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SYNAPTICHNIUM TRACKS FROM THE MIDDLE MUSCHELKALK (MIDDLE TRIASSIC, ANISIAN) BERNBURG SITE (SAXONY-ANHALT, GERMANY)

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Abstract: The Solvay Quarry of Bernburg is one of the most important ichnosites from the Muschelkalk of the Germanic Basin. Extensive surfaces with long chirotheriid trackways have been discovered and assigned to *Chirotherium* and *Isochirotherium*. Some undescribed step cycles from this site are analysed here and assigned to *Synaptichnium* isp. These footprints belong to a “thick-digit” *Synaptichnium* morphotype recognised at several Middle Triassic sites of Pangaea that seems to differ from the currently valid *Synaptichnium* ichnospecies. This is the first occurrence of *Synaptichnium* from this site and the only including step cycles one from the track-bearing Muschelkalk successions of N Germany and the Netherlands. A comparison between the tetrapod ichnoassociations of marginal marine and alluvial units of the Muschelkalk of the Germanic Basin reveals a similar ichnofaunal composition but different relative proportions between ichnotaxa. *Rhynchosauroides* and *Procolophonichnium* occur more often in tidal units, whereas the alluvial units show a higher abundance of chirotheriid tracks and an overall greater track diversity.

Key words: Triassic, tetrapod footprints, ichnotaxonomy, chirotheriid tracks, Germanic Basin, tidal palaeoenvironments.

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INTRODUCTION

Tetrapod footprints from the Muschelkalk of the Germanic Basin have been known since Faber (1958) described them from the Lower Muschelkalk site of Winterswijk, the Netherlands (e.g., Demathieu and Oosterink, 1983, 1988; Marchetti *et al.*, 2019a; Fig. 1). Holst *et al.* (1970) described the first footprints from the Lower Muschelkalk of Germany, from Haarmühle (NW Germany). During the past 20 years, several studies revealed a high abundance of footprints from the marginal marine limestone deposits of the Lower and Middle Muschelkalk of N Germany, between the North Rhein-Westphalia, Hessen, Thuringia and Saxony-Anhalt regions (see Diedrich, 2015 and references therein). Further sites were described from the alluvial siliclastic Muschelkalk units of NE Bavaria, Germany (e.g., Haubold and Klein, 2002; Klein and Lucas, 2018). All localities in the Netherlands and N Germany are representative of tidal flat palaeoenvironments and are characterised by a high abundance of small tracks of *Rhynchosauroides* and *Procolophonichnium* and by the rarity of chirotheriid tracks, forming low-diversity ichnoassociations. Therefore, chirotheriid tracks are generally scattered and isolated. A notable exception is represented by the trampled surfaces from the Solvay Quarry of Bernburg, between the cities of Magdeburg and Halle, Saxony-Anhalt. Several long and well-preserved trackways of *Chirotherium barthii* and *Isochirotherium herculis* have been documented from this locality (Diedrich, 2012). These track-bearing surfaces include *Rhynchosauroides*, *Procolophonichnium* and supposed limulid tracks, reported from 12 different layers of the lower Middle Muschelkalk (Karlstadt Formation, Anisian; e.g., Diedrich, 2015). Nevertheless, some of these trampled layers remained undocumented. Here we describe, for the first time, a selection of chirotheriid footprints found in layers 5 and 6 of Diedrich (2012), including incomplete step cycles and trackways. Although this material is generally not well-preserved, the recognised diagnostic features differ from *Chirotherium* and *Isochirotherium* and are instead close to *Synaptichnium*. *Synaptichnium* is unknown from the Bernburg site and it is rare in the Muschelkalk of N Germany and the Netherlands. In fact, it was reported from only two localities in the Muschelkalk of NW Germany (Germete and Grossenlüder), with only an isolated single track being illustrated (Diedrich, 2009, fig. 5c). Therefore, the trackways described here are of great interest. The scope of this contribution is to correctly assign the morphotype found in layers 5 and 6 of the Bernburg site through a selection of the best-preserved material and the use of photogrammetric techniques. The results are compared with other possible *Synaptichnium* occurrences from the Muschelkalk of the Germanic Basin. Finally, palaeoecological and faunistic inferences are provided.

GEOLOGICAL SETTING

The economically important carbonates of the Solvay Quarry Bernburg (GPS: 51°49′11.9″ N 11°43′23.7″ E) are part of the Triassic Muschelkalk successions of the Tethyan periphery Germanic Basin (Fig. 1).

During the earliest Triassic (lowermost Buntsandstein) the Germanic Basin, or Central European Basin, was completely enclosed by extensive Precambrian and Palaeozoic massifs, namely the London-Brabant Massif in the W and SW, the Fennosarmatian Massif in the N and NE and the Vindelician-Bohemian Massif in the S and SE, and therefore separated from the Tethys ocean to the South (Szulc, 2000; Matysik and Szulc, 2019; Fig. 1). The spreading of the Tethys domain resulted in the opening of the East Carpathian and Silesian-Moravian gates (or “Silesian Gate”) during the Olenekian (middle-upper Buntsandstein facies), and in the deposition of basin-wide carbonates, that began during the middle Anisian transgression (Muschelkalk facies). The deposition continued during a second transgression with the opening of the Western Gate (or “Burgundy Gate”), during the late Anisian (Szulc, 1999, 2000; Götz, 2002). These transgressions were followed by a

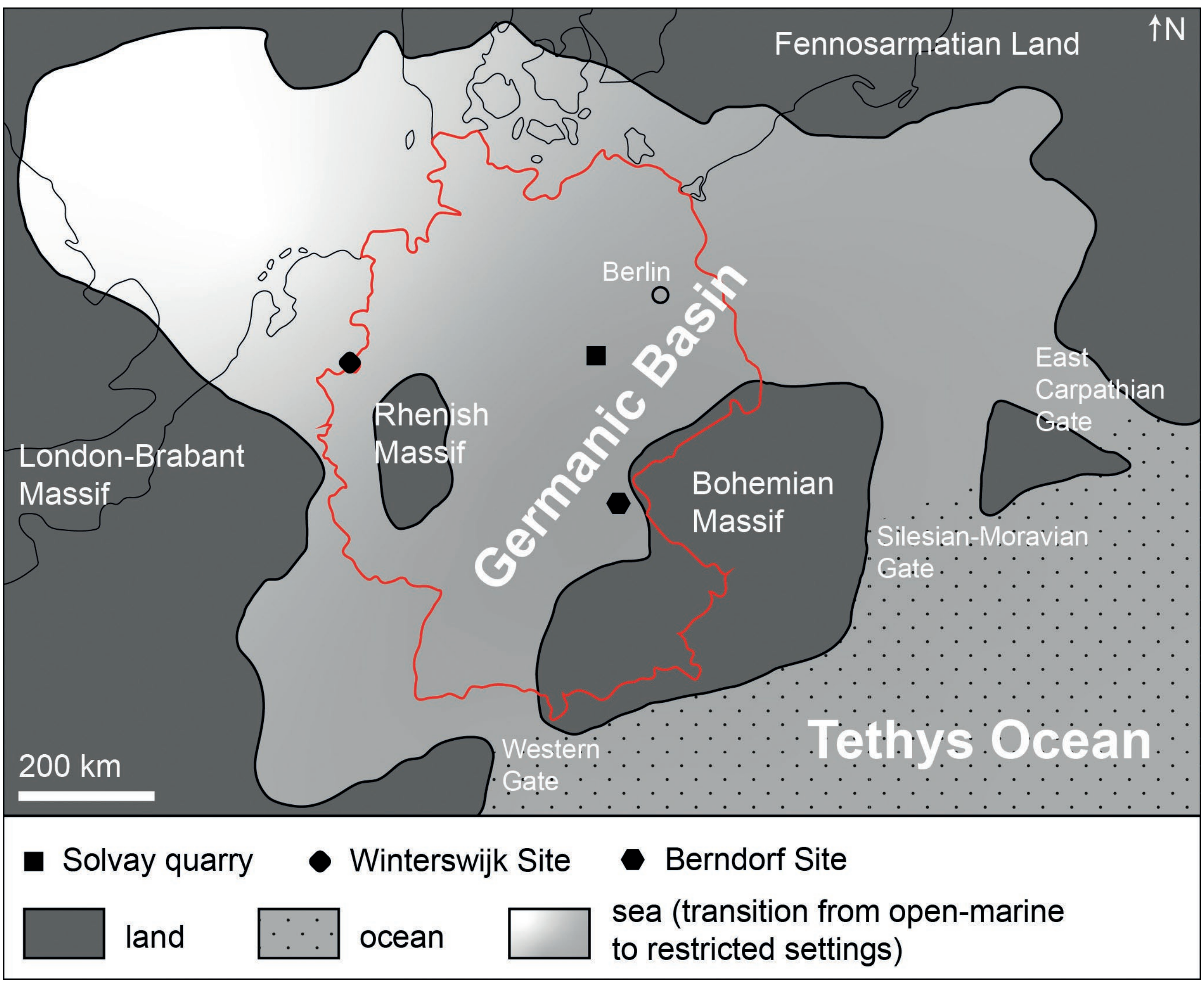

Fig. 1. Palaeogeographic position of Germany (red border) and, in particular, of the Solvay Quarry and the Berndorf site (both Germany) as well as the Winterswijk site (the Netherlands) in the Middle Triassic Germanic Basin; modified after Szulc (2000), Matysik and Szulc (2019).

regression resulting in the deposition of evaporites located in the western Germanic Basin, and of lenticular carbonates and "Wellenkalk facies" in the central and eastern areas of the basin (Götz, 2002). The basin margins are dominated by marly-clayey dolomite successions, which are partly sandy in the western margin (Schwarz, 1970). During the Ladinian, the Germanic Basin became separated from the Tethys domains, as all the gates were closed due to intense crustal uplift in the Polish province.

The Middle Triassic carbonates of Bernburg have a total thickness of 125 m (Diedrich, 2015; Fig. 2). The succession yields track-bearing carbonates and dolomites of the Aegean Röt Formation (uppermost Buntsandstein), followed by carbonates of the Jena Formation (Lower Muschelkalk; Wellenkalk facies) and track-bearing laminated limestones of the overlying basal Karlstadt Formation (Middle Muschelkalk; Fig. 2C, D). The facies reveals high current and wave activity for the Lower Muschelkalk, changing into a very shallow marine depositional realm with increasing salinity for the Middle Muschelkalk.

Twelve track-bearing beds have been documented from the basal Karlstadt Formation of the Bernburg section (Fig. 2A). Their host sediment is described as laminated mudstones and thin micritic to arenitic carbonate layers. The tracks show different preservational states but are usually displayed as only very shallow footprint reliefs. However, in some layers, preservation of scalation patterns on digit traces and heel pads is common. According to Diedrich (2015), sedimentological patterns include wave ripples, drift marks, mud cracks and slickensides.

The track-bearing layers we focus on here (beds 5 and 6) are part of a sequence of beds, in which each bed is about 10 cm thick. These mostly flat beds consist of finely laminated calcilutites and calcarenites. The uppermost laminae are visibly deformed by the footprints (Fig. 2B). The very shallow and non-collapsed footprints preserving some morphological details suggest the presence of a relatively dry microbial mat covering the original surface (see Marchetti *et al.*, 2019b, fig. 25). Ripple marks occur, if recognizable, with low crest heights. Mud cracks are common and form polygons of several tens of centimetres in width (Fig. 2E). This can be interpreted as recording shallow water deposition with alternating phases of submersion and temporary subaerial exposure.

The track-bearing sediments from this site have been assumed to represent mainly storm-related deposits of the upper tidal flats under the influence of strong seismic activity (Diedrich, 2015). However, the bedding surfaces show no evidence of strong wave or storm activity such as intensive cross-bedding or intercalated shell deposits. Moreover, the footprints do not show signs of erosion. So, we reject the hypothesis of storm-related deposits. Extensive NNE–SSW parallel cracks (shifting to E-W) are described by Diedrich (2015) as synsedimentary slickenside vein structures induced by seismic activity. However, these veins cut the whole bed, including tracks and mud cracks (Figs 2B, 5C). We, therefore, assume a post-sedimentary tectonic-driven origin, probably related to the rifting of the Tethys, that was associated with the reactivation of ancestral lineaments (Matysik and Szulc, 2019).

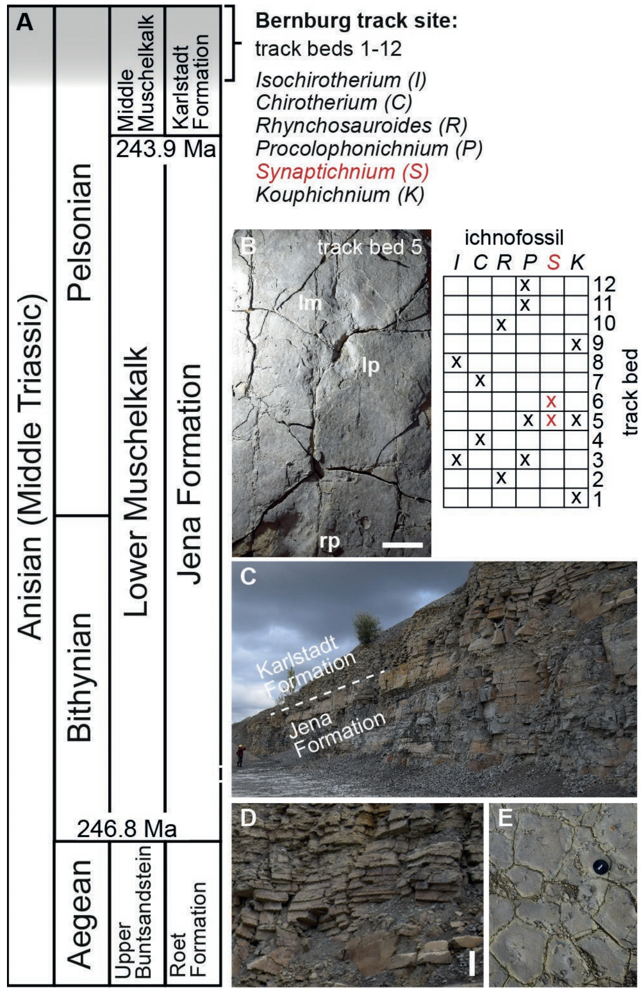

Fig. 2. Stratigraphy, ichnology and lithostratigraphy of the Bernburg Solvay Quarry track site locality. **A.** Stratigraphic position and ichnotaxa of the track-bearing horizons; after Radzinski (2008), Diedrich 2015; **B.** LVH-F-V-38. *Synaptichnium* isp. right pes (rp), left pes (lp) and left manus (lm) cut by linear, parallel and partly polygonal post-sedimentary cracking on track bed 5, scale 10 cm; *Synaptichnium* isp. is also revealed in track bed 6; compiled after Diedrich (2015). **C.** Lithological transition from the Jena Formation (Lower Muschelkalk) to the Karlstadt Formation (Middle Muschelkalk) in the quarry outcrop. **D.** Mainly planar bedded, laminated limestones of the Lowermost Karlstadt Formation, partly tetrapod track-bearing, scale 1 m. **E.** Upper plane bedding surface of the Karlstadt Formation reveals intensive polygonal desiccation cracking.

MATERIAL AND METHODS

All material comes from the track-bearing layers 5 and 6 of Diedrich (2012) in the upper part of the stratigraphic section of the Solvay Quarry of Bernburg (Germany). These layers are part of the Karlstadt Formation, lower Middle Muschelkalk, Middle Triassic (Anisian) (Fig. 2).

Specimens are stored in the collection of the Landesmuseum für Vorgeschichte, Halle (Saale), Landesamt für Denkmalpflege und Archäologie Sachsen-Anhalt (acronym LVH).

All slabs were studied first-hand and photographed with oblique light. 3D photogrammetric models were obtained with standard techniques (e.g., Mallison and Wings, 2014) for the most significant specimens. The material was selected by employing morphological preservation *sensu* Marchetti e*t al.* (2019b), to exclude extramorphologies from the systematic analysis. The track measurements follow the conventions of Leonardi (1987).

SYSTEMATIC PALAEONTOLOGY

Synaptichnium Nopcsa, 1923
Synaptichnium isp.
Figs 3–5

Material: LVH-F-V-3, incomplete step cycle with footprints of three consecutive pes-manus couples; LVH-F-V-13, trackway with footprints of four consecutive pes-manus couples; LVH-F-V-18, trackway with three consecutive pes-manus couples; LVH-F-V-29, incomplete step cycle with tracks of two consecutive right pes-manus couples; LVH-F-V-30, incomplete step cycle with three consecutive right pes imprints; LVH-F-V-34, trackway with three consecutive pes-manus couples; LVH-F-V-38, incomplete step cycle with two consecutive pes-manus couples; LVH-F-V-43, incomplete step cycle with footprints of three consecutive pes-manus couples; LVH-F-VI-88, right pes-manus couple; all footprints preserved in concave epirelief.

Description: Semiplantigrade to semidigitigrade, pentadactyl footprints of a quadruped. The pes imprint is longer than wide, about 10–13 cm in length and 8–10 cm in width. Anterior digit group I–IV compact and well-separated from the postero-laterally positioned and laterally everted digit V. The latter is preserved with a robust, proximally expanded basal pad impression and lacks a distinct phalangeal portion. Digit group I–IV wider than long, with subparallel digit imprints increasing in length continuously between digits I and III. Digit III imprint is about as long as or slightly longer than digit IV. Digit imprints are straight, thick, with

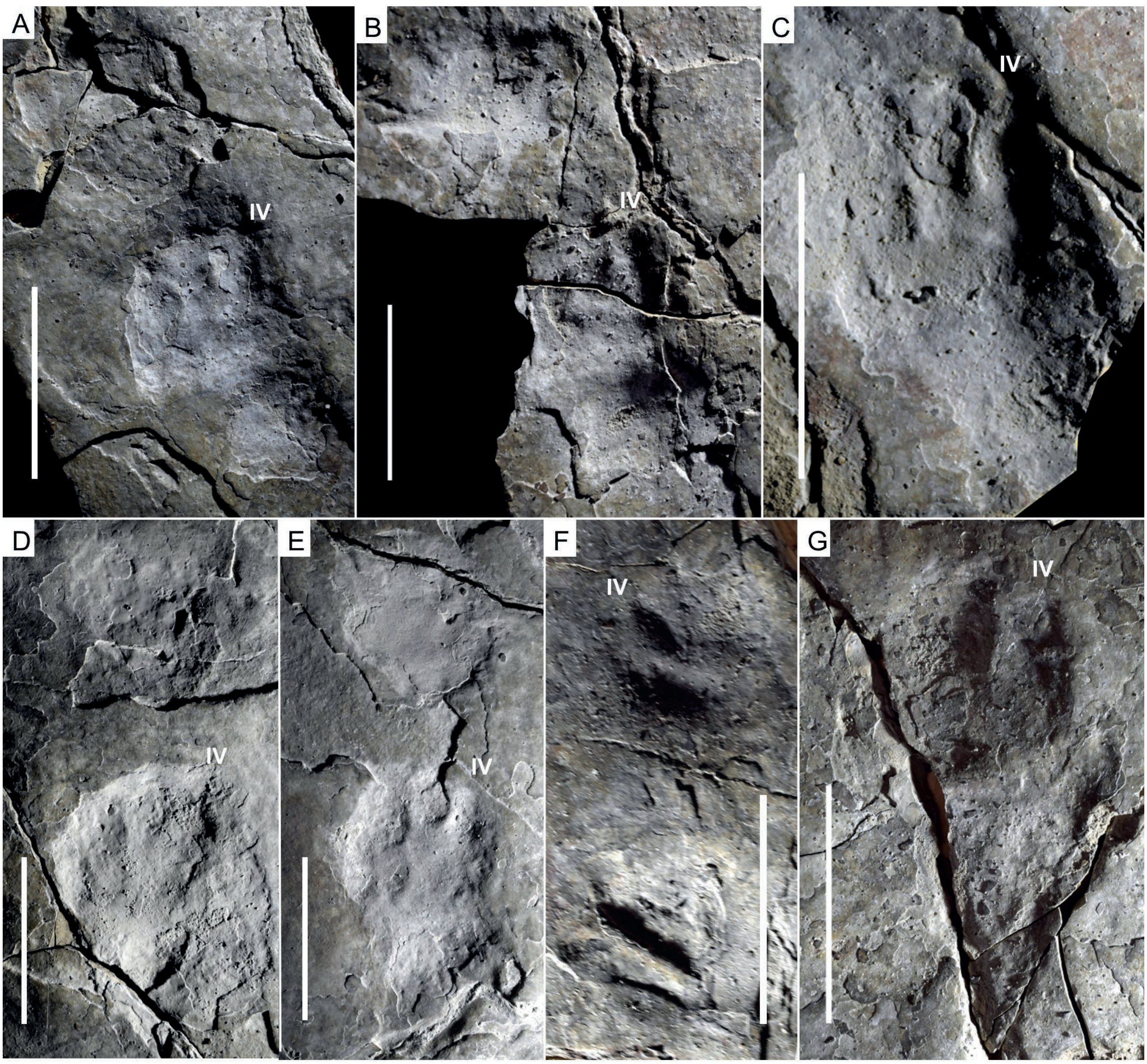

Fig. 3. Footprints of *Synaptichnium* isp., concave epirelief. **A.** LVH-F-V-18. Right pes-manus couple. **B.** LVH-F-V-13. Right pes-manus couple. **C.** LVH-F-V-38. Right pes imprint. **D.** LVH-F-V-37. Right pes-manus couple. **E.** LVH-F-VI-88. Right pes-manus couple. **F.** LVH-F-V-34. Left pes-manus couple. **G.** LVH-F-V-3. Right pes imprint. IV – digit IV imprint. Scale bars 10 cm.

rounded phalangeal and metatarso-phalangeal pad traces preserved in some specimens, and with indistinct small claw impressions. Manus imprint incomplete and smaller than pes imprint. It is about 6–7 cm long, wider than long or as long as wide and semiplantigrade. Relatively short digit imprints, ending in rounded terminations or small claw marks. Digit III imprint seems to be the longest, digit V is postero-laterally positioned and separated from digit group I–IV. Trackways narrow with relatively long stride length (pes: 93–103 cm, manus: 92–96 cm) and pace length (pes: 45–52 cm, manus: 45–50 cm) and high pace angulation (pes: 167–175°, manus: 159–167°), characterised by a simple alternating arrangement of pes-manus couples. The manus is positioned anterior to the pes, and the pes is strongly outwards-oriented relative to the midline.

Remarks: Although not well-preserved, these footprints have a clear chirotheriid morphology, because of the compact digit I–IV group with the sharply-defined proximal margin and the well-separated and proximal digit V (Figs 3–5). They differ from both *Isochirotherium* and *Chirotherium*, the two chirotheriid ichnogenera known from Bernburg (e.g., Diedrich, 2012), in digit proportions and relative size of the manus. In fact, the pes digit II is too short and the manus is too large compared to *Isochirotherium*, while pedal digit IV is too long for both *Isochirotherium* and *Chirotherium*. Also, the digit I–IV group forms a consolidated block (Figs 3–5), different from both ichnogenera with the exception of *C. sickleri* (e.g., Klein and Lucas, 2010a). The ichnogenus *Isochirotherium* is characterised by dominating pes digits II and IV while pes digits I and IV are much shorter. *Chirotherium* has a functionally tridactyl (II, III, IV), mesaxonic pes. The digit proportions are slightly similar with those of *Protochirotherium*, but the latter is characterised by a shorter, often laterally diverging digit IV and a broad digit V with a massive basal pad impression (e.g., Fichter and Kunz, 2004; Klein and Niedźwiedzki, 2012).

Overall morphology, digit proportions and digit arrangement (Figs 3–5) are in agreement with the ichnogenus

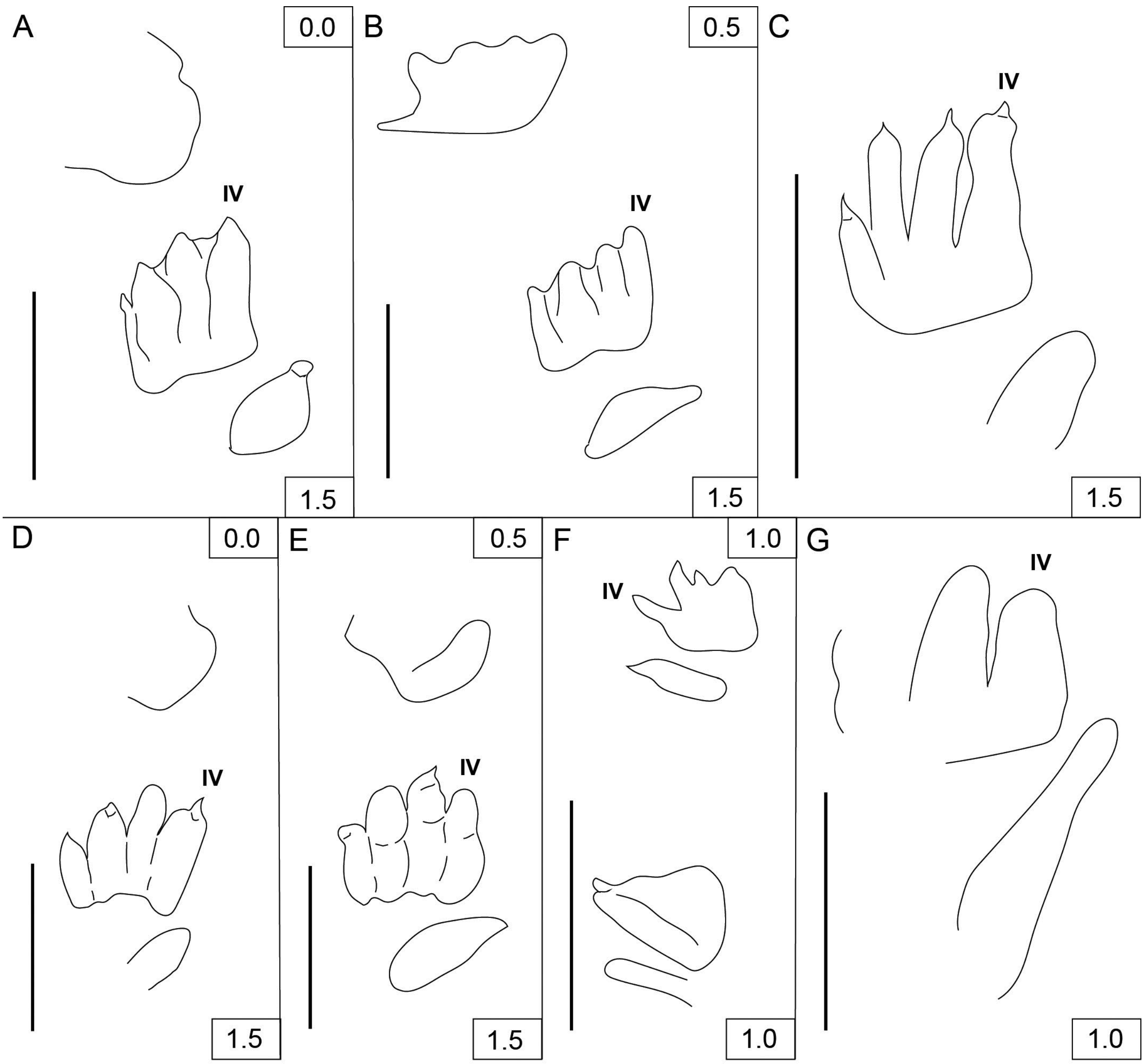

Fig. 4. Footprints of *Synaptichnium* isp. described here from the Solvay Quarry, interpretive drawings. **A–G.** See caption of Fig. 3. Numbers in the boxes beside tracks refer to the preservation scale of Marchetti *et al.* (2019b). IV – digit IV imprint. Scale bars 10 cm.

Synaptichnium, especially because of the parallel digits I–IV and the relative length of digits III and IV (e.g., Avanzini and Mietto, 2008; Klein and Lucas, 2018; Fig. 6A, C). Additionally, the orientation and morphology of pedal digit V and the mesaxonic manus are consistent with this ichnogenus. Nevertheless, some features such as the relatively thick digits, sometimes with rounded terminations, and the relatively long pes digit III differ from the ichnospecies *S. pseudosuchoides, S. cameronense* and *S. diabloense* (e.g., Klein and Lucas, 2010a; 2018) and are instead similar to several Lower-Middle Triassic footprints originally assigned to *Brachychirotherium* and later considered a *Synaptichnium* morphotype showing *Brachychirotherium*-like features (Klein and Lucas, 2010b, 2018; Fig. 6). This morphotype includes the ichnospecies "*Brachychirotherium*" *hessei* (Soergel, 1925), "*B.*" *harrasense* (Haubold, 1967) and "*B.*" *praeparvum* (Haubold, 1967) from the Buntsandstein of Germany, "*B.*" *circaparvum* Demathieu 1971 and "*B.*" *pachydactylum* Demathieu and Gand, 1973 from the Middle Triassic of France and "*B.*" *paraparvum* Demathieu and Oosterink, 1988 from the Muschelkalk of the Netherlands (Fig. 6D). Further occurrences of this morphotype are known from the Middle Triassic of Argentina (Melchor and De Valais, 2006, fig. 4a) and Italy (Brandner, 1973, pl. 1.3). It has also been found in the alluvial Muschelkalk of SE Germany (Klein and Haubold, 2004; Klein and Lucas, 2018). All this material, currently considered as *Synaptichnium* by some authors (e.g., Klein and Lucas, 2010, 2017), needs to

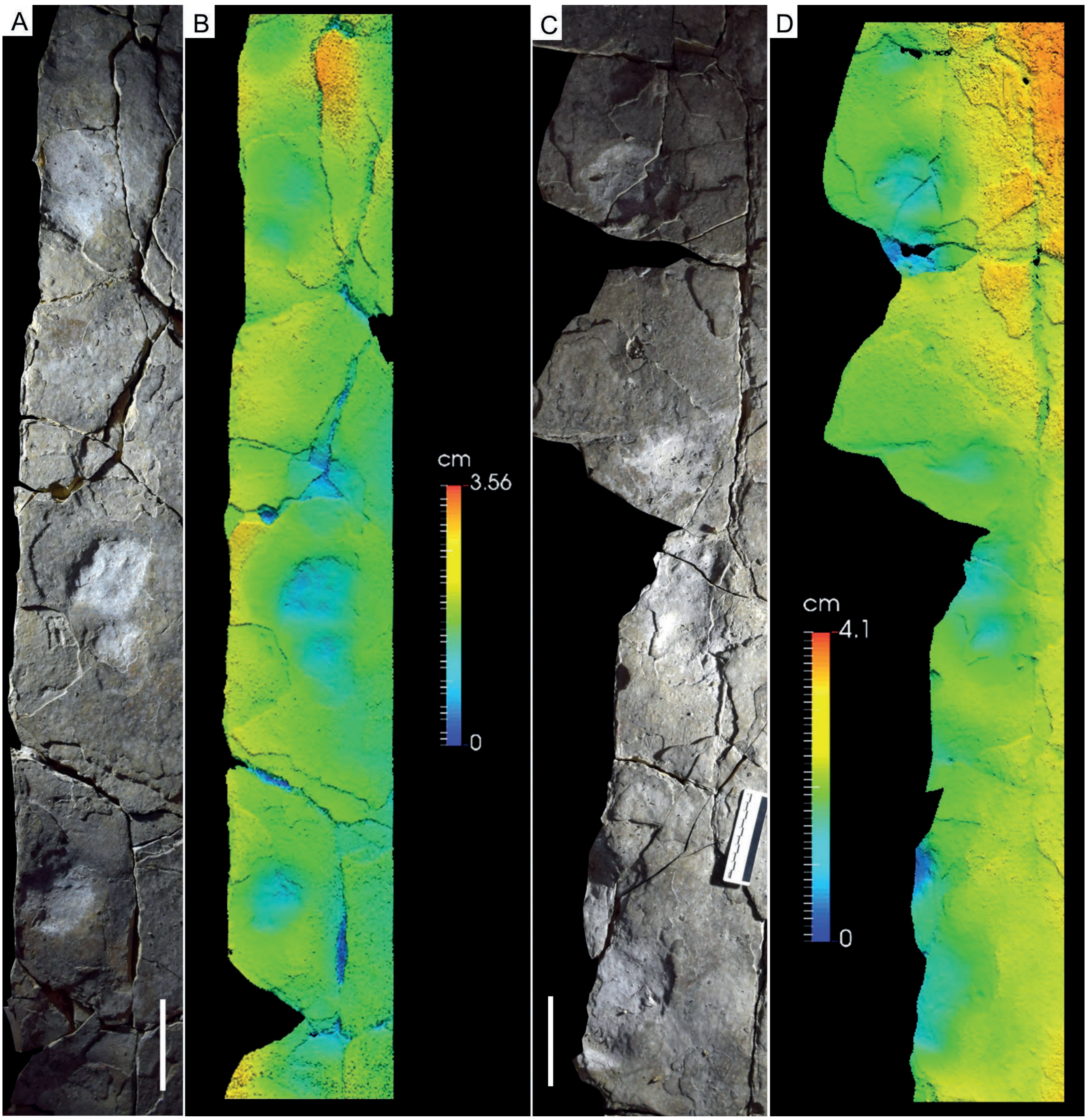

Fig. 5. Trackways of *Synaptichnium* isp., concave epirelief. **A.** LVH-F-V-18. Three consecutive pes-manus couples. **B.** LVH-F-V-18. False-colour depth map. **C.** LVH-F-V-13. Three consecutive pes-manus couples. **D.** LVH-F-V-13. False-colour depth map. Scale bars 10 cm.

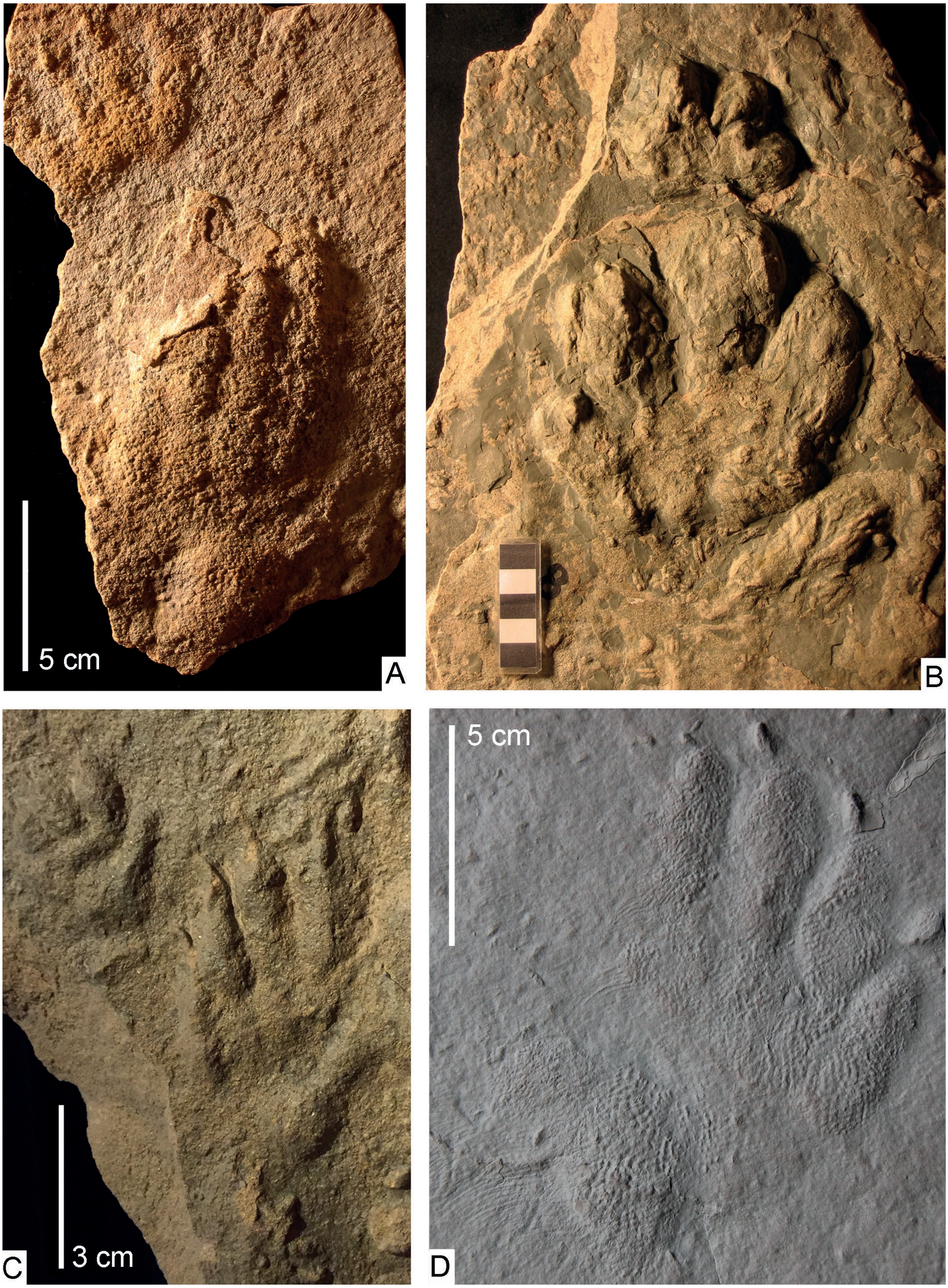

Fig. 6. Comparison with morphologically-similar material. **A.** *Synaptichnium pseudosuchoides*, pes-manus set, Eschenbach Formation (Middle Triassic, Anisian), NE Bavaria, Germany. **B.** *Brachychirotherium thuringiacum,* pes-manus set, Hassberge Formation (Upper Triassic, Carnian), N Bavaria, Germany. **C.** *Synaptichnium* isp., pes-manus set, Roet Formation (Anisian), N Bavaria, Germany. **D.** "*Brachychirotherium*" *paraparvum*, pes imprint with skin texture, Vossenveld Formation (Anisian), Winterswijk, the Netherlands. Scale bar in B = 1 cm. A, B. From Klein and Lucas (2018, 2010a). C, D. Photographs by Ikuko Tanaka and Henk W. Oosterink.

be comprehensively revised in order to be eventually assigned to an ichnospecies, that may be the first introduced for this material, "*Brachychirotherium*" *hessei* (Soergel, 1925). The possibility that this morphotype is related to extramorphological variability is not plausible, because several specimens, although not those from Bernburg, show an optimal morphological preservation *sensu* Marchetti *et al.* (2019b), indicating that the observed differences could be diagnostic. Nevertheless, Klein and Haubold (2004) and Klein and Lucas (2018) observed a possible morphological transition between characteristic *Synaptichnium* and a morphotype similar to "*Brachychirotherium*" *hessei* and "*Brachychirotherium*" *paraparvum* on same surfaces. These authors, however, emphasised that their conclusions were first based on studies and observations in the Eschenbach Formation (Muschelkalk, Anisian) of south-eastern Germany, so they did not formally re-assign Middle Triassic "*Brachychirotherium*" to *Synaptichnium*. Also, it cannot be excluded that some of the former represent an ichnogenus different from *Synaptichnium*. This can only be resolved by a comprehensive future study.

We concur that the Middle Triassic "*Brachychirotherium*" morphotype is clearly different from the *Brachychirotherium* type ichnospecies *B. hassfurtense* and also from *B. thuringiacum* (Fig. 6B) from the Upper Triassic Hassberge Formation (Carnian) of Germany (e.g., Klein and Lucas, 2010b; see also Karl and Haubold, 1998). The differences include: 1) thicker and shorter pes digit impressions, 2) a wider digit divarication, 3) a relatively longer pes digit II, 4) a relatively shorter pes digit IV (IV < II), 5) a relatively smaller and differently-oriented pes digit V, and 6) a relatively smaller manus imprint in *B. hassfurtense* and *B. thuringiacum* (Fig. 6B) The ichnospecies *Brachychirotherium parvum* (Hitchcock, 1889) from the Upper Triassic of North America is certainly more similar to this morphotype, because of the more parallel and relatively longer pes digit imprints. This is especially true for the type material described as *Chirotherium parvum* (Syn. *C. copei* Bock, 1952) by Baird (1957). However, the digit proportions still differ from this morphotype, and the manus is relatively smaller compared to the pes. So, pending a comprehensive revision of the ichnogenera *Synaptichnium* and *Brachychirotherium*, we assign the studied material to *Synaptichnium* isp. avoiding ichnospecific assignments, because of the overall poor preservation of the specimens (preservation grade 1.5 or lower; Fig. 4).

Synaptichnium is a very abundant ichnotaxon in Lower (Olenekian) and Middle Triassic units, and it has been found from a number of sites in North America, South America, North Africa and Europe (e.g., Haubold, 1971a, 1971b; Avanzini and Mietto, 2008; Klein and Lucas, 2010a, 2010b; Klein *et al.*, 2011; Klein and Niedźwiedzki, 2012). Its trackmakers are considered archosauromorphs with a non-derived pes structure (e.g., Klein *et al.*, 2011).

DISCUSSION

The marginal marine units of the Lower and Middle Muschelkalk of the Germanic Basin currently include the ichnogenera: *Chirotherium, Isochirotherium, Synaptichnium, Procolophonichnium* and *Rhynchosauroides* (Table 1). These palaeoenvironments were dominated by small tracks of *Rhynchosauroides* and *Procolophonichnium*, as emphasised by Diedrich (2000, 2002a, b), who interpreted the track-bearing laminated limestones as intertidal environments. Chirotheriid footprints are significantly rarer and, although the Bernburg site seems to constitute an exception, the finding of more chirotheriid trackways is probably due to extensive exposures compared to other sites rather than to a real difference in the ichnotaxa abundance. Among the chirotheriid tracks of the Bernburg site, *Chirotherium* is the most abundant ichnotaxon, while larger *Isochirotherium* and smaller *Synaptichnium* are significantly rarer. The Muschelkalk ichnoassociation from tidal units of N Germany and the Netherlands can be compared with the alluvial Muschelkalk units of SE Germany (e.g., Klein and Lucas, 2018; Table 1). All the above-mentioned ichnogenera occur in both settings, but the ichnospecies often differ. Other ichnogenera are also found in alluvial settings, such as *Atreipus-Grallator, Rotodactylus, Gwyneddichnium* and some tracks resembling *Dicynodontipus* (Klein and Lucas, 2018). Moreover, the relative abundance of ichnotaxa is very different: chirotheriid tracks, especially *Chirotherium* and *Synaptichnium*, are numerically predominant, *Rhynchosauroides* is less common, and *Procolophonichnium* is rare (Klein and Lucas, 2018). Therefore, while the overall ichnofaunal composition in different palaeoenvironmental conditions, such as tidal flats and alluvial plains, is similar, there are evident differences in ichnospecies, relative proportions between ichnotaxa, and diversity that can probably be attributed to a different palaeoecology of the trackmakers. Some marginal marine ichnosites with a similar age from Spain and Italy, interpreted as sabkha and alluvial environments, are also characterised by abundant *Rhynchosauroides* tracks and rarer chirotheriid tracks (e.g., Avanzini and Renesto, 2002; Mujal *et al.*, 2018). This, as suggested by Diedrich (2002b) and Mujal *et al.* (2018), may be interpreted as a distinct ichnocoenoses linked to marginal marine settings.

CONCLUSIONS

The analysis of undescribed footprints from the lower Middle Muschelkalk of the Solvay Quarry of Bernburg documents the occurrence of *Synaptichnium* isp. for the first time, not only from this site but from Saxony-Anhalt (N Germany). *Synaptichnium* is a rare ichnotaxon in the Lower and Middle Muschelkalk tidal facies of the Germanic Basin. Furthermore, these are the first *Synaptichnium* step cycles described from this unit. Previous works reported only isolated tracks or pes-manus couples assignable to this ichnotaxon. The studied material differs from other known *Synaptichnium* ichnospecies and is similar to other "*Brachychirotherium*-like" *Synaptichnium* footprints, which are in need of revision because some of the characterising features appear unrelated to extramorphological variability. The tidal units of the Lower and Middle Muschelkalk of the Germanic Basin, including the Bernburg site, show a low-diversity ichnoassociation dominated by tracks of *Rhynchosauroides* and *Procolophonichnium*, while chirotheriid tracks are rarer. This clearly differs from

Table 1

Occurrences of tetrapod ichnogenera in the Muschelkalk of the Germanic Basin.

	Lower Muschelkalk				Middle Muschelkalk		
	The Netherlands	N Germany		SE Germany	N Germany		SE Germany
	Vossenveld	Osnabrück	Jena	Eschenbach	Karlstadt	Diemel	Grafenwöhr
Ichnogenus	tidal	tidal	tidal	alluvial	tidal	tidal	alluvial
cf. *Dicynodontipus*				X			
Procolophonichnium	X	X	X	X	X	X	
“Coelurosaurichnus”	X						
Rhynchosauroides	X	X	X	X	X	X	X
Gwyneddichnium				X			
Rotodactylus				X			
Synaptichnium				X	X	X	
“Brachychirotherium”	X						
Isochirotherium				X	X		
Chirotherium					X		X
“Sphingopus”				X			
Atreipus-Grallator				X			

the ichnoassociation of the alluvial Muschelkalk facies of SE Germany, which is more diverse and numerically dominated by chirotheriid tracks, although the overall ichnofaunal composition is similar. Further studies are needed to correctly relate the differences between Middle Triassic alluvial and marginal marine tetrapod ichnoassociations to the different depositional palaeoenvironments and to, eventually, revise the related tetrapod.

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