



The Great Ordovician Biodiversification Event: Reviewing two decades of research on diversity's big bang illustrated by mainly brachiopod data

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Abstract

The Great Ordovician Biodiversification Event (GOBE) laid the foundation for present-day biodiversity levels and set an agenda for marine life against a background of modern-type climates. The event was protracted, commencing at the beginning of the Ordovician and unfolding during 40 million years (myr) of the period. The first diversity acme (Tremadocian–Floian) was strongly diachronous across both the paleoblocks and groups of organisms. But within a 10 myr interval, during mainly the Middle Ordovician (Darriwilian), the global marine species richness was tripled, i.e., the second diversity acme. The third acme (Katian) was much more unified across both taxonomic groups and terranes. This diversification trend continued into the Silurian and Devonian making GOBE the most sustained marine biodiversity pulse of the entire Phanerozoic. The GOBE was also marked by three major faunal turnovers based on the brachiopod data, in the mid-Darriwilian, end-Katian, and end-Hirnantian, respectively. Each turnover was followed by an explosive radiation of new faunas, especially in the shallow-marine shelly benthos. Potential intrinsic or extrinsic drivers for this event are widely debated, but a causal narrative remains elusive.

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Keywords: Biodiversification; Brachiopods; Diversity acme; Ordovician; Baltica; South China

1. Introduction

The 'Great Ordovician Biodiversification Event' (GOBE) is the most significant and sustained increase of marine biodiversity in Earth history. During a relatively short time interval of some 40 myr, a marked expansion in diversity at the lower taxonomic ranks such as family, genus, and species occurred against a background of climatic and environmental change. Remarkably, however, this event and its significance has only been recognized relatively recently. The fossil record is the primary archive for paleobiodiversity data but is now being subjected to intense and rigorous numerical scrutiny, revealing the clear impact of the GOBE. One of the first attempts to quantify the history of life was that of Phillips (1860) who published, within

a year of Darwin's publication of 'On the Origin of Species,' a semi-quantitative analysis of the biodiversity of Phanerozoic life. Phillip's curve defined three stratigraphically-based marine faunas, the first corresponding to 'Palaeozoic life'. Although some of the numerical compilations of fossil range data during the 1950s (e.g., Newell, 1952) indicated that the Ordovician Period was a locus of biodiversity, it was not until Sepkoski (1995) provided a first detailed analysis of diversity based on his global database (e.g., Sepkoski, 1981, 1995, 2002), and Droser and Sheehan (1997) published an initial dissection of the paleoecology of the event. Sepkoski's diversity counts confirmed the major radiations of marine diversity during the Paleozoic, including the Cambrian Explosion and Ordovician Radiation, clearly illustrating that the most spectacular increase of animal marine diversity at the family level took place during the Ordovician (Fig. 1). Not only a rapid increase in taxonomic diversity is obvious, but also very dramatic changes within the paleoecological context of the biotas, with the development of the 'Paleozoic Evolutionary Fauna' in the Ordovician, that replaced

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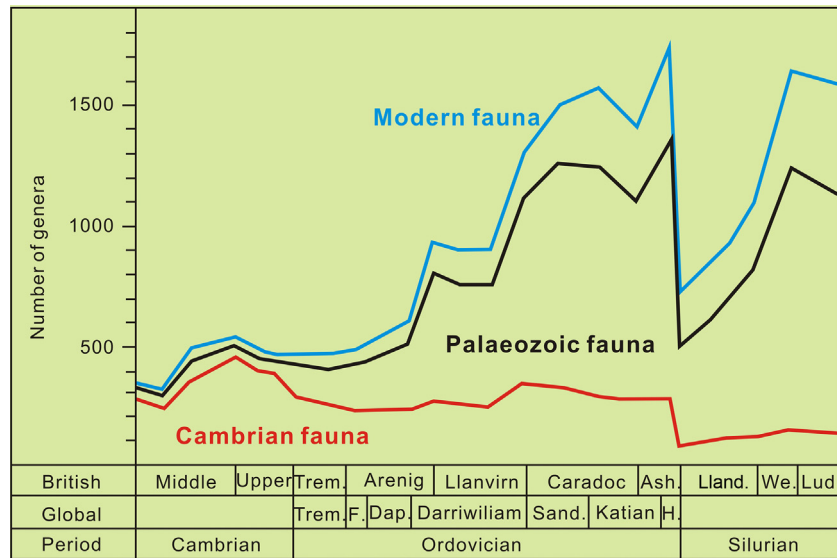


Fig. 1. The Great Ordovician Biodiversification Event (GOBE) as a composite of Sepkoski's Cambrian, Paleozoic, and Modern evolutionary faunas (Sepkoski, 1995). Abbreviations: Trem., Tremadoc; F., Floian; Dap., Dapingian; Sand., Sandbian; H., Hirnantian; Ash., Ashgill; Lland., Llandovery; We., Wenlock; Lud., Ludlow.

progressively the 'Cambrian Evolutionary Fauna' in the marine ecosystem (e.g., Sheehan, 1996; Harper, 2006; Miller, 2012). It is highly probable that the very complex GOBE was linked to a variety of coincident factors, intrinsic and extrinsic, regional and global, many of which were interconnected, and segue into each other. Moreover, these data provide tests of a whole variety of environmental hypotheses, framed to explain the event (Miller, 2012).

2. Databases fit for purpose

During the past three decades, a formidable amount of fossil range data, both spatial and temporal, have been captured by the mining of the literature, initially by Sepkoski (e.g., Sepkoski, 1981, 1995, 2002), and during three highly-successful IGCP projects, 410 'The Great Ordovician Biodiversification Event', 503 'Early Palaeozoic palaeogeography and palaeoclimate', and 591 'The Early–Middle Paleozoic Revolution'. These compilations were aided by an improved taxonomy of all the major fossil groups, an agreed global chronostratigraphy for the Ordovician System and refined paleogeographic maps for the period. IGCP 410 (1997–2003) had a primary focus on biotic data through the period, assembled by a large number of inclusive clade teams and mapped against the then new global stages for the Ordovician and much finer stage slices (Bergström et al., 2009). The successor project IGCP 503 (2005–2010) developed a more holistic approach to the event (Harper et al., 2013), relating biodiversity to changes in the Ordovician earth system. The substantial books and thematic volumes generated by the projects illustrate some of the key research themes developed during the past two decades: Ordovician biodiversity (Webby et al., 2004), climate and sea-level (Munnecke et al., 2010), paleoecology (Servais and Owen, 2010), paleoclimate and paleogeography (Munnecke and Servais, 2007), Ordovician earth system (Finney and Berry, 2010), biogeography and paleogeography (Harper and Servais, 2013), global change (Calner et al., 2014). These and other

review papers (e.g., Servais et al., 2009; Zhang et al., 2010; Zhan et al., 2013) have firmly established the GOBE as a pivotal interval in the history of life. High-quality global and regional datasets are now available for the system. The project IGCP 591 (2011–2015) has been paying more attention to the causes of GOBE and the multidisciplinary investigations on this major biotic event and related geologic events.

Analyses of these databases have demonstrated a number of important properties. Firstly, during the Ordovician diversification individual fossil groups show different curves with diversity peaks at different levels (Zhan and Liu, 2010). Some important Paleozoic fossil groups, e.g., graptolites, showing a diversity acme during the Tremadocian-Floian transition (Chen et al., 2006), and brachiopods, experienced a dramatic increase of diversity during a relatively short time span in Darriwilian (Middle Ordovician) (e.g., Zhan and Rong, 2003; Harper et al., 2004; Harper, 2006). Other fossil groups, e.g., corals, diversified much later, but also very rapidly, during the Sandbian, in the Late Ordovician (Webby et al., 2004). Although it is clear that there was a spectacular Ordovician diversification in some fossil groups, other organisms did not demonstrate such a rapid and dramatic increase in the Ordovician, but display a continuous and long-term biodiversification that, for some fossil groups, started already in the Cambrian. Such groups include trilobites (e.g., Zhou et al., 2006), some subphyla of the echinoderms (e.g., Nardin and LeFebvre, 2010), and the phytoplankton (e.g., Servais et al., 2008). Secondly, there was a marked regional diachroneity, with the diversification strongly focussed on areas of tropical Gondwana, such as South China (e.g., Zhan and Harper, 2006), during the earlier Ordovician. The first diversity acme, on a global scale, occurred during the Darriwilian (Middle Ordovician) with not only South China but also other major blocks (e.g., Baltica, Laurentia, etc., Rasmussen et al., 2007) experiencing a rapid biodiversification within the marine ecosystem (Webby, 2000; Harper et al., 2004); and the strongest signals were in the middle–late Katian (Late Ordovician) (Zhan et al.,

Table 1
Key driving (intrinsic) factors for the Great Ordovician Biodiversification Event.

Intrinsic driving factors	Mechanism	References
Competition	Increasing need for space generates narrower niches, burrowing and tiering and expansion into new habitats	Waisfeld et al., 2003; Servais et al., 2008
Plankton revolution	Marked increase in phytoplankton and zooplankton fuelled diversifications at all levels in the food chain	Servais et al., 2008, 2009, 2010
Predation	Diversification of predators ignited GOBE arms race, increased burrowing, mobility and skeletal protection	Servais et al., 2010

2006, 2013). Such studies convincingly highlight the importance of regional studies as the building blocks of any global datasets and the individuality of both clades and continents.

The studies previously mentioned are less elegant. More elegant analyses have established taxon-age distributions for the system (Candela, 2014). In addition to many genera that appeared at the base of the Ordovician System, the age space is successively filled by taxa that develop longevity and presumably resilience, expanding geographically to fully embrace the World's oceans.

3. Drivers and enablers of the diversification

The causes for the GOBE fall into two, in some cases, overlapping categories: intrinsic (essentially biological) and extrinsic (essentially environmental). This partitioning of causes has the potential to frame the former in terms of the Red Queen model (Van Valen, 1973) and the latter through the Court Jester hypothesis (Barnosky, 1999, 2001). Another way of considering these factors is a division into enabling factors (mainly extrinsic environmental causes) and driving factors (mainly biological causes) that together providing the ambience and impetus for the event to take place. There is thus strong evidence to suggest that the transition from the Cambrian Evolutionary Fauna to the Paleozoic Evolutionary Fauna is associated with an important change at the base of the food chain between the Cambrian and Ordovician periods. Whereas Precambrian and Cambrian metazoan communities were mostly limited to the seabed, the Ordovician radiation began to fill the water column, as animals adapted to life in previously unoccupied ecospace. Benthic organisms were extending higher above the substrate, developing a complex tiering strategy and increasing their depth of burrowing into the substrate; the plankton was also increasing dramatically in diversity, suggesting also an increase in abundance. Furthermore, habitats that had been occupied in the Cambrian were invaded by many new groups that were adapting to these habitats and occupying more finely defined ecological niches. The establishment of an open marine food chain, sustainable enough for the development of a diverse fauna of large cephalopod predators was achieved by the Middle Ordovician. Ecological escalation on the seabed was signalled by a diversification of new groups of predators, mobile organisms and by increasing complexity and depths of bioturbation. Thus diversifications at the base and the top of food chain provided important drivers

for diversification and a reorganization of community structures (Table 1).

Environmental causes (Table 2) have included the intense magmatic and tectonic activities during the period, creating island arcs and chains together with microcontinental archipelagos, eustatic changes in sea-level, related to fluctuations in the area and volume of ice sheets and magmatic activity along mid-oceanic ridges (McKenzie et al., 2014). The Ordovician was also characterized by exceptional volcanic activity together with a possible superplume (Barnes, 2004). Apart from generating a variety of greenhouse gases and contributing to global warming, volcanic eruptions also provided increased amounts of inorganic nutrients to the world's oceans; these, together with the erosional products of the developing orogenic belts such as the Caledonides, contributed to the base of the food chain during this exceptional event. A large increase in shelf area, significantly in the tropics, was related to marine transgression and the global greenhouse effect, creating a unique mosaic of large epicontinental seas during the period. On the other hand, intervals of global cooling may also have driven the radiation, providing more amenable water temperatures for animal metabolism (Trotter et al., 2008) and the precipitation of calcium carbonate. Oxygen levels continued to rise during the period, supporting the growth and metabolism of progressively larger animals (Berner et al., 2007). Finally, an extraterrestrial cause associates the increased flux of asteroids hitting the surface of the Earth, resulting from the breakup of a giant body in the asteroid belt some 470 Ma ago, to the biodiversification (Schmitz et al., 2008). The increased frequency of impact craters, asteroid fragments, and extraterrestrial chromite in Scandinavia match precisely that huge hike in biodiversity demonstrated by the brachiopod faunas in eastern Russia (Rasmussen et al., 2007).

There has also been a strong focus on unravelling the various types of biodiversity and assessing the origin and significance of each in relation to global diversity patterns and trends for the entire period (Harper, 2006, 2010). Thus alpha, or intra-community diversity, packs more species into communities by expanding or multiplying ecological niches; beta diversity, or inter-community, generates whole new communities, during the Ordovician associated with the offshore movement of communities (Bassett et al., 2002) and the generation of new community-types ranging from flat-bottom to mud mounds and reefs (e.g., Zhan et al., 2006); gamma diversity captures global diversity patterns and is commonly associated with the global

Table 2
Key enabling (extrinsic) factors for the Great Ordovician Biodiversification Event.

Extrinsic driving factors	Mechanism	References
Asteroid impact	Intermediate disturbance hypothesis, clearing the seabed for recolonization	Schmitz et al., 2008
Erosion	Emergent mountain chains provided erosional products and nutrients	Miller and Mao, 1995
Global cooling	Amelioration in temperature more compatible with metazoan metabolism and skeletal growth	Achab and Paris, 2007; Trotter et al., 2008
High sea levels	Increased habitable platform area	Kiessling et al., 2003; Nardin and LeFebvre, 2010
Oxygenation	Pulse of atmospheric oxygen aids metabolism, production of collagen and skeletal material	Berner et al., 2007; Diamond, 2013
Substrate change	General trend from carbonate to siliciclastic substrates favoured particular groups of organisms	Miller and Connolly, 2001
Superplume activity	Source of nutrients	Barnes, 2004
Tectonic and magmatic activity	Creation of island habitats, providing intra-oceanic nurseries, museums and stepping stones for taxa	Bruton and Harper, 1981; Harper, 1992; Harper et al., 1996, 2008, 2009; Servais et al., 2009
Volcanicity	Products of submarine volcanoes provided nutrients	Vermeij, 1995; Servais et al., 2009

provinciality. All these processes, however, are aggregated into a total diversity for the planet and perhaps no single trigger or suite of explanations is necessary. Darwin's model predicted the expansion of life from a single species to the 10–20 million species today. A key property of life is its ability to diversify and the Ordovician Period clearly provided the essential ambient earth system and relevant drivers and enablers.

4. Examples of regional case studies: from the Baltic to South China

The global signals of the GOBE are now known with increasing clarity and precision. Less well known are the underlying regional contributions to the event that are many and varied, although there are now many detailed regional compilations and descriptions of data (e.g., [Benedetto, 2003](#)). Some of the regions have exhibited very distinctive patterns of biotic change during the event or have been prominent in unravelling key aspects of the GOBE. For example, new studies in the Welsh sector of Avalonia suggest the diversity of sponge faunas have been seriously underestimated as important components of the GOBE ([Muir et al., 2014](#)), in an area that has proved useful in unravelling parts of the ecology of the event through its exceptionally preserved faunas ([Botting and Muir, 2008](#)). In the Moroccan part of North-west Gondwana an Ordovician Lagerstätte has exposed relicts of the Cambrian Explosion such as anomalocarids, occupying deep-water environments, suggesting an offshore displacement of these faunas during the GOBE ([Van Roy et al., 2010](#)). Key localities across Laurentia have demonstrated firstly changes in the dominant components of shell beds, indicating a shift from trilobites to brachiopods as the most abundant shells in concentrations and pavements ([Finnegan and Droser, 2008](#)), a phenomenon reported also from South China ([Liu et al., 2010](#)). The diversification, particularly into deeper-water habitats, of trace fossils through the event has been documented in a wide range of publications; but tiering in some taxa, for example

Thalassinoides ([Jin et al., 2013](#)) across Laurentia, was a key part of the increased bioturbation of the substrate. Finally the transition from microbial to metazoan reef complexes was the key in establishing a new range of habitats not least cryptic communities ([Harper, 2006](#); [Adachi et al., 2011](#)).

We have focussed on just two of the many regional case histories available to demonstrate the importance and significance of such studies in deconstructing the many complex strands of this major event.

One key region is the Baltic Craton. During the Early–Middle Ordovician (Tremadocian–Darriwilian), Baltica moved rapidly from cool temperate zones to warmer temperate latitudes, with the more shallow-water facies of this paleobasin characterized by cool-water carbonates. Siliciclastic input was extremely limited, derived from a peneplaned hinterland of mainly the Precambrian rocks. The Floian–Darriwilian rocks were intensively sampled, bed-by-bed, during several field seasons in the St. Petersburg region, Russia and northern Estonia. The resulting dataset, based on more than 30 000 rhynchonelliformean brachiopods, precisely identifies the initiation of the GOBE during the early Darriwilian ([Rasmussen et al., 2007](#)). These data are supplemented by 15 000 trilobites, providing an exceptional mid-latitude paleoecological window on the biotic changes on the paleocontinent of Baltica ([Fig. 2](#)).

- (1) During this short time interval there was a massive diversity spike at the species, genus, and family levels particularly amongst the brachiopods ([Rasmussen et al., 2007](#)).
- (2) The diverse brachiopods can be organized into a series of onshore-offshore communities in a transect from Estonia to western Russia, signalling the expansion of both alpha and beta diversities ([Rasmussen et al., 2009](#)).
- (3) Changes in brachiopod diversity and ecological changes can be tracked through a number of sections as the diversification proceeded ([Rasmussen and Harper, 2008](#)).

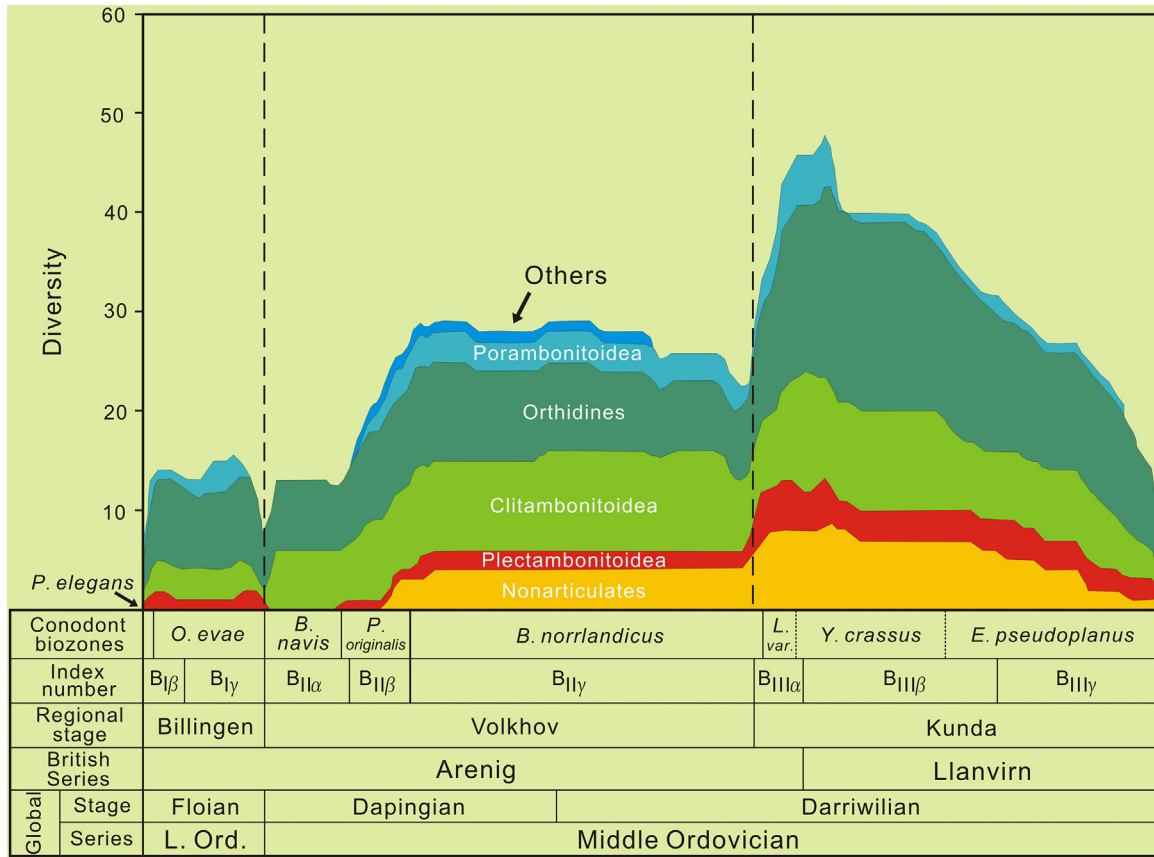


Fig. 2. Massive hike in brachiopod species diversity in the lower Darriwilian (Kundan) in western Russia. The rapid diversification coincides with evidence of meteorite impacts, cooling, and regression (after Rasmussen et al., 2007). Abbreviations: B_{Iβ}, lower Billingen Stage (middle Floian); B_{Iγ}, upper Billingen Stage (upper Floian); B_{IIα}, lower Volkhov Stage (lower Dapingian); B_{IIβ}, middle Volkhov Stage (middle Dapingian); B_{IIγ}, uppermost Volkhov (upper Dapingian); B_{IIIα}, lower Kundan Stage (lower Darriwilian); B_{IIIβ}, middle Kundan Stage (lower Darriwilian); B_{IIIγ}, upper Kundan Stage (lower Darriwilian).

- (4) The hike in diversity is precisely coincident with a high abundance of meteorite fragments, extraterrestrial chromite and other geochemical proxies (Schmitz et al., 2008) together with widespread soft-sediment deformation structures (Pöldsar and Ainsaar, 2013).
- (5) The rapid diversification is also associated with cooling and a regression possibly coincident with the development of small ice caps on the continent of Gondwana (Rasmussen et al., 2009).

In this context the early Darriwilian diversification was associated with a clearing of ecospace by meteorite impacts but also enabled by cooling and a focus for migrations and originations in shallow-water marine habitats.

A series of case studies, conducted in South China over the past 15 years, has greatly aided our understanding of the event. Here within a platform-slope-basin setting during the Early Paleozoic, particularly the Cambrian and Early–Middle Ordovician, complete rock sequences and abundant fossils of various marine organisms, have formed the basis for some detailed studies of changes in the patterns of regional diversity.

- (1) The radiation lasted for tens of million years during which all major marine organisms participated in three diversity

acmes during the GOBE; apparent diachroneity, however, occurred among different organisms. For example, brachiopods experienced radiation acmes in the early Floian, Darriwilian, and late Katian respectively (Zhan and Jin, 2008a), whereas graptolites diversified during late Tremadocian, early Darriwilian, and mid Katian (Chen et al., 2006; Zhang et al., 2010), trilobites in the early Sandbian, early Katian, and late Katian (Zhou et al., 2006).

- (2) The radiation was characterized by faunal replacements, in at least three major fossil groups, spanning a range of ecotypes: graptolites (from anisograptid to dichograptid to diplograptid faunas), trilobites (from *Ibex* to *Whiterock* faunas), and brachiopods (from *Sinorthis* fauna to *Saucrorthis* fauna to *Altaethyrella* fauna) (Zhang and Chen, 2006; Zhou et al., 2006; Zhang et al., 2007; Zhan and Jin, 2008a) (Fig. 3).
- (3) For the benthos, each diversity acme was associated with strong global provincialism manifested by the radiation of a regional fauna. The brachiopod *Sinorthis*, *Saucrorthis* and *Altaethyrella* faunas are all typical regional faunas occupying normal marine benthic regimes (Zhan et al., 2002, 2007; Rong and Zhan, 2004; Zhan and Jin, 2008b). The GOBE was always coincident with strong provincialism which may be an important trigger for this major bioevent (Williams, 1973; Zhan et al., 2014).

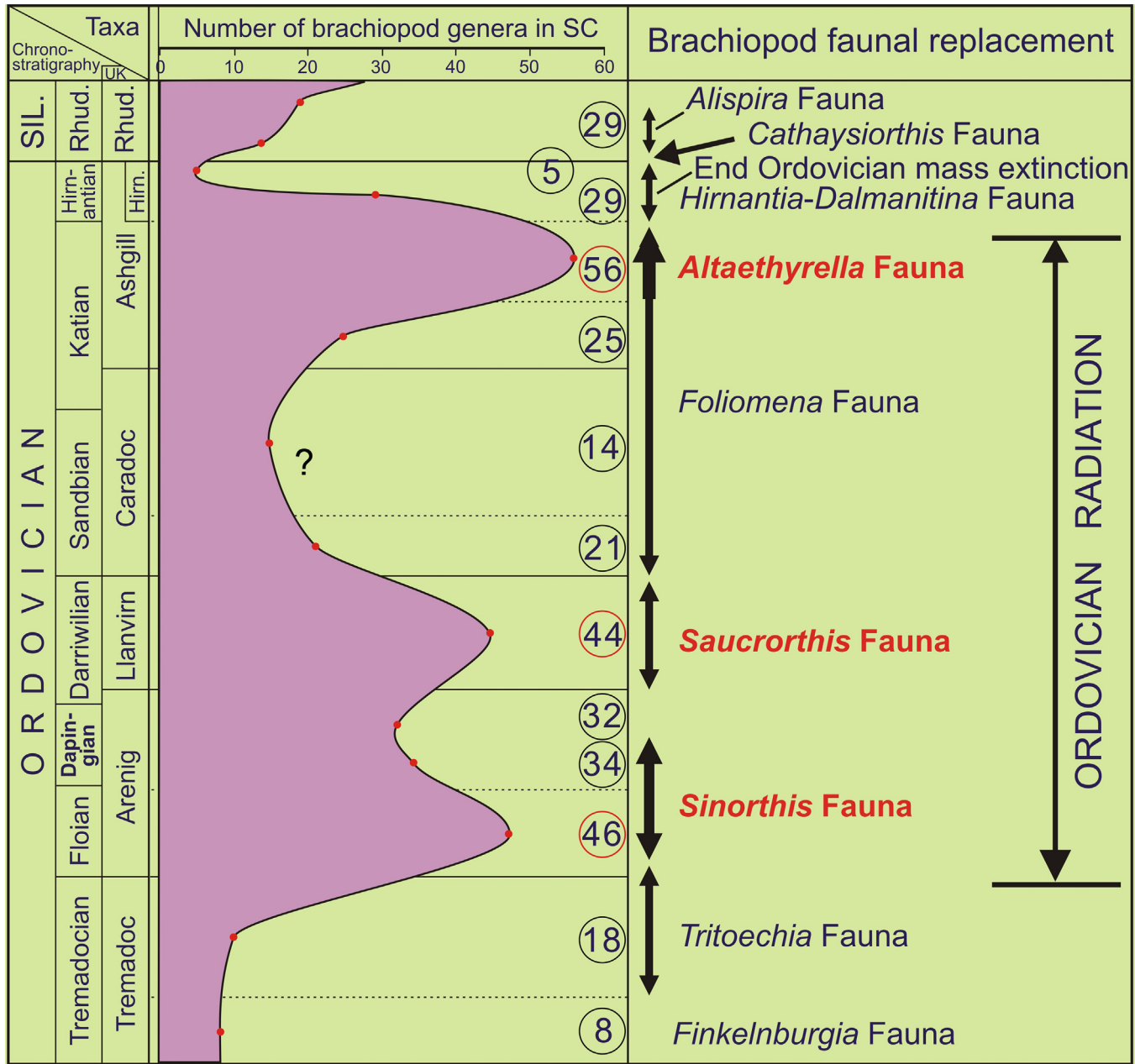


Fig. 3. Brachiopod generic diversity change during the Ordovician in South China (shown by circled numbers), brachiopod faunas on the Yangtze Platform, and the *Altaethyrella* Fauna on the Zhe-Gan Platform. Note three diversity maxima marked by the *Sinorthis* Fauna, the *Saucrorthis* Fauna, and the *Altaethyrella* Fauna, respectively. The question mark around late Sandbian refers to the subjective diversity value because of systematic study, in progress, on the *Foliomena* fauna from the Pagoda Limestone (Sandbian–lower Katian). The *Hirnantia-Dalmanitina* Fauna is confined largely between the two pulses of mass extinction, and the *Cathaysiorthis* Fauna ranges from the latest Ordovician to the lowermost Silurian (basic data partially from Zhan et al., 2005 and Rong et al., 2013). Abbreviations: SIL., Silurian; Hirn., Hirnantian; Rhud., Rhuddanian.

(4) The first acme of brachiopod Ordovician radiation in South China could be further differentiated into three phases: originating in the relatively deeper benthic regimes (such as the upper part of the Jiangnan Slope), radiating in normal marine environments (the central part of the Yangtze Platform), and ending in near shore shallow water localities (Zhan and Jin, 2014) (Fig. 4). But, paleoecologically, most of the new arrivals in South China first appeared in the central part of the Yangtze Platform and only a few in near shore or offshore localities, challenging the general ‘onshore

origination and offshore expansion’ model posited by Jablonski et al. (1983).

(5) The dynamics of GOBE are most probably a combination of intrinsic and extrinsic factors, exemplified by the data from South China. During its outward migration from the supercontinent Gondwana, South China accommodated a sympatric environmental background for the relatively early biodiversification in Early Ordovician. The Kwanghsian Orogeny commenced in the late Middle Ordovician (coincident with tectonic activity during the Caledonian

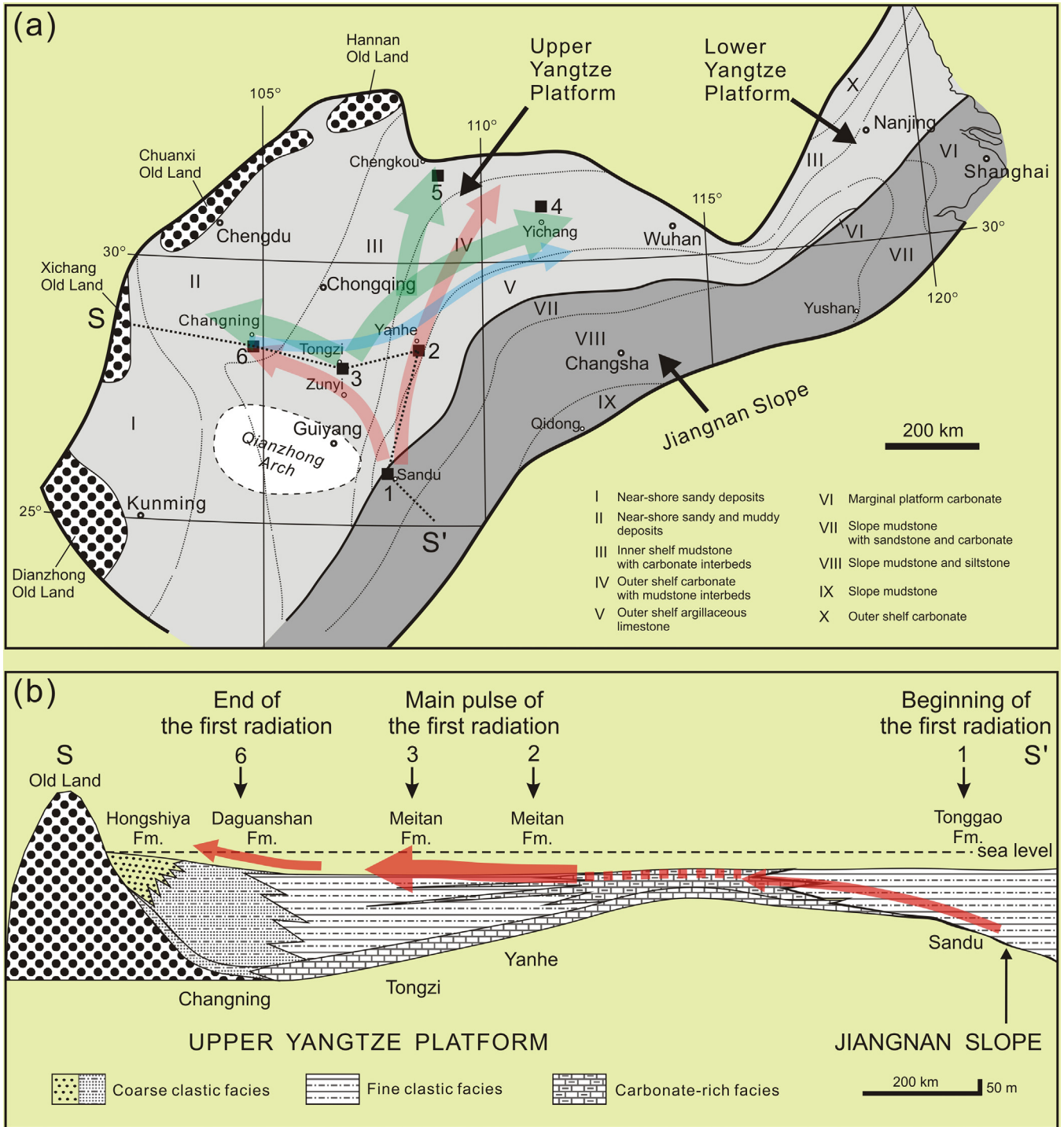


Fig. 4. (a) Paleogeographic positions of six classical Ordovician sections representing the case studies conducted in South China, and the migration routes of some key brachiopod taxa. Light red arrows indicate dispersal of taxa from the upper Jiangnan Slope in the onshore direction; light green arrows denote dispersal of taxa on the central Upper Yangtze Platform in both onshore and offshore directions; light blue arrow indicates dispersal of taxa from near-shore to offshore localities. (b) Stratigraphic cross-section (S–S') from the Upper Yangtze Platform to the upper Jiangnan Slope showing deposits of mainly Floian age in different paleogeographic settings. The transparent red arrows indicate the stepwise pulses of diversity acmes during the first radiation of the brachiopod Great Ordovician Biodiversification Event (GOBE) in South China in the offshore-onshore direction. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and Taconic orogenies in Europe and North America respectively), accelerating the process of diversification of all marine organisms (Chen et al., 2012). The rapid expansion of the Cathaysian Oldland aided and supported the climax of

GOBE for almost all fossil groups, by establishing a unique paleogeographic setting in South China (Rong and Chen, 1987), which included the formation of a narrow Zhe-Gan Platform and the Zhexi Slope.

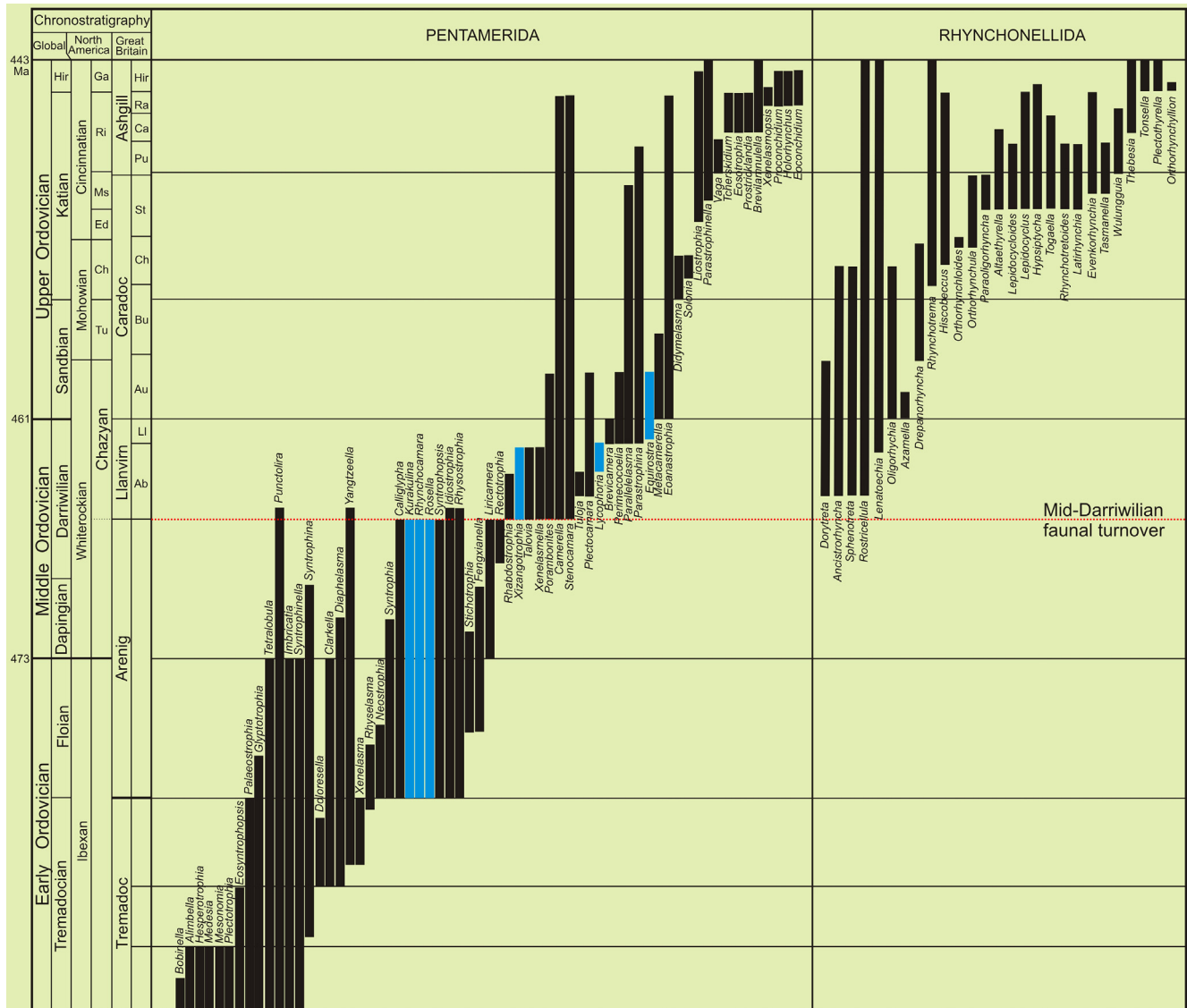


Fig. 5. Chronostratigraphical range chart of some key taxa (genera) of Ordovician pentamerids and rhynchonellids, showing a major faunal turnover disrupting pentamerid evolution in the middle Darriwilian which was also followed by the first appearance of rhynchonellids. Abbreviations: Ab, Abereiddian; Au, Aurelucian; Bu, Burrellian; Ca, Cautleyan; Ch, Chatfieldian; Ed, Edenian; Ga, Gamachian; Hir, Hirnantian; Li, Llandeilian; Ms, Maysvillian; Pu, Pusgillian; Ra, Rawtheyan; Ri, Richmondian; St, Streffordian; Tu, Turinian.

5. Sustaining a direction of travel through the next decade

The Ordovician biodiversification was rooted in the Cambrian and is a logical extension of the Cambrian Explosion. Body plans had to be in place before diversifications at lower taxonomic levels, such as families, genera, and species, could follow. The 'Cambrian Explosion' and the 'Great Ordovician Biodiversification Event' are, nevertheless, linked as part of a single, large scale evolutionary progression of marine life, including the Devonian Nekton Revolution (Klug et al., 2010), that developed over some 100 myr; the significant time lag between the two still requires explanation. On the global scale, some of the terrestrial processes that may have promoted the GOBE were part of a continuum from the Cambrian into the Middle Ordovician: for example, continental divergence with the origin of island arcs

and the development of new terranes with their own provincial structures, the increase in shelf area related to marine transgression and global warming. Volcanic activity and tectonism may have been more episodic as, clearly, was asteroid impact. Many of the terrestrial processes were interrelated and impinged on both the benthos and the plankton, and the revolution in the latter probably had a major effect on the former and both probably fuelled the later nekton revolution. The GOBE thus may be associated more with positive feedbacks and the crossing of thresholds than abrupt triggers; a similar model has been recently proposed for the Cambrian Explosion (Smith and Harper, 2013). The recent international research effort has enhanced our understanding of many of the processes involved. The cumulative effect of these processes was a massive increase in diversity within the major clades that developed in the Cambrian Explosion and constructed a resistant and resilient marine ecosystem

that set the agenda for the rest of the Phanerozoic. To further penetrate the essence of the GOBE, we require high-quality case studies for those major continents or blocks where fossiliferous and well-preserved Ordovician sequences are exposed. Detailed systematic paleontology and high-resolution chronostratigraphy are critical aspects of these kinds of investigations. Precise regional paleontological and stratigraphical correlation is essential to describe and refine the reality and significance of the GOBE. Moreover, detailed investigations of geochemistry, sedimentology, and structural geology of these key sections are critical in understanding triggers of this major biotic event.

A new research direction and perspective on the GOBE is focused on the critical role played by a few progenitor taxa during the drastic faunal turnovers and subsequent diversity booms. The mid-Darriwilian benthic shelly faunal turnover, for example, has not attracted much attention among GOBE-related IGCP projects. For the brachiopods, as an example of the predominant fossil group, the ‘Early Ordovician’ brachiopod fauna globally was replaced largely by a new fauna of ‘Late Ordovician aspect’ at this faunal turnover. From the few progenitors, the pentameride, rhynchonellide, and atrypide orders went through rapid, stepped radiation pulses, and radiated into the highly diverse Late Ordovician benthic shelly fauna (Fig. 5). Another striking example is the origin and diversification of the Silurian pentamerids, the signature shallow-marine shelly benthos for the period, stemmed from a single thread, the *Brevilamnulella* lineage, which was a markedly inconspicuous taxon of the Hirnantian fauna. Future study of such faunal turnover events, especially regarding the biological and environmental causes for the survival of progenitors (often perceived as insignificant component of a fauna) and their subsequent diversification, may shed much light on the patterns, processes, and causes of large-scale and long-term biodiversity fluctuations like the GOBE.

In conclusion, the refined chronostratigraphy for the system, advancing taxonomic knowledge of the majority of the fossil groups, and a reliable paleogeographic framework are providing the foundations for yet more quantum leaps in understanding the GOBE. The more accurate and refined paleogeographic maps for the period (Harper and Servais, 2013) are providing a much greater prospect to identify species pumps and refugia, migrational pathways and associated upwelling and oceanic currents (Servais et al., 2014). While a new emphasis on a model-based approach (e.g., Godderis et al., 2014), particular to climate change, is providing a range of new hypotheses to test with the massive amounts of new data that continue to be generated by the IGCP projects.

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