



Unveiling trampling history through trackway interferences and track preservational features: a case study from the Bletterbach gorge (Redagno, Western Dolomites, Italy)

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ABSTRACT

A slab from the Upper Permian Arenaria di Val Gardena Formation, bearing hundreds of tracks of different tetrapods, has been studied in order to reconstruct the trampling history through standard ichnological analysis and 3D photogrammetry. Analysis of crossed trackways to determine the relative timing of passages, as well as preservational features of the tracks qualitatively considered with trackmaker dimensions, has elucidated the nature of the trampled layer and the preservational mode of the tracks, especially the different conditions (i.e., sediment cohesion) that characterized the trampled layer during trackmaker crossings. Moreover, the analysis of an event timeline strongly suggests that caution should be exercised in analyzing track interferences, especially when multiple lines of evidence are lacking. As a consequence, the timeline of events may be masked, misleading and misinterpreted with obvious repercussions on general reconstructions (e.g., palaeoecological and behavioural). This study highlights the reliability of this type of analysis in untangling the preservational history of trampled surfaces; a useful investigative tool to be employed prior to traditional ichnological analyses aimed at classification of tetrapod tracks.

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INTRODUCTION

The historical and idiographic nature of tetrapod ichnology, focusing on unique and unrepeatable events, is evident in the context of the dynamics of track formation. This process does not always occur in the same conditions, often leading to very different footprints largely depending on substrate properties as well as trackmaker anatomy and behaviour. As stated by several authors, the footprint itself should be considered as the result of *in continuum* interactions between the substrate and the trackmaker foot (e.g., Gatesy et al., 1999; Fornós et al., 2002; Gatesy, 2003; Milàn et al., 2006). The parts of the footprint and their formation can be considered “diachronous” in the time interval in which they were impressed (Romano et al., 2015). The physical properties (e.g., substrate consistency) of the tracking surface and the substrate exert a strong control on the footprint’s three-dimensional morphology, as highlighted by several papers that stress the specificity of some track features in relation to the moisture content of the substrate (e.g., Avanzini, 1998; Nadon, 2001; Milàn, 2006; Milàn and Bromley, 2006, 2008; Jackson et al., 2009, 2010; Bates et al., 2013).

Both of the main variables involved in the process of track formation have a prominent historical nature, but at very different timescales. The historical nature of the trackmaker and track is evident in the context of the irreversible process of evolution, considering the acquisition of anatomical and behavioural characters that are mirrored in the footprint’s three-dimensional morphology (Avanzini et al., 2001; Carrano and Wilson, 2001; Romano et al., 2015). The historical nature of the substrate, acting on a smaller timescale, involves variations in the physical and mechanical properties that can alternate or coexist on a trampled surface; these variations are detectable from footprint structure and substrate-related extramorphologies (for the concept of extramorphologies in tetrapod ichnology see Peabody, 1948; Haubold, 1996, 1998), as well as from other abiotic structures (e.g., Citton et al., 2012; Cariou et al., 2014). Thus, the identification and understanding of the main events and substrate conditions is deemed essential in order to reconstruct the dynamics of track formation.

Ancient surfaces with multiple tracks and trackways are quite common in the ichnological record; in these cases, the spatial distribution of tracks and trackways, as well as the trackmaker’s advancement direction, bending, interferences

(i.e., interruptions and intersections) and overlapping, represent valuable data for ichnological analyses giving insights for general interpretations. A popular example is the recognition of herd behaviour in different groups of dinosaurs based on the analysis of parallel trackways (e.g., Currie and Sarjeant, 1979; Currie, 1983; Carpenter, 1992; Casanovas Cladellas et al., 1993; Barnes and Lockley, 1994; Cotton et al., 1998; Castanera et al., 2011), as well as the interpretation of interrupted trackways as evidence of predatory interactions between both vertebrate and invertebrate trackmakers in the continental Permian ichnological record (Lockley and Madsen, 1993; Hunt et al., 1994; Kramer et al., 1995, but see Hunt and Lucas, 1998 and Citton et al., 2012 for different interpretations).

At the same time, interferences between tracks and trackways have proved to be a significant source of direct and indirect information about trackmakers and substrate conditions during track formation (Lockley et al., 1986; Farlow et al., 1989; Mezga and Bajraktarevic, 1999; Matsukawa et al., 2001; Romero-Molina et al., 2003; Gangloff et al., 2004; Rainforth, 2005; Latorre Macarrón et al., 2006; Melchor and De Valais, 2006; Torcida Fernández-Baldor et al., 2006; Zhang et al., 2006; Nicosia et al., 2007; Wilson et al., 2009; Alcalá et al., 2012; Citton et al., 2012; Hornung et al., 2012; Razzolini et al., 2014), indirectly allowing reconstruction of the sequence of trackmaker passages.

Here, we analyze a single surface trampled by different types of tetrapods crossing in different directions. On the slab surface hundreds of tracks and traces are preserved. Ten trackways have been identified in addition to many isolated footprints and some probable invertebrate traces. Nine of the trackways and some *Pachypes dolomiticus* isolated tracks reciprocally interfere with one or more trackways by overprinting and/or intersections, allowing tracing back a relative timing of surface crossings. The analysis enabled a detailed narrative of events that is crucial for the understanding of the substrate conditions before, during and after the trampling, as well as for the recognition of the preservational mode of the tracks (Milàn and Bromley, 2006; Marty et al., 2009).

Geological Setting of the Arenaria di Val Gardena Formation in the Southern Alpine Domain

Two main, unconformity-bounded tectonosedimentary cycles have been recognized in the Late Carboniferous to early Middle Triassic stratigraphic

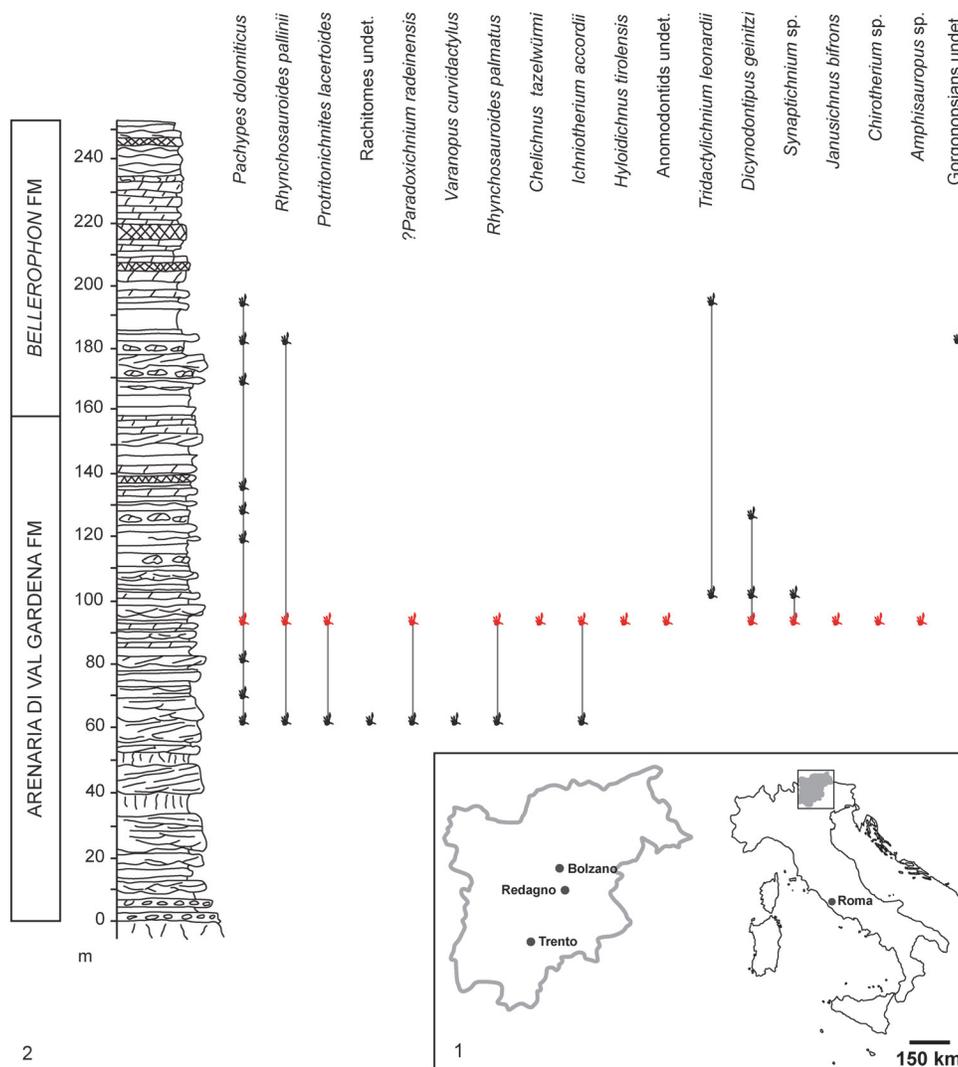


FIGURE 1. 1, Location map of the Butterloch-Bletterbach area – Redagno; 2, Schematic drawing of the Butterloch-Bletterbach section with the distribution of ichnotaxa; red tracks indicates the stratigraphic level from which the studied footprints came (from Ceoloni et al., 1988, redrawn and slightly modified).

succession of the Southern Alps (Massari et al., 1994). The lower cycle typically consists of volcanic rocks and alluvial to lacustrine sedimentary rocks deposited in small graben or half-graben. The upper cycle is characterized by an interruption of volcanic activity and is mainly represented by fluvial, coastal sabkha and shallow marine sediments (Cassinis et al., 1988). Radiometric data and palynomorph assemblages (Cassinis and Doubinger, 1992; Cassinis et al., 2002) indicate an Artinskian-Kungurian age for the lower cycle (Early Permian), whereas the upper cycle is regarded as Wuchiapingian (Late Permian) on the basis of spore morphs and foraminifera (Cassinis et al., 2002).

The arenaceous and silty terrestrial red beds of the Arenaria di Val Gardena Formation, first

described by von Richthofen (1860), belong to the second cycle and can lie directly on the crystalline basement, on conglomeratic lenses (Bosellini and Dal Cin, 1968) or on volcanic rocks of the “Gruppo Vulcanico Atesino” (Avanzini et al., 2008). The unit is laterally and upwardly replaced by the shallow marine *Bellerophon* Formation related to westward transgressions, which is in turn overlain by the Lower Triassic Werfen Formation (Cassinis et al., 2012; Roghi et al., 2014).

One of the most important localities to study the Late Permian evolution of the Southern Alpine domain is, undoubtedly, the Butterloch-Bletterbach section, close to the town of Redagno (Bolzano, Italy; Figure 1.1), where a thick sequence of the Arenaria di Val Gardena Formation and *Bello-*

phon Formation crops out. The Bletterbach gorge was extensively studied in the past and more recently, with regard to sedimentological and stratigraphical features (e.g., Accordi, 1958; Conti et al., 1986, 1997; Massari et al., 1988; Cassinis et al., 1999, 2002, 2012), the palaeobotanical and palynological associations (e.g., Leonardi, 1948; Klaus, 1963; Kustatscher et al., 2012, 2014; Bauer et al., 2014) and the rich tetrapod footprint ichnofauna (e.g., Kittl, 1891; Abel, 1929; Leonardi, 1951; Leonardi and Nicosia, 1973; Leonardi et al., 1975; Conti et al., 1975, 1977, 1979; Valentini et al., 2007, 2008, 2009).

The rich track-bearing levels belong to a stratigraphic interval that shows a wide range of facies, as highlighted by Conti et al. (1986; Figure 1.2). According to Massari et al. (1988), the spectrum comprises channel-fill sandstones, red to grey mudstones, small thin-bedded intervals of sandstones, commonly wave-rippled at the top, and mudstones sometimes cracked, crinkled and with gypsum nodules and, finally, laminated and bioturbated siltstones and fine sandstones; intervals with pedogenic properties, such as carbonate nodules or concretions, have also been observed. The facies associations have been related to the transition between the distal portion of a fluvial system and a coastal sabkha that was susceptible to floods by very shallow water, as suggested by the thin-bedded sequence of wave-rippled fine sandstones with mud drapes (Conti et al., 1986; Massari et al., 1988, 1994).

MATERIAL AND METHODS

Much of the terminology used here was introduced and discussed by Leonardi (1987). The study of the relative timing of passages, main advancement directions and preservational features of the tracks were carried out directly on the slab. A grid, consisting of three rows and eight columns indicated with letters from A to C and Arabic numerals from 0 to 7, respectively, has been superimposed on the interpretive drawing to facilitate the description of the main intersection points and interferences between tracks. Each trackway is indicated by an acronym that is followed (only for trackways of the same ichnotaxon) by an Arabic numeral according to the relative time of formation. The acronyms are: 'G11–7' for *Ganasauripus ladinus* tracks and trackways, 'Jb' for *Janusichnus bifrons* trackway, 'Ct1–2' for *Chelichnus tazelwürmi* trackways and 'Pd' for *Pachypes dolomiticus* tracks

and trackway. Sedimentary structures are indicated by the acronyms 'rip' (i.e., ripple marks) and 'dcr' (i.e., possible desiccation cracks).

The slab MPUR NS 34/28 (MPUR NS: Museo di Paleontologia Università di Roma Nuova Serie) was collected in the 1980s from the Butterloch-Bletterbach section (Ceoloni et al., 1988). Digital 3D models of MPUR NS 34/28 were constructed in order to obtain a quantitative assessment of the relief of the studied tracks (qualitatively evaluated during the firsthand analysis). The model was achieved using the high resolution Digital Photogrammetry method. This technique is based on Structure from Motion (SfM) (Ullman, 1979) and Multi View Stereo (MVS) (Seitz et al., 2006) algorithms and takes advantage the computational power of modern computers, low cost digital cameras and high quality photos.

A full 3D scaled model of any object in space can be reconstructed, starting from a suitable number of photographic images (2D object projection) of a static scene taken from different points of view. To achieve suitable results for scientific applications, it is crucial that objects possess locally unique texture, and numerous photos are taken in order to maintain a high "overlay redundancy index" and a small angular separation between images. The former index can be thought as the average number of photos in which surveyed surface points are present. This technique produces high-quality, dense point clouds with no spatial information that can be used to generate 3D models comparable to those obtained from LiDAR technology.

A number of software solutions do exist for digital photogrammetry; the software package used (Agisoft PhotoScan Pro, www.agisoft.com) is geared toward semi-automatic processing of images with the end goal of the creation of 3D textured meshes. PhotoScan can handle a wide range of digital images and automatically calculates camera calibrations.

The photogrammetric process used images that were acquired using an 8 Megapixel Canon Digital ixus 80 IS and a 10 Megapixel Canon EOS 400D with 18 mm focal length. In order to achieve good image overlap, 270 images were used in 3D model construction. In order to correctly scale the calculated model, a metric reference marker was applied on the surface. A dense cloud mean resolution of less than 1 mm was obtained.



FIGURE 2. Orthophoto of the slab MPUR NS 34/28. Scale bar is 50 cm.

RESULTS

The Slab

The slab is composed of about 20 parts, some of which were obtained by gluing together blocks of small sizes. When reconstructed, the slab is about 2.5 m long, a maximum of 1 m wide and about 3 cm thick (Figure 2). The slab is composed of a dark-red siltstone. Tracks and traces are preserved as convex hyporeliefs, thus representing the infills of the original impressions. In section, well below the alleged upper limit of the filling depositional event, silty sediments are characterized by very fine, undeformed, parallel laminae. Sediments constituting the filling of the tracks are instead unstructured, suggesting that the burial of the tracking surface (*sensu* Fornós et al., 2002) likely occurred in a relatively rapid sedimentation event forming natural casts (see “track burial model” in Marty et al., 2009). The surface on which the tracks are preserved is slightly undulatory and characterized by weakly developed, discontinuous, straight-crested ripple marks. The ripple marks are symmetrical and were likely produced by oscillatory flow acting, after a flooding event, on silty sediments. The discontinuity of the ripples can be ascribed to an original topographical heterogeneity of the tracked surface.

Brief Description of Ichnotaxa

The studied slab has been previously described with regard to ichnotaxonomy and track-maker identification (Ceoloni et al., 1988; Valentini et al., 2007, 2008, 2009). A general description of the studied tracks is briefly provided; for a detailed discussion of ichnotaxonomy, which is beyond the aim of this paper, reference should be made to the cited literature and references therein.

According to Ceoloni et al. (1988), *Chelichnus tazelwürmi* refers to footprints with a marked affinity with ‘mammalian reptiles’ belonging to ‘pelycosaurs’ (Figure 3.1-2). Manus and pes are pentadactyl, semiplantigrade and mesaxonic, the pes with a marked internal functional prevalence; digit traces are straight and almost parallel to each other and relative to the trackway midline (Ceoloni et al., 1988).

Ceoloni et al. (1988) also established the ichnotaxon *Janusichnus bifrons* (Figure 3.3) for pentadactyl, plantigrade manus and pes footprints. The pes shows some ‘mammalian’ features, among which a reduced phalangeal formula and internal functional prevalence are the most prominent. The manus has digits increasing in length from I to IV, with the fifth reduced (Ceoloni et al., 1988).

Ganasauripus ladinus was established by Valentini et al. (2007) as part of the review of the lacertoid footprints of the Arenaria di Val Gardena Formation. It indicates pentadactyl, semiplantigrade to plantigrade footprints of a quadruped ‘reptile’, showing a mesaxonic manus and an ectaxonic pes and sinusoidal tail drag marks; digits increase in length from I to IV, with the fifth ending behind the base of digit IV (Figures 3.4, 4.1).

Pachypes dolomiticus was coined by Leonardi et al. (1975) and recently re-evaluated by Valentini et al. (2009). The ichnotaxon refers to semiplantigrade, pentadactyl footprints of a quadruped track-maker identified as a pareiasaur (e.g., Valentini et al., 2008, 2009). The pes, sub-parallel with respect to the trackway midline, exhibits a total functional prevalence, whereas the manus is mesaxonic and often turned inward with respect to the trackway midline. Digits are short and sturdy, sub-parallel; external digits are shorter (Figure 4.2-4).

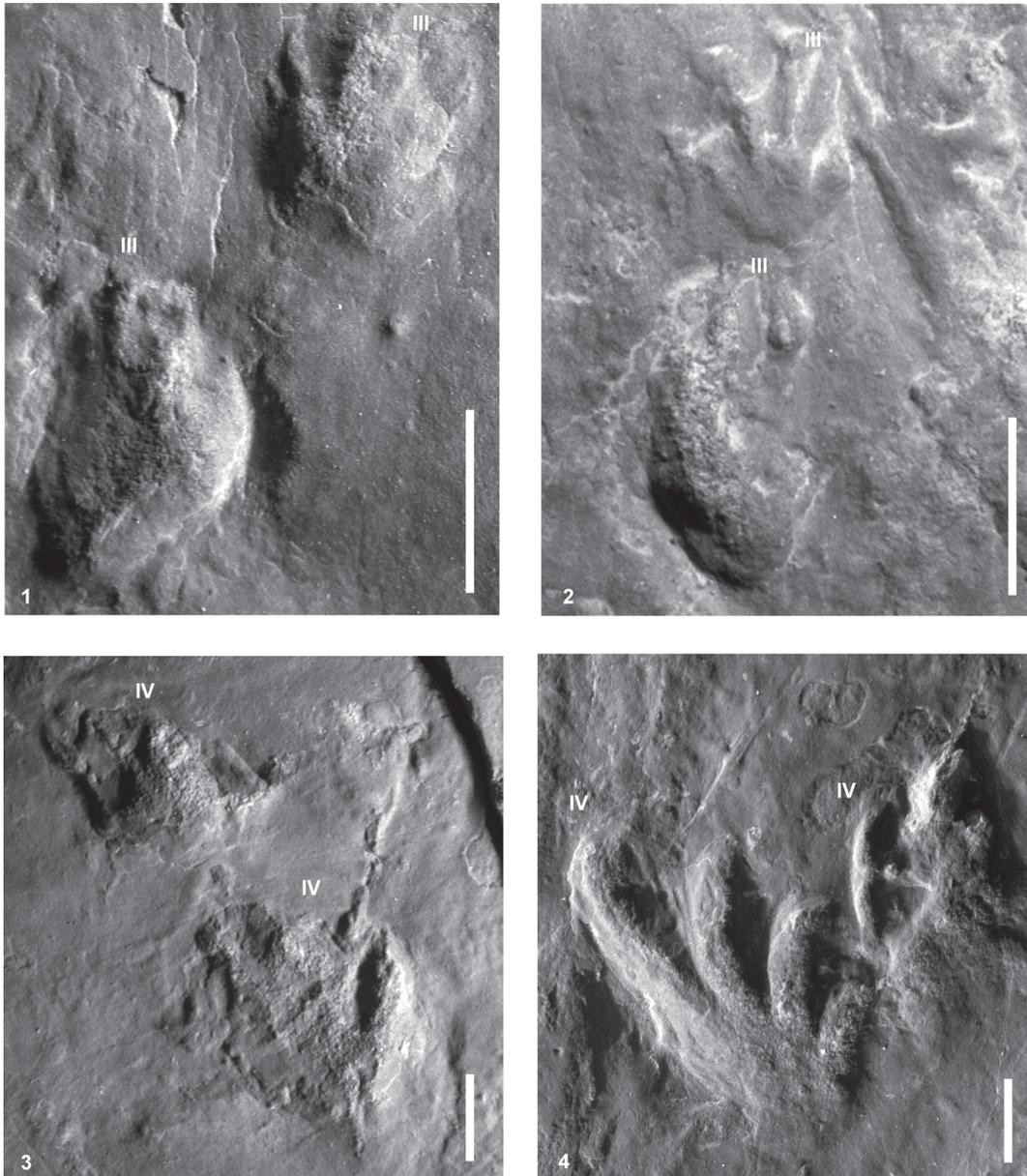


FIGURE 3. 1-2, *Chelichnus tazelwürmi*; 3, *Janusichnus bifrons*; 4, *Ganasauripus ladinus*. Scale bar is 1 cm. Roman numerals refer to digits.

Event Timeline

The analysis of interferences between trackways, and between tracks and sedimentary structures, allows us to define a relative timeline for when different crossing events occurred (Figure 5.1-9). G13 tracks and some isolated tracks do not interfere with any other trace, so their relative timing by means of intersection points cannot be defined. Footprints Pdx and Pdy (Figure 5.8-9) were not considered in the analysis due to their

poor quality and the uncertainty in referring them confidently to any single trackway.

The formation of ripple marks represents the most likely first event recorded on the submerged surface, as indicated by their interference by some tetrapod tracks (Figure 5.1, meshes B5–B6; e.g., Figure 6). In many cases, ripple crests are interrupted at track margins or, when present, at the lateral edge of the expulsion rims.

According to Valentini et al. (2007), G11 tracks, assigned to *Ganasauripus ladinus* (meshes B3–B4, Figure 5.1), exhibit a more digitigrade pos-

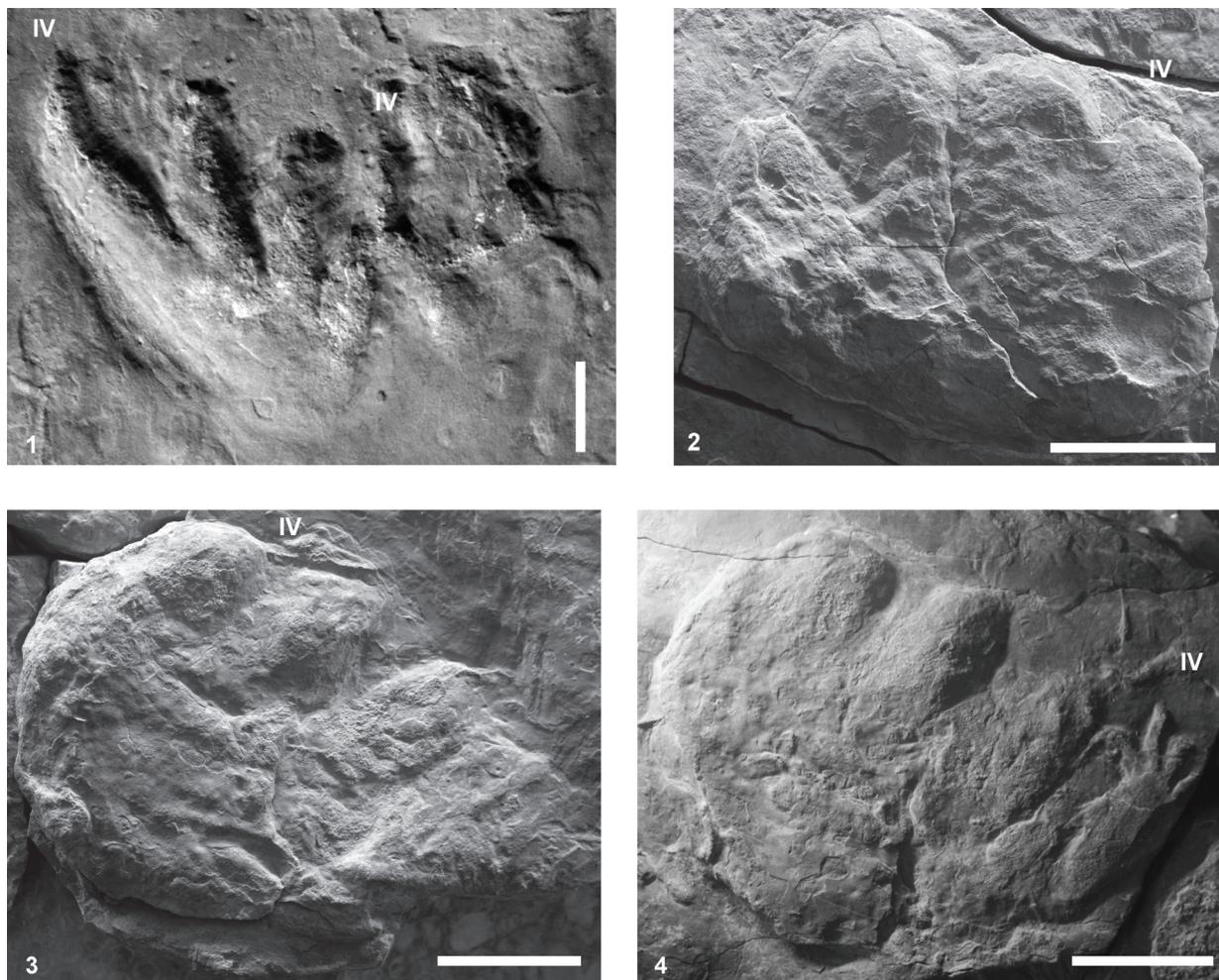


FIGURE 4. 1, *Ganasauripus ladinus*; 2, *Pachypes dolomiticus* manus; 3-4, *Pachypes dolomiticus* pedes. Scale bar is 1 cm (1) and 5 cm (2-4). Roman numerals refer to digits.

ture of the trackmaker's feet and lack impressions of the first and the fifth digits; digit traces are widened and have claw scratch marks (Figure 7). These features characterize GI1 tracks as swimming traces (Valentini et al., 2007). According to the same authors, these tracks were likely produced by a trackmaker that was moving on a thin sheet of water partially floating, just touching the substrate surface by pushing off with the distal ends of digit.

After the GI1 trackmaker, the animal that produced trackway GI2, and likely the GI3 tracks, crossed the surface (Figure 5.2, meshes B0–B6). The tetrapod, which produced 13 strides and a faint tail trace, interfered with some ripple marks (mesh C6). The relative antecedence of this crossing is derived by different points of intersection between the trackway GI2 and the trackways GI4,

GI5, GI6, GI7 and Pd (see Figure 5.9, meshes B0–B2 and C3–C6, and 5.10).

Later, the producer of the GI4 trackway passed (Figure 5.3, meshes A1–C5). The interferences preserved on the slab indicate the relative antecedence of this trackway to the GI5, GI6, Jb and Pd trackways (Figure 5.9–10, meshes B2–B4; Figure 8.1). Subsequent to GI4, the Jb trackmaker crossed the surface (Figure 5.4, meshes A3–B3), trampling on the tail trace and a pes print of the GI4 trackway. The Jb trackway disappears at the intersection with a pes impression belonging to the Pd trackway, thus indicating its relative subsequence.

Before the impression of the GI5 trackway, the trackmaker of Ct1 left about 10 poorly preserved footprints (Figure 5.5, mesh A1–B1). The GI5 trackway, made of about 14 sets and by a sinusoidal tail trace, was left by a trackmaker (Figure 5.5, meshes A0–C3) interfering with the GI2, GI4 and

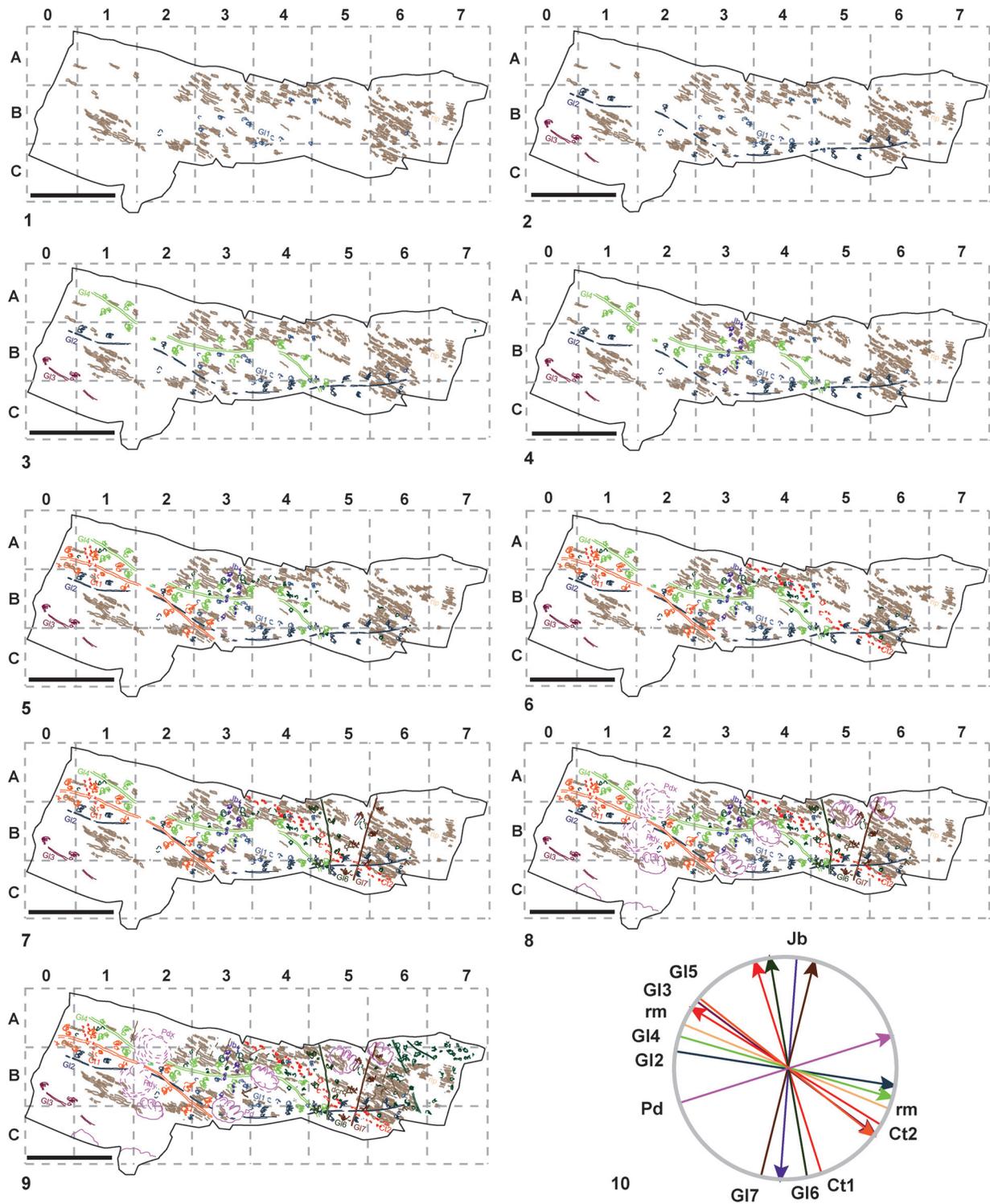


FIGURE 5. Event timeline. **1**, Ripple marks and G1 tracks formation; **2**, G2 and G3 tracks formation; **3**, G4 trackway formation; **4**, Jb trackway formation; **5**, G5 and Ct1 trackways formation; **6**, Ct2 trackway formation; **7**, G6 and G7 trackways formation; **8**, Pd trackway formation; **9**, Final interpretative drawing of the slab MPUR NS 34/28; **10**, Trackmakers advancement directions. **rip**, ripple marks; **Pd**, *Pachypes dolomiticus* trackway; **Ct1-Ct2**, *Chelichnus tazelwürmi* trackways; **G11-G17**, *Ganasauripus ladinus* trackways; **Jb**, *Janusichnus bifrons* trackway; **dcr**, ? desiccation cracks. Scale bar is 50 cm.

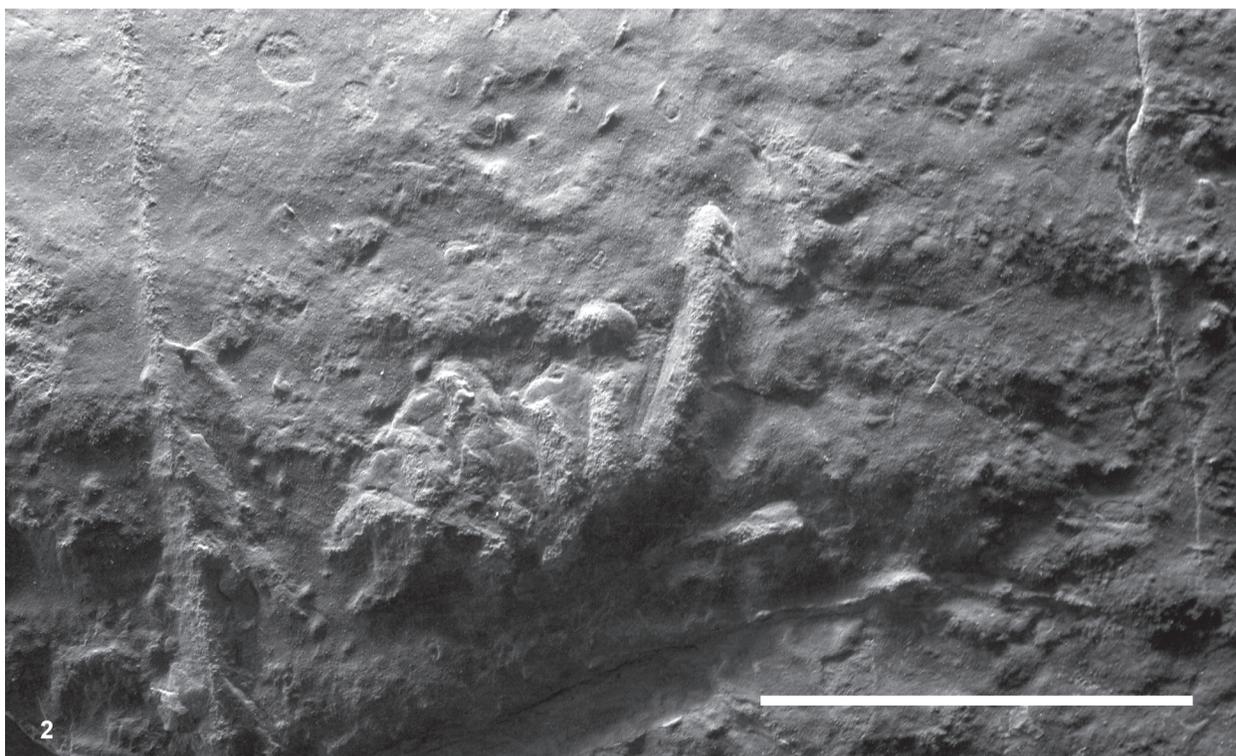
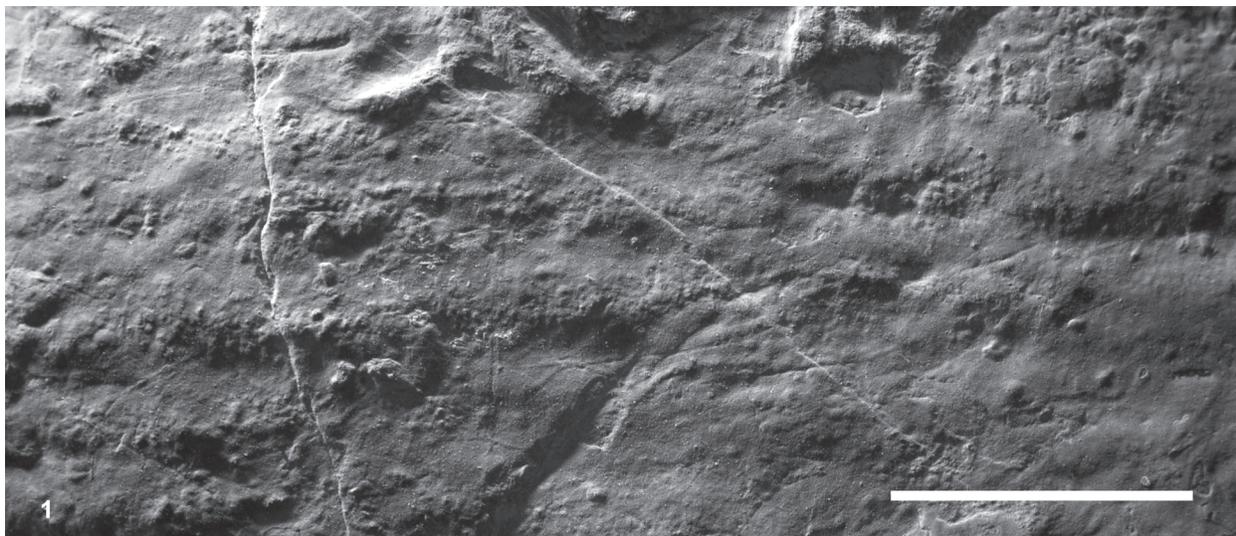


FIGURE 6. Slab MPUR NS 34/28. **1**, Ripple marks counterprints; **2**, Interference between ripple marks counterprints and GI7 trackway. Scale bar is 5 cm.

Ct1 trackways (Figure 5.9-10, mesh A1–B1). Trackway Ct2 was produced before GI6 and GI7. While crossing the surface, the Ct2 trackmaker interfered with ripple marks, some swimming traces and with the trackway GI2 (Figure 5.6, meshes B4–B5 and C5–C6). Afterward, the GI6 trackmaker crossed the surface, interfering with the

GI2, GI4 and Ct2 trackways (Figure 5.7, mesh A5–C5).

Trackway GI7 is comprised of six sets, two of which are incomplete, and a sinusoidal tail trace. The penultimate pes impression of this trackway shows a trace probably left by the tarsal-ankle joint pad, as highlighted by Valentini et al. (2007).

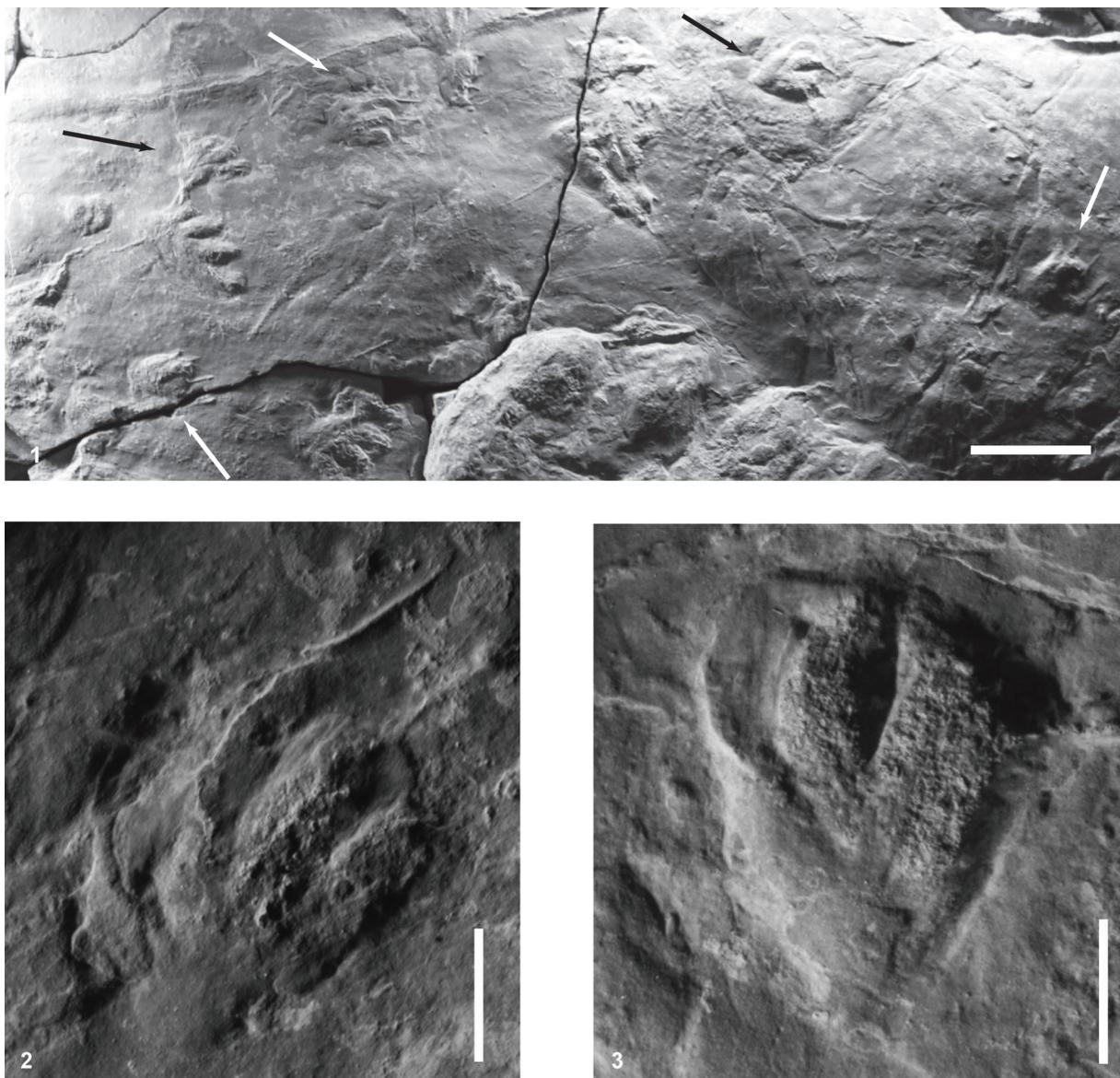


FIGURE 7. Slab MPUR NS 34/28. **1**, Swimming traces (indicated by black and white arrows) belonging to trackway GI1; **2-3**, Close-up of the best GI1 tracks. Scale bar is 5 cm (**1**) and 1 cm (**2-3**).

Regarding the relative timeline, it can only be stated that this trackway was left by a trackmaker crossing the surface after the impression of the GI2 and Ct2 trackways, with which it interferes (Figure 5.7, mesh B5), and before the Pd trackway.

The last trackmaker leaving traces of its passage was the producer of the Pd trackway, inferred to be a member of Pareiasauridae (Valentini et al., 2008; Avanzini et al., 2011). The trackway is made of three sets, the first of which is incomplete. The trackmaker crossed the surface and interfered with ripples marks and the GI2, GI4, GI5, GI6, GI7 and

Jb trackways (Figure 5.8-10, meshes A6–B1; Figure 8.2).

The tracked surface also possesses structures tentatively interpreted as desiccation cracks (indicated as dcr in Figure 5.9-10, meshes B5, B6), very likely formed well after track formation.

Preservational Features

The tracks are not uniformly preserved on the surface; instead preservational variations can be observed between and within trackways. At the same time, many of the natural casts clearly show some recurrent features providing significant infor-

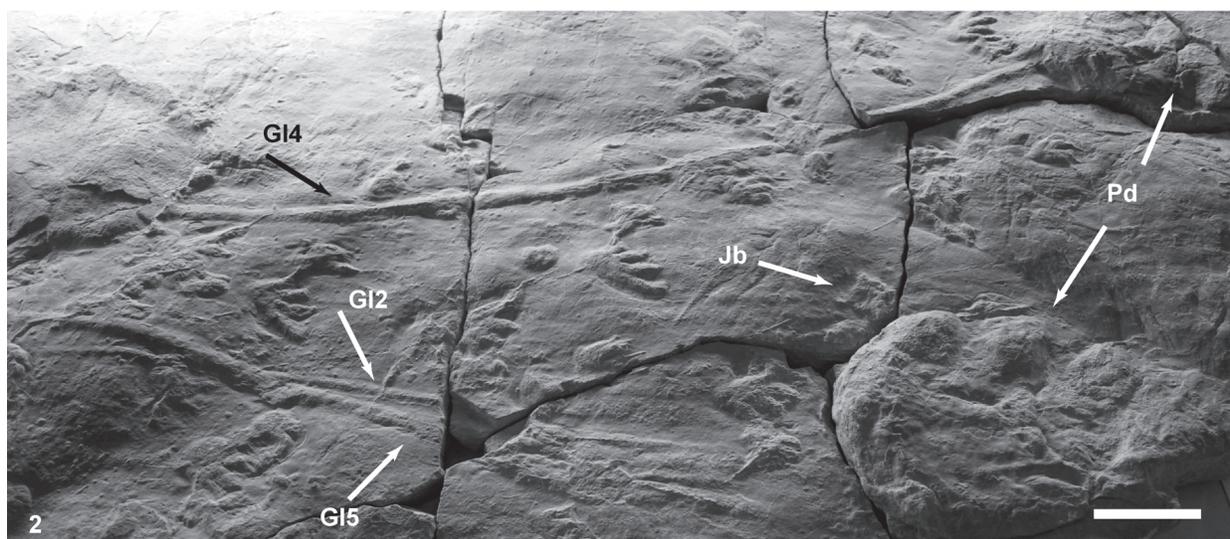


FIGURE 8. Slab MPUR NS 34/28. **1**, Interference between trackways G14 and Pd indicating the relative antecedenence of G14 trackmaker; **2**, Trackway Pd, sets 2 and 3 interfering with G12, G14, G15 and Jb trackways. Scale bar is 5 cm.

mation about the substrate conditions during and after trampling. All the tracks seem to have been impressed at the same depth, regardless of footprint morphology and trackmaker anatomy. Maximum variation in track relief is within a centimetre. Tracks with greatest relief are those left by the pareiasaurian, as illustrated in the 3D photogrammetric model (Figure 9.2, Appendix).

Trackways G14, G15, G16, Ct2, Pd and, with lesser emphasis, G17 and Jb, are generally characterized by very well-preserved footprints showing

several anatomical characters of the trackmakers' foot, as also stated by Valentini et al. (2007) for *Ganasauripus ladinus* trackways. In many cases footprints belonging to these trackways exhibit expulsion rims extending up to the proximal margin of the footprint. The rims are almost vertical, high and sharp. Track walls (*sensu* Brown, 1999) and lateral walls of digits are vertical, and no traces of collapse are observed. These features suggest that trampled sediments were highly cohesive and plastic during trackmaker crossings. In contrast,

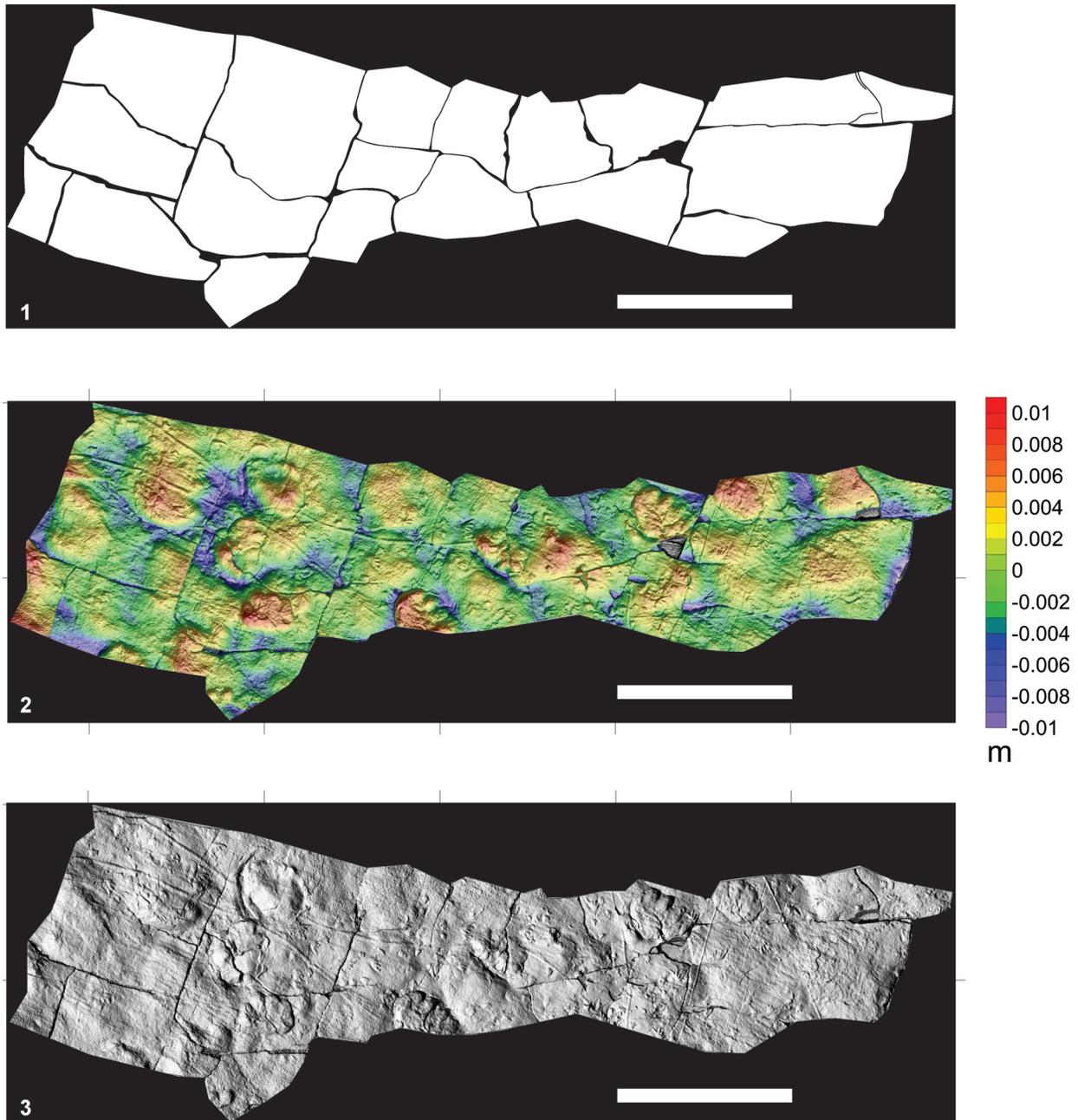


FIGURE 9. 1, Drawing of different parts making up the slab; 2, 3D photogrammetric false coloured model; 3, 3D photogrammetric shaded grey model. Scale bar is 0,5 m.

GI1 footprints are characterized by weak expulsion rims and are more developed horizontally, suggesting that sediments were less cohesive and more fluid, likely due to water logging, during trackmaker advancement.

A different substrate condition can be inferred from the crossing of the trackmakers of GI2 and GI3. These trackways share similar preservational features; the right side of both trackways is not pre-

served, whereas the left one is incomplete, being made of shallowly impressed sets and often lacking the manus impressions. In these cases, the preservational bias causing the failure of the impression of the right side was likely controlled by different substrate conditions, in a restricted space.

Trackway Ct2 shows the greatest internal preservational variability. In the first segment of the trackway, like trackway Ct1, footprints are some-

times faintly preserved and sets are incomplete, although some retain the main anatomical characters. From the fifteenth set up to the end of the trackway, however, footprints are very well preserved and are characterized by almost vertical walls and definite expulsion rims. These features again suggest a wet and cohesive substrate during trackmaker crossing, at least for the central and final portion of the trackway.

A noteworthy feature is represented by the interferences that trackway Pd forms with some ripple marks and with GI7, further indicating the conditions of the surface during the crossing of the huge trackmaker. In four cases, ripple marks overlap different *Pachypes dolomiticus* footprints (e.g. Figure 4.3-4; see Figure 5.8, meshes C2, C3; B5, B6), thus seemingly subsequent in time. However, the antecedence of ripple marks is assured by the slight displacement affecting these structures at the intersections with the Pd tracks (e.g., mesh B5, B6 in Figure 5.8). Therefore, it is evident that the heavy trackmaker crossed the surface after the ripples formed, causing dislocation and overprinting, without obliterating the trampled structures.

A similar configuration is observable between the Pd and GI7 trackways (Figure 10.1). The tail trace of GI7 is clearly interrupted in correspondence to the proximal margin of the foreprint of set 6 of Pd, but it can still be observed as superimposed on the Pd manus with a right displacement of less than 1 cm. The last set of GI7 is preserved close to the tail trace and at the same distance as in the preceding sets, although it appears smaller than the previous sets (Figure 10.2-5). As in the case of ripple marks, the Pd trackmaker crossed the surface after the passage of the GI7 trackmaker. As the giant animal walked and interfered with the GI7 trackway, the tail trace was interrupted and dislocated, but at the same time the overprinted structures were preserved under the animal's weight. Similar configuration is shown by the preceding pes impression of GI7 (see Valentini et al., 2007 for a discussion of this track) and the pes impression of the Pd trackway (Figure 5.8, mesh A5, B5).

DISCUSSION

The conducted analyses enabled important information about footprint preservation and substrate conditions during and after the tetrapods' crossings to be gained. By integrating the collected evidence in a broader perspective, additional interpretations can be made.

The configuration of Pd interferences with ripple marks and GI7 trackways (i.e., interruption and displacement plus lowering and overprinting) requires an explanation that accounts for both the observed track preservational features and substrate properties during track formation. The observed interferences can occur within the substrate, with the trackmaker of Pd walking well above the trampled surface (i.e., Pd tracks should be the filling of undertracks or transmitted tracks or ghost prints *sensu* Marty et al., 2009). However, the lack of a stack of transmitted prints and no sediment interposition (nor differential compaction) between the fillings of *Ganasauripus ladinus* and *Pachypes dolomiticus* suggests that there were no important sedimentation events between the two crossings. Thus Pd tracks are likely not undertracks, but natural casts similar to the other tracks on the surface. The most parsimonious explanation for Pd-GI7 interference is that when the Pd trackmaker crossed the surface, the trampled sediments were deformed under the trackmaker's weight and, simultaneously, the ripple crests, GI7 tracks and the tail trace were lowered and displaced without being distorted, fractured or obliterated. At the time of the impression of the Pd trackway, some tracks were still so fresh as to be effaced (e.g., Jb), whereas the sediments affected by ripple marks and already trampled by other tetrapods probably had expelled part of the water. The surface hardened, allowing for the preservation of some ripple marks, the tail trace and the last set of the GI7 trackway during the Pd trackmaker passage. The surface was still relatively plastic and ductile enough, however, not to collapse or crack under the pressures applied by the heavy trackmaker whose tracks are rather detailed. It can be envisaged that differential hardening of the substrate may have been triggered by progressive general dehydration of the sediments or by microbial activity. At the same time, small time scale variations of the sediment moisture, which may have been driven by the daily variation in humidity or rainfall, could also have occurred, thus explaining the co-existence of slightly different substrate conditions during Pd trackmaker crossing.

Moreover, the facts that i) tracks left by trackmakers of different relative sizes, morphologies and modes of locomotion, which crossed the same surface under different substrate conditions, were impressed to the same depth and that ii) track elements and substrate-related extramorphologies (e.g., anatomical details, track walls, expulsion rims, associated traces) of these tracks co-occur

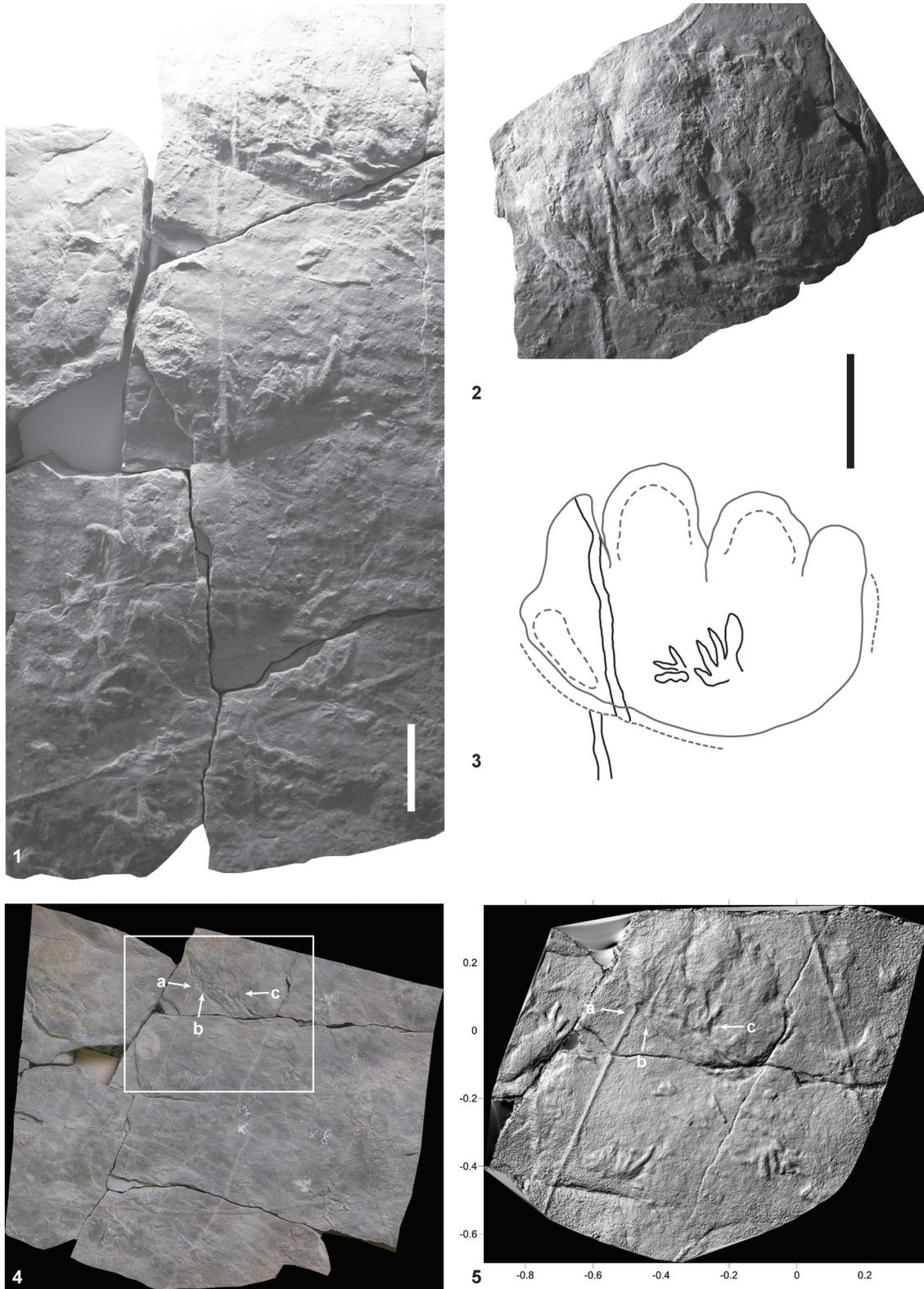


FIGURE 10. 1, Trackway GI6; 2, Close up of the GI6-Pd interference; 3, Interpretative drawing of GI6-Pd interference; 4, Orthophoto of trackway GI6; 5, Shaded grey photogrammetric model of the interference. White arrows and letters a, b and c indicate interruption (a), displacement (b) of the tail trace, and trackway GI6 last set (c). Scale bar is 5 cm.

and share similar features, suggest that i) a sub-surface consolidated layer underlay the trampled sediments, as also suggested by Valentini et al. (2007, see also Falkingham et al., 2011), and that ii) all the tracks were likely produced within days or, perhaps, weeks of each other. If trackmakers of different weights crossed the surface simultaneously under homogeneous substrate conditions, then the footprints produced would probably have different characteristics in relation to different pressure-sediment relationships, regardless of the existence of a firm subsurface layer.

A general consideration regards the overprinting of tracks and the clear difficulties in establishing the correct timeline of passages, especially when subsidiary evidences (i.e., more than one intersection point, interruption, displacement) are lacking or not observed. A vivid example is the overprinting between GI7 and Pd tracks discussed above. In this case, assuming no record of interruption and displacement (e.g., trackmaker's tail lifted from the ground during locomotion; substrate not compliant to record displacement), the reverse timing between the two crossings would probably have been interpreted as correct.

Finally, the maximum sediment thickness able to compact during the trampling history was roughly equal to that showed by the overprinted cases (e.g., the sum of Pd manus plus GI7 set thickness), thus shedding further light on the role of fossil tracks as paleo-penetrometers (see Falkingham et al., 2011). Pd being the last set of tracks preserved along with the displaced tail trace of GI6, it also possible to infer that during its trampling, the pareiasaurian trackmaker likely never reached the alleged consolidated layer underlying the trampled sediments.

CONCLUSIONS

The analysis carried out on a rich Late Permian ichnocoenosis preserved on the studied slab indicates a complex trampling history involving at least four different types of trackmaker crossing the surface during different times, in different directions, and under variable conditions of substrate consolidation. Interferences between tracks and trackways, as well as several track features and some substrate-related extramorphologies, have proved to be a meaningful reservoir of information about the timeline of events and the track preservational history.

The tracks, preserved as convex hyporeliefs, are natural casts representing the filling of foot-

prints left by tetrapods on the tracking surface. Tracks were left over days or weeks, during which time the surface passed through different conditions with respect to sediment cohesion and hardening. At the same time, minor differences in substrate conditions probably occurred simultaneously and in a restricted space, ruling the dynamics of track formation and the variability within single trackways. Optimal conditions for track recording, with respect to trackmakers' weight, occurred at different times during the trampling history. At the time of the crossing of the Pd trackmaker, the substrate was still in optimal condition with respect to the trackmaker's weight to record the passage of the heavier producer, but likely not the lighter ones. The progressive hardening of the trampled layer, still without achieving desiccation, enabled the preservation of those tracks and traces, which were lowered and displaced under the limbs of the giant.

The analysis of interferences has stressed the importance of secondary evidence when establishing the relative antecedence or subsequence of events. Caution should be exercised in general reconstructions based on track interferences alone. In the studied case, the tracks of the pareiasaurian trackmaker turned out to be crucial in refining the timeline of events and in further constraining the trampling history as well as the original thickness of the trampled layer.

The need to deeply understand, case-by-case, the close interdependence between the momentary substrate conditions, trackmaker morphology, dimensions and behaviour, and the 3D track morphology is highlighted. This understanding is pivotal in the context of tetrapod ichnology, as it allows the direct investigation of the processes leading to track formation. In this regard, this type of analysis is strongly recommended whenever possible. While time-intensive, it could be a useful investigative tool prior to traditional ichnological analyses, for which the control on the mode of preservation of the footprints is crucial.

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APPENDIX

Three-dimensional interactive model of the slab MPUR NS 34/28 (.stl). Please see online for zipped file (palaeo-electronica.org/content/2016/1499-bletterbach-gorge-trackways).