Co-evolution of oceans, climate, and the biosphere during the ‘Ordovician Revolution’: A review

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1. Introduction

The Ordovician Period (~485–444 Ma) was an interval of major, causally interconnected changes in the Earth’s biotic, climatic, and environmental systems. The diversity of marine life increased sharply during the Great Ordovician Biodiversification Event (GOBE; [Webby et al., 2004](#); [Fig. 1](#)). The GOBE was terminated by the end-Ordovician mass extinction, the first of the ‘Big Five’ Phanerozoic mass extinctions ([Sepkoski, 1996](#)), which coincided with the Hirnantian glaciation, the first ice age since the late Neoproterozoic. This event was the culmination of a cooling trend that had begun in the Early or Middle Ordovician ([Trotter et al., 2008](#); [Vandenbroucke et al., 2010](#)), and that was linked to some combination of reduced volcanic arc outgassing ([McKenzie et al., 2016](#)), enhanced silicate weathering ([Young et al., 2009](#); [Lefebvre et al., 2010](#); [Nardin et al., 2011](#)), and increased organic carbon burial ([Brenchley et al., 1994](#); [Yan et al., 2009](#); [Zhang et al., 2010](#); [Hammarlund et al., 2012](#)). Also important were contemporaneous bioevolutionary events, i.e., the appearance of various zooplankton clades ([Servais et al., this volume](#)) and the earliest land plants ([Lenton et al., 2012](#)), oceanographic changes, e.g., intensified ocean circulation related to climatic cooling ([Kidder and Tomescu, this volume](#)), and (3) geotectonic processes, e.g., a possible mid-Ordovician superplume ([Algeo, 1996](#); [Barnes, 2004a](#)). The relationships among these many co-occurring developments are complex, which makes the Ordovician a classic example of co-evolution of Earth systems and a fascinating geologic period for study.

This special issue of *Palaeogeography Palaeoclimatology Palaeoecology* is thematically dedicated to the ‘Ordovician Revolution’. It builds on earlier organized research efforts, in

particular those of International Geoscience Programme (IGCP) projects 410 (2000-2004), 503 (2005-2010), and 591 (2011-2016), which have yielded many advances in our understanding of the Ordovician Revolution. The 13 contributions in this volume cover many aspects of the major changes that characterize the Ordovician Period. In addition to this introductory review paper, various contributions investigate the relationship of surface-ocean circulation patterns to atmospheric CO₂ levels (Pohl et al.), major changes in marine phytoplankton communities (Servais et al.), changes in the marine silica cycle possibly linked to increased radiolarian productivity (Kidder and Tomescu), marine carbonate and/or organic carbon isotope records (Pruss et al., Quinton et al., Jones et al., Edwards and Saltzman, Zhang and Munnecke), the operation of the marine sulfur cycle (Kah et al.), redox changes associated with the onset of the GOBE (Marenco et al.), the interplay of the marine carbon and sulfur cycles (Young et al.), and diagenetic influences on conodont REE and trace-element compositions (Zhang et al.). The geographic and stratigraphic ranges of these studies are shown in Figures 2 and 3, respectively. Below, we discuss the significance of these contributions in the context of broader research issues pertaining to the ‘Ordovician Revolution’.

2. Stratigraphic framework

The Ordovician System is subdivided into lower, middle, and upper series (Fig. 3; Cooper and Sadler, 2012). The Lower Ordovician consists of the Tremadocian and Floian stages, the Middle Ordovician of the Dapingian and Darriwilian stages, and the Upper Ordovician of the Sandbian, Katian, and Hirnantian stages. All stage boundaries have been formally ratified by the International Commission on Stratigraphy (<http://www.stratigraphy.org/gssp/>). The most recent international geologic timescale (Gradstein et al., 2012) dates the start and end of the Ordovician Period at 485.4 and 443.8 Ma, respectively, yielding a duration of 41.6 Myr (Cooper and Sadler, 2012).

Biostratigraphic control for the Ordovician is provided mainly by conodonts in shallow-water settings and graptolites in deep-water settings, although zonation schemes for trilobites, brachiopods, acritarchs, and other fossil types have been developed (Cooper and Sadler, 2012). Both the conodont- and graptolite-based schemes have individual zones averaging ~2 Myr in duration and separate zonal successions for warm-water and cool-water provinces. An integrated scheme was generated by Sadler et al. (2009) using the CONOP (constrained optimization) method applied to a dataset of 430 stratigraphic sections globally, an analysis that provided the foundation for the present standard Ordovician timescale (Cooper and Sadler, 2012).

Carbonate carbon isotopes represent an important tool for international correlations of the Ordovician System (Bergström et al., 2009, 2010; Azmy et al., 2014; Edwards and Saltzman, 2014). A series of positive excursions has been identified (Fig. 3), among which the middle Darriwilian carbon isotope excursion (MDICE), the Guttenberg carbon isotope excursion (GICE), and the Hirnantian carbon isotope excursion (HICE) are the best documented. All three isotopic events were of global extent, having been identified in North American, European, and Chinese sections at a minimum. The MDICE was an event spanning the mid to late Darriwilian Stage (*Didymograptus artus*-*Pygodus serra* zones), dating to ~464-460 Ma (Ainsaar et al., 2010; Leslie et al., 2011; Schmitz et al., 2011; Thompson et al., 2012; Albanesi et al., 2013; Calner et al., 2014; Zhang and Munnecke, this volume). The GICE was an event correlative with the Sandbian-Katian boundary, dating to ~453 Ma (Ludvigson et al., 2004; Kaljo et al., 2004; Tobin

et al., 2005; Young et al., 2005, 2008; Bergström et al., 2008; Buggisch et al., 2010; Ainsaar et al., 2010; Zhang et al., 2010; Munnecke et al., 2011; Pancost et al., 2013; Quinton et al., this volume). The HICE was an event spanning the early Hirnantian Stage (*Normalograptus extraordinarius* Zone), dating to ~445-444 Ma (Marshall and Middleton, 1990; Brenchley et al., 1994; Finney et al., 1999; Zhang et al., 2000; Kaljo et al., 2004, 2007; Melchin and Holmden, 2006; LaPorte et al., 2009; Fan et al., 2009; Yan et al., 2009; Ainsaar et al., 2010; Zhang et al., 2010; Jones et al., 2011; Zhang and Munnecke, this volume).

The utility of carbonate carbon isotopes for correlation in the Ordovician System is demonstrated in the study of **Zhang and Munnecke (this volume)**. They generated high-resolution $\delta^{13}\text{C}$ curves for nine sections from the Tarim Basin in northwestern China, which was an isolated terrane on the northeastern Gondwanan margin during the Ordovician. They identified the well-known MDICE and GICE excursions in multiple sections, as well as several lesser-known excursions, allowing detailed correlations among the study sections as well as to global C-isotope reference profiles. In some of the study sections, stratigraphic incompleteness owing to large sea-level fluctuations resulted in stacking of carbon isotope excursions, as a result of which integrated biostratigraphic-isotopic control was essential in establishing the ages and depositional histories of these study sections.

3. Marine ecosystems and biodiversification

Although the fossil records of most animal phyla were established by the end of the Cambrian Radiation, the Ordovician experienced a huge diversification of marine taxa at the family, genus, and species levels known as the Ordovician Radiation (Miller, 1997) or Great Ordovician Biodiversification Event (GOBE; Webby et al., 2004; Harper, 2006, 2015; Servais et al., 2010; Fig. 1). This event ushered in the change in dominance from the Cambrian Evolutionary Fauna to the Paleozoic Evolutionary Fauna, which was the primary component of marine communities until the end-Permian mass extinction. Recent work suggests that evolutionary diversification during the GOBE occurred in a series of pulses (Harper, 2006; Servais et al., 2010). However, generally low ecosystem stability is suggested by background rates of extinction that were significantly higher than for younger geologic intervals (Gilinsky, 1994).

Marine ecosystems underwent major structural changes during the Ordovician. Trophic chains lengthened as archaic predators such as the anomalocarids disappeared (Collins, 1996) and new, larger predatory organisms evolved. In particular, nautiloid cephalopods, which appeared in the late Cambrian, diversified and increased in abundance greatly during the Ordovician, although perhaps being mainly scavengers at that time (Brett and Walker, 2002). The Middle Ordovician also witnessed the appearance of eurypterids, asteroids, varied arthropods, and drilling gastropods (Brett and Walker, 2002). Rates of species origination, although generally high throughout the Cambrian-Ordovician, appear to have peaked in the Middle Ordovician (Bambach et al., 2004). Diversity increased among some groups such as brachiopods, trilobites, and echinoderms during the Floian, but the main pulse of diversification of the GOBE occurred later, during the Darriwilian (Webby et al., 2004; Fig. 1).

New communities of marine organisms developed largely during the Ordovician. Deepwater communities diversified as a result of offshore migration of certain previously shallow-water clades (Jablonski et al., 1983). Infaunal burrowing increased markedly (Bottjer et

al., 1988; Droser and Bottjer, 1989; Mángano and Droser, 2004). Encrusting organisms found on both hardgrounds and shelly substrates undergo a radiation during the Middle Ordovician, with the appearance of new groups of holdfast-bearing pelmatozoans, tube-dwelling annelids, and encrusting bryozoans (Brett, 1988). The Ordovician is also characterized by the first records of many endolithic organisms, with borings produced by cyanobacteria, green algae, red algae and heterotrophic microbionts from the Upper Ordovician Cincinnati Series (Vogel and Brett, 2009). Larger borers, such as rock-boring bivalves, also evolved during the Late Ordovician (Brett, 1988).

Hardgrounds are far more common in the Ordovician than in the preceding Cambrian Period (Taylor and Wilson, 2003). The prevalence of hardgrounds during the Ordovician may have been due to a combination of factors: (1) high sea levels and extensive cratonic flooding (Algeo and Selslavinsky, 1995; Haq and Schutter, 2008), and (2) global cooling (Trotter et al., 2008; Nardin et al., 2011; Chen et al., 2013; Fig. 1), which caused shallowing of the aragonite and calcite compensation depths (ACD and CCD, respectively). The latter condition favored the development of ‘calcite seas’ (i.e., seawater that is comparatively less saturated with respect to all forms of calcium carbonate; Wilkinson et al., 1985), resulting in dissolution of aragonite and precipitation of secondary calcite cements at shallow depths (Palmer et al., 1988; Taylor and Wilson, 2003). The contemporaneous radiation of boring organisms was due to a combination of the increased availability of both hardgrounds and shelly substrates, the latter itself a consequence of the GOBE, which greatly expanded the range of hard-substrate niches available to borers (Wilson and Palmer, 2006). In addition, the intensity of boring, as measured by the number of borings per unit area of hard substrate, increased sharply during the Ordovician, a pattern termed the ‘Ordovician Bioerosion Revolution’ by Wilson and Palmer (2006).

Two contributions to the present volume address an aspect of Ordovician biodiversification that has received comparatively little study to date: the evolution of the marine plankton community. Servais et al. (this volume) document changes in diversity among acritarchs, radiolarians, graptolites, and chitinozoans. They also review evidence for contemporaneous changes in life modes, i.e., a switch from the benthon to the plankton by certain groups of arthropods and molluscs, and the origin of planktotrophy in invertebrate larvae. The most important changes in the marine plankton community (termed the ‘Ordovician Plankton Revolution’) appear to date to the late Cambrian-Early Ordovician interval, preceding and possibly contributing to the subsequent GOBE. Although the trigger for the Ordovician Plankton Revolution is unknown, they may have been linked to oceanic changes during the late Cambrian, e.g., a major organic carbon burial event (reflected in the Steptoean Positive Carbon Isotope Excursion, or SPICE; Gill et al., 2011) and concurrent increases in atmospheric O₂ (from 10-18 % to 20-29 %) (Berner, 2006; Saltzman et al., 2011) and oceanic nutrient levels. In turn, changes in the plankton community may have instigated major changes in sedimentation patterns and biogeochemical cycling. Although radiolarians had appeared in the Cambrian, they increased greatly in abundance and diversity during the Ordovician. Kidder and Tomescu (this volume) explore the hypothesis that an increase in radiolarian productivity during the Ordovician was responsible for (1) a shift in the dominant locus of chert deposition from shallow peritidal to deep-shelf and basin settings, and (2) a consequent drawdown of dissolved silica in ocean-surface waters that forced siliceous sponges to move into deeper waters.

4. Paleooceanography and paleoclimate of the Ordovician

4.1. Paleoocean-climate connections

Major climatic changes occurred during the Ordovician. A gradual cooling through most of the Ordovician has been inferred on the basis of conodont O-isotope data (Bassett et al., 2007; Buggisch et al., 2010; Nardin et al., 2011; Rosenau et al., 2012; Quinton and MacLeod, 2014; Rasmussen et al., 2016; Fig. 1), although the low resolution of the longest-ranging O-isotope record (Trotter et al., 2008) leaves the details of timing uncertain at present. This cooling trend has been attributed to enhanced burial of organic carbon linked to higher marine productivity (Qing and Veizer, 1994; Patzkowsky et al., 1997; Yan et al., 2009; Zhang et al., 2010; Hammarlund et al., 2012; Lenton et al., 2012) and, thus, to drawdown of atmospheric $p\text{CO}_2$ (Gibbs et al., 1997; Herrmann et al., 2004a). In this scenario, the Hirnantian glaciation represents the culmination of a long-term cooling trend, when a critical $p\text{CO}_2$ threshold (or ‘tipping point’) was overstepped. Contemporaneous mega-volcanic eruptions do not appear to have measurably influenced climate (Herrmann et al., 2010).

The vigor of global-ocean circulation is closely linked to global climate and the steepness of pole-to-equator temperature gradients (Rind, 1998; Meehl et al., 2007; Toggweiler and Russell, 2008). Greenhouse conditions produce flatter latitudinal temperature gradients and less vigorous ocean circulation, whereas climatic cooling produces a steeper latitudinal temperature gradient and more vigorous ocean circulation. In this context, major cooling during the Ordovician is predicted to have intensified ocean circulation. The study by Pohl et al. (this volume) reconstructs Ordovician ocean-surface circulation patterns based on simulations using FOAM, a coupled ocean-atmosphere general circulation model, and state-of-the-art paleogeographic reconstructions (Torsvik and Cocks, 2009, 2013). Although their modeled surface-ocean circulation patterns are similar to those given in a conceptual model of Wilde (1991) and earlier GCM models (Poussart et al., 1999; Herrmann et al., 2003, 2004a,b), the present study shows that ocean-surface circulation patterns were highly sensitive to atmospheric CO_2 levels, with substantial differences for high- CO_2 (16 PAL), medium- CO_2 (8 PAL) and low- CO_2 (4 PAL) simulations. The role of atmospheric CO_2 variation was discerned by Pohl et al. owing to a larger CO_2 range (4-16 PAL vs. 8-18 PAL), greater climate sensitivity (3-11 °C/ CO_2 doubling vs. 2.5 °C/ CO_2 doubling), and larger modeled temperature variation (14 °C vs. 5.5 °C) than in Herrmann et al. (2004a). In addition, Pohl et al.’s simulations revealed a climate threshold at transitions between 4 and 8 PAL CO_2 that triggered large (11 °C) temperature changes.

4.2. Marine carbon isotope events

The late Cambrian was characterized by strong perturbations to the global carbon cycle as recorded by a series of positive $\delta^{13}\text{C}_{\text{carb}}$ excursions (Saltzman et al., 2000; Bergström et al., 2008; Fig. 1). These fluctuations have been attributed to unstable redox conditions and intermittent expansion of euxinia in the global ocean (Saltzman et al., 2000; Hurtgen et al., 2009; Gill et al., 2011). The Early-Middle Ordovician is characterized by relatively stable $\delta^{13}\text{C}_{\text{carb}}$ of ca. -1 ‰ with a few small isotopic excursions that ended in the Floian, possibly due to a better-oxygenated global-ocean system (Taylor et al., 2004; Edwards and Saltzman, 2014; Saltzman et al., 2015). The relative stability of the global carbon cycle during this interval is reflected in the $\delta^{13}\text{C}_{\text{carb}}$ record from Cow Head Group carbonates in western Newfoundland generated by Pruss et al. (this volume). The only significant feature in their record, which spans the Upper

Cambrian (mid-Croixian) to Lower Ordovician (uppermost Arenigian), is a ~2 ‰ negative excursion (from ~+1 to -‰) in the upper Tremadocian. The relatively stable oceanic conditions implied by such limited $\delta^{13}\text{C}_{\text{carb}}$ variation were favorable for benthic marine communities and skeletal carbonate production, possibly contributing to the GOBE (Pruss et al., 2010; Saltzman et al., 2011).

More volatile carbon-cycle conditions reappeared during the latest Middle Ordovician and continued into the Late Ordovician, as recorded by the MDICE, GICE and HICE carbon isotope events (Brenchley et al., 1994; Patzkowsky et al., 1997; Pancost et al., 1999, 2013; Young et al., 2008, 2010; LaPorte et al., 2009; Zhang et al., 2010; Jones et al., 2011; Metzger and Fike, 2013; Melchin et al., 2013; Calner et al., 2014; Fig. 1). The MDICE is a relatively broad event (spanning several million years) of modest amplitude (typically +1 to +2 ‰). The GICE is a much shorter event (≤ 0.5 Myr) of somewhat larger amplitude (typically +2 to +4 ‰). The HICE event, which is closely connected to the Hirnantian glaciation and, thus, has a duration between 0.5 and 1.0 Myr, shows an even larger amplitude than the earlier events (typically +3 to +7 ‰). The HICE event has been interpreted as evidence of widespread burial of organic carbon and consequent ^{13}C enrichment of seawater dissolved inorganic carbon (Saltzman and Young, 2005; Zhang et al., 2011). An alternative hypothesis linked the HICE to enhanced carbonate weathering during the Hirnantian glaciation (Kump et al., 1999; Jones et al., 2011), but this process seems unlikely to have yielded such large carbon isotopic excursions at the scale of the global ocean (LaPorte et al., 2009; Holmden et al., 2012).

Several studies in the present volume show that the record of Ordovician carbon-isotope excursions was influenced locally by sequence stratigraphic factors. The study by Quinton et al. (this volume) identified the GICE in one of four Upper Ordovician sections from northeastern Alabama, representing the southern margin of early Paleozoic Laurentia. This 1.5 ‰ positive excursion is located just above the Millbrig K-bentonite, a well-studied volcanic tephra layer (Kolata et al., 1987; Haynes, 1994; Sell et al., 2015) that has been radiometrically dated to 454–453 Ma (Cooper and Sadler, 2012). The absence of the GICE event in their other three study sections was attributed to unconformities. The study by Jones et al. (this volume) generated high-resolution $\delta^{13}\text{C}_{\text{carb}}$ records for five sections of the Ely Springs Dolostone in Utah and Nevada, forming a transect across the eastern Great Basin. Correlation with the late Katian Cincinnati reference curve from eastern North America shows that the mid-Katian Whitewater negative excursion and the HICE are present. The HICE $\delta^{13}\text{C}$ maximum exhibits a pronounced lateral gradient, diminishing from basinal areas (+7.5 ‰) to inner-shelf areas (+2.5 ‰). This gradient is attributed to a combination of factors including development of a regional unconformity during the Hirnantian glacio-eustatic lowstand that truncated the Upper Ordovician more deeply on the periphery of the Ibex Basin than in its center, as well as local incorporation of authigenic carbonate phases driven by methanogenesis.

4.3. Climate connections to global carbon-sulfur cycles

Major climate changes during the Ordovician appear to have been intimately connected to global carbon cycle perturbations. The positive marine carbonate carbon isotope excursions discussed above are generally attributed to enhanced organic carbon burial, which lowered atmospheric $p\text{CO}_2$ and induced global cooling (Brenchley et al., 1994, 2003; Saltzman and Young, 2005; Gill et al., 2007; Young et al., 2008, 2010; Zhang et al., 2009, 2011). Anoxia was widespread in Ordovician oceans, especially during the pre-Hirnantian as reflected in black shale

deposition (Berry et al., 1989; Berry, 2010) and positive sulfur isotope excursions (Zhang et al., 2011; Thompson and Kah, 2012). The GICE event has been linked to an increase in phosphate and chert deposition in the Laurentian epeiric sea that may record intensified upwelling (Patzkowsky and Holland, 1996; Pope and Steffen, 2003). However, local influences on carbon cycling are apparent in gradients of inorganic carbon isotopes within restricted epicontinental seas (Holmden et al., 1998; Panchuk et al., 2005; Quinton et al., this volume).

The Early Paleozoic was a critical interval with regard to oceanic redox conditions, representing a transition from mainly anoxic deepwater conditions in the pre-Phanerozoic to mainly oxic deepwater conditions in the post-Devonian. During the Cambro-Ordovician, oceanic anoxia may have expanded recurrently (Zhuravlev and Wood, 1996; Hough et al., 2006; Hurtgen et al., 2009; Thompson and Kah, 2012; Marenco et al., 2013), serving as a trigger for local bioturbation events (Saltzman et al., 2015). Major pulses of evolutionary diversification associated with the GOBE did not begin until after a prolonged period without positive isotopic excursions during the Early Ordovician, interpreted to reflect increasing oxygenation of the deep ocean (Saltzman et al., 2015). The study by Marenco et al. (this volume) tests this idea by looking at Th/U ratios in marine carbonates through the Lower and Middle Ordovician. They show that a significant decline in Th/U ratios occurred at the end of the Tremadocian, concurrently with the last bioturbation extinctions (Saltzman et al., 2015), reflecting decreased removal of U to anoxic facies in response to increasing deepwater oxygenation.

Atmospheric $p\text{CO}_2$ is thought to have declined strongly during the Ordovician in response to enhanced organic carbon burial. One test of this idea is based on $\Delta^{13}\text{C}_{\text{carb-org}}$, as calculated from paired carbonate and organic carbon isotope records, which can serve as a proxy for photosynthetic fractionation by marine phytoplankton (Popp et al., 1989; Kump and Arthur, 1999). Under low (high) atmospheric $p\text{CO}_2$ conditions, phytoplankton are expected to fractionate carbon isotopes to a smaller (larger) degree. Paired isotopic records show a ~ 3 ‰ increase in $\Delta^{13}\text{C}_{\text{carb-org}}$ through the Early–Middle Ordovician, implying rising atmospheric CO_2 levels (Edwards and Saltzman, this volume). This seems unlikely, however, on two counts: (1) estimated atmospheric CO_2 levels for the Ordovician (e.g., Berner and Kothvala, 2001) were too high to trigger large changes in photosynthetic fractionation, and (2) the implied secular trend toward higher $p\text{CO}_2$ runs counter to other evidence for falling $p\text{CO}_2$ during the Ordovician (e.g., climatic cooling; Nardin et al., 2011). Alternative explanations for the increase in $\Delta^{13}\text{C}_{\text{carb-org}}$ invoke changes in phytoplankton communities, cell growth rates, or changes in O_2/CO_2 ratios (Popp et al., 1998; Pancost et al., 2013; Edwards and Saltzman, this volume). However, global cooling during this interval may account for more than half of this C isotopic shift, as a ~ 14 °C cooling (Trotter et al., 2008; Nardin et al., 2011) would translate into a 1.7 ‰ change in ϵ_p based on a temperature dependence of 0.12 ‰/°C (Hayes et al., 1999).

The relationship between organic carbon burial and global cooling continued into the Hirnantian Stage (Brenchley et al., 1994; Saltzman and Young, 2005; Zhang et al., 2009, 2011; Young et al., 2010; Jones and Fike, 2013). Indeed, a positive feedback between enhanced thermohaline circulation, marine productivity, drawdown of atmospheric $p\text{CO}_2$, and global cooling may have contributed to the intense but brief nature of the Hirnantian glaciation. Approximately correlative excursions in $\delta^{13}\text{C}_{\text{org}}$ and $\delta^{34}\text{S}_{\text{py}}$ have been widely reported (Wang et al., 1993, 1997; Chen et al., 2006; Yan et al., 2009; Zhang et al., 2009, 2011). Whereas the positive $\delta^{13}\text{C}_{\text{carb}}$ shift at the Katian–Hirnantian boundary (base of *N. extraordinarius*–*N. ojsuensis*

Zone) is globally correlative, the positive shift in $\delta^{13}\text{C}_{\text{org}}$ records appears to be regionally diachronous, commencing variably below the Katian-Hirnantian boundary (within the *D. mirus* Subzone; [Yan et al., 2009](#)), at the boundary ([Melchin and Holmden, 2006](#)), or above it (mid-*N. extraordinarius*–*N. ojsuensis* Zone; [Zhang et al., 2009](#)). The diachroneity in the $\delta^{13}\text{C}_{\text{org}}$ records is probably due to regional variation in the timing and intensity of changes in marine productivity and organic carbon burial.

Sulfur isotope evidence also is relevant to an understanding of coeval climate-carbon cycle changes. [Young et al. \(this volume\)](#) document co-variation in C- and S-isotopes for Middle-Late Ordovician successions from the Appalachian Basin and Arbuckle Mountains, finding two major events in which large (12 ‰) negative shifts in $\delta^{34}\text{S}_{\text{CAS}}$ are linked to positive shifts in $\delta^{34}\text{S}_{\text{pyrite}}$ (+10 ‰) and $\delta^{13}\text{C}_{\text{carb}}$ (+2 ‰). Their geochemical model suggests that reductions in the global pyrite burial rates or in S-isotopic fractionation between seawater sulfate and sedimentary pyrite can account for the observed relationships. These changes may have been driven by increasing oceanic oxygenation, which reduced microbially mediated pyrite burial and organic matter remineralization rates. Although a large increase in the pyrite weathering flux is also a possible cause, geologic and geochemical proxy evidence do not support multiple continental weathering pulses.

The marine sulfate system has conventionally been viewed in terms of a single reservoir model, wherein the isotopic composition of marine sulfate is primarily controlled by burial of sedimentary pyrite ([Claypool et al., 1980](#); [Bottrell and Newton, 2006](#); [Young et al., this volume](#)). [Kah et al. \(this volume\)](#) contend that the utility of this model is limited during times of persistent marine euxinia, when the oxic and anoxic marine sulfur reservoirs can become decoupled. At such times, seawater sulfate concentrations are low ([Thompson and Kah, 2012](#); [Algeo et al., 2015](#)), and short-term fluxes that act between the two reservoirs (e.g., sulfate reduction and sulfide oxidation processes) often dominate over the long-term fluxes (e.g., weathering and pyrite burial) that control the single reservoir ocean model. Based on sections from Argentina, western Newfoundland, and South China, they demonstrate relative stability of the marine sulfur cycle from the Floian through the Dapingian, followed by a major reorganization in the early Darriwilian driven by ocean ventilation. This ventilation event resulted in a rapid change in the isotopic composition of marine sulfate in surface oceans, and ultimately led to the near depletion of hydrogen sulfide within the anoxic reservoir, as recorded by formation of superheavy pyrite. This ventilation event was coeval with a decline in sea-surface temperatures that ultimately led to the late Ordovician glaciation.

4.4. A tectonic or paleobotanic driver?

The cause(s) of the GOBE and concurrent climate-ocean changes remain under debate ([Munnecke et al., 2010](#)). Although a purely bioevolutionary driver within the marine ecosystem cannot be completely ruled out, most researchers favor an external forcing of some type. One possible external forcing is unusual levels of tectonic activity. Major plate tectonic shifts took place globally during the Ordovician as a raster of peri-Gondwanan terranes, including the South China Craton, were dispersed northward ([Chen et al., 2004](#)). The Iapetus Ocean closed and the Rheic Ocean opened as Armorica and Avalonia shifted positions relative to Baltica and Laurentia ([Murphy et al., 2010](#); [Nance et al., 2012](#); [Van Staal et al., 2012](#); [Keppie and Keppie, 2014](#)). Increased MOR spreading rates related to rapid continental dispersion led to globally high

sea levels (Miller et al., 2005; Haq and Shutter, 2008) and widespread continental flooding (Algeo and Seslavinsky, 1995). Regionally, mountain-building events such as the Taconian Orogeny were important (van Staal and Hatcher, 2010). However, it is unclear that any of these tectonic events were of sufficient magnitude (i.e., larger than other Phanerozoic events of the same type) to have triggered contemporaneous organic carbon burial and global climatic cooling. Furthermore, any cooling induced by enhanced silicate weathering may have been offset by higher volcanic degassing during the Middle Ordovician (Young et al., 2009; McKenzie et al., 2016).

One tectonic event of possible significance in this regard is a putative Ordovician superplume (Algeo, 1996; Barnes, 2004a) or unknown large igneous province (Lefebvre et al., 2010). Direct evidence for an event of this type has been lost owing to subduction of nearly all Ordovician-age oceanic crust, but a number of lines of circumstantial evidence support it. The Middle-early Late Ordovician is characterized by widespread deposition of black shales (Barnes, 2004b) and volcanic massive sulfides (VMS) (Eastoe and Gustin, 1996), formation of ophiolites (Vaughan and Scarrow, 2003), and declining seawater $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (McArthur et al., 2001; Shields and Veizer, 2004; Edwards et al., 2015), all of which are consistent with intensified oceanic magmatism. An important, but widely overlooked, line of evidence supporting a superplume is the existence of a Middle to Late Ordovician magnetic superchron (Algeo et al., 1996; Pavlov and Gallet, 2005; Fig. 1), a feature analogous to the mid-Cretaceous Normal Polarity Superchron, whose relationship to a Pacific superplume appears well-established (Larson, 1991). A steep decline in seawater $^{87}\text{Sr}/^{86}\text{Sr}$ ratios during the Middle Ordovician Darriwilian Stage has been interpreted to reflect weathering of young volcanic rocks on the continents (Young et al., 2009; Saltzman et al., 2014) but may also mark the start of this poorly known superplume event (Shields et al., 2003).

An alternative external forcing mechanism is the evolution of the earliest land plants (Lenton et al., 2012). Multicellular plants first became established on land during the Ordovician, prior to which only microbial crusts are thought to have existed (Retallack, 2013). These plants were bryophyte grade, i.e., lacking a vascular system, and thus structurally equivalent to modern mosses and lichens. Their origin was probably from a freshwater green alga, although the closest modern sister group remains under debate, with various researchers favoring Charales ('stoneworts') or Zygnematales ('pond scum'; Wodniok et al., 2011; Timme et al., 2012). Evolution of the earliest land plants is hypothesized to have had measurable effects on climate and the environment. A likely vector for influencing the marine environment is through intensified weathering and elevated riverine nutrient fluxes, stimulating marine phytoplankton productivity and, thus, organic carbon burial and global climatic cooling (Lenton et al., 2012), a mechanism that is functionally identical to the effects of the better-documented spread of vascular land plants during the Devonian (Algeo et al., 1995, 2001).

The timing of the appearance of land plants is key to this hypothesis, although the sparseness of the present fossil record makes evaluation difficult. The oldest cryptospores are from the Dapingian (Middle Ordovician) of Argentina (Volkheimer et al., 1980; Wellman and Gray, 2000; Rubinstein et al., 2010; Fig. 1). Slightly younger cryptospores, of Darriwilian age, have been reported from the Czech Republic (Vavrdova 1984, 1990) and Saudi Arabia (Strother et al., 1996; Steemans et al., 2009). The oldest cryptospores in Baltica, *Tetrahedraletes medinensis*, *T. grayii* and *Pseudodyadospora* sp., are of late Katian age (Badawy et al., 2014). The first trilete spores are from the Katian or Hirnantian of Turkey (Steemans et al., 2009;

Lenton et al., 2012). Other paleobotanic developments include the earliest glomalean fungi from the late Sandbian of Wisconsin (Redecker et al., 2000) and the earliest sporangial mesofossils from the Katian of Oman and Saudi Arabia (Wellman et al., 2003; Steemans et al. 2009). Although the extent of such early plant cover on continents is highly uncertain (Pohl et al., this volume), the available fossil evidence is consistent with a rapid spread and diversification of non-vascular early land plants during the Middle and Late Ordovician.

6. The end-Ordovician crisis

6.1. The end-Ordovician mass extinction

The end-Ordovician mass extinction collectively eliminated 22-26 % of families, 49-61 % of genera, and ~86 % of species of marine invertebrate animals (Jablonski, 1991; Sheehan, 2001; Harper, 2010; Fig. 1), making it possibly the second most severe biocrisis after the Permian-Triassic boundary event. Among the clades strongly affected were trilobites, brachiopods, graptolites, conodonts, corals, and chitinozoans. The extinction occurred in two steps, the first coinciding with the onset of the Hirnantian glaciation in the *N. extraordinarius*-*N. ojsuensis* Zone at ~445 Ma, and the second coinciding with its termination in the early *N. persculptus* Zone at ~444 Ma (Rong, 1984; Rong et al., 2002; Fan et al., 2009; Harper et al., 2014; Fig. 1). The fauna affected by the second extinction pulse was the cool-water-adapted Hirnantia Fauna, which had appeared around the beginning of the Hirnantian glaciation and had established a wide distribution during the *N. extraordinarius*-*N. ojsuensis* Zone of the early Hirnantian Stage (Rong, 1984; Rong et al., 2002; Zhan et al., 2010).

Microbial community changes are less well documented. The intervals preceding and following the Hirnantian ice age were characterized by relatively greater microbial influence, with abundant evidence of nitrogen-fixing and denitrifying archaea (Rohrssen et al., 2013; Luo et al., 2015). This is consistent with widespread suboxic to anoxic conditions in marine environments, which limited the availability of fixed nitrogen (LaPorte et al., 2009; Melchin et al., 2013; Luo et al., 2015). During the Hirnantian cooling, a contraction of marine anoxia and an increase in biologically available nitrogen fueled the proliferation of eukaryotic organisms of the Hirnantia Fauna. This inference is supported by hydrocarbon biomarker records showing a decreased fraction of prokaryotes compared with eukaryotes (Rohrssen et al., 2013) and an increased diversity of microphytoplankton such as acritarchs (Melchin et al., 2013, and references therein). However, the abundance and diversity of graptolites declined as the intensity of denitrification waned because the preferred habitat for graptolites was eutrophic, low-oxygen waters (Cooper et al., 2012; Melchin et al., 2013).

Climatic cooling is widely viewed as the main trigger of the end-Ordovician biocrisis (e.g., Finnegan et al., 2012), although other kill mechanisms such as oceanic euxinia (Hammarlund et al., 2012) have been proposed. As with all mass extinctions, multiple causation is possible. However, the close association of the two pulses of extinction with the abrupt onset and termination of the Hirnantian glaciation make temperature change the most likely culprit.

6.2. The Hirnantian glaciation

The Hirnantian glaciation (or ice age; Fig. 1) was a relatively short but intense climatic event linked to the formation of icesheets formed on Gondwana, which was located in the South

Polar region at that time (Brenchley et al., 1994; Ghienne, 2003; Le Heron and Dowdeswell, 2009; Delabroye and Vecoli, 2010; Finnegan et al., 2011). The onset of the Hirnantian glaciation was marked by an abrupt eustatic fall at the base of the *N. extraordinarius*–*N. ojsuensis* graptolite Zone, which corresponds to the base of the Hirnantian Stage (Bergström et al., 2009, 2010; Finnegan et al., 2011; for a local record, see Chen et al., 2004). The glacial maximum, corresponding to the maximum eustatic lowstand, occurred within the *N. extraordinarius*–*N. ojsuensis* graptolite Zone. The end of the glaciation, which was marked by an abrupt eustatic rise, came in the early *N. persculptus* Zone of the late Hirnantian Stage.

The maximum amplitude of late Ordovician glacio-eustatic fluctuations has been estimated at ~70–100 m (Zhang and Barnes, 2002; Brenchley et al., 2003; Finnegan et al., 2011). These large fluctuations are recorded in major lithofacies changes, e.g., as on the South China craton where deep-water graptolitic black shales of the pre-glacial Wufeng Formation are overlain by shallow-water shelly limestones of the syn-glacial Kuanyinchiao Formation and then graptolitic black shales of the post-glacial Longmaxi Formation (Chen et al., 2004; Zhou et al., 2015). The estimated ~500-kyr (Brenchley et al., 1994) to ~1.0-Myr (Holmden et al., 2012) duration of the glaciation subsumed about five glacial-interglacial cycles (Ghienne et al., 2007; Yan et al., 2010; Turner et al., 2012), suggesting possible modulation by the Earth's ~100-kyr short-eccentricity and/or 405-kyr long-eccentricity orbital cycles (Sutcliffe et al., 2000; Elrick et al., 2013).

The mechanisms for both the beginning and the termination of the Hirnantian glaciation are uncertain. The cause of the Hirnantian glaciation is generally attributed to the cooling trend that had begun in the Early or Middle Ordovician, for which the ultimate driver was a lowering of atmospheric $p\text{CO}_2$ (Gibbs et al., 1997; Herrmann et al., 2004). Reduced CO_2 levels may have been driven by some combination of reduced volcanic arc outgassing (McKenzie et al., 2016), enhanced silicate weathering (Young et al., 2009; Lefebvre et al., 2010; Nardin et al., 2011), and enhanced burial of organic carbon linked to higher marine productivity (Qing and Veizer, 1994; Patzkowsky et al., 1997; Yan et al., 2009; Zhang et al., 2010; Hammarlund et al., 2012). In this scenario, the Hirnantian glaciation represents the culmination of a long-term cooling trend, when a critical $p\text{CO}_2$ threshold (or 'tipping point') was overstepped. An alternative idea is that the onset of glaciation was triggered by changes in the marine nitrogen cycle, specifically, rates of denitrification and their attendant control of nitrous oxide production (Luo et al., 2015). Nitrous oxide (N_2O) is a potent greenhouse gas whose heat-trapping efficiency per molecule is ~300× greater than that of CO_2 and which has a long residence time (>100 year) in the atmosphere (Naqvi et al., 1998; Galloway, 2003). A large reduction in its production rate would have contributed to global cooling and, ultimately, glaciation. Although the termination of the Hirnantian glaciation has been attributed to increasing atmospheric $p\text{CO}_2$ (Kump et al., 1999; Young et al., 2010), it is also possible that the marine nitrogen cycle played a leading role in this event (Luo et al., 2015). Specifically, a sharp negative $\delta^{15}\text{N}$ shift at the end of the glacial interval signals intensified denitrification, which may have resulted in increased N_2O production and enhanced greenhouse warming.

The Hirnantian glaciation is widely thought to have developed under conditions of high atmospheric $p\text{CO}_2$, an idea based largely on the Phanerozoic carbon cycle models of the late Robert Berner (Berner, 1991, 1994; 2006; Berner and Kothavala, 2001) and possibly reinforced by C-isotope studies of soil minerals as CO_2 paleobarometers (Yapp and Poths, 1992; Mora et al., 1996). However, this would be highly unusual given the strong positive correlation between

low $p\text{CO}_2$ and glaciation for the Phanerozoic as a whole (Royer, 2006) and for the Pleistocene in particular (Cuffey and Vimeux, 2001; Shakun et al., 2012). Various hypotheses have been proposed to account for this supposed anomaly, including a weak early Sun (Ramstein, 2011), high cloud albedo caused by cosmic ray flux (Shaviv and Veizer, 2003), and diminished silicate weathering owing to extensive ice cover (Kump et al., 1999). However, it is also possible that the inference of high atmospheric $p\text{CO}_2$ during the Hirnantian is simply incorrect: Berner's $p\text{CO}_2$ curves have only a 10-Myr resolution and, thus, are likely to have completely missed a short-lived (~1-Myr-long) $p\text{CO}_2$ minimum during the Hirnantian glaciation. The significance of the Yapp and Poths (1992) study is uncertain as well: they studied the late Richmondian (late Katian) Neda Formation, which predated the Hirnantian glaciation by several million years. A recent investigation inferred that $p\text{CO}_2$ in the early Katian, ~8 million years prior to the Hirnantian glaciation, was <8× present atmospheric level (PAL), or less than half of earlier estimates (Pancost et al., 2013). Thus, atmospheric $p\text{CO}_2$ during the Hirnantian glaciation may well have been lower than previously thought.

8. Summary

The importance of the Ordovician Period as a transitional interval in Earth history characterized by a dynamic interplay among biotic, climatic, and environmental systems cannot be overemphasized. For most of geologic time prior to the Ordovician, the Earth was inhabited exclusively by single-celled organisms or, in the immediately preceding ~200 million years, by primitive metazoans. The Great Ordovician Biodiversification Event represented the first full 'flowering' of advanced animal life. At the same time, changes in global climate and environmental conditions were occurring in an episodic manner, possibly in sync with major bioevolutionary developments (although this issue has not yet been investigated to the point of resolution). Despite uncertainties about the nature of biota-environment relationships, cause-and-effect relationships among coeval oceanic-atmospheric developments are better understood: some combination of reduced volcanic arc outgassing, enhanced silicate weathering, and increased organic carbon burial resulted in lower atmospheric CO_2 levels, triggering climatic cooling that culminated in the Hirnantian glaciation, the first ice age of the Phanerozoic. Cooler climatic conditions appear to have increased the pole-to-equator temperature gradient, invigorating global-ocean circulation and thus leading to improved oxygenation of the deep ocean. It seems possible that a positive feedback between enhanced thermohaline circulation, marine productivity, drawdown of atmospheric $p\text{CO}_2$, and global cooling may have contributed to the intense but brief nature of the Hirnantian glaciation. With regard to diversification patterns, one of the paradoxes of the Ordovician is that a modest cooling during the Middle to early Late Ordovician appears to have promoted a radiation of marine life but the intense cooling of the latest Ordovician Hirnantian Stage triggered a mass extinction. The relationships among these many co-occurring events are complex, which makes the Ordovician a classic example of co-evolution of Earth systems and a fascinating geologic period for study.

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Figure captions

Fig. 1. Major Ordovician events. GOBE = Great Ordovician Biodiversification Event; HICE = Hirnantian carbon isotope excursion; GICE = Guttenberg carbon isotope excursion; MDICE = mid-Darriwilian carbon isotope excursion. Paleobotanic data: 1 – Volkheimer et al. (1984, 1990), 2 – Wellman and Gray (2000), Rubinstein et al. (2010); 3 – Steemans et al. (2009); 4 – Servais et al. (2009); 5 – et al. (2009); 6 – B. S. S. (2009).

Fig. 2. Paleogeographic distribution of studies in this volume globally (A) and in North America (B). Middle Ordovician paleogeographic base maps courtesy of Ron Blakey (www2.nau.edu/rcb7). Numbered sections are keyed to the papers in this volume: (1) Algeo et al., (2) Servais et al., (3) Kidder and Tomescu, (4) Pohl et al., (5) Pruss et al., (6) Quinton et al., (7) Marengo et al., (8) Jones et al., (9) Edwards and Saltzman, (10) Young et al., (11) Kah et al., (12) Zhang and Munnecke, and (13) Zhang et al.

Fig. 3. Stratigraphic distribution of studies in this volume. Stratigraphic framework adapted from Cooper and Sadler (2012). The numbered ranges are keyed as in Figure 2. See Figure 1 for abbreviations.

Figure 1

Figure 3