Fossil vertebrate footprints in the Coconino Sandstone (Permian) of northern Arizona: Evidence for underwater origin

Leonard R. Brand, Thu Tang
Department of Natural Sciences, Loma Linda University, Loma Linda, California 92350

ABSTRACT

Numerous fossil vertebrate trackways in the Coconino Sandstone of northern Arizona exhibit several features that imply that these trackways were not made in subaerial conditions. Some trackways begin or end abruptly on undisturbed bedding planes, and in other trackways the individual prints are oriented in a different direction from that of the trackway. These features indicate buoyancy of the animals in water. The animals were swimming in the water part of the time and at other times walking on the substrate, and they were sometimes orienting upslope on the surface of the underwater dunes, while being drifted sideways by lateral currents. Observations on salamander locomotion in a sedimentation tank with flowing water support this model.

INTRODUCTION

There has been increased research on ancient eolian sands in the past decade (e.g., Blakey, 1988; Brookfield and Ahlbrandt, 1983; Hesp and Fryberger, 1988; Kocurek, 1988; Kocurek and Dott, 1981; Loope, 1984; McKee, 1979). The Coconino Sandstone of northern Arizona is generally interpreted as an eolian deposit of desert sand (Blakey, 1988; Loope, 1984; McKee, 1933, 1947, 1979; McKeever, 1991; Middleton et al., 1990; Spamer, 1984), and the fossil footprints that are abundant in this deposit have been used as evidence for eolian deposition. Lockley and Rice (1990) and McAllister (1989) discussed the criteria for recognition of subaqueous trackways, and some recent work has indicated that the fossil footprints in the Coconino Sandstone most closely resemble footprints made underwater in the laboratory (Brand, 1979). We present here additional data on fossil footprints that have features pertinent to an understanding of the depositional environment of the Coconino Sandstone.

METHODS

Exposures of the Coconino Sandstone in Arizona were surveyed for trackways: these were photographed, and in some cases molds of the trackways were made. Localities studied are listed in Appendix 1.[1] Trackway collections were also studied and photographed in the following museums: Smithsonian Institution, Peabody Museum at Yale University, American Museum in New York, Raymond Alf Museum at the Webb Schools in Claremont, California, and Museum of Northern Arizona in Flagstaff. Most of the tracks in Coconino Sandstone in these museums were from the localities listed in Appendix 1 (see footnote 1).

In photographs, the directional orientation of trackways was determined in relation to an arbitrary reference direction (Fig. 1). The orientation of individual footprints was then measured in relation to the same reference direction. A line was drawn through each individual footprint parallel to the direction in which the toe prints were pointing. The orientation of an equal number of left and right and/or back and front prints (depending on whether it was possible to determine right and left or back and front for the prints) was determined for each trackway or section of trackway, and the mean of these directions was used for comparison with the trackway direction. Differences between the trackway direction and the mean print direction were evaluated with the Hotelling test for paired samples of angles, which calculates a value of F (Zar, 1984) as a basis for determining the probability (p) that there is no difference between the directions of the trackways and the individual prints.

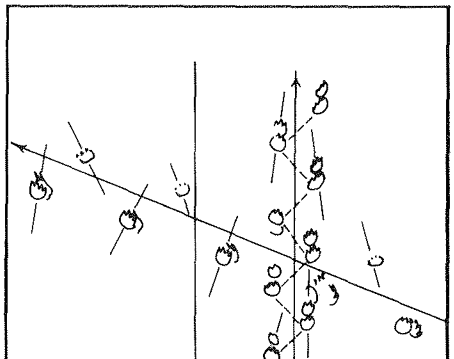

Figure 1. Two intersecting trackways showing method of comparing trackway and print orientation. Orientation of each solid line was measured relative to reference line.

Underwater locomotion of western newts, *Taricha torosa*, was observed in an acrylic sedimentation tank, 1.83 m long, 30.5 cm wide, and 45.7 cm high. The newts were allowed to walk on a flat bed of fine sand, with water 4 cm deep flowing the length of the tank at ~8 cm/s, while their behavior was taped with a stationary video camera. The video tape was replayed one frame at a time, and the position of each foot when placed on the substrate and the orientation of the animal's body were traced on a transparent overlay taped to the front of the monitor. A total of 238 underwater trackways were studied. Line drawings of the fossil trackways, traced from photographs, were compared with the tracings of underwater newt locomotion. The animal body positions suggested by this analogue as explanations for the orientation of the fossil prints were drawn on to the fossil trackway drawings.

FOSSIL TRACKWAYS AND A LABORATORY ANALOGUE

Trackways of Animals Moving Sideways

Trackways in the Coconino Sandstone and De Chelly Sandstone usually go up the faces of the cross-beds (McKee, 1947; Vaughn, 1963). In these deposits, we have observed only one trackway that appeared to be going downhill. Most upslope fossil tracks (see Fig. 4A) show the features of normal walking—a regular alternation of left and right feet, and toe marks that point approximately in the direction of movement or are slanted toward the midline of the trackways. In all in situ specimens observed, these trackways were headed up the slope of the cross-beds. In contrast, in a significant minority of the trackways ($N = 87$) (Fig. 2) the toe marks of all visible prints point in one general direction, which is not the direction in which the animal is moving. In some cases (Fig. 2, B, D,

[1]Appendix 1, Location of Coconino Sandstone Fossil Trackway Study Localities (Arizona), GSA Supplementary Data 9135, is available on request from Documents Secretary, GSA, P.O. Box 9140, Boulder, Colorado 80301.

Note: Additional material for this article is Supplementary Data 9135, available on request from the GSA Documents Secretary (see footnote 1).

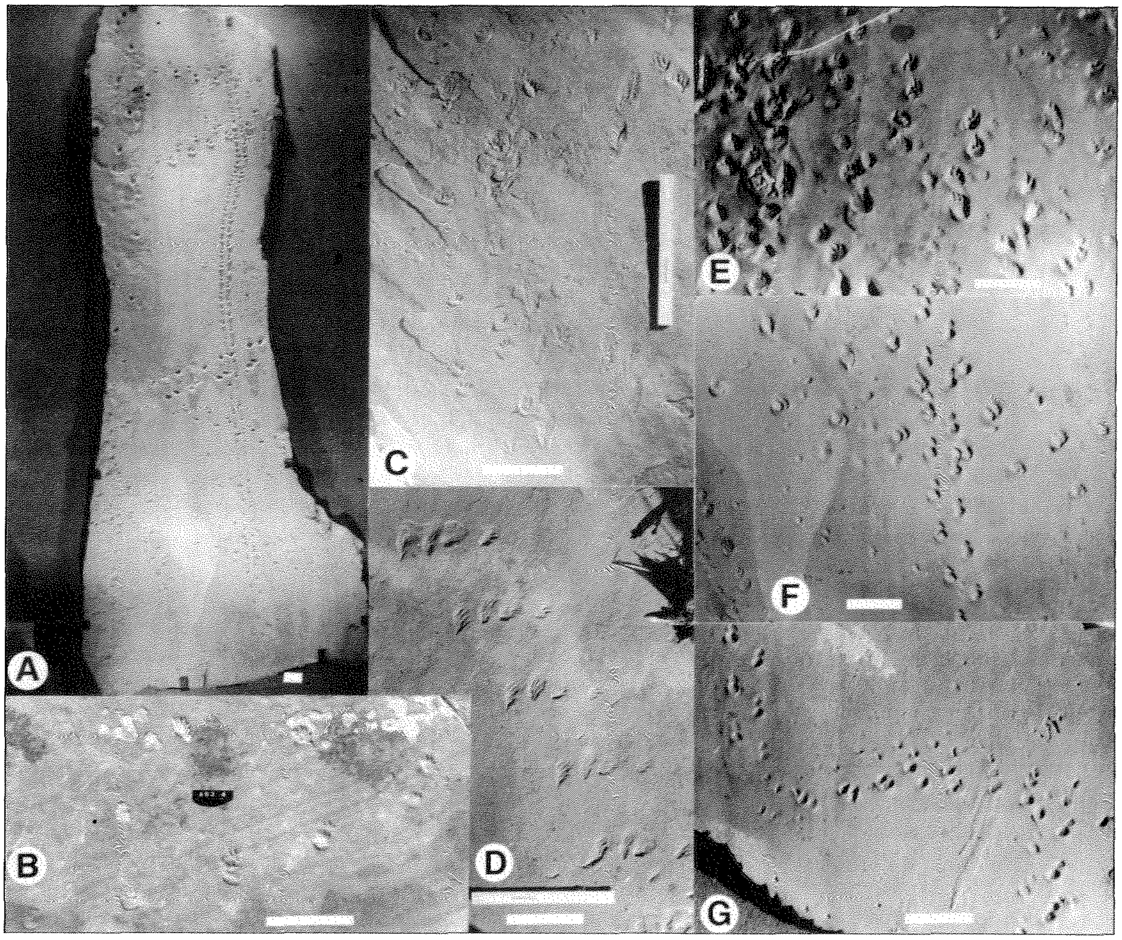

Figure 2. Trackways showing oblique movement of animals across Coconino Sandstone surfaces. A, E, F, G: Alf Museum, collected at Seligman, Arizona. B, C, D: In situ tracks in Grand Canyon; B—Grandview Trail; C and D—Kaibab Trail. Bar scales = 10 cm.

and G) the trackway is headed at almost right angles to the direction in which the prints are pointed. Tracks of this type were found in situ or in museum specimens of the Coconino Sandstone from all localities studied. For all in situ specimens, these trackways were oriented across the slope, the prints pointed up the slope.

The trackway in Figure 2D is the most unusual; each set of four prints is arranged in a straight line at right angles to the trackway orientation. A very similar trackway was also found at Seligman.

In the laboratory, salamanders walking underwater sometimes walked directly into or with the current (Fig. 3A), but often the current drifted them sideways. They then continued to walk, while drifting at some angle to the direction in which their bodies were oriented. Figure 3, B–F, shows representative tracings of their body orientations and the position of each foot as it was placed on the substrate while they drifted sideways. These trackways are very similar to the trackways observed in the Coconino Sandstone in which print direction and trackway direction were not the same. Interpretations of these trackways are shown in Figure 4.

The rose diagrams in Figure 5 compare the trackway orientation with individual print orientation for several slabs containing multiple trackways on each. Data from four slabs from the same locality (Seligman) were combined and tested for significance. In eight upslope trackways, the print and trackway orientations were the same (<2° difference). For the remaining 36 trackways, the trackway orientations were significantly different from the print orientations ($N = 36$; $F = 48.53$; $p < 0.0005$).

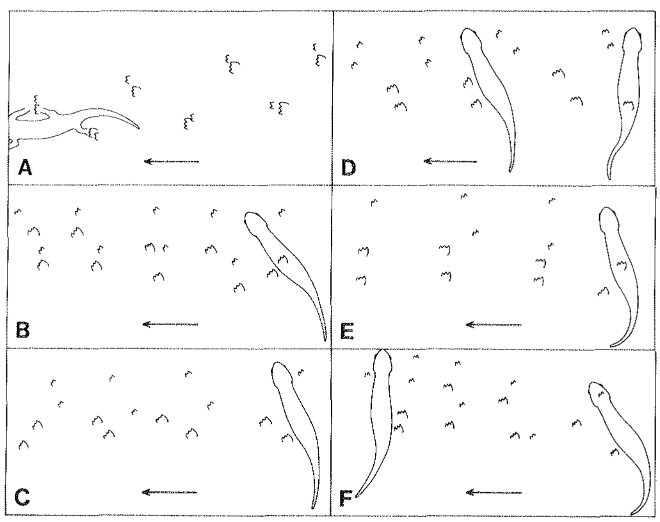

Figure 3. Foot placement and body orientations of live salamanders walking underwater in sedimentation tank. A: Normal locomotion. B–F: Drifting sideways with current; arrows indicate current direction. Shape of footprints is stylized: three toes indicate pes: two toes indicate manus. Scale arrows = 3 cm.

Tracks That Start or Stop Abruptly

Several trackways begin suddenly in the middle of a smooth surface, with no evidence of slumping or other erosional or sedimentary processes that could have obscured part of the trackway (Fig. 6). In one case (Fig. 6C), a trackway angles across the slope, then suddenly ends. The same trackway (or another trackway of the same type) begins about 0.6 m farther up the slope and angles across the slope at the same angle as the lower part of the trackway. In Figure 6A the deeply impressed trackway begins in the middle of the slab and goes upward. The upper trackway in Figure 6B also begins in the middle and goes up and to the left. The trackway in Figures 2B and 4G (upper part) also begins and ends abruptly on a smooth, undisturbed surface.

DISCUSSION AND CONCLUSIONS

Any depositional model for the Coconino Sandstone must account for the behavior of the animals reflected by the abundant footprints that resulted from that behavior.

Trackways that angle across the face of the cross-beds have been previously reported from Hermit basin in the Grand Canyon (Brand, 1979). It is now apparent that they are a common, widespread feature in the Coconino Sandstone. Comparison of the laboratory observations of living salamanders with the fossil tracks suggests the interpretations in Figure 4. This comparison, however, does not indicate whether the track makers were amphibians or reptiles capable of underwater locomotion. The fossil trackways are ascending the 15° to 25° slopes of the cross-beds, and some trackways are as much as 4 m long. This indicates a water depth much greater than the height of the track makers. Thus if the tracks were made underwater, the track makers were not swimming at the surface, but were entirely underwater while walking on the substrate.

The upper part of Figure 4G (and Fig. 2B) is a trackway that starts at the left, angles across the slope to the right, then abruptly changes direction and angles back across to the left. Another trackway (Figs. 4I and 2G) starts up the slope, then turns to the left and slightly downslope, and then resumes its original direction. In all of these prints, the toe marks point directly up the slope, indicating that the animal is oriented in that direction. Figure 4B (and Fig. 2C) shows that the animal moved sideways to the left, walked forward a short distance, then moved sideways to the right. These trackways suggest shifting or intermittent lateral currents to account for the sudden changes in direction of movement.

The unusual trackway in Figure 4F (and Fig. 2D) was apparently the result of a fortuitous combination of body orientation and rate of sideways drift, as occurred occasionally in the laboratory. The salamander walking underwater shown in Figure 3F drifted to the left, and as its body orientation changed, its footprint pattern also gradually changed until the back and front feet were placed in a straight-line relation, just as they are in the fossil trackway in Figure 4F. If the animal in Figure 3F continued to drift in the same position, it appears that a trackway like that shown in Figure 4F would be produced. Some other fossil trackways, such as the upper trackway in Figure 4H (and Fig. 2E), approach the extreme arrangement of the prints seen in Figure 4F. These trackways can be most easily explained if the animals were walking under water. If the submerged animals were walking on the sand but were partially buoyed up by the water (as is typical in modern salamanders; Brand, 1979), they could easily drift sideways when pushed from the side by a lateral current. Because the animal's weight is not resting on the substrate, it can be moved sideways by a fairly gentle current.

If the animal was not in water but was walking on an eolian sand dune, there is no apparent mechanism that could account for the marked sideways drift evident in many of the fossil trackways. If the wind were strong enough to impede an animal's progress, it could cause the animal to go back down the slope or to turn and walk laterally along the dune, but there would be no medium to lift the animal's body weight off the substrate so that it could drift slowly sideways while facing directly up the slope. A wind strong enough to move an animal would also probably obliterate any trace of its trackways.

Another feature of the sideways-drifting trackways is that they often show definite impressions from only the back feet, front foot impressions being indistinct or absent. It is unlikely that these can be explained as ghost prints or underprints (Lockley and Rice, 1990; Sarjeant, 1988) because of the fine detail preserved in many of them. Because the Permian tetrapods most likely responsible for most of these trackways did not show evidence of bipedal adaptations, this evidence also is most easily explained

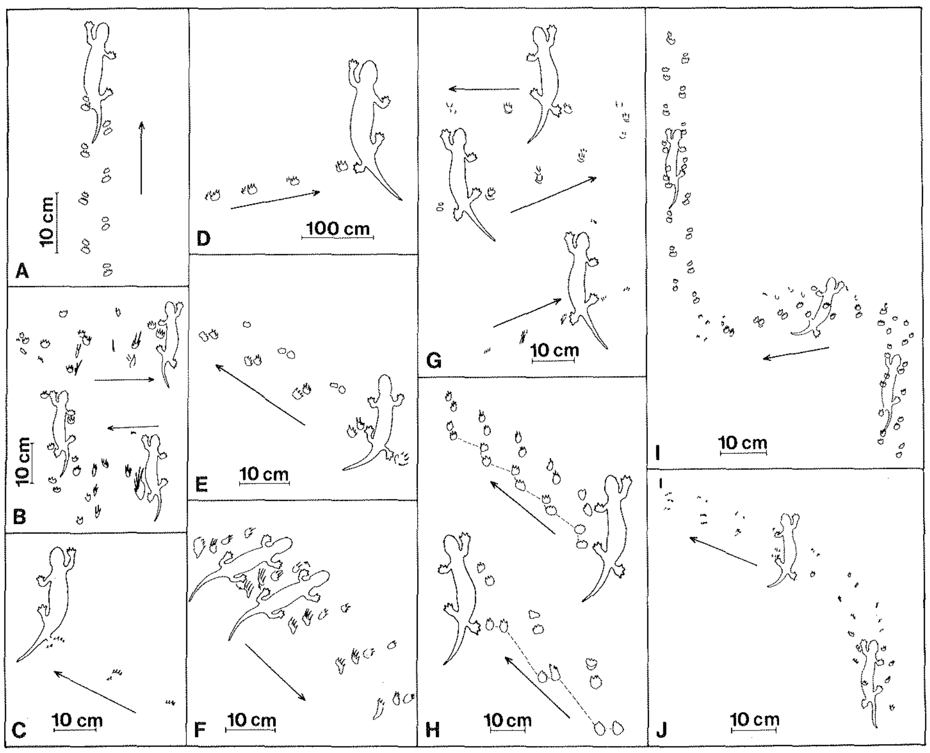

Figure 4. Fossil trackways from Coconino sandstone, traced from photographs (Fig. 2 and additional photographs); superimposed drawings show presumed orientation of animals as they made these trackways. Arrows indicate presumed current direction (see text). A, E, H, I: Alf Museum, collected at Seligman, Arizona. C: 9.2 km north-northeast of Ashfork, Arizona. B, D, F, G, and J: In situ trackways in Grand Canyon; B, F, J—Kaibab Trail; D—Hermit Trail; G—Grandview Trail. B = Figure 2C; F = Figure 2D; G (upper part) = Figure 2B; H (upper part) = Figure 2E (circled tracks); I = Figure 2G.

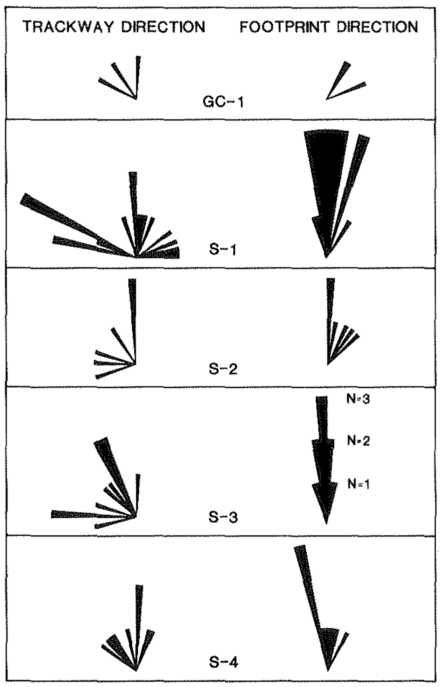

Figure 5. Rose diagrams comparing trackway orientation with orientation of individual prints for five slabs of Coconino Sandstone. GC-1 is in situ slab along Kaibab Trail; S-1 to S-4 are slabs in Alf Museum, all collected at Seligman, Arizona.

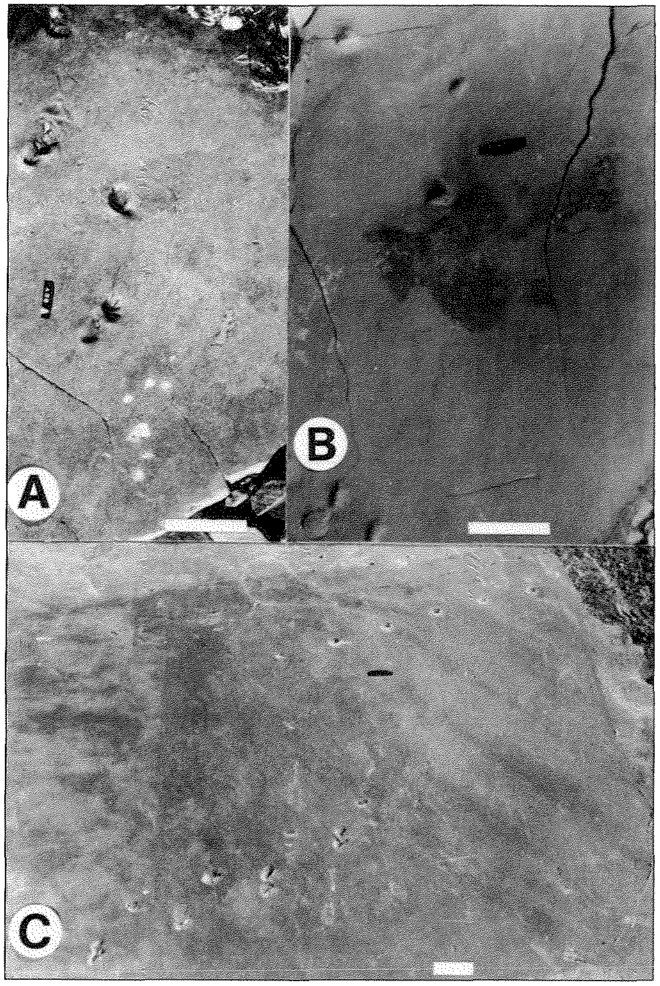

Figure 6. Coconino Sandstone trackways that begin and/or end abruptly. A: From quarry 14.7 km north of Ashfork. B: In situ, from Seligman. C: In situ, from 9.2 km north-northeast of Ashfork. Bar scales = 10 cm.

if the animal was in a medium that supported much of its weight, so that the front feet only lightly touched the substrate. The long scratches seen in some prints (Fig. 2, C and D; Fig. 4, B and F) also are similar to scratches made by live salamanders under water.

Fossil tracks that start or stop suddenly could result (1) from slumping or other sedimentary or erosional processes that have obliterated part of the trackway, making it appear to start or stop suddenly; or (2) from the animals walking on the bottom and abruptly being buoyed up by the current or simply swimming upward.

Fossil slump features in the Coconino Sandstone are sometimes associated with fossil footprints. However, the trackways in Figure 6 do not show any evidence of slumps or other disturbances that could have obliterated the missing parts of the trackways. These unusual trackways can be explained most readily by a depositional environment that allowed the tracks to be made underwater. Some irregular trackways appear to have been made in water by animals that touched the substrate only occasionally.

The best criteria for recognition of subaqueous trackways are any features that indicate buoyancy of the track maker in water (McAllister, 1989). The trackways described above, which are widely distributed in the Coconino Sandstone, are quite different from the tracks discussed by McAllister (1989), but they also show several features that are strong evidence of track-maker buoyancy. These features include trackways that drift sideways, trackways that start or stop abruptly, and irregular trackways in which a floating animal would have only occasionally touched the substrate. These data and other features of the trackways reported by Brand (1979) indicate that the fossil trackways do not lend support to the hypothesis of an eolian sand-dune origin, but rather they point to subaqueous deposition for at least part of the Coconino Sandstone.

REFERENCES CITED

Blakey, R.C., 1988, Superscoops: Their significance as elements of eolian architecture: Geology, v. 16, p. 483–487.

Brand, L.R., 1979, Field and laboratory studies on the Coconino Sandstone (Permian) vertebrate footprints and their paleoecological implications: Palaeogeography, Palaeoclimatology, Palaeocology, v. 28, p. 25–38.

Brookfield, M.E., and Ahlbrandt, T.S., eds., 1983, Eolian sediments and processes: Amsterdam, Elsevier, 660 p.

Hesp, P., and Fryberger, S.G., eds., 1988, Eolian sediments: Sedimentary Geology, v. 55, 184 p.

Kocurek, G., ed., 1988, Late Paleozoic and Mesozoic eolian deposits of the western interior of the United States: Sedimentary Geology, v. 56, 413 p.

Kocurek, G., and Dott, R.H., Jr., 1981, Distinctions and uses of stratification types in the interpretation of eolian sand: Journal of Sedimentary Petrology, v. 51, p. 579–595.

Lockley, M.G., and Rice, A., 1990, Did "*Brontosaurus*" ever swim out to sea?: Evidence from brontosaur and other dinosaur footprints: Ichnos, v. 1, p. 81–90.

Loope, D.B., 1984, Eolian origin of upper Paleozoic sandstones, southeastern Utah: Journal of Sedimentary Petrology, v. 54, p. 563–580.

McAllister, J.A., 1989, Dakota Formation tracks from Kansas: Implications for the recognition of tetrapod subaqueous traces, *in* Gillette, D.D., and Lockley, M.G., eds., Dinosaur tracks and traces: Cambridge, England, Cambridge University Press, p. 343–348.

McKee, E.D., 1933, The Coconino Sandstone—Its history and origin: Carnegie Institution of Washington Contributions in Paleontology No. 440, p. 77–115.

—— 1947, Experiments on the development of tracks in fine cross-bedded sand: Journal of Sedimentary Petrology, v. 17, p. 23–28.

—— ed., 1979, A study of global sand seas: U.S. Geological Survey Professional Paper 1052, 429 p.

McKeever, P.J., 1991, Trackway preservation in eolian sandstones from the Permian of Scotland: Geology, v. 19, p. 726–729.

Middleton, L.T., Elliott, D.K., and Morales, M., 1990, Coconino Sandstone, *in* Beus, S.S., and Morales, M., eds., Grand Canyon geology: New York, Oxford University Press, p. 183–202.

Sarjeant, W.A.S., 1988, Fossil vertebrate footprints: Geology Today, v. 4, no. 4, p. 125–130.

Spamer, E.E., 1984, Paleontology of the Grand Canyon of Arizona: 125 years of lessons and enigmas from the late Precambrian to the present: Mosasaur, v. 2, p. 45–128.

Vaughn, P.P., 1963, A downslope trackway in the DeChelly Sandstone, Permian of Monument Valley: Plateau, v. 36, p. 25–28.

Zar, J.H., 1984, Biostatistical analysis (second edition): Englewood Cliffs, New Jersey, Prentice-Hall, 718 p.

ACKNOWLEDGMENTS

Supported by a grant from the Geoscience Research Institute. We thank Art Chadwick and Adam Chilson for field assistance.

Manuscript received April 29, 1991
Revised manuscript received August 23, 1991
Manuscript accepted August 29, 1991

Reviewer's comment

Reinterprets a long-standing paradigm using a completely novel line of evidence.

Kevin Padian

Printed in U.S.A.