Persistent oceanic anoxia and elevated extinction rates separate the Cambrian and Ordovician radiations

Matthew R. Saltzman^{1*}, Cole T. Edwards^{1,2}, Jonathan M. Adrain³, and Stephen R. Westrop⁴

¹School of Earth Sciences, The Ohio State University, Columbus, Ohio 43210, USA

²Department of Earth and Planetary Sciences, Washington University, Saint Louis, Missouri 63130, USA

³Department of Earth & Environmental Sciences, University of Iowa, Iowa City, Iowa 52242, USA

⁴Sam Noble Oklahoma Museum of Natural History and ConocoPhillips School of Geology & Geophysics, University of Oklahoma, Norman, Oklahoma 73072, USA

ABSTRACT

Recurrent mass extinction events (at "biomere"-a biostratigraphic unit-boundaries) characterize the middle Cambrian to Early Ordovician (Tremadocian) time interval that is between the major Cambrian and Ordovician radiations of animal life. A role for anoxia in maintaining elevated extinction rates in the late Cambrian has been proposed based on coincidence of an extinction with positive excursions in $\delta^{13}C_{_{carb}}$ and $\delta^{34}S_{_{CAS}}$ (CAS—carbonate-associated sulfate). Here we examine an Early Ordovician extinction event at the base of the North American Stairsian Stage (upper Tremadocian), and demonstrate concurrent onset of positive excursions in $\delta^{13}C$ and $\delta^{34}S$ inferred to reflect enhanced organic matter burial under anoxic waters. Sea-level rise may have brought anoxic waters onto the shelf to initiate extinctions. The evidence for δ^{13} C excursions and elevated extinction rates appears to wane in the Tremadocian, consistent with progressive oxygenation of the oceans reaching a threshold that helped facilitate initial stages of the Great Ordovician Biodiversification Event.

INTRODUCTION

The late Cambrian (Furongian Series) to Middle Ordovician records a plateau in animal diversity between the Cambrian and Ordovician radiations that was maintained by repetitive extinction and recovery (Bambach et al., 2004). Extinction events at stage or "biomere" (biostratigraphic unit) boundaries (Stitt, 1983; Palmer, 1984; Westrop and Ludvigsen, 1987; Taylor et al., 2012) occurred at least 5 times over the ~20 m.y. of the Furongian to mid-Early Ordovician (Tremadocian Stage) (Adrain et al., 2009). Processes that underlie this distinctive macroevolutionary regime (Fig. 1) are not well understood, but an emerging theme focuses on fluctuations in oceanic redox state over a range of time scales (e.g., Hurtgen et al., 2009; Pruss et al., 2010; Saltzman et al., 2011; Gill et al., 2011; Thompson and Kah, 2012; Marenco et al., 2013).

It has been hypothesized that O₂ deficiency was widespread below the surface mixed layer of late Cambrian oceans, and that upwelling of anoxic waters during sea-level rise may have been a primary cause of the global extinction at the base of the Paibian Stage (Gill et al., 2011). Although the spatial and temporal extent of early Paleozoic oceanic anoxia is debated (e.g., Dahl et al., 2010; Landing, 2012; Chen et al., 2015), periodic expansion of anoxic waters in the late Cambrian is supported by the positive shift in δ^{13} C of marine carbonate (i.e., Steptoean Positive Isotope Carbon Excursion, SPICE, event; Saltzman et al., 2000) and δ^{34} S of carbonateassociated sulfate (Gill et al., 2011). The possibility that a link between δ^{13} C excursions, anoxia, and extinctions persisted into the Early Ordovician is beginning to be explored (e.g., Taylor et al., 2004); efforts have been hampered by extensive dolomitization (e.g., Knox Dolomite in the Appalachian Basin). An understanding of the timing and areal extent of Early Ordovician anoxia may ultimately help explain the evidence of a major post-Tremadocian transition in marine life marked by the termination of biomere extinctions (Adrain et al., 2009), an increased abundance of skeletal carbonate (Pruss et al., 2010), and the onset of the Ordovician



Figure 1. Composite δ¹³C with Cambrian data from the Great Basin (Saltzman et al., 2000; for other sources, see the Data Repository [see footnote 1]) and Ordovician from Argentina (Buggisch et al., 2003; see also Edwards and Saltzman, 2014). Biomere positions are after Adrain et al. (2014) and Taylor et al. (2012), and Great Ordovician Biodiversification Event (GOBE) pulses are after Servais et al. (2010). See Figure DR4 (see footnote 1) for entire Phanerozoic extinction percentages. Time scale of International Commission on Stratigraphy (ICS, www.stratigraphy.org/index.php/ics-chart-timescale). VPDB—Vienna Peedee belemnite; extinct.—extinction; Ser.—Series; ORDOV.—Ordovician; Dap.—Dapingian; Darriwil.—Darriwilian.

radiation or Great Ordovician Biodiversification Event (GOBE) (Servais et al., 2010).

This study examines the relationship between a prominent positive $\delta^{13}C_{carb}$ excursion and a biomere-like extinction event near the base of the North American Stairsian Stage (Tremadocian) in the Ibex area of Utah. Stitt (1983) first reported the trilobite extinction in Oklahoma, and Ethington et al. (1987) demonstrated subsequent turnover of conodonts. We aim to establish a link between these extinctions, sea-level change, and anoxia (e.g., Landing et al., 2012), and positive $\delta^{13}C_{carb}$ (carbonate) (Buggisch et al., 2003; Taylor et al., 2004; Hong et al., 2011) and $\delta^{34}S_{CAS}$ (carbonate-associated sulfate) excursions (Edwards, 2014).

BACKGROUND

Trilobite extinctions, sometimes used to define stage-level biostratigraphic units termed biomeres (Palmer, 1984; Taylor et al., 2012), are well documented in middle Cambrian to lower Ordovician shelf successions of Laurentian North America. The basal Paibian (base Steptoean) extinction has been identified worldwide (Palmer, 1984; Saltzman et al., 2000), and it is becoming apparent that younger events are also global in scope (Westrop and Adrain, 2013). The youngest well-studied extinc-

^{*}E-mail: saltzman.11@osu.edu

tion in North America is near the base of the Early Ordovician Stairsian Stage (top Symphysurinid biomere, Stitt, 1983; upper Tremadocian Stage in global terms, Adrain et al., 2014). An even younger trilobite extinction discovered at the top of the Stairsian (Adrain et al., 2009) has not yet been characterized geochemically.

The base of the North American Stairsian Stage coincides with the base of the *Paraplethopeltis genacurva* trilobite zone (Adrain et al., 2014; equivalent to the base of the *Paraplethopeltis* zone of Taylor et al., 2012). The trilobite extinction begins at the base of this zone in Utah, Oklahoma, and western Texas (Stitt, 1983; Ethington et al., 1987; Miller et al., 2003; Taylor et al., 2004, 2012; Adrain et al., 2014), and is nearly coincident (within 5 m of section) with a conodont extinction at the transition from the *Rossodus manitouensis* zone to the so-called Low Diversity Interval (Ethington et al., 1987; Ji and Barnes, 1993). Miller et al. (2003) suggested that extinctions in Utah were driven by sea-level fluctuations (Miller et al., 2003, their Sequence 13, and Tule Valley lowstand).

METHODS AND RESULTS

Integrated study of trilobite biostratigraphy, sequence stratigraphy, and δ^{13} C was conducted at three sections in the Ibex area of Utah centered on Universal Transverse Mercator coordinates, Zone 12: E 296,000 m; N 4,304,000 m (Fig. DR1 in the GSA Data Repository¹). The δ^{13} C was derived from micritic limestone microdrilled from least-altered portions of fresh rock surfaces. The δ^{18} O does not covary with δ^{13} C (Fig. DR2), as might have been expected if primary δ^{13} C was reset during meteoric diagenesis (e.g., Jones et al., 2015). The δ^{13} C decreases from ~+1‰ in the *Symphysurina* trilobite zone to -1‰ in the *Bellefontia* zone (Fig. 2) and begins to increase just below the base of the Stairsian Stage (Fig. 3).



Figure 2. δ^{13} C for composite at Ibex, Utah (UT.; locality map in Fig. DR1 [see footnote 1]). Biostratigraphy is from Ethington et al. (1987), Miller et al. (2003), and Adrain et al. (2014). Fillm.—Fillmore Formation; VPDB—Vienna Peedee belemnite; st.—stage; fm.—formation; con.—conodont zone; *P. helli—Paraplethopeltis helli*; *P. genacur.—Paraplethopeltis genacurva*; *R.—Rossodus*; an.—*Cordylodus angulatus* zone; L.D.I.—low diversity interval.

The δ^{13} C continues rising above an erosion surface overlain by silty, laminated dolostone containing the youngest pre-extinction trilobites (Fig. 3). The trilobite extinction is within an overlying succession of intraclastic rudstone and rhynchonelliform brachiopod shell beds above the sequence boundary, and thus not the result of stratigraphic bias (Patzkowsky and Holland, 2012). Above the extinction, the "top bed" of the House Limestone (Fig. DR3A) begins with a condensed succession (Fig. DR3B) including thrombolitic buildups. The δ^{13} C peaks at +1.4‰ in the basal Fillmore Formation (*Paraplethopeltis helli* zone; Figs. 2 and 3).

DISCUSSION

Extinctions and Excursions in $\delta^{\rm 13}C$ and $\delta^{\rm 34}S$

The stratigraphic coincidence between a trilobite extinction event and the onset of a positive $\delta^{13}C$ excursion has been firmly established previously only for the late Cambrian where the SPICE (Fig. 1) begins near the base of the Paibian Stage (e.g., Saltzman et al., 2000). Gill et al. (2011) used $\delta^{13}C$ and $\delta^{34}S$ from SPICE sections around the world to corroborate the hypothesis put forth by paleontologists (Palmer, 1984) that upwelling of anoxic waters contributed to the extinction. Two younger Cambrian trilobite extinction events at the bases of the North American Sunwaptan



Figure 3. δ^{13} C, trilobite biostratigraphy, and sequence stratigraphy at Lava Dam North (N.) and B-Top with detailed measured section after Adrain et al. (2014). Brown siltstone overlies a low rank sequence boundary (Fig. DR3A; see footnote 1) and may represent a lowstand systems tract (LST) (Miller et al., 2003). Brachiopod shell bed marks base of transgressive interval; remainder of the House Limestone is a cycle with a small-scale transgressive systems tract (TST) and highstand systems tract (HST) (Fig. DR3B; see footnote 1). The lower Fillmore Formation correlates into an unconformity in parts of Laurentia (e.g., Landing et al., 2012), and likely represents an extended LST of a high rank (third order) sequence. *P. helli—Paraplethopeltis helli; P. genacur.—Paraplethopeltis genacurva*; gen. nov.—genus novum; s.s.—sensu stricto.

¹GSA Data Repository item 2015274, Figure DR1 (locality map), Figure DR2 (C-O isotope cross plot), Figure DR3 (field photos of House-Fillmore Formation transition), Figure DR4 (Phanerozoic extinction percentages) and text with citations for composite C-isotope curve, is available online at www.geosociety.org /pubs/ft2015.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

and Skullrockian Stages also appear to coincide with positive shifts in δ^{13} C (Fig. 1) (Saltzman et al., 1995; Ripperdan and Miller, 1995), and Taylor et al. (2004) first documented that the extinction at the base of the Early Ordovician Stairsian Stage was linked to a positive δ^{13} C excursion.

Our data from Ibex, Utah (Figs. 2 and 3), correlate well with sections in Texas and New Mexico (studied by Taylor et al., 2004) and at Shingle Pass, Nevada (Edwards and Saltzman, 2014), where a positive $\delta^{34}S_{CAS}$ excursion is also documented (Edwards, 2014) (Fig. 4). Recognition of the basal Stairsian δ^{13} C excursion in Argentina (Buggisch et al., 2003) and South Korea (Hong et al., 2011) may be possible using conodont zones, but detailed study of trilobites and δ^{34} S is needed. The most plausible hypothesis for the relationship between the basal Stairsian $\delta^{13}C$ and $\delta^{34}S$ excursions and extinction event is expansion of anoxic waters into parts of the shelf, analogous to the SPICE (e.g., Gill et al., 2011), rather than changes in weathering fluxes. A possible time lag in which the onset of the global $\delta^{13}C$ excursion precedes the mass extinction (represented by several meters of rock; Figs. 2 and 3) in Utah could reflect progressive expansion of anoxia in deeper water masses (upper slope; e.g., Landing, 2012) prior to upwelling in shelf environments. Above the top of the Stairsian, stability in the remainder of the Early–Middle Ordovician δ^{13} C curve is apparent (Fig. 1) and suggests that progressive oxygenation of oceans reached a threshold in the Floian Stage, beyond which anoxic events were greatly diminished in scale in shelf environments. Higher oxygen concentrations would also have increased the oversaturation of surface waters with respect to calcite and aragonite, and possibly provided a mechanism for the renewed radiation of heavily skeletonized invertebrates and algae (Pruss et al., 2010).

Although the redox state of the Ordovician oceans (e.g., Saltzman et al., 2011; Thompson and Kah, 2012; Landing et al., 2012; Marenco et al., 2013) and the broader context of early–middle Paleozoic oxygen with links to animal diversity (e.g., Berner et al., 2007; Dahl et al., 2010; Chen et al., 2015) are still debated, our results are consistent with the view that oceanic oxygen levels were at a relative low point in between the Cambrian explosion and Ordovician radiation (i.e., GOBE). Oceanic oxygenation near the base of the Cambrian (e.g., Chen et al., 2015) was thus periodically reversible during the late Cambrian to Early Ordovician. This view fits with an emerging picture of the late Neoproterozoic–early Paleozoic based on molybdenum isotopes (Kendall et al., 2015) in which episodes of extensive

oxygenation break up intervals of less oxygenated oceans. Regardless of any absolute change in global O_2 concentrations between the Early and Middle Ordovician, increasingly homogeneous redox conditions (i.e., less geographic and bathymetric variability) could create greater stability in shelf environments that facilitated the GOBE if, as proposed for the Cambrian radiation by Sperling et al. (2013), this increased the proportion of carnivores (e.g., cephalopods; Servais et al., 2010) and overall diversity.

Sea-Level Driver?

Although periodic expansion of anoxic waters into shelf environments may have triggered repeated extinctions that extended into the Early Ordovician Tremadocian Stage, the driver remains poorly understood. The SPICE (Fig. 1) was presumed to be triggered by sea-level rise (Gill et al., 2011), with the peak in δ^{13} C associated with a reversal back to falling sea level. Our new data suggest that the base Stairsian δ^{13} C and δ^{34} S excursions and trilobite mass extinction may generally follow a similar pattern. We interpret the silty, laminated dolostone containing the youngest preextinction trilobite fauna in the upper House Limestone as a thin lowstand systems tract (Fig. 3) (Miller et al., 2003), although, in addition to sea level, it is possible that some sedimentologic features (e.g., dissolution surfaces) were influenced by changing carbonate saturation as a function of oxygen levels (cf. Pruss et al., 2010). This pre-extinction lowstand systems tract in Utah may correlate to a stratigraphic break in New Mexico (near the base of the Sierrite Limestone; Taylor et al., 2004), but correlations to discontinuity surfaces further east in Laurentia and other continents are less certain (Ethington et al., 1987; Ji and Barnes, 1993; Miller et al., 2003). The trilobite extinction horizon in Utah is within the overlying fining-upward succession of intraclastic rudstone and rhynchonelliform brachiopod shell beds that is interpreted as a high-energy transgression (Fig. 3). The sea-level rise in the early Stairsian appears to have been terminated by a fall in sea level near the $\delta^{13}C$ peak in the lower Fillmore Formation (Miller et al., 2003).

The base Stairsian extinction likely resulted from ecological factors triggered in part by spread of anoxic and/or dysoxic water and possibly sea-level–related habitat destruction in the outer shelf (Westrop and Ludvigsen, 1987). Consistent with the observation that the positive δ^{13} C excursion was initiated just below the base Stairsian sequence boundary (Fig.



Figure 4. Correlation of base Stairsian Stage positive δ¹³C excursion in Utah (UT) to New Mexico (NM) (Taylor et al., 2004), Korea (Hong et al., 2011), Argentina (Buggisch et al., 2003), and Shingle Pass, Nevada (NV) (Edwards and Saltzman, 2014). For Shingle Pass, δ³⁴S is plotted and generally tracks the δ¹³C excursion in the upper House Limestone (Edwards, 2014). VPDB—Vienna Peedee belemnite; VCDT—Vienna Canyon Diablo Troilite; Trilo.—trilobite; Cono.—conodont; Fm.—formation; *Bell.-Xen.—Bellefontia-Xenostegium; Leio-Kain.—Leiostegium-Kainella*; *R. manit.—Rossodus manitouensis*; L.D.I.—low diversity interval; *M. dianae—Macerodus dianae*; Mbr—member; Fill.—Fillmore; Par. Spr—Parker Spring; Laws.—Lawsonian; Flo.—Floian; SJF—San Juan Formation; *G. quad.—Glyptoconus quadraplicatus*.

3), multiple carbon cycle drivers in addition to sea level are likely superimposed to produce the complex signal (e.g., changes in ocean circulation and ventilation or weathering fluxes); this could also explain why some large Ordovician sea-level changes (e.g., basal Stonehenge transgression; Miller et al., 2003; Taylor et al., 2012; Landing et al., 2012) are not associated with isotopic excursions or extinctions.

ACKNOWLEDGMENTS

We thank John Taylor, Thomas Servais, Ed Landing, and two anonymous reviewers for strengthening the manuscript. J. Miller, B. Gill, and R. Ethington provided valuable discussion. This is a contribution to International Geoscience Programme (IGCP) Project 591. Field work was supported by National Science Foundation grants EAR-9973065 and EAR-0308685 (Adrain and Westrop), DEB-07166065 (Adrain), and the Evolving Earth Foundation (Edwards).

REFERENCES CITED

- Adrain, J.M., McAdams, N.E.B., and Westrop, S.R., 2009, Trilobite biostratigraphy and revised base of the Tulean and Blackhillsian stages of the Ibexian Series, Lower Ordovician, western United States: Australasian Association of Palaeontologists Memoirs no. 37, p. 541–610.
- Adrain, J.M., Westrop, S.R., Karim, T.S., and Landing, E., 2014, Trilobite biostratigraphy of the Stairsian Stage (upper Tremadocian) of the Ibexian Series, Lower Ordovician, western United States: Australasian Association of Palaeontologists Memoirs no. 45, p. 167–214.
- Bambach, R., Knoll, A.H., and Wang, S., 2004, Origination, extinction, and mass depletions of marine diversity: Paleobiology, v. 30, p. 522–542, doi:10.1666 /0094-8373(2004)030<0522:OEAMDO>2.0.CO;2.
- Berner, R.A., VandenBrooks, J.M., and Ward, P.D., 2007, Oxygen and evolution: Science, v. 316, p. 557–558, doi:10.1126/science.1140273.
- Buggisch, W., Keller, M., and Lehnert, O., 2003, Carbon isotope record of Late Cambrian to Early Ordovician carbonates of the Argentine Precordillera: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 195, p. 357–373, doi: 10.1016/S0031-0182(03)00365-1.
- Chen, X., et al., 2015, Rise to modern levels of ocean oxygenation coincided with the Cambrian radiation of animals: Nature Communications, v. 6, 7142, doi: 10.1038/ncomms8142.
- Dahl, T.W., et al., 2010, Devonian rise in atmospheric oxygen correlated to the radiations of terrestrial plants and large predatory fish: National Academy of Sciences Proceedings, v. 107, p. 17,911–17,915, doi:10.1073/pnas.1011287107.
- Edwards, C.T., 2014, Carbon, sulfur, and strontium isotope stratigraphy of the Lower–Middle Ordovician, Great Basin, USA: Implications for oxygenation and causes of global biodiversification [Ph.D. thesis]: Columbus, Ohio State University, 248 p.
- Edwards, C.T., and Saltzman, M.R., 2014, Carbon isotope (δ¹³C_{carb}) stratigraphy of the Lower–Middle Ordovician (Tremadocian–Darriwilian) in the Great Basin, western United States: Implications for global correlation: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 399, p. 1–20, doi:10.1016/j .palaeo.2014.02.005.
- Ethington, R.L., Engel, K.M., and Elliott, K.L., 1987, An abrupt change in conodont faunas in the Lower Ordovician of the Midcontinent Province, *in* Aldridge, R.J., ed., Palaeobiology of conodonts: Chichester, UK, Ellis Horwood Limited, p. 111–127.
- Gill, B.C., Lyons, T.W., Young, S.A., Kump, L.R., Knoll, A.H., and Saltzman, M.R., 2011, Geochemical evidence for widespread euxinia in the later Cambrian ocean: Nature, v. 469, p. 80–83, doi:10.1038/nature09700.
- Hong, S.K., Lee, Y.I., and Jeong, S.Y., 2011, Carbon isotope composition of Upper Cambrian to Lower Ordovician carbonate in Korea, and its bearing on the Cambrian-Ordovician boundary and Lower Ordovician paleoceanography: Journal of Asian Earth Sciences, v. 40, p. 252–260, doi:10.1016/j.jseaes.2010 .07.007.
- Hurtgen, M.T., Pruss, S.B., and Knoll, A.H., 2009, Evaluating the relationship between the carbon and sulfur cycles in the later Cambrian ocean: An example from the Port au Port Group, western Newfoundland, Canada: Earth and Planetary Science Letters, v. 281, p. 288–297, doi:10.1016/j.epsl.2009.02.033.
- Ji, Z., and Barnes, C.R., 1993, A major conodont extinction event during the Early Ordovician within the midcontinent realm: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 104, p. 37–47, doi:10.1016/0031-0182(93)90118-3.
- Jones, D.S., Creel, R.C., Rios, B., and Santiago Ramos, D.P., 2015, Chemostratigraphy of an Ordovician–Silurian carbonate platform: δ¹³C records below glacioeustatic exposure surfaces: Geology, v. 43, p. 59–62, doi:10.1130/G36236.1.
- Kendall, B., et al., 2015, Uranium and molybdenum isotope evidence for an episode of widespread ocean oxygenation during the late Ediacaran Period: Geochimica et Cosmochimica Acta, v. 156, p. 173–193, doi:10.1016/j.gca.2015.02.025.
- Landing, E., 2012, Time-specific black mudstones and global hyperwarming on the Cambrian–Ordovician slope and shelf of the Laurentia paleocontinent: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 367-368, p. 256–272, doi:10.1016/j.palaeo.2011.09.005.

- Landing, E., Adrain, J.M., Westrop, S.R., and Kröger, B., 2012, Tribes Hill–Rochdale formations in east Laurentia: Proxies for Early Ordovician (Tremadocian) eustasy on a tropical passive margin (New York and west Vermont): Geological Magazine, v. 149, p. 93–123, doi:10.1017/S0016756811000598.
- Marenco, P.J., Marenco, K.N., Lubitz, R.L., and Niu, D., 2013, Contrasting longterm global and short-term local redox proxies during the Great Ordovician Biodiversification Event: A case study from Fossil Mountain, Utah, USA: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 377, p. 45–51, doi: 10.1016/j.palaeo.2013.03.007.
- Miller, J.F., Evans, K.E., Loch, J.D., Ethington, R.L., Stitt, J.H., Holmer, L.E., and Popov, L.E., 2003, Stratigraphy of the Sauk III interval (Cambrian–Ordovician) in the Ibex area, western Millard County, Utah: Brigham Young University Geology Studies, v. 47, p. 23–118.
- Palmer, A.R., 1984, The biomere problem: Evolution of an idea: Journal of Paleontology, v. 58, p. 599–611.
- Patzkowsky, M.E., and Holland, S.M., 2012, Stratigraphic paleobiology: Chicago, Illinois, University of Chicago Press, 256 p.
- Pruss, S.B., Finnegan, S., Fischer, W.W., and Knoll, A.H., 2010, Carbonates in skeleton-poor seas: New insights from Cambrian and Ordovician strata of Laurentia: Palaios, v. 25, p. 73–84, doi:10.2110/palo.2009.p09-101r.
- Ripperdan, R.L., and Miller, J.F., 1995, Carbon isotope ratios from the Cambrian-Ordovician boundary section at Lawson Cove, Wah Wah Mountains, Utah, *in* Cooper, J.D., ed., Ordovician odyssey: Short papers for the seventh International Symposium on the Ordovician System: Pacific Section, Society for Sedimentary Geology Book 77, p. 129–132.
- Saltzman, M.R., Davidson, J.P., Holden, P., Runnegar, B., and Lohmann, K.C., 1995, Sea-level-driven changes in ocean chemistry at an Upper Cambrian extinction horizon: Geology, v. 23, p. 893–896, doi:10.1130/0091-7613(1995) 023<0893:SLDCIO>2.3.CO;2.
- Saltzman, M.R., Brasier, M.D., Ripperdan, R.L., Ergaliev, G.K., Lohmann, K.C., Robison, R.A., Chang, W.T., Peng, S., and Runnegar, B., 2000, A global carbon isotope excursion during the Late Cambrian: Relation to trilobite extinctions, organic-matter burial and sea level: Palaeogeography, Palaeoceanography, Palaeoclimatology, v. 162, p. 211–223, doi:10.1016/S0031-0182(00)00128-0.
- Saltzman, M.R., Young, S.A., Kump, L.R., Gill, B.C., Lyons, T.W., and Runnegar, B., 2011, A pulse of atmospheric oxygen during the late Cambrian: National Academy of Sciences Proceedings, v. 108, p. 3876–3881, doi:10.1073/pnas .1011836108.
- Servais, T., Owen, A.W., Harper, D.A.T., Kroger, B., and Munnecke, A., 2010, The Great Ordovician Biodiversification Event (GOBE): The palaeoecological dimension: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 294, p. 99–119, doi:10.1016/j.palaeo.2010.05.031.
- Sperling, E.A., Frieder, C.A., Raman, A.V., Girguis, P.R., Levin, L.A., and Knoll, A.H., 2013, Oxygen, ecology, and the Cambrian radiation of animals: National Academy of Sciences Proceedings, v. 110, p. 13,446–13,451, doi:10.1073 /pnas.1312778110.
- Stitt, J.H., 1983, Trilobite biostratigraphy and lithostratigraphy of the McKenzie Hill Limestone (Lower Ordovician), Wichita and Arbuckle Mountains, Oklahoma: Oklahoma Geological Survey Bulletin 134, 54 p.
- Taylor, J.F., Myrow, P.M., Ripperdan, R.L., Loch, J.D., and Ethington, R.L., 2004, Paleoceanographic events and faunal crises recorded in the Upper Cambrian and Lower Ordovician of west Texas and southern New Mexico, *in* Nelson, E.P., and Erslev, E.A., eds., Field trips in the southern Rocky Mountains, USA: Geological Society of America Field Guide 5, p. 167–183, doi:10.1130/0-8137-0005-1.167.
- Taylor, J.F., Repetski, J.E., Loch, J.D., and Leslie, S.A., 2012, Biostratigraphy and chronostratigraphy of the Cambrian-Ordovician great American carbonate bank, *in* Derby, J.R., et al., eds., The Great American carbonate bank: The geology and economic resources of the Cambrian–Ordovician Sauk megasequence of Laurentia: American Association of Petroleum Geologists Memoir 98, p. 15–35, doi:10.1306/13331488M983497.
- Thompson, C.K., and Kah, L.C., 2012, Sulfur isotope evidence for widespread euxinia and a fluctuating oxycline in Early to Middle Ordovician greenhouse oceans: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 313-314, p. 189–214, doi:10.1016/j.palaeo.2011.10.020.
- Westrop, S.R., and Adrain, J.M., 2013, Biogeographic shifts in a transgressive succession: The Cambrian (Furongian, Jiangshanian; latest Steptoean–earliest Sunwaptan) agnostoid arthropods *Kormagnostella* Romanenko and *Biciragnostus* Ergaliev in North America: Journal of Paleontology, v. 87, p. 804–817, doi:10.1666/12-111.
- Westrop, S.R., and Ludvigsen, R., 1987, Biogeographic control of trilobite mass extinction at an Upper Cambrian "biomere" boundary: Paleobiology, v. 13, p. 84–99.

Manuscript received 24 March 2015 Revised manuscript received 24 June 2015

Manuscript accepted 5 July 2015

Printed in USA