



HAL
open science

Polar front shift and atmospheric CO₂ during the glacial maximum of the Early Paleozoic Icehouse

T.R.A. Vandembroucke, Howard-A. Armstrong, Mark Williams, Florentin Paris

► To cite this version:

T.R.A. Vandembroucke, Howard-A. Armstrong, Mark Williams, Florentin Paris. Polar front shift and atmospheric CO₂ during the glacial maximum of the Early Paleozoic Icehouse. Proceedings of the National Academy of Sciences of the United States of America, 2010, 107 (34), pp.1483-1486. 10.1073/pnas.1003220107 . insu-00605031

HAL Id: insu-00605031

<https://insu.hal.science/insu-00605031>

Submitted on 23 Apr 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Polar front shift and atmospheric CO₂ during the glacial maximum of the Early Paleozoic Icehouse

Thijs R. A. Vandenbroucke^{a,b,c,1,2}, Howard A. Armstrong^{a,1}, Mark Williams^{d,e,1}, Florentin Paris^f, Jan A. Zalasiewicz^d, Koen Sabbe^g, Jaak Nõlvak^h, Thomas J. Challands^{a,i}, Jacques Verniers^b, and Thomas Servais^c

^aPalaeoClimate Group, Department of Earth Sciences, Durham University, Science Labs, Durham, DH1 3LE, United Kingdom; ^bResearch Unit Palaeontology, Department of Geology, Ghent University, Krijgslaan 281-58, 9000 Ghent, Belgium; ^cGéosystèmes, Université Lille 1, Formation de Recherche en Evolution 3298 du Centre National de la Recherche Scientifique, Avenue Paul Langevin, bâtiment SN5, 59655 Villeneuve d'Ascq Cedex, France; ^dDepartment of Geology, University of Leicester, University Road, Leicester, LE1 7RH, United Kingdom; ^eBritish Geological Survey, Kingsley Dunham Centre, Keyworth, NG12 5GG, United Kingdom; ^fGéosciences, Université de Rennes I, Unité Mixte de Recherche 6118 du Centre National de la Recherche Scientifique, Campus de Beaulieu, 35042 Rennes-cedex, France; ^gProtistology and Aquatic Ecology, Department of Biology, Ghent University, Krijgslaan 281-58, 9000 Ghent, Belgium; ^hInstitute of Geology, Tallinn University of Technology, Ehitajate tee 5, 19086 Tallinn, Estonia; and ⁱTotal E&P UK Limited, Geoscience Research Centre, Crawpeel Road, Aberdeen AB12 3FG, United Kingdom

Edited by Jeffrey Kiehl, National Center for Atmospheric Research, Boulder, CO, and accepted by the Editorial Board July 1, 2010 (received for review March 16, 2010)

Our new data address the paradox of Late Ordovician glaciation under supposedly high $p\text{CO}_2$ (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 $p\text{CO}_2$ 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 $p\text{CO}_2$ 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 $p\text{CO}_2$ 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 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 $p\text{CO}_2$ was set at 8×

PAL (5). A GCM experiment parameterized with the same $p\text{CO}_2$ 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 $p\text{CO}_2$ 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 $p\text{CO}_2$ 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 $p\text{CO}_2$.

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

Author contributions: T.R.A.V., H.A.A., M.W., J.A.Z., J.V., and T.S. designed research; T.R.A.V. performed research; F.P., J.N., and T.J.C. contributed new reagents/analytic tools; T.R.A.V., H.A.A., M.W., and K.S. analyzed data; T.R.A.V., H.A.A., and M.W. wrote the paper; and J.V. and T.S. supervised the project.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. J.K. is a guest editor invited by the Editorial Board.

¹T.R.A.V., H.A.A., and M.W. contributed equally to this work.

²To whom correspondence should be addressed. E-mail: Thijs.vandenbroucke@univ-lille1.fr.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1003220107/-DCSupplemental.

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

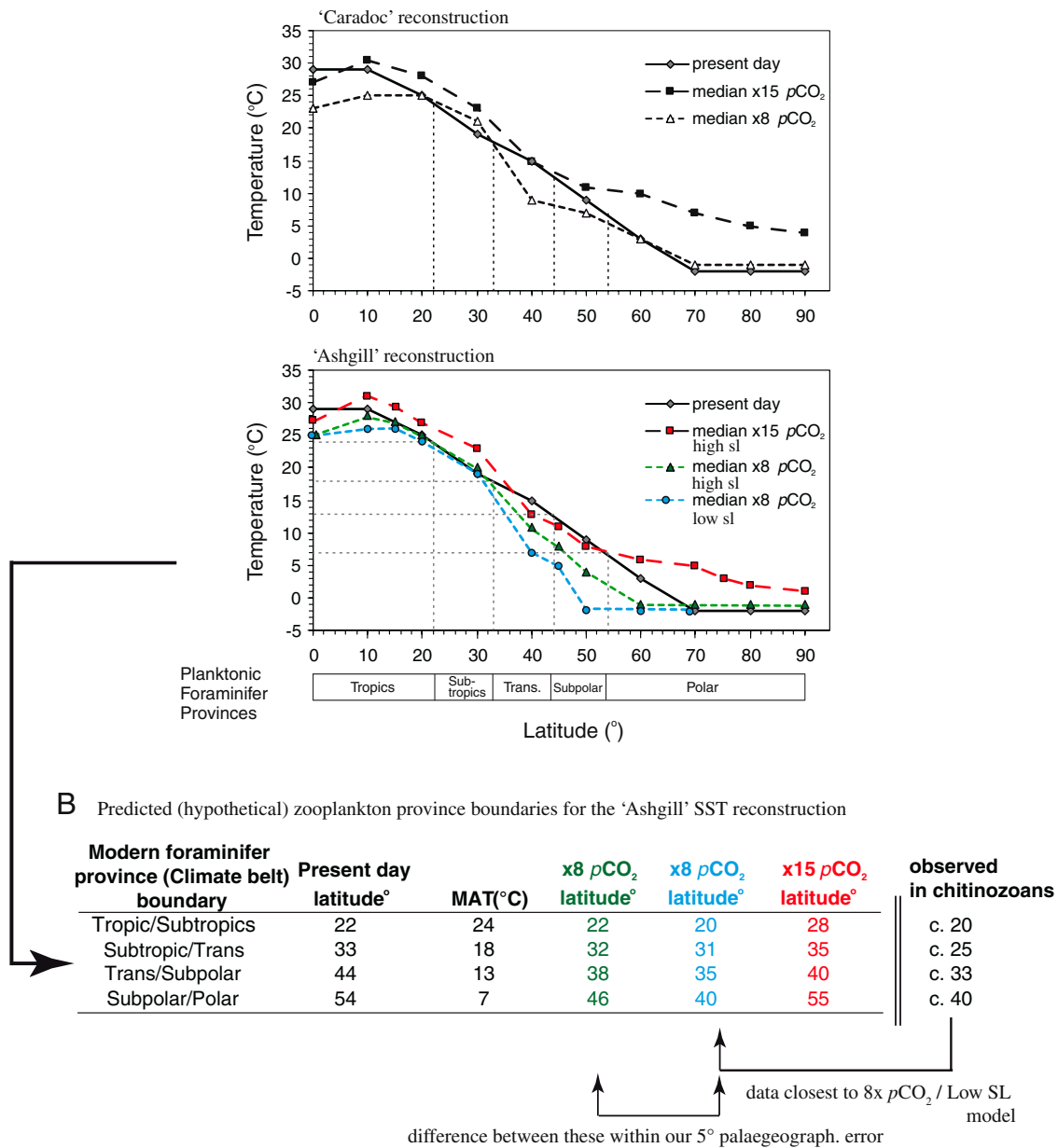


Fig. 1. Model predictions. (A) Latitudinal SST gradients and profiles from Sandbian and Hirnantian (Caradoc and Ashgill) SST models ($\times 8$ and $\times 15$ PAL $p\text{CO}_2$) (5) compared with present-day SST (ref. 30, central Pacific Ocean, taken from <http://www.noaa.gov>). Modern day planktonic foraminifer provinces in terms of SST (29). (B) Using SST simulations of Herrmann *et al.* (5) at $\times 8$ (high sea level/low sea level) and $\times 15$ PAL $p\text{CO}_2$ we estimate the position of these zooplankton provinces/belts and their boundaries during the Hirnantian, for different $p\text{CO}_2$ 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 $p\text{CO}_2$ estimates (Fig. 3 C and E).

Discussion

There is an ongoing debate as to how Hirnantian continental scale ice sheets could exist at high $p\text{CO}_2$ levels of 8 to 22 \times 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

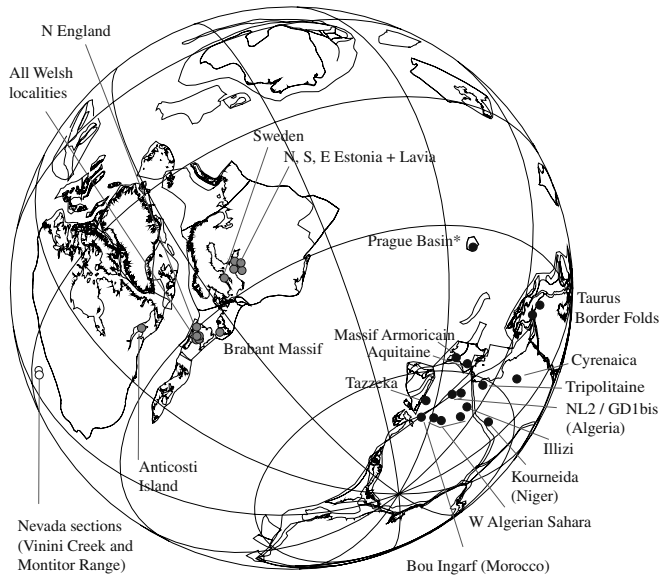


Fig. 2. Hirnantian paleogeographical reconstruction (27). The shading represent TWINSPLAN clusters, i.e. Polar (black), Tropical (white), and Subpolar to Subtropical localities (gray; *SI Materials and Methods*). *We do not follow this reconstruction for the Prague Basin on the wandering Perunica “micro-continent,” 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

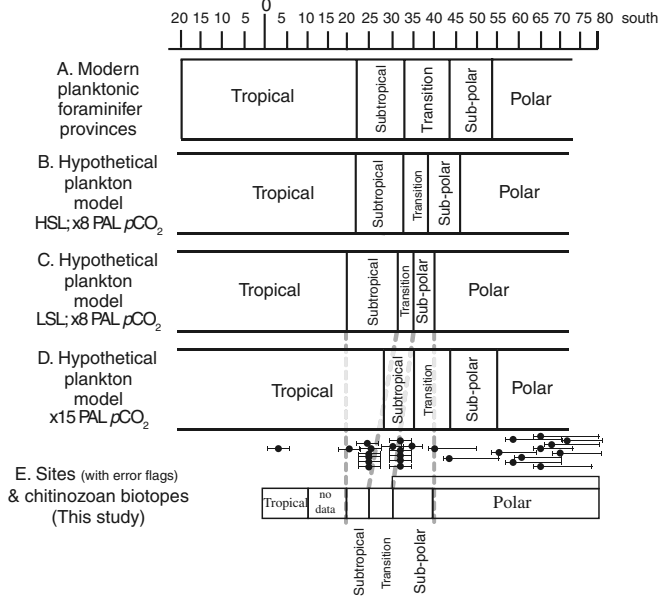


Fig. 3. Plankton maps. (A) Map of modern planktonic foraminifer provinces. (B, C, D) Hypothetical plankton models based on GCMs parameterized as indicated. (E) Comparing inferred chitinozoan biotopes with the hypothetical plankton models allows us to identify Hirnantian Tropical to Polar chitinozoan biotopes, with key boundaries at $\sim 20, 25, 30, 40^\circ$ 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 $\times 8$ 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.

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 $8\times$ 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 $\sim 40^\circ$ 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 $\sim 60^\circ$ N to $\sim 40^\circ$ 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

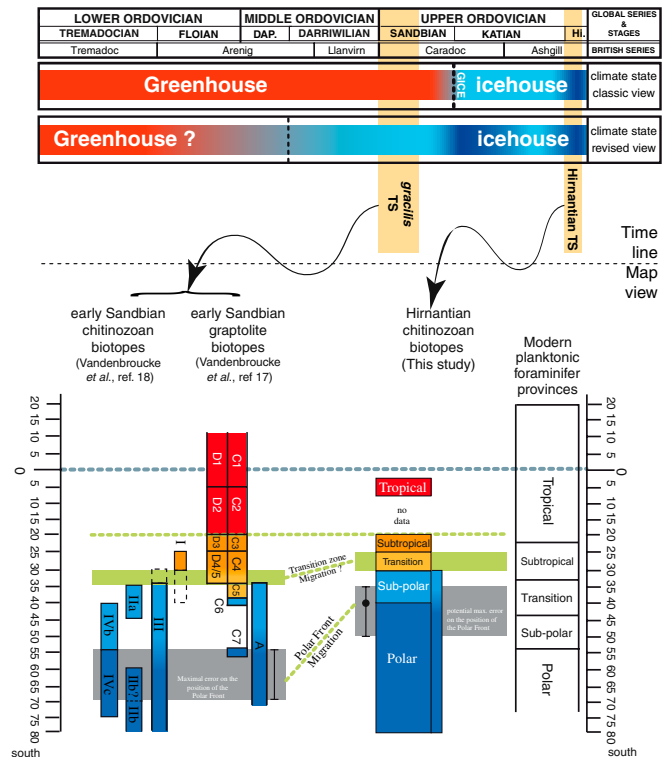


Fig. 4. Late Ordovician Polar Front migration. Time line showing a Katian (2) start of Late Ordovician cooling and a revised view with an earlier onset (15). Our Sandbian data (17, 18) support the latter. The map view compares Sandbian and Hirnantian chitinozoan biotopes; these maps demonstrate an equatorward 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 glacial. 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 $p\text{CO}_2$ was the same during the Ordovician and the Pleistocene (see ref. 21) then we further hypothesize that $p\text{CO}_2$ 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 $p\text{CO}_2$ (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/ $p\text{CO}_2$ relationship for the Pleistocene, a fall in $p\text{CO}_2$ from 8× PAL to ~5× PAL. The onset of Hirnantian glaciation was likely controlled by mechanisms and feedbacks that lead to falling $p\text{CO}_2$. 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).

ACKNOWLEDGMENTS. T.R.A.V. acknowledges the Research Foundation, Flanders (FWO-Vlaanderen) for postdoc-project funding. J.N. benefitted from Grant 7640 of the Estonian Science Foundation (ESF). We thank Alan Haywood, Yves Goddérís, and Vincent Lefebvre for discussion, and James Baldini and Stephen Louwye for constructive comments on an earlier version of the text. We acknowledge the helpful comments of three anonymous referees.

- Sutcliffe OE, Dowdeswell JA, Whittington RJ, Theron JN, Craig J (2000) Calibrating the Late Ordovician glaciation and mass extinction by the eccentricity cycles of Earth's orbit. *Geology* 28:967–970.
- Page AA, Zalasiewicz JA, Williams M, Popov LE (2007) Were transgressive black shales a negative feedback modulating glacioeustasy in the Early Palaeozoic Icehouse? *Deep Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies*, eds M Williams, AM Haywood, JF Gregory, and DN Schmidt (Micro-palaeontological Society Special Publications, Geological Society of London, London), pp 123–156.
- Crowley TJ, Baum SK (1995) Reconciling Late Ordovician (440 Ma) glaciation with very high (14×) CO_2 levels. *J Geophys Res-Atmos* 100:1093–1101.
- Gibbs MT, Barron EJ, Kump LR (1997) An atmospheric $p\text{CO}_2$ threshold for glaciation in the Late Ordovician. *Geology* 25(5):447–450.
- Herrmann AD, Haupt BJ, Patzkowsky ME, Seidov D, Slingerland RL (2004) Response of Late Ordovician paleoceanography to changes in sea level, continental drift, and atmospheric $p\text{CO}_2$: Potential causes for long-term cooling and glaciation. *Palaeogeogr Palaeoclimatol Palaeoecol* 210:385–401.
- Herrmann AD, Patzkowsky ME, Pollard D (2004) The impact of paleogeography, $p\text{CO}_2$, poleward ocean heat transport and sea level change on global cooling during the Late Ordovician. *Palaeogeogr Palaeoclimatol Palaeoecol* 206:59–74.
- Sheehan PM (2001) The Late Ordovician mass extinction. *Annu Rev Earth Pl Sc* 29:331–364.
- Armstrong HA (2007) On the cause of the Ordovician glaciation. *Deep Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies*, eds M Williams, AM Haywood, JF Gregory, and DN Schmidt (Micro-palaeontological Society Special Publications, Geological Society of London, London), pp 101–121.
- Armstrong HA, et al. (2005) Origin, sequence stratigraphy and depositional environment of an Upper Ordovician (Hirnantian), peri-glacial black shale, Jordan. *Palaeogeogr Palaeoclimatol Palaeoecol* 220:273–289.
- Clark PU, et al. (2009) The last glacial maximum. *Science* 325:710–714.
- Petit RJ, et al. (1999) Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* 399:429–436.
- McIntyre A, Ruddiman WF, Jantzen R (1972) Southward penetrations of the North Atlantic polar front—faunal and floral evidence of large-scale surface water mass movements over the last 225,000 years. *Deep-Sea Res* 19:61–77.
- Eynaud F, et al. (2009) Position of the Polar Front along the western Iberian margin during key cold episodes of the last 45 ka. *Geochem Geophys Geosy* 10:Q07U05.
- Armstrong HA, Baldini J, Challands TJ, Gröcke DR, Owen AW (2009) Response of the Inter-tropical Convergence Zone to Southern Hemisphere cooling during Upper Ordovician glaciation. *Palaeogeogr Palaeoclimatol Palaeoecol* 284:227–236.
- Trotter JA, Williams IS, Barnes CR, Lecuyer C, Nicoll RS (2008) Did cooling oceans trigger Ordovician biodiversification? Evidence from conodont thermometry. *Science* 321:550–554.
- Shields GA, et al. (2003) Sr, C, and O isotope geochemistry of Ordovician brachiopods: A major isotopic event around the Middle-Late Ordovician transition. *Geochim Cosmochim Acta* 67:2005–2025.
- Vandenbroucke TRA, Armstrong HA, Williams M, Zalasiewicz JA, Sabbe K (2009) Ground-truthing Late Ordovician climate models using the paleobiogeography of graptolites. *Paleoceanography* 24:PA4202.
- Vandenbroucke TRA, et al. (2010) Epipelagic chitinozoan biotopes map a steep latitudinal temperature gradient for earliest Late Ordovician seas: Implications for a cooling Late Ordovician climate. *Palaeogeogr Palaeoclimatol Palaeoecol*, 10.1016/j.palaeo.2009.11.026, in press.
- Tajika E (2003) Faint young sun and the carbon cycle: Implication for the Proterozoic global glaciations. *Earth Planet Sc Lett* 214:443–453.
- Gough DO (1981) Solar interior structure and luminosity variations. *Sol Phys* 74:21–34.
- Royer DL (2006) CO_2 -forced climate thresholds during the Phanerozoic. *Geochim Cosmochim Acta* 70:5665–5675.
- Herrmann AD, Patzkowsky ME, Pollard D (2003) Obliquity forcing with 8–12 times preindustrial levels of atmospheric $p\text{CO}_2$ during the Late Ordovician glaciation. *Geology* 31:485–488.
- Breecker DO, Sharp DZ, McFadden LD (2010) Atmospheric CO_2 concentrations during ancient greenhouse climates were similar to those predicted for AD 2100. *Proc Natl Acad Sci USA* 107:576–580.
- Lunt DJ, et al. (2010) Earth system sensitivity inferred from Pliocene modelling and data. *Nat Geosci* 3:60–64.
- Jansen E, et al. (2007) Palaeoclimate. *Climate Change 2007: The Physical Science Basis, IPCC AR4*, eds S Solomon et al. (Cambridge Univ Press, Cambridge and New York), Chapter 6.
- Loi A, et al. (2010) The Late Ordovician glacio-eustatic record from a high-latitude storm-dominated shelf succession: The Bou Ingarf section (Anti-Atlas, Southern Morocco). *Palaeogeogr Palaeoclimatol Palaeoecol*, 10.1016/j.palaeo.2010.01.018, in press.
- Torsvik TH, Cocks LRM (2009) *BugPlates: Linking Biogeography and Palaeogeography* Software manual, available at <http://www.geodynamics.com>.
- Cocks LRM, Torsvik TH (2002) Earth geography from 500 to 400 million years ago: A faunal and palaeomagnetic review. *J Geol Soc London* 159:631–644.
- Kucera M (2007) Planktonic foraminifera as traces of past oceanic environments in proxies in late Cenozoic palaeoceanography. *Developments in Marine Geology*, eds C Hillaire-Marcel and A De Vernal (Elsevier, Amsterdam), Vol 1, pp 213–262.
- Locarnini RA, Mishonov AV, Antonov JI, Boyer TP, Garcia HE (2005) Temperature in NOAA Atlas NESDIS 61. *World Ocean Atlas 2005*, ed S Levitus (US Government Printing Office, Washington, DC), Vol 1.
- Paris F (1998) Early Palaeozoic paleobiogeography of northern Gondwana regions. *Acta U Carol Geol* 42:473–483.