FIRST WELL-ESTABLISHED TRACK-TRACKMAKER ASSOCIATION OF PALEOZOIC TETRAPODS BASED ON ICHNIOTHERIUM TRACKWAYS AND DIADECTID SKELETONS FROM THE LOWER PERMIAN OF GERMANY

Authors: VOIGT, SEBASTIAN, BERMAN, DAVID S., and HENRICI, AMY C.

FEATURED ARTICLE

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SEBASTIAN VOIGT,[*, 1] DAVID S BERMAN,[2] and AMY C. HENRICI[2]

[1]Institute of Geology, Freiberg University of Mining and Technology,
Bernhard-von-Cotta-Str. 2, D-09596 Freiberg, Germany, s.voigt@geo.tu-freiberg.de;
[2]Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213-4080, U.S.A.,
bermand@carnegiemnh.org, henricia@carnegiemnh.org

ABSTRACT—As a single stratigraphic source and site of high-fidelity vertebrate trackways and superbly preserved skeletons, the Lower Permian Tambach Formation, lowermost unit of the Upper Rotliegend, of the Bromacker locality in the middle part of the Thuringian Forest near Gotha, central Germany, provides a unique opportunity of matching late Paleozoic trackways with their trackmakers. Here the track-trackmaker association is firmly established between two species of the ichnogenus *Ichniotherium*, *Ichniotherium cottae* and *Ichniotherium sphaerodactylum*, and the skeletal fossils of the closely related diadectids *Diadectes absitus* and *Orobates pabsti*, respectively. These are the first well-documented species-level identifications of the trackmakers of Paleozoic trackways. The *Ichniotherium* ichnospecies are principally separated by the relative lengths of the digits of the pes imprint and the degree of overstepping of the pes and manus imprints. Both characters are shown to be clearly due to differences in the number and lengths of phalangeal elements and the number of presacral vertebrae of the diadectid species. The unique methods employed here in establishing the track-trackmaker associations provide not only an innovative data source for studying the evolutionary biology, paleobiogeography, and locomotor behaviour of the trackmakers, but also a valuable methodology for evaluating taxonomic concepts in vertebrate ichnology.

INTRODUCTION

Tetrapod footprints are a common phenomenon in late Paleozoic terrestrial deposits, having been documented by several thousand specimens from Africa, Europe, European Russia, North America, and South America. Due to their abundant record, global distribution, and autochthonous origin vertebrate tracks are often used as collateral evidence in reconstructing terrestrial tetrapod communities for paleoecological, biostratigraphic, and biogeographic analyses (e.g., Matsukawa et al., 2005; Van Allen et al., 2005). The accuracy of such studies is facilitated by confident identification of a biospecies as the progenitor of an ichnospecies. Unfortunately, this approach is typically obstructed severely by two commonly encountered obstacles: (1) biotaxa are typically based mainly on cranial features, whereas ichnotaxa are based strictly on features of the tracks and trackways; and (2) even if the structures of the manus and pes of a biotaxon are well known, there remains the difficulty of matching them to imprints that reflect a soft-tissue encasement of skeletal structures. Due to this taphonomic bias, tetrapod ichnogenera and ichnospecies are usually more or less vaguely referred to families or orders within paleobiological classifications (Haubold, 2000). This practice is necessitated in essence by an insufficient skeletal fossil record. Despite the large number of late Paleozoic track sites and tracks, there is only a small portion of sufficiently well-preserved specimens to which anatomical differences of the imprint morphology or trackway pattern can be used to differentiate ichnospecies. On the other hand, the skel-

etal fossil record typically lacks sufficiently preserved postcrania to allow detailed comparisons with ichnospecimens. Moreover, relevant tracks and skeletal remains are predominantly preserved in different sedimentary facies and often in different formations that are widely separated stratigraphically and spatially, further raising the suspicion about the accuracy of track-trackmaker associations.

Here we present well-documented examples in which the origins of two vertebrate ichnospecies of *Ichniotherium* can be ascribed to two biospecies of closely related genera of Diadectidae that occur with tracks at essentially the same stratigraphic level of the Lower Permian Tambach Formation of the Bromacker locality in central Germany. These are the first such examples of Paleozoic track-trackmaker associations at the species level and are based on anatomical features of the trackmaker's postcranial skeleton that are clearly transcribed in the imprint morphology and trackway pattern of the ichnotaxa.

MATERIALS AND METHODS

This study is based on 53 trackways of the Permo-Carboniferous tetrapod ichnogenus *Ichniotherium* Pohlig, 1892, which include 11 specimens of *Ichniotherium cottae* (Pohlig, 1885) and 42 of *Ichniotherium sphaerodactylum* (Pabst, 1895) collected from the Lower Permian Tambach Formation of the Bromacker locality in Thuringia, central Germany. Collectively, these specimens comprise more than 600 manus and pes imprints, as well as several hundred *Ichniotherium* tracks of incompletely preserved trackways. The difference in the abundances of the two ichnospecies trackways does not reflect a selective bias of the specimens studied, but rather a tally of all the *Ichnioth-*

erium trackways encountered by the senior author during a 5-year research program of reviewing Permo-Carboniferous tetrapod footprints. To assess the variability of the trackways, they were photographed both in overview and as individual imprints. Most importantly, the trackways were outlined on transparency film in order to record measurements of 28 different parameters of imprint morphology and trackway pattern (Appendices 1, 2). All of the measurements are widely accepted as standard, procedural practice and have been fully described in other such studies (e.g., Haubold, 1971; Leonardi, 1987; Voigt and Haubold, 2000).

The Tambach Formation of the Bromacker locality has yielded about a dozen partial to complete, articulated skeletons of the diadectids *Diadectes absitus* Berman, Sumida, and Martens, 1998, and *Orobates pabsti* Berman, Henrici, Kissel, Sumida, and Martens, 2004 (see Appendix 3), which are described here as the trackmakers of the ichnospecies *Ichniotherium cottae* and *Ichniotherium* s*phaerodactylum*, respectively. Before the description of *Diadectes* Cope, 1878, from the Bromacker locality (Berman et al., 1998), this well-known genus had an exclusively North American distribution, whereas the occurrence of *Orobates* (Berman et al., 2004) is restricted to the Bromacker locality. Unfortunately, only a few specimens of the two Bromacker diadectids are useful in identifying them as the trackmakers of *I. cottae* and *I.* s*phaerodactylum*. Of the Bromacker *D. absitus* specimens, the greater portion of the articulated postcranial skeleton of MNG 7721 provides the first example of a complete, articulated manus (a right). Examples of the pes in *D. absitus*, however, are limited to a partial right tarsus in the holotype MNG 8853, which consists of the greater portion of an articulated skeleton with skull, and a partial pes in MNG 10650, which consists of an articulated right tibia, fibula, partial tarsus, and metatarsals 1–4 (Berman et al., 1998; Berman and Henrici, 2003). In the absence of an example of a complete pes in *D. absitus* the present analysis uses a large, mature *Diadectes* sp. specimen, CM 41700, from the Permo-Carboniferous of North America that consists of a superbly preserved, dorsally exposed, articulated posterior half of the postcranial skeleton (Berman, 1993; Eberth and Berman, 1993; Berman and Henrici, 2003). In this specimen both hind limbs are extended directly outward from the pelvis and the pedes are splayed out and present mirrored images of one another. Except for a missing medial centrale in the left tarsus, the pedes exhibit the full complement of elements in their correct relative positions to each other. This substitution is justified by the fact that the partial pedes in the Bromacker specimens MNG 8853 and 10650 exhibit no noticeable deviations from those in CM 41700 (Berman and Henrici, 2003) and that there is only one *Diadectes* species, *D. absitus*, known from the locality. CM 41700 is also important to this study in possessing a complete, articulated tail, which is not preserved fully in any of the *D. absitus* specimens.

The holotype of *Orobates pabsti*, MNG 10181, a complete, superbly preserved, articulated skeleton, exhibits all the structures necessary for this study in dorsal view: (1) a complete vertebral column that includes the presacral region and the entire tail; (2) both manus, with the right exposed in dorsal view, and all the elements in nearly their correct relative positions to each other; and (3) both hind limbs extend outward from the pelvis with the pedes exposed splayed out and presenting mirrored images of one another with all the elements occupying their correct positions relative to each other. Because the North American and German *Diadectes* specimens are structurally identical in their postcranial characters (Berman et al., 1998), they collectively provide a reliable basis for comparison with *O. pabsti*. All of the measurements of postcranial structures included herein have been made directly from the study specimens.

Institutional Abbreviations—**BGR**, Bundesanstalt für Geowissenschaften und Rohstoffe; Außenstelle Berlin-Spandau, Germany; **BUW**, Bauhaus-Universität Weimar, Germany; **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; **FG**, Geologisches Institut der Technischen Universität Bergakademie, Freiberg, Germany; **GZG**, Geowissenschaftliches Zentrum Göttingen, Germany; **HF**, Institut für Geologische Wissenschaften und Geiseltalmuseum, Martin-Luther-Universität Halle-Wittenberg, Germany; **HLMD**, Hessisches Landesmuseum Darmstadt, Germany; **LMJG**, Landesmuseum Joanneum Graz, Austria; **MB**, Naturkundemuseum Berlin, Germany; **MLP**, Museum of Natural History La Plata, Argentina; **MNG**, Museum der Natur Gotha, Germany; **MSEO**, Museum Schloß Ehrenstein, Ohrdruf, Germany; **NHMM**, Naturhistorisches Museum Magdeburg, Germany; **NHMS**, Naturhistorisches Museum Schloß Bertholdsburg Schleusingen, Germany; **NHMW**, Naturhistorisches Museum Wien, Austria; **NME**, Naturkundemuseum Erfurt, Germany; **PMJ**, Phyletisches Museum Jena, Germany; **RE**, Ruhrlandmuseum Essen, Germany; **SMMGD**, Staatliches Museum für Mineralogie und Geologie Dresden, Germany; **UGBL**, Urweltmuseum Geoskop Burg Lichtenberg, Thallichtenberg, Germany.

Anatomical Abbreviations—**as**, astragalus; **ca**, calcaneum; **fe**, femur; **fi**, fibula; **h**, humerus; **i**, intermedium or its portion of astragalus; **lc**, lateral centrale; **mc**, medial centrale; **pc**, proximal centrale or its portion of astragalus; **pi**, pisiform; **r**, radius; **ra**, radiale; **ti**, tibia; **tib**, tibiale or its portion of astragalus; **u**, ulna; **ul**, ulnare; **1–4**, distal carpals and tarsals.

Ichnological Abbreviations—**A**, distance between manus and pes; **B**, width of pace; **C**, apparent body length; **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; **S**, length of stride; **α**, pace angulation; **β**, divarication of manus or pes from midline, plus = outward rotation, minus = inward rotation; **γ**, interdigital angle I–V; **I–II–III–IV–V**, first to fifth digit, numbered from medial to lateral side of imprint.

GEOLOGICAL CONTEXT

With one exception (postcranial skeletal of *Diadectes*, CM 41700) the present study is based entirely on vertebrate skeletal fossils and tracks or trackways from the Lower Permian Bromacker locality, an area of small abandoned and intermittently active quarries scattered over an area of less than 0.5 km^2 in the middle part of the Thuringian Forest approximately 1.5 km north of the village of Tambach-Dietharz and about 20 km south of the town of Gotha, central Germany (Fig. 1). This is the type locality of the Tambach Sandstone, a 50–100 m thick, midmember of an informal, tripartite division the Tambach Formation, which forms the base of the Upper Rotliegend Group or Series in this area and comprises a 200–400 m thick unit of conglomerates, sandstones, and mudstones. The red beds of the Tambach Formation, whose outcrops are now restricted to an area of about 50 km^2, were deposited in a small, internally drained paleograben, termed the Tambach Basin, approximately 250 km^2 in original aerial extent. The Bromacker locality lies near the center of the former Tambach Basin. The vertebrate tracks and skeletons occur in a 10 m thick stratigraphic interval of the Tambach Sandstone exposed in the commercial quarries of the Bromacker locality. Eberth and colleagues (2000) interpreted the deposition of the Bromacker sediments and its associated fossil assemblage of the Tambach Basin as representing a rarely described paleoenvironment of a 'truly upland' terrestrial setting that was far removed and up-dip from coal-swamps or extensive coastal or alluvial plains bordering non–coal-forming wetlands, which has been the overwhelming source of Late Pennsylvanian-Early Permian vertebrates.
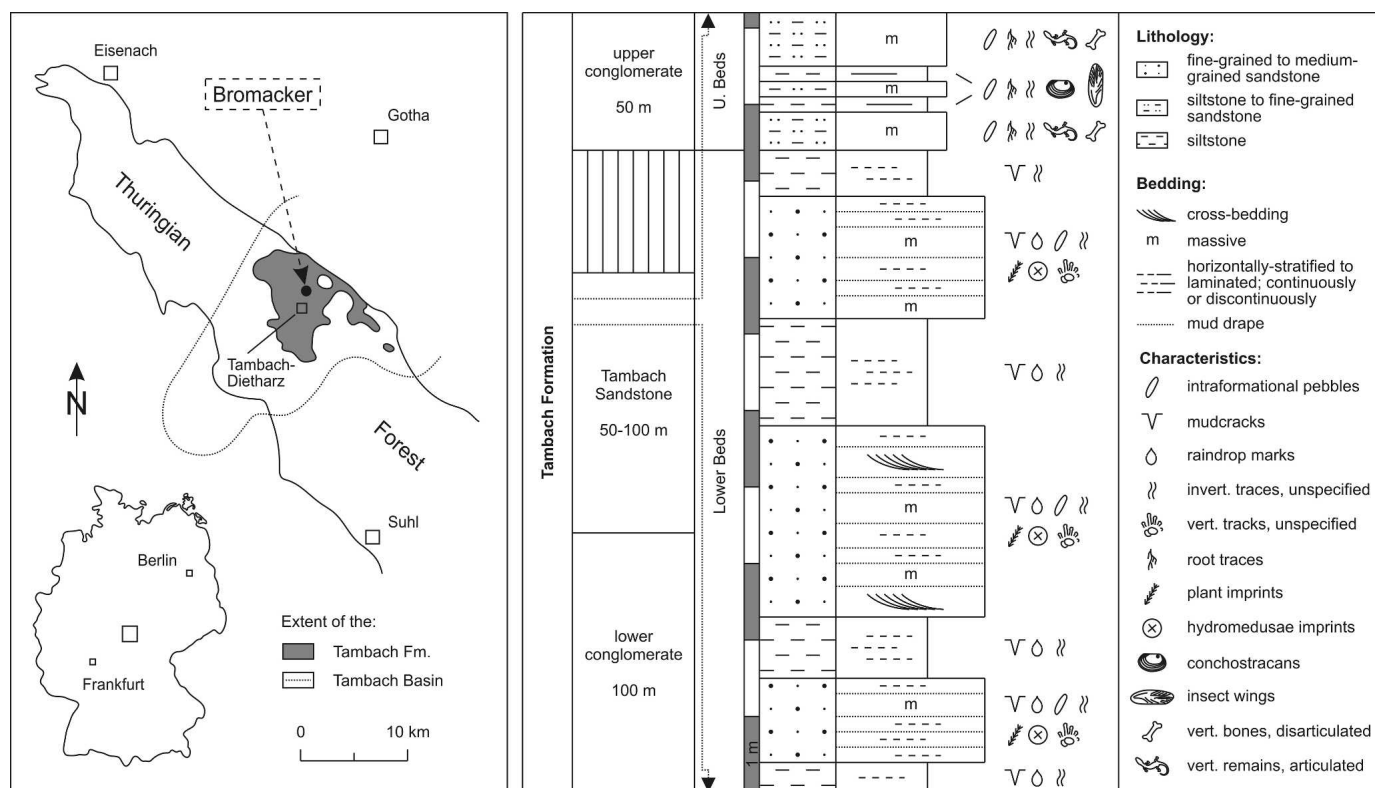
FIGURE 1. Location map and generalised stratigraphic section of the track- and bone-bearing red-bed succession of the Lower Permian Bromacker locality, Thuringia, central Germany (after Knoth, 1970, and Eberth et al., 2000).

Based on different facies content the Bromacker section was divided into two conformable stratigraphic intervals by Eberth and colleagues (2000; Fig. 1), a sandstone-dominated Lower Beds and a mudstone-dominated Upper Beds. The Lower Beds consist of several decimeter-thick massive to bedded sandstones with millimeter-to-centimeter thick laterally-extensive mud-drapes along which they are easily split into the commercial sandstones slabs. Desiccation cracks, macroplant and jellyfish impressions, invertebrate trace fossils, the vertebrate tracks for which the Bromacker locality is famous, as well as evaporation and raindrop marks, are commonly preserved on the lower surface of the sandstone slabs (Haubold, 1973b; Martens, 1975; Barthel and Rößler, 1994; Eberth et al., 2000; Voigt, 2002b). The sandstone bodies alternate with decimeter-thick laminated to bedded siltstones. The Upper Beds are dominated by two facies: basal, decimeter-scaled massive siltstones to very fine-grained sandstones, which are sharply overlain by beds of finely laminated siltstone and claystone. Essentially all of the hundreds of vertebrate skeletal specimens collected from the Bromacker, ranging from isolated elements to partial and complete, articulated skeletons, including the diadectid specimens that are the subject of this study (e.g., Boy and Martens, 1991; Berman and Martens, 1993; Berman et al., 1998, 2004; Berman, Henrici, et al., 2000; Berman, Reisz, et al., 2000), were recovered from two closely associated sheetflood deposits within a stratigraphic interval of 1.2 m within the massive siltstones of the Upper Beds. The overlying facies of very finely interlaminated siltstone and claystone beds, up to 15 cm thick, have yielded impressions of conchostracans, insect wings, and myriapod fragments (Martens et al., 1981).

According to Eberth and colleagues (2000) the red beds of the Bromacker locality were probably deposited on an upland alluvial plain with minor stream channels. Fossil biota and bedding plane markings indicate seasonal wet-dry cycles of a savanna-type climate. The sandstone sheets and their mudstone drapes of the Lower Beds were interpreted as recurrent alluvial paleochannel and interfluvial deposition, respectively. The sandstones sheets were deposited as low-sinuosity, shallow, paleochannel fills during high-energy flooding events. A cessation of the flooding events due to a blockage or back up of the channels was followed by mud-laden, slack-water conditions that drowned the channels and resulted in the laterally extensive deposition of the mud drapes. The Upper Beds were interpreted as an upper-flow-regime sheetflood deposit and waning flood deposits in an ephemeral-lacustrine to flood basin setting. The sheetfloods probably originated at the margins of the Tambach Basin and, when sufficiently intense, spread across the low-sloping land surface of the basin center. The fine-grained sandstone lenses were interpreted as shallow, locally developed, channel fills. Because the depositional style of the Lower and Upper Beds represents cyclic deposition of coarser-grained flood sediments followed by slack-water conditions with suspension deposition that are very similar to one another, sedimentation of the Bromacker red-bed succession from the Lower Beds to the Upper Beds is thought to have occurred without a significant stratigraphic break. On this basis it is probable that the taxa represented by the skeletal remains in the Upper Beds are the same as those that made the tracks in the Lower Beds.

BROMACKER TETRAPOD ICHNOTAXA RECORD

Preservation and Ichnofauna

The Bromacker locality has long been known for exceptionally well-preserved tetrapod footprints (Pohlig, 1892; Pabst, 1895, 1908; Voigt, 2002a). Approximately 300 large trackway slabs that

collectively include thousands of single imprints have been recovered during the past 120 years of commercial quarrying activities in the area (e.g., Müller, 1954; Steiner and Schneider, 1963; Haubold, 1973b; Fichter, 1998). The superb preservation and abundance of the tracks in the Lower Beds was undoubtedly the result of the unusual sedimentary conditions in which they were made: (1) the tracks were made on the uppermost surface of thin, mm-to-cm-thick drying mud layers of the mud drapes and, therefore, represent true surface footprints with the potential of preserving ultra-fine anatomical details such as skin impressions; (2) the underlying sandy substrate of the paleochannel fill was sufficiently coarse-grained and thick-layered to provide firm support and only shallow penetration by the trackmakers; and (3) the sand grains of the overlying channel fill that filled in the imprints were of sufficient fineness to form detailed natural casts of the tracks. The tetrapod tracks of the Tambach Sandstone are, therefore, exclusively preserved as convex hyporeliefs on the bottom surface of the sandstone channel fills. The Bromacker locality can be regarded as presenting optimum conditions for the preservation of tetrapod tracks.

To date, five vertebrate ichnogenera are currently recognized from the Tambach Sandstone of the Bromacker locality (Haubold, 1998; Voigt, 2005): (1) *Amphisauropus* Haubold, 1970, referred to the seymouriamorph amphibians; (2) *Ichniotherium* Pohlig, 1892, referred to the diadectomorph Diadectidae; (3) *Dimetropus* Romer and Price, 1940, referred to the primitive basal synapsid sphenacodontids or caseids; (4) *Varanopus* Moodie, 1929, referred to the reptilian Captorhinomorpha; and (5) *Tambachichnium* Müller, 1954, of uncertain origin and tentatively referred to the parareptilian bolosaurids or primitive basal synapsid Varanopidae (Haubold, 1998; Voigt, 2005). *Ichniotherium* is by far the most common ichnogenus from the Tambach Sandstone, representing more than 95% of all tetrapod footprints recovered (Haubold, 1998).

Ichniotherium Pohlig, 1892

Ichnotaxonomic Aspects—Since the beginning of ichnologic studies of the Bromacker site in the late 19th century, researchers discerned minor morphological differences in the *Ichniotherium* footprint record, which they used as a basis for ichnospecies recognition. Shortly following the description of *Ichniotherium cottae* (Pohlig, 1885), two additional ichnospecies or ichnosubspecies of *Ichniotherium* were recognized (Pabst, 1895, 1908) at the Bromacker locality, the more common *Ichniotherium sphaerodactylum* (Pabst, 1895) and the rather rare *I. sphaerodactylum minor* (Pabst, 1895). Nopcsa (1923), Lotze (1928), and Korn (1933) not only accepted the subspecific separation of the Bromacker *Ichniotherium* tracks, but also proposed a greater ichnotaxonomic separation on the basis of differences in trackway patterns. Haubold (1971, 1973a) initially argued that *I. sphaerodactylum*, *I. sphaerodactylum minor*, and *I. cottae* are the tracks of a single species which reflected different gaits, and so he synonymized the former two ichnospecies with *Ichniotherium cottae*, the first named ichnotaxon (Pohlig, 1885, 1892). However, in a recent revision of the *Ichniotherium* assemblage of the Bromacker locality Voigt and Haubold (2000) recognised two morphotypes of *Ichniotherium* that they referred to as A and B, which differ in the relative length of digit V of the pes imprint and the trackway pattern. They noted that the imprints of the more common morphotype A exhibits a longer digit V and a trackway pattern indicative of a slow to moderate rate of locomotion by the trackmaker, whereas the imprints of the rarer morphotype B exhibits a shorter digit V and a trackway pattern indicative of a more rapid rate of locomotion. On this basis Voigt and Haubold (2000) concluded, as Haubold (1971, 1973a) had earlier, that morphotypes A and B were made by individuals of the same species, and their differences merely reflect different

gaits and speeds. The short digit V of the morphotype B, which is represented only by the rounded imprint of the digit tip, was interpreted by Voigt and Haubold (2000) as indicating a greater speed and less plantigrade gait of the trackmaker. This explanation for the differences in the two types of *Ichniotherium* tracks was abandoned, however, with the discovery in 2002 of the second most prolific *Ichniotherium* track site in the Permo-Pennsylvanian red beds of the Maroon Formation near Maroon Bells, central Colorado (Voigt et al., 2005). Here numerous trackway segments and hundreds of isolated imprints of *Ichniotherium* were recorded that are identical to the morphotype B tracks of the Bromacker locality. Thus, it was concluded (Voigt et al., 2005) that morphotypes A and B of *Ichniotherium* were made by very closely related animals that differ in some postcranial characters, such as the relative length of digit V of the pes and the ratio of the body length to that of the limbs. This significant expansion of the ichnological database revealed clearly that two different ichnospecies of *Ichniotherium* occur at the Bromacker locality: *I. sphaerodactylum* (Pabst, 1895) and *I. cottae* (Pohlig, 1885), which are synonymous with morphotypes A and B, respectively, of Voigt and Haubold (2000). The taxonomy of both ichnospecies is complex and beyond the goal of this study (cf. Voigt, 2005). Yet, it can be stated that *Ichniotherium* undoubtedly represents the best example of all late Palaeozoic tetrapod ichnogenera in which ichnospecies can be distinguished on anatomically controlled characters of the imprint morphology and trackway pattern that correlate with well-preserved body fossils.

Ichniotherium Characterization—Based on the abundant track record from the Bromacker locality *Ichniotherium* is the trackway of a quadrupedal tetrapod with pentadactyle, plantigrade footprints between 5.5 and 13.0 cm in length (Fig. 2). In both the manus and pes footprints digits I-IV exhibit a serial increase in length, whereas the length of digit V is ichnospecies specific in being either shorter than II or as long as III. In well-preserved manus and pes tracks the digits, particularly their
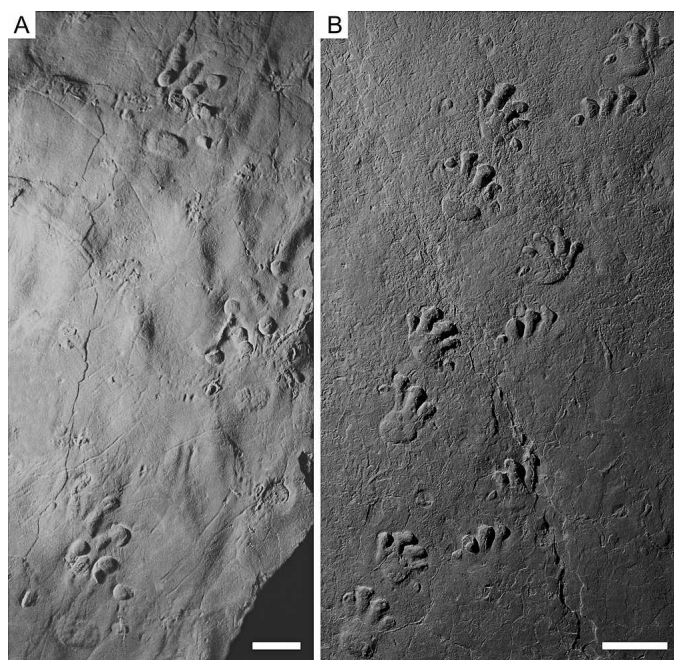

FIGURE 2. *Ichniotherium* trackways from the Bromacker locality. **A**, *Ichniotherium cottae* (Pohlig, 1885), MNG 1352; **B**, *Ichniotherium sphaerodactylum* (Pabst, 1895), MNG 1351. Quality of preservation is typical of locality. Scale bars equal 5 cm in A and 10 cm in B.

proximal portions, are segmented transversely by short, very narrow, slightly irregularly curved grooves. The distal portions of digits II–IV of the manus imprint are distinct from those of the pes in being more strongly bent or angled toward the trackway midline. The manus and pes impressions of *Ichniotherium* can be easily recognized by a large, mediolaterally expanded, oval sole-pad impression that is clearly separated from the digit impressions. In contrast to the sole-pad impression of the manus, however, that of the pes is more clearly defined marginally and is larger in relief. Also typical of the pes, the digits terminate in expanded, rounded margins that give them a drumstick-like outline. The length of the manus imprint is about 80% of that of the pes, with a width that exceeds its length by about 20%, whereas the pes imprint is about as long as it is wide.

Other than the manus imprint always being positioned in front of the pes track, the trackway pattern of *Ichniotherium* is variable. Trackways with a long manus-pes separation are usually characterised by the manus imprint of one side being contralateral to the pes imprint of the opposite side (=alternating arrangement of single imprints). The shorter the manus-pes separation the greater is the tendency for an alternating arrangement of coupled manus-pes imprints (Fig. 2A). Although primary overstepping occurs in trackways showing a distinctly alternating arrangement of footprint sets, it is, however, never greater than partial, with the digits of the pes imprint never reaching the base of the digits of the manus imprint. The trackway width and length of pace of the manus imprints are somewhat smaller than those of the pes imprints. The pace angulation ranges between 70° and 130°, the ratio of the stride length to pes length is 2.5–5.5:1, and the ratio of the stride length to the apparent body length is 0.8–1.7:1. Both the manus and pes imprints are directed inward, approximately 25° and 8°, respectively. A tail-drag mark is very rare and always discontinuously preserved.

***Ichniotherium cottae* (Pohlig, 1885) Characterization**—The most diagnostic features of the manus and pes imprint morphology of *Ichniotherium cottae* are the lengths of digit V and the shape of the sole pad. In both the manus and pes imprints digit V is short, measuring about 50% of the length of digit IV (Fig. 3A–C, Appendix 1). The sole pad impression of the manus track exhibits an oval-to-subcircular outline with a mediolateral width that exceeds only slightly its proximodistal length and lies opposite digits II and III. Preservation of the sole pad impression of the pes track occurs as two, co-joined semicircular outlines: a medial, oval-to-subcircular outline that lies opposite digits II–IV and a smaller outline that joins its proximolateral margin as an oval-to-semicircular extension that lies opposite digit V (Fig. 3A–C). The appearance of the latter portion of the impression is apparently dependent on the impression of the sole pad being sufficiently deep to include it. The entire sole pad impression has a greatest mediolateral width that exceeds its greatest proximodistal length by about 53%. The manus and pes lengths range between 5.5 and 7.6 cm and 6.6 and 8.4 cm, respectively (see Appendix 1).

The trackway pattern ranges from a nearly alternating arrangement of single imprints to an alternating arrangement of coupled manus-pes imprints (Fig. 4A–C). The latter pattern is more common and may exhibit a partial overstepping of the pes up to the proximal margins of the manus digits. The pace angulation ranges between 80° and 130°, the ratio of the stride length to pes length ranges from 3.5–5.5:1, and the ratio of the stride length, based on pes imprints, to the apparent body length ranges from 1.2–1.7:1. A tail-drag mark has never been reported in Bromacker specimens of *Ichniotherium cottae* nor has it been observed in this study.

***Ichniotherium sphaerodactylum* (Pabst, 1895) Characterization**—The manus and pes imprints of *Ichniotherium sphaerodactylum* exhibit a relatively long digit V, measuring about 66% and 80% the length of digit IV in the manus and pes, respectively
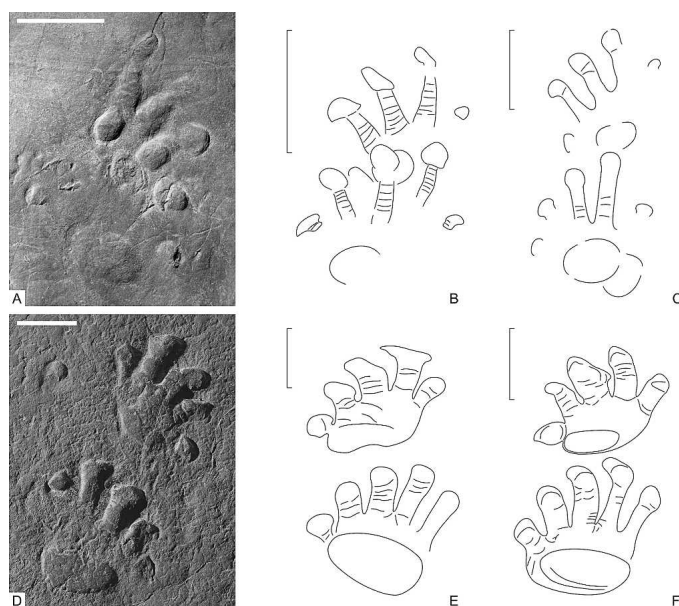

FIGURE 3. Imprints and outline drawings of coupled manus-pes impressions (manus anterior to pes) of **A–C**, *Ichniotherium cottae* and **D–F**, *Ichniotherium sphaerodactylum* from the Bromacker locality. **A**, MNG 1352; **B**, MSEO 4; **C**, drawing based on photograph of a non-preserved trackway slab from the Bromacker locality recovered in 1995; **D**, MNG 1351; **E**, MB.1969.54.257; **F**, MB.ICV.4. Scales equal 5 cm.

(Fig. 3D–F). The sole impression of the pes can be distinguished by its greatly expanded, mediolateral oval outline that measures approximately twice its proximodistal length and lies opposite digits II–V. In the manus imprint there is often a comparable but much smaller, less clearly defined sole impression that is narrower and positioned opposite digits II and III, although it sometimes appears to be elongated proximolaterally to about the level of the mid-width of digit IV. Typically, the distal portions of the manus digits II–IV are narrowly pointed, sharply bent or angled medially, and sub-parallel with each other. Commonly, the outline of the entire imprint of the first manus digit is narrowly triangular. The manus and pes lengths range between 4.4 and 10.6 cm and 5.7 and 12.9 cm, respectively (Appendix 2).

Trackway pattern ranges from an alternating arrangement of single imprints to an alternating arrangement of coupled manus-pes imprints (Fig. 4D–F). However, even trackways with a distinctly alternating arrangement of coupled manus-pes imprints exhibit only minor overstepping in which the digit tips of the pes imprints at most overlap slightly the proximal posterior margin of the manus imprints. The pace angulation ranges between 70° and 110°, the ratio of the stride length to the pes length ranges from 2.5–4.4:1, and the ratio of the stride length, based on pes imprints, to the apparent body length ranges from 0.8–1.4:1. A discontinuous tail-drag mark may be present (e.g., BUW 1, MB.ICV.2).

BROMACKER TETRAPOD BIOTAXA REPRESENTATION

Preservation and Faunal Composition

Vertebrate bone fragments were first found at the Bromacker locality in 1974 (Martens, 1980, 1982), more than 80 years after the first recovery of tetrapod tracks from the Bromacker. This initiated a program of systematic excavation of the Tambach Formation at the Bromacker locality, which yielded the first articulated vertebrate remains in 1979, a nearly complete, partially
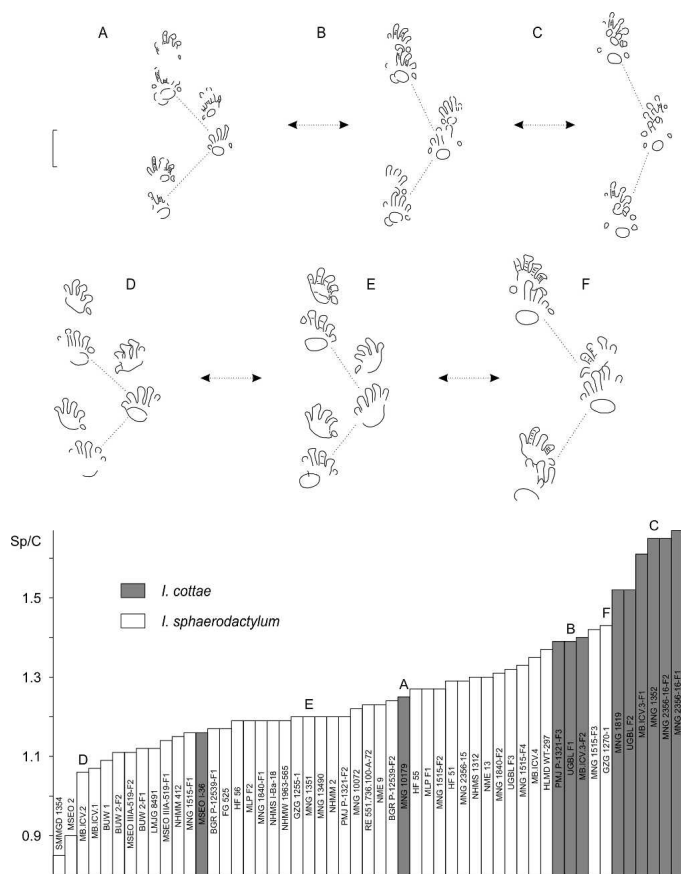
FIGURE 4. Graphic and numerical expressions of the range of *Ichniotherium* trackway patterns. Sp/C, the ratio of stride length of pes to apparent body length (glenoid-acetabular distance; data source Appendices 1, 2), indicates clearly that the trackmaker of *Ichniotherium cottae* was capable of significantly longer strides relative to its body length than the trackmaker of *Ichniotherium sphaerodactylum*. **A–C** and **D–F** indicate catalogued specimens of *I. cottae* and *I. sphaerodactylum*, respectively, whose trackways are illustrated. Scale equals 10 cm in **A–E** and 15 cm in **F**.

disarticulated postcranial skeleton of *Diadectes* (Martens et al., 1981; Berman et al., 1998). In terms of abundance of specimens, diversity of taxa, and quality of preservation the Bromacker locality had become the most productive locality for Lower Permian terrestrial vertebrates in Europe by the end of the century (Martens, 1988, 1994, 2001a, b; Boy and Martens, 1991; Berman and Martens, 1993; Berman et al., 1998, 2001; Berman, Henrici, et al., 2000; Berman, Reisz, et al., 2000; Sumida et al., 1996, 1998; Eberth et al., 2000). To date, a minimum of 11 vertebrate taxa have been identified from the Bromacker locality that are collectively represented by 50 or more partial-to-complete skeletons and hundreds of isolated elements (Eberth et al., 2000; Martens et al., 2005). Anamniotes (amphibians) include the trematopid *Tambachia trogallas*, Sumida, Berman, and Martens, 1998, unidentified dissorophids (Anderson et al., 2004), and the seymouriamorph *Seymouria sanjuanensis* Vaughn, 1966, (Berman and Martens, 1993; Berman, Henrici, et al., 2000; Martens et al., 2005; Klembara et al., 2005, 2006). Amniotes are represented by two diadectids, *Diadectes absitus* Berman, Sumida, and Martens, 1998, and *Orobates pabsti* Berman, Henrici, Kissel, Sumida, and Martens, 2004, the captorhinomorph *Thuringothyris mahlendorffae* Boy and Martens, 1991, the bolosaurid *Eudibamus cursoris* Berman, Reisz, Scott, Henrici, Sumida, and Martens, 2000, the primitive basal synapsid *Dimetrodon teutonis* Berman,

Reisz, Martens, and Henrici, 2001, and two undescribed primitive basal synapsids, a caseid and varanopid (Berman et al., 2004; Martens et al., 2005).

Although the Bromacker vertebrate assemblage shares many taxa in common with those of well-documented, lowland terrestrial environments (almost exclusively found in the United States), it is unique in exhibiting marked differences in the composition and abundances of its constituents that suggest a direct relationship between their paleobiology and occurrence in a 'truly upland' paleoenvironment (Berman, Henrici, et al., 2000; Eberth et al., 2000; Martens et al., 2005): (1) a complete absence of aquatic and semi-terrestrial forms (fish and obligatory aquatic and semi-terrestrial amphibians); (2) an unusually high abundance and variety of herbivores (*Diadectes*, *Orobates*, *Eudibamus*, and the undescribed caseid) capable of subsisting on a diet of high-fiber plants; and (3) an unusually low abundance and variety of top predators (*Dimetrodon* and the undescribed varanopid).

The Bromacker is uniquely characterised by a remarkable abundance of specimens that occur fully or nearly complete, articulated, and exceptionally well preserved in fully extended, near natural poses (e.g., Fig. 5C; Berman et al., 2001, 2004; Berman, Henrici, et al., 2000; Eberth et al., 2000). This indicates that death and burial were in these instances almost certainly coeval events. Often two, three, or four articulated specimens of one or two taxa were preserved in small groups or clusters. These observations indicate that rates of sedimentation were high and the specimens were not transported great distances during the flooding events that preserved them in the sheet-flood deposits. It was also reasoned that those specimens clustered together occurred together at the time of death and probably indicate gregarious behavior. Furthermore, specimens represented by isolated bones of reworked carcasses were transported with little or no subaerial exposure from proximal to more central parts of the basin. Also judging from the description of the paleoenvironment of the Tambach Basin and its Bromacker locality (Eberth et al., 2000), there is reasonably good evidence to assume that the vertebrates are representatives of a single, local community: (1) most significantly, the sheet-flood deposit in which the vertebrates occur represent essentially a single, catastrophic flooding event that was restricted to the internally drained Tambach Basin and was of very short duration but had a very wide aerial extent and an apparent magnitude capable of preserving individuals much larger than those recovered; and (2) specimens of specific taxa are randomly distributed throughout the sheet-flood deposits without any signs of taphonomic sorting to a particular level. Taken together, these taphonomic features suggest strongly that the Bromacker quarry not only preserves only those vertebrates that inhabited the Tambach Basin, but also provides a fairly reliable census of their diversity, relative abundances, and maximum sizes. Until now, these two aspects of the Bromacker assemblage have never before been demonstrated in an Early Permian terrestrial assemblage, and they strongly indicate that the tetrapod taxa preserved in the Upper Beds most likely also represent those whose numerous tracks are preserved in the sandstone facies of the Lower Beds.

Diadectid Representation

The Late Pennsylvanian to Early Permian Diadectidae, along with the Late Pennsylvanian Limnoscelidae and Early Permian Tseajaiidae, best or solely represented by the type genera *Limnoscelis* and *Tseajaia* (Vaughn, 1964; Moss, 1972; Fracasso, 1983; Berman and Sumida, 1990; Berman, 2000) comprise one of the best-known and most diverse late Paleozoic tetrapod clades, the Diadectomorpha. Although widely regarded as the sister group to all amniotes (e.g., Carroll, 1995; Laurin and Reisz, 1995, 1997), Berman and colleagues (1992) and Berman (2000) placed the

Diadectomorpha within Amniota as sharing a most recent common ancestor with Synapsida, as well as linking them as the sister clade of Reptilia. Diadectids include five more or less well-established genera, *Diadectes* Cope, 1878, *Desmatodon* Case, 1908, *Diasparactus* Case, 1910, *Orobates* Berman, Henrici, Kissel, Sumida, and Martens, 2004, and *Ambedus* Kissel and Reisz, 2004, and all are exclusively known from the Permo-Carboniferous of North America except for the Bromacker occurrence of *Diadectes* and the exclusively Bromacker occurrence of *Orobates* (Olson, 1947; Berman et al., 1992, 1998; Berman and Sumida, 1995). A combination of autapomorphic and plesiomorphic characters, mainly cranial but also some postcranial, clearly distinguishes *Orobates pabsti* not only as most closely related to *Diadectes* among the diadectids, but also as the sister taxon to all other diadectids (Berman et al., 2004), with the possible exception of *Ambedus* Kissel and Reisz (2004), which is based solely on jaw elements with teeth similar to diadectids. *Phanerosaurus* Meyer, 1860, and *Stephanospondylus* Stappenbeck, 1905, are poorly defined diadectids from Germany, and about all that can be said of them is that they are probably diadectids (Berman et al., 1998).

The Bromacker locality is unique among Early Permian terrestrial vertebrate localities not only in having yielded a very large number of diadectid specimens (Appendix 3), but also in the great abundance of diadectids compared to the other members of the Bromacker assemblage (Eberth et al., 2000). Based on a count of minimal number of individuals, diadectids represent 35% of the Bromacker vertebrate population with *Diadectes absitus* and *Orobates pabsti* comprising 24% and 11% of this total, respectively. Most significantly, using the same abundance index, the herbivores (*Diadectes*, *Orobates*, *Eudibamus*, and the undescribed caseid) outnumbered the top predators (*Dimetrodon* and the undescribed varanopid) 7:1.

Diadectid Postcranial Characters and Implications for Ichnospecies Identification

Diadectes absitus Berman, Sumida, and Martens, 1998—An unusual character of the axial skeleton of *Diadectes* among late Paleozoic tetrapods, including the holotype of *Diadectes absitus* (MNG 8853; Fig. 5A), is the reduction of the number of presacral vertebrae to 21. The postaxial presacral neural arches are of the type typically referred to as swollen, with the zygapophyses extending well beyond the lateral margins of the centra. In addition to the two sacral vertebrae, at least 34 caudals are present in the complete tail of the North American specimen CM 41700 (Fig. 5B). The ulna exceeds the radius in length by about 20%, whereas the fibula exceeds the tibia in length by 10% (Appendix 4).

As far as is known, the right manus in the Bromacker *Diadectes absitus* MNG 7721 includes the only known example of a complete, or nearly complete, articulated carpus of the genus

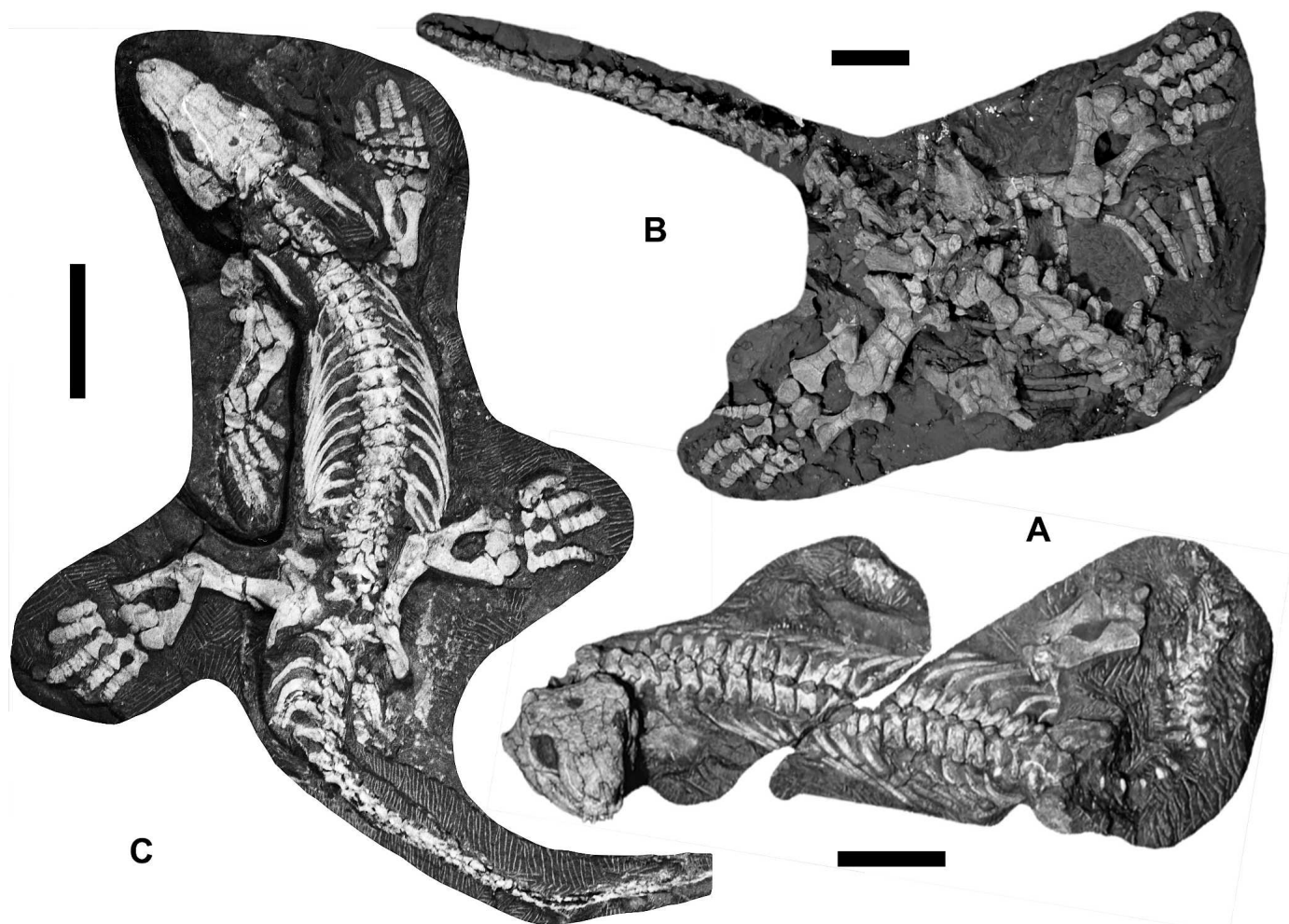FIGURE 5. **A**, greater part of articulated skeleton exposed mainly in dorsal view of *Diadectes absitus* Berman, Sumida, and Martens, 1998, holotype, CM 8853; **B**, partial postcranial skeleton exposed in dorsal view of *Diadectes* CM 41700; **C**, essentially complete articulated skeleton exposed mainly in dorsal view of *Orobates pabsti* Berman, Henrici, Kissel, Sumida, and Martens, 2004, holotype, MNG 10181. Scales equal 10 cm.

(Berman et al., 1998) and comprises all the expected elements, an ulnare, intermedium, radiale, lateral centrale, and distal carpals 1–5, except for perhaps the medial centrale and pisiform (Fig. 6A). The pisiform may be present, however, as a displaced element located between the metacarpals 2 and 3. The carpal elements are tightly packed and the five distal carpals provide a strong bony link between the carpus and digital complex. In size the oval ulnare is clearly the dominate element of the carpus. Because the proximodistally elongated distal carpal 2 is unusually large and contacts not only nearly the entire medial margin of the lateral centrale, but also the distal end of the radiale, it was suspected of either including or excluding the medial centrale. Distal carpal 4 is typical in being large with a broad contact with metacarpal 4, but is unusual in having a proximally extended angular margin that wedges partially between the medial centrale and the ulnare. In general, the metacarpals and digits exhibit a gradual serial increase in size from the first to the fourth. The fifth digit is shorter than the fourth, but its exact length is unknown due to probable incomplete preservation. Only two phalanges are present in the digit V, but a count of three is suspected to be the correct number, inasmuch as this is would give *Diadectes* the typical phalangeal formula of late Palaeozoic terrestrial vertebrates of 2–3-4-5-3 (e.g., Sumida, 1997). All of the phalanges are short and broad and decrease serially in length distally, but with an extreme shortening of the penultimate phalanges of digits II-IV. The terminal phalanges end in a bluntly rounded margin, giving them a spade-like outline in which the width slightly exceeds the length, but are longer than the non-terminal phalanges.

As noted earlier in this paper, the description of the pes in *Diadectes absitus* relies heavily on the superbly preserved examples in the *Diadectes* sp. specimen CM 41700 from the Permo-Carboniferous of North America (Figs. 5B, 7A; Berman and Henrici, 2003). The tarsus exhibits a reduction in the number of elements to five: astragalus, calcaneum, medial centrale, and distal tarsals 1 and 4. The partial Bromacker pes of *D. absitus* MNG 10650 may represent an exception to this pattern, in that an extremely small ossification may represent the fifth distal tarsal (Berman and Henrici, 2003:fig. 5). The obvious reduction in size or lack of ossification of some elements has resulted in large unoccupied areas. These spaces were presumably occupied by the standard series of tarsals, either totally represented by cartilage or as greatly reduced ossifications surrounded by a thick envelope of cartilage. The astragalus is extremely thick and, as is typical of late Paleozoic terrestrial amniotes, is L-shaped, although the vertical and horizontal limbs are greatly shortened. Its origin is clearly the result of a fusion of the amphibian tibiale, intermedium, and proximal centrale (Berman and Henrici, 2003). The calcaneum is oval in outline and considerably thinner than the astragalus, but the two elements have a broad contact with one another and were probably bound strongly together by ligaments and a peg-and-socket locking mechanism (Berman and Henrici, 2003). The greatest mediolateral width of the pair exceeds their greatest proximodistal length by about 30%. A small, oval, nodular medial centrale lies adjacent to the distomedial curvature of the astragalus. The small, oval distal tarsals 1 and 4 are apparently the only bony links between the proximal tarsal elements and the metatarsals. The first through fourth metatarsals and digits gradually increase in size serially, with the fifth being subequal to the second. The non-terminal phalangeal elements are short and broad, and decrease serially in size distally except for, as in the manus, an extreme shortening of the penultimate phalanges of digits II-IV. The terminal phalanges, as in the manus, are spade-like in outline with the width slightly exceeding the length, but are longer than the non-terminal phalanges (Fig. 7A). The phalangeal formula of the pes is 2–3–4–5–3, and thus identical to that of the manus.
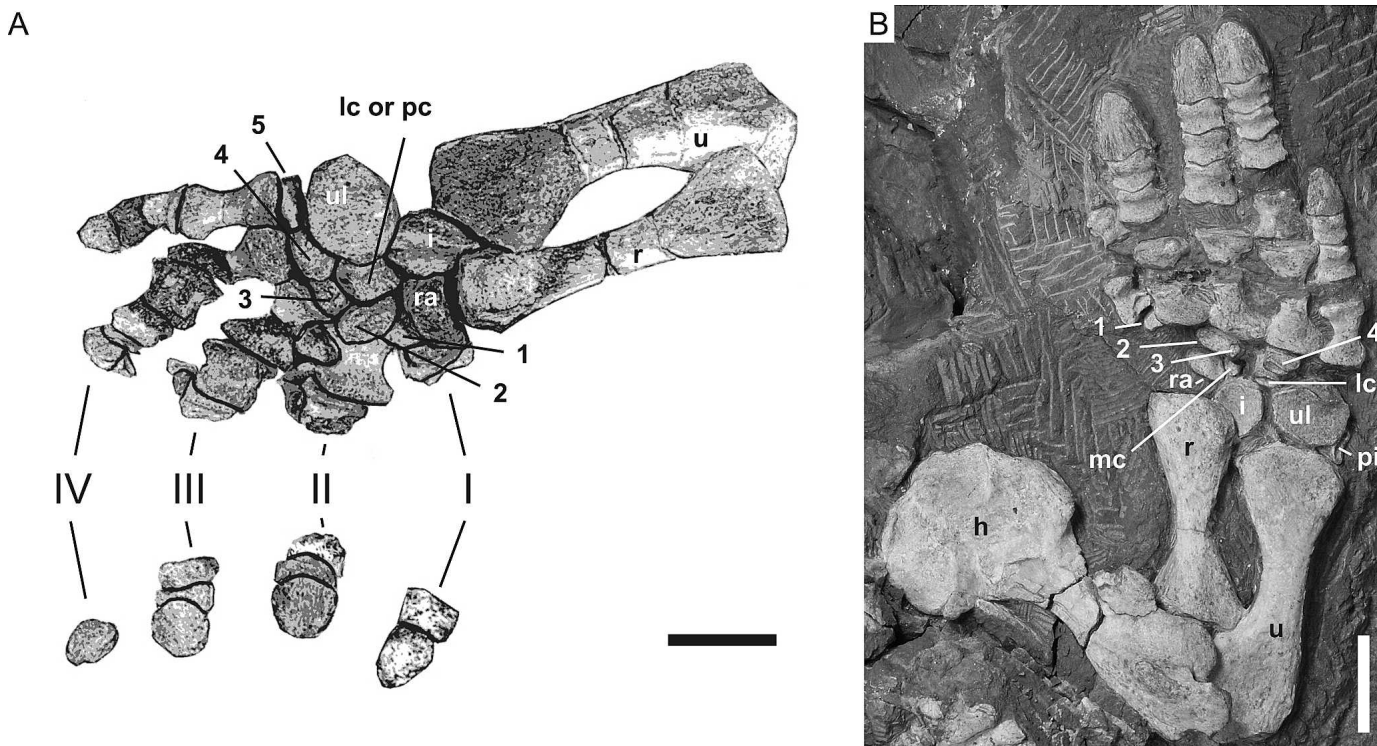
FIGURE 6.   **A**, articulated right radius, ulna, and manus of *Diadectes absitus* Berman, Sumida, and Martens, 1998, paratype, MNG 7721, in dorsal view. Distal phalanges of digits I–IV are hyperflexed against plantar surface of manus and shown separately. **B**, articulated right forelimb and manus of *Orobates pabsti* Berman, Henrici, Kissel, Sumida, and Martens, 2004, holotype, MNG 10181, in dorsal view. Scale equals 4 cm in **A** and 2 cm in **B**. Abbreviations given in the text.
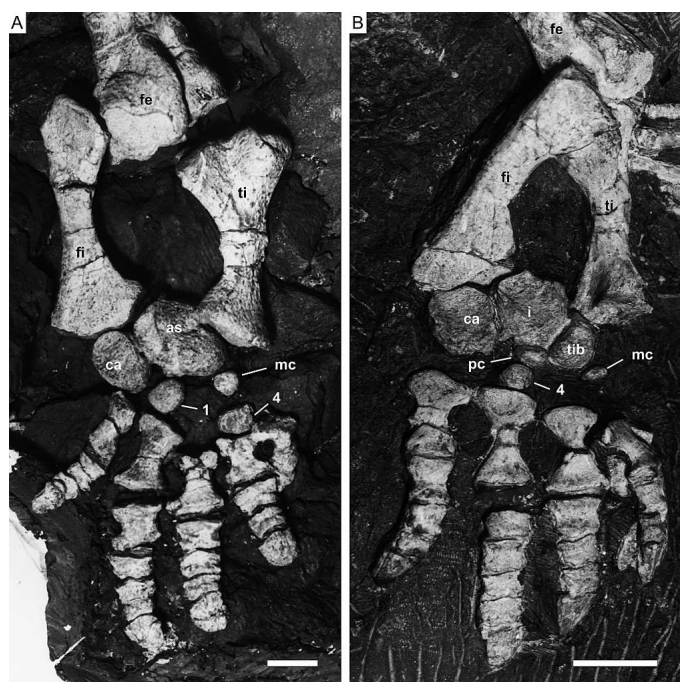
FIGURE 7. Dorsal views of articulated right crus and pes of **A**, *Diadectes* CM 41700 (Berman and Henrici, 2003) and **B**, *Orobates pabsti* Berman, Henrici, Kissel, Sumida, and Martens, 2004, holotype, MNG 10181, respectively. Scale equals 4 cm in **A** and 2 cm in **B**. Abbreviations given in the text.

Orobates pabsti **Berman, Henrici, Kissel, Sumida, and Martens, 2004**—The vertebral column of *Orobates pabsti* consists of 26 presacral and 2 sacral vertebrae, and a caudal count that apparently varies widely, with counts of 34 and 46 for the holotype MNG 10181 and paratype MNG 8980, respectively. The postaxial, presacral neural arches are of the type typically referred to as swollen, with the zygapophyses extending well beyond the lateral margins of the centra. The ulna exceeds the radius in length by about one fourth to one third, whereas the fibula exceeds the tibia in length by about 13% (see Appendix 4).

The carpus of *Orobates pabsti* is believed to consist of ten elements that include the radiale, intermedium, ulnare, medial and lateral centrales, distal carpals 1–4, and pisiform (Fig. 6B). There is an unusual reduction or even absence of ossification of some elements, which has resulted in large unoccupied areas. These spaces were presumably occupied by the standard series of carpal elements either totally represented by cartilage or as greatly reduced ossifications surrounded by a thick envelope of cartilage. The ulnare and intermedium are the dominant elements of the carpus, whereas in comparison the oval radiale is relatively small. Berman and colleagues (2004) assumed that the fourth distal carpal provided the only bony link, albeit weak, between the carpus and the digital complex. The first through fourth metacarpals and digits gradually increase in size serially, with the fifth being intermediate between the first and second. The non-terminal phalanges are short and broad and exhibit very little serial decrease in size distally, with 1 and 2 of the second digit, 2 and 3 of the third digit, and 2–4 of the fourth digit being subequal. The terminal phalanges are slightly longer than wide and considerable longer than the non-terminal phalanges and terminate in a bluntly pointed margin. Terminal phalanges of the digits I-IV are unique among diadectids in possessing a small, proximally directed, narrow, triangular extension at their proxi-

molateral corner, giving them an asymmetrical appearance (Fig. 6B). The phalangeal formula of the manus is 2–3–4–5–3.

The tarsus of *Orobates pabsti* is reduced to six elements: tibiale, intermedium, proximal centrale, calcaneum (= amphibian fibulare), medial centrale, and fourth distal tarsal (Fig. 7B). The tibiale, intermedium, and proximal centrale are tightly united suturally into a single structural unit considered to be the equivalent of the amniote astragalus (Berman and Henrici, 2003). The greatest mediolateral width of the astragalus-calcaneum pair exceeds its greatest proximodistal length by about 70%. The slightly oval fourth distal tarsal articulates between the proximal centrale and the fourth metatarsal to provide the only bony link between the tarsus and the digital complex. An extremely small, oval-shaped element, presumably the medial centrale, lies adjacent to the distolateral corner of the tibiale portion of the astragalus. Thus, the tarsus, as in the carpus, exhibits large, unoccupied areas for which the same explanation was offered (Berman and Henrici, 2003). The first through fourth digits and metatarsals gradually increase in size serially, with the fifth of both being subequal to the third. The non-terminal phalangeal elements are short and broad and decrease serially in size distally, although the first and second penultimate phalanges of the third and fourth digits are subequal in size. As in the manus, the terminal phalanges are slightly longer than wide and considerably longer than the non-terminal phalanges. Also as in the manus, the terminal phalanges of digits I–IV possess a small, proximally directed, narrow, triangular extension at their proximolateral corner, giving them an asymmetrical appearance (Fig. 7B). The phalangeal formula of the pes is 2–3–4–5–4.

DISCUSSION

Biotaxon Correlation With *Ichniotherium*

The ichnotaxon *Ichniotherium* has been referred to very different groups of late Paleozoic tetrapods since its first description 120 years ago. Pohlig (1885, 1887, 1892, 1893) interpreted *Ichniotherium* alternately as the tracks of protorosaurs, archegosaurs, and branchiosaurs. Fritsch (1887, 1901) preferred a relationship to temnospondyls, first proposing a 'giant salamander', then a melanerpetontid branchiosaur as the possible trackmaker. Whereas the diagnosis of Nopcsa (1923) more correctly recognised a relationship to eryopids and diadectids, Lotze (1928) stressed a closer relationship to the latter on the basis of the pentadactyle imprints and the inferred, reptilian-like phalangeal formula of manus and pes. Schmidt (1927) was the first to presume a primitive or pelycosaurian-grade basal synapsid origin of the *Ichniotherium* trackmaker. Based on detailed anatomical studies Romer and Byrne (1931) rejected a relationship to diadectids, because they reconstructed the pes of *Diadectes* with the digit tips pointing at a vertical angle to the ground, which they reasoned would produce somewhat shorter digit impressions rather than the plantigrade, long-toed imprints of *Ichniotherium*. Nevertheless, subsequent studies preferred a relationship to diadectids (e.g., Korn, 1933; Abel, 1935; Czyzewska, 1955; Schmidt, 1959; Steiner and Schneider, 1963) or the lesser likelihood of a relationship to procolophonids (Korn, 1933; Müller, 1955). Haubold (1971, 1973a, b, 1996) opposed the diadectid trackmaker, referring to the study of Romer and Byrne (1931), and instead proposed a primitive basal synapsid origin, such as edaphosaurids or caseid precursors. Fichter (1983) and Gand (1988) followed this interpretation. The recovery of abundant and excellently preserved diadectid remains from the Bromacker locality during the 1990s presented the crucial turning point in the biotaxon interpretation of *Ichniotherium* trackways. A striking coincidence in the size distribution, anatomy, and abundance of the diadectid specimens from the Bromacker locality provided quickly accepted, convincing evidence of a diadectid-origin of

Ichniotherium trackways (Fichter, 1998; Haubold, 1998, 2000; Eberth et al., 2000; Voigt and Haubold, 2000; Voigt, 2001, 2005; Berman et al., 2004; Voigt et al., 2005).

Biotaxa Correlations with *Ichniotherium cottae* and *Ichniotherium sphaerodactylum*

General—Comparisons of the *Ichniotherium* record at the Bromacker locality suggests the presence of two very closely related species of diadectid trackmakers. The ichnospecies *Ichniotherium cottae* (Pohlig, 1885) and *Ichniotherium sphaerodactylum* (Pabst, 1895) differ in some details of their manus and pes morphologies and trackway patterns, but most significantly in the: (1) relative lengths of digits I and V of the manus and pes; (2) shape of the terminal phalanges of digits II–IV; (3) shape of the distal portions of digits II–IV of the manus and the degree of their orientation toward the midline of the trackway; (4) shape and size of the sole pad; (5) degree of overstepping of the manus and pes; and (6) presence or absence of a tail drag mark. Despite numerous differences between the postcrania of *Diadectes absitus* and *Orobates pabsti*, albeit many of seemingly minor importance (Berman et al., 1998, 2004; Berman and Henrici, 2003), only a few can be directly or potentially related to the differences in the tracks and trackway patterns of the two ichnospecies of *Ichniotherium*. As noted earlier, because a complete pes of *D. absitus* was not available for this study, those of the superbly preserved mature *Diadectes* sp. specimen CM 41700 (Figs. 5B, 7A; Berman and Henrici, 2003) from the Permo-Carboniferous of North America provide much of the basis for the following comparisons.

Footprint Morphology versus Autopod Skeletal Anatomy—An association of the ichnospecies *Ichniotherium cottae* and *Ichniotherium sphaerodactylum* with the biospecies *Diadectes absitus* and *Orobates pabsti*, respectively, is supported strongly by the relative lengths of the pes digits (Fig. 8) when expressed as a percentage of the length of digit IV (Appendices 5, 6). This is especially true of digit V in the pes, which in *I. cottae* and *D. absitus* have lengths equal to about 48 and 52% of digit IV, respectively, compared to 80 and 79% in *I. sphaerodactylum* and *O. pabsti*, respectively. Differences in the relative lengths of digit V of the pes can be attributed to, at least in part, the smaller phalangeal count of three in *D. absitus* compared to four in *O. pabsti*. Similarly, the length of digit I in the pedes of *I. cottae* and

presumably *D. absitus* are 35 and 38% of digit IV, respectively, whereas in *I. sphaerodactylum* and *O. pabsti* the respective measurements are 45 and 48%. There is also a strong correlation between the relative lengths of digits II and III compared to that of digit IV in the pes of *I. cottae* and presumably *D. absitus* of 62 and 58%, and 82 and 78%, respectively, whereas in *I. sphaerodactylum* and *O. pabsti* the same measurements are 67 and 60%, and 86 and 81%.

The associations between ichno- and biospecies is less clear based on the lengths of the manus digits (see Fig. 8) expressed as a percentage of the length of digit IV of the manus (Appendices 5, 6). Using this measure of comparison, there is a considerable discrepancy between the relative lengths of digits I-III in *Ichniotherium cottae* and *Diadectes absitus*. This could be due to an affectation of preservation, since in the only complete carpus of *D. absitus* available for this study, MNG 7721, the distal phalanges are hyperflexed against the plantar surface of manus with some being slightly telescoped on each other (digit III), and the two phalanges of digit I were lost due to weathering and restored using their enclosing matrix as a natural mold to cast them in epoxy (Berman et al., 1998). In the same manner, the only significant discrepancy between the relative lengths of digit V the ichno- and biospecies is the higher value of *I. sphaerodactylum* compared to that in *O. pabsti*. Disregarding a few apparent minor discrepancies, the relative lengths of the middle digits of the manus of *I. sphaerodactylum* and *O. pabsti* exceed those of *I. cottae* and *D. absitus* by fairly consistent values.

There are two anatomical features that may have contributed to why the manus and pes digit traces in *Ichniotherium cottae* are relatively shorter than those in *Ichniotherium sphaerodactylum*, assuming their respective origins are *Diadectes absitus* and *Orobates pabsti*: (1) in *D. absitus* there is a unique, extreme shortening of the penultimate phalanges of digits I–IV of the manus and pes (see Figs. 6, 7); and (2) the terminal phalanges of digits II–IV in *D. absitus* end in a bluntly rounded margin, giving them a spade-like outline in which the width slightly exceeds the length, whereas in *O. pabsti* the terminal phalanges are bluntly pointed and the length exceeds slightly the width.

The size and shape of the sole pad imprint of the pes in both *Ichniotherium* species are undoubtedly moulded, probably entirely, by the closely articulated astragalus (or its tightly sutured component elements) and calcaneum, which greatly dominate the tarsus. Outlines enclosing the articulated astragalus and calcaneum in *Diadectes* CM 41700 and *Orobates pabsti* MNG 10181 have a strong similarity to the outlines of the soles pad imprints of the pedes in *Ichniotherium cottae* and *Ichniotherium sphaerodactylum*, respectively (compare Figs. 3 and 7). A distinctive feature of the sole pad impression of the pes track of *I. cottae* is its partial division into two, co-joined impressions (Fig. 3C): an oval-to-subcircular medial impression and a smaller, semi-oval to semi-circular impression that extends from its proximolateral margin that were likely made by the astragalus and calcaneum, respectively. As already noted, the appearance of the latter portion of the impression was apparently dependent on the sole pad being pressed deep enough into the substrate to include it. This is seemingly due to a much greater vertical thickening of the ventral surface of the astragalus over that of the calcaneum. In *Diadectes*, although the dorsal surfaces of the articulated astragalus-calcaneum occupy essentially a single horizontal plane, the astragalus is about 60% thicker, giving it a much greater ventral dimension and undoubtedly a more dominant influence than the calcaneum in the formation of the sole pad impression (Berman and Henrici, 2003). On the other hand, the astragalus and calcaneum in *Orobates pabsti* are about equal thicknesses, and when articulated their dorsal and ventral surfaces occupy essentially parallel planes (Berman et al., 2004).

The trackways of both species of *Ichniotherium* indicate a plantigrade contact of the autopodes with the substrate at the
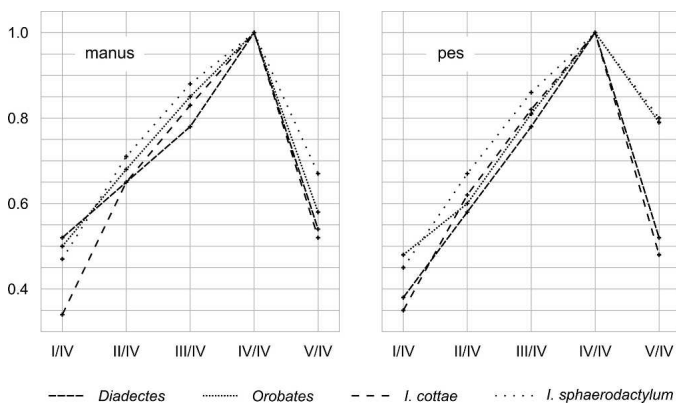
FIGURE 8. Graphic comparisons of the relative lengths of the manus and pes digit lengths of *Ichniotherium cottae* and *Ichniotherium sphaerodactylum* and their presumed trackmakers *Diadectes* and *Orobates* expressed as a percentage of the length of digit IV (data source Appendices 5, 6). Note that a strong congruence is indicated only between the digit length proportions of the pedes of *I. cottae* and *I. sphaerodactylum* and *Diadectes* and *Orobates*, respectively.

initiation of the power stroke with a uniform medial divarication toward the midline of the trackway that averages about 25° and 5–10° for the manus and pes, respectively (Appendices 1, 2). The lesser degree of angulation of the pes toward the midline might be accounted for by a highly mobile joint between the epipodials and proximal tarsal elements, particularly between the tibia and the astragalus, which is not only present in the diadectids, including *Diadectes absitus* and *Orobates pabsti*, but also in Paleozoic amniotes as well (Berman and Henrici, 2003). Here a condyle-like tibial facet on the medial half of the dorsal surface of the astragalus is unusual in being much larger than the opposing facet on the distal end of the tibia, allowing for a rotational sliding motion of the pes about the long axis of the tibia. This permitted the pes to remain directed nearly anteriorly at all phases of the power stroke, so as to maximize the force of the posterior thrust during locomotion. A similar or comparable joint is not apparent between the epipodials and proximal carpal elements of the manus and may account for the higher medial divarication of the manus.

A distinctive feature of the imprints of the manus in *Ichniotherium sphaerodactylum* that distinguishes it from that of *Ichniotherium cottae* is the greater and more abrupt medial angulation or bending of the distal portions of digits II–IV, whereas this feature is negligible in the pes tracks of both ichnospecies. Differences in the expression of this feature may be attributable to differences in the ranges of rotational movement at joints between the epipodials and the proximal carpals and tarsals and between the distal carpals and tarsals and the metapodials. It is assumed that at the termination of the power stroke and the initiation of the retraction of the limbs to begin the next power stroke, the autopodes were lifted from the substrate progressively from their proximal margin to their digit tips. Just before the distal portions of the digits lost contact with the substrate, particularly the longer digits I–IV, there would have been a tendency for them to rotate significantly medially through a horizontal plane as the upper portion of the limb was swung anteriorly. In the pedes of both *Diadectes absitus* and *Orobates pabsti* this tendency might have been diminished strongly not only by a well-developed joint between the epipodials and the proximal tarsals, but also by an unusually mobile joint between the distal tarsals and metatarsals. Berman and Henrici (2003) proposed that large areas of reduction or absence of ossification of some of the central and distal tarsal bones in *D. absitus* and *O. pabsti* (at that time unnamed) provided a unique structural pattern in which the only bony link between the tarsus and the digital complex is via the fourth distal tarsal. This, they argued, produced a crude facsimile of the highly mobile lacertilian mesotarsal joint that served, along with the joint between the epipodials and the proximal tarsals, to maintain an anteriorly directed pes during the power stroke to maximize the force of the posterior thrust during locomotion. In the manus of *O. pabsti*, although there is some reduction in the number and ossification of the central and distal carpals, the mobility at the mesocarpal joint would have been far less than that at the mesotarsal joint. This, combined with the far less mobile epipodial-carpal joint compared to the equivalent joint of the hind limb, may account for the strong medial bending of the distal portions of digits II–IV of the manus imprint of *I. sphaerodactylum*. However, in *D. absitus* the carpal elements are strongly ossified and tightly packed, which likely minimized or eliminated any horizontal rotation of the digital complex about the mesocarpal joint. Yet, the distal portions of the imprints of digits II–IV of the manus of *I. cottae* exhibit little medial angulation or bending. Perhaps this is due in part to the relatively shorter digits in *Diadectes*, allowing for a more abrupt lifting of the manus from the substrate at the initiation of the limb retraction. The greater degree of medial bending or angulation of the distal portions of the digital imprints of the manus in *I. sphaerodactylum* than in *I. cottae* may also be directly related to a greater lateral undulation or flexion of the vertebral column during locomotion in *O. pabsti* than in *D. absitus*. In tetrapods with a sprawling-limb type of posture the degree of lateral undulation of the presacral vertebral column during locomotion is directly related to its length. Inasmuch as vertebral structure in *Diadectes absitus* and *Orobates pabsti* is essentially identical, the greater number of 26 presacral vertebrae in the latter, compared to 21 in the former, might have significantly increased its degree of lateral undulation during locomotion and therefore the medial bending or angulation of the distal portions of the digit imprints of the manus.

Trackway Pattern versus Axial Skeletal Anatomy—The two ichnospecies are distinguishable by consistent patterns of overstepping (Fig. 9). In *Ichniotherium cottae* overstepping is partial, with the pes track reaching the proximal ends of the manus digit impressions, whereas in *Ichniotherium sphaerodactylum* overstepping is minor, with the pes track reaching at its maximum the posterior margin of the manus sole impression (see Fig. 4). Differences in the extent of overstepping can be attributable to three variables: (1) the locomotory speed of the trackmaker, (2) length ratios of the limbs to the presacral portion of the vertebral column (= glenoid-acetabular distance), and (3) the length of the presacral vertebral column. Considering the abundant ichnological data examined for both ichnospecies, which includes 53 trackways, the full range of variation of their trackway patterns is probably represented. For this reason the differences in the upper limits of the range of overstepping exhibited by the two ichnospecies is considered to be of anatomical origin rather than differences in locomotory speed. Differences in the length proportions of the limbs to the presacral vertebral column can also be ruled out, as the proportional relationships of the propodials to the epipodials in *Diadectes absitus* and *Orobates pabsti* are identical (see Appendix 4). The third alternative explanation, however, dealing with differences in the glenoid-acetabular distance of the trackmakers, can be verified. The presacral columns in *D. absitus* and *O. pabsti* differ essentially only in the number of vertebra, with 21 in the former and 26 in the latter. Assuming equal-sized limbs in both genera, it is clear that the relatively shorter trunk in *D. absitus* would explain the more pronounced overstepping of its trackway pattern. In addition, trackway measurements of the ratio of the pes stride length to the apparent body length (glenoid-acetabular distance) of both ichnospecies of *Ichniotherium* indicate clearly that the trackmaker of *Ichniotherium cottae* was capable of significantly longer strides relative to its body length than the trackmaker of *Ichniotherium sphaerodactylum* (see Fig. 4).

The occasional inclusion of a tail-drag impression with the trackways of *Ichniotherium sphaerodactylum* and its absence in trackways of *Ichniotherium cottae* may be due to simply a difference in the tail lengths of their presumed trackmakers. The tail of the *Diadectes* CM 41700 (see Fig. 5B) appears to be complete and possesses 32 vertebrae, whereas counts of 34 and 46 were reported (Berman et al., 2004) for the holotype (see Fig. 5C) and paratype, respectively, of *Orobates pabsti*, which appear to represent complete or nearly complete counts. If it is assumed that the presence or absence of a tail-drag mark in *I. cottae* and *I. sphaerodactylum* is related to their tail lengths, then it would support their biospecies identifications as *D. absitus* and *O. pabsti*, respectively.

Ichnospecies as Indicators of Relative Body Size and Abundance of Biospecies—The maximum sizes of the manus and pes imprints of *Ichniotherium cottae* are significantly smaller than those of *Ichniotherium sphaerodactylum* (Appendices 1B, 2B), which, because of the close relationship of the ichnospecies, would be expected to reflect a corresponding similarity in the overall body sizes of *Diadectes absitus* and *Orobates pabsti*. However, the size distinction based on tracks is not reflected in the Bromacker skeletal record of *D. absitus* and *O. pabsti* if skull size
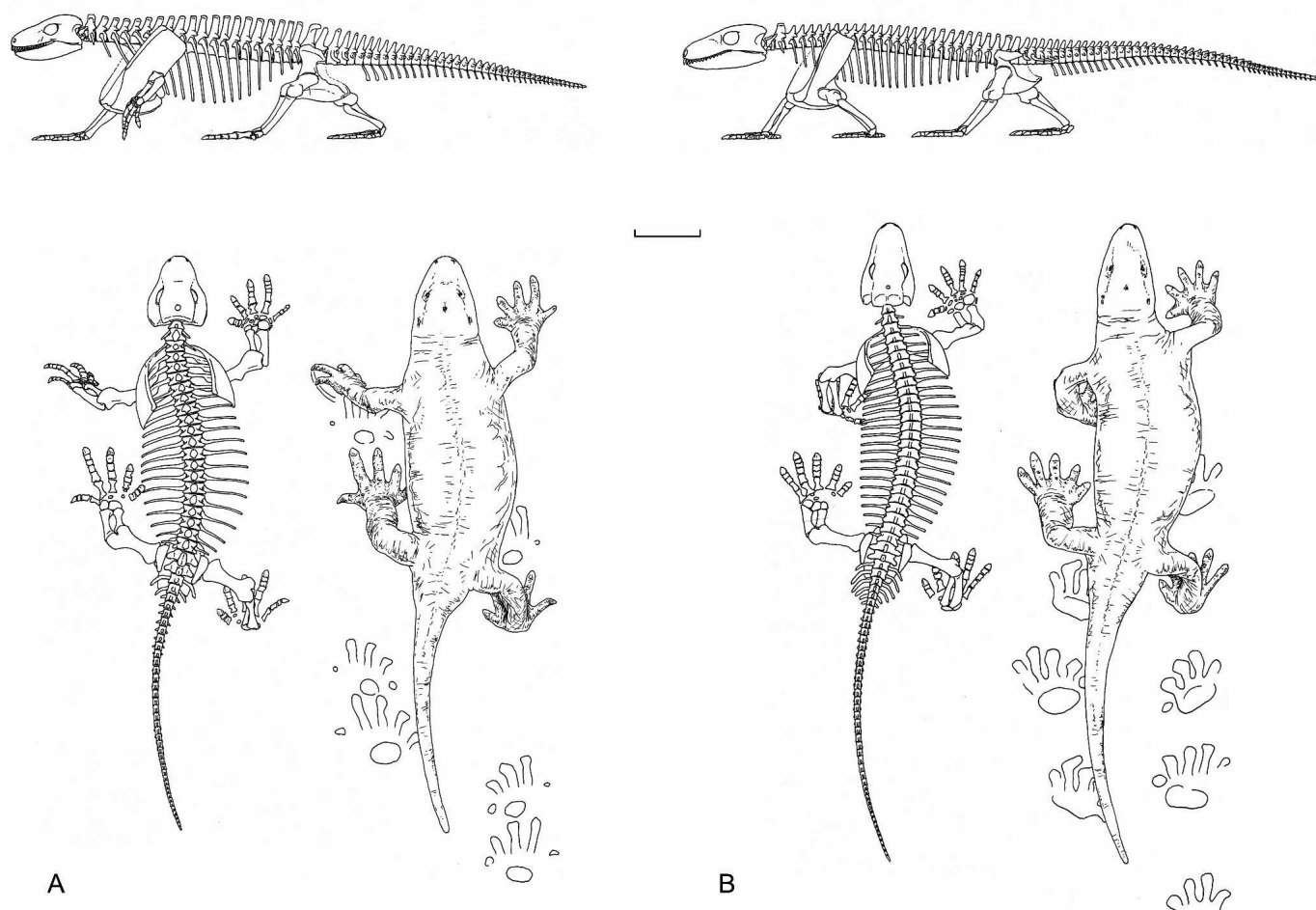
FIGURE 9.   Skeletal reconstruction and body shape illustration of **A**, *Diadectes* and **B**, *Orobates* fitting outlined tracks of **A**, *Ichniotherium cottae* and **B**, *Ichniotherium sphaerodactylum*, respectively. The figure is based on the skeletal remains of specimens MNG 8853 and MNG 10181 as well as the trackway specimens MNG 1351 and MNG 1352. Scale equals 10 cm.

is used, as the maximum skull size of the former exceeds substantially that of the latter (see Appendix 3). Several explanations can be offered for this apparent contradiction: (1) shortening of digits in *Diadectes* due to a reduced number of phalangeal elements and an extreme proximodistal shortening in some; (2) trackways of the *I. cottae* studied herein often lack the proximolateral extension of the pes sole pad, which obscures their true length; and (3) the skeletal record is typically far inferior to the ichnological record in providing complete size distribution data.

From another perspective, the long head, short trunk and tail, and long limbs and feet in *Diadectes* compared to the reversed body proportions in *Orobates* might be explained by morphodynamic and heterochronic developmental patterns, as demonstrated for example in dinosaurs and dinosaur tracks (Lockley, 2005; Lockley and Kukihara, 2005). This approach considers the organism as an integrated complex system ruled by extrinsic, as well as intrinsic, shape affecting factors. That means, if the trunk of *Diadectes* has been shortened and the limbs have been extended due to the acquirement of a more efficient locomotion, then the shortening of the tail and feet, as well as the extension of the head, may represent non-functional, corresponding or compensatory morphologic changes due to growth dynamics.

Inasmuch as all of the trackway specimens of this study were collected from the Bromacker locality and were selected on the basis of providing adequate data for comparisons, the numerical disparity of 11 *Ichniotherium cottae* and 42 *Ichniotherium*

sphaerodactlyum specimens is strong reason to expect an approximately 1:4 ratio in the local community abundances of the trackmakers *Diadectes absitus* and *Orobates pabsti*. Furthermore, *Ichniotherium* is reported to represent more than 95% of all tetrapod footprints recovered from the Bromacker (Haubold, 1998). Yet, as already noted above, minimum number of individuals counts indicate that *D. absitus* outnumbered *O. pabsti* by a nearly 2:1 ratio and that in abundance they collectively represented about 35% of the Bromacker population.

There are several possible explanations for disparity between abundances based on trackways and skeletal fossils: (1) tracks are not necessarily good census indicators, as one individual can make numerous trackways; (2) the high percentage of *Ichniotherium* trackways may indicate that the diadectids were more successful than other vertebrates at reoccupying the alluvial plain of the Tambach Basin after flooding events; (3) the track-bearing mudflats were exposed for weeks to months, recording continuous activity by the same animals, whereas death and burial of the vertebrates by the sheetfloods were essentially coeval events representing a very brief moment of time and that preserved a relatively accurate census of the diversity and abundances of the Bromacker vertebrate community; and (4) the recovery of skeletal fossils by quarrying is best described as serendipitous or the result of fortunate, accidental discoveries influenced by strongly biased techniques that may produce a skewed picture of relative abundances and size ranges. The above comments are intended

to indicate that at present tracks cannot be relied on to determine accurately the body size distributions and relative abundances of the trackmakers, just as the body fossil record may not accurately reflect the track census.

CONCLUSIONS

An extensive record of tetrapod tracks and articulated vertebrate remains from the Lower Permian Bromacker locality of central Germany provides strong evidence for a diadectid trackmaker of *Ichniotherium* footprints. Cross-checked comparative analysis of imprint morphology based on autopod structure and trackway pattern based on axial skeleton structure firmly establishes the track-trackmaker association between two species of the ichnogenus *Ichniotherium* Pohlig, 1892, *Ichniotherium cottae* (Pohlig, 1885) and *Ichniotherium sphaerodactylum* (Pabst, 1895), and the skeletal fossils of the closely related diadectids *Diadectes absitus* and *Orobates pabsti*, respectively. These are the first well-documented species-level correlations between trackmakers and Paleozoic trackways.

Orobates pabsti and *Ichniotherium sphaerodactylum* are known only from the Bromacker locality. On the other hand, *Ichniotherium cottae* occurs in all six formations of the Thuringian Forest Permo-Carboniferous succession that precedes the Tambach Formation (Voigt, 2005). This stratigraphic distribution is unexpected, inasmuch as *Orobates* is, with the possible exception of *Ambedus* Kissel and Reisz, 2004, the basal-most members of Diadectidae, which are known in North America from the Upper Pennsylvanian to the Lower Permian (Berman et al., 2004). In this context it is noteworthy that the accumulation of the clastic sediments of the Tambach Formation began after a significant break in sedimentation that was accompanied by denudation and remarkable tectonic movements (Knoth, 1970; Lützner, 1981). Undoubtedly, it was this change in basin configuration and the creation of unique paleoenvironmental and paleobiological conditions that allowed *Orobates pabsti*, as well as other members of the Bromacker vertebrate assemblage, to colonize the Tambach Basin, which has been described as representing the earliest and best documented example of the rarely encountered 'truly upland' paleoecosystem (Eberth et al., 2000; Berman et al., 2001). In this scenario *O. pabsti* probably existed outside the Tambach Basin area long before the time span represented by the Lower Permian sedimentary rocks of the Tambach Formation. Therefore, the discovery of *O. pabsti* or *I. sphaerodactylum* at any other locality of Permo-Carboniferous beds in the world could provide an important key to the geographic origin and dispersal routes of diadectids (see also Berman et al., 1997). This goal could realistically be achieved by a careful restudy of the global *Ichniotherium* record, which is presently restricted to Europe and North America.

In addition, the recognition of the close relation between *Ichniotherium* species and diadectid genera offers a unique opportunity to evaluate principals and taxonomic concepts in vertebrate ichnology. Permian tetrapod footprints, which alone have been assigned to nearly 400 ichnospecies (Haubold, 2000), are based mostly on poorly preserved specimens and rely on obscure, weakly defined, or little understood features of imprint morphology and trackway pattern, as well as stratigraphic or even geographic occurrences. In several aspects, the superb *Ichniotherium* record from the Bromacker locality is an outstanding example of why those practices should be rejected in favor of diagnoses based on an abundant record of well-preserved tracks and trackways. Only then can anatomically controlled characters be clearly recognized and rigidly defined, so as to provide the most reliable criteria for diagnosing tetrapod ichnotaxa. Moreover, due to the extensive database available for *Ichniotherium*, it promises to be an invaluable and welcome subject to test the accuracy of bivariate and multivariate statistical methods often argued as the most objective and modern approach in recognizing tetrapod ichnotaxa (e.g., Demathieu and Demathieu, 2002; Tucker and Smith, 2004).

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APPENDIX 1.

A. Trackway parameters of *Ichniotherium cottae* (in mm and degrees).

Trackway	Sp	Sm	Pp	Pm	A	Bp	Bm	C	αp	αm	βp	βm
MB.ICV.3-F1	371.2	358.5	225.2	219.8	46.7	132.7	120.3	231	110	112	−13.6	−30.3
MB.1CV.3-F2	327	335	203	195.5	64	119	104	233	111	115	−9.7	−21.5
MNG 1352	456	441	254	251.5	51.7	113	122.5	276	129	124	−22	−30.3
MNG 1819	303	300	182.5	182.5	48.7	103	103.5	199	111	111	2.3	−20.3
MNG 2356-16-F1	366.3	366.3	222.8	222.8	34.4	128.3	125.8	219.7	110	110.7	−3	−25.5
MNG 2356-16-F2	407.3	401.5	244.3	238.3	45	134.8	128.3	246.5	113	115.5	−7	−16.5
MNG 10179	289	306.7	218.8	195	79.4	169.3	116.8	231.7	82.7	105	2.6	−20
MSEO I-36	272	260.5	227	219.7	80	181.3	171.7	233.5	90	87	−2.8	−26.3
PMJ P-1321-F3	312	343.5	219.3	202.7	60.5	146	113	225	95	112.5	−13	−33.5
UGBL F1	343.7	350.8	203.3	229.4	73.6	110	148.8	248	115	99	−17.2	−20.8
UGBL F2	384	392.2	243.2	241	61	152	137.2	252.8	103.3	108.8	−16.4	−21.4
Minimum	272.00	260.50	182.50	182.50	34.40	103.00	103.50	199.00	82.70	87.00	2.60	−16.50
Maximum	456.00	441.00	254.00	251.50	80.00	181.30	171.70	276.00	129.00	124.00	−22.00	−33.50
Mean	348.32	350.55	222.13	218.02	58.64	135.40	126.54	236.02	106.36	109.14	−9.07	−24.22

B. Imprint parameters of *Ichniotherium cottae* (in mm and degrees).

Trackway	pI	pII	pIII	pIV	pV	mI	mII	mIII	mIV	mV	pl	pb	ml	mb	γp	γm
MB.ICV.3-F1	14	25.8	35.3	42.8	21	15.5	25.3	29.6	34.5	17	73	—	61	66.5	—	—
MB.ICV.3-F2	14.3	25.7	35	41	—	11.3	24	32	37.5	19	73	81	—	64	—	—
MNG 1352	17	33.3	43.3	51	23.7	13.5	30.5	40	46	23	84	92	76	84	—	—
MNG 1819	13	19.5	27	37.5	18	11	20.5	26.5	30.5	15.5	71	63	55	62.3	—	—
MNG 2356-16-F1	16	26	35	42.3	—	13	26	32.3	40.7	22.5	72.3	—	68	—	—	—
MNG 2356-16-F2	16.7	28.3	37	43	—	12	27	30	40.5	—	73	—	67	—	—	—
MNG 10179	12	26	34.5	40	17	11.3	21.7	29.7	36	22	80	77	61.5	74.7	104	120
MSEO I-36	17.5	30	35.3	42	—	15	20.5	27	34	17	78.7	—	60.5	79	—	137
PMJ P-1321-F3	16	26.7	34.5	42	21	12	26	32.5	40.5	16	66	79	57	58	—	—
UGBL F1	15.3	26	36.5	43.4	23.3	13	26	33.5	38.7	20.5	83	86.3	61.3	70	97	114.5
UGBL F2	15	27.5	36	47.5	21.3	13	27.5	36	42	25	81.5	85.5	65.5	74.3	105	—
Minimum	12.00	19.50	27.00	37.50	17.00	11.00	20.50	26.50	30.50	15.50	66.00	63.00	55.00	58.00	97.00	114.50
Maximum	17.50	33.30	43.30	51.00	23.70	15.50	30.50	40.00	46.00	25.00	84.00	92.00	76.00	84.00	105.00	137.00
Mean	15.16	26.80	35.40	42.95	20.76	12.78	25.00	31.74	38.26	19.75	75.95	80.54	63.28	70.31	102.00	123.83

APPENDIX 2.

A. Trackway parameters of *Ichniotherium sphaerodactylum* (in mm and degrees).

Trackway	Sp	Sm	Pp	Pm	A	Bp	Bm	C	αp	αm	βp	βm
BGR P-12539-F1	332.7	338.7	221	230.3	125.6	151.3	157	285	91.7	89.3	−11.6	−23.6
BGR P-12539-F2	316	319	225	209	96.6	158	135.3	255.3	85.7	100	—	−26.3
BUW 1	350.3	344	251.9	233.3	141.4	180.3	155.2	321	88.2	98.6	−6	−74.5
BUW 2-F1	301.5	318.5	207	221.3	115.3	142	166	269	92.5	84	−9	−17
BUW2-F2	309	330	231	232.5	122.3	171	162.5	278	84	90	−20	−23.7
FG 525	384.3	372.5	270.8	261.7	130	194.5	181.3	328	90	97	−10.4	−18.8
GZG 1255-1	406	399.4	287.5	279.5	138	197.5	198.5	339.6	89	90.8	−15.7	−17.3
GZG 1270-1	429.7	432	280.5	283.7	88.8	177.3	186.3	300	102	98	−10.6	−34
HF 51	351.3	357.4	266.1	265	88.4	183.4	187.8	272.5	85.3	84	−12	−21.1
HF 55	348	355.7	228.3	228.8	101.5	152.7	132	274	95	100.7	−12.5	−21.4
HF 56	342	336.3	232	216.3	124.8	153.3	134	287.5	87.5	98.7	−0.3	−19.4
HLMD WT-297	352.3	349	228.5	224.8	81	144.8	142.6	256.3	100	100	−14.2	−25
LMJG 8491	352.7	335.5	264.3	240.5	137.8	198.5	159.5	314	85	92	−11	−26.8
MB.ICV.1	318.3	316.7	255.1	250.9	140.1	202.7	187.4	297.8	76.7	79.5	−2.1	−17.8
MB.ICV.2	290	296.7	221.8	208	130.4	151.3	155.3	274.5	82.7	86.5	11.5	−11.2
MLP F1	447	405	286.7	284	149.8	162.7	197.3	351	97.5	90	−3.3	−9.3
MLP F2	411.3	417.5	293	317.5	132.8	208.7	223.5	345	88.5	86	−16.6	−18.3
MB.ICV.4	367	367	242.2	253.4	87.4	159.2	178.4	272	98.8	93.5	−12.4	−33.1
MNG 1351	360.1	351.2	240.1	237.9	126.4	160.3	165.6	299.5	96.4	95.2	−12	−24.8
MNG 1515-F1	313.5	338.4	252.3	239.1	103.3	195.7	176.1	270.9	77.2	88.4	−2.5	−30.2
MNG 1515-F2	340.6	339.9	228	235.6	94.9	148.9	164.7	268.7	96.6	92	−5.1	−20.4
MNG 1515-F3	394.1	407.4	258.1	265.1	73.3	170.4	172.9	277.3	98.4	100.7	−9.4	−22.7
MNG 1515-F4	374.7	379.2	243.4	254.7	91.1	155.8	171.7	281.8	101.4	95	−13.5	−32.2
MNG 1840-F1	324.7	327	249.5	238.2	112.1	192.2	174.2	272.2	81	88.2	−5.6	−24.5
MNG 1840-F2	430.8	438.3	288.8	309.8	113.5	194.8	219.6	328.8	93.5	87.5	−16.8	−24
MNG 2356-15	428.8	428.7	308.4	305	118	218.4	219	332.7	90.5	90	−5.8	−17.4
MNG 10072	358.5	362.8	275.3	251.7	112.7	211.3	170.4	294.2	81.6	94.6	−5.7	−30.6
MNG 13490	395.6	387.8	293.8	295.3	141	215.5	209.8	330.8	84.8	84.6	2.5	−22.5
MSEO IIIA-519-F1	347.7	346.3	259	242	129.6	194.3	161.5	305.7	81.7	94.7	−3.6	−10.2
MSEO IIIA-519-F2	343.8	333.7	276.4	263.5	141.2	217.8	197.8	311	79.3	77.3	−5.2	−19.8
MSEO nn-2	326.3	329.3	287	269	170.3	235.5	216	343.5	70.3	73	−4.8	−14.7
NHMM 2	389	386.1	259.3	278.1	131.9	175.8	199.3	322.9	95.6	87.3	−3.5	−29.3
NHMM 412	306	314	221.3	218.3	108.8	156	145.8	265.5	85	92	−4.3	−19.8
NHMS I-Ba-18	388	372	265	221.3	153	180.3	109	326	94	118.5	7.8	−35.3
NHMS 1312	438	440	278	264	102	171.5	128.5	337	107	118	6.3	−38
NHMW 1963-565	359.5	358.6	257.1	275.2	119.1	186.2	204.5	301.9	87.7	83.4	−12.9	−24.2
NME 9	160.7	163.0	125.3	122.3	51.6	96.3	87.5	131.0	81.7	88.0	10.8	−11.5
NME 13	385.5	373	252	272	104.5	165	199.7	297.5	101	89	−10	−16
PMJ P-1321-F2	406.5	423	310.7	277.3	128	226	188.7	340	87.5	96.5	−2.7	−24.7
RE 551.736.100A72	333	371.5	258.5	273	94.7	191	210.3	271	82	86	−15.5	−16
SMMGD 1354	306.3	320	273.8	286	143.7	225	195	360	72.3	83	9.3	−25.7
UGBL F3	458.8	463	308.3	343.3	121.3	210.9	252.1	347.8	95	84.3	−7.8	−25.9
Minimum	160.70	163.00	125.30	122.30	51.60	96.30	87.50	131.00	70.30	73.00	11.50	−9.30
Maximum	458.80	463.00	310.70	343.30	170.30	235.50	252.10	360.00	107.00	118.50	−20.00	−74.50
Mean	359.68	360.32	256.19	253.79	117.64	180.32	174.86	299.20	89.26	91.70	−6.27	−23.98

B. Imprint parameters of *Ichniotherium sphaerodactylum* (in mm and degrees).

Fáhrte	pI	pII	pIII	pIV	pV	mI	mII	mIII	mIV	mV	pl	pb	ml	mb	γp	γm
BGR P-12539-F1	19.3	32	40.5	44.5	35.7	17.7	27.3	32.4	37.4	24.6	92.5	97.5	77.3	97.5	78	100.5
BGR P-12539-F2	19	29.3	40.7	46.7	36.5	15.5	27.5	35	42.3	28	90	89.5	71.3	88	—	—
BUW 1	14	28	44	46	40	19.5	27	27	34	20	116	114	80.5	106	85.5	137
BUW 2-F1	—	—	38	47	40	20	23	33	36	23	91.3	96	75.7	90.5	62	101.5
BUW 2-F2	28	33	41	46	36	17	24	30.7	36.3	23.7	91	103	75.7	99	54	96.5
FG525	23	38.3	50.5	57.3	44.5	17	27.5	43	49	36	123.3	122.3	98	122.3	76	83
GZG 1255-1	27.4	45.7	58.3	70.4	55.3	21.5	34.2	41.6	51.2	36.4	124.1	127.5	97.7	127.2	68.8	103.5
GZG 1270-1	27	36.7	51.3	61.7	49	23	35.3	41	47.8	33	115	119	80.8	121.5	64	103.7
HF 51	22	36	43.7	51.5	38.2	17	30.4	37.1	40.4	27	101.8	109.3	79.3	92	83.3	105
HF 55	20	34	43.5	47.7	37	15	27	37	43.3	29	97.5	87	86.7	91	—	96
HF 56	23.3	34.3	41.7	39.3	39.3	16.4	28.3	37.6	41.4	30.5	110.3	105	81.5	97.5	71.5	109
HLMD WT-297	17.7	31.2	39.2	45.4	38	17.8	26	32	37	25.4	88.4	94.5	67	93	69	101.5
LMJG 8491	18.5	29	37	45.5	38.5	21.7	28.3	33	36.7	23.3	105.3	112.8	83	107	71.5	97
MB.ICV.1	25.5	36.5	44	56.3	40.5	16.7	33.3	36	37	25	109.5	115	93.3	114.5	79.3	120
MB.ICV.2	20.3	33	41.8	46	36.5	18	28	35	38.7	23.7	92	100.7	74	94.3	74.5	119
MLP F1	26	41.5	53.8	66	54.3	23.5	33.5	41	51	38.7	123	144.3	96	132.5	68	86
MLP F2	30	41	53	68	54	25	36.7	44.5	52	38.8	129.3	141.3	106.3	127.3	83.5	97
MB.ICV.4	20.5	29.4	37.4	42.6	32.8	16.3	26.7	31.5	35.7	23.3	94.7	108.4	73.2	104	84.2	100.3
MNG-1351	22.7	33.2	43.6	51.3	38.7	19	28.6	36.6	45.3	28.4	108.5	111.2	87	107.4	82.5	116.5
MNG 1515-F1	22	32.3	42.8	49.2	42	19.4	31.1	36	39.8	25	96.7	106.4	79.1	94.6	79.7	104
MNG 1515-F2	—	33	45	49		20	29	35.9	40.8	25.5	93.5	96	73	93.5	—	110
MNG 1515-F3	17	32	41.6	45.3	38.5	—	28.9	36.5	41	26.4	100.3	100.8	84	95.2	75	108.5
MNG 1515-F4	19	34.3	41.8	48.7	39	19.5	30	35.3	39.8	26.5	94.7	104	—	95.5	73	—
MNG 1840-F1	25.7	36.1	43	49.9	36.4	24.1	30.3	35.1	38.8	26.2	100.6	107.2	79.3	106.3	65.4	89.2

APPENDIX 2.   B.   (*Continued*)

Fáhrte	pI	pII	pIII	pIV	pV	mI	mII	mIII	mIV	mV	pl	pb	ml	mb	γp	γm
MNG 1840-F2	28.3	39.3	50.5	59.8	50	18	35	45.4	51.2	35.5	111	113	88	106	—	—
MNG 2356-15	28	43.5	54.8	63	46.5	20.8	35	46.3	53	32.3	128.3	138	95.3	124.7	72	95
MNG 10072	21.4	31.9	39.4	43.9	34.7	29.3	30.2	34	36	22.9	103.3	110.2	77.4	100	72	113.3
MNG 13490	23	34.8	46.5	55	42.6	18	27.3	35	38	25	123	125.3	83	116.5	65.7	104
MSEO IIIA-519-F1	26.3	35.3	42.8	51	42.8	19.3	30.8	37	40.3	28.8	110	113.5	85.3	106.7	64.3	102.5
MSEO IIIA-519-F2	24.8	37.2	44.4	51.4	39.6	18.7	27.3	33.3	38.3	26	106	106	87	99.5	70.8	96
MSEO nn-2	—	—	53	—	—	25	41	48.7	55.3	41	122.8	128.7	95.7	128.3	60	97.5
NHMM-2	27	39.2	46.8	53	36	24.6	34	41.2	43.6	28.1	105.5	122.8	83.6	115.4	91.3	93.8
NHMM 412	28	34	44.3	54.5	45	23.3	32.3	39.4	45.2	30.7	121	106	78.8	108.3	91	94
NHMS I-Ba-18	30	43	56	63.7	51	21.7	33.3	42.8	51	36	117	113.5	94	110.3	66.5	101.3
NHMS 1312	22.5	31.5	47.5	61.5	43	17	26	39	44.3	30	122	111	94	100	79	100
NHMW 1963-565	21.6	31.4	38.7	45.8	36.7	23	30.8	37.9	39.2	28.4	105.3	111.4	83.6	116.8	68.9	98.8
NME 9	11.0	20.8	28.0	33.0	24.0	10.3	15.3	22.0	25.0	16.0	57.3	62.0	44.0	48.0	74.0	96.8
NME 13	28	39.5	47	49.5	41	17.3	28.8	35	42.8	29.7	87.5	97	72	87	78	90.3
PMJ P-1321-F2	24	32	42	53	44	19.3	32.3	37.5	44	29.7	111	112.5	87.3	110.7	76	80
RE 551.736.100A72	25.5	39	46.5	55.5	49	21	33.7	40.3	44.3	28	96	118	81	98.5	70	105
SMMGD 1354	23.3	36	48	61.7	50.5	21.5	30	34.3	41.3	27.7	104	120	79.3	109.5	83.5	90
UGBL F3	29.5	41.5	51.5	59	48	20	31	39.5	48.5	35.7	120.7	137.5	88.7	117.3	72.3	97.3
Minimum	11.00	20.80	28.00	33.00	24.00	10.30	15.30	22.00	25.00	16.00	57.30	62.00	44.00	48.00	54.00	80.00
Maximum	30.00	45.70	58.30	70.40	55.30	29.30	41.00	48.70	55.30	41.00	129.30	144.30	106.30	132.50	91.30	137.00
Mean	23.28	34.89	44.84	52.00	41.44	19.69	29.81	36.88	42.19	28.56	105.98	110.76	82.92	104.94	73.89	100.93

APPENDIX 3.   Articulated diadectid remains from the Bromacker locality.

Taxon	Specimen No.	Material	Length of skull	Snout-sacrum distance	Ontogenetic stage
Diadectes absitus	MNG 2955	postcranium	—	?	?
Diadectes absitus	MNG 7721	postcranium (paratype)	—	?	?
Diadectes absitus	MNG 8747	skull (paratype)	ca. 13 cm	?	adult
Diadectes absitus	MNG 8853	skeleton (holotype)	ca. 13 cm	?	adult
Diadectes absitus	MNG 8978	postcranium (paratype)	—	?	?
Diadectes absitus	MNG 10552	postcranium	—	?	?
Diadectes absitus	MNG 10556	skeleton	?	?	?
Diadectes absitus	MNG 10559	skeleton	?	?	?
Orobates pabsti	MNG 8760	skeleton (paratype)	10.7 cm	—	adult
Orobates pabsti	MNG 8980	skeleton (paratype)	7.0 cm	41 cm	subadult?
Orobates pabsti	MNG 10181	skeleton (holotype)	9.7 cm	48 cm	subadult?

APPENDIX 4.   Absolute and relative lengths of forelimb and hind limb elements of *Diadectes* and *Orobates* based on *Diadectes absitus* manus MNG 7721, *Diadectes* pes CM 41700, and *Orobates absitus* manus and pes MNG 10181.

Element or ratio	*Diadectes*	*Orobates*
humerus/radius/ulna	—/61 mm/72 mm	80 mm/46 mm/60 mm
femur/tibia/fibula	146 mm/98 mm/108 mm	85 mm/55 mm/62 mm
manus digit IV/ pes digit IV	33 mm/59 mm	38 mm/44 mm
radius:humerus	—	58%
ulna:humerus	—	75%
radius:ulna	85%	77%
tibia:femur	67%	65%
fibula:femur	74%	73%
tibia:fibula	91%	89%
manus digit IV:humerus	—	48%
manus digit IV:radius	54%	83%
manus digit IV:ulna	46%	63%
pes digit IV:femur	40%	52%
pes digit IV:tibia	60%	80%
pes digit IV:fibula	55%	71%

APPENDIX 5. Lengths of manus and pes phalangeal elements of *Diadectes* and *Orobates pabsti* (data in mm) based on *Diadectes absitus* manus MNG 7721, *Diadectes* pes CM 41700, and *Orobates pabsti* manus and pes MNG 10181.

Taxon–autopodium	Plananx	I	II	III	IV	V
Diadectes–manus	1	6.5	7.5	10.0	11.0	6.5
	2	11.5	4.0	4.5	6.5	5.0
	3	—	11.0	2.0	5.5	7.0
	4	—	—	10.5	2.5	—
	5	—	—	—	9.0	—
	Summa	18.0	22.5	27.0	34.5	18.5
Diadectes–pes	1	10.5	10.5	12.5	19.5	10.5
	2	12.0	8.5	10.5	8.5	6.5
	3	—	16.0	8.0	8.0	14.0
	4	—	—	15.5	7.0	—
	5	—	—	—	17.0	—
	Summa	22.5	35.0	46.5	60.0	31.0
Orobates–manus	1	7.0	6.0	7.0	8.5	7.0
	2	11.5	6.0	6.0	6.0	6.0
	3	—	13.0	6.0	5.5	8.5
	4	—	—	12.5	5.0	—
	5	—	—	—	12.0	—
	Summa	18.5	25.0	31.5	37.0	21.5
Orobates–pes	1	6.5	6.5	9.0	10.5	10.0
	2	12.5	6.0	6.0	7.5	7.5
	3	—	11.5	5.5	6.0	5.5
	4	—	—	12.0	5.5	8.5
	5	—	—	—	10.5	—
	Summa	19.0	24.0	32.5	40.0	31.5

APPENDIX 6. Lengths of digits of diadectids *Diadectes* and *Orobates* and *Ichniotherium cottae* and *Ichniotherium sphaerodactylum* relative to length of digit IV based on *Diadectes absitus* manus MNG 7721, *Diadectes* pes CM 41700, and *Orobates pabsti* manus and pes MNG 10181.

Taxon and autopodium	I/IV	II/IV	III/IV	IV/IV	V/IV
Diadectes–manus	0.52	0.65	0.78	1.0	0.54
Diadectes–pes	0.38	0.58	0.78	1.0	0.52
Orobates–manus	0.50	0.68	0.85	1.0	0.58
Orobates–pes	0.48	0.60	0.81	1.0	0.79
I. cottae–manus	0.34	0.65	0.83	1.0	0.52
I. cottae–pes	0.35	0.62	0.82	1.0	0.48
I. sphaerodactylum–manus	0.47	0.71	0.88	1.0	0.67
I. sphaerodactylum–pes	0.45	0.67	0.86	1.0	0.80