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A link in the chain of the Cambrian zooplankton: bradoriid arthropods invade the water column

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Abstract – Bradoriids are small bivalved arthropods that had global distribution for about 20 million years beginning at Cambrian Epoch 2 (*c.* 521 Ma). The majority of bradoriids are considered to be benthic, favouring oxygenated waters, as suggested by their anatomy, lithofacies distribution, faunal associates and provinciality. Most bradoriids were extinct by the end of the Drumian Age (middle of Cambrian Epoch 3). The post-Drumian is characterized by widespread dysoxic shelf lithofacies in southern Britain and Scandinavia and by the abundance of phosphatocopid arthropods. This interval is also associated with two bradoriid species with wide intercontinental distribution: *Anabarochilina primordialis*, which had a geographical range from the palaeo-tropics to high southern palaeo-latitude, and *Anabarochilina australis*, which extended through the palaeo-tropics from Laurentia to Gondwana. The wide environmental and geographical range of these species, coupled with a carapace anatomy that suggests an active lifestyle, is used to infer a zooplanktonic lifestyle. A possible driver of this widespread Cambrian bradoriid zooplankton was sea-level rise coupled to the periodic spread of low oxygen conditions onto continental shelves, acting in tandem with anatomical pre-adaptations for swimming. Parallels exist with the myodocope ostracod colonization of the water column during Silurian time, which may also have been influenced by extrinsic environmental controls acting on anatomical pre-adaptations for swimming. Similar biological and environmental mechanisms may have facilitated arthropod zooplankton colonizations across Phanerozoic time.

Keywords: Cambrian, Bradoriida, zooplankton, biogeography, marine ecosystems.

1. Introduction

During Precambrian time plankton communities were microbial, comprising the primary producing phytoplankton and the bacterial biomass that degraded dead phytoplankton and returned the nutrients to the water column to be recycled into the next generation of phytoplankton. This ecosystem changed dramatically through the late Proterozoic – earliest Palaeozoic interval with the evolution of metazoans, the colonization of the water column by zooplankton and the development of the complex marine ecosystems of the Phanerozoic Eon (Butterfield, 2011). Arthropods were likely in the vanguard of early plankton colonization and have been a numerically important component of the ocean zooplanktonic ecosystem since Cambrian time (Signor & Vermeij, 1994; Rigby & Milsom, 2000; Peterson *et al.* 2004; Vannier, 2007). In modern planktonic ecosystems, arthropod zooplankton are essential intermediates between the primary producers and secondary and tertiary consumers (Falkowski, 2012). Arthropod zooplankton are important consumers of phytoplankton, bacterioplankton, marine snow and other zooplankton, repackaging carbon via their faecal pellets and delivering this to other parts of the water column, including to the seabed. They are fundamental to the transfer of energy, carbon and biomass through the marine ecosystem. They also provide a food source for organisms on higher trophic levels (Rigby & Milsom, 2000).

Many groups of organisms that have colonized the water column have benthic antecedents, for example, ostracods (Siveter, Vannier & Palmer, 1991), foraminifera (Hart, 2000; Hart *et al.* 2003), hemichordates (Hou *et al.* 2011) and chitinozoans (Shen *et al.* 2013). However, despite numerous groups of extant and fossil zooplankton (for a comprehensive summary see Rigby, 1997; Rigby & Milsom, 2000), few studies have attempted to identify the environmental and anatomical feedbacks that facilitate a zooplanktonic lifestyle. Furthermore, although arthropods are a major component of modern marine zooplankton, the fossil record of arthropod zooplankton as a whole is scarce and evidence of this important component of marine ecosystems is largely absent. This is exemplified by copepods, numerically the most abundant component of modern arthropod zooplankton, but which have virtually no fossil record (see summary in Selden *et al.* 2010). Examples of arthropod zooplankton colonizations are fundamental to understanding the drivers of a zooplanktonic lifestyle and the likely modes of recolonization of the water column post-dating major extinction events in the marine ecosystem.

Here we examine a component of the early zooplankton within a major group of Cambrian bivalved

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arthropods, the Bradoriida. Bradoriida were small as adults (typically 0.2–1 cm long) and a common component of shelly marine Cambrian assemblages (Williams *et al*. 2007). They are numerically the most important component of the Burgess Shale (e.g. see Siveter & Williams, 1997) and Chengjiang Lagerstätten (e.g. see Hou *et al*. 2002) and are presumed important primary consumers in basal positions in many Cambrian ecosystems. Bradoriida were a globally distributed component of seabed and near-seabed marine shelf communities for about 20 million years during Cambrian epochs 2 and 3 (Williams *et al*. 2007). Thereafter, their biodiversity apparently collapsed, with only a few taxa persisting into late Cambrian time (Furongian Epoch). This change may be linked to sea-level rise and the spread of anoxic conditions onto continental shelves (Williams *et al*. 2011). Bradoriids are an ideal group with which to assess the mechanisms of a planktonic colonization in arthropods: there is abundant evidence of their geographical and lithofacies distribution, of their faunal associates through Cambrian space and time (Williams *et al*. 2007, 2011), of their soft-part anatomy (Hou *et al*. 1996, 2010; Shu *et al*. 1999), and of their physiology (Vannier, Williams & Siveter, 1997; Williams *et al*. 2011). Geological and palaeobiological evidence supports a zooplanktonic lifestyle for two *Anabarochilina* bradoriid species (see also Collette, Hughes & Peng, 2011), namely *Anabarochilina primordialis* (Linnarsson) and *Anabarochilina australis* (Hinz-Schallreuter). We assess the possible biological and environmental drivers of this lifestyle and show how these may relate to other arthropod zooplankton colonizations elsewhere during Phanerozoic time.

2. The distribution of Cambrian Bradoriida

The geographical and temporal distribution of Bradoriida is summarized by Williams *et al*. (2007, 2011). The group occurs in many regions of the world during Cambrian epochs 2 and 3, but is best known from palaeocontinental Laurentia (e.g. Siveter & Williams, 1997), Baltica (e.g. Diez Álvarez *et al*. 2008), Avalonia (Williams & Siveter, 1998), South China (Hou *et al*. 2002; Zhang, 2007) and various regions of palaeocontinental Gondwana including Antarctica (e.g. Wrona, 2009), North Africa (e.g. Hinz-Schallreuter, 1993) and especially Australia (e.g. Jones & Laurie, 2006; Topper *et al*. 2011). Bradoriid arthropods are interpreted as benthos and demersal swimmers and favoured well-oxygenated seas, as indicated by their lithofacies distribution (Williams *et al*. 2011) and well-developed integumental circulatory systems (Vannier, Williams & Siveter, 1997). In general, Bradoriida are absent where phosphatocopid arthropods (=labrophoran eucrustacea; see Siveter, Waloszek & Williams, 2003) are common, in the black shale successions of the Avalonian and Baltic regions during the upper part of Cambrian Series 3 and the Furongian (Williams *et al*. 2011). However, bradoriids and phosphatocopids occur together in the Monastery Creek Phosphorite Formation (Cambrian Stage 5, Series 3) of Australia (Jones & Laurie, 2006).

At the species level, and to some degree at the genus level, bradoriid arthropods are highly provincial and map out different regions of Cambrian palaeogeography (see Williams *et al*. 2007). This suggests that the vast majority of bradoriid species lacked the capacity for intercontinental (trans-oceanic) distribution, and supports their interpretation as benthic organisms (see Schallreuter & Siveter, 1985 for similar distribution patterns in Ordovician ostracods). This interpretation is also endorsed by rare instances of soft-part anatomy preservation in bradoriids, which suggest that their appendages were useful for locomotion but not specifically adapted for swimming or permanent occupation of the water column (see Hou *et al*. 2010). While this pattern of bradoriid provinciality persisted for much of Cambrian epochs 2 and 3, species of one bradoriid genus (namely *Anabarochilina*) have a markedly different palaeogeographical distribution (Fig. 1). *Anabarochilina* species (Fig. 2) are the most widespread of all bradoriids, with taxa recorded from North America (Siveter & Williams, 1997), southern Britain (Williams & Siveter, 1998), Scandinavia (Siveter *et al*. 1993), Siberia and Kazakhstan (Melnikova, Siveter & Williams, 1997; Melnikova, 2003), India (Collette, Hughes & Peng, 2011) and Australia (Hinz-Schallreuter, 1993; Jones & Laurie, 2006; Collette, Hughes & Peng, 2011). Two species in particular are widely distributed, *A. australis* at low palaeo-latitude, and *A. primordialis* from low to high palaeo-latitude during Cambrian Epoch 3 (Fig. 1).

3. Temporal and biogeographical distribution of *Anabarochilina*

Species of *Anabarochilina* are present in strata of Cambrian series 2, 3 and the Furongian (Fig. 3). The biogeographical and temporal distribution of *Anabarochilina* species is summarized in Figures 1 and 3. Trilobite biozones referred to in the text are summarized in Figure 4.

Anabarochilina species first appear in the rock record of the upper part of Cambrian Stage 3 (Series 2). These early *Anabarochilina* occur in the low palaeo-latitude Taconic Allochthon succession of Laurentia and possibly in the high palaeo-latitude assemblages of peri-Gondwanan Avalonia (see Figs 1, 3). This material consists of *Anabarochilina*? sp. A of Williams & Siveter (1998) from the Red Callavia Sandstone of Shropshire, UK (*Callavia* trilobite Biozone; see Williams & Siveter, 1998), and *Anabarochilina rotundata* (Walcott) from limestones interbedded with mudstones containing the *Elliptocephala asaphoides* fauna (level equivalent to the *Olenellus* trilobite Biozone) of New York State, USA (Siveter & Williams, 1997).

During Cambrian Epoch 3 the distribution of *Anabarochilina* species became global (Fig. 1).

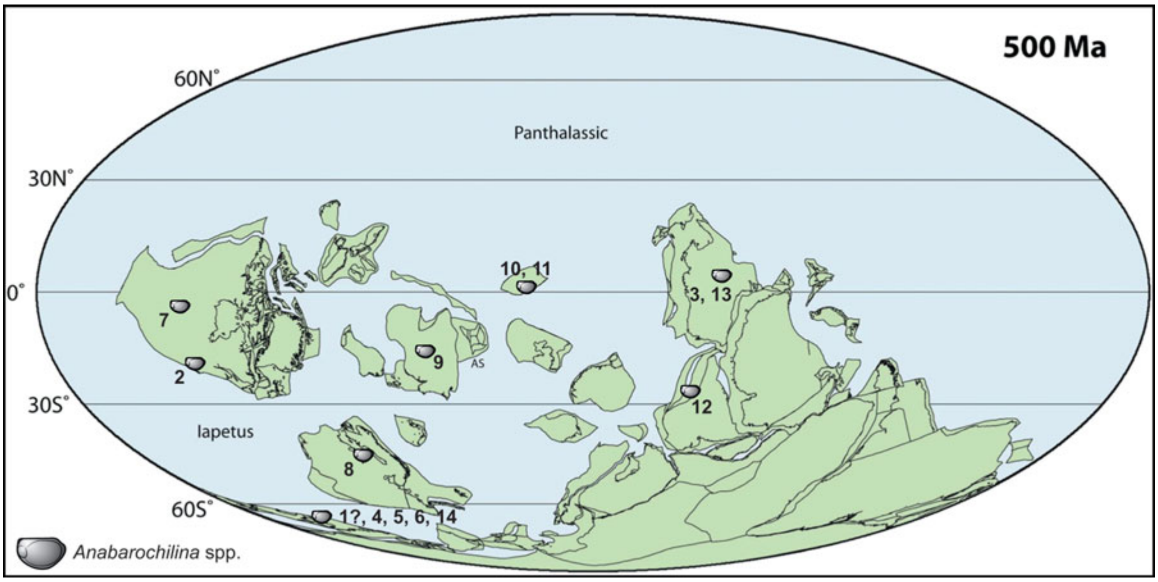

Figure 1. (Colour online) Geographical distribution of *Anabarochilina* species plotted onto a Cambrian base map for 500 Ma (from Torsvik & Cocks, 2013). Occurrences are cross-referenced (by number) with the temporal occurrence of *Anabarochilina* species depicted in Figure 3. For locality references see text. Numbers 1 and 2 are Cambrian Epoch 2 occurrences; 3–10, 12, 13 are Epoch 3; 11 is uncertain (either Epoch 3 or Furongian); and 14 is Furongian. 1, *Anabarochilina*? sp. A of Williams & Siveter (1998), Red Callavia Sandstone, Shropshire, England. 2, *Anabarochilina rotundata*, *Elliptocephala asaphoides* fauna, 'upper Taconic', New York, USA. 3, *Anabarochilina australis*, Monastery Creek Phosphorite Formation, Queensland, Australia. 4, *Anabarochilina hicksii*, Menevian Group of South Wales, and Abbey Shale Formation of Warwickshire, England, UK. 5, *Anabarochilina corpulenta*, Rushton Brook Bed, Shropshire, UK. 6, *Anabarochilina primordialis*, Mancetter Shale Formation, Warwickshire, England, UK. 7, *Anabarochilina australis*, Weeks and Marjum formations, Utah, USA. 8, *Anabarochilina primordialis*, Alum Shale Formation, Sweden. 9, *Anabarochilina primordialis*, vicinity of the River Kotui, East Siberia, Russia. 10, *Anabarochilina australis*, Kyr-Shabakty section, Maly Karatau, Kazakhstan. 11, *Anabarochilina konevae*, Edrei Beds, Agyrek Mountains, Kazakhstan. 12, *Anabarochilina australis*, Zanskar Valley, northern India. 13, *Anabarochilina chummyensis*, Mungerebar Limestone, Australia. 14, Undescribed *Anabarochilina* species are also known from the Outwoods Shale Formation, Furongian, southern Britain (Williams & Siveter, 1998).

Anabarochilina australis has its earliest occurrence in strata of Cambrian Stage 5 (*Ptychagnostus gibbus* trilobite Subzone of the *Ptychagnostus paradoxissimus* trilobite Biozone, at *c.* 507 Ma) of Australia. *A. australis* is notable for a temporal range that may exceed four million years (see Collette, Hughes & Peng, 2011 for a summary distribution of this species). Its early occurrence is notable, because this species became pandemic in low palaeo-latitude regions within the *Lejopyge laevigata* trilobite Biozone of the Guzhangian Stage (*c.* 503 Ma; Collette, Hughes & Peng, 2011). *Anabarochilina* is represented in Avalonia in the Drumian Stage of Series 3 by *Anabarochilina hicksii* (*Tomagnostus fissus* to *Hypagnostus parvifrons* trilobite subzones of the *P. paradoxissimus* Biozone, see Fig. 4), being recorded from the Abbey Shale Formation of Warwickshire and from the Menevian Group of South Wales (Williams & Siveter, 1998; see also Fig. 2). *Anabarochilina corpulenta* occurs in the Rushton Brook Bed (formerly known as the Paradoxides forchhammeri Grits, see Rushton & Berg-Madsen, 2002), late Drumian of Shropshire, UK (for stratigraphical context see Figs 3, 4).

In the upper part of the *P. forchhammeri* Biozone (through an interval equivalent to the *L. laevigata* trilobite Biozone of the Guzhangian Stage) species of *Anabarochilina* extended their range to become global (Fig. 1), occurring in the palaeocontinental areas of Avalonia, Baltica, Laurentia, Siberia, Kazakhstan and Gondwana (see Williams *et al*. 2007; Collette, Hughes & Peng, 2011; see also Fig. 3). *A. primordialis* extended its latitudinal range from high palaeo-latitude Gondwana to palaeo-tropical Siberia (Fig. 1). At the same time, *A. australis* extended from western Laurentia, across the palaeo-tropics to Gondwana in the east (Fig. 1).

4. Palaeoenvironmental setting of *Anabarochilina*

Individual species of *Anabarochilina* traverse environments from platform carbonates to deep-shelf and deep-marine fan environments. Coupled with anatomical evidence from the carapace that suggests an active lifestyle (see Section 5), the lithofacies distribution of certain *Anabarochilina* species supports the interpretation that they had a zooplanktonic lifestyle.

Early occurrences of *Anabarochilina* are typically associated with benthic assemblages of trilobites and small shelly fossils. The Red Callavia Sandstone, Lower Comley Group, Shropshire (see Harvey *et al.* 2011 for a description of these strata) was deposited in a shelf marine setting on the eastern margins of the early Palaeozoic Avalonian Welsh Basin. It contains the bradoriid *Anabarochilina*? sp. A of Williams & Siveter (1998), which is known only from a single specimen that has an anterior node, well-developed

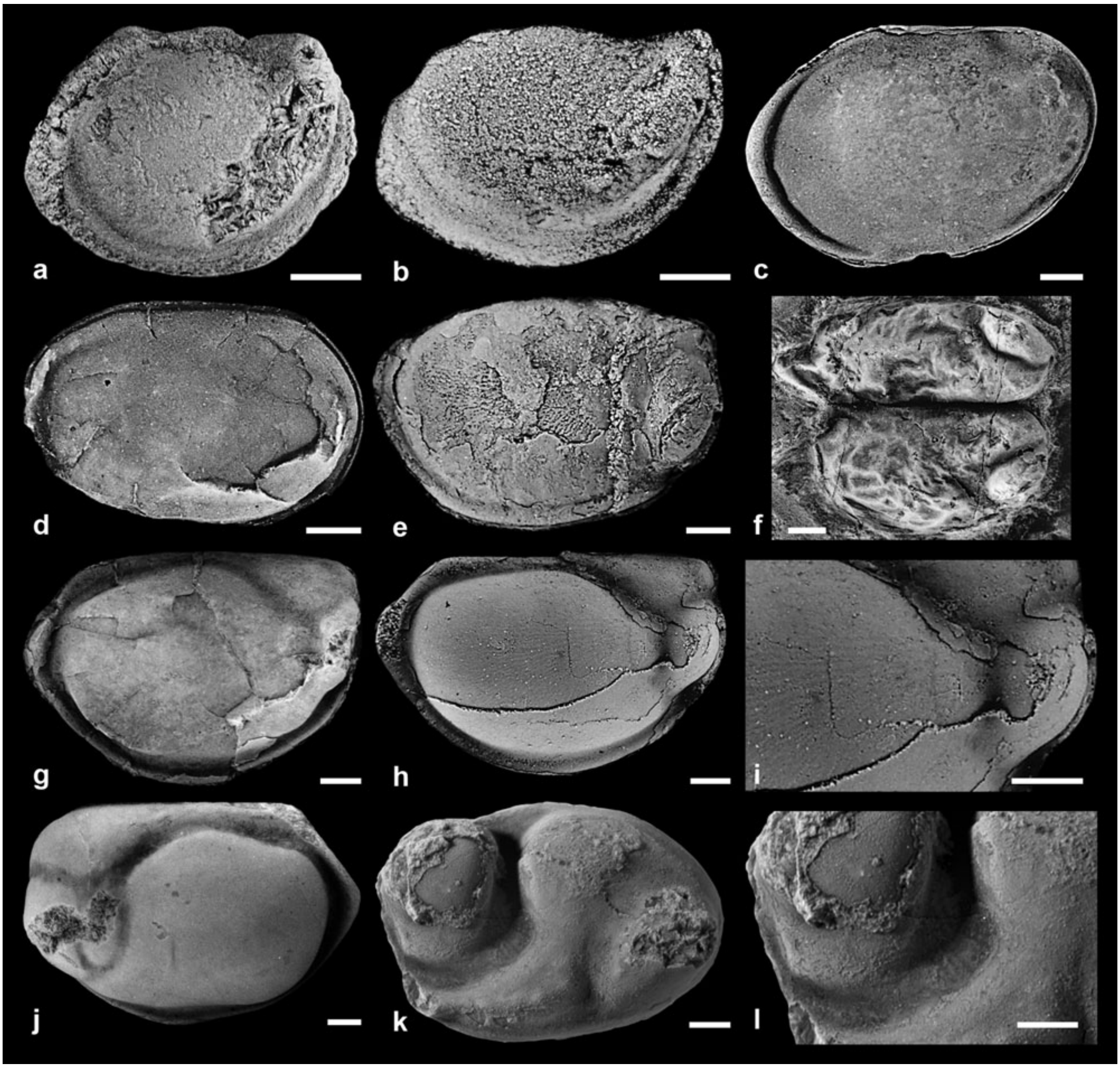

Figure 2. Morphology of *Anabarochilina* species from Cambrian epochs 2 and 3, and comparison between the carapace anatomy of *Anabarochilina primordialis* and the Silurian myodocopid ostracod *Parabolbozoe bohemica*? (after Perrier, Vannier & Siveter, 2011). Both *Anabarochilina australis* (e), and *A. primordialis* (h, i) show the clear development of an anastomosing integumental circulatory system extending from the area of the adductor muscle attachment (see also Fig. 5). (a, b) *Anabarochilina rotundata* (Walcott), lateral view, internal mould of right valve and silicon rubber cast of right valve respectively, USNM 17446, 4.76 mm long. (c, d) *Anabarochilina hicksii* (Jones): (c) internal mould of carapace, right lateral view, NMW 80.34G.1095, 8.3 mm long; (d) lateral view of internal mould of flattened left valve, BGS Zs4582, 6.25 mm long. (e, f) *Anabarochilina australis* (Hinz-Schallreuter): (e) right valve, lateral view, PIN N4343/55, 8 mm long; (f) KUMIP 1129844, open carapace, 6.5 mm long. (g–j) *Anabarochilina primordialis* (Linnarsson); (g) internal mould of flattened right valve, BGS BDA2313, 8.3 mm long; (h, i) right valve, lateral view, and close-up of anterior features, SGU 8622, 8.89 mm long; (j) left valve, lateral view, PIN 4342/62, 10 mm long; (k, l) *Parabolbozoe bohemica*? (Barrande) internal mould of carapace, left lateral view and close up of anterior features, UMC-IP-VP 1, 8.51 mm long. USNM – United States National Museum, Washington DC; NMW – National Museum of Wales, Cardiff; BGS – British Geological Survey, Nottingham; PIN – Palaeontological Museum of the Palaeontological Institute, Russian Academy of Sciences; KUMIP – University of Kansas, Museum of Invertebrate Paleontology; SGU – Sveriges Geologiska Undersokning, Uppsala; UMC-IP-VP – University of Montpellier. (a, b) Washington County, New York, USA; (c) Porth-y-rhaw, South Wales, UK; (d) Nuneaton, Warwickshire, UK; (e) Maly Karatau, Kazakhstan; (f) Millard County, Utah, USA; (h, i) Vastergotland, Sweden; (j) East Siberia, Russia; (k, l) La Combe d'Yzarne, Montage Noire, France. Scale bars are 1 mm.

continuous marginal rim and smooth and broadly convex valves (Williams & Siveter, 1998, p. 23). It occurs with the bradoriids *Indiana lentiformis* (Cobbold) and *Liangshanella salopiensis* (Cobbold), which are interpreted as a benthic association of species (Williams & Siveter, 1998), consistent with the overall fauna of the Red Callavia Sandstone. *Anabarochilina* species are absent from the contemporaneous sedimentary deposits of the open marine shelf Purley Shale Formation of Warwickshire on the Midland Platform (see Rushton

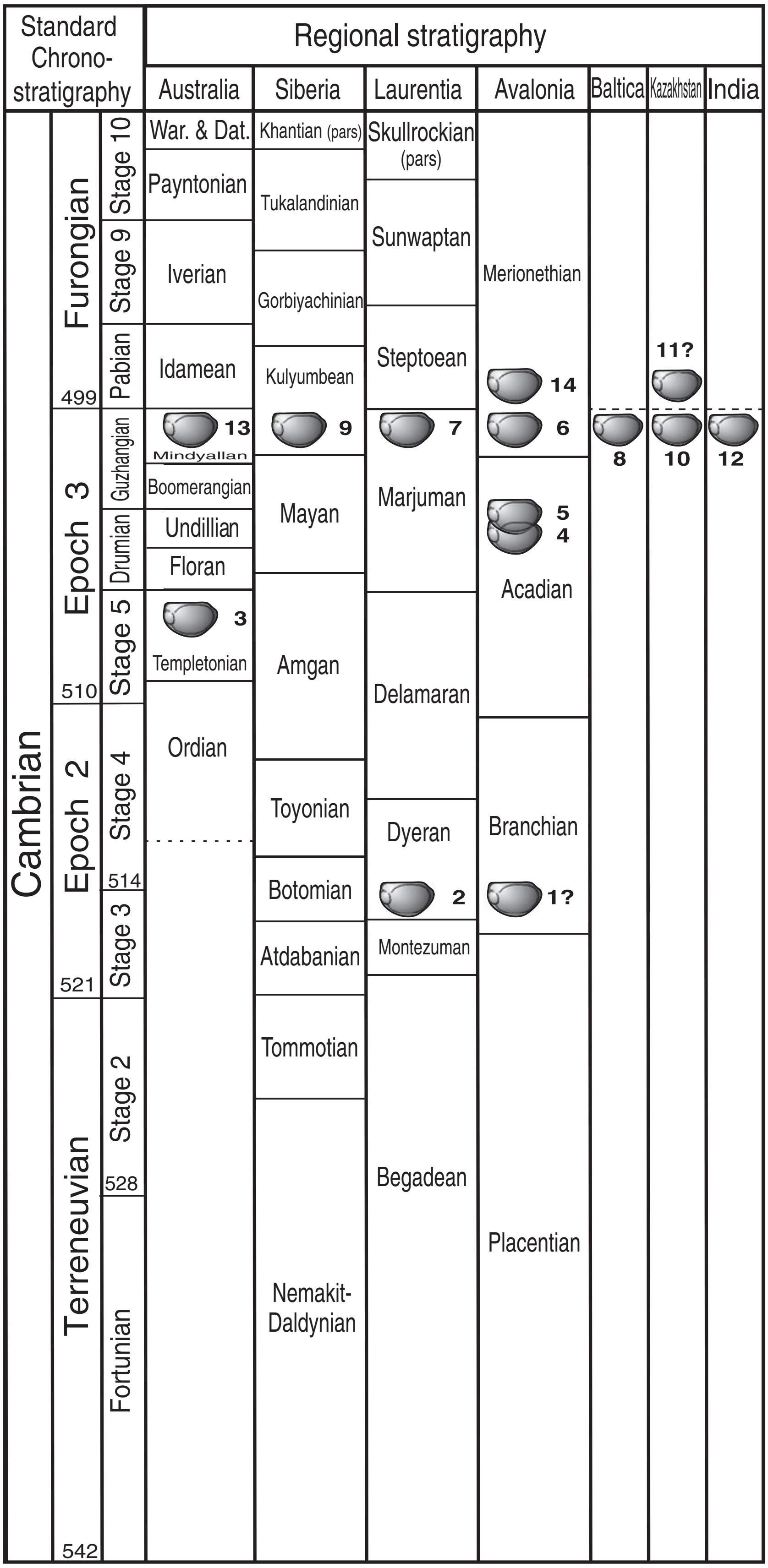

Figure 3. Temporal distribution of *Anabarochilina* species plotted against the international and selected regional chronostratigraphic subdivisions of the Cambrian (chronostratigraphy from Zhu, Babcock & Peng, 2006). For geographical distribution of these *Anabarochilina* species and relevance of numbers adjacent icons see Figure 1. Note that ‘8’ represents the occurrence of *A. primordialis* in the Alum Shale Formation of Sweden, at the same level as the late Guzhangian occurrence of this species in Siberia and Avalonia.

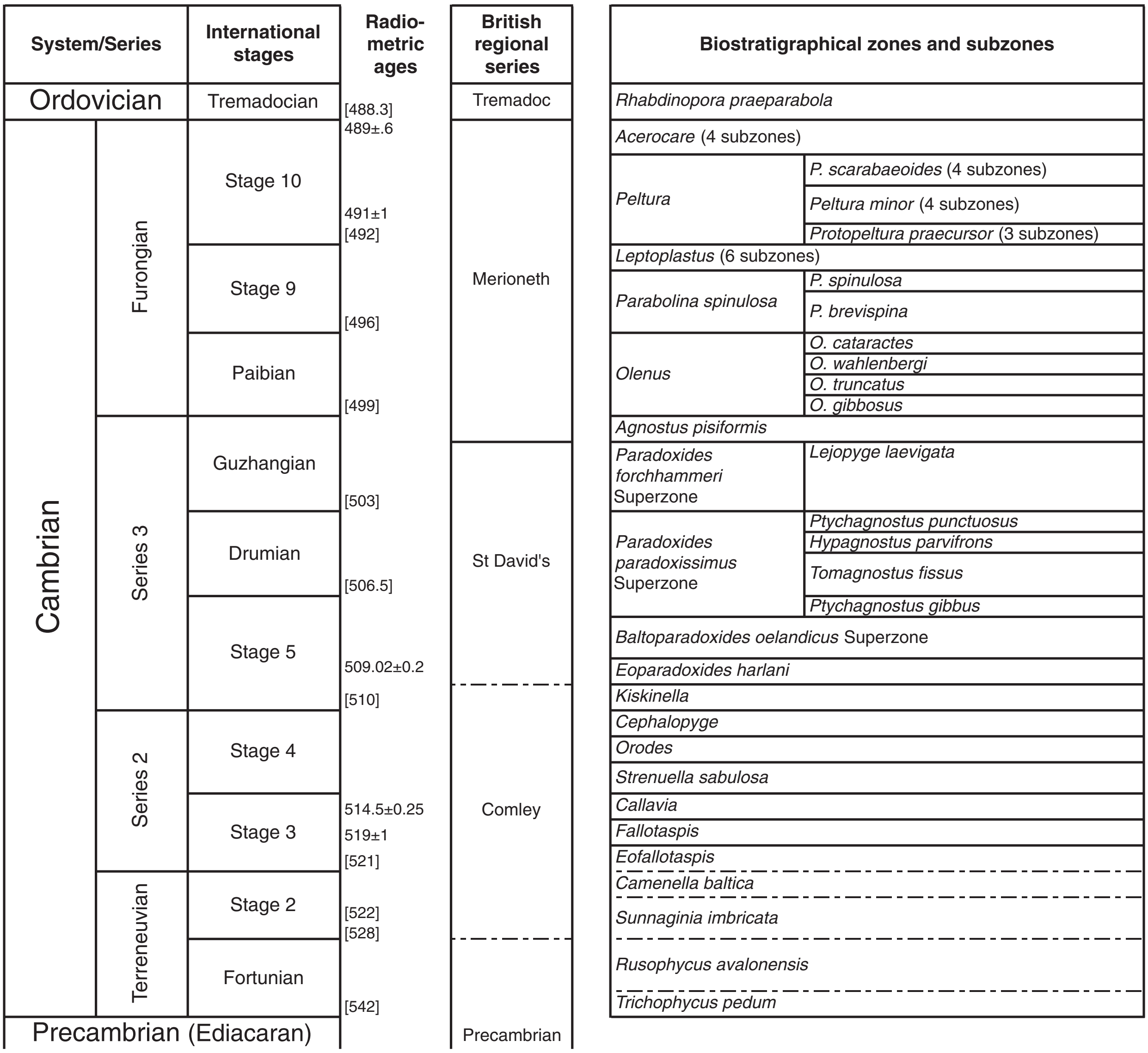

Figure 4. Trilobite biozones referred to in the text and their correlation with the International and British regional stages of the Cambrian, and with available radiometric dates for the Cambrian (based on the detailed summary in Rushton *et al*. 2011, radiometric ages in brackets are inferred). Boundaries shown by dashed lines are of uncertain correlation with the standard.

et al. 2011; Williams *et al*. 2013), which however contains the bradoriid *Matthoria* sp. (see Williams & Siveter, 1998). *Matthoria* forms an important faunal link between the southern British succession and the *Elliptocephala asaphoides* fauna of New York State (*Olenellus* trilobite Biozone), where *Matthoria troyensis* (Ford) is recorded from near the city of Troy, New York State (Ford, 1873; Siveter & Williams, 1997). The *Elliptocephala asaphoides* fauna is a component of the lower Palaeozoic Taconic Allochthon succession of eastern New York State, considered to be an outboard and deep-marine setting along the Iapetus-facing margin of the Laurentia palaeocontinent (e.g. Landing & Bartowski, 1996). The *Elliptocephala asaphoides* fauna has long been considered to contain a biogeographically mixed assemblage of organisms that reflect different environmental settings (e.g. Lochmann, 1956). Other bradoriids within the ‘upper Taconic’ of the New York Cambrian succession include *Anabarochilina rotundata* (Walcott) and *Indiana dermatoides* (Walcott) from Washington County (Walcott, 1887; see Siveter & Williams, 1997). Collectively, the bradoriids suggest a significant faunal similarity at the genus level with Avalonia. There is no clear suggestion from these early palaeogeographical patterns that *Anabarochilina* species were zooplanktonic, and their occurrence with other benthic marine organisms (including other bradoriids that have been interpreted as benthic) would be consistent with a lifestyle at or near the seabed.

During Cambrian Epoch 3 the distribution of *Anabarochilina* species became global, extending westwards through the palaeo-tropics (Collette, Hughes & Peng, 2011). The earliest (Cambrian Age 5) occurrence of the widespread and long-lived (*c*. 4 Ma duration, see Fig. 4) *A. australis* is in offshore phosphatic limestones of the Monastery Creek Phosphorite Formation, Queensland, Australia (see Jones & Laurie, 2006), a region of palaeocontinental Gondwana (see Collette, Hughes & Peng, 2011). *A. australis* occurs with a diverse bradoriid fauna and with arthropods interpreted as endemic phosphatocopids (see Jones & Laurie, 2006). During the Guzhangian, *A. australis* is found both in platform carbonates and distal fan settings (Collette, Hughes & Peng, 2011), while its likely synonym '*A. burkensis*' is recorded from carbonates (Devoncourt Limestone) in Queensland, Australia (see Jones & Laurie, 2006).

Anabarochilina hicksii occurs in the Drumian Stage of Series 3 (Figs 3, 4), in the Abbey Shale Formation of Warwickshire and from the Menevian Group of South Wales (Williams & Siveter, 1998; Fig. 2). The Abbey Shale Formation consists of pyritic mudstones that were probably deposited on a shallow shelf during a period of low seabed oxygenation, punctuated by intervals when the sea bed became colonized by a diversity of benthic trilobites (Rushton, 1999). The mudstones of the Lower and Middle Menevian Group represent deposition below storm wave base, probably in low but fluctuating oxygen conditions (Prigmore & Rushton, 1999). *Anabarochilina corpulenta* occurs in the (upper Drumian) Rushton Brook Bed of Shropshire (Williams & Siveter, 1998; see Rushton & Berg-Madsen, 2002 for revised correlation of the Paradoxides forchhammeri Grit).

During Guzhangian time, the lithofacies distribution of *Anabarochilina* species includes deeper shelf mudstones. *A. australis* occurs in both shelf and more deep-water marine lithofacies. *A. primordialis* (synonyms: *A. ventriangulosa* and *A. ventriarcuata*, see Siveter *et al.* 1993) occurs in a range of lithofacies that include the Mancetter Shale Formation (formerly the Mancetter Grits and Shales) of Warwickshire (Bridge *et al.* 1998), and also in low palaeo-latitude fine-grained and laminated limestones in Siberia (Melnikova, Siveter & Williams, 1997; see Fig. 2). Undescribed *Anabarochilina* species are also present in the succeeding Outwoods Shale Formation of Warwickshire, in strata that comprise black pyritic mudstones with a fauna of putative chemoautotrophic olenid trilobites (Fortey, 2001), possible pelagic agnostid trilobites and phosphatocopid arthropods. In particular, these levels of the Outwoods Shale Formation record seabed conditions that were, at least intermittently, anoxic (see Woods *et al.* 2011). *A. primordialis* is also preserved in the Alum Shale Formation of Scandinavia (Berg-Madsen, 1985), a unit which is also associated with probable dysoxic seabed conditions (Ahlberg *et al.* 2009): here it occurs with the trilobites *Tomagnostella exsculpta* and *L. laevigata*. The late Guzhangian (Mindyallan) *Anabarochilina chummyensis* is recorded from a carbonate setting in Australia and may yet prove to be conspecific with *A. australis*. *Anabarochilina karatauensis* Melnikova was considered conspecific with *A. australis* by Collette, Hughes & Peng (2011), and occurs in fine-grained bedded limestones in the Kyr-Shabakty section, Maly Karatau, Kazakhstan. This setting represents a marine environment at the edge of a carbonate platform, located on an isolated submarine mount (L. Melnikova, pers. comm., November 2014).

Anabarochilina konevae occurs in a block of limestone within a succession dated as Furongian Epoch (regional Aksayan Stage) of the Agyrek Mountains, Kazakhstan, but is sourced from an olistolith (Williams *et al.* 2007) and may represent material reworked from an older horizon.

5. Possible pre-adaptations of *Anabarochilina* for life in the water column

There is no known soft-part anatomy for species of *Anabarochilina*, and inferences about functional morphology are based on the carapace morphology. Nevertheless, certain anatomical characteristics of the carapace suggest that *Anabarochilina* possessed a well-developed integument circulatory system (see Figs 2e, h, i, 5a–c) that suggests an active mode of life and occupation of an oxygenated water column. That *Anabarochilina* was restricted to environmental settings characterized by oxygenated waters is also suggested by species in shelf successions with typical Cambrian marine benthic faunas (e.g. in the Rushton Brook Bed). An integumental circulatory system was noted in the earliest description of *A. rotundata* from the Cambrian Taconic Allochthon (Walcott, 1887, pl. 1, fig. 9) and is well developed in *A. primordialis*, with anastomosing structures extending across the entire lobal area of the carapace and converging on an ovoid lobe immediately posterior of the pronounced mid-anterior lobe (Figs 2e, h, i, 5a–c). This is analogous to structures in myodocopid ostracods and leptostracan phyllocarids where hemolymph enters the anastomosing circulatory network of both valves around the adductor muscles (Fig. 5d, e; Vannier & Abe, 1995). It is reasonable to suppose that provision of an integumental circulatory system facilitated an active metabolism and aided swimming.

The convergence of the anastomosing structures onto a lobal structure in *Anabarochilina* and the composition of this lobe from numerous small tubercles (Figs 2e, h, i, 5b–c) suggest that this is the site of adductor muscle attachment in *Anabarochilina*. The strongly inflated mid-anterior lobe (already present in *A. rotundata*, Fig. 2a, b) lying immediately anterior of these adductor muscles might, by analogy with the dorsal bulb of Silurian myodocopid ostracods (Siveter, Vannier & Palmer, 1991; Fig. 2k, l), have accommodated a well-developed basipodite of strong swimming appendages of the second antenna. If this interpretation is correct, *Anabarochilina* may have had well-developed swimming abilities. However, we note that in the Chengjiang bradoriid *Kunmingella douvillei* (Hou *et al.* 2010), all of the post-antennal appendages (barring the trailing terminal appendage pair) have identical biramous morphology (Hou *et al.* 2010) with no specifically adapted swimming appendages.

The preservation of many benthic bradoriid arthropods in butterfly orientation (e.g. Hou *et al.* 2002) and

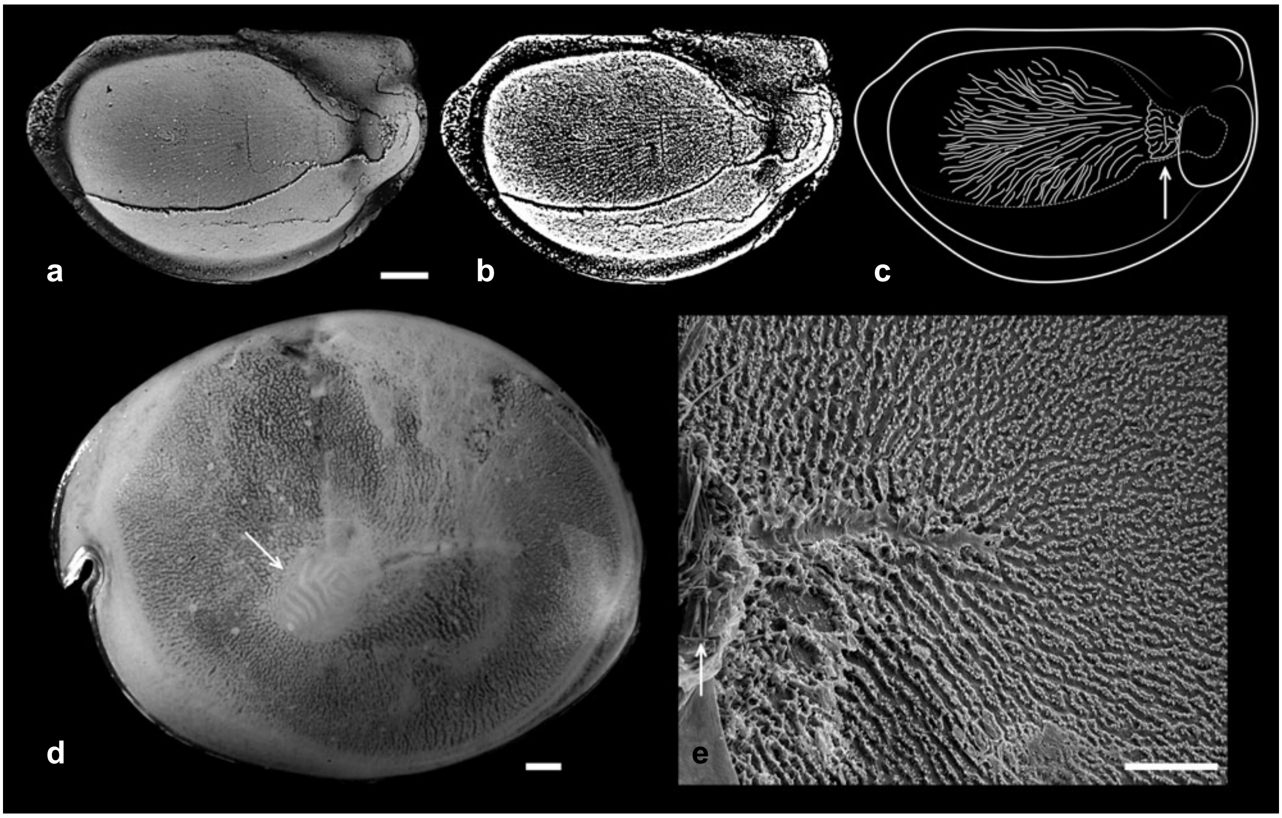

Figure 5. *Anabarochilina primordialis* (Linnarsson). (a–c) Right valve, lateral view, of specimen SGU 8622, 8.89 mm long (the same specimen as Fig. 2h, i); (b) is shown with elevated contrast to pick out the morphology of the anastomosing structures while (c) is a camera lucida drawing of these structures showing their convergence on the area interpreted as an adductor muscle scar (arrowed). (d, e) Recent myodocope, *Azygocypridina* sp. (muscle scar arrowed) from New Caledonia, Université Claude-Bernard Lyon-1 collections. As with *A. primordialis*, this animal has a well-developed integumental circulatory system imprinted on the carapace that converges on the adductor muscle area. All scale bars are 1 mm.

the general absence of muscle scars across all the main groups of bradoriids suggests that most (possibly nearly all) of these arthropods lacked the ability to articulate and close their valves tightly. However, *A. primordialis* and possibly other *Anabarochilina* species may have possessed adductor muscles and may have had the ability to articulate and possibly close the carapace. This would have provided an advantage to an organism occupying the water column, where predation would be a constant threat.

Eyes are recorded in the Chengjiang bradoriid *Kunmingella douvillei* (Shu *et al*. 1999; Hou *et al*. 2010), and are situated in a dorsal position. In *A. primordialis* the area dorsal of the mid-anterior lobe is clearly inflated, with a specific 'node' at its anterior extremity (Figs 2g–j, 5a–c) that might have accommodated eyes with excellent forward vision. *K. douvillei* also provides evidence that bradoriids brooded their eggs (Duan *et al*. 2014), and such a strategy would have been highly beneficial if *Anabarochilina* species reproduced in the water column.

In summary, *Anabarochilina* species have an integumental circulatory system that suggests an active metabolism. They may have had well-developed anterior swimming appendages and good vision. Their ability to close the carapace via adductor muscles would have protected swimming appendages and possibly eggs, and would have been useful anatomical adaptations to facilitate a life in the water column.

6. Environmental drivers of a widespread bradoriid zooplankton

Anabarochilina species reveal a distribution pattern with three phases: (1) early (Cambrian Epoch 2) distribution focuses on the Iapetus-facing Taconic Allochthon of Laurentia and possibly in Avalonia, and these *Anabarochilina* co-occur with essentially benthic assemblages of trilobites and small shelly fossils; (2) early–middle Cambrian Epoch 3 (Age 5 and Drumian) species of *Anabarochilina* (e.g. *A. hicksii*) are found in a wider spectrum of lithofacies, some of which suggest dysoxic sea beds but no species is cosmopolitan; and (3) during the Guzhangian Age (late Epoch 3, *L. laevigata* trilobite Biozone) two species of *Anabarochilina* became widely distributed, occurring in both inner and outer shelf settings, some of these environments being characterized by dysoxic sea beds. During phase 3, individual species had trans-oceanic (*A. australis*) and trans-latitude (*A. primordialis*) distribution. These patterns suggest that post-Drumian *Anabarochilina* species were zooplanktonic.

The earliest *Anabarochilina* species may have been distributed between Avalonia and Taconic Laurentia

(Fig. 1), suggesting that *Anabarochilina* species could disperse between continental areas separated by oceans. However, there is no firm evidence that these earliest *Anabarochilina* were zooplanktonic.

The geographically widespread *A. australis* occurs in Cambrian Stage 5 limestones of Australia (Jones & Laurie, 2006), and approximately 4 million years later this taxon extended its range through the palaeo-tropics (Fig. 1). Based on its geographical and lithofacies distribution (Collette, Hughes & Peng, 2011) and on the morphology of *Anabarochilina* species in general, *A. australis* is considered to be a zooplanktonic arthropod. Given this interpretation, why did *A. australis* remain exclusively Gondwanan until the Guzhangian Age of Cambrian Epoch 3, approximately 4 million years after its first occurrence? The absence of *A. australis* from other regions during the interval of mid Epoch 3 might represent a collection bias, as in general specimens of *Anabarochilina* are rare. However, bradoriids are recorded from successions of this age in other palaeocontinental regions and include *Anabarochilina* species (e.g. *A. hicksii* and *A. corpulenta* in Avalonia; see Williams & Siveter, 1998).

Both *A. hicksii* and *A. primordialis* occur in sedimentary successions that have intermittent levels with pyritic mudstones, suggesting that seabed conditions were sometimes characterized by low oxygen. The spread of black shales onto the shelf during early Guzhangian time is associated with the development of phosphatocopid assemblages in Avalonia and Baltica that were probably adapted for dysoxic seabed conditions (Williams *et al.* 2011) and which are characteristic of the Alum Shale Formation of Sweden (e.g. Ahlberg *et al.* 2009) and the Outwoods Shale Formation of England (e.g. Williams *et al.* 1994; Williams & Siveter, 1998). The Drumian–Guzhangian boundary signals the demise of much of the benthic bradoriid fauna that occupied well-oxygenated shelf marine settings (Williams *et al.* 2011). *Anabarochilina hicksii* is recorded from Drumian age strata in Avalonia that are assignable to the *T. fissus* and *H. parvifrons* subzones of the *P. paradoxissimus* Biozone (Figs 3, 4). By comparison with the carbon isotope curve of the Alum Shale Formation of Scandinavia (Ahlberg *et al.* 2009, fig. 4), this equates to the interval immediately following the peak negative excursion of the Drumian Carbon Isotope Excursion (DICE) event, when carbon isotope values were rising with a positive trend. *A. primordialis* is characteristic of the (Guzhangian Stage) *L. laevigata* Biozone. Its first occurrence in the Scandinavian succession occurs at the inflection point of the carbon isotope curve as it begins to rise towards the Steptoean Positive Carbon Isotope Excursion (SPICE) event (Ahlberg *et al.* 2009, figs 2, 4): *A. primordialis* characterizes the same interval in the Avalonian succession (Williams & Siveter, 1998). The pattern of distribution of Drumian and Guzhangian *Anabarochilina* species, which includes the dispersal of *A. australis* to Kazakhstan and Laurentia (Fig. 1), suggests that *Anabarochilina* species may have been pre-adapted to cope with sea-level rise and the spread of intermittent seabed anoxia onto the shelf, and that this was an important driver of their widespread distribution.

The wide latitudinal range of *A. primordialis* during the interval of the *L. laevigata* trilobite Biozone is remarkable. It either suggests an organism with tolerance of a range of surface water temperatures (across nearly 70° of southern latitude), a low thermal gradient from the Cambrian tropics to the poles (not suggested by the apparent restriction of *A. australis* to the palaeo-tropics) or the possible extension of warm surface water currents to Avalonia. Alternatively, *A. primordialis* may have occupied deeper-water settings at the level of the thermocline and was therefore not subject to surface temperature gradients.

7. Comparison with other early putative arthropod zooplankton colonizations

The Cambrian (epochs 2 and 3) bivalved arthropod *Isoxys* had a global distribution in the palaeo-tropics (Williams, Siveter & Peel, 1996; Vannier & Chen, 2000), often occurring in black shale deposits such as those of the Sirius Passet Lagerstätte of Greenland (e.g. Williams, Siveter & Peel, 1996). However, Stein *et al.* (2010) have noted that no single species of *Isoxys* has a cosmopolitan distribution; at present, a zooplanktonic mode of life for *Isoxys* is therefore speculative. Similarly, the Ordovician bivalved arthropod *Caryocaris* (Vannier *et al.* 2003) has been interpreted as a zooplanktonic phyllocarid. It may have occupied the water column during Early Ordovician time (see Vannier *et al.* 2003). It occurs in graptolite-bearing black mudstones but like *Isoxys* no single species has a cosmopolitan distribution, in contrast to contemporaneous macro-zooplanktonic graptolites.

A more direct comparison with zooplanktonic *Anabarochilina* is afforded by Silurian myodocopid ostracods. The early (Llandovery and Wenlock) myodocopid genus *Pauline* is recorded from England, Greenland and China (Siveter *et al.* 2013; Perrier *et al.* 2014; unpub. data). However, no single species is palaeogeographically widespread. Later during Silurian time, myodocopids show a well-documented plankton colonization following the middle Homerian biotic crisis (Siveter, Vannier & Palmer, 1991) with transoceanic distribution at the species level (Perrier, Vannier & Siveter, 2007, 2011). This colonization event may be associated with sea-level change, the spread of ocean anoxia onto the continental shelf and the restoration of the planktonic ecosystem (including zooplanktonic graptolites) post-dating the middle Homerian extinction (Siveter, Vannier & Palmer, 1991; Porebska, Kozlowska-Dawidzuik & Masiak, 2004; Cramer *et al.* 2012). Extrinsic environmental drivers may have acted on physiological and anatomical pre-adaptations already present in myodocopids from Llandovery time (or possibly earlier; Siveter *et al.* 2014) that included an active metabolism and well-developed swimming appendages, the latter evident in exceptionally preserved ostracods from the Wenlock Herefordshire Lagerstätte of England (e.g. Siveter *et al*. 2003, 2007, 2010, 2013). Parallels with *Anabarochilina* include biological pre-adaptations acted upon by environmental drivers that include sea-level rise and the spread of anoxia onto the marine shelf. Although the record of arthropod zooplankton is scarce in the fossil record, similarities between the context and nature of Cambrian and Silurian arthropod zooplankton suggest that similar processes may have acted across time, and may have been important following major extinction events for the restoration of an arthropod zooplanktonic component of marine ecosystems.

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Declaration of interest

None.

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