

The age of tubes: A window into biological transition at the Precambrian-Cambrian boundary

James D. Schiffbauer

University of Missouri, Department of Geological Sciences, 101 Geology Building, Columbia, Missouri 65211, USA

Flashback to 1997, Spring semester: as a freshman biology major at West Virginia University (USA), I was enrolled in Dr. Kammer's *Fossils and Evolution* course. Like nearly every kid, I had at least had a passing fascination with dinosaurs in the 2nd grade, briefly rekindled in the early 90's with the *Jurassic Park* hype, but this course was my first true exposure to paleontology. I remember that the syllabus had a unit titled "Precambrian Life: Mostly Microbes." I didn't know much about early life and, in truth, I wasn't very excited, but I learned quickly just how wrong my first intuition was. In this course, outside readings, in addition to Gould's *Wonderful Life* (1989), were expected throughout the semester. For the Precambrian and Paleozoic Life units, I distinctly recall poring over Schopf's (1993) report of the ca. 3.5 Ga Apex Chert (Australia) microfossils and the amazing reconstruction of *Anomalocaris* from the Cambrian Burgess Shale (Canada) by Whittington and Briggs (1985). We learned about Seilacher's Vendobionta (1992) of the, at the time, unratiated Ediacaran Period (Knoll et al., 2004), but understanding how exactly these "classic Ediacaran organisms" fit in the evolutionary sequence of life between earlier microbes and later animals seemed to be both incomprehensible and captivating.

Flashing forward nearly two decades to the present day, my initial bewilderment toward Precambrian-Cambrian life has instead turned into true zeal. And apparently I wasn't alone; the Ediacaran-Cambrian interval, encompassing ~25 m.y. on either side of the 541 Ma boundary, has become one of the most intensively studied time slices in the geological and paleontological records. The past twenty years have brought significant new data to the table regarding the Ediacaran-Cambrian Earth system and biosphere, but a great many questions remain unanswered. Foremost of which, the pattern(s) of and mechanism(s) for biotic change during the Ediacaran-Cambrian transition are still largely unresolved.

Three general models exist for the departure of the Ediacara biota from the fossil record (Laflamme et al., 2013): categorized as environmental, taphonomic, and ecological.

The environmental model suggests a catastrophic perturbation to Earth surface environments and geochemical cycles, denoted in the rock record by an unprecedented terminal Ediacaran negative carbon isotope excursion (e.g., Amthor et al., 2003; Fike et al., 2006; Verdel et al., 2011). Conceivably corresponding to a flood of oxygen (Fike et al., 2006) and certainly reflecting a major perturbation to the carbon cycle (Schrag et al., 2013), this excursion likely signaled a momentous abiotic stress to Ediacaran organisms, but additionally may have supported the diversification of active and motile (multicellular, and possibly metazoan organisms capable of motion) life modes with higher oxygen requirements than the dominantly sessile, probably passive feeding organisms of the Ediacara biota.

In turn, this leads to the taphonomic, or "Cheshire Cat", model of Laflamme et al. (2013), in which matgrounds conducive to Ediacara-type fossil preservation (e.g., Gehling, 1999; though see also Tarhan et al., 2016, p. 951 in this issue of *Geology*) may have been eradicated or greatly diminished by the evolution of motile grazing behaviors. If correct, the Ediacara biota may have persisted into the Phanerozoic, although their record as fossils should be few and far between, if not entirely

absent. As such, the Cheshire Cat model is impractical to evaluate with fossil evidence, as it is necessarily based on the lack thereof. Recent evidence suggests that microbial mat-covered sediments persisted into the Cambrian; however, coupled with an abrupt increase in ichnodiversity, matgrounds may have become environmentally restricted during the Ediacaran-Cambrian transition (Buatois et al., 2014; 2016). Nonetheless, we observe that the fossil record of Ediacara organisms was truncated at this transition—whether by disappearance of their preservational regime or by disappearance of the organisms themselves.

The final model, which has received much attention recently (e.g., Darroch et al., 2015, 2016; Laflamme et al., 2013), broadly suggests that a growing diversity of true animals faced off in an increasingly antagonistic landscape with the likely non-metazoan taxa of the Ediacara biota, eventually driving the latter to extinction. The environmental catastrophe and biological revolution models are not mutually exclusive, and arguments for one, the other, or a combination of both have been offered (among many others, Amthor et al., 2003; Butterfield, 2009; Seilacher, 1992; Sperling et al., 2013). Evaluation of these arguments, however, has been hindered by a deficiency of stratigraphic sections that preserve fossil indicators of the Ediacaran-Cambrian transition within carbonate lithologies suitable for isotopic analyses.

Smith et al. (2016, p. 911 in this issue of *Geology*) accomplish exactly this task, from a detailed study of Ediacaran-Cambrian rocks of the Great Basin, Nevada. Investigating carbonate strata of the Deep Spring Formation at Mount Dunfee, Smith et al. provide an integral contribution to the timing of the large end-Ediacaran carbon isotope excursion, with direct reference to the occurrence of (1) *Cloudina*- and *Conotubus*-bearing tubular fossil assemblages, known as index fossils for the last ~10 m.y. of the Ediacaran (Cai et al., 2010; Cortijo et al., 2015; Grant, 1990); and (2) the Cambrian-defining ichnofossil *Treptichnus pedum* (Knoll et al., 2004).

Within 100 m of stratigraphy, Smith et al. not only observed the last occurrence of the Ediacaran tubicolous animals and the first occurrence of *T. pedum*, but also show a tightly constrained negative $\delta^{13}\text{C}$ excursion, dipping as low as -9.5% VPDB (Vienna Peedee belemnite), between the tubular and trace index fossil horizons. While they recovered no classic Ediacarans, the tubular fauna observed occupy Nama-aged assemblages (ca. 551–541 Ma), which have been shown recently from other localities to have meaningfully low generic diversity of iconic Ediacaran forms (Darroch et al., 2015). Additionally, the tubular fossils reported (including *Conotubus*, *Gaojiashania*, and *Wutubus*) provide a new Laurentian analogue to other Nama-aged tubular fauna, such as from the Gaojiashan Lagerstätte and Shibantan Member of the Dengying Formation, China (see fossil comparisons in Fig. 1) (Cai et al., 2010, 2011, 2012, 2013, 2014; Chen et al., 2014; Schiffbauer et al., 2014).

These tubular and other vermiform (worm-like) organisms have recently been implicated in marginalizing and competitively wedging out the classic Ediacaran forms, owing to such ecological novelties as ecosystem engineering and macropredation (Schiffbauer et al., 2016). However, as shown here in direct context with an isotopic record of environmental perturbation, perhaps the combined ecological and environmental stressors provided



Figure 1. Examples of tubular fossils from Mount Dunfee (Nevada, USA; top row), and their proposed Chinese equivalents (bottom row; white arrow in *Wutubus* frame indicates fossil, black arrow indicates burrow). Gaojiashan photos courtesy of Yaoping Cai; Shibantan photo courtesy of Shuhai Xiao.

an insurmountable double whammy, forcing a coda for the classic Ediacarans. While the terminal Ediacaran of the Deep Spring Formation had been previously examined (e.g., Gevartzman and Mount, 1986; Signor et al., 1987), Smith et al.'s new work has served to prop the window open for further refinement of the taxonomy of these tubular forms, as well as detailed investigation of their taphonomy and paleoecology. These “worm-world” organisms (Schiffbauer et al., 2016) inhabit an important transition, and their continued investigation may yield clarity into the patterns and mechanisms of biotic turnover at the Ediacaran-Cambrian boundary.

ACKNOWLEDGMENTS

I thank Y. Cai, S.A.F. Darroch, J.W. Huntley, M. Laflamme, A.D. Muscente, and S. Xiao for conversations that helped shape my thoughts on this topic and timeframe.

REFERENCES CITED

Amthor, J.E., Grotzinger, J.P., Schröder, S., Bowring, S.A., Ramezani, J., Martin, M.W., and Matter, A., 2003, Extinction of *Cloudina* and *Namacalathus* at the Precambrian–Cambrian boundary in Oman: *Geology*, v. 31, p. 431–434, doi:10.1130/0091-7613(2003)031<0431:EOCANA>2.0.CO;2.

Buatois, L.A., Mángano, M.G., Olea, R.A., and Wilson, M.A., 2016, Decoupled evolution of soft and hard substrate communities during the Cambrian Explosion and Great Ordovician Biodiversification Event: *Proceedings of the National Academy of Sciences of the United States of America*, v. 113, p. 6945–6948, doi:10.1073/pnas.1523087113.

Buatois, L.A., Narbonne, G.M., Mángano, M.G., Carmona, N.B., and Myrow, P., 2014, Ediacaran matground ecology persisted into the earliest Cambrian: *Nature Communications*, v. 5, p. 3544, doi:10.1038/ncomms4544.

Butterfield, N.J., 2009, Oxygen, animals and oceanic ventilation: An alternative view: *Geobiology*, v. 7, p. 1–7, doi:10.1111/j.1472-4669.2009.00188.x.

Cai, Y., Hua, H., Schiffbauer, J.D., Sun, B., and Yuan, X., 2014, Tube growth patterns and microbial mat-related lifestyles in the Ediacaran fossil *Cloudina*, Gaojiashan Lagerstätte, South China: *Gondwana Research*, v. 25, p. 1008–1018, doi:10.1016/j.gr.2012.12.027.

Cai, Y., Hua, H., Xiao, S., Schiffbauer, J.D., and Li, P., 2010, Biostratigraphy of the late Ediacaran pyritized Gaojiashan Lagerstätte from southern Shaanxi, South China: Importance of event deposits: *Palaeos*, v. 25, p. 487–506, doi:10.2110/palo.2009.p09-133r.

Cai, Y., Hua, H., and Zhang, X., 2013, Tube construction and life mode of the late Ediacaran tubular fossil *Gaojiashania cyclus* from the Gaojiashan Lagerstätte: *Precambrian Research*, v. 224, p. 255–267, doi:10.1016/j.precamres.2012.09.022.

Cai, Y., Schiffbauer, J.D., Hua, H., and Xiao, S., 2011, Morphology and paleoecology of the late Ediacaran tubular fossil *Conotubus hemiannulatus* from the Gaojiashan Lagerstätte of southern Shaanxi Province, South China: *Precambrian Research*, v. 191, p. 46–57, doi:10.1016/j.precamres.2011.09.002.

Cai, Y., Schiffbauer, J.D., Hua, H., and Xiao, S., 2012, Preservational modes in the Ediacaran Gaojiashan Lagerstätte: Pyritization, aluminosilicification, and

carbonaceous compression: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 326–328, p. 109–117, doi:10.1016/j.palaeo.2012.02.009.

Chen, Z., Zhou, C., Xiao, S., Wang, W., Guan, C., Hua, H., and Yuan, X., 2014, New Ediacara fossils preserved in marine limestone and their ecological implications: *Nature Scientific Reports*, v. 4, p. 4180.

Cortijo, I., Mus, M.M., Jensen, S., and Palacios, T., 2015, Late Ediacaran skeletal body fossil assemblage from the Navalpino anticline, central Spain: *Precambrian Research*, v. 267, p. 186–195, doi:10.1016/j.precamres.2015.06.013.

Darroch, S.A.F., Boag, T.H., Racicot, R.A., Tweedt, S., Mason, S.J., Erwin, D.H., and Laflamme, M., 2016, A mixed Ediacaran–metazoan fossil assemblage from the Zaris Sub-basin, Namibia: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 459, p. 198–208, doi:10.1016/j.palaeo.2016.07.003.

Darroch, S.A.F., et al., 2015, Biotic replacement and mass extinction of the Ediacara biota: *Proceedings of the Royal Society of London. Series B, Biological Sciences*, v. 282, p. 1–10, doi:10.1098/rspb.2015.1003.

Fike, D.A., Grotzinger, J.P., Pratt, L.M., and Summons, R.E., 2006, Oxidation of the Ediacaran ocean: *Nature*, v. 444, p. 744–747, doi:10.1038/nature05345.

Gehling, J.G., 1999, Microbial mats in terminal Proterozoic siliciclastics: Ediacaran death masks: *Palaeos*, v. 14, p. 40–57, doi:10.2307/3515360.

Gevartzman, D.A., and Mount, J.F., 1986, Paleoenvironments of an earliest Cambrian (Tommotian) shelly fauna in the southwestern Great Basin, USA: *Journal of Sedimentary Research*, v. 56, p. 412–421, doi:10.1306/212F8931-2B24-11D7-8648000102C1865D.

Gould, S.J., 1989, *Wonderful Life: The Burgess Shale and the Nature of History*: New York, Norton, 347 p.

Grant, S.W.F., 1990, Shell structure and distribution of *Cloudina*, a potential index fossil for the terminal Proterozoic: *American Journal of Science*, v. 290-A, p. 261–294.

Knoll, A.H., Walter, M.R., Narbonne, G.M., and Christie-Blick, N., 2004, A new period for the geologic time scale: *Science*, v. 305, p. 621–622, doi:10.1126/science.1098803.

Laflamme, M., Darroch, S.A.F., Tweedt, S.M., Peterson, K.J., and Erwin, D.H., 2013, The end of the Ediacara biota: Extinction, biotic replacement, or Cheshire Cat?: *Gondwana Research*, v. 23, p. 558–573, doi:10.1016/j.gr.2012.11.004.

Schiffbauer, J.D., Huntley, J.W., O’Neil, G.R., Darroch, S.A.F., Laflamme, M., and Cai, Y., 2016, The latest Ediacaran wormworld fauna: Setting the ecological stage for the Cambrian explosion: *GSA Today*, v. 26, p. 4–11, doi:10.1130/GSATG265A.1.

Schiffbauer, J.D., Xiao, S., Cai, Y., Wallace, A.F., Hua, H., Hunter, J., Xu, H., Peng, Y., and Kaufman, A.J., 2014, A unifying model for Neoproterozoic–Palaeozoic exceptional fossil preservation through pyritization and carbonaceous compression: *Nature Communications*, v. 5, p. 1–12, doi:10.1038/ncomms6754.

Schopf, J.W., 1993, Microfossils of the Early Archean Apex Chert: New evidence of the antiquity of life: *Science*, v. 260, p. 640–646, doi:10.1126/science.260.5108.640.

Schrag, D.P., Higgins, J.A., Macdonald, F.A., and Johnston, D.T., 2013, Authigenic carbonate and the history of the global carbon cycle: *Science*, v. 339, p. 540–543, doi:10.1126/science.1229578.

Seilacher, A., 1992, Vendobionta and Psammocorallia: Lost constructions of Precambrian evolution: *Journal of the Geological Society*, v. 149, p. 607–613, doi:10.1144/gsjgs.149.4.0607.

Signor, P.W., Mount, J.F., and Onken, B.R., 1987, A pre-trilobite shelly fauna from the White-Inyo region of eastern California and western Nevada: *Journal of Paleontology*, v. 61, p. 425–438, doi:10.1017/S0022336000028614.

Smith, E.F., Nelson, L.L., Strange, M.A., Eyster, A.E., Rowland, S.M., Schrag, D.P., and Macdonald, F.A., 2016, The end of the Ediacaran: Two new exceptionally preserved body fossil assemblages from Mount Dunfee, Nevada, USA: *Geology*, v. 44, p. 911–914, doi:10.1130/G38157.1.

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: *Proceedings of the National Academy of Sciences of the United States of America*, v. 110, p. 13446–13451, doi:10.1073/pnas.1312778110.

Tarhan, L.G., Hood, A.S., Droser, M.L., Gehling, J.G., and Briggs, D.E.G., 2016, Exceptional preservation of soft-bodied Ediacara Biota promoted by silica-rich oceans: *Geology*, v. 44, p. 951–954, doi:10.1130/G38542.1.

Verdel, C., Wernicke, B.P., and Bowring, S.A., 2011, The Shuram and subsequent Ediacaran carbon isotope excursions from southwest Laurentia, and implications for environmental stability during the metazoan radiation: *Geological Society of America Bulletin*, v. 123, p. 1539–1559, doi:10.1130/B30369.1.

Whittington, H.B., and Briggs, D.E.G., 1985, The largest Cambrian animal, *Anomalocaris*, Burgess Shale, British Columbia: *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, v. 309, p. 569–609, doi:10.1098/rstb.1985.0096.

Printed in USA