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ICHNOTAXONOMY AND TRACKMAKER ASSIGNMENT OF TETRAPOD TRACKS AND SWIMMING TRACES FROM THE MIDDLE PERMIAN HORNBURG FORMATION OF SAXONY-ANHALT (GERMANY)

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Abstract: Here we describe new material of tetrapod tracks and swimming traces from the Konberg quarry, a tracksite of the late middle Permian Hornburg Formation in Saxony-Anhalt, central Germany. A relatively well-preserved trackway and several isolated imprints are assigned to *Capitosauroides* isp. Among others, toe proportions in the manus and pes footprints of the newly described specimens and the long, proximal and detached pedal digit V imprint are similar to the type ichnospecies *Capitosauroides bernburgensis* from the Early Triassic of Bernburg, Saxony-Anhalt. In these features the new Konberg material differs from other ichnotaxa, such as *Amphisauropus* and *Varanopus*, which may look similar in their relative length of the sole, digit proportions and/or in the digit tip imprint morphology. The comparatively large manus imprint, which is wider than long, the relative length and shape of the sole impression, the digit proportions that are indicative for a more ectaxonic manus a more mesaxonic pes, the low pace angulation and the low imprint-size-normalized stride length in the Konberg track type are distinct from *C. bernburgensis.* It shares, however, a certain similarity with recently described material of *Capitosauroides* from middle–late Permian tracksites. These observations are in agreement with the results of a multivariate analysis including *Capitosauroides* and morphologically similar ichnotaxa. Our findings would justify the erection of a new ichnospecies if more trackways with a similar or slightly better preservation were at hand. Hornburg Formation material previously assigned to *Amphisauropus* is herein considered as indetermined tetrapod tracks, whereas the occurrence of *Dromopus* isp. is confirmed. This reassignment shortens the stratigraphic range of the ichnogenus *Amphisauropus*, which appears to be restricted to the early Permian, since younger occurrences are questionable. In agreement with the attribution of *Capitosauroides* to eutheriodont producers, we regard the Konberg material assigned to this ichnogenus as tracks of small and possibly semi-aquatic therapsids. Abundant tetrapod swimming traces that co-occur with *Capitosauroides* isp. on the same bedding planes are interpreted as having been made by the same group of producers. The subaquatic traces often consist of short parallel claw mark sets. In agreement with a derived amniote producer group, they indicate propulsion by parasagittal limb movement rather than axial undulation.

Key words: Rotliegend, tetrapod ichnology, *Capitosauroides*, *Amphisauropus,* Therapsida, Konberg.

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INTRODUCTION

Tetrapod tracks, when supported by an anatomy-consistent ichnotaxonomy and track-trackmaker correlation (e.g., Voigt *et al.*, 2007), are an important source of information on the extinct tetrapod faunas, especially in those units with few or no skeletal remains preserved. Throughout the Permian, this is especially true for the low-latitude tetrapod ichnofaunas of Euramerica, which are very extensive in terms of abundance and diversity compared to the skeletal record in the time interval comprised between the late early Permian and the end of the late Permian (e.g., Schneider *et al.*, 2020). Nevertheless, while the late early Permian and late Permian tetrapod ichnoassociations of low-latitudes are extensive and well-understood, those from the middle Permian are generally fewer and in need of revision (e.g., Voigt and Lucas, 2018; Marchetti *et al.*, 2019a). These records are mainly from France and include the La Lieude Formation of the Lodève Basin (e.g., Gand *et al.*, 2000) and the Pradineaux, Mitan, Muy, and Pelitique formations of the Provence basins (e.g., Heyler and Montenat, 1980; Gand, 1989, 1995; Demathieu *et al.*, 1992). The main difference between these ichnofaunas and the late early Permian ones is the occurrence of therapsid synapsid tracks, such as *Brontopus*, a trait they have in common with the middle Permian mid-high latitude tetrapod ichnofaunas of Gondwana (e.g., Marchetti *et al.*, 2019b). A further potential source of information on low-latitude middle Permian ichnofaunas may come from the Hornburg Formation of central Germany. This deposit is known for its noteworthy trace fossil content, mostly coming from the Blätterton Member of the Konberg locality and a few other sites (e.g., Haubold and Katzung, 1975; Walter, 1978, 1982). It includes abundant and diverse invertebrate trace fossils, especially arthropod tracks, numerous tetrapod swimming traces and relatively abundant but generally poorly-preserved tetrapod tracks. The latter have been tentatively assigned to *Amphisauropus* and *Dromopus* in the last review (Voigt, 2012). The recent discovery of a relatively well-preserved tetrapod trackway and swimming traces associated with tetrapod tracks raised new interest in this ichnofauna and demands a thorough description of the newly-discovered material – in order to put it adequately in the context of the sparse middle Permian low-latitude record of tetrapod tracks.

In this approach we provide a short synopsis of the geology and stratigraphy of the Hornburg Formation and of the Konberg site in particular, while the main part focusses on the following issues: (1) description and ichnotaxonomy of the recently discovered and previously described/collected tetrapod tracks, (2) support of their systematic assignment by methods of multivariate statistics, (3) trackmaker assignment and biostratigraphic implications, (4) interpretation of the abundant tetrapod swimming traces in terms of producer behaviour.

GEOLOGICAL BACKGROUND

The successions of the late Carboniferous−early Permian Saale Basin and the successor depositional areas linked to the Southern Permian Basin of central and northern Germany are mostly covered by Mesozoic and Cenozoic sediments, but well known through the study of drilling core data (e.g., Schneider and Gebhardt, 1993; Plein, 1995; Schneider *et al.*, 2005; Ehling and Gebhardt, 2012). s an end-Variscan subsidence structure, the Saale Basin had an extension of 150 km by 90 km, extending from the present-day State of Thuringia in the southwest to the State of Brandenburg in the northeast. The Hornburg Anticline (Saxony-Anhalt) in the north-eastern part of the basin (Fig. 1A), exposes clastic sedimentary rocks in several outcrops; its Permian strata were lithostratigraphically subdivided into the 'Halle', 'Hornburg' and 'Eisleben' Formations (Ehling and Gebhardt, 2012). The Unterrotliegend (pre-Illawarra Reversal) Halle Formation (301±3 Ma to 292±3 Ma; radiometric ages in Ehling and Gebhardt, 2012, table 1) comprises volcanic intrusions, lava flows and volcanic tuffs hosted in clastic greyish and reddish sediments. In contrast, the Hornburg Formation represents a postvolcanic stage of basin development. Since Falk *et al.* (1979) the deposits of this formation were regarded as representing the last filling-up stage of the Saale basin in an only restricted basin remnant during the early Permian. This was supported by the biostratigraphic determination of the tetrapod track fauna by Haubold (1973) as of late Autunian (upper part of the Lower Rotliegend) age. Re-investigations of the Hornburg Formation in drilling cores and comparison with the facies pattern and cyclicity of the middle to late Permian deposits of the Southern Permian Basin as well as magnetostratigraphic data have changed this picture (as discussed by Gebhardt *et al.*, 2018; Fig. 1B): Magnetostratigraphic data of Menning *et al.* (1988) and especially the new data of Gebhardt (2011) and Gebhardt and Lützner (2012) point to a position of the Illawarra Reversal within the lower part of the Hornburg Formation. Based on the position of the Illawarra Reversal inside the Parchim Formation of the Southern Permian Basin (Menning *et al.*, 1988; Menning and Bachtadse, 2012), its lower cycle can be correlated with the Hornburg Formation. This correlation would be in agreement with the cyclostratigraphic correlations by Gebhardt and Lützner (2012) whose results support the basal conglomerate of the Hornburg Formation (Unteres Quarzitkonglomerat) as being coeval with the basal conglomerate of the Parchim Formation, which marks the beginning of subsidence of the huge Southern Permian Basin. The correspondence between the Hornburg and Parchim Formations leads us to the conclusion that the start of deposition of the Hornburg Formation is caused by the same geodynamic processes – long-lasting thermal subsidence in superposition with extensional faulting (e.g., Stollhofen *et al.*, 2008 and references therein). Consequently, the depositional area of the Hornburg Formation cannot be linked to the Carboniferous − early Permian Saale Basin but is considered as a new minor basin (herein termed "Hornburg Basin") close to the southern border of the Southern Permian Basin and its mega-playa system.

Due to the lack of biostratigraphically significant fossils and volcanic ashes suitable for radiometric dating, the

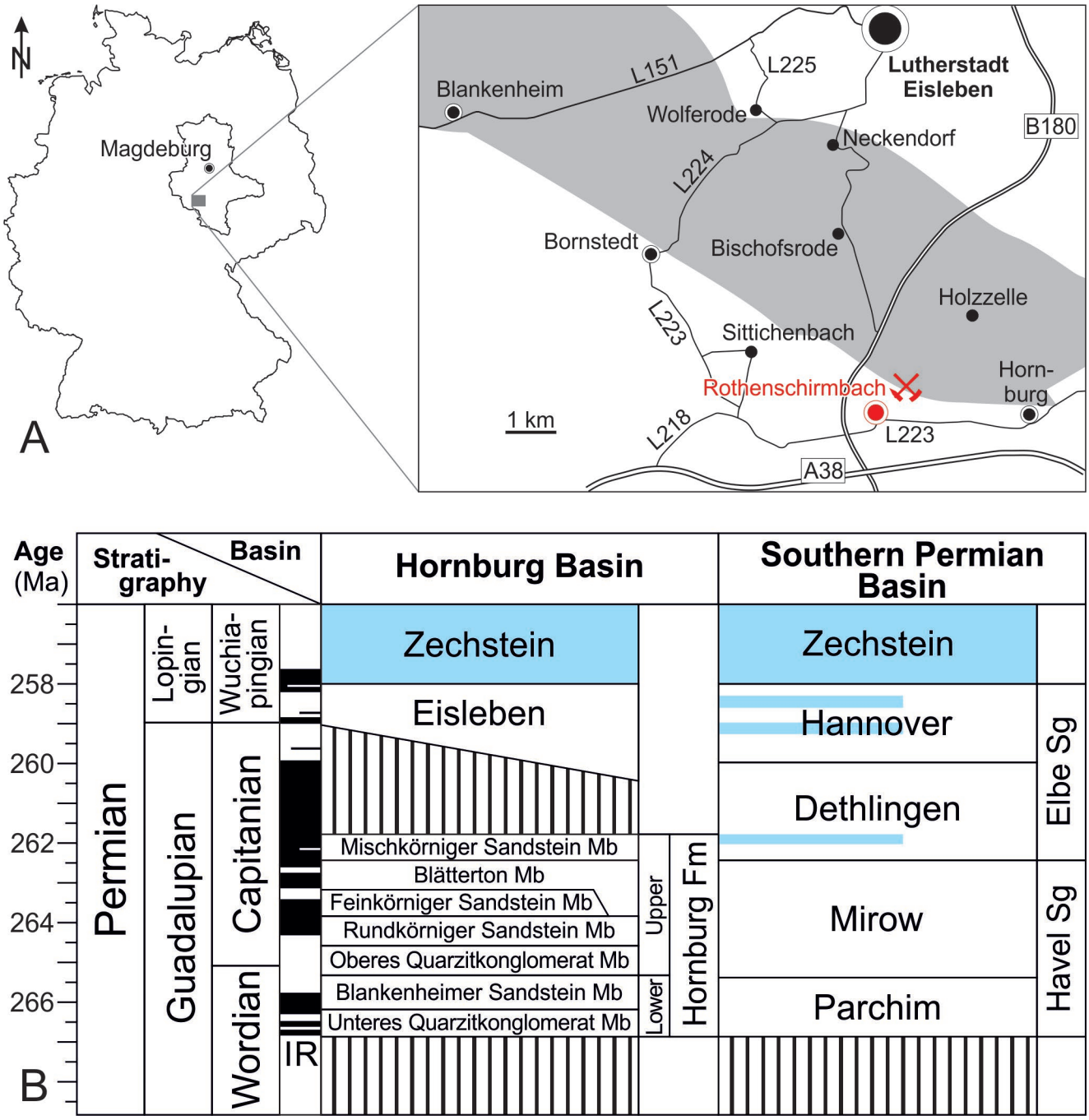


Fig. 1 Location and stratigraphic succession of the late middle Permian Hornburg Formation. **A.** Position of the Hornburg Anticline within Germany and map of the Hornburg Formation outcrop area, including Konberg (Ost) quarry (red mining symbol). The NW–SE striking anticline and distribution area of Palaeozoic bedrock (Rotliegend and Zechstein) is grey-shaded. **B.** Schematic lithostratigraphic successions of the Hornburg basin and Southern Permian basin; marine ingressions are marked with light blue colour. Map data based on OpenStreetMap; magnetostatigraphy after Hounslow and Balabanov (2018).

Illawarra Reversal is the only available age indicator. It is regarded to be of Wordian age (266 to 265 Ma; Steiner, 2006; Szurlies, 2013; Hounslow and Balabanov, 2018) and implies a Capitanian age for the tetrapod-track-bearing Blätterton Member (Schneider *et al.*, 2020, Figs 1B, 2).

The Hornburg Formation is exposed in several outcrops of the Hornburg anticline, a WNW–ESE striking structure to the south of the town of Eisleben (Saxony-Anhalt), and in several former copper shale shafts. Its succession has been studied through four drillings (Strenz 1/62, Hornburg 1/61, Bottendorf 1/61, Querfurt 1/64) and recently by very detailed mapping of surface outcrops at the Hornburg anticline (Falk, 2014). Based on these data, the Hornburg Formation consists of two fining-upwards mega-cycles, which comprise six to seven lithofacies members (Hoyningen-Huene, 1960; Gebhardt, 2011; Falk, 2014; Fig. 1B) – from the base to the top: (1) the Unteres Quarzit Konglomerat (Lower Quartzite Conglomerate) Member and (2) the Blankenheim Sandstein (Blankenheim Sandstone) Member of the lower cycle; the upper cycle comprises (3) the Oberes Quarzit

Konglomerat Member, (4) the Rundkörniger Sandstein Member, (5) the Feinkörniger Sandstein Member, (6) the Blätterton Member. A further unit, (7) the Mischkörniger Sandstein Member, has been described based on drilling core data. The conglomerates, siltstones and sandstones of members 1–3 represent alluvial fan to braid plain system deposits. They are laterally and vertically overlain by sandy and silty braid plain and evaporitic sand flat deposits of members 4 and 5. Aeolian transport is indicated by bimodal coarse to fine grained sandstones successions and spatially restricted well-sorted, fine- to medium-grained fluvially reworked and redeposited aeolian sandstones. They are overlain by fossiliferous lacustrine, fine clastic deposits including laminated silty claystones, pure claystones with intercalated thin relicts of evaporitic horizons and intercalated channel sandstones bearing in places small halite crystal marks (member 6). In general, the sedimentological and palaeontological features of the Hornburg Formation are indicative of dry playa red beds deposited under semiarid to arid climatic conditions (Schneider *et al.*, 2006, 2015; Ehling and Gebhardt, 2012).

Fossils from the Hornburg Formation are relatively rare (e.g., Schneider and Gebhardt, 1993; Ehling and Gebhardt, 2012). Nevertheless, the siltstones and mudstones of the Blätterton Member host a diverse Rotliegend ichnofauna, but also impressions of conchostracans and jellyfish (Müller, 1978; Martens, 1983; Walter, 1983; Falk, 2014). Different from the diverse invertebrate ichnofauna (e.g. Walter, 1982, 1983; Falk, 2014), only few morphotypes of tetrapod tracks have been distinguished based on often poorly preserved material from the localities Konberg/Rothenschirmbach, Sittichenbach and Neckendorfer Grund/Wolferode Süd (Haubold and Katzung, 1975; Walter, 1982, 1983; Falk, 2014). Tetrapod tracks often occur as swimming traces, which were produced under water cover by a buoyant tracemaker or highly deformed/collapsed imprints left in water-saturated mud. Voigt's (2012) assessment that only *Amphisauropus* and *Dromopus* are known from the Hornburg Formation represents the current state of knowledge prior to this study. Recent excavations (between 2012−2020) in the fine clastic successions of the abandoned Konberg (Ost) quarry to the northwest of the village Rothenschirmbach (51°27′28.3″N, 11°33′14.8″E, municipality of Lutherstadt Eisleben) revealed new material of tetrapod tracks (Figs 3−5). In the present study these specimens are compared to previously described finds and similar ichnotaxa (Figs 6–11), but also related to the abundant co-occurring swimming traces (Figs 12−13).

At Konberg quarry the uppermost part of the Feinkörniger Sandstein Member and an about 10 m thick succession of the Blätterton Member are exposed (Fig. 2A). The latter is well accessible along the southern wall of the quarry (Falk, 1979; Falk, 2014) and has since long been targeted by ichnologists and private fossil collectors due to its abundant invertebrate trace fossils and tetrapod tracks. An about 4.5 to 5.0 thick claystone horizon (unit 18 of Falk, 1979, unit one in Fig. 2B) forms the lower part of the Blätterton Member and is overlain by a 2.5 m succession of alternating clay-rich siltstones and fine sandstones to siltstones. The uppermost 2.5 m of the Hornburg Formation exposed at the Konberg site are dominated by claystone and clay-rich siltstone. Within the alternating succession of the Blätterton Member invertebrate and vertebrate ichnia are often preserved either within laminated shales or as convex hyporelief on slabs of fine sandstone to siltstone. The highest abundance and fidelity of tetrapod footprints and swimming traces has been observed in a cm-thick horizon of clay-rich siltstone, covered by a light-coloured, ten to 15 cm thick layer of fine sandstone which also yielded most of the new material presented here (unit 5c in Fig. 2B).

Institutional abbreviations

FG, Geoscientific Collections of the TU Bergakademie Freiberg; MfNMD, Museum für Naturkunde Magdeburg; HF, Geologisches Institut der Martin-Luther-Universität Halle-Wittenberg; MNG, Museum der Natur Gotha; NML, Naturkundemuseum Leipzig. NML-G (TRO) refers to specimen numbers in the former private collection of Frank Trostheide, Wolmirstedt that have been assigned a new Leipzig specimen number.

MATERIAL

Specimens from the Konberg quarry (Rothenschirmbach, municipality of Eisleben) that were excavated during the years 2012/2013, 2017/2018 and 2020 by Hartmut Knappe, Frank Trostheide and Michael Buchwitz include:

– slabs of fine sandstone from a 10 to 15 cm thick horizon in the middle part of the Blätterton succession (unit 5C, Fig. 2B) with tracks preserved in convex hyporelief: NML-G 2020/0004 (TRO 6721) a 50 cm-long slab with a tetrapod trackway consisting of five pes-manus couples and one additional manus imprint, several isolated footprints and tetrapod swimming traces (Figs 3, 4, 7D, 8E−F); MfNMD P-21704, a 90-by-90-cm-large slab from the same horizon that bears various tetrapod swimming traces including the long "swimming trackway" of a floating tetrapod and invertebrate traces; MfNMD P-21704a and 21704b; two small associated slabs with relatively well-preserved footprints (Figs 5A, 5D, 7F−G, 13E−G); NML-G 2020/0005 (TRO 5579) and NML-G 2020/0006 (TRO 5580) two slabs with mostly parallel-oriented tetrapod swimming traces on the convex bottom of channel filling (Fig. 12F−G); NML-G 2020/0007 (TRO 5621), a further slab with tetrapod swimming traces (Fig. 12D); NML-G 2020/0011 (TRO 5909), MfNMD P-21733 and P-21734, slabs with tetrapod swimming traces and desiccation cracks (Fig. 12E); NML-G 2020/0013 (TRO 5927) swimming tracks associated with long parallel claw drag marks (Fig. 13A−D);
– slabs of shale from the alternating succession of siltstones and fine sandstones above the main track horizon (units 6–11, Fig. 2B): NML-G 2020/0008 (TRO 5622), a short trackway with indistinct imprints, concave epirelief; NML-G 2020/0009 (TRO 5795) slab with a tetrapod trackway consisting of deformed tracks and several arthropod trackways, concave epirelief (Fig. 12A); NML-G 2020/0010 (TRO 5808) one side of a tetrapod trackway with indistinct tracks, convex hyporelief (Fig. 5H); NML-G 2020/0012 (TRO 5914) deformed pes-manus

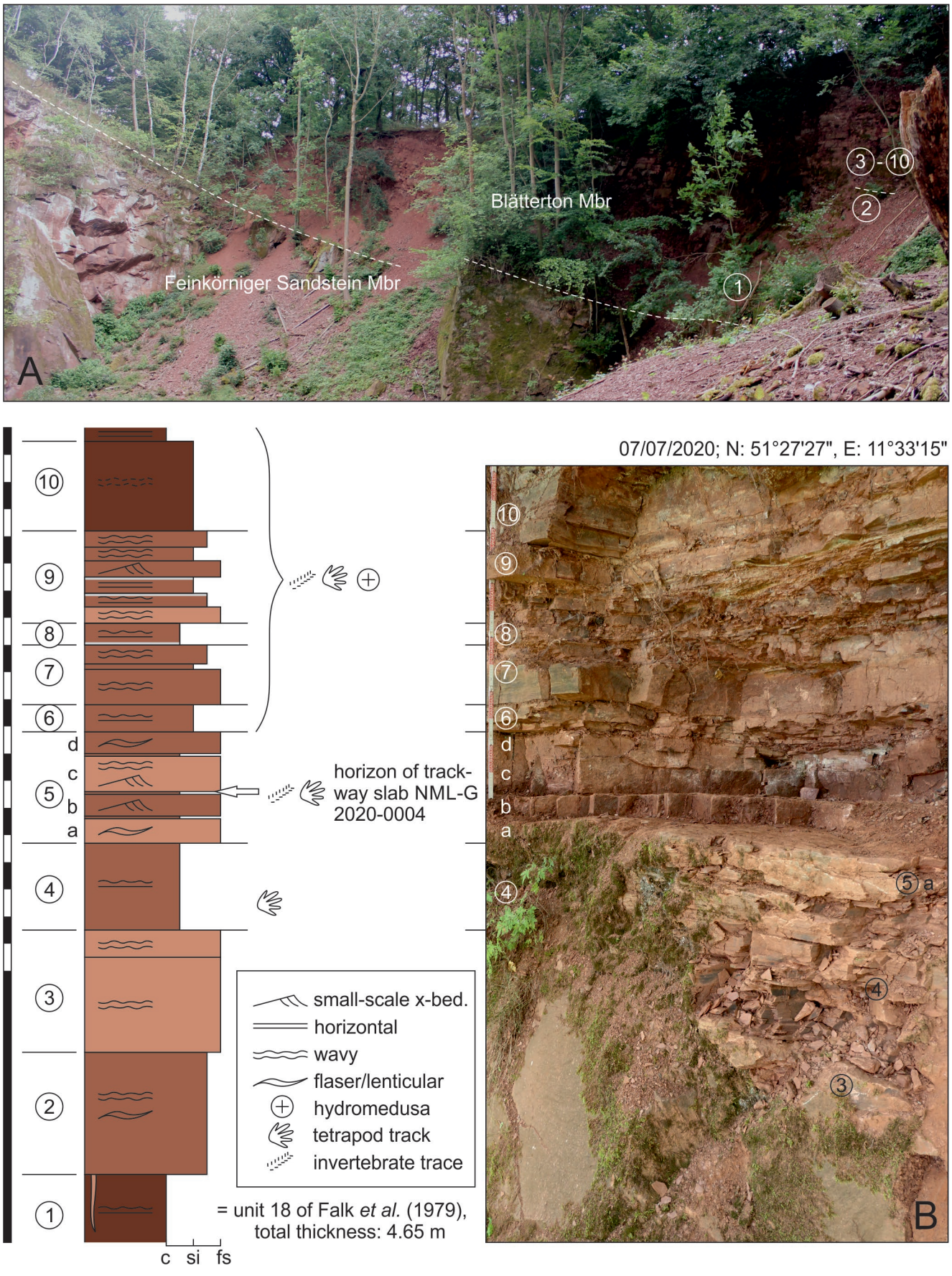


Fig. 2. Studied succession of Konberg (Ost) quarry near Rothenschirmbach, municipality of Lutherstadt Eisleben. **A.** Outcrop panorama with the excavation site in the right half of photograph. **B.** Grain size profile and outcrop photo for the fossiliferous part of the Blätterton Member at Konberg quarry. Abbreviations: c – claystone, si – siltstone, fs – fine sandstone. Small scale unit: 10 cm.

couple, concave epirelief (Fig. 12B); MfNMD P-21402, right pes imprint, convex hyporelief (Fig. 5B); MfNMD P-21859, pes-manus couple showing an undertrack-like preservation, part and counterpart (Fig. 5F).; MfNMD P-21860 with a relatively well preserved pes imprint, convex hyporelief (Fig. 5E).

Further material: Specimens MfNMD -P-9550 and MfNMD -P-9544, both convex hyporelief, were collected in the 1970s to 1980s at the Sittichenbach site of the Hornburg Formation and were donated to the Natural History Museum of Magdeburg by Gerald Kopp (Figs 5C, 11C, D); a specimen preserved as part and counterpart with footprints

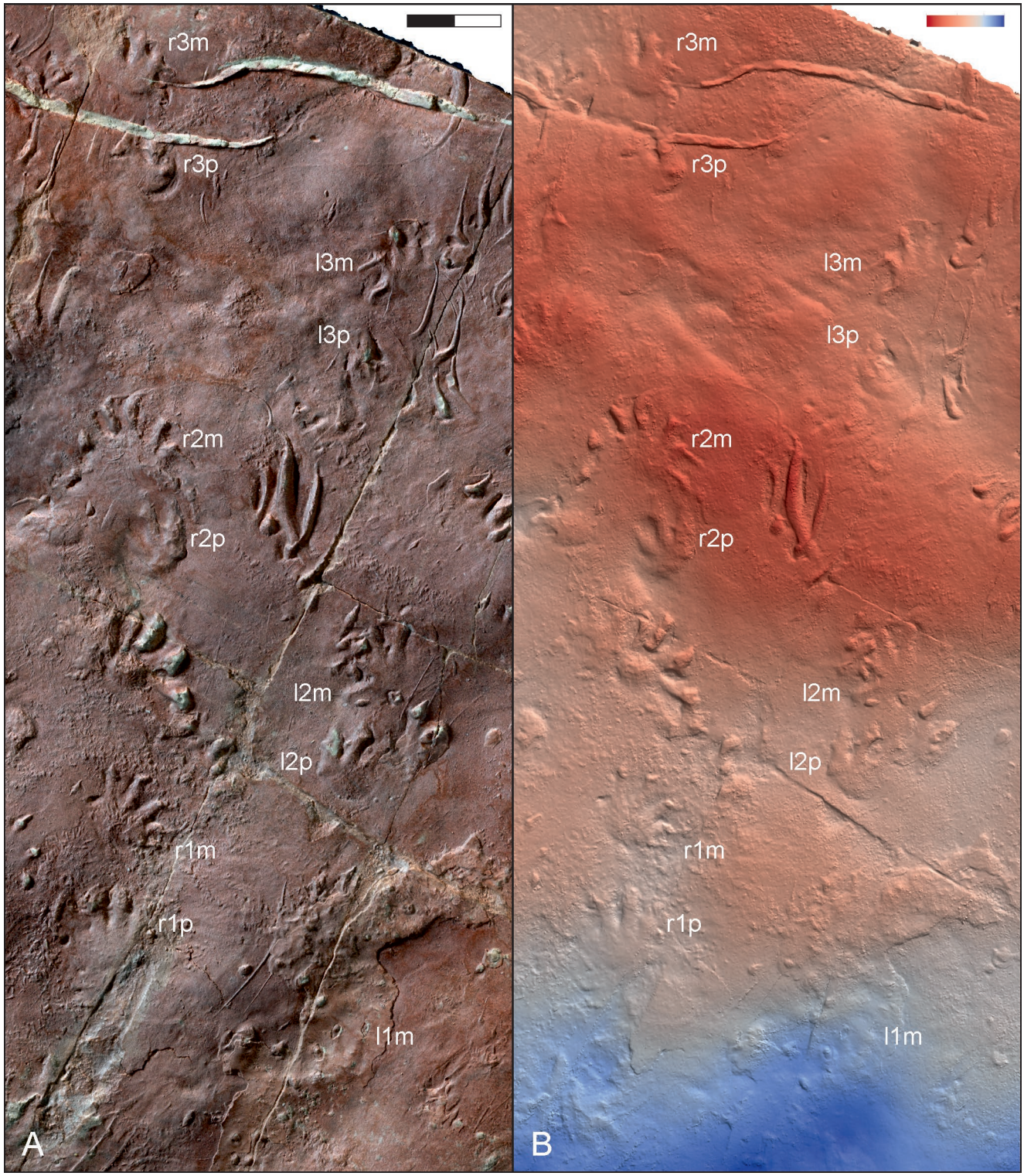


Fig. 3. Specimen NML-G 2020-0004 (TRO 6721), assigned to *Capitosauroides* isp., siltstone slab with a trackway, several isolated footprints and invertebrate traces preserved in convex hyporelief. **A.** Orthophoto (azimuth view) of a textured surface model. **B.** Combination of a shaded relief and blue-white-red false colour image depicting depth variation. Left and right manus and pes imprints are numbered from first to last. Scale bar: 2 cm; the colour scale represents 1.6 cm of depth.

collected by Marcus Schipplick from Braunschweig (MS 2347, Fig. 5G) in the early 2010s; specimens FG 250/193, FG 292/1, FG 292/4 and FG 295/5 represent material published by Harald Walter and colleagues (Figs 11A, B, 12C; Walter *et al*., 1978, 1982); specimens MNG 2365/HF 58, MNG 2365/HF 65, HF 77 and HF 78 were described by Haubold and Katzung (1975) and are addressed in the systematic part and in the discussion.

The type material (HF 24, 25) of *Capitosauroides bernburgensis* and one additional sandstone slab with tracks (HF 26) were described by Haubold (1971) (Figs 6, 7A−C). Additional specimens for the multivariate analysis have been taken from Voigt (2005) and Marchetti *et al.* (2019a, b) and the respective repositories are listed in these publications.

METHODS

The tetrapod footprints used for ichnotaxonomy have been selected by means of morphological preservation *sensu* Marchetti *et al.* (2019c). Only the footprints showing an anatomy-consistent morphology have been considered for the assignments, thus trying to identify and exclude the morphological features highly influenced by substrate

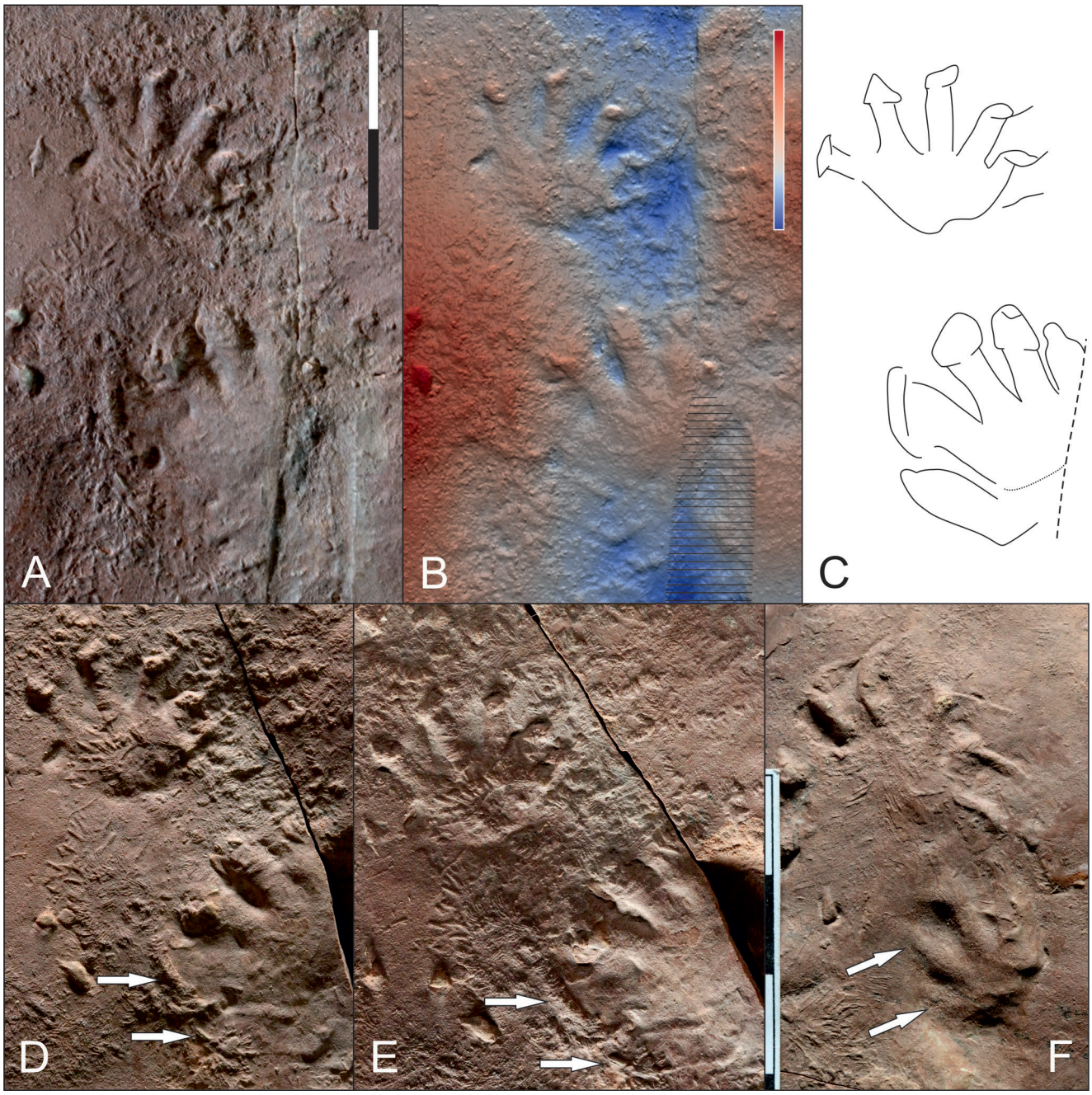


Fig. 4. *Capitosauroides* isp., specimen NML-G 2020-0004. **A–E.** First right footprint couple preserved in convex hyporelief: as orthophoto (A), combined false colour/shaded relief image (B), interpretation drawing (C) and photos with differently positioned light source (D, E). **F.** Second right footprint couple with incomplete preservation of pedal digits IV and V. The dashed area marks a missing part of the trackway surface (replaced by glue). The arrows indicate the position of pedal digits IV and V. Scale unit: 1 cm.

conditions and secondary behaviour. These are commonly known as extramorphologies (e.g., Peabody, 1948; Haubold *et al.*, 1995). The footprint and trackway measurements (Tables 1–3, Appendix, Supplement I) follow the conventions of Leonardi (1987). The terms mesaxony and ectaxony are herein referred exclusively to the relative length of the digit imprints within a footprint.

Based on a set of digital photos taken with a 100 mm macro lense, photogrammetric models have been calculated for specimen NML-G 2020-0004 with Agisoft Metashape Standard 1.9.x (Agisoft LLC, 2020). Postprocessing included cropping and scaling of the model with MeshLab v. 2020.1 (Cignoni *et al.*, 2008). The result is included as a STL file in the online supplementary material (Supplement II). For illustration in this manuscript orthorectified images of the textured model and combined shaded relief and height-scale false-colour images were generated with ParaView v. 5.8.0 (Ayachit, 2019), following the procedure outlined by Lallensack *et al.* (in press).

To define their degree of similarity and whether they can be separated based on standard imprint and trackway measurements (Tables 1–3, Appendix, Supplement I), we compare the following trackway samples in a multivariate approach (employing the statistics software package PAST3; Hammer *et al.*, 2001): five trackways of *Varanopus microdactylus* and 46 trackways of *Amphisauropus kablikae* from the Cisuralian of the Thuringian Forest Basin (Voigt, 2005), two trackways and two pes-manus couples of *Capitosauroides bernburgensis* from the Middle Buntsandstein of Bernburg (Haubold, 1971). They form the basis for the comparison with one trackway on specimen NML-G 2020-0004 from the Konberg site of the Hornburg Formation. In a further step, we include three specimens assigned to *Capitosauroides* isp. and cf. *Capitosauroides* isp. that have been described from middle to late Permian

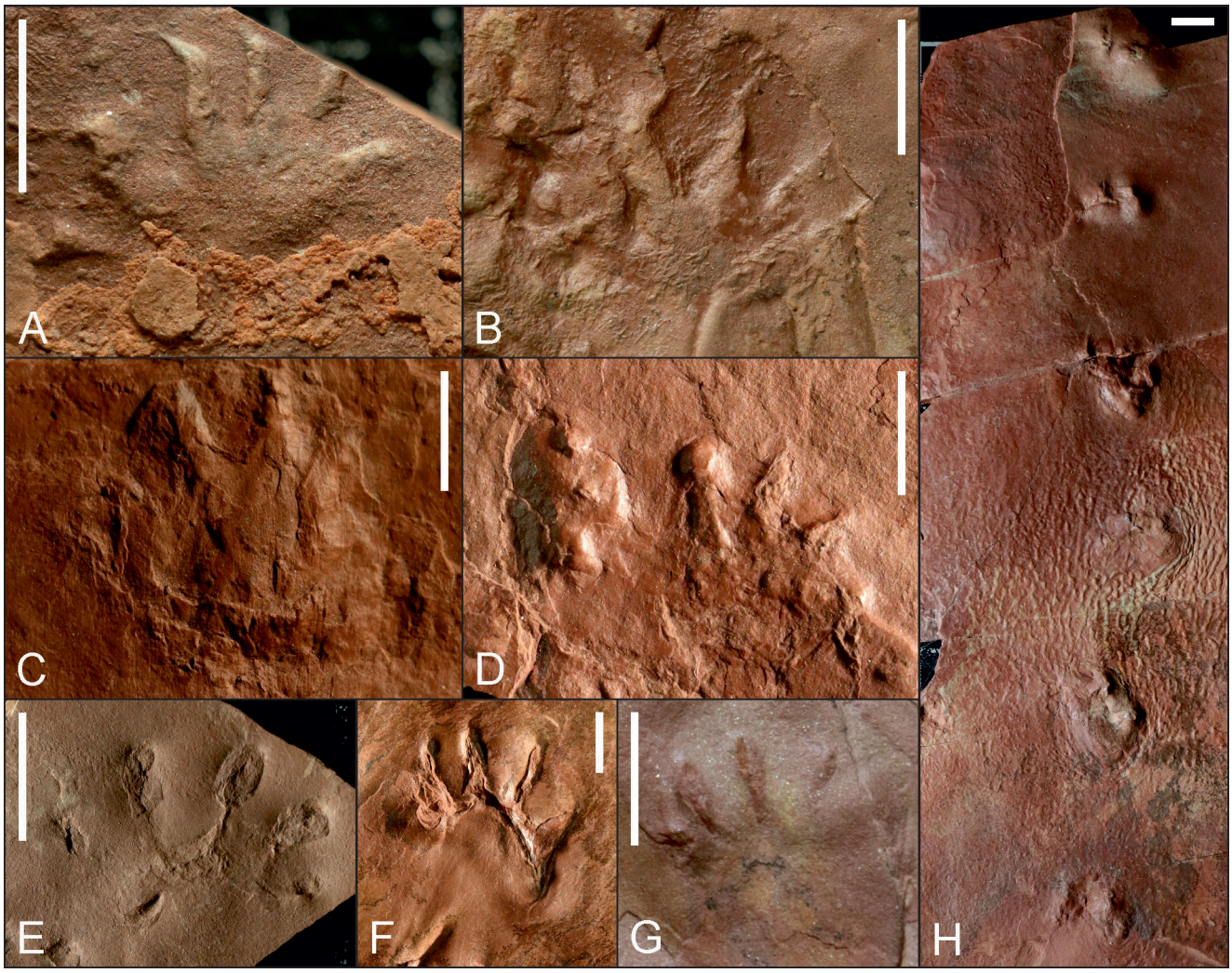


Fig. 5. Isolated footprints and a succession of footprints from the Blätterton Member/Hornburg Formation, displaying varying preservation qualities. **A–C.** *Capitosauroides* isp.: A, MfNMD P-21704a, right manus imprint, convex hyporelief; B, MfNMD P-21402, right pes imprint, convex hyporelief; C, MfNMD P-9550, left manus imprint, concave epirelief. **D–F.** cf. *C. Capitosauroides* isp.: D, MfNMD P-21704b, right manus imprints, convex hyporelief; E, MfNMD P-21860, right pes imprint on the right and undetermined track on the left, convex hyporelief; F, MfNMD P-21859, left pes imprint, convex hyporelief. **G**. Undetermined tetrapod track on specimen MS 2347, convex hyporelief. **H.** Undetermined tetrapod trackway with deformed tracks, NML-G 2020/0010 (TRO 5808), convex hyporelief. Scale bars: 1 cm.



Fig. 6. *Capitosauroides bernburgensis* Haubold, 1971 from the type locality of Bernburg, Germany. Middle Buntsandstein, Early Triassic. **A.** HF 24. Holotype trackway, concave epirelief. **B, C.** Enlargements of A, left pes-manus couples. Note the triangular claw marks of the manus imprints. **D.** HF 24. Paratype trackway with shallow tail impression, wider digit imprints and higher digit divergence, convex hyporelief. **E.** Enlargement of D. Right manus imprint. Note the low digit divergence. **F.** HF 26. Right pes-manus couple, convex hyporelief. Note the slender and parallel pes digit imprints, which are distally bent outwards. **G.** HF 26. Left pes-manus couple, convex hyporelief. Note the outwards-bent claw marks of pes digits II–IV. Scale bars: A and D = 5 cm, F, G = 2 cm.

Table 1

Pes imprint measurements for six trackways and individual footprints assigned to *Capitosauroides*. Abbreviations: pI–pV, digit lengths I–V [mm]; pL, total length [mm]; pW, total width [mm]; pDIV, divarication angle between digits I and V [°] (see also Appendix and Supplement I for individual measurements).

Specimen	pI	pII	pIII	pIV	pV	pL	pW	pDiv
HF 24	15	18.5	23	26.5	19	53	56	107
HF 25	13	16	23	28	26	56	73	142
HF 26/1	18	24	34	36	28	65	76	98
HF 26/2	10	20	29	35	25	58	62	88
NML-G 2020-0004	6	8	9	9	7	19	24	56
MfNMD P-21402	5	8	9	9	8	20	24	108

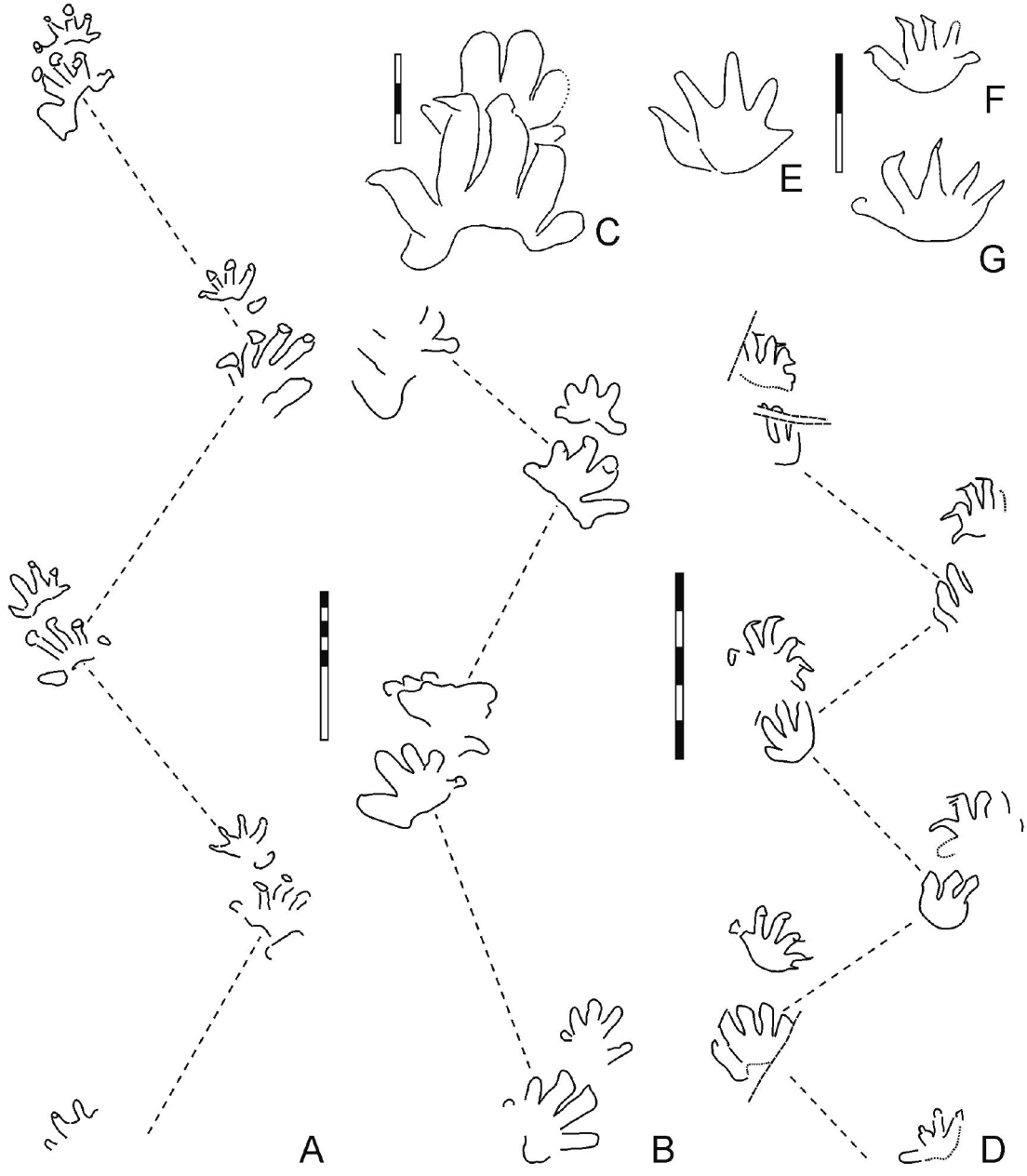


Fig. 7. Outline drawings of *Capitosauroides bernburgensis* footprints and tracks (**A–C**) and the Konberg morphotpye of *Capitosauroides* (**D–G**): A, HF 24; B, HF 25; C, HF 26; D, NML-G 2020-0004; E, MfNMD P-21402; F, MfNMD P-21704a; G, MfNMD P-21704b. Scale bars: 10 cm for A, B, 3 cm for C, 5 cm for D, 2 cm for E–G.

Table 2

Manus imprint measurements for seven trackways and individual footprints assigned to *Capitosauroides*. Abbreviations: mI–mV [mm], digit lengths I–V [mm]; mL, total length [mm]; mW, total width [mm]; mDIV, divarication angle between digits I and V [°] (see also Appendix and Supplement I for individual measurements).

Specimen	mI	mII	mIII	mIV	mV	mL	mW	mDiv
HF 24	10	13.5	16.5	16	13.5	34.5	44	135
HF 25	8.5	14	15.5	18.5	17	41	47.5	160
HF 26/1	10	19	23	23	14	41	49	123
HF 26/2	8	16	NA	NA	8	38	46	108
NML-G 2020-0004	4.5	7	8	8.5	7	16	24	128
MfNMD P-21704a	6	7	8	9	8	16	25	111
MfNMD P-21704b	3	(5)	6	7	7	13	17	112

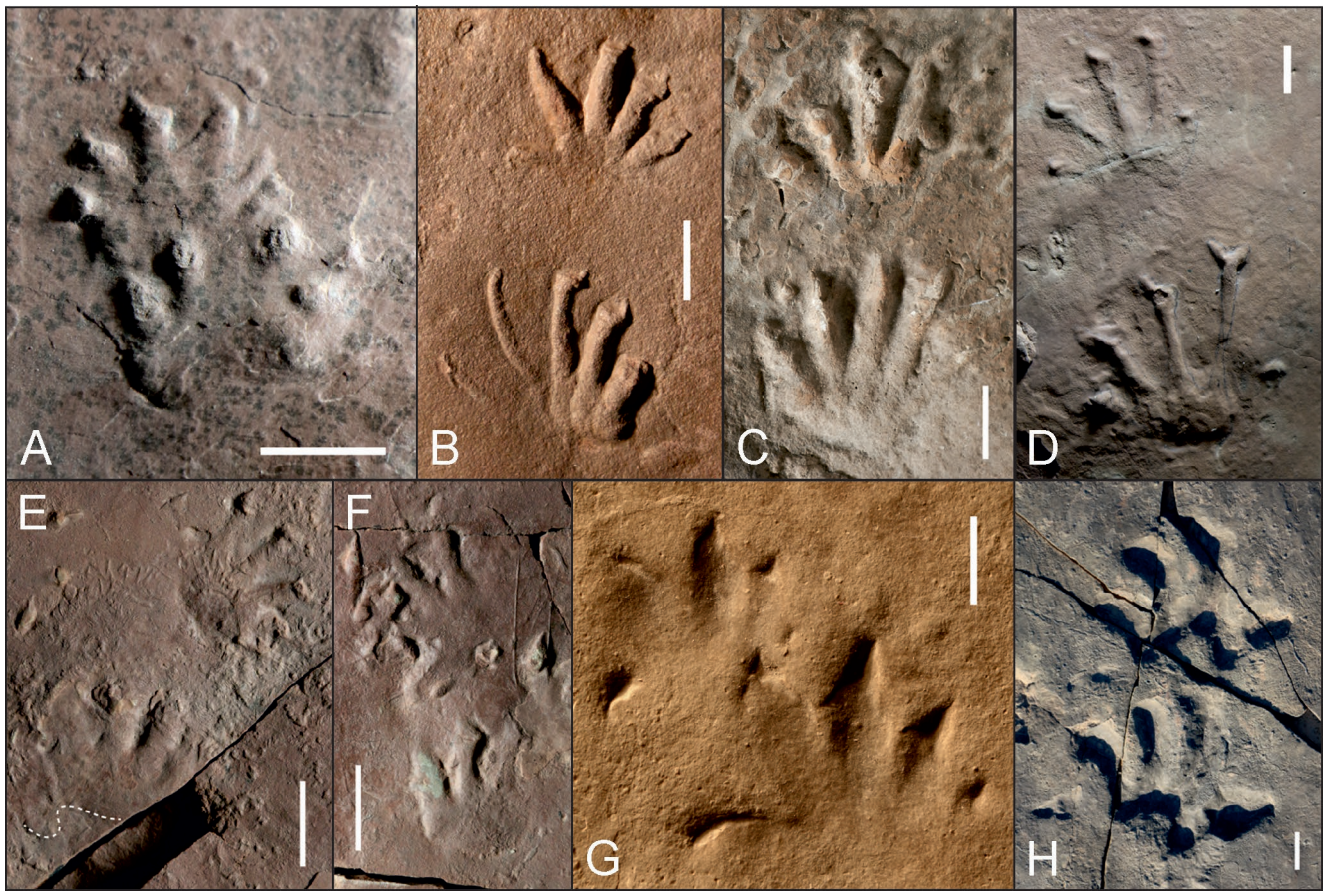


Fig. 8. *Capitosauroides* isp. from Konberg and morphologically similar ichnotaxa. **A.** MNG 7891. *Amphisauropus kablikae*. Left pes-manus couple, convex hyporelief. Oberhof Formation, Cisuralian, Germany. **B.** PMJ-P 1322. *Varanopus microdactylus*. Right pes-manus couple, convex hyporelief. Tambach Formation, Cisuralian, Germany. **C.** NHMUK-PV-R 3173. *Procolophonichnium nopcsai*. Left pes-manus couple, convex hyporelief, plaster cast (plastotype). Balfour Formation, Palingkloof Member, Permian-Triassic transition, South Africa. **D.** USNM 11518. *Hyloidichnus bifurcatus*. Left pes-manus couple, convex hyporelief (holotype). Hermit Formation, Cisuralian, Arizona. **E–F.** NML-G 2020-0004 (TRO 6721). *Capitosauroides* isp., convex hyporelief. Hornburg Formation, Guadalupian, Germany: E, right pes-manus couple; F, left pes-manus couple. **G.** NML-G (TRO -4562b). *Procolophonichnium haarmuehlensis*. Left pes-manus couple, concave epirelief. Middle Muschelkalk, Middle Triassic, Germany. **H.** GF-TR 1. *Karoopes gansfonteinensis*. Right pes-manus couple, concave epirelief (holotype). Teekloof Formation, Guadalupian-Lopingian transition, South Africa. All scale bars: 1 cm, except for H: 5 cm.

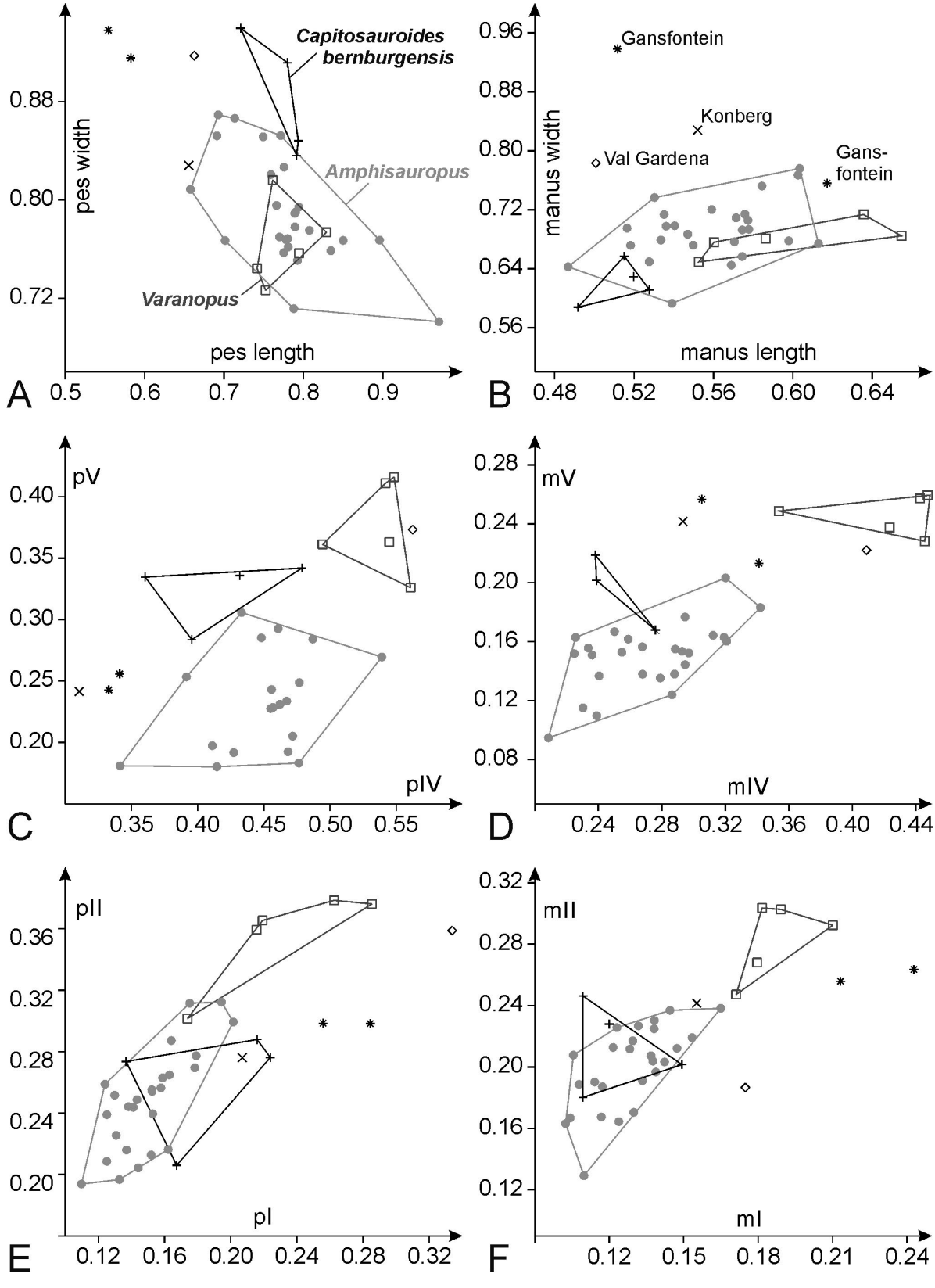


Fig. 9. Bivariate plots depicting the variability in normalized length measurements that reflect trackway morphology for trackways of *Capitosauroides bernburgensis* from the Buntsandstein of Saxony-Anhalt (plus), *Amphisauropus kablikae* (dot) and *Varanopus microdactylus* (square) from the Thuringian Forest, Konberg specimen NML-G 2020-0004 (cross) and cf. *Capitosauroides* from the middle Permian Gansfontein Site (star) and from the late Permian of Val Gardena (rhombus). **A.** Normalized pes width versus normalized pes length. **B.** Normalized manus width versus normalized manus length. **C.** Normalized length of pedal digits IV and V. **D.** Normalized length of manual digits IV and V. **E.** Normalized length of pedal digits I and II. **F.** Normalized length of manual digits I and II. As a body size proxy for normalization the square-root of the sum of manus width multiplied with manus length and pes length multiplied with pes width was used.

Table 3

Trackway measurements for three specimens assigned to *Capitosauroides*. Abbreviations: Sp, pedal stride length [mm], Pp, pedal pace length [mm], GWp, pedal gauge width [mm], Dpm, along-track distance between pes and manus [mm]; Wmp, difference in gauge width between manus and pes (negative values indicate more lateral manus) [mm]; PAp/PAm, pedal/manual pace angulation [°]; Op/Om, orientation of pes/manus with respect to trackway midline [°] (negative values indicate outward orientation) (see also Appendix and Supplement I for further trackway parameters and individual measurements).

Specimen	Sp	Pp	GWp	Dpm	Wmp	PAp	PAm	Op	Om
HF 24	373.5	231	133	42	11	109	111	-32	-6
HF 25	370	232	103.5	56	-21	118	122	-34	-4
NML-G 2020-0004	81	63	48	22	-7	82	69.5	-9	0

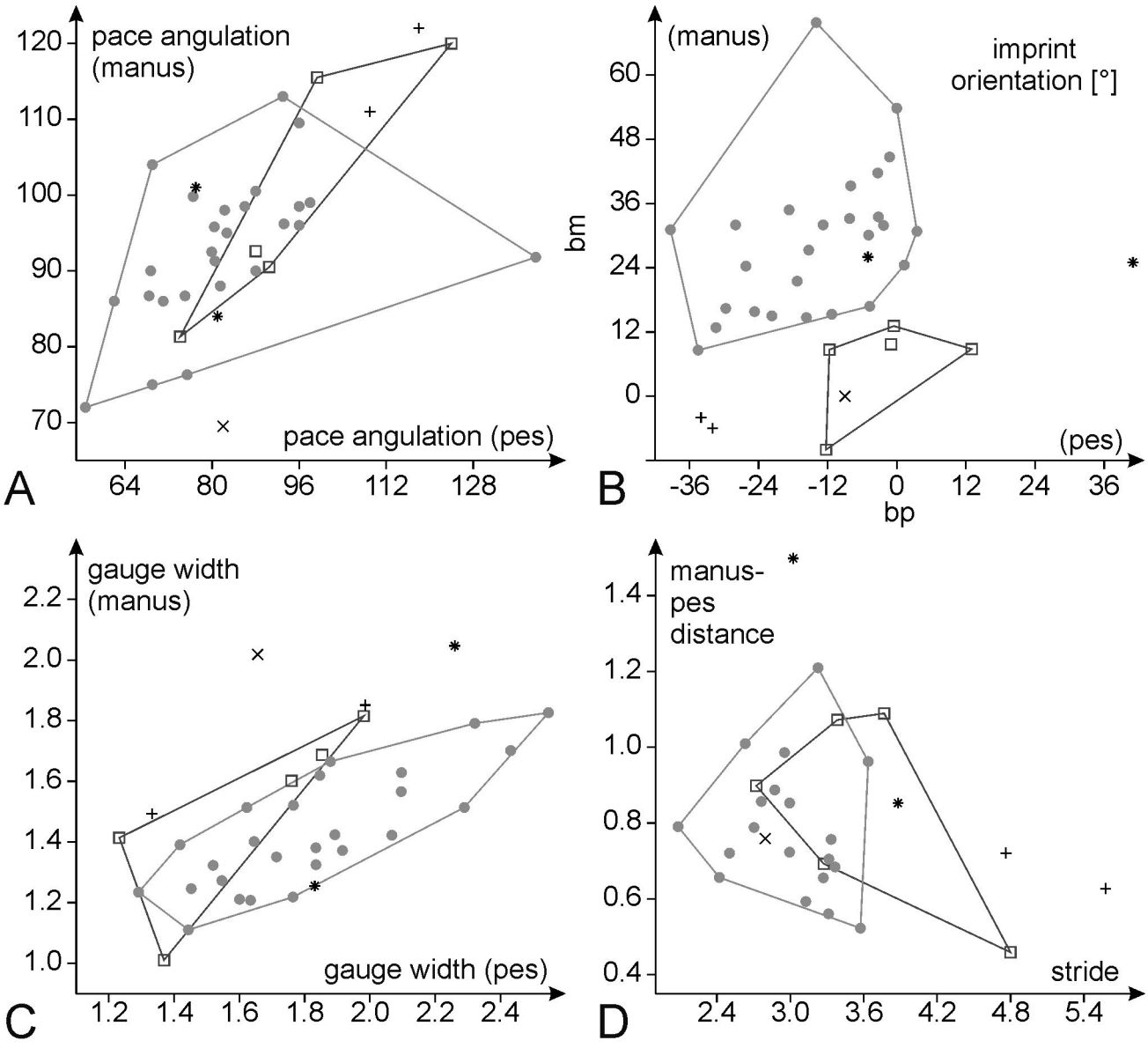


Fig. 10. Bivariate plots depicting the variability of *Capitosauroides bernburgensis*, Permian trackways assigned to *Capitosauroides*, *Amphisauropus kablikae* and *Varanopus microdactylus* in parameters that describe their trackway pattern. **A.** Pace angulation for the manus vs pace angulation for the pes (in degree). **B.** Imprint orientation of the manus versus imprint orientation of the pes (with respect to trackway midline, in degree). **C.** Normalized gauge width for the manus versus normalized gauge width for the pes. **D.** Normalized manus-pes distance (in direction of walk) vs normalized stride length for the pes.

deposits of South Africa and Italy, respectively (Marchetti *et al.*, 2019a, b).

The Thuringian samples have been chosen because they represent the largest homogeneous (spatially and temporally confined) trackway samples for two well-established ichnogenera, *Varanopus* and *Amphisauropus*; they display a general similarity to the Konberg tracks in terms of imprint proportions and because of the earlier assignment of some Hornburg Formation material to *Amphisauropus* (Haubold und Katzung, 1975; Walter, 1982; Voigt in Gebhardt, 2009; Voigt, 2012). Despite the younger age of the tracks (late Early Triassic), *Capitosauroides* from Bernburg has been included as third reference sample due to its alikeness in the structure of the pedal imprints. Other Permian tracks assigned to *Capitosauroides* have been included in a further set of analyses for the purpose of testing their assignment.

To remove the influence of body size, we test two different approaches: (1) normalization of length values with an elaborate body size proxy (called "BSP" here) as denominator (based on the assumption that the length of a producer is proportional to the square-root of imprint area): BSP = (manus width * manus length + pes width *pes length)^0.5); (2) for datasets that include only imprint length measurements a principal component analysis (PCA) is carried out and, under the assumption that PC 1 represents body size, statistic tests are applied on the remaining PCs 2 to 14 that are assumed to include non-body-size-related variation.

BSP-normalized length values are also used to depict variation in imprint length proportions through bivariate plots of normalized length ratios (Fig. 9) and for illustrating trackway pattern similarities (Fig. 10C, D). Angle measurements, i.e. pace angulation and the angles of manus and pes orientation with respect to the trackway midline (Fig. 10A−B), are plotted as unnormalized values.

We employ standard multivariate normality tests implemented in PAST3 (Mardia tests, Doornik and Hansen omnibus) to find out whether empirical distributions follow a multivariate normal distribution. Five different sets of variables were considered as separate test cases: (a) principal components 2 to 14, calculated for 14 unnormalized imprint measurements (10 digit lengths, manus width and length, pes width and length); (b) normalized values of 10 digit lengths; (c) normalized values of 14 imprint measurements; (d) six trackway measurements, including two normalized lengths (orientation angles for manus and pes, pace angulation of manus and pes, normalized pedal pace length, normalized distance between manus and pes parallel to trackway midline); (e) six trackway measurements including four normalized lengths (orientation angles, normalized pedal stride length, normalized pedal gauge width, normalized distance between manus and pes parallel to trackway midline and perpendicular to trackway midline) (test cases a−e are represented by separate columns in Table 4). If the null hypotheses of these tests were not declined, multivariate analysis of variance (MANOVA) had been applied in order to test the overall distinctiveness of the predefined groups via two different test statistics (Wilk's lambda, Pillai trace) and also the distinctiveness between pairs of groups (pairwise tests for *A. kablikae* vs. *V. microdactylus*, *A. kablikae* vs. *C. bernburgensis* and C. *bernburgensis* vs. *V. microdactylus*) has been considered. If the null hypothesis of multivariate normality test was declined, we applied permutational analyses of variance (PERMANOVA) including pairwise tests as non-parametric alternative to MANOVA.

In the next step, we use linear discriminant analysis (LDA) to address the question on how well the three reference samples can be separated from each other and to understand to which sample the unassigned specimens may belong according to the inferred linear discriminant functions. In a first series of LDAs the separability of the three groups *A. kablikae, V. microdactylus* and *C. bernburgensis* and the assignment of NML-G 2020-0004 to one of these groups are tested for five sets of variables: (a) principal components 2 to 14, calculated for 14 imprint measurements; (b) normalized values of 10 digit lengths; (c) normalized values of 10 digit lengths and four other imprint measurements; (d) six trackway measurements, including two normalized

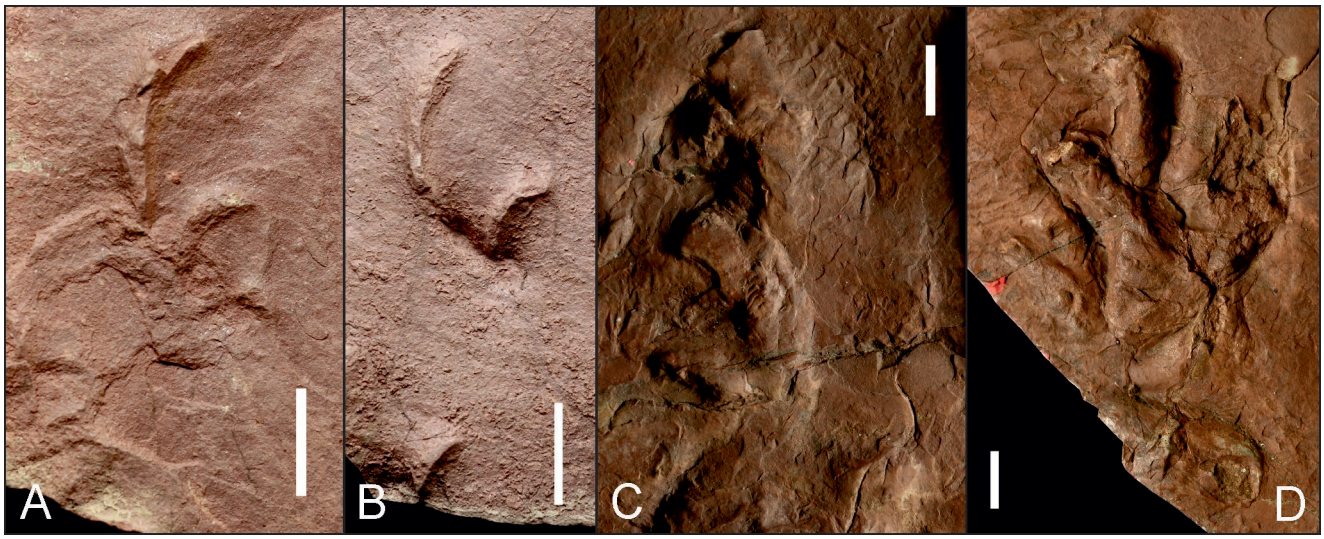


Fig. 11. *Dromopus* isp. from the Hornburg Formation, locality Sittichenbach. **A, B.** FG 250/193, right pes imprints, convex hyporelief. **C, D.** MfNMD P-9544, right pes-manus couples showing partial primary overstep, convex hyporelief. Scale bars: 1 cm.



Fig. 12. Swimming traces and deformed tracks generated under water cover from the Blätterton Member/Hornburg Formation of Konberg quarry. **A.** NML-G 2020/0009 (TRO 5795). **B.** NML-G 2020/0012 (TRO 5914). **C.** FG 292/4. **D.** NML-G 2020/0007 (TRO 5621). **E.** NML-G 2020/0011 (TRO 5909). **F.** NML-G 2020/0006 (TRO 5580). **G.** NML-G 2020/0005 (TRO 5579). Small scale unit: 1 cm.

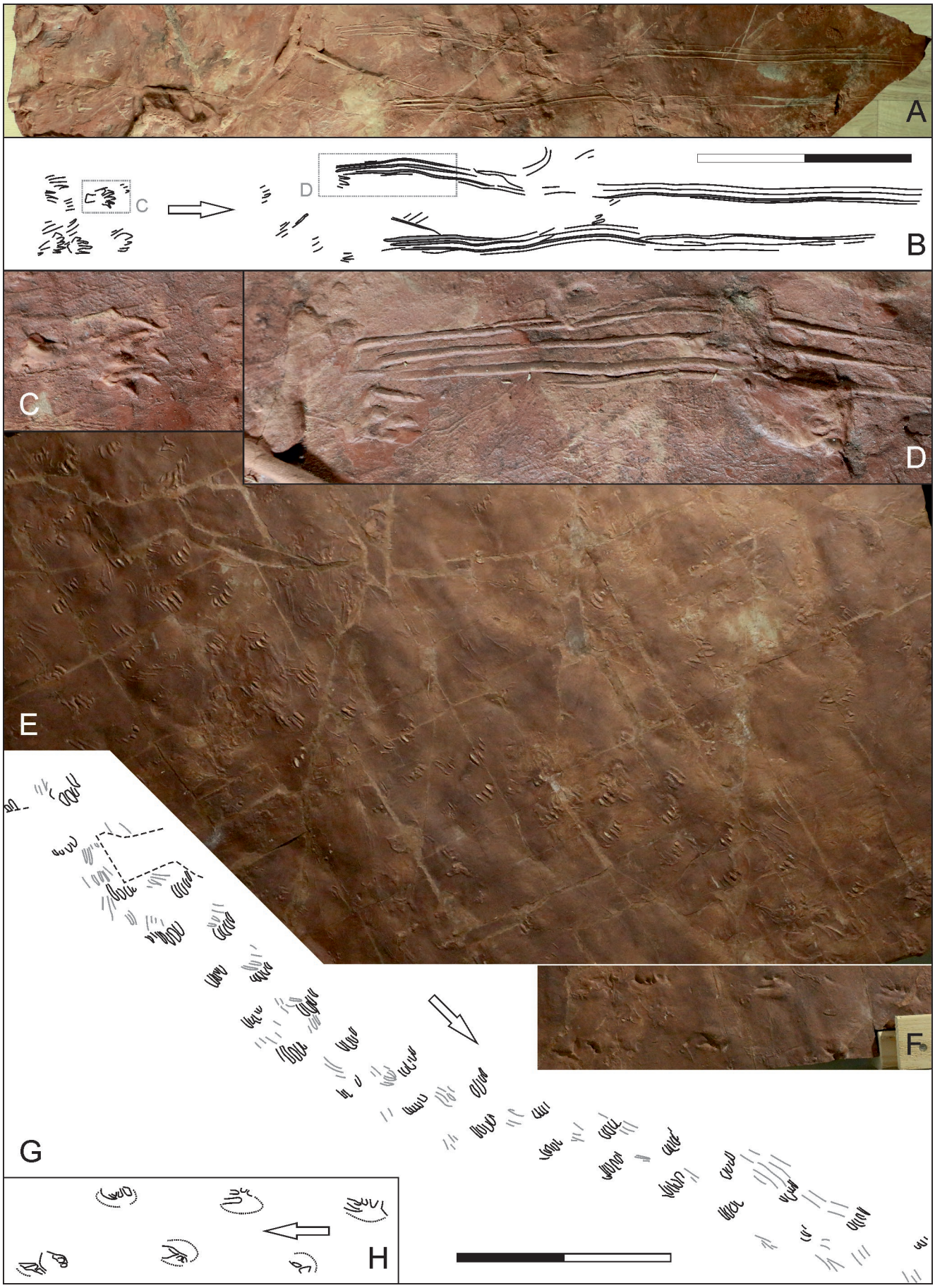


Fig. 13. Swimming traces from the Blätterton Member/Hornburg Formation of Konberg quarry. **A–D.** NML-G 2020/0013 (TRO 5927); E–H, MfNMD P-21704. Arrows mark direction of movement. Scale bars: 20 cm.

Table 4

Results of multivariate normality tests and multivariate analyses of variance based on different sets of measurements and 27 specimens assigned two three reference groups. Insignificant results (p-values or Bonferroni-corrected p-values > 0.05) are set in bold font.

Test	PC-based	Analyses with normalized length values			
	imprint measurements (PCs 2-14)	digit lengths (10)	imprint measurements (14)	trackway measurements	
				Set A (6)	Set B (6)
Mardia tests	declined	not declined	declined	not declined	not declined
D&H omnibus	$2.341*10^{-5}$	**0.2899**	**0.09414**	**0.5625**	**0.4167**
MANOVA (W.)	–	$5.061*10^{-5}$	–	0.0001254	$3.782*10^{-5}$
MANOVA (P.)	–	0.0001706	–	0.0002141	$4.576*10^{-5}$
PERM-ANOVA	0.0001	0.0005	0.0002	0.0003	0.0001
A vs V	0.0001	0.001054	0.0002	0.00059052	0.00073397
A vs C	0.0017	0.0042845	0.0037	0.014314	0.004671
V vs C	**0.018**	fail	**0.0701**	fail	fail

lengths; (e) the combination of 14 normalized imprint measurements and 6 trackway measurements (test cases a−e are represented by separate columns in Tables 5 and 6).

In a second series of analysis, the specimen NML-G 2020-0004 is predefined as belonging to the '*Capitosauroides*' sample (together with *C. bernburgensis*) and we test the assignment of two Gansfontein trackways from the Teekloof Formation of South Africa (GF-TR 9 and GF-TR 11; Marchetti *et al.*, 2019b) and a specimen from the Arenaria di Val Gardena Formation of Italy (UR-NO NUM 1; Marchetti *et al.*, 2019a). Given the lack of complete step cycles or pes-manus couples apart from the only trackway specimen from the Hornburg Formation, we refrain from including the newly described morphotype of *Capitosauroides* as a separate group.

SYSTEMATIC PALAEONTOLOGY

Capitosauroides Haubold, 1971

Figs 3−7, 8E, F, Tables 1–3

Type ichnospecies: *Capitosauroides bernburgensis* Haubold, 1971

Type locality: Bernburg, Germany. Middle Buntsandstein, Early Triassic. While information about the type locality was all but lost at the time of description, Haubold (1971) concluded based on a label on the backside of HF 26 that the three specimens come from a Buntsandstein quarry in the Bernburg area, Saxony-Anhalt, and named the ichnospecies accordingly.

Type material: HF 24. Holotype of *Capitosauroides bernburgensis* Haubold, 1971. Trackway with footprints belonging to five consecutive pes-manus couples, concave epirelief. HF 25. Paratype. Trackway with footprints belonging to four consecutive pes-manus couples and shallow tail impression. Two incomplete step cycle with two consecutive right pes-manus couples each. Convex hyporelief. HF 26. Additional specimen from the type locality. Four isolated pes-manus couples, convex hyporelief.

Diagnosis of the ichnogenus (modified from Haubold, 1971 in accordance with the inclusion of a new morphotype): Semiplantigrade pentadactyl tracks (different from *Limnopus*, that has a tetradactyl manus; different from *Ichniotherium* and most synapsid tracks, that are plantigrade). Pes larger than the manus (different from *Karoopes* and *Merifontichnus*, characterised by homopody). Relatively long and robust digit imprints that can be distally bent inwards or outwards (different from *Hyloidichnus*, *Merifontichnus*, *Procolophonichnium jageri, P. nopcsai, P. tirolensis, Robledopus* and *Varanopus* that do not show outward bending) and end in rounded terminations or wide triangular claw impressions (different from *Amphisauropus* and *Ichniotherium*, that do not have claw marks). Digit IV imprint of the manus and pes is of equal length or slightly longer than digit III imprint, indicating a mesaxonic to slightly ectaxonic manus and slightly ectaxonic pes (different from *Amphisauropus*, *Hyloidichnus, Ichniotherium*, *Karoopes*, *Merifontichnus*, *Procolophonichnium jageri*, *P. nopcsai*, *P. tirolensis*, *Robledopus* and *Varanopus* that are ectaxonic). Shallow impression of digit I which is often very short (different from *Amphisauropus, Hyloidichnus*, *Merifontichnus*, *Procolophonichnium jaegeri, P. nopcsai, P. tirolensis, Robledopus* and *Varanopus* that have a deep impression of digit I). Pedal digit V imprint is relatively long, set proximally and slightly separated from the digit I–IV group (different from *Amphisauropus, Hyloidichnus*, *Merifontichnus*, *Procolophonichnium jageri, P. nopcsai P. tirolensis, Robledopus* and *Varanopus* in which digit V imprint is connected with the digit I–IV group; different from chirotheriid tracks, in which the digit V imprint is much more proximal and separated from the digit I–IV group). As a consequence of this particular condition of digit V, the total length of the pes imprint exceeds that of

the longest digit by more than 50% and the proximal margin of the sole impression may either have a markedly concave and semi-circular appearance or feature a relatively longer sole impression with a less evident concavity.

Short to relatively long manual digit V imprint (different from *Amphisauropus, Hyloidichnus*, *Ichniotherium*, *Merifontichnus*, *Procolophonichnium jageri, P. nopcsai, P. tirolensis, Robledopus* and *Varanopus* that have a relatively short manual digit V imprint). Trackway pattern with regular alternating arrangement of close pes-manus couples, pace angulation is usually between 70° and 120° (lower than most chirotheriid tracks), the manus is in line with the pes (different from *Amphisauropus, Hyloidichnus, Merifontichnus*, *Procolophonichnium jageri, P. nopcsai, P. tirolensis, Robledopus* and *Varanopus* in which the manus is more medial than the pes); manus oriented parallel to the midline and pes is parallel to laterally-oriented (different from *Hyloidichnus* and *Merifontichnus* that show a more medially-oriented pes).

Diagnosis of the type ichnospecies *Capitosauroides bernburgensis*: Unlike the Konberg morphotype, the manus is considerably smaller than the pes and, in both manus and pes, the total footprint width does not exceed the total footprint length by more than 25% (see also Fig. 9A−B). In agreement with a slightly stronger ectaxony of the pes and mesaxony of the manus compared to the Konberg morphotype, pedal digit I imprint is relatively shorter and the pedal digit IV and V imprints are relatively longer, whereas the digit V imprint of the manus is often considerably shorter and the digit III imprint is the longest (see also Fig. 9C−F). Unlike the Konberg morphotype, manus and pes display a relatively short sole impression with a markedly concave proximal margin, which reflects the semi-circular arrangement of the digit basal pads. The trackway pattern of *C. bernburgensis* looks derived in comparison to the Permian *Capitosauroides* due to its relatively high pace angulation (>100°) and high body-size-normalized stride length (see also Fig. 10A, D). Marked outward orientation of the pes (over 20°) and parallel to slight outward orientation of the manus (Fig. 10B).

Capitosauroides isp., Konberg morphotype

Figs 3, 4, 5A−C, 7D−F, 8E, F, Tables 1−3

Material: NML-G 2020-0004 (TRO 6721), trackway with footprints belonging to five consecutive pes-manus couples, convex hyporelief; MfNMD P-21704a, isolated right manus imprint, convex hyporelief; MfNMD P-21402, isolated right pes imprint, convex hyporelief. MfNMD P-9550, an isolated left manus imprint excavated from strata of the Blätterton Member/Hornburg Formation outcropping at Sittichenbach (Fig. 1A) is also referred to this track type.

Diagnostic features: The manus imprint is relatively wider than in *C. bernburgensis* and not much smaller than the relatively short pes imprint (Fig. 9A, B). With digit IV imprint as the longest, a relatively long digit V imprint, and relatively short digit I and II imprints, the manus has a slightly ectaxonic appearance – unlike *C. bernburgensis*, in which digit III imprint is longest and digit V imprint is relatively short (Fig. 9D, F). Proportionally shorter pedal digits IV and V imprints and longer digits I and II imprints than in *C. bernburgensis* give to the pes a slightly more mesaxonic appearance (Fig. 9C, E). Digit imprints look not as thick, especially in the manus. Palm and sole impressions are relatively longer than in *C. bernburgensis* and only in a few imprints a slight indentation/concavity of the proximal margin of the palm/sole impression is visible. Pace angulation (<100°) and imprint-size-normalized stride length are lower than in *C. bernburgensis*; the pes is slightly less outward-oriented (Fig. 10).

Description: Relatively small, semiplantigrade and pentadactyl tracks of a quadruped. The pes imprint is wider than long and slightly larger than the manus. The digit imprints are relatively long, thick and straight and can be distally bent medially or laterally. They end in large triangular or flat claw impressions or, when the claw marks are not preserved, in enlarged and rounded terminations. The pes imprint is characterised by the following digit length proportions: I<V<II<III≤IV. The digit I imprint of the pes is short and shallowly impressed, the digit II–IV imprints of the pes are well-impressed and the digit V of the pes is proximal and slightly detached from the digit I–IV imprint group. The sole impression is generally shorter than half foot length, the proximal margin is slightly convex to concave. The manus imprint is characterised by the following digit length proportions: I<V≤II<III<IV. The palm impression is relatively short, and its proximal margin is slightly convex to concave. The trackway pattern is characterised by a simple alternating arrangement of pes-manus couples, with the manus imprint in line or slightly more lateral than pes imprint, the pace angulation is generally low (70–100°) and the gauge is high. The pes imprints can be slightly outwards-oriented, while the manus imprints are generally parallel to the midline. No pes-manus overstep nor tail/body impressions have been observed (Fig. 7A, B, D).

Remarks: Tracks of small quadrupeds, generally associated with swimming traces, have been known since a long time from the Hornburg Formation (Haubold and Katzung, 1975; Walter, 1978, 1982). These tracks have been assigned to *Amphisauropus imminutus*, *A. latus* and *Gilmoreichnus* cf. *brachydactylus* by Haubold and Katzung (1975).

The ichnotaxa *Gilmoreichnus brachydactylus* Pabst, 1900, *A. imminutus* Haubold, 1970 and *A. latus* Haubold, 1970 have been revised by Voigt (2005), who considered them junior synonyms of *Amphisauropus kablikae* (Geinitz and Deichmüller, 1882). In the last study listing the Hornburg Formation tetrapod footprint material, Voigt (2012) confirmed the potential occurrence of *Amphisauropus*. The analysed material is superficially similar to *Amphisauropus* because of the relatively long sole impression, the relatively robust digit imprints with blunt, often rounded tips, the pentadactyly, the slight ectaxony and the trackway pattern. Also, *Amphisauropus* is commonly associated with swimming traces in the Cisuralian (e.g., Voigt, 2005).

The overall poor morphological preservation (*sensu* Marchetti *et al.*, 2019c) and incompleteness of the material from the Hornburg Formation hampered a thorough ichnotaxonomic revision so far. Nevertheless, some recently found material is more complete and better preserved (e.g., Buchwitz *et al.*, 2019). The trackway on specimen NML-G

2020-0004 (TRO 6721) shows complete and well-preserved footprints. The digit imprints terminate often in large triangular claw impressions, but this feature is not observed in *Amphisauropus*, which does not have claw marks (e.g., Voigt, 2005; Marchetti *et al.*, 2017a; Fig. 8A). Moreover, the most deeply-impressed pes digits are II–IV (Figs 4, 8E–F), whereas in *Amphisauropus* are I–III (Fig. 8A). Also, the manus digit V imprint is much longer than that of *Amphisauropus* (Fig. 8A, E, F). This is observable also in the isolated manus imprints of MfNMD P-9550 and MfNMD P-21704 a/b, of specimens MNG 2365/HF 58 and 65 illustrated by Walter (1982, plates III.4 and IV.2) and of specimen HF 78. Specimens MfNMD P-9550 and MfNMD P-21704a show a proximal manus digit V imprint, different from *Amphisauropus*. The concave proximal margin of the palm in MfNMD P-9550, however, is absent in MfNMD P-21704 a, b and NML-G 2020-0004 (TRO 6721) which show a rather convex proximal margin, so being more similar to *Amphisauropus*. Nevertheless, the convex appearance of the proximal margin of the palm impression may be also due to incompletely impressed digit I and V bases.

In NML-G 2020-0004 (TRO 6721) and MfNMD P-21402, the pes digit V imprint is proximally-positioned and slightly separated from the digit I-IV group, forming a slight concavity in the proximal margin of the sole (despite the relatively long sole, Figs 4, 8E), whereas *Amphisauropus* shows the digit V in line with the other digits and normally a convex proximal margin of the sole (e.g., Voigt, 2005; Fig. 8A). A further difference from *Amphisauropus* can be found in the trackway pattern: NML-G 2020-0004 (TRO 6721) lacks an inward-rotated manus, which is more inward-positioned than the pes (Figs 7D, 10B−C). Considering all features together, this material cannot be assigned to *Amphisauropus*.

Some reptile ichnotaxa with semiplantigrade and pentadactyl footprints, large claw marks and robust digit imprints such as *Hyloidichnus*, *Merifontichnus*, *Procolophonichnium jaegeri, P. nopcsai*, *P. tirolensis*, *Robledopus* and *Varanopus* may resemble this material as well (e.g., Haubold and Lucas, 2001, 2003; Voigt, 2005; Gand and Durand, 2006; Voigt *et al.*, 2013; Klein *et al.*, 2015; Marchetti *et al.*, 2019b). However, they are all characterized by a median-lateral decrease in the relief of the pes (see Mujal *et al.*, 2020) ; thus, their pes digit I is well-impressed (Fig. 8B–D). This is not the case of the described material, in which digit imprint I of the pes is relatively shallow and the most deeply impressed digits are II–IV (Fig. 8E, F). Also, the relative length of manus digit V is longer than that of these ichnotaxa, and such proximal position of the digit V in both the pes and the manus is also not observed. Consequently, this material cannot be assigned to any of the above-mentioned ichnotaxa.

The newly found material shows instead features diagnostic of *Capitosauroides* Haubold, 1971, including: pentadactyl and semiplantigrade tracks with robust digits ending in large triangular claws or with blunt roundish terminations, digit imprints that may be distally bent outward, weak ectaxony to mesaxony, very small and shallow digit I imprint, markedly concave proximal margin of the palm/sole, proximal digit V somewhat separated from the digit I–IV group but not as proximal as in chirotheriid tracks (e.g., Haubold, 1971; Klein and Lucas, 2010). So, we assign this material to the ichnogenus *Capitosauroides*.

Nevertheless, notable differences from the type ichnospecies *C. bernburgensis* can be observed, including a more ectaxonic manus imprint, a relatively longer manus digit V, thinner but still robust digit imprints and lower pace angulations. Some of these features are also observed in other Permian material recently assigned to *Capitosauroides* isp. or cf. *Capitosauroides* isp. (Marchetti *et al.*, 2017b, 2019a, b, d) which, however, usually lack the relatively long sole impressions because the proximal part of the pes imprints is generally less-completely impressed. We consider these features as potentially diagnostic for an ichnospecific differentiation within the ichnogenus *Capitosauroides*. Although the Hornburg Formation material is more complete and better preserved than most Permian tracks assigned to *Capitosauroides*, we refrain here from erecting a new ichnospecies, because the diagnostic features are observed in few footprints apart from those of the only known trackway on specimen NML-G 2020-0004.

The ichnotaxa *Procolophonichnium haarmuehlensis* and *Karoopes gansfonteinensis* (e.g., Klein *et al.*, 2015; Marchetti *et al.*, 2019b) show also similarities with the studied material, but they differ because of the relatively shorter digit V imprint and manus mesaxony (*Procolophonichnium haarmuehlensis*) and homopody, marked ectaxony and higher pace angulation (*Karoopes gansfonteinensis*). *P. haarmuehlensis* has recently been considered to be improperly assigned to the ichnogenus *Procolophonichnium* (e.g., Marchetti *et al.*, 2019b). Thus, its relation with *Capitosauroides* should be investigated in case of revision of this ichnotaxon. In certain features, especially the relatively large size of the manus, the Konberg morphotype of *Capitosauroides* is more similar to *P. haarmuehlensis* and *K. gansfonteinensis* than to *C. bernburgensis*. On the other hand, the relatively short palm/sole with markedly concave proximal margin observed in *P. haarmuehlensis*, *K. gansfonteinensis* and *C. bernburgensis* is unlike the *Amphisauropus*-like expanded sole in the Konberg material.

Similar material: The specimens MfNMD P-21860, right pes imprint, convex hyporelief, MfNMD P-21704b, isolated right manus imprint, convex hyporelief, and MfNMD P-21859, left pes imprint, convex hyporelief, are assigned to cf. *Capitosauroides*. isp. (Fig. 5D–F) because they are generally more incomplete and/or deformed than the type material. Some other specimens, such as MS 2347 and NML-G 2020/0010 (TRO 5808) include incomplete, deformed/collapsed footprints of generally similar size and shape (Fig. 5G–H). Due to the poor morphological preservation, we consider these footprints as indeterminate tetrapod tracks. The specimens MNG 2365/HF 58 and MNG 2365/HF 65 include several isolated tracks and pes-manus couples preserved in convex hyporelief, generally incomplete and associated with swimming traces. These tracks are among the material assigned to *A. imminutus* by Haubold and Katzung (1975), and include at least a pentadactyl manus each (e.g., Walter, 1982, plates III.4, IV.2). The specimen HF 78 includes a right pes-manus couple preserved in concave epirelief, with a pentadactyl manus. This specimen is among the material assigned to *A. latus* by Haubold and

Katzung (1975). Because of the incompleteness and poor preservation of the material assigned to *Amphisauropus* and *Gilmoreichnus* by Haubold and Katzung (1975), we re-assign these specimens to indeterminate tetrapod tracks, although some features are similar to the *Capitosauroides* morphotype herein described. Walter (1982) erected a new ichnospecies based on material from the Hornburg Formation, ?*Laoporus rothenschirmbachi*. However, the step cycle on specimen FG 292/1 described by Walter (1982, figs 7, 8, p. V.1) and used as holotype features only one recognizable pentadactyl track along an incomplete step cycle. This footprint is poorly preserved because all the digits were laterally dragged and their outline is not well recognizable, therefore important information regarding morphology and proportions is not available or not reliable. Since the holotype is not assignable with certainty, even the finding of better-preserved material of similar morphology could not help to emend this ichnotaxon. Thus, we consider ?*Laoporus rothenschirmbachi* a *nomen dubium* and re-assign this material to indetermined tetrapod tracks. An incomplete step cycle on specimen FG 295/5 was instead assigned to *Foliipes* isp. by Walter (1982, fig. 9, p. V.2). Nevertheless, the footprints belonging to this specimen are completely collapsed and none of the observed morphological features can be considered as diagnostic. We re-assign this material to indetermined tetrapod tracks.

Ichnogenus *Dromopus* Marsh, 1894
Dromopus isp.
Fig. 11

From the Hornburg Formation localities Sittichenbach and Neckendorfer Grund (near Wolferode) another track type of medium size (4–6 cm long) has been reported. The tracks are marked by long and inwards-curved digit imprints ending in sharp claw impressions, generally superimposed at the base, markedly ectaxonic, with a proximal and laterally-oriented digit V imprint and pes and manus imprints of the same morphology, but with the manus imprint being slightly smaller. In some cases, a primary partial pes-manus overstep is also observed (Fig. 11C, D). These tracks can be assigned to *Dromopus* isp. in agreement with classifications of Haubold and Katzung (1975) and Voigt (2012). The specimen HF 77 includes a right pes-manus couple preserved in convex hyporelief and is among the material originally assigned to *Dromopus* by Haubold and Katzung (1975).

Swimming traces and tracks that formed in wet sediment
Figs 12, 13

Swimming traces have been found with deposits of the Blätterton Member at different Hornburg Formation localities (e.g., Falk, 2014). Here we focus on specimens excavated between 2012 and 2018 at Konberg (Ost) quarry. The tetrapod traces produced under water cover are represented by a spectrum of morphologies:

– Within silt- and claystones of the upper part of the Konberg succession (unit 6 and above) deformed footprints occur which consist of thin (collapsed), elongated, and diverging digit imprints that are irregularly connected at their bases but without a distinct palm/sole impression. These represent collapsed walking traces of tetrapods that sunk deeply into water-saturated mud. In some specimens, several pes-manus couples of these deformed footprints form a trackway – as in specimens NML-G 2020/0009 (TRO 5795) and NML-G 2020/0012 (TRO 5914) (Fig. 12A, B). In specimen NML-G 2020/0009 several millimetre-thick laminae are visibly bent by plunging and withdrawal of the limb. A series of strongly deformed undertracks that might have been formed through back-swinging wet sediment are preserved in concave hyporelief (i.e. not as a convexity as usual) on MfNMD P-21704 (Fig. 13G, H);
– The most abundant morphotype are sets of three to five short pointed or long parallel claw marks that may be arranged in a trackway-like pattern. Most of these traces come from horizon 5b (see Fig. 2B), among others the specimens MfNMD P-21704, NML-G 2020/0005 (TRO 5579), NML-G 2020/0006 (TRO 5580), NML-G 2020/0007 (TRO 5621), NML-G 2020/0011 (TRO 5909) (Figs 12C−G, 13E, F). The orientation of the claw marks may be oblique to the orientation of the trackway and the pattern may be asymmetric (i.e. zigzag-like), as in case of the long swimming track on slab MfNMD P-21704 (Fig. 13E, F). This pattern can be interpreted as pes imprints of a tetrapod half-floating in shallow water and trying to adjust the direction of movement against the water current to avoid drifting. Specimen FG 292/4 represents another example of this type of swimming track FG 292/4 (Fig. 12C). Swimming traces with similar morphologies have been assigned to the ichnogenus *Characichnos* (Whyte and Romano, 2001) but we refrain here from such a designation because most traces yet assigned to this ichnogenus display no more than three parallel claw marks and they are usually related to archosauromorph swimmers.
– Sometimes between 1 and 2 cm wide sets of three to five very thin, parallel, linear and continuous impressions occur. These structures may be paired, separated by a gap of 2.5 to 6 cm and up to 46 cm centimetres long; they may re-appear after an interval of non-impression with a certain lateral shift. Traces of this type have been found on NML-G 2020/0013 (TRO 5927) (Fig. 13A−D) and on the large slab MfNMD P-21704. They may be interpreted as marks of an individual floating in shallow water with claws only gently dragging on the bottom of the water body and possibly transported by the flow current, since the marks are very long and weakly curved to straight (no undulations are observed). On slab MfNMD P-21704 it is possible to observe a transition between a trackway and these traces, in fact the trackway ends in correspondence of the two parallel sets of scratches, has a similar width and additionally, one set clearly departs from the digit tips of a laterally-oriented pes footprint (Fig. 13C).

RESULTS OF THE MULTIVARIATE ANALYSES

According to all multivariate analyses of variance – including either only imprint length measurements or only trackway measurements – significant differences between the three reference groups occur (see MANOVA and PERMANOVA p-values listed in Table 4). According to pairwise testing, *Amphisauropus kablikae* from the Thuringian Forest Basin can be well separated from both *Varanopus microdactylus* and *Capitosauroides bernburgensis*. For *V. microdactylus* and *C. bernburgensis* however, which are both represented by only small samples, the pairwise statistic tests either fail or they show no significant difference ("V vs C" in Table 4).

Notwithstanding their problematic separability according to multivariate variance analyses, the three groups appear to occupy distinct morphospace sections in linear discriminant analyses (LDAs) based on varying combinations of measurement parameters (between 96% and 100% correct classification, see Table 5; Fig. 14). Despite its dissimilarity to the Bernburg type material in certain aspects, the Konberg trackway NML-G 2020-0004 is included in the *Capitosauroides bernburgensis* group in three out of five LDAs. In the LDA based on 14 normalized lengths, it is included in the *Amphisauropus kablikae* group, but close to the distribution field of *C. bernburgensis* (Table 5, Fig. 14C). If only six parameters that describe the trackway pattern are considered, NML-G 2020-0004 appears to be distinct from *C. bernburgensis* and is included in the *A. kablikae* group (Table 5, Fig. 14E).

In a further set of LDAs, we changed the composition of the reference groups by inclusion of the Konberg specimen NML-G 2020-0004 in a common *Capitosauroides* group together with *C. bernburgensis*; alleged *Capitosauroides* records from the Permian of South Africa and Italy were included as priorly unassigned specimens. The results demonstrated that these additional records to some degree exceed the range of *C. bernburgensis* and the Konberg type of *Capitosauroides*: Specimen UR-NO NUM 1 fell in the range of the *Amphisauropus* or *Varanopus* groups, GF-TR 9 fell in the range of *Capitosauroides* or *Varanopus* and GF-TR 11 was classified as *Capitosauroides* or *Amphisauropus* (Table 6). When only normalized digit lengths were considered, all *Capitosauroides* records came out as morphologically close to each other (Fig. 14B).

DISCUSSION

Quantitative approaches to the diagnosis of the ichnogenus *Capitosauroides*

Results of the multivariate analyses demonstrated that (a) *Capitosauroides bernburgensis* can be distinguished from *Amphisauropus kablikae* and, to a lesser degree, from

Table 5

Results of linear discriminant analyses including 27 specimens assigned to 3 reference groups and NML-G 2020-0004 from Konberg (Ost) quarry, Hornburg Formation.

Classification:	PC-based	Analyses with normalized length values			
	imprint measure-ments (PCs 2-14)	digit lengths (10)	imprint measurements (14)	trackway measurements (6)	imprint & trackway measurements (20)
Correct classification	27/27 100%	27/27 100%	27/27 100%	25/26 96.15%	26/26 100%
NML-G 2020-0004	*Capitosauroides*	*Capitosauroides*	*Amphisauropus*	*Amphisauropus*	*Capitosauroides*

Table 6

Results of linear discriminant analyses including 28 specimens assigned to three reference groups and three additional specimens from the Permian of South Africa and Italy.

Classification:	PC-based	Analyses with normalized length values			
	imprint measurements (PCs 2-14)	digit lengths (10)	imprint measurements (14)	trackway measurements (6)	imprint & trackway measurements (20)
correct classification	28/28 100%	28/28 100%	28/28 100%	24/27 88.9%	27/27 100%
UR-NO NUM 1	*Amphisauropus*	*Varanopus*	*Amphisauropus*	NA	NA
GF-TR 9	*Varanopus*	*Capitosauroides*	*Capitosauroides*	*Varanopus*	*Varanopus*
GF-TR 11	*Amphisauropus*	*Capitosauroides*	*Amphisauropus*	*Amphisauropus*	*Amphisauropus*

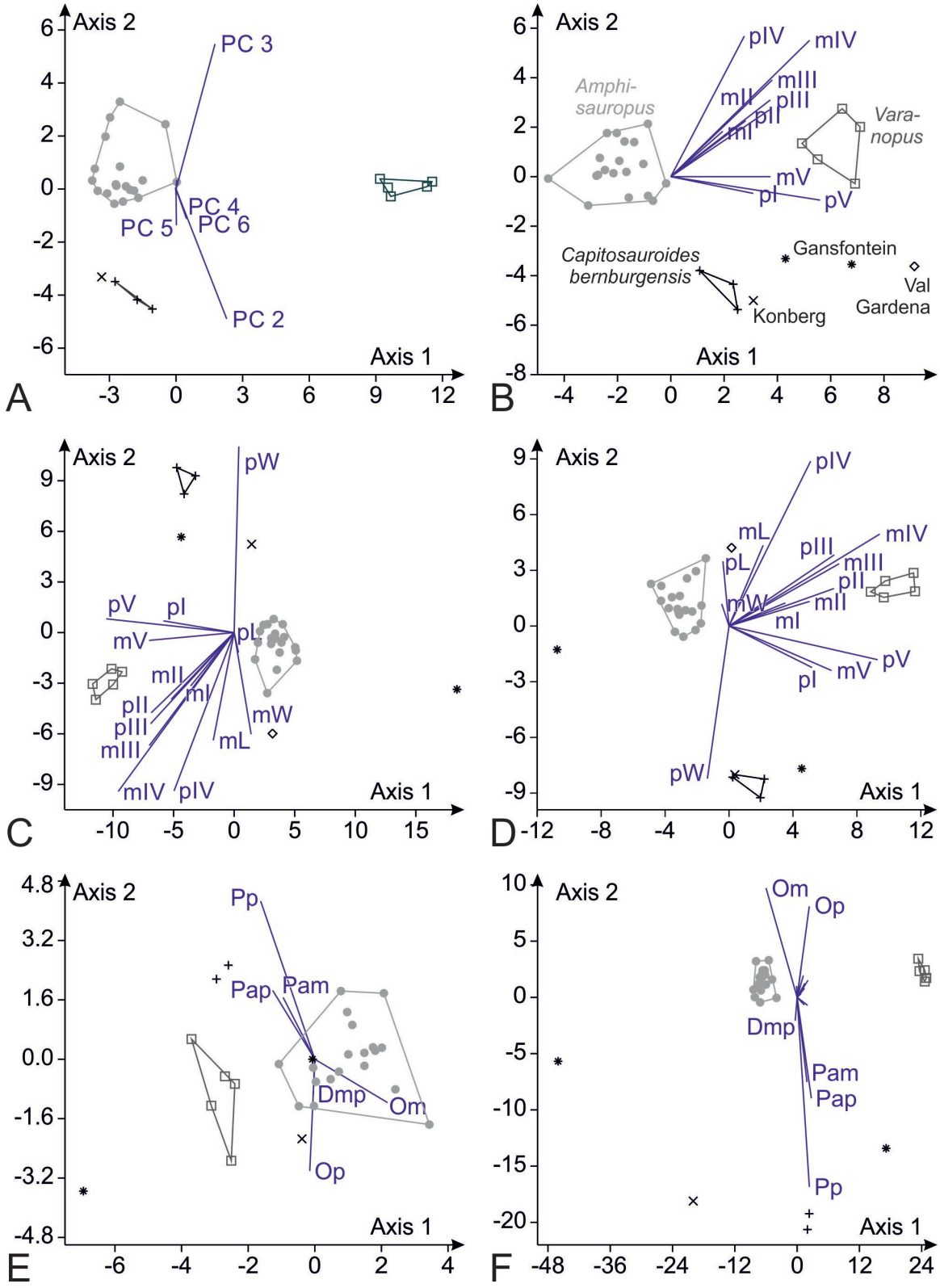


Fig. 14. Results of linear discriminant analysis for three reference groups (*Capitosauroides, Amphisauropus* and *Varanopus*) based on different variables and sample sizes; coordinate axes represent axes of discrimination. With one exception (in D) Konberg specimen NML-G 2020-0004 (cross), cf. *Capitosauroides* from the middle Permian Gansfontein Site (star) and from the late Permian of Val Gardena (rhombus) are included but are not priorly classified. **A.** LDA result for principal components 2–14, based on 14 normalized imprint lengths. **B.** LDA result for ten normalized toe lengths. **C.** LDA result for 14 normalized imprint lengths (i. e. toe lengths plus length and width of manus and pes). **D.** LDA result for 14 imprint lengths with the Konberg specimen defined "*Capitosauroides*". **E.** LDA result for six trackway parameters (including two normalized lengths and four angles). **F.** LDA result for 14 normalized imprint lengths plus six trackway parameters. Abbreviations: Dmp, manus-pes distance (along trackway); mI to pV, normalized manual digit length I to pedal digit length V, mL, manus length, mW, manus width, Om, orientation of the manus; Op, orientation of the pes; Pam, manual pace angulation, Pap, pedal pace angulation, pL, pes length, pW, pes width; Sp, pedal stride length.

Varanopus microdactylus based on imprint length measurements taken from reasonably well-preserved couples and trackways; (b) the Konberg trackway NML-G 2020-0004, assigned to *Capitosauroides* isp., often falls in or is close to the *Capitosauroides bernburgensis* spectrum and a combined *C. bernburgensis* and Konberg type group is equally well separable from *A. kablikae* and *V. microdactylus;* (c) at least two cf. *Capitosauroides* trackways from the Gansfontein Site (middle Permian of South Africa) appear to fall in close range of the combined *Capitosauroides* group; (d) trackway parameter distributions of the ichnogenera overlap and the trackway pattern is less well suitable for the distinction of *Capitosauroides* from the other two ichnotaxa but may have potential for description of the internal variability of this ichnogenus.

In conflict with the assignment of the Konberg trackway NML-G 2020-0004 to *Capitosauroides*, this specimen fell in the *Amphisauropus* group in a merely trackway-parameter-based LDA and in an analysis including 14 normalized imprint length measurements (Table 5). While the differences between the trackway patterns of *C. bernburgensis* and the Konberg trackway are obvious (and therefore the deviant classification result is unsurprising), the imprint-length-based classification result might be to some degree a methodological artifact: Datasets that include all 14 normalized imprint length measurements are somewhat problematic, given that four of these imprint lengths (total manus length, manus width, pes length, pes width) are also used for the calculation of the body size proxy (as denominator for normalization) and with this kind of redundancy a certain bias is introduced. Arguably, the PC-based approach and the analyses based on only ten normalized digit lengths (first and second column in Tables 5 and 6, Fig. 14A, B) are better suited because they avoid redundant consideration of certain length measurements.

Even though an expanded definition of the ichnogenus *Capitosauroides* to include Permian material appears to be justified according to our multivariate analysis results, its quantitative separation from other Permian to Triassic ichnotaxa, such as *Karoopes gansfonteinensis*, *Procolophonichnium haarmuehlensis* (supposed therapsid tracks according to Marchetti *et al.*, 2019b, e) and a variety of similarly-looking reptilian tracks types (other ichnospecies of *Procolophonichnium, Erpetopus, Robledopus, Hyloidichnus*) should be tested in future approaches, depending on the availability of a minimum number of specimens. The numbers of distinct pes-manus couples and trackways per group should be larger than the number of compared groups.

Trying to avoid the disadvantages of using conventional imprint size measures, such as (overall) pes length and the length of pes digit IV, which is often the longest digit in Palaeozoic pentadactyl tracks (Voigt, 2005; Buchwitz and Voigt, 2018), as body size proxies, we suggested two alternatives: (1) normalization by a combined measure that is calculated from four lengths (total manus length, manus width, pes length, pes width) and so a more robust body size indicator, especially in the case of vastly different track shapes and trackmakers representing varying degrees of heteropody (unequal manus and pes imprint size); (2) PCA of imprint lengths and subsequent use of all principal components except PC 1 (which is assumed to include all body-size-related variance) for variance analysis and classification approaches. Both procedures have certain disadvantages, e.g. interpretation difficulties and the effects of outliers in case of the PC-based approach and unequal contribution of different length measures in case of the mixed body size proxy normalization approach. Thus, they may be considered together as complementary approaches in length-measurement-based studies of tracks.

The combination of normalized imprint lengths with trackway measurements, such as normalized stride length, gauge width, pace angulation and imprint orientation (divarication from the trackway midline) in the same analysis still represents a challenge, given the different size ranges of these variables and in case of doubt, imprint and trackway measurements (especially angle measurements) might be considered in separate multivariate classification approaches.

Possible producers of *Capitosauroides* tracks

In his description of the new ichnogenus and ichnospecies, Haubold (1971) named several features that support the assignment of *C. bernburgensis* to anamniote trackmakers: (1) roundish toe tips without claw impressions; (2) lack of a metatarsal-phalangeal connection, which he regarded as typical at least for semiplantigrade reptiles; (3) the proximal end of the sole impression is indistinct/not sharply defined. He compared these footprints to the typical amphibian feet of salamanders and, considering the contradiction of the four-fingered manus of extant amphibians and most temnospondyls, provided a list of genera for which a manus with five fingers has once been observed or discussed: *Eryops* Cope, 1877, *Trematops* Williston, 1909, *Cacops* Williston, 1910, *Paracyclotosaurus* Watson, 1958 and *Branchiosaurus* Fritsch, 1875. He concluded that capitosaurs and trematosaurs, whose skulls had been excavated from the Buntsandstein strata of Merkel's quarry in Bernburg, were among the potential trackmakers and ruled out trematosaurs as marine dwellers, assigning the tracks to capitosaurs and erecting a new ichnogenus with the interpretative name *Capitosauroides*.

Contrary to Haubold's (1971) observations, we have found that some of the imprints on the type specimens of *C. bernburgensis* do in fact display triangular claw impressions (e.g., Fig. 6D, E). Although from the description of Haubold (1971) the meaning of metatarsal-phalangeal connection is not clear, we suppose that it refers to the basal digit pad lateral connection, which may be absent between the basal pad of pes digits IV and V in *Capitosauroides*. Contrary to Haubold's (1971) statements, this condition is only found in amniote tracks, such as chirotheriid tracks, or certain therapsid tracks, such as *Karoopes* (e.g., Klein and Lucas, 2010; Marchetti *et al.*, 2019b). Anamniote tracks, such as *Batrachichnus*, *Limnopus*, *Amphisauropus* and *Ichniotherium*, do not show this trait (e.g., Voigt, 2005). Also, in contrast with Haubold's (1971) suggestions, several reptiliomorph and temnospondyl tracks display a plantigrade condition with well-defined structures of the sole

and proximal margins (see the Thuringian Forest Basin ichnotaxa *Batrachichnus*, *Limnopus, Amphisauropus* and *Ichniotherium* as documented by Voigt, 2005). Unlike the two short trackways of the *C. bernburgensis* type material, the trackway pattern of the probable temnospondyl ichnotaxa *Batrachichnus* and *Limnopus* is marked by a generally low pedal pace angulation and manual imprints that are inward-rotated and somewhat more medially-positioned with respect to the pedal imprints. Furthermore, in accordance with the recent assessment of the manus structure in temnospondyls and discussion of temnospondyl tracks (Fröbisch *et al.*, 2014; Marsicano *et al.*, 2014; Mujal and Schoch, 2020; Konetzko-Meier *et al.*, 2020), there is only one specimen of a derived stereospondyl from the late the Triassic of Poland that clearly displays a five-toed manus whereas most evidence points to four manual digits (Konetzko-Meier *et al.*, 2020).

Given the improbability of a temnospondyl producer, alternative producers were hypothesized for material recently assigned either to *Capitosauroides* isp. or cf. *Capitosauroides* isp. from the late Permian of northern Italy, the middle Permian of South Africa and the late Permian of Scotland: (a) reptiliomorph amphibians, such as seymouriamorphs and chroniosuchians (Marchetti *et al.*, 2019a), or (b) parareptiles, such as procolophonomorphs (Marchetti *et al.*, 2017b), or (c) theriodont therapsids that lack the plantigrade condition of cynodonts (Marchetti *et al.*, 2019b, 2019d). Even though chroniosuchian reptiliomorphs have been reported from the late Permian and Lower Keuper of Germany (Witzmann *et al.*, 2008; Witzmann and Schoch, 2019; Witzmann *et al.*, 2020), the presence of claw marks, the concave proximal margin of the sole, the proximal position of the pedal digit V base and the relatively high pace angulation of *C. bernburgensis* are in disagreement with the trackmaker attribution of Marchetti *et al.* (2019a). Marchetti *et al.* (2017b) tentatively assigned certain imprints from the late Permian of Italy to *Capitosauroide*s and, following Mietto (1995), they suggested a parareptilian affinity for *Capitosauroides*, based on the proximal position of the pes digit V imprint, observed in the *C. bernburgensis* type material and in some tracks attributed to parareptiles such as *Erpetopus*. However, this interpretation does not take into account that *C. bernburgensis* lacks fundamental traits of parareptile tracks, such as the low total digit divergence and the marked medial-lateral decrease in relief of the pes.

In their more recent approach on South African tracks and their producers, Marchetti *et al.* (2019b) provided an extensive discussion for the interpretation of *Capitosauroides* and *Karoopes* as track types of non-cynodont theriodont therapsids: These two ichnotaxa combine relatively short and shallow palm/sole impressions with continuous digit impressions which may be more shallow in the middle (between tip and basal pads), a feature caused by the so-called synapsid digital arcade (see Kümmell and Frey, 2012). The pedal semi-plantigrady and distal bending of digit impressions may be interpreted as being related to the gorgonopsid and therocephalian intra-tarsal joint, which allowed for mobility between the astragalus and the calcaneum and may have enabled an overall increase in lateral limb mobility (Kemp, 2005). Furthermore, the semi-circular arrangement of basal digit pads and the proximally positioned digit V are interpreted as reflecting the arrangement of distal carpals and tarsals in the theriodont limb skeleton: due to the absence of distal tarsals/carpals for digit V, the phalanges may have been in direct contact with the calcaneum/ulnare and thus the digit V impression appears to diverge more proximally. Marchetti *et al.* (2019b) noted that *Capitosauroides* and *Karoopes* share with other ichnotaxa allegedly produced by synapsid trackmakers a medial-lateral increase of imprint relief (lateral functional prevalence, see also Mujal *et al.*, 2020).

Following their assignment of *Capitosauroides* and *Karoopes* to derived therapsids of the clade Theriodontia, Marchetti *et al.* (2019b) discuss features that may be used to support a more exact track-trackmaker correlation and suggest that pedal ectaxony, manual mesaxony, footprint heteropody (pes notably larger than manus) and reduction of lateral digit impressions in *Capitosauroides* are consistent with the group Therocephalia, whereas these features are absent in *Karoopes*, which could have been produced by members of the closely related Gorgonopsia.

With the revised diagnosis of *Capitosauroides* and inclusion of the Konberg material in the present study, the morphological spectrum for this ichnogenus is larger than according to previous considerations by Marchetti *et al.* (2019a, b, d) and thus the producer group might be less exclusive. Critical features that distinguish *Capitosauroides* from *Karoopes*, i.e. pedal ectaxony, manual mesaxony, heteropody and reduction of lateral digit impressions, are not as distinct in *Capitosauroides* isp. from Konberg as in the type ichnospecies. However, due to their morphology, maximum size and conspicuous trackway pattern, marked by very high pace angulations and primary pes-manus overstep, trackways of *Karoopes* are well distinguishable from *Capitosauroides*. Among others, the shape and the relative length of the sole impression and the low pace angulation give the Konberg *Capitosauroides* a more primitive appearance than *C. bernburgensis*. This difference could be explained by the higher stratigraphic age of the Konberg material and a more basal therocephalian or related non-therocephalian therapsid trackmaker. After the interpretation of *Procolophonichnium haarmuehlensis* from the Muschelkalk (Middle Triassic) of Winterswijk as a probable therocephalian track type (Marchetti *et al.*, 2019e), the track-trackmaker correlation may become even more complex because the herein redefined ichnogenus *Capitosauroides* may cover some, yet not all therocephalian tracks. In agreement with the earlier assessment of Marchetti *et al.* (2019b, e) we rule out anamniote, reptilian or non-theriodont synapsid producers.

Stratigraphic ranges of *Capitosauroides*, *Amphisauropus* and their producers

According to the revisions of Voigt (in Gebhardt, 2009; 2012) *Dromopus* and *Amphisauropus* are the only valid tetrapod ichnotaxa with convincing records from localities of the Hornburg Formation. Their co-occurrence and the lack of modern ichnotaxa would be a weak indication for an early Permian age (*Dromopus* footprint biochron sensu Voigt and Lucas, 2018) and in conflict with the late

middle Permian age inferred from lithostratigraphic correlation and magnetostratigraphic data (see Gebhardt and Lützner, 2012). In this study we have, however, assigned superficially *Amphisauropus*-like tracks of varying quality to *Capitosauroides* isp., cf. *Capitosauroides* isp. or indeterminate tetrapod tracks and regard *Amphisauropus* as absent from the Hornburg Formation until better evidence emerges. Neither can swimming traces of the Hornburg Formation that are usually associated with *Capitosauroides* or *Capitosauroides*-like tracks be assigned to *Amphisauropus*. Since the supposed *Amphisauropus* tracks of the Hornburg Formation represented the youngest record of this ichnogenus apart from a questionable Moroccan pes-manus imprint couple (Hminna *et al.*, 2012; Voigt, 2015; Schneider *et al.*, 2020) and some poorly-preserved tracks described from a different Moroccan site by Moreau *et al.* (2020), our re-interpretation of the Hornburg Formation record leaves *Amphisauropus* restricted to the Cisuralian. The new *Amphisauropus* LAD (Last Appearance Datum) is therefore from the late Kungurian Pizzo del Diavolo Formation of Italy (e.g., Marchetti *et al.*, 2017a). Even though anamniote reptiliomorphs as potential producers of *Amphisauropus* tracks persist to the late Middle Triassic (Witzmann *et al.*, 2008; Schoch *et al.*, 2010), skeletal remains are rare and the predominantly aquatic lifestyle of these late occurring representatives means that no or only sparse track records can be expected.

The Konberg morphotype falls within the previously known late middle Permian to late Early Triassic range of *Capitosauroides* according to the stratigraphic ages of the type ichnospecies and of additional occurrences described by Marchetti *et al.* (2017b, 2019a, b, c). The stratigraphic range of *Capitosauroides* is roughly corresponding to that of therocephalian therapsids whose latest surviving lineage reached the Anisian (Abdala *et al.,* 2014), but it would also be in agreement with "non-cynodont theriodonts" as a less exclusive producer group that includes a considerably larger spectrum of Permian taxa. If the assumption of a late therocephalian trackmaker for *Procolophonichnium haarmuehlensis* is correct (Marchetti *et al.*, 2019e), the record of theriodont tracks from Saxony-Anhalt would span more than 20 Million years from the late middle Permian Konberg type of *Capitosauroides* to the late Anisian *P. haarmuehlensis*, which is an abundant track type in the Middle Muschelkalk tidal flat deposits that are outcropping close to the Early Triassic type locality of *C. bernburgensis* (Diedrich and Trostheide, 2007; Diedrich, 2011).

Inference from Hornburg Formation swimming traces

At Konberg quarry, the tetrapod swimming traces of the three morphotypes distinguished above are associated with tracks assigned to *Capitosauroides* isp. Swimming traces of the most common type – sets of four to five shorter or longer parallel or slightly curved claw marks, that may form a continuous trackway-like pattern – have also been documented from other Hornburg Formation localities (Falk, 2014). They are reminiscent of similar-shaped scratches that have been described from other Permian and Triassic sites, where they usually feature only three parallel claw marks per set

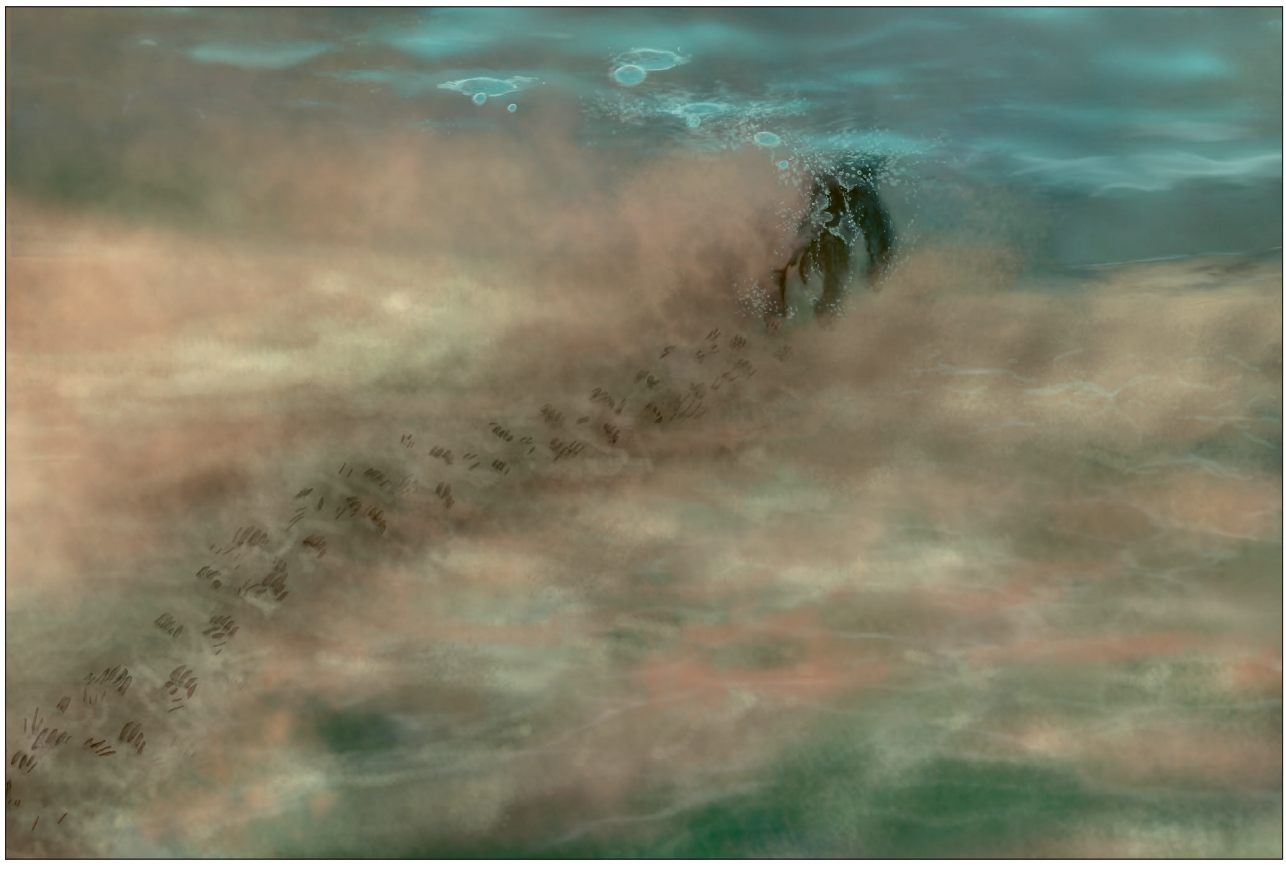


Fig. 15. Artistic reconstruction of the formation of a long sequence of swimming traces found on slab MfNMD P-21704 (see also Fig. 13E, F).

(Swanson and Carlsen, 2002; Thomson and Lovelace, 2014; Thomson and Droser, 2015; Reolid *et al.*, 2018, Sadlok and Pawełczyk, 2020).

This type of swimming traces has been interpreted as the product of derived reptilian or synapsid producers generating propulsion through parasagittal limb movements and occasionally or regularly scratching the substrate during backstroke (Swanson and Carlsen, 2002; Sadlok and Pawełczyk, 2020; Fig. 15). Long and curved or sigmoidal-shaped traces only rarely occur in the most densely scratched horizon (5c) at Konberg quarry among the mostly straight claw mark sets. Clear indications for tetrapods swimming through lateral undulation of the body axis or continuous limb motion with a considerable lateral component are missing. Due to clear transitions between swimming traces and locomotion traces assigned to *Capitosauroides* isp., we find it likely that all yet documented swimming traces were produced by the trackmakers of this ichnogenus and find it no evidence for additional producer groups with a more amphibian-like aquatic locomotion. The question whether these Hornburg Formation swimming traces are indicative for a certain set of palaeoenvironmental conditions, i.e. the *Characichnos* tetrapod ichnofacies (*sensu* Hunt and Lucas, 2007), requires a broader consideration of other ichnological and sedimentological evidence and shall be discussed elsewhere.

CONCLUSIONS

According to our description of a recently found, well-preserved trackway and further footprints and swimming traces from the Konberg quarry and their qualitative and quantitative comparison with Permian and Triassic track types, the new material does not represent one of the ichnotaxa previously described from the middle Permian Hornburg Formation but can be placed in the ichnogenus *Capitosauroides* with some justification based on imprint proportions, digit arrangement and the structure of the palm/sole. In accordance with previous assumptions about *Capitosauroides* tracks, this track type from Konberg may be referred to a small therapsid trackmaker and we find likely that some, if not all, co-occurring tetrapod swimming traces were made by the same group of producers. Hornburg Formation tracks that were previously assigned to *Amphisauropus* are considered here as indeterminate tetrapod tracks. They may represent poorly preserved footprints of the same trackmaker.

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Appendix

Measurement tables for *Capitosauroides* trackways

Abbreviations: pI–pV, pedal digit lengths I–V [mm]; pL, total pes length [mm]; pW, total pes width [mm]; pDIV, divarication angle between pedal digits I and V [°]; mI-mV, manual digit lengths I–V [mm]; mL, total manus length; mW, total manus width [mm]; mDIV, divarication angle between manual digits I and V [°]; Sp/Sm, pedal/manual stride length [mm]; Pp/Pm, pedal/manual pace length [mm]; GWp/GWm, pedal/manual gauge width [mm]; Dpm, along-track distance between pes and subsequent manus [mm], GAL, glenoaccetabular length [mm]; PAp/PAm, pedal/manual pace angulation [°]; Op/Om, orientation of pes/manus with respect to trackway midline [°]. DIV negative = manus/pes outwardly rotated, beta positive = manus/pes inwardly rotated; Wmp negative = manus more outward than pes.

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Couple no.	pI	pII	pIII	pIV	pV	pL	pW	pDIV
l1	NA	NA	NA	NA	NA	NA	NA	NA
r1	6	8	9	9	9	20	24	56
l2	NA	7	8	8	NA	16	NA	NA
r2	NA	8	9	10	5	19	NA	NA
l3	NA	8	10	NA	NA	NA	NA	NA
r3	NA	NA	NA	NA	NA	17	NA	NA
median	6	8	9	9	7	18	24	56

Couple no.	mI	mII	mIII	mIV	mV	mL	mW	mDIV
l1	4	7	7	NA	NA	NA	NA	NA
r1	4	6	8	8	7	16	22	129
l2	5	7	7	NA	NA	NA	24	NA
r2	4	7	10	9	7	NA	24	127
l3	6	8	8	NA	NA	16	NA	NA
r3	5	8	8	NA	NA	NA	NA	NA
median	4.5	7	8	8.5	7	16	24	128

Step cycle	Sp	Sm	Pp	Pm	GWp	GWm	Dpm	GAL	PAp	PAm	Op	Om
l1-r1-l2	NA	87	NA/65	72/66	NA	54	25	NA	NA	77	-9	24
r1-l2-r2	82	79	65/61	66/73	48	58	22	62	89	69	-13	3
l2-r2-l3	81	83	61/60	73/71	45	59	22	64	82	70	-22	0
r2-l3-r3	79	78	60/68	71/75	50	61	24/22	63	74	65	25/-5	0/-5
median	81	81	63	72	48	58.5	22	63	82	69.5	-9	0

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Couple no.	pI	pII	pIII	pIV	pV	pL	pW	pDIV
r1	NA	NA	NA	NA	NA	NA	NA	NA
l1	15	19	20	17	NA	58	53	107
r2	NA	18	24	27	19	40	54	NA
l2	19	28	32	30	24	60	62	83
r3	12	17	22	26	15	48	58	110
median	15	18.5	23	26.5	19	53	56	107

Couple no.	mI	mII	mIII	mIV	mV	mL	mW	mDIV
r1	NA	NA	NA	NA	NA	NA	NA	NA
l1	11	14	16	16	15	38	41	137
r2	6	13	20	21	13	33	43	144
l2	11	16	16	16	14	36	45	133
r3	9	13	17	16	9	27	45	129
median	10	13.5	16.5	16	13.5	34.5	44	135

Step cycle	Sp	Sm	Pp	Pm	GWp	GWm	Dpm	GAL	PAp	PAm	Op	Om
r1-l1-r2	NA	362	NA	220/218	NA	124	44	NA	NA	111	-18	10
l1-r2-l2	364	376	224/231	218/242	136	132	40	230	106	109	-41	-22
r2-l2-r3	383	379	231/232	242/202	130	116	54/34	236	112	117	-27/-38	1/-13
median	373.5	376	231	219	133	124	42	233	109	111	-32	-6

HF 25

Couple no.	pI	pII	pIII	pIV	pV	pL	pW	pDIV
l1	NA	18	30	33	26	65	67	NA
r1	11	16	22	30	26	56	73	151
l2	13	16	23	28	27	56	73	142
r2	18	NA	NA	NA	NA	NA	NA	136
median	13	16	23	28	26	56	73	142

Couple no.	mI	mII	mIII	mIV	mV	mL	mW	mDIV
l1	9	16	18	20	18	42	48	131
r1	NA	NA	NA	NA	NA	NA	NA	NA
l2	8	12	13	17	16	40	47	189
r2	NA	NA	NA	NA	NA	NA	NA	NA
median	8.5	14	15.5	18.5	17	41	47.5	160

Step cycle	Sp	Sm	Pp	Pm	GWp	GWm	Dpm	GAL	PAp	PAm	Op	Om
l1-r1-l2	436	426	244/232	255/231	96	116	59/56	271	132	122	-35/ -30	-5/ NA
r1-l2-r2	304	NA	232/150	231/NA	111	NA	49	NA	104	NA	-34	-3
median	370	426	232	243	103.5	116	56	271	118	122	-34	-4

Supplement I and Supplement II are available online: http://www.asgp.pl/90_2.