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PHYLOGENETIC ANALYSIS AND ORDINAL CLASSIFICATION OF THE BRACHIOPODA

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ABSTRACT. The long-standing division of the lophophorate Phylum Brachiopoda into two units of Class rank, the Articulata and Inarticulata, is not supported by phylogenetic (cladistic) analysis. Using the PAUP program, two separate analyses, for seven extant brachiopod orders/suborders and for the combined extant and extinct groups, respectively, are consistent in identifying all chitinophosphatic-shelled stocks as a sister group to the carbonatic-shelled brachiopods, which include both 'inarticulates' and 'articulates' of previous schemes. The chitinophosphatic-shelled stocks are united in the Class Lingulata, but within the Brachiopoda, contrary to the proposals of Gorjansky and Popov (1985). The carbonatic-shelled brachiopods form the Class Calciata, embracing the Subclass Craniformea (including Craniida, Craniopsida, and Trimerellida), and a yet un-named Subclass that includes the Obolellida, Kutorginida, and the 'articulates'. The precise affinities of the kutorginides remain enigmatic, although they are clearly calciate. The proposed relationships suggest that brachiopods are monophyletic and had consistently separate shell chemistries from early in their phylogeny, removing the need for the repeated transformations in biomineralization inherent in previous evolutionary models.

OUR recent outline summary of the higher level classification of the lophophorate Phylum Brachiopoda (Popov *et al.* 1993) recognizes two taxonomic units of Class rank, the Lingulata and Calciata, embracing three units of Subclass rank, the Lingulatea, Craniformea, and 'Articulata'. Such a scheme of systematic classification and nomenclature differs markedly from the previous long-accepted subdivision of the Phylum into the classes Inarticulata and Articulata (e.g. Williams and Rowell 1965, pp. H214–234), and stems essentially from the conclusion that the chitinophosphatic-shelled 'inarticulates' of former classifications constitute a natural group that has little in common with the carbonatic-shelled 'inarticulates', apart from the fact that both lack an articulatory mechanism incorporating a hinge with teeth and sockets and are thus not 'articulates' in the commonly accepted sense, as expounded by Gorjansky and Popov (1985, 1986), Holmer (1991a), and Popov (1992).

Following Hennig's (1966, fig. 47; Text-fig 1A herein) original use of a cladistic (phylogenetic) methodology to analyse the phylogeny and systematics of the Brachiopoda, there has been considerable subsequent debate on the subject, in which a variety of theories has been proposed to explain relationships within the Phylum (see Popov *et al.* 1993; Carlson 1995). A number of these subsequent analyses has also employed phylogenetic methods, generally with significantly different results. In the latest of these studies prior to our own work, Carlson (1991, 1995) rejected the revised scope and status of the 'Inarticulata' proposed by Gorjansky and Popov (1985, 1986); some of the points of difference in these analyses and interpretations have already been the subject of preliminary discussion (Carlson 1994; Bassett *et al.* 1994). In this context, it is immediately interesting to note that Hennig's (1966) analysis, which was based on the taxonomically definitive characters of brachiopods propounded by Helmcke (1939, fig. 227), lends strong support to the Gorjansky and Popov model.

The purpose of this paper is therefore two-fold. First, to assess previous cladistic models of brachiopod phylogeny as a means of understanding the differences from and implications for our own model (Popov *et al.* 1993). And then to incorporate any common views into an expanded

discussion of proposed relationships and their nomenclatorial expression. Our analysis is confined to systematic relationships between the major groups assigned conventionally to the Brachiopoda, and does not address the further question of the origins of the Phylum. A number of authors have outlined the current, widely divergent views on this latter question as part of the debate surrounding the origin and early evolution of metazoans as a whole (e.g. Ghiselin 1989; Bergström 1991, fig. 4; Dzik 1991, fig. 4; Schram 1991; Schopf and Klein 1992). Our ultimate conclusion as to brachiopod monophyly is an obvious contribution towards this debate, in support of other recent analyses of phylogenetic relationships within the group (e.g. Rowell 1981, 1982; Carlson 1991, 1995).

Note. For brevity and convenience throughout this paper we refer to chitinophosphatic-shelled and carbonatic-shelled brachiopods as phosphatic and calcareous, respectively.

METHODS

Data matrices (Tables 1 and 2) derived from our selection of what we take to be taxonomically significant characters (see below) have been analysed cladistically using the PAUP program (Phylogenetic Analysis Using Parsimony 3.1.1; Swofford 1993). A total of 40 characters was selected from both extant and extinct brachiopod stocks. The data were analysed separately for the seven extant groups of Order and Suborder rank alone, and secondly for combined characters from the ten living and fossil stocks. In the first analysis the exhaustive search option was used on a data matrix derived from 35 unordered and unweighted characters (Table 1). For the analysis of the combined data, the exhaustive search option was used in analysing 26 unordered and unweighted characters (Table 2).

Character selection

What we take to be diagnostic characters were selected both from the soft-body of brachiopods and from the shell.

Any attempt to reconstruct soft-body anatomy in extinct stocks is clearly interpretative and/or highly speculative. We thus consider it best to make separate analyses of phyletic relationships for the extinct and extant lineages of brachiopods. At the same time, however, we emphasize the point that some features of soft anatomy (mainly the muscle systems, mantle and pedicle) can be inferred confidently in the majority of extinct lineages from an interpretation of shell morphology.

Our work stems initially from our joint evaluation of all the 'inarticulate' brachiopods of previous classifications for the forthcoming revision of Part H of the *Treatise on invertebrate paleontology*; as such, it is beyond our remit, and the scope of this paper, to analyse in detail all the extinct 'articulate' stocks and their relationships. However, because of the implications of relationships between some groups of the 'inarticulates' and the 'articulates' it is necessary to consider some details of the latter, and therefore as representatives of all these groups we use characters derived from the superfamilies Orthoidea and Protorthoidea, based on the commonly held consensus that the earliest Cambrian orthides were among the most plesiomorphic 'articulates' (Williams and Rowell 1965, p. H174; Williams and Hurst 1977, p. 92); in this regard the nisusiids and the calcareous-shelled genera *Kotujella* and *Matutella* were excluded because they require further study before their affinities can be determined.

Characters not used

The limited available knowledge of the ontogeny, and sometimes also the soft anatomy (e.g. nervous system and coelomic partitioning in various 'articulates') of most Recent brachiopods, make it highly speculative to use several features that might otherwise be important for the definition of major clades and their phylogenetic relationships. Thus, for example, the interpretation and homology of subdivisions of the coelom in various brachiopod larvae is a matter of ambiguity, with a separation

into proto-, meso- and metacoel remaining a subject of speculation and numerous different interpretations (Gorjansky and Popov 1985, 1986). The larva of *Neocrania* has as many as four pairs of coelomic sacs (Nielsen 1991), and that of *Terebratulina* only two pairs (Percival 1944). In other calciates, coelomic partitioning has not been investigated. Carlson's (1991, fig. 2; 1995, Appendix 2, character 22) proposed character, based on an imperfect separation of the mesocoel and metacoel, is therefore of doubtful use. The origin of holoperipheral growth in one or both valves is another good example of doubtful homology. We have not used such characters, in an attempt to reduce the influence of homoplasy on the results.

Similarly, unlike some previous investigations, we also question the use of 'functional characters', such as 'large number of gametes released per spawning event', 'larval propulsion accomplished with lophophoral cilia', 'brooding uncommon', etc. Characters of this kind can hardly be homologous and must surely reflect extreme homoplasy; it is difficult to see what use they can have in cladistic analyses. The assumption by Carlson (1991, 1995) that the introduction of a large number of such character conflicts will not outweigh the homologous characters is not proven (see further below, p. 735).

Another complex of rejected characters is related to various plesiomorphic 'absence features', which have been used by some authors for definition of different lineages. We have commented previously on this practice (Bassett *et al.* 1994, p. 3; see also Forey 1990, p. 432), and reiterate our view that it is unsatisfactory to define any group mostly on characters that are absent.

Outgroup selection

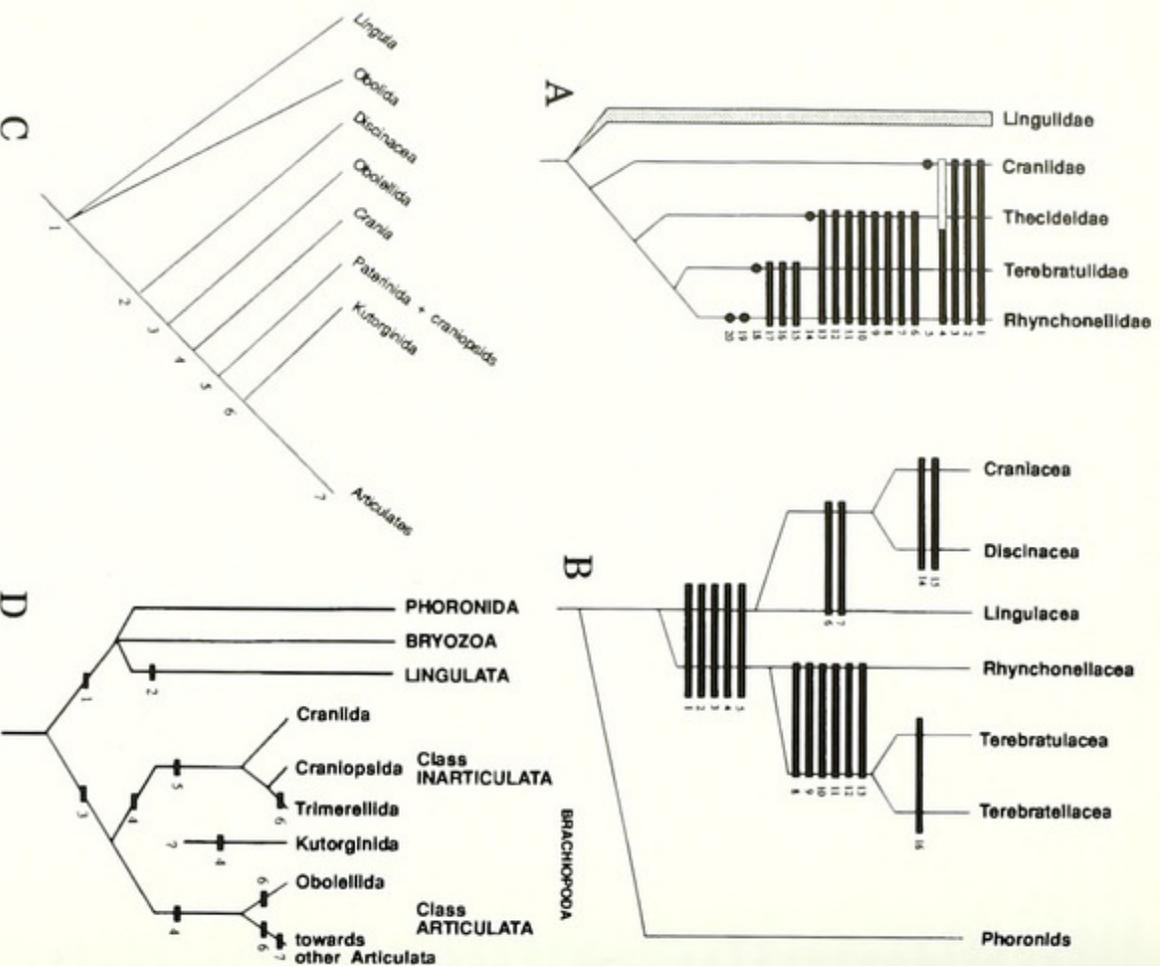
As noted by Carlson (1991, 1994, 1995) the selection of outgroups for determining the polarity of character transformations in brachiopods presents a number of problems. Bryozoans and phoronids are potential candidates, but Carlson (1995) also used Pterobranchia and Sipunculida. Priapulids have also been linked with the brachiopods (Runnegar and Curry 1992; Conway Morris 1994) and might also be outgroup candidates. However, because all these groups lack a bivalved shell, their body plans are fundamentally different and cannot be used to polarize most brachiopod characters.

In our previous analysis (Popov *et al.* 1993) we rooted our trees using a 'phoronid-like' ancestor, apart from the few instances where this group would appear to have derived characters. Notwithstanding the fact that the use of a 'hypothetical' outgroup has validity for some uncertain states (Maddison *et al.* 1984), it can be regarded as a way of *a priori* manipulation of the data set (Carlson 1994); in order therefore to avoid this possibility, in this paper we have chosen to use phoronids as an outgroup.

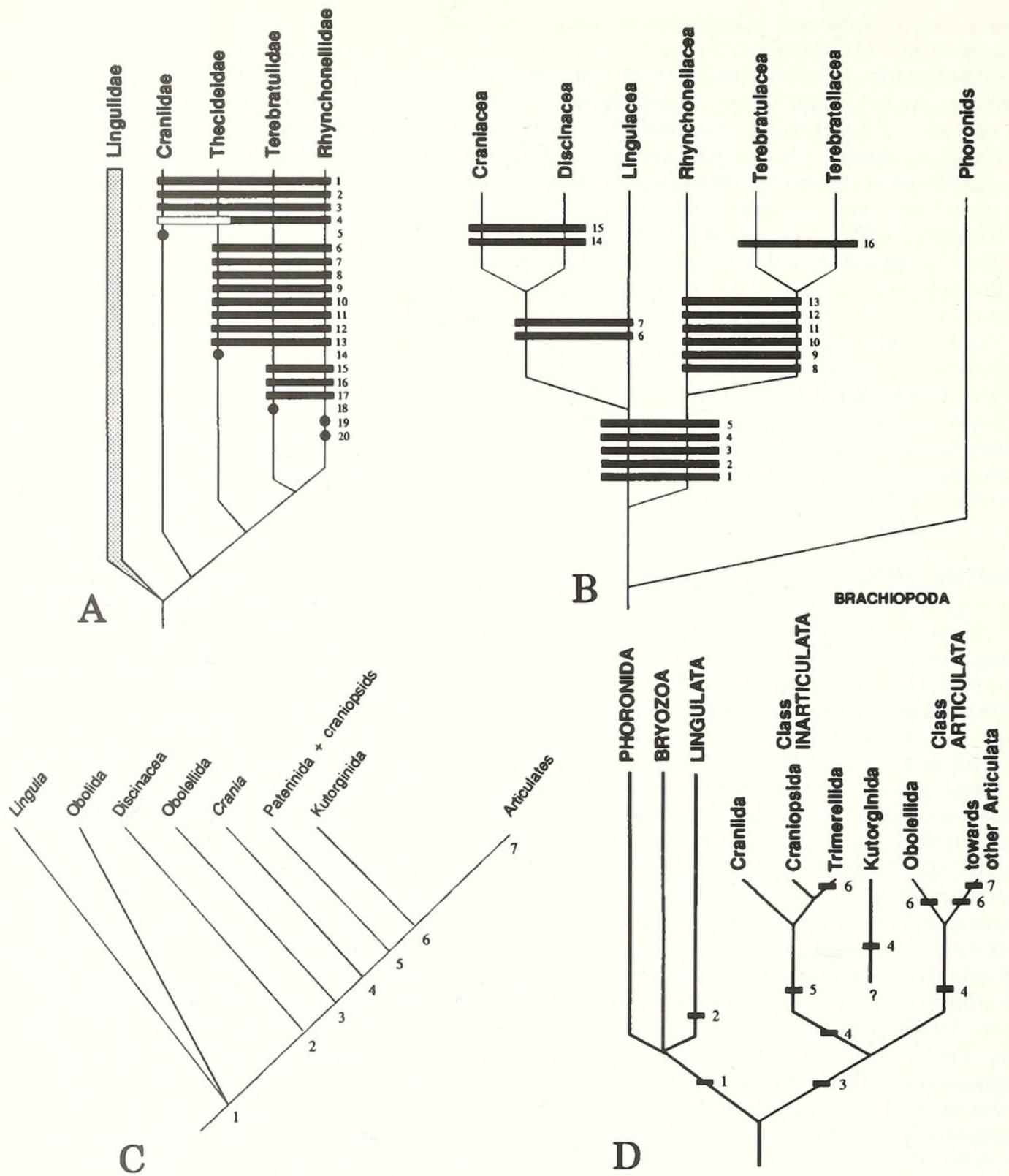
As noted by Nielsen (1991), brachiopods may not have originated from an ancestor within the Phoronida, but it might be argued that the lophophore anatomy, as well as the nervous system of phoronids, may retain primitive characters. The organization of the brachiopod body plan is dependent largely on its formation within an enclosed filtering chamber (Valentine 1981; Valentine and Erwin 1987), and it is not unreasonable to assume that the characters of the phoronid lophophore, functioning without a filtering chamber, are more primitive.

As we have noted previously (Bassett *et al.* 1994), we consider the bryozoans to be less useful as an outgroup. The bryozoan lophophore also functions without a filtering chamber, but is highly modified through a complex process of metamorphosis during ontogeny (Nielsen 1985, 1987). In any event, bryozoans are highly polymorphic in their anatomy and morphology, and it remains extremely difficult to select generalized characters for a 'typical' bryozoan body plan. In this respect, the phoronids constitute a much smaller and more homogeneous group.

Although the choice of an outgroup (or combination of outgroups) obviously influences the result of any analysis, it is not without interest to note that the topology of our proposed cladogram supporting the Lingulata and Calciata (Popov *et al.* 1993; Text-figs 3–4 herein), was also produced in a revised analysis of Carlson's (1995) character state matrix, using the bryozoans, phoronids, pterobranchs, and sipunculids as outgroups (see Text-fig. 5 and discussion on pp. 734–735).



TEXT-FIG. 1. A. Hennig's (1966, fig. 7) cladogram of relationships among the major taxa of the extant Brachiopoda. Synapomorphies shown by bars connecting taxa are: (1) shell consisting of calcium carbonate; (2) anterior part of body parenchymatous; (3) marginal lacuna not developed; (5) dorsal mantle lobes widely separated from the remaining visceral sac; (6) central portion of the shell cavity only partly filled with organs; (7) intestine ending in a blind sac; (8) muscle bundles not penetrated medially by a transverse plate of connective tissue; (9-11) dorsal and ventral mantle lobes united posteriorly; valves articulated by tooth and socket arrangement; dorsal valve with ridges that support lophophores; (14) musculature consisting of only three pairs of muscle bundles; the base of the arm of the oldest tentacle is transformed into organs of brood



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REVIEW AND DISCUSSION OF PREVIOUS CLADISTIC ANALYSES

Hennig 1966

The first cladistic analysis of Recent brachiopods was published by Hennig (1966). This was based exclusively on a revised version of 'kinship relationships' [verwandtschaftlichen Beziehungen] among five Recent brachiopod 'families' published in a highly informative, but unfortunately rarely available and little known work by Helmcke (1939, p. 224, fig. 227). The scheme of classification used by Hennig and Helmcke can be reconciled with and transformed readily into the superfamilial system of current usage, and Hennig's proposed cladogram (Text-fig. 1A) corresponds very closely with that derived from our own analysis (Text-fig. 3). The fact that Hennig's selected synapomorphies were based on the extremely detailed and accurate descriptions of Helmcke allows them to be adopted with only minor modification in order to correct a few misinterpretations. For example, Hennig's character 15 (gonads present only in mantle canals) was assumed erroneously by him to be apomorphic only for rhynchonelloideans and terebratuloideans (1966, p. 152). However, it is a characteristic of all calcareous-shelled brachiopods (Williams and Rowell 1965, p. H44).

From his analysis, Hennig concluded that only the 'family Lingulidae' (including discinides) could not be established as a monophyletic group; although not stated explicitly by him, his cladogram implies that these form a kind of 'outgroup' for the calcareous-shelled taxa.

Rowell 1981, 1982

Cladograms for both extant and extinct taxa were constructed by Rowell (1981, 1982) as part of a critical analysis of models of polyphyletic brachiopod origins proposed by Valentine (1973; see also Valentine 1975; Wright 1979). Rowell's conclusions support brachiopod monophyly.

For six superfamilies of Recent brachiopods (the Thecideoidea were excluded from the analysis), and with phoronids as an outgroup, Rowell's cladograms (1981, fig. 7, 1982, fig. 4) were based on 16 synapomorphies (Text-fig. 1B herein). Of these, the five characters uniting living brachiopods are: (1), filaments in a single palisade about the lophophore axis; (2), double row of filaments on adult lophophores; (3), brachial lip bounding food groove; (4), two mesocoelic cavities in lophophore; and (5), mantle canals. As discussed by Rowell (1982, p. 305), the structural features of the lophophores of all brachiopods are so similar and are consistently different from those of other lophophorates that it seems most probable that they are true homologies. However, it should be noted that his

care; (15) gonads present only in mantle lobes; (16) pedicle without a cavity; (17) middle portion of muscles tendonized; (18) right and left arms of the lophophore separated; (19) two pairs of metanephridia; (20) absence of mantle papillae. The nature of the 4th, 12th and 13th synapomorphies is not defined clearly by Hennig. B, Rowell's (1982, fig. 4) cladogram showing the relationships between major taxa of the extant brachiopods. Synapomorphies shown by bars connecting taxa are: (1) filaments in a single palisade about the lophophore axis; (2) double row of filaments on adult lophophore; (3) brachial lip bounding food groove; (4) two mesocoelic cavities in lophophore; (5) mantle canals; (6) hydraulic mechanism for opening valves; (7) presence of larval shell; (8) diductor muscles and hinge mechanism; (9) posterior fusion of mantles; (10) fibrous secondary shell; (11) pedicle as larval rudiment; (12) mantle reversal on settlement; (13) no larval shell; (14) closely comparable oblique internal and oblique lateral muscles paths; (15) holoperipheral growth in both valves; (16) presence of loop. C, Forey's (1982, fig. 4) cladogram derived for eight nested sets of taxa covering both the extinct and Recent stocks (note that definition of the nodes is based in some cases on combinations of characters; see text for further explanation). D, Gorjansky and Popov's (1986, fig. 2) diagram illustrating their view of a diphyletic course of brachiopod evolution. Major autapomorphies and synapomorphies indicated are: (1) schizocoelic coelom, metasomal pouch and settlement on the ventral body wall; (2) bivalved calcium phosphate shell; (3) enterocoelic coelom with reduced metacoel and settlement on the posterior part of the body; (4) bivalved calcareous shell; (5) pedicle and metasome reduced; (6) the origin of articulation; (7) pedicle as cartilaginous stalk and blind alimentary canal.

Note. In this Text-figure and in Text-figures 2 and 5 and Table 5 the endings used for brachiopod superfamily names (*acea*) are as used in the original publications by the respective authors; throughout the text we use the ending *oidea* for these same units of Superfamily rank as now recommended generally by the ICZN.

character 2 (Rowell 1982, fig. 4) is a generalization. Thus, in the extant genera of the Lingulata, a double row of filaments occurs in the trocholophe stage, whereas in Recent calcareous-shelled forms a double row of filaments does not develop until the post-trocholophe stage (Williams and Rowell 1965, p. H32; see further below, p. 722).

Eight further synapomorphies were then identified by Rowell (his characters 6–13; Text-fig. 1B herein) that support the traditional two-fold division of brachiopods into inarticulates and articulates, but some of these also require further discussion in the light of subsequent studies. Thus his synapomorphy 7, the presence of larval shell in calcareous and phosphatic shelled 'inarticulates', is not confirmed by recent studies of craniide larvae (Nielsen 1991), and synapomorphy 6 (hydraulic mechanism for opening valves) represents a functional character of doubtful homology (see earlier discussion, p. 715). Although closely comparable oblique lateral muscles are present in these groups (synapomorphy 14) they appear to have some fundamental differences in position and function. In craniides they are attached to the anterior body wall, which is an important difference from discinides (e.g. Bulman 1939, fig. 4).

Forey 1982

Brachiopods were used by Forey (1982, pp. 125–136) as an example in debating the distinction between and comparative utility of cladograms and phylogenetic trees. His cladogram (1982, fig. 4; Text-fig. 1C herein), which was not based on outgroup comparison, was constructed for eight nested sets of taxa covering both the extinct and Recent stocks, but excluding the acrotretides for which Forey did not identify any unique synapomorphy. Monophyly is identified for the brachiopods as a whole and for the 'articulates', with the 'inarticulates' being paraphyletic.

Of the characters, or groups of characters taken as synapomorphies by Forey, only that in support of his node 1 (branch point) can now be accepted; dorsal and ventral valves secreted by mantle is a character uniting all brachiopods. Node 2 is not supported by either of the listed characters; for example craniides have no pedicle throughout ontogeny (Nielsen 1991), and many linguloids and oboloids are also inequally valved. The presence of a laminar secondary shell layer cannot support node 3 as this feature is present only in craniides, obolellides, and some 'articulates'; in addition there is no delthyrium in craniides and craniopsides. At node 4, the identification of a straight posterior margin to the ventral valve is too vague to be definitive, whilst in any case obolellides have strophic shells to which this character could be applied. Definition of a subapical foramen or open gap (node 5) is similarly tenuous, together with the fact that stocks such as chileides and eichwaldiides have similar primitive openings of uncertain function. This node is also unsupported by the presence of a deltidium, since deltidial structures are variably defined, or absent, in 'articulates'. And finally, the morphology of some obolellide taxa removes support for both nodes 6 and 7. Narrow muscle attachment scars similar to those of 'articulates' originated in obolellides such as *Naukat* (Popov and Tikhonov 1990) and *Bynguanoia* (Roberts and Jell 1990), whilst primitive teeth and sockets were also present in the same group.

Forey (1982, p. 136, caption to fig. 4) makes particular reference to the incongruent placing of the phosphatic shelled Paterinida in his cladogram, where they are interpolated between calcareous stocks. In suggesting that 'placing this group to the left of the obolellids is unparsimonious', he gives no supporting comment, but concludes that 'a division of brachiopods into non-calcareous and calcareous may be over simplistic'. It is pertinent to repeat here that our original summary (Popov *et al.* 1993) was in direct contradiction to this view, and that the present paper is a further exploration of these relationships.

Gorjansky and Popov 1985, 1986

The phylogenetic importance of shell mineralogy in brachiopod evolution is emphasized by Gorjansky and Popov (1985, 1986) and Popov (1992). These authors do not list synapomorphies for Recent superfamilies, but they can be deduced from the descriptions of phosphatic and

calcareous-shelled taxa in the text; together with the modified cladogram they are reproduced here in Text-figure 1D.

The first two synapomorphies are based on a new interpretation by Gorjansky and Popov of the coelomic subdivision in some brachiopods. Lingulates (discinioideans + linguloideans) would appear to have a mesocoel, restricted to the coelomic spaces in the lophophore (1), and with metacoelic cavities in the remaining part of body (2). These states are regarded as derived for this lineage. The loss of coelomic partitioning in adult 'articulates' also represents a derived feature. In view of limited knowledge of the ontogeny of Recent 'articulate' taxa, as well as craniides, these synapomorphies are regarded here as highly hypothetical. The ambiguous nature of recent information on coelomic partitioning and embryology of extant brachiopods is discussed above (see pp. 714–715).

The fundamental conclusion by Gorjansky and Popov (1985, 1986) that the Lingulata (i.e. all phosphatic-shelled stocks) represent a phylum separate from the Brachiopoda is not now supported by our joint studies. The morphology, anatomy and ontogeny of extant stocks support instead the recognition of two major clades as sister groups within the brachiopods; it is more parsimonious to regard the origin of two different kinds of shell mineralization as a result of initial divergence within the phylum. The subsequent radiation of the lingulate and calciate orders are explained by Gorjansky and Popov in much the same way as in our analysis (see further below).

Carlson 1991, 1995

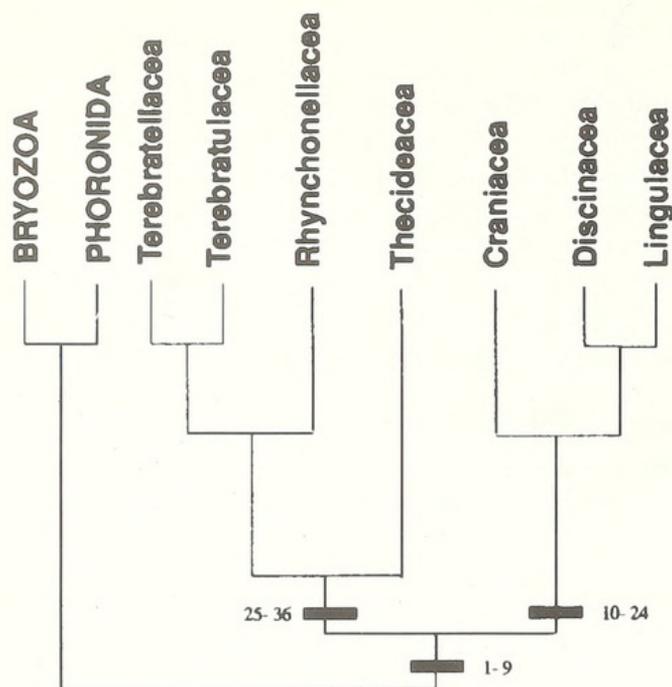
The most exhaustive published analysis of brachiopod phylogeny employing cladistic methodology is that by Carlson (1995), which builds on her earlier preliminary study (Carlson 1991) by considerably revising and expanding the data matrix. In both cases her results support a monophyletic origin for the brachiopods as a whole, and separately for the 'articulates' and 'inarticulates'.

The summary nature of Carlson's 1991 paper precluded a presentation of a data matrix; whilst we note that her detailed 1995 account eliminates some redundant characters and adds other informative features, it remains useful for us to comment separately on both papers as a means of emphasizing our views on the utility or otherwise of various potentially useful characters. Such a discussion is essential in order to understand the fundamental differences in our models and conclusions.

1991. In her initial study Carlson produced five different cladograms, but for our purposes discussion can be restricted to the model proposed for the Recent superfamilies (Carlson 1991, fig. 2; Text-fig. 2 herein). Nine synapomorphic characters uniting all brachiopods were proposed. They are: sex usually separate (1); imperfect separation of metacoel and mesocoel (2); pedicle present (3); primary ganglion below oesophagus (4); sensory cells present in juvenile stage only (5); ectodermal epithelium in three distinct zones (6); lophophore palisade bears a single row of filaments (7); lophophore suspended between mantles (8); mantle secreting shell material (9).

Of these, only characters 4 and 8 are acceptable without discussion. The other seven are defined ambiguously or represent what we consider to be plesiomorphic states that characterize not only brachiopods, but also other lophophorates.

The first two characters can be rejected as synapomorphies because they are common within other invertebrates. Character 7 requires clarification in its wording, but we take it to be valid in referring to the single palisade about the lophophore axis as opposed to the double palisade in phoronids. The remaining four features (3, 5, 6, 9) can be used only with emendation. They are not synapomorphic for all brachiopods, but characterize various lineages. It has long been known that the pedicle (character 3) is not homologous in linguloids and discinoids on the one hand and 'articulates' on the other (Williams and Rowell 1965). Character 5 is also ambiguous, because statocysts, for example, are developed in linguloid and discinoid larvae and persist in adults (Chuang 1977). Moreover, lingulate taxa lack sensory organs comparable to those of the 'articulate' larvae. The ability of the mantle to secrete a mineralized shell (character 9) is not a



TEXT-FIG. 2. Carlson's (1991, fig. 2) cladogram showing phylogenetic relationships between the extant brachiopod superfamilies. Synapomorphies are distributed as follows. Brachiopoda: Characters 1–9: sexes usually separate; imperfect separation of metacoel and mesocoel; pedicle present; primary ganglion below oesophagus; sensory cells present in juvenile stages only; ectodermal epithelium in three distinct zones; lophophore palisade bears a single row of filaments; lophophore suspended between mantles; mantles secreting shell material present. Inarticulata: Characters 10–24: development relatively direct; median tentacle of lophophore present initially, then lost; larval propulsion accomplished with lophophoral cilia; large subenteric ganglion only present; one row of adlabial and ablabial filaments on adult lophophore; large number of gametes released per spawning event; brooding uncommon; mantle rudiment does not reverse; ventral and dorsal mantles always discrete; mantle epithelium underlain by thin muscular layer; muscle system complex; laminar shell layer present; valves do not rotate in contact about a hinge axis; pair of teeth and sockets absent; calcareous lophophore supports absent. Articulata: Characters 25–36: coelomic spaces originate by enterocoely, mouth does not originate from blastopore, coelom divided into two principal spaces, the mesocoel and metacoel; postlarval initiation of shell formation; duration of a free-swimming larval stage short; adult lophophore lacks brachial muscles; brachial canal system simple; alimentary canal, pedicle, mixonephridia, and lophophore develop after settlement; gametes develop in mantle canals; gametes released more or less in a single burst; alimentary canal ends blindly; elevator and protractor muscles absent from the lophophore.

characteristic of brachiopods alone, but also of various unrelated invertebrate stocks. And finally, the meaning and implication of character 6 are unclear to us.

Carlson then defines 15 characters as synapomorphies for all 'inarticulates', including craniides. They are: development relatively direct (10); median tentacle of lophophore present initially, then lost (11); larval propulsion accomplished with lophophoral cilia (12); large subenteric ganglion only present (13); one row of adlabial and ablabial filaments on adult lophophore (14); large number of gametes released per spawning event (15); brooding uncommon (16); mantle rudiment does not reverse (17); ventral and dorsal mantles always discrete (18); mantle epithelium underlain by thin muscular layer (19); muscle system complex (20); laminar shell layer present (21); valves do not rotate in contact about hinge axis (22); paired teeth and sockets absent (23); calcareous lophophore support absent (24).

Apart from character 18, none of these characters are acceptable as synapomorphies for the combined calcareous- and phosphatic-shelled 'inarticulates'. Characters 13, 17 and 19 are known only in discinides and lingulides, and are absent or the condition is unknown in craniides. Recent work on the early ontogeny of *Neocrania* (Nielsen 1991) shows that a direct development (character 10) is not a character of craniides, and the absence of mantle reversion (character 17) is probably plesiomorphic for all brachiopods. Craniides have a paired subenteric ganglion rather than a single one as suggested by Carlson (character 13). The presence of a thin muscular layer in the mantle

epithelium of lingulides and discinides (character 19) might indicate the presence of well-developed dermal muscles, and this type of musculature is poorly developed in craniides (Blochmann 1892, 1900). The presence of a median tentacle, lost during later ontogeny, in craniides and lingulides (character 11) appears to be related to the spirolophous lophophore, because it is present also in rhynchonellides (Beecher 1897, p. 106; Rowell 1960, p. 49; Williams and Rowell 1965, fig. 36). Characters 12, 15 and 22 are not features of shell morphology or anatomy, but instead functional processes which, as noted above (p. 715), we consider to be of dubious application in phylogenetic analysis. One row of adlabial and ablabial filaments on the adult lophophore (character 14) is strictly a characteristic of all brachiopods (see also earlier comments on characters in Rowell's 1982 cladogram). With regard to character 20, we have commented previously (Bassett *et al.* 1994) that the use of such extremely generalized characters is of little value in investigating fundamental trends in brachiopod phylogeny; complexity is in the eye of the beholder. The presence of a laminar secondary layer (character 21) is a characteristic only of craniides; the shell structure of lingulides and discinides differs markedly from the laminar shell of craniides and cannot be described in such terms. Problems of denoting similarities based on the absence of any one particular feature (characters 23 and 24) are discussed above (p. 715).

In characterizing the 'articulates', Carlson then lists the following further 12 synapomorphies: coelomic spaces originate by enterocoely (25); mouth does not originate from blastopore (26); coelom divided into two principal spaces, the mesocoel and metacoel (27); postlarval initiation of shell formation (28); duration of free-swimming larval stage short (29); adult lophophore lacks brachial muscles (30); brachial canal system simple (31); alimentary canal, pedicle, mixonephridia and lophophore develop after settlement (32); gametes develop in mantle canals (33); gametes released more or less in a single burst (34); alimentary canal ends blindly (35); elevator and protractor muscles absent from lophophore (36).

The problematical nature of characters 25–29, 32, 34 is discussed above (p. 715). With regard to the brachial muscles in the articulate lophophore (30), they are not lacking but are less organized than in craniides and lingulides, a state that is related apparently to the presence or absence of brachial structures (Williams and Rowell 1965, p. H32), as is the case with the presence or absence of elevator and protractor muscles (36). Mantle canals with gonads (33) are known to be present in all calcareous-shelled brachiopods, including craniides.

1995. The data matrix for Carlson's more detailed analysis of extant brachiopods was built from 112 morphological and embryological characters. In some cases, modifications from her 1991 data set are noted, partly in line with some of our discussion immediately above.

Apart from our own initial study (Popov *et al.* 1993), this thorough analysis by Carlson is the first to present a published data matrix in support of cladograms. Our above review of previous cladistic analyses discusses each of the synapomorphies selected as a means of understanding the resulting theory in the absence of a full matrix. In the case of Carlson (1995) it is more useful to analyse her matrix directly, and in the light of our conflicting results it is more meaningful to do so as a comparative discussion after the presentation of our own analysis (see Discussion, p. 734).

DIAGNOSTIC CHARACTERS AND CHARACTER STATES

Our original analysis (Popov *et al.* 1993) of extant brachiopods of Order rank identified 29 diagnostic morphological and anatomical characters as a basis for the construction of a character state matrix. In the light of our continuing studies we have modified the original data set by merging and changing the character coding, while also adding 15 new characters, a combination of which is used in both the analyses presented below. Our revised data take into account published comment on our earlier analysis (Carlson 1994), together with numerous critical points made on initial versions of this manuscript.

Note. For ease of cross-reference, bracketed abbreviations of the numbered characters listed below are those set out in Tables 1–3.

TABLE 1. Character State Matrix used in PAUP analysis of characters (1–31, 33–34, 37–38) as listed in the text for the seven extant brachiopod orders and suborders.

| Character no. | 1 | 2 | 3 | 4 | 5 | 6 | 7a | 8 | 9 | 10 | 11 | 12 |
|------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| Abbreviation | clo | bli | fil | ctl | mfl | man | fus | set | mcl | mar | mas | pds |
| Phoronida | 0 | 0 | 0 | 0 | 0 | 0 | N | 0 | N | N | N | 2 |
| Lingulida | 1 | 1 | 2 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 2 |
| Discinida | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 2 |
| Craniida | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 0 |
| Terebratellidina | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Terebratulidina | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Thecideidina | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 |
| Rhynchonellida | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Character no. | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 |
| Abbreviation | gab | gon | sta | snt | sup | pmn | dem | obl | ob2 | did | olm | lan |
| Phoronida | U | 1 | 0 | 0 | 0 | N | 1 | N | N | N | N | N |
| Lingulida | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| Discinida | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| Craniida | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
| Terebratellidina | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| Terebratulina | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| Thecideidina | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| Rhynchonellida | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| Character no. | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 33 | 34 | 37 | 38 | |
| Abbreviation | dbv | lpl | ppb | ovm | phs | cal | lsh | css | pun | shr | tee | |
| Phoronida | N | 0 | 0 | 0 | 0 | 0 | 0 | N | N | N | N | |
| Lingulida | 0 | 0 | 0 | 1 | 1 | 0 | 1 | N | N | 0 | 0 | |
| Discinida | 0 | 0 | 0 | 1 | 1 | 0 | 1 | N | N | 0 | 0 | |
| Craniida | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 2 | 0 | 0 | |
| Terebratellidina | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | |
| Terebratulina | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | |
| Thecideidina | 0 | 1 | 0 | 0 | 0 | 1 | 0 | P | 1 | 1 | 2 | |
| Rhynchonellida | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | |

Lophophore

The primary feature that characterizes the functional organization of brachiopods is the ability to carry out filtration in an isolated chamber (see also Rowell 1982).

Phoronids have a single coelomic cavity in the lophophore, lacking a brachial lip as well as cartilage-like connective tissue. Despite the considerable morphological similarity of the lophophore in all extant Brachiopoda, there are consistent differences in detail between the main clades. In all extant Lingulata, there is a double row of lophophore filaments in the trocholophe stage (character 3, state 2), whereas in extant Calciata (i.e. Craniformea and 'articulates'), the trocholophe stage has only a single row of filaments (character 3, state 1; see also Williams and Rowell 1965, p. H32). In the phoronid lophophore, a single row of filaments persists throughout the ontogeny (character 3, state 0); this state is also present in the adult stage of Recent thecideidoideans.

TABLE 2. Character State Matrix used in PAUP analysis of characters (6–9, 13, 19–25, 27–40) as listed in the text for the extant and extinct brachiopod orders.

| Character no. | 6 | 7b | 8 | 9 | 13 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 27 |
|----------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| Abbreviation | man | fus | set | mcl | gab | dem | obl | ob2 | did | olm | lan | dbv | ppb |
| Phoronida | 0 | N | 0 | N | N | 1 | N | N | N | N | N | N | 0 |
| Lingulida | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Siphonotretida | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Acrotretida | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Paterinida | 1 | 0 | 1 | 1 | 0 | U | U | U | 2 | 0 | 0 | 0 | U |
| Craniida | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |
| Trimerellida | 1 | 1 | U | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| Craniopsida | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 |
| Obolellida | 1 | 0 | U | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| Kutorginida | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| Orthida | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| Character no. | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 |
| Abbreviation | ovm | phs | cal | lsh | pss | css | pun | hom | psd | shr | tee | csp | kut |
| Phoronida | 0 | 0 | 0 | 0 | N | N | N | N | N | N | N | N | N |
| Lingulida | 1 | 1 | 0 | 1 | 0 | N | N | 0 | N | P | 0 | 0 | 0 |
| Siphonotretida | 1 | 1 | 0 | 1 | 0 | N | N | 0 | N | 1 | 0 | 0 | 0 |
| Acrotretida | 1 | 1 | 0 | 1 | 1 | N | N | 0 | N | P | 0 | 0 | 0 |
| Paterinida | U | 1 | 0 | 1 | 0 | N | N | 1 | N | 0 | 0 | 0 | 0 |
| Craniida | 0 | 0 | 1 | 0 | N | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| Trimerellida | 0 | 0 | 1 | 0 | N | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Craniopsida | 0 | 0 | 1 | 0 | N | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Obolellida | 0 | 0 | 1 | 0 | N | 1 | 0 | 0 | 1 | P | 1 | 0 | 0 |
| Kutorginida | 0 | 0 | 1 | 0 | N | U | U | 0 | 2 | 0 | 0 | 0 | 1 |
| Orthida | 0 | 0 | 1 | 0 | N | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 |

Lophophoral muscle fibres are smooth in phoronids (character 5, state 0), but partly striated in brachiopods (character 5, state 1; James *et al.* 1992).

1. Coelomic cavities in lophophore (*clo*).

States (0) one coelomic cavity; (1) two coelomic cavities.

2. Lophophore palisades and brachial lip (*bli*).

States (0) two palisades, brachial lip absent; (1) filaments in a single palisade, with brachial lip, bounding a food groove.

3. Arrangement of lophophore filaments (*fil*).

States (0) one row of lophophore filaments; (1) double row of filaments in the post-trocholophe stage; (2) double row of filaments in the trocholophe stage.

4. Cartilage-like connective tissue in lophophore (*ctl*).

States (0) absent; (1) present.

5. Muscles fibres in lophophore (*mfl*).

States (0) smooth; (1) striated.

Mantle

The presence of dorsal and ventral mantles with coelomic cavities forming a filtration chamber (character 6, state 1) is another distinctive feature uniting all brachiopods, as is the development of mantle setae (character 8, state 1). The latter character was also used by Rowell (1981, 1982). Setae

were previously thought to be lacking in craniids, but Nielsen (1991) identified marginal setae in juvenile *Neocrania*, and they have also been found in the Lower Cambrian 'craniopside' genus *Heliomedusa* (Jin and Wang 1992) as well as in paterinides from the Burgess Shale (e.g. Whittington 1985). However, marginal setae appear to be absent in Recent thecideidines, and Recent phoronids also lack a mantle with setae.

Mantle lobes that are fused along the posterior margin have been considered to represent a distinctive 'articulate' character (character 7a, state 1 for extant lineages; character 7b, state 0 for extinct lineages; see also Rowell 1982), whereas the phosphatic and calcareous 'inarticulates' have discrete ventral and dorsal mantles (Williams and Rowell 1965, p. H9; Carlson 1991, fig. 2). However, it is apparent that *Lingula anatina* passes through an ontogenetic stage in which the mantle lobes are fused along the posterior margin (character 7, state 1; Yatsu 1902; Williams and Rowell 1965, p. H46). Only in craniids and discinides do the mantle lobes appear to be discrete throughout ontogeny (character 7a, state 2 for extant lineages; character 7b, state 1 for extinct lineages). For the extinct brachiopods with a strophic shell (Paterinida, Obolellida, Kutorginida, Orthida) the absence of setal follicles along the straight posterior margin suggests that the mantle lobes were somewhat modified and might therefore have been fused. Moreover, in view of the absence of any kind of articulatory structures in paterinides, the axis of rotation may have been fixed only by fused mantle lobes.

Differences in the direction of the *vascula terminalia* also differentiate the two main brachiopod lineages. Thus, in lingulates the *vascula terminalia* are directed both peripherally and medially (character 9, state 0), whereas all calcareous stocks have only peripherally directed vascular trunks (character 9, state 1; Williams and Rowell 1965, figs 136, 138).

Reversion of the mantle through ontogeny is a diagnostic character of Recent 'articulate' lineages (character 10, state 1). The available information on the ontogeny of lingulates (Yatsu 1902; Chuang 1977) confirms the absence of reversion in these stocks (character 10, state 0). In the craniids, the change in direction of the larval setae during ontogeny (Nielsen 1991) indicates that some kind of mantle reversion takes place during the complex metamorphosis.

The marginal sinus (character 11, state 0; 'marginal lacuna' of Hennig 1966) is a separate coelomic channel that runs near the mantle edge in *Discinisca* and *Lingula*; it does not appear to be present in calcareous-shelled brachiopods (Hyman 1959, p. 533).

6. Mantles with coelomic cavities forming a filtration chamber (*man*).
States (0) absent; (1) present.
- 7a. Fusion of mantle lobes (for analysis of extant stocks) (*fus*).
States (0) fused in embryonic stage, separate in adults; (1) fused along the posterior margin in adults; (2) separate in larvae and adults.
- 7b. Fusion of mantle lobes (for analysis of extinct stocks) (*fus*).
States (0) no mantle; (1) separate in adults; (2) fused along the posterior margin in adults.
8. Setae (*set*).
States (0) absent; (1) present.
9. Mantle canals (*mcl*).
States (0) *vascula terminalia* directed peripherally and medially; (1) *vascula terminalia* directed peripherally only.
10. Mantle reversion (*mar*).
States (0) absent; (1) present.
11. Marginal sinus (*mas*).
States (0) present; (1) absent.

Digestive system

In adult brachiopods there are three types of digestive tracts. In the Lingulata the gut is U-shaped and placed anteriorly close to the right nephropore (character 12, state 2). A U-shaped gut is also present in phoronids (Hyman 1959, p. 245). In *Neocrania* the anus is placed posteromedially

(character 12, state 0; Williams and Rowell, 1965, pp. H17–21). The third type occurs in the ‘articulates’, where the gut is blind (character 12, state 1; Hyman 1959, p. 552).

The attachment scars of the gastroparietal bands (character 13, state 1) can be traced on dorsal valves of various lingulate taxa (paterinides are the only exception) back to the Cambrian (Mickwitz 1896, p. 100; Blochmann 1900, p. 118). This suggests that in the majority of the extinct lingulate lineages the morphology of the digestive tract was probably comparable essentially with that of Recent taxa. These types of scars are lacking in all craniides; in ‘articulates’ the gastroparietal bands never leave attachment scars, and because they do not bear gonads their homology with those of lingulates is questionable and even unlikely.

12. Digestive system (*pds*).

States (0) straight with posteromedially placed anus; (1) straight, blind; (2) U-shaped with anteriorly placed anus.

13. Dorsal attachment of gastroparietal bands (*gab*).

States (0) present; (1) absent.

Reproductive system

In Recent craniides and ‘articulates’ the gonads are placed in the mantle canals (character 14, state 0), whereas phosphatic brachiopods and phoronids are characterized by gonads occupying the free edges of the peritoneal bands (character 14, state 1; Hyman 1959, p. 564).

14. Location of gonads (*gon*).

States (0) in coelomic canals; (1) on free edges of peritoneal bands.

Nervous system

According to Chuang (1977, p. 53), statocysts develop in lingulide and discinide larvae and persist through ontogeny into the adult stage (character 15, state 1).

The presence of subenteric ganglionic in brachiopods distinguishes them from all other lophophorates, but different states occur in each of the main brachiopod lineages (Hyman 1959, p. 560). Lingulates have only one subenteric ganglion (character 16, state 1) and lack a supraenteric ganglion (character 17, state 0); craniides are characterized by the presence of paired subenteric ganglia (character 16, state 2; Williams and Rowell 1965, p. H42); and ‘articulates’ have small transverse supraenteric ganglia (character 17, state 1) and a larger subenteric ganglion (character 16, state 1). These types of ganglionic are not present in phoronids (Hyman 1959, p. 239).

A ring nerve formed by the confluence of the peripheral ends of the mantle nerves occurs in the margin of each mantle lobe of lingulides and discinides (character 18, state 1; Hyman 1959, p. 560).

15. Statocysts (*sta*).

States (0) absent; (1) present.

16. Subenteric ganglion (*snt*).

States (0) absent; (1) present, single; (2) present, paired.

17. Supraenteric ganglion (*sup*).

States (0) absent; (1) present.

18. Peripheral mantle nerves (*pmn*).

States (0) absent; (1) present.

Muscle system

The muscle system of lingulates is characterized mainly by well developed dermal muscles (character 19, state 1) as well as the presence of transmedian muscles (character 20, state 1) and two or three additional pairs of oblique muscles (character 21, state 0; Rowell *in* Williams *et al.* 1965, p. H273). We do not consider the transmedian muscles to be homologous with any of the oblique muscles in craniides.

Dermal muscles are absent or only weakly developed both in Recent craniides and ‘articulates’ (character 19, state 0) (Rowell *in* Williams *et al.* 1965, p. H273). The craniides have a musculature

that is simpler than that of discinides (Williams and Rowell 1965, p. H28), with only the paired internal oblique muscles being similar to the numerous oblique muscles of lingulates (character 21, state 1). On the other hand, both the paired outside lateral muscles, which are attached anteriorly to the body wall (character 23, state 1), as well as the unpaired *levator ani* (character 24, state 1) are unique to the craniides (Blochmann 1892). This kind of muscle system is also known in the Craniopsida and Trimerellida (Gorjansky and Popov 1985, 1986).

The musculature of 'articulates' consists of three main groups of muscles: paired anterior and posterior adductors, and paired oblique muscles attached posteromedially to the dorsal valve and serving as diductors (character 22, state 1).

Emig (1982, p. 188; see also Williams and Rowell 1965, p. H29) suggested that the dermal musculature in lingulates may be used for the hydraulic opening of the shell, and this was later demonstrated experimentally by Trueman and Wong (1987). Dermal muscles are also well developed in phoronids (Hyman 1959, p. 237). By contrast, they are developed only weakly in *Neocrania* (Hyman 1959, p. 533), and the exact type of opening mechanism is not known, although Gorjansky and Popov (1985, p. 6) suggested that the outside lateral muscles, which attach anteriorly to the body wall (Williams and Rowell 1965, fig. 29), may be used for hydraulic opening of the shell. A similar type of opening mechanism was proposed for lingulides by Gutmann *et al.* (1978), but this is clearly not a viable suggestion because there are no muscles attaching to the anterior body wall in the adult animal.

19. Dermal muscles (*dem*).

States (0) weakly developed or absent; (1) strongly developed.

20. Transmedian muscle (*obl*).

States (0) absent; (1) present.

21. Number of other oblique muscles (*ob2*).

States (0) one pair; (1) more than one pair.

22. Diductor muscles (*did*).

States (0) absent; (1) oblique muscles acting as diductors attached posteriorly to dorsal valve; (2) oblique muscles attached posteriorly to the inner side of homeodeltidium.

23. Outside lateral muscles attached anteriorly to body wall (*olm*).

States (0) absent; (1) present.

24. *Levator ani* (*lan*).

States (0) absent; (1) present.

Body wall

The attachment of the dorsal body wall to the dorsal valve in five separate areas is a character unique to the craniides (character 25, state 1; Beauchamp 1960, fig. 1287) whereas in lingulates, 'articulates', craniopsides, and trimerellides it is attached to only one area (character 25, state 0).

25. Attachment of dorsal body wall to shell (*dbv*).

States (0) attached in five areas; (1) attached to one area.

Pedicle

The pedicle is not homologous within the different lineages of brachiopods (Williams and Rowell 1965, p. H13; see also Carlson 1995, Appendix 2, character 30). In extant lingulides and discinides, the pedicle possesses a coelomic cavity and arises as an outgrowth of the inner epithelium of the ventral mantle, and is attached only to the ventral valve. This feature is diagnostic of all lingulate taxa (character 28, state 1). In 'articulates', the pedicle originates from the larval peduncular lobe (character 26, state 1); in the adult stage it has a core of firm, cartilage-like connective tissue and lacks coelomic cavities (character 27, state 1; Hyman 1959, p. 537). In craniformeans there is no pedicle, nor is there a peduncular lobe in the larva (Nielsen 1991). Based on subdivisions of the coelomic space, Gorjansky and Popov (1985, 1986) have interpreted the anal papilla of the craniides as being homologous with the pedicle of the 'articulates', but supporting evidence is inconclusive.

Nielsen (1991, p. 25) asserted that the larva of *Neocrania* settles on the posterior part of its dorsal side, such that the 'pedicle valve' represents a 'posterior dorsal valve', and the 'brachial' valve an 'anterior dorsal valve'. However, it is difficult to determine where dorsal and ventral meet on the posterior part of a larva lacking a peduncular lobe. This, in addition to the difficulty that Nielsen (1991, p. 21) had in following the fate of the blastopore, makes his interpretation difficult to confirm.

In extinct lingulate taxa, the presence of a *Lingula*-type pedicle is confirmed in some taxa in which the soft anatomy is preserved (e.g. *Lingulellotreta*; Jin *et al.* 1993) and can be deduced convincingly in many taxa in which an impression of the pedicle nerve is retained as a scar (Holmer 1991b).

- 26. Larval peduncular lobe (*lpl*).
States (0) absent; (1) present.
- 27. Pedicle forming from posterior part of body (*ppb*).
States (0) absent; (1) present.
- 28. Pedicle as outgrowth of ventral mantle lobe (*ovm*).
States (0) absent; (1) present.

Chemical composition of the shell

There are two main types of brachiopod shell, one in which the predominant inorganic component is calcium phosphate (character 29, state 1), and the other in which it is calcium carbonate (character 30, state 1). In the extant phosphatic-shelled forms, exemplified by lingulides and discinides, calcium phosphate accounts for 74.7–93.7 per cent. of the shell, the remainder being organic material comprising mostly chitin and protein. In calcareous-shelled forms, calcium carbonate makes up 94.6–98.6 per cent. of the shell material in the 'articulates' and 87.8–88.6 per cent. in craniides (Clarke and Wheeler 1922; Vinogradov 1953; Jope 1965); the remainder is organic material, consisting largely of protein.

We have emphasized previously (Popov *et al.* 1993, p. 3) that evolutionary transformations in brachiopod shell chemistry from a phosphatic to a calcareous composition, or *vice versa* (Carlson 1995), are at best weakly founded (Runnegar 1989; Runnegar and Bengtson 1990). Bengtson and Runnegar (1992, p. 450) have also recently reiterated this case in stating that 'there are no convincing examples of a phylogenetic transition from phosphate to carbonate in the history of lineages'. The pattern and timing of biomineralization of the earliest brachiopods remains incompletely known and too poorly understood for defining the polarity (Bengtson 1992, fig. 7.7.1; Bengtson and Runnegar 1992). We therefore separate the two types of mineralization as two characters.

- 29. Phosphatic mineralization (*phs*).
States (0) absent; (1) present.
- 30. Calcareous mineralization (*cal*).
States (0) absent; (1) present.

Shell formation and structure

Several discrete features of shell formation and structure in both phosphatic and calcareous brachiopods serve in differentiation of major lineages. The initial states of formation show remarkable differences with both extant and extinct lingulate taxa characterized invariably by the presence of a larval shell (character 31, state 1; Holmer 1989). By contrast, craniides (Nielsen 1991) and 'articulates' develop a shell only after settlement (character 31, state 0).

The majority of lingulate taxa are characterized by alternating phosphatic and organic shell layers (character 34, state 2), which become somewhat more complicated in the acrotretides with the further addition of a columnar structure (character 32, state 1; Holmer 1989; Williams and Holmer 1992).

In addition to shell chemistry, craniides, craniopsides and obolellides also have a shell structure fairly similar to that of many of the 'articulate' groups in that they have a periostracum covering

a primary mineral layer consisting of inclined acicular crystallites, and a laminar secondary layer (character 32, state 1; Williams and Wright 1970; Williams 1990, p. 74). Among 'articulate' taxa, a laminar secondary layer is a distinctive character of billingselloideans, strophomenides and other related stocks, whilst a fibrous secondary layer is diagnostic for the Orthida (character 33, state 0). The possible acquisition of an aragonitic shell with its distinctive structure (Jaanusson 1966) is an equally unique character of the trimerellides (character 33, state 2).

An impunctate shell (character 34, state 0) is typical of the majority of Cambrian calcareous brachiopods (*Kotujella* is possibly one of the only exceptions) but according to Williams (1990, p. 71, text-fig. 4F), punctation evolved subsequently several times in 'articulate' lineages. In craniformeans, only craniides have acquired a dendroid punctuation (character 34, state 2; Williams and Wright 1970).

31. Larval shell (*lsh*).

States (0) absent; (1) present.

32. Phosphatic columnar shell structure (*pss*).

States (0) absent; (1) present.

33. Calcareous shell structure (*css*).

States (0) with fibrous secondary layer; (1) with laminar secondary layer; (2) aragonitic.

34. Punctate shell (*pun*).

States (0) impunctate; (1) endopunctate with simple porosity; (2) endopunctate with dendroid porosity.

Modifications of the posterior shell margin

The presence of a convex homeodeltidium covering the delthyrial opening (character 35, state 1) is a diagnostic character of the paterinides (Laurie 1987).

An open delthyrium is characteristic of both the earliest obolellides (*Obolella*, *Bicia*, *Magnicanalis*) and orthides (*Glyptoria*, *Israeleria*, *Leioria*; character 36, state 1). The various types of delthyrial covers thus probably originated later in their evolution. Several Lower Cambrian 'articulate' stocks with delthyrial covers, such as the nisusiides, have usually been placed within the orthides, but this now seems improbable. *Nisusia* lacks characters such as teeth and brachiophores, and the unusual pattern of its articulation (Rowell and Caruso 1985; Popov and Tikhonov 1990) suggest to us a close affinity with kutorginides.

In all Craniformea, there is no trace of a pedicle opening or gap between the valves in any of the Recent or extinct stocks (character 36, state 0); as in *Neocrania*, this indicates to us that all craniformeans lacked a pedicle.

Shell resorption is a rather rare phenomenon in Lower Palaeozoic brachiopods. It is commonplace within the siphonotretides (character 37, state 1), but the only other documented occurrences within the phosphatic brachiopods are in the acrotretide *Curticia* (Rowell and Bell 1961) and in the lingulide family Dysoristidae (Popov and Holmer 1994). It is also recorded in obolellides (Rowell 1965) and in the cyrtomatodont teeth of 'articulates' (Jaanusson 1971).

The nature of the diverse but primitive articulatory structures is one of the important characteristics of the majority of the earliest 'articulate' lineages (Popov and Tikhonov 1990), but among Lower Cambrian stocks only obolellides (character 38, state 1) and orthides (character 38, state 2) acquired paired deltidiodont teeth or denticles on the lateral margins of the delthyrial opening.

In the craniformeans, articulatory structures comprising a cardinal socket and socket plate are found only in the extinct Trimerellida (character 39, state 1; Norford and Steele 1969).

The simplest pattern of articulation, in which the dorsal propareas fit into furrows on both sides of the pseudodeltidium, is known only in the kutorginides (character 40, state 1; Popov and Tikhonov 1990).

35. Homeodeltidium (*hom*).

States (0) absent; (1) present.

36. Pseudodeltidium and delthyrium (*psd*).

States (0) absent; (1) with open delthyrium; (2) with pseudodeltidium.

TABLE 3. Synapomorphy scheme for internal nodes of the cladogram shown in Text-figure 3.

| Node | Character states |
|--------------|---|
| 1 | — |
| 2 | 1:1, 2:1, 4:1, 5:1, 6:1, 8:1, 16:1 |
| 3 | 3:2, 13:1, 15:1, 18:1, 20:1, 28:1, 29:1, 31:1 |
| Lingulida | 7a:0 |
| 4 | 3:1, 8:11, 10:1, 11:1, 12:0, 14:0, 19:0, 21:1, 32:1 |
| Craniida | 16:2, 23:1, 24:1, 25:0, 33:1, 34:2 |
| 5 | 7a:1, 12:1, 17:1, 22:1, 26:1, 37:1; 38:2 |
| Thecideidina | 8:2 |
| 6 | 27:1 |

TABLE 4. Synapomorphy scheme for internal nodes of the cladogram shown in Text-figure 4.

| Node | Character states |
|--------------|------------------------|
| 1 | — |
| 2 | 5:1, 6:1 |
| 3 | 20:1, 28:1, 29:1, 31:1 |
| Paterinida | 23:2, 35:1 |
| 4 | 7b:1, 9:0, 13:1, 37:1 |
| Acrotretida | 32:1 |
| 5 | 19:0, 21:1, 32:1 |
| 6 | 7b:1, 23:1, 24:1 |
| Trimerellida | 22:1, 33:2, 39:1 |
| Craniida | 25:0, 34:2 |
| 7 | 22:1, 27:1, 36:1 |
| Kutorginida | 36:2 |
| Obolellida | 38:1 |
| Orthida | 33:0, 38:2 |

For brevity, we cross reference throughout in the following way: character 1, state 1 = 1:1, character 3, state 0 = 3:0 etc. (see also Tables 3–4).

Seven synapomorphies are diagnostic in discrimination of the Recent brachiopods, supporting node 2 in Text-figure 3 and indicative of a monophyletic origin for the Phylum Brachiopoda:

1. Two coelomic cavities in the lophophore (1:1).
2. Filaments arranged in a single palisade about the lophophore axis, with a brachial lip, bounding a food groove (2:1).
3. Cartilage-like connective tissue in the lophophore (4:1).
4. Striated muscle fibres in the lophophore (5:1).
5. Dorsal and ventral mantles with a coelomic cavity forming a filtration chamber (6:1).
6. Mantle with marginal setae (8:1).
7. Single subenteric ganglion (16:1).

At a similar level in the analysis of the combined extinct and extant stocks (Text-fig. 4, node 2), two of the synapomorphies listed above (5 and 6) were generated (Table 4).

Both analyses lend strong support to the recognition of the Lingulata as a natural group within the Brachiopoda (Popov *et al.* 1993; Carlson 1995). The following eight synapomorphies are in support of node 3 for Recent lingulates (Table 3; Text-fig. 3):

8. Double row of filaments in the trocholophe stage (3:2).

9. Dorsal attachment scars of gastroparietal bands (13:1).
10. Statocysts in larvae and adults (15:1).
11. Peripheral mantle nerves (18:1).
12. Transmedian muscles (20:1).
13. Pedicle as outgrowth of the ventral mantle lobe (28:1).
14. Phosphatic mineralization (29:1).
15. Larval shell (31:1).

Four of these synapomorphies (12–15) also support the same point for the combined extinct and extant orders (Text-fig. 4, node 3; Table 4).

The apomorphic character no. 9 also supports the clade consisting of lingulides, discinides, siphonotretides and acrotretides in the combined analysis (Text-fig. 3A, node 4; Table 4) together with two further synapomorphies:

16. Separate mantle lobes in adults (7b:1).
17. *Vascula terminalia* directed peripherally and medially (9:0).

The Order Paterinida appears to be a sister stock of this clade, characterized by two autapomorphies (Text-fig. 4; Table 4):

18. Oblique muscles attached posteriorly to the inner side of the homeodeltidium (23:2).
19. Homeodeltidium present (35:1).

In the combined analysis, the unresolved trichotomy for the Acrotretida, Siphonotretida and Lingulida (Text-fig. 4, node 4; Table 4) cannot be resolved from the characters available. The Order Acrotretida is characterized by a single autapomorphy (Text-fig. 3A; Table 4):

20. Phosphatic shell with columnar structure (32:1).

The Order Lingulida lacks derived characters according to the combined analysis, but in the analysis of Recent stocks a single autapomorphy (Text-fig. 3; Table 3) was found:

21. Mantle lobes fused in embryonic stage, separate in adults (7a:0).

The unity of all calcareous-shelled brachiopods in a clade as a sister group to the lingulates is supported by both analyses. These are the Class Calciata of Popov *et al.* (1993). Six selected synapomorphies (of nine) characterize the extant stocks alone (Text-fig. 3, node 4; Table 3):

22. Double row of filaments in the post-trocholophe stage (3:1).
23. *Vascula terminalia* directed peripherally only (9:1).
24. Mantle reversion developed (10:1).
25. Gonads in the mantle canals (14:0).
26. Dermal muscles weakly developed or absent (19:0).
27. One pair of oblique muscles (21:1).
28. Calcareous mineralization (32:1).

The three last of these were also confirmed in the combined analysis (Text-fig. 4, node 5; Table 4).

Recognition of a Subclass Craniformea (Popov *et al.* 1993) is supported by both analyses, linking the craniides, craniopsides and trimerellides as proposed originally by Gorjansky and Popov (1985, 1986). For Recent craniides this discrimination is supported by six autapomorphies (Text-fig. 3; Table 3):

29. Paired subenteric gangliation (16:2).
30. Outside lateral muscles attached anteriorly to the body wall (23:1).
31. *Levator ani* present (24:1).
32. Attachment of dorsal body wall in five areas (25:0).
33. Calcareous shell structure with laminar secondary layer (33:1).
34. Punctate with dendroid porosity (34:2).

The same separation in the combined extant and extinct taxa (Text-fig. 4, node 6; Table 4) is supported by two of the synapomorphies above (30, 31) and an additional derived character:

35. Mantle lobes separate (7b:1).

This analysis thus indicates that the appearance of separated mantle lobes took place convergently within lingulates and craniformeans.

In the combined analysis, the unresolved trichotomy for the Craniopsida, Trimerellida, and Craniida (Text-fig. 4, node 6; Table 4) cannot be resolved from the characters available.

The Order Craniopsida appears to lack derived characters and it might possibly be closely comparable with the ancestral stock for all craniformeans. It is characterized by a three-layered impunctate shell with a laminar secondary layer, large, submedially placed visceral fields on both valves, a well-developed pleurocoel, and the absence of a pedicle opening. The muscle system of the craniopsides can be interpreted from the pattern observed in craniides (Gorjansky and Popov 1985).

The early divergence of craniformeans and other calcareous-shelled taxa has been confirmed by the recent discovery of craniopsides in Lower Cambrian (Botomian) strata. The genus *Heliomedusa* from Yunnan, China (Jin and Wang 1992) is characterized by a slightly inequivalved shell with mixoperipheral growth of the ventral valve and holoperipheral growth of the dorsal valve. The position of the visceral fields on both valves suggests a relatively large visceral cavity with a well-developed posterior body wall. There is no trace of a pedicle. The mantle canal system was probably pinnate with paired *vascula lateralia* on both valves, and is similar to that of Ordovician craniides like *Pseudocrania*. Marginal mantle setae are also present in *Heliomedusa*.

The Order Craniida includes the only extant craniformeans. The shell morphology of the earliest known Ordovician genera (*Pseudocrania* and *Orthisocrania*) is closely comparable with that of the extant *Neocrania*. A similar muscle system, with paired anterior and posterior adductors, internal oblique muscles and outside lateral muscles attached anteriorly to the body wall, is also present in the earliest representatives of the Order. The presence of the *levator ani* attachment scar on the dorsal valve of extinct taxa suggests a similar position of the digestive tract, with a postero-medially placed anus throughout phylogeny.

The Order Trimerellida is characterized, as are other craniformeans, by the lack of a pedicle opening; they possibly had an open digestive tract with a postero-medially placed anus, indicated by the possible scar of the *levator ani* on the socket plate of the dorsal valve (Gorjansky and Popov 1985). The mantle canal system is characterized by peripherally-directed *vascula terminalia*. The following autapomorphic characters were obtained (Text-fig. 4; Table 4):

36. Oblique muscles acting as diductors, attached posteriorly to dorsal valve (22:1).
37. Aragonitic shell (33:2).
38. Cardinal socket and socket plate (39:1).

The origin and initial radiation of the 'articulates' (as represented here by the orthides) and related calcareous shelled lineages is outside the scope of this paper, but it is possible that the synapomorphies of the extant stocks obtained in our analysis reflect a common origin of the Recent 'articulate' lineages, as a clade that arose after the divergence from the Craniformea (see also Rowell 1981, 1982; Carlson 1991, 1995). The list of proposed synapomorphies (Text-fig. 3, node 5; Table 3) for 'articulates' includes:

39. Mantle lobes fused along posterior margin in adults (7a:1).
40. Digestive system straight, blind (12:1).
41. Supraenteric gangliation (17:1).
42. Oblique muscles acting as diductors, attached posteriorly to dorsal valve (22:1).
43. Larva with peduncular lobe (26:1).
44. Deltidodont teeth (38:2).

Character 42 was also selected in the combined analysis (Text-fig. 4, node 7; Table 4), which suggests that the 'articulate' type of opening mechanism originated convergently in trimerellides (autapomorphy 36) and 'articulates' (synapomorphy 42); the same analysis also produced the following two synapomorphies:

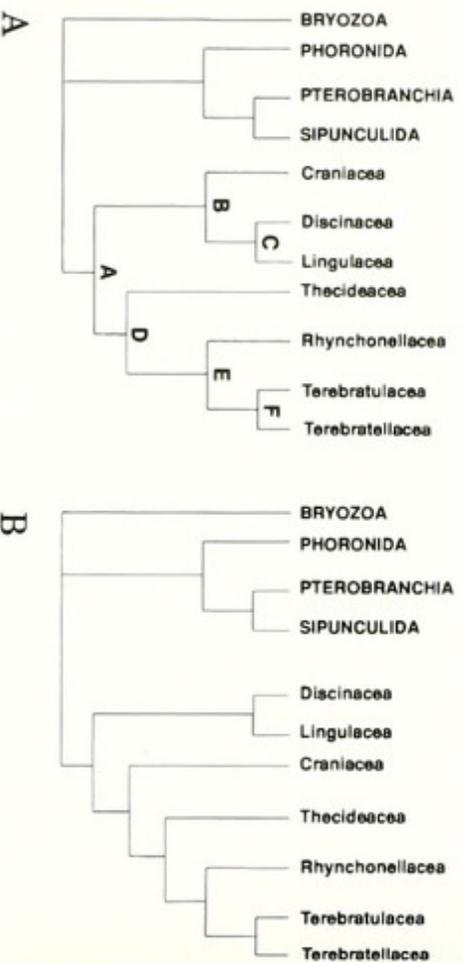
45. Pedicle forming from posterior part of body (27:1).
46. Open delthyrium (36:1).

There is growing evidence that rudimentary articulation developed in parallel within several lineages of calcareates in the early-mid Cambrian, including protorhoids, muscids, kutorginids and obolellids (Cooper 1976; Rowell and Caruso 1985; Ushatinskaya 1988; Popov and Tikhonov 1990; Roberts and Jell 1990). In this regard it is worth emphasizing that Cambrian obolellids and kutorginids are interpreted here as primitive calcareate 'articulates' (Text-fig. 4, nodes 7 and 8; Table 4).

DISCUSSION

The scheme of classification summarized in Text-figures 3 and 4 removes the implication inherent in previous subdivision of the Brachiopoda into articulates and inarticulates of repeated evolutionary transformations in shell chemistry, either from a phosphatic to a calcareous composition (e.g. Williams and Hurst 1977) or initially from calcareous to phosphatic as proposed by Carlson (1991, 1995). Experiments with the matrices for our two analyses show that removal of the two characters based on chemical composition (characters 29, 30) does not change the topology of the resulting cladogram in the analysis of the Recent stocks. However, the same change in the combined analysis including the extinct stocks leads to a highly unresolved topology, supporting only two of the nodes (4 and 5) depicted in Text-figure 4, and indicating the need for further studies to resolve such instability.

Carlson (1995) analysed the relationship between seven superfamilies of extant brachiopods, using 112 characters. The topology of her single resulting cladogram (reprinted here as Text-fig. 5)



TEXT-FIG. 5. A, Carlson's (1995) cladogram derived from analysis of 112 characters within seven superfamilies of extant brachiopods. B, Cladogram derived from analysis of Carlson's (1995) 112 characters plus 6 additional characters from our matrix (113–118; Table 5), with a single change in her character 38 (state of Rhynchonellacea changed from 0 to U).

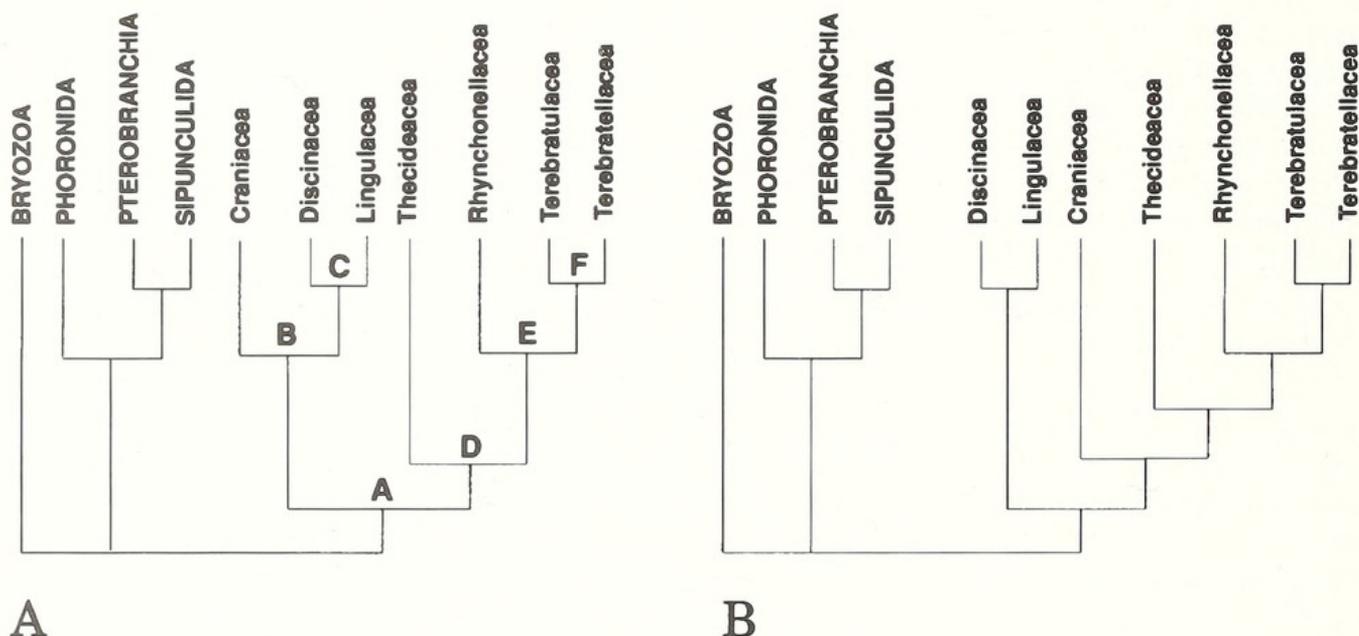
is identical to that published earlier (Carlson 1991; see also above, p. 720), in giving support to the identity of the Class Inarticulata as a monophyletic group. Whilst we do not attempt to analyse all 112 characters used by Carlson, we have already noted the doubtful homology of many 'functional' characters that are used (see above, p. 715). However, some additional comment is also required, because, despite the very large set of characters used in her study, it is apparent that a number of others used in our studies (Popov *et al.* 1993 and herein) are absent from her matrix: in order therefore to test further the stability of her results, we simply added some of these missing characters

There is growing evidence that rudimentary articulation developed in parallel within several lineages of calciates in the early-mid Cambrian, including protorthoids, nisusiids, kutorginides and obolellides (Cooper 1976; Rowell and Caruso 1985; Ushatinskaya 1988; Popov and Tikhonov 1990; Roberts and Jell 1990). In this regard it is worth emphasizing that Cambrian obolellides and kutorginides are interpreted here as primitive calciate 'articulates' (Text-fig. 4, nodes 7 and 8; Table 4).

DISCUSSION

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to her otherwise unchanged matrix. For example, the development of dermal muscles (character 113, *dem*; Table 5) does not appear as any of her 112 original characters. The addition of this single character alone is enough to modify the analysis by producing two equally parsimonious trees, with the topologies represented in Text-figure 5A–B. Carlson herself noted that removal of her characters 38 (median tentacle in lophophore) or 40 (internal musculature of adult lophophore) (Table 5), as well as removing data for the thecideoideans completely, also significantly changed the result in producing trees that are consistent with our model. We have already commented (p. 721) on the fact that the development of a median tentacle in the 'Inarticulata' might be related to the presence of a spirolophous lophophore, and if we re-code Carlson's interpretation of the possible presence of a 'median tentacle' in rhynchonelloideans (her character 38) to missing (that is, 'Unknown'), the resulting cladogram also supports our model (Text-fig. 5B). The addition of a further five characters from our matrix (114–118; Table 5) gives yet more strength to the resulting single tree (Text-fig. 5B). This kind of instability in Carlson's (1995) analysis might possibly be related to the presence of a large number of homoplastic characters (Bassett *et al.* 1994, p. 385). Such effects are probably particularly strong in analyses involving relatively 'simple' invertebrate groups with relatively few 'good characters' and an ancient geological record (causing problems with outgroups). Unlike vertebrates, for example, the brachiopod body plan does not involve many characters that have a clear-cut homology, and thus it is possible that analyses introducing a large number of homoplastic characters will be more disturbed by this 'noise' by comparison with analyses of other groups.

In comparing the conflicting conclusions reached by Carlson and ourselves, recent studies of brachiopod ontogeny and biochemistry lend strong support to our proposals. Nielsen's (1991) study of the larval development of *Neocrania* indicated that 'the "articulates" and *Crania* [= *Neocrania*] appear to represent one line of evolution and *Lingula* and *Discinisca* another'. Jope's (1986) summary of her data on the shell protein and other biochemical characteristics of *Crania* [= *Neocrania*] emphasized a greater similarity to the 'articulates' than to the phosphatic-shelled brachiopods. Whilst noting the 'anomalous taxonomic position of the Craniacea', Jope (1986, p. 106) stressed that the 'zoological evidence for connection with the Inarticulata is equally cogent'. Two particular features are given in support of this latter association. These are, the low glycine in the shell protein and the presence of chitin as pads at the site of muscle attachment (Williams and Wright 1970; Jope 1986). However, thin layers of chitin have been discovered in the laminated carbonate shells of molluscs (Weiner and Traub 1984) and Jope (1986) believes that such thin layers will be found eventually in calcareous brachiopods. Although Jope herself recognized the strength of her biomolecular evidence for classifying craniids with the articulates she did not do so, preferring to explain part of this evidence by developing a genetic scenario for the derivation of the Craniida from the phosphatic brachiopods. However, the need for such genetic perturbations is greatly reduced and the biochemical similarities much more easily explained if the Craniformea share a common ancestry with the 'articulates'. Similarly, the 'uneasy phylogenetic placement' of *Lingula* and its phosphatic-shelled relatives pointed out in studies of shell protein by Tuross and Fisher (1989) is resolved by our conclusions. It is unlikely that differences between shell proteins of brachiopods can be explained simply by the different patterns of mineralization of the shell, because the proteinous chain-length of the phosphatic-shelled *Lingula* is comparable with that of bivalve molluscs, but both *Lingula* and the *Bivalvia* differ markedly in this character from *Crania* and 'articulate' brachiopods (Jope 1986, fig. 1). The differences are more strongly indicative of a considerable genetic difference between lingulates and calciates.

CONCLUSIONS

The conflicting patterns of brachiopod relationships reviewed above largely reflect the selection of, and relative taxonomic importance ascribed to characters used in the various analyses; such factors also include the choice and coding of the outgroup. As we have pointed out previously (Bassett *et al.* 1994), a level of subjectivity is inevitable and we certainly reiterate the view that degrees of objectivity cannot be evaluated simply by comparing the size of matrices that support competing

TABLE 5. Character state matrix (see text for explanation) used in PAUP analysis by Carlson (1995). Characters 113–118 (marked as bold text) have been added to Carlson's original 112 characters. The coding of character 38 (marked with **bold**) was changed in one of the analyses run herein.

| Character no. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 |
|-----------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| Bryozoa | U | 0 | 1 | U | U | 0 | P | 1 | 1 | 1 | 1 | 2 | N | 0 | 1 | U | 0 | 1 | U | 1 | P | 1 | U | 0 | N |
| Craniacea | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 3 | 1 | 1 | 2 | 1 | 1 | 0 | 2 | 1 | 1 |
| Discinacea | 1 | 1 | 1 | 1 | 0 | 1 | U | U | 1 | U | 0 | 1 | 0 | 1 | 1 | 3 | 1 | 1 | U | 1 | 1 | 1 | U | 1 | 1 |
| Lingulacea | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 4 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| Phoronida | 2 | 1 | 1 | 0 | N | P | P | 1 | 1 | 1 | P | 1 | 3 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 1 | 0 | U | 0 | N |
| Pterobranchia | 1 | 1 | 1 | 1 | N | P | 1 | 0 | 0 | U | U | 0 | 2 | 1 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 0 | U | 0 | N |
| Rhynchonellacea | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | U | 2 | 1 | 1 | P | 2 | 1 | 2 | 2 | 1 | 2 | 1 | U | 1 | 0 |
| Sipunculida | 0 | U | 0 | 0 | N | P | U | 0 | 0 | U | 1 | 0 | 0 | P | 1 | 0 | 0 | 0 | 0 | 0 | U | N | U | 0 | N |
| Terebratulacea | 1 | 1 | 1 | 1 | 1 | P | 1 | 0 | 2 | U | U | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 1 | 0 |
| Terebratulacea | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | U | 1 | 1 | 1 | P | 2 | 1 | 2 | 2 | 1 | 2 | 1 | U | 1 | 0 |
| Thecideacea | 1 | 0 | 1 | 1 | 1 | 1 | 1 | U | 1 | 1 | U | 2 | 1 | 1 | 1 | 2 | 1 | 2 | U | 1 | 2 | 1 | U | 1 | 0 |
| Character no. | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 |
| Bryozoa | N | N | N | 0 | 0 | N | N | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | N | 1 | 0 | 0 | U |
| Craniacea | 1 | 1 | 0 | 0 | 0 | N | N | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 3 | 1 | 1 | 0 | 1 | 2 | 2 | 1 |
| Discinacea | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 0 | 2 | 2 | 1 | 0 | 2 | 0 | 2 | 1 |
| Lingulacea | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 0 | 2 | 6 | 1 | 0 | 1 | 1 | 2 | 1 |
| Phoronida | N | N | N | 0 | 0 | N | N | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 3 | 0 | 1 | 1 |
| Pterobranchia | N | N | N | 0 | 0 | N | N | 2 | 2 | 4 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 2 | N | 1 | 1 | 0 | 1 |
| Rhynchonellacea | U | U | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | U | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 1 | 1 | 2 | U |
| Sipunculida | N | N | N | 0 | 0 | N | N | 0 | 2 | 4 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 5 | 1 | 0 | 2 | 0 | 2 | 0 |
| Terebratulacea | U | U | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 3 | 1 | 0 | 1 | 1 | 2 | 1 |
| Terebratulacea | U | U | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 3 | 1 | 0 | 1 | 1 | 2 | U |
| Thecideacea | U | U | 2 | 0 | 4 | 1 | N | 1 | 1 | 3 | 1 | 0 | U | 1 | 0 | 1 | 1 | 1 | 4 | 1 | 0 | 1 | 1 | 2 | U |
| Character no. | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 |
| Bryozoa | 0 | 0 | 1 | N | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 2 | N | N | N | N | N | 0 | 0 | 0 | N | N | N | N |
| Craniacea | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | N | 0 | 1 |
| Discinacea | 1 | 0 | 1 | 0 | 0 | U | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 0 | N | N | 0 | 0 | 1 | 0 | 0 | N | 0 | 1 |
| Lingulacea | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 3 | 1 | N | N | 0 | 0 | 0 | 0 | 0 | N | 0 | 2 |
| Phoronida | 2 | 0 | 0 | N | 1 | 0 | N | 2 | 0 | 0 | 0 | N | N | N | N | N | N | N | 0 | N | 1 | N | N | N | N |
| Pterobranchia | 0 | 0 | 0 | N | 1 | U | 0 | 2 | 1 | 0 | 0 | 2 | 1 | 2 | 1 | 0 | 3 | 0 | 0 | 1 | 0 | 1 | 2 | 1 | 1 |
| Rhynchonellacea | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 2 | 1 | 0 | U | U | 0 | U | 0 | N | 1 | 2 | 1 |
| Sipunculida | 0 | 0 | 0 | N | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 2 | N | N | N | U | U | 0 | 0 | U | 0 | N | N | N | N |
| Terebratulacea | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 2 | 1 | 0 | N | 2 | 2 | 1 | 0 | 1 | 1 | 2 | 2 |
| Terebratulacea | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 2 | 1 | 0 | 1 | 2 | 2 | 1 | 0 | 1 | 1 | 2 | 2 |
| Thecideacea | 1 | 1 | 1 | 1 | 1 | U | 0 | 2 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | N | 2 | 2 | 1 | 1 | 1 | 0 | 2 | 0 |

| Character no. | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 |
|-----------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|----|----|----|----|----|----|-----|
| Bryozoa | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N |
| Craniacea | 1 | N | 2 | 1 | 1 | 2 | 0 | 0 | 0 | N | 3 | N | 0 | N | N | N | 0 | 0 | 0 | N | N | 1 | N | 0 | N |
| Discinacea | 1 | N | 0 | 0 | 0 | 0 | 0 | 0 | 0 | N | 0 | N | U | 0 | 0 | 0 | 1 | 1 | 1 | N | 0 | 0 | 0 | 0 | 1 |
| Lingulacea | 0 | N | 0 | 0 | N | 1 | 1 | 0 | 0 | N | 2 | 0 | U | 0 | 2 | 1 | 1 | 1 | P | N | 0 | 0 | 3 | 1 | 2 |
| Phoronida | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N |
| Pterobranchia | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N |
| Rhynchonellacea | 0 | 2 | 2 | 1 | N | 1 | 3 | 2 | 0 | 0 | 1 | 1 | 3 | 2 | 3 | 1 | 2 | 0 | 0 | 2 | 1 | 0 | 1 | 0 | 2 |
| Sipunculida | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N |
| Terebratulacea | 0 | 1 | 1 | 1 | N | 1 | 1 | 0 | P | 1 | 1 | 1 | 3 | 2 | 2 | 1 | 2 | 0 | 1 | P | 1 | 0 | 1 | P | 1 |
| Terebratulacea | 0 | 1 | 1 | 1 | N | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 3 | 1 | 4 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 |
| Thecideacea | 1 | N | 1 | 2 | 2 | 1 | 2 | 0 | 0 | N | 1 | 1 | 1 | 3 | 2 | 0 | 2 | 0 | 1 | 0 | N | 0 | 0 | 0 | 1 |
| Character no. | 101 | 102 | 103 | 104 | 105 | 106 | 107 | 108 | 109 | 110 | 111 | 112 | 113 | 114 | 115 | 116 | 117 | 118 | | | | | | | |

| | dem | mcl | pmn | sta | dbv | lan |
|-----------------|-----|-----|-----|-----|-----|-----|
| Bryozoa | U | N | N | N | N | N |
| Craniacea | 0 | 0 | 0 | 0 | 1 | 1 |
| Discinacea | 1 | 1 | 1 | 1 | 0 | 0 |
| Lingulacea | 1 | 1 | 1 | 1 | 0 | 0 |
| Phoronida | 1 | N | N | N | N | N |
| Pterobranchia | 1 | N | N | N | N | N |
| Rhynchonellacea | 0 | 0 | 0 | 0 | 0 | 0 |
| Sipunculida | 1 | N | N | N | N | N |
| Terebratulacea | 0 | 0 | 0 | 0 | 0 | 0 |
| Terebratulacea | 0 | 0 | 0 | 0 | 0 | 0 |
| Thecideacea | 0 | U | 0 | 0 | 0 | 0 |
| Character no. | 112 | 113 | 114 | 115 | 116 | 117 |
| Bryozoa | N | U | N | N | N | N |
| Craniacea | 3 | 0 | 0 | 0 | 0 | 1 |
| Discinacea | 2 | 1 | 1 | 1 | 1 | 0 |
| Lingulacea | 3 | 1 | 1 | 1 | 1 | 0 |
| Phoronida | N | 1 | N | N | N | N |
| Pterobranchia | N | 1 | N | N | N | N |
| Rhynchonellacea | 2 | 0 | 0 | 0 | 0 | 0 |
| Sipunculida | N | 1 | N | N | N | N |
| Terebratulacea | 2 | 0 | 0 | 0 | 0 | 0 |
| Terebratulacea | 2 | 0 | 0 | 0 | 0 | 0 |
| Thecideacea | U | 0 | U | 0 | 0 | 0 |
| Character no. | 111 | 112 | 113 | 114 | 115 | 116 |
| Bryozoa | N | N | N | N | N | N |
| Craniacea | 2 | 3 | 0 | 0 | 0 | 0 |
| Discinacea | 1 | 2 | 0 | 0 | 0 | 0 |
| Lingulacea | 1 | 3 | 1 | 1 | 1 | 1 |
| Phoronida | N | N | 1 | N | N | N |
| Pterobranchia | N | N | 1 | N | N | N |
| Rhynchonellacea | 3 | 2 | 0 | 0 | 0 | 0 |
| Sipunculida | N | N | 1 | N | N | N |
| Terebratulacea | 4 | 2 | 0 | 0 | 0 | 0 |
| Terebratulacea | 4 | 2 | 0 | 0 | 0 | 0 |
| Thecideacea | U | U | 0 | 0 | 0 | 0 |
| Character no. | 110 | 111 | 112 | 113 | 114 | 115 |
| Bryozoa | N | N | N | N | N | N |
| Craniacea | N | 2 | 3 | 0 | 0 | 0 |
| Discinacea | N | 1 | 2 | 1 | 1 | 1 |
| Lingulacea | N | 1 | 3 | 1 | 1 | 1 |
| Phoronida | N | N | N | 1 | N | N |
| Pterobranchia | N | N | N | 1 | N | N |
| Rhynchonellacea | 1 | 3 | 2 | 0 | 0 | 0 |
| Sipunculida | N | N | N | 1 | N | N |
| Terebratulacea | 2 | 2 | 1 | 0 | 0 | 0 |
| Terebratulacea | 2 | 4 | 1 | 0 | 0 | 0 |
| Thecideacea | 3 | 2 | 0 | 0 | 0 | 0 |
| Character no. | 109 | 110 | 111 | 112 | 113 | 114 |
| Bryozoa | N | N | N | N | N | N |
| Craniacea | 0 | N | 2 | 3 | 0 | 0 |
| Discinacea | 0 | N | 1 | 2 | 1 | 1 |
| Lingulacea | 0 | N | 1 | 3 | 0 | 0 |
| Phoronida | N | N | N | N | N | N |
| Pterobranchia | N | N | N | N | N | N |
| Rhynchonellacea | 0 | 1 | 3 | 2 | 1 | 1 |
| Sipunculida | N | N | N | N | N | N |
| Terebratulacea | 0 | 2 | 2 | 1 | 0 | 0 |
| Terebratulacea | 0 | 2 | 4 | 1 | 0 | 0 |
| Thecideacea | 1 | 3 | 2 | 0 | 0 | 0 |
| Character no. | 108 | 109 | 110 | 111 | 112 | 113 |
| Bryozoa | N | N | N | N | N | N |
| Craniacea | 1 | 0 | N | 2 | 3 | 0 |
| Discinacea | 2 | 0 | N | 1 | 2 | 1 |
| Lingulacea | 2 | 0 | N | 1 | 3 | 0 |
| Phoronida | N | N | N | N | N | N |
| Pterobranchia | N | N | N | N | N | N |
| Rhynchonellacea | 0 | 0 | 1 | 3 | 2 | 0 |
| Sipunculida | N | N | N | N | N | N |
| Terebratulacea | 1 | 0 | 2 | 2 | 1 | 0 |
| Terebratulacea | 1 | 0 | 2 | 4 | 1 | 0 |
| Thecideacea | 0 | 1 | 3 | 2 | 0 | 0 |
| Character no. | 107 | 108 | 109 | 110 | 111 | 112 |
| Bryozoa | N | N | N | N | N | N |
| Craniacea | 1 | 1 | 0 | N | 2 | 3 |
| Discinacea | 2 | 2 | 0 | N | 1 | 2 |
| Lingulacea | 2 | 2 | 0 | N | 1 | 3 |
| Phoronida | N | N | N | N | N | N |
| Pterobranchia | N | N | N | N | N | N |
| Rhynchonellacea | 0 | 0 | 0 | 1 | 3 | 2 |
| Sipunculida | N | N | N | N | N | N |
| Terebratulacea | 1 | 0 | 2 | 2 | 2 | 1 |
| Terebratulacea | 1 | 0 | 2 | 4 | 1 | 0 |
| Thecideacea | 0 | 1 | 3 | 2 | 0 | 0 |
| Character no. | 106 | 107 | 108 | 109 | 110 | 111 |
| Bryozoa | N | N | N | N | N | N |
| Craniacea | 0 | 0 | 1 | 0 | N | 2 |
| Discinacea | 0 | 0 | 0 | 1 | 2 | 1 |
| Lingulacea | 0 | 0 | 0 | 1 | 3 | 0 |
| Phoronida | N | N | N | N | N | N |
| Pterobranchia | N | N | N | N | N | N |
| Rhynchonellacea | 1 | 1 | 0 | 3 | 2 | 0 |
| Sipunculida | N | N | N | N | N | N |
| Terebratulacea | 2 | 1 | 1 | 2 | 1 | 0 |
| Terebratulacea | 2 | 0 | 2 | 3 | 1 | 0 |
| Thecideacea | N | N | 1 | 3 | 2 | 0 |
| Character no. | 105 | 106 | 107 | 108 | 109 | 110 |
| Bryozoa | N | N | N | N | N | N |
| Craniacea | 0 | 0 | 0 | 1 | 2 | 3 |
| Discinacea | 0 | 0 | 0 | 0 | 0 | 0 |
| Lingulacea | 0 | 0 | 0 | 0 | 0 | 0 |
| Phoronida | N | N | N | N | N | N |
| Pterobranchia | N | N | N | N | N | N |
| Rhynchonellacea | 1 | 1 | 0 | 1 | 2 | 3 |
| Sipunculida | 0 | 0 | 0 | 0 | 0 | 0 |
| Terebratulacea | 1 | 0 | 1 | 1 | 1 | 1 |
| Terebratulacea | 1 | 0 | 1 | 1 | 1 | 1 |
| Thecideacea | 2 | 0 | N | 1 | 3 | 2 |
| Character no. | 104 | 105 | 106 | 107 | 108 | 109 |
| Bryozoa | N | N | N | N | N | N |
| Craniacea | N | 0 | 0 | 0 | 1 | 2 |
| Discinacea | N | 0 | 0 | 0 | 0 | 0 |
| Lingulacea | N | 0 | 0 | 0 | 0 | 0 |
| Phoronida | N | 0 | 0 | 0 | 0 | 0 |
| Pterobranchia | N | 0 | 0 | 0 | 0 | 0 |
| Rhynchonellacea | 1 | 1 | 0 | 0 | 0 | 0 |
| Sipunculida | N | 0 | 0 | 0 | 0 | 0 |
| Terebratulacea | 1 | 1 | 1 | 1 | 1 | 1 |
| Terebratulacea | 1 | 1 | 1 | 1 | 1 | 1 |
| Thecideacea | 2 | 2 | 0 | N | 1 | 3 |
| Character no. | 103 | 104 | 105 | 106 | 107 | 108 |
| Bryozoa | N | N | N | N | N | N |
| Craniacea | 1 | N | 0 | 0 | 0 | 1 |
| Discinacea | 0 | N | 0 | 0 | 0 | 0 |
| Lingulacea | 0 | N | 0 | 0 | 0 | 0 |
| Phoronida | N | N | 0 | 0 | 0 | 0 |
| Pterobranchia | N | N | 0 | 0 | 0 | 0 |
| Rhynchonellacea | 2 | 1 | 1 | 1 | 0 | 0 |
| Sipunculida | N | N | 0 | 0 | 0 | 0 |
| Terebratulacea | 2 | 1 | 1 | 1 | 1 | 1 |
| Terebratulacea | 2 | 1 | 1 | 1 | 1 | 1 |
| Thecideacea | 2 | 0 | 2 | N | 1 | 3 |
| Character no. | 102 | 103 | 104 | 105 | 106 | 107 |
| Bryozoa | N | N | N | N | N | N |
| Craniacea | 0 | 0 | 0 | 0 | 0 | 0 |
| Discinacea | 0 | 0 | 0 | 0 | 0 | 0 |
| Lingulacea | 0 | 0 | 0 | 0 | 0 | 0 |
| Phoronida | N | N | N | N | N | N |
| Pterobranchia | N | N | N | N | N | N |
| Rhynchonellacea | 1 | 1 | 0 | 0 | 0 | 0 |
| Sipunculida | 0 | 0 | 0 | 0 | 0 | 0 |
| Terebratulacea | 1 | 1 | 1 | 1 | 1 | 1 |
| Terebratulacea | 1 | 1 | 1 | 1 | 1 | 1 |
| Thecideacea | 2 | 2 | 0 | N | 1 | 3 |
| Character no. | 101 | 102 | 103 | 104 | 105 | 106 |



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