# PHYLOGENY AND EVOLUTION OF 'PENTAMERIDE' BRACHIOPODS

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ABSTRACT. Despite their importance in articulate brachiopod evolutionary history, relatively little is known in detail about the phylogenetic relationships among 'pentameride' taxa, and of 'pentamerides' to other articulates. Phylogenetic relationships among all named 'pentameride' families and rhynchonellide superfamilies were reanalysed using outgroup methods of polarity determination. A detailed working hypothesis of 'pentameride' phylogeny and the supporting evidence on character distribution is presented. As currently diagnosed, Pentamerida and Syntrophiidina are paraphyletic, while Rhynchonellida and Pentameridina are monophyletic. Generally acknowledged patterns of morphological change may now be examined in detail, as they are expressed in a comprehensive pattern of relationship. In the evolutionary history of these taxa, strophic hinge line length decreased steadily and astrophic hinge lines evolved twice. Interlocking hinge structures arose twice from the non-interlocking condition, and muscle platforms in the dorsal and ventral valves evolved several times independently. These phylogenetic results have significant implications for several issues relevant to the study of brachiopod systematics. Agreement between the stratigraphical first appearance of 'pentameride' families and their cladistic rank is quite good, suggesting that both outgroup and palaeontological methods indicate the same direction of character polarity in the evolution of 'pentamerides'. The paraphyletic 'syntrophiidines' suffer pseudoextinction in transforming to the monophyletic rhynchonellides (extant) and the monophyletic pentameridines (extinct), which possess a combination of characters (very strong biconvexity, large adult size, lack of pedicle, non-interlocking dentition) that apparently rendered them less able to adapt over time to changes in their habitat. A highly corroborated phylogenetic hypothesis provides an explicit framework within which causal hypotheses of macroevolutionary phenomena may be generated and tested.

'PENTAMERIDE' brachiopods occupy a particularly important place, both temporally and morphologically, in the evolution of articulate brachiopods. 'Pentamerides' are among the earliest articulates in the fossil record, first appearing in the Lower Cambrian of Siberia (Andreeva 1987). The Pentamerida is one of the first articulate brachiopod orders to become extinct (with the Atrypida, at the end of the Devonian). Several morphological transformations of great significance in articulate brachiopod evolution are manifest within the 'pentamerides'. For example, the 'pentamerides' include the first cyrtomatodont articulates, making the transition from non-interlocking to interlocking hinge structures (Jaanusson 1971). They also include the first astrophic articulates, evolving curved hinge lines from those that were long and straight. Shell biconvexity increases dramatically from the earliest to the latest 'pentamerides'. A number of derived features associated with extant brachiopods first appear quite early in 'pentameride' evolution. On the other hand, various types of muscle platforms are developed in both the dorsal and ventral valves and are a prominent feature of 'pentameride' internal shell morphology. Similar platforms are present in several groups of Palaeozoic brachiopods, but are generally lacking in Recent forms (see Rudwick 1970). Considering their early appearance in the fossil record, 'pentameride' brachiopods thus present interesting combinations of both primitive and unexpectedly derived morphological features.

In the most general sense, 'pentamerides' are thought to have evolved from the orthides and given rise to the rhynchonellides (see Text-fig. 1). Despite their considerable importance in our understanding of brachiopod evolution and the origin of the modern brachiopod fauna, a detailed
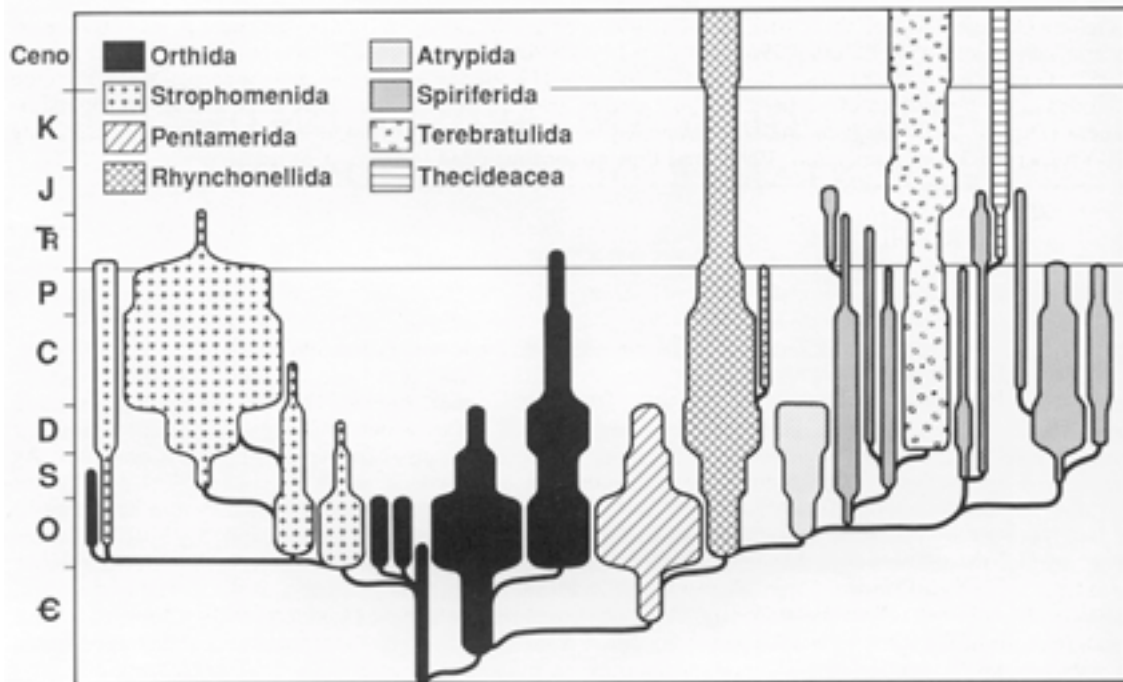
TEXT-FIG. 1. Stratigraphical ranges of articulate brachiopod superfamilies plotted according to their familial diversity and pattern-coded by their ordinal classification; redrawn from Williams (1968). The hypothetical phylogenetic relationships are as illustrated by Williams (1968).

reconstruction of phylogenetic relationships among the 'pentamerides', and of 'pentamerides' to other articulates, is lacking. No comprehensive study of 'pentameride' phylogeny and character evolution has been completed since G. A. Cooper's pioneering work in the 1930s (e.g. Schuchert and Cooper 1932; Ulrich and Cooper 1938). The number of 'pentameride' genera has more than doubled in the last thirty years alone, since the publication of the brachiopod volumes of the *Treatise on invertebrate paleontology* (Williams and Rowell 1965). It it time to re-examine assumptions of character homology and polarity among all members of the order.

The primary goal of this study is to investigate phylogenetic relationships among 'pentameride' brachiopod families. Without a detailed and strongly supported phylogenetic hypothesis, morphological transformations among the 'pentamerides' may be understood only in the most general terms. The results of four experimental phylogenetic analyses using outgroup criteria for polarity determination are compared and contrasted, and the implications of each to several issues relevant to the study of brachiopod systematics are discussed: morphological character evolution within the group; comparison of outgroup and stratigraphical methods of polarity determination; past, present, and future interpretation of 'pentameride' classification; and the macroevolutionary significance of the extinction of the paraphyletic 'pentamerides'.

METHODS

Taxa

Two 'pentameride' suborders are recognized currently (Amsden 1965; Biernat 1965; see Table 1). The Pentameridina includes the stereotypical 'pentamerides'; large, highly biconvex brachiopods with long, curved beaks in both dorsal and ventral valves. The Syntrophiidina includes a diverse group of brachiopods with a number of morphological characteristics intermediate between the

TABLE 1. Classification of the Order Pentamerida used in this study. Primary reference is the *Treatise on invertebrate paleontology* (Biernat 1965; Amsden 1965), with additions from Nikiforova (1960), Amsden *et al.* (1967), Gauri and Boucot (1968), Boucot and Johnson (1979). Syntrophiidine genera named since 1965 are included in the families to which they were assigned by their authors. Three additional Chinese syntrophiidine genera (*Disepta, Fengxiangella,* and *Limstrophina*) were only recently brought to my attention by Dr Rong Jia-Yu (personal communication, 1993), and thus are not included in these analyses.

PENTAMERIDA
  SYNTROPHIIDINA
    PORAMBONITACEA
    Alimbellidae: *Alimbella, Medessia, Mogoktella*
    Clarkellidae: *Acanthoglypha, Calliglypha, Clarkella, Diaphelasma, Stichotrophia,*
      Syntrophina, Syntrophinella, ?Syntrophioides, Thaumotrophia, Yangtzeella
    Eostrophiidae: *Cambrotrophia*
    Huenellidae: [Huenellinae] *Huenella, Huenellina, Palaeostrophia, Plectotrophia;*
      [Mesonomiinae] *Glyptotrophia, Mesonomia;* [Rectotrophiinae] *Rectotrophia*
    Lycophoriidae: *Lycophoria*
    Porambonitidae: *Porambonites, Porambonitoides, Rosella, Talovia*
    Syntrophiidae: [Syntrophiinae] *Rhyselasma, Syntrophia;* [Xenelasmatinae]
      Euorthisina, Xenelasma, Xenelasmella, Xenelasmopsis
    Syntrophopsidae: *Altunella, Bobinella, ?Cuparius, Hesperotrophia, Rhabdostrophia,*
      Rhysostrophia, Syntrophopsis, Tcharella
    Tetralobulidae: *Doloresella, Imbricatia, Pseudoporambonites, Punctolira, Tetralobula*
    Karakulinidae: *Karakulina*
    Uncertain: *Triseptata*

    CAMERELLACEA
    Brevicameridae: *Brevicamera*
    Camerellidae: [Camerellinae] *Bleshidimerus, Bleshidium, Camerella, Idiostrophia,*
      Kokomerena, Liricamera, Llanoella, Neostrophia, Perimecocoelia,
      Plectocamara, Plectosyntrophia, Psilocamerella, Tuloja, Xizangostrophia;
      [Stenocamarinae], *Boreadocamara, Stenocamara*
    Parastrophinidae: *Anastrophia, Eoanastrophia, Grayina, Jolkinia, Liostrophia,*
      Maydenella, Parastrophina, Parastrophinella

    UNCERTAIN
    Branconia, Schizostrophia, Swantonia

  PENTAMERIDINA
    PENTAMERACEA
    Parallelelasmatidae: *Didymelasma, ?Metacamerella (= Parallelelasma), Salonia*
    Clorindidae: *Antirhynchonella, Clorinda, Clorindella, Clorindina*
    Enantiosphenidae: *Enantiosphen*
    Gypidulidae: *Barrandina, ?Biseptum, Carinagypa, Devonogypa, Gypidula,*
      Gypidulella, Gypidulina, Ivdelinia, Leviconchidiella, Levigatella,
      Pentamerella, ?Procerulina, Sieberella, Wyella, Zdimir
    Pentameridae: *Brooksina, Callipentamerus, Capelliniella, Harpidium, Jolvia,*
      Lissocoelina, ?Pentamerifera, Pentameroides, Pentamerus, ?Pleurodium,
      Rhipidium
    Stricklandiidae: *Costistricklandia, Kulumbella, Microcardinalia, Plicostricklandia,*
      Stricklandia
    Subrianidae: *Aliconchidium, Conchidium, Cymbidium, Lamelliconchidium,*
      Plicocoelina, Severella, Spondylopyxis, Spondylostrophia,
      Stricklandistrophia, Subriana, Vagranella, Vosmiverstum
    Virgianidae: *Holorhynchus, Platymerella, Virgiana*

strophic orthides and the astrophic rhynchonellides and terebratulides. The 'syntrophiidines' are thought to serve as the ancestors of both the pentameridines, which represent a derived, short-lived but highly successful 'dead end' of 'pentameride' evolution (see Johnson 1977; Boucot and Johnson 1979), and the rhynchonellides, which have persisted to the present day remarkably unchanged.

Choosing terminal taxa in a preliminary phylogenetic study of this sort presents a chicken-and-egg dilemma. Which comes first, the phylogenetic analysis or the taxa? Terminal taxa should represent systems of common ancestry (i.e. be monophyletic; see Wiley 1981). The monophyly of named 'pentameride' higher taxa has not been tested; it is highly likely that at least some are not clades. A species level analysis of the 'pentamerides' would appear to be a necessary first step, assuming that biological species represent 'basic taxonomic units' (although see de Queiroz and Donoghue 1988, 1990; Nixon and Wheeler 1990) and that fossil species are comparable in some sense to biological species. However, a minimum estimate of several hundred named fossil 'pentameride' species exist. It is not reasonable to expect interpretable results from a phylogenetic analysis, either by hand or by computer, that includes such a large number of terminal taxa. Even at the genus level, which is commonly considered to represent a realistic operational taxonomic unit in brachiopod palaeontology (Cooper 1970), well over one hundred taxa exist.

As a compromise between feasibility and taxonomic detail, phylogenetic relationships among families of 'pentamerides' were chosen for analysis. Specimens were examined, when possible, in addition to descriptive literature on all named genera assigned to each family. Character states per family were coded as a consensus of character states present in each genus assigned to that family. This strategy runs the risk of coding a taxon as a combination of characters that are not present in that particular combination in any single individual. Nevertheless, if the taxon is monophyletic, the character combination should represent the clade as a whole. Phylogenetic analyses of genera and species within at least the 'syntrophiidine' families are being conducted currently (Carlson in preparation), and the results of these ongoing studies have the potential to affect the results presented here.

Fifteen 'syntrophiidine' families (four of which are monogeneric), eight pentameridine familes or subfamilies, and two rhynchonellide superfamilies comprise the ingroup in these analyses (Table 1). The diagnoses and generic composition of 'syntrophiidine' families, as listed in Table 1, largely reflect the classification in Biernat (1965). Genera named since 1965 are included in the families to which they were assigned by their authors. My knowledge of the Syntrophiidina is much greater than for the Pentameridina; thus I have relied largely on the Amsden (1965) classification and diagnoses to characterize the pentameridine families (but also consulted Amsden et al. 1967; Gauri and Boucot 1968; Boucot and Johnson 1979). Many new pentameridine genera have been named since then, but because I have had limited exposure to the specimens, I chose to exclude them from this analysis.

The purpose of this study is to investigate phylogenetic relationships among 'pentameride' families. Revising 'pentameride' higher-level classification is a separate, subsequent endeavour, and will not be accomplished here. Genus-level phylogenetic analyses of the 'pentamerides', particularly the most primitive 'pentamerides' and the orthides, must be completed before final decisions of classification can be reached. Decisions involving the redefinition of established higher taxa are particularly delicate; they deserve the consideration of the full body of morphological evidence on all articulates, which is currently under active investigation.

Throughout, informal taxon designations are used (e.g. orthides for Orthida, 'syntrophiidines' for Syntrophiidina, rhynchonellaceans for Rhynchonellacea, porambonitids for Porambonitidae) that refer to groups of brachiopods currently classified in various higher taxa. The phylogenetic status, relative taxonomic rank, and lower-level classification of these named taxa are all in the process of being evaluated; thus, the informal name is used to convey some sense of the brachiopods in question, without placing undue emphasis on the rank or current definition of the taxon name itself. In the interest of consistency, suspected or identified paraphyletic taxa are always referred to in quotation marks, following Gauthier (1986).

Finally, it is very likely that components of the research of several Russian palaeontologists (e.g. Nikiforova, Sapelnikov, Andreeva, Kulkov, Tcherkesova, among others) who have produced extensive publications on the 'pentamerides' have been inadvertently overlooked. My knowledge of the Russian literature is limited by the amount that has been made accessible through translation, which represents only a small portion of the total body of research. Sapelnikov (1980, 1982, 1985) in particular, has published phylogenetic reconstructions of the 'pentamerides'. His assignment of genera to families does not agree with the classification (Table 1) used as a starting point for these analyses; thus, our conclusions about 'pentameride' relationships will necessarily differ.

Characters

The list of characters (Appendix A), data matrix (Appendix B), and list of apomorphies for cladogram five, discussed below, (Appendix C) have been deposited with the British Library, Boston Spa, Yorkshire, UK, as Supplementary Publication No. SUP 14043.

Because all but one of the terminal taxa in this study are extinct, all the characters used in the analysis are necessarily those that fossilize, namely characters of skeletal anatomy. Homoplasy (convergence or parallelism) in brachiopod skeletal anatomy is common (e.g. Buckman 1906; Cooper 1930, 1972; Cloud 1941), and raises a legitimate concern that perhaps too few homologous characters will be identified to generate a phylogenetic 'signal' above the homoplastic 'noise'. Such concerns may never be put to rest entirely in phylogenetic studies of extinct groups. However, ignoring all extinct taxa is a highly unsatisfactory alternative to attempting an analysis with the available morphological data and then critically evaluating the results. In this case, homology was tested primarily by phylogenetic congruence (Patterson 1982) with other putative homologues.

Information was compiled on seventy-four morphological characters of skeletal anatomy, including valve form and ornament, shell structure, the hinge region, and dorsal and ventral valve interiors, especially the cardinalia (SUP 14043, Appendix A). Only characters that vary among two or more terminal taxa were included. Autapomorphous characters are essential in identifying individual taxa, but do not provide information on relationships among taxa. No attempt was made to eliminate characters thought to be homoplastic prior to performing the analyses, under the assumption that homoplasy would be revealed in the analysis itself by phylogenetic congruence (Patterson 1982). Both binary and multistate characters were recognized. All characters were initially unordered, allowing the outgroup (primitive) character states to polarize the direction of character transformation. None were constrained to be irreversible. All were weighted equally in the first analysis; all were reweighted according to their rescaled consistency indices (Farris 1989) in the second analysis.

Many characters were coded as missing (SUP 14043, Appendix B), for one of three different reasons: (1) the character is not applicable to the taxon (e.g. spondylium type in a taxon lacking a spondylium); (2) it is not known for the taxon; or (3) the states are variable (polymorphic) among genera in a family. Intentional ambiguity in coding polymorphic taxa as missing, enables the polarity of the various character states to be reconstructed from the results of the phylogenetic analysis. In other words, coding variability itself as a separate character state (e.g. shell ornament: smooth [0], costate [1], both smooth and costate [2]) will tend to group polymorphic taxa together. It is more likely that one of the two character states is primitive, as revealed in the analysis, and has transformed within the polymorphic taxon. The cladogram topology is structured on the basis of coded characters; missing characters do not play a role in cladogram construction (although see Nixon and Davis 1991; Platnick *et al.* 1991; Novacek 1992).

Polarity determination

Traditional palaeontological methods of phylogenetic inference polarize the direction of character transformation using (primarily) stratigraphical criteria (i.e. stratigraphically lowest fossils are most primitive). Relying largely on stratigraphical polarity in phylogenetic reconstruction is problematic for several reasons. Using this method, the 'primitive condition' is fundamentally empirical and

defined solely on the basis of characteristics observable in the oldest known fossils. As older and older fossils are discovered, the concept of 'primitive' must necessarily change to accommodate them. Also, stratigraphical resolution may be poor at times of critical evolutionary importance. For example, diverse morphotypes appear nearly simultaneously in the Cambrian (e.g. Rowell 1977), making it difficult to decide which of the conflicting characters is 'the' most primitive.

Outgroup criteria for polarity determination (Watrous and Wheeler 1981; Maddison et al. 1984) were used to test the relationship between stratigraphical first appearance data and cladistic rank among the 'pentamerides' (see Gauthier et al. 1988; Norell and Novacek 1992). Using outgroup criteria, character states present in outgroup taxa presumed to share most recent common ancestry with the ingroup taxa function as the reference for the primitive state. Outgroup analyses generate a phylogenetic framework that is not exclusively dependent upon the quality of preservation of the fossil record, and allow predictions to be made about possible character combinations in fossils not yet discovered. Ideally, both methods will indicate the same polarity, but use different criteria. If they do not, new insights into the nature of character evolution or fossil preservation may be gained.

Three orthide taxa were chosen as outgroups (Nisusiidae, Billingsellidae, and Orthacea), using Williams' (1968) phylogenetic tree as a working hypothesis of relationships among all articulates (Text-fig. 1). The orthides function as outgroups, but they also happen to occur earlier in the fossil record than most of the ingroup taxa. Because of logical problems with coding relative stratigraphical position as a character in a morphological analysis, analyses were conducted independently of stratigraphical position; stratigraphical and morphological results were then compared. Stratocladistics methods (Fisher 1980, 1982, 1988, 1991, 1992; Maddison and Maddison 1992), in which stratigraphical data can be incorporated directly into a morphological analysis but analysed in a manner necessarily different from morphological data, will soon be used and the results compared with these.

Phylogenetic methods

A phylogenetic systematic methodology was employed to analyse genealogical relationships among the 'pentamerides' (see Hennig 1966; Eldridge and Cracraft 1980; Wiley 1981; Wiley et al. 1991). The goal of this method of inference is to identify evolutionary patterns of common ancestry that result from the process of descent with modification. The phylogenetic systematic approach can be viewed 'not as an alternative to traditional evolutionary methods, but as a refinement of them' (de Queiroz 1988, p. 244). Phylogenetic methods produce explicit, testable working hypotheses of relationship.

All analyses were conducted using the microcomputer program PAUP 3.0 (Swofford 1990). PAUP is a parsimony-based program that seeks to find the shortest (most parsimonious) branching diagram compatible with the available data, as it is coded in a taxon-by-character data matrix (SUP 14043, Appendix B). Despite the widespread use of parsimony-based methods, parsimony is a contentious principle in phylogenetic inference (e.g. Felsenstein 1978, 1983; Sober 1983, 1985). Much (but not all) of the controversy surrounds the use of parsimony methods when rates of evolution vary considerably among the taxa being analysed. I have assumed that significantly different rates of taxic evolution are not an issue in this study of 'pentameride' brachiopods, but this is admittedly difficult to estimate.

Any phylogenetic analysis is only as robust as the assumptions implicit in its methods, including character homology, taxon monophyly, polarity determination, etc. Particularly given the ease with which microcomputer programs designed to reconstruct phylogenetic patterns can be used, and results (of greatly varying quality) obtained, it is important to experiment extensively with the data matrix and the program, to avoid accepting uncritically the first (or most favoured) result (e.g. Cann et al. 1987; Templeton 1992).

Four analyses and four of the cladograms that resulted from them form the basis of this study. A heuristic search using global branch swapping methods with random addition of taxa in each of ten replicate analyses was first employed. Branch and bound searches and bootstrap replications

were prohibitively slow due to the size and structure of the data matrix and have not yet been completed. One of the several equally most parsimonious cladograms that resulted was compared with the fifty percent majority rule consensus cladogram of all the equally most parsimonious cladograms. In the second analysis, each of the characters was re-weighted based on its rescaled consistency index (the more stable characters receive proportionally more weight) from the first analysis, and a heuristic search was then performed. The rhynchonellides were removed in the third analysis, revealing their significance in structuring relationships among the 'pentamerides'. Finally, I experimented with selectively weighting four characters concerning the development of muscle platforms, to investigate their effect in 'pentameride' classification.
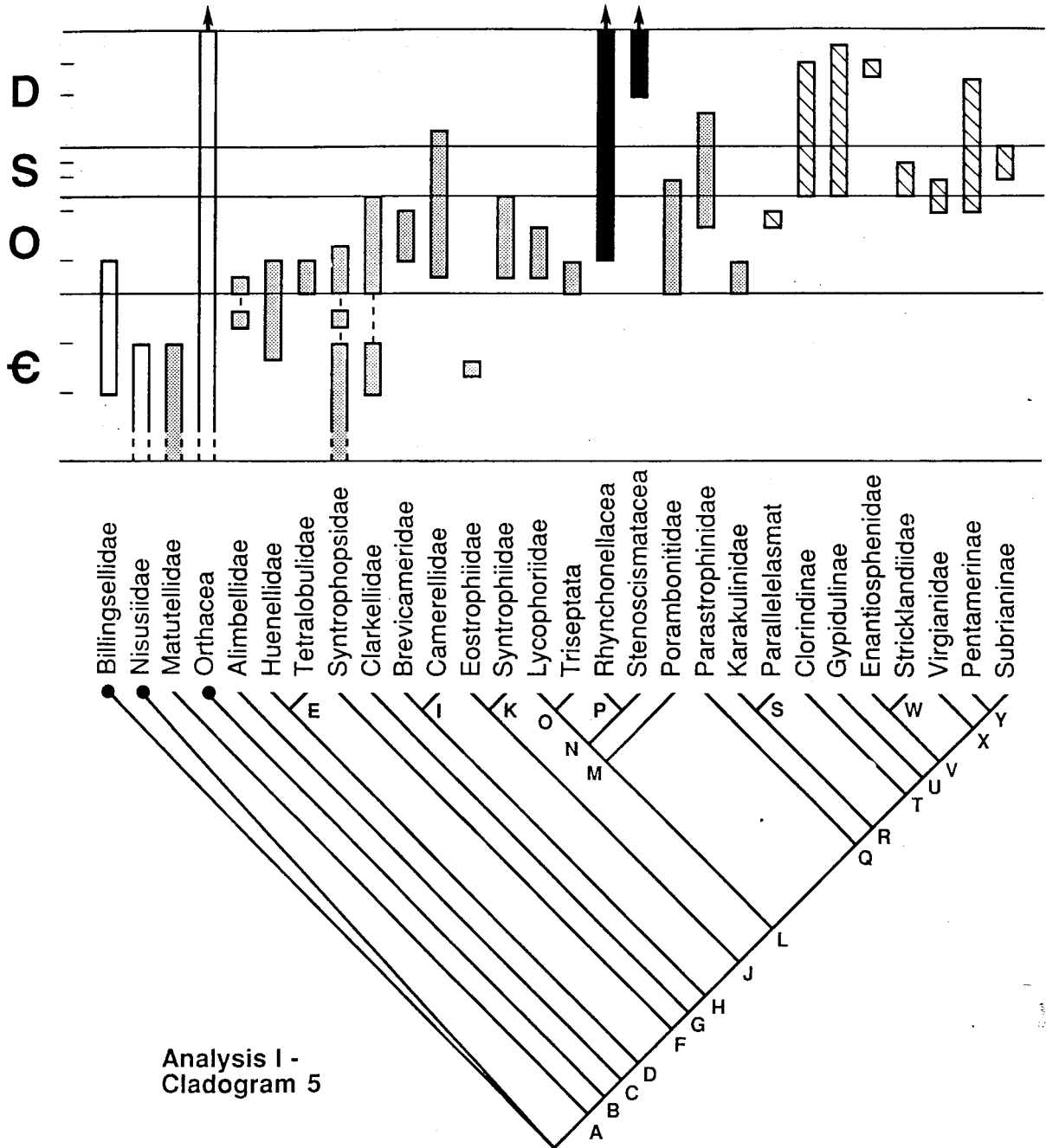
RESULTS

Analysis I – Cladogram 5

The first analysis yielded twelve equally most parsimonious cladograms, each of length 286 and consistency index of 0·389. Although the consistency index appears to be relatively low, it is still well within the norm for analyses of twenty-eight taxa (see Sanderson and Donoghue 1989; Klassen *et al.* 1991). The pattern of relationships that emerges (Text-fig. 2) is not at all unexpected, given traditional concepts of 'pentameride' phylogeny. Moreover, it is quite consistent with the order of first appearance of these taxa in the fossil record. At the family level, 'pentamerides' (currently defined) are paraphyletic. Rhychonellides and pentameraceans each form clades, and each shares most recent common ancestry with different 'syntrophiidine' groups.

More than merely confirming several sister-group pairs recognized in the traditional 'pentameride' phylogenies (e.g. Eostrophiidae ancestral to Syntrophiidae; Huenellidae ancestral to Tetralobulidae; Virgianidae ancestral to the Pentameridae and Subrianidae), the analysis presents a parsimonious and detailed working hypothesis of relationships among all the taxa included in the analysis. To construct the pattern of relatedness among the 'pentamerides' and their relatives at this level of detail, patterns of character homology and homoplasy must be evaluated more or less simultaneously. In the past, certain selected characters ('good' or less variable characters) were used to establish taxon diagnoses, while the distribution of highly variable or conflicting characters was ignored. However, these 'bad' characters may be less problematic in other taxa and may even define them. An explicit branching diagram, with apomorphies defining each node, serves as a basis for discussion of homology and homoplasy in character evolution. Points of disagreement can be established clearly when character distributions across the entire diagram are known.

Remarkable examples of brachiopod homeomorphy – specimens with identical external morphologies and different internal morphologies (e.g. the orthide *Platystrophia* and the spiriferide *Spirifer*) – are relatively common. Such striking convergence in whole suites of characters makes one suspicious that less obvious examples of homoplasy are likely to be common among brachiopods. The analysis bears out this prediction; most of the characters have a consistency index of considerably less than 1·0 (the average is, of course, 0·389), indicating numerous reversals, convergences, or parallelisms.

Given the great geological age of the ingroup and the extinction of all but one of its members, it makes evolutionary sense to expect fairly low consistency among characters. Examining patterns of relationship established over a period of two hundred million years among higher (presumably monophyletic) taxa extinct for over three hundred and fifty million years, it is entirely reasonable to expect relatively high levels of homoplasy. This is particularly true when the pool of characters included in the analysis is limited to morphological characters as they are expressed in organisms less morphologically complex than, for example, arthropods or vertebrates. This is not to say that lower morphological complexity renders cladistic analyses ineffective, only that expectations of high ('statistically significant') levels of congruence among characters is perhaps unrealistic from an evolutionary perspective.

To facilitate discussion of the results, seven groups of taxa are recognized. Some correspond to named higher taxa, others do not. Four of the seven together comprise the order Pentamerida

TEXT-FIG. 2. Cladogram number five; one of twelve equally most parsimonious cladograms resulting from Analysis I, using outgroup polarity. Solid dots under taxon names identify outgroup taxa. The cladogram is rooted at an internal node with a basal polytomy. Note that the ingroup is not strictly monophyletic; Orthacea appears to share more recent common ancestry with certain 'syntrophiidine' taxa than with other orthide taxa. Nodes are identified by the letters beside them; apomorphies of each node are listed in the Appendix. The known stratigraphical range of each taxon is plotted above the taxon names. Outgroup ranges are unshaded, 'syntrophiidine' families are shaded, rhynchonellides are black, and pentameridines are diagonally hatched.

(Amsden 1965; Biernat 1965); three of the seven comprise the Syntrophiidina (Biernat 1965). Characters that distinguish each group will be discussed and compared to current taxon diagnoses.

Pentamerida. Lower Palaeozoic biconvex brachiopods with impunctate shells, open delthyria, distinctive dorsal cardinalia, and ventral spondylia are typically assigned to the order Pentamerida (Amsden 1965; Biernat 1965; see Text-fig. 3). The spondylium, a spoon-shaped structure formed
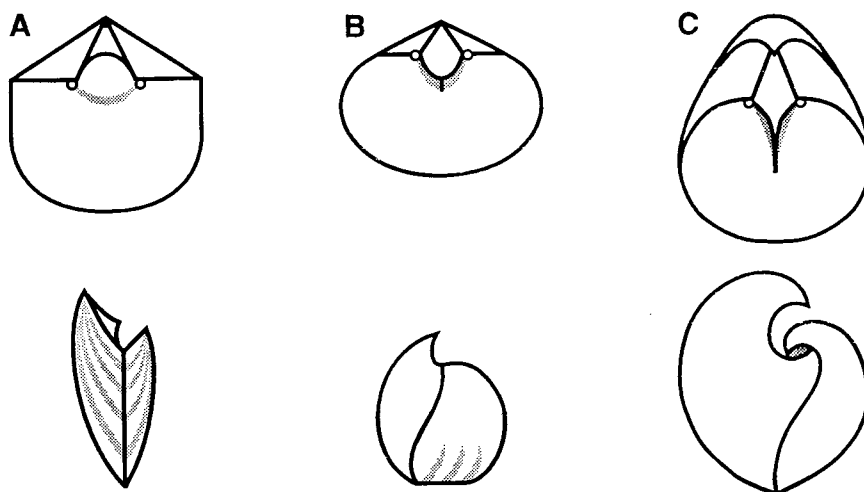
TEXT-FIG. 3. Highly schematic reconstructions to facilitate comparison of relative biconvexity, hinge line shape and length, and development of ventral muscle platforms. Upper row: dorsal view of interior of ventral valves; lower row: lateral view of articulated valves, ventral valve on left. A, early orthide; B, generalized syntrophiidine; C, derived pentameridine.

from the uniting of convergent dental plates and the ventral median septum, is particularly diagnostic of the 'pentamerides', in concert with the other characters mentioned. The results of the phylogenetic analysis (Text-fig. 2; Appendix; SUP 14043, Appendix C) are consistent with this general characterization of the 'pentamerides', but the shared derived characters of the group span several nodes (A–D) in the cladogram, rather than being clustered conveniently at a single node.

The cladogram in Text-figure 2 suggests three possibilities for the definition of Pentamerida. Either the Pentamerida includes the matutellids, making the orthaceans (and alimbellids?) an early offshoot from the 'pentameride' clade, or it includes only the alimbellids, or it excludes both matutellids and alimbellids. Andreeva (1987) classified the matutellids in the Pentamerida and considered them to be the ancestors of the alimbellids, while Williams and Bassett (1991) tentatively suggest that the alimbellids may be more appropriately classified with the Orthida. Matutellids appear to be morphologically intermediate between early orthides and 'pentamerides'. They possess a long, straight hinge line and an apical or supra-apical foramen like early orthides, but also possess a very strong fold and sulcus and mantle canal markings similar to the 'syntrophiidines' (Andreeva 1987). Ultimately, the hierarchic pattern of acquisition of derived characters (Appendix) is more informative phylogenetically than deciding how to define the taxon Pentamerida.

Syntrophiidina. The 'syntrophiidines' have long been considered to be a paraphyletic, early group of 'pentamerides' (Schuchert and Cooper 1932; Williams 1968; see Text-fig. 2). They possess derived characters of the Pentamerida (e.g. open delthyrium, spondylium, strong biconvexity, fold and sulcus), but lack derived characters of the pentameraceans and rhynchonellides (Table 2).

'*Early Syntrophiidina*'. Huenellidae and Tetralobulidae, Syntrophopsidae, and Clarkellidae (and

possibly Alimbellidae and/or Matutellidae) together comprise the earliest 'syntrophiidines', a grade of Cambro-Ordovician 'pentamerides' (Text-fig. 2). They possess derived 'pentameride' features, while retaining certain primitive characters of the orthides (e.g. relatively long hinge lines and extensive interareas, moderate to small adult size). It is the morphological combination of both primitive and derived characters that gives this early paraphyletic group a certain morphological 'integrity'.

'*Camerellacea*'. Nikiforova (1960) established the Camerellacea as a superfamily distinct from the 'porambonitaceans' largely by the combined possession of a spondylium duplex in the ventral valve (a typical pentameracean character) and retention of a 'syntrophiidine' type of dorsal cardinalia and muscle field. The Camerellidae, some parastrophinids, and the Stricklandiidae were originally classified in this superfamily (Nikiforova 1960). Many 'camerellaceans' may possess a spondylium simplex rather than duplex (Biernat 1965). The camerellids alone are a fairly morphologically and taxonomically diverse group; they may not be monophyletic. In this analysis (Text-fig. 2), the brevicamerids and camerellids are sister taxa characterized by a very reduced hinge line, a cruralium (functionally comparable to a spondylium in the dorsal valve), and valve ornament and fold and sulcus restricted to the anterior portions of the valves. Camerellacea redefined in this manner would include only these two families; it is doubtful that these characters alone justify superfamily status for the group. Nevertheless, genus-level analyses within these families may shed light on the distribution and acquisition of characters in the clade and clarify its phylogenetic status. As originally defined, however, the Camerellacea (Nikiforova 1960) does not represent a clade; according to this analysis, its diagnostic characters are homoplastic.

'*Late Syntrophiidina*'. Eostrophiidae and Syntrophiidae, Porambonitidae, Lycophoriidae and *Triseptata*, and Parastrophinidae comprise a poorly resolved grade of (largely) Ordovician 'pentamerides' (Text-fig. 2). Compared to the other 'pentamerides', these brachiopods together possess unusual combinations of primitive and derived characters. They have short (but occasionally long) hinge lines, a weak fold and sulcus, and a strong dorsal septalium. Spondylia are either lacking entirely or are present as duplex spondylia; several have interlocking hinge structures, and many reach large adult sizes. *Cambrotrophia* (the sole eostrophiid) is widely considered to be ancestral to the syntrophiids (Biernat 1965), despite a considerable stratigraphical gap between them (Text-fig. 2). The location of *Cambrotrophia* near the centre of the cladogram is somewhat anomalous considering its early first appearance in the fossil record.

Despite the fact that *Porambonites* serves as the type genus for the superfamily, the porambonitids represent a significant morphological departure from other 'syntrophiidines' because of their large size, characteristic fenestrate ornament, robust hinge teeth (that interlock in some), and in lacking a spondylium. The classification of *Lycophoria* has long been problematical as well. The genus has been classified as a strophomenide (Lahusen 1886; St Joseph 1939), an orthide (Schuchert and Cooper 1932), and a 'pentameride' (Biernat 1965). Although this analysis resolves the *Lycophoria* plus *Triseptata* clade as sister-group to the rhynchonellides, future analysis may reveal that *Lycophoria* (and perhaps *Triseptata*) is more closely related to nonsyntrophiidine brachiopods. The parastrophinids share a number of derived characters with the pentameridines (e.g. astrophic hinge line), but retain a 'syntrophiidine' dorsal cardinalia, including a strong septalium.

Rhynchonellida. Rhynchonellacea and Stenoscismatacea are sister taxa, consistent with their classification in the order Rhynchonellida. Rhynchonellides are characterized by astrophic hinge lines, extremely strong valve biconvexity with a deep fold and sulcus (primitively retained). Most possess a characteristic costate ornament. The delthyrium is partly closed by deltidial plates. The spondylium is absent in the rhynchonellaceans, but present and elaborated in the steno-scismataceans. Brachiophores, bounding the socket, are longer than in the 'syntrophiidines' and brachial processes (in the form of crura) are present. Many rhynchonellaceans possess a strong dorsal septalium either retained primitively from their 'syntrophiidine' ancestry or (possibly)

TABLE 2. Comparison of distinguishing characteristics of the four main groups in this study. Descriptions derive from taxon diagnoses, as referenced. Descriptions in brackets not present explicitly in diagnosis, but characteristic of taxon nevertheless.

Character/Taxon	Porambonitacea (Davidson, 1853) [Biernat 1965]	Camerellacea (Nikiforova 1960)	Pentameracea (M'Coy, 1844) [Amsden 1965]	Rhynchonellacea (Gray, 1848) [Ager 1965]
Size	Variable	Variable	Variable, usually large	[Variable, usually small]
Valve convexity	Unequally biconvex	[Strongly biconvex]	Strongly biconvex	[Strongly biconvex]
Ornament	Smooth, costate, or costellate	(On anterior 1/3 to 2/3)	Smooth, costate, or costellate	[Costate or smooth]
Fold and sulcus	Present	Present	Variable	Usually present and strong
Delthyrium	Open	[Open]	Open or partly covered	Partly closed deltidial plates
Spondylium	Lacking, simplex, or duplex	Duplex (incorrect)	Simplex or duplex	Normally absent
Cardinal process	Absent or rudimentary	[Absent]	Absent, present in few [Reduced]	[Normally absent]
Brachiophores (socket ridges)	United by supporting plates (brachial)	[Like Porambonitacea]		[Well-developed]
Brachial plates	[Generally short] [One part: brachiophore plate] Do not enclose muscles	Like Porambonitacea	Long or short In three parts: inner plate, brachial process, outer plate Enclose muscles in some, but not all	[Normally short] [Hinge plates and crura] [Do not enclose muscles]
Lophophore supports	?None	[?None]	Brachial processes. [not homologues of brachiophores]	Crura [homologues to brachial processes]

developed independently from them. This phylogenetic hypothesis reveals the possible evolutionary origins of characters that typify the rhynchonellides. In other words, the rhynchonellides embody a mosaic of primitive and derived characters at various stages of transformation from their 'syntrophiidine' ancestry.

Pentameridina. Pentameridines typically attain large adult size; some pentameridines are among the largest brachiopods known. They retain a deep spondylium and strong valve biconvexity. The delthyrial (pedicle?) opening is frequently obscured or obstructed by the growth of the strongly rostrate dorsal and ventral beaks. The most distinctive changes involve the dorsal cardinalia which become elaborated (Text-fig. 4) from a single supporting plate (brachiophore plate) to a three-part
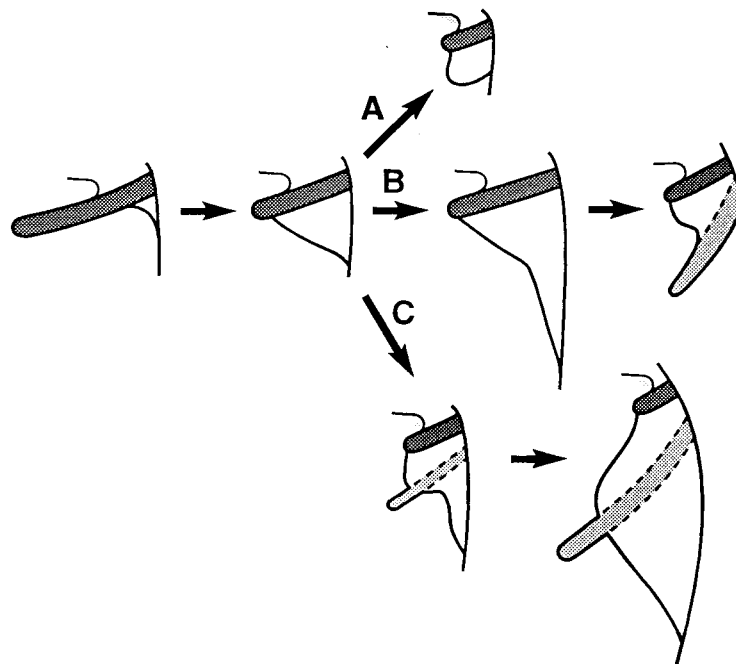
TEXT-FIG. 4. Highly schematic reconstructions of the dorsal cardinalia (left side only, as seen from the sagittal plane) of generalized 'pentameride' taxa. Brachiophores (socket ridges) are black, brachiophore/brachial plates are unshaded, brachial processes/crura are shaded. Sockets are represented as shaded 'hooks' on top of brachiophores. Orthide morphology transforms to the generalized 'syntrophiidine' morphology, which then transforms in one of three general ways: A, to the 'camerellacean' type; B, to the porambonitid and rhynchonellide types; or C, to the parastrophinid and pentameridine types.

brachial plate (consisting of an inner plate, brachial process, and outer plate). Brachial processes (not homologous with brachiophores) are likely to have served as lophophore supports. Pentameridine brachial plates are typically longer than 'syntrophiidine' brachiophore plates. For this reason, they often (but not always) enclose the adductor muscle field, unlike in the 'syntrophiidines'.

Just as the position of the Pentamerida is debatable, so is the position of the Pentameridina. Node Q, R, or T (Text-fig. 2) could serve to delimit the pentameridines, depending on the inclusion of the parastrophinids, and/or the parallelelasmatids and *Karakulina*. Node R corresponds to the point at which pentameridines are generally recognized today; twelve apomorphies characterize the node, many of which are typical pentameridine features. *Karakulina*, originally classified as a 'porambonitacean' (Andreeva 1972), consistently clusters with the pentameraceans in this analysis,

although many characters of this genus are still poorly known. Parallelelasmatidae, first classified as a 'syntrophiacean' (Cooper 1956), was later considered to be a 'porambonitacean' family (Williams 1962), and later still was placed in the Pentameracea (Amsden 1964, 1965); it also consistently clusters with the pentameraceans in this analysis.

Consensus of results from Analysis I

The fifty percent majority rule consensus cladogram of the twelve equally most parsimonious cladograms obtained in Analysis I is illustrated in Text-figure 5. This type of consensus diagram
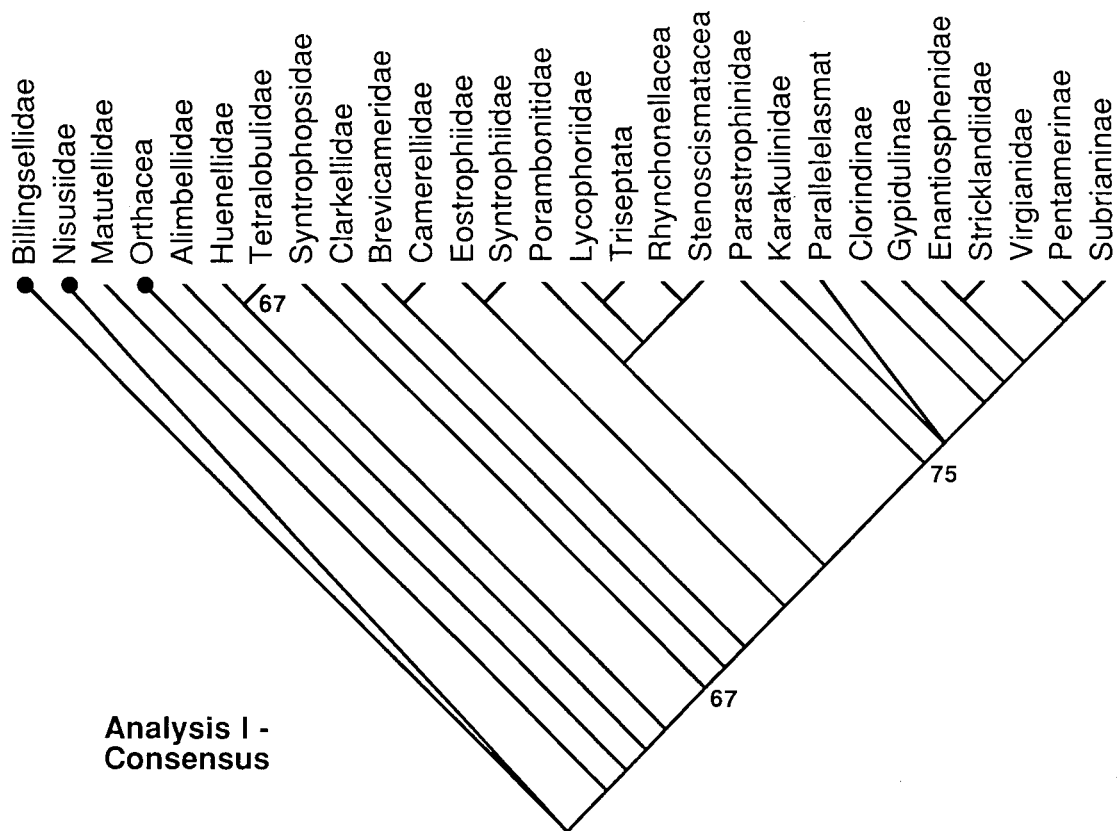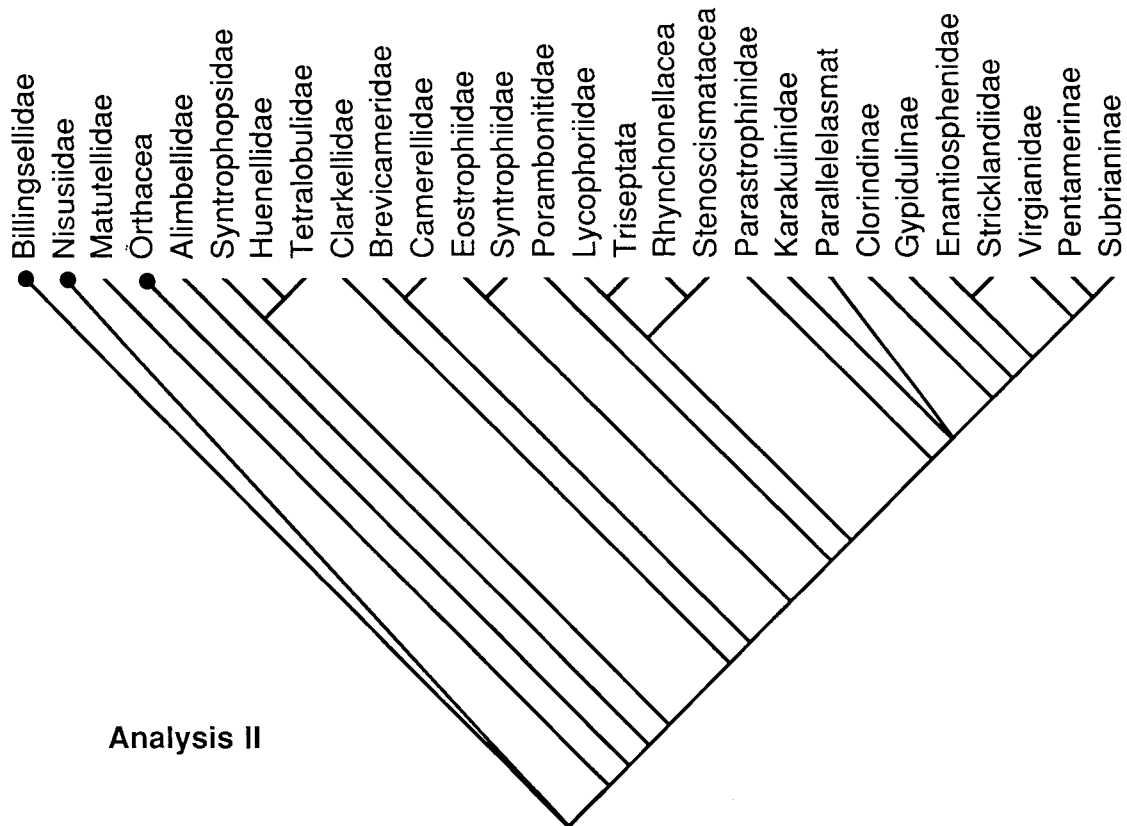

TEXT-FIG. 5. Fifty percent majority rule consensus cladogram of twelve equally most parsimonious cladograms from Analysis I. The numbers beside each node represent the percentage of the twelve cladograms that support that node; unmarked nodes are supported by one hundred percent of the cladograms.

provides a good estimate of the nodes that are more or less consistently supported by the data. Only three nodes are relatively poorly supported (by seventy-five percent or fewer of the cladograms); the rest are quite robust. The topology of the consensus diagram is very similar to cladogram five (Text-figs 2, 5). The *Karakulina* plus Parallelelasmatidae clade collapses to a polytomy with the pentameridines at this level of consensus.

Analysis II

In the second analysis, characters were weighted by the value of their rescaled consistency indices precisely according to their performance in the first analysis. The analysis produced three equally most parsimonious cladograms of length 70 163 (weights are scaled to a base weight of 1000 = 1·0) with a consistency index of 0·503 (Text-fig. 6). The consensus topology is generally similar to
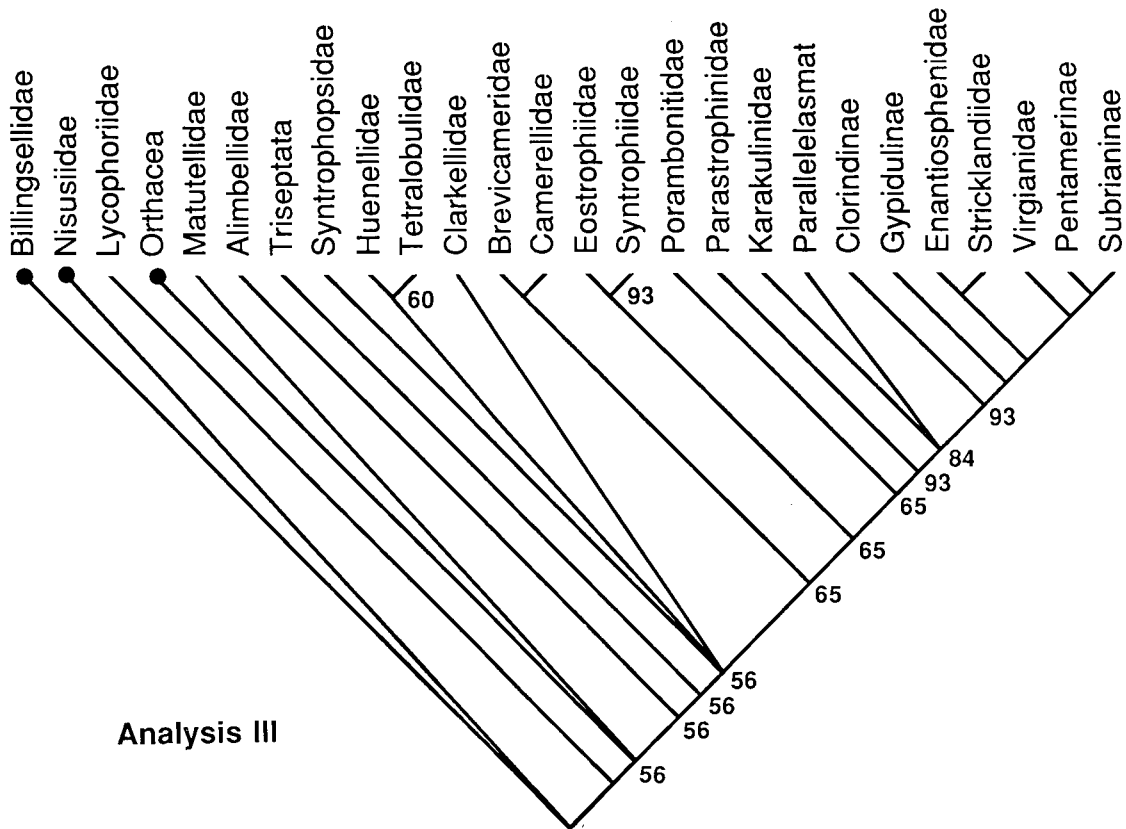

Analysis II

TEXT-FIG. 6. Fifty percent majority rule consensus cladogram of three equally most parsimonious cladograms from Analysis II. Following Analysis I, characters were reweighted according to the value of their rescaled consistency indices.

cladogram five (Text-fig. 2), although a few taxa change positions. Among the early 'syntrophiidines', the syntrophopsids become the sister group to the (Huenellidae plus Tetralobulidae) clade. Porambonitids become the sister group to all the remaining derived 'pentamerides' and rhynchonellides. No major changes in the interpretation of character evolution are required.

Analysis III

The rhynchonellides were removed from the analysis as an experiment, to see if the topology of relationships among the 'pentamerides' would remain stable in their absence. The results are different in several interesting respects. Forty-three cladograms of length two hundred and sixty-eight, each with a C.I. of 0·404, were obtained. The consensus diagram of these forty-three cladograms (Text-fig. 7) shows that resolution among the early 'syntrophiidines' collapses entirely;
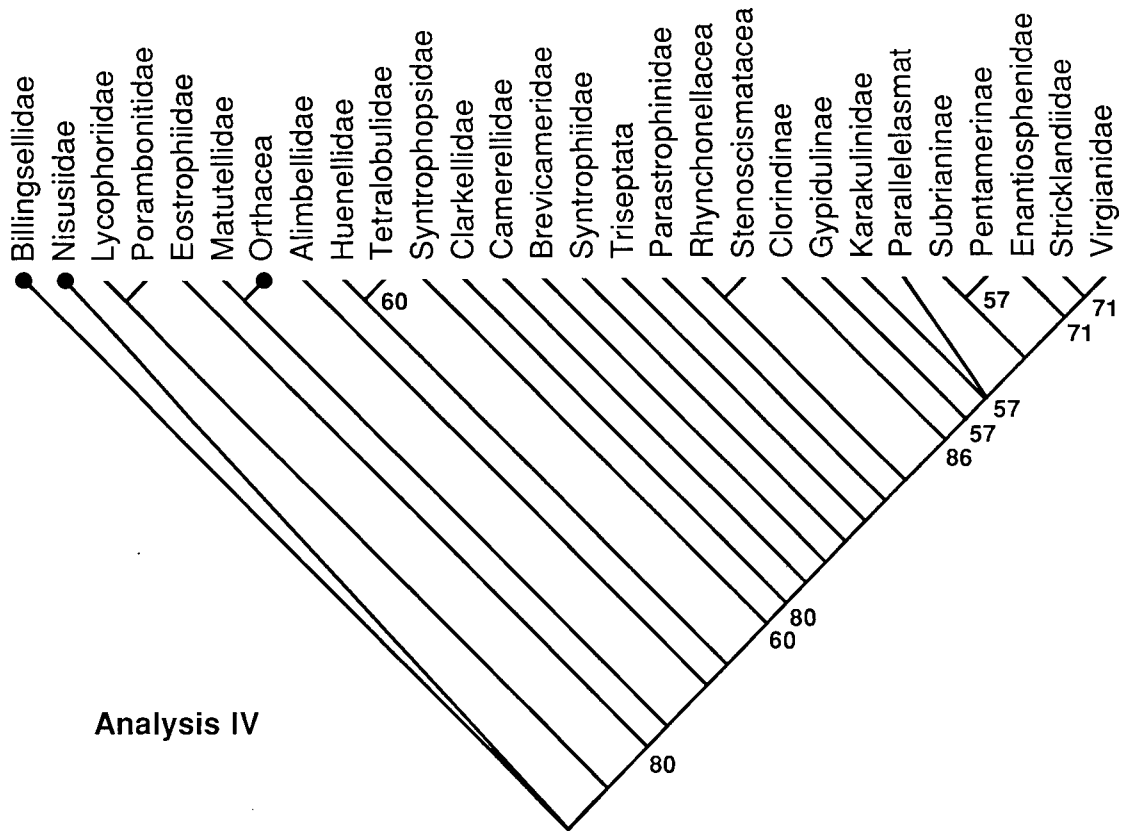
TEXT-FIG. 7. Fifty percent majority rule consensus cladogram of forty-three equally most parsimonious cladograms from Analysis III, in which rhynchonellides were removed. The numbers beside each node represent the percentage of the cladograms that support that node.

most other nodes are very poorly supported, except among the pentameridines. Perhaps most significantly, the *Lycophoria* and *Triseptata* clade breaks apart, and both taxa move down towards the base of the cladogram. *Lycophoria* moves to the branch between the nisusiids and the matutellids (in spite of a sizeable stratigraphical gap between them) consistent with their earlier assignment to the orthides (Schuchert and Cooper 1932). Thus, without the influence of rhynchonellide morphology, this problematic taxon shifts phylogenetic affinities significantly. Stratocladistic methodology would seem to offer a potential resolution of this dilemma, by considering both morphological and stratigraphical information simultaneously.

Analysis IV

In the final experiment, four characters (numbers 33, 37, 57, 60) were arbitrarily weighted four times greater than the other characters. These particular characters, which all relate to the presence and type of spondylium, cruralium, and septalium, were chosen because earlier investigations of 'pentameride' phylogeny (e.g. Schuchert and Cooper 1932; Ulrich and Cooper 1938) emphasized the importance of characters related to the size and orientation of dental plates and brachial plates, and the attachment of muscles relative to these plates. The results are quite different again from the other topologies. Thirty-five cladograms of length three hundred and thirty-one, each with a C.I. of 0·400, were obtained. In the consensus of these cladograms (Text-fig. 8), most of the nodes are

TEXT-FIG. 8. Fifty percent majority rule consensus cladogram of thirty-five equally most parsimonious cladograms from Analysis IV, in which four characters were selectively weighted. The numbers beside each node represent the percentage of the cladograms that support that node.

strongly supported, except within the pentameridines. *Lycophoria*, the porambonitids, and *Cambrotrophia*, lacking muscle platforms, shifted towards the base of the cladogram, among the orthides. A paraphyletic group in the middle of the cladogram, possessing well-developed spondylia, septalia, and cruralia, bears some resemblance to the 'Camerellacea' (*sensu* Nikiforova 1960), including (among others) the camerellids, brevicamerids, and parastrophinids. The rhynchonellides, which lose the ventral platform, and pentameridines, which lose the dorsal platforms, become sister taxa; relationships within the pentameridines are rearranged.

DISCUSSION

The evolution of character complexes

The evolutionary process of descent with modification necessarily results in character transformation over time. Phylogenetic analysis can reveal the nature and direction of transformations, and provide an evolutionary context for the identification and interpretation of evolutionary trends (see Carlson 1992). Recall that characters derived with respect to one node are, at the same time, primitive with respect to the next higher node in a cladogram. The everchanging perspective on the relative state of primitive and derived, moving from the base of a cladogram to the final pair of sister taxa, reveals the dynamic (mosaic) evolution of character complexes.

The stereotypical 'primitive' articulate brachiopod, which derives largely from a composite of early orthide fossils (see Williams and Wright 1965), includes the following elements: dorsal valves of low convexity and ventral valves of generally low convexity; strong radial ornament common; impunctate shell structure; long, straight hinge lines; weak, non-interlocking (deltidiodont) teeth and sockets; wide interarea; large triangular delthyrial openings, often covered by a pseudo-deltidium or deltidial plates, and notothyrial openings; a variably sized foramen at or near the apex of the ventral valve; no mineralized support for the lophophore. As noted earlier, some of these characters are retained by all 'pentamerides', while others are transformed slightly, and some dramatically.

Relationship to substrate. The wide hinge lines and broad interareas in early brachiopods provide a somewhat stable surface upon which the animal rested on soft, but presumably firm substrates (Rudwick 1970; McGhee 1980 b). The earliest articulates possess delthyrial and notothyrial openings in addition to a foramen at or near the apex of the ventral valve. The foramen is generally interpreted as the pedicle opening, while the delthyrial opening may have accommodated only the body of the adductor and diductor muscles extending from one valve to the other (see Rudwick 1970; Rowell and Caruso 1985; Carlson 1989). In brachiopods lacking an apical foramen (e.g. 'pentamerides'), the pedicle, if present, is thought to have emerged from between the valves at the delthyrial/notothyrial opening, although to my knowledge no direct fossil evidence exists to support this assumption.

The hinge line is primitively wide in the 'syntrophiidines' with respect to both outgroup and stratigraphical polarity. It first shortens and then lengthens somewhat in several groups independently. Hinge line width can vary considerably among 'syntrophiidines', even within a species; some specimens have essentially an astrophic (curved) hinge, while conspecifics may possess distinct hinge lines. Astrophic hinges evolved twice from the strophic (straight) condition, first in the rhynchonellides and again in the most recent common ancestor of the parastrophinids and pentameridines. Most pentameridines are astrophic; stricklandiids and some gypidulids present interesting exceptions. The delthyrial openings in pentameridines commonly become obstructed by the growth of the beaks in very strongly biconvex ventral and dorsal valves, apparently preventing the passage of a pedicle. In addition to preservational and palaeoenvironmental evidence, this has lead to the interpretation that at least some pentameridines lacked pedicles entirely and became free-living on soft substrates (i.e. Ziegler *et al.* 1966, 1968). Rhynchonellaceans, the only extant taxon in these analyses, are astrophic, live on hard substrates attached by a pedicle, and possess well-developed pedicle openings.

Hinge structures. The transition from deltidiodont to cyrtomatodont hinge structures has been documented on a broad scale among all articulate brachiopods (Jaanusson 1971; Carlson 1989, 1992). The transition can be observed within the 'pentamerides' as well. In comparison with inarticulate brachiopods, the lack of hinge structures in nisusiids and matutellids is primitive, small teeth with non-interlocking articulation are derived, and large teeth with interlocking articulation are derived relative to non-interlocking structures. Interlocking hinge structures appear to have evolved twice independently among these taxa: in camerellids and in the porambonitid clade (at Node M; Text-fig. 2). Taphonomic evidence (Sheehan 1978) also supports the morphological evidence for cyrtomatodont dentitions in these taxa; they are only infrequently preserved in the fossil record as disarticulated valves.

The possession of a cyrtomatodont dentition does not appear to be a shared derived character of a single monophyletic subclade within the 'pentamerides', thus, cyrtomatodonts are not strictly monophyletic. At a more universal level of analysis, however, cyrtomatodont dentitions in the most recent common ancestor of the rhynchonellides and porambonitids may be a synapomorphy of the cyrtomatodonts, with camerellids (possibly other brachiopods as well; see Jaanusson 1971) convergent on the cyrtomatodont condition. More detailed phylogenetic analyses of all articulate brachiopods will resolve this issue.

Mantle cavity volume. Overall body size increases considerably over the course of 'pentameride' evolution, as does valve convexity (Sapelnikov 1982). 'Syntrophiidines' are generally small, but occasionally reach a fairly large size (e.g. *Porambonites*); they commonly possess a strong fold and sulcus as well. 'Syntrophiidines' first appear to increase convexity in lateral profile, by decreasing their rate of whorl expansion during growth (*sensu* McGhee 1980*a*). With shorter hinge lines, the dorsal profile of more derived 'syntrophiidines' also becomes more rounded over time. Several taxa approach a spherical shape (e.g. *Lycophoria*), which maximizes the ratio of body volume to surface area.

As McGhee (1980*a*) has pointed out, several groups of biconvex articulate brachiopods appear to maximize their mantle cavity volume, possibly as an adaptation for increasing the lophophore's size and food-gathering capabilities (see also Carlson 1992). Unfortunately, the 'pentameride' lophophore type is not known, but is presumed to be a spirolophe, which is the primitive condition for brachiopods (by comparison with living inarticulates). Pentameridines achieve extremes in body size and valve convexity, which is also consistent with the assumption that they were spirolophous (La Barbera 1986). Rhynchonellides remain small to medium-sized and retain the near-spherical mantle cavity shape. They are spirolophous, supporting only the proximal end of the lophophore on short prong-like crura, which are probable homologues to pentameridine brachial processes.

Muscle platforms. Muscle platforms are structures in the posterior of either valve that serve to raise the site of muscle attachments above the valve floor, to varying degrees. The elaboration of muscle platforms and dorsal and ventral cardinalia are among the most significant evolutionary trends within the 'pentamerides'. Nearly all extant brachiopods possess tendinous muscles, in which relatively short muscle bundles that attach to each valve are connected to one another by tendon crossing the expanse of the mantle cavity (Rudwick 1970). Only thecideides, tiny brachiopods with a small ventral platform, today possess columnar muscles in which the muscle bundle extends from one valve to the other, with no tendon in between. Rudwick (1970) proposed that muscle platforms evolve as an adaptive response in brachiopods that (1) possess columnar, rather than tendinous, muscles and (2) are under selection for increasing valve convexity, presumably because of the greater food-gathering capabilities a larger lophophore can attain.

Although ventral muscle platforms of various types have evolved independently several times in articulate brachiopods (e.g. clitambonitaceans, gonambonitaceans, certain atrypides, etc.), the spondylium appears to be a shared derived character of the 'pentamerides'. A variety of types of spondylia have been recognized (Kozlowski 1929; Schuchert and Cooper 1932). In a spondylium simplex, the dental plates have converged and are supported by a single median septum. A spondylium duplex is supported by a single structure that appears to have been formed by the coalescence of two septae, possibly the distal extension of the dental plates themselves (Williams and Rowell 1965, p. H153). The evolutionary transformation of spondylium type in this analysis appears to change from pseudospondylia to sessile to simplex to duplex spondylia. Unfortunately, neither the developmental origin nor the functional significance of the simplex versus duplex spondylium is clear, making it difficult to evaluate the significance of this particular pattern of character transformation. However, given the differences in the structure of these spondylia, the multiple independent origins of simplex spondylia from the sessile condition and duplex spondylia from parallel dental plates seem more likely (and just as consistent with the distribution of characters in Text-fig. 2), although less parsimonious overall (Kozlowski 1929). Old (gerontic) individuals of *Porambonites* commonly develop structures very similar to spondylia and cruralia (Schuchert and Cooper 1932; Biernat 1965). If individuals can develop spondylium-like structures within a life cycle, the multiple, peramorphic (*sensu* Alberch *et al.* 1979) origins of spondylia over evolutionary time are plausible.

Muscle platforms may also develop in the dorsal valve. The brachiophores (socket ridges) in 'syntrophiidines' are supported and united by short brachiophore plates (Text-fig. 4). When these plates unite with and are supported by a median septum, the structure is called a septalium, which may support the diductor muscles (functioning as a cardinal process), but never the adductor
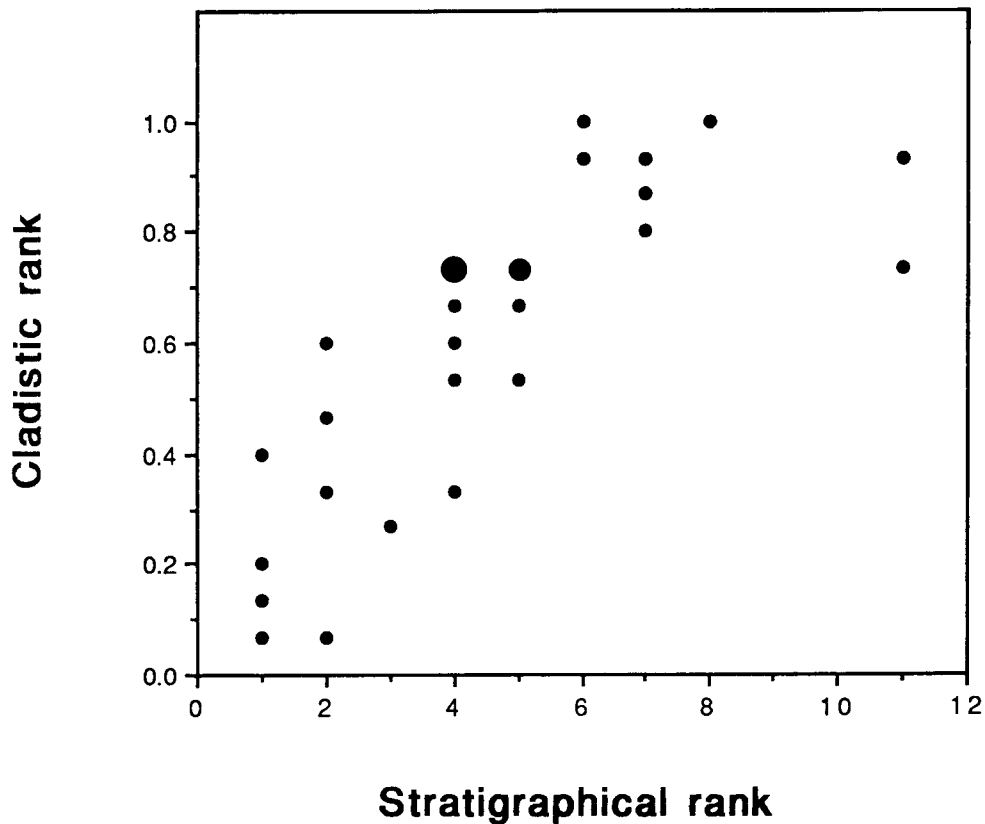
TEXT-FIG. 9. Plot of cladistic rank as it varies according to stratigraphical rank (following Gauthier *et al* 1988). Stratigraphical rank was assigned at the series level (e.g. Lower Cambrian = 1, Middle Cambrian = 2, etc.) according to the first appearance of the taxon in the fossil record. Cladistic rank was determined by counting the number of nodes from the base of the cladogram to each taxon, and is scaled from 0 to 1·0.

muscles (Williams and Rowell 1965). A septalium is present in all 'syntrophiidines' except *Cambrotrophia, Lycophoria,* and the porambonitids, but appears to have evolved four times independently. It is absent in the rhynchonellides and pentameridines. In some 'syntrophiidines' and pentameridines (and stenoscismataceans as a camarophorium), a cruralium develops anterior to the septalium, which supports the adductor muscles and functions as a spondylium in the dorsal valve. According to the results of Analysis I, a cruralium has evolved six times independently among the 'pentamerides'. Muscle platforms in 'pentamerides' appear to have been relatively easy to construct and the selection pressure to construct them high.

In summary, morphological transformations previously known to occur within the 'pentamerides' can now be discussed with respect to a specific phylogenetic hypothesis of relationships among all the named 'pentamerides' families. The pattern of transformations in all characters can be compared simultaneously; the distribution of homologues, both primitive and derived, as well as homoplastic characters is revealed. The order of acquisition of evolutionary novelties (polarized by methods of outgroup comparison), including the loss or secondary transformation of characters, may be traced on the cladogram and compared with the known stratigraphical ranges of the analysed taxa.

Comparison of outgroup results and stratigraphical position

The fossil record provides series of morphologies in an ordered temporal sequence related to the evolutionary time of origin and the direction of transformation of characters and character states. Nevertheless, it is clear that the fossil record represents a more or less erratic sampling of the history and diversity of life. Some critics have claimed that the record is too incomplete to record accurately the true sequence of character transformation (Nelson 1978) and that ancestral taxa may either never have been preserved as fossils or they may not appear in the record as early as their actual time of origination (see Patterson 1981; Norell 1992). Despite these difficulties, agreement between cladistic rank and stratigraphical rank is often quite good (Gauthier *et al.* 1988; Donoghue *et al.* 1989; Norell and Novacek 1992), as is the case in this analysis (Text-fig. 9).

Outgroup analyses provide criteria independent of relative first appearance in the fossil record for evaluating the direction of character change in evolution. Studying the pattern of acquisition of evolutionary novelties (apomorphies) in a cladogram obtained using outgroup methods, in conjunction with the available geological evidence, may help to distinguish between alternative explanations of the preserved stratigraphical record. One of the advantages of employing stratocladistic methods (Fisher 1991, 1992) is that morphological and stratigraphical information can be combined in a single analysis and the results compared with previous hypotheses.

Analysis I. A method for comparing stratigraphical first occurrence data with cladistic rank was developed by Gauthier *et al.* (1988; further elaborated by Norell and Novacek 1992). If two sources of information on polarity are congruent, they are positively correlated; the greater the congruence, the stronger the correlation. This method was used to compare the first occurrences of 'pentameride' families with their ranking in cladogram five (Text-fig. 2), although no attempt was made to accommodate redundant ranks (Norell and Novacek 1992). A clear positive relationship exists between the two variables (Text-fig. 9). Using ranked stratigraphical first occurrence as the independent variable, a linear regression yields a correlation coefficient of 0·602. Two outliers are noticeable, the Enantiosphenidae and the Stenoscismatacea; eliminating them and recalculating the correlation yields a coefficient of 0·748. Both first appear in the fossil record much later than would be predicted on the basis of their cladistic ranking alone, indicating one of two things. Either their true stratigraphical ranges extend further back in the record than currently known, or they share common ancestry with a late-appearing and derived species in their sister taxon. Overall, the order of appearance of 'pentameride' families in the fossil record agrees well with their ranking in a phylogenetic diagram constructed independently of stratigraphical position.

An empirical example. An example from the 'pentameride' literature illustrates one of the difficulties in relying exclusively on stratigraphical polarity in phylogenetic reconstruction. Prior to 1987, the Eostrophiidae was the stratigraphically lowest 'pentameride' family, occurring in the Middle Cambrian. The assignment of *Syntrophioides* to Clarkellidae (by Schuchert and Cooper 1931), which extends the stratigraphical range of the clarkellids to the Middle Cambrian, is tentative and may not survive revision of the group. As the stratigraphically lowest, *Cambrotrophia* has assumed the role of 'typical ancestral pentameride' (e.g. Sapelnikov 1980). Therefore, I had predicted that it would appear as a fairly primitive member of the 'pentamerides' in my analyses. Contrary to expectations, eostrophiids appear near the middle of the cladograms, possessing an interesting mixture of primitive and derived morphological features.

In 1987, Andreeva described a new genus, *Tcharella*, from the Lower Cambrian of Siberia. She classified *Tcharella* in the Syntrophopsidae (and moved *Cambrotrophia* to this family as well, although my analyses do not support her reassignment). With this new discovery, if the family assignment is justified, Syntrophopsidae becomes the oldest 'pentameride' family known from the fossil record. It also appears much closer to the base of the 'pentameride' clade in all cladograms (Text-figs 2, 5–7) than does Eostrophiidae. In this instance, cladograms generated using outgroup methods of polarity determination provided a basis for predicting where previous collecting biases

had existed. In other words, recent collecting in the Cambrian of Siberia revealed that brachiopods morphologically more primitive than *Cambrotrophia* (on the basis of this analysis) existed in the fossil record earlier than previously thought, but were only recently collected and named. It is likely that the stratigraphical ranges of some of the other primitive families (e.g. Huenellidae, Tetralobulidae) will be extended further back in time, as collecting in Cambrian strata of less well-known regions proceeds. This process of discovery cannot proceed indefinitely, but it is clear that exploration and description of Cambrian fossils and strata in a number of remote areas is active and ongoing, and yields new information regularly (e.g. Ushatinskaya 1986; Andreeva 1987; Popov and Tikhonov 1990).

Phylogenetic analyses of the sort presented here establish morphological states and their evolutionary transformations within systems of common ancestry without having to rely on the collections of particular specimens from particular stratigraphical horizons that exhibit particular combinations of characters. In other words, characteristics likely to have been present in the common ancestor can be hypothesized based on the distribution of features in known specimens, irrespective of whether a specimen has been collected that exhibits all those ancestral features (de Queiroz and Gauthier 1990). As they are collected, new specimens will test existing hypotheses.

Previous views of 'pentameride' phylogeny and classification

A very brief review of the history of 'pentameride' classification reveals much controversy over the status of 'pentamerides' as a unified group, and the identification of the group of brachiopods with which 'pentamerides' share most recent common ancestry (see Muir-Wood 1955). The current view (Williams 1968; Text-fig. 1) considers 'pentamerides' to have evolved from the orthides and given rise to the rhynchonellides; each of these three groups is classified in a separate order of the Articulata.

Schuchert and Cooper (1932) remains today the most detailed discussion of phylogenetic relationships among 'pentameride' genera. In their tentative phylogenetic reconstructions, genera that would today all be classified in the superfamily Porambonitacea (Biernat 1965) were placed in four separate lineages and assigned to three different superfamilies (Text-fig. 10). Two lineages derived from the Billingsellidae, one that gives rise to the pentameraceans via Syntrophiidae, and one that leaves no descendant higher taxa. Two other lineages emerge from Orthidae, deep within the Orthacea. Ulrich and Cooper (1938) briefly discuss possible phylogenetic relationships among these brachiopods and are in general agreement with Schuchert and Cooper (1932). They tentatively suggest that the rhynchonelloids may have evolved from the syntrophiids, which also gave rise to the camerellids, and culminated in the parastrophinids. Comparing the phylogenetic tree in Text-figure 10 to the cladogram in Text-figure 8 (where ventral and dorsal cardinalia were weighted preferentially), certain similarities emerge, suggesting that these characters may have been given particular weight in structuring relationships among the 'pentamerides'.

In 1965, Biernat (in the *Treatise on invertebrate paleontology*) proposed a classification that differs considerably from that of Schuchert and Cooper (1932), but is comparable to the (partial) classification in Cooper (1956). The Porambonitacea are united as a single (?monophyletic) superfamily in the suborder Syntrophiidina (Table 1). Cooper (1956) placed both superfamilies Pentameracea and Rhynchonellacea in the suborder Pentameroidea, perhaps as a reflection of the close phylogenetic relationship envisioned between these taxa. Unfortunately, neither Cooper nor Biernat presented much in the way of phylogenetic analysis of named 'pentameride' genera or families; some sense of phylogeny must be inferred from the grouping of taxa into higher taxa (although classifications may be arrangements of convenience and explicitly *not* phylogenetic in structure; Cooper 1944).

Sapelnikov (1980) proposed a classification substantially different from previous sources. The assignment of genera to families bears little resemblance to earlier schemes, and a number of genera named prior to 1980 appear to have been omitted in the analysis. In addition to a new classification, a hypothesis of phylogenetic relationships among the (newly reconstituted) families and subfamilies
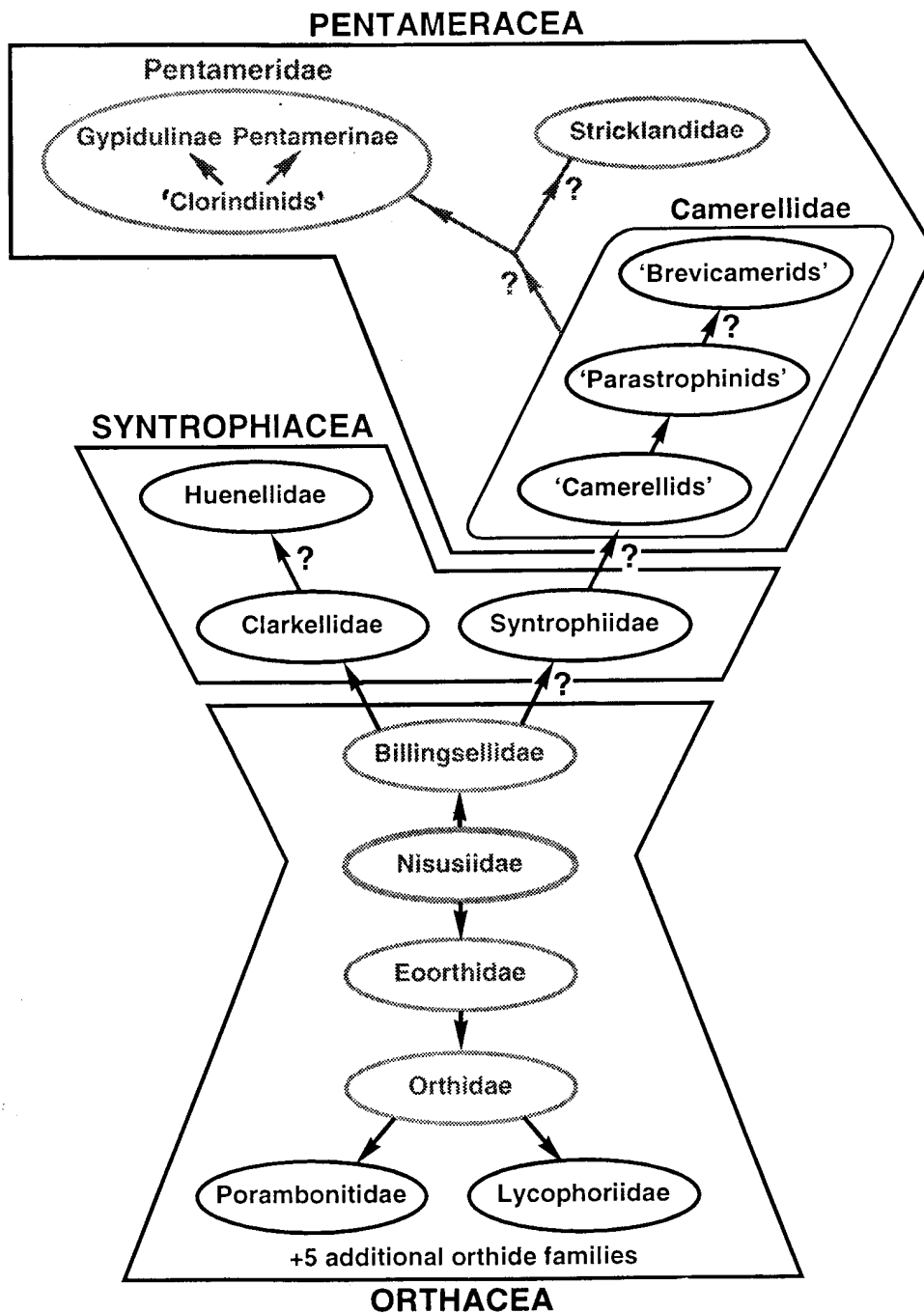
TEXT-FIG. 10. Phylogenetic relationships among 'syntrophiacean' (= 'porambonitacean'), pentameracean, and selected orthacean families (compiled and redrawn from Schuchert and Cooper 1932), illustrating the apparently fragmented phylogenetic relationships among families (outlined in heavy black ovals) currently classified in the Porambonitacea (Biernat, 1965). The Orthacea, as illustrated here, was reorganized by Williams and Wright (1965) for the *Treatise on invertebrate paleontology*; billingsellids and nisusiids were removed and placed in a separate superfamily, the Billingsellacea. The Orthacea chosen as an outgroup in this study reflects the more recent definition of the superfamily.

was presented. Seven higher taxa emerge from the Huenellinae simultaneously at the base of the Ordovician (Sapelnikov 1980, fig. 1); phylogenetic resolution is low.

It seems clear that classification of the 'pentamerides' has been fairly contentious for more than a century. Major differences among systematists in both the naming and relative ranking of higher taxa have resulted primarily from differences in the interpretation of 'pentameride' phylogeny, specifically levels of character homology, relative to articulate brachiopod evolution.

Implications for 'pentameride' classification

As they are currently defined (Amsden and Biernat 1965), the Pentamerida, Syntrophiidina, and Porambonitacea are each paraphyletic, the Camerellacea (Nikiforova 1960) is polyphyletic, and the Pentameridina and Rhynchonellida are each monophyletic with respect to the result of the analyses described here. Establishing the phylogenetic status of each of these named higher taxa with reference to a working hypothesis of relationship (Text-fig. 2) is valuable and necessary if named higher taxa are to play an interpretable role in macroevolutionary studies.

Controversy surrounds the field of classification, particularly in assessing the phylogenetic status of existing higher taxa, and in naming new taxa and ranking those taxa in some kind of a hierarchic scheme (see de Queiroz and Gauthier 1992). Newly named or rediagnosed higher taxa should be monophyletic. Characters (synapomorphies) diagnose monophyletic taxa, and enable us to determine whether a given organism is representative of the taxon or not. However, monophyletic entities are systems of common ancestry that exist independent of our ability to recognize them (de Queiroz and Gauthier 1990). Thus, we recognize snakes as tetrapods even though they lack limbs; in this case, evolutionary character transformation is expressed as the loss of a character. It may also be expressed as dramatic transformation (e.g. avian wing, mammalian inner ear).

While most systematists will admit that named taxa should have phylogenetic significance, there is debate about whether or not paraphyletic groups (as only partial systems of common ancestry) have phylogenetic significance. Many neontologists argue against the naming of paraphyletic groups (e.g. de Queiroz and Gauthier 1990), while palaeontologists commonly argue in their favour (e.g. Waller 1978). Particularly when dealing with fossils, a paraphyletic taxon has been named to designate the group of plesions (*sensu* Wiley 1981) excluded from a derived clade; each taxon is often given the same taxonomic rank (e.g. suborders Syntrophiidina and Pentameridina in the order Pentamerida). If phylogenetic relationships among the organisms of interest are unknown, or very poorly known, it is possible that paraphyletic taxa can be named by accident. However, when a working hypothesis of phylogenetic relationship has been constructed (e.g. Text-fig. 2), paraphyletic taxa can only be named on purpose (de Queiroz and Gauthier 1990), regardless of which taxonomic philosophy one adopts.

In discussions of macroevolutionary phenomena, it is often useful to recognize groups of organisms that share ecologically or functionally significant suites of primitive characters, particularly if they also share similar extinction histories (Fisher 1985, 1991). Referring to these known paraphyletic groups as, for example, non-avian dinosaurs or non-mammalian synapsids is acceptable, but perhaps unnecessarily awkward. Informally, known paraphyletic groups are denoted as such by enclosing their names in quotation marks (Gauthier 1986). To avoid confusion, explicit reference should be made to an existing phylogenetic hypothesis (branching diagram) in which membership in the paraphyletic group is clear. Without such a reference, dinosaurs could represent either the paraphyletic group of fully terrestrial archosaurs or the monophyletic group that also includes birds.

Taxonomic revisions necessarily invite confusion. Old taxon names rediagnosed have different meaning; new taxon names are unfamiliar. The status of 'pentameride' higher taxa, as they are currently diagnosed, with respect to these cladograms (Text-figs 2, 5-8) is clear. It is possible formally to rediagnose the Pentamerida and Pentameridina on the basis of this phylogenetic analysis. However, this paper focuses on characters rather than taxa – on the pattern of acquisition of shared derived characters as represented in the branching diagrams themselves. It is debatable

whether Pentamerida is the most appropriate taxon name (irrespective of taxonomic rank) for the clade of 'pentamerides', rhynchonellides, and their relatives. Such a decision must await the completion of additional, complementary analyses by other brachiopod systematists, particulary those working at lower taxonomic levels on the orthides and rhynchonellides.

Extinction of a paraphyletic taxon

Paraphyletic groups are characterized by the possession of derived characters *and* the retention of primitive characters. The 'syntrophiidines' possess derived 'pentameride' features and can thus be recognized as 'pentamerides', but also retain more primitive orthide characteristics than do either of their descendants. The rhynchonellides and pentameridines retain primitive 'pentameride' features, but also possess unique sets of derived characters that distinguish them, as clades, from their ancestors.

Of what evolutionary significance is the extinction of the paraphyletic 'syntrophiidines'? Of the monophyletic pentameridines? Or the survival of the monophyletic rhynchonellides? The extinctions were apparently not clustered in time (at this level of resolution; Text-fig. 2); no mass extinction eliminated all (and only) the primitive 'pentameride' families. The evolution of character complexes over time, the acquisition of derived characters and the loss or transformation of primitive characters, resulted in the recognition of successively younger groups of organisms as distinct taxa. Thus, the process of evolution itself results in the pseudoextinction (Smith and Patterson 1988; Fortey 1989) of paraphyletic taxa such as the 'syntrophiidines' or, more universally, the 'pentamerides'.

Comparing the features of the monophyletic survivors and victims, some interesting patterns emerge. 'Syntrophiidines' are relatively small brachiopods with primarily strophic hinge lines and non-interlocking hinge structures, strong biconvexity and fold and sulcus, no calcareous lophophore supports, with variously developed muscle platforms in both the ventral and dorsal valves. They lived on soft substrates, anchored by a pedicle in a manner presumably similar to their orthide ancestors. Rhynchonellides retained the small 'syntrophiidine' adult size, strong biconvexity, and fold and sulcus. However, they evolved astrophic hinge lines with interlocking teeth and sockets, and live today attached to hard substrates by a strong pedicle. They also developed distinct supports for at least the base of the lophophore. Some lost the ventral platforms; some elaborated platforms in each valve. 'Pentamerides' retained the non-interlocking hinge structures and also, in general, developed astrophic hinges, retained ventral but lost dorsal muscle platforms, retained a soft substrate habitat but lost a functional pedicle as adults, and retained strong valve biconvexity but grew to very large size. They also developed brachial processes thought to support the base of the lophophore. The combination of astrophic hinge lines and non-interlocking teeth and sockets in 'pentamerides' was thought to be fundamentally unstable (Jaanusson 1971). Together with the lack of a pedicle, these features may have contributed to the extinction of the group. Rhynchonellides survived because of the particular combination of characters they possessed (interlocking hinge structures and hard substrate habitat), given the environmental changes occurring at the end of the Devonian (see Copper 1990).

Although this scenario makes logical sense, viewing the pattern of 'pentameride' extinction and survival in these terms alone oversimplifies a more complex pattern. In other words, it successfully accounts for a portion of the existing evidence, but ignores conflicting evidence. For example, many strophomenides lacked a pedicle, lived on soft substrates, grew to large sizes, and had non-interlocking hinge structures, but were very abundant and diverse through the entire Palaeozoic. Was the additional combination of strong biconvexity and astrophic hinge lines sufficient to put 'pentamerides' at a strong selective disadvantage in the middle Palaeozoic? If so, why were 'pentamerides' themselves so abundant while they were extant (Ziegler *et al.* 1968; Amsden 1969)? They are often depicted as a classic specialized group, very well adapted for one mode of life (apediculate, with their weighted posterior buried in the sediment) that they exploited in great numbers, and were then eliminated by some change in their habitat to which they could not adapt

(see Boucot and Johnson 1979). Detailed palaeoenvironmental investigations are more appropriately suited to answer the how and why of patterns of extinction and survival. Nevertheless, a phylogenetic context provides an explicit framework within which causal hypotheses of extinction and adaptation may be generated and tested.

SUMMARY AND CONCLUSIONS

1. 'Pentamerides' played an important role in the early evolution of articulate brachiopods, yet their phylogenetic relationships have not been studied in detail for the past several decades. Phylogenetic relationships among named 'pentameride' families and rhynchonellide superfamilies were reanalysed, using outgroup methods of polarity determination. A detailed working hypothesis of 'pentameride' phylogeny and the supporting evidence on character distribution is presented. The paraphyletic 'syntrophiidine pentamerides' gave rise, through the process of descent with modification, to two clades: the pentameridines, a distinctive apediculate group extinct by the end of the Devonian, and the rhynchonellides, which are represented little changed in the modern fauna. This phylogenetic hypothesis will be tested in the future as genus-level analyses and stratocladistic analyses (Fisher 1992; Maddison and Maddison 1992) are completed.

2. The phylogenetic hypothesis obtained can serve as a foundation for detailed studies of character evolution within this important, early group of brachiopods. Strophic hinge line length decreases steadily to the astrophic condition, interlocking hinge structures arise twice from the non-interlocking condition and muscle platforms in the dorsal and ventral valves evolve several times independently. These generally acknowledged patterns of morphological change, among others, may now be examined in detail as they are expressed in a comprehensive pattern of relationship. Levels of homology and patterns of convergence and parallelism are revealed; primitive absence can be distinguished from derived loss of characters. It is possible to study the dynamic mosaic of character evolution among large numbers of characters simultaneously.

3. Outgroup methods can serve as an independent test of stratigraphical polarity methods. In this study, agreement between the stratigraphical first appearance of 'pentameride' families and their cladistic rank is quite good, suggesting that, at least in this example, both methods indicate the same direction of character polarity in evolution. Outgroup methods can generate predictions about ancestral character combinations independent of the empirical record, and provide a means of generating phylogenetic hypotheses among taxa that appear more or less simultaneously in the fossil record.

4. The phylogenetic status of named 'pentameride' higher taxa is established, at least with respect to one hypothesis of relationship. Rhynchonellida and Pentameridina are monophyletic; Pentamerida and Syntrophiidina are paraphyletic. More than simply categorizing the status of named taxa, the nature of paraphyly is revealed explicitly. Comparisons between older classifications and newer phylogenetic reconstructions reveal the macroevolutionary roles that named paraphyletic taxa have played in the past.

5. What is the significance of the extinction of a paraphyletic taxon? In this instance, the extinction of the 'pentamerides' signifies the end of an early stage in the evolutionary transformation of articulate brachiopods. The 'syntrophiidines' suffer pseudoextinction in transforming to the rhynchonellides (extant) and the pentameridines, which possess a combination of characters (strong biconvexity, large adult size, lack of pedicle, non-interlocking dentition) that apparently rendered them less able to adapt to changes in their habitat. There is value in recognizing, if only informally, paraphyletic groups of taxa that possess unique and functionally or ecologically relevant combinations of derived and primitive characters. This is particularly true when the derived state of a character that defines a named subclade takes the form of loss or extreme transformation from its primitive state. Paraphyletic groups should always be interpreted with respect to a specific phylogenetic hypothesis so the nature of their paraphyletic status is clear. In this context, they may be useful and informative in studies of character evolution.

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APPENDIX

Descriptions of shared derived characters (and the primitive states from which they transformed) for all internal nodes on cladogram number five.

Pentamerida

Node A: Ventral valve convexity greater than dorsal valve (from equal convexity); strong fold and sulcus present (from absent); open delthyrium (from delthyrium covered by pseudodeltidium); pseudospondylium present (from absent); mantle canal markings digitate (from saccate); brachiophore plates rudimentary (from short); short dorsal median septum present (from absent).

Node B: Radial ribs present as costae (from costellae); pedicle opening as delthyrium (from foramen); dental plates distinct (from absent).

Node C: More or less spherical lateral valve profile (from anteriorly compressed); strong valve biconvexity (from moderate); dorsal valve convexity greater than ventral valve (from ventral valve greater); convergent

dental plates (from divergent); dental plates united with median septum (from not united); short ventral median septum present (from absent); weak septalium present (from absent).

Node D: Valve outline subpentagonal (from subquadrate); short hinge line (from long); spondylium present (from pseudospondylium); spondylium deep (from shallow); deep notothyrial cavity (from shallow); brachiophore plates short (from rudimentary); convergent brachial plate orientation (from divergent).

'Early Syntrophiidina'

Node E: Posteriorly compressed lateral valve profile (from more or less spherical); dorsal and ventral valve convexity approximately equal (from dorsal valve more convex); dorsal valve interarea orientation anacline (from apsacline); hinge line of medium width (from short); four lateral septae in dorsal valve (from two); dorsal adductor muscle attachment area quadrilobate (from other than quadrilobate).

Node F: Small adult valves (from moderate); fold and sulcus present on anterior two-thirds of valve only (from entire valve); small hinge teeth (from large).

Node G: Ventral valve interarea reduced (from extensive); dorsal valve interarea reduced (from extensive); spondylium simplex (from sessile); weak callosities around muscle attachment area in dorsal valve (from absent).

Node H: Sulcus not extended into distinct tongue (fron tongue present); accessory septae supporting spondylium not prolonged in front of spondylium (from prolonged); anterior dorsal adductor muscle scars larger than posterior (from posterior larger); well-developed adductor muscle attachment area present anterior to cruralium (if present) (from absent); dorsal adductor muscle attachment area quadrilobate (from other than quadrilobate).

'Camerellacea'

Node I: Lateral valve profile compressed posteriorly (from more or less spherical); bumpy or pustulose valve ornament, if not radial ribs (from fenestrate); ornament present on anterior third of valve only (from entire valve); fold and sulcus present on anterior third of valve only (from anterior two-thirds); extremely short hinge line (from short); cruralium present (from absent).

'Late Syntrophiidina'

Node J: valve ornament smooth (from radial ribs); spondylium duplex (from simplex); ventral median septum absent (from present and short); dorsal median septum long (from short); septalium absent (from present and weak); callosities around muscle attachment area in dorsal valve absent (from present and weak).

Node K: Valve outline subquadrate (from subpentagonal); anteriorly compressed lateral valve profile (from more or less spherical); weak fold and sulcus (from strong); fold and sulcus ornament smooth (from costate); hinge line medium width (from short); cruralium simplex (from duplex).

Node L: Dorsal valve interarea obsolete (from reduced); spondylium wide (from narrow); brachial plates long (from short); brachial processes blade-like (from absent); outer brachial plates present and short (from absent); long septalium (from short); septalium on septum (from sessile); strong callosities around muscle attachment area in dorsal valve (from absent).

Porambonitid clade

Node M: Large adult valves (from small); valve ornament as radial ribs (from smooth); interlocking hinge structures (from non-interlocking); large hinge teeth (from small); dental plate orientation subparallel (from convergent); spondylium absent (from present).

Node N: Valve length approximately equal to width (from width greater); subtriangular valve outline (from subpentagonal); very strong valve biconvexity (from strong); well-developed cardinal process (from absent); brachial plates short (from long); outer brachial plates absent (from present and short); brachial plates united with cardinal process (from not united).

Node O: Valve length greater than width (from approximately equal); valve outline more or less spherical (from subtriangular); radial ribs costellate (from costate); fold and sulcus lacking (from present and strong); dorsal valve interarea reduced (from obsolete).

Rhynchonellida

Node P: Small adult valves (from large); posteriorly compressed lateral valve profile (from more or less spherical); moderately rostrate ventral valve beak (from not rostrate); growth lines absent (from present and weak); ventral valve interarea orientation anacline (from apsacline); hinge line astrophic (from strophic); delthyrium may be partly covered by deltidial plates (from open delthyrium); brachiophores long and curved (from short and blunt).

Node Q: Moderately rostrate ventral beak (from not rostrate); ventral valve interarea obsolete (from reduced); astrophic hinge line (from strophic); pedicle opening absent (from present as delthyrium); spondylium supported on high septum (from low); ventral median septum long (from absent); ventral valve muscle impressions confined to spondylium (from not confined).

Pentameracea

Node R: Valve length approximately equal to width (from width greater); ventral valve convexity greater than dorsal valve (from dorsal valve greater); strongly rostrate ventral valve beak (from moderately rostrate); growth lines absent (from present and weak); fold and sulcus extends the entire length of the valves (from anterior $\frac{2}{3}$ only); medium hinge width (from short); ventral median septum does not extend anterior to spondylium (from extends beyond); mantle canal markings pinnate (from digitate); dorsal median septum absent (from long); adductor muscle attachment area anterior to cruralium absent (from present and well-developed); adductor muscle attachment area quadrilobate in shape (from other than quadrilobate); callosities around muscle attachment area in dorsal valve absent (from present and strong).

Node S: Valve convexity equal (from ventral valve greater); valve ornament present only on anterior $\frac{2}{3}$ of valve (from present on entire valve); fold and sulcus absent (from present and strong); if present, fold and sulcus only on anterior third of valve (from present on entire valve); ventral valve muscle impressions not confined to spondylium (from confined); subparallel brachial plates (from convergent).

Node T: Very deep spondylium (from deep); brachiophores poorly developed (from short and blunt); long outer brachial plates present (from short).

Node U: Large adult valves (from small); valve outline subtriangular (from subpentagonal); valve biconvexity very strong (from strong); delthyrial cavity shallow (from deep); short ventral median septum (from long).

Node V: Very large adult valves (from large); fold and sulcus absent (from present and strong); shallow notothyrial cavity (from deep); rod-like brachial processes (from blade-like); outer brachial plates absent (from present and long); adductor muscle attachment area anterior to cruralium well-developed (from absent); outer lamellar shell layer in dorsal and ventral valves not intersecting (from intersecting).

Node W: Anteriorly compressed lateral valve profile (from more or less spherical); moderate valve biconvexity (from very strong); ventral valve beak not rostrate (from strongly rostrate); outer lamellar shell layer in dorsal valve not continuous (from continuous); inner lamellar shell layer in dorsal valve present (from absent); lamellar layer in ventral median septum absent (from present).

Node X: Valve length greater than width (from equal proportions); valve ornament as radial ribs (from smooth); weak growth lines present (from absent); long spondylium (from short); deep spondylium (from very deep); short outer brachial plates present (from absent); prismatic layer in ventral valve wedged (from not wedged).

Node Y: Subparallel dental plate orientation (from convergent); long ventral median septum (from short); cardinal process occasionally present as a longitudinally striated mound (from absent); subparallel brachial plates (from convergent); adductor muscle attachment area anterior to cruralium absent (from well-developed); outer lamellar shell layer in dorsal and ventral valves intersect (from not intersecting).