Phylogenetic relationships of leptellinid brachiopods

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The relationships among the diverse genera comprising the family Leptellinidae (Brachiopoda) are reviewed in the light of the revised edition of the *Treatise on Invertebrate Palaeontology*. Taxonomic work reassessed all the genera identified as Leptellinidae in the most current classification. Four genera were discarded, namely *Bekkerella, Benignites, Leptastichidia* and *Nikitinamena*. Cladistic analysis reveals the paraphyly of these genera; their abandonment leading to more morphologically coherent subdivisions of the family. Two subfamilies, Leptellininae and Palaeostrophomeninae, are emended and taxonomically restructured. The palaeogeographical history of the Leptellinidae is complicated. The Leptellinidae are first recorded in Baltica in the late Floian (Early Ordovician) and rapidly dispersed to circum-Iapetus palaeocontinents by the Dapingian, thence to most terranes composing Gondwana by the Darriwilian (Middle Ordovician).

LEPTELLINIDAE is an important family both palaeoecologically and phylogenetically. The family is constrained almost exclusively to the Ordovician (a single genus has been described from the Silurian). It is found in many terranes across Gondwana and also in all the peri-Iapetan palaeocontinents. Genera from this family are also common components of brachiopod faunas of this age (see for example Patzkowsky 1995), and are described as belonging to Benthic Associations 2 to 4 (see for example Nikitina *et al.* 2006, Potter & Boucot 1992) and seldomly BA 5 (Candela 2006) environments. The Leptellinidae evolved early among the plectambonitoid brachiopods, appearing first in Baltica during the Floian. The family diversified in the Dapingian, achieving maximum diversity during the Darriwilian to Sandbian (Fig. 1). The generic diversity dropped drastically (to half the number of genera) in the late Katian, although a third articulated brachiopod radiation occurred at the beginning of late Katian (Harper 2006). This pattern has been observed among other brachiopod clades as diversity dropped, and extinction rates exceeded origination rates in the later phases of the Ordovician (Harper *et al.* 2004). The Leptellinidae collapsed in diversity and almost disappeared through the Hirnantian, which witnessed a radical climate change that lead to a severe drop in sea level. A single genus belonging to the Leptellinidae is recorded in the upper Llandovery of North China and England, which are the last occurrences of the family. At a higher taxonomic level (i.e. families) the faunal dynamics show a slightly different pattern. In the Llanvirn, ten families of Plectambonitoidea are distributed worldwide (Fig. 1). By the late Caradoc, four families became extinct, and two more families were affected by the Hirnantian extinction events. In total, two of these ten families continued to thrive up to the Devonian. As a whole, the Plectambonitoidea were affected significantly by the Late Ordovician glaciation events with six genera

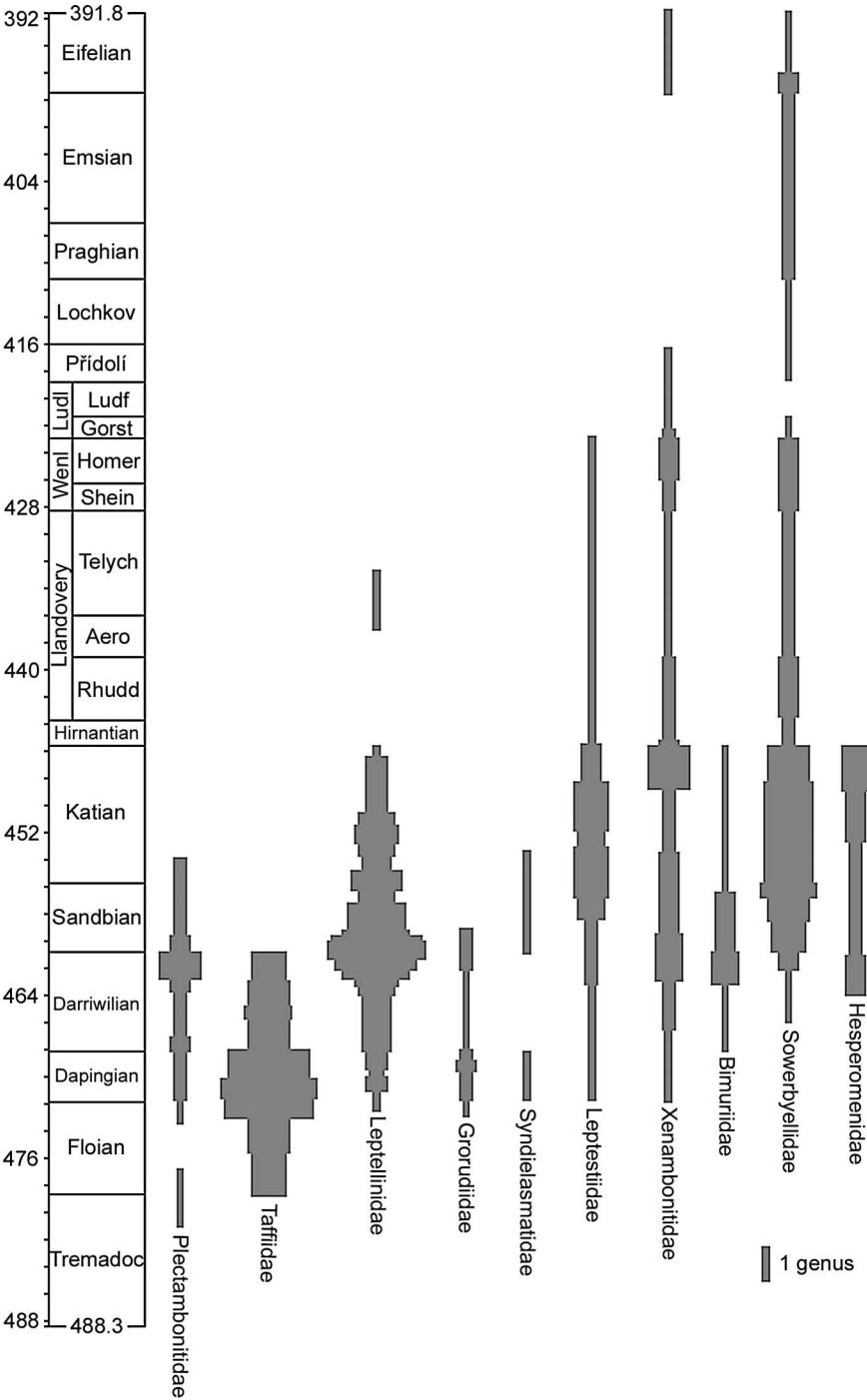*Fig. 1.* Stratigraphical range of the Plectambonitoidea families, as defined by Cocks & Rong (2000, 2007), with absolute abundance of genera, arranged in chronological order of first appearance (left to right). Tremadoc = Tremadocian, Rhudd = Rhuddanian, Aero = Aeronian, Telych = Telychian, Wenl = Wenlock, Shein = Sheiwoodian, Homer = Homerian, Ludl = Ludlow, Gorst = Gorstian, Ludf = Ludfordian, Lochkov = Lochkovian.

recorded at the beginning of the Silurian against 21 genera pre-Hirnantian.

The Plectambonitoidea are phylogenetically important. Strophomenoidea are interpreted to derive from the former probably in the early Arenig; the earliest known strophomenoid being from North China (Rong *et al.* 1999). Rong & Cocks (1994) also argued that strophomenoid brachiopods have their ancestors within the Leptellinidae. It is, therefore, important to understand the phylogenetic affiliations within the Leptellinidae in order to understand the relationships of the Strophomenoidea.

Since the work undertaken by Cocks & Rong (1989), new genera have been described and added to the family Leptellinidae, which is divided into the subfamilies Leptellininae and Palaeostrophomeninae, as described in the revised edition (and addenda) of the Treatise on Invertebrate Paleontology (Cocks & Rong 2000, 2007). These taxa form the core of the present study. However, careful review of the Leptellinidae has revealed discrepancies in the classification. Some generic descriptions are not consistent with the diagnosis of the family and/or subfamilies. For example, *Benignites* possesses a simple cardinal process instead of a trifid cardinal process.

Review of the Leptellinidae genera

Cocks & Rong (1989) undertook the first review of the plectambonitoid brachiopods by compiling and analyzing the new genera described since Williams (1965). This work and their later updated classification of the plectambonitoids (Cocks & Rong 2000, 2007) in general and the leptellinids in particular is generally accepted as the foundation for current brachiopod research. Laurie (1991), however, critically discussed the 1989 classification and argued that the system employed by Cocks & Rong is based on the combination of seven states and three characters resulting in 'a simple permutational taxonomy, the ten combinations of which were all assigned a family name'. Nevertheless, Laurie (1991) assigned the Leptellinae Williams, 1965 back to the Leptellinidae, rather than to the Taffiidae where Cocks & Rong (1989) had placed it, on the basis of differences in dorsal mantle canal system and musculature with the latter. In this instance, Laurie (1991) grouped genera both lacking and possessing a cardinal process. I contend that the updated classification by Cocks & Rong (2000) should be followed in separating the Leptellinae from the Leptellinidae.

Laurie (1991) also criticized the argument by Cocks & Rong (1989) that genera with a trifid cardinal process were a 'more advanced group of genera' than those with a simple cardinal process. I agree with Laurie's criticism in that the evolution of the cardinal process is not as simple as that. The cardinal process is a plesiomorphic character, and as Laurie pointed out, a simple cardinal process is a recurrent character in the phylogeny of the Leptellinidae.

Cocks & Rong (1989, 2000) defined the Leptellinidae as follows: 'concavo-convex to resupinate shells; dental plates present; trifid cardinal process not undercut; no side septa; no bema'. The family was divided into two subfamilies: the Leptellininae were differentiated from the Palaeostrophomeninae on the basis of a restricted ventral muscle field. The latter possesses a large, open ventral muscle field and deeply impressed mantle canal markings. This classification poses problems because dental plates are not always present within the family (e.g. *Kajnaria* Nikitin & Popov in Klenina, Nikitin & Popov, 1984 and *Lepidomena* Laurie, 1991 as in Cocks & Rong 2000, p. 322, 326). Moreover, the broad criteria dividing the two subfamilies do not seem to be supported morphologically. For example, *Titanambonites* Cooper, 1956 and

Glyptambonites Cooper, 1956 are both palaeostrophomenine brachiopods with, respectively, an open and a restricted ventral muscle field. Cocks & Rong (2000, p. 324) stated that a 'large open ventral valve muscle field' is diagnostic of the subfamily Palaeostrophomeninae). Cocks & Rong (1989) did not assign *Goniotrema* Cooper, 1956 to any family with confidence, although they stated that the 'correct systematic position of the genus remains unknown' (p. 148) but that it 'may perhaps be a leptellinid' (p. 148). The genus is characterized by a weak platform. It was questionably assigned to the Palaeostrophomeninae within the Leptellinidae (Cocks & Rong 2000). However, the same authors noted that the presence of 'faint traces of possible side septa' did not exclude its inclusion in the Syndielasmatidae. In conclusion, they considered that *Goniotrema* is 'not certainly leptellinid'. *Goniotrema* is internally very similar to *Sowerbyites* Teichert, 1937 (see also Cooper 1956, p. 711). It possesses a ventral muscle field open anteriorly and restricted laterally by a pair of bounding ridges, and dorsally, an identically trifid cardinal process and a median septum flanked by a pair of oblique ridges. Cocks & Rong (1989, 2000) described a platform in the dorsal interiors. That feature is in my opinion due to the concavity of the dorsal valve that is expressed internally and is not a consistent morphological character developed throughout ontogeny (a similar pattern is evident in dorsal interiors of *Sowerbyites*). Moreover, Cooper (1956, p. 711) did not mention that feature in his diagnosis and closely compared *Goniotrema* with *Sowerbyites*. Therefore, *Sowerbyites* is best placed within the Leptellinidae with *Goniotrema* based on the presence of dorsal oblique septa in the muscle field, similar trifid cardinal process and similar ventral muscle field. Laurie (1991) was correct in pointing out that the classification by Cocks & Rong (1989) shows, in some places, 'bizarre' assignments (for example *Sowerbyites vesciseptus*

Percival, 1979 synonymized with *Bilobia*). Moreover, Laurie criticized the choice by Cocks & Rong of synonymizing *Sowerbyites* and *Syndielasma*. I agree with Laurie that these two genera do not possess similar side septa. Therefore, the paired systematic position of *Syndielasma* and *Sowerbyites* should be revised. Cocks & Zhan (1998) included *Bekkerella* Reed, 1936 in the Leptellinidae on the basis that some of the specimens possessed a trifid cardinal process. However, no illustration was provided to warrant the description. The dorsal adductor scars are dalmanelloid-like, arranged postero-anteriorly in two pairs, which is peculiar for the Leptellinidae. The ventral muscle scar is also very unusual for the family. Cocks & Rong (2000) overlooked the description of the cardinal process as trifid. The lack of photographic evidence in support of the description favours exclusion of *Bekkerella* from the Leptellinidae.

Benignites Havlíček, 1952 was synonymized with *Leptellina* Ulrich & Cooper, 1936 by Havlíček (1967, p. 27). This opinion was followed by Cocks & Rong (1989, p. 104) in their review of the plectambonitoid brachiopods. However, Havlíček (1952, 1967) stated that the dorsal valves of *Benignites* possess a simple cardinal process. Therefore, this genus can not be maintained within the Leptellinidae.

Leptastichidia Zhan & Jin, 2005, *Anchoramena* Benedetto, 1995, *Nikitinamena* Popov & Cocks, 2006 and *Tesikella* Popov, Cocks & Nikitin, 2002 are recent additions to the family Leptellinidae that were included in volume 6 of the Treatise on Invertebrate Paleontology dedicated to the Brachiopoda (Cocks & Rong 2007). Zhan & Jin (2005) assigned *Leptastichidia*, from the Middle Ordovician of China, to the family Leptellinidae and subfamily Leptellininae (p. 34, 35). It is characterized by a 'ventral muscle field small, trilobed with straight anterior margin' and a 'cardinal process bulbous or ridge-like'. Cocks & Rong (2007)

assigned *Leptastichidia* to the subfamily Palaeostrophomeninae. However, the diagnosis for the Palaeostrophomeninae provided in volume 2 (Cocks & Rong 2000) states that specimens assigned to this subfamily must possess a 'large open ventral valve muscle field'. Moreover, the Leptellinidae groups genera having a trifid cardinal process.

Popov & Cocks (2006, p. 266) compared *Nikitinamena* with *Apatomorpha* Cooper, 1956, *Titanambonites* and *Sowerbyites* based on the 'single cardinal process and bilobed ventral muscle field with short adductor scars completely separating large, diverging diductor scars' (p. 266). Leptellinidae possess a trifid cardinal process, therefore, *Nikitinamena* has to be discarded from the family.

On the other hand, *Anchoramena* and *Tesikella* possess the diagnostic features of the Leptellinidae. Moreover, *Lepidomena* possesses a trifid cardinal process with a high median crest projecting posteriorly to the hinge line.

Laurie (1991) also viewed *Ishimia*, *Lepidomena*, *Goniotrema* and *Titanambonites* as a single familial unit, namely the Titanambonitidae, on the basis of the mantle canal systems and the ventral muscle field anatomy. These four genera have differences in their dorsal valve interiors (*viz.* relating to the presence or absence of a platform and a trifid or a high simple cardinal process). I do not follow Laurie's (1991) concept of Titanambonitidae. Moreover, Laurie (1991) criticized the fact that Cocks & Rong (1989) placed *Ishimia* in synonymy with *Toquimia*. This was corrected in the revised classification (Cocks & Rong 2000). In the light of the discussion above, *Bekkerella*, *Benignites, Leptastichidia* and *Nikitinamena* are rejected from the Leptellinidae and are not included in the present study.

A new genus described by Candela & Harper (2010), *Kilbuchomena*, was based on material from the lower Katian of Pomeroy, Northern Ireland and Kilbucho, Scotland. It possesses the diagnostic characters of the Leptellinidae, i.e. trifid cardinal process, no side septa and no bema, hence it is included in the present study.

Methods

The morphological data were collected from various bibliographical sources, in particular Cocks & Rong (2000, 2007) and those containing the original descriptions of the genera. Scoring of the taxonomically significant characters (Appendix 1) produced a data matrix (Appendix 2) that was analysed using the PAUP program (Swofford 1992).

The Taffiidae was considered by Cocks & Rong (1989) to form the ancestral stock for the Leptellinidae. Plesiomorphic states of the characters are those of *Taffia* Butts, 1926. The lower Arenig *Taffia* is characterized by the absence of a cardinal process and a median septum, and the presence of a low platform. It does not possess the trifid cardinal process or side septa typical of some later plectambonitoids.

Phylogenetic analysis

Fifty-five character states were determined for 20 unordered and unweighted characters. A heuristic search was performed using tree bisection and reconnection (TBR) and a Fitch optimization criterion, in which characters are unordered and reversible and fewer assumptions than other optimization criteria available in the software are taken.

Seven trees were produced with a consistency index (CI) of 0.376, a retention index (RI) of 0.513, a homoplasy index (HI) of 0.624 and a re-scaled consistency index (RCI) of 0.193 (Fig. 2A shows the strict consensus tree). The analysis was run a second time with data re-weighed using the RCI to determine the most consistent characters (see Farris 1989). Nine trees were obtained. A strict consensus tree (Fig. 2B) has a CI of 0.507, a RI of 0.656 and a HI of
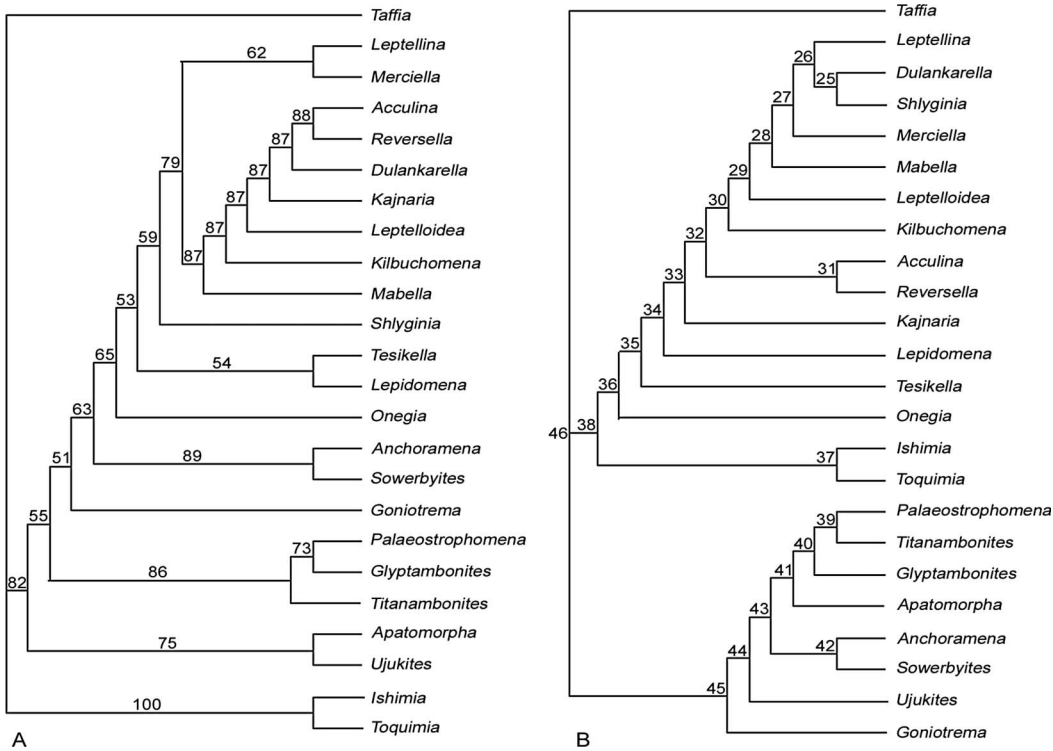
Fig. 2. **A**, 50% majority-rule consensus of 7 trees. Consistency index (CI) = 0.376; Retention Index (RI) = 0.513; Homoplasy Index (HI) = 0.624; Rescaled Consistency Index (RCI) = 0.193. Numbers above the branches indicate the percentage of trees that support each branch. **B**, After re-weighting using the RCI, nine trees were produced. 50% majority-rule consensus of nine trees: CI = 0.507; RI = 0.656; HI = 0.493. Nodes are numbered 43–41.

0.493. A list of synapomorphies is presented in Appendix 3.

The cladogram shows two groups (Fig. 2B; Node 46–38 and Node 46–45). All genera from both groups share a trifid and not undercut cardinal process. Group 1 (from Node 38) contains genera that were assigned to the Leptellininae and Palaeostrophomeninae subfamilies as described by Cocks & Rong (2000). This group is characterized by concavo-convex shells (rarely resupinate), with a rectimarginate to uniplicate anterior profile, and the presence of a platform, to which merges a median septum.

Group 2 (from Node 45) clusters genera that were included solely in the Palaeostrophomeninae, as described by Cocks & Rong (2000, 2007). The taxa belonging to this group are characterized by concavo-convex

to resupinate shells with a rectimarginate anterior profile, acute cardinal extremities, ventral muscle scars that are not restricted anteriorly, and the absence of a platform (Node 46–45; 17: 1→0, CI = 0.600). The genera assigned to this group are *Palaeostrophomena*, *Glyptambonites*, *Titanambonites*, *Apatomorpha*, *Sowerbyites*, *Goniotrema*, *Ujukites* and *Anchoramena*.

In the light of the analysis, emended diagnoses for the subfamilies are as follows:

Subfamily Leptellininae Ulrich & Cooper, 1936

Diagnosis. Anterior profile rectimarginate to uniplicate; presence of platform; median septum merging with platform; oblique ridges in dorsal muscle field absent.

Subfamily Palaeostrophomeninae Cocks & Rong, 1989

Diagnosis. Anterior commissure rectimarginate; cardinal angles acute; median septum present; dorsal muscle field with oblique ridges variably marked; platform absent.

Geographic distribution of the Leptellinidae

Although the oldest member of group 1, *Onegia*, is first recorded during the late Floian in Baltica (Fig. 3), the origin of this group is uncertain. *Onegia* is characterized by, in contrast to younger genera from group 1, a weak trifid cardinal process. This morphological character is shared with a coeval genus from group 2 originating from Kazakhstan, *Ujukites*, and by contemporaneous and older plectambonitoid brachiopods (e.g. *Taffia*, *Borua*, *Ahtiella*). *Onegia* disappeared by the middle Dapingian and is the sole element of group 1 recorded from Baltica until the appearance of *Leptelloidea* and *Leptellina* in the early Sandbian (Fig. 3). The dispersal history of *Leptellina* is interesting because it is a cosmopolitan genus during the Ordovician. It can serve as a template for understanding the dis-
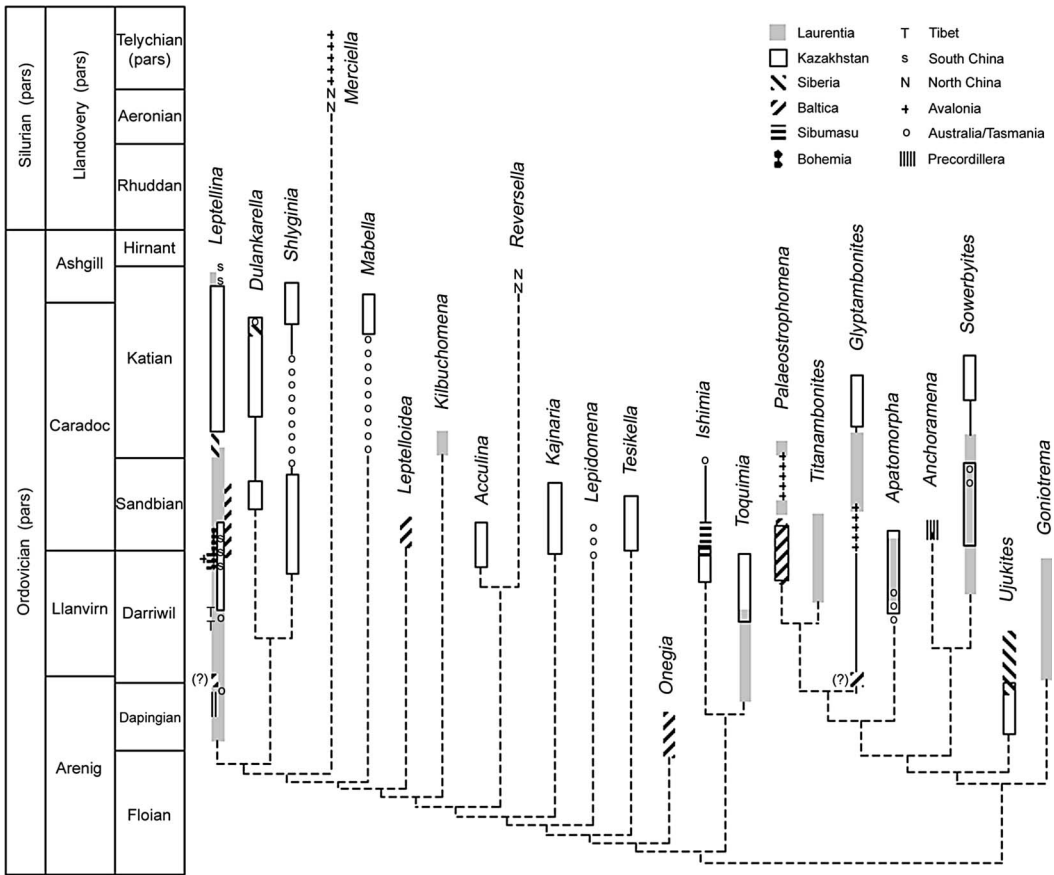
Fig. 3. Stratigraphical ranges and inferred phylogenetic relationships of the Ordovician leptellinid brachiopods. Darriwil. = Darriwilian; Hirnant. = Hirnantian; Rhuddan. = Rhuddanian.

persal pattern of the Leptellinidae during the early Palaeozoic. Modern palaeogeographical models constructed by Torsvik (2009) help comprehend this. The first known occurrence of the genus is from the early Dapingian in Laurentia (Fig. 4). The genus expanded its range quickly to the Precordillera and 'Australian' terranes during the late Dapingian. A putative

occurrence is listed by Rasmussen *et al.* (2007) in Baltica in the early Darriwilian (Fig. 3). This westward dispersal route can be explained by the relative closeness of the Precordillera terrane that acted as a 'stepping stone' for the genus to reach the eastern margins of Gondwana during the early Middle Ordovician. The coeval occurrence in Baltica is not contradictory, as

Fig. 4. Palaeogeographic reconstructions (Mollweide projection) for (**A**) the Dapingian (470 My) and (**B**) the late Darriwilian to early Sandbian (460 My) showing the distribution of key leptellinid brachiopod genera. Black square: *Leptellina*, black diamond: *Onegia*, black star: *Ujukites*, black triangle: *Sowerbyites* and concentric circles: *Glyptambonites*. Redrawn from Torsvik (2009).

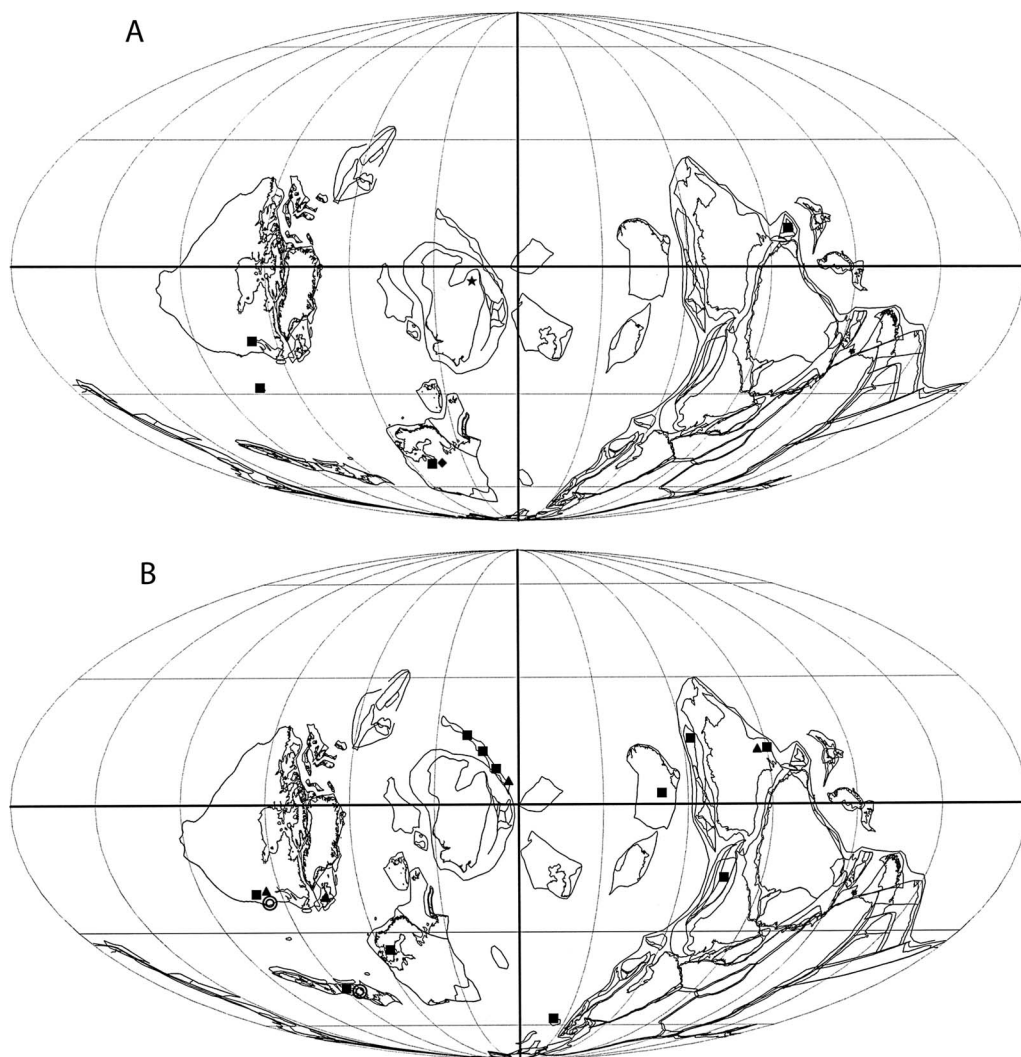palaeo-oceanographic models proposed by Christiansen & Stouge (1999) explain this hypothesis with a westerly gyre towards the eastern margins of Gondwana and an anti-clockwise gyre circulating in the Iapetus. During the middle Darriwilian, *Leptellina* reached the Kazakh terranes, Tibet, and in the late Darriwilian colonized the western margins of 'East' Gondwana (*sensu* Fortey & Cocks 2003) and adjacent terranes, i.e. Sibumasu and South China (Fig. 4). By the early Sandbian, occurrences of *Leptellina* are known from the Bohemian terrane and Avalonia. Nevertheless, the origination of the Leptellinidae in Baltica, supported by the fossil evidence, is plausible as the main peak in brachiopod diversity occurred, according to Rasmussen *et al.* (2007), in Baltica, at the Volkhov–Kunda boundary (late Dapingian–early Darriwilian).

During the late Darriwilian to early Sandbian, the leptellinid brachiopods favoured a distribution in terranes distributed around the eastern margin of Laurentia (*Leptellina, Titanambonites, Apatomorpha, Sowerbyites* and *Goniotrema*) and also the Kazakh terranes (*Shlyginia, Acculina, Kajnaria, Tesikella, Ishimia, Toquimia* and *Apatomorpha*; Fig. 3). Several genera first recorded from Kazakh terranes (*Dulankarella, Ishimia* and *Shlyginia*) extended their geographical distribution to Australia; the reciprocity is also true (*Apatomorpha* and *Mabella*). *Dulankarella* is also found in Siberia in the middle Katian, whereas *Shlyginia* and *Ishimia* are found in the complex Altai-Sayan terrane, which by the Early Ordovician had accreted to Siberia (Cocks & Torsvik 2007). Percival (1995) identified a close affinity of Middle to Late Ordovician benthic faunas inhabiting Kazakhstan, South China and Australia, using the distribution of trimerellide brachiopods. A total of ten occurrences of Leptellinidae are recorded during the late Darriwillian to early Sandbian on the Kazakh terranes, of which six genera

(*Dulankarella, Shlyginia, Acculina, Kajnaria, Tesikella* and *Ishimia*) originated there. This represents almost 50% of the Leptellinidae genera originating at that time. The Kazakh terranes can then be identified as a biodiversity hotspot in the late Darriwilian to early Sandbian.

In the early Katian, *Leptellina*, is recorded on the Siberian Platform. Two migration paths are possible: either from Laurentia or from the Kazakh terranes, as it has already been documented in those areas from the late Darriwilian to early Sandbian. By the middle Katian, the diversity of the Leptellinidae had dramatically decreased with only six genera distributed mainly around the Kazakh terranes (for example *Leptellina, Glyptambonites* and *Sowerbyites*, see Fig. 5) and the northern edge of Gondwana (Australia, for example *Mabella* and *Shlyginia*) and rare, later occurrences on the eastern margin of Laurentia, South China (*Leptellina*, see Fig. 5) and Siberia (*Dulankarella*).

Ujukites, in group 2, is first represented in the lower Dapingian of Kazakhstan (Fig. 3) and dies out in the middle Darriwilian in the Siberian palaeocontinent. Recent advances in palaeogeography have shown that the Kazakh terranes and Siberia were geographically closer than previously hypothesized (Cocks & Torsvik 2007, Torsvik 2009). By the early Darriwilian, taxa from group 2 rapidly extended their geographical range by invading the margins of Laurentia and the tropical province of marginal Gondwana (Liljeroth & Harper 2008). By the Sandbian, group 2 was greatly diversified and had colonized the Baltic-Avalonian province and the Precordillera terrane. However, taxa were more strongly established in Laurentia and the Kazakh terranes, marginal to Siberia, than in any other area. This can be explained by their closer affinities associated with the warm waters of the equatorial Laurentian and Siberian platforms (Liljeroth & Harper 2008).
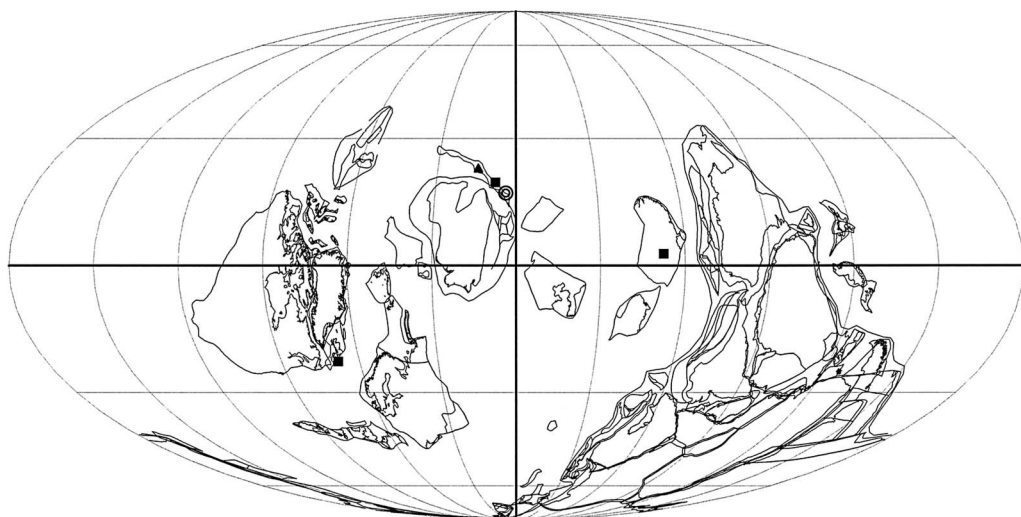
Fig. 5. Palaeogeographic reconstructions (Mollweide projection) for the middle Katian (450 My) with position of key genera. Key as in Fig. 4. Redrawn from Torsvik (2009).

Conclusion

Morphological reassessment of the Leptellinidae has permitted removal of four genera previously assigned to the family (*Bekkerella*, *Benignites*, *Leptastichidia* and *Nikitinamena*). This is supported by the cladistic analysis and leads to a morphologically more consistent group that is divided into two better-defined subfamilies. Leptellininae possess, in dorsal valves, a platform and lack oblique ridges in the muscle field. Palaeostrophomeninae, in dorsal valves, lack a platform but possess oblique ridges variably marked in the muscle field. Plotting the distribution through time of some key genera has permitted a preliminary appraisal of the dispersal route of the Leptellinidae. Originating from Baltica in the late Floian (*Onegia*), the group is recorded on the eastern margins of Laurentia by the Dapingian (*Leptellina*), and colonized circum-Iapetus terranes by the late Darriwilian. From the Sandbian, the group diversified to the east, reaching the Kazakh terranes and subsequently the western margins of Gondwana. The Kazakh terranes appear to constitute a pole of origination for many genera at the Darriwilian–Sandbian boundary. An alternative postulated route of dispersal envisages the group colonizing, to the west, the Precordillera terrane during the Dapingian, to reach the eastern margins of Gondwana (Australia/Tasmania) during the Darriwilian.

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Appendix 1

Characters and character states in the phylogenetic analysis.

Shell shape

1. Outline: subquadrate (0); transversely semioval (1).
2. Profile (Longitudinal): concavo-convex (0); resupinate (1); plano-convex (2).
3. Profile (Transverse): rectimarginate (0); uniplicate (1).
4. Cardinal extremities: rectangular-obtuse (0); acute (1).
5. Shell size (Length): <5 mm (0); 5–10 mm (1); 10–15 mm (2); >15 mm (3).

Ornamentation

6. Radial: unequally parvicostellate (0); parvicostellate (1).

7. Concentric: weak (0); comae (1); lamellae (2).

Delthyrium and notothyrium

8. Delthyrial cover: apical (0); deltidial plates (1); pseudodeltidium (2).
9. Notothyrial cover: absent (0); chilidium (1); chilidial plates (2).

Articulation

10. Dental plates: absent (0); present (1).
11. Socket ridges: short straight (0); long straight (1); short curved (2).

Musculature

12. Ventral scar: triangular (0); bilobed (1); flabellate (2); cordate (3).
13. Ventral scar: not restricted anteriorly (0); restricted anteriorly (1).
14. Bounding ridges: absent (0); present (1).
15. Cardinal process position: projecting anterior to the hinge line (0); projecting posterior to the hinge line (1); absent (2).
16. Median septum (dorsal): not merging with platform (0); merging with platform (1).
17. Platform: absent (0); not elevated (1); elevated undercut (2); elevated not undercut (3).
18. Sub-peripheral rim: absent (0); present (1).

Mantle canal

19. Ventral systems: unclear (0); saccate (1); lemniscate (2); pinnate (3).
20. Dorsal systems: unclear (0); saccate (1); apocopate (2); lemniscate (3).

Appendix 2

Data matrix used in the cladistic analysis.

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Taffia	1	2	0	1	2	1	0	2	1	1	0	0	0	0	2	0	1	1	0	0
Leptellina	1	0	0	1	2	0	1	2	0	1	0	1	1	1	0	1	3	1	1	1
Merciella	1	0	0	1	1	0	1	2	0	1	0	1	1	1	0	1	2	1	0	0
Acculina	1	1	0	1	2	0	1	2	1	1	2	1	1	1	0	1	2	0	1	3
Dulankarella	1	0	1	1	3	0	1	2	2	1	1	1	1	1	1	1	3	0	1	0
Kajnaria	1	0	0	1	3	0	1	2	1	0	1	1	1	1	1	1	2	1	1	1
Leptelloidea	0	0	0	0	2	0	0	1	1	1	1	1	1	1	1	1	2	1	1	0
Mabella	1	0	0	0	1	0	0	2	0	1	0	3	1	1	1	1	2	1	2	0
Reversella	1	1	0	1	3	0	0	?	?	1	0	3	1	1	1	1	2	0	3	3
Shlyginia	1	0	0	1	1	1	0	2	2	0	0	2	1	1	0	1	3	1	0	0
Kilbuchomena	1	0	0	0	3	0	0	0	1	1	0	0	1	1	1	1	2	1	1	2
Palaeostrophomena	1	1	0	1	3	0	1	2	1	1	0	1	0	1	0	0	0	0	2	3
Apatomorpha	0	0	0	1	1	0	0	2	1	1	0	2	0	1	0	0	0	0	1	1
Glyptambonites	1	0	0	1	1	0	1	2	1	1	0	1	0	1	0	0	0	0	2	3
Ishimia	0	0	0	1	3	0	1	2	1	1	1	2	0	0	0	1	3	1	2	0
Onegia	1	0	0	1	0	0	0	2	?	0	0	1	0	0	0	1	2	1	0	0
Titanambonites	1	0	0	1	3	0	2	2	1	0	2	2	0	1	0	0	0	0	2	3
Toquimia	0	0	0	1	3	0	0	2	1	1	0	2	0	0	1	1	1	1	2	3
Ujukites	1	1	0	1	1	0	0	2	1	1	1	2	0	0	0	0	0	0	0	0
Tesikella	1	1	0	0	1	0	1	2	2	0	0	1	0	1	0	1	1	1	1	1
Lepidomena	0	0	0	1	2	0	0	2	1	0	0	1	0	1	1	1	1	1	1	1
Anchoramena	1	1	0	1	2	0	2	2	0	0	1	1	0	0	1	0	0	0	1	0
Sowerbyites	1	0	0	1	2	0	2	2	2	0	0	1	1	0	0	0	0	1	1	1
Goniotrema	1	0	0	3	?	?	0	1	1	0	0	1	0	1	0	0	0	1	0	0

Appendix 3

List of synapomorphies supporting the numbered nodes in Fig. 2B. Characters and character states are marked as in Appendices 1 and 2. The consistency index is shown in parentheses.

Node 46—*Taffia*. Profile (longitudinal) 2: 0→2 (0.333); shell size (length) 5: 3→2 (0.250); radial ornamentation 6: 0→1 (0.500); ventral muscle scar shape 12: 1→0 (0.333); cardinal process position 15: 0→2 (0.286).

Node 46—38. Median septum 16: 0→1 (1.000).

Node 38—36. Dental plates 10: 1→0 (0.167).

Node 36—35. Bounding ridges 14: 0→1 (0.333); ventral mantle canal system 19: 0→1 (0.375); dorsal mantle canal system 20: 0→1 (0.333).

Node 35—34. Cardinal process position 15: 0→1 (0.286).

Node 34—33. Ventral scar 13: 0→1 (0.500); platform 17: 1→2 (0.600).

Node 33—32. Dental plates 10: 0→1 (0.167); dorsal mantle canal system 20: 1→0 (0.333).

Node 32—30. Cardinal extremities 4: 1→0 (0.333).

Node 30—29. Shell size 5: 3→1 (0.250).

Node 29—28. Notothyrial cover 9: 1→0 (0.400).

Node 28—27. Cardinal extremities 4: 0→1 (0.333); concentric ornamentation 7: 0→1 (0.222); cardinal process position 15: 1→0 (0.286).

Node 27—26. Platform 17: 2→3 (0.600).

Node 26—*Leptellina*. Shell size (length) 5: 1→2 (0.250); dorsal mantle canal system 20: 0→1 (0.333).

Node 26—25. Notothyrial cover 9: 0→2 (0.400).

Node 25—*Dulankarella*. Profile (transverse) 3: 0→1 (1.000); shell size (length) 5: 1→3

(0.250); socket ridges 11: 0→1 (0.250); cardinal process position 15: 0→1 (0.286); subperipheral rim 18: 1→0 (0.250).

Node 25—*Shlyginia*. Radial ornamentation 6: 0→1 (0.500); concentric ornamentation 7: 1→0 (0.222); dental plates 10: 1→0 (0.167); ventral scar 12: 1→2 (0.333); ventral mantle canal system 19: 1→0 (0.375).

Node 27—*Merciella*. Ventral mantle canal system 19: 1→0 (0.375).

Node 28—*Mabella*. Ventral scar 12: 1→3 (0.333); ventral mantle canal system 19: 1→2 (0.375).

Node 29—*Leptelloidea*. Outline 1: 1→0 (0.250); shell size (length) 5: 1→2 (0.250); delthyrial cover 8: 2→1 (0.667); socket ridges 11: 0→1 (0.250).

Node 30—*Kilbuchomena*. Delthyrial cover 8: 2→0 (0.667); ventral scar 12: 1→0 (0.333); dorsal mantle canal system 20: 0→2 (0.333).

Node 32—31. Profile (longitudinal) 2: 0→1 (0.333); platform 18: 1→0 (0.250); dorsal mantle canal system 20: 0→3 (0.333).

Node 31—*Acculina*. Shell size (length) 5: 3→2 (0.250); concentric ornamentation 7: 0→1 (0.222); socket ridges 11: 0→2 (0.250); cardinal process position 15: 1→0 (0.286).

Node 31—*Reversella*. Ventral scar 12: 1→3 (0.3333); ventral mantle canal system 19: 1→3 (0.375).

Node 33—*Kajnaria*. Concentric ornamentation 7: 0→1 (0.222); socket ridges 11: 0→1 (0.250).

Node 34—*Lepidomena*. Outline 1: 1→0 (0.250); shell size (length) 5: 3→2 (0.250).

Node 35—*Tesikella*. Profile (longitudinal) 2: 0→1 (0.333); cardinal extremities 4: 1→0 (0.333); shell size (length) 5: 3→1 (0.250); concentric ornamentation 7: 0→1 (0.222); notothyrial cover 9: 1→2 (0.400).

Node 36—*Onegia*. Shell size 5: 3→0 (0.250); platform 17: 1→2 (0.600).

Node 38—37. Outline 1: 1→0 (0.250); ventral muscle scar shape 12: 1→2 (0.333); ventral mantle canal system 19: 0→2 (0.375).

Node 37—*Ishimia*. Concentric ornamentation 7: 0→1 (0.222); socket ridges 11: 0→1 (0.250); platform 17: 1→3 (0.600).

Node 37—*Toquimia*. Cardinal process position 15: 0→1 (0.286); dorsal mantle canal system 20: 0→3 (0.333).

Node 46—45. Platform 17: 1→0 (0.600).

Node 45—44. Shell size (length) 5: 3→1 (0.250); subperipheral rim 18: 1→0 (0.250).

Node 44—43. Ventral mantle canal system 19: 0→1 (0.375); dorsal mantle canal system 20: 0→1 (0.333).

Node 43—41. Bounding ridges 14: 0→1 (0.333).

Node 41—40. Concentric ornamentation 7: 0→1 (0.222); ventral mantle canal system 19: 1→2 (0.375); dorsal mantle canal system 20: 1→3 (0.333).

Node 40—39. Shell size (length) 5: 1→3 (0.250).

Node 39—*Palaeostrophomena*. Profile (longitudinal) 2: 0→1 (0.333).

Node 39—*Titanambonites*. Concentric ornamentation 7: 1→2 (0.222); dental plates 10: 1→0 (0.167); socket ridges 11: 0→2 (0.250); ventral scar 12: 1→2 (0.333).

Node 41—*Apatomorpha*. Shell outline 1: 1→0 (0.250); ventral scar 12: 1→2 (0.333).

Node 43—42. Shell size (length) 5: 1→2 (0.250); concentric ornamentation 7: 0→2 (0.222); notothyrial cover 9: 1→0 (0.400); dental plates 10: 1→0 (0.167).

Node 42—*Anchoramena*. Profile (longitudinal) 2: 0→1 (0.333); socket ridges 11: 0→1 (0.250); cardinal process position 15: 0→1 (0.286); dorsal mantle canal system 20: 1→0 (0.333).

Node 42—*Sowerbyites*. Notothyrial cover 9: 0→2 (0.400); ventral scar 13: 0→1 (0.500); subperipheral rim 18: 0→1 (0.250).

Node 44—*Ujukites*. Profile (longitudinal) 2: 0→1 (0.333); socket ridges 11: 0→1 (0.250); ventral scar 12: 1→2 (0.333).

Node 45—*Goniotrema*. Delthyrial cover 8: 2→0 (0.667); dental plates 10: 1→0 (0.167); bounding ridges 14: 0→1 (0.333).