Polar front shift and atmospheric CO_2 during the glacial maximum of the Early Paleozoic Icehouse

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Author Contributions

TVDB, HAA and MW contributed equally: they designed the project together with JAZ, conceived the concept, interpreted the data and wrote the paper. TVDB assembled the data. FP, JN and TJC provided chitinozoan distribution data. KS established the biostatistical protocol and performed the analysis. JV and TS supervised the project. All authors discussed the results and implications and commented on the manuscript.

Competing Financial Interests statement

The authors declare no competing (financial) interests.

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Supplementary information accompanies this paper:

- Materials and Methods
- Results
- Literature sources for Late Ordovician pCO_2 estimates
- Figs. S1, S2, S3, S4.

Our new data address the paradox of Late Ordovician glaciation under supposedly high *p*CO_2 (8 to 22x PAL: Pre-industrial Atmospheric Level). The paleobiogeographical distribution of chitinozoan ("mixed layer") marine zooplankton biotopes for the Hirnantian glacial maximum (440Ma) are reconstructed and compared to those from the Sandbian (460Ma): they demonstrate a steeper latitudinal temperature gradient, and an equator-wards shift of the Polar Front through time from 55-70°S to ~40°S. These changes are comparable to those during Pleistocene interglacial-glacial cycles. In comparison with the Pleistocene, we hypothesize a significant decline in mean global temperature from the Sandbian to Hirnantian, proportional with a fall in *p*CO_2 from a modeled Sandbian level of ~8x PAL to ~5x PAL during the Hirnantian. Our data suggest that a compression of mid-latitudinal biotopes and ecospace in response to the developing glaciation was a likely cause of the end-Ordovician mass extinction.

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Introduction

The Hirnantian glaciation (~440 Ma) was a discrete event of a few hundred thousand years (1) during the longer Early Paleozoic Ice Age (2). A Laurentide-scale continental ice sheet was located in the Southern Hemisphere despite previous *p*CO_2 estimates ranging from 8 to 22x PAL (Pre-industrial Atmospheric Level; 3-6; for a full review, see supporting online text). The Hirnantian glaciation is linked to one of the major mass-extinctions in the Phanerozoic (7). New causal hypotheses for the Hirnantian glaciation (2; 8) draw on a comparison with Pleistocene glacial maxima, driven by orbitally-forced ice margin feedback mechanisms (9; 10), and set against a background of long term *p*CO_2 decline (11). Glaciations during the late Pleistocene resulted in a steepening of the latitudinal temperature gradient and a shift in the position of the Polar Front from ~60° to ~40°N (12, 13). It is therefore predicted that as the Hirnantian ice sheet grew and the intensity of the South Polar high pressure zone increased, there would be an equatorward shift in the location of the Polar Front and adjacent climate belts (14).

Stable oxygen isotope data from conodonts suggest equatorial temperatures approached modern values from the Middle Ordovician (15; see ref. 16 for an alternative explanation) a view supported by our previous work on plankton distribution (17, 18). Proxy paleoclimate maps reconstructed for the Sandbian (~460 Ma), marine zooplankton (graptolite and chitinozoan) biotopes, and General Circulation Models (GCMs), show tropical sea surface temperatures (SSTs) and austral latitudinal temperature gradients were similar to present, and the Polar Front lay between 55° to 70°S (5, 6, 17, 18; Fig. 1). These maps support GCMs in which Sandbian pCO_2 was set at 8x PAL (5). A GCM experiment parameterized with the same pCO_2 value, high relative sea level and a modern equator-to-pole heat transport (6) returns a mean global surface temperature prediction of 15.7°C for the Sandbian. Energy Balance Models (19) suggest that the elevated pCO_2 levels of 8x PAL could have been balanced, to a large degree, by reduced solar flux from a “faint young Sun” (20) to produce mean global surface temperatures that approach the modern. All this is consistent with the early Late Ordovician (Sandbian) being a ‘cool’ world *sensu* Royer (21).

SST maps derived from a Hirnantian GCM (assuming pCO_2 of 8xPAL, and a low relative sea level) indicate a steepening of the temperature gradient relative to the Sandbian (5; Figure 1). However, key uncertainties remain relating to the parameterization of Ordovician GCMs (17, 18) and these have never been independently tested. Here we present an entirely new compilation of the distribution of chitinozoan zooplankton biotopes during the Hirnantian, that we use to reconstruct a proxy SST-map and hence to map the position of critical climate boundaries as the Earth moved into the glacial maximum of the Early Paleozoic Icehouse. We use this new information to evaluate the validity of Hirnantian GCMs and estimates of Hirnantian global surface temperatures and for qualitative assessments of pCO_2.

Our primary analysis is the same as used in our previous studies (17, 18) but here is based upon an entirely new compilation of published chitinozoan species presence/absence data for the glacial Hirnantian (Supplementary Figure S1). Suitable collections for this interval are largely restricted to continents that fringed the southern part of the Early Paleozoic Iapetus Ocean, within the southern hemisphere (Figure 2).

Results: Hirnantian chitinozoan biotope distribution

Figure 3 shows the distribution of chitinozoan biotopes and the inferred climate belts during the Hirnantian. The boundary between the Tropical and Sub-tropical chitinozoan biotopes lies between 5° and 20°S; the southern edge of the Sub-tropics is at 25°S and the northern edge of the Sub-polar biotope is at 30°S. The Transitional biotope lies between 25° and 30°S. The Polar Front, i.e. the northernmost extent of the South Polar fauna, lies between ca. 35°S and 40°S.

Comparing the distribution of equivalent chitinozoan biotopes in the Sandbian and the Hirnantian reconstructions, these key findings are reported:

(i) An expansion of the Polar Biotope and equator-wards shift of the Polar Front from 55°-70°S to ~40°S. This shift has the consequence of narrowing the Sub-Polar biotope and inferred climate belt (Figure 4).

(ii) Within the error of our analysis there is a minimal change in the width of the Tropical and Sub-tropical climate belts.

(iii) Species richness within biotopes appears to correlate with latitudinal extent. The narrower Hirnantian Sub-polar biotope has reduced species richness (nine species compared to 35 species in the Sandbian, see ref. 18), whilst the more extensive Hirnantian Polar biotope has an increased species richness of 19 species compared to the four species identified with certainty in Sandbian Polar faunas (18).

(iv) Hirnantian chitinozoan biotope distribution indicates a steeper latitudinal temperature gradient than would be predicted from equivalent hypothetical plankton provinces derived from the GCM with the lowest pCO_2 estimates (Fig. 3c, e).

Discussion: implications for Late Ordovician global temperature and pCO_2 levels

There is an ongoing debate as to how Hirnantian continental scale ice sheets could exist at high pCO_2 levels of 8 to 22x PAL (3-6; see supporting online text). Herrmann et al. (22) identified this issue and addressed it using coupled ice-sheet and atmospheric GCM modeling, but concluded that initiation of glaciation was possible at the lower end of these estimates. The lack of well-dated Late Ordovician direct pCO_2 proxies (21) hampers a critical evaluation of these modeled values. Furthermore, this paradox between climate state and assumed pCO_2 concentrations is exacerbated by recent studies that conclude that Earth's climate, in the Paleozoic and Pliocene, was more sensitive to atmospheric CO_2 than previously thought (23, 24).

Our results (point iv above) show a variance between our zooplankton maps and the hypothetical distributions of plankton provinces predicted by the SSTs derived from the GCM. This variation is less for the climate model with the lowest pCO_2 of 8x PAL and implies a re-parameterization of the GCM is necessary, e.g. by using other pCO_2 levels. Here we provide a qualitative assessment of what Hirnantian pCO_2 may have been.

Our Late Ordovician zooplankton biotope map and climate belt reconstruction shows a similar response of the Earth's climate-ocean system during the Hirnantian Glacial Maximum to that reported for Pleistocene glacials. As the Hirnantian ice sheet grew, the latitudinal temperature gradient steepened and the austral Polar Front shifted to ~40°S. The scale of shift in position of the Polar Front matches that documented during Pleistocene glacial maxima and associated Heinrich Events (12, 13), and is consistent with independent studies that show a coeval northward shift in the Intertropical Convergence Zone (ITCZ) towards the Hirnantian (14). During Pleistocene glacial maxima the boreal Polar Front moved from ~60°N to ~40°N as the Laurentide ice sheet grew (12, 13) with a concomitant fall in mean global surface temperature of between 3° to 5°C (based on estimated cooling between the present day and the Last Glacial Maximum; 25) and a reduction of pCO_2 from 280 ppm to 180 ppm (thus at a ratio of 0.64; see ref. 11). Loi et al. (26) calculated a fall in Hirnantian ice-equivalent sea-level of at least 148 m, relative to the earliest Hirnantian and 222 m relative to the late Katian. These are values that are equivalent to those of the total ice cover of the LGM (190-210 m; 26). We therefore hypothesize that the Sandbian to Hirnantian transition resulted in similar changes in ice cover, and thus ice-albedo feedback, as between Pleistocene interglacials and glacials. Combining this with our results that identify similarities in amplitude of Polar Front shift, we predict a similar fall in Hirnantian mean global surface temperature as during Pleistocene interglacials – glacials, from 16°C pre-Hirnantian (Sandbian) to values between ~13°C and ~11°C during the Hirnantian. Assuming the relationship between temperature and pCO_2 was the same during the Ordovician and the Pleistocene (see 21) then we further hypothesize that pCO_2 fell from ~8 x PAL during the Sandbian to ~5 x PAL in the Hirnantian.

Conclusions

Our data show that Late Ordovician SST gradients were much more similar to modern oceans than previously hypothesized. Elevated pCO_2 (8x PAL) for the early Late Ordovician appears to have balanced the reduced solar flux from a fainter Sun, resulting in mean global surface temperatures that approach those of the present day. Severe cooling resulted in an equatorward shift in the position of the Hirnantian austral Polar Front from 55-70°S to 40°S. This is deduced from an equator-ward expansion of the Polar Biotope, and is an equivalent shift to that between Pleistocene interglacials and glacial maxima. We conclude that during the Hirnantian glaciation there was an equatorward shift in climate belts, commensurate with a fall in mean global surface temperature from ~16°C to ~13-11°C and, assuming an equivalent temperature/pCO_2 relationship for the Pleistocene, a fall in pCO_2 from 8x PAL to ~5x PAL. The onset of Hirnantian glaciation was likely controlled by mechanisms and feedbacks that lead to falling pCO_2. Significantly, our data suggest that a disruption of marine habitats and a net reduction in ecospace in mid-latitude biotopes, as a consequence of rapid climate change, resolves as a likely cause of the mass extinction in the zooplankton at the end of the Ordovician.

Materials and Methods

A detailed Time Slice definition of the glacial Hirnantian (*extraordinarius* and lower *persculptus* graptolite biozones, Supplementary Figure S1) and the literature sources for the chitinozoan data of each site in this compilation are given in the "Materials and methods" section of the supporting information. The paleolatitudes for the localities are taken from the most recent paleogeographic reconstruction of Torsvik & Cocks (27, updated from base maps published in 28; see supporting online text for a full justification). The relatively small variance between this and earlier paleogeographic reconstructions (Plate tectonic maps and "Point tracker" software by C. R. Scotese, PALEOMAP Project; http://www.scotese.com) is used to define a 5° paleogeographical error for most areas, but the position of some of the Gondwanan localities varies by *ca*. 10° (Figure 3). Chitinozoan biotopes are defined using a combination of Detrended Correspondence Analysis (DCA), TWINSPAN and constrained seriation (17, 18; Materials and methods are available as supporting material; Supplementary Figures S2-S4). The distribution of chitinozoan biotopes is then compared to the hypothetical positions of modern zooplanktonic (foraminifer) provinces (SST temperature boundaries from Kucera, 29), mapped onto the Hirnantian paleogeography using the SST predictions from the GCMs (5; Figures 1, 3).

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Figure Legends

Fig. 1. Model predictions. (*A*) Latitudinal SST gradients and profiles from Sandbian and Hirnantian (Caradoc and Ashgill) SST models (x8 and x15 PAL pCO_2, ref. 5) compared with present day SST (ref. 30, central Pacific Ocean, taken from http://www.noaa.gov). Modern day planktonic foraminifer provinces in terms of SST (29). (*B*) Using SST simulations of Herrmann *et al.* (5) at x8 (High Sea Level/Low Sea Level) and x15 PAL pCO_2 we estimate the position of these zooplankton provinces/belts and their boundaries during the Hirnantian, for different pCO_2 scenarios.

Fig. 2. Paleogeographical reconstruction (27). The shading represent TWINSPAN clusters, i.e. Polar (black), Tropical (white) and Sub-Polar to Sub-tropical localities (grey; Materials and methods are available as supporting material). *We do not follow this reconstruction for the Prague Basin on the wandering Perunica 'microcontinent', which is shown to have been at higher paleolatitudes (31).

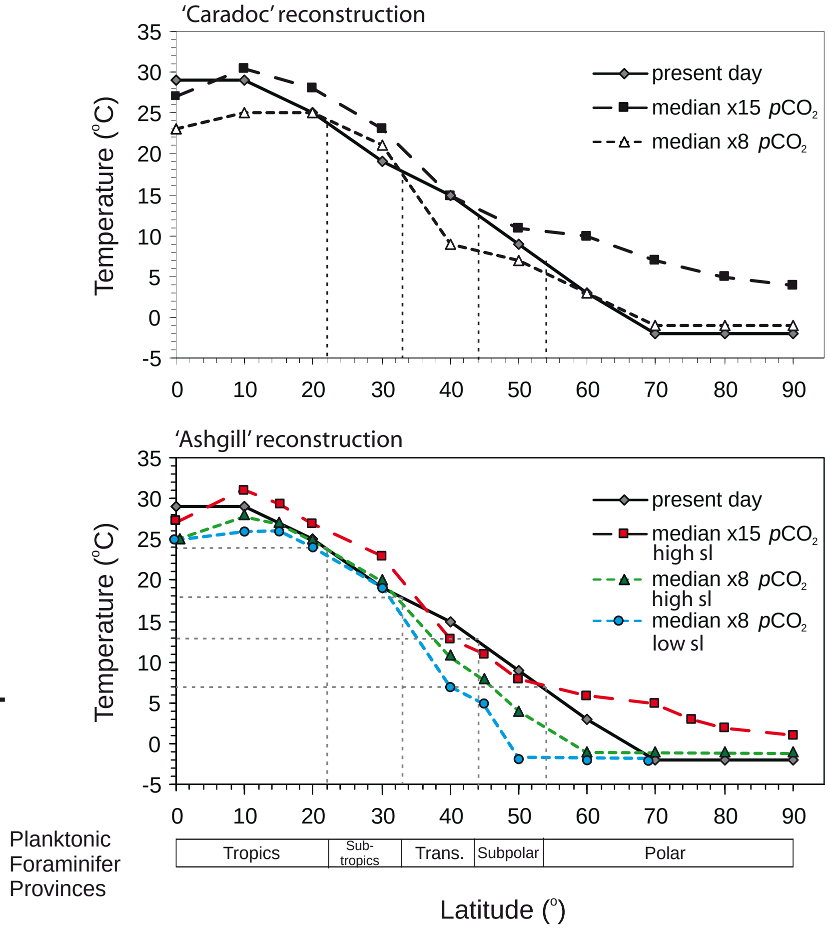
Fig. 3. Plankton maps. (*A*) Map of modern planktonic foraminifer provinces. (*B*, *C*, *D*) Hypothetical plankton models based on GCMs parameterized as indicated. (*E*) Comparing inferred chitinozoan biotopes with the hypothetical plankton models allows us to identify Hirnantian Tropical to Polar chitinozoan biotopes, with key boundaries at ~20, 25, 30, 40°S. Hence we can map oceanic climate belts during the major glaciation of the Early Paleozoic and compare these to the pre-glacial Sandbian climate belts (see Fig. 4). The chitinozoan biotopes and their inferred climate belts are most similar to the patterns for the hypothetical planktonic provinces for a SST-model

at x8 PAL pCO_2 and low relative sea levels, but nevertheless indicate an even steeper faunal and hence latitudinal temperature gradient than the model. The dots represent localities and the error bars reflects variance with regard to PALEOMAP reconstructions (http://www.scotese.com) with a minimum of 5° of latitude.

Fig. 4. Late Ordovician Polar Front migration. Time line showing a Katian (2) start of Late Ordovician cooling and a revised view with an earlier onset (15). Our Sandbian data (17, 18) support the latter. The map view compares Sandbian and Hirnantian chitinozoan biotopes; these maps demonstrate an equatorward shift in the position of the Polar Front from 55°-70°S to likely 40°S, which involves an equatorward incursion of Polar water and a compression of the Sub-polar belt and fauna (diversity). The sub-tropical belt moves slightly northwards. The shift of the Polar Front maps onto well-known patterns of late Cenozoic glacial-interglacial Polar Front migration.

Figure 1

(a) Predicted SST gradients (Herrmann *et al.* - ref 5) versus modern



(b) Predicted (hypothetical) zooplankton province boundaries for the 'Ashgill' SST reconstruction

Modern foraminifer province (Climate belt) boundary	Present day latitude °	Present day MAT (°C)	x8 pCO_2 latitude °	x8 pCO_2 latitude °	x15 pCO_2 latitude °	observed in chitinozoans
Tropic/Subtropics	22	24	22	20	28	c. 20
Subtropic/Trans	33	18	32	31	35	c. 25
Trans/Subpolar	44	13	38	35	40	c. 33
Subpolar/Polar	54	7	46	40	55	c. 40

data closest to 8x pCO_2 / Low SL model

difference between these within our 5° palaeogeograph. error

Figure 2

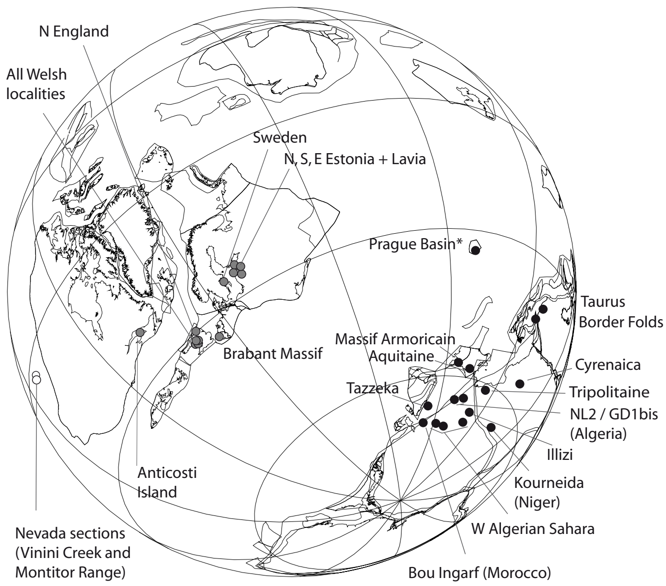
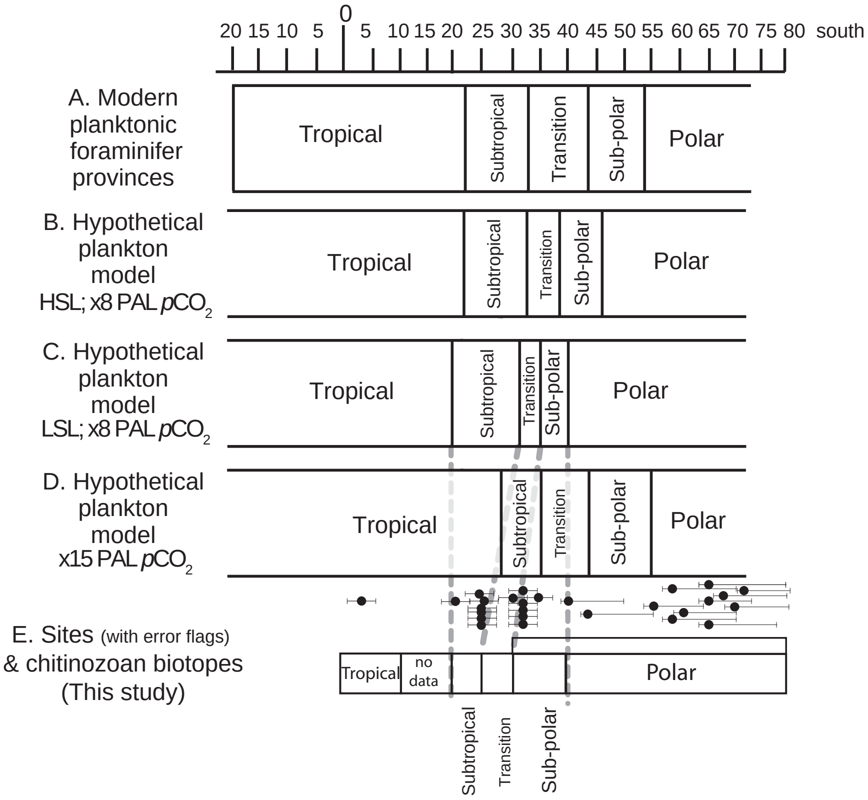
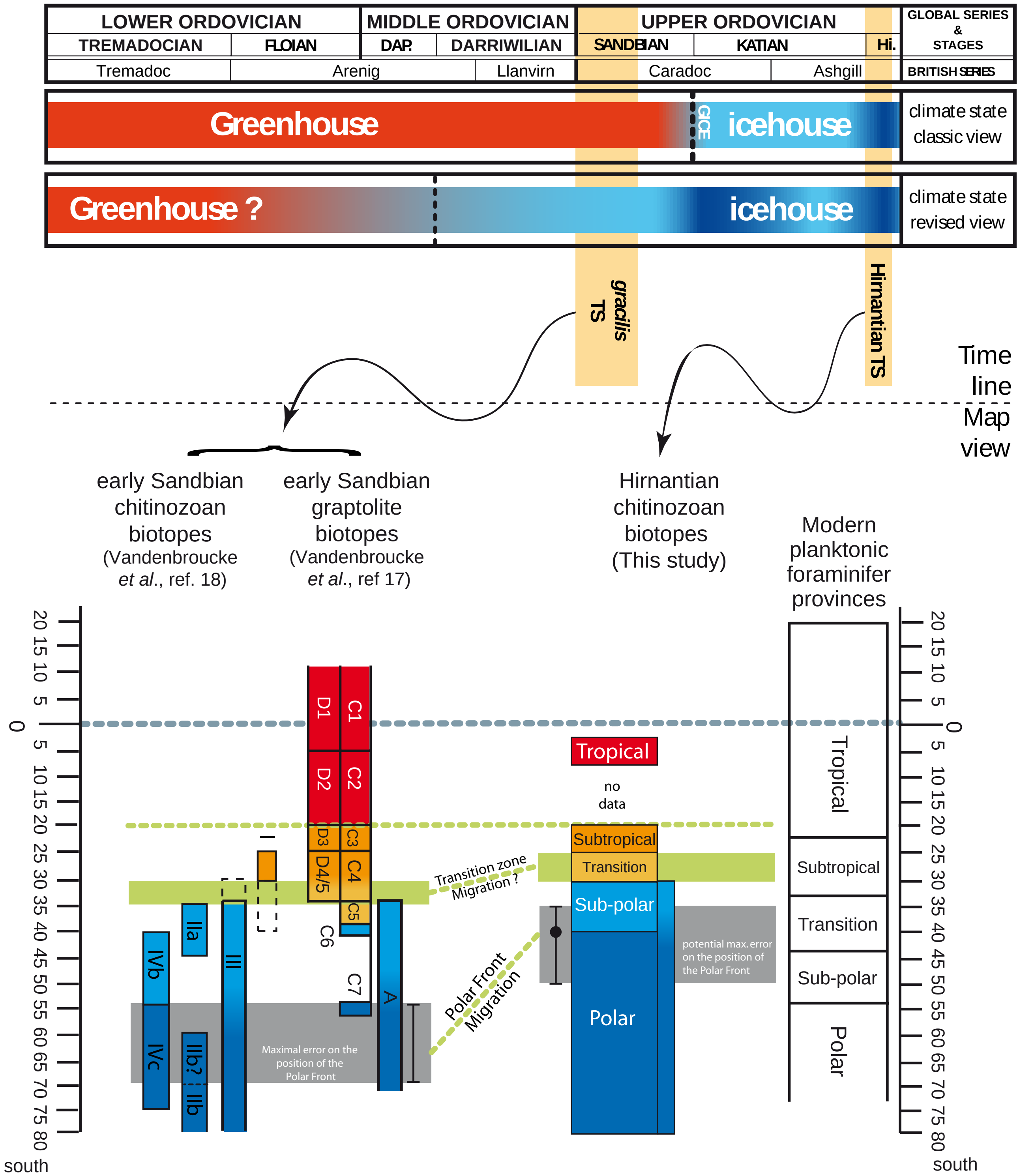

N England
All Welsh localities
Sweden
N, S, E Estonia + Lavia
Prague Basin*
Taurus Border Folds
Massif Armoricain
Aquitaine
Brabant Massif
Cyrenaica
Tazzeka
Tripolitaine
NL2 / GD1bis (Algeria)
Illizi
Anticosti Island
Kourneida (Niger)
W Algerian Sahara
Nevada sections (Vinini Creek and Montitor Range)
Bou Ingarf (Morocco)

Figure 3



0
20 15 10 5 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 south
A. Modern planktonic foraminifer provinces
Tropical
Subtropical
Transition
Sub-polar
Polar
B. Hypothetical plankton model HSL; x8 PAL pCO_2
Tropical
Subtropical
Transition
Sub-polar
Polar
C. Hypothetical plankton model LSL; x8 PAL pCO_2
Tropical
Subtropical
Transition
Sub-polar
Polar
D. Hypothetical plankton model x15 PAL pCO_2
Tropical
Subtropical
Transition
Sub-polar
Polar
E. Sites (with error flags) & chitinozoan biotopes (This study)
Tropical
no data
Polar
Subtropical
Transition
Sub-polar

Figure 4



LOWER ORDOVICIAN
MIDDLE ORDOVICIAN
UPPER ORDOVICIAN
GLOBAL SERIES & STAGES
TREMADOCIAN
FLOIAN
DAP.
DARRIWILIAN
SANDBIAN
KATIAN
Hi.
Tremadoc
Arenig
Llanvirn
Caradoc
Ashgill
BRITISH SERIES
Greenhouse
GICE
icehouse
climate state classic view
Greenhouse ?
icehouse
climate state revised view
gracilis TS
Hirnantian TS
Time line
Map view
early Sandbian chitinozoan biotopes (Vandenbroucke et al., ref. 18)
early Sandbian graptolite biotopes (Vandenbroucke et al., ref 17)
Hirnantian chitinozoan biotopes (This study)
Modern planktonic foraminifer provinces
20 15 10 5 0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80
south
D1
C1
D2
C2
D3
C3
D4/5
C4
C5
C6
C7
A
IIa
IVb
IVc
III
IIb?
IIb
Maximal error on the position of the Polar Front
Transition zone Migration ?
Polar Front Migration
Tropical
no data
Subtropical
Transition
Sub-polar
Polar
potential max. error on the position of the Polar Front
Tropical
Subtropical
Transition
Sub-polar
Polar