

Chapter 24

Late Ordovician zooplankton maps and the climate of the Early Palaeozoic Icehouse

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Abstract: Chitinozoans and graptolites are the main components of preserved Ordovician zooplankton. As with much of the modern plankton, the 'first-order' species distributions of Ordovician plankton reflect water masses defined on the basis of sea surface temperatures. For 'time slices' of less than a few million years, zooplankton distribution patterns can be used to infer latitudinal sea surface temperature gradients, key palaeoceanographical boundaries and the position of Ordovician climate belts. Here, using two Late Ordovician time intervals – the early Sandbian and Hirnantian – we review how zooplankton distribution patterns identify Late Ordovician cooling and reflect the development of severe icehouse conditions.

Supplementary material: Additional information on methods and material is available at: <http://www.geolsoc.org.uk/SUP18670>

The spatial distribution of modern-day marine plankton is controlled by seawater temperature, salinity, food supply and light penetration. These factors, in turn, reflect the prevailing geography and climate, which control ocean circulation patterns and temperature distribution at the surface of the oceans. Understanding past sea surface temperature (SST) distribution is one of the most useful targets for reconstruction in palaeoceanography (Haywood *et al.* 2005). SSTs help decipher the past behaviour of ocean circulation and ocean heat transport and provide critical input and validation data for numerical climate reconstructions using General Circulation Models (GCMs) (Wefer *et al.* 2000; Haywood *et al.* 2005).

A 'best practice' example of how fossil plankton can be used to help reconstruct ancient climates is the 'Pliocene Research, Interpretation and Synoptic Mapping' (PRISM) palaeoenvironmental reconstruction program of the US Geological Survey. It consists of several generations and series of global-scale datasets of marine fossil distributions (foraminiferans, diatoms, etc.) and deduced climate proxy data (SST using transfer functions, modern analogue techniques, but also Mg/Ca ratios, etc.) that are in turn used to improve GCM reconstruction (Dowsett 2007; Dowsett *et al.* 2010). PRISM also includes extensive continental vegetation datasets that have enabled model–data comparisons (e.g. Salzmann *et al.* 2008).

The use of fossil plankton to reconstruct late Cenozoic palaeoclimates has the advantage of using species that are either still extant or are closely related to modern ones, even if ecological tolerances of these taxa most likely change with time. The challenge for Palaeozoic workers now is to try to reconstruct these ecological tolerances for their extinct fossil groups and species where there are no close descendants.

Ordovician zooplankton

Graptolites

Graptolites were an important part of the Ordovician to Early Devonian macro-zooplankton and various models using palaeo-depth, palaeolatitute and water mass-specific controls to explain species distribution have been developed (e.g. Cooper *et al.* 1991; Finney *et al.* 2007). Graptolites, in essence, resolve into three broad ecological groups based on their facies associations (see Cooper *et al.* 1991 and Cooper & Sadler 2010 for an overview and more details): (a) a group found in distal, deeper water, outer shelf to continental slope facies; (b) a low-diversity group confined to proximal, shallower water, mid to inner shelf deposits; and (c) a group that ranges across these settings, from the inner shelf into outer shelf to slope facies. These groups were distinguished on the basis of the benthic lithofacies in which the graptolites accumulated, and comprise a mix of assemblages within the overlying water column. Two hypotheses exist to explain these groupings: the first emphasizes depth stratification as the primary control on the species groupings ('biotopes'), which were indicative of discrete water masses at various depths (Cooper *et al.* 1991; Cooper 1998; Cooper & Sadler 2010, and references therein). In this model, the first group represents a deep-water biotope and the third one an epipelagic biotope (Fig. 24.1). Recent evidence in favour of such a scenario includes Cooper & Sadler's (2010) constrained optimization experiments that showed differences in mean species duration between species of their epipelagic and those of their deep-water groups: species of the deep-water group generally have much shorter

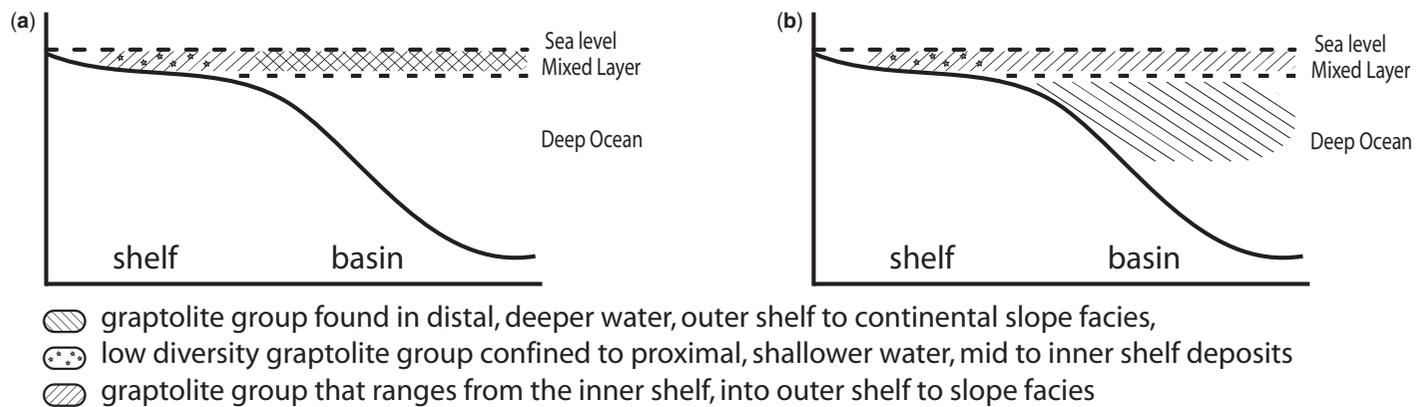


Fig. 24.1. Two hypotheses to explain graptolite facies associations: (a) onshore/offshore variation in species distribution (e.g. Finney & Berry 1997; Williams *et al.* 2003; Mitchell *et al.* 2008; Vandenbroucke *et al.* 2009); (b) depth-controlled species biotopes (e.g. Cooper *et al.* 1991).

biostratigraphical ranges than the ones from the epipelagic groups. According to Cooper & Sadler (2010), this difference in mean species duration between the groups reflects environmental differences, and implies that these groups could not have shared the same habitat (i.e. could not have lived at the same depth). The second hypothesis emphasizes horizontal on-shore/off-shore differentiation as the main control on the graptolite environmental groupings (e.g. Finney 1984, 1986; Finney & Berry 1997; Williams *et al.* 2003; Mitchell *et al.* 2008), and suggests that groups (a)–(c) inhabited water masses at largely the same depth, but at different areas on a shelf to basin transect (Fig. 24.1). Finney & Berry (1997), for example, identified ‘margin dwellers’ (in contrast to the ‘deep-water’ group) and cratonic invaders (in contrast to the epipelagic group).

Cooper *et al.* (1991) also showed that graptolites had broad ‘provincial’ distributions, identifying a low-latitude Pacific and a high-latitude Atlantic province for the ‘Arenig’ (also see Skevington 1974). Vandenbroucke *et al.* (2009) developed this idea, and in a review of global species distribution for the early Sandbian showed that SST was the primary ecological control on graptolite distributions. Early Sandbian graptolite species could be grouped into planktonic provinces (in their paper called biotopes) that reflected climate belts. Vandenbroucke *et al.* (2009) noted that, within the ocean mixed layer, apparently deeper and shallow-water species (of groups (a) and (c)) displayed a similar degree of latitudinal differentiation, implying that any depth stratification was within the ocean mixed layer (i.e. above the thermocline) and was controlled by primary ecological factors other than temperature. Difference in depth between these two groups seems to have been small, if present at all.

Chitinozoans

Chitinozoans are very useful in Ordovician to Devonian biostratigraphy and inter-basin correlations; a relatively high-resolution record of their occurrences has been established in many parts of the world (see references in Paris 1996; Paris *et al.* 1999). However, and in comparison with other fossil groups, they still are much less frequently used for palaeoenvironmental studies and reconstructions, and the ecology of the group is much less well understood than their temporal distribution.

The chitinozoan organic-walled microfossil egg cases and/or their enigmatic metazoan parent organisms were part of the epipelagic zooplankton. As with the graptolites, Late Ordovician species distributions were parallel to palaeolatitude and SST has been hypothesized as the primary ecological factor controlling their distribution, subsequently potentially modified by palaeocurrents (Paris *et al.* 1999; Vandenbroucke

et al. 2010a, b). The main evidence for this interpretation is summarized here:

- (1) The distribution of chitinozoan species is largely facies-independent. This was recently quantified by Vandenbroucke *et al.* (2010a) for an early Sandbian time slice. Data from this interval show that chitinozoan species occur in shelf to off-shelf deposits and that the majority of species occur in both shelf and off-shelf settings. This indicates that the chitinozoan animal lived within the shallow ‘mixed layer’ of the ocean, independent of any seafloor facies control.
- (2) Chitinozoans occur in widespread anoxic deposits, such as the early Silurian black graptolitic ‘hot’ shales of northern Gondwana and the widespread Ordovician–Silurian anoxic facies in Scotland and Wales. Fossil groups occurring in these deposits must have lived high in the water column, and must have had an epipelagic/nektonic mode of life, considering the lethal anoxic seafloor conditions over large areas.
- (3) Chitinozoans occupy a series of latitudinally discrete biotopes, reflecting the latitudinal equator-to-pole temperature gradient and the distribution of climate belts. Chitinozoans must therefore have lived in the topmost ‘mixed layer’ of the oceans as, below the thermocline, at the base of this layer, there is little latitudinal variation in seawater temperature.

The Ordovician was a period of increasing continental dispersion (Cocks & Torsvik 2002). Historically, chitinozoan research has been focused on North America (Laurentia), NE Europe (the circum-Iapetus palaeocontinents of Baltica and Avalonia) and North Africa and the Middle East (Gondwana). Each had an at times endemic chitinozoan fauna that is reflected in the development of separate biozonal schemes for each palaeocontinent (Paris *et al.* 1999). As chitinozoans were epipelagic and each of these palaeocontinental areas was located at different palaeolatitudes, it is likely that these chitinozoan ‘provinces’ largely reflect SST and palaeoclimate belts. In contrast, the Ordovician continental dispersion also reflected increasing endemism of the shelf benthos (see elsewhere in this volume). A number of geographical provinces of benthic organisms living on the shelves of the individual continents provide a good palaeogeographical tool for continent identification. It is important not to confuse the meaning of, and main control on, benthic (palaeocontinent) and planktonic (SST) provinces, as each has its value for better understanding of the Ordovician world.

Here we demonstrate how Late Ordovician chitinozoan and graptolite zooplankton distribution patterns can be used to develop and evaluate Ordovician climate models. We use the new ‘BugPlates’ (used throughout this volume; Torsvik & Cocks 2009; Figs 24.2 & 24.3) palaeogeographical reconstruction for



Fig. 24.2. Early Sandbian chitinozoan localities on the 'BugPlates' palaeogeographical reconstruction. The 'BugPlates' reconstruction gives no position for the Argentine Precordillera. The Argentine localities used by Vandenbroucke *et al.* (2010a) have here been excluded from the plots.

our zooplankton distribution patterns, and evaluate how these influence previous reconstructions of Ordovician plankton distribution.

The 'BugPlates' palaeogeographical reconstruction

'BugPlates' is a modified version of a GIS-orientated palaeogeographical reconstruction software package, which interfaces with fossil databases and which has been developed at the Centre for Geodynamics at the Geological Survey of Norway (Torsvik & Cocks 2009). Reconstructions are based on palaeomagnetic and (predominantly benthonic) palaeobiogeographical data. The base maps used in the reconstructions are updated versions of those published by Cocks & Torsvik (2002, 2004). The advantages of using 'BugPlates' are (a) that these are the most recently revised maps available for the Ordovician, (b) that the data they are based on are available as case studies (Cocks & Torsvik 2005, 2007) and (c) that it is in a user-friendly, digital format.

Vandenbroucke *et al.* (2009, 2010a) compiled graptolite and chitinozoan presence/absence data for an early Sandbian time slice, which is equivalent to the entire temporal range of the graptolite *Nemagraptus gracilis* (see Vandenbroucke *et al.* 2009, for further discussion), and not to the *gracilis* graptolite Biozone as variously defined in different palaeogeographical regions (see Williams *et al.* 2004 for a fuller explanation). The Sandbian data compilation of Vandenbroucke *et al.* (2009, 2010a) predates the publication of the 'BugPlates' palaeogeography and their data was plotted using the PALEOMAP reconstruction. The Sandbian data are here replotted using 'BugPlates'. Vandenbroucke *et al.* (2010b) compiled chitinozoan presence/absence data for the glacial Hirnantian (equivalent to the *extraordinarius* and lower *persculptus* graptolite biozones) from localities largely within the circum-Iapetus region. These Hirnantian distribution data have been published using the new 'BugPlates' reconstruction and can therefore be considered in our analysis here without replotting.

Differences in the latitudinal position of our Sandbian localities inferred from the 'BugPlates' and the earlier PALEOMAP

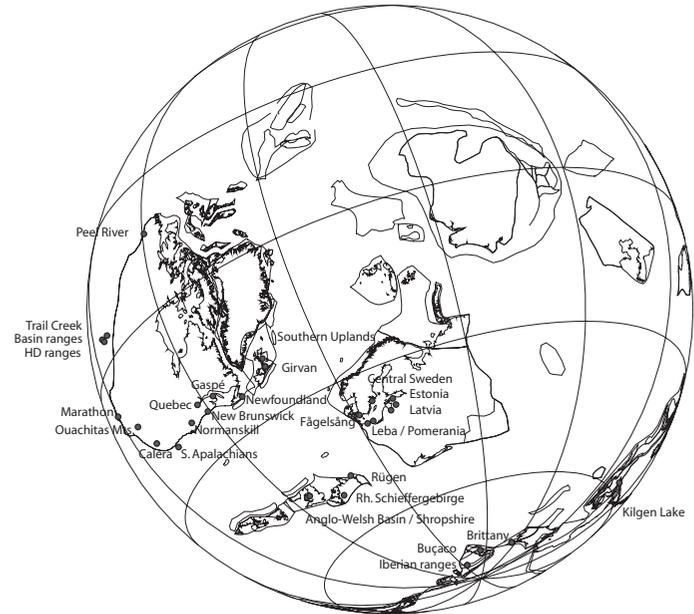


Fig. 24.3. Early Sandbian graptolite localities on the 'BugPlates' palaeogeographical reconstruction. Localities not shown on the map are Australasia, Chaqimayo in Peru and Atocha in Bolivia. The 'BugPlates' reconstruction gives no position for the Argentine Precordillera; the Argentine localities used by Vandenbroucke *et al.* (2009) have here been excluded from the plots.

palaeogeographical reconstructions are shown in supplementary material: the differences are usually within our defined 5° bin of palaeolatitudinal error, with the exception of three site-clusters where the palaeogeographical error is systematically larger. Of these three areas, the large uncertainty on Avalonian localities causes most problems and these sites will not be used to pinpoint the positions of important climate boundaries in this study.

We re-plot the groups of species obtained by multivariate analyses by Vandenbroucke *et al.* (2009, 2010a) and called biotopes, on the new 'BugPlates' palaeogeographical reconstructions. The individual species are not shown, although the full species lists are given in the supplementary material and the relatively small differences between the published biotopes (Vandenbroucke *et al.* 2009, 2010a) on the one hand and the biotopes in Figures S1 and S2 on the other, are listed in Table S2. The full data matrices are uploaded as supplementary Figures S3 and S4.

The general pattern of Sandbian biotope distribution is little affected by the use of the 'BugPlates' palaeogeographical base-maps, compared with previously published distributions using PALEOMAP (Vandenbroucke *et al.* 2009, 2010a). The biotopes (e.g. C1–C7) group into 'bioprovinces', which appear comparable to modern plankton foraminiferan provinces and, following comparison with various numerical climate models, are used to define Sandbian climate belts (exactly how this is done is discussed in full in the supplementary material). This produces a robust pattern for all available biogeographical reconstructions for the early Sandbian.

Late Ordovician zooplankton provinces

Definitions of Sandbian zooplankton provinces

We define the Sandbian chitinozoan and graptolite zooplankton biotopes as follows (and based on the 'BugPlates' reconstruction):

- a Tropical province from c. 0 to 20° latitude (graptolite biotopes C1, C2, D1–D3);

- a Sub-tropical province from *c.* 20 to 35° latitude (including chitinozoan biotope I and graptolite biotopes C3, C4, D4 and D5);
- a narrow Transition province at *c.* 35° latitude (graptolite biotope C5);
- a Sub-polar province from *c.* 35° latitude to 55–70° latitude (chitinozoan biotopes IIa, IVb and III, graptolite biotopes C6, A);
- a Polar province from 55–75° latitude to the poles (chitinozoan biotopes IIb and III, graptolite biotope A).

In our previous papers, we chose to use ‘biotope’ rather than ‘province’ as the latter has a benthic connotation in Ordovician studies, which is linked with palaeogeographically–palaeocontinentally controlled benthic faunal units. However, we now opt to formalize usage and define planktonic ‘provinces’, following the practice used for modern planktonic foraminiferans (Kucera 2007). The spatial distribution of these provinces is summarized in Figure 24.4.

Sandbian palaeoceanographical boundaries

Diverse graptolite assemblages thrived at low latitudes, in warmer (sub)tropical waters. Chitinozoans, in contrast, seemed to have

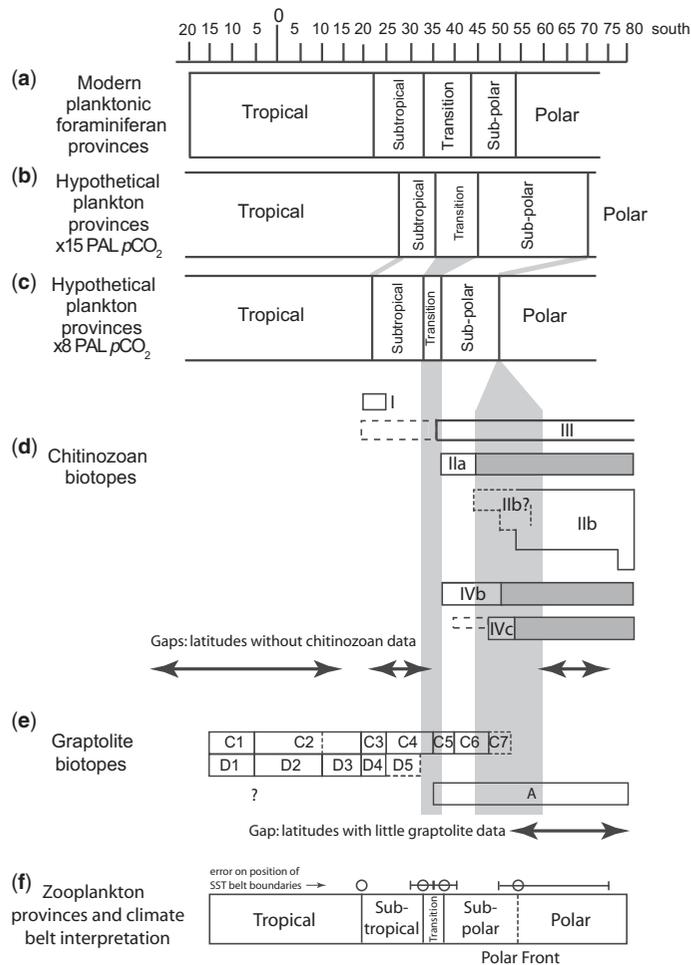


Fig. 24.4. (a) Modern-day planktonic foraminiferan provinces: boundaries in terms of SST defined by Kucera (2007); the mapped latitudinal positions of the SSTs are those in the central Pacific Ocean (www.noaa.gov; Locarnini *et al.* 2006). (b, c) Hypothetical position of plankton provinces for the Sandbian are based on the hypothetical distribution of modern foraminiferan provinces, using SST data derived from the Sandbian GCM of Herrmann *et al.* (2004a) at $\times 8$ and $\times 15$ PAL $p\text{CO}_2$. (d) Chitinozoan biotope distributions; species with the narrowest ranges define the plotted latitudinal width of the biotopes. (e) The graptolite biotope distributions. (f) Climate belt interpretation combining all information. Figure after Vandenbroucke *et al.* (2009, 2010a).

preferentially diversified in the relatively colder surface waters at intermediate to high latitudes (Vandenbroucke *et al.* 2009, 2010a; Fig. 24.4). The oceanographic boundary known as the Sub-tropical convergence, that divides essentially warm tropical water from cold polar water and marks the edge of the (sub)tropics in the modern ocean, lies at *c.* 35°S in our new reconstruction (Vandenbroucke *et al.* 2009, 2010a). Equator-wards of this boundary, there are several latitudinally distinct biotopes within the Tropical (see supplementary material: graptolite biotopes C1, C2, D1–D3) and Sub-tropical (C3, C4, D4 and D5) regions. These are non-symmetrically distributed around the Equator and may reflect regional patterns of productivity or surface currents.

The fossils also map the Sandbian austral Polar Front, that is, the northernmost extension of the Polar waters, between 55 and 75°S. The range of positions is due to a combination of palaeogeographical errors (*c.* 10°) and potential multiple indicators for this oceanographic boundary. We speculate that these apparent multiple indicators of the Polar Front during the early Sandbian demonstrated by our dataset (see Fig. 24.4) could be due to temporal variation in the position of this important oceanographic boundary during the *gracilis* time slice, as this spans at least 3 myr.

Not all the species have a narrow latitudinal range, and only the ones that do have been used to define the biotopes and provinces. To the south of the Sub-tropical convergence (Transition zone/province), some graptolite species (defined as ‘wide’ on Fig. S1) had geographical ranges across the Sub-polar and Polar provinces. We have speculated earlier that these could reflect mixing and/or re-distribution by the Southern Gondwanan Current (see also Herrmann *et al.* 2004a; Poussart *et al.* 1999; Wilde 1991). The same ocean surface current system could also be responsible for the redistribution of the wider-ranging elements in the Sub-polar chitinozoan biotopes.

Definitions of Hirnantian zooplankton provinces

Hirnantian chitinozoan provinces (Fig. 24.4) have already been formally defined (Vandenbroucke *et al.* 2010b) as Tropical (0 to 5–20°); Sub-tropical (5–20 to 25°S); Transition (25–30°); Sub-polar (30–40°S) and Polar (40° to the poles). The error bars on the boundaries are based on comparison of palaeogeographical reconstructions.

Late Ordovician climate

Climate proxy data derived from stable isotope analyses of biogenic materials remain controversial (e.g. see contrasting views in Shields *et al.* 2003; Trotter *et al.* 2008) and depend on assumptions about primary ocean chemistry. The value of GCMs (Herrmann *et al.* 2004a, b) for reconstructing Late Ordovician palaeoclimate is limited by our incomplete knowledge of prevailing boundary conditions for this interval, but the use of zooplankton distribution data can help constrain GCM outputs (Vandenbroucke *et al.* 2009, 2010a, b).

Graptolite and chitinozoan surface water biotopes are latitudinally strongly differentiated through the Southern Hemisphere during the Late Ordovician. The faunal equator-to-pole gradient expressed in the combined graptolite and chitinozoan data is much steeper than would be expected for a greenhouse climate. As an analogue, the present-day global distribution of planktonic foraminiferans, representative of an icehouse world, is characterized by nine SST-controlled provinces, while in the greenhouse world of the Late Albian there are only five provinces (Hart 2007, and references therein).

The steeper early Sandbian faunal gradient is comparable to that found at present, and probably suggests a comparable SST

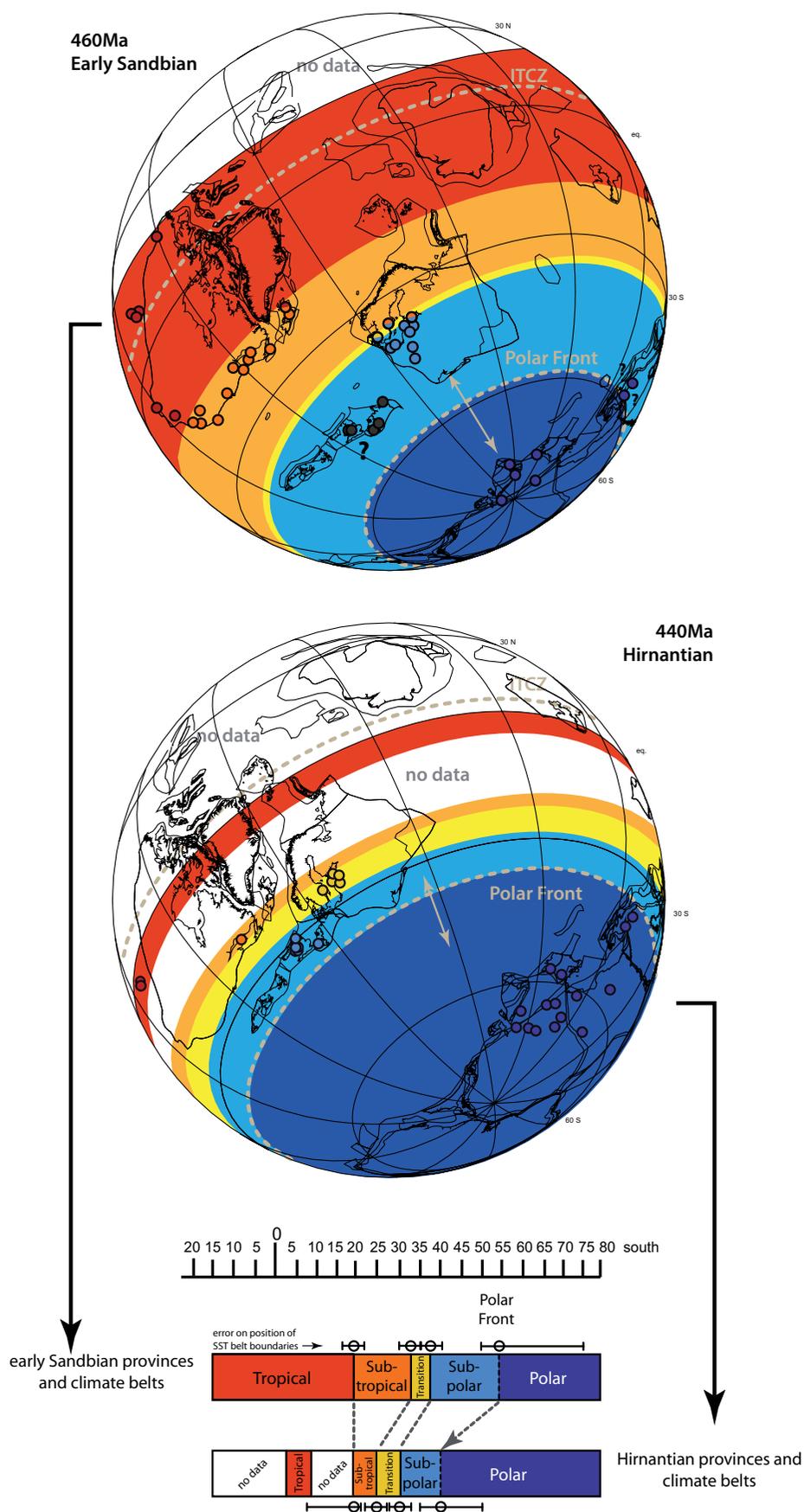


Fig. 24.5. Compilation globes and maps showing the inferred Sandbian climate belts from Figure 24.4, compared with the Hirnantian climate belts as inferred from chitinozoan distribution data by Vandenbroucke *et al.* (2010b). Coloured circles are localities and their climate belt interpretation: for information on localities, see Figures 24.2 and 24.3; double coloured localities represent ‘conflicting’ interpretations by graptolites and chitinozoans (note that these are in the transition zone). Grey circles are early Sandbian Avalonian localities: owing to large variance in the position of Avalonia between palaeogeographical reconstructions for the early Sandbian, these are not used to map climate boundaries. Intertropical Convergence Zone (ITCZ) position from Armstrong *et al.* (2009).

gradient. If this interpretation is correct, then the faunal data indicate that a ‘modern-type’ climate and cooling towards the Hirnantian glacial maximum was already underway by the early Sandbian (see also Trotter *et al.* 2008; Vandenbroucke *et al.*

2009, 2010a). This is a hypothesis that contrasts markedly with other interpretations of the ‘background’ climate mode during the Ordovician, historically regarded as a ‘Cretaceous-style greenhouse’.

The distribution of graptolite and chitinozoan provinces during the Sandbian best fits the SST simulation from the GCM model (Herrmann *et al.* 2004a), constrained at a $p\text{CO}_2$ of eight times the Pre-industrial Atmospheric Level ($8 \times \text{PAL} \approx 2240$ ppm) and returning a mean global surface temperature of 15.7°C . These values compare relatively well with more advanced Middle Ordovician GCM model runs using the GEOCLIM model (Nardin *et al.* 2011).

As the climate further cooled towards the Hirnantian glacial maximum, the chitinozoan provinces indicate a steeper latitudinal temperature gradient than in the Sandbian, the Sub-tropical Convergence at $25\text{--}30^\circ\text{S}$ and the austral Polar Front at $c. 40^\circ\text{S}$. In this reconstruction the Polar belt had expanded, while the Sub-tropical belt may have slightly narrowed (but note our 5° error bars) and the sub-polar belt had contracted radically (Fig. 24.5). Vandenbroucke *et al.* (2010b) hypothesized this loss of ecospace as a possible cause of extinction within the Sub-polar province. The equator-ward migration of the Polar Front to $c. 40^\circ$ latitude during the Hirnantian is identical to that reported for the (boreal) Polar Front during late Cenozoic glaciations (McIntyre *et al.* 1972; Eynaud *et al.* 2009), and suggests a similar fall in mean global temperature of between 3 and 5°C . This would equate to a fall in $p\text{CO}_2$ from $c. 8 \times \text{PAL}$ to $c. 5 \times \text{PAL}$ during the Hirnantian glaciation (Petit *et al.* 1999; Vandenbroucke *et al.* 2010b).

Conclusions

The primary control on Ordovician graptolite and chitinozoan species distribution was SST (depth probably was not a primary factor). Biogeographical province boundaries for both of these groups reflect latitudinally restricted climate belts, and can therefore be used to define the position of climate-sensitive palaeoceanographical boundaries and their movement through time. In this review, early Late Ordovician zooplankton distribution patterns (Vandenbroucke *et al.* 2009, 2010a) have been re-evaluated using 'BugPlates'. During the Sandbian the Earth had a 'cool world' climate (*sensu* Royer 2006) similar to that of the present day, supporting the hypothesis that global cooling had started during the Mid Ordovician or earlier. During the Hirnantian glacial maximum, the distribution of the Sub-tropical Convergence and Polar front indicates a climate not dissimilar to that during late Cenozoic glaciations. The distribution of graptolite and chitinozoan provinces during the Late Ordovician indicates that the zooplankton responded in a very similar way to modern planktonic groups. The reconstruction of climate–ocean–biosphere interactions during the Palaeozoic is entirely possible.

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