



SPOTLIGHT

LAGERSTÄTTEN THROUGH TIME: A COLLECTION OF EXCEPTIONAL PRESERVATIONAL PATHWAYS FROM THE TERMINAL NEOPROTEROZOIC THROUGH TODAY

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INTRODUCTION

While the study of taphonomic processes has elucidated numerous biases within the fossil record of life on Earth (for recent examples, see contributions within Allison and Bottjer, 2011), perhaps the most striking example comes in the form of preserved soft tissues and softbodied organisms. Deposits with these exceptionally conserved tissues, known as Konservat-Lagerstätten (Seilacher, 1970), represent one of the richest sources of paleontological data available in the fossil record. Yet, these exceptional faunas have classically been excluded in the examination of evolutionary patterns through time due to considerations of their rarity and perceived atypical paleoenvironments that are conducive to their preservation (Conway Morris, 1985; Allison and Briggs, 1993;). Konservat-Lagerstätten, however, have contributed vastly to the documentation of major evolutionary and biogeochemical shifts through numerous important intervals in geologic history (e.g., Butterfield, 2003) due to the extraordinary biological and mineralogical conservation of these fossils.

Konservat-Lagerstätten are unevenly distributed through geologic time (Allison and Briggs, 1993; Fig. 1). From such Proterozoic examples as the three-dimensionally preserved microbes of the Bitter Springs biota (e.g., Schopf, 1968; Schopf and Blacic, 1971; Schopf and Oehler, 1976), phosphatized acritarchs, algae, and possible animal embryos of the Doushantuo biota (e.g., Xiao et al., 1998; Xiao and Knoll, 1999; Huldtgren et al., 2011, 2012; Cunningham et al., 2012; Schiffbauer et al., 2012; Xiao et al., 2012), and the first appearance of complex macrofossils in globally distributed Ediacaran successions (e.g., Waggoner, 2003; Narbonne, 2005; Xiao and Laflamme, 2009), to Phanerozoic representatives such as the soft-bodied Tully Monster of Mazon Creek (e.g., Richardson, 1966), marine reptiles of the Smoky Hill Chalk (e.g., Williston, 1898; Frey, 1972), and the famous Archaeopteryx specimens from the Solnhofen Plattenkalk (e.g., Hecht et al., 1985; Rietschel, 1985; Wellnhofer, 1988), exceptional preservational pathways offer unique glimpses of diversity, disparity, and biology that, without the preservation of soft tissues, would have remained poorly known or merely speculated.

Our knowledge about the paleobiology and taphonomy of Konservat-Lagerstätten, in addition to the paleoenvironmental, biogeochemical, and sedimentological settings surrounding them, continues to grow with new discoveries of such exceptional deposits as the Ordovician Burgess Shale-type Fezouata biota (e.g., Van Roy et al., 2010), and novel approaches to understanding preservational pathways (e.g., Gaines et al., 2012a). The dissection of the processes and factors that lead or contribute to exceptional preservation, and further the relationships between ex-



James D. Schiffbauer (left) is research faculty at Virginia Tech's Institute for Critical Technology and Applied Science Nanoscale Characterization and Fabrication Laboratory, with primary research interests involving processes responsible for fossil preservation and mineralization in the Neoproterozoic and Paleozoic. His recent studies have centered on the investigation of the phosphatized Doushantuo microfossils, including possible early animal embryos and contained intracellular structures, as well as the carbonaceous compression taphonomic pathway apparent in numerous terminal Ediacaran-lower Cambrian fossil deposits. Jim is highly involved with the use of electron, ion, and X-ray microbeam analytical techniques, such as variable pressure scanning electron microscopy, focused ion beam scanning electron microscopy, secondary ion mass spectroscopy, and microcomputed X-ray tomography, for detailed micro- to nano-scale structural and compositional investigation of exceptionally preserved fossils at the early stages of animal evolution. Marc Laflamme (right) is a Smithsonian Institution Postdoctoral Fellow at the National Museum of Natural History with research interests in the classification and preservation of the Ediacara biota, the oldest large and complex organisms in the rock record. His studies focus on the enigmatic rangeomorphs and erniettomorphs, which likely represent extinct lineages on par with animals and plants. He has applied morphometric techniques to study the growth and differentiation in closely related species, and recently utilized modeling techniques to evaluate the likely feeding strategies employed by these enigmatic organisms. Marc is also interested in the taphonomic pathways that allowed for the preservation of soft-bodied Ediacara biota in coarse sediments.

ceptional taphonomic pathways and the resultant expression of fossil organisms, are paramount to the direction and growth of taphonomic and paleontological studies. These factors can be divided into two distinct but complementary categories. First, factors that have a more distal influence, such as paleoenvironmental and diagenetic processes, can chemically or mechanically serve to delay decay processes effectively shielding organic materials from destruction and allowing for preservation. These include such facilitating factors as burial within dysoxic or anoxic sediments, a lack of bioturbation, or early diagenetic

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FIGURE 1—Updated compilation of the distribution of exceptional faunas in marine deposits (adapted from Allison and Briggs, 1993, fig. 1), with added localities throughout the Phanerozoic and Ediacaran. Locales included: Ediacaran: Ediacara Hills (H⁺), Mistaken Point-Avalon Peninsula, Nama Group, Doushantuo Formation, White Sea, Gaojiashan Formation (G), Miaohe biota, Khatyspyt Formation, Tsagaan Gol Complex; Cambrian: Burgess Shale, Chengjiang biota-Maotianshan Shale, Sirius Passet, Emu Bay Shale, House Range-Marjum Formation-Wheeler Shale (F), Alum Shale-Orsten, Kinzers Formation, Spence Shale (E), Kaili Formation; Ordovician: Beecher's Trilobite Bed, Fezouata biota (D), Walcott-Rust Quarry, Soom Shale, Winneshiek, Llanfawr Mudstones-Welsh Gold; Silurian: Lesmahagow, Waukesha, Wenlock-Herefordshire; Devonian: Hunsrück Slates, Wissenbach Slate, Cleveland Shale, Canowindra-New South Wales, Gogo Formation, Arkona Shale; Carboniferous: Granton Lower Oil Shale, Bear Gulch Limestone, Mecca-Logan, Mazon Creek; Triassic: Grès à Voltzia, Montral-Alcover, Monte San Giorgio; Jurassic: Osteno, Holzmaden-Posidonia Shale, Christian Malford, La Voulte-sur-Rhône, Cordillera de Domeyko, Solhnhofen Plattenkalk; Cretaceous: Montsech, Santana Romualdo-Crato Formations, Haqel-Hadjula-al-Nammoura, Smoky Hill Chalk, Cenozoic (Paleogene-Neogene combined): Monte Bolca, Chita, Fur Formation. Fossils shown in A-H (with approximate geologic time represented by labeled arrows) taken from papers assembled as part of this special issue: A*) SEM micrograph of transverse sections of Larix conifer leaf needles from the middle Miocene Ballast Brook Formation, Banks Island, Canada (Witkowski et al., 2012, fig. 2B); B*) Damselfly from the upper Eocene Florissant Formation, Colorado, United States (Smith, 2012, fig. 1A); C) articulated Eldredgeops rana cluster from the Middle Devonian Hamilton Group, Windom Shale, New York, United States (photo courtesy of Matt Phillips and Rich Spencer; Brett et al., 2012, fig. 5D); D) concretion-hosted anomalocaridid specimen from the Lower Ordovician Fezouata biota, eastern Anti-Atlas, Morocco (photo courtesy of Peter Van Roy; Gaines et al., 2012b, not figured); E) middle Cambrian Spence Shale trilobite Leanchoilia superlata?, Utah, United States (Olcott Marshall et al., 2012, specimen shown in fig. 1); F) middle Cambrian Wheeler Shale coiled algal morphotype, House Range, Utah, United States (Handle and Powell, 2012, fig. 3); G) Shaanxilithes ribbonlike fossil and associated discoidal structures from the terminal Ediacaran Gaojiashan biota, Dengying Formation, southern Shaanxi Provence, South China (Meyer et al., 2012, fig. 2H); H⁺) Modern experimental replication of Ediacara-type death mask preservation using larvae of Galleria mellonella as model organisms (Darroch et al., 2012, fig. 2); *indicates nonmarine deposits, †indicates modern laboratory experimental approach to investigate taphonomic pathway.

cementation—all of which can assist but do not necessarily ensure softtissue preservation. Second, more constructive and proximal factors serve to stabilize and replicate the organic soft tissues themselves, typically through mineralization (Briggs, 2003) and are, therefore, imperative for the survivability of these tissues within the fossil record (Cai et al., 2012). Studies engaging distal and proximal factors, and their resultant taphonomic pathways, serve as functional guides for interpreting not only the biology of fossil remains, but also the paleoenvironmental, biogeochemical, sedimentological, and diagenetic influences responsible for exceptional, and likewise not-so-exceptional, fossil deposits.

SCOPE OF THIS ISSUE

The papers contained herein come directly from research presented in the topical session "T117. Lagerstätten through Time: An Examination of Exceptional Preservational Pathways from the Terminal Proterozoic through Today" from the 2010 annual Geological Society of America meeting in Denver, Colorado. The reports here range from the terminal Neoproterozoic through the Pliocene, and focus on proximal and distal taphonomic factors, in addition to technological approaches to the investigation of exceptionally preserved biotas and laboratory experimentation in an effort to replicate taphonomic processes responsible for preservation.

Experimentally, Simon Darroch and colleagues (Darroch et al., 2012) investigated the tempo and mode of Ediacaran soft-tissue preservation through a series of decay experiments in their paper entitled "Experimental formation of a microbial death mask." Their studies confirm a strong positive influence of microbial mats in controlling the fidelity of fossil impressions cast in coarse sands, and suggest that the presence and influence of microbial mats prolonged the taphonomic window allowing for soft-tissue preservation up to several weeks, when compared to normal marine settings. The generation of a black halo, composed of common aluminosilicates and likely iron sulfides, may help explain similar geochemical associations found in Ediacaran fossils and predicted by the Death Mask hypothesis of Gehling (1999). Michael Meyer and colleagues (Meyer et al., 2012), in their contribution "Taphonomy of the upper Ediacaran enigmatic ribbonlike fossil Shaanxilithes," investigate a potential regionally significant biostratigraphic indicator, Shaanxilithes ningqiangensis, from the upper Ediacaran Gaojiashan Lagerstätte of the Dengying Formation, southern Shaanxi Province, southern China. By applying scanning electron microscopy (SEM), energy dispersive X-ray spectroscopy

(EDS), Raman spectroscopy, and morphological analyses to this enigmatic ribbon-like fossil preserved by aluminosilicate molds (e.g., Gabbott, 1998; Orr et al., 1998; Anderson et al., 2011; Laflamme et al., 2011; Cai et al., 2012; Handle and Powell, 2012), they resolve previous debates surrounding the affinities of Shaanxilithes (Shen et al., 2007; Weber et al., 2007; Zhuravlev et al., 2009; Cai and Hua, 2011). Kimberly Handle and Wayne Powell (Handle and Powell, 2012), in "Morphologically simple enigmatic fossils from the Wheeler Formation: A comparison with definitive algal fossils," also use an SEM-EDS and Raman spectroscopic approach in addition to electron probe microanalyzer-based (EPMA) wavelength dispersive X-ray spectroscopy (WDS) to characterize numerous potential algal forms from the middle Cambrian Wheeler Shale of the House Range, western Utah. Their investigation indicates preservation as a combination of carbonaceous compression with an aluminosilicate and iron oxide (from pyrite weathering) association, which they use to interpret contributing paleoenvironmental factors and conditions. In "Raman spectroscopic investigations of Burgess Shale-type preservation: A new way forward," Alison Olcott Marshall and collaborators (Olcott Marshall et al., 2012) report Raman spectroscopic examination of Burgess Shale-type fossils (a technique already gaining popularity in the investigation of similar exceptional fossils: see Handle and Powell, 2012; Meyer et al., 2012) and the implications of this analytical approach for investigation of numerous other preservational windows. In their contribution "Preservation of giant anomalocaridids in silicachlorite concretions from the Early Ordovician of Morocco," Robert Gaines and coauthors (Gaines et al., 2012b) detail remarkably preserved anomalocaridids captured in large silica-chlorite concretions from the recently discovered Early Ordovician Fezouata biota of Morocco (Van Roy et al., 2010). A suite of technical approaches, including SEM-EDS, X-radiography, X-ray diffraction and fluorescence, and carbon isotopic analyses, are used to explore the formation of massive concretions. The authors suggest that rapid mineralization, a highly reactive sediment composition, and accelerated microbial degradation of a large quantity of organic material were ultimately responsible for the anomalocaridid preservation. Carlton Brett and colleagues (Brett et al., 2012) thoroughly investigate several prominent trilobite Lagerstätten in the article entitled "Mid-Paleozoic trilobite Lagerstätten: Models of diagenetically enhanced obrution deposits," which identifies two dominant taphonomic facies that are distinguished based on the amount of associated seafloor disturbance. These deposits were also at the mercy of subsequent sediment accumulation, which affected the severity of postburial diagenetic overprints, suggesting that the best-preserved specimens resulted from rapid burial and subsequent sediment starvation. Dena Smith (2012), in "Exceptional preservation of insects in lacustrine environments," surveys and details preservational pathways and paleoenvironments associated with exceptional lacustrine insect preservation from the Jurassic-Cretaceous transition through the Miocene. Finally, Caitlyn Witkowski and colleagues (Witkowski et al., 2012) utilize a combination of SEM and pyrolysis gas chromatography mass spectrometry for high-resolution imaging and molecular analysis of exceptionally preserved conifers from a middle Miocene through Pliocene fluvial setting in their contribution, "Molecular preservation of Cenozoic conifer fossil Lagerstätten from Banks Island, the Canadian Arctic." For representative fossil images from these contributions, see Figures 1A-H (in reverse chronologic order).

CONCLUDING REMARKS

While providing an avenue to discuss current research into exceptional preservational pathways, we also hope that this issue will serve to widen the scope of future analytical approaches into processbased investigation of Konservat Lagerstätten. By spotlighting varying modes of exceptional preservation across a wide breadth of geologic time, we are confident that future taphonomic studies will build on this volume to further our understanding of constructive taphonomic factors and processes, as well as paleoenvironmental, biogeochemical, sedimentological, and diagenetic conditions that may be shared by seemingly disparate Lagerstätten deposits.

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