

GR Focus Review

Ordovician palaeogeography and climate change

L. Robin M. Cocks¹, Trond H. Torsvik^{2,3*}

¹Department of Earth Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

²Centre for Earth Evolution and Dynamics (CEED), University of Oslo, PO Box 1028, Blindern NO-0315, Norway

³School of Geosciences, University of Witwatersrand, Johannesburg 2050, South Africa

*Corresponding author

E-mail addresses: r.cocks@nhm.ac.uk, t.h.torsvik@geo.uio.no

ABSTRACT

New palaeogeographical reconstructions for the earlier Ordovician (480 Ma), and later Ordovician (450 Ma) integrate revised longitude-calibrated palaeomagnetic reconstructions and the inclusion of synthetic plate margins within the now-vanished oceanic areas. There are substantial published differences from the previous placing of some of the continents and terranes in Asia; for example, Siberia and Gondwana have previously been placed at varied distances and relative positions in relation to the Kazakh terranes, South and North China, and Tarim. But there are only minor changes for most of the world, particularly in the North American and European areas. The global distributions of benthic trilobites and brachiopods within faunal provinces and their changes through the Ordovician are plotted, including the new term Cathay-Tasman Province for some pan-equatorial brachiopod faunas from China and Australia, and key sites and provinces are shown on the revised maps.

The 30 Myrs from 470 to 440 Ma (mid Ordovician to early Silurian) saw some of the most varied and changeable climates of the whole Phanerozoic culminating in the ‘Hirnantian’ ice age. Those changes in turn much affected the rates of evolution of many benthic and pelagic animal groups which were driven by both biological and environmental causes. Global cooling during the Ordovician was a prime factor by reducing sea surface temperatures which challenged life to evolve faster and more substantially than before. That cooling was driven by decreasing atmospheric CO₂, for reasons that are not fully resolved, but probably included reduced sourcing (reduced continental arc activity) combined with increased silicate weathering due to the advent of land plants and perhaps the progressive exhumation of low-latitude collisional arcs. Since long-term CO₂ sinks are largely controlled by palaeogeography, the general increase in the

concentration of continents in the tropics during the Ordovician increased the overall global weathering.

Keywords: Ordovician, palaeogeography, climates, Kazakh Terranes, benthic brachiopod provinces

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1. Introduction

The Ordovician has long attracted the interest of palaeogeographers because there was a particularly large number of diverse continents and terranes in those times which were well dispersed in equatorial and southerly latitudes (Figs. 1 and 2). However, the majority of the previously published research has been concerned with today's Europe and North American areas, and the remaining three-quarters of the world have been less intensively studied. No *in situ* Ordovician oceanic crust is preserved, and thus the principal quantitative tool for establishing the ancient geography has been through palaeomagnetic studies, but those only indicate the palaeolatitudes and rotations of the former continents and terranes, not their longitudes, and the original primary magnetic signature has in many places been overprinted (reset) by subsequent tectonics. The margins of all the terranes can also be defined by analysis of their separating sutures, which indicate subduction, obduction, or strike-slip activity at the time of closure, but they do not place the terranes' positions on the globe in relation to their neighbours until that suturing occurred. Although more qualitatively than quantitatively based, the distributions of the differing benthic faunal assemblages, for example of brachiopods and trilobites, have often proved effective indicators of relative palaeolongitudes as well as latitudes. Fortey and Cocks (2003) reviewed the shallower-water benthic faunas helpful in the placing of continents in the Ordovician and Silurian, but that account was written before the technical advances mentioned in the following paragraph, and thus those provinces and their changing distributions from the beginning to the end of the Ordovician are revised here. All the benthic and planktonic animal phyla underwent a massive evolutionary radiation during the Ordovician, known as the Great Ordovician Biodiversification Event (GOBE), which was reviewed by Webby et al. (2004) and is briefly discussed in Section 4 below.

Fresh insights have transformed our understanding of pre-Mesozoic palaeogeography since 2008, when the plume generation zone reconstruction method was identified as useful in placing some of the major continents in longitude through the occurrences of large igneous provinces (LIPs) and kimberlites within them (Torsvik, 2019; Torsvik and Cocks, 2017; Torsvik et al., 2008; 2014). In addition, the generation of mathematically objective and kinematically coherent successive synthetic ocean models has provided a base for conjecturing where the plate boundaries lay under many of the oceans, thus making much more realistic Palaeozoic maps for much of the Earth (Domeier and Torsvik, 2014; Domeier, 2016; 2018).

We have constructed new global maps within a revised GPlates (Boyden et al., 2011) framework for the earlier Ordovician (near the end of the Tremadocian Stage) at about 480 Ma (Fig. 1), and the later Ordovician at 450 Ma during the Katian Stage (Fig. 2), shortly before the advent of the end-Ordovician Hirnantian global cooling. During those thirty million years the Iapetus Ocean narrowed and the Rheic Ocean widened in today's western hemisphere; and the many terranes mostly now in Asia and southern Europe performed a complex dance round the

northern border of the immense Gondwanan continent and to the then east of Siberia. Figs 1 and 2 also show representative sites of the shallower-water brachiopod benthic faunal provinces. Those provinces and their positions on the globe are revised in broad terms and discussed below in Section 5.

The Ordovician saw some of the most varied climates and sea level variations of the whole Phanerozoic (Fig. 3). At the beginning of the Ordovician the Earth was very warm with tropical sea surface temperatures of around 45°C or more, and by ~450 Ma sea levels were so high (Fig. 3d) that they have only since been exceeded in mid-Cretaceous times. At the Ordovician's end at 444 Ma there occurred one of only three glacial episodes known in the most recent half billion years but it is noteworthy that the 'Hirnantian' glaciation lasted only for perhaps less than a million years: a sharp contrast to the 40 Myrs Late Palaeozoic ice age (Carboniferous-Permian) and the End Cenozoic ice age, first recorded by glaciations in Antarctica from about 34 Ma and peaking from ~2.7 Ma in the current Plio-Pleistocene glaciation (which has not yet ended). The 'Hirnantian' glaciation is shown in quotation marks throughout this paper since it is probable that the glaciation commenced at some time in the latter half of the preceding Katian Stage in a few places, as well as icecaps continuing on into the early part of the Silurian, certainly in Brazil. The description and possible causes of those Ordovician climate fluctuations are discussed in Sections 6 and 7.

2. Main continental and oceanic regions

2.1. Outline

There is only a brief summary here – much more can be found in Torsvik and Cocks (2017).

2.1.1. The North Atlantic area, Laurentia, and Baltica

The Iapetus Ocean, which lay largely between the continents of Laurentia, Baltica, and Gondwana (Figs. 1, 2), was over 4,000 km wide at the start of the Ordovician at 487 Ma. The ocean extended northward over the Equator between north-east Laurentia and Siberia, and was united with the Panthalassic at its north. By the end of the Ordovician at 444 Ma the central region of Iapetus between Avalonia and Laurentia had narrowed to about 1,200 km across the British sector in eastern Avalonia and ~500 km between Ganderia and Laurentia in western Avalonia. In contrast, the Rheic Ocean only originated in the latest Cambrian when rifting started to separate the newly independent microcontinent of Avalonia from the main mass of Gondwana at about 490 Ma, the end of Tremadocian time (Cocks and Fortey, 2009), but by the end of the Ordovician, the Rheic had widened to over 3,500 km between the South American sector of Gondwana and Laurentia, and to about 6,000 km between the North-west African sector of

Gondwana and Avalonia. That steady widening of the Rheic was reflected in the increasing faunal disparity on the shelves at their respective edges as Ordovician time progressed.

Laurentia was a large continent, comprising most of the USA, Canada, Greenland, much of Mexico, Scotland, and part of Ireland, a high proportion of whose craton was flooded by shallow seas during most of the Early Palaeozoic. Its equatorial position made it warm enough to host many carbonate sediments and bioherms, with thicker, deeper-water origin sediments including turbidites in the surrounding and less stable tectonically-active continental shelves. Because of the passive margins which surrounded it on all sides, Baltica underwent little tectonism during the entire Ordovician and also contained many carbonates, although those limestones were initially of cooler-origin (Jaanusson, 1973), when the continent was at a much higher southern latitude (Fig. 1) than later, when it neared the Equator (Fig. 2). In contrast, the much more tectonically active microcontinent of Avalonia included substantial volcanism, which peaked at around 455 Ma, and the substantial Welsh Basin within Avalonia deepened throughout the period and was largely filled with many thick turbidites often interbedded with volcanics (reviewed in Branchley and Rawson, 2006).

The Iapetus contained many oceanic island arcs, but by the end of the Ordovician at 444 Ma it was much narrowed and most of those volcanic islands previously within the western part of the ocean had become accreted to Laurentia within the Appalachians of North America and those in the eastern sector to the Caledonides of north-western Europe to the north-west of Avalonia and Baltica. Many of those arc terranes were reviewed by Domeier (e.g. 2016) whose papers we have used in the changes to our previous published maps. Offshore from Avalonia and separated from it by the Tetagouche-Exploits back-arc basin, was the composite microcontinent of Ganderia (sometimes termed Western Avalonia), which included Maine, Tetagouche (Miramichi), and various Newfoundland units today on the American side of the Atlantic; as well as Tramore, Bellewstown, Anglesey, and others which are now parts of north-west Europe (Pothier et al., 2015).

2.1.2. *Gondwana and its periphery*

As reviewed by Torsvik and Cocks (2013), the large part of the margin of Gondwana stretching from Peru, around southern Africa and East Antarctica, and to the eastern coast of Australia was active throughout the Ordovician, in contrast to the margin from north-east Australia, around India, Arabia, and northern Africa, which was mostly passive. During the Ordovician, much new material, mostly previous island arcs, was accreted to the already-large Gondwanan continent, particularly to form today's eastern Australia as well as western South America (Chile, Peru, and Argentina). The South Pole lay beneath northern Africa and the extensive area of high-latitude shelves in that region includes many pockets of coarse sandstone, collectively termed the Grès Armoricaïn, some deposited on the inner shelf and others within shallow seas on top of the

craton. In the Middle Ordovician, Gondwana remained about the same size and had moved very little in latitude, but the subduction and volcanic arc activity continued all along the extensive southern margin. In contrast, its opposite margins were largely passive with the widening of the Rheic Ocean between Gondwana on one side and Laurentia, Baltica, and the Avalonian collage on the other.

As well as Avalonia, which rifted away from Gondwana at about 490 Ma (Fig. 1), there were also numerous and varied terranes now in southern Europe south of the Trans-European Suture Zone and which were mostly within the Armorican Terrane Assemblage (some forming the Franconia and Saxothuringia terranes). These units form most of France, Spain, Germany, and the Czech Republic, as well as many parts further east which survive only as fragments within the much later Alpine collage. Other southern and eastern areas, principally now parts of Italy, were constituent parts of the Palaeo-Adria terrane. All these were integral parts of the higher-latitude sector of Gondwana for much of the Ordovician, but those composite units, many with Precambrian cores, were subsequently isolated or tectonically much affected as they progressively split off from the main Gondwana continent initially during the Ordovician and Silurian but more so during the Upper Palaeozoic Variscan Orogeny (Franke et al., 2017). In the later Palaeozoic, that Variscan area extended westwards into the Alleghenian area of Laurentia and north-western Africa and into the dismembered Central American terranes surrounding Mexico (Torsvik and Cocks, 2017, fig. 9.7), all during the assembly of the supercontinent of Pangea. However, as can be seen on Fig. 2, some of those tectonic separations had already started in the Ordovician; for example, when Franconia and Saxothuringia became detached from the rest of the Armorican Terrane Assemblage.

2.1.3. *The Panthalassic fringes*

As can be seen in Figs 1 and 2, the Panthalassic Ocean covered nearly half the globe and lay chiefly in the northern hemisphere. From west to east its fringes were formed of western Laurentia and the nearby Arctic-Alaska Chukotka microcontinent; Siberia and the adjacent Central Mongolian Terranes (later to be parts of the Amuria microcontinent) with the latter two separated by the relatively small Mongol Okhotsk Ocean. There was also a large sector of Gondwana which stretched northward over the Equator, near which lay the extensive Kazakh archipelago discussed further below in Section 3. There was Ordovician subduction of the Panthalassic under the western margin of Laurentia, but much of that off-shelf margin has been lost through subsequent tectonics. At the opposite Panthalassic margin, in the areas today south of Antarctica and South America, there were yet more island arcs, such as those in Argentina described in Benedetto (2003), although there are none preserved today in Antarctica between the early Ordovician and the early Devonian. An enormous subduction zone lay immediately south of Gondwana at its Panthalassic rim, which might have been continuous from Peru to Australia.

3. Palaeogeographical disagreements on Siberia and central and eastern Asia

3.1. Background

Apart from the large continental plate of Siberia, whose Palaeozoic positions and faunas were summarised by Cocks and Torsvik (2007) and whose palaeomagnetic inversion and progressively changing palaeolatitudes as it drifted northwards have been widely accepted for many years, there is little unanimity on the divisions and development of the many terranes and continents which made up most of the rest of central and eastern Asia during the Ordovician. As well as the Siberian craton itself, there are numerous terranes, many with Cambrian or Precambrian cores, which were independent entities during the Ordovician. Some were substantial continents during the Ordovician, including the closely-related South China and Annamia (Indochina), North China (including the Sino-Korean Peninsula), and Tarim (today within south-west China), and others which were smaller (Cocks and Torsvik, 2013). Between the Baltica-Siberia sector of Eurasia and the remnants of the old Gondwana in Africa and India there stretches today a wide tectonised swathe from the Black Sea to the Pacific, variously termed the Altaids or the Central Asian Orogenic Belt, an extensive collage most of which was not finally united until the Late Carboniferous and Permian during the assembly of the supercontinent of Pangea. Central within this belt, and occupying much of south-western Asia today, are the so-called ‘Kazakh Terranes’, which not only occupy much of Kazakhstan, but also Kyrgyzstan, Uzbekistan, Tajikistan, and adjacent countries, and which extend eastwards for a relatively short distance into south-western China.

Because so many different definitions and names have been used for the numerous Kazakh terranes, we have constructed Fig. 4, each part of which has a modern base-map, to help orientate the reader. Fig. 4a is essentially the same as Torsvik and Cocks (2017, fig. 3.7) but modified to denote those terranes, such as South Tien Shan, whose rocks are entirely of post-Ordovician (largely Devonian) ages and which can thus be discounted in the present discussion. Fig. 4b is a slightly simplified variant of Domeier (2018, fig. 5), and Fig. 4c is based on Şengor et al. (2018, fig. 5), which was largely unchanged from Şengor et al. (1993). Popov and Cocks (2017), discussed further below, largely followed the modern-day boundaries of the Şengor et al. (2018) terrane units, but postulated a different Ordovician palaeogeography.

As well as those three relatively recent reconstructions discussed further below, numerous other authors, including Golonka (2007), Metcalfe (e.g. 2011), Wilhem et al. (2012), Li et al. (2018), and those in the book edited by Kröner (2015), have also presented different and variable versions of how the Altaid fragments were distributed during the Lower Palaeozoic. Unfortunately, particularly when attempting to synthesise the palaeogeography of the whole Ordovician globe, yet many more papers simply omit the Kazakh terranes altogether or depict them as a single entity. In addition, various authors have postulated that the continent of

Kazakhstan, which did eventually incorporate the majority of the Kazakh terranes, existed as an entity during the Ordovician. For example, Zhao et al. (2018, fig. 9) show only ‘Kazakhstan’ in their Cambrian to Ordovician (500–460 Ma) reconstruction and linked it to Siberia with little discussion, as well as placing a substantial Paleo-Asian Ocean between those two continents and Gondwana, which they considered as including North and South China as well as Alex, Qaidam, and Tarim: an interpretation which can only be wrong. After detailed analysis of the many different local rocks throughout the region, Popov and Cocks (2017, fig. 15) demonstrated that Kazakhstan was only united to become a substantial continent from Devonian times onwards, and thus the name should not be used for periods before then.

However, still not yet finally resolved are the precise Ordovician positions of Tarim and North China. Domeier (2018) placed Tarim over 50° south of North China in the middle Cambrian at 500 Ma and moving steadily northward until being adjacent to North China by the end of the Ordovician (Fig. 5b), separated only by the Qilian-Qaidam-North Qinling island arcs. Qilian (now part of Tibet) was very orogenically active and includes Ordovician and Early Silurian diorite dykes which were formed during northward subduction of the South Qilian oceanic slab from 472 Ma (Early Ordovician: Floian) to 432 Ma (mid-Silurian: Wenlock) (Yang et al. 2018). North China has a variety of Cambrian to mid-Ordovician (Darriwilian) shelly faunas in rocks underlying an unconformity beneath mid-Carboniferous rocks, indicating that it was largely a land area from the Sandbian onwards. The Japanese arc islands, today adjacent to North China and in which only relatively few Ordovician rocks are found, were either immediately offshore or integral constituents of the South China continent during the early Palaeozoic rather than North China (Isozaki et al., 2010). The whole region was described and reviewed by Cocks and Torsvik (2013), but here we further analyse and compare the three differing palaeogeographies of Şengor et al. (2018), Popov and Cocks (2017), and Domeier (2018).

3.1.1. Şengor et al. (2018)

A milestone paper was by Şengor et al. (1993), and its essentials were repeated with only minor changes for the Kazakh region in several subsequent papers including Şengor et al. (2018). Their scenario (summarised here in Fig. 5a) shows a single enormous Kipchak Arc curving all the way from Baltica to Siberia; an island arc which included many of the relatively small microcontinents and terranes now making up the Kazakh Terranes and adjacent areas of central Asia. The palaeolatitudes which they showed for Baltica and Siberia at either end of the arc were originally derived (within errors) from those of Torsvik et al. (1992). The Şengor et al. interpretation was heavily influenced by their assessment of the history of the large and obvious orocline in Kazakhstan which had been noted for many years; however, that orocline was more fully investigated by Abrajevitch et al. (2007), who, by using a substantial amount of then new

palaeomagnetic data from the widespread and abundant Devonian volcanics, established that the orocline was entirely formed during the Devonian. Also after analysis, Fortey and Cocks (2003) found that the Ordovician benthic trilobite (particularly the unmistakeable *Taklamakania*) and brachiopod faunas show a close relationship of the Kazakh terranes to Gondwana and South China and had no links with either Siberia or Baltica. Thus it can be reaffirmed here that the Kipchak Arc scenario can definitely be discounted. In contrast, the reality of the extensive Tuva-Mongol Arc with its many terranes today to the south-west and in the Ordovician to the north of Siberia (Fig. 5a), also originally postulated by Şengör et al. (1993), is a probable scenario for those areas.

3.1.2. *Popov and Cocks (2017)*

These authors presented a new palaeogeographical map for the Late Ordovician of the Kazakh terrane area as well as the adjacent North and South China, Tarim, and part of Gondwana, summarised here on Fig. 5c. They concluded that the majority of those Kazakh terranes formed an archipelago which straddled the palaeoequator west of the Australian sector of Gondwana throughout the Ordovician. After analysis of 94 brachiopod faunas from later Ordovician (Sandbian and Katian) sites of many of the Kazakh terranes, chiefly Boshchekul, Chingiz-Tarbagatai, and Chu-Ili, Popov and Cocks (2017) demonstrated that those terranes can be grouped into three clusters, with progressively closer links between contemporary faunas in South China and nearby Australia, the latter an integral part of Gondwana in the Ordovician (Figs 1, 2). However, in contrast to Domeier (2018), Popov and Cocks (2017) placed the Kokchetav, Boshchekul, and Chingiz terranes between North China and Gondwana.

3.1.3. *Domeier (2018)*

Following other innovative papers (e.g. Domeier, 2016) on the Iapetus and Rheic oceans, Domeier (2018) constructed a synthetic model for the oceanic plates throughout Lower Palaeozoic time in the Asian area, summarised here for the Ordovician in Fig. 5b. However, he grouped all the Kazakh terranes into just three units, the first the combined Boshchekul and Chingiz terranes, the second North Tien Shan (including Chu-Ili), and the third the Stepnyak, Selety, and Kokchetav terranes. From the Middle Cambrian at 500 Ma to the Middle Ordovician just before 460 Ma, Domeier showed the Boshchekul and Chingiz terranes as forming integral parts of the Siberian Plate (Fig. 5b). However, the Cambrian and Ordovician benthic faunas of the Chingiz terrane are well known, including the brachiopods described by Popov and Cocks (2014), and have almost nothing in common with contemporary Siberian faunas and thus the placing of those Kazakh Terranes as integral parts of the Siberian Plate is in error. Domeier (2018) plotted Boshchekul-Chingiz and the other Kazakh terranes as adjacent to Siberia at the

western end of a long ribbon proceeding through Tarim, North China, and South China and ending in the east close to the Tibetan-Thai sector of Gondwana.

3.1.4. Our compromise conclusions

In contrast to Domeier (2018), we conclude here from all the geophysical and faunal evidence that the Boshchekul-Chingiz terrane group and the Siberian Plate must have been quite separate from each other, and our new reconstructions (Figs 1 and 2) show oceanic separation of over 1000 km between Siberia and the other terranes and continents to its east. However, we have followed Domeier (2018) rather than Popov and Cocks (2017) in placing the Kazakh terranes to the west of North China rather than to the east, since the faunal data previously used by Popov and Cocks is suggestive rather than objectively definite, and Domeier's continental placings have more kinematically consistent geophysical evidence to support them.

4. Ordovician evolutionary radiations of the biota

The term GOBE was introduced in the book edited by Webby et al. (2004), to which many individual experts in all the early Palaeozoic major animal and plant groups contributed: its conclusions have since been used and amplified by many subsequent workers (e.g. Servais and Harper, 2018). It is noticeable from that volume that, although every organic group did indeed diversify greatly during the Ordovician, most of those evolutionary peaks were not simultaneous for all the different groups, both benthic and planktonic, during the period or even within the various subgroups (Orders etc) within each phylum.

The definition of GOBE has varied between authors. Biodiversity patterns differ between various continents, various animal groups and the kind of statistical analysis used. Stigall et al. (2019) reviewed the increases in numbers of genera and orders of many phyla including zooplankton, phytoplankton, and both swimming and benthic invertebrates during the later Ordovician. From that paper we have taken their data on the genera of articulated brachiopods (green thick global curve in Fig. 3a). Stigall et al. (2019) also concluded that the term GOBE should be restricted to the particularly rapid diversification which started during the Darriwilian and continued on up into the Katian when peak GOBE occurred. That is in contrast to the term 'Ordovician Radiation', which they used when discussing all the diversifications which took place throughout the Ordovician. However, we continue to use GOBE here in the original sense of Webby et al. (2004) and confine its use to within the Ordovician. The global biodiversity curve in Rasmussen et al. (2019) show gross similarities with that of Stigall et al. (2019) but with a more distinct rise in Mid-Ordovician richness during the late Dapingian-early Darriwilian (blue curve of global biodiversity in Fig. 3a). They found peak biodiversity levels in the early Katian and argued for a three-phased diversity reduction, which actually ended in the Early Silurian, and not the 'Hirnantian'. In Fig. 3a we also show yet another diversity curve (in red) estimated from

marine invertebrate data but which was based only on Chinese sections, overwhelmingly from the South China Plate (Fan et al., 2020). They noted a nearly threefold increase in species diversity during the Early Ordovician and recognized GOBE as a ~20 Myrs continual diversity increase from the Early Ordovician until the Dapingian-Darriwilian. Fan et al. (2020) observed peak richness in the Sandbian and viewed the end-Ordovician ‘Hirnantian’ mass extinction as a rapid diversity decline from the Late Katian (shortly after the Boda warming event). Many previous authors had also noticed substantial Early Ordovician radiations in South China (termed ‘pre-GOBE’ by Stigall et al., 2019; Fig. 3a) that are not seen on other continents, but it is questionable if the diversity curve of Fan et al. (2020) is globally representative. All these areas in China were located within a narrow latitude belt centred at around 15°S from 485 to 465 Ma (Fig. 1), and subsequently on the Equator from ~455 to 445 Ma (Fig. 2).

The Hirnantian period showed the very dramatic end-Ordovician biotic extinctions (Fig. 3a), which occurred in two separate phases according to Webby et al. (2004), and ended with 85% of species and 61% of genera becoming extinct. Rasmussen et al. (2019) estimated a three-phased Ordovician diversity reduction, starting in the Early Katian, but rather unexpectedly their Figure 2 plotted the peak of both the ‘end-Ordovician Mass Extinction’ and also the lowest sea level in the Rhuddanian Stage of the early Silurian rather than in the Hirnantian Stage of the latest Ordovician (Fig. 3a).

5. The changing distributions of benthic faunal provinces

Since the pioneering works of Whittington (1966) on trilobites and Williams (1969) on brachiopods, as reviewed by Fortey and Cocks (2003), it has been known that the distribution of the various benthic provinces (Fig. 6) often reflect the contemporary Ordovician palaeogeography, particularly at the margins of the larger oceans. The opportunity is taken here to plot some of the key brachiopod provincial sites on our new maps (Figs 1, 2). However, each benthic phylum has different faunal provinces, as upgraded in the book edited by Harper and Servais (2013), particularly the analysis of Harper et al. (2013) for the brachiopods. As a generality the distribution of both benthic and planktonic faunal provinces are subparallel to the palaeolatitudes, but by no means entirely, probably indicating that the distribution of many of the provinces were much influenced by the prevalent colder or warmer ocean currents and gyres of Ordovician times. The distances between some of the major continents, particularly near the old Equator, were sufficiently wide enough so that separate shallower-water benthic provinces were hosted on some of the different continental margins at the same lower latitude. The development of the various provinces is now reviewed at successive times.

5.1. Earlier Ordovician

5.1.1. Mediterranean Province

In the earlier Ordovician, Gondwana was so large (Fig. 1) that the Mediterranean brachiopod Province (which largely coincided with the calymenoidean-dalmanitoidean, sometimes termed *Neseuretus*, trilobite Province) was widely developed on the fringes of its margins at higher and intermediate latitudes (Fig. 6a). The province has two principal aspects, whose sites are separately distinguished on Fig. 1; firstly, the higher-latitude faunas with their distinctive large inarticulated lingulide brachiopods, notably *Lingulobolus brimonti*, *Lingulobolus hawkeii*, *Pseudobolus salteri*, *Ectenoglossa leseueuri*, and *Lingulepis crassipixis*, whose distributions primarily lay within northern Africa, and the then adjacent polar parts of Gondwana, notably Iberia, Armorica, and Bohemia (Torsvik and Cocks, 2011, fig. 6).

The second aspect of the Mediterranean Province, which covered a more widespread area, (Fig. 6a), is less eye-catching but still includes distinctive brachiopod faunas including assemblages initially dominated by *Prantlina*, *Ranorthis*, *Nocturniella*, and others during the Floian and Dapingian, and in slightly later (Darriwilian) times by *Tissintia* and *Tafilaltia*. These faunas occur in South America and the Middle East as well as in slightly lower latitudes in Avalonia (see ‘Celtic’ Province below), and some parts of the Armorican Terrane Assemblage such as France and Bohemia. In addition to these and over a similar wide latitudinal belt largely between 30° and 60°S, there were also communities of varied composition and diversity. Variably diverse Ordovician shallow-marine benthic faunas, such as the brachiopods and trilobites described in the volume edited by Benedetto (2003), occur in the island arcs now in Argentina which fringed south-western Gondwana. Also abundant in some mid-shelf assemblages was the large porambonitacean brachiopod *Yangzteella*, which was originally described from South China, but is also known from southern Turkey, Karakorum, and Iran: however, those *Yangzteella* Community sites can only loosely be included within the Mediterranean Province: they also lived in rather lower latitudes.

Included as well in those Mediterranean Province more diverse regions are those with assemblages of the ‘Celtic’ Province. That province was originally defined by Williams (1969) to include two Early Ordovician faunas in Anglesey and south-eastern Ireland, which are both very comparable to the fauna now revised from south-west Wales (Cocks and Popov, 2019). All were then in the microcontinent of Avalonia, which had separated from Gondwana at about 490 Ma, only 10 Myr beforehand. Williams’ concept of the Celtic Province has been much expanded by various later authors, as summarised in Liljeroth et al. (2017). For example, North China’s Dapingian to Darriwilian brachiopods were linked to the Celtic Province by Harper et al. (2013), although there seem to be few genera in common and those few appear to reflect latitudinal rather than geographical similarities. Thus Celtic is recognised here as a sub-province, perhaps comparable in status to the *Yangzteella* faunas mentioned above, particularly since there are no distinctive particular brachiopod genera found in all of its sites which would normally

characterise a province, although some endemic genera are known from many of the individual Celtic terranes.

5.1.2. *Baltic (or Baltica) Province*

This province, based on the distinctive benthic faunas of many phyla identified by numerous authors in classic monographs since Linnaeus in the eighteenth century nineteenth century, was largely centred around today's Baltic Sea area (Fig. 6a) but extended eastwards to the Urals and north-eastwards to Nova Zemlya, and was bounded to its modern south by the Trans-European Suture Zone (apart from the Holy Cross Mountains of Poland, which is to the south-west of that zone and contains characteristic Baltic trilobites and brachiopods). As summarised by many authors, for example Öpik (1935), Whittington (1966), Williams (1969), and Fortey and Cocks (2003), the province was particularly distinctive in the Early Ordovician, notably in its megistaspiniid trilobites and the brachiopods *Lycophoria* (which is occasionally abundant to the extent of being rock-forming and is also the only genus known within its family) and many endemic clitambonitoideans. That distinctiveness reflected the relative isolation of the Baltica continent during the later Cambrian and earlier Ordovician (Fig. 1) before its northward migration to lower palaeolatitudes (Fig. 2).

5.1.3. *Laurentian Province*

In the Early Ordovician of the USA and Canada, many of the abundant and diverse previously termed Ozarkian and Canadian (now Tremadocian) brachiopod faunas were largely endemic. These faunas were originally described by Ulrich and Cooper (1938), although they are in some need of modern revision, and were succeeded by equally diverse brachiopod and trilobite faunas locally known as Whiterock, for example by Ross (1970). In addition, the widespread bathyurid trilobite Province dominated both Siberia and Laurentia in shallower waters, but the deeper-water trilobite faunas in the same regions have been termed the olenid Province, which is less significant when analysing the continental palaeogeography since the ambient sea temperature is always globally more equable in the deeper parts of the oceans. Both the bathyurid and the dikelokephalinid provinces lay in similar tropical latitudes but were far enough apart to have hosted largely different benthic faunas, even though there is a bathyurid record from a single site in North China (Fortey and Cocks, 2003). The Laurentian Province (Fig. 6a) hosted the largest benthic diversity of the period, not just trilobites and brachiopods, but many representatives of several other phyla, including echinoderms and corals (Harper and Servais, 2013).

We include within the Laurentian Province the so-called Toquima-Table Head Province, originally erected by Ross and Ingham (1970) and modified by Neuman and Harper (1992). However, that consists essentially of the deeper-water marginal faunas found offshore from some

of the main shallower-water benthic Laurentian Province, and is therefore recognised as only having subprovincial status here.

The Cuyania (or Precordillera) Terrane of north-western Argentina (Fig. 1) also hosted trilobites and brachiopods of largely North American aspect at that time (Benedetto, 2003), very different from the medium-latitude peri-Gondwanan faunas of the rest of South America adjacent to Cuyania today. That indicates its lower Early Ordovician palaeolatitude as well as its relative proximity to the south-western USA.

Although Siberia is grouped here as within the main Laurentian Province at this time, its trilobite and brachiopod benthic faunas may only be differentiated as a Siberian Subprovince in the Early Ordovician, partly because they were so much less diverse there than in Laurentia itself. Nevertheless, we show that subprovince from the rest of the Laurentian Province separately in Fig. 6a. Although there were some distinctive shallow-water Siberian endemic trilobites (Fortey and Cocks, 2003), heralding the even more distinctively different faunas seen there in the subsequent parts of the Ordovician, there were no endemic earlier Ordovician brachiopods. Siberia also shared the olenid trilobite ‘Province’ with Laurentia, but again that merely reflected the deeper-shelf biota.

5.1.4. *Cathay-Tasman Province*

The most characteristic trilobites of the Kazakh terranes, North China, South China, and the Australian sector of Gondwana are all representatives of the dikelocephalinid trilobite Province. In contrast to the fauna within the Laurentian Province, the Australian pan-tropical shores of Gondwana hosted both the dikelocephalinid trilobite Province and the Cathay-Tasman brachiopod Province in the same equatorial palaeolatitudes. The latter is a new term, coined here to recognise the brachiopod faunas (Fig. 6) found in both the Gondwanan margin, for example in Tasmania (Laurie, 1991) and in China (which was historically named Cathaysia). However, earlier Ordovician brachiopod diversity was often locally very low; for example, at some shallow-water localities in Australia and western Malaysia only numerous specimens of the plectambonitoidean *Spanodonta* occur in a virtually monospecific community (Cocks and Torsvik, 2013), although the species diversity of both brachiopods and trilobites rose soon afterwards to reflect the GOBE radiation (Webby et al., 2004). A few Ordovician benthic faunas have been found in the continent of Amuria, particularly in the substantial Khinggan area (then part of the Khanka-Jiamusu-Bureya sector of Amuria) which today spans the junction between Siberia, China, and Mongolia. However, the described faunas from Khinggan are rather sparse and, since they were identified with few rather poor illustrations over a hundred years ago, are much in need of modern systematic revision before their provincial affinities can be confidently assessed.

5.2. *Later Ordovician*

Particularly during the approximately 30 Myr between the end of the Tremadocian at 478 and the middle of the Katian at about 450 Ma, not just the brachiopods and trilobites but all the benthic faunas evolved and expanded in diversity very dramatically as parts of the GOBE radiation (Webby et al., 2004). For example, the bivalve molluscs were insignificant during the Cambrian, but radiated sharply, firstly in the temperate latitudes of Gondwana soon after the start of the Ordovician before spreading from there to lower latitudes, where they later became more generally diverse (J.C.W. Cope and J. Kříž in Harper and Servais, 2013).

5.2.1. *Mediterranean Province*

Gondwana remained so large that the Mediterranean brachiopod Province was still developed on the fringes of its southern margins (Fig. 6b), but now without the previously-distinctive large inarticulated brachiopods or widespread quartzites. However, the trilobites remained grouped within the calymenoidean-dalmanitoidean Province, albeit with different genera (Fortey and Cocks, 2003). In general, only clastic rocks continued to be deposited at those higher latitudes, which was a major factor in keeping the diversities of most shelf benthic communities relatively low. However, for example, in Bohemia (then still an integral sector of Gondwana) Havlíček et al. (1994) identified 38 brachiopod genera in their later local Beroun stage (late Katian), of which over half were endemic to the province. During the later Katian, the Boda warming Event was reflected even in the higher-latitude parts of Gondwana, such as Morocco, which were host to relatively small bioherms of cooler-water origin largely formed of bryozoans: which are locally very conspicuous since they are the only carbonates seen in the whole thick Ordovician succession there (Fortey and Cocks, 2005).

5.2.2. *Baltic-Anglo-Welsh Province*

With the dwindling of the Tornquist Ocean, Avalonia became progressively closer to Baltica at its eastern end, and the two continents merged obliquely very close to Ordovician-Silurian boundary time at 444 Ma (Torsvik and Rehnström, 2003). Thus the benthic faunas of the previously separable Baltic and Anglo-Welsh Provinces became gradually more similar, and comparably those areas had progressively fewer benthos in common with the higher-latitude Mediterranean Province as the Rheic Ocean widened. Although Harper et al. in Harper and Servais (2013) had recognised a separate Baltic Province in the later Ordovician, when Liljeroth et al. (2017) revised the brachiopods occurring in the Iapetus Ocean and elsewhere and plotted their Ordovician distributions at 463 Ma (Darriwilian) and 457 Ma (Sandbian), they reclassified the Baltic assemblages as within the Anglo-Welsh-Baltic Province, and we follow them here (Fig. 6). The changing distributions of the trilobites in these areas were also comparable to the brachiopods (Fortey and Cocks, 2003).

5.2.3. *Siberian Province*

By comparison with the other large continents, Siberia became progressively more isolated as the Ordovician progressed and as it drifted steadily northwards to straddle the Equator, and thus its benthic faunas had become progressively more endemic by the late Ordovician so as to merit full provincial status, especially for the trilobites. From the Sandbian to the end of the Ordovician, endemic trilobites were particularly distinctive, particularly emphasised by the Subfamily Monorakinae, eight out of ten of whose genera are confined to Siberia, and which formed a large part of the shallower-water monorakine-cheirurid-illaenid Association (Ebbestad and Fortey, 2019). Their distribution confirms that the New Siberian Islands in today's Arctic Ocean were part of Siberia, as concluded on other grounds by Cocks and Torsvik (2007), and their presence in the Khinggan (or Xing'an) area also supports the integration of that block within Siberia as suggested by Domeier (2018). In addition, Ebbestad and Fortey (2019) confirmed that the trilobites in the Arctic-Alaska Chukotka terrane were typically monorakine and therefore also within the Siberian Province, which is why we have included a queried line on Fig. 2 to indicate that Arctic-Alaska Chukotka may have been nearer Siberia than previously shown by Cocks and Torsvik (2011), although the brachiopods from that terrane require revision. As also noted by Cocks and Torsvik (2011), monorakine trilobites have been found in the Farewell terrane of Alaska, although since the Ordovician location of that enigmatic and relatively small terrane is poorly constrained, it is not shown on Figs 1 and 2.

Ebbestad and Fortey (2019) also pointed out that the deeper-water trilobites in the Siberian area were much more cosmopolitan, and are comparable with the Scoto-Appalachian 'Province' originally identified by Williams (1969). However, the shallower-water brachiopods and trilobites in the Siberian area still had a much lower diversity than in most other parts of the world and the relatively few brachiopods are notably represented by largely cosmopolitan genera, which also emphasises the difficulties that their spat must have had in successfully crossing the very wide oceans which surrounded the Siberian continent (Fig. 2).

5.2.4. *Cathay-Tasman Province*

South China, North China, the peri-Australian pan-tropical shores of Gondwana (including Sibumasu, which extended into today's south-western China), and nearby areas (Fig. 2) continued to host largely equatorial brachiopod and trilobite shallow-water benthic provinces with only a small minority of genera in common with the Laurentian Province. This included the distinctive Sandbian to Katian Pagoda trilobite Province, updated by Zhou et al. (2016), which is the approximate geographical equivalent of the Cathay-Tasman brachiopod Province, certainly in the areas in and around the South China continental area. The Pagoda trilobite communities lived at various depths, but there are many endemic or partially endemic trilobite genera within those

faunas, notably *Ovalocephalus* and *Paraphillipsinella*. The Pagoda faunas are mostly known from South China, but they also occurred in southern Thailand within the nearly Sibumasu sector of Gondwana (Fortey, 1997). The brachiopod faunas from the various Kazakh terranes analysed by Popov and Cocks (2017) also include some Sandbian to Katian genera otherwise endemic to North and South China, but those faunas are very different from the sparse faunas known from Siberia, which also straddled the Equator by that time (Fig. 2). Tarim, which is not firmly positioned palaeomagnetically, hosted typical Cathay-Tasman brachiopods, including the *Altaethyrella-Schachriomonia* Assemblage described by Sproat and Zhan (2019). Percival (1991) monographed the extensive Late Ordovician brachiopods found in New South Wales which lived within the volcanic arcs immediately offshore of Australia in those times, many of which genera are also only found elsewhere in the Kazakh terranes.

5.2.5. Laurentian Province

By the later Ordovician (Fig. 2), the Iapetus had become much smaller than before, with the Rheic Ocean much wider and thus the Avalonian faunas underwent progressive interchange with those in both Baltica and Laurentia. During the latest Sandbian to earlier Katian there was a major marine transgression after which Sproat and Jin (2017) identified the dominance of the relatively diverse Scoto-Appalachian Fauna (not here recognised as a benthic province) in the deeper waters off the eastern margin. There is also a widespread but less diverse epicontinental fauna (Fig. 6b) in much of shallower waters covering the craton, often known as the Richmondian brachiopod and coral faunas, which have sometimes been termed a province. Those Richmondian faunas remained distinctively different from their European contemporaries until almost the end of the Ordovician, when the majority of them became extinct, although from Katian times onwards they had been joined by an increasing proportion of immigrants from Baltica.

Before the end-Ordovician ice age, during the later Katian at around 447.5 Ma (Fig. 3a), there was relatively brief global warming termed the Boda Event (Fortey and Cocks, 2005), in which extensive bioherms developed in the low latitudes of Laurentia (particularly north-eastern USA and south-eastern Canada), as well as in Baltica (Boda itself and elsewhere in Sweden, Norway, and Estonia), and Avalonia (Kildare, Keisley, Portrane, and others), both of which had drifted northwards into much lower latitudes comparable to Laurentia (Fig. 2). Numerous endemic brachiopods, trilobites, and other phyla are known from within each individual bioherm and its immediate surroundings.

5.3. The Hirnantian finale

Near the close of the Ordovician at about 445 Ma, the ‘Hirnantian’ Ice Age (Fig. 3a) much affected the planet but for substantially less than a million years, although there may have been

some minor glaciation at the highest latitudes of Gondwana in the late Katian which certainly continued into the earliest Silurian in Brazil (Grahn and Caputo, 1992) (Fig. 7). But within that relatively short time two different extinction phases showed a massive faunal turnover, notably including the demise of the distinctive Richmondian brachiopod faunas in Laurentia (Harper et al., 2013). However, the palaeogeography did not undergo any substantial changes and, in contrast to the earlier half of the Ordovician, there were few active orogenic areas.

A direct result of the ‘Hirnantian’ glaciations was better oceanic circulation which led in turn to increased oxygenation to lower depths within the oceans, thus enabling some more enterprising pioneer benthic forms, for example the brachiopod *Hirnantia* and its community associates, to colonise deeper depths than hitherto on the continental shelves over much greater areas of the globe. The diversity of that *Hirnantia* Fauna varied considerably from just a very few brachiopod genera including *Hirnantia* itself as well as *Eostropheodonta* and *Cryptothyrella* and the trilobite *Mucronaspis*, to over twenty genera, which were mostly brachiopods, but there were also sometimes a few representatives of other phyla (Rong and Harper, 1988). Although some authors have divided the *Hirnantia* Fauna into two separate provinces, we do not follow them and conclude that the variable diversity and detailed composition of the fauna depended on local factors, including variable depths and palaeolatitudes rather than relative palaeogeography. Thus the *Hirnantia* Fauna seems best considered as cosmopolitan rather than provincial.

6. Ordovician Climates and Biodiversity

Much has been published on the possible causes of the Ordovician climatic and evolutionary changes, some of which have been included in Fig. 3, including variations in biodiversity, sea surface temperatures (SST), atmospheric CO₂ and O₂, continental arc-activity, global sea level and continental connectivity expressed in terms of the width of some important oceans.

Plate tectonics plays an intricate role in shaping the long-term climate by controlling the distribution of continents and oceans (palaeogeography), mountain building, arc-volcanism, topography and weathering. Plate tectonics also has a major effect on the hydrosphere because the variation in seafloor spreading is the most important driver of sea-level rise and falls. In turn, that also affects the biosphere and biodiversity, which is strongly influenced by continental flooding, intercontinental connectivity, the link between latitudes of the various continents and their overall average temperature, habitat, and oceanic-atmospheric circulation. It is perhaps naïve to assume that radiations in biodiversity can be linked to any single specific cause, but for some time there has been much agreement (e.g. Trotter et al., 2008) that changes in the marine biosphere during the Ordovician (Fig. 3a), can be at least partly related to a steady falling in SSTs, from ~45°C in the Early Ordovician to near modern equatorial SSTs (27-32°C) by the mid-Ordovician (Fig. 3b).

6.1. Sea-surface temperatures and biodiversity

Global mean sea surface temperatures (SSTs) may differ substantially and are commonly a blend of $\delta^{18}\text{O}$ measurement from phosphate and carbonate (less reliable in more ancient rocks) fossils that lived at variably different latitudes. We have used the SST dataset of Song et al. (2019), assuming an invariant oxygen isotope composition of seawater to calculate SSTs, and data-selection only include $\delta^{18}\text{O}$ from 648 phosphate fossils (apatite conodonts) that once thrived near the tropics (absolute mean latitude: $12 \pm 4^\circ \text{N/S}$ based on our own Ordovician-Early Silurian reconstruction parameters). Our mean curve (Fig. 3b; in one Myr increments and averaged over 2 Myr bins; Table 1) shows gross similarities with the pioneering curve of Trotter et al. (2008). We notice the same overall decline in temperatures during the Early Ordovician but our curve has slightly higher (and fluctuating) temperatures until the late Sandbian, followed by distinct cooling (about 5° to $28^\circ \pm 2^\circ \text{C}$ between 454-446 Ma), which coincides with the onset of reduced Late Ordovician biodiversification (Fig. 3a). Both curves show a pronounced drop during the Hirnantian, essentially coinciding with the end-Ordovician mass extinction, and recovered temperatures (and diversity) during the Early Silurian. Thus both increasing (early-mid Ordovician) and decreasing biodiversity (Late Ordovician) are associated with cooling! Increased diversity during cooling contrasts modern associations between warm climates and diversity, but the increased richness during the early Ordovician was probably simply a result of cooling to habitable temperatures, i.e. to biological tolerance levels. Thus there were feedback loops from increased skeletonisation which led to increased tiering within communities which enabled development into new ecological niches and leading in turn to fresh speciation.

6.2 Temperature, atmospheric CO_2 and biodiversity correlations

During the Early Ordovician, modelled CO_2 levels were high (~ 3500 ppm at 490 Ma) with SSTs around 45°C . CO_2 levels were steadily falling to about 460 Ma and then flattening out with CO_2 level at around 2500 ppm whilst SSTs was reduced to about 28°C . In the GEOCARBSULF model (Royer et al., 2014), atmospheric CO_2 is averaged to 10 Myr bins (Table 1), but by comparing SSTs and CO_2 levels at that time resolution we notice a reasonable correlation between SSTs and atmospheric CO_2 (Pearson correlation, $r=0.92$). We also compared mean SSTs with the COPSE (results in Mills et al., 2019) and GEOCLIMTech (Godd ris and Donnadieu, 2019) models but these gave lower correlations, $r=0.8$ and 0.57 , respectively. All three climate models show a general CO_2 reduction during the Ordovician but the actual levels can differ by as much as 1500 ppm, and during the ‘Hirnantian’ (~ 445 Ma), CO_2 levels range from nearly 2600 ppm (GEOCARBSULF) to 1600 ppm (COPSE).

If we compare SSTs and CO_2 variations (Fig. 3b) with the three diversity curves in Fig. 3a (Table 1) we estimate that the diversity of global articulate brachiopods show the strongest (negative) correlation with temperature ($r=-0.83$) and CO_2 ($r=-0.92$) from the Early Ordovician to

the Early Silurian. But this negative correlation is factored by the general reduction in SSTs and CO₂ during the Early Ordovician that allowed certain life-forms to flourish.

Cooler oceans would store more dissolved oxygen and Edwards et al. (2017) argued for a strong temporal link between GOBE and O₂ concentrations. The O₂ level in the early Ordovician was about 10-13%, but then there was a sharp rise from the early Darriwilian up to about 24% by the mid-Katian (red curve in Fig. 3c). That was followed by a major reduction in O₂ immediately before and during the Hirnantian. Edwards et al. (2017) therefore argued that oxygen levels played an important role in regulating Ordovician biodiversity; we find a fair (negative) correlation between O₂ levels and SSTs ($r=-0.74$) whilst there is a respectable positive correlation between atmospheric O₂ and the diversity of global articulate brachiopods ($r=0.86$).

6.3. *The link between palaeogeography and biodiversity.*

It is perhaps also naïve to consider only one parameter (e.g. temperature) as the chief cause for diversity changes. Variations in the geographical distribution and diversity of species are also affected by tectonic and magmatic pressures, for example from LIPs. As discussed by Stigall (2018), plate tectonic divergence causes physical isolation and can drive natural selection via allotropic speciation whilst habitat reconnections during plate convergence leads to competition between species occupying similar niches. Continental ‘block-fragmentation’ was tentatively correlated with diversity by Zaffos et al. (2017); however, although they observed peak Palaeozoic block fragmentation in the Mid-Ordovician, they identified no changes at all during Ordovician to Early Silurian times, which is surprising since that was a period with much major reorganization of the palaeogeography. The Iapetus closed progressively during the Ordovician (Figs. 1-2) and from the mid-Silurian, Avalonia and Baltica collided with Laurentia to form Laurussia. The Rheic Ocean, at the expense of the Iapetus, widened considerably during the Ordovician and reached a width of about 7000 km by the Early Silurian (Fig. 3e). We notice that the width of the most important Ordovician oceans, such as the Iapetus, Rheic, but also Ægir (separating Baltica from Siberia) were all in the order of 3000-4000 km at around 465 Ma and at the main GOBE initiation (Fig. 3a,e).

6.4. *What led to cooler Ordovician oceans?*

When discussing Ordovician temperature fluctuations there are two main questions; firstly, what led to the initial and progressive cooling during the Early Ordovician, and secondly what caused the more abrupt cooling that is contemporaneous with mass extinctions during the ‘Hirnantian’?

CO₂, the most important greenhouse gas in the Earth’s atmosphere, regulates planetary temperature, and on a geological time-scale its changes have been principally controlled by plate tectonics and the consequent developing palaeogeography. Long-term magmatic-related degassing occurs at mid-ocean ridges, island arcs, continental arcs, and continental rifts. Zircons

in the sedimentary record provide a way to track the past presence of continental arc systems, and temporal changes in continental arc-activity has been argued to play an important role in regulating long-term climate changes (McKenzie et al., 2016); in other words, high continental arc activity is linked to warm climate (greenhouses) and reduced arc activity explains icehouse climates. Subduction fluxes derived from full-plate models provide a powerful means of estimating plate tectonic CO₂ degassing (sourcing) through time (Torsvik et al., 2020), and correlate well with zircon age frequency distributions. No reliable global full-plate model (Domeier and Torsvik, 2014) is available before 410 Ma (Devonian) and therefore we have re-scaled and normalized arc-related zircon frequencies to subduction flux for the past 410 Ma and extended the normalized (1 = present day) zircon frequency curve to pre-Devonian times. In the Early Ordovician (Fig. 3d), we note peak arc-activity of ~1.7 (i.e. 70% higher than modern activity), after which there was a marked drop during the Floian-early Dapingian. However, the Ordovician is essentially characterised by a 35% reduction in continental arc-activity, starting at 480 Ma. Reduced plate tectonic CO₂ degassing is compatible with a generally cooler climate during the Ordovician but cannot explain the abrupt temperature/diversity shift during the ‘Hirnantian’.

Silicate weatherability and cooling can be explored by calculating the fraction of the total continental area that is located in the tropics (currently $\pm 23.5^\circ$), i.e. subjected to potentially warm and wet climates with high weatherability. During the Cambrian at around 510 Ma, 35% of the landmasses were located within the tropics, but maximum tropical exposure (Fig. 3d) is seen in the Ordovician between 460 and 440 Ma (45-46%, Table 1). That was followed by a dramatic reduction during the Silurian resulting in about 30% exposure of land in the tropics by the Early Devonian. The Ordovician therefore had the highest exposure of landmasses within the tropics, which potentially cooled the climate through silicate weathering. Estimates naturally depend on plate models and effective weatherability would be lowered by high sea levels. Climate gradients also appear much different during most of the Ordovician with evaporites commonly found at tropical latitudes, and thus pointing to an arid equator with low silicate weatherability. Globally, this was the case for the entire Ordovician (Fig. 7), except perhaps for the Katian and Hirnantian, when low-latitude evaporites were mostly confined to Laurentia (Fig. 8).

Low atmospheric CO₂ is a principal variable in controlling continental-scale glaciations (Royer, 2006), but the short-lived Hirnantian cooling event (~445 Ma) is paradoxical because of its apparent association with high atmospheric CO₂ levels. However, the sun was 3-5% fainter then and the CO₂ threshold for nucleating ice sheets at that time could have been 4-8 times (1120-2240 ppm) higher than pre-industrial levels of ~280 ppm (Gibbs et al., 2000; Herrmann et al., 2003; Royer, 2006; Lowry et al., 2014). GEOCARBSULF models atmospheric CO₂ levels of 2536 ppm (450 Ma) and 2600 ppm (440 Ma), and it is perhaps interesting to see how our revised estimates of ‘plate tectonic degassing’ (continental arc-activity in Fig. 3d) affects the

GEOCARBSULF model. Changes in seafloor production rates is an important time-dependent parameter in long-term climate models and named f_{SR} in GEOCARBSULF, but subduction flux must equal the seafloor production rate to a first order. We use normalized arc-related zircon frequencies as a measure of subduction flux and as a proxy for f_{SR} . If we recalculate atmospheric CO₂ in GEOCARBSULF (all other parameters similar to those in Royer et al. 2014) we notice that early Ordovician CO₂ levels are slightly higher, but end-Ordovician/early Silurian levels are reduced by ~200 ppm (450 Ma) and 350 ppm (440 Ma) 354 ppm at 440 Ma (stippled black curve in Fig. 3b). The two models are quite similar but the Pearson correlation between sea surface temperatures and our revised estimates for atmospheric CO₂ is slightly improved ($r=0.94$).

6.5. *The end-Ordovician mass extinction: links with cooling or a Large Igneous Province?*

Peak weatherability (at least theoretically) during the Mid-Late Ordovician can be estimated by other proxies for silicate weathering, e.g. strontium (Saltzman et al., 2014) and neodymium (Swanson-Hyell and Macdonald, 2017), which along with reduced plate tectonic degassing during the Ordovician (Fig. 3d) provide an explanation for the general cooling of the Ordovician oceans. Swanson-Hyell and Macdonald (2017) also postulated that an exceptional amount of tropical weathering of mafic and ultramafic rocks exhumed during the Taconic arc-continent collision along the margin of North America Laurentia (Fig. 2), may have been a factor in driving the ‘Hirnantian’ glaciation, although other authors, e.g. Landing (2018) have queried their conclusions.

Most Phanerozoic mass extinctions and oceanic anoxia events show causal links to continental large igneous provinces (LIPs) and global warming conditions. Examples include the ~252 Ma Siberian Traps, linked to the end-Permian mass extinction, and the end-Triassic mass extinction linked to the ~201 Ma Central Magmatic Igneous Province. Rasmussen et al. (2019) argued that the end-Ordovician mass extinction was linked to intense volcanism during the mid-Late Ordovician, but citing a so-called LIP event in South Korea (Ogcheon Volcanics) with reference to Kravchinsky (2012) who had assigned a rather imprecise age (480–430 Ma) for that intrusion in his LIP compilation. But the South Korean rocks in question are in fact Neoproterozoic (~750 Ma; Kim et al., 2006), and the end-Ordovician mass extinction cannot be linked to any known continental LIP (Torsvik et al., 2020).

Might the end-Ordovician extinction also have been triggered by an oceanic LIP which has since vanished through subduction? That was mooted by Jones et al. (2017) who documented unusually high concentrations of mercury in the late Katian and mid-Hirnantian of South China and the Hirnantian of Nevada, then part of Laurentia (Fig. 8), which they suggested might be the products of an undiscovered or a now-vanished (subducted) LIP. This was reinforced by Bond and Grasby (2020), who analysed deeper-water sediments, including the type Ordovician-Silurian boundary section at Dob’s Linn, Scotland, then offshore from Laurentia, and found comparable

levels of mercury. However, oceanic LIPs are limited in terms of the production of volatiles through contact metamorphism and/or crustal contamination, and environmental impacts must be considered much less severe than their continental counterparts (Torsvik et al., 2020). Thus, even if there was an end-Ordovician LIP, it is unlikely to have been more than a minor factor in causing the ‘Hirnantian’ glaciation.

7. The development of Ordovician climates

7.1. *The climate before 460 Ma.*

There is general agreement that the latest Cambrian and earlier Ordovician were relatively very warm (Fig. 3b); a warmth reflected in the massive carbonates widespread in many continents, some even in high paleolatitudes such as Sardinia. That warmth was matched by high atmospheric CO₂ levels, and that was echoed in turn by the great variety and increased speciation not only of benthic phyla, particularly trilobites, brachiopods, and echinoderms, but also swimmers including cephalopods and conodonts (Harper and Servais, 2013). However, the speed and detailed nature of the subsequent changes are not yet precisely clear. There is steady progressive, albeit fluctuating, reduction in sea-surface temperature from a surprising high of 45° C at the start of the Ordovician at 489 Ma to about 32° C in the late Darriwilian-Sandbian, a substantial fall to temperatures around 28° C during the Late Sandbian-Katian, and then another substantially fall near the end of the Katian to mean temperatures around of about 25°C during the ‘Hirnantian’ glaciations (Fig. 3b).

Although Rasmussen et al. (2016) concluded that the GOBE of Webby et al. (2004) was triggered by an emerging mid-Ordovician icehouse, there are no known mid-Ordovician glacial deposits from anywhere to firmly support any icecaps anywhere: for example, those glacial pavements previously reported from Morocco by Hamoumi (e.g. 2001) from the Sandbian of Morocco have been falsified, as summarised in Torsvik and Cocks (2017). Saltzman & Young (2005) had also postulated that there was glaciation as early as late Sandbian or early Katian (locally termed the Chatfieldian Stage) in Laurentia as reflected in a $\delta^{13}\text{C}$ excursion in the Monitor and Antelope ranges of Nevada, but, although there may well have been some cooling at that time, there seems no proof of any icecaps or glaciations either near there or anywhere else.

7.2. *Climate from 460 Ma (late Darriwilian) to 450 Ma (Katian).*

It was during the Middle Ordovician, between 460 Ma (late Darriwilian) and just after 450 Ma (early Katian), that there were the highest sea-level stands in the Palaeozoic (Fig. 3d). Many parts of the old cratons were flooded and the resultant warm-water shallow seas were enhanced centres of evolution for the benthic faunas, particularly those at low latitudes such as around and over the partially flooded craton of the continent of Laurentia (Fig. 2), as well as around some of the many

contemporary microcontinents such as the Chu-Ili Terrane of Kazakhstan (Popov and Cocks, 2021).

Bergström et al. (e.g. 2010) identified a substantial $\delta^{13}\text{C}$ isotope excursion at 453 Ma (Fig. 3c), approximately the Sandbian-Katian boundary, which they named the Guttenberg Excursion (GICE), and which they documented in detail in many sections in Baltica and Laurentia. Somewhat prior to the GICE, in the later Sandbian at 454 Ma, there occurred one of the largest known volcanic explosions ever, probably at a now-subducted site under the North Sea, of calc-alkaline magmatism beneath Avalonia, and which caused massive and very widespread bentonites to be laid down. Since Avalonia was nearing Baltica at that time (Torsvik and Rehnström, 2003): those bentonites are termed the Kinnekulle Bentonite in Baltica. It was once thought that the extensive Millbrig Bentonite in eastern Laurentia was a product of the same eruption, but it is now known that the two are not of precisely the same age and have different geochemical composition (Haines et al., 1995), but nevertheless Millbrig confirms the roughly contemporary very active arc volcanism. Bergström et al. (2010, fig. 17) accurately located both the GICE excursion as well as the Kinnekulle Bentonite some 4 m below it in the Fjäckå section and the nearby Smedsby Gård borehole in the Siljan area of Sweden. What precise effect those volcanic outpourings had on both the GICE and the longer-term climate change is uncertain.

7.3. Climate from 450 Ma (Katian) to 444 Ma (end Hirnantian).

A relatively short warm period was named the Boda Event by Fortey and Cocks (2005), which peaked in the early late Katian at around 447.5 Ma and saw numerous bioherms in several continents as plotted on Fig. 8. Those bioherms are of two very different types, the ‘normal’ and often very substantial bioherms up to several hundred metres in lateral extent and largely made up of crinoids, calcareous algae, and stromatoporoids, with subsidiary corals and bryozoans, as well as epifaunal benthic brachiopods, trilobites, and other phyla. These major rock-forming structures were in marginally subtropical areas, notably in Europe (as far east as the Ural Mountains) and North America. The second category are cooler-water bioherms, usually less than 20 m wide and which are chiefly dominated by bryozoans: those are vividly seen as relatively small white carbonate structures which stand out in stark contrast to the surrounding thick and substantial darker-coloured clastic deposits, notably in the high cliffs of the Anti-Atlas Mountains of Morocco, and other regions of North Africa. Before the Boda Event was named, Boucot et al. (2003) had previously identified some ‘Warm-Water’ faunas in various previously colder places outside Laurentia during the Katian. However, by the time of the Boda Event the overall biodiversity was past its Ordovician maximum (Rasmussen et al., 2019) (Fig. 3a).

After the Boda Event, the sea level remained high until around the end of the Katian (Fig. 3c), which increased the endemism within, for example, the brachiopods (Jin et al., 2014). Villas et al. (2002) interpreted the substantial increase in carbonate platform sedimentation at

around the time of the Boda Event, particularly in North America, as a major triggering factor in the subsequent ‘Hirnantian’ glaciations because of the cooling caused from the enormous amounts of CO₂ which would have been locked up in those limestones and dolostones. Finnegan et al. (2011) documented a gradual and protracted global oceanic cooling from about 457 Ma onwards decreasing from 37°C to 32°, with a ‘short-sharp’ minimum during the Hirnantian Stage down to 27°C, followed in contrast by a further protracted gradual increase in temperature to 37°C at some time past the end of the Aeronian Stage of the Llandovery at 439 Ma; however, we have constructed a revised plot (Fig. 3b) which largely echoes Song et al. (2019) and shows only a gradual dip until just after 456 Ma when the sea surface temperature dipped below the level seen today (shown as a light blue band in Fig 3b), after which it was not until the middle of the Llandovery at about 438 Ma that modern sea temperature were again matched.

It was largely during the Hirnantian Stage that the dramatic cooling event caused the formation of a very substantial icecap covering more than half of Gondwana as described by many authors. However, it is not clear to what extent there were in reality any truly glaciogenic deposits laid down before Hirnantian time. Outcrops from many areas of various late Ordovician ages are recorded in the substantial work of Boucot et al. (2013), but there are typically recorded only as ‘Ashgillian’, thus having a potential wide time range from 453 to 444 Ma, astride the ‘Hirnantian’ glaciation. Many do show undoubted glaciogenic features, in particular the striated glacial pavements originally described from North Africa, but most of their individual ages are poorly constrained, and thus the glacial reality of some have been controversial, both in the interpretation of their sedimentology as well as in their dates. However, an important paper, which incorporated the much earlier pioneer results of Beuf et al. (1971), is the compilation from northern Africa by Ghienne et al. (2007), which demonstrated clearly the reality of a late Ordovician ice cap there. That cap appears to have extended to cover a large part of central Africa as well as South America, Arabia and adjacent parts of south-eastern Asia. There are also contemporary glaciogenic sediments in South Africa, notably the Pakhuis Tillite (I.C. Rust in Holland, 1981), although it is unknown whether or not the icecap there was connected with the main polar icecap and what proportion of the whole Gondwanan continent was covered by a continuous sheet of ice.

Icebergs from the polar ice sheet are known to have travelled at least 3,500 km northwards before generating dropstone deposits on the subtropical shelf of Baltica (now within Poland) after melting (Porębski et al., 2019); however, that does not indicate that the icecap extended anything like as far towards the Equator as the low latitudes in which Baltica was then situated, and the icebergs are almost certainly comparable to those seen near the coast of Newfoundland today.

7.4. Climate immediately after the Ordovician.

Although a few icecaps persisted in the Brazilian sector of Gondwana for much of the early Llandovery (Fig. 7), they had largely vanished from most of that vast continent very soon after the start of the Silurian. The melting ice and the slowly rising average global temperature caused the volume of water in the oceans to expand. The consequent rise in sea level caused major transgressions during the early Silurian in a great number of places, many documented in the volume edited by Landing and Johnson (2003). Those transgressions continued in many regions at least until the end of the Llandovery at 433 Ma.

8. Conclusions

We have combined newly generated maps with calibrated longitude and plotted on them revised benthic faunal distributions to produce palaeogeographical and biogeographical maps for the earlier and later Ordovician, with the boundaries of lands, continental shelves, and oceans updated from those in Torsvik and Cocks (2017). Largely following Domeier (2016; 2018), the maps show the plate boundaries within most of the oceans apart from the immense Panthalassic. Those plate boundaries are synthetic since no *in situ* Ordovician oceanic crust is preserved today, although the postulated boundaries are kinematically consistent with each other through time. The new maps presented here supersede the reconstructions in our various previous papers (e.g. Cocks and Torsvik, 2007; Torsvik and Cocks, 2013; 2017). The benthic faunal provinces defined by the brachiopods in the earlier and later Ordovician are also shown (Fig. 8), after assessment of the assemblages from many sites across the world, some shown in Figs 1 and 2.

Other reconstructions are reviewed, including Popov and Cocks (2017), who, from analysis of later Ordovician brachiopods of the Kazakh terranes, concluded that those faunas demonstrate progressively closer links between contemporary faunas in South China and nearby Australia (Fig. 5b); and Domeier (2018), who, in his full-plate model of the whole of Asia throughout the Early Palaeozoic, published successive Ordovician maps which showed the Kazakh terranes, together with Tarim and North China, as stretching between South China and Siberia, with the Boshchekul terrane as actually on the same plate as Siberia in the early Ordovician (Fig. 5c). Although we largely follow most of Domeier's terrane and continental placings in Figs 1 and 2, we show Siberia as more than 1,000 km distant from all of the Kazakh terranes, largely because of their very different faunas, as well as the Kazakh terranes in revised positions to the west of North and South China.

Further modifications in the arcs and microcontinents in the Iapetus Ocean area follow Franke et al. (2017) and Liljeroth et al. (2017), particularly in the individual recognition of the many units within the Armorican Terrane Assemblage, Avalonia, and Ganderia microcontinents and associated terranes; and we also largely follow Liljeroth et al. (2017) in their brachiopod distributions in the Iapetus region. Thus the new maps presented in the present paper help to reconcile some of the differences in published reconstructions by ourselves and other authors.

The chief changes lie in the positions of North and South China, particularly with reference to each other, to adjacent terranes, and particularly with Siberia; the Kazakh terranes; and the Armorican terranes; as well as including the possible (although synthetic) oceanic plate boundaries in the new maps.

The Ordovician is known for worldwide tectonic activity and volcanism, major plate tectonic reorganizations and changes in palaeogeography, and wide oceans separating many of the major continents, which must have contributed to distinctive faunal provinces found in the marine benthos of the continental shelves. The Ordovician is also very special since virtually all the continents were located in the southern hemisphere (although some spanned the Equator) and the northern hemisphere was dominated by a single huge ocean named the Panthalassic. The Ordovician was also an exceptional period for biological and climatic changes, including the advent of land plants (which might have begun as early as the Late Cambrian; Morris et al. 2018), as well as the Great Ordovician Biodiversification Event (GOBE), which progressively increased the biota, particularly from the early Darriwilian onwards (Fig. 3a). The Early Ordovician Earth was a greenhouse planet with high temperatures (around 45°C) and high atmospheric CO₂ levels, but a 40 Myrs cooling trend culminated in the ‘Hirnantian’ glaciations in the high latitude parts of Gondwana, and the subsequent lowering of global sea level and the associated first Phanerozoic mass extinction at the end of the Ordovician period at 444 Ma. This is the only Phanerozoic mass extinction that cannot be linked to or explained by a contemporaneous LIP event (or an asteroid impact) and all other mass extinctions or anoxia events occurred during greenhouse conditions (Torsvik et al., 2020). A yet unidentified LIP or an oceanic LIP now vanished through subduction has been suggested to explain the end-Ordovician mass extinction but there is no evidence for that. Such a LIP would have triggered an abrupt global warming event superimposed on the cold climate at that time for which there is no evidence.

Although the GOBE was driven by a combination of biological and environmental factors, global cooling during the Ordovician must have been the prime factor, by reducing SSTs to temperatures that challenged life to evolve faster and more substantially than before. Cooling probably also caused the modelled increase in atmospheric O₂. Temperature and oxygen levels are anti-correlated and both echo the diversity of global articulate brachiopods. Global cooling was probably driven by decreasing atmospheric CO₂, which is most noticeably recognized from the earliest Ordovician to the Late Darriwilian in the GEOCARBSULF model. Although the reason for reduced CO₂ levels is not fully resolved, it probably reflects a combination of causes in this extraordinarily dynamic period in Earth evolution. These include *reduced sourcing* (reduced continental arc activity in Fig. 3d) and *increased silicate weathering* due to the advent of land plants (Lenton et al., 2012; 2016; Porada et al., 2016; Morris et al., 2018) as well as the progressive exhumation of low-latitude collisional arcs. Ultimately, long-term CO₂ sinks are largely controlled by palaeogeography, and the general increase in the concentration of continents

in the tropics during the Early Ordovician (Fig. 3d) appears to have increased the overall global weatherability.

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TEXT-FIGURE EXPLANATIONS

Fig. 1. Earlier Ordovician (late Tremadocian) lands and oceans at about 480 Ma, with representative sites of the various brachiopod provinces described in the text. Lambert azimuthal equal area projection centred on the South Pole. AAC, Arctic-Alaska Chukotka; AN, Annamia; ATA, Armorican Terrane Assemblage; AV, Avalonia; BC, Boshchekul-Chingiz; CU, Cuyania; F, Florida; K, Kara; K-O, Kolyma-Omolon; NT, North Tien Shan (including Ch-Ili); PA, Palaeo-Adria; SK, Stepnyak, Selety, and Kokchetav; SP, South Pole; T, Tarim.

Fig. 2. Later Ordovician (Katian) lands and oceans at about 450 Ma, with representative sites of the various brachiopod provinces described in the text. Lambert azimuthal equal area projection centred on the South Pole. The line extending with a query from the eastern end of AAC indicates the uncertain position of that terrane. AAC, Arctic-Alaska Chukotka; AN, Annamia; A-S, Altai-Sayan; ATA, Armorican Terrane Assemblage; BC, Boshchekul-Chingiz; CA, Carolinia; CU, Cuyania; F, Florida; F-S, Franconia-Saxothuringia; G, Ganderia; K, Kara; K-O, Kolyma-Omolon; NT, North Tien Shan (including Ch-Ili); NZ, New Zealand; PA, Palaeo-Adria; SK, Stepnyak, Selety, and Kokchetav; SP, South Pole; T, Tarim.

Fig. 3. Ordovician and Early Silurian stages with their ages in million years (Ma). **(a)** Calculated generic biodiversity (blue curve) from Rasmussen et al. (2019) and scaled (Palaeozoic) diversity (red curve) according to Fan et al. (2020) which is based on only Chinese sections, and mostly from South China. For comparison, we also show a global genera curve (thick green) from articulate brachiopods (Stigall et al. 2019, Table 1), who defined a pre-GOBE phase in South China, a main GOBE initiation in the Darriwilian, a peak GOBE phase, and the Boda warming event. In the Rasmussen et al. (2019) analysis, GOBE is defined as a distinct phase of increased biodiversity during late Dapingian-early Darriwilian (~467 Ma), whilst Fan et al. (2020), defined GOBE as a 20 Myr interval from the Tremadocian to the late Dapingian. Vertical background colour bars after Stigall et al. (2019). **(b)** Sea surface temperatures (SST, Table 1) shown as mean values at one Myrs interval (averaged over 2 Myr bins) with a 95% confidence envelope (transparent yellow background), calculated from Song et al. (2019), based on $\delta^{18}\text{O}$ measurements from apatite conodonts that once lived within the ancient tropics ($12 \pm 4^\circ \text{N/S}$), and the pioneering temperature curve of Trotter et al. (2008). Both curves assume seawater compositions as today. We also show a modelled atmospheric CO_2 curve (thick black line; GEOCARBSULF model) shown with 95% confidence levels in grey shading from Royer et al. (2014), and a revised CO_2 curve (stippled black) by substituting the f_{SR} parameter in the GEOCARBSULF model with the scaled zircon age frequency (arc environment) curve in panel d. **(c)** $\delta^{13}\text{C}$ variations (black line; Rasmussen et al. 2019) with abrupt positive values during the Hirnantian along with modelled atmospheric O_2 (red line) with 95% confidence envelope

(Edwards et al. 2017). **(d)** Global sea level curve in shaded light blue from Rasmussen et al. (2019) and scaled zircon age frequency (Modern=1) generated by arc environments (adapted from Domeier et al., 2018; Torsvik et al., 2020). We also show the amount of landmasses in the tropics (percentage of all land) which peaks in the mid-late Ordovician (Table 1). **(e)** The widths of the Iapetus across the UK sector (Laurentia/Scotland vs. Avalonia/England) and between Laurentia/Scotland and Baltica/Norway. Rheic ocean width is measured between Avalonia/England and Gondwana/NE Africa whilst Ægir width is measured between Baltica/Urals Margin and Siberia/Taimyr (Fig. 8). GICE, Guttenberg Isotope Carbon Excursion (Hatch et al., 1987; Bergström et al., 2010); GOBE, Great Ordovician Biodiversification Event; HICE, Hirnantian Isotope Carbon Excursion (Bergström et al. 2006).

Fig. 4. The central Asian area, including the Kazakh terranes (surrounded by a thick black line) on modern maps. The terranes between Chingiz-Tarbagatai and the Siberian Craton all formed parts of peri-Siberia and the Tuva-Mongol Arc in the Ordovician. **(a)**, modified from Torsvik and Cocks (2017, fig 3.7). The solely post-Ordovician terranes (largely Devonian island arcs), e.g. South Tien-Shan, are left uncoloured, since they can be discounted in this discussion. The Tourgai Terrane was part of peri-Baltica. The Karakum to Qiantang terranes in the south of the figure were parts of peri-Gondwana. **(b)**, simplified version of Domeier (2018, fig. 5). **(c)** From Şengor et al. (2018, fig. 5) with the terranes numbered (e.g. 13.2) as in their successive papers. Ba-Aq, Baidulet-Aqbastau belt; EZ, Erementau zone; KM, Kokchetav Massif; SE, Selety zone; SM, Shat Massif; ST, Stepnyak zone; U, Urumbai zone.

Fig. 5. Contrasting palaeogeographical maps of parts of Asia, eastern Europe, and sectors of Gondwana as previously published by **(a)** Şengor et al. (2018) with terrane numbers as in Fig 4c, **(b)** Domeier (2018), and **(c)** Popov and Cocks (2017). Af, Afghan terranes. For discussion see text.

Fig. 6. The distributions of the major Ordovician shallow-water brachiopod benthic faunal provinces in **(a)** Tremadocian (at about 480 Ma) and **(b)** Katian (at about 450 Ma) times. Mollweide projections. For discussion see text.

Fig. 7. New global equal-area palaeogeographical maps at selected times in the Ordovician and early Silurian showing the sites of both glacial deposits and the distribution of evaporites (including data sourced from Boucot et al., 2013; Torsvik and Cocks 2017). The evaporites were virtually all in latitudes below 30° both south and north of the Equator and indicate that that zone was largely dry. The Panthalassic Ocean covered most of the northern hemisphere. ATA, Armorican Terrane Assemblage of southern Europe; SP, South Pole.

Fig. 8. Middle Late Ordovician 450 Ma (Katian) palaeogeography, showing the ‘normal’ substantial bioherms of the Boda Event developed in subequatorial latitudes as well as evaporite deposits at 447.5 Ma and the cooler-water bryozoan-dominated bioherms in much higher latitudes. At 450 Ma, Avalonia was located at palaeolatitudes comparable to those of Baltica with subduction beneath Avalonia as recorded by Andean-type calc-alkaline magmatism in southern England (Torsvik and Rehnström, 2003). Explosive vents associated with that subduction were the source for gigantic Late Ordovician ash falls in Baltica (Kinnekulle Bentonite, KB). ATA, Armorican Terrane Assemblage; CA, Carolina Terrane; F, Florida; F-S, Franconia-Saxothuringia terranes; G, Ganderia Terrane; MB, Millbrig Bentonite; SP, South Pole.

Biographies

L. ROBIN M. COCKS



Scientific Associate in the Department of Earth Sciences at the Natural History Museum, London, UK, where he was formerly Keeper of Palaeontology. He has been President of the Geological Society of London, the Palaeontological Association, the Geologists' Association and the Palaeontographical Society. In 1995 he was awarded the Geological Society's Coke Medal, and in 2010 the Lapworth Medal, by the Paleaontological Association, its highest honour.

TROND H. TORSVIK



Professor of Geodynamics and Founding Director of the Centre for Earth Evolution and Dynamics (CEED), University of Oslo, Norway, and Honorary Professor at Wits University, Johannesburg. He is a Member of the Norwegian Academy of Sciences, a Fellow of the American Geophysical Union, and awarded the prestigious Arthur Holmes Medal (European Union of Geosciences) in 2016, among various other awards and prizes.

Table 1. Some parameters shown in Figure 3a-d.

AGE (Ma)	Scaled Palaeozoic Diversity ("China") [Fan <i>et al.</i> 2020]	Global Genera (articulate brachiopods) [Stigall <i>et al.</i> 2019]	Generic Biodiversity [Rasmussen <i>et al.</i> 2019]	Modelled atmospheric O ₂ (%) [Edwards <i>et al.</i> 2017]	Sea Surface Temperature (°C) [2 Myr bins calculated from Song <i>et al.</i> 2019]	Modelled atmospheric CO ₂ (ppm) [Royer <i>et al.</i> 2012] (recalculated here)	% Land within the Tropics (23.5°N/S) [calculated from plate model]	Scaled Arc "Activity" [adapted from Domeier <i>et al.</i> 2018, Torsvik <i>et al.</i> 2020]
485	0.30	37.98	702.31	12.0	43.9			
484	0.31	41.27	783.92	11.9	43.2			
483	0.34	44.52	874.17	11.9	42.6			
482	0.34	47.77	911.33	11.9	41.7			
481	0.36	51.06	901.98	12.1	41.0			
480	0.36	54.62	906.22	12.5	40.8	3171 (3591)	41	1.69
479	0.40	58.34	901.28	12.6	41.0			
478	0.44	61.81	857.42	12.7	38.7			
477	0.47	65.05	784.03	12.7	37.9			
476	0.47	68.22	741.90	12.7	40.0			
475	0.51	71.34	779.70	12.7	39.8			
474	0.55	74.25	819.58	12.7	39.8			
473	0.58	77.31	855.44	13.1	39.3			
472	0.61	80.63	849.80	12.9	35.8			
471	0.64	83.32	844.76	12.3	35.7			
470	0.63	85.39	811.55	11.4	37.1	2837 (2775)	45	1.48
469	0.72	88.06	791.60	11.0	37.3			
468	0.73	86.94	873.14	10.5	34.4			
467	0.78	85.66	1110.98	10.4	34.1			
466	0.75	98.30	1386.39	11.8	33.1			
465	0.74	108.60	1312.61	13.5	33.1			
464	0.72	117.98	1293.28	15.0	36.4			

463	0.78	125.99	1324.97	16.0	35.1			
462	0.76	134.30	1365.30	16.2	35.4			
461	0.77	143.64	1396.78	15.8	38.2			
460	0.74	164.14	1452.04	16.3	31.2	2435 (2281)	47	1.44
459	0.69	182.51	1528.22	17.2	31.2			
458	0.74	202.14	1608.31	18.6	31.8			
457	0.77	212.52	1665.23	20.5	33.1			
456	0.79	205.80	1689.13	22.0	33.3			
455	0.82	202.50	1727.83	22.4	32.1			
454	0.80	202.83	1774.58	21.8	26.5			
453	0.79	205.88	1807.09	23.0	28.2			
452	0.73	208.03	1858.38	24.6	28.1			
451	0.67	208.22	1843.92	24.6	27.8			
450	0.58	195.16	1644.93	24.1	28.9	2536 (2352)	46	1.42
449	0.61	181.04	1516.09	23.0	28.9			
448	0.54	199.26	1509.07	21.0	28.4			
447	0.57	213.24	1562.24	16.5	29.0			
446	0.54	216.89	1567.09	14.8	28.6			
445	0.43	118.54	1407.44	18.4	24.8			
444	0.43	139.06	1343.13	17.1	24.2			
443	0.45		1153.60	19.7	25.9			
442	0.51		1116.54	22.6	26.5			
441	0.55		1130.52	25.9	28.2			
440	0.58		1212.65	27.2	28.9	2600 (2246)	46	1.37
439	0.53		1280.99	27.8	29.8			

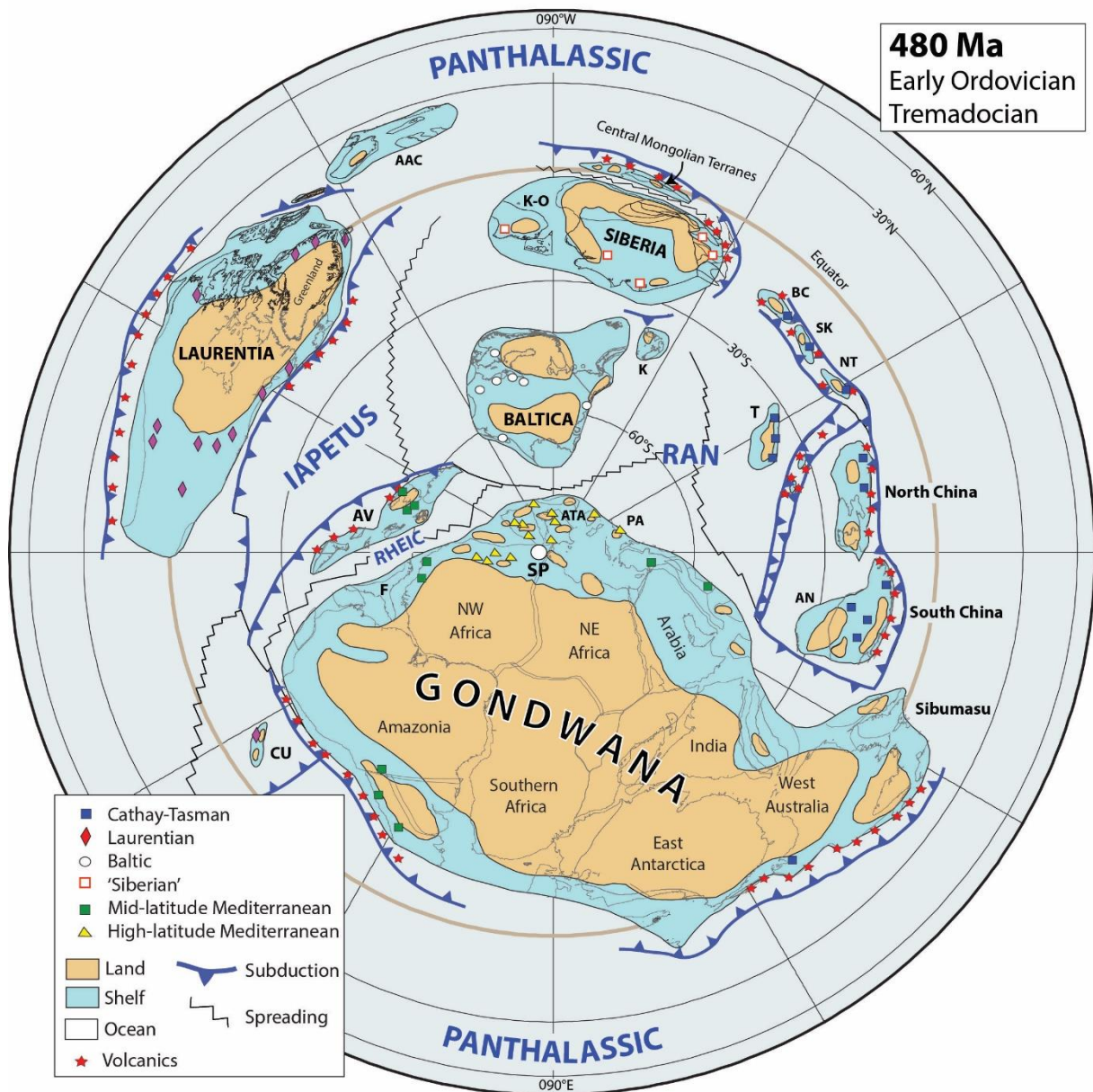


Figure 1 (Cocks & Torsvik)

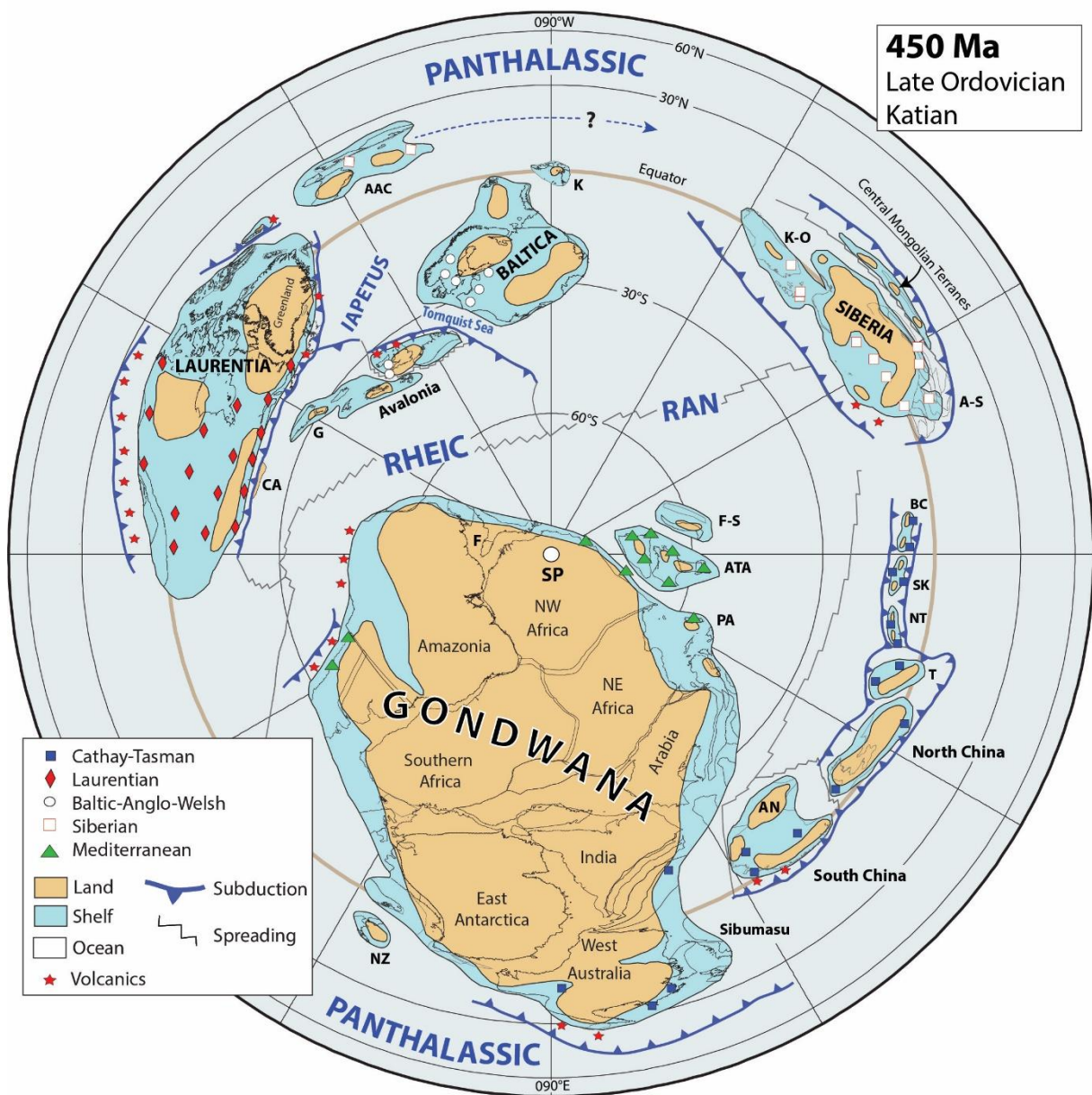
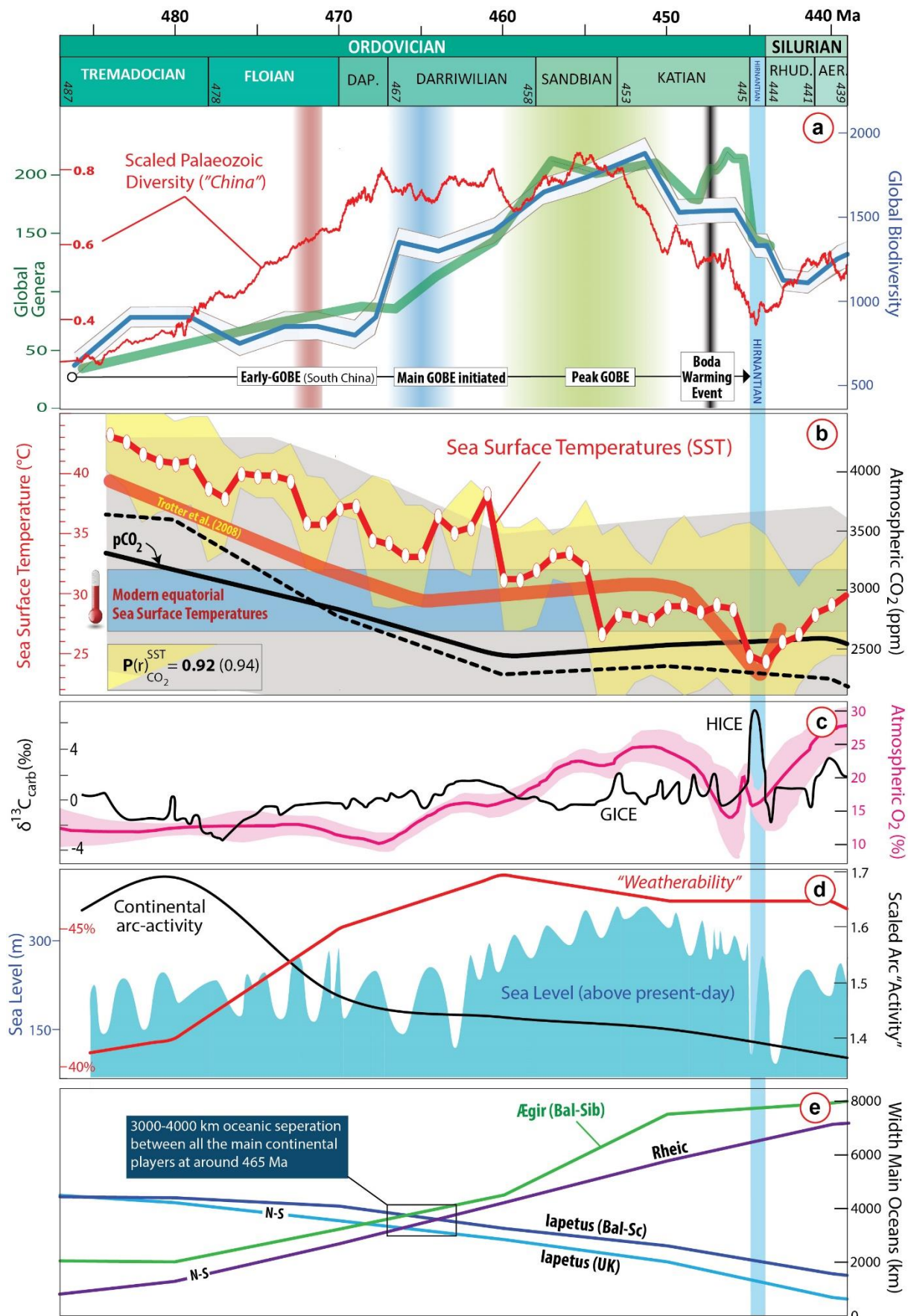


Figure 2 (Cocks & Torsvik)



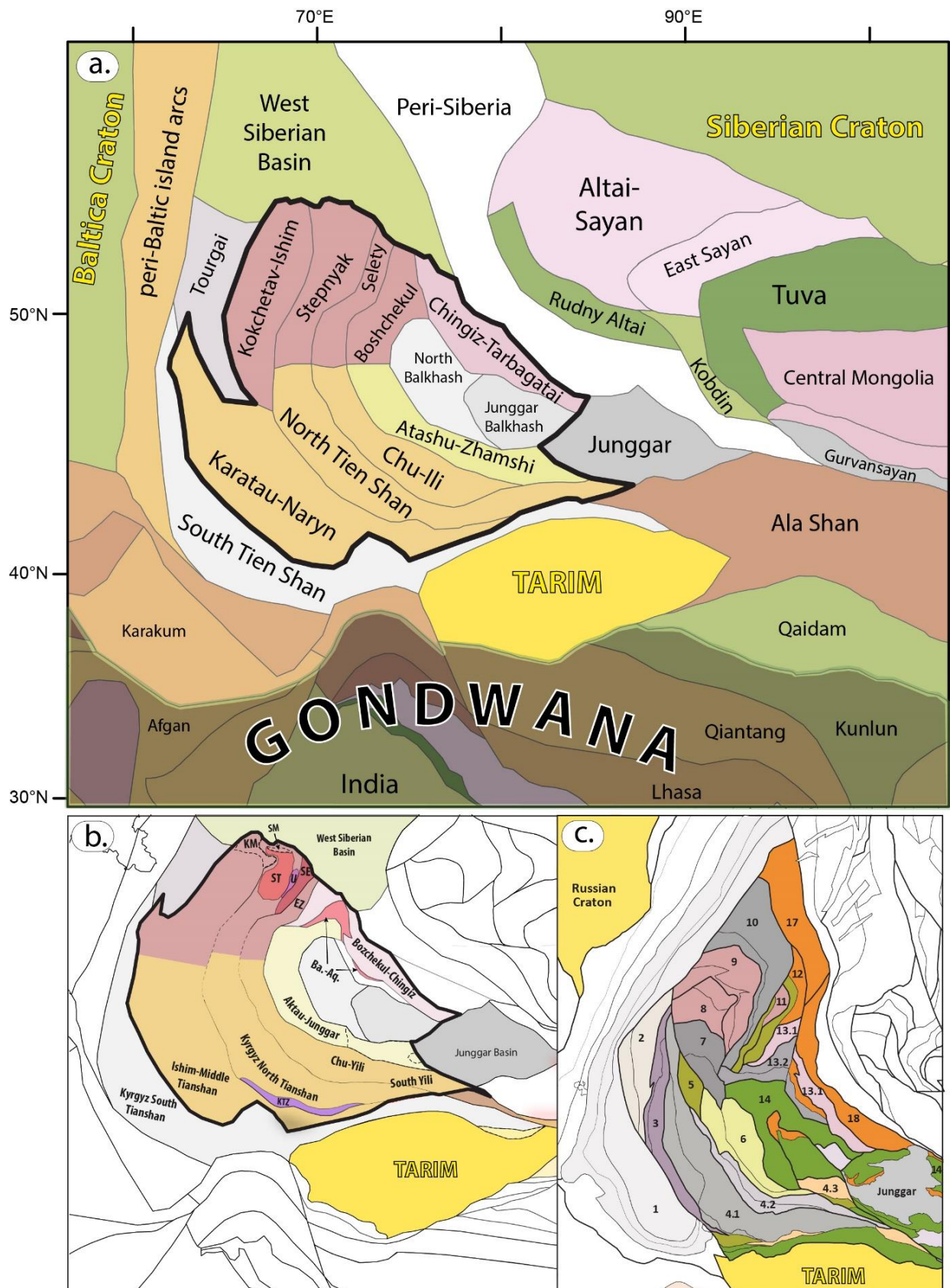


Figure 4 (Cocks & Torsvik)

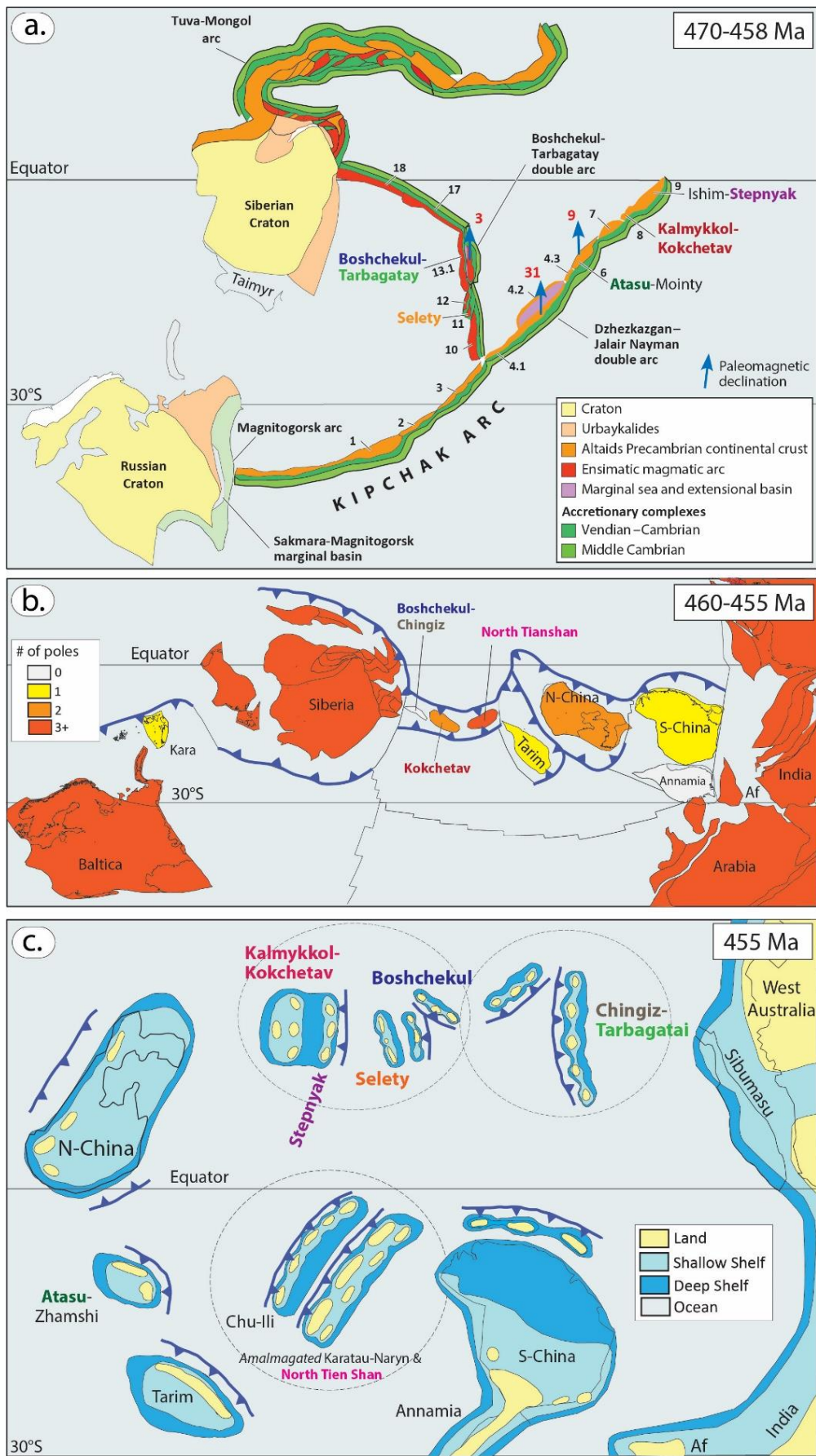


Figure 5 (Cocks & Torsvik)

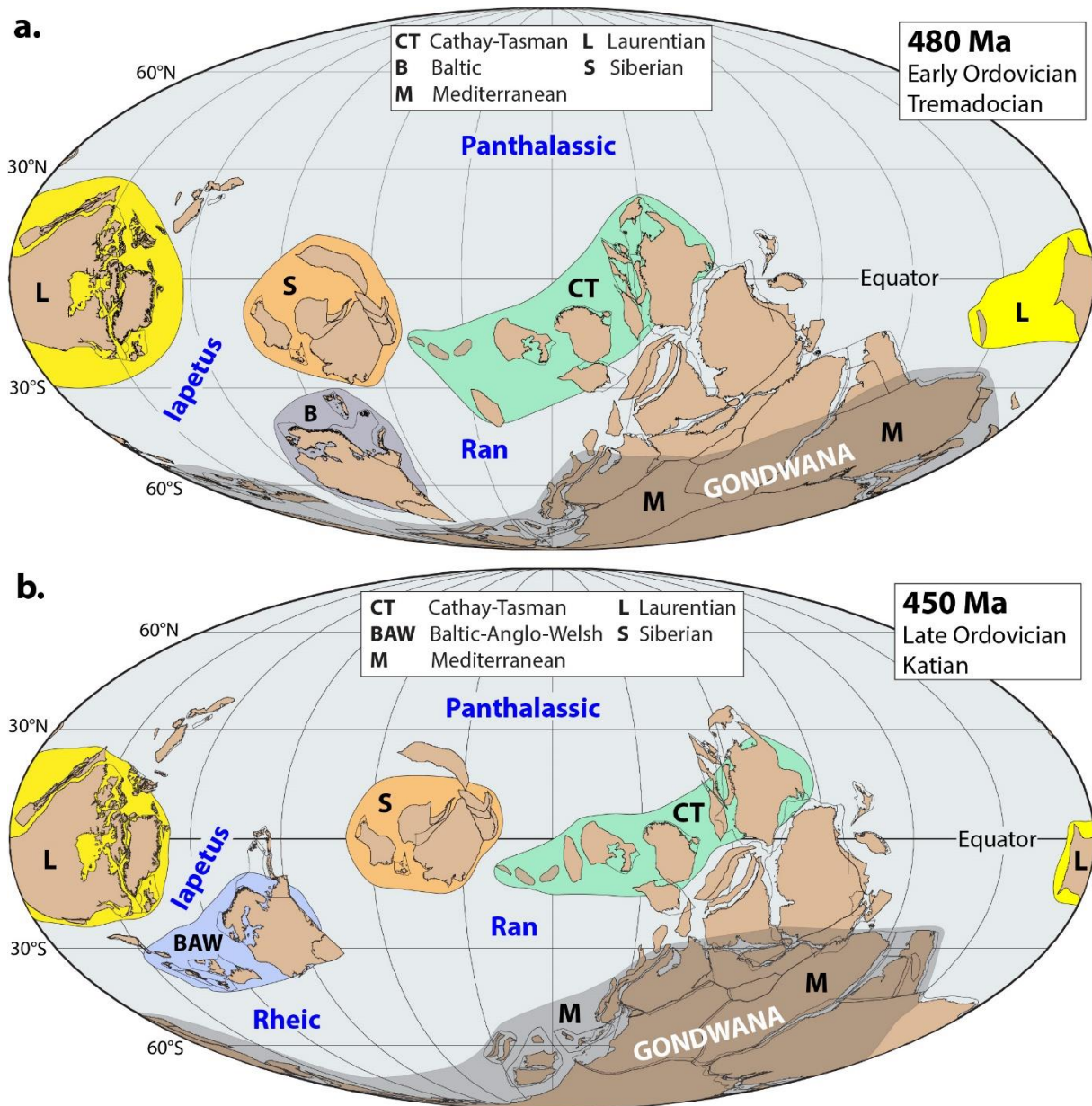


Figure 6 (Cocks & Torsvik)

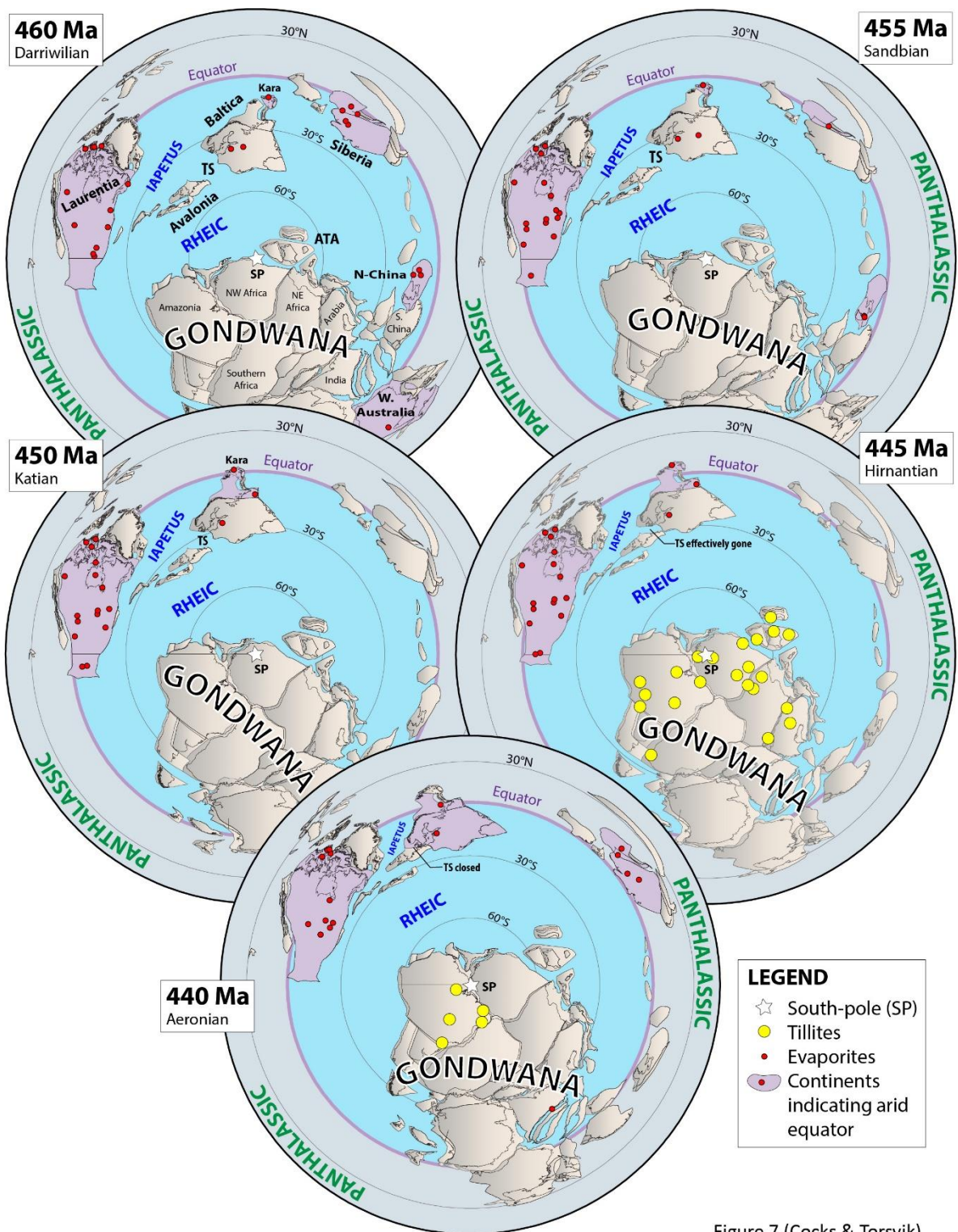


Figure 7 (Cocks & Torsvik)

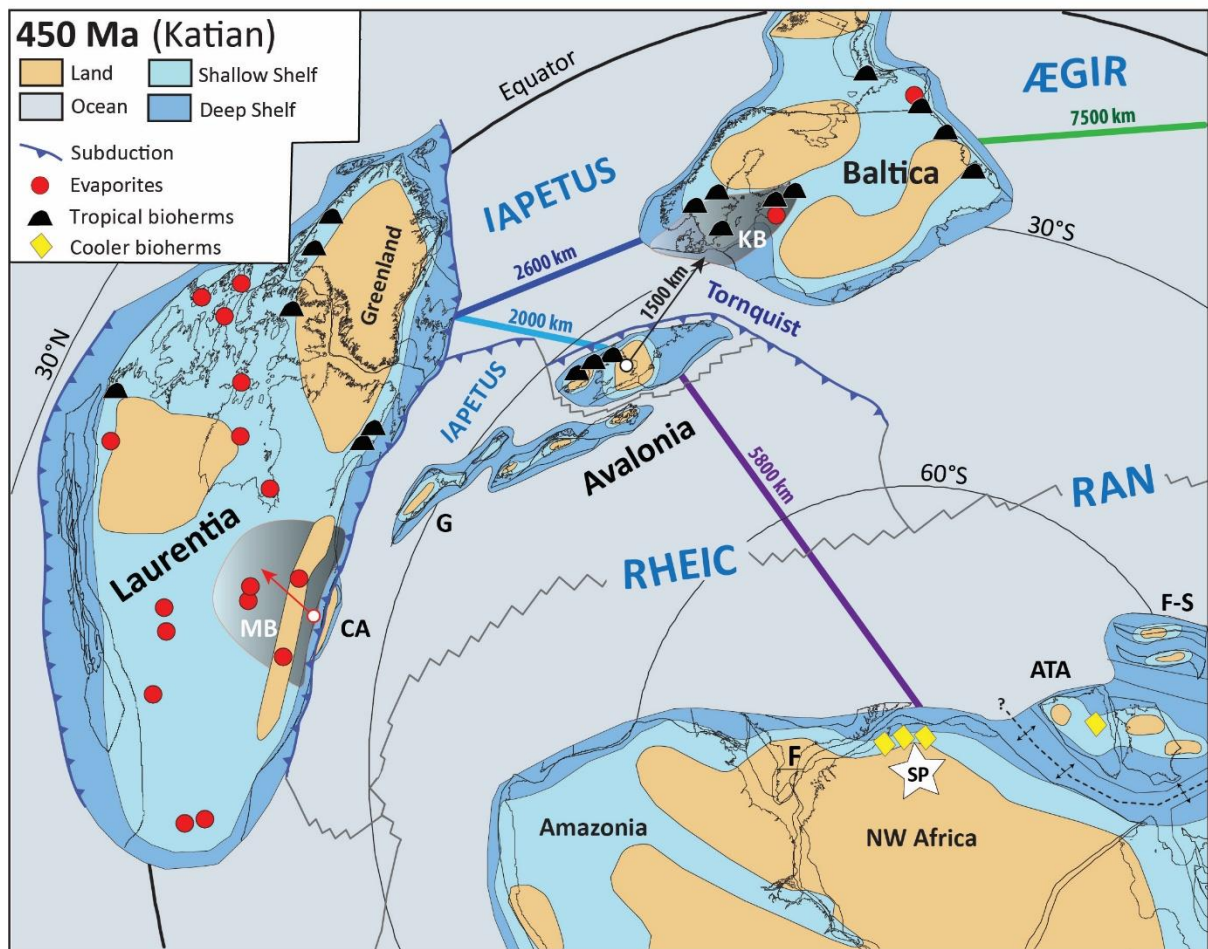


Figure 8 (Cocks & Torsvik)