



New clues from Foresta/Devil's Trails: The elephant trackway and the puzzling trunk's impressions

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ABSTRACT - This research provides a critical reappraisal of the elephant footprints left by a young elephant on an ignimbrite deposit of the Roccamonfina volcano (Tora-Picilli, Central Italy) and the associated problematic trunk traces. The note discusses the most conceivable direction followed by the walking elephant and the reliability of the impressions that the elephant's distal trunk would have left. The elephant's traces are currently visible at the upper edge of the steep slope and on the sub-horizontal pathway that runs at the top of the ≈ 350 ka old pyroclastic ignimbrite (LS7 unit) of the Roccamonfina's Brown Leucitic Tuff (385-230 ka). We discussed how challenging it could be to accurately recreate the dynamics of the elephant's movements, the morphological features of alleged distal trunk traces, and the modality of the trunk resting on the substrate. The latter depends on the modifications of the distal trunk's shape caused by the dynamics of the trunk's contact with the ground. According to the scant information that is now available, the elephant walked along the F/DT prehistoric pathway from east to west. An alternative hypothesis also deserves attention. The elephant might have climbed the steep slope diagonally, proceeding from southeast to northwest and then westward along the pathway. It possibly used its trunk to support itself when it reached the pathway.

Keywords: footprints; trunk traces; Middle Pleistocene; Roccamonfina volcano; *Palaeoloxodon antiquus*.

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1. INTRODUCTION

Elephant footprints (ichnogenus *Proboscipeda*) have been documented since the Paleogene in a couple of Asian ichnosites. The earliest proboscidean footprints have been reported from the Middle Eocene deposits of the Gonjo (eastern Tibetan Plateau, China), about 45 Ma old (Tahir et al., 2024), and from the Late Eocene ichnosites of the Tarom Mountains (Avaj region, Iran). The latter, assigned to *Proboscipeda enigmatica* and *Proboscipeda* sp., are particularly significant. They document for the first time the presence of proboscideans in this region during the Late Paleogene (see Abbassi et al., 2017, 2024, and references therein).

During the Neogene, the number of ichnosites increased slightly. For instance, proboscidean footprints were reported from America, Africa, and Eurasia. In Europe, Panin and Avram (1962) described 100 footprints left by a herd of large individuals from a Middle Miocene ("Vindobonian") trampled surface at Prisaca-

Putna (Romania). Based on these footprints, the authors proposed the earliest name erected for proboscidean tracks, *Proboscipeda* ichnogenus (type ichnospecies *P. enigmatica*). The footprints are characterised by an oval shape, with five toes and traces of roughness. The authors attribute the cushion's roughness to sediment granulometry and humidity, not to a natural feature. They attributed the tracks to a deinother, a rather common Old World Miocene proboscidean. Pérez-Lorente et al. (1999) described an isolated footprint found in an old quarry of the Jumilla-Ontur tertiary basin (Murcia province, Spain). The trace was impressed on a gypsum sediment, likely deposited in the Late Miocene, during the Messinian Salinity Crisis (5.97-5.33 Ma).

The tracks of a proboscidean herd were recorded from the Late Miocene site of Mleisa 1 (United Arab Emirates), where the trackways of at least 13 individuals of varying size, diagonally crossed by that of a single large individual, are remarkably preserved (Higgs et al., 2003;

Bibi et al., 2012). Scrivner and Bottjer (1986) assigned to *Proboscipeda* sp. some proboscidean trackways from the Miocene of southern California, which were re-described by Reynolds (1999).

In the Late Miocene-Early Pliocene (Hemphillian North American Land Mammal Age) of North America, some gomphotherid, several birds, and mammal footprints were found on the bedding surfaces of the playa-lake carbonates of the Copper Canyon Formation (Death Valley National Monument, southern California) (Scrivner and Bottjer, 1986). In the Late Pliocene of Africa, *Loxodonta exopata* and *Deinotherium* sp. left their footprints on the cinerite deposit at the well-known Laetoli ichnosite (Leakey and Hay, 1979). During the Early Pleistocene, proboscidean footprints are still not frequent. Among others, two manus, or pes, prints, left by either a mammoth or a mastodon, were found in the early Irvingtonian NALMA deposits of the Bacons Castle Formation at the Stratford Hall site (Westmoreland County, Virginia) (Weems, 2018), and several proboscidean footprints, likely impressed by *Stegodon aurora*, were discovered in the Lower Pleistocene deposits of the Uonuma Formation (Tagawa River, Tokamachi City, Japan) (Nagamori and Hayashi, 2001). Conversely, Elephantinae footprints (*Proboscipeda panfamilia*) have been recorded from several Middle or Late Pleistocene ichnosites. The footprints were mainly left by the African bush elephant, *Loxodonta africana* (e.g., Roberts et al., 2008; Bennett et al., 2010; Helm et al., 2019, 2020, 2021, 2022, 2024, and references in those papers); mammoths, especially from North and Central America (e.g., Lofgren et al., 2006; Lucas et al., 2006, 2007 a,b; Remeika, 2006; McDonald et al., 2007; McNeil et al., 2006, 2007; Hunt and Lucas, 2016; Retallack et al., 2018; Bennett et al., 2019, 2020; and references in those papers), and straight-tusked elephants from Europe (e.g., Fabiano and Zucchelli, 2003; Neto de Carvalho, 2009, 2011; Silva et al., 2013; Muñiz et al., 2019; Altamura, 2020; Neto de Carvalho et al., 2019, 2020 a,b,c, 2021, 2022, 2023; Mayoral et al., 2022; Altamura and Serangeli, 2023) and Asia (e.g., Nojiriko Fossil Footprint Research Group, 1992; Kim et al., 2010; Matsukawa and Shibata, 2015; Takahashi, 2020). Footprints of a dwarf insular mammoth were left only from the Sardinian endemic *Mammuthus lamarmorai* (Pillola and Zoboli, 2017; Zoboli and Pillola, 2018) and dwarf straight-tusked elephants from the Mediterranean islands (e.g., Milàn et al., 2007, 2015). Despite the large amount of worldwide footprint of Pleistocene elephants, the only described fossil putative trunk impression was that left by *L. africana* on a moderately sloping aeolianite surface exposed along the Cape Town coast in the Goukamma Nature Reserve (Helm et al., 2022). The traces consist of two sequential, elongate, wide, and rather deep grooves, roughly aligned with the longitudinal trackway's axis. Fossil impressions left by elephant distal trunks have neither been reported nor described so far. Sometimes, authors reported the presence of elephant footprints in research focusing on other subjects, such as, for instance,

the 43 footprints found in the last interglacial deposit of Alathar paleolake (Arabian Peninsula), together with those of other mammals and generically referred to *Proboscipeda* isp. (Stewart et al., 2020).

This research aims to: i) critically update the description of the elephant trackway provided by Palombo et al. (2018); ii) describe and discuss the fossil trace of the trunk and those of two puzzling hearth-shaped herein tentatively ascribed to the trunk tip; and iii) discuss the difficulty of clearly reconstructing the dynamics of the elephant's movements and the dynamics and causes of the trunk's resting on the substrate.

The traces were impressed on the ignimbrite deposit of the Roccamonfina volcano, dating to about 0.35 Ma (MIS 10), at the Foresta/Devil's Trails (F/DT hereinafter) (Tora-Picilli, Central Italy) (Mietto et al., 2022, and references therein) (Fig. 1). We re-examined the area where Palombo et al. (2018) recognised the elephant's traces for various purposes: i) to better define the nature of the track doubtfully identified as left by the trunk and of some tracks associated with the track but not identifiable as prehistoric elephant footprints already discussed in Palombo et al. (2018); ii) to verify the possibility that some incomplete and poorly preserved tracks present on the path at the top of the slope could or could not be in continuity with those of elephants already identified and described; iii) to identify the possible way (or ways) followed by the elephant trackmaker.

The elephant traces could be regarded as the most attractive documentation of the mammals that visited the F/DT ichnosite nearly at the same time as the hominins did. The ichnosite is especially known for at least 81 footprints impressed by hominins (*Homo heidelbergensis* s.l.). The hominins went down along zigzagged trackways on a ≈ 350 ka old pyroclastic still unconsolidated ignimbrite (LS7 unit) of the Brown Leucitic Tuff (385-230 ka). The latter was deposited at the end of MIS 10, in a time close to the Climatic Termination IV, during Plinian eruptions of the second period of the activity of the Roccamonfina stratovolcano (Palombo and Panarello, 2023, 2025; Panarello et al., 2023).

At the ichnosite, a few other mammal traces were identified. The footprints were left very shortly after the emplacement of pyroclastic flows, on the top of the cooling and still unconsolidated surface (Panarello et al., 2020). The best-preserved mammal footprints, belonging to a middle-sized ruminant artiodactyl (ichno-order Artiodactipedia *sensu* Vialov, 1966). The footprints have been detected on the sub-horizontal surface pathway running at the top of the slope (Panarello et al., 2017a-b), whereas two trackways, crossing and flanking the human trackway, can be ascribed to the *Hippipedia* ichnotaxon. Among other problematic and badly preserved footprints, one, maybe two, impressed on the thin mud layer interbedded between the surface of the pyroclastic flows LS7 and LS8, were tentatively ascribed to *Ursichnus europeus* (Panarello et al., 2017 a,b; Pillola et al., 2020).

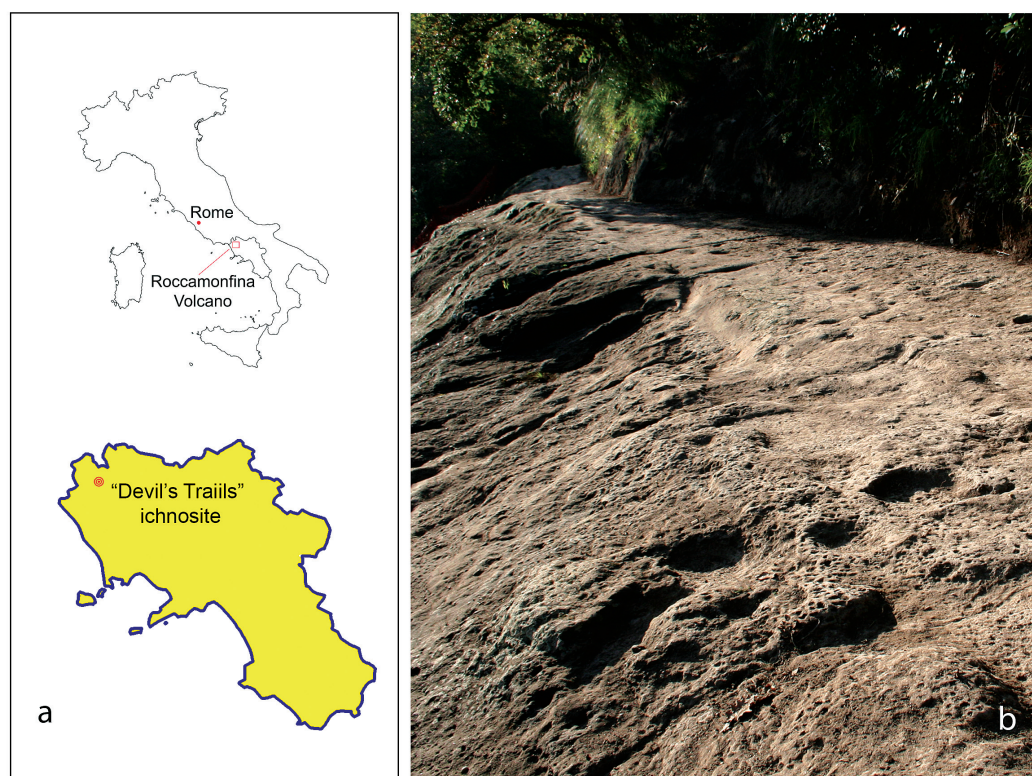


Fig. 1 - The Foresta "Devil's Trails" ichnosite: a) Geographical location; b) eastern view of the prehistoric human pathway with elephant ichnites (in the foreground).

2. MATERIALS AND METHODS

Twelve or thirteen elephant traces have tentatively been identified at the top and the edge of the F/DT ignimbrite slope on a surface of about 4.50 x 2.00 square meters. They include the four, maybe five manus and pes footprints already recorded by Palombo et al. (2018), five putative footprints present on the prehistoric path in the area modified in historical time by anthropogenic activity (Panarello, 2016; Panarello et al., 2017 a,b; Pillola et al., 2020), and one trunk trace. Two other problematic traces are present along the elephant trackway. Herein, the footprints' labels are based on the most likely manus-pes succession according to the analysis of data currently available. The labels T2, T1, and T3 indicate the trunk and the two problematic traces, respectively (Fig. 2).

We measured the dimensions of the traces at different times, using 3D models scaled by means of a metal comparator. For prints with a well-defined structure, we fixed some landmarks for taking more precise measurements.

We fixed landmarks on both its most medial and most lateral borders for measuring each trace. We fixed some additional landmarks for measuring some morphological features of the T1 trace.

We carried out photogrammetric surveys of the entire studied area with APS-C Canon PowerShot G9 (12 mpx), APS-C Canon EOS 550D (18 mpx), and Sony NEX-

6 (16.1 mpx) cameras with Canon 7.4-44.4 mm f/2.8, Sony E PZ 16-50 mm f/3.5-5.6 OSS, and Canon EF-S 18-200mm f/3.5-5.6 IS lenses, respectively. We scaled the models based on 10-cm-long metal bars and carried out the 3D processing using AgisoftPhotoScanPro™ (ver. 0.9.0 build 1586) and KitwareParaView™ (ver. 3.98.1.64) software. Supplementary Information with a table reporting the modelling details (compiled following Lockley et al., 2015) is available in the online version of the manuscript.

Furthermore, detailed photogrammetries and 3D models were produced for the impact zones of the T1, T2, and T3 traces (Fig. 2). A depth map and a planimetry of the entire considered area and of each new trace were produced. To better analyse the trace's structural morphology and the preserved and still detectable anatomical details, we realised maps and planimetries with contour lines differing in height of 1 mm.

3. SYSTEMATIC PALAEOICHOLOGY

3.1. ELEPHANT TRACES

Ichnogenus *Proboscipeda* Panin & Avram, 1962

Type Ichnospecies *Proboscipeda enigmatica* Panin & Avram, 1962

Ichnospecies *Proboscipeda panfamilia* McNeil, Hills, Tolman & Kooyman, 2007

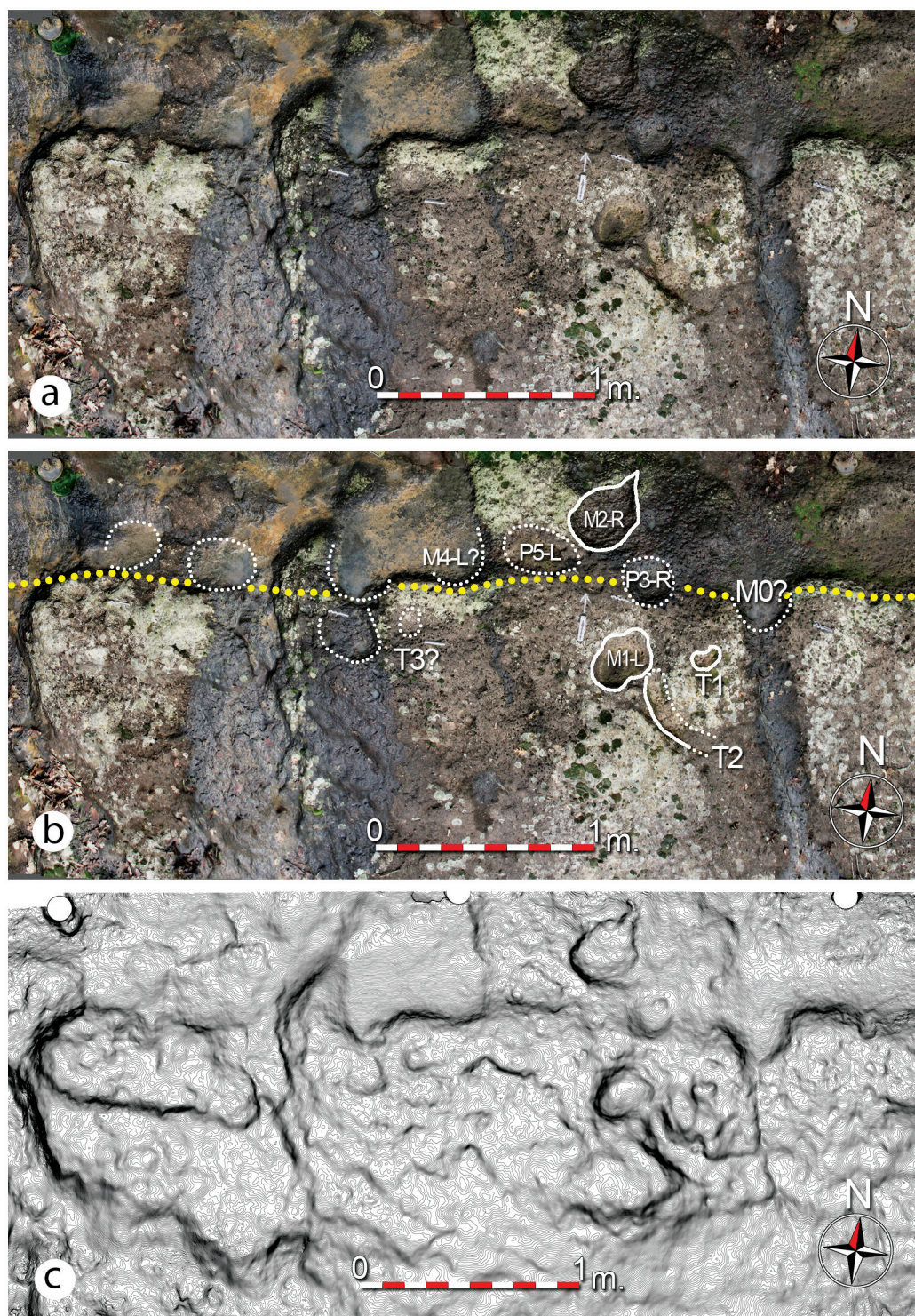


Fig. 2 - The Foresta "Devil's Trails" ichnosite: a) 3D generated zenithal image of the trampled paleosurface area trampled by the elephant; b) topographic location of the discussed traces; the dotted yellow line indicates the boundary between the prehistoric path and the slope; c) contour map 1mm (Scale bar=1 m).

We ascribed to an elephant trackmaker some footprints and a trunk trace detectable on the F/DT pathway, which runs at the top of the ignimbrite slope and at its edge on the uppermost part of the slope. In the elephant's traces, impressed on the F/DT ichnosite's ignimbrite deposits, two discrete components can be identified, resulting from

the activity of a single trackmaker that simultaneously behaves in various distinct ways, walking and exploring the substratum with its trunk (compound traces *sensu* Bertling et al., 2006). Consequently, according to the principles of ichnotaxonomy of invertebrates, two different specific names should be applied to the tracks left

by the feet and the proboscis. Lucas (2007a) and Lockley and colleagues (2007) debated the question about the opportunity to apply the same rules to the invertebrate and vertebrate footprints, taking into account that nearly all the fossil vertebrate traces identified in the fossil record are trackways produced by locomotion and vertebrate ichnologists relate those tracks to the taxon that left them (Yang et al, 1995; Carrano and Wilson, 2001). Hence, we refer to *Proboscipeda* both the foot and trunk traces.

3.2. DESCRIPTION

3.2.1. Elephant's footprints

The identified footprints consist of at least two manus, two less-preserved pes, and a partial putative manus. Some other putative footprints are present on the sector of the prehistoric path that was affected during historical time by invasive alterations of the original ground due to both natural and anthropogenic actions (Panarello et al., 2017a-b; Pillola et al., 2020) (Fig. 2).

In the best-preserved footprints (M1-L and M2-R), already described by Palombo et al. (2018), some anatomical details are still more or less discernible. M1-L, located on the slope just below the path's edge, shows an oval outline, with the width being the greatest dimension (length=257.34 mm; width=298.59 mm) (Fig. 3). Four toe imprints are present on the footprint's anterior part. Toe impressions are typically found in young elephants' footprints because a wild elephant's walking behaviour (e.g., playing and running) is more varied and intensive throughout youth (e.g., playing and running).

The major pressure zones correspond to the front and, to a slightly lesser degree, the left lateral side parts of the footprint (Fig. 3).

This distribution only partially supports the Panagiotopoulou et al. (2012, 2016) conclusion, according to which the highest pressures would be encountered in digit 3 in both Asian and bush African extant elephants.

The M2-R footprint is also rather well-preserved; its morphological peculiarities are less identifiable than those of the M1-L footprint. The expulsion rim and the cushion's pressure are evident anteriorly and a little less accentuated on the right side. The footprint's left edge is less defined, and the expulsion rim is hardly detectable on the left side. A typical "dragging" trace, probably left during the foot-off event, characterised the footprint's right-posterior side. Its occurrence could account for the rather larger dimensions of M2-R (length=329.43 mm; width=334.82 mm) with respect to those of M1-L. The available data suggest that the M2-R's stride was ESE-WNW directed, with a slight convergence towards the M1-L direction.

Palombo et al. (2018, fig. 1a) illustrated but did not describe two smaller pes footprints. The best preserved P3-R pes footprint (P1-R in Palombo et al., 2018) (length=210 mm; width=215 mm) is located on the path at its edge close to the left posterior corner of the M2-R medial side. The expulsion rim is detectable and the

major pressure is set prevalently on the medial (left) side, suggesting that the PR-3's stride was E-W directed. The second pes trace, P5-L, (P2-R in Palombo et al., 2018), is present between the M2-R footprint and the incomplete M4-L one. The oval shape of the cushion (length=251.5 mm; width=313.3 mm) is clearly detectable, but the expulsion rim and the footprint's border show a rather anomalous feature on the left, lateral side, whereas both are barely appreciable on the medial one (Fig. 2).

The M4-L footprint, situated on the path near the ignimbrite slope's edge, consists of a portion of the medial edge, where the expulsion rim can be discerned, and the posterior one is visible. The size (max measurable width=~300 mm) could be similar to that of the other manus footprints. There are a few other large traces along the path, but natural and human factors have erased most of the traits that would have identified them as the footprints of the elephant that continued its way towards the west (Fig. 2). Moving on the prehistoric path from east to west, the first potential elephant footprint is the incomplete trace M0-R, which is visible just at the beginning of the slope (Fig. 2). Only the medial half is preserved, whereas the part on the path was destroyed by the human activity that in historical time seriously altered the original shape of several footprints left by the humans and mammals that walked on the path about 350 ka ago. The available dimensions of the M0-R hypothetical footprint (max measurable width=~305 mm) are consistent with those of M1-L and M2-R.

3.2.2. The trunk's trace

The putative trunk trace (T2) extends southeast up the slope from the rear edge of M1-L. The maximum distance between the medial margin of T2 and the western margin of T1 is about 222 mm (Fig. 2). The cavity is arched and slightly sinuous, with its concavity facing the prehistoric path. An expulsion rim is present along the most convex margin. The uppermost termination is rounded and gently turned towards E. T2 becomes wider and deeper in the lower part. The latter was damaged by historical anthropological breakages, probably made with metal tools to facilitate the flow of rainwater along the slope and prevent rainwater's stagnation on the above subplanar path (Fig. 4). T2 width ranges from 7.0 cm of the uppermost segment to 11.8 cm of the best-preserved lower portion. The lengths of the western and eastern external ridges are ~540 mm and ~490 mm, respectively, and the chord total length is ~590 mm.

3.2.3. Remarks

The footprint morphology suggests that the M1-L stride was W-NW directed, conforming to the peculiar dynamic of cushion deformation and the support offered to the limb rotational movement during the limb and foot rotational movements (Hutchinson et al., 2006, 2011). The nail impressions are generally present in footprints left by young individuals but not in those of adults. They could be hardly detectable even in footprints left

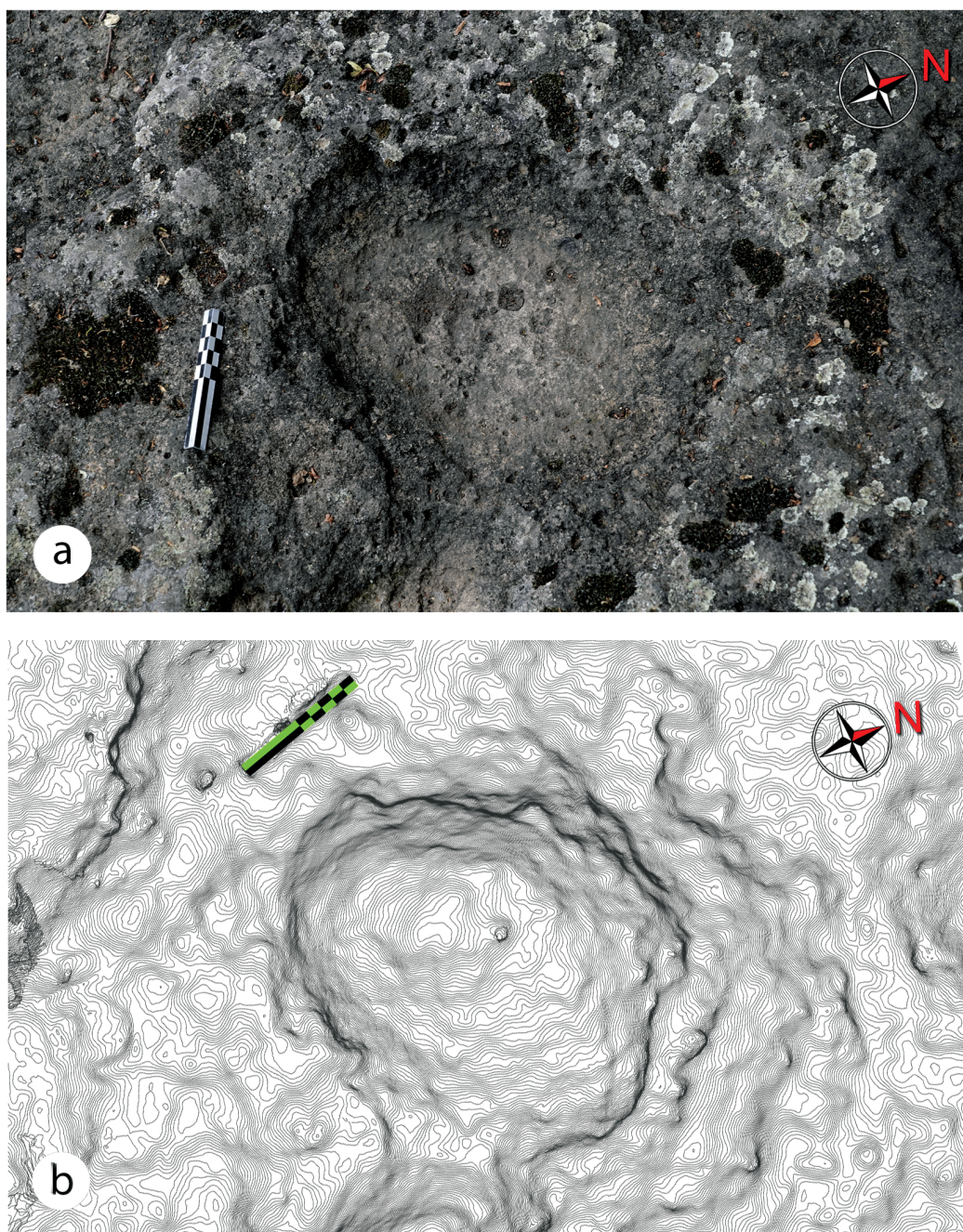


Fig. 3 - The Foresta "Devil's Trails" ichnosite - M1-L footprint: a) zenithal photograph; b) contour map 1 mm (Scale bar=10 cm).

by a young elephant, depending on the type of substrate (Pasenko, 2017).

No evident nail traces are detectable in the M2-R right manus footprint, and the expulsion rim and the cushion's pressure are clearly evident only on the footprint's anterior side. The position of the typical "dragging" trace left during the foot-off event indicates the right-posterior side of the M2-R footprint (Fig. 5). The available data suggest that the M2-R's stride was ESE-WNW directed and slightly convergent towards the M1-L direction.

The shape of the T1 trunk impression shows some

similarity with the dragging trace left by extant Asian elephants in muddy sediments (MRP personal observation), but is rather different from the elongate, wide, poorly undulate trunk drag-like described by Helm et al. (2022). Although the extremely coarse nature of the substrate and the trace incompleteness due to historical human cuts, the hypothesis that it could result from a dragging action during walking seems reasonable. However, the possibility that the elephant used its trunk to support itself when it reached the pathway deserves attention.

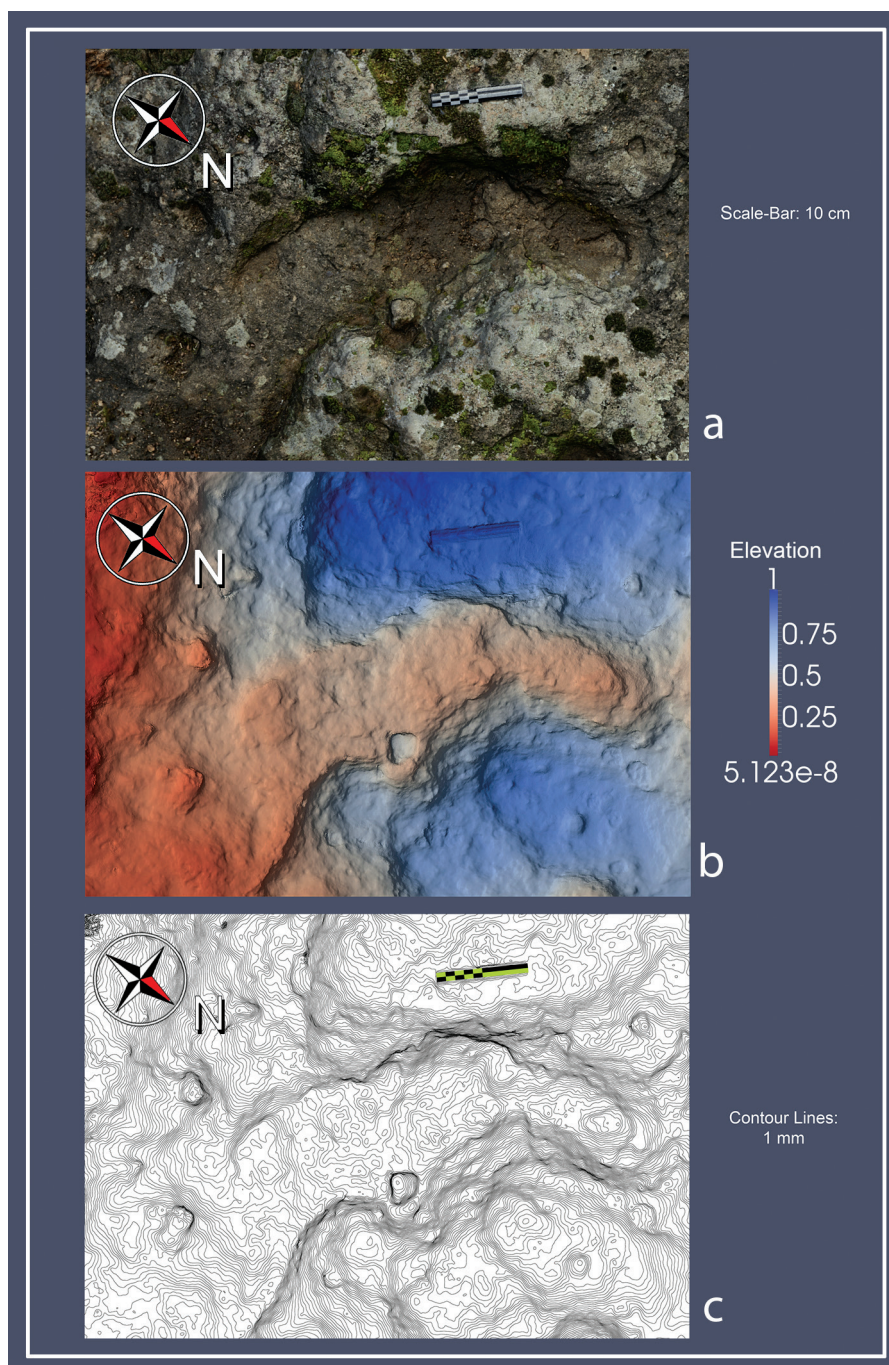


Fig. 4. The Foresta “Devil’s Trails” ichnosite - The drag-like trunk trace T2: a) 3D-generated zenithal image; b) depth map; c) contour map 1 mm (Scale bar=10 cm).

4. THE PUZZLING HEART-LIKE SHAPED TRACES

Two rather small heart-shaped footprints visible along the elephant trackway are of difficult systematic attribution.

4.1. DESCRIPTION

The fairly well-preserved T1 trace is located on the ignimbrite slope, behind the M1-L footprint, at a short distance from the semi-trace M0-R (Fig. 2). The trace, seen from the prehistoric path, shows an inverted heart-like shape; it shows evident expulsion edges, in particular

on the right and left lateral sides (Figs. 6, 7).

Some morphological details can be detected, but their characterisation is rather variable depending on the light conditions and the irregular coarse-grained texture of the pyroclastic sediment.

The impression of the pointed anterior part is rather well defined. It consists of a marked subtriangular imprint, which appears to be preceded by a rapid sequence of phases of contact with the ground. A well-marked and deeper impression runs along the trace’s posterior edge. In

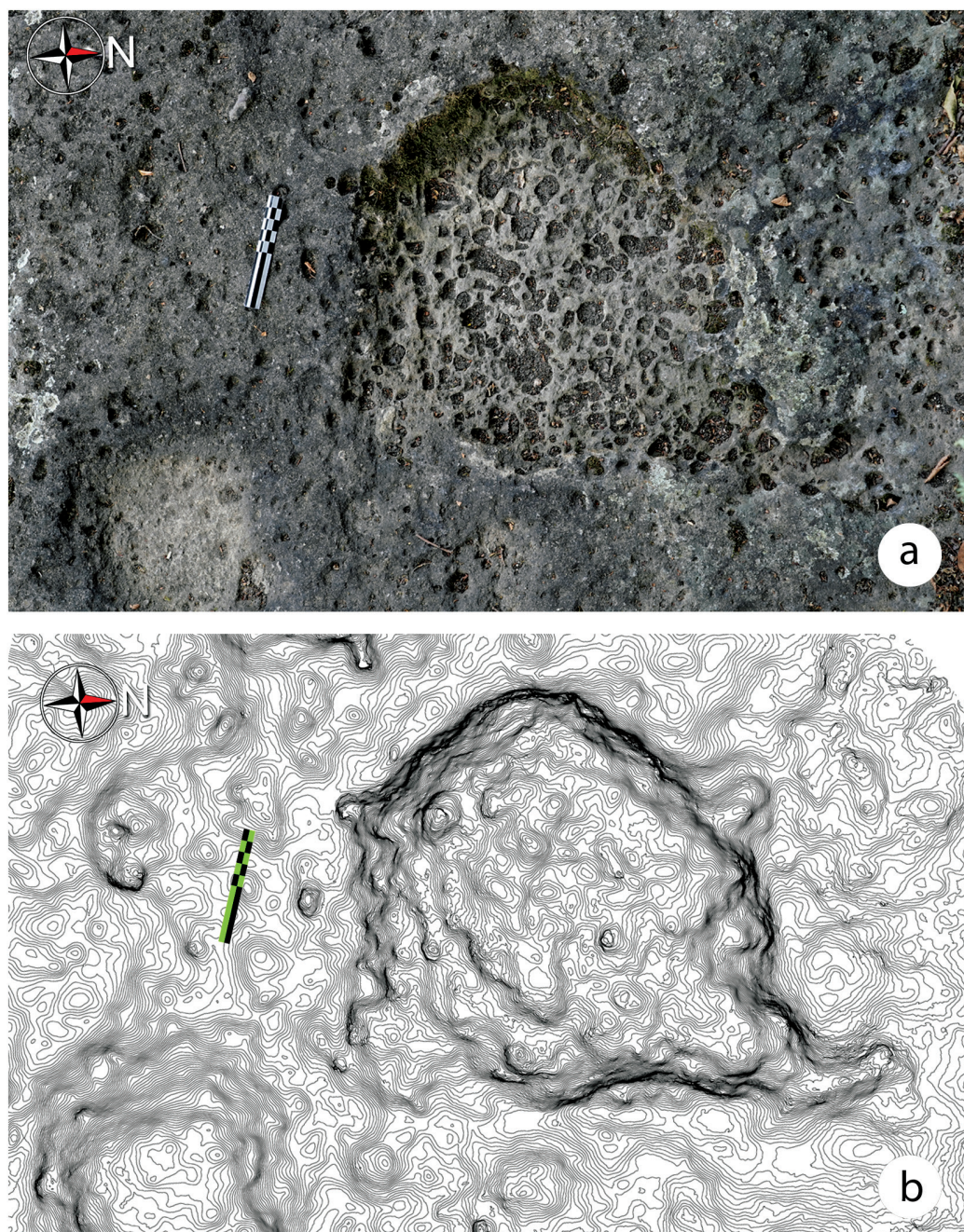


Fig. 5 - The Foresta "Devil's Trails" ichnosite - M2-R footprint: a) zenithal photograph; b) contour map 1 mm (Scale bar=10 cm).

its central part, a less deep triangular impression extends forwards into the T1 trace, separating the posterior parts of the two central impressions. Two roughly rounded oval impressions, with badly defined outlines, take up the middle and posterior parts of the trace. Their forward extension cannot be properly defined, even if they occupy less than two-thirds of the T1 trace, and their anterior limit is far from reaching that of the T1.

We could measure its dimensions (maximum length=123 mm; maximum width=125 mm; distance between the dorsal and the ventral margins=109 mm, whereas those of the sub-oval central impressions have been roughly

inferred because the substrate's coarse nature hampers sound measurements. The tentative dimensions of their deepest areas (measured on the 3D generated model (Fig. 7) are as follows: right impression, maximum length=155 mm, right impression, maximum breadth=48 mm, and left impression, maximum breadth =45 mm.

A similar impression, T3, is visible on the slope to the west of M1-L. The trace's centroid is about 67 cm and 100 cm away from those of P5-L and M2-R, respectively (Fig. 2). T3 shows general shape, orientation, and size (external maximum width of T1 and T3=15.15 cm and 14.57 cm) consistent with those of T1, but the anatomical

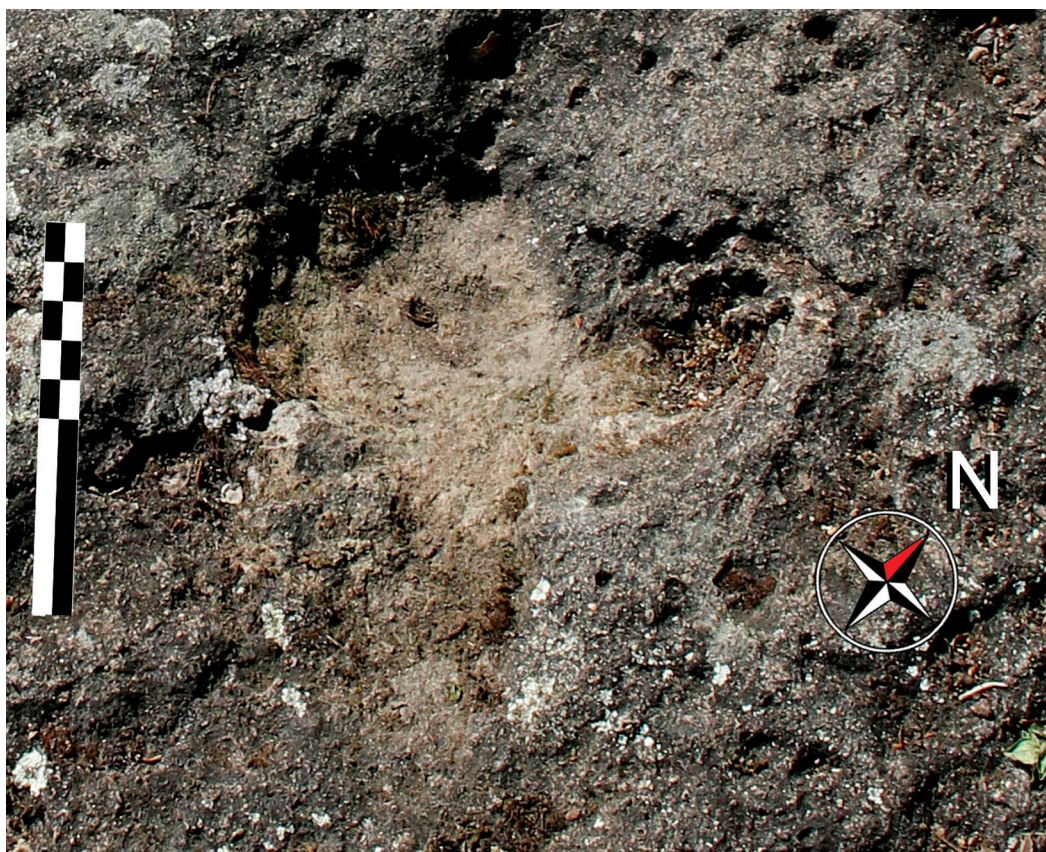


Fig. 6. The Foresta "Devil's Trails" ichnosite: the T1 trace (Scale bar=10 cm) (Photograph credit: A. Panarello, 2021).

details are unclear, and the expulsion rims are poorly appreciable (Fig. 8).

4.1.1. Remarks on the puzzling T1 and T2 traces

The T1 and T3 traces are located along the elephant trackway. T1 is in proximity to the trunk T2 trace, behind the M1-L footprint, and at a short distance from the semi-trace M0-R (Fig. 2). This location could raise the presumption that the traces may be related to some elephant activity, such as that of the trunk tip. However, T1 differs from the traces that an elephant would produce if it simply impressed and left the trunk tip on the substrate without producing any other additional movements. For instance, the heart shape is distinctly different from the trunk tips observed in a frontal (Deiringer et al., 2023). When the proboscis is inactive, the finger-like process, especially the dorsal one, extends from the tip, protruding forwards in a slightly advanced plane with respect to the nostrils. Therefore, a finger-like process is expected to produce in the sediment a deeper impression than the latter. However, trunk tip shape changes during its activity according to its motion dynamics (e.g., Soppelsa et al., 2022), as well as with the elephant's ontogenetic age (Deiringer et al., 2023).

The presence of two roughly symmetrical sub-oval impressions in the T1 middle part makes it difficult to

imagine that tracks T1 and T3 can be explained as being due to other biological phenomena of elephants, such as urination impressions. Urination depressions that living elephants leave in sandy sediments are circular to irregular in shape. They might have steep or slightly sloping sides and be surrounded by a raised rim. Small fans of sediment radiating around the track, this rim might be interrupted by. On the ground surface, a concentric ring of coarse sediment grains may be present around the track at a distance of up to tens of centimetres (see Platt and Hasiotis, 2014).

Further, T1 at first glance might look like a bilobate artiodactyl hoofprint. When the F/DT ignimbrite was deposited, two artiodactyl species (*Cervus elaphus* and *Bos primigenius*) with footprint sizes roughly comparable to those of T1 and T3 were present in the Latium region (cfr Palombo, 2023). The size of the *Cervus elaphus* hoofprints (*Bifidipes* isp) varies according to the trackmaker's ontogenetic age and sex, reaching a length of 9-10 cm in adult males. The elongate hearth-shape hoofprints and the pointed drop-like and arch shape of the III and IV digit impressions, which open onwards, are hardly comparable to the T1 morphology.

The *B. primigenius* hoofprints reported and described in Pleistocene deposits are rather rare (e.g., Nojiriko Fossil Footprint Research Group, 1992; Neto de Carvalho

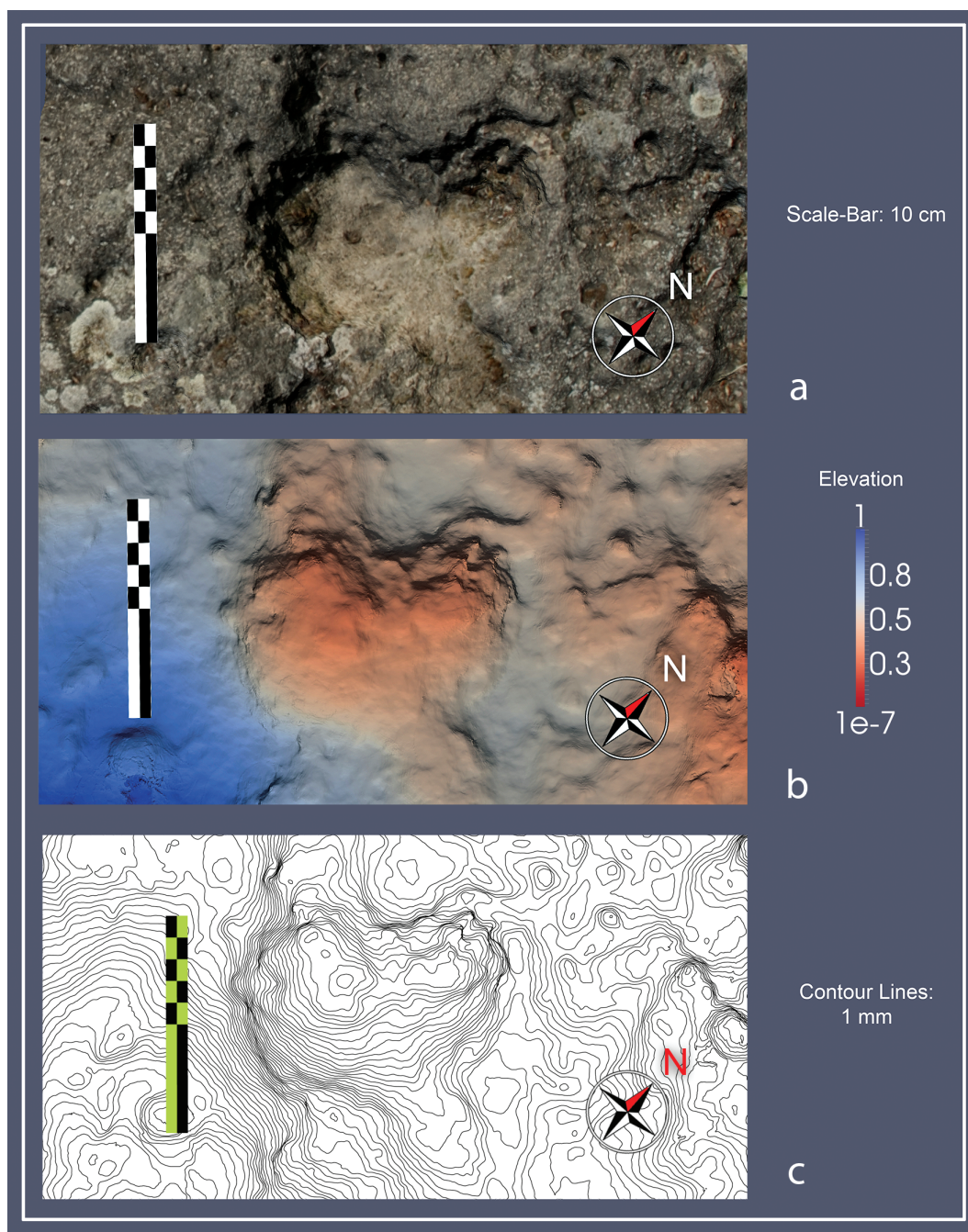


Fig. 7. The Foresta "Devil's Trails" ichnosite - T1 trace: a) 3D-generated zenithal image; b) depth map; c) contour map 1 mm (Scale bar=10 cm).

et al., 2022; Tanaka et al., 2021; Hsieh et al., 2023). Neto de Carvalho et al. (2022) erected the new ichnogenus *Bovinichnus* (type ichnospecies *Bovinichnus uripeda*) for some *B. primigenius* hoofprints found in the Late Pleistocene (MIS 5) beach and eolian deposits of Cape Trafalgar (Cadiz Province, South of Spain).

Some morphological features of T1 raise doubts about the consistency of the idea that a young auroch walked on the F/DT ignimbrite surface. In particular, the T1 central impressions would hypothetically be left by the III and IV digits, but they are proportionally smaller,

and their forward extension is definitely inferior to that characterising the central (III-IV) digit impressions of *B. uripeda*. These impressions nearly occupy the entire surface of the hoofprint, whereas in T1, the impressions' distal part ends far from the footprint apex. Moreover, in the *B. uripeda* hoofprints, the V-shaped impressions that in T1 protrude forward from the anterior margin and the triangular impression that extends forward into the trace, separating the posterior parts of the two central impressions, are not visible.

All things considered, the idea that the T1 and T3

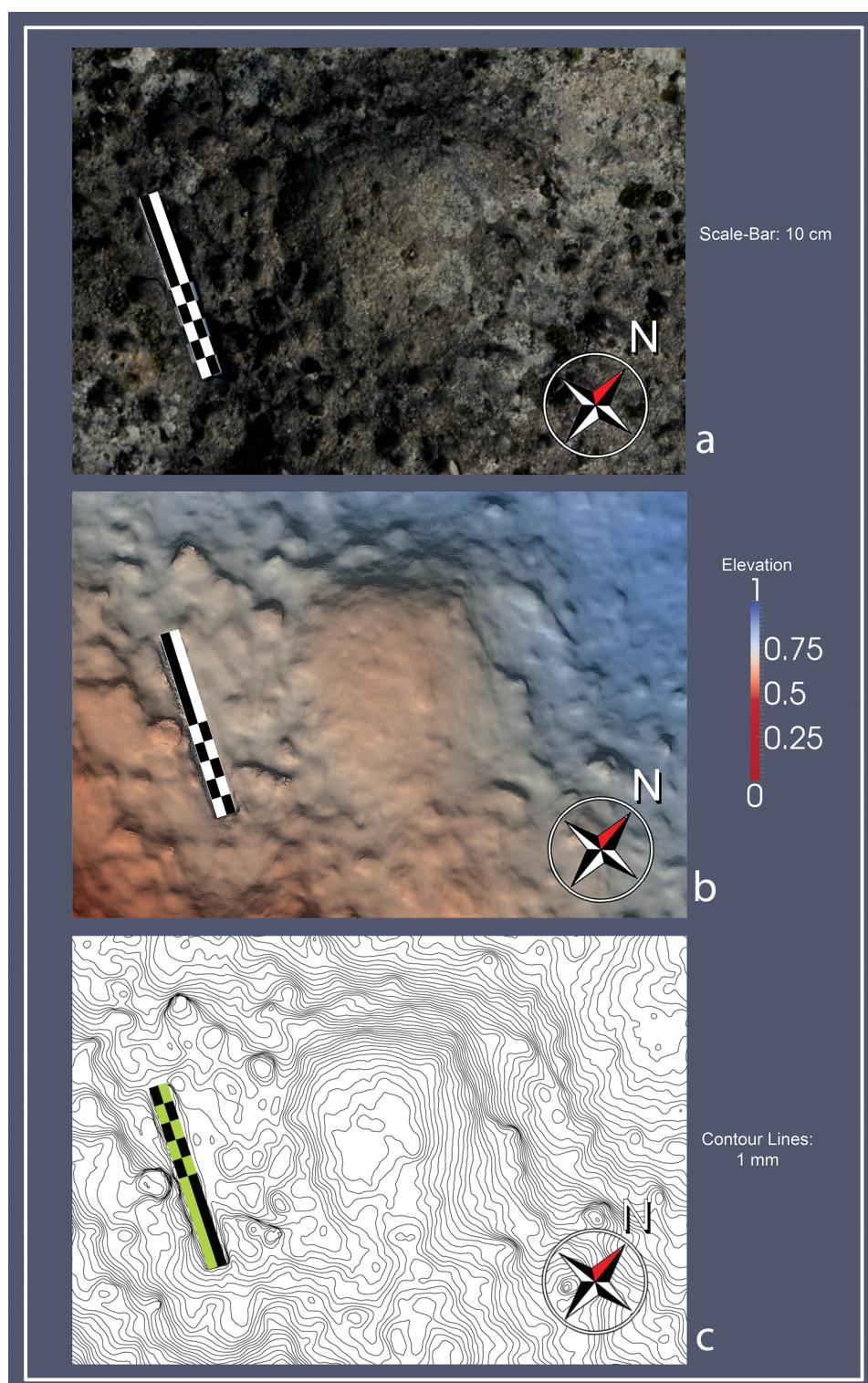


Fig. 8. The Foresta "Devil's Trails" ichnosite - The distal trunk trace T3: a) 3D-generated zenithal image; b) depth map; c) contour map 1 mm (Scale bar=10 cm).

impressions could be left by an artiodactyl results in something rather inconsistent.

The position of the T1 and T3 imprints, located along the elephant trackway, and that of the T1 two central impressions, which hint that the distal trunk trace is

roughly N-S oriented, justify the hypothesis that would be left by the elephant walking at the top and on the F/DT prehistoric path.

Accepting the idea that T1 might correspond to a trunk tip impression, we could tentatively describe the central

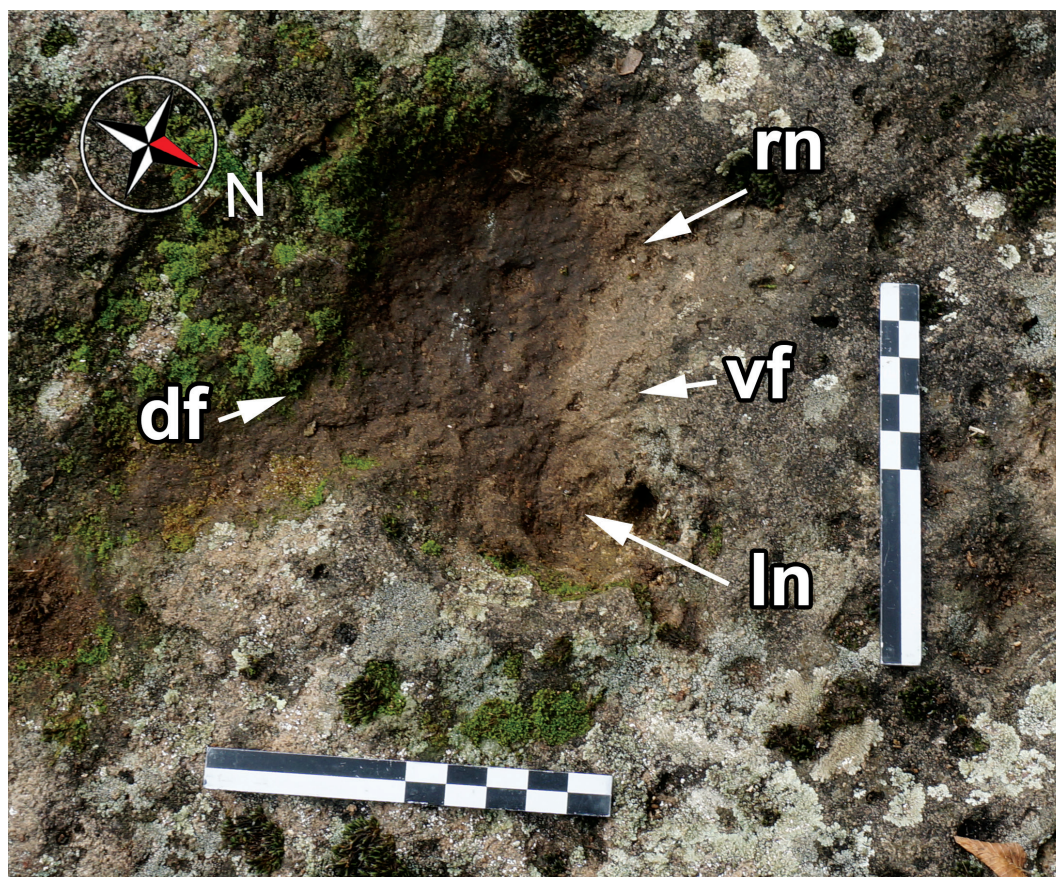


Fig. 9 - The Foresta "Devil's Trails" ichnosite: Tentative explanation of the morphological features of the T1 trace. Zenithal photograph of the distal trunk-trace T1. df=dorsal finger; vf=ventral finger; ln=left nostril; rn=right nostril (Scale bar=10 cm).

impressions as the right and left nostrils, the impression of the pointed anterior part as the dorsal finger-like process, and hypothesise that the triangular impression that extends forwards into the T1 trace might be left by some actions of the ventral finger-like process (Fig. 9).

Nevertheless, evident abnormal differences in depth exist between the slightly more deeply impressed central impressions and those of the anterior and posterior processes, which would hypothetically correspond to the nostrils and the dorsal and ventral finger-like processes, respectively.

To justify this incongruity, we could speculate that the trunk tip had been resting lightly on the substrate while the elephant breathed out and then slightly dragged backwards as the elephant lifted it after momentary contact with the ground. This hypothesis is consistent with the morphology of the trace's most anterior part. The dorsal finger trace shows some hints of a moderate dragging movement, while the ventral finger contracted and rested more firmly on the ground, which might explain the slightly deeply impressed medial region, which putatively would correspond to the nostrils.

Speculating that the T1 trace was left by the trunk tip, the shape of the trunk tip of the F/DT elephant is more similar to that of African elephants that have a dorsal and a

ventral finger, while Asian elephants only have one dorsal finger. The fairly inflated dorsal shape of the F/DT imprint morphology differs from that of *Mammuthus primigenius*, which shows a more triangular and narrower distal trunk with considerably longer and thicker dorsal and rather bilobate ventral finger-like processes (see Plotnikov et al., 2015; Liu, 2021, and references therein). Regrettably, no data are available for confirming whether the other *Mammuthus* representatives shared this so specialised tip morphology, even if the hypothesis that *Mammuthus* had a similar basic structure seems to be conceivable. The F/DT imprint morphology differs from the sometimes more triangular one of *Loxodonta*. Though the shape of elephants' trunk tip generally varies, especially during ontogenetic growth and also when contacting the ground or grasping objects on the substrate for feeding (e.g., Schulz et al., 2023, 2024).

Nonetheless, given 1) the inconsistencies among T1 morphological features; 2) the absence of documented neoicnological evidence and direct fossil analogues; 3) the coarse nature of the sediment, not suitable to preserve anatomical details; 4) the objective impossibility of reconstructing the dynamics of the movement that the trunk tip would have made while resting on the substrate; and 5) the coherence of the position of T1 and T3 with

the elephant's trackway, we consider any consistent and sound conclusion about the actual trackmaker of T1 and T2 to be premature.

5. DISCUSSION

The definition of the primary characteristics of the F/DT elephant's trackway is complicated and hampered by several factors, including i) the number and progression of footprints and, in turn, ii) the trackmaker's path direction; iii) the causes and dynamics of trunk support; iv) the distal trunk's anatomical details, particularly those of finger-like processes; and v) the potential affinities of the F/DT individual with one or another elephant species.

5.1. ISSUES RELATED TO THE NATURE OF THE SUBSTRATE AND ITS MODIFICATION OVER TIME

Random factors (e.g., the nature of the substrate, topography, locomotion dynamics, and ways in which feet or other anatomical parts rest on the ground) could affect the traces' preservation and their morphology, hampering the chance of properly reconstructing the trackmaker's movement dynamics, especially when the detectable traces are few. For instance, the preservation state, the nature, and the geometry of the substrate may affect the shape and dimensions of some traces. Doughless, the morphology of a footprint is determined by the structure of the trackmaker's foot, whose morphology varies according to the nature of and the interaction with the substrate, the latter resulting in extramorphological variation. The main characteristics of the sediment play a significant role in ichnites' preservation. They include, among others, i) sediment macrofabric; grain size (e.g., in coarse sediments such as that of the F/DT ichnosite, anatomical features are less preserved); 2) moisture content; cohesion and plasticity; 3) and acclivity (e.g., Frey and Pemberton, 1986; Allen, 1997; Milàn, 2006; Fanelli et al., 2007; Marty et al., 2009; Eren et al., 2010; Platt et al., 2012; Morse et al., 2013; Bennett and Morse, 2014; Falk et al., 2017; Marchetti et al., 2019).

Furthermore, at the F/DT ichnosite, natural factors (e.g., weathering, including substrate surface crumbling caused by thermal shocks, and surface colonization by mosses and lichens) and historical anthropological activity by means of metal tools (Panarello, 2016; Panarello et al., 2017a, b; Palombo and Panarello, 2023) have deeply altered or obliterated some traces and strongly modified the shape and extension of others, erasing their expulsion edges.

5.2. ISSUES RELATED TO THE DISTAL TRUNK AND TRUNK-DRAG-LIKE IMPRESSIONS

The elephant trunk exhibits an impressive versatility in its prehension capabilities that depends on the peculiar structure of this organ, which involves no rigid tissues. It functions as a muscular hydrostat and consists of hundreds of thousands of muscle fascicles, which give the trunk an impressive degree of freedom in movement.

The coordinated contractions of antagonist muscles allow the trunk to elongate, shorten, bend, twist, pick up small and large objects, etc., without the support of an articulated skeleton, but through shape changes. The changes are mainly allowed by the constant volume of self-supporting tissues (e.g., Shoshani, 1985; Kier and Smith, 1985; Dehnhardt and Sachser, 1997; Lefeuvre et al., 2020; Dagenais et al., 2021, and references therein). The functionality of Asian and African elephants' trunks is, however, rather different. For instance, Asian elephants have a more flexible trunk and pick up objects mainly wrapping clockwise around them, while the trunk of African elephants is firmer, and they may pick up objects using ventral and dorsal finger-like processes. However, African bush elephants may grasp either with the finger-like processes, sometimes helping the pinch with a suction, or wrapping the trunk around a food item. The grasping technique differs between elephants feeding in different habitats (Costes et al., 2024). Wild roaming elephants actually are mixed feeders, acting either as grazers or browsers, picking vegetation from grasslands or trees, respectively, depending on the environmental conditions.

When elephants pick up small food items or other objects from the ground, the shape of the trunk tip might change. The research by Soppelsa et al. (2022) showed that three out of the six analysed African bush elephants changed the shape of the tip of their trunk to match the object they were picking up and that the finger-like parts of the trunk change when the tip touches the ground or rests flat on it (Soppelsa et al., 2022 - SI 1_Experimental design visualisation).

The T1 ichnite's anatomical details indicate that the elephant placed its trunk tip on the ground, but they do not explain if this was done to hold food or other objects from the ground or because it was necessary for support. A grasping motion would be consistent with the narrow and deep trace of the ventral finger-like process and the presence of potential traces at the top of the dorsal finger-like process. The latter could suggest a short sequence of dragging phases.

Wild roaming elephants are actually mixed feeders that act as either grazers or browsers, grasping vegetation from grassland or trees, respectively.

5.3. WHAT ABOUT THE DRAG-LIKE IMPRESSION OF THE TRUNK (T2)?

The arched and slightly sinuous shape of the T2 trace, on the one hand, resembles the tracks left by modern elephants dragging the distal end of their trunk on muddy ground (Fig. 10). On the other hand, we cannot exclude that the imprint was left by the trunk resting sinuously on the ground (see 5.4 below). The lack of exhaustive documentation and the lack of studies dealing with this theme hamper the comparison with the tracks left by modern elephants. The only possible elephant trunk-drag impressions analysed thus far are those identified on the slightly sloping dune aeolianite deposits exposed at the



Fig. 10 - Picture of a Sri Lankan *Elephas maximus* that climbs a slope leaning against the trunk (Photograph credit: M.R. Palombo, 2016).

Goukamma Nature Reserve (Cape South Coast, South Africa) (Helm et al., 2022). The trunk-drag traces consist of two elongated grooves that run along a 5 m long trackway at a distance varying from about 60 cm to a few cm from its median axis.

The best-preserved proximal groove (length about 270 cm) shows slight displacement rims at the medial and lateral margins. Three smaller successive areas with outer convexity precede this trace towards the southeast (Helm et al., 2022). The Goukamma trunk-drag impression is almost straight, differing in this feature from the T2 trace present at the F/DT ichnosite (Fig. 11).

All things considered, at the moment, too few data are available for disentangling how the F/DT elephant acted to generate the T2 impression.

5.4. THE CHALLENGING ISSUE OF DECONSTRUCTING THE DYNAMICS OF THE ELEPHANT'S MOVEMENTS

The low number of well-preserved footprints, the indefiniteness of some, the ambiguous position of others, and the relative position of footprints and trunk traces hinder recreating the walking direction, properly contextualising the trunk traces, and, in turn, better understanding the dynamics of its movement. For example, 1) the alteration due to water runoff hampers confirming the presence of footprints in the upper part of the slope; and 2) the cuts made in the 19th and

20th centuries for the extraction of lithoid tuff blocks (Panarello, 2016; Mietto et al., 2022) prevent us from verifying whether or not footprints were present in the sector of the slope located east of M1-L. Palombo et al. (2018) hypothesised that the F/DT young elephant climbed the ignimbrite slope to reach the path's subplanar zone, implicitly assuming that it moved from SE to NW. However, at least one fact makes this hypothesis questionable. The position of M0-R, assuming it is reliable, appears inconsistent with the walking direction of the best-preserved ones (M1-L and M2-R). On the other hand, it is unrealistic to imagine that a second young individual advanced from east to west along the prehistoric path due to the absence of any other evidence of this hypothetical trackway. The position of the toenails and whisker traces in M1-L and M2-R, respectively, indicates that the elephant proceeded from east-southeast to west-northwest. This hypothesis is weakly supported by the M2-R peak pressure, which partially confirms the tendency to concentrate the pressure on the lateral digits of the feet during walking, observed in modern elephants roaming in near-wild captive conditions (Panagiotopoulou et al., 2012, 2016). Panagiotopoulou et al. (2016) and Hutchinson et al. (2006) observed in modern elephants roaming in near-wild captive conditions. Indeed, the deepest zone corresponds to the anterior foot part in both footprints, even though in the F/DT M1-L footprint, some cushion pressure is detectable



Fig. 11 - A trunk-drag impression from the Goukamma Nature Reserve (Cape South Coast, South Africa) (modified from Helm et al., 2022).

on the lateral footprint side. However, variations in the pressure magnitude might vary as a function of the body mass, substrate characteristics, and gait, even in elephants of similar age.

In this context, the direction of the distal trunk trace T1, which was not detected at the time of Palombo et al. (2018) preliminary study, is a pivotal element for substantiating an alternative hypothesis. The shape and the dorsal finger-like process would indicate that the elephant, walking along the southern edge of the prehistoric trail from east to west, momentarily turned toward the slope. We might speculate that the elephant unbalanced itself toward the slope by placing one limb (see the M0-R footprint) partially on it and then resting its distal trunk for support. The balance lost might be caused by excessive stretching of the trunk for grasping something on the slope. The possible dragging trace left by the dorsal finger-like process may support this supposition. The elephant might have turned back toward the slope, as supported by the M1-L orientation. We could also assume that the T2 trace was left by the back of the trunk. Indeed, extant elephants may occasionally rest the back of their trunk when climbing a slope. Then the elephant resumed walking along the prehistoric path from east to west, impressing the M2-R as well as the other, less detectable footprints. In this context, the lack of the left pes footprint could be due to the current deteriorated conditions of the substrate. We cannot,

however, rule out the possibility that the elephant from the slope ascended to the ancient trail and continued uphill, moving slowly and using its trunk for exploring the ground. Indeed, we are unable to validate it due to the impossibility of confirming whether footprints were there at the hypothetical area where the elephant first moved.

6. CONCLUSIONS

This research 1) describes for the first time the fossil traces left by a non-African elephant's trunk; 2) discusses the possible identification of two problematic earth-shaped impressions present along the elephant trackway, which we eventually regarded as hypothetically left by the elephant's distal trunk; and 3) critically reappraises the elephant's footprints preliminarily described by Palombo et al. (2018). It discusses the dynamics of the elephant's movements, the possible direction followed by the elephant trackmaker walking on the uppermost edge of the F/DT ignimbrite slope and along the prehistoric path, as well as the modality of the trunk drag-like and trunk tip impressions. The few available pieces of evidence suggest that the elephant followed one or another of two potential routes. The first, most conceivable, hypothesis would indicate that it walked from east to west first on the border and then on the path, and that a temporary balance lost forced it to impress a manus footprint on the slope. A second theory, suggesting that it diagonally climbed the slippery slope from southeast towards northwest, helping

itself with its trunk when it reached the pathway, and then walked on the path towards the west, deserves attention. Unfortunately, the altered preservation status of the ignimbrite surface prevents us from verifying if any other footprint is present on the slope along this hypothetical route.

The morphology of the hypothetical trunk tip impression (T1), if confirmed by more sound evidence, would provide some useful hints for the trackmaker's taxonomical identification. The occurrence of the finger-like dorsal and ventral finger-like processes seems to be more consistent with the trunk tip of the African savanna elephants. Assuming as true this rather speculative hypothesis, it may suggest that the trackmaker was a young straight-tusked elephant. Indeed, mitogenomic evidence indicates that *P. antiquus* was a close relative of the extant African elephants, particularly of the African forest elephant (*Loxodonta cyclotis*) (Meyer et al., 2017; Palkopolou et al., 2018; Roca, 2019). Moreover, Palombo et al. (2018) results of analysis, which provided the estimated height at the shoulder (not more than 1.9 m) and body mass (2300-2600 kg), enable the authors to infer for the F/DT elephant an ontogenetic age that ranges from a to 9 years, depending on its sex.

All things considered, the reappraisal of the elephant footprints from the F/DT ichnosite, taxonomically identified as *Proboscipeda panfamilia*, confirms that the best-preserved footprints and the trunk traces likely belong to a young individual. The footprint dimensions and the sharp edges of the M1 toe impressions support the elephant's young age because nails are usually worn down in adult elephants. Unfortunately, the lack of data prevents us from soundly asserting that the T1 and T3 traces were left by the trunk tip and allows us just to speculate about the direction of travel and the factors causing the trunk impressions. Only the discovery of new pieces of evidence and new tracks left by fossil and extant elephants will answer these open questions.

Author Contributions

M.R.P. conceived the manuscript. M.R.P. wrote the original draft of the manuscript and analysed data and validated the manuscript with the valuable support of A.P.; A.P. collected and graphically elaborated the data. M.R.P. reviewed and edited the manuscript with the support of A.P.

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