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THE PROBLEM OF SMALL FOOTPRINTS IN PALEOICHNOLOGY: REMARKS ON THE EARLY PERMIAN ICHNOTAXON *ERPETOPUS CASSINISI*, A LOCAL SPECIES FROM SOUTHERN ALPS (NORTHERN ITALY)

LORENZO MARCHETTI [1], GIUSEPPE SANTI [2] & MARCO AVANZINI [3]

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Abstract. Based on well-preserved specimens, and strictly considering the influence of extramorphological (substrate-related) factors, the use of modern techniques (computer drawings, 3D acquisitions), permitted a reliable study on footprints smaller than 20 mm. Footprints of this size were mostly considered as too small and being affected by a lot of deformation, thus preventing a substantiated analysis. Our case study focuses on the *Erpetopus/Camunipes* dualism. Ichnologists disagree on the value of a separation of these ichnogenera, and their discussion appears rather "philosophical" than being conducted by an accurate analysis and objective data. We restudied the holotype of *Camunipes cassinisi* (sp. MBS 319), together with a new specimen from Southern Alps (sp. MBG 12465) that shows five well-preserved long trackways, and compared them to selected material, including the *Erpetopus willistoni* holotype (sp. UGKU C-8). Results suggest a synonymy of *Camunipes* with *Erpetopus* and the new combination *Erpetopus cassinisi* which is distinct from *E. willistoni* by the following anatomical features: the pes of *E. cassinisi* shows higher divarication angles between digits IV-V (>50°) and I-V (>130°) and a longer and variably oriented digit V, which is long about as digit II. This has interesting paleobiogeographical consequences: *E. cassinisi* was probably a local ichnospecies of *Erpetopus* in the Southern Alps.

Introduction

The study of small-sized tetrapod footprints (under 20 mm length) has been a challenge for paleoichnologists so far. These tracks are scarcely preserved under optimal conditions. In addition, they seem to be strongly affected by extramorphological deformation blurring the anatomically-controlled shape and hindering their unequivocal assignment.

An emblematic example is the revision of the Early Permian ichnotaxon *Erpetopus willistoni* Moodie, 1929, from the ichnofauna of Castle Peak (Texas) by Haubold & Lucas (2001, 2003). The lack of a larger material with well-preserved specimens and the influence of extramorphological effects prevented a substantiated anatonomically-based analysis of this ichnotaxon. The result was a simple description containing few data only.

In comparison with similar-shaped ichnotaxa such as *Camunipes cassinisi* Ceoloni et al., 1987, *E. willistoni* was differently evaluated. Haubold & Lucas (2001, 2003) described *Camunipes cassinisi* as an extramorphological variant of *E. willistoni*, considering the wide outward rotation of pedal digit V as not diagnostic. Contrary, Santi (2007a) evaluated this feature to be anatonomically-controlled, and therefore the ichnospecies as valid.

The discussion appears to be rather "philosophical", because objective data that might support these opinions were not presented. In summary, these ichnotaxonomic problems are the result of: 1) lack of well-preserved specimens, 2) increase of extramorphological effects in footprints below the critical size of 20 mm, 3) inadequacy of traditional techniques, 4) difficulty of correlation between different paleogeographical settings.

In order to add reliable data on this matter we studied new material from Southern Alps and revised the holotype of *Camunipes cassinisi*, with an appropri-

1 Dipartimento di Geoscienze, Università degli Studi di Padova, via Gradenigo 6, 35131 Padova, Italy. E-mail: lorenzo.marchetti@studenti.unipd.it
2 Dipartimento di Scienze della Terra e dell'Ambiente, Università di Pavia, via Ferrata 1, 27100 Pavia, Italy. E-mail: gsanti@unipv.it
3 MUSE Museo delle Scienze, Corso del Lavoro e della Scienza 3, 38123 Trento, Italy. E-mail: marco.avanzini@muse.it

ate evaluation of extramorphological effects. A comparative study on the holotype of *Erpetopus willistoni* and selected material from Texas, France and Morocco was carried out to draw ichnotaxonomic conclusions.

Geological Setting

In the Southern Alps, the Late Carboniferous to Permian continental sequence is characterized by two tectono-sedimentary cycles separated by a clear and regional unconformity (about 10 Ma) (Cassinis et al. 2011). On the Variscan basement, the Lower Cycle or Cycle 1 (Early Permian) is defined by a thick fluvio-lacustrine and acidic to intermediate volcanic deposits; the Upper Cycle or Cycle 2 (Middle?-Late Permian) is composed by alluvial sediments of the Verrucano Lombardo-Val Gardena red-beds complex (Cassinis et al. 2011).

The Early Permian of Southern Alps is characterized by the formation of pull-apart basins, which was probably caused by the opening of the Paleo-Tethys to the East, or by the existence of a mega-shear zone between Gondwana and Laurasia that generated transtensional tectonic forces on the Variscan Orogeny (Muttoni et al. 2003; Schaltegger & Brack 2007).

The most important of these are the Collio and Orobic basins and the Athesian Volcanic Complex. The first is characterized by the deposition of alluvial-to lacustrine fine-grained sediments (Collio Formation), interfingering in the upper part with sandstones and conglomerates of prograding alluvial fans (Dosso dei Galli Formation). It also includes volcanic beds (Dasdana beds) and bodies (Auccia Volcanics, Macaone Formation). Tetrapod footprints come from fine-grained laminated sediments of the Collio Formation, from both the Pian delle Baste and Val Dorizzo members (Cassinis et al. 2011). In the latter Berruti (1969) discovered the holotype of *Camunipes cassinisi* (sp. MBS 319), at a locality known as Malga Dasdana Busa (Fig. 1). After radiometric datings (Schaltegger & Brack 2007), the age of this basin was calculated between 283.1 ± 0.6 Ma and 279.8 ± 1.1 Ma (Early Kungurian).

In the Orobic Basin the stratigraphic succession of the Lower Permian is represented by the deposition of the Laghi Gemelli Group (Boriani et al. 2012) (Fig. 1). From the bottom, is generally characterized by a sequence of clastic sediments mainly of quartz fragments coming from the metamorphic basement (i.e. Dozy & Timmermans 1935; Cadel et al. 1996 in Cassinis et al. 2011) and by sandstones with rare volcanic fragments (Basal Conglomerate). In this body, are intercalated beds of red purple siltite, locally bioturbated. At the top, the Monte Cabianca Formation overlies. It is composed by acid to intermediated acidity (andesites) volcanic deposits belonging to two volcanic cycles (Cassinis et al. 2011 cum bibl.) with intercalated sandstones and conglomerates. The upper part of the Laghi Gemelli Group is the Pizzo del Diavolo Formation, composed by a thick sequence of lacustrine fine-grained laminated mudstones and coarse-grained (sandstones to conglomerates) fan bodies; evaporites, lacustrine carbonates and volcanites also occur (Cassinis et al. 2011).

The specimen MBG 12465 was found in laminated limestones of the latter unit, at a locality known as Pizzo del Diavolo (Fig. 1). After radiometric dating, the age of this basin is probably Artinskian-Roadian (288 Ma, Cadel et al. 1987; 280 Ma, Philippe et al. 1987; 279 and 270 Ma, Berra et al. 2008). However, the vertebrate ichnoassociation lists the same taxa of the Collio Basin, so it is probably Kungurian (Marchetti et al. 2013a) (Fig. 1).

Ichnotaxonomic remarks

Small footprints

The classification of fossil footprints may follow two kinds of approaches: anatomically-based or behavioral. Both are suitable, but a mixture of both should be avoided. The study of fossil tetrapod footprints is typically focusing on the anatomy of the trackmaker, and from parameters and measurements of footprints and trackways we try to reconstruct their autopodia and even their complete body.

This excludes features related to behavior (like speed of locomotion, gait, etc.) and also effects due to substrate (grain size, wetness, compactness), stratigraphic level (undertracks and overtracks, see the works of Hitchcock 1858; Allen 1989; Lockley 1991) and size of the trackmaker. These are known as extramorphological effects, as first noticed by Peabody (1948). They blur the anatomically controlled impressions of the autopodia of the trackmaker, resulting in different deformations such as elongation, truncation, bifurcation, bending, widening, thinning, non-impression, rotation.

It is essential for ichnotaxonomic studies to recognize extramorphological features because these effects are sometimes so pervasive, thereby inflating every kind of objective analysis. In addition, they cannot be compensated by statistical methods and large samples, respectively (Haubold et al. 1995). Consequently, an extreme taxa oversplitting took place in former studies, especially in those on Early Permian footprints. A large number of so-called phantom-taxa that were based mostly on extramorphological features, have later been synonymized (Haubold et al. 1995; Haubold 1996, 2000; Voigt 2005).

In the case of small tetrapod footprints (under the critical size of 20 mm), extramorphological phenomena

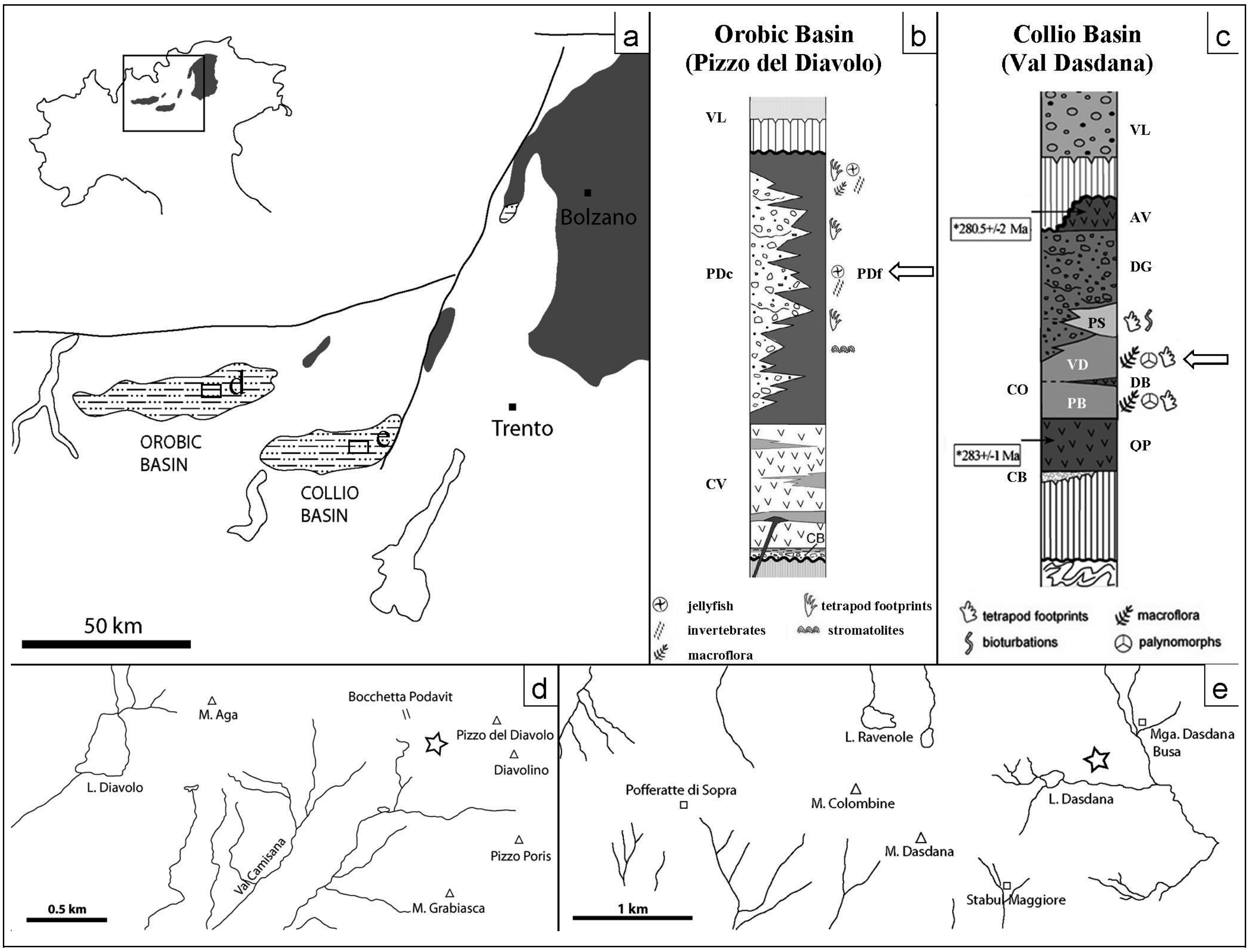

Fig. 1 - Geological setting and localities. a) Location of Collio and Orobic basins. b) Stratigraphy of Orobic Basin (from Ronchi et al. 2005) with position of body fossil and footprint levels. c) Stratigraphy of Collio Basin (from Cassinis & Perotti 2007) with position of body fossil and footprint levels. d) Pizzo del Diavolo locality (sp. MBG 12465). e) Malga Dasdana Busa locality (sp. MBS 319).
CB= Basal Conglomerate, PD= Pizzo del Diavolo Fm., c= coarser, f= finer, VL= Verrucano Lombardo Fm., QP= Lower Quartz Porphyries, CO= Collio Fm., PB= Pian delle Baste Mb., DB= Dasdana Beds, VD= Val Dorizzo Mb., PS= Pietra Simona, DG= Dosso dei Galli Fm., AV= Auccia Volcanics.

seem to become more frequent. This was noticed in a study and revision of Early Permian ichnotaxa from New Mexico and Europe by Haubold et al. (1995) and Haubold (1996). They showed that the influence of extramorphological effects on small footprints was responsible for the description of 50 phantom-taxa that can all be synonymized with *Batrachichnus salamandroides* and *Chelichnus bucklandi* which include the smallest ichnotaxa under examination. Furthermore Haubold (1996) noted: *"Die Deformation nimmt speziell unter 30 mm Fusslänge zu. Bei 20 mm - 15 mm, gleichsam an der Untergrenze der Erhaltbarkeit der Fusseindrücke von Tetrapoden im Sediment, erreicht die Variabilität der Überlieferung ein Maximum"* (p. 84). "The deformation refers specifically to the foot length smaller than 30 mm. At 20-15 mm, almost the lower limit of the footprint preservation in the sediment, the variability reaches a maximum".

Captorhinomorph tracks

The ichnotaxonomy of Early Permian captorhinomorph tracks is problematic since the first studies by Gilmore (1927, 1928) on material from the Grand Canyon of Arizona and by Moodie (1929, 1930) from Castle Peak, Texas. Still there is no consensus on the validity of some ichnospecies and ichnogenera, especially for small footprints. After the revision of Haubold (2000) the following ichnospecies were considered as valid: *Hyloidichnus bifurcatus* and *H. major*, *Gilmoreichnus* (*Hylopus*) *hermitensis*, *Varanopus curvidactylus* and *V. microdactylus*, *Erpetopus willistoni*. Whilst *Hyloidichnus* and *Varanopus* are widely accepted, the validity of *Gilmoreichnus* was questioned by Voigt (2005) and Gand & Durand (2006), leaving the status of *Hylopus hermitensis* unresolved. Gand & Durand (2006) also recognized a further ichnotaxon, *Varanopus rigidus*, possibly a synonym of *Hylopus hermitensis*. The ichnotaxonomy of *Erpetopus* is even more complex, because besides their small size, the provenance from different basins hampers their comparison. Haubold & Lucas (2001, 2003), in their revision of the original material from Castle Peak, invalidated the ichnogenus *Microsauropus* as well as some French specimens previously attributed to *V. curvidactylus* and the Italian *Camunipes cassinisi*. This was not accepted by Gand & Durand (2006), who supported the validity of *Microsauropus acutipes* and related ichnotaxa from France. In addition, Santi (2007a) did not accept the invalidation of *Camunipes cassinisi* and instead proposed a second ichnospecies being distinct from *Erpetopus willistoni*. In order to get a solution of these problems, a more detailed study on captorhinomorph tracks is needed.

Material and methods

The material consists of several longer trackways with numerous pes-manus sets preserved as true tracks or natural casts. The specimens from Southern Alps (Italy) are stored in the Natural History Museums of Bergamo (MBG, MBG-PF), Milano (MSNM-V), Morbegno (MSNM) and Gerola Alta (EMVG) for the Orobic Basin; Natural History Museums of Brescia (MBS), Trento (MUSE), and University "La Sapienza" of Roma (NS-43) for the Collio Basin. The specimens from Texas and France (Haubold personal collection) are stored in Urweltmuseum GEOSKOP of Tallichtenberg, Germany (UGKU). The specimens from Morocco are stored in the University of El Jadida, Morocco (CDUE).

To avoid incorrect determinations due to extramorphological overprinting, only the best-preserved tracks were considered for measurement of footprint parameters. Criteria are (1) completeness of digit numbers, (2) distinct impression of digits and palmar/plantar surface, (3) morphology not affected by deformations.

To reduce errors in measurements and obtain the most precise and objective drawings of tracks, an integration of modern and traditional techniques was utilized. Final digital drawings are based on outline drawings on transparent films, high-resolution photos under controlled artificial light conditions and 3D acquisitions from an optical laser scanner (e.g. Petti et al. 2008; Remondino et al. 2010).

Ichnological parameters were measured following the principles of Leonardi (1987) and Voigt (2005). Elaborations were made with the appropriate software (ScanStudio HD®, Polyworks®, Adobe Illustrator®, Gimp2®).

Trackways of sp. MBG 12465 are numbered from Tr1 to Tr5, manus-pes couples have Roman numbers from I to XXIII, following the direction of locomotion. Measurements were taken from following tracks: TR1 pes V, IX, XI, manus I, IV, VIII, IX, XI, XII, XIII, XIV; TR 2 pes II, III, IV, VI, VII, manus I; TR 3 pes I, III, VIII, XII, XIII, XIV, manus IX, X, XII, XIV, XV, XVI, XVII, XVIII, XIX, XX, XXII; TR 4 pes IV, V, manus III, IV, VIII, IX, X; TR 5 pes III, IV, manus I, III, V. In the holotype, sp. MBS 319: pes II, IV, V, VI, VII, manus II, IV, V, VI, VII.

Systematic paleoichnology

Ichnogenus *Erpetopus* Moodie, 1929

Ichnospecies **Erpetopus willistoni** Moodie, 1929

Diagnosis [after Moodie (1929), emended]: Small to very small tracks, length of manus and pes 5 to 10 mm on average, smallest recognized size about 3 mm. Manus and pes usually close in sets along quadrupedal trackways. Dependent on size and related stride length, which measures 28 to 110 mm, pace angulation about 90°; observed maximum of pace angulation about 120 ° (specimens NMMNH P-32408, 32410). Manus partially overstepped by pes. In tiny forms (pes length 5 mm and less), trackway pattern may become less regular, as in UC 443 A (holotype). If tracks are optimally recorded on a firm substrate, they show 5 digits in manus and pes. Length increases from digit I to IV; digit V as short as digits I or II and in opposition to group of digits I to IV, which are often laterally directed outward. All digits pointed, ending in small claws, which appear in imprints as curved or directed inward. This, however, is influenced by mode of movement. In several cases, digit tips appear bifurcated. Trace of digit tip V may appear curved backward. In relatively soft substrate, tips of digits II to IV can be extended into elongated trailing marks (Haubold & Lucas 2003: 251).

Remarks. The ichnogenus was introduced by Moodie (1929) in a study of some specimens from the Choza Formation of Castle Peak (Texas), a locality first described by Williston (1908). The material was later revised by Sarjeant (1971), Haubold (1971) and Haubold & Lucas (2001, 2003). Despite some similarities of *Erpetopus* with *Varanopus*, Haubold & Lucas (2001; 2003) convincingly explained the differences between these ichnogenera. Contrary to *Erpetopus*, *Varanopus* footprints are oriented parallel to the midline, their pedal digits show a total divergence of about 90° and pedal digit V is directed forward and not curved backward as in the former; it is about as long as digit III. In addition, it is mostly of larger size (foot length>20 mm), however, this is not a diagnostic feature.

Material assignable to *Erpetopus* (*Microsauropus*) has been reported:

– from North America (Moodie 1929, 1930; Sarjeant 1971; Haubold 1971; Haubold & Lucas 2001, 2003; Minter et al. 2007; Voigt et al. 2013),

– from France, where it is usually named *Varanopus curvidactylus* (Gand & Haubold 1984; Gand 1987, 1993; Demathieu et al. 1991; Haubold & Lucas 2001; Gand & Durand 2006; Barrier et al. 2009),

– from Italy, where it is often assigned to *Camunipes cassinisi* (Berruti et al. 1969; Ceoloni et al. 1987; Conti et al. 2000; Santi & Krieger 2001; Confortini et al. 2001; Gianotti et al. 2002; Santi 2003; Arduini et al. 2003; Ronchi et al. 2005; Santi 2007a, 2007b; Bernardi & Avanzini 2011; Marchetti et al. 2012, 2013a, 2013b),

– Morocco (Hminna et al. 2012).

The trackmakers were probably small captorhinids of uncertain affinity (Haubold & Lucas 2003; Minter et al. 2007) or small captorhinids/protorothyridids (Bernardi & Avanzini 2011).

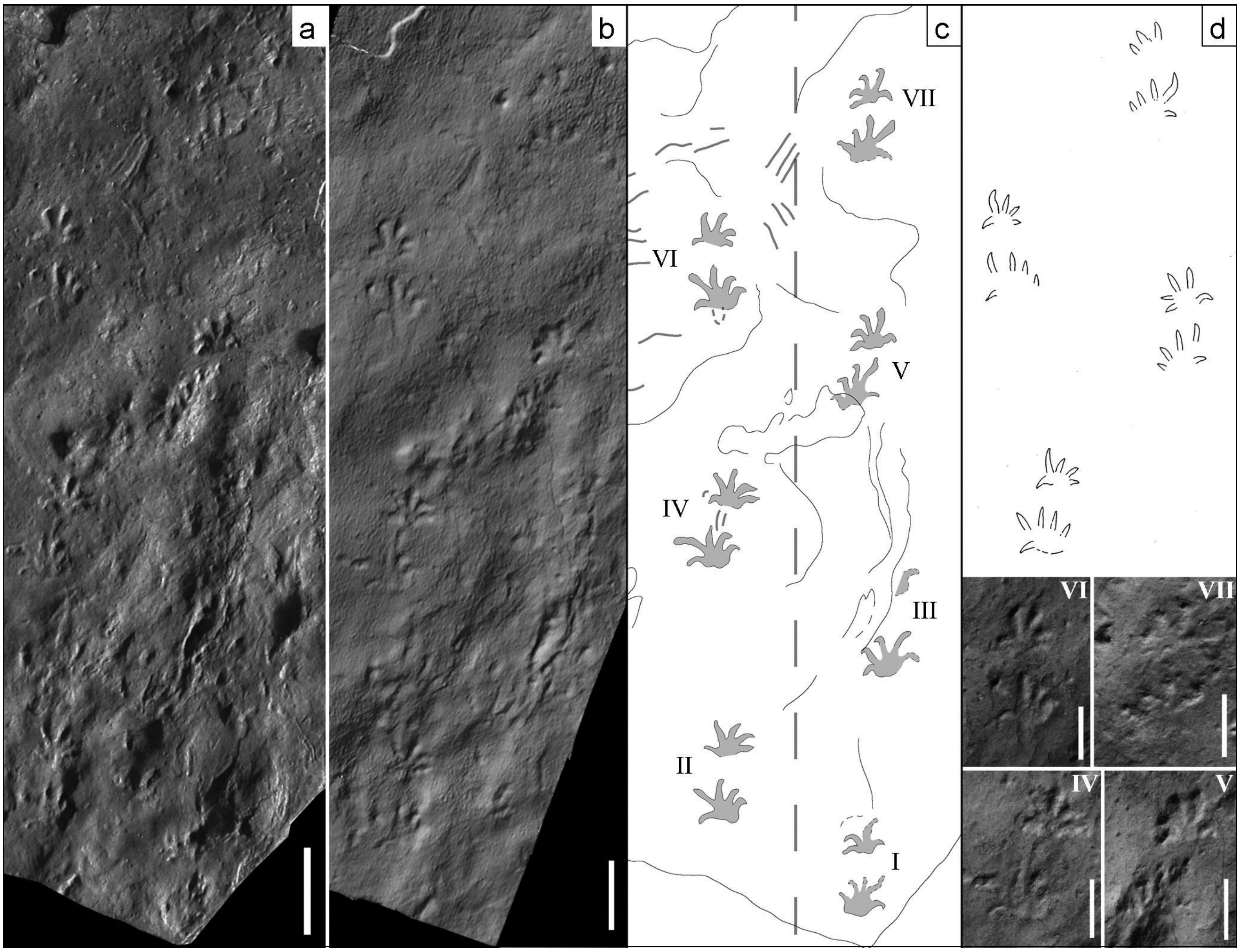

Fig. 2 - Holotype of *Erpetopus cassinisi* (Ceoloni et al., 1987) from Malga Dasdana Busa (Collio Basin, North Italy) (MBS 319). a) Photo of the specimen. b) 3D model of the specimen from optical scanner acquisition. c) Interpretative drawing. d) The original drawing of Ceoloni et al. 1987 and photos of the best-preserved manus-pes couples (IV-VII, scale 10 mm). Scale: 20 mm.

Ichnogenus *Erpetopus* Moodie, 1929

Ichnospecies **Erpetopus cassinisi** (Ceoloni et al., 1987) comb. nov.

Figs 2-4, Tabs 1-4

1969 *Prochirotherium permicum* Leonardi vel *Ichnium acrodactylum tambachense* Pabst - Berruti, p. 19, 21, fig. 5, 7

1975 *Amphisauropus imminutus* Haubold - Haubold & Katzung, p.116

1987 *Camunipes cassinisi* Ceoloni et al., p. 221-222, pl. 1, fig. 8

2001 *Erpetopus willistoni* Moodie - Haubold and Lucas, p. 91, fig. 10a

2013b *Erpetopus willistoni* Moodie - Marchetti et al., p. 59, fig. 3

Holotype: MBS 319 (single trackway with 7 pes-manus sets) (Fig. 2).

Paratype: MBG 12465 (Trackways 1, 3, 4 with 17, 23, and 11 pes-manus sets, respectively) (Fig. 3-4).

Additional material: MBG 12480, MBG-PF 8, EMVG 2, MSNM 27, MSNM-V 2856, MSNM-V 7012, MSNM-V 7073, NS 43-311, MUSE 7086.

Type horizon: Val Dorizzo Member, Collio Formation.

Type locality: Malga Dasdana Busa, Brescia, Italy.

Repository: Natural History Museum of Brescia, Italy.

Diagnosis [after Ceoloni et al. (1987), emended]: Ectaxonic, pentadactyl, semiplantigrad footprints, slightly larger than long; the functional prevalence is slightly medial and, in the pes, on the distal part of lateral digits. The manus is a little smaller than pes. Digits are thin, slightly falcate, and increasing in length from I to IV. V digit of the pes is as long as II and slightly turned backwards. Digit divergence is high between digits IV-V and I-V. All the digits have sharp claws. Palm and sole are short and rectangular. The trackways are disposed in a slightly irregular alternating arrangement of pes-manus sets, with the pes close to the manus, overstepping is also observed. The gait is variable, usually moderately fast. The axis of IV digit of manus and of III digit of pes are subparallel to midline.

Description

Tracks of a small quadruped. The pes is pentadactyl, plantigrade to semi-digitigrade and less distinctly impressed than the manus, a median-lateral decrease in relief is common. It is wider than long or as wide as long (length 11 mm, width 13 mm, length/width ratio 0.85.

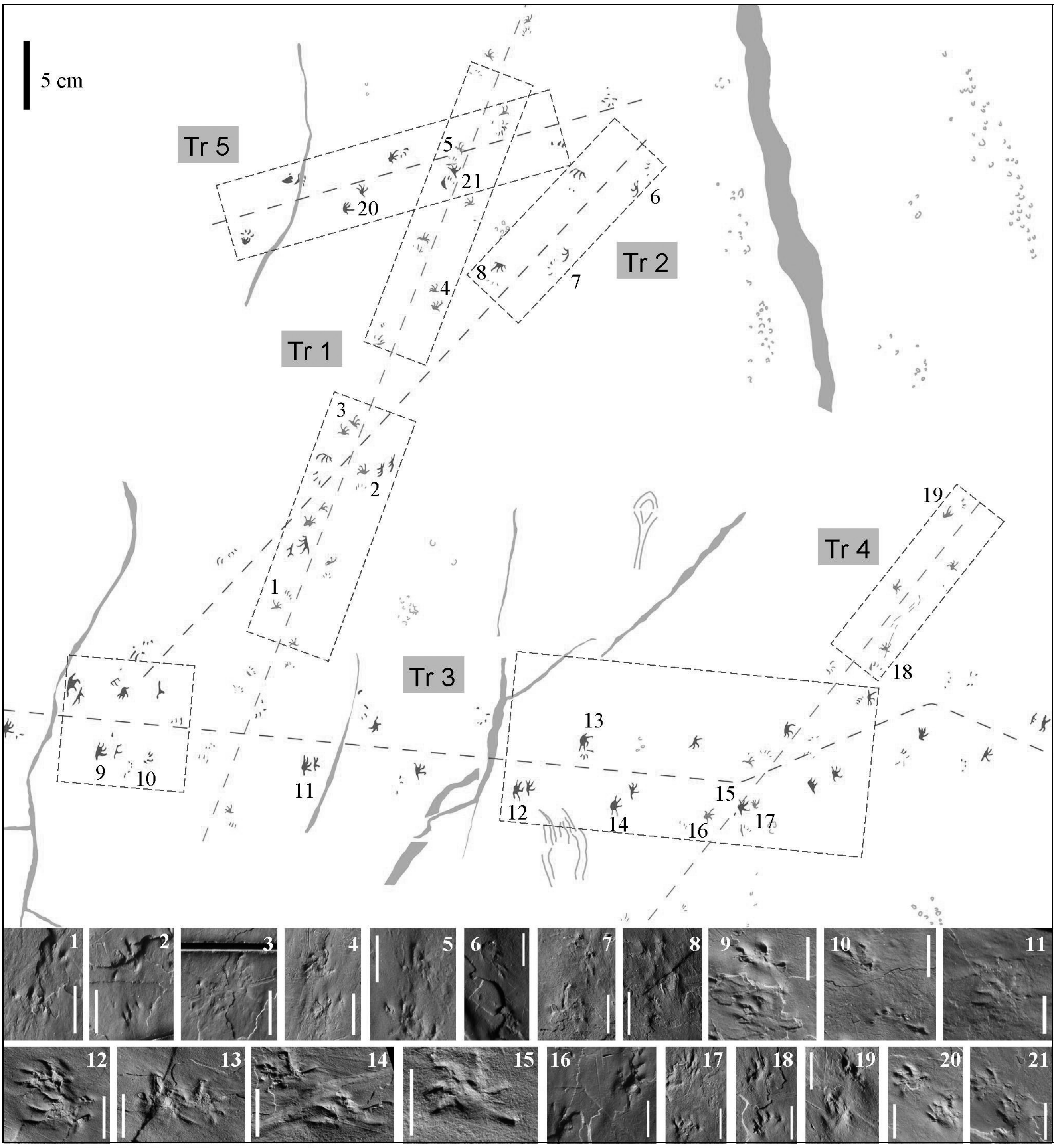

Fig. 3 - MBG 12465 from Pizzo del Diavolo Fm. (Orobic Basin, northern Italy). Interpretative drawing with three *Erpetopus cassinisi* trackways (Tr1, Tr3, Tr4) and two possible *Erpetopus willistoni* trackways (Tr2, Tr5).
1-21 – Photos of manus-pes couples corresponding with numbers in the trackway map. 1-5) Tr1, note the pes digit V curved backward. 6-8) Tr2, digitigrade preservation. 9-15) Tr3, with deformed imprints [10]; overstep of the manus by the pes [15]; digits IV-V outward oriented [12, 14]. 16-19) Tr4, with outward-oriented pes and deformed imprints [19]. 20-21) Tr5, note the short pes digit V. Scale: 10 mm.

Values on average). Digits are thin, long and straight and end in small sharp claws, the distal part of digits I-IV is typically curved inward. Digit length increases between digits I and IV (length of digit IV 6 mm, on average), digit V is shorter and subequal with digit II. It is laterally spread and often curved backward. The divarication angle between central digits II-III and III-IV, respectively, is relatively small (25°and 27°), larger between digits I-II (34°) and digits IV-V (58°); the total divergence is 146°. Values on average. In digitigrade imprints, only the tips of the digits are preserved, mostly those of central digits II-IV. The digit V is often preserved with the tip only or completely missing. The sole, if preserved, is short and rectangular (length 5 mm, width 7 mm, on average). It represents 2/5 of the pes length.

The manus is pentadactyl, plantigrade to semi-digitigrade and slightly smaller than the pes. It is wider than long (length 9 mm, width 11 mm, length/width ratio 0.85. Values on average). Digits are thin, long and straight and end in small sharp claws, the distal part of digits I-IV is typically curved inward. Digit length increases slightly between digits I and IV (length of digit IV 5 mm, on average), digit V is shorter, as long as digits I-II and directed outward. Divarication angles in the manus are small between central digits II-III and III-IV (31°) and larger between external digits I-II and IV-V (41° and 64°, respectively). The total divergence is larger than in the pes (169°). Values on average. In digitigrade imprints, only the distal parts of digits are preserved, commonly those of digits I-IV. The palm is short and rectangular but not always impressed and constitutes about half of the pes length (length 4 mm, width 6 mm, on average).

The trackway pattern shows a slightly irregular alternating arrangement of manus-pes couples, with the manus being positioned close to the pes in a distance of 15 mm, on average. In some cases the manus is slightly to completely overstepped by the latter. The stride length of the pes is 67 mm, that of the manus 65 mm; the pace length of the pes is 51 mm, that of the manus 45 mm, on average. Values are variable depending on different size, speed and gait of the trackmaker. The pace angulation ranges between 21-112° (85° on average) in the pes and between 28-127° (96° on average) in the manus. The stride length/foot length ratio is 2.8-10.7 (7 on average). Compared with the pes, the manus is positioned more close to the midline. The width of pace of the pes is 37 mm, that of the manus is 29 mm, on average. The orientation of the pes is parallel to the midline or slightly rotated inward or outward (3° on average); the manus is directed inward (22° on average). The calculated body length is 47 mm, the stride length/body length ratio 1.4, on average (Figs 3, 4).

Specimen MBG 12465. The trackways of specimen MBG 12465 (Tr1-Tr5) (Figs 3-4) are the longest *Erpetopus* trackways recorded from Southern Alps. The state of preservation is good enough to allow taxonomic considerations.

Trackways 1 and 4 (*E. cassinisi*; Fig. 4a, c, d, g) are directed to the upper and to the upper-right parts of the figure and record footprints pertaining to 17 and 11 manus-pes couples, respectively. Both show similar features and the trackmaker must have had the same size (pes length and width about 8 mm) and speed of locomotion. The latter was quite high (pace angulation 107° and 96° in the pes, 121° and 124° in the manus, stride length/foot length ratio 8.3 and 9.1, respectively). Digit V of the pes is outward directed and curved backward, this causes a large divarication angle IV-V (67° and 79°, respectively). This is distinct in 8 different pes imprints (Tr1: III, V, IX, X, XI, XIV; Tr4: IV, V), only in one imprint digit V is forward directed (Tr4: XI), but it is clearly deformed. The others do not preserve digit V. Pes digit V is about as long as digit II. The most striking feature of these trackways is the semiplantigrade-digitigrade preservation of footprints, in particular of the pes imprints with the lack of a palm impression and the proximal part of digits, possibly also of external digits.

Trackway 3 (*E. cassinisi*, Fig. 4c, f) is directed to the right part of the figure and crosses trackways 1 and 4, slightly changing direction at the end. It records footprints pertaining to 23 manus-pes couples. They are plantigrade, wider than long and slightly bigger than those of trackways 1-4. The speed of locomotion was lower (low pace angulation and SL/FL ratio). State of preservation, dimensions and speed of locomotion are similar to the *E. cassinisi* holotype. Pes digit V is about as long as II and it is directed outward, in the holotype also curved backwards. The divarication angle between pedal digits IV and V is about 50°, due to the slightly outward directed digit IV (feature evident in the central part of the specimen, pes XII, XIV, Fig. 4c and in the holotype in pes I, II, III, IV, V, VI, Fig. 2). This could be an effect of slow gait, so the differences with Trackways 1-4 reflect simply different morphotypes linked to gait and extramorphological variation. Pes II, XIII show a short forward directed digit V, this is clearly an extramorphological feature. The first part of the trackway reflects slow movement with low stride length (23-43 mm) and pace angulation (21-56°), more reasons can have caused this, maybe a wetter substrate that prevented faster locomotion (Fig. 4f).

Trackways 2 and 5 (cf. *E. willistoni*, Figs 4a, b, d, e) cross trackway 1 and are directed to the lower left part and to the upper right part of the specimen, showing 9 and 8 manus-pes couples, respectively. Dimensions (pes length ~ 9 mm) and trackway pattern reflecting speed of locomotion (high pace angulation 105-125°, stride length/foot length ~ 9-10) are similar, but trackway 2 is more digitigrade. The interesting feature is the pes digit V preservation, it is forward directed (divarication IV-V ~30°) and long about as digit I. If this is indeed an anatomically controlled feature, it might justify a determination as *E. willistoni*, however, it cannot be excluded that this is an extramorphological feature. Therefore, we tentatively refer this trackway to cf. *E. willistoni*.

Remarks. The ichnotaxon *Camunipes cassinisi* was established in 1987 by Ceoloni et al. from the study of some specimens from northern Italy. The holotype (specimen MBS 319) was previously attributed to *Prochirotherium permicum* Leonardi (1951)/*Ichnium acro-*

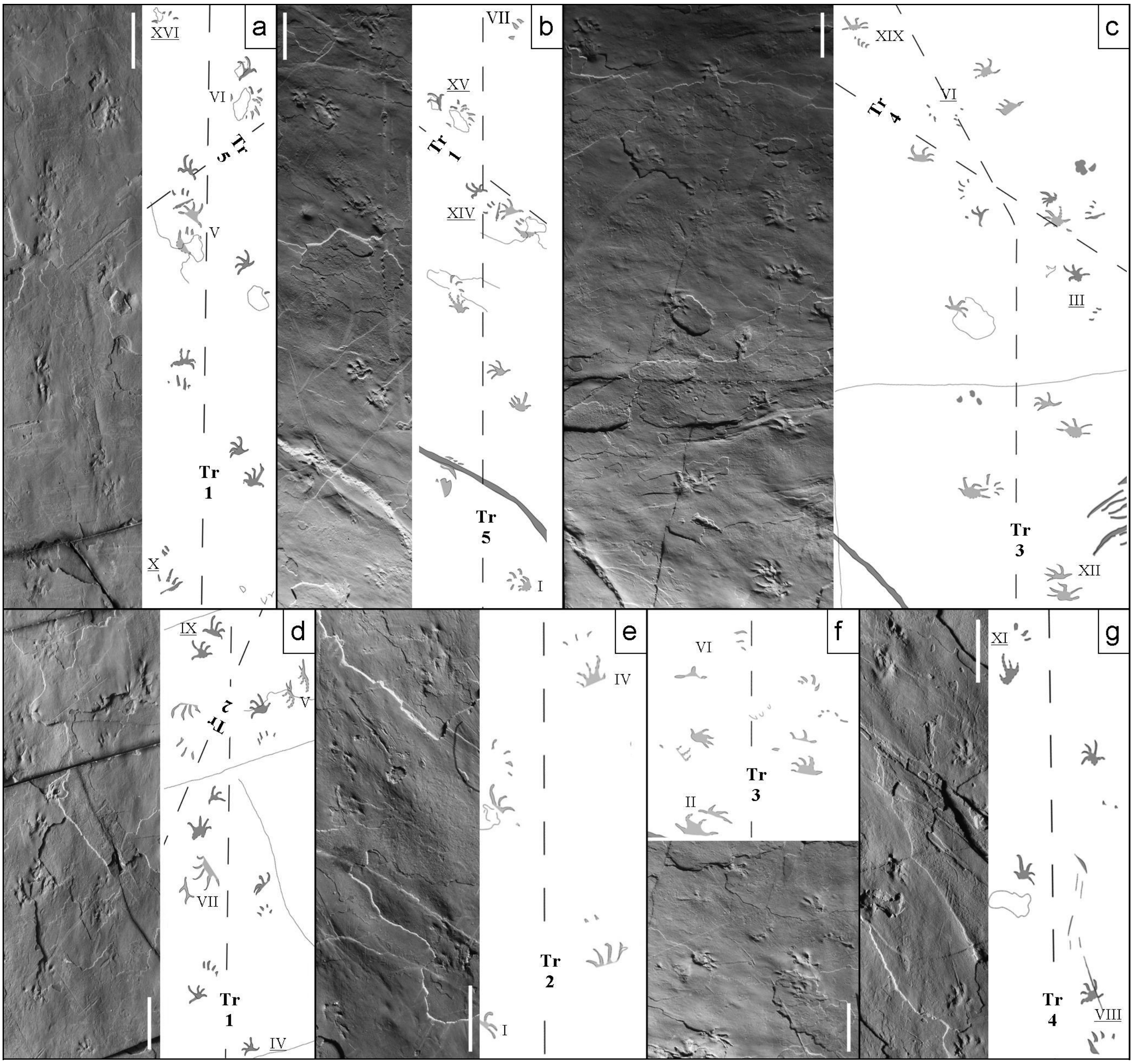

Fig. 4 - MBG 12465, photos and interpretative drawings of trackways (rectangles in Fig 3). a) Final part of Tr1, intersecting with Tr5. b) Trackway Tr5, intersecting with Tr1. c) Trackway Tr3, turning to the left in the final part and intersecting with Tr4. d) First part of Tr1, intersecting with Tr 2. e) First part of Tr2. f) First part of Tr3 reflecting very slow movement. g) Final part of Tr4. Scale bar: 20 mm.

dactylum tambacense Pabst (1908) by Berruti (1969); and to *Amphisauropus imminutus* Haubold, 1970 by Haubold & Katzung (1975). It comes from the Malga Dasdana Busa, in the Brescian prealps (Val Dorizzo Member, Collio Formation, Collio Basin) and is stored in the Natural History Museum of Brescia (Fig. 2).

Further reports of *Camunipes* and *Erpetopus* from Italy were reported by Conti et al. (2000), Confortini et al. (2001), Gianotti et al. (2002), Arduini et al. (2003), Ronchi et al. (2005), Santi (2003, 2007a, b), Bernardi & Avanzini (2011), Marchetti et al. (2012, 2013a, b). The material assigned to *Varanopus curvidactylus* by Santi & Krieger (2001), clearly shows the diagnostic features of *Erpetopus*. Instead the material from the Val Gerola site (Santi & Krieger 1999; Nicosia et al. 2000), and the specimen MBG 8834 from the Val Brembana site (the latter assigned to *Dromopus lacertoides* in Santi & Krieger 2001), might be *Varanopus* (Marchetti et al. 2013a) (Fig. 5).

Ichnotaxonomical comparisons

In order to understand and interpret correctly the studied material from the Southern Alps, a comparison with material coming from Texas, France and Morocco was carried out.

The selected specimens (Fig. 5, Tabs 1-4) include: an artificial cast of the *Erpetopus willistoni* holotype

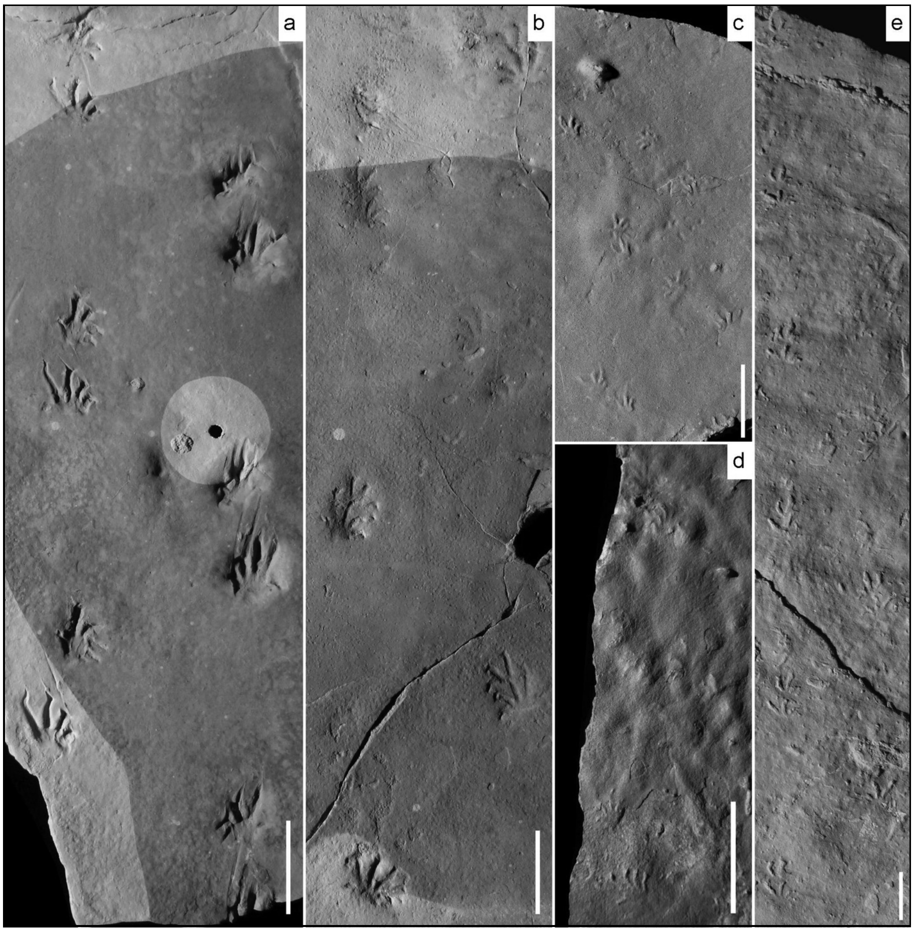

Fig. 5 - Photos of selected *E. willistoni* specimens of from Texas (a, b, c) Morocco (d) and France (e). a) UGKU 1803, plantigrade trackway with 6 pes-manus sets, note the short pes digit V. b) UGKU 1820, plantigrade trackway with 7 pes-manus sets and partial overstepping. c) UGKU C-8, artificial cast of the *E.willistoni* holotype. d) CDUE 357, natural cast. e) UGKU 1825, semiplantigrade trackway with 10 pes-manus sets, natural cast. Scale bar: 20 mm.

(UGKU C-8) and two optimally-preserved trackways (UGKU 1803, 1820) from the site of Castel Peak, Texas (Choza Formation, Kungurian); two trackways (UGKU 1823, 1825) from the Estérel Bas-Argens Basin, southern France (Pradineaux Formation, Roadian); a trackway (CDUE 357) from the Argana Basin, Morocco (Ikakern Formation, Guadalupian).

Specimen UGKU C-8 (*E. willistoni* holotype) shows a trackway with 7 incomplete pes-manus sets. The size of footprints is small (pes foot length 6 mm, on average) and the trackway pattern is irregular, with a probable change in direction and a different manus-pes distance on the two sides of trackway. Tracks are characterized by a median-lateral decrease in relief and the pes digit V is long about as digit I. UGKU 1803 displays a plantigrade trackway with 7 manus-pes couples, larger footprints (pes foot length 12 mm, on average), in a more regular pattern. The pes is long as wide, its digit length strongly increases between digits I-IV, digit V is less deeply impressed, outward bent and long about as digit I, and the total divergence is low. UGKU 1820 shows a trackway (Tr 1) with 7 manus-pes couples, in a slightly faster gait, in this case a partial overstep of the pes on the manus is observed. The other features are similar to UGKU 1803.

Specimen UGKU 1823 displays three semiplantigrad manus-pes couples, pes lenght of 9 mm (on average), and relatively short pes digit V, long about as digit I. UGKU 1825 shows a long semiplantigrad trackway (Tr1) with 10 manus-pes couples, the pes length is about 9 mm (on average). Footprints are evidentely larger than long, with relatively high digit divergences. The pes digit V is long about as digit I.

Specimen CDUE 357 displays three manus-pes couples, pertaining to the same trackway. The track size is quite small (pes length of 7 mm, on average). Footprints are as long as wide and digit divergences are quite low. The pes digit V is long about as digit I.

The study of morphology and the evaluation of the ichnological parameters of these specimens (Fig. 5, Tab. 1-4) permitted to advance some considerations: 1) all the material is assignable to the ichnogenus *Erpetopus* Moodie 1929, 2) some features of the pes structure differentiate the material from Southern Alps from the other *Erpetopus* specimens.

Discussion

From the study of the holotypes of *C. cassinisi* and *E. willistoni* and new material we obtained reliable parameters that are useful for different taxonomic con-

Sp	TR	FL	FW	FL/FW	psL	psW	I L	II L	III L	IV L	V L	div I-II	div II-III	div III-IV	div IV-V	div II-IV	div
MBG 12465	1	8.3	8.4	1.00	2.8	3.7	2.2	2.8	3.5	4.6	3	51.1	25.6	36.4	67.1	62.0	181.3
	2	9.4	11	0.84	4.7	7.6	2.8	4.1	4.9	5.7	2.2	27.5	28.6	16.7	26.3	45.3	82.4
	3	8.7	14.6	0.60	4.7	7.3	3.5	3.8	3.7	4.8	3.5	27.4	42.0	42.6	50.4	84.7	162.5
	4	8.4	8.7	0.96	3.4	4.7	2.8	3	3.6		2.6	52.1	26.5	15.4	78.7	41.9	172.8
	5	9.3	8.8	1.07	3.9	4.9	2.8	3.1	3.9	4.7	2.1	40.5	17.3	18.6	33.3	36.0	109.7
MBG 12480		12.5	13.1	0.97	5.1	5.8	2.6	3.1	4.1	6.5	3.6	29.6	19.2	22.1	52.6	41.2	120.0
MBG-PF 8	3	7.9	7.7	1.05	2.9	3.9	2.7	3.2	4	4.8	2.6	24.7	6.0	13.9	77.0	19.9	121.6
EMVG 2	2	15.8	15	1.05	6.7	7.6	5.1	6.2	7.2	9.9	5.2	35.4	25.1	18.6	54.6	43.7	138.6
MSNM 27	2	18.2	19.6	0.93	6.4	8.8	4.9	7.8	9.6	10.5	6.1	7.4	37.2	-5.3	62.7	31.9	102.0
MSNM-V 2856	1	13.2	13.7	0.97	6.6	7.4	3.1	4	5.8	6.8	3.3	40.8	26.1	28.1	61.6	54.1	156.4
MSNM-V 7012		8.3	10.3	0.80	2.5	4.4	2.8	2.4	3.6	6.2	2.7	64.2	20.4	25.9	66.4	46.3	176.8
MSNM-V 7073	2	5.1	6.6	0.78	2.5	3.6	1.8	1.7	2.2	3	1.6	40.3	28.3	44.0	74.1	72.3	205.2
MBS 319		10.8	12.9	0.85	5.5	6.1	3	3.8	5.2	6.3	3.6	28.3	20.0	41.5	51.3	61.5	141.2
NS 43-311		9.4	11.5	0.83	4.8	6.2	2.3	2.9	3.5	4.1	3.1	31.4	35.9	27.3	60.9	65.5	160.5
MUSE 7086	2	10.9	16	0.72	5.7	9.4	4.4	4.1	4.2	5.9	3.8	30.8	19.6	24.8	51.7	44.4	130.6
	3	9.8	13.7	0.72	4.7	7.8	4	4.1	4.8	6	3	22.3	16.0	11.1	57.6	27.1	111.2
UGKU C-8		5.6	6.4	0.92	2.3	3.1	1.7	2	3.2	4.4	1.5	46.4	35.7	40.5	40.4	76.1	150.7
UGKU 1803		11.9	11.2	1.06	4.7	6.4	2.7	4.4	6.4	8.4	2.5	15.6	18.9	25.3	38.6	44.3	98.4
UGKU 1820	1	11.7	10.9	1.09	3.7	6.1	2.8	4	5.5	8	2.5	25.0	34.2	17.2	40.0	51.4	120.0
UGKU 1823		9.3	9	1.06	3.9	5.7	2	3.1	4.2	5.4	1.7	41.6	38.3	12.6	46.9	50.9	165.5
UGKU 1825	1	9.1	12.9	0.71	3.6	6	3	3.7	5.1	7.6	3.2	38.7	28.8	39.2	37.9	68.0	144.6
CDUE 357		6.6	6.1	1.09	2.4	3.3	2.5	3.2	3.8	4.7	2.1	14.9	5.1	22.5	41.6	27.6	84.1

Tab. 1 - Ichnological parameters of pes footprints. Sp= specimen, TR= trackway, FL= foot length, FW= foot width, FL/FW= foot length/width ratio, psL= sole length, psW= sole width, L= digit length, div= divergence, I-V= digit number. Metrical measures in mm, angular measures in degrees, values on average.

siderations. This is the result of: 1) restriction to optimally preserved specimens, 2) identification of extramorphological features and strictly anatomically based determinations, 3) integration of modern and traditional techniques. Footprints smaller than 20 mm are not always affected by extramorphological factors as previously thought. The examined footprints are extremely small and only 5 and 18 mm in size. The "critical size" has to be lowered or restricted to a certain kind of footprints, for example *Batrachichnus salamandroides* (Geinitz, 1861), a small ichnotaxon examined in the studies of Haubold (1996) and Haubold et al. (1995), that shows a huge variability of preservational modes (see also Melchor & Sarjeant 2004; Stimson et al. 2012). A new acceptable limit for the study of small footprints could be 7 mm, such as the dimensions of the *Erpetopus* holotype (specimen UC443A, Yale Peabody Museum) that has footprints smaller than 7 mm and that shows widely varying parameters. All tracks of this study larger than 7 mm have more stable values.

The diagnostic characters of *E. cassinisi* are observed in MBS 319 (holotype) and MBG 12465 (paratype), in trackways 1-3-4, as well as in the additional material. The material from Texas (including the cast of the *E. willistoni* holotype, sp. UGKU C-8), France and Morocco was utilized to better define *E. willistoni*.

Here follows a description of these features (Fig. 6, Tabs 1-4): tracks of a small pentadactyl quadruped, slightly bigger than *E. willistoni* (pes length 5-18 mm in *E. cassinisi*, 5-13 mm in *E. willistoni*). The pes morphology is the main diagnostic difference between the two ichnospecies. We observed a different position, orientation and length of digit V with respect to digits I-IV. In *E. cassinisi*, digit V is outward oriented and distally curved backward. This is reflected in the large divarication angle between digits IV-V, which is about 58°, compared with 40° in *E. willistoni*, and the larger total divergence of 146°, compared with 125° in the latter. The relative length of digit V is longer, in fact the digit V/IV ratio is 0.63 in *E. cassinisi* (as II/IV) and 0.36 in *E. willistoni* (as I/IV). Values on average. Another difference is the less pronounced increase in length between digits I-IV, and the higher relative footprint width in *E. cassinisi*. The manus structure is analogue, in *E. cassinisi* the ex-

Sp	TR	FL	FW	FL/FW	psL	psW	I L	II L	III L	IV L	V L	div I-II	div II-III	div III-IV	div IV-V	div II-IV	div I-V
MBG 12465	1	7.5	8	0.94	2.6	3.7	2.5	2.2	3	4.1	2.5	58.7	36.1	31.2	72.1	67.3	198.0
	2	11	8	1.38	4.7	3.4	4	3	3.2	4.8		39.7	93.8	18.7		112.5	
	3	9.1	11.2	0.82	4.1	5.4	3	3.2	3.7	4.2	3.5	41.2	35.1	44.1	63.3	79.2	183.7
	4	8.1	8.2	0.99	3.9	4.1	2.5	2.2	2.7	4.2	2.3	52.3	41.9	36.8	42.5	78.7	173.4
	5	7.9	8.9	0.82	3.7	4.9	2.7	3	3.8	3.8	2.3	57.7	42.9	23.8	82.0	66.6	185.2
MBG 12480		9.1	10.3	0.88	4	5.5	2.8	3.4	4.2	5.2	2.3	33.5	34.5	29.5	63.0	63.7	161.3
MBG-PF 8	3	6.8	4	1.70	2.7	3	1.5	2.3	2.4	2.2	2.5	12.5	-3.4	37.9	103.0	34.5	149.9
EMVG 2	2	13.2	14.2	0.93	5.9	7.6	3.6	5.7	6.4	7.5	4.2	43.1	30.9	14.1	70.2	48.3	150.7
MSNM 27	2	11.3	15.4	0.73	4.2	8.8	3.4	5.6	7	7.5		8.3	8.4	14.3	69.6	22.8	100.6
MSNM-V 2856	1	10.3	11.8	0.88	5.2	6.8	2.8	3.2	4.6	6.3	3.5	35.8	29.3	30.3	59.2	59.6	153.2
MSNM-V 7012		7	9.8	0.72	2.7	4	1.7	2.4	3.3	4.4	3	84.8	52.0	11.7	41.2	63.6	198.6
MSNM-V 7073	2	4.9	6.6	0.74	2	2.4	1.8	2.4	2.7	3.2	2.2	32.6	26.0	68.2	62.2	94.2	189.0
MBS 319		8.6	10.5	0.82	4	4.9	3.4	3.5	4.5	5.5	3.1	34.2	38.0	37.5	60.0	75.5	169.6
NS 43-311		9.2	9.5	0.97	4.1	5.1	2.4	3	5.2	4	2.5	31.1	26.0	14.6	106.0	40.6	177.6
MUSE 7086	2	8.8	12	0.76	4.2	7.7	3.2	3.3	5.2	4.9	3.2	21.8	15.1	19.8	56.9	34.9	105.6
	3	9.7	14.3	0.69	5	9.5	4	3.3	4.4	5.6	3.3	47.0	6.2	15.9	59.9	5.6	119.5
UGKU C-8		4.8	5.8	0.83	2.1	2.6	1.4	1.9	2.7	3.3	1.7	55.9	29.5	35.9	56.0	65.3	177.2
UGKU 1803		9.4	10	0.95	4.6	5	2.5	3.5	4.4	6.2	2.3	36.3	28.4	24.2	55.2	52.7	144.2
UGKU 1820	1	7.9	11	0.74			2.6	3.8	5.4	5.5	2.9	55.5	29.2	9.6	47.7	38.7	119.7
UGKU 1823		8	9.6	0.84	3.2	5.8	1.9	2.6	3.4	5.5	2.6	22.3	37.5	19.3	48.0	56.8	127.1
UGKU 1825	1	7.4	10.6	0.71	2.7	5.7	2.3	3.2	5.3	5.3	1.9	44.9	34.1	50.6	69.7	84.7	168.8
CDUE 357		5.4	5.7	0.96	2.5	2.8	1.5	2.5	3	4	1.1	26.7	36.2	24.6	33.5	60.8	122.5

Tab. 2 - Ichnological parameters of manus footprints. Sp= specimen, TR= trackway, FL= foot length, FW= foot width, FL/FW= foot length/width ratio, psL= palm length, psW= sole width, L= digit length, div= divergence, I-V= digit number. Metrical measures in mm, angular measures in degrees, values on average.

ternal digits are slightly longer. The trackway pattern is very similar; the only possible difference is the manus-pes distance, higher in *E. cassinisi*. For morphology of the tracks and the trackway pattern, see descriptions of the ichnogenus above.

The length of the trackways with abundant imprints, the state of preservation and the evaluation of extramorphological variation, permitted us to relate these features to the anatomy of the autopodia. Their constant occurrence along the trackways indicates that they are not controlled by gait, size or substrate. The trackways of the holotype and of trackway 3 were left by bigger and slower animals than those of trackways 1 and 4, and also the sediment and depositional environment is different (siltstone from alluvial plain in MBS 319, limestone from playa environment in MBG 12465). Nonetheless, all show the features diagnostic of *E. cassinisi* missing in all other *Erpetopus* specimens. Therefore, we consider *E. cassinisi* as a valid ichnospecies. This distinction preserves the meaning of the original descriptions of the two ichnogenera, avoiding an excessive splitting of nomenclature (the problem of the "phantom taxa") and also an excessive simplification of ichnological diversity.

The comparison with previously studied material is difficult, because of the small number of available data. For example digit V of the pes is frequently missing or badly impressed, as happens for the holotype of *E. willistoni*. We agree with Santi (2007) that a holotype should contain all features of the ichnogenus, and this is not the case.

In the Castle Peak material only a few specimens preserve digit V of the pes along the trackways (YPM 1124, Haubold & Lucas 2001, fig 3c and NMMNH P-32410/411, Minter et al. 2007, fig 14c). The latter is the best preserved and shows a pes digit V/IV ratio of 0.4 and a total divarication angle of the pes of 129°, the pes divergence IV-V is about 30° (Voigt et al. 2013). These characters are in line with those of the studied specimens (UGKU 1803, 1820), that are clearly different from *E. cassinisi* material, and don't seem to be effected by extramorphological factors (Fig. 6, Tabs 1-4).

Sp	TR	SLp	PLp	PAp	LPp	WPp	DIVp	SLm	PLm	PAm	LPm	WPm	DIVm	Dmp	BL	SL/BL	SL/FL
MBG 12465	1	69.0	44.4	107.1	35.2	26.6	0.7	69.0	40.4	120.5	34.7	20.3	26.4	12.5	47.5	1.55	8.32
	2	92.0	54.1	110.2	43.7	33.2	1.6	90.2	50.7	116.7	41.7	27.7	15.8	12.6	54.3	1.71	9.79
	3	62.3	60.0	62.2	29.7	49.9	18.6	64.0	49.9	77.3	31.1	36.9	31.7	13.9	40.0	1.42	7.16
	4	75.6	50.0	95.7	34.6	32.1	-18.0	74.4	41.7	123.5	36.6	19.9	23.8	16.0	52.2	1.44	9.05
	5	79.0	49.7	105.0	39.6	29.7	8.2	78.6	45.6	125.2	40.5	19.7	36.3	9.5	45.3	1.60	8.54
MBG 12480		63.8	60.0	70.5	37.8	44.0	-14.0	63.4	51.6	72.3	30.4	41.3	4.7	19.3	50.3	1.29	5.11
MBG-PF 8	3	48.3					-3.8	49.9					24.3	10.6			6.11
EMVG 2	2	85.6	56.9	88.5	39.0	39.4	-26.7	75.0	49.2	92.4	38.4	29.9	4.1	25.1	64.2	1.33	5.42
MSNM 27	2		74.4		51.8	53.2	3.9		68.0		52.7	43.2	20.4	13.1			
MSNM-V 2856	1	71.9	52.6	86.4	34.6	38.6	9.0	72.4	48.1	96.0	34.0	32.5	20.6	20.0	53.9	1.35	5.45
MSNM-V 7012		78.4	49.9	104.1	39.3	30.6	3.3	73.6	47.6	100.9	36.8	30.2	28.4	12.0	50.5	1.55	9.50
MSNM-V 7073	2	47.9	36.3		28.3	22.9	-11.5	53.0	30.5	119.0	26.4	15.1	38.0	7.3			9.39
MBS 319		57.9	46.3	75.9	28.6	35.8	0.6	58.6	45.4	78.4	28.6	34.9	14.5	13.2	41.5	1.40	5.46
NS 43-311		49.7	35.1	93.7	25.0	24.1	-11.4	49.7	34.0	91.2	24.3	23.5	23.9	17.7	42.4	1.16	5.29
MUSE 7086	2	73.0	52.3	85.8	37.0	35.4	28.2	70.2	51.4	94.1	37.8	32.1	29.5	13.5	50.7	1.49	6.76
	3	65.0	39.2		20.0	28.4	13.7	56.6	41.6	77.6	23.8	32.0	17.5	16.3	50.8		6.63
UGKU C-8		39.1	31.7	75.9	19.9	24.2	-15.1	38.0	26.9	96.1	17.2	20.0	16.8	10.2	26.7	1.41	6.99
UGKU 1803		68.9	53.4	80.5	34.4	40.8	-3.5	67.2	46.7	92.0	33.6	32.5	24.8	17.7	51.6	1.33	5.79
UGKU 1820	1	79.5	55.7	89.8	39.1	39.1	4.8	83.3	52.4	106.6	41.1	32.1	22.4	6.3	46.0	1.79	6.79
UGKU 1823		64.7	47.7	84.6	32.3	34.3	7.2	63.5	39.8	105.5	31.5	23.2	10.0	9.7	41.7	1.55	6.96
UGKU 1825	1	73.6	54.0	83.8	36.1	40.0	-3.8	75.0	53.5	88.1	37.3	38.4	15.0	9.4	47.3	1.55	8.08
CDUE 357		33.7	37.3		29.8	22.3	-7.0	38.3	32.0	75.6	18.5	25.0	20.0	9.3			5.11

Tab. 3 - Ichnological parameters of trackways. Sp= specimen, TR= trackway, p= pes, m= manus, SL= stride length, PL= pace length, PA= pace angulation, LP= length of pace, PW= width of pace, DIV= divarication from midline (inward positive, outward negative), Dmp= distance manus-pes, BL= calculated body length. Metrical measures in mm, angular measures in degrees, values on average.

The material from France is difficult to compare because *Erpetopus* is often assigned to *Varanopus curvidactylus* or, after Gand & Durand (2006), to *Microsauropus acutipes* (see above), without giving a figure or description. Haubold & Lucas (2001), identified and figured some French specimens as *Erpetopus*. Unless the material is not properly described and the assignment to *Erpetopus* (*Microsauropus*) or *Varanopus* sufficiently discussed, we suppose that it might be either attributed to *Erpetopus willistoni* or *E. cassinisi*. The

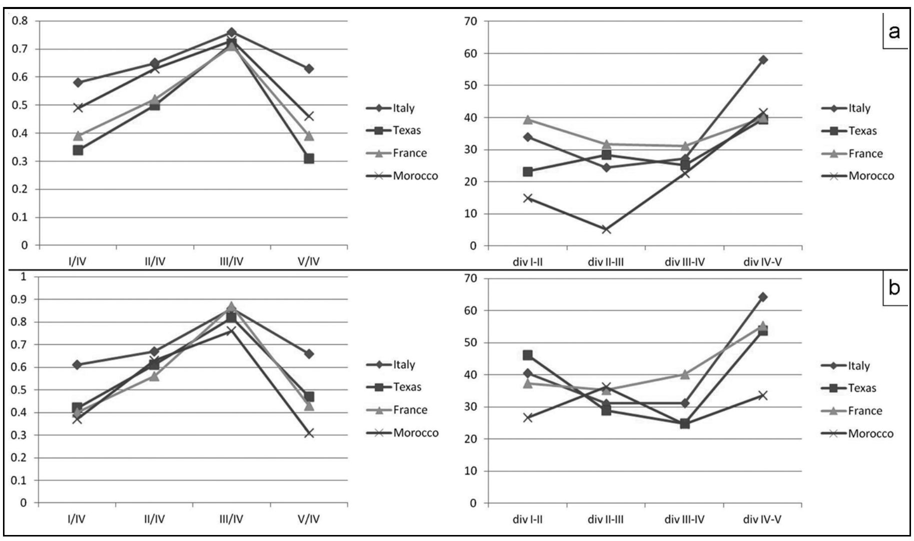

Fig. 6 - Relative length of digits I, II, III, V respect to digit IV and digit divergences (div). Comparison between specimens of *E. cassinisi* (Italy) and *E. willistoni* (Texas, France, Morocco). a) Measures relative to the pes. b) Measures relative to the manus. Angular measures in degrees, values on average.

Sp	TR	I/IV	II/IV	III/IV	V/IV	I/IV	II/IV	III/IV	V/IV
		p	p	p	p	m	m	m	m
MBG 12465	1	0.54	0.59	0.72	0.77	0.62	0.56	0.74	0.64
	2	0.50	0.70	0.83	0.44	0.83	0.63	0.67	
	3	0.72	0.79	0.77	0.73	0.80	0.82	0.90	0.94
	4					0.57	0.54	0.67	0.57
	5	0.60	0.66	0.84	0.46	0.72	0.77	1.03	0.36
MBG 12480		0.42	0.50	0.66	0.63	0.54	0.66	0.85	0.44
MBG-PF 8	3	0.62	0.68	0.83	0.59	0.68	1.05	1.09	1.14
EMVG 2	2	0.50	0.60	0.72	0.56	0.49	0.79	0.85	0.56
MSNM 27	2	0.47	0.74	0.91	0.58	0.45	0.75	0.93	
MSNM-V 2856	1	0.46	0.62	0.87	0.51	0.43	0.50	0.72	0.55
MSNM-V 7012		0.44	0.31	0.58	0.43	0.31	0.57	0.78	0.73
MSNM-V 7073	2	0.61	0.56	0.76	0.57	0.57	0.76	0.84	0.70
MBS 319		0.47	0.60	0.83	0.57	0.64	0.65	0.83	0.57
NS 43-311		0.48	0.61	0.80	0.80	0.52	0.81	1.31	0.64
MUSE 7086	2	0.80	0.75	0.71	0.65	0.62	0.67	1.13	0.64
	3	0.76	0.76	0.86	0.69	0.83	0.58	0.80	0.63
UGKU C-8		0.36	0.45	0.73	0.35	0.43	0.60	0.85	0.54
UGKU 1803		0.32	0.53	0.77	0.30	0.40	0.57	0.72	0.38
UGKU 1820	1	0.34	0.50	0.68	0.31	0.48	0.69	0.99	0.53
UGKU 1823		0.36	0.58	0.78	0.30	0.34	0.47	0.62	0.47
UGKU 1825	1	0.40	0.49	0.68	0.42	0.43	0.60	1.00	0.35
CDUE 357		0.53	0.68	0.82	0.46	0.37	0.63	0.76	0.31

Tab. 4 - Relative length of digits I, II, III, V respect to digit IV. Sp= specimen, TR= trackway. p= pes, m= manus. Values on average.

studied material (UGKU 1823, 1825) suggest some features similar to *E. cassinisi* (footprints wider than long, high total divergences), but the pes digit V is short as digit I, as in *E. willistoni* (Fig. 6, Tab. 1-4).

The material from Morocco has been described by Hminna et al. (2012). Unfortunately, specimens and trackways are few, more material is needed to draw reliable conclusions. The studied specimen CDUE 357 shows features closer to *E. willistoni*, as the short pes digit V, footprints long as wide and low digit divergences (Fig. 6, Tabs 1-4).

Conclusions

The separation between *E. willistoni* and *E. cassinisi* is justified. The former is characterized by a short digit V (as long as digit I with the digit V/IV ratio being 0.36) which is less curved outward; the pes shows a divergence of digits IV and V of about 40° and of digits I and V of 125°. Instead the latter shows a slightly longer digit V (as long as digit II with the digit V/IV ratio being 0.63) which is curved backward; the divergence between digits IV and V is 58°, that of digits I and V 146°. Values on average. All other characters seem to correspond. A separation of the two ichnospecies within a single ichnogenus (as proposed by Santi 2007) is followed here. Furthermore, we consider *E. cassinisi* as a new combination according to the congruence with the diagnostic features of the ichnogenus *Erpetopus.*

E. cassinisi appears to be a local ichnotaxon (as supposed by Santi & Krieger 2006).

A future task would be to explain the possible coexistence of the two ichnospecies in the Alps. *E. cassinisi* hypothetically reflects an adaptation to restricted conditions in the small Orobic and Collio basins by a higher mobility of digit V.

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