

Millions of reptile tracks—Early to Middle Triassic carbonate tidal flat migration bridges of Central Europe—reptile immigration into the Germanic Basin

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Abstract

Discoveries of vertebrate track sites in Central Europe have occurred in 75 localities in carbonate tidal flats of the Middle Triassic. In the Germanic Basin carbonate tidal flats were wide-span mapped, resulting in the finding of millions of small- to medium-sized reptile tracks. In the west of the basin the sediment of the Lower Muschelkalk to basal Upper Muschelkalk contains at least 21 track horizons, whereas in the eastern part more typically marine conditions were present. Here, tidal flats with additional track beds started earlier during the Upper Bunter and demonstrated marine ingression from the eastern Silesian gate. During low stands these tidal flats comprised inter-peninsula bridges, which allowed migration of reptiles. Only two medium to small prolacertilian reptiles, which were fully adapted to these environments, left any kind of track. A large thecodont reptile such as *Euparkeria* was the potential predator that may rarely have hunted the main small trackmakers *Macrocnemus* and *Hescherleria*.

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1. Introduction

The first tracks in the Bunter (Lower Triassic) of Europe were found in 1834 in siliciclastic fluvial environments of a red desert landscape in Central Europe. These became the famous “hand of ferocious animal” *Chirotherium* footprints, the oldest reported reptile tracks in the world (Sickler 1834). Many geoscientists and collectors in Europe tried to find vertebrate tracks in terrestrial environments; numerous tracks were found in the Carboniferous, Permian, Lower

and Upper Triassic—but always in sandy or terrestrial environments, which were influenced by fresh water.

In 1958, tracks were found for the first time in limestone sediments of the Dutch locality Winterswijk (Faber, 1958). This remained for some time the only locality in which different track types were recognized (Demathieu, Oosterink, 1983, 1988) and also showed a diverse, mainly marine-adapted, vertebrate fauna (Oosterink, et al. 2003). The track bed age was initially unclear, but was thought to be from the Lower Muschelkalk (Middle Triassic); this was verified much later by detailed track bed and stratigraphic work (Diedrich, 2001a). This section of Winterswijk contains the boundary from the Upper Bunter up to the Oolitic

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Zone (Lower Muschelkalk) and about 11 track beds (Diedrich, 2001a). A second site was discovered in 1970 at Haarmühle in north-western Germany (Holst et al., 1970), the exact stratigraphic position of which in the Lower Muschelkalk is still unknown. Much later, in 1996, a new site was found by chance in Borgholzhausen in north-western Germany and was excavated systematically (Diedrich, 2000a,b). From this location systematic prospecting were initiated to the east and west, which were relatively successful. Many of these sites provided new information on ichnotaxonomy, and, more importantly, detailed ichnofacies analyses (Diedrich, 1998a).

In the last 10 years, approximately 75 new track sites (Fig. 1) have been found by the “Middle Triassic megatrack site Project of Europe” (Diedrich, 1998a,b, 2000a,b, 2001a,b,c, 2002a,b,c, 2005, 2006). It became clear quite early on that tracks could be found only in biolaminates. Such fossil microbial mats went almost unrecognized, and generations of geologists who described hundreds of sections and outcrops, the

sedimentology, stratigraphy and fossil content of the “Germanic Muschelkalk”, nevertheless overlooked millions of small reptile tracks.

This was astonishing, but one explanation is that no one expected tracks in marine environments, and especially not in the “well known and studied” Germanic Muschelkalk. Therefore none of the researchers looked for the tracks, which indeed are often difficult to identify. More surprising is the enormous density of small reptile tracks found, which was demonstrated in the first detailed track mappings at Borgholzhausen (Diedrich, 2002b). There must be millions of tracks preserved in the special environment of the lower and upper intertidal to lower sabkha environment of the coastal zone of the southern Germanic Basin.

2. Materials and methods

Seventy-five quarries were found in Germany in which track bearing biolaminates occur. Only one, in The Netherlands, had been previously discovered.

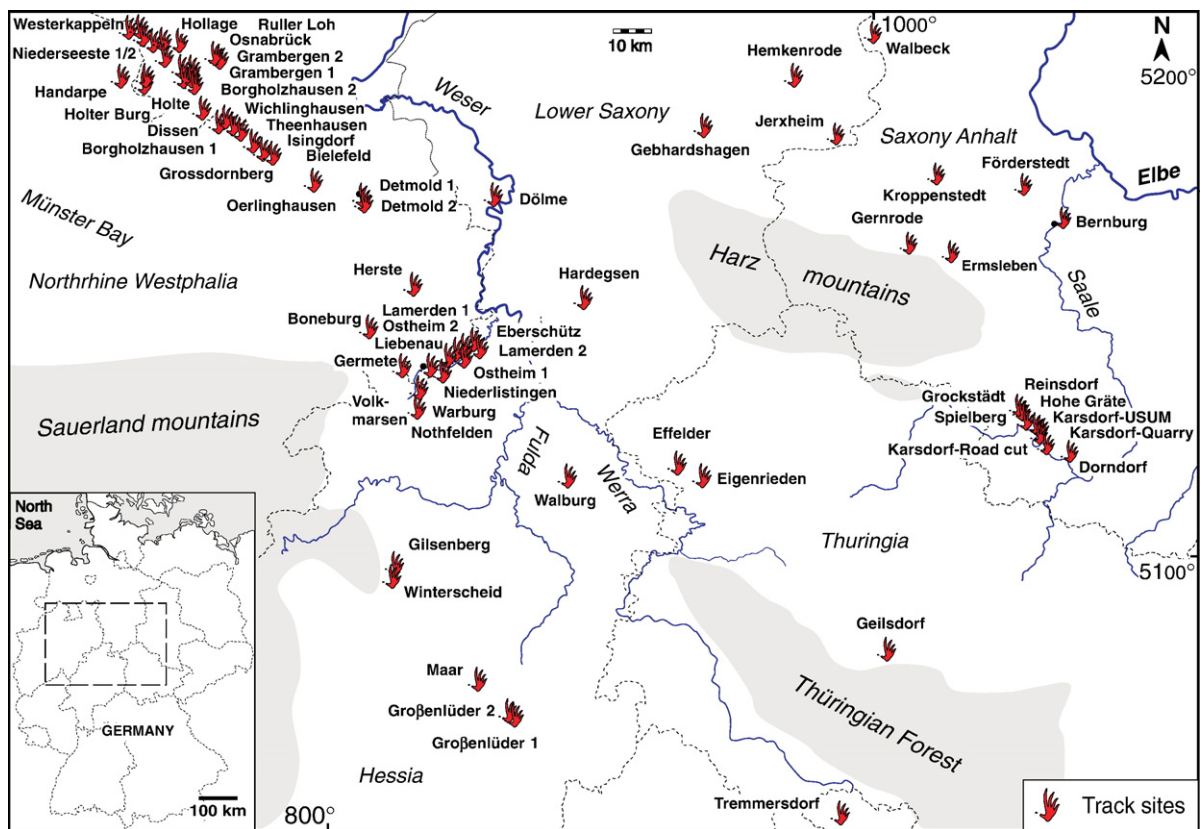


Fig. 1. Seventy-five Triassic track sites in fossilized carbonate tidal flat limestones. Here reptiles migrated from the Bohemian Massif to the Rhenish Massif—an inter-peninsula faunal exchange over tidal zones. Two different small reptiles lived permanently in these tidal flats and left millions of tracks.

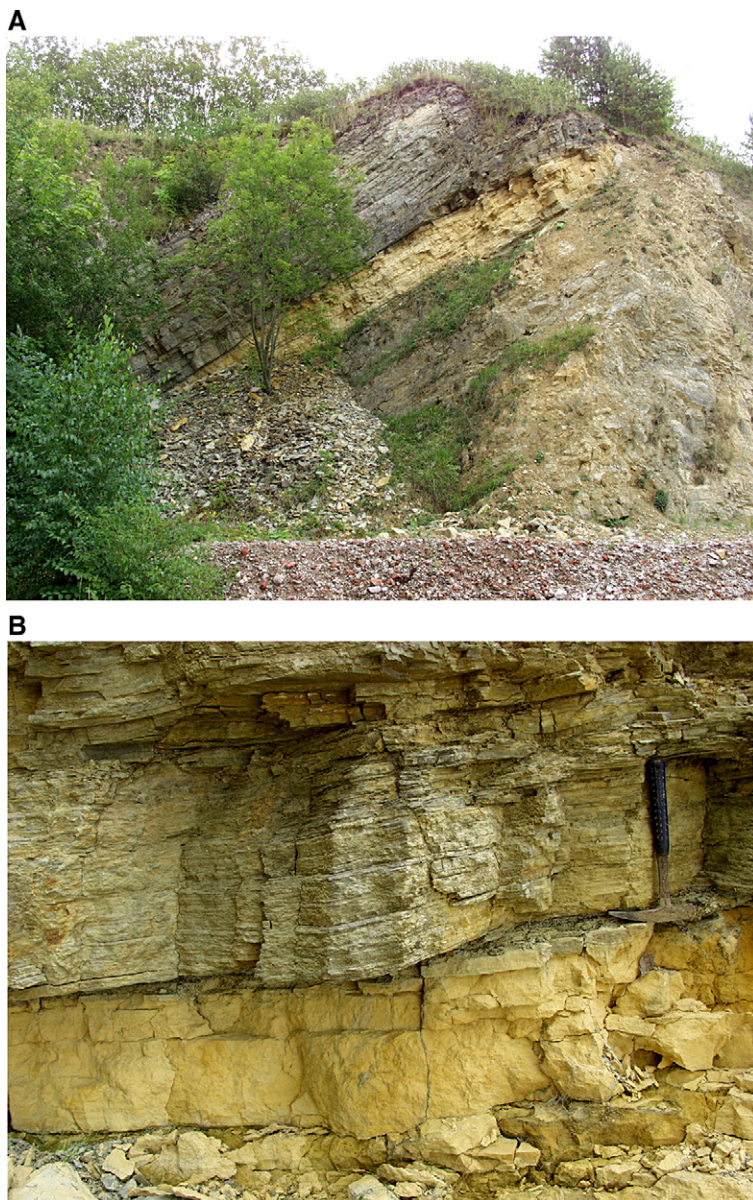


Fig. 2. A. Yellow dolomites of the sabkha facies in the Lower Muschelkalk (muW3 top) of northern Germany (quarry Hardeggen, Lower Saxony). B. The dolomites are overlain by 60 cm thick mud cracked biolaminates (track bed XIV, see Fig. 1), in which several track horizons of *Rhyncho-sauroides* and *Procolophonichnium* were found. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Systematic prospecting between 1996 and 2007 followed similar sediments, mud cracked biolaminates, which are relatively easy to distinguish from other sediments in the Muschelkalk of the Triassic marine intertidal carbonates. In those several thousands of tracks were found, of which in most cases tracks were taken from vertical sections. In a few places such as Winterswijk, Borgholzhausen, Detmold, Großenlütder or Bernburg track slabs of a few square meters were

rescued, especially in active quarries. At those mentioned few sites systematic surface excavations were possible. Here the important trackways were mapped; an attempt was made to map at least six manus/pes sets for speed and other characteristics of the trackmaker. The mapping indicated different facies zones with different track associations (ichnocoenosis types). Actuopalaeontological experiments were carried out in the carbonate tidal flats south of the Arabian Gulf in the United Arab

Emirates (UAE), using the modern *Iguana* and *Uromastix* to produce similar tracks to those found in the Triassic record. Production of recent tracks that are similar to the fossils allows details of the anatomy, speed, type of locomotion (such as slow or fast moving) and swimming activities of the trackmaker to be deduced from the fossil record. At all track sites the stratigraphical high-resolution work, combined with information about the sedimentology and fossil content (invertebrates, ichnology, vertebrates), resulted in regional and international correlations of track beds over hundreds of kilometres. This work was the basis for the development of megatrack site and palaeogeographical maps. Finally, the dating was supported by the few Ceratite finds, which helped to create a general track horizon stratigraphy in the entire southern Germanic Basin. These cephalopods are important in correlating the track beds of the Germanic Basin with sediments of the northern Tethyan realm, especially the Alps, but also with the eastern Germanic Basin (Upper Silesia).

3. Geology and environment

The track sediments were consistently biolaminates, the products of cyanobacterial and algal mats in the intertidal zones. These track rich sediments are often found close to the yellow dolomites of the sabkha facies. Both environments occurred close together and overlapped as a result of eustatic and facies changes, which were tectonically controlled. The millimetre-thick bedded biolaminate limestones occasionally, of which some thin sections were made, built up to 2.5 m thick laminate packages, whereas in most cases they are between 10 and 80 cm thick. In many cases the biolaminates are in close contact stratigraphically to yellow dolomites (Fig. 2A–B). This results in two facies types, the sabkha and the tidal flats, being adjacent. During flooding or regression, changes occur in these facies, which can be observed at many locations in Germany. Only on mud cracked biolaminates are tracks preserved (Fig. 3), as a result of rapid drying and the early diagenetic cementation processes of the microbial mats after tide regressions.

The study of 75 track sections in Central Europe has shown the high complexity of carbonate tidal flat megatrack sites (Fig. 4), which range from the Bithynian (Upper Bunter/*Myophoria* Beds) to the basal Anisian (Lower Upper Muschelkalk), with a maximum of 31 track beds (Fig. 4). The more westernly within the basin the sections, the more track beds were found to be present (Diedrich, 2006).

In the Winterswijk locality, the highest density of track beds is present in the Upper Bunter to basal

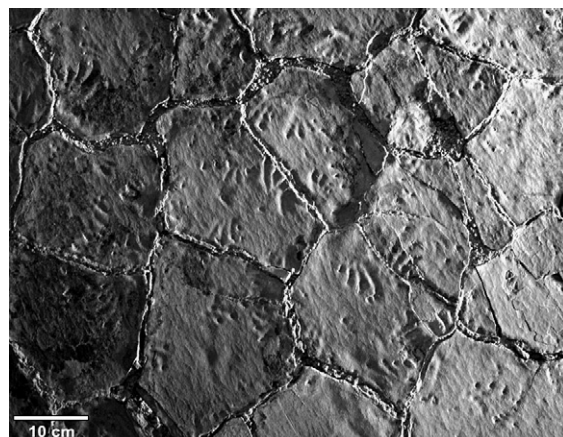
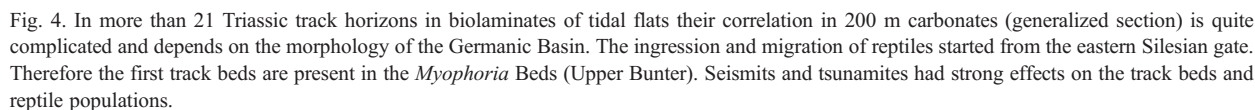


Fig. 3. Mud cracked Middle Triassic (Lower Muschelkalk, Oolitic Zone) biolaminates with many imprints of *Rhynchosauroides* tracks from Borgholzhausen, north-western Germany (= *Rhynchosauroides* ichnofacies).

Lower Muschelkalk, as a result of the mainly flat tidal conditions in this region, the western flat ramp margin. In the Osnabrücker Bergland, Teutoburger Wald and northern Hessa of northern Germany 27 track beds were dated precisely using high-resolution stratigraphy, including rare cephalopods (cf. Wunsch, 1960; Urlichs, Mundlos, 1985; Kaim, Niedzwiedzki, 1999), as biozone fossils in the Lower Muschelkalk (Diedrich, 2006) and uppermost Bunter (*Myophoria* Member). The track horizon number decreases towards central Germany (central Hessa, Thuringia, Saxony Anhalt), whereas in the centre of the basin the “Hessa/Thuringia Depression” (Fig. 1) has been under subtidal marine conditions since the Bunter/Muschelkalk boundary marine ingression. No tidal flats have developed here and therefore tracks are absent. The southern basin coast seems to be influenced excessively by siliciclastic sediments, which prevented a facies development of carbonate tidal flats (Hagdorn et al., 1987).

A recent analogue of the Triassic intercontinental Lower Muschelkalk Basin is the Persian Gulf (Knaust, 1997). Here similar track types and preservations of the Middle Triassic Ichnogenus *Rhynchosauroides* were produced in an experiment in carbonate tidal flats of the UAE using the lizard *Iguana* (Diedrich and Gardner, 2004). Those demonstrated different degrees of preservation and locomotion types, comprising basking, slow movements, fast movements and even subaquatic movement and swimming (Fig. 5), of the Triassic trackmakers that left the *Rhynchosauroides* trackways (Diedrich, 2005).



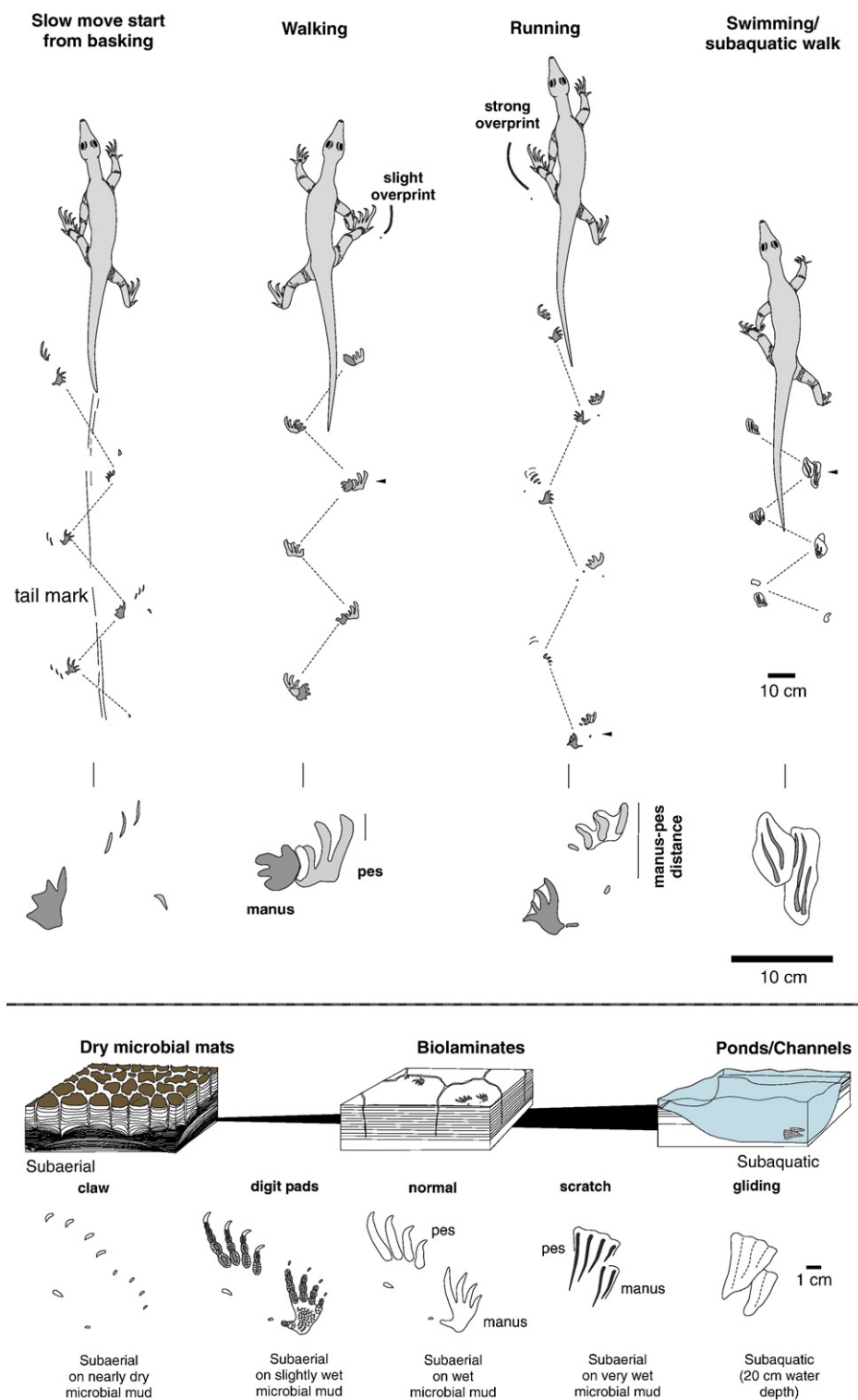


Fig. 5. Trackway preservation and different moving activities from slow movement, to fast movement and up to swimming of the track ichnospecies *Rhynchosauroides*.

4. Track types and their possible trackmakers

Trackways of *Rhynchosauroides* were mapped at systematically excavated sites such as Winterswijk (Diedrich and Oosterink, 2000), Borgholzhausen (Diedrich, 2002b) and Großenlütder (Diedrich and Fichter, 2003). In most cases *Rhynchosauroides* trackways lack tail marks in all three trackway types (slow or fast movements and swimming activities). In only one case was a tail mark observed, this could have marked the transition from basking to slow movement. It may be the result of an incomplete tail. If the prolacertilian *Macrocnemus* is believed to be the trackmaker, the anatomy represented in earlier illustrations must be corrected.

These track types also occur in the Triassic of the Alps (Abel, 1926), and were ascribed to the same trackmaker (Avanzini and Renesto, 2002). In both regions the sediments are from coastal zones, but the preservation of the tracks is quite different as a result of different substrates and facies. *R. tirolicus* (Abel 1926) (created for the alpine sites) and *R. peabodyi* (Faber 1958) (created for the Dutch site) appear to represent only a single track ichnospecies (Fig. 5).

Unique to this Middle Triassic track is the “overstepping” of the hind limb over the forelimb. It gives evidence for the long legs of the trackmaker. The long-legged trackmaker *M. bassani* was found in the Middle Triassic, with a few skeletons in the black shales of the Monte San Giorgio (Switzerland) (Peyer, 1937). *Macrocnemus* must have lived primarily in the coastal zones, on sandy beaches or carbonate tidal flat facies, where it left millions of tracks and trackways. This species walked with its pelvic girdle elevated, therefore the long legs are consistent with the tail-less trackway types. This medium-sized reptile, which was about 1.2 m long, was adapted to beach zones and could swim or walk through tidal ponds and channels. Populations of juvenile to adult animals searched here for food, possibly small crustaceans (Diedrich and Schulz, 2003) and other marine invertebrates, or even fish carrion. The main activity zone of this prolacertilian was the lower intertidal zone of the carbonate tidal flats, close to the ocean. The *Rhynchosauroides*-ichnofacies types provide evidence for this (Diedrich, 1998a,b, 2002b.). *Macrocnemus* most probably fed on freshly drifted food directly in the splashing zone.

The second small common track type, *Procolophonichnium* (Demathieu and Oosterink, 1988), was a little smaller and generally showed the characteristic sinuous tail mark (Fig. 6), which indicates, together with the normal lacertoid footprint order (fore foot behind hind foot imprint), a different reptilian anatomy. *Procolopho-*

nichnium harmühlensis (Holst et al., 1970) is synonymous with the later-described Dutch find of *P. winterswijkensis* (Demathieu and Oosterink, 1988). Ichnofacies analyses and mappings prove this smaller reptile to have lived more in the dryer upper intertidal zone (Diedrich, 1998a,b, 2002b). Here they left very dense trampled mud cracked biolaminates, but often only their claw marks, which is a further reason for their late discovery at many other localities. The track preservation types were proved to be similar to those of *Rhynchosauroides*. Again, subaquatic, slow movement and running was documented on trackways from different sites (Diedrich, 1998a,b, 2002b). An important reptile find is a single disarticulated skeleton of the most probably *Procolophonichnium* trackmaker from the Anisian/Ladinian boundary in the Black Shales of the Monte San Giorgio, which Peyer (1936) described as *Hescherleria ruebeli*. Other Dutch skeleton finds in-between the Lower Muschelkalk biolaminates are only from aquatic sauropterygians (Oosterink et al., 2003). The pedal anatomy of the Swiss find is consistent with the track type of *Procolophonichnium*, also, the body size matches the trackways. It can be demonstrated that these reptiles lived permanently in coastal beach environments, especially carbonate tidal flats, where they searched for food.

Other tracks are very rare in carbonate tidal flats (Fig. 7) and are each represented only by a single footprint or part of a trackway. *Brachychirotherium paraparvum* (Demathieu and Oosterink, 1988) has been found in Winterswijk (The Netherlands, boundary of Bunter/Lower Muschelkalk) and in Germete (Germany, Grenzgelbkalk Member, basal Upper Muschelkalk), which shows the wide stratigraphical range of this rare chirotherid track type. In the latter location it was imprinted in sediments of the lower sabkha facies, whereas it was found in lower intertidal mud cracked biolaminates in The Netherlands. Here the preservation shows a gliding motion, and proves the difficulty of moving on slimy microbial mats and tidal flat environments for the large protosuchid trackmaker (cf. Demathieu and Haubold, 1974). It appears that only in extreme situations, such as times of seasonal migration times or lack of prey, did these largest of Triassic carnivores step onto the tidal muds. Hunting of the first two trackmakers described could have been the reason for the presence of *Euparkeria* or *Ticinosuchus*, which have been found in Europe (Krebs, 1965; Ewer, 1965; Kuhn, 1971).

Coelurosaurichnus ratumensis (Demathieu and Oosterink 1988) is another large rare track, which has been recorded from the boundary Bunter/Lower Muschelkalk of Winterswijk, referred here to *Isochirotherium* tracks,

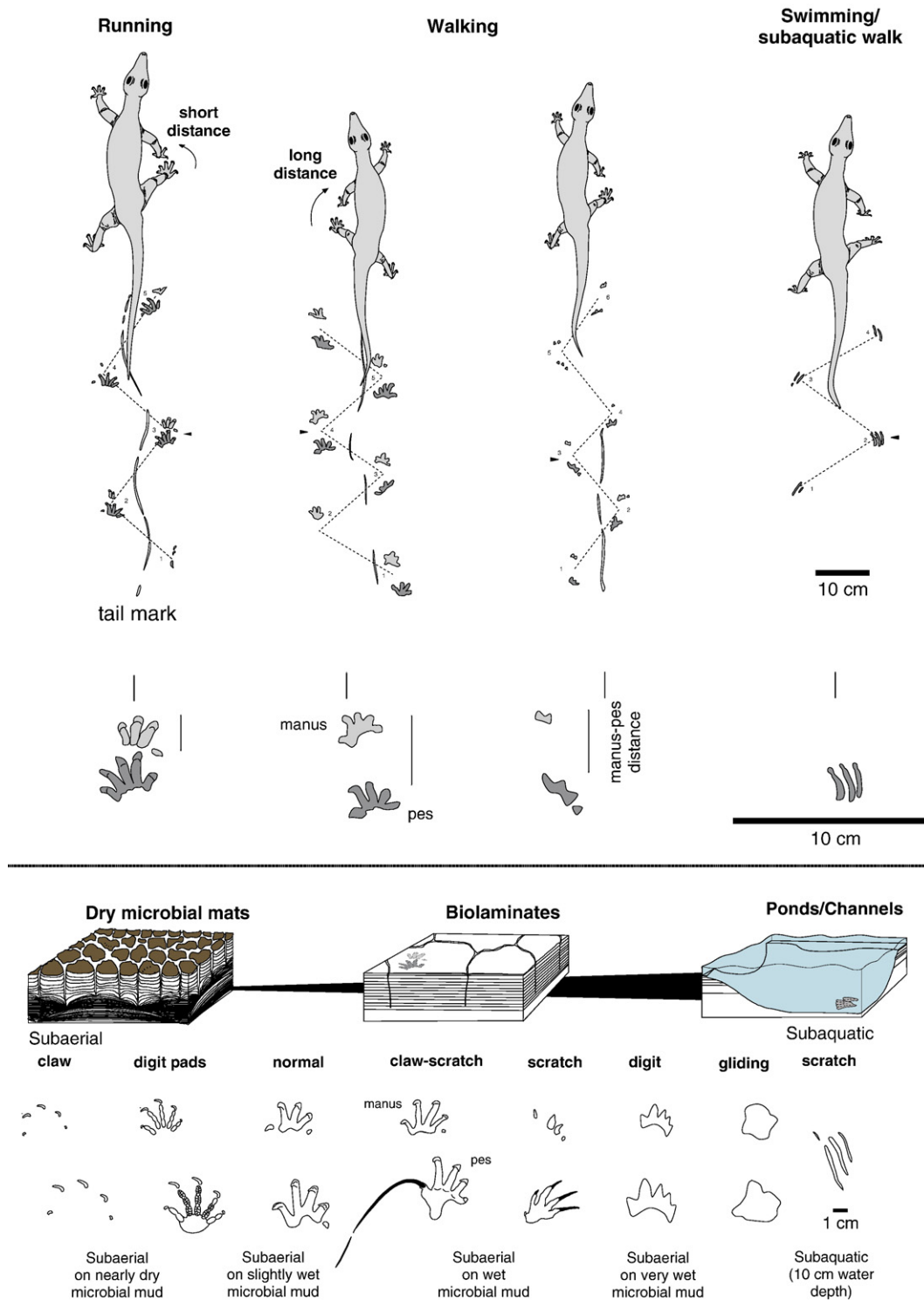


Fig. 6. Trackway preservation and different movement activities from slow movement, to fast movement and up to swimming for the track ichnospecies *Procolophonichnium*.

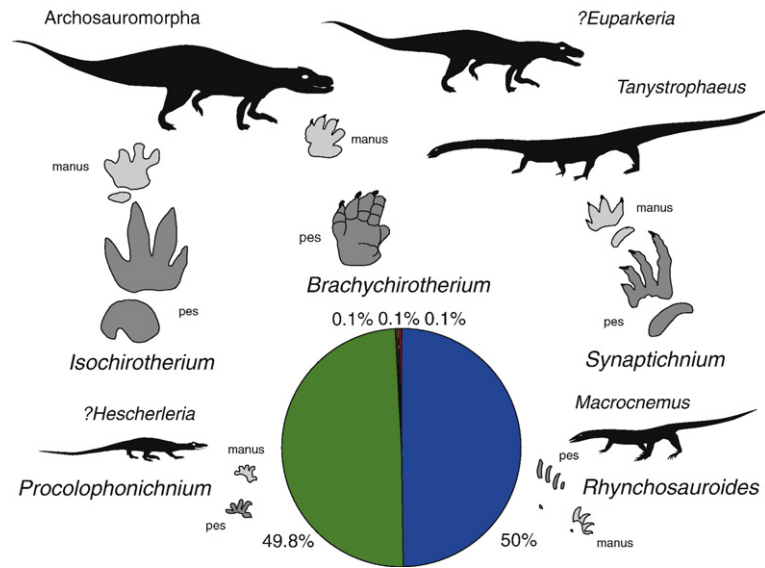


Fig. 7. In the carbonate tidal flats of the Lower/Middle Triassic (Muschelkalk) the two track ichnogenera *Rhynchosauroides* and *Procolophonichnium* predominate. The large predator tracks of *Brachychirotherium* are rare. Other tracks are represented only by single prints of unidentified trackmakers ($N=1.200$ tracks).

were found in a similar old strata (Basalkonglomerate Member, Lower Muchelkalk) of Central Germany (Diedrich and Fichter, 2003). It has been suggested recently that *Tanystropheus antiquus*, which was demonstrated by the presence of bone material in the Lower Muschelkalk of The Netherlands and Germany (Oosterink et al. 2003), could have been the trackmaker of *Synaptichnium* tracks.

Finally, the question of the tracks and traces of the abundant marine sauropterygians remains open. *Placodus*, *Nothosaurus*, *Cymatosaurus*, *Pachypleurosaurus*, *Serpianosaurus* and *Anarosaurus* are common aquatic adapted reptiles, which were found not only in the carbonates of Winterswijk (Oosterink et al. 2003) but also in different German and Polish uppermost Lower to Middle Triassic marine influenced areas (Rieppel, 2000). Such reptiles must have moved onto the coastal beaches for reproduction and hidden their eggs in the beach zones. They may also have bred on the coast. This may have attracted the *Macrocnemus* or *?Hescherleria* to feed on their eggs. However, whether marine-adapted sauropterygians moved on the tidal flats is unclear, particularly in the case of paraxial swimming reptiles, such as the early smaller *Nothosaurus* species, which must have crawled on land in a similar way to modern crocodiles. The many fine parallel scratch-marks, which were also found on the fossil Triassic biolaminates, may have been produced by their body scales. How far *Coelurosaurichnus* could be a possible track of these

sauropterygians is unclear, due to the problem of missing or incompletely mapped trackways.

The phenomenon of “Triassic carbonate tidal flat megatrack sites in Central Europe” (Diedrich, 2002d), and the presence of trackmaker skeletons or bones in the biolaminates and many Triassic bonebeds in the Germanic Muschelkalk, is unique, and gives rise to new palaeoceanographic (Fig. 8), stratigraphic and palaeoecological interpretations of the Germanic Basin.

5. Paleooceanography and reptile migrations

The first terrestrial reptile migrations into the Germanic Basin started already before, but mainly during the *Myophoria* Member (Fig. 8A) with the marine ingression. Five track beds in the marine Upper Bunter limestones prove the small- to medium-sized reptiles by their abundant footprints in Germany. The main extension of tidal flats and sabkhas in the southern Basin was at the boundary Bunter/Lower Muschelkalk (upper Röt, see also Backhaus, 1981). In the western but also Central Basin (Diedrich, 2000a, 2002b) the most extended tidal flats/sabkha were present as a result of a first sea level high stand maximum to the west. During a slight regression reptiles could migrate from east to west perfectly. In the Oolitic Member of the Lower Muschelkalk (Fig. 8B) there was one small bridge, which was usable for the east–west exchange: the Eichsfeld Swell south of the Harz Mountains. Here it is

still unclear, if this area connected also to the Harz Swell. This megatrack site is distributed over 200 km around the northern and eastern part of the Rhenish Massif (cf. [Diedrich, 1998b](#)) and the northern Bohemian Massif. During the maximum flooding (Terebratula Member, see also [Knaust, 2000](#)) the tidal flats and sabkha disappeared nearly in relict small zones along the coast. With the end of the Lower Muschelkalk (Schaumkalk Member) another low stand resulted again a period of maximum tidal flat extensions in the southern Germanic Basin. The maximum of the low stand was reached in the basal Middle Muschelkalk (*orbicularis* Member, mm1). Those megatrack sites were again extensively distributed in the entire southern Germanic Basin (cf. [Diedrich, 2002d](#)).

During the Lower Muschelkalk tsunamites and seismits are proved for the entire Basin ([Rüffer, 1996](#); [Szulc, 1993](#); [Knaust, 2000](#)) and could be presented here in an overview for the studied area. The sea-earthquake induced tsunamites leave typical mixed and chaotic sediments in intertidal zones, which were described for recent deposits in Japan ([Minoura and Nakaya, 1991](#)). Very typical are the flat intraclasts in these beds ([Knaust, 2000](#)), which are built of reworked beach rocks or in the intertidal zones of the biolaminates. Even reworked red terrestrial marls were found in the western basin (Osnabrücker Bergland, [Diedrich, 2002c](#)). Therefore in the coastal shallow and intertidal zones of the western Germanic Basin around the Rhenish Massif (especially Osnabrück Mountains) such intraclast beds are well

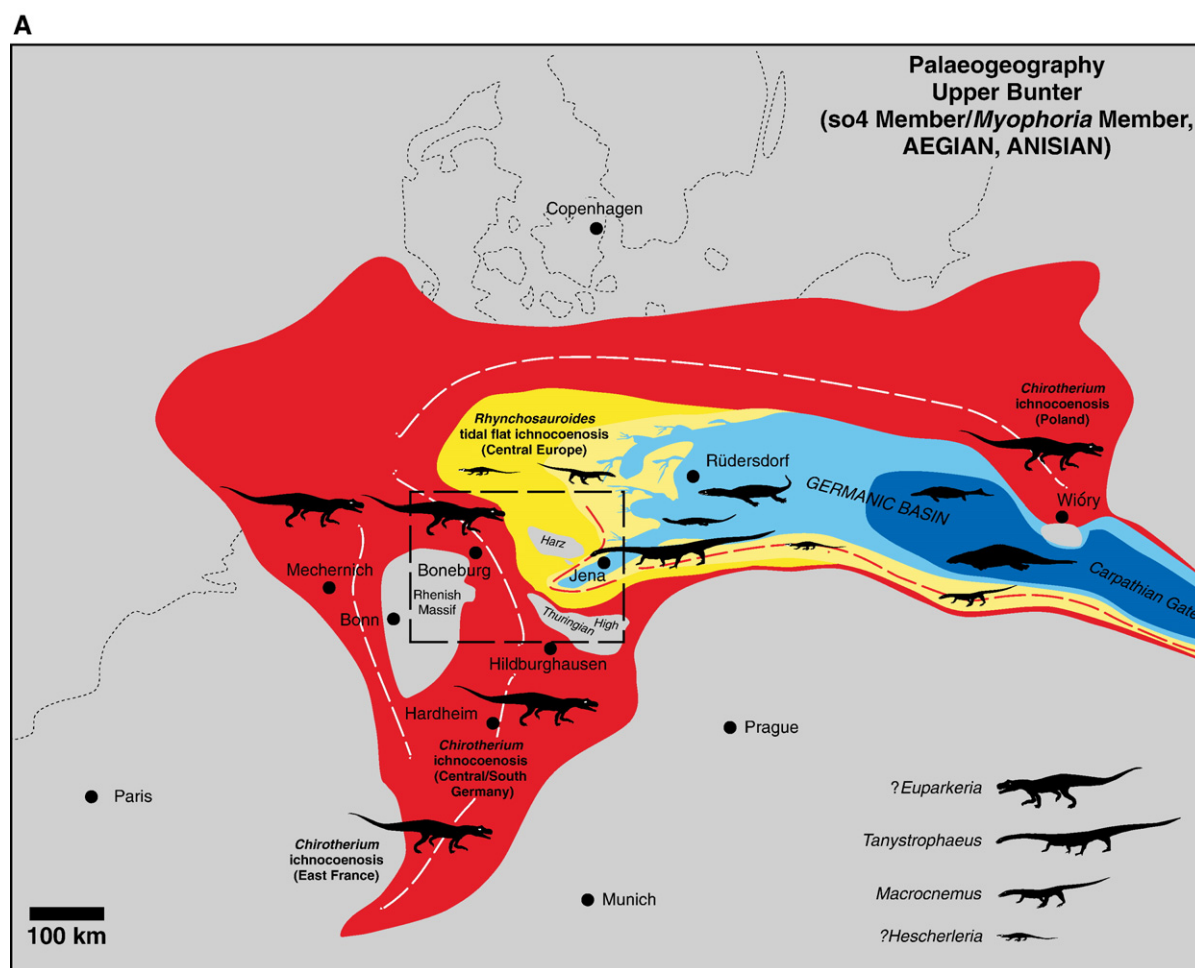


Fig. 8. First intertidal flats and sabkha zones in the Germanic Basin during the Anisian. A. *Myophoria* member (Upper Bunter, Lower Triassic, Aegian) and B. Oolitic Member (Lower Muschelkalk, Middle Triassic, Bithynian). These flat marine zones moved during the Germanic Basin ingress from east to west. Possibly the Palaeozoic Harz and Thuringian mountains already built peninsulas. Whereas in the terrestrial facies *Chirotherium* dominated track associations are well known, at the same time other immigrating reptiles left the *Rhynchosauroides*/*Procolophonichnium* dominated ichnocoenosis in intertidal flat and sabkha zones (frame see. [Fig. 1](#)).

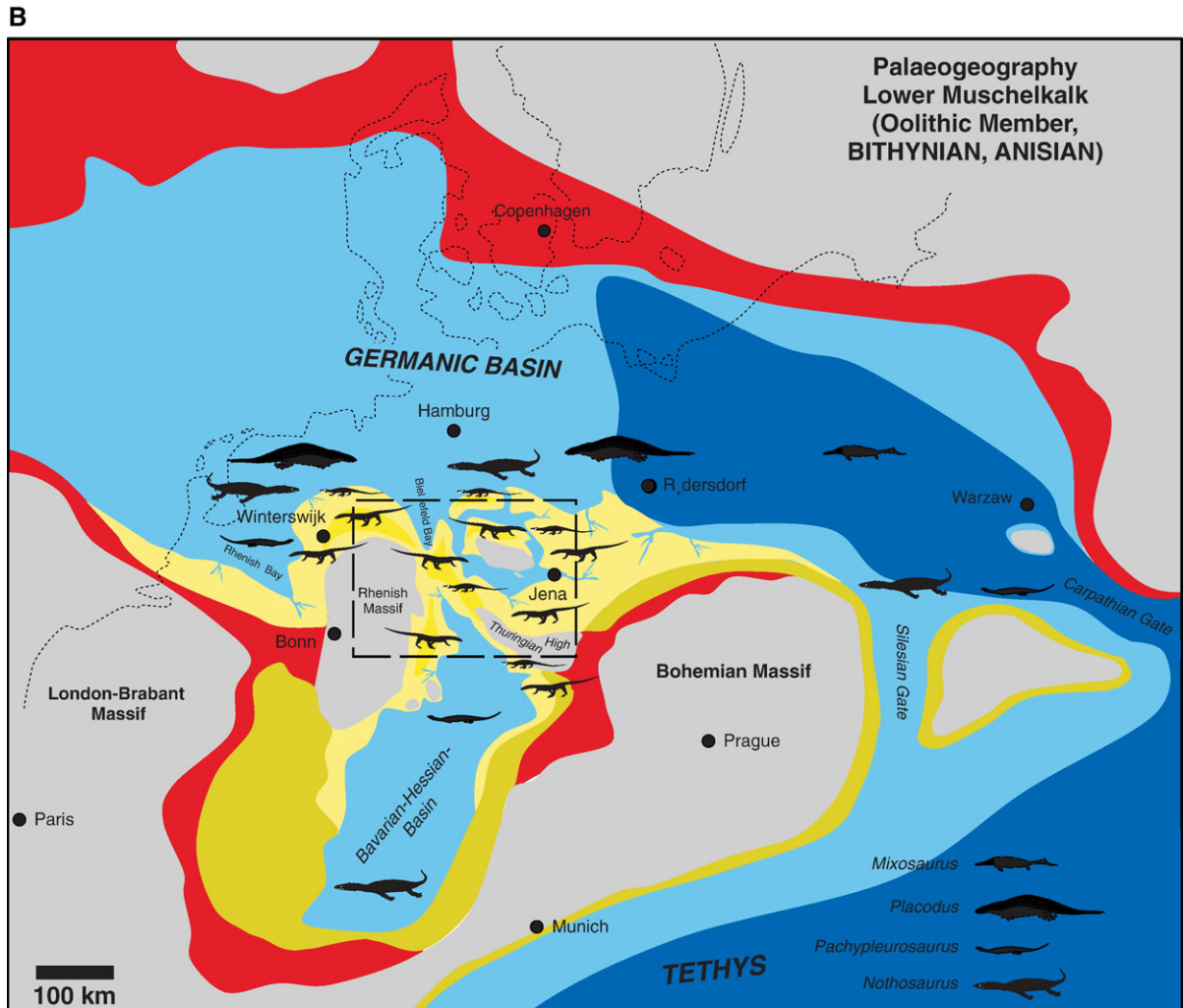


Fig. 8 (*continued*).

developed and interpreted sensu [Knaust \(2000\)](#) here as tsunamites. Tsunamites are the Basiskonglomerate Bed I, the Basiskonglomerate Bed III (=Sorges Bed in [Knaust, 2000](#)), the Red flat pebble Bed (Osnabrücker Bergland) at the base of the muW1F, and the Schaumkalk Bed II. All these beds are also described for the Basin by [Knaust \(2000\)](#), who additionally interpreted beds in the muW2 as tsunamites, which presently cannot be proved for the western Germanic Basin, yet.

Seismites sensu [Knaust \(2000\)](#) seem to be present with phacoidic structures in the Osnabrücker Bergland in three horizons. In the muW1G below the Oolithic beds and in the muW2B up to 50 cm large phacoids seem to be the result of syndimentary massive slumps (cf. [Knaust, 2000](#)). A third one can be recognized in the muW3C below the *Pentacrinus* Bed. The presence of the tsunamites and seismites supports the model of the

basin dynamics, which was mainly tectonically controlled (Knaust, 2000). The subsiding tectonics of the Germanic Basin had the main effect onto the intertidal flat distribution and movements. However, especially tsunamites would have killed complete reptile populations in the intertidal zones. The trace makers of *Rhynchosauroides* and *Procolophonichnium* trackways must have been killed periodically in huge numbers in their populations by such tsunamite events. Such rapid depositional events would additionally explain the preservation of many track beds. As shown in the section, the track beds are overlain generally by tsunamites/tempestite beds or first by sabkha sediments.

The Lower Muschelkalk comprises a time of about 3 Ma years (240–237 Ma, after [Menning, 1995](#)). In such a time frame an evolution of the trackmakers might be expected, but cannot be proved on the tracks

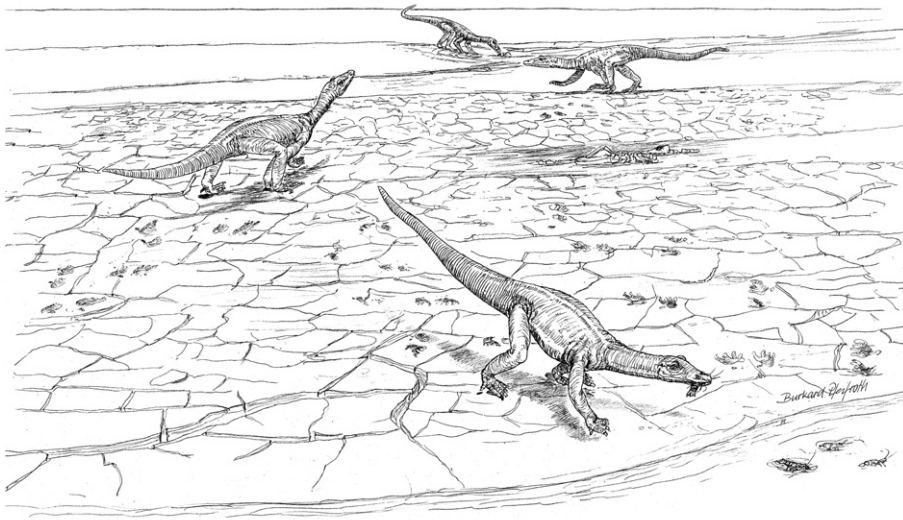


Fig. 9. *Macrocnemus* in a mud cracked carbonate tidal flat in which marine invertebrates (here the crustacean *Clytiopsis*) and vertebrates were caught in ponds. Daily tidal change and activities of many animals of different ages and varying movement and swimming activities left millions of tracks of *Rhynchosauroides* around the entire southern Germanic Basin during the Triassic (Illustration © B. Pfeifroth, Reutlingen).

(*Rhynchosauroides*/*Procolophonichnium*). The similar tracks are found even up to the basal Upper Muschelkalk and range over a time of more than 4 millions years.

6. Tidal flat and sabkha adapted reptiles

The tidal flats and lower sabkha environments were the habitats of two specialized medium to small reptile species (Diedrich, 2001b). The track maker of *Rhynchosauroides*, possibly the prolacertilian *Macrocnemus*, must have searched for food mainly in the lower intertidal zone (Fig. 9). Crustaceans of the tidal flats (cf. Diedrich and Schulz, 2003) and other marine animals could have been the nutrition source. This reptile even could swim through ponds and channels, which is proved by many swimming trackways and claw scratch mark imprints (Diedrich, 2002b). The smaller reptile, possibly *Hescherleria*, left the tracks of *Procolophonichnium*, but more often in the upper intertidal to lower sabkha environment. Whereas one of the track maker skeletons of *Hescherleria* was found, as mentioned in the alpine Middle Triassic of the Monte San Giorgio, bones are not known yet from this prolacertid reptile in the Germanic Basin. The tracks of *Brachychirotherium* are believed to be produced by the protosuchid *Euparkeria* (cf. Demathieu and Haubold, 1974).

In the Middle Triassic carbonate tidal flats coastal zones the two main small reptiles left the *Rhynchosauroides* (nearly 50%) and *Procolophonichnium* (nearly 50%) dominated track ichnocoenoses (Diedrich, 1998b). In sandy coastal areas such as the eastern Massif Central a

different association is represented during the Middle Triassic. Here a more terrestrial influence was proved by the main presence of *Isochirotherium* (40%) left by herbivore herds, *Brachychirotherium* and *Synaptichnium* produced by large carnivores (15%). *Rhynchosauroides* and *Rotodactylus* tracks are only represented less than 25% (Demathieu, 1985). *Procolophonichnium* is rarely represented in the sandy beach facies (Demathieu, 1970). *Anchisauripus* and *Coelosaurichnus* or *Sphingopus* tracks were left by predators such as *Coelophys* or *Halticosaurus* (Demathieu, 1985). This track-ichnocoenosis is similar to the terrestrial Lower Triassic assemblages from the Upper Buntsandstein (so4 Member) of southern Germany (Bräuhäuser, 1910; Jux and Pflug, 1958; Demathieu and Müller, 1978; Demathieu and Leitz 1982; Haderer et al., 1995), or the Middle Buntsandstein (so2–3 Members) localities in Central, southern Germany (Soergel, 1825; Kaup, 1835; Haubold, 1971; Demathieu and Haubold, 1982; Fichter and Lepper 1997), eastern France (Demathieu and Haubold 1974), Poland (Ptaszyński, 2000) or England (Tresise and Sarjeant, 1997).

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