



Middle Triassic horseshoe crab reproduction areas on intertidal flats of Europe with evidence of predation by archosaurs

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A systematically excavated track site in a 243.5 Myr old Middle Triassic (Karlstadt Formation, Pelsonian, middle Anisian) intertidal carbonate mud-flat palaeoenvironment at Bernburg (Saxony-Anhalt, central Germany) has revealed extensive horseshoe crab trackways attributable to the *Kouphichnium* Nopsca, 1923 ichnogenus. The exposed track bed of a Germanic Basin-wide spanned intertidal megatrack site is a mud-cracked biolaminate surface on which detailed tracks have been preserved because of rapid drying and cementation as a result of high temperatures, followed by rapid covering with a protective layer of arenitic storm or tsunami sediments. The different trackway types and their orientations have allowed a tidal sequence to be reconstructed, with the initial appearance of swimming horseshoe crabs followed by half-swimming/half-hopping limulids under the shallowest water conditions. The Bernburg trackways, which have mapped lengths of up to 40 m, were all produced by adult animals and exhibit a variety of shapes and patterns that reflect a range of subaquatic locomotion behaviour more typical of mating than of feeding activities. The closest match to the proportions and dimensions of the horseshoe crab tracks at Bernburg is provided by the largest known Middle Triassic limulid *Tachypleus gadeai*, which is known from the north-western Tethys in Spain. The horseshoe crab body fossils recognized in the German Mesozoic intertidal zones, instead, are from juveniles. The uniformly adult size indicated by the trackways therefore suggests that they may record the oldest intertidal reproductive zones of horseshoe crabs known from anywhere in the world, with the track-makers having possibly migrated thousands of kilometres from shallow marine areas of the north-western Tethys to reproduce in the intertidal palaeoenvironments of the Germanic Basin. *Chirotherium* trackways of large thecodont archosaurs also appeared on these flats where they appear to have fed on the limulids. With the tidal ebb, smaller reptiles such as *Macrocnemus* (*Rhynchosauroides* trackways) appeared on the dry intertidal flats, probably feeding on marine organisms and possibly also on horseshoe crab eggs. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **103**, 76–105.

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INTRODUCTION

Xiphosurid (horseshoe crab) trace fossils are much more abundant than their body fossils in the post-Palaeozoic fossil record (Nopsca, 1923; Anderson, 1975; Hunt, Lucas & Lockley, 1993; Wang, 1993; Schweigert & Dietl, 2002; Romano & Whyte, 2003; Harris & Lacovara, 2004; Minter, Braddy & Davis, 2007; Seilacher, 2008); they provide important palaeoenvironmental and ethological information on the

track-makers (Seilacher, 2008). In most descriptions of the fossil record, however, only small slabs or fragments of trackways have been analyzed and given ichnotaxonomic binominal names. No trackways have been analyzed and mapped in the same detail as this new European locality in Bernburg, central Germany (Fig. 1A), nor have any been studied over similar lengths of up to 40 m. Horseshoe crab trace fossils have previously been mainly described ichnotaxonically from these small slabs, with each being given a different ichnospecies name, although a few unnamed tracks from France are the only ones known

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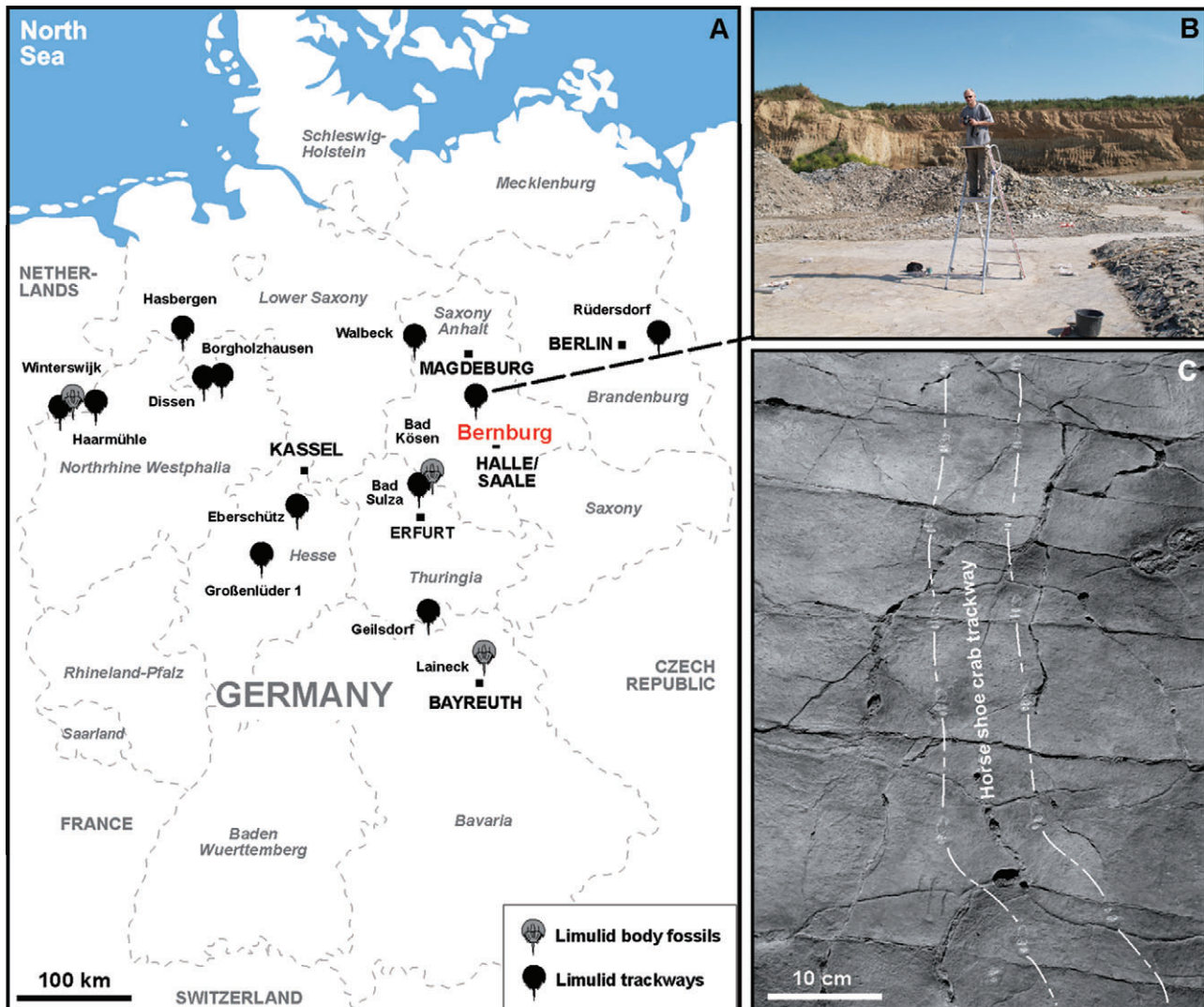


Figure 1. A, localities in Germany with ‘Muschelkalk’ (Middle Triassic) horseshoe crab trackways and body fossils in shallow marine and intertidal carbonate sediments. B, AUTOCAD documentation (Diedrich, 2009b). C, part of a documented horseshoe crab trackway, after colouring.

from the Middle Triassic ‘Muschelkalk’ of the Germanic Basin of central Europe (Demathieu, 1985). Detailed palaeobiological analyses as well as critical ichnotaxonomic analyses have, however, now been completed for the horseshoe crab tracks at Bernburg.

Only a very few limulid body fossils have been found from this Middle Triassic marine period, in Germany (Muenster, 1839; Fritsch, 1906; Krause, Hauschke & Wilde, 2009), Spain (Vía Boada & de Villalta, 1966; Romero & Vía Boada, 1977; Vía Boada, 1987a, b), and the Netherlands (Hauschke, Oosterink & Wilde, 2009; Fig. 1A), all in shallow marine deposits. However, no European Middle Triassic ‘Muschelkalk’ fossil trackways have previously been attributed with certainty to horseshoe crabs. Invertebrate track-

ways from the eastern edge of the Massif Central (in the south-western part of the Germanic Basin) that have previously been described as ‘arthropod trackways’ (Demathieu, 1985) can now be identified as having been, at least in part, made by limulids as a result of comparisons with the recent extensive discoveries at Bernburg (Diedrich, 2009a), as well as with other new sites at Winterswijk in the Netherlands, and at Hasbergen, Borgholzhausen, Bad Sulza, and other sites in Germany (Fig. 1A). These newly-discovered trackways and single tracks, scattered over distances of several hundreds of kilometres, reveal that limulid traces in the Middle Triassic ‘Muschelkalk’ of Europe are far more abundant than the few known body fossils of their track-makers,

although they have either not been preserved or have been simply overlooked.

The presented study makes use of evidence from extensive trackway material and long horseshoe crab trace fossils (Fig. 1C) aiming to interpret the palaeoecology of ancient intertidal flats from the Middle Triassic of Europe, approximately 245–237 Mya. Trace fossils are the structures left behind by behavioural interactions between organisms and substrates (Bromley, 1990; Seilacher, 2008). Trace fossils such as those described in the present study from the Middle Triassic are preserved *in situ* and hence provide palaeoecological information as well as evidence of animal behaviour and interactions (Ekdale, Bromley & Pemberton, 1984). Associations of different trace fossils or ichnofacies types therefore provide a window into past ecosystems (Ekdale *et al.*, 1984; Bromley, 1990). Such ichnocoenoses for the Middle Triassic intertidal flats of Europe were originally considered to contain only reptile tracks (Diedrich, 1998), although the presence of such large numbers of small reptile tracks in these plant-free zones remained enigmatic (Diedrich, 2008a). Their presence can now, however, be better understood in the light of the abundant arthropod trackways that have now been recognized.

Trace fossils of both reptiles and invertebrates such as those discussed in the present study are generally identified and named using a parataxonomic binomial nomenclature, with trace fossil genera (ichnogenera), and trace fossil species (ichnospecies; e.g. Ekdale *et al.*, 1984); all horseshoe crab trackways therefore belong to the *Kouphichnium* Nopsca, 1923 ichnogenus. The binomial name given to a trace fossil is based solely on its morphology, although the morphology of each trace fossil can vary within its own trackway, as is clearly demonstrated in the long horseshoe crab trackways from Bernburg that have been mapped for this contribution. The morphology of a trace fossil is dependant on three main factors: (1) the anatomy of the organism producing the traces; (2) the behaviour of that organism at the time (including the type of locomotion being used); and (3) the substrate conditions (Seilacher, 2008), the effects of which have recently been studied at the Bernburg site in relation to reptile track preservation (Diedrich, 2011). A single organism can therefore produce different types of trace fossils as a result of different types of behaviour and different substrate conditions. Conversely, taxonomically different but morphologically similar organisms can produce similar trace fossils as a result of either similar or completely dissimilar behaviour. The best examples of this are provided by the ‘scratch marks’ that have been frequently recorded at the studied locality. In particular, scratch marks left by archosaur claws at the possible archosaur

‘predation’ trace fossil site reported in the present study appear very similar to the abundant scratch marks left by limulids. Single small slabs are therefore often misinterpreted, whereas the mapping of longer trackways over large surfaces permits far more reliable interpretation.

The producer of a trace fossil can, in most cases, only be inferred, although this process can be refined by comparing the trace fossils with the anatomy of known body fossils, as well as by observing the traces produced by modern organisms, and by experimentation. Only in rare cases, such as in the additional Jurassic horseshoe crab material, has the trace-maker been found at the end of its last tracks (Schweigert & Dietl, 2002; Seilacher, 2008), allowing its positive identification as the track producer. At the German Triassic Bernburg locality, however, only the recently discovered trackways are available. These trackways are, however, present in large quantities and can be excavated as beautifully preserved horseshoe crab trackways some tens of metres in length, together with abundant trackways of reptiles that range from small to large sizes, and are quite unique in the world, providing valuable palaeoenvironmental information.

MATERIAL AND METHODS

EXCAVATION OF PALAEONTOLOGICAL SURFACES AT BERNBURG

The largest modern excavation of a Triassic track site in Europe was performed in June 2008 at Bernburg, in central Germany (51°49′13.94″N, 11°43′33.30″E; Fig. 1B), over a large surface covering approximately 2500 m² (cf. details in Diedrich, 2009a). As well as multiple trackways ascribed to each of the five ichnogenera *Procolophonichnium*, *Rhynchosauroides*, *Chirotherium*, *Isochirotherium*, and *Prosauropodichnus*, a large number of arthropod trackways were identified and mapped over lengths of up to 40 m. Despite thorough cleaning of the track-bearing mud-cracked biolaminar surfaces by brushing, the arthropod trackways were initially very difficult to identify. Only in the low angle light of morning and evening, or by using artificial light at night, was it possible to locate and map most of the several thousand single imprints and link them together into long trackways. The deepest, elongated to kidney-shaped imprints from large arthropods were identified first and marked with circles of particular colours (Fig. 1C) to allow the various trackways to be better followed and photographically documented (Fig. 1B). Even after the colour-marking, it was often difficult to follow the trackways on site because of the large number of overlapping tracks, the sinuous or unusual circular

patterns of the trails, and because of interruptions in the trails as a consequence of the different states of preservation that resulted from variations in the moisture content of the substrate at the time that the track-maker traversed the sediments. Thousands of small arthropod track imprints were mapped photographically and were equalized using AUTOCAD (Autodesk, Inc.) to obtain the best possible resolution. Between 30 and 40 complete and incomplete arthropod trackways were mapped on a single track bed surface (Track Bed 7), providing the longest and largest quantity of fossil arthropod (*Kouphichnium*) trackways documented anywhere in the world. Although most of the trackway material from Bernburg was mapped, very little of it could be preserved as a result of the large size of the excavated surface that had the dimensions of about half a football field. Only a few selected slabs of original track material could be saved and are now stored in the Landesmuseum at Sachsen-Anhalt (LSDA). Some isolated slabs were also collected from other arthropod track-bed layers within the Bernburg section (Fig. 2).

In 2010 another, smaller, excavation of an area outside the original 2008 Bernburg excavation site, focussing on chirotherid reptile trackways, revealed an important thecodont archosaur trackway (*Chirotherium*) that included within its tracks the traces of an area used as a 'feeding/playing' site by the thecodont, and its possible prey, a horseshoe crab. A perfectly preserved trackway of mating horseshoe crabs was also documented and a length of approximately 9 m was preserved. All of the material saved from the 2010 excavation is in the local Bernburg Museum (MB).

EXPLORATION OF OTHER LOCALITIES

Subsequent to the discovery of the extensive Bernburg tracks and the exploration of a small part of this site (which is still continuing), systematic exploration of other localities known to contain biolaminates and vertebrate footprint records has revealed two more arthropod track sites (one at Winterswijk in the Netherlands and another at Bad Sulza in central Germany) (Fig. 1A) in which track beds have been recorded from three different layers of Middle Triassic carbonates. Material recovered from an excavation at Hasbergen, near Osnabrueck, in north-western Germany has also been incorporated into this study; this material is partly housed at the Geozentrum in Hasbergen (GZH), whereas the remainder is at the TERRA.Vita UNESCO-Geopark site (Diedrich, 2008b, 2010b). Also included are unpublished surfaces with arthropod scratch marks and vertebrate track beds that were excavated in 1996 at Borgholzhausen in western Germany (Diedrich, 2002b), and are stored at

the ErdZeitMuseum in Borgholzhausen (EZMB). A small quantity of material collected from Winterswijk in 2009 is from the same facies as the earlier discoveries and has extended the time range of these arthropod tracks in the Germanic Basin; this material has been stored in the Freriks Museum (MF). There are also several other vertebrate track sites, such as those at Dissen, Eberschütz, Grossenluder 1, Geilsdorf, and Rüdersdorf, where at least some arthropod scratch marks and single pusher-foot imprints have been noted, although no systematic research has been carried out. Many other known track sites between Winterswijk in the eastern Netherlands and Rüdersdorf in eastern Germany (Diedrich, 2009b; Fig. 1A) may be included in future, more extensive studies, although, because most of these localities do not permit large-scale surface excavations, Bernburg remains the most important recent excavation locality.

HORSESHOE CRAB BODY FOSSILS

In addition to the tracks and traces mentioned above, a few limulid body fossils have been recorded in track-rich biolaminates from various German sites, ranging from Aegean to Illyrian (Middle Triassic) in age. A nonprepared Middle Triassic limulid body fossil has recently been reported from Winterswijk (Hauschke *et al.*, 2009). Limulid material from Spain in the Museo Geológico del Seminario de Barcelona (MGSB) and a single small specimen from Ohrdruf in central Germany, stored in the Naturkundemuseum at Erfurt (NME), have been included in this study aiming to improve our understanding of the possible track-makers in the Middle Triassic.

Additionally Upper Jurassic trackways and *Mesolimulus* specimens from the Solnhofen Plattenkalk in the Senckenbergmuseum, Frankfurt (SMF), have been included for comparison purposes, in particular a large slab with a looping trackway that includes the track-maker's body fossil at the end of the track.

ACTUALISTIC EXPERIMENTS

A neoichnological study was conducted, aiming to improve our understanding of the above-mentioned track variability and of the species responsible for the large arthropod trackways at Bernburg. A modern Japanese/Chinese horseshoe crab (*Tachypleus tridentatus* Leach), with a prosoma width of 18 cm, was used because of its apparent similarity in size to the Triassic horseshoe crab species that made the Bernburg trackways. The first experiment involved the animal walking on exposed, almost dry, sand. The second sediment type used in this experiment (very

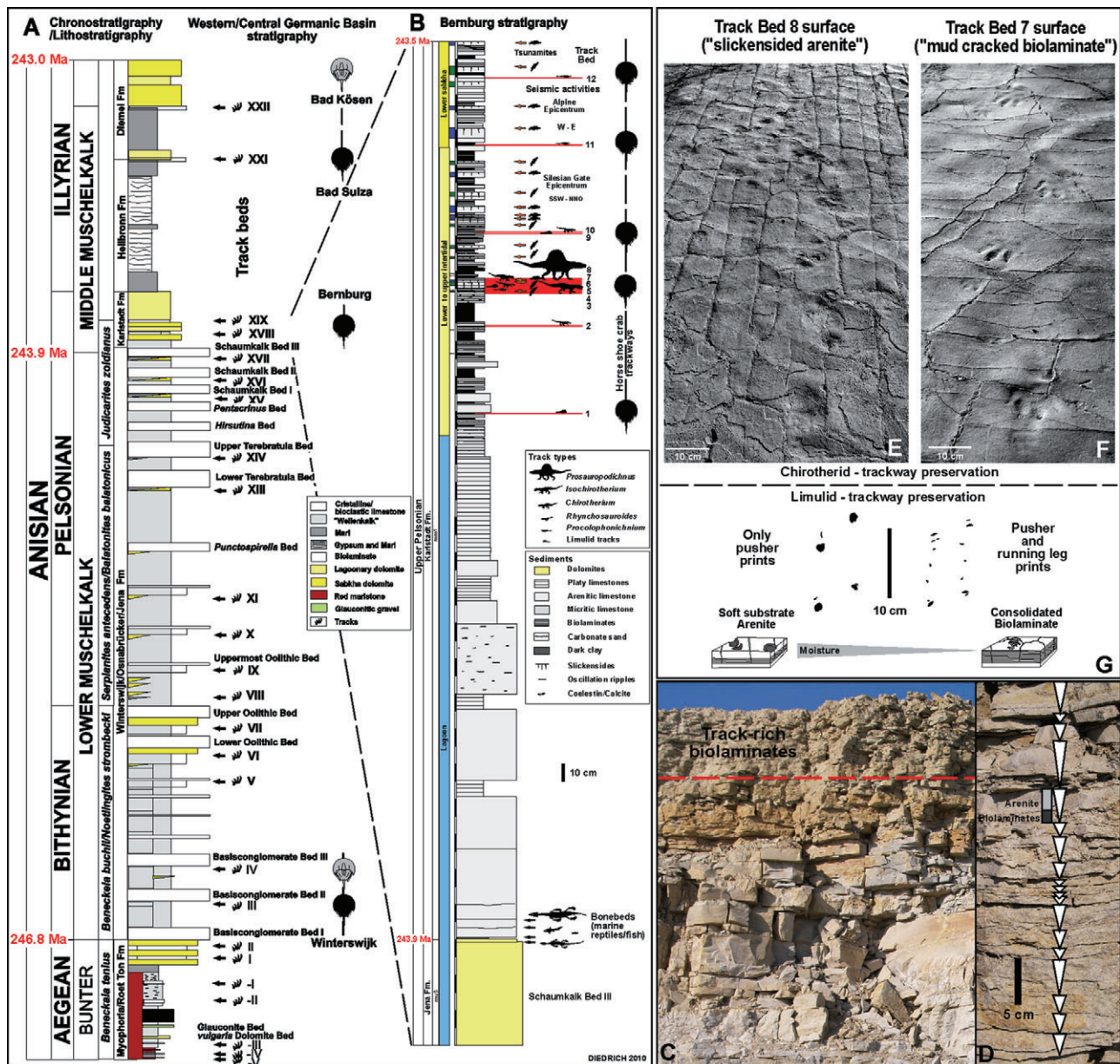


Figure 2. A, generalized Lower to Middle Muschelkalk (Middle Triassic) section for the central to western part of the Germanic Basin, including the horseshoe crab track beds and body fossil locations. B, C, high resolution stratigraphy for the limulid trackway site at Bernburg; D, with the biolaminate/arenite series; E, in which the arenites are mostly slickensided; F, the mud-cracked autochthonous biolaminates with chirotherid reptile trackways on the main documented surface, together with the horseshoe crab trackways. G, preservation varies between the two main sediment types and with their moisture contents (stratigraphy *sensu* Diedrich, 2008a, 2009b, 2011).

fine-grained carbonate) was taken from the intertidal flats west of Abu Dhabi (UAE) to ensure a grain size similar to the sediments that subsequently became the micritic limestones found at Bernburg. This 'pudding-like' barely stabilized carbonate mud was smoothed onto the floor of a tank. In the first experiment, under subaerial exposure, the horseshoe crab produced predominantly looped or even circular

trackways and left deep impressions of all of its extremities, as well as its telson, as it crawled or walked across the surface. When the carbonate sediment surface was covered with slightly less than 10 cm of saline water, the limulid produced very different kinds of trackways that were more sinuous and recorded only impact marks from the running legs and the pusher-feet, produced by a combination of

hopping and swimming motions. The under-water experiment was more difficult because, once the water had been drained from the tank, the mud tended to collapse very quickly as a result of dehydration and tank movements, which destroyed the tracks. These subaquatic walking experiments were therefore repeated several times and the resultant trackways documented very quickly after dewatering the tank, before being eventually redrawn digitally.

GEOLOGY

STRATIGRAPHY

Horseshoe crab tracks and body fossils overlap stratigraphically within the marine deposits of the Middle Triassic (Anisian/Ladinian) 'Muschelkalk' of the Germanic Basin, with the trackways appearing only in intertidal biolaminates (Track Horizons within the stages, and Track Beds within the formations), whereas body fossils have been recorded from a variety of shallow marine facies and sediment types, including Lower Muschelkalk 'Wellenkalk' shallow subtidal carbonates, intertidal biolaminates, and sabkha deposits (Fig. 2A). The Anisian of the Germanic Basin includes the substages described below.

Bithynian

The oldest horseshoe crab track material used in this research is from Winterswijk, based on the chronostratigraphic subdivision of the Middle Triassic by Kozur & Bachmann (2008) and high resolution vertebrate track-bed stratigraphy by Diedrich (2008a, 2009a, b) which ascribe an early to middle Bithynian age (lower Anisian; Fig. 2A) to the Winterswijk Formation. This formation consists mainly of mud-cracked intertidal biolaminate facies (Diedrich, 2001), from which the tracks and trackways described in the present study were collected. Horseshoe crab tracks from Borgholzhausen are from slightly younger layers in the late Bithynian Oolitic Beds, which form the base of the Osnabrück Formation in the Lower Muschelkalk (Diedrich, 2002b; Fig. 2A).

Pelsonian

The material from Bernburg was also found in biolaminates, and included additional material from seismically influenced and slickensided intertidal facies arenites (Diedrich, 2009a, 2011; Fig. 2B, C, D). High resolution track bed stratigraphy has placed these sediments in the Karlstadt Formation, which is of late Pelsonian age (Fig. 2A, B). The repeated seismic influence within the approximately 5-m thick Karlstadt Formation at the Bernburg arthropod track site, over a time frame of some 500 000 years, has

recently been documented: nineteen horizontal slickenside zones, separated vertically by 15–25 cm, have been recorded within arenaceous carbonate layers (Fig. 2E) with parallel fracture zones within the section (Diedrich, 2011; Fig. 2B). Several horseshoe crab trackways have even been found on seismically influenced, 2–4 cm thick, arenite layers (Fig. 2C) that intercalate with the autochthonous biolaminates (Fig. 2D), on which trackway details are best preserved (e.g. in most of the material described in the present study from Track Bed 7).

Illyrian

The stratigraphically youngest material came from the Bad Sulza section, where new dating has placed this track bed (Track Horizon 21) into the middle Illyrian (middle Anisian) Diemel Formation (Fig. 2A).

PALAEOENVIRONMENTS

All vertebrate and arthropod tracks in the northern Germanic Basin have been found in intertidal to lower sabkha carbonate facies, and are most commonly preserved in biolaminates (Diedrich, 2002a, b, 2008a, 2011). These intertidal carbonate mud to sand flats were widely distributed in the central Germanic Basin, especially on the shallow marginal ramps of the western and central basin area. On several occasions during the Middle Triassic they extended over hundreds of kilometers (Fig. 2A) and even formed 'bridges' between the Rhenish and Bohemian Massifs (e.g. during early Middle Muschelkalk times when the Bernburg tracks were formed) (Diedrich, 2009b). These maximal extents of intertidal and sabkha environments were especially evident during the three intervals in which arthropod tracks have been found: the early Lower Muschelkalk, the early Middle Muschelkalk, and the late Middle Muschelkalk (Diedrich, 2009b; Fig. 2A). During these times the shallow carbonate ramp of the Germanic Basin was tectonically controlled (Schwarz, 1975; Knaust, 1997) and affected by seismically generated waves as result of the subsidence of this intracratonic basin and collision of the African and European plates (Knaust, 2000; Föhlisch, 2007).

PALAEONTOLOGY

ICHNOGENUS *KOUPHICNIUM* NOPSCA, 1923

KOUPHICNIUM ICHNOSP. (FIGS. 3–14)

Ichnotaxon: *Koupichnium* is a horizontal, bilaterally symmetrical trackway that can be quite variable in its expression depending on the substrate and sediment moisture at the time of formation (Figs 2G, 3, 4,

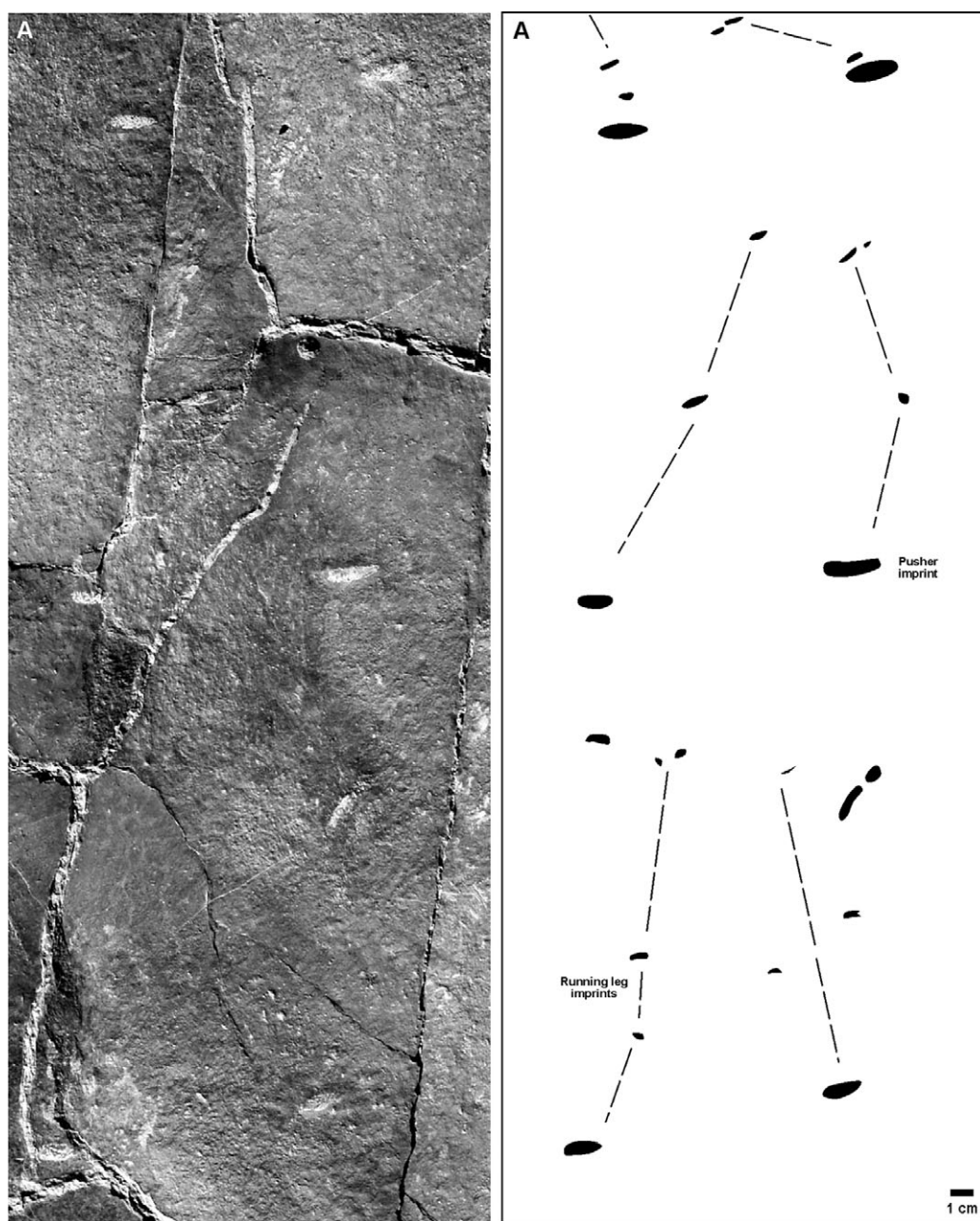


Figure 3. *Koupichnium* Nopsca, 1923 horseshoe crab traces from the Middle Triassic intertidal flat facies of the Germanic Basin. A, part of a subaquatic trackway, with deep pusher-foot and small running-leg imprints, from Track Bed 7 (part of Trackway A; Fig. 12) in the Karlstadt Fm. (upper Pelsonian, middle Anisian) at Bernburg (positive).

5, 6, 7, 8) but, in the best examples, it exhibits birdfoot-type prints with an associated medial telson drag-mark. Its track and trace-maker was a horseshoe crab moving in either a subaqueous or subaerial marine environment (Seilacher, 2008). The variables that typically control the morphology of the tracks and traces are the sediment type (see descriptions of neoichnology and actualistic experiments), the size and age of the animal, the speed and type of locomotion

(Figs 12, 14), the facies in which the tracks and traces were made (Fig. 2G), and various other more subtle factors. These main variables are considered in the description below.

Material: Between 30 and 40 trackways from Bernburg, which range in length between 10 and 40 m (Figs 11, 12, 13, 14). The precise number of trackways is uncertain because some are only parts of track-

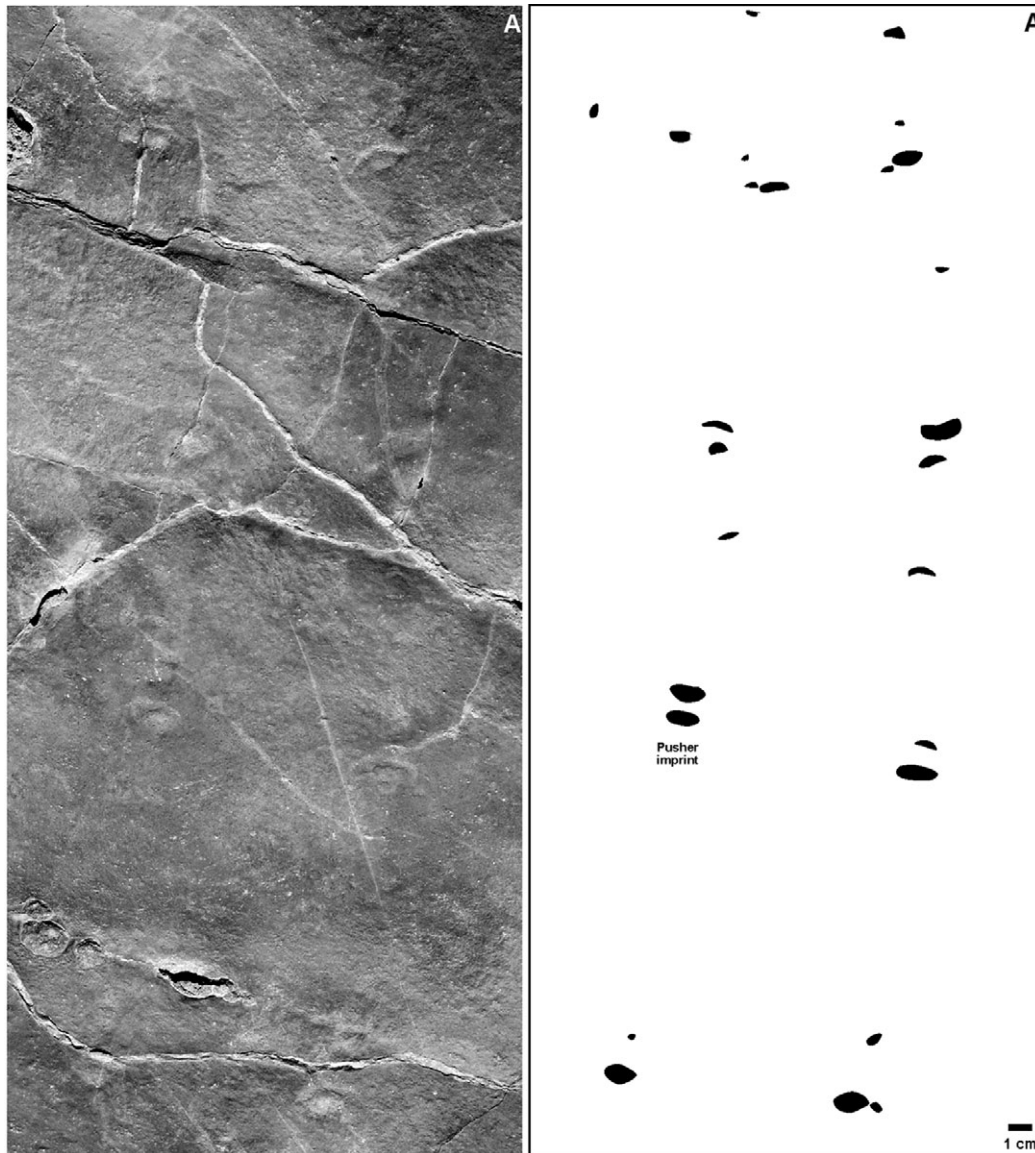


Figure 4. *Koupichnium* Nopsca, 1923 horseshoe crab traces from the Middle Triassic intertidal flat facies of the Germanic Basin. A, part of a subaquatic trackway, with deep pusher-foot imprints, from Track Bed 7 (part of Trackway B; Fig. 12) in the Karlstadt Fm. (upper Pelsonian, middle Anisian) at Bernburg (positive).

ways, terminating within the mapped area but possibly belonging to a single trackway: connecting them up is problematic because of loops and directional changes within the trackways.

Description: Trackway types A–C described below reflect differences in behaviour and would normally receive separate ichnotaxonomic names. However, in some cases, the changes occur within a single trackway, and new ichnospecies names have therefore not been ascribed to each of the different trackway types: all are simply referred to as *Koupichnium* but with three main types of locomotion being distinguished

within the trackways, as well as traces that were possibly formed by drifting carcasses and a possible feeding site.

A. Parallel pusher-foot imprint trackways: These footprints vary in their individual shapes. In most cases, only the pusher-foot imprints are preserved (Figs 3, 4, 5, 6, 7, 8), which are usually long, kidney-shaped or oval depressions with small ridges along their leading edges. These are the tracks that can be most easily seen (Figs 3, 4, 5). In a few instances, a series of tracks were arranged *en echelon*, with those on either side of the trackway having opposite symmetries that

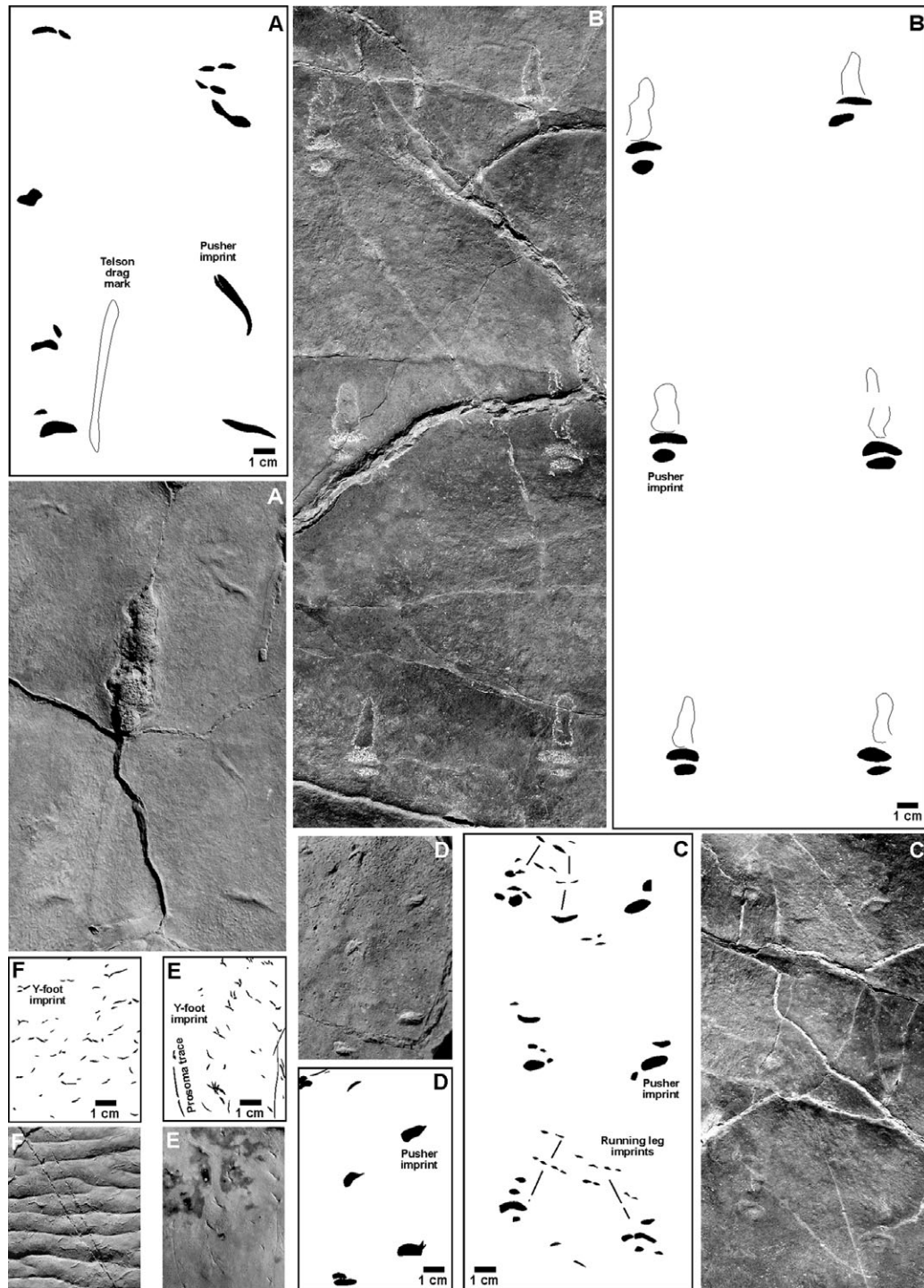
include both pusher-foot and running-leg foot impressions (Figs 3A, 5C, 13). These running-leg foot impressions are mostly spread-foot impressions and, depending on the completeness of the imprint and/or the state of preservation, appear to split into at least two parts (Fig. 5E, F); when fully imprinted, they can be seen to be Y-shaped. This can best be seen on track slabs from Bernburg and Bad Sulza that have similarly-shaped foot impressions (Fig. 5E, F). Most of the trackways have mainly pusher-foot imprints preserved (Fig. 12A, B, C) and, in some cases, only pusher-foot imprints (Fig. 12D). The trackways are often irregular as a result of the diverse types of motion represented, sometimes including rapid, sinuous movements (Figs 10, 12). In most cases, the trackways of a single individual could be followed over long distances (Figs 11, 12) but, in several cases, the trackways were interrupted and it is unclear whether this was a result of poor preservation, shallow original imprints, or a combination of both movement along the sediment surface and swimming. A normal trackway consists of large, elongated to kidney-shaped, pusher-foot imprints in a pattern that ranges from slightly curved to extremely sinuous. Ninety-six percent of the Bernburg trackways fit into this 'normal' category of preservation, and the track slab from Winterswijk also exhibits a similar type of locomotion and preservation (Fig. 5E). One of the few trackways that has telson drag-marks preserved (in places), forming straight, elongated traces that are only 1–2 mm in depth, is shown in Figure 5A. The trackways are parallel to each other in many cases, and their main orientation on the excavated surface is west-south-west–east-north-east (Fig. 11).

B. Alternating/zigzagging pusher-foot imprint trackways: Two long trackways of this type were mapped in the 2008 and 2010 excavations. The first trackway is illustrated in Figure 12E; the second, 9-m long saved trackway (Fig. 6), has similar alternating foot prints, in which the pusher-foot imprints have irregular posterior margins allowing the direction of motion to be inferred in this trackway. Important details can

be seen in the pusher-foot imprints of both trackways, which end distally with a 'comb-like' pattern (Figs 6F, G, H, 7A), suggesting the presence of at least three smaller distal appendage segments. One of the trackways crosses a chirotherid trackway, with the *Chirotherium* footprint overprinted by the by the horseshoe crab trackway (Fig. 6E).

C. Pusher-foot scratch-mark trackways: Parallel scratch marks that can be related to four long appendages are present in a swimming trackway illustrated in Figure 8B. This anatomical detail is important in understanding the other scratch-mark trackways (cf. Figs 7C, D, E, 8, 9) that must have also resulted from these pusher-foot appendages. Several very sinuous trackways (Figs 7C, 12C, D, E), consisting only of two or three small, parallel scratch marks and other scratch marks, angled at approximately 45° to the direction of travel, appear to be left from the above-mentioned pusher-foot appendages and can therefore be attributed to the same track-maker; these can be well seen in the trackway segment shown in Figure 8B. Other fine, parallel scratches that are mostly elongate, and often comprised of only two scratch traces, are different from those mentioned above and are more or less parallel to the direction of movement; these were made either by the prosoma margins or, once again, by the pusher-foot appendages but during swimming, when the pusher-feet were not being used but simply hung beneath the body, thus leaving thin scratch marks running parallel to the direction of travel (Figs 8A, B, 9). Further evidence supporting the attribution of these swimming traces to limulids is provided by the similarity in trackway widths (from 6–10 cm) between the half-swimming trackways and the trackways consisting of scratch marks and pusher-foot impressions. The traces from full swimming movements can be very sinuous and may include complete loops (Fig. 14C, E). In one instance, a circular scratch-mark was documented at the intersection of two trackways (Fig. 12A). It is interesting to note that, on the excavated surface, all of these types of trackways have a completely different

Figure 5. *Kouphichnium* Nopsca, 1923 horseshoe crab traces from the Middle Triassic intertidal flat facies of the Germanic Basin. A, part of a subaquatic trackway, with deep pusher-foot imprints and a telson drag mark, from Track Bed 12 (Fig. 2B) in the Karlstadt Formation (upper Pelsonian, middle Anisian) at Bernburg (positive). B, part of a subaquatic trackway, with deep pusher-foot imprints from Track Bed 7 (part of Trackway D; Fig. 12D) in the Karlstadt Formation (upper Pelsonian, middle Anisian) at Bernburg (positive). C, part of a subaquatic trackway, with deep pusher-foot imprints from Track Bed 7 (Fig. 2A) in the Karlstadt Formation (upper Pelsonian, middle Anisian) at Bernburg (positive). D, partial trackway of a half-swimming animal with deep pusher-foot imprint, from track beds in the Winterswijk Formation (Bithynian, lower Anisian) of Winterswijk (negative). E, trackway of a running animal with marginal prosoma scratch marks and Y-shaped running-leg impressions, from Track Bed 9 (Fig. 2B) in the Karlstadt Fm. (upper Pelsonian, middle Anisian) at Bernburg (positive). F, trackways with Y-shaped running-leg impressions, from Track Horizon 22 (Fig. 2A) in the Diemal Fm. (upper Pelsonian, upper Anisian) at Bad Sulza (positive).



orientation to the previously described track types and are quite restricted to parallel north-north-west-south-south-east orientations (Fig. 13).

D. Elongated traces: Elongated drag marks on the excavated surface might have been caused by horseshoe crabs, or alternatively by drifting carcasses

which generally rest upside down on the sea floor. There are two types of trace: most of the traces are hyporeliefs (Fig. 7B) but, in one trace (Fig. 13I), the long drag mark is an epirelief. The predominant north-west-south-east orientation of these traces on the excavated surface appears to reflect the current (and transport) direction.

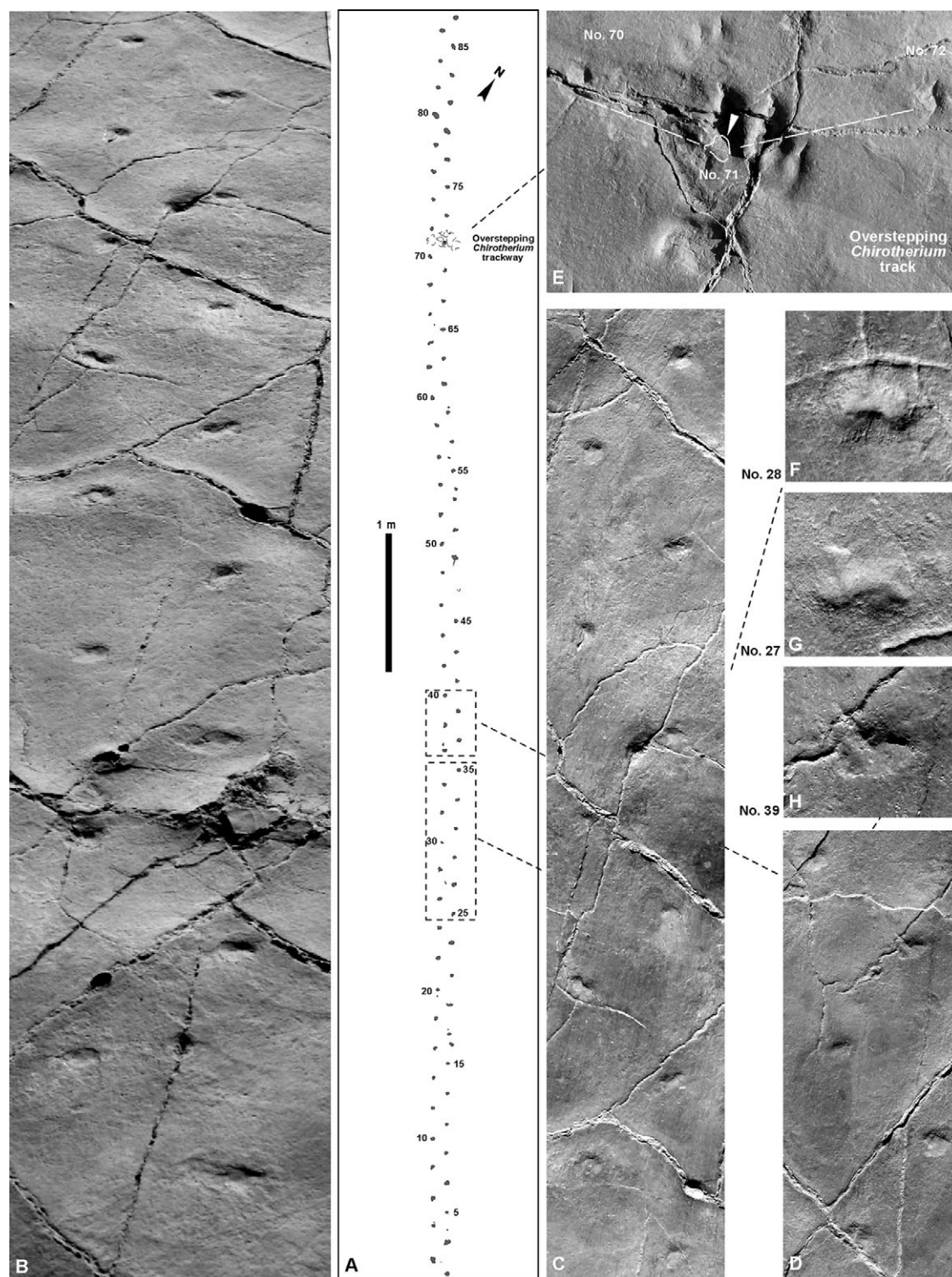


Figure 6. *Koupichnium* Nopsca, 1923 horseshoe crab traces from the Middle Triassic intertidal flat facies of the Germanic Basin. A, B, C, D, E, F, alternating, zigzagging, mating trackway type consisting of 87 right and left pusher-foot imprints from Track Bed 7 in the Karlstadt Fm. (upper Pelonian, middle Anisian) at Bernburg (positive): A, track map; B, oblique view; C, D, trackway parts; E, crossing a reptile trackway and overprinting by a *Chirotherium* footprint (no. 71); F, G, H, enlarged pusher-foot imprints (Excavation 2010, coll. MB).

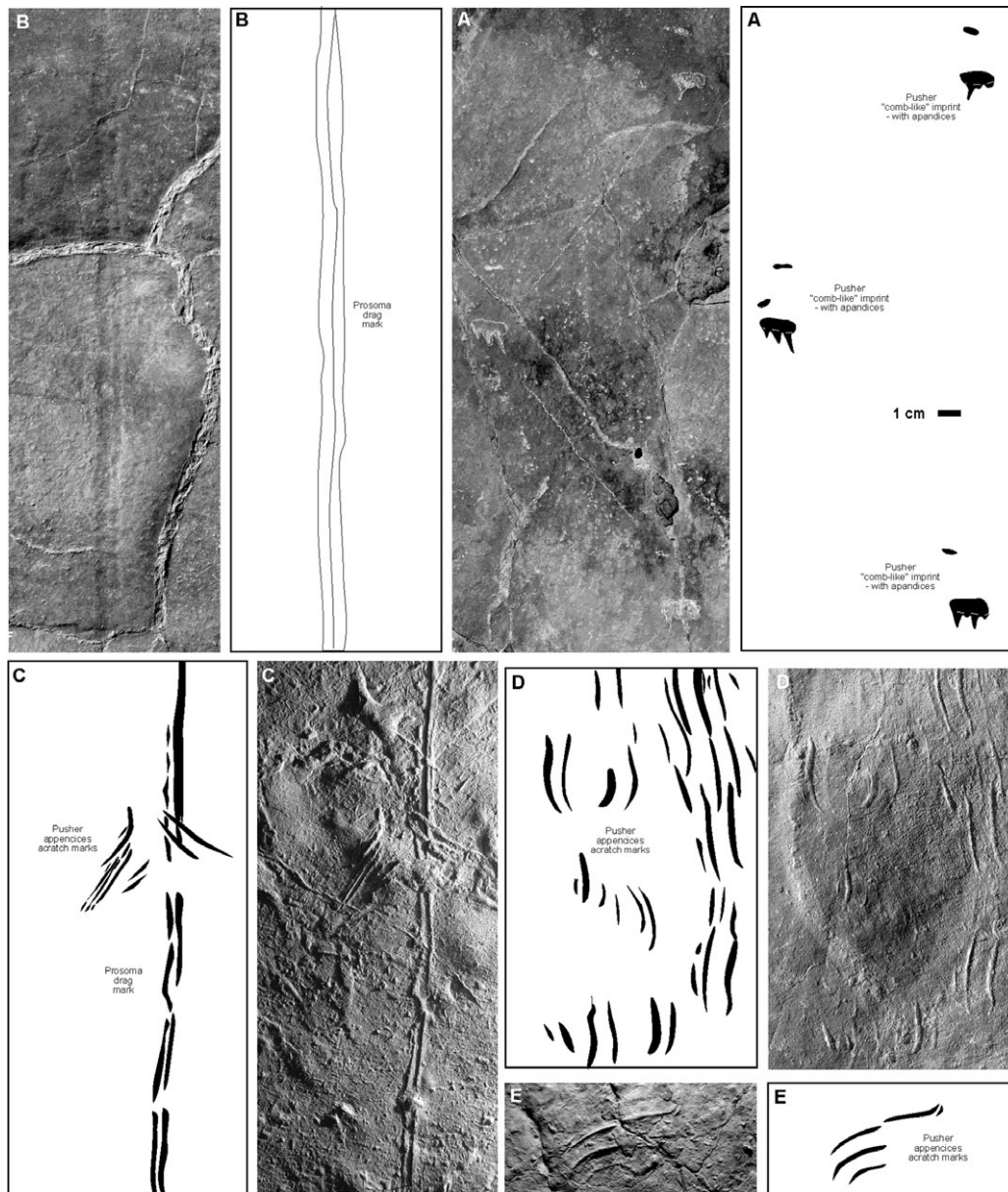


Figure 7. *Kouphichnium* Nopsca, 1923 arthropod traces from the Middle Triassic intertidal flat facies of the Germanic Basin. A, part of a mating, zigzagging, alternating, trackway type leaving deeply impressed pusher-foot prints with appendage details (3–4, ‘brush-like’, posterior pointing) from Track Bed 7 (part of Trackway E; Fig. 12E) in the Karlstadt Fm. (upper Pelsonian, middle Anisian) at Bernburg (positive). B, part of a subaquatic drifting carcass drag mark (?) as hyporelief, from Track Bed 7 (part of Trackway A; Fig. 14A) in the Karlstadt Fm. (upper Pelsonian, middle Anisian) at Bernburg (positive). C, part of a subaquatic, drifting carcass (?) trace from Track Bed 2 (Fig. 2) in the Osnabrueck Fm. (upper Aegean, lower Anisian) at Hasbergen (negative). D, scratch marks from pusher appendages, from Track Bed 9 (Fig. 2) in the Karlstadt Fm. (upper Pelsonian, middle Anisian) at Bernburg (negative). E, scratch marks from pusher appendages, from Track Horizon 2 (Fig. 2) in the Osnabrück Fm. (upper Aegean, lower Anisian) at Hasbergen (negative).

E. Thecodont archosaur predation site on horse shoe crab: During the 2010 Bernburg excavation, a unique archosaur-horseshoe crab activity trace was discovered within a mapped and preserved *Chirotherium* trackway (Fig. 10). The *Chirotherium* trackway was

unfortunately destroyed before the activity place (which is almost complete) but it continues irregularly beyond the feeding site, initially with only two hind limb footprints but then gradually resuming a normal locomotion modus. This archosaur trackway

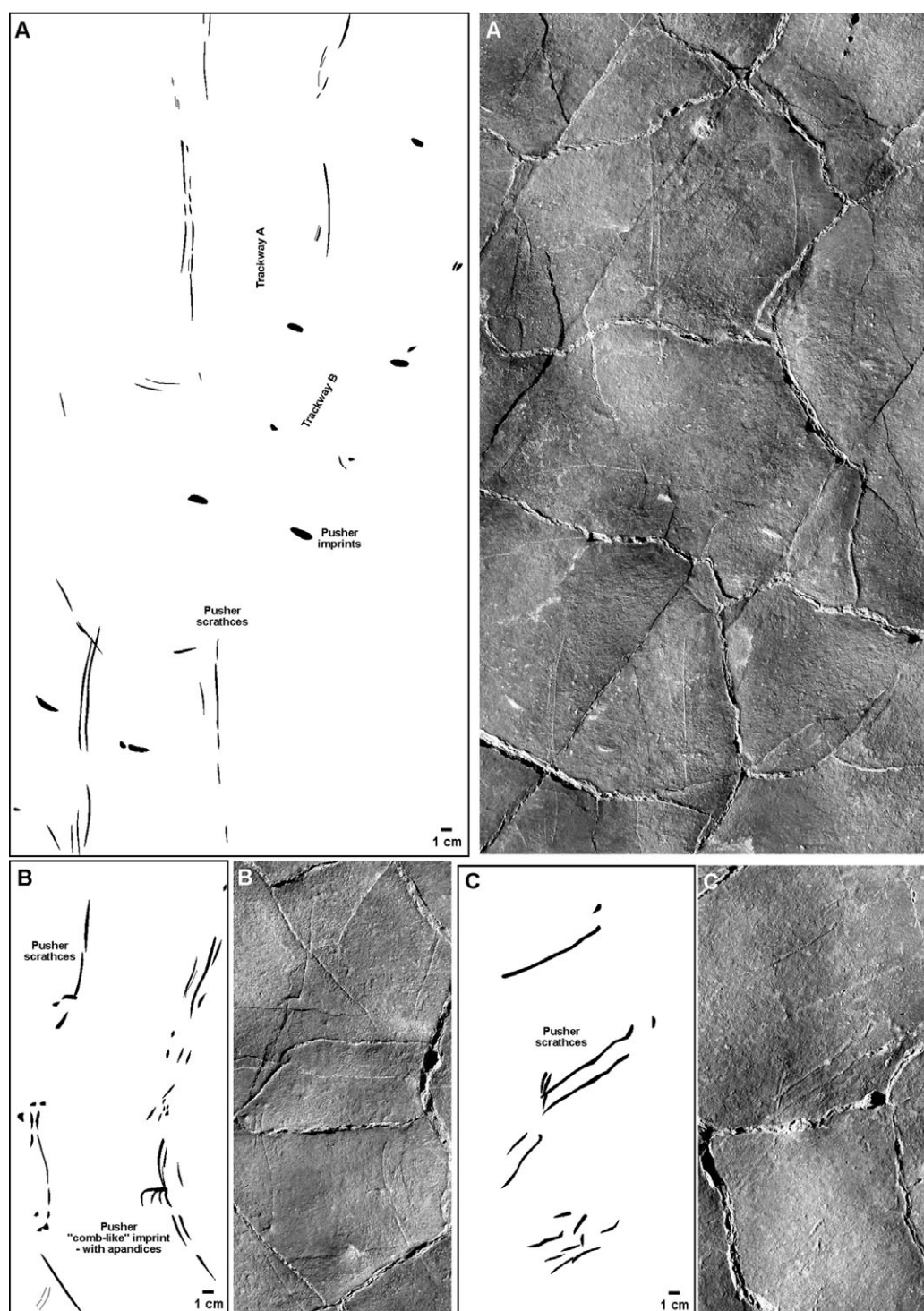


Figure 8. *Koupichnium* Nopsca, 1923 arthropod traces from the Middle Triassic intertidal flat facies of the Germanic Basin. A, swimming trackway with parallel scratch marks from the pusher-foot appendages (part of Trackway E; Fig. 14E), from Track Bed 7 in the Karlstadt Fm. (upper Pelsonian, middle Anisian) at Bernburg (positive). B, swimming trackway with parallel scratch marks from the pushers and well printed fork- or brush-like pusher appendages; all scratch marks are from a single trackway (part of Trackway E; Fig. 14E), from Track Bed 7 in the Karlstadt Fm. (upper Pelsonian, middle Anisian) at Bernburg (positive). C, swimming trackway (part) with parallel scratch marks from the pusher appendages (part of Trackway D; Fig. 14D), from Track Bed 7 in the Karlstadt Fm. (upper Pelsonian, middle Anisian) at Bernburg (positive).

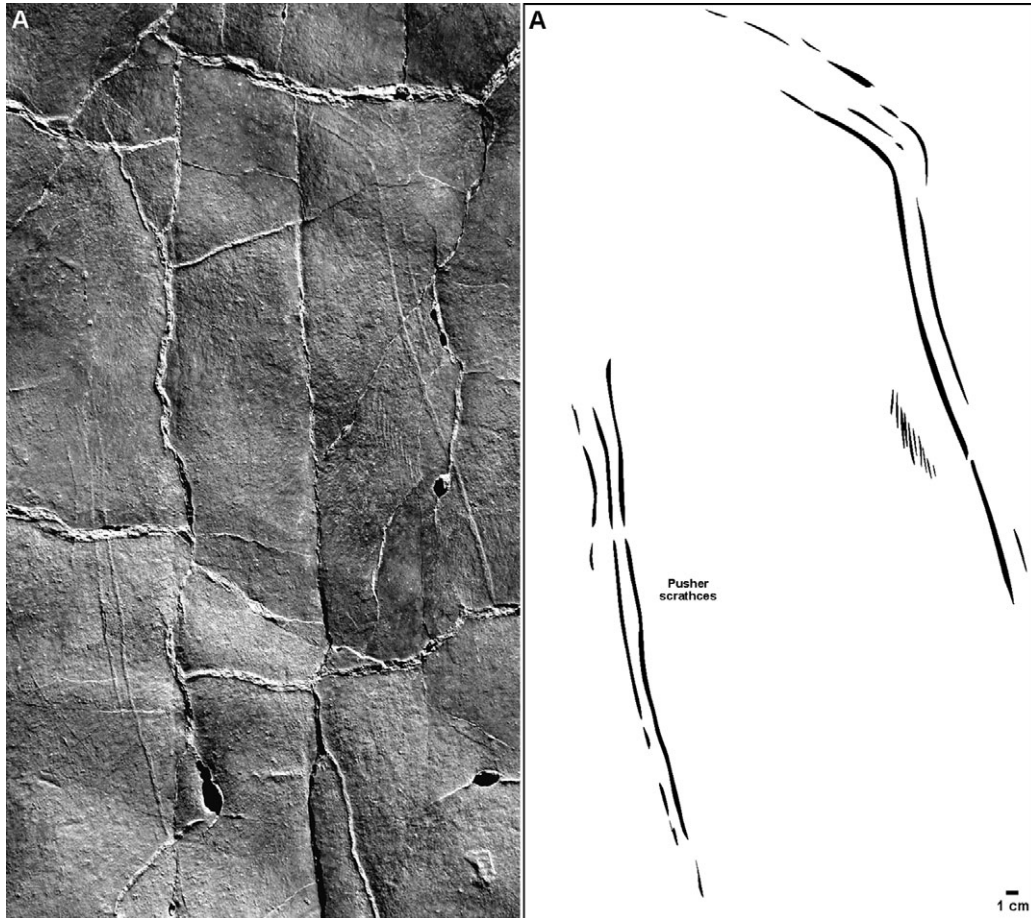


Figure 9. *Koupichnium* Nopsca, 1923 arthropod traces from the Middle Triassic intertidal flat facies of the Germanic Basin. A, two long, parallel scratches from pusher-foot appendages (Trackway F; Fig. 13F), from Track Bed 7 in the Karlstadt Fm. (upper Pelsonian, middle Anisian) at Bernburg (positive).

continues only with two hind limb footprints after the place, and starts then slowly a normal locomotion modus. Traces of a horseshoe crab can be identified additionally at this site following the description of extensive traces found on Track Bed 7 at Bernburg, and in particular compared to the quite similar circular trace shown in Figure 12A. A similar circular trace can be seen within the archosaur trackway activity place, made up of hundreds of small oval to triangular impact marks only 1–2 mm across, densely covering the surface (Fig. 10G). In some cases, the spread feet imprints are in rows and can be identified best as horseshoe crab running-leg imprints. A horseshoe crab trackway of type A was also mapped nearby, although it is unclear whether this trackway ends at the ‘feeding site’ or could still be from a second individual. In addition to the archosaur footprints, the 3–5 mm wide scratch marks from its claws, and the hundreds of small horseshoe crab foot imprints, there are also oval, chain-ordered depressions around the

horseshoe crab prints, circling around the limulid tracks.

DISCUSSION

MIDDLE TRIASSIC HORSESHOE CRAB TRACK RECORDS IN PANGAEA

Following comparisons with Palaeozoic and Mesozoic ichnogenera, the Middle Triassic material described and illustrated in the present study can be attributed to the very variable arthropod track ichnogenus *Koupichnium* (Romano & Whyte, 2003; Buta, Rindsberg & Kopaska-Merkel, 2005; Seilacher, 2008), of which the best examples for comparison are the shallow lagoonal subaquatic trackways found in the platy limestones of the Upper Jurassic (Kimmeridgian) ‘Solnhofener Plattenkalk’ (Schweigert & Dietl, 2002; Romano & Whyte, 2003; Buta *et al.*, 2005; Seilacher, 2008). Such a Solnhofener trackway is

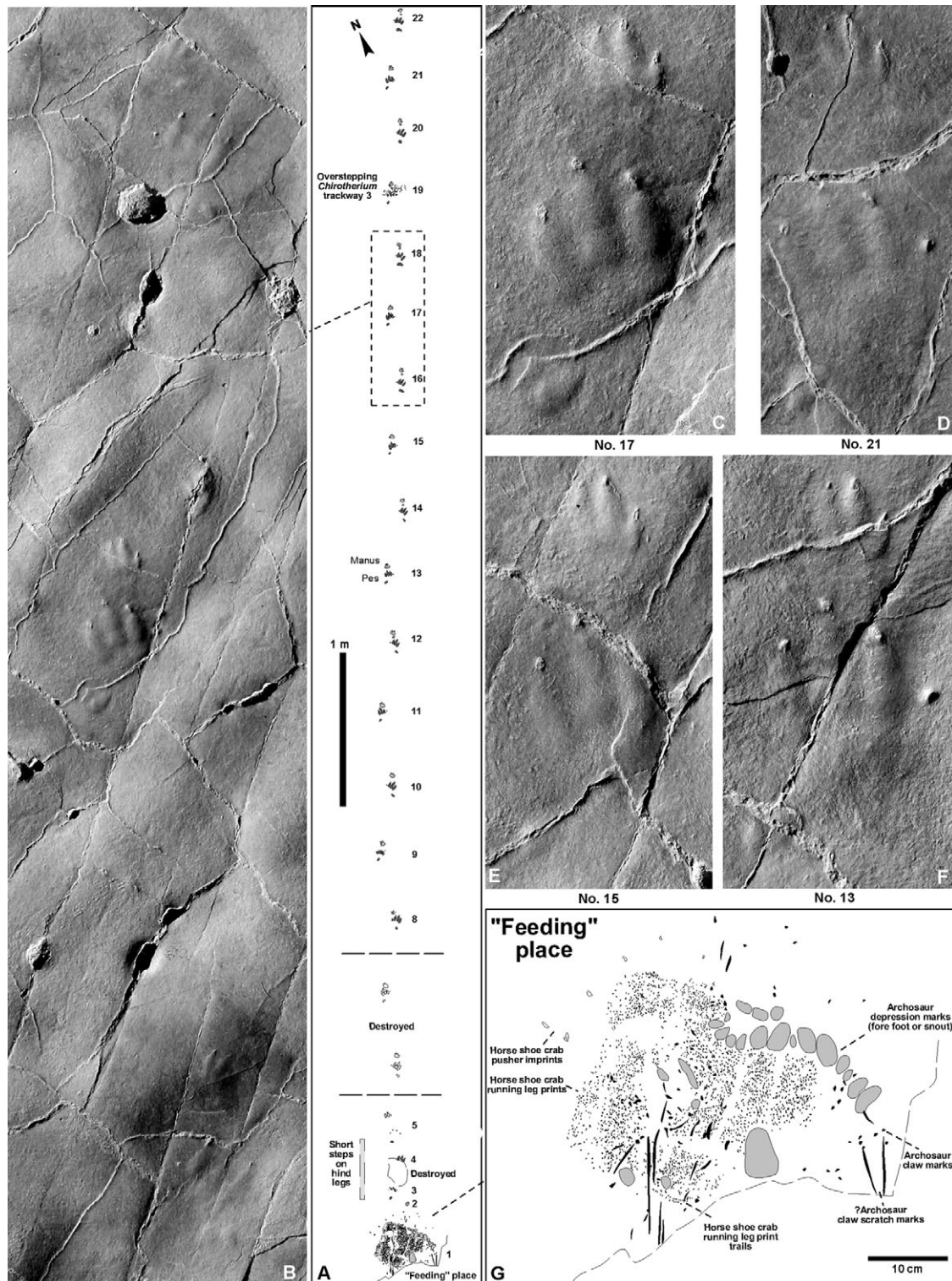


Figure 10. *Chirotherium* trackway 3 of a medium sized carnivorous thecodont archosaur track-maker, from Track Bed 7 in the Karlstadt Fm. (upper Pelsonian, middle Anisian) at Bernburg (positive). A, 22 tracks (tracks 6–7 destroyed) and 18 preserved manus/pes sets which have been interrupted over a length of approximately 1 m as a result of modern damage. B, trackway part. C, D, E, F, individual manus/pes sets from the trackway. G, possible site of feeding on horseshoe crab; enlarged (Excavation 2010, coll. MB).

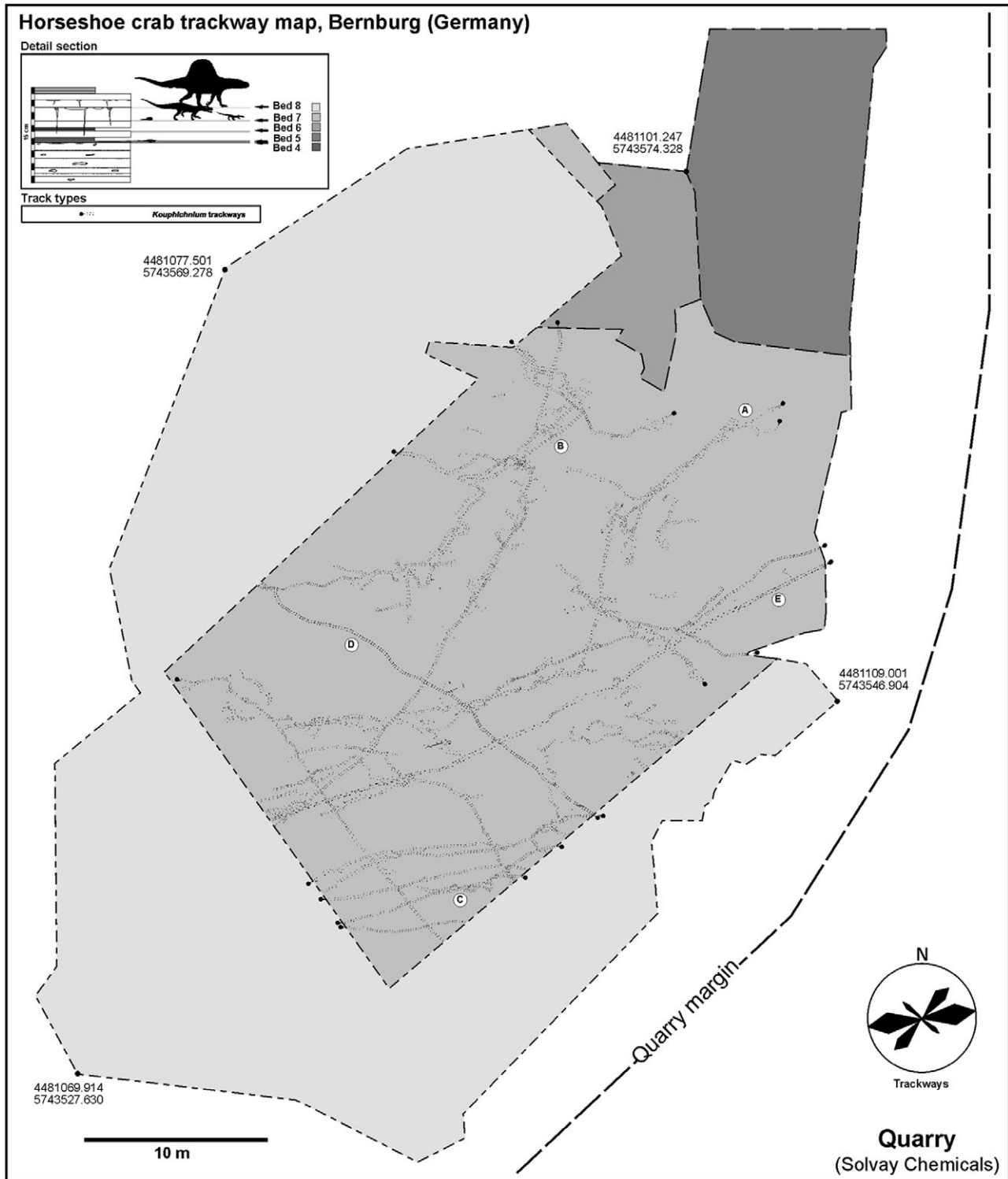


Figure 11. Overview of subaquatic horseshoe crab walking/crawling trackways on the surface of Track Bed 7 at the Bernburg track site. The trackways show differences in preservation and are sometimes incomplete. This is a result of slow wetting and drying out processes on the surface within a complete tidal cycle, during which limulids travelled over the surface (for trackway details, see Fig. 12).

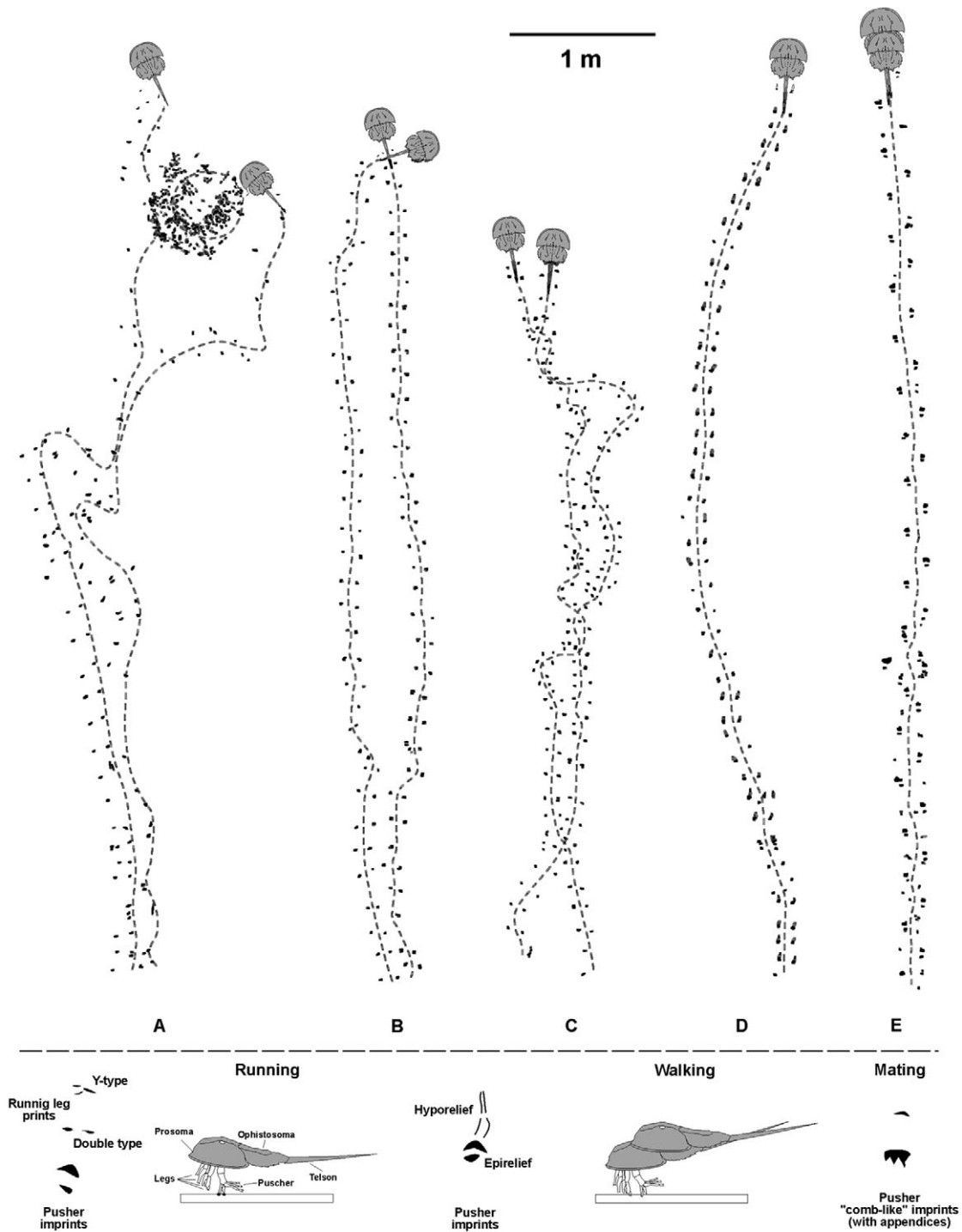


Figure 12. Subaquatic horseshoe crab walking trackways on Track Bed 7 in the Karlstadt Fm. (upper Pelsonian, middle Anisian) at Bernburg, central Germany. A, two crossing trails, in which one trail is sometimes only printed on one side indicating one individual attached on the other. At the end of the trackway, there appears to be a mating circle. B, two trails, more or less parallel to each other. C, two trails that cross each other several times. D, single trackway with hyporeliefs in front of the pusher-foot prints indicate scratching and sliding over the surface by the pusher-feet. E, trackway with deep zig-zagging impressions resulting from different modes of movement, possibly caused by two limulids mating. The trackway form changes in the middle of the trail, when only one pusher-foot is used (for trackway positions on the excavation surface, see Fig. 11).

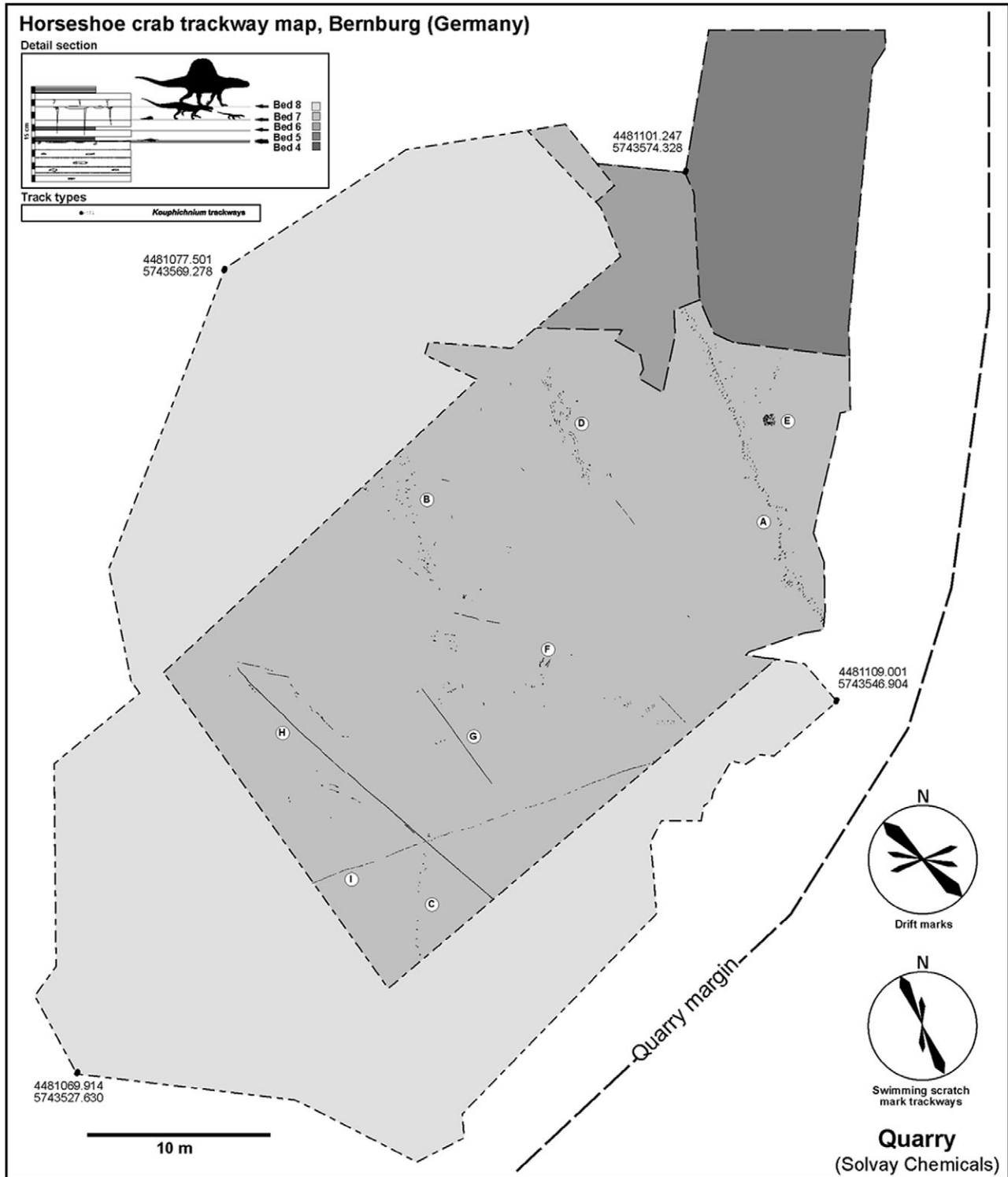


Figure 13. Overview of horseshoe crab drifting/swimming trackways on the surface of Track Bed 7 at the Bernburg track site (compare details of trackways with Fig. 14A, B, C, D, E).



Figure 14. Subaquatic horseshoe crab drifting carcass and swimming trackways from Track Bed 7 (upper Pelsonian, Anisian) at Bernburg, central Germany. A, straight drifting carcass (?) trace (Fig. 13H). B, interrupted drifting carcass (?) trace (Fig. 13G). C, sinuous swimming trace with scratch marks from the pusher-foot appendages (Fig. 13B). D, sinuous swimming trace with scratch marks from the pusher-foot appendages (Fig. 13A). E, looping swimming trace with scratch marks from the feet and traces from a pusher-foot appendage on one side (Fig. 13D) (positions on the excavation area in Fig. 13).

illustrated in Figure 15C and includes a new *Mesolimulus* specimen not previously described; one of the best known specimens of a *Kouphichnium* trackway and its horseshoe crab track-maker. Many different *Kouphichnium* track 'ichnospecies' have been described ranging from Carboniferous to Jurassic in age, including *Kouphichnium didactylus*, *Kouphichnium gracilis*, *Kouphichnium variabilis*, *Kouphichnium walchi* (Fig. 15C), *Kouphichnium lithographicum* and others; these have been produced by both subaquatic and supratidal movements that resulted in different types of trackways (Romano & Whyte, 2003; Buta *et al.*, 2005; Seilacher, 2008), as demonstrated by the experiments described herein (Fig. 15A, B).

Attribution of the *Kouphichnium* trackway types A–C at Bernburg to different ichnospecies does not make sense in view of the enormous variability demonstrated, both between and within, the long, continuous trackways described in the present study. This research demonstrates for the first time the wide range of variability in *Kouphichnium* behavioural reflecting tracks, even without including any of the types of supratidal trackways that horseshoe crabs make today along sandy beaches when laying their eggs that are presented in the experiments shown in Figure 15B.

Very similar unnamed arthropod trackways from the eastern border of the Massif Central (France), not previously identified or described in detail and only briefly documented but attributed to *Kouphichnium*, have been illustrated from Middle Triassic track slabs formed in intertidal sandy beach deposits that are also rich in vertebrate tracks (Demathieu, 1985). Comparable Middle Triassic subaquatic arthropod trails made by limulids found in Triassic–Jurassic deposits of America (Peabody, 1956; Morales, 1987; Hunt *et al.*, 1993; Harris & Lacovara, 2004), which have only been documented from small slabs and from a much more limited amount of material than at Bernburg, have also been found in association with a very similar, partly coastal, vertebrate track assemblage, similar to those in France (Demathieu, 1985) within the *Chirotherium* and *Isochirotherium* reptile track dominated ichnocoenosis. As at Bernburg, invertebrate half-swimming traces (Diedrich, 2009a) are also very common in the North American lower Middle Triassic Moenkopi Formation of northern Arizona (Peabody, 1956; Morales, 1987; Hunt *et al.*, 1993).

Such arthropod tracks have, to date, not been studied from any other 'Muschelkalk' sites in the Germanic Basin of Europe, although the extensive discoveries at Bernburg (Diedrich, 2009a) suggest that they now can be expected to be present at many of the 75 recently recognized German intertidal track

sites (Diedrich, 2009b) because, as mentioned previously, such arthropod tracks can easily be overlooked, especially when concentrating on vertebrate tracks.

EXPERIMENTS AND TRACK VARIABILITY

Neoichnological experiments with juvenile horseshoe crabs have previously been performed (Martin & Rindsberg, 2007), although there was also a need for experiments with modern adult horseshoe crabs on different substrates and moistures. No deeply printed 'classical *Kouphichnium* trackways' (Nopsca, 1923; Seilacher, 2008) on sand (Fig. 15B) have been found at Bernburg or anywhere else in the intertidal sediments of the Middle Triassic Germanic Basin. This emphasizes the importance of subaquatic locomotion modes on these intertidal flats and therefore supports the conclusion that they were used only as mating zones.

The 'comb-like' tracks (Fig. 15A, B) that are best preserved in the tracks on sandy sediments are horseshoe crab pusher-foot traces, which are only rarely well preserved in the Bernburg trackways and have been referred to in the past as 'bird or pterosaur footprint-like traces' (Nopsca, 1923; Seilacher, 2008). Between two and four parallel scratch marks were produced if the pusher-foot did not reach the ground during subaquatic swimming but simply scratched the surface (Fig. 15A, B), which would explain the origin of the 'Pusher-foot scratch-mark trackways type C'. In view of this interpretation, scratch marks from other Middle Triassic intertidal flat track sites, such as Borgholzhausen (Diedrich, 2002b) can, in several cases, now also be revised as being of horseshoe crab origins and not formed by reptile claws. Previous suggestions of a 'sauropterygian marine reptile origin' for the scratch marks at Bernburg (Diedrich, 2009a) must also be fully revised. None of the scratch marks in the present study can be attributed to either a marine reptile or the terrestrial reptile *Macrocnemus*.

The frequency of telson drag marks decreases from the subaerial walking to subaquatic swimming modus (Fig. 15B). This explains the almost total absence of telson drag marks in the 'Parallel pusher-foot imprint trackways type A'. In subaquatic locomotion under a covering of 15–25 cm of water (tidal scenario), the horseshoe crab trackway appears quite different from the classical '*Kouphichnium*', with only occasional telson drag marks preserved but with predominant pusher-foot impact marks, sometimes accompanied by imprints of the pusher-leg itself (Fig. 15B). The experiments were able to clarify that, with the incoming tide, horseshoe crabs first appear under very shallow water conditions, and then are eventually able to swim thereby leaving the scratch mark track-

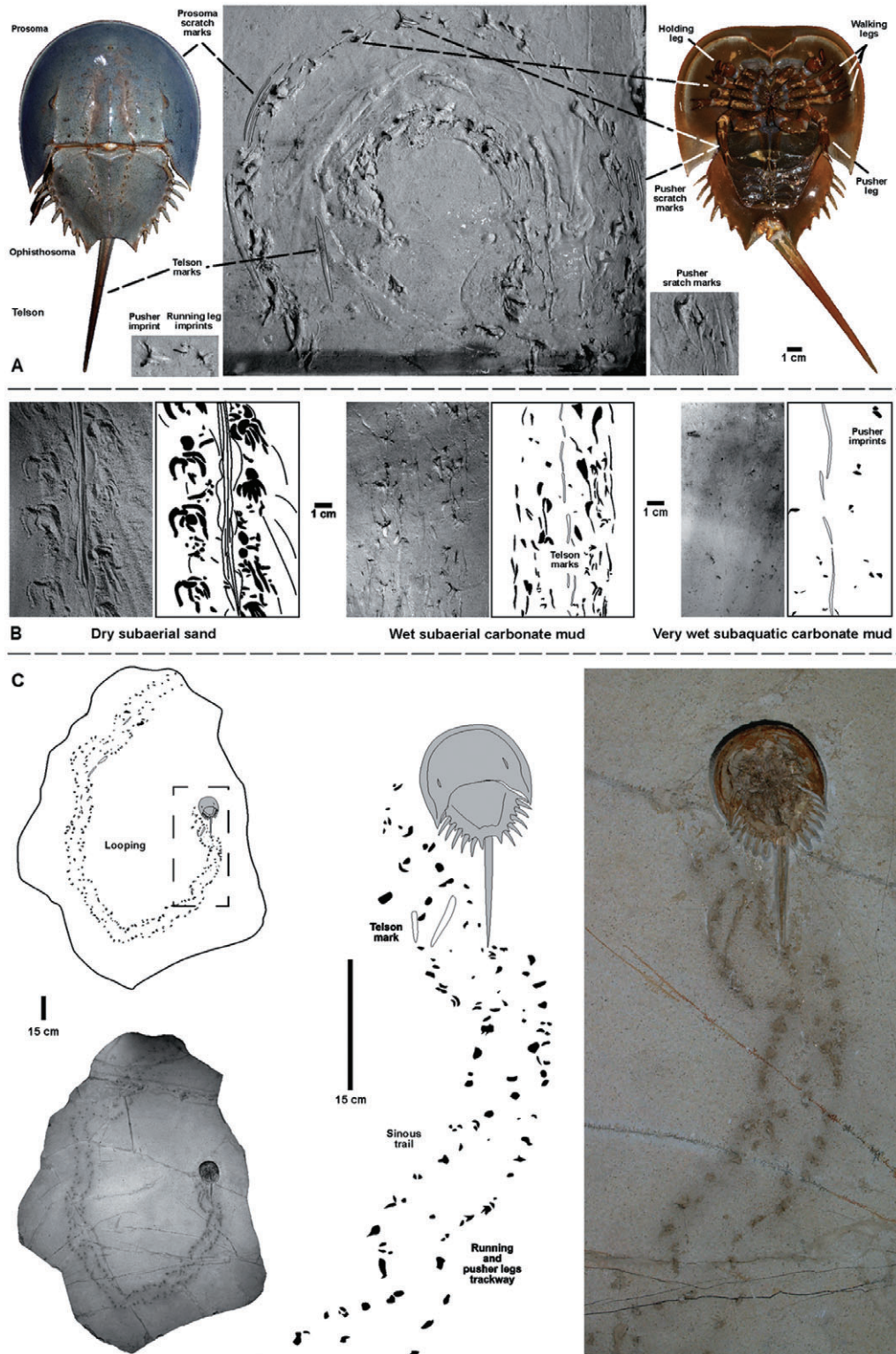


Figure 15. A, modern Japanese/Chinese horseshoe crab *Tachypleus tridentatus* Leach in dorsal and ventral views and its resulting traces and looping tracks. B, neoichnological trackway types of *Kouphichnium* Nopsca, 1923 produced by modern horseshoe crabs on different substrates. C, platy limestone slab with the subaquatic locomotion trackway of *Kouphichnium walchi* and its track-maker at the end, a *Mesolimulus walchi*, from the Upper Jurassic (Kimmeridgian) of southern Germany (coll. SBM exhibition (SBM = Senckenberg museum)).

way types. Finally, the experiments were also able to demonstrate the looping trackways produced by subaquatic-swimming horseshoe crabs, as well as the variety of traces and tracks produced by all other body parts (Fig. 15A).

THE PROBABLE HORSESHOE CRAB TRACK-MAKERS

The most probable track-maker was a limulid that lived, walked and swam along the sea floor, thereby leaving the trackways and traces that were first recognized in Germany and that were incorrectly described from the lagoonal platy limestones of Solnhofen as 'pterosaur trackways' (see history of this ichnotaxon in Schweigert & Dietl, 2002; Seilacher, 2008). These trackways exhibit traces of a typical limulid locomotion, in which the first large impressions were left by the feet on the last pair of legs, the pusher-legs (Seilacher, 2008). As the experiments have demonstrated, the Bernburg trackways are subaquatic, and are almost identical to the trackways on a slab of Upper Jurassic Solnhofen platy limestones on which the track-maker, a *Mesolimulus* horseshoe crab, was found at the end of a looping trackway (Fig. 15C). This trackway provides the main evidence that the Middle Triassic trackways at Bernburg were made by horseshoe crabs. Not only the trackways (Fig. 15), but also present-day horseshoe crabs are almost identical in shape to fossil horseshoe crabs as far back as 380 Mya, with the main difference being in their sizes which, on average, have increased over time. Although the maximum width of the 'front-shield' (prosoma) during the Middle Triassic (246–228 Mya) was only approximately 15 cm, it can reach approximately 30 cm in Neogene and modern specimens (Hauschke & Wilde, 1991). Limulids in the Middle Triassic Muschelkalk of Europe are known to have had a prosoma width that ranged from approximately 1 cm (Fig. 16D-1) up to approximately 15 cm (Fig. 16D-2) (Fritsch, 1906; Schmidt, 1928; Romero & Vía Boada, 1977; Hauschke & Wilde, 1991).

The earliest known limulids from the Middle Triassic 'Muschelkalk' of the European Germanic Basin at Winterswijk are known as ?*Limulitella* sp. (Hauschke *et al.*, 2009), which have been dated as Bithynian, lower Anisian (Diedrich, 2001), and horseshoe crab trackways newly reported in the present study from the same site, age, and intertidal facies can be attributed to *Kouphichnium*. Fritsch (1906) described *Limulus henkeli* (now *Limulitella henkeli sensu* Størmer, 1952) from the Lower Muschelkalk (?Wellenkalk facies) of the Jena Formation (Pelsonian, lower Anisian), and it may also occur in the slightly younger layers of the Diemel Formation (Illyrian, middle Anisian) at Bad Kösen (Thuringia, central Germany). A small limulid found at Laineck

near Bayreuth in the lower sabkha dolomites of the same Diemel Formation (mm5 substage, lower Illyrian, middle Anisian), with a prosoma width of only 1 cm, has been described as *Limulus priscus* Muenster & Graf, 1839; it was previously named *Limulus agnotus* (Muenster, 1839). These limulids were subsequently identified as juveniles by Størmer (1952), who changed the genus name to *Limulitella priscus*, although it is unclear whether those juveniles really belong to *Limulitella* or to the larger species from Spain discussed below. A very similar small limulid has been recorded more recently from the same facies and the same age at Ohrdruf-Hopbach in Thuringia, central Germany (Krause *et al.*, 2009; Fig. 16D-1). It is possible that the only species present in the Germanic Basin during the Lower and Middle Muschelkalk (Anisian) was *L. henkeli*.

Other material from the Upper Muschelkalk (Ladinian) has been described from the Alcover-Montral site in Spain, where large specimens of '*Heterolimulus*' *gadeai* have prosoma widths of approximately 15 cm (Vía Boada & de Villalta, 1966; Fig. 16D-2): from the point of view of size, these specimens would provide the best fit with the limulid trackways at Bernburg. This horseshoe crab body fossil genus is in need of revision but, in the present study, it is considered to be synonymous with *Tachypleus* because of its lateral immobile ophistosoma spines that are typical of this genus. Its genus is therefore changed preliminarily herein to *Tachypleus gadeai*. Two other smaller limulids with movable ophistosoma lateral spines have been described from the Muschelkalk in Spain: *Terracolimulus rieki* (Romero and Vía Boada, 1977) and *Mesolimulus crepelli* (Vía Boada, 1987a, b). As noted by Hauschke *et al.* (2009), a full revision of the Middle Triassic limulids is overdue, especially with respect to the recognizing different sized limulid body fossils as being juvenile and adult specimens of a few known genera. The intertidal flats of the Germanic basin may, however, have also been used by two different sized limulids.

HORSESHOE CRAB BEHAVIOUR

The trackways on Track Bed 7 at Bernburg are between 6 and 10 cm wide, with an average width of approximately 8 cm. From these measurements the prosoma width of the limulid track-makers can be estimated to have been between 10 and 15 cm, which would fit well with the size of fully grown adult *T. gadeai* limulids from the Middle Triassic of Spain (Vía Boada & de Villalta, 1966). All documented trackways from Track Bed 7 (Figs 9, 11) are therefore considered to be from large, fully grown or almost fully grown limulids of reproductive age.

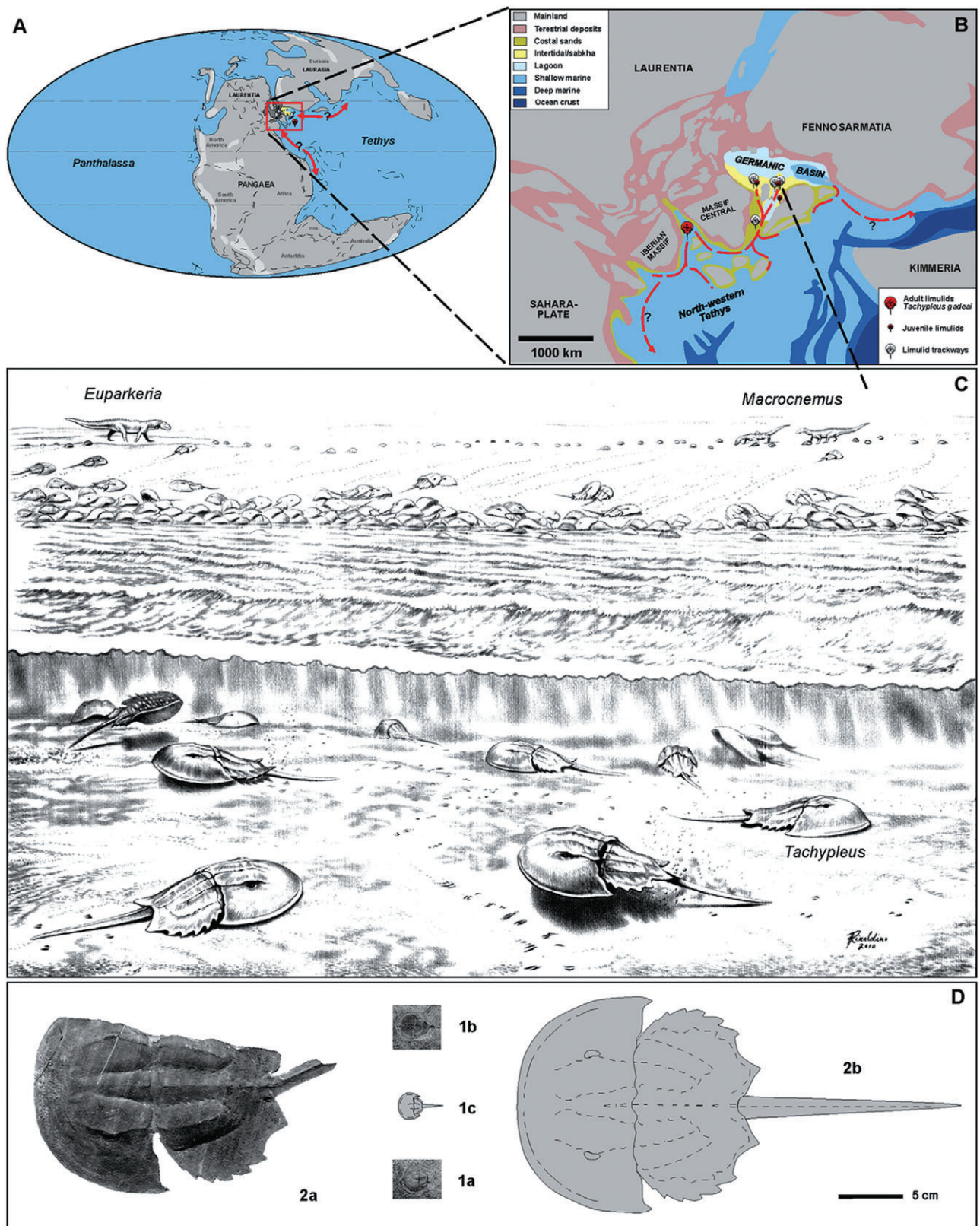


Figure 16. A, B, north-western Tethys and the connected cratonic, shallow marine Germanic Basin, with its extensive intertidal and sabkha zones during the Middle Triassic. Horseshoe crabs possibly migrated from the steeper coastal environments of the north-western Tethys for reproduction on the extensive, shallow ramp, intertidal zones of the Germanic Basin [Palaeogeography redrawn and compiled from Ziegler, 1982 (north-western Tethys) and Diedrich, 2009b (Germanic Basin)]. C. Flooding tide scenario on the shallow intertidal beach zone at Bernburg. Horseshoe crabs used this shallow water zone as a reproduction area, close to the supratidal beach areas. Small *Macrocnemus* reptiles (*Rhynchosauroides* track producer), as permanent intertidal inhabitants, appear to have fed on horseshoe crab eggs. These reptiles were in turn prey for the large archosaur predators such as *Euparkeria* (*Chirotherium* track producer), *Ticinosuchus* (*Isochirotherium* track producer) or *Arizonasaurus* (*Prosauropodichnus* track producer). D, 1a, b, c, small, probably juvenile, limulids preserved in dolomitic biolaminates from a lower sabkha facies in the Diemel Fm. (Illyrian, Middle Triassic) of Ohrdruf-Hopbach (Thuringia, central Germany; coll. NME) (a, negative; b, positive cast; c, reconstruction). 2. Large European limulid *Tachypleus gadeai* (Vía Boada & de Villalta, 1966) from the platy limestones (Ladinian, Middle Triassic) of Alcover-Montral (Tarragona, Spain; coll. MGSB) (a, positive cast; b, reconstruction).

The hypothesis proposed in the present study is that the intertidal mud flat area served as a mating zone but not as a breeding ground, as has been reported for modern situations (Lee, 2010), in that only adult forms were present for at least part of the time. This would explain the high level of variability in the trackway types, which are mainly from patrolling and half-swimming activities rather than from walking, as well as the scarcity of telson drag-marks. The breeding area must have been in the lower sabkha zone (close to the northern Rhenish Massif), above the regularly flooded intertidal zone, where tracks are less well preserved than they are in the biolaminates of the intertidal zone, although some vertebrate tracks have been reported (Diedrich, 2009a, b). Juvenile early Middle Muschelkalk limulid remains from this lower sabkha zone (dolomitic biolaminate facies) at Bad Kösen (Krause *et al.*, 2009) provide support for this theory, as do similar late Middle Muschelkalk discoveries from Bayreuth (Muenster, 1839; Størmer, 1952).

On the basis of published observations of modern horseshoe crabs (Brockmann & Penn, 1992), the trackways at Bernburg show no suggestion of sexual dimorphism, although this is probably a result of the state of preservation and problems in mapping the trackways, together with the small size and rare preservation (or rare observation) of running-leg foot imprints. Sexual dimorphism in modern horseshoe crabs is expressed by a difference in the first pair of running-legs (Brockmann & Penn, 1992), although it has not been possible to distinguish this in the trackways preserved at Bernburg. The front running-legs are small pincers that resemble those of crabs or scorpions, and these would have left the well documented Y-shaped imprints found both at Bernburg and at Bad Sulza (Fig. 5E, F). The first pair of running-legs in males, however, have distinctively shaped graspers that are adapted to hold on to the female during mating (Brockmann & Penn, 1992). At least one long mating trackway, in which a male was

on top of a female, appears to have been documented at Bernburg (Fig. 10E). This trackway started out with a similar form to most of the others as a normal limulid trackway, although the locomotion then changed in the middle of the trackway, after which the pusher-foot imprints became much more deeply impressed into the sediment and the motion started to alternate in an zigzagging fashion, presumably as a result of the increased weight on the female track-maker.

The illustration in Figure 16 of a horseshoe crab with different types of locomotion and swimming in different positions, matches well with other documented trackways. Swimming trackways have only two or three parallel scratch marks, which can be demonstrated to have been produced mainly by the pusher-foot appendages (Fig. 15A). The long, hyporelief drag marks were probably left by drifting carcasses (Fig. 14A, B). When running over a surface, limulids leave only the typical single or double kidney-shaped impressions that are produced by its pusher-feet and not by its other appendages (Fig. 13E). In a slower locomotion (but not a crawling motion) such as would be expected on the supratidal beaches, the impact marks of its running-leg feet have, in some cases, been preserved (Fig. 13D). One of the trackways may represent a feeding trackway, this being the trackway illustrated in Figure 12D, although the fact that this type of trackway is quite rare supports the possibility that this area may have been mainly a 'reproduction beach zone'. Observations of foraging Modern *Limulus* revealed that individual predators dig multiple pits during a single high tide, with little disturbance to the sediments in between (Lee, 2010), which is what appears to be the case in the trackway of Figure 12D. In most cases, however, running-leg foot prints do not appear to have been imprinted, which supports the interpretation that limulids arrived with the tide onto the extended carbonate flats, partly swimming and partly walking close to the bottom using mainly their

pusher-feet. This type of locomotion does not produce any telson drag-marks, and it also matches the trackways documented at Bernburg from which such marks are usually absent. Exactly the same trackway type (*K. walchi*), representing subaquatic locomotion, has been described previously (Caster, 1941; Malz, 1964) and is best documented in a fossil slab from the Upper Jurassic (Kimmeridgian) Solnhofen Plattenkalk of southern Germany in which, as mentioned previously, the *Mesolimulus walchi* trackmaker died and was preserved at the end of its looping and sinuous trackway (Fig. 15C).

PALAEOBIOGEOGRAPHY AND SEASONAL MIGRATION

In the Middle Triassic 'Muschelkalk' of the north-western Tethys, only medium-sized limulids such as the Spanish *T. gadeai* (Vía Boada & de Villalta, 1966) have dimensions that could match those of the Bernburg trackways. In the Germanic Basin, by contrast, only the very small *L. henkeli* and juvenile forms generally appear to be present, and these are only commonly found in lower sabkha deposits, not in intertidal mud flat zones. These observations compare favourably with the mating and reproductive behaviour of present-day horseshoe crabs, which congregate annually for reproduction in beach zones to which they return over many years (Brockmann & Penn, 1992; Almendral & Schoppe, 2005; Lee, 2010). This explains the high amount of horse shoe crab track beds within the Muschelkalk, and in more high resolution at Bernburg. Mating takes place in shallow water close to the beach, although the eggs are deposited in nests on the nearby nursery beach (Rudloe, 1980; Penn & Brockmann, 1994; Almendral & Schoppe, 2005; Lee, 2010).

The Germanic Basin was a intracratonic basin, with very shallow ramps and extensive intertidal and sabkha zones during the Lower and Middle Muschelkalk, providing an ideal environment for limulid reproduction in the very shallow waters of its extremely extensive, flat, intertidal zones. Such coastal areas would not have existed only at Bernburg: considering the Middle Triassic geometry of the Germanic Basin, and especially the central part of the basin, such favourable palaeoenvironments would have been present over hundreds of kilometres of intertidal flats extending east-west across the basin (Diedrich, 2008a, 2009a). From the fossil record, it would appear that, during the Middle Triassic, large limulids were only present in the north-western Tethys (in Spain), whereas only small or juvenile forms of these species were present in the Germanic Basin. Although it is only speculation at this stage, a model involving migration followed by mating (Fig. 16A, B, C) would provide the best explanation

for the unusual distribution of Middle Triassic horseshoe crab juvenile and adult body fossils, and their track records documented herein.

ACTUALISTIC COMPARISON WITH THE ECOLOGY OF PRESENT-DAY HORSESHOE CRABS

At present, there are four species of horseshoe crabs inhabiting different coastal areas of the earth's oceans. The most abundant species, which is also the best studied, is *Limulus polyphemus*, which is found from a latitude of approximately 42°N in southern Maine, extending southward along the east coast of North America and around the Gulf of Mexico to the Yucatan peninsula at approximately 19°N. Its peak abundance is in the Delaware Bay (Botton & Ropes, 1987; Shuster, Brockmann & Barlow, 2003). Two other species, *Tachypleus gigas* and *Carcinoscorpius rotundicauda*, live in the Indo-Pacific region and range from the Bay of Bengal to Indonesia and Borneo. The fourth species, *Tachypleus tridentatus*, used in the present study for trackway experiments, is found from the Philippines to the south-western Sea of Japan (Shuster *et al.*, 2003; Almendral & Schoppe, 2005), mating on mangrove beaches (Almendral & Schoppe, 2005).

The North Atlantic *L. polyphemus* species is most often found in the more saline parts of estuaries but is reported to be euryhaline (Shuster *et al.*, 2003), which is of interest because hypersaline situations were present during many periods in the development of the Germanic Basin, and especially during the deposition of the Karlstadt Formation in which the highest concentrations of limulid tracks occur. The biogeographic distribution of this *L. polyphemus* species appears to be similar to the population distribution of Middle Triassic limulids in that they also appear to have shown a biogeographic restriction to particular shallow marine habitats, in the north-western Tethys and Germanic Basin. Similarly, the population sizes of *L. polyphemus* show a distinct latitudinal gradient such that the larger animals and the largest population centres occur today in the Delaware Bay region of Delaware and New Jersey, whereas smaller animals are mainly found away from this area, both northward and southward toward the limits of its range (i.e. north of Cape Cod, and along the Florida coast and in the Gulf of Mexico) (Botton & Ropes, 1987). A similar difference in animal sizes and proportions appears to have existed during the Middle Triassic in Europe, when large limulids occurred in Spain but, in the Germanic Basin near the northern limit of their distribution, only small (juvenile) individuals have been found (Fig. 16A, B). It still remains unclear, however, whether there may have been two, or even three, different Middle Triassic species within this region.

Beach morphology and wave energy are important parameters in present-day reproductive zones of the horseshoe crab, as has been demonstrated for *L. polyphemus* in the USA from Delaware Bay to Florida (Smith *et al.*, 2002) where a strong relationship was observed between beach morphology and the quantity of live eggs found in surface sediments. Not only are beach morphology and wave energy associated with the quantity of eggs near the sediment surface, but, in bay-front beaches, horseshoe crabs also prefer to spawn on the more narrow, landward side of the beach, perhaps because of the reduced wave energy. These beaches also provide a quicker route back into shallow waters to escape from predators. Particular beach types may also be critical for protection from foraging shore birds (Smith *et al.*, 2002). By analogy with the modern situation, the low-relief intertidal zones and beaches of the Triassic Germanic Basin were similarly optimal for limulids, with their shallow and extensive intertidal flats that were perfect for reproduction, and their widespread availability, particularly during the Middle Triassic (Aegean to Illyrian) of the central Germanic Basin (Diedrich, 2009a). Horseshoe crabs are long-lived and slow to mature. Males reach sexual maturity between 9 and 11 years of age, and females mature between 10 and 12 years (Cohen & Brockmann, 1983). Their average life span is believed to be approximately 20–40 years (Botton & Ropes, 1987). Because the Bernburg trackway widths are all quite similar (including all 30–40 trackways mapped on Track Bed 7) and match the maximum sizes of *T. gadeai*, they were probably made by mature animals of reproductive age.

Both adult and juvenile horseshoe crabs employ 'epibenthic crawling' or 'hopping' as their primary means of locomotion (Smith *et al.*, 2002), as was confirmed in the track experiments (Fig. 15B), which explains why fossil trackways of this type predominate at Bernburg. Occasionally, a horseshoe crab will turn onto its back and swim upside-down, using its book-gills to propel itself through the water (Shuster *et al.*, 2003). Less of such behaviour, as in more passively drifting carcasses, would explain the long straight hyporelief trails at the Bernburg site, which are oriented at an angle of approximately 90° to seismically induced slickensides. Despite the inherent opportunity for wide-spread dispersion during their free-swimming stage, many horseshoe crab larvae have been shown to settle in shallow waters close to the beaches where they were spawned (Shuster *et al.*, 2003; Almendral & Schoppe, 2005; Botton, Tankersley & Loveland, 2010). The shallow intertidal habitats of the Germanic Basin have yielded, to date, only small, juvenile forms and no adult specimens. This bias toward the preservation of juvenile forms would appear to be perfectly compatible with a nesting beach environment. Although *L.*

polyphemus generally lives in sublittoral environments, it spawns near sandy beaches (Shuster *et al.*, 2003). This behaviour explains the presence of abundant adult trackways in the shallow, water-covered intertidal zones of the Germanic Basin. Unfortunately, there is no record left of the carbonate sand beach environments because they have been removed by post-Triassic erosion. In the spring, *Limulus* males, which often outnumber females many times over, patrol along the foot of the beach waiting for the arrival of females (Shuster *et al.*, 2003). Such fossil patrol trails of 'swimming-hopping' locomotion, which appear to be the most common type of trail represented in the Bernburg intertidal zones, are very similar to the trails that were produced in the modern horseshoe crab experiments. Horseshoe crabs typically locate mates, achieve amplexus, and then migrate to the high tide mark in the intertidal zone to deposit and fertilize eggs before returning to deeper water at the end of the spawning season (Shuster *et al.*, 2003).

ARCHOSAUR PREDATION ON HORSESHOE CRABS AND THEIR EGGS

For the first time in the global fossil record, the possible predation by a carnivorous thecodont archosaur (possibly *Euparkeria*, or a related species) on a horseshoe crab has been documented, in the same track-rich layer at Bernburg on which the other trackways described herein were mapped (Fig. 10). It remains unclear, however, whether the archosaur was actually feeding on the limulid or just playing with it. The oval depressions within the ichnites appear to have been left as a result of the front foot of the archosaur being used to trap the horseshoe crab, although it is also possible that these depressions were left by the animal's snout as it tried to catch and feed on the limulid. The prey must have remained alive for quite a long time, perhaps in a protected alive position on the biolaminates, where the archosaur may have trodden on the crab and then tried to flip it onto its back. Trapped and under stress, the limulid appears to have tried to escape, used its running-legs in a rapid circular motion that produced the large number of prints observed. The deep claw marks from the archosaur's manus that are all around the activity zone may have been a result of it treading on the crab to hold it down or, as noted above, trying to flip it over. These unique traces therefore appear to indicate a thecodont archosaur (*Chirotherium*) track-maker trying to feed on a living horseshoe crab. From this 'feeding place', the archosaur continued on its hind legs for first few steps: the pes imprints are very closely spaced and there are no manus imprints. The archosaur possibly remained on its hind legs to be able to raise its head and swallow the horseshoe crab.

Thecodont archosaurs are well represented in the same layer of Track Bed 7, forming a restricted, lower intertidal, *Rhynchosauroides/Chirotherium/Kouphichnium* dominated ichnocoenosis on the mud-cracked biolaminates (Diedrich, 2009a, 2011). The predation of thecodont archosaurs that are approximately 2 m long on horseshoe crabs is, however, quite astonishing and unexpected, although it supports the theory of a chain reaction to the horseshoe crab migrations within Pangaeian archosaur populations which, together with other small reptiles, appear to have fed on the crabs or on their eggs (Diedrich, 2011).

Present-day predators (especially seabirds) do not feed on horseshoe crabs when they are on their reproductive beaches but, instead, focus on the abundant horseshoe crab eggs for their nutrition (Crenson, 2003). The ecological niche filled today by seabirds deriving their nourishment from the eggs of thousands of horseshoe crabs was, during the Middle Triassic of Europe, filled by small reptiles such as *Macrocnemus* and *Hescheleria*, whose presence is demonstrated by 'millions of footprints' (*Rhynchosauroides*, *Procolophonichnium*; Diedrich, 2001, 2002a, b, 2008a, b, 2009a, b, 2010a, b, 2011) and abundant long *Rhynchosauroides* trackways on the Bernburg horseshoe crab trackway bed (Diedrich, 2009a). These small reptiles, which were abundant in this plant-free intertidal palaeoenvironment, may in turn have been food for small to very large carnivorous thecodont archosaurs such as *Euparkeria* and *Ticinosuchus* (Diedrich, 2011), which are also documented by perfectly preserved footprints and long trackways on Track Bed 7, the same limulid track-rich horizon at Bernburg. The bones and skeletons of these thecodont archosaurs have also been occasionally found in different parts of Pangaea (Diedrich, 2011). The above-mentioned site suggesting predation on (or playing with) a horseshoe crab would also appear to support the suggested feeding of thecodont archosaurs on invertebrates. Finally, other reptiles (aquatic sauropterygians, such as *Nothosaurus*, *Serpianosaurus* or *Anarosaurus*) whose presence at Bernburg has been demonstrated by discoveries of bones (Diedrich, 2009a) and skeletons not far away at Heteborn (Diedrich & Trostheide, 2007), may also have derived some of their nutrition from horseshoe crab eggs laid in the shallow marine intertidal zones (Fig. 16C).

CONCLUSIONS

Horseshoe crab tracks have been recorded from several German sites indicating a megatracksite covering some hundreds of kilometres of intertidal carbonate mudflats within the central Germanic Basin of Europe. The widespread distribution of these carbonate tidal flat megatracksites during the basin's development

between 248.6 and 243 Mya suggests that the tidal zones surrounding the Germanic Basin were regularly used by horseshoe crabs as mating and reproduction areas. This has best been documented in the Bernburg section, where many horseshoe crab track layers occur within a 2.5-m thick biolaminate/arenite sequence. The orientation of stress fracture overlapping mud cracks in the tsunamite overlying the slickensided, seismically influenced carbonates is also at 90° to the current direction, supporting the interpretation of submarine earthquakes and small-scale tsunami waves that might nevertheless be dangerous for horseshoe crab and archosaur populations on such low-relief tidal flats. The presence of approximately 19 slickensided layers within the Karlstadt Formation indicates the repetitive nature of these unique dangers presented to horseshoe crab reproduction areas by the initial phases of Alpine tectonic activity.

The abundant horse shoe crab trackways of the *Kouphichnium* Nopsca, 1923 ichnogenus found in several layers of the Karlstadt Formation (upper Pelsonian, Anisian, Middle Triassic) at Bernburg have provided a rare insight into the intertidal flat palaeoenvironments of central Europe, as well as their invertebrate and vertebrate ecosystems and interactions.

Trackway experiments with a modern horseshoe crab (*Tachypleus tridentatus*) on sand and very fine-grained intertidal carbonate sediments with different moisture and water coverage have confirmed that the mapped trackways were not formed subaerially, but rather that they were all formed by subaquatic locomotion, possibly during limulid migration onto the tidal flats with a single flooding tide. The three main track shape types most closely match those associated with swimming-hopping motions, during which the crabs mostly left only pusher-foot imprints, with occasional prosoma scratch marks and rare telson drag-marks or running-leg footprints. In some cases, full-swimming trackway types are evident, documented solely by parallel scratch marks from the pusher appendices. In addition, traces that appear to have been left by carcasses drifting towards the north-west provide an indication of current direction, with many horseshoe crab 'patrolling trackways' running at 90° to the interpreted current direction (i.e. running north-east-south-west).

The broad trackway widths of between 6 and 10 cm indicate the presence of only large, 'reproduction sized' individuals. These trackways of limulids with prosomas 10–15 cm wide may have been left by the largest known European Middle Triassic limulid *T. gadeai*, which must have been present throughout the Germanic Basin even though this cannot be demonstrated from the body fossil record. Horseshoe crab body fossils appear to have mainly drifted with the daily tides onto

the lower and upper supratidal sabkha environments, where they are occasionally found in Europe. In the lower sabkha facies, which was only periodically flooded, small individuals with prosomas 1–2 cm wide, apparently representing only juvenile forms, are known from three German localities within the Lower to Middle Muschelkalk of the Germanic Basin where extensive intertidal zones were present along the distal shallow carbonate ramps.

Additional trackways and traces attributable to limulids can be reported from several sites in the present study, in intertidal facies of a similar age, supporting the theory that the extensive intertidal mud flat zones in the central Germanic Basin served as reproductive areas for large populations of limulids that may have migrated to these areas from the northern Tethys Sea over the Burgundian and Silesian Gates. Large Muschelkalk horseshoe crab species in the north-western Tethys of Spain are therefore possible track-makers for the Bernburg *Kouphichnium* trackways. The abundant horseshoe crab trackways of Bernburg, together with similar discoveries across the entire central Germanic Basin, support the idea of an extensive coastal, shallow, intertidal, beach reproductive zone along which patrolling males left many trackways, with circling tracks and evidence of attachment to other individuals also appearing to indicate an intertidal beach mating zone.

From comparisons with present day situations, it is likely that millions of horseshoe crab eggs have been produced in these reproductive areas. These eggs would then have provided a major food source for higher-trophic-level consumers in the coastal zone food-chain, offering a good explanation for the abundance of trackways from small, coastal-dwelling reptiles, such as *Macrocnemus* (*Rhynchosauroides* trackways), which were probably seasonally dependant on these eggs as a major food source. At the Bernburg site, there is also evidence of an unusually large number of larger reptilian thecodont archosaur predators, in the form of *Chirotherium*, *Isochirotherium* or *Prosauropodichnus* trackways, suggesting that these predators may have hunted the smaller reptiles. A unique record of traces that appear to have been formed by a thecodont archosaur feeding on a horseshoe crab provides the first evidence world-wide that horseshoe crabs may have formed part of thecodont archosaurs diet, and may possibly also explain the seasonal migrations of these Pangaeen predators.

Fossil bones of small to medium-sized shallow marine sauropterygian reptiles are relatively common in the Germanic Basin, and have also been found in various layers at Bernburg, with some even washed into in some chirotherid footprints, such as recorded with *Pachypleurosaurus*, *Serpianosaurus*, and *Notho-*

saurus. Those shallow marine reptiles might also have consumed horse shoe crabs or at least their eggs.

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