Palaeontology The Palaeontological Association www.palass.org

[Palaeontology, Vol. 60, Part 5, 2017, pp. 609–631]

FRONTIERS IN PALAEONTOLOGY

BRACHIOPODS: ORIGIN AND EARLY HISTORY

by DAVID A. T. HARPER[1,2], LEONID E. POPOV[3] *and* LARS E. HOLMER[4,5]

[1]Palaeoecosystems Group, Department of Earth Sciences, Durham University, Durham, DH1 3LE, UK; david.harper@durham.ac.uk
[2]Department of Geology, Lund University, Sölvegatan 2, Lund, 223 62, Sweden; david.harper@geol.lu.se
[3]Department of Geology, National Museum of Wales, Cathays Park, Cardiff, CF10 3NP, UK
[4]Department of Earth Sciences (Palaeobiology), Geocentrum, Uppsala University, Uppsala, 752 36, Sweden; lars.holmer@pal.uu.se
[5]Early Life Institute & Department of Geology, State Key Laboratory for Continental Dynamics, Northwest University, Xi'an, 710069, China

Typescript received 21 September 2016; accepted in revised form 10 May 2017

Abstract: Despite many major advances in recent years, three key challenges remain in bringing clarity to the early history of the phylum: (1) identifying the origin, morphology and life modes of the first brachiopods; (2) understanding the relationships of the major groups to each other and higher sister taxa; and (3) unravelling the roles of the Cambrian and Ordovician radiations that set the agenda for much of subsequent brachiopod evolution. Since some 95% of all brachiopod taxa are extinct, the fossil record is the primary source of data to frame and test models for the evolution of the phylum. The acquisition of new, and the redescription of existing faunas, in precise spatial and temporal frameworks, using new and well-established analytical and investigative techniques, are as important as ever.

Key words: brachiopod, Cambrian, Ordovician, phylogeny, diversity.

OUR current understanding of the Cambrian origin and early history of the brachiopods is far from complete; nonetheless the Brachiopoda provides a rich source of data for addressing major research questions relevant to their evolution and that of other invertebrate phyla. Although the monophyletic Brachiopoda remains firmly placed amongst the lophotrochozoan protostomes, the detailed internal topology of the brachiopod clade and its putative sister taxa have advanced significantly since the benchmark analysis of Williams *et al.* (1996). In particular, the revised brachiopod *Treatise* volumes (part H, volumes 1–6, 1997–2007; see also Carlson 2016) still represent a comprehensive and detailed snapshot of research on and across the phylum. This snapshot, however, has been complemented by recent discoveries of both exceptionally-preserved and skeletal stem group taxa within the time-frame of the Cambrian Explosion, and commonly associated with Lagerstätten, prompting a more detailed picture of the basal-most taxa on the brachiopod tree (Zhang *et al.* 2011*a*, *b*, 2013; Zhang & Holmer 2013). There is also a large body of new data which has a bearing on the broad-frame classification of the phylum, established by Williams *et al.* (1996) with subsequent and significant modifications (e.g. Carlson 2016) that merit discussion.

THE EARLY PALAEOZOIC FOSSIL RECORD OF BRACHIOPODS

The brachiopods or lamp-shells are a distinctive and diverse group of marine, mainly sessile, benthic invertebrates with a long and varied geological history dating back to the early Cambrian (Fig. 1A). They are one of the few groups of marine animals, which have an enviably complete fossil record, from the emergence of the earliest skeletonized representatives in the early Cambrian (Terreneuvian) to a sporadic distribution in modern oceans (Ushatinskaya 2008; Clausen *et al.* 2015; Skovsted *et al.* 2015). Over 12 000 fossil species and approximately 350 living species have been reported, belonging to nearly 6000 genera (see e.g. Harper 2005). Significant information on their relatively simple body anatomy can be extracted from their hard parts: a bivalved shell together with skeletonized brachial supports, including impressions of their muscle system, mantle canals, pedicle and other attachment structures, features of the lophophore, and even some features of the nervous system (e.g. pedicle nerve impressions in lingulids; Holmer *et al.* 2016). Detailed studies of the brachiopod shell ultrastructure continue to reveal important details about the early evolution of shell secretion within the phylum (e.g. Williams

© 2017 The Authors.
doi: 10.1111/pala.12307

Palaeontology published by John Wiley & Sons Ltd on behalf of The Palaeontological Association.
This is an open access article under the terms of the Creative Commons Attribution License,
which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

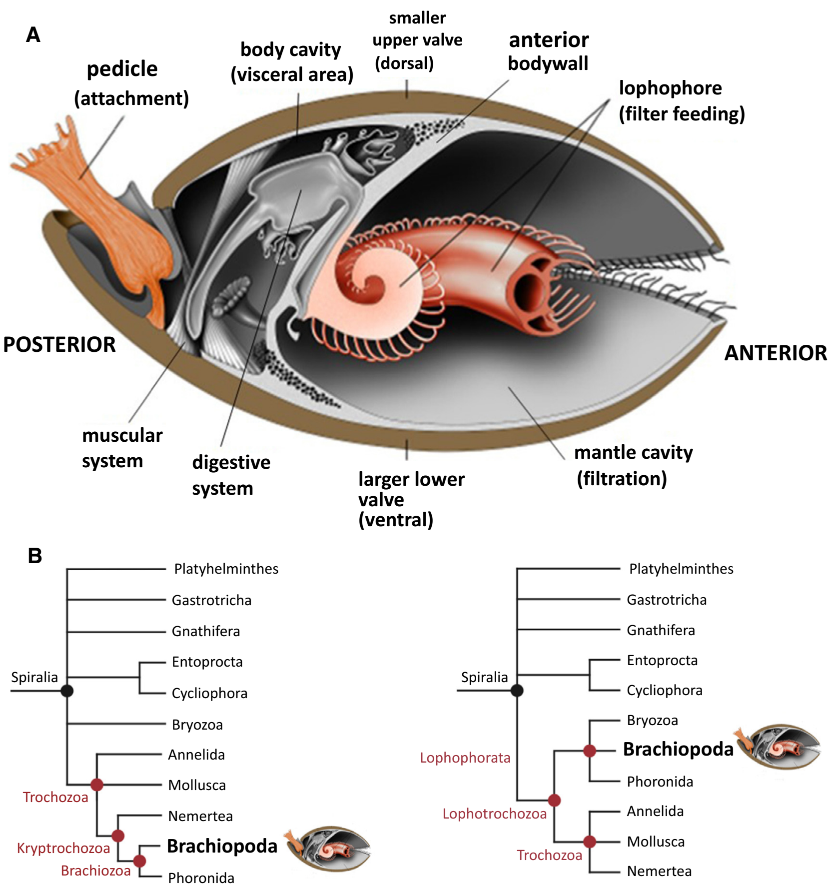


FIG. 1. A, reconstruction of a rhynchonelliform terebratulide brachiopod, cut along the plane of symmetry to reveal internal anatomy (modified from Harper 2005 by Holmer; original drawn by Lisa Belhage, Geological Museum, Copenhagen). B, possible relationships of Brachiopoda to sister phyla, from Hejnol *et al.* 2009 (left) and Nesnidal *et al.* 2013 (right).

& Cusack 2007; Holmer *et al.* 2008*a*). Recent discoveries of exceptionally-preserved specimens with soft parts, which are mostly from the lower Cambrian Chengjiang Konservat Lagerstätte of Kunming, southern China, provide an important window into soft body anatomy of the extinct brachiopod groups, close to the initial divergence of major lineages within the phylum, as well as confirming the early origin of the U-shaped gut and the lingulide-type pedicle in linguliforms (Zhang & Holmer 2013). It has also been possible to infer the existence of lophophore and setal structures in the earliest non-bivalved, stem-group brachiopods (e.g. Holmer *et al.* 2008*b*). Important advances in understanding the early stages of ontogeny in Early Palaeozoic brachiopods have also been made; the preserved protegulum and larval shell in juveniles preserve important information on the possible feeding habit of the larva, timing and characters of metamorphosis, including the number of larval setal sacs, secretion of protegulum at or prior settlement, characters of initial larval attachment and other characters (Freeman & Lundelius 2005; Popov *et al.* 2007*b*, 2009, 2012; Bassett *et al.* 2008). Finally, there has been significant progress in studies of brachiopod molecular phylogeny, although they are still in the pioneering stage, and with sometimes contradictory results (Passamaneck & Halanych 2006; Paps *et al.* 2009; Hausdorf *et al.* 2010; Sperling *et al.* 2011; Nesnidal *et al.* 2013).

RELATIONSHIPS BETWEEN MAJOR BRACHIOPOD GROUPS

Recent brachiopods are distributed across three major groups, which are currently referred to three subphyla: Linguliformea, Craniiformea and Rhynchonelliformea (Williams *et al.* 1996). These subphyla may have split from each other at an early stage in brachiopod evolution, and probably prior to the acquisition of a mineralized shell in the early Cambrian (Gorjansky & Popov 1985, 1986; Ushatinskaya 2008; Holmer *et al.* 2011). In any event, the living representatives of these three major lineages are clearly separated from each other in major aspects of shell morphology, soft-body anatomy and early ontogeny in the early fossil record of the group (Carlson 1991*a*; Popov *et al.* 1993).

The key characteristics of each subphylum are outlined in Table 1. In addition, each possesses a double row of tentacles throughout their ontogeny, which was previously considered to be an apomorphic feature of linguliform brachiopods (Holmer *et al.* 1995; Williams *et al.* 1997).

TABLE 1. Key anatomical characteristics of the three brachiopod subphyla.

Subphylum	Linguliforms	Craniiforms	Rhynchonelliforms
Shell	Organophosphatic; stratiform	Organocalcitic, possibly aragonitic with laminar tabular secondary layer	Calcitic, mainly fibrous, or less commonly, laminar secondary layer
Articulation	Lack of advanced articulatory structures	Generally lacking but with hydraulic shell-opening mechanisms	Well developed with ventral teeth and dorsal sockets
Gut	U-shaped with anterior anus	Axial with posteromedian anus	Blind, lacking anus
Pedicle	Outgrowth from ventral mantle	Lack of pedicle attachment	Developed from posterior lobe of larva
Body wall	Muscular with dermal muscles	Muscles lacking	Muscles lacking
Outer mantle lobes	Without lobate cells	Lacking reversion and delayed	Fused
Gonads	Restricted to body cavity	In mantle canals	Anterior extension of coelom
Larvae	Probably planktotrophic	Lecithotrophic	Lecithotrophic

Based on data from Gorjansky & Popov (1985); Holmer *et al.* (1995); Williams et al. (1996, 1997); Lüter (2001); Nielsen (2005); Balthasar & Butterfield (2009); Popov *et al.* (2009); Zhang *et al.* (2009); see Carlson & Leighton (2001) for similar, earlier summary.

Emig (*in* Zhang *et al.* 2009, fig. 4) demonstrated that a single row of tentacles is present on the trocholoph of the discinid *Pelagodiscus atlanticus*, and thus not a characteristic of only the linguliforms, but most probably plesiomorphic for all groups of the brachiopods. Differences between the three subphyla (Table 1) are apparent by the end of the Ordovician; however, recent studies of Early Palaeozoic brachiopods have revealed a more complex and intricate picture.

A key problem in unravelling the early evolution of major brachiopod clades concerns our understanding of the polarity of morphological characters in phylogenetic analyses. According to some recent molecular studies (e.g. Helmkampf *et al.* 2008; Nesnidal *et al.* 2013, fig. 1) brachiopods are placed at the base of lophotrochozoan clade, while in others they represent the most advanced lophotrochozoans (e.g. Paps *et al.* 2009; Nesnidal *et al.* 2013, fig. 4); thus any attempt at outgroup selection is a fundamental problem and the available choices (e.g. annelids, molluscs, bryozoans and phoronids) will inevitably influence the result, because all of them may be derived in one way or another in relation to the brachiopods (see e.g. Fig. 1B).

BRACHIOPOD PHYLOGENY: AN OVERVIEW

Brachiopods are commonly considered to be a monophyletic group and, for most of the history of their study, a two-fold subdivision into ‘inarticulates’ and ‘articulates’, with an emphasis on the presence or absence of articulatory structures along the hinge, endured (e.g. Carlson 1991*a*). An alternative phylogenetic model, developed by Gorjansky & Popov (1985), proposed a bi-phyletic origin with the lingulates (brachiopods with organophosphatic shells) placed apart from other brachiopod groups (calcareous-shelled ‘inarticulates’ and ‘articulates’). Popov *et al.* (1993) and Holmer *et al.* (1995) indicated that separation of organophosphatic and calcareous shell types does not necessarily require a polyphyletic origin for the brachiopod body plan (but see e.g. Valentine 1977; Wright 1979 for an alternative view and Carlson 1995 for discussion); this was supported by phylogenetic analyses that remarkably recalled the earlier brachiopod phylogenetic analysis published in the pioneering book by Hennig (1966). These data were assimilated and reworked in a later phylogenetic analysis by Williams *et al.* (1996), with the recognition of three brachiopod subphyla, namely Linguliformea, Craniiformea and Rhynchonelliformea; craniiforms and rhynchonelliforms were considered to be sister taxa and the enigmatic chileates as basal rhynchonelliforms (see also discussion in Carlson 2007).

Implications of molecular data

Traditionally brachiopods, together with phoronids and bryozoans (Lophophorata *sensu* Hyman 1959), were considered to be the sister group of the Deuterostomia. However, with progress in phylogenetic molecular studies, most analyses currently place lophophorate phyla close to the trochozoan clades, firmly establishing the monophyly of the Lophotrochozoa (for more details see Telford 2006; Nesnidal *et al.* 2014). As discussed below, however, the precise phylogenetic position of the various lophophorate clades, including the brachiopods, remains controversial.

The most comprehensive (ribosomally-based) analyses of lophophorate and brachiopod molecular phylogeny, in terms of the number of species sequenced, have been published by Cohen (2000, 2013) and Cohen & Weydmann (2005). In their earlier analyses, trees were rooted in either the chiton *Acanthopleura* (Cohen *et al.* 1998; Santagata & Cohen 2009) or more distantly in the sponge

Clathrina (Cohen 2000); their results consistently placed phoronids as an ingroup within the brachiopods. Cohen (2013) favoured a molecular clock-based rooting of potential ingroup taxa. The outcome also positions phoronids as an ingroup within brachiopods, while craniiforms and linguliforms combined emerge as a sister group of the phoronids. Moreover, discinids appeared to form a sister group of the craniides, which is in strong contradiction with available morphological and ontogenetic data.

Sperling *et al.* (2011), however, correctly pointed out that alternative morphological and molecular (ribosomally-based) phylogenies have similar topologies, but differ in rooting; they tested the monophyly of brachiopods using a combined set of seven nuclear housekeeping genes plus three ribosomal subunits (5.8S, 18S, 28S rDNA) as well as analysing the distribution of specific-microRNA (miRNA) genes. The combined analysis (Sperling *et al.* 2011, fig. 2A) supported brachiopods and phoronids as sister groups, with the monophyly of brachiopods moderately supported (posterior probability of 0.82) and placed craniiforms at the base of the brachiopod clade. It was also noted that analyses of 'homogeneous sites only' and 'heterogeneous sites only' datasets resulted in different topologies and position of the root, with the latter supporting brachiopod paraphyly with phoronids appearing as a sister-group of craniides. Moreover, Sperling *et al.* (2011) demonstrated that the brachiopod-specific microRNAs favoured brachiopod monophyly, and their absence in phoronids cannot be readily explained by loss of morphological characters. This conclusion, however, was challenged by Cohen (2013, p. 89). Regarding brachiopod interrelationships, Sperling *et al.* (2011) grouped craniiforms and linguliforms into a single cluster, but as discinids were not included in their analyses, the result remains inconclusive. Nevertheless, Sperling *et al.* (2011) acknowledged that in 'molecular phylogenetic analyses, the craniides behave as a 'rogue taxon' with little statistical resolution at the base of Brachiopoda'.

In the outcomes of the analysis of nuclear-encoded housekeeping genes presented by Helmkampf *et al.* (2008, figs 2, 3), brachiopods, represented by craniiforms and rhynchonelliforms, are placed at the base of lophotrochozoan clade, as a sister group of all other lophotrochozoans; bryozoans and phoronids share a common ancestry with annelids and molluscs. Thus, lophophorates appear to be paraphyletic. Data on linguliforms (lingulids and discinids) were not part of that analysis; it is thus of little help in resolving phylogenetic relationships within the Brachiopoda.

Lophotrochozoan phylogeny assessed using LSU (large subunit) and SSU (small subunit) data (Passamaneck & Halanych 2006) indicates that the lophophorates and brachiopods (including rhynchonelliforms, craniiforms and linguliforms) in particular, exhibit extreme polyphyly. Cohen (2013), however, noted that the sequence of *Novocrania* (= *Neocrania*) used by Passamaneck & Halanych (2006) may in fact belong to the polychaete *Chaetopterus* which introduces a source of some considerable confusion.

The analyses by Nesnidal *et al.* (2013, 2014) have re-introduced support for the Lophophorata as a monophyletic clade, and moreover suggested sister-group relationships with bryozoans and phoronids. Nesnidal *et al.* (2013, 2014) also supported Lophophorata as a sister group of the Nemertea, together forming a sister group to the Annelida. They are thus derived in relation to molluscs and imply that lophophorates evolved from ancestors with a trochophoran larva. Nesnidal *et al.* (2013, 2014) have also claimed that brachiopods are distinctly separate from phoronids, in contrast to other phylogenetic analyses (e.g. Cohen & Weydmann 2005; Cohen 2013). However, the linguliform taxa (e.g. extant lingulids and discinids) were not included. Thus, while the clear separation of phoronids from craniiforms and rhynchonelliform brachiopods is justified, the phylogenetic relation of that group to linguliforms remained unresolved in the molecular phylogeny presented by Nesnidal *et al.* (2014).

Investigation of the role of hox gene clusters (Schiemann *et al.* 2017) suggests that the hard tissues of the annelids, brachiopods and molluscs (i.e. the chaetae and shells) share a common origin dating back to the early Cambrian. This implies that *Wiwaxia* belongs to the lophotrochozoan stem (see also Smith 2014), although the latter taxon possesses distinctly molluscan characters. In these analyses, it is significant that the phoronids are presented as a sister group to the phylum Brachiopoda.

In summary, molecular data show good support for lophotrochozoan monophyly, with the identification of some key novelties, but neither the position of the brachiopods in relation to other phyla within the lophotrochozoan clade, nor the interrelationships between the three major brachiopod subphyla can be resolved with any certainty. The current state of flux in lophotrochozoan molecular phylogeny was predicted by Nielsen (2002), who concluded that based on the 18S rDNA gene sequences, only the branch leading to the Deuterostomia in strict sense can be recognized; the sequence of older speciation events within lophotrochozoan phyla cannot be convincingly resolved at present.

Possible brachiopod stem and sister groups

Although data from embryology and comparative anatomy have been used in support of lophophorate polyphyly, with brachiopods placed as a sister-group of the deuterostomes (Lüter 2001; Nielsen 2002), rapidly accumulating molecular data (discussed above) now firmly support the position of brachiopods within the lophotrochozoan clade (Fig. 1B). Nevertheless, the monophyletic nature of the Lophophorata, which has been placed in doubt by some earlier studies (e.g. Halanych *et al*. 1995; Lüter 2001; Paps *et al*. 2009), finds some support in published studies on molecular phylogeny (e.g. Nesnidal *et al*. 2013, 2014) and more traditional comparative anatomic studies (Temereva & Tsitrin 2015). It implies that the lophophores in brachiopods, phoronids and bryozoans are homologous, and probably the only recognizable synapomorphy for the group. Moreover, new evidence from exceptionally-preserved specimens from the middle Cambrian Burgess Shale and Spence Shale suggests that the hyoliths too may be members of this clade (Moysiuk *et al*. 2017). However, the phylogenetic relationships of brachiopods with ectoproct bryozoans remain controversial (Nielsen 2001, 2002, 2005).

The phoronids have frequently been considered to be a sister group of brachiopods (e.g. Peterson & Eernisse 2001; Sperling *et al*. 2011) while recent analysis by Nesnidal *et al*. (2014) has suggested a closer relationship to ectoproct bryozoans. In contrast (as discussed above) Cohen (2000, 2013) and Cohen & Weydmann (2005) have persistently argued that phoronids form an ingroup within Brachiopoda, and this view was supported by Balthasar & Butterfield (2009); the latter argued that the soft-shelled early Cambrian lingulide *Lingulosacculus nuda* Balthasar & Butterfield, could be interpreted as secondary loss of mineralization in some lingulates and as a possible brachiopod link to the phoronids. However, *Lingulosacculus nuda* is from the upper *Nevadella* Biozone (transition from Cambrian Stage 2 to Stage 3) which would make it among the oldest yet recorded lingulate brachiopods. Existing records of the earliest occurrences of lingulates (excluding the paterinates) in Siberia, Kazakhstan, South China and Baltica are well established in the lower Cambrian Stage 3 (Holmer & Popov 2000; Zhang *et al*. 2015), while reports of the occurrence of lingulides in the upper *Judomia* Biozone of Siberia are poorly documented and require confirmation (Bassett *et al*. 1999; Ushatinskaya 2008). *Lingulosacculus* may on the other hand represent a ‘pre-mineralized’ shell condition in the lingulellotretides, but it is more likely that the shell of *Lingulosacculus* was ‘loosely’ mineralized, as manifest in mickwitziids and some siphonotretides (Skovsted & Holmer 2003; Holmer & Caron 2006). The earliest lingulate assemblages from the Cambrian Stage 3 show significant morphological diversity, suggesting earlier divergence, which probably occurred before development of a strongly phosphatized shell (Popov 1992, p. 419; Ushatinskaya 2008).

Thus, the position of brachiopods within the lophotrochozoan clade cannot be determined with any accuracy (see Fig. 1B). With the exception of phoronids, there is no other lophotrochozoan group that can be nominated as a stable outgroup for phylogenetic analyses; moreover, the position of phoronids in relation to brachiopods remains controversial. Nielsen (2005, p. 439) noted that the trochophore larva represents an important character, which most probably evolved only once; it is also supported by cell-lineage studies (Nielsen 2012). This indicates that brachiopods and phoronids together form sister groups at the base of all other lophotrochozoan phyla. Another common feature of the phylum is the radial cleavage pattern, which may confirm the close relationship between brachiopods and phoronids or represent a plesiomorphic state. Nielsen (2002, p. 44) stated that ‘although traces of spiral pattern have been reported by a few authors it is now agreed that cleavage is radial’. Thus, ‘secondary’ references to the presence of a spiral cleavage pattern in phoronids (e.g. Nesnidal *et al*. 2013) are probably erroneous.

THE FIRST BRACHIOPODS

Can we predict the morphology and life mode of the first brachiopod? There is a view that the sessile mode of life in the lophophorates is a secondary adaptation which evolved from a vagile, ‘slug-like’ life style (e.g. Nesnidal *et al*. 2014); but this view is not conclusively supported by either the general anatomical and morphological organization of the animal (i.e. having a lophophore rather than a foot) or by the available data from the palaeontological record. In fact, a ‘tubular’ sessile life habit may be primitive within the lophotrochozoans (e.g. Zhang *et al*. 2013, 2014; Zhuravlev *et al*. 2015). Strong palaeontological support for this hypothesis is provided by the uniquely well-preserved tubular fossil *Yuganotheca* Zhang, Li & Holmer *in* Zhang *et al*., 2014 from the Cambrian Stage 3 Chengjiang Lagerstätte (Yunnan, China) that exhibits an unusual combination of phoronid and brachiopod characters, notably a pair of agglutinated valves, enclosing a horseshoe-shaped lophophore, supported by a lower bipartite tubular attachment structure with a long pedicle (Zhang *et al*. 2014). *Yuganotheca* was placed phylogenetically as a sister group to organophosphatic taxa (Fig. 2). Apart from indicating the rooting of brachiopods into the sessile lophotrochozoan *Yuganotheca*, this taxon also suggests that the origination of the brachiopod twin-shelled Bauplan preceded the biomineralization of bivalved shells in crown-group brachiopods (Zhang *et al*. 2014). The lophophore anatomy of *Yuganotheca* also indicates that it may not have had a real brachiopod-like, laminar filter-feeding

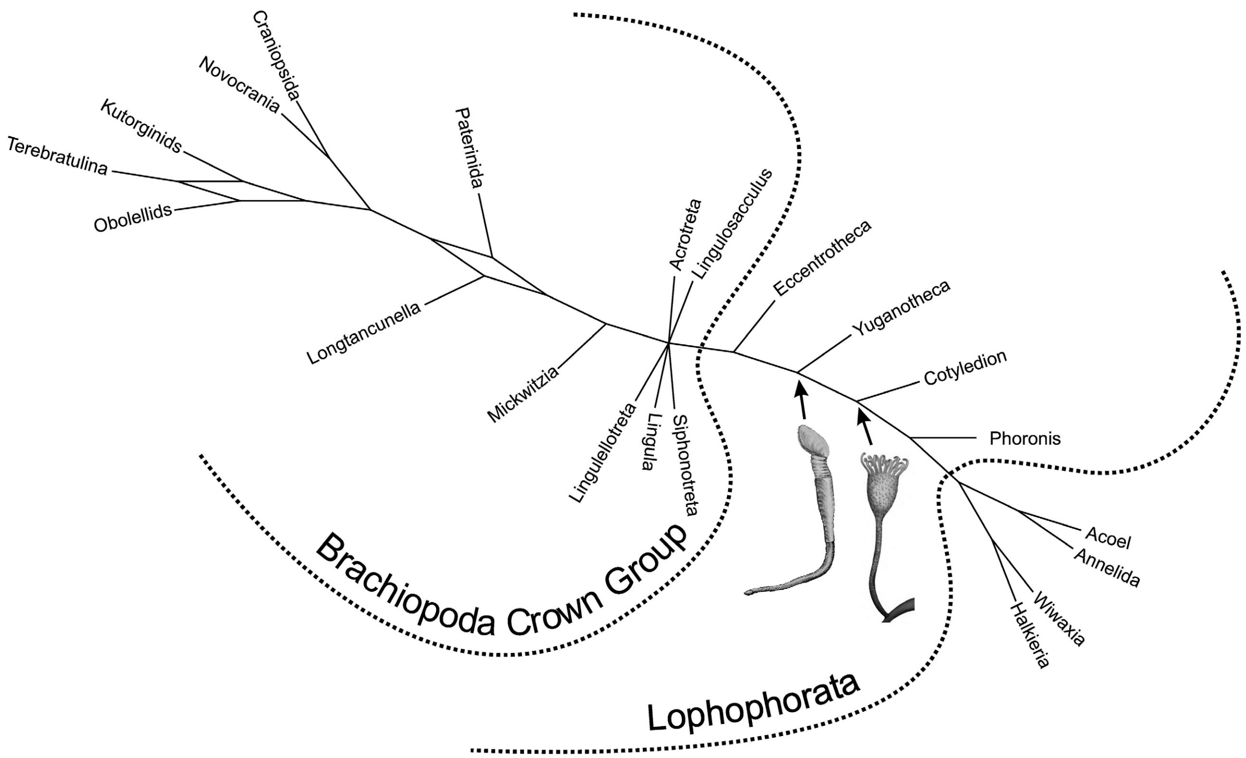


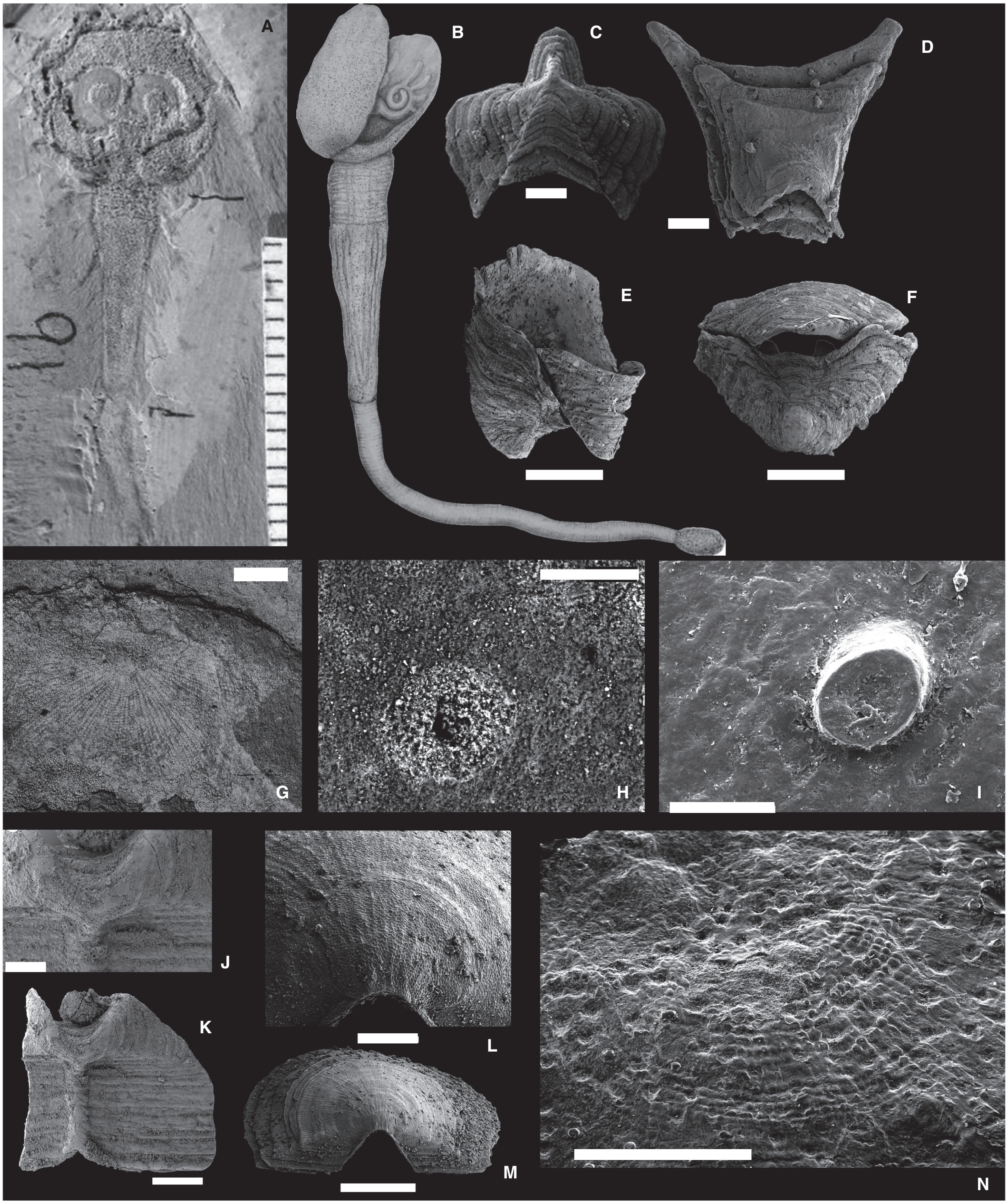
FIG. 2. Stem groups and relationships to crown taxa (From Zhang *et al.* 2014); see Figure 3 for illustrations of key taxa.

organ, directed laterally through the lophophore as in all living brachiopods, but rather had a more phoronid-like filtration system with the current directed towards the mouth (Fig. 3). The more expansive hypothesis of the relationships between crown-group brachiopods and the tommotiids (e.g. Holmer *et al.* 2011) has been criticized on the basis of its dependence, in part at least, on a brachiopod construct (Murdock *et al.* 2014). Thus, in the opinion of Murdock *et al.* (2014), the specialization of sclerites with paired sclerite associations surrounding attachment organ, the presence of setal tubes and a closed filtration chamber are all assumptions generated by adherence to and an expectation of the brachiopod bauplan. The phylogeny presented is a hypothesis and, although there is paucity of data, Murdock *et al.* (2014) do not necessarily falsify it, merely urge caution in the analysis of incomplete data sets.

Some of the key characters of the tommotiid-brachiopod hypothesis that were questioned by Murdock *et al.* (2014) have now been supported by further

FIG. 3. Key brachiopod taxa associated with the brachiopod stem; see Figure 2. A–B, *Yuganotheca elegans* Zhang *et al.*, early Cambrian Chengjiang Lagerstätte, Yunnan, China. A, holotype ELI BLW-0091, showing the elongate tubular body with agglutinated dorso-ventral valves, lower conical tube from which the linguloid-like pedicle emerges (mm scale bar); B, reconstruction (Zhang *et al.* 2014). C–D, *Paterimitra pyramidalis* Laurie, early Cambrian Arrowie Basin, Flinders Ranges, South Australia; C, SAMP46315, 'ventral' (S2) sclerite; D, SAM P46319, 'dorsal' (S1) sclerite (Holmer *et al.* 2011). E–F, *Micrina etheridgei* (Tate), early Cambrian Todd River Dolostone, Northern Territory, Australia; E, CPC39703, 39704, lateral view of artificially produced bivalved scleritome with conjoined 'ventral' (mitral) and 'dorsal' (sellate) sclerites; F, posterior view of artificially conjoined valves; (Holmer *et al.* 2008*b*). G–H, *Heliomedusa orienta* Sun & Hou, NIGP11, early Cambrian Yu'anshan Formation, Chengjiang Lagerstätte, South China; G, apex of dorsal valve exterior, showing delineated juvenile shell, with rows of pustules; H, detail of one canal showing wall and central canal, width may have been enlarged during taphonomy; (Holmer & Popov 2000). I, N, *Mickwitzia monilifera* (Linnarsson), RMBr1609, early Cambrian File Haidar Formation (Mickwitzia beds), Västergötland; I, detail of one canal showing wall and central canal; N, juvenile partly exfoliated ventral exterior showing pustulose ornamentation; (Holmer & Popov 2000). J–K, *Salanygolina obliqua* Ushatinskaya, early Cambrian, Salany-Gol, Mongolia, PMU25065; J, detail of ventral umbo, showing larval shell; K, posterior view of ventral exterior, showing colleplax, pseudodeltidium and delthyrial opening. L–M, *Askepasma toddense* Laurie, early Cambrian Ajax Limestone, Mount Scott Range, South Australia, SAM P47072; L, detail of ventral larval shell, scale bar 0.5 mm; M, ventral valve, scale bar 1 mm (Topper *et al.* 2013). Scale bars represent: 0.1 mm (C, D); 0.5 mm (E–G, L, M); 0.05 mm (H, I); 0.2 mm (J, K); 1 mm (N).

evidence. Notably, the presence of exceptionally-preserved phosphatized setae within the setal canals of the tommotiid *Micrina* (Butler 2015) has now been demonstrated. These setal structures are identical to the setal canals and exceptionally preserved setae in mickwitziid brachiopods, including *Mickwitzia* and *Heliomedusa* from the lower Cambrian of Baltica and China, respectively, and the shell structure of the mickwitziids also includes columns that are closely similar to the columnar shell structure of both *Micrina* and more derived



linguliform brachiopods (Fig. 3G–I, N; Holmer & Popov 2007; Holmer *et al.* 2008*a*; Butler 2015). A similar shell structure with setal canals, indicating a homology with those of *Micrina* and *Setatella*, within the brachiopod stem has been described in early Cambrian *Oymurania* (Kouchinsky & Bengtson 2017). Moreover, no alternative reconstruction of the clearly bi-membrate scleritome has been proposed, for example, for *Micrina* (Fig. 3E, F; Holmer *in* Holmer *et al.* 2008*a*) and both *Micrina* and *Paterimitra* also possess a brachiopod-like, bivalved larval shell that in the latter taxon includes the odd colleplax-plate covering a triangular anterior notch in the larval shell; this is identical in growth and morphology to the colleplax found in, for example, the enigmatic brachiopod *Salanygolina* (Fig. 3J, K; Holmer *et al.* 2009, 2011; see also below). Furthermore, the mode of skeletal secretion in tommotiids and brachiopods is identical to the point where fragments of *Paterimitra* and the paterinate *Askepasma* (Fig. 3L, M) cannot be distinguished from each other (Balthasar *et al.* 2009).

Halkieria-like, possible lophotrochozoan ancestors (Conway Morris & Peel 1995) have been invoked as palaeontological support for an early origin of a vagile, slug-like lophophorate life style, with *Halkieria* interpreted as a stem group of annelids plus brachiopods. *Halkieria* has been subsequently assigned to the molluscs and considered to be representative of the separate class Diplacophora, which may itself have a sister-group relationship with Polyplacophora (Vinther & Nielsen 2005). Moreover, the position of the slug-like *Halkieria* within the Mollusca has been recently further strengthened by studies of a broadly similar taxon from the Ordovician of Morocco, better contextualising their morphology and life modes (Vinther *et al.* 2017).

The view that a sessile life style may be primitive for the lophophorates is further supported by the fact that the gymnolaemate bryozoans, as well as rhynchonelliform and craniiform brachiopods, completely lack a muscular body wall, while the lingulates, phylactolaemate bryozoans as well as phoronids have well developed dermal muscles (Hyman 1959; Holmer *et al.* 1995; Schwaha & Wanninger 2012). If we assume that the absence of dermal muscles is a plesiomorphic feature, while the body wall musculature evolved convergently in the derived groups of those phyla, an ancestry of the lophophorates from vagile lophotrochozoans looks extremely unlikely. As convincingly demonstrated by Nielsen (2005), it is most likely that the trochophore larva evolved just once and may represent a key synapomorphy within lophotrochozoans. Thus the secondary loss of this larval type in the lophotrochozoans (Nesnidal *et al.* 2014), secondary loss of the dermal muscles in selected groups of bryozoans and gymnolaemates, and loss of the trochozoan coelom (involving the 4d-cell and a spiral cleavage; Lüter 2000) appear extremely unlikely. Instead we strongly support lophophorates as an early lophotrochozoan offshoot, or as a paraphyletic branch from stem-group lophotrochozoans.

EARLY PALAEOZOIC RADIATION OF THE BRACHIOPODA

Three major events dominated the diversity and evolution of the Early Palaeozoic Brachiopoda: The Cambrian Explosion, the Great Ordovician Biodiversification Event and the end Ordovician Extinction.

The Cambrian explosion and Cambrian Evolutionary Fauna

Cambrian faunas were dominated by a range of nonarticulated groups, together with groups of disparate articulated taxa, such as the chileates, naukatides, obolellides, kutorginides, billingsellides, protorthides (Fig. 4), orthides and pentamerides (Fig. 5). These groups participated in a variety of loosely-structured, nearshore palaeocommunities but with a clear partition between shallow-water carbonate and siliclastic environments characterized by higher proportions of rhynchonelliforms, and deeper-water finer-grained deposits, often dysoxic, commonly with linguliforms. Key evidence has been extracted from some of the early–mid Cambrian Lagerstätten, preserving not only a diversity of form but also exquisite anatomical features (see below). By the early Cambrian, the phylum had already evolved a spectrum of life styles (Topper *et al.* 2015) exploiting its diversity across a variety of ecological niches. In fact, most of the key life modes had been established prior to the Great Ordovician Biodiversification Event (Topper *et al.* in press). Challenges, however, exist in understanding the relationships between the individual groups near the base of the stem, particularly in clarifying the relationships between and within the tommotiids.

Origin and early history of the linguliforms

Subphylum Linguliformea, as presently defined (Williams *et al.* 1996), includes all brachiopods with organophosphatic mineralized shells, and is subdivided into two classes. One of these, the short-lived Paterinata, includes the oldest known brachiopods, which appeared at the base of the Cambrian Stage 2 (*Aldanocyathus sunnaginicus* Biozone) in Siberia (Pelman *et al.* 1992) and vanished during the Hirnantian Mass Extinction Event at the end of the Ordovician (Harper *et al.* 2014). The second, Lingulata, appeared late in Cambrian Stage 2 and can still be found in Recent seas. The linguliforms represent an important component of the Cambrian Evolutionary Fauna and, by the beginning of the Ordovician, they show remarkable ecological expansion extending from near-shore to basinal environments. They often occur in benthic assemblages from marine marginal environments such as eutrophic basins, mobile sands in shore-face zones, and as pioneers of the abyssal depths associated with hexactinellide sponges and pterobranchs (Bassett *et al.* 1999; Tolmacheva *et al.* 2004).

While separation of lingulates from craniiforms and rhynchonelliforms is robust, paterinates display a mosaic combination of characters, also typical of chileates and rhynchonellates (Williams *et al.* 1996, 1998; Holmer *et al.* 2011). The group is probably polyphyletic, rooted in different taxa of the stem group brachiopods. The lingulates share features such as a canaliculated condition of the stratiform shell, a mantle permeated by the intermedial and marginal *vascula terminalia*, gonads confined exclusively to the body cavity, outer mantle lobes without lobate cells, whereas a single subenteric gangliation is plesiomorphic for the clade (Holmer *et al.* 1995; Williams *et al.* 1996). A U-shaped alimentary canal with the anteriorly placed anus and a pedicle developed as the ventral mantle outgrowth with the extension of the coelomic cavity as a core is present even in the earliest lingulates from the Chengjiang Konservat Lagerstätte (Zhang & Holmer 2013), although they have a muscular body wall unlike rhynchonelliforms and craniiforms; however, these features are also present in the phoronids and may represent plesiomorphic characters evolved in some stem-group brachiopods. The paterinates, unlike lingulates, are characterized by a mantle canal system including gonad sacs and with exclusively marginal *vascula terminalia*, grouped posteromedially-located adductor muscle scars in both valves, and a strophic shell probably fused along the hinge by the strip of periostracum. All these features also occur in the rhynchonelliforms (Williams *et al.* 1996, 1998).

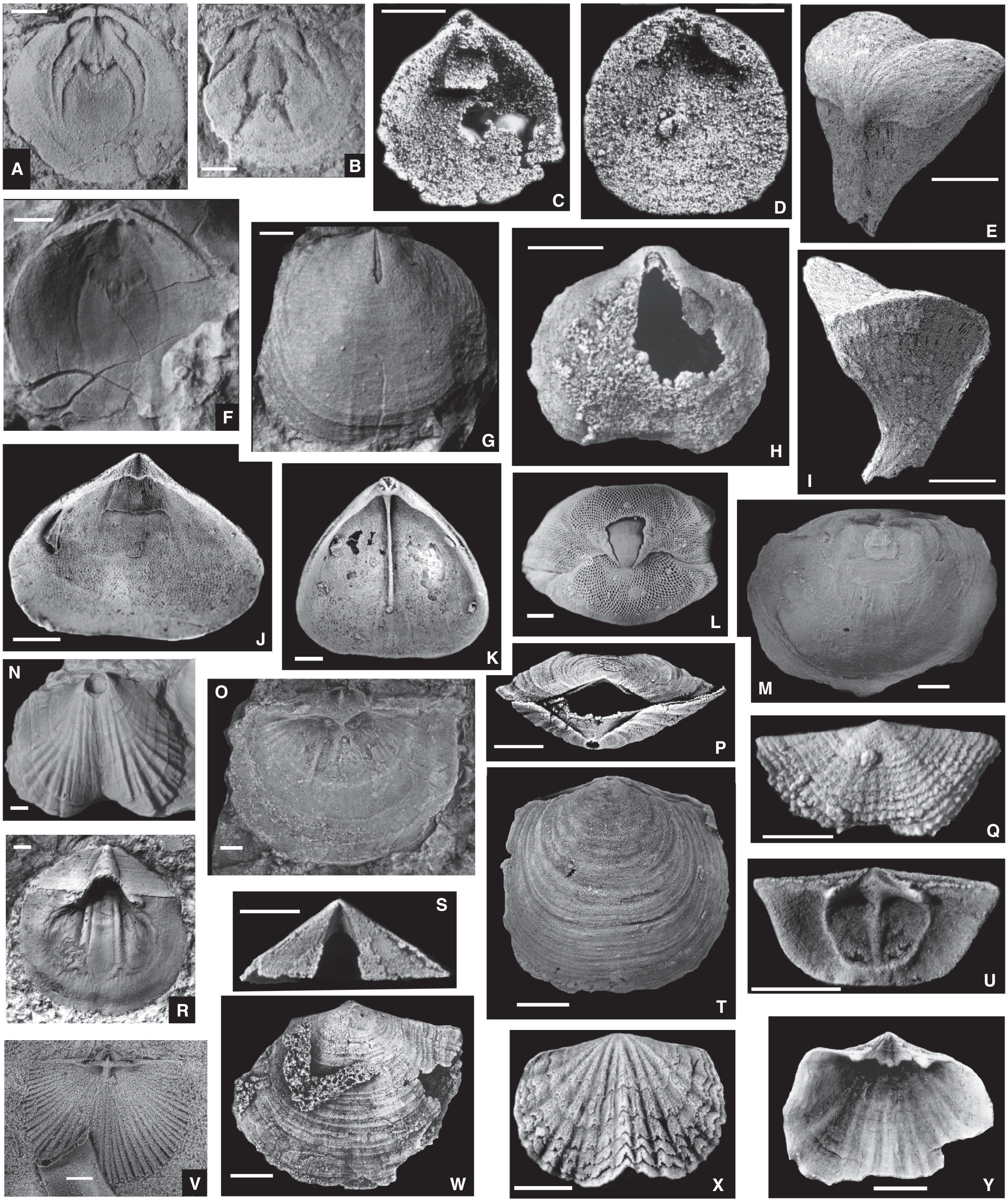
The earliest lingulates exhibit considerable morphological disparity (Bassett *et al.* 1999); they had already acquired a conveyor-belt system for shell secretion, which probably evolved at the 'pre-mineralized' state. By contrast, the earliest paterinates (e.g. *Askepasma*, *Pelmanotreta* and *Solanygolina*) exhibit a simple 'stacking' pattern of mineralized shell secretion, probably, predating the origin of the conveyor-belt system, which first became evident only within the family Paterinidae (Williams *et al.* 1998), although the canaliculated condition, characteristic of lingulates, did not evolve within the paterinates.

The Great Ordovician Biodiversification Event

During the Ordovician, the craniiforms diversified with the craniopsides and trimerellides appearing for the first time. Within the rhynchonelliforms, two major clades, the rhynchonellates and strophomenates, have been identified within the broad-frame classification of the phylum (Williams *et al.* 1996). Two types of dentition, the simple deltidiodont and the more complex cyrtomatodont, are both phylogenetically and ecologically significant (Jaanusson 1971). Within the two rhynchonelliform subclasses, a laminar secondary shell layer characterizes many of the strophomenates whereas a fibrous secondary layer typifies the rhynchonellates. During the Ordovician radiation, the deltidiodont orthides and strophomenides dominated faunas. Many taxa were first generated around Early–Middle Ordovician island complexes (Neuman 1984; Bruton & Harper 1985) and later dominated the platforms, where they participated in an offshore movement of palaeocommunities (Rong *et al.* 1999; Bassett *et al.* 2002) and the occupation of carbonate mudmound and reef structures (Harper *et al.* 2004; Harper 2006); the latter environments became progressively occupied by the cyrtomatodont athyridides, atrypides and rhynchonellides. By the end of the Ordovician the majority of shell morphologies, excluding perhaps oyster-like forms exemplified by the bizarre Permian lyttonioids, had evolved occupying a wide variety of niches on the seabed. The expansion of the subphylum was evident with increased α-diversity as more species were packed into communities, β-diversity as communities expanded offshore and into carbonate structures and γ-diversity as the fragmentation of provinces, particularly during the Early–Middle Ordovician (Harper *et al.* 2013), drove allopatric speciation (Harper 2006, 2010). Following the end Ordovician extinction event, spire-bearing brachiopods reached their dominance, particularly in the carbonate environments of the mid-Palaeozoic (Harper & Rong 2001); the strophomenates lost their dominance.

Origin and early history of the craniiforms

The Craniiformea is a small, but distinctive group of calcareous-shelled nonarticulated brachiopods, which emerged early in the Ordovician as a minor component of the Palaeozoic Evolutionary Fauna (Popov *et al.* 2013*a*). They reached maximum morphological disparity in the Late Ordovician and Silurian, where they are represented by three orders: Craniida, Craniopsida and Trimerellida (Fig. 5A-C). Only the craniides survived through all five major extinctions and can be found in modern oceans. While the monophyly of craniiforms is presently well defined (Gorjansky & Popov 1985, 1986; Holmer *et al.* 1995; Popov *et al.* 1996, 2007*a*), their relationship to other major brachiopod clades remains controversial. Recent attempts to root craniiforms in some Cambrian taxa have failed. The enigmatic *Heliomedusa* from the early Cambrian Chengjiang Lagerstätte, Yunnan Province, earlier thought to be the ancestral craniopside (Popov *et al.* 2000*a*; Zhang *et al.* 2003) is now placed near *Mickwitzia* within the brachiopod stem (Holmer & Popov 2007; Zhang & Holmer 2013). The brachiopod



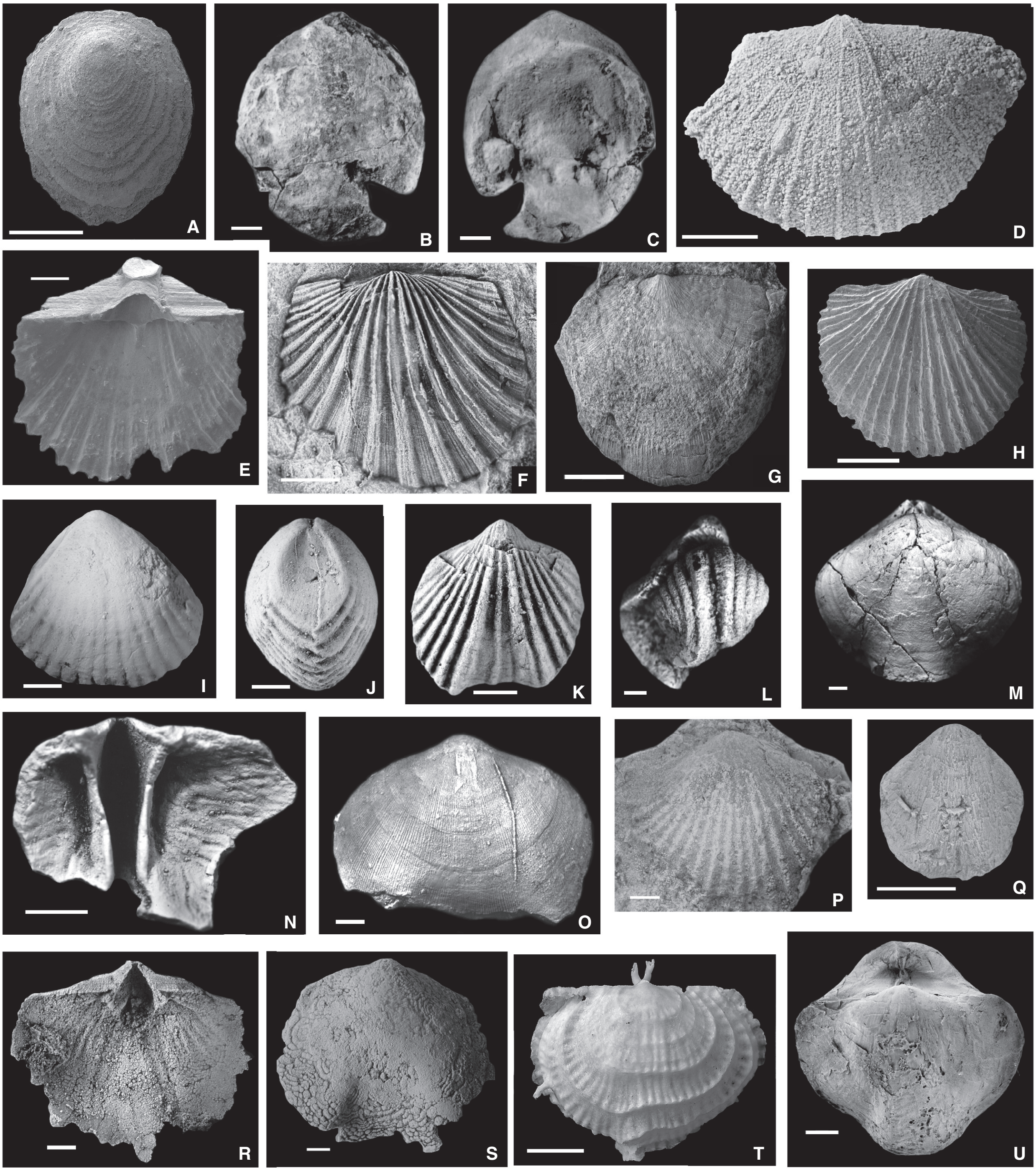
affinity of the poorly known *Discinopsis* Matthew *in* Hall & Clarke, 1892, previously associated with the craniiforms (Popov *et al.* 2000*a*), is doubtful. The earliest craniides are from the Tremadocian of the Mediterranean peri-Gondwana region (Sdzuy *et al.* 2001; Mergl 2002), while trimerellides and craniopsides emerged only during the early Sandbian (Popov *et al.* 2013*a*).

The craniiforms are characterized by a foliated shell, constructed of high magnesium calcite, which can be punctate (craniides) or impunctate (craniopsides); the original aragonitic composition of the trimerellid shell (Jaanusson 1966) has been confirmed by Balthasar *et al.* (2011). Recent craniiforms lack articulation and open their shells hydraulically with the assistance of the outside lateral muscles attached anteriorly to the body wall (Robinson 2014). This shell-opening mechanism differs markedly from that found in the lingulates, which have well developed dermal muscles (Hyman 1959; Popov *et al.* 1993; Holmer *et al.* 1995). Trimerellides are the only craniiforms which developed an effective hinge mechanism (Gorjansky & Popov 1985, 1986) and are also among the largest Early Palaeozoic brachiopods. The craniiforms lack a pedicle attachment during all ontogenetic stages in which an encrusting or ambitopic (initially attached but later free-living) life mode is adopted.

The alimentary canal of craniiforms is axial, supported by complete ventral and dorsal mesenteria, and terminated with an anus placed posteromedially on the posterior body wall. They have paired subenteric ganglia. Some extinct craniiforms (trimerellides) developed rudimentary articulation and a direct shell-opening mechanism, using diductor muscles evolved from the internal oblique muscles (Gorjansky & Popov 1985, 1986). Some features, such as mantle canals containing gonads, a peripheral arrangement of *vascula terminalia* and lecithotrophic larvae without shells, are shared by the craniiforms and rhynchonelliforms (Holmer *et al.* 1995; Williams *et al.* 1996). Mantle lobes in the craniiforms developed without reversion and the appearance of the ventral mantle lobe is significantly delayed. The larva in craniiforms is lecithotrophic with mineralized shell secretion occurring only after settlement, while secretion of the ventral valve is delayed until the end of metamorphosis (Popov *et al.* 2010, 2012; Altenburger *et al.* 2013).

FIG. 4. Representative photographs of key brachiopod genera illustrating their morphological diversity, related to the Williams *et al.* (1996) supra-ordinal classification of the Brachiopoda (see Fig. 6): Cambrian–Silurian taxa. A–B, *Obolella crassa* Hall, 1847, Class Obolellata, Superfamily Obolelloidea; Cambrian Stage 2, Troy, New York, USA; A, USNM 51951f, ventral valve; B, USNM 51951, dorsal internal mould; (Popov & Holmer 2000). C–D, *Pelmanella borealis* Popov *et al.*, 1997, Class Obolellata, Superfamily Naukatoidea; Cambrian Stage 4, Paralleldal Formation, Peary Land, central North Greenland; C, MGUH23743, holotype, ventral valve interior; D, MGUH23747, dorsal valve interior; (Popov *et al.* 1997). E, I, *Tomteluva perturbata* Streng *et al.*, 2016, Class Obolellata, Superfamily Naukatoidea; Cambrian Stage 5, Stephen Formation, Odaray Mountain, British Columbia, Canada; E, ROM63413.2, oblique posterior view of a pair of conjoined valves; I, ROM63413.3, side view of a pair of conjoined valves (photo, M. Streng). F–G, *Trematobolus pristinus bicostatus* Gorjansky *et al.*, 1964, Class Obolellata, Superfamily Obolelloidea, Cambrian Stage 4, Rassokha River, Siberia; F, CNIGR 7/8362, ventral valve interior; G, CNIGR 5/8362, ventral valve exterior; (Gorjansky *et al.* 1964). H, *Chile mirabilis* Popov & Tikhonov, 1990, Class Chileata, Superfamily Matutelloidea, Cambrian Stage 3, Chilesai, Alai Range, Kyrgyzstan; CNIGR 3/12859, holotype, ventral valve, exterior (Popov & Tikhonov 1990). J, K, *Eodictyonella gibbosa* (Hall, 1868), Class Chileata, Superfamily Matutelloidea, Silurian, Decatur Formation, Linden, Tennessee, USA; J, USNM 459702b ventral valve interior; K, USNM 459702, dorsal valve interior; (Popov & Holmer 2000). L, *Eodictyonella reticulata* (Hall, 1868), Class Chileata, Superfamily Matutelloidea, Silurian, Waldron Shale, Waldron, Indiana, USA; AMNH 36636, posterior view of a pair of conjoined valves (Popov & Holmer 2000). M, *Trifissura transversa* (Salter *in* Davidson, 1866), Class Chileata, Superfamily Matutelloidea, Silurian, Wenlock, Homerian, Coalbrookdale Formation, Dudley, England; NHMUK B820a, ventral view of internal mould of conjoined valves (Holmer *et al.* 2014). N, *Matutella grata* Andreeva, 1962, Cambrian Stage 5, Rassokha River, Siberia; Class Chileata, Superfamily Matutelloidea; CNIGR 8202, ventral valve exterior. O, *Billingsella*? *fortis* Popov *et al.*, 2013*b*, Cambrian, Furongian, Mila Formation, Tuyeh-Darvar, Alborz Mountqains, Iran, NMW2011.16G.459, dorsal valve interior (Popov *et al.* 2013*b*). P, T, *Kutorgina* sp., Class Kutorginata, Superfamily Kutorginoidea, Cambrian Stage 4, east Dead Sea coast, Jordan; P, NMW 98.69G.20, posterior view of a pair of conjoined valves; T, NMW 98.69G.30, ventral valve exterior; (Bassett *et al.* 2001). Q, S, U, *Arctohedra pyramidalis* Aksarina, 1975, Class Strophomenta, Superfamily Billingselloidea, Cambrian Series 3, Arpatektyr Mountain, Alai Range, Kyrgyzstan; Q, CNIGR 1/12761, dorsal valve exterior; S, CNIGR 23/12761, ventral valve posterior view showing interarea; U, CNIGR 6/12761, dorsal valve interior; (Popov & Tikhonov 1993). R, *Billingsella* sp., Class Strophomenata, Superfamily Billingselloidea, Cambrian, Furongian, Kujandy Formation, east side of Olenty River north-western slope of Aksak-Kujandy mountain, north-central Kazakhstan (Popov *et al.* 2001); CNIGR 1/12604, ventral valve interior. V, *Tritoechia tenuis* Popov *et al.*, 2015, Class Strophomenata, Superfamily Polytoechioidea, Lower Ordovician, Tremadocian, Mila-Kuh, Alborz Mountains, Iran; NMW2012.45G.326, holotype, latex cast of dorsal valve interior (Kebria-ee Zadeh *et al.* 2015). W, *Psiloria dayi* Cooper, 1976, Class Rhynchonellata, Superfamily Protorthoidea; Cambrian Stage 4, east Dead Sea coast, Jordan; NMW 98.69G.21, ventral view of a pair of conjoined valves. X–Y, *Glyptoria gulchensis* Popov & Tikhonov, 1993, Class Rhynchonellata, Superfamily Protorthoidea; Cambrian Series 3, Arpatektyr Mountain, Alai Range, Kyrgyzstan; X, CNIGR 22/12761, dorsal valve exterior; Y, CNIGR 20/12761, ventral valve interior; (Popov & Tikhonov 1993). All scale bars represent 2 mm except: E, I, Q, U (1 mm); M, T (5 mm). The CC license does not apply to images A–M, O–V, X, Y; reproduced here with the permission of the copyright holder as noted in citations above.

Many similarities in ontogenetic characters are shared between Recent craniides and the earliest Cambrian brachiopods of the Family Salanygolinidae (*Salanygolina* and *Pelmanotreta*), which also show delayed ventral valve formation and larval attachment by the ventral side of the body (Holmer *et al*. 2009; Skovsted *et al*. 2015). The larva of *Pelmanotreta* possessed three pairs of larval setal sacs, a character otherwise documented only in the Recent Craniida. However, larvae of Salanygolinidae were planktotrophic and probably acquired their shell during a free-swimming stage. As pointed by Holmer *et al.* (2009), *Salanygolina* exhibits a combination of features intermediate between the paterinates and chileates. In particular, attachment structures with ventral umbonal perforation and colleplax, and a ridge-like pseudodeltidium can be found also in chileates, while hemiperipheral growth of



dorsal valve and organophosphatic shell mineralization occur in the paterinides. Nevertheless, it is unlikely that the Salanygolinidae represent a transitional form between the organophosphatic paterinates and calcareous chileates (Fig. 4H, J–N). The primitive character of a densely laminate shell structure, which is characterized by a stacking honeycomb pattern with individual units, was probably enclosed by the organic membranes. Similar shell structure is also known in the tommotiids (Balthasar *et al.* 2009) and it clearly suggests the absence of the conveyor-belt system of shell secretion characteristic of other brachiopods. Thus, phosphatic shell mineralization may have evolved independently, within stem group brachiopods at the base of the craniiform clade. Although the Class Chileata may not belong to the basal rhynchonelliform clade as presented in previous phylogenetic analyses (e.g. Williams *et al.* 1996) it may represent a stem group craniiform, probably linked with the tommotiides (Holmer *et al.* 2009). Craniides may have evolved as paedomorphic chileates, retaining larval attachment by the retardation of the secretion of mineralized ventral valve and acquiring holoperipheral growth of both valves. It is also likely that calcareous mineralization of the shell in craniiforms evolved independently from that in rhynchonelliforms. An aragonitic shell is confined exclusively to the craniiform clade, being inferred for the chileate families, Isogrammidae and Trifissuridae (Fig. 4M) in addition to the trimerellides (Popov & Holmer 2000; Holmer *et al.* 2014).

Origin and early history of the rhynchonelliforms

The rhynchonelliforms are generally characterized by a fibrous, calcareous shell, a distinctive pedicle developing from a larval lobe, and a blind gut (Table 1); they are the

FIG. 5. Representative photographs of key brachiopod genera illustrating their morphological diversity, related to the Williams *et al.* (1996) supra-ordinal classification of the Brachiopoda (see Fig. 6): Ordovician and Silurian taxa. A, *Craniops implicata* (Sowerby, 1839), Class Craniata, Superfamily Craniopsoidea, Silurian, Wenlock, Mulde Formation of Fröjel, Gotland, Sweden; RM Br24286e, dorsal valve exterior. B–C, *Ussunia incredibilis* Nikitin & Popov, 1984, Class Craniata, Superfamily Trimerelloidea; Upper Ordovician, Sandbian, Bestamak Fortmation, Bestamak, Chingiz Range, Kazakhstan; CNIGR 1/12095, holotype, dorsal valve exterior (B), interior (C); (Nikitin & Popov 1984). D, *Plectella uncinata* (Pander, 1830), Class Strophomenata, Superfamily Plectambonitoidea, Lower Ordovician, Floian, Mäekula Member, Popovka River, Ingria, Russia; RM Br137127 ventral view of a pair of conjoined valves. E, *Antigonambonites planus* (Pander, 1830), Class Strophomenata, Superfamily Billingselloidea; Middle Ordovician, Dapingian, Volkhov Formation, east side of Volkhov river near Simankovo, Ingria, Russia; NMW 2001.39G.557, ventral valve interior (Popov *et al.* 2007*b*). F, *Paralenorthis semnanensis* Popov *et al.*, 2009, Class Rhynchonellata, Superfamily Orthoidea; Lower Ordovician, Tremadocian; Simeh-Kuh, vicinity of Damghan, Iran; NMW 2004.22G.872, latex cast of ventral valve exterior (Popov *et al.* 2009). G, *Dirafinesquina globosa* Cocks & Zhan, 1998, Class Strophomenata, Superfamily Strophomenoidea; Middle Ordovician, Darriwilian, Lashkarak Formation; NMW 2014.26G.11 ventral valve exterior (Popov *et al.* 2016). H, *Paurorthis parva* (Pander, 1830), Class Rhynchonellata, Superfamily Dalmanelloidea, Middle Ordovician, Dapingian, Volkhov Formation, east side of Volkhov River, Babino quarry, Ingria, Russia, NMW 2009.3G.240, dorsal valve exterior. I–J, *Idiostrophia tenuicostata* Popov *et al.*, 2005, Class Rhynchonellata, Superfamily Camarelloidea; Middle Ordovician, Dapingian, Volkhov Formation, Volkhov river, east side between Obukhovo and Simankovo, Ingria, Russia; CNIGR 15⁄13101, dorsal and side views of conjoined valves; (Popov *et al.* 2005). K, *Sulcatospira prima* Popov *et al.*, 1999, Class Rhynchonellata, Superfamily Atrypoidea; Upper Ordovician, Katian, Tauken Formation, Shollakkarasu river west of Sarybulak, north-central Kazakhstan; NMW 98.30G.49, ventral view of a pair of conjoined valves (Nikitin *et al.* 2003). L–M, *Kellerella pilata* Nikitin *et al.*, 2006, Class Rhynchonellata, Superfamily Meristelloidea; Upper Ordovician, Katian, Odak Beds, Odak, east side of Shiderty river, Kazakhstan; L, NMW 98.65G.1887, dorsal view of broken shell showing laterally directed spiralial cones; M, NMW 98.65G.1883, dorsal view of a pair of conjoined valves; (Nikitin *et al.* 2006). N–O, *Eoporambonites latus* (Pander, 1830), Class Rhynchonellata, Superfamily Porambonitoidea, Lower Ordovician, Floian, Mäekula Member, Popovka river, vicinity of Pavlovsk, Ingria, Russia; N, CNIGR 105⁄222, dorsal valve interior; O, CNIGR 107⁄222, ventral view of a pair of conjoined valves; (Popov *et al.* 2005). P, *Ancistrorhyncha modesta* Popov *in* Nikiforova & Popov, 1981, Class Rhynchonellata, Superfamily Ancistrorhynchoidea; Upper Ordovician, Sandbian, area west of Alakul Lake; west Balkhash Region, Kazakhstan; NMW 98.28G.1976, dorsal valve exterior. Q, *Rozmanospira mica* (Nikitin & Popov, 1984), Class Rhynchonellata, Superfamily Protozygoidea, Upper Ordovician, Sandbian, area west of Alakul Lake; west Balkhash Region, Kazakhstan; NMW 98.28G.1989, ventral view of a pair of conjoined valves. R–S, *Syntrophioides tersus* Popov *et al.*, 2011, Class Rhynchonellata, Superfamily Porambonitoidea, Cambrian, Furongian, Mila Formation, Deh-Molla, vicinity of Shahrud, Alborz Mountains, Iran; R, NMW 2011.16G. 61, ventral valve interior; S, NMW 2011.16G.62, ventral valve exterior; (Popov *et al.* 2011). T, *Streptis undifera* (Schmidt, 1858), Class Rhynchonelliformea, Superfamily Triplesioidea, Upper Ordovician, Hirnantian, Arina Formation, Porkuni quarry, North Estonia; GIT 626-64, neotype, dorsal valve interior (Hints *et al.* 2013). U, *Eospirifer ghobadiae* Popov & Cocks, 2013, Class Rhynchonelliformea, Superfamily Cyrtioidea, Silurian, Aeronian, Qarabil Limestone Formation, Pelmis, Kuh-e Saluk Mountains, Kopet-Dagh Region, Iran; NMW 60473, holotype, a pair of conjoined valves (Popov & Cocks 2013). All scale bars represent 2 mm except: A (500 μm), H (1 mm); B, C, G, N, O, U (5 mm). The CC license does not apply to images B, C, E–G, I–O, R–U; reproduced here with the permission of the copyright holder as noted in citations above.

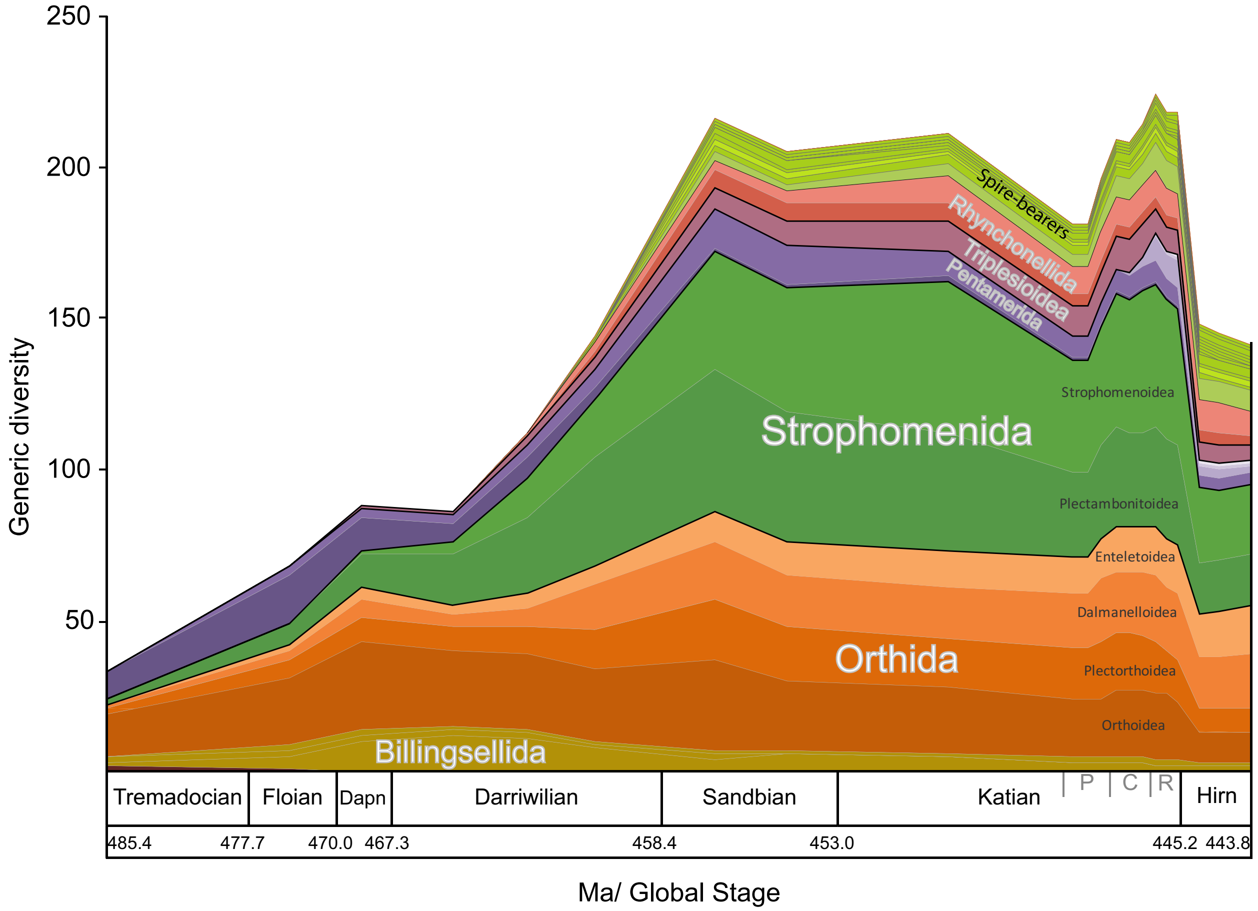


FIG. 6. Diversification of the Ordovician rhynchonelliform Brachiopoda (modified from Rasmussen 2014; original courtesy of C. Rasmussen). *Contractions*: Dapn, Dapingian; Hirn, Hirnantian; spire-bearers include the athyridides, atrypides and spiriferides.

typical ‘modern’ brachiopods and diversified, substantially, during the Ordovician (Fig. 6). In the earliest taxa, the pedicle probably emerged through the delthyrial notch or delthyrium, but a minute apical foramen is reported in some groups that is of doubtful function. The pedicle, together with the type of interactions between the valves and the development later of lophophore supporting structures, were critical in evolving new taxa and life styles within the class. Some of the earliest rhynchonelliforms occur in the upper Tommotian, including the obolellides (Fig. 4A, B, F, G) and kutorginides (Fig. 4P, T). By the Atdabanian the fauna includes nisusiids (Fig. 4C–E, I), again lacking teeth but nevertheless hinged, whilst the earliest of the more typical rhynchonelliform exemplars, the protorthids (Fig. 4W–Y) appeared during the latter part of Cambrian Stage 4. All these early forms have rudimentary articulation but apparently effective hinging mechanisms. Many groups demonstrate considerable morphological diversity and plasticity, particularly in articulatory structures and musculature (e.g. Bassett *et al.* 2001). The most recent rhynchonelliformean phylogenies, founded on Williams *et al.* (1996), are fairly robust in the broadest sense with the establishment of the rhynchonellate and strophomenate clades (Figs 4, 5) in the Cambrian while additional traits, mainly focused on lophophore supports, sequentially define new groups throughout the Ordovician. Thus, crown group taxa such as the Lingulida appeared deep in the Cambrian, and were joined by the craniides (Fig. 5A–C) and by more diverse and dominant rhynchonellide (Fig. 5D–U) faunas later in the Ordovician.

Thus, many of the key body plans were already in place by the Cambrian, but in terms of an escalation of families, genera and species, the Ordovician was critical (Fig. 6; Harper & Drachen 2010; Harper *et al.* 2015). The two main clades, the rhynchonellates and strophomenates, presented alternative life modes; both had deltidiodont dentition, cardinal areas and simple brachial supports but the former taxa were mainly pedunculate whereas the latter were mainly ambitopic or recumbent, taking advantage of both hard and soft substrates. The two clades also differ in their broad

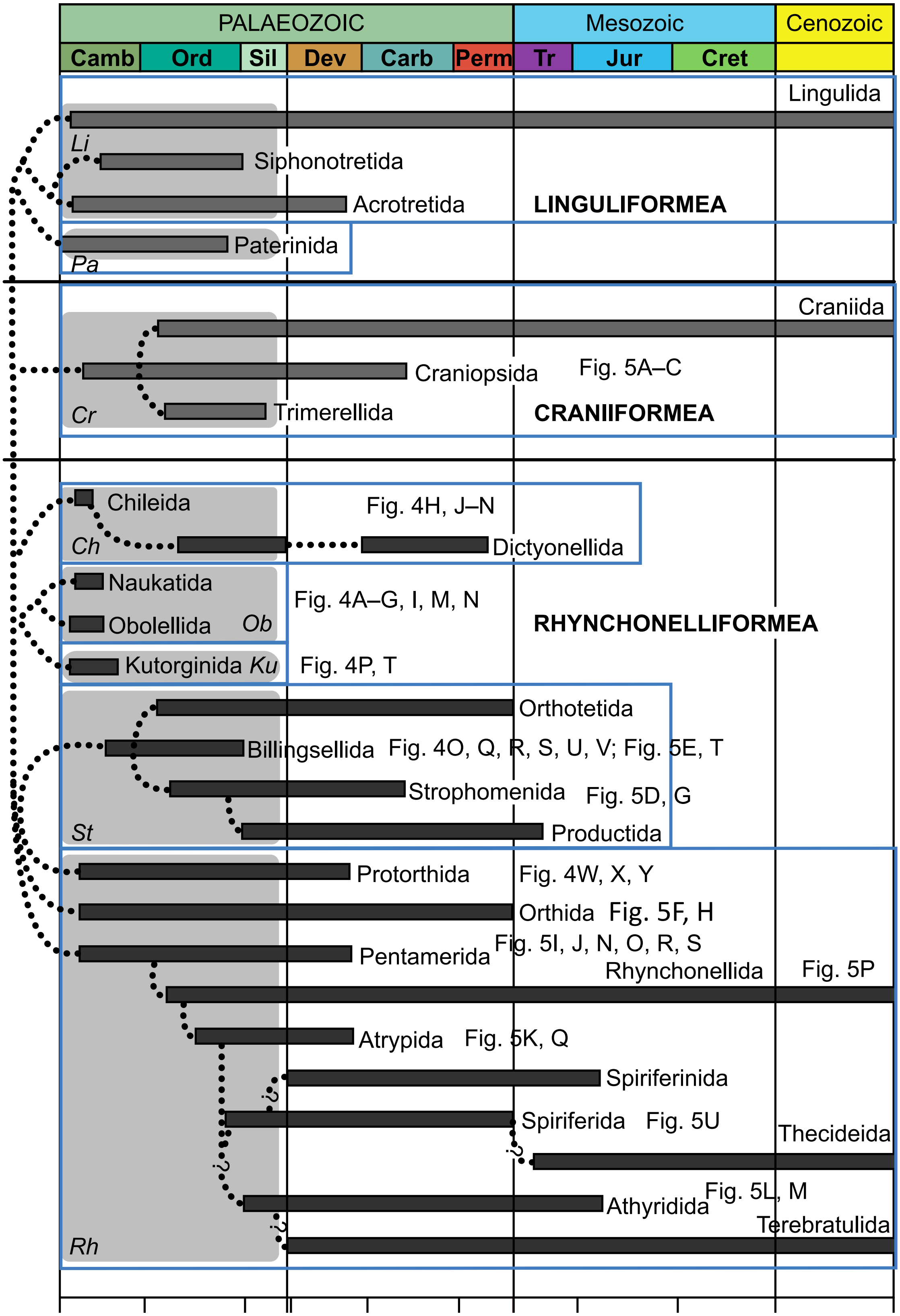


FIG. 7. Broad-frame classification (after Williams *et al.* 1996), annotated with an indication of the taxa illustrated in Figures 4 and 5. Li, Lingulata; Pa, Paterinata; Cr, Craniata; Ch, Chileata; Ob, Obolellata; Ku, Kutorginata; St, Strophomenata; Rh, Rhynchonellata.

biogeographical distribution, with pentamerides (Fig. 5I, J, N, O, R, S) generally dominating in lower latitudes and the orthides (Fig. 5F, H) and strophomenides (Fig. 5D, G) widespread but commonly diverse in higher latitudes (Harper *et al.* 2013). In the stem of the strophomenates, an understanding of the billingsellides (Fig. 4O, R; Fig. 5E) is critical in deciphering the origins of the polytoechiids (Fig. 4V) and clitambonitides (Popov *et al.* 2001; Topper *et al.* 2013) together with the position and role of *Arctohedra* (Fig. 4Q, S, U) and its relationship to the protorthides and clitambonitides. The diversity of the strophomenate clade accelerated during the mid-Ordovician with the expansion of the Plectambonitoidea (Fig. 5D) and in the later Ordovician, the Strophomenoidea (Fig. 5G) (Cocks & Rong 1989; Rong & Cocks 1994; Cocks & Rong 2000). Recent phylogenetic analyses of parts of the group (e.g. Candela 2011*a*, *b*; Congreve *et al.* 2015) have provided more clarity to the classification and evolution of the strophomenides during the Ordovician and Silurian, but questions remain regarding the placement of a number of groups such as the toquimiids, that apparently possess orthoid characters. The cladistic classification of the orthidines (Williams & Harper 2000) remains relatively robust, but that of the dalmanellidines (Harper 2000) is more fragile, with the suggestion that punctuation in that group may be polyphyletic (Benedetto & Muñoz 2017). This, together with the addition of much new morphological data from taxa near the base of the clade since publication of the *Treatise*, offers the prospect of a better understanding of this complex and currently, poorly-resolved group.

End Ordovician extinction

This extinction, the first major such event affecting animal-based communities, is one of the ‘big three’ in taxonomic terms (Bambach 2006). It appears not to have been particularly taxon selective, targeting deep-water and warm-water communities (Finnegan *et al.* 2016) and generating a large number of Lazarus taxa (Rong *et al.* 2006). Importantly, though, it had a relatively mild impact on the marine ecosystem (Bambach *et al.* 2004; Bambach 2006; Harper *et al.* 2014). In terms of the four levels of ecological impacts of extinction crises (see Droser *et al.* 2000) only third- and fourth-level palaeoecological changes were triggered during the end Ordovician mass extinction, invoking only community or community-type changes during the event. The ecological severity of the event was deemed even less significant than that of the Serpukhovian (McGhee *et al.* 2012) and is currently ranked only sixth within the eleven largest Phanerozoic ecological crises (McGhee *et al.* 2013). The two-phased extinction, nevertheless, provided the first real test of the resilience and sustainability of brachiopods, tipping the balance in favour of more derived rhychonelliform morphologies, such as those of the atrypides (Fig. 5K, Q), athyridides (Fig. 5L, M), pentamerides and spiriferides (Fig. 5U) (Harper & Rong 2001; Huang *et al.* 2017).

THE BROAD-FRAME CLASSIFICATION: CHALLENGES MOVING FORWARD

There have been no substantive attempts to reassess the phylogeny of the Brachiopoda in its entirety since the landmark study of Williams *et al.* (1996; Fig. 7). Attempts prior to this, with the exception of the cladistics analysis of Carlson (1991*a*) focused on several key characters (e.g. Williams 1956; Williams & Rowell 1965; Rudwick 1970; Williams & Hurst 1977) rather than total evidence. Nevertheless, new data, new investigative techniques and the more precise location of fossil data in time and space provide the opportunity to test existing phylogenetic hypotheses and suggest alternatives. Morphological data remain crucial. New data, particularly from those groups originating in the Cambrian, provide some exciting challenges to conventional wisdom. We focus on some of the recent research (see also above) pertinent to any substantive revision of the broad-frame classification of the phylum.

We have briefly indicated six key areas that merit discussion and exploration:

1. The paterinates as a natural outgroup for the phylum. Morphological and stratigraphic data suggest this group offers to be the most appropriate outgroup for phylogenetic rooting.
2. The significance of the chileates. This group is increasingly important for understanding initial divergence of craniiform, strophomenate and rhynchonellate clades, as well as for early evolution of the attachment structures in the brachiopods. They include the oldest known brachiopods with a calcareous and strophic shell, and an unusual pedicle emerging through a vertical umbonal penetration; a colleplax, typical of the chileates, is also present in the phosphatic *Salanygolina* and this structure may have equivalents in the craniiforms and strophomenides. The group thus demonstrates a puzzling mosaic of characters developed elsewhere in apparently more distantly related taxa.
3. Mutual relationships amongst the kutorginides, naukatides and obollelides and with the strophomenates. New morphological and stratigraphical data on the first three groups requires a re-evaluation of their relationships with each other and the strophomenates. The attachment structures of the kutorginates and

strophomenates are probably homologous and quite distinct from those of the rhynchonellates. Investigation of the early ontogenetic stages of the kutorginides is key to resolving their relationship with the strophomenates.

4. The position of the pentamerides within the rhynchonelliformeans. Pentameride dentition has been considered intermediate between cyrtomatodont and deltidiodont modes or to include both types. While many pentamerides are astrophic, the cyrtomatodont condition has not been established with any veracity. Moreover, the presence of platforms in both valves might suggest a lack of muscles with tendons in contrast to those of the orthides. On this basis it would seem unlikely that the pentamerides are members of the brachiopod crown group.
5. The composition and mutual relationships of the three great clades. The three subphyla, the Linguliformea, Craniiformea and Rhynchonelliformea were clearly separated by the Early Ordovician (possibly earlier) on the basis of their shell structures and compositions together with their respective morphologies. Thus, there is a definite possibility that all three major brachiopod lineages were phylogenetically distinct, prior to mineralization of their respective shells.
6. Evolution and timing of shell mineralization. The origin of the phylum and its earliest evolution is associated with the development of different types of secretory mechanisms and regimes together with the utilization of different shell substances. Understanding the respective origins and evolutionary trajectories of the different types of mineralization is still in its infancy but the new many new taxa, recognized in the brachiopod stem, show considerable prospect for unravelling this complex problem.

Institutional abbreviations. AMNH, American Museum of Natural History, New York City, USA; CNIGR, Central Scientific Research Geologic Exploration Museum, St Petersburg, Russia; CPC, Commonwealth Palaeontological Collection, Australian Geological Survey, Canberra, Australia; ELI, Early Life Institute, Northwest University, Xi'an, China; GIT, Institute of Geology, Tallinn University of Technology, Tallinn, Estonia; MGUH, Geological Museum, University of Copenhagen, Denmark; NIGP, Nanjing Institute of Geology & Palaeontology, Chinese Academy of Sciences, China; NHMUK, Natural History Museum, London, UK; NMW, National Museum of Wales, Cardiff, Wales, UK; PMU, Paleontological Museum, Uppsala, Sweden; RMBr, Swedish Museum of Natural History, Stockholm, Sweden; ROM, Royal Ontario Museum, Toronto, Canada; SAM, Iziko South African Museum, Cape Town, South Africa; USNM, Smithsonian National Museum of Natural History, USA.

Acknowledgements. We thank Dr Andrew Smith for his invitation to contribute to the Frontiers series. Both he and Dr Sally Thomas improved the manuscript with their decisive and helpful editorial comments. Dr Michael Streng kindly provided unpublished photographs of *Tomteluva* presented in the paper. Substantial improvements were suggested by two anonymous referees and Dr Robin Cocks. DATH thanks the Leverhulme Trust and the Wenner-Gren Foundation for support. LEP is grateful to the National Museum of Wales for logistical support. LEH was supported by a grant from the Swedish Research Council (VR 2012-1658) and his research visits to Xi'an associated with this paper were financially supported by the Zhongjian Yang Scholarship from the Department of Geology, Northwest University, Xi'an. This is a contribution to IGCP 653 'The onset of the Great Ordovician Biodiversification Event'.

Editor. Andrew Smith

REFERENCES

AKSARINA, N. A. 1975. Brakhiopody [Brachiopods]. 91–100. *In* REPINA, L. N., JASKOVICH, B. V., AKSARINA, N. A., PETRUNINA, Z. E., PONIKLENKO, I. A., RUBANOV, D. A., BOLGOVA, G. V., GOLIKOV, A. N., KHAJRULINA, T. I. and OSOKHOVA, M. M. (eds). *Lower Palaeozoic stratigraphy and fauna of the northern slopes of the Turkestan and Alay ranges*. Trudy Instituta Geologii i Geofiziki, Akademiya Nauk SSSR, Sibirskoye Otdelenye, 278 pp. [in Russian]

ALTENBURGER, A., WANNINGER, A. and HOLMER, L. E. 2013. Metamorphosis in Craniiformea revisited: *Novocrania anomala* shows delayed development of the ventral valve. *Zoomorphology*, **132**, 379–387.

ANDREEVA, O. N. 1962. Some Cambrian brachiopods of Siberia and Central Asia. *Paleontologicheskii Zhurnal*, **1962**, 87–96. [in Russian]

BALTHASAR, U. and BUTTERFIELD, N. J. 2009. Early Cambrian "soft–shelled" brachiopods as possible stem–group phoronids. *Acta Palaeontologica Polonica*, **54**, 307–314.

—— SKOVSTED, C. B., HOLMER, L. E. and BROCK, G. A. 2009. Homologous skeletal secretion in tommotiids and brachiopods. *Geology*, **37**, 1143–1146.

—— CUSACK, M., FARYMA, L., CHUNG, P., HOLMER, L. E., JIN, J., PERCIVAL, I. G. and POPOV, L. E. 2011. Relict aragonite from Ordovician–Silurian brachiopods: implications for the evolution of calcification. *Geology*, **39**, 967–970.

BAMBACH, R. K. 2006. Phanerozoic biodiversity mass extinctions. *Annual Review of Earth & Planetary Sciences*, **34**, 127–155.

—— KNOLL, A. H. and WANG, S. C. 2004. Origination, extinction and mass depletions of marine diversity. *Paleobiology*, **30**, 522–542.

BASSETT, M. G., POPOV, L. E. and HOLMER, L. E. 1999. Organophosphatic brachiopods: patterns of biodiversification and extinction in the early Palaeozoic. *Geobios*, **32**, 145–163.

—— —— —— 2001. Functional morphology of articulatory structures and implications for patterns of musculature in Cambrian rhynchonelliform brachiopods. 163–176. *In*

BRUNTON C. H. C., COCKS, L. R. M. and LONG, S. L. (eds). *Brachiopods past and present*. Systematics Association Special Volume, **63**. CRC Press, 441 pp.

—— —— —— 2002. Brachiopods: Cambrian–Tremadoc precursors to Ordovician radiation events. 13–23. *In* CRAME J. A. and OWEN, A. W. (eds). *Palaeobiogeography and biodiversity change: a comparison of the Ordovician and Mesozoic–Cenozoic radiations*. Geological Society London, Special Publications, **194**, 212 pp.

—— —— and EGERQUIST E. 2008. Early ontogeny of some Ordovician–Silurian strophomenate brachiopods: significance for interpreting evolutionary relationships within early Rhynchonelliformea. *Fossils & Strata*, **54**, 13–20.

BENEDETTO, J. L. and MUÑOZ, D. F. 2017. Plectorthoid brachiopods from the Lower Ordovician of north-western Argentina; phylogenetic relationships with *Tarfaya* Havlíček and the origin of heterorthids. *Journal of Systematic Palaeontology*, **15**, 43–67.

BRUTON, D. L. and HARPER, D. A. T. 1985. Early Ordovician (Arenig–Llanvirn) faunas from oceanic islands in the Appalachian-Caledonide Orogen. 359–368. *In* GEE, D. G. and STURT, B. A. (eds). *The Caledonide Orogen: Scandinavia and related areas*. Wiley.

BUTLER, A. D. 2015. Decoding the fossil record of early lophophorates: systematics and phylogeny of problematic Cambrian Lophotrochozoa. PhD thesis, Uppsala University, Sweden. *Digital Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology*, **1284**, 65 pp. http://urn.kb.se/resolve?urn=urn:nbn:se:uu:diva-261907

CANDELA, Y. 2011*a*. Phylogenetic relationships of leptellinid brachiopods. *Alcheringa*, **35**, 413–426.

—— 2011*b*. A systematic revision of the Ordovician plectambonitoidean brachiopods *Chonetoidea* and *Sericoidea*. *Journal of Systematic Palaeontology*, **9**, 499–522.

CARLSON, S. J. 1991*a*. Phylogenetic relationships among brachiopod higher taxa. 3–10. *In* MACKINNON, D. I., LEE, D. E. and CAMPBELL, J. D. (eds). *Brachiopods through time*. Proceedings of the 2nd International Brachiopod Congress. Balkema Press.

—— 1991*b*. A phylogenetic perspective on articulate brachiopod diversity and the Permo-Triassic extinctions. 119–142. *In* DUDLEY, E. C. (ed.) *The unity of evolutionary biology, vol. 1*. Proceedings of the 4th International Congress of Systematics & Evolutionary Biology Dioscorides Press, Portland, Oregon.

—— 1995. Phylogenetic relationships among extant brachiopods. *Cladistics*, **11**, 131–197.

—— 2007. Recent research on brachiopod evolution. 2878–2900. *In* KAESLER, R. L. and SELDEN, P. A. (eds). *Treatise on invertebrate paleontology. Part H (revised), Brachiopoda (Revised) 6*. Geological Society of America & University of Kansas Press.

—— 2016. The evolution of Brachiopoda. *Annual Review of Earth & Planetary Sciences*, **44**, 409–438.

—— and LEIGHTON, L. R. 2001. The phylogeny and classification of Rhynchonelliformea. *The Paleontological Society Papers*, **7**, 27–51.

CLAUSEN, S., AVARO, J., DEVAERE, L., AHLBERG, P. and BABCOCK, L. E. 2015. The Cambrian explosion: its timing and stratigraphic setting. *Annales de Paléontologie*, **101**, 153–160.

COCKS, L. R. M. and RONG, J. Y. 1989. Classification and review of the brachiopod superfamily Plectambonitacea. *Bulletin of the British Museum (Natural History), Geology Series*, **45**, 77–163.

—— —— 2000. Strophomenida. 216–349. *In* KAESLER, R. L. (ed.) *Treatise on invertebrate paleontology. Part H. Brachiopoda (Revised) 2*. Geological Society of America & University of Kansas Press.

—— and ZHAN, R. 1998. Caradoc brachiopods from the Shan States, Burma (Myanmar). *Bulletin of the British Museum (Natural History), Geology Series*, **54**, 109–130.

COHEN, B. L. 2000. Monophyly of brachiopods and phoronids: reconciliation of molecular evidence with Linnaean classification (the subphylum Phoroniformea nov.). *Proceedings of the Royal Society B*, **267**, 225–231.

—— 2013. Rerooting the rDNA gene tree reveals phoronids to be 'brachiopods without shells'; dangers of wide taxon samples in metazoan phylogenetics (Phoronida; Brachiopoda). *Zoological Journal of the Linnean Society*, **167**, 82–92.

—— and WEYDMANN, A. 2005. Molecular evidence that phoronids are a subtaxon of brachiopods (Brachiopoda: Phoronata) and that genetic divergence of metazoan phyla began long before the Early Cambrian. *Organisms, Diversity & Evolution*, **5**, 253–273.

—— GAWTHROP, A. B. and CAVALIER-SMITH, T. 1998. Molecular phylogeny of brachiopods and phoronids based on nuclear-encoded small subunit ribosomal RNA gene sequences. *Philosophical Transactions of the Royal Society B*, **353**, 2039–2061.

CONGREVE, C. R., KRUG, A. Z. and PATZKOWSKY, M. E. 2015. Phylogenetic revision of the Strophomenida, a diverse and ecologically important Palaeozoic brachiopod order. *Palaeontology*, **58**, 743–758.

CONWAY MORRIS, S. and PEEL, J. S. 1995. Articulated halkieriids from the Lower Cambrian of North Greenland and their role in early protostome evolution. *Philosophical Transactions of the Royal Society B*, **347**, 305–358.

COOPER, A. G. 1976. Lower Cambrian brachiopods from the Rift Valley (Israel and Jordan). *Journal of Paleontology*, **50**, 269–289.

DAVIDSON, T. 1866. *British fossil Brachiopoda, vol. 3. Silurian, part 7 (1)*. Palaeontographical Society Monographs, London, 88 pp.

DROSER, M. L., BOTTJER, D. J., SHEEHAN, P. M. and McGHEE, G. R. Jr 2000. Decoupling of taxonomic and ecologic severity of Phanerozoic marine mass extinctions. *Geology*, **28**, 675–678.

FINNEGAN, S., RASMUSSEN, C. M. Ø. and HARPER, D. A. T. 2016. Biogeographic and bathymetric determinants of brachiopod extinction and survival during the Late Ordovician mass extinction. *Proceedings of the Royal Society B*, **283** (1829), 20160007.

FREEMAN, G. and LUNDELIUS, J. W. 2005. The transition from planktotrophy to lecithotrophy in larvae of Lower Palaeozoic Rhynchonelliform brachiopods. *Lethaia*, **38**, 219–254.

GORJANSKY, V. YU. and POPOV, L. E. 1985. Morfologiya, systematicheskoe polozheniye i proiskhozhdeniye bezzamkovykh brachiopod s karbonatnoy rakovinoy [Morphology, systematic position and origin of the inarticulate brachiopods with carbonate shells]. *Paleontologicheskii Zhurnal*, **1985**, 3–14. [in Russian]

—— —— 1986. On the origin and systematic position of the calcareous-shelled inarticulate brachiopods. *Lethaia*, **19**, 233–240.

—— EGOROVA, L. I. and SAVITSKII, V. E. 1964. On the Lower Cambrian fauna of the northern slope of the Anabar shield. *Nauchno-Issledovatelskii Institut Geologii Arktiki (NIIGA), Trudy*, **4**, 5–32. [in Russian]

HALANYCH, K. M., BACHELLER, J. D., AGUINALDO, A. M. A. and LIVA, S. M. 1995. Evidence from 18S ribosomal DNA that the lophophorates are protostome animals. *Science*, **267**, 1641–1643.

HALL, J. 1847. *Palaeontology of New York, vol. 1. Containing descriptions of the organic remains of the lower division of the New-York System*. C. van Benthuysen, New York, 338 pp, 100 pls.

—— 1868. *Note on the genus* Eichwaldia. Twentieth Annual Report of the Regents of the University of the State of New York, on the Condition of the State Cabinet of Natural History, 274–278.

—— and CLARKE, J. M. 1892. *Palaeontology, vol. 8, part 1. An introduction to the study of the genera of Palaeozoic Brachiopoda*. Geological Survey of the State of New York, 367 pp, 20 pls.

HARPER, D. A. T. 2000. Dalmanellidina. 782–844. *In* KAESLER, R. L. (ed.) *Treatise on invertebrate paleontology. Part H. Brachiopoda (Revised) 3*. Geological Society of America & University of Kansas Press.

—— 2005. Brachiopods. 301–310. *In* SELLEY, R. C., COCKS, L. R. M. and PLIMER, I. R. (eds). *Encyclopedia of geology*. Elsevier.

—— 2006. The Ordovician biodiversification: setting an agenda for marine life. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **232**, 148–166.

—— 2010. The Ordovician radiation: roles of alpha, beta and gamma diversity. *Geological Society of America, Special Paper*, **466**, 69–83.

—— and DRACHEN, A. 2010. The Orthida: the rise and fall of a great Palaeozoic clade. *Special Papers in Palaeontology*, **84**, 107–117.

—— and RONG, J.-YU. 2001. Palaeozoic brachiopod extinctions and recoveries. *Geological Journal*, **36**, 317–328.

—— COCKS, L. R. M., POPOV, L. E., SHEEHAN, P. M., BASSETT, M. G., COPPER, P., HOLMER, L. E., JIN, J. and RONG, J.-Y. 2004. Brachiopods. 157–178. *In* WEBBY, B. D. E., PARIS, F., DROSER, M. L. and PERCIVAL, I. G. (eds). *The Great Ordovician Biodiversification Event*. Columbia University Press.

—— RASMUSSEN, C. M. Ø., LILJEROTH, M., BLODGETT, R. B., CANDELA, Y., JIN, J., PERCIVAL, I. G., RONG, J., VILLAS, E. and ZHAN, R. 2013. Biodiversity, biogeography and phylogeography of Ordovician rhynchonelliform brachiopods. *Geological Society London, Memoirs*, **38**, 127–144.

—— HAMMARLUND, E. U. and RASMUSSEN, C. M. Ø. 2014. End Ordovician extinctions: a coincidence of causes. *Gondwana Research*, **25**, 1294–1307.

—— RENBIN, Z. and JISUO, J. 2015. The Great Ordovician Biodiversification Event: reviewing two decades of research on diversity's big bang illustrated by mainly brachiopod data. *Palaeoworld*, **24**, 75–85.

HAUSDORF, B., HELMKAMPF, M., NESNIDAL, M. P. and BRUCHHAUS, I. 2010. Phylogenetic relationships within the lophophorate lineages (Ectoprocta, Brachiopoda and Phoronida). *Molecular Phylogenetics & Evolution*, **55**, 1121–1127.

HEJNOL, A., OBST, M., STAMATAKIS, A., OTT, M., ROUSE, G. W., EDGECOMBE, G. D., MARTINEZ, P., BAGUÑÀ, J., BAILLY, X., JONDELIUS, U. and WIENS, M. 2009. Assessing the root of bilaterian animals with scalable phylogenomic methods. *Proceedings of the Royal Society of London B*, **276**, 4261–4270.

HELMKAMPF, M., BRUCHHAUS, I. and HAUSDORF, B. 2008. Multigene analysis of lophophorate and chaetognath phylogenetic relationships. *Molecular Phylogenetics & Evolution*, **46**, 206–214.

HENNIG, W. 1966. *Phylogenetic systematics*. University of Illinois Press, 263 pp.

HOLMER, L. E. and CARON, J. B. 2006. A spinose stem group brachiopod with pedicle from the Middle Cambrian Burgess Shale. *Acta Zoologica*, **87**, 273–290.

—— and POPOV, L. E. 2000. Class Lingulata. 30–146. *In* KAESLER, R. L. (ed.) *Treatise on invertebrate paleontology. Part H. Brachiopoda (Revised) 2*. Geological Society of America & University of Kansas Press.

—— —— 2007. Class Lingulata. 2532–2590. *In* SELDEN, P. A. (ed.) *Treatise on invertebrate paleontology. Part H. Brachiopoda (Revised) 6*. Geological Society of America & University of Kansas Press.

—— —— BASSETT, M. G. and LAURIE, J. 1995. Phylogenetic analysis and classification of the Brachiopoda. *Palaeontology*, **38**, 713–741.

—— —— and STRENG M. 2008*a*. Organophosphatic stem group brachiopods – implications for the phylogeny of the Subphylum Linguliformea. *Fossils & Strata*, **54**, 3–11.

—— SKOVSTED, C. B., BROCK, G. A., VALENTINE, J. L. and PATERSON, J. R. 2008*b*. The Early Cambrian tommotiid *Micrina*, a sessile bivalved stem group brachiopod. *Biological Letters*, **4**, 724–728.

—— PETTERSSON STOLK, S., SKOVSTED, C. B., BALTHASAR, U. and POPOV, L. E. 2009. The enigmatic early Cambrian *Salanygolina* – a stem group of rhynchonelliform chileate brachiopods? *Palaeontology*, **52**, 1–10.

—— SKOVSTED, C. B., LARSSON, C., BROCK, G. A. and ZHANG, Z. 2011. First record of a bivalved larval shell in Early Cambrian tommotiids and its phylogenetic significance. *Palaeontology*, **54**, 235–239.

HINTS, L., POPOV, L. E. and HOLMER, L. E. 2013. Morphology, ontogeny and affinities of the Hirnantian triplesiid brachiopod *Streptis undifera* from Baltoscandia. *Palaeontology*, **56**, 961–970.

HOLMER, L. E., POPOV, L. E. and BASSETT, M. G. 2014. Ordovician–Silurian Chileida–first post-Cambrian records of an enigmatic group of Brachiopoda. *Journal of Paleontology*, **88**, 488–496.

—— POPOV, L., KLISHEVICH, I. and GHOBADI POUR, M. 2016. Reassessment of the early Triassic lingulid brachiopod '*Lingula*' *borealis* Bittner, 1899 and related problems of lingulid taxonomy. *GFF*, **138**, 519–525.

HUANG, B., HARPER, D. A. T., RONG, J. I. and ZHAN, R. 2017. Brachiopod faunas after the end Ordovician mass extinction from South China: testing ecological change through a major taxonomic crisis. *Journal of Asian Earth Sciences*, **138**, 502–514.

HYMAN, L. H. 1959. *The Invertebrates, vol. 5. Smaller coelomate groups, Chaetognatha, Hemichordata, Pogonophora, Phoronida, Ectoprocta, Brachiopoda, Sipunculida, the coelomate Bilateria*. McGraw-Hill, 783 pp.

JAANUSSON, V. 1966. Fossil brachiopods with probable aragonitic shell. *GFF*, **88**, 279–281.

—— 1971. Evolution of the brachiopod hinge. *In* DUTRO, J. T. Jr (ed.) *Paleozoic perspectives: a paleontological tribute to G. Arthur Cooper*. Smithsonian Contributions to Paleobiology, **3**, 33–46.

KEBRIA-EE ZADEH, M. R., GHOBADI POUR, M., POPOV, L. E., BAARS, C. and JAHANGIR, H. 2015. First record of the Ordovician fauna in Mila-Kuh, eastern Alborz, northern Iran. *Estonian Journal of Earth Sciences*, **64**, 121–139.

KOUCHINSKY, A. and BENGTSON, S. 2017. X-ray tomographic microscopy tightens affinity of the early Cambrian *Oymurania* to the brachiopod stem group. *Acta Palaeontologica Polonica*, **62**, 39–43.

LÜTER, C. 2000. The origin of the coelom in Brachiopoda and its phylogenetic significance. *Zoomorphology*, **120**, 15–28.

—— 2001. Larval brooding and development of the micromorph rhynchonellid *Tethyrhynchia mediterranea* (Brachiopoda: Recent). *Journal of the Marine Biological Association of the United Kingdom*, **81**, 939–942.

McGHEE, G. R. Jr, SHEEHAN, P. M., BOTTJER, D. J. and DROSER, M. L. 2012. Ecological ranking of Phanerozoic biodiversity crises: the Serpukhovian (early Carboniferous) crisis had a greater ecological impact than the end-Ordovician. *Geology*, **40**, 147–150.

—— CLAPHAM, M. E., SHEEHAN, P. M., BOTTJER, D. J. and DROSER, M. L. 2013. A new ecological-severity ranking of major Phanerozoic biodiversity crises. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **370**, 260–270.

MERGL, M. 2002. Linguliformean and craniiformean brachiopods of the Ordovician Třenice to Dobrotiva formations of Barrandian, Bohemia. *Acta Musei Nationalis Pragae, Series B, Historia Naturalis*, **58**, 1–82.

MOYSIUK, J., SMITH, M. R. and CARON, J.-B. 2017. Hyoliths are Palaeozoic lophophorates. *Nature*, **541**, 394–397.

MURDOCK, D. J. E., BENGTSON, S., MARONE, F., GREENWOOD, J. M. and DONOGHUE, P. C. J. 2014. Evaluating scenarios for the evolutionary assembly of the brachiopod body plan. *Evolution & Development*, **16**, 13–24.

NESNIDAL, M. P., HELMKAMPF, M., MEYER, A., WITEK, A., BRUCHHAUS, I., EBERSBERGER, I. and HAUSDORF, B. 2013. New phylogenomic data support the monophyly of Lophophorata and an Ectoproct-Phoronid clade and indicate that Polyzoa and Kryptrochozoa are caused by systematic bias. *BMC Evolutionary Biology*, **13**, 253.

—— —— BRUCHHAUS, I., EBERSBERGER, I. and HAUSDORF, B. 2014. Lophophorata monophyletic – after all. 127–142. *In* WAGELE, J. W. and BARTOLOMAEUS, T. (eds). *Deep metazoan phylogeny: the backbone of the tree of life: new insights from analyses of molecules, morphology and theory of data analysis*. Walter De Gryter, Berlin.

NEUMAN, R. B. 1984. Geology and paleobiology of islands in the Ordovician Iapetus Ocean: review and implications. *Geological Society of America Bulletin*, **95**, 1188–1201.

NIELSEN, C. 2001. *Animal evolution: interrelationships of the living phyla*. 2nd edn. Oxford University Press.

—— 2002. The phylogenetic position of Entoprocta, Ectoprocta, Phoronida, and Brachiopoda. *Integrative & Comparative Biology*, **42**, 685–691.

—— 2005. Trochophora larvae: cell-lineages, ciliary bands and body regions. 2. Other groups and general discussion. *Journal of Experimental Zoology B: Molecular & Developmental Evolution*, **304**, 401–447.

—— 2012. *Animal evolution: interrelationships of the living phyla*. 3rd edn. Oxford University Press.

NIKIFOROVA, O. I. and POPOV, L. E. 1981. New data on the Ordovician Rhynchonellidae of the Kazakh SSR and Central Asia. *Paleontologicheskii Zhurnal*, **1981**, 54–67.

NIKITIN, I. F. and POPOV, L. E. 1984. Part II. Brachiopods from the Bestamak and Sargaldak Formations (Middle Ordovician). 126–166. *In* BANDALETOV, S. M. (ed.) *Brachiopods and biostratigraphy of the Middle and Upper Ordovician of the Chingiz Range*. Nauka, Alma-Ata, 196 pp.

—— —— and BASSETT M. G. 2003. Late Ordovician brachiopods from the Selety river basin, north Central Kazakhstan. *Acta Palaeontologica Polonica*, **48**, 39–54.

—— —— —— 2006. Late Ordovician rhynchonelliformean brachiopods of north-central Kazakhstan. *In* BASSETT M. G. and DEISLER, V. K. (eds). *Studies in Palaeozoic palaeontology*. National Museum of Wales Geological Series, **25**, 223–294.

PANDER, C. H. 1830. *Beiträge zur Geognosie des Russischen Reiches*. K. Kray, St Petersburg, Russia, 165 pp.

PAPS, J., BAGUNA, J. and RIUTORT, M. 2009. Lophotrochozoa internal phylogeny: new insights from an up-to-date analysis of nuclear ribosomal genes. *Proceedings of the Royal Society B*, **276**, 1245–1254.

PASSAMANECK, Y. J. and HALANYCH, K. M. 2006. Lophotrochozoan phylogeny assessed with LSU and SSU data: evidence of lophophorate polyphyly. *Molecular Phylogenetics & Evolution*, **40**, 20–28.

PELMAN, YU. L., AKSARINA, N. A., KONEVA, S. P., POPOV, L. E., SOBOLEV, L. P. and USHATINSKAYA, G. T. 1992. *The most ancient brachiopods of the territory of northern Euroasia*. United Institute of Geology, Geophysics & Mineralogy, Siberian Branch, Russian Academy of Sciences, Novosibirsk, 145 pp. [in Russian]

PETERSON, K. J. and EERNISSE, D. J. 2001. Animal phylogeny and the ancestry of bilaterians: inferences from morphology and 18S rDNA gene sequences. *Evolution & Development*, **3**, 170–205.

POPOV, L. E. 1992. The Cambrian radiation of brachiopods. 399–423. *In* LIPPS, J. H. and SIGNOR, P. W. (eds). *Origin and early evolution of Metazoa*. Pergamon.

—— and COCKS, L. R. M. 2013. The radiation of early Silurian spiriferide brachiopods, with new taxa from the Llandovery of Iran. *Alcheringa*, **37**, 558–564.

—— and HOLMER, L. E. 2000. Class Chileata. 193–196. *In* KAESLER, R. L. (ed.) *Treatise on invertebrate paleontology. Part H. Brachiopoda (Revised) 2*. Geological Society of America & University of Kansas Press.

—— and TIKHONOV, JU. A. 1990. Early Cambrian brachiopods from southern Kirgizia. *Paleontologicheskii Zhurnal*, 1990, 33–46. [in Russian]

—— —— 1993. New findings of the Middle Cambrian silicified articulated brachiopods in South Kyrgyzstan. 33–40. *In* MAMBETOV, A. M. (ed.) *New data on the Precambrian and Palaeozoic biostratigraphy of Kyrgyzstan*. Ilim, Bishkek, 159 pp. [in Russian]

—— BASSETT, M. G., HOLMER, L. E. and LAURIE, J. 1993. Phylogenetic analysis of higher taxa of Brachiopoda. *Lethaia*, **26**, 1–5.

—— HOLMER, L. E. and BASSETT, M. G. 1996. Radiation of the earliest calcareous brachiopods. 209–213. *In* COPPER, P. and JIN, J. (eds). *Brachiopods*. Proceedings of the 3rd International Brachiopod Congress, Sudbury, Ontario, Canada. .

—— —— ROWELL, A. J. and PEEL, J. S. 1997. Early Cambrian brachiopods from North Greenland. *Palaeontology*, **40**, 337–354.

—— NIKITIN, I. F. and SOKIRAN, E. V. 1999. The earliest atrypides and athyridides (Brachiopoda) from the Ordovician of Kazakhstan. *Palaeontology*, **42**, 625–661.

—— BASSETT, M. G. and HOLMER, L. E. 2000*a*. Class Craniata. 158–164. *In* KAESLER, R. L. (ed.) *Treatise on invertebrate paleontology. Part H. Brachiopoda (Revised) 2*. Geological Society of America & University of Kansas Press.

—— —— —— 2000*b*. Class Obolellata. 200–208. *In* KAESLER R. L. (ed.) *Treatise on invertebrate paleontology. Part H. Brachiopoda (Revised) 2*. Geological Society of America & University of Kansas Press.

—— VINN, O. and NIKITINA, O. I. 2001. Brachiopods of the redefined family Tritoechiidae from the Ordovician of Kazakhstan and South Urals. *Geobios*, **34**, 131–155.

—— EGERQUIST, E. and ZUYKOV, M. A. 2005. Ordovician (Arenig–Caradoc) Syntrophiidine brachiopods from the East Baltic region. *Palaeontology*, **48**, 739–761.

—— BASSETT, M. G. and HOLMER, L. E. 2007*a*. Craniata. 2590–2594. *In* KAESLER, R. L. and SELDON, P. A. (eds). *Treatise on invertebrate paleontology. Part H. Brachiopoda (Revised) 6*. Geological Society of America & University of Kansas Press.

—— EGERQUIST, E. and HOLMER, L. E. 2007*b*. Earliest ontogeny of Middle Ordovician rhynchonelliform brachiopods (Clitambonitoidea and Polytoechioidea): implications for brachiopod phylogeny. *Lethaia*, **40**, 85–96.

—— BASSETT, M. G., HOLMER, L. E. and GHOBADI POUR, M. 2009. Early ontogeny and soft tissue preservation in siphonotretide brachiopods: new data from the Cambrian–Ordovician of Iran. *Gondwana Research*, **16**, 151–161.

—— —— —— SKOVSTED, C. B. and ZUYKOV, M. A. 2010. Earliest ontogeny of Early Palaeozoic Craniiformea: implications for brachiopod phylogeny. *Lethaia*, **43**, 323–333.

—— GHOBADI POUR, M., KEBRIA-EE ZADEH, M.-R. and SHAHBEIK, S. 2011. First record of silicified Cambrian (Furongian) rhynchonelliform brachiopods from the Mila Formation, Alborz Range, Iran. *Memoirs of the Association of Australasian Palaeontologists*, **42**, 193–207.

—— BASSETT, M. G. and HOLMER, L. E. 2012. Earliest ontogeny of Early Palaeozoic Craniiformea: compelling evidence for lecithotrophy. *Lethaia*, **45**, 566–573.

—— HOLMER, L. E., GHOBADI POUR, M. and PERCIVAL, I. G. 2013*a*. Biogeography of Ordovician linguliform and craniiform brachiopods. *In* HARPER, D. A. T. and SERVAIS, T. (eds). *Early Palaeozoic biogeography and palaeogeography*. Geological Society London, Memoir, **38**, 117–126.

—— KEBRIA-EE, ZADEH, M. R., GHOBADI POUR, M., HOLMER, L. E. and MODZALEVSKAYA, T. L. 2013*b*. Cambrian (Furongian) rhynchonelliform brachiopods from the Eastern Alborz Mountains, Iran. *Bulletin of Geosciences*, **88**, 525–538.

—— HAIRAPETIAN, V., EVANS, D. H., GHOBADI POUR, M., HOLMER, L. E. and BAARS, C. 2015. Review of the Ordovician stratigraphy and fauna of the Anarak Region in Central Iran. *Acta Geologica Polonica*, **65**, 403–435.

—— KEBRIAEE-ZADEH, M. R. and GHOBADI POUR, M. 2016. Emergence of the *Saucrorthis* Fauna in the Middle Ordovician of northern Iran. *Australasian Palaeontological Memoirs*, **49**, 485–514.

RASMUSSEN, C. M. Ø. 2014. Phylogeography of Ordovician–Silurian rhynchonelliformean brachiopods: tracking higher order distributional patterns, radiations and extinctions in 4D. *GFF*, **136**, 223–228.

ROBINSON, J. 2014. The muscles, body wall and valve-opening mechanism of extant craniid (inarticulated) brachiopods. *Journal of Natural History*, **48**, 1231–1252.

RONG, J. Y. and COCKS, L. R. M. 1994. True *Strophomena* and a revision of the classification and evolution of strophomenoid and 'strophodontoid' brachiopods. *Palaeontology*, **37**, 651–694.

—— REN-BIN, Z. and HARPER, D. A. T. 1999. The late Ordovician (Caradoc-Ashgill) *Foliomena* (Brachiopoda) fauna from China: implications for its origin, ecological evolution and global distribution. *Palaios*, **14**, 412–431.

—— BOUCOT, A. J., HARPER, D. A. T., ZHAN, R.-B. and NEUMAN, R. B. 2006. Global analysis of brachiopods through the Ordovician and Silurian transition: reducing the role of the Lazarus effect. *Canadian Journal of Earth Sciences*, **43**, 23–39.

RUDWICK, M. 1970. *Living and fossil brachiopods*. Hutchinson University Library, London, 199 pp.

SANTAGATA, S. and COHEN, B. L. 2009. Phoronid phylogenetics (Brachiopoda; Phoronata): evidence from morphological cladistics, small and large subunit rDNA sequences, and mitochondrial cox1. *Zoological Journal of the Linnean Society*, **157**, 34–50.

SCHIEMANN, S. M., MARTÍN-DURÁN, J. M., BØRVE, A., VELLUTINI, B. C., PASSAMANECK, Y. J. and HEJNOL, A. 2017. Clustered brachiopod Hox genes are not expressed collinearly and are associated with lophotrochozoan novelties. *Proceedings of the National Academy of Sciences*, **114**, E1913–E1922.

SCHMIDT, F. 1858. Untersuchungen über die silurische Formation von Ehstland, Nord-Livland und Oesel. *Archiv für die Naturkunde Liv-, Ehst- und Kurlands*, Serie 1 (2), Dorpat, 250 pp.

SCHWAHA, T. and WANNINGER, A. 2012. Myoanatomy and serotonergic nervous system of plumatellid and fredericellid Phylactolaemata (Lophotrochozoa, Ectoprocta). *Journal of Morphology*, **273**, 57–67.

SDZUY, K., HAMMAN, W. and VILLAS, E. 2001. The Upper Tremadoc fauna from Vogtendorf and the Bavarian Ordovician of the Frankenwald. *Senckenbergiana Lethaea*, **81**, 207–261.

SKOVSTED, C. B. and HOLMER, L. E. 2003. The Early Cambrian (Botomian) stem group brachiopod *Mickwitzia* from Northeast Greenland. *Acta Palaeontologica Polonica*, **48**, 1–20.

—— USHATINSKAYA, G., HOLMER, L. E., POPOV, L. E. and KOUCHINSKY, A. 2015. Taxonomy, morphology, shell structure and early ontogeny of *Pelmanotreta* nom. nov. from the lower Cambrian of Siberia. *GFF*, **137**, 1–8.

SMITH, M. R. 2014. Ontogeny, morphology and taxonomy of the soft-bodied Cambrian 'mollusc' *Wiwaxia*. *Palaeontology*, **57**, 215–229.

SOWERBY, J. de C. 1839. Shells. 589–712. *In* MURCHISON, R. I. (ed.) *The Silurian System*. John Murray, London, 768 pp.

SPERLING, E. A., PISANI, D. and PETERSON, K. J. 2011. Molecular paleobiological insights into the origin of the Brachiopoda. *Evolution & Development*, **13** (3), 290–303.

STRENG, M., BUTLER, A. D., PEEL, J. S., GARWOOD, R. J. and CARON, J. B. 2016. A new family of Cambrian rhynchonelliformean brachiopods with an aberrant coral-like morphology. *Palaeontology*, **59**, 269–293.

TELFORD, M. J. 2006. Animal phylogeny. *Current Biology*, **16**, R981–R985.

TEMEREVA, E. N. and TSITRIN, E. B. 2015. Modern data on the innervation of the lophophore in *Lingula anatina* (Brachiopoda) support the monophyly of the lophophorates. *PLoS ONE*, **10** (4), e0123040.

TOLMACHEVA, T., HOLMER, L., POPOV, L. and GOGIN, I. 2004. Conodont biostratigraphy and faunal assemblages in radiolarian ribbon-banded cherts of the Burubaital Formation, West Balkhash Region, Kazakhstan. *Geological Magazine*, **14**, 699–715.

TOPPER, T. P., HARPER, D. A. T. and BROCK, G. A. 2013. Ancestral billingsellides and the evolution and phylogenetic relationships of early rhynchonelliform brachiopods. *Journal of Systematic Palaeontology*, **11**, 821–833.

—— STROTZ, L. C., HOLMER, L. E. and CARON, J.-B. 2015. Survival on a soft seafloor: life strategies of brachiopods from the Cambrian Burgess Shale. *Earth-Science Reviews*, **151**, 266–287.

—— ZHANG, Z., GUTIÉRREZ MARCO, J. C. and HARPER, D. A. T. in press. The dawn of a dynasty: life strategies of Cambrian and Ordovician brachiopods. *Lethaia*.

USHATINSKAYA, G. T. 2008. Origin and dispersal of the earliest brachiopods. *Paleontological Journal* **42**, 776–791. [English translation]

VALENTINE, J. M. 1977. General patterns in metazoan evolution. 27–54. *In* HALLAM, A. (ed.) *Patterns of evolution as illustrated by the fossil record*. Elsevier, 591 pp.

VINTHER, J. and NIELSEN, C. 2005. The Early Cambrian *Halkieria* is a mollusc. *Zoologica Scripta*, **34**, 81–89.

—— PARRY, L., BRIGGS, D. E. G. and ROY, P. VAN 2017. Ancestral morphology of crown-group molluscs revealed by a new Ordovician stem aculiferan. *Nature*, **542**, 471–474.

WILLIAMS, A. 1956. The calcareous shell of the Brachiopoda and its importance to their classification. *Biological Reviews*, **31**, 243–287.

—— and CUSACK, M. 2007. Chemicostructural diversity of the brachiopod shell. 2396–2521. *In* SELDEN, P. A. (ed.) *Treatise on invertebrate paleontology. Part H. Brachiopoda (Revised) 6*. Geological Society of America & University of Kansas Press.

—— and HARPER, D. A. T. 2000. Orthida. 714–782. *In* KAESLER, R. L. (ed.) *Treatise on invertebrate paleontology. Part H. Brachiopoda (Revised) 3*. Geological Society of America & University of Kansas Press.

—— and HURST, J. M. 1977. Brachiopod evolution. *Developments in Palaeontology & Stratigraphy*, **5**, 79–121.

—— and ROWELL, A. J. 1965. Evolution and phylogeny. 164–199. *In* MOORE, R. C. (ed.) *Treatise on invertebrate paleontology. Part H*. University of Kansas Press, 927 pp.

—— CARLSON, S. J., BRUNTON, C. H. C., HOLMER, L. E. and POPOV, L. E. 1996. A supra-ordinal classification of the Brachiopoda. *Philosophical Transactions of the Royal Society B*, **35**, 1171–1193.

—— JAMES, M. A., EMIG, C. C., MACKAY, S. and RHODES, M. 1997. Anatomy. 7–188. *In* KAESLER, R. (ed.). *Treatise on invertebrate paleontology. Part H. Brachiopoda (Revised) 1*. Geological Society of America & University of Kansas Press.

—— POPOV, L. E., HOLMER, L. E. and CUSACK, M. 1998. The diversity and phylogeny of the paterinate brachiopods. *Palaeontology*, **41**, 221–262.

WRIGHT, A. D. 1979. Brachiopod radiation. 235–252. *In* HOUSE, M. R. (ed.) *The origin of major invertebrate groups*. Systematics Association Special Volume, **12**, Academic Press, 515 pp.

ZHANG, A. and HOLMER, L. E. 2013. Exceptionally preserved brachiopods from the Chengjiang Lagerstätte (Yunnan, China): perspectives on the Cambrian explosion of metazoans. *Science Foundation in China*, **21**, 66–80.

ZHANG, X.-G., HOU, X.-G. and EMIG, C. C. 2003. Evidence of lophophore diversity in Early Cambrian. *Proceedings of the Royal Society of London B*, **270** (Suppl. 1), S65–S68.

ZHANG, Z., LI, G., EMIG, C. C., HAN, J., HOLMER, L. E. and SHU, D. 2009. Architecture and function of the lophophore in the problematic brachiopod *Heliomedusa orienta* (Early Cambrian, South China). *Geobios*, **42**, 145–150.

ZHANG, A., HOLMER, L. E., POPOV, L. E. and SHU, D. 2011*a*. An obolellate brachiopod with soft-part preservation from the early Cambrian Chengjiang Fauna of China. *Journal of Paleontology*, **85**, 460–463.

—— —— QIANG, Q., HAN, J. and SHU, D. 2011*b*. The exceptionally preserved early Cambrian stem rhynchonelliform brachiopod *Longtancunella* and its implications. *Lethaia*, **44**, 490–495.

—— —— SKOVSTED, C., BROCK, G. and BUDD, G. E. 2013. A sclerite-bearing stem group entoproct from the early Cambrian and its implications. *Scientific Reports*, **3**, 1066.

—— LI, G.-X., HOLMER, L. E., BROCK, G. A., BALTHASAR, U., SKOVSTED, C. B., FU, D.-J., ZHANG, X.-L., WANG, H.-Z., BUTLER, A., ZHANG, Z.-L., CAO, C.-Q., HAN, J., LIU, J.-N. and SHU, D.-G. 2014. An early Cambrian agglutinated tubular lophophorate with brachiopod characters. *Scientific Reports*, **44**, 4682.

—— HOLMER, L. E. and LI, G. 2015. First report of linguloid brachiopods with soft parts from the lower Cambrian (Series 2, Stage 4) of the Three Gorges area, South China. *Annales de Paléontologie*, **101**, 167–177.

ZHURAVLEV, A. YU., WOOD, R. A. and PENNY, A. M. 2015. Ediacaran skeletal metazoan interpreted as a lophophorate. *Proceedings of the Royal Society B*, **282**, 20151860.