Ancestral billingsellides and the evolution and phylogenetic relationships of early rhynchonelliform brachiopods

Timothy P. Topper [a] , David A.T. Harper [a] [b] & Glenn A. Brock [c]

[a] Geologisk Museum, Statens Naturhistoriske Museum, Øster Voldgade 5-7, DK-1350, København K, Denmark

[b] Department of Earth Sciences, Durham University, Durham, DH1 3LE, UK

[c] Department of Biological Sciences, Macquarie University, NSW, 2109, Australia
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Timothy P. Topper[a]*, David A.T. Harper[a,b] and Glenn A. Brock[c]

[a]*Geologisk Museum, Statens Naturhistoriske Museum, Øster Voldgade 5-7 DK-1350, København K, Denmark; [b]Department of Earth Sciences, Durham University, Durham DH1 3LE, UK; [c]Department of Biological Sciences, Macquarie University, NSW 2109, Australia*

The relationship of many Cambrian rhynchonelliform brachiopods is poorly understood, with many genera displaying a combination of morphological features that are taxonomically confusing. The study of middle Cambrian–early Tremadocian brachiopods is critical because this interval is sandwiched directly between the two largest radiation phases in the early Palaeozoic and provides raw data for deciphering the events leading up to the explosion of brachiopod genera in the Ordovician. Here we present a parsimony analysis of a wide selection of Cambrian and Ordovician brachiopod genera with a particular focus on the evolution and phylogeny of Billingsellida. The billingselloids were widespread by the late Cambrian and the group was originally thought to represent the ancestral stock of many Ordovician brachiopod lineages. The phylogenetic analyses portray the polytoechioids as derived billingselloids separate from the clitambonitoids that form a sister group. The Gondwanan brachiopod *Roanella* is interpreted as ancestral to the clitambonitoids within the Billingsellida and is reassigned to Clitambonitoidea within a new monogeneric family, Roanellidae nov. *Antigonambonites* displays no obvious relationship with the clitambonitoids and should be formally transferred to the polytoechioids. The monogeneric family Chaniellidae exhibits characters reminiscent of members of the polytoechioids and is transferred to the superfamily Polytoechioidea. The recently reappraised clitambonitoid *Arctohedra* is interpreted as a basal member of the entire order Billingsellida.

Introduction

Brachiopods dominated the benthic marine realm during the Palaeozoic, both in terms of relative abundance and species diversity. The Ordovician in particular represented a pivotal period for brachiopods, with the phylum undertaking a spectacular surge in biodiversity driven by an exponential increase in numbers at family, genus and species levels (Sepkoski 1981; Droser *et al.* 1997; Harper *et al.* 2004; Harper 2006; Alroy 2010). However, brachiopods had a significant history prior to the Ordovician, with the majority of higher-level taxa already established during the Cambrian 'explosion'; all three subphyla are represented (Williams & Carlson 2007), as well as 12 out of a total of 26 orders described for the entire phylum (Curry & Brunton 2007). Cambrian faunal assemblages were dominated by organophosphatic-shelled Linguliformea (especially Lingulida and Acrotretida), which account for more than 50% of total Cambrian brachiopod diversity (Curry & Brunton 2007; Ushatinskaya 2010). In general, the calcareous-shelled rhynchonelliform brachiopods tended

to be minor and relatively short-lived components of early–late (Furongian) Cambrian communities, with several members within the orders Obolellida, Kutorginida and Chileida becoming extinct by the end of the Middle Cambrian (e.g. Popov & Holmer 2000; Holmer *et al.* 2001, 2011). Some rhynchonelliform groups, including the orthidines and the billingsellides, endured, forming communities in the shallow-marine, inshore settings of tropical Gondwana (e.g. Bassett *et al.* 2002; Benedetto & Sanchez 2003) and Laurentia (e.g. Ulrich & Cooper 1936, 1938; Freeman & Stitt 1996). These brachiopod assemblages had already formed trophic and tiering structures characteristic of younger Palaeozoic faunas, but their relationship with succeeding brachiopod faunal assemblages is poorly understood (Bassett *et al.* 2002).

One of the more distinctive groups of brachiopods that became almost cosmopolitan by the Furongian were the billingselloids, a group interpreted by many workers to represent ancestors to the characteristic stocks of the younger Ordovician faunal assemblages (Brock & Talent 1999; Popov *et al.* 2001, 2007, 2009; Bassett *et al.*

*Corresponding author. Email: timothy.topper@snm.ku.dk

2002). Sharing many features with the early orthides, the billingselloids were originally classified as such (see Williams 1965); however, the presence of a modified delthyrium, a chilidium and, significantly, the possession of a laminar secondary shell layer prompted a reassignment of the superfamily to Strophomenida (Williams *et al.* 1996), although the group was given eponymous ordinal status in the Strophomenata by Williams & Harper (2000). The new order provisionally includes the clitambonitoids and polytoechioids, pending further information on shell structure and a greater understanding of the closure of the delthyrium (Williams & Harper 2000). In a reassessment of tritoechiid (= polytoechiid) phylogeny, Popov *et al.* (2001) doubted that the billingselloids were ancestral to the clitambonitidines, alternatively presenting evidence that the tritoechiids and billingselloids formed a monophyletic clade. The clitambonitidines formed a separate clade potentially representing an ingroup within Protorthida or a sister group of Orthida (Popov *et al.* 2001, fig. 12).

The exact stem and crown group relationships of the earliest rhynchonelliform orders are still poorly understood and indeed many Cambrian rhynchonelliform genera have been taxonomically perplexing, displaying a mosaic of morphological characters that has subsequently led to uncertainties regarding their systematic placement and evolutionary relationships. For example, *Arctohedra* Cooper, 1936, an aberrant mid-Cambrian genus transiently assigned to Protorthida, displays a notothyrial platform reminiscent of some orthids (Williams & Harper 2000). However, the possession of a free spondylium, deltidiodont articulation, advanced cardinalia and quadripartite dorsal adductor scars could also point to a close relationship with the clitambonitidines (Vinn & Rubel 2000; Popov *et al.* 2001, 2007). This relationship has recently been recognized formally by Rubel (2007), transferring Arctohedridae (excluding *Loperia* Walcott, 1905) to the clitambonitidines based on the confirmed presence of a cardinal process and the discovery of a free spondylium in juvenile clitambonitidines (Popov *et al.* 2001). The enigmatic early Furongian brachiopod *Roanella platystrophioides* (Chapman) from the Dolodrook River limestones, eastern Victoria, Australia (Brock & Talent 1999; Paterson & Laurie 2004), has frustrated taxonomists for over a century. The biconvex, strongly costellate nature of the shells, presence of a well-developed deltidium and absence of dental plates have seen the taxon misidentified as *Platystrophia biforata* (Chapman, 1907), redescribed as *Orthis* (*Plectorthis*) *platystrophioides* (Chapman, 1911), transferred to *Eoorthis* (Chapman, 1917) and finally incorporated into the new genus *Roanella* by Brock & Talent (1999). Brock & Talent (1999) tentatively assigned this genus to Billingselloidea; however, the family-level assignment was left open due to the unusual combination of billingselloid and clitambonitidine features. The genus has since been reassigned to Eoorthidae based on morphological features, particularly present in the dorsal valve (such as an open notothyrium), that are more typically orthoid (Harper 2007). The unusual set of morphological characters and the resulting phylogenetic analysis presented here has prompted the erection of a new family, Roanellidae fam. nov., to accommodate the genus. A recent addition to Billingselloidea is the genus *Chaniella* Benedetto, 2009, documented from the lower Tremadocian of north-west Argentina. The particular combination of clitambonitid and polytoechioid features in *Chaniella*, for example, the presence of narrow lateral deltidial plates and a pseudospondylium, excluded the genus from all known families and led to the erection of the new monotypic family Chaniellidae within the superfamily Billingselloidea. The possession of dental plates and a pseudospondylium, however, suggest that Chaniellidae may be better accommodated within Polytoechioidea.

Despite their undoubted significance, the taxonomic position and phylogenetic relationship of many mid–late Cambrian brachiopod genera is not well understood. Study of middle Cambrian–early Tremadocian brachiopods is essential to fill the gap between the two major radiation phases in the early Palaeozoic and to search for the origin of these keystone organisms in the lead-up to the explosion of the phylum during the Ordovician. The purpose of this study is to evaluate the taxonomic position of several critical Cambro-Ordovician brachiopod genera, in particular to elucidate the complex relationships among billingsellides and basal rhynchonelliform taxa. Of particular interest is the phylogenetic relationship of the problematic *Roanella*. The phylogenetic analyses presented here support earlier statements that portray the Polytoechioidea as derived billingselloids (Popov *et al.* 2001, 2007) separated from the clitambonitidines (Popov *et al.* 2001, 2007). However, the enigmatic late Cambrian *Roanella* is here interpreted as ancestral to the clitambonitidines within Billingsellida, with the newly assigned clitambonitidine *Arctohedra* representing a basal member of the entire order Billingsellida.

Phylogenetic analysis and results

To assess the systematic position of key Cambro-Ordovician brachiopod genera the taxon-character matrix designed by Benedetto (2009) was implemented, expanded and updated to include recent revisions and new taxonomic information (Online Supplementary Material). The character matrix remains largely the same, consisting of 28 characters (one character added) but we add nine new taxa to the matrix (total 40 taxa) and revise the character codings of Benedetto (2009). Many genera employed in this study represent early members of their respective groups and some display a combination of morphological characters that suggest a basal position, in brachiopod groups that would become prevalent in the late Cambrian and Ordovician. More derived genera are utilized to include the full range of morphological characters of the particular

groups under investigation. A wide selection of Cambrian and Ordovician genera were included in the analysis, representing five major rhynchonelliformean orders including Billingsellida, Orthida, Pentamerida, Protorthida and Kutorginida. As the main focus is to delve into the phylogeny of basal billingsellides, half of the taxa included in the analysis are representatives of Billingsellida, with all six families (including Roanellidae fam. nov.) incorporated. Orthida are represented by six families, including members of Plectorthoidea, such as euorthisinids, giraldiellids and finkelnburgiids, in conjunction with the Cambrian eoorthids that are presently thought to represent a link between the plectorthoids and orthoids (Williams & Harper 2000). In an attempt to incorporate a variety of shell morphotypes, representing a wide range of ancestral and derived early orthides, *Wimanella* Walcott, 1908 and *Bohemiella* Schuchert & Cooper, 1931 were selected in addition to the more derived anomalorthids. Protorthides possess very rudimentary cardinalia but have paired teeth and a free spondylium and for this reason the protorthide taxon *Glyptoria* Cooper, 1976 was included in the analysis. In both analyses *Glyptoria* was chosen as the outgroup taxon for rooting the phylogenetic trees. This genus is interpreted as one of the most ancestral protorthides (Popov *et al.* 2001) and was also the selected outgroup taxon in the cladistic analysis undertaken by Benedetto (2009).

Unlike most protorthides, *Leioria* Cooper, 1976 has derived cardinalia with dental sockets and brachiophores, characters which prompted Jin & Popov (2008) to consider the genus within the primitive Syntrophiidina. Consequently, *Leioria* and three Cambrian Syntophiidina genera were included in the analysis. The lower Cambrian kutorginide *Nisusia* Walcott, 1905 was also incorporated as one of the earliest known rhynchonelliformean brachiopods.

No single species was chosen to represent each genus in the analysis. Some morphological features, such as presence of a fold and sulcus and external ornament are quite variable within genera and although the type species was commonly chosen to code, we attempted to quantify each genus holistically as the type may not accurately reflect the morphological features for the entire genus. Analysis of the 28-character matrix (see Online Supplementary Material) was performed using the parsimony program TNT, version 1.1 (Goloboff *et al.* 2008), using a traditional, heuristic method with multiple random addition sequences plus the tree bisection reconnection (TBR) branch-swapping algorithm, holding 10 trees in each addition sequence. Two parsimony analyses were performed. In the initial analysis all characters were unordered and unweighted, yielding 60 shortest trees of 186 steps (consistency index (CI) 0.328; retention index (RI) 0.618), the strict consensus of which is shown in Fig. 1. The second analysis involved the differential weighting of particular character states prior to the cladogram construction and produced eight shortest trees

of 622 steps (CI 0.402; RI 0.739), the strict consensus of which is shown in Fig. 2. Character states were weighted in the analysis according to their recognized importance in previous classifications – these include characters 5–9, 14–16 and 21–24 (see Online Supplementary Material). Weighted characters appertain to the modification of the delthyrium and notothyrium, the nature of the dental plates, presence/absence of spondylium or pseudospondylium, nature of the notothyrial platform, and cardinalia. Some morphological characters are variably present within a single genus, their presence or absence possibly being polymorphic. Consequently, the selected weighted characters are interpreted as diagnostic and hold greater taxonomic significance than the remaining characters that may be evolutionary holdovers with reduced bearing on systematic relationships, or display variability or ambiguity within the selected genus.

The results of the analysis should be viewed as a preliminary attempt to comprehend the phylogenetic relationships of taxa within Billingsellida and other Cambro-Ordovician rhynchonelliform brachiopods. The moderate level of homoplasy in character transformations resulted in modest values of consistency index (0.328 and 0.402, respectively). These values, however, are comparable to consistency indices displayed in other phylogenetic analyses incorporating Cambro-Ordovician brachiopod taxa, such as the cladograms presented by Popov *et al.* (2001, fig. 12, CI 0.585), Jin & Popov (2008, fig. 6, CI 0.3189) and Benedetto (2009, figs 5–6, CI 0.438). The consistency or retention indices were not stated for the cladograms presented by Benedetto (2009, figs 5–6); the value stated here was obtained by re-running the matrix provided (Benedetto 2009) using TNT and under the instructions outlined by Benedetto (2009, p. 399). The modest consistency indices are attained because many characters used in these phylogenetic analyses, such as shell profile, ventral interarea height and inclination, presence of a fold and sulcus, ornament, muscle fields and mantle canal systems, exist across many brachiopod lineages and are not particularly useful for elucidating phylogenetic relationships. This is especially evident in classifying the early orthides (top branch of Figs 1 and 2) due to the scarcity of clear, synapomorphic characters. However, there are some characters present in the analysis that do contribute some synapomorphy to the resulting cladograms, such as modification of the delthyrium and notothyrium, presence of a spondylium or pseudospondylium, and development of cardinal process and dental plates; this is reflected in the comparatively high values of RIs in the cladograms presented herein (0.618 and 0.739). The level of homoplasy, combined with a limited number of informative features that can be applied to the large number of analysed taxa, should be viewed as a valuable insight into elucidating the complex relationships of Cambro-Ordovician rhynchonelliform brachiopods, but is clearly not a concrete basis for revising the entire systemat-

Figure 1. Cladogram depicting inferred phylogenetic relationships of billingsellides and other selected brachiopod taxa discussed in the text based on character data in Online Supplementary Material. Consistency idex (CI) = 0.328; retention index (RI) = 0.618. Analysis involved unordered and unweighted characters. Superfamily level assignment is indicated.

ics of the group. The few taxonomic revisions made in this paper are not based solely on the cladistic analysis presented herein – they are also supported by morphological information, phylogenetic analyses and taxonomic assessments presented previously (e.g. Popov *et al.* 2001, 2007, 2009; Benedetto 2009).

There are many broad similarities in the two cladograms presented below (Figs 1 and 2). The relationships within the order Billingsellida in both cladograms are essentially in agreement, with the monophyletic grouping of the billingselloids and the more derived polytoechioids. The clitambonitoids form a separate, monophyletic sister group. Of particular note is the inclusion of the clitambonitid *Antigonambonites* Öpik, 1934 as a derived polytoechioid in both trees (Figs 1, 2). This entire clade, representing the Order Billingsellida, emerges as a sister group to the clade
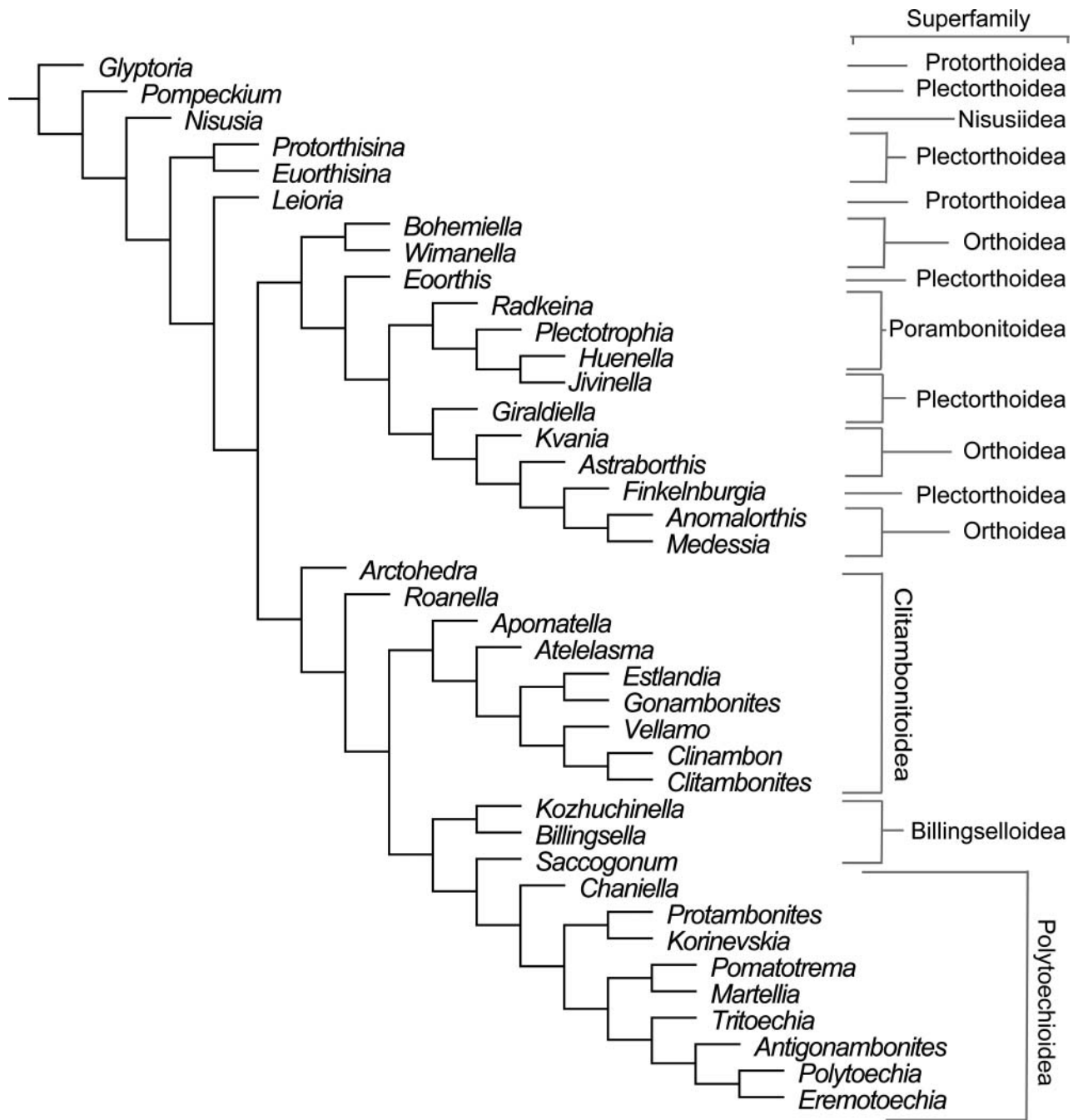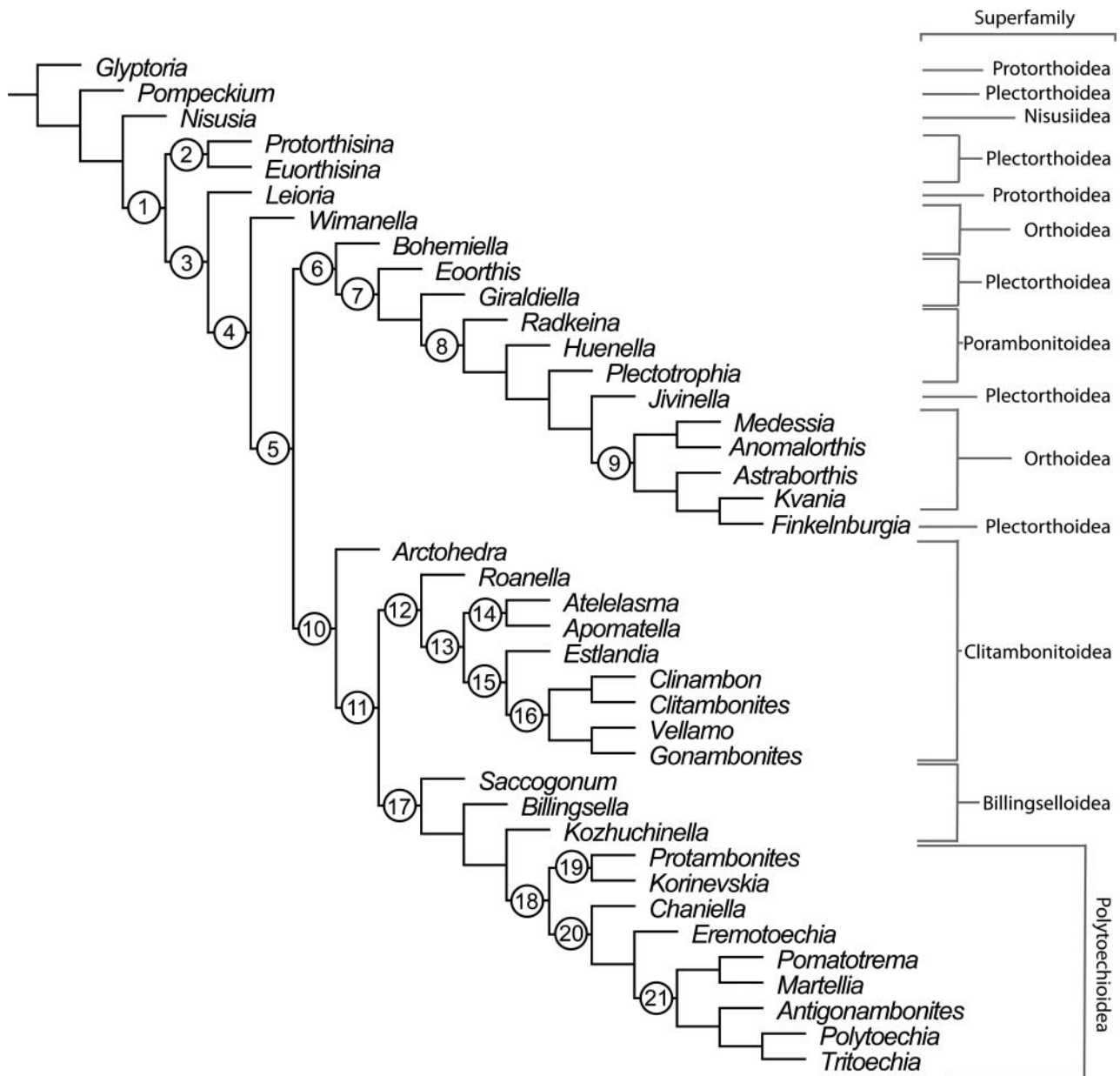
Figure 2. Cladogram depicting inferred phylogenetic relationships of billingsellides and other selected brachiopod taxa discussed in the text, based on character data in Online Supplementary Material. CI = 0.402; RI = 0.739. Analysis involved the differential weighting of characters 5–9, 14–16 and 21–24. Numbered nodes are supported by character states discussed in the text, and superfamily level assignment is indicated.

consisting of selected members of Orthida and Pentamerida. The major problem evident from the phylogenetic tree with unordered and unweighted characters (Fig. 1) is that many of the synapomorphies recognized in the cladistic analysis are focused on the presence of a fold and sulcus, muscle fields and mantle canal systems in both ventral and dorsal valves. Saccate and pinnate mantle canal systems are, for example, present in a number of the earliest Cambrian rhynchonelliformean groups and are seen as homoplas-

tic features that cannot be reliably used to establish close phylogenetic relationships. There are a few minor stratigraphical discrepancies in both cladograms (see Figs 1, 2), most notably the basal position of the late Cambrian–lower Ordovician Euorthisinidae genera (see Fig. 3 for first appearance data), *Euorthisina* Havlíček, 1950 and *Protorthisina* Benedetto, 2007, the ancestral position of which is based entirely on the acquisition of a septalium (Fig. 2, node 2). Furthermore the non-weighted phylogenetic tree (Fig. 1)

Figure 3. Cladogram reproduced from Fig. 2 calibrated to chronostratigraphical scale. Black squares indicate the first appearance datum of the genus.

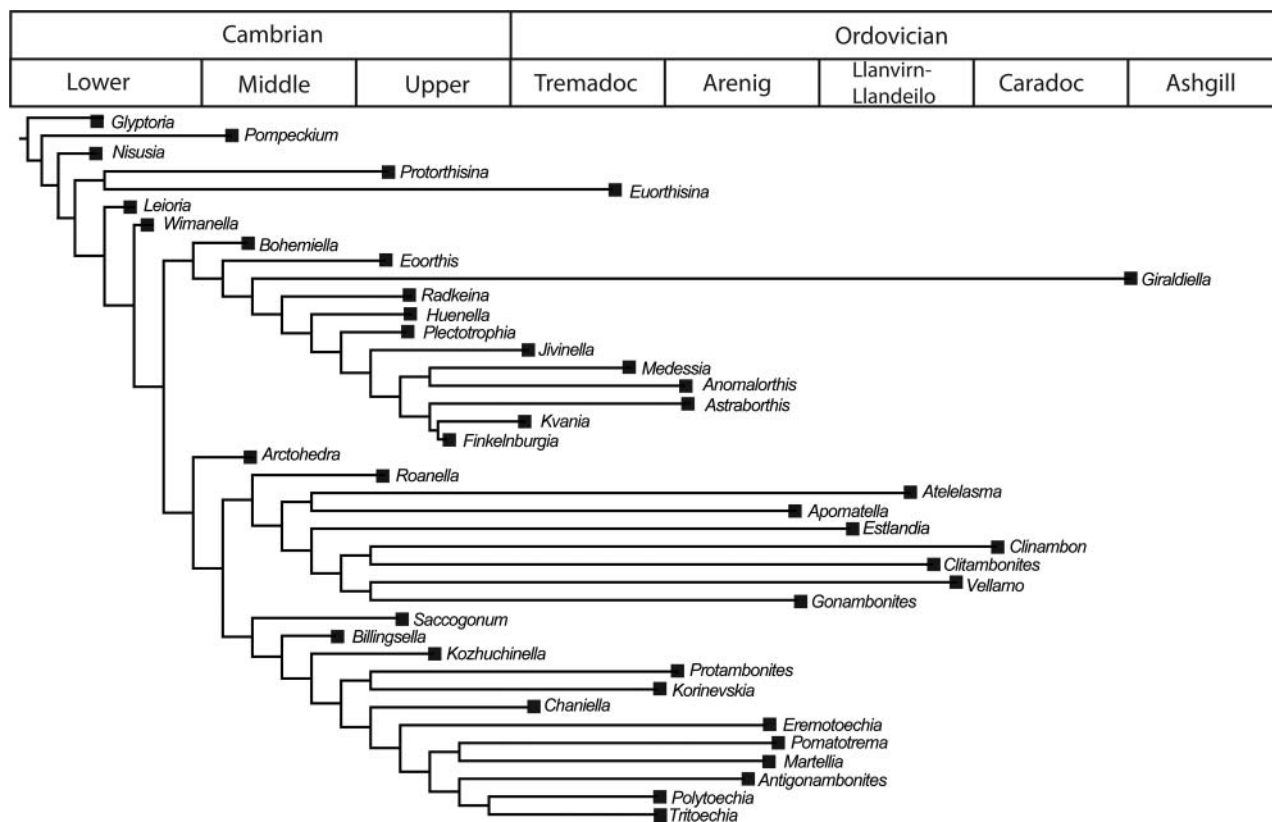displays a lower CI (0.328 compared to 0.402), diminishing its overall utility. As a result, the following discussion will predominantly centre on the cladogram (Fig. 2) produced with the differential weighting of characters interpreted here as being more taxomically significant that produced a stratigraphically compatible tree with a higher CI.

The cladogram shows the billingselloids and polytoechioids as a single, consistent monophyletic clade (Fig. 2, node 17) linked predominantly by homologous structures, such as the presence of chilidial plates or chilidium and a well-developed pseudodeltidium, an apomorphy not shared with the lower Tremadocian *Chaniella*. The Furongian genus *Saccogonum* Havlíček, 1971 is expressed as the most basal of the billingsellides displaying 'ancestral' morphological features such as an open, unmodified notothyrium and the absence of dental plates and a pseudospondylium. The billingselloid genus *Chaniella* clusters within Polytoechioidea, representing a basal member of the superfamily based on the peculiar combination of character states such as the lack of a pseudodeltidium but possession of dental plates and a pseudospondylium (Fig. 2, node 18). Interestingly, the basal members of the derived Polytoechioidea, *Korinevskia* Popov *et al*., 2001 and *Protambonites* Havlíček in Havlíček & Josopait, 1972, possess a pseudodeltidium

but lack a pseudospondylium, in addition to exhibiting a near orthocline ventral interarea (Fig. 2, node 19). *Antigonambonites,* which possesses a pseudospondylium rather than a spondylium, clusters in this clade as a derived polytoechioid, alongside the type genus *Polytoechia* Hall & Clarke, 1892 and *Tritoechia* Ulrich & Cooper, 1936, as a result of the presence of separate chilidial plates (Fig. 2).

The above clade does not include the clitambonitidines (*Antigonambonites* is excluded), which form a monophyletic sister group of Billingsellidina (Fig. 2, node 12). The basal member of the group is the late Cambrian *Roanella* (Fig. 4), which is associated with the clade because it possesses a deltidium; however, this feature is not recognized as synapomorphic in the cladistic analysis. *Roanella* lacks the spondylium triplex, characteristic of the clitambonitoids (Fig. 2, node 13), and consequently takes up an ancestral position within the group. Brock & Talent (1999, p. 112) previously raised the possibility that *Roanella* "may be an early member of [the clitambonitidine] lineage". *Apomatella* and *Atelelasma*, which are characterized by narrow deltidial plates and separate chilidial plates (Fig. 2, node 14), are a sister group of the clade formed by genera having a complete deltidium, such as *Vellamo* Öpik, 1930, *Clitambonites* Pander, 1830,
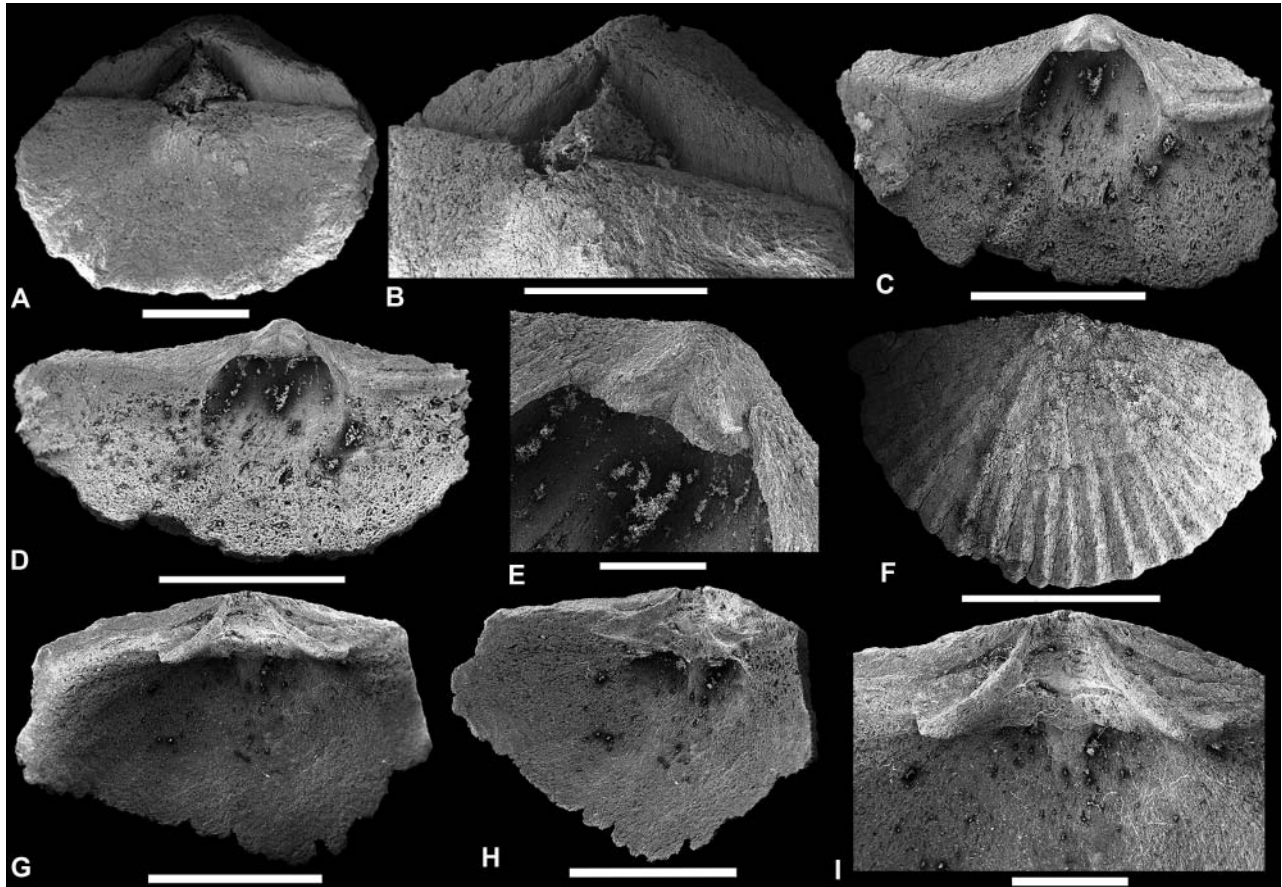
Figure 4. *Roanella platystrophioides* (Chapman) from locality D-RH 21.7, Dolodrook River limestones of Victoria, Australia. All scale bars 5 mm, unless otherwise indicated. **A, B,** articulated specimen, NMV P17252; **A,** dorsal view, scale bar 2 mm; **B,** enlarged, lateral view, scale bar 2 mm. **C–E,** ventral valve, NMV P17253; **C,** interior view; **D,** oblique interior view; **E,** enlargement of deltidium, scale bar 1 mm. **F,** exterior view of dorsal valve, NMV P 17254. **G–I,** dorsal valve, NMV P17255; **G,** interior view; **H,** lateral view of interior; **I,** enlargement of cardinal area, showing short, median ridge, scale bar 2 mm.

Clinambon Schuchert & Cooper, 1932 and the gonambonitids (Fig. 2, node 15). The mid-Cambrian clitambonitide genus *Arctohedra* is interpreted as ancestral to the entire Billingsellida clade (Fig. 2, node 10). *Arctohedra* had already acquired a free spondylium, deltidiodont articulation and quadripartite dorsal adductor scars, but retains an open and unmodified delthyrium and notothyrium, similar to many orthide and protorthide genera. The modification of the delthyrium is perceived as the synapomorphy characterizing the entire Billingsellida clade (Fig. 2, node 11).

The other branch of the cladogram is still speculative because of the sparse fossil record of many of the selected genera and the lack of well-defined evolutionary trends. The branch includes members from a number of families representing Orthidina (such as anomalorthids, bohemieliids and eoorthids) and Syntrophiida (huenellids and tetralobulids). Synapomorphies for the group include an unmodified delthyrium and notothyrium (Fig. 2, node 6)

and the possession of dental plates (Fig. 2, node 7). The basal member of the group is the middle Cambrian orthidine genus *Bohemiella* Schuchert & Cooper, 1931 which lacks dental plates but possesses a simple cardinal process (Fig. 2, node 5). The syntrophiidines appear as a monophyletic group based on a well-developed notothyrial platform (Fig. 2, node 8), with the late Cambrian Australian genus *Radkeina* Laurie, 1997 the basal member, a result of its possession of a sessile spondylium rather than a pseudospondylium. The anomalorthids (*Anomalorthis, Astraborthis* and *Medessia*) appear as a derived group of the syntrophiidines based on possessing a quadripartite dorsal muscle field and outwardly curved brachiophores (Fig. 2, node 9). *Kvania* Havlíček, 1994 and *Finkelnburgia* Walcott, 1905 represent the most derived genera of the clade based on the rudimentary cardinal process and small notothyrial chamber (Fig. 2), despite the fact that both genera are present in the late Cambrian. In the unweighted cladogram (Fig. 1), *Wimanella* and *Bohemiella* appear as a sister

group to the rest of the orthides and pentamerides that are anchored by the plectorthoid genus *Eoorthis* Walcott, 1908.

Systematic palaeontology

Figured specimens of *Roanella platystrophioides* are deposited in the Museum of Victoria; catalogue numbers are indicated in the figure captions.

<div align="center">

Class **Strophomenata** Williams *et al*., 1996
Order **Billingsellida** Schuchert, 1893
Suborder **Clitambonitidina** Öpik, 1934
Superfamily **Clitambonitoidea** Winchell & Schuchert, 1893
Family **Roanellidae** fam. nov.
(Fig. 4)

</div>

Diagnosis. Ventribiconvex, unequally costellate shell with semicircular to subquadrate outline. Ventral valve with deltidium poorly defined, small teeth, lacking dental plates; mantle canal system saccate. Dorsal valve with open notothyrium, lacking chilidium; ridge-like cardinal process.

Type genus. *Roanella* Brock & Talent, 1999.

Discussion. The new family is based on the unique character states of the genus *Roanella*. The unusual set of morphological characters, including the presence of a well-developed deltidium, open notothyrium, well-developed notothyrial platform and the absence of dental plates, chilidium and spondylium, means that the genus cannot be accommodated in any established family within the order Billingsellida (Fig. 4). The phylogenetic analysis presented herein supports assignment within the suborder Clitambonitoidea (see text for discussion). The new family is monogeneric; the type species of *Roanella*, *R. platystrophioides* (Chapman), has been previously documented and described comprehensively. For further information regarding material, type locality and detailed description, refer to Brock & Talent (1999, figs. 2A–R, 3A–U, pp. 112–118).

<div align="center">

Suborder **Billingsellidina** Schuchert, 1893
Superfamily **Polytoechioidea** Öpik, 1934
Family **Chaniellidae** Benedetto, 2009

</div>

Type genus. *Chaniella* Benedetto, 2009.

Discussion. Based on the new cladistic analysis and on the presence of both dental plates and a pseudospondylium, the monogeneric family Chaniellidae is transferred to the superfamily Polytoechioidea. The type genus *Chaniella* possesses an open delthyrium flanked by narrow deltidial plates, which led Benedetto (2009) to exclude assignment to Polytoechioidea. However, morphological similarities between *Chaniella* and members of Polytoechioidea, e.g.

Korinevskia and *Protambonites*, have been discussed here and by Benedetto (2009) who provides further information regarding material and discussion of Chaniellidae.

<div align="center">

Family **Polytoechiidae** Öpik, 1934
Genus *Antigonambonites* Öpik, 1934

</div>

Type species. *Gonambonites plana* Pander, 1830.

Discussion. There has been much discussion regarding the taxonomic position of *Antigonambonites* (see Wright & Rubel 1996; Vinn & Rubel 2000) and suggestions have been made to move the genus into Polytoechiidae (Popov *et al.* 2001); however, no formal taxonomic reassignment has been made. The genus possesses a pseudospondylium rather than a spondylium and appears to be a derived polytoechioid, alongside the type genus *Polytoechia* and *Tritoechia*, in the phylogenetic analysis (Fig. 2). The discrete dental plates and partly or entirely raised ventral muscle field in *Antigonambonites* can be unambiguously identified as a polytoechiid pseudospondylium; as a result the genus is transferred to Polytoechiidae.

Discussion

The grouping of billingselloids and clitambonitoids into a new order, Billingsellida, was prompted by the phylogenetic analysis of Williams *et al.* (1996) and was implemented by Williams & Harper (2000). Originally considered to belong to Orthida (Schuchert & Cooper 1932; Ulrich & Cooper 1936; Williams 1965), the presence of a pseudodeltidium and chilidium and the discovery that the secondary shell layer of *Billingsella* is laminar in the manner of most strophomenates (Williams 1970), prompted reassignment to Strophomenida (Williams & Harper 2000). This reassignment has been generally accepted (e.g. Benedetto 2009; Popov *et al.* 2009, 2011), with the new order consisting of three Cambro-Ordovician superfamilies: Billingselloidea, Clitambonitoidea and Polytoechioidea (see Williams & Harper 2000). The ancestral stocks of the clitambonitoids and polytoechioids were thought to have arisen from within the billingselloid plexus (Williams *et al.* 1996) and, although this theory may still hold true for the polytoechioids, the position of the clitambonitoids is uncertain, with a possible origin from Furongian orthide stocks with an open delthyria and dental plates (Wright 1996), or a protorthid-like brachiopod from the mid-Cambrian (Vinn & Rubel 2000).

The clitambonitidines form a distinctive group of brachiopods that thrived in shallow shelf environments throughout the Ordovician, but were particularly prevalent in Baltic faunas (e.g. Pander 1830; Egerquist 2003; Rubel & Popov 1994; Popov *et al.* 2007). The suborder was divided into two superfamilies by Williams (1965), based essentially on the impunctate nature of the clitambonitoid shell and the pseudopunctate shell of the gonambonitoids.

This relationship was later revised by Williams & Harper (2000), who incorporated the gonambonitoids with the clitambonitoids and erected a new superfamily Polytoechioidea, bearing a pseudospondylium. The suborder Clitambonitidina has been considered to represent a derived group within the Order Billingsellida (Rubel & Wright 2000), but recent evidence has shown that the clitambonitidines are polyphyletic, embracing two very different groups of brachiopods (Popov *et al.* 2001, 2007). The polytoechioids represent derived billingsellids, in contrast to the clitambonitoids that display many features in common with the protorthides (Popov *et al.* 2001, 2007). This view is partially supported by the phylogenetic analysis herein (Fig. 2): Clitambonitidina constitutes a polyphyletic clade, Polytoechioidea derived from Billingselloidea (Fig. 2, node 18) with Clitambonitioidea representing a monophyletic sister group (Fig. 2, node 12). Further evidence is required to support suggested ancestral relationships with the protorthides.

The mid-Cambrian *Arctohedra* appears as the basal member of the entire Order Billingsellida. The combination in *Arctohedra* of deltidiodont teeth, dorsal cardinalia (well-developed notothyrial platform and simple cardinal process), open delthyrium and a free spondylium are seen as ancestral morphological features of the group (Fig. 2, node 10). The presence of a free spondylium originally placed *Arctohedra* within the protorthids (Cooper 1936; Havlíček, 1977; Popov 1992); however, after much discussion (Brock 1998; Popov *et al.* 1996, 2001, 2007) the genus was relocated in the clitambonitoids (Rubel 2007). The position of *Arctohedra* in our cladogram (Fig. 2) and the possession of a free spondylium support the earlier claim by Vinn & Rubel (2000) that the clitambonitoids arose from a protorthid-like brachiopod in the mid-Cambrian. However, it is important to note that the possession of a free spondylium does not automatically indicate a protorthid ancestry. Havlíček (1977) noted that the spondylium-like plate present in protorthid taxa predated the development of dental plates, which emerged in late Cambrian orthide taxa and as such the development of the protorthid free plate probably had no link with dental plates. Consequently the free or spondylial plate is seen as probably rising independently in a number of brachiopod lineages (Brock 1998).

The enigmatic genus *Roanella* also emerges as an early member of the clitambonitidine clade. It was tentatively placed within Billingselloidea (Brock & Talent, 1999) and recently transferred to Plectorthoidea (Harper 2007), but the presence of a deltidium suggests a more suitable placement within Clitambonitoidea (Fig. 2, node 12). Other early clitambonitid genera, like *Apomatella* Schuchert & Cooper, 1931 and *Atelelasma* Cooper, 1956, lack a deltidium, instead exhibiting small deltidial plates, but they share saccate ventral mantle canals, a similar notothyrial platform and a simple cardinal process. Brock & Talent (1999) noted that *Roanella* displayed an unusual combina-

tion of billingselloid and clitambonitidine features to the extent that confident family level assignment was difficult. As a result of the current phylogenetic analysis and evidence presented previously (Brock & Talent 1999), a new monogeneric family within Clitambonitoidea, Roanellidae fam. nov., is herein erected to accommodate *Roanella*, a genus that may represent an early member of the clitambonitidine lineage. For a detailed description and other systematic details of *Roanella*, see Brock & Talent (1999). Significantly, *Roanella* lacks the diagnostic clitambonitidine spondylium, although Brock & Talent (1999, fig. 3B, C, H, I) reported a consistent and prominent thickening of the shell in the umbonal region, which could be interpreted as an elevated muscle pad/platform that was an early, rudimentary form of the spondylium.

In the clitambonitidines *sensu stricto* there is a spondylium simplex, formed by the fusion of the dental plates onto a single median septum (Wright & Rubel 1996). This is modified in gonambonitids into a spondylium triplex, with a pair of lateral septa extending from below the spondylium towards the valve floor on either side of the median septum (Wright & Rubel 1996). *Estlandia* appears less derived than Clitambonitidae, which displays fully-fledged deltidia (Fig. 2), supporting the ontogenetic information presented by Popov *et al.* (2007). *Gonambonites* appears more derived and clusters with *Vellamo*, based on the acquisition of dental plates. Ontogenetic studies have recently been used in phylogenetic reconstructions of clitambonitidine brachiopods, Popov *et al.* (2007) citing the planktotrophic larvae of clitambonitoids and lecithotrophic nature of polytoechioids as evidence of polyphyly in the group. Differentiation was primarily based on the dimensions of the first-formed shell, with lecithotrophic larvae displaying a first-formed shell that rarely exceeded 200 μm in width (Freeman & Lundelius 2005; Popov *et al.* 2007). The silicified nature of the *Roanella* specimens does not allow for an accurate discrimination of the first-formed shell, making it difficult to validate the position of the genus within the clitambonitoids. The early ontogeny of many Cambrian rhynchonelliform brachiopods remain poorly understood and consequently ontogenetic details were excluded from the matrix used in the current analysis.

Available information on shell morphology together with the phylogenetic analysis presented here suggests a close affinity between Polytoechiidae and Billingsellidae. The polytoechioids have long been considered to be derived from billingsellids (e.g. Havlíček 1977; Popov *et al.* 2001), sharing such morphological features as the presence of chilidial plates or a chilidium, simple cardinal process and a well-developed pseudodeltidium. Two important acquisitions in the polytoechioid shell (both features are present in *Chaniella*) are dental plates and the pseudospondylium (Fig. 2, nodes 18 and 20, respectively). The presence of dental plates was once considered a characteristic feature of *Billingsella* (Schuchert & Cooper 1932; Williams &

Harper 2000); however, numerous authors (Nikitin 1956; Popov *et al.* 2001, 2011) have noted that these structures have been erroneously interpreted and are not homologous to the dental plates possessed by orthides and polytoechioids. Popov *et al.* (2001, 2011) maintained that none of the *Billingsella* species possess dental plates and considered the presence of dental plates as diagnostic of the more advanced Polytoechioidea. Despite this, a recently described faunal assemblage from the upper Furongian of China (Zhan *et al.* 2010) documented dental plates in specimens of *Billingsella guangxiensis* Zeng, 1977 and *B. costata* Zhan *et al.*, 2010. It is possible that the generic diversity of Billingsellidae in the Furongian has been underestimated and, in conjunction with the problems surrounding the correct designation of the type species (see Freeman & Stitt 1996; Popov *et al.* 2011), the group in general appears to require revision. Dental plates are very weakly developed in *Kozhuchinella* cf. *mariiniea* Severgina, 1967 from the upper Cambrian of western Queensland (Laurie 1997) and are further developed in the lower Tremadocian genus *Chaniella* Benedetto, 2009. It is *Chaniella* that clusters within the polytoechioids (Fig. 2, node 20), possessing short dental plates and a pseudospondylium but differing in lacking a pseudodeltidium and displaying a different dorsal muscle field (Fig. 2, node 21 represents the acquisition of a radially arranged dorsal muscle field). Interestingly, Vinn & Rubel (2000) hypothesized that the polytoechioids may have been derived from a late Cambrian billingselloid that possessed dental plates, a view supported by the cladogram here (Fig. 2). Benedetto (2009) erected the new monogeneric family, Chaniellidae, based on specimens from the lower Tremadocian of Argentina. The reasons for the inclusion of Chaniellidae in Billingselloidea are not clear as billingselloids possess a pseudodeltidium and lack a pseudospondylium, quite distinct from the pseudospondylium-bearing *Chaniella*. Benedetto (2009) documented the close resemblance between *Chaniella*, *Protambonites* and *Korinevskia*, recognizing similarities in shell profile, dental plates and ventral muscle fields, with *Chaniella* differing in lacking a pseudodeltidium. Furthermore, the cladistic analysis presented by Benedetto (2009, fig. 5) portrayed *Chaniella* as closely related to both polytoechioid genera. *Korinevskia* and *Protambonites* differ in lacking a pseudospondylium, which is why these genera appear as a sister group to *Chaniella* and the rest of the polytoechioids (Fig. 2, node 19). The possession of short dental plates and a pseudospondylium is considered here to represent morphological characters more indicative of Polytoechioidea and we propose that *Chaniella* be transferred to Polytoechioidea based on the cladistic analyses presented here (Fig. 2) and previously (Benedetto 2009, fig. 5). The polytoechioids as a group display strong conservatism and the basic morphological characteristics of the group, including muscle fields, general shell shape, ornament and

mantle canal system, persisted until the later Ordovician (Popov *et al.* 2001), making the investigation of relationships between the other members of the group difficult.

The endemic Baltoscandian genus *Antigonambonites*, which possesses a pseudospondylium rather than a spondylium, clusters in this clade as a derived polytoechioid, alongside the type genus *Polytoechia* and *Tritoechia*, as a result of the presence of separate chilidial plates (Fig. 2). The placement of *Antigonambonites* within the Clitambonitoidea has been a matter of discussion for many years (e.g. Wright & Rubel 1996; Vinn & Rubel 2000), with Popov *et al.* (2001, p. 139) suggesting that both *Antigonambonites* and *Raunites* Öpik, 1939 be reassigned to Polytoechiidae. The presence of discrete dental plates and partly or entirely raised ventral muscle field in *Antigonambonites* can be unambiguously identified as a polytoechiid pseudospondylium (Wright & Rubel 1996; Vinn & Rubel 2000; Popov *et al.* 2001). The position of the genus in the Polytoechioidea has been verified by ontogenetic information presented by Popov *et al.* (2007) and phylogenetic information shown in Popov *et al.* (2001) and Benedetto (2009), and is supported by the current analysis (Fig. 2).

The other branch of the cladogram is weakly supported and thus largely unresolved because of the sparse fossil record of some of the selected genera and the lack of well-defined evolutionary trends. Included are members from a number of families representing Orthidina and Syntrophiidina. Many of the synapomorphies recognized in the cladistic analysis are focused on the presence of a fold and sulcus, muscle fields and mantle canal systems in both ventral and dorsal valves. Saccate and pinnate mantle canal systems are, for example, present in a number of the earliest Cambrian rhynchonelliformean groups and are seen as homoplastic features that cannot be reliably used to establish close phylogenetic relationships. Consequently the phylogenetic relationships of many of the Orthida are far from clear and require detailed revision. The plectorthoid clade appears paraphyletic, the acquisition of a pseudospondylium in the genera *Jivinella* and *Finkelnburgia* portraying both genera as derived despite their presence in the late Cambrian–early Tremadocian (see Fig. 3). The suggestion that *Kvania* is in a stem group position on the lineage leading to nanorthids and other plectorthoid lineages (Benedetto 2007, fig. 5) is not supported here. *Kvania* and *Finkelnburgia* represent the most derived genera on the branch based on a rudimentary cardinal process and small notothyrial chamber (Fig. 2). The syntrophiidines appear as a monophyletic group, with the late Cambrian Australian genus *Radkeina* Laurie, 1997 as the basal member, a result of possessing a sessile spondylium rather than a pseudospondylium (Fig. 2, node 8).

In light of the current cladistic analysis the clitambonitoids should be classified as the sole superfamily within Clitambonitidina, with Polytoechioidea better supported as a clade within the suborder Billingsellidina, congruent

with trees produced by Popov *et al.* (2001) and Benedetto (2009). Recognition of lower taxonomic levels within the billingsellidines is a difficult task and a number of families could be potentially recognized. *Antigonambonites* should be formally recognized as a member of the polytoechioids, showing no clear relationship with the rest of the clitambonitoids. On the basis of current morphological criteria, *Roanella* is better placed within Billingsellida; however, the genus cannot be assigned consistently to any family within the order. According to the cladistic analysis presented here *Roanella* should be reassigned to the Superfamily Clitambonitoidea and assigned to a new monogeneric family, Roanellidae fam. nov., characterized by the presence of a deltidium, an open notothyrium, a well-developed notothyrial platform and a simple cardinal process, but also lacking chilidium, dental plates and spondylium. The monogeneric family Chaniellidae is here transferred to Polytoechioidea because it possesses dental plates and a pseudospondylium. Recent reassignment of *Arctohedra* to the clitambonitids is supported by the analysis and represents an ancestral member of the entire Billingsellida clade.

Acknowledgements

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1	Shell profile: subequally biconvex or ventribiconvex 0; convexiplane to dorsibiconvex 1; strongly dorsibiconvex 2; concavoconvex to planoconvex 3; ventral valve subpyramidal 4
2	Fold and sulcus: absent: 0; present: 1
3	Ventral interarea (height): low 0; medium 1; very high 2
4	Ventral interarea (inclination): strongly apsacline to orthocline 0; apsacline 1; procline to catacline 2
5*	Delthyrium: entirely open, unmodified 0; modified 1
6*	Pseudodeltidium: absent 0; present 1
7*	Deltidium: Absent 0; present 1
8*	Deltidial plates: absent 0; present 1
9*	Notothyrium: open 0; separated chilidial plates 1; chilidium complete 2
10	Ornament: costate 0; coarsely costellate or fascicostellate 1; multicostellate 2; parvicostellate 3; ramicostellate 4; none (smooth) 5
11	Pseudopuncta: Absent 0; present 1
12	Aditicules: absent 0; present 1
13	Deltidiodont teeth: absent 0; present 1
14*	Dental plates: absent or rudimentary 0; short recessive 1; well developed 2
15*	Spondylium: absent 0; supported by one septum 1; supported by three septa 2; free anteriorly 3
16*	Pseudospondylium: absent 0; present 1
17	Ventral median septum: absent 0; short 1; extended beyond the muscle field 2; supporting spondylium 3
18	Ventral muscle field: indistinct 0; adductor scars as long as diductors 1; adductors longer than diductors 2
19	Ventral mantle canals: indistinct 0; saccate 1; pinnate 2; digitate 3
20	Dorsal mantle canals: indistinct 0; pinnate 1; digitate 2
21*	Notothyrial platform: underlined by a transverse plate 0; absent or rudimentary 1; well developed 2; notothyrial chamber 3; brachiophore plates converging to form septalium 4
22*	Septalium: absent 0; small 1; large, supported by a septum 2
23*	Cardinal process: absent or rudimentary 0; simple, ridgelike 1; simple with enlarged myophore 2
24*	Sockets/socket ridges: sockets absent or rudimentary, built on primary shell 0; sockets well developed, bounded by short socket ridges 1; socket ridges long, subparallel to hinge 2
25	Dorsal septum: absent or rudimentary 0; short, broad 1; long, bladelike 2; supporting septalium 3; short, supporting notothyrial platform 4
26	Dorsal muscle field: indistinct 0; quadripartite 1; muscle scars arranged radially 2
27	Dorsal peripheral rim: absent 0; present 1
28	Brachiophores: absent 0; short, divergent 1; rod-like divergent 2; outwardly curving 3; short knobs 4; forming septalium 5

	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	26	27	28
Glyptoria	0	1	1	1	0	0	0	0	0	4	0	0	1	0	3	0	0	0	2	0	2	0	0	0	0	2	0	4
Nisusia	4	0	2	2	1	1	0	0	0	1	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0
Pompeckium	0	1	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	2	3	0	0	0	1	0	0	0	0	2
Leioria	0	1	1	1	0	0	0	0	0	5	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1
Wimanella	0	0	1	1	0	0	0	0	0	4	0	0	1	0	0	0	0	2	1	0	1	0	0	1	1	2	0	0
Bohemiella	0, 3	0	1	1	0	0	0	0	0	4	0	0	1	0	0	0	0	1	1	1	1	0	1	1	0	1	0	4
Eoorthis	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	1	1	0	1	0	1	1	1	0	0	1
Euorthisina	0	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	4	1	0	1	3	0	0	5
Protorthisina	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	4	1	0	1	3	0	0	5
Giraldiella	1	1	0	0	0	0	0	0	0	1	0	0	1	2	0	0	0	0	0	0	1	0	1	1	1	0	0	1
Radkeina	0	1	0	1	0	0	0	0	0	1	0	0	1	2	1	0	3	1	0	0	2	0	1	1	1	2	0	1
Plectotrophia	0	1	0	1	0	0	0	0	0	2	0	0	1	1	0	1	1	1	0	0	2	0	1	1	1	2	0	1
Huenella	2	1	1	1	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	2	0	0	1	1	2	0	1
Jivinella	0	1	1	1	0	0	0	0	0	1	0	0	1	1	0	1	1	?	?	?	2	0	1	1	0	?	0	2
Medessia	0	1	0	1	0	0	0	0	0	2	0	0	1	2	0	1	0	1	3	0	2	0	1	1	1	1	0	3
Anomalorthis	0	1	2	1	0	0	0	0	0	2	0	0	1	2	0	1	1	0	3	0	2	0	1	1	1	1	0	3
Astraborthis	0	1	0	1	0	0	0	0	0	1	0	0	1	2	0	1	1	1	0	0	3	0	1	1	1	1	0	3
Kvania	0	0	0	1	0	0	0	0	0	1	0	0	1	2	0	0	0	1	0	0	3	0	0	1	1	1	0	1
Finkelnburgia	0	0	0	1	0	0	0	0	0	2	0	0	1	2	0	1	1	1	3	3	3	0	0	1	0	2	0	1
Arctohedra	4	0	2	2	0	0	0	0	0	1	0	0	1	0	3	0	0	0	1	0	2	0	1	1	1	1	0	0
Roanella	0	0	1	1	1	0	1	0	0	1	?	0	1	0	0	0	0	0	1	0	2	0	1	1	1	0	0	0
Apomatella	4	0	2	2	1	0	0	1	1	1	0	0	1	0	1	0	3	1	1	0	2	0	1	1	1	1	0	0
Atelelasma	0	0	1	1	1	0	0	1	1	1	0	1	1	0	1	0	3	1	1	1	2	0	1	1	1	1	0	0
Gonambonites	0	0	1	1	1	0	1	0	2	2	1	0	1	2	1	0	3	1	0	0	2	0	1	1	1	2	1	0
Estlandia	1	0	1	1	1	0	1	0	2	2	1	1	1	0	2	0	3	1	1	1	2	0	1	1	2	1	1	0
Vellamo	4	0	2	1	1	0	1	0	2	1	0	1	1	2	1	0	3	1	2	1	2	0	1	1	1	1	1	0
Clitambonites	4	0	2	2	1	0	1	0	2	1	1	1	1	0	1	0	3	2	2	1	2	0	1	1	1	1	1	0
Clinambon	4	1	2	2	1	0	1	0	2	1	1	1	1	0	1	0	3	2	0	1	2	0	1	1	2	1	1	0
Saccogonum	1	0	1	1	1	1	0	0	0	2	0	0	1	0	0	0	1	2	1	0	2	0	1	1	1	1	0	0
Billingsella	0,3	0	2	0	1	1	0	0	1	2	0	0	1	0	0	0	0	2	1	2	2	0	1	1	1	1	0	0
Kozhuchinella	3	0	1	1	1	1	0	0	2	3	0	0	1	1	0	0	0	1	3	2	2	0	1	1	1	1	1	0
Chaniella	1	0	1	1	1	0	0	1	1	3	0	0	1	1	0	1	1	2	1,2	1	2	0	1	2	1	1	1	0
Korinevskia	1	0	2	0	1	1	0	0	2	4	0	0	1	1	0	0	1	2	1	1	2	0	1	2	2	2	0	0
Protambonites	1	0	2	0	1	1	0	0	2	4	0	0	1	1	0	0	1	2	2	1	2	0	1	2	1	2	0	0
Martellia	0	1	2	1	1	1	0	0	2	2	0	0	1	2	0	1	1	1	1	1	2	0	1	2	4	2	1	0
Pomatotrema	0, 3	0	2	1	1	1	0	0	2	1	0	1	1	2	0	1	2	1	1	1	2	0	1	2	4	2	1	0
Eremotoechia	2	0	1	1	1	1	0	0	2	2	0	0	1	2	0	1	0	1	0	0	2	0	2	2	0	2	0	0
Tritoechia	0, 4	0	2	1	1	1	0	0	1	2, 3	0	1	1	2	0	1	1	1	2	1	2	0	1	2	4	2	0	0
Antigonambonites	1	0	2	1	1	1	0	0	1	2	1	0	1	2	0	1	0	1	2	1	2	0	1	1	4	2	1	0
Polytoechia	4	1	2	1	1	1	0	0	1	2	0	0	1	2	0	1	3	1	2	0	2	0	1	2	4	2	0	0