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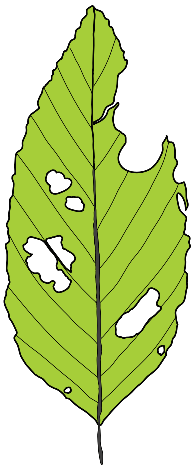

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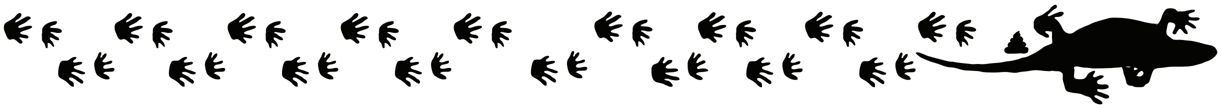
Halle (Saale), Germany; 23rd - 29th September



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Abstracts of
Presentations

Quantification of morphological variation in Late Triassic to Early Jurassic theropod tracks of southern Africa

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Abstract:

The Upper Triassic-Lower Jurassic of southern Africa preserves a plethora of dinosaur tracks. In this study, we examine ~200, high-quality tridactyl tracks attributed to theropod trackmakers in the Elliot [subdivided into the lower (lEF) and upper (uEF)] and basal Clarens formations to quantify track morphological variation across a time span of ~35 million years.

Statistical methods, such as canonical variance and principal component analysis (PCA), show that the tracks in the lEF and Clarens Formation form two distinct morphological clusters, while the tracks in uEF span across these two tight domains. Stratigraphic trends, from oldest to youngest, include: an average increase in track lengths (TL) and track widths (TW), a slight increase in TL/TW ratios, and a decrease in digit III projection. These temporal changes can be summarized into an overall decrease in mesaxony. These results, though to different degrees, are mirrored in statistical tests comparing the ~200 tracks based on the size class of these tridactyl tracks (e.g., small < 15 cm, large > 25 cm). This correlation between stratigraphic and size class trends would be expected, because the size class distribution is closely linked to stratigraphy; e.g., lEF primarily preserves tracks that are < 25 cm long, while the Clarens Formation predominantly preserves tracks that are > 30 cm long. Classical systematic ichnological treatment combined with PCA mostly assign these theropod tracks to the Grallator-Anchisauripus-Eubrontes plexus, within which an increase in track size and a decrease in digit III projection are observed (OLSEN et al., 1998).

Keywords: Upper Triassic, Lower Jurassic, Karoo Basin, theropod tracks, geostatistics

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Trace fossils, water table and depositional evolution in eolian systems (Cretaceous Mulichinco Formation, subsurface of western Argentina)

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Abstract:

Our knowledge of the ichnology of eolian systems is expanding at a relatively fast pace. However, previous research is based either on modern environments or on outcrops, with essentially no ichnologic work performed on core. Study of cores from the Lower Cretaceous (Valanginian) Mulichinco Formation, El Mangrullo oil field, Neuquén Basin, western Argentina, allows reconstructing trace-fossil distribution as a response to temporal changes in the position of the water table. Accordingly, this study yields insights into how ichnologic information may help to reconstruct depositional evolution in eolian systems. A combined ichnofacies-ichnofabric approach was used. In addition, ichnologic information was integrated with sedimentologic and sequence-stratigraphic datasets.

Four ichnofabric associations comprising ten ichnofabrics have been recognized. The eolian dune ichnofabric association comprises the *Digitichnus* isp., *Arenicolites* isp., and dwelling burrow ichnofabrics, as well as some occurrences of the *Skolithos linearis* ichnofabrics 1 and 2. This association occurs in the lower and middle intervals of the studied unit. The eolian sand sheet ichnofabric association comprises the *Planolites* isp.-*Palaeophycus* isp. ichnofabric 1 and the laminated filled vertical burrow ichnofabric, as well as some occurrences of the *Skolithos linearis* ichnofabrics 1 and 2. It is present in the lower and middle intervals of the Mulichinco Formation. The interdune ichnofabric association comprises the *Planolites* isp.-*Palaeophycus* isp. ichnofabric 2 and the *Taenidium* isp. ichnofabric 1. This association occurs in the middle interval of the studied unit. The fluvial sheet flood ichnofabric association is represented by the *Taenidium* isp. ichnofabric 2. It is present in the upper interval of the Mulichinco Formation.

The studied succession comprises a 3rd-order depositional sequence, which has been subdivided into three 4th-order sequences. The latter are stacked in a backstepping pattern as a result of a rise in the water table. The base of the 3rd-order sequence is represented by the intra-Valanginian unconformity that in the study area separates marine deposits below from continental deposits above. Overall, the 3rd-order sequence reflects the vertical transition from a dominance of eolian dune deposits to eolian sand sheet and fluvial sheet flood deposits, the latter intercalating with marginal-marine intervals. Integration of ichnologic, sedimentologic and sequence-stratigraphic datasets indicates a temporal evolution from hyper-arid to arid and semi-arid conditions.

Both the *Scoyenia* and *Entradichnus-Octopodichnus* ichnofacies are identified. The *Scoyenia* ichnofacies is present in damp interdune and ephemeral fluvial deposits. The *Entradichnus-Octopodichnus* ichnofacies occurs in eolian dune and sand sheet deposits. This study provides further support to the notion of an archetypal eolian ichnofacies.

Keywords: bioturbation, dunes, interdunes, continental ichnology, Neuquén Basin, reservoirs

Overview of the Permian and Triassic tetrapod trackway localities in Saxony-Anhalt, Germany

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Abstract:

Permian tetrapod track localities in Saxony-Anhalt have been listed by VOIGT (2012) in his review on tetrapod ichnology of the German Rotliegend deposits: In addition to ichnotaxonomically problematic occurrences in the Ilfeld Basin (southern Harz Mountains) and Saale Basin, Early Permian anamniote and reptilian tracks, including the ichnotaxa *Batrachichnus, Ichniotherium* and *Dromopus*, have been described from the Flechtingen and Föhrberg Formations of the Flechtingen-Rosslau Block. Tetrapod footprints from different localities in Saxony-Anhalt include various types of swim traces and trackways referred to the ichnogenera *Amphisauropus* and *Dromopus* from the late Middle Permian (Hornburg Formation, Hornburg Saddle) and *Erpetopus* from the Late Permian (Eisleben Formation, Sangerhausen Trough) of the Saale Basin.

Here we discuss recent finds from two localities, which will also be visited during the ICCI 2019 field trip: (1) a relatively well-preserved trackway of *Amphisauropus* from the Konberg Quarry (Hornburg Formation) that differs morphologically markedly from the Thuringian Forest specimens of *Amphisauropus*, (2) a recently discovered rich ichnofauna from the late Middle to early Late Permian deposits of the Mammendorf Quarry (Elbe Subgroup, Flechtingen-Rosslau Block, Southern Permian Basin) that includes, among others, the ichnogenus *Erpetopus* and therapsid tracks. The most abundant type of vertebrate traces from Mammendorf are up to 28-cm-wide oval-shaped to elongate paired scratches and hole-like perforations indicative for a shallow burrowing behavior.

Triassic tetrapod footprints are known from Early and Middle Triassic strata: A few older finds of isolated chirotheriid imprints have been documented from continental Middle Buntsandstein deposits of the Subhercynian Basin (central Saxony-Anhalt), outcropping in the Merkel and Baalberge quarries in the vicinity of Bernburg. DIEDRICH & TROSTHEIDE (2007) described six new trackway localities in the Subhercynian Basin and eight occurrences in the Querfurt and Freyburg troughs (southern Saxony Anhalt). These finds come from marginal marine deposits of the Upper Buntsandstein (Röt) and Lower to Middle Muschelkalk. In this depositional environment, unlike the abundant ichnotaxa *Procolophonichnium* and *Rhynchosauroides*, chirotheres usually constitute only a minor ichnofaunal element. The Solvay Quarry in Bernburg (Saale) has yielded the richest yet described ichnofauna within marlstones of the Middle Muschelkalk. It includes trackways of *Rhynchosauroides tirolicus, Procolophonichnium haarmuehlensis, Isochirotherium herculis* and *Chirotherium barthii* in addition to limulid tracks and other invertebrate traces typical for tidal flat deposits (see also DIEDRICH 2011 and ICCI 2019 field guide).

Keywords: Mammendorf Quarry, Konberg Quarry, Solvay Quarry, Hornburg Formation, Muschelkalk

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The Late Jurassic vertebrate footprint collection of the Sociedade de História Natural in Torres Vedras (Portugal)

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Abstract:

The Late Jurassic of the Lusitanian Basin (Portugal) has yielded significant theropod and sauropod tracksites (e.g.: Pedra da Mua, Avelino, Cabo Mondego) plus recent findings of isolated dinosaur tracks. The Sociedade de História Natural (SHN) in Torres Vedras houses a significant collection of yet mostly undescribed dinosaur tracks from the Late Jurassic. The footprints have been collected from different Kimmeridgian-Tithonian geological formations (Amoreira-Porto Novo, Alcobaça, Sobral and Freixial formations) that mainly outcrop across the Consolação and Turcifal sub-basins of the Lusitanian Basin. The footprints have been collected in different localities at the base of the cliffs, mainly isolated and dispersed. The collection is composed of more than a hundred of footprints and the majority of them are preserved as isolated sandstone natural casts. Nonetheless, some specimens are preserved as microconglomerate natural casts or in limestones (either as casts or true tracks). The majority of the footprints are tridactyl dinosaur tracks of variable sizes. Among them, several symmetric with high interdigital angle and low mesaxony tracks probably produced by ornithopod/ornithischian dinosaurs are noteworthy. Three main morphotypes (*Anomoepus*-like, *Dineichnus*-like and Iguanodontipodidae) have been identified. In addition, medium to large sized theropod tracks (*Megalosauripus transjuranicus*-like) have been also identified. Small (grallatorid-like) and gigantic theropod and sauropod tracks, plus some possible crocodylomorph traces complete this outstanding collection. These new occurrences increase the previously known Late Jurassic ichnodiversity in the Lusitanian basin.

Keywords: Ornithopoda, Theropoda, Sauropoda, Crocodylomorpha, Kimmeridgian, Tithonian

An overview to the Cenozoic tracksites of Aragón (Spain)

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Abstract:

The southern margin of the Pyrenees and its foreland Ebro Basin in Aragon (northeastern Spain) presents a great wealth of Cenozoic tracksites that range from the Late Eocene to the Miocene. Recently, a palaeoichnological itinerary through the main sites has been proposed emphasizing the value of this palaeontological heritage as a tourist and educational resource and the geoconservation work carried out on the tracksites. The site of Bailo-Arrés is located in a transitional stratigraphic unit (Yeste-Arrés sandstone unit, Late Eocene) and has preserved at least two different types of artiodactyl, as well as perissodactyl and carnivore (feliform-like) footprints. The Peralta de la Sal and La Sagarreta tracksites occur in an alluvial unit (Peralta Formation, Early Oligocene) and show bird and mammal (artiodactyl, perissodactyl and carnivore) tracks. The Abiego tracksite is located in a lacustrine unit (Peraltilla limestones, Early Oligocene) and displays three different types of artiodactyl tracks. Casa de la Tejera is preserved in a fluvial unit (Uncastillo Formation, Late Oligocene-Early Miocene) and shows indeterminate mammal tracks. Sierra de Luna is a lacustrine unit site (Alcubierre Formation, Early Miocene), where large quadrupedal mammal tracks (mainly perissodactyls) can be distinguished. The new sites of Alto del Poyero must be added to the itinerary. They occur in younger lacustrine-palustrine deposits of the Alcubierre Formation (Middle-Late Miocene), and are characterized by a high diversity of mammal (carnivor, artiodactyl, proboscidean) and bird tracks. Altogether, they show variation of the ichnofauna within a time range of 20-25 million years.

Keywords: birds, mammals, Eocene, Oligocene, Miocene

Plant-insect interactions of the Passo das Tropas outcrop, Santa Maria Formation, southern Brazil (Late Ladinian)

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Abstract:

This work focuses on traces produced in vegetative organs of the Triassic *Dicroidium* Flora, demonstrating a high rate of the damage types in corystosperm plants. The data correspond to *Dicroidium* Flora strata Lagerstätten from the Ladinian (Passo das Tropas outcrop = PTO), Santa Maria Formation, Paraná Basin. We use a qualitative and quantitative approach for morphological characterization of the traces, together with ontogenetic aspects of the plant-hosts for interpretation. The insect traces on Ladinian plants are composed principally of an infestation of scales (324 units). Furthermore, 16 mine traces and 76 traces interpreted as scars of oviposition are also registered. The different damage types were grouped in 17 damage types (DT), six of which are new. The correlation two-tailed test was applied for the pinna-pinnule height ($p = 0.07$) and width ($p = 0.37$) of corystosperms. The maximum scale diameter (new DT C) is not significantly correlated to the limb measures of the corystosperms, suggesting that a significant relation between the scale and the leaf size does not exist. The leaves of the corystosperms with scales appear significantly larger in width (Mann-Whitney, $U = 11639$, $p < 0.0001$), suggesting that herbivore organisms selected larger leaves. The external feeding indexes (11,45%), DT diversity and choice of host plants exhibit patterns that are similar to those found in Carnian sites from the Molteno Formation (Middle-Upper Triassic) of southern Africa.

Keywords: *Dicroidium* Flora, endophytic habit, scale insect, Santa Maria Formation, lagerstätten

The Triassic strata studied here is located in the City of Santa Maria, southern Brazil (29°44´37, 85´´S and 53°47´31, 12´´W), along the BR 392 highway. The phytofossils were extracted from 2.20 m of laminated mudstone. This mudstone alternates with massive, planar, and trough cross-bedded sandstones and conglomerates, the latter containing gravels and boulders of mud.

The material consists of 550 plant samples of the *Dicroidium* Flora, being composed of partial and entire corystosperm, ginkgoalean, cycadophyte, and voltzialean leaves, and stems of sphenophytes (Equisetaceae). The *Dicroidium* Flora assemblage comprises the following corystosperm genera that were determined based on the presence of their diagnostic features: *Xylopteris* (Frenguelli) Stipanicic & Bonetti 1996, Zuberia Frenguelli 1946 and *Dicroidium* Gothan 1912. Ginkgoalean taxa were previously identified by Barboni & Dutra (2015) and Barboni et al. (2016).

The record of damage types by order of diversity is the following: oviposition (6 DTs), surface feeding (3 DTs), piercing and sucking (4 DTs), mines (2 DTs), margin feeding (1 DTs), hole feeding (1 DT) (Fig. 1). The *Dicroidium* flora of the PTO shows an abundance of scales (piercing-and-sucking) in corystosperms (82%), its distribution being related to the wide of the foliar organ of the host plants.

Corystosperms have different leaf morphotypes, where the congeneric *Dicroidium* related forms are the most used as host (42.2%), followed by congeneric *Zuberia* forms (27.4%) and the congeneric *Xylopteris* forms (10.2%). Ginkgo congeneric hosts have similar rates of trace proportion compared with *Zuberia* forms (*Baiera*/24.1%, *Sphenobaiera*/33.3%). In addition, the Ginkgoaceae forms are the second most abundant host and have a lower rate of herbivorized proportion (25.5%) compared with corystosperms. However, Ginkgoaceae have the highest rate of interacted hosts when the ovipositions are summed (57.5%). The *Baiera* (51.7%) and *Sphenobaiera* (75%) morphotypes present the highest rates of interacted leaf proportions, but with a low number of specimens (47 leaves) compared with the corystosperms (424 leaves).

The Molteno Formation (Middle to Late Triassic) are examples compatible with trace patterns from PTO. At least 14 locations from the Molteno Formation have DT diversity (106 localities studied) that are comparable to PTO. Furthermore, damage types that occurred in PTO showed a diversity of ovipositions of 6 DTs similar to the maximum indexes of diversity of the Triassic from the Molteno Formation (see Labandeira et al., 2013). Labandeira et al. (2013) also register one of the localities of Ladinian age with a lower diversity of 11 DTs from PTO (16 DTs). The DT diversity recorded from PTO has similar indices to the localities of Carnian sites from Africa. Lara et al. (2016) record the DT12 and oviposition on a stem of a sphenophyte from the Potrerillos Formation (Carnian) of the Cuyana Basin, Mendoza, Argentina; both traces are registered in the PTO, and, as well, in the same plant groups.

African strata document the largest variety of damage types in Mesozoic strata so far, mainly the Aasvoëlberg 411 site. The similarity in DTs from the Aasvoëlberg 411 site and from PTO is demonstrated by the occurrence of 6 equal DTs, which are hosted by the same groups of plants (*Heidiphyllum*, *Dicroidium*, ginkgoalean leaves) (Labandeira et al. 2013).

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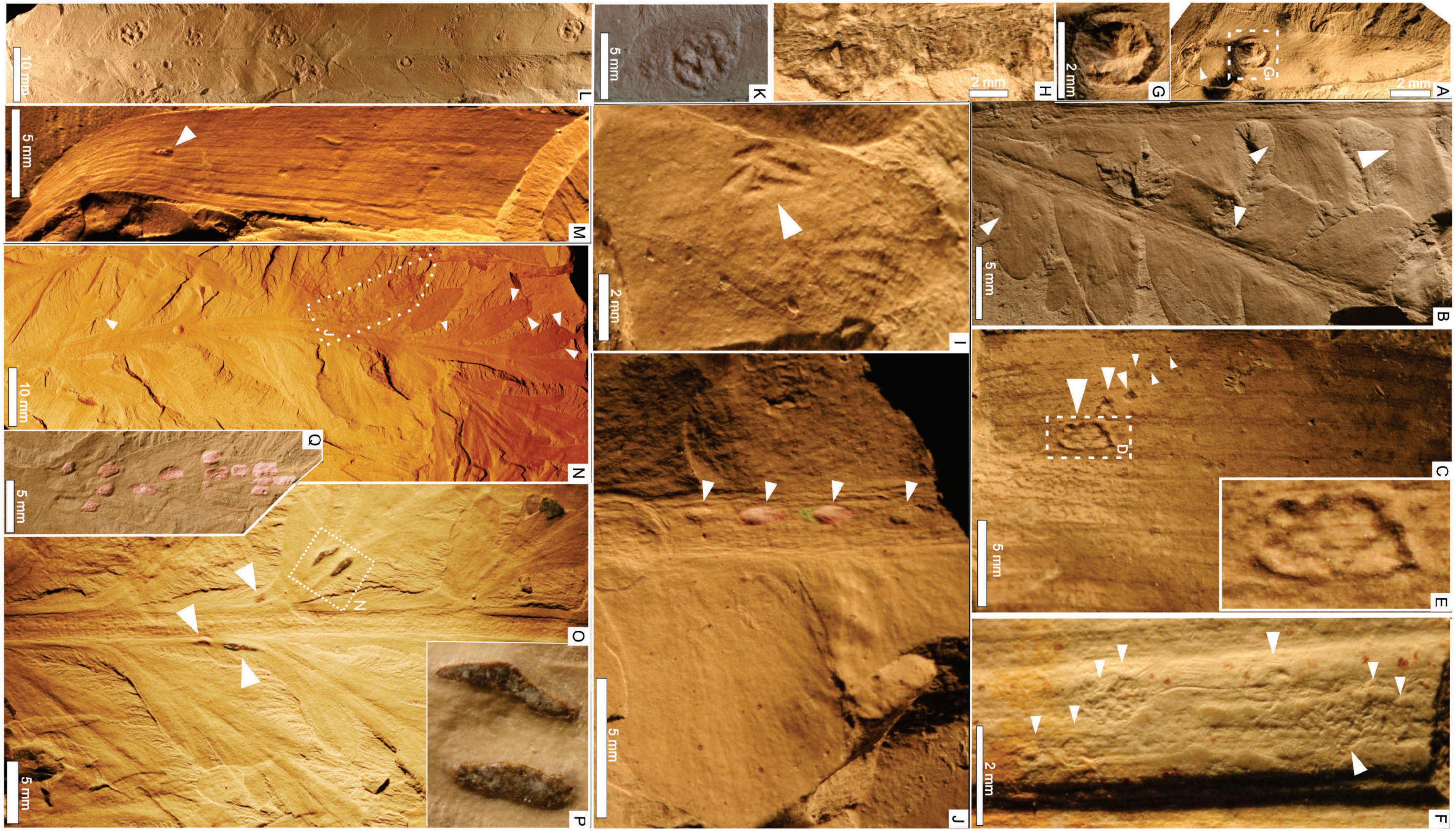

Fig. 1. Damage type representatives of the PTO. Scales and mines in the left side area: A, G: Large scale (pinna) and juvenile scales on *Dicroidium longifolium* (ULVG11137/new DT C). H: Scale distributed on *Zuberia* sp.; the region with scales were enlarged (ULVG11028/new DT C). K, L: Scales in the most infested specimen distributed in the entire leaf area on *Dicroidium odontopteroides* (ULVG9353/new DT C). M: Mine in *Heidiphyllum* sp.; oviposition site (arrow) (ULVG9297/DT71). External feeding traces in the upper right area: B: Three margin feeding in different pinnae of *Dicroidium odontopteroides* (ULVG11070/DT12). C, D: Surface feeding in five spots on *Heidiphyllum* sp., see detail in figure D (ULVG11124/new DT A). F: Wrinkled marginal tissue reacted by the insect puncturing in the lamina on *Sphenobaiera sulcata* (ULVG-9763/new DT B). Oviposition in the lower right area: I: Oviposition overlapping egg scars without reaction tissue on *Dicroidium odontopteroides* (ULVG11194/new DT D). J: Egg scars in one oviposition action on *Dicroidium odontopteroides;* egg scars (pinkish areas) and the tissue reaction below (yelowish area) (ULVG9163b/new DT E). N, Q: Oviposition on *Xylopteris* sp., the egg scar is in pinkish color (ULVG11389/DT102). O, P: Egg scars on *Xylopteris rigida* (ULVG11397/DT76).

Possible death marks of coccomorphs (life position) on *Dicroidium odontopteroides* from the Passo das Tropas outcrop (Late Ladinian), Paraná Basin, Brazil

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Abstract:

We analyzed a compression of a Triassic phytofossil specimen of *Dicroidium odontopteroides* presenting a probable coccoid fossil with the trace fossil representing the last activity of the tracemaker (*Mortichnia*). The phytofossil sample presents a high-quality preservation. That sample comes from an interval of 2.2 meters-thick of laminated mudstone of the Passo das Tropas outcrop, Santa Maria Formation, Paraná Basin. The trackway produced by the coccomorph is composed of two pared track rows with a total of 1.6 mm in length and 1.5 mm in width. The imprints have a scratch shape and are regularly spaced, forming an angle of 40° to the mid-line. The trace fossil has 14 imprints that can be attributed to the *Diplichnites* ichnogenera, produced before the compression of the coccomorph. The preserved insect presents 3.75 mm in length and 2.87 mm in width. The dorsal-posterior anal ring is exposed. The absence of dorsal wax plates ornamentation is probably due to a fine clay of sediment that overlays the dorsal view. Although dorsal comprehension is not visible, the interpretation of coccomorphs affinities is enhanced by the association with 29 coccomorph dorsal compressions bearing dorsal wax plates ornamentation in the same plant from that stratigraphic interval. Female specimen is suggested by compressions of elongated posterior wax plates. The association of life position of the coccomorph and its trackway on the *Dicroidium odon-topteroides* indicate an event of fast burial in the depositional site. The tracemaker evidence will be examined by techniques of Micro-CT for further interpretations [CNPq e CAPES].

Keywords: coccoid, Coccoideae, Ortheziidae, *Dicroidium* Flora, lagerstätten

Application of a deltaic ichnological model to Holocene deltaic deposits: examples from the Nakdong River delta in the Southeastern Korean Peninsula

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Abstract:

Since sensitive reaction of organic behavior to an environmental change, ichnological analyses have given the information about a variety of physicochemical stresses of delta environments. While many analyses have been performed in ancient deltaic settings, little has been done in modern deltas. Through this study we applied ichnological models to the unconsolidated Holocene deltaic deposits of the Nakdong River delta, Korea, at core site ND-2, in order to track the sedimentary evolution and early Holocene sea-level jump recorded in discontinuity surface. Quantitative grain size data and age dating results helped a little interpretation of depositional settings.

The study interval (35-9 m depth) can be divided into six facies associations (lower shoreface, lower offshore, distal prodelta, proximal prodelta, distal delta front, and delta front). Around 8.5 ka ago, the sea-level jumped abruptly, and preserved as *Glossifungites* surface between lower shoreface and lower offshore. Deltaic deposition initiated around 6 ka ago with decelerating sea-level rise. The fining-upward succession of lower shoreface and lower offshore under transgressive system tract changes to coarsening-upward succession at the lower boundary of the distal prodelta facies association. Dominance of deposit feeding structures in sandy substrate of the distal delta front indicates high water turbidity representing proximity to river mouth.

Wave-dominated lower shoreface, lower offshore, prodelta, and distal delta front show uniform and moderate to high bioturbation indices (BI=3-5). Low sedimentation rate indicates a wide colonization window, and stressful condition to trace makers induced by freshets had been buffered by wave agitation. The mixed wave-, storm-, and river-dominated delta front represents a uniform and low bioturbation index (BI=0-2). High sedimentation rate indicates a narrow colonization window. Wave processes were still dominant, but hyperpycnal flow caused by intense storm and flood events easily overprinted original structures. With the proximity to the river mouth, organisms were affected by persistent stressful environments from riverine outflow.

Consequently, this study suggests that the ichnological models of ancient deltaic settings can be applied to the modern Nakdong deltaic setting, and ichnological analysis also might be a valuable tool in reconstruction of Holocene paleoenvironments.

Keywords: delta, Holocene, ichnology, *Glossifungites* surface, depositional processes, Nakdong River

Sedimentary evolution

The postglacial transgression of the study area was initiated around 15 ka ago (Park et al., 2000) and then the sea-level rise was decelerated around 6 ka ago (Park et al., 1996, Yang et al.). According to the result of radiocarbon and OSL age dating analysis of ND-2 sedimentary core, FA1 was deposited around 8.5-9 ka ago. This age dating result and fining upward succession of FA1 indicate that this unit belongs to transgressive system tract. At this age, the BH-1 core site, which is approximately 20 km landward of the ND-2 site, was in an estuary environment, and the ND-1 core site, which is 6 km landward of the ND-2 site, was in a river mouth area. Also, pre-studied Holocene sea-level curves represent the water depth of ND-2 site, at that time, was within the range of fair-weather wave-base. With integrated consideration with facies analysis, intercalated sand with mud facies totally disturbed by intense bioturbation, it can be determined that FA1 was lower shoreface environment at about 8.5-9 ka ago.

According to the research conducted for sea-level fluctuations of the southeastern Korean Peninsula, a sea-level jump occurred caused by rapid transgression around 8 ka ago. The transgressive erosion and non-deposition period because of the rapid landward shift of the depocenter led the formation of firm-ground, which is associated with the *Glossifungites* Ichnofacies observed at the boundary between FA1 and 2. This boundary can be defined as a within-trend flooding surface which is not a surface of sequence stratigraphy, but represents notable facies change owing to rapid transgression (Embry, 2002; Catuneanu, 2006). Reconstructions show the BH-1 site, 6-8 ka ago, as a bay environment, and the ND-1 site as an inner shelf environment. Also, the sea-level curves represent the water depth at this time was within the range of storm wave-base. Consequently, this integrated consideration of facies analysis of landward sites and the sea level curve support the environmental interpretation. The massive mud deposition of FA2 (lower offshore) occurred near storm wave-base, and this environment was seldom influenced by a riverine outflow. The accumulation rate at this period calculated from age dating analyses is very low.

The highstand system tract began 6ka ago, and the sea-level rose to the present level. The boundary between FA2 and FA3 is a maximum flooding surface, since the upward-fining succession changed to a coarsening upward trend at this boundary. A riverine outflow started to affect the sedimentary processes. The initiation of the Nakdong delta also developed during this period. Holocene worldwide delta initiations are within the time range of 6.5-8.5 ka ago. The deceleration of sea-level might cause the deltaic progradation. Despite the deltaic progradation caused by sea-level deceleration, the ND-2 site was located still far from the river mouth, and the sedimentation rate might be very low. Relatively high bioturbation index supports this low sedimentation rate. The opportunistic colonizers such as *Skolithos*, *Diplocraterion*, and *Bergaueria* concomitant with sand layers have relatively small sizes and relatively high abundance. These characteristics infer that these colonizers comprised r-selected populations, and it means that this prodelta environment was unstable to filter feeders. Settling from buoyant plume is the dominant depositional process under low energy conditions, and the sand layers such as tempestites and turbidites were deposited intermittently. Step-wised age dating errors of the upper FA4 can be considered as the intense bioturbation.

Around 3 ka ago, the sediment discharge slightly increased, and the sedimentary environment changed from prodelta (FA4) to distal delta front (FA5). Despite mud-dominated deposits, relatively regular tempestites intervals suggest that FA5 was seasonally influenced from storm or flooding events, and that the sedimentary rate slightly increased. Trace fossils were observed concomitant with sand layers dominated by deposit feeders rather than by filter feeders. These aspects are archetypal in deltaic settings, and with the increase of sediment discharge, water turbidity might become high in these periods. Generally in this facies association trace fossil assemblages represent high diversity, and have moderate size. These characteristics indicate the trace fossils formed r-selected population in this facies association. The moderate to intense bioturbation infers that the sedimentation rate was still low. The deposition might occur under a fair-weather wave-base.

The association of fluid mud and hummocky beds, and sparse bioturbation indicate that FA5 is a delta front facies association. Since the high sedimentation rate and the salinity fluctuation, the bioturbation intensity is very low. The lamination within fluid mud suggests wave processes were the dominant controlling factor in the Nakdong delta system.

Dominant controlling factor during the Nakdong delta evolution

The planform morphology of modern deltas can be classified as three end members by the dominant processes of river, wave, and tides, and there were many attempts to determine this classification by ichnological analyses mainly in ancient deltaic environments (Olariu et al., 2005; 2010; Olariu & Bhattacharya, 2006; Gingras et al., 1998; McIlory, 2004a; 2004b; Carmona et al., 2009). On the other, recent ichnological analyses proposed the mixed influence processes of river, wave, current, storm, and tide in delta evolution rather than the tripartite delta classification (Gani et al., 2008). Likewise the pre-conducted ichnological analyses of the ancient deltaic environments, the integrated analyses of sedimentology and ichnology of the mid to late Holocene deltaic deposits recovered from the ND-2 core site represent the changes of relative influence of river, wave, and storm in response to the Nakdong delta evolution.

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Ichnofossils of the Eocene Fossillagerstätte Geiseltal (Saxony-Anhalt, Germany)

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Abstract:

The Eocene Geiseltal fossillagerstätte (approximately 47.5-42.5 million years old; MP 11-MP 14) was discovered ca. 20 km SW of Halle (Saale), Saxony-Anhalt (Germany) during open cast lignite mining in the 1920's. Excavations took place until the early 2000's when the pits were flooded. The resulting Geiseltal Collection is part of the Natural Sciences Collections of the Martin Luther University Halle-Wittenberg. More than 50,000 specimens – about half of them vertebrates – from at least three Eocene depositional environments provide a detailed look at the flora and fauna of a subtropical peat bog ecosystem comprising six different habitats (Krumbiegel et al. 1983).

Local influx of carbonate-rich waters buffered humic acids, preserving both hard and soft tissues. Hence, several specimens preserved features such as feathers, scales, hair, and/or colour preservation (Voigt 1988).

Although lignite deposits are not known as important trace fossillagerstätten, a variety of ichnologically relevant specimens belongs to the Geiseltal Collection. Several ichnofossils were likely produced by crocodilians (Fig. 1A, B). This includes presumed and approved bite marks on mammal bones (early equids and the tapir-like perissodactyl *Lophiodon*) and turtle shells, as well as coprolites and stomach stones (geo-gastroliths)(Hellmund 2001, Wings 2012).

Beside their appearance in other crocodilian taxa including the planocraniid *Boverisuchus*, clusters of gastroliths are present in most articulated specimens of the alligatoroid taxon *Diplocynodon*, often still within the gastric area (Fig. 2). They are mostly composed of mm to cm sized vein quartz pebbles, which have otherwise rarely been found in the Geiseltal lignites. Isolated clusters of quartz pebbles without any connection to vertebrate fossils have been interpreted as evidence for crocodilian body remains completely dissolved in the acidic peat bog environment. While this is a likely scenario and a valid explanation for the clusters, the reported identification criteria of these gastroliths (e.g., etched surface texture; Hellmund 2001) are currently under critical review.

Aside from crocodilians, gastroliths also occur in the palaeognath bird *Palaeotis*. The composition and superficial appearance of these pebbles are similar to the crocodilian gastroliths from the Geiseltal.

Interestingly, there are at least eleven coprolite specimens from the Geiseltal which contain gastroliths (Fig. 1B).

About 100 complete coprolites and approximately the same number of coprolite fragments are preserved from the Geiseltal lignites. Most of them exhibit shapes ranging from flat and oval to elon-

gate; however, in rare cases the coprolites possess a sausage-like or ovoid outline (Fig. 1A). Geiseltal coprolites range in size from a few millimetres to a decimetres scale. They occasionally contain bone fragments, claws or plant remains. Plant remains from lophiodontid coprolites as well as gut contents revealed an herbivorous diet including grass and foliage (Weigelt 1935, Fischer 1964).

Gut contents are also known from other taxa including *Palaeotis*, the artiodactyl *Amphirhagatherium* and the equid *Propalaeotherium*. They were only studied from the latter (Weigelt 1940, Wilde & Hellmund 2010). Extracted plant matter, pollen and seed imprints from the equid digestive contents reveal a mixed diet, dominated by foliage and including flowers and seeds/fruits (Wilde & Hellmund 2010).

Aspects of invertebrate ichnology, including plant-insect-interactions such as feeding traces on leaves, are not yet investigated. However, due to the wide spectrum of fossils of phytophagic invertebrates from Geiseltal (i.e. about 150 insect taxa), feeding traces are likely to occur. A preliminary survey among the palaeobotanical Geiseltal collection revealed several leaves unambiguously damaged by feeding insects as well as a much higher number of potential occurrences of feeding damage (Fig. 1C, D). Furthermore, Weigelt (1935) shortly mentions insect burrows in several excavated seeds.

The insect feeding traces on the Geiseltal flora may help advance our understanding of the evolution of a very specific set of plant-insect interactions: latex defences in plants and pre-ingestion behaviours of insect to deactivate these defences including vein-cutting strategies to drain the latex and make the leaf safe to eat (Dussourd & Denno 1991). The Geiseltal flora includes one of the earliest fossil examples of latex (called 'Monkeyhair', from an undetermined member of the family Apocynaceae) (Hagel et al. 2008, Wilde & Riegel 2010). An ongoing study investigates insect damage on Apocynaceae leaves from the Geiseltal, looking specifically for the distinctive vein-cutting damage, in order to reveal if insects had already developed this latex-circumventing behaviour in the Eocene.

A peculiar ichnofossil might have been created by fly larvae of the family Calliphoridae interacting with *Lophiodon* remains. Larvae were mainly discovered inside the spongy bone, between bones, inside the nasal parts of the skull, inside *Lophiodon* gut content and also in the coal surrounding the skull (Weigelt 1935, Weigelt 1940). We currently aim to reconstruct traces of larvae penetration, feeding or moving on bone, in gut contents or surrounding sediment.

Keywords: coprolites, gastroliths, fly larvae, plant–insect interaction, bite marks

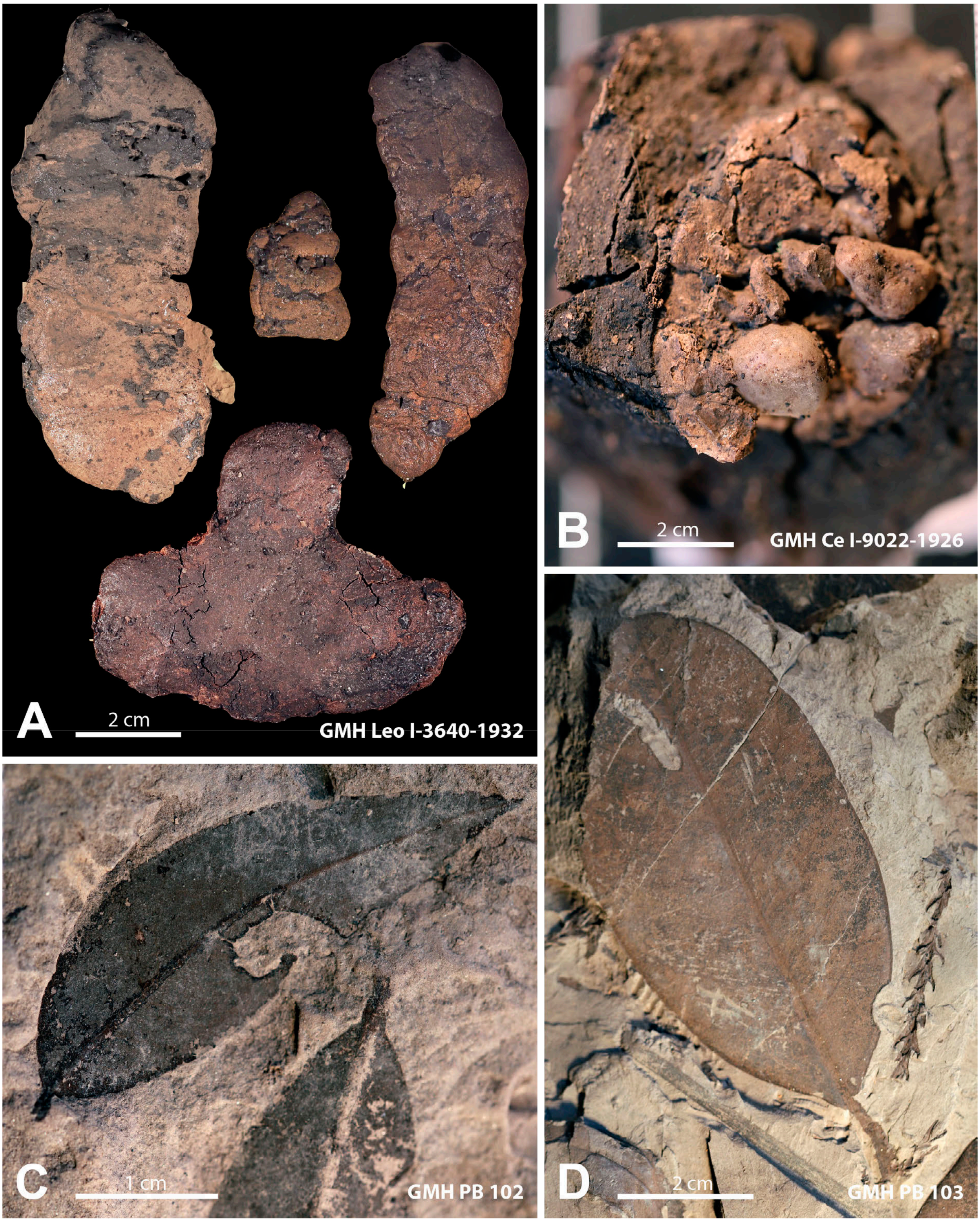

Fig.1: Selected ichnofossils in the Geiseltal Collection, Halle (Saale); A: Coprolites (GMH Leo I-3640-1932) of different shapes and sizes, possibly from crocodilian producers; B: Coprolite (GMH Ce I-9022-1926), still embedded in coal, containing several gastroliths; C: Undetermined angiosperm leaf (GMH PB 102) with insect feeding damage; D: Undetermined angiosperm leaf (GMH PB 103) with insect feeding structures on the lower right margin and close to the leaf axis.

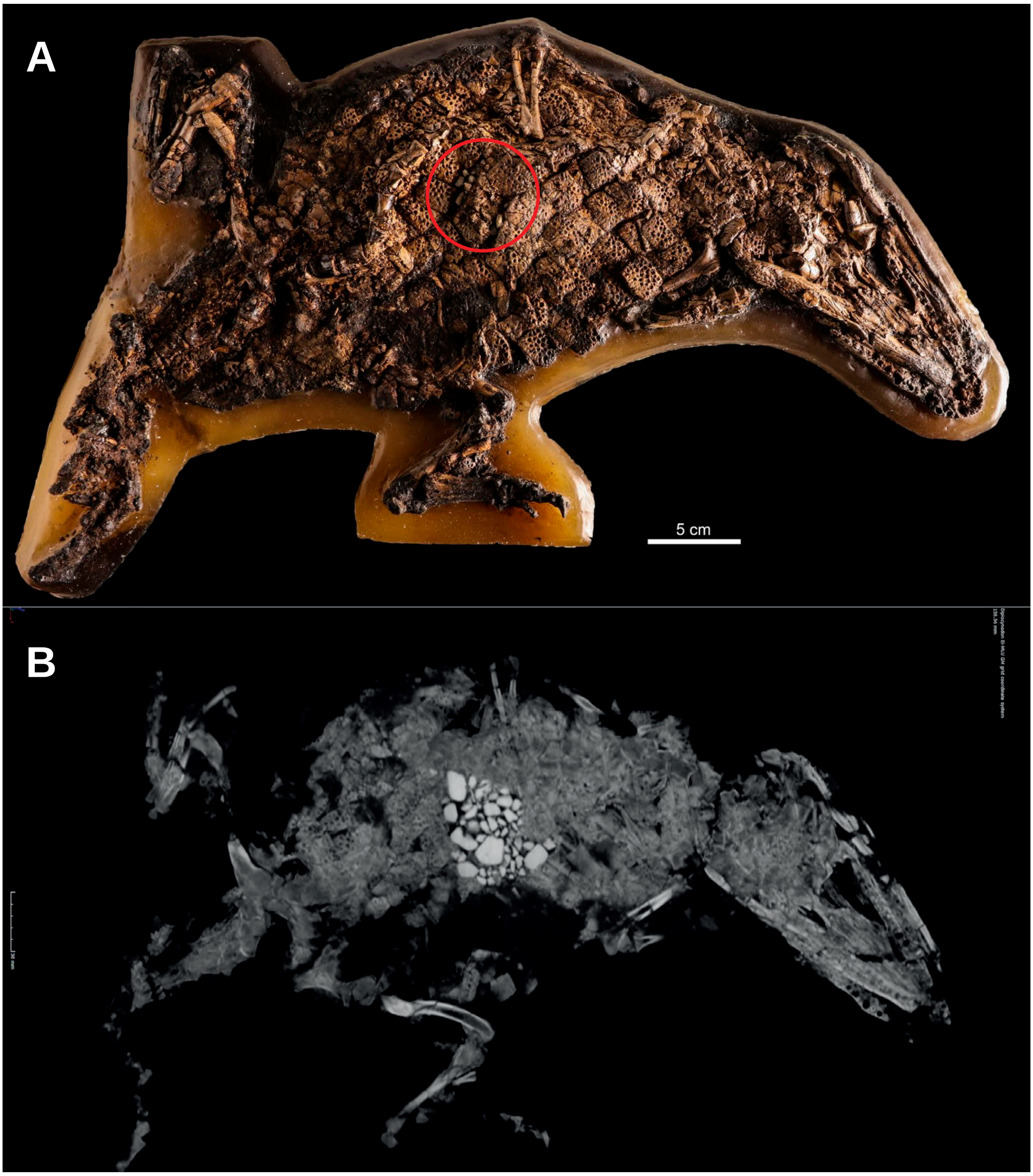

Fig. 2: Articulated skeleton of the alligatoroid crocodilian *Diplocynodon* (GMH Leo II-9000-1932); A: The skeleton GMH Leo II-9000-1932 reveals gastroliths (red circle) in the gastric area; B: CT-scan of GMH Leo II-9000-1932 at the Leibnitz-Institute for Zoo- and Wildlife Research Berlin revealed a much higher number of the gastroliths underneath the osteoderms.

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Track formation mechanisms elucidated by computer simulation and bi-planar X-ray

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Abstract:

We demonstrate, through the use of computer simulation and bi-planar X-ray data, that track volumes formed by narrow-toed feet, such as those of theropods and birds, may be penetrative, rather than transmissive in nature. Penetrative tracks and undertracks do not look like the feet that made them, which has made them less attractive to study. Despite the lack of anatomical correlates, penetrative tracks can be exquisitely preserved and provide a wealth of information about their track makers and vertebrate track formation more broadly.

Key words: simulation; dinosaur; DEM; digitization; biomechanics

Tracks are three-dimensional structures whose initial morphology is defined entirely by the anatomy of the foot, consistency of the substrate, and dynamics of the lower limb (and ultimately the whole animal). This Anatomy-Substrate-Dynamics concept has been invoked by several authors in different forms, including ternary diagrams (Padian and Olsen 1984), Venn diagrams (MINTER, BRADDY, & DAVIS 2007) and multi-dimensional axes (FALKINGHAM 2014). Understanding the formational process then, can potentially shed light on soft-tissue anatomy, environmental conditions when the track was made, and locomotor kinematics of the track maker.

Whilst anatomy will remain relatively constant throughout a trackway (indeed, throughout many trackways left by that animal), substrate and dynamics will vary far more dramatically. Changes in substrate can be highly localized (e.g. walking on a beach from dry sand to the water's edge), and as substrates become softer, the foot will sink deeper. Relative to a firm substrate standard, deeper sinking entails altered movement and the potential for greater step-step kinematic variation. Tracks made in deep, soft, substrates will necessarily record a more complete and complex foot-substrate interaction (GATESY et al. 1999; MILÀN, CHRISTIANSEN & MATEUS 2005; COBOS et al. 2016) than tracks left on shallow firm substrates. The deeper the foot sinks, the more motion is recorded in the reorganisation of sediment grains.

When the sediment behaviour includes an element of flow, grains and particles are free to move around pedal structures under load. The weight of the animal will not be supported and the foot will descend, perforating superficial layers before reaching its maximum depth. We refer to tracks created by this mechanism as 'penetrative' tracks, because the foot does not simply deform, but actually perforates the surface (and subsurface; 'penetrative undertracks') layers (GATESY & FALKINGHAM , in Review). The result is a sequence of interfacial surfaces below the original tracking surface that record the motion of the foot.

The concept of a 'track volume' is not new. Indeed, it was the 'father of ichnology' EDWARD HITCHCOCK that first illustrated the concept of 'undertracks' (HITCHCOCK 1858, 1841). HITCHCOCK's figures have generally been interpreted as describing the transmission of displacement beneath the foot-sediment interface, producing 'transmitted undertracks'. As we have discussed elsewhere (GATESY & FALKINGHAM, in review), it is not clear if this was in fact HITCHCOCK's original understanding.

Undertracks were an under-acknowledged phenomenon in vertebrate ichnology for well over 100 years, until work in the 1980's and onwards emphasised the importance of sub-surface deformations (Allen 1989, 1997; Jackson, Whyte & Romano 2010; Jackson, Whyte & Romano 2009; Manning 2004; Milàn & Bromley 2006, 2008; Milàn, Clemmensen & Bonde 2004; Falkingham et al. 2011). Much of this work concerned transmission of displacement beneath the foot-sediment interface, producing progressively less defined copies of the "True track" with depth.

However, our experimental work with a chicken-like bird, the guineafowl, employing bi-planar X-rays and computer simulation (Falkingham & Gatesy 2014; Gatesy & Falkingham 2017), has shown that very little deformation is actually transmitted below the sinking foot, at least for relatively narrow-toed feet such as birds and other theropods. Instead, the narrow toes penetrate sediment layers, leaving behind a series of nested V's beneath the tracking surface, all of which are "direct tracks" that have been formed through explicit contact with the trackmaker's foot (Gatesy 2003).

To illustrate sediment flow and penetrative track and undertrack formation, Figure 1 shows a computer simulation carried out using the discrete element method to simulate particle motions around a vertically indenting cylinder. The simulation shows how sediment collapses behind the descending cylinder and creates v-shaped penetrative tracks. This phenomenon is not limited to arbitrary indenters, but occurs with real foot morphologies and motions too, with individual toes behaving just like the cylinder in our simulation (Ellis & Gatesy 2013; Milàn & Bromley 2008).

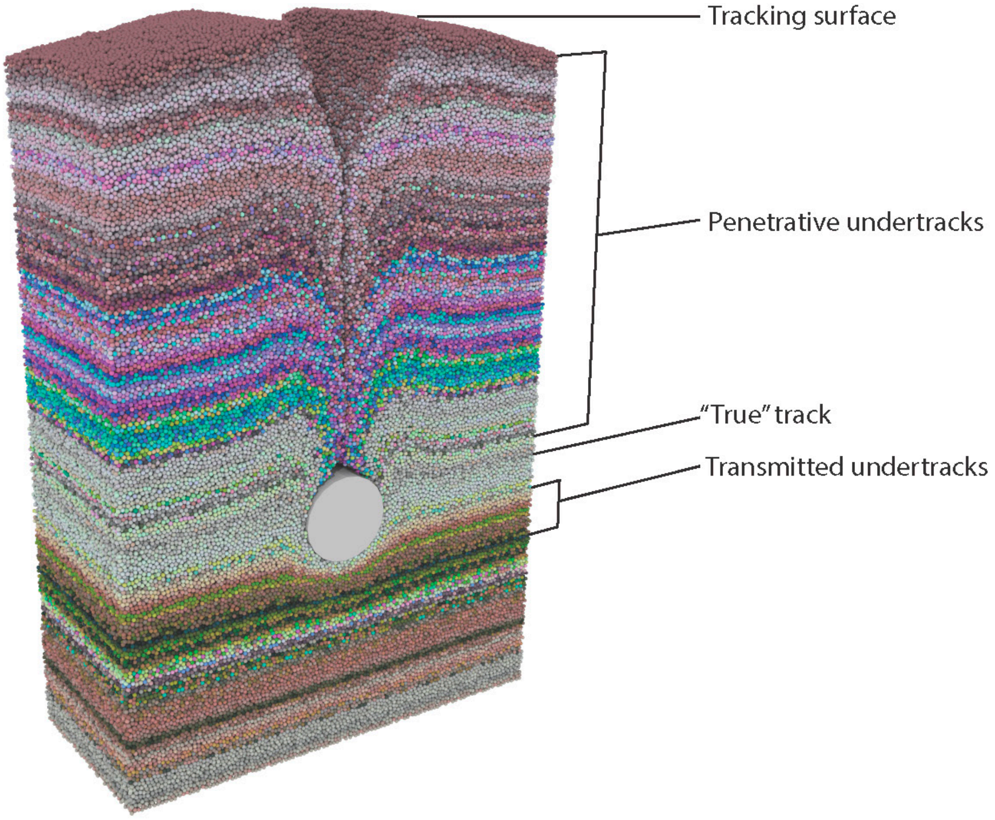

Fig. 1 - Discrete Element simulation demonstrating penetrative track and penetrative undertrack formation. Note that the depth beneath the indenter that transmitted undertracks occur is very shallow compared to the distance over which penetrative undertracks occur. From Gatesy and Falkingham (in review).

We have previously demonstrated the 3D capture of subsurface foot motions in guineafowl traversing soft substrates (Falkingham & Gatesy 2014), through the use of XROMM; X-ray Reconstruction of moving morphology (Gatesy et al. 2010; Brainerd et al. 2010). Incorporating the foot motions captured with XROMM into our DEM simulations results in surface tracks almost identical to the real tracks, but allows us to expose subsurface deformations as layers or slices.

Vertical slices through our simulations exhibit nested 'V' shapes where the toe has passed through laminations. These are identical to our abstract indenter simulations, but also to cut sections through dinosaur tracks (Figure 2), demonstrating that this mechanism occurs in both computational and real-world cases.

Our footprint simulations also provide a means of identifying what these tracks will look like if exposed at some surface beneath the original layer the animal walked on. The fossil track collections held at the Beneski Museum of Natural History, Amherst College – many of which were collected and curated by Edward Hitchcock, contain a wide range of penetrative dinosaur tracks. Hitchcock collected many tracks that appeared to have been made by animals with extremely thin toes. Hitchcock named these tracks 'leptodactylous' to reflect this interpretation. However, exposing our simulated penetrative tracks on sub-surface layers presents thin impressions much narrower than the toes that made them. Flow and collapse of soft sediment behind the sinking digits creates slit-like impressions. The degree to which these slits are prepared or naturally broken can determine how thick they appear.

Knowing that toes have penetrated through the exposed surface can provide information regarding the path of the foot. Many of the tracks in the Hitchcock collection appear on both upper and lower surfaces of specimens, and sometimes over multiple slabs. Tracking foot features over multiple surfaces can provide a means of documenting the path the foot took, and providing information about foot anatomy and motion, as well as substrate behaviour, that would not be available from a single surface.

Ironically, these highly informative tracks are often ignored or treated superficially in the literature, cast aside in preference of 'footprints' that appear more like a mould of an animal's foot. This second class status extends to terminology; the terms 'well preserved' or 'elite' have been used by some authors to exclusively refer to those tracks with clear anatomical features. We have previously made the case that such deep and 'messy' tracks should be considered no less well-preserved than a perfect impression of a foot in firm clay, if we are to maintain any consistency between osteological and ichnological vocabulary (Gatesy & Falkingham 2017). This has met with some resistance (e.g. Marchetti et al. 2019), but we maintain that calling the guineafowl tracks in Figure 3, recorded immediately after they were made, anything but 'well preserved' is misleading and incorrect. Further, to focus on anatomical correlates is to take vertebrate ichnology back to a time when ichnotaxa were analogous to species taxa, and raises points for discussion about what ichnotaxonomy is for; is it purely to communicate morphology, or is it to attempt to quantify biological diversity?

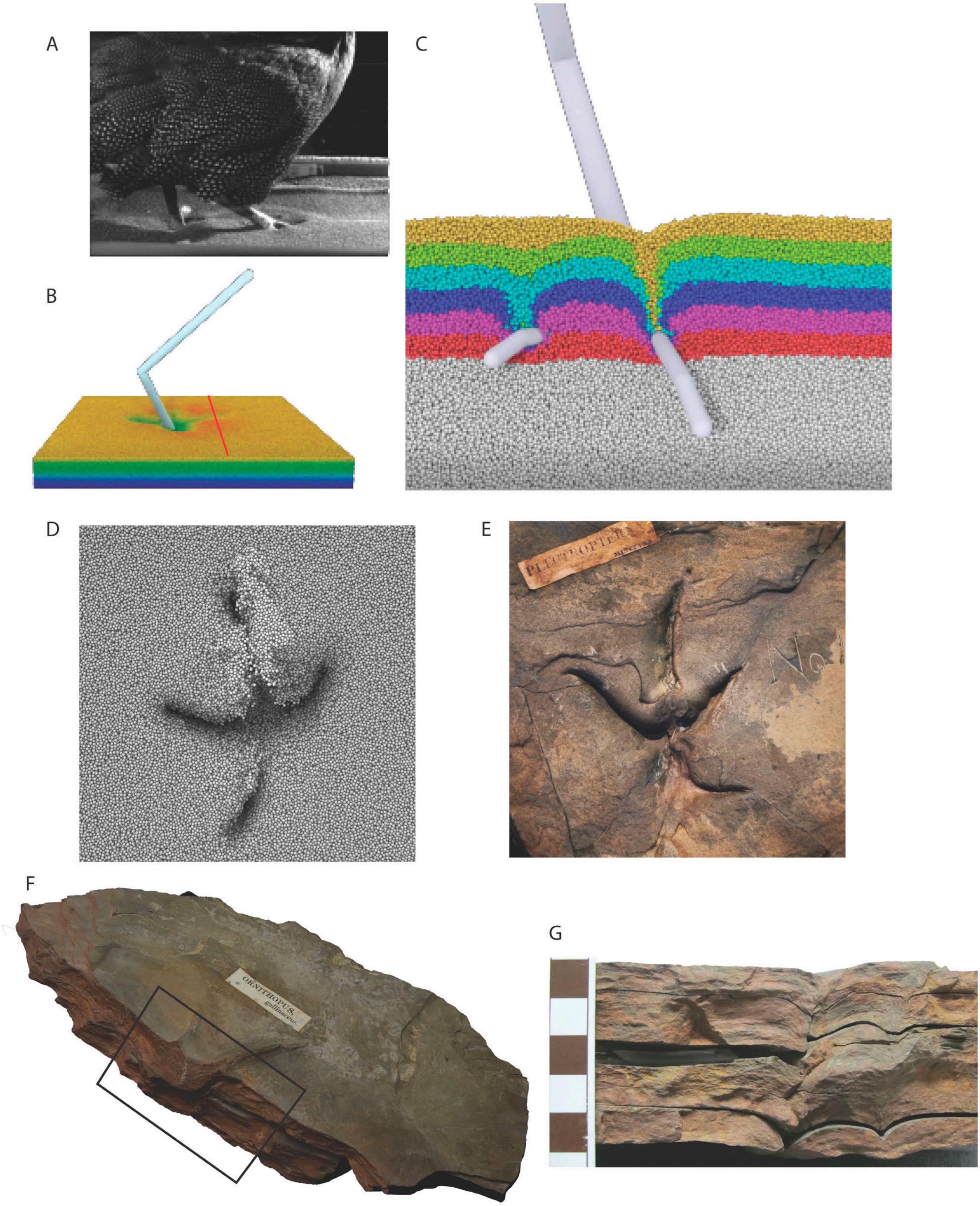

Figure 2 - Simulations and fossil tracks showing penetrative formation. Video (A) and XROMM-DEM simulation (B) of guineafowl track formtion, presented as a cross section in C. D) sub-surface layer exposed as though the track volume was broken along a lamination, displaying narrow, V-like digits very similar to the fossil specimen (E) ACM-ICH 32/28 from the Beneski Museum of Natural History. F & G show a track preserved in cross-section (specimen ACM-ICH 41/4).

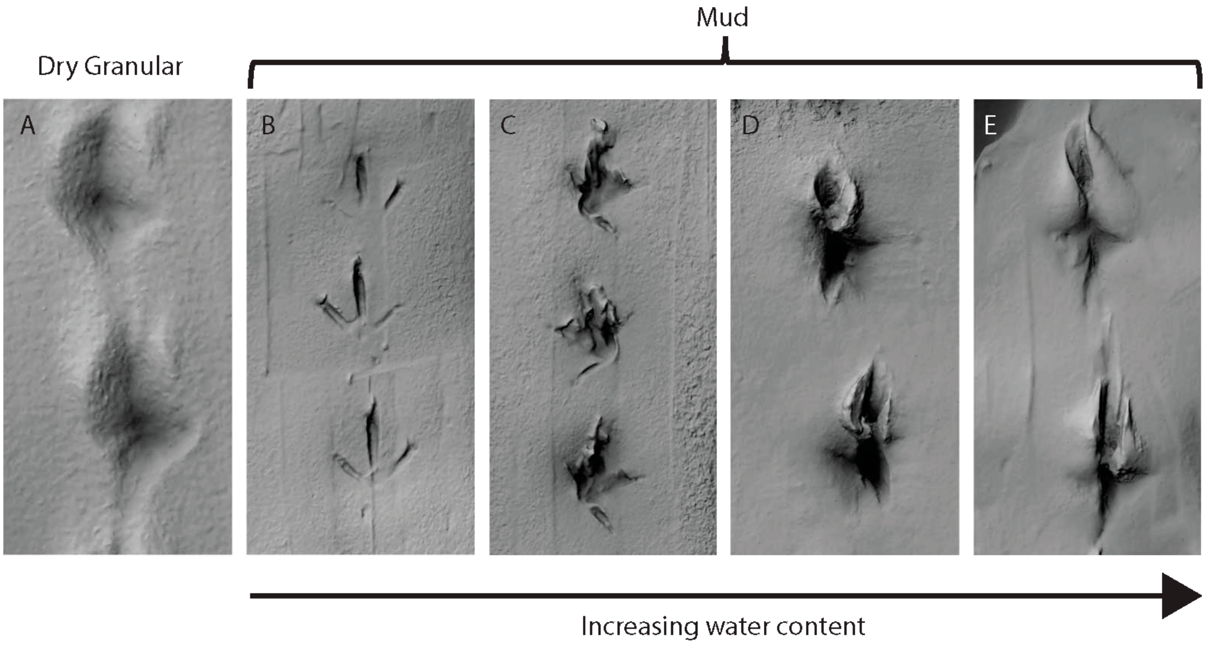

Figure 3 - Photogrammetric models of Guineafowl tracks recorded immediately after formation. A Dry granular medium (poppy seeds, behaving similar to dry sand). B-E Tracks left in a clay mixture at various levels of hydration. Note that only when walking over a firm mud (B) does the Guineafowl leave tracks that record anatomical correlates. Fossil tracks similar to those in A, C-E are often referred to incorrectly as 'poorly preserved' due to a lack of anatomical fidelity. Modified from Gatesy and Falkingham (2017).

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Revisiting and exploring Middle-Late Triassic vertebrate tracksites in Ardèche (southern France)

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Abstract:

The southeastern border of the Massif Central is a key area for ichnology in France. Indeed, it concentrates many Middle-Late Triassic vertebrate tracksites in which several vertebrate ichnospecies have been defined since the 1960s. Many of these localities are now part of the Regional Natural Park of the Ardèche Mounts that became a UNESCO Geopark in 2015. Given the major scientific and patrimonial interest of this area, we have started a detailed, updated inventory of vertebrate tracks and trackways, checking already known sites and prospecting for new ones. At present, about 15 sites have been referenced and more than 600 tracks have been recorded. Anisian/Ladinian ichnoassemblages are dominated by pentadactyl chirothere tracks (*Chirotherium*, *Isochirotherium*, *Brachychirotherium*, *Sphingopus*), tridactyl *Coelurosaurichnus*-type tracks and small pentadactyl lacertoid *Rhynchosauroides*. Norian ichnoassemblages are largely dominated by tridactyl *Grallator* tracks but also contain *Otozoum*/*Pseudotetrasauropus* footprints and rare chirothere trackways. Interestingly, many of these fossil traces have been preserved in coarse sediments, apparently without any contribution of microbial mats. Using field observations, thin sections, as well as image contrasting techniques and 3D modelling, our project aims at revising the ichnodiversity of these sites based on statistical grounds, at understanding the taphonomic pathways involved and at protecting this remarkable ichnological patrimony.

Keywords: Ardèche, Triassic, ichnoassemblage, vertebrates, Geopark

Dinosaur footprints from Dinosaur State Park (East Berlin Formation, Lower Jurassic, Rocky Hill, Connecticut, USA)

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Abstract:

Dinosaur State Park (DSP) in Connecticut preserves a spectacular occurrence of tridactyl dinosaur footprints from the Lower Jurassic East Berlin Formation. The tracks are impressed in sediments that accumulated in a rift valley created during the early stages of separation of North America from Africa that led to creation of the Atlantic Ocean (McDonald 2010). These footprints have repeatedly received brief attention in the literature (e.g. Farlow & Galton 2003; Galton & Farlow 2003). Using maps and photographs created by Galton when the track occurrences were initially discovered, subsequent on-site examinations of the trackways by Farlow, and laser-scanning and digital modeling by Hyatt, we embarked on a project of full-scale documentation of the DSP footprints, part of which is presented here.

There are two occurrences of footprints at DSP, a larger East Tracksite that was re-buried after Galton's fieldwork, and a smaller West Tracksite (Fig. 1; informally known as the "Trackway") that is presently protected by a surrounding building. Most of the footprints accessible to study are in the West Tracksite. Footprints occur in two beds, the uppermost of which (Tier 1) immediately overlies the other (Tier 0). Some trackways in Tier 1 can be traced beyond the limits of Tier 1 onto Tier 0, and some footprints truncated by the edge of Tier 1 can also be seen in Tier 0, indicating that the Tier 0 prints are undertracks. Prints in Tier 1 vary in depth and clarity, some of them being clearly impressed (Fig. 1 insert), and others very faint. Although some trackways may parallel each other, for the site as a whole there is little indication of preferred direction of travel by the dinosaurs.

Clearly registered West Tracksite Tier 1 footprints are longer than broad, sometimes show acuminate toetips, and sometimes a slight sigmoid curvature of digit III. With increasing size among footprints attributed to theropods, there is a tendency for prints to become relatively broader, and for the portion of the print distal to the tips of digits II and IV to become shorter relative to the portion of the print proximal to the terminal ends of digits II and IV (Fig. 2). DSP footprints are generally similar in size and shape to such named theropod ichnotaxa as *Eubrontes*, *Kayentapus*, and larger forms of *Anchisauripus*.

The mean length ("heel" to toetip III) across Tier 1 trackways is 35.9 cm (range 31-41; maximum/minimum = 1.3; CV = 7.4 %; N = 35). This is a rather small range of sizes (the East Tracksite, in contrast, had a few trackways made by considerably smaller animals). This could be consistent with trackmakers having been a single species, but does not require that interpretation; many dinosaur skeletal faunas have more than one large theropod species of comparable size (cf. Farlow & Pianka 2002). Considerations of overall footprint shape in fact suggest that more than one kind of large trackmaker may have been present at the site.

Keywords: vertebrate ichnology, Theropoda, Newark Supergroup, digital imaging

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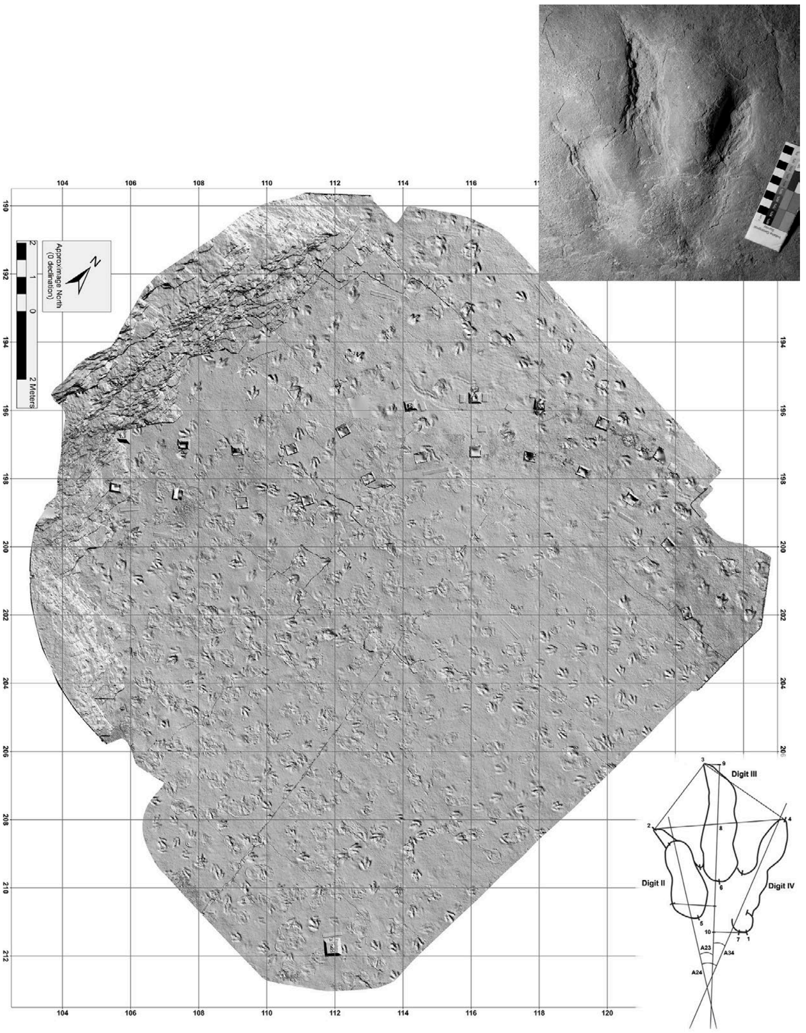

Fig. 1. Digital model of the West Tracksite, Dinosaur State Park (DSP). Top right insert: Footprint 7 (a right) of trackway G in Tier 1, one of the more clearly registered footprints at the site; scale bar in cm. Lower right insert: Landmarks on DSP footprints: 1 = "heel"; 2 = toetip II; 3 = toetip III; 4 = toetip IV; 5 = proximal end of digit II; 6 = proximal end of digit III; 7 = proximal end of digit IV (sometimes, but not always, the same point as the "heel"); 8 = intersection of long axis of digit III (as seen on a 3D model of the footprint, which may not always be the same as a midline through the toemark as seen in a 2D drawing) with line connecting toetips II and IV; 9 = projection of toetip III onto the long axis of digit III; 10 = projection of "heel" onto long axis of digit III. Other, unlabeled landmarks drawn on the footprint were not used in the present analysis.

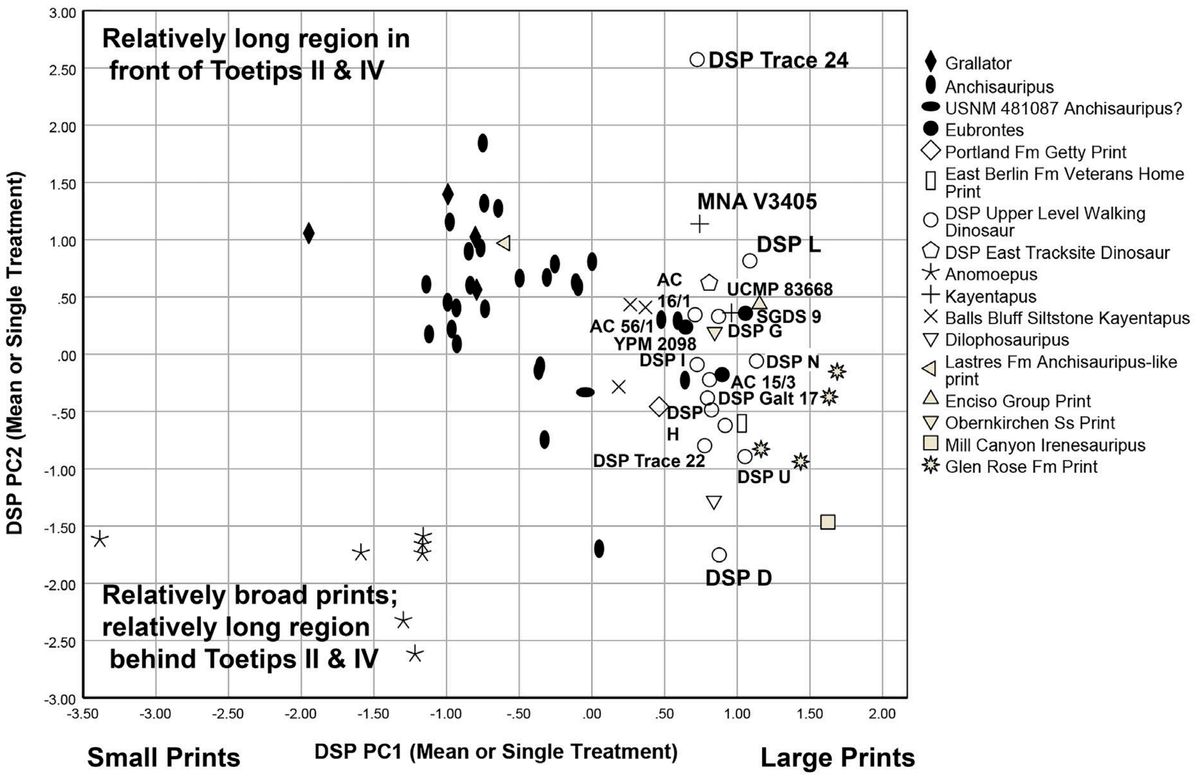

Fig. 2. Principal components analysis (PCA) of measurements of DSP footprints, along with those from other Newark Supergroup sites (data from Farlow et al. 2018), from Early Jurassic sites in the western USA, and from later Mesozoic tracksites from around the world. Measurements of toetip distances (II-III [landmarks 2-3], III-IV [landmarks 3-4], and II-IV [landmarks 2-4; = toetip width]), projection of digit III beyond the distal limits of digits II and IV [landmarks 8-9], length of the print behind toetips II and IV [landmarks 8-10], distances between the proximal ends of digits II-III [landmarks 5-6], and III-IV [landmarks 6-7], and distances from the "heel" to toetips II [landmarks 1-2] and IV [landmarks 1-4], were made on actual footprints, casts of footprints, or digital models of footprints; where measurements for more than one footprint in a trackway were available, mean values were used. Measurements were log-transformed before PCA. PC1 is mainly associated with overall print size. PC2 is a contrast between parameters associated with the length of the print ahead of digits II and IV (more positive values), and parameters associated with broad prints and a relatively long region behind the tips of II and IV (more negative values). *Anomoepus* is a likely ornithischian print, while all others are interpreted as made by theropods. Note tendency for prints attributed to theropods to take lower values of PC2 with increasing size. Where possible without clutter, selected individual points of interest are labeled. Although there is considerable scatter along PC2 in the DSP prints, they mostly plot close to values for *Eubrontes*, *Kayentapus*, and larger forms of *Anchisauripus*. AC = Amherst College, DSP = Dinosaur State Park, MNA = Museum of Northern Arizona, SGDS = St. George Dinosaur Site (Utah), UCMP = University of California Museum of Paleontology.

Climatic implications for modern continental traces from high latitude terrestrial environments: examples from Svalbard

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Abstract:

We report on the extraordinary occurrence of modern traces assignable to *Cochlichnus*, *Planolites*, and *Treptichnus* in a high polar latitude terrestrial setting near Svea, Svalbard. Svea is an old mining community that sits at 77º45′00″N, 16º43′50″E. The coldest average daily mean temperature is approximately –17ºC from January to March. The warmest daily mean temperature ranges from 1–5ºC from June to August. The remaining months experience daily mean temperatures below freezing. Average precipitation varies between 13 mm (May) to 29 mm (March), and comes in the form of snow, ice, fog, and/or rain. The traces were discovered on near-saturated, patchy grass-covered surfaces of a glacial outwash plain during an expedition in early June 2017. They were most visible in patches of sediment between grasses that were above the very high-water table; no traces were visible in pools of water between grass patches or in large areas underwater and/or barren of vegetation. Thin, regular sinusoidal trails < 1 mm in diameter attributed to *Cochlichnus* were most common. No tracemaker was visible producing these traces. Thin, curvilinear to irregular trails < 1 mm in diameter attributed to *Planolites* were common, but not as abundant as *Cochlichnus*. Thin, feather-stitch-like patterns < 1 mm in diameter attributed to *Treptichnus* were present, but less common than the other two morphotypes. Dipertan pupae were visible producing these traces. This trace association marks the highest known latitudinal occurrence of summer-produced invertebrate behaviors for an interstadial period, which can be used to interpret potential occurrences in deep time.

Keywords: *Cochlichnus*, *Treptichnus, Planolites,* polar, Svea

Ichnology, paleopedology, & sedimentology of the Cubango Megafan core: Using bioturbation to interpret environment, soil formation, sediment accumulation rate, hydrology, & climate

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Abstract:

The ichnology of the Kalahari Group is explored through a 400-m deep core taken from the Tertiary deposits of the Cubango Megafan in the Owambo Basin of northern Namibia. The megafan is 350-km long and was deposited by the paleo Cubango-Okavango River with an extremely low gradient of ~0.017°. The strartigraphy of the Kalahari Group is complex, but in Namibia it consists of the Ombalantu, Beiseb, Olukonda and Andoni formations, in ascending order. The Kalahari Group was deposited in at least seven subbasins within the main basin that encompasses Angola, Namibia, Botswana, Congo, South Africa, and Zambia. Deposits comprising these formations in the Owambo Basin of northern Namibia include conglomerates, mudstones, siltstones, sandstones, marl, and calcrete, and were deposited in alluvial fan, fluvial, palustrine, and lacustrine settings. The age of the lower part of the Kalahari Group is unknown but the upper part is Neogene in age. The core consists of unconsolidated and locally carbonate-cemented, mostly fine-grained sand, silt, and clayey sediments deposited in fluvial and lacustrine settings. The relationships between bioturbation patterns and lithofacies associations are used to interpret paleoenvironment, pedogenesis, sediment accumulation rate, hydrology, and climate during deposition of this portion of the Cubango Megafan. The Kalahari succession accumulated in a seasonal, semiarid, grassland savannah environment dominated by C4 grasses. Summer rains in the Angolan highlands catchment to the north produced runoff that transported sediments onto the megafan. Here, deposits became part of the vadose zone after each flood event, which allowed pedogenesis mostly by bioturbation to take place. The vast majority of traces are composed of packets of backfill meniscate assigned to *Naktodemasis bowni*, which were likely produced by beetle larvae and soil bug nymphs. Burrows with nondescript fill that appear massive with a sharp wall are assigned to *Planolites* isp. Burrows are often associated with rhizoliths, rhizohaloes, and possible rhizotubules. This postdepositional process plus other pedogenic processes destroyed much of the original bedding based on the frequency of depositional events. Frequent events produced weakly developed compound paleosols; less frequent and intermittent events produced moderately–well-developed composite paleosols and weakly–moderately developed cumulative paleosols.

Keywords: compound paleosols, composite paleosols, cumulative paleosols, rhizoliths

Vertebrate burrows in deposits of an eolian system, Lower Jurassic Navajo Sandstone, Moab, Utah, area, U.S.A.

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Abstract:

Two types of vertebrate burrow morphotypes are preserved in stabilized interdune and dune deposits of the Lower Jurassic Navajo Sandstone in the Moab area of southeastern Utah. The Navajo Sandstone represents the largest eolian system preserved ever known. The burrow morphologies are similar to those of the ichnotaxa *Reniformichnus* isp. (subhorizontal to inclined tunnel, simple architecture) and Fractussemita isp. (complex, multicomponent architecture). The overall architectural and surficial morphologies and comparison to other ancient and extant burrows indicates the Navajo burrows were constructed by therapsids and mammals. The burrows are associated with interdune and fluvial environments associated with large-scale bounding surfaces.

Keywords: interdune, bounding surfaces, fluvial, mammals, paleosols

Introduction

Multiple examples of vertebrate burrows (Fig. 1) were discovered along extensive bounding surfaces that cross multiple depositional environments comprising the eolian system preserved in the Lower Jurassic Navajo Sandstone (Ss) in several localities in Moab, Utah, area. Vertebrate burrow occurrences are associated with bounding surfaces that exhibit various stages of pedogenic development. Two major types of burrow morphologies are documented: 1) Simple burrow systems: subhorizontal, inclined tunnel that likely terminates in a chamber >1.5x wider than the tunnel width and 3–4x longer than the width of the chamber; and 2) Complex burrow systems: short vertical shafts and/or a subhorizontal, inclined tunnel leading to a network of interconnected long and short tunnels, some of which likely terminate in an elliptical chamber 1.5–2x wider than the tunnel width and 2x longer than the width of the chamber.

Type 1 burrows: *Reniformichnus* (Fig. 1A, B)

Type 1 burrows are likely assignable to the ichnotaxon *Reniformichnus* isp., which represents large-diameter (~10–20 cm) burrows that exhibit subhorizontal orientation from a paleosurface with an elliptical to bean-shaped cross section containing a medial ridge in the burrow floor. Burrow walls and floors contain longitudinal scratches, whereas the burrow ceiling is often free of scratches. These features, however, are only preserved when the enclosing sediment is finer grained (siltstone and mudstone). A few of the burrows do exhibit a chamber at the termination that tends to be >1.5x wider than the tunnel width.

The Navajo Ss burrows can be placed within this burrow morphotype, with the majority of samples represented by partially preserved burrows in outcrop. The existence of a terminal chamber is currently unknown based on samples from which *Reniformichnus* was defined (KRUMMUCK & BORDY, 2017). Further exploration for additional complete specimens in areas adjacent to those outcrops may provide enough material to define a new ichnotaxon of burrow morphology that represent vertebrate behavior.

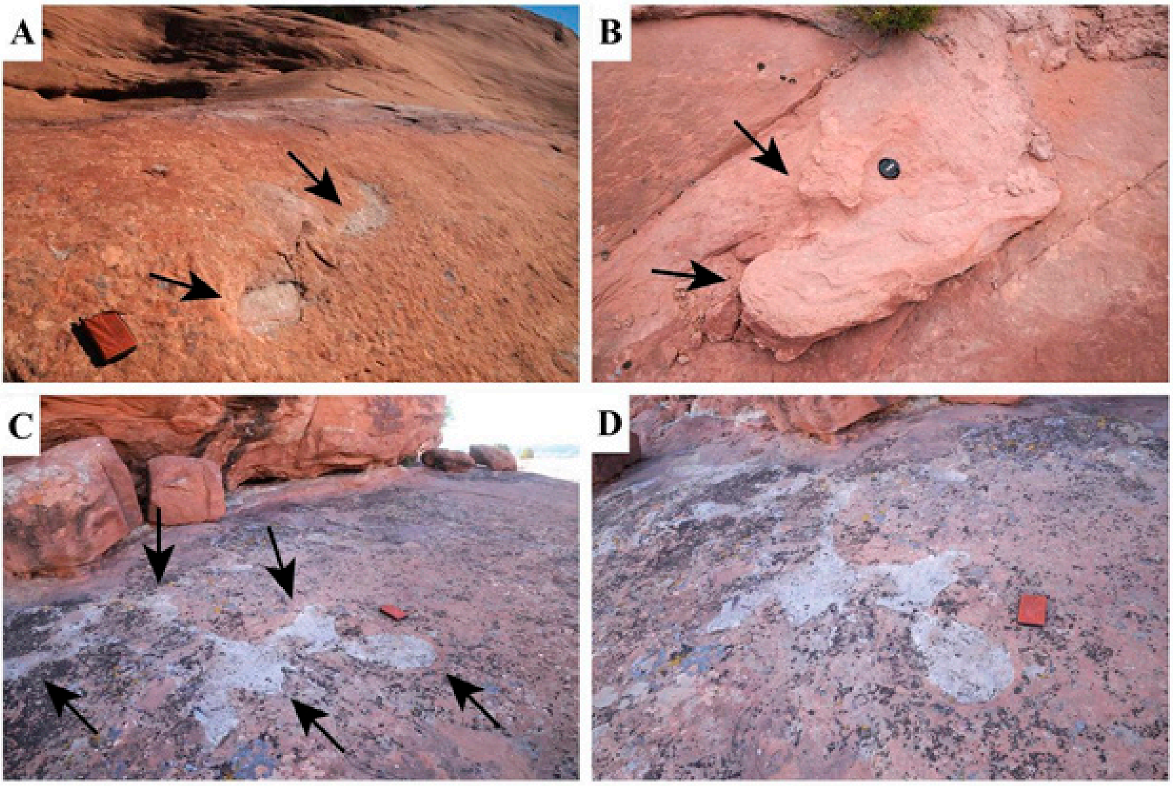

Fig. 1. Vertebrate burrows at a pedogenically modified complex surface, SFRA. Notebook 22 cm tall; lens cap 6.7 cm wide. A) Two examples of *Reniformichnus* isp. (arrows) in a moderately developed paleosol. B) Two closely occurring, different diameter *Reniformichnus* isp. (arrows) in a weakly developed paleosol; smaller burrow with medial ridge in the burrow floor; larger burrow with terminal chamber. C–D) Example of *Fractussemita* isp. (arrows) with multiple tunnels and chambers in a well-developed paleosol.

Reniformichnus in the Navajo Ss are interpreted to have been constructed by therapsids based on their elliptical, bean-shaped cross section. Similar burrow morphologies have been described from Triassic and Jurassic alluvial and fluvial floodplain deposits in Antarctica, Argentina, Poland, South Africa, and the United States (e.g., Hasiotis et al. 2004; Bordy et al. 2011; Talanda et al. 2011; Krapovickas et al. 2013). No body fossils have been found within any of those burrows, however, therapsid body fossils have been found in isolated terminal chambers in Antarctica (Sidor et al. 2008). Burrows assigned to Reniformichnus were likely used as seasonal to semipermanent dwellings to escape temperature extremes, as well as to rear young (e.g., Hasiotis et al. 2004; Bordy et al. 2011).

Type 2 burrows: *Fractussemita*

Type 2 burrows are likely assignable to a new ichnospecies of the ichnotaxon *Fractussemita* isp., which represents burrow systems composed of circular to subcircular, large-diameter (~10–20 cm) shafts (vertical orientation) and subhorizontal tunnels of low to high angle with respect to the paleosurface (Raisanen & Hasiotis, 2018). These burrow elements exhibit a variety of branching angles between 45–90° from the main tunnel and form an irregular boxwork pattern that extends several meters or more laterally in outcrop and to a depth of ~1 m. The *Fractussemita* isp. in SFRA exhibit a similar range in branching angles, but also exhibit one or more chambers associated with the burrow complex that are 1.5–2x wider than the tunnel diameter and ~2x longer than the width of the chamber. The SFRA burrows also tend to have larger diameter tunnels and shafts, do exhibit the irregular boxwork system, do not appear to contain the medial ridge on the burrow floor. They do exhibit a burrow system in which tunnels and shafts of different diameters are connected to a main subhorizontal tunnel.

Fractussemita are interpreted to have been constructed likely by mammals that exhibited some degree of social behavior, based on the complexity of the burrow system as well as the circular to subcircular diameter of the burrows. Similar burrow morphologies have been described from late

Paleozoic, Mesozoic, and Cenozoic alluvial and fluvial floodplain deposits in Antarctica, Morocco, South Africa, and the United States (see Voigt et al. 2011; Hasiotis et al. 2004). Burrows in Paleozoic deposits with similar morphology were likely constructed by therapsids or reptiles (see Voigt et al. 2011; Hasiotis et al. 2004). The SFRA *Fractussemita* burrow systems were likely the work of multiple individuals, all part of a social group. Such burrow systems required a great deal of work to construct, and maintenance was likely continuous or seasonal. Burrow networks were used for multiple purposes: protection from both predators and diurnal temperature extremes, food storage, foraging tunnels close to the surface to feed on plant roots and other soil biota, and denning to raise young.

Implications

Occurrences of the ichnotaxa *Reniformichnus* isp. and *Fractussemita* isp. in the deposits of the eolian system preserved in the Navajo Ss have several significant implications to paleoenvironmental, paleoecological, and paleoclimatic reconstructions, and the use and creation of ichnofacies. The overall architectural and surficial morphologies and comparison to other ancient and extant burrows indicates the Navajo burrows were constructed by therapsids and mammals. Both types of burrow morphologies reflect seasonal to semipermanent and permanent dwellings used to escape temperature extremes, as well as to rear young (*Reniformichnus*) and to forage and store food (*Fractussemita*), indicating abundant food, water, and stability of the local landscape to sustain the occupation populations of vertebrates in those areas. These ichnotaxa occur in association of large-scale bounding surfaces that cross dune, interdune, and fluvial environments within the Navajo eolian system, indicting a larger, more stable landscape likely produced by a shift of the climate to wetter and/or more humid conditions. This association is significant as the burrowing Navajo vertebrates did not have to contend with burial by migrating dunes across dry or wet interdune environments. The presence of lakes and rivers also indicates higher water table conditions, such that lakes produced carbonate deposits and rivers flowed through small valleys with associated floodplain deposits with the eolian system.

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Neoichnological evidence of predatory behavior in soil arthropods and its application to continental trace fossils

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Abstract:

Predatory arthropods are known from terrestrial environments since the Silurian. Many of these animals have acquired specialized behavioral adaptations including various burrowing styles and even permanently fossorial habits. Our knowledge of arthropod predators in Paleozoic soil ecosystems, however, is limited. Ichnofossils are abundant in Paleozoic paleosols and may record a hidden diversity of predatory arthropods. Laboratory experiments were conducted with various species of predatory soil arthropods to better understand the morphology and use of their burrows. Specimens were placed in sediment-filled terrariums and observed for 10-30 days. Open burrows were cast and ichnofabric was observed through serial sections. The morphology of the traces was described qualitatively and quantitatively and compared using statistical methods. The animals burrowed through intrusion, excavation, and backfilling. Burrow morphology ranged from simple vertical shafts to complex boxworks that served as temporary to permanent dwellings. Burrows also served a role in hunting and were used as sites for concealment for ambush or as prey traps. While complexity of burrows was not related to their use, distinct morphologies could be linked to predatory behaviors. Data collected from these experiments can be applied to ichnofossils found in Paleozoic paleosols to improve our understanding of the evolution of predatory arthropods, their geographic distribution through time, and their response to changes in soil environments, as well as improve interpretations of the paleoecology of ancient soil ecosystems. This knowledge is especially important given the relatively poor preservation potential of predatory soil arthropods in the environments they inhabit.

Keywords: neoichnology, arthropod, paleosol, burrow, predator

Preliminary studies of a new dinosaur track locality from the Candeleros Formation (Cenomanian, Upper Cretaceous), Neuquén Basin, Argentina

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Abstract:

A new Upper Cretaceous (Cenomanian) dinosaur track locality “El Chocón Medio” from northwestern Patagonia, Argentina, is reported here. More than 30 true tracks (concave epireliefs) were recognized in fine-grained sandstone beds, interpreted as floodplain deposits. The only distinct trackway consist of six deep and medium-sized tridactyl tracks poorly preserved with distinct metatarsal impressions (about 50 cm long and 20 cm wide). This trackway does not reflect changes in footprint features such as track length, depth, pace and height of displacement rims, suggesting that the consistency of the substrate was homogenous along the complete distance. About 20 m from this trackway, several deeper and large tridactyl tracks (30 to 40 cm in length) with very pronounced rims have been identified. They are positioned close to each other and show different orientations, accordingly were considered as isolated tracks. They are poorly preserved and lack anatomical features, making it difficult to determine a theropod or ornithopod affinity. Finally, in the underlying bed (10 cm below) several subcircular (70 cm in diameter) and crescent-shaped (50 cm in width) natural cast tracks (pes-manus) of sauropods were documented. At least three sauropod pes from the same side (left or right) where arranged in an incomplete trackway, so the type of gauge could not be determined. Preliminarily, considering the similar morphology and heteropody, these tracks can be assigned to cf. *Sauropodichnus giganteus* Calvo, 1991, from the same unit and tracksite proximity. The present track assemblage shows that this site was repeatedly visited by different groups of dinosaurs.

Keywords: tridactyl footprints, metatarsal impressions, sauropod tracks, Cenomanian, Patagonia

Gregariousness among non-avian theropods: a case study from a Patagonian dinosaur tracksite, Candeleros Formation (Cenomanian), Argentina

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Abstract:

Gregarious behaviour is an important aspect of dinosaur paleoecology and has been inferred from several evidences: monospecific bonebeds, skeletal morphology, phylogenetic inferences, comparison with modern ecosystems and parallel trackways. Nevertheless, it is relatively poorly documented and understood among non-avian theropods. In the Cenomanian Candeleros Formation (northwestern Patagonia) several parallel tridactyl trackways were recorded, including five theropod trackways of medium track size (average length of 28 cm). These trackways possess similar stride, speed estimation, preservational features, uniform depth, and the same direction as non-overlapping tracks. They are preserved as shallow under tracks in a medium-grained sandstone bed interpreted as floodplain deposits. The tracking surface would have been an immediately overlying thin layer of muddy-siltstone containing a minor percentage of expandable clays (smectite). The latter gave a certain degree of coherence and plasticity to the substrate, sufficient to preserve several anatomical track features. Considering the theropod taxa documented in the same unit as well as the size and track morphology, abelisaurid or carcharodontosaurid theropods are suggested as trackmakers. Physical barriers (i.e., large fluvial channels or perennial lakes) that could control the moving direction of the theropods were not recognized in the track-bearing level, nor were revealed by the analysed interval. Taking into account that there are no evidences of physical constraints and that all parallel trackways possess similar features such as stride, speed, preservation, depth, and direction, a gregarious behaviour of their producers can be suggested.

Keywords: theropod footprints, gregarious behaviour, Upper Cretaceous, Neuquén Basin

The Late Triassic archosaur ichnogenus *Brachychirotherium*: First complete step cycles from Morocco, North Africa, with implications for trackmaker identification and ichnotaxonomy

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Abstract:

Trackways of Late Triassic *Brachychirotherium* (archosaur) are known from few specimens, mostly from North America. Complete step cycles have been found on the upper and lower bedding surface in laminated mudstone and fine sandstone of the upper Oued Oum Er Rbiaa Formation (Late Triassic). This is the first trackway of the ichnogenus in North Africa. It consists of 7 successive pes (pl = 12 cm, pw = 8 cm) and manus (ml = 5-6 cm, mw = 5-6 cm) tracks. Imprints show the characteristic broad pes, with digit proportions III > II > IV> I > V, with digit V preserved as a large oval basal pad. Skin impressions are present in several tracks. Striking feature is the large distance between pes and manus imprints, possibly due to the early ontogenetic stage of the small individual.

In some associated isolated tracks, pedal digit V is oriented in line with digit IV. These tracks are similar to *Brachychirotherium parvum* (Hminna et al., 2013), whereas pes imprints from the trackway show similarities to *B. thuringiacum* and *B. hassfurtense* from the Hassberge Formation (Carnian) of Germany (Beurlen, 1950; Karl & Haubold, 2000), with pedal digit V, being laterally spread.

The footprints from Morocco are determined as *Brachychirotherium parvum* and *B. thuringiacum* based on the presence of features diagnostic of the ichnospecies such as the orientation of pedal digit V (Hunt & Lucas, 2007a). Probable trackmakers are archosaurs of the crocodylian stem-group (Crurotarsi). Associated tetrapod ichnofauna from the unit consists of small *Rhynchosauroides* (archosauromorph/lepidosauromorph) tracks.

Keywords: North Africa, chirothere footprints, Crurotarsi, Rhynchosauroides, Archosauromorpha

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Why ornithopod feet rotate inward

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Abstract:

Inward rotation of hindfoot axis (orientation of digit III relative to the trackway midline) is commonly observed in both bipedal and quadrupedal trackways of ornithopods, suggesting in-toed gait of the trackmakers. The origin of quadrupedalism of ornithopods has been often discussed in previous research, but the cause of in-toed orientation of the pes is largely unknown.

We investigated 14 ornithopod trackways, all showing inward rotation of the hindfoot. The average pace angulation of 14 trackways based on the measurement connecting the center of the footprints is 158°. In contrast, the value based on the measurement connecting the tip of digit III is 166°. The latter value is close to that of the average pace angulation of theropods.

The observation of shorebirds has proven that birds with long legs and high-positioned acetabular joints do not have inward rotated feet. In contrast, birds with short legs and low positioned acetabular joints have inward rotated feet.

Based on these data, we interpret this as follows. The inward rotation of the hindfoot axis: 1) increases the stability of the body against the lateral overturning moment; 2) compensates for the short distance between knee and ground, and resolves the disadvantage of short legs when placing the foot closer to the trackway midline (center of mass) for maintaining body balance.

Keywords: dinosaur, footprint, trackway, in-toed, pronation

Reconstruction of an ancestral amniote trackmaker based on trackway data, track – trackmaker correlation and phylogeny

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Abstract:

Trackway measures, such as pace angulation, pace length, stride length, gauge width, manus-pes distance (along track) and imprint orientation vary notably among amphibian, stem-amniote and early amniote tracks from Late Carboniferous to Early Permian deposits. Some of this variability can be attributed to evolutionary changes in trackmaker anatomy and locomotion style close to the origin of amniotes. This variability may be explored through phylogenetic approaches following the assignment of certain track types to distinct producer groups.

Based on trackway averages of various parameters measured for eight tetrapod ichnotaxa from the Early Permian of the Thuringian Forest Basin as well as two additional Late Carboniferous ichnotaxa we infer ancestral states for functionally controlled trackway measures by means of parsimony and maximum likelihood.

We use basal amniote trees from recent literature and consider two alternative trackmaker phylogenies, where: (1) diadectomorphs as probable producers of Late Carboniferous to Early Permian *Ichniotherium* tracks form the sistergroup to all amniotes; (2) they form the sistergroup of more derived synapsids within Amniota.

According to our results, the ancestral amniote trackmaker had a body size higher than the sampled amphibian and reptilian track producers but was smaller than diadectomorph and early synapsid trackmakers. Its tracks were characterized by higher pace angulations, somewhat narrower gauges and lower normalized stride lengths than those of its non-amniote predecessors, whereas neither the normalized distance between consecutive manual and pedal imprints nor the orientation of the pedal imprints appear to have changed much on the amniote stem. The manual imprints were more outward positioned and had a more parallel orientation than those made by earlier stem-amniote producers. Early Permian *Ichniotherium* trackways display certain similarities to contemporaneous synapsid tracks, whereas other measures, most notably the orientation of manual and pedal imprints, differ considerably, demonstrating their limited use as model tracks of basal amniotes.

Keywords: ichnotaxa, track-trackmaker correlation, Ancestral State Reconstruction (ASR), Carboniferous

A taphonomic study of the exceptionally preserved arthropod trackway in chemically precipitated silica of the Cretaceous Uhangri Formation (Haenam Basin, South Korea)

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Abstract:

The Upper Cretaceous Uhangri Formation (Haenam Basin, southwestern Korea) is well-known for its ichnofauna with footprints of dinosaurs, pterosaurs, birds and traces of invertebrates. MINTER et al. (2012) reported trackways of arthropods as *Lithographus hieroglypichus* abundantly preserved on a single horizon of cherty mudstone. More than 50 trails and about 30 burrows formed by the same trace maker, show a delicate and peculiar morphology with chevron marks. The cherty mudstone layer is composed of inorganically precipitated silica deposited in a saline-alkaline paleolake when supersaturated silica suffered a pH decline. Although trace fossils preserved in lacustrine precipitated silica are very unusual, especially superficial trails, the arthropod trace fossils in the Uhangri Formation are well-preserved with different morphotypes. Such morphotypes may be attributed to surface moisture of substrates while being shortly exposed under subaerial conditions. Furthermore, saturated-mud size sediments might have controlled the preservation of trails. The trace fossils in this study indicate an exceptional taphonomic process: 1) a temporary exposure of precipitated silica substrates; 2) overlay by ash-fall tuff; 3) presence of cherty-mud substrates. Moreover, this paleoenvironmental condition means that possible trace makers of *Lithographus*, which have been interpreted as pterygote insects, can inhabit a saline-alkaline lake environment with burrowing. Therefore, ongoing investigations and further studies could be expected to elucidate the possible trace maker and contemporary environment of the Haenam Basin.

Keywords: ichnology, taphonomy, *Lithographus*, saline-alkaline lake, precipitated chert

Subaqueous tracks of marine tetrapods – indications to trackmakers based on new surfaces from the Middle Triassic of Guizhou Province, China

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Abstract:

Tracks documenting subaqueous activity of terrestrial or semi-aquatic tetrapods are common in the Mesozoic record. Numerous examples of swimming dinosaurs or other tetrapods, in particular turtles, phytosaurs and crocodylomorphs are known. Marine forms, however, rarely left their imprints on the bottom of shallow water while buoyant, drifting or actively swimming, touching the ground with distal parts of digits, or during bottom walking. China nothosaur foraging tracks have been reported from Middle Triassic marginal marine deposits (Guanling Formation) of Yunnan Province. Recently a large surface with similar traces was found in this unit. Associated foot impressions and trackways show strong morphological similarities with the feet and limb performance of placodonts. Characteristic are four robust digits (probably II–V), showing proportions IV = III > II > V and a broad trackway pattern with outwardly rotated imprints positioned opposite to each other, suggesting swimming activity of the trackmaker. According to digit proportions, with a relatively short digit IV, and the large trackway width, it is likely that the traces were left by the forefeet of placodont sauropterygians. The latter are common and well-known from finely preserved skeletons from the Guanling and Xiaowa formations (Anisian-Carnian) of the area. Further candidates such as saurosphargids and turtles are also considered, even if the skeletal evidence of the latter, restricted to rare findings, does not appear before the Carnian. Other groups such as thalattosaurs, nothosaurs, ichthyosaurs or archosaurs can be excluded because of different limb posture, digit proportions or the presence of fin-like autopodia.

Keywords: Guanling Formation, placodonts, saurosphargids, turtles, nothosaurs

First evidence of borings in calamitean stems and other plant-arthropod interactions from the late Pennsylvanian of the Saale Basin

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Abstract:

Hitherto, plant-arthropod interactions have been rarely reported from the late Pennsylvanian (Gzhelian, Stephanian C) of the Saale Basin (Saxony Anhalt, Germany). A re-examination of material from the collections of the Martin-Luther-University Halle-Wittenberg and private collections revealed the presence of different damage types on plants. Among them are at least three types of endo- and exophytic oviposition, the first evidence of borings in calamitean stems, margin feeding, and leaf mining.

Keywords: plant-arthropod interactions, Gzhelian, oviposition, boring, leaf feeding

Introduction

Since Germar (1844-1853) published his monographs about the fossils of the Wettin coal mines, the rich flora and fauna of the late Pennsylvanian of the Saale Basin has been subject of intensive research. Nevertheless, only a few plant-insect interactions have been described yet. Among them are approximately semicircular excisions of the leaf margins of *Odontopteris subcrenulata*, which were interpreted by Müller (1982) as leaf mines and described as *Cuniculonomous (Acrophionomus) undulatus*. Recently, this damage type is regarded as margin feeding and assigned to the ichnospecies *Phagophytichnus ekowskii* Van Amerom 1966 (see also damage type DT12 according to Labandeira et al. 2007).

Furthermore, Laass & Hoff (2014) reported the earliest record of damselfly-like endophytic oviposition in the fossil record from the Wettin Subformation of the Siebigerode Formation (see Fig. 1g).

As described in the following section, new observations on fossils from the Wettin Subformation revealed that the number of plant-arthropod interactions was higher than previously thought.

New plant-arthropod interactions from the Wettin Subformation

The palaeontological collections of the Martin Luther Universität Halle-Wittenberg are an important archive of fossils, particularly from Central Germany (Hauschke 2018). One of these collections houses palaeontological objects from the coal mine district of Plötz-Wettin-Löbejün (Saxony-Anhalt). E.F. Germar (1786-1853) was the first, who collected systematically fossil plants, invertebrates and vertebrates from the Wettin Subformation. A re-examination of this material brought to light new evidence of leaf feeding on Neurodontopteris auriculata (Brongniart) Potonié (Fig. 1a), which strongly resembles the ichnotaxon *Cuniculonomous (Acrophionomus) undulates* Müller (1982) on *Odontopteris subcrenulata*. In some cases, undulating leaf mines can be observed. This supports Müller´s interpretation of this ichnotaxon as leaf mines. In other cases, it cannot be excluded that some traces represent margin feeding (*Phagophytichnus ekowskii* Van Amerom, 1966). Typically, damaged leaf margins are thickened, which resulted from the growth reaction of tissue. On some leaves of the same species mines can be observed, which run parallel to the venation (Fig. 1c).

Borings in wood from the Carboniferous are well-known from gymnosperms and tree ferns (e.g. Cichan & Taylor 1982, Rössler & Fiedler 1996, Barthel, Krings & Rössler 2010). Hitherto unknown are borings in Calamite stems. In this paper two new types of this kind of plant-arthropod interaction are described (Fig. 1b, e). The first type is characterized by three-dimensionally preserved boring casts, which run almost parallel to the impressions of the vascular bundles (Fig. 1b). This suggests that these borings were situated in soft tissue of the pith cavity and/or in the region of the metaxylem of a young calamitean stem. Similar borings were described by Rössler & Fiedler (1996, Fig. 4: Type 2) in wood of the gymnosperm genus *Dadoxylon* from the Lower Permian of Chemnitz. Another type of borings in a calamitean stem is depicted in Fig. 1e. These borings form a three-dimensional meshwork consisting of straight to meandering canals, which often run nearly perpendicular (Fig. 1e:1), but sometimes also parallel to the vascular bundles (Fig. 1e:2). In some cases, the borings enter the pith cavity of the stem (Fig. 1e:3).

Fig. 1d shows the earliest evidence of possible insect egg masses attached on the surface of plant foliage (exophytic oviposition) (Laass & Hauschke 2019).

In contrast, Figs. 1f, g show examples of endophytic oviposition, i.e. the eggs were inserted by the insects with their ovipositors into plant tissue. This damage caused the growth of elliptical scars. In Fig. 1f the ovipositor slits of the scars are still visible. As shown in Fig. 1g the scars are often arranged in rows. A similar arrangement of the eggs can also be observed in some extant damselflies (Hellmund & Hellmund 1996).

These new results suggest complex relationships between plants and arthropods in late Pennsylvanian ecosystems.

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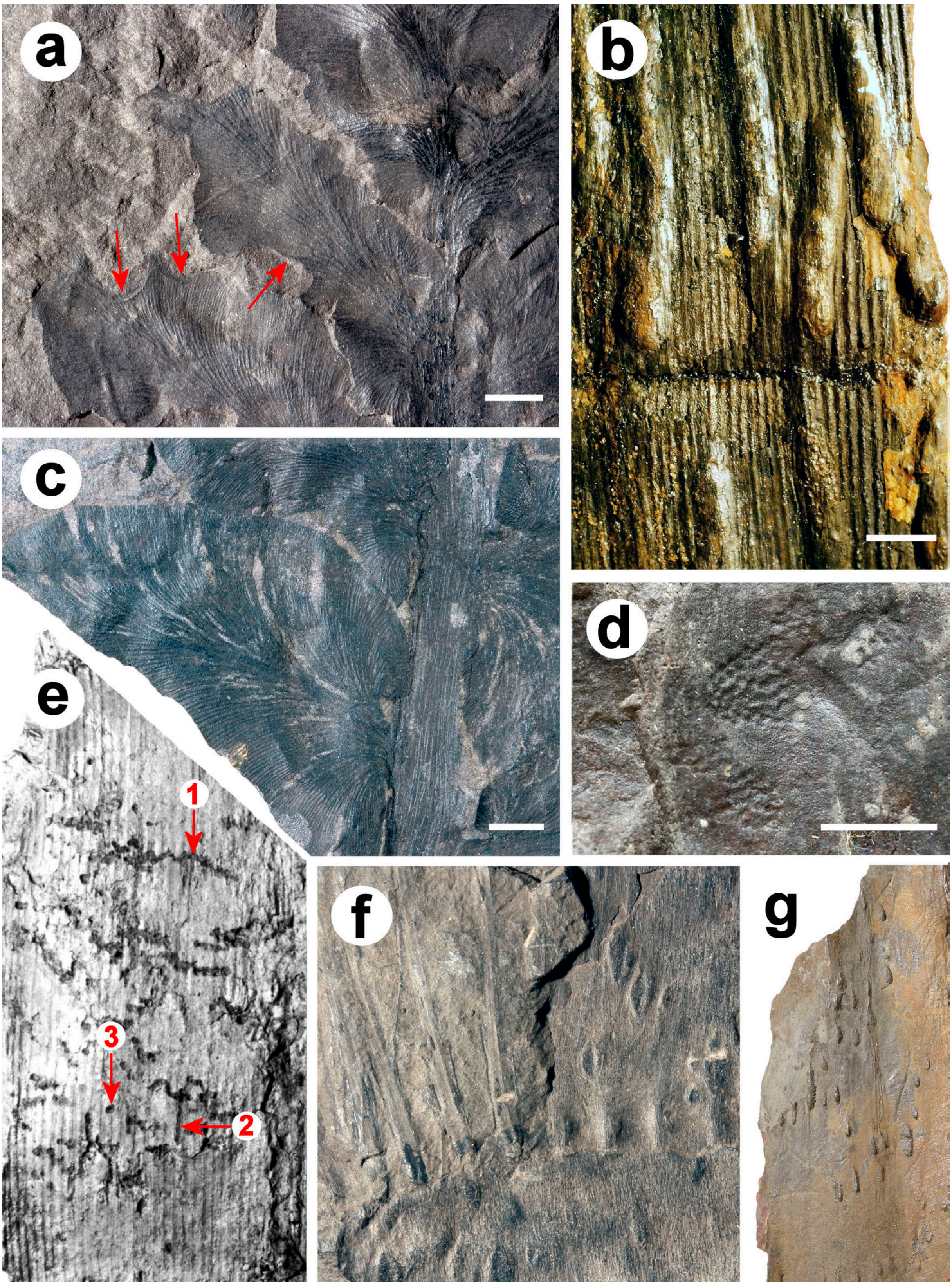

Fig. 1: Plant-arthropod interactions from the late Carboniferous of the Saale Basin. a: Leaf feeding on *Neurodontopteris auriculata* (arrows), b: Borings (Typ 1) in a calamitean stem, c: Mines on a leaf of *Neurodontopteris auriculata*, d: Possible exophytic insect eggs on plant foliage (from Laass & Hauschke 2019), e: Borings (Typ 2) in a calamitean stem (arrows 1-3), f: Endophytic oviposition on the outer cortex of a calamitean stem, g. Endophytic oviposition on plant foliage (from Laass & Hoff 2014). Scale bar = 5 mm.

Automated outline and landmark generation of footprints based on 3D-models

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Abstract:

The lack of widely applicable methods to objectively define the margins of footprints remains a central problem in ichnology, especially when the margins are indistinct. Any characterisation of footprint shape is thus unavoidably affected by the subjectivity of the observer. Interpretive outline drawings remain the main means for capturing footprint shapes, although outlines drawn by separate ichnologists can drastically differ especially when conflicting preconceptions about the responsible trackmaker taxon are involved. The resulting subjectivity equally affects measurements and landmark coordinates. As was argued in a recent publication, results of quantitative analyses based on subjective data can only be equally subjective.

To address this unsolved issue, a program is presented that generates objective outlines, landmarks, and measurements based on 3D-models of footprints in a single step. The program fits the model to the horizontal plane and extracts a fixed number of contour lines. Relevant contours are selected, and the points of the steepest slope detected along the footprint wall. The resulting outline is then rotated so that the digit impressions point upwards. For tridactyl footprints, an automatic landmark generation is implemented, from which objective measurements can be derived. The method was tested on tridactyl dinosaur tracks from the Lower Cretaceous of Münchehagen, Germany, reproducing results made by an earlier study based on interpretive outlines. While not an adequate replacement of interpretive drawings, generated outlines may form an objective basis for the latter. Most importantly, the method for the first time allows for fully objective quantitative analyses of footprint shapes.

Keywords: vertebrate ichnology, objective data analysis, shape analysis, landmark detection, algorithm

Invertebrate trace fossil-bearing wairakite layer from the Cretaceous Haman Formation, Gyeongsang Basin, Korea: Occurrence, origin, and paleoenvironmental implications

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Abstract:

An abundant invertebrate burrow-bearing white bed was found in the Cretaceous Haman Formation of the Hayang Group, Gyeongsang Basin, Korea. The Haman Formation is composed of reddish mudstones and sandstones deposited in a sheetflood–dominated alluvial-plain environment under a seasonal, semi-arid climatic regime. The white bed is 2–3.5 cm thick developed in a reddish mudstone sequence, and burrows are well exposed on the bedding plane. Burrow-fills are composed of reddish sand and show a distinct color contrast with surrounding white matrix materials. The burrows were identified as *Taenidium barretti, Planolites beverleyensis*, and *Planolites montanus.* Various analyses including microscopic observation, XRD, X-ray CT, and FE-EPMA were carried out to characterize burrow architecture, mineralogy and origin of the white bed, and its paleoenvironmental and tectonic implications. Based on the XRD analysis, the mineralogy of the white materials consists mostly of wairakite, a zeolite mineral with an analcime structure but containing a calcium ion, and quartz. Although zeolites are commonly found as a secondary mineral in volcanogenic sediments, wairakite is rarely reported due to its high formation temperatures (about 200–400 °C). We investigated the maximum paleotemperatures that the Haman Formation experienced and the Ca source needed for the wairakite formation. The results of this study provide important information on burial diagenesis and/or hydrothermal alteration associated with volcanic activity during the Cretaceous Hayang period in Korea which was located in the active continental margin setting.

Keywords: trace fossil, Haman Formation, wairakite, Cretaceous

Continental invertebrate and plant trace fossils in space and time: State of the art and prospects

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Continental invertebrate ichnology has experienced a substantial development during the last quarter of century. From being a field marginal to mainstream marine ichnology, represented by a handful of case studies, continental ichnology has grown to occupy a central position within the field of animal-substrate interactions. This evolution is illustrated not only through the accumulation of ichnologic information nurtured by neoichnologic observations and a detailed scrutiny of ancient continental successions, but also through the establishment of new concepts and methodologies.

From an ichnofacies perspective, various recurrent associations were defined (BUATOIS & MÁNGANO 1995; GENISE et al. 2000, 2010, 2016; HUNT & LUCAS 2007; EKDALE et al. 2007; KRAPOVICKAS et al. 2016), a situation sharply contrasting with the sole recognition of the *Scoyenia* ichnofacies as the only valid one during the seventies and eighties (Table 1; Fig. 1). The ichnofacies model now includes not only freshwater ichnofacies, but also terrestrial ones, most notably those reflecting the complex nature of paleosol trace fossils (GENISE 2017).

Trace fossils are now being increasingly used to establish a chronology of the colonization of the land and to unravel the patterns and processes involved in the occupation of ecospace in continental settings (e.g. BUATOIS & MÁNGANO 1993; BUATOIS et al. 1998, 2016; KRAPOVICKAS et al. 2016; GENISE et al. 2016; MINTER et al. 2016b,c, 2017). These studies have helped to identify trends of colonization in specific environments, such as deserts (KRAPOVICKAS et al., 2016), yield insights into the evolution of insects (e.g. GENISE et al. 2016), and reconstruct evolutionary events, such as Paleozoic colonization of continental settings (e.g. BUATOIS & MÁNGANO 1993; MINTER et al. 2016b,c, 2017; FRANCISCHINI et al. 2019) and the Mesozoic Lacustrine Revolution (e.g. BUATOIS et al. 2016).

Another line of research that has been successful in recent years is the study of modern traces as a tool to decipher complex behavior and scrutinize the fossil record (e.g. HASIOTIS et al. 1993; SÁNCHEZ & GENISE 2008, 2015; SARZETTI et al. 2013; 2014; CANTIL et al. 2014, 2015). In particular, experimental neoichnology allows identifying a variety of burrow architectures and their potential producers (e.g. HEMBREE 2009, 2013, 2016; CATENA & HEMBREE 2014). These studies are instrumental to establish more accurate paleobiologic interpretations of continental trace fossils and to better understand the requirements and solutions of different groups to life in land. Neoichnology is providing paleoichnology with a solid ground to establish paleobiologic and paleoecologic inferences, including both qualitative and quantitative data.

Continental ichnology has been benefitted through the use of conceptual and methodological tools derived from the ichnofabric approach. In particular, a framework for the analysis of paleosol ichnofabrics has been proposed and successfully applied to accurately characterize complex paleosol ichnofabrics (GENISE et al. 2004; BEDATOU et al. 2009; BELLOSI et al. 2016; GENISE 2017). The concept of taphonomic pathways provides a way of analyzing the origin of ichnofabrics in freshwater environments, allowing to unravel the generation of composite ichnofabrics (BUATOIS & MÁNGANO 2004).

The need of integrating invertebrate and vertebrate ichnology has been noted long ago (BUATOIS & MÁNGANO 1996). Although these two fields still remain quite separate and this may be considered a pending item, a number of recent studies have documented assemblages comprising both invertebrate and vertebrate trace fossils, helping to bridge the gap between these two areas of research (e.g. KRAPOVICKAS et al. 2015; MENEZES et al. 2019). Unifying approaches to the study of invertebrate and vertebrate trace fossils is desirable (the so-called "one ichnology"), but there has to be room for a plurality of conceptual and methodological tools that take into account the peculiarities of these two fields.

The study of plant bioturbation in paleosols is another pending item that deserves further attention. Many paleosols do not display burrowing and nesting structures and are instead dominated by rhizoliths or other structures recording the activities of plants. Melchor et al. (2012) proposed a "potential rhizolith ichnofacies" to embrace these assemblages dominated by plant bioturbation, commonly devoid of discernible animal activity. With the required temporal and spatial recurrence, specific assemblages could define several "potential rhizolith ichnofacies". Indeed, these assemblages can offer valuable information and, in many cases, they can alternate with other continental Ichnofacies, highlighting significant changes in climate and other paleoenvironmental conditions.

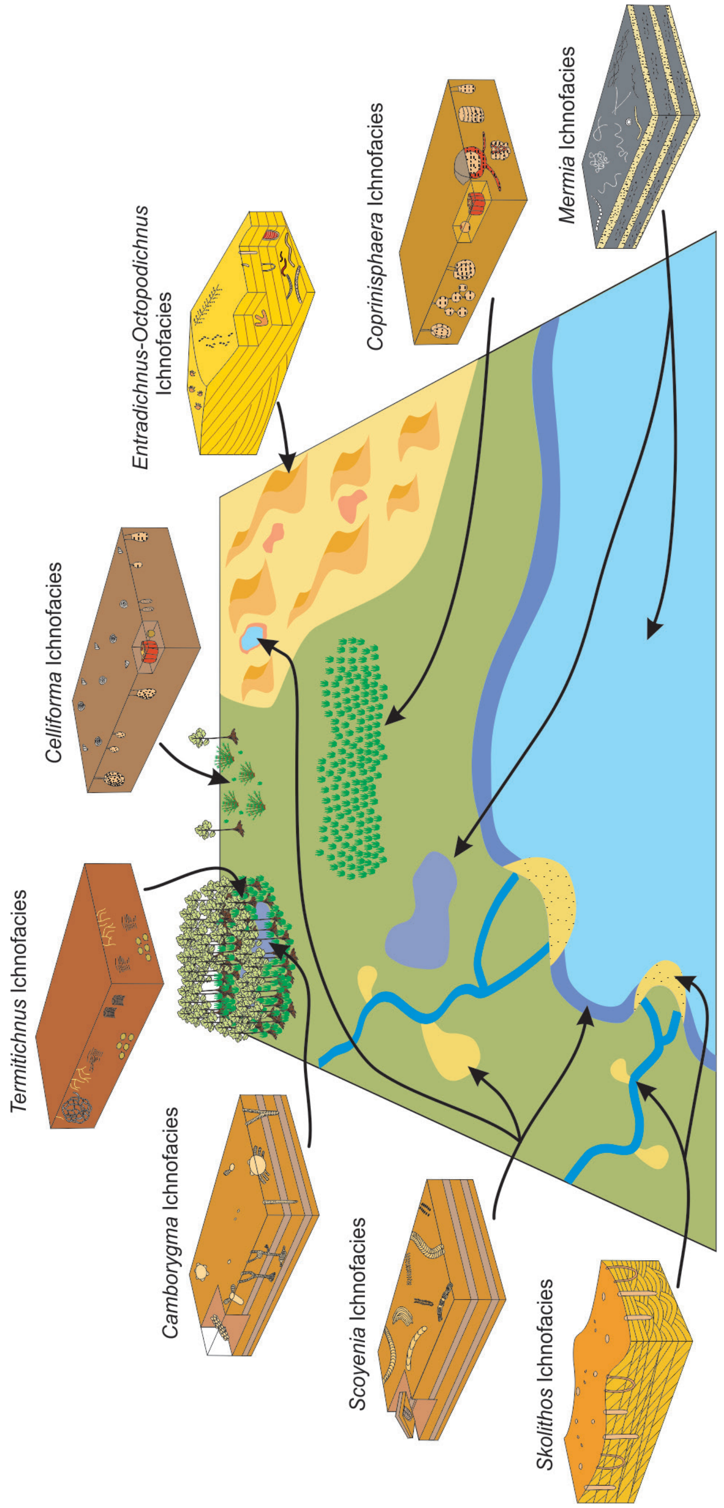

Fig. 1. Environmental distribution of invertebrate continental ichnofacies.

Another need is to attain a better articulation of ichnological and sedimentological datasets within a stratigraphic framework in order to enhance the utility of trace fossils in paleoenvironmental analysis. In this regard, continental ichnology still lags behind marine ichnology. However, studies providing a more refined integration of these lines of evidence are becoming gradually available (e.g. Eberth et al. 2000; Ronchi 2008).

Last but not least, the field will benefit from increased exploration of continental environments that so far remain poorly studied. This is the case of saline lakes and hotsprings, which are typically regarded as stressful and mostly devoid of metazoan life. However, integration of high-resolution sedimentological studies and ichnology reveals the persistence of microbial-animal interactions and a variety of traces recording adaptations and the biological complexity of the inhabitants of these settings (e.g. Scott et al. 2007, 2010, 2019; Buatois et al. 2017).

Keywords: bioturbation, continental ichnology, ichnofacies, evolutionary paleoecology

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Ichnofacies	**Characteristics**	**Representative ichnogenera**	**Implications**
Scoyenia	Abundance of horizontal meniscate backfilled traces; abundance of locomotion traces, including both trackways and bilobate trails; presence of vertical domiciles; a mixture of invertebrate (mostly arthropod), vertebrate and plant traces; low to moderate ichnodiversity, and localized high abundance.	*Scoyenia*, *Beaconites*, *Taenidium*, *Umfolozia*, *Merostomichnites*, *Diplichnites*, *Hexapodichnus*, *Permichnium*, *Acripes*, *Cruziana*, *Rusophycus*, *Planolites*, *Palaeophycus*, *Cochlichnus*, *Skolithos*, *Cylindricum* and *Fuersichnus.*	Sediments periodically exposed to air or periodically inundated, and intermediate between aquatic freshwater and terrestrial environments. Low-energy. Silty-sandy, soft to firm substrates. Fluvial overbank settings, such ponds, levees, and crevasse splays. Lake-margin areas in both open and closed lacustrine basins, and in both ephemeral and perennial lakes. Wet interdunes.
Mermia	Dominance of horizontal to subhorizontal grazing and feeding traces produced by mobile deposit feeders; subordinate occurrence of locomotion traces; relatively high to moderate ichnodiversity; high abundance, and low degree of specialization of grazing and feeding patterns.	*Mermia*, *Gordia*, *Helminthopsis*, and *Helminthoidichnites*, *Cochlichnus*, *Treptichnus*, *Circulichnis*, *Undichna* and *Diplopodichnus.*	Permanent subaqueous freshwater environments. Low-energy. Silty-sandy, soft substrates. Well-oxygenated settings. Abundant food supply. Open perennial lacustrine basins, typically hydrologically open. Floodplain water bodies under subaqueous conditions. Fjord settings under freshwater conditions due to glacial melting.
Coprinisphaera	Dominance of trace fossils of bees, wasps, ants, and beetles; subordinate presence of termite ichnofossils; dominance of nesting traces or calichnia; tiering structures that result from variable depths of emplacement of hymenopterous, termite, and dung-beetle nests; moderate to relatively high ichnodiversity, and high abundance.	*Coprinisphaera*, *Pallichnus*, *Eatonichnus*, *Monesichnus*, *Fontanai*, *Teisseirei*, *Celliforma*, *Uruguay*, *Ellipsoideichnus*, *Palmiraichnus*, *Rosellichnus*, *Chubutolithes*, *Attaichnus*, and *Parowanichnus.*	Paleosols associated with herbaceous plant communities, mostly savannas, grasslands, prairies, and steppes. Climatically ranging from dry and cold to humid and warm conditions. Various depositional systems subject to subaerial exposure and soil development, such as alluvial plains, overbank, and eolian environments.
Termitichnus	Dominance of trace fossils of termites; low ichnodiversity, and high abundance.	*Termitichnus*, *Vondrichnus*, *Fleaglellius*, *Krausichnus* and *Masrichnus.*	Paleosols formed in closed forests with plant growth under warm and humid conditions. Abandoned channels and overbank areas.

Celliforma	Dominance of halictid bee nests; association with hackberry endocarps, and freshwater and terrestrial snail shells; dominance of callichnia; presence of pupichnia; moderate ichnodiversity, and high abundance.	*Celliforma*, *Rosselichnus*, *Pallichnus*, *Rebuffoichnus*, *Palmiraichnus*, *Teisseirei* and *Taenidium*.	Carbonate-rich paleosols associated with scrubs and woodlands. Palustrine environments and calcretes.
Camborygma	Dominance of burrows produced by crayfishes and earthworms; common cross-cuttings relationships; low ichnodiversity; and high abundance.	*Camborygma*, *Loloichnus*, *Dagnichnus*, *Cellicalichnus meniscatus*, and *Edaphichnium*.	Paleosols formed in forests, scrubs, and open herbaceous communities, particularly in marshes, bogs, swamps or wetlands. High and fluctuating water table, mostly under warm climates. Various depositional systems subject to subaerial exposure and soil development, such as abandoned channels, floodplains, levees, crevasse splays, and loessic, ponds.
Octopodichnus-Entradichnus	Low-to more rarely moderate ichnodiversity; dominance of simple sub-superficial dwelling traces produced mostly by members of Coleoptera, Orthoptera and Arachnida, with horizontal and/or vertical orientation; superficial locomotion traces produced by arthropods, especially arachnids; and subordinate feeding simple and meniscate traces.	*Octopodichnus*, *Paleohelcura*, *Entradichnus*, *Digitichnus*, *Planolites*, *Palaeophycus*, *Taenidium*, *Arenicolites* and *Skolithos*.	Mobile and temporary stabilized sandy substrates, subject to frequent erosion and deposition, and to strong seasonality. Environments with reduced humidity and low nutrient availability. Sand dune, dry interdune, and sand sheet deposits of wet eolian systems typically associated with arid deserts and/or in arid intervals of hyper-arid deserts.

Table 1. Summary of continental invertebrate ichnofacies (after Minter et al., 2016a). A continental equivalent of the typically marine *Skolithos* Ichnofacies may be present as well (Fig. 1).

Update of ichnofaunal units and link with footprint biochrons in the late Palaeozoic to early Mesozoic of the Southern Alps: towards a better correlation with the marine realm

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Abstract:

Tetrapod footprints have recently proven to be a valid and useful stratigraphic tool in the late Palaeozoic-early Mesozoic continental stratigraphy. The Southern Alps of Italy (SA) show a number of very thick and well-exposed successions and preserve one of the best tetrapod footprint records of this time interval, either for the abundance, quality and diversity of the ichnoassociations. Furthermore, the stratigraphy of this area is well-constrained by radiometric datings, microfloras from both continental and marine units, invertebrate fossils and microfossils, sequence stratigraphy, carbon stable isotopic stratigraphy and magnetostratigraphy from interspaced marine units (Fig. 1).

We revised the stratigraphic record of tetrapod footprints of this area, updating existing ichnofaunal units (IFUs) and describing ichnoassociations that may represent IFUs. IFUs are informal ichnoassemblages of possible biostratigraphic value (CONTI et al., 1997; AVANZINI et al., 2001a). IFUs and ichnoassociations have been correlated with tetrapod footprint biochrons as listed in the following.

A) The oldest tetrapod footprint record in the SA occurs in the latest Carboniferous (Ghzelian) continental Corona Formation (Carnic Alps), which yielded probable anamniote tracks (MIETTO et al., 1986). This record is considered too small to represent a proper IFU.

B) The first extensive ichnoassociation is from the Lower Permian (Kungurian) continental Collio, Dosso dei Galli, Pizzo del Diavolo, Monte Luco and Tregiovo formations, all well-constrained by radioisotopic methods (e.g., SCHALTEGGER & BRACK, 2007; MAROCCHI et al., 2008). It is characterized by common non-archosauromorph eureptile and parareptile tracks, anamniote tracks and rare synapsid tracks (e.g., CEOLONI et al., 1987; SANTI & KRIEGER, 2001; MARCHETTI et al., 2015a, b, c; MARCHETTI, 2016). It constitutes the Collio IFU (CONTI et al., 1997), characterized by the lowest occurrence (LO) of *Erpetopus* and the highest occurrence (HO) of *Amphisauropus* (Fig. 1). The Collio IFU is the reference for the *Erpetopus* footprint biochron in the Kungurian (VOIGT & LUCAS, 2018) and represents the reptile radiation started by the mid Cisuralian (MARCHETTI et al., 2019a).

C) The subsequent tetrapod ichnoassociation follows a hiatus of at least 15 Ma marked by a regional unconformity, and occurs in the continental marginal marine Val Gardena Formation, dated through sporomorphs as late Permian (late Wuchiapingian/Changhsingian; e.g., PITTAU, 2001). This ichnoassociation is characterized by common diapsid and parareptile tracks, synapsid tracks and rare anamniote tracks (e.g., CONTI et al., 1977; CEOLONI et al., 1988; VALENTINI et al., 2007, 2009; MARCHETTI et al., 2017). It constitutes the Bletterbach IFU (CONTI et al., 1997), characterized by the *Rynchosauroides* LO and the *Pachypes* last appearance datum (LAD) (Fig. 1). It is the reference for the *Paradoxichnium* footprint biochron (VOIGT & LUCAS, 2018). However, the lack of *Erpetopus* and *Hyloidichnus* and the possible first appearance datum (FAD) of *Protochirotherium* (e.g., BERNARDI et al., 2015; PETTI et al., 2015) differ from other Late Permian assemblages.

D) The Lower Triassic is characterized by scattered neodiapsid footprints found in the continental

to shallow marine Werfen Formation (almost entirely Lower Triassic according to the conodont and bivalve biozones; e.g., Posenato, 2019), in the Campil and Cencenighe members (e.g., Avanzini & Mietto, 2008), but findings are too scarce to build a valid IFU. This ichnoassociation coincides with the *Rhynchosauroides schochardti* Assemblage of Avanzini & Mietto (2008).

E) Middle Triassic ichnoassociations are found in the continental-to-marginal marine Lower Serla, Gracilis, Voltago, Giovo, Richthofen and Morbiac formations. All these units are well dated through biostratigraphy (ammonoids, conodonts), macro and microfloras, magnetostratigraphy, sequence stratigraphy and stable isotopic chemostratigraphy from intercalated/correlated marine units in the Dolomites area, all considered to be of Anisian age (e.g., De Zanche et al., 1993; Mietto & Manfrin, 1995; Gianolla et al., 1998).

The Anisian ichnoassociations coincide with the *Rhynchosauroides tirolicus* Assemblage of Avanzini & Mietto (2008).

The lower Anisian Lower Serla and Gracilis ichnoassociation includes few neodiapsid and synapsid tracks (e.g., Avanzini & Mietto, 2008; Petti et al., 2013), therefore it is not informative enough to build a valid IFU.

The mid-upper Anisian ichnoassociation from the Voltago, Giovo, Richthofen and Morbiac formations is characterized by abundant archosauromorph tracks, non-archosauromorph eureptile and synapsid tracks and rare dinosauromorph tracks (e.g., Avanzini & Lockley, 2002; Avanzini & Renesto, 2002; Avanzini & Mietto, 2008; Todesco et al., 2008; Todesco & Bernardi, 2011). It is characterized by the LOs and HOs of *Chirotherium* and *Isochirotherium* (Fig. 1). This ichnoassemblage, here named *Chirotherium-Isochirotherium* Ichnoassociation, has the potential to become a valid IFU. The most significant localities are the Gampenpass/Passo Palade site (Voltago-Giovo formations) and the Piz da Peres site (Richthofen Formation). This is largely coincident with the *Chirotherium barthii* footprint biochron, although the upper part may be transitional with the *Atreipus-Grallator* biochron (Klein & Lucas, 2010) because of the LO of *Sphingopus* (Avanzini & Wachtler, 2012).

The Ladinian units are devoid of tetrapod footprints.

F) The Upper Triassic tetrapod ichnoassemblage is preserved in the Carnian continental marginal marine Val Sabbia, Travenanzes and Monticello formations, dated with sporomorphs in these units and ammonoids and conodonts in intercalated marine units (e.g., Assereto & Casati, 1965; Preto et al., 2005; Roghi et al., 2010), and in the late Carnian-Rhaetian Dolomia Principale Formation, dated with brachiopods, conodonts and sequence stratigraphy (e.g., Mietto, 1977; Gianolla et al., 1998; Belvedere et al., 2008).

The lower Carnian ichnoassociation, preserved in the Val Sabbia Formation (Zone locality, near the lake of Iseo; Petti et al., 2009), includes only non-dinosauromorph archosauromorph tracks, and coincides with the Assemblage 1 of Bernardi et al. (2018). It is characterized by the FO of *Brachychirotherium*, here named *Brachychirotherium* ichnoassociation, and may become a valid IFU after further findings. More track occurrences are reported from the lower Carnian Dolomia Cassiana Formation (Mietto et al., 2012), but they are unfortunately poorly-preserved.

The upper Carnian ichnoassociation comes from the Travenanzes, Monticello and Dolomia Principale formations and is characterized by abundant dinosaur tracks, archosauromorph tracks and rarer dinosauromorph tracks (e.g., Mietto, 1988; Dalla Vecchia, 1996; Dalla Vecchia & Mietto, 1998; D´Orazi Porchetti et al., 2008; Avanzini et al., 2010; Bernardi et al., 2013). It coincides with the Assemblages 2 and 3 of Bernardi et al. (2018) and probably represents the first dinosaur radiation with a contemporary reduction of the non-dinosauromorph archosauromorphs. It is characterized by the FAD of *Eubrontes* and *Evazoum*, the first occurrence (FO) of *Grallator* and the LO of *Brachychirotherium* (Fig. 1). This ichnoassemblage, here named *Eubrontes-Grallator* ichnoassociation, has the potential to become a valid IFU. The most representative locality is San Gottardo near Mezzocorona (Travenanzes Formation).

The Late Triassic ichnoassociations coincide with the *Brachychirotherium* footprint biochron (Klein & Lucas, 2010).

G) The Lower Jurassic ichnoassociation comes from the tidal Hettangian-Sinemurian Monte Zugna

Formation and from the Pliensbachian Rotzo Formation (both pertaining to the Calcari Grigi Group), dated with marine fossils (e.g., Avanzini et al., 2007). It is characterized by diverse dinosaur tracks (e.g., Leonardi & Mietto, 2000; Mietto et al., 2000, Avanzini et al., 2001b, 2003; Avanzini & Petti, 2008), with the LO of *Kayentapus*, *Anomoepus* and *Parabrontopodus*, and the HOs of *Grallator* and *Eubrontes* (Fig. 1). This ichnoassemblage, here named *Kayentapus-Parabrontopodus* ichnoassociation, has the potential to become a valid IFU. The most representative locality is the famous megatracksite of the Lavini di Marco near Rovereto (Monte Zugna Formation). This is coincident with the Lower Jurassic footprint biochron (*Eubrontes* acme) (Lucas, 2007).

In conclusion, two IFUs based on tetrapod footprints have been revised and four ichnoassociations that may become IFUs have been described for the late Palaeozoic-early Mesozoic continental-marginal marine ichnoassociations from the Southern Alps. In our view, because of the quality of the ichnofossil record and the high-resolution stratigraphic record in the marine units, this area constitutes an ideal reference for the continental-marine stratigraphic correlations and the combined study of the continental-marine biota during climatic crises.

Keywords: tetrapod footprints, biostratigraphy, ichnofaunal units, Palaeozoic-Mesozoic, Southern Alps

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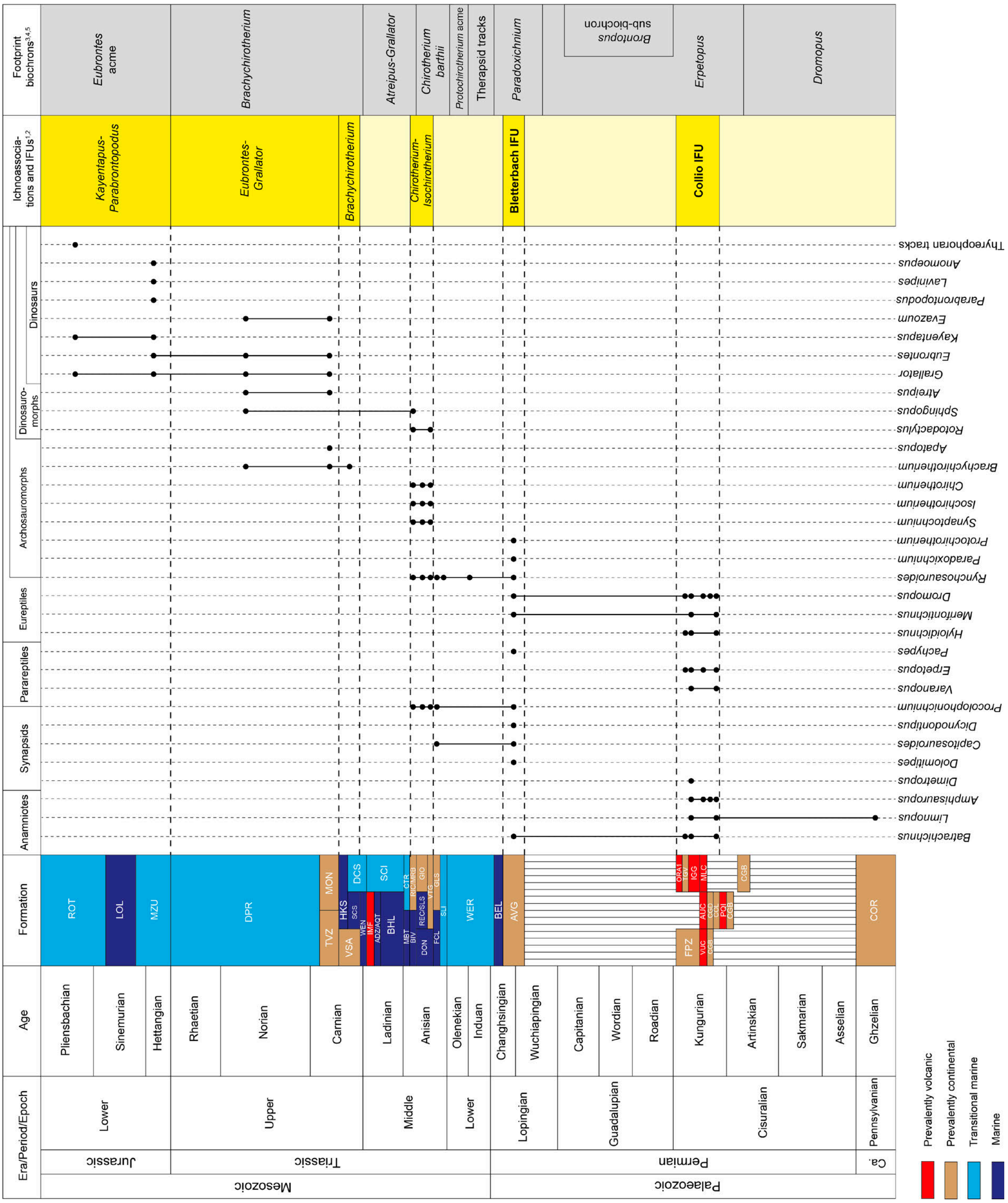

Fig. 1: Chronostratigraphic scheme of the Southern Alps with the Palaeozoic-Mesozoic continental and marginal marine units containing tetrapod footprints, and intercalated or correlated marine units; ichnotaxa ranges (occurrences centered in the middle of the formations); supposed trackmaker groups; ichnoassociations/ichnofaunal units (IFUs) and footprint biochrons. Note that pre-Late Triassic *Brachychirotherium* and *Parasynaptichnium* are not represented because probably assignable to different ichnogenera (e.g., Petti et al., 2013). The tracks from the Corona Formation (Mietto et al., 1986) are assigned to *Limnopus*, and the crocrodilomorph tracks from the Monticello Formation (Dalla Vecchia, 1996) are assigned to *Apatopus*. The Palaeozoic units are dated with radiometric ages and palynology, the Mesozoic units mostly with marine macro- and microfossils from intercalated or coeval marine formations. Formation acronyms: COR=Corona, CGB=Basal Conglomerate, VUC=Auccia Volcanite, FPZ=Pizzo del Diavolo, PQI=Lower Porphyries, COL=Collio, CGD=Dosso dei Galli, AUC=Auccia, MLC=Monte Luco, IGG=Gargazzone, TGV=Tregiovo, ORA1=Ora Formation, Predonico Member, AVG=Val Gardena, BEL=Bellerophon, WER=Werfen, SLI=Lower Serla, FCL=Coll´Alto Limestone, GLS=Gracilis, DON=Dont, VTG=Voltago, REC=Recoaro Limestone, SLS=Upper Serla, GIO=Giovo, BIV=Bivera, RIC=Richthofen, MRB=Morbiac, MBT=Ambata, CTR=Contrin, BHL=Livinallongo/Buchenstein, ADZ=Zoppè Sandstone, AQT=Acquatona, IMF=Fernazza Volcanite, SCI=Sciliar, WEN=Wengen, SCS=San Cassiano, DCS=Cassian Dolomite, HKS=Heiligkreuz, TVZ=Travenanzes, VSA=Val Sabbia, MON=Monticello, DPR=Dolomia Principale, MZU=Monte Zugna, LOL=Loppio Oolitic Limestone, ROT=Rotzo. 1=this work, 2=Conti et al., 1997, 3=Klein & Lucas, 2010, 4=Voigt & Lucas, 2018, 5=Marchetti et al., 2019b.

Three-dimensional methodology for photogrammetric reconstruction of ichnofossils

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Abstract:

Photogrammetry is a common method, which is used for 3D reconstruction purposes. It shows exceptional results in broad paleontology field (MALLISON & WINGS 2014), as well as in ichnological applications (REMODINO ET AL. 2010; FALKINGHAM ET AL. 2018). This study presents an experimental approach of the usage of photogrammetry in situ for reconstruction of large rock plates, covered with multiple ichnofossils. The studied material and locality is a Silurian limestone from Ohessaare cliffs, Saaremaa, Estonia, where rich bioturbations can be observed at a horizontal outcrop on the sea coast.

Photogrammetric survey was done by using a Canon 80D camera with 24 mm lens. Several GCPs were placed on each rock block and measured with RTK GNSS equipment. Reconstruction was done in Agisoft MetashapePro. Half of all GCPs were used for alignment corrections and another half for model clarification. As a result, orthomosaic and DEM were produced and exported to QGIS software for interpretation.

Reconstructed 3D models of rock plates show that *Rhizocorallium* from the Ohessarre coast has a thinner marginal tube and a burrow outline with the shape of a widely rounded curve and sprite organization more similar to Zoophycos. The outlined studies show prominent results of photogrammetry application in. The authors suggest the usage of this method for reconstruction of ichnofossils in situ.

Keywords: photogrammetry, ichnofossils, 3D reconstruction

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New dinosaur tracks from the Late Cretaceous El Molino Formation of Toro Toro (Dep. Potosi, Bolivia)

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Abstract:

The El Molino Formation in the Toro Toro syncline (Department of Potosi, Bolivia) has long been known for it's Cretaceous dinosaur tracks. They were briefly mentioned by Branisa (1968). Giuseppe Leonardi led the first expedition in 1983 and mapped several surfaces. In 1984 he published the description of a trackway, *Ligabueichnium bolivianum* attributed to an ankylosaur. In his atlas (Leonardi 1994) five larger surfaces with tracks and trackways of theropods and sauropods are figured. Most of the sauropod trackways can be attributed to the ichnotaxon *Calorckosauripus lazari* Meyer, Marty & Belvedere, 2018. Apesteguía et al. (2011) describe purported dromaeosaurid tracks from the Toro Toro Formation, however the site is in the El Molino Formation. The latter has been deposited in a lacustrine to fluvial environment.

We report here on several new surfaces situated on the Cerro de Huayllas, the Rio T'iratani and the Quebrada Chiflon. They are situated at the base and the top of the Middle member of the El Molino Formation (Maastrichtian: see Vignol et al. 2018).

The Cerro de Huayllas surfaces show tracks and trackways of minute (FL 13 cm) to large sized theropods (FL 35 cm) as well as parallel trackways of *C. lazari*. The Quebrada Chiflon comprises two surfaces of 1300 and 1600m2 respectively, containing more than 1000 footprints of small to medium sized theropods. The Quebrada del Rio T'iratani site shows a surface with 30 theropod footprints in four trackways. One of the trackways consists of three consecutive imprints of a crouching theropod that may be attributed to Maniraptoriformes.

Keywords: lacustrine environment, dinosaur tracks, El Molino Formation, Maastrichtian, Toro Toro (Bolivia)

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On the occurrence of *Ichniotherium* from the Lodève Basin (Southern France): reappraisal of ‘*Cyclopus aequalis*’ Heyler & Lessertisseur 1963

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Abstract:

The early Permian continental succession from the Lodève Basin (Southern France) yields a very rich tetrapod ichnological record. However, the ichnotaxonomy of some morphotypes is still unclear. This is the case of *Cyclopus aequalis* Heyler & Lessertisseur (1963), defined on the basis of ~30 large footprints, currently preserved on a plaster cast of the original surface (MNHN-LOD 83), coming from the Autunian Lunas locality (Fig. 1). We re-describe these tracks by using up-to-date data and techniques (e.g. photogrammetry). Manus tracks (120-130 mm long, 150-160 mm wide) are semiplantigrade to plantigrade, whereas pes tracks (150-170 mm long, up to ~160 mm wide) are plantigrade. Both manus and pes tracks are pentadactyl and ectaxonic (digit IV impression is the longest). Digit impressions are relatively wide and short, slightly bent inwards and deeper in their rounded tips. In manus tracks, digit III impression is the deepest. In pes tracks, impressions of digit I and II are the deepest. In pes tracks, impression of digit V is about as long as III. Two broad trackways are arranged in alternated manus-pes sets (stride: 500 to 550 mm; pace: 400 to 460 mm), with pes tracks behind and in line with manus tracks. Manus tracks are rotated inwards, whereas pes tracks are parallel to the midline. Although this material is not well-preserved (preservation grade 2.0 or lower), the new analysis permits a confident assignment to *Ichniotherium* (the first not dubious from Lodève localities) confirming the hypotheses of Haubold (1971) and Gand (1988). These footprints suggest the presence of large diadectomorph reptiliomorphs in Southern France, and increase the ichnofaunal diversity of Central Pangaea.

Keywords: ichnotaxonomy, *Ichniotherium*, diadectomorph footprints, Early Permian, Lodève

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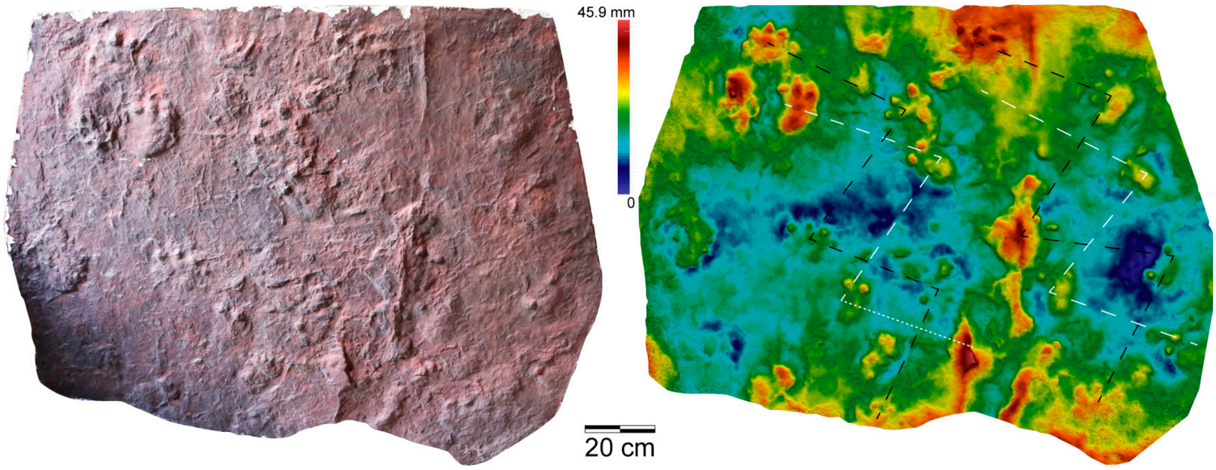

Fig. 1. Photo of the plaster cast surface and false colour map from 3D photogrammetric model of MNHN-LOD 83. Dashed lines indicate the manus and pes paces of trackways (in black and white, respectively).

Making use of a track-trackmaker association: locomotor inference of an early amniote with help of "fossilized behavior"

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Abstract:

A deeper understanding of an extinct species' paleobiology is a common goal of studies into the functioning of the musculo-skeletal system which is only fragmentarily preserved in fossil tetrapod remains. The combination of a body fossil and ichnofossils stemming from the same species offers the chance to link fossilized anatomical features with "fossilized behavior". In a recent project, a unique combination of an articulated complete specimen of *Orobates pabsti* (Diadectidae) and *Ichniotherium sphaerodactylum* tracks to which *O. pabsti* has previously been assigned as the trackmaker was exploited for an in-depth reconstruction of the locomotion of this species. Phylogenetic analyses place *O. pabsti* close to the crown group node of amniotes and often recover the diadectids as the fossil sister taxon to modern amniotes. Early amniotes became increasingly independent of aquatic habitats and this key evolutionary transition is reflected in the reconstructed locomotor behavior of *O. pabsti*. Research into the fossil's anatomy, the fossil's potential joint mobility and potential movements within the *I. sphaerodactylum* tracks, a comparative analysis of extant tetrapod locomotor mechanics, and finally into a fossil-inspired walking machine (OroBOT) will be summarized.

Keywords: *Orobates*, locomotion, *Ichniotherium*, robot, simulation

Introduction

Early four-limbed vertebrates (i.e., early tetrapods) evolved the salient capability to move on land. It has been argued that the transition from fully aquatic ancestors to fully terrestrial forms was not completed before the appearance of the amniote egg accompanying terrestrial reproduction (e.g., Romer 1957). Soon after the appearance of the first amniotes, the clade underwent a rapid radiation which has previously been linked to the evolution of advanced terrestrial locomotion (Sumida & Modesto 2001). An understanding of locomotor capabilities of early amniotes (both stem representatives and basal members of the crown group) indicative of how well a species was adapted to an terrestrial lifestyle thus has the potential to elucidate further this key event of tetrapod evolution. New, integrative and interdisciplinary approaches allow for reconstructions of locomotor characteristics grounded on quantified empirical evidence (McInroe et al. 2016; Nyakatura 2016).

In the study summarized here, a unique combination of a pristinely preserved, complete and articulated specimen of *Orobates pabsti* (MNG 10181), a basal diadectid (Berman et al. 2004), and fossil tracks of the ichnospecies *Ichniotherium sphaerodactylum* (MNG 1840) assigned to *O. pabsti* as the trackmaker (Voigt et al. 2007) was used to study the locomotor capabilities of this species (Fig. 1). Both utilized fossil specimens stem from the same locality of the Thuringian forest in central Germany, the Early Permian Tambach Formation of the Bromacker quarry near Tambach-Dietharz (Martens 2018). The Tambach Formation of the Bromacker locality has produced dozens of articulated, partially or completely preserved tetrapod body fossil specimens several of which are diadectids including the here used holotype specimen (MNG 10181) and paratypes of *O. pabsti* (Berman et al. 1998; Berman & Henrici 2003; Berman et al. 2004; Martens 2018). The locality has also yielded hundreds of vertebrate tracks including the MNG 1840 tracks of *I. sphaerodactylum* (Eberth et al. 2000; Voigt 2005; Voigt et al. 2007). The Bromacker is furthermore the type locality of the Tambach Sandstone, which in part forms the base of the Upper Rotliegend Group in this area (Eberth et al. 2000; Voigt et al. 2007). All skeletons and tracks stem from a 10m thick stratigraphic interval of this Tambach Sandstone and first fossil finds were exposed in commercial quarries (Voigt et al. 2007). Voigt et al. (2007) were able to establish an association of the tracks of *I. sphaerodactylum* with *O. pabsti* as the trackmaker based on the relative lengths of the digits of the pes imprint and the degree of overstepping of the manus and pes imprints.

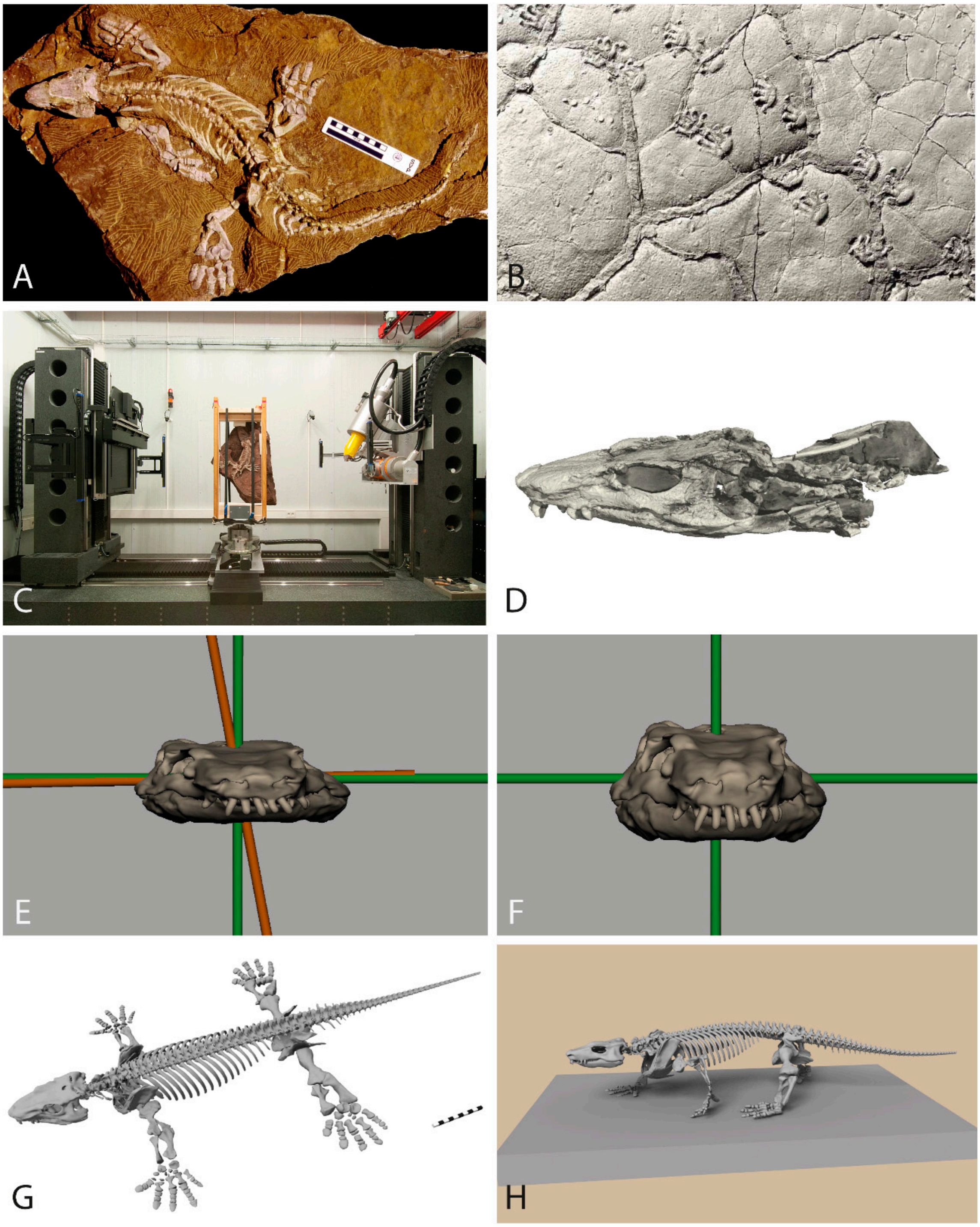

Fig. 1.: Digital reconstruction of *O. pabsti* (figure modified from Nyakatura 2017). A: The holotype specimen of *O. pabsti* MNG 10181; B: The *I. sphaerodactylum* ichnofossil MNG 1840; C: Computed tomography scan of MNG 10181 at the Technical University Dresden, Germany; D: Volume render of the high detail skull scan; E,F: Correcting distortion using symmetry and other evidence (cf. Nyakatura et al. 2015); G: Complete digital reconstruction; H: Virtual mount of MNG 10181.

Thus, the *I. sphaerodactylum* tracks typify "fossilized behavior" of *O. pabsti* and present an intriguing opportunity to study the locomotion of this fossil species. Diadectids are usually recovered as stem amniotes close to the crown group node of amniotes (Laurin & Reisz 1995; Ruta & Coates 2007). However, a couple of recent studies found *O. pabsti* to be an early member of the amniote crown group in at least some of the conducted analyses (Berman 2013; Marjanovic & Laurin 2019). The conjunction of a complete body fossil, assigned tracks, and a key phylogenetic position in the tetrapod tree of life motivated the here summarized investigation into the locomotion of *O. pabsti*.

The methodological approach advocated in this project integrated i) the digital reconstruction of the type specimen of *O. pabsti* MNG 10181, ii) two sets of simulations constrained by the fossil tracks (MNG 1840) and informed by biomechanical insight into sprawling tetrapod locomotion of extant species, and iii) a fossil-inspired, motor-actuated physical replica of *O. pabsti*, a robot dubbed OroBOT (Nyakatura et al. 2019). This combination of empirically grounded quantitative evidence was employed to narrow down the range of plausible locomotor characteristics of *O. pabsti* in a transparent and reproducible way.

A digital reconstruction of *Orobates pabsti*

Despite the superb preservation of the holotype specimen MNG 10181, the fossil was affected by taphonomic and diagenetic processes. As a result the almost 300 million year old specimen is fragmented and suffers from plastic deformation (Nyakatura et al. 2015). Furthermore, the specimen is mostly restricted to a two-dimensional analysis since the skeleton was only superficially prepared out of the surrounding rock matrix to prevent potential damage. To allow a quantitative analysis of the specimen's functional anatomy, it was therefore digitally reconstructed using microfocus computed tomography (µCT) scanning and subsequently virtually repaired. For scanning, the v|tome|x L450 (GE phoenix x-ray systems, Wunstorf, Germany) was used at the Technical University of Dresden, Germany (Fig. 1). For the main slab of MNG 10181 (ca. 1.0 m x 0.8 m x 0.35 m; approx. 35 kg) containing most of the trunk, tail, pelvic girdle, a forelimb and both hindlimbs a resolution of 150 µm was achieved. A slab of MNG 10181, which was separated during preparation (Berman et al. 2004), contained the skull, the cervical vertebrae, the pectoral girdle, and the left forelimb and allowed a more detailed scan with a resolution of 62 µm (Fig. 1).

Taphonomic and diagenetic alterations of the fossil material lead to a high heterogeneity of grey levels between fossil bone and surrounding rock matrix in the µCT images. This prevented the use of automated segmentation algorithms and made a time-consuming manual segmentation necessary. Segmentation was done using the segmentation editor in Amira® 6.0.0 (Thermo Fischer Scientific, Hillsboro, Oregon, U.S.A.). Bone fragments were fused in Autodesk Maya® (Autodesk Inc., San Rafael, California, U.S.A.) and subsequently plastic deformation was corrected using symmetry criteria and circumstantial evidence from additional material (specifically an isolated vertebra MNG 8966) as explained in detail in a previous publication (Nyakatura et al. 2015). It was not possible to virtually reconstruct in sufficient quality large parts of the trunk and tail. These parts were modelled according to the detailed descriptions provided in the literature (Berman et al. 2004). Only the left limbs were reconstructed and were subsequently simply mirrored to obtain right limbs assuming perfect bilateral symmetry. Finally, this idealized digital reconstruction of the holotype specimen of *O. pabsti* was mounted in Maya® (Fig. 1), was made publically available (http://dx.doi.org/10.17880/digital-reconstruction-of-orobates-pabsti-mng10181), and served as the basis for the estimation of body mass (ca. 4kg), the body segments' centers of mass, the mobility in the hip and shoulder joints (Nyakatura et al. 2015), and was the basis for a digital marionette that was used for subsequent simulations of the locomotion (Nyakatura et al. 2019).

Simulating the locomotion using constraints posed by fossil tracks

To identify common principles of sprawling tetrapod locomotion that can also be assumed to have pertained to *O. pabsti*, an in-depth comparative analysis of the locomotor mechanics of a sample of extant species was conducted. Previous work demonstrated the importance of lateral bending of the spine, of retraction in the shoulder and hip joints, and of long-axis rotation of the stylopodial limb elements (humerus and femur) for the generation of propulsion in sprawling gaits (Barclay 1946, Edwards 1977; Ashley-Ross 1994; Karakasiliotis et al. 2013; Nyakatura et al. 2014). These kinematic properties were thus quantified in metamorphic Mexican salamanders (*Ambystoma mexicanum*), blue-tongued skinks (*Tiliqua scincoides*), green iguanas (*Iguana iguana*) and spectacled caimans (*Caiman crocodilus*) using x-ray motion analysis (Nyakatura et al. 2019). Synchronously, ground reaction forces for individual limbs in contact with the ground were recorded (Fig. 2).

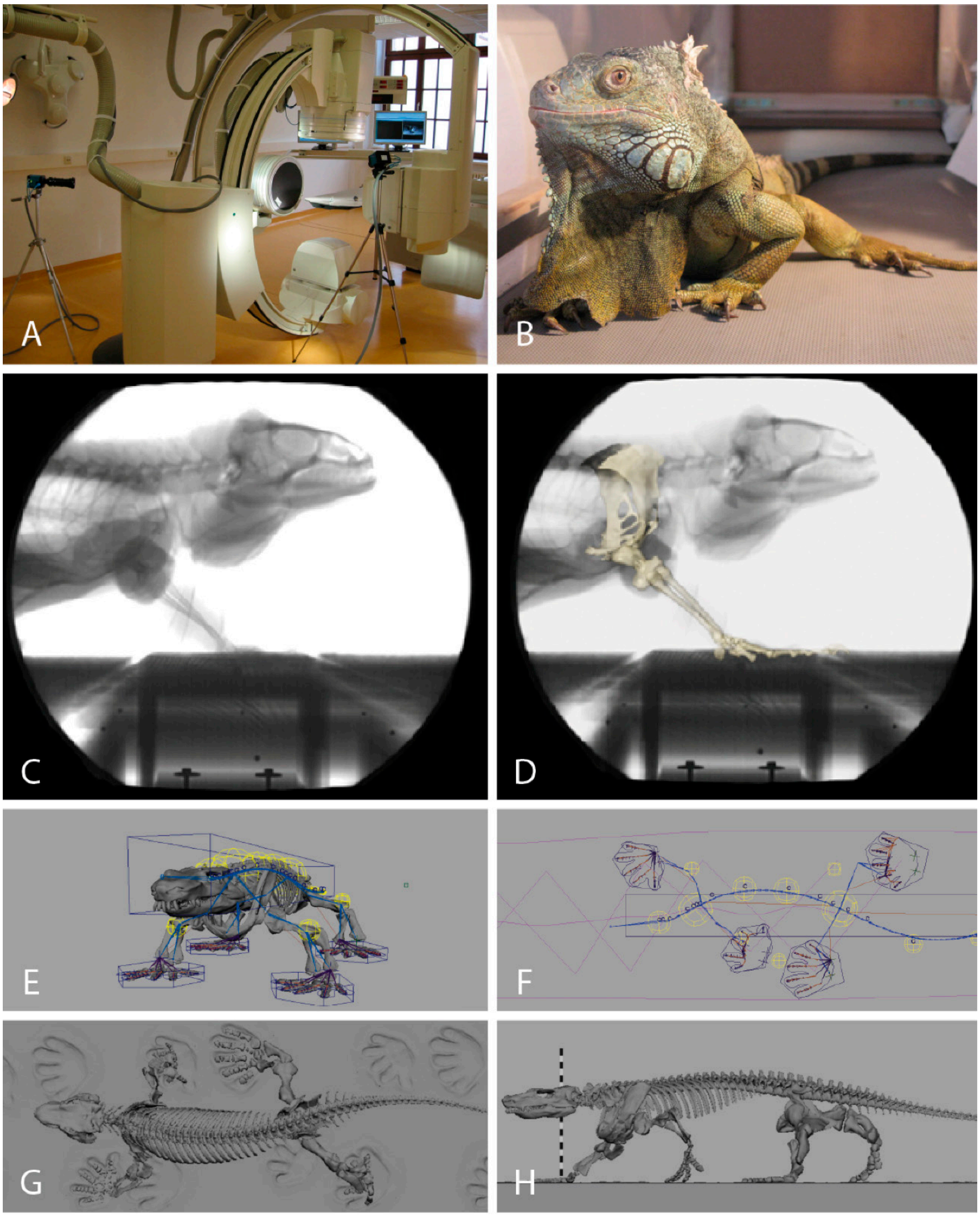

Fig. 2: Kinematic simulation of *O. pabsti* (figure modified from Nyakatura 2017). A: The biplane high-speed x-ray facility of the Friedrich Schiller University Jena, Germany, where all x-ray motion analyses have been conducted; B: Green iguana on a treadmill; C, D: Video stills from x-ray motion analysis that involves superimposition of three-dimensional bone models on x-ray images to visualize and quantify three-dimensional kinematics (cf. Nyakatura et al. 2014; Nyakatura et al., 2019); E: Digital marionette of *O. pabsti*; F: Locomotion is constrained within the MNG 1840 tracks; G, H: The kinematic simulation allows systematic variation of kinematic variables to test for anatomical plausibility.

The sampled extant animals covered a reasonable portion of the mechanical diversity in extant sprawling tetrapods due to differing morphology (e.g., body length to limb length ratio) and different ecologies (terrestrial, semi-aquatic, arboreal). The extant sample also phylogenetically bracketed the anamniote to amniote transition (Witmer 1995). In brief (this data is detailed in Nyakatura et al. 2019), this comparative analysis revealed significant differences between more erect limb postures (fore- and hindlimbs in the caiman and forelimbs in the iguana) and hyper-sprawled limb postures (fore- and hindlimbs in the salamander and the skink, hindlimbs in the iguana). More erect limb postures were accompanied by less long-axis rotation and increased stylopodial retraction. The most important kinematic properties were visualized in a three-dimensional plot, that was termed the sprawling gait space. These plots allow for the direct comparison of the complex gait characteristics. Despite the observed differences between more erect and hyper-sprawled limb postures, the patterns of the vertical ground reaction force component was remarkably similar within our sample of diverse extant taxa, which indicates that dynamic similarity is maintained across extant sprawling taxa (Nyakatura et al. 2019).

The *I. sphaerodactylum* tracks MNG 1840, as "fossilized behavior" of *O. pabsti*, preserved information about stride length, stride width, and pace angulation for a locomotor sequence of the fossil. The fossil's trackway information was thus compared to the tracks of extant species, too (Curth et al. 2014). The MNG 1840 tracks were intermediate to those of the extant species implying that locomotor mechanics of *O. pabsti* likely did not deviate substantially from those of the extant sampled species (Nyakatura et al. 2019). In accordance with the kinematic principles observed in the comparative analysis of extant sprawling tetrapods, the digital marionette of the digitally reconstructed holotype specimen MNG 10181 was animated in Maya® (Fig. 2). The skeleton's movements were hard constrained by the tracks of MNG 1840 (i.e., the autopodia of the digital marionette were forced to contact the ground within the MNG 1840 tracks), which were also digitized and imported into Maya® together with the digital marionette.

The animated digital marionette of *O. pabsti* walking within the MNG 1840 tracks allowed for a systematic variation of the most important kinematic variables (lateral spine bending, long-axis rotation/retraction, body height) in a virtual experiment. 100 parameter combinations were tested for each the forelimb and the hindlimb (Nyakatura et al. 2019). For each parameter combination of *O. pabsti* anatomical plausibility was evaluated and by this regions within the sprawling gait space plot were identified that were characterized by no or just minimal bone collisions or joint de-articulations. These anatomically plausible gaits exhibited little-to-moderate humeral and femoral long-axis rotation, intermediate-to-high body height and moderate lateral spine bending (Nyakatura et al. 2019).

OroBOT – an actuated physical replica of *Orobates pabsti*

A physical walking machine, dubbed OroBOT, was built to mimic the fossil reconstruction of *O. pabsti* and to test reconstructed plausible gaits under realistic conditions (real-world physics). For the construction, three-dimensionally printed parts that were designed after the morphology of *O. pabsti* were used together with off-the-shelf actuators. OroBOT was based on a previous robotic platform, Pleurobot (Karakasiliotis et al. 2016), but was designed to closely mimic properties of *O. pabsti* (e.g. positioning of the girdles along the spine, position of the center of mass, limb lengths etc.; cf. Nyakatura et al. 2019). Pleurobot already was a tetrapod walking machine that was able to replicate salamander stepping locomotion, including lateral bending of the spine, long-axis rotation and retraction in the proximal limb joints, and different body heights (Karakasiliotis et al. 2016). Importantly, OroBOT was simulated first in Webots® (Cyberbotics ltd., Lausanne, Switzerland), an open source robotics simulation software. This allowed dynamic simulation of the robot locomotion. Thus, in addition to the anatomic criterion of plausibility (termed a "filter" in Nyakatura et al. 2019) described above, additional dynamic filters were utilized to further narrow down the likely locomotion of *O. pabsti*. These filters were a power expenditure criterion, a balance criterion, a precision criterion, and a ground reaction

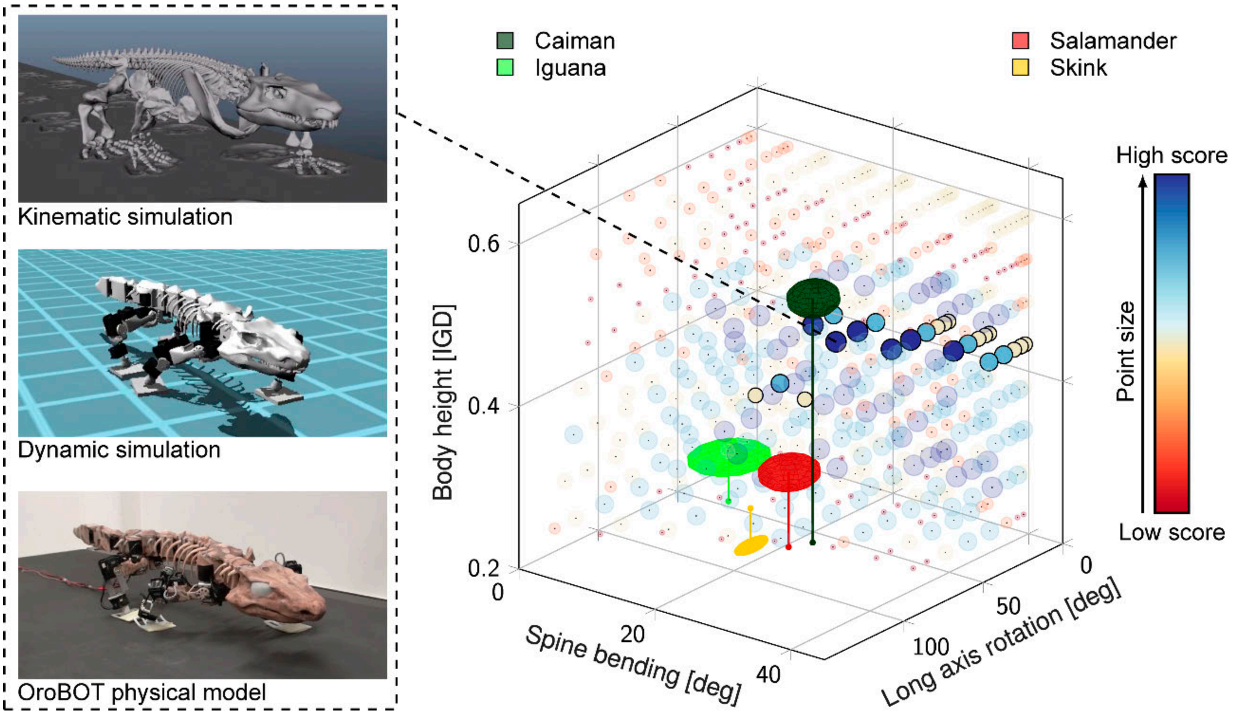

Fig. 3: Several plausible gaits are found after employing all kinematic and dynamic filters and visualized in the three-dimensional sprawling gait space plot (large, dark blue spheres). Pale spheres represent evaluation of dynamic filters only, before being filtered for anatomical plausibility. For comparison, kinematics of extant species are plotted in the sprawling gait space, too. Body height of different species has been normalized by inter girdle distance (IGD). Plausible gaits found for *O. pabsti* resemble the locomotion of the caimans. Figure modified from Nyakatura et al. 2019.

Finally, it was tested for a number of parameter combinations across the sprawling gaits space whether the physical robot OroBOT matches the simulated gaits in Webots®, which was the case. The robot was able to replicate the track parameters of MNG 1840 in the reconstructed plausible gaits (Nyakatura et al. 2019).

Discussion and implications

Consistent with previous qualitative assessments of the locomotion of *O. pabsti* (Berman & Henrici 2003; Voigt et al. 2007), we reconstructed a relatively erect (within the spectrum of sprawling tetrapod locomotion) gait. Locomotion of *O. pabsti* further appeared to be balanced and mechanically power-saving (Nyakatura et al. 2019). In comparison to earlier tetrapods, this combination points to advanced terrestrial locomotor capabilities. Thus, if diadectids are indeed stem amniotes (e.g., Laurin & Reisz 1995; but see Marjanovic & Laurin 2019), these results suggest that advanced terrestrial locomotion can be assumed to have evolved before the crown group and predates the subsequent radiation of amniotes.

In addition to the paleobiological insight outlined above, the study summarized here has methodological aspects worth discussing. First, it is important to point out that it was not aspired to find the *one correct solution* for the problem of how has *O. pabsti* has moved. Instead, hard constraints in form of anatomical features of MNG 10181 and track parameters of MNG 1840 were combined with different dynamic filters and together were used to stepwise exclude unlikely parameter combinations (i.e., gaits). This approach was first suggested by Gatesy et al. (2009). All data supporting the quantitative assessment of *O. pabsti* locomotion have been made publicly available (Nyakatura et al. 2015; Nyakatura et al. 2019) and is aimed to allow future studies to complement and/or revise the current state of knowledge. Additionally, a website was created that allows users to interactively explore the sprawling gait space of *O. pabsti*, give different weights to the filters, and to compare the reconstructed locomotion with that of the analyzed sample of extant sprawling tetrapods (https://go.epfl.ch/Orobates). New insight could lead to completely new filters, that could be used to further narrow down the locomotion of *O. pabsti*. Also, the here advocated approach, coined "robotic paleontology" (Nyakatura et al. 2019), could be transferred to similar problems where a deeper understanding of the functional morphology holds the potential for enabling more fine-grained concepts of key evolutionary transitions (e.g., the origin of active flight in birds and bats or the origin of bipedal locomotion of human ancestors).

Further, this study demonstrates the potential use of robotics for the understanding of biological problems, in contrast to the more common approach of studying biological systems to inform new technical solutions. Compared to motion analyses of living animals, robots allow to systematically test individual parameters similar to computer-aided simulations (Nyakatura 2017). In such simulations, too, systematic analysis of individual parameters provides an opportunity to test the limits of what is plausible and beyond to exhaustingly explore a search space. "Virtual palaeontology" (Cunningham et al. 2014), as utilized in the study summarized here, is a prerequisite for such "virtual experiments" (Nyakatura & Demuth 2019).

Finally, as part of the current study experts from design disciplines concerned with computer generated imagery and computer animation developed together with (paleo-)biologists new tools for the analysis of *O. pabsti*. This constitutes an example of how new technology-driven research strategies in addition to the traditional scientific illustration can increasingly become a means to generate new knowledge rather than "merely" helping to communicate scientific output to peers and the public (Amelung 2019). Consequently, the scientific illustrators were included directly in the author list, instead of being mentioned in the acknowledgements only (cf. Nyakatura et al. 2015; Nyakatura et al. 2019).

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First record of cf. *Polyonyx* sauropod trackway outside the Iberian Peninsula: Insight from Middle-?Late Jurassic red beds of Morocco

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Abstract:

A new dinosaur tracksite was discovered in continental red beds of the Isli Formation (late Bathonian-?Callovian) along the northern flank of the Aït Ali ou Ikkou Syncline in the Imilchil area, Central High Atlas, Morocco.

The area has an extraordinary scientific potential, as the layers, which have been deposited in a fluvio-lacustrine environment, contain at least fourteen track-bearing levels, which reveal a diverse dinosaur-dominated ichnofauna including the footprints of crocodylomorphs, pterosaurs, theropods, sauropods and ornithischians; and numerous invertebrate traces.

In this work, we focus on a longer sauropod trackway from the new locality, which is morphologically similar to the ichnogenus *Polyonyx* and which represents the first record of this morphotype outside of the Iberian Peninsula. The trackway is moderately to well-preserved and comprises nine consecutive manus-pes sets preserved as concave epireliefs. Characteristic features are low heteropody and asymmetry of manus prints with a large digit I (pollex) trace which is oriented medially, and with a large triangular claw I trace which is posteriorly oriented. Pes prints show four claw marks, I–II with an anterior orientation, and III–IV laterally oriented. Different from typical *Polyonyx* is the narrow gauge pattern vs. the wide gauge observed in the type trackway from Portugal.

This study suggests that the trackmaker, interpreted here as basal eusauropod, lived in an intra-continental silty-sandstone depositional environment, different from the limestone environments of the Iberia province, and compared with both marginal-sea (Portugal) or lacustrine (Spain) environments. The stratigraphic age of the High Atlas deposit is younger than the sites in Portugal (Bajocian-Bathonian) and older than the Spanish localities (Tithonian-Berriasian).

The new data from the Moroccan High Atlas give evidence of basal eusauropods in the Middle Jurassic-Early Cretaceous interval of northwestern Gondwana.

Keywords: Sauropod trackway, Bathonian, Isli Formation, Imilchil, Central High Atlas, Gondwana

Dinosaur track-bearing deposits of the Cretaceous Gyeongsang Supergroup, Korea: Stratigraphic occurrences and paleoecological implications

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Abstract:

Dinosaur track-bearing deposits are common in the Cretaceous Gyeongsang Supergroup (Hauterivian to Maastrichtian) (Fig. 1), Korea. The Gyeongsang Supergroup consists of alluvial fan, fluvial plain, and lacustrine deposits and is composed of a variety of siliciclastic and tuffaceous rocks, some carbonates and evaporites. The dinosaur track-bearing deposits of the Gyeongsang Supergroup show variation in stratigraphic occurrences. Whereas dinosaur bone fossils occur in the lowermost Nakdong Formation (alluvial fan with some ponds) and are common in the overlying Hasandong Formation (fluvial with some lakes), dinosaur tracks are absent in the Nakdong Formation and scarcely present in the Hasandong Formation. Body fossils of dinosaurs are very rare throughout the Gyeongsang Supergroup except the Hasandong Formation, however, dinosaur tracks are common in the upper part of the Jinju Formation (lacustrine), the Haman Formation (alluvial plain with some ponds) and the Jindong Formation (alluvial plain and playa lakes). It is unusual that dinosaur tracks are absent in the Chilgok Formation overlying the Jinju Formation in spite of its similar depositional setting to that of the Haman Foramtion. In the pyroclastic deposit-dominated Yucheon Group (the uppermost Group) overlying the Jindong Formation dinosaur tracks are very rare. In summary the occurrences of dinosaur tracks in the Gyeongsang Supergroup shows the recurrent pattern of increase and decrease in abundance and a preferred occurrence in lake-related deposits rather than in alluvial fan and fluvial sediments. It is suggested that dinosaurs migrated into the Gyeongsang Basin during the Barremian, then thrived during Aptian to Cenomanian, and finally declined in the Campanian. The stratigraphic shifts of dinosaur occurrences might have been resulted from paleoenvironmental changes of the Gyeongsang Basin related to the evolution of regional tectonism inducing volcanic activity and paleoclimate changes on the Korean Peninsula during the Cretaceous.

Keywords: Cretaceous, dinosaurs, track deposits, paleoenvironments, Korea

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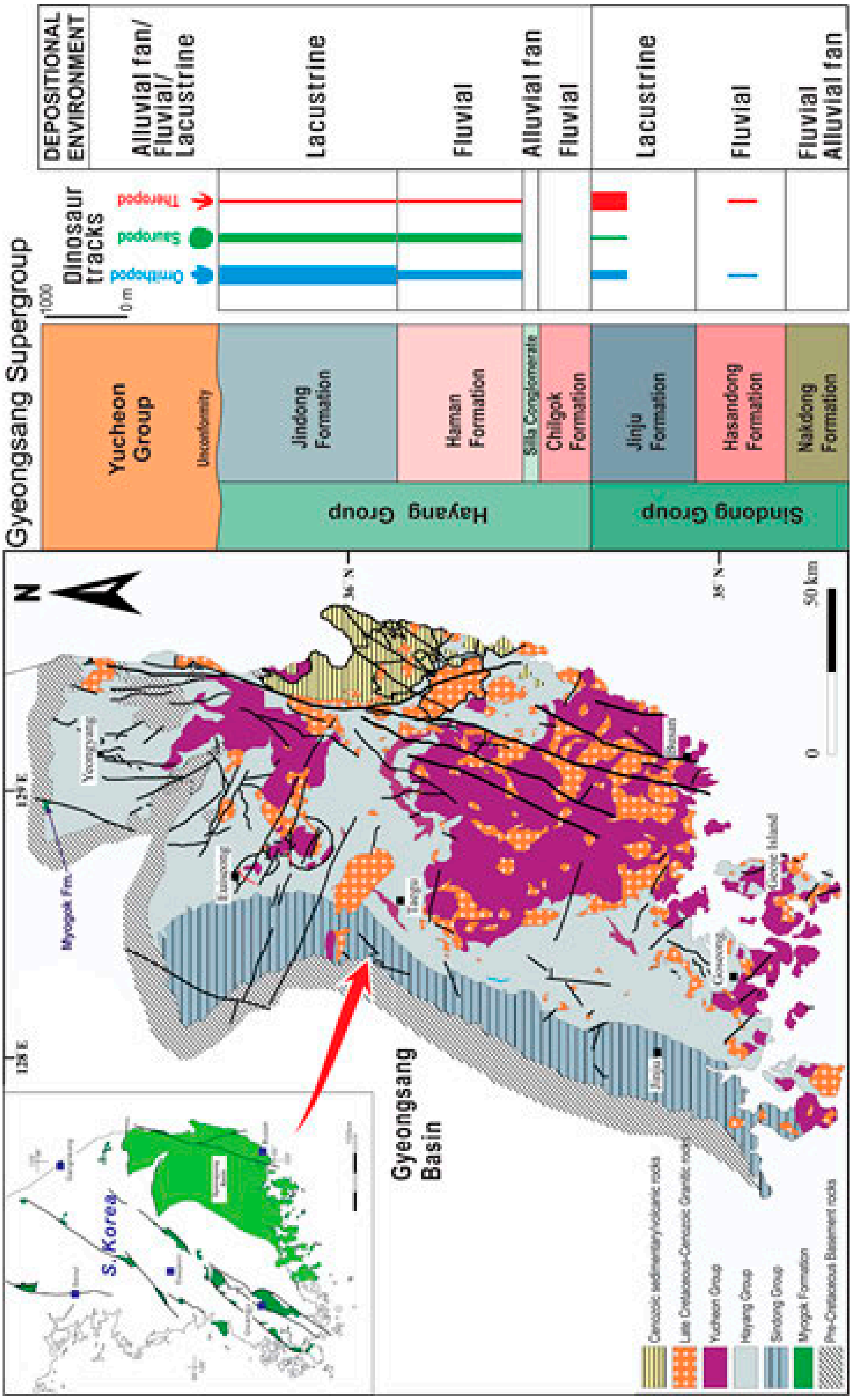

Fig. 1. Geological map of the Gyeongsang Basin (modified after KANG et al., 1995) and stratigraphic occurrences of the dinosaur tracks in the Gyeongsang Supergroup.

The Temijbek ichnological site from the Early Pleistocene of the Caucasus foreland (Russia): Taphonomy and identification of fossil burrows

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Keywords: fossil burrows, rodents, ichnotaphonomy, diagnostic features, preservation

Introduction

Although fossil burrows have long been known to occur in the Pleistocene paleosols of the steppes of Eastern Europe, they have received only a cursory mention in geological descriptions. No ichnological sites with fossil burrows have previously been described here. In this paper, we give the first description of a fossil burrow ichnoassemblage from this region. The young age of the locality presents an opportunity to identify burrows by reference to burrows of extant species of the same genera (Ponomarenko & Ponomarenko 2018). Additionally, the study of preservational features and forms of burrows is instructive for the interpretation of older fossil burrow localities.

Geological Location

The Temijbek fossil locality occurs within the Early to Late Pleistocene section exposed in the Kuban River bend of the Caucasus foreland (Dodonov et al. 2006). The lower half of the section consists of alluvial deposits and hydromorphic paleosols which have been dated from scarce small mammal fossils (*Clethrionomys* cf. *kretzoii*, *Mimomys reidi*, and *Mimomys* sp.) to the Gelasian (Tesakov 2010). In addition to skeletal fossils, which occur in the lower, alluvial deposits, the section contains paleosols with ichnofossils, called "calcified krotovinas" by Dodonov et al. (2006), but previously undescribed. Fossil burrows occur in two carbonate paleosols in the middle of the section, intercalated between colluvial deposits, at the transition from hydromorphic to automorphic soils. These paleosols have a reverse magnetic signature (Matuyama) and are dated to the late Calabrian (ca. 1 Ma). Overlying the middle part of the section are Upper Pleistocene loessic deposits with paleosols without calcified fossil burrows.

Another paleosol with carbonate fossil burrows was found during our fieldwork in 2017 within a previously undescribed outcrop 2 km upstream of the described locality. The exact stratigraphic correlation of this outcrop with the dated section is yet unclear. A colluvial sedimentology including carbonate paleosols point to a Calabrian age coeval with the dated burrow-bearing paleosols.

Materials and Methods

32 fossil tunnel casts were documented in the field, 12 tunnel casts were collected for further study. In describing and identifying the fossil burrows we made use of the reference collection of mammal burrow casts at the Borissiak Paleontological Institute and our descriptions of subrecent burrows observed in archaeological, geological, and soil sections. The taxonomically diagnostic features identified from these two sources have been described in another paper (Ponomarenko & Ponomarenko 2018). The reference collection includes burrows of the following mammal taxa: Insectivora: Talpidae (*Talpa europea*, *Parascalops breweri*), Rodentia: Spalacidae (*Myospalax myospalax*, *Spalax microphthalmos*), Sciuridae (*Marmota monax*, *Tamias striatus*, *Spermophilus fulvus*, *S. major*), Cricetidae (*Ellobius talpinus*, *Cricetus raddei*, *C. cricetus)*.

Results

The studied fossil burrows occur as carbonate-permeated infills. The degree of cementation varies from complete cementation of the entire infill to carbonate rims from precipitation along the interface between the infill and the encasing material. In modern climatic conditions of the Kuban River valley, calcrete does not form within the burrow fill, but similar processes are known from slightly more arid conditions (e.g., see Imbellone, Teruggi 1988). The burrowed paleosol levels contain both Mg concretions and carbonate nodules, which indicates rapid drying of water-logged deposits.

The structure of the bioturbation horizon is different in the three studied paleosols. The upper paleosol in outcrop 1 contains a shallow bioturbation horizon (25–30 cm), which has to do with the predominance of dense horizontal tunnel networks. The lower bioturbation horizon in outcrop 1 (Fig. 1) is 150–180 cm deep and is crossed by both inclined and subvertical, in addition to horizontal, tunnels. In outcrop 2, the visible bioturbation horizon is 40–50 cm deep, dominated by chambers with a smaller number of horizontal and subvertical spiral tunnels. The horizon is truncated at the top and possibly covered by talus below.

Five morphological types of fossil burrows occur in the locality:

1. Horizontal, vertical and rarely inclined tunnels. Diameter 6.0–8.0 cm. Vertical tunnels gradually level out into deep horizontal tunnels below. No chambers found. cf. *Nannospalax* (Fig. 2).
2. Tunnel diameter 8.5–9.5 cm with chambers up to 12 cm. Bends 20–40 cm long. Elliptic cross-section, height > width. Sculpture contains paired divergent crests 10–15 mm long. cf. *Spermophilus* (small species) (Fig. 3).
3. Cross-section strongly asymmetrical, height >> width (12×7 cm). A single straight inclined tunnel found. If the cross-sectional shape reflects the shape of the original tunnel, then even in the absence of other morphological features the tunnel should be identified as a jerboa species similar to *Allactaga major* in size. The shape and size of the cross-section correspond to the shape of jerboa entrances (Fenyuk 1928, 1929).
4. Surficial tunnels within the upper carbonate burrow-bearing paleosol. Diameter strongly variable, from 4.5 to 8.0 cm. No vertical or inclined tunnels were found, tunnels occur in a dense network. In the absence of other features it is referred to Arvicolidae.
5. Spiral vertical tunnels, horizontal tunnels, chambers (Fig. 4). Diameter: vertical tunnels 5.5–6.0 cm, horizontal 6×7.5 (width > height). The only species having this kind of spiral tunnel in the studied region is the mole-vole, *Ellobius* (see Ponomarenko & Ponomarenko 2018).

Conclusion

From fossil data it is known that small mammal fauna of the studied region during the Eopleistocene was similar to the present. The fossorial rodents were represented by modern genera. The particularity of the Temijbek locality is the occurrence of a large variety of burrow morphotypes within a small outcrop area. The large diversity of fossil burrows likely reflects changing conditions over the lifetime of the paleosol, rather than a strictly contemporaneous assemblage. No skeletal fossils have so far been described from the paleosols, and the diversity of taxa represented by burrows (5) is larger than the diversity of skeletal fossils in the underlying alluvium (3). The taxonomic diagnostics of fossil burrows within paleosols therefore directly complements the skeletal fossil record. Given the state of preservation of the Eopleistocene burrows in the Kuban River valley, the most important tools for burrow diagnostics are architecture, followed by diameter and sculpture.

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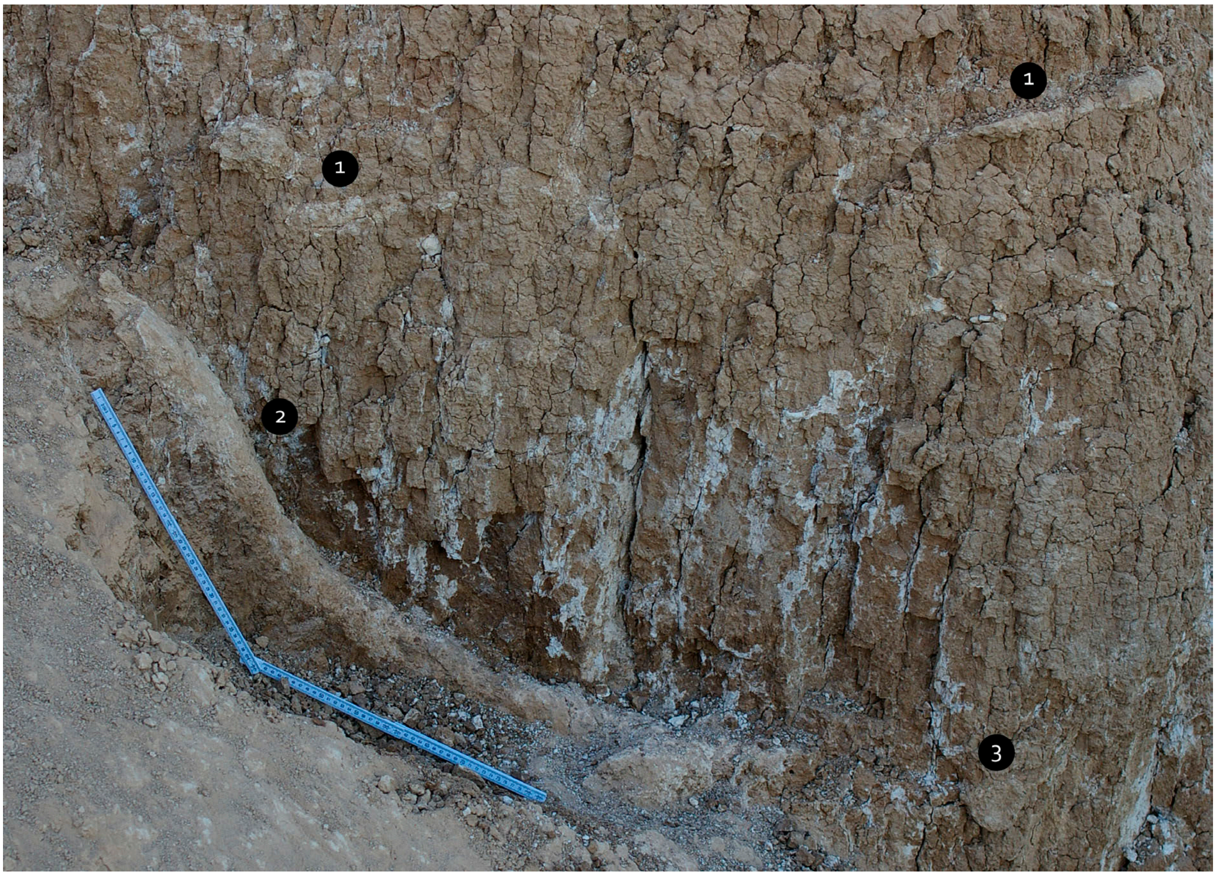

Fig. 1. Outcrop 1. Portion of the bioturbation horizon: 1) inclined tunnels, 2) subvertical tunnel, 3) deep horizontal tunnel of morphotype 1.

Fig. 2. Temijbek fossil burrow morphotype 1. Inclined and horizontal burrows in outcrop.

Fig. 3. Temijbek fossil burrow morphotype 2 in plan view. Bends and sculpture.

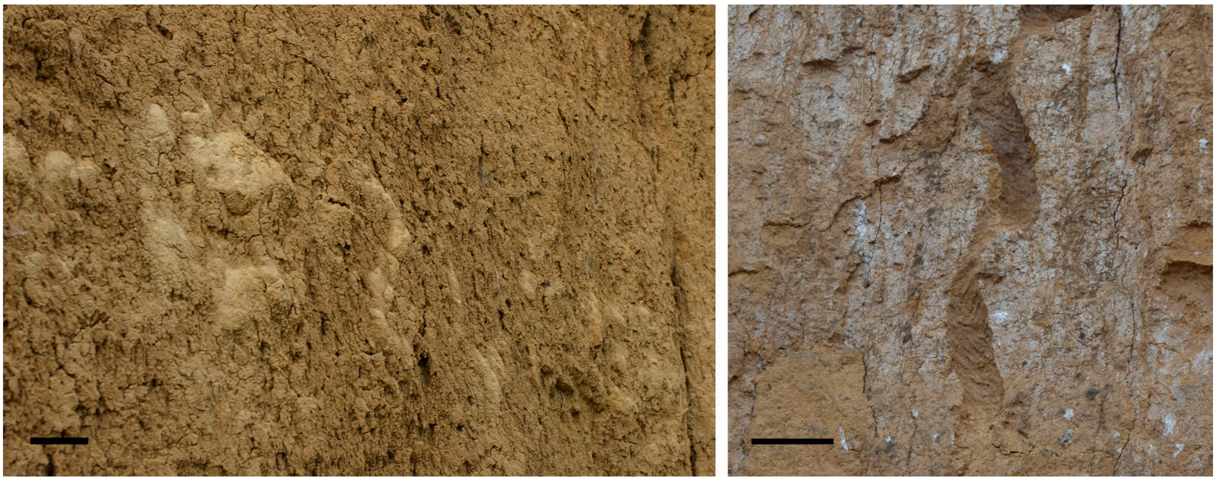

Fig. 4. Chambers and spiral subvertical tunnels. Left, Temijbek locality, outcrop 2, morphotype 5. Right, subrecent *Ellobius talpinus* spiral tunnels (confluence of the Kama and the Volga Rivers).

Chambered trace fossil from the Lower Tipam Formation (Pliocene) of Tripura, Northeast India

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Abstract:

The medium grained, cross bedded fluvial sandstone of the Lower Tipam Formation, Pliocene age, of Amarpur area in Tripura, India is considered to have been deposited in a fluctuated intertidal to tidal environment with occasional brackish water and fluvial influence. The unit is characterized by a trace fossil composed of filled chambered burrows, more or less ellipsoidal in outline, and interconnected by shafts/tunnels. The burrows show variable dimensions with length 30–160 mm, width 30–100 mm, and height 20–60 mm; and the tunnels are 8–9 mm in average diameter. Small forms of *Thalassinoides* isp. and *Skolithos* isp. are the other traces observed. The chambered burrows are possibly related to social insects, such as ants or termites. The discovery is remarkable because of the rare occurrence, and for it was not previously reported from Asia; and at the same time no other exactly similar ichnospecies has been reported so far. Thus, the morphology of the studied traces points toward a likely new ichnospecies of *Vondrichnus* belonging to the ichnofamily Krausichnidae. The presence in the Lower Tipam Formation also suggests a probably warm climatic condition for the environment of this unit.

Keywords: interconnected, fluvial, sandstone, Krausichnidae, warm climate

Unusual occurrence of termite nests close to shoreline: neoichnological insights

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Abstract:

Termites are social insects inserted in the Blattodea order, generally characterized by their complex nests. These insects feed on cellulosic material from the interior of the nest, and they control the microclimate, mainly the local humidity and the relative heat of the nest. Insect trace fossils attributed to the activity of ants and termites occur in eolian deposits of the Pleistocene barrier-lagoon system III of the Rio Grande do Sul Coastal Plain (PCRS), Brazil. The search for modern analogues in a correlated environment (barrier-lagoon system IV, Holocene to recent) revealed the presence of a termite nest in eolian dunes that compose the backshore deposits covered by incipient vegetation. A cast of the nest allowed a comparison with the ichnogenus *Termitichnus*. The average diameter of the mound is 25 cm, with underground galleries reaching an area up to 140 cm2 and 90 cm in depth. The nest was composed of a rounded convex epigeal portion and a hypogeal portion formed by interconnecting spherical to semispherical chambers. Considering that termites normally colonize more mature, vegetated soils due to the need of abundant cellulosic material, the occurrence of a termite nest in backshore dunes close to the shoreline opens a discussion about the distribution and habit of termites in medium latitudes. This may (1) result from an opportunistic behavior, due to the urban expansion in the study area or any other stressing process acting during the establishment of a new colony or (2) may represent a particular habit still unknown from these insects, or (3) even reflect a modern adaptation, in response to environmental changes. Thus, to prospect new occurrences of modern termite nests in backshore dunes is crucial to solve this puzzle and further studies will be carried on to evaluate the distribution of termite nests in the PCRS, in order to better understand the Pleistocene record.

Keywords: *Termitichnus*, Blattodea, Pelotas Basin, Rio Grande do Sul, barrier-lagoon system

Early Jurassic dinosaur ecosystems in southwestern Gondwana: steps towards refining its palaeoecology

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Abstract

The Triassic-Jurassic transition records a pivotal phase in terrestrial vertebrate evolution. During this time, dinosaurs emerged as the preeminent terrestrial species, and continued their dominance for ~135 Ma. This rapid radiation allowed dinosaurs to occupy a variety of ecological niches and populate diverse habitats around the world.

In southern Africa, this dynamic period in dinosaur evolution is best recorded in the red-beds of the Elliot Formation and the overlying sandstone-dominated Clarens Formation. These units collectively document the Late Triassic-Early Jurassic palaeolandscape and habitat changes of a semi-arid to arid southwestern Gondwana. Although vertebrate tracks are abundant, palaeontological focus has been placed on the body fossils recovered from these strata. As a result, relatively little is known about vertebrate behaviour, and habitat preferences. Contrastingly, vertebrate trace fossils are preserved in situ and therefore present an independent proxy on the environment, climate, ecology.

We herein present high resolution sedimentological and ichnological findings of five dinosaur track sites, consisting of *Eubrontes*-like and *Anomoepus*-like tracks, from the transition of the Elliot and Clarens formations. Our reconstructions show that during this aridifying period in the late Sinemurian, these theropod and ornithischian communities inhabited a mosaic of fluvial, lacustrine and aeolian environments. Within these continental strata, theropod footprints are distinctly prevalent, suggesting that these animals were an essential component of this ecosystem despite their heavy underrepresentation in the body fossil record. Furthermore, our study highlights the importance of integrating ichnofossils with body fossils and sedimentological data in order to obtain a refined view of ancient ecosystems.

Keywords: vertebrate ichnology, dinosaurs, ecosystems, Triassic-Jurassic, southern Gondwana

The Late Sinemurian ichnofossils from Mampoboleng (Upper Moyeni), Lesotho

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Abstract:

The Mampoboleng ichnosite (Upper Moyeni, SW Lesotho) is a newly documented vertebrate track-bearing surface in the highly-fossiliferous upper Elliot Formation, ~35 m below the conformably overlying Pliensbachian Clarens Formation. The ~60 tridactyl tracks and trackways are preserved among ripple marks on top of a 1.5 m thick, fine- to medium-grained, upward-fining sandstone unit. The tracks range from 17.5 to 48 cm in length and preserve digital pad impressions, claw marks and expulsion rims. Their morphometric parameters are consistent with *Eubrontes*. Five tracks with pes length <25 cm can be classified as either *Grallator* or *Anchisauripus*, though the latter is considered a synonym of *Eubrontes* by some authors (Milner et al. 2006). However, tracks with lengths of up to ~48 cm are comparable in overall shape, size and L/W ratios with *Megalosauripus* (Lockley et al. 1996), which previously has not been reported from southern Africa. In addition to these theropod tracks, an isolated, semi-horizontal burrow cast (diameter: ~23 cm; height: 10 cm) with a bilobate cross-sectional shape and chevron scratch marks is located within a silty mudstone, ~13 m below the track-bearing palaeosurface. This burrow cast is the second one reported from the upper Elliot Formation (Bordy et al. 2017), and can be assigned to *Reniformichnus* (Krummeck & Bordy 2018). Based on sedimentological and ichnological evidence, the Late Sinemurian ichnofossils at Mampoboleng were generated in a palaeolandscape with small rivers and shallow lakes by a variety of biped dinosaurs (theropods) and burrowing vertebrates, potentially mammaliaforms.

Keywords: tridactyl, upper Elliot Formation, *Megalosauripus*, Lower Jurassic, vertebrate burrow cast

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Swimming and related traces of a Late Triassic freshwater community from the lower Elliot Formation, South Africa

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Abstract:

Here, we report, for the first time, on traces related to swimming and other sub-aqueous activity by a freshwater pond community in the Upper Triassic lower Elliot Formation (Stormberg Group, Karoo Basin, South Africa). The palaeosurface preserves several generations of ichnites forming a seemingly chaotic ichnofossil assemblage. The ichnites, together with abiotic traces (e.g., tool marks), are preserved on the upper bedding plane of a fine-grained sandstone. This is in turn overlain by a khaki, laterally continuous, ~1-m-thick, laminated, pedogenically-unaltered mudstone unit. Several sinuous trails on the palaeosurface can be assigned to *Undichna* ANDERSON 1976. A didactyl track of *Grallator*-like affinity is associated with a single sickle-shaped digit-drag mark as well as disorderly striations that are 3–8 cm long and show variable morphology (e.g., narrowly incised, V-shaped, straight to slightly sinuous grooves). Additionally, unique yet indistinct, <2 cm-long, partially preserved ichnites with three (or possibly four) slender digit impressions and associated, shallowly incised, curving trail-like striation are also preserved. Together these trace fossils provide evidence for animals currently unrecorded in the osteological record of the lower Elliot Formation. Based on cross-cutting relationships, the timeline of events within this shallow, freshwater pond suggests an initial fully aqueous period, when the first generation of tracemakers (likely small fish such as *Semionotus*) produced swimming traces. This was followed by a semi-aqueous period, when invertebrates burrowed and tetrapods waded and walked along the shoreline. The unfossiliferous, laminated pond sediments represent the final phase and suggest uninterrupted silting up of the pond.

Keywords: *Undichna*, lower Elliot Formation, fish, Upper Triassic, swim traces

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Re-evaluating the wealth of the Late Triassic Phuthiatsana ichnosite, Maseru District, Lesotho

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Abstract:

Late Triassic ichnites attributable to quadrupedal basal sauropodomorphs (prosauropods) are known from several palaeosurfaces from the main Karoo Basin in Lesotho (southern Africa). The Phuthiatsana tracksite (Maseru District, Lesotho) was briefly documented by Ellenberger ET AL. (1963). This palaeosurface yielded a diversity of well-preserved tridactyl, tetradactyl and pentadactyl ichnites, which are attributed to theropods, prosauropods and dicynodonts, respectively. Our re-documentation of the ~320 m2 Phuthiatsana palaeosurface revealed new ichnological, stratigraphic and sedimentological details. The more refined palaeoenvironmental reconstruction of this tracksite has yielded palaeobiological and palaeoecological implications. Stratigraphically, we now firmly place this site and others with similar ichnoassemblages (e.g., Subeng, Ha Falatsa) into the lower Elliot Formation. Moreover, via detrital zircon geochronology, we have recently dated these sites as being as old as middle Norian. Many ichnites are modified true tracks with expulsion rims and sediment collapse features. Associated interference ripples and desiccations cracks assist in determining the substrate consistency and its impact on track morphology. Several tetradactyl pes and manus impressions are registered in some of the trackways, and are considered to have been made by quadruped sauropodomorphs with pronounced heteropody and possibly flexed limb postures. Pes tracks, of both quadruped and biped animals, show little morphological variability along the individual trackways, in which toe-drag and tail-drag marks are locally present. Phuthiatsana provides comprehensive insights into a middle Norian dinosaur-dominated vertebrate community in southern Gondwana, and broadens the discussion concerning the evolution of locomotion mode (i.e., quadrupedality) in basal sauropodomorph dinosaurs (e.g., lessemsaurids).

Keywords: sauropodomorphs, Elliot Formation, Upper Triassic, tetradactyl, quadrupedalism

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Late Cretaceous insect trace fossils from the Capacete Formation, Sanfranciscana Basin, Brazil

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Abstract:

The Late Cretaceous Capacete Formation of the intracratonic Sanfranciscana Basin, Brazil, consists of epiclastic sediments with an important eolian contribution. This unit is currently interpreted as deposited by distal alluvial fans grading to braided rivers in an arid- to semiarid climate within the central part of western Gondwana. Locally, recently described expositions with great lateral continuity show architectural elements representative of deposition in meandering rivers, such as overbank fines (FF) associated with crevasse splay (CS) deposits from floodplain settings, lateral accretion bars (LA) and channels (CH). We quantified the degree of bioturbation of the meandering fluvial deposits (bioturbation degree = BD) on a scale from 0 to 6, based on a visual scale. The fluvial bars preclude ichnofossils while climbing sandstones (CS) have sparse occurrences (BD 1-2) of meniscated vertical trace fossils with 8 to 11 mm in diameter identified as *Taenidium*. Vertical simple excavations with diameter varying from 9 to 13 mm identified as *Skolithos* occur associated with *Taenidium* in sandstone facies (CS), as well as rhizoliths. Sparse subspherical excavations (BD 1) with thick walls were identified in mudstone facies from the floodplain setting, with a diameter of 62 mm and with an internal chamber measuring 27 mm in diameter. This morphology was identified as *Coprinisphaera*. The setting attests the episodic colonization of the vegetated flood plains by insects. Furthermore, the sedimentologic and ichnological data reveal the unexpected presence of meandering river deposits in the Capacete Formation. Despite the general interpretation of an arid climate for the Late Cretaceous of the Sanfranciscana Basin, these new data support punctual deposition under humid conditions.

Keywords: meandering fluvial systems, coprinisphaera, paleoclimate, paleoenvironment

Vertebrate tracks in the upper part of the Omma Formation (Pleistocene) of west-central Japan

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Abstract:

Vertebrate footprints are preserved in two horizons of a locality in the Pleistocene Omma Formation (approximately 90Ma) in Kanazawa, west-central Japan. The depositional environment of the site is a typical floodplain (Muddy sand- fine sand). Dominant proboscid and scattered cervid tracks occur on the upper horizon (Approximately 5 tracks on approximately 13m^2), while a ruminant trackway is recognized together with rare avian and proboscid footprints on the lower horizon (Approximately 20 tracks on the bearing surfaces is approximately 10m^2). Vertically undulated bedding between the horizons may represent cross sections of large footprints. The trace fossils indicate flourishment of vertebrates that migrated from an adjacent continent when a land bridge was formed, but no longer inhabit the island arch today.

Keywords: large footprint, ruminant, land bridge

Ichnofabrics in Quaternary inland dunes of SE Poland

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Abstract:

Inland sand dunes were deposited on a large area of western-middle Europe in the so-called European Sand Belt during post-glacial times of Late Pleistocene – early Holocene. During the Late Pleistocene, the southern margin of the ice cap went through southern Scandinavia. The dunes were stabilized during the Holocene and rarely re-mobilized. Recently, they are usually forested or covered by pasture vegetation. The dunes were partly influenced by human activity. They are intensively bioturbated below the recent soil or below buried soils, but usually this fact is overlooked in investigations. The presented investigations concern the southern margin of the European Sand Belt in the Sandomierz Basin, SE Poland (50°–51° N), where the morphology of dunes is still well preserved and their internal structure available in sand pits. The dunes were deposited by generally westerly winds.

The bioturbated zone in the dunes is 1.5–2.2 m thick. Its upper portion (about 0.3–0.9 m thick) is totally bioturbated. The primary sedimentary structures are completely altered. In recent times, various bioturbating animals can be encountered in this zone, mostly insects, e.g. hymenopteran solitary bees and wasps, ants, antlion (*Myrmeleon*) larvae, beetles (e.g. tiger beetles of the subfamily Cicindelinae). Moreover, oligochaetes (earth worms) and mammals (e.g. the European mole *Talpa europaea* in more organic-rich places, and the red fox *Vulpes vulpes* on the slopes) are present. Earth worm burrows (usually 2–4 mm wide) are associated with burrows of the European mole (branched, 40–60 mm wide). Usually, they are well visible in the subsoil below thicker organic rich soils, mostly in the lower dune slopes and in the interdune areas. The sand is also disturbed by roots of trees and other vascular plants.

The totally bioturbated zone passes downward through a partly bioturbated zone (0.8-1.3 m thick) and to a non-bioturbated zone with well visible lamination. In the partly bioturbated zone, primary lamination is cross cut by mostly vertical/subvertical meniscate burrows, which can be ascribed to *Taenidium*, *Entradaichnus* or *Naktodemasis* (irrespective of their ichnotaxonomic problems). They are 5–20 mm thick and can be traced at a distance of several tens of centimetres. Their menisci, usually poorly visible, are usually concave down. The burrows can be concentrated in wedge zones which have been formed after decomposition of thick tree roots ("ghosts of roots"), or they can follow thinner roots. Recent pine roots (*Pinus*) may extend a few metres down the surface. They can follow disturbances after old frost wedges. The lower boundary of the totally bioturbated zone is uneven. Commonly, it deflects down around thicker ghosts of roots.

The meniscate burrows are produced by insects and their larvae or nymphs. They fed on organic matter, mostly on dead or living roots. In the totally bioturbated zone, the burrows are differently oriented. In the deeper zone, they are vertical or steeply oblique. The latter are interpreted as burrows of insects which overwinter below the level of frost (usually 1 m) and migrate into the ground mostly along thin roots. The concavity of the menisci shows that they returned to surface or subsurface along the same path. Probably, the way up was easier along the already used burrow. Stabilized sand dunes seem to be a good place to overwinter for insects, because they are well drained, with very low probability of flooding, well aerated, and with deep roots, which are the basis of the trophic chain.

In non-ploughed areas, the transition between topsoil and the burrowed subsoil is gradual. In the ploughed fields, even if the field was abandoned by tens of years, contact between the topsoil and the subsoil is sharp. In both cases, burrows filled with the topsoil dark particles are well contrasted with the lighter subsoil sediments. In some burrows, sediment from the subsoil is introduced into the topsoil. Visibility of burrows in the totally bioturbated zone can be low, so that the sand seems to be massive. Their visibility depends on moisture and light. Usually, the ichnofabric is less visible in dry sand. In some places, the visibility of burrows is enhanced by mineralization, mainly ferruginization. Locally, ferricretes are present. Shallowly buried soils can be re-burrowed from recent soils and ichnofabrics formed during different times can overlap.

Investigations in old sand pits, which are vegetated and abandoned since a few tens of years, show much thinner and less developed ichnofabrics below the exploitation surface. The laminated sand occurs very shallowly below the soil developing on such surface. This shows that the thick ichnofabrics observed below natural surfaces/soils developedduring at least hundreds of years.

Keywords: aeolian environment, soil, meniscate burrows, Late Pleistocene, Holocene, Central Europe

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Plant-insect interactions in deep time

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Abstract:

Fossil evidence of insect herbivory dates back to the early Devonian, and all of the fundamental feeding strategies of herbivorous insects, except leaf mining, were established by the Late Carboniferous. Over the last 400 million years, trophic complexity (the relationship between the number of species and the density of trophic interactions) and insect feeding diversity (the number of distinct ways in which insects consume plants) have increased. Today, food webs incorporating plants, phytophagous insects, and carnivorous insects account for up to 75% of non-microbial global terrestrial biodiversity. Thus, plant-insect interactions affect practically all terrestrial life. Paleobiological studies of insect damage on fossil plants can provide valuable information about insect diversity, ecological interactions, and evolutionary adaptation.

For example, the Paleozoic–Mesozoic transition is characterized not only by the most massive Phanerozoic mass extinction at the end of Permian, but also extensive aftermath and a prolonged period of major biotal recovery during the succeeding Middle to Late Triassic. This delayed recovery is generally attributed to the effects of extreme environmental conditions inflicted on Early Triassic ecosystems.

Studies of insect damage on plants are often the only way to learn about how insect diversity and ecological associations respond to environmental changes. Both paleobiological and ecological studies provide valuable information on how insects might have been affected.

Keywords: herbivory, insects, gymnosperms, angiosperms, climatic fluctuations

Open questions regarding identification and function of gastroliths

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Abstract:

Stomach stones (geo gastroliths) are considered a rather special case of ichnologic objects, but they occur commonly in fossil and extant lithophagic vertebrates and can reveal valuable insights into the paleobiology and spatial distribution of their bearers. These stones and their use are still surrounded by many puzzles. Two pressing questions are discussed.

1. Gastroliths identification. Gastroliths have a high potential for paleogeographic and lithogenetic reconstructions, but this potential can only be accessed when stomach stones can be unambiguously identified. There are very few comparable published studies about gastroliths identification which hold up to a scrutinized evaluation of scientific methods. For example, polish was often regarded as a prime criterion for gastroliths identification, but it occurs rarely on verified gastroliths and is more commonly formed by several geologic processes (e.g., wind polish or tectonics). Additional research on parameters like rock type, surface texture, or shape will reveal the variety of existing appearances among gastroliths and support the identification of isolated stomach stones.

2. Gastroliths function. Herbivorous birds utilize grit to triturate and to mix foodstuffs. No sufficient explanation has been found for the purpose of gastroliths in other vertebrates. While lithophagy has also been reported from several insectivorous clades, this is especially relevant for aquatic taxa. In extinct as well as extant clades, such as Permian tetrapods, plesiosaurs, crocodilians, and pinnipeds, gastroliths were or are utilized on a regular basis. For aquatic taxa, several functions were proposed and need crucial reinvestigation. The two most plausible hypotheses are digestive help and buoyancy alteration as ballast in water. However, evidence for both hypotheses is poor and investigations are hampered because gastroliths distribution and amounts within individuals of certain taxa are highly variable and gastroliths functions may overlap.

Consequently, an investigation of relevant stomach contents of lithophagic animals is essential. While the gastroliths collection at the ZNS is still growing, acquisition of new material from lithophagic animals from varied sources is limited, encumbering future research. Hence, acquiring material from other regions and/or taxa would be an invaluable help. If you would like to donate or participate in gastroliths research, please contact the author.

Keywords: lithophagy, gastroliths identification, surface textures, gastroliths function, sample acquisition

Middle–Late Triassic ichnoassemblages from Irohalene area (Argana Basin, Western High Atlas, Morocco): sedimentological and ichnological analyses

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Abstract:

Middle to Late Triassic redbeds of the Timezgadiouine Formation (T4-T5, Anisian-Carnian) in the Irohalene area (Argana Basin, Western High Atlas, Morocco) consist of cyclical clastic sedimentary rocks, which are mainly composed of conglomerates, sandstones, siltstones, claystones and mudstones, that were deposited in an alluvial plain to mudflat environment with ephemeral rivers and lakes. Sedimentological analysis allowed identification of seventeen different facies, grouped into fluvial, alluvial fan, flood plain and lacustrine associations. These sequences contain numerous ichnogenera of vertebrates and invertebrates, associated with plants, conchostracans and isolated fish remains.

Vertebrate tracks and trackways, are assigned to *Parachirotherium* isp., *Atreipus-Grallator* isp. *Grallator-Eubrontes* isp., *Brachychirotherium* isp., *Apatopus lineatus*, *Rhynchosauroides* isp., and indeterminate ichnotaxa, attributed to dinosauromorphs/crocodylian-stem archosaurs, and lepidosauromorphs/archosauromorphs. Invertebrate traces include the ichnogenera *Arenicolites* isp., *Scoyenia gracilis*, *Taenidium barretti*, *Palaeophycus tubularis*, *Lockeia* isp., *Spongeliomorpha carlsbergi*, *Petro-xestespera* isp., *Skolithos verticalis* and *Rhizoconcretion* isp. They can be assigned to annelid and/or polychaete worms, mayfly larvae, beetles and bivalves.

Ichnoassemblages provide the opportunity to observe palaeoecological diversity and allow more detailed palaeoenvironmental reconstructions, reflecting energy changes and palaeohydrological fluctuations. The ichnoassemblages from Irohalene area show a subtle change in ichnocoenoses. Five ichnocoenoses were distinguished: 1) *Scoyenia–Rhizoconcretion*, generated in low-energy floodplain environment; 2) *Arenicolites*, developed in higher flow velocities of active palaeochannels; 3) *Taenidium-Scoyenia*, formed in low energy sandy colonization of inactive palaeochannels; 4) *Arenicolites* horizontal meniscate burrows, the most common ichnocoenosis in the Irohalene, reflecting intermediate conditions between ichnocoenoses 2 and 3; 5) *Lockeia-Petroxestes*, formed in a marginal lake.

Keywords: ichnocoenosis, invertebrates, vertebrates, palaeoenvironment, Argana, Morocco

3rd International Conference of Continental Ichnology

2019

Field Trip Guide

MICHAEL BUCHWITZ, DANIEL FALK, HENDRIK KLEIN

& OLIVER WINGS

Acknowledgements:
We would like to thank JOGI SCHNEIDER (Freiberg) and MICHAEL SCHLIRF (Haßfurt) for providing explanatory texts and/or photographs to some field stops, as well as Maren Jansen for proof-reading. We are very grateful to the families Hauck (Schönbachsmühle), Gleußner (Neubrunn), and Stadler (Schlehenberg) as well as the Wesling company and the Dinosaurier-Park Münchehagen for the permissions to enter their quarries and outcrops.

ICCI 2019 Field Trip Schedule

Day 1 – Friday, 27th September 2019

Departure: Domplatz Halle (Saale) at 7.45 am.

Stop 1. Schlehenmühle at the river Rotmain, SE Bayreuth at 10.30 am.
Lunch at Ausflugsgaststätte Schlehenberg.

Stop 2. Schönebachsmühle at 2 pm..

Stop 3. Neubrunn/Hassberge at 3.45 pm.

Stop 4. Hildburghausen at 5.30 pm.

Stop 5. Schloss Bertholdsburg in Schleusingen at 7 pm.
Supper in Schleusingen.

Overnight: Hirschbach, Gasthof „Zum Goldenen Hirsch" at 10 pm.

Day 2 – Saturday, 28th September 2019

Breakfast at the hotel at 7 am and **departure from Hirschbach** at 8 am.

Stop 6. Bromacker Quarry / Tambach-Dietharz at 9 am.

Stop 7. Museum collection, Gotha at 11 am.
Lunch: packages handed out in Gotha. The participants are visiting the collection facility in two groups - with time for lunch in the nearby park area for the non-visiting group.

Stop 8. Konberg Quarry / Rothenschirmbach at 2.30 pm.

Stop 9. Solvay Quarry / Bernburg at 4.30 pm

Overnight: Hotel (Slotel Budget) in Bernburg will be reached at 6.30 pm.

Diner/supper – possibilities in the city centre of Bernburg.

Day 3 – Sunday, 29th September 2019

Breakfast at the hotel at 7.30 am and **departure from Bernburg** at 8.15 am

Stop 10. Mammendorf Quarry at 9.30 am.

Stop 11. Dinosaurier-Park Münchehagen at 1 pm
Lunch in the Dinopark restaurant.

Stop 12. Obernkirchen Quarry at 3.30 pm.

Return to Halle (Saale) and **arrival at 8 pm**.

The stops are situated in northern Bavaria, Thuringia, Saxony-Anhalt and Lower Saxony (Fig.I); they cover a stratigraphic range from the Carboniferous/Permian boundary to the Early Cretaceous (Fig. II).

Fig. I. Geographic position of ICCI 2019 field trip stops no. 1 – 12 and hotels in Hirschbach and Bernburg (based on https://commons.wikimedia.org/wiki/File:Relief_Map_of_Germany.svg).

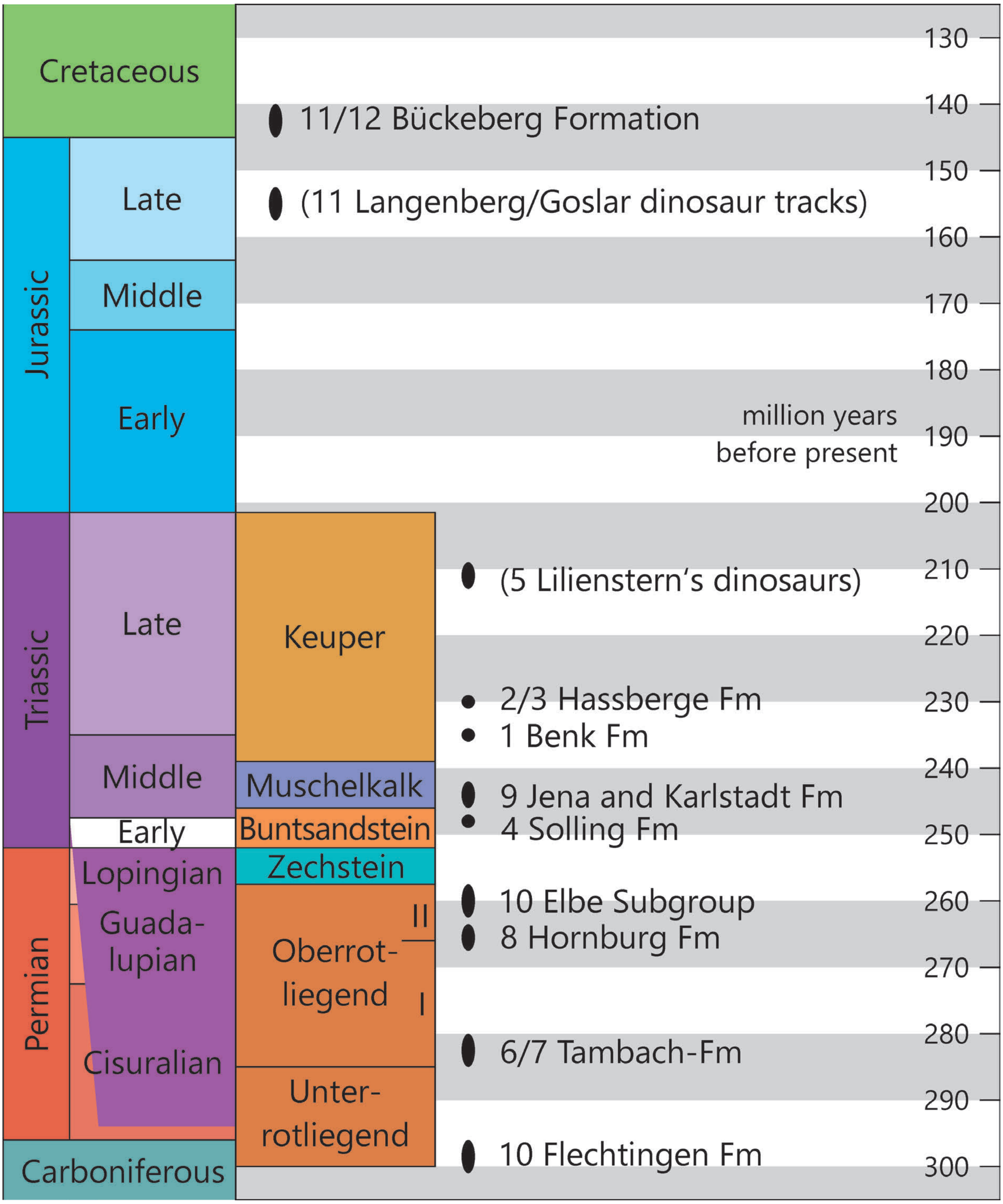

Fig. II. Stratigraphic position of localities 1 – 12.

Day 1 – Friday, 27 September 2019

The Triassic of the Germanic Basin

General overview: The Germanic Basin, or Central European Basin is one of the most important regions for ichnological research and extremely rich in trace fossil horizons and localities (see distribution of vertebrate tracks in Figs. 1-2). This is an epicontinental (Peri-Tethyan) depositional area that extended from Great Britain in the west to Poland in the east and from the North Sea to southern Germany. Borders were the Fennoscandian Massif to the north and northeast, the London-Brabant and Gallian Massifs to the west, and the Bohemian-Vindelician Massif to the east and southeast. These mainlands were the source of clastic deposits transported into the basin by fluvial activity. In northern Germany about 3000 meters of Triassic sediments have been deposited. The early formation of this structure goes back to the end of the variscan orogeny in the latest Carboniferous and Permian. Connections to the Tethyan ocean in the south existed by the Burgundy Gate, the Silesian-Moravian Gate and the East Carpathian Gate.

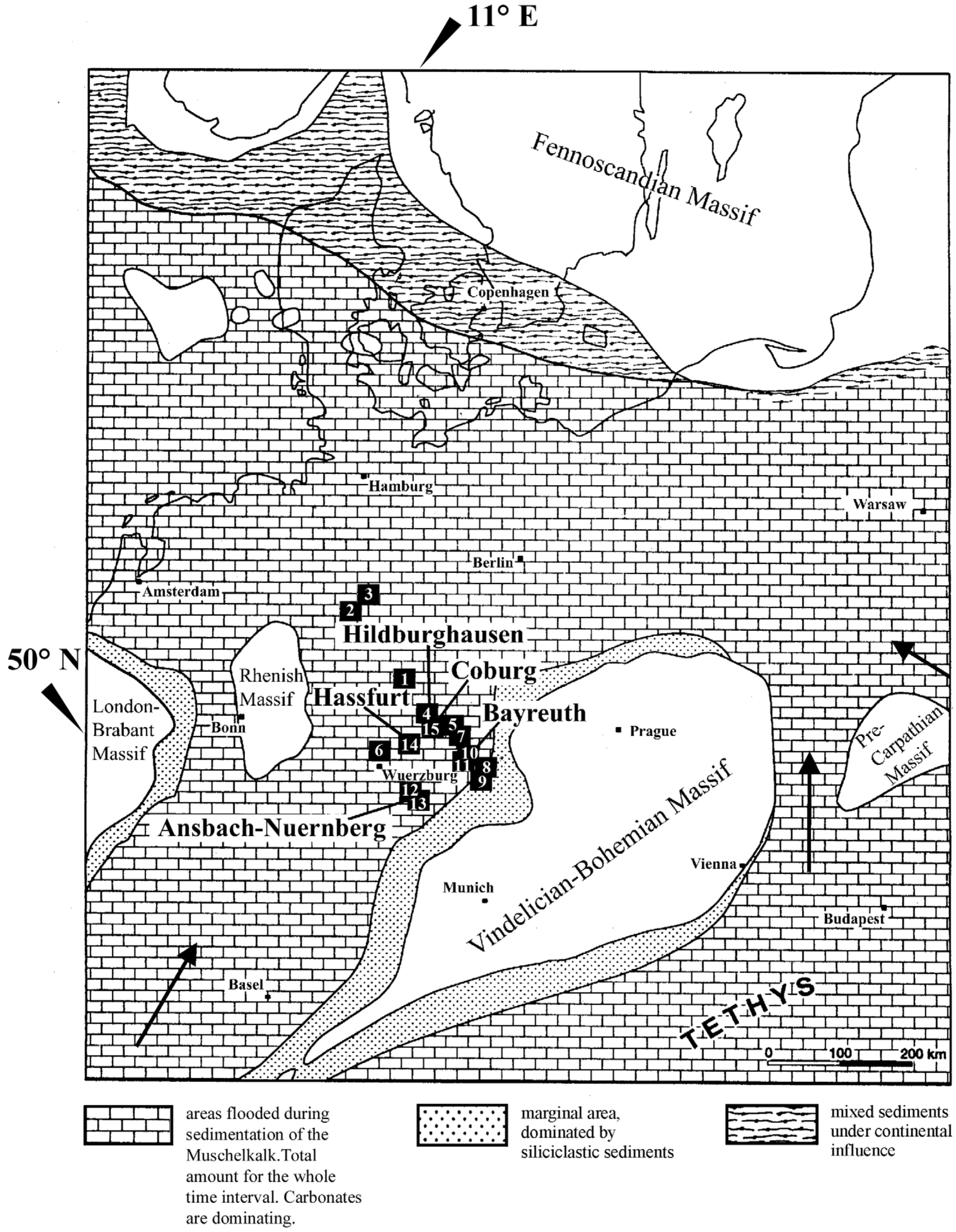

Fig. 1. Paleogeographic map of the Germanic Basin during deposition of the Muschelkalk (Middle Triassic, Anisian-Ladinian), with distribution of track localities of the whole Triassic along the Bohemian-Vindelician massif. Numbers correspond to those in Fig. 2. Base map from Geyer (2000) and Ziegler (1982).

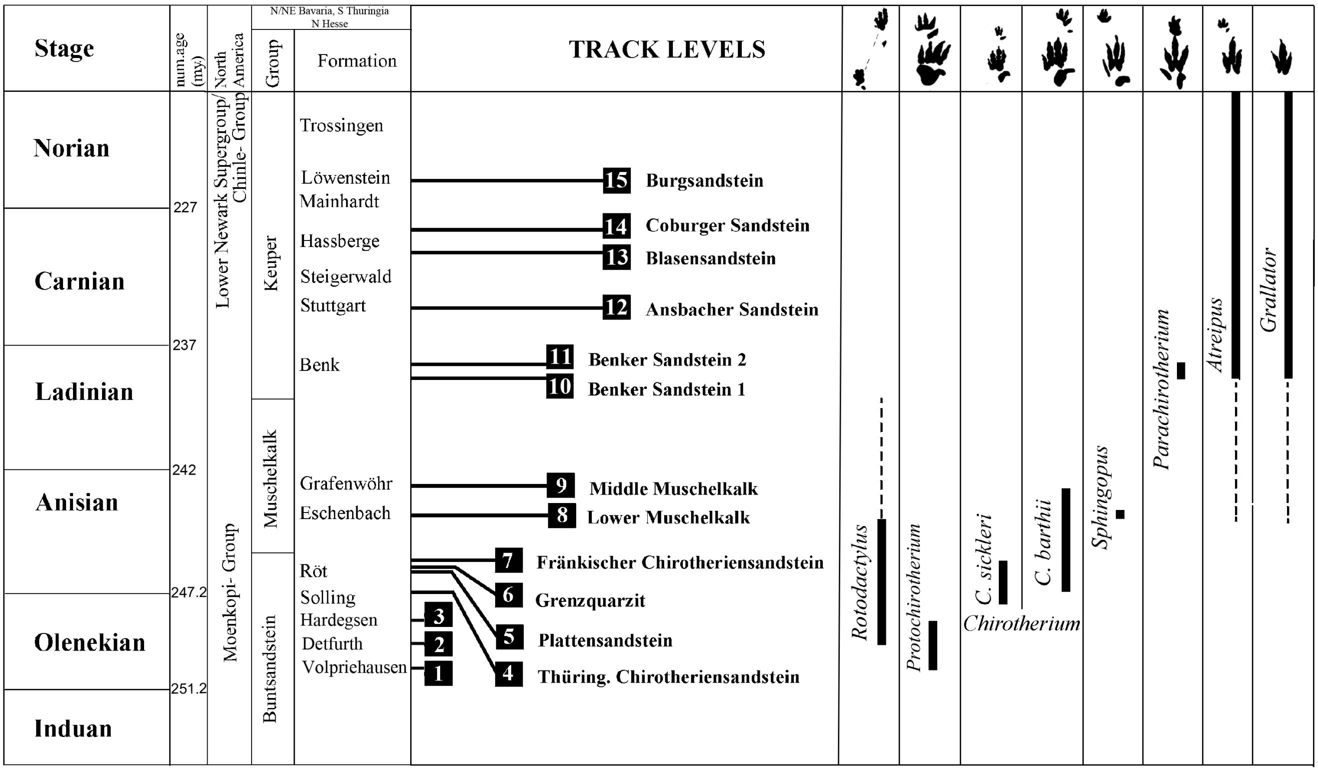

Fig. 2. Tetrapod footprint horizons and range chart of archosaur tracks from the Lower-Upper Triassic of the Germanic Basin of northern and northeastern Bavaria, southern Thuringia and Hesse. Numbers correspond to those in the map of Fig. 1.

Classical stratigraphy devides the Triassic deposits of the Germanic Basin into lower, continental redbeds (Buntsandstein), the middle part that is characterised by carbonatic and evaporitic, essentially marine sedimentation (Muschelkalk), and an upper continental redbed succession (Keuper). The continentally dominated deposits furthermore show marine transgressions in the upper part of the Buntsandstein (Roet Formation) and a transition from marine to continental sedimentation in the lower part of the Keuper (Erfurt Formation).

Lithologically the Buntsandstein is composed mostly of sandstones and shales deposited in fluvial and playa depositional environments. The upper part (Roet Formation) yields gypsum, anhydrite, halite and carbonates. The Muschelkalk is dominated by limestones and marls, with abundant dolomites, gypsum, anhydrite and halite forming the middle part. The Keuper shows marine dolomites and continental siliciclastic deposits such as sandstones and shales in the lower part (Erfurt Formation), and playa deposits with siliciclastic beds, partly alternating with gypsum, anhydrite and dolomite layers in the middle part. The Schilfsandstein of the Stuttgart Formation represents a fluvial deposit that has its origin in the Fennoscandian Massif of the north. The upper part of the Keuper (Rhaetian) has marine sandstones and shales.

Buntsandstein: The Buntsandstein succession in the Germanic Basin (Fig. 3) has a thickness of about 500-1200 meters. It is subdivided into a lower (Calvörde and Bernburg formations), middle (Volpriehausen, Detfurth, Hardegsen, Solling formations) and upper part (Roet Formation). Formations can be cross-correlated to the international time scale, with the Bernburg and Calvörde formations representing the Induan, the Volpriehausen, Detfurth, Hardegsen formations and most of the Solling Formation representing the Olenekian, and the uppermost Solling Formation and the Roet Formation belonging to the early Anisian. Known ichnofossils include rich vertebrate track assemblages and invertebrate traces (see below), bodyfossils are vertebrate skeletal remains such as fishes, temnospondyl amphibians, procolophonids, and archosaurs, invertebrates with crustaceans, insects and bivalves, furthermore plants. Biostratigraphically conchostracans as well as some chirothere tracks are important (Lepper & Röhling, 1998; Bachmann & Kozur, 2004; Klein & Lucas, 2010).

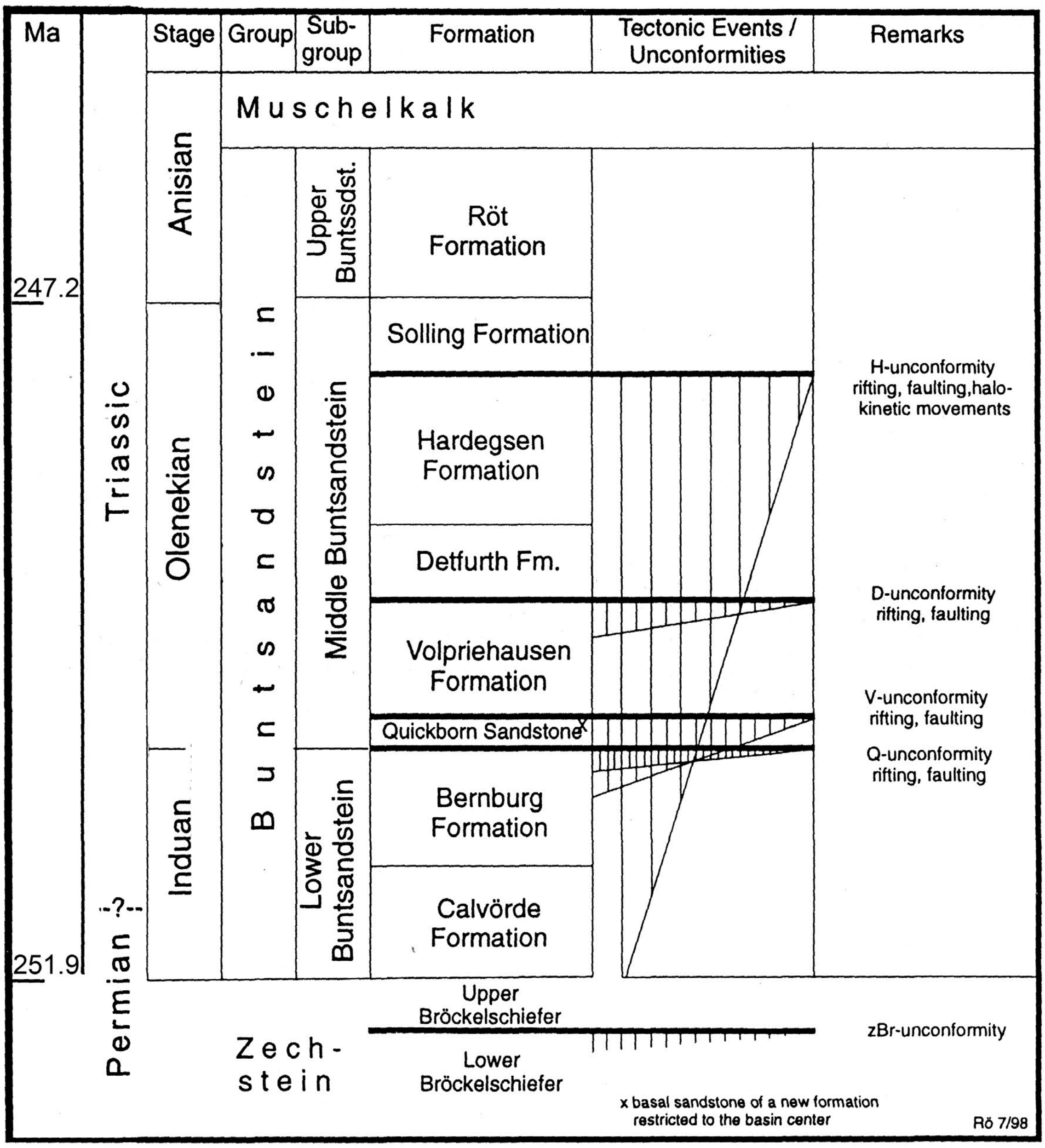

Fig. 3. Chronostratigraphy and lithostratigraphy of the Buntsandstein in Germany. From Lepper & Röhling (1998). Numerical ages updated according to Cohen et al. (2013).

Muschelkalk: The Muschelkalk succession in the Germanic Basin (Fig. 4) has a maximum thickness of about 250 meters. It is subdivided into the lower part (Jena Formation), middle part (Karlstadt, Heilbronn, Diemel formations), and upper part (Trochitenkalk, Meißner formations). These can be cross-correlated to the international time scale with the Jena to Diemel formations representing the Anisian, and the Trochitenkalk Formation belonging to the Ladinian. Ichnofossil assemblages from marginal marine deposits of the Muschelkalk include abundant vertebrate tracks and invertebrate trace fossils (see below), bodyfossils are vertebrates with fishes and marine reptiles, furthermore rich invertebrate faunas with cephalopods, crustaceans, bivalves, brachiopods and echinoderms. Biostratigraphically, in particular cephalopods (ceratites), conodonts, brachiopods, bivalves, echinoderms, ostracods and marine reptiles are important as well as some plant fossils (HAGDORN et al., 1998).

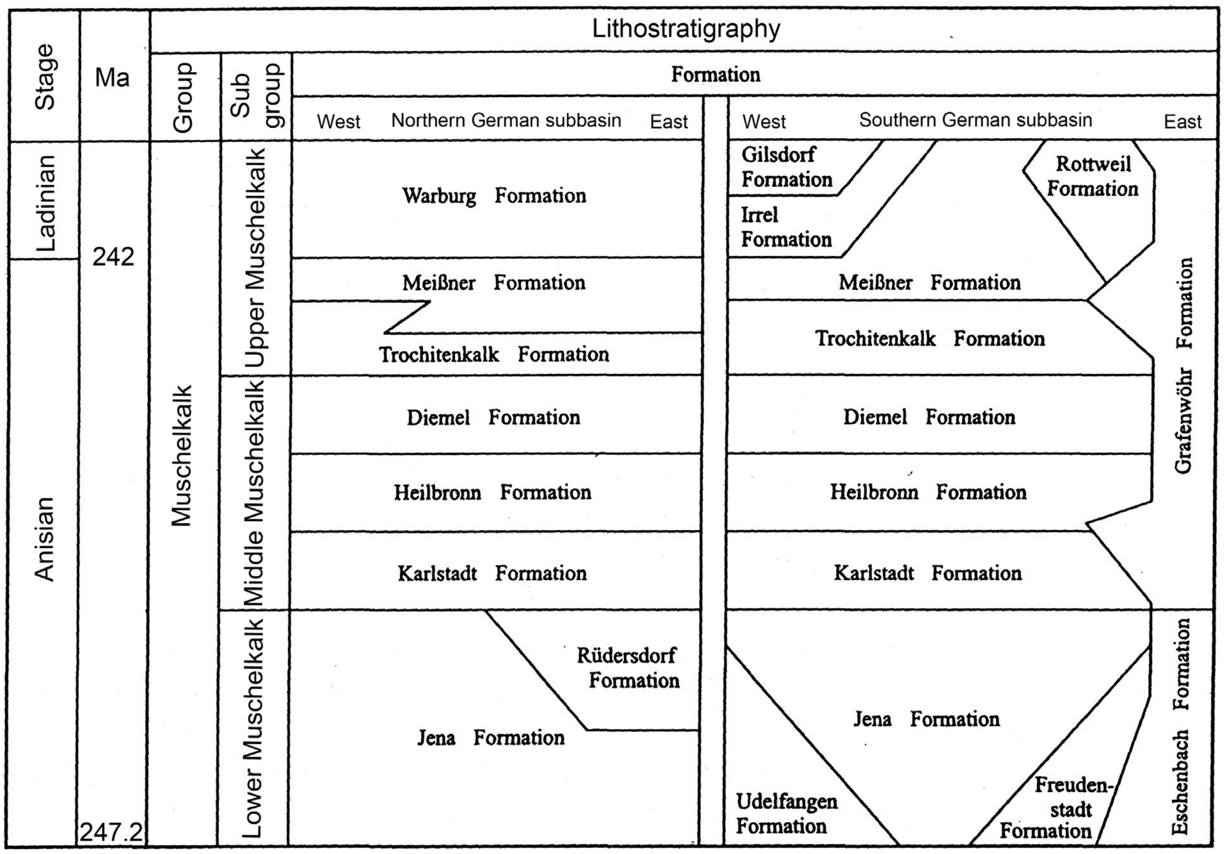

Fig. 4. Chronostratigraphy and lithostratigraphy of the Muschelkalk in Germany. From HAGDORN et al. (1998). Numerical ages updated according to COHEN et al. (2013).

Keuper: The Keuper succession in the Germanic Basin (Fig. 5) has a maximum thickness of 700 meters, except in some graben structures where it can reach several thousand meters.

It is subdivided into the lower part (Erfurt Formation), the middle part (Grabfeld, Weser, Arnstadt formations), and upper part (Exter Formation) with equivalents at the southern margin along the Bohemian-Vindelician Massif, such as the Grafenwöhr, Benk, Stuttgart, Steigerwald, Hassberge, Mainhardt, Löwenstein and Trossingen formations. Correlations to the international time scale are Ladinian (Erfurt Formation-lower Grabfeld Formation), Carnian (upper Grabfeld Formation-Weser Formation), Norian (Arnstadt Formation) and Rhaetian (Exter Formation). Ichnofossils occur with abundant invertebrate traces in all units of the Keuper, vertebrate tracks are present with diverse assemblages in particular in the middle Keuper. Bodyfossils include vertebrates with fishes, temnospondyl amphibians, procolophonids, turtles, archosaurs including phytosaurs, aetosaurs and dinosaurs like plateosaurs and theropods. Invertebrates are also present and reveal bivalves, crustaceans, insects and abundant plants. Biostratigraphically palynomophs, ostracods and bivalves are important (BEUTLER, 1998).

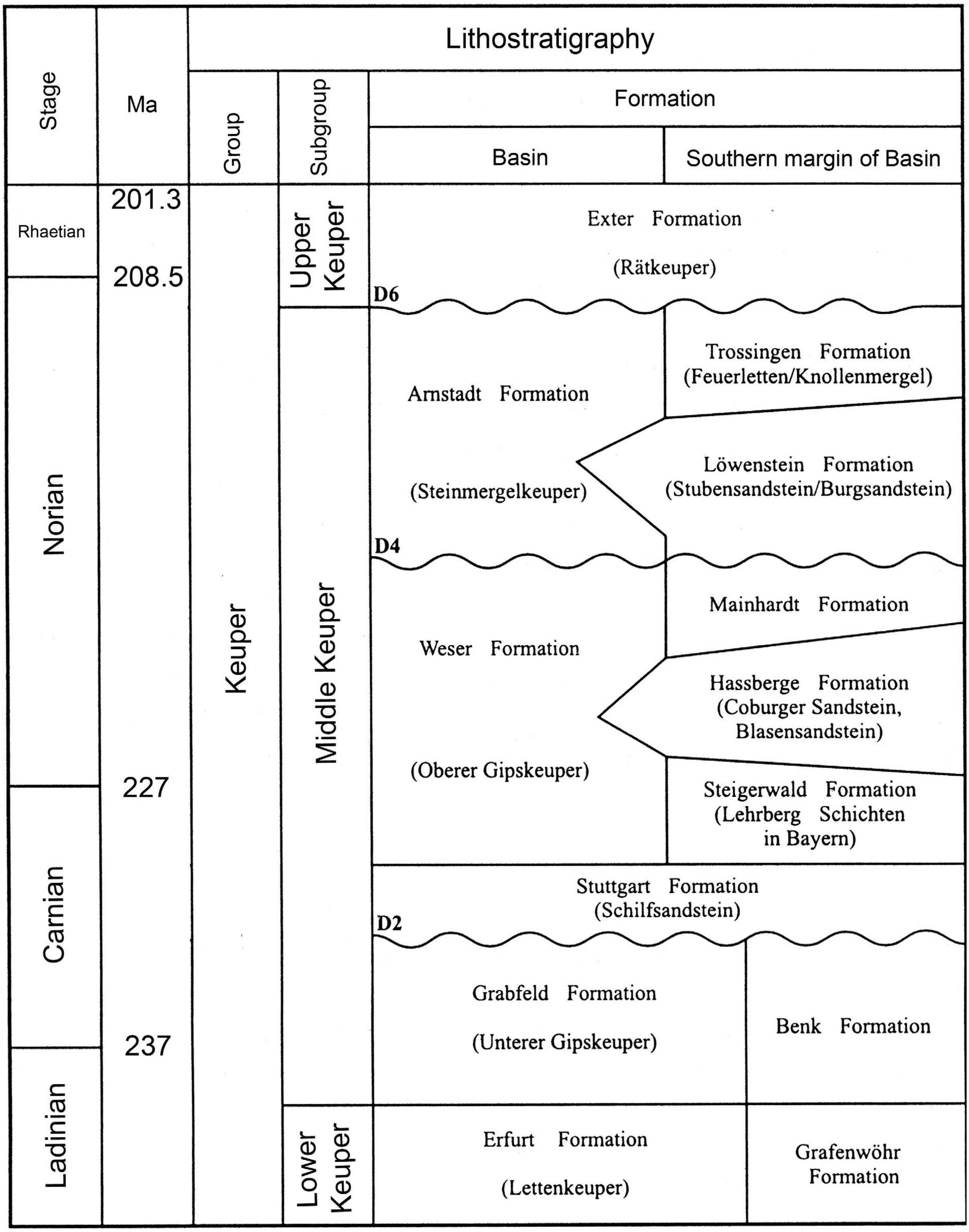

Fig. 5. Chronostratigraphy and lithostratigraphy of Middle-Upper Triassic units in Germany. From Beutler (1998). Numerical ages updated according to Cohen et al. (2013).

Fig. 6. Outcrop along the Red Main River SE of the city of Bayreuth, with sandstone-claystone succession of the trace-fossil bearing Benker Sandstein (Benk Formation, Middle Triassic, late Ladinian) as overview (top) and detail (bottom).

Stop 1. Schlehenmühle, SE Bayreuth

Location. Outcrop along the bank of the Red Main River, which belongs to the headwaters of the Main River, where the city of Frankfurt is situated. It lies in a hilly and wooded area southeast of the city of Bayreuth with continental and marine Triassic-Jurassic rocks, commonly exposed in isolated fault-blocks. The succession is in the lower Benk Formation of the Middle Keuper (Middle Triassic, latest Ladinian).

GPS. 49°54’28.2”N 11°37’19.6”E

Features to be seen.

1. Section in fluvial siliciclastic rocks with archosaur and other tetrapod tracks, including the chirotheriid ichnotaxon “*Parachirotherium*” *postchirotherioides*.
2. abundant invertebrate traces.

Geology/Ichnology. The outcrop consists of arcosic white to yellowish, mostly medium to fine-grained sandstones and siltstones, alternating with red and green claystone layers (Fig. 6). Characteristic features are crossbedding, rip-up clasts, mudcracks, halite crystal casts. The succession belongs to the Benk Formation (Middle Triassic, latest Ladinian), that interfingers with the marginal marine-playa Grabfeld Formation of the basin (Figs. 5, 7). Deposition took place along the Bohemian Massif in an alluvial fan/alluvial plain environment with occasional sheetflood events. This is the type locality of the chirotheriid “*Parachirotherium*” *postchirotherioides* (Fig. 8A). The ichnotaxon is characterized by the trackways of a quadruped with a functionally tridactyl pes imprint that has strongly reduced and posteriorly shifted digits I and V. Trackmakers are considered to be dinosauriform archosaurs. The late Ladinian is an important time interval for the evolution of dinosauriforms. Deposits of this age also contain mesaxonic tridactyl pes imprints, that are occasionally accompanied by a manus trace, documenting trackways of a facultative biped. They can be assigned to the *Atreipus-Grallator* plexus and represent some of the oldest representatives of these ichnotaxa (Fig. 8B), that have their very first appearance in the late Anisian. This has been documented from a global record (Klein & Lucas, 2010). Co-occurring tetrapod tracks are “*Brachychirotherium*“ isp. (Fig. 8C) and *Rhynchosauroides* isp. that can be attributed to basal archosaurs and archosauromorphs/lepidosauromorphs, respectively. Invertebrate traces are present with abundant *Skolithos* and *Scoyenia* (Fig. 8A, C). For vertebrate ichnofauna see Haubold & Klein (2000, 2002). Bodyfossils present in the Benk Formation are plants, conchostracans and bivalves. A skull of a capitosaurian temnospondyl is also known (Kamphausen, 1990).

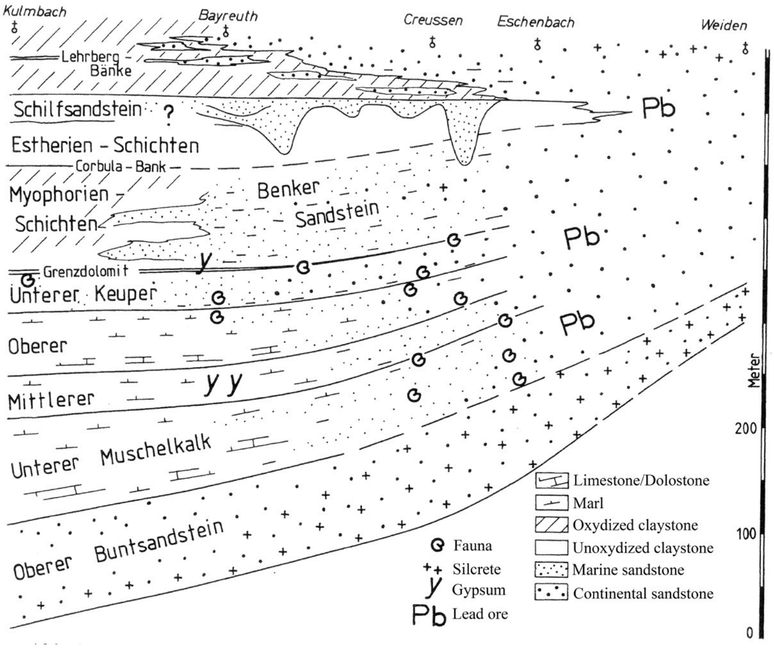

Fig. 7. Lithologic section with Middle-Upper Triassic (Anisian-Carnian) deposits SE of the city of Bayreuth. From Schröder et al. (1998).

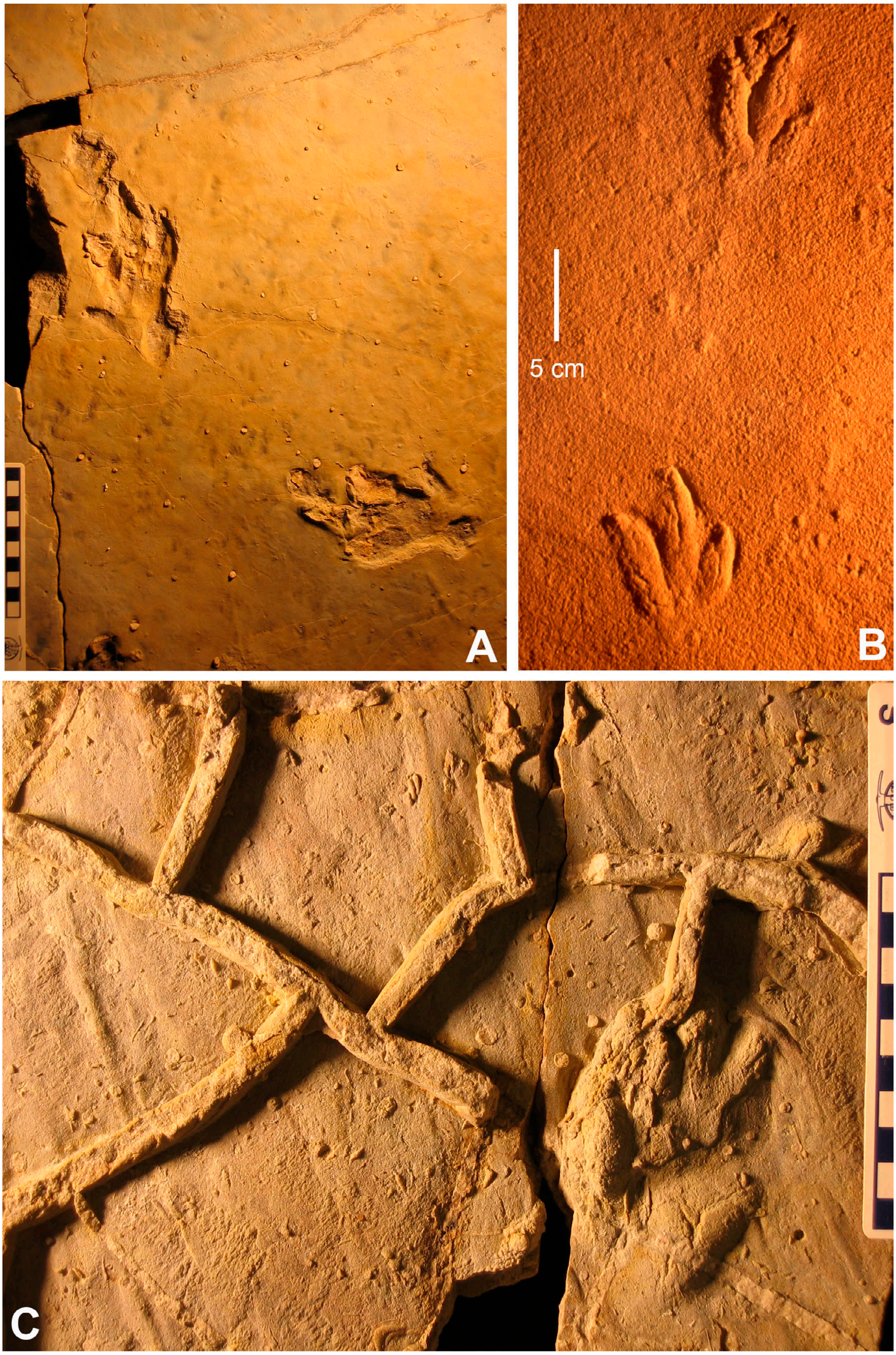

Fig. 8. Trace fossils from the Benker Sandstein (Benk Formation, Middle Triassic, late Ladinian) southeast of Bayreuth City. A. Section with detail of crossing trackways of "*Parachirotherium*" *postchirotherioides* from the type locality, showing two pes-manus sets preserved as concave epirelief, together with numerous *Skolithos* isp. B. Section of trackway with two pes and overstepped manus imprints of tridactyl *Atreipus-Grallator*, preserved as convex hyporelief. C. Mudcracked surface with "*Brachychirotherium*" isp., pes-manus set (right), together with small *Rhynchosauroides* isp. footprints, scratch marks and *Skolithos* isp. Scale bar increments 1 cm.

Stops 2 and 3. Schönbachsmühle and Neubrunn, Hassberge, NW Bamberg.

Location. Two (largely abandonded) quarries in the Coburger Sandstein of the Hassberge Formation (Middle Keuper, Upper Triassic, Carnian). They are situated in the Hassberge, smooth forested hills (altitude ~500 m) northwest of the city of Bamberg and north of the Main River, that gave the name to the formation. At their basis they consist of continental deposits of the Upper Triassic Keuper (Carnian-Rhaetian). Exposed in the quarries is a section of about ten meters, with thick channel sandstones at the base that have been quarried for building stones.

GPS. 50°00‘42.0“N 10°40‘15.8“E and 50°01‘56.7“N 10°40‘10.5“E

Features to be seen.
1. Characteristic fluvio-lacustrine Keuper succession.
2. Archosaur tracks, including *Brachychirotherium*, *Atreipus-Grallator* and *Apatopus*.
3. Rich invertebrate ichnofauna with *Planolites*, cf. *Asterosoma*, *Skolithos* and others.

Geology/Ichnology. The Coburger Sandstein forms the upper part of the Hassberge Formation (Fig. 9). Deposits are Late Triassic (Late Carnian) in age. The quarries show a perfect architecture of a fluvio-lacustrine environment with successions of deep sandstone channels and playa-lacustrine overbank deposits with claystones, siltstones and sandstones, partly exhibiting extensive layers of ochre-coloured carbonatic concretions, as well as overlying crevasse-splay sandstones (Figs. 10A, B, 11). Features are trough bedding, tabular cross bedding, horizontal bedding, with some layers showing carbonate concretions, intraclasts, mud cracks, halite crystal casts, rootlets and more extensive bioturbation.

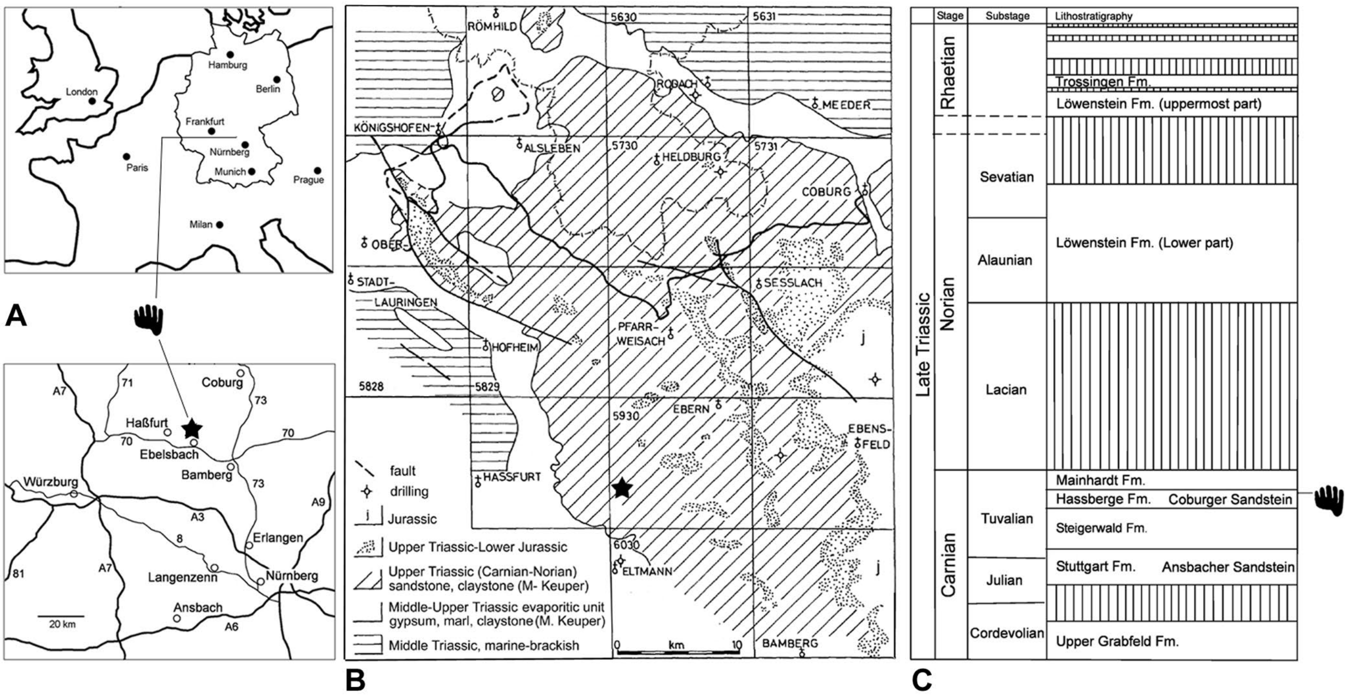

Fig. 9. Geographic and geologic maps (A-B), and lithostratigraphic section of the Upper Triassic in southern Germany (C), with position of outcrops and tetrapod footprints in the Coburger Sandstein. From Klein & Lucas (2013).

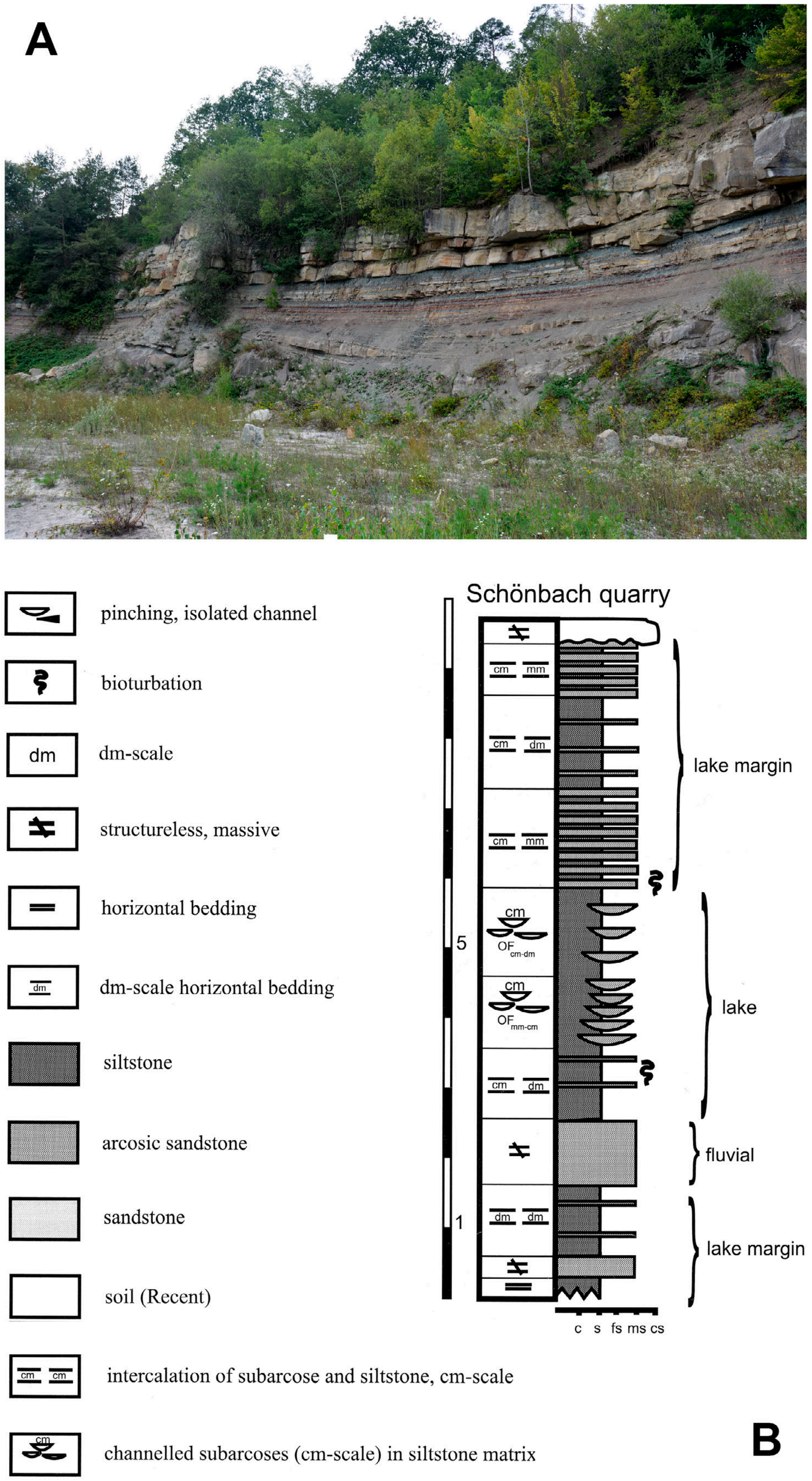

Fig. 10. Quarry in the Coburger Sandstein unit (Hassberge Formation, Upper Triassic, Carnian) at Schönbachsmühle locality. A. Overview photograph showing fluvio-lacustrine succession with thick channel sandstones at the base, followed by overbank playa and crevasse splay deposits. B. Lithological section with sedimentary features and distribution of trace fossils. From Schlirf et al. (2001).

The Coburger Sandstein is the type horizon of the ichnogenus *Brachychirotherium* Beurlen 1950 that has been documented thus far from a global distribution (Karl & Haubold, 1998; Klein & Lucas, 2010). It is present in this unit with two ichnospecies: *B. hassfurtense* (type ichnospecies) and *B. thuringiacum* (Karl & Haubold, 1998)(Fig. 12A). *Brachychirotherium* can be attributed to crocodylian-stem archosaurs, that were either aetosaur or rauisuchid pseudosuchians. Characteristic are pes and manus imprints with short broad digit traces and tiny claw marks. *Brachychirotherium* has also some biostratigraphic significance, being the index fossil of the Late Triassic *Brachychirotherium* biochron (Klein & Lucas, 2010). Associated vertebrate tracks are tridactyl dinosauromorph tracks of the *Atreipus-Grallator* plexus (Fig. 12B) as well as small lacertoid *Rhynchosauroides* representing lepidosauromorph and/or archosauromorph trackmakers. In recent years further ichnotaxa such as *Apatopus lineatus* (phytosaur) and a new ichnotaxon *Procolophonichnium lockleyi* (therapsid) have been described from the Coburger Sandstein (Klein & Lucas, 2013; Klein et al., 2015)

(Fig. 12C-D). The unit has also a rich invertebrate ichnofauna with the ichnogenera *Skolithos*, *Scoyenia*, *Taenidium*, *Lockeia*, *Rusophycus*, *Cruziana*, *Polykladichnus*, *Helminthoidichnites*, *Planolites* and others (Schlirf et al., 2001)(Fig. 13A-B). Body fossils are known with crustaceans (*Triops*), insects, fishes and plants. The lower part of the Hassberge Formation (Blasensandstein) has yielded a rich vertebrate fauna with skeletal remains of temnospondyls and phytosaurs (Kuhn, 1936).

Fig. 11. Quarry in the Coburger Sandstein unit (Hassberge Formation, Upper Triassic, Carnian) W of Neubrunn village with fluvial channel sandstones and overbank deposits. This locality yielded a rich vertebrate ichnofauna with *Brachychirotherium*, *Atreipus-Grallator*, *Apatopus*, *Rhynchosauroides* and *Procolophonichnium*.

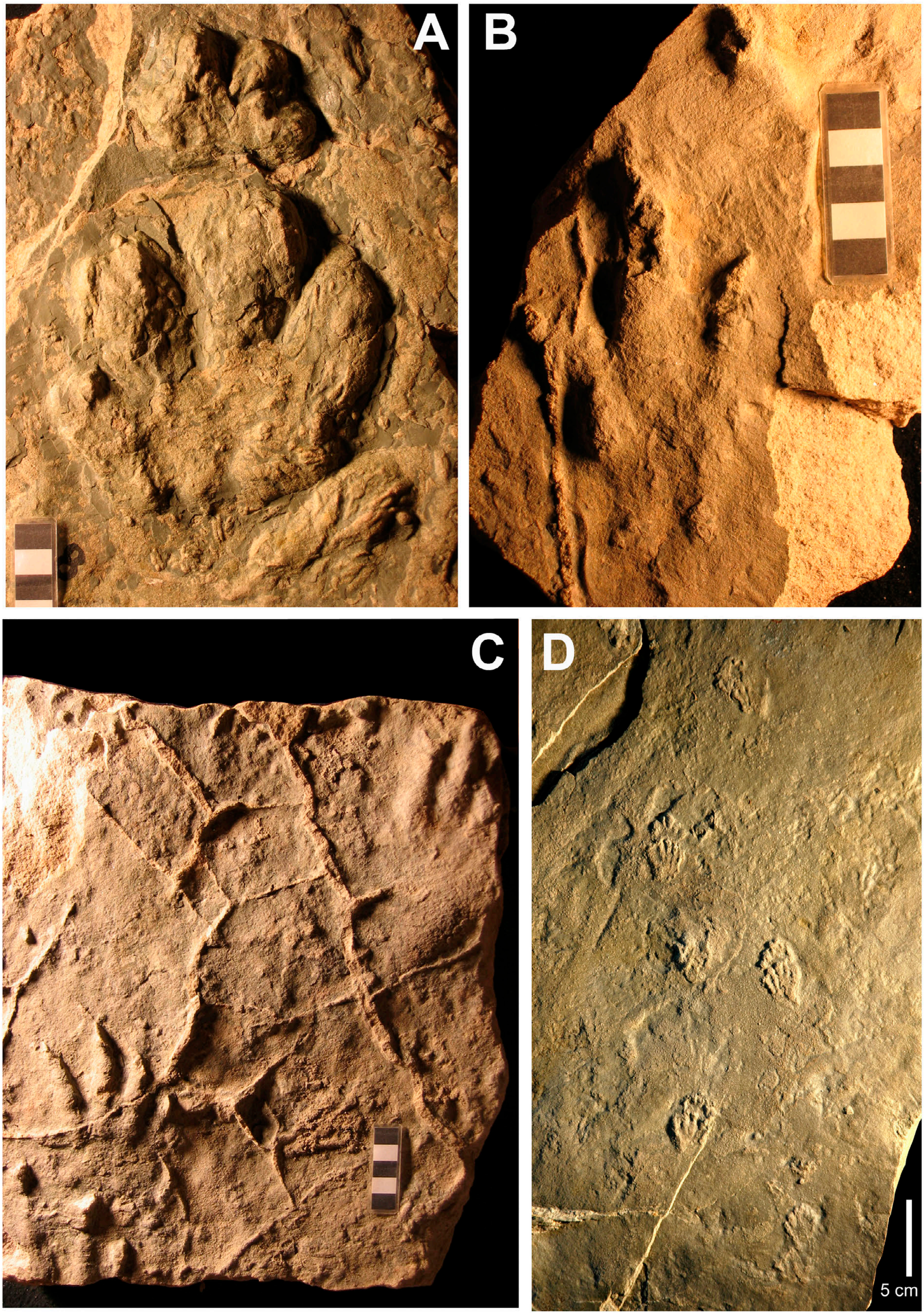

Fig. 12. Trace fossils from the Coburger Sandstein unit (Hassberge Formation, Upper Triassic, Carnian) of the Germanic Basin. A. *Brachychirotherium thuringiacum*, pes-manus set. B. *Atreipus-Grallator*, pes-manus set. C. *Apatopus lineatus*, partial trackway with pes-manus set and pes imprint. D. *Procolophonichnium lockleyi*, holotype trackway. Scale bar increments 1 cm.

Fig. 13. Invertebrate trace fossils from the Coburger Sandstein (Hassberge Formation, Upper Triassic, Carnian) of the Germanic Basin. A. cf. *Asterosoma*. B. *Planolites* isp. (pers. comm. M. Schlirf, Haßfurt).

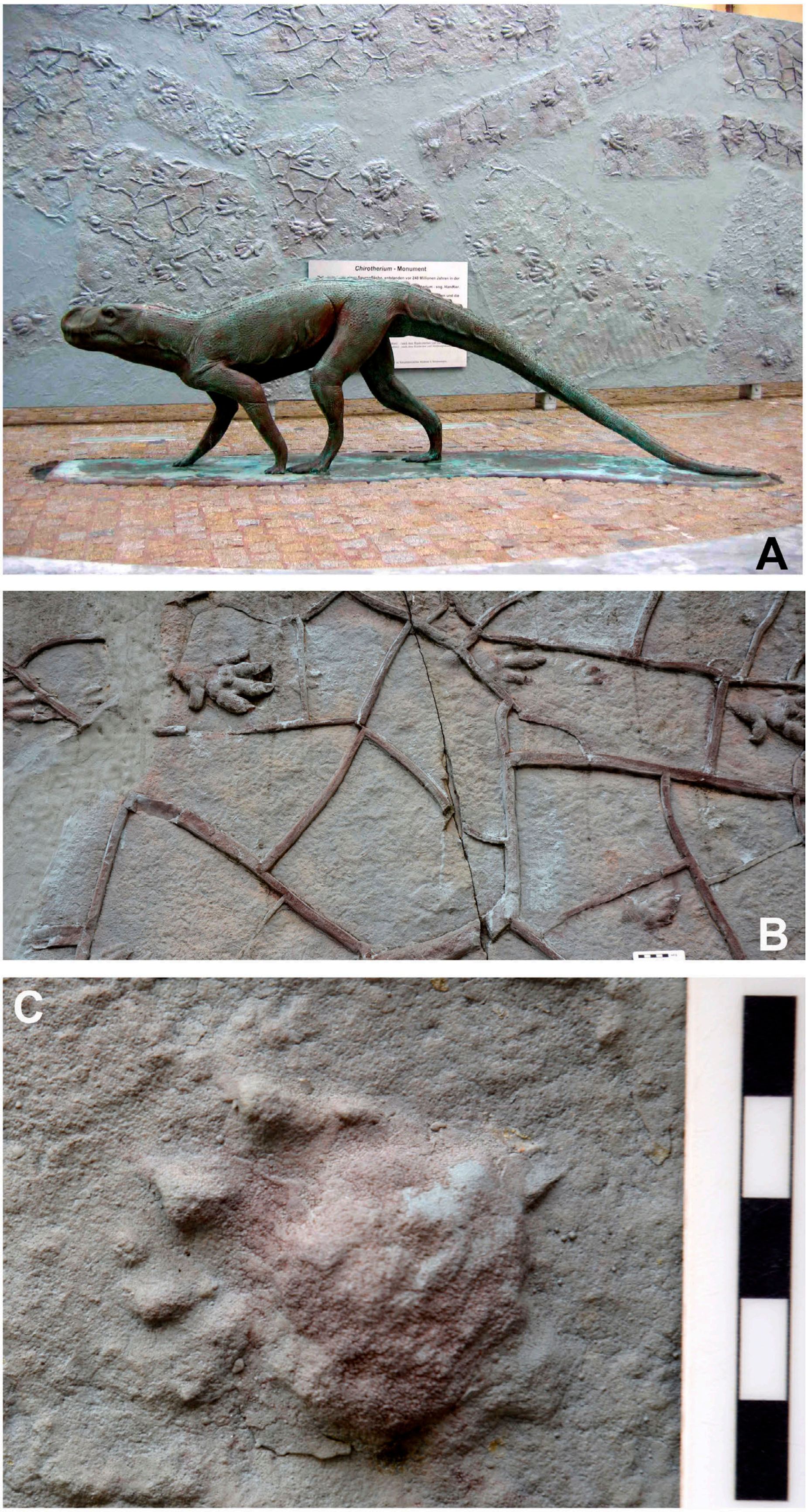

Fig. 14. Chirotherium Monument, market place of Hildburghausen, southern Thuringia, Germany. A. reconstructed type surface of *Chirotherium barthii* and *Chirotherium sickleri* and lifesize model of *C. barthii* trackmaker by Hartmut Haubold and Martin Kroniger. B. Section of reconstructed type surface with trackways of *C. barthii* (top) and *C. sickleri* (bottom). C. Associated synapsid tracks *Dicynodontipus geinitzi*. Scale bar increments 1 cm. Photograph in A: Ralf Werneburg, Schleusingen.

Stop 4. Hildburghausen

Location. Chirotherium Monument on the historical market place of the city.

GPS. 50°25'34.4"N 10°43'47.6"E

Features to be seen.
1. Replica of original *Chirotherium* type surface from the Middle Buntsandstein of Hildburghausen, with numerous trackways; top reference for tetrapod ichnological research.
2. Associated tetrapod ichnofauna.
3. Lifesize model of *Chirotherium barthii* trackmaker.

Ichnology. This is a reconstruction of the type surface of *Chirotherium barthii* and *C. sickleri*, which was discovered in 1833 by the school director F. K. L. Sickler and described and scientifically named by Kaup (1835a, b) from the Winzer Quarry (named after the owner) at Hessberg in the surroundings of Hildburghausen (Fig. 14A). The quarry was in the uppermost Solling Formation (Thüringischer Chirotheriensandstein, Anisian). Hartmut Haubold, renowned ichnologist from the University of Halle-Wittenberg spent several years, puzzling together different slabs with the footprints that were scattered in various institutions and museum collections all over Europe (Haubold, 2006). The original map of Winzer with sketches of the trackways gave a first idea of the orientation, however, it was soon clear that Winzer had made this drawing from memory, after the slabs were sold to the different institutions. Therefore Haubold, besides concrete features from the trackways, used significant landmarks from sedimentary structures such as mud-cracks to reconstruct the original relationship of the pieces. Together with the preparator Martin Kroniger, he made replicas of the slabs in the collections and puzzled them together step by step. Furthermore he made a reconstruction of the *C. barthii* trackmaker as a lifesize model in bronze, based on the skeletons of the archosaurs *Saurosuchus galilei* and *Euparkeria capensis*. The replicas of the slabs show all details, with accompanying ichnofauna such as *Rotodactylus matthesi* (dinosauromorph) and *Dicynodontipus geinitzi* (cynodont therapsid) tracks (Fig. 14B-C).

Stop 5. Schleusingen

Location. Museum of Natural History, Schloss Bertholdsburg.

GPS. 50°30’33.5”N 10°44’59.3”E

Features to be seen.
1. Rich collections of Paleozoic-Mesozoic fossils from the Thuringian Forest, including famous specimens of Permian tetrapods, invertebrates, plants, Triassic dinosaurs and tetrapod tracks.
2. Old castle from the 13th century (Fig. 15).

Ichnology/paleontology. The museum has one of the best collections of Paleozoic-early Mesozoic ichno and body fossils in Germany. Important are vertebrate, invertebrate and plant body fossils from well-known Permian localities in Thuringia such as Friedrichroda, Manebach and Tambach. Ichnofossils are *Ichniotherium*, *Dimetropus*, *Amphisauropus*, *Dromopus*, *Tambia* and many others. Also present are fossils from the Zechstein (Late Permian) period and finally original slabs with tetrapod footprints from the Buntsandstein (Middle Triassic, Anisian) of Hildburghausen and other localities, showing trackways of *Chirotherium*, *Isochirotherium*, “*Brachychirotherium*”, *Rotodactylus*, *Rhynchosauroides*, *Dicynodontipus* and *Chelonipus*. The latter are one of the oldest known turtle tracks. Further fossils and reconstructions on display concern the marine Muschelkalk (Middle Triassic, Anisian-Ladinian), fluvio-lacustrine depositional environments with temnospondyl amphibians from the Middle Triassic (Ladinian) lower Keuper and finally dinosaur fossils from the Norian locality “Großer Gleichberg”. The latter is well-known for the dinosaur skeletons of *Liliensternus* and *Ruehleia,* found by Hugo Ruehle v. Lilienstern who lived in nearby Bedheim castle. Other attractions of the museum are minerals from the Thuringian Forest and rich zoological collections.

Fig. 15. Museum of Natural History Schloss Bertholdsburg, Schleusingen, southern Thuringia. Old castle from the 13th century hosting the museum (top). Exhibition with dinosaur skeletons. Photos: https://www.museum-schleusingen.de.

Day 2 – Saturday, 28th September 2019

Stop 6: Bromacker Quarry near Tambach-Dietharz

Location: The Bromacker sandstone quarry and the nearby tetrapod excavation site are located in proximity to the town Tambach-Dietharz in the northern Thuringian Forest. This locality is now part of the National Geopark of Thuringia and its "Saurian Event Path" (Saurier-Erlebnispfad). Due to its rich ichnofauna and well-preserved tetrapod skeletons the Bromacker lagerstätte represents the most important European site for Early Permian tetrapods and their tracks.

GPS: 50°48'35.8"N 10°37'17.4"E.

Features to be seen:
1. Inactive sandstone quarry and the former excavation site of the Museum der Natur Gotha. Sedimentary succession of the Tambach Formation (Artinskian, Early Permian) including trace-bearing sandstones and mudflow deposits which yielded bones and skeletons of various tetrapod species (Fig. 16).
2. Trackways of *Ichniotherium sphaerodactylum*, tetrapod scratches and scrabbling/ shallow burrowing traces (*"Megatambichnus"*). Mudcrack horizons with tetrapod tracks usually display impressions of plant detritus and invertebrate ichnia (Fig. 17A-B).
3. Invertebrate burrowing traces, especially *Tambia spiralis* in varying morphologies (Fig. 17C).

Fig. 17: Tambach sandstone slabs with A, tetrapod scratches ("*Megatambichnus*"); B, the diadectid ichnotaxon *Ichniotherium sphaerodactylum*; C, the invertebrate burrowing trace *Tambia spiralis*.

Fig. 16. Sites of the Bromacker lagerstätte: A, Bromacker Quarry, featuring sandstones of the Tambach Sandstone Member that are overlain by the Bromacker Siltstones; B, Excavation site of Thomas Martens and his former Museum der Natur Gotha team.

Geology of the Thuringian Forest Basin*: The Thuringian Forest Basin, an approximately 40 to 60 km wide NW-SE orientated depression, is largely exposed in the horst structure of the Thuringian Forest. It belongs to the classical Rotliegend areas in Europe (Fig. 18) because of the mining of Permian Zechstein Kupferschiefer deposits along the borders of this horst, sulfide ores in Rotliegend lacustrine black shales, Stephanian and Rotliegend coals, and Mesozoic vein deposits. In 1775 F.G. Gläser published one of the worldwide oldest hand-coloured geological maps that included parts of the Thuringian Forest. Nowadays, this Rotliegend basin is one of the biostratigraphically best investigated and correlated basins in the Variscan area (Schneider, 1996, 2001; Lützner et al., 2007; Andreas et al., 2005; Schneider & Werneburg, 2006; Werneburg & Schneider, 2006, 2012). The basin is situated on deeply eroded Variscan basement of the Saxothuringian Zone in the southeast, Visean granites in the center, and the inverted Mid-German Crystalline Zone (MGCZ) as well as the Rhenohercynian zone in the northwest. Basin development, sedimentation and volcanism were controlled by various distinctly striking fault systems, which caused a changing pattern of subsiding and uplifting blocks during sedimentation. In consequence, small sub-basins with partially strong relief gradients were created (see Andreas, 1988, 2014; Lützner, 1988; Lützner et al., 2007, 2012).

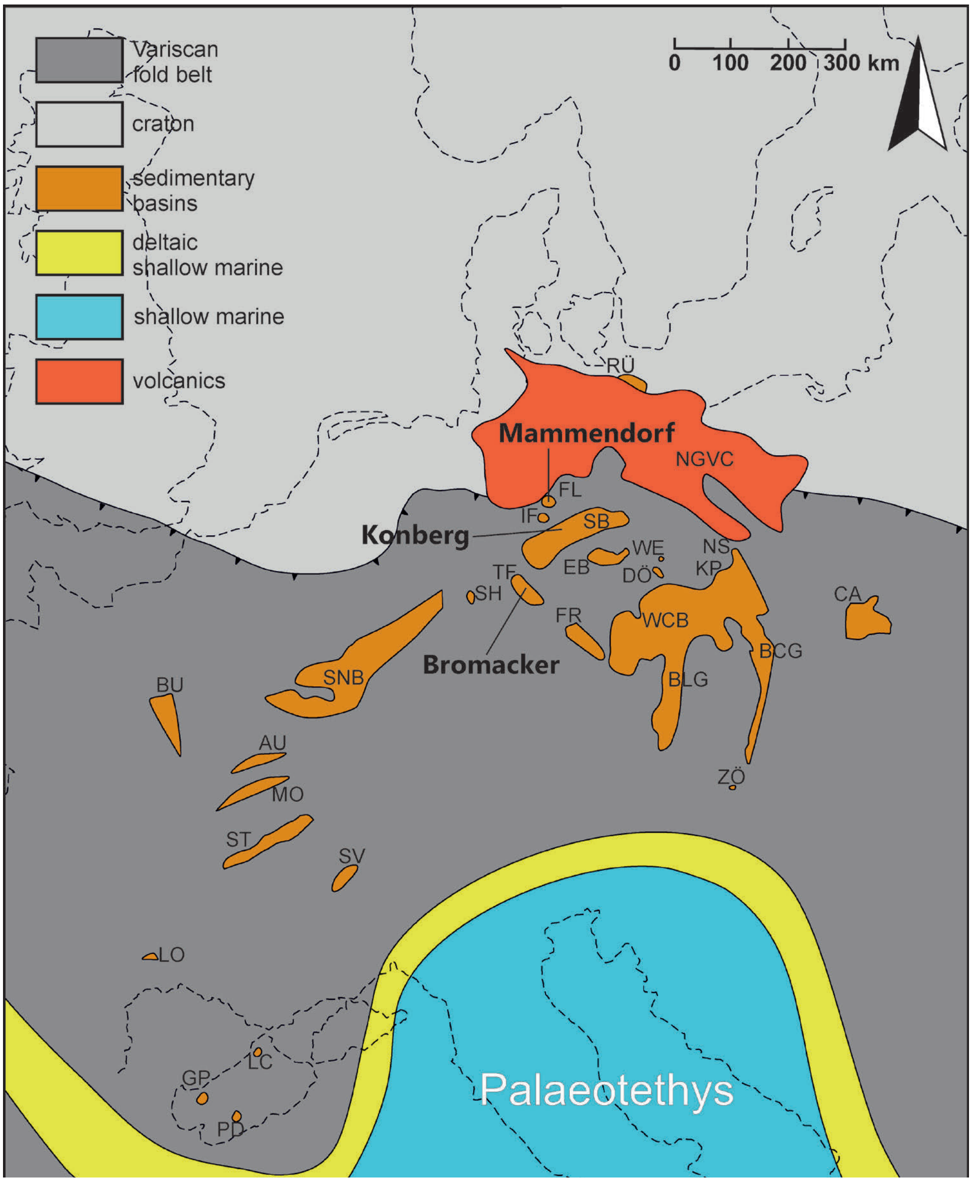

Fig. 18: Simplified maps of Central European Rotliegend basins: EB – Erzgebirge Basin, FL – Flechtingen depositional area, IF – Ilfeld Basin, SB – Saale Basin, SNB – Saar-Nahe Basin, TF – Thuringian Forest Basin. The map was provided by Jan Fischer of the Urweltmuseum Geoskop in Kusel.

After deposition of the Rotterode Formation and a hiatus, the up to 250 m thick **Tambach Formation** was deposited on a volcanic relief dissected in part by canyons (Lützner & Mädler, 1994; Lützner et al., 2007). Facies patterns range from very coarse, matrix supported wadi-fill conglomerates to proximal and distal debris-flow dominated alluvial fan clastics as well as floodplain sandstones and floodbasin siltstones. The sandstones are interpreted as fluvial reworked aeolian sandstones, primarily accumulated in the hinterland (Schneider & Gebhardt, 1993). Scoyenia-facies, indicative for wet red beds, is typical of these alluvial plain deposits (Martens et al., 1981). The flora consists of xerophilous walchians and cones of the drought-adapted *Calamites gigas*.

Tambach is famous for complete, articulated vertebrate skeletons, preserved in mud flows (Martens, 1988; Berman & Martens 1993; Eberth et al., 2000). The fauna includes reptiles and terrestrially adapted amphibians, which at the genus level are close to North American Early Permian tetrapod faunas. Based on tetrapods and insects (*Moravamylacris kukalovae*), the Tambach Formation is correlated with the North American late Wolfcampian/early Leonardian, i.e. the Artinskian/earliest Kungurian (Schneider & Werneburg, 2006; Lucas, 2006). The Tambach Formation is followed by the 400 m to 600 m thick completely red-coloured sediment revealing Eisenach Formation.

Facies, paleoecology and paleoenvironment of the Tambach Formation*: The red beds of the Tambach Formation have been deposited in an S-N stretching depression on and at the flanks of the Oberhof Volcanite Complex; drainage was possibly to the North into the Saale basin (Lützner et al., 2012). Simplified, the formation starts with up to 125 m alluvial fan conglomerates (Bielstein conglomerate Member), which laterally and vertically grade into the up to 100 m thick Tambach Sandstone Member (Mb). Tectonical activity caused the progradating of a new alluvial fan and braid plain system, the up to 50 m thick upper conglomerate (Finsterbergen Conglomerate Member). The basal conglomerates were deposited as debris flows and hyperconcentrated flash flood-flows. The upper conglomerate represents shallow alluvial fans with transitions into a braid plain environment. Regardless the longer transport distances from a crystalline and granitic source (Ruhla Crystalline Complex) the roundness of the pebbles is much lower than in the basal conglomerates. The fossiliferous Tambach sandstone originates in an alluvial braid plain environment. Typical are flat channels and sheetflood bodies with intercalated short-termed pontic claystones and siltstones as well as lateral and vertical transitions into floodplain siltstones. Horizons rich in mud clasts and containing articulated tetrapod skeletons result from repeated catastrophic flood events.

Exposed in the quarry areal are the **Tambach Sandstone Mb.** with the Bromacker Siltstones in the top. The mostly well sorted fine to middle grained sandstones form stacked decimetre to metre thick internally indistinct horizontal plane to rarer distinct small to large scale trough bedded horizons. The single sandstone bodies fill elongated decameter long shallow channels. Decimeter deep and meter wide gutter casts are common. Single beds are mostly separated by centimeter thick desiccation crack horizons of mud drapes. Those features indicate that these single sandstone beds correspond to single flood events. The mud drapes are settled down after floods. They contain a variety of tetrapod tracks, invertebrate traces and in places the freshwater jellyfish *Medusina limnica*. The tracks and traces were later dissected by desiccation cracks. Concentric and parallel water level marks in about 0.5 cm to 1 cm distance from one another are interpreted as the result of strongly changing day/night (noctidiurnal) temperatures and therefore evaporation rates as known from modern semiarid to arid climates. Counting of those marks result in time durations of 30 to 100 days of water fill of those puddles and ponds. The about 4 m thick **Bromacker Siltstones** are dominated by two facies: about 1.5 m 2 m basal, decimeter-scaled massive siltstones to very fine-grained sandstones, which are sharply overlain by beds of finely laminated siltstone and claystone. Essentially all of the hundreds of vertebrate skeletal specimens collected from the Bromacker, ranging from isolated elements to partial and complete, articulated skeletons were recovered from two closely associated sheetflood deposits within a stratigraphic interval of 1.2 m within the massive clay pebble containing siltstones. The overlying facies of very finely interlaminated siltstone and claystone beds, up to 15 cm thick, have yielded impressions of conchostracans, insect wings, and myriapod fragments (Martens et al., 1981). Altogether these fine clastics were interpreted as an upper-flow-regime sheetflood deposit and waning flood deposits in an ephemeral-lacustrine to flood basin setting. The sheetfloods originated in the wadis at the margins of the Tambach Basin and, when sufficiently intense, spread across the low sloping land surface of the basin center. Bedding planes with densely packed adult conchostracans, buried in living position, represent in analogy to modern examples dried up puddles and ponds on the flood plain. The duration of the ontogenetic development of conchostracans from their dry-resistant eggs to adult stages, which takes place in minimally 4 weeks, coincide well with the standing duration of the water bodies in the sandstone facies.

Fossil content*: The Bromacker locality became well-known for the well-preserved and very common tetrapod tracks discovered here since more than 100 years (Pabst, 1895; for details see Voigt, 2005). In 1974 the first tetrapod bone was discovered by Thomas Martens, since then about 40 skeletons of 13 different early terrestrial tetrapods were excavated by a German – North American team (Martens, Berman, Sumida, Henrici), documented in numerous publications (e.g., Voigt et al., 2007, 2010), and allow unique insights into a rare Permian terrestrial upland ecosystem. With respect to the unique finds of tetrapod tracks and skeletons, the Bromacker locality has consequently emerged to one of the most important sites of Late Palaeozoic vertebrates in Europe. It is also the place with the first well-documented species-level identification trackmakers among Palaeozoic vertebrates: *Ichniotherium cottae* are the tracks of *Diadectes absitus*, and *Ichniotherium sphaerodactylum* are the tracks of *Orobates pabsti* (see Voigt et al., 2007).

The flora is dominated by walchians and *Calamites gigas*; callipterids are very rare. Aquatic invertebrates a represented by *Medusina limnica* and conchostracans. Terrestrial invertebrates include the relatively common wings of blattids (*Moravamylacris kukalovae*, *Phylloblatta* sp.) and one 8 cm long (?)orthopteran wing fragment, diplopods and arachnids. Very common are invertebrate traces, such as *Tambia spiralis* (Fig. 17C), *Striatichnium bromackeri*, *Scoyenia gracilis*. Skeletons of several distinct tetrapod taxa have been excavated: the temnospondyl amphibians *Georgenthalia clavinasica*, *Rotaryus gothae* and *Tambachia trogallas*, the reptiliomorph anamniotes *Seymouria sanjuanensis*, *Diadectes absitus* and *Orobates pabsti*, the reptiles *Eudibamus cursoris* and *Thuringothyris mahlendorfae*, the synapsids *Tambacarnifex unguifalcatus*, *Dimetrodon teutonis*, an unnamed microsaur and an unnamed caseid (Wings & Eckert 2018). Tetrapod tracks have been referred to five ichnotaxa: *Ichniotherium cottae*, *Ichniotherium sphaerodactylum*, *Dimetropus leisnerianus*, *Varanopus microdactylus* and *Tambachichnium schmidti*.

**These paragraphs have largely been replicated with friendly permission from Schneider, J. W., Rössler, R., Werneburg, R., Scholze, F. & Voigt, S. (2014): Part II. The Carboniferous–Permian basins in Saxony, Thuringia, and Saxony-Anhalt of East Germany. In: Schneider, J.W., Oplustil, S. & Scholze, F. (Eds.): CPC-2014 Field Meeting on Carboniferous and Permian Nonmarine–Marine Correlation. July 21st–27th, Freiberg, Germany. Excursion Guide. – Technische Universität Bergakademie Freiberg, Wissenschaftliche Mitteilungen des Institutes für Geologie, 4: 55–121.*

Stop 7: Museum der Natur Gotha – Bromacker collection

Location: The Museum der Natur (Museum of Nature) in Gotha belongs to the foundation Stiftung Schloss Friedenstein Gotha and its exhibition is housed in the eponymous Friedenstein castle in the centre of Gotha. The Bromacker collection is currently stored in a nearby building.

GPS: 50°56’51.7”N 10°42’38.6”E

Features to be seen:
1. Tambach Formation sandstone slabs with *Ichniotherium*, *Varanopus*, *Dimetropus*, *Tambachichnium*, *“Megatambichnus”* and invertebrate trace fossils. Some of the specimens show skin impressions of the belly, tail and legs associated with in association footprints (Fig. 19).
2. Skeletons and partially articulated skeletons of Bromacker tetrapods – including amphibians, reptiliomorph anamniotes (*Seymouria*, *Orobates*), synapsids and reptiles (Fig. 20; some of the material is currently under study by researchers of the Museum für Naturkunde Berlin and may not be available during our visit).

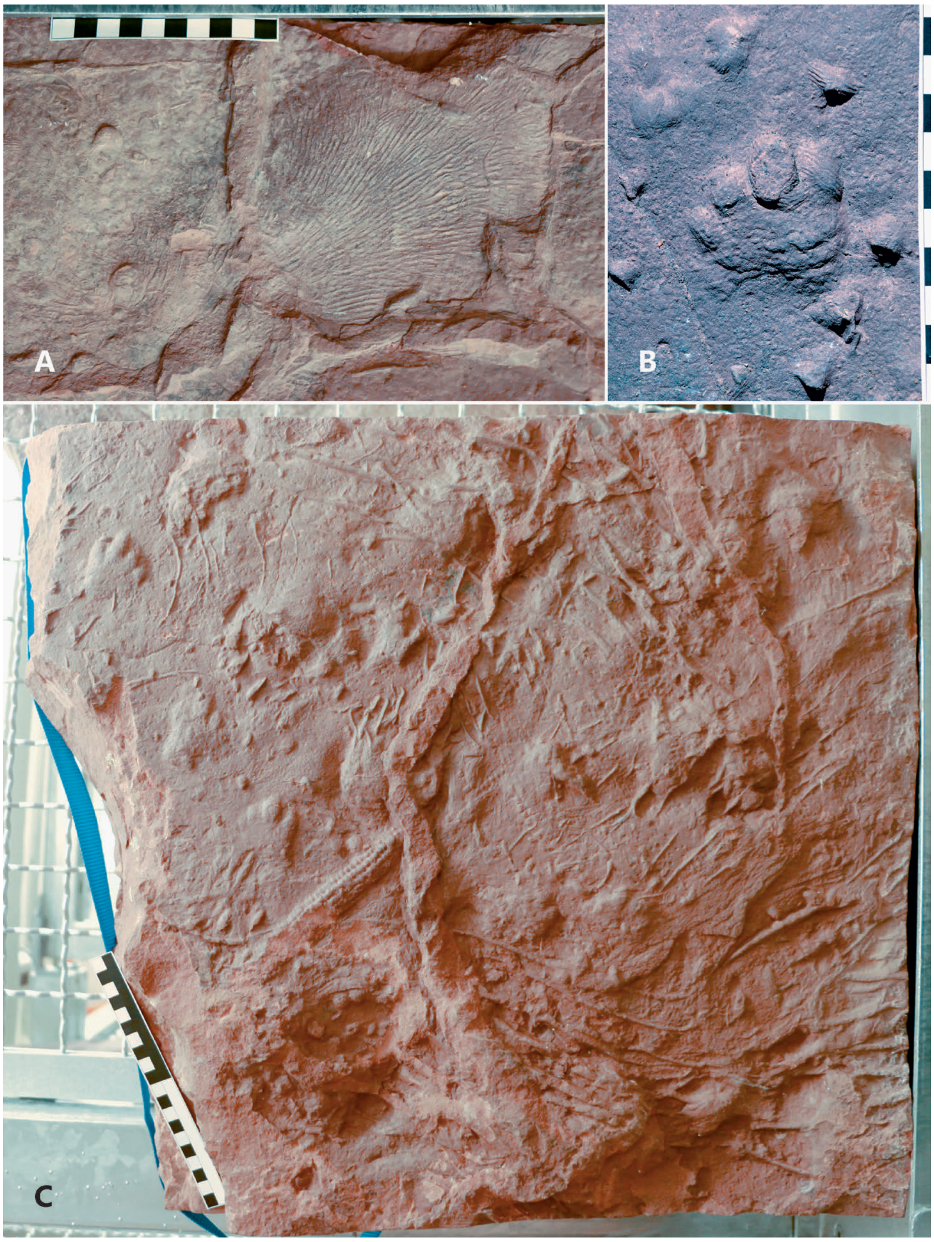

Fig. 19. Trace fossils of the Bromacker collection: A, *Striatichnium bromackerense*; B, Footprint of *Dimetropus leisnerianus*, C, Slab with skin imprints of the body and tail that are associated with *Dimetropus* footprints as well as scratch marks.

Fig. 20. Skeletal specimens of the Bromacker collection stored in the external collection building of the Museum der Natur Gotha: A, *Seymouria sanjuanensis*, the "Tambach Lovers"; B, left hindlimb of *Dimetrodon teutonis*; C, partial skeleton of *Orobates pabsti*.

Stop 8: Konberg Quarry in Rothenschirmbach

Location: In the Konberg Quarry, sedimentary rocks of the Hornburg Formation (Upper Rotliegend, Middle Permian) are exposed. The now inactive sandstone quarry lies in a small forest at the north-eastern margin of the village Rothenschirmbach, which now forms a part of the town Eisleben.

GPS: 51°27'28.3"N 11°33'14.8"E

Features to be seen: Sandstones of the Feinkörniger Sandstone Member and laminated shalestones and thin-bedded sandstones of the Blätterton Member with arthropod tracks, tetrapod swimming traces and impressions of hydromedusae (Figs. 21 and 22).

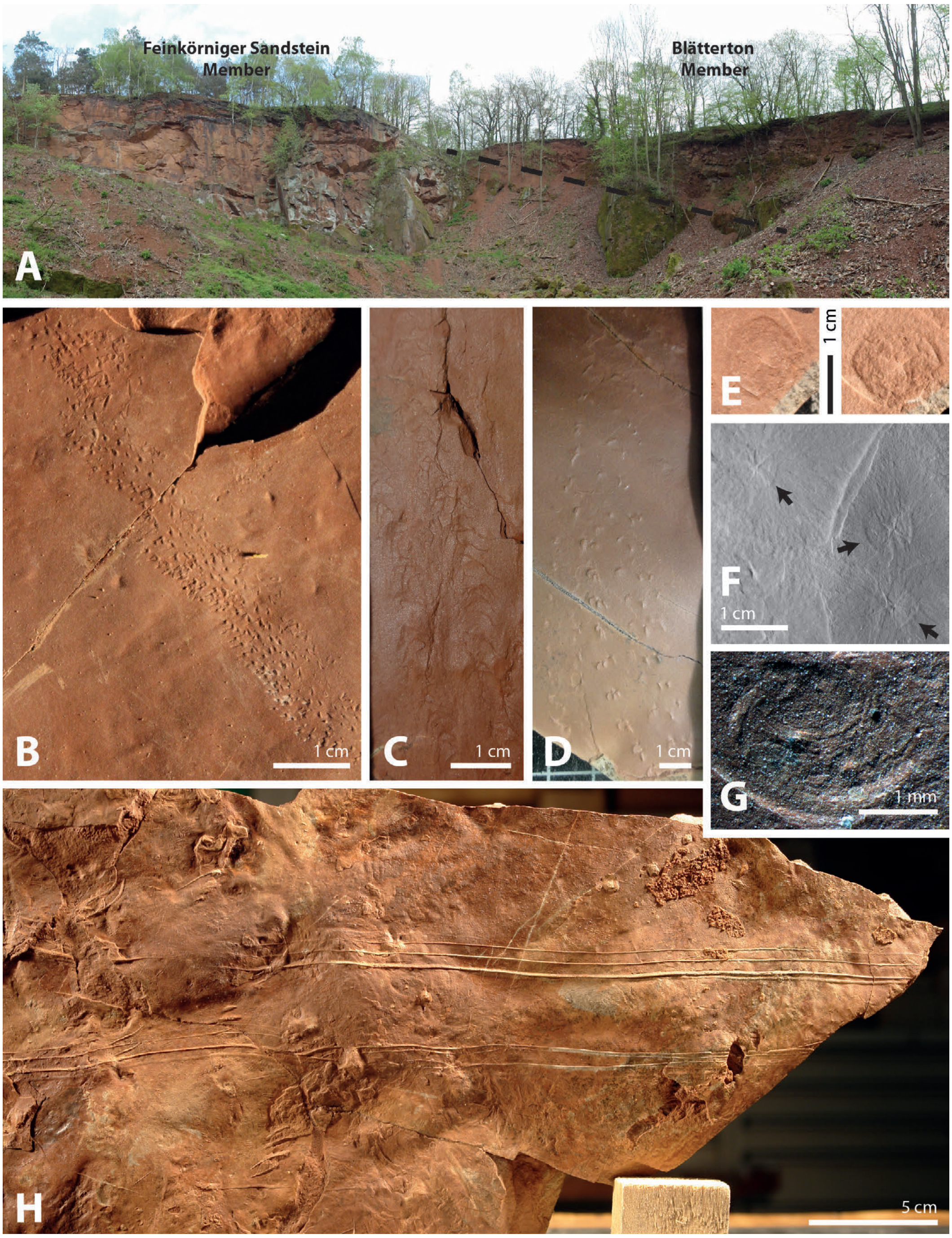

Fig. 21. Konberg Quarry: A, exposed strata of the Hornburg Fm; B-D, arthropod tracks; E-F, impressions of hydromedusae; G, conchostracan shell imprint; H, tetrapod swim traces.

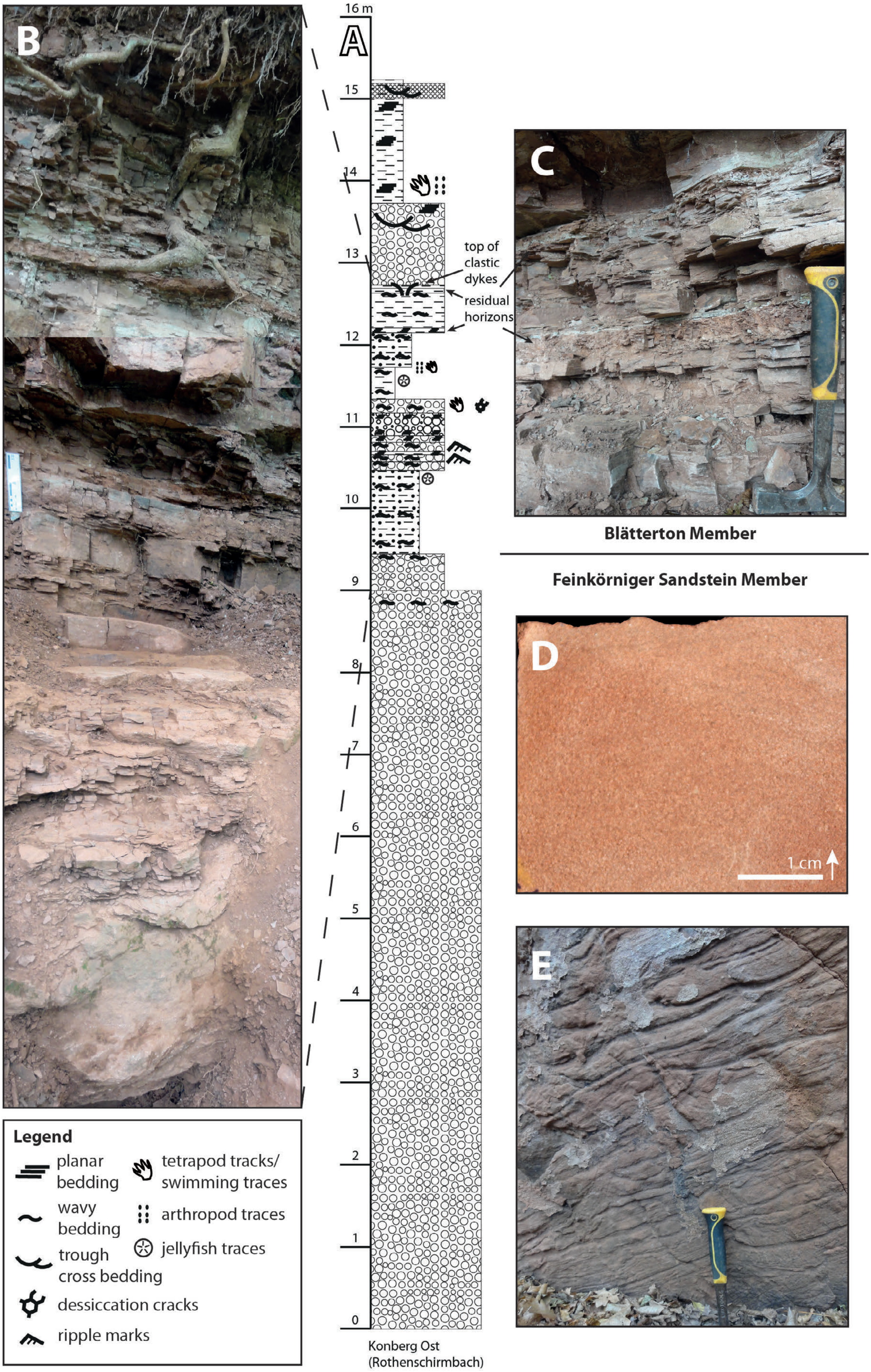

Fig. 22. Succession of sedimentary rocks at Konberg-East.

Stratigraphy of the Hornburg anticline/Saale Basin: The nowadays Hornburg anticline (Saxony-Anhalt) was part of the northeastern margin of the Carboniferous -Permian Saale Basin (150 km x 90 km). The Rotliegend basin fillings of that area are lithostratigraphically subdivided into the Halle, Hornburg and the Eisleben Formation (Ehling & Gebhardt 2012). Whereas the Unterrotliegend (pre-Illawarra) Halle Formation (»300 Ma to »285 Ma) comprises volcanic intrusions, lava flows and volcanic tuffs hosted in clastic greyish and reddish sediments, the Hornburg Formation represents a postvolcanic stage of basin development (Ehling & Gebhardt 2012). Due to erosion, faulting and a lack of absolute and relative age dating requirements the exact age of the base of the Hornburg Formation is still uncertain. Magnetostratigraphy revealed a lower Oberrotliegend II syn- to post-Illawarra age for the lower cycle (Menning et al. 1988). Lithostratigraphical correlations with sediments of the Northern German Depression lead also to the post-Illawarra-Oberrotliegend (Oberrotliegend II, Gebhardt & Lützner 2012). The top of the upper cycle is overlain by an unconformably bedded conglomerate of the Eisleben Formation which further includes reddish fanglomerates and sand- and siltstones interpreted as marginal deposits of the Northern German depression. The top of the Eisleben Formation is associated with the end of the Oberrotliegend II, which is followed by the deposits of the marine Zechstein transgressions (»257 Ma, Ehling & Gebhardt 2012).

Hornburg Formation: The Middle Permian syn- to post-Illawarra Hornburg Formation is located a few kilometers southern of the town of Eisleben (Saxony-Anhalt). It was deposited in a small playa basin south of and transitional to the mega-playa system of the Southern Permian Basin. The outcrops of the Hornburg Formation are an exceptional window into the continental environment and biota of the Euramerican mid-Permian northern trade wind zone. Sedimentary and paleontological features are indicative for the semi-arid to arid dry red beds that are in contrast to the Late Carboniferous - Early Permian wet red-beds of the study area (Schneider et al. 2006, Ehling & Gebhardt 2012).

At the Hornburg anticline, the Hornburg Formation consists of two fining-up mega-cycles, which contain six lithofacies members (Mb) (Hoyningen-Huene 1960, Falk 2014, 2016, 2018). The lower cycle starts with (1) the Unteres Quarzit Konglomerat Mb and is followed by (2) the Blankenheim Sandstein Mb. The upper cycle comprises in ascending order (3) the Oberes Quarzit Konglomerat Mb, (4) the Rundkörniger Sandstein Mb, (5) the Feinkörniger Sandstein Mb, and (6) the Blätterton Mb.

The members forming a complete fan and playa system with its biota which is rarely preserved in the Permian of Europe. The playa basin is filled with conglomerates and sandstones of an alluvial fan to braid plain system (members 1-3), laterally and vertically followed by braid plain and evaporitic sand flat deposits (members 4 and 5) (Fig. 23). Aeolian transport is indicated by bimodal coarse to fine grained sandstones outcropping at the Wickenberg site (in the north of Hornburg) and by well-sorted, fine- to medium-grained fluvial reworked and redeposited aeolian sandstones, which were formerly quarried in the abandoned Konberg Quarry (to the north of Rothenschirmbach, Fig. 22D, E). They are overlain by fossiliferous lacustrine laminated silty claystones, pure claystones and intercalated channel sandstones of up to a thickness of 10 cm (member 6). Those playa lake successions partly outcrop in the Konberg Quarry, too (Fig. 21A, Fig. 22A-C).

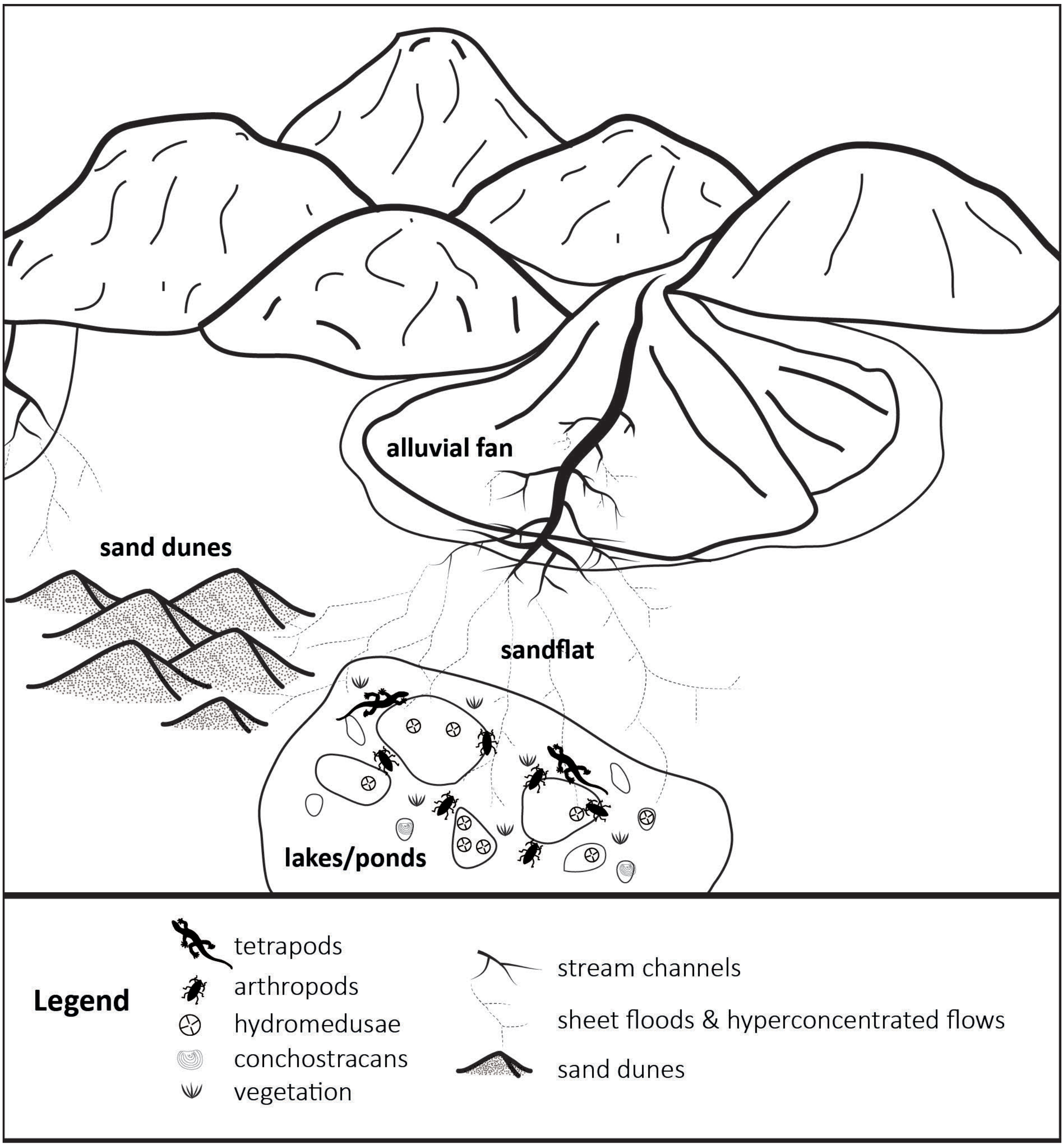

Fig. 23. Reconstruction of Hornburg Formation palaeoenvironment.

The **Konberg Quarry** site reveals a fine to medium and angular grained quartz sandstone of several meters thickness (Feinkörniger Sandstein Mb). The centimeter- to 10-centimeter-thick, homogeneous beds are mainly horizontally bedded, but rarely show trough crossbedding. Local occurrences of wavy sediment and convolute bedding indicate deformation due to slumping. The sandstone beds are fossil-free and represent fluvial redeposited aeolian sediments (Fig. 21A, Fig. 22A, D, E).

The sandstone is overlain by an alternating succession of bedded sandstones and laminated claystones (Blätterton Mb). Both units are highly ichnofossiliferous (see below, Fig. 21B-H). The lacustrine claystones represent lake and pond slack water deposits, whereas the intercalated, well-sorted, fine grained horizons of quartz sandstone indicate conditions of the higher flow regimes (flash floods). Sometimes, these beds show ripple marks on the upper surface as well as load casts and hyporeliefs of desiccation cracks on the lower surface. Halite pseudomorphs may be common on mudstone surfaces. Furthermore, residual horizons point to temporarily hypersaline conditions. A curiosity is displayed by clastic dykes (desiccation crack fillings) with more than 2 meters in length crosscutting several clay and silt stone horizons (Falk 2014, Schneider & Gebhardt 1993).

Fossil finds: Plant remains are extremely rare and only represented by one cone of a conifere. Ichnofossils have only been found in the Blätterton Mb (Fig. 21B-H, Fig. 22A). Tetrapod tracks, tetrapod scratch marks/swimming traces (Fig. 21H), local mass occurrences of imprints of jellyfish (Fig. 1E, F) as well as arthropod trackways (Fig. 21B-D) were excavated during systematic study of different profiles including the site "Konberg Ost". Rarely, conchostracan shell imprints were found (Fig. 1G). The investigation was focused on the relation between sedimentology and track preservation as well as on biostratigraphy (Falk 2014). Poorly preserved and undetermined small tetrapod tracks (up to four cm in length and width) are embedded in mud- to siltstone layers. Tracks and swimming trails of tetrapods as e.g. *Dromopus* (Geinitz 1861) and cf. *Amphisauropus* (Geinitz & Deichmüller 1882) are preserved at the bottom of the small intercalated fluvial channels and in lacustrine claystone, too.

Circular-shaped imprints (2 to 10 mm in diameter) are assigned to jellyfish *Medusina limnica* Müller 1978. Traces of hydromedusa and microbial mats are most common and indicative for dry lake and pond deposits. Conchostracan shell imprints belong to *Pseudestheria graciliformis* Martens 1983. They were excavated from restricted single fine silt- and claystone beds.

Locally, mass occurrences of arthropod (mainly insect) tracks are associated with claystones, fluvial siltstones and silty sandstones. After Walter (1983), the following genera are known: *Lineatichnus, Multipodichnus, Acripes, Euproopichnus, Heteropodichnus, Permichnium, Lithographus*, *Secundumichnus, Heterotripodichnus, Etterwindichnus, Tarsichnus, Striatichnium, ?Tripodichnus, ?Taslerella* and *Avolatichnus*. They include up to 21 different arthropod ichnospecies described by Walter 1983, which reveal trackways, landing traces from flying invertebrates ("Volichnia") and potential invertebrate swimming traces ("Natichnia"). Neither traces of burrowing organisms nor body fossils were found. Considering all ichnological observations taken together, the biota can be referred to a new type of ichnofacies which is in many aspects similar to the *Scoyenia* ichnofacies, but under much drier climatic conditions and without appearance of *Scoyenia* itself.

Stop 9: Solvay Quarry in Bernburg

Location: In the western part of the Solvay Quarry, where the Wesling Mineralstoffe GmbH has its production area, yellowish strata of the Middle Muschelkalk are exposed and form the top of bedrock. This area is accessible from the west via Federal Street (Bundesstraße) B 71.

GPS: 51°49'11.9"N 11°43'23.7"E

Features to be seen:

1. Stratigraphic section through shallow marine and coastal deposits of the Germanic Basin, ranging from the Upper Wellenkalk Member of the Lower Muschelkalk to the lower part of the Middle Muschelkalk (Fig.24A).
2. Mud crack horizons within laminated marlstones of the Middle Muschelkalk (Fig. 24B) with limulid tracks of *Kouphichnium*, invertebrate burrows, tetrapod scratches, and the tetrapod footprint ichnogenera *Rhynchosauroides* and *Procolophonichnium* (Fig. 25).

Fig. 24: Muschelkalk sediments exposed in the western part of the Solvay Quarry: A, the display part of the succession ranges from the Upper Wellenkalk Member of the Lower Muschelkalk (Jena Formation) to the yellowish Middle Muschelkalk beds (Karlstadt Formation) with the harder Schaumkalk limestone beds in the middle. B, Excavation site in Middle Muschelkalk layers exposed on the bedrock surface; the track-bearing horizons usually display a pattern of polygonal mudcracks.

Fig. 25: Examples for *Rhynchosauroides* and *Procolophonichnium* tracks on laminite slabs from the Middle Muschelkalk of Bernburg. A, Slab with manus and pes imprints of *Rhynchosauroides* and several couples of small *Procolophonichnium* footprints. B, *Rhynchosauroides* manus imprint with scalation pattern preserved as shallow relief.

Geology/Ichnology: The Solvay Quarry represents one of 14 (mostly in Anisian age) tetrapod track localities in Saxony-Anhalt listed by Diedrich & Trostheide (2007), six of whom lie in the Subhercynian Basin in central Saxony-Anhalt. These localities cover a succession of limestones, marlstones and dolomites, reaching from the Upper Buntsandstein through the Middle Muschelkalk. It was deposited in a subtidal to supratidal environment and includes several distinct layers with tracks, most of them represent biolaminites. In Bernburg twelve track horizons have been documented within the Middle Muschelkalk (Diedrich 2011). Five of these horizons, which lie in close succession, are still exposed just below the bedrock surface and can be accessed from the western (Wesling) quarry entrance.

The ichnofossil horizons are usually structured by mudcrack polygons and display only very shallow footprint reliefs. However, in some layers preservation of scalation patterns on digit traces and heel pads are common. The Bernburg tetrapod track record is dominated by *Rhynchosauroides tirolicus* and (to a lesser degree) *Procolophonichnium haarmuehlensis*, whereas chirotheriid archosaur tracks occur more rarely, even if several long trackways have been documented. Diedrich & Trostheide (2007) considered this pattern as indicative for a *Rhynchosauroides*-dominated tidal flat ichnocoenosis, which they distinguished from a more continental *Chirotherium*-dominated ichnocoenosis that occurred along the outer margins of the Germanic Basin. Tanystropheid archosauromorphs are suggested to be likely producers of the *Rhynchosauroides* tracks, whereas *Procolophonichnium* can be attributed to therapsids or parareptiles.

In terms of abundance and quality of the tracks, the Solvay Quarry turned out to be the most important locality in Saxony-Anhalt. It represents one of the few Triassic tracksites that exposed very long trackways of *Chirotherium barthii*, *Isochirotherium herculis* and *Rhynchosauroides*, including dozens of step cycles, which were documented in detail before they were finally collected. Some material discovered during original exploration work between 2006 and 2007 is now stored in the Museum für Naturkunde Magdeburg. The longest and most complete trackways were discovered during the later extensive excavations of the Landesmuseum für Vorgeschichte Halle led by C. G. Diedrich and are now part of the Landesmuseum collections. Apart from tetrapod tracks this quarry also yielded an extensive record of long *Kouphichnium* trackways produced by limulids. Furthermore, nothosaur and hybodont skeletal remains have been found in association with the tracks.

Day 3 – Sunday, 29th September 2019

Stop 10: Mammendorf Quarry

Location: This andesite quarry is located about 10 km to the northwest of the city of Magdeburg between Mammendorf and Irxleben (Hohe Börde community), where the Flechtingen-Rosslau block becomes visible as an elevation (Flechtingen High). In the Flechtingen-Rosslau block greywackes and quartzites of the Rhenohercynian basement are unconformably overlain by post-Variscan volcanic and subvolcanic rocks and by sedimentary rocks of the Southern Permian Basin. The quarry is run by Cronenberger Steinindustrie (https://www.cronenberger-steinindustrie.de).

GPS: 52°10’34”N 11°26’23”E

Features to be seen:
1. Sedimentary successions of (a) Lower Rotliegend (?Eiche Member, Flechtingen Formation, Earliest Permian) with abundant tuff horizons and (b) Upper Rotliegend (Elbe Subgroup, late Middle to early Late Permian) including sheet flood deposits of a distal alluvial fan and sand flat deposits (Figs. 26-27).
2. Sedimentary structures, such as desiccation cracks, various ripple types, halite crystal marks, rain droplets. Traces of haloturbation and calcrete formation.
3. Slabs with tetrapod scratches and tetrapod burrowing traces of varying size and shape (Fig. 28C); invertebrate burrows.
4. Examples for tetrapod footprints (cf. *Pachypes*, indet. therapsid tracks) and *Erpetopus* trackway (Fig. 28A-B)

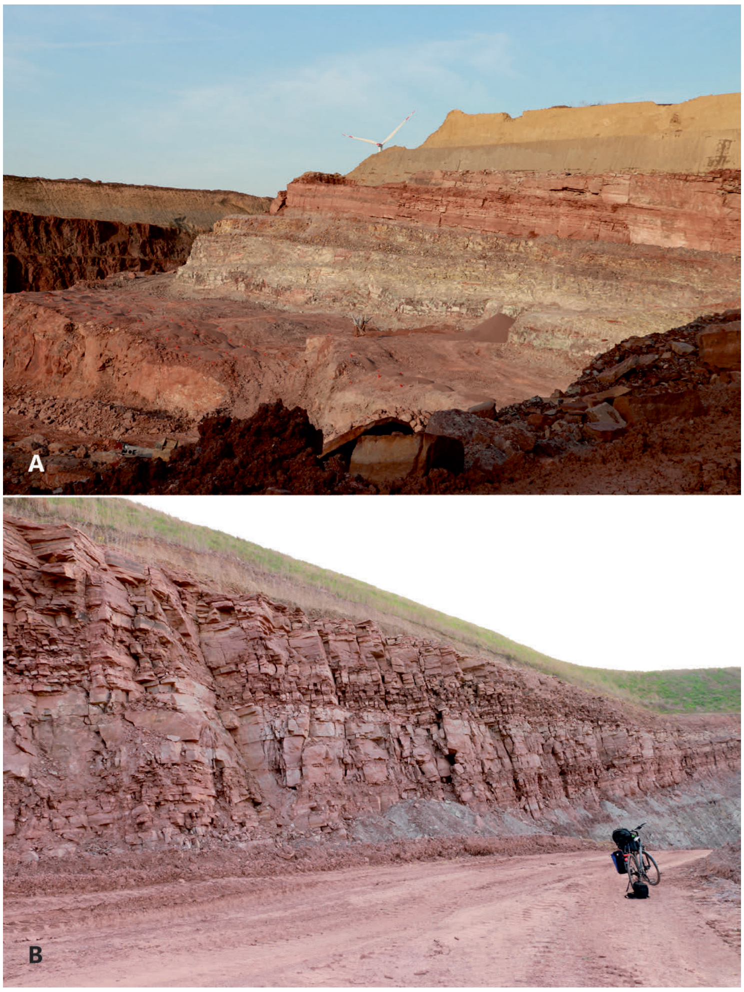

Fig. 26. The Mammendorf Rotliegend succession features light-coloured pyroclastic-rich mudstones of the Lower Rotliegend (Eiche Member, Flechtingen Formation) that are unconformably overlain by mostly red-coloured conglomerates and sandstones of the Upper Rotliegend II.

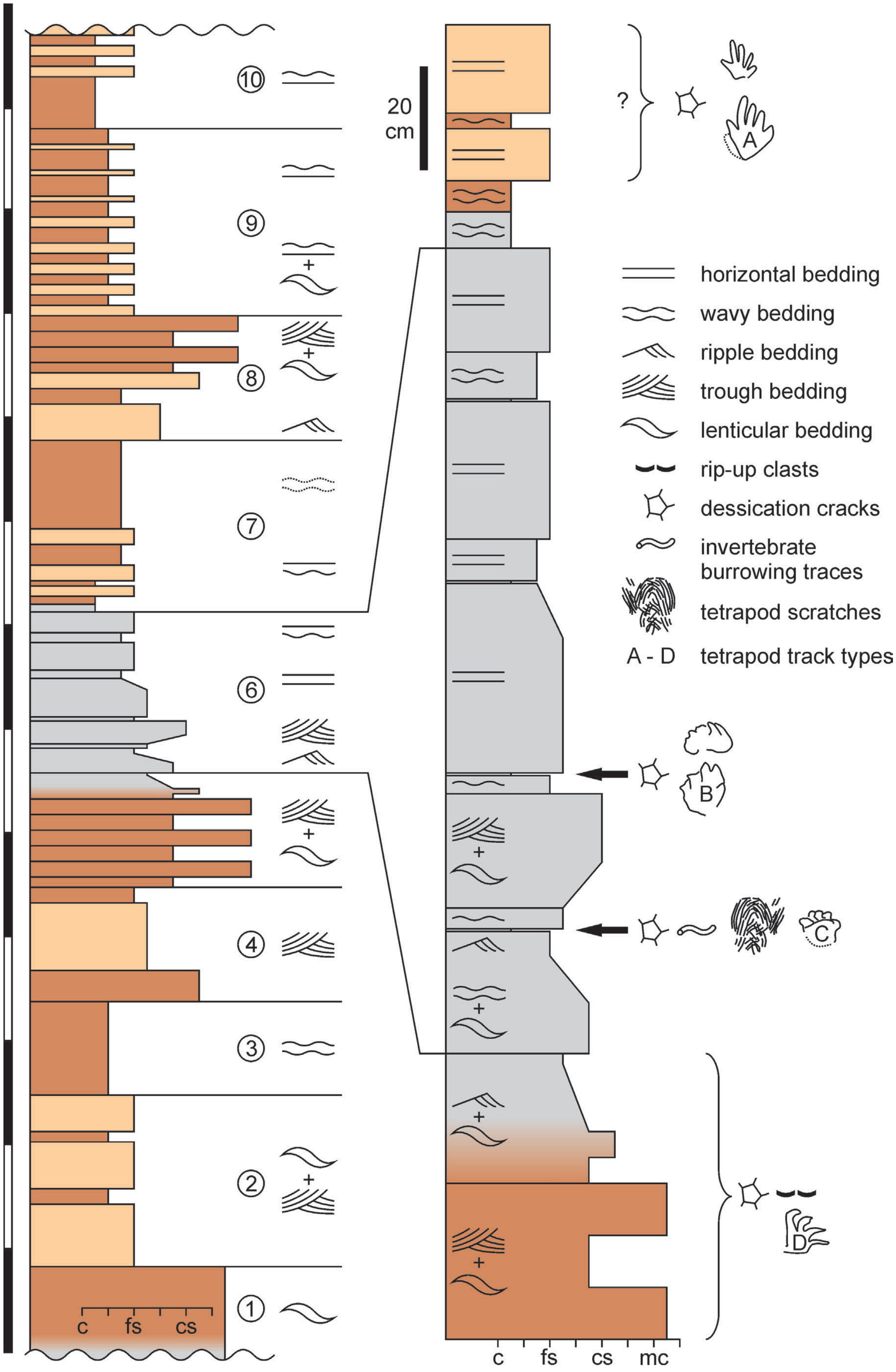

Fig. 27. Simplified stratigraphic section for 2016 excavation site at the southeastern end of Mammendorf Quarry. Tetrapod tracks: A, cf. *Procolophonichnium*, B, cf. *Pachypes*, C, indeterminate therapsid tracks, D, *Erpetopus* isp.

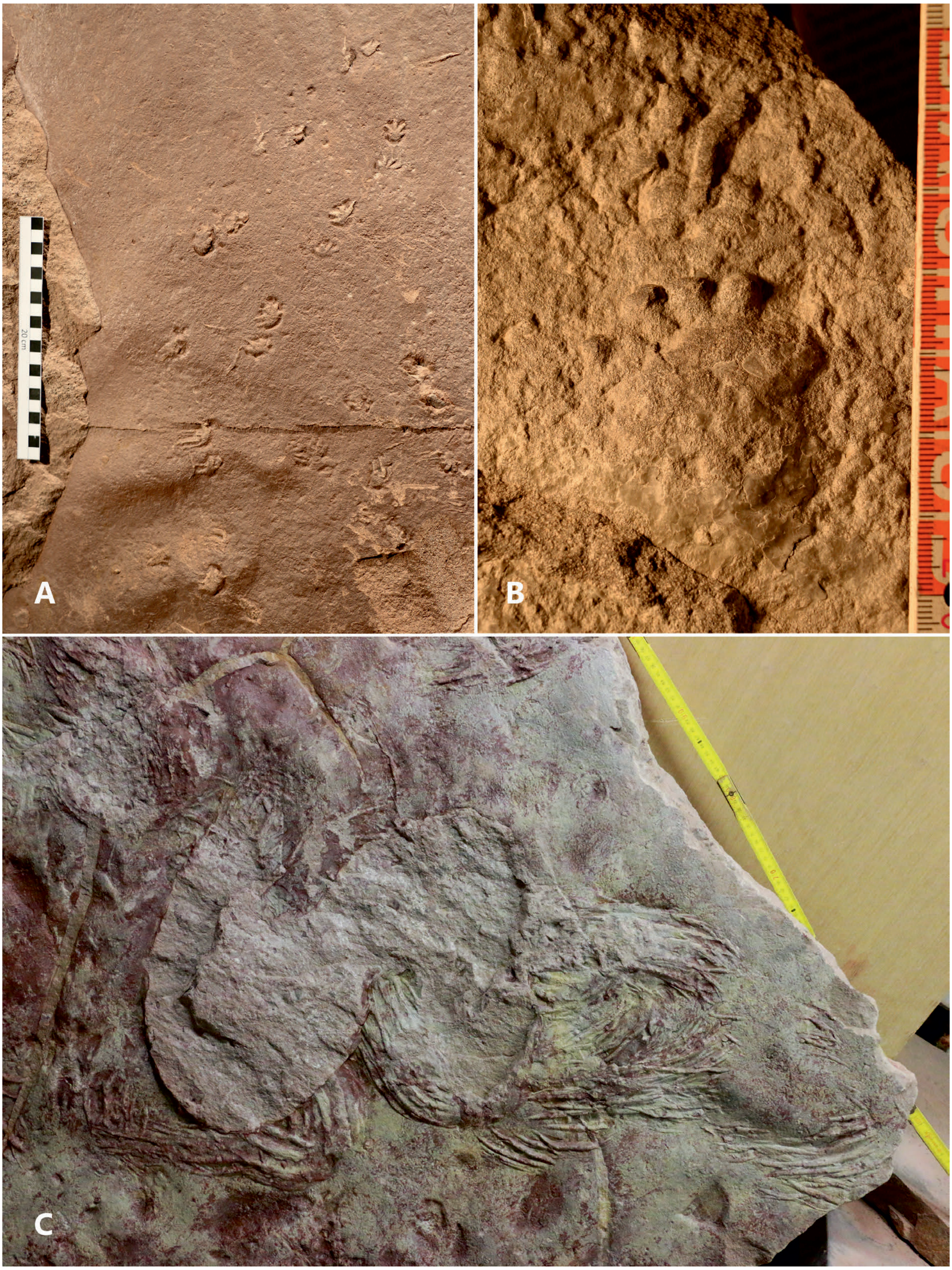

Figure 28. Tetrapod trace fossils: A, trackway of *Erpetopus* isp.; B, therapsid footprint couple; C, tetrapod scrabbling traces and distinct outlines of hole-like perforations due to shallow burrowing behavior.

Geology of the Southern Permian Basin*: During the deposition of the Upper Rotliegend succession Mammendorf was located at the southern margin of the **Southern Permian Basin,** which formed as an intracontinental basin in Northern Pangea at palaeolatitudes of 10–15° N. Arid to semi-arid conditions prevailed, leading to deposition in a desert environment (Glennie, 1972; Roscher & Schneider, 2006). The 1700×600 km large Southern Permian Basin stretched from England over the North Sea and Northern Germany to Poland. Approximately 2500 m thick continental sediments were deposited in the depocentre within a period of 6 to 10 Ma. The general facies distribution reveals alluvial deposition at basin margins and a centripetally adjoined belt of dominantly aeolian sediments. In the basin centre a huge saline lake existed (Gast, 1995). The Rotliegend saline lake covered an area of approximately 17,000 km^2 during lake level lowstands, but doubled to quadrupled its size during wet periods (Gebhardt, 1994) and then covered wide areas of northeastern Germany, Schleswig-Holstein and the North Sea. Zechstein transgression terminated the continental Rotliegend deposition. Rotliegend sedimentation was controlled by two main parameters, tectonics and climatic fluctuations. Gebhardt et al. (1991) described the Altmark I to IV tectonic movements. They resulted in a restructuring of the basin and triggered the formation of fining upward successions with coarse clastics (fanglomerate or sandstone) at the base of the Parchim, Mirow, Dethlingen, and Hannover formations. The duration of deposition of each formation can be estimated at 2 to 3 Ma.

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Schneider, J. W., Rössler, R., Werneburg, R., Scholze, F. & Voigt, S. (2014): Part II. The Carboniferous–Permian basins in Saxony, Thuringia, and Saxony-Anhalt of East Germany. In: Schneider, J.W., Oplustil, S. & Scholze, F. (Eds.): CPC-2014 Field Meeting on Carboniferous and Permian Nonmarine–Marine Correlation. July 21st–27th, Freiberg, Germany. Excursion Guide. – Technische Universität Bergakademie Freiberg, Wissenschaftliche Mitteilungen des Institutes für Geologie, 4: 55–121.

Stratigraphic assignment and ichnology: The exact stratigraphic position of the Mammendorf Upper Rotliegend deposits is still unclear – their facial patterns appear to be distinct from those of the nearby Bebertal sites (Hünenküche, Sventesius Quarry) and they are likely to represent either Dethlingen or Hannover Formation and thus have a Capitanian or early Wuchiapingian age. About 50 metres of siliciclastics have been documented in exploration drillings in the SE of the Mammendorf Quarry (Drilling No. 4/12, Luthardt 2013) but only the basalmost 20 meters are exposed along the southwestern quarry wall as of 2019. A 10-m-thick succession of mass flow and sheet flow deposits on a distal alluvial fan, which is marked by three distinct conglomeratic horizons and a stable facies architecture (flow units ranging over hundreds of meters), is overlain by fine sandstones and siltstones of an alluvial plain. The latter are altered by haloturbation and pedogenesis. Tetrapod and invertebrate traces have mainly been found within thin mudstone horizons close to the second conglomerate and adjacent sandstone layers. Apart from invertebrate burrowing traces, paired tetrapod scratches of varying shape (half-oval or elongate/rail-like, bilobate or flat) in transition to hole-like shallow tetrapod burrowing traces (width between 8 and 27 cm) represent the most common type of ichnia. Finds of tetrapod footprints include several slabs with multiple tracks and one longer trackway of *Erpetopus* isp., one other small reptilian track type (cf. *Procolophonichnium*), a few roundish footprints and a trackway which may represent *Pachypes* and paw-like therapsid tracks and short trackways that are most similar to *Dicynodontipus* and *Dolomitipes*. Only one slab with plant root traces has been found; traces of algae mats are more common.

Stop 11: Dinosaurier-Park Münchehagen

Location: Münchehagen, about 50 km west of Hannover, is a popular tourist destination because of its large dinosaur park featuring more than 230 life-sized reconstructions of dinosaurs and other extinct vertebrates. On a 2.5 km circuit trail you can explore the vertebrate evolution throughout the Phanerozoic. The park was created around an old quarry – now protected as a National Monument – yielding the only Lower Cretaceous sauropod tracks found in Germany. Since 2004, the active Wesling Quarry adjacent to the Dinosaurier-Park Münchehagen has produced further track-bearing levels in Berriasian strata.

GPS: 52°26'32.4"N 9°11'58.6"E

Features to be seen:
1. Several trackways of sauropods, ornithopods and theropods that occur in silty mudstones and sandstones of the Early Cretaceous (Berriasian) Bückeberg Formation. Many tracks are excellently preserved as concave epireliefs and/or natural casts. Among recently excavated dinosaur tracks are least eight trackways of theropod dinosaurs with a total of >100 footprints.
2. Late Jurassic (Kimmeridgian) dinosaur tracks and other fossils from Langenberg Quarry near Goslar.

Fig. 29. The Dinosaurier-Park Münchehagen: A variety of life size reconstructions of Meszoic vertebrates surrounds the hall built for the protection of the sauropod trackways.

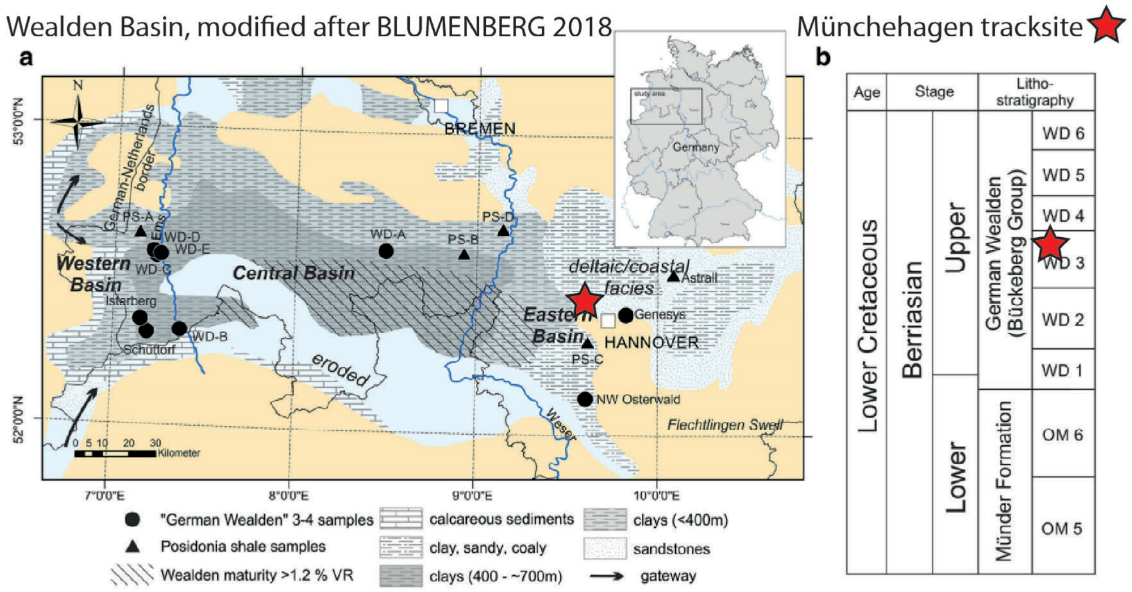
Stratigraphy: The Münchehagen tracksite is located on the southwestern flank of the Rehburg Mountains/Rehburg anticline about 50 km west of Hannover. Although the Berriasian (approx. 145-140 Ma) clastic sediment successions of Lower Saxony are mainly covered by Cenozoic sediments, several outcrops unveil Mesozoic era sediments along the flanks of the Rehburg anticline (Jordan 1979). Geological uplift took place by basin inversions, revealing the buried Jurassic and Cretaceous sediments. The uplift processes were triggered by local halotectonics of Permian evaporites since the Late Cretaceous. Erosion of Jurassic marls and mudstones uncovered the underlying Cretaceous clastic successions. The exposed, more weathering-resistant sandstones are quarried since medieval times and still unveil palaeontological treasures (Jordan 1979, Wings et al. 2012, Wings et al. 2016). Stratigraphically, the strata of the Münchehagen quarries belong to the Obernkirchen Sandstone which is a sub-unit of the Bückeberg Formation (= 'German Wealden', Fig. 29A; Hornung et al. 2012). Palaeogeographically, the Münchehagen site is situated in the Eastern Lower Saxony Basin (Fig. 30A), the southern part of the North German Basin (Fischer 1998, Blumenberg 2019).

Fig. 30. A. Sauropod trackways in the protection hall of the Old Wesling Quarry. B. Tridactyl theropod and ornithopod tracks during excavation in the New Wesling Quarry in 2011. C. The New Wesling Quarry with the excavation site in 2011.

The Obernkirchen Sandstone has an age between 142 and 138 Ma (Hornung & Böhme, 2012). The clastic sediments were part of a prograding delta system of a large river which probably matured the sand grains in the Münchehagen and especially in the Obernkirchen sandstones (Pelzer, 1998; Hornung & Böhme, 2012). Formation of barrier systems was facilitated by landward transport of sand during storm events, and possibly also by longshore currents (Pelzer, 1998).

The Natural Monument 'Saurierfährten Münchehagen' includes large sauropod dinosaur tracks, which were discovered in the 1970s at the so-called "Old Wesling-Quarry" (Figs. 29A, 31F). After protection as a Natural Monument by the Federal State of Lower Saxony during the following years, continuing dinosaur track research has been successfully associated with public outreach. The Dinosaur Park Münchehagen opened in the early 1990s for the public and displays real-sized dinosaur and other prehistoric animal models as well as the original sauropod tracksite ("National Geotope", Fig. 29A). Excellently preserved tridactyl iguanodontid and 'allosauroid' trackways were discovered in the active Wesling-Quarry adjacent to the Dinosaurier-Park in 2004 and subsequently excavated since then (Figs. 29B, 31E).

A



B Legend (Profile Documentation)

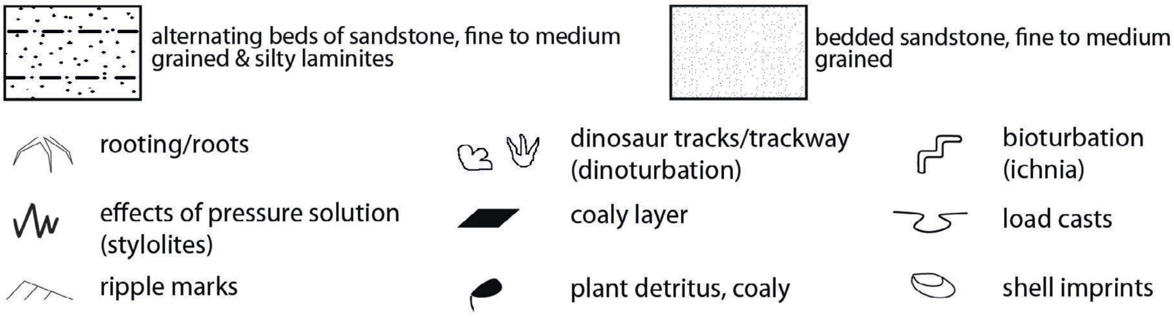


Fig. 31. Palaeogeographic and stratigraphic position of the Münchehagen tracksite (A) and legend for the sedimentary log (B) that is displayed in Fig. 32.

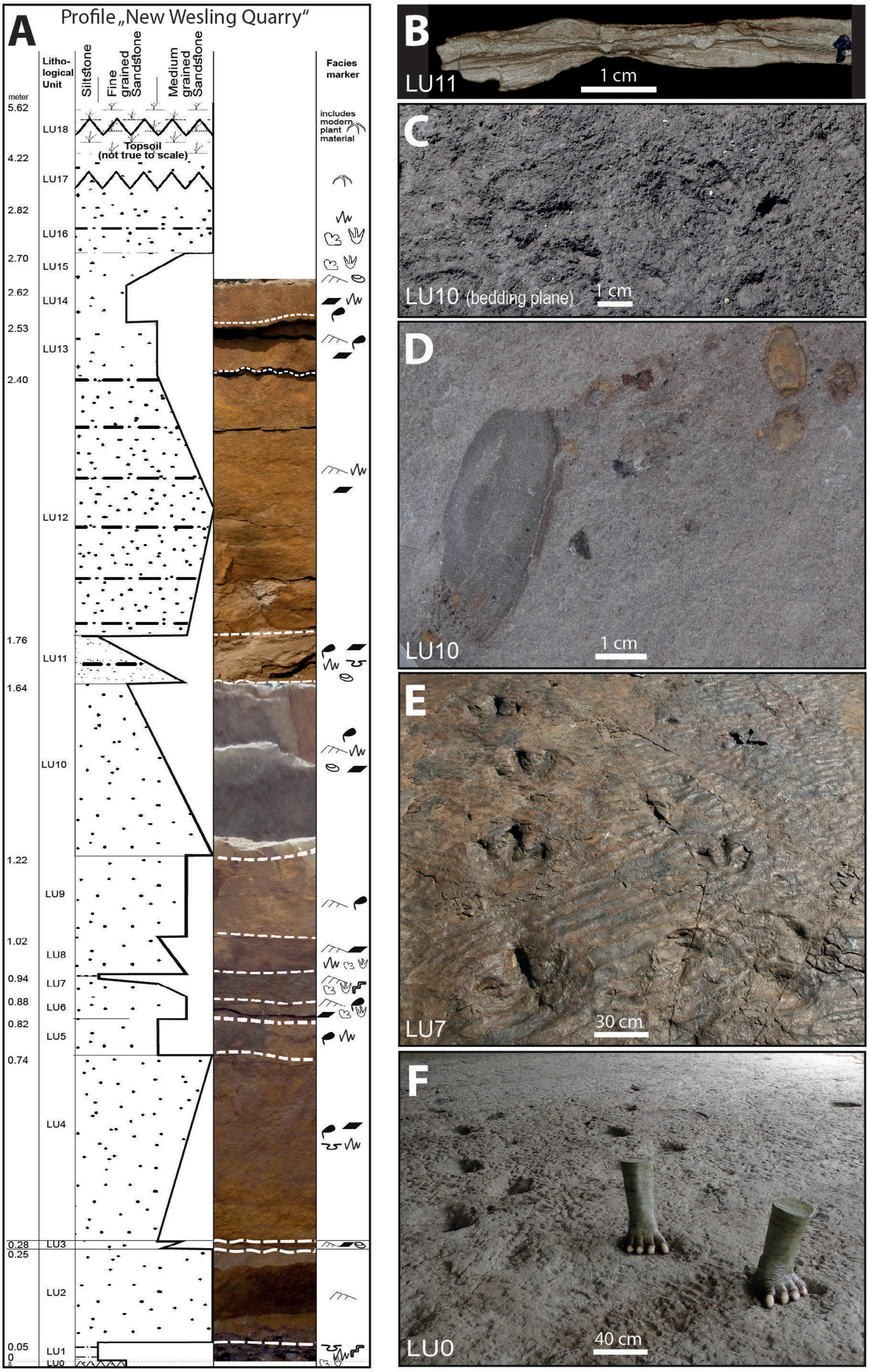


Fig. 32. Lithostratigraphic profile (A) and ichnofossils (B-F) of the active Wesling Quarry.

The Wesling Quarry is still active, producing brownish to yellow-grey sandstones as working stones and road gravel (Fig. 30C). Both Wesling Quarries yield predominantly fine- to medium-grained quartz sandstones which are siliceously cemented (Fig. 32A, D). True (tridactyl) tracks are embedded in thin mud- to siltstone layers, interpreted as slack water deposits. Undertracks are preserved in fine-grained sandstones, indicating higher flow regimes. In addition to dinosaur bioturbation, invertebrate bioturbation occurs in some beds. The sandstone beds show colorful dark brown-grey dissolution sutures/cracks, and bioturbation by invertebrates and dinosaurs. Ripple marks are often present on bedding planes and may show a rough jagged surface (Figs. 30A, B, 32A, E, F). Some bedding planes have drainage structures and/or are partially covered with coaly layers, which often coincide with pressure dissolution sutures (Fig. 32A, C). Inhomogenously embedded coal particles from mainly terrestrial plant detritus are very common. Chemical (dis)coloration ('Liesegang rings') was probably caused by organic carbon and/or mineral ions. Small (1–3 cm) oval impressions are interpreted as bivalve shell imprints (Fig. 32A, D; Wings et al. 2012).

The exposed geological profile of the active Wesling Quarry has a total thickness of 5.62 m (Figs. 31B, 32A). Individual beds can be traced on a centimetre to decimetre scale but are often laterally variable (Wings et al. 2012).

Sauropod trackways, as part of the natural monument, and invertebrate bioturbation are common at the quarry base (LU0, Fig. 31F). In the upper part of LU7, the sandstone is overlain from a layered 0.5–2 cm thick silty mudstone. True iguanodontid and theropod tracks are embedded in that silty mudstone layer, which contains the best-preserved tracks in the profile (Fig. 30 B, 32E, Wings et al. 2012). Drag marks, probably made by drifted plant remains, occur rarely. LU6 and LU5 reveal the clearly visible undertracks of the LU7-footprints. Furthermore, extensive dinoturbation occurs in LU8, LU15 and LU16 on thin silty layers on top of medium-grained sandstone beds.

Siltstone and mudstone layers or beds represent slack water deposits whereas sandstone beds indicating temporarily higher flowing regimes (e.g. storm events) (Schwennicke 1998, Wings et al. 2012). Small-scale wave ripple marks occur on many bedding planes and were generated by an unidirectional undulating consistent water flow (foreset laminae) in shallow water offshore areas with a temporary influence of currents. The minimal water depth has been calculated within the range of 2.7 cm to 5.4 cm, the maximum water depth cannot be determined (Wings et al. 2012, Schwennicke 1998).

The Münchehagen locality is part of the Eastern Lower Saxonian Basin which is dominated by the clastic successions of the German Wealden. The basin is characterized by mainly freshwater conditions and high sediment influx by fluvial-deltaic transport. Based on sedimentology, fossil content and palaeogeography, a distal deltaic realm for the Münchehagen tracksite is assumed (Fig. 31A) (Fischer 1998, Falk 2011, Blumenberg 2019).

Ichnology: Sauropod track impressions (Figs. 30A, 32F) were originally described as '*Rotundichnus muenchehagensis*' (Wright 2005), but lack enough morphological details to be considered diagnostic of any particular type of sauropod or trackway (Wright 2005). They reveal an oval to elongated-oval shape, appearing slightly triangular, with the longest 'peak' pointing backwards. The tip of the triangular oval is the deepest point altogether. The medial sides of the imprints are always deeper, which indicates medial sides bearing more weight. The same applies for the tip of the toes I and II. Even on imprints that show better preservation features, there is still a lack of claw or single toe imprints preservation (Fischer 1998, Wings et al. 2012). Some imprints show ripple marks in their inner floor (Fig. 32F). More than seven sauropod trackways yield at least 256 footprints. Most imprints were discovered not only in the old quarry, but new exposures of the track bearing surface in the "new" Wesling Quarry resulted in additional findings too. The same sandstone bed at the quarry base also produced poorly preserved tridactyl tracks as well as hollow sandstone casts of shark spines.

Most tridactyl imprints were discovered and excavated in the active quarry (Figs. 30 B, C, 32E). These well-preserved imprints have been the basis for several publications (Wings et al. 2005, Wings et al 2012, Lallensack et al. 2016, Wings et al. 2016, Lallensack 2019). The imprints belong to the ichnotaxa *Iguanodontipus* (iguanodontid trackmaker) and *Megalosauripus* ('allosauroid' theropod trackmaker). The wide size ranges indicate subadult and adult individuals for both groups. All tridactyl trackways show bipedal gaits.

Several excavations on different quarry levels revealed more than 150 imprints – more than 100 imprints (three trackways) were exposed on the single bedding plane of LU7 (the so-called Lower Level, Falk et al. 2013). Theropod trackways are crossing iguanodontid trackways. The longest trackway (LU16) comprised 57 consecutive well-preserved and two weakly preserved *Iguanodontipus* imprints (Wings et al. 2012).

Siltstone and mudstone layers yield at least partly horizontal invertebrate burrows (millimetre-scale), which disturbed the fine laminated strata (Fig. 31A). *Thalassinoides* and *Planolites* can be found in such "pre-storm sediments" (Schwennicke 1998). Rough jacked, partly coaly surfaces are often linked to microbial mats, which stabilized the wet sediment and supported the track preservation (Falk et al. 2013). Bivalve imprints due occur in nests (Fig. 31C). The sandstone rarely yields Gingko leaf or horsetail fossils, usually preserved by a thin coaly layer.

Langenberg tracks: Apart from Early Cretaceous tracks of the Obernkirchen Sandstone, the Dinosaurier-Park Münchehagen has also stored and exhibited materials from Langenberg Quarry, a Late Jurassic (late Oxfordian to Kimmeridigian) limestone quarry close to the town of Goslar at the northern margin of the Harz Mountains. Sedimentary rocks exposed in this quarry include limestones and mudstones, which were deposited in a shallow marginal basin of the Late Jurassic Germanic Basin (Fischer 1999, Zuo et al. 2018). The Langenberg locality is well-known for skeletal remains of the dwarfed sauropod *Europasaurus holgeri* and other terrestrial vertebrates, which are thought to have inhabited islands within this part of the Germanic Basin (e.g., Sander et al. 2006, Wings & Sander 2012, Martin et al. 2019). Tridactyl dinosaur tracks has been reported from the upper part of the Langenberg section (bed 93) – about 5 m above the *Europasaurus* horizon. Some of these tracks belong to large theropods and may indicate that the existence of an isolated insular fauna ended due to a sea level decrease that led to the immigration of large carnivores (Lallensack et al. 2015).

Stop 12: Oberkirchen

Location: This locality represents another example for the Berriasian track-bearing sandstones from the Obernkirchen Sandstone unit in the Bückeberg Formation. It was the first site in the region were dinosaur tracks have been found - more than two centuries ago!

GPS: 52°15'36.9"N 9°11'58.9"E

Features to be seen: Obernkirchen Quarry (Fig. 33) is well-known for its moderately to heavily dinoturbated "Chicken Yard" (Fig. 34). This site is characterised by an extraordinary high density of true tracks including several morphotypes and size classes of theropods and ornithopods. Additionally, there is an upper track level in the Obernkirchen Quarry, which has produced mainly iguanodontian tracks (Fig. 35A).

Fig. 33. The Obernkirchen Quarry is also known for its well-sorted quartz sandstones producing high quality workstones.

Ichnology: Apart from abundant tridactyl dinosaur tracks, the Obernkirchen tracksite has produced remarkable didactyl tracks (Fig. 35B) of a new deinonychosaurian ichnotaxon (Richter & Böhme 2016). It is assumed that the exceptional preservation of most tracks is due to microbial mats covering sandy lagoonal flats (Richter et al. 2011).

The "Chicken Yard" (Fig. 34) footprints comprise 424 tridactyl theropod, 55 didactyl deinonychosaurian dinosaur, 196 medium-sized and large iguanodontid ornithopod, and only 20 small possible ornithopod tracks. The tracks appear to represent multiple generations of trackmakers and show no preference in walking direction. Some of the didactyl tracks may be referred to troodontids that had sizes between 3 and 4 m. Some of the ornithopod tracks can be assigned to *Iguanodontipus* isp. The Upper Level of tracks at the northern margin of the Obernkirchen quarry differs from the "Chicken Yard" in its preservation and types of tracks and is more similar to other tracksites of the Oberkirchen Sandstone. The Obernkirchen site has also produced well-preserved impressions of bones in the sandstone, the original bone material dissolved during diagenesis.

Fig. 34. The "Chicken Yard", a heavily dinoturbated sandstone layer.

Furthermore, the Obernkirchen Quarry is known for peculiarly preserved hollow moulds of larger bones such as crocodyliform skulls (Fig. 35C) and turtle shells.

Fig. 35. Vertebrate remains from the Obernkirchen Quarry. A. Typical large tridactyl footprint (?*Iguanodontipus)* from Obernkirchen. B. Well-preserved didactyl track of a ?troodontid producer. C. Natural hollow sandstone mould of the skull of the crocodyliform *Goniopholis*.

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