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Our new data address the paradox of Late Ordovician glaciation under supposedly high pCO_2 (8 to 22× PAL: preindustrial atmospheric level). The paleobiogeographical distribution of chitinozoan ("mixed layer") marine zooplankton biotopes for the Hirnantian glacial maximum (440 Ma) are reconstructed and compared to those from the Sandbian (460 Ma): They demonstrate a steeper latitudinal temperature gradient and an equatorwards 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 pCO_2 from a modeled Sandbian level of ∼8× PAL to ∼5× PAL during the Hirnantian. Our data suggest that a compression of midlatitudinal biotopes and ecospace in response to the developing glaciation was a likely cause of the end-Ordovician mass extinction.

chitinozoans | Ordovician | zooplankton biotopes | Hirnantian glaciations | climate belts

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 pCO_2 estimates ranging from 8 to 22× PAL (preindustrial atmospheric level (3–6); for a full review, see *SI 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 pCO_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 that tropical sea surface temperatures (SSTs) and austral latitudinal temperature gradients were similar to present-day, and that 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 8× 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 8× 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 8× PAL and a low relative sea level) indicate a steepening of the temperature gradient relative to the Sandbian (5; Fig. 1). However, key uncertainties remain relating to the parameterization of Ordovician GCMs (17, 18) and these have never been independently tested. Here we present a 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 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 that used in our previous studies (17, 18), but here it is based upon a unique compilation of published chitinozoan species presence/absence data for the glacial Hirnantian (Fig. 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 (Fig. 2).

Results

Fig. 3 shows the distribution of chitinozoan biotopes and the inferred climate belts during the Hirnantian. The boundary between the Tropical and Subtropical chitinozoan biotopes lies between 5° and 20° S; the southern edge of the Subtropics is at 25° S and the northern edge of the Subpolar biotope is at 30° S. The Transitional biotope lies between 25° and 30° S. The Polar

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The authors declare no conflict of interest.

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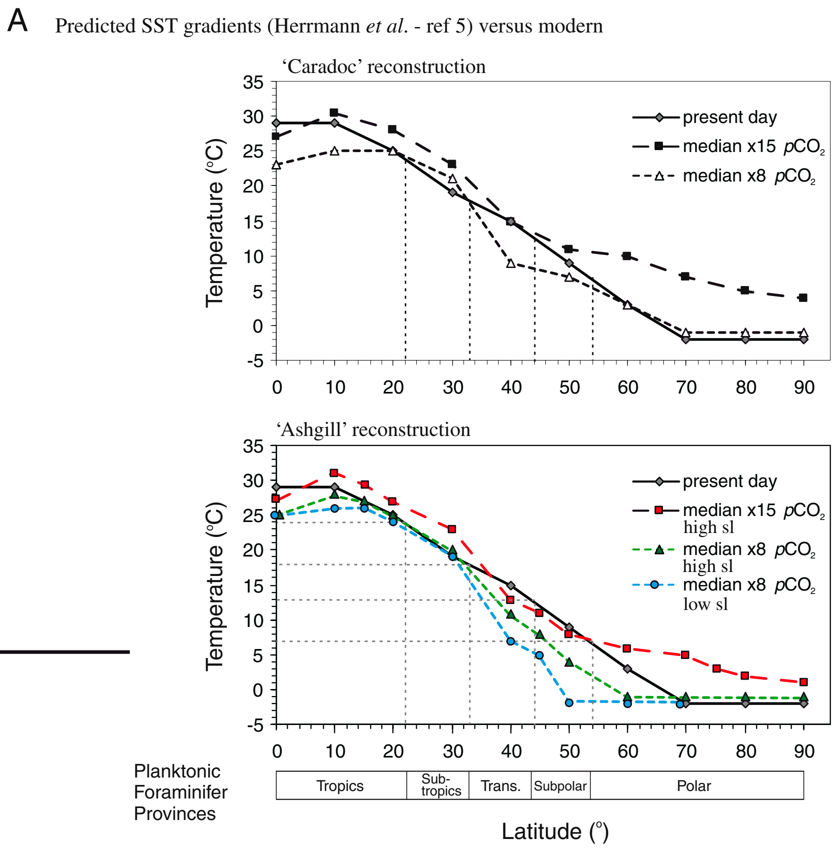

B Predicted (hypothetical) zooplankton province boundaries for the 'Ashgill' SST reconstruction

Modern foraminifer province (Climate belt) boundary	Present day latitude°	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° palaegeograph. error

Fig. 1. Model predictions. (*A*) Latitudinal SST gradients and profiles from Sandbian and Hirnantian (Caradoc and Ashgill) SST models (×8 and ×15 PAL pCO_2) (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 ×8 (high sea level/low sea level) and ×15 PAL pCO_2 we estimate the position of these zooplankton provinces/belts and their boundaries during the Hirnantian, for different pCO_2 scenarios. MAT: mean annual temperature.

Front, i.e. the northernmost extent of the South Polar fauna, lies between *ca.* 35° and 40° S.

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

i. An expansion of the Polar biotope and equatorwards shift of the Polar Front from 55°–70° S to ~40° S. This shift has the consequence of narrowing the Subpolar biotope and inferred climate belt (Fig. 4).
ii. Within the error of our analysis there is a minimal change in the width of the Tropical and Subtropical climate belts.
iii. Species richness within biotopes appears to correlate with latitudinal extent. The narrower Hirnantian Subpolar biotope has reduced species richness (9 species compared to 35 species in the Sandbian, see ref. 18), while the more extensive Hirnantian Polar biotope has an increased species richness of 19 species compared to the 4 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. 3 *C* and *E*).

Discussion

There is an ongoing debate as to how Hirnantian continental scale ice sheets could exist at high pCO_2 levels of 8 to 22× PAL (3–6; *SI 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

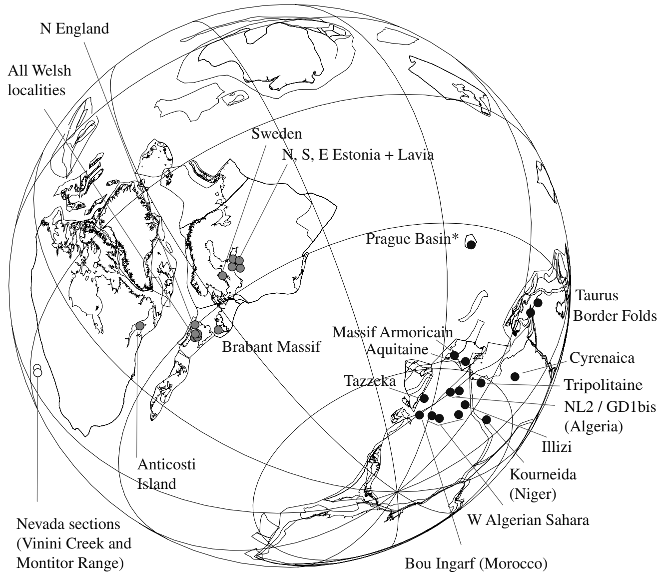

Fig. 2. Hirnantian paleogeographical reconstruction (27). The shading represent TWINSPAN clusters, i.e. Polar (black), Tropical (white), and Subpolar to Subtropical localities (gray; *SI Materials and Methods*). *We do not follow this reconstruction for the Prague Basin on the wandering Perunica "microcontinent," which is shown to have been at higher paleolatitudes (31).

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 8× PAL and implies a reparameterization 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 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° and 5 °C [based on estimated cooling between the present-day and the Last Glacial Maximum (LGM)] (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

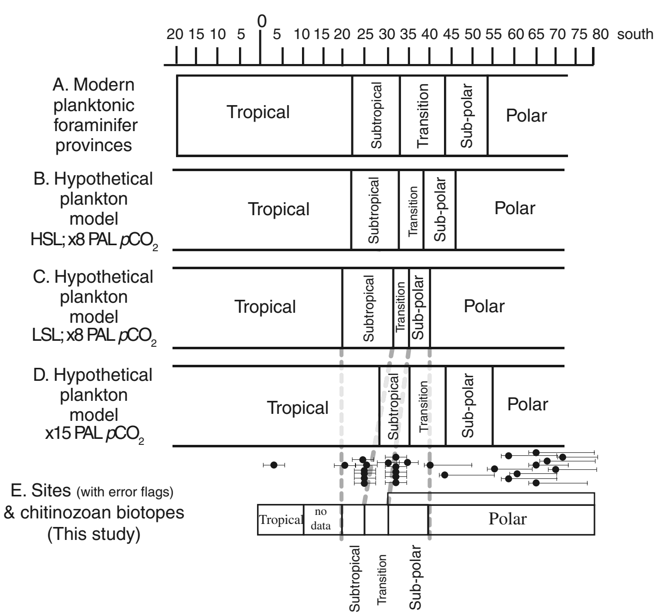

Fig. 3. Plankton maps. (*A*) Map of modern planktonic foraminifer provinces. (*B*, *C*, *D*) Hypothetical plankton models based on GCMs parameterized as indicated. (*E*) Comparing inferred chitinozoan biotopes with the hypothetical plankton models allows us to identify Hirnantian Tropical to Polar chitinozoan 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 preglacial 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 ×8 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.

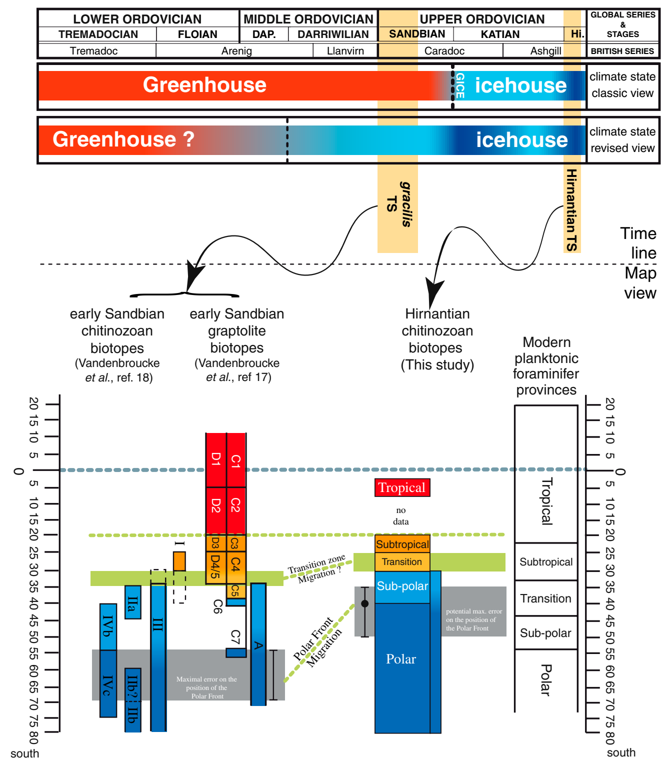

Fig. 4. Late Ordovician Polar Front migration. Time line showing a Katian (2) start of Late Ordovician cooling and a revised view with an earlier onset (15). Our Sandbian data (17, 18) support the latter. The map view compares Sandbian and Hirnantian chitinozoan biotopes; these maps demonstrate an equatorward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

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 ref. 21) then we further hypothesize that pCO_2 fell from ∼8× PAL during the Sandbian to ∼5× 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 (8× 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 equatorward 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 8× PAL to ∼5× 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 midlatitude biotopes, as a consequence of rapid climate change, emerges 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, Fig. S1) and the literature sources for the chitinozoan data of each site in this compilation are given in the *SI Materials and Methods*. The paleolatitudes for the localities are taken from the most recent paleogeographic reconstruction of Torsvik and Cocks (ref. 27, updated from base maps published in ref. 28; see *SI 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° (Fig. 3). Chitinozoan biotopes are defined using a combination of Detrended Correspondence Analysis, TWINSPAN (two way indicator species analysis), and constrained seriation (17, 18; *SI Materials and Methods*; and Figs. S2–S4). The distribution of chitinozoan biotopes is then compared to the hypothetical positions of modern zooplanktonic (foraminifer) provinces [SST boundaries from Kucera (29)], mapped onto the Hirnantian paleogeography using the SST predictions from the GCMs (5) (Figs. 1 and 3).

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