Senckenbergiana maritima | 35 | (2) | 203–220 | Frankfurt am Main 13.10.2005

Actuopalaeontological trackway experiments with *Iguana* on intertidal flat carbonates of the Arabian Gulf – a comparison to fossil *Rhynchosauroides* tracks of Triassic carbonate tidal flat megatracksites in the European Germanic Basin

Cajus Diedrich

With 14 Figures

Keywords: Trackway experiments, *Iguana*, Arabian Golf, carbonate tidal flat, fossil *Rhynchosauroides* trackways, megatracksites, Middle Triassic, Europe

Abstract

[Diedrich, C. (2005): Actuopalaeontological trackway experiments with *Iguana* on intertidal flat carbonates of the Arabian Gulf – a comparison to fossil *Rhynchosauroides* tracks of Triassic carbonate tidal flat Megatracksites in the European Germanic Basin. – Senckenbergiana maritima, 35 (2): 203-220, 14 Figs.; Frankfurt a. M.]

In the recent carbonate tidal flats of the lower to upper intertidal zone of the Khor Al Qirqishan Bay western of Abu Dhabi at the southern Arabian Gulf actuopaleontological trackway experiments with the lizard *Iguana* were made. The different moving activities such as basking, slow walk or running over dry to wet biolaminate surfaces and swimming or walking activities through ponds and tide channels have left a variety of quadruped track preservations. *Iguana* has produced trackways on nearly dry microbial mats of the upper intertidal only with claw marks. On slightly wet substrates detailed imprints of the subdigital lamellae were produced, while in wet mud a medium impressed imprint type without subdigital structures was typical. On very wet mud scratch marks were left by the long claws combined with medium impressed imprints. In about 25 cm deep intertidal channels or ponds *Iguana* began to swim and touched the ground. In less deep water the lacertid left swimming and subaquatic walk scratch marks. In slow move the tail produced a more or less straight deep impression and the pes was printed behind the manus. By running activities the pelvic girdle was uplifted, the tail did not touch the ground and the pes was printed besides the manus. Astonishing is the identical track preservation of the fossil European Triassic trackways on biolaminates. The experiment results are very similar to the fossil record with the very abundant Lower to Middle Triassic track genus *Rhynchosauroides* in the southern margin of the Germanic Basin with its ancient carbonate tidal flat megatracksites. With the study of the recent lower or upper intertidal environments in the Arabian Gulf fossil footprints can be positioned in the palaeoenvironments of the old tidal flats, tidal ponds or channels. Also the biolaminate consistence of the fossil Middle Triassic carbonate tidal flats and moving activity zones of the most possible trackmaker *Macrocnemus*, a fossil Middle Triassic prolacertilian of Europe, can be reconstructed. These old reptiles must have lived primary in the carbonate tidal flats, especially searching for food in the lower intertidal, where they left the highest density of their trackways in the entire surrounding Germanic Basin coastline about 240 Mio. years ago under the same subtropical arid conditions as in the recent Ana logon, the southern Arabian Gulf.

Author's address: Cajus Diedrich, Nationalmuseum Prague, Department of Palaeontology, Václavské náměsti, 68 CZ-11579 Prague <cdiedri@gmx.net>; www.paleologic.de

Introduction

Numerous fossil vertebrate track sites have been discovered recently in the upper Lower to Middle Triassic marine carbonate tidal flat deposits of Europe (Diedrich 1997, 1998a-d, 2000, 2001a–c, 2002a–d, 2003, Diedrich & Oosterink 2000, Diedrich & Fichter 2003, Diedrich & Schulz 2003). These include over 35 localities in Germany, discovered by the MTMP (Middle Triassic Megatracksite Project, Diedrich 2002c). This project aims to elucidate the fossil carbonate tidal flat ecosystem, its palaeogeography and movement during time and space and the reptiles that lived in this environment permanently or only periodically. The situation in Europe appears to be unique, with the discovery of partial skeletons of the putative track makers in the Netherlands, associated with the track beds (Diedrich 2002c, Oosterink et al. 2003).

Comparisons between fossil and recent marine biolaminates and their trackways are important for the understanding of the facies, the palaeogeography and the track makers. Sedimentological comparisons between the Germanic Basin (Middle Triassic, 240 MBP) and the recent Arabian Gulf were studied by Knaust (1998). Both basins were/are flat marginal basins with high salinity in dry subtropical latitudes. In both basins, biolaminates were/are present on the flat southern carbonate ramp coastlines. The recent carbonate tidal flats at the southern Arabian Gulf coast of the Abu Dhabi region (Evans & Kirkham 2001) are an ideal comparative locality and were used in this study for the experiments.

Firstly biolaminates were studied sedimentological in Khor Qirqishan (Fig. 1). Then, a large individual of the iguanid lizard *Iguana iguana* was used for a series of trackway experiments in the carbonate tidal flats of Al Dabb'iya Peninsula (Fig. 1), west of Abu Dhabi. This animal has a similar footprint size, as well as the overprinting of the forelimb, that has been observed in the fossil record of the most common Middle Triassic trackways of the Ichnogenus *Rhynchosauroides*. In the experiments (see also Diedrich & Gardner 2004, Diedrich 2005 a), tracks on microbial mats of varying texture and wetness were prepared to compare track imprinting and preservation. Tracks produced by slow walking to fast running, and also swimming activities were documented and compared with the fossil material.

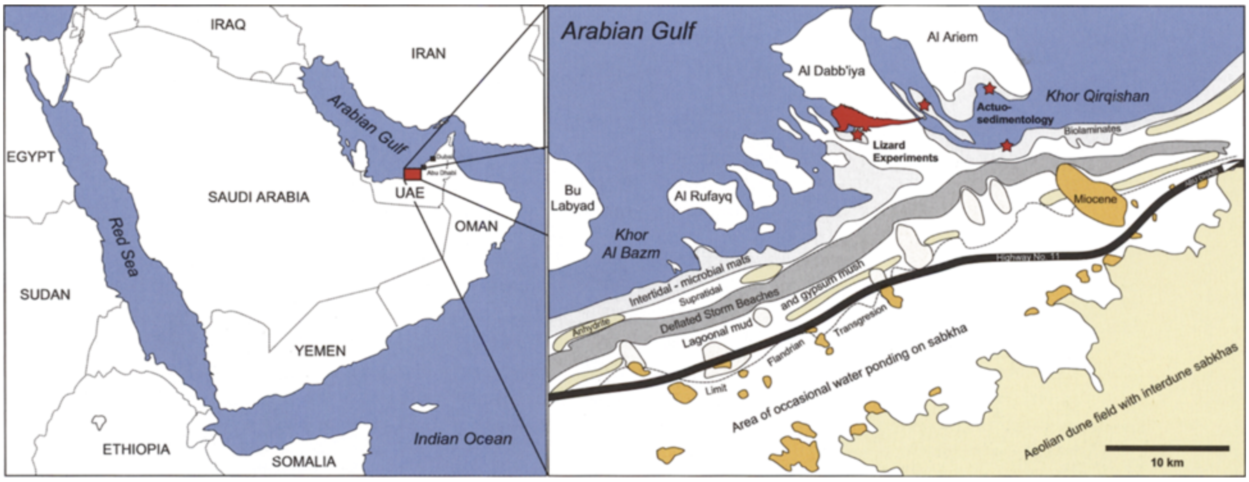

Fig. 1: Studied carbonate tidal flat regions in the Khor Al Qirqishan bay and carbonate tidal flat zones along the coast western of Abu Dhabi, and experiment area in the West of Al Dabb'iya, U.A.E (Graphics: PaleoLogic).

The fossil track record

Fossil *Rhynchosauroides* trackways were found with thousands of imprints at the margins of the Rhenish and the Vindelizic Massif at many sites that were discovered mainly in the last six years of field work (Fig. 2). In The Netherlands a single track site was discovered in 1958 by Faber near Winterswijk (Demathieu & Oosterink 1983, Oosterink 1986, Demathieu 1988) in the first quarry of the Steen-en Kalkgroeve at Ratum. Nearby, the track site Haarmühle was the first known place with vertebrate tracks of the Middle Triassic in Germany (Holst et al. 1970). More than 35 new vertebrate track localities were discovered in Germany between 1996 and 2001 by the use of a successful prospecting scheme (Diedrich 1997, 1998a–d, 2001, Fig. 2). In the Osnabrücker Bergland tracks of *Rhynchosauroides* were found at Halen, Hagen, Hellern, Handarpe, Rulle, Osnabrück, Grambergen, Holte, Eistrup and Bissendorf. In the Teutoburger Wald the localities Dissen, Borgholzhausen, Wichlinghausen, Halle/Westphalia, Bielefeld, Oerlinghausen and Detmold have delivered material. In the Eggegebirge and Nordhessische Bergland tracks of *Rhynchosauroides* were collected stratigraphically from Herste, Boneburg, Eberschütz, Lamerden (cf. also Fichter 1997), Ostheim, Liebenau, Warburg, Nothfelden and Volkmarsen and on a systematic excavation in Großenlüder (Diedrich & Fichter 2003). In south-western Germany the most recently discovered track sites are Tremersdorf, Geilsdorf, Grockstädt, Reinsdorf, Karsdorf and Dorndorf (Figs. 2–3).

The tracks of *Rhynchosauroides* (Fig. 4) and other track Ichnospecies such as *Procolophonichnium, Coelurosaurichnus,* and *Brachychirotherium* were always found in biolaminates. There are differences in track beds and track horizons after the defi-

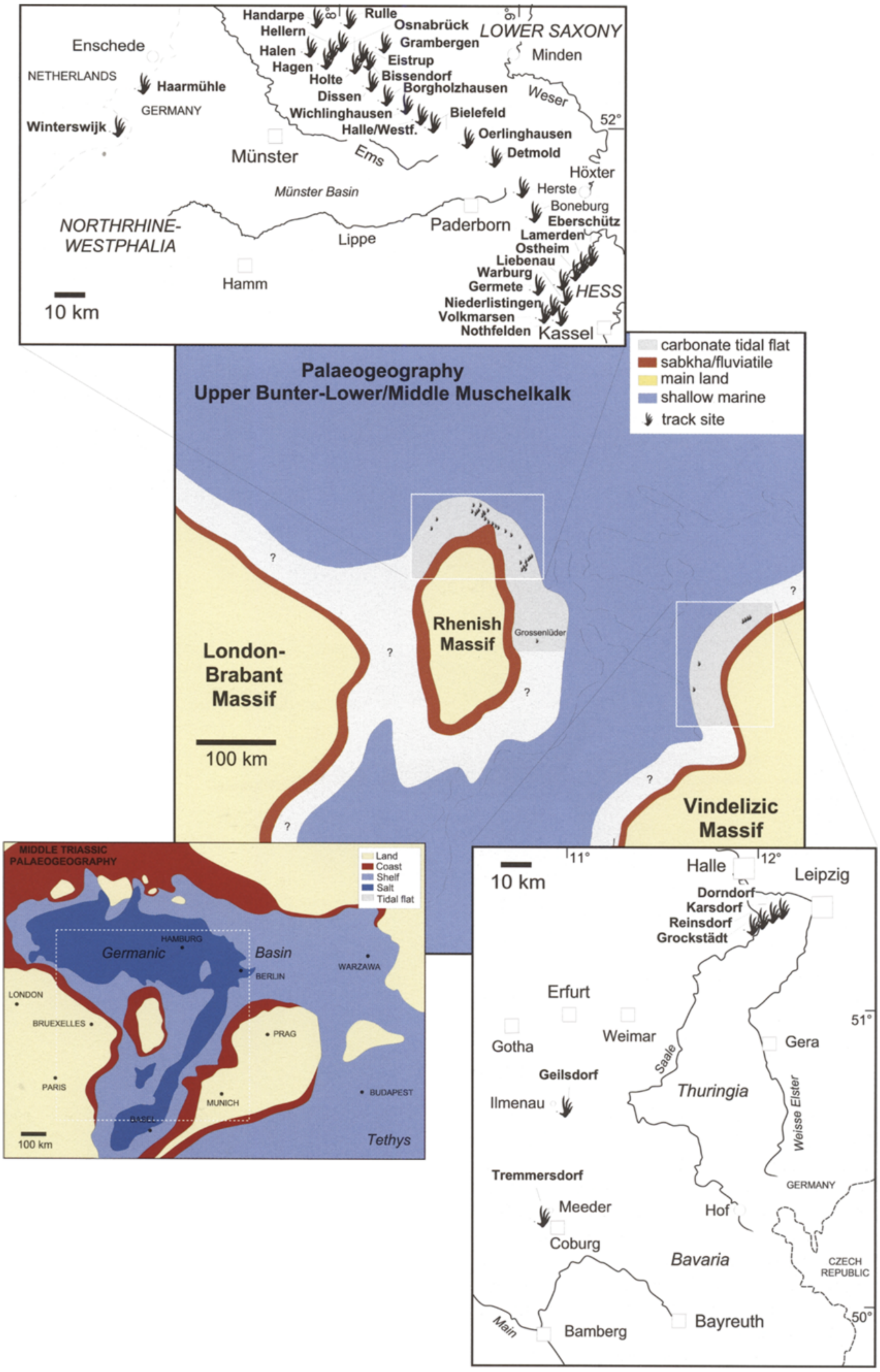

Fig. 2: Studied fossil track bearing carbonate tidal flat regions of the Lower/Middle Triassic in the Germanic Basin. – About 35 carbonate tidal flat track sites from the Upper Bunter, Lower and Middle to basal Upper Muschelkalk are known. Some of them built isochronous megatracksites (see Fig. 3), that span over 100 km (Graphics: PaleoLogic).

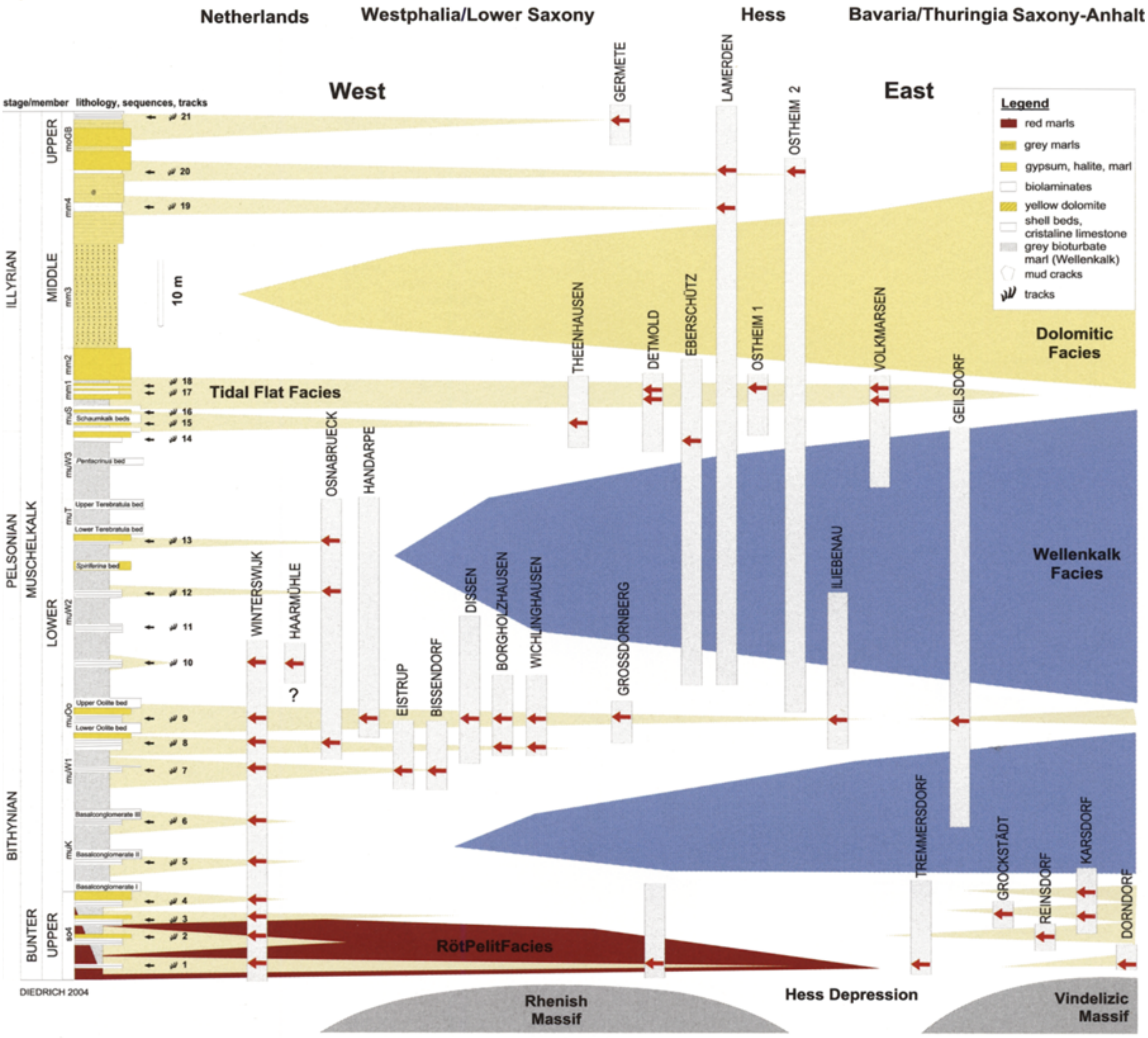

Fig. 3: Generalized section of 25 stratigraphically detailed studied Lower to Middle Triassic biolaminate track site beds in the northern Germanic Basin building in some levels wide spanning Megatracksites in carbonate tidal flat environments surrounding the old Rhenish and Vindelizic Massifs (Graphics: PaleoLogic).

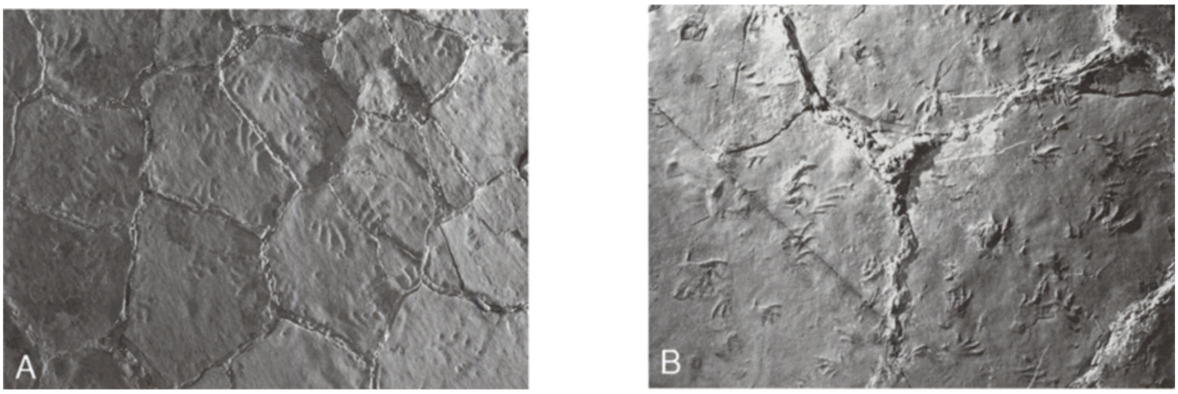

Fig. 4: Sediments of the Middle Triassic track sites of the Germanic Basin. –
A: Track slab with hundreds of *Rhynchosauroides* track imprints (positive, coll. ErdZeitMuseum Borgholzhausen) on polygonal cracked biolaminates from the Lower Muschelkalk (Oolith Member) of the track site Borgholzhausen, NW Germany (cf. Diedrich 2002b).
B: Track slab with hundreds of *Rhynchosauroides* track imprints (negative, coll. Naturkundemuseum Bielefeld) on polygonal cracked biolaminates from the Upper Bunter/Lower Muschelkalk boundary (Basiskonglomerat Member) of the track site Winterswijk, W Netherlands (cf. Diedrich 2001a). – Track sizes of the pes imprints about 10 cm.

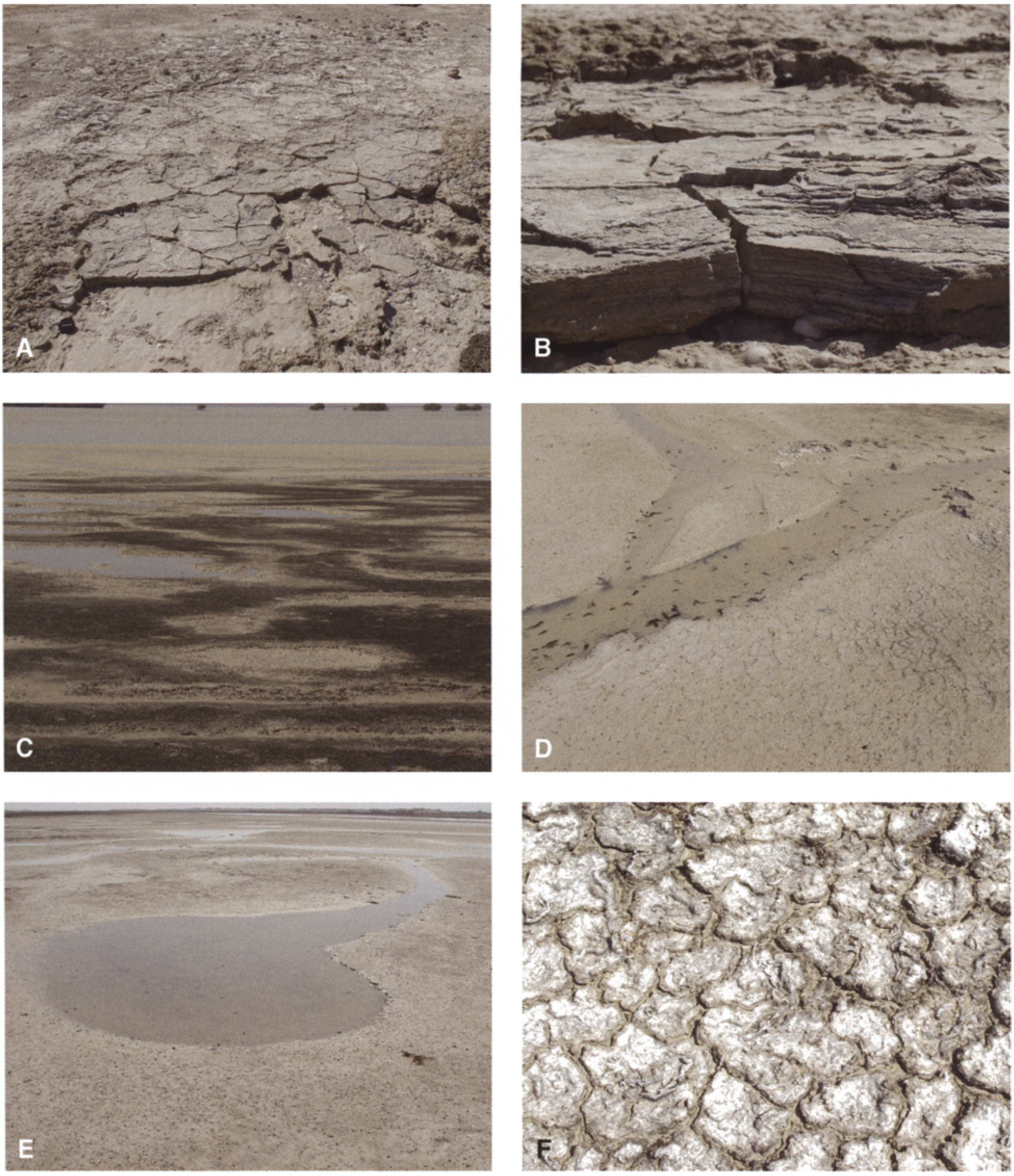

Fig. 5: A-B: Holocene microbial mats in the Khor Al Qirqishan bay, Abu Dhabi, U.A.E. –
A: Recent mud cracked non-active microbial mats (algae, cyanobacteria) at the beach, **B:** section of these microbial mats with millimetre thinly lamination. –
C-F: The active carbonate tidal flats of Al Dabb'iya. –
C: Overview of the carbonate tidal flat, proximal are light carbonate muds partially mud cracked in which channels and ponds were left at the low tide; brownish are the dried microbial mats in the distal upper tide zone. This part is flooded only during spring or storm tides, **D:** tidal channels and mud cracks in the lower intertidal, **E:** tidal pond, **F:** in small polygons cracked microbial mats of the upper intertidal (Photos: PaleoLogic).

Fig. 6: The North and South American lacertilian *Iguana iguana* Linnaeus 1758 used for the experiments. –
A: Mrs. McQuarry and her Californian *Iguana* pet, **B:** A. Gardner the and the author left deep mammal trackways in the mud of the lower intertidal, **C:** left lateral side of *Iguana* touching the ground with its tail, **D:** ventral side with sharp scutes, **E:** right pes with long and spiky claws, **F:** right manus with long and spiky claws (Photos: PaleoLogic).

Fig. 7: *Iguana iguana* Linnaeus 1758 – moving story 1 in the upper to lower intertidal flat. –
A: Sitting for warming up in the lower intertidal flat, **B:** fast move with uplifted hind limbs in the upper intertidal flat, **C:** slow move with non-uplifted hind limbs through a pond in the upper intertidal flat, **D:** sitting in 20 cm deep water in a pond of the lower intertidal flat, **E:** start of swimming in a 25 cm deep water of a lower intertidal flat channel, **F:** paraxial swimming in a 30 cm deep intertidal flat channel – the animal does not try to touch the ground with its extremities (Photos: PaleoLogic).

Fig. 8: *Iguana iguana* Linnaeus 1758 – moving story 2 in the lower intertidal flat. –
A: Swimming through a 30 cm deep channel, **B:** walking scratch mars left in 10 cm deep water, **C:** change of the trackway preservation from unshaped underwater to clear visible track and tail marks by slow moving onto the intertidal flat mud, **D:** differences in the footprint and tail mark impressions on a very short distance of 60 cm, depending on the sediment moisture and relief. Remember: on the left side combined normal imprints with partially scratches and scratch marks on the right side as a result of diagonally moving on a very low relief dipping surface (Photos: PaleoLogic).

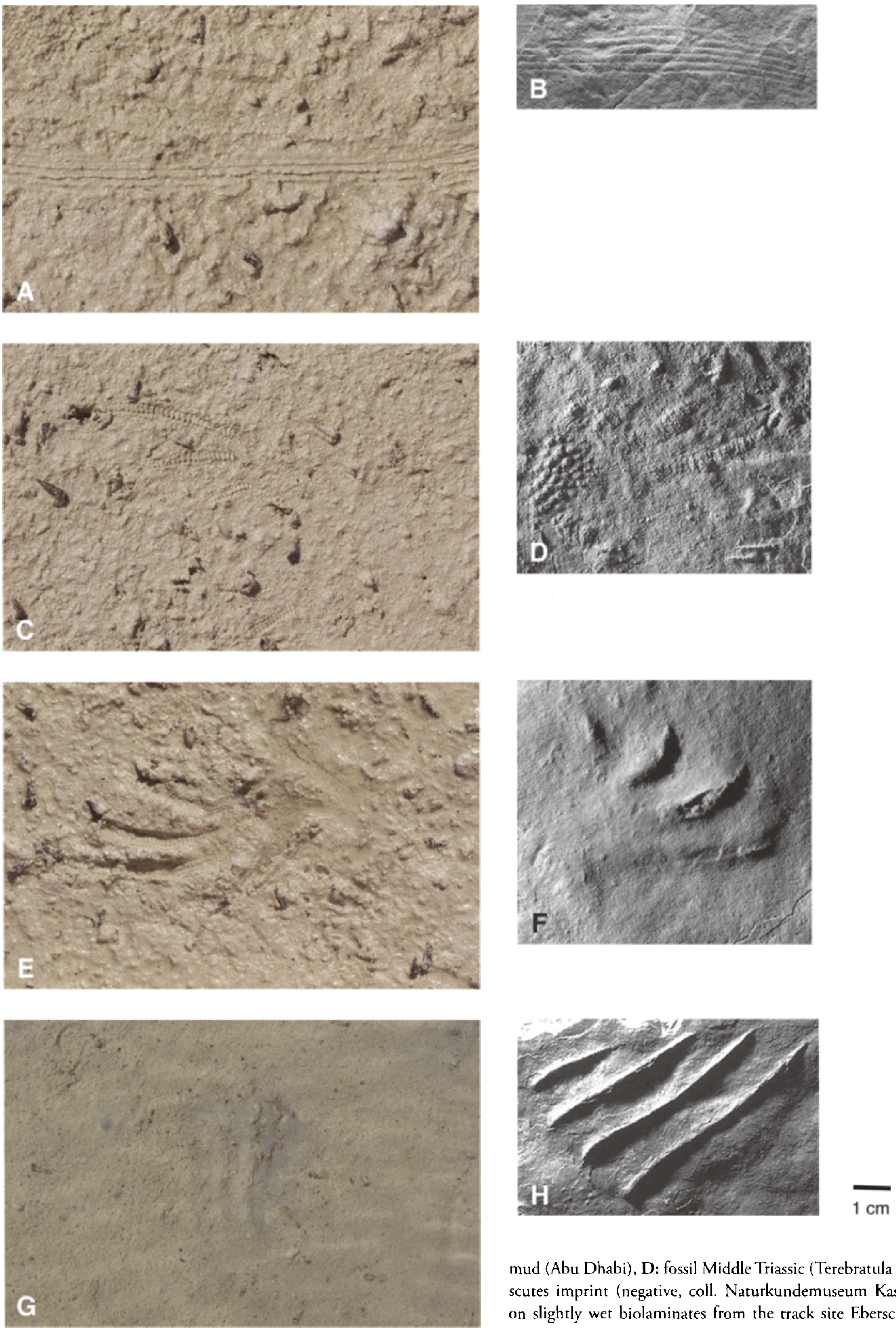

Fig. 9: Imprint preservation of the recent *Iguana* tracks and the fossil *Rhynchosauroides* track type. –
A: Scutes scratch marks of the tail left on recent drying biolaminates surface (Abu Dhabi), **B:** fossil Middle Triassic (Terebratula Member) scutes scratch marks (negative, coll. Naturkundemuseum Kassel) in slight wet biolaminates from the track site Eberschütz (Germany), **C:** detailed dermal scutes imprint preservation on slightly wet microbial mat covered mud (Abu Dhabi), **D:** fossil Middle Triassic (Terebratula Member) dermal scutes imprint (negative, coll. Naturkundemuseum Kassel) preservation on slightly wet biolaminates from the track site Eberschütz (Germany), **E:** normal deep impressed print preservation on very wet microbial mat covered mud (Abu Dhabi), **F:** fossil Middle Triassic (Basiskonglomerat Member) manus imprint of *Rhynchosauroides tirolicus* (coll. GPI Museum University Münster) in very wet biolaminates from the track site Winterswijk (The Netherlands), **G:** under water scratch mark track in a recent 25 cm deep channel (Abu Dhabi), **H:** fossil Middle Triassic (Oolith Member) subaquatic scratch marks (negative, coll. ErdZeitMuseum Borgholzhausen) from the track site Borgholzhausen (Germany) (Photos: PaleoLogic). – Scale bar: 1cm.

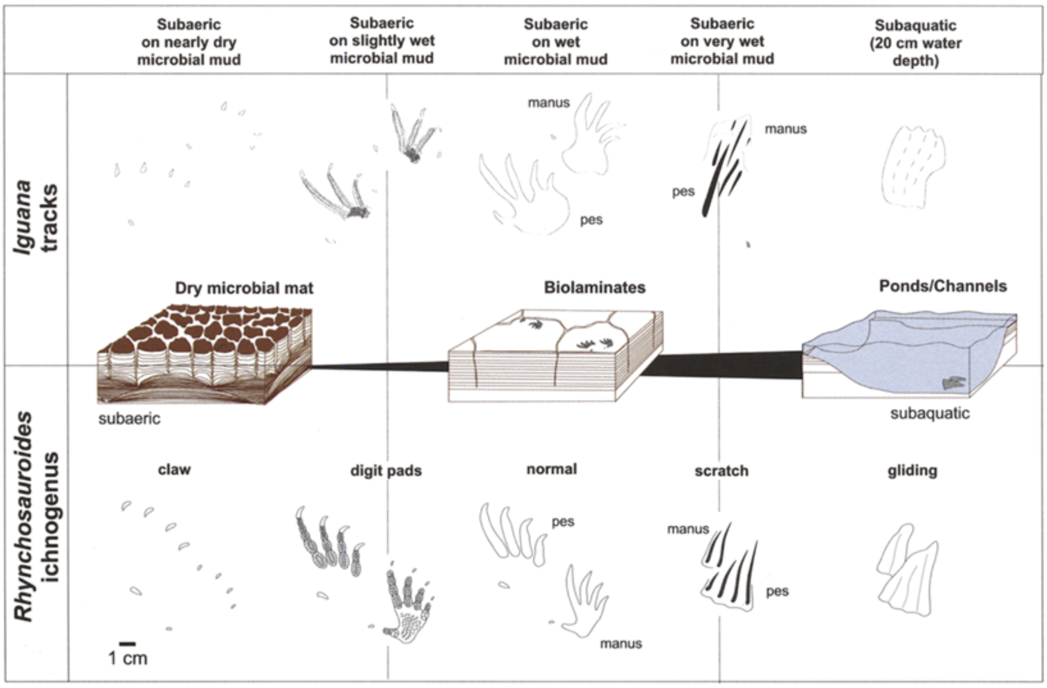

Fig. 10: Comparison of the track preservation of recent *Iguana*-tracks after the experiments in the carbonate tidal flats in the Arabian Gulf western Abu Dhabi, U.A.E. and the Middle Triassic Fossil tracks of the Ichnogenus *Rhynchosauroides* from carbonate tidal flats of the Germanic Basin in Europe (Graphics PaleoLogic).

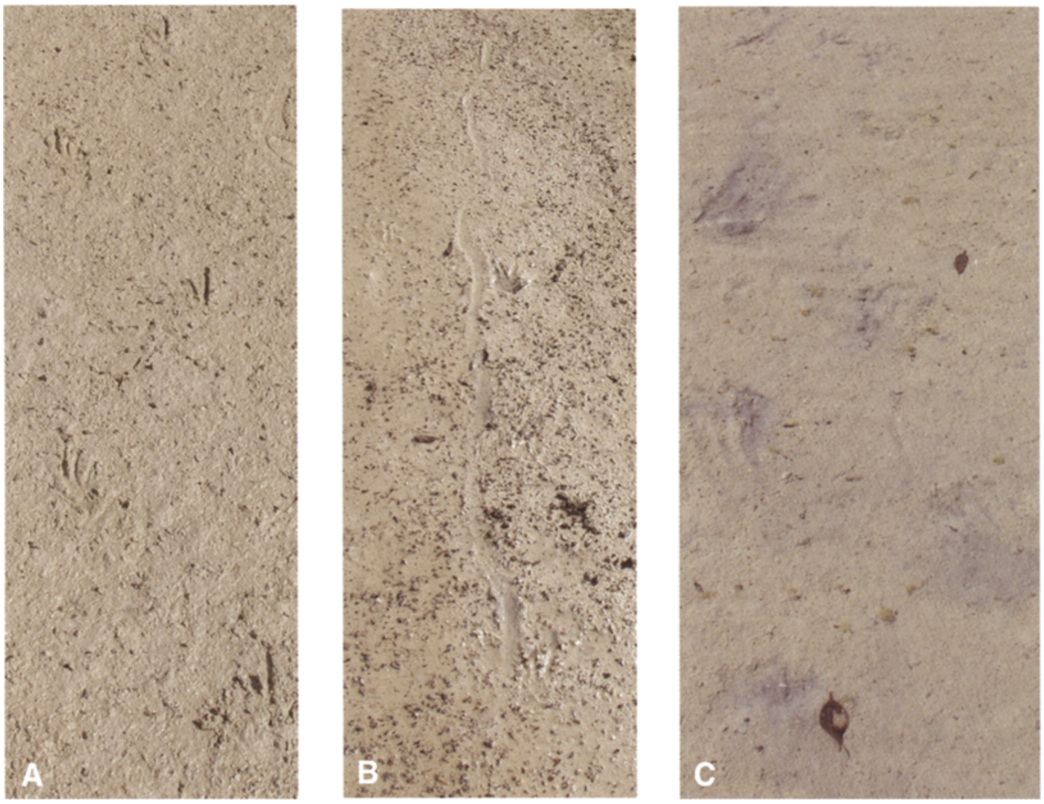

Fig. 11: Preservation of *Iguana iguana* LINNAEUS 1758 trackways depending on different moving styles and substrate moistures. –
A: Fast move with overprinting of the pes on slightly wet surfaces, with lacking of the tail mark impression as a result of uplifting of the pelvis and tail, **B:** slow move with non-overprinting on wet surfaces with the presence of a tail mark, **C:** underwater walking trackway with half scratch mark and half deeply normal preservation with lacking tail mark (Photos: PaleoLogic).

nition (cf. Diedrich 2002b). One "track bed" is situated at the top of a sedimentary shallowing upward sequence and is built of 10 to 250 cm massive biolaminates containing itself many "track horizons". It is nearly impossible to find all track horizons in the millimetre thinly bedded biolaminates at one locality, but in the most studied sections one to ten track horizons are present per 10 cm sedimentation. A detailed studied section is described from the site Borgholzhausen, in which 36 track horizons were mapped in 250 cm biolaminates as a result of special excavation technique (Diedrich 1998a, b, 2002b). These mud cracked carbonates are products of cyanobacterial and microbial mats (Diedrich 2000b) of the lower to upper intertidal zone. Such carbonates are typical in the recent tidal flats of the Arabian Gulf. Some yellow dolomite beds (= "Gelbkalke") with tepee structures and sometimes bird eye structures were found sometimes above the more planar biolaminates in the Germanic Lower to Upper Muschelkalk indicate supratidal sabkha environments (cf. modern sabkha environments in: Garvish et al. 1985, Gerdes et al. 1985, Warren 1989). Oscillation ripples, mud cracks and granular surface marks are present in the track bearing beds typical of carbonate tidal flat environments. The track bed sediments of the Germanic Triassic are planar laminated petee, mud cracked, grey mudstones of the lower intertidal flat to laminated, yellow coloured dolomites to the upper intertidal to supratidal sabkha zone and can be compared to the recent Arabian Gulf intertidal to sabkha zone (cf. modern sabkha in: Kirkham 1997, 1998) or to Cenomanian/Turonian intertidal to sabkha carbonates of the Adriatic Carbonate Platform (cf. Diedrich 2005b). Only at the track site Wichlinghausen tracks were discovered in hematite rich and red coloured, laminated and mud cracked carbonate deposits that were influenced by an outer fan of an ancient river floating from the Rhenish Massif into the Germanic Basin (Diedrich 1998). The tidal flat belt must have spanned many km in width surrounding the old massif coastal zones in the entire southern Germanic Basin (cf. Fig. 2).

During the Muschelkalk Formation this intertidal carbonate flat belt must have changed its position many times during low stand systems tracts basin wards or during transgressive system tracts landwards indicated by the enormous amounts of track bed levels (Fig. 3).The result are more than 21 track beds (Fig. 3) in 250 m thick carbonates of the marginal coastal zones of the Germanic Basin during the Upper Röt (Bunter) to the Gelbe Basisschichten Member (basal Upper Muschelkalk) of the Lower to Middle Triassic (Fig. 3). The palaeogeography and density of track beds to the west (Fig. 3) indicates a more flat ramp position of the western part of the Germanic Basin and fit to the basin model presented by Knaust (1998).

The first track beds were found in the biolaminates of the Upper Bunter (upper Lower Triassic). These tracks were dug from the Grenzdolomit in the Upper Röt Pelit Member in Winterswijk or East-Germany at Dorndorf (Diedrich 2001c). In the Middle Triassic they are abundant in many track beds. The first track beds in tidal flat carbonates occur with the increase of the marine Tethyan influence over the Upper Silesian and Carpathian seaway of the eastern Germanic Basin during the Upper Röt Pelit Member. Here the first track beds 1–3 are located at the margin of the Vindelizic Massif (Fig. 3). Track bed 4 occur in the Grenzdolomit Member of the uppermost Upper Bunter followed by two track beds in the Basiskonglomerat Member (track bed 5–6, muK), track bed 7 (muW1B), and track bed 8 in the Lower Wellenkalk Member (muW1C, Lower Muschelkalk), track bed 9 in the Oolith Member (muOo, Lower Muschelkalk), track bed 10–13 (muW2A-E), in the Middle Wellenkalk Member (Lower Muschelkalk), track beds 15 and 16 in the Schaumkalk Member (muS, Lower Muschelkalk), track beds 17 and 18 in the *orbicularis* Member (mm1, Middle Muschelkalk), track beds 19 and 20 in the Upper Marl/Dolomite Member (mm 4, Middle Muschelkalk) and finally track bed 21 in the Gelbe Basisschichten (moGB) of the basal Upper Muschelkalk.

Actuoenvironmental observations in the Arabian Gulf

The track sites of the Middle Triassic period in Europe represent fossil carbonate tidal flat regions consisting of mud-cracked microbial biolaminates. These mats were studied western of Abu Dhabi, to compare this type of sediments to the ones of the European upper Lower to Middle Triassic (241–238 MBP) track sites (Figs. 1–2).

The Holocene non-active microbial mats at the Western Abu Dhabi coast in the Khor Al Qirqishan bay (Figs. 5A–B) are built up to 60 cm laminated and mud-cracked fine to medium-grained carbonate sands/silts. The consistency of these biolaminates is still soft, but when the cementation is completed, they form hard beach rocks (cf. Evans et al. 2002) that also can be found along the recent coastline of the Khor Al Qirqishan bay. In the daily inundated carbonate tidal flats of the Al Dabb'iya experiment site (Figs. 5 C–F), the living microbial mats have not yet accumulated many centimetres of laminated beds. Here the process of biolaminate accretion is still in progress. The fossil Middle Triassic biolaminates only differ macroscopically from the recent ones of the Abu Dhabi region in their grain size, being built in most cases of silty and finer carbonate particles and not of carbonate sand.

Track experiments

The experiments at Al Dabb'iya were conducted at low tide from 9 a.m. until the tide turned at noon, rapidly flooding over the channels onto the low-relief flats (Figs. 5C, 6B). The lizard used in the trackway experiments was a large, male green iguana (*Iguana iguana* Linnaeus 1758) a Central and South American species. The green iguana is primarily an arboreal herbivore, but known to be an accomplished swimmer (Müller 1972). This individual was approximately 80 cm in snout to vent length and 4 kg in weight. Although more than one third of the distal tail had previously been lost, but this was not considered of importance for the track experiments (Fig. 6C). The body is completely covered by small, spiny-tipped scutes (Fig. 6D). The sharp and well developed claws of the manus and pes (Fig. 6A, E–F) did cut deeply into the mud (Fig. 10).

Track imprinting of *Iguana* on different biolaminate surface consistencies

An attempt was made to duplicate the different track imprint types found in the fossil record by utilising a range of different surfaces of the lower and upper intertidal. Nearly dry and slightly mud-cracked surfaces, soft carbonate mud, very soft channel mud, and under water surfaces in channels and ponds were used for the experiments.

Mud-cracked surfaces of dry microbial mats: (Fig. 5F). The microbial mats towards the landward edge of the upper intertidal flats are only periodically flooded and built 2–3 mm thick, in very small irregular, 5–10 cm in diameter cracked polygon surfaces with a dry, leather-like consistency. In this environment no footprints or even claw marks could be imprinted by the lizard.

Mud-cracked surfaces of slightly wet microbial mats: Here in the upper intertidal flat zone the microbial mats built 2–3 mm thick, soft, leathery cracked dry planar surfaces (Fig. 5D). On these biolaminates only boomerang shaped claw marks of the footprints were left, also fine parallel scratch marks of the ventral body scales (Figs. 9A, 10).

Soft carbonate mud of wet microbial mats: Under these conditions in the lower intertidal zone the best and most detailed preservation of the tracks was produced. Here the fine parallel scratches of the ventral scutes of the tail (Figs. 6D, 9C, 10), ventral body scales (Fig. 6D), the digital pads and the scales of the feet pads (Figs. 10, 11C) were left as shallowly impressed tracks and traces.

Very soft subaeric channel and pond mud: These soft substrates of the lower intertidal allow an imprint, usually without scale or digital pad structures (Figs. 9E, 10, 11B). Often not all digits are impressed well (digits 1 and 5 imprints usually are not preserved and give a "three toed" form). On the channel margins scratch marks and deep tail marks of *Iguana* were left after swimming through a tidal channel. The most impressive track is illustrated in Fig. 8. Over a short distance of six metres the animal used several types of locomotion and crossed varied surfaces of carbonate mud, leaving a range of track impressions on subaquatic to slightly dry microbial mat surfaces.

Extremely soft subaquatic channel and pond mud: These wet mud conditions in the lower intertidal do not preserve detailed track impressions. In many cases only scratch marks were left on the channel or pond bottom (Figs. 8B, 9G).

Track forms of *Iguana* depending on the different locomotion types

Different movement speeds and swimming activities have a strong effect on the tracks produced, leaving impressions that differ enormously. This is especially important to document as such differences have been used in track ichnotaxonomy to create erroneous fossil track Ichnospecies.

Basking: The iguana basked to raise its body temperature, with its pelvis on the mud substrate and the forelimbs uplifted (Figs. 6C, 7A, D). While the animal was sitting for warming up on dry biolaminates of the upper intertidal (Fig. 7A), or in the tide channels (Fig. 7D) not well imprinted tracks were left.

Slow movement: While walking slowly the pes reached the side of the manus print but did not overstepped it. The hind limbs were not strongly raised off the substrate and the tail touched the ground (Figs. 7C, 8C). The slow moving *Iguana* produced a trackway with non-overprinting of the hind limb and a sinous tail mark in the middle of the trackway (Figs. 7C, 11B). The trackway width is in this case broad and the pace angulation is low.

Fast movement: During running, the pes overprinted the manus. The hind limbs were well raised from the substrate (Fig. 7B). The tail generally did not touch the ground. During fast movement the hind limbs were raised and overstepped therefore the forelimbs, but no tail marks were left in the trackways (Figs. 7B, 11A). The pace angulation of the trackway is very high.

Swimming: The lacertilian swimmed paraxially (Figs. 7F, 8A) in water deeper than 30 cm. In shallower water (<20 cm) the manus and especially the pes were sometimes used for locating and touching the bottom (Fig. 7E). Paraxial swimming did not generally left any tracks. When the animal touched the ground with its extremities it usually produced scratches in the soft mud (Figs. 7E, 9G).

Comparison of the *Iguana* to the fossil tracks of the Triassic Germanic Basin

Experiments on intertidal carbonate tidal flat zones were made for the first time, whereas trackway experiments with lizards and amphibians were studied not in the origin environment or mostly in siliciclastic environments by e.g. FICHTER (1982) or BRAND (1996) for the comparison of fossil Permian tracks.

The experiments in a recent carbonate tidal flat environment with *Iguana* successfully illustrated a range of track impressions under different substrate moisture and bacterial mat conditions in the lower to upper intertidal zone. Different locomotory activities in an original habitat allowed a detailed comparison with the fossil record of Triassic tracks (Figs. 9, 10).

Fossil **fine parallel scratches** found at many track sites in the Germanic Basin, such e.g. of the track site Eberschütz (Province Hess, Germany, Fig. 9B), are the result of the ventral body and tail scutes scratching on smooth slightly dried biomats in the upper intertidal zone (Fig. 9A).

From the fossil *Rhynchosauroides* commonly **claw mark impressions** are known and were produced by *Iguana* on the drying biomats of the upper intertidal zone. The claws mostly did not get strongly into the mud and therefore left combined claw and very short scratch marks. At most of the studied track sites oval shaped scratches left by the claws are very common. Even in the other track preservation types the claws can be seen on the tip of the toes by pointing (Figs. 9D–F).

On the slightly wet biomats of the upper intertidal the best and most detailed **skin prints** were left by *Iguana* (Fig. 9C). The same preservation with digital pads and detailed scutes impressions are found not very often in the fossil record for *Rhynchosauroides*, here demonstrated by a track from the track site Eberschütz (Province Hess, Germany, Fig. 9D).

Normal imprints relatively deeply imprinted into medium soft wet biolaminates were produced by *Iguana* in the lower intertidal or at the margins of tide ponds and channels (Fig. 9E). Such preservations are the most common types in the fossil record for *Rhynchosauroides* (Winterswijk, Netherlands, Fig. 9F). At most fossil track sites this preservation type is found on smooth biolaminate surfaces that are cracked in up to 60 cm large petee polygons (Fig. 4).

At least **scratch marks** are produced by *Iguana* in the tide channels or ponds by swimming or subaquatic walking activities (Figs. 9H, 11C) or in the channel margin when *Iguana* walked out of the water diagonally (Fig. 8D). Such scratch marks, sometimes found on ripple marked surfaces, are very common in the Triassic track sites (Fig. 9H). There is also only one documented fossil trackway from the track site Borgholzhausen (Fig. 12A), that proves the theory of a reptile scratching the subaquatic mud by swimming or walking through a channel or tide pond.

Iguana and *Rhynchosauroides* trackway similarities

There are three main different trackway types left by *Iguana* on the biolaminates.

1. A fast move trackway with overprinting of the pes was left by *Iguana* on slightly wet surfaces. Here the tail mark impression lacks as a result of the uplifting of the pelvis and tail (Fig. 11A).
2. A slow move trackway with non-overprinting of the pes that was produced on wet surfaces. Important is the presence of a sinous and interrupted tail mark (Fig. 11B).
3. A walking trackway under subaquatic surface conditions produced in a flat tide channel. Here only scratches were left (Fig. 11C).

Hundreds of track imprints (single imprints and manus/pes sets) of *Rhynchosauroides* were collected in last six years by high resolution track bed and track horizon stratigraphy in Germany and the Netherlands (Diedrich 1997–2003, Diedrich & Oosterink 2000, Diedrich 2002a–d, Diedrich & Fichter 2003). In most cases only samples of the sections were taken and short trackways were mapped. Therefore mostly single manus or pes imprints in different preservations were found and deposited in several museums (see Diedrich 1997–2005a). There are some partly new trackways of *Rhynchosauroides* found at different track sites which were mapped for the trackway comparisons. The longest trackways were excavated and mapped in Winterswijk. They are about 8 m in length (= *R. peabodyi* (Faber) after Diedrich & Oosterink 2000). All other trackways are shorter (3–4 m). This is mostly the result of the outcrop situations and resulting of the impossibility to map long trackways. For an impressive comparison between trackway types a set of six manus-pes impressions is enough to present the main differences to understand the locomotion and speed of the track makers (see Fig. 12).

The figured *R. tirolicus* trackways (Fig. 12C, E) were documented in the quarry Steen-en Kalkgroeve near Winterswijk (Netherlands, Diedrich & Oosterink 2000), the old quarry Silbersee near Hagen (Figs. 12D, F; Diedrich 2001b) and the sports field Borgholzhausen (Figs. 12 A, B; Diedrich 2002b), all situated in north-western Germany in the Teutoburger Wald. Some of them are published here for the first time in detail (Hagen Silbersee, Germany, Figs. 12D, F).

As shown by the experiments the trackway Fig. 12A was left by an animal that walked slowly through a tide pond or a channel, that was not deeper that about 25 cm. Typical are the scratches in the sinous grooves, and also the slow pace angulation as a result of slow movement through the water. Animals in normal medium speed (Figs. 12B, C) can be observed at many localities. The reptiles left the low pace angulated trackways with a manus-pes set in nearly the same high as a result of non-overprinting. Trackways of animals that walked in very soft (Fig. 12B), and soft biolaminates (Fig. 12C) of the lower intertidal environment are very common at all track sites in the Germanic Basin. Also trackways of running prolacertilians are typical at many sites and were mapped mostly from the upper intertidal zones (Figs. 12D, E).

That the Middle Triassic carbonate intertidal flats were inhabited by large populations of the *Rhynchosauroides* track makers is not only documented by the "*Rhynchosauroides* ichnofacies" (Diedrich 1998d) and many trackways of large "adult" prolacertilians. Every size from very small to large imprints of the type *Rhynchosauroides* can be found at any site sometimes in high tracking densities (100 imprints per square meter, Diedrich 2002b). Here only one trackway is shown as a first example for a juvenile trackmaker (Fig. 12F). Its trackway would fit into the trackways of the running large animals, but the discussion of the possible trackmaker, the prolacertilian *Macrocnemus*, show the different body proportions of juvenile and old animals that resulted different pace angulations and strides in trackways of young and adolescent track makers. Especially the very long legs in comparison to the body length of *Macrocnemus* juveniles seem to be the result of the strong stride and pace, and not the speed. Therefore it seemed that the figured trackway (Fig. 12F) was left by a slow moving young trackmaker.

The prolacertilian *Macrocnemus* – trackmaker of Rhynchosauroides tracks in Europe

The recent tracks of *Iguana* are so close in morphology to the ones preserved in the fossil record of the European Middle Triassic, that the observed fossil tracks of the name *Rhynchosauroides* seemed to be produced by the prolacertilian *Macrocnemus* (cf. Peyer 1931, 1937, Rieppel 1989), as previously suggested (Diedrich 1998–2002, Avanzini & Renesto 2002).

Fortuitously, the proportions of *Iguana* are very close to those ones of the *Rhynchosauroides* track maker, but both show some differences (Fig. 10). Other similarities include the overprinting and the partially lacking tail mark during fast movement. One argument for *Macrocnemus* as the trackmaker of the *Rhynchosauroides* tracks to walk more uplifted with longer extremities, could have resulted the common lack of tail marks in the fossil trackways.

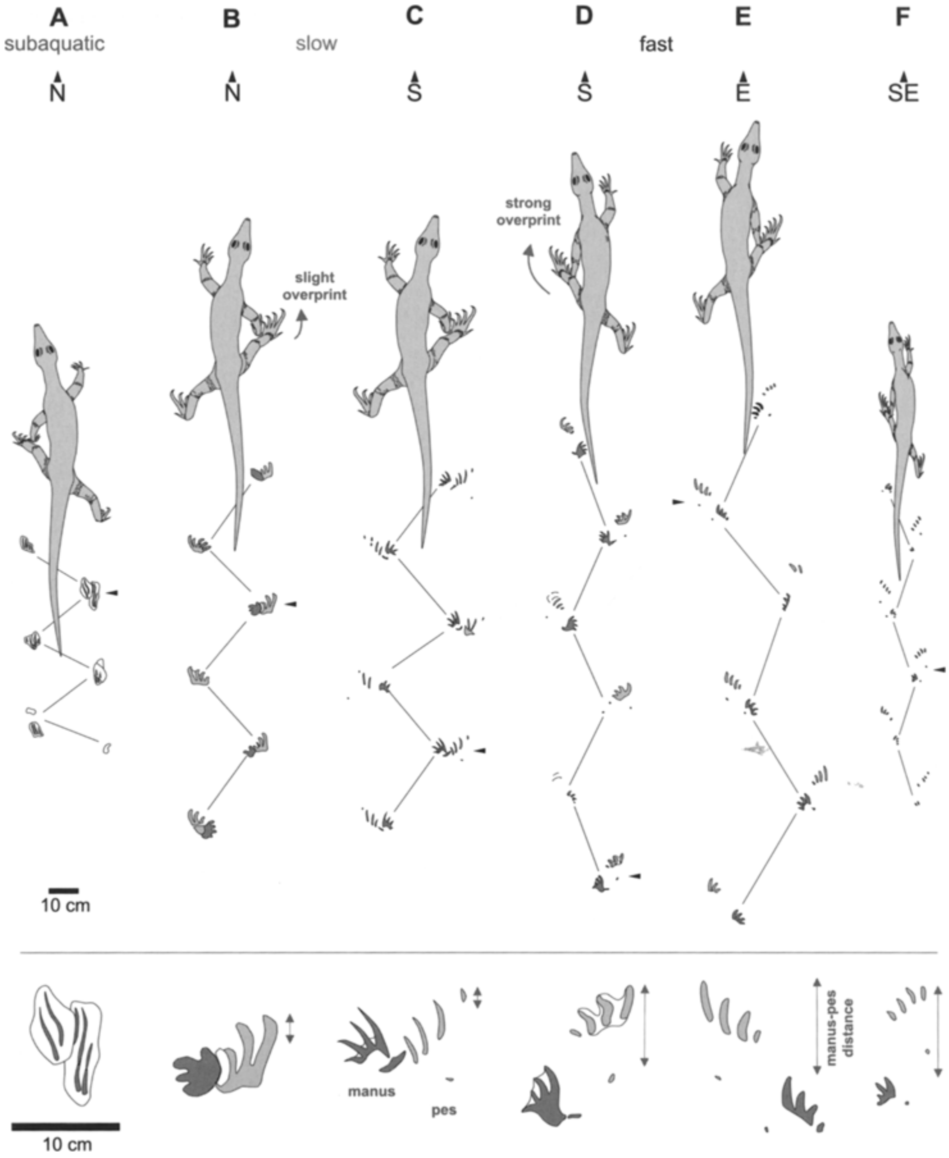

Fig. 12: Variability of tracks outlines, manus/pes distances and pace angulations of *Rhynchosauroides tirolicus* Abel in dependence on life activity and substrate moisture. Only six manus/pes sets are figured per trackway. – **A:** trackway of an subaquatic walking adult individual, track bed 9 (Oolithic member, Lower Muschelkalk Formation) from Borgholzhausen, **B:** trackway of an adult individual moving slow on very wet mud, track bed 9 (Oolithic member, Lower Muschelkalk Formation) from Borgholzhausen, **C:** trackway of an adult individual moving slow on wet mud, track bed III (Grenzgelbkalk member, Upper Bunter Formation) from Winterswijk, **D:** trackway of an adult individual moving fast on slightly wet mud, track bed IV (Grenzgelbkalk member, Upper Bunter Formation) from Hagen, **E:** trackway of an adult individual moving fast on slightly wet mud, track bed III (Upper Röt Pelit member, Upper Bunter Formation) from Winterswijk, **F:** trackway of an adolescent individual moving fast on slightly wet mud, track bed IV (Grenzgelbkalk member, Upper Bunter Formation) from Hagen (Graphics: PaleoLogic).

Undoubtedly the Middle Triassic trackmaker was not a modern lacertilian, but it had very close proportions with a few longer extremities or shorter body length and walked in the same modus. Therefore only *Macrocnemus* (Fig. 13) can be suggested as the only possible trackmaker, although there are reptiles in the track beds of the track site Winterswijk all representing sauropterygians (Oosterink et al. 2003), except *Sphenosphargus* (described in Oosterink et al. 2003 as *Dactylosaurus* sp., in Diedrich 2002e as *Cymatosaurus*). This prolacertilian has a pedal anatomy that fits more to the tracks of *Procolophonichnium* and is recently under study to focus on this trackmaker. The described reptiles from the Upper Bunter/ Lower Muschelkalk boundary of Winterswijk (cf. Diedrich 2001a) such as *Nothosaurus, Neusticosaurus, Anarosaurus, Tanystropheus* or *Placodus* (Oosterink et al. 2003) do not fit into the pedal anatomy of the *Rhynchosauroides* tracks. The *Macrocnemus* manus and pes anatomy (Fig. 13B) in contrast fits very well into those tracks (Figs. 13C, D).

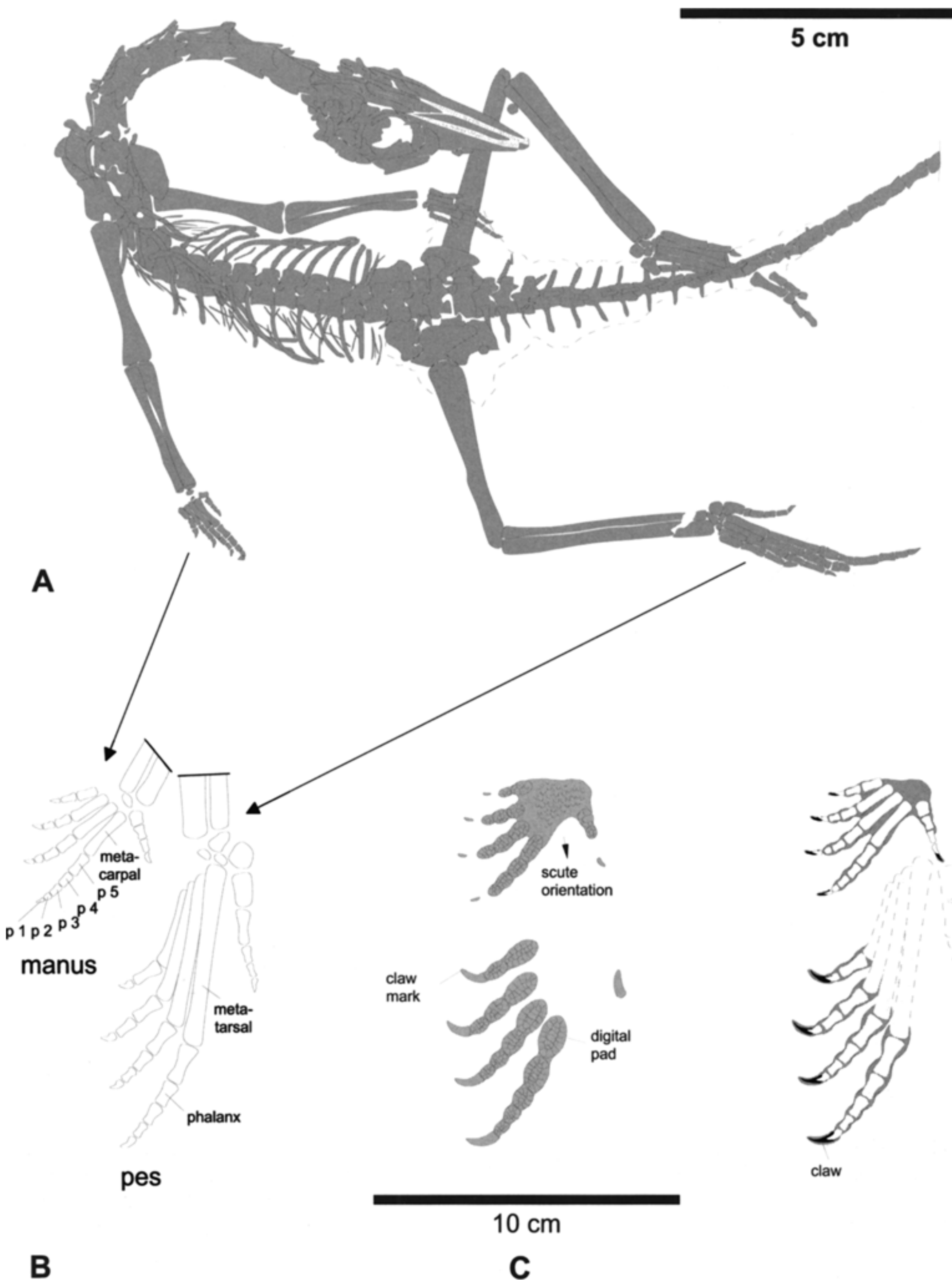

Fig. 13: The possible producer of *Rhynchosauroides tirolicus* Abel trackways in the Lower to Middle Triassic: the prolacertilian *Macrocnemus bassani* (Nopcsa 1930). –
A: Skeleton of a juvenile individual from the Genzbitumen Zone of the Middle Triassic of Switzerland (redrawn from Brinkmann 1994), **B:** reconstruction of the manus and pes anatomy, **C:** Reconstruction of the *Rhynchosauroides tirolicus* Abel manus/pes imprint set with digital pads and dermal scutes structure, **D:** projection of the pedal skeleton of *M. bassani* onto the *R. tirolicus* track (Graphics: PaleoLogic).

The habitat "Middle Triassic carbonate intertidal flat"

Thinking about *Macrocnemus* as the trackmaker of *Rhynchosauroides* trackways in carbonate intertidal flat environments of the Germanic Basin, but maybe also sandy coastal zones in the European Alps (cf. Avanzini & Renesto 2002) and eastern border of the Massif Central (cf. Demathieu 1985), the following palaeoecological model can be presented.

The intertidal carbonate flats of the entire southern Middle Triassic Germanic Basin surrounded the old massifs such as the Rhenish and the Vindelizic Massif. These tidal flat regions were more wide spanned about decakilometers in the western (The Netherlands, Northwest Germany) and less in width hundreds of meters to about thousand meters in the eastern Basin as a result of the basin morphology with its western oriented carbonate ramp (subtidal basin reconstruction see also

Knaust 1998). Sequencially these intertidal biolaminate flats moved basin- or landwards depending on regressions or transgressions more than 20 times during the upper Lower to upper Middle Triassic. The mostly shallowing upward sequences of the Muschelkalk Formation were caused mostly by basin tectonics, proved by submarine slumps in the basin centre (cf. Knaust 1998).

In the lower and upper intertidal flats two reptile species must have used this special carbonate tidal flat environment as their primary permanent habitat. Unfortunately there are recently no lizards living in the carbonate tidal flats to compare their ecology. The one small non-identified trackmaker left fossil tracks of *Procolophonichnium*, which were found more commonly in the biolaminates of the upper intertidal zones (= *Procolophonichnium* ichnofacies, cf. Diedrich 1998a). In the lower intertidal mostly the second ichnofacies of *Rhynchosauroides* is abundant, but the Ichnogenus also known from the upper intertidal. The possible trackmaker *Macrocnemus* must have foraged daily in these carbonate tidal flats. A non-diverse invertebrate fauna is known from this hypersaline intertidal environment and figured especially from the track site Winterswijk (cf. Oosterink 1986), but here from levels above the track beds, which represent a different facies. One of the invertebrates the *Rhynchosauroides* track makers could have preyed upon, suggested in Diedrich & Schulz (2003), might have been crustaceans such as *Clytiopsis*. This medium sized shrimp has lived in the upper intertidal zones, and environments that were influenced periodically by fresh water. Therefore a scenario of a *Macrocnemus* population feeding in the lower intertidal on crustaceans in the tide ponds and channels is presented here. By feeding and hunting they left thousands of tracks by basking, running, slow moving and by walking and swimming paraxially through the channels and ponds. The thoughts of Rieppel (1989), that *Macrocnemus* could run bipedal on its hind limbs over short distances can not be proved yet at the Middle Triassic trackways.

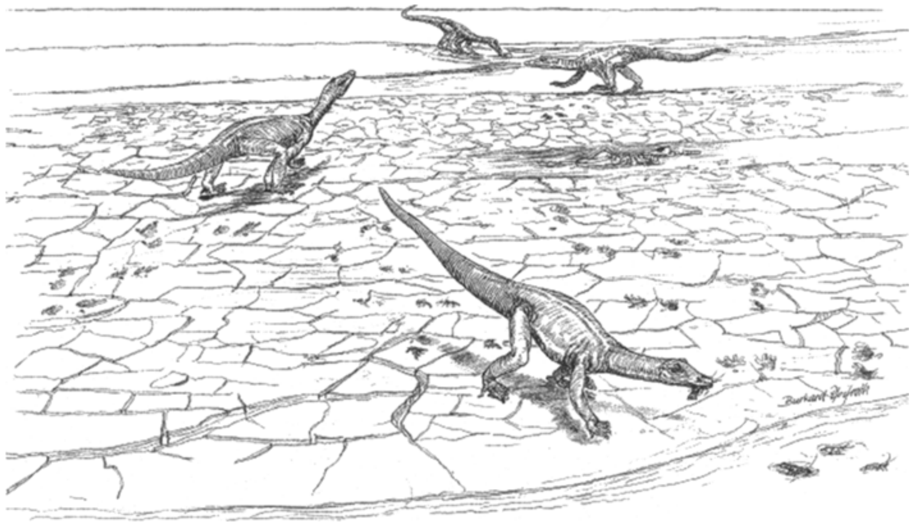

Fig. 14: *Macrocnemus* in a mud cracked carbonate tidal flat covered by bio films and cut by tide channels and ponds in which marine invertebrates (here the crustacean *Clytiopsis*) and vertebrates like fishes were caught in theses traps being the food for prolacertilians. Daily tide change and activities of many animals of different age and varying moving to swimming activities left thousands of tracks around the entire Germanic Basin during the Middle Triassic (Muschelkalk) (Illustration: B. Pfeifroth).

Acknowledgements

I am most grateful to Molly McQuarrie for allowing using her pet iguana for the experiments, for accompanying us in the field, and for persuading the animal to make the right tracks in the right mud! Thanks to Dr. D. Gardner of the Zayed University of Abu Dhabi for his managements and collaboration in the field. I am very grateful to the quarry director of the Steen-en Kalkgroeve near Winterswijk, Dr. J. Mentink, who kindly gave a permission to study the quarry-section, Mr. Brockmeyer of the Landschaftsbehörde Osnabrück, for prospecting and excavation permission, Mrs. A. Leipner of the Museum am Schölerberg Osnabrück, Natur und Umwelt for assistance of the excavations at the Silbersee near Hagen and H. Oosterink, who gave me access to invaluable information on the occurrence of invertebrate and vertebrate remains of Winterswijk. Dr. M. Bertling integrated kindly the excavated track slab of Winterswijk, Prof. Dr. R. Springhorn of the Lippische Landesmuseum Detmold supported the study of the material in the Detmold region. Also thanks to the city Osnabrück, especially the UNESCO-Geopark *Terra. Vita* manager H. Escher for collecting permission at the Westerberg and other localities in the Lower Saxony area of the Osnabrücker Bergland. Dr. Fichter of the Naturkundemuseum Kassel Ottoneum and Dr. E. Mönnig of the Naturkundemuseum Coburg integrated the material in their regional collections. Financial support for this study was provided by the Lippische Landesmuseum Detmold, Geologisch-Paläontologisches Museum der Westfälischen Wilhelms-Universität Münster, the Museum für Natur und Umwelt Am Schölerberg Osnabrück, the Paläontologische Bodendenkmalpflege of Hess in Wiesbaden, and the palaeontological consulting company PaleoLogic, that sponsored the experiments in the Arabian Gulf. Finally the first manuscript was thankfully reviewed by Dr. G. Köhler and Dr. J. Fichter.

References

Avanzini, M. & Renesto, S. (2002): A review of *Rhynchosauroides tirolicus* Abel, 1926, Ichnospecies (Middle Triassic: Anisian-Ladinian) and some inferences on *Rhynchosauroides* trackmaker. – Rivista Italiana di Paleontologia e Stratigrafia, **108** (1): 51–66; Milano.

Brand, L.R. (1996): Variations in Salamander trackways resulting from substrate differences. – Journal of Paleontology, **70** (6): 1004–1010; London.

Demathieu, G.R. (1985): Trace fossil assemblages in Middle Triassic marginal marine deposits, eastern border of the Massif Central, France. – Society of Economic Paleontologists and Mineralogists Special Publication, **35**: 53–66; Tulsa.

Demathieu, G.R. (1988): New discoveries of ichnofossils from the Middle Triassic of Winterswijk (The Netherlands). – Geologie en Mijnbow, **67** (1): 3–17; Amsterdam.

Demathieu, G.R. & Oosterink, H.W. (1983): Die Wirbeltier-Ichnofauna aus dem Unteren Muschelkalk von Winterswijk (Die Reptilfährten aus der Mitteltrias der Niederlande). – Staringia, **7**: 1–51; Winterswijk.

Diedrich, C. (1997): Erste Ausgrabungsergebnisse einer neuen Wirbeltierfährtenfundstelle aus der Oolith-Zone (Bithyn, Unterer Muschelkalk) von Borgholzhausen (Teutoburger Wald, NW-Deutschland). – Terra Nostra, **97** (7): 42, 138; Daun.

Diedrich, C. (1998a): Saurier und Saurierfährten im -Triassic Park- von Borgholzhausen. – Heimatjahrbuch Kreis Gütersloh, **1998**: 74–78; Gütersloh.

Diedrich, C. (1998b): Stratigraphische Untersuchungen der Ichnofaziestypen einer neuer Wirbeltierfährtenfundstelle aus dem Unteren Muschelkalk des Teutoburger Waldes, NW-Deutschland. – Neues Jahrbuch für Geologie und Paläontologie Monatshefte, **1998** (10): 626–640; Stuttgart.

Diedrich, C. (1998c): Vertebrate tracks of the Oolith-Zone (Bithyn, Lower Muschelkalk) from the middle Teutoburger Wald (NW-Germany) and their stratigraphical and palaeogeographical significance. – Hallesches Jahrbuch Geowissenschaften, B, **5**: 36–37; Halle/Saale.

Diedrich, C. (1998d): Vertebrate track ichnofacies types of the Oolith member (Lower Muschelkalk, Middle Triassic) in the central Teutoburger Wald (NW-Germany) and their stratigraphical, facial and palaeogeographical significance. – Zentralblatt für Geologie und Paläontologie, I, **1998** (7–8): 1–15; Stuttgart.

Diedrich, C. (2000): Neue Wirbeltierfährten aus dem Unteren Muschelkalk (Mitteltrias) des Osnabrücker Berglandes und Teutoburger Waldes (NW-Deutschland) und ihre stratigraphische und paläogeographische Bedeutung im Germanischen Becken. – Neues Jahrbbuch für Geologie und Paläontologie, Abhandlungen, **217** (3): 369–395; Stuttgart.

Diedrich, C. (2001a): Vertebrate track bed stratigraphy of the Upper Bunter and basal Lower Muschelkalk (Middle Triassic) of Winterswijk (East Netherlands). – Geolgie en Mijnbow/Netherland Journal of Geosciences, **80** (2): 31–39; Amsterdam.

Diedrich, C. (2001b): Auf den Spuren von *Rhynchosauroides* und *Procolophonichnium* in den Karbonatwatten der Germanischen Trias – neue Ergebnisse zur Ichnotaxonomie, Stratigraphie und Verbreitung. – Terra Nostra, **01/6**: 148–150; Oldenburg.

Diedrich, C. (2001c): Megatracksites in Triassic carbonate tidal flats of the Germanic Basin in Central Europe and their consequences onto the palaeogeography and sequence stratigraphy. – Schriftenreihe der Deutschen Geologischen Gesellschaft, **14**: 41–42; Hannover.

Diedrich, C. (2002a): Wirbeltierfährten aus dem Unteren Muschelkalk (Mitteltrias) von Thüringen (SE-Deutschland). – Neues Jahrbuch für Geologie und Paläontologie Monatshefte, **2002** (2): 75–91; Stuttgart.

Diedrich, C. (2002b): Die Wirbeltierfährtenfundstelle Borgholzhausen (Teutoburger Wald, NW-Deutschland) aus der Oolith-Zone (Bithyn, Unterer Muschelkalk). – Paläontologische Zeitschrift, **76** (1): 35–56; Stuttgart.

Diedrich, C. (2002c): New megatracksites in the Upper Wellenkalk member (Lower Muschelkalk) and *orbicularis* member (Middle Muschelkalk, MiddleTriassic) of the western Germanic Basin. – Palaeogeography, Palaeoclimatology, Palaeoecology, **2819** (2002): 1–24; Amsterdam.

Diedrich, C. (2002d): Feinstratigraphische Untersuchungen der Wirbeltierfährtenhorizonte des Unteren Muschelkalkes am Westerberg in Osnabrück (NW-Deutschland). – Osnabrücker Naturwissenschaftliche Mitteilungen, **27**: 21–38; Osnabrück.

Diedrich, C. (2002e): Megatracksites in middle Triassic carbonate tidal flats in Central Europe – the sensation – trackmakers in-between trackbeds. – Journal of Vertebrate Paleontology, **22** (3), Abstracts: 49A; Boulder.

Diedrich, C. (2003): Die Wirbeltier-Fauna aus einer Bonebed-Prospektionsgrabung in der *enodis/posseckeri*-Zone des Oberen Muschelkalkes (Unter-Ladin, Mitteltrias) von Lamerden (NW-Deutschland). – Philippia, **2003** (11/2): 133–150; Kassel.

Diedrich, C. (2005a): Actuopalaeontological trackway experiments on intertidal flat carbonates of the Persian Gulf – a comparison to fossil tracks of Middle Triassic carbonate tidal flat Megatracksites in the Germanic Basin. – Abstract, Sediment, **2005**, 18–20. July; Bern.

Diedrich, C. (2005b): Dinosaur megatracksites in Croatia on the Adriatic carbonate platform – stratigraphy, sedimentology, and palaeoenvironment of the shallow subtidal, tidal flat to sabkha in the Middle Cenomanian to Lower Turonian of Hvar Island. – Abstract, Sediment, **2005**, 18–20. July; Bern.

Diedrich, C. & Fichter, J. (2003): Eine erste Saurierfährten-Grabung im Unteren Muschelkalk (Anis, Mitteltrias) von Größenlüder, Nordhessen (NW-Deutschland). – Philippia, **11** (2): 109–132; Kassel.

Diedrich, C. & Gardner, D. (2004): Lacertilian trackway experiments in the carbonate tidal flats of Al Dabb'iya, western Abu Dhabi, U.A.E. – Tribulus, **13** (2): 23–28; Abu Dhabi.

Diedrich, C. & Oosterink, H. (2000): Bergings- en documentatietechniek van *Rhynchosauroides peabodyi* (Faber) – Sauriersporen op de grens Boven- Buntsandsteen/Onder Muschelkalk van Winterswijk. – Grondboor & Hamer, **54** (6): 125–130; Maastricht.

Diedrich, C. & Schulz, M. (2003): Erstnachweis von *Clytiopsis* sp. Bill 1914 im Obersten Röt (Anis, Untertrias) von Schachten, Nordhessen (NW-Deutschland). – Philippia, **2003** (11/2): 103–108; Kassel.

Evans, G. & Kirkham, A. (2001): The Abu Dhabi Sabkha. – In: Barth, H.-J. & Boer, B. [Eds.]: Sabkha Ecosystems: The Arabian Peninsula and adjacent countries: 7–20; Dordrecht (Kluwer).

Evans, G., Kirkham, A. & Carter, R.A. (2002): Quaternary development of the United Arab Emirates Coast: New evidence from Marawah island, Abu Dhabi. – GeoArabia, **7** (3): 441–458; Bahrain.

Fichter, J. (1982): Aktuopaläontologische Untersuchungen an den Fährten einheimischer Urodelen und Lacertilier. Teil I: Die Morphologie der Fährten in Abhängigkeit von der Sedimentbeschaffenheit. – Mainzer naturwissenschaftliches Archiv, **20**: 91–129; Mainz.

Fichter, J. (1997): Vorläufige Mitteilung über ein Vorkommen von Tetrapodenfährten im Mittleren Muschelkalk bei Lamerden, Nordhessen. – Philippia, **8** (1): 61–72; Kassel.

Gerdes, G., Krumbein, W.E. & Holtkamp, E. (1985): 11. Salinity and Water Activity Related Zonation of Microbial Communities and Potential Stromatolites of Gavish Sabkha. – Ecological Studies, 53. In: Friedmann, G.M. & Krumbein, W.E. [Eds.]: Hypersaline Ecosystems, 238–266; Berlin-Heidelberg (Springer-Verlag).

Kirkham, A. (1997): Shoreline evolution, aeolian deflation and anhydrite distribution of the Holocene, Abu Dhabi. – GeoArabia, 2 (4): 403–416; Bahrain.

Kirkham, A. (1998): A Quaternary proximal foreland ramp and its continental fringe, Arabian Gulf, UAE. – In: Wright, V.P. & Burchette, T.P. [Eds.]: Carbonate ramps. Geological Society of London, Special Publications, **149**: 14–41; London.

Knaust, D. (1998): Trace fossils and ichnofabrics on the Lower Muschelkalk carbonate ramp (Triassic) of Germany: tool for heigh resolution sequence stratigraphy. – Geologische Rundschau, **87**: 21–31; Berlin.

Müller, H. (1972): Ökologische und ethologische Studien an *Iguana iguana* L. (Reptilia: Iguanidae) in Kolumbien. – Zoologische Beiträge, **18**: 109–131; Berlin.

Nopcsa, F. v. (1930): Notizen über *Macrochemus Bassani* nov. gen. et nov. spec.. – Centralblatt für Mineralogie, Geologie und Paläontologie, B, **1930**: 252–255; Berlin.

Oosterink, H.W. (1986): Winterswijk, Geologie Deel II. De Triasperiode (geologie, mineralen en fossielen). – Weten. Mede. Konink. Nederl. Natuurhist. Verenig., **178**: 1–120, Winterswijk.

Oosterink, H.W., Berkelder, W., Jong, C. de, Lankamp, J. & Winkelhorst, H. (2003): Sauriers uit de Onder-Muschelkalk van Winterswijk. – Staringia, **11**: 1–144, Winterswijk.

Peyer, B. (1931): *Macrocnemus* nicht *Macrochemus*. – Centralblatt für Mineralogie, Geologie und Paläontologie, B, **1931**: 190–192; Berlin.

Peyer, B. (1937): Die Triasfauna der Tessiner Kalkalpen. XII. *Macrocnemus bassani* Nopcsa. – Abhandlungen Schweizer Paläontologische Gesellschaft, **59**: 3–140; Zürich.

Rieppel, O. (1989): The hind limb of *Macrocnemus bassanii* (Reptilia, Diapsida): Development and functional anatomy. – Journal of Vertebrate Palaeontology, **9**: 373–387; Lawrence.

Warren, J.K. (1989): Evaporite sedimentology. – 285 pp., Prentice Hall Inc.; New Jersey.

Manuscript received 25.02.2005
Revised version accepted 12.08.2005