Geology

Plate tectonic influences on Neoproterozoic–early Paleozoic climate and animal evolution

N. Ryan McKenzie, Nigel C. Hughes, Benjamin C. Gill and Paul M. Myrow

Geology 2014;42;127-130
doi: 10.1130/G34962.1

Notes

Plate tectonic influences on Neoproterozoic–early Paleozoic climate and animal evolution

N. Ryan McKenzie[1,2]*, Nigel C. Hughes[2], Benjamin C. Gill[3], and Paul M. Myrow[4]
[1]Department of Geological Sciences, Jackson School of Geosciences, University of Texas, Austin, Texas 78712, USA
[2]Department of Earth Sciences, University of California–Riverside, Riverside, California 92521, USA
[3]Department of Geosciences, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061, USA
[4]Department of Geology, Colorado College, Colorado Springs, Colorado 80903, USA

ABSTRACT

The initial diversification of animals paralleled some of the most dramatic episodes of climate and environmental change in Earth history. We compiled global Neoproterozoic–early Paleozoic detrital zircon age data to track spatiotemporal variations in continental arc systems to explore the influence of tectonic outgassing of CO_2 on these climatic shifts. These data indicate that global continental arc systems were spatially reduced at the onset of the Cryogenian glacial interval, widespread during the Cambrian greenhouse, and reduced during Ordovician cooling. The Cambrian greenhouse was coincident with ecologically stressed conditions, whereas Ordovician global cooling was accompanied by a major biodiversification event. Thus, variation in the continental arc CO_2 flux likely played a critical role in major climatic fluctuations, which profoundly influenced early animal evolution.

INTRODUCTION

At least two glaciations of global magnitude occurred in the latter half of the Cryogenian (referred to here as the glacial interval 716–635 Ma; Hoffman et al., 1998; Macdonald et al., 2010). In contrast, the Cambrian Period was an interval of extreme greenhouse conditions with the highest modeled atmospheric CO_2 concentrations of the Phanerozoic (Berner, 1990, 2006) (Fig. 1). Cryogenian strata contain the oldest definitive evidence for metazoan life (Love et al., 2009); however, most major metazoan clades do not appear in the fossil record until the early Cambrian "explosion" (Marshall, 2006). The ca. 470 Ma Great Ordovician Biodiversification Event (GOBE) was marked by a rapid increase in taxonomic diversity and profound changes in morphological disparity, ecosystem complexity, and ecospace utilization (Sepkoski et al., 1981; Droser and Finnegan, 2003; Harper, 2006; Alroy, 2010). The Cambrian explosion and GOBE are separated by an interval that is characterized by anomalously high genus-level extinction rates with at least four distinct mass extinction events (Bambach et al., 2004) and the longest metazoan reef gap of the Phanerozoic (Kiessling, 2009), aptly termed the "dead interval" (Miller et al., 2006) (Fig. 1). The success of trilobite faunas adapted to reduced oxygen availability following late Cambrian extinction events prompted the argument for episodic oceanic anoxia during this interval (Palmer, 1984). The model for extensive marine anoxia has been supported by subsequent geochemical investigations (e.g., Gill et al., 2011). This Cambrian dead interval is punctuated by the GOBE, which followed a period of global cooling (Trotter et al., 2008) (Fig. DR1 in the GSA Data Repository[1]).

The late Neoproterozoic–early Paleozoic was a time of widespread convergent tectonism associated with Gondwanan amalgamation (Cawood and Buchan, 2007). On multimillion year time scales, the atmospheric concentration of CO_2, a principal greenhouse gas, is regulated by surface and tectonic processes; volcanism and metamorphism (tectonic outgassing) are the major sources of CO_2 and chemical weathering of silicate rocks is a major CO_2 sink (Berner et al., 1983; Kump et al., 2000). Recent work has shown that variation in the spatial distribution of continental arc systems in particular may play a major role in greenhouse-icehouse transitions via the liberation of CO_2 from carbonate and organic matter–rich bedrock along continental margins (Lee et al., 2013). Rapid CO_2 fluxes from large igneous province (LIP) volcanism can cause dramatic environmental perturbations; however, these are generally short-lived events and numerous successive LIPs are required to influence long-term climate (e.g., Kidder and Worsley, 2010; Lee et al., 2013). Only two LIPs are known from the time interval discussed here, the ca. 720 Ma Franklin LIP (northern Canada; Heaman et al., 1992), which coincides with an episode of global cooling and the first Cryogenian glaciation (e.g., Macdonald et al., 2010), and the ca. 510 Ma Khalkarindji LIP (northern Australia; Glass and Phillips, 2006). Here we use a compilation of new and published U-Pb detrital zircon age data from globally dispersed Cryogenian to Late Devonian strata to evaluate the role of spatiotemporal variation in continental arc volcanism in observed climatic and environmental fluctuations.

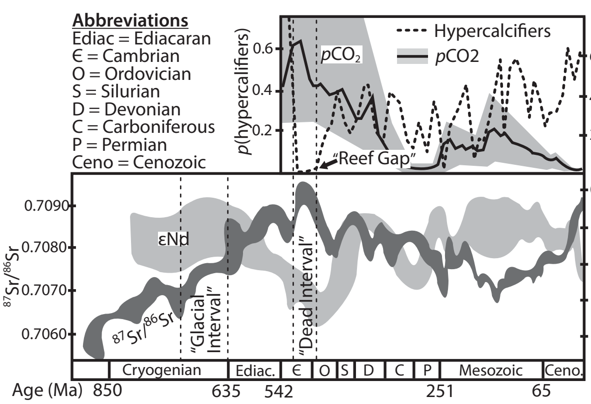

Figure 1. Proterozoic–Phanerozoic seawater strontium and neodymium isotopic trends ($^{87}Sr/^{86}Sr$ and ε_{Nd}), partial pressure of atmospheric carbon dioxide (pCO_2), and proportion (p) of hypercalcifying metazoans relative to macrobenthic metazoans (modified from Berner, 2006; Kiessling, 2009; Peters and Gaines, 2012, and references therein).

UTILITY OF DETRITAL ZIRCON GEOCHRONOLOGY IN PALEOTECTONIC STUDIES

Zircon is a common accessory mineral in felsic-intermediate igneous rock. Age populations from U-Pb dating of individual detrital zircon grains from siliciclastic sedimentary rocks are indicative of the crustal composition of source material. Large populations of relatively young zircon grains are common along convergent margins with continental arcs (ages often within 10 m.y. of the depositional age of the rock), because these systems produce

*E-mail: rmckenzie@jsg.utexas.edu.

[1]GSA Data Repository item 2014034, detrital zircon age data compilation, Figures DR1–DR3, and Table DR1 (U-Pb geochronologic analyses), is available online at www.geosociety.org/pubs/ft2014.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

GEOLOGY, February 2014; v. 42; no. 2; p. 127–130; Data Repository item 2014034 | doi:10.1130/G34962.1 | Published online 6 January 2014

voluminous felsic-intermediate magmas with high zircon fertility, whereas rift and passive margins generally lack abundant young detrital zircon (Cawood et al., 2012). LIPs produce mostly mafic rock that does not contain appreciable zircon. Therefore, detrital zircon age data, when considered in a stratigraphic context, can be used as a proxy to track regional continental arc systems.

For this study we report data from samples with independent depositional age constraints. Age data are presented as regionally and temporally differentiated age probability distributions (Fig. 2) and as normalized temporal global composite age distributions (Fig. 3). We normalized the data by dividing regional age dates into 20 m.y. bins and converting the populations into percentages so that each region has an equal number of age dates (n = 100). To avoid overrepresentation of specific paleogeographic locations, data from regions that were located in proximity on continuous continental margins were normalized and combined prior to inclusion in the global composite, which consisted of (1) north African terranes (North Africa, Arabia, Iran); (2) Cadomia and Iberia; (3) western and northern Laurentia; and (4) eastern Laurentian and Greenland. Silurian and Devonian normalized data were also combined due to the limited Silurian data. Strata from regions with problematic paleogeographic and/or poor depositional age constraints were treated separately (Fig. DR2), although these data are consistent with results and interpretations presented herein.

NEOPROTEROZOIC VOLCANISM AND THE CRYOGENIAN ICEHOUSE

The youngest notable populations of zircon in Cryogenian strata are more than ~100 m.y. older than the depositional age of the rocks, while probability distributions of Ediacaran rocks from African-associated terranes are flooded with young zircon (Fig. 2). In striking contrast, age distributions from Cambrian samples of all non-Laurentian terranes contain large populations of young detrital zircon. Large Cambrian age peaks within ~20 m.y. of the depositional ages of the rock are present in Baltica, South America, and all east Gondwanan terranes, and the largest age peaks from African-associated terranes are of Ediacaran age, thus representing spatially extensive Ediacaran–Cambrian continental arc volcanism. The lack of young zircon grains in Laurentian strata reflects the fact that the terrane was surrounded by rift and passive margins during that time (Hadlari et al., 2012).

Zircon crystallization ages close to the onset of the Cryogenian glacial interval are sparse; this represents a reduction in global continental arc volcanism. Numerous mechanisms have

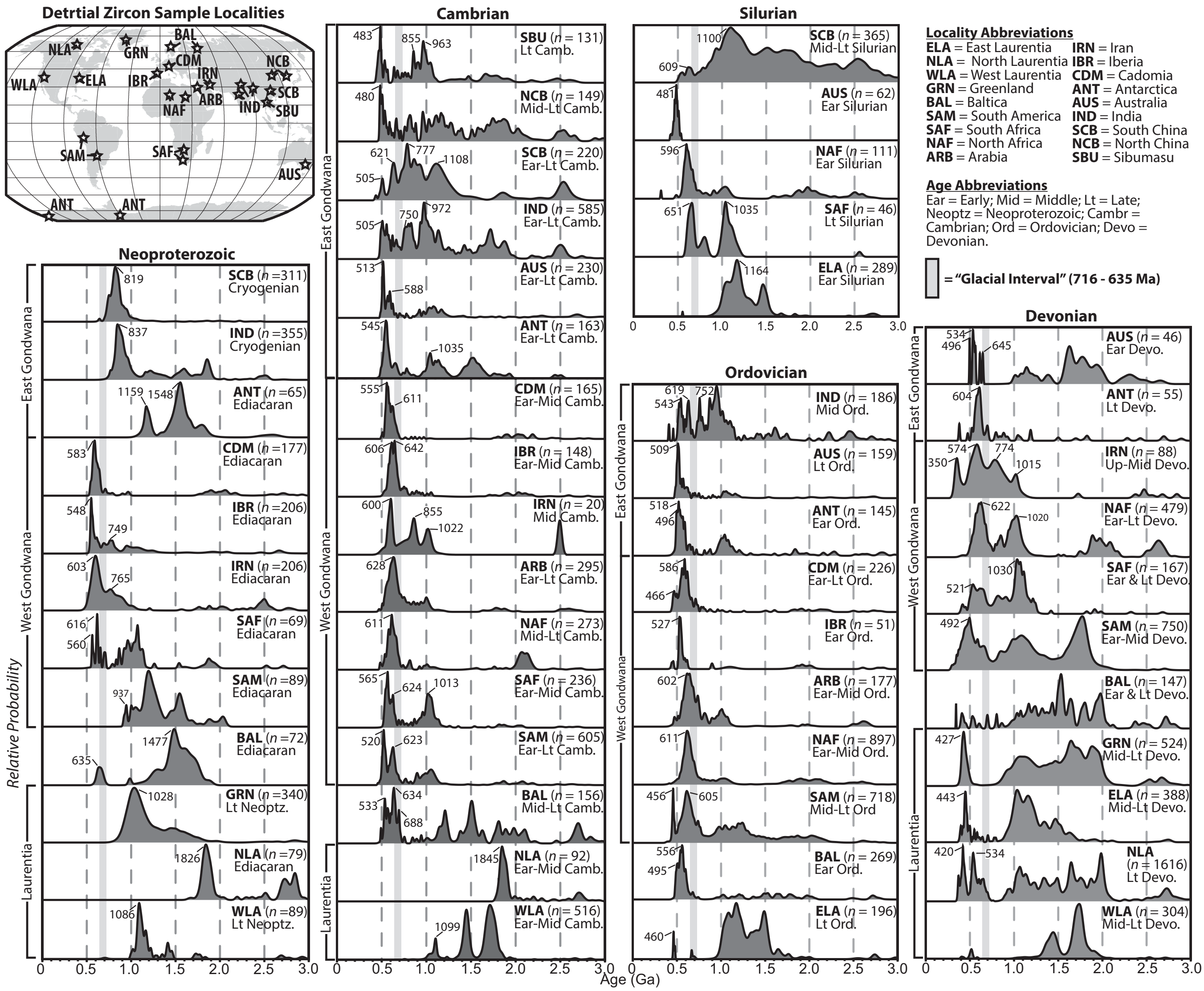

Figure 2. Regionally differentiated U-Pb detrital zircon age probability distributions. All Cryogenian samples include data from ca. 635 Ma Marinoan diamictite. Late Neoproterozoic samples include data from both Cryogenian and Ediacaran samples (see the Data Repository [see footnote 1] for data sources).

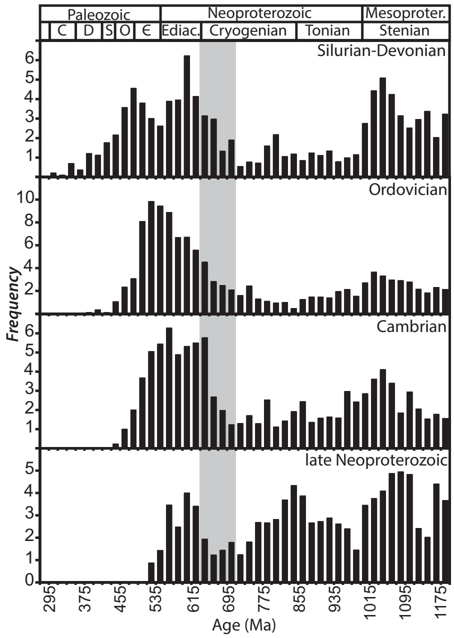

Figure 3. Normalized global composite detrital zircon U-Pb age distributions focused on an interval from 1195 Ma to 275 Ma. Proportion of ages older than 1195 Ma are as follows: late Neoproterozoic = 42%; Cambrian = 37%; Ordovician = 29%; Silurian–Devonian = 45%. Reference bar and abbreviations as in Figure 1.

been suggested for CO_2 drawdown during the Cryogenian icehouse (e.g., Hoffman et al., 1998; Schrag et al., 2002; Donnadieu et al., 2004; Tziperman et al., 2009), and lowered baseline atmospheric CO_2 from reduced volcanic outgassing would have played an important contributing role, permitting one or more of these mechanisms to trigger widespread glaciations. The progressive accumulation of CO_2 from both volcanic emissions and limited weathering has been argued to bring Earth out of the icehouse (Hoffman et al., 1998), and the marked increase in end-Cryogenian and Ediacaran detrital zircon in global distributions supports a major increase in continental arc volcanism at the end of the glacial interval.

EARLY PALEOZOIC TECTONICS, CLIMATE, AND BIODIVERSITY: INSIGHTS FROM A CENOZOIC ANALOG

Young age peaks are prominent throughout Cambrian and Ordovician successions in most regions, although Ordovician distributions are skewed toward the Cambrian populations (Figs. 2 and 3), indicating that the major pulses of volcanism and magmatism occurred during the Cambrian. The persistence of Cambrian grains in Ordovician strata reflects a protracted interval of exhumation and erosion of Cambrian felsic rock, consistent with suggestions that numerous Gondwanan orogens were active until the Middle Ordovician, ca. 480–470 Ma (Cawood and Buchan, 2007). Age distributions from Silurian and Devonian strata maintain strong Ediacaran–Cambrian age peaks, but also include greater concentrations of older zircon grains (and younger Taconic grains in Laurentia) than those from Ordovician rocks. The increased heterogeneity in zircon age populations in Silurian–Devonian strata is consistent with a transition to more mixed crustal sources for detritus that are no longer overwhelmed by the erosion of Cambrian plutons.

The Cenozoic India-Eurasia collision and Himalayan orogeny is a suitable analog for considering these ancient shifts in tectonic regimes. Andean-type subduction emplaced large Cretaceous–Paleogene plutons along the southern margin of Tibet prior to the ca. 50 Ma collision with India (Royden et al., 2008). The transition from Andean-type subduction to continental collision terminated Tibetan arc volcanism and initiated bedrock uplift and exhumation on the north Indian margin. This interval is coincident with the onset of long-term Cenozoic cooling following the Paleocene–Eocene Thermal Maximum (PETM). The cessation of continental arc volcanism (Lee et al., 2013), the chemical weathering of exhumed bedrock, and organic matter burial in Himalayan basins (Raymo and Ruddiman, 1992; Galy et al., 2007) have all been linked to post-PETM cooling. The strontium isotope ratio ($^{87}Sr/^{86}Sr$) of seawater is influenced by the weathering of old continental crust enriched in radiogenic ^{87}Sr, and the intense weathering of ancient bedrock along the Himalayan margin has caused seawater $^{87}Sr/^{86}Sr$ to rise to the second highest values in Earth history, surpassed only by those in the Cambrian (Edmond, 1992) (Fig. 1).

Evidence of increased continental weathering during the Cambrian summarized by Peters and Gaines (2012) includes high $^{87}Sr/^{86}Sr$ and very negative ε_{Nd} seawater values (Fig. 1). High weathering rates in the Himalayan system are facilitated by the South Asian monsoon, which is a function of the geographic position of the orogen (Molnar et al., 2010) and not just the simple fact that it is a continental collision zone. Considering the spatial extent and geometry of convergent Gondwanan margins, especially those in tropical regions of eastern Gondwana (Fig. DR3), one or more these orogenic systems could have generated the anomalously high $^{87}Sr/^{86}Sr$ Cambrian seawater values. Cambrian orogenesis does not, however, explain the continuous increase in seawater $^{87}Sr/^{86}Sr$ throughout the Neoproterozoic (Halverson et al., 2007) (Fig. 1). It is possible that the thick early Paleozoic sedimentary successions that blanketed cratonic interiors (see Peters and Gaines, 2012) covered older crustal sources that were exposed throughout the Neoproterozoic following the amalgamation of Rodinia. The Middle Ordovician decline in $^{87}Sr/^{86}Sr$ (Young et al., 2009) may have also resulted from a combination of increased weathering of juvenile Cambrian rock, as is evident from the detrital zircon record, and a reduction in exhumation of older crust as these orogenic systems shut down.

Cessation of continental arc activity is recorded along the internal sutures and outer margins of Gondwana during the Early Ordovician, although regional metamorphism continued in some regions until ca. 480–470 Ma (e.g., Cawood and Buchan, 2007), reflecting the transition from Andean-type subduction to Himalayan-type collision. The cessation of convergent tectonic activity coincided with the decline in seawater $^{87}Sr/^{86}Sr$ and an interval of rapid global cooling at the onset of the GOBE (Fig. DR1). We suggest that extensive tectonic outgassing fueled the Cambrian greenhouse, and the widespread shutdown of arc systems coupled with continued silicate weathering and organic matter burial along Himalayan-type margins would have caused Ordovician cooling.

We propose a direct relationship between variation in continental arc volcanism, climate, and early metazoan biodiversity. The Cambrian explosion accompanied the transition from the Cryogenian icehouse to the Cambrian greenhouse. Increased oceanic anoxia during the Cambrian dead interval has been attributed to sluggish oceanic circulation and lower oxygen solubility during greenhouse climates (Gill et al., 2011; Thompson and Kah, 2012). These conditions favored morphotypes adapted to stressed environments, such as the lingulid brachiopods and trilobites rich in thoracic segments, which are key components of the Cambrian Evolutionary Fauna (Sepkoski et al., 1981; Droser and Finnegan, 2003; Harper, 2006). The Khalkarindji LIP has been associated with the early Cambrian Botomian mass extinction (Glass and Phillips, 2006), and elevated CO_2 may have lowered the threshold so other eruptive events could affect the carbonate saturation state or pH of the ocean, influencing later Cambrian extinction events and hindering hypercalcifier proliferation (see Knoll and Fischer, 2011). Global cooling that followed the reduction in continental arc volcanism likely improved ocean habitability, allowing the ecological and taxonomic diversification of the GOBE. This cooling continued to the Late Ordovician glaciations and associated mass extinction (Kump et al., 1999; Finnegan et al., 2011). The abundance of Late Ordovician–Silurian detrital zircon in Devonian strata across Laurentia supports the hypothesis that CO_2 outgassing from the Taconic orogeny alleviated the Ordovician icehouse (Kump et al., 1999).

CONCLUSIONS

Data presented here show a distinct relationship between spatiotemporal variations in continental arc volcanism and climate change during the Neoproterozoic–early Paleozoic. Animal biodiversity appears to have responded to these major climatic shifts with extinction events occurring during climatic extremes. Thus climate, as influenced by plate tectonics, played an important role in mediating the evolution of life in Earth's past.

ACKNOWLEDGMENTS

We thank P. Cawood, C. Reinhard, P. Sadler, and T. Lyons for helpful discussions; R. Rainbird and two anonymous reviewers for constructive and insightful comments; and G. Gehrels, M. Ibanez-Mejia, and V. Valencia for analytical assistance. This work was supported by National Science Foundation (NSF) grants EAR-1124303 to Hughes, EAR-1124518 to Myrow, and a University of Texas Austin Jackson Postdoctoral Fellowship to McKenzie. NSF grant EAR-0732436 supports the Arizona LaserChron Center.

REFERENCES CITED

Alroy, J., 2010, The shifting balance of diversity among major marine animal groups: Science, v. 329, p. 1191–1194, doi:10.1126/science.1189910.

Bambach, R.K., Knoll, A.H., and Wang, S.C., 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., 1990, Atmospheric carbon-dioxide levels over Phanerozoic time: Science, v. 249, p. 1382–1386, doi:10.1126/science.249.4975.1382.

Berner, R.A., 2006, GEOCARBSULF: A combined model for Phanerozoic atmospheric O_2 and CO_2: Geochimica et Cosmochimica Acta, v. 70, p. 5653–5664, doi:10.1016/j.gca.2005.11.032.

Berner, R.A., Lasaga, A.C., and Garrels, R.M., 1983, The carbonate-silicate geochemical cycle and its effect on atmospheric carbon-dioxide over the past 100 million years: American Journal of Science, v. 283, p. 641–683, doi:10.2475/ajs.283.7.641.

Cawood, P.A., and Buchan, C., 2007, Linking accretionary orogenesis with supercontinent assembly: Earth-Science Reviews, v. 82, p. 217–256, doi:10.1016/j.earscirev.2007.03.003.

Cawood, P.A., Hawkesworth, C.J., and Dhuime, B., 2012, Detrital zircon record and tectonic setting: Geology, v. 40, p. 875–878, doi:10.1130/G32945.1.

Donnadieu, Y., Godderis, Y., Ramstein, G., Nedelec, A., and Meert, J., 2004, A 'snowball Earth' climate triggered by continental break-up through changes in runoff: Nature, v. 428, p. 303–306, doi:10.1038/nature02408.

Droser, M.L., and Finnegan, S., 2003, The Ordovician radiation: A follow-up to the Cambrian explosion?: Integrative and Comparative Biology, v. 43, p. 178–184, doi:10.1093/icb/43.1.178.

Edmond, J.M., 1992, Himalayan tectonics, weathering processes, and the strontium isotope record in marine limestones: Science, v. 258, p. 1594–1597, doi:10.1126/science.258.5088.1594.

Finnegan, S., Bergmann, K., Eiler, J.M., Jones, D.S., Fike, D.A., Eisenman, I., Hughes, N.C., Tripati, A.K., and Fischer, W.W., 2011, The magnitude and duration of Late Ordovician–Early Silurian glaciation: Science, v. 331, p. 903–906, doi:10.1126/science.1200803.

Galy, V., France-Lanord, C., Beyssac, O., Faure, P., Kudrass, H., and Palhol, F., 2007, Efficient organic carbon burial in the Bengal fan sustained by the Himalayan erosional system: Nature, v. 450, p. 407–410, doi:10.1038/nature06273.

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.

Glass, L.M., and Phillips, D., 2006, The Kalkarindji continental flood basalt province: A new Cambrian large igneous province in Australia with possible links to faunal extinctions: Geology, v. 34, p. 461–464, doi:10.1130/G22122.1.

Hadlari, T., Davis, W.J., Dewing, K., Heaman, L.M., Lemieux, Y., Ootes, L., Pratt, B.R., and Pyle, L.J., 2012, Two detrital zircon signatures for the Cambrian passive margin of northern Laurentia highlighted by new U-Pb results from northern Canada: Geological Society of America Bulletin, v. 125, p. 741–755, doi:10.1130/B30530.1.

Halverson, G.P., Dudas, F.O., Maloof, A.C., and Bowring, S.A., 2007, Evolution of the $^{87}Sr/^{86}Sr$ composition of Neoproterozoic seawater: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 256, p. 103–129.

Harper, D.A.T., 2006, The Ordovician biodiversification: Setting an agenda for marine life: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 232, p. 148–166, doi:10.1016/j.palaeo.2005.07.010.

Heaman, L.M., LeCheminant, A.N., and Rainbird, R.H., 1992, Nature and timing of Franklin igneous events, Canada: Implications for a Late Proterozoic mantle plume and the break-up of Laurentia: Earth and Planetary Science Letters, v. 109, p. 117–131, doi:10.1016/0012–821X(92)90078-A.

Hoffman, P.F., Kaufman, A.J., Halverson, G.P., and Schrag, D.P., 1998, A Neoproterozoic snowball Earth: Science, v. 281, p. 1342–1346, doi:10.1126/science.281.5381.1342.

Kidder, D.L., and Worsley, T.R., 2010, Phanerozoic large igneous provinces (LIPs), HEATT (haline euxinic acidic thermal transgression) episodes, and mass extinctions: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 295, p. 162–191.

Kiessling, W., 2009, Geologic and biologic controls on the evolution of reefs: Annual Review of Ecology Evolution and Systematics, v. 40, p. 173–192, doi:10.1146/annurev.ecolsys.110308.120251.

Knoll, A.H., and Fischer, W.W., 2011, Skeletons and ocean chemistry: The long view, *in* Gattuso, J.P., and Hansson, L., eds., Ocean acidification: Oxford, UK, Oxford University Press, p. 67–82.

Kump, L.R., Arthur, M.A., Patzkowsky, M.E., Gibbs, M.T., Pinkus, D.S., and Sheehan, P.M., 1999, A weathering hypothesis for glaciation at high atmospheric pCO_2 during the Late Ordovician: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 152, p. 173–187, doi:10.1016/S0031-0182(99)00046-2.

Kump, L.R., Brantley, S.L., and Arthur, M.A., 2000, Chemical weathering, atmospheric CO_2, and climate: Annual Review of Earth and Planetary Sciences, v. 28, p. 611–667, doi:10.1146/annurev.earth.28.1.611.

Lee, C.-T.A., and 11 others, 2013, Continental arc–island arc fluctuations, growth of crustal carbonates, and long-term climate change: Geosphere, v. 9, p. 21–36, doi:10.1130/GES00822.1.

Love, G.D., and 12 others, 2009, Fossil steroids record the appearance of Demospongiae during the Cryogenian Period: Nature, v. 457, p. 718–721, doi:10.1038/nature07673.

Macdonald, F.A., Schmitz, M.D., Crowley, J.L., Roots, C.F., Jones, D.S., Maloof, A.C., Strauss, J.V., Cohen, P.A., Johnston, D.T., and Schrag, D.P., 2010, Calibrating the Cryogenian: Science, v. 327, p. 1241–1243, doi:10.1126/science.1183325.

Marshall, C.R., 2006, Explaining the Cambrian "explosion" of animals: Annual Review of Earth and Planetary Sciences, v. 34, p. 355–384, doi:10.1146/annurev.earth.33.031504.103001.

Miller, A.I., Bulinkski, K.V., Buick, D.P., Ferguson, C.A., and Hendy, A.J.W., 2006, The Ordovician radiation: A macroevolutionary crossroads: Geological Society of America Abstracts with Programs, v. 38, no. 7, p. 114.

Molnar, P., Boos, W.R., and Battisti, D.S., 2010, Orographic controls on climate and paleoclimate of Asia: Thermal and mechanical roles for the Tibetan Plateau: Annual Review of Earth and Planetary Sciences, v. 38, p. 77–102, doi:10.1146/annurev-earth-040809-152456.

Palmer, A.R., 1984, The biomere problem: Evolution of an idea: Journal of Paleontology, v. 58, p. 599–611.

Peters, S.E., and Gaines, R.R., 2012, Formation of the 'Great Unconformity' as a trigger for the Cambrian explosion: Nature, v. 484, p. 363–366, doi:10.1038/nature10969.

Raymo, M.E., and Ruddiman, W.F., 1992, Tectonic forcing of late Cenozoic climate: Nature, v. 359, p. 117–122, doi:10.1038/359117a0.

Royden, L.H., Burchfiel, B.C., and Hilst, R.D., 2008, The geological evolution of the Tibetan Plateau: Science, v. 321, p. 1054–1058, doi:10.1126/science.1155371.

Schrag, D.P., Berner, R.A., Hoffman, P.F., and Halverson, G.P., 2002, On the initiation of a snowball Earth: Geochemistry, Geophysics, Geosystems, v. 3, no. 6, p. 1–21, doi:10.1029/2001GC000219.

Sepkoski, J.J., Bambach, R.K., Raup, D.M., and Valentine, J.W., 1981, Phanerozoic marine diversity and the fossil record: Nature, v. 293, p. 435–437, doi:10.1038/293435a0.

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, p. 189–214, doi:10.1016/j.palaeo.2011.10.020.

Trotter, J.A., Williams, I.S., Barnes, C.R., Lecuyer, C., and Nicoll, R.S., 2008, Did cooling oceans trigger Ordovician biodiversification? Evidence from conodont thermometry: Science, v. 321, p. 550–554, doi:10.1126/science.1155814.

Tziperman, E., Halevy, I., Johnston, D.T., Knoll, A.H., and Schrag, D.P., 2009, Biologically induced initiation of Neoproterozoic snowball-Earth events: National Academy of Sciences Proceedings, v. 108, p. 15091–15096, doi:10.1073/pnas.1016361108.

Young, S.A., Saltzman, M.R., Foland, K.A., Linder, J.S., and Kump, L.R., 2009, A major drop in seawater $^{87}Sr/^{86}Sr$ during the Middle Ordovician (Darriwilian): Links to volcanism and climate?: Geology, v. 37, p. 951–954, doi:10.1130/G30152A.1.

Manuscript received 19 July 2013
Revised manuscript received 18 October 2013
Manuscript accepted 22 October 2013

Printed in USA