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The Ordovician ocean circulation: a modern synthesis based on data and models

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Abbreviated title: The Ordovician ocean circulation
Surface currents constitute an efficient transport agent for (larvae of) marine faunas, while the circulation of water masses in the ocean interior drives nutrient redistribution, ventilates the ocean and contributes to shaping surface biological productivity and the benthic redox landscape. Therefore, a robust understanding of ocean circulation, both shallow and deep, and of its response to climate change, is required to interpret paleobiogeographic signals, biological productivity patterns and biodiversity trends. This is especially critical during periods of dynamic biological change, such as the Ordovician. Yet, oceanic circulation patterns leave no direct evidence in the geological record and can therefore be reconstructed solely based on indirect indicators, such as the distribution of faunas and geochemical proxies. General circulation models offer independent, physically robust insights onto the coupling between climate change and ocean circulation. Integrated approaches based on the assimilation of geological data in numerical models thus constitute a promising way forward. We here provide a literature review and updated synthesis of the current understanding of the Ordovician ocean circulation, based on data and models.
Over the past decades, the advent of large, contributive paleontological databases has offered new insights into the evolution of biodiversity in the early Paleozoic (Alroy et al. 2008; Fan et al. 2020). Yet, the drivers of reported biodiversity trends remain poorly constrained (Martin and Quigg 2012; Zaffos et al. 2017; Roberts and Mannion 2019; Close et al. 2020; Harper et al. 2021). Recent work emphasizes the tight coupling between environment and the marine biosphere during the Phanerozoic (Hannisdal and Peters 2011; Mayhew et al. 2012; Zacaï et al. 2021), with abundant work pointing towards a key limitation of animal metabolism and biodiversity by dissolved oceanic oxygen concentrations (Dahl et al. 2010; Saltzman et al. 2011; Deutsch et al. 2015; Vandenbroucke et al. 2015; Penn et al. 2018; Zou et al. 2018; Boag et al. 2021; Stockey et al. 2021).

The ocean circulation plays a key role in shaping the global marine redox landscape (Huang 2009) and thus contributes to driving spatial and temporal marine biodiversity patterns (Deutsch et al. 2015; Penn et al. 2018; Stockey et al. 2021). Currents in the ocean mixed layer define upwelling and downwelling regions and therefore drive spatial patterns of biological productivity in the upper ocean (upper ~500 m) and oxygen consumption through remineralization deeper down, while the deep-ocean circulation modulates ventilation of the ocean interior and the return of nutrients to the upper ocean (Huang 2009). At the regional scale, upper-ocean currents also permit to disseminate planktonic organisms and larvae. They ensure the communication between distant landmasses, with strong implications for speciation dynamics and paleobiogeography (e.g., Rasmussen, 2011; Lam and Stigall, 2015; Muñoz and Benedetto, 2016). Therefore, improving our vision of ocean circulation in ancient times is crucial to better understand changes in spatial and temporal patterns of biodiversity. This is particularly important during periods of highly dynamic biotic evolution, such as the
Ordovician.

Unfortunately, the global ocean circulation leaves no direct evidence in the geological record, and therefore remains very difficult to reconstruct. Sediments testifying of high biological productivity levels, when preserved, can be used as indirect evidence for local upwelling systems (Wilde et al. 1989; Pope and Steffen 2003; Armstrong et al. 2009). Faunal similarities and reconstruction of dispersal pathways can also be used to infer the direction of ancient currents (Popov et al. 2013; Lam and Stigall 2015; Lam et al. 2018, 2021), although the same information also serves as a basis to some paleogeographic reconstructions (Christiansen and Stouge 1999; Scotese and Wright 2018), which potentially implies some degree of circularity. Reconstruction of the deep-ocean circulation is even more challenging. Deep-ocean anoxia may constitute an interesting indicator of seafloor ventilation. However, most of the early Paleozoic seafloor has been recycled during subduction (Granot 2016) and, here again, only indirect clues can be used. Fortunately, a whole suite of redox proxies has been developed and improved over the past decades (Sperling et al. 2015; Dickson 2017; Stolper and Keller 2018; Lau et al. 2019; Lu et al. 2020; Tribovillard 2020; Chen et al. 2021; Nielsen 2021). Yet, local signals are often contradictory (Tostevin and Mills 2020), and proxies for the global extent of anoxia (such as $\delta^{238}$U) (Bartlett et al. 2018; Lau et al. 2019; Zhang et al. 2020; Clarkson et al. 2021) are associated with large uncertainties (Stockey et al. 2020; Zhang et al. 2020). In addition, other factors than ventilation strongly impact seafloor anoxia during the early Paleozoic, with long-term carbon cycle (box) models suggesting a driving role of changing atmospheric oxygen concentrations (Lenton et al. 2012, 2018; Krause et al. 2018; Mills et al. 2021).

General circulation models (GCMs) offer independent insights into past ocean circulation and can constitute a promising, complementary source of information. These models are numerical codes representing, in the form of equations, our understanding of climate physics...
(i.e., energy balance) and dynamics (i.e., atmospheric and oceanic currents). State-of-the-art GCMs represent our current vision of how climate works at the global scale and are used to study ongoing climate change (IPCC 2013). Models used in the deep time are very similar, although often somewhat simpler and coarser in spatial resolution due to technical reasons that make the use of most recent GCMs complex and computationally too heavy (Sepulchre et al. 2020). When appropriate boundary conditions are provided, including continental configuration (Scotese and Wright 2018; Williams et al. 2020; Marcilly et al. 2021), greenhouse gas levels (e.g., Royer et al. 2004; Foster et al. 2017; Witkowski et al. 2018) and solar luminosity (Gough 1981), these models offer a vision of the state of the ocean and atmosphere that may have characterized the investigated period of time (e.g., Zhu et al. 2019; Laugié et al. 2020; Tardif et al. 2020). More importantly, they permit to quantify the sensitivity of the global climate system, including ocean circulation, to key parameters, such as gateways (Niezgodzki et al. 2019; Dummann et al. 2020) and global climate state (Pohl et al. 2017a; Niezgodzki et al. 2019). Of course, results of GCMs should not be taken at face value, since these models are necessarily imperfect, but the assimilation of geological data into climate models has proven efficient to improve our understanding of past climate changes (Vandenbroucke et al. 2010b, a; Chaboureau et al. 2012; Pohl et al. 2016a; Goddéris et al. 2017; Haynes et al. 2020; Dummann et al. 2021).

Here we provide a review of our current knowledge of the Ordovician ocean circulation based on published data and GCMs. Although “intermediate” waters constitute a key component of the Modern global ocean circulation (Waelbroeck et al. 2011; Gonzales et al. 2017), we here adopt the convention of published Ordovician work and successively focus on the upper-ocean (upper ca. 500 m) (section #2) and deep-ocean (deeper than ca. 500 m) (section #3) circulation. We conclude by identifying future research targets (section #4).
Upper-ocean circulation and implications for primary productivity

Upper-ocean currents

The upper-ocean circulation is mainly driven by the location of prevailing wind belts and position of landmasses (Williams and Follows 2011). Wind stress transfers momentum to upper-ocean waters. Currents flow at a 45° angle to the wind at the ocean surface as a result of the balance between the Coriolis force and wind stress. Going deeper in the water column, wind stress gets weaker and the Coriolis force gets comparatively stronger, resulting in an increase of the angle with depth. At the base of the ocean layer undergoing frictional stress – or mixed layer, ocean currents are weak, but opposite to the wind direction. When integrated over the mixed layer, the net flow is 90° to the right in the Northern Hemisphere and to the left in the Southern Hemisphere due to the Earth’s rotation and resulting Coriolis force (Ekman 1905). In the absence of landmasses, the ocean surface circulation would be largely zonal (Ferreira et al. 2011): to the west along the Equator as a result of the wind stress imposed by the Trade Winds, to the east along the mid-latitudinal Westerlies and to the west again along the polar easterlies. Continental meridional boundaries, by deflecting the zonal flow, lead to the establishment of large ocean gyres, therefore promoting heat transport from the low to high latitudes. The most famous of these latitudinal currents today is the Gulf Stream, which results from the deflection of the north equatorial current by the northeastern coast of South America and constitutes the westward limb of the subtropical North-Atlantic Gyre.

Based on these fundamental principles of physical oceanography, and using the continental reconstructions available at the time (Scotese 1986), Wilde et al. (1989) and Wilde (1991) proposed conceptual models of the early Paleozoic (late Cambrian – early Silurian) upper-ocean circulation (Fig. 1). These pioneering studies already featured the most essential characteristics of the Ordovician upper-ocean circulation: in this conceptual model,
the zonal circulation in the essentially oceanic Northern Hemisphere contrasts with a
circulation more similar to the modern one in the Southern Hemisphere, with landmasses
inducing the establishment of large ocean gyres (Fig. 1). A few years later, Christiansen and
Stouge (1999) proposed a revision of this conceptual model accounting for latitudinal shifts
in climatic belts resulting from orbital variations and the faster spinning Ordovician Earth
(Williams 1991). They focused on the Lower Ordovician and used paleobiogeographic
(graptolite, trilobite, brachiopod and conodont) data to refine the continental reconstruction.
The main characteristics of the ocean circulation patterns proposed by Christiansen and
Stouge (1999) remain very similar to the conceptual model of Wilde et al. (1989) and Wilde

Poussart et al. (1999) and Herrmann et al. (2004) confirmed the validity of the previous
conceptual models using numerical climate modeling. Due to technical limitations, they did
not use ocean-atmosphere coupled GCMs, but instead oceanic GCMs forced with
atmospheric (wind) fields independently generated using atmospheric GCMs (Gibbs et al.
1997; Herrmann et al. 2004b). The use of numerical climate models marked a significant step
towards quantification. Poussart et al. (1999) notably demonstrated that the circumpolar flow
characterizing the midlatitudes in the Northern Hemisphere, in their Ordovician model, was
of similar magnitude to the modern Antarctic Circumpolar Current.

Ten years later, Servais et al. (2014) expressed the need for a major update. The authors
noted that, while major advances had been made in Early Paleozoic continental
reconstructions and the paleontological database had been significantly expanded in the
context of the International Geoscience Programs in particular (IGCPs #410, #503 and #591),
the understanding of early Paleozoic ocean circulation had not advanced accordingly, thus
constituting a major limitation to the interpretation of paleobiogeographic signals. Servais et
al. (2014) proposed an updated conceptual model, using the recent continental
reconstructions of Torsvik and Cocks (2013) for three time intervals: 510 Ma (mid Cambrian), 470 Ma (mid Ordovician) and 430 Ma (mid Silurian). In response to Servais et al. (2014), Pohl et al. (2016b) produced the first maps of the Ordovician upper-ocean circulation derived from the results of a fully coupled ocean-atmosphere GCM (Fig. 2). The authors used the continental reconstructions of Torsvik (2012), updated with bathymetric information extracted from regional studies, and conducted simulations for the Early (480 Ma), Mid (460 Ma) and Late (440 Ma) Ordovician at 3 atmospheric CO₂ levels covering Ordovician estimates (1120, 2240 and 4480 ppm). These maps were generated using an ocean-atmosphere GCM of previous generation (Jacob 1997), but constitute the most exhaustive dataset available to date for purposes of paleobiogeographic interpretation (Muñoz and Benedetto 2016; Benedetto et al. 2018; Lam et al. 2018, 2021; Reyes-Abril et al. 2019). They have already proven useful to discuss and interpret faunal migration pathways. For instance, Muñoz and Benedetto (2016) proposed that the faunal affinities observed in brachiopod genera between the Central Andean Basin (Argentina) and the South European microcontinents (red and blue points in Fig. 2) could be explained by two-way upper-ocean circulation connecting these regions, with the Antarctica Current and Southern Westerlies forming the eastward branch and the Gondwana current the westward component (Fig. 2).

**Biological productivity**

Upper-ocean currents largely drive spatial patterns of biological production by marine photosynthetically algae (i.e., phytoplankton) (Williams and Follows 2011). Indeed, converging upper-ocean currents lead to downwelling and low productivity levels, while upper-ocean divergence permits the upwelling of nutrient-rich waters coming from the deeper ocean (where nutrients are returned during the remineralization of sinking organic matter), hence sustaining high levels of primary productivity. Different physiogeographical contexts lead to upwelling. Equatorial upwelling occurs because Ekman transport resulting
from westward equatorial winds is to the north in the Northern Hemisphere and to the south in the Southern Hemisphere, inducing a diverging flow of water away from the equator. Coastal upwelling takes place when the wind direction is parallel to the continent so that Ekman transport is occurring away from the coast.

Using an ocean-atmosphere GCM with biogeochemical capabilities (MITgcm) and the continental reconstructions of Torsvik (2012), Pohl et al. (2017a) simulated the spatial patterns of primary productivity during the Late Ordovician (Fig. 3). In their simulations, primary productivity is high along the western margin of equatorial landmasses, where equatorial upwelling occurs, and at the midlatitudes, mimicking to some extent the behavior of the modern Antarctic Circumpolar Current. It is low elsewhere, along the sinking limb of the tropical convection cells at around 30 °N/S (where downwelling occurs and nutrients are limiting) and at polar latitudes (where incoming solar radiation is limiting) (Pohl et al. 2017b). These model results agree with the conceptual models of Christiansen and Stouge (1999) and Servais et al. (2014), and with the upper-ocean circulation simulated by Pohl et al. (2016b) using another ocean-atmosphere general circulation model. Spatial patterns of primary productivity obtained using the MITgcm are also largely similar to those simulated by Pohl et al. (2021) using the Earth System Model of intermediate complexity cGENIE (Ridgwell et al. 2007-updated), confirming that these results are not overly model-dependent.

Despite the simplicity of the biogeochemical module embedded in their MITgcm setup, Pohl et al. (2017a) notably demonstrated a remarkable match between their results and the black shale compilation of Melchin et al. (2013) during the Katian, with high (low) simulated productivity levels corresponding to the preservation of sediments testifying of anoxic (oxic) depositional settings in the geological record (Pohl et al. 2017b; Fig. 3). Pohl et al. (2017b) extended the modeling to the Early (480 Ma) and Mid (460 Ma) Ordovician and showed that
simulation results satisfactorily compare with the geological record of Ordovician upwelling (Leslie and Bergström 2003; Pope and Steffen 2003; Taylor and Sendino 2010; Fig. 3).

Deep-ocean circulation

Several conceptual models have been proposed in order to explain the coupled changes observed in ocean temperatures, carbon isotopes, black shale depositional settings, platform carbonate accumulation rates and the diversity of marine faunas during the Silurian (Jeppsson 1990; Bickert et al. 1997; Jeppsson and Aldridge 2000; Cramer and Saltzman 2005, 2007; Johnson 2006). The seminal model of Jeppsson and collaborators (e.g., Jeppsson, 1990; Jeppsson and Aldridge, 2000), in particular, considers the alternation between two stable ocean states. ‘Primo’ episodes are characterized by a cool climate and a low eustatic sea level. Deep waters forming at the high latitudes efficiently ventilate and oxygenate the deep ocean, while the weathering of the sediments exposed due to the eustatic regression fosters nutrient delivery to the ocean, primary productivity and black shale deposition in low-latitude shelfal settings. ‘Secundo’ episodes are warmer. In the conceptual model, deep waters form at the mid latitudes during such episodes. These waters are warmer and less oxygenated. These conditions favor anoxia and black shale deposition in the deep ocean, while the high sea levels and limited continental weathering favor carbonate deposition in the shallow ocean at low latitudes. This conceptual model has undoubtedly fostered discussion (e.g., Loydell, 2007, 2008; Munnecke et al. 2010) but found limited support in recent geochemical data (Kaljo et al. 2003; Trotter et al. 2016).

To our knowledge, no such models have been proposed for the Ordovician. The deep-ocean circulation at that time remains poorly constrained. Recently, Rasmussen et al. (2016) coupled relatively high resolution δ18O measurements with new estimates of the eustatic variations derived from the analysis of biofacies to demonstrate the onset of icehouse
conditions during the Mid Ordovician (Dapingian-Darriwilian boundary, around 467 Ma) (see also Vandenbroucke et al. 2009; Dabard et al. 2015; Pohl et al. 2016a), coincident with the highest diversity peaks of the Great Ordovician Biodiversification Events (Trotter et al. 2008). To explain this chronology of events, Rasmussen et al. (2016) suggested that global cooling and glaciation initiated thermohaline circulation. In their hypothesized scenario, the initiation of this “Lower Paleozoic Great Ocean Conveyor Belt” would have promoted primary productivity by the phytoplankton and consequently a revolution in the entire trophic chain. It is not our goal here to discuss the biological aspect of the model of Rasmussen et al. (2016) – a point debated elsewhere in this volume – and we will focus here on the hypothesized changes in the ocean circulation.

The response of the deep-ocean circulation to global cooling during the Ordovician is largely unconstrained. A strengthening and deepening of the deep-ocean circulation in response to global cooling (Rasmussen et al. 2016) is supported by the general circulation models of Poussart et al. (1999) and Pohl et al. (2017a). Modeling results obtained by Herrmann et al. (2004a) are more equivocal: while the main cell of the meridional overturning circulation (in the Southern Hemisphere) significantly strengthens in their model in response to a pCO$_2$ drop from 15 PAL (preindustrial atmospheric level; 1 PAL CO$_2$ = 280 ppm CO$_2$) to 8 PAL using a Sandbian (i.e., Caradoc, early Late Ordovician) continental configuration, it slightly weakens in response to such a pCO$_2$ drop using the Katian (i.e., Ashgill, late Late Ordovician) continental configuration (their Fig. 7). Pohl et al. (2021), using the Earth System Model of intermediate complexity eGENIE (Ridgwell et al. 2007-updated), simulated a more complex response of the deep-ocean circulation to climate change during the latest Ordovician Mass Extinction phase 2 (LOME 2, late Hirnantian, ca. 443 Ma). In their simulations, deep waters form at the high latitudes of both hemispheres under a warm climate (24 PAL, Fig. 4a). When pCO$_2$ is lowered to intermediate values (6–10 PAL), deep-
water formation stops over the North Pole and the southern overturning cell strengthens (Fig. 4b). Upon further cooling to 5 PAL, deep-water formation intensifies in the Northern Hemisphere while the southern cell collapses (Fig. 4c). The model of marine biogeochemistry embedded in cGENIE permits to visualize and quantify the impact of the reorganization of the ocean circulation on benthic dissolved oxygen concentrations (Fig. 4d–f). Unexpectedly, the maximum in Southern Hemisphere overturning simulated for intermediate pCO$_2$ values (Fig. 4b) is associated with the spread of seafloor anoxia globally (Fig. 4e). Indeed, deep waters forming over the South Pole are restricted to the West of the low-latitude continents Laurentia and Baltica at depth, leaving most of the Late Ordovician benthic environment poorly oxygenated. A shift in global ocean circulation similar to the one obtained when decreasing pCO$_2$ from 24 to 8.5 PAL was also simulated in response to global climate cooling in the higher-resolution MITgcm (Pohl et al. 2017b), with a shut-down of deep-water formation over the North Pole and a restriction of southern-sourced oxygenation to the west of Laurentia and Baltica. The resulting deoxygenation of the deep ocean simulated in tandem with global cooling, from 24 to 8.5 PAL (Fig. 4d, e) aligns well with the increase in the extent of global seafloor anoxia reported based on uranium isotope data (carbonate $\delta^{238}$U; Bartlett et al. 2018; Stockey et al. 2020) during the LOME 2 glacial maximum (Pohl et al. 2021).

Taken together, these modeling studies confirm that simulated deep-ocean circulation patterns and their response to climate change are dependent on the numerical model and experimental setup, in line with the spread simulated in the response of the Atlantic meridional overturning circulation in the Paleoclimate Modeling Intercomparison Project (Weber et al. 2007). The cGENIE experiments of Pohl et al. (2021) further show that changes in the ocean circulation can lead to major, and possibly unexpected, reorganizations of the global ocean biogeochemistry and the redox landscape in particular.
Conclusive remarks and future research targets

Despite promising advances in our understanding of the Ordovician ocean circulation, a great deal remains to be done. The assimilation of abundant geological data into numerical models of the ocean probably constitutes a promising way forward. Geological proxy data, on the one hand, constitute the raw material documenting, sometimes in a very indirect manner, the ocean circulation in the deep time. They are required to improve our knowledge, but their interpretation is generally not straightforward, and their preservation is erratic. General circulation models, on the other hand, provide an incomplete and necessary biased vision of the ocean in the past, but they permit to quantify processes. Although data and models both have merits on their own, they become most powerful when used in combination, with numerical models aiding the interpretation of signals born by geological data and permitting to test hypotheses in a quantified numerical framework.

Fortunately, the paleontological database is rapidly growing (e.g., Alroy et al. 2008), permitting to refine our vision of the connectivity of the different regions of the globe and thus providing new insights into possible past upper-ocean currents. This effort benefits from ongoing improvements in the deep-time continental reconstructions, which are increasingly more often based on full plate models and generally permit to calculate the paleo-position of sampling locations based on their present-day latitude-longitude coordinates (Torsvik 2009; Torsvik and Cocks 2013; Scotese 2016; Scotese and Wright 2018; Cocks and Torsvik 2020; Williams et al. 2020; Harper et al. 2021).

Reconstructing the deep-ocean circulation is even more challenging. The vast majority of the Ordovician seafloor has been recycled during subduction (Granot 2016). Only highly indirect proxies can be used; among them, redox proxies representative of the global ocean (as opposed to proxies indicative of local redox conditions) (e.g., δ²³⁸U, δ⁹⁸Mo) provide
information on the state of global ocean oxygenation (Dahl et al. 2010; Bartlett et al. 2018; Stockey et al. 2020; Zhang et al. 2020). The assimilation of such data in an Earth System Model permits disentangling the contributions of changes in the biological pump and ocean ventilation, hence inferring fundamental characteristics of the deep-ocean circulation (e.g., Pohl et al. 2021; Fig. 4).

Numerical models are also rapidly improving. They represent an increasing number of components of the climate system. The explicit simulation of ocean biogeochemistry (Ridgwell et al. 2007), sometimes including some representation of the marine primary producers (Follows and Dutkiewicz 2011; Ward et al. 2018; Wilson et al. 2018), constitutes a major step forward in permitting to directly compare model results to proxy data – including redox proxies (Lu et al. 2018; Pohl et al. 2021). The large computational cost associated with most recent Earth System Models often precludes their use in the deep time when boundary conditions are uncertain and many model parameters have to be tested by means of large gridded ensembles of model experiments (e.g., Pohl et al. 2021; Wong Hearing et al. 2021). However, advances in supercomputers, combined with efforts to develop ‘deep-time’ versions of recent Earth System Models (e.g., Ladant et al. 2020; Sepulchre et al. 2020; Zhu et al. 2020) and the advent of versatile model grids (e.g., Adcroft et al., 2004; Petersen et al., 2019), will undoubtedly facilitate the use of such complex models in the years to come (e.g., Laugie et al. 2021). Using higher-resolution (potentially regional) general circulation models, one could easily imagine quantifying the dispersal potential of marine larvae by simulating the trajectory taken by particles ‘injected’ at specific locations in the model (e.g., Nooteboom et al. 2020). Such approach would further help interpreting paleontological data. Of course, the use of high-resolution models would be fully beneficial only with well-constrained boundary conditions, including land-sea mask and bathymetry, the acquisition of which will necessarily rely on the acquisition of new geological data.
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CONFLICTS OF INTEREST

The authors declare no known conflicts of interest associated with this publication.

DATA AVAILABILITY

Data sharing is not applicable to this article as no datasets were generated during the current study.

AUTHORS CONTRIBUTIONS

AP, EN, TRAV and YD contributed to conceptualization, funding acquisition, investigation and manuscript writing.

FIGURE CAPTIONS

Figure 1: Upper-ocean circulation and water masses in the Late Ordovician (Katian – Ashgill). Northern hemispheric summer and southern hemispheric winter. Redrawn after Wilde (1991).
Figure 2: Map of upper-ocean currents for 480 Ma and 2240 ppm atmospheric CO$_2$. Stream lines represented using the “streamplot” function of the Matplotlib Python package (Hunter 2007). Background shading is current speed. For comparison, the Gulf Stream today regularly exceeds a speed of 1 m s$^{-1}$, an order of magnitude higher than currents in most other ocean regions (e.g., Dong et al. 2019) (see also the high-resolution visualization of Modern ocean currents proposed by the NASA/Goddard Space Flight Center Scientific Visualization Studio at https://svs.gsfc.nasa.gov/3958). Landmasses (at a depth of ca. 200 m) are shaded white. Red and blue points respectively represent the Central Andean Basin and the South European microcontinents. Key upper-ocean currents are shown with thick black arrows: SW, Southern Westerlies, GC: Gondwana Current, AC: Antarctica Current. Beyond 40° N, the ocean circulation is zonal. Equal Earth projection. Adapted after Pohl et al. (2016b).

Figure 3: Late Ordovician (Katian) surface primary productivity simulated using the MITgcm. Landmasses are shaded black. Red and white points represent the preservation of black shales (red) and oxic deposits (white) during the late Katian after Melchin et al. (2013). Grey points represent evidence of upwelling after Pope and Steffen (2003). Adapted from (Pohl et al. 2017b, a).

Figure 4: Response of the Late Ordovician deep-ocean circulation to cooling in the cGENIE model. Meridional overturning circulation (a–c; 1 Sv = 10$^6$ m$^3$ s$^{-1}$) and deep-ocean oxygen concentration at ca. 3900 m water depth (d–f) simulated using a pCO$_2$ of (a, d) 24 PAL, (b, e) 8.5 PAL and (c, f) 5 PAL. In panels (a–c), positive (negative) values in the meridional overturning circulation represent clockwise (anticlockwise) cells. In panels (d–f), results are shown for an atmospheric partial pressure of oxygen of 0.4 PAL and a mean ocean nutrient...
(phosphate) concentration of 0.4 times the present-day value. L: Laurentia; B: Baltica; S: Siberia; G: Gondwana. Modified after Pohl et al. (2021).

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CURRENTS
NP = North Polar Current
NSP = North Subpolar Current
NT = North Tropical Current
NE = North Equatorial Current
M = Monsoonal Counter-Current
SE = South Equatorial Current
ST = South Tropical Current
SSP = South Subpolar Current
SP = South Polar Current

WATER MASSES
Cold
Cool
Warm

LEGEND
Warm Currents
Cool Currents
Subtropical Convergence
Polar Convergence
Center of Oceanic High Pressure