PALAIOS
Emphasizing the impact of life on Earth's history

PALAIOS, 2008, v. 23, p. 344–355
Research Article
DOI: 10.2110/palo.2007.p07-029r

TAPHONOMY OF LACUSTRINE INTERBEDS IN THE KIRKPATRICK BASALT (JURASSIC), ANTARCTICA

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ABSTRACT

The Kirkpatrick Basalt (Jurassic) of South Victoria Land and the Central Transantarctic Mountains, Antarctica, includes sedimentary interbeds representing shallow lakes and ephemeral ponds (some with microbial mat accumulations), deep permanent lakes, and lake-margin areas, especially vegetated wetlands. Fossil assemblages in these sedimentary interbeds are dominated by spinicaudatans (conchostracans), but ostracodes, insect nymphs, actinopterygian fish, and plants are locally abundant. Similar biotas in contrasting contemporaneous deposits allow the taphonomy of these organisms to be compared across lacustrine depositional settings. Spinicaudatan carapaces and fish remains are preserved primarily in calcium phosphate, whereas ostracode carapaces are preserved in calcium carbonate, reflecting the original skeletal composition of the animals. Where microbial mats are present, silica replacement of spinicaudatan carapaces occurs more extensively than in other deposits; microbial processes may have enhanced silicification. This study is the first well-documented example of microbial mat influence on preservation in high-latitude lacustrine systems.

INTRODUCTION

Preservation of fossil material involves a balance between organismal degradation and mineralization. Some of the factors that promote degradation, microbial decay in particular, also promote early mineralization (Allison, 1988a; Briggs and Kear, 1994a; Briggs, 2003). Most analyses of the relationship between decay and mineralization have emphasized fossilization under marine conditions; the sequence of decay and mineralization is less well constrained for continental systems, including lacustrine environments (Elder and Smith, 1988; Allison and Briggs, 1991). In this paper, we describe aspects of the taphonomy, emphasizing early diagenesis, of biomineralizing organisms that range from weakly to more durably biomineralized from high paleolatitude lakes in the Kirkpatrick Basalt (Ferrar Group, Lower Jurassic Series, Toarcian Stage) of Antarctica. Fossils of the Kirkpatrick deposits include nonbiomineralized palynomorphs, plant leaves, and articulated insect nymphs and notostracans, as well as weakly biomineralized spinicaudatans (conchostracans) and more durably biomineralized ostracodes and fishes (Carpenter, 1969; Schaeffer, 1972; Tasch and Lammons, 1978; Ball et al., 1979; Tasch and Gafford, 1984; Shen, 1994; Shang, 1997; Babcock et al., 2006). Preserved microbial mats are associated with some Kirkpatrick lake deposits (Babcock et al., 2006). High-latitude lacustrine deposits are rare in the stratigraphic record, and these deposits, from ~60°S paleolatitude, provide an opportunity to examine some of the factors leading to fossilization in this depositional setting.

Taphonomic studies have documented the preservation of fossils from a variety of depositional environments (e.g., Allison, 1988b; Butterfield, 1990; Speyer, 1991; Briggs, 1995; Kear et al., 1995; Briggs et al., 1998; Erwin and Kidder, 2000; Jones et al., 2001; Toporski et al., 2002a; Mancuso, 2003). Many analyses emphasized a single taxonomic group (e.g., Allison, 1988b; Speyer, 1991; Kear et al., 1995) or a single depositional environment (e.g., Briggs et al., 1998; Jones et al., 2001; Toporski et al., 2002a). These studies provide information critical for interpreting fossil preservation in each case study but can be difficult to extrapolate to other instances. Actualistic studies (e.g., Allison, 1986, 1988a; Plotnick, 1986; Plotnick et al., 1988; Briggs and Kear, 1993; Briggs et al., 1993; Briggs, 1995; Bartley, 1996; Briggs and Wilby, 1996; Hof and Briggs, 1997; Babcock, 1998; Martin et al., 2005) have provided information about specific controls—such as temperature, salinity, and time—on the fossilization process but rarely have accounted for all the complexities of field conditions. An integrated approach, in which multiple taxa are preserved across several contemporaneous environments, can help bridge the gaps among experimental, single-taxon, and single-environment analyses.

This study involved documentation of the preservation of Kirkpatrick fossils, concentrating on spinicaudatan crustaceans, ostracodes, and fishes preserved within a suite of related sedimentary environments from ephemeral ponds to deeper lakes. The fossiliferous interbeds are distributed over ~400 km and have been dated to within 1 myr of each other (Heimann et al., 1994). Consequently, the taphonomy of similar and essentially contemporaneous biotas from deposits formed under broadly similar paleoenvironmental, climatic, and tectonic conditions can be compared and contrasted. This paper provides data and interpretation of the taphonomy of fossils from the Kirkpatrick Basalt lacustrine deposits beyond our earlier overview (Babcock et al., 2006).

GEOLOGIC SETTING

Ferrar Large Igneous Province

The thin lacustrine interbeds investigated in this study developed during times of relative cessation of lava eruption during emplacement of the Kirkpatrick Basalt (Ferrar Group, Jurassic) of Antarctica. Lava flow deposits of the Kirkpatrick Basalt cap the sequence of tholeiitic rocks of the Ferrar Large Igneous Province (FLIP), which occur in a linear belt along the Transantarctic Mountains (Fig. 1), from the Weddell Sea region to North Victoria Land, ~3,500 km in length (Fleming et al., 1997; Elliot et al., 1999; Elliot and Fleming, 2004). The FLIP was emplaced during the initial stages of the breakup of the Gondwanan part of Pangea—specifically, the rifting of East Antarctica and southern Africa. Magmatic

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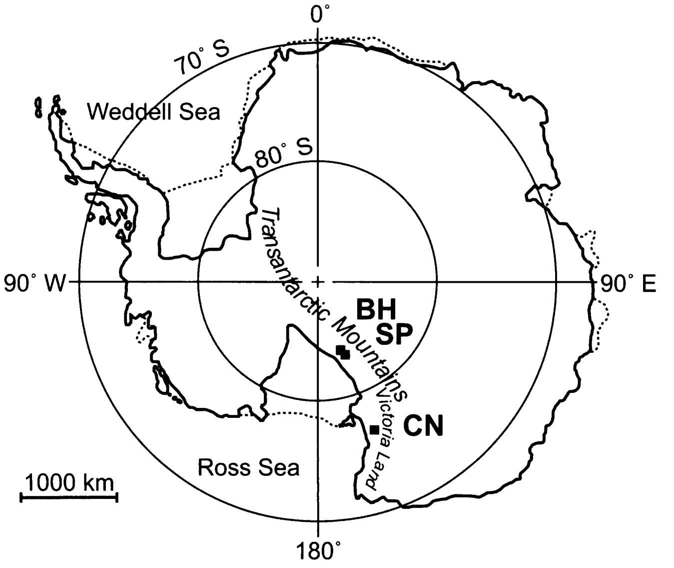

FIGURE 1—Map of Antarctica with field sites noted. The Kirkpatrick Basalt crops out within the Transantarctic Mountains. BH = Blizzard Heights; CN = Carapace Nunatak; SP = Storm Peak.

flow that forms the bulk of the FLIP was controlled by an Early Jurassic zone of extension related to a triple junction in the proto-Weddell Sea region at approximately 55°S (Elliot and Fleming, 2000, 2004). The FLIP comprises, in ascending stratigraphic order, the Dufek intrusion (occurring in deformed supracrustal rocks of the fold belt along the paleo-Pacific Gondwanan margin), the Ferrar Dolerite sills and dikes (sheet intrusions), extrusive rocks consisting of pyroclastic strata, and the Kirkpatrick Basalt lava flows. The total thickness of the Ferrar Group, including gabbroic intrusives in the lower part, sills, dikes, and extrusive volcanics, is variable along the length of the Transantarctic Mountains but exceeds 2 km in places (Elliot and Fleming, 2004).

Tholeiites of the FLIP also extend into areas of Australasia (Tasmania, Victoria, and Kangaroo Island, Australia, and South Island, New Zealand; see Milnes et al., 1982; Hergt et al., 1989; Mortimer et al., 1995), indicating that these areas were adjacent to North Victoria Land during the Paleozoic and early Mesozoic. The original aerial extent of the FLIP is estimated at 3.5×10^5 km^2 (Elliot and Fleming, 2004).

Kirkpatrick Basalt

The Kirkpatrick Basalt consists of a series of lava flows (continental flood basalts and cataclastic rocks), paleosols, and sparse sedimentary interbeds. It ranges in thickness from 380 m to 780 m and consists of a series of stacked flows typically between 10 m and 30 m thick (Heimann et al., 1994). These units were deposited at approximately 60°S latitude in a region with a strongly seasonal, temperate climate (Elliot and Hammer, 1996; Scotese, 2001). The sedimentary interbeds constitute $<1.0\%$ of the total thickness of the Kirkpatrick Basalt (Barrett et al., 1986).

Based on radiometric dating, the entire Kirkpatrick flood basalt sequence was emplaced during a brief interval of <1 myr during the Early Jurassic (Toarcian; Heimann et al., 1994; Fleming et al., 1997). The original analyses calculated an $^{40}Ar/^{39}Ar$ age of 176.6 ± 1.8 Ma for the Kirkpatrick Basalt (Heimann et al., 1994); recalculation of $^{40}Ar/^{39}Ar$ ages using neutron fluence monitor ages, after Renne et al. (1998), results in an age of 180 ± 1.8 Ma. Palynomorph analyses confirm an Early Jurassic age for these strata with biogeographic affinities to the Perth Basin of Australia (Tasch and Lammons, 1978; Shang, 1997; Ribecai, 2007).

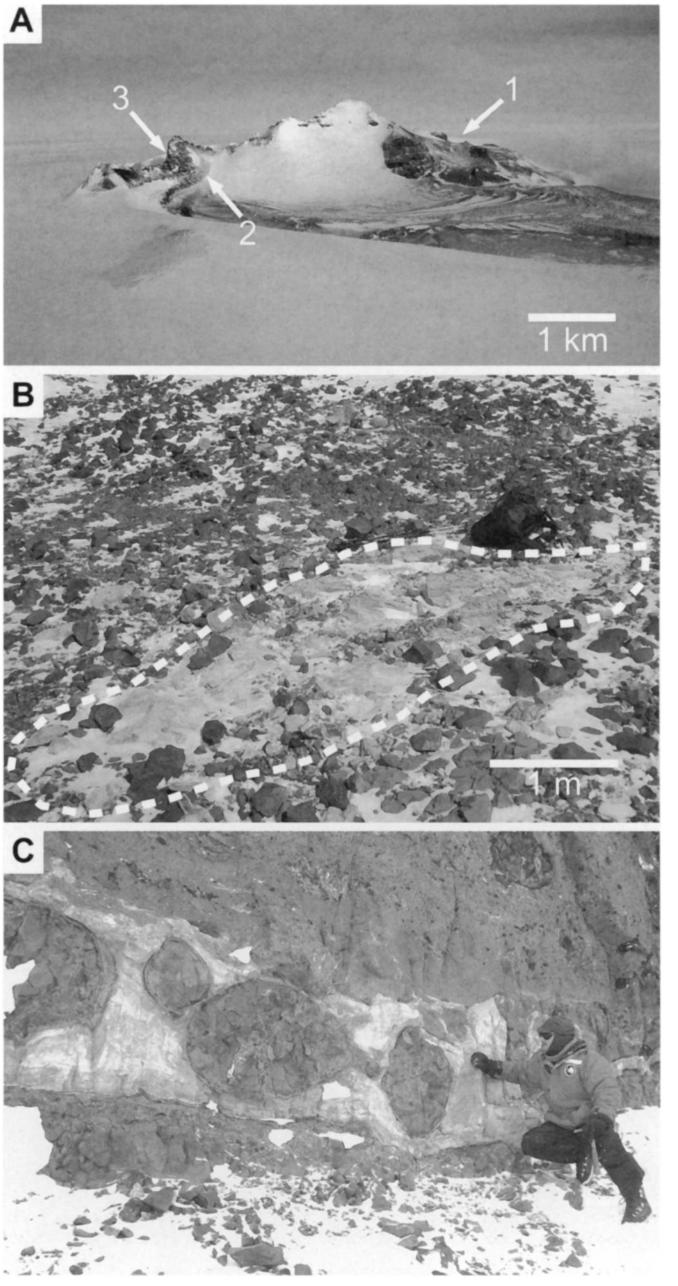

FIGURE 2—Carapace Nunatak, South Victoria Land. A) Outcrop view indicating location of the three sample sites. B) Lens of fossiliferous mudrock (outline) deposited within an ephemeral pond surrounded by basalt flows at location 1. C) Light-colored units represent siliciclastic mudrocks deposited within a relatively deep lake into which basalt pillows were extruded. Soft-sediment deformation features are apparent.

Lacustrine Interbeds of the Kirkpatrick Basalt

The lacustrine sedimentary interbeds vary in inferred depositional setting from shallow ephemeral ponds, some with microbial mat accumulations, to deeper permanent lakes (Tasch, 1977). Fossil assemblages in these rocks are dominated by spinicaudatans, but notostracans, ostracodes, insect nymphs, actinopterygian fish, and plant material are locally abundant (Babcock et al., 2006). Sedimentary interbeds at three localities of the Kirkpatrick Basalt in two regions of the Transantarctic Mountains were investigated during the austral summer of 2003–2004 (Fig. 1). The primary biotic and sedimentary features of the localities that yielded

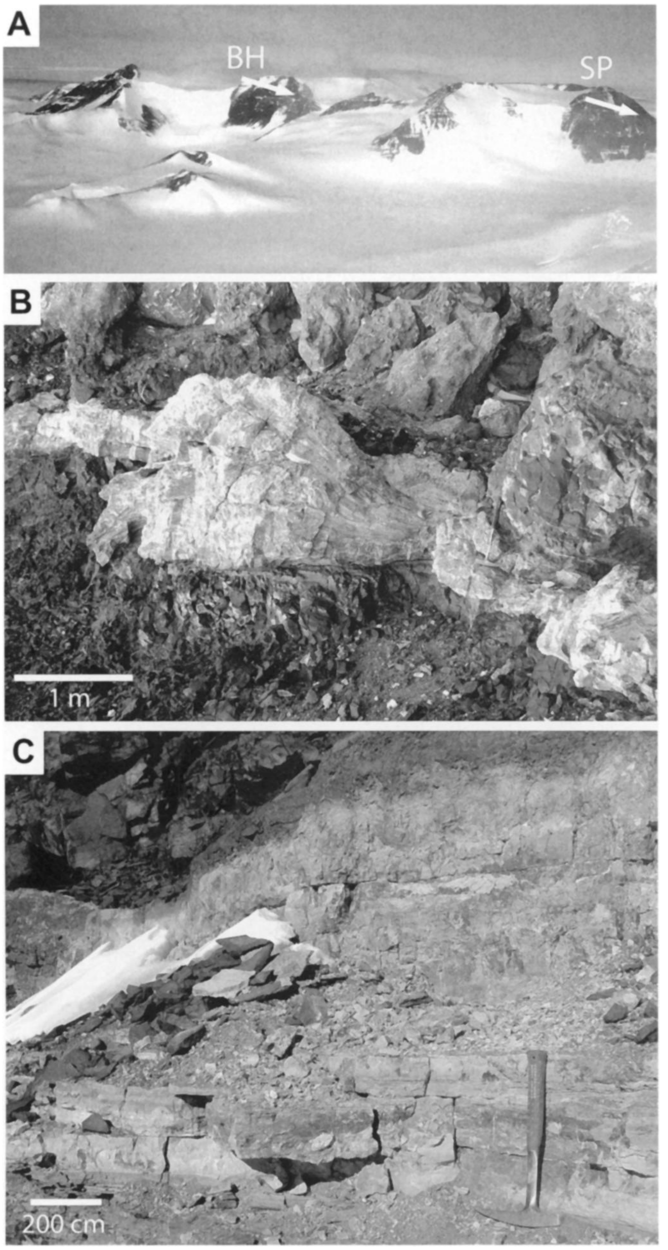

FIGURE 3—Queen Alexandra Range, Central Transantarctic Mountains. A) Outcrop view of Storm Peak (SP) and Blizzard Heights (BH) sites. B) Storm Peak interbeds. Interbeds are deposited above flood basalts. Lithology grades from mudrock into paleosols, and interbeds are overlain by pillow basalt. C) Blizzard Heights interbeds. Platy, laminated mudrock grades into thick paleosol deposits before termination by flood basalts.

specimens analyzed for this study are summarized in Supplementary Data 1 and 2[1], respectively, and reviewed below.

South Victoria Land: Carapace Nunatak.—Fossil-bearing sedimentary deposits at Carapace Nunatak represent two principal depositional environments: ephemeral ponds and deep lakes. Detailed sedimentologic studies of the sedimentary units at Carapace Nunatak were published in Tasch (1977) and Bradshaw (1987). Most fossils were collected from tan or black laminated mudrock lenses at three sites, one on the north spur and two on the south spur of the nunatak (Fig. 2A). These lenses are typically ≤50 cm thick and 2 m in length and contain abundant spinicaudatans, ostracodes, notostracans, insect nymphs, and plant material (Fig. 2B, Supplementary Data 1[1]; see Elliot and Tasch, 1967; Carpenter, 1969; Schaeffer, 1972; Tasch, 1973, 1987; Ball et al., 1979; Tasch and Gafford, 1984; Shen, 1994; Shang, 1997; Babcock et al., 2006). We interpret the depositional setting of these interbeds as shallow ephemeral ponds that likely experienced periodic desiccation, since spinicaudatan life cycles require dehydration of eggs prior to hatching (Weeks et al., 1997). Sedimentary lenses on the south spur of Carapace Nunatak contain alternating light and dark sediment that may reflect seasonal variations in oxygen content or rate of organic accumulation at the surface-water interface in a more permanent lake (Supplementary Data 2[1]). Spinicaudatans occur more sparsely in these units and likely reflect transportation of organisms into deeper water from the shallow margins of the lake. Some sedimentary interbeds contain tightly folded layers; this distortion is interpreted as due to rafting and lateral movement of semiconsolidated blocks during emplacement of the extrusive basalt flows (Barrett et al., 1986; Bradshaw, 1987).

A laterally continuous (≤50 m) and comparatively thick (≤1.5 m) layer of carbonate mudrock overlies the isolated sedimentary rafts on the north spur. Pillow basalts were laterally emplaced within this layer, resulting in soft-sediment deformation that includes flame structures (Bradshaw, 1987; see Fig. 2C). A 34-m-thick hyaloclastite flow overlies this layer and indicates that the sedimentary layers formed in a lake that was at least 34 m deep (Bradshaw, 1987). These relatively deeper-water carbonate-rich lake deposits lack fossils.

Central Transantarctic Mountains.—Localities in the Queen Alexandra Range of the Central Transantarctic Mountains (CTM) contain fossiliferous sedimentary interbeds inferred to be correlative (within 1 myr) with those at Carapace Nunatak in South Victoria Land, based on the total duration of Kirkpatrick Basalt emplacement (Heimann et al., 1994). Sedimentary interbeds were studied at two sites, Storm Peak and Blizzard Heights (Fig. 3A). Interbeds at these locations are thicker than those observed at Carapace Nunatak and include paleosols, silicified logs, and more laterally extensive lacustrine deposits (Supplementary Data 2[1]; see Tasch and Gafford, 1984). Detailed sedimentologic studies of these units have been previously published (Tasch, 1977; Tasch and Gafford, 1984; Elliot et al., 1988), but important features are summarized here.

1. Storm Peak.—Layered basalt flows underlie the sedimentary units at Storm Peak (Fig. 3B). The basalmost sedimentary unit is a mottled paleosol ≤1 m thick that includes large (≤50 cm diameter) silicified logs and occasional pockets of organic-rich sediment. This unit is overlain by 10–20 mm of laminated, orange-tan lacustrine mudrock containing abundant spinicaudatans and occasional fish. The mudrock is overlain by a second well-developed paleosol up to 1 m thick. Lacustrine mudrock pinches out laterally along the outcrop. This sequence of depositional environments suggests a longer hiatus between basalt flows than at Carapace Nunatak, accompanied by extensive weathering. Sufficient time elapsed for the development of thick paleosols and an ephemeral pond system, including connecting streams that supported a fish fauna (Tasch, 1977; Tasch and Gafford, 1984).

2. Blizzard Heights.—The sedimentary succession and inferred depositional environment of Blizzard Heights resemble those of Storm Peak (Tasch, 1977). A basal paleosol developed on the uppermost layered exposed basalt flow. This is followed by 20–30 cm of laminated mudrock, representing lacustrine deposits, and is capped by an upper paleosol ≤1 m thick (Fig. 3C). Large silicified logs and fish are scarce, but spinicaudatans are abundant within the lacustrine interbeds. The sedimentary interbeds vary from tan to gray-green in color, and some contain evidence of microbial fabrics.

MATERIALS AND METHODS

Figured and referred specimens, as well as some additional specimens examined, are deposited in the following museums: Orton Geological Museum, the Ohio State University, Columbus, Ohio (OSU); Yale Uni-

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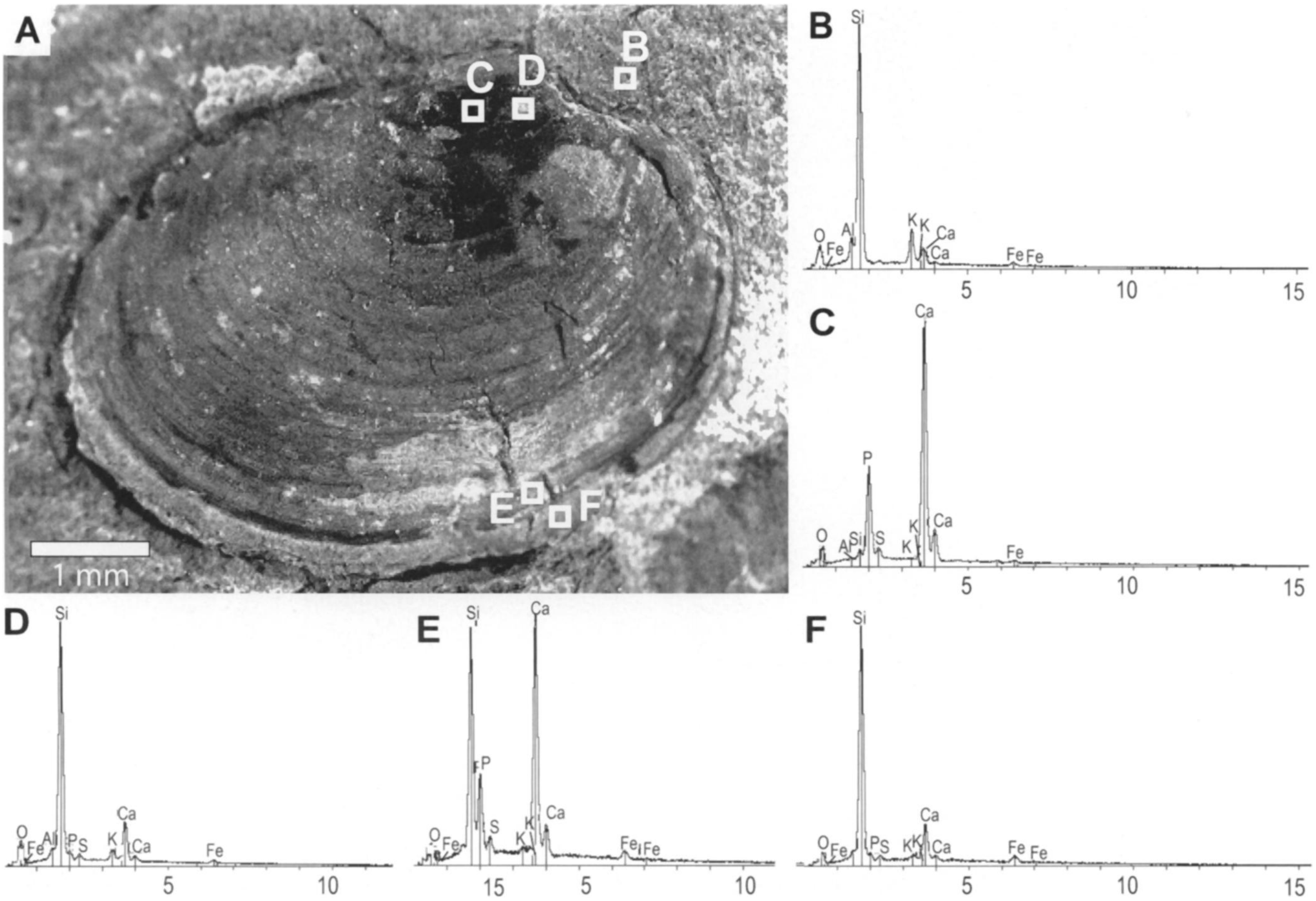

FIGURE 4—*Carapacestheria disgregaris* from shallow lacustrine interbeds, Carapace Nunatak, location 1 (OSU 52701). A) Complete right carapace valve; exfoliation allows sampling of layers. Letters indicate sites of energy dispersive X-ray spectra in B–F. B) Rock matrix, 9000 fs. C) Thick carapace layer, 10,000 fs. D) Exfoliated carapace material, 9000 fs. E) Thin carapace layer, 4000 fs. F) Exfoliated carapace material, 6000 fs. Part A modified from Babcock et al. (2006, fig. 4A), used with permission. Axes in Figs. 4–10: x-axis = X-ray energy (KeV); y-axis = relative number of counts per energy level scaled to given number of fs. fs = femtoseconds.

versity Peabody Museum, Division of Invertebrate Zoology, New Haven, Connecticut (YPM); and Harvard University, Museum of Comparative Zoology, Entomology Division, Cambridge, Massachusetts (MCZ). Species examined, but unfigured, for this project, as well as additional material from the 2003 expedition, are deposited in the United States Antarctic Rock Repository, the Ohio State University, Columbus, Ohio. Collections from previous expeditions, including those of Borns et al. (1968, 1972) and Tasch et al. (1969–1970) are housed at the Natural History Museum, London (Borns et al., 1968), the Museum of Comparative Zoology, Harvard University (Borns et al., 1972), and the National Museum of Natural History, Smithsonian Institution (Tasch et al., 1969–1970).

Taxa Examined

Spinicaudata.—Specimens of *Carapacestheria disgregaris* (Tasch, 1987) occur in all lithologies at all three localities. Valves showed a combination of intact carapace and exfoliated layers (Figs. 4–7). Six specimens were examined from Carapace Nunatak, two (OSU 52701, 52702) from tan mudrock and four (OSU 52703–52706) from laminated black mudrock. Three specimens (OSU 52707–52709) were from a single bedding plane of tan mudrock at Storm Peak, and three (OSU 52710–52712) from gray mudrock at Blizzard Heights.

Carapaces of three modern spinicaudatans were examined for comparison with the fossil material: *Leptestheria compleximanus* (YPM 3619), *Cyzicus mexicanus* (YPM 8297), and *Eulimnadia* sp. (YPM 24263). Of these, *C. mexicanus* is the most closely related to the Jurassic species; both are members of the family Cyzicidae (Shen, 1994; Olesen, 2002). *Leptestheria* is assigned to the Leptestheridae, and *Eulimnadia* to the Limnadiadae.

Ostracoda.—Ostracodes, all identified as *Darwinula* sp., occur commonly in the tan mudrock units at Carapace Nunatak. Only the carapaces are preserved. The carapace of a representative specimen (MCZ 12645) from the tan mudrock at Carapace Nunatak was examined (Fig. 8). Spinicaudatan and ephemeropteran nymph remains occur on the bedding plane with the ostracode specimen.

Actinopterygii.—Fish scales occur in varying numbers throughout the lacustrine deposits in all three localities. Tan mudrock layers at Storm Peak yielded articulated skeletons of *Oreochima ellioti* (Schaeffer, 1972) with scales and, rarely, gut contents in place. Their remains occur in bedding-plane associations with spinicaudatans. One specimen of *O. ellioti* was an articulated, nearly complete specimen showing bones, scales, and alimentary tract material (OSU 52713; Fig. 9).

Analytical Methods

Scanning Electron Microscope and Energy Dispersive X-Ray Spectrometry Analysis.—An FEI XL-30 environmental scanning electron microscope field emission gun was used for scanning electron imaging. Chemical compositions were assessed using a Princeton Gamma Tech energy dispersive X-ray spectrometry (EDS) system with a Ge detector and Spirit data acquisition software. Energy dispersive X-ray spectrometry provides an indication of relative abundances of elements, not

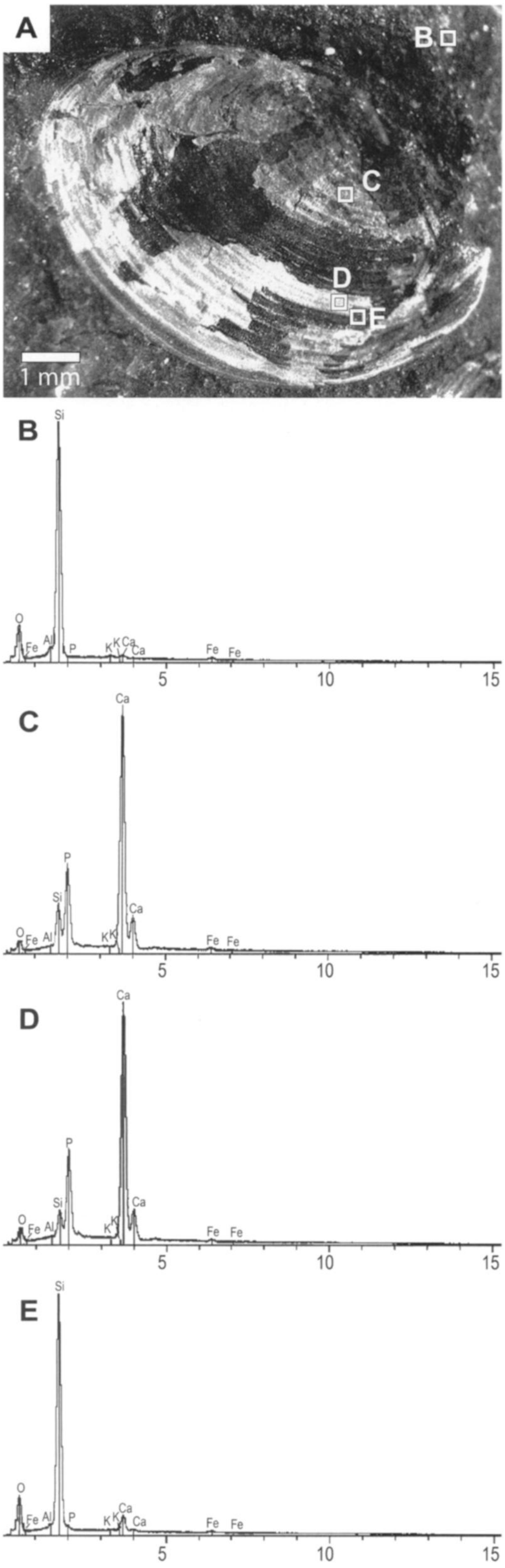

FIGURE 5—*Carapacestheria disgregaris* from deeper lacustrine interbeds, Carapace Nunatak, location 1 (OSU 52703). A) Complete right carapace valve; exfoliation allows sampling of layers. Letters indicate sites of energy dispersive X-ray spectra in B–E. B) Rock matrix, 12,000 fs. C) Thick carapace layer, 10,000 fs. D) Thick carapace layer, 9000 fs. E) Exfoliated carapace material, 12000 fs. fs = femtoseconds.

quantitative values. Uncoated specimens were imaged under low-vacuum conditions in a chamber with water-vapor pressure at 0.93 kPa, an acceleration voltage of 20 KeV, spot size of 3, and working distance of 10 mm. This created a beam width of 1 nm, which samples 1 μm craters of a specimen in a single analysis. Specimens were cleaned with water and alcohol but not removed from their bedding surfaces. Each specimen was analyzed at several sites to obtain information about the composition of specific regions or layers.

Internal tissues and appendages of the modern spinicaudatan carapaces were separated from the carapaces by dissection. The carapaces were dried and mounted on aluminum scanning electron microscope stubs with double-sided carbon tape. Energy dispersive X-ray spectrometry analyses, like those of the fossils, were carried out at 20 KeV. Following EDS analyses, samples were sputter coated with a ~20 nm Au/Pd alloy layer to counteract sample charging for improved imaging. Lastly, specimens were imaged at 10 KeV.

Thin-Section Analysis.—Thin sections (30 μm thick) were prepared to examine fossils in cross section and to determine the sedimentary characteristics of the matrix containing the fossils. Thin sections were examined under transmitted and polarized light conditions.

RESULTS

Spinicaudata

Energy dispersive X-ray spectrometry analyses of modern spinicaudatan carapaces revealed a calcium phosphate composition with accessory amounts of aluminum, silica, sulfur, iron, and zinc (Fig. 10; Supplementary Data 3[1]). These elements were included within minerals that precipitated within a chitinous framework to form cuticular layers. This compositional pattern was the same in all the modern spinicaudatan specimens examined, regardless of familial assignment, suggesting that calcium phosphate is present widely across the order and is likely a symplesiomorphy of the clade. The original composition of the Jurassic spinicaudatan carapaces, therefore, is assumed to have been partly calcium phosphate.

Fossil spinicaudatan valves from the Kirkpatrick Basalt interbeds preserve both original compositional layering and ornamentation of the carapace (Figs. 11, 12). Exfoliation provides access to multiple carapace layers within a single specimen. Spinicaudatan carapaces are preserved as calcium phosphate that was locally or regionally replaced by silica (Figs. 4–7). Within a single valve, different layers or regions are preserved as either calcium phosphate or silica (Fig. 4–7, Supplementary Data 3[1]). The sedimentary matrix at all localities consists of a combination of quartz and clay minerals (Figs. 4–7), and phosphate is essentially absent. Calcium phosphate layers may represent retention of original carapace material, apart from chitin; however, the phosphatic mineralization is commonly coarse, obscuring microstructural details, which suggests some diagenetic recrystallization (Fig. 12). Silica layers are present where calcium phosphate layers have been exfoliated. The silica occurs either basally (forming a cast of the carapace interior; see Fig. 4) or between calcium phosphate layers (Fig. 11). Unlike the recrystallized phosphate layers, the silica layers preserve fine details of the carapace microstructure (Fig. 11). Thus silica replacement of the shell occurred early in diagenesis, before the calcium phosphate was recrystallized.

Whereas compositional layering in spinicaudatan carapaces is common to all lithofacies and localities examined, the relative proportion of carapace material preserved in calcium phosphate and silica varies between localities. Specimens from Carapace Nunatak are preserved in a silt- to mud-sized siliciclastic matrix of quartz and clay mineral grains (Figs. 4, 5). The carapaces consist primarily of calcium phosphate layers, which are brown in color; silica layers occur either basally or replace individual layers within the carapace (Figs. 4, 5, 11). At Storm Peak the sedimentary matrix is of a similar mineralogical composition, but microbial structures are evident (Fig. 13). Calcium phosphate layers within carapaces from this site have a higher iron content compared to those from other sites (Supplementary Data 3–4[1]). Translucent silica layers occur commonly and often constitute a larger per-

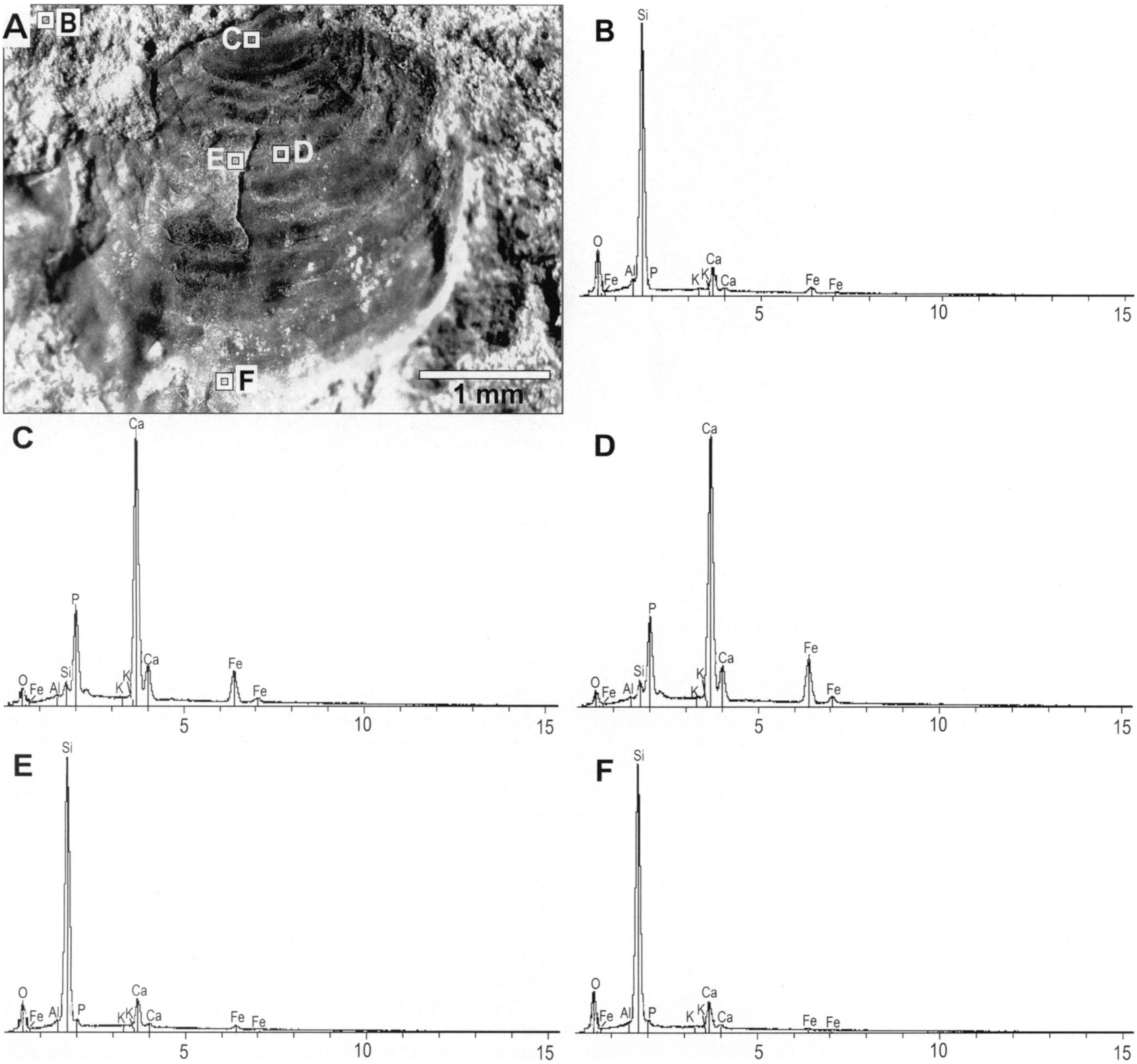

FIGURE 6—*Carapacestheria disgregaris* from microbial mudrock interbeds, Storm Peak (OSU 52708). A) Right carapace valve; exfoliation allows sampling of layers. Letters indicate sites of energy dispersive X-ray spectra in B–F. B) Rock matrix, 12,000 fs. C) Thick carapace layer, 9000 fs. D) Thick carapace layer, 10,000 fs. E) Clear overlayer, 11,000 fs. F) Exfoliated carapace material, 12,000 fs. fs = femtoseconds.

centage of the preserved carapace than calcium phosphate layers (Figs. 6, 13). The sedimentology of Blizzard Heights is similar to that of Storm Peak; microbial fabrics occur throughout a silica-rich matrix (Figs. 7, 13). Carapaces from Blizzard Heights are composed mainly of translucent silica layers. They appear iridescent owing to light refraction from the intervening calcium phosphate layers (Figs. 7, 13).

Ostracoda

Darwinula occurs as white carapaces within the tan mudrock at Carapace Nunatak. Energy dispersive X-ray spectrometry analysis indicated a nearly uniform calcium carbonate composition (Fig. 8, Supplementary Data 3[1]).

Actinopterygii

Oreochima ellioti occurs at Storm Peak and Blizzard Heights. Bones and scales are preserved as calcium phosphate, reflecting their original composition (Fig. 9, Supplementary Data 3[1]), with minor amounts of iron oxide, which imparts an orange hue to the specimens. A complex signature of silica, calcium, iron, aluminum, and phosphorus from material preserved within the alimentary canal indicates high abundance of ferrous and clay minerals. Some of these elements may reflect the diet of the fish: *Oreochima* probably preyed on spinicaudatans, ostracodes, insects, and other fishes.

Sedimentology

Details of sedimentology and biotic content at the South Victoria Land (Carapace Nunatak) and Central Transantarctic sites (Storm Peak and

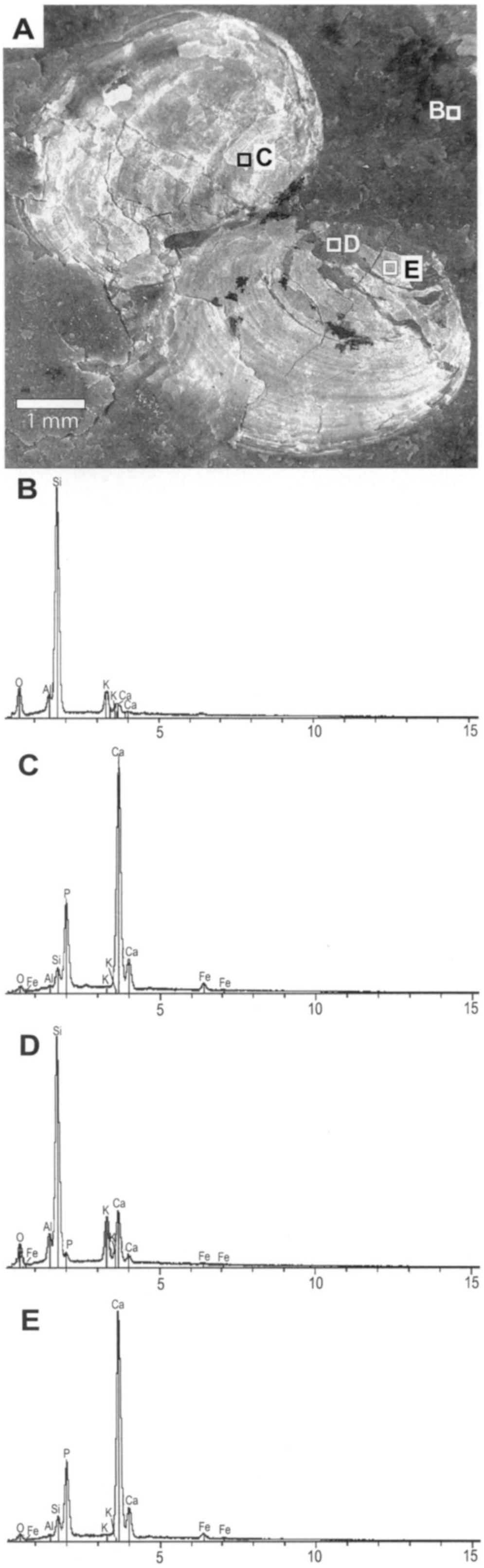

FIGURE 7—*Carapacestheria disgregaris* from microbial mudrock interbeds, Blizzard Heights. A) Complete right carapace valves of two specimens, OSU 52710 (left) and 52711 (right); exfoliation allows sampling of layers. Letters indicate sites of energy dispersive X-ray spectra in B–E. B) Rock matrix, 10,000 fs. C) Thick carapace layer, 10,000 fs. D) Exfoliated carapace material, 8000 fs. E) Thick carapace layer, 10,000 fs. fs = femtoseconds.

Blizzard Heights), summarized in Supplementary Data 1–2[1], suggest that the lacustrine environments represented were different. At Carapace Nunatak, the lacustrine sediments are thinly bedded and characterized by siliciclastic siltstone to mudstone (Fig. 11, Supplementary Data 2[1]). Sparse pyrite grains in some beds indicate dysoxic conditions. The preservation of glass shards and lack of sedimentary structures other than fine laminations indicates a quiet-water setting where sediment was deposited from suspension. At Storm Peak and Blizzard Heights, siliciclastic sediments are thinly laminated and exhibit structures attributable to microbial mats (Fig. 13, Supplementary Data 2[1]); spinicaudatan carapaces are preserved between microbial layers. These microbial textures include wavy-crinkly laminae, clotted texture, and clusters of sand-sized quartz grains within a fine-grained matrix (Fig. 13; cf. Schieber, 1999; Leggitt and Cushman, 2001; Noffke et al., 2001; Noffke, 2004). Microbial mats often occur in the shallow littoral regions of lakes (see examples in Gierlowski-Kordesch and Kelts, 2000). The fish probably inhabited connecting streams because modern spinicaudatans and fish do not normally occur together in a single pond (Smith and Gola, 2001; Martínez-Pantoja et al., 2002). Furthermore, the degree of articulation of the fishes collected from Storm Peak and Blizzard Heights is comparable to that found in articulated fishes from the Los Rastros Formation (Triassic), which are interpreted as having washed in from streams associated with ponds (Mancuso, 2003). The abundance of fossilized spinicaudatan remains is consistent with a lack of predatory fish.

DISCUSSION

Controls on Preservation Preceding Early Diagenesis of Fossils

The fossils in the Kirkpatrick sedimentary interbeds range from insects and plants, which lack a biomineralized skeleton, through weakly to significantly biomineralized carapaces of spinicaudatans and ostracodes, as well as the skeletal remains of fishes. The occurrence of nonbiomineralizing taxa in association with fully articulated vertebrate remains indicates that both skeletal degradation (through predation or scavenging) and physical destruction of the biota were limited. Experimental taphonomic studies have shown that preservation of nonbiomineralizing taxa requires either a reduction in the rate of decay or early mineralization of tissues (Plotnick, 1986; Allison, 1988a; Briggs, 2003).

Evidence for substantial physical abrasion or damage of specimens caused by transport is absent at all localities. Specimens may have been transported short distances after death; some spinicaudatans at Carapace Nunatak were transported from shallow to deeper regions of the lake. At Carapace Nunatak, relatively rapid deposition of sediment under alkaline aqueous conditions is indicated by the preservation of unaltered glass shards (Tasch, 1977). Rapid deposition reduced scavenging on carcasses. Reduced oxygen levels may have promoted bacterially mediated mineralization (Sagemann et al., 1999). At the CTM location, spinicaudatan carapaces and articulated fishes were incorporated into microbial mats shortly after death, which prevented further scavenging or physical transport.

Controls on Early Diagenesis of Fossils

Skeletal Controls on Preservation.—The primary control on the composition of fossils from the sedimentary interbeds of the Kirkpatrick Basalt is the original composition of the organism. This is most obvious in biomineralized skeletons; that is, fish remains are preserved in calcium phosphate, and ostracode carapaces in calcium carbonate.

Extant spinicaudatan carapaces are composed of a mixture of protein and chitin lightly mineralized with calcium phosphate (Fig. 10; see Tasch, 1969). All spinicaudatan carapaces in the Kirkpatrick interbeds are preserved, at least in part, as calcium phosphate. The main source of the phosphate is presumably the carapace itself. Additional phosphate may be required to explain the degree of mineralization in some cases. Phosphate is not present in the sedimentary matrix (Figs. 4–7), and phosphate

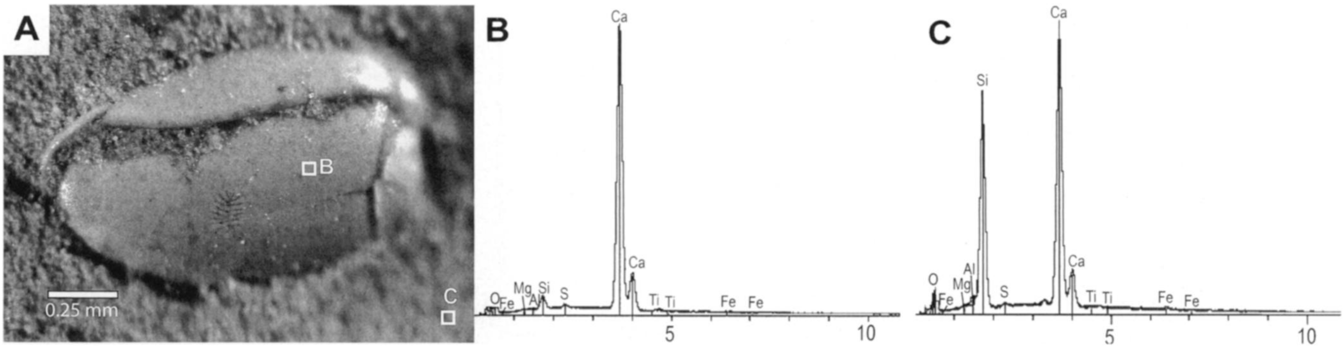

FIGURE 8—*Darwinula* sp. from shallow lacustrine interbeds, Carapace Nunatak, location 1 (MCZ 12645). A) Articulated specimen including muscle scar, anterior to the right. Letters indicate sites of energy dispersive X-ray spectra in B–C. B) Preserved carapace, 10,000 fs. C) Rock matrix, 6000 fs. Part A from Babcock et al. (2006, fig. 4E), used with permission. fs = femtoseconds.

ions are unlikely to have been sufficiently concentrated in the lake water to be a substantial source of phosphate for mineralization (Gierlowski-Kordesch and Kelts, 2000). Geochemical analyses of the Carapace Nunatak and CTM deposits indicate similar water chemistry in these deposits (Tasch, 1977), which suggests that water chemistry cannot account for the preservational differences at these sites. Decaying soft parts of the animals may have contributed additional phosphate to the preserved carapaces. A similar association of phosphate with decay of other crustacean and annelid carcasses has been observed in other studies (e.g., Briggs and Clarkson, 1989; Briggs et al., 1993; Briggs and Kear, 1994a; Hof and Briggs, 1997).

Environmental Controls on Preservation.—At all localities, the mineralogical composition of the matrix is dominated by quartz and clay minerals (Supplementary Data 4[1]). The most significant differences between the Carapace Nunatak sites and the CTM sites are relatively higher levels of iron and lower levels of silica in the latter (Supplementary Data 4[1]). At all localities, the levels of calcium and phosphorus ions present in the sediment are too low to have provided a significant source of ions for fossil preservation. While the amount of silica present in CTM sediment is lower than at Carapace Nunatak (28wt% vs. 40wt%; see Supplementary Data 4[1]), silica is not limiting in either location. The higher degree of silicification of spinicaudatan carapaces at CTM compared to Carapace Nunatak (Figs. 11, 13), therefore, is controlled by decay processes rather than sediment composition.

Specimens from Carapace Nunatak, where microbial mat structures are absent, are preserved almost entirely as calcium phosphate. Original internal laminations are preserved within the calcium phosphate, and silicification occurs only along the external margin of the carapace or between internal layers. Silica constitutes $<10\%$ of the total volume of carapaces at Carapace Nunatak. Carapaces from Blizzard Heights and Storm Peak, where sedimentary structures of microbial origin are present, exhibit almost the converse. Although some calcium phosphate is present in most valves, these specimens are almost entirely silicified. The growth and decay of microbial mats result in local changes in aqueous geochemistry producing anaerobic and strongly reducing conditions beneath mats (Wilby et al., 1996; Schieber, 1999). These conditions favor the growth of anaerobic bacteria, which likely mediated silicification since anaerobes have been shown to promote mineralization (Sagemann et al., 1999).

Influence of Microbes on Preservation.—Microbially mediated silica molded onto the inner surfaces of carapace layers (Fig. 12) and typically preserved a higher fidelity of detail than calcium phosphate layers. Silicification in these spinicaudatan carapaces is fabric replacive rather than fabric destructive. Silica precipitation nucleated and then replaced carapace material along smooth surfaces, either on the exteriors of carapaces or along interfaces (places of weakness) between layers of the carapaces (Fig. 11). The early stages of carapace decay involved weakening of the cuticular structure and separation of carapace layers caused by degradation of protein and chitin within the carapace layers (Hsu and Chen, 1995; Stankiewicz et al., 1998). Silica precipitation was promoted by the chemical gradient set up by microbial degradation of the spinicaudatan carcass. Structural controls resulting in silicification along planar surfaces have also been reported in originally calcitic skeletons (Schmitt and Boyd, 1981; Holdaway and Clayton, 1982; Daley and Boyd, 1996).

Whereas direct evidence for preserved microbes has not been observed within the Kirkpatrick interbeds, the pattern of differential silicification resembles microbially mediated fossilization elsewhere. Microbial mediation has been documented in taphonomic studies of silica formation by modern bacteria, including those by Birnbaum and Wireman (1984, 1985), Jones et al. (2001), and Toporski et al. (2002b). In these studies, hydrothermal or sulfate-reducing bacteria became mineralized in less than one day in a silica-rich solution (Jones et al., 2001; Toporski et al., 2002b). Toporski et al. (2002b) noted that morphological details of the bacteria were destroyed during mineralization. This loss of detail does not occur as commonly when bacterial films are preserved in calcium phosphate (Briggs and Kear, 1993; Toporski et al., 2002a). Furthermore, biofilms are best developed and preserved on outer surfaces of hard parts or within soft parts (Briggs et al., 1993; Briggs and Kear, 1994a, 1994b; Hof and Briggs, 1997; Toporski et al., 2002a). The absence of preserved microbes in the Kirkpatrick interbeds is likely due to the decay of the microbes after their death.

Timing of Mineralization.—The most abundant fossils in the Kirkpatrick Basalt interbeds are lightly or strongly mineralized remains. Both spinicaudatan and ostracode carapaces are preserved with three-dimensional relief, indicating minimal fossil compression. Fish are articulated with scales and fins. Insect exoskeletons and plant materials, which represent refractory organic tissues, are also present (Ball et al., 1979; Shang, 1997; Babcock et al., 2006) but are less common. Other soft and lightly sclerotized tissues, such as arthropod limbs or musculature, are not preserved.

The lack of soft tissue preservation and the initiation of microbially mediated silicification between carapace layers suggest that spinicaudatan carapaces experienced an interval of decomposition prior to mineralization. The high level of detail preserved in the silicified layers of the spinicaudatan carapaces suggests that onset of silicification was rapid—an interval of several days is consistent with experimental taphonomic studies (Birnbaum and Wireman, 1984; Bartley, 1996; Jones et al., 2001). Mineralization may have begun in one region of the carcass, while biodegradation of other portions continued (Briggs, 2003).

CONCLUSIONS

Preservation of lightly to strongly biomineralizing animals in the sedimentary interbeds of the Kirkpatrick Basalt is primary controlled by two

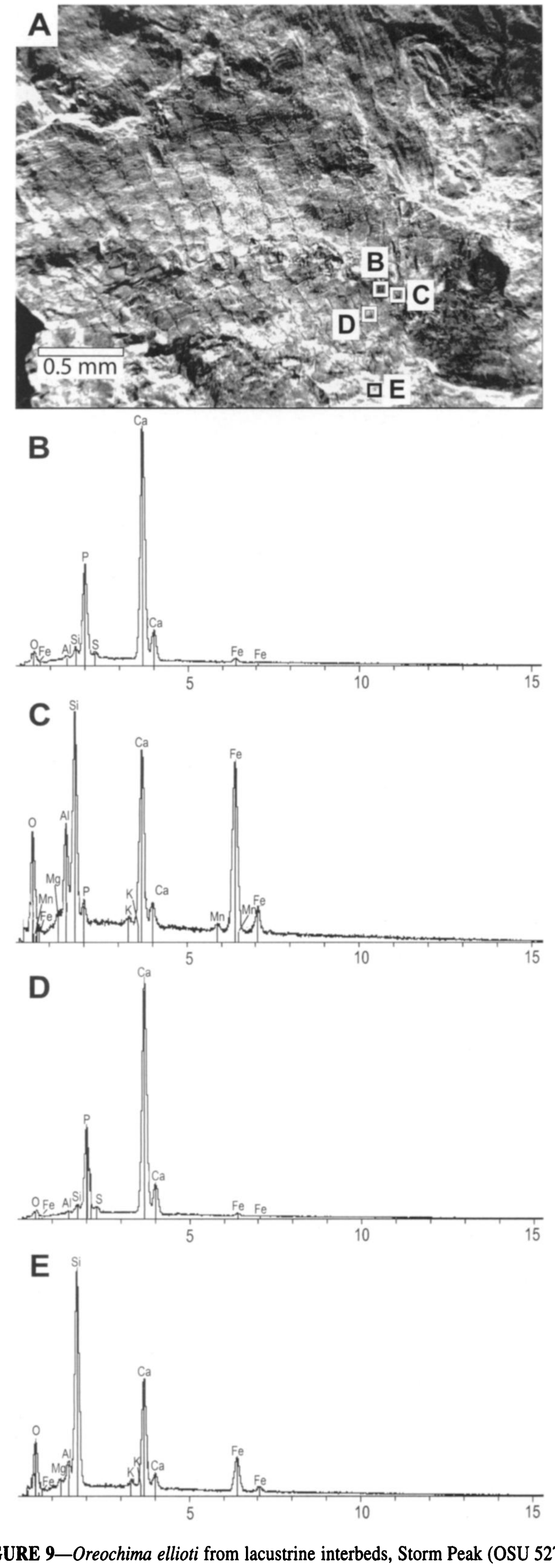

FIGURE 9—*Oreochima ellioti* from lacustrine interbeds, Storm Peak (OSU 52713). A) Mostly complete skeleton including head (toward right) and body scales, vertebral column, gut trace, and right pectoral fin (angled above fish body). Letters indicate sites of energy dispersive X-ray spectra in B–E. B) Vertebral bone, 10,000 fs. C) Gut material, 2750 fs. D) Body scale, 11,000 fs. E) Rock matrix, 6400 fs. fs = femtoseconds.

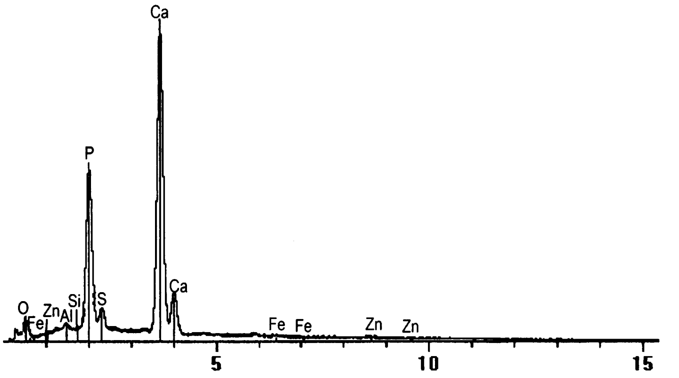

FIGURE 10—Energy dispersive X-ray spectrum from the carapace of a modern spinicaudatan, *Cyzicus mexicanus*, 6400 fs (YPM 8297). fs = femtoseconds.

factors: (1) original skeletal mineralogy of the organisms, and (2) the presence (or absence) of microbial mats within the environment of deposition. Where microbial mats are absent, such as at Carapace Nunatak in South Victoria Land, fossil composition directly reflects the original skeletal composition of the organisms: for example, ostracode carapaces are preserved as calcium carbonate and spinicaudatan carapaces as calcium phosphate. Fish remains at Storm Peak also retain a calcium phosphate composition mirroring original skeletal composition. In the Central Transantarctic Mountains, where microbial mats are present, the originally lightly biomineralized carapaces of spinicaudatans are almost entirely replaced by silica.

Microbially mediated silicification in spinicaudatan carapaces supports the influential role of microbes in fossilization. The importance of microbial mats in exceptional preservation has been noted in marine settings as far back as the Archean (Noffke et al., 2006), and well-documented Phanerozoic occurrences include cases from the Jurassic of France (Wilby et al., 1996) and the Cretaceous of North America (Meyer and Milsom, 2001). This study is the first well-documented case of microbial mat influence on preservation in high-latitude lacustrine systems.

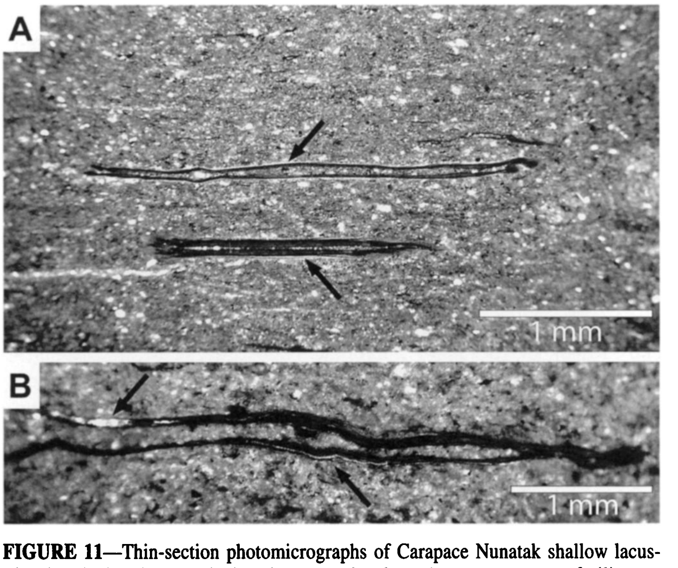

FIGURE 11—Thin-section photomicrographs of Carapace Nunatak shallow lacustrine interbeds, photographed under crossed polars. Arrows = areas of silica replacement. Quartz appears white; hinge of carapaces is to the right. Note the preservation of carapaces as calcium phosphate, including original lamellar framework. Limited silica replacement in carapaces occurs in regions or along layers. A) Wide field of view illustrating siliciclastic nature of interbeds and two spinicaudatan carapaces. B) Close up of articulated spinicaudatan specimen. Part B modified from Babcock et al. (2006, fig. 5A), used with permission.

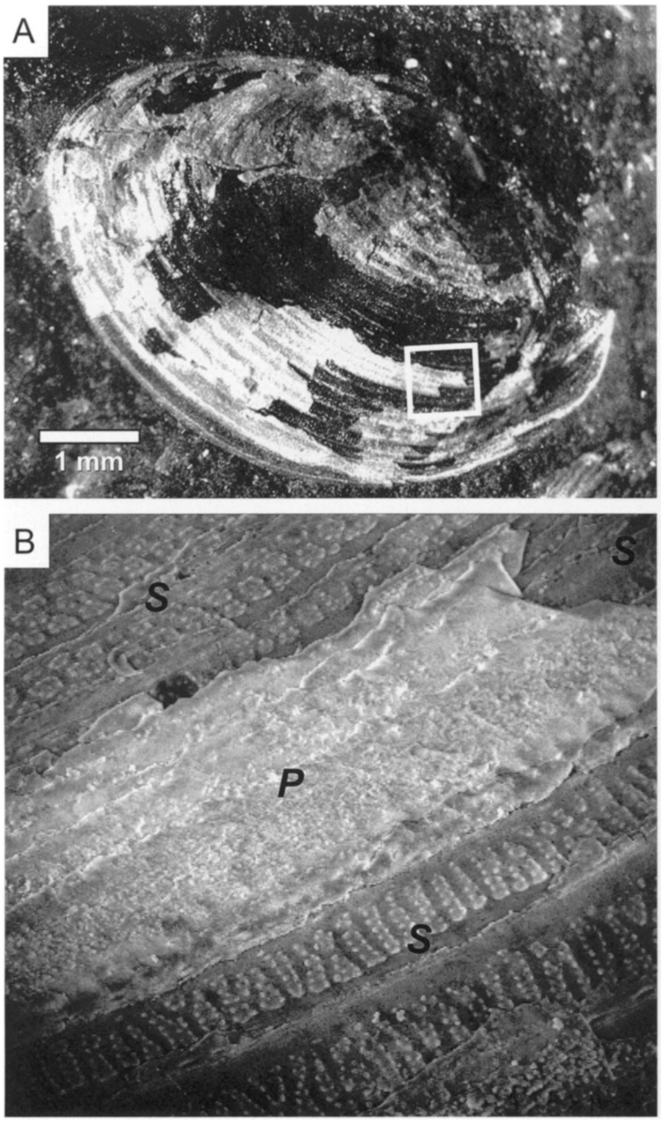

FIGURE 12—Complete right carapace valve of *Carapacestheria disgregaris* from deeper lacustrine interbeds, Carapace Nunatak, location 1 (OSU 52703). A) Lighter areas contain preserved phosphatic carapace material; in dark areas, phosphatic material has exfoliated (see Fig. 5). Square indicates region shown in B. B) Scanning electron microscope image illustrating carapace microstructure preserved as phosphate (*P*) and silica (*S*); silicic preservation records a higher degree of detail.

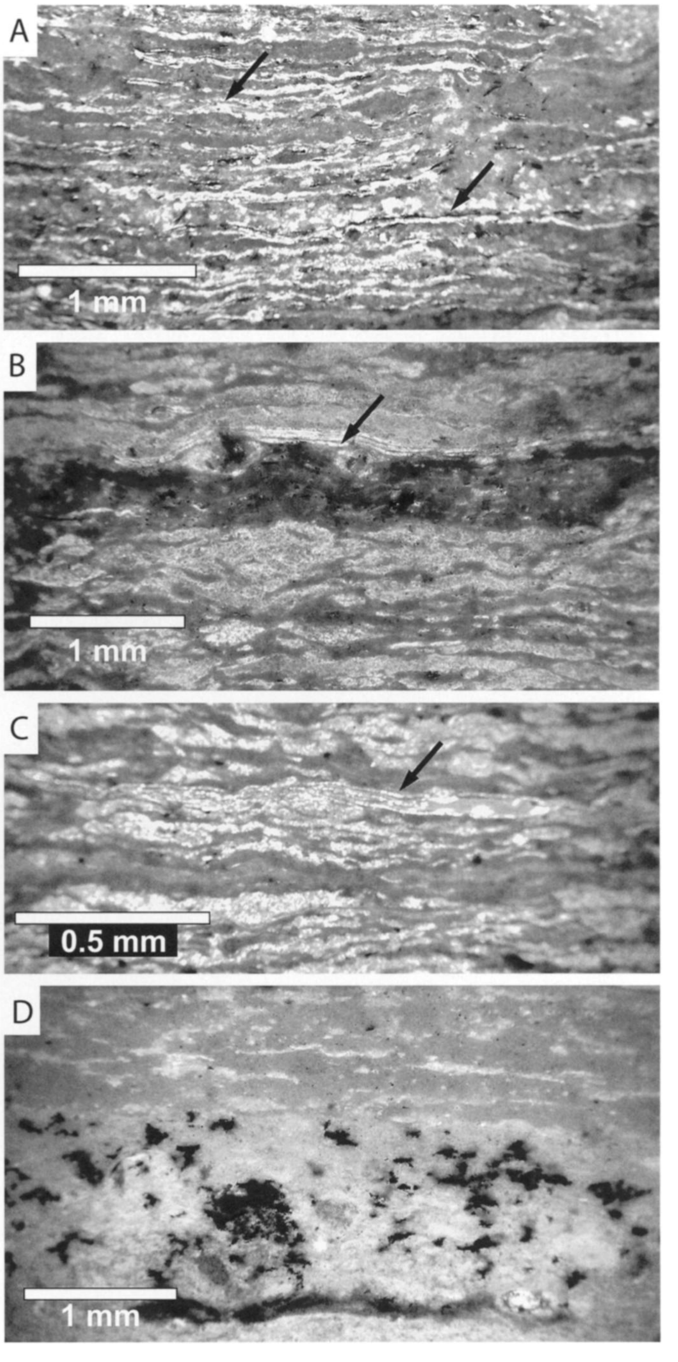

FIGURE 13—Thin-section photomicrographs of Storm Peak (A–C) and Blizzard Heights (D) interbeds, photographed under polarized light. Quartz appears white; black arrows indicate spinicaudatan carapaces. A) View illustrating microbial fabrics. B) Almost entirely silicified spinicaudatan carapace within matrix incorporating microbial textures. C) Articulated, silicified spinicaudatan within matrix exhibiting microbial textures. D) Microbial textures within interbed.

ACKNOWLEDGMENTS

We thank I. Harding and M. Wilson for comments on earlier versions of this paper. Technical assistance with the environmental scanning electron microscope was provided by Z. Jiang, Yale University. Research was conducted partly while A.L.S. was a visiting researcher at Yale University and facilitated by a faculty leave from Ohio University. This research was supported by grants from the National Science Foundation, Office of Polar Programs (OPP-0229757, 0346829) to L.E.B. Field logistics and assistance in Antarctica were provided by the National Science Foundation and Raytheon personnel and contractors. David Elliot provided locality and geological information, Ty Milford served as mountaineer during the fieldwork phase of the work. Susan Butts (Yale University Peabody Museum), Erik Lazo-Wasem (Yale University Peabody Museum), and Philip Perkins (Harvard University, Museum of Comparative Zoology) provided access to collections. Sofie Lindström provided helpful discussion and some reference materials.

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ACCEPTED OCTOBER 19, 2007