# Tetrapod ichnotaxonomy in eolian paleoenvironments (Coconino and De Chelly formations, Arizona) and late Cisuralian (Permian) sauropsid radiation

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## ARTICLE INFO

## ABSTRACT

The tetrapod footprint record of Permian eolian environments has long been underestimated because of overall poor preservation and its apparent monospecifity. The best known and most abundant Cisuralian record of tetrapod footprints is from the Coconino and De Chelly formations of Arizona, which, however, thus far encompassed only the ichnogenera *Chelichnus* and *Dromopus*. We revised the locomotion and taphonomy of these footprints and propose a new model, basing it on: 1) trackways changing direction, 2) trackways heading in different directions on the same surface, 3) trackways in situ, and 4) laboratory experiments with common wall lizards, *Podarcis muralis*. In all cases, the *Chelichnus*-like appearance of footprints is due to digit tip sliding on inclined depositional surfaces, masking the original footprint shape and orientation. Also, the trackway pattern and body position are largely influenced by the angle of inclination (dip) of the substrate being walked on. Based on an anatomy-consistent ichnotaxonomy, *Chelichnus* and *Laoporus* are here considered *nomina dubia*, and the footprints from the Coconino and De Chelly formations are revised and assigned to: parareptiles/captorhinomorph eureptiles (*Erpetopus, Varanopus curvidactylus*), bolosaurid parareptiles/ diapsid eureptiles (cf. *Dromopus*), varanopid synapsid (cf. *Tambachichnium*) and reptiliomorph amphibians (*Amphisauropus, Ichniotherium sphaerodactylum*). The ichnoassociation is dominated by parareptile/captorhinomorph tracks, similarly to all the late Cisuralian marginal marine, floodplain, alluvial fan and ephemeral lacustrine tetrapod ichnoassociations of North America, Europe and North Africa. A review of all the available data including the new results suggests a facies-crossing transition between an early-Cisuralian amphibian- and synapsid-dominated ichnofauna (*Dromopus* track biochron) and a late Cisuralian parareptile/captorhinomorph-dominated ichnofauna (*Erpetopus* track biochron) at low latitudes of Pangea.

## 1. Introduction

Since the 19th century, the study of tetrapod footprints from Permian eolian paleoenvironments has always been a challenging issue subject to several different interpretations (e.g. Jardine, 1853). The abundance of tracks and trackways from these lithofacies is noteworthy, whereas skeletons are generally not preserved. Consequently, an anatomy-consistent ichnotaxonomic interpretation of this footprint material is very important to infer the faunal meaning of the ichnoassociation, as well as the related paleoecology, paleobiogeography and biostratigraphy. The best known and most studied footprints from early Permian eolian units are those of the Coconino and the

De Chelly formations of Arizona (Lull, 1918; Gilmore, 1926, 1927, 1928; Baird, 1952, 1965; Brand, 1979; Brand and Tang, 1991; Spamer, 1984; Lockley et al., 1994, 1995; Haubold et al., 1995a; Morales and Haubold, 1995; Citton et al., 2012). However, the overall poor preservation of this material, together with peculiar locomotory effects (e.g. McKee, 1944, 1947; Vaughn, 1963; Brand and Tang, 1991), has thus far hampered an anatomy-consistent interpretation of the footprints. The ichnoassociation is currently believed to include only the ichnogenera *Chelichnus* and *Dromopus*, the latter known from a single specimen (Haubold et al., 1995a; Haubold, 2000). *Chelichnus* has long been interpreted as the footprint of small to relatively large synapsids (McKeever and Haubold, 1996), whereas *Dromopus* is known as the footprint of bolosaurid parereptiles or of araeoscelid reptiles (Voigt, 2005). Nevertheless, a thorough discussion about locomotion, taphonomy and ichnotaxonomy of the Coconino and De Chelly material has never been attempted.

Because the taphonomy of tetrapod footprints in eolian paleoenvironments is a complex matter, we chose to investigate this issue using different approaches and revising the largest number of specimens with the most recent techniques. The results were used to infer a model of footprint formation in these lithofacies in agreement with what was observed in collection specimens, in specimens in situ and in laboratory experiments on tetrapods of comparable size and locomotor capabilities. Subsequently, the taphonomic effects were separated from the anatomy-consistent morphologic features, and new ichnotaxonomic assignments were proposed. These were used to provide a new faunistic interpretation, with the relevant implications for paleoecology, paleobiogeography and biostratigraphy.

## 2. Geological setting

The Permian geology of Arizona has been long debated, mostly because of the abundance of subsurface outcrops and the frequent vertical and lateral changes in lithofacies, which often hampered reliable and consistent correlations. Moreover, the fossil content of the continental Permian Arizona formations, with the exception of trace fossils, is usually scarce or not suitable for precise biostratigraphy. Several stratigraphic units have been described and variably correlated and grouped (e.g. Blakey and Knepp, 1989; Peirce, 1989). Nevertheless, some features are consistent, such as the repeated occurrence of eolian, fluvial and shelf environments (e.g. Blakey and Knepp, 1989; Peirce, 1989).

The eolian formations repeatedly formed wide sand seas that were surrounded by fluvial environments and marine shelves (Blakey and Knepp, 1989; Mountney and Jagger, 2004). In the study areas, the eolian environments are represented mostly by the Cedar Mesa, De Chelly, Coconino and Glorieta formations. The fluvial environments are represented mostly by the Hermit Shale and Organ Rock Formation (Fig. 1). The marine shelf environments are represented mostly by the Parkoon, Esplanade, Halgaito, Schnebly Hill, Toroweap and Kaibab formations (Fig. 1). The study material comes from the eolian De Chelly and Coconino formations. The De Chelly Formation crops out in northeast Arizona, in the Monument Valley area (sites 10–11, Fig. 1A) and in the Defiance upwarp area (site 12, Fig. 1A). It was named by Gregory (1917) after the De Chelly Canyon in the Defiance upwarp, where it reaches its maximum thickness of about 250 m. It is mostly constituted by large-scale cross-stratified reddish sandstones and it is time-equivalent to the marine lithofacies of the Schnebly Hill Formation of central Arizona, dated as about as middle Leonardian = early Kungurian through marine biostratigraphy (Blakey and Knepp, 1989). The De Chelly Formation overlies the fluvial Organ Rock Shale, interfingers in its upper part with the eolian Coconino Formation westwards, and it is overlain by the eolian Glorieta Sandstone eastwards (Fig. 1B).

The Coconino Formation crops out extensively in northern Arizona, reaching its maximum thickness of about 300 m in central northern Arizona (near Pine). The fossiliferous sites are located in the Grand

Canyon (sites 1–3, Fig. 1A) and in the NW part of the Mogollon Rim (sites 4–9, Fig. 1A). It was named by Darton (1910) after Coconino County. It is composed by large-scale, cross-stratified, whitish quartz sandstones. The Coconino Formation overlies the fluvial Hermit Shale and the marine Schnebly Hill Formation and its lower part interfingers with the upper part of the eolian De Chelly Formation (Fig.1B). Towards north-west Arizona it intertongues with and is overlain by the marine Toroweap Formation. It is also overlain by and it possibly intertongues with the marine Kaibab Formation. Towards the east, it passes laterally into the eolian Glorieta Sandstone. Based on its stratigraphic position, the Coconino Formation is considered late Leonardian = late Kungurian (Blakey and Knepp, 1989).

## 3. Material and methods

In order to achieve a meaningful ichnotaxonomy in Permian eolian paleoenvironments it was necessary to study a large specimen sample (about 500 specimens), strictly evaluating and excluding taphonomic effects in order to identify the footprint morphologies useful for ichnotaxonomy (anatomy-consistent ichnotaxobases). These were then compared to contemporary ichnofaunas. All the specimens were analyzed first-hand and subsequently with photographs in controlled light conditions (oblique artificial light, in at least 2 perpendicular directions), digitized interpretive drawings, 3D models obtained with close-range photogrammetry (using Canon EOS 70D®) that were built through the software Agisoft Photoscan Professional®, elevation that was measured with the software Cloud Compare® and false-color depth maps that were obtained with the software Paraview®. The measurements follow the conventions of Leonardi (1987).

In this work, the tracks from the Permian eolian paleoenvironments of Arizona were compared with the extensive record of late Cisuralian tracks from Arizona, New Mexico, Texas, Morocco, Spain, France, Italy and Argentina (e.g. Haubold et al., 1995b; Haubold and Lucas, 2001, 2003; Lucas et al., 2001; Melchor and Sarjeant, 2004; Gand and Durand, 2006; Voigt et al., 2011; Voigt and Haubold, 2015; Voigt and Lucas, 2015a, 2017; Mujal et al., 2016; Marchetti et al., 2013a, 2015a, 2015b, 2015c; Marchetti, 2016). The Permian eolian tracks from Europe (e.g., the Cornberg Formation of Germany and Corncockle Formation of Scotland), being of a different age (Lopingian), are compared with the contemporary ichnoassociations and discussed in a different paper (Marchetti et al., 2018a).

## 4. Institutional abbreviations

CU = University of Colorado, Denver, CO, USA

DUMFM = Dumfries Museum and Camera Obscura, Dumfries, Scotland

MNA = Museum of Northern Arizona, Flagstaff, AZ, USA

RAM = Raymond M. Alf Museum of Paleontology, Claremont, CA, USA

RSM = National Museum of Scotland, Edinburgh, Scotland

UCMP = University of California, Berkeley, CA, USA

USNM = Smithsonian - National Museum of Natural History, Washington, DC, USA

YPM = Yale Peabody Museum of Natural History, New Haven, CT, USA

## 5. Locomotion and taphonomy

### 5.1. Hypotheses

The first question to be answered in the understanding of the footprint taphonomy in Cisuralian eolian paleoenvironments is: what is responsible for the *Chelichnus*-like morphologies? *Chelichnus* is widely known to represent the footprint of a quadrupedal trackmaker with relatively short subequal and parallel digit impressions and a relatively
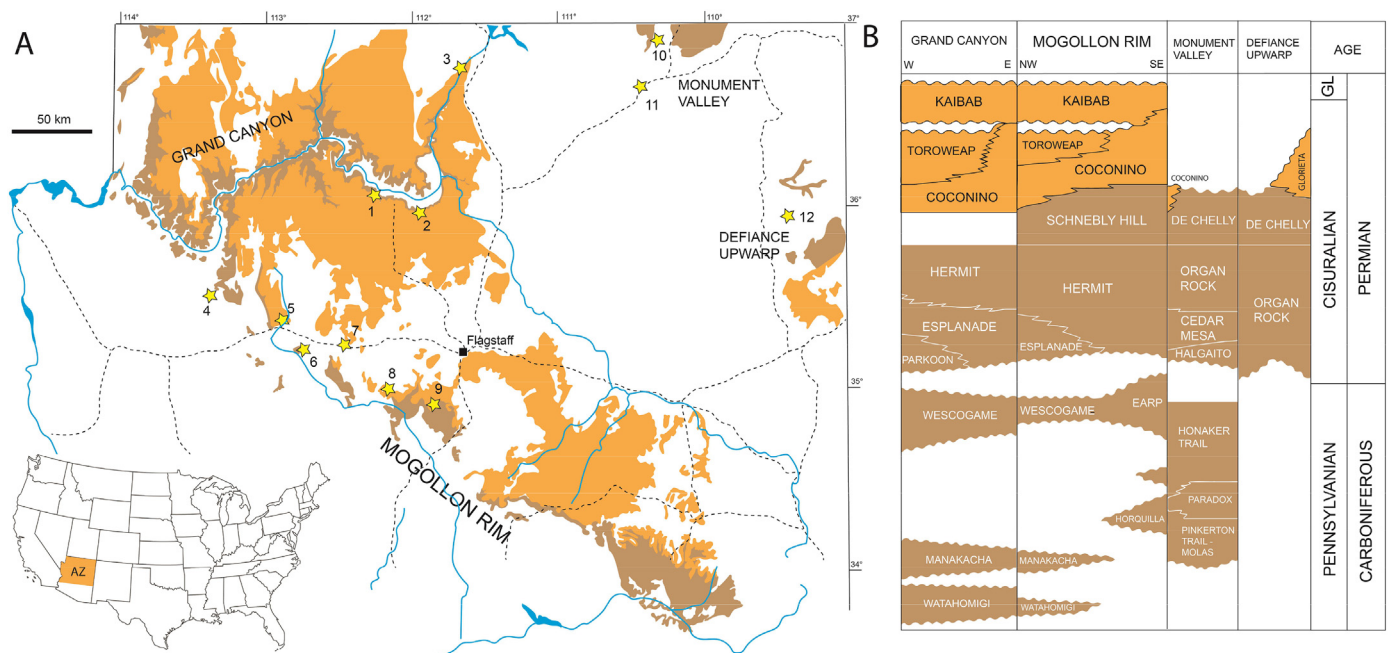
**Fig. 1.** Localities and geological setting. A) Simplified geologic map and localities. 1) Grand Canyon, Hermit Trail. 2) Grand Canyon, Tanner Trail. 3) Soap Creek. 4) Peach Springs. 5) Seligman. 6) Pichacho Butte. 7) Ash Fork. 8) Perkinsville. 9) Sycamore Pass. 10) Boot Mesa. 11) Tsegi. 12) Nazlini Canyon. Localities 1–9 Coconino Formation, Localities 10–12 De Chelly Formation. B) Chronostratigraphic scheme of the fossiliferous area (from Blakey and Knepp, 1989, modified).

large sole impression (McKeever and Haubold, 1996). Nevertheless, its ubiquitous distribution in Cisuralian and Lopingian eolian units globally is rather odd, considering the important faunal replacement that occurred from the Cisuralian to the Lopingian. The analysis of a large number of specimens allowed us to note a peculiar feature: the *Chelichnus* "digit traces" were commonly oriented in a particular direction, which is the same regardless of the trackway direction (Figs. 2-6). There could be two possible explanations for this effect: 1) complete rotation of the footprints along a single direction (e.g. Loope, 1992), or 2) sliding of the producers along a single direction. Tetrapod footprints in eolian paleoenvironments are usually found on the steep slope of the paleodunes, the foresets, which are inclined at about 30° (e.g. Lockley et al., 1995). So, it is not surprising to find unidirectional taphonomic effects, likely due to the slope direction.

In order to verify this assumption, it is necessary to understand the correct trackway direction in relation to the slope direction. The trackway direction was always inferred considering the relative position of the palm/sole impression and the digit tip impressions in every footprint. The palm/sole impression can never be more distal than the digit tip impressions, because this would imply a rotation opposite to the direction of progression, and this would be physically impossible. It turns out that some trackways have a direction of movement opposed to what was initially inferred (e.g. *Dolichopodus tetradactylus* Gilmore, 1926) and in other cases, perpendicular (e.g. Brand and Tang, 1991; Lockley, 1992; Loope, 1992).

After establishing the correct direction of progression, attention was given to the different pace angulation and symmetry of the trackways, which can be very variable, although always in a simple alternating gait. We observed symmetrical trackways with low pace angulation (Fig. 3G), symmetrical trackways with high pace angulation and pes-manus lateral primary overstep (Fig. 2B, 3F), strongly asymmetrical trackways (Fig. 2F, G; Fig. 3B, I), and all the possible asymmetries and pace angulation values in between.

In order to understand if and how these locomotory effects and the digit tip sliding were due to the progression direction in relation to the slope, we chose four different approaches: 1) finding transitions in the trackway direction (slope direction inferred), 2) observing surfaces including different trackway directions (slope direction inferred), 3)

finding different trackway directions in the field (slope direction and angle of dip directly observable), and 4) performing laboratory experiments observing different trackway directions of animals of similar size and structure (slope direction and angle of dip directly fixed). The slope direction of the specimens was inferred from several indications, such as: the direction of the sand avalanches, the position and asymmetry of the expulsion rims, the most common direction of digit sliding and the position of the most deeply impressed footprints in the asymmetrical trackways. The trackway direction was termed downslope for all the trackway directions with an angle of 0–90° from the dip direction, and upslope for all the trackway directions with an angle of 90–180° from the dip direction. The trackways at about 90° have to be considered completely transverse to the dip direction (i.e. contour-parallel), so intermediate between upslope and downslope. The term "lateral component" is used to evidence the angular departure of trackway directions with respect to the downslope and upslope directions. In order to better understand the locomotion mechanism, the position of the body during locomotion was inferred through reconstructing the consecutive positions of the trackmaker's trunk, i.e., gleno-acetabular dimension, inferred from the consecutive position of the pes-manus couples during locomotion (e.g., Leonardi, 1987).

*5.2. Transitions*

The specimens RAM 131 and RAM 235 show a clear change in the direction of progression along the same trackway. The trackway of RAM 131 (Fig. 2A) starts downslope with a high pace angulation and complete primary lateral pes-manus overstep (pace angulation 80–140°) (Fig. 2B) and then it turns in the opposite direction (upslope) with lower pace angulation, only partial and occasional primary lateral pes-manus overstep and a more asymmetrical pattern (pace angulation 60–90°) (Fig. 2D). The transition (Fig. 2C) starts with a lower pace angulation in the final part of the high-pace trackway segment and a subsequent rotation. It is possible to observe two additional pes-manus couples on the right side of the trackway (numbers 1 and 2 in Fig. 2C), produced during the turning, whereas a single left pes-manus couple (circle) probably acted as a pivot (pace angulation 10–75° during the transition).
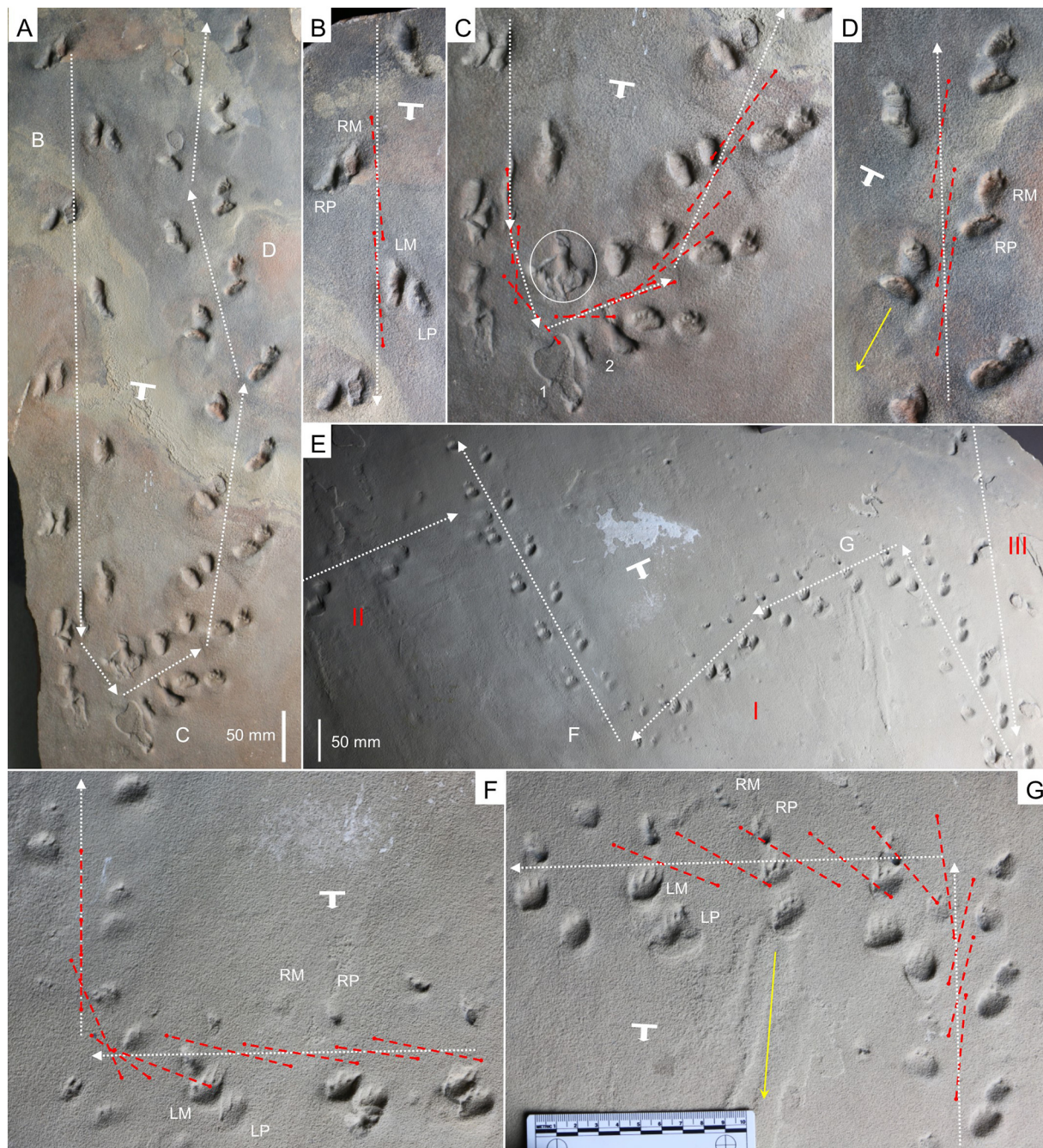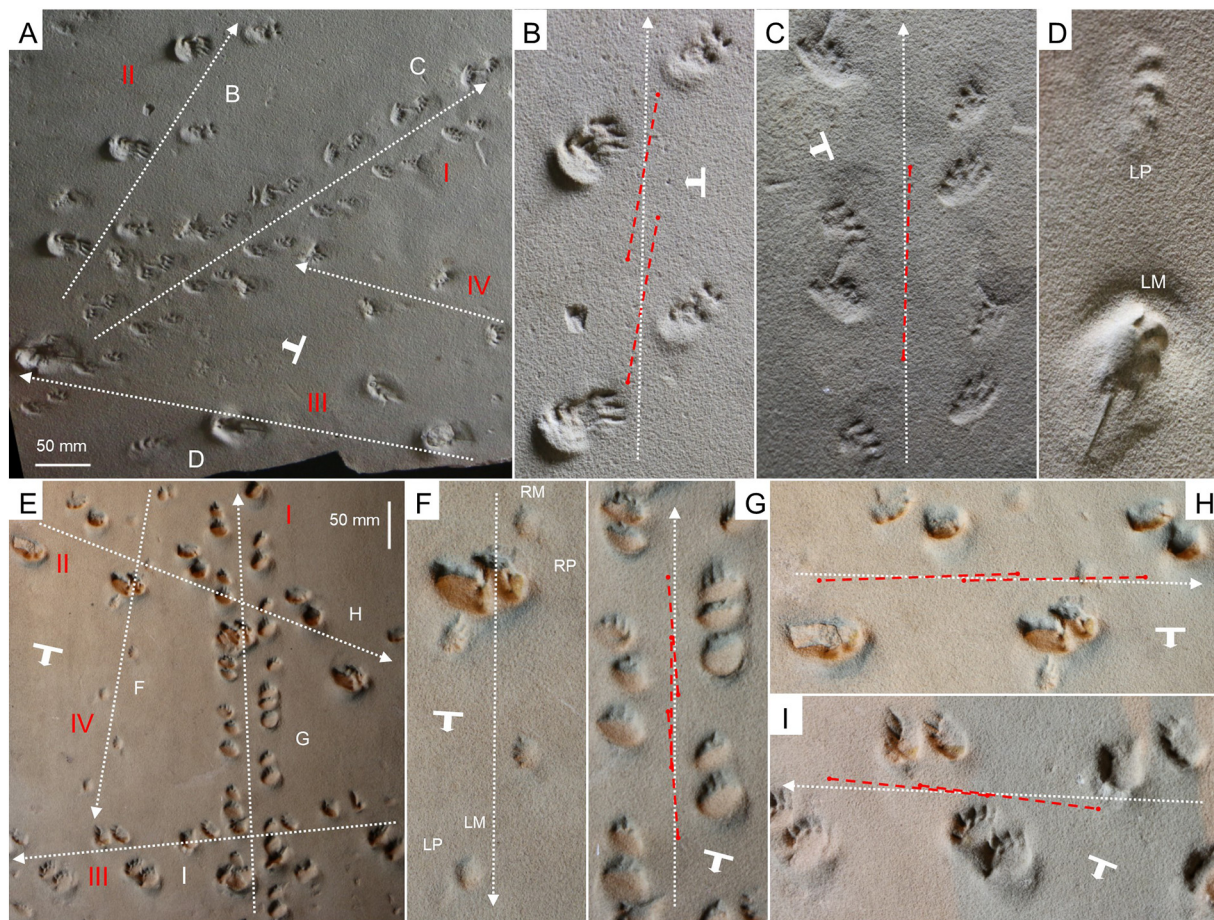
**Fig. 2.** Trackways changing the direction of progression (dip direction inferred and angle of dip unknown). Dashed arrows indicate the direction of progression, red lines the position of the body during locomotion (estimated gleno-acetabular positions), strike and dip symbols the supposed dip of the inclined bedding plane, yellow arrows the direction of the expulsion rims or sand avalanches. L = left, R = right, P = pes, M = manus. All footprints preserved in concave epirelief. A–D) RAM 131. A) Trackway changing direction of progression one time. B) Downslope progression with low lateral component. Note the high pace angulation and the pes-manus primary overstep. C) Transition from downslope to upslope progression with complete rotation of the body. Note the occurrence of two additional pes-manus couples on the right side (1 and 2) and the use of the left limbs as a pivot (circle). D) Upslope progression with lateral component. Note the lower pace angulation, the smaller pes-manus primary overstep and the asymmetry. E–G) RAM 235. E) Trackway changing direction of progression two times (I), trackway directed transverse to the slope (II), trackway directed downslope with low lateral component (III). F) Transition from almost transverse to the slope (asymmetric, left side more deeply impressed) to upslope progression with low lateral component. G) Transition from upslope progression with low lateral component to progression almost transverse to the slope (asymmetric, left side more deeply impressed). In all the asymmetric trackways, the body is rotated in the upslope direction. In all the trackways, the digit tip slide in the dip direction, angular deviations in the progression direction are possible. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

We interpret all this sequence as a single trackway, because there is no other evidence of tracks on the same slab, and the position and orientation of all the couples is consistent with a sudden and complete change in the direction of progression. The dip direction is indicative of an initial long-stride downslope progression, a sudden turning in the opposite direction and a subsequent upslope progression with a lateral component characterized by a short stride and asymmetry. Surprisingly, in the case of trackway asymmetry, the reconstructed gleno-acetabular positions are not parallel to the direction of progression, but they are slightly upslope-turned (Fig. 2C–D). This

**Fig. 3.** Trackways going in different directions on the same stratigraphic surface (dip direction inferred and angle of dip unknown). Dashed arrows indicate the direction of progression, red lines the position of the body during locomotion (estimated gleno-acetabular positions), strike and dip symbols the supposed dip of the inclined bedding plane. L = left, R = right, P = pes, M = manus. A–D) RAM-NN 1, concave epirelief. A) Upslope progression with small lateral component (I), upslope progression with high lateral component (II), downslope progression with small lateral component and high pace angulation (III–IV). B) Enlargement of trackway II. Note the asymmetric pattern and the more deeply impressed left side. C) Enlargement of trackway I. Note the more symmetric pattern with less deformed footprints compared to B. D) Enlargement of trackway III. Left pes-manus couple with complete pes-manus primary overstep. Note the different orientation of digit traces and digit drag marks. E–I) RAM 3301, convex hyporelief. E) Upslope progression with small lateral component (I), downslope progression with higher lateral component (II–III), downslope progression with small lateral component (IV). F) Enlargement of trackway IV. Note the high pace angulation and the primary pes-manus overstep. G) Enlargement of trackway I. Note the low pace angulation and the secondary partial manus-pes overstep. H) Enlargement of trackway II. Note the asymmetry. I) Enlargement of trackway III. Note the asymmetry. In all the asymmetric trackways, the body is rotated in the uspslope direction. In all the trackways, the digit tip slide in the dip direction, angular deviations in the progression direction are possible. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

demonstrates how the track-making animal used the body to oppose the force of gravity, thus creating asymmetry in the trackways (for instance, with manual tracks more medial than those of the pes on one side and more lateral than the pes on the other side), when the direction of progression was not parallel to the dip direction.

The longest trackway of RAM 235 (Fig. 2E) (trackway I) shows two sudden and important (about 90°) changes in the direction of progression. The first part of the trackway shows a relatively low pace angulation with little asymmetry (pace angulation 65–85°) (Fig. 2G). After the first turn, the central part of the trackway is strongly asymmetrical, the left side is more deeply impressed and the left manual tracks are medially positioned with parallel digit scratches oriented perpendicular to the direction of progression (Fig. 2F–G) (pace angulation 50–80°). The right side is weakly impressed or non-impressed, and the manual tracks are laterally positioned. After the second turn, the trackway is again oriented in the same direction as the first, earlier-formed segment and has a similar pace angulation and small asymmetry (pace angulation 75–90°) (Fig. 2F). The slope direction indicates that the trackway is oriented upslope with a small lateral component in the first and last part and directed almost transverse to the dip direction in

the middle part. Therefore, the strong asymmetrical preservation of the trackway in the central part is the result of the gravitational forces acting laterally on the trackmaker and of the different space for the limb extension on the two sides of the trackmaker. This is evident from the inferred sequence of inferred gleno-acetabular positions (Fig. 2F–G), which are not parallel to the direction of progression but upslope-rotated, showing how the trackmaker acted to counteract the gravitational force. The digit tip scratches (parallel to the direction of the slope) show instead the lateral sliding of the trackmaker's body. The other trackways registered on this surface, a strongly asymmetrical one perpendicular to the dip direction in the upper left corner of Fig. 2E (trackway II) and one almost parallel to the dip direction characterized by long pace and complete primary pes-manus overstep in the upper right corner of Fig. 2E (trackway III), are consistent with transverse and downslope progression, respectively, confirming the supposed effects related to the dip direction.

The trackway I of specimen RAM 235 is very important because it was central to the discussion about the possible subaqueous origin of the Coconino Formation (Brand and Tang, 1991; Lockley, 1992; Loope, 1992). The strongly asymmetrical pattern of the central part of this
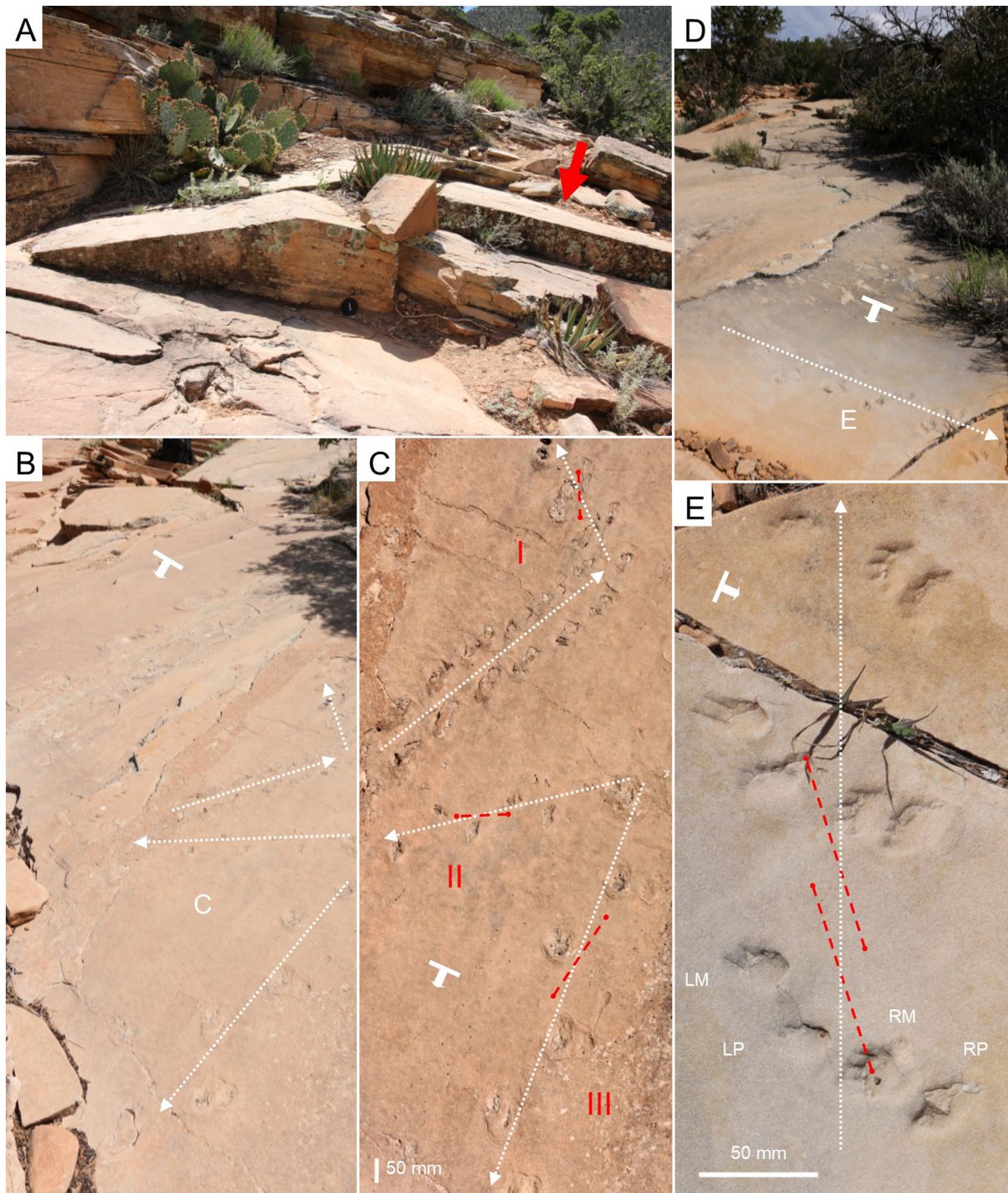
**Fig. 4.** Trackways going in different directions on the same stratigraphic surface in the field (known dip direction and angle of dip). Dashed arrows indicate the direction of progression, red lines the position of the body during locomotion (estimated gleno-acetabular positions), strike and dip symbols the dip of the inclined bedding plane. L = left, R = right, P = pes, M = manus. All the tracks preserved in concave epirelief. A) The trampled foreset dune surface (arrow). B–C) Upslope progression with low (first symmetric part) and high (second asymmetric part) lateral component, low pace angulation (I), downslope progression with high lateral component and asymmetry (II), downslope progression with small lateral component, high pace angulation and pes-manus primary overstep (III). D–E) Upslope progression with high lateral component, note the asymmetry and the right side more deeply impressed. In all the asymmetric trackways, the body is rotated in the uspslope direction. In all the trackways, the digit tip slide in the dip direction, angular deviations in the progression direction are possible. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

trackway was interpreted as a lateral shift of the trackmaker's body during locomotion, due to supposed lateral water currents (Brand and Tang, 1991). In this interpretation, it was important that the supposed orientation of the tracks was apparently perpendicular to the direction of movement. However, the inferred position of the body was not as

these authors suggested, because the left couples were considered pedal tracks and the right couples manual tracks. Two authors criticized this interpretation, suggesting peculiar lateral gaits such as hopping (Lockley, 1992) or a different position of the body (parallel to the direction of movement) with strong asymmetry due to progression
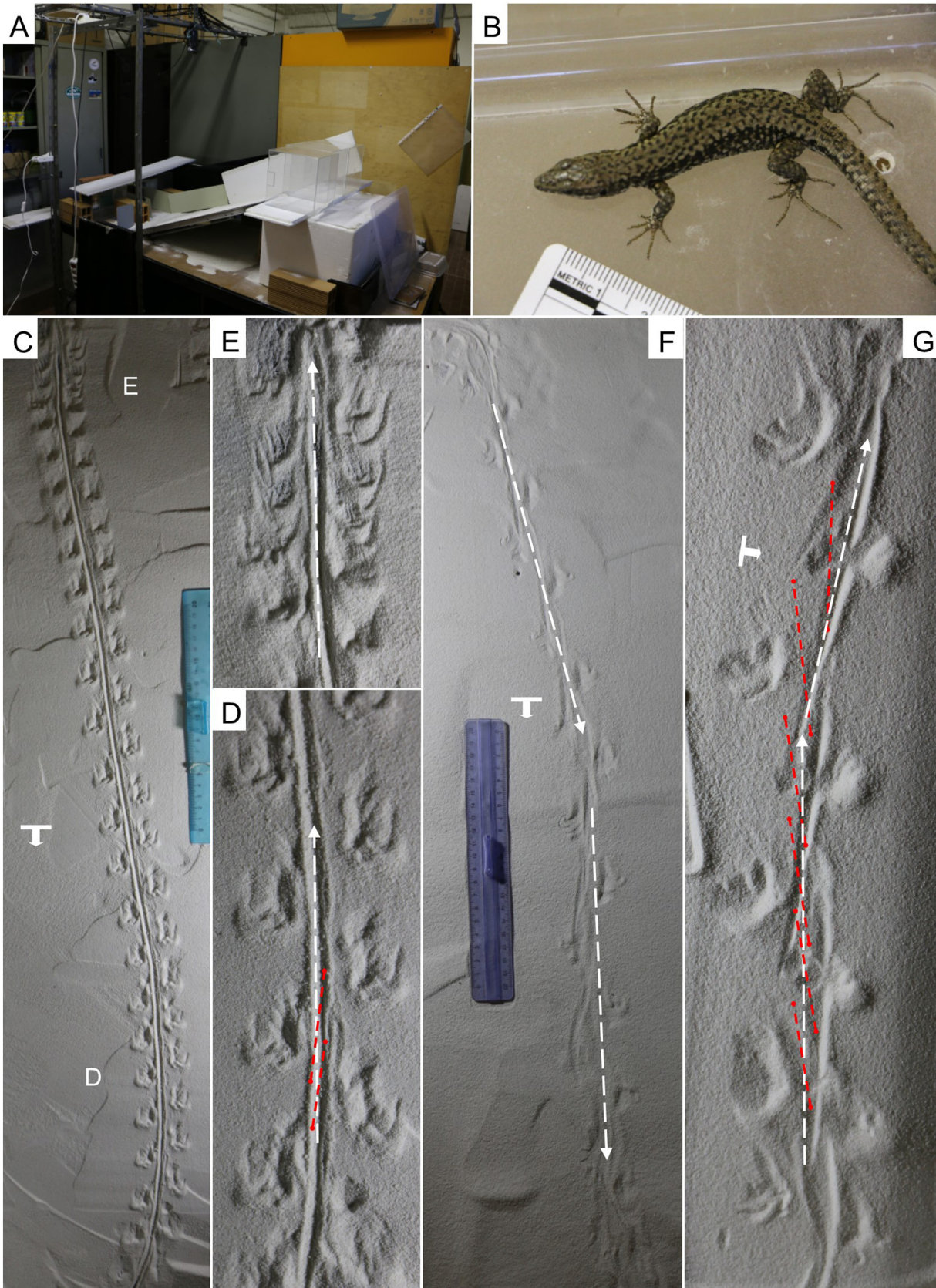
*(caption on next page)*

**Fig. 5.** Laboratory experiments with wall lizards and inclined surfaces covered with well-sorted fine-grained dry sand. Dashed arrows indicate the direction of progression, red lines the position of the body during locomotion (estimated gleno-acetabular positions), strike and dip symbols the dip of the inclined surface. All the tracks preserved in concave epirelief. A) The experimental setting. B) The trackmaker of the footprints in C–G. C–E) Upslope progression with low lateral component and low pace angulation. Note the outward-oriented pedal impression with recognizable lacertid morphology and the digit drag marks forward-directed (D) and the indistinct trackway with *Chelichnus*-like morphology forward-directed in the final part of the trackway, evident result of digit drag marks (E). F) Downslope progression with low lateral component. Note the high pace angulation. G) Almost transverse progression. Note the marked asymmetry. In all the asymmetric trackways, the body is rotated in the upslope direction. In all the trackways, the digit tip slide in the dip direction, angular deviations in the progression direction are possible. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

perpendicular to the slope direction (Loope, 1992). Nevertheless, these explanations could not justify the high footprint rotations (Brand, 1992). Instead, we believe that the footprints and digit impressions are actually much less rotated, and the supposed "digit traces" which were used to infer the footprint direction are actually sliding traces of the digit tips in the direction of the slope.

### 5.3. Different trackway directions

The specimens RAM-NN 1 and RAM 3301 show examples of trackways with a straight course going in several different directions. The specimen RAM-NN 1 (Fig. 3A–D) shows slightly asymmetrical trackways with relatively low pace angulations (75–85°) – upslope progression with a low lateral component (trackway I; Fig. 3A, C), strongly asymmetrical trackways with higher pace angulation (100°-105°) – upslope progression with a high lateral component (trackway II, Fig. 3A, B) and symmetrical trackways with very high pace angulation (120–160°) and complete primary pes-manus overstepping – downslope progression with a low lateral component (trackways III-IV, Fig. 3A, D). The downslope side of the asymmetrical trackways is more deeply impressed and shows the sliding of the digit tips in the direction of the slope, which masks the real footprint direction, whereas the upslope side is less affected by deformation and shows footprints aligned with the direction of progression. The inferred gleno-acetabular positions are upslope-rotated with respect to the direction of progression. In the downslope-directed trackways, the manual tracks are more deeply impressed than the pedal tracks and more rotated inwards.

The specimen RAM 3301 is a very large surface with many different trackways (Fig. 3E–I). It includes a slightly asymmetrical trackway with low pace angulation (35–90°) – upslope progression with a low lateral component (trackway I, Fig. 3E, G), two asymmetrical trackways with higher pace angulation (80–105°) - downslope progression with a high lateral component (trackways II–III, Fig. 3E, H–I) and a symmetrical trackway with high pace angulation (100–130°) and complete primary pes-manus overstepping – downslope progression with a low lateral component (trackway IV, Fig. 3E, F). In the asymmetrical trackways, the inferred gleno-acetabular positions are upslope-rotated with respect to the direction of progression. The downslope side of the trackways is more deeply impressed, and the manual tracks are more deeply impressed in the downslope-directed trackways with a low lateral component. Digit tip drag marks are generally parallel to the dip of the slope (Fig. 3F–H), but their direction can be influenced by the progression direction as well (Fig. 3I).

### 5.4. Trackway directions measured in the field

A stratigraphic surface along the Hermit Trail in the Grand Canyon National Park (Arizona) shows trackways oriented in different directions. These trackways are preserved in the lower part of a foreset surface of known dip direction (210–240° N, dip 20–27°) (Fig. 4A). The trackways of Fig. 4B–C are upslope-directed with a low to high lateral component, low pace angulation and a change in direction (45–75°, trackway I), downslope-directed with a high lateral component and high pace angulation (95–130°, trackway II) and downslope-directed with a low lateral component, high pace angulation and primary pes-manus overstep (95–150°, trackway III). The asymmetrical trackways

always show inferred gleno-acetabular positions rotated upslope with respect to the direction of progression. The digit drag marks are aligned with the slope direction, as can be seen in the two trackways directed downslope. The manus is more deeply impressed than the pes in the symmetrical trackways directed downslope, and the left side of the asymmetrical trackways directed downslope is more deeply impressed than the right side, consistent with the dip direction. The trackway of Fig. 4D–E is upslope-directed with a high lateral component and relatively low pace angulation (70–95°). It is strongly asymmetrical, with a right side more deeply impressed, the inferred gleno-acetabular positions rotated upslope with respect to the trackway direction, and the digit tip drag marks parallel to the dip direction.

### 5.5. Laboratory experiments

The laboratory experiments were performed at the Dipartimento delle Scienze della Terra e dell'Ambiente, University of Pavia, Italy. The work described has been carried out in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki) for experiments involving animals (EU Directive 2010/63/EU) http://ec.europa.eu/environment/chemicals/lab_animals/legislation_en.htm, and the European and Italian laws on animal use in scientific research (Aut. Prot. PNM-2012-0009344 to RS, MM, and SS).

Laboratory experiments were performed using common wall-lizards (*Podarcis muralis*, Fig. 5B), a small Lacertid lizard (snout-to-vent length 45–75 mm) widespread in southern and central Europe (Sillero et al., 2014). We used one adult male (Fig. 5B), previously selected among different individuals as representative of this species digit morphology, to properly evaluate the footprint formation. Lizards walked on an inclined plane (about 30°) covered with well-sorted, fine-grained sand while being video-recorded, in order to correctly interpret the footprint formation (Fig. 5A).

Since the mechanism of footprint formation in eolian paleoenvironments is still unclear we tested different substrate conditions, including dry, damp and wet sand. The animal was unable to leave footprints on the wet sand, because its weight was not sufficient to break the wet sandy crust (as observed by McKee, 1944, 1947). The animal produced very shallow tracks and scratches on the damp sand, together with abundant small breccia of broken surface pieces (McKee, 1944, 1947; Brand, 1979), which has never been reported or observed in association with the eolian trace fossils. Conversely, on the dry sand the animal left clear trackways with complete footprint impressions and digit traces, expulsion rims and effects due to the substrate inclination (in agreement with McKee, 1944, 1947; Loope, 2006 and *contra* Brand, 1979). Moreover, the absence of cracks and breccias, the expulsion rims morphology and the sand avalanches produced by some fossil footprints (Fig. 2F) are consistent with a footprint formation on dry sand. Therefore, we consider the dry sand the most probable medium for the footprint formation in eolian paleoenvironments and used it for the laboratory experiments. Nevertheless, the causes of preservation are still unclear, and include dampening (McKee, 1944, 1947; McKeever, 1991) and/or grainflows possibly generated by the tetrapods themselves (Loope, 2006). In the latter, the progression of animals on the inclined surface may result in small grainflows that delicately cover the previously-formed footprints in a downslope area, preserving them from weathering.
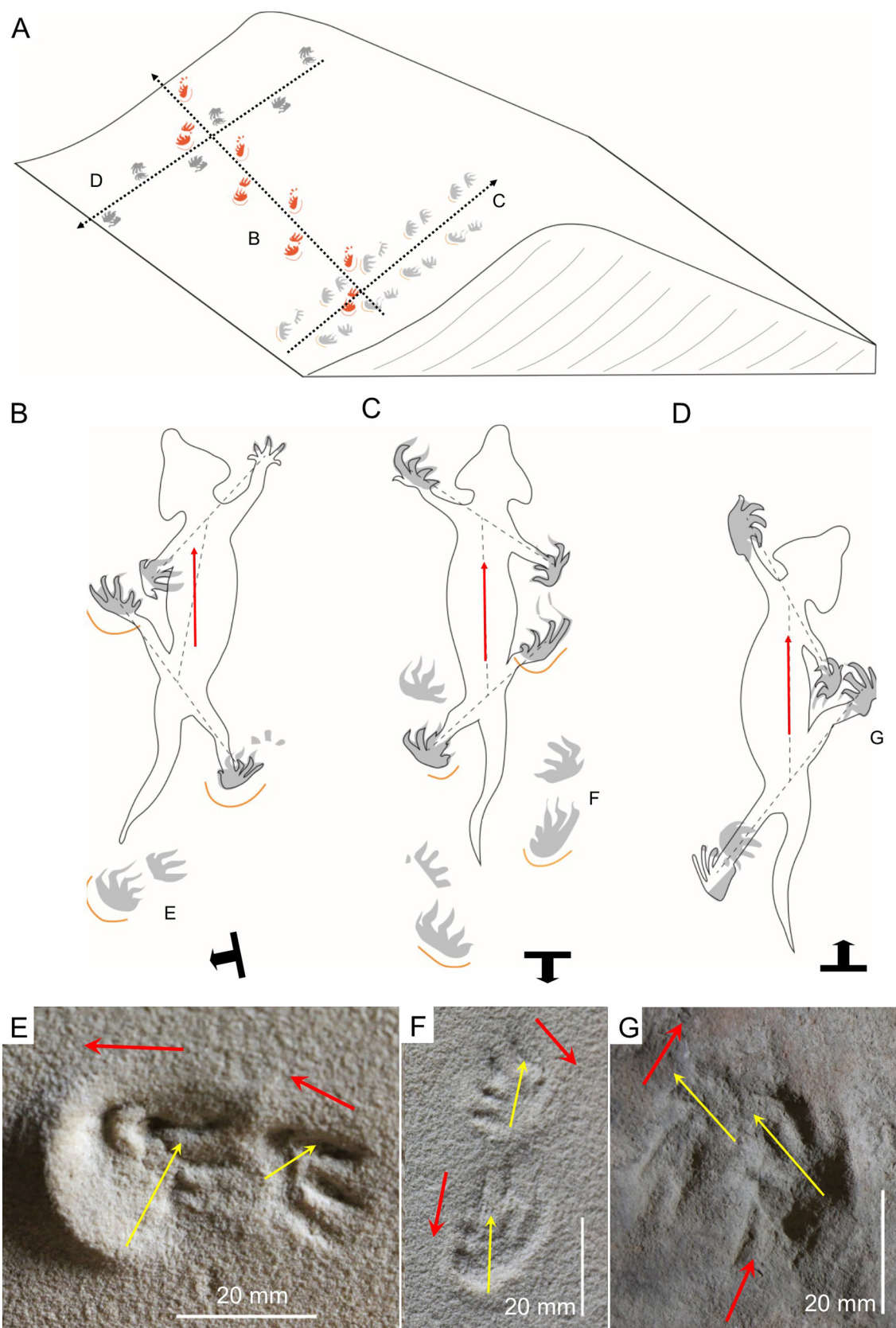
*(caption on next page)*

The upslope progression with a small lateral component produced trackways with low pace angulation (30–90°, Fig. 5C–E) and outward-oriented pedal tracks, smaller manual tracks and continuous tail impressions. The pedal digit tips of the outward-directed footprints scratch in the direction of progression, sometimes blurring the original lacertid morphology and producing *Chelichnus*-like morphologies

**Fig. 6.** Model about locomotion and taphonomy on the inclined surfaces of the foreset dunes. A) Scheme of a dune with trackways preserved on the foreset surface. B–D) Different progression direction compared to the dip. Strike and dip symbols indicate the dip of the inclined surface, red arrows indicate the direction of progression. B) Upslope progression with high lateral component and inferred position of the trackmaker, based on RAM-NN 1. Strongly asymmetric trackways, differential depth, upslope-rotation of the body. C) Upslope progression with low lateral component and inferred trackmaker position, based on RAM-NN 1. Low pace angulation and very small asymmetry. D) Downslope progression with low lateral component and inferred position of the trackmaker, based on UCMP 42944. High pace angulation and pes-manus overstep. E) RAM-NN 1. Left pes-manus couple with partial pes-manus overstep. Formation of *Chelichnus*-like morphologies due to the lateral sliding of the digit tips (red arrows) in the direction of the slope, differently from the real footprint direction (yellow arrows). F) RAM-NN 1. Right pes-manus couple. Formation of *Chelichnus*-like morphologies because of the backward sliding of the digit tips in the down dip direction (red arrows), differently from the real footprint direction (yellow arrows). G) UCMP 42944. Right pes-manus couple. Formation of *Chelichnus*-like morphologies because of the forward sliding of the digit tips in the down dip direction (red arrows), differently from the real footprint direction (yellow arrows). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

oriented in the direction of progression. This is related to a more difficult locomotion and a very low pace angulation (30–50°, Fig. 5E) with respect to the better-preserved trackway segments (80–90°, Fig. 5D).

The downslope progression with a small lateral component produced high pace angulation trackways (100–130°, Fig. 5F) with drag marks oriented in the direction of progression and a discontinuous tail impression. The original footprint morphology is not recognizable and pes-manus overstep is not observed. The almost transverse progression (Fig. 5G) produced strongly asymmetrical trackways with inferred gleno-acetabular positions consistently rotated upslope with respect to the direction of progression (pace angulation 60–110°). The original footprint morphology is not recognizable, and the digit drag marks are mostly aligned with the direction of progression.

### 5.6. Locomotion model

All the trackways observed in the collections, in the field and in experimental settings show consistent features, which reflect the locomotion of quadrupeds on inclined surfaces covered with relatively dry, well-sorted sand (foreset dunes) (Fig. 6A), possibly subject to blowing wind and sand avalanches. The trackways generally follow a straight course with rare and sudden changes in the direction of progression, of variable deviation values (from 30° to 180°). The pace angulation varies consistently from very low (down to a minimum of 30°, upslope progression with a small lateral component) (Fig. 6A, C) to very high with complete pes-manus primary overstep (up to a maximum of 160°, downslope progression with a small lateral component) (Fig. 6A, D).

The trackway symmetry is directly related to the trackway direction with respect to the slope direction. Trackways parallel (both upslope and downslope) to the maximum dip direction are symmetrical (Fig. 6A, C, D), and trackways non-parallel to the slope direction are asymmetrical (Fig. 6A–B). In the asymmetrical trackways, the inferred body direction during locomotion is not aligned with the direction of progression and it is always rotated upslope (upslope-rotated inferred gleno-acetabular position, with manual tracks more medial than pes on one side and more lateral than pes on the other side: Fig. 6A–B). Moreover, the trackway side positioned downslope with respect to the body is generally more deeply-impressed and complete than the trackway side positioned upslope with respect to the body. This evident asymmetry is probably the result of the necessity of the trackmaker to keep the body upright not to fall downslope due to the gravity force. Moreover, the more deeply-impressed downslope tracks can be also the result of the different space available for the limbs on the upslope (less space) and downslope (more space) sides of the trackway. This could have resulted in a sort of limping behavior, with the limbs on the upslope side more flexed than the limbs on the downslope side. This is unlikely to have happened in underwater conditions, and it is not the result of lateral current-driven progression as suggested by Brand and Tang (1991).

The unidirectional orientation of the *Chelichnus*-like footprints, regardless of the trackway orientation, could be explained by: 1) very high footprint rotation (e.g. Loope, 1992), or 2) deformation of the anatomy-controlled footprint morphology and orientation due to dip-controlled sliding.

Hypothesis 1) is rather unlikely because it implies a constant footprint inward-rotation of up to 90° on one side and a footprint parallel to the progression direction on the other side in certain trackways (e.g. Fig. 2E–G). This either would have been physically impossible for the trackmaker, or at least very inefficient. Hypothesis 2) is instead more realistic, because it does not imply a high degree of foot rotation but just sliding of the digit tips (Fig. 6 E–G). This is not easy to observe because usually only the distal trace of the digit is preserved in these lithofacies, but it is rather clear that the distal digit traces are commonly bent and elongated in the direction of dip, with possible angular deviations in the progression direction. Consequently, the footprint is deformed into a *Chelichnus*-like morphology, and the real digit trace (and thus footprint) orientation is only visible in the part of the digit traces proximal to the bending and sliding effects of the digit tips (Fig. 6E–G). Therefore, the *Chelichnus/Laoporus*-like morphologies do not reflect the anatomy-controlled footprint morphologies, but are taphonomic artifacts due to the combined effects of digit drag due to sliding and locomotion that deformed the actual footprint shape and orientation.

This is evident in trackways showing morphological variation along their course (Fig. 5D–E) and in trackways that change completely in their direction compared to the slope (Fig. 2): the track morphology disparity is high, and it is directly related to the slope-controlled taphonomic effects acting during locomotion, clearly the trackmaker foot morphology cannot vary (the trackmaker is the same along the same trackway). Therefore, for ichnotaxonomic purposes it is necessary to exclude these effects from the footprint assignments and select the better-preserved material that is less-affected by these deformations and that shows recognizable and possibly complete digit traces and palm/sole impressions that are an expression of the anatomy of the trackmaker.

With this perspective, we discard the use of *Chelichnus* Jardine, 1853 and *Laoporus* Lull, 1918 for ichnotaxonomic purposes, because their type material (DUMFM 5 and YPM 2143, respectively) is not adequately preserved and their morphologies are strongly influenced by taphonomic artifacts due to the locomotion on inclined surfaces. Moreover, they were historically used as wastebasket ichnotaxa to classify almost all the footprints subject to the taphonomic effects in Permian eolian environments (e.g. Lockley et al., 1994, 1995; Haubold et al., 1995a; Morales and Haubold, 1995; Citton et al., 2012). Therefore, they are here considered "phantom taxa" (sensu Haubold, 1996) or "taphotaxa" (sensu Lucas et al., 2001) and so *nomina dubia* produced in specific conditions typical of eolian paleoenvironments, rather than anatomy-consistent ichnotaxa related to the eolian paleoenvironments. The same is true for most of the ichnotaxa introduced from the Coconino, Lyons and Supai formations (Table 1).

Moreover, we discard the use of ichnotaxonomy to describe different trackway patterns related to different progression directions on inclined surfaces (e.g. *Dolichopodus tetradactylus* Gilmore, 1926 that shows a peculiar pattern due to the downslope progression with complete pes-manus primary overstep). In fact, in this case the supposed diagnostic features would have been related to the behavior and the substrate conditions rather than to a specific trackmaker. Therefore, the biologic information would be little and confusion may arise because

**Table 1**

List of tetrapod footprint type material from the eolian lithofacies of Coconino, Lyons and Supai formations and new assignments.

| Ichnotaxon | Author | Formation | Holotype | Paratype | Validity | New assignment |
|---|---|---|---|---|---|---|
| *Laoporus schucherti* | Lull, 1918 | Coconino Fm. | YPM 2143 | | *nomen dubium* | cf. *Varanopus* isp. |
| *Laoporus noblei* | Lull, 1918 | Coconino Fm. | YPM 2144 | USNM V 8422 | *nomen dubium* | cf. *Varanopus* isp. |
| *?Limnopus coloradoensis* | Henderson, 1924 | Lyons Fm. | CU-MWC 13238 | | *nomen dubium* | cf. *Varanopus* isp. |
| *Dolichopodus tetradactylus* | Gilmore, 1926 | Coconino Fm. | USNM V 11123 | | *nomen dubium* | undetermined tracks |
| *Nanopus merriami* | Gilmore, 1926 | Coconino Fm. | USNM V 11146 | | *nomen dubium* | cf. *Erpetopus* isp. |
| *Baropezia eakini* | Gilmore, 1926 | Coconino Fm. | USNM V 11137 | | | *Ichniotherium sphaerodactylum* |
| *Agostopus matheri* | Gilmore, 1926 | Coconino Fm. | USNM V 11135 | | *nomen dubium* | cf. *Amphisauropus* isp. |
| *Palaeopus regularis* | Gilmore, 1926 | Coconino Fm. | USNM V 11143 | | *nomen dubium* | undetermined tracks |
| *Barypodus palmatus* | Gilmore, 1926 | Coconino Fm. | USNM V 11134 | | *nomen dubium* | undetermined tracks |
| *?Allopus arizonae* | Gilmore, 1926 | Coconino Fm. | USNM V 11132 | | *nomen dubium* | undetermined tracks |
| *Agostopus medius* | Gilmore, 1927 | Coconino Fm. | USNM V 11509 | | *nomen dubium* | undetermined tracks |
| *Ambylopus pachypodus* | Gilmore, 1927 | Coconino Fm. | USNM V 11511 | | *nomen dubium* | undetermined tracks |
| *Barypodus tridactylus* | Gilmore, 1927 | Coconino Fm. | USNM V 11502 | | *nomen dubium* | cf. *Tambachichnium* isp. |
| *Barypodus metszeri* | Gilmore, 1927 | Coconino Fm. | USNM V 11505 | | *nomen dubium* | cf. *Tambachichnium* isp. |
| *Baropus coconinoensis* | Gilmore, 1927 | Coconino Fm. | USNM V 11514 | | | *Ichniotherium sphaerodactylum* |
| *Nanopus maximus* | Gilmore, 1927 | Coconino Fm. | USNM V 11506 | | *nomen dubium* | Undetermined tracks |
| *Ammobatrachus turbatans* | Gilmore, 1928 | Supai Fm. | USNM V 11691 | | *nomen dubium* | Undetermined tracks |

more ichnotaxa with similar trackmakers are expected to generate such patterns during the progression on inclined sandy slopes.

## 6. Systematic paleontology

### 6.1. *Amphisauropus* Haubold, 1970

*Amphisauropus* isp.

#### 6.1.1. Material

De Chelly Formation: MNA-V 3442A, MNA-V 3442B, MNA-V 3451.

#### 6.1.2. Description

Pentadactyl ectaxonic footprints of a quadruped of intermediate size (pes length about 50 mm), with marked medial-lateral decrease in relief of the pes. Relatively short and thick digit traces with enlarged terminations. Plantigrade pes about as long as wide with large, oval sole impression, semi-plantigrade manus smaller than pes and significantly wider than long. The medial digit traces of the manus can be bent inwards. Simple alternating arrangement with close pes-manus couples, possible primary partial lateral pes-manus overstep at higher gaits. Pace angulation 80–130°. Pedal tracks parallel to the direction of progression, manual tracks parallel or sensibly bent inward. Possible tail impression, discontinuous with a slightly sinusoidal course.

#### 6.1.3. Remarks

The broad sole impression and lack of claw traces are typical of amphibian tracks. The pentadactyl manual tracks (Fig. 7C) distinguish this material from temnospondyl amphibian tracks such as *Limnopus* Marsh, 1894. The manual tracks notably wider than long and directed inward (Fig. 7B–C) are different from the reptiliomorph amphibian track *Ichniotherium* Pohlig, 1892, as is the marked medial-lateral decrease in relief of the pes (Fig. 7D, F). Moreover, the tail impression (Fig. 7A, G) is a very uncommon feature in *Ichniotherium*, whereas it is relatively common in the reptiliomorph amphibian track *Amphisauropus*. Morales and Haubold (1995) assigned the specimens MNA-V 3442A (Fig. 7B–F) and possibly MNA-V 3451 to *Agostopus matheri* Gilmore, 1926. However, the ichnotaxonomic significance of this ichnospecies is dubious (Table 1). Therefore, the most probable assignment is *Amphisauropus* Haubold, 1970. *Amphisauropus* is generally attributed to seymouriamorph reptiliomorph producers (Voigt, 2005; Marchetti et al., 2017a).

#### 6.1.4. Similar material

The study of the type material of *Agostopus matheri* Gilmore, 1926 (USNM V 11135) and *Agostopus medius* Gilmore, 1927 (USNM V 11509)

from the Coconino Formation indicates two trackways that are inadequate for an anatomy-consistent ichnotaxonomy, because the diagnostic morphology and proportions are deformed by taphonomic effects, resulting in a *Chelichnus*-like appearance due to slow upslope progression. Therefore, we consider these two ichnospecies *nomina dubia*, and assign this material to cf. *Amphisauropus* isp. (USNM V 11135) and indeterminate tetrapod tracks (USNM V 11509) (Table 1).

### 6.2. *Dromopus* Marsh, 1894

cf. *Dromopus* isp.

#### 6.2.1. Material

Coconino Formation: UCMP 159262, UCMP 159265.
De Chelly Formation: CU-MWC 139.71.

#### 6.2.2. Description

Relatively small (pes length of about 3 cm), semi-digitigrade, markedly ectaxonic footprints of a quadruped with long and slender digit traces terminating in thin sharp claw traces and with a relatively short palm/sole impression. The pes is pentadactyl, the digit traces I-IV are distally bent inward, tightly grouped and superimposed proximally, digit trace IV is sensibly longer than digit trace III and digit trace V is in a proximal-lateral position, about as long as digit trace III and oriented outward. The manus is smaller and more incomplete, but the morphology and proportions are similar to the pes. Simple, alternating arrangement of close pes-manus couples in broad trackways, the pes is usually directed outward, and the manus is more medial and aligned with the direction of progression. Pace angulation 60–100°. A continuous and straight tail impression can be present.

#### 6.2.3. Remarks

This material matches the diagnostic features of *Dromopus* Marsh, 1894, with regard to the slender digit traces with sharp claw impressions, the markedly ectaxonic footprints with grouped digit traces I–IV, and the proximal digit trace V. The pedal digit trace IV markedly longer than digit trace III (Fig. 8B–F) is different from *Tambachichnium* Müller, 1954. The pedal digit trace V about as long as digit trace III (Fig. 8A, C) is different from *Rhynchosauroides* Maidwell, 1911. Nevertheless, the poor and incomplete preservation of the manual tracks (Fig. 8B–F) hampers a definitive assignment, so we classify this material as cf. *Dromopus* isp. The occurrence of *Dromopus* was already highlighted by Haubold et al. (1995a) for the specimen CU-MWC 139.71, that we re-assign to cf. *Dromopus* isp. because of the poorly-preserved manus. *Dromopus* is generally attributed to araeoscelid eureptile or bolosaurid parareptile producers (Voigt, 2005).
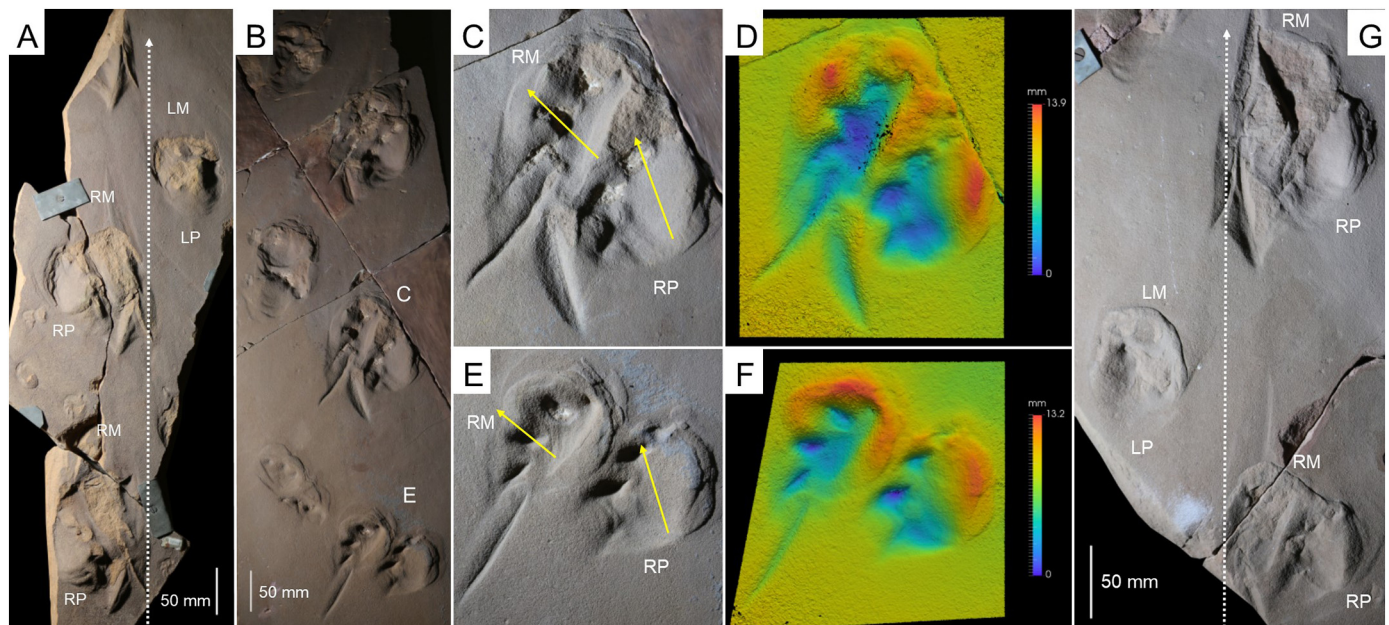
**Fig. 7.** *Amphisauropus* isp. Dashed white arrows indicate the direction of progression, full yellow arrows indicate the orientation of digit trace III. L = left, R = right, P = pes, M = manus. A) MNA-V 3442B, asymmetric trackway and discontinuous sinusoidal tail impression, convex hyporelief. B–F) MNA-V 3442A, concave epirelief. B) Asymmetric trackway. C, E) Right pes-manus couples. C, F) False-color depth map of C and E, respectively. G) MNA-V 3451, asymmetric trackway and discontinuous sinusoidal tail impression, concave epirelief. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
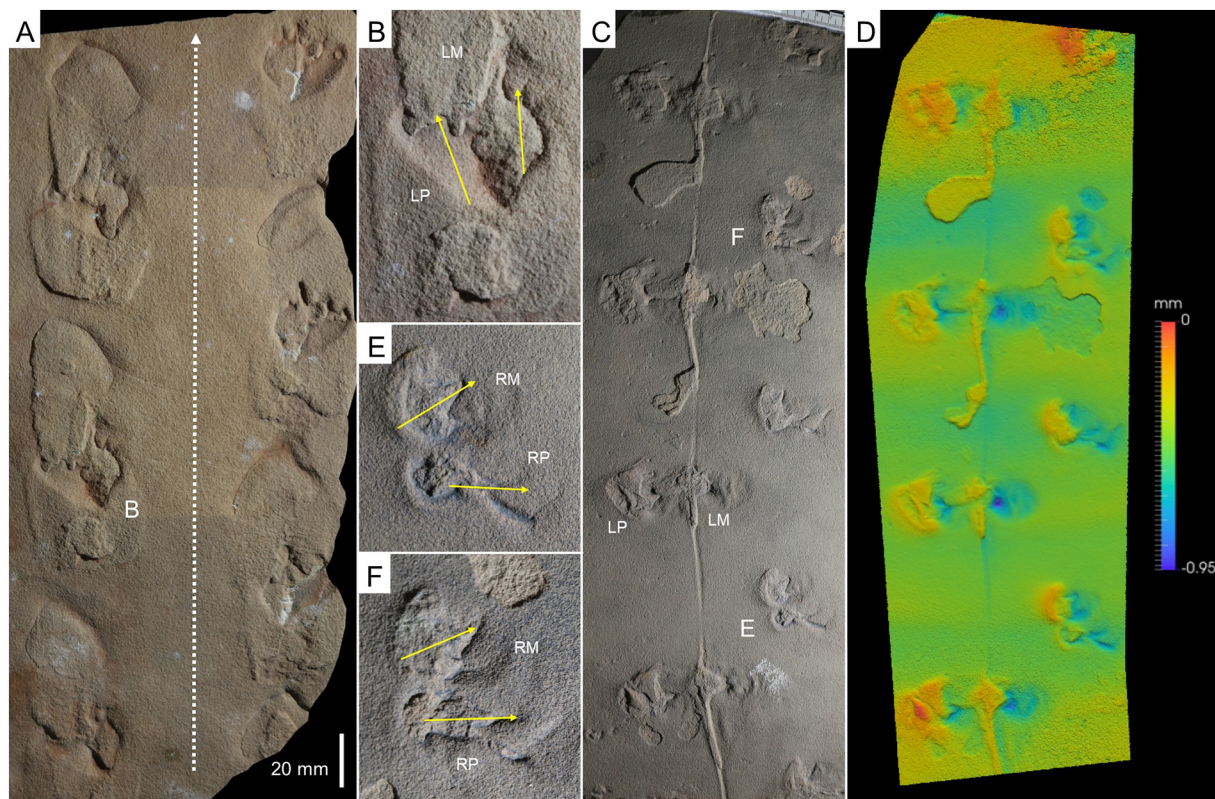


**Fig. 8.** cf. *Dromopus* isp. Dashed white arrows indicate the direction of progression, full yellow arrows indicate the orientation of digit trace III. L = left, R = right, P = pes, M = manus. A–B) UCMP 159265, concave epirelief. A) Symmetric trackway with low pace angulation. B) Left pes-manus couple. C–F) UCMP 159262, concave epirelief. C) Asymmetric trackway with low pace angulation and continuous tail impression. D) False-color depth map. E–F) Left pes-manus couples. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

### 6.3. Erpetopus Moodie, 1929

Erpetopus isp.

#### 6.3.1. Material

Coconino Formation: MNA-V 3343, MNA-V 3379, MNA-V 3385, MNA-V 3439, MNA-V 3440, MNA-V 3682, RAM 385, RAM 7139, RAM 10003, UCMP 36878, UCMP 42940, USNM V 11151, YPM 9843.

De Chelly Formation: MNA-V 3441, MNA-V 3452, MNA-V 3454.

#### 6.3.2. Description

Semi-plantigrade, ectaxonic, pentadactyl and small footprints (pes length of about 10–15 mm) of a quadruped. Long and slender digit traces terminating in thin and sharp claw impressions, digits traces I-IV grouped and distally bent inwards, digit traces III and IV of similar length, digit trace V about as long as digit trace I or II, in a proximal position and distally bent outward. Manus smaller than pes, very short palm/sole impressions, median-lateral decrease in relief of the pes. Simple alternating arrangement of close pes-manus couples in broad to narrow trackways and possible primary lateral pes-manus overstep at higher gaits. Pace angulation 60–125˚. Pes generally oriented outward and manus oriented inward. Thin and slightly sinusoidal tail impression sometimes observed.

#### 6.3.3. Remarks

This material fits the diagnostic features of the ichnogenus Erpetopus Moodie, 1929. The long and slender digit traces terminating in thin sharp claw traces and the short palm/sole impressions are typical amniote track features (Fig. 9D–F). The similar length of digit traces III and IV is different from the reptilian track Dromopus, and the position and relative length of digit trace V (Fig. 9B–H) is different from the reptilian track Dromopus and the synapsid track Tambachichnium. The grouped digit traces I-IV and proximal pedal digit trace V (Fig. 9D–F) are different from captorhinid tracks such as Hyloidichnus and Notalacerta. The relative length of pedal digit trace V (Fig. 9B–H) is smaller than the reptilian tracks Notalacerta and Varanopus. The specimens MNA-V 3441 (Fig. 7H), MNA-V 3454 (Fig. 7G) and YPM 9843 were previously assigned to Laoporus schucherti Lull, 1918. However, the holotype of Laoporus schucherti (specimen YPM 2143) (Table 1) shows a relatively long digit trace V, about as long as digit trace III and parallel to digit trace IV. This is clearly different from this material, therefore it is not assignable to Laoporus schucherti. Consequently, we assign all this material to Erpetopus Moodie, 1929. Erpetopus is generally regarded as a small track of reptilian affinity, possibly captorhinomorph eureptile (e.g. Haubold and Lucas, 2001, 2003) or parareptile (Marchetti, 2016).

#### 6.3.4. Similar material

The holotype of Nanopus merriami Gilmore, 1926, USNM V 11146, from the Coconino Formation shows some features consistent with Erpetopus Moodie, 1929 such as the thin and slender digit traces and the digit trace proportions of the pes. Nevertheless, lacking complete manual impressions and due to the overall poor preservation, we consider this ichnotaxon a nomen dubium and assign this material to cf. Erpetopus isp. (Table 1). Several high-gait trackways of small size have identical manual morphology and similar size with respect to Erpetopus (e.g. RAM 3301, Fig. 3F), and the complete primary lateral pes-manus overstep is known from this genus (LM pers. comm). Nevertheless, the lack of complete pedal footprints hampers a definitive assignment, so we classify this material as cf. Erpetopus isp.

### 6.4. Ichniotherium Pohlig, 1892

Ichniotherium sphaerodactylum (Pabst, 1895).

#### 6.4.1. Material

Coconino Formation: MNA-V 3386, UCMP 42945, UCMP 42951,

USNM V 11137 USNM V 11508, USNM V 11514, YPM 288.

De Chelly Formation: MNA-V 3449.

#### 6.4.2. Description

Relatively large (pes length 50–100 mm), plantigrade, pentadactyl and ectaxonic footprints of a quadruped with stiff straight digit traces, enlarged digit terminations and relatively large and ovoid palm/sole impressions. Pedal digit traces are relatively longer than manual digit traces. Pedal digit trace V is about as long as digit trace III. The pes is slightly longer than wide, and the manus wider than long and smaller than pes. Simple alternating arrangement of pes-manus couples in broad trackways with low pace angulation (60–80˚). Footprints generally aligned to the direction of progression, the pes can be slightly bent outward, the manus slightly bent inward. Partial secondary overstep of the manus on the subsequent pedal impression can be observed.

#### 6.4.3. Remarks

The relatively long stiff digit traces with enlarged terminations and the large ovoid sole impression and the ectaxonic tracks are typical traits of amphibian tracks. The pentadactyl manus (Fig. 10C–F) is different from temnospondyl amphibian tracks such as Limnopus Marsh, 1894. The ovoid sole impression separated from digit traces, the relative length of the manual digit traces and the relative length of digit trace V, about as long as digit trace III, the less evident medial-lateral decrease in relief, the trackway pattern with the footprint aligned with the direction of progression and the very low pace angulation (Fig. 10A–B, G–I) are different from the reptiliomorph amphibian track Amphisauropus Haubold, 1970. These are instead typical traits of the reptiliomorph amphibian track Ichniotherium Pohlig, 1892. The relative length of digit trace V (Fig. 10C–F, J–K) is consistent with the ichnospecies I. sphaerodactylum (Pabst, 1895) and it is different from I. cottae Pohlig, 1885 as demonstrated by Voigt and Haubold (2000), Voigt (2005), Voigt et al. (2007) and Marchetti et al. (2018b). The holotypes of Baropezia eakini Gilmore, 1926 (USNM V 11137, Fig. 10H–I) and Baropus coconinoensis Gilmore, 1927 (USNM V 11514) are considered junior subjective synonyms of Ichiotherium sphaerodactylum. Ichniotherium has been attributed to diadectomorph reptiliomorph amphibian trackmakers (Voigt et al., 2007).

### 6.5. Tambachichnium Müller, 1954

cf. Tambachichnium isp.

#### 6.5.1. Material

Coconino Formation: MNA-NN 1, USNM V 11502, USNM V 11505, USNM V 11506.

#### 6.5.2. Description

Relatively large (pes length 50–100 mm), semi-digitigrade, pentadactyl and ectaxonic footprints of a quadruped. Digit traces I-IV are closely packed, proximally superimposed and distally bent inward. Marked ectaxony with longest digit trace IV and continuous increase in length from digit trace I and IV in the pes. Digit traces are rather thick and terminate in thin, sharp claw impressions. Digit trace V is proximally positioned and oriented outward. Manual tracks smaller, more incomplete and less deeply impressed. Simple alternating arrangement of pes-manus couples arranged in broad trackways with low pace angulation (50–95˚) and possible partial secondary overstep of the manus on the pes at lower gaits. Footprints generally rotated outward with respect to the midline.

#### 6.5.3. Remarks

The combined effect of digit trace superimposition, digit tip drag marks and incomplete preservation provides difficulties for the ichno-taxonomic assignment of this material. In fact, the ichnospecies
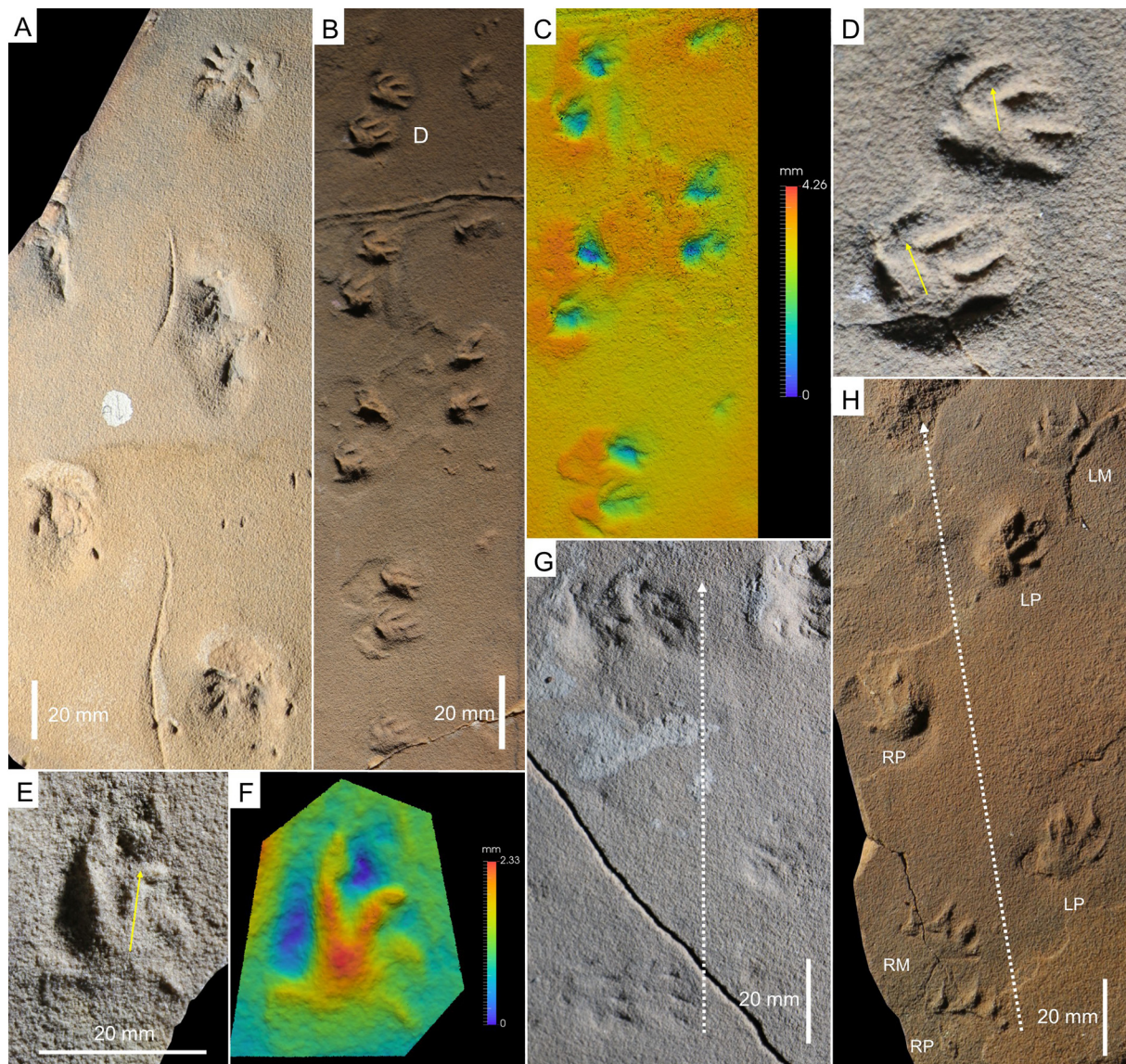
**Fig. 9.** *Erpetopus* isp. Dashed white arrows indicate the direction of progression, full yellow arrows indicate the orientation of digit trace III. L = left, R = right, P = pes, M = manus. A) MNA-V 3343, concave epirelief. Slightly asymmetric trackway, high pace angulation, discontinuous tail impression. B–D) MNA-V 3385, concave epirelief. B) Asymmetric trackway, low pace angulation. C) False-color depth map. D) Left pes-manus couple. E) USNM V 11151, right pes, convex hyporelief. F) False-color depth map of E. G) MNA-V 3454, concave epirelief. Asymmetric trackway. Note the increasing depth of the left pes-manus couples. H) MNA-V 3441, asymmetric trackway, convex hyporelief. Note the relatively short pedal digit trace V in B–H. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

*Barypodus tridactylus* Gilmore, 1927 (holotype USNM V 11502, Fig. 11D–E) and *Barypodus metszeri* Gilmore, 1927 (holotype USNM V 11505, Fig. 11F) were based on a supposed tridactyly and a supposed proximal lateral elongated palm/sole impression, which is instead a partial impression of digit trace V. The marked ectaxony, the close group of digit traces I-IV bent inward distally with sharp claw impressions and the proximal digit trace V are typical of reptilian tracks. The continuous increase in length between pedal digit traces I-IV (Fig. 11A–C) is different from *Dromopus* and *Rhynchosauroides*, which instead show a digit trace IV notably longer than digit trace III. This is instead consistent with *Tambachichnium* Müller, 1954. The apparently stout digit traces (Fig. 11B, E) can simply be a taphonomic artifact due to digit trace superimposition, so it is not considered ichnotaxonomically relevant. Also, the pace lower than usual (Fig. 11A, D, F) is not considered relevant, because of its variability and the probable difficult locomotion for trackmakers with a lacertoid foot on sandy, inclined surfaces. Due to the overall poor preservation and to the

incompleteness of manual tracks, we classify this material as cf. *Tambachichnium* isp. and consider the ichnotaxa *Barypodus tridactylus* and *B. metszeri* to be *nomina dubia* (Table 1).

### 6.6. *Varanopus* Moodie, 1929

*Varanopus curvidactylus* Moodie, 1929.

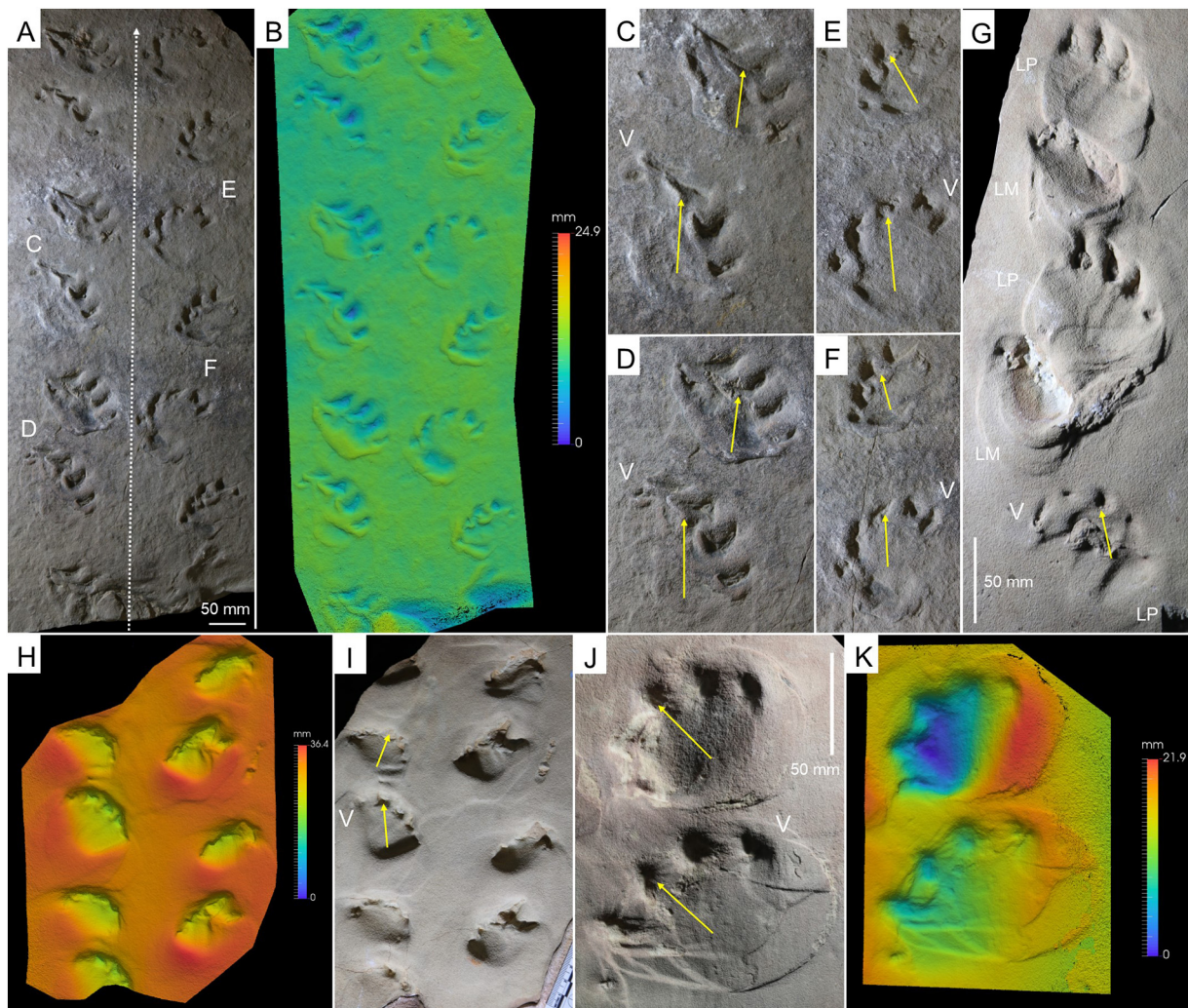#### 6.6.1. Material

Coconino Formation: MNA-NN 2, MNA-V 3327, MNA-V 3336, MNA-V 3339, MNA-V 3347, MNA-V 3376, MNA-V 3454, MNA-V 3470, MNA-V 5193, RAM-NN 1, RAM 141, RAM 214, RAM 226, RAM 236 RAM 342, RAM 350, RAM 410, RAM 420, RAM 422, RAM 7139, UCMP 36852, UCMP 36859, UCMP 42932, UCMP 42944, UCMP 97591.

#### 6.6.2. Description

Semi-plantigrade, ectaxonic, pentadactyl and small footprints (pes

**Fig. 10.** *Ichniotherium sphaerodactylum*. Dashed white arrows indicate the direction of progression, full yellow arrows indicate the orientation of digit trace III. L = left, R = right, P = pes, M = manus, V = pedal digit trace V. A–F) UCMP 42945, concave epirelief. A) Asymmetric trackway, low pace angulation. B) False-color depth map. C–D) Left pes-manus couples. E–F) Right pes-manus couples. G) YPM 288, incomplete step cycle with small pes-manus secondary overstep, concave epirelief. Note the different preservation of the first pes (determinable) and the subsequent pedal impression (*Chelichnus*-like). H–I) USNM V 11137, concave epirelief. Holotype of *Baropezia eakini*. H) False-color depth map. I) Asymmetric trackway with low pace angulation. J) MNA-V 3386, right pes-manus couple, concave epirelief. Note the relatively long pedal digit trace V in all the specimens. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

length of about 15–40 mm) of a quadruped. Long straight digit traces terminating in thin and sharp claw impressions. Pes wider than long, with relatively high digit trace I-IV divarication and digit trace V parallel to digit trace IV. Digit traces I-IV distally bent inward, digit trace V about as long as digit trace III. Manus about as long as wide and slightly smaller than pes, digit trace V about as long as digit traces I-II. Very short palm/sole impressions, medial-lateral decrease in relief of the pes. Simple alternating arrangement of close pes-manus couples in broad to narrow trackways. Pes generally parallel to the midline and manus oriented inward. Low to high pace angulation (50–160°) with possible complete primary pes-manus overstep at higher gaits.

*6.6.3. Remarks*

This is the most common track morphotype, but it is also one of the most difficult to interpret. The distally bent digit traces associated with digit drag marks and an incomplete or unclear preservation of the proximal part of the digit traces (Fig. 12E) and the peculiar trackway pattern relative to the slope direction have thus far hampered an anatomy-based interpretation. This problem was considered in the interpretation of *Laoporus* Lull, 1918 or *Chelichnus* Jardine, 1853

monospecific ichnoassociations in the Coconino and De Chelly formations (Lockley et al., 1995; Haubold, 2000), mostly based on taphonomy-controlled characters. Because of the poor preservation of the type material (YPM 2143, *Laoporus* holotype and DUMFM 5, *Chelichnus* holotype; assignable to cf. *Varanopus* isp. and cf. *Dicynodontipus* isp., respectively), we consider these two ichnogenera as *nomina dubia* that were historically utilized as wastebasket ichnotaxa to classify the Permian footprints from eolian paleoenvironments (e.g. McKeever and Haubold, 1996).

Nevertheless, after excluding the taphonomy-related features and considering the most complete and unequivocal material, some anatomy-controlled features can be observed. The ectaxonic tracks with long and straight digit traces terminating in thin, sharp claws and small palm/sole impressions are consistent with amniote ichnotaxa. The very short palm/sole impressions, the medial to lateral decrease in relief (depth of registration) and the lack of paw-like impressions (Fig. 12F) are different from the synapsid track *Dimetropus*. The position of pedal digit trace V, close to and parallel with digit trace IV (Fig. 12A–C), is different from amniote tracks such as *Tambachichnium, Dromopus* and *Rhynchosauroides*. The relative length of pedal digit trace V (Fig. 12A–C)
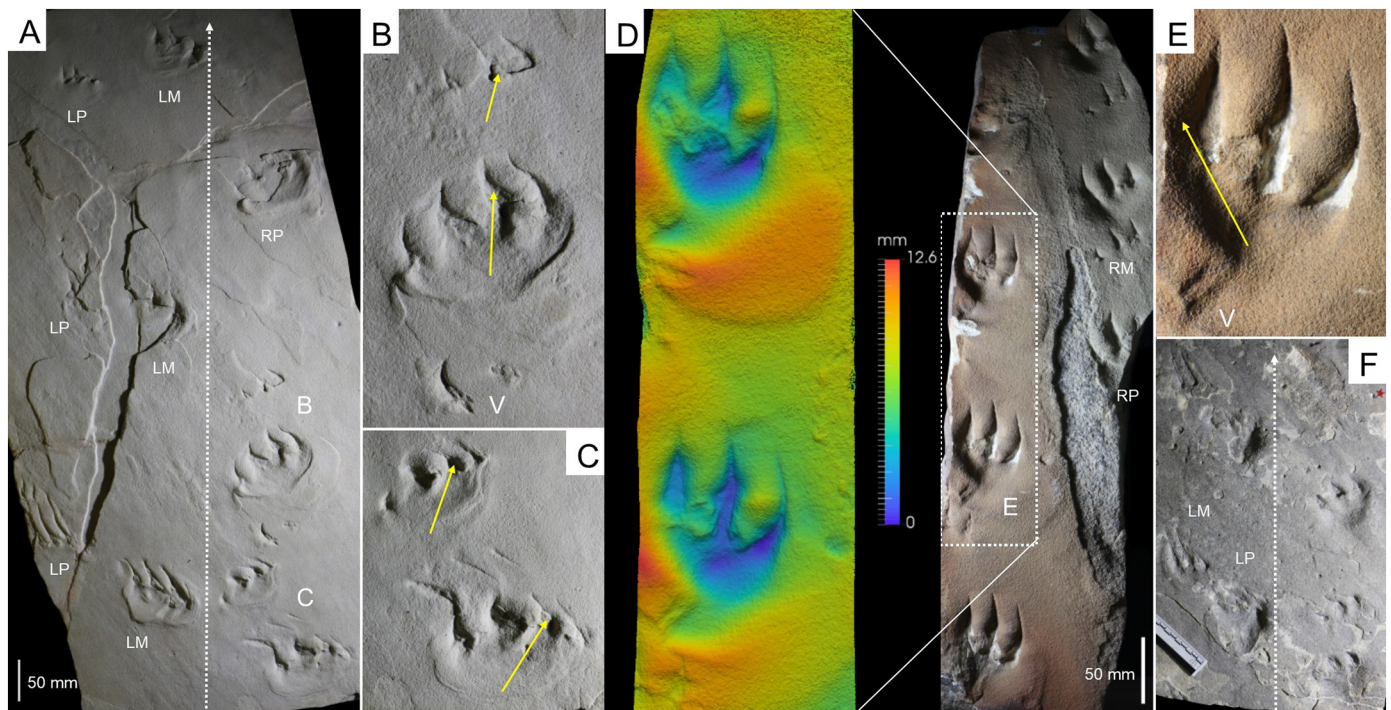
**Fig. 11.** cf. *Tambachichnium* isp. Dashed white arrows indicate the direction of progression, full yellow arrows indicate the orientation of digit trace III. L = left, R = right, P = pes, M = manus, V = pedal digit trace V. A–C) USNM V 11506, concave epirelief. A) Asymmetric trackway with low pace angulation. B–C) Right pes-manus couples. Note the proximal and laterally-oriented pedal digit trace V. D–E) USNM V 11502, holotype of *Barypodus tridactylus*, concave epirelief. D) Symmetric trackway with low pace angulation and false-color depth map. Note the light pes-manus secondary overstep. E) Left pes. Note the proximal and laterally-oriented pedal digit trace V. F) USNM V 11505, holotype of *Barypodus metzleri*, concave epirelief. Asymmetric trackway, low pace angulation. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
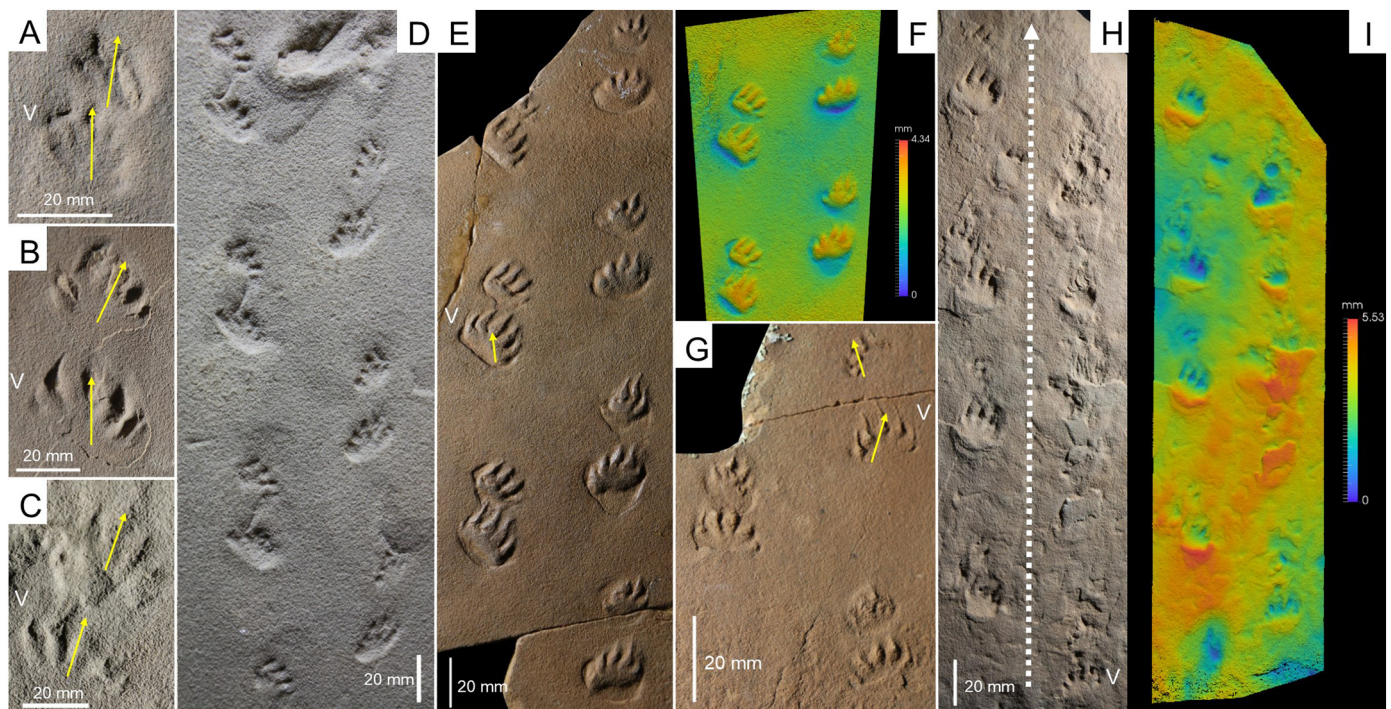


**Fig. 12.** *Varanopus curvidactylus* (A–G), cf. *Varanopus* isp. (H–I). Dashed white arrows indicate the direction of progression, full yellow arrows indicate the orientation of digit trace III. L = left, R = right, P = pes, M = manus, V = pedal digit trace V. A) MNA-V 3454, left pes-manus couple, concave epirelief. B) MNA-V 3376, right pes-manus couple, convex hyporelief. C) RAM 422, left pes-manus couple, concave epirelief. D) RAM-NN 1, concave epirelief. Slightly asymmetric trackway with low pace angulation. E–F) MNA-V 3327, convex hyporelief. E) Slight asymmetric trackway with low pace angulation. F) False-color depth map. G) MNA-V 5193, symmetric trackway, low pace angulation, convex hyporelief. H–I) YPM 2143, holotype of *Laoporus schucherti, nomen dubium*, concave epirelief. H) Slight asymmetric trackway with low pace angulation. Note the relatively long pedal digit trace V in all the specimens. I) False-color depth map. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

is different from the reptilian ichnotaxa *Erpetopus* and *Hyloidichnus*. The morphology and arrangement of pedal digit traces and the relative size of the manus and pes (Fig. 12A–C) are different from the ichnotaxa *Notalacerta, Robledopus* and *Varanopus microdactylus*. The only ichnotaxon showing traces of pes wider than long, straight digit impressions, digit trace V about as long as digit trace III and close to digit trace IV and manus of similar size with respect to the pes is *Varanopus curvidactylus* Moodie, 1929. This ichnotaxon is valid because based on a well-preserved and complete pes-manus couple and a large quantity of well-preserved material including trackways is known from the type locality of Castle Peak, Texas (Haubold and Lucas, 2001, 2003). The wide range of pace angulation, including complete pes-manus overstep at high gaits (Fig. 3D), is a new trait for *V. curvidactylus*, not observable in the type locality because of the scarcity of step cycles (although complete pes-manus overstep is observed in isolated couples; Haubold and Lucas, 2001, 2003). The trackway I of specimen RAM-NN 1 (Figs. 3A, C; 12D) was attributed to *Laoporus noblei/Chelichnus bucklandi* by Haubold et al. (1995a). We re-assign the trackway I of specimen RAM-NN 1 to *Varanopus curvidactylus*. We consider *Laoporus noblei* and *Chelichnus bucklandi* to be *nomina dubia* due to the incomplete and poor preservation of the type material of these ichnotaxa (YPM 2144 and USNM V 8422, holotype and paratype of *L. noblei*, respectively, Table 1; RSM 1875.28.17, lectotype of *C. bucklandi* in McKeever and Haubold, 1996).

*V. curvidactlyus* is usually attributed to a small reptilian trackmaker, such as captohinid eureptiles (Haubold and Lucas, 2001, 2003).

### 6.6.4. Similar material

The holotype of *Laoporus schucherti* Lull, 1918 (YPM 2143, Fig. 12H–I), the holotype of *L. noblei* Lull, 1918 (YPM 2144) and the paratype of *L. noblei* Lull, 1918 (USNM V 8422), all from the Coconino Formation, have features similar to *Varanopus curvidactylus*. In some cases (e.g. YPM 2143, Fig. 12H–I), the traces of the pedal tips are recognizable and consistent with the arrangement and proportions of this ichnotaxon. However, the incompleteness and overall unclear morphology of this material hampers a definitive assignment and does not constitute a good reference for ichnotaxonomy, so we consider the ichnotaxa *L. schucherti* and *L. noblei* as *nomina dubia* and classify this material as cf. *Varanopus* isp. (Table 1) The specimen MNA-V 3456 from the De Chelly Formation is also attributed to cf. *Varanopus* isp.

## 7. Biostratigraphy and paleoecology

The study of the combined effects of locomotion and taphonomy on the tetrapod footprint record of the early Permian Coconino and De Chelly formations of Arizona brought to light concerns that have important implications for new hypotheses about track formation and preservation on the foreset surfaces of eolian paleoenvironments. After a selection of the most complete and significant material for an anatomy-based interpretation, we provide new track assignments for both these formations. Almost all Coconino and De Chelly tracks and most from other Permian eolianites have been previously 'lumped' into *Chelichnus* Jardine, 1853 or *Laoporus* Lull, 1918, and have for historic reasons become a wastebasket ichnotaxa (e.g. Lockley et al., 1994, 1995; Haubold et al., 1995a; Morales and Haubold, 1995; Citton et al., 2012). This study has found many Coconino and De Chelly trackways to be more morphologically diverse, and in some cases better preserved and diagnostic of trackmaker morphotypes. This has underscored concerns that *Chelichnus* and *Laoporus*, including type ichnospecies, and like many ichnotaxa derived from eolianites, exhibit sub-optimal preservation and have to be considered *nomina dubia* (Table 1). In fact, the type material of *Chelichnus* and *Laoporus* (DUMFM 5 *Chelichnus* holotype, assignable to cf. *Dicynodontipus* isp., and YPM 2143, *Laoporus* holotype, assignable to cf. *Varanopus* isp.) are too poorly-preserved to be confidently assigned and to be a reference for ichnotaxonomy. Therefore, they are both considered *nomina dubia* and so they are not

senior subjective synonyms of any anatomy-consistent ichnotaxon.

Therefore, the Coconino Formation track record is here interpreted as including the following ichnotaxa: cf. *Amphisauropus* isp., cf. *Dromopus* isp., *Erpetopus* isp., *Ichniotherium sphaerodactylum*, cf. *Tambachichnium* isp. and *Varanopus curvidactylus* (Table 2). The De Chelly Formation includes: *Amphisauropus* isp., cf. *Dromopus* isp., *Erpetopus* isp., *Ichniotherium sphaerodactylum* and cf. *Varanopus* isp. (Table 2).

These tracks are attributed to small parareptiles/captorhinomorph eureptiles (*Erpetopus, Varanopus curvidactylus*), bolosaurid parareptiles/diapsid eureptiles (cf. *Dromopus*), varanopid synapsid (cf. *Tambachichnium*) and reptiliomorph amphibians (*Amphisauropus, Ichniotherium sphaerodactylum*). The small parareptile/captorhinomorph eureptile tracks seem to be predominant, the reptiliomorph amphibian tracks are rather common and the bolosaurid parareptile/diapsid eureptile and varanopid synapsid tracks are relatively rare in both formations.

The De Chelly Formation is considered to be early Kungurian (middle Leonardian) in age and crops out in Arizona and New Mexico. In the Lucero uplift of New Mexico, the underlying unit is the Abo Formation, which is considered almost completely Wolfcampian (Voigt and Lucas, 2016). In Socorro County (New Mexico), the overlying Abo Formation is overlain by the Arroyo de Alamillo Formation, which is a homotaxial equivalent of the De Chelly Formation. It is characterized by abundant occurrences of *Dromopus, Erpetopus* and *Varanopus* (all here shown to be present in the De Chelly Formation), whereas *Dimetropus* and *Batrachichnus* are rare (Voigt and Lucas, 2017).

The Coconino Formation is considered to be late Kungurian (late Leonardian) and crops out only in Arizona. The Choza Formation of Texas is supposed to be an approximate equivalent of the Coconino Formation. Its abundant track record includes *Erpetopus, Dromopus* and *Varanopus* (Haubold and Lucas, 2001, 2003), with a large predominance of *Erpetopus*. These three ichnogenera occur as well in the Coconino Formation, in which the predominant ichnotaxa are *Varanopus* and *Erpetopus*.

The Coconino and De Chelly tetrapod ichnoassociations of eolian paleoenvironments are therefore very similar to the most important contemporary (late Artinskian-Kungurian) ichnoassociations of water-laid red beds in the western USA, which are all characterized by a predominance of sauropsid tracks and the rarity of temnospondyl amphibian and synapsid tracks, different from the amphibian and pelycosaur-dominated early Cisuralian ichnoassociations (e.g. Sangre de Cristo, Abo and Robledo Mountains formations; *Dromopus* track biochron, Voigt and Lucas, 2018). They both include *Erpetopus*, index taxon of the *Erpetopus* track biochron, which has its first appearance during the late Artinskian (Voigt and Lucas, 2018). In fact, the ichnotaxon *Erpetopus* appears in the late Artinskian (Rabejac Formation of France and topmost Abo Formation of central New Mexico; Haubold and Lucas, 2001; Voigt and Lucas, 2017) and it is widespread in the Kungurian formations of New Mexico, Texas, France and Italy (Haubold and Lucas, 2001, 2003; Voigt and Lucas, 2017; Marchetti et al., 2013b, 2014, 2015a, 2015b, 2015c). *Varanopus curvidactylus*, that occurs in the Coconino Formation, is known from its type locality in Texas, which is Kungurian (Haubold and Lucas, 2001, 2003). Other supposed occurrences of *V. curvidactylus* in New Mexico and France (e.g. Lucas et al., 2001; Gand and Durand, 2006) should be rather assigned to an ichnospecies different from *V. curvidactylus*, because of the much shorter pedal digit trace V. The abundance and diversity of parareptile/captorhinomorph tracks is a common feature of late Cisuralian ichnoassociations, and it is usually associated with rarity and a low diversity of temnospondyl amphibian tracks such as *Batrachichnus* and *Limnopus* (Voigt and Lucas, 2018), which are absent in the Coconino and De Chelly formations. *Amphisauropus* and *Ichniotherium* are typical early Permian ichnotaxa, and their last occurrence is in the Kungurian (Marchetti, 2016; Voigt and Lucas, 2018). The occurrence of *Dromopus* and *Tambachichnium* is generally consistent with an early to middle

**Table 2**

List of tetrapod ichnotaxa from the Coconino, De Chelly and Lyons formations and faunistic attribution.

| Coconino Fm. | DeChelly Fm. | Lyons Fm. | lithofacies | attribution |
|---|---|---|---|---|
| *Varanopus curvidactylus* | cf. *Varanopus* isp. | cf. *Varanopus* isp. | foreset dune | captorhinomoprh eureptile |
| *Erpetopus* isp. | *Erpetopus* isp. | | foreset dune | parareptile |
| cf. *Dromopus* isp. | cf. *Dromopus* isp. | | foreset dune | parareptile/diapsid eureptile |
| cf. *Tambachichnium* isp. | | | foreset dune | varanopid synapsid |
| *Ichniotherium sphaerodactylum* | *Ichniotherium sphaerodactylum* | | foreset dune | reptiliomorph amphibian |
| cf. *Amphisauropus* isp. | *Amphisauropus* isp. | | foreset dune | reptiliomorph amphibian |
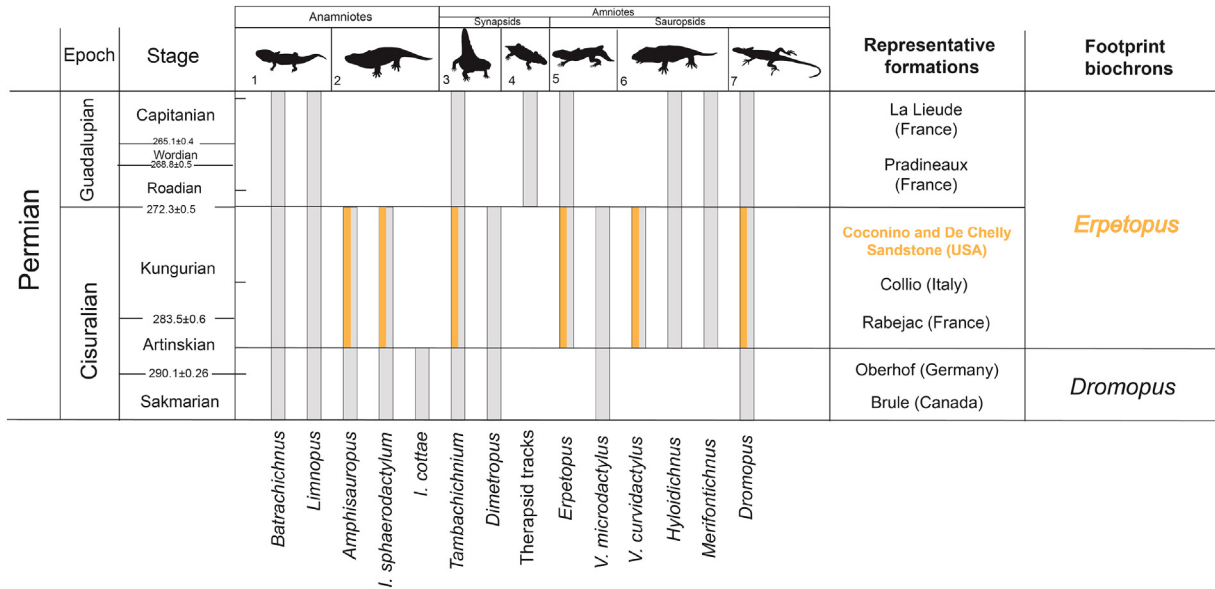


**Fig. 13.** Tetrapod footprint chronostratigraphy in the late Cisuralian and early Guadalupian (Permian). Gray bars are ichnogenera occurrences in non-eolian settings, orange bars are ichnogenera occurrences in eolian settings. 1 = temnospondyl amphibians, 2 = reptiliomorph amphibians, 3 = pelycosaur-grade synapsids, 4 = therapsid synapsids, 5 = parareptiles, 6 = captorhinid eureptiles, 7 = diapsid eureptiles/parareptiles.
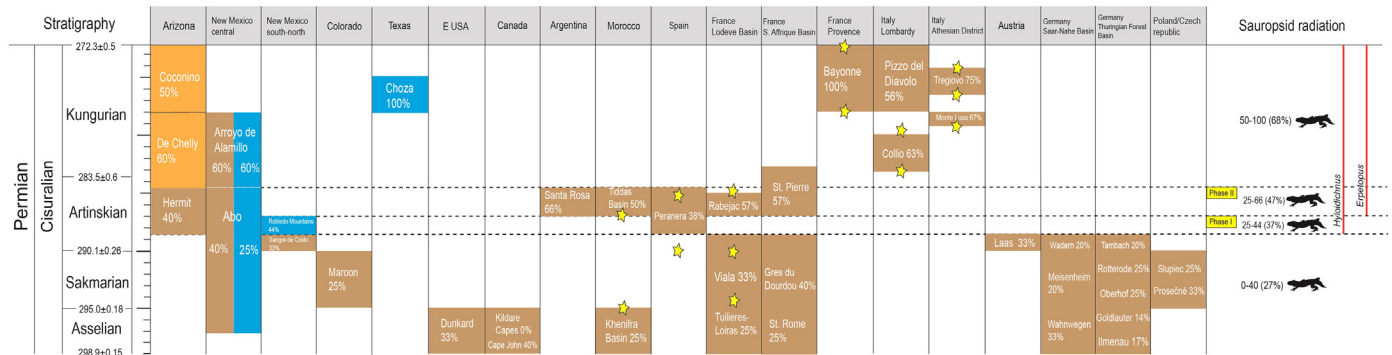


**Fig. 14.** The sauropsid radiation in the Cisuralian. Blue = fluvial-lacustrine coastal units, brown = fluvial-lacustrine inland units, orange = eolian inland to coastal units. Percentages are the relative proportion of ichnogenera attributed to sauropsids, obtained from Table 3. Stars are radioisotopic ages. Radioisotopic ages from Zheng et al. (1992), Schaltegger and Brack (2007), Marocchi et al. (2008), Pereira et al. (2014), Berra et al. (2015), Michel et al. (2015), Ait Lahna et al. (2018) and Youbi et al. (2018). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Permian age (e.g. Voigt, 2005; Gand and Durand, 2006). Therefore, we suggest a latest Artinskian to Kungurian age for the De Chelly and Coconino formations based on the first occurrence of *Erpetopus*, the occurrence of *V. curvidactylus* and last occurrence of *Ichniotherium* (Fig. 13).

**8. The Cisuralian sauropsid radiation**

The Cisuralian has been long considered synapsid- and anamniote-dominated from both the skeleton and the tetrapod footprint record (e.g. Haubold, 2000; Lucas, 2006). Sauropsids, and specifically

captorhinomorphs and parareptiles, and their supposed tracks were known but they were considered local faunas with scarce biostratigraphic and evolutionary meaning (e.g. Clark and Carroll, 1973; Haubold and Lucas, 2001, 2003; Gand and Durand, 2006). The possible evolutionary change found in the footprint record was explained by a different paleoecology due to different paleoenvironments (Hunt and Lucas, 2006, 2007). However, recent discoveries and revisions indicate an evident late Cisuralian radiation of sauropsids in North America with regard to the skeleton record (e.g. Modesto et al., 2014; MacDougall et al., 2017) and a contemporary sauropsid radiation in North America, North Africa and Europe basing on the footprint record (Voigt et al.,

**Table 3**
List of tetrapod ichnogenera in Cisuralian (Asselian-Kungurian) continental units.

| Stratigraphic unit | References | Anamniotes | | | | | Synapsids | | Sauropsids | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Matthewichnus | Batrachichnus | Limnopus | Amphisauropus | Ichniotherium | Dimetropus | Tambachichnium | Hyloidichnus | Merifontichnus | Varanopus | Robledopus | Notalacerta | Erpetopus | Dromopus |
| Coconino | This work | | | | X | X | | | | | X | | | X | X |
| De Chelly | This work | | | | X | X | | | | | X | | | X | X |
| Hermit | Haubold et al., 1995a | | X | | X | | X | X | X | | X | | | | |
| Arroyo de Alamillo | Voigt and Lucas, 2017 | | X | | X | | | | | | X | | | X | X |
| Arroyo de Alamillo | Voigt and Lucas, 2017 | | X | | | | X | | | | X | | | X | X |
| Abo | Lucas et al., 2001, Lucas et al., 2012, Voigt and Lucas, 2017 | | X | X | X | X | X | X | X | | X | | | X | X |
| Abo | Lucas et al., 2001, Lucas et al., 2012, Voigt and Lucas, 2017 | | X | | X | | X | | | | | | | | X |
| Robledo Mountains | Haubold et al., 1995b; Voigt et al., 2011; Voigt and Lucas, 2015a | X | X | X | X | | X | | X | | X | X | X | | X |
| Sangre de Cristo | Voigt and Lucas, 2015b | X | X | X | | X | X | X | | | | | X | | X |
| Maroon | Voigt et al., 2005 | | | | | X | X | X | | | | | | | |
| Choza | Haubold and Lucas, 2001, 2003 | | | | | | | | | | X | | | X | X |
| Dunkard Group | Lucas et al., 2016 | | | X | | | X | | | | | | | | X |
| Cape John | Van Allen et al., 2005 | | | X | X | | X | | | | X | | | | X |
| Kildare Capes | Brink et al., 2012 | | | | X | X | | | | | | | | | |
| Santa Rosa | Melchor and Sarjeant, 2004 | | X | | | | | | X | | X | | | | |
| Tiddas Basin | Voigt et al., 2011a | | X | | X | | X | | X | | X | | | | X |
| Khenifra Basin | Voigt et al., 2011b | | X | | | X | X | | | | | | | | X |
| Peranera | Voigt and Haubold, 2015; Mujal et al., 2016 | | X | X | X | X | X | | X | | X | | | | X |
| Rabejac | Gand, 1988; Haubold and Lucas, 2001; Gand and Durand, 2006 | | X | X | | | X | | X | | X | | | X | X |

**Table 3** (*continued*)

| Stratigraphic unit | References | Anamniotes | | | Synapsids | | Sauropsids | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Viala | Gand, 1988; Gand and Durand, 2006 | X | X | | X | | | | X | | X |
| Tuilieres-Loiras | Gand, 1988; Gand and Durand, 2006 | X | X | X | X | | | | | | X |
| St. Pierre | Gand, 1988; Haubold and Lucas, 2001; Gand and Durand, 2006 | X | X | | X | | X | | X | X | X |
| Gres du Dourdou | Gand, 1988, 1993; Gand and Durand, 2006 | X | X | | X | | | | X | | X |
| St. Rome | Gand, 1988, 1993; Gand and Durand, 2006 | X | X | | X | | | | | | X |
| Bayonne | Gand and Durand, 2006 | X | | | | | | | X | | X |
| Pizzo del Diavolo | Marchetti et al., 2013a, Marchetti et al., 2015a; Marchetti, 2016 | X | X | | X | | X | X | X | X | X |
| Collio | Marchetti et al., 2013b, Marchetti et al., 2015c | X | X | | | | X | X | | X | X |
| Tregiovo | Marchetti et al., 2015b | X | | | | | X | | | X | X |
| Monte Luco | Marchetti et al., 2013a | | X | X | | | | | | | X |
| Laas | Voigt and Marchetti, 2014 | | | X | | | | | | | X |
| Wadern | Voigt, 2007, Voigt, 2012 | X | | X | X | | | | | | X |
| Meisenheim | Voigt, 2007, Voigt, 2012 | X | | X | X | | | | | | X |
| Wahnwegen | Voigt, 2007, Voigt, 2012 | X | | | X | X | | | | | X |
| Tambach | Voigt, 2005, 2012 | | | X | X | X | | | X | | |
| Rotterode | Voigt, 2005, 2012 | X | | X | X | X | | | X | | X |
| Oberhof | Voigt, 2005, 2012 | X | | X | X | X | | | X | | X |
| Goldlauter | Voigt, 2005, 2012 | X | | X | X | X | | | | | X |
| Ilmenau | Voigt, 2005, 2012 | X | | X | X | | | | | | X |
| Prosečné | Voigt et al., 2012 | X | | X | | | | | | | X |
| Slupiec | Voigt et al., 2012 | X | | X | X | | | | | | X |

2011; Voigt and Lucas, 2015a, 2016, 2017, 2018; Marchetti et al., 2013a, 2015a, 2015b, 2015c; Marchetti, 2016; Mujal et al., 2016). The anatomy-consistent ichnotaxonomic revision of the Coconino and De Chelly tetrapod track record has important implications for the understanding of late Cisuralian tetrapod ichnoassociations at low latitudes: the abundance and diversity of pararreptile/captorhinomorph tracks and the rarity of temnospondyl amphibian tracks is consistent with all the Kungurian tetrapod track ichnoassociations in fluvio-lacustrine and eolian inland or marginal marine settings (Fig. 14, Table 3). This is different from pre-Artinskian ichnoassociations, which were instead characterized by more abundant and diverse amphibian tracks. In order to better evaluate this faunal transition, all the most relevant Cisuralian tetrapod ichnoassociations were placed in a chronostratigraphic scheme based on the most recent stratigraphic studies on these formations (through biostratigraphy or radioisotopic ages) (Fig. 14). Subsequently, all the tetrapod ichnogenera attributed to anamniotes, synapsids and sauropsids in every formation were listed in Table 3 and percentages of the number of sauropsid ichnogenera in each formation were calculated and listed in Fig. 14.

The first appearance of the ichnogenera *Hyloidichnus* and *Erpetopus* (the most characteristic ichnotaxa of the post-faunal turnover ichnofaunas) was utilized to define a two-phase faunal transition (I and II). The pre-transition ichnofaunas have a sauropsid track relative abundance of 0–40% (27% on average). This increases during the early Artinskian Phase I to 25–44% (37% on average), with the appearance of *Hyloidichnus*. During the late Artinskian Phase II this value increases to 25–66% (47% on average), with the appearance of *Erpetopus*. In the Kungurian, the faunal turnover is completed, and the ichnoassociations are dominated by sauropsid tracks (50–100%; 68% on average).

This two-phase sauropsid radiation is facies-crossing because it is observable in the track record of fluvial-lacustrine and eolian inland to marginal marine units (Haubold and Lucas, 2003; Marchetti et al., 2017b; Voigt and Lucas, 2016, 2017, 2018) (Fig. 14; Table 3). Therefore, it likely represents a faunal transition from the amphibian- and synapsid-dominated early Cisuralian ichnoassociations (*Dromopus* footprint biochron) to the sauropsid-dominated late Cisuralian ichnoassociations (*Erpetopus* footprint biochron) at all low latitudes of Pangea and in all paleoenvironments.

## 9. Conclusions

A new analysis of footprints preserved on inclined surfaces from the Coconino and De Chelly formations is provided, based on analysis of: 1) different trackway directions from the same trackway, 2) different trackway directions on the same stratigraphic surface, 3) trackway directions in the field, and 4) trackway directions in laboratory experiments. The results indicate several taphonomic effects that deform and modify the anatomy-controlled footprint morphologies and orientations and strongly influence the gait and trackway pattern, the overstep and the trackmaker body and footprint position and orientation during locomotion in these settings. Therefore, new, anatomy-consistent and diagnostic ichnotaxonomic assignments are proposed for tracks mostly previously lumped in the ichnotaxa *Chelichnus* and *Laoporus* which we consider *nomina dubia* because the type material is too strongly influenced by taphonomic effects. The ichnoassociation is characterized by a predominance of pararreptile/captorhinomorph tracks (*Varanopus curvidactylus, Erpetopus* isp.) and a significant occurrence of reptiliomorph amphibian tracks (*Ichnotherium sphaerodactylum, Amphisauropus* isp.), with rare bolosaurid / diapsid tracks (cf. *Dromopus* isp.) and synapsid tracks (cf. *Tambachichnium* isp.).

The meaning of this ichoassociation is now less facies-related and much more similar to contemporary non-eolian ichnoassociations. The faunal diversity and complexity in Cisuralian eolian paleoenvironments are greatly increased, from 2 to 6 different ichnotaxa. A comparison with the main Sakmarian to Kungurian non-eolian ichnofaunas suggests a latest Artinskian to Kungurian age for the Coconino and De Chelly

formations (*Erpetopus* footprint biochron).

Our review of all the available data together with the new results indicates a possible two-phase sauropsid radiation by the mid-Cisuralian, which can now be considered lithofacies-crossing and ubiquitous at low latitudes of Pangea. Therefore, further ichnotaxonomic studies and detailed track-trackmaker correlations of the whole Cisuralian sauropsid track record are required to infer the evolutionary, biostratigraphic, paleobiogeographic and paleoenvironmental meaning of this possibly important faunal transition.

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