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A supra-ordinal classification of the Brachiopoda

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SUMMARY

A new classification of the Brachiopoda is proposed to take into account recent advances in our understanding of the anatomy, shell morphology, ontogeny and phylogeny of the phylum. The use of phylogenetic analysis to help rationalize this new information did not obviate the dilemma facing all previous classifications of how best to reconcile fossil and living data. Over 95% of all recognized genera are founded on extinct species, with the greatest diversity occurring in Cambro-Ordovician times when all but two of the 26 major groups constituting the phylum first appeared. Only five of these groups survive to the present day, albeit as well dispersed representatives of the early diversity. To compare phylogenies extrapolated from these data, phylogenetic analyses of Recent and Cambro-Ordovician groups were conducted independently by using 55 biological characters for the former group and 69 morphological (and inferred anatomical) features for the latter; only 12 characters were common to both exercises.

The cladogram derived for seven Recent suprafamilial taxa, with *Phoronis* and cyclostome and ctenostome bryozoans as outgroups, is virtually the same as that being obtained by studies of the brachiopod genome. It is also largely compatible with the cladogram for 33 Cambro-Ordovician suprafamilial taxa with *Phoronis* as outgroup. This cladogram has, in turn, been subjected to stratocladistic tests and has been shown to be consistent with the stratigraphic records of the taxa analysed.

A reconciliation of the genealogies derived from the Recent and Cambro-Ordovician data, represented by 14 taxa and clades (with *Phoronis* as outgroup), was effected by using the 19 synapomorphies characterizing these groups. The resultant cladogram shows living organophosphatic-shelled lingulids (and discinids) as a sister group to a clade of all other living brachiopods. This clade, however, includes the extinct organophosphatic-shelled paterinids and the organocalcitic-shelled craniids. The inclusion of the craniids, in particular, is a cladistic compromise that is inconsistent with genetic and some anatomical and morphological evidence. It was therefore decided to accommodate these inconsistencies by dividing the Brachiopoda into three subphyla, each typified by Recent species with early Palaeozoic ancestors and defined by easily identifiable synapomorphies. The inarticulated Linguliformea, consisting of two classes (Lingulata and Paterinata), is characterized by an organophosphatic shell with a stratiform secondary layer and by planktotrophic larvae. Its modern representatives are the lingulids and discinids. The inarticulated Craniiformea is primarily distinguished by an organocarbonate shell with a laminar secondary layer and the absence of a pedicle throughout ontogeny. The craniids are the sole Recent descendants. The mainly articulated Rhynchonelliformea is the largest subphylum as it embraces five Classes (Chileata, Obolellata, Kutorginata, Strophomenata and Rhynchonellata). Its synapomorphies include an organocarbonate shell with a fibrous secondary layer, the presence of a pedicle without a coelomic core and the development of a recognizable diductor muscle system controlling the opening of the valves about a hinge axis defined by interareas. All Recent brachiopod species articulating with cyrtomatodont teeth and sockets are rhynchonelliforms.

1. INTRODUCTION

The Brachiopoda, a group of invertebrate bivalves, are normally minor members of present-day marine communities, being represented by no more than a hundred or so genera, albeit cosmopolitan and intertidal to bathyal in distribution. They do, however, have an unexcelled fossil record of morphological diversity and geological continuity, which reflects their dominance as marine benthos throughout the Palaeozoic era. It is therefore understandable that palaeontologists played a leading role in classifying brachiopods once nineteenth century naturalists had determined the anatomy and development of Recent species and had more or less established their relationships with other eumetazoans. Unsurprisingly, brachiopod taxonomy remains greatly influenced by this historic division of labour,

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which accounts for many of the difficulties attending attempts to reclassify the phylum.

As has been well documented by Muir-Wood (1955), the brachiopods known at the beginning of the nineteenth century were assigned, at one time or another, to many different invertebrate groups but were most commonly classified as molluscs (Lamarck 1801, Cuvier 1800–1805) or molluscoides. The latter name was used by Huxley (1853) to accommodate the views of himself and Hancock (1859) that the brachiopods and polyzoans (bryozoans) are related. Morse (1870) concluded that brachiopods are more closely related to annelids than to molluscs and cited the possession of setae as part of the evidence of common ancestry.

Classifications based on molluscan affinities lingered on into the twentieth century and were adopted as late as 1934 in the Russian edition of Zittel's *Textbook of Palaeontology*. By then, brachiopods were being widely recognized as a distinct phylum (Schuchert & Le Vene 1929; Hyman 1940; Cooper 1944). Indeed, in the light of his studies of the life history of a terebratulide, Percival at one time (1944) concluded that articulated brachiopods with organocarbonate shells are so different from inarticulated species with organophosphatic exoskeletons as to warrant the recognition of two phyla.

The precise rooting of the Brachiopoda and related phyla within eumetazoan phylogeny remains in dispute. In the nineteenth century, comparative studies of anatomy and larval development, especially those of *Phoronis* and brachiopods by Caldwell (1882), led Hatschek (1888) to propose a new phylum, the Tentaculata (later more appropriately renamed 'Lophophorata' (Hyman 1959, p. 229)), for brachiopods, bryozoans and phoronids. For almost a century the lophophorates have widely been regarded as protostomes and attempts have even been made to restore Hatschek's original rank of phylum for the group, with the brachiopods, bryozoans and phoronids consequently reduced in hierarchical status to classes (Emig 1984). More recently, Conway Morris & Peel (1995, pp. 343–344) concluded that brachiopods evolved from extinct protostomes, the early Cambrian articulated halkieriids. In our estimation this radical proposal is currently too speculative to warrant the use of the halkieriids as the sister group of the brachiopods.

A deuterostomous origin of some or all lophophorates has also attracted support. 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 Protostoma and Deuterostoma'. Nielsen (1995*a*, p. 6), on the basis of studies and reinterpretations of lophophorate larval development, argued against the monophyly of the lophophorates by assigning the bryozoans to the protostomes and the brachiopods and phoronids to the deuterostomes. In his view, many features, like the lophophore, which are common to all three taxa, are not synapomorphies but homoplasies. The prevalent opinion among zoologists, however, favours all lophophorates as being deuterostomes (Zimmer 1964; Brusca & Brusca 1990; Schram 1991; Meglitsch & Schram 1991; Eernisse *et al.* 1992).

Before the use of outgroups to help determine character polarity, these conflicting views would have had little effect on intra-phyletic brachiopod classification. A broadly based phylogenetic analysis of the Brachiopoda, however, is best conducted with the aid of taxa of indisputably close affinity. This *desideratum* now seems to be fulfilled by molecular evidence, particularly through the use of ribosomal RNA to determine metazoan molecular phylogeny (Conway Morris 1993). So far the unanimous conclusion, based on comparisons of sequences of 18*S* rRNAs and using *Lingula* to represent brachiopods, is that the lophophorates are protostomes (Field *et al.* 1988; Ghiselin 1988; Patterson 1989; Lake 1990; Adoutte & Phillipe 1993), a conclusion accepted by us for this paper.

More detailed genetic studies of the lophophorates, however, are beginning to raise severe intra-phyletic taxonomic problems. An analysis of sequences from one articulated and one inarticulated species of brachiopods, as well as a phoronid and a bryozoan, showed the articulated species and the phoronid as sister taxa that, together with the inarticulated brachiopods, molluscs and polychaete annelids, form a sister clade to the bryozoans (Halanych *et al.* 1995). In contradiction to this possible diphyletic origin of the Brachiopoda, a more comprehensive 18*S* rRNA study of over 30 species, representing all Recent brachiopod superfamilies, showed them to be monophyletic (Cohen & Gawthrop 1996, and personal communication). Even so, Cohen & Gawthrop are unequivocal in nesting the phoronids within the brachiopod clade, either as a sister group of all inarticulated species or of the craniids alone. Their data rather weakly identified molluscs (possibly with annelids among others) as sister group(s) of the brachiopods and phoronids but were inadequate to show the relationship of the bryozoans.

In the light of these studies, we conclude that brachiopods form a clade meriting recognition as a phylum. In so doing we reject poorly founded assertions (Valentine 1975; Wright 1979), first refuted by Rowell (1981*a*, *b*), that the Brachiopoda are polyphyletic. We have also recognized the need to make any classification proposed by us flexible enough to accommodate even the phoronids.

Intra-phyletic classifications of the Brachiopoda have been as contentious as those deciding the intra-metazoan affinities of the phylum. Many schemes were proposed in the nineteenth century but only two have survived in popular usage more or less to the present day. They are based on the presence or absence of teeth and sockets for the articulation of the valves (the classes Articulata and Inarticulata erected by Huxley (1869)), and the ontogeny and presumed phylogeny of shell form and pedicle opening (the orders Atremata, Neotremata, Protremata and Telotremata of Beecher (1892)).

Beecher's more sophisticated classification began falling into disuse when it was found that such key diagnostic features as 'deltidial plates' and 'pseudodeltidia' had developed many times during the evolution of the articulated brachiopods (Cooper 1944) and that his order Protremata had been erected on a misinterpretation of the ontogeny and structure of the thecideidine shell (Williams 1955). By the time Part H, Brachiopoda, of the *Treatise on invertebrate paleontology* came to be published in 1965, all Beecher's orders had been discarded.

The classification adopted for Part H of the *Treatise* was founded on the assumption that it would be both utilitarian and closer to brachiopod phylogeny if it were built up from genera to superfamilies by continual morphological comparison, the pre-eminent palaeontological measure of affinity (Williams & Rowell 1965, p. H223). The superfamilies, with few exceptions, formed well-defined clusters mostly characterized by synapomorphies. Each cluster was given ordinal status and named after its best known genus (Williams 1956). Eleven such orders were recognized and, except for the poorly known Kutorginida, were assigned to the Inarticulata or Articulata, which classes had been retained. Indeed, these classes survived in universal use until recently when it was shown that several kinds of articulation were developed during early brachiopod radiation (Popov 1992).

Within a year of the issue of the brachiopod *Treatise*, a phylogenetic analysis of the phylum had been published by Hennig (1966, pp. 145–154). Some of the data used for the analysis were incorrect; even so, Hennig was prompted to suggest that the inarticulated, carbonate-shelled craniids are more closely related to articulated, carbonate-shelled brachiopods than to inarticulated, phosphatic-shelled species like the lingulids. This point had in fact already been raised within the *Treatise* itself by Jope (1965, p. H159) as a result of her biochemical studies of the brachiopod shell. In effect, the attempt to integrate a classification, based on valve articulation, with one intended to reflect the broad pathways of brachiopod evolution was already under scrutiny. However, phylogenetic analyses of Recent brachiopods by Rowell (1981*a*, *b*; 1982) endorse the higher-level *Treatise* classification.

Later reviews had the advantages of access to new data on early Palaeozoic carbonate-shelled inarticulated species and to computer programs facilitating virtually inexhaustible experiments in phylogenetic analyses. Gorjansky & Popov (1985, 1986), after appraising a mixture of reinterpretations of the development and anatomy of living species and of well-preserved skeletal features of extinct groups, concluded that phosphatic-shelled, inarticulated stocks constituted a distinct class of lophophorates (Lingulata) outside a restricted clade of carbonate-shelled forms (an amended Brachiopoda). This view, entailing bivalve homoplasy among early lophophorates, had been abandoned before the publication of an account by Nielsen (1991) of the development of *Crania*, which supported a close affinity between the craniids and other carbonate-shelled species but refuted brachiopod diphyly.

The dispute over craniid affinity is really a challenge to the use of a single character complex, in this case shell articulation, to define the higher ranks of a Linnean classification of a phylum with a well-recorded genealogy extending throughout the Phanerozoic. It came to a head with recent publications of cladograms constructed from universally accessible biological data characterizing seven extant superfamilies. The broad-frame phylogeny of Carlson (1991, p. 6; 1995) showed brachiopods to be monophyletic with craniids as primitive 'inarticulates'. That of Popov *et al.* (1993, p. 3) and Holmer *et al.* (1995) supported the division of the monophyletic Brachiopoda into two classes, the Lingulata and a new Calciata for all carbonate-shelled species (including the craniids as the most primitive member of that group).

Notwithstanding our lingering differences of opinion on phylogenetic relationships within the phylum, we have all agreed on a broad-frame classification for a revised brachiopod *Treatise*. The revision of Part H of the *Treatise on invertebrate paleontology*, which has involved over 40 contributors from 13 countries for the last seven years, is now in the final stages of completion. Over 4500 genera will be described compared with less than 1700 in the 1965 edition. The morphological revelations of so many of these new taxa, especially those from Asia and Australia and from Cambrian and Permian successions, have changed our views on brachiopod evolution as radically as have recent studies of the molecular and traditional biology of the phylum. Indeed, so much new information has been drawn from these two different sources, fossil and Recent, that it was decided to analyse their evidence independently and thereby check the versatility of any proposed classification by the following procedures.

First, no attempts were made to maximize the overlap between the lists of characters typifying the biology of living species on the one hand and the morphology of fossilized shells on the other. Only 12 of the 55 and 69 characters used to analyse relationships between Recent and Cambro-Ordovician brachiopods, respectively, assess the variability of the same features. Secondly, analyses were made of the phylogenetic relationships between contemporaneous groups at the beginning and the end of the brachiopod record. Consequently there is little direct taxonomic overlap between the groups, even at superfamilial level. *Lingula*, of course, is a spectacular exception but is counterbalanced by Recent terebratulides and thecideidines, the dominant carbonate-shelled, articulated species, which first appeared after Ordovician times.

Finally, the cladograms, representing these two differently characterized and geologically distant assemblages of superfamilies and suborders, were compared and found to be largely compatible with each other except for the location of the craniid branch. We therefore concluded that together they reflect the broad framework of brachiopod phylogeny and could be adapted as a flexible, supra-familial classification of the phylum once allowance is made for the unresolved inconsistencies concerning craniid affinities. Accordingly we propose the recognition of a supra-ordinal hierarchy based upon these cladograms, consisting of three subphyla and eight classes.

2. MATERIALS AND METHODS

Attempts to classify the Brachiopoda phylogenetically have always had to reconcile two kinds of diagnostic data. Over 95% of all described genera are extinct, occurring prolifically as fossilized shells, especially in older Phanerozoic successions. They and the higher taxa accommodating them are distinguished solely on shell morphology (including impressions of the secreting mantle and muscle attachments) with the inevitable complications arising from repeated homoplasy. The numerically insignificant Recent genera are also largely distinguished on their shell morphology; however, at suprageneric levels, anatomical, embryological and, lately, genetic differences become increasingly important and characterize six superfamilial to ordinal groups: the linguloids, discinoids, cranioids, rhynchonellides, thecideidines and terebratulides.

The first four of these Recent groups can be traced back directly to Cambro-Ordovician ancestors that are as different from one another morphologically as their living descendants are biologically. The ancestral stocks are contemporaneous with 31 extinct groups of superfamilial to ordinal status; a reconciliation of these relicts of early Palaeozoic brachiopod radiation with a cladistic extrapolation of living data seems a good way to construct a comprehensive classification. This could have been done as a single analysis based on a full array of the morphological and biological characters used to distinguish extinct and living groups. There are, however, taxonomic as well as procedural advantages to deriving phylogenies for the two groups separately. In particular, a comparison of genealogies, based on independently assembled character sets and extrapolated from contemporaneous groups at the first branches and at the tips of the brachiopod evolutionary tree, would test the validity of a reconstructed phylogeny as a basis for a supra-ordinal classification.

A large quantity of data was processed during this investigation but only lists of characters defining the Operational Taxonomic Units (OTUS) and matrices prepared for phylogenetic analyses need be recorded. Such lists and matrices are given at Appendix A.

(*a*) *Sources of data*

The data used in this investigation have been provided by many brachiopodologists, all involved in the forthcoming revision of the brachiopod volumes of the *Treatise on Invertebrate Paleontology*. Two of the authors of this paper have written some or all of the chapters on brachiopod anatomy and development, shell structure and morphology; and all five of us have, between us, described most of the taxa recorded in Cambro-Ordovician successions. We have also been given free access to relevant chapters and sections by other contributors listed in the acknowledgements. Thus we have been able to use up-to-date taxonomic information that has been carefully evaluated by over 20 specialists and will be published within the next few years.

(*b*) *Characterization of living brachiopods*

A hundred or so Recent genera are presently recognized and are assigned to 29 families. These families aggregate into six OTUS of differing hierarchical rank. The linguloids, discinoids, craniidines, rhynchonellides and thecideidines are well-defined clades of superfamilial to ordinal status. The sixth unit, the ordinal Terebratulida, is a clade with a more elaborate evolutionary history. The traditional view that Recent species assigned to the order are separable into short-looped (terebratulidines) and long-looped (terebratellidines) sister groups is upheld by studies of the genome (Cohen & Gawthrop 1996). However, students of the order now recognize at least six extant subclades including the zeillerioids, long regarded as having become extinct before the end of the Cretaceous (P. G. Baker, personal communication). Notwithstanding the identification of *Macandrevia* as a zeillerioid and the difficulties of placing aberrant groups such as the kraussinids, megathyrids and platidiids in relation to other Recent terebratulides, it remains phylogenetically valid and is operationally convenient to restrict the representation of this largest extant order to the two subordinal terebratulidines and terebratellidines.

As noted in the Introduction, the protostomous sister group of the Brachiopoda has not yet been genetically identified with certainty. Even so, representatives of the other lophophorates have been used for this analysis despite Nielsen's contention (1995*a*, *b*) that 'deuterostomous' brachiopods and phoronids are unrelated to the protostomous bryozoans. The vermiform phoronids, which lack biomineralized skeletons, can be identified only as trace fossils; and microscopic burrows in Devonian brachiopods (MacKinnon & Biernat 1970) seem to be the oldest plausible record of the phylum. In contrast, fossilized bryozoans are abundant in post-Cambrian rocks, and character suites of two Recent orders that first appeared in the Ordovician have been chosen to represent the phylum. They are the tubuliporates and ctenostomates, with organocalcitic and chitinoproteinaceous zooecia respectively. New evidence (Weedon & Taylor 1995, p. 282) that bryozoan biomineralization is more diverse than envisaged when a unified secretory model for bryozoans and brachiopods was first proposed (Williams 1984), does not weaken the use of a tubuliporate as an outgroup.

The 55 characters used to analyse present-day relationships between seven brachiopods, a phoronid, a tubuliporate and a ctenostome are listed in Appendix A(*a*)(i); and the matrix, showing character differentiation between these 10 OTUS, is given in Appendix A(*a*)(ii). The characters describe the morphological, anatomical and developmental states of the lophophorates and, except in one respect, differ little from those of other recently compiled lists. Differentiation of the integument and mantle, however, has been treated in greater detail than in the past. It has been summarized by 11 characters instead of the two or three used in previous analyses. Many comparative studies of the integument have been made within the past 30 years and have provided new insights into relationships between extinct and Recent taxa as well as between living species.

(*c*) *Characterization of extinct brachiopods*

In 1995, 28 brachiopod orders (or suborders) were widely recognized. All but two, the Terebratulida and Thecideidina, are present in Cambro-Ordovician successions with nine recorded among the early Cambrian fossil assemblages and thirteen first appearing in the Ordovician. These taxa are distinguished on shell morphology and some have been erected for rare, poorly preserved specimens as well as aberrant species of dubious affinities. Consequently, some of the orders are provisional groupings and cannot be satisfactorily represented by a single stock. The Orthida, for example, which includes some of the earliest known articulated brachiopods, is more informatively represented by five superfamilies, the Orthoidea, Billingselloidea, Skenidioidea, Plectorthoidea and Protorthoidea. In all, 33 orders, suborders and superfamilies have been used to represent the Cambro-Ordovician radiation and are listed in the matrix (Appendix A(*b*)(ii)).

The choice of one or more appropriate outgroups to analyse variations in the shell morphology of Cambro-Ordovician brachiopods poses a problem. The use of other lophophorates, which lack a bivalved shell, would give little guidance on the polarity of the morphological characters that mainly distinguish early Palaeozoic brachiopods. However, only the stratigraphically oldest taxa can be reasonably assumed to include species that could serve as an ancestral outgroup. The oldest known brachiopods are the organophosphatic paterinide cryptotretids of early Cambrian (Tommotian) age (J. Laurie, personal communication). The oldest recorded calcitic brachiopods are obolellides and chileides of the succeeding Atdabanian and Botomian stages respectively. All three were used, along with other lophophorates, in the early rounds of analysis of the Cambro-Ordovician taxa to identify the most appropriate outgroup.

The 69 characters defining the Cambro-Ordovician taxa are listed in Appendix A(*b*)(i) and set out as a matrix in Appendix A(*b*)(ii). Twelve characters, which are also used for Recent taxa, describe the composition, structure and form of the shell, the nature of the mantle canal systems, the disposition of the gonads on the valve floors and the nature and attachment of the pedicle and muscle systems. The remainder are morphological features of the shell, which were subject to repeated homoplasy. For example, the spondylia of protorthoids (and possibly skenidioids), porambonitoids and clitambonitoids evolved independently but, being similar in form, development and function, cannot be easily categorized. Other complications arise when a character state, such as a uniplicate shell, is a synapomorphy of all known species in one family but merely one aspect of familial or even generic variability in another. Indeed, in terms of the current brachiopod classification, only a minority of morphological characters defining suprafamilial taxa are free of homoplasy.

(*d*) *Analytical procedures*

The data were phylogenetically analysed by the PAUP 3.1.1 program (Swofford 1993), supplemented by the MacClade 3.0 program (Maddison & Maddison 1992). Heuristic searches were undertaken by stepwise addition of taxa (a random sequence option of 10 replicates) or by branch-and-bound methods, but exhaustive searches were also made if the data allowed. All characters describing Recent and Cambro-Ordovician taxa were unordered during analyses, enabling polarity to be determined exclusively by outgroup methods. The majority were set up as multistate and, to reduce the effects of homoplasy, were scale-weighted (Swofford & Begle 1993, p. 19). Binary state characters were equally weighted during searches.

3. RESULTS

Although the same procedures were adopted to construct genealogies from data on the diversity of Recent and Cambro-Ordovician brachiopods, different outgroups and character sets warrant independent accounts of the results.

(*a*) *Genealogy of Recent brachiopods*

The conflicting interpretations of genetic data on relationships between brachiopods and other lophophorates prompted analyses of the brachiopods in varying combinations with *Phoronis* and/or tubuliporate and ctenostomate bryozoans as outgroups. With the exclusion of the bryozoans, the craniid was basal to a clade of the remaining brachiopods (figure 1*a*). The exclusion of the tubuliporate (with calcified zooecia) resulted in the nine remaining taxa forming six trees, each consisting of a brachiopod clade relative to the *Phoronis*/ctenostome outgroups. Within these six clades, the craniid served equally as a sister group to either the organophosphatic 'inarticulates' or the organocalcitic 'articulates' (figure 1*b*, *c*). A strict consensus tree (figure 1*d*) portrayed the brachiopod clade as divided into an unresolved trichotomy composed of the craniid, the inarticulated organophosphatic and the articulated organocalcitic branches. In relation to the two other arrangements of both bryozoans with or without *Phoronis*, the brachiopod clade invariably consisted of two subclades, one with the craniid as a sister group to the organophosphatic 'inarticulates' and the other with the rhynchonellid as sister group to various arrangements of the two terebratulides and the thecideid.

As expected, the position of the craniid branch within a lophophorate tree is sensitive to the choice of outgroups. In these circumstances no cladogram can satisfactorily represent the biological data given in Appendix A(*a*); and our choice of one with *Phoronis* and both bryozoans as outgroups can be justified only as retaining representatives of all lophophorate phyla. Irrespective of scale-weighting of characters, analyses of such data by a branch-and-bound search discovered three trees with a length of 129 steps and a retention index of 0.9; the consensus tree is shown in figure 2.

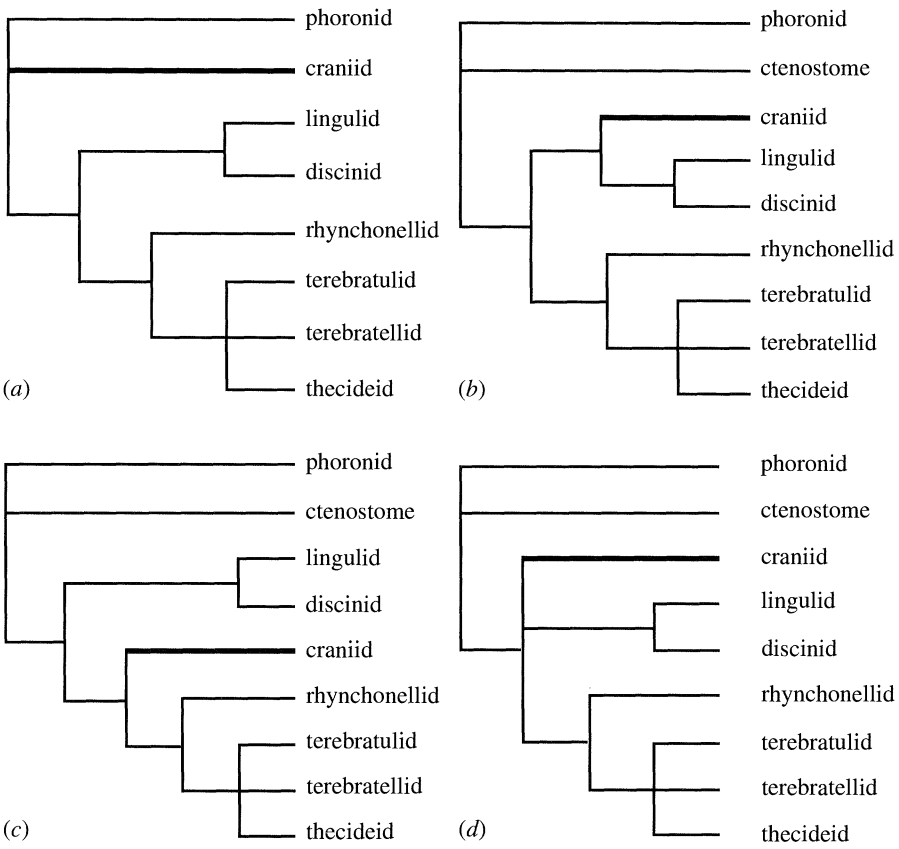

Figure 1. Four trees derived by branch-and-bound analyses of the matrix shown in Appendix A(*a*)(ii) with various combinations of other lophophorates as outgroups; variations in brachiopod branches are restricted to relocations of the craniids and regroupings of the terebratellid/thecideid polytomy within the 'rhynchonellid' clade: (*a*) shows the location of the craniid branch in three of the six trees generated by a phoronid outgroup (the position of the craniid branch in the other three trees relative to all other brachiopods is identical with that shown in (*b*); each of (*b*) and (*c*) shows the location of the craniid branch in three of the six trees derived with a phoronid and ctenostome bryozoan as outgroups; (*d*) is a strict consensus of the six trees represented by cladograms (*b*) and (*c*).

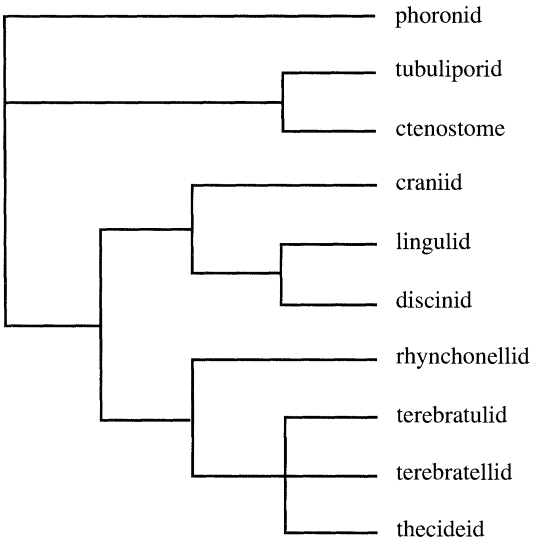

Figure 2. A strict consensus of three trees derived by a branch-and-bound analysis of the matrix shown in Appendix A(*a*)(ii), with *Phoronis* and the tubuliporate and ctenostomate bryozoans serving as outgroups.

The cladogram in figure 2 portrays a strict consensus of all clades containing the rhynchonellide as a sister group of a thecideid–terebratulide trichotomy. Synapomorphies of this 'rhynchonellid' clade include: an astrophic shell articulated by cyrtomatodont teeth and sockets; a proteinaceous, calcitic exoskeleton with a fibrous secondary layer; a reversal of the mantle rudiment during larval development and the closure of the posterior arc of the mantle cavity with concomitant fusion of mantle lobes (Williams 1956); a pedicle developing from a rudiment; and an intestine without an anus. The lingulid and discinid form another 'lingulid' clade characterized by such synapomorphies as: a shell composed of chitin, proteins (including collagen), glycosaminoglycans (GAGS) and apatite in stratiform successions; a double row of tentacles along the entire length of the lophophore; and gonads restricted to the body cavity.

The craniid as a sister group of the lingulid clade is also unique in the tabular growth of the laminar secondary layer of its calcitic shell and the lack of pedicle even during larval development when the initial attachment area of the ventral valve consists of an area of thickened microvillous epithelium with inclusions and fibrils (Nielsen 1991, p. 19).

The equivocal relationship of the craniids with the lingulid and rhynchonellid clades, as shown in figures 1 and 2, reflects their affinities with both groups. An enlarged lingulid clade containing the craniids would be characterized by such synapomorphies as a circumferential mantle cavity, a muscle system consisting

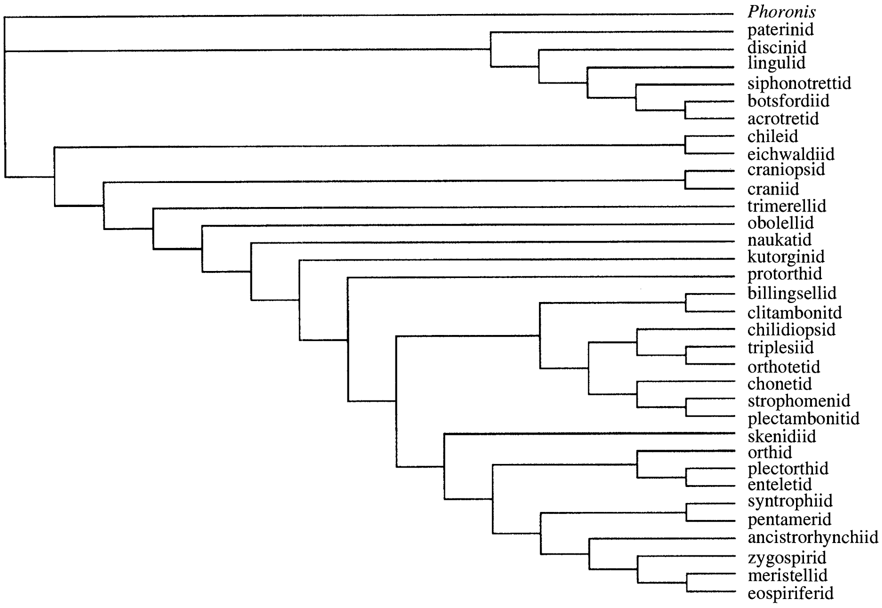

Figure 3. The single tree derived in a heuristic search involving a stepwise random addition of taxa in ten replicates within the matrix shown in Appendix A(*b*)(ii), for which the character states were weighted in the proportions given in Appendix A(*b*)(i).

of obliques and two pairs of adductors, the presence of a transient median tentacle in the early growth of the lophophore and, within that organ, the median division of the brachial canals into two separate cavities. Synapomorphies of a rhynchonellid clade incorporating the craniids would include a proteinaceous calcitic shell with an inner epithelium not involved in the secretion of the periostracum, a single row of tentacles on trocholophous lophophores, gonads suspended in mantle sinuses, and lecithotrophic larvae. Some of these characters can be discerned in fossil brachiopods by studies of either the chemico-structure of the shell or anatomical impressions on valve interiors. Further evidence for resolving relationships between living brachiopods could therefore be expected from an analysis of the early Palaeozoic group.

(*b*) ***Genealogy of Cambro-Ordovician brachiopods***

The greatest difficulty in analysing Cambro-Ordovician data was choosing a means of polarizing characters. With stratigraphic polarity criteria rather than outgroup criteria, the search for an ancestral group was limited to the paterinides, obolellides, kutorginides and chileides, which are among the oldest brachiopods known and well represent the diversification of the phylum during early Cambrian radiation. Excluding stratigraphic first appearances from the analysis, an exploratory use of these taxa, in combination and singly, as outgroups to other Cambro-Ordovician brachiopods as a whole, resulted in a variety of trees. Crucial parts of many of the resultant cladograms were inconsistent with the geological record and with several previously prepared phylogenetic analyses of selected ordinal or supra-ordinal taxa (Carlson 1991; Williams & Brunton 1993; Brunton *et al.* 1995; Holmer & Popov 1996). Differences between the cladograms, however, were relatively simple recombinations of three major groups: an inarticulated, organophosphatic-shelled clade (lingulate); an articulated, calcitic-shelled clade (orthate); and a paraphyletic group in between (chileate). When the obolellide and kutorginide taxa were used singly as outgroups, the chileate group and the lingulate clade formed a larger clade with the paterinide taxon as a sister group. The only difference between the two arrangements was the dissociation of the naukatoids from the chileate segment and their attachment to the orthate clade, which had the kutorginide (or protorthide) taxon as a sister group. With the chileates as the outgroup the remaining taxa formed two sister clades: one composed of the organophosphatic-shelled taxa; and the other comprising the rest of the calcitic-shelled brachiopods. Taking into account stratigraphic age and other analyses previously cited, the most plausible cladograms are those with outgroups of paterinides, obolellides and kutorginides or of the paterinide taxon on its own. These cladograms were identical, with the paterinides providing stratigraphic polarity (Swofford & Begle 1993, p. 26), and other organophosphatic-shelled brachiopods basal to a very large clade consisting of exclusively calcitic-shelled species.

The use of bryozoans as well as *Phoronis* as outgroups gave rise to stratigraphically anomalous derivations such as the paterinids and lingulids from the craniids. *Phoronis*, as the sole outgroup, however, released the paterinids from this primary role and enabled important assumptions to be made on the polarity of many characters distinguishing Cambro-Ordovician groups, as the paterinide shell is extraordinarily diverse in its composition and morphology (see below). A single tree (figure 3), with a retention index of 0.79, was identified in a heuristic search, involving a stepwise random addition of taxa in ten replicates within the matrix (Appendix A(*b*)(ii)) of 34 taxa and 69 scale-weighted characters (Appendix A(*b*)(i)).

To test the stratigraphic consistency of this tree topology, two subsequent analyses were performed. First, a stratigraphic consistency index (SCI) (Huelsenbeck 1996) was calculated, with the program StratCon 1.0 (available from J. Huelsenbeck, University of California, Berkeley). This index represents the number of stratigraphically consistent nodes for a given tree, relative to the total number of possible nodes. The tree in figure 3 has an SCI of 0.61 and a permutation probability of 100, which indicates that none of 100 random permutations of the age ranks to the branch tips had an SCI of 0.61 or more. Secondly, a stratocladistic analysis (Fisher 1992; Maddison & Maddison 1992) was performed by adding the first appearance in the stratigraphic record to the original character matrix (Appendix A(*b*)(ii)) as a designated stratigraphic character. With MacClade 3.0 (Maddison & Maddison 1992), a full search of the tree topology in figure 3 was performed, now including the relative stratigraphic positions in the data matrix. A few minor exchanges in topology resulted: protorthids moved to the base of the skenidiid clade; chonetids moved to the base of the chilidiopsid clade, with strophomenids, plectambonitids and clitambonitids as successively more primitive members of the billingsellid clade; and pentamerids moved to the base of the ancistrorhynchiid clade. These stratigraphic tests suggest that the tree topology in figure 3 is highly robust with respect to both morphological and stratigraphical data.

In the cladogram (figure 3), the paterinides are shown as a sister group of a lingulid clade. Both groups are characterized by an organophosphatic, inarticulated shell although that of the paterinides is also strophic with pseudo interareas indented posteriomedially by a variably covered delthyrium and notothyrium. Moreover, the paterinide valve interiors also bear impressions of gonads, canal systems and posteriomedian muscle scars, which seem to be similar to those of the orthides (Laurie 1987). The paterinides are even like the chileates in one respect at least. No foramen has yet been found but they could have been attached to other living organisms (Conway Morris *et al.* 1982, p. 25, pl. R), and although a 'pedicle' might have emerged between the valves it is also possible that such an organ did not develop and that the pseudointerareas were underlain by a posterior mantle cavity (Williams & Rowell 1965, p. H89) or linked by a bridging periostracal strip that would have been secreted by fused mantle lobes and could have served as a ligament.

The organophosphatic brachiopods, other than the paterinides, are evidently monophyletic although relationships within this lingulid clade are still in some doubt (Holmer & Popov 1996). Synapomorphies of the clade include: a canaliculate shell fabric; a dispersed, specialized musculature that controlled a three-dimensional movement of the inarticulated valves; the confinement of the gonads to the body cavity; and the permeation of the mantles by baculate canal systems with interiomedial as well as marginal fringes of *vascula terminalia*.

Two extinct orders, the Siphonotretida and Acrotretida compose, along with the Lingulida, the Cambro-Ordovician lingulid clade, which has been accorded a supra-ordinal status. An interesting aspect of the analysis is the support for discinoids as having originally been a sister group of the remaining taxa within the clade. Such a relationship accords with the discovery of primitive discinoids in the early Cambrian of China (L. E. H., L. P. & Huo, X. G., personal communication). This would imply that the pedicle notch is an apomorphy of the linguloids and that both superfamilial branches evolved from a stem group with an elongate cylindroid extension of chitin-secreting epithelium and coelom serving as a pedicle. An orbiculid (*Orbiculoidea*) with such a pedicle has recently been found in the Lower Devonian Hunsrück Slate (W. H. Südkamp, personal communication).

Our analysis indicates that all other Cambro-Ordovician brachiopods were derived from a group with an impunctate carbonate shell pre-eminently characterized by a calcitic fibrous secondary layer. This extrapolation refutes the conclusions of Williams and Hurst (1977) but confirms those of Rowell & Caruso (1985, p. 1239) who recognized the antiquity of the fabric. It is also compatible with the stratigraphic ranges of early Cambrian carbonate-shelled species. The chileides are the earliest known calcitic-shelled brachiopods with a strophic hinge line (Popov & Tikhonov 1990) and include the Lower Cambrian *Kotujella* Andreeva, which has a fibrous secondary layer, as have contemporaneous kutorginids (Williams 1968).

The distinctive fibrous fabric, however, was not universally developed. Apart from its polyphyletic replacement by cross-bladed lamination in Ordovician strophomenides and chonetidines (Williams 1970; Brunton 1972), it is unknown in carbonate-shelled inarticulated brachiopods except possibly for the eichwaldioids (Wright 1981). The secondary layer of *Trematobolus*, which is assumed to typify the fabric of all obolellides (including the naukatidines), has been described as laminar (Williams & Wright 1970, p. 45). The constituents of the layer, however, are lenticular rather than parallel-sided in cross section and were probably membrane-bound in life, like ensheathed fibres rather than spirally growing tablets intercalated within proteinaceous sheets.

In contrast with the foliated shell of the obolellides, the secondary layers of three orders, currently classified together (Gorjansky & Popov 1985), are either truly laminar successions of tablets as in craniides and craniopsides (Williams & Wright 1970) or are invariably recrystallized as in the trimerellides and were possibly aragonitic in the original state (Jaanusson 1966). All three orders are widely regarded as having first appeared in the Ordovician but Jin & Wang (1992) have described *Heliomedusa* from the Lower Cambrian (?Botomian) of China, which is probably an early craniopside. The secondary fabrics of carbonate-shelled inarticulated groups might therefore have originated more or less contemporaneously. Yet neither the derivation of obolellide folii from fibres nor the secretion of an aragonitic secondary layer in trimerelloids are as fundamental a transformation as the development of spirally secreted laminae of the craniides. Even the lamination, forming the cross-bladed fabric of strophomenide shells, consists of arrays of lath-shaped constituents that had evolved from fibres in the chonetidines at least (Brunton 1972). Consequently there is a strong possibility that the craniide–craniopside tabular lamination evolved independently of membrane-bound fibres.

The mode of attachment of Cambro-Ordovician brachiopods is extremely variable. Cladistic evidence favours the organ of attachment of the stem group as an outgrowth of the outer epithelium of the ventral mantle. This origin is characteristic of living species of discinoids and craniides even though the latter are cemented by a central pad of ventral ectoderm without a trace of any outgrowth. The ventral perforations of the chileides and the later, related eichwaldioids are also consistent with the development of a cuticular pad arising from the ventral mantle (Williams *et al.* 1997) and usually associated with a colleplax (Wright 1981) or homologous structure.

These prototypic 'pedicles' also varied in location relative to the shell and even encroached on the junction between the outer and inner epithelium of the ventral valve, as is shown by the morphology of the early lingulide shell. The pedicle of most linguloids emerged between the valves as an outgrowth of the inner epithelium (posterior body wall) according to Yatsu's (1902) study of Recent *Lingula*. However, this origin might not have been characteristic of the lingulellotretids and dysoristids with pedicle openings entirely restricted to the ventral valves, which are similar to those of most acrotretoids (Holmer & Popov 1996).

Various openings in the calcitic shells of Cambro-Ordovician brachiopods have been interpreted as pedicle apertures. The delthyria of the chileides could not have accommodated a pedicle if the large perforation in the ventral valve had contained an adhesive cuticular pad. Instead the notch could have indicated the location of the anus on the posterior body wall as postulated by Rowell and Caruso (1985) for the delthyrial/notothyrial gape of the kutorginide *Nisusia*. In the latter group, a small supra-apical foramen probably contained a peduncular structure, as did the internal tube with its external supra-apical opening rather than the open delthyria of early obolellides (Geyer & Mergl 1995). Such an organ would have acted as an adhesive anchor but would not have served as an axis of rotation for the shell as in Recent species. Indeed, no adjustor muscle scars have been recognized within the muscle impressions of protorthides, billingselloids and strophomenides (L. R. M. Cocks, personal communication). Among the clitambonitidines, evidence for adjustor scars in *Clinambon* (see Öpik 1934, pl. xvll, 1) is compromised by the sealing of the pedicle foramen later in the ontogeny of this genus (A. D. Wright, personal communication); the scars so identified are probably lateral lobes of the diductor muscles like those differentiated in many orthidines and strophomenides. Schuchert & Cooper (1932, p. 111) cited pedicle attachment scars in *Hemipronites* and *Deltatreta*, but such impressions would have been made by the cuticular cover of the pedicle and would not have indicated the presence of adjustors. Moreover, Wright (1994) has figured the impressions of *vascula terminalia* along the margins of the ventral interareas of several clitambonitidines. They indicate the presence, *in vivo*, of a posterior body wall that would have precluded the development of a pedicle from a rudiment. The evidence for true adjustor scars in the triplesiidines is equally equivocal. Wright (1963, p. 746) identified two impressions within the ventral muscle field as adjustor scars. They are, however, situated well posterior of the internal opening of a long pedicle tube, sporadically developed in triplesiidines, and could not have operated as adjustors.

Unquestionable impressions of ventral adjustor muscle bases are found in lower Middle Cambrian orthide species assigned to the eoorthids and bohemiellids. Indeed, adjustor scars and pedicle callists are normally impressed on the ventral interiors of all orthidines (excluding the billingselloids) and syntrophiidines. This kind of ventral muscle base, however, was more or less restricted to the umbonal chamber, whereas that of Recent brachiopods is impressed well to the anterior. Anatomical reconstruction suggests that, although the orthidine pedicle probably developed from a rudiment, it had a negligible base that was largely external to the shell. In contrast, the anteriorly placed ventral muscle bases of rhynchonellides, atrypides, spiriferides and terebratulides have always afforded space in the umbonal chamber for the pedicle capsule, an assumed manifestation of mantle reversal (Williams 1956, p. 256).

The evolution of valve articulation, involving teeth and sockets in the delthyrial and notothyrial regions, is another differentiating aspect of the Cambro-Ordovician radiation of carbonate-shelled brachiopods. According to our model, such articulatory devices were not developed in the ancestral brachiopod and are unknown in the phosphatic-shelled groups or the carbonate-shelled craniides, craniopsides, trimerellides and chileides. However, likely descendants of the chileides, the dictyonellidines, are characterized by a cardinal process flanked by a pair of furrows that receive rudimentary 'teeth' of the ventral valve, and by posteriomedian muscle scars feasibly interpreted as diductor bases. The Dictyonellida include the post-Cambrian eichwaldiids and the late Palaeozoic isogrammids, which share a synapomorphy of an articulatory system dominated by a cardinal process (eichwaldiid articulation). In contrast, the articulation of the trimerellids was effected by a dorsal hinge plate fitting into a cardinal socket (Norford & Steele 1969).

The articulatory device, developed in later obolellides, consists of a pair of submedian denticles on either side of a narrow delthyrium fitting into small dorsal sockets; the muscle scar arrangement suggests that internal obliques functioned as diductors (Popov 1992; Geyer & Mergl 1995). The obolellide articulation is essentially the same as that of the naukatidines except that the teeth of the latter are situated on a platform (the anterise of Popov (1992)).

Primitive articulatory devices, flanking delthyrial and notothyrial openings and associated with diductor muscle systems, also evolved independently in the kutorginides as a pair of broadly curved edges to the ventral interarea fitting above obtusely triangular plates in the dorsal valve (Cooper 1936; Rowell & Caruso 1985), and in the protorthides as small teeth at the junctions of the delthyrium and the free spondylium, which fitted laterally of rudimentary outgrowths at the notothyrial edges (Cooper 1976).

The most successful articulatory device ever to have evolved was the orthide/strophomenide type of hinge teeth and dental sockets. It first appeared among early Cambrian species and is ancestral to the system characteristic of Recent articulated species, but its precise origin has yet to be determined. The Lower Cambrian *Leioria* (Cooper 1976) has a protorthide spondylium but deltidiodont teeth, representing the dorsal projections of ridges bounding the delthyrium, and sockets, defined by erect blade-like brachiophores in the manner of orthidines and enteletidines. In contrast, the teeth of the Middle Cambrian bohemiellids are transverse and normally well lateral of the delthyrium, whereas those of billingselloids and strophomenoids are also essentially transverse (but immediately lateral of the delthyrium) and usually fit into shallow sockets defined by flat-lying ridges.

The orthoid deltidiodont teeth and sockets are also characteristic of the pentamerides. However, the intricate interlocking device of cyrtomatodont teeth and sockets first appeared in the astrophic rhynchonellides and are a synapomorphic complex shared with atrypides, athyridides, spiriferides, terebratulides and thecideidines.

One other complex of morphological features plays an important part in the supra-ordinal classification of brachiopods. Skeletal supports of the lophophore have developed independently during the evolution of many groups. Outgrowths from the floors of dorsal valves in the form of plates and platforms (but not necessarily septa partitioning the mantle cavity) almost certainly gave some support to part or all of the lophophore and appeared among acrotretoids, strophomenides and orthides after these groups had become well established (Williams & Rowell 1965). In contrast, apophyses arising from the dorsal hinge line, where they are normally extensions of inner socket ridges, constitute a transformation series in the elaboration of lophophore supports. Comparison of the disposition of the inner socket ridges of Middle and Upper Cambrian billingsellids and eoorthids shows that those of the former were flat-lying whereas those of the latter projected ventrally as brachiophores (Williams & Hurst 1977). The billingselloid socket ridges are precursory to those of the strophomenides (*s.l.*), which functioned only as the inner containing walls of the dental sockets. Among the orthides, brachiophores also served as attachment areas for the dorsal adjustors and, in Ordovician genera such as *Phragmorthis* and *Skenidioides*, extended sufficently anteriorly to have supported the mouth segment of the lophophore (Williams & Rowell 1965).

The growth of apophyses (crura) supporting the mouth segment of the lophophore in the modern style, however, first occurred in early Ordovician rhynchonellides and accompanied transformations of ancestral syntrophiidine cardinalia and articulation, notably the loss of all traces of a notothyrial platform and the differential secretion and resorption of cyrtomatodont teeth and sockets. The further elaboration of skeletal supports of the lophophore in the form of calcareous spiralia first characterized the later-appearing atrypides and then, as descendants from that group, late Ordovician athyridines, meristellids and spiriferide eospiriferids.

No other features of Cambro-Ordovician brachiopods clearly delineate broad phylogenetic trends in shell morphology. Muscle differentiation, as deduced from the distribution of scars on valve interiors, did take place but is better reflected in the development of articulation and the pedicle. Ancillary structures such as spondylia or deltidia developed many times and are not reliable diagnostic features at the supra-ordinal level. Even mantle canal systems were subject to repeated homoplasy in calcitic-shelled species, especially as a result of changes brought about by the enlargement of gonadal sacs during sexual maturity.

(*c*) *Reconciliation of Recent and Cambro-Ordovician genealogies*

The genealogies derived by analyses of the characteristics of Recent and early Palaeozoic brachiopods are compatible and can be reconciled at supra-ordinal levels. Nineteen synapomorphies of ordinal or supra-ordinal significance were identified (Appendix A(*c*)(i)), with seven related exclusively to the morphology and chemico-structure of the shell. Moreover, only two of the remaining twelve have left no trace in the fossil record. They are the distribution of tentacles on lophophore ridges and the presence of lobate cells in the outer mantle lobe (even the presence of an anus has been deduced from presumed faecal evidence in the kutorginides (Rowell & Caruso 1985)). Fourteen groups of brachiopods were analysed in relation to *Phoronis*. Three, the lingulid, craniid and rhynchonellid clades, involve both Recent and extinct groups and contain two to six orders. Four of the wholly extinct groups, the paterinid, trimerellid, kutorginid and protorthid, are single orders, whereas the remainder consist of no more than two orders according to present taxonomic practices. Even these, however, are variable in morphology and shell structure so that all fossil groups are coded for up to three and five multistate and unknown characters respectively, which together constitute nearly one-quarter of the total characterization of the entire ingroup (Appendix A(*c*) (ii)).

Even with the exclusion of tentacular distribution and lobate cell differentiation, the variability or uncertainty of character states generated a large number of trees (438 in a heuristic search involving stepwise random addition of taxa in 10 replicates). Various supra-ordinal groupings can be derived from a 50% majority-rule consensus of these trees (figure 4) including an obolellid–rhynchonellid clade, a paterinid–chileid paraphyletic group, and a lingulid sister group to all other brachiopods. Such grouping is also evident when *Phoronis* is eliminated as an outgroup and relationships between the ingroup are represented as an unrooted tree (figure 5). Two of these units are

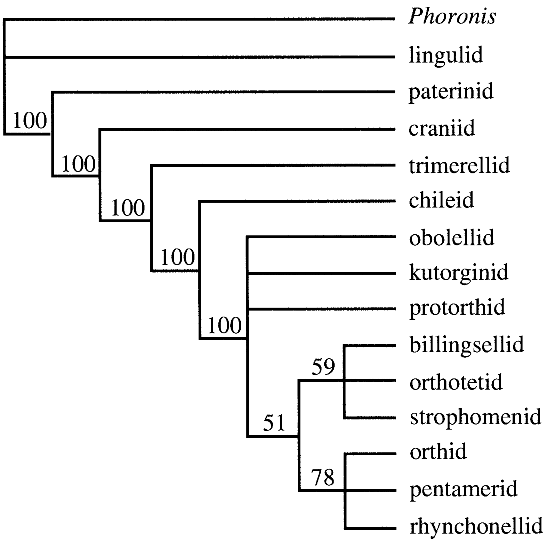

Figure 4. A majority-rule consensus of 438 trees derived in a heuristic search involving a stepwise random addition of taxa in ten replicates within the matrix shown in Appendix A(*c*)(ii) with *Phoronis* as outgroup.

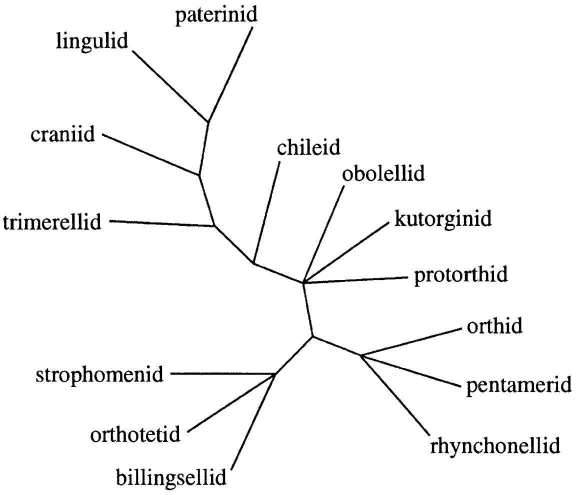

Figure 5. Unrooted representation of the relationships between taxa in figure 4.

distinctive. The lingulid group is characterized by an organophosphatic shell with a stratiform secondary layer and lacks any articulation of the valves. The obolellid–rhynchonellid clade is distinguished by the fibrous secondary layer of their organocarbonate shell and the development of a diductor muscle system signalling valve articulation. For classificatory purposes, the paraphyletic contents of the third group could be redistributed. The paterinids fit well with the lingulids; the fibrous-shelled chileids could be regarded as a sister group to the obolellid–rhynchonellid clade, and the craniids (with trimerellids) could be distinguished as having an organocarbonate (variably aragonitic) laminar shell and lacking evidence of a pedicle or cuticular pad.

With regard to the obolellid–rhynchonellid clade, the true tooth and socket arrangement is a synapomorphy only of the billingsellid/rhynchonellid subclade (figure 4). Morphological evidence of the development of an adjustor-controlled pedicle from a rudiment and the loss of the posterior body wall and anus is first found in the orthid/pentamerid/rhynchonellid group, whereas the development of an astrophic shell and crura in support of the mouth segment of the lophophore and evidence of mantle reversal are restricted to the rhynchonellid constituent, the youngest group to emerge during Cambro-Ordovician times.

4. CONCLUSIONS

The contradictions inherent in current phylogenetic analyses of brachiopods are illustrated in figures 1–4. The use of any of these cladograms as the exclusive basis of a phylogenetic classification would necessarily be insecurely founded. We were therefore left with three options: to choose one of the cladograms and defend its translation into a phylogenetic classification; to defer proposing a classification until more refined data were available to provide a stable pattern of phylogenetic relationships; or to devise an interim workable classification that is not phylogenetic but facilitates current taxonomic studies.

(*a*) *Prospects for a phylogenetic classification*

The constraints governing the erection of a strictly phylogenetic classification are explicit (de Queiroz & Gauthier 1990; Smith 1994). Phylogenetic classifications recognize only monophyletic groups (clades). Paraphyletic higher taxa represent incomplete systems of common ancestry and are *ad hoc* and ambiguous in their delineation. Polyphyletic higher taxa are based on nonhomologous characters and are artificial.

The recognition of monophyletic taxa depends entirely on the structure of a particular cladogram, ideally one that is highly corroborated by several independent sources of data. Our cladograms are clearly unstable. The relative merits of outgroups used for rooting the trees, illustrated in figures 1–4, are currently unresolvable, as are contradictions in character data taken from different sources (the anatomy, embryology, genetics and morphology of extant and extinct species). It would be unwise at this point to erect a classification on any single tree topology constructed for this paper. Rooting difficulties, discussed in §3, lead us to prefer the unrooted tree presented in figure 5. Yet even this analysis could not be transformed into a strict phylogenetic classification appropriate to all the conflicting data at hand. We therefore decided to erect a classification that could accommodate currently recognized taxa and yet be flexible enough to incorporate changes resulting from refinements of outgroup and character data.

(*b*) *A supra-ordinal brachiopod classification*

Our considered view is that a reliable database of all brachiopod characters is unlikely to be established for several years. There are too many imponderables and significant inconsistencies in the anatomical, embryological and genetic evidence to expect an early resolution of data conflicts. Meanwhile there are two existing formal classifications (Williams & Rowell 1965; Popov *et al.* 1993) that inadequately serve

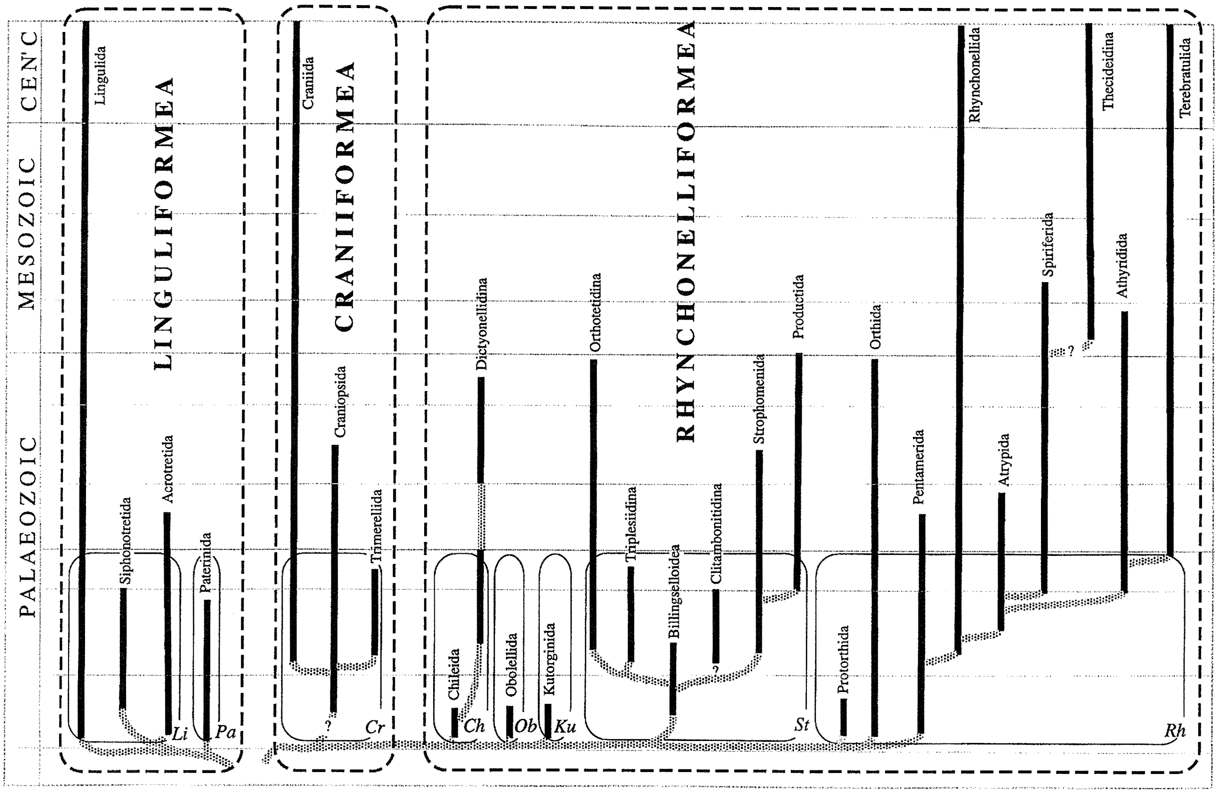

Figure 6. The proposed supra-ordinal classification of the Brachiopoda superimposed on a geological chart with the faint lines representing systemic boundaries proportionately spaced on a vertical radiometric time scale of 545 Ma and showing the chronostratigraphic ranges of the principal taxa within three subphyla (defined by broken-line boxes) composed of eight classes (solid-line boxes) labelled, from left to right, Li (Lingulata), Pa (Paterinata), Cr (Craniata), Ch (Chileata), Ob (Obolellata), Ku (Kutorginata), St (Strophomenata) and Rh (Rhynchonellata).

current taxonomic requirements. We are agreed that the practical necessities of devising a workable classification now heavily outweigh any advantage in waiting for the collation of a definitive database and for the identification of the indisputable brachiopod sister group. We concede that any such interim classification will undergo revision, especially as genetic and embryological variability between extant species becomes better understood. However, we believe that the major features of the classification proposed here are unlikely to be drastically changed for reasons given below.

There is firm evidence to support a continuing recognition of the subphylum, Linguliformea, as a monophyletic group (figures 1 and 3) (Holmer & Popov 1996; Carlson 1995; Cohen & Gawthrop 1996), although it seems to be paraphyletic in figure 4 with *Phoronis* as an outgroup.

We have chosen to erect another subphylum, Craniiformea, specifically because the phylogenetic position of the craniid group is so uncertain. The craniids appear as one branch of an unresolved polytomy in some cladograms (figure 1*a*) and as a sister group to the Linguliformea (figure 1*b*) or of the Rhynchonelliformea (figures 1*c* and 3) in others. These variable relationships could represent real, and as yet unexplained, character conflicts rather than differing interpretations of existing data, and are most conveniently accommodated in a separate subphylum.

A third subphylum is proposed for the rhynchonellid clade, which is constant in all cladograms although variably associated with other branches (figures 1–4). These branches include a number of separate, extinct plesions, mostly of early Palaeozoic age. They are the paterinids, chileids, obolellids, kutorginids and strophomenids (*s.l.*), all of which have been given class status. The wisdom of so recognizing such plesions might be questioned but given the uncertainty of current information on these groups, several of which are poorly known, we feel that recognition can be justified within the taxonomic hierarchy discussed below (see also Patterson & Rosen 1977; Smith 1994).

The supra-ordinal nomenclature proposed for this taxonomic revision of the Brachiopoda has been carefully considered. We were wary of coining terms signifying allegedly distinctive features of new higher taxa. Previous brachiopod classifications have foundered when it became apparent that 'protremata' and 'articulata', for example, were no longer exclusively diagnostic of the brachiopods they embraced. We have therefore adapted generic names to designate all higher taxa. The generic names chosen for defining subphyla are those of members of each of the three main categories of living brachiopods, which are indisputably linked to the oldest stem groups. The subphylum name Linguliformea (Popov *et al.* 1993) was already in circulation and we considered it appropriate to use the same suffix for the Craniiformea and Rhynchonelliformea.

The broad frame of the proposed classification and the assignment of plesions among the subphyla are outlined below and in figure 6 and formally proposed and diagnosed in Appendix B.

The Linguliformea consists of all brachiopods with organophosphatic shells that also covered their planktotrophic larvae. No linguliforms ever developed biomineralized teeth and sockets for shell articulation, although the grouping of the paterinid ventral muscle bases suggests valve movement about a strophic hinge line controlled by a 'ligamental strip' of periostracum. The short-lived paterinate class is also distinguished by mantle impressions of exclusively marginal *vascula terminalia* and gonadal sacs, which are more characteristic of carbonate-shelled brachiopods. The synapomorphies of the Lingulata clade of three orders include the canaliculate condition of the stratiform shell, a mantle permeated by interiomedial as well as marginal *vascula terminalia*, and gonads restricted to the body cavity.

The core of the Craniiformea is a clade consisting of two orders, the inarticulated Craniida and Craniopsida, which, with the articulated Trimerellida, possess a non-fibrous carbonate shell and lack a pedicle; together they compose the class Craniata. The Chileata (including the Dictyonellidina), in contrast, have a fibrous secondary shell and a perforated ventral valve floor that is believed to have housed a cuticular pad serving as a 'pedicle' holdfast. The cladistic position of the chileates relative to the craniates is equivocal. It appears as a paraphyletic associate of the craniid–trimerellid branches in figure 3 but as a sister group to the obolellid–rhynchonellid clade in figure 4. On balance, we favour the inclusion of the chileates in the Rhynchonelliformea.

The Rhynchonelliformea, the largest subphylum with 19 of the 27 recognized orders, is well founded on several important clades including the Rhynchonellata, which embraces all Recent articulated species. The subphylum shares with the Craniiformea the characteristic protegulum of a lecithotrophic larva so that the principal rhynchonelliform synapomorphies are: the fibrous secondary layer of an organocarbonate shell; the presence of a pedicle; and the development of a recognizable diductor muscle system controlling the opening of the valves about a hinge axis defined by interareas.

Three of the plesions herein recognized as classes, the Obolellata, Kutorginata and Strophomenata, share the synapomorphy of a supra-apical pedicle representing a specialized outgrowth of the posteriomedian sector of the ventral mantle. The first two classes are further distinguished by simple articulatory devices and the last by deltidiodont teeth and dental sockets bounded by plates. This classic tooth and socket arrangement is also characteristic of the Orthida as was a novel type of pedicle controlled by adjustor muscles, which occupied the delthyrial opening and almost certainly developed from a rudiment. The strophomenate clade, which underwent a loss of pedicle and articulation in some late Palaeozoic productides, was further involved in the only major transformation affecting the fibrous secondary layer. The typical strophomenate cross-bladed lamination, however, was polyphyletic and possibly indicated a chemico-structural change in the shell of the stem group that led to an inherent tendency for blade-like fibres repeatedly to amalgamate laterally into laminae. Among the reconstituted strophomenates, only the clitambonitidines call for comment. Recently, Wright & Rubel (1996) concluded that the clitambonitidine delthyrial cover is essentially a deltidium rather than a pseudodeltidium and that the delthyrium was open in young shells. This reinterpretation, however, does not necessarily confirm that the clitambonitidine pedicle developed from a rudiment. Apart from the sealing of the foramen in many stocks, other evidence discussed above suggests that the valves were separated by a posterior body wall and, provisionally at least, the clitambonitidines can be relocated within the Strophomenata.

The taxonomic location of the protorthid plesion is equivocal. Protorthides typically had a weakly developed articulatory device that could have evolved independently of deltidiodont teeth and sockets. In contrast, as previously noted, *Leioria* has deltidiodont teeth and brachiophores and, in common with other protorthides, could have had a pedicle rudiment. Pending further study of this poorly known group, we have accorded the uncoded *Leioria* evidence an overriding significance and provisionally assigned the Protorthida to the rhynchonellates. The transformations defining the rhynchonellate Orthida were the foundation of the modern articulated brachiopod. In addition to the inferred development of a pedicle rudiment, other synapomorphies are likely to have been the loss of the posterior body wall, which persisted in the Strophomenata, and the loss of the anus. Projecting brachiophores were also a new development of the orthides and pentamerides; in the latter group an astrophic shell emerged for the first time.

The main synapomorphies of the other orders composing the Rhynchonellata, which range from the rhynchonellides and spire-bearers to the terebratulides and thecideidines, are mantle reversal and those leading to skeletal supports for the lophophore in the form of crura, spiralia and loops. However, endoskeletal spiculation first appeared in some spiriferides (Cooper 1942) and might be homologous with that characteristic of terebratulides and thecideidines, whereas endopunctation with a distal microvillous brush is a synapomorphy of later spiriferides, terebratulides and thecideidines.

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APPENDIX A. DATA USED IN PHYLOGENETIC ANALYSES

(*a*) *Data for analysis of Recent brachiopods*

(i) *The states of the 55 characters used in the phylogenetic analyses of Recent brachiopods and other lophophorates listed in Appendix A*(*a*)(*i*

External cover		
1.	General form	agglutinated tubes (0), zoecia only throughout (1), larval bivalves, adult zoecia (2), bivalved (3)
2.	Bivalves	not developed (0), inarticulated (1), articulated (2)
3.	Hinge-line	no adult bivalves (0), not developed (1), strophic (2), astrophic (3)
4.	Valve growth	none (0), holoperipheral (1), mixoperipheral (2), hemiperipheral (3
Shell composition and structure		
5.	Periostracum	absent (0), simple (1), with infrastructure (2), with elaborate superstructure (3), with both (4)
6.	Infrastructures	lacking periostracum (0), thin GAGS (1), GAGS with proteinaceous fibrils (2), vesicular GAGS with proteinaceous fibrils (3), GAGS with chitinous and proteinaceous fibrils (4), GAGS with chitinous and proteinaceous tubes (5)
7.	Superstructure	lacking periostracum (0), fibrillar (1), sporadic vesicles (2), folded laminae (3), laminated vanes (4), labyrinth (5)
8.	Biomineral components	absent (0), stratiform apatite (1), laminar (tabular) calcite (2), fibrous calcite (3), foliated and laminar calcite (4)
9.	Organic components	mucus (0), mainly GAGS, chitin and collagen (1), glycoprotein (2)
10.	Endoskeletal spiculation	absent (0), present (1)
Mantle		
11.	Mantles	absent (0), present (1)
12.	Inner mantle lobe	no mantle (0), present (1), absent (2)
13.	Inner epithelium secreting periostracum	absent (0), yes (1), no (2)
14.	Lobate cells	no mantle lobe (0), absent (1), present (2)
15.	Vesicular cells	absent (0), present (1), palisade cells (2)
16.	Periostracal slot	no outer mantle lobes (0), absent (1), present (2)
17.	Setae	present (0), absent from post-larval mantles (1), not developed (2)
18.	Canals or punctae	absent (0), canals (1), punctae without brushes (2), endopunctae with brushes (3)
19.	Outer epithelial protrusions	present (0), absent (1)
20.	Vascula terminalia of mantle canals	no mantle (0), peripheral (1), peripheral and interio-medial (2)
21.	Mantle sinuses with gonads	no mantle (0), absent (1), present (2)
22.	Marginal sinuses	no mantle (0), absent (1), present (2)
23.	Mantle cavity	none (0), restricted to anterior (1), continuous posteriorly (2)
Pedicle		
24.	Pedicle	not developed (0), lost in post-larval forms (1), present (2), craniid thickened 'posterior epithelium' (3)
25.	Origin	none (0), from posterior body wall (1), ventral of posterior body wall (2), rudiment (3)
26.	Pedicle core	none (0), coelomic cavity (1), connective tissue (2)
27.	Pedicle muscles	none (0), internal (1), external (2)
Muscle system (dorsal attachment)		
28.	Muscles of body wall	circular (0), parietal sets (1), dispersed (2)
29.	Adductor attachments	none (0), grouped, quadripartite (1), open, quadripartite (2), medial and posteriolateral pairs (3), medial pair and single umbonal (4)
30.	Diductor/oblique attachments	none (0), one pair umbonal (1), three pairs of obliques (2), four pairs of obliques (3), one pair of obliques (4)
Coelomic/circulatory/excretory systems		
31.	Body cavity divided by mesentery	yes (0), no (1)
32.	Gastroparietal bands	absent (0), present (1)
33.	Circulatory system	absent (0), present (1)
34.	Blood type	haemoglobin (0), haemerythrin (1), neither (2)
35.	Mixonephridia	absent (0), one pair (1), two pairs (2)
36.	Nephrostomes	not applicable (0), turned laterally (1), turned dorsally or medially (2)

Nervous system

37.	Supraenteric ganglion	unknown (0), present (1), absent (2)
38.	Subenteric ganglion	nerve ring only (0), single (1), paired (2)

Lophophore

39.	Site of lophophore	in mantle cavity (0), in zoecium (1), at surface (2)
54.	Adult lophophore	trocholophe (0), spirolophe (1), plectolophe (2), ptycholophe (3)
55.	Median tentacle of lophophore	absent throughout ontogeny (0), present initially, then lost (1)
40.	Tentacles	single row (0), double row in post-trocholophous stages (1), double row throughout (2)
41.	Lophophore cavities and canals	intercommunicate (0), separated (1)
42.	Great brachial canals	absent (0), open into body cavity (1), sealed from body cavity (2), two separate cavities (3)
43.	Small brachial canals	absent (0), open into body cavity (1), open into central canal (2)
44.	Lophophore retractor system	absent (0), present (1)
45.	Retractor muscles	absent (0), single muscle (1), muscle complex (2)
46.	Brachial muscles	absent (0), present (1)

Digestive system

47.	Alimentary tract	with anus (0), without anus (1)
48.	Intestine disposition	ending dorso-anteriorly (0), ending posteriorly (1), curving ventrally (2) ending laterally to right (3)
49.	Diverticular ducts	two (0), three (1), four (2), none (3)

Embryology and development

50.	Larvae	planktotrophic (0), lecithotrophic (1)
51.	Coelom formation	schizocoelic (0), modified enterocoelic (1)
52.	Mantle development	without reversal (0), with reversal (1)
53.	Sperm morphology	ect-aquasperm (0), ent-aquasperm (1)

(ii) *Matrix of 55 characters, listed in Appendix A*(a)(*i*), *among seven Recent brachiopod groups and three generalized outgroups representing* Phoronis *and tubuliporate and ctenostomate byrozoans*

	1111111111222222222233333333334444444444555555
	1234567890123456789012345678901234567890123456789012345
phoronid	0000000000000000201000000000001010?02000000000003012110
tubuliporid	1000241420000020220000000000200100200211000011000 30?2100
ctenostome	2000241010000020201000000000200100200211000011000 30?2100
lingulid	3113251110111111011212222111143111111210213100103200011 1
discinid	31114141101111110112122222111221111212221021320210010 00?11
craniid	3111221220121111120121230001240012122220113202101011 0111
rhynchonellid	3232231320112211001121123221111112222110112100012011 1010
terebratulid	3232112321112212030121123221111112121101121000120111020
terebratellid	3232315321112212030121123221111112121101121000120111020
thecideid	32221113211122122 30?2111300131111212110112100012011 1?3?

(*b*) *Data for analysis of Cambro-Ordovician brachiopods*

(i) *The states of 69 characters used in the phylogenetic analysis of Cambro-Ordovician brachiopods and* Phoronis, *as listed in Appendix A*(*b*)(*ii*)

The different weights, given to the characters during analysis (Swofford & Begle 1993), are recorded in brackets at the end of each character description.

Shell structure

1.	Secondary layer	fibrous (0), foliated (1), tabular laminar (2), cross-bladed laminar (3), recrystallized, possibly aragonitic (4), stratiform (5), no shell (6) [7]
2.	Perforation	impunctate (0), extropunctate (1), endopunctate (2), punctate (3), caniculate (4), no shell (5) [8]
3.	Pseudopunctation	absent (0), present in some species (1), pseudopunctate (2), taleolate pseudopunctate (3), extropunctate (4), no shell (5) [8]
4.	Aditicules	absent (0), present (1), no shell (2) [16]

Shell shape

5.	Outline	subcircular/oval (0), subquadrate (1), transversely semioval (2), elongately semioval (3), protean (4), rostrate (5), conical (6), ostreiform (7), no shell (8) [5]
6.	Neanic profile	biconvex (0), concavoconvex (1), convexoconcave (2), no shell (3) [12]

7.	Profile (long.)	biconvex (0), dorsibiconvex (1), ventribiconvex (2), planoconvex (3), concavoconvex (4), convexoconcave (5), resupinate (6), geniculate (7), planoconical (8), no shell (9) [4]
8.	Profile (trans.)	rectimarginate (0), unisulcate (1), sharply unisulcate (2), uniplicate (3), sharply uniplicate (4), strangulate (5), no shell (6) [7]

Ornamentation

9.	Radial	smooth (0), costate (1), coarsely costellate (2), ramicostellate (3), fascicostellate (4), multicostellate (5), parvicostellate (6), no shell (7) [6]
10.	Capillae	absent (0), sporadically present (1), present (2), no shell (3) [12]
11.	Concentric	growth lines (0), imbricate (1), lamellose (2), spiny bands (3), nodular lamellose (4), filate (5), reticulate (6), no shell (7) [6]
12.	Superficial	absent (0), honeycomb (1), pustulose (2), radiating pits (3), post-larval pustules (4), no shell (5) [8]

Delthyrium

13.	Pedicle opening	ventral valve (0), supra-apical (1), posterior cleft (2), absent (3), between valves (4), no shell (5) [8]
14.	Posterior cleft	absent (0), delthyrial (1), other (2), secondarily lost (3), no shell (4) [10]
15.	Delthyrium	not developed (0), rudimentary (1), widely divergent (2), subparallel, narrowly divergent (3), no shell (4) [10]
16.	Delthyrial cover	open delthyrium (0), apical plate (1), deltidial plates (2), deltidium (3), convex pseudodeltidium (4), pseudodeltidium with keel (monticule) (5), concave pseudodeltidium (6), no delthyrium (7), homeodeltidium (8), no shell (9) [4]
17.	Foramen (ontogeny)	absent (0) delthyrial (1), supra-apical (2), ventral (3), in young shells only (4), secondarily lost (5), not developed (6), no shell (7) [6]
18.	Pedicle callist	absent (0), present, adnate (1), present as apical plate (2), pedicle collar (3), not developed (4), no shell (5) [8]
19.	Notothyrium	absent (0), rudimentary (1), widely divergent (2), subparallel, narrowly divergent (3), no shell (4) [8]
20.	Notothyrial cover	absent (0), antigydium (1), chilidial plates (2), chilidium (3), grooved plates (4), no notothyrium (5), no shell (6) [6]

Cardinal areas, interareas, pseudo-interareas

21.	Ventral	absent (0), vestigial (1), present (2), pyramidal/conical (3), lost/ginglymus (4), protean (5), no shell (6) [7]
22.	Disposition	absent (0), anacline (1), orthocline (2), apsacline (3), catacline (4), procline (5), hypercline (6), no shell (7) [6]
23.	Dorsal	absent (0), vestigial (1), present (2), no shell (3) [10]
24.	Disposition	absent (0), anacline (1), orthocline (2), apsacline (3), catacline (4), procline (5), hypercline (6), no shell (7) [6]

Articulation

25.	Ventral articulating structures	absent/rudimentary (0), simple, pointed (1), transverse plate (2), delthyrial ridges (3), flexed cardinal margin (kutorginid) (4), cardinal sockets (5), no shell (6) [6]
26.	Delthyrial ridges	no ridges (0), deltidiodont (1), deltidiodont with crural fossettes (2), transverse (3), transverse denticulate (4), cyrtomatodont (5), no shell (6) [6]
27.	Dental plates	absent/rudimentary (0), present (1), replaced by free spondylium (2), no shell (3) [10]
28.	Dorsal articulating sockets	absent (0), present (1), denticular pits (2), for delthyrial ridges (3), oblique furrows (4), propareas (5), hinge plate (6), no shell (7) [5]
29.	Socket buttress	no sockets (0), hollows (1), nubs (2), plates/rods, parallel with hinge-line (3), brachiophores (4), brachiophores and plates (5), brachiophores and fulcral plates (6), inner socket ridges (7), no shell (8) [4]
30.	Brachiophores/crura	absent (0), brachiophore rods/blades (1) crura (2), anderidia (3), no shell (4) [10]
31.	Brachiophore supporting plates	absent (0), parallel (1), convergent (2), as septalium (3), divergent (4), no brachiophores (5), no shell (6) [7]
32.	Fulcral plates	absent (0), present (1), no brachiophores (2), no shell (3) [12]
33.	Hinge line/cardinal margin	not developed (0), astrophic (1), strophic (2), no shell (3) [12]

Musculature

34.	Ventral adductors	dispersed posteriorly/anteriorly (0), grouped posterio-medianly (1), posterior pair attached to apical part in the umbonal area, anterior pair vestigial or reduced (2), no shell (3) [12]

35.	Dorsal adductors	medial and posterio-lateral pairs (0), grouped quadripartite (1), linear (2), elongate, radiating (petaloid) (3), dispersed quadipartite (4), dispersed (5), vestigial or lost (6), no shell (7) [6]
36.	Ventral diductors	not developed (0), interspersed with adductors (1), flanking/enclosing adductors (2), asymmetrical (3), attached to homeodeltidium or delthyrial margins (4), no shell (5) [8]
37.	Dorsal diductor impressions	not developed (0), posterio-median plate or cavity (1), notothyrial platform and/or cardinal process (2), notothyrium and/or cardinal process (3), no shell (4) [10]
38.	Ventral scar impressions	on valve floor (0), on callist/pseudospondylium (1), on raised structures (2), no shell (3) [12]
39.	Raised structures	none (0), spondylium simplex/triplex (1), free spondylium (2), colleplax (3), raised platform (4), adductor chamber (5), myocoelidium (6), sessile spondylium (7), camarophorium (8), no shell (9) [4]
40.	Notothyrial platform	absent/rudimentary (0), transverse 'plate' (1), platform (2), platform and notothyrial ridges (3), not developed (4), no shell (5) [8]
41.	Cardinal process	absent/rudimentary (0), median ridge (1), differentiated median ridge (2), variations of two lobes (3), median and submedian ridges (4), forked (5), undercut trifid (6), bilobate (7), no notothyrial structures (8), no shell (9) [4]
42.	Dorsal median partition	absent/low ridge (0), septum (1), no shell (2) [16]
43.	Subperipheral rim	absent (0), present (1), sporadic (2), geniculation (3), no shell (4) [10]
Mantle canals		
44.	Ventral	saccate/convergent *vascula media* (0), saccate/divergent *vascula media* (1), digitate (2), lemniscate (3), pinnate (4), baculate (5), absent (6), bifurcate (7), no bivalved mantle (8) [5]
45.	Dorsal	saccate (0), digitate (1), lemniscate (2), pinnate (3), apocopate (4), baculate (5), absent (6), bifurcate (7), no bivalved mantle (8) [5]
Addenda		
46.	Valve growth	holoperipheral (0), mixoperipheral (1), hemiperipheral (2), ventral valve mixoperipheral, dorsal valve hemiperipheral (3), ventral valve variable, dorsal valve mixoperipheral (4), no shell (5) [8]
47.	Colleplax	absent (0), present (1), no shell (2) [16]
48.	Ventral pseudointerarea	absent (0), present (1), not differentiated (2), other structures (3), no shell (4) [10]
49.	Attachment scar	absent (0), cicatrix (1), encrusting (2), no shell (3) [12]
50.	Hollow spines	absent (0), along hinge line (1), concentric rows (2), no shell (3) [12]
51.	Brachial markings	absent (0), sporadically developed (1), no shell (2) [16]
52.	Crural extensions	absent (0), spiralia (1), no shell (2) [16]
53.	Orientation of spiralia	no spiralia (0), medial (1), dorsal (2), lateral (3), no shell (4) [10]
54.	Jugum	absent (0), incomplete (1), complete (2), resorbed (3), no spiralia (4), no shell (5) [8]
55.	Hinge plate	absent (0), present (1), divided by cardinal pit (2), with raised boss (3), no shell (4) [10]
56.	Crural bases	absent (0), present (1), no crura (2), no shell (3) [12]
57.	Shell mineral	carbonate (0), phosphate (1), no shell (2) [16]
58.	Larval shell	absent (0), present (1) [24]
59.	Larval shell ornamentation	smooth (0), pitted (1), pustulose (2), no larval shell (3) [12]
60.	Larval shell spines	absent (0), present (1), no larval shell (2) [16]
61.	Transverse muscle scars	absent (0), present (1), attached ventrally to inner side of (acrotretoid) pseudointerarea (2), no shell (3) [12]
62.	Ventral cardinal muscle scars	absent (0), present (1), different muscle system (2), no shell (3) [12]
63.	Dorsal cardinal muscle scars	absent (0), present (1), different muscle system (2), no shell (3) [12]
64.	Outside lateral muscle scars	present (0), absent (1), combined with middle lateral muscle scars (2), no shell (3) [12]
65.	Dorsal scars of gastroparietal bands	absent (0), present (1), no shell (2) [16]
66.	Listrium	absent (0), present (1), no shell (2) [16]
67.	Vascula terminalia	peripheral only (0), peripheral and medial (1), no bivalved mantle (2) [16]
68.	Adjustor muscles	absent (0), present (1), no pedicle (2) [12]
69.	Gonads	in body cavity (0), extending into mantle (1), no mantle (2) [16]

(ii) *Matrix of 69 characters, listed in Appendix A(b)(i), among 33 Cambro-Ordovician brachiopod groups and Recent* Phoronis
The states of character 70 represent the first appearances of taxa in the geological record and have been used in a separate stratocladistic analysis of the data.

							1111	111	1	11222222	22	2	23	3	3	3333	3	3344	444	4	4444555555555	5	66666666667
	1	23	45	67	8	9	0123	456	7	89012345	67	8	90	1	2	3456	7	8901	234	5	6789012345678	9	01234567890
Phoronis	6	55	28	39	6	7	3755	449	7	44667376	63	7	84	6	3	3375	4	3959	248	8	5243322454320	3	3333322222?
paterinid	5	?0	01	02	(03)	0	1000	228	6	42500000	00	0	00	5	2	2004	1	0048	00(04)	(04)	1010000040211	2	0102?000010
lingulid	5	40	04	0(012)	0	0	1004	207	6	40500000	00	0	00	5	2	0050	0	0048	005	5	101000004021(01)	0	01000101002
discinid	5	40	00	0(012)	0	0	0000	207	6	40500000	00	0	00	5	2	0050	0	0048	005	5	0010000040211	(01)	0100111100A
botsfordiid	5	40	00	02	0	0	0040	207	6	40500000	00	0	00	5	2	0050	0	0048	005	5	4020000040211	1	11000101002
siphonotretid	5	40	00	02	0	0	0000	207	6	40500000	00	0	00	5	2	0050	0	0048	005	5	4010200040211	0	01000101005
acrotretid	5	40	04	02	0	0	0000	207	6	40500000	00	0	00	5	2	0260	0	0048	005	5	4030000040211	1	02112101002
naukatid	?	?0	04	0(013)	(013)	(02)	0002	136	(12)	03023212	00	(02)	00	5	2	210(01)	(01)	2420	00?	?	1000000040200	3	2022100?0?3
obolellid	1	00	03	00	0	0	200(12)	136	(12)	0302322(01)	00	(02)	10	5	2	200(01)	(01)	0000	005	5	1000000040200	3	20221000?01
chileid	0	30	01	0(123)	(03)	(02)	0000	234	3	00500000	00	0	00	5	2	2?00	0	??00	004	?	3110000040200	3	20221000013
eichwaldiid	0	30	05	00	0	0	0030	221	3	00553000	00	4	00	5	2	2?10	1	?301	10?	3	3100000040200	3	202210000?E
kutorginid	0	00	0(023)	0(02)	0	0	0001	124	2	02023244	00	5	00	5	2	2?3?	1	0000	00?	3	1000000040200	3	20221000?11
craniopsid	2	00	00	00	0	0	0003	007	0	00500000	00	0	00	5	2	0040	0	1000	02?	?	0011000040200	3	202210000?3
craniid	2	30	00	00	0	0	0003	007	0	00500000	00	0	00	5	2	0040	0	0000	014	4	0002000040200	3	20221000019
trimerellid	4	00	00	00	0	0	0003	007	0	00523005	00	6	00	5	2	2001	1	2400	00?	?	1000000040200	3	202210000?D
orthid	0	00	0(01)	0(25)	1	3	1502	120	1	12023213	21	3	41	0	0	2112	2	0021	000	1	1000000040200	3	20221000114
billingsellid	3	00	01	00	1	5	0001	124	2	02323213	30	3	30	0	0	2112	2	0021	020	1	1000000040200	3	20221000014
skenidiid	0	00	02	03	1	5	0002	120	1	02033213	12	3	61	3	1	2112	2	2202	100	1	1000000040200	3	20221000113
plectorthid	0	00	1(01)	0(25)	(013)	5	0002	120	1	12023213	21	3	61	2	1	2112	3	0002	000	2	1000000040200	3	20221000117
enteletid	0	30	1(01)	0(25)	(013)	5	0002	120	1	12023213	21	3	61	1	1	2112	3	0002	003	2	1000000040200	3	20221000118
triplesiid	3	01	04	01	(013)	2	1201	125	2	01623113	11	3	30	0	0	2112	3	0005	000	1	1000000040200	3	20221000?1C
clitambonitid	0	0(02)	11	0(04)	0	(56)	0201	123	2	02323213	12	3	30	0	0	2132	2	0121	024	3	1000000040200	3	20221000?16
strophomenid	3	0(23)	02	14	(013)	6	0001	124	2	02323213	30	3	30	0	0	2132	2	0023	030	0	1000010040200	3	20221000019
plectambonitid	(03)	03	02	14	(013)	6	0001	124	2	02223213	11	3	30	0	0	2132	2	0024	022	3	1000010040200	3	20221000016
chilidiopsid	3	01	04	0(18)	(01)	5	0501	124	2	02323213	11	3	3(03)	0	0	2132	2	0023	00?	2	1000000040200	3	2022100001D
orthotetid	3	0(24)	04	0(18)	(01)	5	0503	125	5	02323113	11	3	31	(04)	(01)	2132	3	0003	00?	?	1001000040200	3	2022100001G
chonetid	3	03	02	14	(013)	5	0001	124	2	02323213	13	3	33	0	0	2132	3	002(34)	10?	?	1000110040200	3	2022100001G
protorthid	?	??	02	00	1	2	0002	120	1	02023211	02	1	20	0	0	2122	1	2210	000	?	1000000040200	3	20221000?13
syntrophiid	0	00	02	01	4	0	0002	120	1	01013103	1(01)	3	61	2	1	2131	3	2100	002	1	1000000040200	3	20221000114
zygospirid	0	00	00	00	1	2	0002	120	1	10512003	50	3	72	0	1	1112	1	0000	000	1	1000001121000	3	2022100011D
ancistrorhynchid	0	00	05	01	4	1	0002	122	1	11013003	51	3	72	3	1	1132	3	0000	00?	?	1000000041100	3	2022100011B
meristellid	0	00	03	02	3	0	0002	310	1	20000003	51	1	52	3	0	2112	3	0000	004	3	1000001322100	3	2022100011H
eospiriferid	0	00	02	02	3	5	0002	12(02)	1	?0023113	51	3	72	0	0	2122	3	0000	00?	?	1000001301100	3	2022100011G
pentamerid	0	00	03	02	0	0	0002	120	1	00011003	12	1	52	1	0	21??	3	2100	00?	?	1000000040200	3	2022100011F

(*c*) *Data for analysis of Recent and Cambro-Ordovician brachiopods*

(i) *The states of 19 synapomorphies, identified in the phylogenetic analysis of Recent and Cambro-Ordovician brachiopods and used to analyse the suprafamilial groups and Recent* Phoronis *listed in Appendix A(c)(ii)*

Shell

1.	Composition	chitinophosphatic (0), carbonate (1), no shell (2)
2.	Structure	stratiform (0), fibrous (and foliated) (1), tabular laminar (2), cross-bladed laminar (3), recrystallized (4), no shell (5)

Morphology

3.	Shell growth	holoperipheral (0), mixoperipheral (1), hemiperipheral (2), no bivalved shell (3)
4.	Cardinal areas	absent (0), pseudointerareas (1), strophic interareas (2), astrophic interareas (3), no bivalved shell (4)
5.	Pedicle opening	absent (0), ventral valve floor (1), supra-apical (2), posterior cleft (3), delthyrial (4), between valves (5), no bivalved shell (6)
6.	Articulatory devices	absent (0), other kinds (1), deltidiodont teeth and sockets (2), cyrtomatodont teet and sockets (3), no bivalved shell (4)
7.	Lophophore supports	absent (0), inner socket ridges (1), brachiophores (2), crura (3), crura and spiralia (4), no bivalved shell (5)

Anatomy

8.	Pedicle	absent (0), from body wall (1), from rudiment (2)
9.	Posterior body wall	present (0), absent (with fused mantle lobes) (1), not applicable (2)
10.	Muscles operating articulation	none (0), regrouped internal obliques (1), diductors (2), no bivalved shell (3)
11.	Muscles operating pedicle	no pedicle (0), absent (1), present (2)
12.	Interiomedial *vascula terminalia*	absent (0), present (1), no bivalved mantle (2)
13.	Gonadal distribution	restricted to body cavity (0), also in mantle sinuses (1)
14.	Anus	present (0), absent (1)
15.	Tentacles	doubled (0), doubled in post-trocholophous segments (1), single row (2)
16.	Shell perforations	absent (0), canals (1), punctae (2), pseudopunctae (3), endopunctae (4), no bivalved shell (5)
17.	Mantle reversal	no (0), yes (1), no bivalved mantle (2)
18.	Planktotrophic larval shell	present (0), post-larval shell only (1), no shell (2)
19.	Lobate cells in mantle lobe	absent (0), present (1), no bivalved mantle (2)

(ii) *Variations of 19 synapomorphies, listed in Appendix A(c)(i), among 14 brachiopod groups and Recent* Phoronis

11		11111	111							
12	3	4	5	6	7	8901	23456	789		
	Phoronis	25	3	4	6	4	5	0230	20005	222
	paterinid	00	1	1	0	0	0	0?10	01??0	?0?
	lingulid	00	(12)	1	(15)	0	0	1001	10001	000
	craniid	12	(01)	(01)	0	(01)	0	0000	0101(02)	010
	chileid	11	1	2	1	(01)	0	1011	0???0	???
	trimerellid	14	1	2	0	1	0	0010	01??0	?1?
	obolellid	11	1	2	2	1	0	1?11	00??0	???
	kutorginid	11	1	2	2	1	0	1021	010?0	???
	protorthid	11	1	2	4	(12)	(02)	212(12)	011?0	?1?
	billingsellid	13	1	2	2	2	1	1?21	01??0	?1?
	orthotetid	13	1	2	2	2	1	1?21	01??(03)	?1?
	strophomenid	1(13)	1	2	2	2	1	1?21	01??3	?1?
	orthid	11	1	2	4	2	2	2122	011?(02)	?1?
	pentamerid	11	1	(23)	4	2	(23)	2122	011?0	?1?
	rhynchonellid	11	1	3	4	3	3	2122	0111(04)	111

APPENDIX B. DIAGNOSES OF SUBPHYLA AND CLASSES

Subphylum LINGULIFORMEA nov.

Brachiopods with organophosphatic inarticulated shells developed without mantle reversal; larvae planktrophic with variously ornamented shell; pedicle emerging between valves or supra-apically with extensions of coelomic cavity as core; alimentary tract with anus; lophophore initially with median tentacle, lost during growth, tentacles in double row throughout ontogeny. *Early Cambrian* (*Tommotian*)–*Recent*.

Class LINGULATA Gorjansky & Popov, 1985

[Gorjansky & Popov, 1985, p. 13]
Linguliform brachiopods with smooth or pitted larval shell; dorsal and ventral mantle lobes completely separated in adults; marginal setae forming continuous rows along mantle margin; posterior body wall usually well developed; musculature composed of single or paired posterior adductor, three or four pairs of oblique muscles (partly reduced in acrotretides) and paired anterior adductor; mechanism of shell opening hydraulic, by means of muscles in body wall; digestive tract of living taxa open, recurved with anteriorly placed anus; nervous system with only one subenteric ganglion and peripheral mantle nerves; gonads confined to body cavity; statocysts in larvae and adults; mantle canals usually baculate, with *vascula terminalia* directed peripherally and medially. *Early Cambrian* (*late Atdabanian*)–*Recent*.

Incl.: Order LINGULIDA Waagen, 1885
Order SIPHONOTRETIDA Kuhn, 1949
Order ACROTRETIDA Kuhn, 1949

Class PATERINATA nov.

Linguliform brachiopods with pustulose larval shell; strophic cardinal margins lacking setae, possibly associated with fused mantle lobes; incipient, divergent notothyrium and delthyrium covered by homeodeltidium; paired dorsal adductor muscles grouped medially and posteriolaterally, diductor muscles possibly attached ventrally to homeodeltidium or delthyrial margin and dorsally inserted in posteriomedian cavity; saccate, rarely pinnate mantle canal system, possibly accommodating gonads. *Early Cambrian* (*Tommotian*)–*Late Ordovician*.

Incl. Order PATERINIDA Rowell, 1965

Subphylum CRANIIFORMEA Popov, Bassett, Holmer & Laurie, 1993

[*nom. transl.*, *nom. correct.*, herein (*pro*, Subclass Craniformea POPOV, BASSETT, HOLMER & LAURIE, 1993, p. 2).
Brachiopods with calcitic, laminar (tabular) inarticulated shells; valves developed discretely without mantle reversal; larvae lecithotrophic without shell; posterior body wall complete, pedicle not developed, ventral valve attached by larval epithelium; muscle system with a single pair of internal obliques and with paired outside lateral muscles attached anteriorly to the body wall; alimentary tract more or less axial with anus; lophophore initially with median tentacle lost during growth, tentacles in double row in post-trocholophous growth stages only; paired ganglia developed; mantle canal systems without interiomedial *vascula terminalia*, normally pinnate, containing gonads. *Early Cambrian* (?*Botomian*)–*Recent*.

Class CRANIATA nov.

As for Subplylum. *Early Cambrian* (?*Botomian*)–*Recent*.

Incl.: Order CRANIOPSIDA Gorjansky & Popov, 1985
Order CRANIIDA Waagen, 1885
Order TRIMERELLIDA Gorjansky & Popov, 1985

Subphylum RHYNCHONELLIFORMEA nov.

Brachiopods with calcitic, basically fibrous articulated shells; mantle in later groups undergoing embryonic reversal, larvae lecithotrophic without shell; hingeline formed by posterior cardinal margins of shell secreted by fused mantle lobes; articulatory structures, essentially a pair of ventral teeth and dorsal sockets on either side of median indentations (delthyrium and notothyrium respectively) of cardinal margins; pedicle normally developed from rudiment and occupying delthyrial area, filled with connective tissue and controlled by adjustor muscles; adductor muscles grouped, normally located posteriomedianly, diductor muscles flanking adductors ventrally, inserted in notothyrial region dorsally; alimentary tract without anus; lophophore without median tentacle, tentacles double in post-trocholophous stages of growth; lophophore supported in later groups by calcitic extensions from dorsal hingeline in the form of crura, spiralia or loops; mantle canal systems variable in branching, containing gonads, without marginal sinuses. *Early Cambrian* (*Atdabanian*)–*Recent*.

Class CHILEATA nov.

Rhynchonelliform brachiopods with strophic, normally inarticulated shell, variably punctate, fibrous; ventral and dorsal valves with mixoperipheral and hemiperipheral growth respectively; mantle lobes possibly fused posteriorly; ventral valve with cardinal interarea; ventral umbo with perforation enlarged anteriorly by resorption and usually covered posteriorly by colleplax; mantle canals pinnate. *Early Cambrian* (*Botomian*)–*Permian*.

Incl.: Order CHILEIDA Popov & Tikhonov 1990
Order DICTYONELLIDA Cooper, 1956

Class OBOLELLATA nov.

Rhynchonelliform brachiopods with foliated, impunctate, biconvex shell; both valves with hemiperipheral growth and well defined interareas; ventral interarea with delthyrium, usually covered by concave pseudodeltidium, rarely open articulatory structures variably developed as submedian denticles on either side of a narrow delthyrium or on a ventral platform; musculature probably with internal oblique attached to dorsal valve posteriomedianly. *Early Cambrian (Atdabanian)–Middle Cambrian (Amgaian).*

Incl.: Order OBOLELLIDA Rowell, 1965
Order NAUKATIDA Popov & Tikhonov, 1990

Class KUTORGINATA nov.

Rhynchonelliform brachiopods with fibrous, impunctate, ventribiconvex, strophic shell; posterior margin with large median opening, partly covered by convex, widely triangular pseudodeltidium, and bounded laterally by furrows; beak, with small, rounded apical foramen; dorsal interarea divided by wide notothyrium; dorsal adductor scars radially arranged; diductors probably attached dorsally to floor of notothyrial cavity; articulation by edges of the interareas, without teeth and dental sockets; mantle canals pinnate; digestive tract probably open with anus placed posteriomedianly. *Early Cambrian (Atolabnanian)–Middle Cambrian (Mayaian).*

Incl.: Order KUTORGINIDA Kuhn, 1949

Class STROPHOMENATA nov.

Rhynchonelliform brachiopods with cross-bladed laminar secondary shell, exceptionally fibrous impunctate in early stocks, commonly pseudopunctate with or without taleolae or extropunctate (some orthotetidines); shell outline and profile variable, especially in productides, but commonly planar to weakly concavoconvex in strophomenides; strophic hinge, commonly with high ventral interarea and reduced dorsal interarea; delthyrium and notothyrium variably covered by pseudodeltidium and chilidium; supra-apical foramen universal, but becoming lost in adults or stratigraphically younger taxa, some of which are umbonally cemented; tubular spines uniquely developed in late Palaeozoic productides; deltidiodont teeth simple, transverse or peg-like but lost in strophodontids and post-Famennian productidines, dental sockets commonly defined by flat-lying ridges; dorsal bases of diductor muscles inserted on notothyrial platform or normally on prominent cardinal process of varied morphology, ventral bases attached laterally of medianly placed adductor scars; lophophore supports rare, as brachiophores or raised dorsal ridges; mantle canal systems saccate to pinnate, poorly known in later groups. *Middle Cambrian (Amgaian)–Late Permian (Tatarian).*

Incl.: Order STROPHOMENIDA Öpik, 1934
  Suborder ORTHOTETIDINA Waagen, 1884
  Superfamily BILLINGSELLOIDEA Schuchert, 1893
  Suborder TRIPLESIIDINA Moore, 1952
  Suborder CLITAMBONITIDINA Öpik, 1934
Order PRODUCTIDA Sarytcheva & Sokolskaya, 1959

Class RHYNCHONELLATA nov.

Rhynchonelliform brachiopods with fibrous, endopunctate or impunctate, biconvex, strophic or astrophic shells, articulated by deltidiodont or cyrtomatodont teeth and sockets buttressed by brachiophores or supported by parallel socket or hinge plates that may converge to form septalium or cruralium; pedicle opening as delthyrium or rounded foramen; cardinal areas and notothyrium commonly vestigial or absent, wide in some later groups; dental plates less commonly converge to form spondylium posteriomedial ventral adductor scars flanked or enclosed by ventral diductor and laterally placed adjustor scars; dorsal adductor scars petaloid or grouped and quadripartite; crura present in later groups and commonly extended as spiralia or loops; mantle canal systems variable as saccate, digitate, pinnate, or lemniscate impressions. *Early Cambrian (?Botomian)–Recent.*

Order ORTHIDA Woodward, 1852
Incl: Suborder PROTORTHIDINA Schuchert & Cooper, 1931
Order PENTAMERIDA Schuchert & Cooper, 1931
Order RHYNCHONELLIDA Kuhn, 1949
Order ATRYPIDA Rzhonsnitskaya, 1960
Order SPIRIFERIDA Waagen, 1883
Order SPIRIFERINIDA Ivanova, 1972
Order ATHYRIDIDA Boucot, Johnson, & Staton, 1964
Order TEREBRATULIDA Waagen, 1883
Order THECIDEIDA Elliott, 1958