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Underprints of vertebrate and invertebrate trackways in the Permian Coconino Sandstone in Arizona

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The only fossils in the Permian Coconino Sandstone of northern Arizona are abundant fossil trackways. A slab of Coconino Sandstone contains underprints of both vertebrate and invertebrate animals, exposed at two levels separated by a 1–2 mm layer of sand. The underprints on the lower level are deeper and much more distinct than the same trackway exposed on the higher level. The tracks on the upper level were partly infilled by the fine sand, which does not contain clays or other material that could provide cohesiveness. The trackways on this upper level also appear to be underprints, but formed closer to the surface. Many other fossil trackways in the Coconino Sandstone are probably also underprints, since they closely resemble the documented underprints. The mechanics of underprint formation may also explain the origin of some tracks that are very deep, with steep sides that even overhang the front of the track.

Key Words: underprints, trace fossils, Coconino Sandstone, Permian.

INTRODUCTION

The cross-bedded Coconino Sandstone (Permian; Leonardian) is widespread in northern Arizona. The only fossils that have been found in this formation are vertebrate and invertebrate trackways. The vertebrate trackways have been variously interpreted as tracks of amphibians (Lull, 1918), or reptiles (Baird, cited in Spamer, 1984; Peabody, 1959). Other authors indicated uncertainty of their identity (Gilmore, 1926, 1927; McKee, 1947). Haubold (1971, 1974, 1984) classified the ichnogenus *Baropezia* as amphibian, and *Laoporus* (the most common trackways in the Coconino Sandstone) as caseid pelycosaur tracks.

It has been suggested (Lockley, 1989, 1991; Thulborn, 1990) that a large proportion of fossil tracks are actually underprints, produced when the shape of a footprint is pressed down into laminae below the surface that the animal walked on. In some contexts underprints may have a higher potential for preservation than the true prints on the sediment surface, because underprints are not subject to the reworking that can occur on the surface (Hitchcock, 1858; Lockley, 1987; Lockley and Rice, 1990). Underprints may also have a better chance for preservation than true prints if the surface sediment is not suitable for preservation of tracks (Lockley, 1991). In these situations underprints may be the only traces preserved. Similarly, where underprints are preserved below true tracks, the surface with true tracks may be eroded away before burial or after the sandstone is exposed to erosion. Lockley and Conrad (1989) suggested that trackways made in desert dunefield environments may have good preservation potential if they are impressed into "moist or well-laminated underlayers."

It has been observed by many authors (Hitchcock, 1858; Sarjeant, 1988; Allen, 1989; Lockley and Rice, 1990; Sundberg et al. 1990; Thulborn, 1990; Lockley, 1991) that underprints are generally less well defined than the true tracks, but there are exceptions to this (Lockley and Conrad, 1989, Fig. 14.2D; Thulborn, 1990). The varying characteristics of true tracks and underprints has the potential to contribute to taxonomic confusion. Padian and Olsen (1984a,b) emphasized that the actual features of a trackway are affected by the conditions of the substrate as well as by the anatomy of the foot and the kinematics of the limb. This paper presents the first documented evidence for underprints in the Permian Coconino Sandstone and compares their characteristics with other underprints.

THE UNDERPRINTS

Two matching slabs (part and counterpart) of Coconino Sandstone from Seligman, Arizona, bear intersecting trackways of an invertebrate and two tetrapods with well preserved underprints of both invertebrates and tetrapods (Fig. 1). The invertebrate and one tetrapod trackway are exposed on two levels, separated by a 1–2 mm thick layer of sandstone. The trackway traversing vertically through Figure 1A has parallel rows of multiple impressions (trackway width 4.5 cm) as is characteristic of arthropod trackways in Permian sandstones (Brady, 1947; Sadler, 1993). Individual prints are 2–2.5 mm deep on the lower

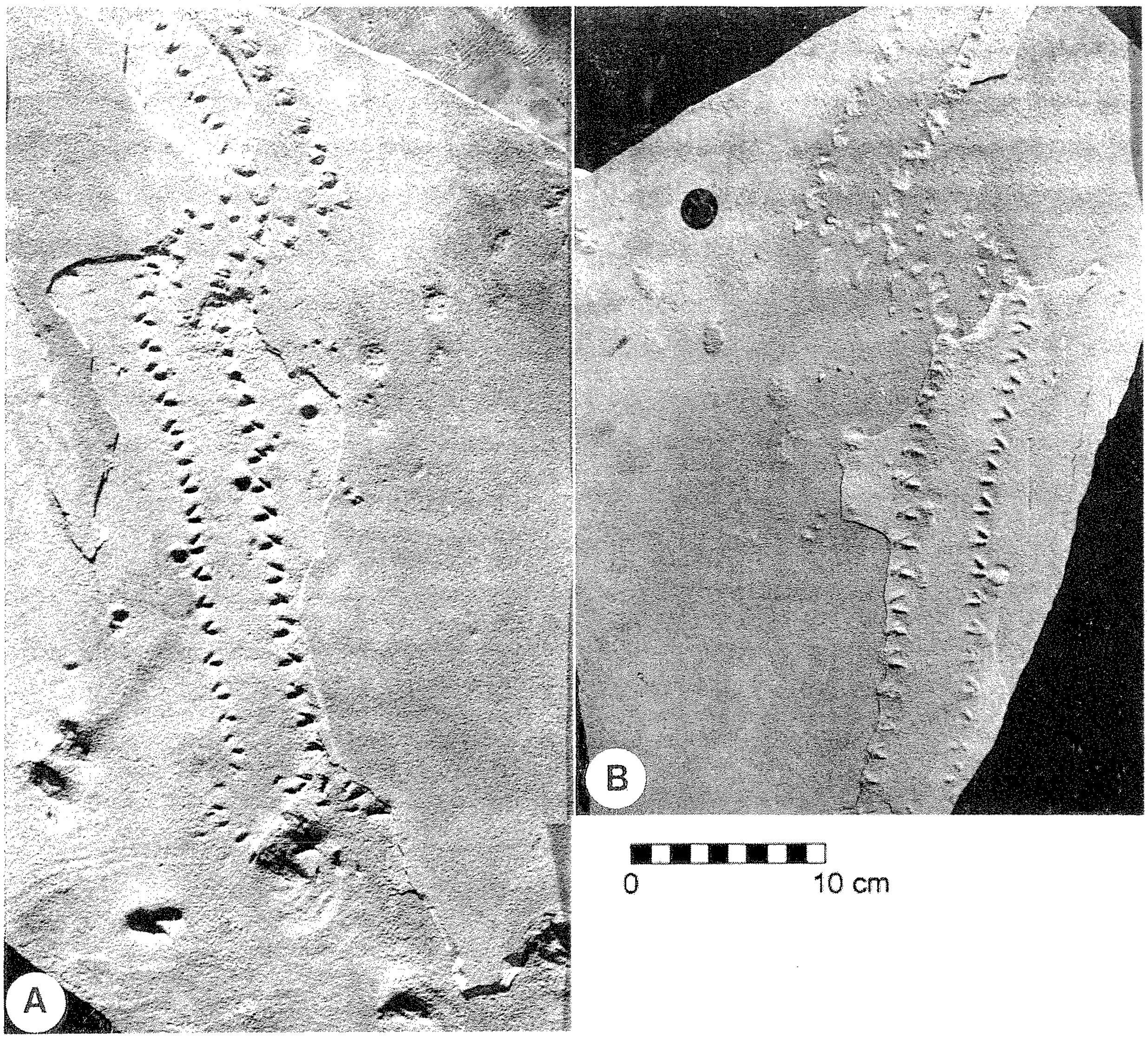

Fig. 1. (**A**) Fossil trackways showing trackways on the upper level and the more distinct underprints exposed on the lower level. (**B**) Natural mold of a part of the slab in A. From Seligman, Arizona. The bottom of these photographs is toward the upslope direction on the cross-bed surface.

level and 1 mm deep on the upper level. This trackway is currently being described elsewhere.

The other two trackways have the stride characteristics of tetrapods. The smaller of these trackways has a mean stride length of 4.53 cm, and looks like *Laoporus* (Haubold, 1984). Impressions of the left feet are visible at the right side of Figure 1A, but fade out toward the left lower end of the trackway. The tracks that can be best compared between the two levels are the right pes prints. They are 9 mm wide and 2–2.5 mm deep on the lower level and 10–13 mm wide and 1–1.5 mm deep on the upper level. The larger trackway at the bottom of Figure 1A has a stride length of 13.3 cm. It is only exposed on the lower level and the prints are 3–5 mm deep. It is not as well defined as the smaller tetrapod trackway, but it also appears to be *Laoporus*.

The underprints on the lower level (Fig. 1A) are very distinct, deep depressions with uniformly rounded edges, while the tracks on the upper level, which also appear to be underprints, are shallower and much less distinct. The evidence suggesting that the upper level of tracks is an upper level of underprints, rather than true surface tracks, is seen in a thin section (Fig. 2A) cut vertically through the invertebrate trackway just above the top of Figure 1B. Large sand grains have been pushed down through the upper level of tracks from the distinct layer of larger grains above this upper level. Splitting of the laminae, to expose the upper level visible in Figure 1 occurred 1.4 mm

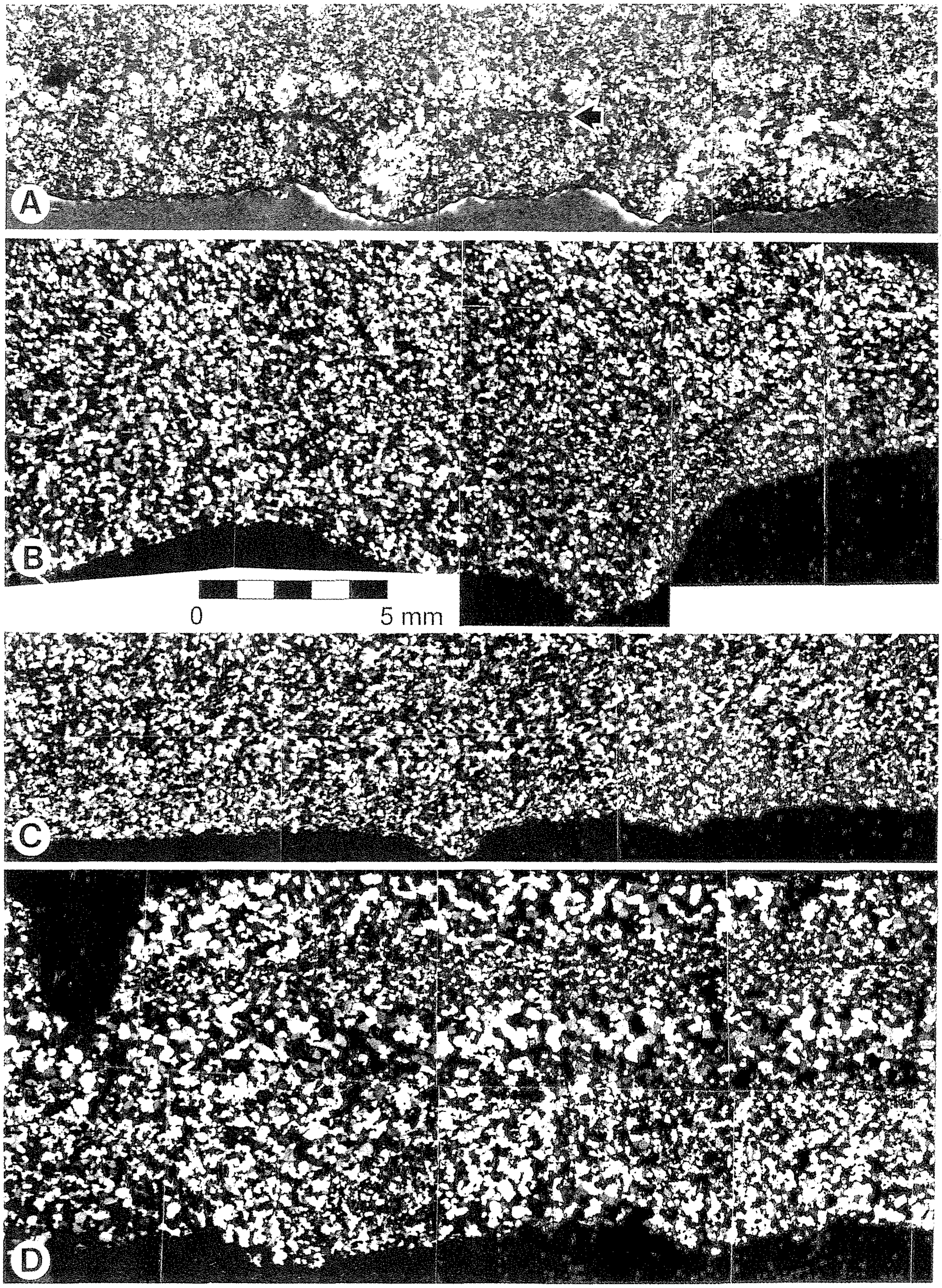

Fig. 2. Polarized light photographs of thin sections through natural molds of Coconino Sandstone trackways. (**A**) Two of the invertebrate underprints from Figure 1. Arrow marks the level of the surface of the upper layer in Figure 1A. (**B–D**) Vertebrate trackways. All from Seligman, Arizona, and all to the same scale.

below the top of this layer of large grains, at the dark line marked by an arrow in Figure 2A. If the layer of large grains had been deposited after the trackway was formed, the large grains would not have been pushed so far down into the tracks. Figure 3 illustrates the sequence of events suggested by the evidence in Figure 2A. The animal walked on the surface above the layer of large grains, pushing them down at least as far as the lower level of underprints which resulted from deformation of the sand laminae below the surface. As the legs were withdrawn, these large grains remained deep in the trackway. Infilling of the depression by sand decreased the clarity of the tracks close to the surface (the upper level), but did not affect deeper layers. There may have been only slight visible evidence of the trackway on the surface immediately after the trackway was made.

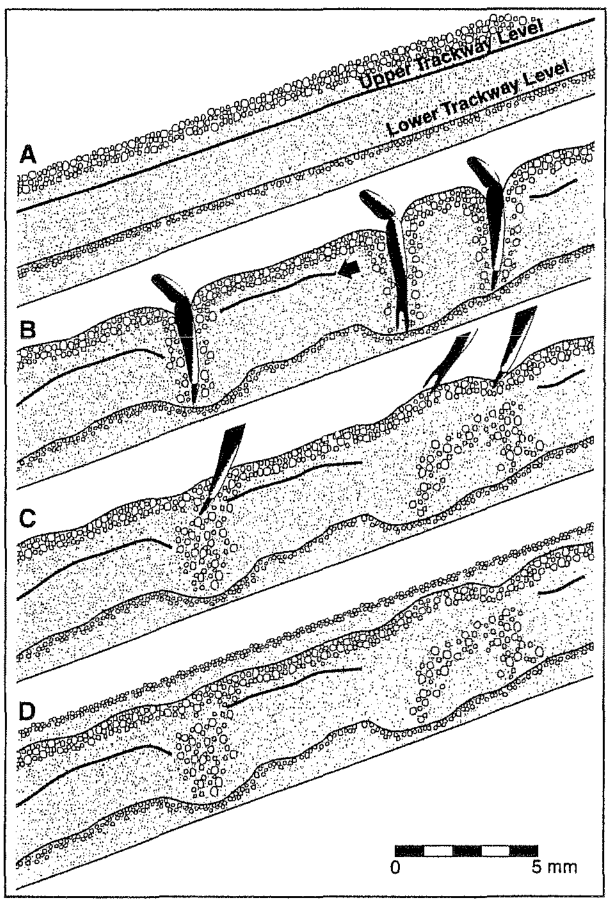

Fig. 3. An interpretation of the formation of the tracks in Figure 2A, oriented as it was on the sloping cross-bed surface. **(A)** Sand surface upon which the animal walked. **(B)** Arthropod legs enter the sand, pushing large surface sand grains down into lower layers, and deforming the sand laminae below the surface. Direction of animal movement was from left to right. **(C)** As the legs are removed the large grains fill the space where the legs were, and the surface depressions are partly filled. **(D)** The trackway is covered by more sand.

IMPLICATIONS FOR OTHER TRACKS

Comparison of this slab with other fossil trackways from the Coconino Sandstone suggests that a number of these other trackways may also be underprints. Evidence favoring this interpretation is the clarity and depth of the footprints and their uniformly rounded edges (Fig. 4A–C), compared with the shallower footprints with more diffuse margins that we have observed on fine sand in the laboratory (Brand, 1979) or on desert sand dunes. Thin sections of nine other Coconino Sandstone natural casts of fossil trackways were examined, to evaluate the usefulness of thin sections for detecting underprints. Some of these trackways appear to be underprints, based on the above criteria, but grain size differentiation (Fig. 2B,C) is not seen clearly as in Figure 2A. The evidence for underprints in Figure 2A is provided primarily by the layer of large sand grains fortuitously present and pushed downward. The tracks in Figure 2B and C were impressed into a fairly homogenous sand, without grain size differences that could indicate whether they were underprints. Grain size differentiation is evident in Figure 2D, but if these tracks are underprints, the true print level would apparently be below the layer of large sand grains across the middle of the picture, since there is no mixing of the large grains down into the lower layer. Thin sections are only helpful for identifying underprints if the sand is in layers with distinct grain-size differentiation. If these layers are not present, underprints can still be recognized if a trackway is exposed at two or more levels as in Figure 1.

If many of the trackways in the Coconino Sandstone are underprints this also suggests an explanation for some footprints that are so deep that the sand on the front edge of the track overhangs the footprint impression (Fig. 5). The Coconino Sandstone is composed of fine sand and

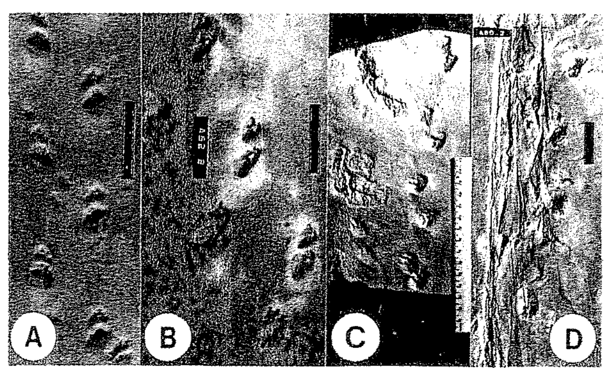

Fig. 4. **(A–C)** Coconino Sandstone trackways with surface detail suggesting that they are underprints. **(D)** A Coconino Sandstone trackway that appears to be a true print. Localities in Arizona: A, Seligman; B, Ashfork; C, Hermit Basin, Grand Canyon; D, Grandview Trail, Grand Canyon, traversing a slump feature. Bar = 5 cm.

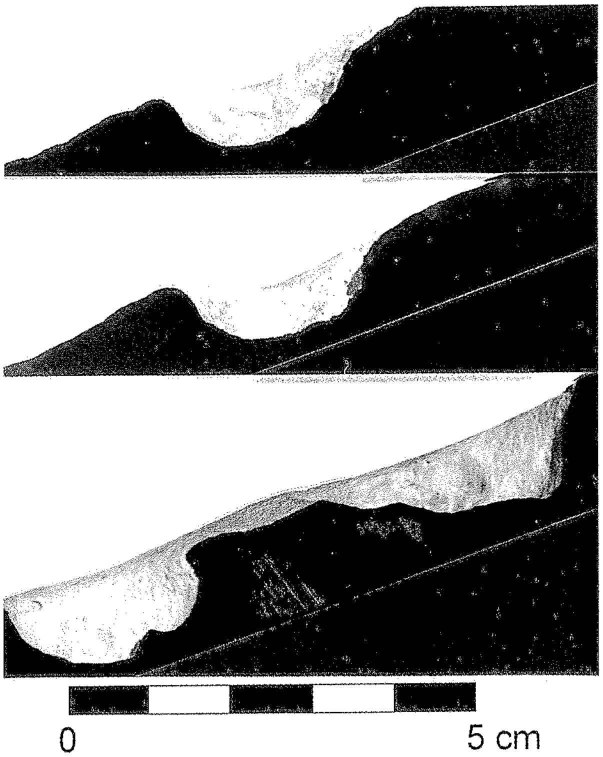

Fig. 5. Cross sections through unusually deep footprints from three tetrapod trackways in the Coconino Sandstone, from Seligman, Arizona.

generally does not show evidence of clays or other material that could provide the cohesion to retain such steep, even overhanging, surfaces. If these footprints are underprints, the deep, undercut impressions may have been preserved by the undisturbed continuity of the underlayers while the surface depressions were partly infilled by sand, as in Figure 3C.

CONCLUSIONS

A previous paper (Brand and Tang, 1991) concluded that the Coconino trackways were unlikely to be underprints because of the fine detail preserved in them. Data reported here indicate that, contrary to the usual situation in other types of sediments, underprints in pure, fine sand may contain more detail than the true tracks. A substrate, such as a mudflat, with an ideal consistency for preserving tracks produces true surface prints that are more distinct and detailed than the underprints. In contrast, when animals walk in non-cohesive, pure, fine sand, infilling of the sand at the surface can obliterate details in the surface tracks while these details are preserved in the underprints. Underprints close to the surface may also be lower in quality than those farther below the surface.

An alternate hypothesis for the data presented here should be considered. It could be proposed that the more distinct tracks are the true tracks, and the upper tracks are not as clearly defined because they are overprints, formed by layers of sand deposited after the tracks were formed. This hypothesis is refuted by the presence of the large sand grains pushed down to the lowest level of tracks in Figure 2A, indicating that the animal pushed its feet down to that level from above the layer of large grains. It is possible that some tracks in the Coconino Sandstone are overprints, but that does not seem to be an adequate explanation for the trackways discussed in this paper. It also is difficult to explain the deep tracks in Figure 5 if they are not underprints.

The Coconino Sandstone sometimes splits apart in thin sheets, but often it only breaks out as slabs several centimeters thick. As can be seen in thin sections, there may be several distinct, alternating layers of fine-grained and coarser-grained sand between two cleavage planes, even in a thin slab (Fig. 2D), indicating complex sedimentation not represented by modern exposed surfaces for each sediment layer. What type of trackway preservation is discovered will be determined by the sedimentary processes that produce cleavage planes, such as variations in grain size, shape, or alignment. These factors may be independent of the features of the original exposed surfaces on which the animals walked. Thus in this sandstone there may not be any reason to expect that the original exposed surface with true tracks is more likely to be found than underprints. Where trackways were made on clay drapes, such as some of the specimens studied by McKeever (1991), it is possible that the clay layers may control cleavage of the rock and produce a bias in favor of true tracks.

REFERENCES

Allen, J.R.L. 1989. Fossil vertebrate tracks and indenter mechanics. Journal of the Geological Society, London, 146:600–602.

Brady, L.F. 1947. Invertebrate tracks from the Coconino Sandstone of northern Arizona. Journal of Paleontology, 21:466–472.

Brand, L. 1979. Field and laboratory studies on the Coconino Sandstone (Permian) vertebrate footprints and their paleoecological implications. Paleogeography, Palaeoclimatology, Palaeoecology, 28: 25–38.

Brand, L.R., and Tang, T. 1991. Fossil vertebrate footprints in the Coconino Sandstone (Permian) of northern Arizona: evidence for underwater origin. Geology, 19:1201–1204.

Gilmore, C.W. 1926. Fossil footprints from the Grand Canyon. Smithsonian Miscellaneous Collections, v. 77, no. 9, p. 1–41.

Gilmore, C.W. 1927. Fossil footprints from the Grand Canyon: second contribution. Smithsonian Miscellaneous Collections, v. 80, no. 3, p. 1–78.

Haubold, H. 1971. Ichnia Amphibiorum et Reptiliorum fossilium. Handbuch der Paläoherpetologie, Teil 18, Gustav Fischer Verlag, Stuttgart, ix + 124 p.

Haubold, H. 1974. Die Fossilen Saurierfährten. Die Neue Brehm-Bücherei, A. Ziemsen Verlag, Wittenberg Lutherstadt, 168 p.

Haubold, H. 1984. Saurierfährten. Die Neue Brehm-Bücherei, A. Ziemsen Verlag, Wittenberg Lutherstadt, 232 p.

Hitchcock, E. 1858. A report on the sandstone of the Connecticut Valley, especially its fossil footmarks. W. White, Boston (reprinted by Arno Press 1974), p. 31–33.

Lockley, M.G. 1987. Dinosaur tracks symposium signals a renaissance in vertebrate ichnology. Paleobiology, 13:246–252.

Lockley, M.G. 1989. Summary and prospectus. *In* Gillette, D.D., and Lockley, M.G. (eds.), Dinosaur Tracks and Traces. Cambridge University Press, N.Y., p. 441–447.

Lockley, M.G. 1991. Tracking Dinosaurs. Cambridge University Press, N.Y., p. 23–29, 130, 138, 141.

Lockley, M.G., and Conrad, K. 1989. The paleoenvironmental context, preservation and paleoecological significance of dinosaur tracksites in the western USA. *In* Gillette, D.D., and Lockley, M.G. (eds.), Dinosaur Tracks and Traces. Cambridge University Press, N.Y., p. 121–134.

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

Lull, R.S. 1918. Fossil footprints from the Grand Canyon of the Colorado. American Journal of Science, 45:337–346.

McKee, E.D. 1947. Experiments on the development of tracks in fine cross-bedded sand. Journal of Sedimentary Petrology, 17:23–28.

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

Padian, K. and Olsen, P.E. 1984a. The fossil trackway Pteraichnus: not pterosaurian, but crocodilian. Journal of Paleontology, 58:178–184.

Padian, K., and Olsen, P.E. 1984b. Footprints of the Komodo Monitor and the trackways of fossil reptiles. Copeia, 1984, p. 662–671.

Peabody, F.E. 1959. Trackways of living and fossil salamanders. University of California Publications in Zoology, 63:1–71.

Sadler, C.J. 1993. Arthropod trace fossils from the Permian De Chelly Sandstone, northeastern Arizona. Journal of Paleontology, 67: 240–249.

Sarjeant, W.A.S. 1988. Fossil vertebrate footprints. Geology Today, 4: 125–130.

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

Sundberg, F.A., Bennington, J.B., Wizevich, M.C., and Bambach, R.K. 1990. Upper Carboniferous (Namurian) amphibian trackways from the Bluefield Formation, West Virginia, USA. Ichnos, 1:111–124.

Thulborn, T. 1990. Dinosaur Tracks. Chapman and Hall, N.Y., p. 24–28.