Toward the origin of amniotes: Diadectomorph and synapsid footprints from the early Late Carboniferous of Germany

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Ichnotaxonomic revision of two extended sequences of large tetrapod footprints from the Westphalian A Bochum Formation of western Germany suggests assignment of the specimens to the well-known Permo-Carboniferous ichnogenera *Ichniotherium* and *Dimetropus*. Trackway parameters and imprint morphology strongly support basal diadectomorphs and "pelycosaurian"-grade synapsid reptiles, respectively, as the most likely trackmakers. The ichnofossils thereby extend the first appearance of these two important groups of basal tetrapods by about 5–10 million years, to the early Late Carboniferous, which is in accordance with the minimum age for the evolutionary origin of the clades following widely accepted phylogenetic analyses. These trackways provide not only direct evidence bearing on activity and behaviour of large terrestrial tetrapods close to the origin of amniotes, but also serve as a valuable benchmark for the assessment of controversially interpreted vertebrate tracks from other localities of similar age.

Key words: *Ichniotherium*, *Dimetropus*, Cotylosauria, tetrapod tracks, Westphalian, Germany.

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Introduction

The Carboniferous is an important period in the evolution of terrestrial tetrapods including the first appearance of amniotes (Clack 2002). Recent findings suggest a remarkable radiation of amniotes soon after their origin about 320 Ma ago (e.g., Reisz and Dilkes 2003; Kissel and Reisz 2004a; Müller and Reisz 2005). Most clades of early synapsids, sauropsids, and closely allied anamniotes, however, are represented by ghost lineages only, indicating a significant lack of data from the skeletal fossil record (Reisz 1997, 2007; Reisz and Müller 2004). Tetrapod footprints are an abundant source of information that may supplement the skeletal record in multiple ways (Carrano and Wilson 2001; Voigt et al. 2007). The present paper is intended to demonstrate the importance of vertebrate ichnology for timing the origin and evolutionary history of two important groups of terrestrial tetrapods based on the revision of two extended sequences of reptiliomorph and amniote tracks from the early Late Carboniferous of western Germany.

Pre-Stephanian Late Carboniferous tetrapod footprints are relatively rare in European coal beds and associated strata. Tracks are only known from a few horizons of Westphalian age and include the following stratigraphic units: (i) Faisceau de Dusouich, Westphalian C, Bully-les-Mines, Pas-de-Calais Basin, northern France (Dollé et al. 1970); (ii) Sulzbach Formation, Westphalian C, Neunkirchen, Saar area, western Germany (Weingardt 1961; Fichter 1982; Voigt 2007); (iii) Radnice Member, Kladno Formation, Westphalian C, Radnice Basin, western Bohemia, Czech Republic (Turek 1989); (iv) Alveley Member, Salop Formation, Westphalian D, Alveley, southern Shropshire, Great Britain (Haubold and Sarjeant 1973, 1974; Tucker and Smith 2004); and (v) Zwickau Formation, Westphalian D, Zwickau and Lugau-Ölsnitz, Erzgebirge Basin, eastern Germany (Geinitz 1885; Beck 1915; Müller 1962; Haubold 1970, 1971, 1984). The tracks from the Bochum Formation, Westphalian A, of the Ruhr area, western Germany (Kukuk 1924, 1926; Schmidt 1956, 1963), which are the focus herein, represent an outstanding occurrence, because they are the stratigraphically oldest record of Late Carboniferous vertebrate footprints outside of North America.

In recent years, much progress has been achieved in the study of Permo-Carboniferous tetrapod ichnofaunas from central Europe regarding recognition of anatomically based characters of Late Palaeozoic tetrapod footprints (Haubold 1996, 2000; Voigt and Haubold 2000; Voigt 2005, 2007) and the identification of potential trackmakers (Voigt 2005; Voigt et al. 2007). Reanalysis of the tetrapod tracks from the Westphalian A of the Ruhr area provides strong arguments for their referral to two ichnogenera which are substantially affiliated with Stephanian and Early Permian red-beds. For

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both taxa there is a broad consensus on the trackmakers within reptiliomorph amphibians (diadectomorphs) and basal synapsids ("pelycosaurs"), respectively. Taking into account the fact that the tracks are about the same age as the oldest known definitive amniotes from Joggins, Nova Scotia (Carroll 1964; Falcon-Lang et al. 2006), we present a unique record of large terrestrial tetrapods from an early phase of amniote evolution.

Institutional abbreviations.—DBM, Deutsches Bergbau-Museum, Bochum, Germany; GZG, Geowissenschaftliches Zentrum, Göttingen, Germany; MB, Museum für Naturkunde, Berlin, Germany; MNG, Museum der Natur, Gotha, Germany; UGBL, Urweltmuseum Geoskop, Burg Lichtenberg, Thallichtenberg, Germany.

Other abbreviations.—A, distance between manus and pes; B, width of pace; C, apparent body length; L, left manus-pes couple; m, manus imprint; mb, width of manus imprint; ml, length of manus imprint; mI to mV, length of digit I to V of the manus imprint; P, length of pace; p, pes imprint; pb, width of pes imprint; pl, length of pes imprint; pI to pV, length of digit I to V of the pes imprint; R, right manus-pes couple; S, length of stride; α, pace angulation; β, deviation of manus or pes from midline, plus β outward rotation, minus β inward rotation; γ, interdigital angle I–V; I–II–III–IV–V, first to fifth digit, numbered from medial to lateral side of imprint.

Material and methods

In 1923 an assemblage of 30 tetrapod tracks was discovered in the subsurface "Präsident" coal mine at Bochum, western Germany, during tunnel preparation work at the roof of the "Plaßhofsbank" coal seam, lower Bochum Formation, Westphalian A, 430 m below ground level (Kukuk 1924, 1926). The imprints were solely preserved in convex hyporelief on a thick slab of sandstone; the underlying mud rock with the original footprints had already been destroyed by mining activities. One year after its discovery, the 2 × 2 m large trackway surface was moulded in plaster; copies were made for display in the geological museum of the Westfalian trade union for mining (Westfälische Berggewerkschaftskasse, WBK), Bochum; and in the conference hall of the "Präsident" coal mine. In preparation for a more detailed cast in 1952, the subsurface outcrop of the original trackway slab was expanded to 9 m^2, then showing about 80 single tracks (Schmidt 1956). A new and now coloured cast replaced the mould from the 1920s in the exhibition of the WBK geological museum (Fig. 1A, B). Before closing the "Präsident" coal mine in 1965, the WBK was able to salvage ten fragments of the original trackway surface for public display (Hahne 1966; Ganzelewski et al. 2008; Fig. 1C–F). During the 1970s the WBK fossil collection moved to the German Mining Museum at Bochum (Deutsches Bergbau-Museum, DBM). The oversized mould of the tetrapod footprint slab of the "Präsident" coal mine proved cumbersome and had to become remodelled for easy handling. The resulting four-part plastic cast, together with the ten fragments of the original specimen, represents the material base for our study of the Bochum trackway slab.

At the same stratigraphic level, another long trackway was discovered in the "Erin" coal mine at Castrop, Ruhr area, western Germany, in 1957. The 0.5 × 2.25 m large slab containing about 30 single imprints is completely preserved; five successive pieces of the natural cast and two plaster casts are housed at the DBM.

Our trackway analysis is based on natural and artificial casts of the Bochum and Castrop specimens. To assess the variability of the trackways they were photographed both in overview and as individual imprints. Outline drawings on transparency film were made in order to record measurements of 28 different parameters of the trackway patterns and individual imprint morphologies (Appendices 1, 3). Data acquisition follows widely accepted standards of tetrapod ichnology fully described in related papers (e.g., Haubold 1971; Leonardi 1987; Voigt and Haubold 2000).

Systematic palaeoichnology

Ichniotherium praesidentis (Schmidt, 1956) comb. nov.

Figs. 1–4, Appendices 1, 2.

1956 *Megapezia praesidentis* Schmidt, 1956: 200–204, figs. 1, 2, pl. 14.

1970 *Schmidtopus praesidentis* Haubold, 1970: 94–95, fig. 4D.

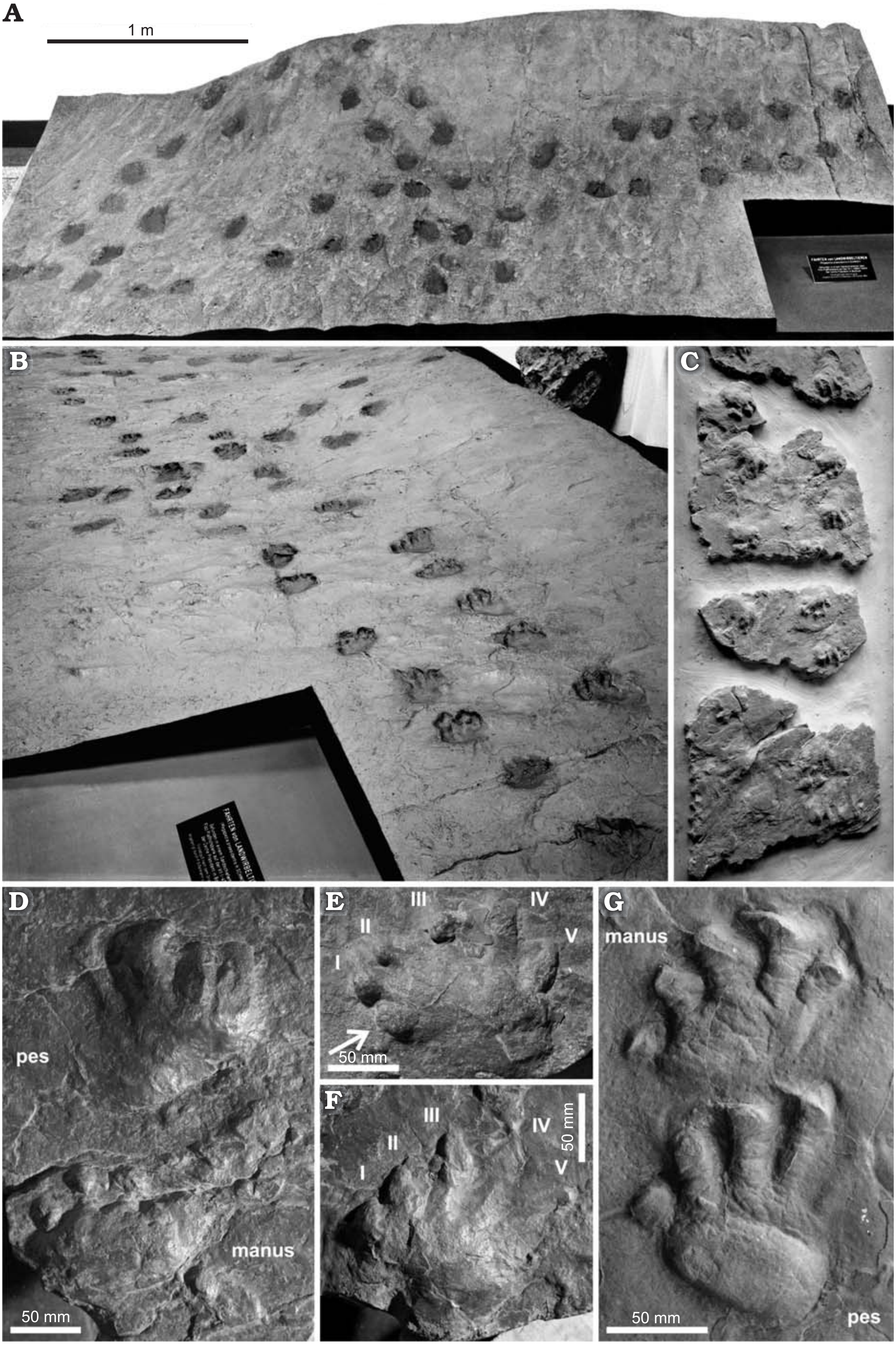
1982 *Schmidtopus praesidentis*; Fichter 1982: 68–72, figs. 29, 30, 32, tables 1, 7.

1984 *Schmidtopus* (*Megapezia*) *praesidentis*; Haubold 1984: 64, fig. 43: 1.

Holotype: DBM 060003259001 to DBM 060003259010, original material, preserved as convex hyporelief, and DBM 060003309001 to DBM 060003309004, plastic cast, four-part. All segments are part of the same trackway surface, 2 × 4.6 m in size, covered by about 80 monospecific imprints of three trackways (Fig. 1A–C). Owing to a mistake that occurred when the replica of the slab was reconstructed during the 1950s, the first two imprints of the best preserved trackway are portrayed twice (Fig. 2).

Type locality: Former coal-mine „Präsident“ at Bochum, Ruhr area, western Germany (Kukuk 1924, 1926).

Fig. 1. Tetrapod footprints of *Ichniotherium praesidentis* (Schmidt, 1956) from the Late Carboniferous Bochum Formation, Ruhr area, Germany (**A**–**F**) and *Ichniotherium sphaerodactylum* (Pabst, 1895) from the Early Permian Tambach Formation, Thuringian Forest, Germany (**G**). **A**, **B**. Historical photographs from the 1960s showing a subsequently lost plaster replica of the holotype of *Ichniotherium praesidentis* in the vestibule of the Geological Museum of the Ruhr mining industry. **C**. Original fragmentary material of the holotype of *Ichniotherium praesidentis* arranged in loose sand (Geological Museum of the Ruhr mining industry, ca. 1965). **D**–**F**. Close-up views of natural casts of *Ichniotherium praesidentis* tracks based on the holotype (DBM 060003259001 and DBM 060003259003); the arrow in E marks the distinct pad at the base of the first digit of the manus imprint. **G**. Right manus-pes couple of *Ichniotherium sphaerodactylum* (MB I.058.19). →



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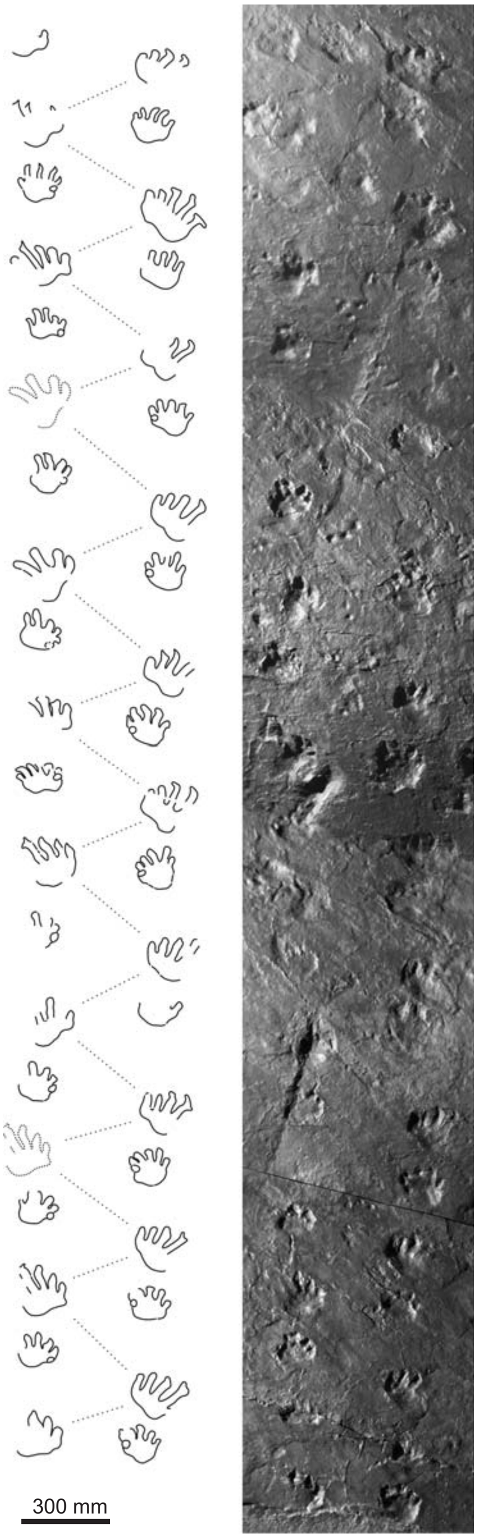


Fig. 2. Tetrapod footprints of *Ichniotherium praesidentis* (Schmidt, 1956) from the Late Carboniferous Bochum Formation, Ruhr area, Germany, represented by the longest and best preserved trackway of the holotype. Photograph and drawing are based on the four-part resin replica (DBM 060003309001 to DBM 060003309004). Note: the first two imprints are erroneously replicated twice and therefore not shown in the outline drawing. Dotted zigzag line links the pes imprints, and dotted track outlines indicate the position of imprints, which are reasoned from the step cycle but not preserved on the cast.

Type horizon: Above seam "Plaßhofsbank", lowermost Bochum Formation, Westphalian A2, Langsettian, Late Carboniferous.

Lithology.—Based on the original material, the tracks were made in dark grey silt. Natural casts are preserved in light grey medium-grained sandstone showing mud-crack casts up to 6 mm in width.

Description.—Trackway of a quadrupedal tetrapod with pentadactyl, plantigrade footprints; manus and pes imprints are distinct in size and shape (Figs. 1, 2; Appendix 1). Pes imprints measure up to 15 cm in length and up to 17 cm in width. Digits I to IV of the pes imprint exhibit a serial increase in length, whereas digit V is about as long as III. Due to a significant decrease in relief from digit I to V, the outer digit is either reduced to a faint imprint of the digit tip or missing entirely (Fig. 1D, F). Digit tips I to IV are bent toward the trackway midline. The sole of the pes imprint is represented by a deep and structure-less impression.

The manus imprints average about 11 cm in length and 12 cm in width. Digits I to III of the manus imprints exhibit serial increase in length. Digit III is of nearly the same length as IV, in some cases shorter, in others slightly longer than IV. Digit V varies in length between digits II and III. Digit imprints I to IV commonly with hemispherical, slightly enlarged tips. The digits of the manus tracks are more evenly deep impressed than those ones of the pes tracks. The sole is a deep impression either showing a convex, straight, or slightly concave proximal margin. Some of the tracks notably possess a clearly distinct oval pad proximal to the first digit (Fig. 1E).

The trackway pattern is characterised by an alternating arrangement of inversely coupled manus-pes imprints (Fig. 2). Inversion means that associated tracks belong to consecutive couples, with the manus imprint lying closely behind the pes imprint of the succeeding step cycle. Low pace angulation, the relatively short length of stride, and a relatively wide gait are further characteristics of the trackway pattern (Appendix 1). The pes imprints are pointed outwardly about 30° on average, whereas the manus imprints are placed almost parallel to the trackway midline.

Remarks.—Kukuk (1924, 1926) interpreted the anterior track of coupled imprints of this trackway to be the imprint of the manus, judged from the trackway pattern and the apparent tetradactyl tracks. Abel (1935) equivocated about the number of digits present in the questionable imprints, whereas Schmidt (1956) and, later, Haubold (1970, 1971) agreed with Kukuk's interpretation of a four-toed manus. Fichter (1982) proposed the alternative view that both, manus and pes imprints are pentadactyl and that the larger of the two, though placed in front of two closely spaced footprints, corresponds to the pes. The debate stems from two unusual features of the trackway: (i) the mediolateral decrease in relief of the pes imprints, which prevents a distinct impression of the fifth digit (Fig. 1D); and (ii) the relatively short length of stride, which causes an alternating arrangement of inversely coupled manus-pes imprints (Fig. 2).

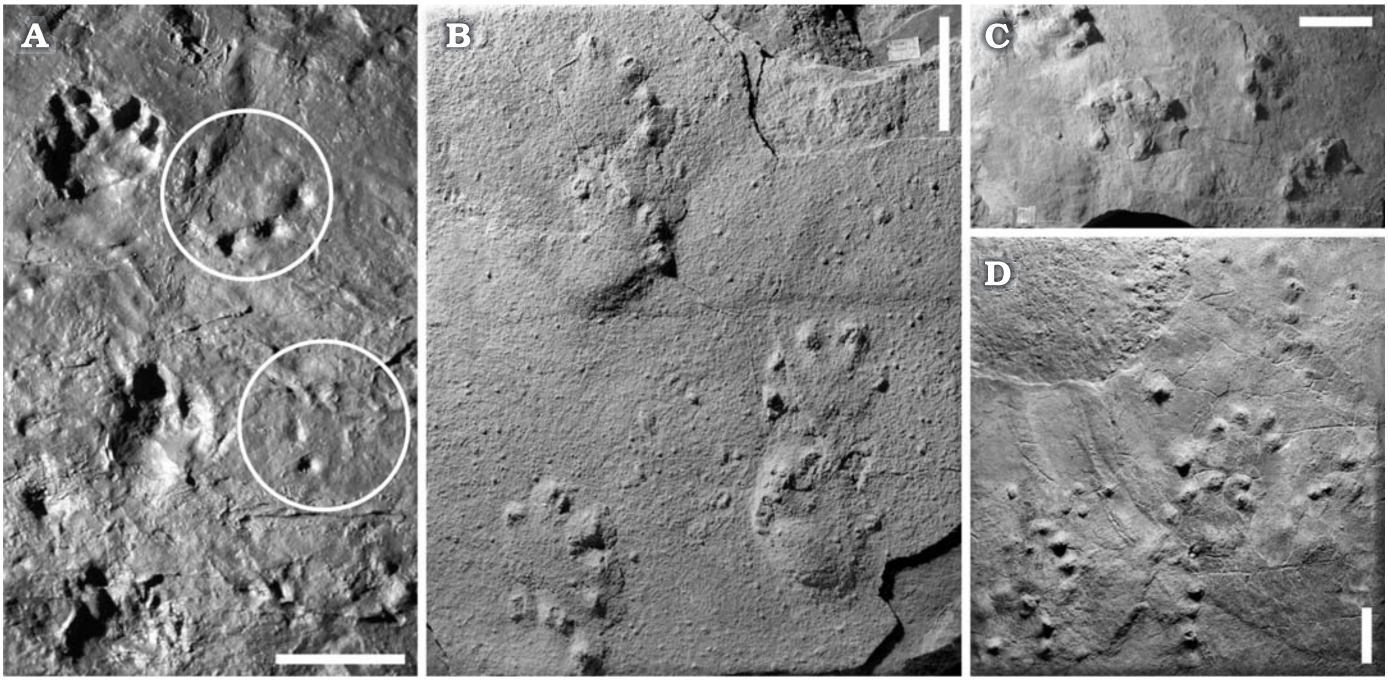


Fig. 3. Undertrack preservation in *Ichniotherium* tetrapod footprints. **A**. *Ichniotherium praesidentis* (Schmidt, 1956) from the Late Carboniferous Bochum Formation, Ruhr area, Germany; DBM 060003309003. **B**–**D**. *Ichniotherium cottae* (Pohlig, 1885) from Early Permian strata of the Thuringian Forest area, Germany; MNG 2049 (**B**), MNG 1871 (**C**), and MNG 2016 (**D**). Semicircularly arranged spherical imprints of the digit tips of the digits I–III or I–IV, which are typical in appearance to the undertrack preservation of Ichniotherium. Scale bars 100 mm.

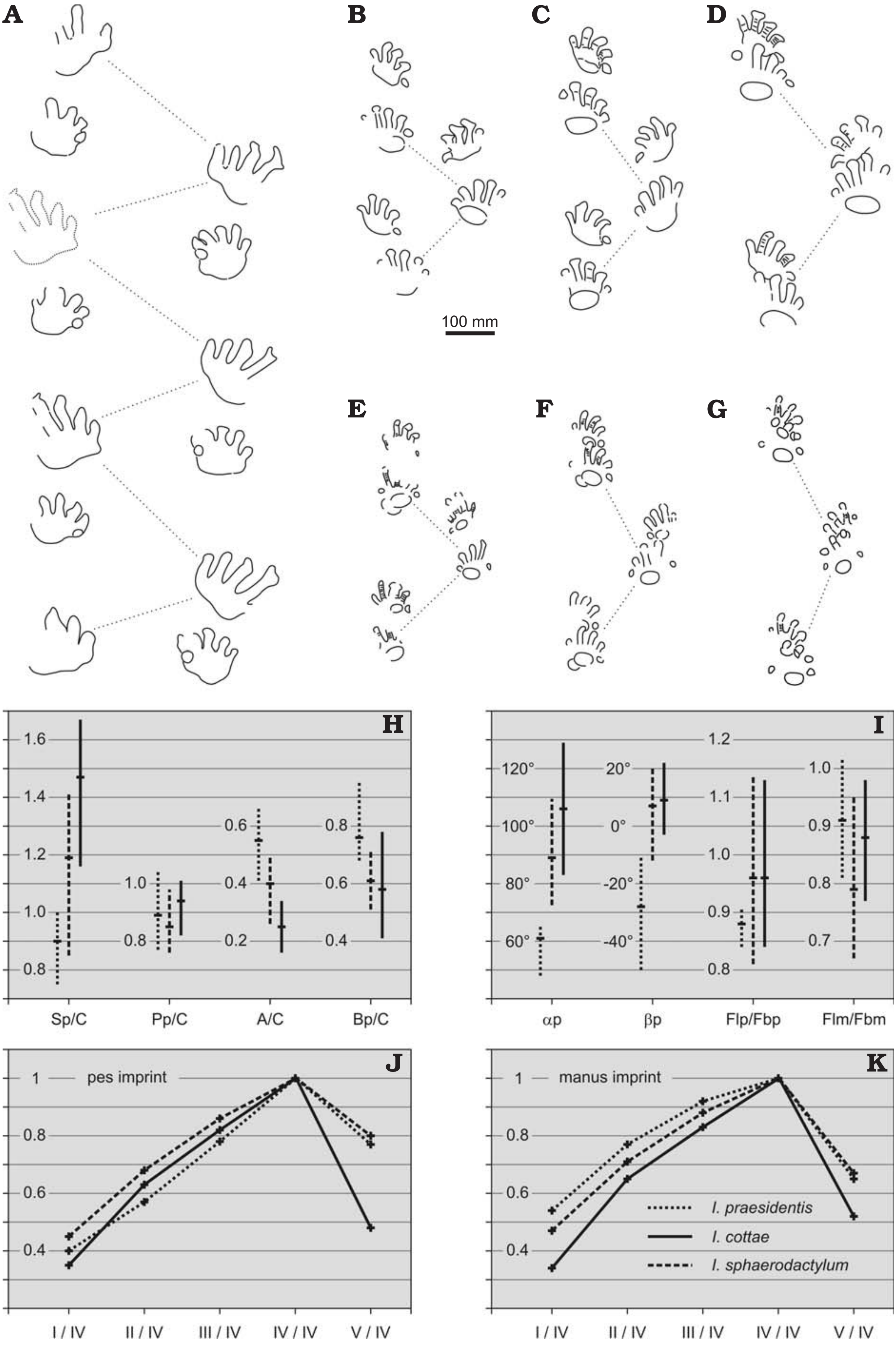
Schmidt (1956) assigned the tracks of the Bochum slab to *Megapezia* Matthew, 1903 from the Mississippian of Nova Scotia. From his point of view, both track morphs share a tetradactyl manus imprint with a posteriorly extended sole. Haubold (1970) agreed that the "manus imprints" are similar, but stressed the short and wide "pes imprint" of the Bochum tracks as being unique. Therefore, he introduced the new ichnogenus *Schmidtopus* Haubold, 1970. Even though setting right the interpretation of the trackway pattern, Fichter (1982) maintained *Schmidtopus* as a separate ichnotaxon referred to the Bochum tracks.

Based on careful reanalysis of the type material, we assign the Bochum tracks to the well-known Permo-Carboniferous ichnogenus *Ichniotherium* Pohlig, 1892. Both track morphs share several main imprint characters (Fig. 1D–G): (i) pentadactyl manus and pes imprints; (ii) distally rounded digit imprints with enlarged tips ("drumsticks" sensu Korn 1933); (iii) pes imprints with a mediolateral decrease in relief; (iv) manus imprints with evenly distributed relief; and (v) inwardly curved digit tips (I–IV). In addition, *Ichniotherium praesidentis* exhibits the typical preservation of *Ichniotherium* undertracks (Fig. 3).

In comparison to the well-established Permian ichnospecies *Ichniotherium sphaerodactylum* (Pabst, 1895) and *I. cottae* (Pohlig, 1885), *I. praesidentis* differs in its inversely coupled manus-pes sets of the trackway pattern (Fig. 4A–G). The Bochum trackway indicates a very slow-moving individual with respect to the low stride, short manus-pes distance, high width of pace, and small pace angulation (Fig. 4H, I). The relative length of pace lies within the range of variation obtained for the other Permian ichnospecies (Fig. 4H). This is possible because the short stride is accompanied by a relatively high width of pace. Another difference concerns the strongly outward rotation of the pes imprints of *I. praesidentis* (β in Fig. 4I). More similar are the imprint and digit proportions (Fig. 4I–K) with pes imprints being one third longer than the manus imprints (Appendix 2; Voigt et al. 2007). The digit proportions of *I. praesidentis* are almost congruent with those of *I. sphaerodactylum*, but differ significantly from the digit proportions of *I. cottae* by the relatively longer digit V of the pes imprint (Fig. 4J). *I. sphaerodactylum* has the most extended digit V of all Late Carboniferous to Early Permian tetrapod ichnotaxa (Voigt 2005). The relatively long outer digit of the pes imprint clearly separates the Bochum trackway specimen from similar forms such as *Amphisauropus* Haubold, 1970, and provides strong basis for placing the tracks within *Ichniotherium*.

I. praesidentis differs from all other *Ichniotherium* ichnospecies in having a distinct pad at the base of the first digit. *I. willsi* Haubold and Sarjeant, 1973, from the Westphalian D of Great Britain, has outwardly rotated pes imprints similar to the Bochum trackway. Both ichnospecies, however, differ significantly by the relative length of the fifth digit of the pes imprint.

Nomenclature.—The tracks of the Bochum slab are most similar to *Ichniotherium* Pohlig, 1892 and are thus assigned to that ichnogenus herein. *Schmidtopus*, which was introduced for these tracks by Haubold (1971), is considered as a junior synonym of *Ichniotherium*. Being different from all previously defined *Ichniotherium* ichnospecies in having a


A
B
C
D
100 mm
E
F
G
H
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
Sp/C
Pp/C
A/C
Bp/C
I
120°
100°
80°
60°
20°
0°
-20°
-40°
1.2
1.1
1.0
0.9
0.8
0.7
αp
βp
Flp/Fbp
Flm/Fbm
J
1
pes imprint
I / IV
II / IV
III / IV
IV / IV
V / IV
K
manus imprint
I. praesidentis
I. cottae
I. sphaerodactylum

← Fig. 4. Graphic comparisons of the trackway pattern and selected parameters of three *Ichniotherium* ichnospecies. **A**. *Ichniotherium praesidentis* from the Bochum Formation, Late Carboniferous, Germany; DBM 060003309001 to DBM 060003309004, part). **B**–**D**. *Ichniotherium sphaerodactylum* from the Tambach Formation, Early Permian, Germany; MB ICV.2 (**B**), MNG 1351 (**C**), and GZG 1270 (**D**). **E**–**G**. *Ichniotherium cottae* from the Tambach Formation, Early Permian, Germany; MNG 10179 (**E**), UGBL F1 (**F**), and MNG 1352 (**G**). **H**, **I**. Derived trackway and imprint parameters graphically expressing the mean, minimum, and maximum values. **J**, **K**. Relative lengths of the manus and pes imprint digit lengths expressed as a percentage of the length of digit IV. Data source for H–K, see Appendix 2.

distinct pad at the base of the first digit and a pes imprint that is outwardly rotated, the Bochum track represents a separate ichnospecies. Using the first available specific epithet, the valid name for the discussed tracks is *Ichniotherium praesidentis* (Schmidt, 1956).

Osteological interpretation.—Kukuk (1924) supposed the trackmaker of the Bochum tracks to be a Late Palaeozoic batrachomorph based on the salamander-like trackway pattern and the apparently tetradactyl nature of what were interpreted as manus imprints. Later, he included early amniotes as potential trackmakers, suggesting that the pointed digit tips of some tracks resulted from the presence of claws or nails (Kukuk 1926). Abel (1935) agreed that the tracks were made by a clawed animal, before Kukuk (1938) speculated on a pareiasaurian-like reptile as the potential trackmaker. Schmidt (1956) stressed the tetradactyly of the misinterpreted manus imprint as the most crucial character identifying the trackmaker as a large temnospondyl such as an eryopid. Haubold (1970, 1971, 1973, 1984) agreed with this interpretation, as did Fichter (1982), who referred to reconstructions of Palaeozoic temnospondyls showing a pentadactyl autopodium of the fore limb.

For about the past decade, *Ichniotherium* tracks have been regarded as belonging to diadectids (Fichter 1998; Haubold and Stapf 1998; Haubold 2000; Voigt and Haubold 2000; Voigt 2001, 2005; Berman and Henrici 2003; Kissel and Reisz 2004a; Voigt et al. 2005, 2007). This interpretation is based on the abundant record of *Ichniotherium* tracks and diadectid skeletal remains at the Early Permian Bromacker locality in central Germany (Berman et al. 1998, 2004; Haubold 1998; Voigt and Haubold 2000; Voigt et al. 2007). Diadectids are the most diverse clade of the Late Carboniferous to Early Permian Diadectomorpha, which also includes limnoscelids (Williston 1912; Romer 1946) and the monotypic Tseajaiidae (Vaughn 1964; Moss 1972). Even though some differences in the appendicular skeleton of limnoscelids, tseajaiids, and diadectids exist (Romer 1946; Berman and Henrici 2003; Pelletier et al. 2007), discrimination of the three biotaxa by tracks is not possible at the current state of knowledge because of inadequate knowledge of the hind limbs, e.g. for *Tseaja campi* Vaughn, 1964 (cf. Moss 1972). Without associated skeletal remains, as is the case for the discussed Westphalian footprints, biotaxon assignment of *Ichniotherium* tracks should be conservatively posited no lower than Diadectomorpha.

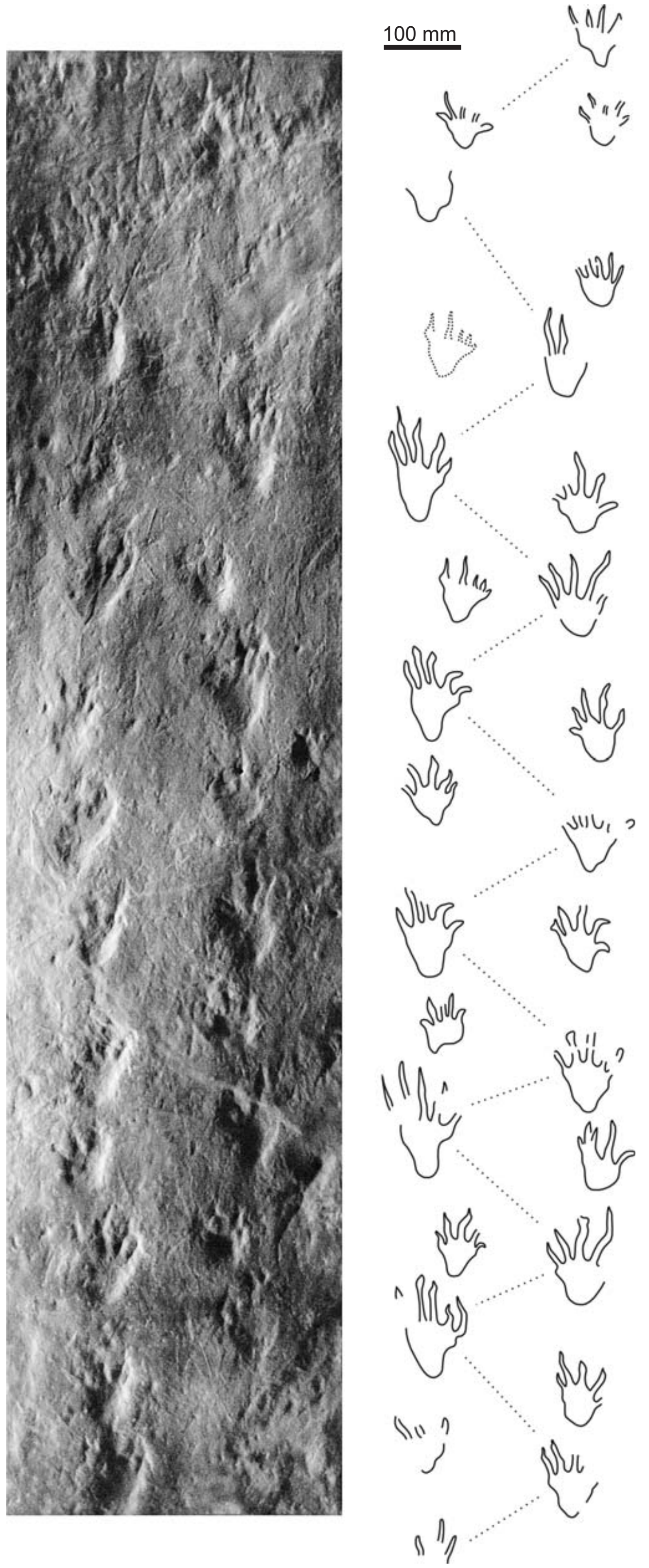


Fig. 5. Tetrapod footprints of *Dimetropus* sp. indet., from the Late Carboniferous Bochum Formation, Ruhr area, Germany. The photograph shows one of the two plaster casts of the trackway (DBM 060003357001); it is restricted to the most detailed tracks excluding faint imprints at the beginning and end of the trackway. The outline drawing illustrates the complete trackway as preserved on the five separated blocks of the original material.

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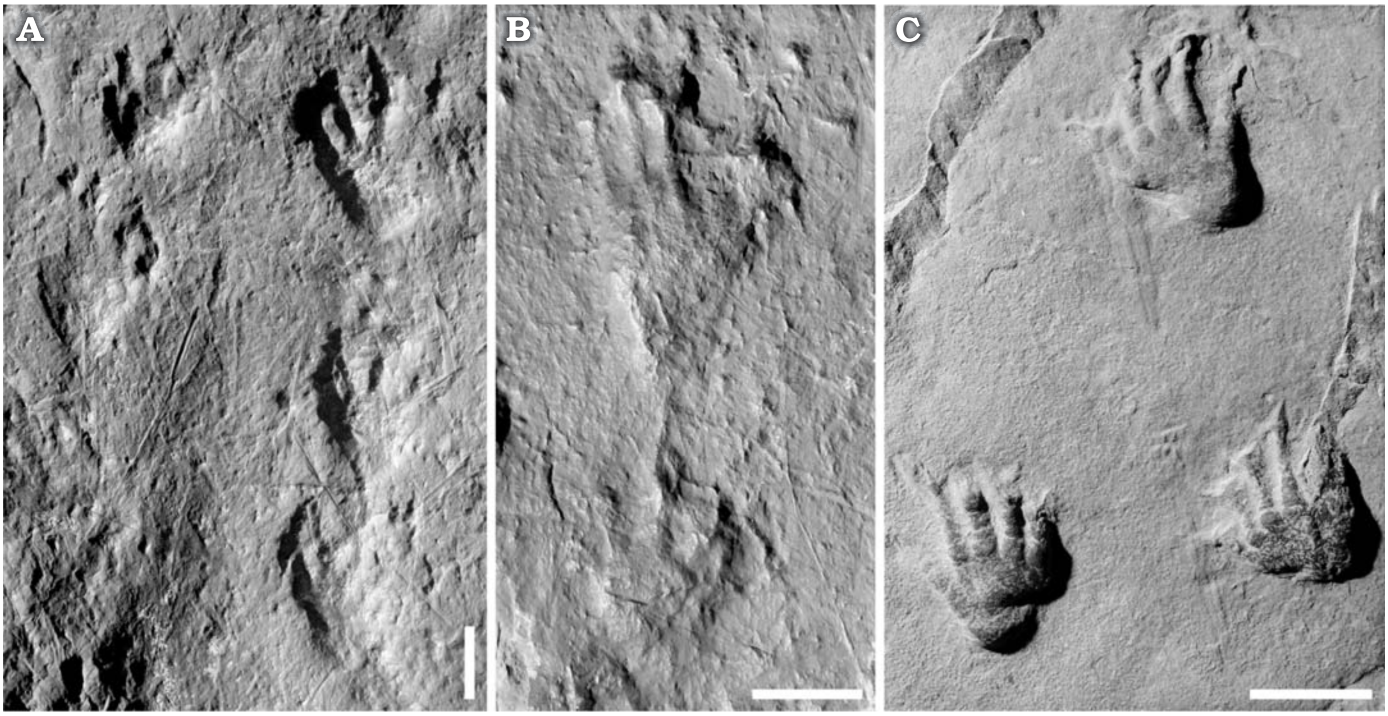

Fig. 6. Comparison between tracks of *Dimetropus* sp. from the Late Carboniferous Bochum Formation, Ruhr area, Germany, DBM 060003260001 (**A**) and DBM 060003260003 (**B**) and *Dimetropus leisnerianus* (Geinitz, 1863) from the Early Permian Tambach Formation, Thuringian Forest, Germany, MNG 1762 (**C**). Scale bars 100 mm.

Dimetropus ichnosp. indet.

Figs. 5–7, Appendices 3, 4.

1963 *Herpetichnus erini* Schmidt, 1963: 179–184, fig. 1, pl. 13.
1971 *Pseudobradypus* (*Herpetichnus*) *erneri* [sic]; Haubold 1971: 27, fig. 16: 3.
1982 *Pseudobradypus erini*; Fichter 1982: 50–59, figs. 7–10, 15, tables 1, 4.
1984 *Pseudobradypus* (*Herpetichnus*) *erini*; Haubold 1984: 64, fig. 42: 2.

Material.—DBM 060003260001 to DBM 060003260005, original material, preserved as convex hyporelief; DBM 060003357001 and DBM 060003357002, plaster casts. All of the original material belongs to the same slab, 0.5 × 2.3 m in size, composed of five segments showing 27 monospecific imprints of one trackway (Fig. 5).

Locality.—Former coal-mine „Erin“ at Castrop, Ruhr area, western Germany (Hahne 1957).

Horizon.—Above seam “Sonnenschein”, lower Bochum Formation, Westphalian A2, Langsettian, Late Carboniferous.

Lithology.—Based on the original material the tracks were made in dark grey mudstone. Natural casts are preserved in light grey siltstone to fine-grained sandstone. The track-bearing surface is partially covered by imprints of macrofloral remains and isolated tetrapod footprints of other trackways that are indeterminable due to faint or incomplete preservation (cf. Schmidt 1963).

Description.—Trackway of a quadrupedal tetrapod with pentadactyl, plantigrade footprints; manus and pes imprints are similar in shape but different in size (Figs. 5, 6A, B, Appendix 3). Imprints are always longer than wide, with distally pointed slender digits and proximally elongated heel. Sole of the pes may cover almost half of the length of the imprint. In both manus and pes imprints, digits I to IV exhibit a serial increase in length; digit V is longer than II in the pes imprint, but shorter than II in the manus imprint. Pes imprints measure up to 14 cm being about 50% larger than the manus imprints. Manus imprints up to one third longer than wide, with a total digit angulation of 77.5° on average. Pes imprints more than 50% longer than wide with a mean total digit angulation of 61.5°.

The trackway pattern shows a more or less alternating arrangement of imprints, where the manus imprint of the one side of the trackway is nearly opposite a contralateral pes. In some parts of the trackway the manus-pes couples are so closely spaced that the trackway pattern merges into an alternating arrangement of inversely coupled imprints similar to that described for *I. praesidentis*. The trackway pattern is characterised by a relatively short stride, wide gait, and low pace angulation. Deviation of the manus and pes imprints from trackway midline is highly variable; both imprints may be significantly pointed inwardly or outwardly; on average, however, the imprints are placed almost parallel to the trackway midline (Appendix 3).

Remarks.—Schmidt (1963) compared the Castrop tracks with *Ichnium acrodactylum* Pabst, 1895 from the Early Permian of central Germany. He recognised an overall similarity regarding the relative length of the digits, their specific shape with pointed digit tips, and the posteriorly extended sole of the im-

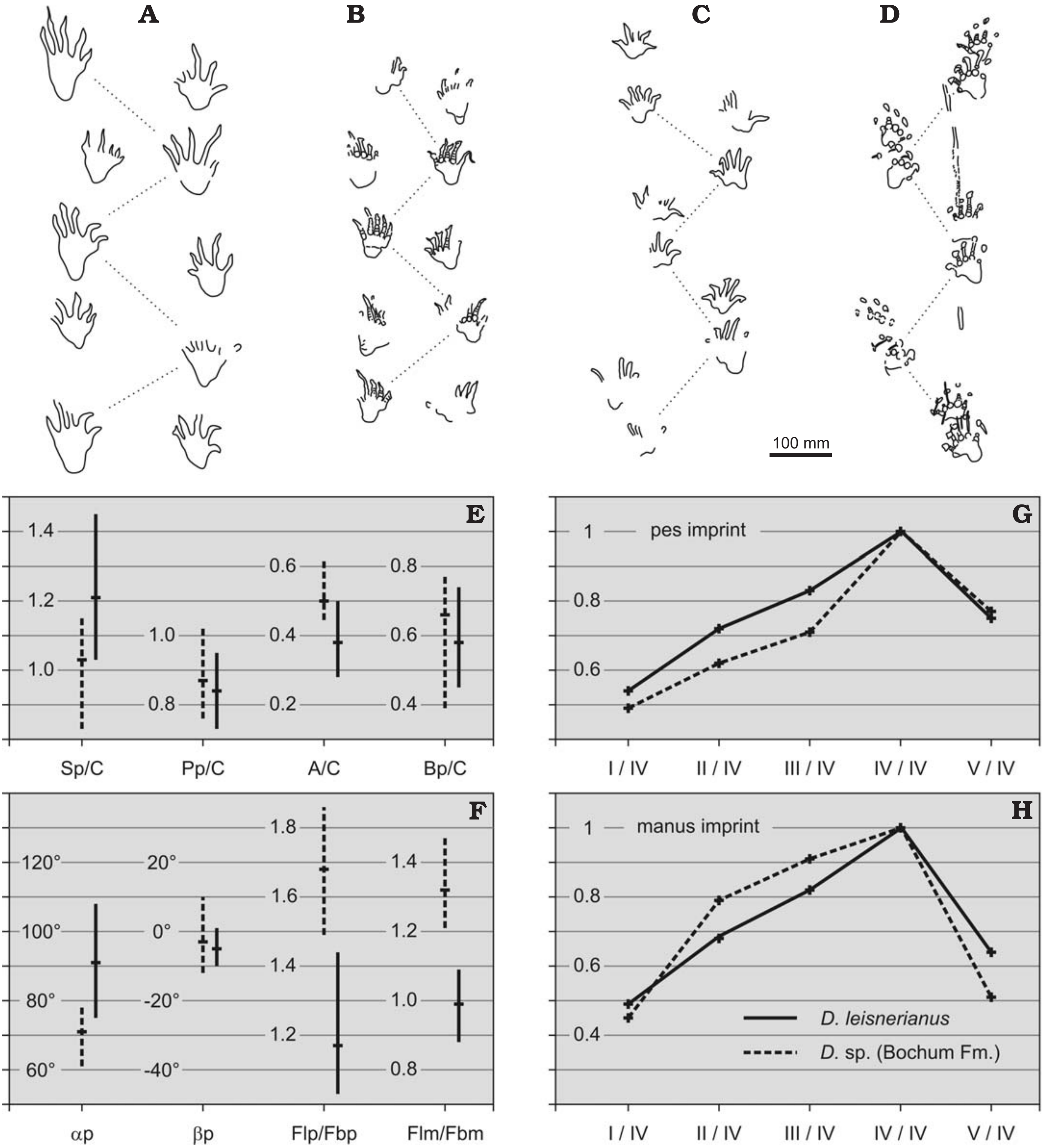

Fig. 7. Comparison of trackway pattern and selected parameters of *Dimetropus* sp. from the Late Carboniferous Bochum Formation, Ruhr area, Germany, DBM 060003260001 to DBM 060003260005 (**A**) and *Dimetropus leisnerianus* from the Early Permian Tambach Formation, Thuringian Forest, Germany, MNG 1762 (**B**), MNG 1828 (**C**), MNG 13490 (**D**). **E**, **F**. Derived trackway and imprint parameters graphically expressing the mean, minimum, and maximum values. **G**, **H**. Relative lengths of the manus and pes imprint digit lengths expressed as a percentage of the length of digit IV. Data source for E–H, see Appendix 4.

prints. Following the proposal of Nopcsa (1923), who had assigned *Ichnium acrodactylum* to *Herpetichnus* Jardine, 1850 from the Early Permian of Scotland, Schmidt (1963) introduced *Herpetichnus erini* but without an appropriate ichnospecies definition. Haubold (1971) did not accept the synonymy of *Herpetichnus* Jardine, 1850 and *Ichnium acrodac-*

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tylum (= *Dimetropus leisnerianus* (Geinitz, 1863) according to Haubold 1971) and assigned the Castrop tracks to *Pseudobradypus* Matthew, 1903 from the Early Pennsylvanian of Nova Scotia. Fichter (1982) supported this referral on the basis of trackway parameters and the extended heel of the pes imprints. On the other hand, he conceded that the type material of the generic type, *Pseudobradypus unguifer* (Dawson, 1872), is lacking crucial details of the imprint morphology. The ambiguity of the *Pseudobradypus* type material is expressed by the wide morphological range of Carboniferous tracks that have recently been assigned to this ichnotaxon (Lucas et al. 2004; Falcon-Lang et al. 2007; Wood and Miller 2007).

Our results support the determination of Schmidt (1963) who firstly stressed the similarity of the Castrop footprints with *Dimetropus* Romer and Price, 1940 (*Herpetichnus* in the usage of Schmidt 1963). Neither imprint morphology nor trackway pattern support ichnogeneric separation. As Schmidt (1963) observed, the digit imprints of these tracks are characterised by their narrow middle part. This is a typical feature of *Dimetropus* tracks, whose most deeply impressed segments are the metatarsal- and metacarpal-phalangeal pads and the claws (cf. Voigt 2005). Fichter (1982: 58) and even Haubold (1971: 27) noted the striking similarity between the Castrop tracks and *Dimetropus*; the reservation of these authors on the ichnogeneric identity might be due to stratigraphic age discrepancies.

Eleven ichnospecies of *Dimetropus* have been named, of which three were accepted as valid taxa by Haubold (2000): *D. leisnerianus* (Geinitz, 1863), *D. berea* (Tilton, 1931), and *D. nicolasi* Gand and Haubold, 1984. Lacking reliable criteria for ichnotaxonomic discrimination other than stratigraphy and locality, Voigt (2005, 2007) argued for a monospecific ichnogenus *Dimetropus*. The trackway pattern of the Castrop specimen is similar to trackways of *D. leisnerianus* made by slow-moving individuals (Fig. 7A–D). All differences of the trackway pattern, including the shorter length of stride, the higher manus-pes distance, and the lower pace angulation, can be explained by a reduced speed of gait. Coincidence is given for the relative length of pace and the deviation of the pes imprints from midline (Fig. 7E, F). The Castrop specimen differs from *D. leisnerianus* in having relatively longer manus and pes imprints (Fig. 7F); minor differences concern the digit proportions (Fig. 7G, H). The relatively higher length of imprints and the relatively shorter digit V of the pes imprint of the Castrop tracks might be of ichnospecific relevance. Because consistency of the features can not be assessed by a single specimen, the Castrop tracks are tentatively referred to *Dimetropus* with open nomenclature on the ichnospecies level.

Nomenclature.—The Castrop tracks are indistinguishable from *Dimetropus* Romer and Price, 1940 and are consequently assigned to that ichnogenus. *Dimetropus* is a valid, widely accepted, and well characterised taxon for Palaeozoic tetrapod footprints. *Herpetichnus* was erroneously used for *Dimetropus* tracks from the Early Permian of central Germany by Nopcsa (1923), but there is no synonymy of that ichnotaxa as repeatedly stated by several authors (Haubold 1971, 1984, 1996, 2000; Fichter 1982; Voigt 2005).

Osteological interpretation.—The Castrop tracks were referred to an amniote trackmaker by all previous authors (Schmidt 1963; Haubold 1971, 1973, 1984; Fichter 1982). Whereas Schmidt (1963) and Fichter (1982) proposed an association with early edaphosaurids, Haubold (1971) compared the specimen with footprints of supposed captorhinomorph affinity, but conceded that the tracks could also have been made by basal synapsids ("pelycosaurs") due to the large size of the imprints.

Dimetropus is usually referred to Eupelycosauria, which include edaphosaurids, sphenacodontids, ophiacodontids, and varanopids (Tilton 1931; Romer and Price 1940; Haubold 1971, 1984, 1996, 2000; Fichter 1976, 1979, 1983; Gand 1988; Haubold et al. 1995; Voigt 2005; Voigt et al. 2005). With the exception of some large caseids such as *Cotylorhynchus*, the manus and pes structure of basal synapsids ("pelycosaurs") are generally similar (Reisz 1986). Varanopids are unique in that the fourth digit appears to be extended showing digital proportions similar to the tracks of *Tambachichnium* Müller, 1954 (cf. Voigt 2005). At the current state of knowledge, the ichnogenus *Dimetropus* subsumes tracks of a wide range of non-therapsid synapsids.

Discussion

Osteological interpretations of fossil tetrapod footprints are commonly ambiguous because of the limited number of anatomical features which can be adequately reflected by tracks and trackways. The reliability of candidate trackmaker identifications commonly relies to some extent on isochronistic occurrences of bio- and ichnotaxa. Therefore, we will compare the taxon distribution of *Ichniotherium* with diadectomorphs, and *Dimetropus* with "pelycosaurian"-grade synapsids, respectively.

The oldest known occurrence of *Ichniotherium* is that of *I. willsi* Haubold and Sarjeant, 1973 from the Salop Formation, Westphalian D (Kasimovian) of Alveley near Birmingham, Great Britain (Haubold and Sarjeant 1973, 1974; Tucker and Smith 2004). Diadectomorphs, the most likely progenitors of *Ichniotherium* trackways, are known from Late Pennsylvanian to Early Permian (about Bashkirian to Artinskian) deposits (Berman and Henrici 2003; Kissel and Reisz 2004b; Reisz 2007). Excluding very fragmentary questionable limnoscelids, such as *Limnostygis relictus* Carroll, 1967, from the Westphalian D of Florence, Nova Scotia, the diadectid *Desmatodon* Case, 1908 from the Missourian (Stephanian A) Red Knob and Sangre de Cristo formations of Pennsylvania and Colorado, respectively, represents the first appearance of diadectomorphs (Kissel and Reisz 2004b). According to the present state of knowledge, the supposed diadectomorph track record only slightly antedates the diadectomorph body fossil record.

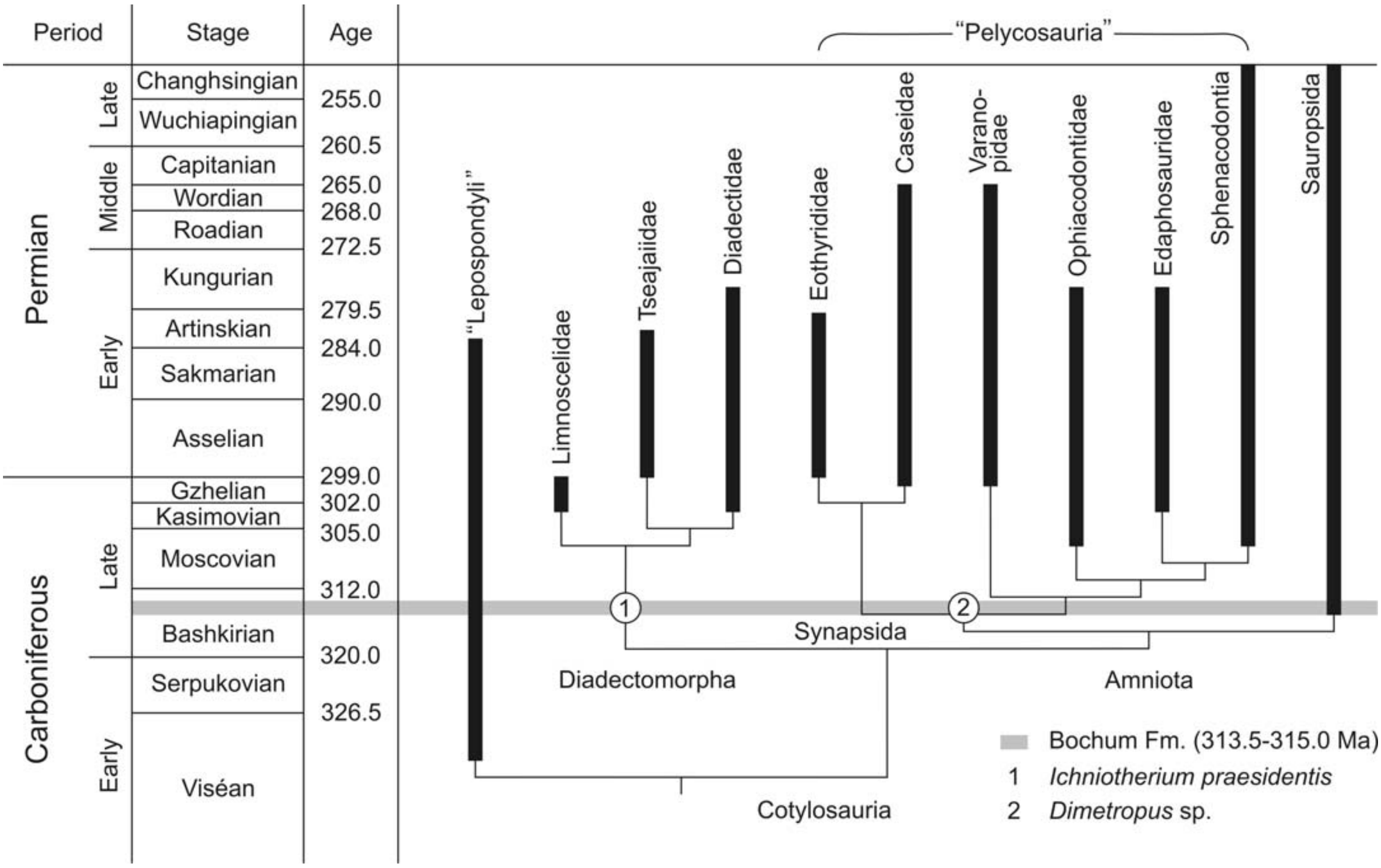

Fig. 8. Stratocladogram of tetrapod phylogeny. Although extending the known body fossil record, the stratigraphic position of the diadectomorph and synapsid footprints from the Bochum Formation of western Germany fits well the phylogenetic pattern. Black bars indicate the known record of skeletal remains (Reisz 1986; Kissel and Reisz 2004a, b). Cladogram topology and minimum times of divergence are based on Kissel and Reisz (2004a, b), Müller and Reisz (2004), and Reisz (2007). The chronostratigraphic scale is adopted from Menning (2005).

Dimetropus salopensis Haubold and Sarjeant, 1973 from the Salop Formation, Westphalian D (Kasimovian) of Alveley near Birmingham, Great Britain is the oldest known occurrence of the ichnogenus *Dimetropus* (Haubold and Sarjeant 1973, 1974; Tucker and Smith 2004; Voigt 2005). Hunt and Lucas (2004) and Hunt et al. (2005) assigned tracks from the Westphalian A Pottsville Formation in the Black Warrior basin of Alabama to *Dimetropus*; however, because the specimens are undertracks (as noted by the authors), their assignation is questionable. Skeletal remains of Late Carboniferous synapsids as the most likely producers of *Dimetropus* trackways have been reported from nearly 20 localities in North America and Europe (cf. Kissel and Reisz 2004a). *Protoclepsydrops haplous* Carroll, 1964 from the Westphalian A Joggins Formation of Nova Scotia was identified as an ophiacodontid synapsid in the original description (Carroll 1964), which would be the oldest known synapsid ("pelycosaur"). However, the poor quality of the holotype and the three referred specimens leave doubt about the identity of the taxon (Kissel and Reisz 2004a). With the ophiacodontids *Archaeothyris florensis* Reisz, 1972 and *Echinerpeton intermedium* Reisz, 1972, an unnamed sphenacodontid, and two unnamed, indeterminate forms, the earliest definitive synapsids come from the Westphalian D Florence locality of Nova Scotia (Reisz 1972). About the same age are findings of *Archaeothyris* from Linton, Ohio, and Nýřany, Czech Republic (Reisz 1975). Thus, the unquestionable record of Synapsida and referred tracks currently dates to the Middle Pennsylvanian.

Ichniotherium praesidentis and *Dimetropus* sp. from the early Late Carboniferous of Germany predate the first occurrence of diadectomorphs and synapsid reptiles by about 5–10 Ma to the Early Pennsylvanian (313.5–315 Ma, Westphalian A, Bashkirian; Fig. 8). This might be used as an argument against the proposed trackmaker interpretation. However, based on widely accepted phylogenetic analyses, the diadectomorphs comprise the sister taxon to all amniotes (Gauthier et al. 1988; Laurin and Reisz 1995, 1997; Lee and Spencer 1997), which on their parts are characterised by a basal dichotomy of synapsids and sauropsids (Reisz 1997; Laurin and Reisz 1999; Kissel and Reisz 2004a). Accepting the analyses means that the origin of diadectomorphs must be at least as old as the oldest known amniote and synapsid origin must date at least to the age of the oldest known sauropsid. The earliest definitive amniote is the sauropsid *Hylonomus* from the Joggins Formation of Nova Scotia (Carroll 1964; Falcon-Lang et al. 2006). The Joggins Formation is currently placed in the Langsettian stage (314.5–313.4 Ma; Falcon-Lang et al. 2006) and about the same age as the

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Bochum Formation (315.0–313.5 Ma; Menning et al. 2005). Thus, giving credit to the phylogenetic relationship of early tetrapods (Gauthier et al. 1988; Laurin and Reisz 1995, 1997, 1999; Lee and Spencer 1997), diadectomorphs and "pelycosaurian"-grade synapsids must have existed by the Westphalian A, which is in full agreement with the proposed trackmaker identification of the footprints discussed herein (Fig. 8).

Conclusions

The tracks from the early Late Carboniferous of Germany provide substantial data for an interpretation in favour of basal diadectomorph and synapsid origin, respectively. As stated by various authors (e.g., Milner 1987; Reisz 1997, 2007; Reisz and Müller 2004), the large, heavily-built diadectomorphs and basal synapsids (edaphosaurids, sphenacodontids, haptodontids etc.) which appear for the first time in the Stephanian of North America and Europe must have had antecedents in the Westphalian faunas. Long ghost lineages of early amniotes and close relatives probably result from taphonomic bias, considering that our knowledge of Westphalian tetrapods is ecologically restricted to lowland faunas with preservation of rather small terrestrial tetrapods (Reisz 1997, 2007; Reisz and Müller 2004). The Bochum and Castrop tracks clearly indicate the existence of reptiliomorphs and early amniotes of more than 400 mm snout-vent length during the Early Pennsylvanian, suggesting that the vertebrate fossil record from the lycopod tree stumps of the contemporaneous Joggins Formation of Nova Scotia is highly selective with respect to body size (Reisz 1997). Therefore, the described trackways may represent one of the rare fossil records of large terrestrial tetrapods from early Late Carboniferous upland ecosystems.

Phylogenetic analyses suggest that the palaeoequatorial regions of central Laurasia, which are western and central Europe today, served as a centre of origin for several Late Palaeozoic amniote clades especially parareptiles and eureptiles (Müller and Reisz 2005; Müller et al. 2006, 2008). This pattern might be also true for basal synapsids and diadectomorphs taking into account that the first appearance of these groups is now given by tetrapod footprints from Germany. Besides, the German tracks may be a useful correlative for the controversial interpretation of large tetrapod footprints from similarly aged strata, such as the Pottsville Formation of Alabama (cf. Haubold et al. 2005; Hunt and Lucas 2004; Hunt et al. 2005).

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Appendix 1

A. Trackway parameters of *Ichniotherium praesidentis*, DBM 060003309001 to DBM 060003309004 (in mm and degrees).

Imprint couple	Sp	Sm	Pp	Pm	A	Bp	Bm	C	D	E	αp	αm	βp	βm
R1-L1-R2	–	434	– / 379	410 / 362	– / 267 / 304	– / 352	320 / 324	–	-9 / -128	– / -1 / 29	–	66	– / -21 / -40	6 / 0 / 4
L1-R2-L2	423	408	456	432	254	361	366	489	-20	-54	63	64	-33	-7
R2-L2-R3	456	391	358	454	238	314	427	464	-80	-59	65	54	-27	25
L2-R3-L3	426	347	436	440	174	355	395	421	15	19	64	47	–	-18
R3-L3-R4	391	457	454	438	304	428	345	451	-37	64	54	68	-16	–
L3-R4-L4	361	484	442	416	297	383	360	481	-79	-41	48	62	-11	-12
R4-L4-R5	421	395	395	394	276	350	349	499	-97	42	66	59	-29	-29
L4-R5-L5	494	418	454	442	224	347	357	499	18	-52	66	65	-29	-35
R5-L5-R6	441	430	385	378	264	355	330	471	-74	77	64	61	-27	2
L5-R6-L6	405	445	440	391	260	368	300	459	-6	-9	61	67	-18	20
R6-L6-R7	412	444	377	386	298	347	336	476	-108	20	58	72	-30	-8
L6-R7-L7	435	446	460	428	272	363	339	505	-15	4	59	70	-38	-2
R7-L7-R8	451	464	402	384	311	367	327	516	-107	36	64	67	-33	5
L7-R8-L8	442	444	450	398	276	360	326	504	-37	-2	64	67	–	-9
R8-L8-R9	474	414	420	388	254	368	346	495	-81	24	64	66	-33	-22
L8-R9-L9	459	444	462	442	259	368	350	486	12	-6	59	62	-21	12
R9-L9-R10	419	419	402	372	253	370	340	481	-106	36	62	63	-28	-24
L9-R10-L10	435	432	470	445	256	374	342	474	30	-4	58	64	-20	–
R10-L10-R11	407	–	394	–	–	372	–	–	-132	–	58	–	-50	–
Minimum	361	347	358	362	174	314	300	421	-132	-59	48	47	-50	-35
Maximum	494	484	470	454	311	428	427	516	30	77	66	72	-11	25
Mean	430.67	428.67	422.95	410.53	265.32	363.26	346.26	480.65	-52.05	6.47	60.94	63.56	-28.00	-5.11

B. Imprint parameters of *Ichniotherium praesidentis*, DBM 060003309001 to DBM 060003309004 (in mm and degrees).

Imprint couple	pI	pII	pIII	pIV	pV	mI	mII	mIII	mIV	mV	pl	pb	ml	mb	γp	γm
R1	–	–	–	–	–	28	41	45	36	25	–	–	117	125	–	72
L1	30	49	76	–	–	28	38	45	40	–	–	–	105	–	–	–
R2	45	64	71	94	–	–	–	32	28	26	149	–	102	116	65	–
L2	33	52	73	92	–	25	35	38	–	21	162	–	98	118	–	67
R3	37	47	64	83	–	31	36	40	48	33	144	–	116	118	–	74
L3	–	–	–	–	–	24	34	45	–	–	–	–	–	–	–	–
R4	47	50	64	76	–	–	–	–	–	30	140	–	–	–	–	–
L4	–	–	64	–	–	19	28	44	–	–	–	–	–	–	–	–
R5	30	48	67	88	–	23	33	46	48	27	146	–	125	122	–	62
L5	38	48	72	96	–	–	–	37	42	25	168	–	115	–	–	97
R6	–	–	–	–	–	25	43	48	49	31	–	–	113	126	–	108
L6	34	44	71	–	–	17	23	31	49	38	–	–	109	122	–	96
R7	32	51	58	–	–	24	37	–	50	25	–	–	–	117	–	57
L7	32	52	72	81	–	31	39	46	48	–	153	–	114	115	–	56
R8	25	42	63	81	–	23	37	36	37	28	140	–	104	129	–	56
L8	–	–	–	–	–	20	22	44	48	27	–	–	95	118	–	51
R9	–	–	59	79	–	–	43	46	54	36	150	–	–	119	–	–
L9	33	50	66	99	80	–	–	–	–	–	154	169	115	126	54	83
R10	–	–	67	81	60	20	32	42	46	33	151	179	109	118	52	49
L10	–	–	–	–	–	23	–	–	–	–	147	–	–	–	–	–
R11	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Minimum	25	42	58	76	60	17	22	31	28	21	140	169	95	115	52	49
Maximum	47	64	76	99	80	31	43	48	54	38	168	179	125	129	65	108
Mean	34.67	49.75	67.13	86.36	70.00	24.07	34.73	41.56	44.50	28.93	150.33	174.00	109.79	120.64	57.00	71.38

Appendix 2

A. Trackway parameters of *Ichniotherium* ichnospecies (in mm and degrees). Data for *Ichniotherium cottae* and *Ichniotherium sphaerodactlyum* adopted from Voigt (2005) and for *Ichniotherium praesidentis* from Appendix 1.

Trackway	Sp	Sm	Pp	Pm	A	Bp	Bm	C	D	E	αp	αm	βp	βm
I. cottae (11 trackways)	272.0	260.5	182.5	182.5	34.4	103.0	103.5	199.0	52.0	-18.4	82.7	87.0	-2.6	16.5
	456.0	441.0	254.0	251.5	80.0	181.3	171.7	276.0	172.5	23.8	129.0	124.0	22.0	33.5
	348.3	350.6	222.1	218.0	58.6	135.4	126.5	236.0	116.8	4.25	106.4	109.1	9.1	24.2
I. sphaero-dactylum (41 trackways)	290.0	296.7	207.0	208.0	73.3	142.0	109.0	255.3	-9.4	-20.5	70.3	73.0	-11.5	9.3
	458.8	463.0	310.7	343.3	170.3	235.5	252.1	360.0	130.3	48.0	107.0	118.5	20.0	74.5
	363.9	365.4	259.4	257.5	118.7	182.6	177.9	302.6	64.6	2.0	89.3	91.7	6.9	24.1
I. praesidentis (1 trackway)	361	347	358	362	174	314	300	421	-132	-59	48	47	-50	-35
	494	484	470	454	311	428	427	516	30	77	66	72	-11	25
	430.7	428.7	423.0	410.5	265.3	363.3	346.3	480.7	-52.1	6.5	60.9	63.6	-28.0	-5.1

B. Derived trackway and imprint parameters of *Ichniotherium* ichnospecies. Data for *Ichniotherium cottae* and *Ichniotherium sphaerodactlyum* adopted from Voigt (2005) and for *Ichniotherium praesidentis* from Appendix 1.

Trackway	Sp/C	Pp/C	A/C	Bp/C	pI/pIV	pII/ pIV	pIII/ pIV	pV/ pIV	mI/mIV	mII/mIV	mIII/mIV	mV/mIV	Flp/Fbp	Flm/Fbm
I. cottae (11 trackways)	1.16	0.82	0.16	0.41	0.30	0.52	0.72	0.43	0.29	0.60	0.74	0.40	0.84	0.77
	1.67	1.01	0.34	0.78	0.42	0.71	0.86	0.54	0.45	0.73	0.87	0.61	1.13	0.98
	1.47	0.94	0.25	0.58	0.35	0.62	0.82	0.48	0.34	0.65	0.83	0.52	0.96	0.88
I. sphaero-dactylum (41 trackways)	0.85	0.76	0.26	0.51	0.30	0.51	0.77	0.68	0.35	0.56	0.79	0.59	0.81	0.67
	1.42	0.98	0.50	0.72	0.61	0.87	1.06	1.00	0.81	0.90	0.97	0.76	1.14	0.95
	1.19	0.85	0.40	0.61	0.45	0.68	0.86	0.80	0.47	0.71	0.88	0.67	0.96	0.79
I. praesidentis (1 trackway)	0.75	0.77	0.41	0.68	0.31	0.50	0.67	0.74	0.35	0.46	0.63	0.50	0.84	0.81
	1.01	1.04	0.67	0.95	0.62	0.66	0.89	0.81	0.81	1.14	1.17	0.78	0.91	1.02
	0.90	0.89	0.55	0.76	0.40	0.57	0.78	0.77	0.54	0.77	0.92	0.65	0.88	0.91

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Appendix 3

A. Trackway parameters of *Dimetropus* sp., DBM 060003260001 to DBM 060003260005 (in mm and degrees).

Imprint couple	Sp	Sm	Pp	Pm	A	Bp	Bm	C	D	E	αp	αm	βp	βm
L1-R1-L2	326	284	228 / 284	224 / 255	160 / 133 / 118	194 / 206	225 / 187	283	-40 / 74	-16 / -15 / 34	79	69	- / 2 / -4	-30 / 6 / 5
L2-R2-L3	298	290	210	210	126	190	185	271	-26	-29	72	83	-3	15
R2-L3-R3	276	291	274	270	133	197	197	269	58	29	66	73	-5	-2
L3-R3-L4	258	302	228	214	172	217	183	282	-59	5	62	76	-5	-4
R3-L4-R4	257	300	280	278	176	207	207	308	12	-5	61	77	-11	-5
L4-R4-L5	316	296	246	236	152	209	210	322	-42	4	73	67	10	20
R4-L5-R5	349	286	294	254	132	118	165	301	54	49	73	69	-12	6
L5-R5-L6	307	294	224	200	135	193	162	290	-20	-18	78	83	-4	-4
R5-L6-R6	316	–	268	–	–	187	–	–	70	–	77	–	6	–
Minimum	257	284	210	200	118	118	162	269	-59	-29	61	67	-12	-30
Maximum	349	302	294	278	176	217	225	322	74	49	79	83	10	20
Mean	300.3	292.9	253.6	237.9	143.7	191.8	191.2	290.8	8.1	3.8	71.2	74.6	-2.6	0.7

B. Imprint parameters of *Dimetropus* sp., DBM 060003260001 to DBM 060003260005 (in mm and degrees).

Imprint couple	pI	pII	pIII	pIV	pV	mI	mII	mIII	mIV	mV	pl	pb	ml	mb	γp	γm
L1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
R1	42	49	–	–	–	23	50	38	37	–	–	–	104	–	–	83
L2	47	30	54	67	58	–	13	43	46	22	137	92	91	66	48	73
R2	38	48	58	68	–	25	45	43	56	32	133	–	91	75	–	62
L3	–	54	72	83	68	17	31	–	39	17	155	–	77	60	60	52
R3	29	45	–	–	38	26	38	–	36	17	–	91	–	78	63	92
L4	22	32	–	–	35	20	31	44	48	–	–	84	96	75	68	67
R4	–	–	–	–	–	16	36	54	64	38	–	–	109	81	77	96
L5	25	31	49	63	47	–	–	–	–	–	143	85	93	69	59	–
R5	39	49	54	76	–	–	–	56	–	29	118	–	106	–	57	95
L6	27	52	60	79	51	–	–	–	–	–	156	84	–	–	60	–
Minimum	22	30	49	63	35	16	13	38	36	17	118	84	77	60	48	52
Maximum	47	54	72	83	68	26	50	56	64	38	156	92	109	81	77	96
Mean	33.6	43.3	57.8	72.7	49.5	21.2	34.9	46.3	46.6	25.8	140.3	87.2	95.9	72.0	61.5	77.5

Appendix 4

A. Trackway parameters of *Dimetropus* ichnospecies (in mm and degrees). Data for *Dimetropus leisnerianus* adopted from Voigt (2005) and for *Dimetropus* sp. from Appendix 3.

Trackway	Sp	Sm	Pp	Pm	A	Bp	Bm	C	D	E	αp	αm	βp	βm
D. leisnerianus (8 trackways)	263.5	261.5	172.9	189.2	65.3	111.5	130.0	211.0	12.0	-17.6	75.3	80.1	-9.9	-25.0
	343.2	341.4	256.0	233.3	129.0	198.7	159.0	287.5	104.0	18.5	108.3	101.4	0.9	6.4
	297.1	294.2	207.6	210.5	94.8	142.7	144.7	247.3	55.7	0.8	91.4	89.3	-5.1	-3.8
D. sp. (Bochum Fm.; 1 trackway)	257	284	210	200	118	118	162	269	-59	-29	61	67	-12	-30
	349	302	294	278	176	217	225	322	74	49	79	83	10	20
	300.3	292.9	253.6	237.9	143.7	191.8	191.2	290.8	8.1	3.8	71.2	74.6	-2.6	0.7

B. Derived trackway and imprint parameters of *Dimetropus* ichnospecies. Data for *Dimetropus leisnerianus* adopted from Voigt (2005) and for *Dimetropus* sp. from Appendix 3.

Trackway	Sp/C	Pp/C	A/C	Bp/C	pI/pIV	pII/ pIV	pIII/ pIV	pV/ pIV	mI/mIV	mII/mIV	mIII/mIV	mV/mIV	Flp/Fbp	Flm/Fbm
D. leisnerianus (8 trackways)	1.03	0.73	0.28	0.45	0.49	0.64	0.73	0.68	0.43	0.60	0.76	0.56	1.03	0.88
	1.45	0.95	0.49	0.74	0.57	0.78	0.97	0.81	0.56	0.80	0.87	0.76	1.44	1.09
	1.21	0.84	0.38	0.58	0.54	0.72	0.83	0.75	0.49	0.68	0.82	0.64	1.17	0.99
D. sp. (Bochum Fm.; 1 trackway)	0.83	0.76	0.44	0.39	0.34	0.49	0.59	0.65	0.25	0.56	0.77	0.44	1.49	1.21
	1.16	1.02	0.61	0.77	0.66	0.71	0.95	0.87	0.72	1.06	1.13	0.59	1.86	1.48
	1.03	0.87	0.50	0.66	0.49	0.62	0.71	0.77	0.45	0.79	0.91	0.51	1.68	1.32