Mud-filled *Ophiomorpha* from Upper Cretaceous Continental Redbeds of Southern Mongolia: An Ichnologic Clue to the Origin of Detrital, Grain-Coating Clays

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At Flaming Cliffs—a famous vertebrate locality in southern Mongolia—sand grains in red sandstones of fluvial and eolian origin within the Upper Cretaceous Djadokhta Formation are coated with detrital clay. The nearest correlative marine deposits are thousands of kilometers distant. Structureless sandstones with stringers and lenses of reworked caliche pebbles lie laterally adjacent to sets of eolian cross-strata up to 20 m thick. These pebbly sandstones, interpreted as the deposits of intermittent streams that occupied interdune positions, contain abundant Ophiomorpha. *Burrows are 1 to 3 cm in diameter, with a knobby exterior. The traces occur not only as simple tubes, but also as* Teichichnus-*like spreiten, produced by the systematic upward and lateral migration of a spiral burrow. Spreiten can reach vertical extents greater than 3 m and widths of 30 cm. Although they commonly appear in stratal sequences that contain no mudstone beds, many of the burrows are filled by mud. The best modern analog is provided by freshwater crustaceans that excavate deep burrows to the water table in order to escape desiccation during drought. Mud was emplaced during fluvial flood events when the open, near-vertical shafts acted as storm sewers through the vadose zone. Spreiten probably were generated by systematic offsets from the original burrow axis during repeated re-excavations.*

One mechanism for emplacing detrital clays in sandstones calls upon infiltration of muddy water through the vadose zone during flood events. The burrow fills within the fluvial facies of the Djadokhta Formation provide corroborative, independent evidence for the passage of muddy water through the strata. Like the Callianassa *burrows that fill with coarse, shelly debris during the passage of Caribbean hurricanes ("tubular tempestites"), burrows in continental settings also can provide unique testimony to important depositional events and early diagenetic processes.*

INTRODUCTION

Most flows of air and water across Earth's surface that entrain sediment are turbulent; therefore, clay and sand are segregated into bedload and suspended load and deposited in different settings. In thin-sections and SEM images of sandstones, however, coatings of detrital clay are common on sand grains (Walker et al., 1978). These grain coatings have received considerable attention from petrologists because they can promote pressure solution, inhibit formation of syntaxial quartz overgrowths, and act as nucleation sites for authigenic clays (Matlack et al., 1989; Wilson, 1992). Clay coatings similar to those in sandstones have been observed in Holocene sediments and have been generated in the laboratory. Evidence indicates that most detrital clay coatings are emplaced within sand bodies that lie near or above the water table and are subjected to infiltration by vadose water carrying suspended clay. Many clay coatings in eolian and shelf sandstones show evidence of transport from their site of origin—the inherited clay rims of Wilson (1992)—suggesting that they can survive considerable transport. Two mechanisms have been suggested to explain the abundance of clay coatings on sand grains within modern and ancient eolian dunes. (1) Airborne dust that falls on dune slopes or crests is carried directly into the sand by infiltrating rainwater (Walker, 1979); this process may be especially important on vegetated dune surfaces where dust particles are not easily resuspended (Pye and Tsoar, 1987; Winspear and Pye, 1995). (2) Mud-sized particles also can be emplaced in coarse alluvium that lies above the water table when flood waters infiltrate channel deposits during flooding (Crone, 1975; Walker et al., 1978); deflation later moves the clay-coated sand onto nearby dunes (Wilson, 1992).

In the Gobi Desert of southern Mongolia, a diverse continental fauna of dinosaurs, mammals, and lizards is spectacularly preserved in Upper Cretaceous redbeds of the Djadokhta Formation (Dasheveg et al., 1995; Loope et al., 1998). Strata of the Djadokhta Formation (as well as over- and underlying rocks) are entirely nonmarine, representing eolian and fluvial environments (Jerzykiewicz et al., 1993; Eberth, 1993). The nearest known correlative marine rocks are 2800 km away, in Kazakhstan (Averianov, 1997). The Djadokhta Formation, thus, represents a rare glimpse of the climate and biota of the interior of a large continent during the Cretaceous (Barron and Washington, 1982).

At our study site, Flaming Cliffs (= Bayan Dzak, Fig. 1), both the structureless and the cross-stratified sandstones that we interpret as the deposits of intermittent streams and eolian dunes are composed of clay-coated sand grains. Although many outcrops of these sandstones at Flaming Cliffs are completely free of mudstone interbeds, near-vertical, mud-filled *Ophiomorpha* burrows are common in

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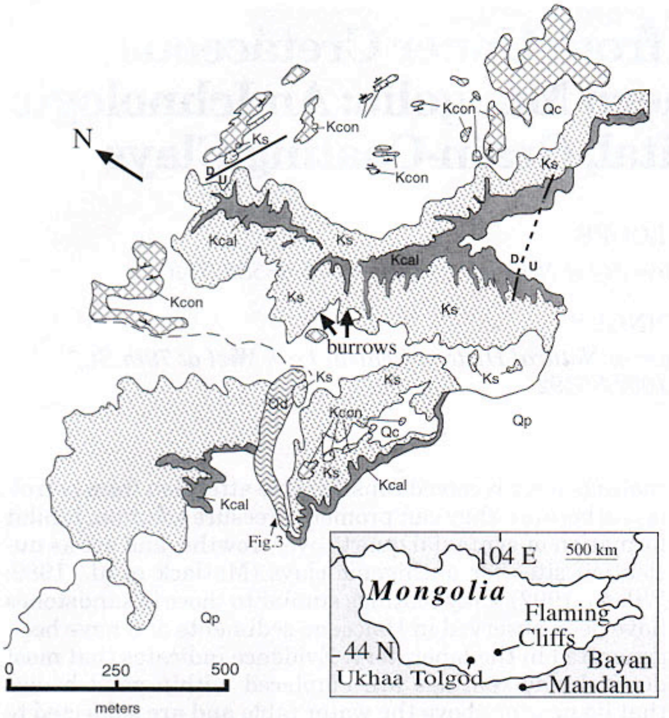

FIGURE 1—Central portion of Flaming Cliffs showing location of burrows, structureless sandstone (Ks), cemented dune foresets with rhizoliths (Kcon), caliche horizons (Kcal), and orientation of camera for Figure 3. Inset–Location of study site (Flaming Cliffs) and two other sites where trace fossils (Bayun Mandahu; Jerzykiewicz et al., 1993) and clay rims (Loope et al., 1998) from Djadokhta Formation red beds have been described.

these exposures and bear testimony to the passage of numerous mud-rich floods.

Ophiomorpha, a distinctive, knobby-walled trace fossil that is abundant in the rock record (Weimer and Hoyt, 1964; Bromley, 1990) is typically found in marine or marginal marine settings and is typically composed of simple or branched cylinders. The *Ophiomorpha* specimens within our study area are atypical on both of these counts. They were built within intermittent stream deposits in a fully continental setting and are preserved not as individual burrows, but instead as *Teichichnus*-like spreiten. Our goal in this paper is to describe these unusual trace fossils and to highlight their implications for the origin of clay coatings on sand grains.

From a tropical, shallow marine setting, Wanless et al. (1988) demonstrated the potential of open burrows as recorders of energetic events. Our study of ancient fluvial deposits shows that deep, open burrows acted as storm sewers that carried mud-rich flood water through a thick vadose zone. Our evidence corroborates the findings of Crone (1975) and Walker et al. (1978), who demonstrated that abundant clay rims are generated by the flooding of desert-stream courses.

STRATIGRAPHIC AND SEDIMENTOLOGIC SETTING

During the late Mesozoic, repeated intervals of block faulting across east central Asia produced a complex mosaic of graben and semigraben structures which were infilled with bone-bearing strata (Jerzykiewicz and Russell, 1991). Rivers entered the basins from surrounding mountains and provided a source of sand for dune fields, much as occurs along the southern margins of the Junggar and Tarim basins in modern China (Eberth, 1993). Our site, Flaming Cliffs, is the type locality of the Djadokhta Formation, first described by Berkey and Morris (1927) and studied by Lefeld (1971). On the basis of its vertebrate fauna, the sequence has been correlated to Upper Cretaceous (Campanian) strata of western North America (Lillegraven and McKenna, 1986) and Kazakhstan (Averianov, 1997). The Darbasa Formation of southern Kazakhstan, in contrast to rocks of Late Cretaceous age in Mongolia and China, yields both marine and nonmarine fossils (Averianov, 1997).

About 30 m of strata are exposed at Flaming Cliffs (Fig. 2). Caliche horizons, identical to those that were well described and illustrated from correlative rocks at Bayan Mandahu in China (Fig. 1) by Eberth (1993), form prominent benches near the top of our section. Sheets of caliche pebble conglomerate lie near the top of the section, and one-meter-wide, channel-filling ribbons and thin stringers of this material are present in the lower beds that contain abundant trace fossils (Fig. 2).

A single set of calcite-cemented cross-strata is present in the lower part of the stratigraphic section. The set is up to 15 m thick and is discontinuous laterally (Figs. 2, 3). The scale of the foresets and the texture of the deposit suggest a dune origin, and in a few locations it is possible to see inverse-graded mm-scale laminations (Hunter, 1977) that confirm an eolian interpretation.

Rhizoliths, ranging in diameter from about 1 cm to about 1 mm (Fig. 4) are abundant in the prominent, carbonate-cemented cross-strata. The larger rhizoliths typically lie parallel to stratification. In many cases, primary sedimentary structures (laminae and beds) within the eolian rocks are absent owing to intense burrowing and rooting; the orientation of the obscured foresets typically is best recorded by sheets of preferentially cemented sediments with abundant small rhizoliths and, in a few cases, by the orientation of large rhizoliths.

We interpret the rhizoliths that lie parallel to dune cross-strata as a record of the growth of xerophytic dune vegetation. Plants grew on the large eolian bedforms and their roots derived water strictly from the vadose zone. Because tightly packed sands retain more water after wetting than those that are loosely packed (Hillel, 1980), vadose water would have been most available to plants in foresets dominated by wind ripple deposits rather than grainflows, which have higher porosity (Hunter, 1981). In the vadose zone, any anisotropy to flow within a porous medium is greatly enhanced relative to the anisotropy of the same material under saturated conditions (Stephens, 1996). McCord et al. (1991) showed that for a dune sand that was nearly isotropic at saturation, the unsaturated permeability parallel to bedding was as much as 20 times greater than that perpendicular to bedding. Therefore, plant roots that grow parallel to bedding are best able to exploit the limited water resources in dune sand. Under saturated conditions, there would be little advantage to this growth pattern.

At the west end of our study area, a lens of red mudstone is present in the lower part of the section (Lefeld, 1971, fig.

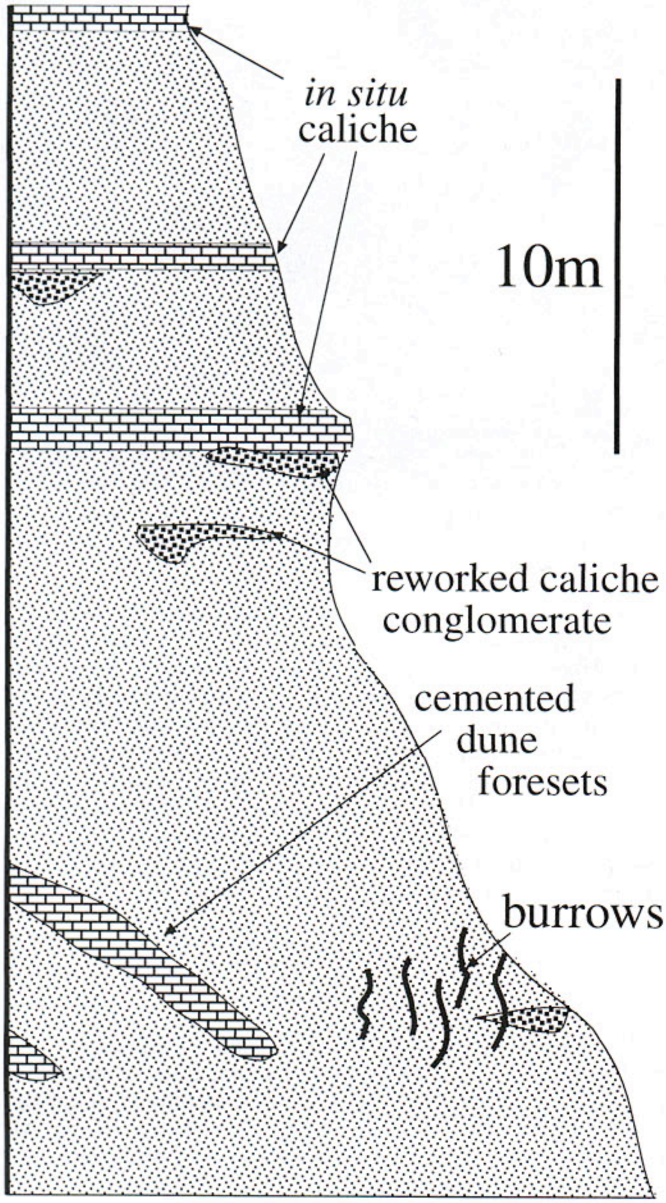

FIGURE 2—Stratigraphic section, central Flaming Cliffs. Section is dominated by structureless sandstone; note absence of mudstones.

5). It reaches a maximum thickness of 7 m and extends over approximately 1 km². The lowermost 30 cm of mudstone is cut by sandstone dikes that form polygons that are about 25 cm in diameter. A 1-cm-thick sandstone caps the polygons. A set of dune cross-strata lies within 100 m of the edge of the mudstone outcrop, and the cross-strata dip toward the lens. Mud-filled trace fossils are present in the sandstone that underlies the mudstone lens, but the large spreiten structures described below are absent. We interpret the mudstone lens as the fill of an interdune swale that was flooded during major runoff events. Eolian sand filled the polygonal desiccation cracks that formed after the first preserved flood event.

The soil carbonates of the study area—both the caliche horizons and the rhizoliths—suggest a semi-arid climatic setting. The absence of evidence of perennial surface water is notable. In Quaternary dune fields, especially those stabilized by vegetation like the Nebraska Sand Hills, interdune lakes are numerous, but they are restricted to areas that lack throughgoing stream courses (Loope et al., 1995). Although large eolian dunes were present within the study area during deposition of the Djadokhta Formation, they apparently did not block stream courses. The environmental interpretation offered by Eberth (1993, fig. 19) and Jerzykiewicz et al. (1993, fig. 14 I) for strata in China that are correlative to the Djadokhta Formation apply very well to our site. The configuration of streams and dunes may have resembled the modern Channel Country of central Australia (Gibling et al., 1998).

FIGURE 3—View to the northeast toward the main escarpment at Flaming Cliffs. Calcite-cemented foresets (foreground) dip away from camera. Burrows exposed at base of escarpment (see Fig. 1).

DETRITAL CLAYS IN SANDSTONES OF THE DJADOKHTA FORMATION

Description

Scanning electron microscopy of sand grains in the walls of the *Ophiomorpha* traces (described below) shows abundant clay bridges (Fig. 5) and clays that lie parallel to sand-grain surfaces. Clays are absent at points of contact between framework grains. X-ray diffraction reveals the

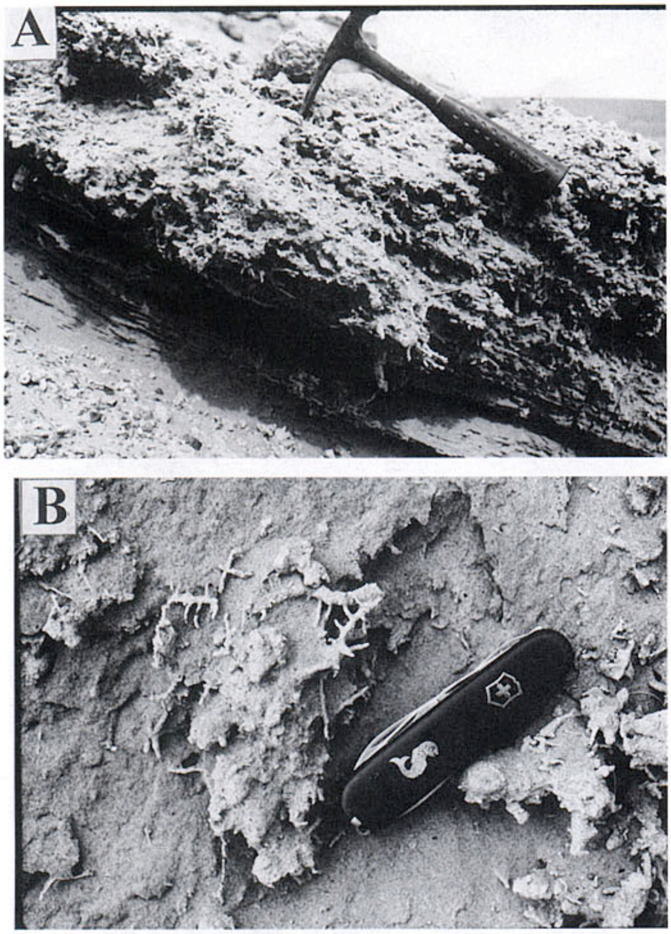

FIGURE 4—Evidence for plant growth on dunes. (A) Rhizoliths within preferentially cemented dune cross-strata. (B) Close-up showing branching of rootlets. Knife is 9 cm long.

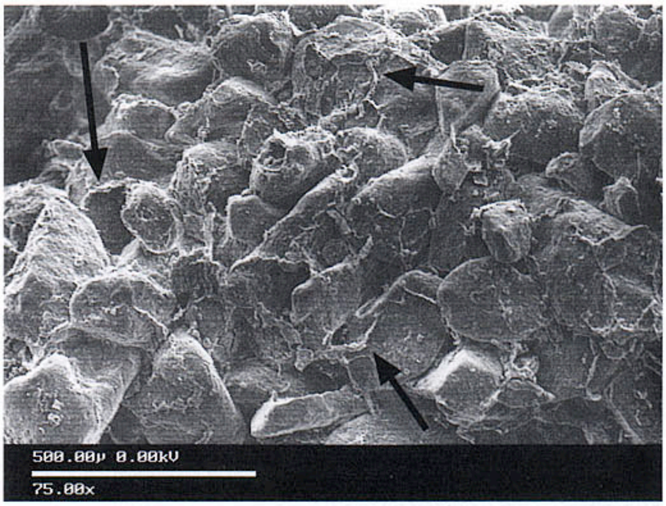

FIGURE 5—SEM image of sandstone from burrow wall, showing clay bridges (arrows) on broken surfaces. Scale bar is 0.5 mm long.

presence of mixed-layer illite/smectite and chlorite; samples from burrow fills and the mudstone lens described above contain the same minerals. Our samples from the calcite-cemented dune deposits do not contain clay bridges and clays are present at points of contact.

Interpretation

Based on application of criteria and terminology suggested by Wilson (1992), the fluvial sandstones that we have examined contain abundant infiltration clays (*in situ* accumulations), whereas the eolian rocks are dominated by inherited clay rims (transported after infiltration). Cross-stratified eolian sandstones in Djadokhta Formation outcrops at Ukhaa Tolgod, 100 km west of Flaming Cliffs, also contain abundant inherited clay rims (Loope et al., 1998). Although positioned in the vadose zone relatively near the surface of a vegetated sand dune, the sand grains associated with the rhizoliths that we examined show no evidence of *in situ* grain-coating detrital clay.

We have not done an exhaustive study of the distribution and characteristics of detrital clay within Djadokhta Formation sandstones. Although our limited petrographic observations support the view that clays were emplaced in a fluvial setting and were later recycled to the dunes, we believe that another post-depositional process makes interpretations that are based solely on petrography equivocal. After transport of clay-coated grains (which removes bridges) and their deposition in a second sand body (as inherited clay rims), those clays can be removed from their host grains by infiltrating water and can provide material for a second generation of bridges on grains a few centimeters away. In this case, the presence of clay bridges between sand grains in the second sand body could mislead the petrographer to the conclusion that the observed clays are primary infiltrates.

Ophiomorpha

Description

The trace fossils that are the focus of this paper are within generally structureless, friable, fine- to medium-grained sandstone, and they are best displayed along the bases of cliffs that are exposed to very strong winds. Although isolated cylindrical burrows with knobby exteriors are present in some exposures (Fig.6B, E), strap-like, *Teichichnus*-like spreiten (Bromley, 1990, p. 133) with the same knobby ornamentation are much more abundant and prominent (Fig. 6A-F). The outside diameter of the isolated cylinders and the thickness of the cumulative spreiten structures range from about 1 to 3 cm. The width of the cumulative structures (measured perpendicular to the long axis of individual burrows) can reach at least 30 cm. Burrows within the cumulative structures typically are nearly vertical and the spreiten commonly twist into helices (Fig. 6A, D, E). Both right-handed and left-handed helical segments have been observed in a single, elongate specimen. Cumulative structures reach at least 3 m in vertical extent (Fig. 6A).

Details of burrow-wall morphology are visible only along overhung cliff exposures where differential wind erosion brings trace fossils into nearly full relief. The knobby appearance of the exterior walls is produced by protruding hemispheres of friable sandstone ranging from 3 to 5 mm in diameter (Fig. 6B, C, E). These hemispheres contain no more clay than the matrix and are free of cal-

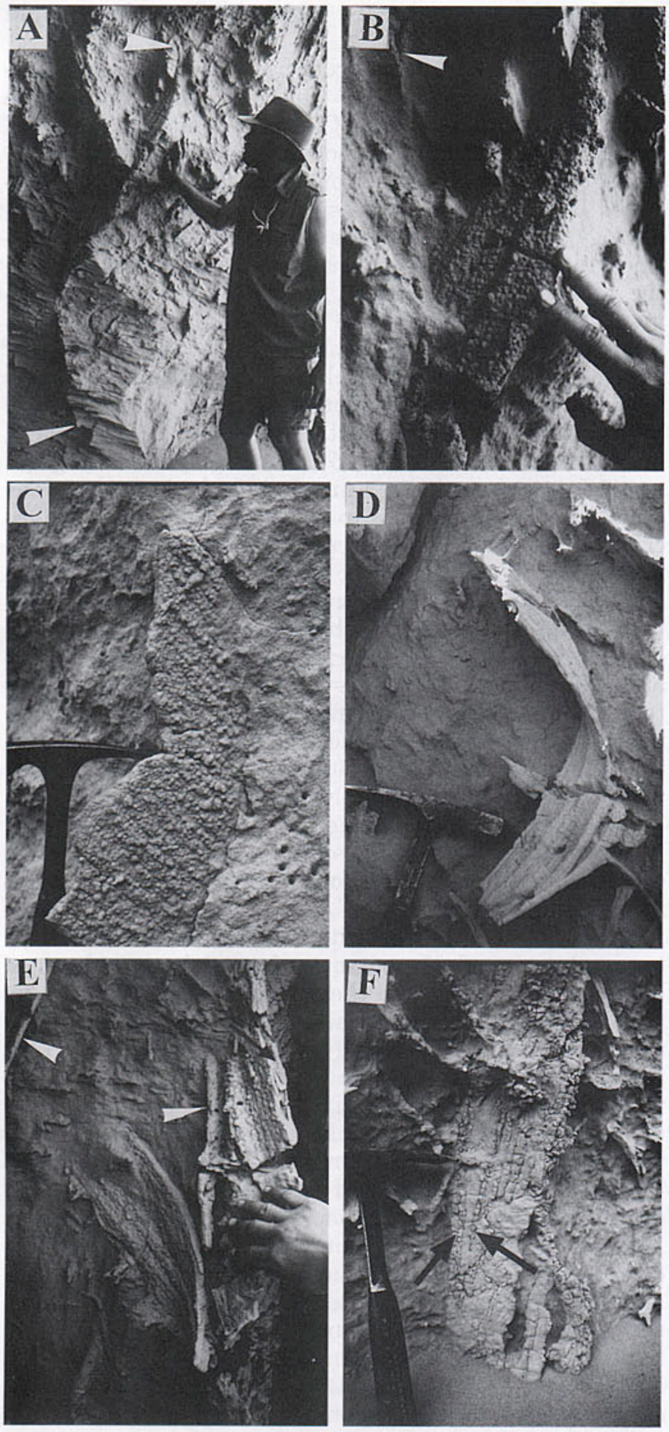

FIGURE 6—In situ *Ophiomorpha* spreiten at Flaming Cliffs. (A) 2-m-long spreite with large radius of curvature. Arrows mark highest and lowest preserved parts of burrow. (B) Closer view of same specimen; two small cylinders with nodular wall ornamentation in upper left (arrow). (C) Nodular surface of spreite; note linear alignment of surface ornamentation. (D) Broken specimen with small radius of curvature. (E) Portions of two spreiten; note broken cross-sections showing concave-up structure (black arrows) and simple cylinders with nodular wall ornamentaion (white arrows). (F) Deeply eroded specimen showing multiple mud (arrows) and sand fills.

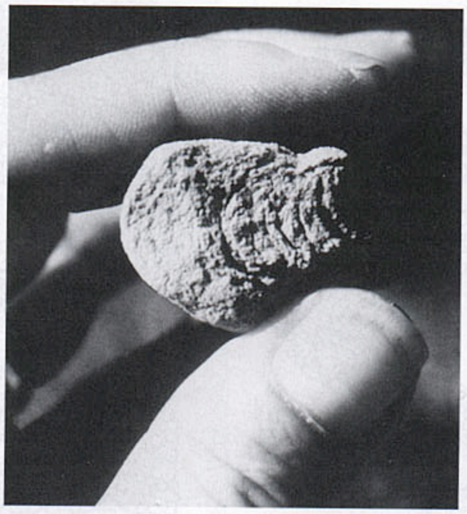

FIGURE 7—Transverse section of 5 cm long fragment of a spreite showing concave-up structure. Top is to right; specimen is 3 cm wide. Compare with lower right portion of Fig. 8B.

cium carbonate cement. The inner walls, although rarely visible, are smooth (Fig. 6E).

Cross-sections of the spreite reveal thin sandy laminae, interbedded sand and mud (Figs. 6F, 7), or structureless mudstone. Some laminae in the sandy fills are concave-up, others are nearly planar. Mud is a major component of the fill of some spreiten, but it is totally absent in many others.

Interpretation

Ophiomorpha is a knobby-walled burrow (Hantzschel, 1975) that is common in high-energy, clean sand deposits from Ordovician to Recent age. Hester and Pryor (1972) described blade-shaped spreiten traces from Eocene sandstones near Starkville, Mississippi, that share several key characteristics with the Cretaceous traces from Mongolia (compare their figs. 3 and 4 with Figs. 6 and 7). Noting that their traces have the knobby exterior of *Ophiomorpha* but an overall form similar to *Teichichnus,* they made a compelling case for the use of the former ichnogenus name, arguing that the trace was made by the same organism that produced typical (non-spreite) *Ophiomorpha* in the same deposit. Bromley (1990, p. 161) pointed out that a logical alternative name for the trace described by Hester and Pryor (1972) would be *Teichichnus nodosus.*

A major difference between the Mississippi and Mongolia examples, however, is that the spreite in the Mongolian material is produced by upward and lateral migration of a steeply inclined cylinder; in the Mississippi traces, a similar blade-like morphology is produced by simple upward migration (retrusion) of a horizontal cylinder. Trace fossils more similar to the Mongolian material are present in Upper Cretaceous shallow marine strata of the Book Cliffs of central Utah (Ekdale, personal communication, 1999). Although *Ophiomorpha annulata* at the Utah locality most commonly display a horizontal maze geometry, they also uncommonly form subvertical, slightly twisted, *Teichichnus*-like spreiten.

Frey et al. (1978, fig. 6c), Hobbs (1981, p. 31,34), and Bromley (1990, fig. 5.22) have noted the tendency of both

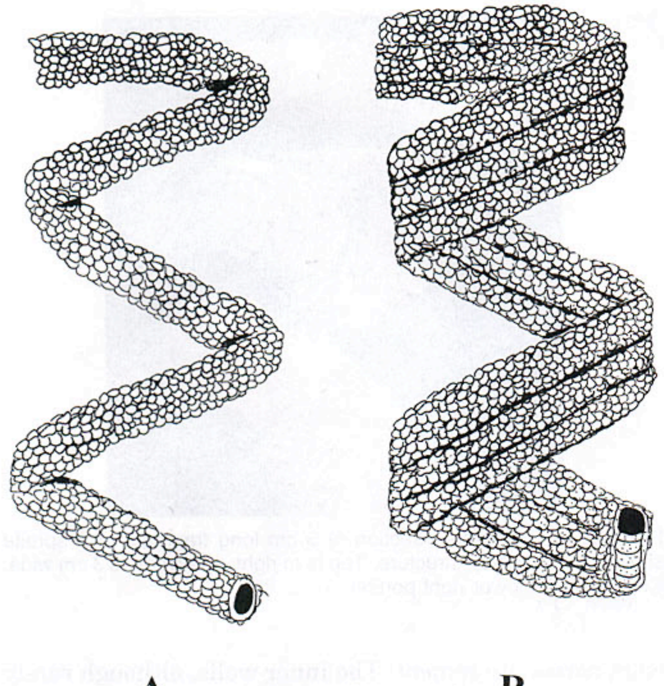

FIGURE 8—Upward migration (retrusion) of a spiral-shaped *Ophiomorpha* burrow (A; after Frey et al., 1978) generates the "twisted strap" morphology (B) described in this paper.

marine and freshwater crustaceans to build spiral burrows. We interpret the helical, twisted strap form of our traces to be the result of repeated re-excavations of a near-vertical, spiral burrow (Fig. 8).

Laminae within sandy fills that are concave-up represent the migration of the smooth inner wall and were produced actively by the burrower. The concave-up aspect indicates that the spreiten are retrusive—the burrow moved obliquely upward with each renewed episode of excavation. The planar-laminated sand probably represents passive fill, which was deposited as sand fell from the roof or slipped down the steeply sloping floor of the spiral burrow. Mud is absent from many spreiten but is the nearly exclusive kind of fill of others, so we interpret the mud fills as passive. We think mud was emplaced in the burrows when muddy water from stream floods flushed downward through the channel sands toward the regional water table. According to Dunne (1990), when water infiltrates a porous medium under unsaturated conditions, it migrates only within the matrix, avoiding burrows, open fractures, and other macropores. Any water within macropores moves outward into the unsaturated matrix. Under saturated conditions, however, the pressure gradient is reversed, and water flows into the macropore from the matrix. When desert streams flood, channel sands become saturated, forming an inverted water table. Unsaturated flow, however, would occur between the inverted water table and the deeper, regional water table (Stephens, 1996, p. 116–117). Some of the mud in the burrows probably was deposited from suspension and some as a filter cake that accumulated against the burrow walls as water flowed outward from the burrow into the unsaturated sands that lay below the inverted water table and above the regional water table.

The similarities in wall structure and morphology of the Mongolian trace fossils to *Ophiomorpha* from marine rocks of Eocene and Late Cretaceous age (Hester and Pryor, 1972; Ekdale, personal communication, 1999) strongly suggest that the Mongolian structures were produced by crustaceans. The surface ornamentation, morphology, and geometry of the Mongolian burrows are distinct from those of modern crayfish burrows, but because the Mongolian trace fossils are present in fluvial sediment, crayfish appear to be the only living crustaceans that can provide behavioral clues for the interpretation of our material. We do not imply that the Mongolian traces were produced by crayfish, only that they were produced by animals that had important anatomical, behavioral, and ecological similarities to modern crayfish. The great vertical extent (at least 3 m) of individual traces at our study site is comparable to the length of some modern crayfish burrows. Because crayfish must keep their gills moist, they live at the water table. Therefore, the vertical extent of their burrows is a direct indication of the distance from the surface to the water table (Hasiotis and Bown, 1992). Many hyper-arid desert settings are unsuitable habitat for crustaceans—the regional water table lies tens of meters below the floors of stream channels and surface flows are ephemeral. The presence of *Ophiomorpha* in the Mongolian fluvial deposits suggests to us that surface water was present seasonally and that, although the paleo-water table may have fluctuated seasonally, it typically lay within 2 to 3 m of the surface. The trace fossils thus corroborate other sedimentological evidence for a semi-arid climatic setting.

Hobbs (1981) and Horowitz and Richardson (1986) attempted to classify the burrows of crayfish on the basis of behavior and relation to the water table. Hasiotis et al. (1993) showed that these classifications can be applied to ancient traces. The vertically elongate, unbranched burrows that dominate our study site are most similar to those in Hobbs' (1981) "tertiary burrows" category. Modern crayfish species that make such burrows live in open water and retreat to the burrows (1) to get below the frost line in winter; (2) to lay and brood eggs; and (3) to avoid desiccation when the body of water begins to disappear. Because Late Cretaceous climates were mild, even within continental interiors at relatively high latitude (Barron and Washington, 1982), air temperatures probably did not reach freezing. The deep burrows of the Djadokhta Formation may reflect reproductive behavior or, since the host sediments were deposited between eolian dunes and show evidence of vadose conditions, may have provided refuge from desiccation. It seems likely that seasonal droughts were terminated by flooding events that filled the open burrows with sand and or mud. Rather than excavate the fresh fill, the buried animals offset from the axis of the burrow and constructed the new burrow in adjacent, firm parent material.

DISCUSSION

From Djadokhta Formation outcrops in China, Jerzykiewicz et al. (1993, p. 2193, fig. 13b) were the first to describe and illustrate examples of the trace fossils similar to those discussed here. Their Chinese site is about 360 km southwest of our study area. The structure that these workers called *Teichichnus* is very similar to the trace fossils described here, but those authors did not describe any knobby-walled or mud-filled specimens. They speculated that the spreiten may have been produced by a selective deposit feeder, and they took this as an indication that the sediment originally contained a substantial quantity of organic material. Deposit-feeding behavior by crayfish has not been described, but at least one marine decapod crustacean, *Callianassa californiensis,* is mainly a deposit feeder (Bromley, 1990). Like most deposit feeders, *Callianassa californiensis* lives in intimate contact with reducing pore waters and builds burrows that have poorly reinforced walls.

We do not favor the deposit-feeder interpretation, because the spreiten burrows from the Djadokhta Formation were excavated in strongly oxidized sediment and have reinforced walls. Not only does the host sediment have a very low organic matter content, but its red color indicates that oxidizing conditions persisted during diagenesis (Walker et al., 1978).

Hasiotis et al. (1993) have pointed out that many freshwater crayfish excavate deep burrows in order to escape desiccation—a problem faced by few marine crustaceans. They described burrows more than 3 meters in vertical extent with few horizontal elements. We interpret the Djadokhta spreiten burrows as products of either long-lived individuals or colonies of surface-feeding crustaceans. Instead of reflecting a feeding strategy, we interpret the lateral shifts of the cylindrical burrow to be a response to sedimentation events that filled an open, near-vertical spiral shaft. Rather than removing the freshly deposited material from the original shaft, the shut-in burrow occupant(s) offset slightly and, moving upward, excavated a parallel shaft. Hobbs (1981, p. 31, 35) noted that modern crayfish that construct deep, tertiary burrows commonly plug them, presumably to prevent their infilling with sediment. If the Djadokhta Formation burrows were originally plugged, it seems likely that the plugs were removed during fluvial floods.

The *Ophiomorpha* described here are unusual not only for their spreiten structure, but also for their presence in an unequivocally non-marine setting. The utility of *Ophiomorpha* as a marine indicator has been a subject of dispute for about 20 years. To illustrate their warning that all *Ophiomorpha* should not be interpreted as indicators of marine or marginal marine environments and products of the shrimp *Callianassa* in particular, Frey et al. (1978, p. 215) noted that if a freshwater crayfish were found to produce knobby-walled burrows, and the structures were fossilized, those burrows would have to be called *Ophiomorpha*. In the same year, Stewart (1978) identified *Ophiomorpha* in a Late Cretaceous fluvial sequence on the Isle of Wight. Later, Bown (1982) included *Ophiomorpha* in the ichnofauna of an Oligocene sequence from Egypt that he considered to be nonmarine. Goldring and Pollard (1995) argued more recently that the British examples described by Stewart (1978) actually lack the pelleted wall structure of *Ophiomorpha,* and, therefore they reassigned those traces to *Beaconites*. Hasiotis and Bown (1992) reinterpreted the *Ophiomorpha*-bearing portions of the Oligocene strata in Egypt to represent an estuarine environment. Only the *Ophiomorpha* described from Eocene fluvial rocks by Merrill (1984) now appear to be widely accepted as an example of a nonmarine occurrence of the ichnogenus (Anderson and Droser, 1998). The abundant specimens of *Ophiomorpha* described here from Late Cretaceous redbeds of central Asia must now be added to a very short list of nonmarine examples of this distinctive trace fossil.

CONCLUSIONS

(1) Upper Cretaceous fluvial sandstones of the Djadokhta Formation at Flaming Cliffs, southern Mongolia contain speiten trace fossils best assigned to *Ophiomorpha*. These sandstones were deposited in a continental interior setting under a semi-arid climatic regime. Intermittent streams carrying abundant mud in suspension flowed seasonally between large, vegetated eolian dunes. In the vicinity of fluvial channels, the water table sometimes dropped 3 m below the surface. *Ophiomorpha* and rhizoliths within dune cross-strata have provided new insights into the environmental setting of this important vertebrate fossil locality.

(2) The spreiten structure of *Ophiomorpha* resulted from repeated, bottom-to-top re-excavation of spiral burrows that were passively filled during fluvial floods.

(3) Petrographic observations suggest that grain-coating clays within sandstones of the Djadokhta Formation were emplaced by fluvial processes. This interpretation is corroborated by the presence of mud-filled *Ophiomorpha* burrows in the fluvial deposits. Mud-filled trace fossils should be sought in other sand-dominated fluvial sequences.

(4) We found no evidence that rainwater infiltrating the dunes emplaced dust-derived, primary clays on grain surfaces. Fluvial sediments were apparently the source of both sand and clay for the dunes.

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