *Crania*) have developed a much more extended planktonic period of several days or even weeks. The larva develops much further, into an actively swimming and feeding organism, before settling finally on to the substratum; such larvae have often been taken in mid-oceanic plankton.

The presence of possible brood pouches is the only primarily sexual dimorphism that can be detected in fossil brachiopods. Dimorphism in general form of the shell has been claimed in several fossil brachiopods (e.g., *Cyrtospirifer*, *Dielasma*), and may be a secondary sexual character.

## POPULATION STRUCTURE

Very little is known about the rates of growth and mortality in brachiopod populations. Growth lines on the shells of some species, especially those from shallow water, are sometimes grouped together in fairly regular "annual rings," which probably represent seasonal conditions unfavorable for shell growth (18, 23). This indirect evidence, which has yet to be checked by long-term study of growing individuals, suggests that sexual maturity may be reached after two or three years, and that shell growth continues at a gradually decreasing rate throughout life, some individuals having a life span of seven or eight years or perhaps even longer. These tentative figures are based on a study of *Waltonia inconspicua*; but probably different species vary greatly.

The age distribution or even the size distribution of a population cannot easily be determined, because the extremely patchy settlement of the individuals makes it difficult to collect a representative sample. Observations on shallow-water species, which can be studied easily *in situ,* suggest a fairly symmetrical distribution about a mean corresponding to a "mature" shell form. Generally no great preponderance of small and young individuals is found, which implies that if a high rate of juvenile mortality affects populations, it must occur in the larval stage before or at spatfall. Once an individual has survived the larval period and settled successfully on to a suitable substratum, it has a relatively good chance of surviving to maturity. In detail, the distribution is commonly bimodal or multimodal; this may be due either to the growth of successive year-classes of individuals, or to their irregular settlement.

Most assemblages of fossil brachiopods have a rather similar symmetrical size distribution; even where the state of preservation is good and there is little risk of collection bias, small shells are generally rare. This has been used to argue that such assemblages cannot be true life-assemblages, that the shells have drifted from their position of life, or that the smallest shells have been winnowed out after death by bottom currents or destroyed by predators. It is true that empty brachiopod shells, especially the normal biconvex forms, can be shifted even by very gentle currents, and it is also probable that such movements may produce few apparent signs of abrasion or breakage. Many or most fossil brachiopods may indeed have been shifted a little from their position of life; but it has yet to be proved that fossil assemblages do not usually approximate to life-assemblages. If, as the slender available evidence of living species suggests, the highest rate of juvenile mortality occurs before or at spatfall, fossil assemblages would not be expected to contain any preponderance of small shells. This conclusion is supported by an analysis of fossil brachiopods preserved in well-defined "clusters" or "nests," which almost certainly represent undrifted life-assemblages (11). These show a roughly symmetrical size distribution, which in detail may be bimodal or multimodal.

So-called "dwarf" faunas of fossil brachiopods have been described frequently, but their ecological significance is uncertain (6). Although some may be due to true physiological dwarfing by unfavorable conditions, others may be due to a relatively high early mortality, or to a concentration of small shells by drifting after death.

Many populations of living brachiopods show a high degree of variability, especially in characters such as shell form, length-breadth-height ratios, etc. In a few instances it is clear that some of the variation is purely phenotypic, depending on factors such as the degree of exposure. It is probable that many similar intraspecific variants in fossil brachiopods have been described as separate "species."

## BIOTIC RELATIONS

Almost nothing is known about predators on living brachiopods. Potential predators, by analogy with known predators on sessile mollusks, may include fishes, crustaceans, starfishes, and gastropods. It is possible that predation may be relatively heavy during the earlier stages of growth, while the shell is small, thin, and not yet camouflaged by encrusting organisms.

Numerous fossil brachiopod shells show injuries which were healed by subsequent regeneration at the valve edges. Like similar injuries in the shells of living bivalve mollusks, they may have been due to attempted predation. An analysis of injuries to some Carboniferous productoids, for example, suggested that they were due to *(a)* sharp bites, possibly by the horny beaks of cephalopods, and *(b)* broader crushing bites, possibly by the flat crushing teeth of elasmobranch fishes such as *Petalodus*. Circular borings with bevelled edges, which almost certainly indicate predation by carnivorous gastropods, are found occasionally in brachiopod shells as far back as the Upper Ordovician.

True parasitism is little known in living brachiopods and difficult to establish in fossils. Parasitic trematodes have been reported in *Glottidia* and monocystid protozoa in *Crania*. In a Devonian *Atrypa,* the boring organism *Diorygma* maintained an aperture on the inner side of the shell, opening into the mantle cavity, and was probably parasitic (2). Other boring organisms, possibly sponges or "worms," utilized the shells of some other Paleozoic brachiopods, but probably only for protection; their adverse effect on the brachiopods was probably mild.

The shells of living brachiopods commonly are thickly encrusted with other sessile organisms, especially in shallow water where there may be intense competition for settling space (18). Like the brachiopods themselves, these organisms are predominantly suspension-feeders (e.g., sponges, hydroids, tube worms, bryozoans, young brachiopods). Similar encrusting organisms, or at least those with preservable hard parts, are commonly found on the shells of fossil brachiopods (1); they include sponges, small corals, tube worms, bryozoans, and other brachiopods. Some of these organisms may have colonized the brachiopod after death, using the shell merely as a piece of hard substratum on an otherwise soft bottom. But some probably encrusted the brachiopod during life, if only because the dangers of sedimentation would have been lessened by the frequent snapping movements of the host shell. A few of these organisms clearly grew in such a way as to maintain themselves at the valve edges of the brachiopod, suggesting that they intercepted the food-bearing currents created by the brachiopod. One such organism was the coral *Aulopora,* and it has been suggested that the nematocysts of the coral conferred some protection on the brachiopod, making the association mutually beneficial. In fact, however, any encrustation might be of some mutual benefit; while the brachiopod provides the encrusting organisms with settling space, the latter may serve to camouflage the brachiopod and protect it from predators.

Color marking on the shell may also be a form of camouflage. It occurs on the shells of a few living brachiopods from shallow water (e.g., *Argyrotheca, Frenulina*), and traces of color patterns have been seen on the shells of a few fossil brachiopods (e.g., *Cranaena*).

## INORGANIC FACTORS

At the present day, all brachiopods normally live in water of full marine salinity, almost all are intolerant of any lowering of the salinity, and none are adapted to brackish- or fresh-water conditions. The lingulids can survive occasional brief periods of immersion in brackish or fresh water (e.g., a tropical storm while exposed at low tide); but they do so by closing their shells tightly and by retreating into their burrows, i.e., by temporarily suspending all normal metabolic activities. No other living brachiopods possess even this limited tolerance of nonmarine conditions.

The evidence of sediments and associated faunas suggests that the environments of fossil brachiopods were also invariably marine. The presence of fossil lingulids unaccompanied by other brachiopods is not a reliable indicator of brackish conditions of deposition. Such assemblages may indicate conditions that were normally marine but liable to occasional brief periods of brackish water. But lingulids are ecologically abnormal in several other respects, and other explanations are therefore possible.

All living brachiopods seem to require well-oxygenated water, and are not known from environments such as black organic-rich muds. This seems to be true also of fossil brachiopods. With certain exceptions, fossil brachiopods are conspicuously absent from the "black-shale" facies. The few that do occur are most plausibly interpreted as epiplanktonic, living suspended from floating vegetation or other organisms in the surface waters, away from the poorly oxygenated bottom conditions.

It is possible that living brachiopods, like other marine invertebrates, are limited in their distribution by narrow ranges of temperature tolerance, especially perhaps for reproduction, but of this little is known. At the present day, brachiopod faunas are most abundant and diverse in cool and temperate waters. Those found in subtropical or tropical latitudes are mainly confined to deeper water; the exceptions, which are presumably adapted to relatively high temperatures, include (among others) species of *Lingula, Glottidia, Discinisca,* and *Frenulina.* There is no apparent correlation between the size of brachiopods and the climatic region in which they live.

It is clearly hazardous to extrapolate such frail evidence to fossil brachiopods. The ecology of living species does not encourage the use of fossil species as indicators of paleotemperature. Nevertheless, certain fossil brachiopods have a circumscribed geographical distribution which does not seem to be attributable to limitations of present outcrops, original bottom conditions, possibilities of dispersal, etc., and which may be climatic in origin. In the Permian, for example, the Enteletidae, Richthofeniidae, and Oldhaminidae have a distinctive circumglobal distribution which may represent the tropical and subtropical belt of the time. The Permian brachiopod faunas within this belt are certainly remarkable for the diversity, abundance, and large size of many of their species, which recalls the character of the tropical molluscan faunas (but not brachiopod faunas) of the present day.

As in other marine animals, the range in depth of brachiopods is probably related closely to their range of temperature tolerance. The greatest abundance of living species occurs in the shallower waters of the continental shelves. Most of these species are limited to depths of a few hundred meters, but some extend through a remarkable range from shallow water into abyssal depths (e.g., *Terebratulina retusa* to 3,600 m.; *Macandrevia cranium* to 4,000 m.). A few species are confined to abyssal depths (e.g., *Abyssothyris wyvillei, Chlidonophora chuni*); none are known from hadal faunas. At the opposite extreme, very few species extend into the littoral (intertidal) zone. Here the chief limitations are of course the reduced time available for feeding and the risk of desiccation. Species of *Lingula, Glottidia,* and *Discinisca,* among the inarticulates, and *Terebratalia* and *Waltonia*, among the articulates, are known to extend up to mid-tide level. At low tide the lingulids retreat into their burrows; the other brachiopods can only close their shells tightly, but they tend to occur in situations where they are protected from desiccation (e.g., undersides of boulders). None of these species, however, is more than marginally intertidal; all of them are most abundant below low-tide level.

Like the evidence of temperature, that of depth is too indecisive to allow extrapolation to fossil brachiopods. Moreover, it is clear that many modes of life, some of which may have been related to definite conditions of depth, are unrepresented among the surviving species of the present day. It has been asserted that brachiopods as a phylum have tended to migrate into deeper water in the course of time; but this is doubtful, except in the most general sense that brachiopods have become less abundant members of the shallow-water faunas. Few fossil brachiopods can be used as indicators of depth; but the occurrence of fossil lingulids without other brachiopods may, if there are no indications of toxic conditions, be taken to reflect possibly littoral (intertidal) conditions of deposition.

It is commonly asserted that living brachiopods require clear water and cannot tolerate turbid conditions. While this perhaps may be true of some species, it is certainly not true of all. For example, among the shallow-water species that can be studied *in situ,* the inarticulate *Lingula* and the articulate *Waltonia* are well adapted to living in water that is generally turbid. Few if any direct observations on turbidity have been made on deeper-water brachiopods, but at least some species are known from muddy bottoms, and some can tolerate turbid conditions in laboratory aquaria. Tolerance of turbidity is clearly related to the feeding mechanisms. The digestive system, like that of other unselective suspension-feeders, is adapted to the extraction of food particles from a relatively large volume of other material (silt, etc.); and the highly developed rejection mechanisms enable the brachiopod to cope with any sudden large influx of inorganic material in suspension. In the last resort, the shell can be tightly closed, and can remain closed for several hours. Living brachiopods are less well adapted, however, to cope with any substantial sedimentation; unlike bivalve mollusks, for example, they lack the mobility to maintain themselves at the surface of a substratum on which rapid sedimentation is taking place (the infaunal burrowing habit of the lingulids gives them in this respect a unique advantage among brachiopods). Small or young brachiopods, especially, have to keep their shells clear of sediment by frequent and vigorous snapping of the valves and by turning around on the pedicle. Some species are commonly found in positions (e.g., undersides of boulders) which afford not only protection but also relative freedom from sedimentation.

A high tolerance of turbidity, with lesser tolerance of actual sedimentation, is likely to have been a general characteristic of brachiopods in the past; for there is no reason to suppose that the controlling physiological characters have changed radically. This is confirmed by the fact that fossil brachiopods commonly are abundant in muddy or silty sediments and in fine-grained limestones. Perhaps in some instances such sediments accumulated discontinuously, giving long periods without active sedimentation; but many must represent bottom environments of high turbidity with at least some degree of sedimentation.

Living brachiopods are generally found in bottom conditions that are relatively quiet and not swept by powerful currents. Those that occur in shallow turbulent water are commonly confined to the more protected micro-environments. This ecological preference, however, is probably dependent simply on the mode of anchorage of the shell. Attachment by a pedicle is probably not strong enough to withstand highly turbulent conditions. It is significant that *Crania,* with its ventral valve firmly cemented to a rock surface even in the earliest stages of growth after settlement, is able to survive on rocky bottoms with strong current action.

The mode of anchorage of the shell clearly influences to a great extent the types of substratum that can be utilized by brachiopods. Since most living species seem to be dependent on hard material for attachment, they are correspondingly limited to bottom environments in which such materials (rock, shell, coral, etc.) are abundant. This, however, is not a reliable guide to the ecology of fossil brachiopods, since many fossil species may have shared with the living *Chlidonophora* the ability to root into soft sediments. Others apparently lived freely on the surface of such sediments, or were stabilized by other means (spines, etc.). The living *Gwynia,* by its extremely small size and by other adaptations, is able to utilize the "difficult" environment of marine sand, as a member of the interstitial fauna.

Brachiopods were common members of "reef" faunas during the Paleozoic, but have been rare in similar environments in more recent periods. This has been attributed to the predation of the brachiopod larvae by coral polyps (10). But at the present day coral reefs support a large fauna of other organisms, some of which have planktonic larvae. The more sheltered parts of reefs should provide abundant sites of attachment suitable for brachiopods; yet very few (e.g., *Frenulina*) are in fact found there. It may be significant that deep-water ahermatypic corals, on the other hand, characterize an environment in which living brachiopods may be abundant. Brachiopods may have been rare on true reefs since the Paleozoic simply because the conditions of temperature or depth are generally unsuitable, or because predation by fishes, etc., is too great.

## REFERENCES

The sources of information on the ecology and paleoecology of brachiopods are so scattered that a comprehensive list of references cannot be given here. This list therefore contains only *(a)* a few compilations and other works with large bibliographies, and *(b)* some recent works on more specialized topics, which summarize research done in the last few years. The list excludes papers cited in the compilative works and also papers which, although they contain ecological material, are primarily concerned with systematics (a few exceptions to this have been included, however). The chapter also incorporates some of the author's unpublished work on the physiology and ecology of living and fossil brachiopods.

**Ager, D. V.**
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# CLASSIFICATION

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The history of brachiopod classification reveals a bewildering succession of taxonomic practices which have varied greatly in utility and popularity but have not yet given rise to a scheme that meets with general and lasting approbation. The principal reason for this confusion is, of course, the never-ending search for a classification that is not only workable and decisive in its application but also consistent with the known facts of brachiopod evolution, a requisite of special significance for a phylum founded mainly on paleontological data. These two qualifications, desirable though they be, are essentially incompatible with each other. Taxonomic procedure is a practical method of segregating organisms into identifiable groups, each with a clearly defined status within a classificatory scheme, whereas the theory of evolution postulates continuity between all such groups within the framework of time. This incompatibility has long been known, but the problems generated by attempts to satisfy both conditions in a classification of the Brachiopoda were not fully appreciated until some 50 years after BEECHER (2,3) had published his classic systematized interpretation of brachiopod phylogeny. Indeed, so important are his writings to the development of a sophisticated brachiopod classification that it is convenient to review various procedures adopted in the past according to whether they were proposed before or after the period 1891 to 1929, when the impact of BEECHER's ideas was most felt. Since, however, the full history of brachiopod systematics has recently been admirably summarized by MUIR-WOOD (31), the following account is concerned only with a comparison of those classifications that have most influenced modern practices.

The earliest classifications involving more than one suprageneric group, like those of MENKE (29), VON BUCH (9, 10), GRAY (18), PHILLIPS (37), M'COY (27) and KING (22) were attempts to formalize the profound differences existing between genera that were then known and at the same time to provide a simplified key for quick diagnosis. Thus KING recognized ten families (one embracing the coral *Calceola*), while VON

BUCH contrived to establish a hierarchical arrangement dependent primarily on external form. But a feasible monothetic classification, i.e., one in which the diagnostic set of features for any taxon is unique (47), did not appear until 1848, when GRAY (19) proposed to assign the brachiopods to two subclasses, the Ancylopoda and Helictopoda, based on the disposition of the lophophore and the structure of the shell (a third unnamed category for the rudist pelecypods was also tentatively listed). This segregation was carried to its logical conclusion. The Ancylopoda, which were described as having "recurved" brachia, were further divided into those with lophophores forming "hoops" (i.e., plectolophes), the Ancylobrachia; or "sunk into grooves" (e.g., thecideid lobate trocholophes), the Cryptobrachia. Again, among the Helictopoda a distinction was drawn between those in which the spirally disposed brachia were either supported by variably developed outgrowths from the "hinge margin" (Sclerobrachia) or lacking any such support (Sarcibrachia). In this way GRAY disposed of 8 families accommodating nearly 1,000 fossil species.

The most interesting feature of this classification was the assurance with which GRAY interpreted the anatomy of extinct groups. With commendable perspicacity, he indicated a relationship between rhynchonellids, pentamerids and spiriferids; and in concluding that an unsupported spirolophe was typical of his Productidae (comprising *Orthis, Leptaena, Strophomena,* etc.) was able to effect an integrated classification for both living and fossil species. No fundamental distinction, however, was drawn between the articulates and inarticulates, for the latter were all included as families in the Sarcibrachia, although DESHAYES (16) had already proposed the segregation of species with free (Libres) or articulated (Articules) valves, and OWEN (36) was shortly to erect two orders, Lyopomata and Arthropomata, on these differences and others like shell composition and proportions of viscera to shell space.

GRAY's scheme was accepted by many systematists (e.g., KING, 23, and, with some emendation, BRONN, 7) although others, like M'COY (28) and DAVIDSON (15) continued to recognize only familial divisions. DAVIDSON's reluctance to indulge in any monothetic classification was particularly noteworthy. After devoting his life to an unrivalled study of the phylum, he would not commit himself to anything more than assigning the 139 genera ultimately recognized by him to 29 suprageneric groupings, 7 of which were listed as Tretenterata KING (=Inarticulata HUXLEY) and the remainder as Clistenterata KING (=Articulata HUXLEY). Incidental comments on the lack of fossil evidence in support of the theory of evolution suggest that DAVIDSON found no relationships between these groups that were strong enough to warrant any closely integrated classification, although he was obliged to use the superfamilial rank. Throughout his researches DAVIDSON carefully discriminated in an appropriate systematic manner between family (-idae) and subfamily (-inae). Yet in bringing together all the loop- and spire-bearing brachiopods, he used the collective nouns "Terebratulacea" and "Spiriferacea," listed as "families," but actually embracing several orthodox families and subfamilies. DAVIDSON was thus among the first to appreciate the need for a taxonomic rank intermediate between family and order.

WAAGEN's classification (52) was altogether much more elaborate, for like that of GRAY, it was essentially monothetic and consisted of inarticulate suborders based on the presence and attitude of the pedicle, and articulate suborders founded mainly on the nature of the lophophore supports. Neither procedure was original. The former feature had been used for suprageneric classification by VON BUCH (11) and EUDES-DESLONGCHAMPS (17), and the latter by GRAY; but WAAGEN employed them with a much greater understanding of their classificatory merits. He was certainly the first to attempt any subordinal arrangement of the inarticulates which he knew by OWEN's term Lyopomata. Thus the Gasteropegmata was erected for forms, like the craniids, that lacked a pedicle and were attached by their "ventral valve"; the Daikaulia embraced the discinids, siphonotretids and genera which would now be included in the trematids and acrothelids, all with a pedicle which "pierces one of the valves"; his third suborder, the Mesokaulia, included the lingulids, obolids and trimerellids which WAAGEN believed had a pedicle that protruded between the valves. The articulates (i.e., Arthropomata of OWEN) were divided into four suborders, the Kampylopegmata for brachiopods with "curved" skeletal supports to the lophophore, the Helicopegmata for those with spiral skeletal supports, the Aphaneropegmata for those without any calcareous lophophore supports, and the Coralliopsida for the Richthofenidae.

Even in the light of contemporary knowledge, there were incongruities to WAAGEN's scheme, like the exalted rank of the richthofeniids, which, in contrast to the lyttoniids, had been separated at the subordinal level from the productids, and the assignment of the rhynchonellids and thecideids, as well as all loop-bearing brachiopods, to the Kampylopegmata. These weaknesses were generally recognized by others who used the classification, and emendations accordingly were made. ZITTEL (61), for example, replaced the Kampylopegmata by the Ancylopegmata, which included all the loop-bearers (compare the Ancylobrachia of GRAY), and the Ancistropegmata for brachiopods like the rhynchonellids that were equipped with crura. In this manner modified versions of WAAGEN's classification continued in use as late as 1949 (49), and would probably have enjoyed a much wider popularity if SCHUCHERT had not so actively promoted BEECHER's classification as one that faithfully reflected brachiopod evolution.

BEECHER's ordinal segregation of the Brachiopoda (2) was undoubtedly inspired by the Haeckelian theory of recapitulation. His prefatory remarks include references to the efficacy of HYATT's law of morphogenesis and to methods of elucidating the evolutionary history of phyla by applying the "principles of growth, acceleration of development, and mechanical genesis" in the light of the "geological sequence of genera and species." Therefore, he believed that the study of a relatively few stocks, the selection of which was fortuitously determined by what was then known of brachiopod ontogeny would provide the key to a broad classification in harmony with the main evolutionary changes affecting the group.

According to BEECHER, the generalized morphology of the brachiopod protegulum represents the most primitive condition of the shell and is closely comparable with that of adult *Paterina*, which may therefore be regarded as typifying the "early primordial form." Subsequent diversification of the phylum was essentially related to an increasing dissimilarity in the form and relationship of the valves and to a ventral migration of the pedicle. BEECHER recognized that one of the most distinctive features to develop in the brachial valve was a skeletal support for the lophophore. Yet he maintained that internal structures like these grew independently of the valves and could safely be ignored in any interpretation of brachiopod history based on shell form. In contrast, the type of pedicle opening and even the length of pedicle were regarded as important factors in shell growth and, in the belief that they indicated the existence of four distinct groups which came into being during the evolution of the phylum, BEECHER proposed four new orders, the Atremata and Neotremata to embrace all inarticulate genera, and the Protremata and Telotremata to include all articulates. The diagnoses of these taxa include comments on the nature of the protegulum and subsequent shell growth and on the occurrence of articulation and supports for the lophophore; but, judging from the preamble to his classification, BEECHER gave pride of place to the location of the pedicle opening. Thus, the pedicle of the Atremata was described as lying in the commissural plane and emerging between both valves, while that of the Neotremata was stated to be disposed normal to the commissural plane and confined to the "lower" valve where the pedicle opening may be a slit opening posteriorly or entirely surrounded by shell and even subcentrally located. The Protremata were believed to have been derived from the Neotremata, although the pedicle opening remained in a submarginal position and posterodorsally was either constricted by a pseudodeltidium *(Strophomena)* or open through resorption of that structure *(Orthis)*. BEECHER also noted that the pedicle of young Telotremata is oriented like that of the Atremata but with further growth of the shell is normally restricted to the pedicle valve by deltidial plates. The affinities suggested by such comparisons were contrary to those implicit in the recognition of the Articulata and Inarticulata and led BEECHER to reject these terms (or their synonyms) as formal taxa. His comparative review (3) of the embryology of certain brachiopods belonging to all four orders seemed to vindicate his earlier conclusions because he interpreted KOVALEVSKIY's study (24) of the development of the "protrematous" *Lacazella* as showing the pseudodeltidium to originate independently of the pedicle valve.

The repercussions of this ingenious analysis were not immediately felt. The classification used by HALL & CLARKE in their definitive review of the Brachiopoda (20), for example, was an inconsistent mixture of earlier schemes; although three of BEECHER's orders were used, the systematic validity of the Inarticulata and Articulata was still upheld. WAAGEN's division of the inarticulates into three suborders was adopted in its original form, except for a minor etymological correction of two subordinal names to Mesocaulia and Diacaulia, and the listing of Atremata as an alternative to the former. The adoption of BEECHER's Protremata and Telotremata as ordinal taxa for the articulates was, however, attended by some important changes within the latter group, which was divided into three suborders, Rostracea (first used by SCHUCHERT) for the rhynchonellids, Ancylobrachia (of GRAY) for the loop-bearers, and Helicopegmata (of WAAGEN) for the spire-bearers. The text accompanying this classification suggests that HALL & CLARKE accepted BEECHER's ideas on brachiopod phylogeny without realizing how irreconcilable they were with those systematic treatments of the phylum based solely on morphological comparison. This incompatibility was, however, fully appreciated by SCHUCHERT, who for the next quarter of a century conducted a prolific and spirited defense of BEECHER's thesis that classifications must be founded on the facts of evolution.

In 1893, SCHUCHERT (42) was content to employ BEECHER's orders as subdivisions of the Lyopomata (Inarticulata) and Arthropomata (Articulata), but by 1897 he had completely revised (43) the brachiopod classification, then embracing more than 6,000 species, to conform strictly with *his* interpretation of the evolutionary history of the phylum. WALCOTT (53) had already shown that, in contrast to the brachiopod protegulum, *Paterina* possesses a "cardinal area." Yet SCHUCHERT persisted in the belief that the ancestor to the phylum must have been like the protegulum and continued to use the term "Paterina" to denote this theoretical stage in brachiopod evolution. The "third shell," identified by BEECHER in the development of *Lacazella* and named the "prodeltidium" by HALL & CLARKE, was the source of even greater speculation. SCHUCHERT, consolidating tentative observations by MÜLLER (32) and BROOKS (8), not only homologized the prodeltidium with a "plate somewhat loosely attached to the ventral shell" of *Discinisca,* but also with a posteromedian thickening in the brachial valve of *Lingula.* He therefore concluded that the prodeltidium, supposedly secreted by the pedicle, was invariably present except in the Telotremata, and was attached to the pedicle valves of the Neotremata and Protremata and to the brachial valve of the Atremata. On this basis he was able to define two superorders: the Homocaulia, embracing the Atremata and Telotremata, and the Idiocaulia containing the Neotremata and Protremata. Since this grouping is contrary to that resulting from the use of Inarticulata and Articulata, SCHUCHERT sought to show that the latter categories had neither phylogenetic nor morphological worth. Hence, he contended that the so-called "perforations" in the "dorsal beaks" of a number of fossil Protremata and Telotremata must have been anal openings; that articulation was developed in many Atremata and even in the Neotremata, yet was hardly functional in the protrematous *Kutorgina*; and that the Telotremata were represented in the Lower Cambrian by *"Protorhynchia antiquata"* (now referred to *Swantonia,* a genus of uncertain taxonomic position) and must have evolved from the Atremata and not from the protrematous orthids as postulated by HALL & CLARKE (20).

The infraordinal classification advocated by SCHUCHERT in 1897 involved the standardization of taxa with the termination

"-acea" (previously used by WAAGEN and DAVIDSON for suprafamilial units of varying rank) as superfamilies. In this manner, 31 families were arranged within 10 superfamilies, the atrematous Obolacea and Lingulacea, the telotrematous Rhynchonellacea, Terebratulacea and Spiriferacea, the neotrematous Acrotretacea, Discinacea and Craniacea, and the protrematous Strophomenacea and Pentameracea.

In all but the last of his later writings on the Brachiopoda, SCHUCHERT maintained these views on the nature and phylogenetic importance of the relationship between the pedicle and the shell. Some strictly systematic rearrangements were promulgated from time to time but no allowance was made for the growing body of evidence that was steadily undermining the very foundations of his classifications. In 1913 he again emphasized (44) the need to build a classification on "the history of the class (chronogenesis) and the ontogeny of the individual," and declared that there are "certain primary characters," like the nature of the pedicle opening and the stages of shell development, which can be used to define orders, while "persistent internal characters" may be employed for superfamilial division. The classification put forward had been enlarged by the addition of three superfamilies, the Rustellacea (Atremata), Siphonotretacea (Neotremata) and Orthacea (Protremata). More significantly, WALCOTT's studies of the Cambrian brachiopods (54) had caused SCHUCHERT to shift the Kutorginacea from the Protremata to the Atremata and to acknowledge that the Telotremata first appeared not in the Lower Cambrian but in the Ordovician. He did not, however, realize how contradictory these revisions were to the arguments he had used in 1897 for the abolition of the Inarticulata and Articulata and the derivation of the Telotremata from the Atremata rather than the Protremata. In fact, the sole concession made by SCHUCHERT was to conclude that the Telotremata and Neotremata had evolved from the Obolacea (Atremata) and the Protremata from the Kutorginacea (by then transferred to the Atremata), a relationship that necessitated the abandonment of the superorders Homacaulia and Idiocaulia.

Even in 1929 SCHUCHERT (with LEVENE) continued (46) to use BEECHER's orders (together with Palaeotremata of THOMSON) as the basis for the classification of the 700 or so brachiopod genera then known. In all, 56 families were recognized and distributed among 19 superfamilies, five of which were new. One of these, the Paterinacea, was removed to the Palaeotremata. The others, Trimerellacea (Atremata), Clitambonacea (Protremata), Rostrospiracea and Atrypacea (Telotremata) simply represented hierarchical promotions of families within the same orders to which they had been assigned in 1913. Indeed, SCHUCHERT did not admit any suspicions about the validity of his phylogenetic and systematic practices until 1932 when he held it likely (45) that the Telotremata arose from the Protremata and the "prodeltidium" had been misinterpreted. By then, however, the BEECHER-SCHUCHERT classification had become so firmly established in literature that even when its inadequacies were known, paleontologists were generally content to recast it rather than advocate its discard. KOZLOWSKI (25), for example, in his systematic study of the Silurian brachiopods of Poland used BEECHER's orders but, in contradiction to the reasoning that led to their erection, assigned the Atremata and Neotremata to the Inarticulata and the Protremata and Telotremata to the Articulata. After demonstrating the polyphyletic origin of the spondylium, he also moved the Pentameracea from the Protremata to the Telotremata in the misapprehension that what delthyrial covers developed in that group originated in the same way as the telotrematous deltidia.

The chief reason for the survival of the BEECHER-SCHUCHERT classification for so long after the exposure of the fallacies that had prompted its construction was, paradoxically, THOMSON's critique on brachiopod morphology and systematics (50). In an enquiry into the naturalness of BEECHER's orders, he reviewed embryological researches that flatly contradicted the generalizations propounded by BEECHER and later assumed by SCHUCHERT, and pointed out further deficiencies that had arisen from their disregard of the delthyrium, articulation, and shell structure. THOMSON concluded that in living brachiopods differences in the development of the pedicle are far more fundamental than the nature of the pedicle opening, and since these were associated with other distinguishing features that had previously been used for the separation of the Inarticulata (or Lyopomata) and Articulata (or Arthropomata), he urged the continued recognition of two similarly constituted subclasses. For this purpose he proposed Gastrocaulia and Pygocaulia, which were broadly synonymous with the Inarticulata and Articulata, respectively, but, in his estimation, sufficiently different in content and emphasis to warrant new names. Actually, the changes introduced by him for the definition of his new subclasses were much less important than the revision he considered necessary at the ordinal level. Thus, he maintained that the Neotremata as understood by BEECHER and SCHUCHERT was diphyletic and he revised the grouping of the inarticulates by assigning the Obolacea, Lingulacea and Siphonotretacea to the Atremata, and the Paterinacea, Acrotretacea, Discinacea and Craniacea to the Neotremata. The rearrangement of the articulates was equally drastic because, although the Orthacea, Strophomenacea and Pentameracea were still allocated to the Protremata, and the Rhynchonellacea, Spiriferacea, and Terebratulacea to the Telotremata, a new order, Palaeotremata, was introduced for the Kutorginacea and Rustellacea with their undifferentiated shell and incompletely developed articulation and delthyrium. In effect, the emendations advised by THOMSON were incompatible with the intention behind BEECHER's orders. Yet so established had those orders become that, in contrast to his treatment of the subclasses, THOMSON preferred to recast their diagnoses entirely rather than abandon them for a new classification. This ambivalence, especially in conjunction with his well-reasoned criticisms, was undoubtedly the signal for excessive caution from other paleontologists and greatly extended the life of a classification that had long ceased to have any intrinsic merit.

The response to the mounting evidence that militated against the retention of BEECHER's orders was varied. Some students, like KUHN (26) were content to accept THOMSON's emended version of the classification *in toto* and do nothing more than change the status of some taxa. Others adopted bits of it. This selective practice seems to have been started by ULRICH & COOPER (51), who used THOMSON's subclasses as well as the orders Atremata and Neotremata; although in describing the articulates they omitted reference to any rank above the subordinal level, a position then held by their Orthoidea, Strophomenoidea and Syntrophioidea. No explanation was given for this action, but in 1944, COOPER (13) produced a provisional systematic arrangement of the phylum and briefly listed the reasons for introducing certain emendations. COOPER's classification was basically that of THOMSON, although he had by that time reverted to the use of Inarticulata and Articulata in preference to Gastrocaulia and Pygocaulia, respectively. He retained the Atremata and Neotremata but transferred the Siphonotretacea back to the latter order. The only articulate order to survive, however, was the Palaeotremata. The remaining articulate genera were assembled into superfamilies which in turn were grouped together according to shell structure. Thus, the impunctate Articulata contained the Orthacea, Clitambonacea, Syntrophiacea [Porambonitacea], Pentameracea, Triplesiacea, Rhynchonellacea, Spiriferacea, Atrypacea and Rostrospiracea; the pseudopunctate Articulata, the Strophomenacea and Productacea: and the punctate Articulata, the Dalmanellacea [Enteletacea], Terebratulacea and Punctospiracea. COOPER emphasized that such an arrangement, based on shell structure, was not intended as a "genetic classification" but as an informal guide for quick identification of genera. This qualification was reiterated in 1956 when the same scheme was used in his study of Ordovician brachiopods (14), although the subclasses Gastrocaulia and Pygocaulia were reinstated without comment.

Despite the cautionary note struck by COOPER, his views stimulated contrasted systematic activity. Both ROGER (38) and MOORE (30) adopted the orders Atremata, Neotremata and Palaeotremata as understood by COOPER (13). ROGER also accepted COOPER's demonstration of the systematic value of shell structure but not his criticisms of the Protremata and Telotremata, because in a gesture of uninhibited compromise he set up five composite orders, the Protremata Impunctata, Protremata Pseudopunctata, Protremata Punctata, Telotremata Impunctata, and Telotremata Punctata. Moore, on the other hand, concurred with Cooper on the need to abandon the Protremata and Telotremata, but concluded that the grouping of superfamilies solely on shell structure was inconsistent with other morphological evidence and should not be formalized. Instead, he proposed the elevation of most suborders then known to ordinal rank (the "Clitambonitoidea" were not included presumably through oversight), thereby filling the gap in the hierarchy left by the rejection of the Protremata and Telotremata. Excluding members of the Palaeotremata, all articulate genera were assigned to twelve suborders (denoted by the termination—"-acea") and seven orders—("-ida"). They were (1) Orthida (including the Orthacea and Dalmanellacea [Enteletacea]), (2) Pentamerida (Syntrophiacea [Porambonitacea], Pentameracea), (3) Triplesiida, (4) Rhynchonellida (Rhynchonellacea, Rhynchoporacea), (5) Strophomenida (Strophomenacea, Productacea), (6) Spiriferida (Atrypacea, Spiriferacea, Rostrospiracea, Punctospiracea), (7) Terebratulida.

In her history of brachiopod classification, Muir-Wood (31) went even further toward the abolition of Beecher's classification. She discarded the order Palaeotremata and assigned the Kutorginacea to the Orthoidea (the Rustellacea being cited as *"incertae sedis"*). She also predicted that a comprehensive revision of the inarticulates would lead to the rejection of the Atremata and Neotremata, although they were provisionally retained in the classification presented by her. She foresaw difficulties in using shell structure or any other single character as the basis for an ordinal classification of the articulates and, pending the completion of several independent studies that were then being undertaken for the *Treatise*, used only suborders and superfamilies to accommodate the 108 articulate families known at that time. In this manner 15 suborders were recognized: Orthoidea, Dalmanelloidea, Clitambonitoidea, Syntrophioidea, Pentameroidea, Triplesioidea, Strophomenoidea, Oldhaminoidea, Productoidea, Rhynchonelloidea, Atrypoidea, Spiriferoidea, Chonetoidea, Terebratuloidea and Terebratelloidea, of which the last three were new.

The shortcomings of the systematic schemes propounded by Beecher and Schuchert have all been stated at one time or another but are worth reiterating at this juncture.

The chief attraction of Beecher's thesis has always been his contention that a few features, and especially the pedicle opening, not only provide a simple classificatory key for the Brachiopoda but also indicate the main lines of descent within the phylum. The principal novelty of the resultant classification was undoubtedly the assumption that the Telotremata were not related to the Protremata but derived out of the Atremata. Yet even in the light of contemporary knowledge, Beecher was not really justified in arriving so confidently at such controversial conclusions. He interpreted the relationship between the pedicle and the shell in much too mechanistic a fashion and naively ignored both the anatomy of that organ and the structure of various openings accommodating it. The studies of Hancock (21), which must have been known to him, had already shown how much the pedicle of *Lingula* differed from those of *Terebratulina* and *Hemithiris,* while the likeness between the open delthyria of certain Protremata and Telotremata, as pointed out by Thomson (50), ought at least to have been considered.

Apart from the attitude of the pedicle, the distinction drawn between the protrematous and telotrematous delthyrial covers also played an important rôle in ordinal diagnosis. The difference as then understood depended entirely on Beecher's opinion (3) that the third shell (prodeltidium) of the Protremata was secreted not by the mantle but by the pedicle and only later became ankylosed to the pedicle valve during subsequent growth. Since its publication, this assertion has been the subject of increasing criticism, culminating in the proof that the pseudodeltidium has always been similar in shell structure to the rest of the valve, even in *Lacazella* (56, 57), and that Beecher misinterpreted Kovalevskiy's work (1). The shell substance figured by Kovalevskiy as originating on the pedicle rudiment and homologized by Beecher with the pseudodeltidium is not, as he believed, a discrete plate but the lateral view of a ring continuous with the pedicle valve.

Finally, the location of the teeth of articulate brachiopods invariably flanking the delthyrium and fitting into dorsal sockets, the differences between the muscle systems of the inarticulates and articulates, and the fibrous nature of the secondary shell shown by CARPENTER (12) to be typical of the articulates, should not have been so lightly disregarded by BEECHER during his enquiry into the relationship between the Protremata and Telotremata.

It may be said that the mistakes perpetrated by BEECHER are only obvious in retrospect, but even so, their perpetuation by SCHUCHERT is less excusable. By 1913, when SCHUCHERT repeated without any basic modification his views on brachiopod phylogeny, BLOCHMANN (5, 6) had decisively demonstrated the essential anatomical homogeneity of the inarticulates, and YATSU (60) had shown that the development of *Lingula* is greatly different from that of living articulates and does not include the secretion of a third shell. In the face of this evidence and that of WALCOTT (54) on the post-Cambrian origin of Telotremata, the views held by SCHUCHERT are inexplicable.

In a bid to retain BEECHER's orders there has been a tendency to revise their diagnoses in such a way as to emphasize the exclusiveness rather than the derivation of their chief characteristics. Such emendations were really attempts to change a phylogenetic classification into a monothetic one. THOMSON (50), for example, contrasted the hemiperipheral succeeded by mixoperipheral growth of both valves of the Atremata with the holoperipheral growth of, at least, the pedicle valve of the Neotremata. But, since he included the Obolacea, Lingulacea, and Siphonotretacea in the former order and the Paterinacea, Acrotretacea, Discinacea, and Craniacea in the latter order, he was obliged to concede that in members of both taxa the pedicle might have emerged between both valves or through an opening of the pedicle valve. The important differences cited for the segregation of the articulates (excluding the Palaeotremata) were for the Protremata "ventral delthyria closed only by impunctate deltidia" and "brachial supports absent or rudimentary"; and for the Telotremata "ventral delthyria partially or completely closed by deltidial plates, pseudodeltidia or symphytia which are punctate in punctate shells," and "brachial supports generally well developed." Even generalized statements of this sort, however, do not promote the merits of BEECHER's orders sufficiently to warrant their retention, as can be shown by reviewing some of the discrepancies.

In terms of shell growth, THOMSON was justified in assigning the Paterinacea to the Neotremata. But the nature of the posterior opening between the valves is anomalous and apart from the subconical form of the pedicle valve there are few resemblances between the paterinaceans and other genera included within the Neotremata. The only satisfactory solution, as was realized by COOPER (14), is to place *Paterina* and its related genera in a taxon outside both the Atremata and Neotremata, but this, of course, means that "holoperipheral growth" as a taxonomic feature is no longer unique to members of the Neotremata. Other examples may be cited which contradict any reasonably designed diagnoses for the two orders. *Curticia* has commonly been regarded as belonging to the Atremata (54) because adults have a triangular opening in the posterior margin of the pedicle valve. This opening, however, is not homologous with the lingulid pedicle groove. It was formed during ontogeny by a dorsally directed resorption of the shell and the pedicle was initially restricted to a small slitlike foramen near the apex of the valve. Hence, juvenile *Curticia* would undoubtedly be placed in the Neotremata and indeed many of the characters of the genus suggest that it was derived from some acrotretacean stock (40). Similar difficulties arise in the classification of the Obolellidae. *Alisina,* with an apical pedicle foramen, and *Trematobolus,* which has a pedicle foramen opening anterior of the apex, would unquestionably be referred to the Neotremata. Yet *Obolella* and *Magnicanalis,* which in all other respects appear to have been very closely related, would have to be placed in the Atremata, since their pedicle seemingly emerged between the valves.

Morphological differences between the Protremata and Telotremata are even less exclusive. Like that of the Telotremata, the delthyrial cover developed in any protrematous stock is deposited by outer epithelium in exactly the same way as the shell and is therefore similar in microstructure to the rest of the pedicle valve (57). Moreover, the protrematous cover is not always a pseudodeltidium. Deltidial plates, identical in genesis with those of the telotremates, are known in the orthacean *Barbarorthis* and the enteletacean *Phragmophora,* and the apical plates commonly found in the spiriferides are also known among the pentameraceans.

The use of the lophophore skeletal supports to distinguish between the Protremata and Telotremata is contrary to the advice of Beecher, but even when employed in the manner advocated by Thomson, no mutually exclusive scheme of classification, consistent with other morphological data, can be arranged. Among groups assigned to the Protremata, apophyses that probably functioned like the telotrematous crura, are known in a minority of Orthidina (57) and in most pentameraceans; while loops developed in the enteletacean *Tropidoleptus* and the pentameracean *Enantiosphen* (58) and spiralia in the davidsoniacean *Thecospira* (55). Among members of the Telotremata, the spiriferide leptocoeliids lacked spiralia (33) and in a few terebratulides, like *Gwynia*, it has long been known that only vestiges of a loop or dorsal median septum are retained for the support of the lophophore.

In summary, it may be said that no possible benefit can accrue from the retention of Beecher's classification or any emended version of it that contrives to maintain any of the original assumptions on which it was based. It in no way reflects brachiopod phylogeny as we now understand it, nor can it be adopted as a workable morphological key for the quick identification of brachiopod groups.

Following the collapse of Beecher's classification only a few attempts have been made to erect a monothetic classification. The use of shell structure in the classification of articulates has lately exercised some attraction but, although the impunctate, endopunctate, and pseudopunctate shell types are all distinctive enough to be categorized, the resultant classification would be intolerably artificial. Abundant evidence now suggests that although pseudopunctate and endopunctate brachiopods descended from impunctate stocks, all three shell conditions reappeared continually during evolution of the phylum. The earliest endopunctate enteletaceans, the paurorthids, angusticardiniids, and dalmanellids are so unlike in other features that they possibly arose independently of one another from diverse orthaceans. The rhynchonellide *Rhynchopora* was certainly unrelated to any other endopunctate group, and although the Terebratulida appear always to have been endopunctate, the relationships within their probable ancestors, the Spiriferida, are complex. The earliest spire-bearers are all impunctate but the endopunctate condition ultimately became characteristic of four distinct groups, three of which, the suessiaceans, spiriferinids, and syringothyridids, are reputed to include some impunctate descendants. The relationship between the impunctate and pseudopunctate conditions, surprisingly enough, is also complex. The latter type of shell is generally thought of as being exclusively diagnostic of the Strophomenida. In fact, it is also characteristic of the Gonambonitacea (35), and although this group may actually have had a common ancestry with the Plectambonitacea rather than the Clitambonitacea, with which it is now associated systematically, the impunctate condition of certain Strophomenida, like early species of *Christiania* (48), the plectambonitacean *Ukoa* (34), and early davidsoniaceans (57) is equally misleading.

Deficiencies of a classification based exclusively on lophophore supports have been recognized generally since the turn of the century, but they did not deter Beurlen (4) from proposing a monothetic scheme based on the known or inferred disposition of the lophophore. He erected two orders: the Orthoconata, to include the Orthacea, Triplesiacea, Clitambonitacea, Strophomenacea, Dalmanellacea [Enteletacea], Rhynchonellacea, Atrypacea, and Terebratulacea; and the Tropoconata to embrace the Syntrophiacea [Porambonitacea], Pentameracea, and Spiriferacea. According to Beurlen, who relied mainly on shell shape to interpret the attitude of the lophophore, orthoconate brachiopods possessed a lophophore disposed as a pair of low spires lying in the plane of the commissure with the apices directed submedianly; in the tropoconates, the spiral brachia were normal to the commissural plane, thereby conforming with the strong biconvexity and reduced hinge line of primitive stocks. Neither ordinal diagnosis, of course, is consistent with the attitude of the terebratulide plectolophe, but a much graver fault is the unprecedented systematic importance given to shell shape on the assumption that it invariably reflects one of two basic attitudes of the lophophore. The prevalence of homeomorphy throughout the history of the phylum shows how unsuited this feature is for the construction of an acceptable classification. Among the orthacean plectorthids alone, such great variation in shell shape is found that it is possible to draw close comparisons with members of other superfamilial groups. *Plectorthis* is gently biconvex and would probably be classified as a typical orthoconate brachiopod. Its near relatives, however, include *Herbertella,* dorsibiconvex like *Atrypa, Cyclocoelia,* almost rostrate in the rhynchonellid fashion, and *Platystrophia,* strongly reminiscent of *Spirifer,* all of which would have to be assigned to different suborders or even orders.

The disadvantages of any monothetic classification of the Brachiopoda have been reviewed by WILLIAMS (57), who demonstrated that all such schemes proposed in the past are incompatible with the evolutionary history of the phylum. This limitation does not necessarily preclude the use of a monothetic classification, provided that it always is acknowledged to be only a catalogue of brachiopods, deliberately arranged for the quick identification of stocks. A grouping of the articulates based upon differences in shell structure or lophophore supports as used by COOPER and WAAGEN respectively, falls into this category. No one, however, admits to being entirely satisfied with a classification which is merely a key to the identification of specimens. An awareness of the effects of evolution so pervades paleontological thought that preference is rightly given to those schemes purporting to reflect the main lines of descent. Hence the attraction exercised by classifications like those of BEECHER, SCHUCHERT, and BEURLEN derives not so much from their simplicity as from the claim that they represent a synopsis of the history of the phylum. Brachiopod evolution, however, so obviously pursued a far more complicated course than is indicated by such classifications that they do not even constitute plausible monothetic groupings. It can be shown that every character which has played a fundamental role in classifications of this kind arose independently in unrelated stocks, and the inescapable conclusion is that no satisfactory ordinal arrangement will ever emerge from the use of a few selected features of shell morphogeny.

It is apparent then that the only way to erect a classification which approximates to brachiopod evolution and is at the same time utilitarian is to build one up from a series of basic units—the genus is best suited for this purpose in paleontology—by a process of continual morphological comparison. Such a classification is more objective than one contrived by the fragmentation of predetermined orders because each character is assigned a taxonomic value largely uninfluenced by preconceptions. Moreover, morphological comparison is the paleontological measure of affinity, so that when genera are assembled into families, families into superfamilies, and so on, it becomes evident that each taxon within the hierarchy spanned by a particular group is typified by a certain combination of features which commonly can be related to morphogenetic developments within the group. This does not mean that the hierarchical status of character combinations for any one group of brachiopods can be used unconditionally for similar character combinations in any other group, as advocated by SCHUCHERT (43). Each group should be built up separately, because features which persist unmodified in one group and have therefore a high systematic value, appear only sporadically or are subject to extreme variation in another group and so possess a low systematic value. In effect, the classificatory importance of a character is normally a function of the number of species (or genera) in which it appears. Thus variably developed deltidial plates or symphytia are always present in members of the Terebratulida and so have a diagnostic value at the ordinal level. Yet the occurrence of deltidial plates in *Barbarorthis,* of the Hesperorthinae, a well-defined group deserving no more than a subfamilial rank in the orthacean hierarchy, does not necessitate the separation of that genus from its hesperorthin relatives and its promotion to ordinal rank.

The range of each genus compared with that of the group to which it is morphologically related can also affect the design of a classification, because the variability of even persistent characters was frequently an inverse function of time as measured by phyletic existence. Thus the form of the loop in established terebratulides is sufficiently stable to play a very important part in classification, but it is highly variable even within a generic stock when the order first appeared (25). Consequently, if the diverse loops found in early Devonian *Mutationella* were assigned the taxonomic value they undoubtedly possess in stabilized Mesozoic Terebratellidina, almost every individual would constitute a genus and every population a family.

The time range of a genus is another important factor influencing taxonomic procedure. Along with detailed morphological comparison it serves to distinguish convergent elements in unrelated and related groups. Many paleontologists (e.g., Kozlowski, 25) have commented on the similarity between dorsal interiors of thecideaceans and certain plectambonitaceans. On morphological grounds these two groups might appear to have some affinity but there cannot be any genetic relationship between them, because the last plectambonitacean is recorded from the Middle Devonian and the earliest thecideacean from the Triassic. A more striking example of external and internal homeomorphy exists between the orthacean *Phragmorthis* and the enteletacean *Mystrophora* (14). Apart from differences in shell structure, only minor morphological details serve to separate them; yet heterochronous convergence is the only explanation for this likeness because the former is restricted to the Ordovician and the latter to the Devonian.

These considerations led Williams (57) to emphasize the value of superfamilies as taxa made up of demonstrably related stocks. It remains to be seen whether, through processes of systematic trial and error, this rank has become, as suggested by him, a rough measure of successful paedomorphic changes that have dictated the course of brachiopod evolution. Nonetheless the superfamilies, as at present conceived, are highly distinctive taxa. Genera included in the Davidsoniacea, for example, can be confidently described as constituting a basically homogeneous group diversified by the loss or exaggerated growth of dental plates, the differential development of cardinal area, the acquisition of pseudopunctation and secondary ornamentation, etc. Yet the affinities of their impunctate progenitors can only be described vaguely as strophomenidine.

Although superfamilies can be defined in terms of distinctive character combinations, their contents are not necessarily morphologically unique. Indeed, as disputes over superfamilial affiliations of a minority of genera, like *Christiania,* show, some stocks exhibiting morphological overlap between allied superfamilies can be expected to have persisted beyond the early stages of group divergence, thereby indicating the more feasible ways of combining superfamilies into suborders and orders. Williams contended that the articulate superfamilies, except for the Triplesiacea and Thecideacea, could be marshalled into six groups, each typified by a well-known brachiopod (*Orthis, Strophomena, Pentamerus, Rhynchonella, Spirifer, Terebratula*) epitomizing the generalized morphology of its group. No formal taxa were then proposed for these groups, although it was pointed out that the complex processes of morphological duplication that characterized brachiopod evolution make it impossible to define the assemblages by diagnoses that are not mainly repetitive. The superfamilies making up the groups were: (1) *Orthis* group: Orthacea, Dalmanellacea [Enteletacea], Clitambonitacea, ?Triplesiacea; (2) *Pentamerus* group: Syntrophiacea [Porambonitacea], Pentameracea, ?Triplesiacea; (3) *Strophomena* group: Plectambonitacea, Strophomenacea, Orthotetacea, Oldhaminacea [Lyttoniacea], Productacea, Richthofenacea, Chonetacea, Cadomellacea; (4) *Rhynchonella* group: Rhynchonellacea, Stenoscismatacea; (5) *Spirifer* group: Atrypacea, Spiriferacea, Athyracea [Athyridacea]; (6) *Terebratula* group: Terebratulacea, Terebratellacea, ?Thecidacea [Thecideacea].

In the introduction to the brachiopod section of the *Osnovy Paleontologii* (41), SARYCHEVA reiterated the arguments given above for building up a classification from a generic foundation and presented what was admitted to be a provisional arrangement constructed in this manner. The most significant advance was the abandonment of BEECHER's Atremata and Neotremata and the allocation of inarticulate genera to six orders embracing 11 superfamilies: (1) Rustellida: Rustellacea; (2) Lingulida: Obolacea, Lingulacea, Trimelleracea; (3) Craniida: Craniacea; (4) Acrotretida: Acrotretacea, Discinacea; (5) Siphonotretida: Obolellacea, Siphonotretacea; (6) Kutorginida: Paterinacea, Kutorginacea.

No explanation was given for this revision in either the introduction or the systematic chapter on the inarticulates prepared by GORYANSKY, and the orders appear to have been introduced to produce some degree of parity between the ordinal classification of the Inarticulata and Articulata. Articulata genera were assembled into 8 orders and 26 superfamilies: (1) Orthida: Orthacea, Rhipidomellacea, Enteletacea, Clitambonitacea; (2) Pentamerida: Porambonitacea, Camerellacea, Pentameracea; (3) Strophomenida: Plectambonitacea, Strophomenacea, Stropheodontacea, Orthotetacea; (4) Productida: Chonetacea, Productacea, Lyttoniacea; (5) Rhynchonellida: Rhynchonellacea, Rhynchoporacea; (6) Atrypida: Cyclospiracea, Atrypacea, Coelospiracea, Dayiacea; (7) Spiriferida: Spiriferacea, Delthyriacea, Spiriferinacea; (8) Terebratulida: Terebratulacea, Terebratellacea, ?Thecidacea [Thecideacea]. In addition, the Triplesiacea, which were believed to have features in common with the Pentamerida and Strophomenida, and the Athyracea [Athyridacea], which were considered to be an unnatural grouping, were listed as *incertae ordinis,* as were the Eichwaldiidae, although near relatives, the Isogrammidae, were assigned to the Productida.

The classification used herein has also been built up by continual morphological comparison of genera, subfamilies, families, etc. It is the product of several contributors and at suprafamilial levels consists of 48 superfamilies, 20 suborders, and 11 orders. For purposes of comparisons with earlier classifications, it is necessary to list only orders and their constituent superfamilies, which are: (1) Lingulida: Lingulacea, Trimerellacea; (2) Acrotretida: Acrotretacea, Discinacea, Siphonotretacea, Craniacea; (3) Obolellida: Obolellacea; (4) Paterinida: Paterinacea; (5) Kutorginida: Kutorginacea; (6) Orthida: Billingsellacea, Orthacea, Enteletacea, Clitambonitacea, Gonambonitacea, Triplesiacea; (7) Strophomenida: Plectambonitacea, Strophomenacea, Davidsoniacea, Chonetacea, Cadomellacea, Strophalosiacea, Richthofeniacea, Productacea, Lyttoniacea; (8) Pentamerida: Porambonitacea, Pentameracea; (9) Rhynchonellida: Rhynchonellacea, Stenoscismatacea, Rhynchoporacea; (10) Spiriferida: Atrypacea, Dayiacea, Retziacea, Athyrisinacea, Athyridacea, Koninckinacea, Cyrtiacea, Suessiacea, Spiriferacea, Spiriferinacea, Reticulariacea; (11) Terebratulida: Stringocephalacea, Cryptonellacea, Dielasmatacea, Terebratulacea, Zeilleriacea, Terebratellacea.

The first four orders constitute the Inarticulata; the last six, together with the Eichwaldiacea and Thecideacea as *incertae ordinis,* the Articulata. The Kutorginida cannot at present be assigned confidently to either class.

This classification differs importantly from that adopted for the *Osnovy Paleontologii.* The rejection of the Atremata and Neotremata was certainly opportune but reinvestigation of inarticulate genera has shown that a number of emendations of GORYANSKY's classification are necessary. The order Lingulida is accepted with only minor changes in content. The Acrotretida is also deemed valid but it has been enlarged to embrace not only the forms assigned to it by GORYANSKY, but also the majority of genera comprising his Craniida, which is now regarded as superfluous. Changes of this kind are always, in the last resort, subjective, but since it is highly probable that the craniaceans developed from either the acrothelids or discinaceans, it appears desirable to indicate this relationship taxonomically. The Siphonotretida of GORYANSKY is considered to be polyphyletic and to embrace two distinct stocks

(39). The phosphatic-shelled siphonotretaceans, whose early members suggest that they may have developed from the acrotretaceans, have been emended and transferred to the Acrotretida. The calcareous-shelled Obolellacea (emended), on the other hand, are here regarded as sufficiently distinctive morphologically to merit a separate order, the Obolellida. The Kutorginida, as proposed by GORYANSKY, is likewise thought to include two independently derived groups. The order is retained for the kutorginaceans and also the poorly known *Rustella,* which thereby loses its ordinal status: but the phosphatic-shelled paterinaceans are now known to differ greatly from all other brachiopods in the posterior margins of both valves and have been promoted to a new order, the Paterinida.

The reduction of articulate orders from eight to six is consistent with the superfamilial groupings advocated by WILLIAMS (57) and has led to the demotion of the Productida and Atrypida, proposed in the *Osnovy Paleontologii,* to suborders. This revision is ultimately a matter of preference, but, as shown in the chapter on Evolution, there is little doubt about the origin of either group and the taxonomic distance between Strophomenidina and Productidina or the Atrypidina and the Spiriferidina is considered to be significantly less than that between any of the orders recognized here. The order Triplesiida, proposed by MOORE, has also been rejected. WRIGHT (59) has recently reviewed the possible affinities of this group and his conclusions justify its classification as a suborder of the Orthida. Indeed, only two subordinal groups remain to be placed within the present scheme, the Dictyonellidina (Eichwaldiacea) and the Thecideidina; their relationships with other articulates have already been explored in the chapter on Evolution.

The infraordinal arrangement of the articulates is quite different from that put forward by Russian contributors to the *Osnovy Paleontologii,* both in the number and grouping of the superfamilial units. In contrast to ALICHOVA's treatment of the Orthida, WRIGHT has found no reason to retain her Rhipidomellacea, as well as the Enteletacea, while WILLIAMS believes that the morphological heterogeneity of the Orthacea and Clitambonitacea as described by her, can be reduced profitably by using some stocks previously assigned to them as the basis for the new superfamilies Billingsellacea and Gonambonitacea, respectively. Similarly, WILLIAMS believes that stropheodontids are not sufficiently different from other members of the Strophomenacea to warrant a separate superfamily within the Strophomenida, as proposed by SOKOLSKAYA; and although the Productida of SARYCHEVA, LIKHAREV, and SOKOLSKAYA has not been retained, MUIR-WOOD has continued to recognize the Cadomellacea, as well as the Chonetacea, and the Strophalosiacea and Richthofeniacea, as well as the Productacea, as necessary superfamilial assemblages.

In her preparation of the Pentamerida, NIKIFOROVA erected a new superfamily (Camerellacea) and used Porambonitacea for the remaining porambonitaceans, whereas BIERNAT prefers to retain both groups within the Porambonitacea; the remaining group, the Pentameracea as prepared by AMSDEN, conforms more or less with that of NIKIFOROVA. The higher ranks of the Rhynchonellida as set out by AGER, GRANT, MCLAREN, and SCHMIDT differ from those used by RZHONSNITSKAYA, LIKHAREV and MAKRIDIN in the continued recognition of the Stenoscismatacea, in addition to the Rhynchonellacea and Rhynchoporacea.

The spire-bearing brachiopods show the most radical differences in treatment. Not only is the order Atrypida RZHONSNITSKAYA relegated to subordinal status by BOUCOT, JOHNSON & STATON, but both the Cyclospiracea and Coelospiracea are discarded and their contents reallocated, mainly to the Dayiacea. Moreover the Athyracea, as understood by LIKHAREV, MAKRIDIN, NIKIFOROVA, and RZHONSNITSKAYA has been promoted to two suborders, Retziidina and Athyrididina, each sufficiently diverse in morphology to warrant the recognition of two superfamilies, the Retziacea and Athyrisinacea, and the Athyridacea and Koninckinacea, respectively. In a like manner, PITRAT's studies of the Spiriferidina have led him to propose a classification quite different from IVANOVA's arrangement of the Spiriferida. The genera assigned by IVANOVA to the Delthyriacea have been redistributed, partly to the Spiriferacea and partly to two new superfamilies, the Cyrtiacea and Reticulariacea, while the Cyrtinidae and Suessidae have been removed from the Spiriferinacea, as understood by IVANOVA, and assembled into the new superfamily Suessiacea. Lastly, the twofold division of the Terebratulida into the Terebratulacea and Terebratellacea as used by LIKHAREV, MAKRIDIN, and RZHONSNITSKAYA has proved quite inadequate for MUIR-WOOD, ELLIOTT, HATAI, and STEHLI in their classification of the order. Genera included in the former superfamily are here allocated to two suborders (and three superfamilies), the Centronellidina (Stringocephalacea) and Terebratulidina (Terebratulacea and Dielasmatacea); and those attributed to the latter are now distributed among the Cryptonellacea and Zeilleriacea, as well as the Terebratellacea.

In conclusion, it seems appropriate to offer a few words in defense of the systematic procedure adopted here. The classification is far more complicated than any monothetic scheme, but, because it has been built up by empirical methods of morphological comparison, it has two important advantages. First, it is sufficiently versatile in its construction to survive drastic revisions of any of its ordinal sections. Second, since it involves all characters initially used to define genera and subsequently repeatedly sieved to determine the limits of each successive rank within the systematic hierarchy, it is bound to reflect to some degree or other the phylogenetic complexities of brachiopod evolution. As in any other classification, all taxa are admittedly subjective, but this concerns their ranking rather than their relationships with one another, which are real in so far as one can rely on shell morphology to reflect true affinities among extinct stocks. Hence, it is the nature and composition of the major groups making up the phylum that should be scrutinized closely, rather than their ranges within the systematic hierarchy which change with the fashion of the time.

Few paleontologists would now dispute the validity and status of the Inarticulata and Articulata as classes within the phylum Brachiopoda. The morphological, anatomical and embryological differences between them, which are fully discussed in the appropriate systematic sections, are decisive enough in living representatives. But morphological interpretation suggests that, within the dimension of brachiopod history, some of these distinctions are lost and that definable boundaries, which are also indicative of affinities, can only be maintained between the two classes if the Kutorginida are excluded from both. This dilemma is not new, as is shown by the way the allocation of *Kutorgina* (with *"Rustella"*) vacillated between the Protremata and Atremata of BEECHER and SCHUCHERT. In isolating the stock as an order of uncertain systematic allegiance, it is anticipated that further study will confirm its derivation independently of both the articulates and inarticulates (see chapter on Evolution) and lead to its recognition as a distinct class.

The Inarticulata and Articulata, as interpreted herein, embrace four and six orders, respectively, which can be arranged in a gradient of change from the Lingulida at one end to the Terebratulida at the other. It might, therefore, be argued that, with some revision of existing orders, a more refined classification involving subclasses to indicate these inferred relationships, might be achieved. Thus, in the chapter on Evolution, reasons are advanced for segregating the phylum (excluding the Kutorginida) into the following five grades: (1) Lingulida, Obolellida, Acrotretida; (2) Paterinida; (3) Strophomenida, Clitambonitidina, Triplesiidina, Billingsellacea; (4) Pentamerida, Orthacea, Enteletacea, ?Dictyonellidina; and (5) Rhynchonellida, Spiriferida, Terebratulida, ?Thecideidina. The differences between them are not based on any one set of characters, as was used by BEECHER to establish his fourfold division of the phylum. The Paterinida are isolated from other inarticulates because the pattern of their muscle impressions is unique; the Strophomenida, etc., are separated from other articulates because their pedicle is inferred to have developed in the same way as that of the inarticulates: while the fifth group is believed to be the only one characterized by mantle reversal. Nonetheless, it is at least premature to erect subclasses on interpretations such as these and nothing is gained by recasting the Orthida to conform with the segregation adopted for the third and fourth groups. The pseudodeltidium is mainly diagnostic of the nature of the pedicle in stocks assigned to the third group, but is not one of those persistent features that provide an unambiguous classification, because it is wanting in a few Clitambonitidina and Strophomenida. Moreover, although the morphology of the Clitambonitidina is reminiscent of both the Strophomenida and Orthidina, the modal characters of the Billingsellacea and Triplesiidina are certainly more like those of early Orthacea than primitive Strophomenidina.

A total of 232 subfamilies, 202 families, 48 superfamilies, and 20 suborders have been used to accommodate the 1,700 or so brachiopod genera described to date. About one-fifth of these suprageneric categories are new, but most of them represent promotion of pre-existing taxa, and in view of the fact that this compilative work is the most comprehensive review of the phylum to be undertaken since 1913, the treatment is not unduly lavish. All suprageneric taxa, with the exception of those assigned to the Dictyonellidina and Thecideidina, have been incorporated within the ordinal classification. It is possible that the former group will prove to have arisen independently of other articulates and so merit ordinal status, but the latter is more likely to be ultimately allocated to the Spiriferida, Terebratulida, or even the Strophomenida.

Finally, it is noteworthy that diagnoses of all suprageneric taxa have been so composed as to emphasize their definitive characteristics. The repetitious nature of diagnoses for suprafamilial groups, however, may prove disconcerting at first, because, in many of them, only changes in emphasis serve to indicate the individuality of the group. This morphological overlap is, of course, a manifestation of the replicating processes in evolution. The modal features of the Strophomenida, for example, are unique and include a concavo- to planoconvex, strophic, pseudopunctate, unequally parvicostellate shell with pseudodeltidium and chilidium, bilobed cardinal process, teeth and socket ridges without brachiophores, and muscle bases impressed directly on the internal surfaces of valves. Yet genera, rightly assigned to the order, may lack one or more of all these characters, while everyone of them is known to occur among members of the Orthida. Despite such convergences, most genera can be referred immediately to their ordinal groups and even the closest homeomorphs identified unequivocally.

## OUTLINE OF CLASSIFICATION

The following outline of the classification of the Brachiopoda summarizes taxonomic relationships, geologic occurrence, and numbers of recognized genera and subgenera in each family group and higher-rank taxon.[1] Where a single number is given, it refers to genera; where two numbers are given, the second indicates subgenera. Authorship of the systematic descriptions is indicated by recording with each division the initial letters of the author's name as shown by the tabulation below:

*Authorship of Systematic Descriptions*

| | |
|---|---|
| Ager, D. V. | A |
| Amsden, T. W. | AM |
| Biernat, Gertruda | B |
| Boucot, A. J. | BO |
| Elliott, G. F. | E |
| Grant, R. E. | G |
| Hatai, Kotora | H |
| Johnson, J. G. | J |
| McLaren, D. J. | ML |
| Muir-Wood, H. M. | MW |
| Pitrat, Charles W. | P |
| Rowell, A. J. | R |
| Schmidt, Herta | SC |
| Staton, R. D. | ST |
| Stehli, F. G. | S |
| Williams, Alwyn | W |
| Wright, A. D. | WR |

### *Main Divisions of Brachiopoda*

- Inarticulata *(class)* (129). *L.Cam.-Rec.* (R)
  - Lingulida *(order)* (51). *L.Cam.-Rec.* (R)
    - Lingulacea *(superfamily)* (46). *L.Cam.-Rec.* (R)
      - Lingulidae (7). *?Ord., Sil.-Rec.* (R)
      - Obolidae (27). *L.Cam.-U.Ord.* (R)
        - Obolinae (10). *L.Cam.-M.Ord.* (R)
        - Lingulellinae (6). *L.Cam.-U.Ord.* (R)
        - Glossellinae (7). *L.Ord.-U.Ord.* (R)
        - Acanthamboniinae (1). *M.Ord.-U.Ord.* (R)
        - Subfamily Uncertain (3). *Ord., ?Sil.* (R)
      - Elkaniidae (3). *U.Cam.-L.Ord.* (R)
      - Lingulasmatidae (1) *M.Ord.-U.Ord.* (R)
      - Andobolidae (1). *Ord.* (R)
      - Paterulidae (3). *Ord.-Sil.* (R)
      - Craniopsidae (4). *M.Ord.-L.Carb.* (R)
    - Trimerellacea *(superfamily)* (5). *M.Ord.-U.Sil.* (R)
      - Trimerellidae (5). *M.Ord.-U.Sil.* (R)
  - Acrotretida *(order)* (65). *L.Cam.-Rec.* (R)

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[1] Numbers given in the following tabulation are exclusive of genera recorded in the Addendum.

- Acrotretidina *(suborder)* (50). *L.Cam.-Rec.* (R)
  - Acrotretacea *(superfamily)* (32). *L.Cam.-Dev.* (R)
    - Acrotretidae (21). *L.Cam.-U.Sil., ?L.Dev.* (R)
      - Acrotretinae (8). *?L.Cam., M.Cam.-U.Ord.* (R)
      - Linnarssoniinae (3). *L.Cam.-U.Cam.* (R)
      - Ceratretinae (2). *U.Cam.-L.Ord.* (R)
      - Scaphelasmatinae (3). *M.Ord.-U.Sil.* (R)
      - Torynelasmatinae (2). *M.Ord., ?U.Sil.* (R)
      - Ephippelasmatinae (1). *M.Ord., ?U.Ord.* (R)
      - Subfamily Uncertain (2). *Ord.* (R)
    - Curticiidae (1). *U.Cam.* (R)
    - Acrothelidae (6). *L.Cam.-L.Ord.* (R)
      - Acrothelinae (4). *L.Cam.-L.Ord.* (R)
      - Conodiscinae (2). *?M.Cam., U.Cam., ?L.Ord.* (R)
    - Botsfordiidae (3). *L.Cam., ?M.Cam.* (R)
      - Botsfordiinae (2). *L.Cam., ?M.Cam.* (R)
      - Neobolinae (1). *L.Cam.* (R)
    - Family Uncertain (1). *L.Ord.* (R)
  - Discinacea *(superfamily)* (11). *Ord.-Rec.* (R)
    - Trematidae (2). *M.Ord.-Dev.* (R)
    - Discinidae (9). *Ord.-Rec.* (R)
      - Orbiculoideinae (5). *Ord.-Perm.* (R)
      - Disciniscinae (3). *?Carb., ?Trias., L.Jur.-Rec.* (R)
      - Discininae (1). *Rec.* (R)
  - Superfamily and Family Uncertain (2). *L.Ord.-Dev.* (R)
  - Siphonotretacea *(superfamily)* (5). *U.Cam.-Ord.* (R)
    - Siphonotretidae (5). *U.Cam.-Ord.* (R)
- Craniidina *(suborder)* (15). *?M.Cam., L.Ord.-Rec.* (R)
  - Craniacea *(superfamily)* (15). *?M.Cam., L.Ord.-Rec.* (R)
    - Craniidae (11). *?M.Cam., L.Ord.-Rec.* (R)
    - Eoconulidae (1). *M.Ord.-U.Ord.* (R)
    - Genera Doubtfully Referred to Craniacea (3). *Ord.-L.Sil.* (R)
- Obolellida *(order)* (5). *L.Cam.-M.Cam.* (R)
  - Obolellacea *(superfamily)* (5). *L.Cam.-M.Cam.* (R)
    - Obolellidae (5). *L.Cam.-M.Cam.* (R)
- Paterinida *(order)* (7). *L.Cam.-M.Ord.* (R)
  - Paterinacea *(superfamily)* (7). *L.Cam.-M.Ord.* (R)
    - Paterinidae (4). *L.Cam.-M.Ord.* (R)
    - Genera Doubtfully Referred to Paterinida (3). *L.Cam.-L.Ord.* (R)
- Addendum, Class Inarticulata (1). *M.Ord.* (R)
  - Ptychopeltidae (1). *M.Ord.* (R)
- Class Uncertain (3). *L.Cam., ?M.Cam.* (R)
  - Kutorginida *(order)* (3). *L.Cam., ?M.Cam.* (R)
    - Kutorginacea *(superfamily)* (3). *L.Cam., ?M.Cam.* (R)
      - Kutorginidae (2). *L.Cam., ?M.Cam.* (R)
      - Yorkiidae (1). *L.Cam.* (R)
- Articulata *(class)* (1584;44). *L.Cam.-Rec.* (A,AM,B,BO,E,G,H,J,ML,MW,P,R,SC,ST,S,W,WR)
  - Orthida *(order)* (189;9). *L.Cam.-U.Perm.* (W,WR)
    - Orthidina *(suborder)* (156;7). *L.Cam.-Perm.* (W,WR)
      - Billingsellacea *(superfamily)* (8). *L.Cam.-L.Ord.* (W)
        - Billingsellidae (4). *M.Cam.-L.Ord.* (W)
        - Nisusiidae (4). *L.Cam.-M.Cam.* (W)
      - Orthacea *(superfamily)* (82;7). *L.Cam.-U.Dev.* (W)
        - Eoorthidae (7). *L.Cam.-L.Ord.* (W)
        - Protorthidae (3). *M.Cam.* (W)
        - Hesperonomiidae (3). *L.Ord.* (W)
        - Orthidiellidae (5). *L.Ord.-U.Ord.* (W)
        - Orthidae (21). *M.Cam.-L.Dev.* (W)
          - Orthinae (17). *M.Cam.-L.Dev.* (W)
          - Productorthinae (3). *Ord.* (W)
          - Poramborthinae (1). *L.Ord.* (W)
        - Dolerorthidae (11). *L.Ord.-U.Sil.* (W)
          - Dolerorthinae (1). *M.Ord.-U.Sil.* (W)
          - Hesperorthinae (5). *L.Ord.-U.Sil.* (W)
          - Glyptorthinae (5). *L.Ord.-U.Sil.* (W)
        - Plaesiomyidae (7;7). *Ord.* (W)
          - Plaesiomyinae (5;7). *Ord.* (W)
          - Evenkininae (1). *M.Ord.* (W)
          - Metorthinae (1). *L.Ord.* (W)
        - Finkelnburgiidae (4). *U.Cam.-L.Ord.* (W)
        - Plectorthidae (14). *L.Ord.-U.Sil.* (W)
          - Plectorthinae (10). *L.Ord.-L.Sil.* (W)
          - Platystrophiinae (2). *M.Ord.-U.Sil.* (W)
          - Cyclocoeliinae (1). *U.Ord.* (W)
          - Rhactorthinae (1). *M.Ord.-U.Ord.* (W)
        - Cremnorthidae (2). *M.Ord.* (W)
          - Cremnorthinae (1). *M.Ord.* (W)
          - Phragmorthinae (1). *M.Ord.-U.Ord.* (W)
        - Skenidiidae (3). *L.Ord.-U.Dev.* (W)
        - Tuvaellidae (1). *L.Sil.* (W)
        - Saukrodictyidae (1). *U.Ord.* (W)
      - Enteletacea *(superfamily)* (66). *L.Ord.-U.Perm.* (WR)
        - Enteletidae (17). *M.Ord.-U.Perm.* (WR)
          - Enteletinae (4). *M.Carb.-U.Perm.* (WR)
          - Draboviinae (6). *M.Ord.-U.Ord.* (WR)
          - Schizophoriinae (7). *U.Ord.-U.Perm.* (WR)
        - Paurorthidae (2). *L.Ord.-M.Ord.* (WR)
        - Dalmanellidae (20). *L.Ord.-L.Carb.* (WR)
        - Dicoelosiidae (1). *U.Ord.-M.Dev.* (WR)
        - Kayserellidae (4). *M.Dev.-U.Dev.* (WR)
          - Kayserellinae (1). *M.Dev.* (WR)
          - Prokopiinae (3). *M.Dev.-U.Dev.* (WR)
        - Mystrophoridae (1). *M.Dev.* (WR)
        - Hypsomyoniidae (1). *M.Dev.-U.Dev.* (WR)
        - Harknessellidae (4). *M.Ord.-U.Ord.* (WR)
        - Heterorthidae (3). *M.Ord.-U.Ord.* (WR)
        - Rhipidomellidae (5). *L.Sil.-U.Perm.* (WR)
        - Linoporellidae (5). *M.Ord.-U.Sil.* (WR)
        - Angusticardiniidae (2). *L.Ord.-U.Ord.* (WR)
        - Tropidoleptidae (1). *L.Dev.-U.Dev.* (WR)
    - Clitambonitidina *(suborder)* (23;2). *Ord.* (W)

- Clitambonitacea *(superfamily)* (13;2). *Ord.* (W)
  - Polytoechiidae (4). *L.Ord.-M.Ord.* (W)
  - Clitambonitidae (9;2). *Ord.* (W)
    - Clitambonitinae (7;2). *Ord.* (W)
    - Atelelasmatinae (2). *L.Ord.-M.Ord.* (W)
- Gonambonitacea *(superfamily)* (10). *Ord.* (W)
  - Gonambonitidae (9). *Ord.* (W)
    - Gonambonitinae (6). *L.Ord.-M.Ord.* (W)
    - Anomalorthinae (3). *L.Ord.* (W)
  - Kullervoidae (1). *M.Ord.-U.Ord.* (W)
- Triplesiidina *(suborder)* (10). *L.Ord.-Sil.(Wenlock.).* (WR)
- Triplesiacea *(superfamily)* (10). *L.Ord.-U.Sil.(Wenlock.).* (WR)
  - Triplesiidae (10). *L.Ord.-U.Sil.* (WR)
- Order Uncertain (4). *M.Ord.-Perm.* (R)
- Dictyonellidina *(suborder)* (4). *M.Ord.-Perm.* (R)
- Eichwaldiacea *(superfamily)* (4). *M.Ord.-Perm.* (R)
  - Eichwaldiidae (2). *M.Ord.-U.Sil.* (R)
  - Isogrammidae (2). *Carb.-Perm.* (R)
- Strophomenida *(order)* (375;26). *L.Ord.-L.Jur.* (MW,W)
- Strophomenidina *(suborder)* (150;26). *Ord.-Trias.* (W)
- Plectambonitacea *(superfamily)* (53;4). *Ord.-Dev.* (W)
  - Plectambonitidae (6). *L.Ord.-M.Ord.* (W)
    - Plectambonitinae (3). *L.Ord.-M.Ord.* (W)
    - Ahtiellinae (3). *L.Ord.-M.Ord.* (W)
  - Taffiidae (4). *L.Ord.(U.Canad.-Whiterock.).* (W)
  - Leptestiidae (15). *L.Ord.-U.Ord.* (W)
    - Leptestiinae (11). *L.Ord.-U.Ord.* (W)
    - Isophragmatinae (3). *L.Ord.-M.Ord.* (W)
    - Taphrodontinae (1). *L.Ord.* (W)
  - Leptellinidae (12). *L.Ord.-U.Sil.* (W)
    - Leptellininae (4). *L.Ord.-L.Sil.* (W)
    - Leptellinae (2). *L.Ord.* (W)
    - Leptestiininae (6). *M.Ord.-U.Sil.* (W)
  - Sowerbyellidae (14;4). *Ord.-M.Dev.* (W)
    - Sowerbyellinae (6;4). *Ord.-M.Dev.* (W)
    - Ptychoglyptinae (1). *Ord.* (W)
    - Xenambonitinae (1). *M.Ord.-U.Ord.* (W)
    - Aegiromeninae (6). *M.Ord.-L.Sil.*
  - Bimuriidae (2). *M.Ord.*
- Strophomenacea *(superfamily)* (68;20). *Ord.-Carb.* (W)
  - Strophomenidae (29;2). *M.Ord.-L.Dev.* (W)
    - Strophomeninae (9). *M.Ord.-U.Sil.* (W)
    - Furcitellinae (4). *M.Ord.-L.Sil.* (W)
    - Rafinesquininae (4;2). *M.Ord.-U.Ord.* (W)
    - Glyptomeninae (5). *L.Ord.-M.Ord.* (W)
    - Oepikinae (5). *M.Ord.-U.Ord.* (W)
    - Leptaenoideinae (2). *U.Sil.-L.Dev.* (W)
  - Foliomenidae (1). *U.Ord.*
  - Christianiidae (1). *Ord.* (W)
  - Leptaenidae (10). *M.Ord.-L.Carb.* (W)
  - Stropheodontidae (27;18). *U.Ord.-U.Dev.* (W)
    - Stropheodontinae (7;10). *U.Ord.-U.Dev.*
    - Leptostrophiinae (5). *L.Sil.-U.Dev.* (W)
    - Douvillininae (6;2). *U.Sil.-U.Dev.* (W)
    - Pholidostrophiinae (2;4). *U.Sil.-M.Dev.* (W)
    - Shaleriinae (3;2). *L.Sil.-Dev.* (W)
    - Leptodontellinae (3). *L.Dev.-M.Dev.* (W)
    - Liljevalliinae (1). *M.Sil.* (W)
- Davidsoniacea *(superfamily)* (29;2). *Ord.-Trias.* (W)
  - Davidsoniidae (3). *L.Dev.-M.Dev.* (W)
  - Meekellidae (11;2). *M.Ord.-Perm.* (W)
    - Meekellinae (9;2). *Dev.-Perm.* (W)
    - Fardeniinae (2). *M.Ord.-U.Sil.* (W)
  - Schuchertellidae (7). *Dev.-Perm.* (W)
    - Schuchertellinae (4). *Dev.-Perm.* (W)
    - Streptorhynchinae (3). *Carb.-Perm.* (W)
  - Orthotetidae (7). *Carb.-Perm.* (W)
    - Orthotetinae (4). *Carb.-Perm.* (W)
    - Derbyiinae (3). *Carb.-Perm.* (W)
  - Thecospiridae (1). *Trias.* (W)
- Chonetidina *(suborder)* (29). *?U.Ord., L.Sil.-L.Jur.(U.Lias.).* (MW)
- Chonetacea *(superfamily)* (29). *?U.Ord., L.Sil.-U.Perm.* (MW)
  - Chonetidae (23). *?U.Ord., L.Sil.-U.Perm.* (MW)
    - Chonetinae (1). *L.Dev.-L.Carb.* (MW)
    - Strophochonetinae (1). *?U.Ord., L.Sil.-L.Dev.* (MW)
    - Devonochonetinae (4). *M.Sil.-M.Dev.* (MW)
    - Anopliinae (5). *L.Dev.-L.Perm.* (MW)
    - Retichonetinae (1). *L.Dev.-L.Carb.(Miss.).* (MW)
    - Rugosochonetinae (7). *L.Dev.-U.-Perm.* (MW)
    - Chonetinellinae (3). *U.Carb.(Penn.).-U.Perm.* (MW)
    - Semenewiinae (1). *L.Carb.(Tournais.-Visean).* (MW)
  - Eodevonariidae (1). *L.Dev.-M.Dev.* (MW)
  - Chonostrophiidae (1). *U.Sil.-M.Dev.* (MW)
  - Daviesiellidae (4). *?M.Dev., U.Dev.-L.Carb., ?U.Carb.(Namur.).* (MW)
    - Daviesiellinae (1). *L.Carb.(Visean.).* (MW)
    - Delepineinae (2). *?M.Dev., U.Dev.-L.Carb., ?U.Carb.(Namur.).* (MW)
    - Airtoniinae (1). *L.Carb.(Visean).* (MW)
- Suborder and Family Uncertain (1). *L.Carb.(Tournais.).* (MW)
- Cadomellacea *(superfamily)* (1). *L.Jur.(U.Lias.).* (MW)
  - Cadomellidae (1). *L.Jur.(U.Lias.).* (MW)
- Productidina *(suborder)* (179). *L.Dev.-Perm.* (MW)
- Strophalosiacea *(superfamily)* (42). *L.Dev.-Perm.* (MW)
  - Strophalosiidae (15). *L.Dev.-U.Perm.* (MW)
    - Strophalosiinae (5). *M.Dev.-U.Perm.* (MW)

Heteralosiinae (9). *L.Dev.-U.Perm.* (MW)
Ctenalosiinae (1). *L.Perm.* (MW)
Teguliferinidae (3). *U.Carb.(Penn.)-L.Perm., ?U.Perm.* (MW)
Aulostegidae (18). *U.Penn.-U.Perm.* (MW)
Aulosteginae (3). *L.Perm.-U.Perm.* (MW)
Echinosteginae (8). *U.Penn.-L.Perm.* (MW)
Chonosteginae (3). *U.Carb. or L.Perm., ?Perm.* (MW)
Institellinae (1). *L.Perm., ?U.Perm.* (MW)
Rhamnariinae (2). *L.Perm.-U.Perm.* (MW)
Costellariinae (1). *L.Perm.* (MW)
Sinuatellidae (1). *L.Carb.-U.Carb.(Namur.).* (MW)
Chonetellidae (1). *?L.Perm., U.Perm.* (MW)
Spyridiophoridae (1). *U.Penn.-L.Perm.* (MW)
Tschernyschewiidae (1). *L.Perm.-U.Perm.* (MW)
Scacchinellidae (2). *U.Penn.-L.Perm., ?U. Perm.* (MW)
Richthofeniacea *(superfamily)* (6). *L.Perm.-U.Perm.* (MW)
Richthofeniidae (5). *L.Perm.-U.Perm.* (MW)
Richthofeniinae (2). *L.Perm.-U.Perm.* (MW)
Prorichthofeniinae (1). *L.Perm.* (MW)
Gemmellaroiinae (2). *L.Perm.* (MW)
Family Uncertain (1). *Perm.* (MW)
Loczyellinae (1). *Perm.* (MW)
Productacea *(superfamily)* (131). *L.Dev.-U. Perm.* (MW)
Productellidae (16). *Up.L.Dev.-U.Miss.* (MW)
Productellinae (9). *L.Dev.-L.Miss.* (MW)
Chonopectinae (7). *U.Dev.-L.Carb.(L.Miss.-U.Miss).* (MW)
Institinidae (3). *L.Carb.(Visean), ?U.Carb.* (MW)
Leioproductidae (11). *M.Dev.-L.Perm.* (MW)
Leioproductinae (7). *U.Dev.-L.Perm.* (MW)
Devonoproductinae (2). *M.Dev.-U.Dev.* (MW)
Productininae (2). *L.Miss.-L.Carb.(Visean).* (MW)
Overtoniidae (19). *U.Dev.-L.Perm., ?U.Perm.* (MW)
Overtoniinae (16). *U.Dev.-L.Perm., ?U.Perm.* (MW)
Plicatiferinae (1). *L.Carb.(Visean).* (MW)
Institiferinae (2). *L.Carb.(Visean).* (MW)
Marginiferidae (22). *L.Carb.-U.Perm.* (MW)
Marginiferinae (8). *L.Carb.-U.Perm.* (MW)
Costispiniferinae (8). *U.Miss.-U.Perm.* (MW)
Retariinae (5). *U.Carb.(Moscov.-Ural.)-L. Perm.* (MW)
Probolioniinae (1). *L.Perm.*
Productidae (2). *L.Carb.(Visean)-U.Carb. (Westphal.).* (MW)
Echinoconchidae (8). *L.Carb.(Miss.)-U.Perm.* (MW)
Echinoconchinae (7). *L.Carb.(Miss.)-L.Perm.* (MW)
Waagenoconchinae (1). *U.Penn.-U.Perm.* (MW)
Buxtoniidae (11). *U.Dev.-U.Perm.* (MW)
Buxtoniinae (9). *U.Dev.-U.Perm.* (MW)
Juresaniinae (2). *U.Carb.(L.Penn.-U.Penn.)-L.Perm.* (MW)
Dictyoclostidae (16). *L.Carb.(Tournais.-Visean)-U.Perm.* (MW)
Dictyoclostinae (14). *L.Carb.(Tournais.-Visean)-U.Perm.* (MW)
Horridoniinae (1). *Perm.* (MW)
Levitusiinae (1). *L.Carb.(Visean).* (MW)
Linoproductidae (18). *L.Carb.(L.Miss.-U. Miss.)-U.Perm.* (MW)
Linoproductinae (11). *L.Carb.(L.Miss).-U. Perm.* (MW)
Proboscidellinae (1). *L.Carb.(Visean).* (MW)
Monticuliferinae (1). *L.Perm., ?U.Perm.* (MW)
Paucispiniferinae (3). *U.Carb.(Penn.)-U. Perm.* (MW)
Striatiferinae (2). *L.Carb.(Visean)-Perm.* (MW)
Gigantoproductidae (5). *U.Dev.-U.Carb.(Namur.).* (MW)
Gigantoproductinae (2). *L.Carb.(Visean).* (MW)
Semiplaninae (2). *U.Dev.-U.Carb.(Namur.).* (MW)
Kansuellinae (1). *L.Carb.(Visean).* (MW)
Oldhaminidina *(suborder)* (16). *U.Carb.-U. Trias.* (W)
Lyttoniacea *(superfamily)* (16). *U.Carb.-U. Trias.* (W)
Lyttoniidae (10). *U.Carb.-Perm.* (W)
Poikilosakidae (4). *U.Carb.-Perm.* (W)
Bactryniidae (1). *U.Trias.(Rhaet.).* (W)
Spinolyttoniidae (1). *U.Perm.* (W)
Pentamerida *(order)* (84;3). *M.Cam.-U.Dev.* (B, AM)
Syntrophiidina *(suborder)* (40;3). *M.Cam.-L. Dev.* (B)
Porambonitacea *(superfamily)* (40;3). *M.Cam.-L.Dev.* (B)
Eostrophiidae (1). *M.Cam.* (B)
Huenellidae (6). *U.Cam.-L.Ord.* (B)
Huenellinae (4). *U.Cam.-L.Ord.* (B)
Mesonomiinae (2). *U.Cam.-L.Ord.* (B)
Tetralobulidae (4). *L.Ord.* (B)
Alimbellidae (2). *L.Ord.* (B)
Clarkellidae (8). *U.Cam.-U.Ord.* (B)
Syntrophopsidae (3). *L.Ord.* (B)
Lycophoriidae (1). *L.Ord.-M.Ord.* (B)
Porambonitidae (1;3). *L.Ord.-L.Sil.* (B)
Syntrophiidae (2). *L.Ord.* (B)
Syntrophiinae (1). *L.Ord.* (B)
Xenelasmatinae (1). *L.Ord.* (B)
Brevicameridae (1). *Ord.* (B)
Camerellidae (7). *L.Ord.-Sil.* (B)

Camerellinae (6). *L.Ord.-Sil.* (B)
Stenocamarinae (1). *L.Ord.* (B)
Parastrophinidae (4). *M.Ord.-L.Dev.* (B)
Pentameridina *(suborder)* (44). *?M.Ord., U.Ord.-U.Dev.* (AM)
Pentameracea *(superfamily)* (44). *?M.Ord., U.Ord.-U.Dev.* (AM)
?Parallelelasmatidae (4). *M.Ord.* (AM)
Stricklandiidae (5). *L.Sil.-U.Sil.(Wenlock.).* (AM)
Virgianidae (3). *U.Ord.-L.Sil.* (AM)
Pentameridae (31). *U.Ord.-U.Dev.* (AM)
Pentamerinae 13). *U.Ord.-L.Dev.* (AM)
Gypidulinae (14). *L.Sil.-U.Dev.* (AM)
Clorindinae (4). *Sil.-M.Dev.* (AM)
Enantiosphenidae (1). *M.Dev.* (AM)
Rhynchonellida *(order)* (270;2). *M.Ord.-Rec.* (A,G,ML,SC)
Rhynchonellacea *(superfamily)* (258;2). *M.Ord.-Rec.* (A,ML,SC)
Ancistrorhynchidae (2) *M.Ord.* (SC)
Oligorhynchiidae (4). *M.Ord., ?Sil.* (SC)
Rhynchotrematidae (14). *M.Ord.-M.Dev.* (SC)
Rhynchotrematinae (7). *M.Ord.-L.Dev.* (SC)
Orthorhynchulinae (7). *M.Ord.-M.Dev.* (SC)
Trigonirhynchiidae (13). *M.Ord.-L.Carb.(Miss.).* (ML-SC)
Uncinulidae (19;2). *Sil.-U.Dev., ?Perm.* (SC)
Uncinulinae (7;2). *L.Dev.-U.Dev., ?Perm.* (SC)
Hebetoechiinae (8). *Sil.-M.Dev.* (SC)
Hypothyridininae (3). *Sil.-U.Dev.* (SC)
Hadrorhynchiinae (1). *M.Dev.(Givet.).* (SC)
Eatoniidae (7). *Sil.-L.Dev.* (SC)
Pugnacidae (6). *L.Dev.-L.Carb.* (SC)
Family Uncertain (?aff. Pugnacidae) (5). *Sil.-L.Carb., ?Perm.* (SC,ML)
Camarotoechiidae (20). *?L.Sil., U.Sil.-Perm.* (SC)
Camarotoechiinae (16). *?L.Sil., U.Sil.-Perm.* (SC)
Septalariinae (4). *L.Dev.-M.Dev., ?U.Perm.* (SC)
Camerophorinidae (1). *M.Dev.* (ML)
Yunnanellidae (7). *?M.Dev., U.Dev., ?L.Miss.* (ML-SC)
Dimerellidae (21). *?Dev., Trias.-L.Cret.* (A)
Dimerellinae (1). *Trias.* (A)
Rhynchonellininae (10). *U.Trias.-U.Jur.* (A)
Norellinae (7). *M.Trias.-U.Jur., ?L.Cret.* (A)
Halorellinae (2). *?Dev., Trias.* (A)
Peregrinellinae (1). *?Dev., M.Jur.-L.Cret.* (A)
Tetracameridae (3). *L.Carb.(Miss.).* (ML)
Rhynchotetradidae (3). *L.Carb.-L.Perm.* (ML)
Wellerellidae (30). *L.Carb.-U.Cret.* (SC,A)
Wellerellinae (9). *L.Carb.-U.Perm.* (SC)
Wellerella Group (2). *U.Carb.-Perm.* (SC)
Pseudowellerella Group (4). *Permocarb.-U.Perm.* (SC)
Allorhynchus Group (3). *L.Carb.-U.Perm.* (SC)
Cirpinae (13). *Trias.-U.Jur.* (A)
Lacunosellinae (8). *L.Jur.-U.Cret.* (A)
?Cardiarinidae (1). *Penn.* (ML)
Rhynchonellidae (60). *Trias.-U.Cret.* (A)
Rhynchonellinae (4). *Trias.-U.Jur.* (A)
Acanthothyridinae (3). *M.Jur.-U.Jur.* (A)
Tetrarhynchiinae (23). *U.Trias.-L.Cret.* (A)
Cyclothyridinae (30). *L.Jur.-U.Cret.* (A)
Septirhynchiidae (1). *U.Jur.* (A)
Austrirhynchiidae (1). *Trias.* (A)
Cryptoporidae (1). *Eoc.-Rec.* (A)
Basiliolidae (9). *Cret.-Rec.* (A)
Basiliolinae (6). *Eoc.-Rec.* (A)
Aphelesiinae (1). *Eoc.-Plio.* (A)
Aetheiinae (2). *Cret.-Mio.* (A)
Hemithyrididae (4). *Eoc.-Rec.* (A)
Frieleiidae (5). *?Eoc., ?Mio., Plio.-Rec.* (A)
Erymnariidae (1). *Eoc.* (A)
Family Uncertain (20). *M.Ord.-L.Perm.* (S,ML)
Stenoscismatacea *(superfamily)* (11). *M.Dev.-U.Perm.* (G)
Atriboniidae (7). *M.Dev.-U.Perm.* (G)
Atriboniinae (3). *M.Dev.-L.Perm.* (G)
Psilocamarinae (4). *U.Carb.-U.Perm.* (G)
Stenoscismatidae (4). *M.Dev.-U.Perm.* (G)
Stenoscismatinae (2). *M.Dev.-U.Perm.* (G)
Torynechinae (2). *?U.Carb., L.Perm.* (G)
Rhynchoporacea *(superfamily)* (1). *Miss.-Perm.* (ML)
Rhynchoporidae (1). *Miss.-Perm.* (ML)
Spiriferida *(order)* (305). *M.Ord.-Jur.* (BO,J,ST,P)
Atrypidina *(suborder)* (56). *M.Ord.-U.Dev.* (BO,J,ST)
Atrypacea *(superfamily)* (42). *M.Ord.-U.Dev.* (BO,J,ST)
Atrypidae (29). *M.Ord.-U.Dev.* (BO,J,ST)
Zygospirinae (8). *M.Ord.-L.Sil.* (BO,J,ST)
Atrypininae (1). *L.Sil.-L.Dev.* (BO,J,ST)
Carinatininae (9). *U.Ord.-M.Dev.* (BO,J,ST)
Atrypinae (8). *L.Sil.-U.Dev.* (BO,J,ST)
Karpinskiinae (1). *Sil.-M.Dev.* (BO,J,ST)
Palaferellinae (2). *L.Dev.-M.Dev.* (BO,J,ST)
Lissatrypidae (12). *M.Ord.-M.Dev.* (BO,J,ST)
Lissatrypinae (6). *L.Sil.-M.Dev.* (BO,J,ST)
Septatrypinae (6). *M.Ord.-M.Dev.* (BO,J,ST)
Family and Subfamily Uncertain (1). *Sil.* (BO,J,ST)
Dayiacea *(superfamily)* (13). *M.Ord.-M.Dev.* (BO,J,ST)
Dayiidae (4). *M.Ord.-L.Dev.* (BO,J,ST)
Cyclospirinae (1). *M.Ord., ?L.Sil.* (BO,J,ST)
Dayiinae (2). *U.Sil.(Wenlock.)-L.Dev.* (BO,J,ST)

Aulidospirinae (1). *M.Ord., ?U.Ord.* (BO,J,ST)
Anoplothecidae (4). *U.Sil.(Wenlock.)-M.Dev.* (BO,J,ST)
Coelospirinae (1). *U.Sil.(Wenlock.)-M.Dev.* (BO,J,ST)
Anoplothecinae (3). *L.Dev.-M.Dev.* (BO,J,ST)
Kayseriidae (1). *M.Dev.* (BO,J,ST)
Leptocoeliidae (4). *L.Sil.-M.Dev.* (BO,J,ST)
Superfamily Uncertain (1). *M.Dev.* (BO,J,ST)
Uncitidae (1). *M.Dev.* (BO,J,ST)
Retziidina *(suborder)* (16). *U.Sil.(Wenlock.)-Trias.* (BO,J,ST)
Retziacea *(superfamily)* (11). *U.Sil.(Wenlock.)-Perm.* (BO,J,ST)
Retziidae (9). *L.Dev.-Perm.* (BO,J,ST)
Rhynchospirinidae (2). *U.Sil.-L.Dev.* (BO,J,ST)
Athyrisinacea *(superfamily)* (5). *M.Dev.-Trias.* (BO,J,ST)
Athyrisinidae (5). *M.Dev.-Trias.* (BO,J,ST)
Athyrididina *(suborder)* (46). *U.Ord.-Jur.* (BO,J,ST)
Athyridacea *(superfamily)* (41). *U.Ord.-Trias.* (BO,J,ST)
Meristellidae (13). *U.Ord.-U.Miss.* (BO,J,ST)
Meristellinae (6). *U.Ord.-U.Dev.* (BO,J,ST)
Meristinae (2). *L.Sil.-M.Dev.* (BO,J,ST)
Camarophorellinae (2). *M.Dev.-Miss.* (BO,J,ST)
Hindellinae (3). *U.Ord.-L.Dev.* (BO,J,ST)
Athyrididae (27). *U.Sil.(Wenlock.)-Trias.* (BO,J,ST)
Protathyridinae (4). *U.Sil.(Wenlock.)-M.Dev.* (BO,J,ST)
Athyridinae (10). *L.Dev.-Trias.* (BO,J,ST)
Diplospirellinae (4). *Trias.* (BO,J,ST)
Subfamily Uncertain (9). *L.Dev.-Trias.* (BO,J,ST)
Nucleospiridae (1). *U.Sil.-L.Carb.(Miss.).* (BO,J,ST)
Koninckinacea *(superfamily)* (5). *Trias.-Jur.* (BO,J,ST)
Koninckinidae (5). *Trias.-Jur.* (BO,J,ST)
Spiriferidina *(suborder)* (185). *L.Sil.-L.Jur.* (P)
Cyrtiacea *(superfamily)* (28). *L.Sil.-Perm.* (P)
Cyrtiidae (9). *L.Sil.(Llandover.)-M.Dev.(Couvin.).* (P)
Cyrtiinae (3). *L.Sil.(U.Llandover.-Dev. (Ems.-?Couvin.).* (P)
Eospiriferinae (6). *L.Sil.(Llandover.)-M.Dev. (Couvin.).* (P)
Ambocoeliidae (19). *?U.Sil., L.Dev.-Perm.* (P)
Suessiacea *(superfamily)* (12). *Sil.-L.Jur.* (P)
Cyrtinidae (11). *Sil.-U.Trias.* (P)
Suessiidae (1). *L.Jur.* (P)
Spiriferacea *(superfamily)* (89). *L.Sil.-U.Perm.* (P)
Delthyrididae (21). *L.Sil.(Llandover.)-M.Dev. (Couvin.).* (P)
Delthyridinae (5). *U.Sil.(Wenlock.)-M.Dev. (Couvin.).* (P)
Acrospiriferinae (10). *L.Sil.(Llandover.)-U. Dev.(Frasn.).* (P)
Kozlowskiellininae (2). *U.Sil.(Wenlock.)-L. Dev.(Ems.).* (P)
Paraspiriferinae (3). *L.Dev.(Siegen.)-M.Dev. (Couvin.).* (P)
Cyrtinopsinae (1). *M.Dev.(Couvin.).* (P)
Mucrospiriferidae (5). *L.Dev.(Ems.)-L.Carb. (Visean).* (P)
Fimbrispiriferidae (1). *L.Dev.(Ems.)-M.Dev. Givet.).* (P)
Spinocyrtiidae (6). *L.Dev.(Ems.)-U.Dev. (Frasn.).* (P)
Syringothyrididae (15). *U.Dev.-U.Perm.* (P)
Syringothyridinae (7). *U.Dev.-Perm.* (P)
Licharewiinae (8). *U.Carb.-U.Perm.* (P)
Costispiriferidae (5). *L.Dev.(Siegen.)-U.Dev. (Frasn.), ?L.Carb.* (P)
Cyrtospiriferidae (13). *?M.Dev., U.Dev. (Frasn.)-L.Carb.(Visean).* (P)
Spiriferidae (10). *L.Carb.-Perm.* (P)
Brachythyrididae (12). *?U.Dev., L.Carb.-Perm.* (P)
Family Uncertain (1). *U.Dev.(Frasn.).* (P)
Spiriferinacea *(superfamily)* (19). *L.Carb.-L. Jur.* (P)
Spiriferinidae (19). *L.Carb.-L.Jur.* (P)
Reticulariacea *(superfamily)* (36). *?U.Sil., L. Dev.-Perm., ?Trias.* (P)
Reticulariidae (18). *?U.Sil., L.Dev.-L.Carb., ?U.Carb.-Trias.* (P)
Elythidae (7). *M.Dev.-Perm.* (P)
Martiniidae (11). *L.Carb.-Perm., ?Trias.* (P)
Superfamily and Family Uncertain (1). *Dev., ?L.Carb.* (P)
Suborder, Superfamily, and Family Uncertain (2). *Carb.-L.Jur.* (P)
Terebratulida *(order)* (290;4). *L.Dev.-Rec.* (MW, S,E,H)
Centronellidina *(suborder)* (39). *L.Dev.-Perm.* (S)
Stringocephalacea *(superfamily)* (39). *L.Dev.-U.Perm.* (S)
Centronellidae (12). *L.Dev.-M.Dev.* (S)
Centronellinae (2). *L.Dev.-M.Dev.* (S)
Rensselaeriinae (5). *L.Dev.-M.Dev.* (S)
Eurythyridinae (3). *L.Dev.* (S)
Meganteridinae (2). *L.Dev.* (S)
Stringocephalidae (7). *M.Dev.* (S)
Rensselandiinae (3). *M.Dev.* (S)
Bornhardtininae (1). *M.Dev.* (S)
Stringocephalinae (3). *M.Dev.* (S)
Rhipidothyrididae (5). *L.Dev.-M.Dev.* (S)
Rhipidothyridinae (2). *M.Dev.* (S)
Globithyridinae (3). *L.Dev.* (S)
Mutationellidae (13). *L.Dev.-Perm.* (S)
Brachyzyginae (1). *L.Dev.* (S)

Mutationellinae (8). *L.Dev.-M.Dev.* (S)
Cimicinellinae (1). *L.Dev.* (S)
Cryptacanthiinae (3). *?L.Dev., Miss.-U.Perm.* (S)
Family Uncertain (2). *M.Dev.-U.Miss.* (S)
Terebratulidina *(suborder)* (132;2). *L.Dev.-Rec.* (S,MW)
Dielasmatacea *(superfamily)* (42;2). *L.Dev.-U.Trias., ?L.Jur.* (S,MW)
Cranaenidae (5). *L.Dev.-Miss.* (S)
Cranaeninae (3). *L.Dev.-U.Miss.* (S)
Girtyellinae (2). *Miss.* (S)
Dielasmatidae (24). *L.Carb.-U.Trias., ?L.Jur. (Lias.).* (S,MW)
Dielasmatinae (13). *L.Carb.-U.Trias.* (S, MW)
Centronelloideinae (1). *U.Miss.* (S)
Nucleatulinae (3). *U.Trias., ?L.Jur.(Lias.).* (MW)
Juvavellinae (5). *U.Trias.* (MW)
Subfamily Uncertain (2). *M.Trias.-L.Jur.(M. Lias.-U.Lias.).* (MW)
Heterelasminidae (4). *U.Dev.-U.Perm.* (S)
Notothyrididae (5;2). *U.Miss.-U.Perm.* (S)
Labaiidae (3). *M.Penn.-U.Perm.* (S)
Family Uncertain (1). *Perm.* (S)
Terebratulacea *(superfamily)* (90). *U.Trias.-Rec.* (MW)
Orthotomidae (1). *L.Jur.(M.Lias.).* (MW)
Terebratulidae (56). *U.Trias.-Rec.* (MW)
Terebratulinae (41). *U.Trias.-Rec.* (MW)
Sellithyridinae (3). *L.Cret.-U.Cret.(Cenoman.).* (MW)
Rectithyridinae (5). *L.Cret.-U.Cret.* (MW)
Gibbithyridinae (3). *U.Cret.(Cenoman.-Senon.).* (MW)
Carneithyridinae (2). *U.Cret.(Senon.-Dan.).* (MW)
Inopinatarculinae (1). *U.Cret.(Santon.).* (MW)
Subfamily Uncertain (1). *U.Jur.(Oxford.).* (MW)
Cheniothyrididae (1). *M.Jur.(U.Infer.Ool.).* (MW)
Dictyothyrididae (1). *M.Jur.(Bathon.)-U.Jur. (Oxford.-?Kimmeridg.).* (MW)
Tegulithyrididae (1). *U.Jur.(Callov.).* (MW)
Pygopidae (5). *?L.Jur.(Lias.), M.Jur.-L.Cret. (Neocom.).* (MW)
Dyscoliidae (4). *?U.Jur., U.Cret.(Cenoman.)-Rec.* (MW)
Cancellothyrididae (21). *?L.Jur.-?M.Jur., U. Jur.-Rec.* (MW)
Cancellothyridinae (6). *U.Jur.-Rec.* (MW)
Chlidonophorinae (3). *U.Cret.-Rec.* (MW)
Eucalathinae (2). *?U.Cret., Rec.* (MW)
Agulhasiinae (1). *Rec.* (MW)
Orthothyridinae (1). *U.Cret.* (MW)
Subfamily Uncertain (8). *L.Jur. (Gt. Ool. Ser.)-L.Cret.(Apt.-Alb.).* (MW)
Terebratellidina *(suborder)* (117;2). *L.Dev.-Rec.* (MW,E,H,S)
Cryptonellacea *(superfamily)* (4). *L.Dev.-Perm.* (S)
Cryptonellidae (4). *L.Dev.-Perm.* (S)
Zeilleriacea *(superfamily)* (22). *Trias.-L.Cret.* (MW)
Zeilleriidae (21). *Trias.-L.Cret.* (MW)
Eudesiidae (1). *M.Jur.(Bathon.).* (MW)
Terebratellacea *(superfamily)* (91;2). *U.Trias.-Rec.* (E,H)
Megathyrididae (5). *U.Cret.-Rec.* (E,H)
Platidiidae (2). *Eoc.-Rec.* (E,H)
Kraussinidae (6). *Mio.-Rec.* (H)
Dallinidae (39;2). *U.Trias.-Rec.* (E,H)
Dallininae (14;2). *L.Cret.-Rec.* (E)
Gemmarculinae (1). *L.Cret.-U.Cret.* (E)
Kingeninae (4). *U.Jur.-U.Cret.* (E)
Trigonellininae (3). *L.Jur.-U.Jur.* (E)
Frenulininae (3). *Mio.-Rec.* (H)
Nipponithyridinae (5). *Mio.-Rec.* (H)
Subfamily Uncertain (9). *U.Trias.-L.Cret.* (E)
Terebratellidae (32). *L.Cret.-Rec.* (E,H)
Terebratellinae (7). *Oligo.-Rec.* (H)
Bouchardiinae (3). *U.Cret.-Rec.* (E,H)
Magadinae (9). *L.Cret.-Rec.* (E,H)
Trigonoseminae (3). *U.Cret.* (E)
Neothyridinae (10). *Oligo.-Rec.* (H)
Laqueidae (4). *Mio.-Rec.* (H)
Laqueinae (1). *Mio.-Rec.* (H)
Pictothyridinae (2). *Plio.-Rec.* (H)
Kurakithyridinae (1). *Plio.* (H)
Family Uncertain (3). *Jur.-Rec.* (E,H,MW)
Suborder, Superfamily, and Family Unknown (2). *Eoc.-Mio.* (MW)
Order Uncertain (12). *Trias.-Rec.* (E)
Thecideidina *(suborder)* (12). *Trias.-Rec.* (E)
Thecideacea *(superfamily)* (12). *Trias.-Rec.* (E)
Thecidellinidae (4). *Trias.-Rec.* (E)
Thecideidae (8). *L.Jur.-Rec.* (E)
Order, Suborder, and Family Uncertain (53). *M. Cam.-Trias.*

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# STRATIGRAPHIC DISTRIBUTION

By ALWYN WILLIAMS

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The known stratigraphic distribution of the Brachiopoda is a reflection not only of the evolutionary history of the phylum and the control exercised by shifting facies throughout time, but also of the fortuity of fossil preservation and paleontological tradition. The first two factors have determined the main pattern of distribution; the last two are responsible for its imperfect presentation. Any general survey of the brachiopods in time and space needs to take account of limitations of the available data and insofar as possible, to segregate the relative effects of nature and artifice.

By any standard of measurement, it appears that the phylum has passed through its climactic phase of evolution and is now in decline. In effect, brachiopods have been replaced by other invertebrates as the principal constituents of benthic marine faunas. This process seems to have been gathering momentum since early Mesozoic times but it followed an era of remarkable generic proliferation and phyletic diversity which, as shown graphically in Figs. 148-150, reached their acme during the Devonian. It is not surprising to find that the generic and superfamilial patterns of distribution are comparable, since frequency of the latter is normally a function of the former. Superfamilial ranges, however, provide a better picture of evolutionary design because the inauspicious beginnings and decimated endings of extinct groups are commonly obscured by the numerical preponderance of their more flourishing contemporaries. Thus all six articulate orders are represented in Devonian rocks (including the earliest Terebratulida and the last Pentamerida) and although four persisted into the Jurassic they included the last of the Strophomenida and Spiriferida. In fact, since the Ordovician and Devonian, when maxima of eight orders were simultaneously in existence, there has been a steady reduction in the more basic diversity of the phylum.

The occurrence of living brachiopods in almost every known marine environment from brackish-water tidal flats (e.g., *Lingula*) to abyssal regions over 5,000 m. deep (e.g., *Abyssothyris*) is undoubtedly a relic of past adaptability. Certainly ample evidence suggests that extinct stocks, as burrowers, sedentary benthos, or even epiplankton, successfully colonized as many ecological niches as their modern descendants. Consequently, brachiopods have been

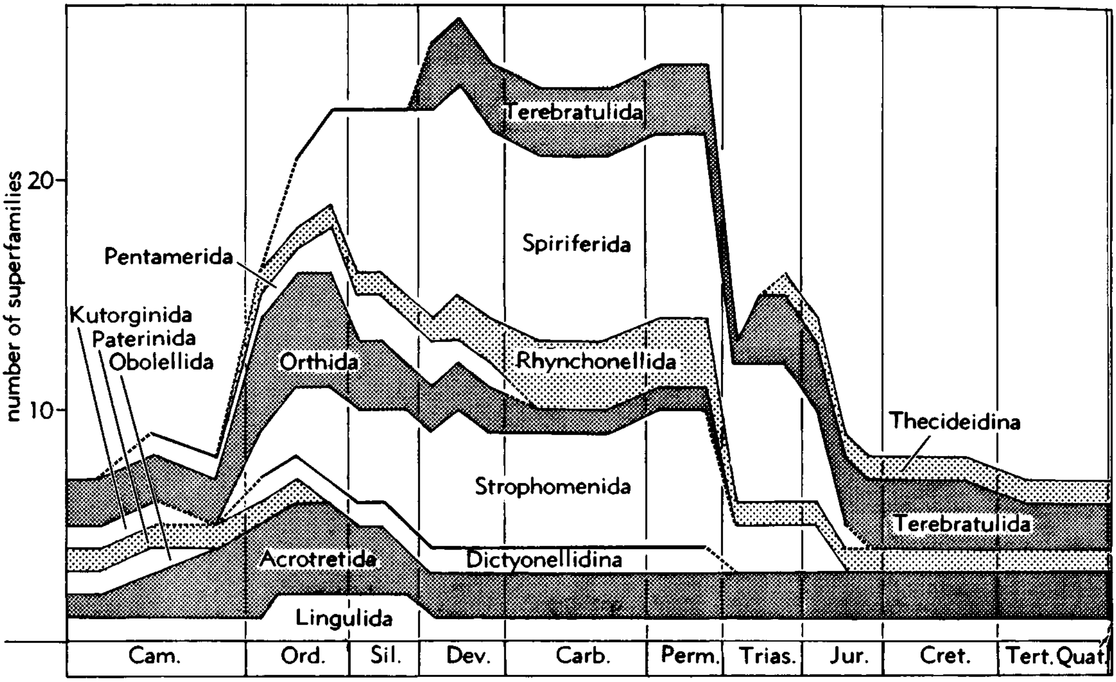

FIG. 148. Stratigraphic distribution of Brachiopoda according to number of superfamilies (5).

taken from most sedimentary rocks of marine origin, but with a clear majority from assorted shallow-water deposits. It is also becoming apparent that communities maintained by subtle differences in facies and associations endemic to major provinces were as common in the past as they are today. In all, the relationships between and within faunas in time and space have always been complex and are likely to be grossly misinterpreted through incompleteness of the fossil record.

Some of the effects of such facies controls may be identified in a time-frequency chart of all known genera (Fig. 149). The distribution shows the Late Silurian and Late Carboniferous as times of relatively few brachiopod genera, isolating the Ordovician, Devonian, and early Permian maxima from one another. This disparity can be explained in a number of ways. The minima may represent phases of depressed speciation immediately precursory to evolutionary accelerations affecting, for example, the Devonian Spiriferida and the Permian Strophomenida. They may represent faunas that for reasons of geographical inconvenience or personal taste have not been subjected to the same intensity of systematic research as, say, the Devonian assemblages. Yet it is also significant that the location of maxima and minima are mainly determined by systemic or subsystemic boundaries and, since these boundaries are related in general to important facies changes, generic variation could have been due to equally profound changes in past environments. Thus, the drop in number of genera recorded from the Upper Carboniferous coincided with the deposition of the largely nonmarine Coal Measures of Europe and North America, the two regions of the world with the longest tradition for systematic study of the brachiopods. Indeed, a good example of the difficulties involved in interpreting stratigraphic distributions of this sort is afforded by the Ordovician record.

The Ordovician was a period of unrivaled increase in the number of brachiopod genera. More than six times as many genera are recorded from the mid-Ordovician as from the Cambrian, and this proliferation

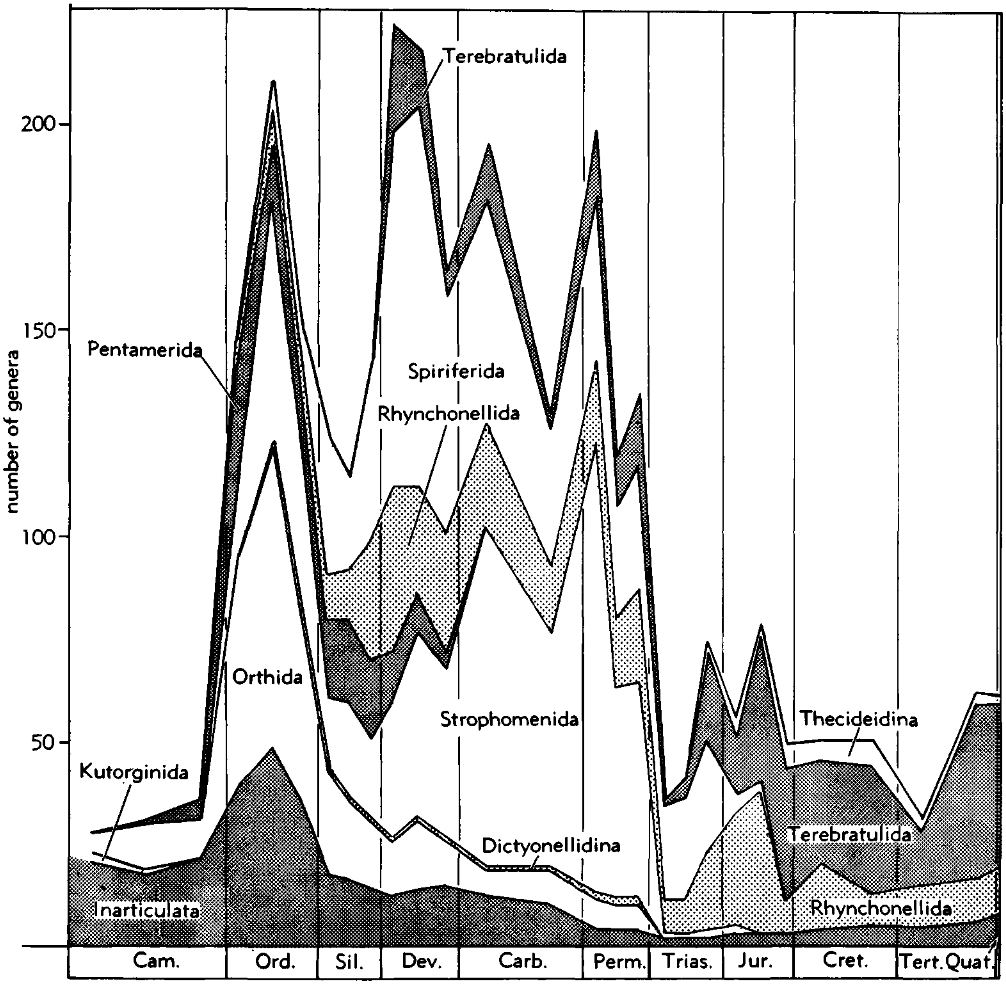

FIG. 149. Stratigraphic distribution of Brachiopoda according to number of genera (5).

is generally conceded to signify the most important radiation that affected the phylum. About 330 genera made their first appearance during the Ordovician, including 117 from the Early Tremadocian and 84 from oldest members of the Caradocian (or Porterfield) (Fig. 151). The former influx is as yet not well documented, but the latter is known to coincide with a marine transgression that occurred during the existence of the ubiquitous graptolite *Nemagraptus gracilis* and seems to have affected much of the Northern Hemisphere.

By establishing new channels of communication between hitherto isolated basins and opening up newly flooded areas for exploitation by marine faunas, transgressions on this scale can promote rapid migration and speciation, each contributing to an increase in the number of genera registered for a given area. Both influences seem to have been operative during early Caradocian times and may be identified in the following manner. A cluster analysis of brachiopod assemblages recovered from the shelly facies of North America and Europe shows that at least two well-defined indigenous faunas existed in this part of the world during mid-Ordovician time (Fig. 152). One extended from Nevada to Scotland, the other from the eastern Baltic to North Wales, although both were affected by diversification, as can be seen in the low correlations of the Ward Cove and Spy

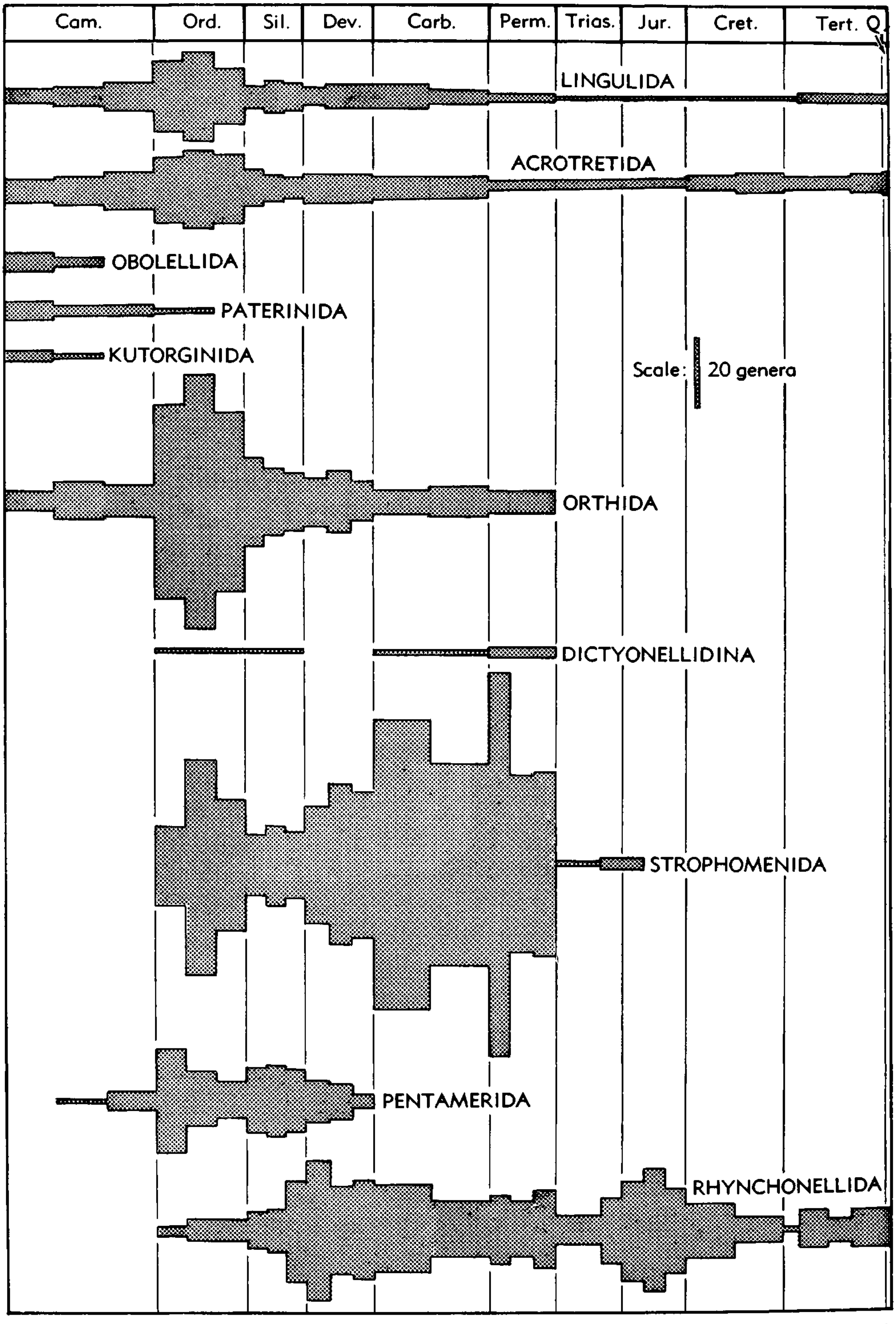

Fig. 150. Stratigraphic distribution of Brachiopoda in orders or suborders and proportionate to numbers of genera (5).

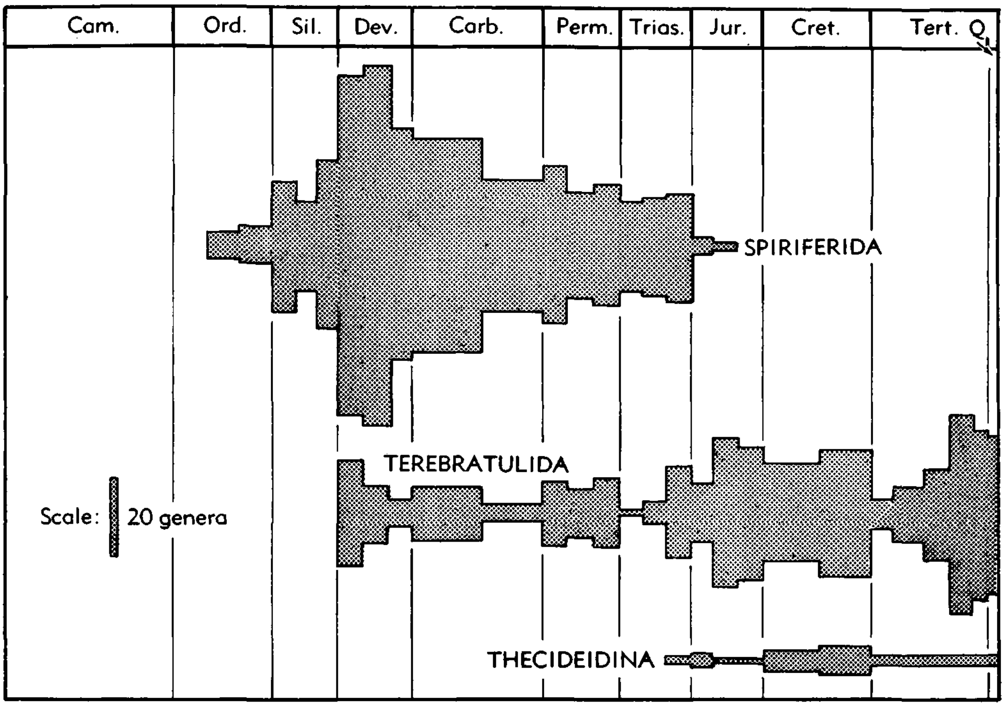

FIG. 150. *(Continued.)*

Wood Grit assemblages within their respective provinces. Various elements of the early Caradocian influx, however, appeared everywhere and can be segregated into two distinct groups. Among new genera, 52 of 84 belong to families or subfamilies already represented in one or both provinces and could conceivably have arisen by rapid speciation *in situ*. The remainder are the earliest members of families or subfamilies to which they have been assigned. They include inarticulates like the craniopsids, and scaphelasmatinids, and articulates like the dolerorthids, linoporellids, kullervoids, parastrophinids, xenambonitinids, bimuriids, and rafinesquinids. Such stocks are so different from their contemporaries that they must have had a long evolutionary history in an unidentified basin (or basins) which first became connected with the North American and European provinces during mid-Ordovician time. Moreover, it is possible that this massive immigration also included some members of the first group which had evolved more gradually elsewhere. Hence the sudden increase of genera registered for the mid-Ordovician may not be so realistic an index of an acceleration in evolution as is generally believed.

Complications comparable with those outlined above must continually have affected the geological record of the Brachiopoda and important changes in distribution are to be expected as systematic study proceeds. It is possible, however, that sampling is already thorough enough to give a reasonably accurate picture of the relative importance of various groups from one system to another. Some idea of the changes in faunal composition that occurred throughout time may, therefore, be profitably gauged from the distributions shown in Figures 153 and 154, and the following comments may be appropriate.

Except for the Cambrian, the Paleozoic may be described as the era of the Orthida, Spiriferida, and Strophomenida. The inarticulates were certainly conspicuous elements in the earlier phases of brachiopod descent, for they comprise about two-thirds of the Cambrian faunas. Yet only the Acrotretida were comparable in generic representation with the Orthida, which soon became so prolific as to outnumber the entire

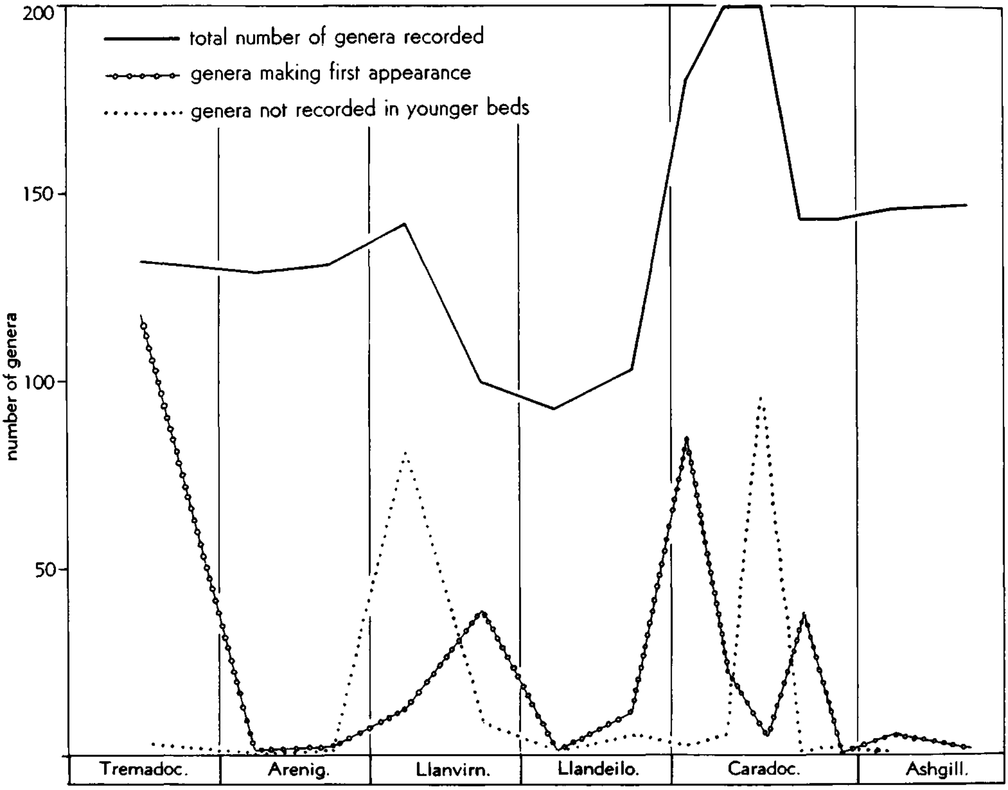

FIG. 151. Variations in total number and first and last appearances of brachiopod genera throughout Ordovician time (5).

class of inarticulates by early Ordovician times. Throughout the Ordovician, the Orthida, notably orthaceans and enteletaceans, remained dominant. They embraced about one-third of the brachiopod faunas and their supremacy was never seriously challenged by either the Strophomenida, which superseded the inarticulates in the Middle and Late Ordovician successions as the second most diverse group, or the pentameroid porambonitaceans, which had first appeared in the mid-Cambrian and were quite common in the Early Ordovician. These oldest strophomenoids were initially represented exclusively by the plectambonitaceans and strophomenaceans, since the davidsoniaceans are not now recorded from successions older than Middle Ordovician. Of the remaining groups that arose during the period, early Rhynchonellida and Spiriferida were indisputably the most significant to future development of the phylum. The Clitambonitidina are noteworthy for their restricted range, being unknown outside the Ordovician; they were relatively rare constituents of most faunas, however.

The history of the Spiriferida illustrates the rapidity with which new stocks may become established. By early Silurian time Athyrididina, Spiriferidina and especially Atrypidina amounted to about one-quarter of the total brachiopod faunas; and, apart from the mid-Silurian, when they were temporarily ousted by the strophomenoids (principally strophomenaceans), they remained dominant throughout the period. The replacement of the Orthida was equally decisive. They remained as the second most common group of brachiopods during the Early Silurian but thereafter their relative importance became greatly diminished, despite persistence of the enteletaceans and a minority of orthaceans into the Middle Paleozoic (triplesiaceans became extinct before

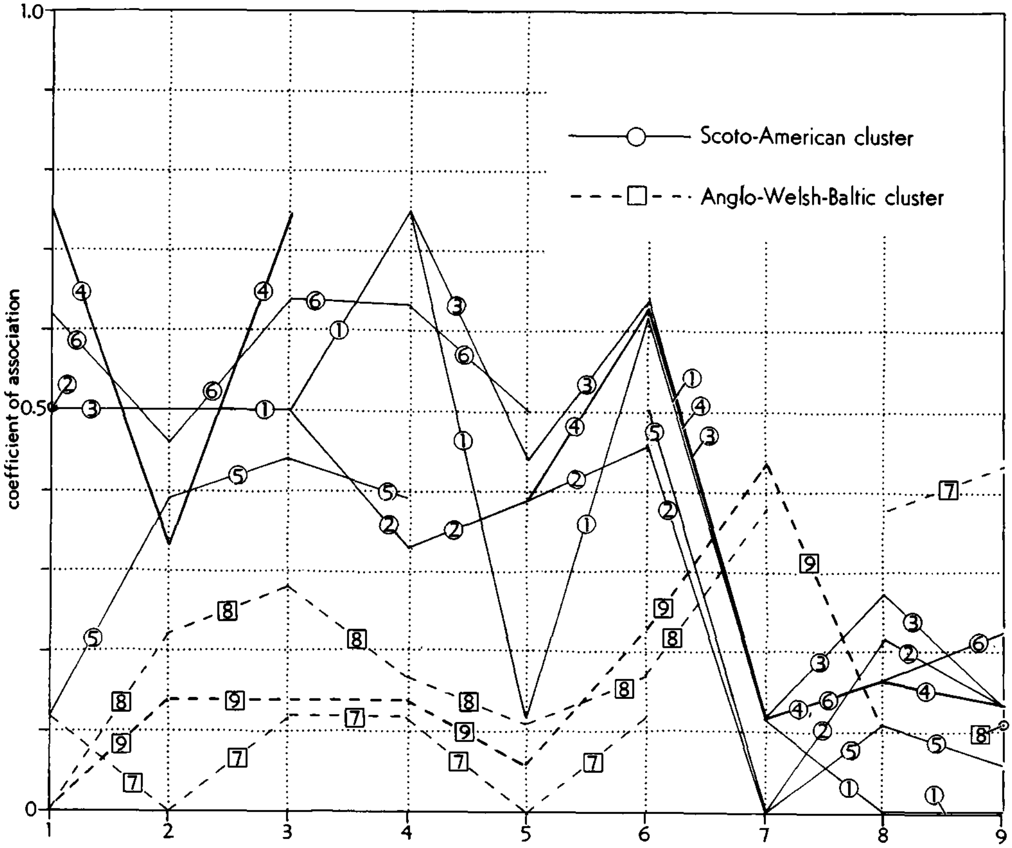

FIG. 152. Correlation profiles of nine Ordovician brachiopod faunas (*1*, Yellow Ls., Nev.; *2*, Mountain Lake, Okla.; *3*, Pratt Ferry and Little Oak, Ala.; *4*, Arline, Tenn.; *5*, Ward Cove, Va.; *6*, Stinchar Limestone, Scot.; *7*, Derfel Limestone, North Wales; *8*, Spy Wood Grit, Eng.; *9*, Kukruse Stage $C_{II}$, Eastern Baltic (refs. 1-4 and unpublished data). The coefficient of association was calculated by eliminating genera recorded in all successions and expressing the residue in common between any two faunas as a proportion of the smaller assemblage (5).

the end of the Silurian). Pentamerida, mainly pentameraceans, are widely regarded as typical of the Silurian as well as the Devonian. But this impression is a reflection of their restricted range, rather than their profusion, because they were consistently only the third most commonly occurring group and were even surpassed in respect of generic numbers by the Rhynchonellida throughout the Late Silurian. The most significant additions to the phylum during this period included the Spiriferida, Chonetidina, Stenoscismatacea, and Terebratulida, which first occur in transitional beds between the Silurian and Devonian.

Well more than one-third of the brachiopod genera recorded from the Devonian were Spiriferida, which persisted as the most important group throughout the period. There was, however, a subtle replacement within the order in that the spiriferaceans superseded the atrypaceans, which dwindled and became extinct by the end of the Devonian. Moreover, the rhynchonelloids were displaced by the strophomenoids as the second most common group throughout the Middle and Late Devonian. This transposition took place despite the extinction of the plectambonitaceans. It resulted from a late proliferation of the strophomenacean stropheodontids and particularly of the Productidina, which became the dominant Strophomenida during late Devonian times. The Terebratulida were initially conspicuous mainly through the advent of a number of centronellidine genera. They were, however,

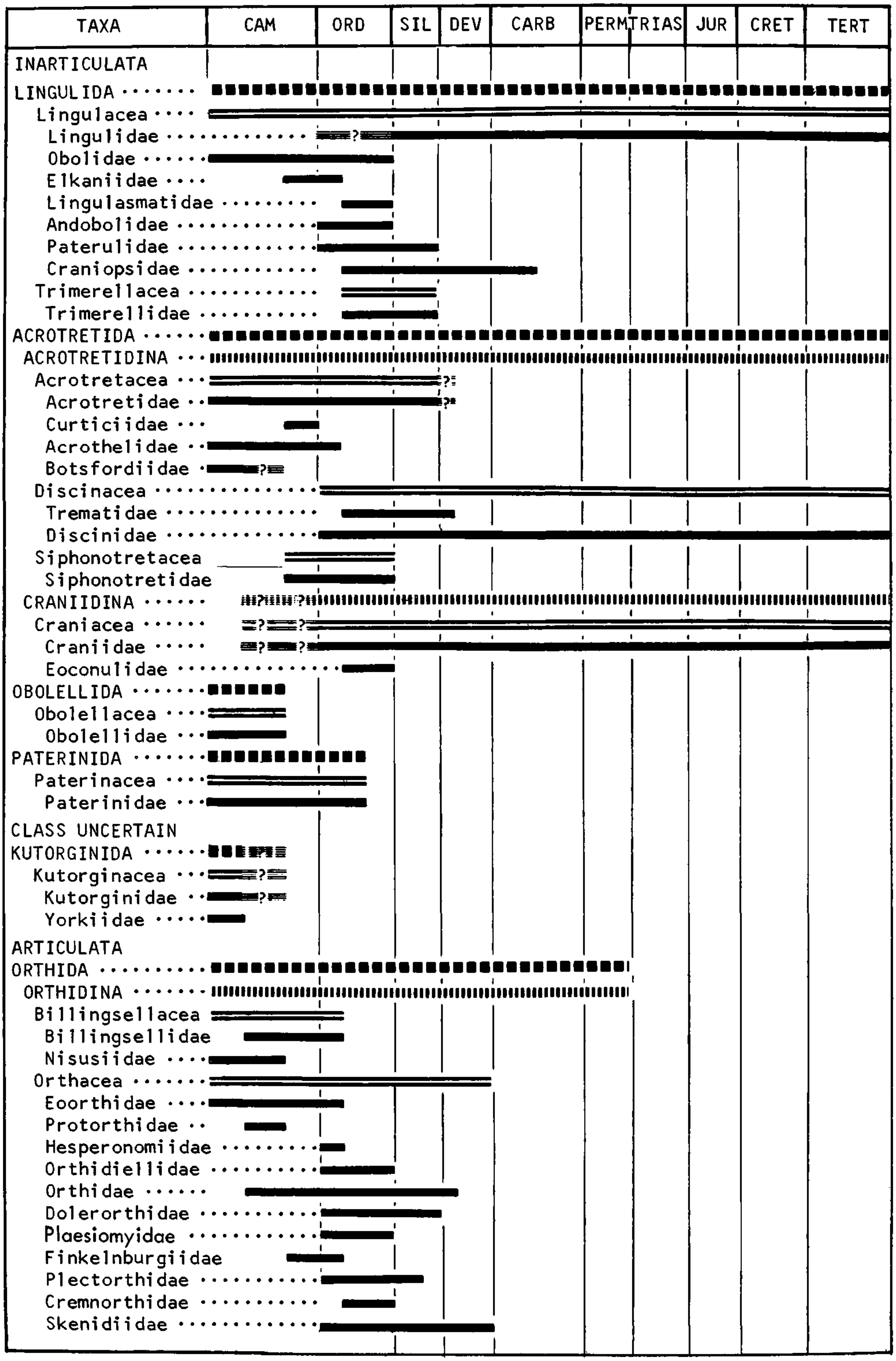

FIG. 153. Stratigraphic distribution of families and higher taxonomic units of Brachiopoda (5).

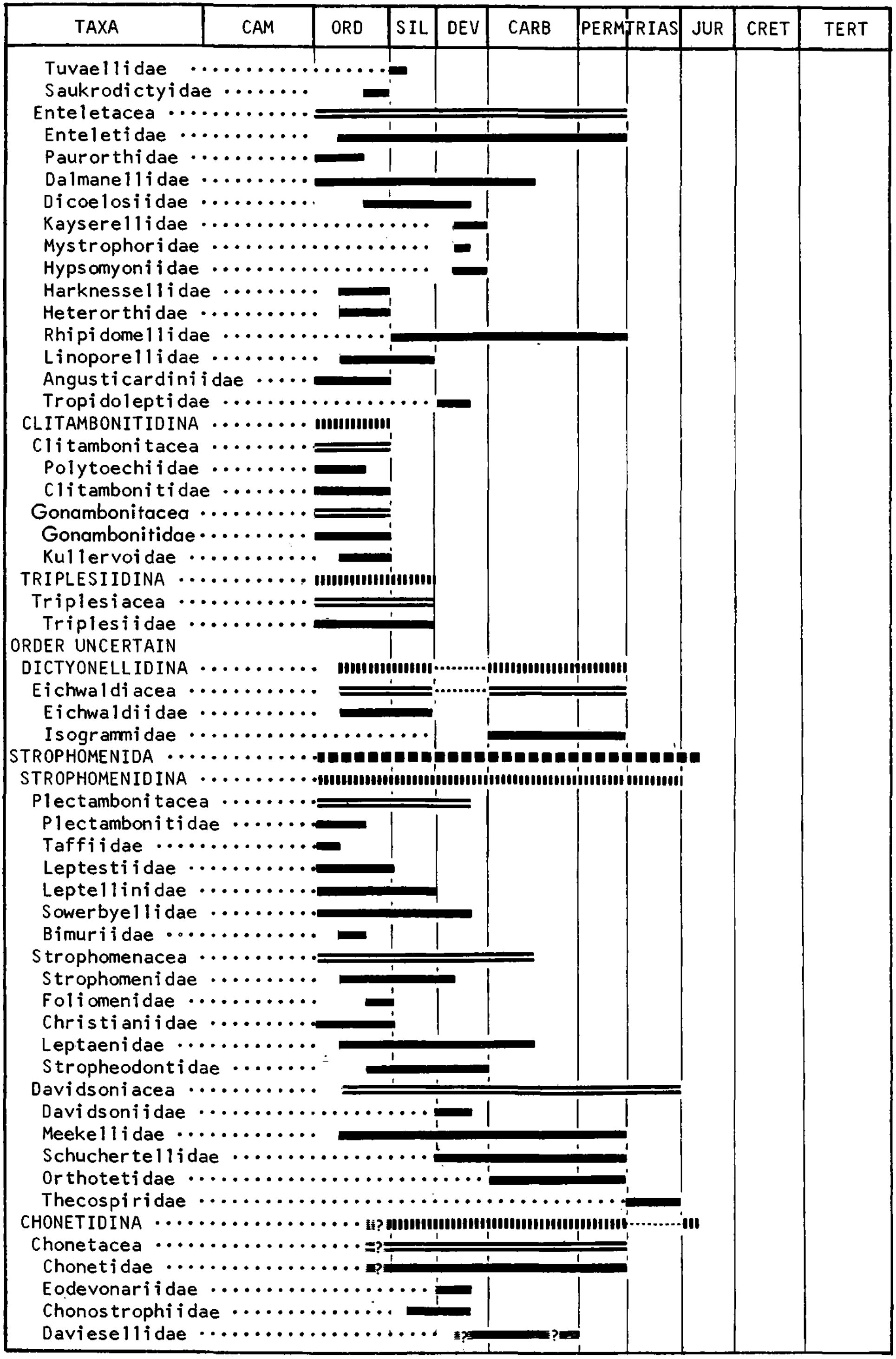

Fig. 153. (Continued.)

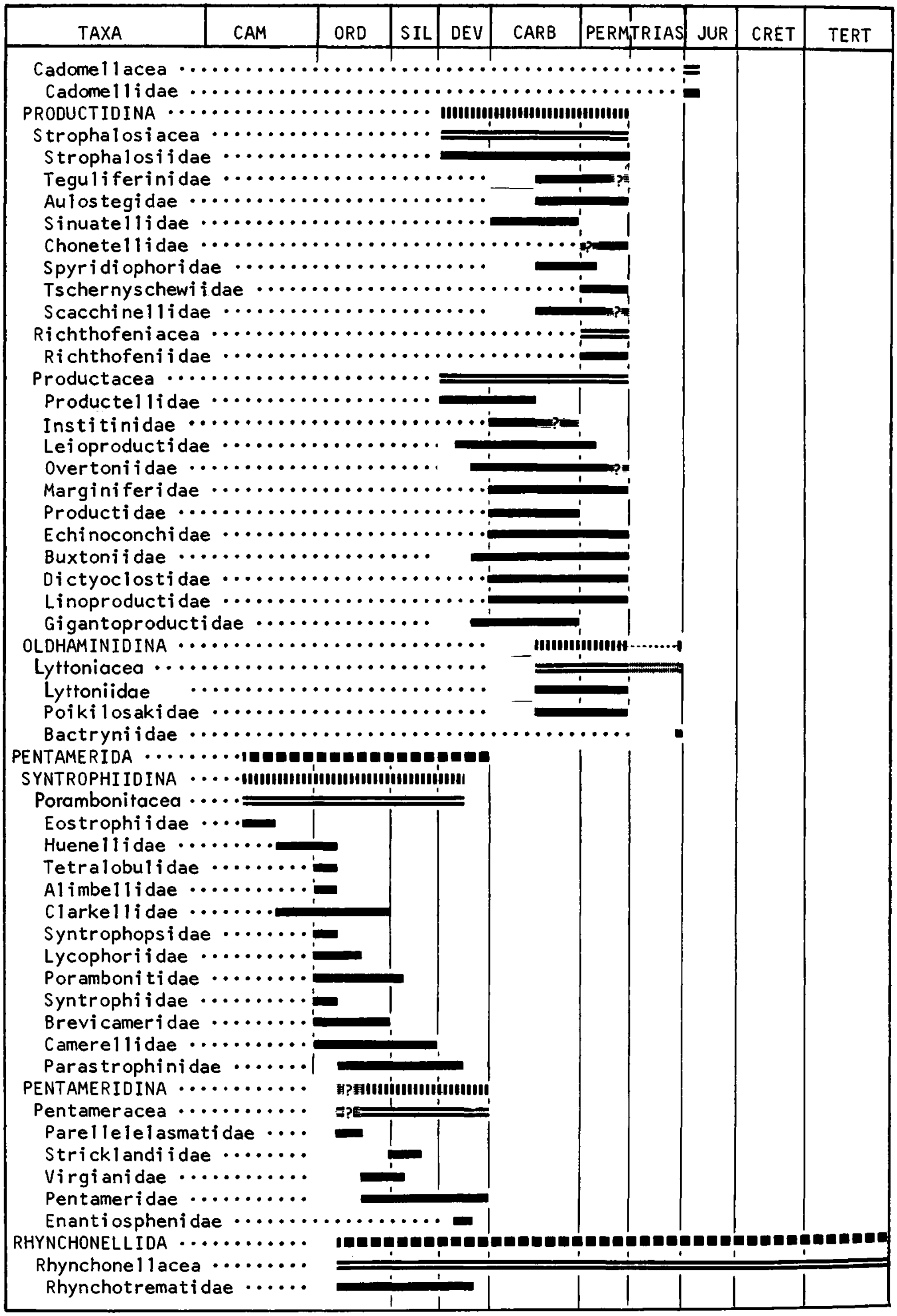

Fig. 153. *(Continued.)*

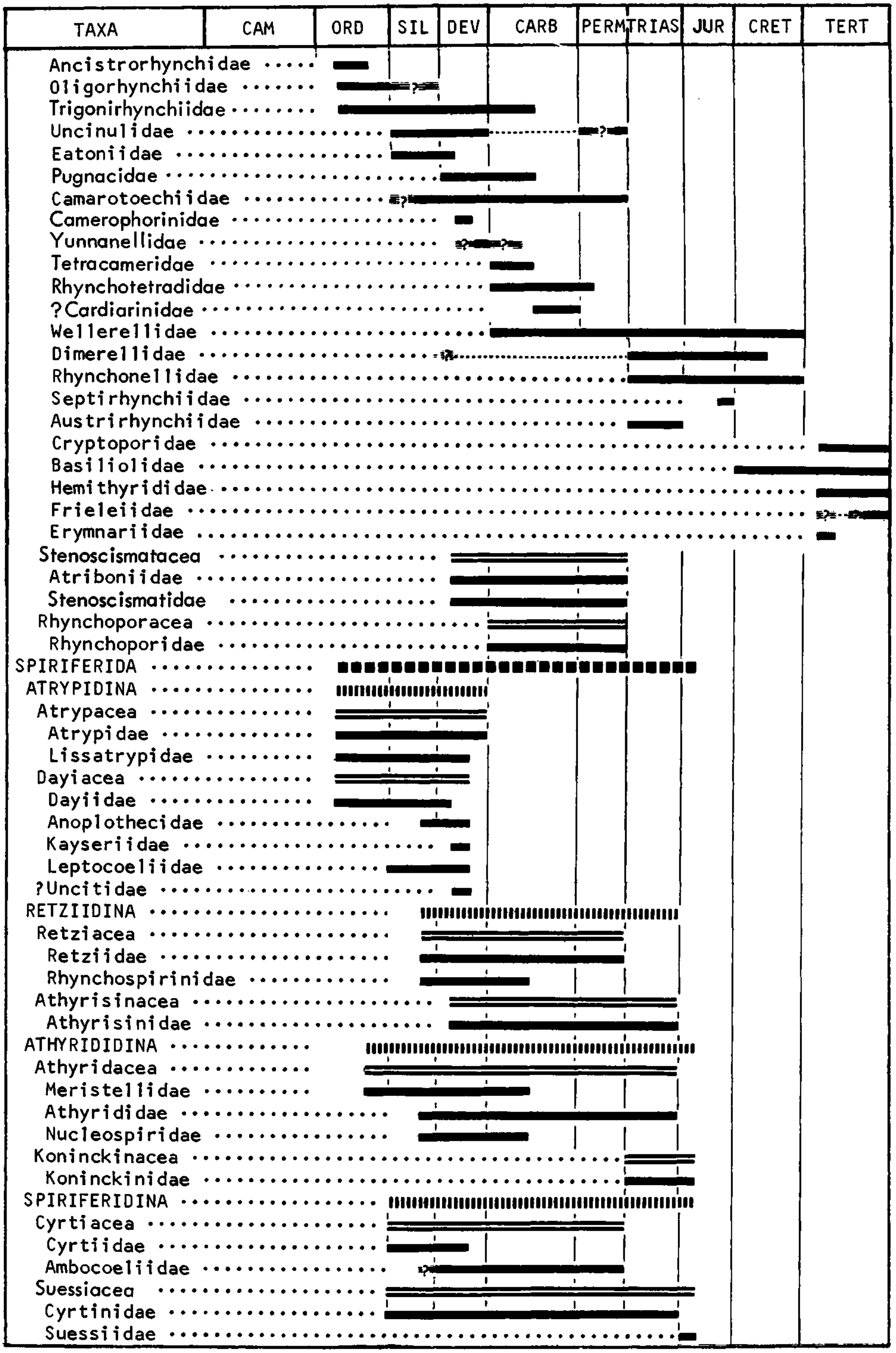

FIG. 153. *(Continued.)*

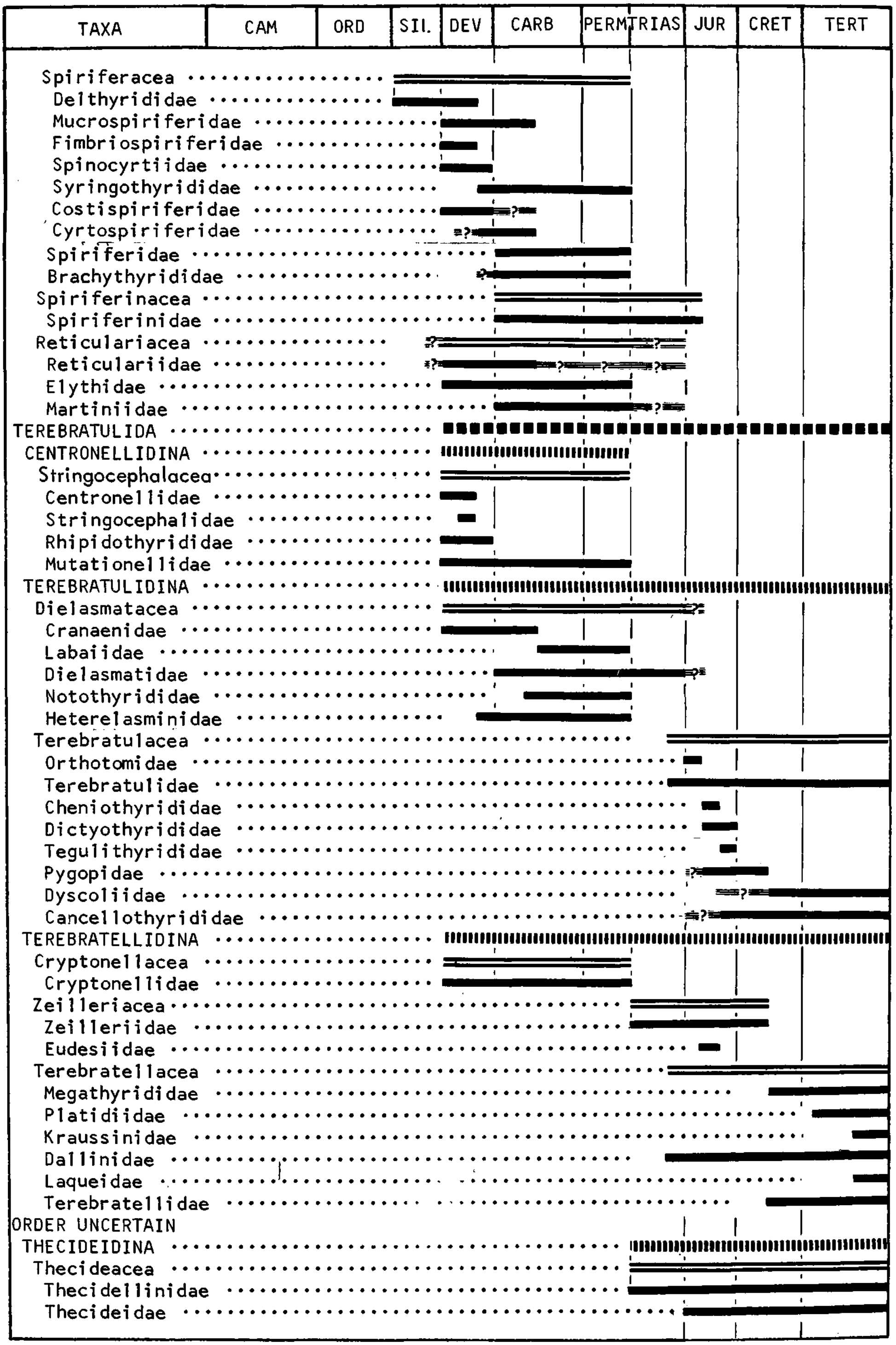

FIG. 153. *(Continued.)*

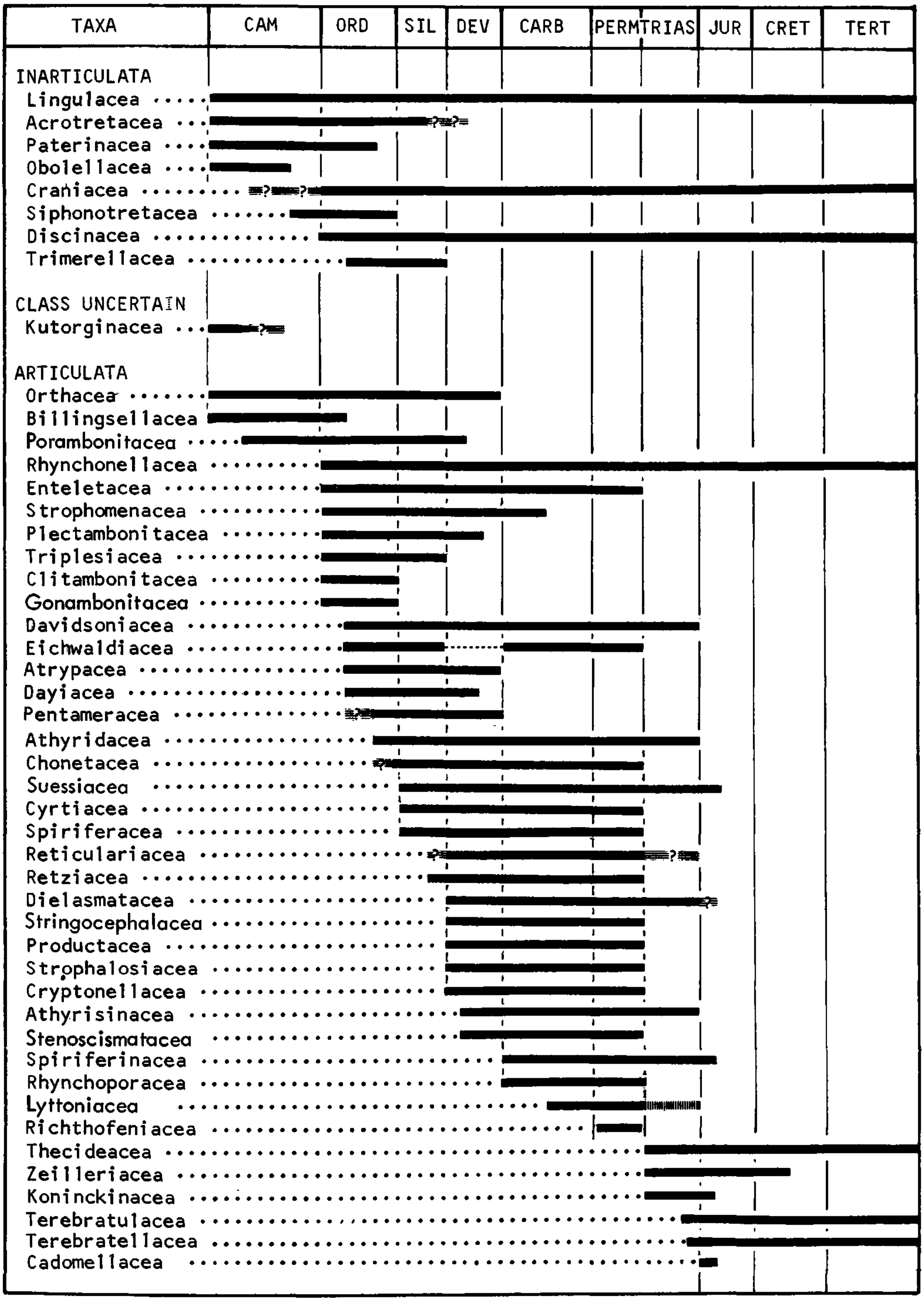

FIG. 154. Stratigraphic distribution of brachiopod superfamilies plotted according to order of their appearance (5).

less common than the Orthida throughout the rest of the period, although the orthaceans themselves became extinct before the beginning of the Carboniferous, leaving the enteletaceans as sole representatives of the order.

The ascendancy gained by the Productidina within the strophomenoid group became even more marked during the Permo-Carboniferous and indeed greatly contributed toward establishing the Strophomenida as the most diverse order throughout both periods. The productaceans formed the largest superfamily, with more genera during the Carboniferous than those assigned to all other groups. Yet by early Permian times, the chonetaceans, davidsoniaceans, Oldhaminidina, which are first known from the Late Carboniferous, and strophalosiaceans together became more numerous. The spiriferoids and especially the spiriferaceans and reticulariaceans, which thrived in more or less equal strength, were as consistently the second most commonly occurring group as were the rhynchonelloids the third. In fact, more than 80 percent of the brachiopod faunas then extant belong to these three orders and the remarkable changes that took place during the Mesozoic were mainly the consequence of a widespread extinction. Thus no member of the enteletaceans, productaceans, davidsoniaceans, richthofeniaceans, strophalosiaceans, spiriferaceans, cyrtiaceans, stenoscismataceans, rhynchoporaceans, Centronellidina, and dielasmataceans have yet been recovered from post-Paleozoic successions. This unprecedented reduction affected all taxonomic ranks of the Brachiopoda and not only marked the end of the Orthida, the first-established articulate order, but also the prelude to disappearance of the strophomenoids and spiriferoids. Admittedly, the spiriferoids, chiefly athyridaceans, survived in sufficient strength to become the commonest Triassic brachiopods; but along with a few strophomenoid derivatives they ultimately became extinct in the Jurassic.

With the elimination of such large and long-established orders, the Rhynchonellida and Terebratulida ultimately emerged as the dominant articulate brachiopods, although both groups remained subordinate to remnants of the Spiriferida during Triassic time. Throughout much of the Triassic and on into the Early Jurassic, the rhynchonellaceans were more numerous than the Terebratulida, which were represented mainly by the terebratulaceans. But by mid-Jurassic time, the terebratuloids, especially the terebratulaceans and zeilleriaceans, replaced the rhynchonelloids as the most prolific brachiopod order. This position has been maintained up to the present day by an increase in the number of terebratellacean stocks, which has more than counterbalanced the extinction of the zeilleriaceans and the decline of the terebratulaceans during Cretaceous time. The only other brachiopods living today are, significantly, descendants of two of the oldest orders, the inarticulate Lingulida and Acrotretida, and the youngest group to come into being, the thecideaceans.

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### ADDITIONAL SOURCE OF ILLUSTRATIONS

(5) **Williams, Alwyn,** new

# TECHNIQUES FOR PREPARATION OF FOSSIL AND LIVING BRACHIOPODS

By ALWYN WILLIAMS
[The Queen's University of Belfast]

Brachiopods have flourished at some period or another in nearly every type of marine environment since Cambrian times, so that, like representatives of many other phyla, their occurrence is registered in such a variety of ways that a number of techniques have come into use to facilitate the study of their record. These modes of preservation are all ultimately related to the degree to which closed or gaping shells or disarticulated valves remain unaltered after their burial. Skeletal remains may have been so unaffected by diagenesis as to permit detailed studies of their shell structure, a state of preservation that is found even among Cambrian articulate brachiopods. Quite commonly, however, the original shell substance has been partially or completely recrystallized or replaced by dolomite, pyrite, or silica. It may even have been dissolved away completely, without replacement, leaving external and internal molds which bear the impressions of exterior and interior surfaces of the shells or valves. Clearly, the techniques involved in the study of molds or altered shells serve only to reveal morphological detail, but those employed in the examination of unaltered shells may also furnish information on shell deposition and growth.

In general, molds are eminently satisfactory for purposes of morphological reconstruction, because the counterparts can be used to prepare casts of both internal and external features. A number of casting materials, including waxes and plastics (18) are widely favored but modeling clays, like plasticene, and various latex solutions, with or without plaster fills, are among the simplest and most efficient media in use. Plasticene, with a wetted surface to prevent adhesion, provides adequate impressions for day-to-day purposes; but permanent casts, especially of molds that accommodated long, obliquely disposed apophyses, are best obtained by using latex solution. Good casts free of air blisters are usually obtained by wetting the mold surface with a diluted detergent to reduce surface tension, and applying a thin first coat of latex carefully decanted into undercut indentations of the mold. Further coats should then be added to build up a thick but pliable cast. The translucency of dried natural latex is disadvantageous to the microscopic examination and photographing of casts even when they are coated by a sublimate like ammonium chloride, but casts can be opaquely colored by adding small quantities of india ink or organic dyes to the liquid latex stock.

A profitable examination of shells that have been recrystallized or dolomitized depends on how distinguishable they are from their containing matrix, which, more often than not, has been similarly affected. Selective silicification that has commonly resulted in the replacement of articulate shells in carbonate rocks, however, has proved a boon for the study of morphological variation.

The process of dissolving silicified organic remains out of carbonate rocks by dilute acids has been known for a long time (8, 21) but was not practiced on a large scale until the 1930's when COOPER began his systematic investigation of the American Ordovician brachiopods and his studies (5, 17) are a testimony to the efficacy of this technique. Dilute hydrochloric acid may be used to etch silicified shells out of limestone blocks, but this acid also attacks the unsilicified chitino-phosphatic shells of inarticulates and, following BELL (2), dilute acetic acid or the more quickly acting formic acid are now more popular etching agents because their use ensures the recovery of the inarticulate elements in the fauna. During etching, certain delicate structures, like loops or spires, that gradually appear may break away in the final stages of solution of their supporting matrix. To prevent such destructive collapses, COOPER (12) has used paraffin wax as a temporary embalming medium which may later be removed with xylol; and CLOUD (4) has advocated the painting of those parts of the fossil content requiring strengthening and protection with cellulose acetate. Silicified shells recovered by etching are normally brittle and may even be hollow, and thus subject to collapse, because replacement may have been limited to thin external and internal skins to the original shells. It is therefore advisable to harden specimens by thinly painting them with liquids, like polyvinol acetate emulsion (12) or "lustrex" dissolved in acetone, which dry out to form a tough protective binding cover.

The preparation of unaltered shells and valves for examination is nearly always a more exacting task than those just described. Even when specimens have been washed out from clays and sands it is likely that adherent particles obscure the finer morphological details, and although the penetrative effects of ultrasonic tanks and detergents are invaluable aids in the final stages of cleaning, patches of matrix may still have to be removed by mechanical means. The simplest method, and also one over which the most delicate control can be exercised, is, of course, the scratching away of matrix with needles, either permanently mounted or held in chucks. COOPER (5) has found that if the needle points are beveled they can be used as fine chisels and such microscopic cutting edges greatly facilitate the scraping away of material and minimize the damage done to the shell surface. During such preparation, surfaces are best kept wet, not only to soften some types of matrix but also to accentuate the visible contrast between shell and matrix. Even for specimens in rock, the final cleaning is best performed in this manner, although there are other means for reducing the volume and toughness of the enclosing matrix.

Dental equipment with electrically driven cutting wheels and chisels or similarly fitted percussive implements can be safely used for removing much of the matrix. Certain chemicals like caustic potash (17), hydrogen peroxide, and gasoline (see SOHN in 16) have been used in an attempt to find effective methods of disintegrating argillaceous or arenaceous rocks. Carefully applied dilute acid may also be used to remove carbonate matrix (see, for example, 5), but, in general, such methods are only partially successful, because of the wide range of bonding properties of rock cements; accordingly, they should be regarded only as ancillary to the more painstaking process of mechanical dissection. Indeed, the rock containing brachiopods may be so intractable that removal of the shell, thereby providing external and internal molds, is an easier and less hazardous operation. Thus, dilute acid may be used to dissolve away shells embedded in noncarbonate rocks, especially tough mudstones and siltstones which give very fine external and internal impressions; although slight carbonate diffusion into the matrix immediately adjacent to the shell may ultimately leave the mold surfaces friable enough to require hardening.

Specimens embedded in matrix which is sufficiently calcareous to preclude the use of acids may be transformed into molds by calcining the shell. This method was first recorded by BUCKMAN (3), who suggested that specimens should be heated until the shell becomes powdery and then should be plunged into cold water. The technique can be very wasteful of material because most matrices, including the finely grained ferric ones which provide the best molds, are liable to crack and explode, not only during their immersion in water, but even while they are being heated. On the whole, the more cautious approach adopted by COOPER (5) of removing the calcined shell by dissection, rather than by slaking, is preferred.

Under certain conditions of deposition, buried shells may be so tightly closed as to contain only a small quantity of sediment, and during diagenesis the remaining shell space may become filled with clear calcite. Such a matrix has been used to great advantage in the study of internal features because, being soft and transparent, it can easily be cut and chiseled to expose the skeletal remains. In this medium it is possible even to dissect out such fragile structures as loops and spires (GLASS, 8). But, generally, nothing more is required for studies in the variation of lophophore supports (10) than to chisel away the anterior part of the shell of a number of specimens and then to clear the calcite of abrasive marks by controlled application of dilute acid. Such prepared surfaces coated with glycerine give satisfactory views of the entombed structures.

Other techniques that currently aid in the study of unaltered shells mostly involve the preparation of serial sections. Critical comments have been made in the past about these methods of investigation (14, 17); but they are only justifiable for those procedures which do not provide any permanent record of successive sections through a specimen except for camera lucida drawings or photographs of internal and external outlines of the shell substance. When carried out with all its modern refinements, however, serial sectioning gives an accurate picture not only of the gross morphology but also of the growth relationships and composition of the skeletal parts. Indeed, it can be claimed that no comprehensive review of morphological variation within a group of brachiopods is complete without the kind of supplementary information that is obtained only from the study of serial sections.

The most sophisticated procedure is based on taking impressions of differentially etched sections of a shell. It has been known to paleontology for at least 50 years but apparently was not used for the interpretation of brachiopod morphology until the 1930's when St. Joseph (15) carried out his investigations of lower Paleozoic articulates. Since then a number of refinements have improved the technique, and although individual taste gives rise to some variation in procedure, the following steps are known to yield satisfactory results. Before mounting a specimen for sectioning, it is usually necessary to produce a replica of it. Rubber compounds, like latex, are commonly used to make a pair of mold blocks of the specimen which can then be filled with a solidifying plaster and pressed together until a complete cast has annealed and set (11).

The mounting of a specimen within an appropriately sized block of an acid-resistant substance is essential for reasons that will soon become obvious. Plaster of Paris or dental plaster is still commonly employed for this purpose (11), but any one of the laminar resins (e.g., Marco Resin) is superior because it is much freer of air bubbles and more closely adherent to the external surface, thereby preventing any deep corrosion along this interface; and because the specimen can be clearly seen within such a medium and thus oriented to any desired position for sectioning. The external surface of the specimen may be intricately ornamented or friable or pervaded by microscopic cracks, so that it is advisable first to soak the shell in resin for some hours. In the meantime, the floor of a tray made out of aluminum foil or pliable plastic (individual ice cube trays are big enough for most specimens) is covered to a required depth with polymerizing resin. In due course this hardened resin provides a solid base on which to rest the soaked specimen and polymerizing resin is then added to immerse the specimen either in one operation or, if the shell is big, in successive stages to prevent the development of tension cracks during hardening. When the resin is completely polymerized, only the surface in contact with the atmosphere remains sticky (this can be cleaned with acetone) and the resin, which is easily ejected from the tray, is squared off relative to the preferred orientation of the contained specimen. The base of the prepared block is then soldered by beeswax to the attachment plate of a grinding machine that is calibrated to control the abrasive reduction of the top surface of the resin block by as little as 10$\mu$. The Croft parallel grinding instrument (6), now manufactured by the Cutrock Engineering Co., Ltd., is the best known of these machines; but Hendry, Rowell, & Stanley (9) have recently described equipment which prepares the ground surfaces much more quickly.

Once mounted in position, the top surface of the block is ground down until the shell substance first appears. This exposed area of shell is then etched with dilute acid (dipping the surface about 15 times in 10 percent HCl is normally sufficient), washed, and allowed to dry. A negative impression of the prepared surface can be obtained in a number of ways. The common practice is to apply a thin coat of one of the commercial collodions or a similarly constituted laboratory preparation; for example, cleaned nonsafety film cut into small pieces and added to amyl acetate can be made to any required consistency (7) and has proved eminently successful. But good impressions can also be obtained more quickly by painting the etched surface with amyl acetate and pressing on to it a thin cellulose film. When the preparation has dried, it can be neatly

FIG. 155. Proximal oblique section of spine on brachial valve of *Acanthothiris spinosa* (LINNÉ), showing disposition of fibers in secondary layer, nonfibrous primary layer represented by black rim (cellulose peel, *ca.* ×200) (22).

peeled off the block by first lifting its edges with a razor blade. Subsequent to obtaining the first peel, the instrument is set to grind the block down by required thicknesses and at each interval a peel can be taken until the specimen has been completely abraded (Fig. 155).

Other methods of serial sectioning are practiced. They include the calcining of the shell and the differential staining of the matrix to enhance their contrast; and the drawing or photographing of successive sections (1, 11, 13); but they are certainly less efficient and informative than that described above. The great advantage of the preparation of peels is that they constitute a permanent record that can be used for future studies. Thus they can be projected like negative films to give enlarged photographic prints which in turn can be used as controls for the reconstruction of large-scale models in wax (20). Under high magnifications they show, in negative relief, such details of shell structure as the relationships between fibers comprising the secondary layers of articulate brachiopods. Indeed, these properties of cellulose acetate make it invaluable for rapidly preparing random sections of the shell as well as for determining fine details of the shell surface, like the shell mosaic, which can easily be reproduced without recourse to etching prior to the application of collodion (Fig. 156).

Finally, a few remarks about the preparation of living material seem appropriate here, because interpretive studies of fossil remains cannot really be conducted without reference to the relative distribution of soft parts in living brachiopods. Normally, anatomical sections are prepared by well-known biological techniques subsequent to the decalcification of the shell, the position of which, relative to its secreting epithelium, has to be inferred. It is, however, greatly to the advantage of the palaeontologist to be able to examine sections showing both shell substance and soft parts and the following procedure (19) gives satisfactory results.

A preserved specimen is bulk-stained with some suitable dye, like hematoxylin, and is then taken through a series of liquids in which the preservative is progressively re-

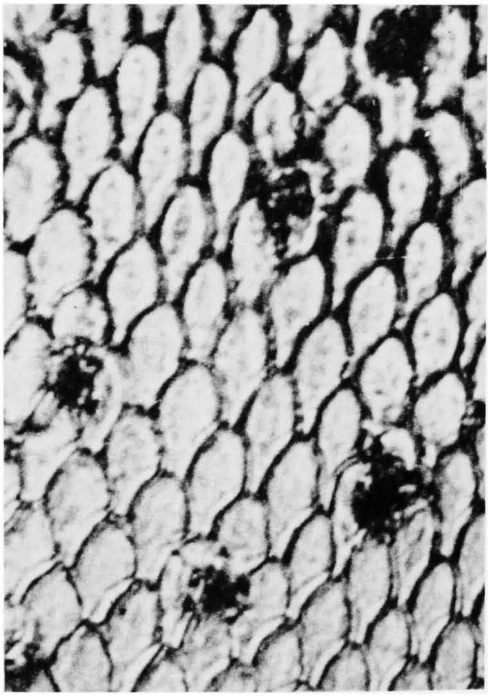

FIG. 156. Internal surface of brachial valve of *Terebratulina caputserpentis* (LINNÉ) showing shell mosaic, which corresponds with cell outlines of outer epithelium (cellulose peel, *ca.* ×550) (22).

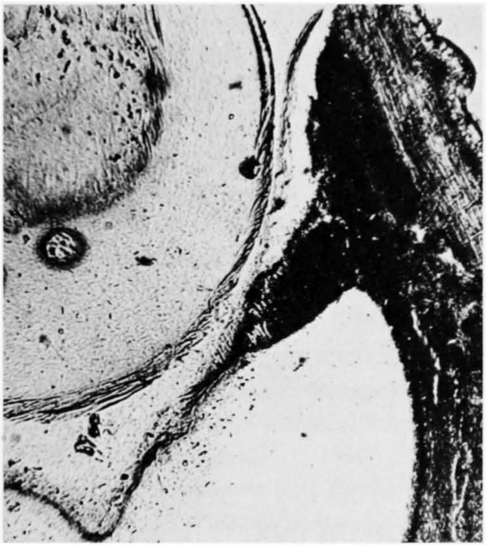

FIG. 157. Part of section through posterior part of *Terebratulina caputserpentis* (LINNÉ) which has been bulk-stained and impregnated with resin before cutting, pedicle at top left, pedicle epithelium disposed in V at bottom left, pedicle valve with periostracum, primary and secondary shell and outer epithelium at right (*ca.* ×60) (22).

duced and acetone proportionately increased (Fig. 157). Once the pure acetone stage is reached the specimen is taken through a second series in which a laminar resin is increased at the expense of acetone (in respective proportions, for example, percentage ratios of 25/75, 50/50, etc.). The longer the interval of time between each transfer (2 or 3 days at least), the more complete the diffusion of increasing concentrations of laminar resin into the tissues. After soaking in laminar resin for a few days, the specimens can be mounted within polymerizing resin in the same way as a fossil shell, and the block containing the specimen can then be cut into a number of thin slices which, like those of rocks or minerals, can be prepared as microscope slides.

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### SOURCE OF ILLUSTRATIONS

(22) **Williams, Alwyn,** new

# SYSTEMATIC DESCRIPTIONS

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