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EARLY PERMIAN DIADECTOMORPH TETRAPOD FOOTPRINTS FROM THE BROMACKER LOCALITY (THURINGIA, GERMANY) IN THE NATIONAL MUSEUM PRAGUE

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Abstract: The Bromacker locality in Thuringia, Germany is world famous for its exceptionally well-preserved early Permian tetrapod footprints. In this paper, we provide the first detailed description of the Bromacker specimen with diadectomorph footprints that was donated to the National Museum Prague in 1916. The specimen shows more than 80 footprints of six trackways and several incomplete step cycles of different morphological qualities assigned to the ichnotaxon *Ichniotherium sphaerodactylum*. Apart from its paleoichnological value, the slab is of historic interest as it fits into a long period of about five decades (1908 to 1954) from which there is almost no information on fossil discoveries at the locality.

Key words: *Ichniotherium*, Diadectomorpha, fossil trackways, Bromacker locality, Tambach Formation

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Introduction

The Bromacker locality refers to an area containing several abandoned sandstone quarries near the village Tambach-Dietharz in the district of Gotha, in Thuringia, Germany. It represents one of the most important sites for early Permian tetrapod ichno- and body fossils in the world (Pabst 1908, Eberth et al. 2000, Voigt et al. 2007, Martens 2018). Fossil footprints from the Bromacker were first recognized in 1887 and shortly after assigned to the ichnogenus *Ichniotherium* Pohlig, 1892 (Pabst 1895). Wilhelm Pabst, a teacher at the Gotha secondary school and later curator of the natural scientific collection of Herzogliches Museum Gotha, was the first who studied the Bromacker tetrapod footprints in detail (Martens 1994). He offered a large number of sandstone slabs with tetrapod tracks to museums and private persons around the world (Text-fig.1) to raise funds for extensive research at the Bromacker locality (Voigt 2002). According to Pabst's original documentation, the first footprint slab was sold in 1896. The sale probably continued after Pabst's death in 1908, but there is no record of specific customers and a lack of scientific publication on new finds for almost fifty years between 1908 (Pabst 1908) and 1954 (Müller 1954).

Here we present a hitherto undescribed slab with numerous diadectomorph tetrapod footprints assigned to the ichnospecies *Ichniotherium sphaerodactylum* (Pabst, 1895) which had been donated to the National Museum Prague in 1916. The slab must have been discovered between 1908 and 1916 and thus represents a very rare specimen as it is from the historically "dark period" of the Bromacker locality during which the site was publicly accessible. A detailed description of diadectomorph tracks and trackways, their taphonomic evaluation and the history of the specimen itself are the main topic of this work.

Geology

The Bromacker locality correlates with the Tambach Formation which is an up to 280 m thick succession of alluvio-fluvial red-beds deposited in a small graben called the Tambach Basin (Lützner 1981, Martens et al. 1981, Lützner et al. 2012). All tetrapod footprints as well as tetrapod skeletal remains come from the uppermost middle part of the Tambach Formation known as the Tambach Sandstone (Eberth et al. 2000, Voigt et al. 2007, Marchetti et al. 2018). The fossil-bearing section at the Bromacker locality is about 10 m thick and subdivided into a lower part

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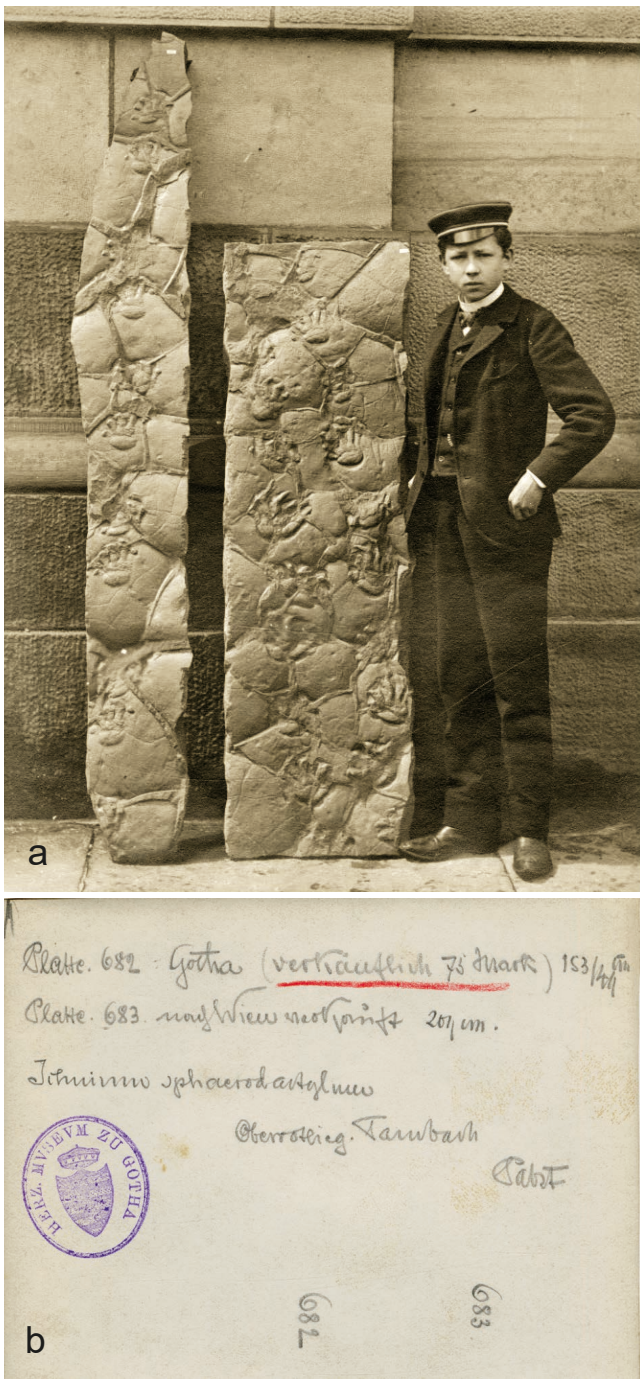


Text-fig. 1. a) Photo of two slabs with *Ichniotherium sphaerodactylum* trackways described by W. Pabst; b) Back side of the same photo. The right slab (no. 682) was for sale for 75 marks, and the left one (no. 683) was sold to Vienna. Archive NMP, NAD 220, cart. no. 15.

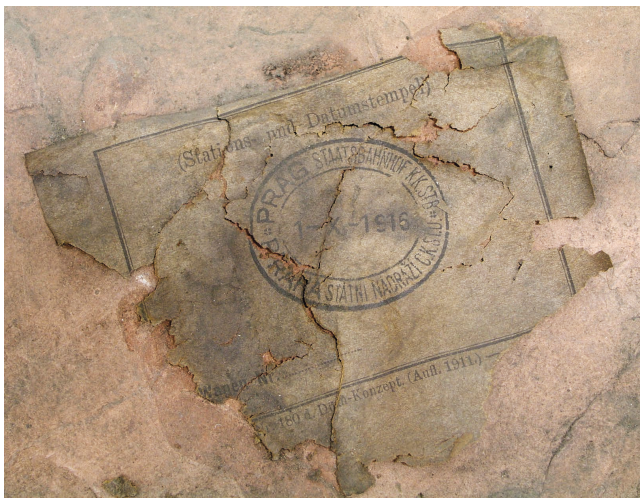
and upper part. The lower part consists of fine- to medium-grained massive to laminated or cross-bedded sandstone with mud-drapes and abundant tetrapod and invertebrate traces. Tetrapod skeletal remains as well as invertebrate body fossils including conchostracans, myriapods, and insects are preserved in massive to laminated fine-grained sandy to pebbly mudstones of the upper part of the section. The paleoenvironment is interpreted to be a fluvial plain with episodic flooding (Eberth et al. 2000). Common mud cracks indicate at least a seasonally dry climate. Cycles of flooding and evaporation probably lasted days to months, and thus provided ideal conditions for the preservation of fossil tracks. The skeletal-bearing mudstones in the upper part of the section are considered to be sheet flood deposits (Eberth et al. 2000).

Tetrapod footprints from the Bromacker locality have been assigned to five ichnotaxa: *Dimetropus leisnerianus* (Geinitz, 1863), *Ichniotherium cottae* (Pohlig, 1885), *Ichniotherium sphaerodactylum* (Pabst, 1895), *Tambachichnium schmidti* Müller, 1954, and *Varanopus microdactylus* (Pabst, 1896). A sixth ichnotaxon, *Notalacerta missouriensis* Butts, 1891 was recently described (Marchetti et al. 2021). However, *I. sphaerodactylum* is by far the most abundant tetrapod ichnotaxon at the site (Voigt 2005).

In 1974, nearly a hundred years after the initial report on the discovery of fossil tetrapod tracks, the first almost complete tetrapod skeletal fossil belonging to *Diadectes absitus* Berman, Sumida et Martens, 1998 was found at this site (Martens 1980). It was the first discovery of a member of Diadectidae outside the American continent (Martens 1980, Martens 1988, Martens et al. 1981, Berman and Martens 1993, Berman et al. 1998). Other well known specimens have also been discovered at the Bromacker locality, e.g., complete or almost complete skeletons of temnospondyls (Sumida et al. 1998, Anderson et al. 2008, Berman et al. 2011), lepospondyls (Henrici et al. 2011), seymouriamorphs (Berman and Martens 1993, Berman et al. 2000a, Klembara et al. 2007), diadectomorphs (Berman et al. 1998, Berman et al. 2004), early reptiles (Boy and Martens 1991, Sumida and Berman 1997, Berman et al. 2000b, Müller et al. 2006) and synapsids (Berman et al. 2001, 2004, 2014, 2020). The body fossils from the Tambach Formation helped to determine the trackmakers of the previously found tracks with relatively high accuracy (Voigt et al. 2007, Marchetti et al. 2016).

Material and Methods

This work is based on the description of tetrapod footprint specimen NMP Sv 1001 (NMP = National Museum Prague) from the Bromacker locality of the Tambach Formation in Thuringia, central Germany. The huge slab (139 × 141 × 13.2 cm) showing more than 80 tracks, came to the museum



Text-fig. 2. Transport label affixed on the specimen NMP Sv 1001.

Table 1. Ichnological parameters of tracks and trackways of *Ichniotherium sphaerodactylum*, NMP Sv 1001. Measurements in mm and degrees.

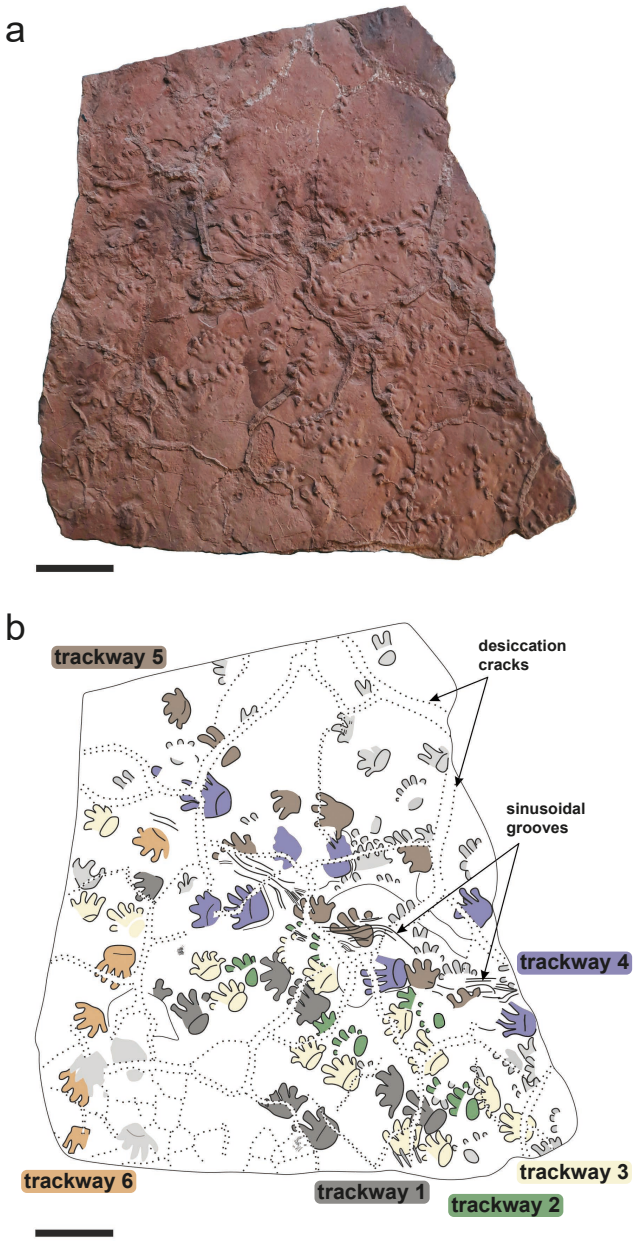
Track parameters		L	W	psL	psW	L/psL	I L	II L	III L	IV L	V L	γ I-V
trackway 1	p	105.48	-	39.82	69.45	2.65	23.88	38.82	45.95	54.54	-	-
	m	79.79	115.74	28.20	66.31	2.83	22.09	24.56	29.52	35.52	23.82	109.63°
trackway 2	p	85.18	94.12	33.94	49.45	2.51	19.68	27.92	31.82	35.73	-	74.451°
	m	-	-	-	-	-	-	-	30.65	33.55	-	-
trackway 3	p	88.89	97.76	32.73	56.13	2.72	21.62	25.27	38.79	46.98	35.64	72.04°
	m	77.44	91.84	22.47	48.52	3.45	14.82	23.05	32.75	38.18	22.55	100.32°
trackway 4	p	105.03	114.09	37.38	72.01	2.81	-	-	-	-	40.05	64.33°
	m	94.49	-	-	56.83	-	-	-	-	-	-	-
trackway 5	p	101.32	-	36.73	68.52	-	25.99	34.49	41.79	49.66	-	-
	m	80.38	108.15	23.74	48.08	3.39	21.44	31.15	32.48	37.69	29.00	106.23°
trackway 6	p	93.80	-	32.12	54.49	-	-	32.14	36.17	48.36	-	-
	m	73.83	103.24	22.9	44.44	3.22	21.83	23.74	33.93	43.03	26.18	120.96°
Trackway parameters:		SLp	SLm	A	BL	Pαp	Pαm	Pwm	Pwp	βm	SL/BL	SL/pL
trackway 1		392.54	398.12	103.29	302.35	84.56°	86.25°	225.7	226.5	37.46°	1.30	3.72
trackway 2		292.37	295,17	64.31	211.90	82.73°	-	205.10	189.72	-	1.39	3.47
trackway 3		295.91	308.43	98.63	252.85	78.74°	68.43°	209.74	192.03	24.27°	1,17	3.33
trackway 4		348.85	-	93.79	268.22	77.25°	-	230.19	232.41	19.10°	1.30	3.32
trackway 5		329.59	321,72	119.812	284.61	74.14°	77.79°	215.67	231.53	35.94°	1.16	3.25
trackway 6		296.30	274.73	127.74	275.89	-	-	-	-	-	1.07	3.16

as a donation during WWI. It was transported to the main railway station in Prague on October 1st, 1916 according to a label affixed on the front side of the slab (Text-fig. 2). The donator was Dr. Eduard Merzinger, co-owner of the Waldes push button factory (since 1939 Koh-i-noor), located in Prague-Vršovice with a branch in Dresden.

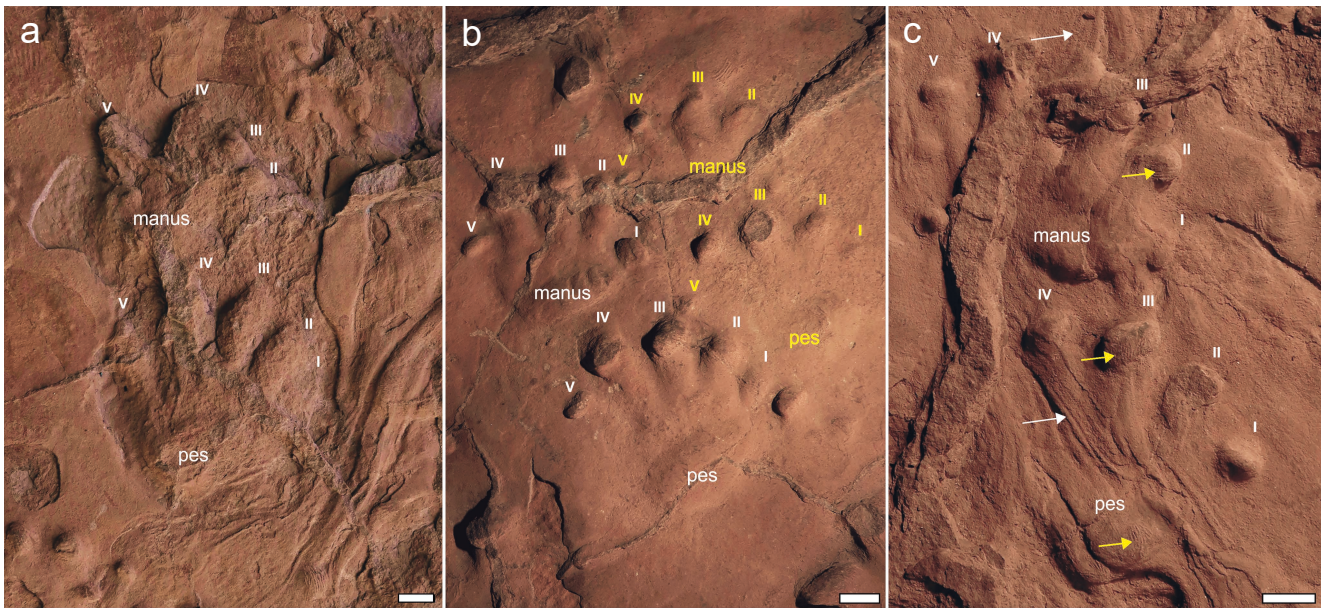
The tetrapod footprints preserved in the red-coloured fine-grained sandstone of NMP Sv 1001 have never been published before. The specimen is not mentioned in the comprehensive work on tetrapod footprints of the Bromacker locality by Pabst (1908). Therefore, we assume that the specimen was discovered at the site between 1908 and 1916, i.e., after Pabst's death in 1908. Eduard Merzinger was an Austrian businessman, who won 20,000 Austro-Hungarian krones in a lottery, which he successfully invested into the Waldes factory in 1902 and later acted as a patron of the arts as a Dresden citizen (Koh-i-noor a.s.; https://www.kin.cz/koh-i-noor/historie; accessed 9. 9. 2022). Since 1897, tetrapod footprint slabs from the Bromacker locality were sold via the Royal Saxony Mining Academy mineral shop in Freiberg near Dresden as a general contractor of the Herzogliches Museum Gotha (Voigt 2002). Merzinger's acquisition could be a first indication that the business selling Bromacker fossil tetrapod footprint slabs between the Gotha Museum and the Freiberg mineral shop continued beyond 1908. In any case, NMP Sv 1001 is the first recorded case of transportation of a specimen in later years, as Bromacker tracks were sold in great numbers around European museums mainly in the years 1895–1908 (Voigt 2002).

The protocol for obtaining track and trackway measurements on NMP Sv 1001 as well as applied footprint terminology follows Leonardi (1987). Tracks were measured using a digital caliper and the software ImageJ. Only clearly defined parameters were measured on the tracks to prevent distortion of the resulting values (Tab. 1). The images were edited in CorelDraw.

Ichnological Abbreviations – **A**, manus-pes distance; **BL**, body length; **L**, length; **m**, manus; **p**, pes; **psL**, palm/sole length; **psW**, palm/sole width; **Pw**, pace width; **Pα**, pace angulation (°); **SL**, stride length; **W**, width; **β**, deviation



Text-fig. 3. *Ichniotherium sphaerodactylum*, **NMP Sv 1001. a) Photo of the slab, convex hyporelief; b) Outline drawing. Scale bars 20 cm.**



Text-fig. 4. a) Poorly preserved manus-pes couple; b) Well-preserved (white) and shallow (yellow) manus-pes couples; c) Post-registration deformation of soft sediment (white narrow) modifying the pes imprint. Invertebrate traces left in the manus-pes couple (yellow narrows). Scale bars 2 cm.

from midline (°), positive value = inward rotation, negative value = outward rotation; **γ I–V**, interdigital angle I–V (°); **I–V L**, length of digits I–V.

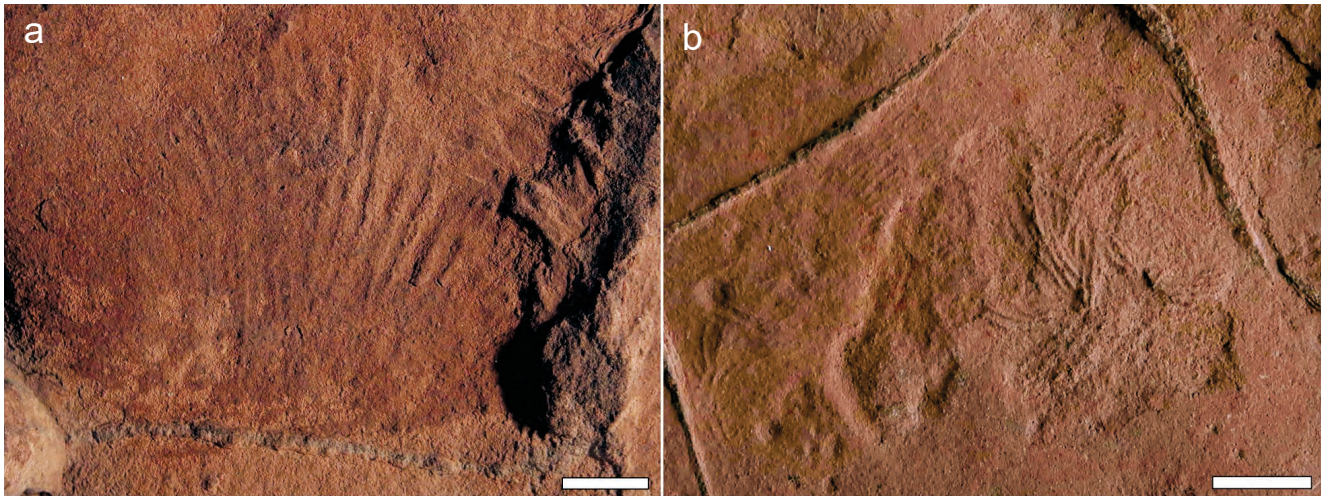
Systematic palaeoichnology

Ichnogenus *Ichniotherium* Pohlig, 1892

Ichnospecies *Ichniotherium sphaerodactylum* (Pabst, 1895)

Reference sample. NMP Sv 1001; approx. 83 footprints concentrated in 6 identified trackways and other incomplete step cycles preserved in convex hyporelief (Text-fig. 3a, b).

Description. Pentadactyl, plantigrade footprints of large sizes (73.83–105.48 mm; Tab. 1, Text-figs 3a, b, 4a–c). The pes imprints are longer than the manus imprints. The manus imprints are wider than long, and the pes imprints are almost as wide as they are long or slighter wider than long. Both the manus and the pes imprints have deeply impressed palm and sole impressions opposite to digits II–V. The palm and sole impressions are wider than long and usually forming elliptical shapes. Digit imprints are thick with oval and deeply impressed distal terminations. In both the manus and pes footprints, digits increase gradually in length from I to IV. The pedal digits V are as long as digits III, whereas the manual digits V are more similar in length to digits II. The pV/pIV ratio of trackway 3 is 0.76. The manual digits II–IV are often bent inwards. The manus imprints are usually turned inward, whereas the pes imprints are parallel to slightly inward to the midline. Trackway patterns show simple alternating arrangements of coupled manus-pes imprints. The manus and pes imprints show medial-median functional prevalence where the pedal digit V impressions are often missing. The body lengths of the individuals are in the ranges of 275.89–302.35 mm. The SL/L ratios are



Text-fig. 5. Invertebrate traces. a) *Striatichnium bromackerense*; **b)** *Tambia spiralis*. **Scale bars 1 cm.**

between 3.16 and 3.72 and the SL/BL ratios are between 1.07 and 1.39. The pace angulations are 77.79–86.25° for the pes imprints, and 74.14–84.56° for the manus imprints (Tab. 1).

Remarks. The footprints on specimen NMP Sv 1001 with their typical features such as relatively long pedal digit V (pV/pIV > 0.6), broad and deeply impressed sole opposite to digits II–V, alternating arrangement of the manus-pes couples and deeply impressed digits II–III enable the assignment to *Ichniotherium sphaerodactylum*. In contrast to *I. cottae*, the specimen NMP Sv 1001 has longer digit V, broader and more elliptical sole and palm impressions, and a relatively lower SL/BL ratio. Another valid ichnospecies *I. praesidentis* (Schmidt, 1956) has an inverse alternating arrangement of manus-pes couples and a prominent digit I basal pad on the manus imprint (see Voigt and Ganzelewski 2010: fig. 1e) which clearly differ from specimen NMP Sv 1001.

The sandstone slab also preserved the typical polygonal desiccation cracks that cross and modify some of the *Ichniotherium* footprints (Text-fig. 3a, b). Further, the tetrapod footprints are accompanied by invertebrate fossil traces such as *Striatichnium bromackerense* Martens, 1982 (Text-fig. 5a) and *Tambia spiralis* Müller, 1969 (Text-fig. 5b) which are typical ichnofossils for the Bromacker locality (see Voigt and Haubold 2000, Martens et al. 2005).

Potential trackmaker. A synapomorphy-based track-trackmaker correlation suggests the diadectid *Orobates pabsti* as a potential trackmaker (see Voigt et al. 2007).

Taphonomic and behavioral interpretation

At least three generations of *Ichniotherium* tracks and trackways can be observed on specimen NMP Sv 1001 which were identified based on their different morphology (Text-fig. 4a, b). The different morphological preservation of footprints was described by Voigt and Haubold (2000), who distinguished three types of *Ichniotherium* track reliefs from the Bromacker locality. Similarly, three types were also observed on specimen NMP Sv 1001: type 1 designation was used for footprints of high relief that were surrounded by displacement rims; type 2 for flatter footprints with laterally shallow relief where digit V impressions were often missing; and type 3 for footprints of very low relief with usually preserved only digit terminations separated from poorly-defined heel impressions (Voigt and Haubold 2000: fig. 7).

The morphology of the footprints and thus also their depth pattern are influenced by many factors such as the character of the substrate (water saturation, microbial mat thickness) as well as the behavior or size of the trackmaker (see Marty et al. 2009, Marchetti et al. 2019).

The deepest and poorly preserved large tracks on NMP Sv 1001 (e.g., trackway 4; Text-figs 3a, b, 4a) with displacement rims and blurred digit terminations were most likely created shortly after a flooding event when the sediment still retained a higher water content (see Milàn 2006, Marty et al. 2009). Large heavy trackmakers could also break the "barrier" through the surface microbial mat and sink their feet into the deeper part of the sediment (see Marty et al. 2009). During the later period, when the substrate was gradually drying and becoming more plastic and water unsaturated, the conditions were suitable for preservation of well-preserved tracks (e.g., trackways 1, 3; Text-figs 3a, b, 4b). The shallowest tracks (e.g., trackway 2) would have been produced in drier and less plastic sediments, but still moist (see Milàn 2006, Marty et al. 2009). As the shallow tracks are overlapped by the deeper ones of similar size (Text-fig. 4b), we assume fluctuation in the substrate water content over several track generations. Further, the footprints of trackway 5 were modified by the post-registration processes, such as the presence of water flow or liquid microbial mats which created the sinusoidal grooves (Text-figs 3b, 4c). Desiccation cracks crossing each track generation indicate that the sediment dried rapidly after the footprints were formed.

The invertebrate trace fossils such as *Tambia spiralis* (Text-fig. 5b), most probably created by an arthropod (Knaust et al. 2022), have often been observed in the deepest parts of the footprints, such as distal parts of the digits and sole impressions (Text-fig. 4c). It seems that arthropods sought out places that retained puddles of water for the longest time.

The measured track and trackway parameters (Tab. 1) refer to the different sizes of individuals walking through the substrate, but most probably with the same intention. A large number of the diadectomorph tracks and trackways at the Bromacker locality (see Pabst 1908, Voigt and Haubold 2000, Voigt 2005, Voigt and Ganzelewski 2010, Buchwitz and Voigt 2018, Marchetti et al. 2018) are most probably associated with foraging and mating behavior (see also Marchetti et al. 2018).

Conclusions

Specimen NMP Sv 1001 with more than 80 footprints from six trackways and several incomplete step cycles of ichnospecies *Ichniotherium sphaerodactylum* from the Bromacker locality in Germany has been an important part of the paleontological collections of the National Museum in Prague for more than a hundred years. The specimen was donated to the National Museum in 1916 making it the first recorded case of Bromacker tracks being transported after 1908. The slab itself was found between 1908 and 1916 when fossil discoveries from the Bromacker locality were extremely rarely reported. The specimen preserves *Ichniotherium* trackways of various morphological qualities reflecting the changing hydrological conditions of the substrate over several track generations. Although ichnospecies *I. sphaerodactylum* is the most common, and at the same time probably the most well-known fossil tracks in Thuringia, each of the preserved specimens represent a unique piece from the large track sequences that can provide completely new information.

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