Tracking ‘transitional’ diadectomorphs in the earliest Permian of equatorial Pangea (#89220)

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Tracking ‘transitional’ diadectomorphs in the earliest Permian of equatorial Pangea

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Diadectomorpha was a clade of large-bodied stem-amniotes or early-diverging synapsids that established a successful dynasty of late Carboniferous to late Permian high-fiber herbivores. Asides from their fairly rich record of body fossils, diadectomorphs are also well-known from widely distributed tracks and trackways referred to as *Ichniotherium*. Here, we provide detailed description of a diadectomorph trackway and a manus-pes couple originating from two different horizons in the Asselian (lowermost Permian) of the Boskovice Basin in the Czech Republic. The specimens represent two distinct ichnotaxa of *Ichniotherium*, *I. cottae* and *I. sphaerodactylum*. Intriguingly, the *I. cottae* trackway described herein illustrates a ‘transitional’ stage in the posture evolution of diadectomorphs, showing track morphologies possibly attributable to a *Diadectes*-like taxon combined with distances between the successive manus and pes imprints similar to those observable in earlier-diverging diadectomorphs, such as *Orobates*. In addition, this trackway is composed of 14 tracks, including six well-preserved manus-pes couples, and thus represents the most complete record of *Ichniotherium cottae* described to date from the Asselian strata. In turn, the manus-pes couple, attributed here to *I. sphaerodactylum*, represents only the second record of this ichnotaxon from the European part of Pangea. Our study adds to the diversity of the ichnological record of Permian tetrapods in the Boskovice Basin which had been essentially unexplored until very recently.

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Abstract. Diadectomorpha was a clade of large-bodied stem-amniotes or early-diverging synapsids that established a successful dynasty of late Carboniferous to late Permian high-fiber herbivores. Asides from their fairly rich record of body fossils, diadectomorphs are also well-known from widely distributed tracks and trackways referred to as *Ichniotherium*. Here, we provide detailed description of a diadectomorph trackway and a manus-pes couple originating from two different horizons in the Asselian (lowermost Permian) of the Boskovice Basin in the Czech Republic. The specimens represent two distinct ichnotaxa of *Ichniotherium*, *I. cottae* and *I. sphaerodactylum*. Intriguingly, the *I. cottae* trackway described herein illustrates a 'transitional' stage in the posture evolution of diadectomorphs, showing track morphologies possibly attributable to a *Diadectes*-like taxon combined with distances between the successive manus and pes imprints similar to those observable in earlier-diverging diadectomorphs, such as *Orobates*. In addition, this trackway is composed of 14 tracks, including six well-preserved manus-pes couples, and thus represents the most complete record of *Ichniotherium cottae* described to date from the

Asselian strata. In turn, the manus-pes couple, attributed here to *I. sphaerodactylum*, represents only the second record of this ichnotaxon from the European part of Pangea. Our study adds to the diversity of the ichnological record of Permian tetrapods in the Boskovice Basin which had been essentially unexplored until very recently.

Keywords: Diadectomorpha, *Ichniotherium*, footprints, Permian, Boskovice Basin, Czech Republic.

Introduction

Diadectomorpha was a widely distributed clade of large-bodied stem-amniotes (Panchen and Smithson 1988, Laurin and Reisz 1997, 1999) ~~or perhaps early-diverging synapsids (Berman 2000, 2013, Marjanović and Laurin 2019, Klembara et al. 2019, Clack et al. 2022)~~ that originated in the Carboniferous (see, e.g., Voigt and Ganzelewski 2010), flourished in late Pennsylvanian and Cisuralian (late Carboniferous and early Permian; e.g., Berman and Sumida 1990, Berman et al 1992, 1998, 2004), and died out in or shortly after the Wuchiapingian (early late Permian; Liu and Bever 2015). Owing to their phylogenetic placement and recognition as one of the earliest tetrapod lineages to evolve high-fiber herbivory (e.g., Beerbower et al. 1992; Hotton et al. 1997, Sues 2000), diadectomorphs are significant contributors to our understanding of the amniote origins and the structure of land ecosystems in the late Paleozoic.

Asides from their fairly abundant body-fossil record, diadectomorphs are also well-known from their fossil tracks and trackways. Three ~~separate~~ ichnotaxa associated with diadectomorph trackmakers are currently ~~being~~ distinguished: *Ichniotherium praesidentis*, *Ichniotherium sphaerodactylum*, and *Ichniotherium cottae*. Among these, *I. praesidentis* is the oldest and rarest morphotype, being only known from the Westphalian A (Moscovian, mid-Pennsylvanian) of Bochum Formation, Germany (Voigt and Ganzelewski 2010); *I. sphaerodactylum* has been reported from the Gzhelian (uppermost Carboniferous) to Artinskian (lower Permian) of Arizona (Francischini et al. 2019), Canada (Brink et al 2012), Germany (Voigt et al. 2007), and Morocco (Voigt et al 2011); and *I. cottae*, the most common and abundant of the ichnotaxa, is known from the Moscovian (upper Carboniferous) to Artinskian of the Czech Republic (Hochstetter 1868, Frič 1887, Calábková and Nosek 2022), France (Mujal and Marchetti 2020), Germany (Voigt and Haubold 2000, Voigt 2005), Great Britain (Haubold ~~H.~~ Sarjeant 1974), Morocco (Lagnaoui et al.

2018), Poland (Voigt et al. 2012), and Colorado (Voigt, Small & Sanders, 2005), New Mexico (Voigt and Lucas 2015), and Ohio (Baird, 1952) in the United States.

Here, we describe a trackway and a manus-pes couple representing two diadectomorph ichnotaxa, *I. cottae* and *I. sphaerodactylum*, respectively. No body-fossil remains of diadectomorphs have been discovered in the Czech Republic so far. However, the presence of tracks ascribed to *I. cottae* has previously been mentioned ~~to derive~~ from two units in the Czech Republic, including the Boskovice Basin (Hochstetter 1868, Calábková and Nosek 2022) and the Krkonoše Piedmont Basin (Frič 1887). Nevertheless, these reports were brief and did not assess the material in detail. In turn, *I. sphaerodactylum* has not been described from the Czech Republic before and, in fact, represents only the second record of this ichnotaxon from the European part of Pangea, the first being from Germany (Voigt et al. 2007).

The material described herein ~~originates~~ from two localities, Čebín and Zbýšov, situated at different horizons in the Asselian (lowermost Permian) of the Boskovice Basin. From the viewpoint of tetrapod fossil record, the lowermost Permian strata of the Boskovice Basin have long been renowned for materials of taxa inhabiting aquatic environment, including extraordinarily abundant specimens of discosauriscid seymouriamorphs (e.g., Špinar 1952, Klembara 1995, 2005, 2016) and rare temnospondyls (Augusta 1947, Milner et al. 2007, Klembara and Steyer 2012, Werneburg et al. 2023). However, recent fieldwork conducted in the basinal strata at several localities provided diverse assemblages of tetrapod footprints which fundamentally enriches our knowledge of the tetrapod biodiversity in the Permian terrestrial settings in this area, revealing the presence of large-bodied seymouriamorphs (Calábková et al. 2022), early-diverging synapsids (Calábková et al. 2023), and now two distinct diadectomorphs.

We provide detailed description of the *Ichniotherium* material from the lowermost Permian of the Boskovice Basin, illustrate it through image-based modeling, and assess its potential trackmakers' affinities using multivariate analyses.

Institutional abbreviations. ~~Czech Republic;~~ MZM, Moravian Museum, Brno, Czech Republic; PM, Podhorácké Museum in Předklášteří, Czech Republic.

Material and methods

Material

This study is based on two specimens: PM PAL113, housed at the collections of the Podhorácké Museum in Předklášteří, Czech Republic, and MZM Ge33302, deposited in the Moravian Museum, Brno, Czech Republic. The specimen PM PAL113 comprises a trackway of *Ichniotherium cottae* tracks preserved in a fine-grained sandstone showing desiccation cracks. PM PAL113 originates from Čebín, a locality that is situated in the lower section of the Letovice Formation of Asselian age. In turn, the specimen MZM Ge33302 comprises a manus-pes couple attributable to *Ichniotherium sphaerodactylum.* The couple is preserved in a fine-grained sandstone discovered at Zbýšov that is situated in the upper section of the Padochov Formation (Asselian). MZM Ge33302 is therefore slightly older than PM PAL113 (see Calábková et al 2022, fig. 1)

Both specimens are preserved in reddish strata of fine alluvial floodplain deposits (Šimůnek and Martínek 2009). For more detailed accounts of the geological and stratigraphic setting of the tracks and trackways from the Boskovice Basin see Calábková et al. (2022), Calábková et al. (2023).

PM PAL113 has been part of the paleontological collections of the Podhorácké Museum in Předklášteří since the first half of the 20th century; MZM Ge33302 was found by Tomáš Viktorýn during fieldwork conducted in 2022. Both samples are preserved as convex hyporelief.

Anatomical terminology and measurements

The anatomical terminology and protocol for obtaining measurements follow those of Leonardi (1987) and Buchwitz and Voigt (2018). Measurements were obtained using a digital caliper and ImageJ.

Multivariate analyses

In order to reconstruct the morphospace occupation of PM PAL113 among diadectomorph trackways we utilized the parameters published by Buchwitz et al. (2021; Supplementary Table 2), Buchwitz and Voigt (2018; average values from measured step cycles of specimen Kletno No.1 and Marieta_NA; supplementary 3 and 4), and Mujal and Marchetti (2020; average values of trackway 1 of MNHN-LOD 83; table 1 and 2), added data obtained from PM PAL113, and performed a principal component analysis (PCA) using PAST 4.12b (Hammer et al. 2001). Prior to the analysis, all raw continuous variables were z-transformed. The original values and z-scores, and the extended results of the PCA, are provided in Supplemental Material I. A .dat file, executable in PAST, is provided in Supplementary Material II.

Image-based modeling

The protocol for three-dimensional (3D) modeling of the studied samples follows that of Porter et al. (2016). We first took 100 photographs of PM PAL113 and MZM Ge33302, each of them in

two elevation positions to fully cover the surface of the samples, using a full frame camera Nikon D750 (lens Tamron 24–75 mm, F2.8). Obtained images were then utilized to reconstruct 3D photogrammetric models through Agisoft Metashape PRO 1.8. The procedure was complemented with scans using the geo-referenced marker grid matrix as it provides a greater precision (and automation of the reconstruction process) than usual geo-referencing of models through one or more scale bars. All models have been reconstructed in the highest possible quality to the final resolution of 3.5 million polygons. Resulting 3D models were visualized and interpreted through CloudCompare 2.10 and Blender 3.0.Three-dimensional models (in the form of meshes) obtained from physical samples using the Structure from Motion method were uploaded to the MorphoSource data archive: https://www.morphosource.org/projects/000546695/temporary_link/9ST98qSfqvYwG6J1Bg3N9HSu?locale=en

Systematic paleoichnology

Diadectomorpha Watson, 1917

Ichniotherium Pohlig, 1892

Ichniotherium cottae (Pohlig, 1885)

Material. PM PAL113, a trackway composed of 14 tracks and including 6 manus-pes couples (Fig. 1A-C).

Locality and horizon. Čebín, South Moravian Region, Czech Republic; upper section of the Letovice formations, Asselian, lowermost Permian, Boskovice Basin.

151

152 **Description and comparisons**

153 The manus and pes imprints are plantigrade and pentadactyl. The pes imprints (104.6 mm long)
154 are larger than the manus imprints (76.08 mm long; Supplemental Material I). The pes imprints
155 are as wide as long, whereas the manus imprint is slighter wider than long. The pedal digit imprints
156 are ~~rather~~ straight, and the manual digits II-IV are often slightly turned inwardly. The digit imprints
157 show typical rounded "drumstick-like" terminations and digital flexure creases. The digit lengths
158 increase from digit I to IV, and the digits V are slightly shorter or the same sized as digits II. The
159 ratio pV/pIV is 0.59. The palm and sole impressions are wider than long. The sole and the palm
160 impressions form elliptical to subcircular shapes lying mostly opposite to digits II – III in the
161 manus, and digits I-IV in the pes imprints. The tracks show the medial-median functional
162 prevalence. The trackway shows an alternating arrangement of successive manus and pes imprints.
163 The overstepping does not occur. The particular trackway parameters (in average values) ~~as~~
164 ~~follow~~: parallel to slightly outward rotation of the pedal imprints (-2.1°) and parallel or slightly
165 inward rotation of the manual imprints (5°) ~~to the midline~~, manual pace angulations is 83.5°, pedal
166 pace angulation is 87.4°, pedal stride length/pes length is 3.06, gauge width~~(pedal)~~/pes length is
167 1.48, pedal pace length/pes length is 2.15, manus-pes distance/pes length ratio is 1.27
168 (Supplemental Material I). All footprints are crossed by desiccation cracks.

169

170 **Remarks**

171 The specimen PM PAL113 shows all diagnostic features of *I. cottae* such as relatively short pedal
172 digit V with ratio~~n~~ pV/pIV 0.59, the palm and the sole impressions forming elliptical to subcircula~~s~~
173 shapes. The ichnospecies *Ichniotherium praesidentis* differs from the PM PAL113 because of

inverse alternating pattern of manus-pes couples, and the prominent manual basal pad I. The ichnospecies *Ichniotherium sphaerodactylum* differs from PM PAL113 with relative long pedal digit V impressions (ratio pV/pIV > 0.60), the palm impressions ~~is~~ usually not clearly delimited, the sole impressions are more extensive lying opposite digits II–V, and distal parts of digits II-IV are often more distinct bend medially. Other early Permian ichnotaxa reaching size similar to that of *Ichniotherium* include *Dimetropus* and *Limnopus*. *Dimetropus* can be clearly distinguished from PM PAL113 based on its typical proximodistally extended palm/sole impressions, deeply impressed metapodial-phalangeal pads, and relatively short and straight digit imprints with deeply impressed clawed terminations. In turn, *Limnopus* differs from PM PAL113 in having a tetradactyl manus imprint, and short, deeply impressed digits which are often not separated from the palm/sole impressions (see, e.g., Voigt 2005).

Ichniotherium sphaerodactylum (Pabst, 1895)

Material. MZM Ge33302, a manus-pes couple (Fig. 2A-C).

Locality and horizon. Zbýšov, South Moravian Region, Czech Republic; upper section of the Padochov Formation, Asselian, lowermost Permian, Boskovice Basin.

Description and comparisons

The manus and pes imprints are plantigrade and pentadactyl. The pes imprints are larger (121.5 mm long; Supplemental Material III) than the manus imprints (93.5 mm long). The manus and the pes imprints are wider than long, while the pes imprints are only slightly. The pedal digits I-III are

straight, whereas distal portions of the pedal digits IV-V are ~~turned~~ outwardly. The manual digits II-III are ~~turned~~ inwardly. The digits show typical rounded "drumstick-like" terminations. The digit length increases from digit I to IV, the pedal digit V is approximately long as the pedal digit III. The manual digit V is poorly preserved or ~~perhaps~~ not preserved at all. The pV/pIV ratio is 0.88. The palm and the sole impressions are broad and elliptical in shape. The tracks show the medial-median functional prevalence.

Remarks

Although the shape of the sole impression MZM Ge33302 is less mediolaterally expanded, the significantly long pedal digit V with the pV/pIV ratio of 0.88, the medial functional prevalence of the pes imprint, the median-medial prevalence of the manus imprint, and the less delimited broad palm impression support the assignment of the MZM Ge33302 to *I. sphaerodactylum*. The ichnotaxon *Ichniotherium praesidentis* differs from MZM Ge33302 based on an inverse alternating pattern of manus-pes couples, and a prominent manual basal pad I. In turn, *Ichniotherium cottae* differs from MZM Ge33302 in having short pedal digit V impressions (pV/pIV >0.60), and less extensive well-defined sole/palm impressions that are often clearly separated from the digit imprints.

Results of the principal component analysis

The results of the principal component analysis (PCA) show broadly overlapping morphospace occupation of trackways assigned to *I. cottae* and *I. sphaerodactylum*, that are concentrated near the center of the biplots and widely separated from a trackway assigned to *I. praesidentis*, which reflects the unique morphology and pattern of that ichnotaxon (Voigt and Ganzelewski, 2010).

In the biplots illustrating the highest percentage of variance (PC1 vs PC2 up to PC1 vs PC 5; PC1 [52.7 %], PC2 [14.1 %], PC3 [9.1 %], PC4 [6.6 %], and PC5 [4.4 %]), PM PAL113 is placed near the center of the plots; on the negative sides of the axes and near or at the overlap of the *sphaerodactylum* morphospace and *cottae* from the "Gottlob-Birkeide type" (Fig. 3A-D; Supplemental Material I). The minimum spanning tree additionally shows that PM PAL113 connects with *I. sphaerodactylum* specimens. For detailed values behind the plots and extended results of the PCA, see Supplementary Material I.

Discussion and conclusion

Trackway pattern and functional implications

Specimen PM PAL113 shows an intriguing combination of features, characterized by presence of tracks parameters diagnostic for *I. cottae* (see above) and a trackway pattern with a high distance between the successive manus and pes imprints (Fig.1A-C, Supplemental Material I). Such features are typically observable in the trackways attributed to *I. sphaerodactylum* (Fig.2A-C) and result from a relatively longer and more flexible trunk of the trackmakers and a more pronounced sprawling posture that allows a shorter stride and thus a lower maximum speed of walking (see Buchwitz and Voigt 2018). It is worth noting, however, that the high degree of sprawling was questioned in the studies by Nyakatura et al (2015) and Nyakatura et al (2019) that explored the locomotion, body mass, and joint mobility of *Orobates pabsti* (using a 3D skeletal reconstruction and *I. sphaerodactylum* tracks), concluding that the *Orobates* movement was relatively erect, balanced, and mechanically power-saving in comparison to earlier tetrapods (Nyakatura et al 2019). Nevertheless, contrary to the condition observable in trackways assigned to *I.*

sphaerodactylum, PM PAL113 shows a lower degree of the inward orientation of the manus and pes imprints, shorter pace length, and a narrower gauge.

The higher distance between the successive manus and pes imprints has been observed in several other specimens attributed to *I. cottae*; these include a specimen from the Gzhelian (uppermost Carboniferous) of the Pittsburgh Formation, Ohio (see Buchwitz et al 2021), included in the "Hainesi-Willsi type" by Buchwitz and Voigt (2018); specimen from the Asselian–Sakmarian (lower Permian) of the Gottlob locality in Thuringia, Germany, included in the "Gottlob-Birkeide type" by Buchwitz and Voigt (2018); and specimen from the Asselian (lowermost Permian) of the Lunas locality, France (Mujal and Marchetti 2020). However, the late Carboniferous "Hainesi-Willsi type" of *I. cottae* shows a distinct outward rotation of the pedal imprints which occurs also in the ~~most archaic~~ *Ichniotherium* tracks referred to as *I. praesidentis* that are Moscovian (middle late Carboniferous) in age (Buchwitz and Voigt 2018). Thus, it differs from PM PAL113 as well as majority of younger *Ichniotherium* ichnotaxa significantly (see Fig 3A-D).

A gradual change of the manus and pes imprint orientation in the *Ichniotherium* trackways has already been observed by Buchwitz and Voigt (2018) who provided detailed description of the evolution of diadectomorph locomotion based on the succession of trackmakers of the "Hainesi-Willsi type" (Moscovian–Gzhelian; middle-upper upper Carboniferous), the "Birkheide-Gottlob type" (Asselian–Sakmarian; lower lower Permian), and the "Bromacker type" (Sakmarian–Artinskian; middle lower Permian). The appearance of these trackways (assigned to *I. cottae*) has been interpreted to exhibit a tendency towards trunk shortening combined with decreasing of its flexibility, narrowing of the sprawling posture, and progressively inward orientation of the manus in the touch-down phase. Such modifications resulted in a higher maximum speed of walking and a higher efficiency of land movement. The youngest "Bromacker type" with its typically

265 'complete' overstepping of the manus-pes couples, the most pronounced inward rotation of the
266 manus and the pes impressions, most obtuse pace angulation, narrowest gauge, and significantly
267 higher pace and stride lengths differs from all of older *Ichniotherium* trackways, including PM
268 PAL113 (Fig 3A-D)
269
270 ***The identity of the trackmaker of PM PAL113***
271 Buchwitz and Voigt (2018) interpreted the morphotypes of *I. cottae* to have been registered by
272 later-diverging representatives of Diadectidae, such as *Desmatodon*, *Diasparactus*, and *Diadectes*.
273 In turn, the nearly complete skeleton of *Diadectes abitus* found at Bromacker was used to correlate
274 the taxon with the "Bromacker type" of *I. cottae* (see Voigt et al. 2007). The trackmaker of PM
275 PAL113 shows a slightly outward to parallel-oriented pedal imprints, parallel to slightly inward-
276 oriented manual imprints, short length of stride and pace, lower pace angulation but narrower
277 gauge and short pedal digits V (Supplemental Material I). These features closely resemble those
278 observed in the "Birkheide-Gottlob type" which may be associated with *Diadectes*-line diadectids
279 (see Buchwitz and Voigt 2018, fig 18). However, unlike the "Birkheide-Gottlob type" trackways,
280 PM PAL113 also shows an unusually high manus-pes distance. Such condition is fundamentally
281 distinct from that typically observed in trackways registered by *Diadectes* (e.g., the "Bromacker
282 type") and instead resembles trackways referred to as *I. sphaerodactylum* which are commonly
283 attributed to earlier-diverging diadectids, such as *Orobates* found at the Bromacker locality (Voigt
284 et al., 2007; Buchwitz and Voigt, 2018), or perhaps early-diverging diadectomorphs in general,
285 such as *Limnoscelis*, which shares with *Orobates* the same phalangeal formula (2-3-4-5-3 for the
286 manus and 2-3-4-5-4 for the pes) and differs from *Diadectes* that shows the same phalangeal
287 formula (2-3-4-5-3) in both, the manus and the pes (Voigt et al., 2007; Kennedy, 2010). These taxa

288 are characterized by a slightly higher number of presacral vertebrae (21 in *Diadectes abitus*, 23 in
289 *Limnoscelis paludis*, 26 in *Orobates pabsti* [Berman and Henrici 2003; Voigt et al 2007; Kennedy
290 2010]) and, thus, more elongated trunks. The combination of features captured in PM PAL113 is
291 also well depicted through the results of our PCA (PC1 vs PC2 up to PC1 vs PC5) where the
292 specimen fall within the overlap of the morphospaces occupied by *I. cottae* and *I. sphaerodactylum*
293 tracks (Fig. 3A-D). Owing to the fact that the propodial-to-epipodial proportions in *Orobates* and
294 *Diadectes* were near-identical (see Voigt et al. 2007), the differences in diadectomorph trackway
295 pattern might additionally stem from differing body mass and limb joint mobility which also
296 largely determine the mode of locomotion (see i.e. Nyakatura et al 2015, 2019).
297
298 ***The significance of MZM Ge 33302 and the identity of its trackmaker***
299 The manus-pes couple of MZM Ge33302 with the relatively longer pedal digit V (pV/pIV ratio =
300 0.88) attributed to *I. sphaerodactylum* represents only the second specimen of this ichnotaxon from
301 the European part of Pangea. Owing to the morphology of the tracks, the manus-pes couple has
302 been likely registered by an *Orobates*-like or perhaps a *Limnoscelis*-like taxon. Interestingly,
303 *Limnoscelis* was also associated with tracks from the Asselian of the Lunas locality in France that
304 were referred to *I. cottae*. This association has originally been based on a high pV/pIV ratio of the
305 Lunas tracks (Mujal and Marchetti 2020). However, the high ratio most likely stemmed from an
306 error in the obtained measurements, caused by poor preservation of the tracks (Mujal, pers.
307 communication 2023).
308 The medial functional prevalence of manual digits I–III, as observed in MZM Ge33302, is also
309 present in the Lunas specimens. Such condition has been associated by Mujal and Marchetti (2020)
310 with plesiomorphic features of basal diadectomorph feet.

Despite that it is impossible to associate a single manus-pes couple with a certain diadectomorph taxon, especially without any associated skeletal record in the Boskovice Basin, MZM Ge 33302 has been clearly registered by an earlier-diverging member of the clade than PM PAL113. Thus, there have been at least two distinct diadectomorphs in the Asselian (earliest Permian) equatorial ecosystem of what is today the Boskovice Basin in the Czech Republic.

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Fig. 1. Trackway of *Ichniotherium cottae*, PM PAL113, convex hyporelief. Image-based modeling of whole slab (A) and the trackway (B). Outline drawing (C).

Fig. 2. Manus-pes couple of *Ichniotherium sphaerodactylum*, MZM Ge33302, convex hyporelief. Photo (A), image-based modeling (B) and outline drawing (C).

Fig. 3. Results of the principal component analysis (PCA). The morphospace occupation of *Ichniotherium* trackways (A, C) and the minimum spanning tree (B, D) along PC 1 vs PC2 (A, B) and along PC1 vs PC3 (C, D).

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Figure 1

Trackway of *Ichniotherium cottae*, PM PAL113, convex hyporelief.

Image-based modeling of whole slab (A) and the trackway (B). Outline drawing (C).

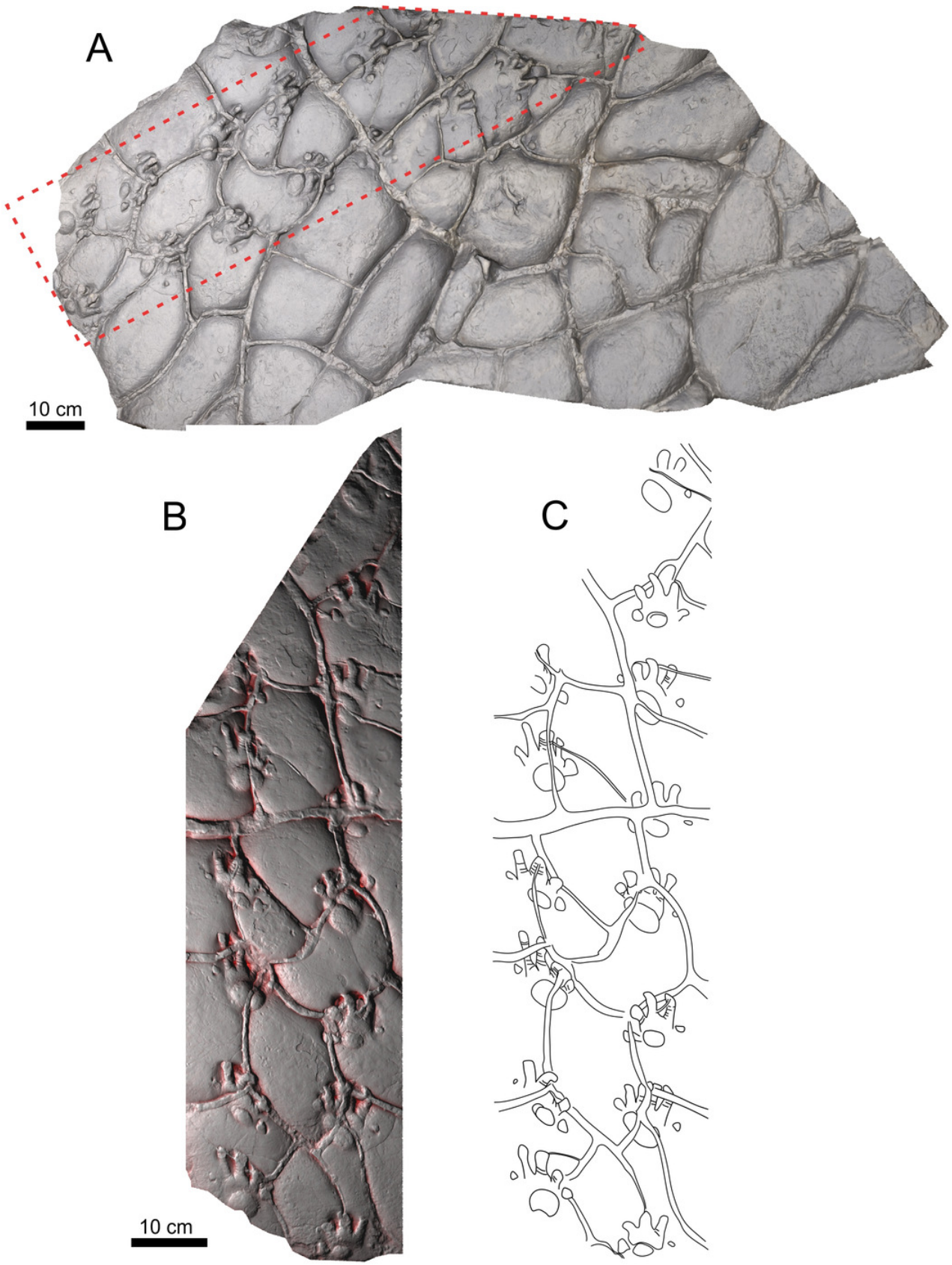
A
10 cm
B
10 cm
C

Figure 2

Manus-pes couple of *Ichniotherium sphaerodactylum*, MZM Ge33302, convex hyporelief.

Photo (A), image-based modeling (B) and outline drawing (C).

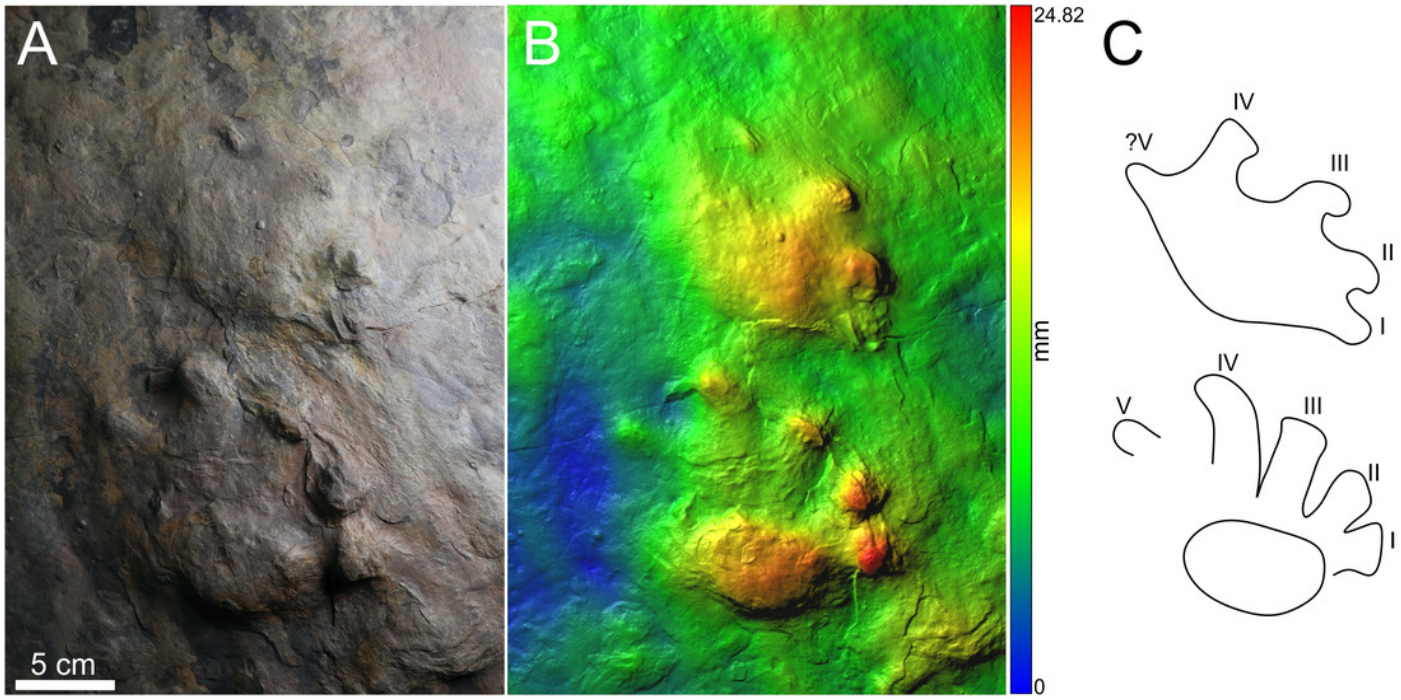

Figure 3

Results of the principal component analysis (PCA).

The morphospace occupation of *Ichniotherium* trackways (A, C) and the minimum spanning tree (B, D) along PC 1 vs PC2 (A, B) and along PC1 vs PC3 (C, D).