AFFINITIES OF BRACHIOPODS AND TRENDS IN THEIR EVOLUTION

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INTRODUCTION

[Alwyn Williams]

Among living, skeletonized metazoans, brachiopods probably have the longest and most complete geological record. Linguliform (paterinate) shells occur in the earliest Cambrian (Tommotian) fossil assemblages; and species of three of the eight Cambro-Ordovician classes that constitute the phylum ubiquitously inhabit modern seas. This wealth of data has sustained two centuries of anatomical, embryological, morphological, and, now, molecular enquiries into the sister group and ancestry of brachiopods. Morphological studies are especially important in postulating ancestral features, not just because of the richness of the fossil record. Brachiopod valves are bilaterally symmetrical with the plane of shell opening (commissural plane) transverse to the bilateralian body. This unusual body plan is a simple but potentially important clue when researching assemblages of earliest Cambrian problematic sclerites for possible sister groups of ancient brachiopods. Such use of fossil data has its place alongside molecular and biological evidence, which is considered in the section on brachiopod affinities (p. 2383 herein).

Despite the distinctiveness of their body plan, brachiopods have often been grouped with other phyla, especially the phoronids. The body plan itself has been regarded as diphyletic in one molecular study, and although this conclusion proved untenable (and is based on artifacts), relationships among brachiopod classes are not always clear. A discussion of brachiopod monophyly and intraphylum relationships is included herein (p. 2830).

The course of brachiopod evolution is documented, albeit incompletely, in the 4800 or so genera described in this revision of *Treatise Part H* (KAESLER, 1997, 2000, 2002, 2006, and herein); but the use of such a formidable quantity of data has been subjective as well as selective. If the hierarchy used to identify the described brachiopods had been wholly phylogenetic and not Linnaean, this chapter would have been a description of those clades that, in our opinion, best exemplify brachiopod evolution. The classification, however, is not yet fully consistent phylogenetically in the way genera have been assembled hierarchically. Some have been assembled cladistically, which has at least the merit of exposing homoplasy. Other parts of the hierarchy have been built up by systematic, mostly morphological, comparison. The data used to establish the hierarchy are also variable in quality and inclusiveness. Ninety-five percent of the classified genera are extinct; and the data distinguishing them are limited to the chemical composition, microstructure, and morphology of their shells, although this can include mantle imprints and skeletal devices for the accommodation and support of various organs. The preponderance of

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[1] Alwyn Williams prepared the initial outline and framework for the components contained within this chapter, derived from a remarkably rich and productive lifetime devoted to the study of brachiopods, their morphology, and evolution. Alwyn and I each wrote separate accounts of our interpretations of brachiopod affinities and trends, with the intention of combining and coordinating our different points of view in the final draft. Sadly, Alwyn passed away before completion of the final draft of this chapter, making such a coordinated effort impossible. Alwyn worked steadily on various drafts up until a week before his death, in keeping with his indefatigable spirit and determination to complete the *Treatise* revision. After his death, numerous studies appeared in the literature that affect some interpretations presented in his drafts. As such, Alwyn's section on affinities in this first chapter is focused more on establishing elements of brachiopod evolution as we understood them just prior to his death. Bracketed notes highlighting recent research were added after his death, and authorship is clearly noted for each section. My section forms a separate, subsequent chapter focused more on raising questions about issues that are not yet understood in light of these more recent studies, with the hope that this approach will encourage others to pursue answers to these questions in the coming years. SJC.

data on brachiopod evolution and trends in morphological evolution is, therefore, weighted in favor of skeletal differentiation, as is evident in the section on brachiopod evolution (herein, p. 2833).

One aspect of brachiopod evolution that has to be taken into account is that material evidence of it is scattered throughout 550 million years of rock successions. This stratigraphic evidence can, on occasion, conflict with phylogenetic relationships inferred from biological and morphological studies and with molecular estimates of time derived from genealogies. These issues are considered in various sections below and in CARLSON, herein, p. 2878.

BRACHIOPOD AFFINITIES

[Alwyn Williams]

Even before the Darwinian theory of evolution and the Haekelian concept of phylogeny had taken root, opinions on the metazoan affinities of the Brachiopoda were being obliquely expressed by classificatory practices. At the beginning of the 19th century, brachiopods were commonly classified as mollusks (LAMARCK, 1801) or molluscoides. The latter name was used by HUXLEY (1869) to accommodate his view (shared with HANCOCK, 1859) that brachiopods and polyzoans (bryozoans or ectoprocts) are related. MORSE (1902), on the other hand, concluded that the brachiopods are more closely related to the annelids and cited the possession of setae as part of the evidence of common ancestry.

CLASSICAL (EMBRYOLOGICAL, ANATOMICAL, AND MORPHOLOGICAL) STUDIES

The formal recognition that brachiopods are bilaterian animals came with HATSCHEK's use of the body plan (1888–1891) as a tool in uncovering metazoan affinities. In particular, the comparative studies of anatomy and larval development of brachiopods and *Phoronis* (CALDWELL, 1882) led HATSCHEK (1888–1891, p. 40) to propose a new phylum for brachiopods, bryozoans, and phoronids: the Tentaculata (later more appropriately renamed Lophophorata [HYMAN, 1959, p. 229]).

Further refinement of metazoan phylogeny, distinguishing the Protostomia from the Deuterostomia, has caused dissension over the precise rooting of brachiopods within the Bilateria. Initially the lophophorates were regarded as protostomes. Reservations on how to interpret the development of the brachiopod gut and coelom prompted HYMAN (1959, p. 230) to suggest that the lophophorates "form some sort of link between the Protostomia and the Deuterostomia." In effect, the lophophorates could be the sister group of either clade; and there is currently some (albeit controversial) support for describing brachiopods as deuterostomes as well as protostomes.

A deuterostomous origin of all lophophorates has attracted support especially among biologists interpreting classical embryological, anatomical, and morphological data. It has been the prevalent opinion among such zoologists as BRUSCA and BRUSCA (1990), SCHRAM (1991), MEGLITSCH and SCHRAM (1991), and EERNISSE, ALBERT, and ANDERSON (1992). A more recent study by LÜTER (2000a) of the development of the mesoderm in brachiopod (rhynchonelliform) larvae suggested that the coelom may be enterocoelic. He concluded that the Brachiopoda and the Deuterostomia are sister groups and rejected a brachiopod sister-group relationship with *Phoronis* so that, in his opinion, the lophophorates are paraphyletic. NIELSEN (1995, p. 6) also regarded the lophophorates as paraphyletic but as a result of different groupings. On the basis of further studies and reinterpretations of lophophorate larval development, NIELSEN assigned the bryozoans to the protostomes and the brachiopods and phoronids to the deuterostomes (Fig. 1890), as sister groups (NIELSEN, 2001). In his view, several features upholding lophophorate monophyly, like the lophophore itself, are not synapomorphies but homoplasies. NIELSEN's conclusions are supported by the immunohistochemical

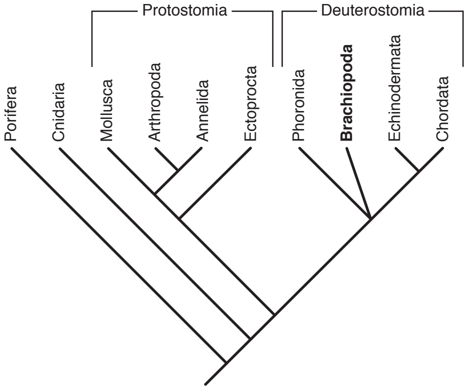

FIG. 1890. Cladogram of major animal groups, showing brachiopods nested among the deuterostomes (adapted from Nielsen, 1995).

study by HAY-SCHMIDT (2000) of the serotonergic larval nervous systems of species representing a number of deuterostomes and protostomes. The brachiopods (*Glottidia*) and phoronids group with the deuterostomes; bryozoans with the protostomes.

MOLECULAR STUDIES

In contrast to the weight of classical data favoring brachiopods as deuterostomes (or a sister group thereof), molecular studies have consistently placed the phylum among the protostomes. These studies have been based on the following: partial and complete sequences of nuclear-encoded, small (18S) and large (28S) subunit ribosomal RNA genes by FIELD and others (1988), LAKE (1990), HALANYCH and others (1995), COHEN and GAWTHROP (1997), COHEN, GAWTHROP, and CAVALIER-SMITH (1998), and COHEN and WEYDMANN (2005); partial and complete sequences of mitochondrial DNA (mtDNA) by COHEN and others (1998) and STECHMANN and SCHLEGEL (1999); and Hox genes, involved in the directional development of bilaterians, by DE ROSA and others (1999). In all but the earliest, pioneering studies, two branches of the Protostomia are recognized: the Lophotrochozoa (HALANYCH & others, 1995) consisting of the lophophorates, mollusks, annelids, and selected other phyla; and the Ecdysozoa.

There was, however, no agreement on the sister group to the brachiopods being within the lophotrochozoans. HALANYCH and others (1995) concluded that brachiopods are not monophyletic because phoronids, not the linguliforms (represented by *Glottidia*), are the sister group of the rhynchonelliforms (represented by *Terebratalia*). The results, which led to the recognition of a new infrakingdom, the Lophotrochozoa, were regarded as premature by CONWAY MORRIS and others (1996), especially on the grounds that these early lophophorate sequences were unreliable.

In their study, which was primarily concerned with the genealogy of 37 brachiopod species representing all extant orders of the phylum, COHEN, GAWTHROP, and CAVALIER-SMITH (1998, p. 2056) found evidence for including the phoronids in a lingulide-craniide clade (the outgroup used for the tree was a chiton). Further study of relevant 18S rDNA gene sequences convinced COHEN (2000) that the phoronids nest within the brachiopod clade (Fig. 1891) with weak support for craniides as a sister group, which, in turn, cluster with lingulides as a sister group to the discinoids (COHEN, 2000, p. 228). COHEN, therefore, reclassified the phoronids as a subphylum (Phoroniformea) of the Brachiopoda. Neither the mtDNA nor the relevant Hox gene sequences of *Phoronis* were used in the analyses of STECHMANN and SCHLEGEL (1999) and of DE ROSA and others (1999). Moreover, their comparative analyses were restricted to *Terebratulina* and *Lingula* respectively so far as the brachiopod genomes were concerned. Interestingly, however, STECHMANN and SCHLEGEL, like COHEN and GAWTHROP (1997) and COHEN and others (1998), found a close affinity between *Terebratulina* and a polyplacophoran mollusk (chiton).

RECONCILIATION OF CLASSICAL AND MOLECULAR STUDIES

Unsurprisingly, several reviews have challenged the reliability of classical or molecular data or have attempted to reconcile the conclusions drawn from them. Different methods have been used to assess the relative merits of classical and molecular evidence. The comprehensiveness of several reviews has inevitably been affected by the pace of later research, especially in the molecular field. Comparisons of some of the more recent reviews, however, are informative in revealing conflicting interpretations of biological and molecular evidence. Thus, attempts by biologists (Lüter & Bartolomaeus, 1997) to reconcile both kinds of data involved the reassessment of seven morphological and embryological complexes that, overall, relate brachiopods to the deuterostomes. They concluded that all but the presence of setae confirmed this relationship. Conversely, strategic insertions of brachiopods or phoronids as a sister group to selected phyla in a spiralian tree required too many convergences to become congruent, in their opinion. In contrast, the protostomous affinity of brachiopods was reaffirmed by de Rosa (2001) in his review of molecular and biological evidence. Six morphological and embryological complexes, largely overlapping those reviewed by Lüter and Bartolomaeus (1997), were assessed as being unreliable evidence for the deuterostomous grouping of brachiopods.

A more comprehensive review by Peterson and Eernisse (2001) involving phylogenetic analyses of classical and molecular (18S rDNA) data, separately and together, appears to resolve several issues of conflict (Fig. 1892). In both separate analyses, brachiopods and phoronids group within the protostomes, although their molecular data do not support brachiopod monophyly. In the combined analyses, however, the Brachiopoda are monophyletic with *Phoronis* as a sister group. The evidence amassed by Peterson and Eernisse (2001, p. 188) appears to be sufficient to "challenge the formal inclusion of phoronids with the brachiopods," as had been proposed by Cohen (2000) and adopted by GenBank (2006) [see Cohen & Weydmann, 2005 for a more recent investigation].

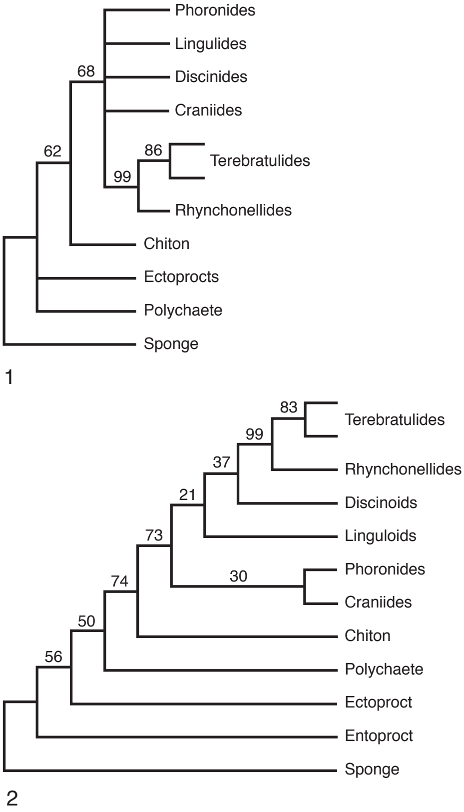

Fig. 1891. Results of phylogenetic analyses of 18S rDNA sequences of representative extant brachiopod species, showing nesting of phoronids among brachiopods. *1,* Maximum parsimony bootstrap 50% majority rule consensus cladogram (nodes with less than 50% support collapsed); *2,* same as in 1, but nodes with less than 50% support not collapsed (adapted from Cohen, 2000).

Reviews of the animal kingdom by Cavalier-Smith (1998) and Zrzavy and others (1998) are both phylogenetic in method and comprehensive in their use of data but are classificatory in aim and are consequently characterized by a plethora of new and amended taxonomic names. Cavalier-Smith (1998, p. 235) recognized the brachiopods and phoronids as sister groups forming a new phylum Brachiozoa which, in turn, is classified as a sister group of the Mollusca within a new protostomous superphylum, Conchozoa, diagnosed as: "vascular system; ancestrally with a calcareous shell,

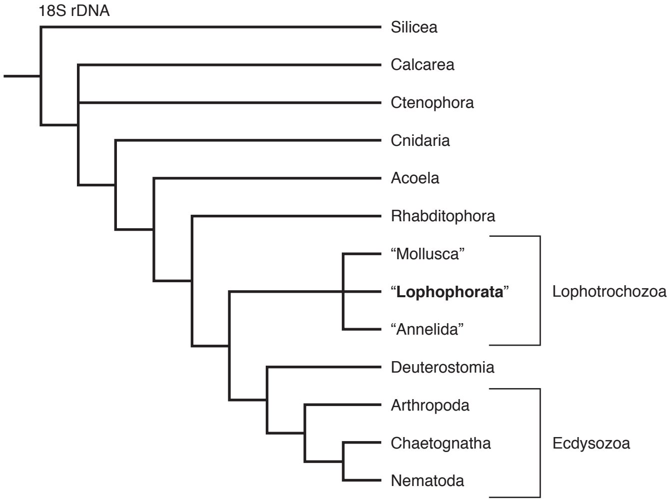

FIG. 1892. Summary of phylogenetic analyses of 18S rDNA sequences of representative extant metazoans with brachiopods in the Lophophorata within the Lophotrochozoa; *quotation marks* indicate possible paraphyly of the taxon named (adapted from Peterson & Eernisse, 2001).

primitively bivalved and unhinged." CAVALIER-SMITH justified the taxonomic demotion of the brachiopods and phoronids (1998, p. 241) on the grounds that they "share a basically similar body plan," contrary to the findings of NIELSEN (1991, p. 25). Likewise, his assertion that the common ancestor of his superphyla Polyzoa and Conchozoa had a bivalved larva (CAVALIER-SMITH, 1998, p. 242) disregarded the disposition of shells relative to the body axes in stocks assigned to these groups.

The unstable nature of the metazoan phylogeny proposed by ZRZAVY and others (1998) is suggested by radical changes to the taxonomic status of the brachiopods and phoronids, proposed by these authors in a postscript. The preferred phylogeny (ZRZAVY & others, 1998, p. 250), which is based on analyses of combined classical and 18S rDNA data, favored the Phoronozoa (a new phylum composed of phoronids and brachiopods) as a sister group of the deuterostomes, although their discussion of this relationship covers all options (ZRZAVY & others, 1998, p. 268). A footnote added in proof (ZRZAVY & others, 1998, p. 271) took into account the newly accessible studies of COHEN, GAWTHROP, and CAVALIER-SMITH (1998) and COHEN and others (1998) and concluded that the Phoronozoa should be reclassified into two phyla, Phoronida and Brachiopoda, the latter with four subphyla: Linguliformea, Disciniformea, Craniiformea, and Rhynchonelliformea. Although the authors equivocated on whether these taxa are deuterostomes or protostomes, the bulk of the defensible evidence now appears to point to a protostome affinity for brachiopods.

FOSSIL EVIDENCE

Several contradictions are exposed in attempts to identify the sister group of the brachiopods by comparing classical and molecular versions of metazoan phylogeny. Both versions recognize the deep divisions within the Bilateria between the deuterostomes and the protostomous lophotrochozoans and ecdysozoans. They do, however, place a minority of phyla, including the brachiopods, within different infrakingdoms; and there is not much satisfactory evidence of reconciliation in reviews using both kinds of data to produce a hybrid metazoan phylogeny.

These two different approaches do have one thing in common: their data are drawn exclusively from living species without regard for fossil evidence. The omission is, of course, inevitable in molecular studies but is a practice of obdurate tradition among biologists that has been defended (PATTERSON, 1981, p. 218) on the grounds that fossil evidence rarely challenges theories of relationships based on living data. This is an indefensible presumption especially when dealing with phyla of controversial affinities, like the brachiopods, that have long geological records incorporating many extinct groups. Twenty-six brachiopod orders are currently recognized, each distinguished by a substantial assemblage of transformations (WILLIAMS & others, 1996). Ten orders are recorded in the Lower Cambrian but only one of these (Lingulida) is represented among the five orders with living species.

This preponderance of extinct groups has determined the kind of characters used to trace early brachiopod evolution. They are overwhelmingly related to the composition and morphology of the shell. Such features may seem superficial but they are biomineralized (and cuticular) manifestations of the mantle (and pedicle) epidermis. Accordingly, morphological analyses, based on the exoskeleton, should enjoy as much credence as molecular analyses (see GEE, 1995; CONWAY MORRIS, 1995), especially in sorting out brachiopod stem groups and identifying feasible sister groups among contemporaneous skeletonized stocks of the Early Cambrian when diversification of metazoan body plans was under way (VALENTINE, JABLONSKI, & ERWIN, 1999; BROMHAM & HENDY, 2000).

The best prospect for identifying the extinct sister group of brachiopods lies among Early Cambrian Problematica, assemblages of sclerites of uncertain taxonomic affiliation. On the basis of bilateral symmetry and devices suggesting articulation, CONWAY MORRIS and BENGTSON (in BENGTSON & others, 1990) described two seemingly calcareous bivalves, *Apisthoconcha* and *Aroonia* as of “possible brachiopod affinity” (1990, p. 164). We concur, however, with their concession that these stocks could also be “products of convergent evolution from other soft-bodied ancestors" (1990, p. 186).

A potentially more promising source of brachiopod ancestry lies in the group of sclerites, sometimes referred to as tommotiids, which were identified as the sister group of brachiopods by CONWAY MORRIS (1993, p. 223). He later homologized the shells on the dorsum of *Halkieria* with brachiopod valves (CONWAY MORRIS & PEEL, 1995; CONWAY MORRIS, 1998) and concluded that brachiopods might have been derived by the folding of the halkieriid bilaterian body across a transverse plane as postulated by NIELSEN (1991) to explain the U-shaped gut of linguliforms (see also COHEN, HOLMER, & LÜTER, 2003).

The tommotiid sclerites, *Tannuolina* and *Micrina,* are perforated by tubes (FONIN & SMIRNOVA, 1967; LAURIE, 1986; QIAN & BENGTSON, 1989; CONWAY MORRIS & CHEN, 1990). More detailed studies of the *Micrina* sclerites by WILLIAMS and HOLMER (2002) showed that they consist of a stratiform succession of laminar sets that might be homologous with those of lingulate shells, complete with internal impressions of muscle bases and gonads; and that the pervading tubes could have contained setae. WILLIAMS and HOLMER (2002, p. 868) further identified *Micrina* sclerites as halkieriid shells (as did USHATINSKAYA, 2002) and postulated a series of transformations that could have changed the sclerites into a linguliform shell (Fig. 1893). Concurrently, the enigmatic, bilaterally symmetrical, apatitic bivalve, *Mickwitzia*, was shown to have a shell structure apparently homologous with the columnar lamination of lingulates and to be pervaded by tubes that, on the ventral pseudointerarea at least, appear to be identical with those of *Micrina* (HOLMER, SKOVSTED, & WILLIAMS, 2002). Shell structure and body plan, therefore, suggest that *Micrina*, a presumed halkieriid, might be

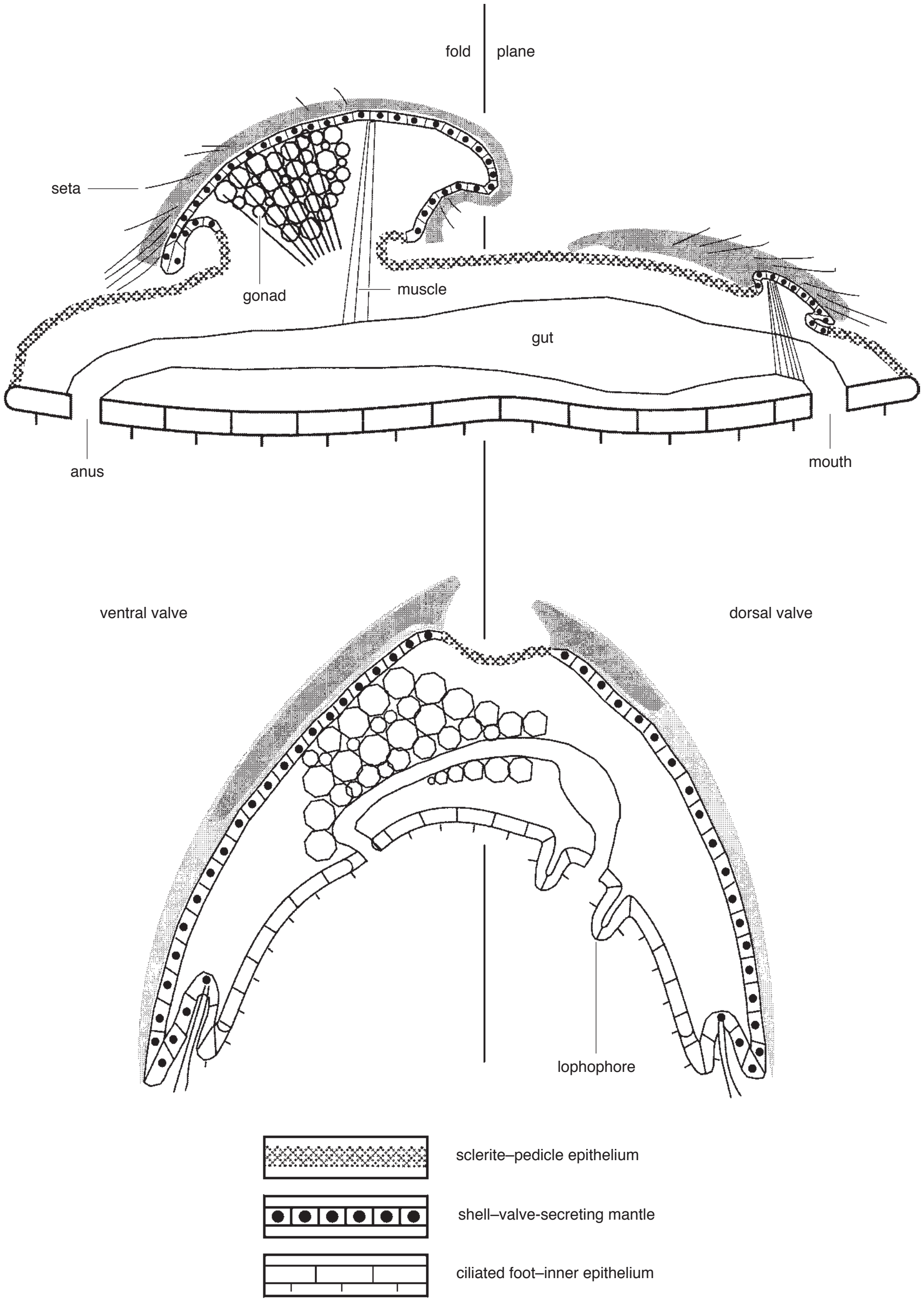

FIG. 1893. Graphical representation of possible evolution of an ancestral brachiopod from a presumed halkieriid, *Micrina* (Williams & Holmer, 2002).

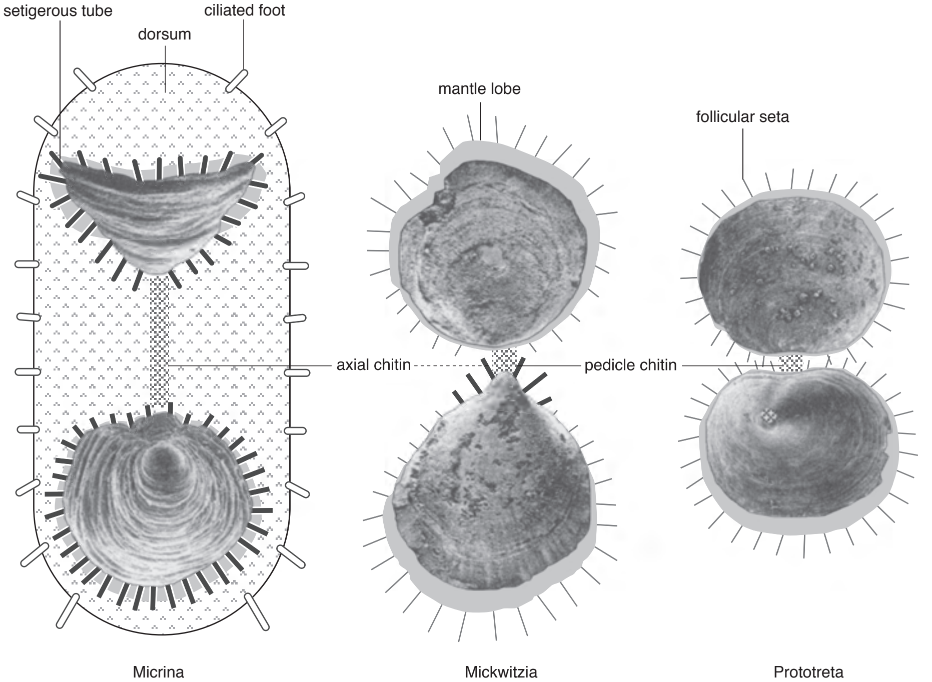

FIG. 1894. Generalized reconstruction of living parts of *Micrina*, *Mickwitzia*, and *Prototreta*, showing *Mickwitzia* as a possible stem-group brachiopod (adapted from Holmer, Skovsted, & Williams, 2002).

the sister group of the Brachiopoda with *Mickwitzia* as a stem-group brachiopod (Fig. 1894).

This version of brachiopod ancestry has been challenged in two ways. LI and XIAO (2002) described the scleritome of *Tannuolina* as consisting of juxtaposed dextral and sinistral mitral sclerites and imbricated sellate sclerites. They concluded that the morphologically similar sclerites of *Micrina* are not homologous with the shells of *Halkieria*, *Mickwitzia*, or brachiopods. They further attributed the similar shell structures of *Micrina*, *Mickwitzia*, and lingulate brachiopods to convergence. WILLIAMS and HOLMER (2002, p. 868) pointed out that the dextral and sinistral mitrals of *Tannuolina* are only homologous with the bilaterally symmetrical mitral sclerite of *Micrina* if they are capped with metameric, juvenile shells. They do not appear to be; only a fused complementary pair of mitral sclerites straddling the bilateral axis of *Tannuolina* could be homologous with the mitral sclerite of *Micrina*. Moreover, it seems improbable that the fine structure of sclerites and shells is homoplastic, while the extremely variable morphology of these skeletal pieces is homologous.

RUNNEGAR (2000), in proposing that the halkieriids were ancestral to chitons, precluded any affinity with organophosphatic brachiopods on the grounds that the scleritome of *Halkieria* was likely to be calcareous. *Micrina,* and possibly *Halkieria,* sclerites are apatitic, as evidenced by their rheomorphically deformed shells (WILLIAMS & HOLMER, 2002, p. 868–869). It is also remotely possible that the embryonic and larval shells of many Early Paleozoic lingulates were calcitic as well as apatitic and siliceous (WILLIAMS, 2003); we cannot yet reject the hypothesis that multimineralic mineralization may have been possible early in shell development.

It is noteworthy that a chiton has emerged as the most proximal outgroup in comprehensive studies of the molecular phylogeny of brachiopods (COHEN, GAWTHROP, & CAVALIER-SMITH, 1998, p. 2040). Such a sister-group relationship is at least consistent with the derivation of polyplacophorans as well as brachiopods from a halkieriid-like ancestor.

MONOPHYLY AND INTRAPHYLUM GROUPINGS OF THE BRACHIOPODA

[Alwyn Williams]

The long-held view that lophophore-bearing animals form a closely related phylogenetic unit of brachiopods, phoronids, and bryozoans (see EMIG, 1977, 1984) has recently been convincingly challenged (NIELSEN, 1995; HALANYCH, 1995). There has never been much doubt, however, of the close relationship between brachiopods and phoronids despite their morphological dissimilarity. This affinity has been recognized taxonomically by classifying them together as a phylum (EMIG, 1997a; CAVALIER-SMITH, 1998; ZRZAVY & others, 1998) with the phoronids as a sister group of the brachiopods, a relationship also upheld when they are both recognized as phyla (PETERSON & EERNISSE, 2001).

There is no indisputable fossil evidence of the first appearance of phoronids notwithstanding the phoronid-style of U-shaped borings (*Diorygma*) in the Devonian (MACKINNON & BIERNAT, 1970). Apart from lacking a shell, *Phoronis* has a U-shaped gut, the outer side of which is ventral and not dorsal as in brachiopods (NIELSEN, 1991, p. 26). Such an orientation suggests that *Phoronis* could not have evolved directly from a halkieriid-like ancestor by an orthodox folding of the body axis (Fig. 1895). The presence of sulphated glycosaminoglycans (GAGs) in the chitinous cuticle of *Phoronis* (HERRMANN, 1997, p. 215) would suggest a link [and quite possibly a plesiomorphic link; COHEN & WEYDMANN, 2005] with linguliforms, as GAGs are unknown in rhynchonelliform shells (Fig. 1891, 1896).

If phoronids are excluded from the brachiopod phylum, three subphyla are presently recognized (WILLIAMS & others, 1996): laminar organophosphatic-shelled linguliforms attached to, or within, the substrate by a pedicle developing as an extension of the posterior body wall; fibrous organocarbonate-shelled rhynchonelliforms attached by a pedicle developing from a larval lobe; and laminar organocarbonate-shelled craniiforms attached by an adhesive ventral valve in place of a pedicle.

Living species of these three subphyla have differently disposed and developed guts (Fig. 1895). The linguliform gut is U-shaped with both mouth (originating near the blastopore) and anus opening into the mantle cavity (NIELSEN, 1991). The rhynchonelliform gut is folded more or less normal to the dorsal valve and lacks an anus, but the mouth, opening into the mantle cavity, also originates near the blastopore (NIELSEN, 1995, p. 318; WILLIAMS & others, 1997, p. 163). Morphological evidence (WILLIAMS, BRUNTON, & MACKINNON, 1997, p. 387) suggested that the distinctive pedicle and gut of living rhynchonelliforms are synapomorphies of all rhynchonellate ordinal taxa originating after the Cambrian. The pedicle of older, extinct rhynchonelliforms, like the protorthides, orthides, and pentamerides, which first occur in the Lower Cambrian, is likely to have been accommodated also in the notch (delthyrium) that indented their ventral valves. We assume that their gut was disposed like that of the crown rhynchonelliforms but possibly with an anus entering the mantle cavity as in linguliforms.

The affinities of the paterinates are ambiguous in that their shells are phosphatic like

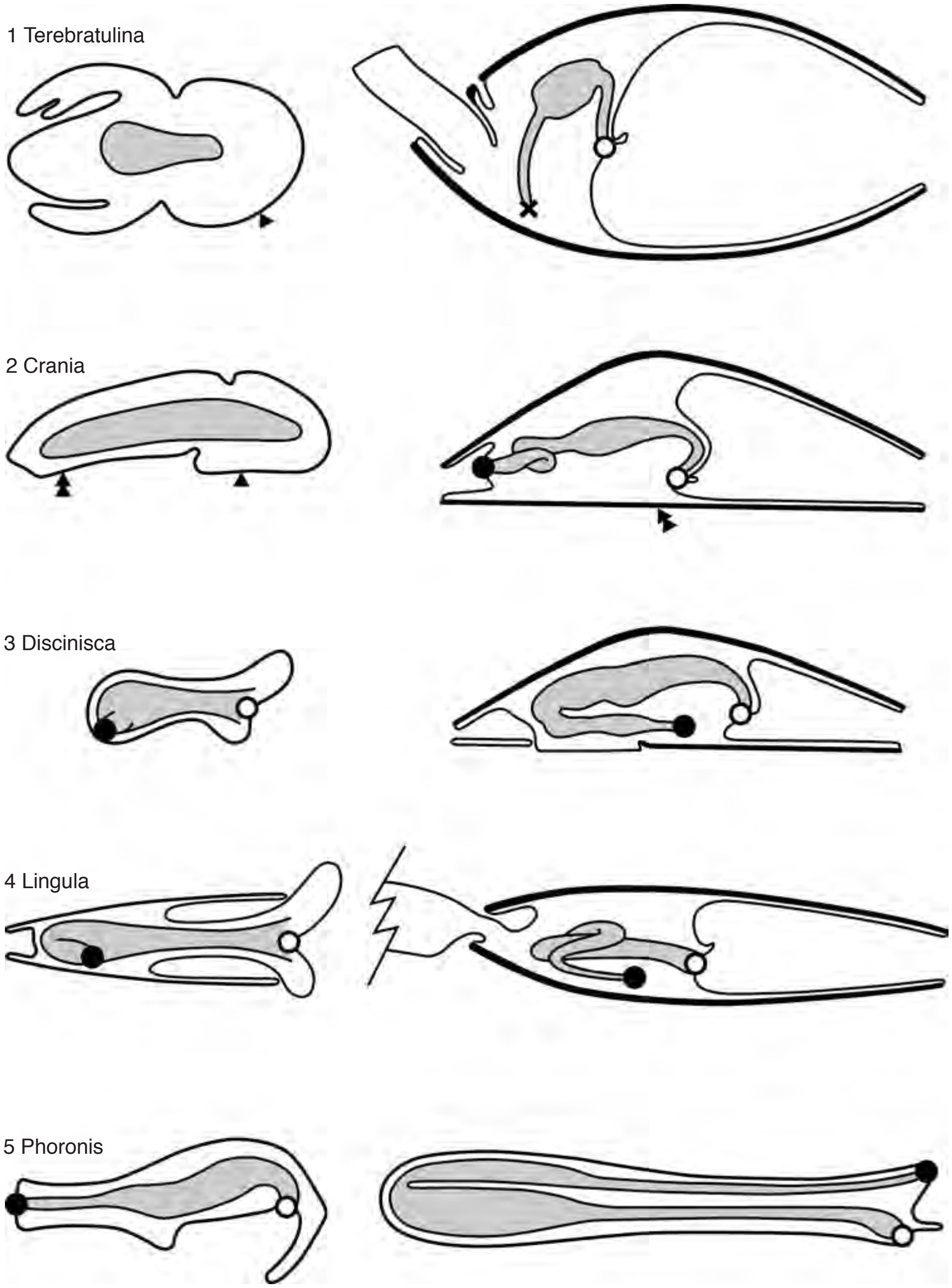

FIG. 1895. Comparison between main body axes and gut orientation of larvae (*left column;* almost to scale) and adults (*right column;* not to scale) of 4 brachiopod genera and *Phoronis* (adapted from Nielsen, 1991); mouth is indicated by *open circle,* the anus by *black dot* (blind intestine marked by *X*), position of closed blastopore by *double arrowhead,* and position of future mouth by *single arrowhead;* anterior part of gut is horizontal in all.

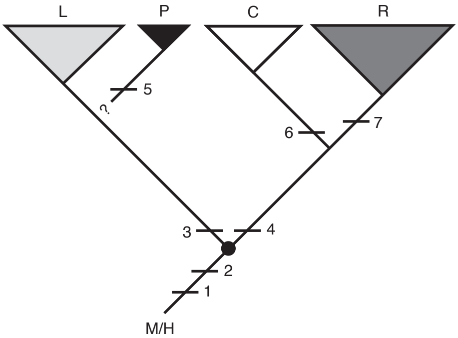

FIG. 1896. Proposed relationships among crown groups of brachiopods Linguliformea (*L*), Phoroniformea (*P*), Craniiformea (*C*), and Rhynchonelliformea (*R*), if they are derived from a halkieriid stem group (*M/H, Micrina-Halkieria*); *numbered dashes* indicate one hypothesis of character evolution: *1,* folded body axis; *2,* pedicle from ventral body wall; *3,* apatitic shell; *4,* calcitic shell; *5,* reoriented body axis, no pedicle, loss of shell; *6,* reoriented body axis, no pedicle; *7,* pedicle from larval lobe (adapted from Williams & Holmer, 2002).

those of other linguliforms, but their body plan is rhynchonelliform (WILLIAMS, POPOV, & HOLMER, 1998, p. 259). Either way, an anus, if developed, would have opened into the mantle cavity. There is, therefore, no need to postulate the existence of a posterior body wall (WILLIAMS, POPOV, & HOLMER, 1998, p. 242) to carry the anus as in craniiforms.

The development and organization of living craniiforms are different. No pedicle develops, and attachment is effected by posteroventral epidermal cells secreting an adhesive ventral valve. The blastopore becomes the site of the future anus on the posterior body wall, and the future mouth breaks through anteriorly into the future mantle cavity (NIELSEN, 1991; FREEMAN, 2000, 2003). The absence of possible pedicle openings from the shells of all groups assigned to the Craniiformea suggests that their body plan has changed very little since the Cambrian. In effect, the anus could always have breached the posterior body wall and never have opened into the mantle cavity with an attendant U-shaped bend in the gut as in linguliforms (Fig. 1895).

There are some early rhynchonelliforms (Chileata, Obolellata, and Kutorginata), in which the anus may have breached a posterior body wall, as has been inferred for the kutorginate *Nisusia* (ROWELL & CARUSO, 1985). Such an intestinal disposition would have accorded with that of the craniiform crown group, as a possible symplesiomorphy.

Despite the divisions between the linguliforms and rhynchonelliforms, their close phylogenetic relationship is confirmed by recent molecular and biological studies. The oldest known rhynchonelliform, a Lower Cambrian (Atdabanian), foliated, carbonate-shelled obolellate, is contemporaneous with the oldest phosphatic-shelled lingulate; both are only slightly younger (<5 million years) than the earliest known brachiopod (a Tommotian phosphatic-shelled paterinate). The apatitic or calcitic composition of brachiopod shells, therefore, seems to have been mutually exclusive *ab initio*.

An interchangeability of these two biomineralizing regimes, however, becomes a possibility if halkieriids were ancestral to brachiopods. The shells of *Micrina* are phosphatic. Those of *Halkieria* are inferred to have been calcareous as were the sclerites coating the dorsum (CONWAY MORRIS & PEEL, 1995, p. 305). The *Halkieria* shells, however, are thought to have been highly rheological in the living state in the manner of linguliform valves (WILLIAMS & HOLMER, 1992). Degradable organophosphatic-shells as part of the *Halkieria* scleritome, which is otherwise chitinocarbonate, cannot, therefore, be ruled out [see VINTHER & NIELSEN, 2005, for an alternative point of view]. In all, the composition of halkieriid scleritomes could have been quite variable. A differentiated secretory system could have given rise to calci-apatitic as well as calcareous or phosphatic scleritomes. *Micrina* could even have been a halkieriid with organophosphatic shells but with the rest of the dorsum covered with discrete, chitinous setae instead of other biomineralized or polymeric sclerites. Such a differentiation would be in keeping with compositional changes apparent in some lingulate shells. It is conceivable that Early Paleozoic lingulates, all with organophosphatic adult shells, may have had apatitic, calcitic, or siliceous juvenile shells (mosaics; WILLIAMS, 2003), but the evidence upon which this is based is highly speculative. An ontogenetic change in biomineral secretion has been documented for living discinids, with their juvenile siliceous mosaics and apatitic adult shells (WILLIAMS & others, 1998; WILLIAMS, LÜTER, & CUSACK, 2001).

The difficulties in relating craniiforms to other brachiopod crown groups, had they evolved from a halkieriid stem group, echoes the contradictions posed by molecular, embryological, and classical phylogenetic studies. Analyses based on 18S rDNA gene sequences place the craniids within living linguliforms (COHEN, 2000) or more recently as their sister group (COHEN & WEYDMANN, 2005; see CARLSON, herein, p. 2883). Some embryological studies suggest a close relationship with the rhynchonelliforms (NIELSEN, 1991), others support a close relationship with the linguliforms (FREEMAN, 2003; see CARLSON, herein, p. 2883), while classical interpretations found their affinities so equivocal as to prompt their provisional classification as a separate subphylum (WILLIAMS & others, 1996, fig. 1). Among the many curious features of craniiforms, the anterior-posterior alignment of the gut is incompatible with a hypothesized transverse folding of the body axis in the midregion. Nor can the craniiform body plan, with the anus at virtually the same site as the linguliform pedicle, be easily interpreted as precursory to folding as inferred in NIELSEN's review (1991, p. 25) of brachiopod evolution. It has, therefore, been claimed (WILLIAMS & HOLMER, 2002) that the Craniiformea is the most derived brachiopod group although so transformed as to defy an unequivocal identification of its sister group (Fig. 1896). The craniiform laminar shell structure is also unique but is, at least, carbonate and, on balance, it has been concluded that the group may have diverged from one of the early rhynchonelliform stocks (WILLIAMS & HOLMER, 2002) [for an alternative point of view, see CARLSON, herein, p. 2883, as well as FREEMAN, 2003].

TRENDS IN BRACHIOPOD EVOLUTION

[Alwyn Williams and Sandra J. Carlson]

As already noted, 95 percent of all brachiopod generic stocks are extinct, so that most of the evidence for the phylogenetic diversity of the phylum is drawn from fossilizable parts of the animal, principally the shell (and endoskeletal spicules). Yet fossilized shells, even from the Lower Cambrian, are a rich source of phylogenetic data on a surprisingly large number of organs. The shape of the shell (itself an intimate record of the integument) and the impressions and apophyses it bears provide evidence of the Phanerozoic evolution of embryological and larval development; the pedicle; shell articulation and its attendant muscle systems; the mantle canal system and gonadal disposition; and the lophophore. Comparative studies of these data in living and fossil brachiopods reveal the chronology of the main transformations that led to many of the basic differences among living species.

The origin of other anatomical differences without a fossil record, like the number of metanephridia, can also be dated in relation to the phylogenetic tree as a whole, as has been shown in conjectures regarding the disposition of the brachiopod gut. Trends in the evolution of these features are outlined below.

EVOLUTION OF EMBRYONIC AND LARVAL MANTLE AND SHELLS

[Alwyn Williams and Sandra J. Carlson]

During ontogeny, three stages in the growth of the brachiopod mantle and shell may be distinguishable: embryonic, larval, and juvenile (postmetamorphic). They can signal not only phases in the development of the animal but also changes in its mode of life. The stages can last for varying amounts of time from species to species: the pelagic larval stage is quite long (weeks to months) in planktotrophic linguliforms and much shorter (days) in lecithotrophic craniiforms and rhynchonelliforms. The terminology used to identify these ontogenetic stages, however, is confused because it has been applied differently by paleontologists and morphologists (WILLIAMS & BRUNTON, 1997; WILLIAMS, LÜTER, & CUSACK, 2001; WILLIAMS, 2003) and neontologists and embryologists (FREEMAN, 1999, 2000, 2001, 2003; FREEMAN & LUNDELIUS, 1999, 2005; G. FREEMAN, personal communication, 2005). In some cases, the same terms (e.g., brephic) have been used to refer to different entities. In order to make the existing literature in each of these two fields more easily accessible to all, both terminologies are discussed below, beginning with the neontological (see also LÜTER, herein, p. 2321). Understanding the processes by which these features of mantle and shell are formed can imbue them with different meanings than can a static view of morphology alone.

Mantle formation and shell deposition are different processes that can occur at different times in brachiopod development. Mantle can form for the first time at different stages of development; it does not form at the same stage of development in all living (or apparently all fossil) brachiopods. Mantle can begin to form during embryogenesis (as in *Lingula*), but not all brachiopods do this. Mantle that forms during embryogenesis is small, roughly the diameter of the egg. Mantle forms more commonly during the larval period (as in *Discinisca*), although mantle lobes are present in the embryos and larvae of both craniiforms and rhynchonelliforms. The mantle reverses during metamorphosis in rhynchonelliforms but does not reverse in craniiforms.

Mantle always forms prior to shell formation, but shells may form on those mantles quite some time following the formation of the mantles; shell can form on mantle that was formed at different developmental stages. Mineralized shell always forms at or immediately after metamorphosis and only very rarely before; this is true for extant representatives of all three subphyla (with shells). Only two exceptions are known: in *Terebratalia* larvae that have been prevented from metamorphosing (FREEMAN, 1993a), and in the siliceous mosaics formed by *Discinisca* swimming larvae (WILLIAMS, CUSACK, & others, 1998), which may or may not be considered the same as more typical shell formation occurring at metamorphosis. Mosaics of mineralized tablets may form during either embryonic or larval periods (*Discinisca*); WILLIAMS, CUSACK, and others (1998), and WILLIAMS (2003) referred to both as the first-formed coat.

Neontological terminology refers to the protegulum as the shell formed on mantle formed during the embryonic or larval stages, before metamorphosis. Brephic shell is the first-formed shell after metamorphosis, laid down on new mantle formed after metamorphosis, during the juvenile stage. WILLIAMS, CUSACK, and others (1998) and WILLIAMS (2003) referred to brephic shell as shell that forms on mantle formed during the larval period, so differs from the neontological definition of the word. Neanic shell refers to shell formed on mantle formed during the adult stage of development.

Traces of the earliest growth stages of the shell can be preserved on mature brachiopod shells irrespective of their geological age or of the composition of the juvenile integument. Because development cannot be observed directly in fossils, a discussion of the terminology of WILLIAMS (2003) is retained here (below) in order to clarify the definitive body of literature by WILLIAMS (1955, 1956, 1970a, 1973, 1997, 2003) on brachiopod shell formation, which dominates the paleontological literature. In WILLIAMS's terminology, embryonic, larval, and juvenile shell refers to shell that has formed on embryonic, larval, or juvenile (postmetamorphic) mantle. Thus, the first-formed coat is that cover secreted by the newly differentiated collective of mantle epithelial cells (the embryonic mantle of FREEMAN & LUNDELIUS [1999, p. 199], which is roughly the "diameter of the egg"). The first-formed shell may be enclosed by mature shell secreted by an incipient mantle lobe developing around the collective. This arrangement signifies that the embryo had settled on the substrate before further growth took place (lecithotrophic larvae). On the other hand, the first-formed shell may be enclosed by the brephic shell (larval in WILLIAMS's terminology; juvenile [from larval mantle] in FREEMAN's), which is separated from the encircling mature shell by a growth disturbance, the lamellar ring of WILLIAMS, LÜTER, and CUSACK (2001). The ring more or less coincides with the settlement of the animal on a substrate and indicates that postembryonic growth (of mantle) took place before settlement (of planktotrophic larvae).

Three styles of development characterize the shell ontogenies of living brachiopods (Fig. 1897). In planktotrophic living lingulids, the first-formed shell (the protegulum of YATSU, 1902) is a single organic sheet that ruptures transversely to the body axis, and the outwardly succeeding brephic shell (formed on larval mantle) consists of separate valves, each delineated by a lamellar ring. In planktotrophic living discinids, the first-formed shell (on embryonic mantle) consists of two separate, opposing valves, each covered externally by a mosaic of siliceous tablets that also ornaments the surface of the brephic shell up to its bounding lamellar ring (WILLIAMS, LÜTER, & CUSACK, 2001). The larvae of living craniiforms (NIELSEN, 1991) and rhynchonelliforms (STRICKER & REED, 1985a, 1985b) are lecithotrophic, and their first-formed coats are two separate valves internally coated with calcitic granules.

The distinctive features of the early ontogeny of living lingulids are unlikely to be older than the Late Paleozoic (Fig. 1897). BALINSKI (1997a) has shown that the first-formed shell of Devonian lingulids are a pair of cup-shaped structures ornamented by pits, tubercles, and radiating setigerous ribs, which must have been secreted by two separate epithelial collectives. Identical structures have been found in a Silurian zhanatellid (L. E. HOLMER, personal communication, 02 September 2002). Traces of the first-formed shells in Lower Paleozoic linguloids are rare, but there is no evidence to contradict BALINSKI's assumption (1997a; see also FREEMAN & LUNDELIUS, 1999). HOLMER (1989, p. 52–67) identified the lamellar rings bounding subcircular to oval juvenile valves in many Cambro-Ordovician linguloids but not a first-formed valve, except in the acrotretide *Eoconulus* where it is an irregularly circular structure that must have been secreted by an independent collective. The entire shells of some linguloids, like those of zhanatellids, are pitted, presumably by the imprints of polymeric vesicles secreted beneath the juvenile cuticle and the mature periostracum.

The prospect that the first-formed shell of Early Cambrian linguloids consisted of independently secreted valves accords with the evidence of embryonic shell secretion in other linguliforms. The siliceous mosaics and bounding lamellar rings of the independently secreted juvenile valves of living discinids also characterize the late Silurian *Opatrilkiella*, the oldest known discinid (WILLIAMS, 2003; but see also CHEN, HUANG, & CHUANG, 2007), although the well-defined larval shells (shell formed on larval mantle) of older discinoids, ranging back to the Ordovician, lack tablet imprints. Yet the juvenile shells of acrotretides, one of the earliest known linguliform groups, are also pitted but with imprints of tablets that, on the basis of their preservation, are less likely to have been siliceous and may even have been calcitic (WILLIAMS, 2003; although the evidence is questionable (CARLSON, herein, p. 2891). The genealogical significance of the possibly different mineralogies of discinoid and acrotretide shell mosaics has yet to be resolved. Was the exocytosis of mosaics, albeit of different composition, a synapomorphy of both groups; or were the possibly differently composed tablets secreted by

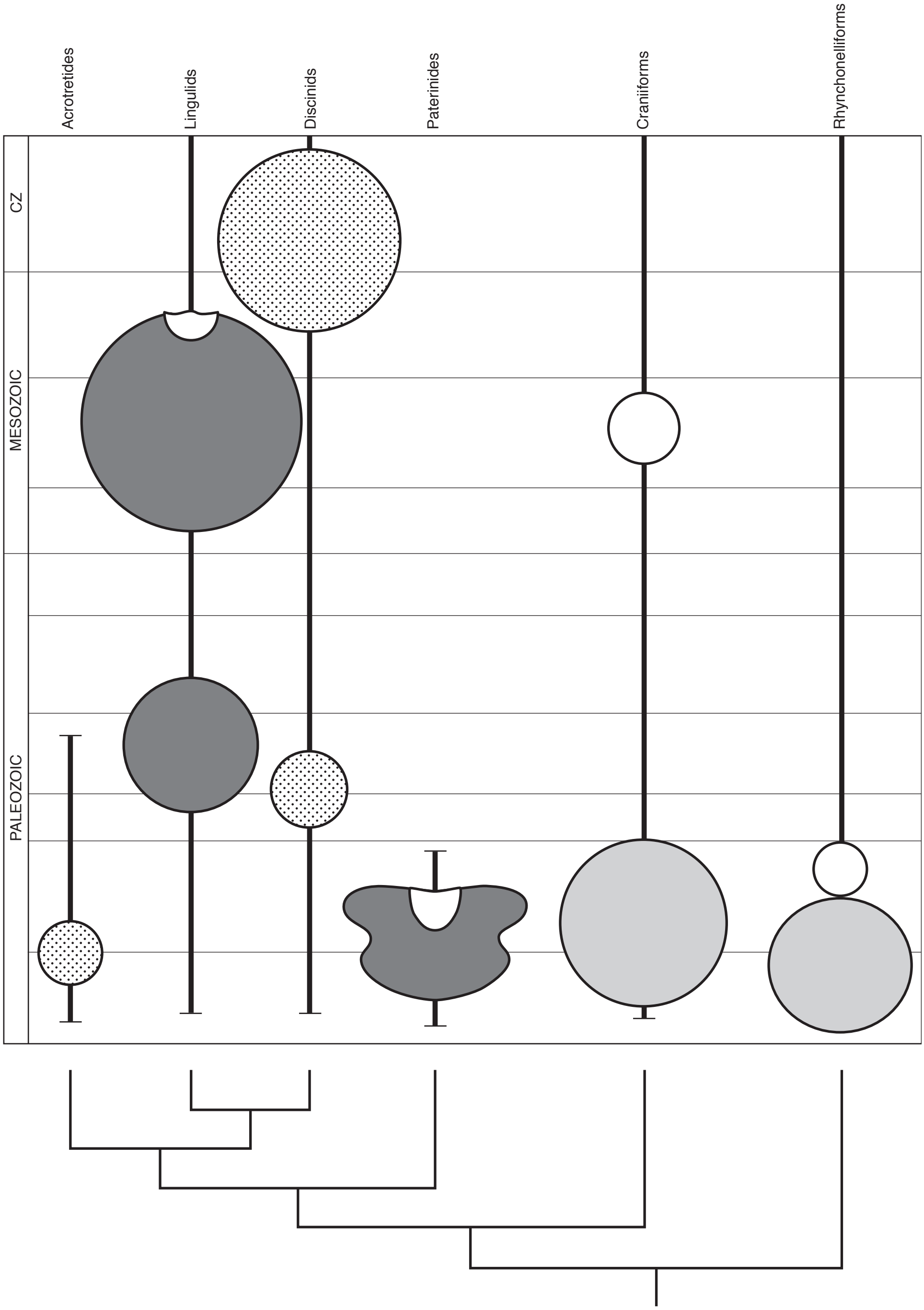

FIG. 1897. Phylogenetic distribution of clearly identified embryonic, larval, or undifferentiated juvenile shells of rhynchonelliforms, craniiforms, and most linguliform groups plotted near their first appearance in the stratigraphic record. Diameter of schematic shells scaled to actual size (5 mm = 50 µm); *open circles* indicate embryonic mantle and shell; *shaded circles* indicate larval mantle and shell; *light shading,* organocalcitic; *dark shading,* organophosphatic; *stippled pattern,* a mineralized mosaic (adapted from Freeman & Lundelius, 1999, 2005; Williams, 2003).

independently developing regimes? Either way, the regime(s) constitutes evidence that at least one group of protostomes secreted a mineralized cover of discrete units before developing a continuous shell. Such mosaics possibly functioned as ultraviolet reflectors during the planktotrophic stage of growth (WILLIAMS, 2003), or possibly as a less dense, lighter weight, and more flexible type of protection from predation prior to settlement [see also herein, p. 2891]. Shells mineralized on larval mantle of the remaining lingulates, the siphonotretides (WILLIAMS, HOLMER, & CUSACK, 2004), are also well defined by lamellar rings, confirming planktotrophic phases in their early ontogeny. An interesting feature of Early Paleozoic lingulate larval shells is that they appear to have been significantly smaller than those of their living descendants. Acrotretide larval shells, for example, are well within the upper limit (225 µm) given by FREEMAN and LUNDELIUS (1999, p. 211) for the diameter of lecithotrophic shells (but see also FREEMAN & LUNDELIUS, 2005). Acrotretides are micromorphs and many species could have been epiplanktonic in adult life, but the larval shells of other contemporaneous lingulates are also small (Fig. 1897).

The embryonic and larval shells of the paterinate linguliforms, the oldest known brachiopod stock, are especially interesting. They may be ornamented by pustules (*Micromitra*) or by pits that cover the entire shell (*Askepasma*) and probably represent imprints of vesicles on a cuticular-periostracal coat. Features of the *Micromitra* juvenile shell are also significant. The first-formed shells of both valves are creased by transverse furrows (possibly metameric traces), while the dorsal valve is quadrilobate and has been interpreted [perhaps incorrectly; see CARLSON, herein, p. 2834] as having accommodated two pairs of larval setae in the manner of lecithotrophic rhynchonelliform larvae (WILLIAMS, POPOV, & HOLMER, 1998).

The modes of life of the lecithotrophic larvae of living craniiforms and rhynchonelliforms and the planktotrophic larvae of living linguliforms are different, but this seems not always to have been so. FREEMAN and LUNDELIUS (1999, p. 211) identified larval shells (shells mineralized on larval mantles), indicative of planktotrophy in all Paleozoic craniiforms, by the presence of lamellar rings (or other morphological changes) with diameters of more than 400 µm. They found that the first signs of lecithotrophy did not appear until the Late Jurassic (in *Craniscus*) and became evident independently and at different times in the genera *Isocrania* and *Crania* during the Tertiary.

Evidence for planktotrophy in the evolution of the rhynchonelliforms is no longer ambiguous (FREEMAN & LUNDELIUS, 2005). Clear evidence for planktotrophy in earlier rhynchonellates appears to be present in shells of Obolellata, Strophomenata, Protorthida, and Orthida. In many strophomenates, early growth stages are morphologically distinguishable from the rest of the shell (KEMEZYS, 1965). The protegular structures of incipient ribs and nodes occupy surfaces approximately 1 mm in diameter that may or may not be part of the mature shell. This interpretation would accord with that of P. RACHEBOEUF's (personal communication, 03 September 2002) interpretation of the early growth stages of chonetidines, where the presumed larval shell, approximately 1.5 mm long, is not delineated by growth disturbances but only by the appearance of costellae flanking a medial juvenile costa. BRUNTON (1966) observed growth banding in productides (ventral grooves, dorsal ridges) delineating umbonal shells, approximately 200 µm in diameter, which is within the size range of overlap indicating either lecithotrophic or planktotrophic larvae.

In general, traces of larval valves on the carbonate shells of early rhynchonelliforms may be less likely to have survived diagenetic crystallization (including silicification) than those on the phosphatic shells of linguliforms, and potentially less reliable evidence has to be used. Thus, the distribution of Early Cambrian *Kutorgina*, which is as widespread as contemporaneous linguliforms that had undoubted planktotrophic larvae, has prompted speculation that kutorginid larvae were also planktotrophic (Popov & others, 1997). No known kutorginids, however, bear growth disturbances that support this assumption (L. E. Popov, personal communication, 04 September 2002). Syntrophiidines, the probable sister group of the rhynchonellides (Carlson, 1996), are among the oldest rhynchonelliforms known, and some, but not all, genera appear to bear umbonal features identifiable as juvenile valves (Freeman & Lundelius, 2005).

Planktotrophy thus appears to be the ancestral condition for brachiopods as a whole, with lecithotrophy evolving independently in craniiforms and rhynchonelliforms, marking a significant feature of brachiopod evolution. The onset of lecithotrophy is first detected in the Pentamerida in the Late Cambrian or Early Ordovician, and in the Rhynchonellida, Atrypida, and Athyridida near the Ordovician-Silurian boundary. The onset of lecithotrophy in the Rhynchonelliformea has been associated with the developmental innovation of mantle reversal (Freeman & Lundelius, 2005), a feature that distinguishes this clade from the Craniiformea and Linguliformea. Why lecithotrophy is not associated with mantle reversal in the Craniiformea is not known at present.

EVOLUTION OF THE INTEGUMENT (MANTLE EPITHELIUM)

[Alwyn Williams]

The brachiopod skeleton affords a comprehensive record of the evolution of the integument even though the mineral components are usually the only recognizable constituents of fossils. Shell surfaces may bear imprints of the periostracum and the secreting outer epithelium. Shell fabrics and textures reveal the nature of the organic substrates on which the mineral constituents were secreted, while cylindroid extensions of the plasmalemma and outer epithelium penetrate the shell through canals and punctae. As for the shell itself, three distinctive compositional and structural types have persisted throughout the geological record: the organophosphatic stratiform successions of linguliforms from the Early Cambrian (Tommotian); the organocarbonate laminar successions of indisputable craniiforms from the Early Ordovician (Arenig); and the organocarbonate fibrous successions of rhynchonelliforms from the Early Cambrian (Atdabanian). There are no known gradations between these types, and each has undergone fabric transformations. Such biomineral and structural differentiation inevitably prompts questions as to how three different secretory systems originated within the monophyletic brachiopods (see discussion herein, p. 2889).

The most profound differentiation of the brachiopod shell is compositional. The mutually exclusive organophosphatic or organocarbonate compositions of adult brachiopod shells throughout the geological record suggest an inability of the mantle to switch from one mineral-secreting regime to another after the initial divergence had taken place. This is not so in living discinids with shells composed of larval siliceous mosaics and adult phosphatic laminae (see also Lüter, 2004). Umbonally, these successions are consecutively secreted by the same epithelial collective but with the secretion of the larval shell ceasing everywhere before the deposition of the adult shell. This hiatus in secretion is presumably brought to an end by a biochemical signal released with the first apatitic exudation initiating the growth of the adult shell (Williams, Lüter, & Cusack, 2001, p. 34). A more relevant switch in composition is that assumed to have characterized the secretion of the acrotretide shell with its inferred (and highly speculative; see Carlson, herein, p. 2891) juvenile calcitic mosaic succeeded by an adult apatitic sequence (Williams, 2003). If it existed, in such a bimineral-secreting regime a neotenous retention of the organic substrates and calcifying proteins ensuring the continuing deposition of an organocarbonate succession could have initiated the development of adult calcareous shells. Suppression of the secretion of a different mineral in larval stages of growth, on the other hand, would have given rise to a monomineral shell that is characteristic of the overwhelming majority of brachiopods. It is important to point out again, however, that the transition from carbonate to phosphate mineralization and respective organic substrates is not known to exist in any extant brachiopod, and the evidence for such a transition in fossil brachiopods is extremely slim and based on the lack of preservation of the purported carbonate larval precursor (see herein, p. 2891). The additional requirement of a heterochronic transition over evolutionary time puts a high burden on this hypothetical scenario.

The larval shell of a stem-group brachiopod, the organophosphatic-shelled *Mickwitzia*, is unknown (WILLIAMS & HOLMER, 2002). *Mickwitzia*, however, appears to be a sister group of organophosphatic-shelled lingulates, including acrotretides with larval mosaics that were possibly calcitic (WILLIAMS, 2003). It may also be chemicostructurally related to the presumed halkieriid *Micrina* with purportedly organophosphatic larval and adult shells and, more remotely, to other halkieriides with shells that were possibly calcareous (and chitinous) as well as phosphatic. In short, the exoskeletons of the presumed brachiopod ancestors must have been diverse in their chemicostructure and flexible in their secretory regimes in order to have been the source of apatitic-shelled and calcitic-shelled stocks, derived independently or one from another [see also discussion herein, p. 2889]. Present understanding of the chemicostructural evolution of the shell in relation to basic features of the body plan (WILLIAMS, HOLMER, & CUSACK, 2004) appears to favor the derivation of the organocarbonate-shelled brachiopods from the paterinates, the sister group of the lingulates (Fig. 1898), unless both mineralogical types evolved from nonmineralized ancestors. The paterinate body plan is essentially rhynchonelliform. The earliest rhynchonelliforms could, therefore, have been derived from a paterinate ancestor by the replacement of an organophosphatic, stratiform shell with GAGs and chitin by an organocarbonate foliate shell. Unless paterinates are actually more closely related to rhynchonelliforms than lingulates and evolved an organophosphatic shell completely independently of the lingulates, this phylogenetic scenario appears no more likely than any other (see CARLSON, herein, Fig. 1908). The conflict between mineralogy and morphology in the paterinates is a continuing puzzle in working out relationships among these early brachiopod groups, which remain unresolved (WILLIAMS, POPOV, & HOLMER, 1998).

The structural transformations of the brachiopod shell are less dramatic than the compositional changes, but they are more helpful in understanding the evolution of the phylum as a whole. The primary layer of all brachiopod shells has always been a uniform mineralized layer secreted on the periostracal substrate. In linguliform shells it is composed principally of GAGs with dispersed apatitic granules; in craniiform and rhynchonelliform shells it is composed mainly of calcite with some glycoprotein. The secondary layer, on the other hand, varies greatly in fabric. The plesiomorphy of the secondary layer of linguliforms is a stratified succession of apatitic laminae alternating with proteinaceous and chitinous substrates (WILLIAMS, 1997). The evolution of this layer involved the periodic secretion of lenses of GAGs with apatite, which, as revealed by postmortem dessication and fossilization, form chambers within the stratiform succession. The chambers may be sporadically distributed with aggregates of residual apatite as in paterinates (WILLIAMS, POPOV, & HOLMER, 1998) and siphonotretides (WILLIAMS, HOLMER, & CUSACK, 2004). More commonly, however, the chambers are arranged in rhythmic laminar sets with well-ordered apatitic structures. The most common fabrics are pillars orthogonal to lamination (columnar) and rods arranged like trellises (baculate). Although both fabrics characterize the earliest lingulates, the columnar sets are probably the

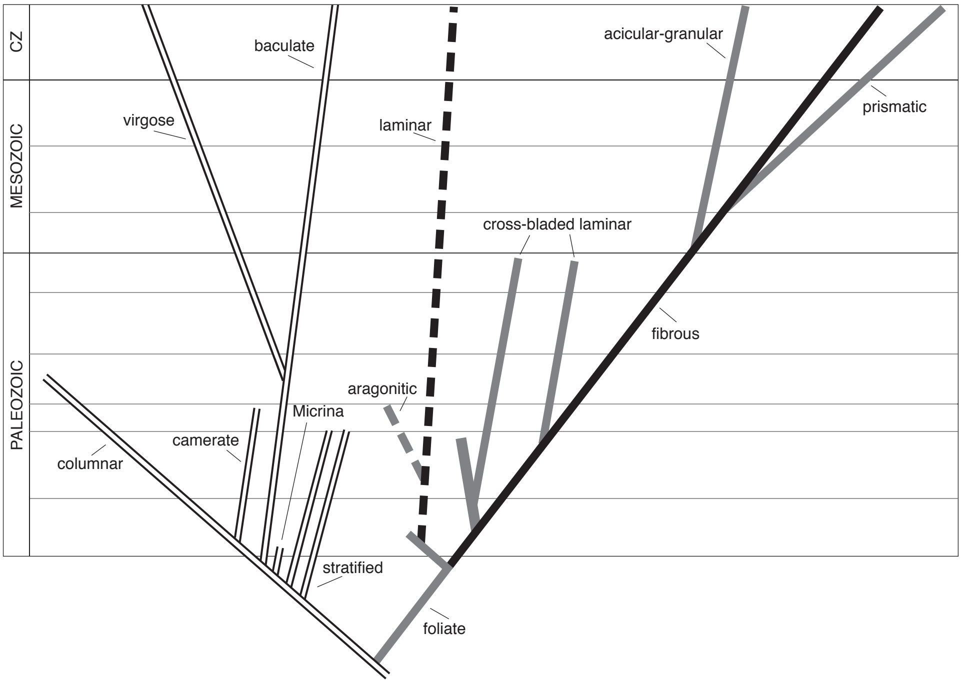

FIG. 1898. Highly schematic stratigraphic and phylogenetic pattern of main microtextures characterizing organophosphatic (linguliform, *open lines*) and organocarbonate (craniiform, *dashed lines;* rhynchonelliform, *shaded lines*) brachiopods (new).

older. Apatitic columns with axial canals are found in *Mickwitzia* (HOLMER, SKOVSTED, & WILLIAMS, 2002), acrotretides (HOLMER, 1989), and lingulide lingulellotretids (CUSACK, WILLIAMS, & BUCKMAN, 1999; WILLIAMS & CUSACK, 1999), which also include genera with baculi that had been secreted as linear aggregates of apatite (L. E. POPOV, personal communication, June 2003). Columnar lamination did not survive beyond the Devonian, and in some acrotretide stocks the columns were replaced by mineralized walls (camerate; HOLMER, 1989), presumably by a change in the specificity of the calcifying proteins. Baculate lamination, on the other hand, survives to the present day, as does a transformation whereby baculi are replaced by spheroidal aggregates and fascicles of apatite (virgose). Both fabrics are associated with a canaliculate system of organic strands free of apatitic columns (CUSACK, WILLIAMS, & BUCKMAN, 1999; WILLIAMS & CUSACK, 1999).

In summary, the chemicostructural evolution of the lingulate shell seems to have involved the phosphatization of an organic scaffold of chitinoproteinaceous laminae and their interconnecting canaliculate strands. The baculate lamination was apparently derived from the columnar lamination with each later giving rise respectively to virgose and camerate successions.

Despite the distinctiveness of these fabrics, some have arisen homoplastically. Partitions simulating camerae, for example, were developed in the baculate obolid *Experilingula* (CUSACK, WILLIAMS, & BUCKMAN, 1999). Siphonotretides, which lack a canaliculate system, were the most derived linguliform descendants of the hypothesized stem-group brachiopod (Fig. 1898). Paterinates, which also lack a canaliculated system, are more like rhynchonelliforms in body plan, while the canals associated with siphonotretide spines may be homologues of the setigerous tubes found in *Mickwitzia* (Williams, Holmer, & Cusack, 2004).

The preeminent secondary shell fabric of the rhynchonelliforms is fibrous. It is a common fabric of the Early Cambrian organocarbonate-shelled brachiopods and overwhelmingly so in living descendants. The fibers, each secreted discretely on a membranous sheath by an epithelial cell, are essentially the same throughout the geological record, differing only in their micromorphology. In contrast, the organic constituents of fibers and the primary and tertiary layers of living species are surprisingly wide ranging in molecular weight. This variability must reflect not only some selective doping with intercrystalline substrates but also molecular transformations of the calcifying proteins (Cusack & Williams, 2001a), which apparently did not greatly affect fiber shape and stacking.

Changes of varying significance, however, did take place. The secondary shells of the Early Cambrian chileates, kutorginates, and obolellates are foliate with irregular laminae of tablets, probably secreted by epithelial collectives on membranous sheets (Williams, Holmer, & Cusack, 2004). This arrangement is possibly ancestral to the orthodox stacking of fibers in rhynchonellates (Fig. 1898 and see Carlson, herein, Fig. 1908).

A more significant change was the transformation of flat fibers into sheets composed of laths. The laths were no longer secreted in glycoproteinaceous sheaths but on organic sheets as laminar aggregates (Williams, 1970a) that became cross-bladed (composite). This composite fabric evolved twice within a group (strophomenates) that was apparently monophyletic in other respects (although see Carlson & Leighton, 2001). Thus, many strophomenates with cross-bladed laminar shells evolved from the laminar-shelled billingsellides, but the productides were derived through the chonetidines from fibrous-shelled plectambonitoids (Fig. 1898; Brunton, 1972) that evolved independently of the rhynchonellate fibrous shells.

More recent transformations effected changes in the standard rhynchonelliform succession (Fig. 1898). In thecideides the fibrous secondary layer became reduced so that the shells of living species are composed mostly or entirely of primary shell (with a granular and acicular texture; Williams, 1973). Prismatic calcite as a tertiary layer (MacKinnon & Williams, 1974) or as lenses among secondary fibers is a homoplastic feature of the shells of the older pentamerides, athyridides, and spiriferides, as well as the terebratulides.

The chemicostructure of the craniiform shell is no more helpful than body plan features in determining the sister group of this subphylum. The inner layer of spirally growing calcitic laminae interleaved with their glycoproteinaceous substrates (Cusack & Williams, 2001a) characterized the craniides from their first occurrence in the Lower Ordovician. The laminar-shelled craniopsides are now accepted as having first been recorded without question in the Ordovician (Llanvirn; L. E. Holmer, personal communication, May 2003), although more questionable occurences extend the range into the Middle Cambrian; they were probably derived from the craniides. The foliate secondary shell of early rhynchonelliforms is, however, structurally comparable with the laths and laminae forming the inner succession of the primary layer of living craniides (Cusack & Williams, 2001a). If the craniide shell succession, currently described as the primary layer, is a homologue of the foliate fabric, it is possible that it shares this feature (primitively) with one of the early rhynchonelliforms, like the chileates.

Rhynchonelliform and craniiform shells are commonly pierced by canals (punctae) or calcitic rods (pseudopunctae) that, contrary to previous widely held views, appear to have limited phylogenetic significance in defining major clades within the phylum. Various papillose outgrowths of the mantle have effected a punctate condition in craniids and most rhynchonelliforms (WILLIAMS, 1997). Only the endopunctae of terebratulides and thecideides, however, with their perforated canopies, can confidently be homologized and possibly derived from a Paleozoic spire bearer (possibly retziidines). In contrast, pseudopunctation, which was long regarded as an important synapomorphy of the strophomenates, involves two different structures that arose independently in four different stocks (WILLIAMS & BRUNTON, 1993).

In review, the chemicostructural evolution of the brachiopod integument broadly accords with the phylogenies of other features of the phylum. The dichotomy between the organophosphatic-shelled and the organocarbonate-shelled brachiopods is out of phase with the most important changes between the lingulate's linguliform and paterinate's rhynchonelliform body plans, however. The origin of the craniiform integument also remains in doubt. Not only is the tabular laminar shell unique (and possibly a novel tertiary layer), but the absence of the inner mantle lobe and lobate cells that develop in all other extant brachiopods is unique as well (WILLIAMS & MACKAY, 1979). This latter difference might reflect the loss of marginal setae during adult growth.

Marginal setae are present in larvae of all extant brachiopods (one pair in linguliforms and two pair in rhynchonelliforms; see LÜTER, herein, p. 2321), except for thecideoids and the terebratellids *Argyrotheca* and *Macandrevia.* They were apparently present in extinct brachiopods as well. They have been documented to occur in juvenile *Novocrania* (three pairs; NIELSEN, 1991) but are absent in adult craniates as well as adult thecideidines and megathyrid terebratulides (WILLIAMS, 1997), both of which are very small bodied as adults. Adult setae, where they occur, are not retained from the larvae but are shed and then redeveloped. Setae appear to have been absent in paterinates, but this is difficult to confirm. *Heliomedusa* exhibits setae, and if classified as a discinid rather than a craniopsid (CHEN, HUANG, & CHUANG, 2007), it indicates that setae were present primitively in at least some of the stratigraphically earliest brachiopods (also *Mickwitzia*, HOLMER, SKOVSTED, & WILLIAMS, 2002; BALTHASAR, 2004a; herein, p. 2888). The presence of setae in linguliforms and rhynchonelliforms could be a derived condition, having evolved twice from nonsetigerous ancestors, or may possibly represent the basal condition, having been lost in the phoronids, paterinates, and adult craniates. GUSTUS and CLONEY (1972) claimed that brachiopod setae are indistinguishable from chaetae in annelids and pogonophorans. Even though they may be very similar structurally, the homology of these structures among phyla is not yet clear (see also LÜTER, 2000a, 2001b), but it is possible that they may be shared more broadly among lophotrochozoans (see BALTHASAR, 2004a).

EVOLUTION OF THE PEDICLE

[Alwyn Williams]

The pedicle is one of the most distinctive features of most Brachiopoda. It is basically an epidermal extension that secretes an adhesive polysaccharide, attaching the animal to the substrate. It is, however, a versatile organ of varying complexity, functioning not only as a holdfast but also as a burrowing device in *Lingula* (EMIG, 1997b, p. 474) or an adjustable tether in the terebratulide *Parakinetica* (RICHARDSON, 1997a, p. 441) and apparently in many strophomenates as well. It may atrophy as in the terebratulide *Neothyris* (RICHARDSON, 1997a, p. 445) or not develop at all, as in craniides and thecideides. In extinct groups, the posterior part of the shell usually serves as a kind of natural cast, recording the morphology of the pedicle as well as its disposition relative to the valves. By this means, it is evident that the diversity in structure and function of the pedicle in living brachiopods has characterized the phylum throughout its geological record. The different modes of attachment can be traced throughout each of the three subphyla, and the evolutionary changes they underwent will be considered within this phylogenetic framework (see also CARLSON, herein, Fig. 1908).

The phylogenetic distribution of pedicles inferred to be present in early brachiopods, however, is far from resolved. It is widely held that true relationships are obscured by the use of the pedicle to identify all organs serving as brachiopods anchors (ROWELL & CARUSO, 1985, p. 1231). There are certainly gross anatomical differences between the coelomic cores of living lingulides and the cartilaginous cores of living terebratulide pedicles. Yet, their basic function of attaching linguliforms and rhynchonelliforms to a substrate is effected in all living species by a distal tip of pedicle epithelium, hypothesized to be homologous in all brachiopods possessing a pedicle that is capable of secreting adhesive mucin and etchants capable of dissolving hard substrates (WILLIAMS & others, 1997, p. 64). Moreover, this distinctive collective is surrounded by a variably developed chitinous cuticle, even in rhynchonellate brachiopods that otherwise lack chitin (WILLIAMS & HOLMER, 2002, p. 870; see also CARLSON, 1995). Accordingly, in this review, the term pedicle is used with the distal homologues of pedicle epithelium (and associated cuticle) in mind; the analogous, proximal parts of the organs will be further distinguished as coelomic or cartilaginous.

These terms, however, are inappropriate for living species of craniiforms, because their cementation is effected by an attachment area that is unlikely to be pedicle epithelium; this attachment area will hereafter be referred to as a holdfast. The developing larva bends or curls ventrally so that the posterior part of the body becomes located ventrally (C. NIELSEN, personal communication, 2005; LÜTER, herein, p. 2321). No pedicle structure develops, and the periostracum of the holoperipherally growing ventral valve also adheres to the substrate.

The site of the pedicle in the ventral valves of lingulides is posterior or posterodorsal to the juvenile part of the valve. It can vary from a groove in a posteromedial, dorsally inclined pseudointerarea to a foramen piercing the valve subcentrally (WILLIAMS, BRUNTON, & MACKINNON, 1997, p. 347–353). These extreme dispositions can be reconciled by taking into account the differential growth of the pedicles and ventral valves of living *Lingula* and *Discinisca* (Fig. 1899). In *Lingula*, the muscle-lined pedicle with its proximal chitinous cuticle and distal adhesive bulb is a cylindroid extension of the ventral body wall and coelom. In *Discinisca*, the muscle-filled pedicle is also an outgrowth of the ventral body wall but rotated ventrally into the plane of the valve so that it and its cuticular border are subtended within a posteromedial notch in the mineralized part of the ventral valve, with the apex of the notch indenting the posterior border of the juvenile valve. With further growth, the mantle lobe, secreting the mineralized valve at the corners of the notch, encroaches posteromedially to fuse into a continuous arc enclosing the pedicle sector (WILLIAMS, HOLMER, & CUSACK, 2004). In Paleozoic adult discinids, like *Orbiculoidea*, the fused lobes secreted an arc of shell that restricted the pedicle to a foramen.

These differences in the accommodation of the pedicles of linguloids and discinoids persisted throughout their geological records but with some variation, such as the lack of mineralization in the posteromedial pedicle sector of the discinoid *Trematis* and the development in the linguloid *Lingulellotreta* of a pedicle foramen within the pseudointerarea by fusion of the trough walls. An interesting deviation was the development of the enclosed pedicle foramen in the ventral valve of the linguloid *Dysoristus.* During adult growth, the pedicle foramen migrated anteromedially from the umbonal area by resorption along the anterior arc and the secretion of a plate along the posterior arc. Such a migration also characterized the siphonotretides (see below), but in *Dysoristus* the young pedicle must have emerged in a trough prior to the growth of an undivided pseudointerarea because all traces of the

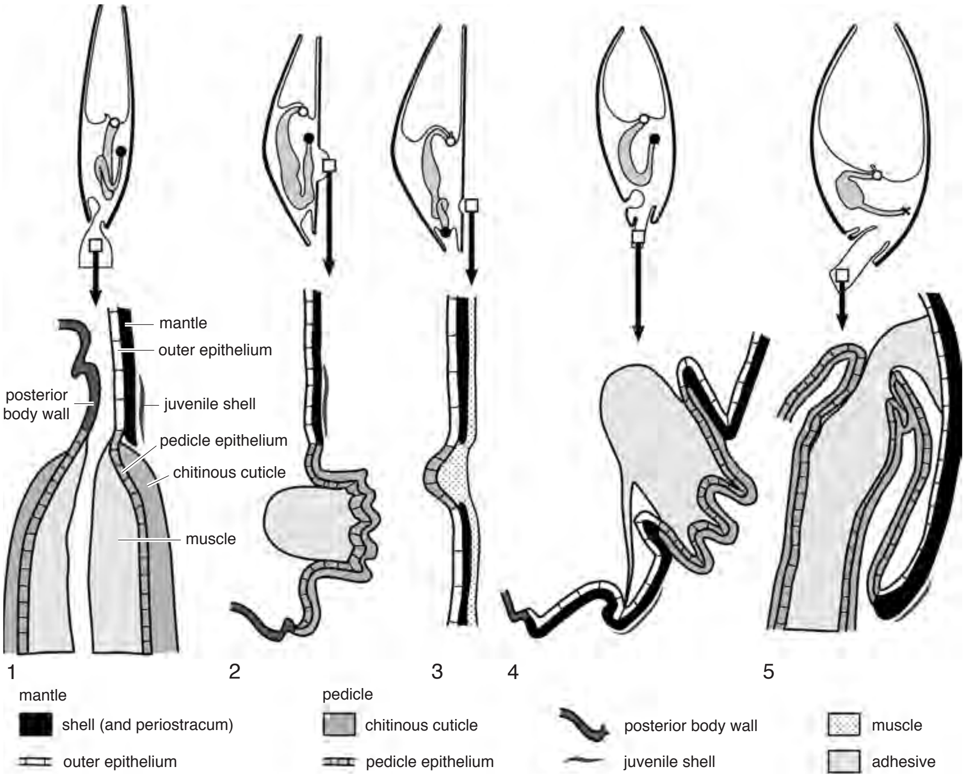

FIG. 1899. Different types of pedicle in relation to ventral valves and body plans as represented by disposition of gut (*open circle,* mouth; *filled circle,* anus; *x,* blind intestine) of *1, Lingula*; *2, Discinisca*; *3, Novocrania*; *4,* a kutorginate (hypothetical); *5, Terebratulina; 1–2,* linguliform type of pedicle growth; *3,* craniiform type; *4,* hypothetical early variant of rhynchonelliform type; *5,* rhynchonelliform type (new).

juvenile ventral valve have been destroyed by resorption.

The pedicle openings in acrotretide ventral valves vary in position from a slitlike foramen in the pseudointerarea of *Keyserlingina* posterodorsal of the apical juvenile ventral valve, to a rounded foramen enclosed within the juvenile valve as in *Ephippelasma*. HOLMER (1989, p. 63) traced the ontogeny of the pedicle opening in the acrotretide *Scaphelasma* from a notch indenting the ventral valve margin just posteromedially of its juvenile pitted mosaic to an oval foramen encroaching anteriorly by resorption into the mosaic and becoming closed posteriorly by the converging edges of the growing pseudointerarea. This growth, in relation to the secretion of the ventral valve, is virtually the same as that of *Discinisca*, and the shifts in the foramen sites can be attributed to the differential rates of growth of pedicle and valve. When the pedicle developed precociously in the juvenile phase of growth, its foramen would have been enclosed by pitted shell. Later development, however, would have resulted in the foramen lying partly, or even entirely, within the adult shell of the pseudointerarea. This is contrary to the views of WILLIAMS, BRUNTON, and MACKINNON (1997, p. 352), who concluded that the pedicle opening initially developed within the juvenile shell and subsequently shifted by resorption to a posterior position during adult growth in some acrotretides.

The pedicle openings of the remaining linguliform brachiopods, the lingulate siphonotretides and the paterinates, cannot be explained in terms of the differential growth of pedicle and shell of living lingulides. In siphonotretides, the pedicle opening originated forward of the posterior margin of the juvenile valve (Fig. 1899). It never indented the ventral pseudointerarea, which is invariably undivided and normally overhung by a beak bearing traces of the juvenile valve. During growth, the enlarging openings migrated anteromedially by the process of anterior resorption and posterior secretion. When surface migration of the foramen ceased, an internal apatitic tube usually developed (presumably secreted by outer epithelium). Pedicle tubes are repeatedly developed in lingulates but no others originated in the same way, although they all must have accommodated the same kind of muscular pedicle. Accordingly, it is assumed that the siphonotretide pedicle differentiated from within the epithelial attachment area that secreted the juvenile ventral valve, and that the pedicle stem cells migrated to that site as a detachment of the posterior body wall attachment area during larval growth (WILLIAMS, HOLMER, & CUSACK, 2004).

Impressions of the paterinate *Dictyonina* attached to the sponge *Choia* are preserved in the Middle Cambrian Burgess Shale (WHITTINGTON, 1980). They show a fringe of setae around the shell except for the wide, straight posterior margin, possibly with a short holdfast. This setal arrangement is consistent with the hypothesis that the paterinate posterior margin is homologous with the strophic posterior margin of rhynchonelliforms (WILLIAMS, POPOV, & HOLMER, 1998). In this context, the paterinate ventral valve has a well-developed orthocline to apsacline interarea that may be divided by a wide delthyrium commonly with a convex mineralized cover (homeodeltidium, structurally indistinguishable from a pseudodeltidium). The shell is not articulated by mineralized devices, but the edge of the ventral interarea of *Askepasma* has been interpreted as bearing traces of an outer or pedicle epithelial junction and the interareas of both valves as having been juxtaposed as in early strophic rhynchonelliforms (WILLIAMS, POPOV, & HOLMER, 1998, p. 242). The presence of a homeodeltidium in some paterinates (and presumably a cuticular arch in others) has prompted the assumption that a posteromedial muscle system, like diductors, passed between the valves beneath a shallow-based pedicle (WILLIAMS, POPOV, & HOLMER, 1998, p. 246). Should this have been so, the paterinate pedicle may have had an axial coelom, but this is highly speculative.

The living craniiforms differ from all other extant brachiopods in their cemented ventral valve without a pedicle and in the orientation of their straight body axis relative to a larval attachment area that is located ventrally but represents the posterior part of the larval body that has bent ventrally (NIELSEN, 1991, fig. 8; C. NIELSEN, personal communication, 2005). The ventral valve grows holoperipherally around this initial holdfast in a plane that is more or less congruent with the straight long axis of the gut lying between the mantle cavity and the posterior body wall (Fig. 1899.4 and 1900). This relationship must have characterized the earliest craniides and the Cambrian craniopsides for even the shells of free-living species bear no openings that could have contained pedicles, only apical cicatrices (L. E. POPOV, personal communication, 2002), indicating that attachment has always been restricted to early stages of growth.

The ontogeny of the pedicle of living rhynchonelliforms has been broadly known for well over a century. But electron microscopic studies of the larval and juvenile pedicle of terebratulides, notably by STRICKER and REED (1985a, 1985b), have revealed further details that also confirm past interpretations of the impressions of pedicle bases in extinct rhynchonelliforms.

In the larval stage, a pedicle lobe is differentiated posterior to a ringlike mantle lobe that, after inversion, develops into the dorsal and ventral valves. In effect, the pedicle arises between the valves despite the fact that during further growth, it is normally confined to the delthyrium of the ventral valve and may become completely

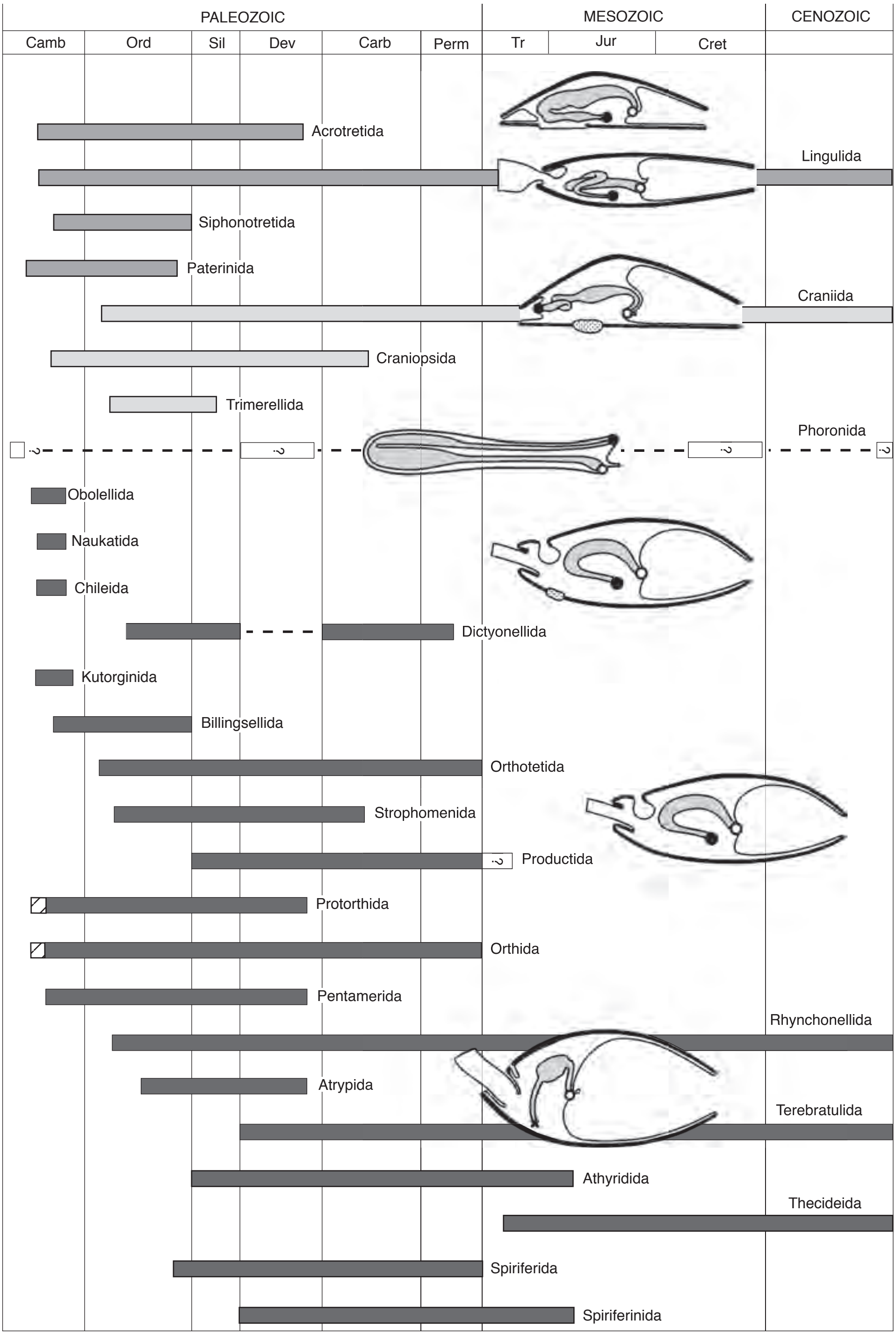

FIG. 1900. Known and inferred structures and dispositions of pedicles, holdfasts, and guts characterizing major groups of brachiopods: discinids and lingulids; craniids; phoronids; hypothetical chileid; hypothetical kutorginate; rhynchonellates (new).

enclosed there by a symphytium (WILLIAMS & HEWITT, 1977). The pedicle also differs from its lingulate analogue in its proximal differentiation into a capsule of connective tissue (STRICKER & REED, 1985b, p. 254), forming a deep-seated pedicle base that fills the umbonal chamber of adult ventral valves (Fig. 1899). Muscles attached to the capsule adjust both pedicle and shell to each other. They may be restricted to one median pedicle muscle attached to the ventral valve forward of the umbonal chamber but more usually consist of two pairs of ventral and dorsal adjustors (WILLIAMS & others, 1997, p. 67).

The development of a pedicle capsule is accompanied by a forward (anterior) shift of muscle systems controlling valve movement with a concomitant displacement of the ventral muscle scars outside the umbonal chambers (WILLIAMS, BRUNTON, & MACKINNON, 1997, p. 387). [Alternatively, the development of a pedicle capsule in derived rhynchonelliforms can be considered as a posterior shift in the umbonal chamber, relative to the valve commissural plane and muscular system; see CARLSON herein, p. 2850.] Such displacements are normally recorded in fossilized adult shells. The geological record confirms that the development of a pedicle from a posterior larval lobe is a synapomorphy of all later rhynchonellates: the rhynchonellides, spirebearers (*s.l.*), and terebratulides. Pedicle lobes also appear to be present in the larvae of cemented thecideides (LACAZE-DUTHIERS, 1861).

In older rhynchonelliforms, the ventral muscle system occupied the umbonal chamber, which suggests that the pedicle capsule was not developed. In orthides and the pentameride syntrophiidines (hypothesized to be the sister group of the later rhynchonellate clade; CARLSON, 1996), the umbonal chamber contained adjustor scars as well as an apical pedicle callist that probably represents the ventral attachment zone of a shallow-based pedicle (WILLIAMS & others, 1996, p. 1179). A shallow-based pedicle must also have characterized protorthides and early strophomenates, although adjustors were not developed or too weakly so to have left identifiable scars (WILLIAMS & others, 1996, p. 1179). The strophomenate pedicle also underwent transformations that resulted in a relocation of the pedicle and its postlarval loss in most lineages. The pedicles of the oldest strophomenates (billingsellides, early strophomenides, and orthotetides) were evidently fully functional albeit restricted to the delthyrial apex by an undivided deltidium or pseudodeltidium. In younger strophomenates, including later strophomenides, the pseudodeltidium is entire, with the pedicle foramen shifted to a supra-apical position. The juvenile pedicle was commonly enclosed in an erect, mineralized tube (pedicle sheath) but was lost in adults that became free-lying or cemented to the substrate by umbonally secreted polysaccharide (orthotetidines) or spines (productides; WILLIAMS, BRUNTON, & MACKINNON, 1997, p. 357–359). It is noteworthy that, in early strophomenates, a medial gap existed between the edges of the pseudodeltidium and a complementary dorsal cover (chilidium). As the gap could not have accommodated the pedicle, it must have been closed by inner epithelium presumably homologous with a posterior body wall (WILLIAMS, BRUNTON, & MACKINNON, 1997, p. 358), as can be postulated for a similar gap in the kutorginate shell described below. This epithelial strip would have covered the diductor muscles passing between the valves and probably would not have been breached by an anus. The shift of the pedicle from an apical to a supra-apical site during strophomenate evolution could have been a manifestation of the migration of pedicle stem cells from a posterior body wall collective as in the lingulate siphonotretides. The transformations effecting these shifts, however, would have occurred convergently and at different phylogenetic rates.

The rhynchonelliforms still to be considered, the chileates, obolellates, and kutorginates, are among the earliest known brachiopods and did not survive beyond the Middle Cambrian, except for the later Paleozoic dictyonellidines, which seem to have an affinity with the chileides (see CARLSON, herein, Fig. 1908). The three groups are morphologically disparate as befits their taxonomic status, but they have two features in common [whether shared due to common ancestry or not is not yet clear; see CARLSON, herein, p. 2878]. First, their body plan, as mirrored by their shells, was essentially that of a strophic rhynchonelliform with devices effecting a crude articulation of the valves that could have been juxtaposed about a transverse plane of folding of the gut. Secondly, there are openings at or forward of the apices of their ventral valves that could feasibly be interpreted as the passageways of holdfasts, like pedicles. The prospect that the groups had folded guts and pedicles emerging from their ventral valves is challenged by the discovery of a complete silicified shell of the kutorginide *Nisusia* with a supra-apical opening in the ventral valve and a cylindroid protrusion, approximately 2 mm in length and in proximal diameter, emerging between the pseudodeltidium and the dorsal interarea (ROWELL & CARUSO, 1985).

If the protrusion between the valves is silicified feces, as suggested by ROWELL and CARUSO (1985), the supra-apical foramen could have accommodated a pedicle (POPOV & WILLIAMS, 2000, p. 210), and the gut would have been aligned like that of craniiforms, not rhynchonelliforms [possibly as a shared primitive feature among early brachiopods; see CARLSON, herein, p. 2883]. ROWELL and CARUSO (1985) gave a detailed account of why they rejected the possibilities that the cylindroids were silicified pedicles or foreign objects in favor of their being coprolites, notwithstanding that feces of living brachiopods are ejected as mucin-bound pellets, 5–10 μm in size, every 15 minutes or so (RUDWICK, 1970, p. 123; JAMES & others, 1992, p. 294).

It is unlikely, but not impossible, that a wholly organic feature like a pedicle could have been silicified. If, however, the protrusion is a silicified pedicle cast composed of sediment, as the morphology of the cylindroids suggests (with ringed furrows replicating the wrinkled state of such pedicles), the kutorginide body plan could have been like that of the later rhynchonelliforms, but this would leave the supra-apical foramen without an orthodox function. In the belief that the protrusion was a fossilized pedicle cast, POPOV (1992, p. 406) advanced the possibility that the supra-apical foramen of *Nisusia* was a "rudiment of a hydrodynamic shell-opening mechanism," like the device he had proposed as occupying the large colleplax-backed opening in the chileate ventral valve. The anatomical topography of such a device, however, which would necessarily have been lined with ciliated epithelium, is too contrived to be feasible. More recently, POPOV (personal communication, 2002) suggested that the supra-apical foramen is a trace of an ancestral larval pedicle and that the cartilaginous pedicle is a later larval development in the kutorginates and such contemporaneous rhynchonellates as the orthides. It is also possible that the cylindroid was not part of the living kutorginates, which may have had a supra-apical pedicle and a body plan similar to that of later rhynchonellates, except possibly for the presence of an anus opening into the mantle cavity.

These conflicting interpretations of the extraordinary features of the *Nisusia* sample have been given in full because they present fundamentally different body plans for early rhynchonelliforms. If the *Nisusia* cylindroids are coprolites, the early rhynchonelliform body plan was similar to that of living craniides, and the holdfast, occupying the supra-apical or ventral apertures, may have been homologous with the craniide attachment area. If, on the other hand, the *Nisusia* cylindroids are pedicle casts, the early rhynchonelliform body plan would have been similar to that of later rhynchonellates (although possibly with an anus opening into the mantle cavity), while the supra-apical foramen is indeed a trace of transient larval attachment.

Both interpretations can be challenged. Most *Nisusia* occur as disarticulated valves, but cylindroids have been found in 15 of the 18 complete shells recovered from numerous thin, resistant beds throughout 12 m of strata (ROWELL & CARUSO, 1985). It is unlikely that excreta could have retained a constant shape in such a high proportion of shells collected (ROWELL & CARUSO, 1985, p. 1227). Yet the other interpretation, that the supra-apical foramen contained a transient larval holdfast prior to the growth of a posteromedial pedicle, also has its weaknesses. It is based on the assumption that two areas of adhesive epithelium differentiated independently in different sites during larval growth. Moreover, even if these areas were cytologically distinct, they could have remained fully functional in some mature kutorginates, like *Trematosia*.

In deciding which of these interpretations is more feasible, account has to be taken of the gross morphology and inferred anatomy of early rhynchonelliforms. All three classes, the chileates, obolellates, and kutorginates, are typified by strophic shells in the rhynchonellate style but with perforated ventral valves and a posteromedial gap subtended by a delthyrium with an apical pseudodeltidium. In some obolellides, the ventral perforation may extend anteriorly by resorption as a slitlike, superficial extension (*Trematobolus*) or may perforate the concave pseudodeltidium (*Naukat*). In chileides and dictyonellides, the opening is greatly enlarged by resorption and is commonly underlain posteriorly by a colleplax, and an open delthyrium may be present. The opening has been interpreted as a means of facilitating the hydraulic opening of the shell (POPOV, 1992), which seems increasingly unlikely. The preferred interpretation is that the subtriangular opening accommodated a cuticular holdfast (WILLIAMS, BRUNTON, & MACKINNON, 1997, p. 360). In the absence of data on the ontogeny of these openings, it is assumed that initially they were underlain by a group of mucus-secreting cells located within the juvenile mantle, as in siphonotretides rather than strophomenates.

It is also feasible to consider the possibility that these three groups had a potentially dual system of attachment, capable of activation at different times in ontogeny and probably involving stem cell collectives with different modes of secretion and organ growth at different phases of phylogenetic differentiation. Thus, in chileates, ventral valve attachment was paramount, presumably by a mucinous pad (compare WILLIAMS, BRUNTON, & MACKINNON, 1997, p. 321). In most kutorginates, on the other hand, attachment was dominantly by a (possibly) coelomic pedicle, like the silicified cylindroid of *Nisusia*, while the supra-apical foramen apparently accommodated nothing more than a transient, larval mucinous pad. In effect, a craniiform-style holdfast may have been as much a feature of the three oldest classes of rhynchonelliforms as a coelomic pedicle but was eliminated with the emergence and evolution of the rhynchonellates.

In review, it seems that brachiopods have attached to the substrate by one of three kinds of holdfast (Fig. 1899–1900): first, a pedicle, developed from the posterior body wall and coelom, tethering a shell with a gut folded parallel with the commissural plane (lingulate type); second, a pedicle developed from a larval pedicle lobe (with or without a capsule), anchoring a shell with a bent gut ending blindly, but possibly evolving from an open gut folded parallel with the commissural plane (rhynchonellate type); and third, an adhesive holdfast within the ventral valve of a shell enclosing the gut lying parallel to the commissural plane (craniate type).

Many transformations affected these attachments during brachiopod evolution. The pedicles of the lingulate siphonotretides and the later strophomenates were accommodated in the ventral valve apparently after having migrated there as epithelial attachment areas. Cementation, with a concomitant loss of pedicle, occurred in the lingulates and especially the strophomenates and rhynchonellates. In craniates, cementation was effected by mucinous holdfasts. Craniate-type holdfasts may also have been present, at least during larval growth, in early rhynchonelliforms, which were additionally equipped with coelomic pedicles. This interpretation necessarily concedes that mucinous holdfasts may have been associated with different developments of the rectum. In living (and presumably stem-group) craniiforms, migration of the holdfast *cum* ventral mantle fold attachment area to the posteroventral side of the larva is followed by the formation of an anus breaching the posterior body wall connecting the two valves. In early rhynchonelliforms, however, an attachment area giving rise to a coelomic pedicle was differentiated early within the posterior body wall, and the rectal region of a bent gut either terminated blindly or breached the anterior body wall in the early phases of rhynchonelliform evolution.

EVOLUTION OF MUSCLE SYSTEMS

[Sandra J. Carlson]

The presence of two mineralized valves is characteristic of all brachiopods (except for phoronids, if they are considered as nesting within Brachiopoda). The muscle systems in extant brachiopods, and those reconstructed from the scars on the interior of fossil brachiopod valves, serve largely to connect the two valves to one another and move them relative to one another (WILLIAMS & others, 1997). Some extant brachiopods (e.g., craniids and discinids) possess muscles that move the lophophore slightly relative to the valves (brachial elevators and protractors); others (e.g., rhynchonellides and terebratulides) have adjustor muscles that move the valves relative to the pedicle. The principal muscles, however, extend between dorsal and ventral valves (originate on the dorsal valve and insert on the ventral valve) and effect movement between them.

Comparing musculature among the major groups of extant brachiopods, it is clear that the brachiopods lacking valve articulation have more muscles overall, particularly more transverse, lateral, and oblique muscles, enabling various types of sliding and twisting movements of the two valves relative to one another. Brachiopods articulating by means of teeth and sockets are limited functionally to the rotation of one valve relative to the other in a plane parallel to the sagittal plane; transverse, lateral, and oblique muscles are not functionally required or present.

Extant brachiopods possess either columnar or tendonous muscles. Extant inarticulated (and thecideide) brachiopods have columnar muscles (HYMAN, 1959; WILLIAMS & ROWELL, 1965d; RUDWICK, 1970). Columnar muscle fibers extend from their origin on one valve to their insertion on the other, are often perpendicular to the valves, and are thus relatively short, like the adductor (central and umbonal) muscles in inarticulated brachiopods. The cross-sectional area of columnar muscles relates to the power they can generate in contraction—the larger the area, the stronger the force the muscle can generate (ALEXANDER, 1968). In contrast, muscle length relates to the total amount of contraction possible (effecting the degree of gape angle)—the longer the muscle, in general, the greater the amount of contraction possible. The various oblique, lateral, and transverse or transmedian muscles typically originate and insert at lower angles (<90 degrees) to the valves and are commonly longer than the adductors.

Extant articulated brachiopods (with the exception of thecideides) have tendonous muscles (HYMAN, 1959; WILLIAMS & ROWELL, 1965d; RUDWICK, 1970), where the contractile muscle fibers extend only a short distance from their origin or insertion on the valves and are united by a tendon spanning the mantle cavity. Tendon is almost inextensible, compared to the muscle fibers themselves, and the power and degree of muscle contraction in articulated brachiopods is dictated by the length and area of the muscle fibers only, not the tendon.

Tracing particular muscles in living organisms from their origin on one valve to their insertion on the other is the most direct way to determine the correspondence of muscle scars among dorsal and ventral valves. In extinct forms only, the scars remain, distinguished by differences in shell fabric and occasionally low ridges or platforms; direct tracing of muscles is not possible. For this reason, multiple interpretations of corresponding muscle origin and insertion scars in extinct brachiopods are to be expected (e.g., WILLIAMS, BRUNTON, & MACKINNON, 1997, p. 385, fig. 346; HOLMER & POPOV, 2000, fig. 75; BASSETT, POPOV, & HOLMER, 2001). Thus, when considering the function and evolution of muscle systems, it is all the more important to be able to construct defensible hypotheses of muscle homology among extinct and extant brachiopods (WILLIAMS & others, 1997; HOLMER & POPOV, 2000; POPOV & HOLMER, 2000a, 2000b, 2000c; BASSETT, POPOV, & HOLMER, 2001). Determining the relative positional relationships of muscle scars to one another is necessary to establish a framework for interpreting the evolution of muscle systems in all brachiopods.

Linguliformea

Musculature is quite variable among linguliform brachiopods, inferred on the basis of muscle scars preserved on the interior of the valves (compare WILLIAMS & others, 1997, p. 83, fig. 82; HOLMER & POPOV, 2000, fig. 7, 39, 44, 51, 75; WILLIAMS, BRUNTON, & MACKINNON, 1997, p. 386, fig. 346). One of the difficulties in reconstructing musculature and determining muscle homologies in all linguliforms is that all are extinct except for a few representatives of the discinids and lingulids. The living lingulids are atypical compared to other inarticulated brachiopods, as a result of their burrowing behavior and infaunal life style, thus rendering them less than ideal to serve as representatives for the entire subphylum. Discinids, therefore, will be referred to as the most plausible example of the primitive type of linguliform musculature.

Discinisca, an extant discinid brachiopod, has paired posterior and anterior adductor muscles that dominate the valve interiors in terms of muscle scar area (WILLIAMS & others, 1997, p. 84, fig. 83). Paired posterior, internal, and lateral oblique muscles are also present, as well as small paired brachial retractor muscles. *Schizotreta* (WILLIAMS & others, 1997, p. 45, fig. 39), an Ordovician-Silurian discinoid, has smaller anterior adductor scars, and the valve musculature appears to occupy a smaller area located more posteriorly in the valves than in *Discinisca* and suggests that closing the valves with the anterior adductors has evolved as the dominant function of the muscular system in living *Discinisca*.

Lower Cambrian (Atdabanian) *Heliomedusa* has recently been assigned to the discinids (CHEN, HUANG, & CHUANG, 2007) and removed from the craniopsoids (JIN & WANG, 1992; HOU & others, 2004) on the basis of characteristic discinid features (e.g., primarily the presence of a ventral pedicle foramen and median ridge) preserved on a larger sample of well-preserved specimens collected from the Chengjiang fauna. The identity of numerous internal features characterized by JIN and WANG (1992) are reinterpreted by CHEN, HUANG, and CHUANG (2007) as entirely different features, including the identity of the dorsal and ventral valves, and underscores the difficulty of attributions of soft anatomy even in abundant, well-preserved, ancient fossils. Muscle scars are not especially well preserved in these fossils, but *Heliomedusa* appears to have elongate, platformlike muscle attachments. A small, pear-shaped central muscle scar is present in the ventral valve (as interpreted by CHEN, HUANG, & CHUANG, 2007, *contra* JIN & WANG [1992] who identify this as the dorsal valve), as is a tear-drop–shaped anterior muscle scar (JIN & WANG, 1992). On either side of the central muscle is a

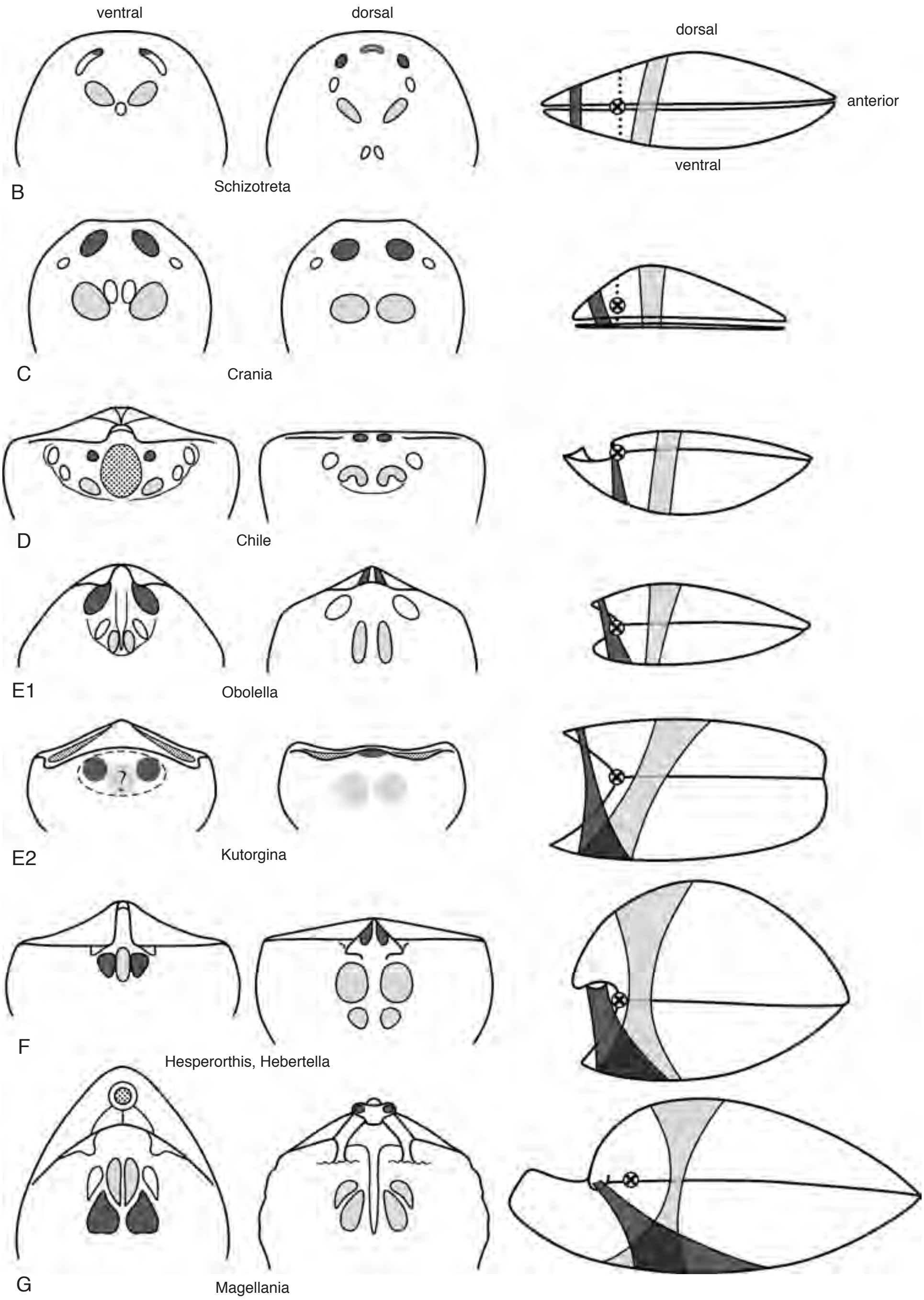

FIG. 1901. *For explanation, see facing page.*

single kidney-shaped anterolateral scar and two slender, elongate posterolateral muscle scars. Homologies with muscles in living discinids are not clear.

Living lingulids have more pairs of muscles than do other lingulides and other inarticulated brachiopods, and more of them extend from one side of one valve to the opposite side of the other valve. *Lingula* possesses a single or paired umbonal muscle, three to four pairs of oblique muscles (transmedian; outside, anterior, and middle laterals), and a central muscle (Williams & others, 1997, p. 83, fig. 82). The complexity in lingulid musculature is almost certainly related to the scissorlike, sliding, or twisting motions of the valves relative to one another, effected by the contraction of the various oblique muscles when burrowing into soft substrates. This is most likely to represent a derived morphology and behavior, despite the early appearance of the group in the fossil record (see Carlson, herein, Fig. 1908). Lingulid umbonal and central muscles may well be homologous with posterior and anterior adductors of discinoids and craniides, based largely on patterns of innervation (Blochmann, 1892, 1900; Williams & others, 1997).

Muscles in Siphonotretida (extinct) appear to be generally comparable to those in early discinids (Fig. 1901 and Table 39), although differences of opinion exist about the correspondence of dorsal and ventral scars and the identity of the particular muscles associated with the scars (Holmer & Popov, 2000, fig. 75). Among acrotretides, the muscles appear to be somewhat similar to, but less numerous than in lingulides. The highly conical ventral valve in many

Table 39. List of different types of valve interactions described in text and reconstructed schematically in Figure 1901 (new).

A. Multi-element, not articulated
Halkieriids
Micrina
Tannuolina

B. Bivalved with hinge axis, but no hinge line
Linguloids
Discinoids
Acrotheloids
Craniopsides
Most siphonotretides
Some acrotretides

C. Strophic posterior valve edges, no articulatory structures
Craniides
Some acrotretides

D. Hinge axis coincident with strophic hinge line, no articulatory structures
Paterinates
Chileates

Valves secondarily lost or primitively absent
Phoronids

E. Articulatory structures rudimentary and diverse
Kutorginates
Most trimerellides
Most obolellates

F. Deltidiodont articulatory structures
Protorthides
Orthides
Most strophomenates
Most pentamerides
Possibly spiriferides and spiriferinides

Articulatory structures lost
Some strophomenates (productides)

G. Cyrtomatodont articulatory structures
Rhynchonellides
Terebratulides
Thecideides
Atrypides
Athyridides
Possibly spiriferides and spiriferinides
Some pentamerides

Fig. 1901. Schematic reconstructions of relative positions of muscle origins and insertions on interior of ventral valve (left column) and dorsal valve (center column), and in lateral view, with valves in life position or articulated (right column); *open circle with X* marks position of hinge axis; *dark shading* indicates muscles functioning to open valves relative to one another (posterior adductors or diductors); *open ellipses* indicate oblique lateral or oblique internal muscles; *light shading* indicates anterior adductors that function to close valves; *letters* correspond to different types of valve interaction, whether inarticulated or articulated, as discussed in the text and listed in Table 39. Ventral and dorsal valve interiors redrawn from *B,* Holmer and Popov (2000); *C,* Bulman (1939); *D,* Popov and Holmer (2000a); *E1,* Popov and Holmer (2000b); *E2,* Popov and Williams (2000); *F,* Rudwick (1970); *G,* Clarkson (1979) (new).

acrotretides makes homologies with lingulides uncertain (WILLIAMS, BRUNTON, & MACKINNON, 1997, p. 385, fig. 346). Dorsal valve originations are most similar in relative position to lingulides and craniides, but the insertions on the ventral valve are quite different. The central muscle is absent in most but may be homologous with the acrotretide anterior lateral muscle; extended discussion of acrotretide muscle systems can be found in HOLMER and POPOV (2000, p. 99–103, fig. 51). These authors suggested that the muscles in the highly conical acrotretides might have been tendonous, not columnar, consistent with the apparent evolution of tendonous muscles in rhynchonellate brachiopods as the valves increased in convexity and globosity (RUDWICK, 1970). A saddle-shaped plate extending from the dorsal valve interior of some acrotretides (e.g., *Ephippelasma*) has been interpreted as a muscle platform (RUDWICK, 1970) or as a lophophore support structure (WILLIAMS & ROWELL, 1965d; WILLIAMS, BRUNTON, & MACKINNON, 1997, p. 384).

Paterinata is now affiliated with Lingulata, in Linguliformea (POPOV & others, 1993; HOLMER & others, 1995; HOLMER & POPOV, 2000), on the basis of shell mineralogy and microstructure, despite considerable differences in musculature and mantle canal systems. The relationship of the paterinates to the lingulates does not appear to be supported strongly (LAURIE, 2000), however, and paterinate monophyly is in question as well (WILLIAMS, POPOV, & HOLMER, 1998; LAURIE, 2000). Paterinates are the first brachiopods to appear in the stratigraphic record (Tommotian), and their muscle scars bear a close correspondence to those in orthide brachiopods (RUDWICK, 1970) and other rhynchonellates with deltidiodont dentitions; their muscle scars are remarkably similar to articulated brachiopods in aspect. In their reconstruction of paterinate muscles, WILLIAMS, POPOV, and HOLMER (1998, fig. 6) recognize separate muscle fields on the dorsal valve for the diductor muscles and the posterior adductor muscles. This reconstruction is contrary to the view of RUDWICK (1970, p. 72; a view shared by SC [Carlson, 2005, personal observation]) that the posterior adductor muscles in inarticulated brachiopods (including paterinates) are likely to be homologous with the diductor muscles in articulated brachiopods. Despite their phosphatic valve mineralogy and lack of articulatory structures, it is at least possible that paterinates may share closer common ancestry with the early rhynchonelliforms than with the linguliforms, or it is perhaps more likely that paterinates share with rhynchonelliforms this more general (primitive, ancestral) pattern of musculature, regardless of valve mineralogy and articulation, which may have evolved multiple times (see CARLSON, herein, p. 2891).

Craniiformea

Craniiform muscle systems are quite similar to discinoids: at least some of the muscles can be identified in corresponding positions on the valves in each group (compare fig. 83–84, p. 84–85, in WILLIAMS & others, 1997) and are assumed to be homologues. The basic pattern of musculature in craniides and craniopsides consists of paired adductor muscles, posterior and anterior, passing more or less directly between the valves, which are considered to be homologous with the paired umbonal and central muscles of lingulids; this may well represent the most primitive condition for brachiopods (WILLIAMS & others, 1997), consistent with the tentative consensus phylogeny in CARLSON (herein, Fig. 1908). An unpaired median muscle is also present near the valve posterior, as are longer, paired internal and lateral oblique muscles. Small, paired brachial elevator and protractor muscles originate on the dorsal valve and insert on the lophophore, allowing some movement of the lophophore relative to the valve.

Trimerelloids have muscle platforms in one or both valves to accommodate (primarily) the origin and insertion of the anterior adductor muscles. Trimerelloid muscle scars are generally similar to craniides in their relative positions on the valves, but appear to be even more similar to those in the chileides (Fig. 1901D). Positional relationships among the muscles scars of trimerelloids and other brachiopods suggest that the posteriormost muscle scars in each valve correspond to the posterior adductors, while the anterior adductor muscles originate at the larger pair of scars in the dorsal valve and insert on the anteromedial scars in the ventral valve. Some trimerelloids exhibit a kind of rudimentary articulation, in that a dorsal hinge plate fits tightly into a cardinal socket in the ventral valve, defining a hinge line about which the valves rotate (Fig. 1901E).

Rhynchonelliformea

Among the rhynchonelliforms, extant rhynchonellides and terebratulides have very similar patterns of musculature, with diductor muscles originating at the posterior of the dorsal valve, often on a cardinal process, and inserting approximately midvalve on the ventral valve (Fig. 1901). Paired anterior and posterior adductor muscles originate approximately midvalve in the dorsal valve and insert slightly posteromedial to the diductor muscles on the ventral valve. Pedicle adjustor muscles may also be present, leaving scars on either dorsal or ventral valve interiors. This general pattern of musculature is characteristic of most rhynchonellate brachiopods, commonly with cyrtomatodont (interlocking) dentitions.

Diductor muscle scars in orthides are typically located on a dorsal cardinal process and on either side of the medial adductor muscle scars in the ventral valve. Two pairs of adductor muscle scars are located midvalve in the dorsal valve. Although a pedicle also emerged from the open (or covered) delthyrial opening, its primary function seems to have enabled the diductor muscles to gain leverage in opening the valves. This general pattern of musculature is characteristic of most strophomenate brachiopods as well. Because of the large number of strophomenates with broad, but rather flat mantle cavities (e.g., *Strophonelloides, Stropheodonta, Chonetes*), ventral muscle scars in particular tend to be quite large and may splay out anteriorly; the muscles intersect the valve interior at a very low angle and thus occupy a relatively larger area on the valve floor, even though their cross-sectional area is not very much larger. Greatly elongated cardinal processes, some bifurcate or trifurcate, evolve within the strophomenates, possibly several times independently. These elongate cardinal processes can function both to increase the mechanical advantage of the valve opening system (CARLSON, 1989) and also effect a type of single tooth valve articulation, helping to reduce torsion or slip between the valves (C. H. C. BRUNTON, personal communication, 2004).

Muscle platforms are often developed in one or both valves of some protorthides (e.g., *Skenidium*), billingsellides (e.g., *Estlandia*), and pentamerides (e.g., *Camerella*) and are thought to have evolved more than once independently. They most likely functioned to reduce the distance between muscle origin and insertion in columnar muscles, as valve globosity increased and before tendonous muscles evolved, possibly as rhynchonellides evolved from pentamerides (RUDWICK, 1970).

Muscle scars are inadequately known for most fossil rhynchonellides (SAVAGE & others, 2002), but we assume they are similar to extant rhynchonellides. Pentameride muscle scars, when visible, are initially orthoidlike (Fig. 1901F) and evolve to more rhynchonellide-like (similar to Fig. 1901G) positions in the valves. Within the evolution of the rhynchonellates, therefore, the ventral insertion of the diductor muscles migrates anteriorly later in time (WILLIAMS & ROWELL, 1965d; CARLSON & others, 2002), which typically improves the mechanical advantage of the valve opening system (CARLSON, 1989). Atrypides (COPPER, 2002), athyridides (ALVAREZ & RONG, 2002), and spiriferides and spiriferinides (CARTER & others, 2006) share the same basic pattern of musculature, although differences in detail obviously exist; muscle scars are commonly impressed clearly on the valve interiors of these taxa. In athyridides, it has been suggested that the single (or fused, paired) juvenile dorsal median attachment of the diductor muscles migrated laterally onto the paired outer hinge plates (cardinal flanges) during ontogeny (ALVAREZ & BRUNTON, 1990; BRUNTON, ALVAREZ, & MACKINNON, 1996).

Obolellate musculature appears to be similar to lingulates, with oblique muscle scars still present, as well as other early rhynchonelliforms, with diductor muscle scars in the extreme posterior of the dorsal valve (Fig. 1901C; see also BASSETT, POPOV, & HOLMER, 2001). Chileates also exhibit somewhat similar muscle patterns (Fig. 1901E). The diductor muscles in these taxa are more likely to be homologous with the posterior adductor muscles rather than with the internal oblique muscles in discinids and craniids because of their position in the valves relative to the other muscle scars. Some naukatides have rudimentary ventral denticles fitting into dorsal sockets (e.g., *Oina*). As articulatory structures evolve in brachiopods, the oblique muscle scars move further laterally on the valves, and the muscles are eventually lost entirely.

In Kutorginata, muscle scars are visible but are not impressed strongly on valve interiors. They appear to be similar to most deltidiodont strophomenates and rhynchonellates, with diductor and adductor impressions in similar positions (POPOV & WILLIAMS, 2000, fig. 127; see also Fig. 1901E). The muscles were located fairly far to the posterior in both valves, as is common in Early Paleozoic brachiopods. The very wide, open notothyrium and delthyrium functioned primarily as a broad notch to allow the muscles to pass from their origin in the extreme posterior of the dorsal valve to their insertion in the ventral valve (RUDWICK, 1970; GUTMANN, VOGEL, & ZORN, 1978; BASSETT, POPOV, & HOLMER, 2001).

Evolutionary Patterns in Musculature Morphology and Function

If halkieriids are provisionally accepted as the brachiopod sister group, it is possible to construct a scenario of the evolution of the muscle system and articulation from their common ancestor. WILLIAMS and HOLMER (2002) outlined a ten-step process by which brachiopods could transform from *Micrina*, which they interpret as a halkieriid (but see also LI & XIAO, 2004) (Fig. 1896). Brachiopods do not necessarily have to be derived from halkieriids directly, only that the two may have shared a common ancestor, perhaps quite distantly (see VINTHER & NIELSEN, 2005). The two shells of halkieriids appear to be located dorsally, one posterior and one anterior, on the organism (CONWAY MORRIS & PEEL, 1995). The posterior shell bears a strong resemblance to certain brachiopod ventral valves (some acrotretides), with a straight (strophic) edge anteriorly and what looks much like a pseudointerarea. The anterior shell is similar to some brachiopod dorsal valves (not acrotretides, interestingly, but more like some craniopsoids or siphonotretoids) with a triangular shape and no strophic posterior edge. The anterior shell retains this basic triangular shape throughout ontogeny; the posterior shell exhibits more pronounced allometric changes as it grows from a similar triangular-shaped shell early in ontogeny. If we hypothesize the halkieriid valves as homologues of brachiopod valves, the halkieriid body plan must be folded transversely in order to place the two shells opposite one another, in an opposing bivalved configuration (see WILLIAMS & HOLMER, 2002; COHEN, HOLMER, & LÜTER, 2003). Alternatively, the common ancestor of both halkieriids and brachiopods could have had a body form (not preserved or not recognized in the fossil record thus far) dissimilar to either of its descendants.

Musculature in halkieriid shells is unknown (even if one accepts *Micrina* as a halkieriid; WILLIAMS & HOLMER, 2002). It is unlikely that the two halkieriid shells interacted directly with one another on an individual organism (CONWAY MORRIS & PEEL, 1995), therefore any musculature they might have possessed is not likely to be homologous with brachiopod musculature. Additional study on a larger sample of halkieriid shells may reveal more useful evidence of soft tissue attachment.

The evolution of musculature in brachiopods closely accompanies the evolution of the two valves. Although not all muscles are associated with the valves, the majority of them are, and it becomes necessary to consider the evolution of muscle systems with respect to the functional morphology of relative valve motion, as well as articulation between the valves. As with articulation, the patterns of musculature preserved on the interior of brachiopods shells as old as the Tommotian demonstrate that a diversity of types of musculature are in place and fully functional in the Early Cambrian.

It is time to reevaluate long-entrenched scenarios of evolutionary polarity in which lingulids figure prominently as the most primitive brachiopods and thus provide a comparison for all other brachiopods, extant and extinct. While they do appear early in the fossil record (mid-Atdabanian; HOLMER, 2001) and have survived as living fossils ever since, many other valve morphologies (those in acrotretides, trematobolids, and kutorginoids; HOLMER, 2001) appear at this early time as well; some (those in paterinates and obolellates) appear even earlier (early Atdabanian; HOLMER, 2001). Among extant brachiopods, discinid and craniid musculature are more similar to one another and are likely to represent a more primitive (phylogenetically; see CARLSON, herein, Fig. 1908) pattern of musculature than what we see in lingulids, because of secondary modifications due to lingulid burrowing behavior and infaunal life mode. This is particularly true now that *Heliomedusa* (Atdabanian) has been reinterpreted as a discinid and not a craniopsid (CHEN, HUANG, & CHUANG, 2007), and the obolid *Xianshanella* (Atdabanian) appears to have been attached to the shells of other organisms by means of a long pedicle (ZHANG & others, 2006).

Major muscle systems in all brachiopods lie primarily (linguloids, trimerelloids, craniopsides, acrotretides) or exclusively (in other inarticulated and articulated brachiopods) in the posterior half of the valves. This nearly universal configuration of musculature, lying with the viscera mostly posterior to the midline, and the lophophore and mantle cavity lying mostly anterior to the midline, ensures that contraction of the posteriormost muscles will result in at least some rotation of the valves, assuming the more anteriorly located muscles (or any muscles anterior to the hinge axis) are capable of some extension and do not contract at the same time as do the more posterior muscles (Fig. 1901). The fulcrum (hinge axis) about which the valves may rotate with respect to one another remains between the posteriormost and the more anterior muscles, regardless of what names they have each been given in different groups of brachiopods. It is quite possible, therefore, that the posterior adductor muscles in inarticulated brachiopods are homologous with the diductor muscles in articulated brachiopods (RUDWICK, 1970). This interpretation is contrary to that outlined in GUTMANN, VOGEL, and ZORN (1978), which appears to oversimplify and thus misinterpret the functional musculature of inarticulated brachiopods. Adductor muscles, which bring the valves together (typically in closure), can effect a separation of the valves at one end (anteriorly) if they are positioned at the other end of the two valves, as is the case for the posterior adductor (umbonal) muscles (RUDWICK, 1970). The axis of rotation remains between these two sets of muscles; the viscera act as a fulcrum about which rotation occurs.

As ventral valves (particularly) evolved from relatively flat (craniids, discinids, lingulids) to more biconvex-cap shapes (acrotretides, kutorginides, orthides), the posterior edges of the valves had to separate in some way in order to accommodate the muscles (GUTMANN, VOGEL, & ZORN, 1978) extending from one valve to the other. This separation took the form of the large, broad delthyrial openings in kutorginides and the open delthyrium in obolellides and other early rhynchonelliforms to allow the muscles to span the distance between the two valves without disruption (RUDWICK, 1970). GUTMANN, VOGEL, and ZORN (1978, fig. 3)

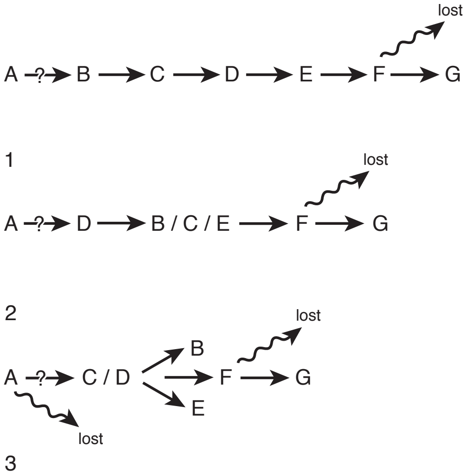

Fig. 1902. Hypothetical scenarios of evolution of valve-to-valve interactions and valve articulation; *letters* refer to types of valve interaction described in text and figured in Figure 1901 and Table 39; *arrows* indicate evolutionary transitions; *1,* a somewhat conventional evolutionary functional scenario; *2,* based on relative stratigraphic position; *3,* following topology in Figure 1908 (new).

assumed erroneously that the anterior edge of the interareas corresponded to the hinge axis; it does not (Fig. 1901). Determining the precise axis of rotation of the valves as they open and close is a critical piece of information; the ability of the muscles to open or close the valves by contraction is specified by the position of the hinge axis relative to the muscles. The position of the umbonal muscles does not shift relative to the hinge axis during this functional-evolutionary transition (*contra* Gutmann, Vogel, & Zorn, 1978), because the hinge axis is not colinear with a hinge line located on the valves (i.e., the edge of the interareas) in brachiopods with musculature similar to that described and illustrated in Figure 1901. The hinge axis always lies between the posterior adductors and the anterior adductors in this functional transition, regardless of which evolutionary pathway is followed (Fig. 1902).

All brachiopods must be able to separate or rotate their valves relative to one another to allow the cilia on the lophophore to establish an incurrent and excurrent water flow through the mantle cavity (LaBarbera, 1977, 1981), enabling the organism to obtain oxygen and food as well as release wastes and gametes. In addition, lingulids alone must be able to open their valves for a very different purpose: to assist the pedicle in penetrating the sediment substrate during burrowing and to help maintain the organism in a vertical position in its burrow (Rudwick, 1970; Thayer & Steele-Petrovic, 1975; Emig, 1981; Trueman & Wong, 1987; Savazzi, 1991; Richardson, 1997a). Trueman and Wong (1987) documented increases in pressure in the perivisceral coelom during the valve-opening phases associated with burrowing. The pressure increases were attributed to contraction of the circumferential muscles in the body wall of the lingulid. These experimental observations led them to conclude that (pedicle and perivisceral) coelomic fluid functions as a hydrostatic skeleton with respect to valve movements—contraction of the circumferential muscles applies pressure to the coelom and pushes the viscera posteriorly, thus forcing the valves open hydrostatically.

If contraction of the thin, sheetlike muscles in the body wall are capable of effecting an increase in pressure in the coelom to the extent that the valves can be opened relative to one another, then it is highly likely that the contraction of the umbonal muscle, which has a much larger cross-sectional area than the myoepithelium of the body wall, could effect a slight opening of the valves as well. If the umbonal (posteriormost) muscle contracts while the central muscle remains relaxed and uncontracted (this can and should be verified experimentally), then both the contraction of the muscles in the body wall and the contraction of the umbonal muscle could effect valve opening in the lingulids. The precise pattern of muscle firing in contraction has not yet been verified throughout the burrowing sequence in lingulids, to our knowledge. A valve-opening scenario in lingulids involving both hydrostatic and muscular forces has broader potential applicability to muscle systems in all brachiopods, not merely in lingulids with their unusual lifestyle. Posterior adductor or umbonal muscles could effect slight (six degrees in *Lingula*) opening of the valves anteriorly if contracted (and not opposed by contraction of the anterior adductors), because the viscera in between the two sets of muscles (in inarticulated brachiopods) acts as a fulcrum (RUDWICK, 1970). The two sets of adductors could contract and relax alternately in time, in a see-saw–like fashion, effecting either opening or closing of the valves anteriorly.

EMIG (1997a, p. 480) stated that "shells of discinids and craniids gape quite widely [presumably more than six degrees] at the anterior edge and more narrowly at the posterior margin," consistent with a scenario involving contraction of the posterior adductor, while the anterior adductor muscles remain relaxed and are allowed to extend. RUDWICK (1970, p. 72) claimed that "the way in which the valves [of living inarticulates] are observed to open by rotation does not support the suggestion that the coelom is used as a hydrostatic chamber." It is difficult to justify a wide gape by contraction of the body wall myoepithelium alone, particularly since *Novocrania* at least does not have a well-developed musculature in the body wall, as *Lingula* does (WILLIAMS & others, 1997). This hypothesis could be tested using electromyography to document the relative timing of muscle contraction. A strophic valve edge immediately posterior to the posterior muscle (as in *Novocrania* or *Cyrtonotreta*) could potentially allow even greater anterior gapes, because the strophic posterior shell edge would not interfere with greater valve rotation as much as a rounded posterior edge.

A comparison of discinids and craniids, assuming them to represent the evolutionarily basal type of musculature among brachiopods, reveals that two pairs of muscles dominate in effecting the opening and closing of the valves. Contraction of the posterior adductors causes the valves to gape somewhat (ATKINS & RUDWICK, 1962; RUDWICK, 1970), and contraction of the anterior adductors closes the gape. The various transmedian and oblique muscles present in discinids, craniids, and lingulids function only in brachiopods that lack both a hinge line and articulatory structures on the valves. As valve rotation about a hinge axis coincident with a hinge line located on the valves (such as seen in paterinates, chileates, and kutorginates, as well as some obolellates and trimerelloids) evolves, the transmedian and oblique muscles are lost evolutionarily. If we compare the position of the discinoid and cranioid posterior adductor muscles across a broader range of brachiopods, assuming them to perform the same function in each (that of effecting a gape angle), these muscles are likely to be homologous with what have been referred as umbonal muscles in lingulids, acrotheloids, acrotretoids, and siphonotretoids (BLOCHMANN, 1892, 1900; WILLIAMS & others, 1997; HOLMER & POPOV, 2000); internal oblique muscles in obolellates (POPOV & HOLMER, 2000c; BASSETT, POPOV, & HOLMER, 2001), trimerelloids (POPOV & HOLMER, 2000a), and chileates (POPOV & HOLMER, 2000b); diductor muscles in paterinates (LAURIE, 1987, 2000; WILLIAMS, POPOV, & HOLMER, 1998) and kutorginates (POPOV & WILLIAMS, 2000; BASSETT, POPOV, & HOLMER, 2001) as well as strophomenates and rhynchonellates (Fig. 1901). Muscles that have been labeled as internal obliques or oblique internals in lingulates and cranioids (where their origin and insertion can be verified directly in extant forms) are not positionally homologous with muscle scars given the same names (oblique internals) in obolellates, trimerelloids, and chileates. Because obolellates, trimerelloids, and chileates are all extinct, it is not possible to test this hypothesis of homology directly, but arguments based on relative muscle position and postulated function in other brachiopods support this hypothesis, which merits further testing.

Assuming that the discinid and craniid type of musculature is primitive for brachiopods, an assumption supported by the stratigraphic record (Atdabanian *Heliomedusa*) as well as molecular systematic data (craniids as primitive among living brachiopods; COHEN & WEYDMANN, 2005; see CARLSON, herein, Fig. 1907–1908; see also WILLIAMS & HOLMER, 2002), it is possible to hypothesize an evolutionary transition from this basal inarticulated pattern of musculature to a more derived, articulated type of musculature (Fig. 1901–1902). In this scenario, the origin of the paired posterior adductor muscles on the dorsal valve, which could rotate the valves open slightly anteriorly as they contract, migrates posteriorly to occupy a posteriormost position, eventually occupying a cardinal process or homologous structure on the dorsal valve. In some taxa, the muscle origin migrated well beyond the posterior edge of the dorsal valve (e.g., *Triplesia*, at the end of a long, hook-shaped cardinal process). It is noteworthy that in such situations the dorsal myophores are positioned anteriorly or even posterodorsally, allowing muscle contraction to effect the maximum rotation of the cardinal process, the dorsal valve, and consequently, the anterior gape (C. H. C. BRUNTON, personal communication, 2004). The insertion of the paired posterior adductor muscles on the ventral valve migrated anteriorly to a position lateral to (in Paleozoic orthides, WILLIAMS & HARPER, 2000, p. 717, fig. 518) and eventually (in extant terebratulides) anterolateral to the anterior adductor muscles (Fig. 1901G), which results in greater mechanical advantage of the diductors in opening the valves. In this evolutionary transition, oblique and transverse muscles of inarticulated brachiopods are lost, the dorsal origin of the posterior adductor (functional diductor) muscle decreases in area, and the ventral insertion of the posterior adductor (diductor) muscle increases in area, due in part to the lower angle at which it intersects the ventral valve interior in articulated brachiopods, and due in part to their tendonous structure. Tendonous muscles cannot generate as great a degree of valve opening as columnar muscles might be able to because of their shorter muscle fiber length, but with large cross-sectional area they could still generate considerable power.

Evolutionary changes in the brachiopod muscle system, as outlined in Figures 1901–1902, can be understood functionally as increasing the mechanical advantage of the posteriormost muscles in opening the valves (CARLSON, 1989). Accompanying these changes in musculature are increases in the convexity of the valves, which have been attributed to selection for increased mantle cavity volume, allowing greater three-dimensional complexity in lophophore geometry and function (MCGHEE, 1980). Apart from the evolutionary migrations of the origin and insertion of the posterior adductor muscles (and their homologues) and the loss of numerous transverse and oblique muscles as valve articulation and articulatory structures evolve, the fundamental arrangement of the major muscles relative to one another and relative to the axis of valve rotation has not changed significantly throughout brachiopod evolution (*contra* GUTMANN, VOGEL, & ZORN, 1978). The size, shape, and geometry of the valves themselves changed in the evolutionary transition from more primitive to more derived brachiopods, from the Tommotian to today, but the relative arrangement of the muscles and hinge axis have not changed significantly, from a functional perspective.

EVOLUTION OF ARTICULATION

[Sandra J. Carlson]

Mapping out the details of the pattern of evolution of valve articulation is one of the great unsolved mysteries of brachiopod evolution. Many of the major changes in the classification of Brachiopoda since the 1965 *Treatise* (MOORE, 1965)—abandoning Inarticulata and Articulata is one prominent example—relate to continuing evolution in our thinking about articulation over the past several decades. Several aspects of the evolution of articulation are clear: the type of tooth and socket structures (and corresponding functions) we associate with extant articulated brachiopods are evolutionarily derived within Brachiopoda and a variety of types of rudimentary articulation, including rotation of the valves about a hinge axis not located on the valves themselves and producing an anterior gape can be found in stratigraphically lower and phylogenetically more basal brachiopods. Are these different types of articulation homologous? How can we test this possibility, and explain the greater variety of valve-to-valve associations that existed early in the history of the phylum?

Any discussion of the evolution of articulation is necessarily related to the evolution of mantle mineralization, which results in two mineralized valves in brachiopods, one dorsal and one ventral (apparently; see also COHEN, HOLMER, & LÜTER, 2003). It is intriguing to note that brachiopods, as a clade excluding phoronids, are defined by a number of morphological synapomorphies (e.g., including a double row of lophophore filaments on only one side of the adult lophophore arms, two coelomic spaces per lophophore arm, and a subenteric primary nervous ganglion) that do not require the possession of two valves (CARLSON, 1995). This suggests that the presence of two valves, whether articulated or not, is not required for membership in the clade Brachiopoda. Thus, it is possible that mineralized valves arose more than once independently within a monophyletic Brachiopoda defined on the basis of other characters unrelated to valves (WRIGHT, 1979); given the major functional advantages to having mineralized valves, it is not unreasonable to consider their multiple independent origins (see also RUNNEGAR, 1982; BENGTSON, 2004). The most parsimonious interpretation involves a single origin of valve mineralization, coincident with the origin of the Brachiopoda (secondarily lost in phoronids if they nest within Brachiopoda), but there is no evidence at present that would allow us to reject definitively several parallel origins of mineralized shells early in brachiopod evolutionary history.

Whether they evolved once or more than once in the Brachiopoda, the two valves can interact with one another in one of several different ways: (1) rotate minimally in a dorsoventral direction about a hinge axis (or hinge plane) that is not located on the valves themselves (Fig. 1901B); (2) slide or twist relative to one another (lingulids only); (3) rotate about a hinge axis not located on the valves, as in #1 (Fig. 1901B and Table 39), but with strophic posterior valve edges, allowing moderate valve rotation to occur (Fig. 1901C); (4) rotate about a hinge axis coincident with a strophic hinge line located on the valves, but lacking articulatory structures (Fig. 1901D); (5) rotate about a hinge line distinguished by the presence of articulatory structures, either rudimentary or well developed (Fig. 1901E–1901G). Each of these combinations of characters, which may characterize either a grade of organization or possibly a clade, is discussed further below, exemplified by the taxa that exhibit them.

Type A: Multi-Element Mineralized Skeleton, Not Articulated

Halkieria possesses three distinct types of sclerites in addition to two dorsal shells, one anterior and one posterior, that are considered to be potentially homologous with the brachiopod dorsal and ventral valves (CONWAY MORRIS & PEEL, 1995). The two shells are not in articulation, and do not even touch one another. If brachiopods share common ancestry with the halkieriids (CONWAY MORRIS & PEEL, 1995; or the tannuolinids, WILLIAMS & HOLMER, 2002), several functional and morphological transformations must have occurred in this evolutionary transition. WILLIAMS and HOLMER (2002) outlined an evolutionary scenario by which brachiopods might have evolved from halkieriids (Fig. 1894), which involves the loss of sclerites and transverse folding of the body axis (COHEN, HOLMER, & LÜTER, 2003), as well as regrouping of the muscles and internal organs, eventually resulting in two shells juxtaposed as in extant brachiopods. The difficult behavioral and

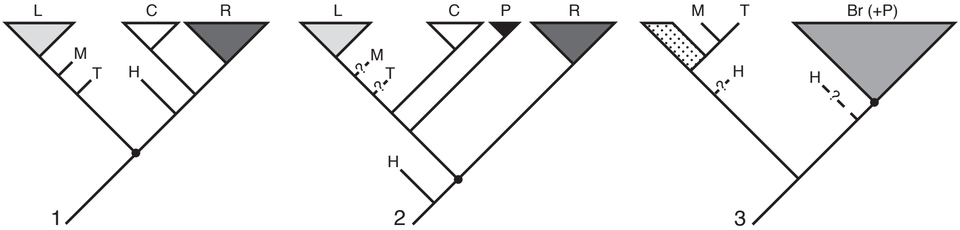

Fig. 1903. Hypothesized phylogenetic relationships among Linguliformea (*L*), Brachiopoda (*Br*), Craniiformea (*C*), Rhynchonelliformea (*R*), Phoroniformea (*P*), *Micrina* (*M*), *Tannuolina* (*T*), and *Halkieria* (*H*). *1,* constructed from discussion in Li and Xiao (2004) following topology in Williams and Holmer (2002); *2,* constructed following topology in Cohen and Weydmann (2005); *3,* constructed from discussion in Li and Xiao (2004) following Bengtson and others (1990); tannuolinids and tommotiids in *stippled box* (new).

whole-organism functional rearrangements that must have accompanied this morphological transition have not yet been thoroughly considered, however (C. Nielsen, personal communication, 2005).

Phylogenetic relationships among these various scleritic Lower Cambrian fossils (*Halkieria, Tannuolina, Micrina*) are not at all widely agreed upon, much less their relationship to brachiopods (Fig. 1896, 1903). Williams and Holmer (2002) considered *Micrina* to be a halkieriid, with the halkieriids (thus defined more broadly) as the phosphatic ancestral stock from which brachiopods evolved (Fig. 1896). This scenario is consistent with the diphyletic origin of brachiopods proposed by Gorjansky and Popov (1986), in which calcareous brachiopods evolved two shells independently from phosphatic brachiopods (see also discussion in Popov, 1992). Li and Xiao (2004) suggested a somewhat different scenario, in which halkieriids (which they consider to be most likely calcareous) might be most closely related to the calcareous brachiopods, while phosphatic *Mickwitzia* (and *Micrina* and *Tannuolina*) might be most closely related to the phosphatic brachiopods (Fig. 1903.1). Unless one considers all these taxa to be included within the clade Brachiopoda, this scenario also renders brachiopods diphyletic, again consistent with Gorjansky and Popov (1986). Both of these scenarios are inconsistent, however, with a growing body of data from molecular systematic analyses of extant taxa (Cohen, 2000; Peterson & Eernisse, 2001; Cohen & Weydmann, 2005) that places the calcareous inarticulated brachiopods more closely related to the phosphatic inarticulated brachiopods than to the calcareous articulated brachiopods (see also Carlson, 1995). This suggests that a calcareous shell might be basal for brachiopods, or at least that a phosphatic shell is less likely to be basal, or that valve mineralogy is largely homoplastic (and phylogenetically unreliable) among these early taxa. Consistent with this overall pattern of relationships, it is conceivable that *Micrina* and *Tannuolina* are most closely related to the phosphatic lingulates, while halkieriids share common ancestry with all brachiopods (Fig. 1903.2).

More traditional views (Bengtson, 1970; Landing, 1984; Laurie, 1986; also Li & Xiao, 2004) of the relationships of these Tommotian fossils considered *Micrina* and *Tannuolina* to be closely related to one another on the basis of sclerite morphology and microstructure, and both closely related to other tommotiids, while more distantly related to all brachiopods (Fig. 1903.3). Halkieriids could still be hypothesized as the sister group to the phoronids and brachiopods but would then be considered more distantly related to the other tommotiids like *Micrina*. At this time, none of these hypotheses can be rejected definitively, but evidence is mounting against the hypothesis illustrated in Figures 1896 and 1903.1. Depending on which pattern of relationships one supports, it is clear that different scenarios of the evolution of articulation result.

Micrina (but not *Tannuolina*) mitral sclerites have paired apophyses, or toothlike structures present just below the deltoid area, suggesting their positional homology to ventral teeth in brachiopods. WILLIAMS and HOLMER (2002, p. 846) claimed, however, that there is no structural evidence that they were used as articulatory devices. It is not clear what the structural evidence would consist of and raises the possibility that the apophyses served as a kind of preadaptation, or functional precursor, for teeth. If *Micrina* apophyses were not teeth used in valve-to-valve articulation, then it is at least possible that the rudimentary teeth (denticles, hinge ridges) in kutorginates, some obolellates, and trimerellates (Fig. 1901E) may also have lacked any valve articulatory function. Very few components of these many linked assertions regarding function and ancestry are known with great certainty.

Mineralized Elements Lost?

If the relationships illustrated in CARLSON (herein, Fig. 1907) (COHEN & WEYDMANN, 2005; see also ZRZAVY & others, 1998) are accurate, phoronids are phylogenetically nested within brachiopods, as the sister group to the linguliform + craniiform clade (Fig. 1903.2). This pattern of relationships suggests that mineralized valves have become secondarily lost in the evolution from a mineralized common ancestor, or possibly that a primitive nonmineralized condition was retained in the phoronids only. If some halkieriid group shares common ancestry with all brachiopods, including phoronids, the most parsimonious scenario posits the loss of a mineralized skeleton in the phoronids, from that common ancestor. If some unmineralized group of organisms, for which we have no fossil record yet, shares common ancestry with brachiopods (and phoronids) instead, then it is possible that phoronids retained their nonmineralized condition, and valves evolved twice independently within brachiopods (Fig. 1903.2).

Phoronids nested within brachiopods remains a somewhat contentious pattern of relationships, however. It is problematic that a fundamental feature like gut orientation would be opposite in two groups thought to be so closely related to one another (Fig. 1895, 1899; C. NIELSEN, personal communication, 2005). Several studies of morphological and molecular data conclude that phoronids lie outside the articulated + inarticulated brachiopod clade, as their sister group (GIRIBET & others, 2000; PETERSON & EERNISSE, 2001; MALLATT & WINCHELL, 2002; see also WILLIAMS & HOLMER, 2002). Using mitochondrial gene arrangements, LARGET, KADANE, and SIMON (2005) suggested (albeit with substantial qualification) that annelids are the sister group to brachiopods. If so, it is possible that the absence of mineralization is basal, with mineralization evolving (twice independently) in brachiopods after divergence from a common ancestor with annelids. The current data are sufficiently conflicted that it is premature to make a definitive statement about the relationship among brachiopods, phoronids, and other protostomes.

Type B: Bivalved Shells Rotate About a Hinge Axis; Hinge Line Absent

Many of the taxa formerly included in Inarticulata can be described by this type of valve-to-valve interaction: linguloids, discinoids (*Schizotreta*), acrotheloids, craniopsides, most siphonotretoids (*Siphonotreta*), and some acrotretoids (*Conotreta*). Valve-to-valve contact during muscle contraction is minimal to nonexistent. The hinge axis about which minimal dorsoventral valve rotation occurs exists between the valves and might be described more accurately as a dorsoventral hinge plane, perpendicular to both the sagittal and commissural planes, passing through the viscera between the posterior (umbonal) and anterior (central) adductor muscles (Fig. 1901). Lingulids represent a special case of this type of valve-to-valve interaction, in which sliding and transverse, twisting motions occur between valves, as well as minimal dorsoventral rotation (see discussion in Evolution of Muscle Systems, herein, p. 2850). Posterior dorsal valve edges are either rounded (*Discina*), or acute (*Glossella*), but almost never strophic. No articulatory structures are present on the valves. Pseudointerareas commonly, but not invariably, exist, but the anterior edge of the pseudointerarea does not serve as a hinge axis (*contra* GUTMANN, VOGEL, & ZORN, 1978).

Type C: Posterior Valve Edges Strophic; Articulatory Structures Absent

Most craniides (*Ancistrocrania*) and some siphonotretoids (*Cyrbasiotreta*) and acrotretoids (*Treptotreta*) have two valves that appear to contact one another posteriorly in an approximately straight (strophic) line (Fig. 1901C) when the posteriormost muscles are contracted. No articulatory structures are present on the valves. The valves can rotate until the straight posterior edges come into contact with one another at the maximum extent of muscle contraction, as in some Recent craniides. This strophic valve edge at least allows the possibility that gapes in taxa with this type of articulation could be wider than in lingulids, which is consistent with RICHARDSON's (1997a) observations on living craniids. ATKINS and RUDWICK (1962, p. 474; and see also C. NIELSEN, personal communication, 2005) stated that "When the shell [of *Crania*] opens, it does so by a rotation of the dorsal valve about an axis corresponding to the posterior side of the shell, where the valve edges remain in contact." Other behavioral observations suggest that no such rotation of the dorsal valve need occur (C. H. C. BRUNTON, personal communication, 2004), even if it is possible to do so. A strophic valve edge also makes it more likely that valve-to-valve contact will occur along a line, in the process of valve rotation, unlike the slight opening effected in lingulids and discinids where no such valve-to-valve contact need occur at all.

Many acrotretoids have ventral valves that are nearly conical in shape (*Ceratreta*, *Ephippelasma*); hypotheses of muscle homology and the nature of valve-to-valve contact in acrotretoids relative to other brachiopods are thus more difficult to reconcile. Nevertheless, many acrotretoids have strophic posterior valve edges, and it is relatively easy to envision a functional scenario in which a lidlike dorsal valve can be rotated open relative to a conical ventral valve about a hinge axis, possibly one coincident with the strophic valve edge, in a manner similar to craniides.

Type D: Hinge Axis Coincident with Strophic Hinge Line; Articulatory Structures Absent

Paterinates, chileates, and some trimerellides have distinct strophic hinge lines and muscle scars arranged in a manner more (*Paterina*) or less (*Chile*) similar to those in strophic articulated brachiopods, leading to the interpretation (POPOV & TIKHONOV, 1990; POPOV, 1992; BASSETT, POPOV, & HOLMER, 2001; WILLIAMS, 2003) that the axis of valve rotation is coincident with the strophic hinge line, with the two valves in contact throughout the process of valve rotation (Fig. 1901D). Yet, all taxa with this type of valve-to-valve contact lack distinct articulatory structures, and all are extinct; the axis of rotation may have been fixed entirely by fused mantle lobes (POPOV & TIKHONOV, 1990; POPOV & HOLMER, 2000a), but this possibility is very difficult to test.

Type E: Articulatory Structures Rudimentary and Diverse

Some trimerelloids (*Eodinobolus*) have what might be called an astrophic hinge line, where the valves contact one another primarily at two points rather than along a straight line (Fig. 1901E). The ventral valve is larger than the dorsal, with a large ventral pseudointerarea present. A dorsal hinge plate fits tightly into a so-called cardinal socket in the ventral valve and appears to have fixed the axis of rotation in a manner similar to that of articulated brachiopods (POPOV & HOLMER, 2000c). This type of valve-to-valve contact has been referred to as a rudimentary form of valve articulation, but one that is lacking in paired teeth and sockets.

In kutorginates (*Kutorgina* and *Nisusia*), which also have a kind of astrophic hinge line, the lateral margins of the pseudodeltidium fit into sockets at the end of furrows or grooves in the dorsal valve located between narrow, elongate socket plates and the so-called interarea (Fig. 1901E); this has been described as a rudimentary articulatory system (Popov & Williams, 2000; Bassett, Popov, & Holmer, 2001) and is quite different from the morphology in trimerelloids. Paired teeth and sockets are lacking, but there are clearly structures of positive relief that fit into structures of negative relief, which could serve to define a hinge axis about which valve rotation could occur.

Most obolellates—naukatides (*Oina*) and obolellides (*Trematobolus*)—possess articulatory structures in the form of paired ventral denticles and dorsal sockets. They are similar to a primitive type of deltidiodont structure, but the homology of obolellate denticles and deltidiodont teeth is not clear. Structures referred to as interareas are present (*Trematobolus* and *Oina)*; the anterior edge of the interareas, where the paired denticles are located, may serve as a hinge axis in these taxa, consistent with Gutmann, Vogel, and Zorn (1978). The muscle serving to rotate the valves open inserts on the posterior side of the hinge axis on the dorsal valve, however, and inserts on the anterior side of the hinge axis on the ventral valve. Rather than requiring a hydraulic opening mechanism, therefore, a standard lever system can effect valve rotation in obolellates, as is apparently also true for kutorginates and trimerelloids (see Bassett, Popov, & Holmer, 2001).

Type F: Deltidiodont Articulatory Structures

Protorthides, orthides, most strophomenates, most pentamerides, and possibly some spiriferides and spiriferinides are characterized by deltidiodont articulatory structures. Minor variations exist among deltidiodont dentitions, but the basic pattern of valve articulation remains more or less the same in each (Jaanusson, 1971; Carlson, 1989). Two ventral teeth sit in two dorsal sockets; the dorsal and ventral valves may be separated from one another easily because the teeth do not interlock with the sockets. Valve rotation is effected by contraction of the diductor muscles to open the valves anteriorly and adductor muscles to close the valves.

Post-Devonian productidines and some pre-Devonian strophomenides have lost the deltidiodont tooth and socket articulation; the lack of articulatory structures is clearly secondary and derived. Despite selection pressures causing the loss of a pair of ventral teeth fitting into dorsal sockets, the functional need for valve-to-valve stability allowed a different but apparently effective type of articulation to evolve. These shells articulated effectively by means of a somewhat peglike cardinal process that extends into the ventral umbonal cavity. On either side of the base of the cardinal process are the median ends of cardinal or lateral ridges that provide articulation surfaces with the edges of the ventral umbo. As these shells are almost universally deeply concavoconvex, commonly with long trails and wide hinge lines coincident with the axis of rotation, the dorsal valve opened within the convexity of the ventral valve and these prevented any differential movement away from the simple rotation about the hinge axis (C. H. C. Brunton, personal communication, 2004). This functional articulation involves a single dorsal tooth (cardinal process) fitting into a ventral socket (umbonal cavity). Multiple denticulations have evolved along the hinge line more than once among strophomenates (e.g., *Strophodonta*, *Leptostrophia*; Rong & Cocks, 1994; Cocks & Rong, 2000) and served largely to prevent torsion of one valve relative to the other.

In general, brachiopods with deltidiodont dentition also have strophic (straight) hinge lines. Thecideides, brachiopods with strophic hinge lines and cyrtomatodont dentitions, present the most unambiguous contradiction to this generalization. JAANUSSON (1971, 1981) argued that all strophic spire-bearers have cyrtomatodont articulation. Examination of a wide variety of strophic spire-bearers (CARLSON, personal observation, 1989) suggests that some are very likely to be deltidiodont, not cyrtomatodont. The detailed nature of hinge structures in the strophic spire-bearers is not entirely clear, however, and merits further, comprehensive investigation.

The rudimentary types of articulation present in many obolellates could be considered deltidiodont, in that articulatory structures are present but do not interlock with one another. Interestingly, these early forms of articulation tend to be associated with astrophic, or curved, hinge lines, rather than strophic, or straight, hinge lines. A number of early brachiopods with strophic hinge lines (paterinates, chileates, some acrotretides) lack any vestige of articulatory structures.

Type G: Cyrtomatodont Articulatory Structures

Rhynchonellides, terebratulides, thecideides, atrypides, athyridides, some pentamerides, and possibly most spiriferides and spiriferinides comprising the rhynchonellate crown group (see CARLSON, herein, Fig. 1908) have cyrtomatodont dentitions. All extant articulated brachiopods have interlocking teeth and sockets that generally prevent easy separation of the valves from one another. The nature of the fit of the teeth in the sockets can limit the degree of valve rotation possible about the hinge axis, which is coincident with an astrophic hinge line in most cyrtomatodont brachiopods. It is possible that cyrtomatodont dentitions have evolved more than once independently (possibly in *Porambonites*, for example), but this does not detract from the hypothesis of synapomorphy for cyrtomatodont dentitions among the derived rhynchonellate brachiopods (see CARLSON, herein, Fig. 1908).

The central role of shell resorption in crafting cyrtomatodont dentitions is undeniable. Interlocking teeth and sockets cannot form and grow through ontogeny without continual resorption and mineralization. It doesn't necessarily follow, however, that taxa with deltidiodont dentitions were not capable of shell resorption. If one looks carefully at the strophomenates (e.g., *Edriosteges, Bathymyonia, Triplesia*), it is possible (but not necessarily required; C. H. C. BRUNTON, personal communication, 2004) that elongated, hook-shaped cardinal processes also involved shell resorption and mineralization in order to form and grow through ontogeny (CARLSON, 1989).

Evolutionary Patterns in Valve Articulation

To move beyond a simple categorization of types of articulation, it is necessary to place these functional groups in some kind of order, ideally an order representing the evolution of the articulatory system. The order in which these various types are listed, from A to G, characterizes a more conventional functional scenario (Fig. 1902.1) in order of increasing complexity in valve-to-valve interaction: hinge axis, but no hinge line (Fig. 1901B); hinge line, but no articulation (Fig. 1901D); articulatory structures primitive, then more derived (Fig. 1901E–1901G).

Stratigraphic polarity alone imposes a structure on these functional groups, but it is a structure dependent on the vagaries of preservation and taphonomic control. The halkieriid sister-group relationship to brachiopods has not yet been tested rigorously, so does not yet impose a clear polarity on these transitions in articulation. Based strictly on relative stratigraphic position, the following order can be deduced (Fig. 1902B): (1) multielement halkieriids appear first in the Nemakit-Daldynian; (2) paterinates, with strophic hinge lines but lacking articulation appear next in the Tommotian; (3) discinoids (*Heliomedusa*) that lack valve-to-valve contact appear in the lower Atdabanian, as do obolelloids with strophic hinge lines bearing small, rudimentary ventral denticles and dorsal sockets (*Trematobolus*) and other obolelloids (*Obolella*) with strophic hinge lines but no articulatory structures; (4) protorthides, orthides, and pentamerides, with deltidiodont articulation of noninterlocking ventral teeth fitting into dorsal sockets, appear in the Toyonian; (5) rhynchonellides with interlocking cyrtomatodont dentition appear in the Llanvirn. This pattern, if truly representative of the order of the evolution of these features, reveals that a strophic hinge line lacking articulatory structures, about which the valves rotate, is the most primitive type of articulation, followed closely in time by three different and coeval functional types of articulation. Stratigraphic polarity cannot yet provide insight into which of these three may be more basal than the others. More typical deltidiodont articulation appears later, and interlocking cyrtomatodont appears later still.

Outgroup polarity may have the power to resolve further the pattern of evolution of articulation (Fig. 1902.3). Among extant brachiopods only, both molecular (Cohen & Gawthrop, 1997; Cohen & Weydmann, 2005) and some (but not all, see Holmer & others, 1995) morphological analyses (Carlson, 1995) support the hypothesis that craniids share most recent common ancestry with discinids and lingulids (see Carlson, herein, Fig. 1907–1908). If so, the nature of valve-to-valve interaction in lingulid and discinid brachiopods (type B) would represent a more derived condition than what exists in craniids (type C). If the various rudimentary articulatory structures seen in kutorginates and some obolellates and trimerelloids (type E) are truly homologous with deltidiodont and cyrtomatodont dentitions (this has certainly not been tested in any rigorous fashion and may well be false), it is reasonable to hypothesize that types B and C, lacking articulatory structures, are more primitive than those with rudimentary structures (type E). Types B, C, D, and E are all more primitive than is F, and it is difficult to say with certainty which of these four types is truly the most basal. When these various articulatory functional groups are mapped onto the pattern of relationships illustrated in Carlson (herein, Fig. 1908), all four types appear near the base of the cladogram.

Consistent with the evolutionary transformation discussed previously for muscle systems, I suggest the following evolutionary transformation in valve articulation, outlined in Figure 1902.3. These morphological transformations can be polarized by stratigraphic or outgroup criteria; both criteria together seem to provide the greatest resolution (Fig. 1902.3; and see Carlson, herein, Fig. 1908), but even that resolution is not particularly clear. It is entirely possible that each of the articulatory types described here represents a grade of functional organization, rather than synapomorphies defining clades (Bassett, Popov, & Holmer, 2001); this would seem to be most plausible for types C, D, and E. With the information that can be gleaned from specimens currently in hand, it is difficult to test these competing hypotheses.

Bassett, Popov, and Holmer (2001) argued that the diverse types of articulation observed among the early rhynchonelliforms are so different that they could not have shared common ancestry and must have evolved independently. Specifically, they argued that the primitive, rudimentary types of articulation seen in obolellates, chileates, and kutorginates evolved independently of one another and that deltidiodont articulation evolved independently in protorthides and orthides. Given the relatively small numbers of specimens collected from these early groups and their variable states of preservation, particularly of anatomical features, it is essentially impossible to reject any hypothesis of relationship of articulatory styles among the Early Cambrian brachiopods at this time.

The lesson of *Heliomedusa* is an important one to remember: numerous conclusions (Jin & Wang, 1992) reached about the identity and position of anatomical features after examination of 185 well-preserved specimens collected by 1992 were rejected upon examination of 1150 specimens collected by 2004 (CHEN, HUANG, & CHUANG, 2007). It is not possible at this time to reject the hypothesis of multiple convergent or parallel evolution of different styles of articulation suggested by BASSETT, POPOV, and HOLMER (2001), but it is not necessarily the most parsimonious interpretation of the evidence currently in hand (Fig. 1902). It is not clear, for example, why articulation in protorthides and orthides is said to have evolved convergently, when these two taxa appear to share the most recent common ancestry (see CARLSON, herein, Fig. 1908; see also CARLSON & LEIGHTON, 2001). Mapping the pattern of articulatory types onto the cladogram illustrated in CARLSON (herein, Fig. 1908), one can construct numerous functional and phylogenetic scenarios to explain the origin and evolution of the pattern. Depending on how one resolves the polytomies or how unwilling one is to accept the pattern of relationships presented here, almost any hypothesis imaginable can be proposed; testing the hypotheses with evidence is the truly challenging aspect of the analysis of the evolution of articulation.

EVOLUTION OF LOPHOPHORE AND SUPPORT STRUCTURES

[Sandra J. Carlson]

Given our current understanding of metazoan phylogeny (ZRZAVY & others, 1998; GIRIBET & others, 2000; NIELSEN, 2001; PETERSON & EERNISSE, 2001; VALENTINE, 2004; LARGET, KADANE, & SIMON, 2005; PASSAMANECK & HALANYCH, 2006), it is likely that the extant sister group to brachiopods does not possess a lophophore. Of the other two lophophorate phyla, phoronids may well cluster within the brachiopod clade (COHEN, 2000; COHEN & WEYDMANN, 2005; see also FREEMAN & LUNDELIUS, 2005), rather than as the brachiopod sister group, but this hypothesized relationship remains controversial (see herein, p. 2880). Bryozoans are now thought to be rather distantly related to brachiopods, and their lophophores not homologous (NIELSEN, 1985; VALENTINE, 2004); pterobranchs have been described as possessing a lophophore-like tentacular crown containing coelomic extensions (BRUSCA & BRUSCA, 2003), even though the mouth lies outside the ring of tentacles, and they are clearly more closely related to the deuterostome taxa. This suggests that the two-armed brachiopod lophophore was a novel feature and evolved from an ancestor lacking a lophophore.

In all brachiopods except thecideides (and phoronids), the lophophore tentacles are paired and located on either one or both sides of the arm axis (EMIG, 1976; WILLIAMS & others, 1997). Given the phylogenetic hypothesis illustrated in CARLSON (herein, Fig. 1908), it is possible to argue either that unpaired tentacles evolved twice independently in phoronids and thecideides (with adlabial tentacles only) or that thecideides alone among brachiopods reversed to a primitive state shared by phoronids. The loss of the ablabial tentacles might be related to their truncation in development, as a result of the small adult size of thecideides (CARLSON, 1995), or might possibly relate to reproduction by brooding rather than dispersal (C. H. C. BRUNTON, personal communication, 2004); both might relate to each other.

Lophophore Ontogeny

The ontogenetic pathways in lophophore geometry observed among extant brachiopods have been amply characterized (ATKINS, 1959a, 1960a, 1961c; RUDWICK, 1962a, 1970; BAKER, 1990, 1991, 2006, EMIG, 1992; WILLIAMS & others, 1997, p. 112, fig. 111). Not surprisingly, geometric complexity of the lophophore increases as body size increases during ontogeny, as more tentacles are required to support the physiological needs of larger individuals. A simple, ring-shaped trocholophe is the first functional lophophore configuration to develop, formed by paired semicircular brachial axes (from which the lophophoral tentacles emerge), one on either side of the mouth.

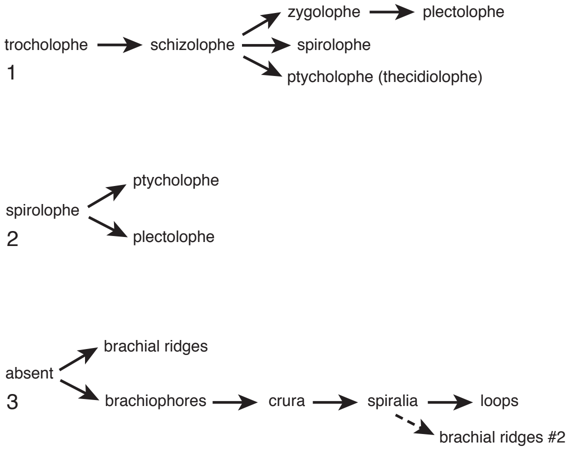

FIG. 1904. Lophophore ontogeny and evolution; *1,* lophophore ontogeny, following RUDWICK, (1970); *2,* lophophore evolution, following topology in Figure 1908; *3,* hypothetical brachidial evolution, following topology in Figure 1908 (new).

The lophophore apices are located anteriorly, opposite the mouth, located posteriorly. The trocholophe stage is followed by a schizolophe or split bilobed configuration (Fig. 1904.1), in which the apices of the lophophore (brachial axis) migrate posteriorly toward the mouth. The brachial axis lies within a plane parallel to the commissural plane in both stages. This initial developmental pattern appears to be shared universally by all extant brachiopods.

Following the schizolophe stage, however, three distinctly different developmental pathways may be pursued, producing either a spirolophe, plectolophe, or ptycholophe lophophore. The ptycholophe is characteristic of thecideide brachiopods today, particularly thecidellinids, and involves additional infolding of the brachial axis in the same plane as the schizolophe. In extant spirolophes, the brachial axis may migrate helically in either a dorsal (craniids, rhynchonellides) or ventral (discinids) direction, or it may rotate 90 degrees to migrate medially, as in lingulids. The plectolophe is characteristic of terebratulide brachiopods and is typically preceded ontogenetically by a zygolophe stage, in which the brachial axis migrates first ventrally and then posteriorly. Eventually the apices of the brachial axis migrate medially, forming an inner planispiral spirolophe (median coil) not unlike that seen in lingulids.

Ontogenetic changes in the calcareous lophophore supports among extant brachiopods include elongation of the crura in rhynchonellides (SAVAGE & others, 2002 and references therein) and increased infolding and lobation in the brachial ridges of thecideides (for example, BAKER, 1969, 1970, 2006). As BAKER (1989) pointed out, our knowledge of ontogenetic changes in the morphology of lophophore support structures is poor for many groups of fossil and Recent brachiopods. Studies by MACKINNON and coworkers (MACKINNON, 1993; MACKINNON & SMIRNOVA, 1995), however, have greatly improved our knowledge of loop ontogeny in terebratellidine brachiopods. Among long-looped terebratulides, teloform (adult) loops can develop in at least two different ways. In most terebratellidines, most elements of the loop develop from a septal pillar arising from the center of the dorsal valve; some of the posterior section of the descending lamellae derive from the cardinalia as well (LEE & others, 2006). Paleozoic terebratulidine teloform loops, almost indistinguishable morphologically from terebratellidine teloform loops, develop in some taxa from the cardinalia (crura) alone (MacKinnon, 1993; Lee & others, 2006; see also Baker, 1972; Richardson, 1975). Among short-looped terebratulidine brachiopods, the loop develops entirely from the cardinalia; no septal pillar exists.

Lacking Recent articulated brachiopods with mineralized spiral brachidia, our knowledge of the details of spiralium development is quite poor (but see Copper, 2002; Alvarez & Rong, 2002). It appears that spiralia developed exclusively from the dorsal cardinalia, largely from the crura.

Lophophore Evolution

What relationship, if any, exists between these ontogenetic pathways and patterns of evolution in lophophore morphology? Among extant brachiopods, a spirolophe lophophore is the most evolutionarily primitive adult form (see Carlson, herein, Fig. 1908), based on either stratigraphic (Williams & others, 1996; Williams, Carlson, & Brunton, 2000) or outgroup (Carlson, 1995) polarity criteria. Emig (1992) stated that the spirolophe has evolved as least twice independently, possibly referring to the fact that the lophophore configuration in many Paleozoic rhynchonelliforms is not known with complete certainty. Spirolophes occur in all inarticulated brachiopods, in phoronids, and in rhynchonellides. Brachiopods with ptycholophe lophophores (thecideides and rare terebratulides, e.g., *Megathiris*) and plectolophe lophophores (most terebratulides) both evolved from ancestors with spirolophe lophophores. Some taxa with small body sizes as adults have retained the primitive juvenile type of trocholophe, zygolophe, or schizolophe lophophore (e.g., *Pumilus*, Williams & others, 1997, fig. 112). Lower Cambrian *Heliomedusa* (Chen, Huang, & Chuang, 2007) appears to possess a distinctive type of spirolophe lophophore, adding further fossil support to the idea that a spirolophe is the basal lophophore state among brachiopods.

Mineralized lophophore support structures are absent in all the more basal brachiopods, as well as phoronids (see Carlson, herein, Fig. 1908). This is thought to result from their absence in the living organisms, rather than nonpreservation in the fossil record. Structures interpreted to have provided support for the lophophore first appear as brachial ridges in most strophomenates and as extensions of the inner socket ridges referred to as brachiophores in early rhynchonellates and in some orthotetidines (Fig. 1904). Brachiophores became elongated and elaborated as crura in derived pentamerides and in rhynchonellides, which became further elaborated as spiralia in the spire-bearing brachiopods and then transformed to loops in terebratulides. If some strophic spire-bearers share closer common ancestry with the impunctate orthoids (Wright, 1979; Gourvennec in Copper & Gourvennec, 1996; Gourvennec, 2000), then spiralia evolved at least twice independently among rhynchonellates, as also did laterally directed spiralia. If thecideides share closer common ancestry with the spiriferides (Baker, 1984, 1990), then brachial ridges have evolved at least twice independently. *Thecospira*, the most basal thecideide (Jaecks & Carlson, 2001), possesses spiralia, supporting this latter possibility.

Brachiophores are considered to be the homologues of crural plates in rhynchonellides (Brunton, Alvarez, & MacKinnon, 1996; Williams, Brunton, & MacKinnon, 1997, p. 369, fig. 329) and socket plates in porambonitoids (Carlson, 2002). It is possible that they may have provided some posterior support to the lophophore in some orthoids, protorthoids (*Enteletes, Skenidioides*), and orthotetidines. Brachiophores are not developed or are very rare in most protorthides, strophomenoids, and clitambonitoids.

Short rodlike or bladelike crura evolved in the clade that includes rhynchonellides and camerelloids as sister taxa (Carlson, 2002). Porambonitoids do not have elongated crura or brachiophores, but very short and morphologically simple socket plates that are unlikely to have provided much lophophoral support. Crura continue to elongate and become more morphologically complex in later rhynchonellides. Diversity in known crural morphology is great, and this diversity provides structure for much of the classification of the superfamilies of rhynchonellides (SAVAGE & others, 2002). Evolutionary relationships among these many, distinct crural types have not yet been determined in detail. Because of their long and delicate structure, crura break easily after death and are thus rather poorly known in a great many rhynchonellides, particularly in the Paleozoic (SAVAGE & others, 2002), complicating the task of determining their phylogenetic relationships.

Because of their considerable morphological complexity and the absence of spire-bearing brachiopods in the Recent fauna, the evolution of spiralia continues to be a contentious topic (RUDWICK, 1970; WRIGHT, 1979; GRUNT, 1982; COPPER & GOURVENNEC, 1996; GOURVENNEC, 2000). The apices of the spiralia point in different directions in different spire-bearing brachiopods: in atrypides they point medially or dorsomedially; in athyridides they point laterally or lateroventrally (ventrally in koninckinoids); in spiriferides and spiriferinides they point laterally or posterolaterally. Several evolutionary hypotheses have been proposed (Fig. 1905) that afford different degrees of importance to the direction in which the spires point, the relative order of appearance of certain features in the stratigraphic record, the significance of a strophic or astrophic hinge line in conjunction with a spiralium, and finally the presence or absence of a complete jugum or medial band connecting the two lamellae of the spiralia.

Monophyly of the spire-bearing brachiopods is supported by COPPER in COPPER and GOURVENNEC (1996; see also DAVIDSON, 1882; WAAGEN, 1883). In this hypothesis, spiralia evolved once, and all spire-bearers (Atrypida, Athyridida, Spiriferida, Spiriferinida) are thus closely related and evolved in relative stratigraphic order from Rhynchonellida (Fig. 1905.1). This hypothesis emphasizes the evolutionary importance of the presence of spiralia and the stratigraphic order of appearance of the different groups characterized by the orientation of the spires.

The diphyletic origin of spiralia was proposed by RUDWICK (1970) and expanded upon by subsequent authors (WRIGHT, 1979; GRUNT, 1982; GOURVENNEC in COPPER and GOURVENNEC, 1996; GOURVENNEC, 2000) proposing several different hypotheses. Strophic spire-bearers (spiriferides and spiriferinides) shared ancestry with strophic orthides, while the astrophic spire-bearers (atrypides and athyridides) shared ancestry with the astrophic rhynchonellides (Fig. 1905.2; RUDWICK, 1970; WRIGHT, 1979). Spiralia evolved twice independently, as also did laterally directed spiralia. Uncertainty about deltidiodont or cyrtomatodont hinge structures contributes to this debate; strophic spire-bearers seem to be deltidiodont (CARLSON & LEIGHTON, 2001, but see also JAANUSSON, 1971), while astrophic are cyrtomatodont. A variant of this hypothesis is discussed by COPPER (in COPPER & GOURVENNEC, 1996), in which both athyridides and spiriferides, the two groups with laterally directed spiralia, evolve from the orthides, while the atrypides with dorsomedially directed spiralia evolve from the rhynchonellides, with dorsally directed lophophore spires (Fig. 1905.3). In this hypothesis, the direction of the spires is granted greater evolutionary importance than the nature of the hinge line. A third diphyletic hypothesis was proposed by GRUNT (1982) in which the atrypides and athyridides each evolved spiralia independently from the rhynchonellides, with the spiriferides (and spiriferinides) evolving subsequently from the athyridides (Fig. 1905.4).

Various aspects of the evolution of the jugum, a calcareous band that connects the two halves of the spiralia in some taxa (athyridides in particular) were discussed in WILLIAMS, BRUNTON, and MACKINNON (1997, p. 374+) and will not be repeated

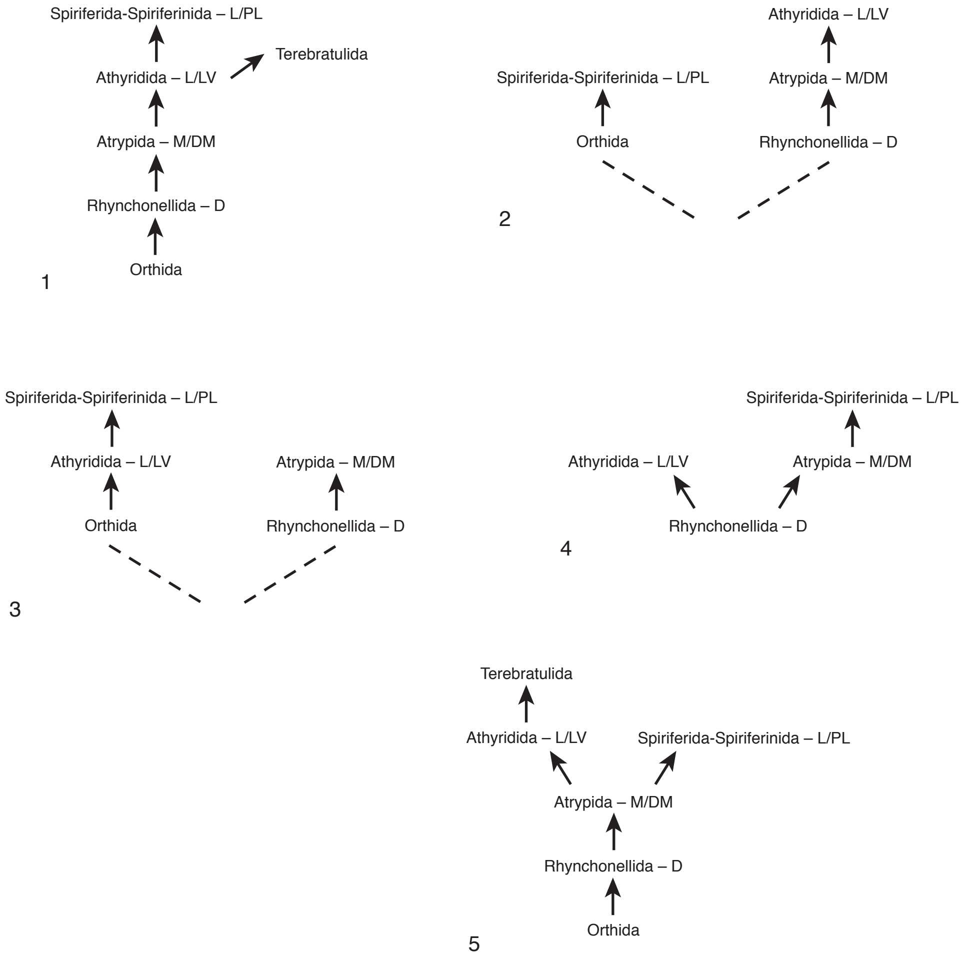

Fig. 1905. Hypotheses of evolution of spiralia among spire-bearing brachiopods; *1,* following Copper in Copper and Gourvennec (1996); *2,* following Rudwick (1970) and Wright (1979); *3,* discussed in Copper and Gourvennec (1996); *4,* following Grunt (1982); *5,* following Rong and Zhan (1996); *L/PL* indicates lateral-posterolateral orientation of spiralia; *L/LV,* lateral-lateroventral; *M/DM,* medial-dorsomedial; *D,* dorsal (new).

here. The presence or absence of a jugum is considered to play an important role in these competing evolutionary hypotheses, however. Copper predicts that finding a complete jugum in the earliest spiriferides (e.g., *Eospirifer*) would support the evolution of the spiriferides from the athyridides (most of which have a complete jugum) and thus the monophyletic origin of spiralia (Copper & Gourvennec, 1996). This scenario would also support the hypotheses illustrated in Figure 1905.3 or 1905.4, however, and does not appear to be as definitive a piece of evidence as Copper asserts. The discovery of additional specimens of *Eospirifer* and *Striispirifer* (Rong & Zhan, 1996) that possess a small jugal process but lack a complete jugum is not consistent with Copper's prediction, which Gourvennec (2000) suggested should lead to a reexamination of the monophyly hypothesis. Rong and Zhan (1996) proposed that the spiriferides and atrypides share closer common ancestry, based on the absence of a complete jugum (Fig. 1905.5). Clearly, some of the characters evaluated in these hypotheses of relationships are homoplastic, not homologous; just which ones they are, however, has yet to be determined.

The presence of a loop in all but the medial (spiral) coil of the plectolophe lophophore is a synapomorphy (shared derived character) of the Terebratulida. As discussed earlier with respect to loop ontogeny, the morphologically simpler of the two loop types (so-called short-looped forms, in Terebratulidina) first appears in the Early Devonian; the loop develops from the crura only. The more derived, long-looped forms in Terebratellidina first appear much later in the Early Triassic; the loop develops from both the crura and the septal pillar (MacKinnon, 1993; Lee & others, 2006). A loop has originated independently of the terebratulides in *Tropidoleptus* (possibly an orthide; Williams & Wright, 1961) and *Enantiosphen* (possibly a pentameride; Boucot, Rong, & Blodgett, 2002). Although their developmental and evolutionary origin is somewhat perplexing, these few instances of homoplasy (possibly due to paedomorphosis) are not sufficient to cause us to reject the hypothesis of the homology of the loop within the terebratulide clade. The occurrence of loops in species outside terebratulides demonstrates that at least a certain amount of developmental flexibility in lophophore mineralization and configuration exists and makes it more difficult to reject the diphyly hypotheses of spiralia evolution.

Brachial ridges are present on the dorsal valve interior in some strophomenides, productides, and thecideides. Their shapes suggest support for schizolophe (*Christiania*, *Reticulatia*, *Anidanthus*, *Urushtenia*), planispiral spirolophe (*Leptaenisca*), or ptycholophe lophophores (most thecideides). Stratigraphy, shell structural changes, and other morphological changes support the evolutionary changes seen in the lophophore supports in plectambonitoids, through Chonetidina to the Productidina and Strophalosiidina (Brunton, 1972). In the very shallow-bodied aegiromenine plectambonitoids, the more usual strophomenate brachiophores are lost, and small anderidia are found in a few genera. These paired ridges on the dorsal interior extend forward from the adductor scars, becoming raised and pointed anteriorly where they are interpreted as supporting the body wall in positions where the lophophore was attached. These structures are found virtually throughout the chonetidines, which do not have well-developed brachial ridges. Anderidia are found also in the three earliest known genera of the productidines and strophalosiidines, but by the Eifelian they are lost, and brachial ridges become increasingly prominent. These features mark the positions on the dorsal valve where the mantle epithelium supported the lophophore, which curved ventrally onto the body wall in which the mouth was placed, and thence anteroventrally on the body wall covering the ventral attachments of the diductor muscles and probably diverticula around the stomach.

The platform of some plectambonitoids (Cocks & Rong, 2000, p. 306) is similar to the tuberculate and ridged borders of dorsal valves in some chonetidines such as *Dyoros (Tetragonetes)* and probably indicates the outline of the lophophore, but the lophophore always remained unsupported by any internal skeletal structures. For this reason, it depended on epithelial attachment that, when intimately associated with the valve interior, caused the growth of shelly brachial ridges.

Brachial ridges are well formed in many productidines and strophalosiidines but are unknown in other groups apart from exaggerated brachial structures in the lyttoniidines and thecideides. In the Productida they probably increased in size and development as these shells grew in size during their range to the Late Permian, with increased demands upon their roles in respiration, collection of food, and clearing of waste products and gametes. The lyttoniidines, a highly derived group of productides, possess a curious, highly lobate internal plate that has a generally ptycholophous shape (Williams, Carlson, & Brunton, 2000).

The most complicated calcified brachidium of GRANT (1972) is found in the Permian strophalosiidine *Falafer* (BRUNTON, LAZAREV, & GRANT, 2000, p. 355). Thecidiolophe (PAJAUD, 1970; BAKER, 1990) supports have evolved in some thecideides (lacazelloids), in which the ptycholophe emerges from the floor of the valve and folds in a ventral and posterior direction, not unlike the folded ptycholophe of *Falafer*. These are exaggerated shelly forms of folded brachial ridges, possibly resulting from the wide gape of these small dorsal valves so that the lophophore became more fully exposed to the surrounding sea (C. H. C. BRUNTON, personal communication, 2005).

Evolution of Coelom, Mantle Canal Systems, and Gonadal Repositories

[Alwyn Williams]

The shape and distribution of the coelom and its contents differ among living representatives of all three brachiopod subphyla. The coelom itself varies in the development of sinuses within the mantle; and, because such patterns are impressed by differential shell secretion on valve interiors, changes in the branching and functions of sinuses have been traced throughout the geological record. Muscles and gonads, being directly attached to the shell, have also left imprints on the interiors of fossil brachiopods. The main evolutionary changes affecting muscle systems have already been discussed in the context of valve movement and articulation. The implications of changes in gonadal imprints are considered here in relation to the development of coelomic sinus systems (mantle canals). Changes in the anatomy and disposition of the gut and the nervous and excretory systems, on the other hand, almost never leave any trace on the fossilized integument. Gut morphology can, to some extent, be inferred from the disposition of the valves relative to one another and to the pedicle. It has been considered in this context elsewhere in the chapter (see Fig. 1899–1900). No such inferences can be made about past nervous and excretory systems. Each, however, has undergone significant changes at the subphylum level, as reflected in living species, and will be briefly addressed here.

Distributional changes in the mantle canals and gonadal repositories in extinct and living brachiopods reflect the evolution of the body cavity relative to muscle and gonadal attachments and the folded epithelial mantles of both valves (Fig. 1906). Sinuses and canals (in up to four orders of branching) invade the connective tissue of the mantle of both brachiopod valves. The sinuses accommodate gonads while each canal branch is divided into two channels by a median ridge of ciliated epithelium, which circulates coelomic fluid in opposite directions throughout the mantles and their marginal setal follicles. Distributional changes in these canals and sinuses are complex in detail in extinct and living species. On the broad scale, however, they reflect the evolution of the body cavity and its mantle extensions relative to the disposition of muscle bases and gonads. Such changes are noteworthy as they suggest that a divergence in body cavity size occurred among stem-group brachiopods and has persisted, with thematic variation, to the present day.

The basic lingulate pattern (Fig. 1906), as impressed on the shells of earliest Cambrian lingulides and acrotretides, is typified by that of living discinoids. Within their relatively large body cavities, gonadal lamellae are attached to gastroparietal and ileoparietal bands or exceptionally lie free. Two primary mantle canals (*vascula lateralia*), controlled by muscular valves and emerging from submedial muscle fields, divide into arcuate, posterior, and anterior trunks. In the dorsal valve, an additional pair of canals emerges anteromedially from the muscle field (*vascula media*). This baculate canal system is more variable in acrotretides, with a stronger development of *vascula media* in Early Cambrian botsfordiids and repeated first-order branching of the *vascula lateralia* of both valves of later acrotretides (pinnate condition). The most dramatic change, however, was the suppression of the *vascula* *media* in the lingulids and their presumed sister group, the pseudolingulids (bifurcate condition).

The distribution and function of mantle canals in living craniids differ from the lingulate system in several respects (Fig. 1906). Adult craniids are without setae (a feature shared with the thecideides, the shells of which are also cemented). Accordingly, mantle distributaries do not exceed third-order branching and end well within the valve margins. Pairs of pinnate *vascula lateralia* and *vascula media* are the only canals developed in the ventral and dorsal valves respectively. There are six gonads: two in the main body cavity and one in each of the principal canals, which are not closed by muscular valves (WILLIAMS & others, 1997, p. 130). The gonads within the canals are supported on genital lamellae developing from the inner epithelium of the mantle.

The earliest (Lower Ordovician) craniides are the cemented *Petrocrania* and the free-lying *Pseudocrania*. The canal systems of the former are convergent with those of lingulids (bifurcate) in that both valves are characterized only by *vascula lateralia*. The key to the vagaries of the craniid canal systems, however, appears to be the pattern characteristic of *Pseudocrania*. In juvenile stages of growth, *Pseudocrania* (with *Orthisocrania*, the presumed sister group of cemented craniids) was attached to the substrate by a transient holdfast in a calcareous sheath. Its canal system was not only baculate but also extended to the shell margins, suggesting that setal follicles were present (see BASSETT, 2000, p. 169, fig. 93). The ensemble may be reminiscent of early lingulid patterns, but the pinnate divisions of the primary canals suggest that the canals contained palmate gonads as in living craniids.

Of the two other orders assigned to the craniiforms, the mantle canal systems of craniopsides are poorly known, while those of the trimerellides are quite variable with *vascula media* being more fully developed in the ventral mantle in some stocks and with bifurcate as well as baculate patterns characterizing others.

All crown-group rhynchonelliforms belong to the Rhynchonellata, with orthides, protorthides, and syntrophiidines well represented in the Cambrian (Fig. 1906). The development of a mantle system to operate articulating valves and the grouping of gonads within mantle sinuses resulted in a significant reduction of the body cavity and a complementary increase in the feeding region, the mantle cavity. This radical anatomical change is reflected in the mantle canal systems that, in the earliest stem-group species, typically consist of a pair of *vascula media* enclosing a pair of gonadal pouches in the ventral valve (saccate condition); and two pairs of primary canals, the *vascula media* and the *vascula myaria* (issuing from the posteromedian adductor field), and a pair of digitating gonads connecting with the posterolateral setal follicles of the dorsal valve (digitate condition). In penecontemporaneous syntrophiidines, the sister group of modern rhynchonellates (CARLSON & others, 2002, p. 922), the gonadal sacs within the ventral mantle were also digitate and the peripheral arcs of the *vascula media* proportionately reduced.

Variations of these basic canal systems characterize descendant rhynchonellates. The most divergent involved the transformation of digitate gonads into repositories of radiating canals that served all but the anteromedial arc of the valve margin (pinnate condition) or a pair of greatly enlarged gonadal sacs dominating a reticulate network of canals (lemniscate condition). The extent to which these patterns repeatedly developed, even within rhynchonellate families, is shown by the variation found in living rhynchonellides and terebratulides (see CARLSON, herein, Fig. 1907). The patterns in both valves of the rhynchonellides *Hemithiris* and *Notosaria* are respectively saccate and lemniscate (WILLIAMS & others, 1997, p. 75).

The saccate-digitate mantle canal systems of the apparent stem-group strophomenates, the Cambro-Ordovician billingsellides, are homologous with those of stem-group rhynchonelliforms (Fig. 1906). Moreover,

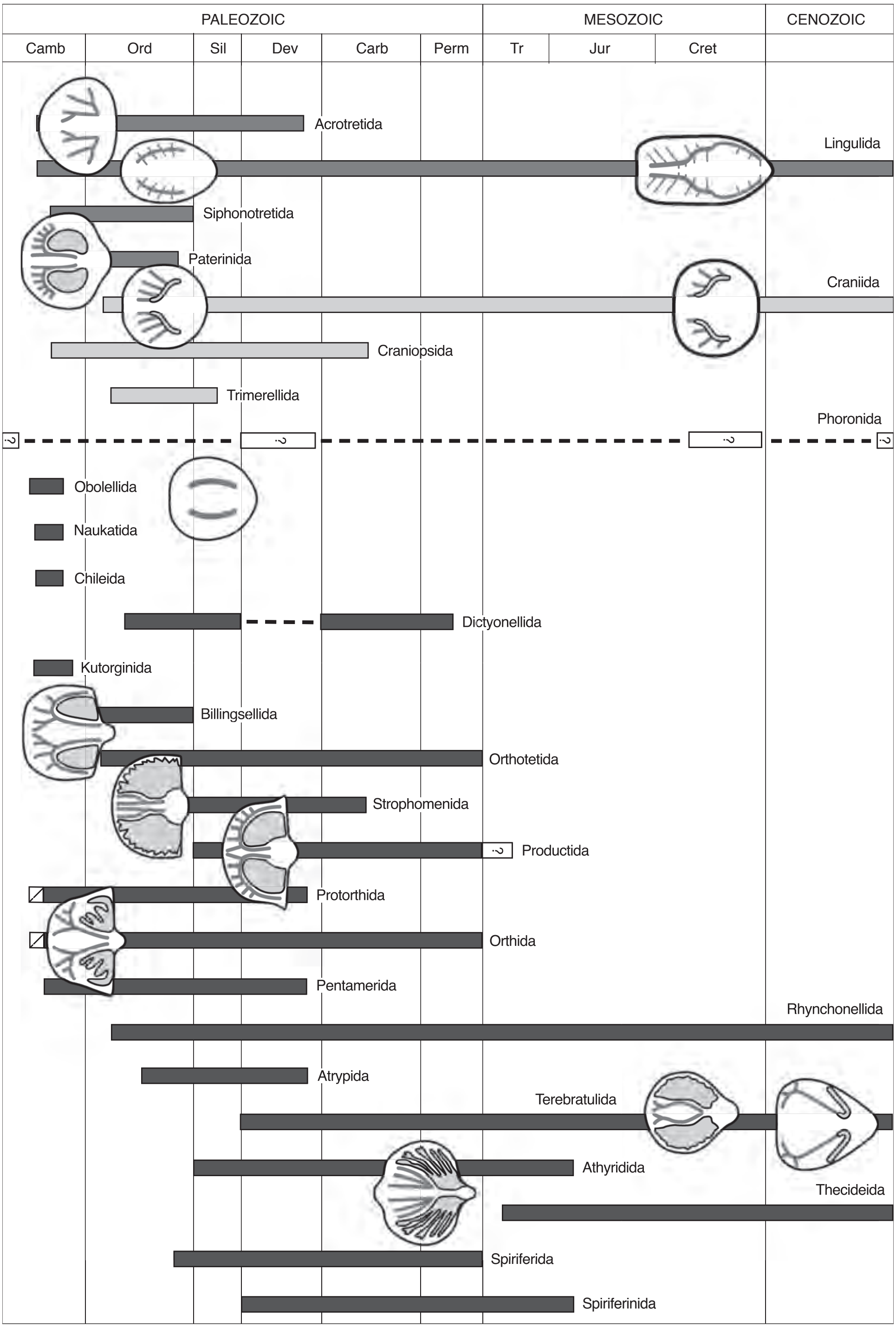

FIG. 1906. Ventral mantle canal and gonadal repository patterns characterizing selected ordinal groups of brachiopods throughout their evolution (new).

during strophomenate evolution, not only is the billingsellide pattern retained (*Leptaena*) but also homoplastic versions of lemniscate (*Strophomena*) and incipient pinnate (*Palaeostrophomena*) patterns developed in many lineages.

The most surprising apparent homology, however, involves the paterinates, which have a saccate canal system at least in the ventral valve (Fig. 1906) and probably in the dorsal valve as well (Williams, Popov, & Holmer, 1998, p. 258; Laurie, 2000, p. 149). In effect, the anatomy of the paterinates is rhynchonelliform despite their linguliform organophosphatic shell.

The mantle canal systems of the remaining rhynchonelliform classes (Fig. 1906) are more like those of derived lingulates than stem-group rhynchonellates or strophomenates. The mantle canal systems of obolellates are baculate, while the absence of gonadal imprints is consistent with the forward disposition of the muscle bases. The canal imprints of chileates are pinnate, but there is no evidence that the canals contained gonads, which is unlikely as the muscle fields of both valves would have to have been housed in a large body cavity. The kutorginate mantle canal system is also pinnate, but unlike the chileates, clearly defined muscle scars have yet to be described and the absence of gonadal extensions into canals is less certain.

EVOLUTION OF EXCRETORY (AND GONODUCT) AND NERVOUS SYSTEMS

[Alwyn Williams]

Apart from very rare nerve imprints on shell interiors, no decipherable traces of the excretory or nervous systems have yet been found in fossil brachiopods. They are briefly considered here, however, because their differentiation in living species has a bearing on brachiopod phylogeny.

All living brachiopods, except for most rhynchonellides, have one pair of metanephridia. In the rhynchonellide *Notosaria*, a second, smaller pair does not develop until the animal is at least 2.5 mm long (Percival, 1960, p. 453). In the micromorphic cryptoporids, however, with adult shells of all three assigned genera varying from 2.4 mm to 4.6 mm in length (Manceñido & others, 2002, p. 1243–1245), only the larger pair develops (Helmcke, 1940; confirmed by C. Lüter, personal communication, 2002; Lüter, herein, p. 2321). The cryptoporids are doubtfully included in the Dimerelloidea ranging back to the Upper Devonian. Living pugnacoids (in the family Basiliolidae) have two pairs of metanephridia; the superfamily extends back to the Lower Devonian.

The presence of a single pair of metanephridia in linguiforms, craniiforms, and most rhynchonelliforms is most likely a shared and primitive condition for all brachiopods, with two pairs of metanephridia evolving only within the rhynchonellides, for an as yet unknown reason. The absence of the second pair of metanephridia in cryptoporids could reflect a paedomorphic loss or some other kind of later, heterochronic transformation (C. Lüter, personal communication, 2002).

Nerve distributaries can vary greatly in detail; the prime zones of sensitivity in the brachiopod include the mantle margins, muscle fields, and pedicle. The only imprints to have been unequivocally identified in fossils, however, are those of the paired pedicle nerves found in the ventral valves of acrotretides as well as lingulides. The main concentration of nerve tissue occurs around the esophagus of all living species studied, where a relatively large subenteric ganglion is responsible especially for the innervation of the mantles, adductor muscles, and pedicles. In rhynchonelliforms, a supraenteric ganglion is also developed and is the principal source of lophophore innervation. In linguliforms and craniiforms, the supraenteric ganglion is absent, being functionally replaced by a circumenteric ring; the craniiform ganglion is divided into two masses. These differences appear not to have been accompanied by any significant changes in the patterns or sources of innervation.

RECENT RESEARCH ON BRACHIOPOD EVOLUTION

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INTRODUCTION

Several issues in brachiopod evolutionary history have become the focus of rather intense scrutiny in the past few years. These issues appear to have become more complicated and more interesting with the discovery of many new fossils and the generation of new data from extant brachiopods. I discuss below five different phylogenetic issues relevant to brachiopod origins and evolution, the evidence presented to support them, and the different perspectives on each that have been raised: (1) relationship of brachiopods and phoronids; (2) relationship of craniiform brachiopods to other brachiopods; (3) relationship of thecideide brachiopods to other brachiopods; (4) relationship of brachiopods to the Tommotian fauna; and (5) relationships among all brachiopods. Against the backdrop of these various evolutionary perspectives, character homology and polarity for each of the character complexes can be evaluated.

All interpretations of the evolution of character complexes and evolutionary trends among brachiopods depend fundamentally on our current understanding of phylogenetic relationships among brachiopod taxa (Carlson, 1995; Holmer & others, 1995; Holmer & Popov, 1996; Williams & others, 1996; Cohen & Gawthrop, 1997; Cohen, 2000; Carlson & Leighton, 2001; Holmer, 2001; Holmer, Skovsted, & Williams, 2002; Williams & Holmer, 2002; Cohen & Weydmann, 2005). In very few cases are these various phylogenetic hypotheses, in part or in whole, fully corroborated and unanimously agreed upon, so differences of opinion necessarily exist. In an attempt to provide a balanced and comprehensive account of character evolution in the brachiopods, I present alternative interpretations that are consistent with existing phylogenetic hypotheses, fully realizing that these interpretations will themselves evolve as new evidence from fossil and Recent brachiopods comes to light.

In order to discuss the evolution of character complexes, hypotheses of character polarity (determining which character states came first and which came later in evolution) must be developed, and some criteria for determining polarity adopted (see also Carlson, 1999). Issues of polarity determination play a particularly fundamental role in shaping our understanding of brachiopod evolution. Character transformation can be polarized by several different methods, none of which is without problems. Outgroup criteria has become the most common method used in most cladistic analyses and relies upon a comparison of the ingroup (in this case, brachiopods) with character states present in the closest relative (sister group); those characters shared between the ingroup and outgroup are more general and thus considered to be shared due to common ancestry (i.e., primitive in the ingroup). The problem with this approach in the study of brachiopod phylogeny is the uncertainty that persists with regard to the identity of the brachiopod sister group. Much anatomical data suggests that other lophophorates, or possibly some deuterostome taxa, are likely sister groups (Emig, 1984; Carlson, 1995; Nielsen, Scharff, & Eibye-Jacobsen, 1996; Lüter & Bartolomaeus, 1997; Lüter, 2000a; Sorenson & others, 2000; Nielsen, 2001). The preponderance of molecular systematic data now argues strongly in favor of protostomes, namely mollusks (Fig. 1907; Cohen & Gawthrop, 1997; Cohen, 2000; Cohen & Weydmann, 2005) or other Eutrochozoa (Valentine, 2004) as the brachiopod sister group. Too few comprehensive morphological studies have been completed at this date to be able to evaluate

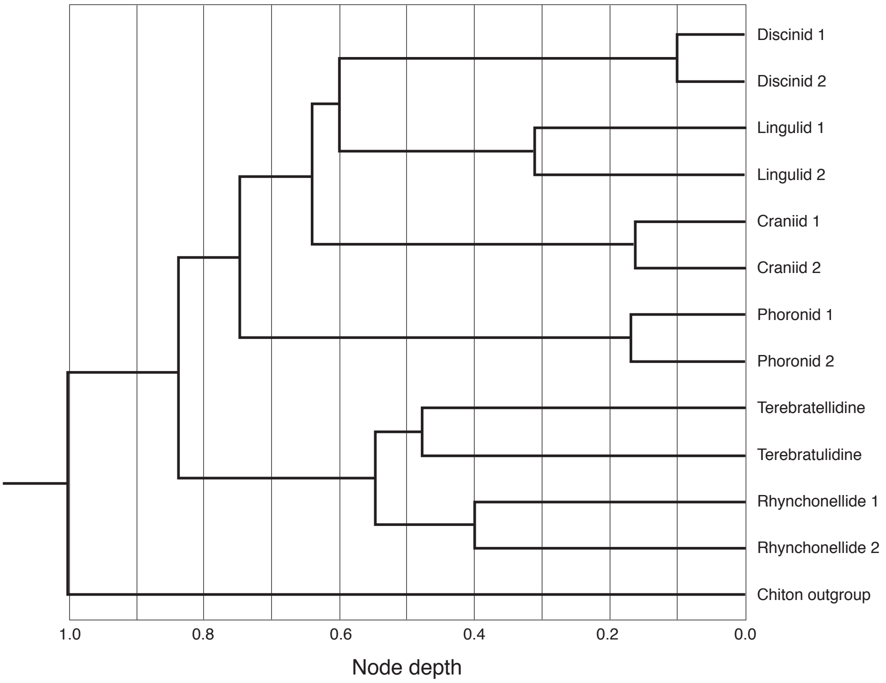

FIG. 1907. Phoronid and brachiopod phylogeny, generated from maximum likelihood (*ML*) heuristic search and bootstrap analysis of 3275 sites of concatenated SSU + LSU alignment. Nonparametric rate smoothing method used to rate-smooth ML chronogram shown; branch lengths proportional to node depth (adapted from Cohen & Weydmann, 2005).

morphological character transformation in brachiopods in detail, with respect to chitons (see VINTHER & NIELSEN, 2005) and other mollusks, rather than other lophophorates and deuterostomes. Because these molecular data have forced a rather fundamental shift in our perspective on brachiopod evolution, this is an exciting, if somewhat unsettled, time to be studying brachiopod evolution.

Apart from outgroup methods, another criterion for polarity determination available to paleontology is relative stratigraphic position (the traditional paleontological approach). Rather than comparing presumed closest relatives, comparisons can be made between the relative appearance of characters in the stratigraphic column; those features appearing earlier (lower) in the fossil record are more likely to be primitive, or general, than those appearing later (higher). As more brachiopod fossils are collected lower in the stratigraphic record, distinctions in relative stratigraphic order that have been made previously on the basis of smaller samples become less distinct, and one could argue that relative stratigraphic position is becoming less and less useful as a polarity criterion for evolutionary events in the critically important Early Cambrian. So much mineralogical and morphological diversity appears within Lower Cambrian strata, a period of perhaps 25 million years only, occurring over 500 million years ago, that it has become increasingly difficult to use relative stratigraphic position as a criterion for polarity determination of features among all brachiopods. Within Brachiopoda, however, stratigraphic data can play an increasingly significant role, in addition to morphological and molecular data, in evaluating hypotheses of phylogenetic relationships (CARLSON & LEIGHTON, 2001).

Ontogenetic transformations (FREEMAN & LUNDELIUS, 1999, 2005; FREEMAN, 2000, 2001), based on our current understanding of the living forms, can also provide an axis for determining polarity of character transformation. Features appearing earlier in ontogeny are considered more general (primitive) and those appearing later more specific (derived) (following NELSON, 1978). Because fewer than 5% of brachiopods are extant, ontogeny cannot provide a detailed determination of polarity for all taxa, but it does appear that early embryogenesis is quite different in living linguliforms, craniiforms, and rhynchonelliforms (NIELSEN, 1991; FREEMAN & LUNDELIUS, 1999, 2005; FREEMAN, 2000, 2001; see FREEMAN, 2003, for a more complete discussion of features in early development), providing additional support for the existence of three separate clades designated as the three brachiopod subphyla. Without an independent criterion of polarity, however, it is difficult to determine whether the characters that appear to be shared (homologous) by any two of these groups are shared and apomorphic (derived; see POPOV & others, 1993; WILLIAMS, CARLSON, & BRUNTON, 2000), shared and plesiomorphic (basal or primitive; CARLSON, 1995; COHEN, 2000; COHEN & WEYDMANN, 2005), or nonhomologous similarities, having arisen independently in different groups (FREEMAN, 2001; FREEMAN & LUNDELIUS, 2005). Fortunately, an approach combining both stratigraphic and ontogenetic polarity criteria is revealing, for example, the independent origination of lecithotrophic larvae among brachiopods and provides strong support for the rejection of lecithotrophy as a shared derived (or shared primitive) character uniting craniiforms and rhynchonelliforms (FREEMAN & LUNDELIUS, 2005).

Finally, the use of parsimony as a criterion for choosing among multiple hypotheses of phylogenetic relationship has come under increasing scrutiny recently (see FELSENSTEIN, 2004). Likelihood methods hold greater promise in their potential to provide a statistical assessment of the likelihood of particular topologies rather than merely choosing the shortest topology given the data in hand. Unfortunately, likelihood methods developed thus far lend themselves much more easily to molecular sequence data than to morphological data (although see WAGNER, 1998; LEWIS, 2001). Results obtained using parsimony analyses should therefore be considered, as always, as testable hypotheses that must be tested empirically, rather than as statements of fact about phylogenetic relationships.

RELATIONSHIP OF PHORONIDS AND BRACHIOPODS

The traditional view of brachiopod relationships has considered phoronids as the most likely sister group to brachiopods (EMIG, 1977, 1984; BRUSCA & BRUSCA, 1990, 2003; WILLMER, 1990; CARLSON, 1995; WILLIAMS & others, 1996; WILLIAMS, CARLSON, & BRUNTON, 2000; NIELSEN, 2001). Phoronids clearly share many developmental and anatomical features with brachiopods, with the major difference between them being the presence of two mineralized valves in brachiopods, which are commonly assumed to have evolved after divergence from a common shell-less ancestor with phoronids. Another significant difference is in the configuration of the gut in adults, which curves ventrally in brachiopods and dorsally in phoronids (NIELSEN, 1991).

Compelling evidence in the form of DNA sequence data is mounting (COHEN, 2000; COHEN & WEYDMANN, 2005) that suggests that phoronids are nested within brachiopods (Fig. 1907–1908), as a derived shell-less clade, rather than being the likely brachiopod sister group (WILLIAMS & others, 1996; WILLIAMS, CARLSON, & BRUNTON, 2000). If phoronids are actually shell-less brachiopods, rather than the brachiopod sister group, our understanding of brachiopod character evolution, as well as monophyly, will require adjustment. It is possible that differences in curvature of the gut in the two groups would preclude the derivation of one from the other (C. NIELSEN, personal communication, 2005). Several scenarios consistent with the topology in Figure 1907 appear equally likely at this time. Mineralized valves might have been lost secondarily in phoronids relative to a shelled common ancestor shared with brachiopods, thus brachiopods retained shells primitively. If the common ancestor was shell-less, then shells originated in brachiopods secondarily, and the absence of a mineralized shell in phoronids could be a primitive condition retained from the common ancestor. Also, brachiopods may have acquired shells twice (once in linguliforms and craniiforms as a clade, and once in rhynchonelliforms as a clade) from a shell-less common ancestor. If the topology illustrated in Figure 1907 cannot be rejected as additional evidence is gathered, the most parsimonious interpretation suggests that a calcareous mineralized skeleton is primitive, shared with the chiton (molluscan) sister group, with shell loss occurring in phoronids, and evolutionary mineralogical transformation (or loss and then gain) of a phosphatic shell occurring in the linguliform brachiopods.

Recent molecular results (Fig. 1907; COHEN & WEYDMANN, 2005) unambiguously place phoronids as a sister group to the craniiform + linguliform clade. If phoronids are simply pruned from this cladogram, brachiopod relationships have the same topology as earlier results using morphological characters to investigate relationships among the major groups of extant brachiopods (CARLSON, 1995). If phoronids are not the sister group to brachiopods, other candidates must be sought; continuing uncertainty in identifying the brachiopod sister group makes it difficult to determine the polarity of character transformation of shells and shell features in brachiopods and remains a necessary and intriguing field of inquiry. COHEN and WEYDMANN (2005) presented molecular evidence that argues in favor of chitons and against annelids as the extant sister group to brachiopods, as CONWAY MORRIS and PEEL (1995) suggest. CONWAY MORRIS and PEEL (1995) rejected a close relationship of halkieriids to chitons, but this position should certainly be reexamined in light of the new molecular evidence (COHEN & WEYDMANN, 2005) and morphological analyses of halkieriids (VINTHER & NIELSEN, 2005).

Similarities in the fate maps and mode of gastrulation between extant phoronids and rhynchonelliforms (G. FREEMAN, personal communication, 2004) provide embryological support (as shared primitive features) for the topology in Figure 1907, in which phoronids are the most basal of the three nonrhynchonelliform groups. Phoronids possess planktotrophic (feeding) larvae, a characteristic they share with linguliforms, basal (but not Recent) craniiforms (see section below; FREEMAN & LUNDELIUS, 1999), and basal (but not Recent) rhynchonelliforms (Fig. 1908; FREEMAN & LUNDELIUS, 2005). Similarities in the relative position of the mouth (anterior) and anus (posterior) in the larvae of brachiopods and phoronids suggest a common larval body plan (see WILLIAMS and CARLSON, herein, Fig. 1895) but do not speak directly to the relative position of phoronids as a brachiopod sister group or as part of the brachiopod ingroup clade. Differences in gut curvature are significant, however, and suggest that two different developmental pathways have been chosen by phoronids and brachiopods (C. NIELSEN, personal communication, 2005).

Lacking a mineralized skeleton, the assignment of fossils to the phoronids is necessarily quite tentative. Phoronid fossils may first appear as early as the Early Cambrian (Atdabanian, lowermost Botomian) in the Chengjiang fauna as *Iotuba* (CHEN & ZHOU, 1997; HOU & others, 2004). It is less than clear that this fossil is actually a phoronid (see COHEN & WEYDMANN, 2005, table 2). The next possible fossil occurrences are vertical burrows (*Skolithos*) in the Devonian (FENTON & FENTON, 1924; MACKINNON & BIERNAT, 1970) attributed to phoronids, but this assignment is extremely tentative, as is

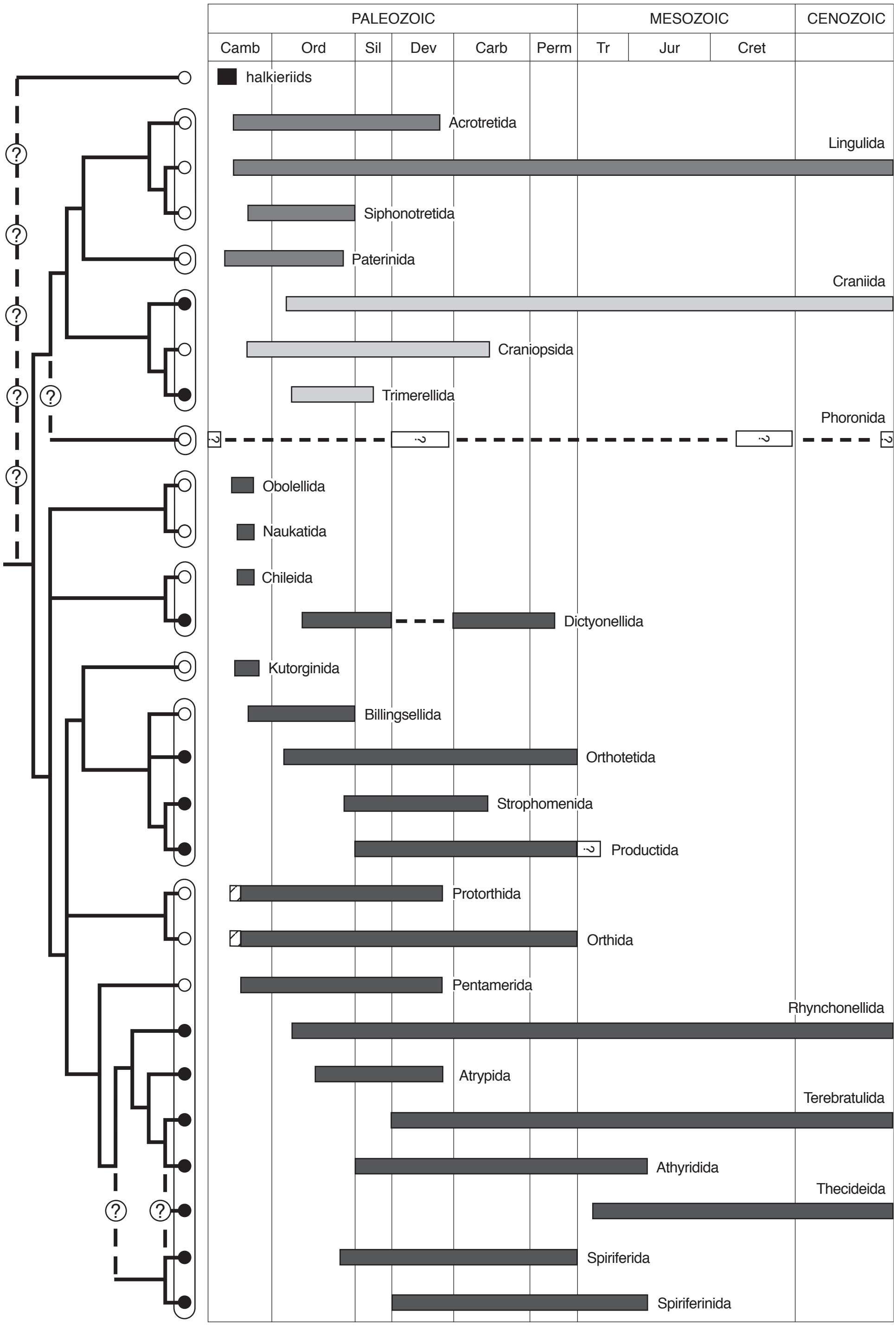

FIG. 1908. *For explanation, see facing page.*

a Cretaceous boring attributed to phoronids (Joysey, 1959).

RELATIONSHIP OF CRANIIFORMEA TO OTHER BRACHIOPODS

As reflected in the 1965 *Treatise* classification of brachiopods (Williams & Rowell, 1965d; also Rowell, 1981a, 1981b, 1982), craniides have traditionally been considered to be more closely related to the other inarticulated brachiopods than to the articulated brachiopods, largely on the basis of a lack of valve-to-valve articulation, although many other characters, both morphological (Carlson, 1995) and molecular (Cohen, 2000; Cohen & Weydmann, 2005), support the hypothesis as well. Following this phylogenetic hypothesis (Fig. 1907–1908), Recent craniiform characters shared with Recent rhynchonelliforms may be either homologous and plesiomorphic (for example, Carlson, 1995; Lüter, 2001b) or nonhomologous (or example, Freeman & Lundelius, 1999, 2005).

Challenges have been raised against the hypothesis that craniiforms are more closely related to linguliforms than to rhynchonelliforms (Gorjansky & Popov, 1985; Holmer, 1991; Nielsen, 1991; Popov, 1992; Popov & others, 1993; Lüter, 2001b; Williams & Holmer, 2002). Craniides have been proposed as the sister group to rhynchonelliforms, and characters they share with rhynchonelliforms are considered to be synapomorphies. Lack of articulation has been argued to be a primitive character (Holmer, 1991; Popov & others, 1993) and therefore cannot be used to diagnose the inarticulates as a clade.

Extant craniiform and rhynchonelliform brachiopods both have lecithotrophic (nonfeeding) larvae that remain in the plankton only a short while before settlement (Nielsen, 1991; Lüter, 2001b). Partly on this basis, Nielsen (1991) suggested that craniides and articulates are likely to be sister taxa. Lüter (2001b) argued, also on this basis, that lecithotrophy is more likely to be a shared and primitive condition for all brachiopods. Freeman and Lundelius (1999), however, argued persuasively that Paleozoic craniiforms possessed planktotrophic larvae. Examining hundreds of fossil brachiopods, they measured the width of the protegulum, mineralized during the embryonic or larval stages of growth; larger valve size is indicative of a planktotrophic larval life history. Lower Paleozoic craniopsides possess a larval shell most likely mineralized during a longer-term planktotrophic larval stage. In a later study, Freeman and Lundelius (2005) argued that Paleozoic rhynchonelliforms also possessed planktotrophic larvae. These studies provide strong support for the hypothesis that planktotrophy (present today in extant linguliforms and phoronids) represents the evolutionarily primitive condition for the brachiopods. Lecithotrophy in extant craniiforms and rhynchonelliforms has evolved independently twice from planktotrophic ancestors. Therefore, lecithotrophy is not an evolutionarily shared (homologous)

Fig. 1908. Stratigraphic ranges and consensus cladogram illustrating one hypothesis of phylogenetic relationship among the 26 orders of brachiopods currently recognized, and phoronids, constructed from data derived primarily from analyses of Cohen and Weydmann (2005) and Cohen (herein, p. 2356) using molecular sequence data from living brachiopods and phoronids; Williams, Carlson, and Brunton (2000), Holmer and Popov (2000), and Popov, Bassett, and Holmer (2000) using morphological data from mostly Cambrian and Ordovician taxa; Carlson (1995) using morphological data from Recent brachiopods; and Carlson and Leighton (2001) using morphological and stratigraphic data together for all rhynchonelliform suborders. *Dark shading* of stratigraphic ranges indicates rhynchonelliforms, *medium shading* linguliforms, and *lightest shading* craniiforms; *open circles* immediately below stratigraphic ranges indicate those orders first appearing in the Cambrian, *closed circles* those first appearing in the post-Cambrian; *elongated ellipses* surrounding circles identify the 8 classes and phoronides; *encircled question marks* indicate uncertainties in topology discussed in text (new).

character and cannot be used to argue for a sister-group relationship between craniides and rhynchonelliforms.

The presence of a calcareous shell is likely to be homologous in craniiforms and rhynchonelliforms but could be either symplesiomorphic (shared and primitive) or synapomorphic (shared and derived). The assumption of synapomorphy led WILLIAMS and HOLMER (2002) to conclude that the craniiforms "diverged from one of the early rhynchonelliform stocks" (p. 871) as a sister clade to Linguliformea + Phoroniformea (see WILLIAMS and CARLSON, herein, Fig. 1896). They suggested that the craniiform "body plan has not changed much since the early Cambrian" (p. 870), yet they somewhat paradoxically claimed that the "craniiforms are the most derived brachiopod group" (p. 871) on the basis of their calcitic shell and differences apparent in development and organization relative to other extant brachiopods. Adult *Novocrania* have a body plan that is quite similar to the larval body plan of linguliforms and phoroniforms (see WILLIAMS and CARLSON, herein, Fig. 1895; NIELSEN, 1991), having a posterior anus and anterior mouth, suggesting that these similarities are more likely to be shared and primitive rather than uniquely derived.

The relative position of the mouth and anus in the larvae of brachiopods and phoronids is similar: posterior anus and anterior mouth (originating from the blastopore in phoronids and linguliforms and from the site of the blastopore in rhynchonelliforms, but only after the blastopore closes completely; LONG, 1964; NIELSEN, 1991) (see WILLIAMS and CARLSON, herein, Fig. 1895). In adults of these taxa, however, differences emerge (NIELSEN, 1991, see also COHEN, HOLMER, & LÜTER, 2003). In craniiforms, the gut does not curve or fold, and the anus remains medioposterior and mouth anterior in both larvae and adult; this straight gut has been considered to be the more primitive condition among metazoans (HYMAN, 1959; CARLSON, 1995). In phoronids, the gut curves into a U-shape and the anus becomes anterodorsal. In linguliforms, the gut curves into a U-shape and the anus becomes right lateral or ventrolateral. In rhynchonelliforms, the gut curves somewhat into a C-shape and the (blind) anus becomes posteroventral in position.

NIELSEN (1991) proposed an intriguing hypothesis regarding body plan evolution in brachiopods (Fig. 1909), which has since come to be known as the brachiopod fold hypothesis (HOLMER, SKOVSTED, & WILLIAMS, 2002; WILLIAMS & HOLMER, 2002; COHEN, HOLMER, & LÜTER, 2003). CONWAY MORRIS and PEEL (1995) adopted this perspective in suggesting the evolution of brachiopods from halkieriids. The fold hypothesis proposes that the anterior-posterior body axis is folded transversely during ontogeny, so that valves now considered to be dorsal and ventral should more accurately be described as dorsal anterior and dorsal posterior. This folding better explains the bilateral symmetry of each of the two valves in brachiopods (COHEN, HOLMER, & LÜTER, 2003) and is consistent with the observation of YATSU (1902) that a single circular embryonic shell in *Lingula* later divides to form a dorsal and ventral valve. Craniiform brachiopods appear to conflict with this hypothesis, however, in that their bodies do not fold during ontogeny (FREEMAN, 2001). According to NIELSEN (1991, fig. 3), *Crania (Novocrania)* larvae develop four coelomic sacs (C1, C2, C3, C4), arranged anteroposteriorly (Fig. 1909). At a later stage in development, coelomic sacs C1 and C4 "curled up ventrally" (NIELSEN, 1991, fig. 3 caption) and came to occupy a position below C2 and C3, respectively. One valve mineralized on the dorsal side of C2 and C3, after C1 and C4 migrated ventrally; this valve is currently considered to be the dorsal valve. At a later time, C1 and C4 can no longer be recognized in older larvae, and a second valve is mineralized topologically ventral to C2 and C3, but on the larval dorsal surface of these coelomic sacs. If this accurately represents the temporal series of events in *Novocrania* ontogeny, then the two valves currently considered to be dorsal and ventral in orientation appear to be topologically dorsal and ventral, yet developmentally dorsal anterior and dorsal posterior. Interestingly, however, the timing of formation of the valves is not coordinated—the dorsal valve forms first. It has been suggested that the dorsal and ventral mantles in strophomenates may also have developed at separate times, but that the ventral mantle (and thus valve) formed first; in rhynchonellates, dorsal and ventral mantle formation appears to be coordinated (Freeman & Lundelius, 2005). Depending on the phylogenetic position of craniiforms and the phylogenetic interpretation of body orientation, the never-folded craniiform body plan could represent either the primitive condition for brachiopods (Carlson, 1995) or a uniquely derived condition within brachiopods (Williams & Holmer, 2002).

Craniiforms lack a pedicle throughout ontogeny, which may represent the primitive condition for brachiopods, a condition shared with phoronids. If so, the pedicles of linguliforms (which are coelomate, muscular, and develop from the inner epithelium as an evagination of the ventral body wall) and rhynchonelliforms (which are not coelomate, not muscular, and develop from the larval pedicle lobe, not from the ventral body wall) are clearly not homologous (Carlson, 1995). The absence of a pedicle in thecideides certainly represents a secondary loss, relative to the ancestral pediculate condition.

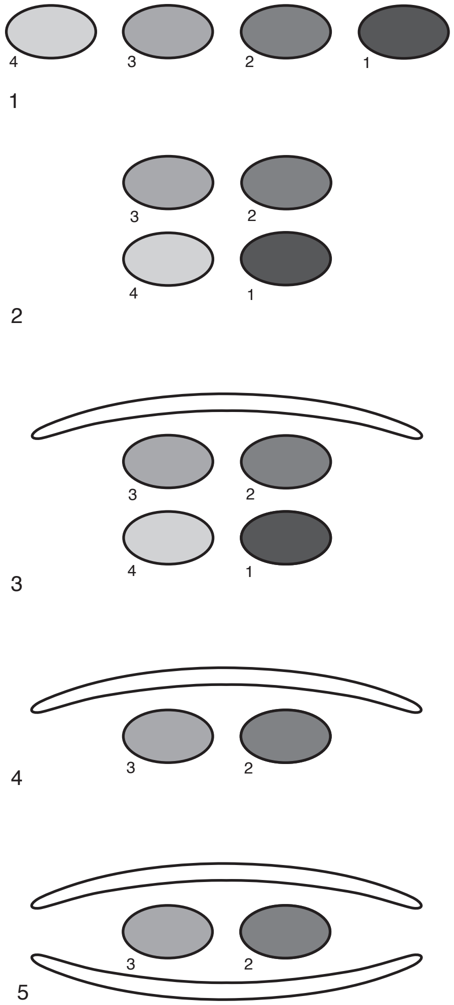

Fig. 1909. Reconstructions of developmental stages of *Novocrania* (adapted from Nielsen, 1991). *Shaded ellipses* represent paired coelomic sacs, numbered from anterior to posterior: *1,* arranged linearly; *2,* later ventral migration of first and fourth pairs of coelomic sacs; *3,* dorsal valve forms; *4,* first and fourth pairs of coelomic sacs can no longer be recognized; *5,* ventral valve forms, after dorsal valve (new).

RELATIONSHIP OF THECIDEIDA TO OTHER BRACHIOPODS

The relationship of thecideides to all other brachiopods has been fraught with controversy for decades; the first *Treatise* named them as a suborder in order Uncertain (Elliott, 1965). Thecideides have very small body sizes as adults, lack pedicles and live cemented to a hard substrate, possess brachial ridges on the dorsal valve interior to support the ptycholophous lophophore, have a strophic hinge line and cyrtomatodont dentition, columnar muscles, and a punctate shell with reduced secondary layer in many species.

Earlier claims (Elliott, 1948) of strophomenide ancestry were abandoned when it was determined (ELLIOTT, 1953; WILLIAMS, 1955) that the shell structure of thecideides was punctate, not pseudopunctate. WILLIAMS (1973) suggested that thecideides might be paedomorphic descendants of the terebratulides (also punctate); preliminary molecular systematic studies appeared to support this hypothesis (COHEN & GAWTHROP, 1997; COHEN & others, 1998) but have since been rejected (COHEN, 2001a). The extensive and meticulous studies of thecideide shell structure and morphology by BAKER (1983, 1984, 1990, 1991) argued convincingly instead for descent from impunctate spiriferides on the basis of a hypothesis of homology of thecideide tubercles with spiriferide denticles; endopunctae thus appear to be homoplastic in these taxa. More recently, however, it has been suggested (BAKER, 2006) that the cytological similarities in the endopunctae of thecideides, terebratulides, and some spire-bearers are too great to be attributed to homoplasy (supported, albeit ambiguously, by the analyses of CARLSON & LEIGHTON, 2001; see also Fig. 1908, 1911).

Spire-bearing *Thecospira* is considered to be the most primitive thecideide (BAKER, 1990; JAECKS & CARLSON, 2001), lending additional support to the hypothesis of spire-bearing ancestry and suggesting that brachial ridges evolved twice independently in strophomenates and more derived thecideides. But which spire-bearers are the thecideide sister group? BRUNTON (1972) and BRUNTON and MACKINNON (1972) argued for a close phylogenetic relationship between *Thecospira* and the koninckinoids (now a suborder in Athyridida; ALVAREZ & RONG, 2002; MACKINNON, 2002), suggesting that thecideides and athyridides may be more closely related than thecideides and spiriferides, a hypothesis supported by analyses of morphology and relative stratigraphic position by CARLSON and LEIGHTON (2001).

In a phylogenetic analysis of morphology, JAECKS (2001) demonstrated that the differences in topology of thecideide relationships polarized by strophomenate and spiriferide outgroups were surprisingly minor, underscoring the combination of strophomenate and spiriferide characters possessed by thecideides. Distinguishing homoplastic from homologous characters, and determining their polarity, will eventually help resolve the question of thecideide ancestry, as will obtaining robust molecular sequence data and reconstructing ontogenetic patterns of shell morphology and shell structure in a broader range of thecideides and other derived rhynchonellate brachiopods.

Molecular sequence data have not yet been as helpful as might be desired in locating the thecideides among the other extant brachiopods. Thecideides are not present in the topology illustrated in Figure 1907 (COHEN & WEYDMANN, 2005). COHEN (herein, p. 2356) considered thecideides as the sister group to the terebratulides, with rhynchonellides a sister group to both thecideides and terebratulides together. If koninckinides are the sister group to thecideides (BRUNTON, 1972; BRUNTON & MACKINNON, 1972) and koninckinides are athyridides (MACKINNON, 2002), this topology is consistent with morphological data from these extinct taxa. The branches connecting thecideides to the terebratulides (COHEN, herein, p. 2356) are very long, however, raising suspicions about the topology (see FELSENSTEIN, 2004); further analyses (molecular, embryological, and developmental, in particular) of more taxa must be completed in order to test this hypothesis of relationships. Abundant morphological data supports thecideides as the sister group to terebratulides + rhynchonellides (CARLSON, 1995), which is at least consistent with thecideides being more closely related to the extinct strophic spire-bearers (spiriferides; BAKER, 1990, 1991, 2006). The trustworthiness of characters supporting this topology is not entirely clear, however; juvenilized thecideide characters might obscure the true pattern of relationships, forcing them down artificially into the most basal position in the topology of all extant brachiopods.

RELATIONSHIP OF BRACHIOPODS TO THE TOMMOTIAN (AND ATDABANIAN) FAUNA

The earliest brachiopods to appear in the Lower Cambrian are diverse mineralogically and morphologically, yet they can be easily recognized as brachiopods. This suggests that the common ancestor of brachiopods may have evolved earlier than the Early Cambrian, leaving no obvious Precambrian fossil record, which is not surprising. This possibility has led to a search for a brachiopod sister group among Lower Cambrian fossils that are less obviously brachiopod-like in their overall morphology but may share certain morphological characters with them because of descent from a common ancestor. A potentially rich source of characters is revealed in the diverse small shelly fossils of the Tommotian and raises numerous issues of character homology and polarity. Some of these are discussed below with reference to particular taxa and particular character complexes.

SIGNIFICANT FOSSIL GROUPS

Halkieriids

CONWAY MORRIS and PEEL (1995) were the first to discuss in any detail the possibility that brachiopods evolved from one group of the (broadly paraphyletic) halkieriids (see also CONWAY MORRIS & PEEL, 1990; YOCHELSON, 1993; HOLMER, SKOVSTED, & WILLIAMS, 2002; WILLIAMS & HOLMER, 2002; COHEN, HOLMER, & LÜTER, 2003). Halkieriids are a curious group of fossils, known from the Nemakit-Daldynian to Atdabanian, with a stratigraphic range extending into Middle Cambrian sedimentary rocks (PORTER, 2004). Discovery of articulated specimens of Atdabanian halkieriids from Greenland (CONWAY MORRIS & PEEL, 1995) establish the spatial relationships of the skeletal elements to one another on the body of *Halkieria evangelista*. Four different elements are known per organism: two shells (one anterior and one posterior) and three different types of sclerities (siculates, cultrates, palmates), each with many elements. The anterior and posterior shells of halkieriids were proposed as homologues of the dorsal and ventral shells, respectively, of brachiopods (CONWAY MORRIS & PEEL, 1995); an evolutionary transformation involving the juxtaposition of the two shells along their median edges and folding of the body axis along this line (see also NIELSEN, 1991; COHEN, HOLMER, & LÜTER, 2003) has been proposed to account for the evolution of brachiopods from halkieriids (see Fig. 1908; see also WILLIAMS and CARLSON, herein, Fig. 1903).

A recent paper by VINTHER and NIELSEN (2005, p. 86–87) asserted that "a comparison of the morphological characters of *Halkieria*, molluscs, brachiopods, and annelids unequivocally supports the interpretation of *Halkieria* as a crown group mollusc" (p. 86) and that "no characters indicate a sister-group relationship" (p. 87) with brachiopods (WILLIAMS & HOLMER, 2002) or annelids (ENDO, 2001). Their argument is based on characters that "are compatible with characters in living molluscs" (p. 81), although no rigorous analysis of the homology or polarity of these characters is presented. VINTHER and NIELSEN argued that halkieriids are likely to be calcareous (following BENGTSON & MISSARZHEVSKY, 1981; BENGTSON & CONWAY MORRIS, 1984; BENGTSON & others, 1990) on the basis of their mode of preservation in the Sirius Passet fauna. In other fossil deposits, mollusks and other calcareous organisms are often preserved as steinkerns of secondary phosphates, while inarticulated brachiopods and tommotiids are preserved with primary mineralogy and ultrastructure. It is not clear, however, that originally mineralized organisms exist as fossils in the Sirius Passet fauna (which includes arthropods, sponges, a palaeoscolecidan, polychaete annelids, and halkieriids: CONWAY MORRIS & PEEL, 1995); certainly none that are unequivocally phosphatic have been found.

Micrina

Micrina and *Tannuolina* together make up the Tannuolinidae, one of four families in the order Tommotiida (Missarzhevsky, 1970 as emended by Landing, 1984) or one of two families in the order Mitrosagophora (Bengtson, 1970). They are found in the Tommotian and Atdabanian, possibly extend into the early Botomian, and consist of two phosphatic elements or sclerites (Laurie, 1986; Holmer, Skovsted, & Williams, 2002; Williams & Holmer, 2002; Cohen, Holmer, & Lüter, 2003; Li & Xiao, 2004) that look superficially similar to brachiopod valves. It is not clear if an individual organism consists of only one of each of these two elements or if other elements or multiples of each element also occur. No articulated *Micrina* individuals have been found, only partially articulated individuals of *Tannuolina* that have been argued to be closely related to *Micrina* (Li & Xiao, 2002, 2004). Are *Micrina* sclerites homologous with brachiopod valves or not?

Controversy exists regarding the status of *Micrina* (and *Tannuolina*) as halkieriids, and their status as possible close relatives to brachiopods. One possibility is that *Micrina* is a halkieriid (based on the similarity in shape of *Micrina* sclerites and halkieriid shells and on their bilateral symmetry), that both *Micrina* and halkieriids were originally phosphatic (based on the nature of the rheomorphic deformation of the exterior surfaces of the sclerites), and that halkieriids (including *Micrina*) give rise to *Mickwitzia* (both sharing the same type of setigerous tubes in the microstructure of the sclerites), which then give rise to other brachiopods in a direct evolutionary sequence (see Williams and Carlson, herein, Fig. 1893; Holmer, Skovsted, & Williams, 2002; Williams & Holmer, 2002).

Li and Xiao (2004) presented a counterargument that, while *Micrina* and *Tannuolina* are likely to be closely related to one another on the basis of shared characters such as spaced growth lamellae and presence of canals (referred to as setigerous tubes by Williams & Holmer, 2002) in the sclerites that open to pores on the exterior surface, the homology of the sclerites in these two taxa is not clear, particularly for the mitral sclerites. They argued that even if *Micrina* and *Tannuolina* are closely related, both are likely to be only distantly related to halkieriids on the basis of the differences in sclerite morphology and body orientation in the articulated specimens of *Tannuolina* (Li & Xiao, 2004) and *Halkieria* (Conway Morris & Peel, 1995). *Tannuolina* sclerites are oriented with their axis of bilateral symmetry perpendicular to the long axis of the individual organism, with sellate sclerites apparently imbricated in anterior-posterior rows, while *Halkieria* shells are oriented with their axis of bilateral symmetry parallel to the long axis of the individual organism, with no imbrication of multiple shells apparent. Similarities in sclerite microstructure are thus thought to be convergent rather than homologous (see Williams & Carlson, herein, Fig. 1903).

Mickwitzia

Mickwitzia possesses an unusual combination of characters, leading to considerable uncertainly regarding its phylogenetic affinities (Laurie, 2000; Skovsted & Holmer, 2000, 2003, 2005; Holmer, Skovsted, & Williams, 2002; Williams & Holmer, 2002; Balthasar, 2004a). It first appears (questionably) in the Tommotian, and extends to the Botomian. Rowell (1965) placed it, with reservation, in the Paterinida; Laurie (2000) removed it to a more uncertain position as a so-called brachiopod-like fossil. Skovsted and Holmer (2000) claimed *Mickwitzia,* originally phosphatic in composition, is a linguliform brachiopod with shells composed of columnar laminae, a feature it appears to share with acrotretide brachiopods (by virtue of common ancestry according to Holmer, Skovsted, & Williams, 2002); it is referred to simply as a stem-group brachiopod by Skovsted and Holmer (2005). *Mickwitzia* also has striated, apatitic tubes indistinguishable from those in *Micrina* (Williams & Holmer, 2002), which are claimed to have held setae in the living animals. Balthasar (2004a, p. 381) argued that the setal tubes in *Mickwitzia* are "distinct from that previously recognized of *Micrina,*" although he acknowledges that *Mickwitzia*-type setae may be homologous to adult setae of extant brachiopods, while *Micrina*-type setae may be homologous to juvenile setae of extant brachiopods. On this basis, Balthasar (2004a) claimed that *Mickwitzia* is closely related to paterinide brachiopods, either as a derived, peramorphic paterinide or as a possible sister group to paterinides.

Heliomedusa

Heliomedusa, from the Chengjiang fauna of the Lower Cambrian (Atdabanian to lowermost Botomian) of southwestern China, was originally classified as a jellyfish (Sun & Hou, 1987) but has since been reassigned among several groups of brachiopods: as an unspecified inarticulated brachiopod (Conway Morris & Robison, 1988); an obolellid (Chen, Hou, & Erdtmann, 1989); and a craniopside (Jin & Wang, 1992; Zhang, Hou, & Emig, 2003; Hou & others, 2004). No original shell material is still preserved associated with these fossils, but it was assumed to have been originally calcareous, not phosphatic, and later replaced diagenetically by iron-rich clays (see also Balthasar, 2004a). Chen, Huang, and Chuang (2007) removed *Heliomedusa* from the Craniopsoidea (Jin & Wang, 1992) and placed it in Discinoidea on the basis of several synapomorphies seen in the soft tissues preserved as impressions in a larger collection of better-preserved individuals: a longitudinally oval pedicle foramen is present in the anterior region of the posterior sector of the ventral valve (which Jin & Wang, 1992, identified apparently erroneously as the dorsal valve) as in discinids; a short, straight pedicle is present, indicating that *Heliomedusa* is not cemented or free-living; elongate scars of paired anterior and posterior adductor muscles are also present; and the lophophore itself is preserved in association with the dorsal valve. These strong similarities to discinoids in soft-part anatomy imply that the *Heliomedusa* shell was chitinous or chitinophosphatic, not calcareous.

MORPHOLOGICAL COMPLEXES AND CHARACTER DISTRIBUTIONS

Mineralized or Not

The hypothesis that mineralized bivalved brachiopod shells evolved multiple times from various unmineralized ancestors has been proposed (Valentine, 1975, 2004; Wright, 1979; Gorjansky & Popov, 1985, 1986; Willmer, 1990), suggesting that brachiopods as a group are polyphyletic (or diphyletic). Among fossil brachiopods, all characters uniting them are related to the two mineralized valves, and it has been difficult to consider what a brachiopod without two valves would look like and how we would recognize it as a brachiopod even if we had collected it as a fossil. And yet, all living brachiopods share certain soft-part anatomical (Rowell, 1981a, 1981b, 1982; Carlson, 1995) and genetic characters (Cohen, 2000) that have little to do with the presence of two valves and provide strong evidence in favor of the monophyly of the group apart from the possession of two valves. If halkieriids prove to be the brachiopod sister group and the two valves of brachiopods can be demonstrated to be homologous with the two shells of halkieriids, then two valves in brachiopods may be most parsimoniously interpreted as a plesiomorphic character, retained from their common ancestor.

Even with brachiopod monophyly supported with confidence on the basis of nonmineralized features, it is quite possible that two valves evolved multiple times within the clade Brachiopoda. Unfortunately, it is not possible to test this latter hypothesis rigorously at this time, because the nonmineralized Proterozoic fossil record of metazoans is sparse and discontinuous in time, space, and morphology. Parsimony encourages us to favor the simplest explanation for a body of data currently in hand, which suggests that two valves evolved once in the evolution of brachiopods and serve as a synapomorphy for the group. It would be foolish, however, not to at least consider that methodological parsimony may be of little relevance to processes of biomineralization early in the Cambrian. Our understanding of processes and constraints in mineralization is so limited for this critically important time in metazoan evolution that we can reject relatively few hypotheses with substantial evidence (B. Runnegar, personal communication, 2004).

Number of Mineralized Elements

Is a multielement mineralized fossil organism the sister group to the brachiopods, rather than a two-element or unmineralized organism? There seems to be no strong evidence in favor of a bivalved sister group to brachiopods, among either the extant or extinct fauna. Halkieriids clearly have multielement skeletons. Although sellate and mitral sclerites of *Micrina* are each bilaterally symmetrical and have been argued to be homologous with the anterior and posterior shells of *Halkieria* (and possibly the dorsal and ventral shells of brachiopods; Williams & Holmer, 2002; see Williams and Carlson, herein, Fig. 1903), the *Micrina* scleritome is generally thought to have been more consistent with a multielement model than a two-shell model (Li & Xiao, 2004). In addition to bearing setae (setigerous), *Micrina* sellate sclerites (located anteriorly) possess internal markings suggesting a pair of muscles, thought to support the mouth, and *Micrina* mitral sclerites (located posteriorly) possess features interpreted as gonadal sacs (similar to saccate mantle canals in brachiopods). But mitral and sellate sclerites are not complementary bivalves (Williams & Holmer, 2002) in the same configuration as brachiopod bivalves, and it seems at least equally plausible that the apparent similarities between the two are homoplastic (convergent) rather than homologous.

Li and Xiao (2004), attempting to accommodate the Williams and Holmer (2002) argument about the homology of shell mineralogy and structure in tannuolinids and brachiopods, presented the independent origin of two shells from a multielement ancestor as a possible scenario for brachiopod origins (see Williams and Carlson, herein, Fig. 1903.1). This scenario implies either that monophyletic brachiopods are primitively multielement and that both tannuolinids and halkieriids can be considered brachiopods or that diphyletic brachiopods evolved independently twice from a multielement ancestor.

The use of a chiton as the outgroup taxon for molecular systematic analyses of brachiopods (e.g., Cohen & Gawthrop, 1997; Cohen & Weydmann, 2005; see also Vinther & Nielsen, 2005) raises the possibility for interesting speculation on morphology and evolution. Chitons have multielement skeletons, today composed of eight separate dorsal plates (called valves) underlain by a thick mantle (girdle) that often has calcareous or chitinous spines. Early chitons may have had more than eight valves (see Vendrasco, Wood, & Runnegar, 2004). This skeletal arrangement is at least reminiscent of the two dorsal shells and multiple small sclerites in halkieriids. The individual plates are imbricated, one behind (posterior to) and under the one in front, with the axis of symmetry of each plate parallel to the long axis of the organism; this is not consistent with the arrangement of sclerites in *Tannuolina* (Li & Xiao, 2004). Chiton plates also possess aesthetes, or sensory structures that sit in canals that penetrate the valves; they bear a certain similarity to endopunctae (containing caecae) in some near-basal brachiopods (e.g., craniids; see Baxter, Sturrock, & Jones, 1990). This similarity has long been thought to indicate no more than convergent similarity, but may now bear closer scrutiny with increased confidence in recent molecular results using chitons as the brachiopod outgroup (Cohen & Weydmann, 2005).

Mineralogy

Both phosphatic and calcitic shells appear very early in the fossil record, at almost indistinguishably different times. Phosphatic shells appear slightly earlier (Williams, Carlson, & Brunton, 2000; Holmer, 2001), supporting the long-held view among brachiopod paleontologists that phosphatic mineralogy is plesiomorphic (primitive) for brachiopods. This runs counter to outgroup analyses suggesting that phosphatic shells are almost certainly derived relative to calcitic shells (within the Eutrochozoa; Valentine, 2004; see also Carlson, 1995; Cohen & Weydmann, 2005).

Is it possible that these evolutionarily early shells were bimineralic or even multimineralic? The unexpected discovery of siliceous tablets in the first-formed shells of discinid brachiopods, which mineralize chitinophosphatic shells for the remainder of their ontogeny (Williams & others, 1998; Williams, Lüter, & Cusack, 2001; see also Williams & Holmer, 2002; Williams, 2003) opens up the hitherto unexplored possibility of bimineralic shells. Secondary diagenetic alteration of primary mineralogy is not at all uncommon in fossil brachiopods, however, and it can be difficult to distinguish primary mineralogy from secondary replacement. For example, the multimineralic state of *Mickwitzia* fossils appears to be diagenetic rather than primary (Balthasar, 2004a).

Apparently building on his discovery of bimineralic discinids, Williams (2003) described microscopic imprints on juvenile shells of Paleozoic linguliform brachiopods and argues that these imprints were likely to have been formed by calcareous discoids and spheroids, rather than phosphatic elements as in the later-formed shell, on the basis of their apparently greater solubility than the phosphatic shell material. No original calcareous shell material remains, however, and it is not clear that relative solubility can be predicted with much certainty in the absence of information about the chemical conditions of diagenesis. Although there is now evidence for the mineralization of siliceous tablets early in the ontogeny of shell secretion in discinids, no extant brachiopod is known to mineralize both calcareous and phosphatic shells over the course of their ontogeny. It is not clear what constraints, if any, might operate to prevent this combination of mineralogies, but no direct evidence yet exists demonstrating calcareous and phosphatic mineralization in the same shell. Opaline silica has a lower specific gravity (2.0–2.5) than either calcite (2.7) or apatite (3.1–3.2); first-formed tablets of less-dense silica would confer lower weight than apatite, an advantage for larval energy expenditure, since in *Discinisca* the tablets begin to be mineralized while the planktotrophic larvae are still in the water column (see also discussion in Freeman & Lundelius, 2005). Interestingly, given our current knowledge of brachiopod biomineralization, a bimineralic shell demonstrating an ontogenetic transformation in mineralogy (siliceous to phosphatic, as in discinids, or calcareous to phosphatic, as hypothesized by Williams, 2003) would suggest that phosphatic shells are derived, using the ontogenetic polarity criterion, which is consistent with the polarity of evolutionary mineralogical transformation suggested by outgroup analyses.

Micrina and *Mickwitzia* were both originally phosphatic (Laurie, 1986; Skovsted & Holmer, 2000; Williams & Holmer, 2002; Balthasar, 2004a), a conclusion based convincingly on details of fossil shell fabric and the fabric of living *Discina*. *Heliomedusa* was originally thought to be calcareous (Jin & Wang, 1992) but is now thought to have been phosphatic (Chen, Huang, & Chuang, 2007). The original mineralogy of halkieriid shells is not clear; no original shell material exists. Halkieriid sclerites were found to be aragonitic (Bengtson & Conway Morris, 1984; Bengtson & others, 1990; Porter, 2004) on the basis of the preservation of needlelike fibers similar to those seen in originally aragonitic skeletons and the similar preservation of other elements of the fauna (Porter, 2004) known to be aragonitic. A calcareous mineralogy for the shells is inferred on the basis of the preservation (decalcified) of associated metazoans (trilobites, hyoliths) known to have had originally calcareous skeletons and the brittle deformation of the anterior shell of *Halkieria* in compaction (Conway Morris & Peel, 1995). No *Halkieria* shells are present in the Monastery Creek Formation (Porter, 2004), even though sclerites (originally aragonitic) are abundant, suggesting a different mineralogy of the shells and the sclerites in the same individuals. This type of simultaneous bimineralic composition of different elements at the same ontogenetic stage is not known in extant brachiopods, even though ontogenetic transformations in mineralogy are known, as discussed above (Williams & others, 1998). Williams and Holmer (2002) argued that halkieriid shells were originally phosphatic, based on the rheomorphic (plastic) deformation of surfaces and the nature of the draping of the shell fabric in shell formation and development similar to the type of deformation seen in fossil brachiopods known to have been phosphatic (acrotretides). They describe a ten-step hypothetical evolutionary transformation from halkieriids (as including *Micrina*) to *Mickwitzia* to brachiopods that relies on the consistency in phosphatic mineralogy, as they interpret it, among all these groups. Given the diversity of opinion cited above, it is clear that the mineralogy of halkieriid shells is currently not universally agreed upon.

Shell Structure

Shell microstructure has long been considered to be a critical source of reliable, if contentious, information on phylogenetic relationships among brachiopods (e.g., Williams, 1956; Williams & others, 1996). For example, Williams (2003; Fig. 1910.4) derived acrotretides from within the linguloids almost exclusively on the basis of shell structural similarities, *contra* Holmer and Popov (2000; Fig. 1910.3), who placed acrotretides as the sister group to the linguloids and all other phosphatic brachiopods except paterinides, and Holmer, Skovsted, and Williams (2002), who placed acrotretoids as basal to all brachiopods, including paterinides (Fig. 1910.5). The microstructures of the various mineralized elements present in Lower Cambrian fossils share similar elements, as well as distinct differences, and currently leave open the question of whether the similarities are homologous or homoplastic.

Determining the level of homology of microstructural features almost certainly plays a major role in deciphering their evolution. Three major types of shell perforations are recognized among brachiopods: canals (extremely fine), punctae (large, lacking distal brushes), and endopunctae (large, with distal brushes). Just as bird, bat, and pterosaur wings are homologous as forearms, but not as wings, these three types of structures may be homologous as shell perforations, but not as punctae. All brachiopods with a canalicular shell structure may be homologous, but they may not be homologous with terebratulide endopunctae, or more generally with chiton aesthetes. More broadly among metazoans, various biomineralized structural features can be notoriously homoplastic (e.g., echinoderm stereom and vertebrate trabecular bone).

The nature of shell lamination and tubes or canals penetrating the shell fabric are the two microstructural features that have figured most prominently in discussions of phylogenetic affinity among the taxa considered here. Acrotretide brachiopods, *Tannuolina*, and *Mickwitzia* are characterized by columnar lamination. *Micrina* sclerites (mitral and sellate) are characterized by stratiform lamination, and these stratified laminar sets are claimed to be indistinguishable from

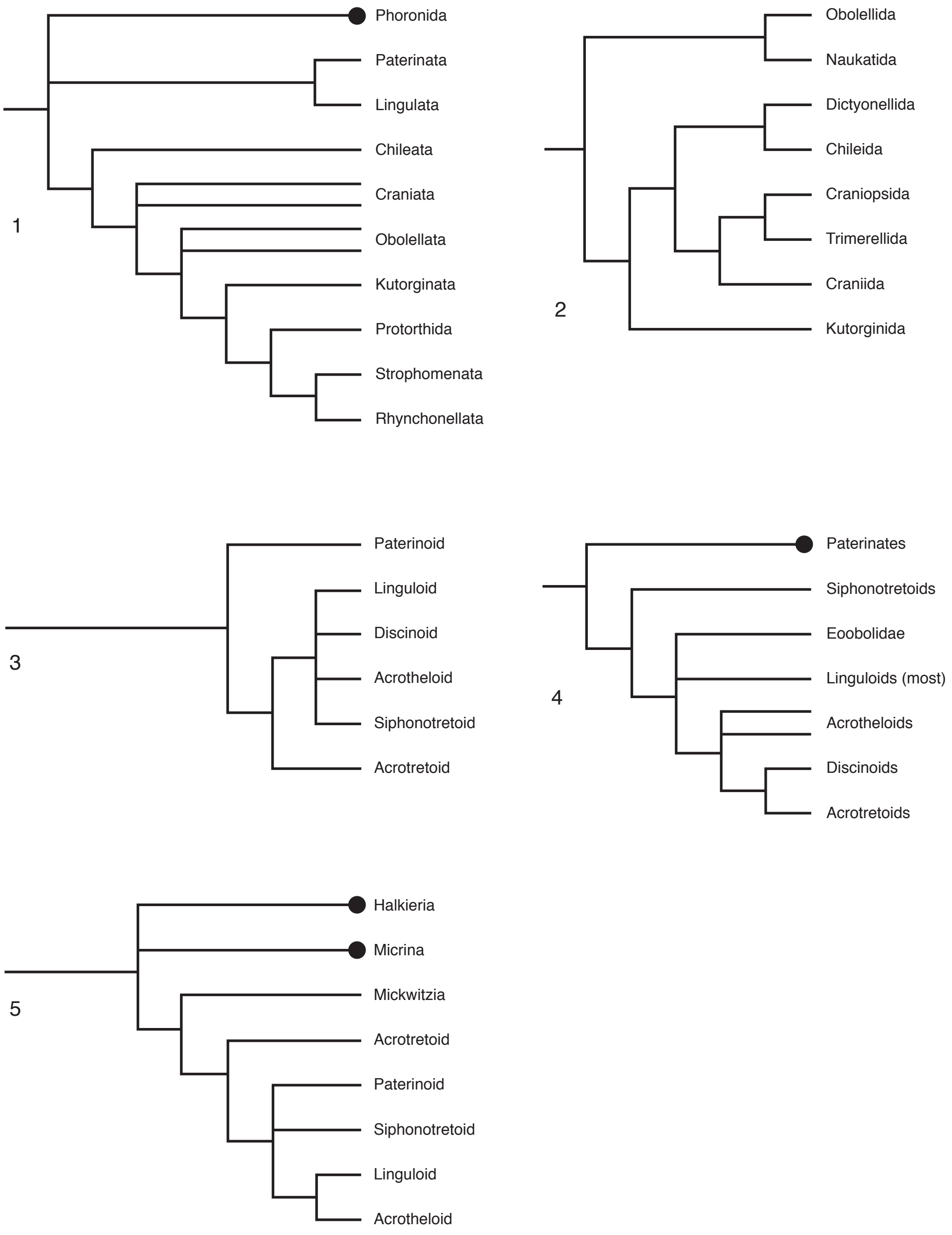

FIG. 1910. Hypothesized phylogenetic relationships among various brachiopod taxa, adapted from sources indicated; *black dots* identify outgroup taxa; *1,* eight brachiopod classes plus phoronides and protorthides (Williams & others, 2000; Bassett, Popov, & Holmer, 2001); *2,* major groups of early calcareous brachiopods (Popov & others, 2000); 3, major groups of phosphatic brachiopods (Holmer & Popov, 2000); *4,* a different view of relationships among major groups of phosphatic brachiopods (Williams, 2003); *5,* major groups of phosphatic brachiopods plus *Micrina*, *Mickwitzia*, and *Halkieria* (Holmer, Skovsted, & Williams, 2002).

those in lingulide brachiopods (WILLIAMS & HOLMER, 2002). Lingulides do not have striated tubes throughout their shell fabric, however; their canalicular structures are not striated and apparently not homologous to striated tubes in *Micrina*. LI and XIAO (2004) characterized the laminar features in *Micrina* simply as basal internal growth lamellae. Nothing is known of halkieriid shell structure, as noted above.

Micrina and *Mickwitzia* possess striated (apparently setigerous) tubes running perpendicularly through the shell fabric (WILLIAMS & HOLMER, 2002; BALTHASAR, 2004a) and secreted independently of the laminar fabric of the shell. A canal system of very small (10–20 µm) striated tubes (spaced concentrically according to WILLIAMS & HOLMER, 2002, but unevenly distributed according to LI & XIAO, 2004) permeate entire sclerites of *Micrina*, but extant brachiopod setae (in follicles, not striated tubes) are restricted to a band in the groove between outer and inner mantle lobes and are never incorporated into the shell (see LÜTER, 2000a), not even (apparently) in Cambrian forms. Micropunctae (canals in linguliforms) are typically around 180–850 µm in diameter, an order of magnitude larger than setigerous canals in *Micrina*. Baculi (apatitic rods) are present in linguloids and acrotheloids and are not homologous with striated tubes in *Micrina*. Spherulitic apatitic aggregates in *Micrina* were apparently formed from a different set of calcifying proteins (WILLIAMS & HOLMER, 2002) than apatitic aggregates in linguloid and acrotretoid brachiopods.

It is possible that the shell structural similarities between *Micrina* and linguliform brachiopods result from shared properties of organic-rich, chitinophosphatic shells, rather than common ancestry—providing some kind of constructional constraint rather than a phylogenetic constraint. If phosphatic biominerals, as well as secondary phosphatic preservation, were more common in the Early Cambrian than today, one could argue on the basis of ocean chemistry that Cambrian phosphatic biominerals and the shell structures that they necessarily form are more likely to be convergent than homologous. This is consistent with the more traditional interpretation of tommotiid relationships (BENGTSON 1970; BENGTSON & others, 1990; CONWAY MORRIS & PEEL, 1995), which posits some halkieriids (as a broadly paraphyletic grouping) sharing common ancestry with brachiopods (and other halkieriids sharing closer common ancestry with annelids) and the phosphatic tommotiids (e.g., *Micrina*) separate from the *Halkieria* + brachiopod clade (see WILLIAMS and CARLSON, herein, Fig. 1903.3). Also, if linguliforms are derived within brachiopods (CARLSON, 1995; COHEN, 2000; COHEN & WEYDMANN, 2005; Fig. 1908; and see WILLIAMS and CARLSON, herein, Fig. 1903.3) rather than basal, then the argument that the similarity of *Micrina* and linguliforms is due to close common ancestry is considerably weakened.

Body Orientation or Plan

Are the two brachiopod valves now referred to as dorsal and ventral actually dorsal and ventral relative to their embryological orientation? It has been claimed that the two valves are more accurately characterized as anterodorsal and posterodorsal (NIELSEN, 1991; COHEN, HOLMER, & LÜTER, 2003; VINTHER & NIELSEN, 2005), having both formed from the originally dorsal surface of the developing embryo (in *Crania* [*Novocrania]*). Recall that YATSU (1902) also observed the formation of a single, nearly circular shell that grows, folds transversely, and divides to form two valves. As discussed earlier, however, it may be that the dorsal valve forms first on the dorsal surface of the embryo, while the ventral valve forms later, on the topologically ventral surface of the embryo (Fig. 1909). Further investigation of the timing of embryological events is necessary to resolve this issue more fully (C. NIELSEN, personal communication, 2005).

There is also little agreement on the arrangement of sclerites in the scleritome of mitrosagophorans. LI and XIAO (2004) discovered partially articulated specimens of *Tannuolina* (thought to be closely related to *Micrina*, implying that these two taxa share the same body plan inherited from a common ancestor) that reveal pairs of articulated (left-right) mitral sclerites oriented with the sagittal plane of the sclerites perpendicular, rather than parallel, to the long axis of the body. This suggests a different body orientation, by 90 degrees, than in the WILLIAMS and HOLMER (2002) reconstruction. Also, the hypothesized body plan of tannuolinids (LI & XIAO, 2004), with symmetrical rows of imbricated sellate sclerites flanking symmetrical pairs of mitral sclerites, appears to be fundamentally different from the body plan of brachiopods with two valves, apparently dorsal and ventral. This argument is based entirely on the assumption of a close phylogenetic relationship between *Tannuolina* and *Micrina*, since the preservational evidence is based entirely on *Tannuolina* specimens. Body orientation of sclerites on *Micrina* individuals is not clear. LAURIE (1986) described the sclerites as anterior (sellate) and posterior (mitral), but it is not yet known whether the sclerite arrangement is comparable to that in *Halkieria*, as USHATINSKAYA (2001, 2002) suggested. Mitral and sellate sclerites of *Micrina* are each bilaterally symmetrical and do not occur in left and right forms.

Metamerism

Were these Early Cambrian forms metameric? If so, what does this imply about possible brachiopod metamerism? *Micrina* is claimed to be initially (ontogenetically) segmented, based on transverse furrows in juvenile mitral sclerites (WILLIAMS & HOLMER, 2002), but this constitutes rather weak supporting evidence for metamerism. Metamerism is consistent with the reconstruction of *Tannuolina* presented in LI and XIAO (2004); if determined to be closely related to *Micrina*, this interpretation could apply also to *Micrina*. *Halkieria* clearly exhibits the serial repetition of sclerites (CONWAY MORRIS & PEEL, 1995), but great caution is urged in interpreting serial repetition as evidence of actual metamerism. Nevertheless, *Halkieria* has been claimed to have a segmented body form (as coded in the data matrix in HOLMER, SKOVSTED, & WILLIAMS, 2002); the data supporting this assertion are not clear. *Eoobolus*, a linguloid brachiopod, has also recently been claimed to be segmented (BALTHASAR, 2004b). If verified with additional evidence, this would suggest that brachiopods might have evolved from a metameric ancestral body form.

EVOLUTIONARY INTERPRETATIONS

Considering the foregoing discussion of these early fossils and the characters they exhibit, three different perspectives on their evolutionary significance emerge.

Homologous and Derived

Morphological and mineralogical similarities among brachiopods and these Tommotian fossils are synapomorphies, or features shared due to common ancestry and derived relative to the ancestral state present among more distant relatives. Supporting this point of view is a phosphatic mineralogy, present in *Mickwitzia* and linguliforms (and inferred to be phosphatic or bimineralic [calcareous and phosphatic] in *Micrina* and halkieriids), the presence of striated, apatitic tubes in *Micrina* and *Mickwitzia* (inferred to have been setigerous), and the columnar lamination of the shell in *Mickwitzia* and acrotretides (Fig. 1910; and see WILLIAMS and CARLSON, herein, Fig. 1896; HOLMER, SKOVSTED, & WILLIAMS, 2002; WILLIAMS & HOLMER, 2002; WILLIAMS, 2003). A modified version of this argument is discussed in LI and XIAO (2004; see WILLIAMS and CARLSON, herein, Fig. 1903.1). If halkieriids were calcareous, as LI and XIAO inferred, they could be the sister group to the craniiforms + rhynchonelliforms, with *Micrina* being the sister group to the linguliforms; this scenario is not consistent with the molecular systematic data (COHEN & WEYDMANN, 2005). This implies that the bivalved body form in brachiopods evolved twice independently from multielement ancestors and that *Micrina, Tannuolina* (if it is closely related to *Micrina*), and halkieriids are nested within the brachiopod crown group, at its base (see WILLIAMS and CARLSON, herein, Fig. 1903.1).

Homologous and Basal (Primitive)

Morphological and mineralogical similarities among brachiopods and Tommotian fossils might be homologous (if halkieriids are calcareous), but plesiomorphic (primitive), not apomorphic. It is possible that *Micrina* shares common ancestry with the linguliforms, via *Mickwitzia*, with halkieriids as a sister group to all brachiopods (see WILLIAMS and CARLSON, herein, Fig. 1903.2), or perhaps even more broadly to a more inclusive group of lophotrochozoans. If the molecular sequence data (COHEN & WEYDMANN, 2005) suggest a more accurate pattern of relationship, then this scenario is much less likely, complicated by the phylogenetic position of the craniides. This scenario (see WILLIAMS and CARLSON, herein, Fig. 1903.2) would require that *Micrina* (and other tannuolinids) retain the primitive multielement body plan after phoronids and craniiforms had diverged from the brachiopod common ancestor. It is much more likely that the similarities *Micrina* appears to share with phosphatic brachiopods are convergent (see WILLIAMS and CARLSON, herein, Fig. 1903.3), as discussed below.

It is also possible that halkieriids are not the sister group to brachiopods at all or may be only much more distantly related, leaving us again with a question mark about the identity of the (extant or extinct) brachiopod sister group. The evidence presented in support of brachiopod ancestry (CONWAY MORRIS & PEEL, 1995; WILLIAMS & HOLMER, 2002) from halkieriids is not particularly robust; the evidence presented in support of molluscan ancestry (with halkieriids within the crown group) is also not especially strong (VINTHER & NIELSEN, 2005). It may be that the existing data are simply not yet sufficient to allow us to reject either hypothesis at this time. Yet another possibility, consistent with both hypotheses, is that halkieriids are part of the stem group of Lophotrochozoa (see WILLIAMS and CARLSON, herein, Fig. 1892; also VALENTINE, 2004) and are distantly related to both mollusks and brachiopods.

Not Homologous

Morphological and mineralogical similarities among brachiopods and the Tommotian fossils are convergent or homoplastic. In other words, they are not homologous, and thus not derived, but result from independent evolutionary events (BENGTSON, 1970; LAURIE, 1986; LI & XIAO, 2004). In this scenario (see WILLIAMS and CARLSON, herein, Fig. 1903.3), halkieriids, if calcareous, might be the sister group to a monophyletic Brachiopoda (CONWAY MORRIS & PEEL, 1995), but *Micrina* and the other tannuolinids and tommotiids are only rather distantly related to the halkieriid + brachiopod clade (see WILLIAMS and CARLSON, herein, Fig. 1903.3). Phosphatic shell mineralogy and associated shell structural similarities are likely to have evolved independently in linguliforms and tannuolinids.

RELATIONSHIPS AMONG ALL BRACHIOPODS

Most brachiopod workers agree that all available data should be brought to bear on the question of determining phylogenetic relationships among all extant and extinct brachiopods. In this spirit, a consensus cladogram was constructed (Fig. 1908), by eye or hand, with data derived primarily from analyses of COHEN and WEYDMANN (2005) and COHEN (herein, p. 2356) using molecular sequence data from living brachiopods and phoronids (Fig. 1907); HOLMER and POPOV (2000), POPOV, BASSETT, and HOLMER (2000), and WILLIAMS, CARLSON, and BRUNTON (2000) using morphological data from mostly Cambrian and Ordovician taxa (Fig. 1910); CARLSON (1995) using morphological data from Recent brachio-

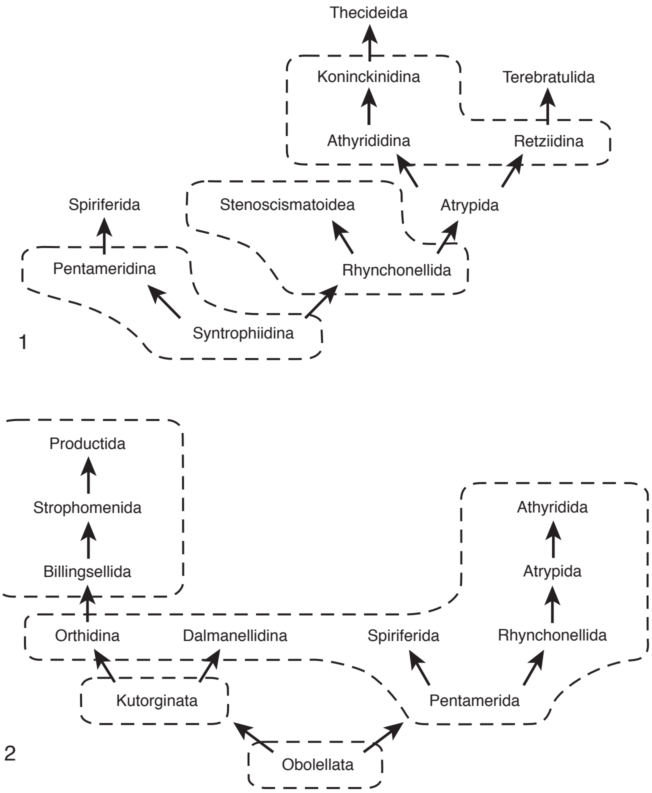

FIG. 1911. Results of two different ANOP (All Nodes Occupied Phylogeny) analyses among selected groups of rhynchonelliform brachiopods, utilizing morphological and stratigraphical data together; *1,* selected derived rhynchonellates, *dashed lines* unite suborders in Pentamerida, Rhynchonellida, and Athyridida; *2,* including more basal rhynchonelliforms as well, *dashed lines* unite suborders in classes Obolellata, Kutorginata, Rhynchonellata, and Strophomenata (adapted from Carlson & Leighton, 2001).

pods; and CARLSON and LEIGHTON (2001) using morphological and stratigraphic data together for all rhynchonelliform suborders (Fig. 1911). All branches of the cladogram should be interpreted as testable hypotheses that may well change over time, but this topology represents the consensus that seems to most accurately and honestly combine the results of the analyses listed above and to concur with our present state of understanding about brachiopod phylogenetic relationships.

Rhynchonelliformea (articulates) is the sister group to a clade that includes Linguliformea, Craniiformea (the inarticulates), and Phoronida; together they comprise the two major clades within Brachiopoda, generally consistent with the old class-level terminology (WILLIAMS & ROWELL, 1965d). Now, however, the inarticulates include phoronids, according to SSU (18S) rDNA evidence (COHEN & WEYDMANN, 2005). COHEN and WEYDMANN (2005) have further suggested modifying the current classification so that Lingulata, Craniata, and Phoronata (each named after the most ancient extant subclade [order]) are recognized as classes within Linguliformea, with Phoronata at the base of this clade. Further study of *Iotuba*, from the Chengjiang fauna, and the complete fossil record of phoronids would be valuable in testing this phylogenetic hypothesis (Fig. 1908). Rhynchonelliforms have a large and diverse (12 orders) stem group; the crown group (7 orders) is long lived, first appearing in the Lower Ordovician.

Relationships among the obolellates and chileates and other early rhynchonelliforms are becoming clearer but are not yet rigorously supported (Popov & others, 1996; Holmer & Popov, 2000; Bassett, Popov, & Holmer, 2001; Holmer, 2001). Rhynchonelliforms are united by the presence of the fibrous secondary layer of an organocarbonate shell, a pedicle, and the development of a recognizable diductor muscle system controlling the opening of the valves about a hinge axis defined by interareas (Williams, Carlson, & Brunton, 2000), discussed in greater detail in the section on articulation below (p. 2899). Each new fossil discovered from the Lower Cambrian has the potential to provide a critical test of the hypotheses of relationships among the early rhynchonelliforms proposed thus far.

The position of orthides and protorthides is not universally agreed upon. They may share most recent common ancestry with the other rhynchonellates, as the revised *Treatise* classification implies (Williams, Carlson, & Brunton, 2000, fig. 6). The evidence supporting this hypothesis is the following: development of a pedicle rudiment (inferred); loss of posterior body wall (which presumably persisted in Strophomenata); loss of the anus; and the appearance of projecting brachiophores in the cardinalia. Alternatively, they may share most recent common ancestry with the kutorginate + strophomenate clade (Carlson & Leighton, 2001, fig. 26.1) or more likely perhaps with the strophomenates, both having evolved from the kutorginates (Fig. 1911.2; Carlson & Leighton, 2001). Given the continuing uncertainty in the patterns of relationship among these early rhynchonelliforms, they are represented in an as yet unresolved tritomy with the kutorginate + strophomenate clade and the other rhynchonellates (Fig. 1908).

It is not clear if the strophic spire-bearers are all nested within the crown-group rhynchonellates (Williams, Carlson, & Brunton, 2000) or if they represent an older, deeper divergence from the pentamerides (Carlson & Leighton, 2001; Fig. 1911). Confusion about the homology and polarity of the calcareous lophophore supports continues to plague this issue, which is discussed in greater detail in the section on the lophophore below (p. 2899). Ideally, resolving relationships among thecideides and the other extant brachiopods (discussed in an earlier section, herein, p. 2885) could clarify the relationships among all spire-bearers to one another.

CONCLUDING SYNTHESIS

EVOLUTION OF MAJOR CHARACTER COMPLEXES

Juvenile Mantles and Shells

Planktotrophy is the primitive state for brachiopods, including phoroniforms (Carlson, 1995; Freeman & Lundelius, 2005). Valves are mineralized at or immediately following metamorphosis in all brachiopods except phoronids. Mineralization on embryonic mantle has evolved several times independently within the linguliforms, which are generally characterized by a long stage of (planktotrophic larval) swimming juvenile growth. Lecithotrophy evolved twice independently: once in the Craniiformea (Craniida) sometime in the mid-Jurassic (Freeman & Lundelius, 1999) and once in the crown-group Rhynchonelliformea sometime in the evolution of rhynchonellides from pentamerides (?Lower Ordovician) (Freeman & Lundelius, 2005). In the Craniiformea, no mantle reversal accompanied the transformation to lecithotrophy, while in the Rhynchonelliformea, mantle reversal did accompany the transformation (Nielsen, 1991; Freeman & Lundelius, 1999, 2005).

Integument and Shell Structure

The presence of mineralized valves appears to be primitive for brachiopods (shared with chitons and other lophotrochozoans, possibly including halkieriids); the absence of shells in phoronids (if they are brachiopods), appears to be derived, but this is far from certain. Two valves appear to be derived for brachiopods (from more than two in chitons and halkieriids), but this is also far from certain. If chitons and halkieriids are only very distantly related to brachiopods, the sister group–ancestor may have been lacking shells altogether, and shells themselves may have evolved more than once. Calcareous laminar shells appear to be primitive for brachiopods; fibrous shell structure is derived within rhynchonelliforms. Phosphatic stratiform shells are derived in the Linguliformea (the most parsimonious interpretation of the distribution of shell mineralogy; other interpretations are possible, but less parsimonious—see discussion in Recent Research section, herein, p. 2891). Punctae have clearly evolved several times independently from the primitive impunctate condition. Pseudopunctae appear to be shared and derived for the Strophomenata, excluding Billingsellida (CARLSON & LEIGHTON, 2001). Various shell fabrics have been identified and named (see WILLIAMS and CARLSON, herein, Fig. 1898) and are almost certainly homoplastic within brachiopods, having evolved several times independently.

Pedicle

Pedicles appear to have evolved twice independently, once in linguliforms and once in rhynchonelliforms (Fig. 1908; see WILLIAMS and CARLSON, herein, Fig. 1899–1900), with different morphology, anatomy, and development. The nature of the attachment of valves to a substrate in several of the early rhynchonelliform groups is not universally agreed upon but may have involved an adhesive holdfast in the form of a mucinous pad. The absence of a pedicle in craniiforms and phoronids appears to represent the primitive state among brachiopods, but this conclusion requires additional investigation of both fossil and living brachiopods.

Muscle Systems

Muscle systems have evolved in concert with changes in articulation. Not surprisingly, the muscles that close the shell are always located anterior to the hinge axis, and the muscles that open the shell are always located posterior to the hinge axis. The insertion of the opening (posterior adductor or diductor) muscles on the ventral valve has migrated anteriorly from a position clearly posterior to the adductors (in linguliforms and craniiforms as well as early rhynchonelliforms; see WILLIAMS and CARLSON, herein, Fig. 1901B, 1901D, 1901E) to a position collinear with or anterior to the adductors (see WILLIAMS and CARLSON, herein, Fig. 1901E–1901G). The origin of the opening muscles on the dorsal valve has migrated posteriorly from a posterior position (see WILLIAMS and CARLSON, herein, Fig. 1901B) to a posteriormost position (see WILLIAMS and CARLSON, herein, Fig. 1901G). This evolutionary transition results in greater mechanical advantage to the valve opening system.

Articulation

The evolution of articulation is complex, with many components in the transition from no articulation to articulation (see WILLIAMS and CARLSON, herein, Fig. 1901B; Table 39). Phoronids have no valves and thus no articulation; craniiforms and linguliforms have no articulatory structures; early rhynchonelliforms have rudimentary articulation. More derived rhynchonelliforms have deltidiodont (noninterlocking) articulation, and cyrtomatodont (interlocking) articulation evolved within the derived rhynchonellates. The complex distribution of different articulatory structures defies, as yet, a simple but more detailed explanation of character evolution across the phylum.

Lophophore

The spirolophe lophophore is primitive; plectolophe and ptycholophe lophophores are both derived from the spirolophe condition. All linguliforms, craniiforms, and early rhynchonelliforms lack mineralized lophophore supports. Brachial ridges evolved within the strophomenates and again a second time in thecideides (from the spire-bearers). Spiralia and then loops, three-dimensional structures supported only at their base by crura, appear to have evolved once in the crown-group rhynchonellates (with unusual genera like *Enantiosphen* and *Tropidoleptus* representing rare, independent originations of mineralized lophophore supports).

Summary

In conclusion, all sources of data, if sufficiently robust and well corroborated, are best analyzed together—morphological, molecular, developmental, and stratigraphic, with additional insights gained from paleobiogeographic and functional analyses. Separate analysis of each alone is essential, and comparative analysis of all together provides the most comprehensive basis for interpreting the evolution of a group like the brachiopods, with a long and rich fossil record and a relatively diminished extant diversity (see also CARLSON, 2001). The evolution of each of the morphological complexes discussed here has been evaluated with respect to hypotheses of phylogenetic relationships structured in part according to several criteria of polarity (outgroup, stratigraphic, and ontogenetic), each of which has strengths and weaknesses, as discussed in WILLIAMS and CARLSON, herein, p. 2833.

Our understanding of brachiopod evolution has increased greatly since the last *Treatise* volumes were published (MOORE, 1965), thanks to greater numbers of fossil specimens collected, improved understanding of living brachiopods, and improved methods for analyzing and comparing these various data. Many questions remain unanswered, however. The phylogenetic hypothesis presented in Figure 1908 must be tested in detail, and the polytomies resolved. Are the thecideides more closely related to the athyridide or spiriferinide spire-bearers? Have mineralized valves, spiralia, and articulation evolved more than once among brachiopods? How are other metazoans and halkieriids and other Early Cambrian fossils related to brachiopods? The evolutionary questions that remain keep the study of brachiopods interesting and compel us to continue searching for evidence that will allow us to reject some of the many alternatives discussed in this chapter.