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Walking, running, hopping
Analysis of gait variability and locomotor skills in *Brasilichnium elusivum* Leonardi, with inferences on trackmaker identification

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ABSTRACT

Synapsids were able to adopt different gaits, including half–bounding and bipedal skipping, since the Early Jurassic, as indicated by a large record of fossil footprints, found in hyper-arid erg–dominated paleonvironments from South and North America. The mammaliamorph origin of these footprints is corroborated by their shape, stance, and gait, in a large number of trackway specimens from the Paraná Basin (Botucatu Formation) of Brazil. This record is interpreted as the expression of the locomotor skills of a single trackmaker population, and might be grouped together under a pre-existing ichnotaxonomic label, *Brasilichnium elusivum* Leonardi, 1981, including one of the few unambiguous Mesozoic records of bipedal saltatory gait in synapsids. This bipedal saltatory gait is associated with desert paleoenvironments, and more specifically with sand dunes with little or no vegetation cover. Decades of collecting has resulted in one of the largest records of synapsid footprints worldwide, and ichnology has proven fundamental to investigate elusive aspects of their natural history.

1. Introduction and aims

Vertebrate ichnology contributes to widening our knowledge of fossil tetrapods, through anatomical, behavioural and ecological study (Sarjeant, 1995; Falkingham, 2014). Fossil footprints are direct evidence of locomotor styles of extinct animals, and occasionally they are the only record of life in specific paleoenvironments (Sarjeant, 1995; Thomson and Droser, 2015). This is the case for the large collection of footprints from the hyper-arid, erg–dominated setting represented by the Botucatu Formation and its equivalents (South America). Thanks to the efforts of Leonardi and co–workers (Leonardi, 1977, 1980, 1981, 1984; Leonardi and Godoy, 1980; Leonardi and Sarjeant, 1986; Leonardi and Oliveira, 1990; Leonardi and Carvalho, 1999), a large and accessible sample is today available for study, enabling us to investigate different palaeobiological aspects of the trackmakers. Most of these footprints are here referred to as *Brasilichnium elusivum* Leonardi, 1981, and are attributed to small, mammal-like synapsids. *B. elusivum* is also known from several stratigraphic units in North America (Lockley and Hunt, 1995; Lockley et al., 1995; Lockley et al., 1998; Rainforth and Lockley, 1996a, 1996b; Rainforth, 1997; Reynolds, 2006; Lockley, 2011; Engelmann and Chure, 2011; Engelmann et al., 2010; Chure et al., 2014; Rowland and Mercadante, 2014) and *Brasilichnium*-like footprints have been recently described from the Twyfelfontein Formation in Namibia (D'Orazi Porchetti and Wagensommer, 2015). Slightly larger footprints from Brazil, informally referred to as "theromorphoid" in the literature, might represent a second ichnospecies of *Brasilichnium* (pers. obs.). *Brasilichnium elusivum* shows a remarkable array of gaits including, among others, bipedal skipping. This footprint record represents a remarkable source of data that sheds light on the origin and diversification of specialized locomotor styles in synapsids. Bipedal saltatory gait is known in extant marsupials, placental mammals, and Aves, but is rarely found in the fossil record. Indeed, *B. elusivum* represents the only record of this specific gait in a Mesozoic quadrupedal trackmaker. In addition to the bipedal skipping gait, we noticed an additional locomotor style, running, for the *B. elusivum* trackmaker. This is exclusively found in downhill oriented trackways and is reported and analyzed here for the first time.

Here we examine the material to determine the extent of taphonomic bias on the sample. The sample is processed in numerical terms to quantify genuine gait variations. We informally ascribe all gaits discussed here to *Brasilichnium elusivum* in order to maintain its ichnotaxonomic stability and reinforce its paleoecologic significance. Footprints are eventually investigated from the paleozoologic

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perspective, in order to constrain as consistently as possible the trackmaker attribution.

2. Geological setting

The age of the Botucatu Formation has been discussed for decades (see Leonardi et al., 2007 for a synthesis). Here we employ the stratigraphic framework proposed by Milani et al. (1994, 2007), in which the Botucatu lithosome is considered as part of the Gondwana III Supersequence, with an age between Late Jurassic and Early Cretaceous. From a lithostratigraphic point of view, the Botucatu Formation is the basal unit of the São Bento Group (Schneider et al., 1974), representing a huge windblown sandstone accumulation in one of the largest paleoergs of Earth history. The areal extent of the Botucatu paleodesert has been approximated to 1.3 million km^2 (Assine et al., 2004). The Botucatu Formation represents a dry eolian system, characterized by large scale cross-bedded sandstone (Bigarella and Salamuni, 1969; Salamuni and Bigarella, 1967), deposited in hyper-arid conditions, with dry interdunes, at least in its southern exposures on the Brazilian territory (Scherer, 2000, 2002).

3. Materials, methods and terminology

This work is based on the analysis of material stored at the Paleontology and Stratigraphy Museum "Prof. Dr. Paulo Milton Barbosa Landim", Rio Claro Campus, São Paulo State University "Júlio de Mesquita Filho"(UNESP), from now on referred to as the "Rio Claro Collection". All slabs at the "Rio Claro Collection" are from the São Bento (also known as Corpedras) sandstone quarry (Araraquara Municipality, São Paulo State). Slabs were extracted from sets of cross–strata inclined at an average angle of 26° (Leonardi, 1980). Footprint-bearing slabs vary from decimetric grain-flow packs to thinner, wind rippled sequences varying in color from pale red to pink, and of fine sand grains. A provenance of the slabs from the lower portion of the dune's foreset is hypothesized, as it is usually not eroded by superimposition of overcoming dunes, and for the presence of climbing ripples layers, which are commonly found at the toe of the lee face.

A total of 109 slabs of various dimensions, including at least 991 *pes*/*manus* prints, mostly organized in trackways (see **Electronic Supplementary Material**) have been analyzed first-hand. Among these, 65 slabs preserve traces that can be ascribed to *Brasilichnium elusivum*. 89 *Brasilichnium* entries have been recorded in the database, mostly as trackways, and rarely as isolated footprints. A total of 669 *pes* prints have been analyzed, associated to 135 *manus* prints. All specimens were photographed and reproduced on transparent acetate peels superimposed to the slabs. Polished sections of a few slabs were produced to investigate sedimentologic features. Three-dimensional models of selected footprints and trackways have also been created based on close-range photogrammetry (Falkingham, 2012). A new labelling for the Botucatu Formation slabs is adopted here, referring solely to the "Rio Claro Collection". The new acronyms, URCR and URCM, are adopted instead of that (ARSB) originally introduced by Giuseppe Leonardi. For the examined material, the correspondence between old and new labelling is given in the **Electronic Supplementary Material**.

For this study, we subjectively limited our quantitative analysis to the *pes* traces, as they are better preserved, more consistent and reliable in shape, and about five times more abundant than the *manus* prints (669 *pes* vs 135 *manus*). A cluster of features have been chosen to test the morphological homogeneity of *pes* tracks in the studied sample. It consists of footprints from different trackways, selected based on their preservation, which must allow a precise identification of digit mark shapes. The number of digits is the main quantitative parameter; additional features include their shape and reciprocal spatial distribution (Fig. 1A–F).

In the following sections an array of anatomical and ichnological terms are employed, as well as other technical words concerning locomotion styles. For the latter, we primarily refer to the mammal gait definitions of Dagg (1973). In the case of bipedal saltatory gait, bipedal

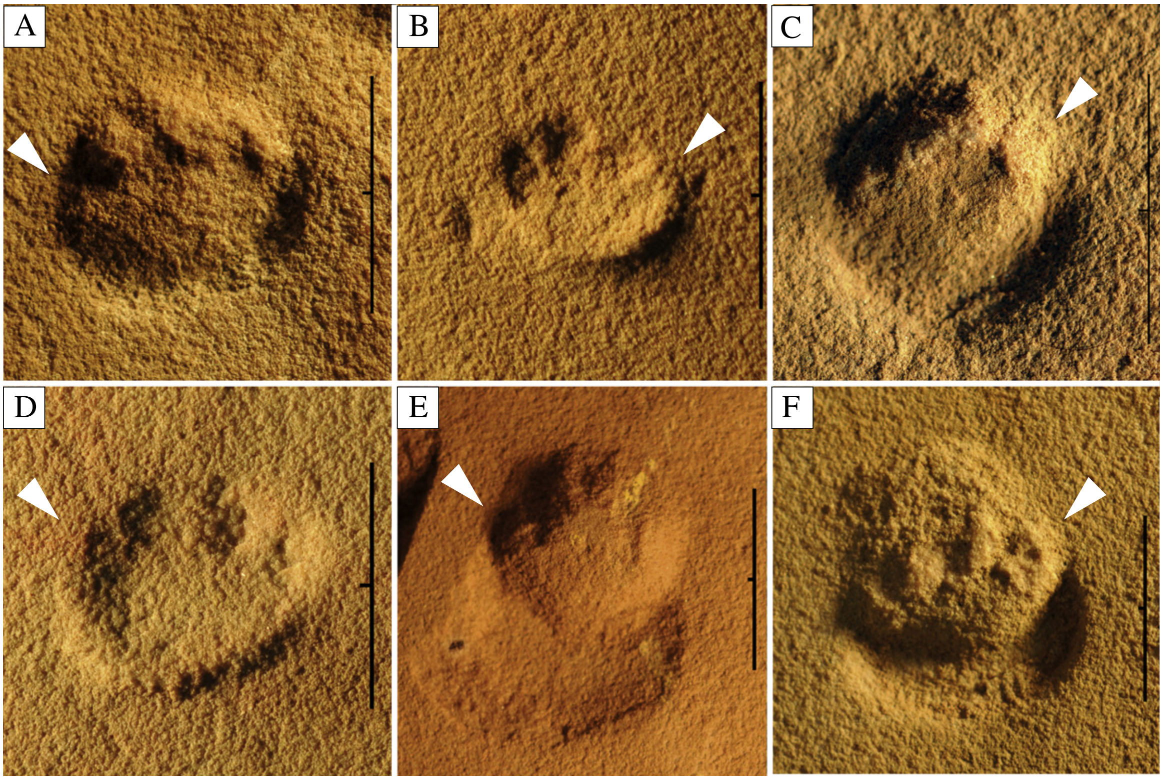

Fig. 1. Selection of *pes* prints from different slabs. A) and F) from URCM.41; B) from URCM.68; C) URCM.62; D) URCR.108; E) URCM.46; All tracks preserved as convex hyporelief, except B) and D). Black arrows mark the lateralmost digit. Scale bars 2 cm.

skipping is distinguished from a ricochetal bounding hop (Alexander, 2004; Bertram, 2016). For a detailed discussion on kinetic and kinematic aspects of the skipping gait see Minetti (1998). Unless otherwise stated, anatomical terms were taken from veterinary anatomy. Ichnological terms were taken after Leonardi (1987) and Thulborn (1990). Expulsion rim and marginal ridge refer to the displacement of sediment upwards generated by foot pressure on the ground. We also use sand crescent and pressure pad as synonyms to indicate expulsion rims on the dune foreset, even if Fornós et al. (2002) originally defined pressure pads as different from sand crescents (see also Melchor, 2015). Stance terminology is taken from Bakker (1971) and Charig (1972).

3.1. Measuring protocol

Linear measurements of footprints were taken directly from the slabs, whereas trackway parameters were measured on the peel drawings. Angle of foot impact on the sediment, depth of the footprint, and position of the sand crescents are all factors that determine the final shape of the footprint. For our purposes, footprint length (FL) is defined as the distance between the most distal and most proximal turbations of sediment with the exclusion of expulsion rims from the measurements. FL is measured, as consistently as possible, at the same reference point, namely at the intersection with the plane of the originally undisturbed slab surface, known as ‘zone of negative vertical displacement’ (see Falkingham, 2016). The width of the footprints is somewhat less exposed to variation, as the medio-lateral axis of the foot always impacts the ground in a parallel way. For this reason, we consider footprint width (FW) to be more consistent than the length (FL), and more useful to compare different footprints. Trackway parameters were taken from equivalent points on successive footprints. As a good portion of the Botucatu footprints consist of featureless hemispheric depressions, an approximate centre was chosen as reference point. Two main angular values are considered relevant here: pace angulation and rotation of the foot relative to the midline. In order to facilitate the collection of data on *pes* rotation, we establish a value of 0 (zero) when the longitudinal axis of the foot is parallel to the midline of the trackway, 1 (one) if the *pes* is rotated inward, and 2 (two) when the *pes* is outward rotated. Measuring the exact value of that angle is, in fact, extremely difficult on such small footprints. All measurements are in millimetres and degrees, and rounded to the closest unit (i.e., 11.8 mm is 12 mm).

3.2. Expulsion rims

Most footprints of the “Rio Claro Collection” are associated with marginal expulsion rims also sometimes referred to as sand crescents, which regularly lay downslope to the footprint. Even if they do not reveal anatomic features of trackmaker's feet (and are, as such, excluded from linear measurements in this work), expulsion rims may show the effect of forces acting on the sediment, adding useful information on locomotion styles. Although the force of gravity has a major role in orientating these crescent marks with the dip of the strata, they are also influenced by load forces generated by the animal pushing and dragging its limbs on and into the sediment. The axis of the expulsion rim might therefore diverge from those of maximum slope of the slip surface of the dune (Fornós et al., 2002). Additionally, the limit of the proximal wall of the sand crescent is difficult to define precisely as it fades evenly inside the footprint shaft. In the examined sample, expulsion rims are always crescent-shaped, but variation occurs in many parameters. The analysis of their genesis is beyond the scope of this work, and only a qualitative description is provided here.

In the future, it would be important to investigate the relationship between sediment properties, forces released during foot contact with the ground, and the inclination of the substrate. Some expulsion rims show a sharp crest and a short antero-posterior base; others have rounded crests and are antero-posteriorly wide. The top of several expulsion rims is eroded, forming a small plateau. According to Loope (2006), this erosion is explained by the occurrence of trackmaker-induced sand avalanches of dry sediment generated during dune crossing.

Interaction between expulsion rims can reveal the timing of feet touching down, as for footprints associated with bipedal skipping, in which an asynchronous touchdown is inferred by the overlapping between marginal rims which cut one another. Pressure pads help determining the direction of travel, based on the different arrangements and relative position of digit marks to which they are associated. As the distal end of digit marks is usually (though not always) oriented in the travel direction, the evidence that the animal is moving uphill is that the digit tips are heading in a direction opposite to the convex edge of the pressure pads. Conversely, digit marks heading to the concave side of the pressure pad indicate the animal was moving downhill. The profile section of tracks is useful to determine the direction of travel when digit marks are not preserved. In *Brasilichnium elusivum* the maximum *pes* penetration occurs at the acropodium (i.e., the phalangeal portion of the foot). In footprints where digits are not preserved, this feature, or better, the spatial relation of this feature to the expulsion rims, indicates the direction of travel.

4. Description

4.1. Morphological homogeneity of the sample: shape of the pes trace in detail

In its original diagnosis, *Brasilichnium elusivum* is a pentadactyl footprint associated with a handprint with an unspecified number of digits (Leonardi, 1981). The emended diagnosis proposed by Fernandes and Carvalho (2008a) re-established the number of digits on the *pes* as four. The *manus* print was defined as tetradactyl in the same work (Fernandes and Carvalho, 2008a). Slabs in the “Rio Claro Collection” show handprints with different degrees of preservation, but none of the specimens show the hand palm. In the sample, forefeet consist of digit prints, from two to three, isolated from one another (Fig. 2A–C). Single digit marks are piriform, with the proximal end more rounded than the distal one, which may be sharpened. The medialmost digit mark is the smallest. The hand mark is ectaxonic. Different portions of the *pes* and *manus* are preserved, but regardless the strong heteropody is interpreted here as a taphonomic bias on the sample. Position of the handprint with respect to the *pes* varies depending on the gait (see below). In the sample, *pes* prints of *Brasilichnium elusivum* are tetradactyl and asymmetric with a subtle ectaxony. Digit marks I, II, and III are slightly separated from digit print IV. Digit mark III extends more anteriorly relative to digit marks II and I, which are shorter. *Pes* impressions reveal a semidigitigrade posture of the autopodium, with the acropodium and the metapodial-phalangeal joints marked deeply into the sediment. Digit mark IV is shallower than group I–III. (Fig. 3).

The average FL/FW ratio is 0.7, as calculated on a sample of 421 footprints of walking, bipedal skipping, and half–bounding trackways. This set of characters defines a morphotype to which all locomotion styles displayed in the sample can be ascribed, and that is the expression of a single anatomical entity (i.e. a similar foot). Therefore, we infer that all trackways dealt with here (see **Electronic Supplementary Material**) pertain to the same trackmaker population.

4.2. Gaits

The studied sample has been divided into different categories, based on direction of travel and gait typology. As the animals were moving on inclined surfaces, the basic division is based on the direction of travel, with two main orientations: uphill and downhill. Further division is based on locomotion styles, with the distinction of four main gaits: walking, half–bounding, bipedal skipping, and running. A running gait has been observed in a small number of trackways. Remarkably, walking, half-bounding, and bipedal skipping are seen exclusively on uphill oriented trackways, whereas downhill trails all share a running gait,

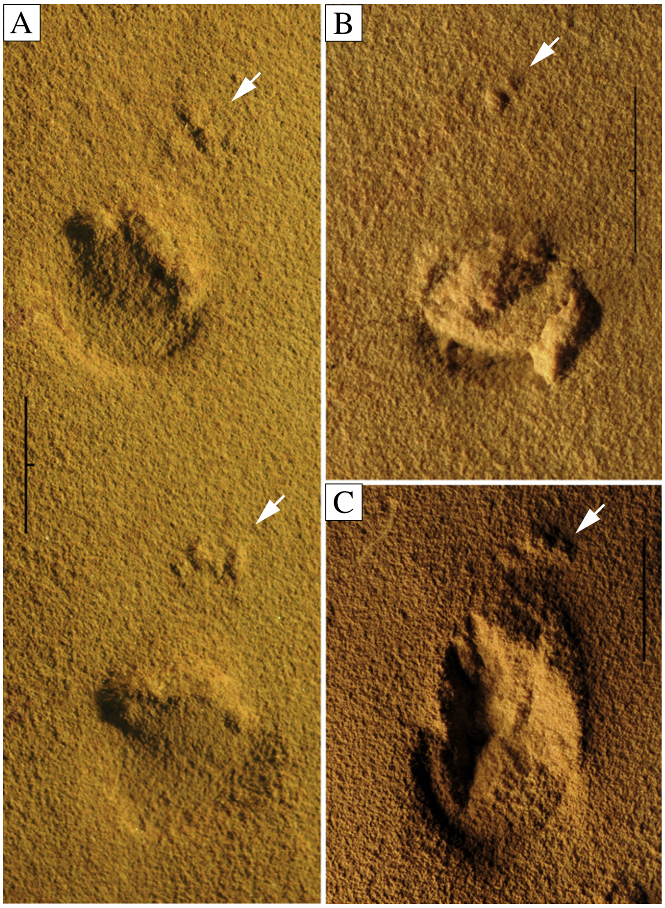

Fig. 2. Detail of *manus* prints (white arrows) from slabs A) URCM.71, B) URCM.34, and C) URCM.44. *Manus* prints are shallower than the *pes* prints, and consist of three (A and B) or two (C) small digit marks. All footprints are preserved as convex hyporelief. Scale bars 2 cm.

with high pace angulation and footmarks closely associated with the handprints. The possible presence of *Brasilichnium* trackways created by a running trackmaker on North American material was first suggested by Lockley and Hunt (1995).

4.3. Uphill trackways

4.3.1. Walking (Fig. 4)

This is the prevalent gait in the studied sample (Fig. 5), with about 68 walking trackways preserved on 57 slabs, representing 75.5% of the total number of sampled trackways. Walking trails record variation in pace, stride, pace angulation of *pes* and *manus* traces, associated with symmetrical and asymmetrical *pes* rotation (see **Electronic Supplementary Material**), and even in the presence/absence of associated *manus* prints. Only 10 out of 68 trackways show *manus* traces. Mean *pes* length (FL) is 12.5 mm ($n = 313$), and mean width (FW) is18 mm ($n = 351$). Total values of FL and FW are, respectively, between 4 mm and 22 mm and between 8 and 30 mm. Mode is 15 mm for both FL and FW. Mean pace value, as calculated on a sample of 296 *pes* prints, is 50.6 mm (min.: 21 mm; max.: 76 mm). The *pes* pace angulation in walking trackways, as calculated on 236 triplets of steps, has a mean value of 131.6°, with a mode of 129° (variation is between 81° and 161°). FL/FW ratio, as calculated on 309 *pes* prints in walking gait, has a mean value of 0.7.

The average pace angulation for *manus* trails is 115° (as calculated on 34 entries), with a range from 74° to 170°, with a median value of 118.5°.

4.3.2. Half–bounding

This gait is represented by a single short trackway on slab URCM.23, with one partial and two complete *manus*–*pes* sets (Fig. 6). Footprints are preserved in convex hyporelief. *Pes* prints are poorly preserved, showing no digit marks. Pes impressions are symmetric relative to the midline. The *manus* prints are about three times smaller than the *pes* prints, lying medially and posteriorly to them. *Manus* shape is only vaguely preserved, in the form of faint bulges. *Manus* prints are not symmetrical with respect to the midline of the trackway. The right mark, corresponding to the left *manus*, is withdrawn relative to the contralateral. Short and narrow expulsion rims are evident in the *pes* marks, but not in the *manus* prints. Average FW is 22.7 mm. At least one other slab with this gait pattern has been recorded in the literature (Leonardi and Sarjeant, 1986, Fig. 9).

4.3.3. Skipping (Fig. 7)

Footprints of jumping animals are not always synchronous, nor symmetrical. The asynchronicity of the foot falls is demonstrated by the presence of contralateral pressure pads cutting one another (Fig. 8). Only an unpaired touchdown of the feet can justify such an interaction between pressure pads. *Pes* position might vary relative to the midline, with one impression advanced in relation to the contralateral. In many cases, orientation also varies, with the mediolateral axis of collateral footprints rotated relative to one another. Stride is also variable, with trackways showing clear changes in jump length, generally with a regular pattern of increase or reduction (Fig. 9A–D). In URCM.66 (Fig. 7A, E), the sequence of steps testifies to a change of gait, from walking to bipedal skipping. In URCM.52, *pes* position is variable, with feet unpaired since the very start of the trackway, the left foot being slightly advanced relative to the right (Fig. 7C, G). On this latter foot, the animal exerted a higher pressure as its expulsion rim is clearly larger than the opposite. The second pair in the sequence is still left-first, becoming right-first from the third step onwards. The length of the aerial

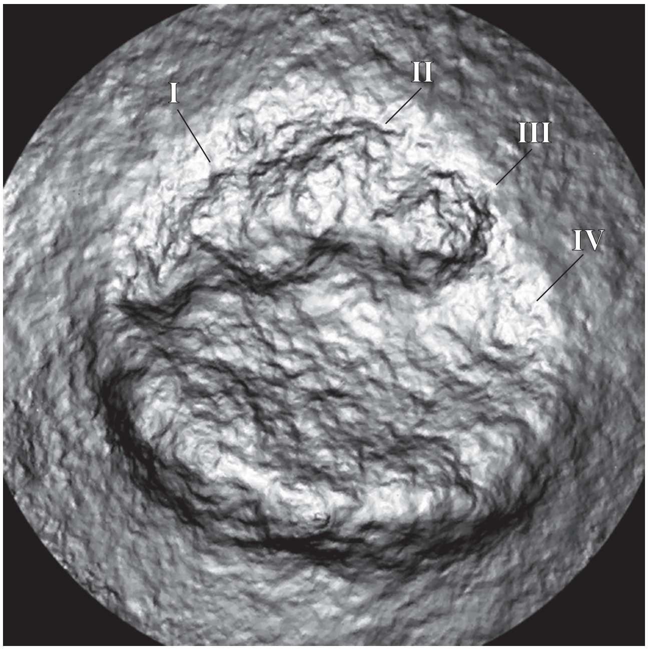

Fig. 3. Three dimensional model of a single footprint from an uphill-oriented trackway (slab URCM.41), to show digit marks morphology and relative arrangement. Penetration into the sediment varies depending on the digit. Indeed, digit mark IV is relatively shallow respect to the other digit marks. Digit marks I-III are deeply impressed, leaving a steep sand wall with three rounded insets at the proximal end of digit marks. This is in relation with the posture of the phalangeal portion of the digits, arranged to form a digital arcade. See text for explanation. Original track preserved as convex hyporelief. Track width 2 cm.

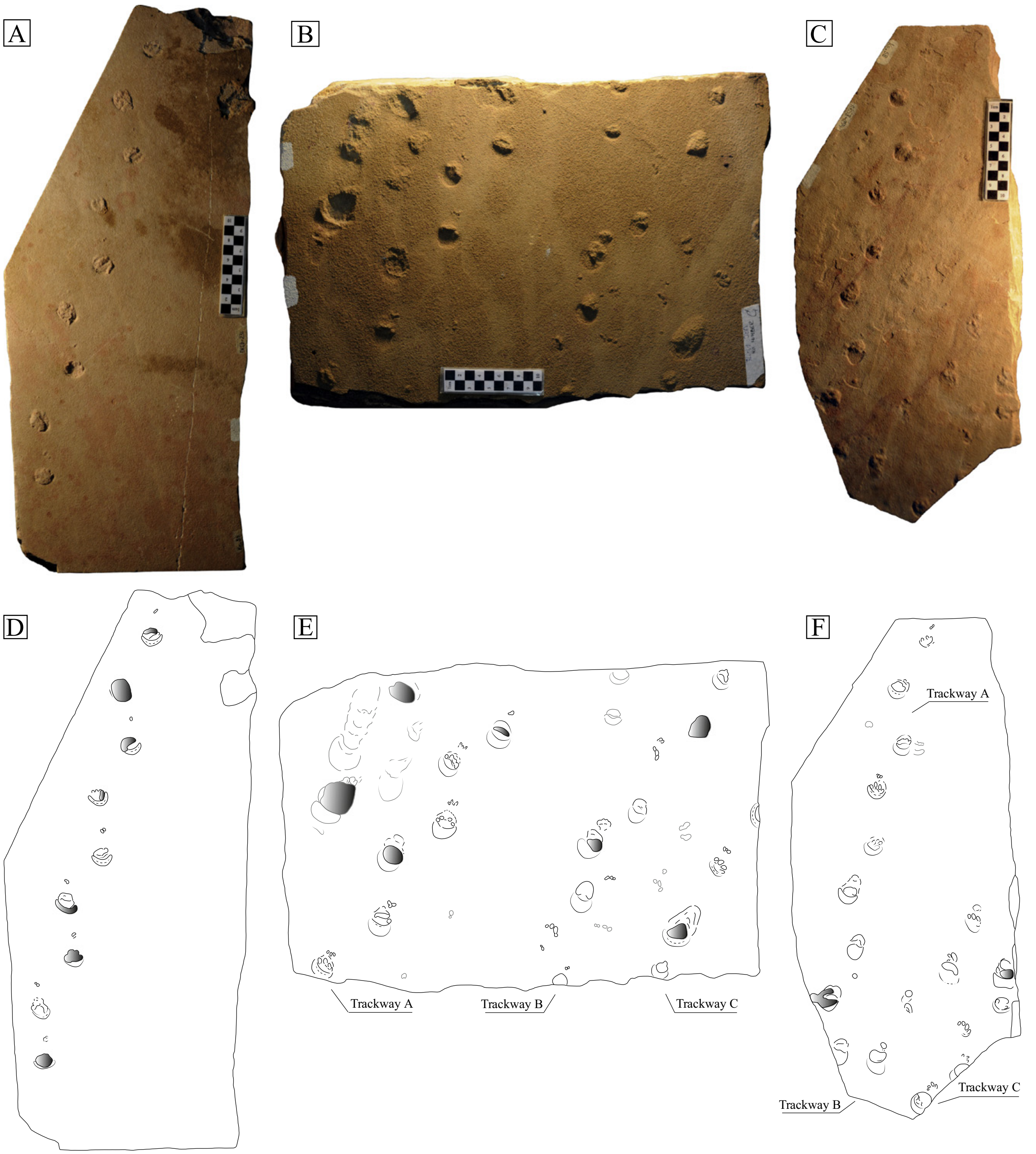

Fig. 4. Selection of slabs with well-preserved trackways in walking gait with *manus* prints. Photograph of slabs A) URCM. 34; B) URCM.71; C) URCM.58, and relative drawings (D–E). Scale bar 10 cm. Drawings at the same scale of the photographs; trackways with *manus* prints are in black, whereas those with no handmarks are in gray. Trackways with *manus* prints are indicated by capital letters (A, B, C). All the footprints are preserved as convex hyporelief.

phase increases throughout the trackway. FL/FW ratio, as measured on 51 *pes* marks, has a mean value of 0.7.

4.4. Downhill trackways

4.4.1. Running (Fig. 10)

A shift in trackmaker gait is associated with downhill oriented trails. All animals heading to the base of the dune's slipface adopt a specific locomotion style; running. This gait can be defined as a run, with high pace angulation, long stride, and *manus* impression (which are consistently preserved) lying close to the *pes* impression. This gait is clearly visible on at least 10 trackways (URCM.27, URCM.35, URCM.41d, URCM.61a, URCM.62c, URCM.62d, URCM.62e, URCM.70-side B, URCM.75b, and URCM.113) even if several others, which we cautiously consider as undetermined, have similarities with this pattern. Yet, the quality of preservation does not allow a robust attribution, and these trails are excluded from the present analysis. Sixty-four *pes* and 61 *manus* impressions represent the current sample of downhill trackways.

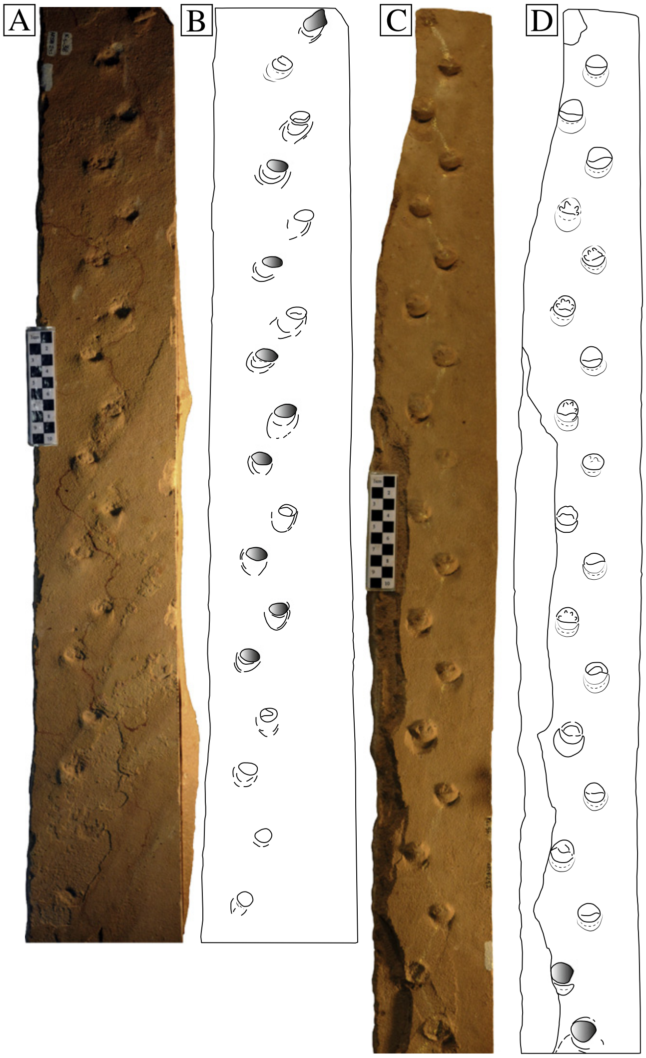

Fig. 5. Selection of slabs with two of the longest trackways in walking gait. Photograph of slabs A) URCM.38; C) URCM.46, and relative drawings (B, D), at the same scale. Footprints are preserved as concave epirelief on URCM.38 and as convex hyporelief on URCM.46. Scale bar 10 cm.

The close association of hand and footmarks reduces the amount of good measurements available for these tracks. Where measured, the mean FL is 10.2 mm for a mean FW of 17 mm.

The *manus* impression can lie anteriorly and in line with the footprint, or more commonly, fall side to side with the *pes*, medially. The position of the *manus* print gives rise to a slightly different configuration.

The first type is exemplified on trackway URCM.61a. This trail consists of four *manus-pes* sets characterized by along pace (mean 154 mm) and high pace angulation (164°). No clear digit marks are visible. The position of the *manus* and *pes* marks relative to the midline varies regularly along the trackway. On step numbers 1 and 3, the longitudinal axes of the *pes* and *manus* are aligned and parallel to the midline. On step numbers 2 and 4 the *manus* and *pes* are also aligned on a common longitudinal axis, but this is rotated outward relative to the midline. In any case, the handprint always precedes the footprint (Fig. 11A–C).

The second and more abundant type of downhill trackway have *manus* and *pes* prints in a different arrangement compared to trackway URCM.61a. The long step and high pace angulation are maintained, but the *pes* longitudinal axis is strongly rotated inward on these trackways, and the *manus* print lies medially in relation to the *pes*. *Manus* and *pes* might be asymmetrically positioned relative to the midline, as in URCM.62d and URCM.75. In general, a bilobate, heart–shaped print results from the association of hand and footmarks on this kind of downhill trackways (Fig. 12A–C).

5. Discussion and remarks

The analysis of the "Rio Claro Collection" allows the discrimination of four gaits (walking, half–bounding, bipedal skipping, and running), which are represented with different percentages in the slab set. Uphill trackways are more abundant (85.6%), and walking is the dominant gait. Downhill trackways are less represented (14.4%), and all display a running gait.

As this work is based on previously collected material, human selection of the sample might have occurred, with preference for trackways that are easier to recognize, or representing slab imperfections, reducing their commercial value. The Corpedras quarry was indeed an economic enterprise, exploiting sandstones for commercial purposes, and bioturbation might have represented a reduction in the product quality. Choice of slabs by quarrymen might have positively selected for those with walking trails, which have the highest ratio of trampling for a given area. On the other hand, almost 30 years of sampling, and the high number of collected slabs may have reproduced stable values for relative gait abundances. As a matter of fact, examination of a comparable number of slabs by Leonardi and Oliveira (1990) revealed percentages of different gaits that are similar to those observed here (D'Orazi Porchetti et al., in review). Dominance of uphill walking trails also occurs among samples of material referred to as *Brasilichnium elusivum* from several localities in North America (Rowland and Mercadante, 2014; Sanders and Picard, 1999). Uphill trackways are numerically dominant in the Coconino Sandstone, which preserves a large amount of Early Permian vertebrate footprints (McKee, 1944, 1947). If sampling bias is discarded, taphonomic factors might explain the numerical dominance of uphill trackways. Seilacher (2007) suggested that an animal moving across a slope exerts different load forces depending on the direction of travel (e.g., up or down), with higher loads applied when climbing uphill. Thus, a causal link between the depth of sediment turbation and its preservation potential has been proposed to explain

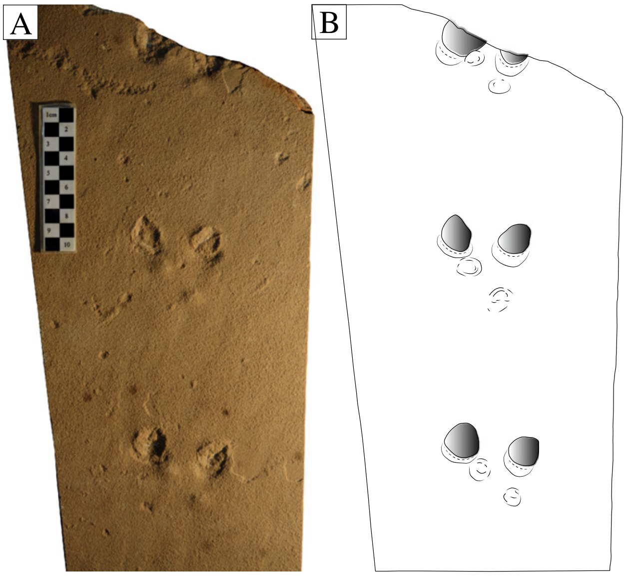

Fig. 6. Photograph A) and drawing B) of slab URCR.23, with a sequence of three consecutive *manus–pes* sets in half–bounding gait. Footprints are preserved as convex hyporelief. The trackway is heading to the top of the image. *Pes* prints are incomplete, partially lost at their top (shaded gray). Hand marks are shallower, and better preserved. The hedges of the expulsion rims are represented with dotted lines. Scale bar 10 cm.

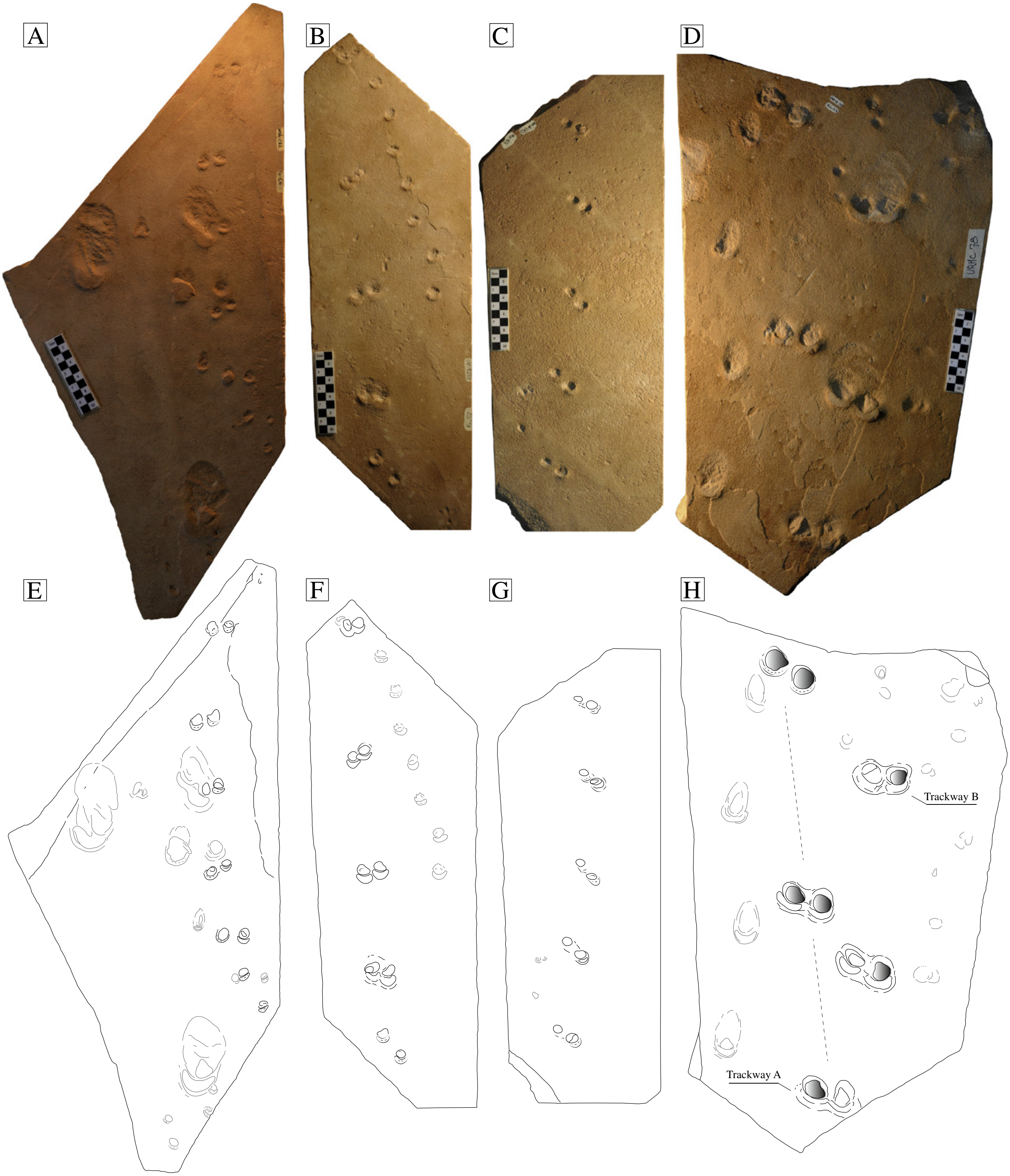

Fig. 7. Selection of slabs with well-reserved trackways in skipping gait. Photographs of slabs A) URCM.66; B) URCM.52; C) URCM.64; D) URCM.43, and drawings of the same slabs (E–H). Scale bar 10 cm. Drawings at the same scale of the photographs; skipping trackways are in black, those with other gaits are in gray. Two different trackways on H) are identified with capital letters (A, and B). Dotted lines to show successive steps of trackway A. All tracks preserved as concave epirelief.

this discrepancy in the record (Seilacher, 2007). A taphonomic cause may not be discounted, even if quantitative studies on this topic are lacking. Indeed, field observations on escape trajectories of two extant Squamata inhabiting sand dune environments, *Callisaurus draconoides* and *Uma scoparia* (Jayne and Ellis, 1998; Irschick and Jayne, 1999), identified no preferences for down- or uphill directions, and heading was determined by the provenience of the threat or the location of shields (burrows or vegetal covers). No field data for extant mammals from similar environmental settings are found in the literature.

5.1. Taphonomic framework

A lasting question, concerning the Botucatu footprints, involves their genesis. Different hypotheses have been proposed to explain how they

Fig. 8. Slab URCM.43, showing interaction between expulsion rims. The medial border of the left rim cuts the controlateral (white arrow), thus proving the asynchronous touch-down of the feet. Footprints preserved as concave epirelief. Scale bar 2 cm.

become preserved and where bioturbation took place; at the sediment/air interface, or at some depth into the sand (Leonardi, 1980, 1981; Fernandes and Carvalho, 2005, 2007a, 2007b, 2008a, 2008b). A subsurface origin is hypothesized here, based on the evidence that follows. As proposed in D'Orazi Porchetti et al. (in review), the paucity of *manus* prints compared to *pes* prints in the sample of uphill walking trackways represents a taphonomic bias. Depending on the direction of travel (uphill or downhill) on the lee side of the dunes, the weight of the trackmaker moves toward the rear (uphill) or front legs (downhill). As such, it is likely that the hands sunk to a lesser extent into the sediment in those trackways heading to the top of the dune (Seilacher, 2007). As a matter of fact, only 10 out of 68 climbing trackways in walking gait show *manus* traces. In contrast, all downhill trackways exhibit clear handprints. Direction of travel and *manus* traces are therefore correlated, and this is explained by the differential distribution of load vectors in fore- and hindlimbs during displacement on inclined surfaces.

In the literature (Leonardi, 1980, 1981), the lack of *manus* prints in walking trails of *Brasilichnium elusivum* has been explained as the effect of foot superimposition. A comparison between trackways produced by a walking gait associated with and without *manus* prints, has been performed to quantify their pattern variation. A scatter plot, based on the mean value for the foot stride against the mean pace angulation value (trackway sample $n = 36$; 5 trackways with *manus* traces), does not identify any difference correlated with the *manus* presence. In other words, when the hand is visible, the walking gait trackways show the same parameters as those where the *manus* is not preserved. This is at odds with the hypothesis of total foot-hand overprinting, but agrees with a taphonomic explanation for the absence of the *manus* print in most uphill-oriented walking gait trackways (Fig. 13).

Bipedal skipping trackways show no handprints in any of the studied specimens. Instead, the single half-bounding trackway in the "Rio Claro collection" shows a stable separation between the *pes* marks, and clear handprints behind the foot traces. As bipedal skipping and half-bounding release much more energy to the ground during touch-down phase than during walking, *manus* prints would easily be transmitted below surficial layers. Hand traces are in fact visible in the half-bound trail, but not in bipedal skipping trails. Therefore, we consider the latter as trails of an animal moving exclusively on the rear legs. Moreover, bipedal skipping traces clearly differ from half-bounding trails, with the former possessing an extremely reduced or no space between *pes* prints.

The Botucatu ichnites were not necessarily left on wet surfaces, and animals might indeed have disturbed dry sediments in their passage. Loope (2006) presented evidence from outcrops of the Navajo Sandstone at Coyote Buttes (Lower Jurassic, USA), showing vertebrate repichnia preserved in dry sand. Ductile deformation of thin sand layers is interpreted as the effects of animals trampling on dry sand (Loope, 2006), and footprints deforming thin sand layers, without breaking their continuity, are documented in the "Rio Claro Collection" (Fig. 14A). The effect of load transmission through sediment is further exemplified by an isolated tridactyl footprint preserved in the "Rio Claro Collection" (Fig. 14B). Parallel striation is found at the rear margin of many

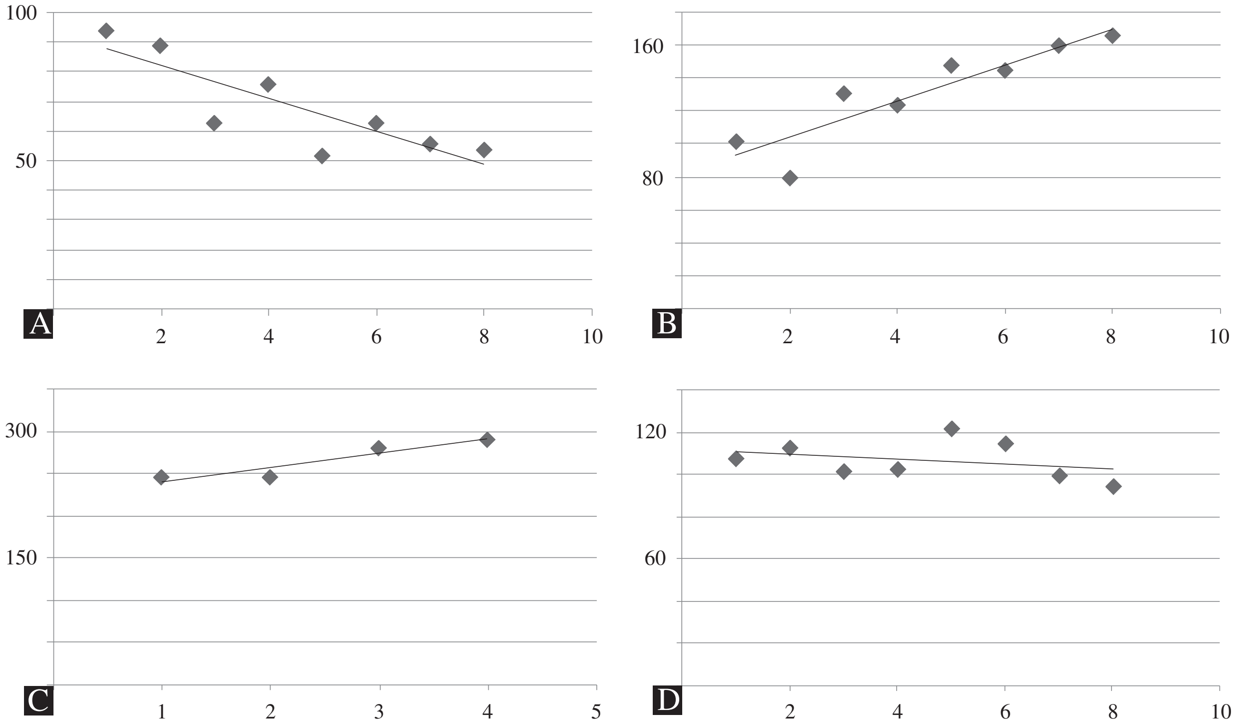

Fig. 9. Scatter plot with linear regression line based on stride distance. Data from biped jumping trackways on slab A) URCM.67; B) URCM.52; C) URCM.43 and D) URCM.64. Step number on the x-axis and distance in mm on the y-axis.

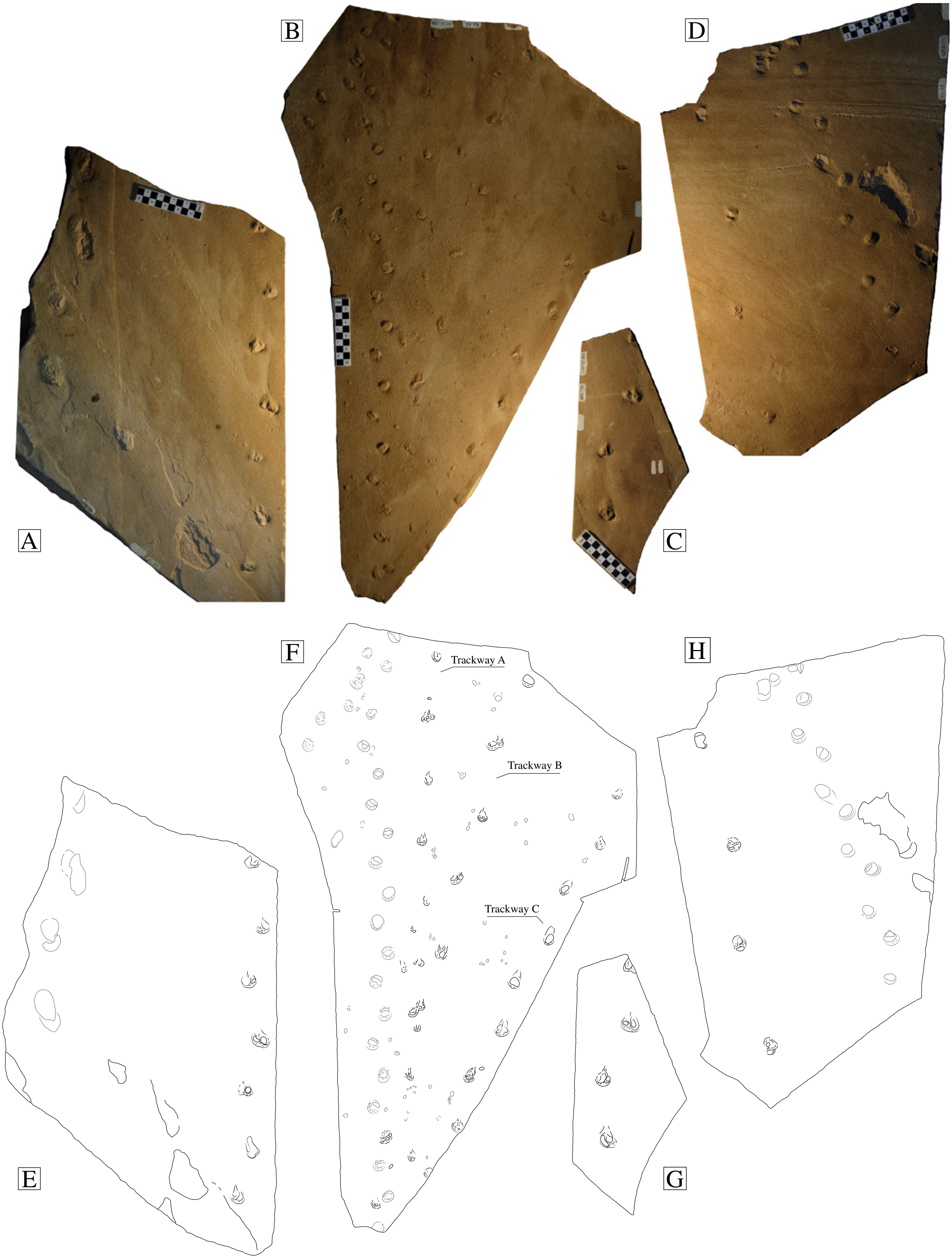

Fig. 10. Selection of slabs with downhill-oriented trackways. Photographs of slabs: A) URCM.27; B) URCM.62; C) URCM.113, and D) URCM.61, and relative drawings (E–H). Scale bar 10 cm. Drawings at the same scale of the photographs; running trackways are in black, those with other gaits are in gray. Three different trackways on F) are identified with capital letters (A, B and C). All the footprints are preserved as convex hyporelief.

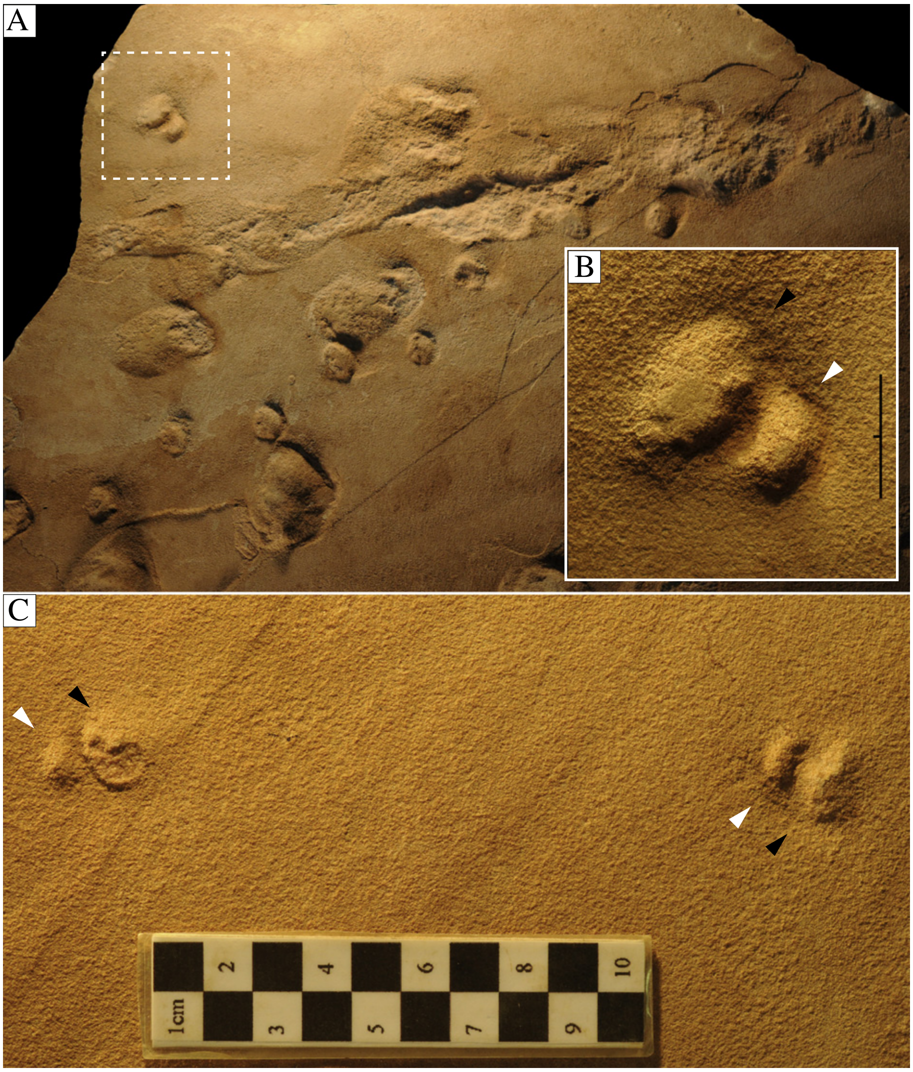

Fig. 11. A) and B) Photograph of slab URCM.41, and C) URCM.61. A single downhill–oriented *manus–pes* set is preserved on slab URCM.41 (dotted line box), which is magnified in B) to show details of the shape and relative *manus–pes* arrangement. The IInd and the IIIrd couples of a longer trackway from slab URCM.61 (see Plate IV–D) are reproduced in C). In these kind of downhill-oriented trackways *manus* (white arrows) usually lies anteriorly to the *pes* (black arrows), and rest separated from the foot marks. All tracks are preserved as convex hyporelief. Scale bar 2 cm in B), 10 cm in C).

tracks in the "Rio Claro collection", as in one of its largest slabs (Fig. 14C). Similar structures have been hypothesized (Fornós et al., 2002, Fig. 21) to appear in subsurficial sections of footprints imprinted on dune foresets as marks of superimposed layers.

Several slabs show the "truncated marginal upfolds" described by Loope (2006, Fig. 2b), in which track expulsion rims are "cut" at their top by avalanches of dry sand (Fig. 14D). In these cases, that surface has an erosional contact with the sandstone layer above.

5.2. *Brasilichnium elusivum* – trackmaker stance

Pace angulation is a useful parameter to determine the stance of tetrapod legs from their trackways, even if categories such as sprawling, semi–erect, and erect (Bakker, 1971) oversimplify a much more variable framework of leg postures (Gatesy, 1991). A quantitative assessment of the relations between pace angulation and leg stance in Permian and Triassic tetrapod trackways has been performed by Kubo and Benton (2009). In their analysis, a vast sample of extant and fossil trackways was compared, establishing a set of categories for different stances (from sprawling to fully erect). In this scheme, an average angle of 151.5° has been retrieved for extant eutherian mammals (none of which are sprawling), spanning from an average of 133° in non-cursors (didelphids, murids, and mustelids) to up to 164°in cursors (felids and canids). The average value for trackways made by a walking gait in our sample is 131.6° (mode = 129°), with minimum values as low as 81° and a top value of 161°. Accordingly, the average value for *Brasilichnium elusivum* falls below the threshold of non-cursor mammals, and a semi-erect posture is therefore suitable for its trackmaker. This is in agreement with the shape of the footmarks observed in the "Rio Claro Collection". *Pes* prints are asymmetrical, ectaxonic, with a lateralmost digit role during the walk cycle. A relationship between a semi-erect leg stance and the function of lateral elements of the acropodium during the walk cycle has been proposed (Kümmel and Frey, 2014).

Several specimens of *Brasilichnium elusivum* display an independent rotation of contralateral *pes* prints relative to the direction of travel. Footprint inward or outward orientations are possibly the expression of the ankle joint mobility. Limitations to foot rotation are imposed by the shape and organization of ankle bones, especially the astragalus and calcaneum. Ankle mobility in extinct and extant mammals has

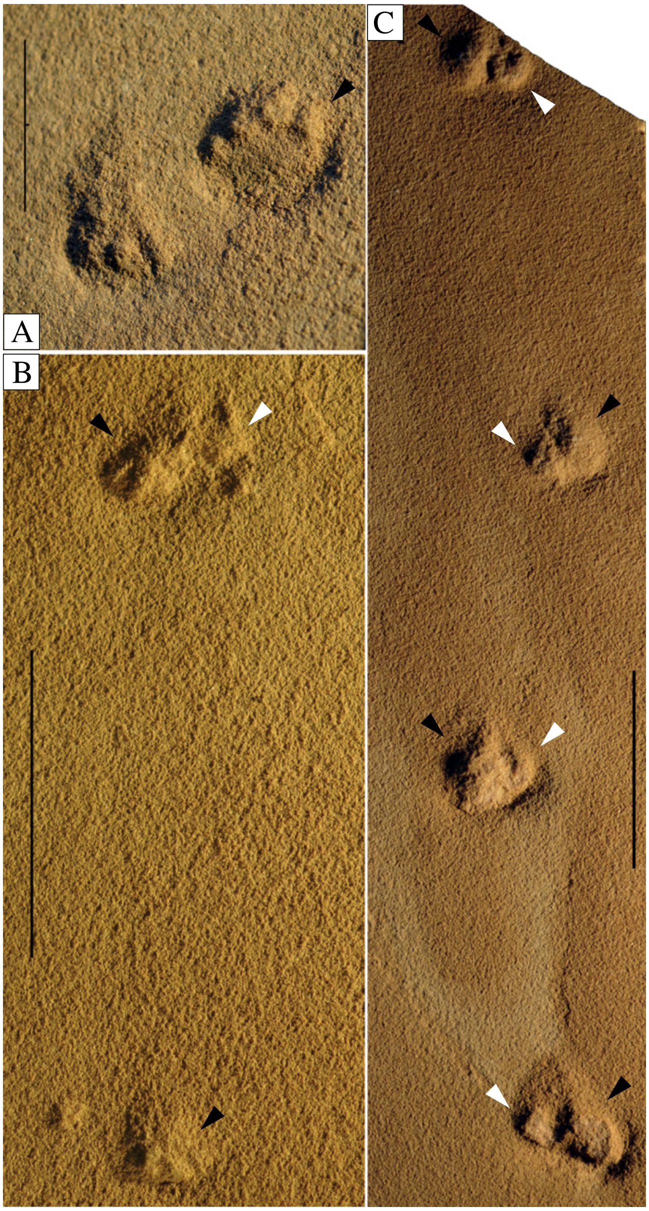

Fig. 12. Close–up of a single A), a couple B), and a sequence C) of four downhill–oriented footprints, all preserved as convex hyporelief. A) and B) from slab URCM.62; C) from slab URCM.27. In A) the downhill–oriented footprint (to the left) is not associated to a hand mark. The right one is an uphill–oriented footprint. Black arrow to mark digit print IV. B) Close–up of two consecutive steps from the same trackway of A). On the upper trace, a hand mark (white arrow) is associated to the footprint (black arrow). The successive track shows only the print of the *pes* (black arrow), with three digit marks, as in A). *Pes* always rests laterally to the *manus* print. C) All footprints (black arrows) are here associated to the handmarks (white arrows). No clear digit marks are discernible. Pes traces are larger and slightly deeper than the handprints. Scale bar is 2 cm in A); 5 cm in B) and C).

been correlated to ecological adaptation, i.e. foot retroversion is functional to scansorial/arboricoral animals, for instance Jenkins and Krause (1983) and Krause and Jenkins (1983) interpreted some multitubercolate forms as scansorial, whereas a stiff ankle and restricted hinge-like movements are typical of cursorial forms (Polly, 2007). It is otherwise possible that the orientation of the *pes* depends not only on ankle mobility, but also on the overall leg posture. The orientation of the body, relative to the maximum dip of the foreset, might have forced the animal to compensate for sliding by re-orienting the downhill leg on the lee face of the dune. Remarkable in this case is the orientation of the foot in running trails, many of which display a strong inward rotation of the *pes*.

5.3. Brasilichnium elusivum – trackmaker gaits

The abundance of walking trackways helps describe in detail this locomotion pattern. The trackmaker of *Brasilichnium elusivum* was primarily a walker, and the variation in pace angulation reveals the ability to vary the stride repeatedly, even along the same trackway. Most of the longer trackways preserved in the studied sample were left by animals moving in a straight line, whereas a minor percentage of trails are sinusoidal. Change in gait is observed in at least two trackways (URCM.67 and URCM.66) where the animal shifted from walking to bipedal skipping. Other records of gait transitions are currently lacking, but these would be extremely important to better understand details of the trackmaker's locomotor skills.

The single bounding trail (URCM.23) records an asynchronous touchdown of the front legs and for this reason represents a half-bounding gait. Considering the other published account of this locomotion style, only two specimens are known so far. Similar bounding trackways have been described from Miocene outcrops of Colorado, and ascribed to rodent mammals (Lockley et al., 2007; Lockley and Milner, 2014).

As described in Section 4.3.3, the analysis of bipedal saltatory trails revealed that the adopted gait is not properly a ricochetal bounding hop, because feet did not touch the ground at the same time. There is a temporal discrepancy between the touchdown of both legs, which might also deliver different amounts of energy, with a change in the leading foot. This gait is therefore better defined as bipedal skipping. Minetti (1998) was among the few to investigate the biomechanics of the skipping gait in humans. Similar studies are lacking for other mammals, but the general conclusions of that study might be extended to our sample. Skipping shows similarities to galloping in terms of stride frequency and energy recovery. At the same time, bipedal skipping delivers a vertical displacement that is two times higher than that observed for bipedal running. On the other hand, it is among the most expensive gaits in terms of energetic costs, at least in humans (Minetti, 1998).

Even if the relative abundance of each gait might be taphonomically biased, the available record allows speculation on some aspects of locomotor patterns. For instance, physical properties of the surface might represent a limitation for adopting specific gaits. Rapid climbing on an inclined surface (up to 30°, as in the case of dune foresets) requires increased walk frequency, or a longer stride in the case of running. Both walking and running strongly relies on the frictional forces on the ground to move the body forward. An inclined surface of loose sand offers low friction during the propulsion phases of walking and running. Conversely, hopping relies on vertical energy vectors, and a sandy surface might offer better resistance and reaction forces to compression. As introduced above, bipedal skipping provides high vertical displacement compared to quadrupedal gaits, and 13 skipping trackways are present in the sample, against a single half-bounding trackway. Even if the relative percentage might be taphonomically biased, half-bounding results in less vertical displacement compared to the skipping gait, and the latter is therefore more effective for rapid uphill dislocation on dune slopes.

We propose that the *Brasilichnium elusivum* trackmaker shifted from walk to half-bound to bipedal skip to increase the speed when rapid uphill movement was required. Running gait is instead uniquely seen in descending trails. As proposed by Rocha et al. (2007) for the spiny torch tail rat, environmental constraints play an important role in shaping locomotor response. Owaki et al. (2013) demonstrated that variation in the distribution of loads among fore and haft legs of a quadrupedal walking drone influences its gait. The same shift in load distribution occurred on the *B. elusivum* trackmaker's legs, depending on the direction of travel (up- or downhill). The effect of this shift

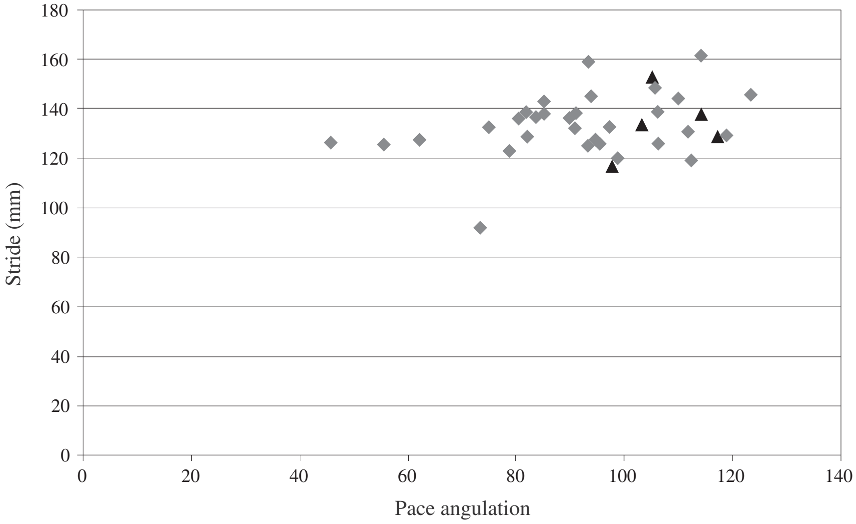

Fig. 13. Scatter plot on the ratio between Stride (in mm) and Pace Angulation values (in degree). Trackways with *manus* prints (black triangles) are not discriminated from those with no hand marks (gray diamonds), as linear and angular parameters are substantially maintained. This is interpreted in support of the taphonomic bias on hand preservation.

might have constrained the adoption of running in downhill movements to increase dynamic stability, manoeuvrability, and compensation of forward fall tendency on declines with an incoherent substrate. Testing this hypothesis is beyond the scope of this paper, but represents a necessary step for future investigation.

5.4. *Brasilichnium elusivum* – *ichnotaxonomic significance*

Brasilichnium elusivum was erected as an ichnotaxonomic label for trails of small synapsid trackmakers in a walking gait. Neither Leonardi (1981) nor Fernandes and Carvalho (2008a) formally included bounding and biped hopping trackways in its diagnosis. Yet, investigation of the "Rio Claro Collection" reveals that all observed gaits are expressions of the same trackmaker. Even if the variety of traces produced by a single biotaxon could each deserve a different name, we recognize the inclusion of non-walking gaits in the same ichnotaxonomic field as not only more convenient and conservative for ichnotaxonomic stability, but also intrinsically more useful than adopting different or new labels. In the Mesozoic framework of purported synapsid tracks, *B. elusivum* is by far the best represented in terms of collected specimens, with at least two large Brazilian collections in São Paulo State (UNESP at Rio Claro and UFSCar at São Carlos) and one at "Museu Nacional do Rio de Janeiro". The ichnotaxonomic stability of *B. elusivum* has been further reinforced by Lockley (2011), with the inclusion of two preservational variants (i.e., *Bipedopus* and *Semibipedopus*).

Brasilichnium elusivum is known from several localities in the United States, with material assigned to this ichnotaxon since the nineties (see Lockley, 2011 and references therein). A thorough comparison in terms of relative abundance of gaits between the South and North American material is currently lacking and future work is envisaged to study the extent of variation between the trackways from Brazil and the United States. According to the available current dating, the track-bearing units in North American outcrops span from the Late Triassic to the Middle Jurassic, and from the latest Jurassic to the Early Cretaceous for the Botucatu Formation of Brazil (Scherer, 2000, 2002). It is interesting to note that original efforts to define the age of the Botucatu Formation relied on ichnites, and an Early to Middle Jurassic age was proposed especially based on the presence of non-mammalian synapsid tracks (Leonardi and Oliveira, 1990). Morphological similarities with the North American forms suggest a similar age for the Botucatu Formation, which would be therefore older than the suggested Early Cretaceous age. As long as a direct dating of samples from the type locality of *B. elusivum* is lacking, the biochronologic significance of this ichnotaxon remains poor.

Lockley (2011) recently proposed the ichnofamily Chelichnopodidae to allocate at a supraichnogeneric rank *Brasilichnium* and *Chelichnus*. These two ichnogenera share a similar morphology in footprint architecture, even if *Brasilichnium* has a tetradactyl *pes* (this work; Fernandes and Carvalho, 2008a), whereas *Chelichnus* footprints have originally been defined as pentadactyl (McKeever and Haubold, 1996). *Chelichnus* has usually a larger handprint as well. This standing, both *Brasilichnium* and *Chelichnus* have been considered as of synapsid origin in the literature (Lockley, 2011 and reference therein), and this view is held in this work too. This has bearing on many aspects, especially because *Brasilichnium* is relevant in facies analysis (the *Brasilichnium* ichnocoenosis of the *Chelichnus* ichnofacies, Hunt and Lucas, 2007), as an index ichnofossil for hyper-arid paleoenvironments dominated by sand dunes. A robust definition of the ichnotaxon *Brasilichnium elusivum* is mandatory for comparison with materials from other regions, such as those from Southern Africa (Lesotho). The Stormberg Group of Lesotho yielded several ichnotaxa of purported synapsid origin (Ellenberger, 1970, 1972, 1974, 1975). Even if their ichnotaxonomic status is problematic (see Lockley et al., 2004 for a review), at least one group of tetradactyl forms from the B/1 biostratigraphic zone of Ellenberger (1970, 1972), informally labelled as "Eotetrapodiscidés", are good candidates for comparison with *B. elusivum*.

6. Re–evaluation of potential trackmakers

Leonardi (1981) proposed *Brasilichnium elusivum* as a label for possible repichnia of undetermined early mammals (op. cit., Leonardi, 1981, pag. 803: "*Classis*:?*Mammalia*"). In successive works (Leonardi and Sarjeant, 1986; Leonardi and Oliveira, 1990; Leonardi and Carvalho, 1999; Leonardi et al., 2007) the synapsid origin of *B. elusivum* was recurrently maintained, with uncertainty on whether they were traces of "true mammals" or "mammal–like reptiles" (Leonardi and Oliveira, 1990, pg. 226). Revision of *B. elusivum* by Fernandes and Carvalho (2008a) retained Leonardi's zoological attribution. North American forms, referred to as *B. elusivum*, have been attributed to tritylodontids (Lockley and Hunt, 1995; Rainforth, 1997; Rainforth and Lockley, 1996b; Rowland and Mercadante, 2014). According to the current dating of the lithostratigraphic units that bear North American specimens of *B. elusivum* (Lucas et al., 2010; Lockley, 2011), the chronologic distribution encompasses Late Triassic to Middle Jurassic strata. The Botucatu Formation is otherwise considered as young as Early

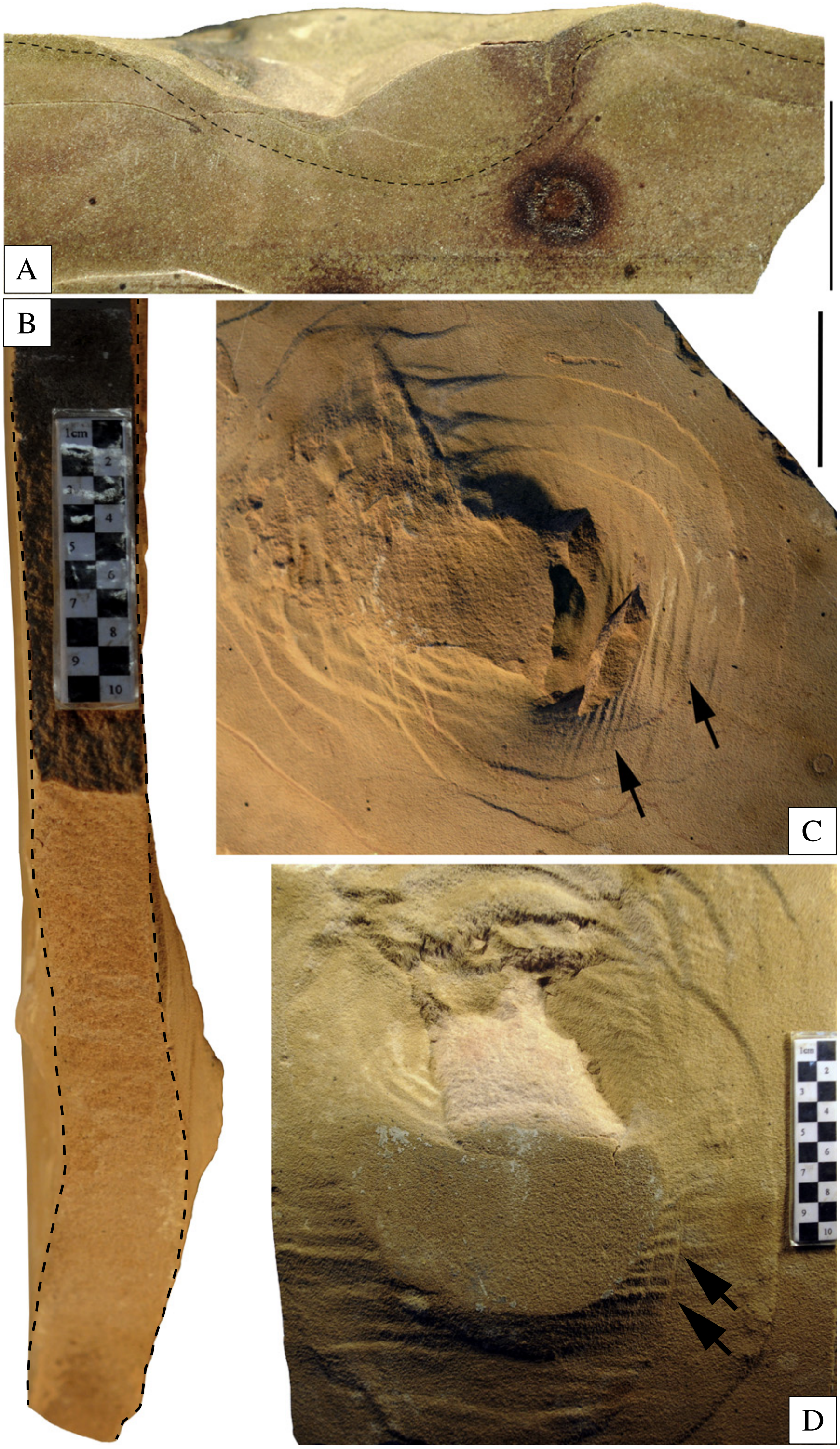

Fig. 14. A) Cross section of slab URCR.125, polished to show the effects of animal trampling on layers of different thickness and granulometry, at different depths. As highlighted by the black dotted line, layers are bended and not broken. Scale bar 5 cm. B) Slab URCR.123 in lateral view showing deep deformation after trampling by small tridactyl dinosaur. The top of the slab is oriented to the left. A bulge protrudes from the original lower surface for about 2 cm. Black dotted lines to remark the upper and lower limits of the slab. Scale bar 10 cm. C) Slab URCR.143 with parallel striation at the back of a tridactyl footprint (black arrows), preserved as convex hyporelief. Striation is here interpreted as the remnants of superimposed sandstone layers, whose fronts are exposed by transverse section below the original air sediment-interface. This striation is not directly the consequence of load deformation, whose effects are otherwise exposed around the track itself. Scale bar 10 cm. D) Top view of slab URCR.128 showing erosion at the top of the expulsion rim. This cut is interpreted here as the result of erosion by sand anvalanche on dune foreset. See also Loope (2006). Parallel striation is visible at the back and around the expulsion rim (black arrows). Concave epirelief. Scale bar 10 cm.

Cretaceous (Scherer, 2000, 2002), at least for its uppermost portion. In general, the age of the footprint-bearing units might have influenced trackmaker identification.

Here, we reconsider the attribution of *Brasilichnium elusivum* based on morphofunctional features revealed by the analysis of foot morphology, stance and gait patterns on the "Rio Claro Collection". The comparative analysis has been arbitrarily limited to Mesozoic forms known in the osteological record worldwide. Non-mammaliaform eucynodonts, in the phylogenetic framework proposed by Sereno (2006) for Mammaliamorpha (Rowe, 1988), are those included in the least inclusive clade containing *Tritylodon longaevus* Owen, 1844, *Pachygenelus monus* Watson, 1913, and *Mus musculus* Linnaeus, 1758.

A consistent outcome of the extensive analyses on *Brasilichnium elusivum* is that the footprint morphology is described in very similar morphological terms by all workers. Yet, a functionally tetradactyl foot is not exclusive to any specific zoological group, and this feature alone is inconclusive in the process of trackmaker attribution. None of the specimens preserved in the "Rio Claro Collection" show pad marks. Testing the pedal phalangeal formula proposed by Leonardi (2–3–3–3–3) is, therefore, unrealistic. No more than three digit marks have been observed on handprints in the "Rio Claro Collection", though Fernandes and Carvalho (2008a) interpret the handprint of *B. elusivum* as tetradactyl. In our view, the shape of the hand mark is too biased by taphonomic issues to be consistently adopted in the process of trackmaker identification. This comes together with the limitation in comparing the size of the hand to that of the foot, although this difference has been quantified in the literature (Leonardi, 1981).

Kümmel and Frey (2012, 2014) performed an extensive and comprehensive analysis on the morphofunctional arrangement of synapsid acropodia, establishing that the digital arcade characterizes this group when occurring in the medial region of the phalangeal sequence. Kümmel and Frey (2012, Fig. 17f) use, among others, a set of *Brasilichnium elusivum* from the Navajo Sandstone (see Lockley and Hunt, 1995, Fig. 4.22) to exemplify how the shape of synapsid footprints is influenced by the architecture of the digital arcade. Digit marks are slightly separated from the sole pad by a stenosis or a gap, which gives an overall paw-like appearance to the tracks. The substantial morphological homogeneity between the North American specimens referred to *Brasilichnium* and the Brazilian forms allows extending the example to the latter. Therefore, the posture of the acropodium represents a robust argument in favour of a synapsid trackmaker for *B. elusivum*.

Trackmakers of *Brasilichnium elusivum* held their legs in a semi-erect posture during walk. Parasagittal leg posture appears late in Mammaliamorpha evolution, and a semi-erect stance is a plesiomorphic trait shared by many Mesozoic synapsids. Kielan-Jaworowska and colleagues extensively discussed the limb posture of fossil mammals (Kielan-Jaworowska and Gambaryan, 1994; Kielan-Jaworowska and Hurum, 2006; Kielan-Jaworowska et al., 2004). A semi-erect posture has been proposed for mammaliaforms such as docodonts, eutriconodonts, multituberculates, "symmetrodonts" and "eupantotherians" on the basis of taphonomic evidence. Based on the assumption that the body posture at carcass burial is an expression of posture in life, the post-burial resting position has been adopted by Kielan-Jaworowska and Hurum (2006) and Kielan-Jaworowska (2013) to infer a semi-erect leg stance for basal mammaliaforms. According to those authors, a true parasagittal stance was achieved only in latter groups of tribosphenidan mammals. Marsupials and placentals with improved leg posture could therefore be excluded as possible trackmakers of *B. elusivum*.

However, Sereno (2006) questioned the semi-erect stance of multituberculate forearms, and argued for a more improved, parasagittal posture. Inferences on leg stance must be cautiously extended to other taxa, as even closely related forms of Cretaceous mammals such as *Akidolestes* and *Zhangheotherium* show great differences in their limbs postures (Chen and Luo, 2013). Indeed, even if limb posture is an important tool in our process of attribution, helping to restrict potential trackmakers to a limited number of clades inside Mammaliamorpha, no definitive clues are available for finer investigation.

An interesting feature of *Brasilichnium elusivum* is the inward orientation of the pedal prints, observed on several trackways in different gaits. Comprehensive data on ankle joint mobility are restricted to Mammaliaformes, and not much is known about other groups of Mesozoic synapsids. In *B. elusivum*, movements are usually limited to the internal rotation of the foot, but the inward orientation of the footprints might also result from the rotation of the entire rear leg. Accordingly, there is no information to unequivocally interpret this feature in terms of trackmaker attribution.

The integrated analysis of locomotion skills may add useful hints to constrain potential trackmakers. A few records of purported ricochetal adaptations in Mesozoic mammaliamorphs are found in literature. *Zalambdalestes* and *Barunlestes* are two Mongolian eutherians from the Late Cretaceous (Campanian) that might have adopted a quadrupedal ricochetal gait, in a way similar to modern macroscoelids (Kielan-Jaworowska, 1978, 2013; Kielan-Jaworowska and Gambaryan, 1994; Kielan-Jaworowska et al., 2004). In an actualistic approach, Chen and Wilson (2015) performed a vast analysis of small extant mammals (less than 5 kg) to infer the locomotion styles of their Mesozoic relatives. This work successfully discriminates parameters for discrete and unequivocal adaptations, but does not include forms with unspecialized skeletal elements, which could have supported a broad array of gaits, such as the trackmaker of *Brasilichnium elusivum*. In fact, Chen and Wilson (2015) did not recover any Mesozoic form adapted for bipedal jumping before the Late Jurassic, and *B. elusivum* is known from strata as old as Late Triassic (Lucas et al., 2010).

The analysis of the characters expressed in *Brasilichnium elusivum* helps discriminating possible trackmakers, but it is limited by the completeness of the record of body fossils, and by interpretation in terms of functional morphology. As far as the osteologic record is concerned, the available evidence helps nest the trackmaker of *B. elusivum* inside Mammaliamorpha, among non-mammaliaforms and "mammals" (Mammaliaformes sensu Rowe, 1988) where a parasagittal leg stance was not yet achieved. Efforts to assign *B. elusivum* to given osteological taxa reveal the limits of such inquiries that, under some respects, might remain frustrating. In fact, *B. elusivum* represents aspects of synapsid evolution that are difficult to elucidate based solely on their osteologic record. A parallel, ecomorphologic approach is suggested to define the role of the ichnologic data in the study of specific aspects of synapsid natural history. *Trinomys yonenagae* Rocha, 1995, is a small Echimyidae rodent inhabiting dune fields along the course of the São Francisco River, in the semiarid Caatinga ecoregion of north-western Brazil. The torch tail rat, as it is popularly known, is a close relative of two other genera *Proechimys* and *Hoplomys* (Rocha et al., 2007), and has at least one congeneric species, *Trinomys albispinus*. *T. yonenagae* adopts an array of gaits (walking, bounding, bipedal hopping) which is not found in the same relative proportions in other echimyids. Rocha et al. (2007) make a strong case for a causal link between preferential locomotion style and the specific environment in which *T. yonenagae* lives, dunes fields with limited vegetation cover. Other authors (Bartholomew and Caswell, 1951; Taraborelli et al., 2003) suggest a relationship between gaits and desert environments, supporting bipedal hopping as more effective for rapid progression than quadrupedal running, providing an ecomorpholgical parallel to the trackmaker of *Brasilichnium elusivum*. There is obviously no attempt to make any systematic link between the trackmaker of *B. elusivum* and *T. yonenagae*, but it is interesting to point out the recurrence of hopping gaits in association with arid environmental conditions, particularly with the presence of dune fields with limited vegetation coverage.

Repeated exploration of ecologic niches has been proposed by Luo (2007) to explain the recurrence of similar body architectures in synapsids. Natatorial, fossorial, or even gliding forms evolved independently in different lineages from the Mesozoic to the present. This interpretation could be expanded to enclose *Brasilichnium elusivum*, as Mesozoic evidence for the recurring evolution of ricochetal gait in Mammaliamorpha. The body architecture of animals able to adopt bipedal jumping (among other gaits) is not necessarily associated to the specialized adaptation of ricochetal forms, as seen, for instance, in some extant Macropodia (e.g., *Macropus*). *B. elusivum* shows that

Mesozoic mammaliamorphs developed locomotor skills to face hyper-arid environments in which rapid dislocation over incoherent slopes was required. Bipedal hopping appears as a good option for this, whereas other gaits were also adopted depending on contingent intrinsic and extrinsic conditions.

7. Conclusions

Four different gaits; walking, half-bounding, bipedal skipping, and running, figure within the locomotor skills of the small mammal-like synapsids that inhabited the Mesozoic Botucatu desert in the Paraná Basin of Brazil. Three of these gaits (walking, half–bounding, and skipping) are found exclusively on uphill trackways, in different percentages. Even with a possible taphonomic bias taken into account, the trackmaker was mainly a walker, able to speed up on four or even two legs when required. Skipping appears more efficient to face rapid displacement on steep slopes with incoherent substrate. Reasons why running is limited to downhill oriented trackways are not clear, but changes in the distribution of loads and shifts in the centre of mass might have constrained downhill gait.

The trackmaker of *Brasilichnium elusivum* was a Mammaliamorpha, with a semi-erect leg posture. According to data from the literature, potential trackmakers can be found among tritylodonts, trithelodonts, as well as mammaliaforms that retained a semi-erect leg posture. No refining in this attribution is possible based on the available osteological data. The search for body fossils matching this footprint might remain frustrating, and the lack of precise osteologic correlates is somewhat problematic. We must assume this ichnofossil as the only one currently available to investigate crucial aspects of locomotion in Mesozoic synapsids. Under an ecomorphologic point of view, skipping trackways of *B. elusivum* fill a gap in data on the evolution of bipedal saltatory gait in the Mesozoic record of mammal-like synapsids. *B. elusivum* also shows the association of bipedal saltatory gait with hyper-arid settings dominated by sand dunes, as previously hypothesized in literature.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2016.10.009.

References

Alexander, R.M.N., 2004. Bipedal animals, and their differences from humans. J. Anat. 204 (5), 321–330.

Assine, M.L., Piranha, J.M., Carneiro, C.D.R., 2004. Os paleodesertos Pirambóia e Botucatu. In: Mantesso–Neto, V., Bartorelli, A., Carneiro, C.D.R., Brito–Neves, B.B. (Eds.), Geologia do Continente Sul–Americano: Evolução da Obra de Fernando Flávio Marques de Almeida, pp. 77–92 (SP, Brasil).

Bakker, R.T., 1971. Dinosaur physiology and the origin of mammals. Evolution 25, 636–658.

Bartholomew Jr., G.A., Caswell Jr., H.H., 1951. Locomotion in kangaroo rats and its adaptive significance. J. Mammal. 32 (2), 155–169.

Bertram, J.E.A., 2016. Understanding Mammalian Locomotion: Concepts and Applications. Wiley–Blackwell, Hoboken, New Jersey.

Bigarella, J.J., Salamuni, R., 1969. Paleowind patterns in the Botucatú Sandstone (Triassic–Jurassic) of Brazil and Uruguay. In: Nairn, A.E.M. (Ed.), Problems of Paleoclimatology. Intersceince, New York, pp. 406–409.

Charig, A.J., 1972. The evolution of the archosaur pelvis and hindlimb: an explanation in functional terms. In: Joysey, K.A., Kempt, T.S. (Eds.), Studies in Vertebrate Evolution. Oliver & Boyd, Edinburgh, pp. 121–155.

Chen, M., Luo, Z.-X., 2013. Postcranial skeleton of the cretaceous mammal *Akidolestes cifellii* and its locomotor adaptations. J. Mamm. Evol. 20, 159–189.

Chen, M., Wilson, G.P., 2015. A multivariate approach to infer locomotor modes in Mesozoic mammals. Paleobiology http://dx.doi.org/10.1017/pab.2014.14.

Chure, D.J., Good, T.R., Engelmann, G.F., 2014. A forgotten collection of vertebrate and invertebrate ichnofossils from the Nugget Sandstone (?Late Triassic–?Early Jurassic), near Heber, Wasatch County, Utah. In: Lockley, M.G., Lucas, S.G. (Eds.), Fossil Footprints of Western North America. New Mexico Museum of Natural History and Sciences, Bulletin 62, pp. 181–196.

Dagg, A.I., 1973. Gaits in mammals. Mammal Rev. 3, 135–154.

D'Orazi Porchetti, S., Wagensommer, A., 2015. A vertebrate trackway from the Twyfelfontein Formation (lower cretaceous), Damaraland, Namibia. Paläontol. Z. 89 (4), 807–814.

D'Orazi Porchetti, S., Bertini, R.J., Langer, M.C., 2016. Proposal for ichnotaxonomic allocation of therapsid footprints from the Botucatu Formation (Brazil). Ichnos (in review).

Ellenberger, P., 1970. Les niveaux paléontologiques de première apparition des Mammifères primordiaux et leurichnologie – establissement de zones stratigraphiques detaillees dans le Stormberg de Lesotho (Afrique du Sud) (Trias Superieur a Jurassique). Second Gondwana Sympospium, Proceedings and Papers: 343–370, Council for Scientific and Industrial Research, Scientia, Pretoria, South Africa.

Ellenberger, P., 1972. Contribution à la classification des pistes de vertébrés du Trias: lês types du Stormberg d'Afrique du Sud (I). Paleovertebrata, Mém. Extraordinaire 1972 (152 pp.).

Ellenberger, P., 1974. Contribution à la classification des pistes de Vertébrés du Trias: lês types du Stormberg d'Afrique du Sud, 2^{e} partie. Palaeovertebrata, Mémoire extraordinaire. Montpellier (170 pp.).

Ellenberger, P., 1975. L'explosion démographique dês petities quadrupèdes a allure de mammifères dans le Stormberg Supérieur (Trias) d'Afrique du Sud a perçu sur leur origine au Permien (France et Karoo). Colloque International C.N.R.S. (1973). Problèmes Actueles de Paléontologie–Évolution des Vertébrés 218, pp. 409–432.

Engelmann, G.F., Chure, D.J., 2011. Up, down, and sideways: abundant therapsid tracks on a dune slipface in the Nugget Sandstone (Early Jurassic) from near Heber, Utah. Society of Vertebrate Paleontology, 71 Annual Meeting, Programs and Abstracts, p. 105.

Engelmann, G.F., Chure, D.J., Loope, D.B., 2010. An occurrence of remarkably abundant *Brasilichnium* tracks (Nugget Sandstone, Early Jurassic, Dinosaur National Monument) and their environmental context. Geol. Soc. Am. Abstr. Programs 42 (5), 642.

Falkingham, P.L., 2012. Acquisition of high resolution 3D modelsusing free, open-source, photogrammetric software. Palaeontol. Electron. 15 (15 pp.).

Falkingham, P.L., 2014. Interpreting ecology and behaviour from the vertebrate fossil track record. J. Zool. 292, 222–228.

Falkingham, P.L., 2016. Applying objective methods to subjective track outlines. In: Falkingham, P.L., Marty, D., Richter, A. (Eds.), Dinosaur Tracks — The Next Steps, pp. 72–80.

Fernandes, M.A., Carvalho, I.S., 2005. Tafonomia para as pistas de tetrápodes amniotas do Paleodeserto Botucatu (Jurássico Superior–Cretáceo Inferior), Brasil. 2° Congresso Brasileiro de Herpetologia, 10–15 Julho 2005, 1.

Fernandes, M.A., Carvalho, I.S., 2007a. A Formação Botucatu (Bacia do Paraná) no Estado de São Paulo: Inferências Paleoambientais e Paleoicnológicas. 4° Simpósio sobre Cronoestratigrafia da Bacia do Paraná. XX Congresso Brasileiro de Paleontologia, 21–26 Outubro 2007 – Búzios, Boletim de Resumos, 23.

Fernandes, M.A., Carvalho, I.S., 2007b. Pegadas fósseis da Formação Botucatu (Jurássico Superior – Cretáceo Inferior): O Registro de um grande dinossauro Ornithopoda na Bacia do Paraná. In: Carvhalho, I.S., et al. (Eds.), Paleontologia: Cenários da Vida Vol. 1. Editora Interciência.

Fernandes, M.A., Carvalho, I.S., 2008a. Revisão diagnóstica para a icnoespécie de tetrápode Mesozóico *Brasilichnium elusivum* (Leonardi, 1981) (Mammalia) da Formação Botucatu, Bacia do Paraná, Brasil. Ameghiniana 45 (1), 167–173.

Fernandes, M.A., Carvalho, I.S., 2008b. A Paleoecnologia da Formação Botucatu (Bacia do Paraná) no Estado de São Paulo: aspectos paleoambientais. 44° Congresso Brasileiro de Geologia, 26–31 Outubro 2008 – Curitiba (PR); Anais, 812.

Fornós, J.J., Bromley, R.G., Clemmensen, L.B., Rodriguez–Perea, A., 2002. Tracks and trackways of *Myotragus balearicus* Bate (Artiodactyla, Caprinae) in Pleistocene aeolianites from Mallorca (Balearic Islands, western Mediterranean). Palaeogeogr. Palaeoclimatol. Palaeoecol. 180, 277–313.

Gatesy, S.M., 1991. Hind limb movements of the American alligator (*Alligator mississippiensis*) and postural grades. J. Zool. 224, 577–588.

Hunt, A.P., Lucas, S.G., 2007. Tetrapod ichnofacies: a new paradigm. Ichnos 14 (1–2), 59–68.

Irschick, D.J., Jayne, B.C., 1999. A field study of the effects of incline on the escape locomotion of a bipedal lizard, *Callisaurus draconoides*. Physiol. Biochem. Zool. 72 (1), 44–56.

Jayne, B.C., Ellis, R.V., 1998. How inclines affect the escape behaviour of a dune–dwelling lizard, *Uma scoparia*. Anim. Behav. 55, 1115–1130.

Jenkins Jr., F.A., Krause, D.W., 1983. Adaptations for climbing in North American multituberculates (Mammalia). Science 220, 712–715.

Kielan–Jaworowska, Z., 1978. Evolution of the therian mammals in the Late Cretaceous of Asia. Part III. Postcranial skeleton in Zalambdalestidae. In: Kielan-Jaworowska, Z. (Ed.), Results of the Polish–Mongolian Palaeontological Expeditions. Part VIII. Palaeontologia Polonica 38, pp. 5–41.

Kielan–Jaworowska, Z., 2013. In Pursuit of Early Mammals. Indiana University Press, Bloomington and Indianalpolis.

Kielan–Jaworowska, Z., Gambaryan, P.P., 1994. Postcranial anatomy and habits of Asian multituberculate mammals. Fossils Strata 36, 1–92.

Kielan–Jaworowska, Z., Hurum, J.H., 2006. Limb posture in early mammals: sprawling or parasagittal. Acta Palaeontol. Pol. 51 (3), 393–406.

Kielan–Jaworowska, Z., Cifelli, R.L., Luo, Z.–X., 2004. Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure. Columbia University Press, New York (630 pp.).

Krause, D.W., Jenkins Jr., F.A., 1983. The postcranial skeleton of North American multituberculates. Bull. Mus. Comp. Zool. 150, 199–246.

Kubo, T., Benton, M.J., 2009. Tetrapod postural shift estimated from Permian and Triassic trackways. Palaeontology 52 (5), 1029–1037.

Kümmel, S.B., Frey, E., 2012. Digital arcade in the autopodia of Synapsida: standard position of the digits and dorsoventral excursion angle of digital joints in the rays II–V. Palaeobiodivers. Palaeoenviron. 92, 171–196.

Kümmel, S.B., Frey, E., 2014. Range of movement in ray I of manus and pes and the prehensility of the autopodia in the Early Permian to Late Cretaceous non–anomodont synapsida. PLoS One 9 (12), e113911. http://dx.doi.org/10.1371/journal.pone.0113911.

Leonardi, G., 1977. On a new occurrence of tetrapod trackways in the Botucatu formation in the state of São Paulo, Brazil. Dusenia 10 (3), 181–183 (Curitiba).

Leonardi, G., 1980. On the discovery of an abundant Ichno–Fauna (vertebrates and invertebrates) in the Botucatu Formation s.s. in Araraquara, São Paulo, Brazil. An. Acad. Bras. Cienc. 52 (3), 559–567.

Leonardi, G., 1981. Novo icnogênero de tetrápode mesózoico da Formação Botucatu, Araraquara, SP. An. Acad. Bras. Cienc. 53 (4), 793–805.

Leonardi, G., 1984. Rastros de um mundo perdido. Ciênc. Hoje 2, 48–60.

Leonardi, G., 1987. Glossary and Manual of Tetrapod Footprint Paleoichnology. Conselho Nacional de Desenvolvimento Cientifico e Tecnologico, Brasil (75 pp.).

Leonardi, G., Carvalho, I.S., 1999. Jazigo Icnofossilífero do Ouro – Araraquara (SP). In: Schobbenhaus, C., Campos, D.A., Queiroz, E.T., Winge, M., Berbert–Born, M.L.C. (Eds.), Sítios geológicos e paleontológicos do Brasil, pp. 39–48 (Brasília).

Leonardi, G., Godoy, L.C., 1980. Novas pistas de tetrápodes da Formação Botucatu no Estado de São Paulo. Anais do XXXI Congresso Brasileiro de Geologia, 1980, pp. 3080–3089 (Balneário de Camboriú, Santa Catarina, SBG 5).

Leonardi, G., Oliveira, F.H., 1990. A revision of the Triassic and Jurassic tetrapod footprints of Argentina and a new approach on the age and meaning of Botucatu Formation footprints (Brazil). Rev. Bras. Geosci. 20, 216–229.

Leonardi, G., Sarjeant, W.A.S., 1986. Footprints representing a new Mesozoic vertebrate fauna from Brazil. Mod. Geol. 10, 73–84.

Leonardi, G., Carvalho, I.S., Fernandes, M.A., 2007. The desert ichnofauna from the Botucatu formation (Upper Jurassic–Lower Cretaceous), Brazil. In: Carvhalho, I.S., et al. (Eds.), Paleontologia: Cenários de Vida 1, pp. 379–391.

Lockley, M.G., 2011. The ichnotaxonomic status of *Brasilichnium* with special reference to occurrences in the Navajo Sandstone (Lower Jurassic) in the western USA. In: Sullivan, R.M., Lucas, S.G., Spielmann, J.A. (Eds.), Fossil Record 3. New Mexico Museum of Natural History and Science, Bulletin 53, pp. 306–315.

Lockley, M.G., Hunt, A.P., 1995. Dinosaur Tracks and Other Fossil Footprints of the Western United States. Columbia University Press, New York.

Lockley, M.G., Milner, A.R.C., 2014. The Ichnotaxonomy of hopping vertebrate trackways from the Cenozoic of the western USA. In: Lockley, M.G., Lucas, S.G. (Eds.), Fossil Footprints of Western North America. New Mexico Museum of Natural History and Science, Bulletin 62, pp. 489–500.

Lockley, M.G., Hunt, A.P., Haubold, H., Lucas, S.G., 1995. Fossil footprints in the DeChelly Sandstone of Arizona: with paleoecological observations on the ichnology of dune facies. In: Lucas, S.G., Heckert, A.B. (Eds.), Early Permian Footprints and Facies. New Mexico Museum of Natural History and Science, Bulletin 6, pp. 225–233.

Lockley, M.G., Hunt, A.P., Meyer, C.M., Rainforth, E., Schultz, R., 1998. A survey of fossil footprints at Glen Canyon National Recreation Area (western USA): a case study in documentation of trace fossil resources. Ichnos 5, 177–211.

Lockley, M.G., Lucas, S.G., Gaston, R., Hunt, A.P., 2004. Ichnofaunas from the Triassic–Jurassic boundary sequences of the Gateway area, western Colorado: implications for faunal composition and correlations with other areas. Ichnos 11, 89–102.

Lockley, M.G., Culver, T.S., Wegweiser, M., 2007. An ichnofauna of hopping rodent and arthropod trackways from the Miocene of Colorado. In: Lucas, S.G., Spielmann, J.A., Lockley, M.G. (Eds.), Cenozoic Vertebrate Tracks and Traces. New Mexico Museum of Natural History and Science, Bulletin 42, pp. 59–66.

Loope, D.B., 2006. Dry–season tracks in dinosaur–triggered grainflows. PALAIOS 21, 132–142.

Lucas, S.G., Spielmann, J.A., Klein, H., Lerner, A.J., 2010. Ichnology of the Redonda Formation. N. M. Mus. Nat. Hist. Sci. Bull. 47 (75 pp.).

Luo, Z.–X., 2007. Transformation and diversification in early mammal evolution. Nature 450, 1011–1019.

Mckee, E.D., 1944. Tracks that go uphill. Plateau 16 (4), 61–72.

Mckee, E.D., 1947. Experiments on the development of tracks in fine cross–bedded sand. J. Sediment. Petrol. 17, 23–28.

McKeever, P.J., Haubold, H., 1996. Reclassification of vertebrate trackways from the Permian of Scotland and related from Arizona andGermany. J. Paleontol. 70, 1011–1022.

Melchor, R.N., 2015. Application of vertebrate trace fossils to palaeoenvironmental analysis. Palaeogeogr. Palaeoclimatol. Palaeoecol. 439 (1), 79–96.

Milani, E.J., França, A.B., Schneider, R.L., 1994. Bacia do Paraná. Boletim Geociências da Petrobras 8 (2), 69–82.

Milani, E.J., Melo, J.H.G., Souza, P.A., Fernandes, L.A., França, A.B., 2007. Bacia do Paraná. Boletim Geociências da Petrobras 15 (2), 265–287.

Minetti, A.E., 1998. The biomechanic of skipping gaits: a third locomotion paradigm? Proc. R. Soc. B 265, 1227–1235.

Owaki, D., Kano, T., Nagasawa, K., Tero, A., Ishiguro, A., 2013. Simple robot suggests physical interlimb communication is essential for quadruped walking. J. R. Soc. Interface 10, 20120669.

Polly, P.D., 2007. Limbs in mammalian evolution. In: Hall, B.K. (Ed.), Fins into Limbs: Evolution, Development, and Transformation. University of Chicago Press, Chicago, pp. 245–268.

Rainforth, E.C., 1997. Vertebrate Ichnological Diversity and Census Studies, Lower Jurassic Navajo Sandstone [M.S. Research Report]. University of Colorado, Boulder (49 pp.).

Rainforth, E.C., Lockley, M.G., 1996a. Tracks of diminutive dinosaurs and hopping mammals from the Lower Jurassic of North and South America. In: Morales, M. (Ed.), The Continental Jurassic. Museum of Northern Arizona Bulletin 60, pp. 265–269.

Rainforth, E.C., Lockley, M.G., 1996b. Tracking life in a Lower Jurassic desert: vertebrate tracks and other traces from the Navajo Sandstone. In: Morales, M. (Ed.), The Continental Jurassic. Museum of Northern Arizona Bulletin 60, pp. 285–289.

Reynolds, R.E., 2006. Way out west: Jurassic tracks on the continental margin. In: Harris, J.D., Lucas, S.G., Spielmann, J.A., Lockley, M.G., Milner, A.R.C., Kirkland, J.I. (Eds.), The Triassic–Jurassic Terrestrial Transition. NewMexico Museum of Natural History and Science, Bulletin 37, pp. 226–231.

Rocha, P.L.B., 1995. *Proechimys yonenagae*, a new species of spiny rat (Rodentia: Echimyidae) from fossil sand dunes in the Brazilian Caatinga. Mammalia 59 (4), 537–549.

Rocha, P.L.B., Renous, S., Abourachid, A., Höfling, E., 2007. Evolution toward asymmetrical gaits in Neotropical spiny rats (Rodentia: Echimyidae): evidences favouring adaptation. Can. J. Zool. 85, 709–717.

Rowe, T., 1988. Definition, diagnosis, and origin of mammalia. J. Vertebr. Paleontol. 8 (3), 241–264.

Rowland, S.M., Mercadante, J.M., 2014. Trackways of a gregarious, dunefield–dwelling, Early Jurassic therapsid in the Aztec Sandstone of southern Nevada. PALAIOS 29 (10), 539–552.

Salamuni, R., Bigarella, J.J., 1967. Botucatu formation. In: Bigarella, J.J., Becker, R.D., Pinto, I.D. (Eds.), Problems in Brazilian Gondwana Geology, pp. 197–206 (Curitiba, PR, Brazil).

Sanders, R.C., Picard, M.D., 1999. Sedimentology and ichnology of a bioturbated interval in the Nugget Sandstone, a Jurassic eolianite, near Peoa, north–eastern Utah. In: Spangler, L.E., Allen, C.J. (Eds.), Geology of Northern Utah and Vicinity. Utah Geological Association Publication 27, pp. 123–140.

Sarjeant, W.A.S., 1995. Footprints in the sands of time. Vertebrate footprints and the interpretation of past environments. Geosci. Can. 21 (2), 77–87.

Scherer, C.M.S., 2000. Eolian dunes of the Botucatu Formation (Cretaceous) in southernmost Brazil: morphology and origin. Sediment. Geol. 137, 63–84.

Scherer, C.M.S., 2002. Preservation of aeolian genetic units by lava flows in the Lower Cretaceous of the Paraná Basin, southern Brazil. Sedimentology 49, 97–116.

Schneider, R.L., Mühlmann, H., Tommasi, E., Medeiros, R.A., Daemon, R.F., Nogueira, A.A., 1974. Revisão estratigráfica da Bacia do Paraná. Anais do XXVIII Congresso Brasileiro de Geologia 1974(1), pp. 41–65 (Porto Alegre).

Seilacher, A., 2007. Trace Fossil Analysis. Springer, Berlin.

Sereno, P.C., 2006. Shoulder girdle and forelimb in a Cretaceous multituberculate: form, functional evolution, and a proposal for basal mammalian taxonomy. In: Carrano, M.T., Gaudin, T.J., Blob, R.W., Wible, J.R. (Eds.), Amniote Paleobiology: Perspectives on the Evolution of Mammals, Birds, and Reptiles. University of Chicago Press, Chicago, pp. 315–370.

Taraborelli, P., Corbalán, V., Giannoni, S., 2003. Locomotion and escape modes in rodents of the Monte Desert (Argentina). Ethology 109, 475–485.

Thomson, T.J., Droser, M.L., 2015. Swimming reptiles make their mark in the Early Triassic: delayed ecologic recovery increased the preservation potential of vertebrate swim tracks. Geology 43 (3), 215–218.

Thulborn, R.A., 1990. Dinosaur Tracks. Chapman and Hall, London.