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FIELD AND LABORATORY STUDIES ON THE COCONINO SANDSTONE (PERMIAN) VERTEBRATE FOOTPRINTS AND THEIR PALEOECOLOGICAL IMPLICATIONS

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ABSTRACT

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The fossil footprints in the Coconino Sandstone have long been considered to be evidence for eolian deposition. I conducted field study of the fossil footprints in Hermit Basin, the Grand Canyon, and laboratory studies of modern amphibian and reptile footprints on dry sand, damp sand, wet sand, and underwater sand. Five species of salamanders all spent the majority of their locomotion time walking on the bottom, under water, rather than swimming. The experimental animals produced footprints under all test conditions, both up and down the 25° slopes of the laboratory "dunes". Toe marks and other details were present in over 80% of the fossil tracks, underwater tracks, and wet sand tracks, but less than 12% of the dry sand and damp sand tracks had any toe marks. Dry sand uphill tracks were usually just depressions, with no details. Wet sand tracks were quite different from the fossil tracks in certain features. The fossil tracks were most similar to the underwater tracks. These data suggest that the Coconino Sandstone fossil tracks should not be used as evidence for eolian deposition of dry sand.

INTRODUCTION

The fossil trackways in the Coconino Sandstone have long been of interest for their paleoecological significance. Matthes (1932) cited them as evidence of eolian deposition. McKee (1947) compared experimental trackways of living animals with the Coconino fossil tracks and also concluded that the tracks are evidence of eolian deposition of the Coconino Sandstone, in a desert environment. There has been considerable study of cross-bedded sandstones in recent years (Stokes, 1968; Marzolf, 1969; Dott and Batten, 1971; Stanley et al., 1971; Visher, 1971; Walker and Harms, 1972; Steidtmann 1974; and Freeman and Visher, 1975), and several authors (Reiche, 1938; Faul and Roberts, 1951; Vaughn, 1963; Walker and Harms, 1972; Sarjeant, 1975) have cited Matthes' (1932) conclusions and McKee's (1947) results as evidence of eolian deposition for some cross-bedded sandstones. I have conducted further field studies on the Coconino Sandstone trackways and laboratory experiments with the trackways of living animals, using a wider variety of experimental conditions than those used by McKee (1947).

METHODS

Fossil footprints in the Coconino Sandstone were studied at the Grand Canyon, in Hermit Basin. The Coconino Sandstone along the Hermit trail was searched for trackways, and 82 vertebrate trackways were located. Each trackway was given an identification number, notes were taken on the presence or absence of toe marks and sole impressions and on other physical features of the tracks, and most trackways were photographed. At each in-situ trackway location the directional heading of the trackways and the slope of the bedding plane was determined with a brunton compass. The study area was surveyed with a brunton compass and steel tape, and a map of the area was prepared.

Trackways of living amphibians and reptiles were studied in the laboratory, in two experimental chambers. One was a wooden box 2.44 m long, 0.61 m wide, 1.22 m high at one end and 0.61 m high at the other end; the other was a plexiglass tank 30.5 cm wide, 45.7 cm high, and 1.83 m long. Sand slopes were formed in these experimental chambers; the animals were then allowed to walk up and down the slope. Each of the 236 experimental trackways was given an identification number, the trackway was photographed, and notes were taken on condition of the sand, the slope of the sand surface, and physical features of the tracks.

Laboratory tracks were studied mostly on 25° slopes, with some observations on 15° and 20° slopes for comparison. Four experimental conditions were used: (1) dry sand (simulating a desert environment); (2) dry sand moistened with a fine spray of water (simulating desert sand moistened by dew or light rain); (3) underwater sand; and (4) wet sand, with standing water at the base of the slope (simulating sand near the water table). Just before each trial on wet sand, the surface was sprinkled until it was beginning to slump. Then the animal was immediately placed on the sand.

Three types of fine-grained sand were tried, but most laboratory trackways were made on sand collected near Mt. Carmel Junction, in southern Utah. This sand was apparently derived from the Navajo Sandstone that forms the surface topography in this area and was used because of its similarity to the sand grains in the Coconino Sandstone. The Coconino Sandstone is composed primarily of whitish, rounded grains, with over 50% fine grains (McKee, 1933). The sand collected from Mt. Carmel Junction is composed of reddish, rounded grains, with the following grain size distribution: silt, 2%; very fine sand, 29%; fine sand, 51%; medium sand, 18%; coarse sand 0.07%. The other two types of sand used were desert sand collected from dunes near Palm Springs, California, and fine-grained silica sand purchased from a sand and gravel company.

Table I lists the animals used in the laboratory studies. The underwater locomotion behaviour of salamanders was observed in the laboratory and in Tenaja Creek, in the Santa Rosa Mountains, Riverside County, California in

TABLE I

Animals used in the laboratory footprint experiments

	Number of individuals	$\bar{x}$ Snout-vent	
		$\bar{x}$ weight (g)	length (mm)
Salamanders			
Taricha torosa	23	10.5	72.3
Taricha granulosa	12	9.7	72.5
Notophthalmus viridescens	9	5.0	45.2
Ambystoma tigrinum	4	75.2	146.0
Cryptobranchus alleganiensis	1	495.0	380.0
Lizards			
Sauromalus obesus	2	159.8	154.0
Sceloporus occidentalis	5	13.8	73.7
Dipsosaurus dorsalis	3	51.0	124.0

March and April, 1975. The amount of time spent swimming or walking on the bottom (with no swimming movements of the tail) was recorded to the nearest second. Each individual was observed for 70 seconds of locomotion time, or until it disappeared from view or stopped moving for a considerable length of time. The lengths and widths of the footprints were measured to the nearest 0.5 mm from photographs, and the resulting data were analyzed for significant differences by use of the Mann-Whitney U Test (Siegel, 1956).

FOSSIL TRACKS

We found fossil trackways distributed through the lower half of the Coconino Sandstone (Fig.1). This distribution is similar to the observation of Gilmore (1927). Within the track-bearing section, trackways occurred on a large number of the exposed surfaces (Fig.2). The trackways were oriented primarily towards the northeast (Fig.3) and, as reported by Gilmore (1927), almost all were going up the slopes of the cross-bedded strata. One indistinct trackway appeared to be going downslope. The trackways occurred on strata with slopes of 21°—26°, with the following distribution: 4 strata at 21°, 3 at 22°, 8 at 23°, 6 at 24°, 3 at 25°, and 1 at 26° (not corrected for regional dip).

Previous work on footprints in the Coconino Sandstone has usually involved primarily the study of the best footprints in each taxon. In the present study the emphasis was not on taxonomic comparison, but on the

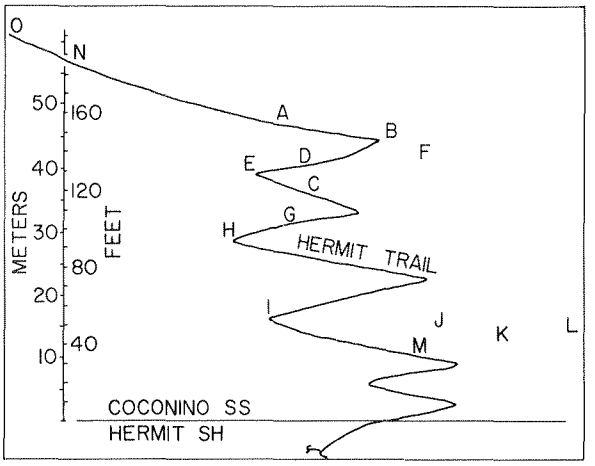

Fig.1. Vertical section through the lower part of the Coconino Sandstone in Hermit Basin, showing footprint locations *A*—*O*. The vertical and horizontal scale is the same.

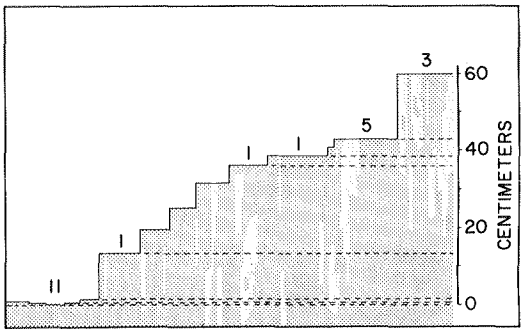

Fig.2. Vertical section through footprint location *A* (see Fig.1). The numbers indicate how many trackways were found on the exposed layers of sandstone.

physical characteristics of the entire population of trackways. The Hermit Basin tracks included some well-defined examples (Fig.4a), but the majority of the tracks were not as well defined or as complete (Fig.4f, g and h). In all trackways the individual footprints were distinct and separate from each other. Some tracks were composed only of toe marks, with no impression of the sole. Some were depressions with no toe marks or other details, and some included both sole impressions and toe marks. Some of the latter type of tracks were as long as they were wide (Fig.4a and c). Others had sole impressions that were short in relation to their width, and thus represent only that part of the sole immediately behind the toes (Fig.4f and i). Fig. 5 illustrates the percentage of trackways with toe marks and sole

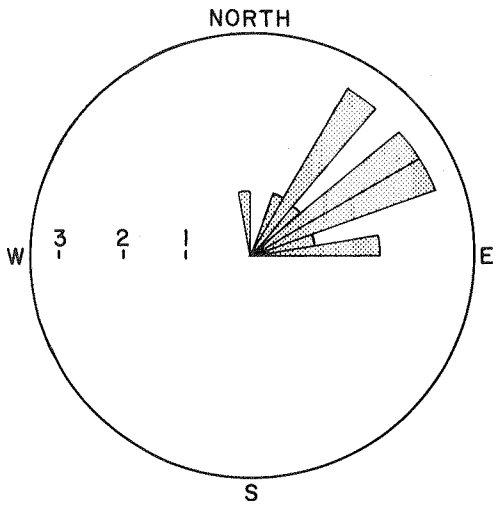

Fig.3. Directional orientation of all in-situ fossil trackways along the Hermit Trail. The length of the bars indicates the number of trackways in each 10° range.

impressions. Tracks with sole impressions sometimes had small ridges of sand pushed up behind them, but these never extended back into the tracks behind them.

One trackway (Fig.4a) was headed up the slope at about 50° to the right of the up-slope direction, but the toemarks on both manus and pes impressions were all pointed up-slope. Trackway 71j (Fig.4b and c) was apparently headed directly across the slope, but with toemarks of manus and pes pointed upslope. The slab also had a number of smaller tracks, all pointed up the slope. These tracks were on a loose slab, and the up-slope direction was deduced from the directional heading of the trackways.

LABORATORY UPHILL TRACKS

The laboratory tracks were not significantly different on the different types of sand we used. This agrees with McKee's earlier conclusions (McKee, 1947).

Dry sand tracks (Fig.6a—e) usually were a series of depressions with no toe marks or other details. There was usually a ridge of sand pushed up behind each footprint; often the sand in these ridges flowed back into the previous footprint. A few salamander trackways had toe marks at the back of each print; these marks were made as the foot was lifted out of the print. Also a few tracks had toe marks that were really marks of the toes being dragged across the sand, from one foot position to the next (Fig.6a and d). All of these were counted as toe marks in Fig.5.

Damp sand trackways always had definite foot impressions, distinct from

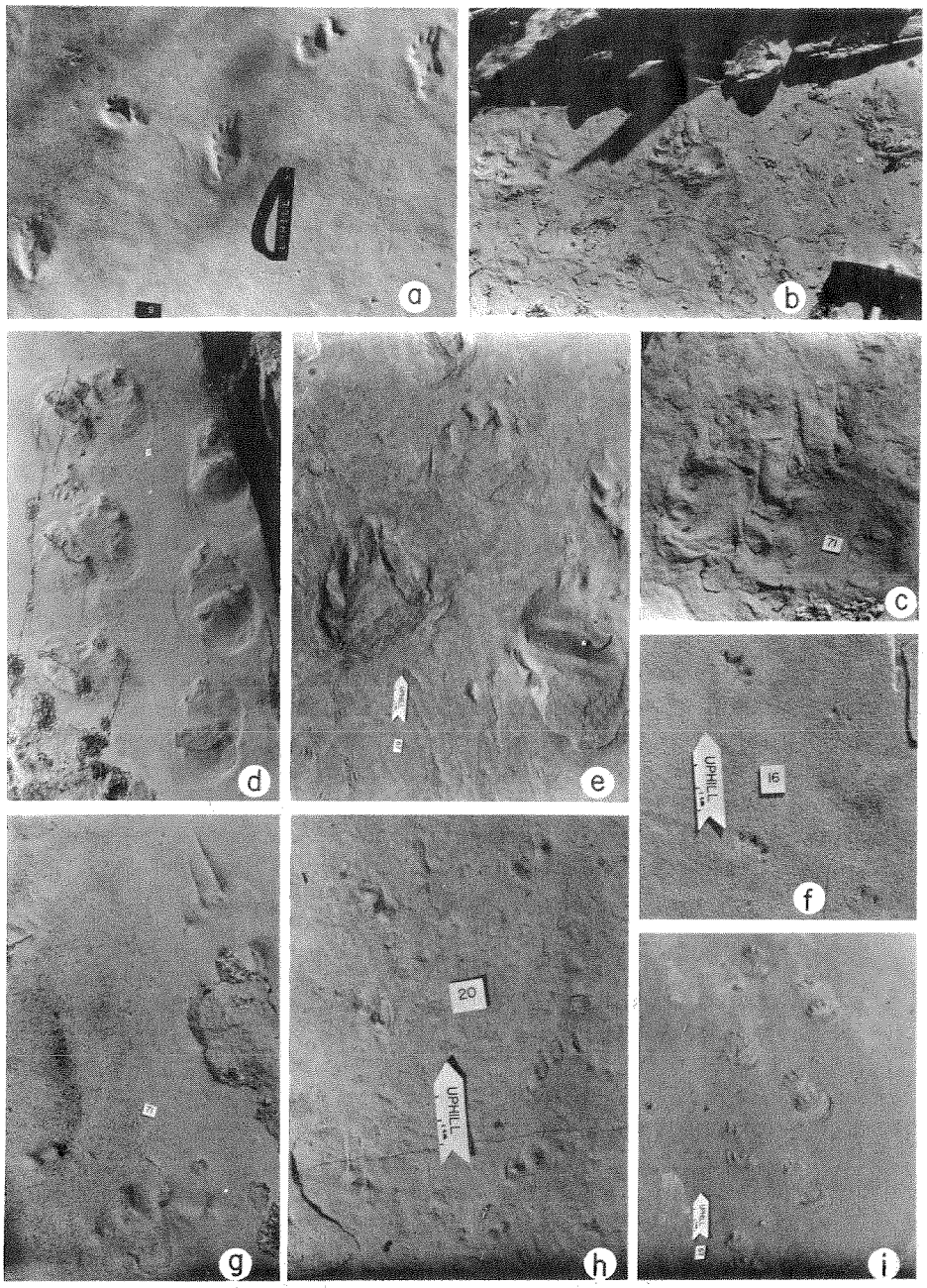

Fig.4. Fossil footprints in the Coconino Sandstone in Hermit Basin. Fig. c is an enlargement of part of b. The trackway in b and c is going across the slope; the others are uphill trackways. All numbers and letters in the photographs were 4.5 mm high.

each other, but toe marks were rarely present (Fig.5; Fig.6f—h). The wet crust on the surface of the sand broke up into many pieces which were sometimes pushed up into a pile at the back of the footprint; in other trackways they were scattered on the surface of the sand. If the damp crust of sand was thick enough so that it did not break up, the only tracks produced were a series of small dimples left by the toes.

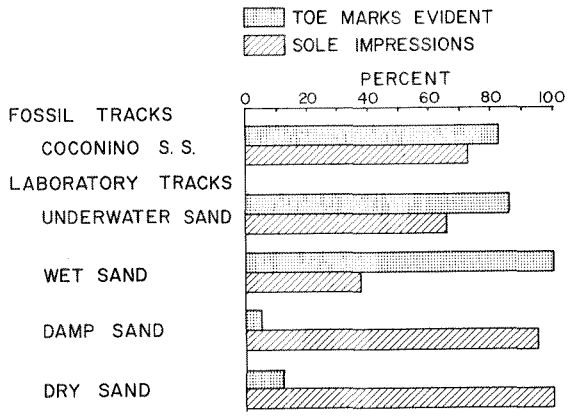

Fig.5. Percent of fossil footprints and laboratory footprints having evident toe marks and sole impressions.

TABLE II

Percent of total locomotion time spent in walking and swimming

Species	Number of animals	Number of trials	walking	swimming
Field observations				
Taricha torosa	30—40*	42	74.5%	25.5%
Laboratory observations				
Taricha torosa	12	20	68.4	31.6
Taricha granulosa	8*	20	51.3	48.7
Notophthalmus viridescens	10*	16	56.4	43.6
Ambystoma tigrinum	3	12	67.4	32.6
Cryptobranchus alleganiensis	1	12	60.0	40.0

* Estimated number

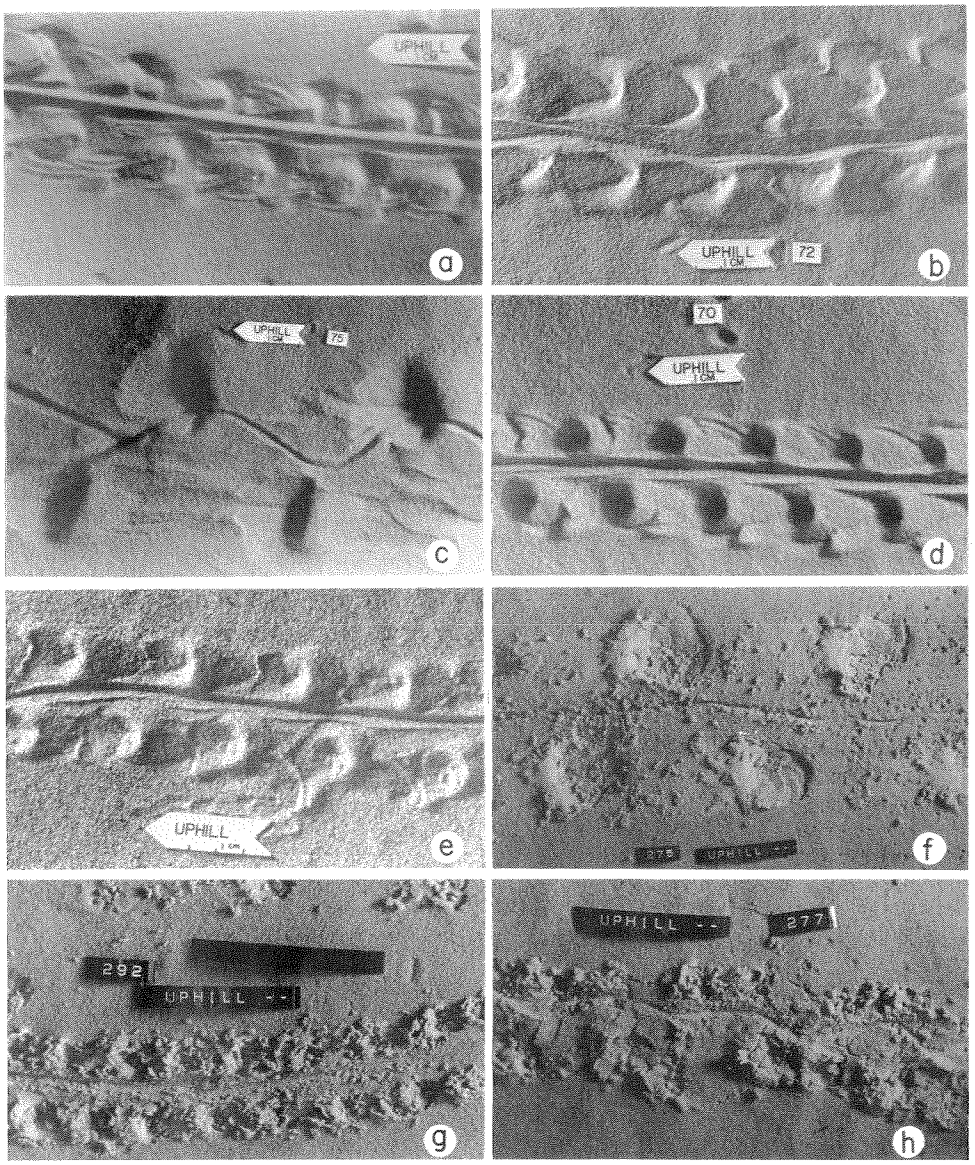

Fig.6. a—e. Uphill laboratory tracks on a 25° dry sand slope: c, *Sceloporus*; a, b, d, e, *Taricha*. f—h. Uphill laboratory tracks on a 25° damp sand slope: f, *Sceloporus*; g, h, *Taricha*.

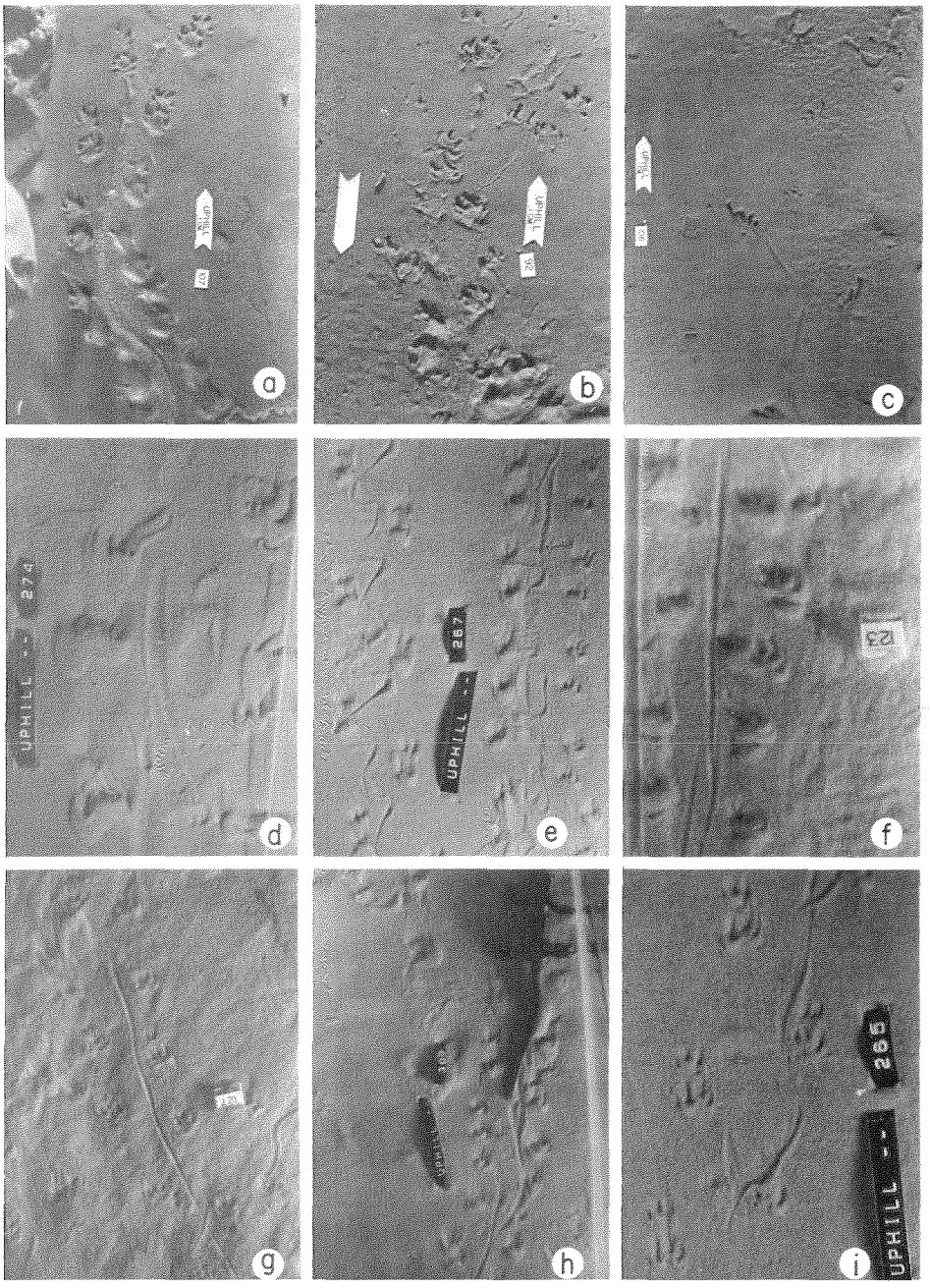

Fig.7. a—c. Uphill laboratory tracks on a 25° wet sand slope: a, b, *Ambystoma*; c, *Dipsosaurus*. d—i. Uphill underwater laboratory tracks on a 25° sand slope: d, *Ambystoma*; all others, *Taricha*.

Tracks in wet sand, above water, were quite variable (Fig.7a—c). The water seeps down through the sand quite rapidly, producing a gradient from highest water content at the base of the slope to lowest water content at the top of the slope. Footprints at the base of the slope were often sloppy and poorly defined, while those higher on the slope, on firmer sand, consisted of toe marks only. The tracks occurring between these two extremes all had toe marks, and some had impressions of all or part of the sole (Fig.5).

Table II summarizes the results of the underwater locomotion observations. All five species of salamanders spent more time walking than swimming. The substrate at the field study site was not suitable for producing footprints, but in the laboratory all five species produced tracks on the sand underwater (Fig.7d—i). These trackways were composed of distinct footprints, which usually had toe marks and sometimes had sole impressions also (Fig.5). Some prints had small ridges of sand pushed up behind them, but these ridges never extended back into the previous footprint.

Forty percent of the laboratory trackways included conspicuous tail drags, but very few of the Coconino fossil trackways have tail drags. The only laboratory tracks that rarely showed tail marks were underwater trackways of the hellbender, *Cryptobranchus alleganiensis*. The hellbender had a much shorter tail than the other animals that I used, and it usually did not drag its tail on the sand enough to leave noticeable tail marks.

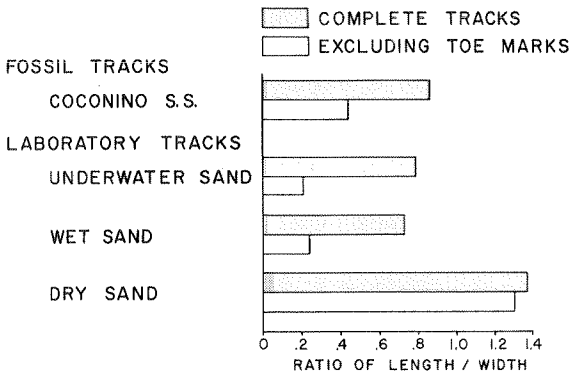

Fig.8. Length/width ratios of individual fossil and laboratory footprints.

Fig.8 compares the ratios of length to width for the fossil tracks and laboratory tracks. Dry sand tracks were longer than they were wide, whereas the fossil tracks, underwater tracks, and wet sand tracks were short in relation to their width. The difference between the fossil tracks (complete tracks) and the dry sand tracks was highly significant ($Z = 5.89$; $p < 0.00001$), but the fossil tracks and the underwater tracks were not significantly different ($Z = 0.07$; $p = 0.47$). The outlines of most of the damp

sand tracks were too poorly defined to allow precise measurements to be made.

DOWNHILL TRACKS

Under all four laboratory experimental conditions the animals produced downhill as well as uphill trackways (Fig.9a—f). On underwater sand, wet

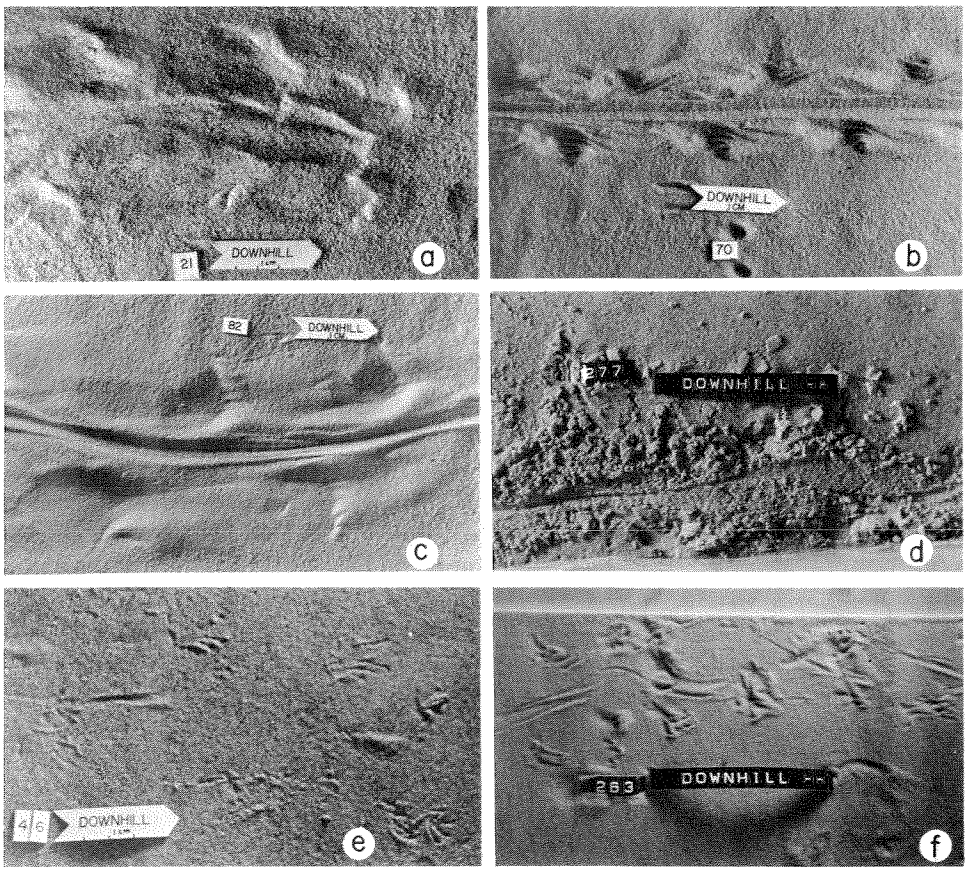

Fig.9. a—c. Downhill laboratory tracks on a 25° dry sand slope: a, *Sceloporus*; b, *Taricha*; c, *Dipsosaurus*. d. Downhill *Ambystoma* laboratory tracks on a 25° damp sand slope. e. Downhill *Sceloporus* laboratory tracks on a 25° wet sand slope. f. Downhill *Taricha* laboratory tracks on a 25° underwater sand slope.

sand, and damp sand almost all downhill trials produced easily recognized trackways, although they were often not as clearly defined as the uphill tracks. On dry sand salamanders walked slowly and produced downhill trackways that were usually reasonably well defined. Lizards produced

distinct downhill trackways on dry sand when they moved at a walking pace or a slow run, but if they were urged into running very fast, their tracks were almost unrecognizable.

DISCUSSION

McKee's (1947) photographs of dry sand and damp sand trackways look very similar to my results. From his experimental results on dry sand, damp sand, and wet sand, and a personal communication from Peabody indicating that salamanders do not make tracks underwater, McKee (1947) concluded that the fossil tracks were most similar to the dry sand trackways. McKee (1947) and others (Faul and Roberts, 1951; Vaughn, 1963; Walker and Harms, 1972; Sarjeant, 1975) have used McKee's data as evidence that the Coconino Sandstone and other cross-bedded sandstone formations were deposited in a desert environment.

Peabody (1959) stated that salamanders usually swim from place to place rather than walking on the bottom, and that when they do walk, they are partially buoyed up by the water and do not leave footprints. He did not indicate how extensive his observations on this phenomenon were. All five species used in my study walked on the bottom a larger percentage of the time than they swam in the water. When salamanders were placed in a laboratory tank, many of them swam vigorously along the surface, against the side of the tank, and tried to climb out. If the tank contained a sand bar or other object that provided a resting place at the water surface, the salamanders' behavior was more like that observed in the field. They would commonly rest on this object, then swim around under the water or walk on the bottom.

Dry sand and damp sand laboratory tracks differed from the Coconino Sandstone fossil tracks in several important features. Dry sand and damp sand tracks rarely had toe marks or other details, while the fossil tracks usually had definite toe marks. Dry sand tracks also differed from the fossil tracks in having larger ridges of sand behind them, which often flowed back all the way into the previous footprint. The jumbled pieces of damp sand crust around the damp sand tracks were never observed in the fossil tracks. Also, the proportions of the fossil tracks were quite different from the dry sand tracks but similar to the underwater sand and wet sand tracks. Consequently the damp sand and dry sand tracks observed in this study do not seem to provide an adequate explanation for the origin of the fossil tracks.

Many of the trackways on wet sand contained some footprints that were very similar to the fossil tracks, but several consistent characteristics of the wet sand tracks were not observed in the fossil tracks. The wet sand trackways almost always showed a definite transition from well-defined prints to toe marks only or almost no prints at all as they ascended the slope, as in Fig.7a. A number of the fossil tracks were several feet long; they were all quite uniform in structure for their full lengths, without the type of

transitions seen in laboratory wet sand trackways. Laboratory wet sand trackways that were made some distance above the water table, where the wet sand was more firm, consisted of small scratches or other marks from the individual toes, and were quite different from many of the fossil tracks.

The laboratory trackways most similar to the fossil tracks were those made underwater. Underwater trackways had toe marks as often as the fossil tracks and were uniform in appearance the full length of the sand slope, as the fossil tracks are. Also, the proportions of the fossil tracks were most similar to the proportions of the underwater tracks. The sole impressions in the underwater tracks tend to be short in comparison to their width. The animals are partially buoyed up by water, and they often push against the sand with their feet almost at right angles to the surface, rather than placing their feet flat on the surface. This produces tracks that usually have only toe marks or toe marks with a shortened sole impression — features that are also found in many of the fossil tracks.

The trackways (Fig. 4a—c) that were headed across the slope but with toes pointed upslope can perhaps be best explained by animals being pushed by a water current moving at an angle to the direction of their movement.

The hellbender, a short-tailed salamander, was the only animal used in this study that did not commonly make tail marks. Some of the known Permian amphibians were heavy-bodied, short-tailed animals. Perhaps this was at least part of the reason why the Coconino Sandstone tracks rarely have tail marks.

McKee suggested that the near-absence of downhill trackways resulted from the animals' tendency to slide downhill, causing their tracks to be obliterated by sliding sand. That explanation does not seem adequate. In my study, the downhill trackways were often not quite as well-defined as the uphill ones, but the majority of the downhill trackways, in all of the experimental conditions, were more distinct than many of the fossil tracks. If the fossil tracks were produced under water, the preponderance of uphill trackways could possibly be the result of some behavioral characteristic of the animals. For example, perhaps they tended to swim when going with the water current but to drop down and walk on the bottom when moving against the current. Of course behavioral traits of extinct animals cannot be tested, but this example merely illustrates that behavior can affect the tracks under water in ways that are not possible above water.

One objection that could be made to the data used in this paper is that many fossil trackways have been removed from the Hermit Basin and deposited in museums, and consequently I studied a biased sample. It is true that some of the trackways removed from the Hermit Basin were taken from the vicinity of the Hermit trail. However, in choosing specimens for museums, it is likely that some preference would be given to the better preserved tracks, which had toe marks and other details useful in classifying them into taxonomic groups. If these specimens had been included in my sample, it would only have increased, rather than decreased, the difference between the fossil tracks and the dry sand and damp sand tracks.

The data presented in this paper suggest that fossil footprints of the type found in the Coconino Sandstone should not be used as evidence for eolian deposition of dry sand. If the Coconino Sandstone was indeed an eolian desert deposit, then several important features of its fossil footprints are as yet unexplained.

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