Aquatic Behavior and Locomotion of Archosauriform Reptiles Interpreted From Early-Middle Triassic Swim Tracks of the Western United States

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Abstract

Subaqueous tetrapod footmarks and traceways attributed to archosauriform reptiles are present in coastal and fluvial Early-Middle Triassic red beds of the Red Peaks Formation of Wyoming, Moenkopi (Torrey Member) and Ankareh (Mahogany Mbr) formations of Utah, and Moenkopi Formation of Arizona (Wupatki Mbr) and New Mexico (Anton Chico Mbr). Footmarks are composed of one, two, or three elongated digit marks preserved in convex hyporelief. One locality in the Moenkopi Formation at Capitol Reef National Park, Utah, exposes two offset traceways containing sequences of 19 and 13 footmarks, respectively. Re-alignment of these offset traceways reveals alternating pace lengths (9-30 cm), fairly consistent strides (39 cm), a front interpace distance (59 cm) significantly wider than the rear (41 cm), consistent pace angulations for front (33°) and rear (43°) footmarks, and high pes divarication angles alternating between 62° and 83°. Footmark positions are consistent with a swimming locomotion characterized by synchronized thrusts of the right and left limbs, respectively, followed by a pause before repetition. Because resistance of the substrate to a full arc of the limb results in posteriorly oriented digits retracting anteriorly to produce posterior overhangs, these overhangs and kick-off scours provide conclusive determination of traceway direction. Swim track surfaces also preserve current crescents that align subequally with traceway directions, demonstrating that the tracemaker swam against the current. Preservation of both manus and pes footmarks shows that all four limbs were used in propulsion. Small interdigit spacing suggests the digits were held together while swimming as opposed to spread at acute angles, like extant crocodylians. Single digit reflectures ("z-traces") have been interpreted as the tracemaker's attempt to maintain grip on the substrate by double kicking at the limit of limb extension. My analysis suggests this z-trace morphology and its behavioral implications are unique to these Early-Middle Triassic footmarks, suggesting that these early archosauriforms swam differently from those recorded by later Mesozoic traces.

Introduction

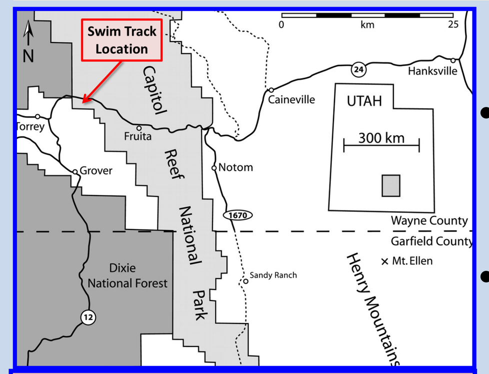


Figure 1: Map showing swim track locality in Capitol Reef National Park, Utah.

- Early-Middle Triassic (Induan to Anisian) red bed deposits from western North America (Moenkopi and Red Peak formations) contain an abundance of tetrapod body and ichnofossils (Lull, 1942; Branson, 1947; Peabody, 1948).
- Body fossil assemblages reported from the Moenkopi are dominated by temnospondyl amphibians with rare archosauriform reptiles and therapsid synapsids (mammal-relatives) (Morales, 1987).
- In contrast, the vertebrate ichnofossil assemblage is dominated by reptile tracks (e.g., *Chirotherium*); and therapsid and amphibian traces are rare (Peabody, 1948).
- Subaqueous tetrapod footmarks and traceways (swim tracks) have been recorded from several members of the Moenkopi Formation (Torrey [McAllister & Kirby, 1998], Lower Red [Mickelson et. al., 2006], Wupatki [Kirby, 1987], and Anton Chico Members [Lucas et al., 2003]), the Ankareh Formation (Mahogany Member [this study]), and the upper Red Peak Formation of Wyoming (Boyd & Loope, 1984).
- One locality in the Moenkopi Fm at Capitol Reef National Park, Utah (**Figure 1**) exposes two offset subaqueous traceways composed of 19 and 13 morphologically variable footmarks (**Figure 2**)
- Due to the paucity of reptile body fossils in the Moenkopi Fm, swim tracks have the great potential for determining the aquatic behavior and swimming locomotion of archosauriform reptiles.

Swim Track Description

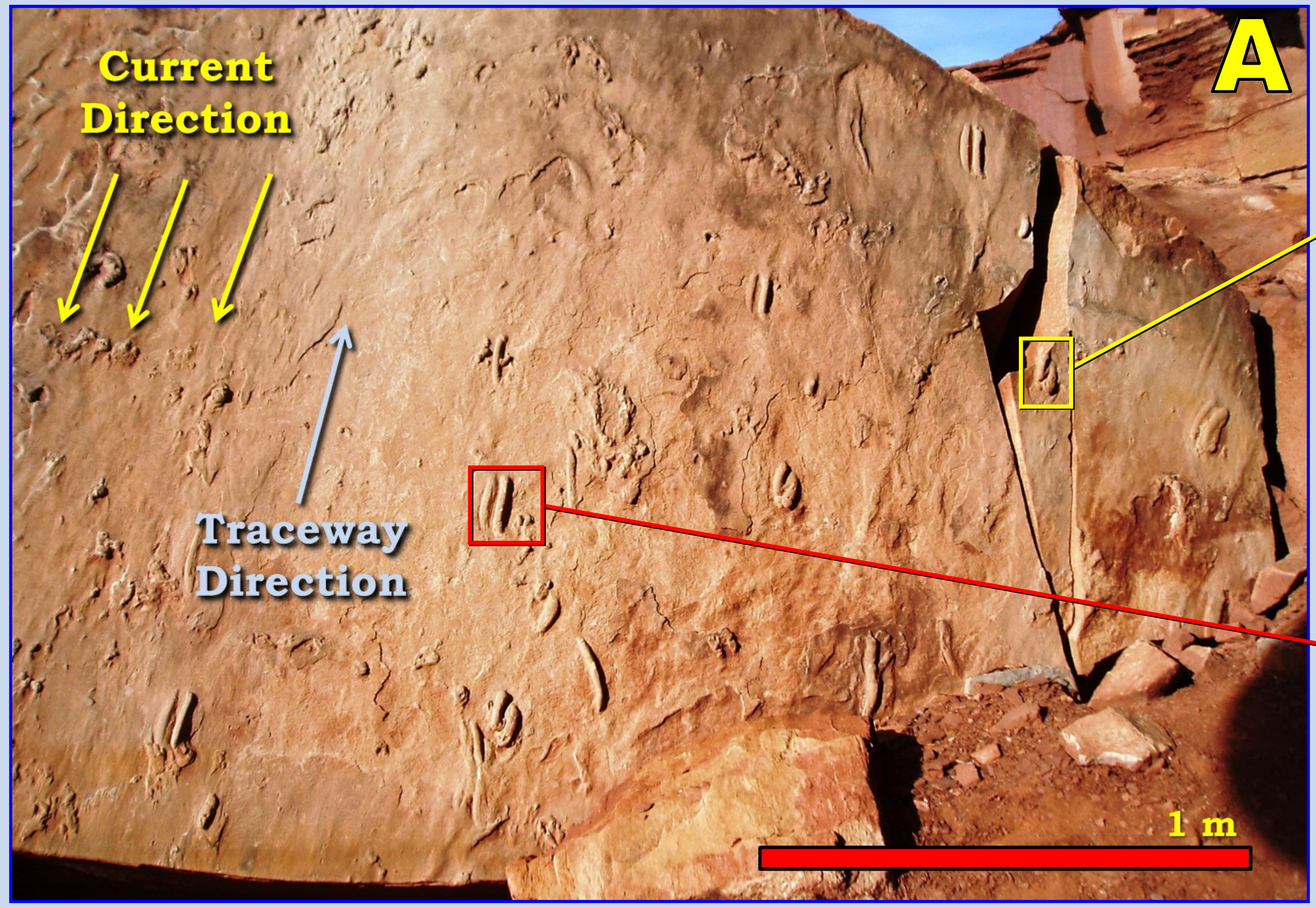
- Surfaces that preserve swim tracks also preserve current crescents with horns indicating the direction of paleocurrent flow along that surface (Peabody, 1947; **Figure 3; Figure 4**).
- Individual footmarks are composed of one, two, or three digit marks preserved in convex hyporelief (**Figure 2**).
- Digit marks one and three are commonly smaller than digit mark two.
- Interdigit spacing is small, commonly half the digit width or less.
- Well preserved footmarks display thin longitudinal striations (**Figure 5**).
- The following two types of footmarks in a traceway can be distinguished:
  - <u>Type 1</u> – Smaller digit widths, shallower footmark impressions, lesser number of preserved digit marks (usually only one or two), higher degree of footmark arc (**Figure 6**).
  - <u>Type 2</u> – Larger digit widths, deeper footmark impressions, larger number of preserved digit marks (usually three), lesser degree of footmark arc (**Figure 7**).
- The posterior margins of individual footmarks are characterized by kick-off scours (**Figure 7**), distinct margins (**Figure 5**), or posterior overhangs (**Figure 8**).
- Single digit reflectures ("z-traces") are a common footmark type (**Figure 8**) and sometimes constitute an entire half of a continuous traceway (**Figure 2A**).
- Z-traces are preserved at a large number of swim track localities (Boyd & Loope, 1984; Kirby, 1987) and are not described from later Mesozoic swim track sites (McAllister, 1989; Whyte and Romano, 2001; Milner et. Al., 2006).

Figure 3 (right): Current crescents (arrows) on traceway surface indicating paleocurrent direction.

Figure 6 (right): Type 1 manus footmark Scale bar = 5 cm

Figure 5 (left): Footmark with thin striations and distinct posterior margin (arrow). Scale bar = 5 cm

Figure 7 (right): Type 2 pes footmark with kick-off scour (arrow). Scale bar = 5 cm



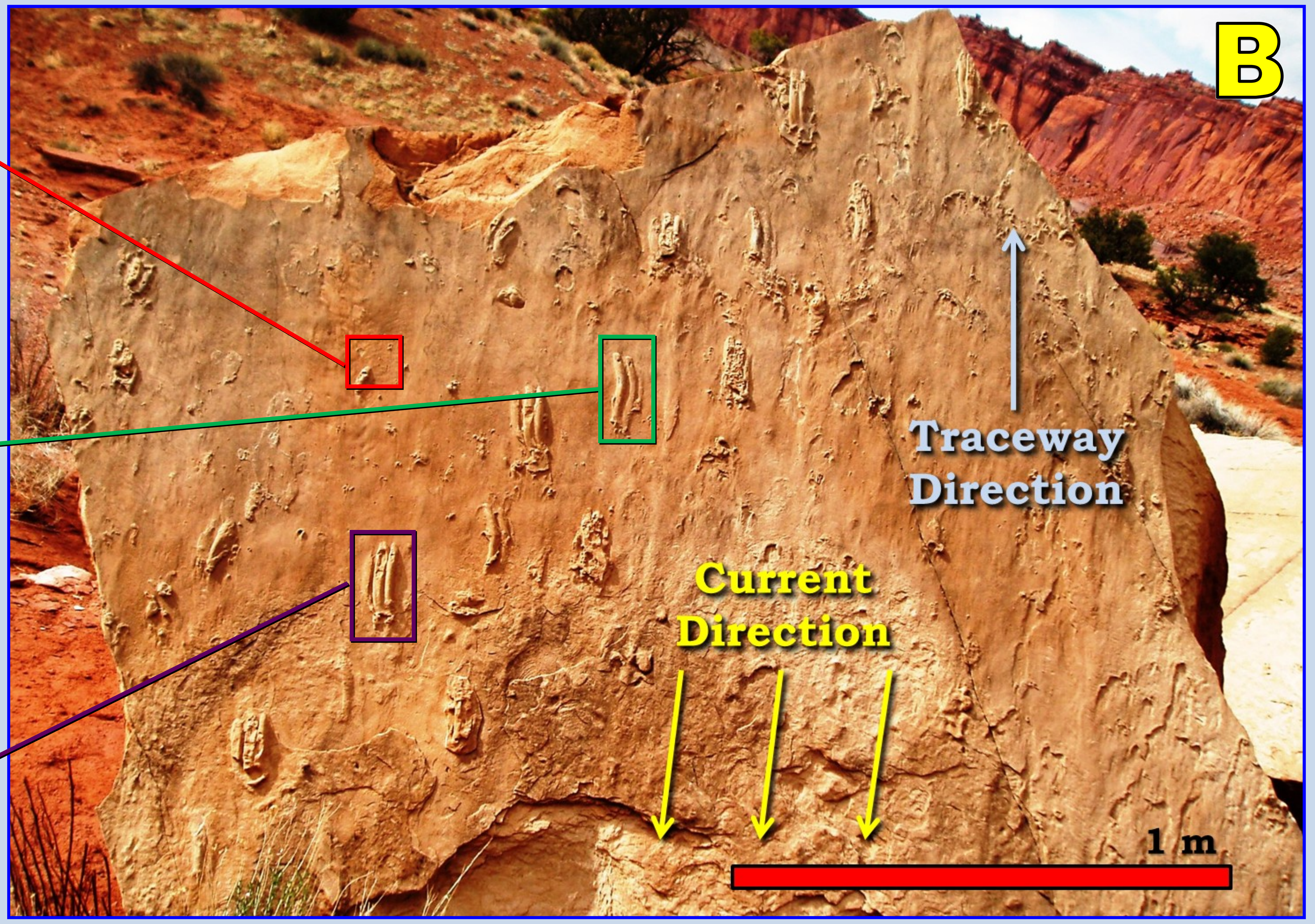


Figure 2: Offset swim traceway surfaces in Capitol Reef National Park; Surface A (13 footmarks) and Surface B (19 footmarks).
Surface A (above) Current direction determined from current crescents, traceway direction determined from footmark posterior overhangs. Z-traces.
Surface B (below) Current direction determined from current crescents, traceway direction determined from footmark kick-off scours. Manus and pes footmarks.

Figure 8 (above): Single digit reflecture (z-trace) with posterior overhang (arrow). Scale bar = 5 cm

Figure 4 (above): Current crescent (arrow) next to a two-digit footmark. Scale bar = 5 cm

Re-alignment of Offset Traceway

- The two types of footmarks in a swim traceway can be assigned to manus and pes limbs as well as to left and right sides based on the following:
  - <u>Type 1 = manus</u> (**Figure 6**) – Smaller digit widths, shallower impressions, and a lesser number of preserved digit marks result from a smaller, shorter, weaker forelimb which is unable to penetrate the substrate as effectively as the hindlimb.
  - <u>Type 2 = pes</u> (**Figure 7**) – Larger digit widths, deeper impressions, and a larger number of preserved digit marks result from a larger, longer, stronger hindlimb which is able to penetrate the substrate more effectively than the forelimb.
- Footmark arcs produced by limb motion point away from the body and therefore distinguish left from right (concave left = right, concave right = left) in both forelimb and hindlimb footmarks.
- Offset swim traceways must be re-aligned through the following steps before useful geometric relationships between footmarks can be described:
  1) Assignment of individual footmarks to manus and pes limbs based on footmark types (**Figure 9**).
  2) Determination of traceway direction through identification of posterior footmark features (posterior overhangs and kick-off scours). Traceway direction will be opposite the posterior margins (*sensu* McAllister, 1989; McAllister & Kirby, 1998) (**Figure 9**).
  3) Drawing tracklines through footmarks parallel to traceway direction (**Figure 9**).
  4) Shifting each footmark along a trajectory perpendicular to traceway direction until all footmarks fall into their respective tracklines (**Figure 10**).
- A significant amount of offset is removed using this process so that useful descriptions of the traceway can be made using the same geometric measurements that describe fully terrestrial tetrapod trackways (**Figure 11**).

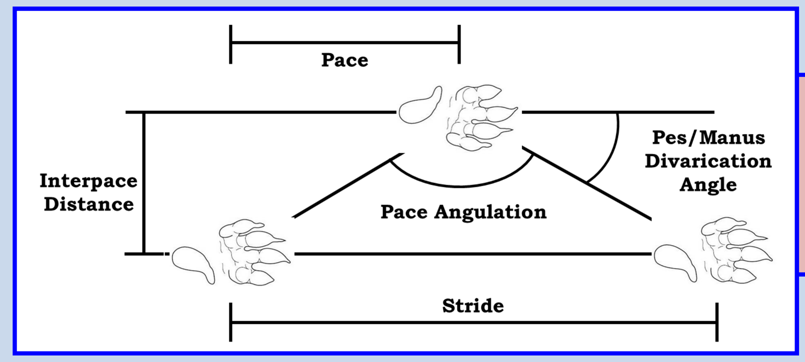


Figure 11 (left): Geometric measurements describing a fully terrestrial trackway (ex. *Chirotherium*) which include interpace distance, pace, stride, pace angulation, and pes/manus divarication angle (*sensu* Peabody, 1948).

Swimming Locomotion and Behavior

- Longitudinal striations on footmarks are produced by claw imperfections or a scaly skin texture sliding through the substrate.
- Small interdigit spacing suggests the digits were held close together while swimming, as opposed to spread out at acute angles like extant crocodylians.
- Preservation of both manus and pes footmarks shows that all four limbs were used for propulsion.
- At nearly all locations where traceway and paleocurrent directions can be determined the preferred swim direction of the tracemaker is nearly opposite to current flow.
- Footmark positions in a re-aligned traceway reveal the following geometric configurations (**Figure 12**):
  - -Alternating pace lengths averaging 9 and 30 cm
  - -Fairly consistent strides averaging 39 cm
  - -Front interpace distance of 59 cm
  - -Rear interpace distance of 41 cm
  - -Front pace angulations averaging 33°
  - -Rear pace angulations averaging 43°
  - -Pes/Manus divarication angles alternating from 62°-83°
- Z-traces are interpreted as a single digit disrupting the substrate twice in a double pumping action by a nearly buoyant tracemaker attempting to regain grip on the bottom (Boyd & Loope, 1984).

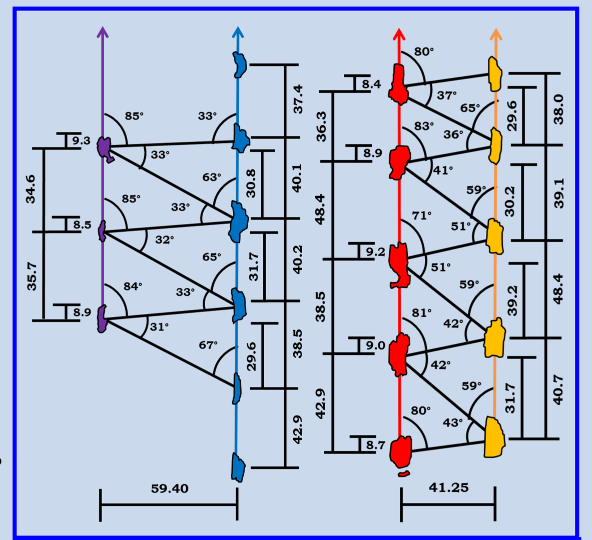


Figure 12 (right): Measurements for a re-aligned swim traceway showing descriptive geometric configurations.
Dimensions in degrees and centimeters.

Conclusions

- Preserved evidence for claws or scaly skin on certain footmarks supports the hypothesis that these swim tracks were produced by reptiles as opposed to temnospondyl amphibians.
- A significant amount of offset in a swim traceway can be removed, thereby allowing useful and descriptive measurements to be taken.
- The following conclusions about the swimming behavior of the trackmaker can be made from footmark morphologies and a re-aligned traceway from Capitol Reef National Park:
  - -Digits were held close together while swimming, unlike extant crocodylians.
  - -Current crescents and posterior overhangs indicate a consistent swim direction opposite to current flow.
  - -Double pumping to regain grip on the bottom ("z-traces").
  - -Preservation of both manus and pes footmarks shows that all four limbs were used in propulsion.
  - -Footmark positions in a re-aligned traceway are consistent with a swimming locomotion characterized by synchronized thrusts of the right and left limbs, respectively, followed by a pause before repetition.
- Z-trace morphology is preserved at a large number of swim track localities in the Moenkopi Fm and its behavioral implications are unique to these Early-Middle Triassic footmarks.
- Apparent absence of z-trace morphologies from Jurassic and Cretaceous swim tracks suggest that these early archosauriforms swam differently from those recorded by later Mesozoic traces.
- Swim tracks comprise and significant portion of the comprehensive vertebrate ichnofossil assemblage of the Moenkopi Fm and as such they provide crucial information about the presence and aquatic behaviors of basal archosauriforms in Early-Middle Triassic ecosystems where body fossils may be lacking.

Figure 9 (below): Re-alignment of offset traceway.
Step 1) Assignment of footmarks to manus and pes, left and right
Step 2) Determination of traceway direction (arrows)
Step 3) Draw tracklines parallel to traceway direction

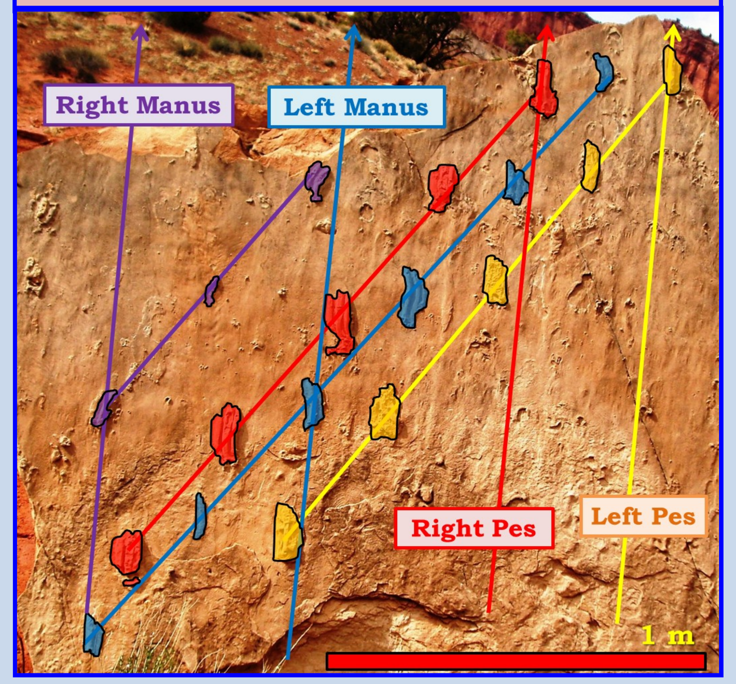
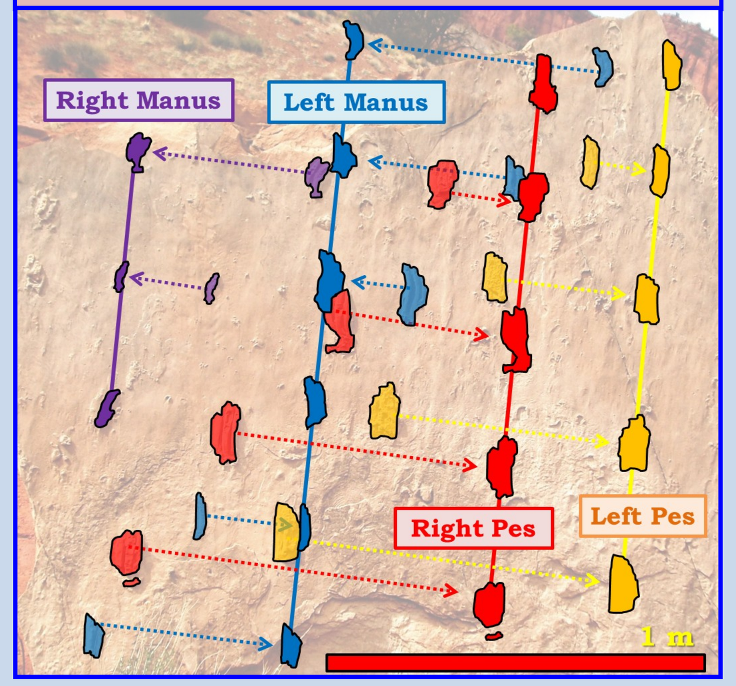


Figure 10 (below): Re-alignment of offset traceway.
Step 4) Shifting footmarks perpendicular to traceway direction into tracklines



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