

# Chronology of early Cambrian biomineralization

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**Abstract** – Data on the first appearances of major animal groups with mineralized skeletons on the Siberian Platform and worldwide are revised and summarized herein with references to an improved carbon isotope stratigraphy and radiometric dating in order to reconstruct the Cambrian radiation (popularly known as the ‘Cambrian explosion’) with a higher precision and provide a basis for the definition of Cambrian Stages 2 to 4. The Lophotrochozoa and, probably, Chaetognatha were first among protostomians to achieve biomineralization during the Terreneuvian Epoch, mainly the Fortunian Age. Fast evolutionary radiation within the Lophotrochozoa was followed by radiation of the sclerotized and biomineralized Ecdysozoa during Stage 3. The first mineralized skeletons of the Deuterostomia, represented by echinoderms, appeared in the middle of Cambrian Stage 3. The fossil record of sponges and cnidarians suggests that they acquired biomineralized skeletons in the late Neoproterozoic, but diversification of both definite sponges and cnidarians was in parallel to that of bilaterians. The distribution of calcium carbonate skeletal mineralogies from the upper Ediacaran to lower Cambrian reflects fluctuations in the global ocean chemistry and shows that the Cambrian radiation occurred mainly during a time of aragonite and high-magnesium calcite seas.

Keywords: Cambrian, radiation, biomineralization, evolution, stratigraphy.

## 1. Introduction

The term ‘Cambrian radiation’ (popularly known as the ‘Cambrian explosion’) is embedded in modern scientific literature and was coined for the early Cambrian geologically rapid diversification of metazoans. Most of these early Cambrian metazoans appear to represent members of the stem lineage of extant clades. The first appearances of these groups are clustered geochronologically by higher-rank phylogeny (Budd, 2003; Landing & Westrop, 2004; Li *et al.* 2007). Budd (2003) and Budd & Jensen (2000, 2003) argued that this clustering reflects the true sequence of divergence of these high-ranking groups and implies rather late origins, probably near the Precambrian–Cambrian boundary, followed by their rapid evolutionary radiation in the early Cambrian. This event is marked in the fossil record by the first appearances and increase in diversity and abundance of many groups of animals, accompanied by the independent acquisition of mineralized skeletons in many lineages.

Skeletal biomineralization was likely an epiphenomenon of the general radiation of body plans and tissues (Bengtson, 2004). Skeletal elements are considered principal aspects of many body plans, and their origin and diversification are thought to have helped spur evolutionary radiation in the Cambrian. Skeletons

certainly diversified along with the taxa that obtained them, with 80 % of modern skeletal morphotypes present by the middle Cambrian (Thomas, Sherman & Stewart, 2000). The diversity of minerals employed in early skeletalized animals suggests a limit to the role of ocean geochemistry in the emergence of skeletons, although the primary acquisition of particular skeletal carbonate mineralogies was likely driven by the ocean geochemistry (Zhuravlev, 1993; Bengtson, 1994, 2004; Ushatinskaya & Zhuravlev, 1994; Hardie & Stanley, 1997; Stanley & Hardie, 1998; Porter, 2007; Zhuravlev & Wood, 2008; Kiessling, Aberhan & Villier, 2008). Mineralized skeletal parts are only one of many strategies to escape predation, since skeletonized species constitute a minority in modern and ancient marine ecosystems (e.g. Conway Morris, 1986). However, it was probably the anti-predatory selective advantage of mineral skeletons that drove early evolution in many clades (Bengtson, 1994, 2004). Further diversification of predators and their increased pressure on epibenthos in the Cambrian may well have triggered the early Cambrian rapid evolutionary radiation in different clades (Bengtson, 1994, 2004).

In order to understand in detail the fossil record of early Cambrian skeletal biomineralization and structure of the Cambrian radiation, a better-resolved sequence of first appearances of mineralized skeletons in the early Cambrian class-to-phylum-level animal groups is presented herein. Our study

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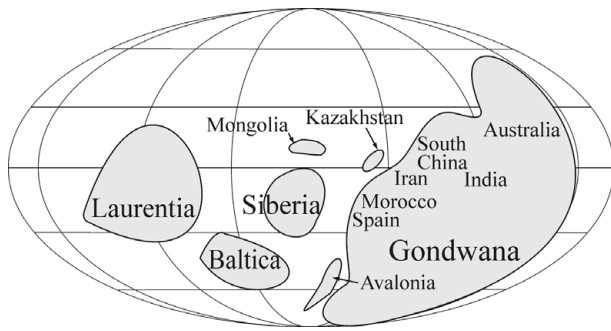


Figure 1. Schematic palaeogeographic map for the early Cambrian with crustal units discussed in this paper (adapted from Fatka, Kraft & Szabad, 2011 and Álvaro *et al.* in press).

incorporates a new carbon isotope chemostratigraphy of the northern Siberian Platform, where a continuous isotopic and fossil record is known from mainly carbonate sections of the Cambrian System (online Fig. S1 at <http://journals.cambridge.org/geo>). The Siberian data are stratigraphically correlated with those from other well-known units of the Cambrian world, such as Western Mongolia, Kazakhstan,

South China, Iran and India, Australia, Avalonia, the Mediterranean region of West Gondwana, Laurentia and Baltica (Fig. 1; online Appendices 1 & 2 at <http://journals.cambridge.org/geo>). This record, supported by available chemostratigraphy and radiometric dating, allows us to constrain the timing of the first appearances of skeletonization in various animal groups (Fig. 2).

2. Stratigraphical setting

The traditional three-fold subdivision of the Cambrian System into Lower, Middle and Upper Cambrian series has been abandoned recently in favour of a subdivision into four series of ten stages (Babcock *et al.* 2005; Babcock & Peng, 2007). The uppermost two series of the revised Cambrian timescale more or less correspond to the traditional Middle and Upper Cambrian series, while the former Lower Cambrian is subdivided into two series. The new Cambrian timescale begins with the Fortunian Stage of the Terreneuvian Series, the base of which is defined as the first occurrence of the trace fossil *Treptichnus pedum*

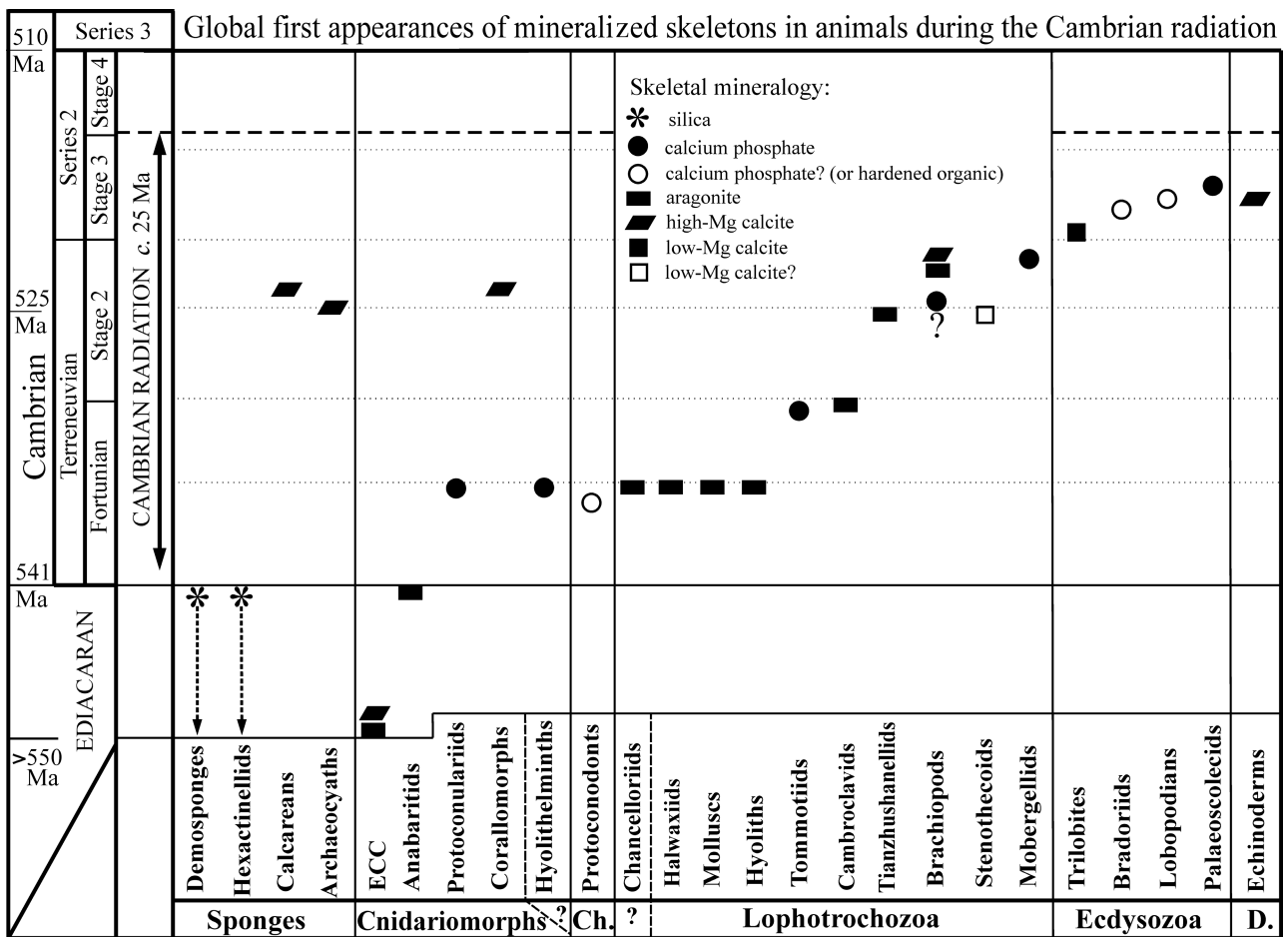


Figure 2. Global first appearances of mineralized skeletons in animals during the Cambrian radiation. Question marks indicate uncertainty in first appearance or place within higher-ranked group; affinities of chancelloriids to the Lophotrochozoa and hyolithelminths to the Cnidaria are uncertain (see main text and online Appendix 1 at <http://journals.cambridge.org/geo>). Cambroclavids (with paracarinachitids included) are tentatively attributed to the Lophotrochozoa. Vertical dashed lines for sponges reflect sporadic occurrence of their presumably biomineralized spicules in the Precambrian (see main text and online Appendix 1 at <http://journals.cambridge.org/geo>). ECC – Ediacaran calcified cnidariomorphs; Ch – Chaetognatha; D – Deuterostomia.

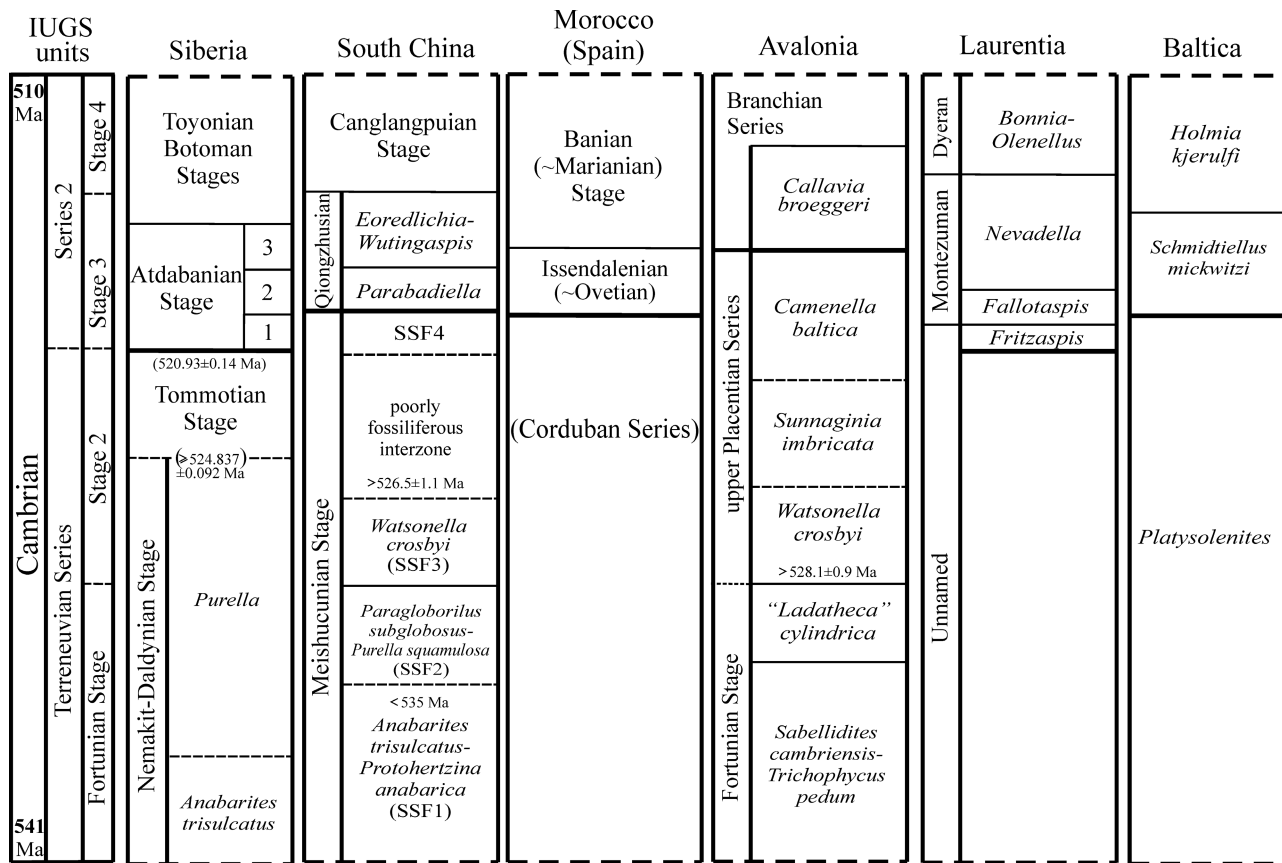


Figure 3. Correlation chart of the major crustal units discussed in this paper. It is formally accepted that the *Purella* Zone corresponds to the entire upper part of the Nemakit–Daldynian Stage (e.g. Rozanov *et al.* 2008). According to the chemostratigraphic record (e.g. Kaufman *et al.* 1996; see also Fig. 4 herein), a hiatus of disputed duration exists, however, at the base of the Tommotian Stage in its stratotype in the southeastern Siberian Platform. The *Purella* Zone is shown herein to cover its duration, since the missing record exists in the northern part of the Platform. The first occurrences of trilobites are highlighted by thick horizontal lines within the Stage 3 interval. The Atdabanian Stage is subdivided into three parts (lower, middle and upper): 1 – *Profallotaspis jakutensis* and *Repinaella* zones; 2 – *Delgadella anabara* Zone; 3 – *Judomia* Zone. SSF4 = *Sinosachites flabelliformis*–*Tannuolina zhangwentangi* Assemblage Zone. Absolute ages for the Precambrian–Cambrian boundary after Bowring *et al.* 2007; Cambrian Series 2–Series 3 boundary after Ogg, Ogg & Gradstein, 2008. Absolute ages of the lower and upper boundaries of the Tommotian Stage are based on data from Morocco (see main text and Maloof *et al.* 2005, 2010a,b). The fossiliferous *Watsonella crosbyi* Zone in China is older than 526.5 ± 1.1 Ma (after Compston *et al.* 2008) and its lower boundary in Avalonia is shown to be older than 530.7 ± 0.9 Ma (Isachsen *et al.* 1994) or 528.1 ± 0.9 Ma (Compston *et al.* 2008). That boundary is, however, younger than 535.2 ± 1.7 Ma, a combined depositional age for Bed 5 (shown as < 535 Ma in figure) from the upper *Anabarites trisulcatus*–*Protohertzina anabarica* Zone (Zhu *et al.* 2009; see main text for discussion).

at Fortune Head in Newfoundland (Landing *et al.* 2007). It is anticipated that the base of Cambrian Series 2 and Stage 3 will coincide with the first appearance of trilobites (Babcock & Peng, 2007), here interpreted to correlate with the base of the Atdabanian Stage in Siberia (Fig. 3). The remaining boundaries within Series 1–2 are less certain. In the present work, we will provisionally correlate the base of Cambrian Stage 2 of the Terreneuvian Series with the base of the *Watsonella crosbyi* Zone of Avalonia and South China (see Landing *et al.* 2007; Li *et al.* 2007) and the base of Cambrian Stage 4 with the lower Botoman Stage in Siberia (Fig. 3). The base of Cambrian Series 3, Stage 5 is presently highly debated, but is here correlated with the first occurrence of the trilobite *Oryctocephalus indicus*, which more or less coincides with the traditional Lower–Middle Cambrian boundary in many areas. The further development of the chronostratigraphy of Cambrian Series 1 and

2 is directly related to our precision in dating and correlation of the first appearances of diverse skeletal fossils in principal Cambrian sequences.

The age of the Precambrian–Cambrian boundary, marked worldwide by a negative carbon isotope anomaly, is dated in the well-constrained section in Oman to 542 ± 0.3 Ma (Amthor *et al.* 2003), later revised to 541 ± 0.13 Ma (Bowring *et al.* 2007). An associated biotic crisis is inferred from the disappearance of the Ediacaran biota (e.g. Kimura & Watanabe, 2001; Narbonne, 2005). As recognized herein, the Cambrian radiation event (‘Cambrian explosion’) occurred within a period of *c.* 25 Ma. The Cambrian radiation began with the diversification of skeletonized bilaterians following this negative anomaly and concluded with the Botoman–Toyonian biotic crisis (Zhuravlev & Wood, 1996; Zhuravlev, 2001; Li *et al.* 2007), which was the first mass extinction episode in the Phanerozoic (Signor, 1992). The onset of the crisis on the Siberian

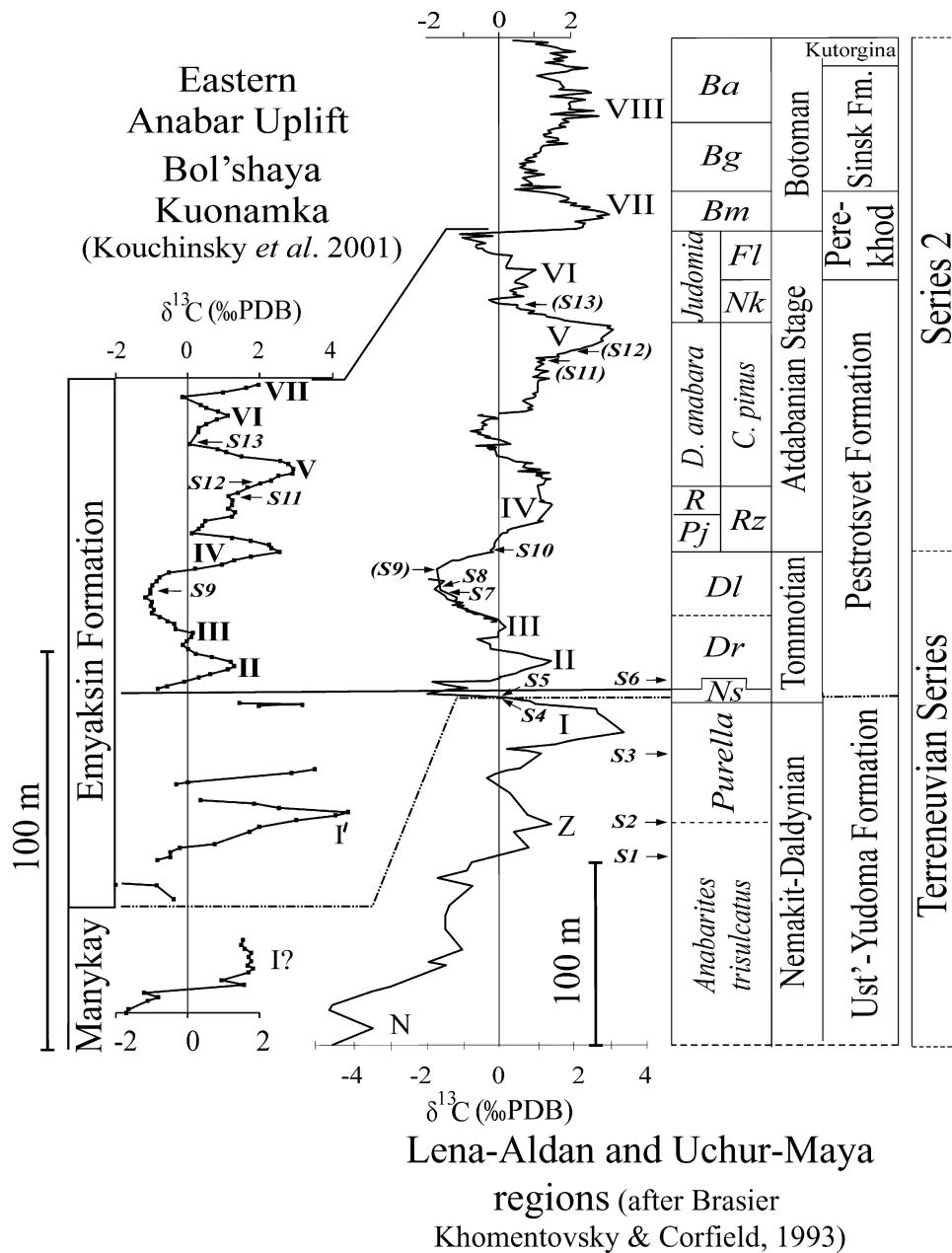


Figure 4. First appearances of skeletal fossil groups on the Siberian Platform (S1–S13, see Appendix 1 for details) in the key sections correlated with the  $\delta^{13}\text{C}$  chemostratigraphy (after Brasier, Khomevtsky & Corfield, 1993; Brasier *et al.* 1994b; Kouchinsky *et al.* 2001). Zones: *Ns* – *Nochoroicyathus sunnaginicus*; *Dr* – *Dokidocyathus regularis*; *Dl* – *Dokidocyathus lenaicus*–*Tumuliolynthus primigenius*; *Rz* – *Retecoscinus zegebarti*; *C. pinus* – *Carinacyathus pinus*; *Nk* – *Nochoroicyathus kokoulini*; *Fl* – *Fansycyathus lermontovae*; *Pj* – *Profallotaspis jakutensis*; *R* – *Repinaella*; *D. anabara* – *Delgadella anabara*; *Bm* – *Bergeroniellus micmacciformis*; *Bg* – *Bergeroniellus gurarii*; *Ba* – *Bergeroniellus asiaticus*. Numbers in brackets are projections of the corresponding first appearances in the Atdabanian Stage of the Anabar Uplift onto the Lena-Aldan reference scale.

Platform (Sinsk event), is marked by decreasing  $\delta^{13}\text{C}$  values above peak VII of the Siberian reference scale (Brasier *et al.* 1994a,b; Zhuravlev & Wood, 1996; Li *et al.* 2007; Fig. 4).

The Cambrian radiation interval shows prominent and frequent oscillations of the carbon isotope ratio (e.g. Brasier *et al.* 1994a,b; Brasier & Sukhov, 1998; Figs 4, 5). An overall rising trend in  $\delta^{13}\text{C}$  values characterizes the sedimentary sequence of the Fortunian Stage in Siberia, Mongolia, China and Western Gondwana. SHRIMP U–Pb zircon analyses from the lower part of this trend in South China provide a revised age of  $539.4 \pm 2.9$  Ma (Compston *et al.* 2008), whereas

secondary ion mass spectrometry (SIMS) of the same tuffite (Bed 5 of the Meishucun section) resulted in a *c.* 533 Ma estimate (Brooks *et al.* 2006). Nano-SIMS measurements by Sawaki *et al.* (2008) provided an age estimate of  $536.5 \pm 2.5$  Ma for Bed 5, whereas SIMS analyses by Zhu *et al.* (2009) yielded an age of  $536.7 \pm 3.9$  Ma. A combined depositional age for Bed 5 was calculated as  $535.2 \pm 1.7$  Ma by Zhu *et al.* (2009). The fauna known from below Bed 5 is considered herein to be older than 535 Ma (Figs 2, 3). The dated bed is situated in the upper part of the *Anabarites trisulcatus*–*Protohertzina anabarica* (SSF1) Assemblage Zone of the lower Meishucunian Stage.

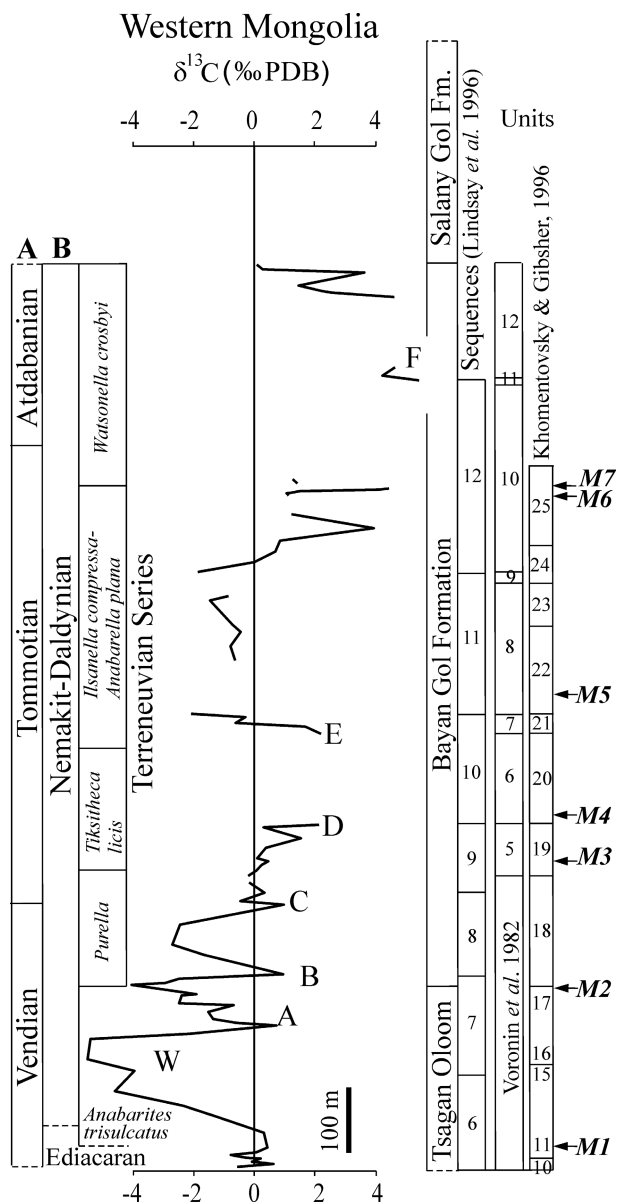


Figure 5. First appearances of skeletal fossil groups in the Tsagan Oloom and Bayan Gol formations of Western Mongolia (M1–M7, see Appendix 2 for details) (after Brasier *et al.* 1996, fig. 6), in the Tsagan Gol, Bayan Gol and Salany Gol sections composite. Features of the  $\delta^{13}\text{C}$  curve, from W to C after Brasier *et al.* (1996, fig. 5) and from D to F after fig. 7 therein; adapted for unit thickness of the Bayan Gol Formation in Brasier *et al.* 1996, fig. 6a. Zones after Brasier *et al.* (1996). A – correlation with Siberia, after Voronin *et al.* (1982), Astashkin *et al.* (1995), Khomentovsky & Gibsher (1996) and Esakova & Zhegallo (1996); B – chemostratigraphic correlation, after Brasier *et al.* (1996).

The rising trend of  $\delta^{13}\text{C}$  values continues into the Cambrian Stage 2, where several highly positive peaks preceding the Tommotian Stage in Siberia top it (Fig. 4). A single preserved prominent positive peak from the same rising trend is present in the *Watsonella crosbyi* (SSF3) Assemblage Zone of the Middle Meishucunian Stage in South China and is older than  $526.5 \pm 1.1$  Ma (after Compston *et al.* 2008). The lower boundary of the Cambrian Stage 2 and *Watsonella crosbyi* Zone has been preliminarily estimated to be

close to 530 Ma (Landing *et al.* 2007). The estimate is based on the absolute age of  $530.7 \pm 0.9$  Ma obtained from the *Watsonella crosbyi* Zone in Avalonia (Isachsen *et al.* 1994), but the date was revised to  $528.1 \pm 0.9$  Ma by Compston *et al.* (2008, p. 417). The uppermost peak in the rising trend of  $\delta^{13}\text{C}$  values within Stage 2 is dated in Morocco to  $525.4 \pm 0.5$  Ma (Malooof *et al.* 2005), later revised to  $525.343 \pm 0.088$  Ma (Malooof *et al.* 2010a,b). The high-resolution successions of  $\delta^{13}\text{C}$  peaks in Morocco and Siberia (Brasier *et al.* 1994b; Kouchinsky *et al.* 2007) proved to be very similar, and their correlation resulted in a *c.* 525 Ma estimate of the age of the Nemakit–Daldynian–Tommotian boundary dated in Morocco to  $524.837 \pm 0.092$  Ma (Malooof *et al.* 2010a,b). Chemostratigraphic  $\delta^{13}\text{C}$  correlation with radiometrically dated sections of Morocco allows dating of the lower boundary of the Atdabanian Stage in Siberia to a maximum age of  $520.93 \pm 0.14$  Ma (Malooof *et al.* 2010a,b), thereby providing an estimate of *c.* 521 Ma for the upper boundary of Stage 2 and the Terreneuvian Series.

A recalculated age of  $515.56 \pm 1.16$  Ma attributed to the upper *Antatlasia gutta-pluviae* Zone of the Moroccan Banian Stage (originally  $517.0 \pm 1.5$  Ma by Landing *et al.* 1998) can be correlated with the Botoman Stage (probably, the *Bergenellius asiaticus* Zone) of Siberia and the *Bonnia–Olenellus* Zone of Laurentia (Zhuravlev, 1995; Landing *et al.* 1998; Malooof *et al.* 2010a). The conclusion of the Cambrian radiation and the onset of the Botoman–Toyonian biotic crisis are, therefore, dated herein to be *c.* 515 Ma (Figs 2, 3). The upper boundary of the Cambrian Series 2 is estimated to be *c.* 510 Ma (Ogg, Ogg & Gradstein, 2008), because it is somewhat younger than the estimated age of  $511 \pm 1$  Ma for the upper Branchian Series of Avalonia (Landing *et al.* 1998).

## 2.a. Siberia

The former Lower Cambrian includes on the Siberian Platform and in the Altai–Sayan Folded Area the Tommotian, Atdabanian, Botoman and Toyonian stages, in ascending order (Rozanov & Sokolov, 1984; Rozanov *et al.* 2008; Varlamov *et al.* 2008). The lowermost Cambrian strata (approximately, Fortunian Stage equivalent) were recognized on the Platform as the Nemakit–Daldynian (or Manykayan Stage by some authors, e.g. Missarzhevsky, 1982, 1989; Val'kov, 1982, 1987; see discussion in Khomentovsky & Karlova, 2002, 2005). The Nemakit–Daldynian Stage is now subdivided into the *Anabarites trisulcatus* and *Purella antiqua* zones, in ascending order (Khomentovsky & Karlova, 1993, 2002). In the Lena–Aldan and Uchur–Maya regions of the southeastern Siberian Platform, the first appearances of taxa are reported from the Ust'-Yudoma Formation (Nemakit–Daldynian Stage) and from the overlying Pestrotsvet Formation (Tommotian–Atdabanian stages) (Figs 4, 6). In the northern part of the Platform, the regional first occurrences are recorded from the Manykay, Medvezh'ya and Emyaksin

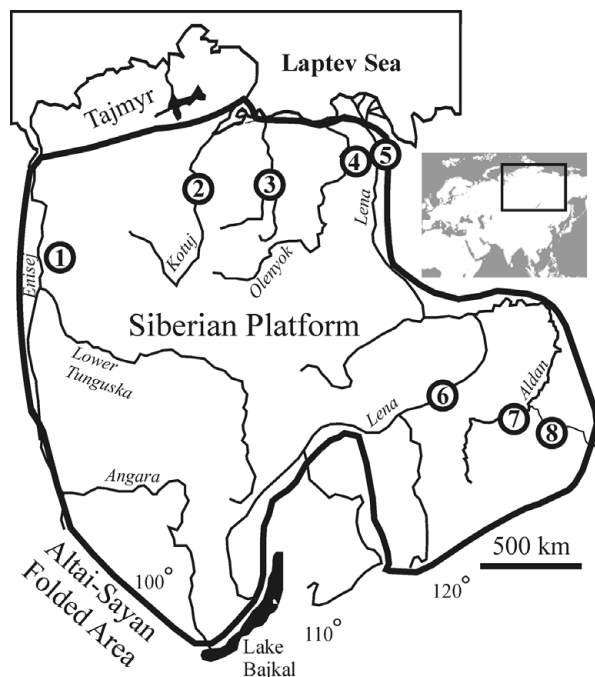


Figure 6. Map of the Siberian Platform with localities referred to in the main text and online Appendix 1 at <http://journals.cambridge.org/geo>. The localities are indicated by circles with the following numbers: 1 – Sukharikha River, middle reaches; 2 – Kotuj River (between the Sergej-Koril-Uoran rapids and mouth of the Kugda Brook) and the lowermost reaches of the Kotujkan River; 3 – Bol'shaya Kuonamka River, lower reaches; 4 – Olenyok River at the mouth of the Erkeket River and Khorbosuonka River at the mouth of the Mattajya River; 5 – Lena River, lower reaches, sections Chekurovka and at the mouth of the Ulakhan-Ald'yarkhaj Brook; 6 – Lena River, middle reaches, between sections Isit' and Achchagyi-Kyyry-Taas; 7 – Aldan River, between sections 'Dvortsy' and Ulakhan-Sulugur; 8 – Uchur-Maya region, sections along the Uchur River, between the Goman and Selinde rivers, including the Mount 1291 m, Mount Konus, Nemnekey, and Selinde localities.

formations of the Anabar Uplift (Nemakit–Daldynian–Atdabanian stages), upper Turkut and Kessyuse formations of the Olenyok Uplift (Nemakit–Daldynian–lower Tommotian), and uppermost Sukharikha–lower Krasny Porog formations abutting the lower Tommotian boundary on the northwestern margin of the Platform (Figs 4, 6). Detailed biostratigraphy and carbon isotope chemostratigraphy was obtained throughout these units and provides the basis for global correlations used herein (Fig. 4).

## 2.b. Western Mongolia

Ediacaran and lower Cambrian beds in Mongolia are better studied in sections of the Khasagt-Khairkhan Ridge in Western Mongolia, where carbon isotope chemostratigraphy and sequence stratigraphy are also available (Brasier *et al.* 1996; Esakova & Zhegalov, 1996). This region represented an isolated Zavkhan Terrane that separated from Eastern Gondwana and collided with Siberia during the Ediacaran–Early Palaeozoic interval (Ruzhentsev & Mossakovsky, 1995; Debrenne, Maidanskaya & Zhuravlev, 1999;

Kheraskova *et al.* 2003). The chemostratigraphic record from this region is fragmentary because of thick intercalations of siliciclastic sediment from which the  $\delta^{13}\text{C}_{\text{carb}}$  values cannot be read (Brasier *et al.* 1996). A composite section through the uppermost Tsagan Oloom and Bayan Gol formations in Western Mongolia is provided herein (Fig. 5).

## 2.c. Kazakhstan

The region was situated in proximity to East Gondwana and embraces Kazakhstani terranes (Holmer *et al.* 2001; Popov *et al.* 2009). Among them, sections in the Lesser Karatau Range that include the Kyrshabakty and Chulaktau formations and the Shabakty Group in ascending order are the best studied and most continuous lower Cambrian sequences in Kazakhstan (Missarzhevsky & Mambetov, 1981; Holmer *et al.* 2001). The Kyrshabakty and Chulaktau formations are biostratigraphically correlated, respectively, with the Nemakit–Daldynian and upper Nemakit–Daldynian–Tommotian stages of Siberia (Missarzhevsky & Mambetov, 1981; Mambetov, 1993). First occurrences in members of the lower Shabakty Group are biostratigraphically correlated with the upper Atdabanian–Botoman stages of Siberia (Missarzhevsky & Mambetov, 1981; Holmer *et al.* 2001).

## 2.d. South China, India and Iran

From the Yangtze Platform (South China), a set of the oldest first appearances of bilaterian taxa with mineralized skeletons is described herein mainly from the Zhujiqing Formation of Yunnan and Maidiping Formation of Sichuan. They are correlated bio- and chemostratigraphically with the Nemakit–Daldynian Stage of Siberia (Qian *et al.* 2002; Li, Zhang & Zhu, 2001; Li *et al.* 2007, 2009; Li & Xiao, 2004; Steiner *et al.* 2007) and comprise in ascending order the assemblage zones *Anabarites trisulcatus*–*Protohertzina anabarica* (SSF1) of the lower Meishucunian Stage, *Paragloborilus subglobosus*–*Purella squamulosa* (SSF2) and *Watsonella crosbyi* (SSF3) of the middle Meishucunian Stage (Steiner *et al.* 2007) (Fig. 3). The upper Meishucunian strata comprise the *Sinosachites flabelliformis*–*Tannuolina zhangwentangi* Assemblage Zone (SSF4) and directly underlie the trilobitic interval of the Cambrian in the shallow water realm of the Yangtze Platform. The first occurrences of skeletonized bilaterians within the *Parabadiella* and *Eoredlichia*–*Wutingaspis* zones of the Qiongzhusian Stage are biostratigraphically correlated (but not directly constrained by chemostratigraphy) with the middle–upper Atdabanian and upper Atdabanian–lower Botoman stages of Siberia, respectively (Qian *et al.* 2002; Li, Zhang & Zhu, 2001; Li *et al.* 2007; Li & Xiao, 2004; Steiner *et al.* 2007; Fig. 3). This interval of earliest trilobitic zones is also more coarsely resolved by the *Pelagiella subangulata* Taxon Range Zone (SSF5) in the shallow water realm, roughly

correlative with the *Ninella tarimensis*–*Cambroclavus fangxianensis* Assemblage Zone and the *Rhombocorniculum cancellatum* Taxon Range Zone at the northern margin of the Yangtze Platform. First appearances of skeletal fossils from sections of the upper Krol and lower Tal formations in the Lesser Himalayas of India and lower Soltanieh Formation in the Elburz Mountains of Iran are correlated with SSF1 of South China (Hamdi, Brasier & Jiang, 1989; Hamdi, 1995; Hughes *et al.* 2005). The three regions belonged to East Gondwana (Fig. 1).

### 2.e. Australia

The first appearances of skeletal fossils in East Gondwana are also derived from South Australia. In the Arrowie Basin, first occurrences are documented herein from the lower Wilkawillina and Ajax Limestones, Wirrapowie Limestone and lower Mernmerna Formation, and the Moorowie Formation. These first appearances span the reportedly pre-trilobitic interval and *Abadiella huoi*–*Pararia janeae* zones, correlated biostratigraphically with the Atdabanian–Botoman stages of Siberia (Bengtson *et al.* 1990; Gravestock *et al.* 2001; Jago, Sun & Zang, 2002; Jago *et al.* 2006; Skovsted, Brock & Paterson, 2006; Topper *et al.* 2010, 2011). In the Stansbury Basin, the earliest skeletal fossils are derived from the Mount Terrible and Winulta formations, broadly correlated with the Nemakit–Daldynian–Tommotian stages of Siberia (Daily, 1976, 1990; Gravestock & Shergold, 2001; Jago, Sun & Zang, 2002; Jago *et al.* 2006). Other first occurrences from the overlying Kulpara Formation and Parara Limestone are reported from pre-trilobitic beds and *Abadiella huoi*–*Pararia janeae* zones (Bengtson *et al.* 1990; Gravestock *et al.* 2001; Jago, Sun & Zang, 2002; Jago *et al.* 2006).

### 2.f. Mediterranean region

Several blocks now in North Africa and Western Europe were situated along the western margin of Gondwana (Fig. 1). Among these, first occurrences from the Corduban Series of central Spain are discussed herein. Based on biostratigraphic correlation with Morocco and chemostratigraphy, the Corduban Series represents a sub-trilobitic part of the lower Cambrian of Western Gondwana (Geyer & Landing, 2004; Fig. 3). The first appearances from the lower Ovetian Stage in W Europe (Spain, France, Germany, Sardinia) are correlated biostratigraphically with those from the lower Issendalenian Stage in the Anti-Atlas Mountains of Morocco (Geyer & Landing, 2004). The base of the Issendalenian Stage in Morocco correlates chemostratigraphically with the *Delgadella anabara* Zone of the Atdabanian Stage of Siberia (Kirshvink *et al.* 1991; Maloof *et al.* 2005, 2010a,b). First appearances of skeletal fossils from the upper Ludwigsdorf limestones of the Saxothuringian microcontinent (Germany) are correlated with the Atdabanian–Botoman stages of Siberia and the upper Qiongzhusian–lower Canglang-

puian stages of South China (Elicki, 1994; Geyer & Elicki, 1995).

### 2.g. Avalonia

The region formed a relatively small terrane of West Gondwanan affinity. In its portion represented by SE Newfoundland, the oldest first appearances are located within the Quaco Road Member of the upper Chapel Island Formation, within the *Ladatheca cylindrica* Zone of the Fortunian Stage and *Watsonella crosbyi* Zone of the Cambrian Stage 2 (Landing, 2004; Landing & Westrop, 1998; Landing *et al.* 1989, 2007). Other important first occurrences are reported from the upper Cuslett and lower Fosters Point formations (*Camenella baltica* Zone, correlated with the lower–middle Atdabanian Stage), as well as from the basal part of the overlying Brigus Formation (*Callavia broeggeri* Zone, correlated with the upper Atdabanian–Botoman stages) (Shergold & Geyer, 2003; Fig. 3). In the portion of Avalonia represented by South Britain, the first occurrences regarded herein are from the Home Farm Member, Lower Comley Sandstone and Comley Limestone (*Camenella baltica* and *Callavia* zones).

### 2.h. Laurentia

In the Northwest Territories of Canada the first appearances are reported from the Ingta Formation of the Wernecke Mountains, correlated with the basal Cambrian *Anabarites*–*Protohertzina* Zone (Pyle *et al.* 2006) and underlain by the Precambrian–Cambrian boundary negative excursion (Narbonne, Kaufman & Knoll, 1994; Pyle *et al.* 2004), and from the Sekwi Formation of the Mackenzie Mountains and basal Rosella Formation of the Cassiar Mountains, correlated with the *Fallotaspis* and *Nevadella* zones (Voronova *et al.* 1987; Dillard *et al.* 2007). In Greenland, important first occurrences are reported from the lower Buen Formation, biostratigraphically correlated with the *Nevadella* Zone and upper Atdabanian Stage (Conway Morris *et al.* 1987; Conway Morris, 1989; Debrenne & Reitner, 2001; Conway Morris & Peel, 2008, 2010), and from the upper Bastion–Ella Island formations, correlated with the *Bonnia*–*Olenellus* Zone and Botoman Stage (Skovsted, 2003, 2004, 2006). First occurrences in California and Nevada are from the Campito Formation, from the *Fritzaspis*, *Fallotaspis* and *Nevadella* zones (Durham, 1971; Hollingsworth, 2005, 2007; Fig. 3).

### 2.i. Baltica

The earliest skeletal fauna (*Mobergella* fauna) on the Baltic Shield known from the Kalmarsund Sandstone and subsurface deposits in southern Sweden is correlated with the *Schmidtellus mickwitzii* Zone (Bengtson, 1968, 1970, 1977). First appearances from the Zawiszyn Beds of the upper Klimontovian Stage in Poland (Lendzion, 1972, 1978; 1983; Bengtson, 1977), Lükati Formation and lower part of the Tiskre Formation in

northern Estonia are also attributed to the *Schmidtiiellus mickwitzii* Zone of the Dominopol' Stage (Bergström, 1973; Mens & Pirrus, 1977; Moczyłowska, 2002). These beds are broadly correlated with the Atdabanian Stage of Siberia (Moczyłowska, 2002). The oldest regional first occurrences are reported from the Lontova Formation in Estonia, *Platysolenites antiquissimus* Zone, broadly correlated with the Terreneuvian Series (Fig. 3).

### 3. First appearances of mineralized skeletal parts in animal groups

#### 3.a. Sponges and spongiomorphs

The oldest fossils attributed to sponges are reported from the Cryogenian Period. One of the earliest lines of evidence for sponges comes from well-preserved molecular biomarkers of demosponges from strata of the Neoproterozoic Huqf Supergroup of the South Oman Salt Basin pre-dating the termination of the Marinoan glaciation and having a minimum age of *c.* 635 Ma (McCaffrey *et al.* 1994; Love *et al.* 2006, 2009). Fossils interpreted as sponge-grade metazoans are also found in the pre-Marinoan Trezona Formation of South Australia with a maximum age of  $659.7 \pm 5.3$  Ma (Malooof *et al.* 2010*c*). *Palaeophragmodictya reticulata* Gehling & Rigby, 1996, from the Ediacaran Rawnsley Quartzite in South Australia, was interpreted as a hexactinellid (Gehling & Rigby, 1996; Debrenne & Reitner, 2001), or a stem-group sponge (Mehl, 1998), but later it was reinterpreted as an attachment disc of a problematic organism of uncertain affinity to sponges or cnidarians (Serezhnikova, 2007). The Late Ediacaran *Fedomia mikhaili* Serezhnikova & Ivantsov, 2007 and *Vaveliksia vana* Ivantsov, Malahovskaya & Serezhnikova, 2004, from the White Sea coast, are likely sponges (Ivantsov, Malahovskaya & Serezhnikova, 2004; Serezhnikova, 2007; Serezhnikova & Ivantsov, 2007).

##### 3.a.1. Demosponges and hexactinellids

The earliest reported sponge spicules from *c.* 750 Ma strata in Nevada were attributed to demosponges (Reitner & Wörheide, 2002; Müller *et al.* 2007). Monaxonus thin-walled and hollow spicules of possible hexactinellids derive from Alaska (Allison & Awramik, 1989; Debrenne & Reitner, 2001), from beds inferred by chemostratigraphy to be Neoproterozoic, most likely pre-Varangerian (Kaufman, Knoll & Awramik, 1992). Skeletal remains of sponges found in thin-sections from the Doushantuo Formation on the South China Platform are interpreted as demosponges, because they consist exclusively of siliceous monaxonal spicules (Li, Chen & Hua, 1998). Their maximum age is *c.* 580 Ma (Condon *et al.* 2005). These latter, however, were regarded as possible pseudofossils (inorganic crystals) by Zhou, Yuan & Xue (1998). Spicule-like objects of hexactinellid habit from the Ediacaran Doushantuo

and Dengying formations of Hubei Province were observed in thin-section (Tang, Zhang & Jiang, 1978; Zhao *et al.* 1988; Steiner *et al.* 1993), but these might also be pseudofossils composed of inorganic crystals (Zhou, Yuan & Xue, 1998) or might instead represent acanthomorphic acritarchs (Zhang, Yuan & Yin, 1998). Spicules with demosponge affinities are known from *Cloudina* reefs of Namibia (Reitner & Wörheide, 2002), with an age of *c.* 550 Ma (after Wood, Grotzinger & Dickson, 2002; Grotzinger, Adams & Schröder, 2005). Disarticulated and clustered tetracts, pentacts, hexacts and polyactines attributed to upper Ediacaran hexactinellids are preserved in iron oxides in chert layers of the upper Tsagan Oloom Formation of Western Mongolia (Brasier *et al.* 1996; Brasier, Green & Shields, 1997), but the stratigraphic position of strata yielding these spicules requires further age constraint. Hexactinellid and/or demospongiid siliceous spicules were mentioned but not illustrated by Brasier & Singh (1987, p. 326), Mazumdar & Banerjee (1998) and Tiwari (1999). These fossils were recovered from the lowermost Cambrian basal Chert-Phosphate Member of the lower Tal Group, in the Mussoorie, Garwhal and Korgai synclines of the Lesser Himalayas and from the lower part of the Gangolihat Dolomite (Deoban Formation) of the Inner Kumaun Lesser Himalayas (inner carbonate belt) (Tiwari, Pant & Tewari, 2000), correlated with the lowermost Cambrian (lower Meishucunian) based on the occurrence of protoconodonts (Azmi & Paul, 2004).

Abundant and extraordinarily preserved hexactinellids and demosponges (including articulated specimens) are well documented from the early Cambrian deep basinal settings of the Yangtze Platform, from the Niutitang black shales of Hunan (Ding & Qian, 1988; Steiner *et al.* 1993) and Hetang black shales of Anhui (Yuan *et al.* 2002). Hexactinellid sponge spicules occur in chert beds of the basal member of the Niutitang Formation of Hunan Province (Steiner *et al.* 1993: p. 6, figs 2–4) and of equivalent strata in Zhejiang Province (Steiner *et al.* 2004*a*, fig. 2h), of which the ages are constrained to the lower Meishucunian Stage owing to the occurrence of *Kaiyangites*. Megasters are not rare in the lower Meishucunian of Shaanxi Province (Steiner *et al.* 2007). By contrast, there are no remains interpreted as sponge spicules from the Meishucunian Stage in its stratotype area of eastern Yunnan (Rigby & Hou, 1995), where the first spicules and sponge body fossils occur in the basal Yu'anshan Formation of the Qiongzhusian Stage (Steiner *et al.* 2001).

In Siberia, siliceous spicules attributed to the Hexactinellida are known from the lowermost Tommotian *Nochorojcyathus sunnaginicus* Zone (Sokolov & Zhuravleva, 1983; Pel'man *et al.* 1990; Rozanov & Zhuravlev, 1992) and traditionally referred to as *Protospongia* sp. (*Protospongia* Salter, 1864). Similar fossils have also been reported by Khomentovsky, Val'kov & Karlova (1990) and Khomentovsky & Karlova (1993) (but not illustrated) from the pre-Tommotian part of the lower Cambrian, from



the upper Ust'-Yudoma Formation (Fig. 4; online Appendix 1 at <http://journals.cambridge.org/geo>). The earliest spicules of demosponges occur in the *Fansycyathus lermontovae* Zone of the upper Atdabanian Stage in northern Siberia (Fedorov in Shabanov *et al.* 1987; online Appendix 1 at <http://journals.cambridge.org/geo>). The earliest articulated hexactinellids and demosponges in Siberia occur in the lower Botoman Sinsk lagerstätten (Goryansky, 1977; Ivantsov *et al.* 2005; Ponomarenko, 2005; Rozanov *et al.* 2010; online Appendix 1 at <http://journals.cambridge.org/geo>).

### 3.a.2. Calcareans

The earliest calcarean sponge spicules of *Dodecaactinella* sp. occur in the lower *Dokidocyathus regularis* Zone of Siberia (Kruse, Zhuravlev & James, 1995; Fig. 2). Pentactines of *Sulugurella sulugurica* Fedorov in Pel'man *et al.* 1990 were originally attributed to the Calcareans and reported from the *Nochorojcyathus sunnaginicus* Zone of the Tommotian (Pel'man *et al.* 1990) and from the probably slightly older uppermost Sukharikha Formation of the Sukharikha River section (Rowland *et al.* 1998), but their hexactinellid affinity is more plausible (A. Zhuravlev, pers. comm., 2008). Calcarean spicules are also known from the Atdabanian–Botoman-equivalent strata of Mongolia, Western Gondwana, Australia and Laurentia (online Appendix 1 at <http://journals.cambridge.org/geo>). The first articulated calcarean *Gravestockia pharetronensis* Reitner, 1992 occurs in Australian beds correlated with the Atdabanian Stage (Reitner 1992; Debrenne & Reitner, 2001; online Appendix 1 at <http://journals.cambridge.org/geo>). According to Zhuravlev & Wood (2008), spicules of first representatives of calcarean sponges are probably high-magnesium calcitic in original composition. Stem-group sponges, which may combine mineralogy and morphology of calcarean and hexactinellid spicules, are also reported from the Cambrian Series 2 (Botting & Butterfield, 2005; Harvey, 2010; see also *Eiffelia* Walcott, 1920 in online Appendix 1 at <http://journals.cambridge.org/geo>).

### 3.a.3. Archaeocyaths and other probable aspicular sponges

First archaeocyaths are known from the lowermost Tommotian Stage of the Siberian Platform (e.g. Rozanov *et al.* 1969, 1992, 2008; Shabanov *et al.* 2008; Riding & Zhuravlev, 1995; Kruse, Zhuravlev & James, 1995). Among them, an undetermined form is reported from the uppermost Ust'-Yudoma Formation (Rozanov *et al.* 1992; Shabanov *et al.* 2008), while several species occur in the basal Pestrotsvet Formation of the Lena-Aldan region (online Appendices 1 & 2 at <http://journals.cambridge.org/geo>; Fig. 2). Archaeocyaths were also reported from the basal Pestrotsvet Formation at Selinde in the southeastern Siberian Platform (Korshunov, Repina & Sysoev,

1969; Khomentovsky & Karlova, 2002) and the uppermost Sukharikha Formation in the Igarka region of the northwestern margin of the Siberian Platform (Rozanov *et al.* 1969, but see Luchinina *et al.* 1997 and Rowland *et al.* 1998). In the latter two localities, carbonates display  $\delta^{13}\text{C}$  oscillations with high positive peaks characteristic of the lower Tommotian boundary beds, although the position of these peaks with respect to this boundary has been questioned (Kouchinsky *et al.* 2001, 2005, 2007). The skeleton of archaeocyaths is thought to have been originally mineralized with high-magnesium calcite (Zhuravlev & Wood, 2008). The radiocyaths and cribricyaths are thought to be different groups of aspicular sponges with, respectively, aragonitic and high-magnesium calcitic biomineralization (Zhuravlev & Wood, 2008). The radiocyaths first appear in the upper Tommotian of the Siberian Platform (Rozanov & Zhuravlev, 1992), whereas the oldest cribricyaths are known from the Altai-Sayan Folded Area in the first half of the Atdabanian Stage (Rozanov & Zhuravlev, 1992).

### 3.b. Cnidariomorphs and problematic tubular forms

Fossils that can be reasonably interpreted as diploblastic-grade metazoans with biomineralized skeletons are represented by a few but locally abundant forms in the upper Ediacaran strata (Grant, 1990; Grotzinger, Watters & Knoll, 2000; Grotzinger, Adams & Schröder, 2005; Wood, Grotzinger & Dixon, 2002; Amthor *et al.* 2003; online Appendix 1 at <http://journals.cambridge.org/geo>). There is also a variety of mineralized solitary and modular calcareous corallomorphs in the lower Cambrian (Debrenne, Lafuste & Zhuravlev, 1990). For convenience, all of these fossils are herein collectively termed cnidariomorphs, including such accretionarily growing mineralized solitary tube-like forms as anabaritids and protoconulariids. Hyolithelminths and 'coleolids' have a more uncertain biological affinity, and their interpretation as bilaterian organisms (such as annelids) cannot be excluded.

#### 3.b.1. Ediacaran calcified cnidariomorphs

The earliest biomineralizing cnidariomorph fossils are represented by such solitary calcareous (probably aragonitic or high-magnesium calcite) tubular forms as *Cloudina* and *Namacalathus* (ECC in online Appendix 2 at <http://journals.cambridge.org/geo> and Fig. 2). Their lowermost occurrence is documented from the Nama Group in Namibia (Germs, 1972; Grant, 1990) and coincides with a pronounced positive carbon excursion reaching 8‰ and dated  $548.8 \pm 1$  Ma (Grotzinger *et al.* 1995; Grotzinger, Watters & Knoll, 2000; Condon *et al.* 2005; Grotzinger, Adams & Schröder, 2005; Zhuravlev *et al.* 2011). *Namapoikia rietoogensis* Wood, Grotzinger & Dixon, 2002 (a calcareous, probably aragonitic, modular form with a robust biomineralized but aspicular skeleton) is of

uncertain affinity to sponges or cnidarians and occurs in the Nama Group of Namibia (Wood, Grotzinger & Dixon, 2002) in the uppermost Ediacaran beds of the same estimated age.

### 3.b.2. *Corallomorphs*

The earliest solitary calcareous corallomorph, *Cysticyathus tunicatus* Zhuravleva, 1955, appears in the lower *Dokidocyathus regularis* Zone of the Tommotian Stage of the Siberian Platform, whereas the oldest modular corallomorphs are the khasaktiids *Vittia* Sayutina and *Khasaktia* Sayutina (Sayutina, 1980) from the upper Tommotian of Siberia (Rozanov & Zhuravlev, 1992; Kruse, Zhuravlev & James, 1995; online Appendices 1, 2 at <http://journals.cambridge.org/geo>). Khasaktiids are reconstructed as originally high-magnesium calcitic (Zhuravlev & Wood, 2008). The oldest known korovinellid- or khasaktiid-like structures described from the uppermost Krol Formation (near the Precambrian–Cambrian boundary) of India (Flügel & Singh, 2003; online Appendix 1 at <http://journals.cambridge.org/geo>) were interpreted as sponges/stromatoporoids (Flügel & Singh, 2003), but their microbial origin was also suggested (Debrenne, Gangloff & Zhuravlev, 1990).

### 3.b.3. *Anabaritids*

Anabaritids are a problematic early Cambrian group with originally calcareous, probably aragonitic, skeletons that typically had triradiate symmetry (Kouchinsky *et al.* 2009). Anabaritids mark the basal Cambrian strata in Siberia, Mongolia, Kazakhstan, China, India, Iran and Laurentia, but may also occur in the uppermost Ediacaran of Siberia (Karlova & Vodanyuk, 1985; Karlova, 1987; Knoll *et al.* 1995) and Western Mongolia (Brasier *et al.* 1996; Esakova & Zhegallo, 1996; Khomentovsky & Gibsher, 1996; online Appendices 1, 2 at <http://journals.cambridge.org/geo>; Fig. 2).

### 3.b.4. *Protoconulariids*

Protoconulariids have a disputed affinity with Palaeozoic conulariids, a group most convincingly placed within the Cnidaria (Van Iten, Zhu & Li, 2010). Calcium phosphatic protoconulariids first appear in the upper *Anabarites trisulcatus–Protohertzina anabarica* Assemblage Zone of the lower Meishucunian Stage of China. They are represented by *Arthrochites emeishanensis* Chen, 1982, *Hexangulaconularia formosa* He in Xing *et al.* 1984 and probably related forms, such as *Carinachites* spp. and *Emeiconularia trigemme* Qian *et al.* 1997 (Brasier, 1989a; Qian, 1989, 1999; Qian & Bengtson, 1989; Conway Morris & Chen, 1992; Qian, Li & Zhu, 2001; Zhu *et al.* 2001; Qian *et al.* 2002; Steiner *et al.* 2004a). *Hexangulaconularia formosa* is also known from the *Anabarites trisulcatus–Protohertzina anabarica* Assemblage Zone of the Lesser Himalayas (Brasier & Singh, 1987;

Hughes *et al.* 2005). A probably coeval occurrence of *Carinachites* sp. is described from the upper Ingta Formation in northwestern Canada (Laurentia), also assigned to the *Anabarites trisulcatus–Protohertzina anabarica* Zone (Pyle *et al.* 2006; online Appendices 1, 2 at <http://journals.cambridge.org/geo>; Fig. 2).

### 3.b.5. *Hyolithelminths*

Hyolithelminths have calcium phosphatic tubes that are circular (*Hyolithellus* Billings, 1871) or oval (*Torella* Holm, 1893) in cross-section. They are similar to *Sphenotallus* Hall, 1847 and *Byronia* Matthew, 1899 also known from the Cambrian Series 2 and may be cnidarians as well, but do not show budding typical of the Cnidaria (Neal & Hannibal, 2000; Van Iten, Zhu & Collins, 2002; Van Iten *et al.* 2005; Peng *et al.* 2005). Hyolithelminths are alternatively compared to annelid tubes (Fisher, 1962; Sokolov & Zhuravleva, 1983; Kiel & Dando, 2009; Johnston *et al.* 2009; Skovsted & Peel, 2011). Hyolithelminths are well known from the lower Tommotian Stage of Siberia (Rozanov *et al.* 1969; Sokolov & Zhuravleva, 1983). Their first representatives are reported, but not illustrated, from the upper *Purella* Zone of the Nemakit–Daldynian Stage (Khomentovsky *et al.* 1983; Khomentovsky, Val'kov & Karlova, 1990; Khomentovsky & Karlova, 1993; Varlamov *et al.* 2008). Probably the earliest hyolithelminths are represented by *Hyolithellus* spp. from the *Anabarites trisulcatus–Protohertzina anabarica* Assemblage Zone of South China (Brasier, 1989a; Qian & Bengtson, 1989; Qian, 1999; Qian *et al.* 2002), Ingta Formation of Laurentia (Pyle *et al.* 2006) and Lower Tal Formation of India (Brasier & Singh, 1987; online Appendices 1, 2 at <http://journals.cambridge.org/geo>; Fig. 2).

### 3.b.6. *Problematic tubular forms*

Other widespread tubular problematics are represented by calcareous, probably aragonitic forms *Coleolella* Missarzhevsky in Rozanov *et al.* 1969, *Coleoloides* Walcott, 1889 and, possibly, *Coleolus* Hall, 1876 (to which '*Coleolus*' *trigonus* Sysoev, 1962 is attributed; see online Appendix 1 at <http://journals.cambridge.org/geo>; Fig. 2). *Coleoloides trigeminatus*, *Coleolella billingsi* (Sysoev, 1962) and '*Coleolus*' *trigonus* Sysoev, 1962 are reported from the lowermost Tommotian *N. sunnaginicus* Zone (Sokolov & Zhuravleva, 1983) of Siberia. They also occur in probably older beds, where carbonates display high positive  $\delta^{13}\text{C}$  peaks, whose position with respect to the lower Tommotian boundary has been questioned (Kouchinsky *et al.* 2005, 2007). *C. typicalis* is known from the *Tiksitheca licis* Zone of Western Mongolia and *Watsonella crosbyi* Zone of Avalonia (Landing *et al.* 1989). *Coleoloides* is also reported from the *Anabarites trisulcatus–Protohertzina anabarica* Zone of India (Brasier & Singh, 1987), but the material requires further revision.

### 3.c. Protoconodonts

The protoconodonts are a group of phosphatic simple-cone-shaped sclerites with a deep cavity, lamellar and often longitudinally fibrous wall, and with accretionary growth on the inner side and basal margin (Bengtson, 1976, 1977, 1983). Protoconodonts are microstructurally different from para- and euconodonts (see Section 3.q); finds of animals with grouped protoconodonts in the Chengjiang fossil lagerstätte (Chen & Huang, 2002; Vannier *et al.* 2007) and partially articulated protoconodont apparatuses of lower Meishucunian species *Mongolodus longispinus* (Vannier *et al.* 2007) demonstrate their affinity with chaetognathans (Szaniawski, 1982, 2002; Hamdi, Brasier & Jiang, 1989; Azmi, 1996; McIlroy & Szaniawski, 2000; Doguzhaeva, Mapes & Mutve, 2002; Azmi & Paul, 2004; Qian *et al.* 2004; Pyle *et al.* 2006; Vannier *et al.* 2007; see also Remarks in section 'Protoconodonts' in online Appendix 1 at <http://journals.cambridge.org/geo>). The primary nature of phosphatization in protoconodonts has been questioned, however, because microstructures rather suggest that in analogy with grasping hooks of modern chaetognaths the protoconodonts had an organic composition, i.e. of hardened chitin (Steiner & Li, 2010).

Among these fossils, *Protohertzina anabarica* and *P. unguiformis* (probably morphotypes within the same species collectively referred to as the *Protohertzina anabarica* group, e.g. by Brasier, 1989b) represent the earliest skeletal remains attributed to protoconodonts and, probably, bilaterian animals in general (Qian & Bengtson, 1989). The first protoconodonts of the *P. anabarica* group appear in the *Anabarites trisulcatus* Zone of the Nemakit–Daldynian Stage on the Siberian Platform and in roughly contemporaneous beds in South China, India, Iran, Laurentia and probably Western Mongolia and Kazakhstan (online Appendices 1 & 2 at <http://journals.cambridge.org/geo>; Fig. 2). With the resolution of stratigraphic correlation available, it is not possible to warrant, however, their earlier appearance than the first calcareous sclerites and shells (see next Section).

### 3.d. Molluscs, hyoliths, halwaxiids and cancelloriids

Coiled, conical or cyrtoconic shells occur frequently in lower Cambrian faunas worldwide. These fossils resemble shells of undisputed molluscs in overall form and shell microstructure. It is largely accepted, therefore, that they are the earliest representatives of the Phylum Mollusca, falling more likely within its stem group (e.g. Peel, 1991; Budd, 2001). Univalved shells with solid walls (not composed of sclerites) presumably represent complete and adult external skeletons (but see Martí Mus, Palacios & Jensen, 2008) and are considered herein to be molluscs. Some other problematic shells or plates, probably parts of multiplated chiton-like exoskeletons, may also belong to this group or to the Halwaxiida (see Section 3.k; online Appendices 1 & 2 at <http://journals.cambridge.org/geo>).

The complete exoskeleton of hyoliths consists of a conical shell (conch), apertural lid (operculum) and may include a pair of curved retractable appendages (helens) protruding between the conch and operculum. These fossils are usually classified either within the Phylum Mollusca or Annelida, or in a separate phylum-level group (e.g. Runnegar *et al.* 1975; Runnegar, 1980; Kouchinsky, 2000).

The Halwaxiida Conway Morris & Caron, 2007 is an apparently monophyletic group that includes biomineralizing calcareous scale-bearing siphogonuchitids and halkieriids. Their compound scleritomes (= full set of sclerites of one individual, after Bengtson, 1985) could also contain conical shells (Bengtson, 1992a). Determining whether specific early Cambrian mollusc-like shells represent the complete skeleton or only a part of the scleritome is not always straightforward (see Section 3.k and 'Other fossils' in online Appendix 1 at <http://journals.cambridge.org/geo>). Representatives of the Halwaxiida have been united with sedentary Cancelloriida in the problematic Coeloscleritophora, whose members share possession of hollow calcareous sclerites secreted at a fixed size by internal soft tissue and a similar skeletal microstructure (Bengtson & Missarzhevsky, 1981; Bengtson & Conway Morris 1992; Conway Morris & Peel, 1995; Bengtson, 2005; Porter, 2008). Halwaxiids can be considered to be stem-group lophotrochozoans, while the general body morphology and affinity of cancelloriids is more problematic (Bengtson & Hou, 2001; Janussen, Steiner & Zhu, 2002; Randell *et al.* 2005; Bengtson, 2005; Sperling, Pisani & Peterson, 2007; Porter, 2008).

These four groups (molluscs, hyoliths, halwaxiids and cancelloriids) appeared in the geological record at about the same time. Their evolutionary radiation in the earliest Cambrian was an important early step for metazoans, which gave rise to numerous forms typical of the lower Cambrian strata worldwide and dominated most of the pre-trilobitic bilaterian fossil assemblages. With the current fidelity of stratigraphic correlation available it is not yet possible to further resolve the relative order of first appearances of molluscs, hyoliths and coeloscleritophorans (Fig. 2).

The oldest such fossils occur at the same level in the upper *Anabarites trisulcatus*–lower *Purella* zones of the Nemakit–Daldynian Stage of the southeastern Siberian Platform (Khomentovskiy, Val'kov & Karlova, 1990) correlated with the lowermost part of the rising trend in the lower Cambrian  $\delta^{13}\text{C}$  values, around feature Z of the Siberian  $\delta^{13}\text{C}$  reference scale (Brasier, Khomentovskiy & Corfield, 1993; Fig. 4). The fossils are represented by mollusc-like shells, such as cyrtoconic planispiral *Oelandiella* Vostokova, 1962 and sinistrally coiled *Barskovia* Golubev, 1976, conchs of hyoliths, siphogonuchitid sclerites and scaly shells of *Purella* Missarzhevskiy, 1974. The earliest hyoliths are also described from the probably time-equivalent basal *Purella* Zone of Western Mongolia (Khomentovskiy & Gibsher, 1996), SSF1 of South China (Qian & Bengtson, 1989; Steiner *et al.* 2004a) and India (Brasier & Singh,

1987; Hughes *et al.* 2005). Siphogonuchitid sclerites and shells of *Maikhanella* Zhegallo in Voronin *et al.* 1982 are also reported from SSF1 beds of South China (Qian & Bengtson, 1989; Steiner *et al.* 2004a), whereas *Purella* defines the base of the *Purella* Zone in Western Mongolia (Khomontovsky & Gibsher, 1996; Fig. 5).

The earliest confirmed appearance of *Chancelloria* is represented by articulated sclerites from the *Purella* Zone of the Nemakit–Daldynian Stage of Siberia (Khomontovsky, Val'kov & Karlova, 1990) and correlated with a trough between Siberian isotopic features Z and I (Brasier, Khomontovsky & Corfield, 1993; Fig. 4). Identification of fossils reported as single rays of *Chancelloria* sp. from the *Anabarites trisulcatus* and basal *Purella* zones of the Nemakit–Daldynian Stage of the southeastern Siberian Platform (Khomontovsky, Val'kov & Karlova, 1990; Khomontovsky & Karlova, 2005; Brasier, Khomontovsky & Corfield, 1993) is questionable (Zhuravlev *et al.* 2011). Likewise, the occurrence of Chancelloriidae in SSF1 of South China (Qian & Bengtson, 1989) has not been confirmed (M. Steiner, unpub. obs.; Online Appendix 1 at <http://journals.cambridge.org/geo>). Single-rayed sclerites of *Cambrothyra* are known, however, from SSF1. This organism is treated as closely related to, but outside the Chancelloriidae *sensu stricto* (Steiner *et al.* 2004a, fig. 2; Moore *et al.* 2010).

### 3.e. Cambroclavids and paracarinachitids

Cambroclaves are originally calcareous (probably aragonitic) sclerites without concentrically arranged growth increments and consist of a basal hollow shield usually bearing a spine (Qian, 1978; Mambetov & Repina, 1979; Bengtson *et al.* 1990; Conway Morris & Chen, 1991; Conway Morris *et al.* 1997; Elicki & Wotte, 2003). Paracarinachitids are probably related forms, but were formed by overlapping growth increments (Qian & Bengtson, 1989). These fossils are regarded as protective sclerites of bilaterally symmetrical animals without reliable systematic position (Bengtson *et al.* 1990). They were alternatively interpreted as receptaculitids (algae or sponges) (Dzik, 1994), protoconodonts (Mambetov & Repina, 1979), acanthocephalans (Qian & Yin, 1984) or such ecdysozoan groups as priapulids (Conway Morris *et al.* 1997) and lobopodians (Qian, 1999; Liu *et al.* 2007). A fragment of an articulated body covered with cambroclavid-type sclerites was reported from the Sirius Passet fauna and has been tentatively assigned to the Ecdysozoa (Conway Morris & Peel, 2010). The fibrous ultrastructure of the wall in cambroclavids and paracarinachitids (Qian & Bengtson, 1989; Conway Morris & Chen, 1991), typical of the other calcareous fossils discussed above, such as molluscs, hyoliths, halwaxiids and chancelloriids, are nevertheless compatible with a lophotrochozoan affinity.

The first sclerites of cambroclavids (*Zhijinites* Qian, 1978) and paracarinachitids (*Paracarinachites* Qian & Jiang in Luo *et al.* 1982) are known from the Yangtze Platform, *Paragloborilus subglobosus*–

*Purella squamulosa* Assemblage Zone (SSF2) of the middle Meishucunian Stage, marked by a rising trend in the carbon isotope record below a prominent positive peak ZHUCE (Qian, 1999; Qian *et al.* 2002; Qian & Bengtson, 1989; Bengtson, 1992b; Steiner *et al.* 2007; online Appendices 1 & 2 at <http://journals.cambridge.org/geo>; Fig. 2).

### 3.f. Tommotiids

Tommotiids are represented by calcium phosphate sclerites with evidence of basal marginal accretionary growth. These fossils have been interpreted as sclerites of larger scleritomes of problematic animals (Bengtson, 1970, 2004; Holmer *et al.* 2008; Skovsted *et al.* 2008, 2009b). The taxonomy of tommotiids was discussed by Landing (1984, 1995), Bengtson (1986), Laurie (1986), Bengtson *et al.* (1990), Conway Morris & Chen (1990), Esakova & Zhegallo (1996) and Skovsted *et al.* (2009a). Based on the organophosphatic shell composition and morphological similarities, tommotiids have been regarded as closely related to brachiopods (Williams & Holmer, 2002). Recent discoveries of articulated tommotiids show distinct affinities to lophophorates, including a sessile habit and brachiopod-like shells within the scleritome (Skovsted *et al.* 2008, 2009b; Holmer *et al.* 2008).

Classical tommotiids, such as *Camenella* Missarzhevsky in Rozanov & Missarzhevsky, 1966, occur in the basal Tommotian Stage deposits of the southeastern Siberian Platform (Rozanov *et al.* 1969). Without description or illustration, they are also reported from apparently older beds of the northern Siberian Platform (Fedorov & Shishkin, 1984; Khomontovsky & Karlova, 1993; Luchinina *et al.* 1997; Meshkova *et al.* 1976; Rozanov *et al.* 1969). These beds contain pre-Tommotian prominent positive carbon isotopic peaks (Kouchinsky *et al.* 2001, 2007; Fig. 4; online Appendices 1 & 2 at <http://journals.cambridge.org/geo>). Probably the earliest appearance of *Camenella* is that reported from Western Mongolian beds at the beginning of the rising trend towards positive peak D (Brasier *et al.* 1996, fig. 9; Fig. 5), which may correspond to the rising trend towards Siberian peaks I or I' (Fig. 4).

*Porcauricula hypsilippis* (Jiang, 1980) is known from lower SSF2 beds (Qian & Bengtson, 1989), in the rising trend towards a prominent positive peak ZHUCE in China (Brasier *et al.* 1990; Li *et al.* 2009). *Lapworthella ludvigseni* Landing, 1984 and *Eccentrotheca kanesia* Landing, Nowlan & Fletcher, 1980 occur in the lower *Watsonella crosbyi* Zone of SE Newfoundland (Landing *et al.* 1989). Hence, the first tommotiids reported from Western Mongolia, South China and Avalonia are probably older than those from the base of the Tommotian Stage in its stratotype in the southeastern part of the Siberian Platform (online Appendices 1 & 2 at <http://journals.cambridge.org/geo>; Fig. 2).

### 3.g. Tianzhushanellids

Tianzhushanellids are bivalved and probably originally aragonitic shelly fossils assigned to the Family

Tianzhushanellidae Conway Morris in Bengtson *et al.* 1990 with uncertain higher-rank taxonomy (see 'Other fossils' in Online Appendix 1 at <http://journals.cambridge.org/geo>). They were referred to molluscs (Parkhaev, 1998), but have more recently been regarded as the best candidates for calcitic-shelled stem-group brachiopods (Balthasar, 2008; Li, 2009). New articulated material of *Apistoconcha* from strata correlative with the Cambrian Stage 3 in Australia seems to support its stem-group brachiopod position (Skovsted *et al.* 2010). The earliest undoubted representatives of the group are known from the SSF3 of China (Qian, 1999; Li & Chen, 1992; Steiner *et al.* 2007) and occur at near the peak of the positive carbon isotope excursion ZHUCE in Sichuan (Brasier *et al.* 1990, fig. 6; online Appendices 1 & 2 at <http://journals.cambridge.org/geo>; Fig. 2).

### 3.h. Brachiopods

The earliest reported brachiopod species with a calcium phosphate (organophosphatic) shell is the paterinid *Aldanotreta sunnaginensis* Pel'man, 1977. It first appears on the Siberian Platform in the *N. sunnaginicus* Zone of the Tommotian Stage (Bengtson *et al.* 1987; Ushatinskaya & Malakhovskaya, 2001; online Appendices 1 & 2 at <http://journals.cambridge.org/geo>; Figs 2, 4). The earliest Siberian brachiopod with a calcareous shell is *Nochoroiella isitica* Pel'man in Grigor'eva, Melnikova & Pel'man, 1983 (assigned to obolellids, although its affinity with brachiopods was questioned: see online Appendices 1 & 2 at <http://journals.cambridge.org/geo>) and *Obolella* sp. from the *D. lenaicus* Zone of the Tommotian Stage (Figs 2, 4). Chemostratigraphic correlation with Siberia (cf. Brasier *et al.* 1996) suggests that these occurrences are likely pre-dated by *Khasagtina primaria* Ushatinskaya, 1987 from Western Mongolia. The latter fossil is originally assigned to kutorginids, but its affinity to brachiopods needs revision (online Appendices 1 & 2 at <http://journals.cambridge.org/geo>; Figs 2, 5).

### 3.i. Stenothecoids

Stenothecoids, a group of probably low-magnesium calcite (Zhuravlev & Wood, 2008) enigmatic bivalved organisms with serial paired imprints sometimes present, occur in Cambrian Series 1–3 (Aksarina, 1968; Yochelson, 1969; Runnegar & Pojeta, 1974; Rozov, 1984; Pel'man, 1985; online Appendices 1 & 2 at <http://journals.cambridge.org/geo>). In Siberia, the first reliable stenothecoids appear in the late Tommotian Stage of the Altai-Sayan Folded Area (Pel'man *et al.* 1992; Rozanov & Zhuravlev, 1992), but the earliest stenothecoids overall (*Stenothecoides* sp. and *S. yochelsoni*) are reported respectively from Western Mongolia (Voronin *et al.* 1982; Khomentovsky & Gibsher, 1996, fig. 13; Fig. 5; online Appendices 1 & 2 at <http://journals.cambridge.org/geo>) and the SSF3 Zone of South China (Yu, 1996; online Appendices 1 &

2 at <http://journals.cambridge.org/geo>). Voronin *et al.* (1982) defined the *Stenothecoides* Zone in Western Mongolia at a level correlated chemostratigraphically (cf. Brasier *et al.* 1996; Fig. 5) with prominent positive peaks of the uppermost Nemakit–Daldynian Stage of the Siberian Platform. Consequently, like brachiopods, the first stenothecoids are reported from Cambrian Stage 2, probably below the lower Tommotian boundary (Fig. 2).

### 3.j. Mobergellids

Mobergellids are low conical or disc-shaped calcium phosphate problematic fossils with evidence of accretionary growth and paired radiating (possibly, muscular) imprints on the interior side (Bengtson, 1968; Conway Morris & Chapman, 1997; Skovsted, 2003; Dzik, 2010). The first occurrence of *Mobergella sibirica* Skovsted, 2003 (formerly *Mobergella radiolata* Bengtson, 1968) in Siberia is known from the lower *Dokidocyathus lenaicus*–*Tumuliolyntus primigenius* Zone of the Tommotian Stage (Rozanov *et al.* 1969; Sokolov & Zhuravleva, 1983; Rozanov & Sokolov, 1984; Missarzhevsky, 1989; Rozanov & Zhuravlev, 1992; online Appendices 1 & 2 at <http://journals.cambridge.org/geo>; Fig. 4). *Mobergella* sp. is also reported from the upper *D. regularis* Zone of the Tommotian Stage (Repina *et al.* 1974), but was not illustrated. Fossils described as *Mobergella*, but without characteristic radiating imprints, are known from the middle Meishucunian Stage of China (Li *et al.* 2007; online Appendix 1 at <http://journals.cambridge.org/geo>), although no definite record of mobergellids exists from China (Qian & Bengtson, 1989; Streng & Skovsted, 2006). The most reliable first appearance of the group is thus in the lower *D. lenaicus* Zone of the Tommotian Stage (upper part of the Cambrian Stage 2), within the carbon isotope trough between peaks III and IV of the Siberian reference scale (Brasier *et al.* 1994a,b; online Appendices 1 & 2 at <http://journals.cambridge.org/geo>; Figs 2, 4).

### 3.k. Other problematic shells and sclerites

Besides shells assigned herein to molluscs, hyoliths, halwaxiids, brachiopods, mobergellids, stenothecoids and tianzhushanellids, there are shells or plates of a calcareous or unknown original composition, often with evidence of accretionary growth. Some of these may represent parts of scleritomes similar to those of halkieriids or chitons (Conway Morris, McIlroy & Rushton, 1998; Vendrasco *et al.* 2009; see 'Molluscs' and 'Other fossils' in online Appendix 1 at <http://journals.cambridge.org/geo>). A number of such problematic shells are reported from China, where they are found in beds of the middle Meishucunian Stage (Bengtson, 1992b; Li *et al.* 2007). Most of them are treated as problematic molluscs by Bengtson (1992b) and Li *et al.* (2007), but some forms among

them are alternatively regarded as ‘brachiopod-like’ or ‘problematic brachiopods’ by Qian, Li & Zhu (2001).

An array of problematic sclerites from Cambrian Series 1–2 is known from Siberia and elsewhere, and some of the sclerites can be assigned to larger groups discussed herein, such as protoconodonts, chancelloriids, halwaxiids, tommotiids and cambroclavids or to ecdysozoan cuticular sclerites and fragments of carapaces, but the others are more problematic (see Bengtson, 1992*b*; Qian *et al.* 2004; Li *et al.* 2007; see ‘Other fossils’ in online Appendix 1 at <http://journals.cambridge.org/geo>).

### 3.1. Trilobites

The Class Trilobita are advanced arthropods (Phylum Arthropoda) with calcareous (low-magnesium calcite) carapaces (Wilmot & Fallick, 1989). The first occurrences of trilobites in the world (highlighted by thick horizontal lines within Stage 3 interval in Fig. 3) post-date or are estimated to be no earlier than those on the Siberian Platform, where their first undoubted appearance is just above the base of the Atdabanian Stage (Lieberman, 2002; Hollingsworth, 2005, 2007, 2008; online Appendices 1 & 2 at <http://journals.cambridge.org/geo>; Fig. 2). The earliest trilobites (Family Archaeaspididae, Order Redlichiida) are represented by *Profallotaspis* Repina in Khomentovsky & Repina, 1965 from Siberia and *Fritzaspis* Hollingsworth, 2007 from Laurentia.

### 3.m. Bradoriids

Bradoriids known from Cambrian to lower Ordovician rocks worldwide have originally weakly or secondarily mineralized (phosphatized) carapaces (Jones & McKenzie, 1980; Landing, 1980; Butterfield, 2003; Zhang, 2007; Zhang, Dong & Maas, 2011). These arthropods are represented by the Order Bradoriida Raymond, 1935 (Bradoriida *sensu stricto*) and Phosphatocopida Müller, 1964 (Hou *et al.* 2002; Maas & Waloszek, 2005; Williams *et al.* 2007; Zhang, 2007). The former are regarded at present as stem-group crustaceans, whereas the latter are considered by some to be crown-group crustaceans (Hou *et al.* 1996, 2010; Shu *et al.* 1999). Although other stem-group crustaceans represented by non-mineralizing *Isoxys zhurensis* Ivantsov, 1990 are known as early as the middle *Profallotaspis jakutensis* Zone of the Atdabanian Stage on the southeastern Siberian Platform (Ivantsov, 1990), the first bradoriid *Cambria* Neckaja & Ivanova, 1956 is reported in Siberia from the middle Atdabanian *Delgadella anabara* Zone (online Appendices 1 & 2 at <http://journals.cambridge.org/geo>; Figs 2, 4). Coeval first occurrences of bradoriids are also known from South China (Hou *et al.* 2002), Gondwana (Hinz-Schallreuter, Gozalo & Liñán, 2008; Topper *et al.* 2011), Avalonia (Brasier, 1989*c*) and Baltica (Streng, Ebbestad & Moczyłowska, 2008).

### 3.n. Lobopodians

Lobopodians have been considered a Cambrian stem group of the Panarthropoda, including such phyla as Onychophora, Tardigrada and Arthropoda (see Budd, 1997; Liu *et al.* 2007; Edgecombe, 2009). These animals were similar to modern onychophorans and are often regarded as members of the Phylum Lobopodia Snodgrass, 1938 (Hou & Bergström, 1995) or Tardipolypoda Chen & Zhou, 1997. Exceptionally preserved in the Chengjiang fossil lagerstätte, they are elongate animals with paired limbs and sclerites (trunk plates) situated along each side of the body (Chen, Hou & Lu, 1989; Chen, Zhou & Ramsköld, 1995; Ramsköld & Hou, 1991; Bergström & Hou, 2001; Hou *et al.* 2004). The sclerites are thought to be of an original calcium phosphatic composition, although their biomineralization has been doubted by Steiner *et al.* (2007).

The first sclerites of *Microdictyon* sp. in Siberia are reported herein from the Emyaksin Formation of the Bol’shaya Kuonamka River, from beds correlated by carbon isotope chemostratigraphy with the upper *Delgadella anabara* Zone of the Atdabanian Stage (Kouchinsky *et al.*, unpub. data; online Appendices 1 & 2 at <http://journals.cambridge.org/geo>; Fig. 2). This occurrence is somewhat older than the previously reported occurrence from the upper Atdabanian *Fansycyathus lermontovae* Zone of Lena River (Varlamov *et al.* 2008). It is correlated chemostratigraphically (Dillard *et al.* 2007; online Appendices 1 & 2 at <http://journals.cambridge.org/geo>) with the regional first occurrence of *Microdictyon* sp. and *Microdictyon* cf. *rhomboideale* Bengtson, Matthews & Missarzhevsky, 1986 in the lower *Nevadella* Zone of Laurentia (Bengtson, Matthews & Missarzhevsky, 1986; Voronova *et al.* 1987; Fig. 3) and, probably, with the first occurrence of *M. sphaeroides* Hinz, 1987 in the *Camenella baltica* Zone of Avalonia (Hinz, 1987) and *Microdictyon depressum* Bengtson in Bengtson *et al.* 1990 in the *Abadiella huoi* Zone of Australia. The first soft-bodied lobopodians with remains of sclerites are already diverse and well known from the Chengjiang fossil lagerstätte, which is time-equivalent with the upper Atdabanian Stage of Siberia.

### 3.o. Palaeoscoleoids

The Class Palaeoscolecida Conway Morris & Robison, 1986 is known from the Cambrian Series 2 to the Upper Silurian. These fossils are morphologically similar to nematomorphs (Hou & Bergström, 1994) and priapulids (Conway Morris, 1997). They are broadly considered as a stem group of the Priapulida (Harvey, Dong & Donoghue, 2010) or Cycloneuralia (Budd, 2001; Conway Morris & Peel, 2010). Complete preservation of their worm-like bodies is known, but far more often they occur as disarticulated calcium phosphate cuticular sclerites. The first palaeoscoleoids, represented by the biomineralized trunk sclerites

*Hadimopanella apicata* Wrona, 1982 are reported herein from the middle *Nochoroicyathus kokoulini* Zone (lower *Judomia* Zone) of northern Siberia (Kouchinsky *et al.*, unpub. data; online Appendices 1 & 2 at <http://journals.cambridge.org/geo>; Figs 2, 4). The earliest soft-bodied preservation of palaeoscolecid is known from the Sirius Passet fauna of Laurentia (Greenland; Conway Morris & Peel, 2010; online Appendices 1 & 2 at <http://journals.cambridge.org/geo>) and the Chengjiang fossil lagerstätte of South China (Hu, 2005), which are time-equivalent with the upper Atdabanian of Siberia.

### 3.p. Echinoderms

The earliest fossils of the phylum Echinodermata are disarticulated and presumably originally high-magnesium calcite plates (Dickson, 2002, 2004). Some of these plates derive from brachiole-bearing echinoderms and thus can be assigned to eocrinoids. The 'class' Eocrinoidea Jaekel, 1918 is paraphyletic and comprises stem-groups of other blastozoan clades (e.g. Sprinkle, 1973). The earliest echinoderm plates like these are reported herein from the upper *Delgadella anabara* Zone of the Atdabanian Stage from Siberia (Kouchinsky *et al.*, unpub. data; Zamora *et al.* in press; online Appendices 1 & 2 at <http://journals.cambridge.org/geo>; Figs 2, 4). First echinoderm plates from the lower part of the *Nevadella* Zone of Laurentia are chemostratigraphically correlated with the upper part of the *Delgadella anabara* Zone of Siberia (Dillard *et al.* 2007; Fig. 3). The earliest isolated echinoderm plates occur in lower Ovetian beds of West Gondwana (Spain) broadly correlated with the *Delgadella anabara* Zone of Siberia and also appear contemporaneously in South China and Australia (Zamora *et al.* in press).

### 3.q. Chordates (paraconodonts and agnathans)

Conodonts (including para- and euconodonts) are characterized by calcium phosphatic dental structures with dentin-like tissue (but see Kemp, 2002a,b). They are regarded as the earliest known biomineralized chordates (Donoghue, Forey & Aldridge, 2000; Donoghue, Sansom & Downs, 2006). There is a microstructural similarity between the two sub-groups as well as a histological and morphological transition from paraconodonts to euconodonts, and therefore they are united as conodonts (Szaniawski & Bengtson, 1993, 1998).

The oldest paraconodonts from Siberia are *Westergaardodina cf. tricuspidata* Müller, 1959 and *Furnishina* sp. from the Paibian Stage-equivalent Kutugunian Horizon, which contains the upper Cambrian (Furongian Series) SPICE carbon isotope excursion (online Appendices 1 & 2 at <http://journals.cambridge.org/geo>; Shabanov *et al.* 2008). *Furnishina* and *Westergaardodina* are known, however, from the Drumian Stage (within the Cambrian Series 3, or traditional Middle Cambrian) in most other crustal units. The oldest

paraconodonts, represented by *Furnishina* sp. and *Westergaardodina* sp., are reported respectively from the *Triplagnostus gibbus* Zone of the uppermost part of Cambrian Stage 5 (lower Series 3) in Sweden (Müller, 1959, 1971; Dong, 2004) and from Stage 5 deposits of Alaska (Dutro *et al.* 1984), but the former is much better preserved and constrained stratigraphically.

The earliest vertebrates with ossification in the dermal skeleton, that contains dentin-like tissue (Smith, Sansom & Repetski, 1996; Karatajute-Talimaa, 1997), are similar to the Ordovician agnathans and represented by disarticulated calcium phosphatic plates of *Anatolepis* sp. from the mid-Sunwaptan Stage of Laurentia (Smith & Sansom, 1995; Smith, Sansom & Cochrane, 2001) corresponding to the upper part of the Cambrian Stage 9 (Furongian Series).

## 4. Discussion

There is no unambiguous evidence of the existence of bilaterian superphyla in the Precambrian (Budd, 2008; Budd & Jensen, 2000, 2003), although some bilaterally symmetrical forms from the late Ediacaran, younger than 555 Ma, are interpreted as their representatives (e.g. Fedonkin & Waggoner, 1997). On the other hand, Ediacara-type fossils have repeatedly been reported from the Early Palaeozoic (Conway Morris, 1993; Jensen, Gehling & Droser, 1998; Samuelson, Van Roy & Vecoli, 2001; Zhang & Babcock, 2001), but none of those is comparable with typical Ediacaran vendobionts in their structure, symmetry and growth pattern (Antcliffe & Brasier, 2008; Zhuravlev *et al.* 2011).

The general succession of first appearances of biomineralized skeletal parts during the Cambrian radiation includes two main sets clustered geochronologically by high-rank phylogeny and reflects two successive phases of diversification of bilaterians (Fig. 2). Such a pulsed diversification accompanied a general increase in generic diversity of the biota towards the early Botoman maximum preceding the Botoman–Toyonian biotic crisis (Brasier *et al.* 1994a; Zhuravlev & Wood, 1996; Zhuravlev, 2001; Li *et al.* 2007).

The first phase recognized herein is marked by a set of first appearances of biomineralization in the Terreneuvian Epoch (*c.* 541–521 Ma), mainly within the Fortunian Age. The latter embraces the first *c.* 10 Ma of the Cambrian Period (Fig. 2). During the Terreneuvian Epoch such major skeletal groups as protoconodonts, halwaxiids, cancelloriids, hyoliths, molluscs, tomotiids, brachiopods, tianzhushanellids, stenothecoids, cambroclavids–paracarinachitids and mobergelids first appeared and diversified, as well as other forms with problematic affinities to these groups (online Appendices 1 & 2 at <http://journals.cambridge.org/geo>; Fig. 2). All of them, except protoconodonts and possibly cancelloriids, can be comfortably placed within the total-group Lophotrochozoa. Among them, such extant biomineralizing lophotrochozoan phyla as Mollusca and Brachiopoda can be recognized. Annelida does not have undisputed biomineralized

representatives during the Cambrian radiation (Conway Morris & Peel, 2008), but such problematic groups as hyolithelminths, hyoliths and halwaxiids may share that affinity (see Section 3 and remarks in online Appendix 1 at <http://journals.cambridge.org/geo>). By contrast, Bryozoa certainly appear relatively late, in the uppermost Cambrian, at the onset of the Ordovician radiation (Landing, English & Keppie, 2010).

Protoconodonts were among the first bilaterians to acquire hardened (probably mineralized calcium phosphatic) skeletal parts (presumably for active predation). These have been interpreted as grasping spines of the Chaetognatha, a protostomian phylum close to the Lophotrochozoa, but most likely its sister-group (Halanych, 2004; Dunn *et al.* 2008). They appeared in the fossil record at about the same time as the first calcareous sclerites of coeloscleritophorans, shells of molluscs and hyoliths. The majority of bilaterian skeletal fossils of the Terreneuvian Series belong to these latter groups. Their first appearances occurred in beds younger than the Precambrian–Cambrian boundary and the carbon isotope negative anomaly associated with this boundary (Narbonne, Kaufman & Knoll, 1994; Brasier *et al.* 1996; Kimura *et al.* 1997; Li *et al.* 2009), but not younger than those with Siberian  $\delta^{13}\text{C}$  feature Z and attributed to the upper *Anabarites trisulcatus*–lower *Purella* zones of the Nemakit–Daldynian Stage (Brasier, Khomentovsky & Corfield, 1993; Brasier, *et al.* 1994a,b). These first appearances can be correlated with the *Anabarites trisulcatus*–*Protohertzina anabarica* (SSF1) Assemblage Zone of the lower Meishucunian Stage of South China, where all of them except shells of molluscs occur in beds older than the tuffite with a combined depositional age of  $535.2 \pm 1.7$  Ma (Zhu *et al.* 2009).

Calcium phosphatic sclerites of tommotiids, probably members of the stem group of organophosphatic brachiopods, have a younger first appearance associated with the same rising trend, but still below highly positive peaks of the lower part of the Cambrian Stage 2. The first reported appearance of tommotiids is older than the estimated *c.* 530 Ma base of the Cambrian Stage 2 in Avalonia (Landing *et al.* 2007). Such groups as cambroclavids–paracarinachitids, other problematic shells with affinities close to molluscs or halwaxiids, and some problematic sclerites also appear during this interval (online Appendices 1 & 2 at <http://journals.cambridge.org/geo>; Fig. 2).

Brachiopods, apparently related to tommotiids, are another major group of lophotrochozoan animals with their first appearance in the Cambrian Stage 2. Together with tianzhushanellids, which probably represent stem-group calcareous brachiopods, and stenothecoids, their first occurrences are registered from Stage 2 strata older than or coeval with the Nemakit–Daldynian–Tommotian boundary of *c.* 525 Ma (Maloof *et al.* 2010a,b). *Mobergella*, *Rhombocorniculum* and some other problematic sclerites appeared during the upper part of Cambrian Stage 2 (online Appendices 1 & 2 at <http://journals.cambridge.org/geo>; Fig. 2).

Biom mineralization in ecdysozoans and deuterostomians did not apparently occur during the first phase of the early Cambrian bilaterian radiation, but these events mark the second phase. Non-biom mineralized ecdysozoans, however, existed before, as evidenced by: (1) fossilized embryos of *Markuelia secunda* Val'kov from the basal Tommotian Stage in Siberia, having already a sclerotized cuticle and representing the Scalidophora, a sub-group of the Cycloneuralia (Bengtson & Yue, 1997; Dong *et al.* 2004, 2005, 2010); embryos and possibly related larvae of *Pseudoooides prima* from the lower Meishucunian Stage of South China, considered as possible stem-group arthropods (Steiner *et al.* 2004b) and (2) the arthropod-type trace fossils in pre-trilobitic strata (Crimes, 1987; Weber & Zhu, 2003; Weber, Steiner & Zhu, 2007).

The second phase of the early Cambrian bilaterian radiation is thus marked by the first appearances of biom mineralization in the Superphylum Ecdysozoa within Cambrian Stage 3, during  $< 5$  Ma (Fig. 2). The earliest undoubted and widespread event in the second phase is the appearance of calcification in carapaces of trilobites at the base of Stage 3, succeeded by the first appearances of calcium phosphate carapaces of bradoriids (Phylum Arthropoda), sclerites of lophopodians (Phylum Tardipolypoda) and palaeoscolecids (?Phylum Priapulida) in that order, in the early and middle parts of Stage 3 (online Appendices 1 & 2 at <http://journals.cambridge.org/geo>; Fig. 2). The diversity of ecdysozoans and their dominance in the Burgess Shale-type fossil communities in upper Stage 3, by the conclusion of the Cambrian radiation, is well documented in such fossil lagerstätten as the Sirius Passet of north Greenland and the roughly time-equivalent Chengjiang of South China (e.g. Conway Morris & Peel, 2008, 2010).

The second phase also involves the Superphylum Deuterostomia, Phylum Echinodermata. The earliest biom mineralizing representatives of echinoderms appear in the middle of Stage 3. Among them eocrinoids, members of the stem-group Echinodermata, can be recognized. The origin of their high-magnesium calcite stereom skeleton is the first documented skeletal biom mineralization event among deuterostomians. Tunicates (Phylum Chordata) may have also existed at that time (Chengjiang fauna, Chen *et al.* 2003, but see Bergström, 2010), and some of them may have produced biom mineralized spicules (see Bengtson *et al.* 1990). Non-mineralizing representatives of the Phylum Chordata were also present during the Cambrian radiation: hagfish-like fossils from Chengjiang are most likely the first vertebrates, but without traces of biom mineralization (Shu *et al.* 1999; Conway Morris, 2006; Bergström, 2010). The first appearances of calcium phosphatic dental mineralization in problematic chordates/conodonts (i.e. paraconodonts) in the upper part of Cambrian Stage 5 (Donoghue, 2002; Donoghue & Sansom, 2002; Kemp, 2002a,b; online Appendices 1 & 2 at <http://journals.cambridge.org/geo>) and dermal biom mineralization in agnathan-like chordates by the end



of the Cambrian (Cambrian Stage 9) (Smith & Sansom, 1995; Smith, Sansom & Cochrane, 2001; Young, 2009) post-date both the Cambrian radiation and the first fossils interpreted as chordates by *c.* 10 and 25 Ma, respectively.

The fossil record of sponges and cnidarians suggests that they acquired skeletal biomineralization in the Precambrian (online Appendices 1 & 2 at <http://journals.cambridge.org/geo>; Fig. 2), but it was not until diverse bilaterian groups become abundant in the fossil record that radiation among skeletonized non-bilaterians like these occurred. Although solitary tubular forms with questionable affinities to cnidarians are already diverse during the first phase of the early Cambrian bilaterian radiation, biomineralized remains of sponges and spongiomorphs are sporadic until the Cambrian Stage 2, where corallomorphs also entered the fossil record (online Appendices 1 & 2 at <http://journals.cambridge.org/geo>; Fig. 2).

Distribution of calcium carbonate skeletal mineralogies from upper Ediacaran to lower Cambrian (Fig. 2) are shown to reflect fluctuations in the magnesium/calcium ratio in the ocean (Zhuravlev, 1993; Ushatinskaya & Zhuravlev, 1994; Porter, 2007; Zhuravlev & Wood, 2008). First appearances of animal groups with aragonite skeletons occur mainly during the Fortunian Age. A few rare and speculative cases of low-magnesium calcite (LMC) biomineralization have been attributed to the Cambrian Stage 2, including *Khasagtina primaria* (kutorginid brachiopod?) and the earliest stenotheccoids (Zhuravlev & Wood, 2008; Fig. 2), but their mineralogy is only suggested from the inferred composition of younger forms, and hence alternative carbonate mineralogies cannot be excluded.

The second phase of the early Cambrian bilaterian radiation occurred after one of the major perturbances in the carbon cycle in the Phanerozoic Earth history, marked with a *c.* 10% negative shift in  $\delta^{13}\text{C}$  record in the middle of Stage 2 (online Fig. S1 at <http://journals.cambridge.org/geo>). The upper part of Stage 2, generally correlated herein with the Tommotian Stage of Siberia, represents a transitional interval with first appearances of high-magnesium calcite (HMC) skeletons, a transition that probably corresponds to decreasing Mg/Ca ratio of the ocean. The second phase, marked by the first appearance of trilobites (Fig. 2), is characterized by the onset of the LMC biomineralization in trilobites and brachiopods and a short-term switch to the calcite sea in the early Atdabanian (Zhuravlev & Wood, 2008). Based on distribution of inorganic precipitates and the relative abundance of genera with aragonite and HMC v. LMC skeletal mineralogies, the remaining part of the second phase is characterized, however, as a reappearance of the aragonite sea (Zhuravlev & Wood, 2008). Hence, despite an increasing number of genera with LMC skeletons during the second phase, the Cambrian radiation interval was generally aragonite and HMC favourable.

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## Appendix 1

### Siberian first appearances in the Nemakit–Daldynian Stage (see Fig. 4)

- S1.** Sclerites of **protoconodonts** *Protohertzina anabarica* and *P. unguiformis* (Nemnekey; Khomentovsky & Karlova, 1991, 1993; projected onto the Siberian  $\delta^{13}\text{C}$  reference scale by Brasier, Khomentovsky & Corfield, 1993).  
*Remarks.* Anabaritids are also reported from this level and below the Precambrian-Cambrian boundary negative excursion (see data in online Appendix 1 at <http://journals.cambridge.org/geo>, not shown in Fig. 4).
- S2.** Shelly **molluscs** *Oelandiella* sp. and *Barskovia* sp., **halwaxiids** *Purella cristata*, *Siphogonuchites* aff. *triangularis*, and orthothecid **hyoliths** *Lophotheca socialis* (Mt Konus; Khomentovsky, Val'kov & Karlova, 1990; projected onto the Siberian  $\delta^{13}\text{C}$  reference scale by Brasier, Khomentovsky & Corfield, 1993).  
*Remarks.* Spicules of **hexactinellids** *Protospongia* sp. and ?sclerites of **chancelloriids** *Chancelloria* sp. are also reported from that level (Gonam; Khomentovsky & Karlova, 1993; projected herein onto the Siberian  $\delta^{13}\text{C}$  reference scale in accordance with Brasier, Khomentovsky & Corfield, 1993).
- S3.** Tubes of **hyolithelminths** *Hyolithellus* sp., sclerites of **chancelloriids** *Chancelloria* sp., problematic sclerites of *Fomitichella* cf. *infundibuliformis* (Gonam;

Semikhatov & Serebryakov, 1983; Khomentovsky *et al.* 1983; Khomentovsky & Karlova, 1993; projected herein onto the Siberian  $\delta^{13}\text{C}$  reference scale in accordance with Brasier, Khomentovsky & Corfield, 1993).

### Siberian first appearances in the Tommotian Stage (see Fig. 4)

- S4.** **Tommotiid** *Sunnaginia imbricata*, **archaeocyaths**, siliceous stauracts and pentacts of the **hexactinellid** sponges (Aldan; Sokolov & Zhuravleva, 1983; Rozanov & Sokolov, 1984; Shabanov *et al.* 2008); problematic tubes **Tommototubulus** *savitzkyi* Fedorov, 1986 (Aldan; Khomentovsky, Val'kov & Karlova, 1990).
- S5.** **Calcium-phosphate brachiopods** *Aldanotreta sunnaginensis* (Aldan; Sokolov & Zhuravleva, 1983; Rozanov & Sokolov, 1984; Bengtson *et al.* 1987; Ushatinskaya & Malakhovskaya, 2001); problematic sclerites **Tumulduria** *incomperta* (Aldan; Sokolov & Zhuravleva, 1983; Rozanov & Sokolov, 1984; Bengtson *et al.* 1987; Rozanov *et al.* 1992) and **Archaeopetatus** sp. (as opercula of *Coleolella billingsi* in Rozanov *et al.* 1969, pl. 7) (Aldan; Rozanov *et al.* 1969; Bengtson *et al.* 1990; Dzik, 1994); problematic tubes *Coleolella billingsi* (Sysoev, 1962) (Aldan; Rozanov *et al.* 1969; Sokolov & Zhuravleva, 1983), '*Coleolus*' *trigonus* Sysoev, 1962 (Aldan; Sysoev, 1962; Rozanov *et al.* 1969), and *Coleoloides trigeminatus* Missarzhevsky in Rozanov *et al.* 1969 (Aldan; Sokolov & Zhuravleva, 1983).
- S6.** Spicules of the **calcarean** sponge *Dodecaactinella* sp. and thecae of **corallomorph** *Cysticyathus tunicatus* (Middle Lena; Kruse, Zhuravlev & James, 1995).
- S7.** *Mobergella sibirica* Skovsted, 2003 (formerly *Mobergella radiolata* Bengtson, 1968) (Aldan; Rozanov *et al.* 1969; Sokolov & Zhuravleva, 1983; Rozanov & Sokolov, 1984; Missarzhevsky, 1989; Rozanov & Zhuravlev, 1992).
- S8.** **Calcium-carbonate brachiopods** *Nochoroiella isitica* and *Obolella* sp. (Middle Lena; Grigor'eva, Melnikova & Pel'man, 1983; Sokolov & Zhuravleva, 1983; Rozanov & Sokolov 1984; Pel'man *et al.* 1992;
- S9.** Problematic sclerites **Rhombocorniculum** *insolutum* (Middle Lena; Sokolov & Zhuravleva, 1983; Rozanov & Sokolov, 1984; Brasier, 1989b; Rozanov & Zhuravlev, 1992. Bol'shaya Kuonamka; Kouchinsky *et al.*, unpub. data and herein).

### Siberian first appearances in the Atdabanian Stage (see Fig. 4)

- S10.** **Trilobites** *Profallotaspis* sp. (Middle Lena; Rozanov & Sokolov, 1984).
- S11.** *Microdictyon* sp. (Bol'shaya Kuonamka; Kouchinsky *et al.*, unpub. data and herein).
- S12.** **Eocrinoidea** indet. (Bol'shaya Kuonamka; Kouchinsky *et al.*, unpub. data and herein).
- S13.** *Hadimopanella apicata* (Bol'shaya Kuonamka; Kouchinsky *et al.*, unpub. data and herein).

## Appendix 2

### Mongolian first appearances (see Fig. 5)

- M1.** **Hexactinellid** spicules (Brasier *et al.* 1996, fig. 5; Brasier, Green & Shields, 1997); **anabaritids** *A. trisulcatus* and *C. decurvatus* (Brasier *et al.* 1996; Esakova & Zhegallo,

1996; Khomentovsky & Gibsher, 1996) or *Anabarites* sp. (Esakova & Zhegallo, 1996).

**M2. Protoconodonts** *Protohertzina unguiformis*; scaly shells of **halwaxiids** *Purella* sp.; orthothecid? **hyoliths** *Pseudorthotheca bicostata* Qian (indicated as *P. bistriata* in Khomentovsky & Gibsher, 1996, fig. 13, p. 386) (Brasier *et al.* 1996, fig. 9; Khomentovsky & Gibsher, 1996, fig. 13).

**M3. Tommotiids** *Camenella applanata* and *Camenella* sp. (Khomentovsky & Gibsher, 1996, fig. 3 on p. 386; Brasier *et al.* 1996), *Camenella* cf. *baltica* (Voronin *et al.* 1982); problematic tubes ***Hyolithellus*** cf. *vladimirovae* (Brasier

*et al.* 1996) or *Hyolithellus* sp. (Voronin *et al.* 1982) and ***Coleolella billingsi*** (Brasier *et al.* 1996, figs 6, 7).

**M4. Shelled molluscs** *Obtusocoelus honorabilis* and *Granoconus trematus* (Khomentovsky & Gibsher, 1996).

**M5. Sclerites of chancelloriids** *Chancelloria* sp. (Voronin *et al.* 1982).

**M6. Calcium carbonate-shelled brachiopod?** ***Khasagtina primaria*** Ushatinskaya, 1987 (described as *Kundatella* sp. by Voronin *et al.* 1982).

**M7. *Stenothecoides*** sp. (Voronin *et al.* 1982; Khomentovsky & Gibsher, 1996, fig. 13).