The "Preservation Paradox": Microbes as a Key to Exceptional Fossil Preservation in the Kirkpatrick Basalt (Jurassic), Antarctica

Loren E. Babcock
School of Earth Sciences, The Ohio State University, Columbus, OH 43210; babcock.5@osu.edu

Alycia L. Stigall
Department of Geological Sciences, Ohio University, Athens, OH 45701; stigall@ohio.edu

Stephen A. Leslie
Department of Earth Sciences, University of Arkansas at Little Rock, Little Rock, AR 77204; saleslie@ualr.edu

Lara A. Ford
School of Earth Sciences, The Ohio State University, Columbus, OH 43210; ford.205@osu.edu

David H. Elliot
School of Earth Sciences, The Ohio State University, Columbus, OH 43210; elliot.1@osu.edu

Derek E. G. Briggs
Department of Geology and Geophysics, Yale University, New Haven, CT 06520; derek.briggs.@yale.edu

ABSTRACT

Thin sedimentary interbeds within the Kirkpatrick Basalt (Jurassic) of Antarctica harbor exquisitely preserved 'soft-bodied' organisms that lived in and around shallow freshwater lakes of the time, some of which were hydrothermally influenced. In the hottest pools, associated with magmatic vents, unusual carbonates were apparently precipitated by Archaea extremophiles adapted to living near active lava flows. In cooler lakes more distant to the vents, fine siliciclastic sediments record other communities of spinicaudatan ("conchostracan") and notostracan crustaceans, larval insects, fishes, and ostracodes much of which may have been sustained by microbial mats, which are also well preserved in the deposits. Along the lake-edge, carbonized leaves, peat or coal, and silicified logs are often found in association with paleosols. Notably, evidence of carnivory, a primary taphonomic filter, is essentially lacking in these sediments. Exceptional preservation of non-biomineralized or lightly skeletonized organisms, therefore, reflects the original diversity of non-biomineralized or lightly skeletonized organisms present.

INTRODUCTION

One of the most striking and paradoxical observations about the evolutionary record is that the most numerous and diverse animals on Earth are represented by a weak fossil record - among them, insects, spiders, scorpions, mites, myriapods, shrimp, nematodes, "worms" of various kinds, and countless other species lacking hard skeletal parts. Conversely, groups best represented in the fossil record constitute a relatively small fraction of total species diversity, including mollusks, brachiopods, corals, echinoderms, vertebrates, and other animals having hard (biomineralized) shells, bones, or teeth, which today constitute less than 20% of animal species. Compensating for this "preservation paradox," in which the most abundant and diverse forms on Earth have a weak fossil record, usually involves the discovery of deposits where both biomineralized fossils and non-biomineralized fossils have been preserved. Such deposits are variously referred to as Konservat-Lagerstätten, Lagerstätten, or deposits of exceptional preservation (DEP's). Well-known examples (see Allison and Briggs, 1991 and references therein) include the Chengjiang deposit (Cambrian of Yunnan, China), the Burgess Shale (Cambrian of British Columbia), the Rhynie Chert (Devonian of Scotland), the Mazon Creek deposit (Carboniferous of Illinois), the Solnhofen Limestone (Jurassic of Germany), and the Green River Formation (Eocene of Wyoming, Colorado, and Utah). Studying fossils from these and similar deposits provide rare snapshots of organisms and ecosystems otherwise not preserved in the fossil record.

Studying exceptionally preserved fossils has a second, and no less important benefit: it provides insight into the processes and timing by which fossilization occurs. Key factors promoting exceptional preservation are the inhibition of tissue degradation by predators, scavengers, and microbial decay agents, and in many cases, rapid diagenesis (commonly preceded by burial). Mounting evidence suggests that microbes (bacteria and fungi) play a central role in the diagenesis process, mediating mineral precipitation within chemical microenvironments inside biofilms generated by decay halos around organic matter (e.g., Schieber, 2002; Borkow and Babcock, 2003; Briggs, 2003).

Here, we describe such an instance of exceptional preservation, and an unusual process of carbonate sedimentation, from the Jurassic of Antarctica. The unusual carbonates were precipitated near a strong hydrothermal source, and nearby cooler and silica-rich hydrothermal waters apparently worked to fossilize organic remains rapidly and produce a "freeze-frame" of macroscopic and microscopic life forms. Microbes seem to have played a vital role in both processes. This example provides an unusual perspective on the fossilization process, and suggests that further insight into taphonomic processes and occurrences of microbial fossils may be gained through expansion of our search strategies, even to igneous-dominated environments.

LOCATION AND STRATIGRAPHY

This paper focuses on thin sedimentary deposits interbedded within lava flows of the Kirkpatrick Basalt (Ferrar Group; Jurassic) of Antarctica, which is exposed in South Victoria Land (Carapace Nunatak) and isolated peaks in the central Transantarctic Mountains (Beardmore and Shackleton Glacier areas; Fig. 1) (Ball et al., 1979; Tasch, 1977, 1987; Barrett et al., 1986; Bradshaw, 1987; Elliot et al., 1991). Two of these sedimentary horizons can be correlated widely and indicate brief periods of relative cessation of extrusive magmatism. The Kirkpatrick Basalt itself forms the cap sequence on tholeiitic rocks of the Ferrar Large Igneous Province (FLIP), which occur in a 3,500 km linear belt along the Transantarctic Mountains from the Weddell Sea region to North Victoria Land (Elliot and Fleming, 2000, 2004). The FLIP was emplaced about 180±3.5 Ma during initial breakup of Gondwana in the Early Jurassic (Toarcian Epoch), from a source

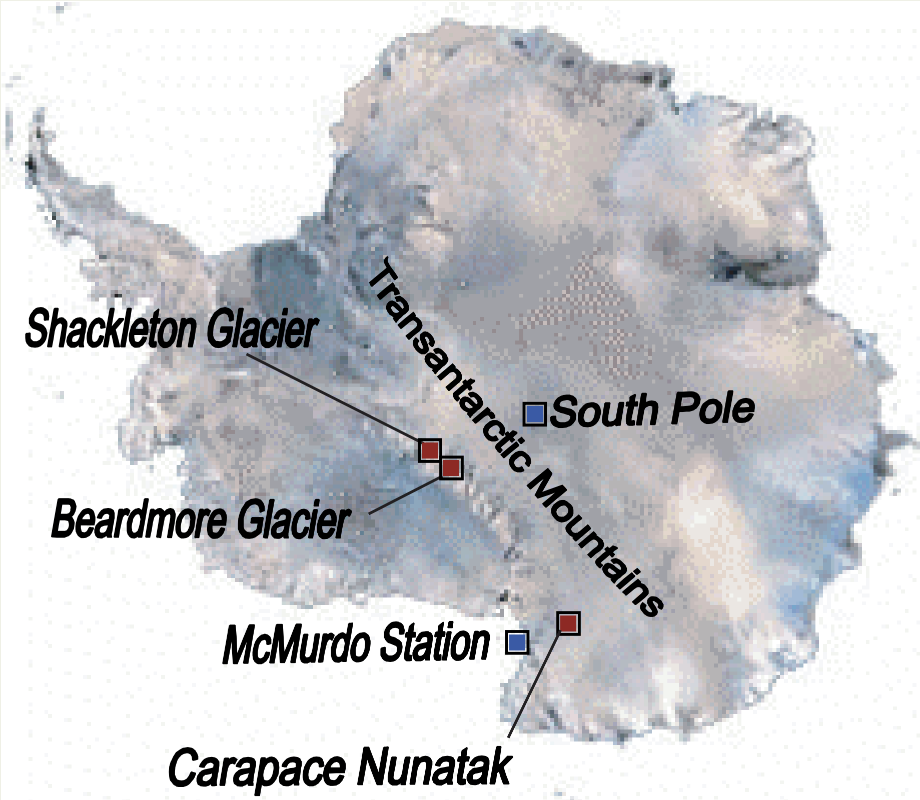

Figure 1. Map of Antarctica showing locations of the Transantarctic Mountains and outcrops of Kirkpatrick Basalt (Jurassic) having sedimentary interbeds. Study localities are Carapace Nunatak (South Victoria Land), and peaks in the Beardmore Glacier area (Central Transantarctic Mountains).

thought to be a triple junction in the proto-Weddell Sea (Elliot and Fleming, 2000, 2004). Radioisotopic dating constrains the duration of FLIP emplacement to a brief interval, less than 1 million years (Heiman et al., 1994). This extrusive magmatism ends with the capping iron-rich lavas of the Kirkpatrick Basalt, which comprises less than 1% of the FLIP rocks that locally exceed 2 km in thickness (Elliot and Fleming, 2004).

SEDIMENTARY INTERBEDS IN THE KIRKPATRICK BASALT

The interbeds of the Kirkpatrick Basalt record sedimentary and biotic processes in relatively shallow lakes and ponds, and in surrounding wetlands to upland areas, during two brief intervals when active magmatic activity had slowed along an expanding rift system in high latitude Pangaea. Among these sedimentary interbeds are two dominant types of subaqueous origin: (1) fine-grained, thinly laminated siliciclastic deposits (Fig. 2) and (2) unusual carbonate deposits rimming and filling spaces between basalt pillows (Fig. 3). Both of these subaqueous deposits transition laterally into thin paleosols and poorly consolidated peat deposits, where large permineralized (silicified) logs occur locally in the Beardmore Glacier region (Taylor and Taylor, 1990).

The siliciclastics were evidently deposited in small, relatively shallow, freshwater lakes and pools (Tasch, 1977, 1987). In many places, synsedimentary deformation of the laminations is associated with igneous extrusions. At Carapace Nunatak, for example, large clasts of lithified or semilithified sediment appear to have been rafted by hot magma (Bradshaw, 1987) (Fig. 2b). Elsewhere, numerous thin dark brown to black laminae and crinkled layers with clotted textures are interpreted as microbial mat communities of photosynthetic bacteria and possibly algae (compare Schieber, 1999; Noffke et al., 2001). The fossil assemblage in these environments is dominated by small (1-2 cm) bivalved spinicaudatan ("conchostracan") arthropods that are today most typical of ephemeral, alkaline pond settings (Fig. 4a) (Tasch, 1987). Other macrofossils include fishes (mostly *Oreochima*), notostracan branchiopods, ostracodes, insect nymphs and wings, and plant leaves (Fig. 4), but macroscopic trace fossils are extremely rare. The animal body fossils are preserved with mineralogies that mimic their original skeletal composition (i.e., spinicaudatan carapaces are preserved as calcium phosphate, while those of ostracods are preserved as calcium carbonate), although portions of spinicaudatan carapaces are silicified (Stigall Rode et al., 2005) (Fig. 5). Overall, the preservation of original skeletal composition and the preservation of carapace layers in spinicaudatan specimens indicate rapid burial and preservation of specimens with little or no alteration of regions of their exoskeleton. The silicification of regions within spinicaudatan carapaces (Fig. 5) may have been microbially mediated.

Weak to distinct laminae in the carbonate beds are aligned subhorizontally to concentrically around basalt pillows (Fig. 3b). The carbonates appear to lack the macroscopic body fossils common in the siliciclastic beds. Backscatter SEM-EDS analyses, however, reveal minute, irregular, organic morphologies preserved with a high concentration of carbon. These organic structures are rimmed by thin silica-rich carbonate 'halos', and the surrounding carbonate mud lacks needles or other indicators of precipitation by macroscopic organisms. Thermoacidophilic microbes likely occurred in this type of setting and may have mediated carbonate, and perhaps also silica, precipitation in pools closely associated with hydrothermal vents and basaltic extrusion. Another untested possibility is that microbial consortia on the surface of cooler basalt pillows created an alkaline chemical microenvi-

Figure 2. Exposure of the Kirkpatrick Basalt at Carapace Nunatak, South Victoria Land; A) Outcrop showing thick lava flows; B) Siliciclastic interbed.

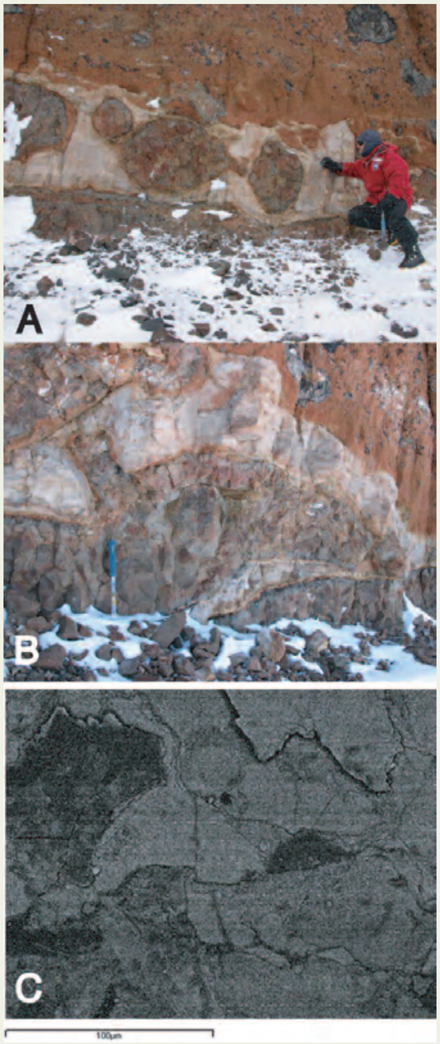

Figure 3. Carbonate interbeds of Kirkpatrick Basalt at Carapace Nunatak; A) View of outcrop showing basalt pillows and limestone interbeds between the pillows; B) Closeup of carbonate interbeds rimming a basalt pillow; C) SEM image of a possible thermophilic archean.

ronment in their immediate vicinity, while water elsewhere in the lakes or pools was reducing.

BIOTIC COMMUNITIES AND TAPHONOMY

Two distinct biotic communities developed within the lake environments of the Kirkpatrick Basalt sedimentary interbeds, their differences probably reflecting distance or access to a magmatic source. Hydrothermal pools near igneous vents close to phreatomagmatic centers were evidently too warm to support multicellular life: only high-temperature-adapted microbes are likely to have survived (see Jones et al., 2001). Thus, larger metazoans are found only in the siliciclastic interbeds of the Kirkpatrick Basalt. Spinicaudatans (dominated by *Carapacestheria*, Fig. 4a) are densely packed in many thin layers at localities in both South Victoria Land and the Central Transantarctic Mountains. Their enormous numbers and nearly uniform lengths presumably reflect a high reproductive (and presumably rapid maturation) rate in pools where they had few predators. The growth lines in the carapaces of *Carapacestheria* in the Kirkpatrick beds indicate that specimens in the individual layers were all of the same age at death. This suggests that each bedding plane represents a single generation of spinicaudatans that hatched simultaneously during the initial spring flooding of the pond, a pattern mimicking that of modern spinicaudatans (Weeks et al., 1997). Carapaces of the freshwater ostracod, *Darwinula* (Fig. 4e), commonly occur on slabs with spinicaudatans.

In South Victoria Land, nymphs of ephemeropteran insects (Fig. 4b) are present in certain thin horizons, apparently confined to narrow time intervals, on Carapace Nunatak. Some localities in the Central Transantarctic Mountains yield abundant remains of fishes (Fig 4c) (mostly *Oreochima*) most of them fully or largely articulated. This again suggests that predaceous and scavenging activity in the Kirkpatrick lakes was minimal. Likewise there is little evidence of bioturbation of benthic muds in the siliciclastic-dominated lakes. Lack of an active infauna may have provided an opportunity for microbial mat communities to flourish.

In numerous other instances of exceptional

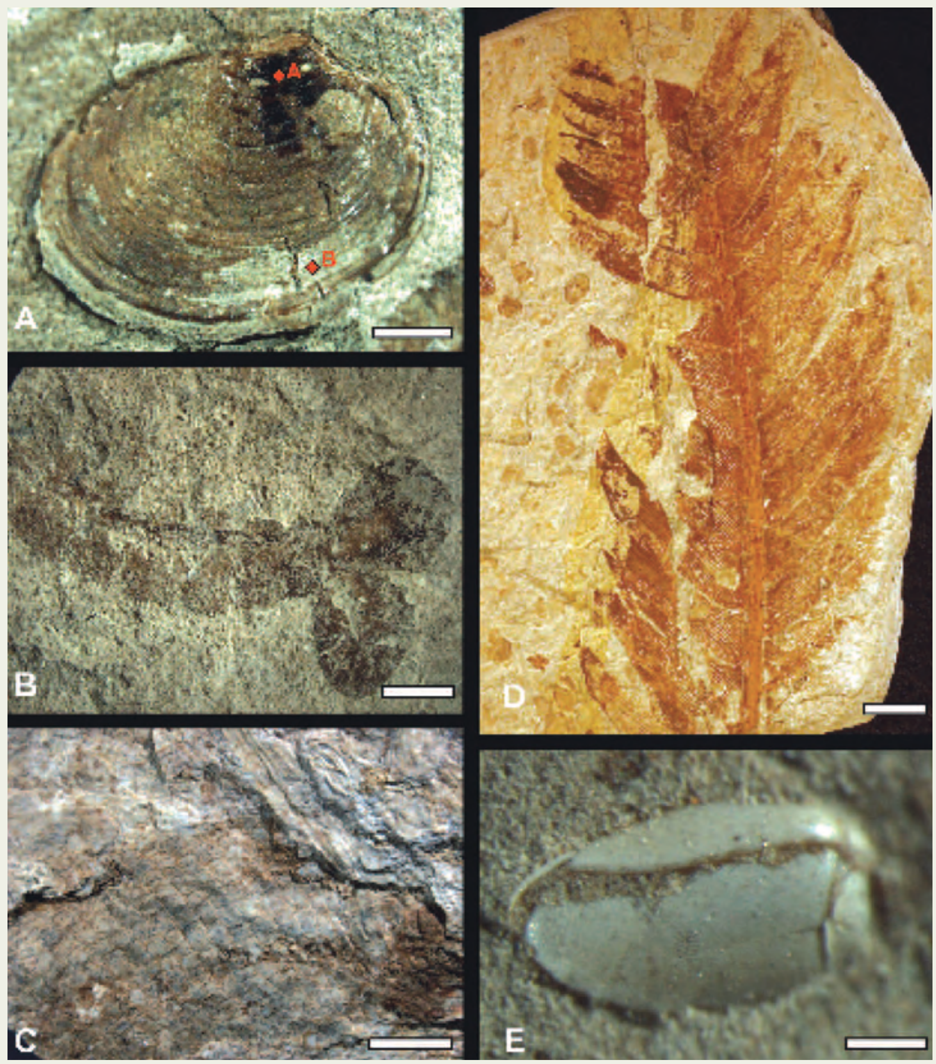

Figure 4. Representative biota from the siliciclastic interbeds. A) spinicaudatan, Carapacestheria disgregaris, *from Carapace Nunatak, scale bar equals 1 cm, B) ephemeropteran nymph, from Carapace Nunatak, scale bar equals 0.25 cm; C) actinopterygian fish,* Oreochima ellioti, *from lower interbeds at Storm Peak, scale bar equals 0.5 cm; D) bennititalean,* Zamites *sp., from Carapace Nunatak, scale bar equals 1 cm; E) ostracod,* Darwinula *sp., from Carapace Nunatak, scale bar equals 0.25 mm.*

preservation in the Phanerozoic, biodegradation, including predation and scavenging, is minimal and sediment bioturbation largely absent. Non-biomineralized remains often survived long enough in the Kirkpatrick lakes to undergo early diagenesis, especially if it were mediated by microbial decay agents within a few weeks (compare Briggs et al., 1993; Wilby et al., 1996; Borkow and Babcock, 2003). Microbial mediation of silicification likely occurred in the siliciclastic interbeds of the Kirkpatrick Basalt. Microbial influence is suggested by differential replacement along zones of weakness between carapace layers as well the increased silicification of carapaces preserved within microbial-mat-influenced versus other sediments (Fig. 5).

Plant remains, including bennettitalean leaves, silicified trunks of gymnosperms, and peat (or low grade coal), are another important constituent of the fossil assemblage in the siliciclastic interbeds of the Kirkpatrick Basalt. Most of the plants lived in wetlands surrounding relatively cool water lakes, or somewhat upland from them. The sizes of the tree trunks, often 50 cm or more in diameter, provide a minimum duration between lava flows. The large diameter of these trunks suggests that some of the trees were several decades to perhaps a hundred years or more in age. Leaves and peat are preserved as hydrocarbons, whereas the logs are permineralized with silica (Taylor and Taylor, 1990) presumably sourced from Si-rich waters derived from nearby volcanic sources.

Silicification of plant material associated with igneous sources is not uncommon (e.g., Chinle Formation, see Sigleo, 1979 and Creber and Ash, 2004; Rhynie Chert, see Rice et al., 2002 and Trewin et al., 2003), but instances where a nearby hydrothermal source for magmatophreatic interactions can be identified are unusual. The Rhynie Chert (Devonian of Scotland) is perhaps the best-known example (Trewin et al., 2003). Silicification of woody material in the Kirkpatrick Basalt provides a window into paleoenvironments and climate of high-latitude Gondwana during the Jurassic (see Taylor and Taylor, 1990; Parrish, 1990).

CONCLUSIONS

Sedimentary interbeds deposited over lava flows of the Kirkpatrick Basalt during the Early Jurassic splitting of Gondwana represent unusual freshwater paleoenvironments. They illustrate an important means of solving some of the issues related to the "preservation paradox" for a critical paleoenvironmental setting-high latitude Gondwana during the early Mesozoic. Hot lakes associated with hydrothermal vents were likely home to thermophilic microbes (archeans) capable of withstanding not only high temperature, but also sulfidic water. They promoted the precipitation of carbonate laminae even around basaltic pillows that extruded into the water. Other freshwater lakes away from direct contact with hydrothermal vents, where water temperatures were cooler, were home to low diversity faunas and microbial mat communities. Vascular plants were rooted beyond the margins of the water. Carnivory was limited, and exceptional preservation of non-biomineralized or lightly mineralized organisms became commonplace. Microbial decay agents contributed to rapid diagenesis.

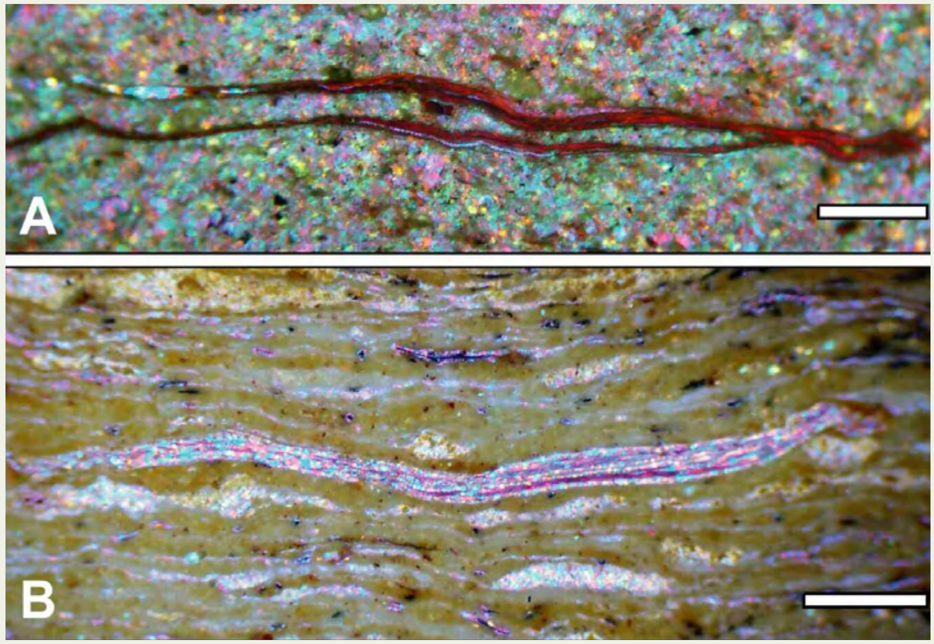

Figure 5. Thin section light micrograph of siliciclastic interbeds; brown coloration of carapace indicates phosphatic composition while purple indicates silica. A) Interbed from Carapace Nunatak without discernable microbial textures, note limited silicification of spinicaudatan carapace. B) Interbed from Strom Peak (lower bed) exhibiting microbial textures, note extensive silicification of spinicaudatan carapace.

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