Comment and Reply on "Fossil vertebrate footprints in the Coconino Sandstone (Permian) of northern Arizona: Evidence for underwater origin"

COMMENT

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Brand and Tang (1991) proposed that certain unusual vertebrate trackways "point to subaqueous deposition for at least part of the Coconino Sandstone." They supported their conclusions by demonstrating that western newts produce similar trackway configurations in aquarium experiments. While it is encouraging to see vertebrate ichnology play such a prominent role in fundamental questions concerning paleoenvironmental analysis, caution must be exercised when using trackways for radical reinterpretation of long-standing hypotheses (Lockley, 1991).

As reviewed by Walker and Middleton (1979), several authors suggested a subaqueous origin for the Jurassic Navajo Sandstone, traditionally regarded as a classic eolian deposit. The presence of tracks, fossil wood, and root zones was subsequently used to argue convincingly for the original interpretation of an eolian origin (Stokes, 1978). Loope (1984) presented similar evidence to argue for an eolian, not subaqueous, origin for the Permian Cedar Mesa Sandstone in eastern Utah. The interpretations of Brand and Tang therefore use vertebrate tracks to revive a controversial debate. The question becomes, Can the presence of footprints in a particular facies be used to suggest a subaerial origin while unusual trackway configurations in the same track assemblages are used to argue for subaqueous deposition? While Brand and Tang are to be congratulated for a thorough experimental study, which presents more Coconino track data than have appeared at any time since the inaugural studies of Gilmore (1926, 1927), several points warrant further comment.

The majority of trackways in question can be assigned to the ichnogenus *Laoporus*, which has usually been attributed to some type of synapsid (see Baird in Spamer, 1984; McKeever, 1991). Moreover, such tracks are common in other contemporary "eolian" deposits, including the Permian Cedar Mesa Sandstone (Loope, 1984, Fig. 7a), the De Chelly Sandstone, and at least four eolian formations in the Permian of the United Kingdom (McKeever, 1991, Table 1). This suggests that Brand and Tang have paid undue attention to the affinity of the track makers, no longer regarded as amphibians as some of the older literature suggests. Moreover they have also not considered the widespread distribution of *Laoporus*-like tracks in Permian deposits of Pangea, which Baird (in Spamer, 1984) considered a facies fauna, or ichnofauna, associated with erg settings. Put another way, we need to ask, Do newts make good analogs for comparison with synapsids that were evidently adapted to arid conditions?

Brand and Tang (1991) suggested that the unusual trackways, which include abrupt appearances and sideways progression across foresets, with toe impressions pointing upslope, can only be explained by postulating buoyant animals in water and are not configurations related to underprints, or the result of slumps or known eolian sedimentary processes. This list of "unacceptable" interpretations leaves out one important category: unusual, or nonwalking, gaits. In their Figures 2G and 4T, Brand and Tang (1991) illustrated a trackway that progressed upslope, then sideways and slightly downslope, then up again (see Monastersky, 1991, p. 5, for enlargement of this illustration, showing what appears to be a small slump leading down from one of the tracks). We need to consider simple explanations that take into account the fact that the trackways change direction and configuration (of manus-pes placements) while still maintaining quite regular patterns not attributable to normal walking progression. Perhaps, quite simply, the *Laoporus* track maker, a habitual dunefield visitor or dweller, was adept at walking sideways or sidling across dune faces with variable gaits. In fact, the trackways illustrated by Brand and Tang (1991, Fig. 4, E–H) are highly reminiscent of various galloping, loping, and jumping gaits, and commonly show the familiar group-intergroup spacing described from mammal trackways by many modern trackers (Murie,

1974; Triggs, 1984, Figs. 3–4; Halfpenny, 1986). In such situations, where animals lope obliquely to one side, individual footprints are *not* oriented in the direction of the trackway. By bringing these unusual gaits to our attention, Brand and Tang have done us a service because they have shown us that the *Laoporus* track maker was evidently an agile animal capable of rapid progression. Indeed, it may be that these are the first convincing reports of various "running" (trotting, loping, galloping) gaits ever reported on the basis of Paleozoic trackways.

Although it *is* frequently claimed that well-preserved trackways are oriented only upslope (McKee, 1944), this is not true, as Brand and Tang and others (Leonardi and Godoy, 1980) have demonstrated for several contour-parallel and oblique trackways. It is also probable that the track makers periodically triggered slip-face avalanches. This would require them to quickly adjust their forward progression and walk, trot, lope, or jump sideways or obliquely for short bursts. If they adjusted their progression on shifting substrates that were underlain by moist underlayers, all manner of irregular trackways could result. Perhaps this explanation is unnecessarily complex also, and we should simply infer that the majority of tracks were made on dune faces that were cohesive as the result of recent wetting, by dew or precipitation, or as the result of accumulation of fine silt drapes. In such situations the track makers would have found firm footing when ascending, and would have left crisp tracks, unlike those observed when animals traverse dry unconsolidated substrates. Indeed, it might be that rapid progression was possible only on such substrates, and that on dry substrates attempts at running uphill would have an excessive energy cost and lead to running in place!

Often geologists are inclined to read complex behavioral interpretations into trackway evidence and to adjust paleoenvironmental models to fit these interpretations. I suggest that the behavioral interpretation is simpler and that the Coconino Sandstone was deposited under eolian conditions, as most geologists have inferred in the past.

COMMENT

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Brand and Tang (1991) offered a dramatic reinterpretation of the origin of vertebrate trackways in the Permian Coconino Sandstone of northern Arizona. On the basis of comparisons of the fossil trackways to tracks made by animals in controlled laboratory experiments, they claimed that the ancient tracks were made not by animals walking on eolian dunes, but, instead, under water by animals drifting sideways in water flows that were at least several metres deep. I find the arguments for an eolian depositional setting for the Coconino to be compelling; my comments here, however, are restricted to the evidence regarding the subaqueous origin of the trackways. My purpose is to introduce an untested alternative hypothesis for some of the unusual features of the trackways that requires no water and is, unlike the Brand-Tang hypothesis, consistent with sedimentological and stratigraphic evidence.

Although the Brand-Tang hypothesis calls upon "sideways drift" of the trackmakers to explain some of the oddities of the Coconino trackways, in doing so it leaves two of the dominant attributes of the "sideways" parts of the trackways unexplained. Locomotion by tetrapods requires a rigidly ordered sequence of precise movements. These movements leave behind a very ordered pattern on the substrate: (1) the stride distance has a characteristic length that is the same for both front (manus) and rear (pes) tracks, and (2) the track of the pes is very commonly near (or is superimposed upon) that of the manus, leading to the formation of paired tracks. The stride distance remains fixed for nearly all of the Permian trackways illustrated by Brand and Tang (1991), including the "sideways" parts. Paired tracks are also present in the parts of the ancient

trackways attributed to lateral drift. My claim is that the Coconino trackways are much too ordered to be explained by the Brand-Tang hypothesis. Animals adrift in fluid flows seem unlikely to repeatedly create such a distinctive pattern.

I interpret all of the pairs of Coconino tracks illustrated by Brand and Tang (1991) as manus-pes couplets; Brand and Tang (1991) viewed many fo these pairs—those in the "sideways" parts of the trackways—as manus-manus or pes-pes. My interpretation of the trackway shown in Brand and Tang's (1991) Figure 4E is that the pairs of smaller, less distinct tracks are those of the manus and pes on the *upslope* side of the trackway; the slope caused rotation of the animal's entire body, shifting the bulk of the weight to the downslope appendages, which left deeper, larger, better preserved, paired impressions. In some trackways (Brand and Tang, Fig. 4, C, D and G), only the impressions of the downslope appendages are recorded; the shallow, upslope tracks were lost to wind erosion.

Fine details are preserved within most of the Coconino tracks, and Brand and Tang (1991) must be correct that these traces cannot be under-tracks (deformations that form below a track). As seen in cross-sectional views of tracks, however, the impression of the foot is emplaced *below* the general depositional surface (see Loope, 1986, Fig. 4a; Allen, 1989, Fig. 1a). The preserved detail in the Coconino tracks does not, therefore, preclude the possibility that many of the tracks are partially eroded. Tracks emplaced to only shallow depths could be totally erased by erosive events that remove only the upper, near-vertical, parts of deeper tracks. My hypothesis requires erasure of some tracks and good preservation of others within the same trackway; careful experimental efforts to erode tracks of different depths in loose sand should be useful in testing this possibility.

The common types of strata in eolian deposits differ in regard to their packing (Hunter, 1977). These differences control the depth of tracks: animals and vehicles (see Bagnold, 1941) sink much deeper into loosely packed grainflow and grainfall sands than into the tighter wind-ripple deposits. Packing (or bulk density) of the sediment substrate should be considered in field and laboratory observations of tracks.

Although their interpretation is based on several lines of evidence, Brand and Tang (1991) placed special emphasis on the high angle between the orientation of the digits and the direction that the animal was moving. I admit my hypothesis lacks a compelling explanation for the puzzling orientation of the digits, but I suggest it may be related to the animals' attempts to move obliquely up or traverse across steeply sloping sand surfaces. Taking into account the effects of compaction, the Permian animals made tracks on surfaces that sloped at 25°–30°. Rather than call upon a dense fluid to carry the animals sideways, I hypothesize that the steepness of the slope caused the animals to systematically place their feet so that the digits were oriented upslope. Brand and Tang (1991) noted that whenever the animals walked directly up the slope, normal trackways (with digits oriented parallel to the direction of movement) were produced. *They explained all movement that is not directly upslope as due to current drift.* Did the animals never *walk* obliquely upslope or along slope? This apparent absence of "normal" trackways that are oblique or perpendicular to depositional dip supports my contention that all parts of all of the trackways were produced by walking (nondrifting) animals and that the unusual placement of the digits is a slope-related (not current-related) phenomenon. In this light, I interpret the remarkable zigzagging trackway in Brand and Tang's (1991) Figure 2A as the walking trail of an animal that systematically moved in a switchback pattern up the slope (rather than as the result of the animal being swept back and forth across the sloping surface by reversing currents).

The steepness of the slope could also explain the unusual all-in-a-row arrangement of tracks in the trackway shown in Brand and Tang's Figures 2D and 4F. Note that, as in the other trackways, the stride distance is the same for all appendages. By changing the placement of one foot (the right manus) in Sarjeant's (1975) Figure 14.4 relative to the other three, the arrangement of tracks becomes similar to that in Brand and Tang's (1991)

Figures 2D and 4F. Here, again, further experiments or field observations of animals are called for.

Brand and Tang used 8 cm/s flows in their experiments; with slightly higher flow velocity (~20 cm/s), they would have produced distinctive physical sedimentary structures with high preservation potential—current ripples. Although thousands of square metres of Coconino bedding planes have been closely perused and photographed in the process of studying these spectacular trackways, no current ripples have been reported from the Coconino Sandstone. On the other hand, several sedimentologists (Loope, 1984; Middleton et al., 1990), using the criteria provided by Hunter (1977), have claimed that lamination produced by the migration and climb of wind ripples makes up a large percentage, if not the bulk, of the formation.

Brand and Tang (1991) have brought some very puzzling aspects of these spectacular trace fossils to the attention of a broad audience. In my view, all hypotheses regarding the origin of the Coconino trackways (including my own) will be unconvincing until (1) the resemblance of the overall pattern of tracks to that of "normal" (walking) trackways is explained; (2) more is known about the trackways made by animals obliquely ascending or traversing steeply sloping surfaces underlain by sands of varying packing densities; and (3) information from biogenic structures is combined with evidence based on physical sedimentary structures and facies associations. Although I strongly disagree with Brand and Tang's conclusion, I find their experimental approach very useful, and hope to incorporate it in the testing of my own hypothesis.

REPLY

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Lockley suggests that we "have paid undue attention to the affinity of the track makers," which are no longer regarded as amphibians, but as synapsids. In our paper we stated that our work "does not indicate whether the track makers were amphibians or reptiles. . . ." The relation between toe-print orientation and movement direction shows common features in amphibians, reptiles, and mammals, and in our experiments we used whatever modern tetrapods were capable of underwater locomotion. The issue is not whether the tracks in the Coconino Sandstone were made by amphibians or reptiles, since some reptiles can also walk underwater. If we had had access to a supply of live Galápagos marine iguanas, which feed on the ocean floor (Eibl-Eibesfeldt, 1984), they also would probably have made good experimental subjects. Perhaps there were aquatic Per-

mian reptiles as well. Our focus was on mechanics of locomotion, not systematic affinities of the track makers.

Some recent research (Brand, 1991) comparing modern tracks made on various substrate conditions indicates that tracks made on cross-beds are particularly unsuitable for identifying the track makers, because the tracks do not accurately reflect the true foot structure of the animal. Thus, I am not convinced that we know what type of animals made the Coconino *Laoporus* tracks.

The principal point that both Lockley and Loope address is that there may be an alternative explanation for the distinctive features of the tracks. They both suggest that instead of the tracks having been made underwater, they were made on desert dunes, and the unusual tracks were normal methods of locomotion of these animals on the faces of dunes. They present different perspectives on essentially the same model. They suggest that the tracks are like the galloping, loping, and jumping gaits of modern mammals (Lockley); that in some cases the track makers moved in a switchback pattern up the dunes (Loope); and that because of the steep slope the animals placed their feet so that the digits were oriented upslope (Loope). Loope also suggests that all the pairs of tracks are manus-pes couplets instead of some being manus-manus or pes-pes as we have concluded.

The first issue that must be clarified involves details of the orientation of the toes. Enlargements (Fig. 1 here) of parts of the trackways from Brand and Tang (1991) show that the upslope orientation of the toes is more consistent and remarkable than may have been evident in Figure 2 of the 1991 paper.

Lockley is correct in stating that "in such situations where animals lope obliquely to one side, individual footprints are *not* oriented in the direction of the trackway." However, this loping obliquely, which is especially common in the dog family (Halfpenny, 1986), involves only a small angle of displacement from the trackway direction (Fig. 2A here). The animal shifts its body slightly to one side, apparently as one way to prevent its back feet from interfering with its front feet. This contrasts strongly with the sharply oblique angles involved in many of the *Laoporus* tracks (Fig. 2, B and C).

The greatest challenge faced by the Lockley and Loope models is to demonstrate that the locomotion mechanics necessary to account for those fossil tracks are possible. It is easy to say that "the steepness of the slope caused the animals to systematically place their feet so that the digits were oriented upslope" (Loope), but to evaluate that statement we must consider what it would take for the animal to accomplish that. One approach would be for the animal to be walking sideways with its toes pointing upslope. Without a current of water to drift it sideways it would have to stretch its left feet far to the left (to the left in Fig. 2, B or C) to the next
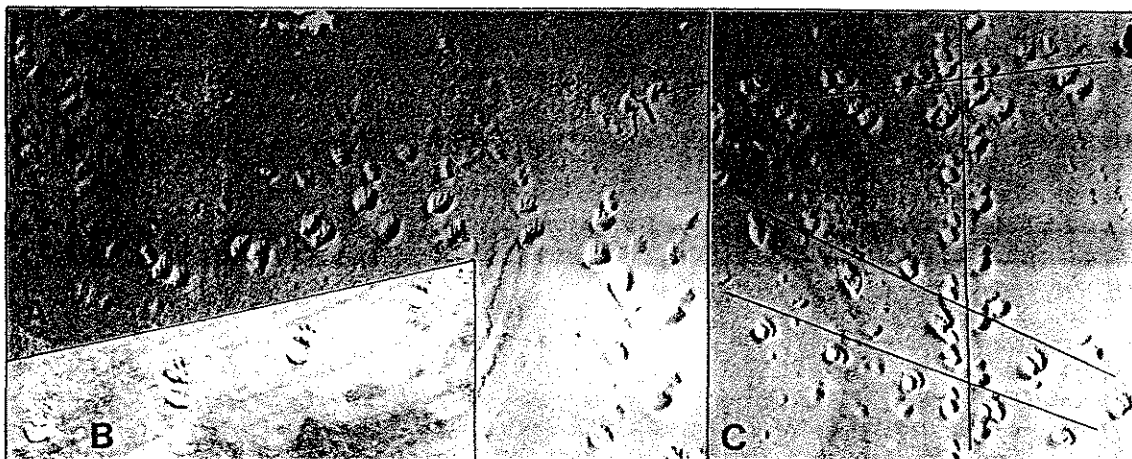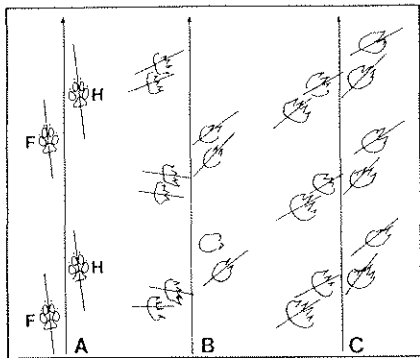

Figure 1. Fossil tracks, Coconino Sandstone. A: Part of Figures 2G and 4I of Brand and Tang (1991). B: Part of Figure 2B of Brand and Tang (1991). C: Lower central part of Figure 2A of Brand and Tang (1991) with lines drawn through axis of principal trackways.

Figure 2. Diagrams of trackways with lines indicating direction of trackway and of each print. A: Tracks of obliquely trotting dog; F = front foot; H = hind foot. B and C: Fossil trackways from Coconino Sandstone, traced from photographs.
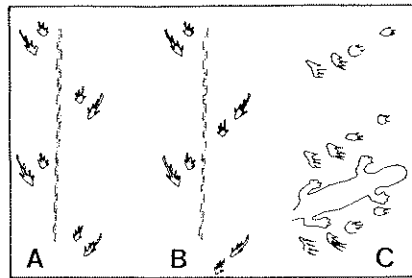

Figure 3. A: Fossil reptile trackway redrawn from Sarjeant (1975, Fig. 14.4). B: Same trackway, modified as suggested by Loope. C: Fossil trackway from Coconino Sandstone, as in Figure 2D and 4F of Brand and Tang (1991), but reversed so orientation will match that in B.

print position, then bring its right feet up under its body, then reach again with the left, sort of like a sideways inchworm. Since that does not seem probable, consider another option, that the animal walks obliquely across the dunes (straight up in Fig. 2, B or C), while twisting its legs so that all four feet point to the right, at nearly right angles to its body. The problems with these options become acute if we accept Lockley's suggestion that these tracks represent rapid progression comparable to mammalian trotting, loping, or galloping, as it would be analogous to a man running down the basketball court with his legs twisted so his feet are both pointing to the right. Or perhaps we would need to consider other possibilities that have *also* never been observed in modern vertebrates, such as progression by a continuous series of sideways leaps. Do we find any Permian tetrapods with unique limb structures that would warrant hypothesizing bizarre locomotion patterns? We cannot propose novel locomotion schemes without considering what they would do to bones, ligaments, and joints.

The oblique tracks of trotting mammals are instructive in another way. In those tracks the hind prints are all on one side, and the front prints are on the other side of the trackway (Fig. 2A), because of the angle of the animal's body (Halfpenny, 1986). If the animal's body were angled more sharply to the side, the hind prints would all be shifted farther to the side of the front prints. Normal locomotion in that position out of water would be improbable, but if, e.g., the animal were being drifted sideways in water the resulting tracks would be just like the interpretations in Brand and Tang (1991, Fig. 4), with the tracks arranged in pes-pes and manus-manus couplets rather than the usual manus-pes couplets as interpreted by Loope.

Loope suggests that the sideways tracks have a stride length and footprint pattern that is too consistent for animals being drifted by a water current. These very consistent patterns are one of the more challenging aspects of the underwater hypothesis, but it is not clear that they could not occur, if the water current velocities are low and fairly consistent. In the laboratory observations of subaqueous newts, the animals continued their normal walking pace while drifting sideways. The result was a consistent stride length evident in almost all of the pes prints (Brand and Tang, 1991, Fig. 3), whereas the manus prints were somewhat more variable. The pes pattern indicates that a consistent stride is not unexpected in a drifting animal, and how closely the manus prints follow that pattern will likely depend on the behavior of the specific animal and how it responds to being drifted off course.

Loope also suggests that "by changing the placement of one foot (the right manus) in Sarjeant's (1975) Figure 14.4 relative to the other three, the arrangement of tracks becomes similar to that in Brand and Tang's (1991) Figures 2D and 4F." That is clearly not correct. If the right manus in Sarjeant's Figure 14.4 (Fig. 3A here) is moved, it will indeed make four prints in a row (Fig. 3B), but the directional headings of the toe marks are not at right angles to the direction of movement of the animal, as they are in the fossil track in question (Fig. 3C). The tracks in Figure 3, B and C imply totally different locomotion processes.

Loope suggests that the tracks are less distinct or absent on the upslope side of some of the Coconino trackways because the upslope tracks were more shallow and were removed by wind erosion, whereas the downslope tracks were deep enough to be only partially eroded. This is a possibility to consider. However, if that had occurred, it seems unlikely that the well-defined ridges pushed up behind many of these tracks would be preserved (Fig. 1).

Neither Lockley nor Loope has offered an alternate explanation for the clear, deep trackways that abruptly appear and/or disappear with no evidence of slumping or other disturbance to explain the missing parts. These still seem best explained as tracks made underwater, where the animals can swim up into the water column.

The locomotion hypothesized by Lockley and Loope does not, as far as I am aware, occur in modern vertebrates, whereas my hypothesis is supported by observations of living animals. At this point the burden of proof is on them, to demonstrate experimentally that their hypothesis is realistic, preferably using modern animals with limb structure as similar as possible to that of the Permian tetrapods.

The tracks seem to be best explained by the analogue of a subaqueous environment, whereas the sedimentologists who work with the Coconino and other similar sandstones are convinced that desert eolian dunes are the best analogue for those sandstones. Finding the solution to this impasse will require continued study of both sides of the problem. In using the present to interpret the past, if none of the analogues that have been studied so far seems to fit all of our data, either we haven't found quite the correct analogue or our understanding of the already studied analogues is not yet adequate. In either case, the seeming incompatibilities in our data simply remind us that there are more discoveries ahead.

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