



Triassic terrestrial tetrapod faunas of the Central European Basin, their stratigraphical distribution, and their palaeoenvironments

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ARTICLE INFO

Keywords:

Triassic
Tetrapod
Footprint
Palaeobiodiversity
Palaeoenvironment
Palaeoecology
Taphonomy
Fossil lagerstätte
Europe

ABSTRACT

Since the early nineteenth century, the Central European Basin (CEB) has been a historically important region for the study of terrestrial tetrapods from the Triassic Period, and continues to yield a wealth of new finds. A review of the fossil evidence permits the recognition of new patterns of diversity for various clades during the recovery period following the end-Permian mass extinction. Unfortunately, the fossil record for tetrapods in the CEB across the Permian–Triassic boundary is virtually non-existent. The lowermost Triassic strata are almost entirely devoid of tetrapod fossils in the CEB, which is in marked contrast with coeval terrestrial deposits in higher-palaeolatitude regions such as South Africa. Temnospondyls were present in many Olenekian horizons and diversified at the beginning of the Anisian, attaining their greatest diversity in the late Ladinian, probably as a response to an increase in available freshwater environments and tolerance of fluctuating salinity in at least some forms. Among amniotes, only procolophonoids have been found in both Olenekian and Anisian strata in Germany, in each instance with two taxa, and they persisted into the late Ladinian. The ichnofaunas tell a rather different (partly complementary) story. Especially in the Olenekian, the poor body fossil record for tetrapods contrasts sharply with the abundance and high diversity of tetrapod ichnofossils, particularly those produced by archosauriform reptiles. Large tetrapod tracks (*Protochirotherium*) suggest that large-bodied archosauriforms were present, but no skeletal remains of such forms have been recovered from known coeval horizons in the CEB to date. Strata of the lower Anisian have recently yielded procolophonids, rhynchosaurs, tanysaurians, a eucrocopodan archosauriform, a ‘sail-backed’ poposauroid pseudosuchian, and a drepanosauriform. For this time interval, the body fossil record (with three temnospondyl and seven amniote taxa) approaches the diversity of the rich tetrapod track record. The differences between Middle and Late Triassic faunas are not as profound as had traditionally been assumed. Whereas there was an almost complete replacement of temnospondyl taxa except for the long-ranging *Gerrothorax pulcherrimus*, the composition of terrestrial amniote assemblages appears to have changed more gradually from the Anisian to the Norian. The Ladinian of southern Germany has yielded a wide range of taxa not otherwise represented in the CEB nor elsewhere. This includes several taxa of lepidosauriforms including a rhynchocephalian, a colognathid, a trilophosaurid, a shell-less stem-turtle, an owenettid and a procolophonid, and four different archosauriform taxa. A recently discovered late Carnian assemblage from the Stuttgart Formation, which is currently under study, includes small diapsids resembling those from the Ladinian. Diverse Early and Late Triassic microvertebrate assemblages have been described from Poland in recent years, and identification of comparable depositional environments elsewhere in the CEB would undoubtedly lead to the discovery of many additional small-sized tetrapod taxa. In summary, the CEB provides an excellent record for studying the evolution of Triassic terrestrial tetrapod faunas along with environmental changes over much of that period.

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<https://doi.org/10.1016/j.earscirev.2025.105085>

Received 31 October 2024; Received in revised form 21 February 2025; Accepted 24 February 2025

Available online 4 March 2025

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1. Introduction

The Triassic was a pivotal period for the evolution and diversification of land vertebrates. It is bracketed by the end-Permian mass extinction event (EPME) and the end-Triassic mass extinction event (ETME). The former is generally considered the greatest extinction event in earth history, especially in the marine realm (see Benton, 2015 for a comprehensive summary) and was most likely triggered by intense volcanism in Siberia (Siberian Traps) (Rampino and Stothers, 1988; Burgess and Bowring, 2015; Dal Corso et al., 2022). This igneous activity caused massive outgassing, which dramatically affected global temperatures and led to extreme temperatures during the earliest Triassic (Sun et al., 2012). The impact of the EPME in the terrestrial realm is difficult to assess and remains contentious (Dal Corso et al., 2022), and some authors have even questioned the synchronicity of the extinctions on land and in the sea (Lucas, 2017; Gastaldo et al., 2020). Among land-dwelling tetrapods, the EPME led to the disappearance of most lineages of the herbivorous dicynodont synapsids and pareiasaurs, and the predatory gorgonopsian synapsids (Benton and Newell, 2014). Other clades of continental tetrapods persisted through this biotic crisis and underwent subsequent diversification, most notably archosauromorph reptiles (Bernardi et al., 2015; Ezcurra and Butler, 2018). Multiple lineages of temnospondyl stem-amphibians similarly not only extended across the Permian–Triassic transition but also greatly increased in diversity during the Early Triassic (Ruta and Benton, 2008).

The Early and early Middle Triassic represented an interval of biotic recovery on land and in the sea. Various tetrapod clades or their respective stem-groups first appeared in the fossil record during this time and/or quickly increased in diversity and geographic distribution (Ezcurra, 2010; Sues and Fraser, 2010; Sues, 2019). Temnospondyls diversified into the small stem-lissamphibians and the predominantly large-bodied stereospondyls, the latter of which became a major component of Triassic terrestrial tetrapod assemblages (Schoch and Milner, 2000, 2014; Schoch and Moreno, 2024). The ascent of diapsid reptiles contributed to a fundamental change of ecosystems both on land and in the sea (Sues, 2019; Romano et al., 2020). By the Late Triassic, all major clades of saurian reptiles or their respective stem-groups had appeared in the fossil record, including turtles, lepidosaurs, crocodylomorphs, and avemetatarsalians (Ford et al., 2021; Nesbitt et al., 2010, 2017).

The end-Triassic mass extinction event (ETME) is one of the five mass extinctions during the Phanerozoic (Van de Schootbrugge and Wignall, 2016; Cribb et al., 2023). It was probably caused by the formation of the Central Atlantic Magmatic Province (CAMP) (Marzoli et al., 2004). It led to the disappearance of most non-dinosaurian archosauriforms (except for crocodylomorphs), non-mammaliomorph synapsids, various other clades such as drepanosauromorphs and procolophonoids, and most temnospondyls near the end of the Triassic; surprisingly, dinosaurs were apparently not affected by this biotic crisis (Olsen et al., 2002).

A major problem in tracing the recovery of terrestrial tetrapod communities from the EPME in the CEB is the still sparse fossil record of skeletal remains of tetrapods in Lower and lower Middle Triassic strata in contrast with the rich record of their tracks (Haubold, 1971a, 1971b; Klein, 2021; Klein and Lucas, 2021). Moreover, the stratigraphically youngest occurrences of Permian tetrapods in the CEB are early Lopin-gian (Wuchiapingian) in age (Sues, 2020) and thus changes in tetrapod communities across the Permian–Triassic boundary cannot be observed in this region. Finally, the stratigraphic position of the Permo-Triassic boundary in the CEB is controversial. The lithostratigraphic boundary between the two periods in Germany is placed at the base of the earliest Triassic Calvörde Formation and is diachronous (Hug-Diegel, 2020). It is not identical with the chronostratigraphic Permo-Triassic boundary as established by the Global Stratotype Section and Point in marine strata at Meishan (China) (Yin et al., 2001). In palynostratigraphic terms, the lithostratigraphic boundary in the CEB lies in the *Lueckisporites virkkiae* zone, which is generally considered diagnostic for the late Permian

(Kürschner and Hengreen, 2010).

Located at palaeolatitudes between 20° and 25° N at the beginning of the Triassic Period, the CEB (also referred to as Germanic Basin) (Fig. 1) represents the classical region for Triassic stratigraphy and tetrapod assemblages, both from terrestrial and marine environments. Germany has a long tradition in the study of Triassic rocks, being the region where Alberti (1834) first recognised and named the period. Historically, the rocks of this period are divided into three facies units and thus were collectively named Triassic, namely the Buntsandstein, Muschelkalk and Keuper, which are widely used on a European scale (Szurliés, 2005; Franz et al., 2013; Hauschke et al., 2021). These units were first used to differentiate the Lower, Middle and Upper Triassic, respectively, with the Buntsandstein representing arid to semi-arid climatic conditions in terrestrial environments, the Muschelkalk more humid conditions in some predominantly marine settings, and the Keuper, again with terrestrial settings with semi-arid to arid conditions. With the modern understanding of stratigraphy, basin analyses, and stratigraphic correlations on a large scale, it is now known that each of these facies types are diachronous.

Triassic tetrapods from the CEB have been studied for nearly two centuries (Jaeger, 1828; Meyer, 1832). Many terrestrial groups – among them temnospondyl stem-amphibians, phytosaurs, aetosaurs, and stem-turtles – were first identified here (Münster, 1836; Meyer, 1837, 1847–1855, 1861; Meyer and Plieninger, 1844; E. Fraas, 1889, 1896; Baur, 1887). Intensified collecting efforts in southern Germany in recent decades have produced a wealth of fossils including many new tetrapod taxa, among them some of the first representatives of several major clades globally (Schoch, 2015a, 2015b; Sobral et al., 2020; Sues and Schoch, 2023a; Sues et al., 2024). At the same time, excavations at new sites in Poland and Switzerland have yielded numerous important new discoveries, extending both the geographical and stratigraphical ranges of known tetrapod taxa (Szczygielski and Sulej, 2016; Scheyer et al., 2022; Czepiński et al., 2023) and adding numerous new taxa (Dzik and Sulej, 2007; Dzik et al., 2008; Sulej et al., 2012; Zahner and Brinkmann, 2019). The CEB is noteworthy for providing an extensive record of tetrapod evolution throughout the Triassic Period along with evidence for environmental changes, especially those related to climatic changes and sea-level fluctuations.

All in all, this extensive fossil record shows that the CEB represents an important palaeogeographic region for understanding the evolution of continental tetrapod communities during the Triassic. Here we review the diversity, stratigraphical distribution, and palaeoecological context for assemblages of Triassic non-marine tetrapods in the CEB. For a more comprehensive overview of these assemblages, we integrate both the osteological and ichnological records. We trace and analyse their changes throughout the Triassic Period, especially those related to palaeoenvironments.

2. Material and methods

This work is intended as a comprehensive overview of the Triassic terrestrial tetrapods from the CEB by analysing the development of their diversity associated with their palaeoenvironments and habitats. First, we documented tetrapod occurrences (Figs. 2, 3; Tables S1, S2) based on both the skeletal and the track records, from the existing literature, as well as our own first-hand examinations of tetrapod fossils from localities in the CEB. We provide an exhaustive list and brief descriptions of all tetrapod faunal and ichnofaunal associations at the species and ichnospecies level, respectively, from all known localities in present-day Germany, Poland, northeastern France, the Netherlands, Switzerland and Austria. It is important to note that the extent and borders of the CEB changed throughout the Triassic. Hauschke et al. (2021) provided an overview of the geological history of this basin, including neighbouring countries as well as southeastern England. Sites in northeastern France and Luxembourg have also yielded important Norian and Rhaetian tetrapod assemblages, but these are part of the Paris Basin, which by the

middle Carnian became a separate basin from the CEB (Bourquin et al., 2006; Schintgen and Förster, 2013).

All tetrapod occurrences are located in their corresponding geological units mainly following the official lithostratigraphical divisions defined by the Deutsche Stratigraphische Kommission (Deutsche

Stratigraphische Kommission, 2005; www.stratigraphie.de) and the coeval stratigraphical units of the CEB outside Germany (Hauschke et al., 2021; see also references throughout the text). In addition, in the corresponding sections, we also note the various historical and local names for individual formations, other subunits, and localities –

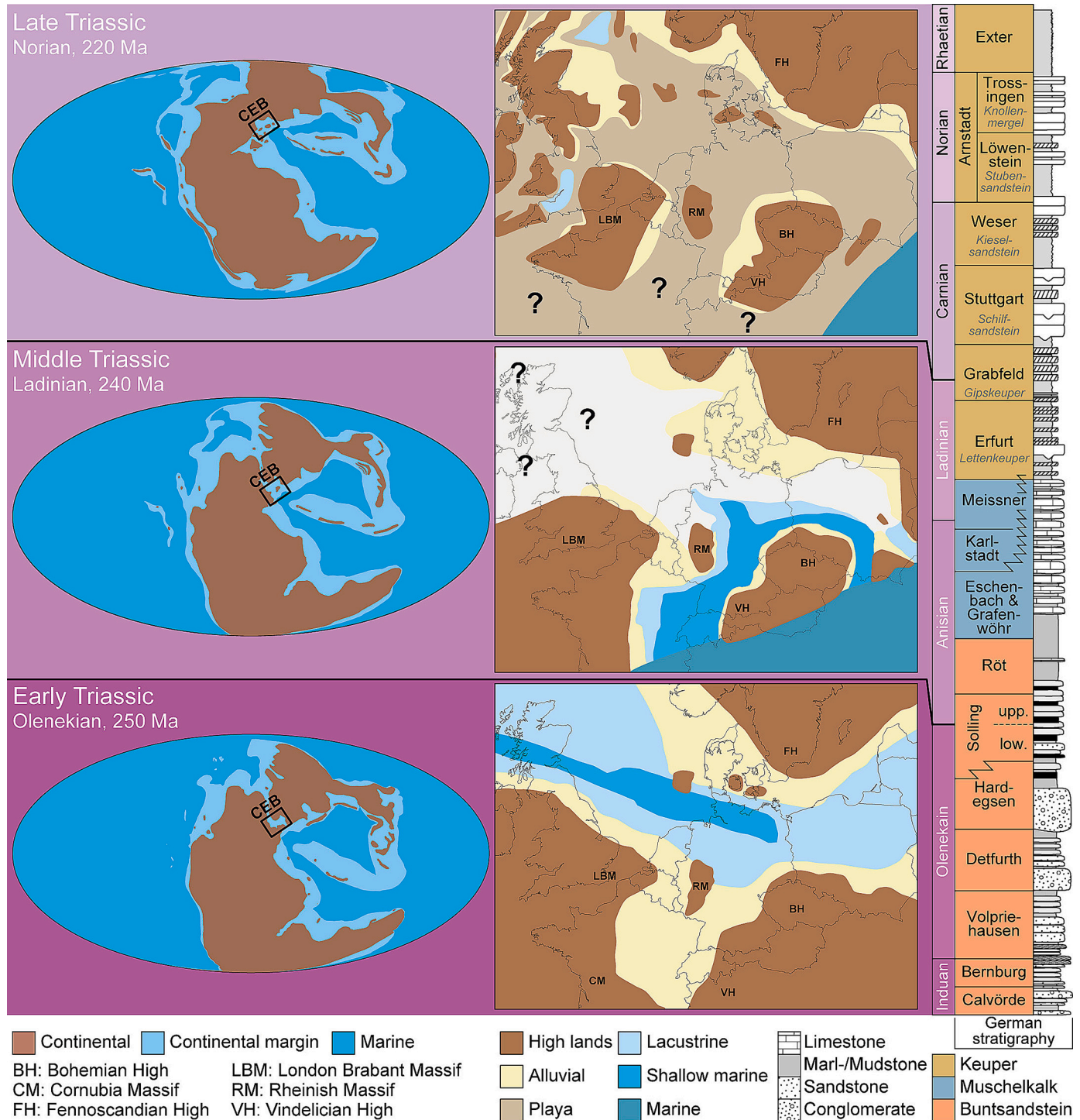
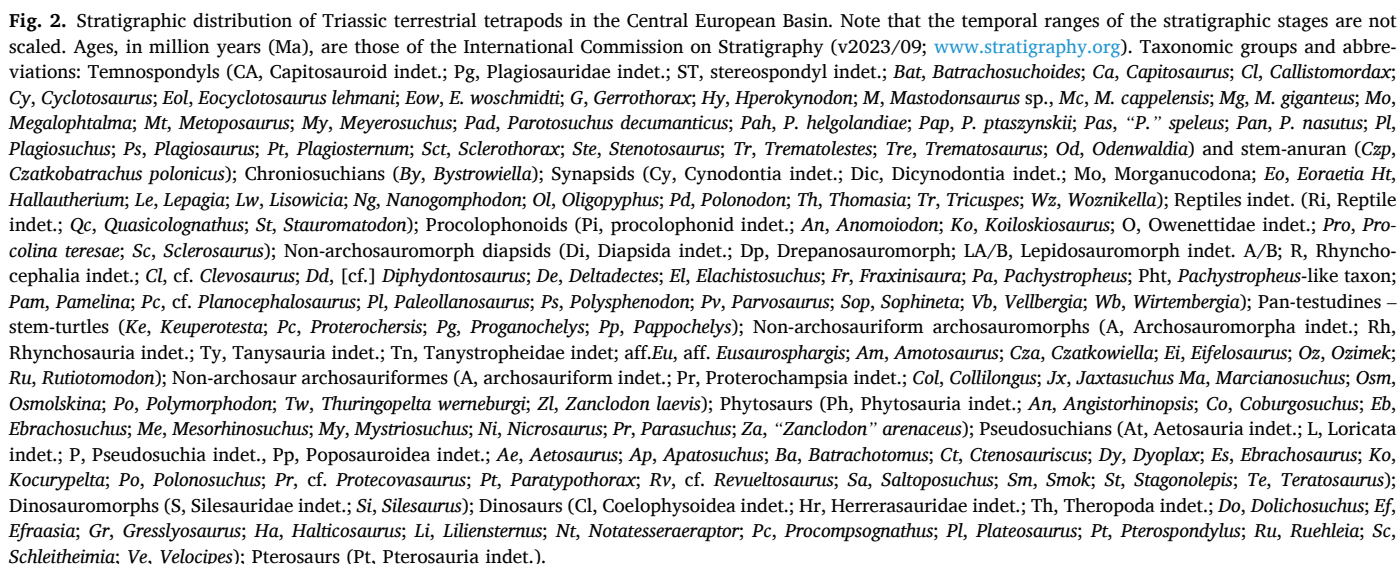


Fig. 1. Palaeogeography of the Triassic of Pangaea and the Central European Basin (CEB), and stratigraphy of the German Triassic. Maps of Pangaea (on the left) from Kocsis and Scotese (2021); the area including the CEB (maps in the middle) is marked with a black square. Maps of the CEB redrawn from: Olenekian, Geluk (2005), Augustsson et al. (2018) and Käsböhrer et al. (2021); Ladinian, Pöppelreiter and Aigner (2008); Norian, Deutsche Stratigraphische Kommission (2005) and McKie and Williams (2009). Note that the CEB maps are rotated to the orientation of present-day Europe (coastline and administrative borders in black line), the palaeo-North is approximately toward the top right corner in each map. On the right, general stratigraphic profile of the Triassic of Germany (modified from Schoch and Moreno, 2024), with the main formations preserving tetrapod fossils; note that stratigraphic or tectonic contacts between formations (e.g., unconformities, hiatuses) are not represented. The temporal ranges of the stratigraphic stages are not scaled (see also Figs. 2, 3).



The palaeoenvironments of each geological unit reviewed here are also reported. We primarily follow the nomenclature summarised in [Hauschke et al. \(2021\)](#) for the principal stratigraphic units in the CEB and additional literature cited throughout the text for more specific interpretations of some localities and/or (sub)units. This results in four

major palaeoenvironmental categories that include all geological units: fluviodeltaic, alluvial plain, playa/sabkha, and coastal/shallow-water marine. We also defined more detailed depositional settings (fluvial, floodplain, lacustrine [including large – $>10\text{ km}^2$ – and small lakes; Behrensmeier and Hook, 1992], coastal, and marine) within the major palaeoenvironmental categories, which correspond to the potential habitats of the tetrapod taxa (based on the skeletal record) here documented. Inferences concerning the habitat preferences of each taxon in each unit are based on the published literature as well as our own palaeoecological interpretations. Those taxa with uncertain ecological preferences and/or absent in their inferred habitat are considered allochthonous.

Classifications of palaeoenvironments and habitat preferences are the base for the descriptive statistical analyses that we carried out following the methodology of De Jaime-Soguero et al. (2021). Tetrapod occurrences of each major taxonomic group (osteological record) and each ichnogenus/morphotype (ichnological record) in each geological unit are scored as present (1) or absent (0), regardless of the absolute number of (ichno)species and specimens known from each unit. Then geological units are grouped at the epoch level (Early, Middle, and Late Triassic), and classified according to their corresponding palaeoenvironments. This generates a picture of the general palaeoenvironmental distribution of tetrapod groups based on both the body fossil and track record. In addition, the inferred habitat preferences of each taxon (based on the skeletal record) are scored in the same way. This allows for comparisons of the actual palaeoenvironmental distribution of tetrapod faunas with their inferred palaeoecology, and the grouping in epochs shows potential faunal and environmental changes throughout the Triassic.

For discussions of tetrapod diversity, species are classified in major taxonomic groups that have been defined phylogenetically (Fig. 2). Tetrapod groups that are generally considered marine are excluded from our analysis. These include sauropterygians, ichthyopterygians, some tanysaurians, and possible thalattosaurs.

Analogous to the skeletal remains, tetrapod track morphotypes are classified at the level of ichnogenus, identifying ichnospecies whenever possible. Track morphotypes that cannot be assigned to any ichnogenus but that are relevant for both diversity and palaeoenvironmental analyses are also reported; they mainly include swimming traces (for which the trackmaker can be inferred in some cases) and other tracks confidently referable to taxonomic groups (e.g., crocodylomorphs or dinosaurs) but not well preserved enough to be assigned to known ichnogenus. Trackmakers are identified primarily following Klein and Lucas (2021) as well as the literature cited throughout the text. In the instances in which producers are still contentious, we employed a synapomorphy-based approach (e.g., Carrano and Wilson, 2001). Such correlations of track to trackmaker allow for a comparison of the ichnological record with the taxonomic groups known from the skeletal record (Figs. 2, 3). As a result, it is possible to get a more complete overview of tetrapod diversity.

3. Tetrapod faunas and ichnofaunas

3.1. Bernburg Formation (Lower Buntsandstein Subgroup)

The largely unfossiliferous Bernburg Formation, the upper unit within the Lower Buntsandstein Subgroup, is Induan in age. It encompasses both aeolian and playa lake deposits. In north-central Germany, braided and low-sinuosity channel deposits have been identified on an alluvial plain with aeolian sediments (Bourquin et al., 2007). Paul and Peryt (1985) reported stromatolites and ooids that formed in these lakes, and Leiber (1970) reported spinicaudatans. The playa lakes were shallow but extended over hundreds of square kilometres on the plain at the centre of the basin. The southern and western margins of the CEB were framed by large alluvial fans with common debris flow and sheet-flood structures (Paul, 2021a).

As in the uppermost Zechstein Group and the lowermost Triassic Calvörde Formation, the climate was less arid than earlier in the Zechstein, and episodes of precipitation led to the formation of playa lakes at the centre of CEB (Paul, 2021b). Palaeogeographically, the CEB was located in the arid belt, which extended from 15° N to at least 45° N during the Early Triassic (Kidder and Worsley, 2004). Paul (2021b) documented that the climatic conditions fluctuated with pronounced cyclicity in the CEB throughout the deposition of the Buntsandstein strata.

Tetrapod body fossils. Schoch (2011a) reported a small stereospondyl mandible originally labelled as stemming from the Eck Conglomerate, but this was shown by Nitsch (2024) to be more likely derived from the substantially younger Vogesensandstein Formation. E. Huene (1943) identified an isolated vertebra from a drill core in the Lower Buntsandstein of Pomorze (former Pommerania) in northwestern Poland as a reptilian caudal.

Tetrapod tracks. The oldest Triassic records of footprints from Germany are poorly preserved tetradactyl or pentadactyl, rounded imprints of relatively small size (3 cm long; Klein and Lucas, 2021). Although these footprints were originally attributed to temnospondyls (Abel, 1935 used the term ‘amphibians’), they are too poorly preserved to be of diagnostic value (Haubold, 1971a, 1971b; Klein and Lucas, 2021).

3.2. Volpriehausen Formation (Middle Buntsandstein Subgroup)

This formation is early Olenekian in age and demarcated by unconformities at its base and top (Bachmann et al., 2021). On Heligoland, which was located at the centre of the CEB, the well-exposed rock sequence includes alternating, low-sinuosity channel and playa deposits. By contrast, the marginal Vosges and Black Forest regions of the basin had large alluvial fans (Nitsch, 2024). The channels were deeply incised and transported large quantities of clasts (now preserved as conglomerates), with seasonally fluctuating water depth. The abundance of thin-bedded aeolian deposits between the North Sea region around Heligoland in the north and Hesse and Thuringia in the south indicates the virtual absence of vegetation over vast areas of the CEB during the deposition of the Lower Buntsandstein strata. This changed during the deposition of the Volpriehausen Formation, when streams alternated with lakes and deltas, with occasional marine incursions into the basin indicated by the presence of bivalves (Backhaus et al., 2014).

Tetrapod body fossils. The land vertebrate fossil record is confined to individual finds from a few localities, with a single taxon at each site, and almost entirely limited to capitosaurian temnospondyls.

Temnospondyli

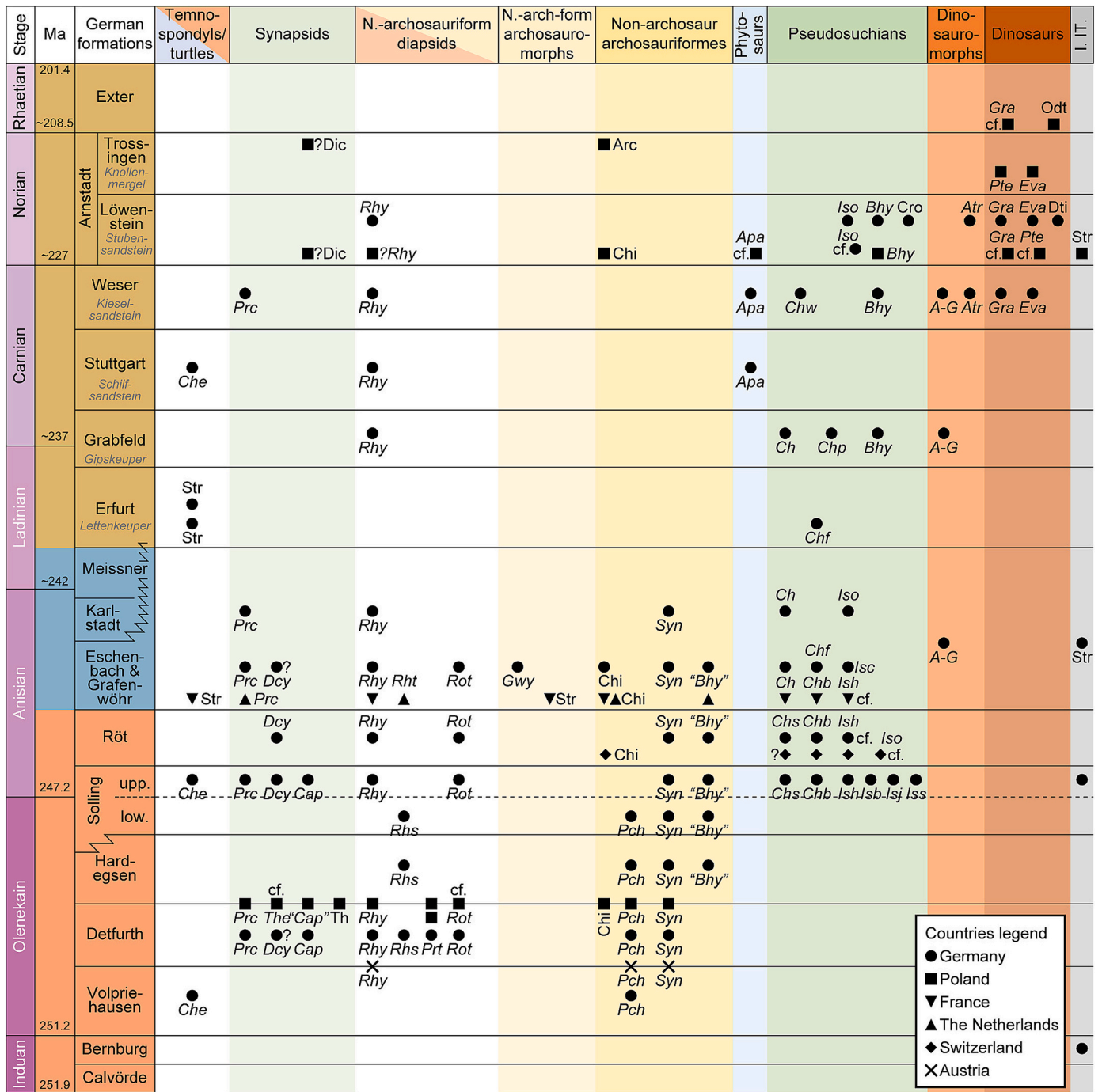
***Parotosuchus helgolandicus*.** The largest known freshwater predator in the CEB during the Early Triassic, this taxon is documented by a skull and an isolated rib from Heligoland (Schroeder, 1913; Staesche and Wolff, 1934).

***Parotosuchus decumanticus*.** Schoch (2011a) reported the natural mould of a palate from the Badischer Bausandstein (earliest Olenekian) of Castle Fautsburg in the Black Forest region that was subsequently placed in a new species, *P. decumanticus* (Schoch and Moreno, 2024).

***Sclerothorax hypselonotus*.** F. Huene (1932a) described this unusual temnospondyl based on skeletal remains from a quarry at Queck near Fulda (Hessen). A phylogenetic analysis by Schoch et al. (2007) found *Sclerothorax* as the sister-taxon to capitosauroids. Its occurrence falls within the Eichsfeld Sandstein (Volpriehausener Geröllsandstein), a basal member of the Volpriehausen Formation.

Reptilia: Archosauriformes

Mesorhinosuchus fraasi is a phytosaur of uncertain affinities (Stocker and Butler, 2013). It was known only from a partial cranium from Parforcehaus near Bernburg (Jaekel, 1910). The holotype and only known specimen was lost during World War II. According to Jaekel, it



Trackmakers and corresponding ichnotaxa / track morphotypes

Temnospondyls/turtles: *Che*, *Chelonipus*. **Synapsids:** *Th*, therapsid tracks indet.; *Dic*, Dicynodont tracks indet.; *Dcy*, *Dicynodontipus*; *Cap*, *Capitosauroides*; *Prc*, *Procolophonichnium*; *The*, *Therapsipus*. **Non-archosauriform diapsids:** *Rhy*, *Rhynchosauroides*; *Rhs*, *Rh. shchohardtii*; *Rht*, *Rh. tirolicus*; *Prt*, *Prorotodactylus*; *Rot*, *Rotodactylus*. **Non-archosauriform archosauromorphs:** *Gwy*, *Gwyneddichnium*. **Non-archosaur archosauriformes:** *Chi*, *chirotheriid* indet.; *"Bhy"*, *"Brachychirotherium"*; *Pch*, *Protochirotherium*; *Syn*, *Synaptichnium*; *Arc*, *Archosaur tracks indet.* **Phytosaurs:** *Apa*, *Apatopus*. **Pseudosuchians:** *Ch*, *Chirotherium* isp.; *Chb*, *Ch. barthii*; *Chs*, *Ch. sickleri*; *Chf*, *Ch. ferox*; *Chp*, *Ch. postchirotherioides*; *Chw*, *"Ch." wondrai*; *Bhy*, *Brachychirotherium*; *Iso*, *Isochirotherium*; *Isc*, *Iso. coureli*; *Ish*, *Iso. herculis*; *Isb*, *Iso. hessbergense*; *Isj*, *Iso. jenense*; *Iss*, *Iso. soergeli*; *Cro*, *Crocodylomorph tracks*. **Dinosauromorphs:** *A-G*, *Atreipus-Grallator*; *Atr*, *Atreipus*. **Dinosaurs:** *Eva*, *Evazoum*; *Gra*, *Grallator*; *Pte*, *Pseudotetrasauropus*; *Dti*, *Dinosaur tracks indet.*; *Odt*, *Other dinosaur tracks*. **Swimming traces:** *Str* (diverse trackmakers). **Indeterminate ichnotaxa and trackmakers:** *I. IT.*

Fig. 3. Stratigraphic distribution of Triassic terrestrial tetrapod tracks in the Central European Basin. Note that ichnotaxa are mainly represented at ichnogeneric level, only the most relevant and recognisable ichnospecies are distinguished (see Klein and Lucas, 2021 for discussions). Stratigraphic framework as in Fig. 2.

was found in the basal layers of the Middle Buntsandstein Subgroup and thus most likely came from the basal Volprie-hausen Formation. If this stratigraphic information is correct, *Mesorhinosuchus* would represent

the oldest known phytosaur to date. However, most authors have questioned the provenance of the fossil (Stocker and Butler, 2013).

Tetrapod tracks. The oldest well-identified tetrapod footprints from

Germany come from the Rhön, Thuringia (Klein and Lucas, 2021). Relatively large chirotheriid tracks have been identified as *Protochirotherium* isp. (Klein et al., 2013). Other 4–5 cm wide tracks and scratches (likely generated during swimming) reported by Gumbel (2009) possibly correspond to *Chelonipus* and/or to temnospondyl tracks (see discussion in Mujal and Schoch, 2020; De Jaime-Soguero et al., 2021).

Palaeoenvironments. The Volpriehausen capitosauroids ranged from 2 to 3 m in total length and were the apex predators in freshwater environments. *Parotosuchus* spp. is also known from probably coeval deposits in Utah and the southern Urals (Lucas and Schoch, 2002) and was one of the largest aquatic tetrapods of its time. In the Black Forest region, streams were smaller and most capitosauroid fossils represent smaller animals. The mode of life of the heavily ossified *Sclerorhax hypselonotus* is more difficult to assess because its skeleton combines features of aquatic temnospondyls with those of terrestrial forms; it could conceivably have coped with seasonal droughts and migrated between water bodies (Schoch et al., 2007). This is consistent with its occurrence in the basal part of the Volpriehausen Formation, which formed under more arid conditions. At Bernburg, the purported presence of a medium-sized archosauriform predator (*Mesorhinosuchus fraasi*) possibly suggests the existence of a somewhat more diverse ecosystem than those with exclusively capitosauroid apex predators, but the loss of the only known specimen precludes confirmation of its provenance. This phytosaur could have been a potential producer of *Protochirotherium*, an ichnogenus correlated with archosauriforms or pseudosuchian archosaurs (Klein and Niedzwiedzki, 2012; Klein et al., 2013; Bernardi et al., 2015; Klein and Lucas, 2021). Regardless of the specific identity of the trackmaker, these footprints indicate that archosauriform reptiles roamed the shores of streams and other water bodies. Swimming traces indicate that some tetrapods, possibly temnospondyls, inhabited the streams.

3.3. Upper Alpine Buntsandstein

In the Upper Alpine Buntsandstein (early Olenekian; approximately correlative to the German Volpriehausen and Detfurth formations) of the Drau Range region in southern Austria, Krainer et al. (2012) reported tetrapod tracks from red siltstone and shale intercalated with sandstone that correspond to shallow channel deposits of a distal braidplain system. These authors also reported tracks from braided river deposits from these strata in southern Austria. The ichnofauna includes chirotheriids (aff. *Protochirotherium* isp. and cf. *Synaptichnium* isp.) and small diapsid footprints (*Rhynchosauroides* isp.).

3.4. Detfurth and Hardegsen formations (Middle Buntsandstein Subgroup)

Following an unconformity after the deposition of the Volpriehausen Formation, the Detfurth Formation forms the oldest Buntsandstein sequence of late Olenekian (Spathian) age, overlain by the Hardegsen Formation (Bachmann et al., 2021). Its age is based on the presence of the spinicaudatan *Magniestheria deverta* and on palaeomagnetic data (Bachmann et al., 2021). The Detfurth Formation represents a phase during which aeolian deposition returned and rivers were confined to small channels. Humidity apparently increased toward the top of the formation (Paul, 2021b). This trend continued in the stratigraphically younger Hardegsen Formation (with the spinicaudatan *Euestheria exsecta*), during which large, high-energy streams and braided rivers provided permanent bodies of water (Mader, 1981).

Tetrapod body fossils. The Hardegsen Formation closely resembles the Volpriehausen Formation in the patchy occurrence of single taxa of capitosauroid temnospondyls. However, the Black Forest region has yielded indeterminate bones at several sites that indicate a greater abundance of these large aquatic predators compared to older deposits

(Schoch, 2011a).

Temnospondyli

Sclerorhax hypselonotus. Morphologically indistinguishable from the type material from the older Volpriehausen Formation; skeletons of this taxon have also been found in the upper Hardegsen Formation sandstones at Heimarshausen near Naumburg in Saxony-Anhalt (Schoch et al., 2007).

Odenwaldia heidelbergensis. Based on a single cranium, this taxon morphologically resembles, but is generically distinct from, *Parotosuchus* (Schoch, 2008a). The holotype was found in the upper conglomerate horizon of Waldkatzenbach near Heidelberg (Morales and Kamphausen, 1984).

Meyerosuchus fuerstenberganus. This taxon is based on a partial palate from Villingen in the Black Forest region and a referred specimen (Schoch, 2011a).

Tetrapod tracks. The record of tetrapod tracks from the upper Olenekian from Germany was reviewed by Fichter and Kunz (2015) who reported a much more diverse ichnofauna from the Detfurth Formation than previously known. As updated by Klein and Lucas (2021), this assemblage comprises nine tetrapod ichnogenes, *Protochirotherium* (including the type material of *P. wolfhagense*; Fichter and Kunz, 2004), *Synaptichnium*, *Prorotodactylus*, *Rotodactylus*, *Rhynchosauroides*, *Procolophonichnium*, *Dicynodontipus* and *Capitosauroides*; of the originally identified taxa, Klein and Lucas (2021) synonymised “*Palaeochirotherium*” with *Protochirotherium*. The largest of these, *Protochirotherium*, has recently been interpreted as having been produced by large-sized archosauriforms with mesaxonic feet and provides the oldest known evidence of an erect gait in this clade (Bernardi et al., 2015; Klein and Lucas, 2021). From the Hardegsen and Solling formations in Hesse, Klein and Lucas (2021) listed chirotheriid-dominated ichnofaunas that include *Protochirotherium* (“*Isochirotherium santacrucense*”, “*I. archaenum*”), *Synaptichnium primum*, S. cf. *S. pseudosuchoides*, S. isp., “*Brachychirotherium*” kuhni, “*B.*” praeparvum, and *Rhynchosauroides schochardti*.

Palaeoenvironments. During the late Olenekian, the number and size of rivers increased. This coincides with the more common occurrence of larger-bodied (2 to 3 m long) capitosauroids as apex predators in fluvial settings. They likely preyed on actinopterygians and dipnoans, although fish remains are rarely preserved. The diverse ichnofauna of terrestrial tetrapods strongly contrasts with the virtual absence of tetrapod skeletons. However, it indicates that stable living conditions existed for small, insectivorous or omnivorous procolophonoids, small-bodied diapsid reptiles (*Rhynchosauroides*, *Rotodactylus*), non-mammalian synapsids (*Procolophonichnium*, *Dicynodontipus*, *Capitosauroides*), and larger archosauriform reptiles (*Protochirotherium*, *Synaptichnium*, “*Brachychirotherium*”). The absence of other characteristic chirotheriid tracks (such as *Chirotherium* and *Isochirotherium*) suggests that pseudosuchians were probably absent.

3.5. Czatkowice cave fill

At Czatkowice near Kraków (Poland), the Palaeozoic Dębnik limestone platform was exposed to karst weathering during the late Olenekian (Paszowski, 2009). It was located within an inland region and the deposits preserve skeletal remains of terrestrial and shallow freshwater tetrapods (Borsuk-Białynicka and Evans, 2009a). Within a cave deposit, a breccia includes countless fossilised remains of diverse tetrapod taxa, some of which are shared with Early Triassic assemblages of the Cis-Urals. Paszowski (2009) dated the particularly rich Czatkowice 1 deposit as late Olenekian (early Spathian), correlating it with the lower Yarenskian Gorizont of Cis-Uralian Russia based on vertebrates and the Detfurth Formation of the CEB.

Tetrapod body fossils. Scores of dissociated bones were reworked from lacustrine deposits and washed into the cave system by run-off, which

explains the unexpected abundance of juvenile specimens of lake-dwelling temnospondyls (Cook and Trueman, 2009). The Czatkowice deposits are not only important because of their tetrapod diversity but also for the often exquisite, three-dimensional preservation of the skeletal remains. It makes this material invaluable for comparison with the typically crushed tetrapod material (especially of small taxa) from other Triassic deposits. However, the dissociated nature of the bones sometimes introduces considerable uncertainty in using taxa based exclusively on specimens from cave fills for phylogenetic analyses. Recently, Sulej et al. (2024) reported tetrapod remains from Stryczowice, a locality from the north-eastern margin of the Holy Cross Mountains that is of similar age to Czatkowice. The assemblage consists of indeterminate trematosaurid temnospondyls and procolophonids.

Temnospondyli

“Parotosuchus” speleus. Juvenile bones of a *Parotosuchus*-like temnospondyl form common finds in the karst deposit (Shishkin and Sulej, 2009).

Batrachosuchoides sp. Shishkin and Sulej (2009) referred several isolated skull bones to this dvinosaurian temnospondyl, but their identification remains uncertain. Alternatively, they could represent plagiosaurids, given that these short-snouted temnospondyls closely resemble *Batrachosuchoides* in cranial features. A clavicle figured by Shishkin and Sulej (2009, fig. 45) bears a markedly tubercular ornamentation, which is typical of most plagiosaurids (Schoch and Milner, 2014).

Lissamphibia: Salientia

Czatkobatrachus polonicus. This taxon is stratigraphically only slightly younger than the earliest known salientian (stem-anuran) *Triadobatrachus massinoti* from Madagascar (Ascarrunz et al., 2016). To date, it represents the only known Triassic record of salientians from Europe (Evans and Borsuk-Białynicka, 2009a).

Reptilia: Procolophonoidea

Procolina teresae. This small-sized procolophonid has a heterodont dentition with unicuspid tooth crowns (Borsuk-Białynicka and Lubka, 2009). It closely resembles *Kapes* spp. from European Russia and southwestern England.

Indeterminate procolophonid. A second procolophonid taxon differs from *Procolina teresae* in the presence of bicuspid teeth and attaining larger adult body size (Borsuk-Białynicka and Lubka, 2009).

Reptilia: Lepidosauromorpha

Sophineta cracoviensis. This tiny lepidosauromorph has pleurodont tooth implantation, a tall facial process of the maxilla, and a small lacrimal. With a reconstructed skull length of only 1 cm, *Sophineta cracoviensis* is the smallest reptile known from the Czatkovice assemblage (Evans and Borsuk-Białynicka, 2009b).

Reptilia: Archosauromorpha

Pamelina polonica. This gracile kuehneosaurian reptile from the CEB that forms one of the rarer components of the fissure fill assemblage (Evans, 2009). It lacked the greatly elongated dorsal ribs of the Late Triassic *Kuehneosaurus latus* and *Icarosaurus sieferi*.

Czatkowiella harae. This early-diverging archosauromorph has greatly elongated cervical vertebrae with low neural spines and a skull resembling that of the late Permian (Wuchiapingian) *Protorosaurus speneri* (Borsuk-Białynicka and Evans, 2009a).

Osmolskina czatkovicensis. Borsuk-Białynicka and Evans (2009b) and Borsuk-Białynicka and Sennikov (2009) described numerous cranial and postcranial bones of a small-bodied euparkeriid archosauriform.

Collilongus rarus. This archosauriform is known only from various postcranial elements (Borsuk-Białynicka and Sennikov, 2009). Its relationships remain unresolved.

Palaeoenvironments. The tetrapod assemblage at Czatkowice comprises both terrestrial and freshwater taxa but lacks marine forms. This is consistent with the geological evidence that, during the late Olenekian, the region was situated in an upland and inland setting (Paszkowski, 2009). The generally very small size of the tetrapod remains suggests sorting by size when the bones were transported into the cave deposits by water. The preservation of juveniles and small-sized adults of a considerable diversity of tetrapods contrasts strongly with the records in most other Lower and Middle Triassic tetrapod lagerstätten. Although the taxonomic diversity as well as the quantity and quality of the skeletal remains make the Czatkowice assemblage highly significant, the isolated nature of the bones often renders their attribution to a particular taxon difficult if not impossible.

3.6. Wióry and Samsonów formations

The Wióry and Samsonów formations of Wióry, Holy Cross Mountains, Poland, date from the late Olenekian (Spathian) based on the presence of the spinicaudatans *Magniestheria deverta*, *Palaeolimnada alsatica defurthensis*, and *Euestheria exsecta* (Sulej and Niedźwiedzki, 2013). Their ichnofaunas closely resemble those of the Middle Buntsandstein Subgroup of Germany (Klein and Niedźwiedzki, 2012). Tetrapod tracks occur in a clastic succession of the Wióry and the lower part of the Samsonów Formation, preserving braided river-channel and floodplain deposits. They include eight reptilian ichnotaxa, *Prochirotherium hauboldi*, *Synaptichnium kotanskii*, other large unidentified chirotheriids, *Prorotodactylus mirus*, cf. *Rotodactylus*, *Rhynchosauroides* (*Rhy. rdzaneki*, *Rhy. brevidigitatus*, *Rhy. isp.*), and *Procolophonichnium polonicum*, and the probably synapsid ichnotaxa cf. *Therapsipus* and “*Capitosauroides*” *fuglewiczi*, as well as other indeterminate therapsid footprints. Niedźwiedzki and Ptaszyński (2007) highlighted the presence of notably large chirotheriid tracks comparable to that of the Solling Formation (see below), as well as in other European and North American localities. Brusatte et al. (2011) reported tracks of what they considered early dinosauromorphs (*Prorotodactylus*) from Wióry and from a slightly older horizon at Stryczowice. However, Fichter and Kunz (2013) and Padian (2013) argued that there is no evidence in support of this identification (see also Mújal et al., 2017). Body fossils include vertebrate bones, plants, and spinicaudatans (which include all Triassic conchostracans or clam shrimps). The capitosauroid *Parotosuchus ptaszynskii* is documented by cranial and mandibular fragments (Sulej and Niedźwiedzki, 2013).

3.7. Lower Solling Formation (Middle Buntsandstein Subgroup)

The Solling Formation was originally considered Olenekian in age in its entirety, but most of it including the Thüringischer Chirotheriensandstein has more recently been redated as early Anisian (Aegean) (Bachmann and Kozur, 2004; Bachmann et al., 2021) and is therefore discussed in section 3.8. At Merkel’s quarry, the famous Bernburg locality in which light grey sandstones were quarried during the nineteenth century, the lower Solling Formation has yielded a rich fossil lagerstätte with plants and temnospondyls. These sandstones (Bau-sandstein) are rich in mud clasts and probably represent delta-channel deposits (Hauschke et al., 2021) in which scores of temnospondyl skulls accumulated and were preserved. The lower Solling Formation of coarse fluvial sandstones and mudstones deposited in a meandering or braided river system (Weber and Lepper, 2002). Paul (2021b) argued for warm semi-arid to seasonally wet conditions during the deposition of the formation.

Tetrapod body fossils. Despite forming a rather short stratigraphic sequence within the Buntsandstein Group, the lower Solling Formation has yielded a more diverse tetrapod fauna encompassing a capitosauroid, trematosaurids, a large-sized procolophonid, and the oldest known pseudosuchian archosaur in the CEB.

Temnospondyli

Parotosuchus nasutus (Fig. 4A). Some 37 diagnostic specimens of this medium-sized capitosauroid were collected at Merkel's quarry of Bernburg during the nineteenth century (Schoch, 2018).

Trematosaurus brauni (Fig. 4B). With 69 identifiable finds, this taxon was the most common temnospondyl found at Merkel's quarry (Schoch, 2019). In Thuringia, *T. thuringensis* is a regional variant (Werneburg, 1993).

Reptilia: Procolophonoidea

Sclerosaurus armatus. This heavily built, up to 50 cm long leptocephalonid procolophonid is represented by an articulated skeleton from the uppermost Middle Buntsandstein of Riehen, Switzerland (Sues and Reisz, 2008). The holotype, a partial postcranial skeleton, was collected from the Upper Buntsandstein at Warmbach near Rheinfelden in Baden (Germany).

Reptilia: Archosauria

Ctenosauriscus koeneni. This 'sail-backed' poposauroid pseudosuchian is represented by a single partial postcranial skeleton from Bremke near Göttingen, which closely resembles that of *Arizonasaurus babbitti* from the Holbrook Member of the Moenkopi Formation in Arizona, USA (Butler et al., 2011). It is especially characterized by the presence of greatly elongated neural spines in the posterior cervical to anterior caudal vertebrae.

Tetrapod tracks. As noted in section 3.4, chirotheriid-dominated ichnofaunas have been reported from the Hardeggen and Solling formations (*Protochirotherium* isp., *Synaptichnium primum*, *S.* cf. *S. pseudosuchoides*, *S.* isp., "Brachychirotherium" *kuhni*, "B." *praeparvum*, and *Rhynchosauroides schochardti* [Fig. 4C]).

Palaeoenvironment. The lower Solling Formation provides evidence of still richer freshwater ecosystems than those of the Hardeggen Formation (Kustatscher et al., 2014), with remains of a locally diverse fauna preserved at Bernburg. The slender-snouted *Trematosaurus* was probably a piscivore and *Parotosuchus nasutus* the apex predator with habits comparable to those of extant crocodylians. The abundance of the widely distributed lycophyte *Pleuromeia sternbergii* in the channel deposits suggests proximity of marine environments (Hauschke et al., 2021). Sedimentary features suggest that some of the *Pleuromeia*-bearing channels were at least partially under marine influence, falling in the beginning of a transgressive phase in the central part of the CEB. The dominance of *Trematosaurus brauni* at Bernburg corresponds to the common occurrence of other trematosaurids in fully marine strata in Svalbard and Madagascar (Schoch and Milner, 2000) and is consistent with the inference that fluctuations in salinity might have played a role in this environment. In the Göttingen region, the lower Solling Formation preserves a more inland terrestrial setting, with fluvial channels and meadows that were framed by diverse vegetation. The Bremke locality preserves freshwater limulids and a rich flora in a crevasse-splay deposit (Kustatscher et al., 2014; Franz et al., 2021a).

3.8. Upper Solling Formation (Thüringischer Chirotheriensandstein, Middle Buntsandstein Subgroup)

The upper part of the Solling Formation is early Anisian (Aegean) in age based on its spinicaudatan assemblage with *Euestheria albertii mahlerselli* and *Palaeolimnada alsatica alsatica* (Kozur and Bachmann, 2005; Kozur and Weems, 2010) and encompasses platey sandstones that were deposited under deltaic to coastal conditions (Paul, 2021b). This rock sequence (Thüringischer Chirotheriensandstein) mostly formed in a shallow-marine setting when the transgressing sea led to the formation of extensive floodplains that provided excellent conditions for the preservation of tetrapod tracks. The famous ichnofauna of Hildburghausen falls into this stratigraphic interval (Haubold, 1971a, 1971b;

Klein and Werneburg, 2021). It should be noted that the term Chirotheriensandstein (or Chirotherien-Sandstein) is used for a variety of roughly coeval local lithostratigraphic units within the Buntsandstein Group of Germany. However, the Thüringischer Chirotheriensandstein sensu stricto corresponds to the upper part of the Solling Formation (Dersch-Hansmann et al., 2013; Bachmann et al., 2021), and we follow this usage in this paper.

Tetrapod body fossils. This time slice has yielded body fossils in a few localities and an excellent ichnofauna from a range of sites particularly from southwestern Thuringia.

Reptilia: Procolophonoidea

Anomoiodon lilienseni. This small-bodied procolophonid is known from an associated pair of articulated skeletons of Thuringia (F. Huene, 1939; Säilä, 2008). It is closely related to *Kapes* spp. from European Russia and southwestern England.

Koiloskiosaurus coburgensis. Three articulated skeletons of this medium-sized procolophonid were found associated at Mittelberg near Coburg (F. Huene, 1912).

Reptilia incertae sedis

An isolated vertebra associated with the holotype of the tanysaurian reptile *Trachelosaurus fischeri* (Spiekman et al., 2024a) is here tentatively identified as aff. *Eusaurosphargis*, a probably terrestrial diapsid reptile (Scheyer et al., 2017).

Reptilia: Archosauromorpha

Archosauriformes. A single end of a limb bone from Merkel's Quarry near Bernburg has been identified as archosauriform (Schoch, 2018).

Tetrapod tracks. The tetrapod track record from the lowermost Anisian upper Solling Formation is well-documented. The classic locality near Hessberg E of Hildburghausen in Thuringia (Haubold, 2006; Klein and Werneburg, 2021) was historically the first to yield tracks of *Chirotherium* (Kaup, 1835). In addition to the synapsid ichnotaxon *Procolophonichnium haarmuehlensis*, somewhat larger tracks of *Rhynchosauroides* and *Rotodactylus* are especially common, and the archosauriform ichnotaxon *Synaptichnium hildburghausense* is also present. An impressive diversity of archosaurian tracks is evidenced by the occurrence of *Chirotherium* (*C. barthii* [Fig. 4D] and *C. sickleri*), *Ischirotherium* (*I. herculis*, *I. hessbergense*, *I. jenense*), and "Brachychirotherium" ("B." *praeparvum*, "B." *harrasense*). From this unit, and from the classic locality, ichnotaxa that most likely were produced by the raptids comprise *Dicynodontipus geinitzi* and *Capitosauroides bernburgensis*. *Chelonipus torquatus* as well as other indeterminate footprints are also present in Hildburghausen (Haubold, 1971a, 1971b; Klein and Lucas, 2021). The slab containing the holotype of *Trachelosaurus fischeri* from Merkel's quarry at Bernburg, which was originally published by Broili and Fischer (1918), and was only recently recognised as a tanysaurian reptile by Spiekman et al. (2024a), also preserves numerous tetrapod tracks most likely corresponding to *Capitosauroides*. An ichnoassemblage from Eisfeld, Thuringia, reported by Klein and Lucas (2021) comprises small chirotheriid footprints (*Chirotherium sickleri*, *Ischirotherium soergeli*, "Brachychirotherium" *praeparvum*, and "B." *harrasense*), which were probably produced by juvenile individuals, associated with *Rotodactylus matthesi*, *Rhynchosauroides bornemanni*, *Rhy. pusillus*, and *Dicynodontipus geinitzi*.

Palaeoenvironments. The extensive coastal facies and its pedogenic horizons suggest a densely vegetated plain. These must have provided excellent habitats for reptiles, as evidenced by the procolophonid skeletons and nine reptilian ichnogenera. The presence of *Trachelosaurus fischeri*, a tanysaurian archosauromorph, together with sedimentary structures preserved on the same slab (Spiekman et al., 2024a) that are also identified elsewhere in the upper part of the Solling Formation (Hauschke et al., 2005) demonstrate the marine influence on the environments populated by diverse tetrapods. The archosaurs include large-bodied pseudosuchians and likely formed a more complex trophic web

than during Olenekian times. The tetrapods range in length from a few centimetres up to 4 or 5 m, as indicated by some large chirotheriid tracks (Haubold, 1971a, 1971b).

3.9. Röt Formation (Upper Buntsandstein Subgroup)

The Röt Formation encompasses a sequence of Aegean- and Bithynian-age strata (Bachmann et al., 2021). The basis of the Bithynian substage lies in the upper portion of the Röt Formation. In southern Germany, the lower part of this formation is formed by the Plattensandstein, a series of sheet sandstone units with conglomerates and intercalated mudstones. A famous mass accumulation of *Mastodonsaurus cappelensis* in the Black Forest is known from the the lower Plattensandstein (Wepfer, 1923a; Schoch et al., 2023). This single occurrence

formed in a small water body in which these fully aquatic temnospondyls probably perished during a drought. Their skeletons were later disarticulated by weak currents. The Plattensandstein is Aegean in age and was deposited in an extensive fluvial system on an arid plain (Nitsch, 2024). Other fossils from this sequence were found in conglomerates, including the rhynchosaurid *Eifelosaurus triadicus* (Kyllburg Member of the Röt Formation) in the Eifel region of southwestern Germany (Sues et al., 2022a) and a poposauroid pseudosuchian from Waldshut in the Black Forest region (Butler et al., 2011). A small sandstone pit, the Kössig quarry at Rotfelden near Nagold in the Black Forest yielded tetrapod remains in sedimentary strata of the upper Plattensandstein (Nitsch, 2024), with temnospondyls occurring in channel sandstones and various disarticulated reptilian skeletons in sheet sandstones (Ortlam, 1970).

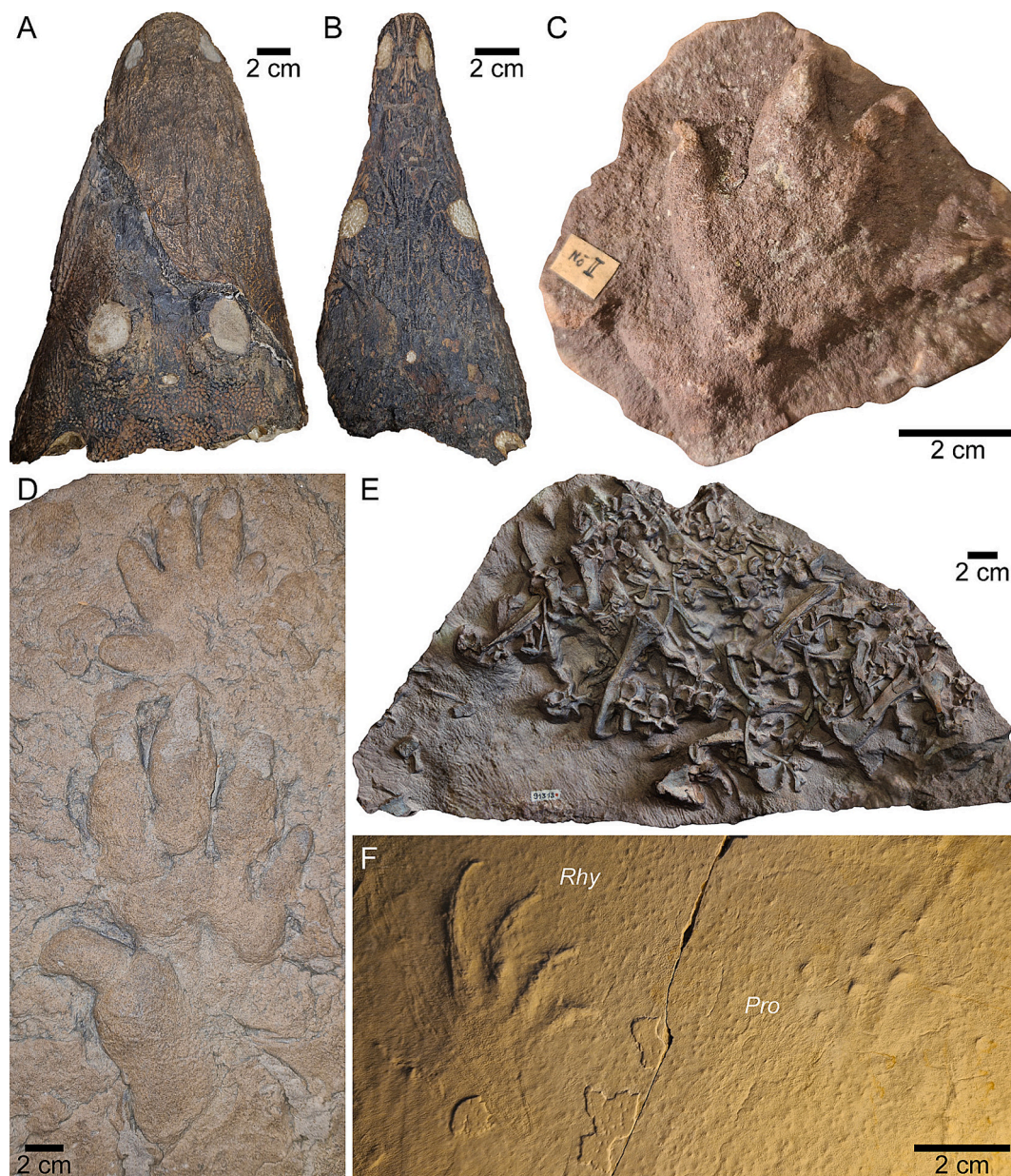


Fig. 4. Selected Triassic tetrapod fossils from the CEB in the Staatliches Museum für Naturkunde Stuttgart (SMNS) collections I. Specimens from the upper Olenekian (A–C) and lower Anisian (D–F). A. *Parotosuchus nasutus* (SMNS 5776), lower Solling Fm. B. *Trematosaurus brauni* (SMNS 6207a), lower Solling Fm. C. *Rhynchosauroides? schochardti*, convex hyporelief (SMNS uncatalogued), middle Buntsandstein. D. *Chirotherium barthii*, convex hyporelief (SMNS 4228), upper Solling Fm. (Thüringischer Chirotheriensandstein). E. *Marcianosuchus angustifrons* (SMNS 91318, holotype), Röt Fm. F. *Rhynchosauroides* isp. (*Rhy*) and *Procolophonichnium* (*Pro*), convex hyporelief (SMNS 51514), Vossenveld Fm.

Tetrapod body fossils. The body fossil record of the Röt Formation is by far the richest of those from the Buntsandstein.

Temnospondyli

Mastodonsaurus cappelenensis. This up to 3 m long capitosauroid, sometimes placed in its own genus *Heptasaurus* (Schoch et al., 2023), is documented by a death assemblage of 40 skulls and many postcranial bones from a single locality at Kappel near Villingen in the Black Forest (Wepfer, 1923a; Schoch et al., 2023).

Stenotosaurus semiclausus. Based on a cranium from Herzogenweiler near Freudenstadt in the Black Forest, this capitosauroid is distinguished by closed otic notches and an unpaired anterior palatal opening (Swinton, 1927). The incompletely known *Stenotosaurus gracilis*, based on an impression of a smaller skull roof from Kronach in Franconia (Bavaria), is probably a subjective junior synonym of *S. semiclausus* (Kamphausen, 1983).

Ecyclotosaurus woschmidtii. This taxon is known from a single skull found in a massive sandstone unit at Rotfelden, in the Black Forest (Ortlam, 1970; Kamphausen, 1989).

Reptilia: Procolophonoidea

Sclerosaurus armatus. The holotype of this large procolophonid was collected from talus of a sandstone quarry near Rheinfelden, Baden (Meyer, 1859; Sues and Reisz, 2008).

Procolophonidae indet. Wild (1998) reported an impression of a skeleton of a small procolophonid resembling *Anomoiodon liliesterni* from the Plattensandstein (lower Röt Formation) of Leinstetten near Freudenstadt in the Black Forest. Ortlam (1967) reported fragmentary procolophonoid material which he described as *Anomoiodon krejci*.

Reptilia: Archosauromorpha

Amotosaurus rotfeldensis. This small-bodied tanystropheid from Rotfelden is the most common tetrapod from the Kössig quarry (Fraser and Rieppel, 2006; Spiekman et al., 2021a). It is known from several partially articulated skeletons preserved in sheet sandstones.

Eifelosaurus triadicus. The holotype and only known specimen of this small-bodied rhynchosaur was found in Oberbettingen near Hillesheim in the Eifel region, southwestern Germany. It is a partial postcranial skeleton exposed in ventral view (Sues et al., 2022a).

Rhynchosauria indet. Three associated juvenile skeletons including partial skulls of an early-diverging rhynchosaur were recovered on a single block from Rotfelden, Black Forest (Sues and Schoch, 2023a). The taxon shares various characters with rhynchosaurids (i.e., rhynchosaurs more derived than *Mesosuchus browni* from the lower Middle Triassic of South Africa). Due to the immaturity of this material and apparent lack of synapomorphies, it is still uncertain whether these specimens can be referred to *Eifelosaurus triadicus* or represent a previously unknown taxon.

Marcianosuchus angustifrons (Fig. 4E). A coarse-grained sandstone layer at Rotfelden yielded the disarticulated skeleton of an about 1 m long eucrocopodan archosauriform (Sues et al., 2024).

Waldshut poposauroid. Butler et al. (2011) reported pseudosuchian postcranial remains with tall dorsal neural spines resembling those of *Ctenosauriscus koeneni* from Waldshut, southern Baden.

Seemannia palaeotriadica F. Huene, 1958 and *Crenelosaurus nigrosilvanus* Ortlam, 1967 were named based on isolated non-diagnostic archosauriform teeth and we consider them *nomina dubia*.

Tetrapod tracks. Tetrapod tracks are common in the Plattensandstein and the Fränkischer Chirotheriensandstein. With numerous occurrences, especially in Upper Franconia and the Würzburg region, the Röt Formation has yielded an ichnofauna that is very similar to that of the upper Solling Formation (e.g., Soergel, 1925; Haubold, 1971a; Demathieu and Fichter, 1989; Haderer et al., 1995; Puff and Klein, 2011; Klein, 2021; Klein and Lucas, 2021). It includes *Rhynchosauroides*, *Rotodactylus*,

Synaptichnium, *Chirotherium* (specifically *C. barthii* and *C. sickleri*), *Isochirotherium*, “*Brachychirotherium*”, and *Dicynodontipus geinitzi*.

Palaeoenvironments. Substantial evaporites in the lower Röt Formation indicate that climatic conditions had become arid again (Paul, 2021b). Later Röt strata formed in a setting with larger streams and intercalated small lakes, with vegetated shores and repeated intervals of soil formation (some of the violet horizons; Ortlam, 1968). The plain was subsequently covered by vast playa lakes in which mudstones and siltstones were deposited. Hence the tetrapod fauna is largely restricted to the fluvial facies in the lower part of the succession (Nitsch, 2024). In this facies, the more numerous temnospondyl taxa suggest richer ecosystems than during the Olenekian, but these aquatic predators are always restricted to a single taxon per site in the Röt Formation. Whereas *Mastodonsaurus* apparently dwelled in lakes, *Ecyclotosaurus* and other heylerosaurines were found in river channel deposits. In terrestrial settings, the poposauroids form the first known pseudosuchian clade to be confirmed by body fossils, and these large-bodied archosaurs likely produced certain types of chirotheriid tracks such as *Chirotherium barthii* and *Isochirotherium*. *Marcianosuchus* from Rotfelden was a medium-sized eucrocopodan archosauriform that resembles Euparkeriidae in some features (Sues et al., 2024).

3.10. Vieux Emosson Formation

This formation at the southern margin of the CEB directly overlies the Palaeozoic metamorphic basement, thus representing the oldest Mesozoic deposits from Switzerland, and is of Olenekian–Anisian age (Klein et al., 2016; Wizevich et al., 2019). The Vieux Emosson Formation consists of a siliciclastic fining-upwards succession in which two different facies associations can be distinguished (Wizevich et al., 2019). The lower one corresponds to a braided alluvial plain, whereas the upper one is characteristic of proximal and distal terminal splay deposits. Klein et al. (2016) thoroughly reviewed the Triassic tetrapod track record from several localities in the upper facies association and identified a variety of ichnotaxa, mainly chirotheriid tracks including *Isochirotherium herculis*, cf. *I. isp. indet.*, *Chirotherium barthii*, and *C. sickleri* (Klein and Lucas, 2021).

3.11. Grès à Voltzia

This unit is younger in age (Bithynian and Pelsonian) than the Röt Formation and correlates with the basal part of the Lower Muschelkalk (Durand and Hagdorn, 2020; Bachmann et al., 2021). It is named for the great abundance of shoots of the conifer *Voltzia heterophylla*. In the Alsace region, a large delta harboured numerous ponds and locally densely vegetated areas during the early Anisian (Gall, 1971). This depositional setting formed along the western margin of the transgressing Muschelkalk Sea, which eventually inundated the region. Starting in the late 1930s, the avocational collector Louis Grauvogel built vast collections of plant and arthropod fossils from these deposits (Gall et al., 2021).

Tetrapod body fossils. Skeletal remains of tetrapods are surprisingly rare in the Grès à Voltzia, with only a few remains of a capitosauroid and three skeletons of small-bodied diapsid reptiles recovered to date from the lower part of the Grès à Voltzia (= Grès à Meules) (Gall et al., 2021).

Temnospondyli

Ecyclotosaurus lehmani. Heyler (1969) reported two skulls and disarticulated postcranial remains of this slender-snouted heylerosaurine capitosauroid from channel sandstones at Graufthal.

Reptilia: Drepanosauromorpha

Two juvenile skeletons of a drepanosauromorph reptile have been identified from the Cocheren locality of northern Alsace (Spiekman et al., in review).

Reptilia: Archosauromorpha

A tiny reptilian skeleton with elongate cervical vertebrae resembling those of tanysaurians was found in a siltstone bed near Bust in northern Alsace. It is currently under study by SNFS.

Tetrapod tracks. From the coastal facies, Gall (1971) reported relatively large (6.5 cm long) tracks of the ‘lacertoid’ ichnogenus *Rhynchosauroides* (probably produced by small diapsid reptiles), including a densely trampled surface, as well as several chirotheriid tracks, most likely corresponding to *Chirotherium* (Gall et al., 2021). Gand et al. (2007) also reported associations of tetrapod footprints from the Alsace region and the Vosges, occurring in both the Grès à Meules and Grès Argileux (lower and upper part of Grès à Voltzia, respectively) that include: “*Chelonichnium vogesiacum*” (nomen dubium according to Klein and Lucas, 2021; possible swimming traces of temnospondyls), *Rhynchosauroides* isp., *Chirotherium* isp., *Ch. barthii*, cf. *Coelurosaurichnus* (most likely indeterminate chirotheriid tracks), and *Isochirotherium* cf. *I. herculis*. Floodplain sandstones and crevasse-like deposits from different outcrops of the upper portion of Grès à Meules contain chirotheriid footprints, *Rhynchosauroides*-like footprints, and swimming traces (likely produced by temnospondyls and large archosauromorphs) (EM and SNFS, pers. obs.).

Palaeoenvironments. The lower portion of the Grès à Voltzia (Grès à Meules) formed in three different depositional settings: river channels, floodplain ponds, and coastal marine settings (Gall, 1972). The channels were lined by dense vegetation, and this is also where the skeletons of the two taxa of small-bodied reptiles were preserved. The streams were inhabited by *Eocyclotus lehmani*. The ponds were too small to harbour large-bodied aquatic tetrapods because their fish fauna consists only of small-bodied taxa (Gall et al., 2021). Large archosauriform reptiles roamed across the coastal flats and left chirotheriid tracks. Potentially, other small- to medium-sized diapsid reptiles were also present in these settings, as indicated by tracks of *Rhynchosauroides*.

3.12. Vossenveld Formation (Lower to Middle Muschelkalk Subgroup)

During a five-million-year interval in the late Anisian and early Ladinian, the CEB was repeatedly inundated by a shallow epicontinental sea, known as the Muschelkalk Sea, which is recorded by the carbonate-dominated Muschelkalk sequence (Hagdorn, 2020). The Vossenveld Formation includes the classic exposures at Winterswijk, the Netherlands, which are famous for the abundance of skeletal remains of a variety of marine reptiles and tetrapod footprints. This succession, of Anisian age, was deposited along the western margin of the Rhenish Massif and consists of carbonates formed in a coastal to shallow-marine setting (During et al., 2019). More specifically, these deposits comprise alternating marlstone, dolostone, limestone and claystone arranged in relatively thinly laminated strata. According to During et al. (2019), the original sediments were deposited in an arid, hypersaline sabkha environment on a very shallow gradient platform along the western margin of the CEB. The only known skeletal remains belonging to a terrestrial tetrapod are isolated vertebrae identified as aff. *Eusauropsphargis* (Sander et al., 2014; Willemse et al., 2019) and a fragmentary rib of an indeterminate capitosauroid (Oosterink and Diepenbroek, 1990). Terrestrial tetrapods from these deposits are mainly documented by abundant footprints usually preserved on mud-cracked surfaces of laminated calcareous mudstones, mostly corresponding to microbial mats on tidal flats. The ichnoassemblage comprises abundant tracks of *Rhynchosauroides* and *Procolophonichnium* (Fig. 4F) and rare occurrences of chirotheriid tracks including “*Brachychirotherium*” and “*Coelurosaurichnus*” (Marchetti et al., 2019a, and references therein). Identification of the latter ichnotaxon is possibly based on poorly or partially preserved chirotheriid footprints (Klein and Lucas, 2021).

3.13. Eschenbach and Grafenwöhr formations (Lower Muschelkalk Subgroup)

The terrestrial Buntsandstein deposits of the CEB generally show an upward trend toward more distal and marine-influenced settings that culminates with the onset of the richly fossiliferous marine carbonates of the Muschelkalk Group (Franz et al., 2013; Hauschke et al., 2021). This implied displacement of terrestrial faunas by the marine transgression, but on the margins of the basin and especially around the Bohemian-Vindelician massif, rich tetrapod ichnoassemblages have been discovered (Klein and Lucas, 2018). These authors reported a locality in fluvial deposits of the Eschenbach and Grafenwöhr formations (Lower Muschelkalk, middle Anisian) near Berndorf (Bavaria). The footprints are preserved within a siliciclastic marginal facies consisting of sandstone and siltstone as well as dolomitic rocks. The tetrapod ichnoassemblage includes: *Synaptichnium pseudosuchoides*, S. cf. *S. diabloense*, S. isp. (morphotype “*Brachychirotherium*”), *Isochirotherium coureli*, *Chirotherium ferox* (formerly ‘*Sphingopus*’ *ferox*; see Klein and Lucas, 2021), *Chirotherium* isp., *Chirotheriidae* indet., *Atreipus-Grallator*, *Rhynchosauroides* isp., *Rotodactylus* isp., *Gwyneddichnium majorae*, plus indeterminate tetradactyl or pentadactyl imprints resembling *Dicynodontipus* (Klein and Lucas, 2018). Klein and Lucas (2021) (see also Marchetti et al., 2020) summarised the record from other marginal marine deposits (including tidal settings) of the Lower Muschelkalk in North Rhine-Westphalia, Hesse, Saxony-Anhalt and Thuringia, with locally abundant tracks of the ichnogenes *Rhynchosauroides* and *Procolophonichnium*. These resemble the ichnoassemblages from Winterswijk, The Netherlands, and more generally those from coastal facies of the Middle Triassic elsewhere in the CEB (Marchetti et al., 2020; De Jaime-Soguero et al., 2021).

The only (sparse) skeletal remains from coeval strata within the CEB represent temnospondyls. Röpke (1930) described *Mentosaurus waltheri* based on fragments of a left mandibular ramus, a skull fragment, and a partial interclavicle of a large capitosauroid (possibly *Mastodonsaurus*) from the predominantly marine Jena Formation (Lower Muschelkalk Subgroup) of Nietleben near Halle an der Saale (Saxony-Anhalt). There are also other records of temnospondyl remains from the Muschelkalk including “*Mastodonsaurus*” *silesiacus*, based on a partial mandible of a capitosauroid from Zakrzów near Gogolin (Poland; Kunisch, 1885) and possibly referable to *Tatrasuchus* (Schoch and Moreno, 2024).

3.14. Karlstadt Formation (Middle Muschelkalk Subgroup)

The basal portion of the Karlstadt Formation consists of laminated mudstones and fine-grained carbonate layers that were deposited on upper tidal flats (Marchetti et al., 2020). The index fossil is the bivalve *Neoschizodus orbicularis*. Some of these beds preserve tetrapod track associations representing a rich assemblage that includes *Isochirotherium*, *Chirotherium*, *Rhynchosauroides*, *Procolophonichnium*, and *Synaptichnium* (Diedrich, 2009, 2012; Marchetti et al., 2020). In addition, relatively large chirotheriid tracks have also been identified in association with limulid traceways (ichnogenus *Kouphichnium*), possibly showing predator-prey interactions (Diedrich, 2012).

3.15. Meissner Formation (Upper Muschelkalk Subgroup)

The uppermost part of this Ladinian aged sequence has occasionally yielded single finds of temnospondyls. These occur in the limestone beds, but are especially abundant in the Grenzbonebed, a condensation horizon containing countless vertebrate remains at the boundary with the Erfurt Formation (Hagdorn and Reif, 1988). The tetrapod fauna includes three temnospondyl taxa, the abundant *Plagiosternum granulosum* (Warren, 1995), and the much less common *Mastodonsaurus giganteus* (Schoch, 1999) and *Gerrothorax pulcherrimus* (Hellrung, 2003). The now lost holotype and only known specimen of “*Cyclotusaurus*” *papilio* (Wepfer, 1923b) probably represented an *Eocyclotusaurus*-like

capitosauroid (Schoch and Moreno, 2024). *Plagiosternum* probably lived in brackish-water or lagoonal settings (Hagdorn et al., 2015). The palaeoenvironment was shallow marine to lagoonal, as indicated by the presence of echinoderms and ceratitid ammonoids. The Grenzbonebed formed as a condensed section in a coastal setting, with extensive reworking of already fossilised bone fragments, scales, and teeth (Hagdorn and Reif, 1988).

3.16. Partnach Beds

The Partnach Formation is a shallow-water marine deposit. Its Furkaska and Wielkie Koryciska units date from around the Anisian–Ladinian transition based on marine invertebrates and conodonts (Kotłowski, 1996). *Tatrasuchus kulczyckii*, a medium-sized capitosauroid with nearly closed otic notches, is based on a skull from the Partnach Beds of the Wielkie Koryciska ravine near Zakopane, western Tatra Mountains, Poland (Maryńska and Shishkin, 1996; Sulej, 2009).

3.17. Miedary Beds (Lower Keuper Subgroup)

The Upper Silesia region (Śląsk) of southwestern Poland has long been known for occurrences of Triassic vertebrate fossils, but early studies largely focussed on the marine fishes and reptiles (Meyer, 1847; Gürich, 1884; Assmann, 1913). More recently, Sulej et al. (2011a) and Pawlak et al. (2022) reported tetrapod remains from lower Ladinian strata at Miedary, and recent excavations have yielded much new material that includes aquatic (both freshwater and marine) and terrestrial tetrapods (Czepiński et al., 2023). The fossils occur in glauconitic sandstones, mudstones, and limestones, and probably date from the early Ladinian (Fassanian) (Franz et al., 2013). The referral of the Miedary Beds to the Lower Keuper is based on facies similarities rather than bio- or chronostratigraphic evidence, and these beds correlate with the uppermost Muschelkalk in the central part of the CEB. The following taxa have been reported by Czepiński et al. (2023) from the Miedary locality.

Tetrapod body fossils. Overall, the assemblage at Miedary is very similar to those from the Meissner and Erfurt formations in the central region of the CEB.

Temnospondyli

***Mastodonsaurus* sp.** Recent material recovered from the M1-M2 layers of Miedary includes a well-preserved partial skull (Czepiński et al., 2023).

***Plagiosternum* sp.** Diagnostic bones of the pectoral girdle of this taxon occur in the M1-M2 layers.

Plagiosaurinae indet. A diagnostic cleithrum was found in layer M1. *Chroniosuchia*

***Bystrowiella* sp.** The M2 layer also yielded an osteoderm of this chroniosuchian that was first recognised in the Erfurt Formation.

Reptilia: Procolophonoidea

Owenettidae indet. A procolophonoid humerus resembling one of the humeri reported by Martinelli et al. (2016) from the Erfurt Formation was recovered from layer M2.

Reptilia: Archosauromorpha

Archosauromorpha indet. A series of associated cervical and dorsal vertebrae with remarkably low neural spines and distinctive osteoderms indicate the presence of a new archosauriform taxon (Czepiński et al., 2023).

***Jaxtasuchus* sp.** An osteoderm resembling armour elements of the posterior trunk region in *Jaxtasuchus salomoni* from the Erfurt Formation was found in layer M3 at Miedary (Czepiński et al., 2023).

Archosauriformes indet. Czepiński et al. (2023) distinguished eight tooth morphotypes in the Miedary sample, among which one

morphotype corresponding to large ziphodont teeth closely resembles tooth type R1 in Schoch et al. (2018) (see also Mujal et al., 2022); they likely represent *Batrachotomus* or a closely related loricatan pseudosuchian.

Palaeoenvironment. The tetrapod assemblage of the Miedary Beds resembles that of the upper Ladinian (Longobardian) Erfurt Formation of Germany (Czepiński et al., 2023) but differs in tanystropheids being the most abundant tetrapods and in the temnospondyl assemblage encompassing taxa also known from the German Upper Muschelkalk (see above). The co-occurrence of *Plagiosternum granulosum* with an enigmatic marine reptile (*Blezingeria ichthyospondyla*) and with eosauroptrygians (*Nothosaurus mirabilis*) resembles the assemblage from the Grenzbonebed in southern Germany (Hagdorn and Reif, 1988). Pawlak et al. (2022) reported a relatively wide range of salinities for the palaeoenvironments of the Miedary Beds by comparing the fishes present in this unit with other, similar assemblages such as that from Vellberg (Schoch and Seegis, 2016). The Miedary Beds may represent depositional environments with more prominent marine influence (see Pawlak et al., 2022) than those from the German Lower Keuper (Schoch and Seegis, 2016; Schoch et al., 2022).

3.18. Erfurt Formation (Lower Keuper Subgroup)

Based on its characteristic palynomorphs (e.g., *Keupersporites baculatus*) and the presence of the spinicaudatan *Euestheria minuta*, the Erfurt Formation (Lettenkeuper or Lower Keuper) is considered to be late Ladinian (Longobardian) in age. It forms a succession of alternating dolostones and mudstones with local channel sandstones (Beutler et al., 1999; Bachmann et al., 2021; Heunisch and Wierer, 2021). The sandstones are confined to a few levels and were deposited in a huge delta that extended across the CEB in a NE–SW direction, with sediment input originating in the southern Scandinavian region (Würster, 1968). Paul (2021b) postulated rather humid climatic conditions, but abundant gypsum suggests extensive arid plains between the water bodies (Nitsch, 2015). The dolostones formed during transgressive phases under usually shallow-water marine or lagoonal conditions, whereas the mudstones document the temporary existence of lakes and swamps, often forming thin coal seams and bonebeds that are rich in fish and tetrapod remains (Nitsch, 2015). A coal deposit at Gaildorf in northern Württemberg yielded the historically first fossils of the giant temnospondyl *Mastodonsaurus giganteus* from the CEB (Jaeger, 1828; Meyer and Plieninger, 1844; E. Fraas, 1889). In the twentieth century, mass accumulations of skeletal remains documenting diverse assemblages of tetrapods were discovered at Kupferzell, Vellberg, and Michelbach an der Bilz in Württemberg and at Bedheim and Molsdorf in Thuringia (Werneburg, 1994; Hagdorn et al., 2015).

Tetrapod body fossils. Most tetrapod deposits in the Erfurt Formation are bonebeds containing reworked bones and teeth or mudstones with occasional finds of skulls and disarticulated postcranial elements. At the historic Gaildorf coal mine, a pyrite-rich siltstone yielded fully articulated skeletons of *Mastodonsaurus giganteus* (Schoch, 1999). A three-month-long salvage excavation at a highway-construction site in the region of Kupferzell in 1977 yielded more than 30,000 specimens, dominated by *Gerrothorax pulcherrimus* and *Mastodonsaurus giganteus* (Schoch et al., 2022). Although less abundant, the presence of the large-bodied loricatan *Batrachotomus kupferzellensis* is noteworthy. Recent excavations at Vellberg produced a wealth of new taxa, both aquatic and terrestrial, which are represented by skeletal remains in various stages of (dis)articulation (Schoch and Seegis, 2016; Schoch et al., 2018).

Temnospondyli

***Mastodonsaurus giganteus* (Fig. 5A).** This up to 5 m long aquatic apex predator is the most abundant tetrapod in many deposits of the Erfurt Formation. It is found at many stratigraphic levels and is especially common at Gaildorf, Kupferzell, Vellberg, Michelbach, and

Wolpertshausen in Württemberg and at Arnstadt and Bedheim in Thuringia (Meyer and Plieninger, 1844; Schoch, 1999; Hagdorn et al., 2015; Schoch et al., 2024).

Tatrasuchus wildi. A smaller, up to 3 m long capitosauroid with a broad-parabolic skull is present at Gaildorf, Kupferzell, Vellberg, Michelbach and Wolpertshausen in Württemberg (Schoch, 1997, 2015a; Schoch and Moreno, 2024). Initially placed in a separate genus *Kupferzellia*, it is now assigned to *Tatrasuchus* (Schoch and Moreno, 2024).

Trematolestes hagdorni (Fig. 5B). This slender-snouted, up to 1.5 m long trematosauroid temnospondyl was first discovered at Michelbach an der Bilz and later identified in samples from Gaildorf, Kupferzell, and two layers at Vellberg (Schoch, 2006; Schoch and Mújal, 2022).

Callistomordax kugleri. This up to about 1.2 m long trematosauroid, a close relative of metoposaurids, is distinguished by large, carinate fangs and is so far known only from two horizons at Vellberg where it is common (Schoch, 2008b).

Gerrothorax pulcherrimus (Fig. 5C). In some localities, especially at Kupferzell, this small-bodied and heavily armoured plagiosaurid is the most common temnospondyl (Hellrung, 2003; Schoch and Witzmann, 2011).

Plagiosuchus pustuliferus. This large-bodied plagiosaurid is present at Gaildorf, Vellberg, and Michelbach in Württemberg and at Molsdorf in Thuringia (Damiani et al., 2009).

Plagiosternum granulolum. In addition to the Grenzbonebed horizon of the Upper Muschelkalk, this plagiosaurid is also found in dolostones and marine bonebeds in many localities in Württemberg, Bavaria and Thuringia (Warren, 1995; Hagdorn et al., 2015).

Megalophthalma ockerti. This plagiosaurid has proportionately enormous orbits and large teeth. It is known from a single skull found in a channel sandstone at Vellberg (Schoch et al., 2014).

Temnospondyli indet. A highly distinctive, robust type of humerus resembles those of terrestrial eryopiforms and was originally interpreted as a dicynodont synapsid (Lucas and Wild, 1995) but has been reidentified as an indeterminate temnospondyl (Maisch et al., 2009).

Chroniosuchia

Bystrowiella schumanni. This late-surviving chroniosuchian stem-amniote is documented by cranial and postcranial remains and is readily distinguished by its dorsal osteoderms. It is known from Kupferzell, Michelbach and Vellberg (Witzmann et al., 2008; Witzmann and Schoch, 2018).

Synapsida: Cynodontia

Nanogomphodon wildi. Hopson and Sues (2006) reported a single molariform tooth of this traversodontid cynodont from Michelbach an der Bilz.

Reptilia: Procolophonoidea

Martinelli et al. (2016) referred two isolated humeri to owenettid procolophonoids.

At Vellberg, jaws with distinctive teeth and a humerus document the presence of procolophonids (Schoch, 2015b; Martinelli et al., 2016).

Reptilia incertae sedis

Quasicognathus eothen (Fig. 5D). Dentaries with an edentulous rostrum and two large bulbous teeth and a tooth-bearing cranial fragment from Vellberg represent a close relative of the North American *Cognathus obscurus*, a still enigmatic tetrapod (Sues et al., 2022b).

Stauromatodon mohli. This distinctive taxon with uncertain affinities is based on a jaw fragment with closely spaced teeth with chisel-shaped crowns from Vellberg (Sobral et al., 2021).

Reptilia: Pan-Testudines

Pappochelys rosinae (Fig. 5E). With 18 partial skeletons and many isolated bones currently known, this up to 25 cm long stem-turtle is common at Vellberg (Schoch and Sues, 2015, 2018b).

Reptilia: Lepidosauromorpha

Vellbergia bartholomaei. This lepidosauromorph reptile has a skull length of only 1.3 cm and was described by Sobral et al. (2020). The phylogenetic analysis by Ford et al. (2021) recovered this species as the sister-taxon to Rhynchocephalia.

Fraxinisaura rozynekae. This taxon is a long-snouted lepidosauromorph with distinctive teeth from Vellberg and is closely related to the Middle-Late Jurassic *Marmoretta oxoniensis* (Schoch and Sues, 2018a; Ford et al., 2021).

Lepidosauromorpha. At least three additional, still undescribed new taxa are known from Vellberg, one of which resembles the Olenekian *Sophineta cracoviensis* from the Czatkovice cave filling (Schoch, 2015b; Sobral and Schoch, in review).

Wirtembergia hauboldae. Jones et al. (2013) first reported rhynchocephalian jaw bones with acrodont dentition from Vellberg. Sues and Schoch (2024) described much additional cranial material and found that this taxon is not only the oldest known evidence of this clade but also represents the sister taxon to all other known rhynchocephalians.

Reptilia

Frequent finds of vertebrae referable to a *Pachystropheus*-like diapsid reptile have been reported from Kupferzell, Vellberg, Wolpertshausen, and Michelbach. Articulated skeletons from Vellberg indicate that this taxon resembles the possible thalattosaur *Pachystropheus rhaeticus* (Schoch, 2015b).

Reptilia: Archosauromorpha

Rutiotomodon tythos. This small-bodied trilophosaurid was identified based on two tooth-bearing jaw fragments from Vellberg (Sues and Schoch, 2023b).

Zanclodon laevis. Plieninger (1847a) reported a distinctive jaw fragment with recurved tooth crowns lacking serrated carinae from the coal mine at Gaildorf. This specimen represents an otherwise unknown archosauriform (Schoch, 2011b).

Jaxtasuchus salomoni. Osteoderms closely resembling those of the archosauriform *Doswellia kaltenbachii* from the upper Carnian Falling Creek Formation of Virginia (USA) are common at Vellberg and other localities in Württemberg. Partially articulated skeletons document a long-necked, gracile doswelliid archosauriform with transverse dorsal rows of four rectangular osteoderms each and with distinctive, slender-crowned teeth (Schoch and Sues, 2014).

Polymorphodon adolfi (Fig. 5F). Two partial skeletons from Vellberg were identified as an early-diverging archosauriform with a tall maxilla and teeth bearing large marginal denticles pointing toward the apex of the crown (Sues, 2020). The phylogenetic analysis by Ezcurra and Sues (2022) found it close to Doswelliidae and Proterochampsidae.

Proterochampsia gen. et sp. nov. Another common reptile at Vellberg is known from a dozen skeletal remains that have osteoderms with deeply serrated margins and slender maxillae and dentaries with numerous closely set teeth (Schoch, 2015b).

Four disarticulated skeletons from Vellberg represent an about 1 m long pseudosuchian with short teeth that bear distinct apicobasal fluting and are bulbous at the bases of the crowns. This new form differs from *Batrachotomus kupferzellensis* in numerous cranial and postcranial features and thus it is unlikely that it represents juveniles of the latter (Schoch, 2011b, 2015b).

Loricata indet. Isolated bones from Vellberg, including a distinctive maxilla (Schoch, 2011b) that shares some features with an isolated maxilla of a much larger loricatan from Carnian strata of the Dockum Group of Texas (Weinbaum and Hungerbühler, 2007).

Batrachotomus kupferzellensis (Fig. 5G). This loricatan pseudosuchian is an up to at least 5 m long terrestrial apex predator. It was originally described based on several partial skeletons found at Kupferzell; later additional remains were recovered at Vellberg, Michelbach, and Wolpertshausen (Gower, 1999; Gower and Schoch, 2009). It is most closely

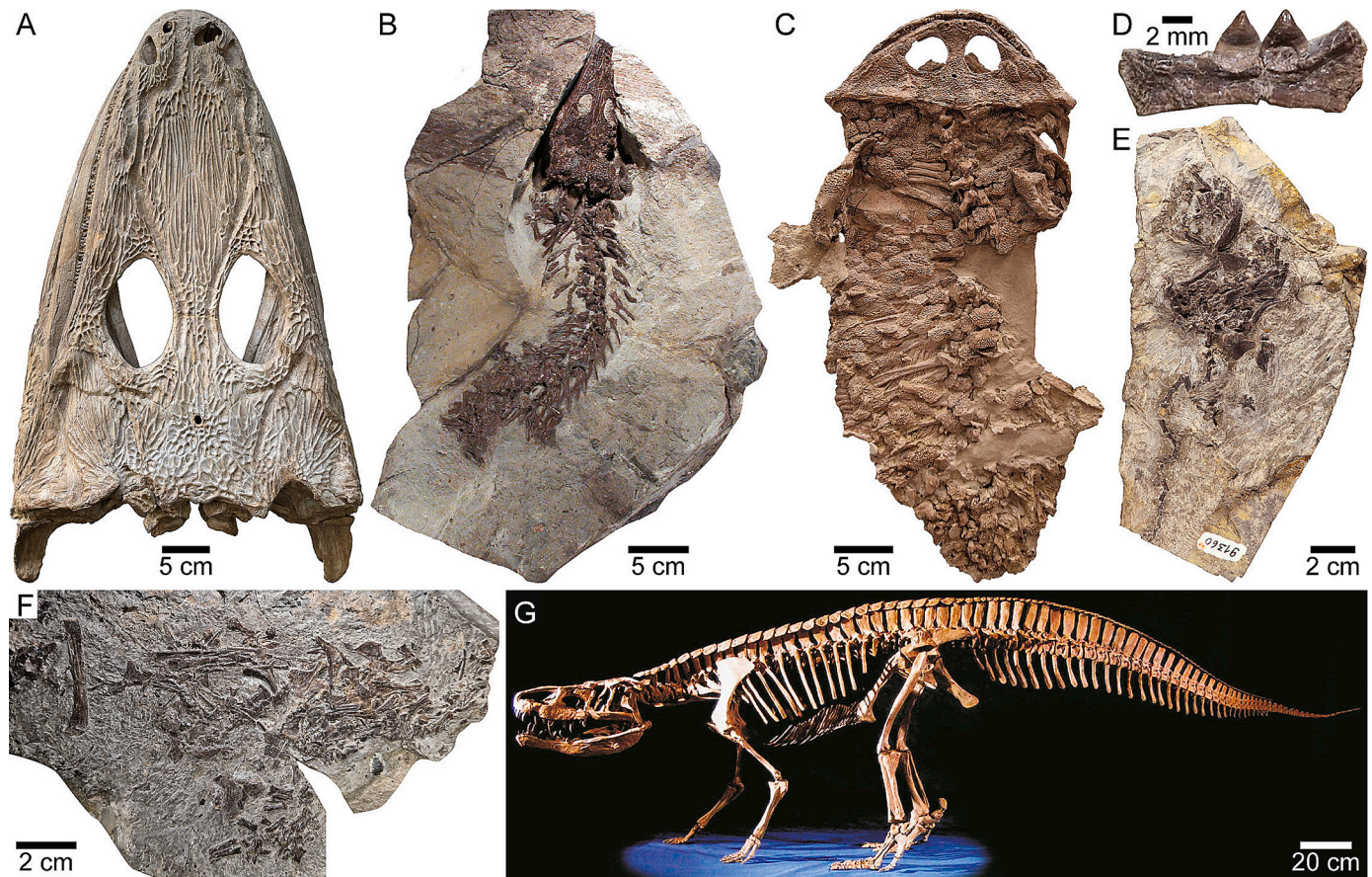


Fig. 5. Selected Triassic tetrapod fossils from the CEB in the Staatliches Museum für Naturkunde Stuttgart (SMNS) collections II. All specimens from the Erfurt Fm. (Lower Keuper, late Ladinian). A. *Mastodonsaurus giganteus* (SMNS 54677). B. *Trematolestes hagdorni* (SMNS 81790, holotype). C. *Gerrothorax pulcherrimus* (SMNS 83866). D. *Quasiclognathus eothen* (SMNS 91315). E. *Pappochelys rosinae* (SMNS 91360, holotype). F. *Polymorphodon adorfi* (SMNS 91343, holotype). G. *Batrachotomus kupferzellensis* (skeleton reconstructed from various specimens).

related to *Heptasuchus clarki* from the Middle or lower Upper Triassic of Wyoming (Nesbitt et al., 2020). An isolated complete tooth described by E. Fraas (1900) as “*Zanclodon schützii*” from the Upper Muschelkalk (Rottweil Formation, formerly Trigonodusdolomit) in the vicinity of Schwäbisch Hall closely resembles teeth of *Batrachotomus kupferzellensis*.

Tetrapod tracks. Only few tetrapod tracks have been identified from the Erfurt Formation to date. The known tracks were collected during fieldwork in different quarries. The first finds correspond to a track referable to *Chirotherium* (formerly ‘*Sphingopus*’) *ferox* (from the Hauptsandstein unit in Ilsfeld) and multiple small digit scratches corresponding to swimming traces likely produced by a temnospondyl (from the Esterienschichten unit in Bitzfeld). More recently, at the Vellberg quarry, Mujal and Schoch (2020) identified tetrapod tracks that were probably produced by a capitosauroid temnospondyl at the base of a dolostone bank (Anthrakonitbank), corresponding to microbial mats in a marginal marine setting.

Palaeoenvironment. The tetrapod assemblage of the Erfurt Formation forms the most diverse in the European Triassic and from the Ladinian worldwide. This probably results from the abundant estuarine environments in which the strata formed, with numerous water bodies existing nearby and with good potential for preserving terrestrial tetrapod remains. Three main environments and their typical tetrapod communities have been identified: (1) marine reptiles in lagoons and shallow-water marine basins, (2) temnospondyls, a chroniosuchian stem-amniote, and a *Pachystropheus*-like reptile in freshwater lakes and extensive swamps, and (3) a non-mammalian cynodont, procopelophonids, lepidosauromorphs, the stem-turtle *Pappochelys*, non-

archosaurian archosauriforms and pseudosuchians along the periphery of the lakes (Schoch and Seegis, 2016; Schoch et al., 2018, 2022). It is noteworthy that the large-bodied pseudosuchian *Batrachotomus kupferzellensis* preyed mostly on large-bodied temnospondyls, especially *Mastodonsaurus giganteus*, and on the predominantly marine reptile *Nothosaurus* (Mujal et al., 2022), thus establishing an ecological connection between aquatic and terrestrial settings.

In the Erfurt Formation, the temnospondyls reached their greatest known diversity and disparity in the CEB, with two trematosauroids, two capitosauroids, and four plagiosauroids inhabiting a variety of lake settings (Hagdorn et al., 2015; Schoch and Moreno, 2024). On land, the diversity of lepidosauromorphs and archosauriforms is particularly compelling, whereas cynodonts are extremely rare and dicynodonts, rhynchosaurs, and avemetatarsalians remain unknown (Schoch, 2015b). As outlined by Schoch et al. (2018), many tetrapods preserved in the Erfurt Formation probably subsisted on fish, whereas herbivores are difficult to identify. Of the currently known tetrapods, only the tiny trilophosaurid *Rutiotomodon tythos* and traversodontid cynodont *Nanogomphodon wildi* probably fed predominantly on plants, and *Polymorphodon adorfi* was possibly an omnivore. Many disarticulated skeletons of smaller tetrapods appear to represent regurgialites from larger predators (Schoch and Seegis, 2016).

Dorka (2002) documented an assemblage of isolated temnospondyl, archosauriform, and cynodont teeth from an upper Ladinian bonebed at Schöningen in Lower Saxony (northern Germany). Although he was uncertain regarding the precise stratigraphic correlation of this horizon, two dental morphotypes of temnospondyls from this bonebed match teeth of temnospondyls known from the Erfurt Formation.

3.19. Grabfeld and Benk formations (Middle Keuper Subgroup)

The Grabfeld Formation (Gipskeuper) formed in a much drier setting with high levels of evaporation and generally hostile conditions for aquatic life in lagoons or playa lakes (Beutler et al., 1999; Paul, 2021b). It is dominated by red or green mudstones with gypsum intercalations and regionally thick layers of salt. Marine transgressions became less frequent. The Grabfeld Formation yields sauropterygian remains at a few localities. At the south-eastern basin margin, in northern Bavaria (Upper Franconia), the Benker Sandstein represents a fluvial sandstone that has yielded a rich tetrapod ichnofauna and a single temnospondyl skull, the holotype and only known specimen of *Capitosaurus arenaceus* (Münster, 1836; Kamphausen, 1990). A dolostone layer at Kaubenheim (northern Bavaria) produced a fragment of a dermal bone referable to the plagiosaurid *Gerrothorax* sp. More surprisingly, incomplete remains of *Metoposaurus* sp., an interclavicle fragment attributable to *Plagios-ternum* sp., and an intercentrum of an indeterminate capitosauroid were collected at Affaltrach, northern Baden-Württemberg, and Neustadt an der Aisch, Bavaria, respectively (Moreno et al., 2024a).

The base of the Estherienschiefer coincides with the lowermost Carnian (Cordevolian) based on the presence of the spinicaudatan *Laxitextella multireticulata* (Bachmann et al., 2021) and on the palynomorph association (Heunisch and Wierer, 2021). In the Bayreuth region, the Estherienschiefer have yielded a low-diversity tetrapod ichnofauna dominated by *Chirotherium* (“*Parachirotherium*”) *postchirotherioides* and *Rhynchosauroides* isp. (Klein and Kneidl, 2015). Additional tetrapod footprints have been reported from the Benk Formation (Haubold and Klein, 2002), which is the stratigraphical equivalent of the Grabfeld Formation in Upper Franconia. This formation is located at the southern margin of the basin and is composed of proximal alluvial deposits. The tetrapod ichnoassociations often include chirotheriid-like footprints that have been identified as “*Parachirotherium*” (= *Chirotherium*; Klein and Lucas, 2021). The upper portion of the formation preserves tracks from the “*Parachirotherium*”-*Atreipus-Grallator* group as well as *Brachychirotherium*.

3.20. Stuttgart Formation (Middle Keuper Subgroup)

This formation encompasses clastic, largely evaporite-free strata that were deposited in large fluvial channels and on floodplains in a basin dominated by vast streams and deltas (Wurster, 1968). Because of its abundance in plant remains (mostly equisetaleans), it was traditionally referred to as Schilfsandstein (“reed sandstone”) (Benton, 1994; Beutler et al., 1999). Palynological data place the formation in the *Aulisporites astigosus* zone, which is Julian in age (Fijałkowska-Mader et al. (2015). Zircon-dated tephra recently provided a radiometric date for the Stuttgart Formation (231 Ma), placing it in the early Tuvanian (Zeh et al., 2021).

The majority of tetrapod fossils was collected from channel deposits that formed in larger streams within the huge delta setting described in detail by Wurster (1962, 1968). The classical localities were discovered during quarrying in the nineteenth century when large building-stone quarries operated at Stuttgart (Feuerbacher Heide) and Heilbronn (Jägerhaus) and include a range of smaller exposures in the Winnenden and Tübingen regions of Württemberg. Benton and Wild (in Benton, 1994) provided a detailed inventory of localities known at the time. In 1932, a fossil-bearing claystone was found in a former clay pit at Mittelhausen (now part of Erfurt), Thuringia (Michael, 1932; Werneburg, 1990). This horizon yielded disarticulated skeletal remains of *Metoposaurus diagnosticus*, *Cyclotosaurus robustus*, and plagiosaurs, as well as osteoderms of a new doswelliid archosauriform (Sues and Schoch, in press). A second type of deposit are conglomerate horizons at Markt Obernzenn and Sulzbach-Laufen, which have yielded fragmentary remains of the temnospondyls *Metoposaurus diagnosticus* and *Gerrothorax pulcherrimus*, archosaurian teeth, and a partial dicynodont mandible (Schoch, 2012). However, the most recent finds, collected by personnel

from the Staatliches Museum für Naturkunde Stuttgart, came from a local lacustrine mudstone deposit within the Stuttgart Formation in the Limpurger Berge near Gaildorf, and are reported here for the first time. These complement the finds from the channel facies that has usually yielded only disarticulated remains of large tetrapods. The newly discovered lacustrine deposit contains a diverse fish fauna associated with disarticulated skeletal remains of tiny reptiles and bones of small specimens of *Metoposaurus diagnosticus*, but plagiosaurs or *Cyclotosaurus robustus* have not been found to date.

Tetrapod body fossils. Currently known taxa include:
Temnospondyli

Cyclotosaurus robustus (Fig. 6A). *Mastodonsaurus keuperinus*, based on a snout fragment (E. Fraas, 1889) from Stuttgart (Meyer and Plieninger, 1844; Quenstedt, 1850), has recently been referred to *C. robustus* (Schoch et al., 2023, 2025).

Cyclotosaurus buechneri. This species, closely related to *C. robustus*, is known from the Stuttgart Formation of Bielefeld-Sieker, North Rhine-Westphalia (Witzmann et al., 2016).

Metoposaurus diagnosticus. This temnospondyl has been recovered from deposits at Feuerbacher Heide in Stuttgart, Hanweiler, Markt Obernzenn, and Mittelhausen near Erfurt (Meyer and Plieninger, 1844; E. Fraas, 1889; Michael, 1932; Werneburg, 1999; Sulej, 2007).

Hyperokynodon keuperinus. Two partial skulls from the Jägerhaus quarry near Heilbronn represent one of the largest and stratigraphically youngest known trematosaurids (Hellrung, 1987; Schoch, 2024).

Gerrothorax pulcherrimus. This plagiosaurid is known from a single dermal bone from Feuerbacher Heide, Stuttgart (Hellrung, 2003; Schoch and Witzmann, 2011).

Synapsida: Dicynodontia

A partial mandible of a kannemeyeriiform dicynodont was reported from a conglomerate horizon at Markt Obernzenn, Bavaria (Schoch, 2012). Szczypiński and Sulej (2023) referred this specimen to *Woznikella triradiata*, which is documented by extensive cranial and post-cranial remains, possibly representing a single individual, from the Grabowa Formation at Woźniki, Poland.

Reptilia: Lepidosauromorpha

Still unidentified jaw elements of a very small reptile (10 mm estimated skull length) with peg-like teeth have been found at the new locality in the Limpurger Berge.

The new Gaildorf locality has yielded several rhynchocephalian jaws with acrodont teeth.

Reptilia

Pachystropheus-like taxon. Mandibular remains resembling those the *Pachystropheus*-like reptile of the Erfurt Formation, indicating skulls with a length of 2–3 cm, have been found at the new locality in the Limpurger Berge.

Reptilia: Archosauromorpha

Uatchitodon sp. A grooved tooth crown from Limpurger Berge closely resembles teeth of the possibly archosauriform reptile *Uatchitodon kroehleri* from the upper Carnian Vinita Formation of Virginia, USA (Sues, 1991).

Thuringopelta werneburgi. Distinctive osteoderms of a new doswelliid archosauriform (originally attributed to *Mastodonsaurus*; Michael, 1932) were recently identified from Mittelhausen near Erfurt in Thuringia (Sues and Schoch, 2025).

“*Zanclodon*” *arenaceus*. A jaw fragment from Feuerbacher Heide, Stuttgart, was named by E. Fraas (1896). Hungerbühler (2001) considered it *incertae sedis* among Archosauriformes, but most authors including Dzik and Sulej (2007) have referred this taxon to phytosaurs.

Dyoplax arenaceus. Known from a complete but poorly preserved natural mould of much of a skeleton from a quarry at Sonnenberg, SE

Stuttgart (O. Fraas, 1867), this taxon is now considered an erpetosuchid pseudosuchian (Maisch et al., 2013; Foffa et al., 2020).

Isolated ziphodont teeth attributable to large pseudosuchians resembling those of *Batrachotomus* have been found at Obernzenn, Sulzbach, and Gaildorf.

Tetrapod tracks. At Feuerbacher Heide, the Stuttgart Formation yielded a track sequence of *Chelonipus* (Fig. 6B), an enigmatic ichnotaxon that has traditionally been referred to stem-turtles (Lichtig et al., 2018) but could also have been produced by capitosaurids or, more generally, temnospondyls (Klein, 2021; Mújal and Schoch, 2020). *Apatopus lineatus*, an ichnotaxon for tracks probably produced by phytosaurs (Baird, 1957), has been reported from the Ansbacher Sandstein within the Stuttgart Formation of northern Bavaria (Klein and Lucas, 2013, 2015). *Rhynchosauroides* is particularly abundant in some horizons (Haubold and Klein, 2002).

Palaeoenvironments. The Stuttgart Formation forms the thickest siliciclastic unit in the German Keuper. It represents the classic example of the Carnian Humid Episode (formerly Carnian Pluvial Event; Ruffell et al., 2016), although Franz et al. (2021b) argued that the humid conditions during the deposition of this unit resulted from eustatic sea level changes rather than a period of increased precipitation. Zeh et al. (2021) argued that the Carnian Humid Episode started in the Stuttgart Formation (Tuvallian 2) three million years later than in the north-western Tethys region. The depositional environments of the Stuttgart Formation resembled those of the upper Ladinian Erfurt Formation, with numerous river channels, floodplains, and lakes in a vast deltaic setting (Beutler et al., 1999; Franz and Barnasch, 2021). Two pulses of deltaic sedimentation were interrupted by a shallow marine transgression (Gaildorfer Bank; Seilacher, 1943). The river channels themselves were probably also under marine influence because Gehrmann and Aigner (2002) reported evidence of tidal features in some rock units at Heilbronn, where the giant trematosaurid *Hyperokynodon keuperinus* was found. This taxon is absent at Feuerbacher Heide and has not been found together with other temnospondyls. The Stuttgart localities yielded phytosaurs and the erpetosuchid *Dyoplax*, and the Mittelhausen site preserved numerous osteoderms of a new doswelliid archosauriform reptile. The absence of skeletal remains of avemetatarsalians is noteworthy, and, unlike in the slightly younger Weser Formation, there are also no tracks indicating the presence of this archosaurian clade. Near the top of the Stuttgart Formation, the formation of gypsum commenced again, suggesting the advent of more arid conditions (Paul, 2021b).

3.21. Weser Formation (Middle Keuper Subgroup)

This upper Carnian (Tuvallian) formation is widespread in southern and central Germany and encompasses fine-grained deposits of playa lakes (Rote Wand, Lehrbergschichten) and sandstones from fluvial systems (Kieselsandstein, Blasensandstein). Its base is marked by the Beaumont horizon, which represents a marine transgression far into northern Germany. The dating of the Weser Formation is based on the appearance of the bivalve *Costatoria vestita* (Bachmann et al., 2021).

Tetrapod body fossils. This formation has yielded tetrapod finds only at a few sites in southern Germany, mostly in the Stuttgart region (Lehrbergschichten; Seegis, 1997), the Swabian Forest (Kieselsandstein, see Brenner, 1973; Milner and Schoch, 2004), and a now abandoned sandstone quarry at Ebrach in Upper Franconia (Blasensandstein; Kuhn, 1933). Benton and Wild (in Benton, 1994) provided a detailed list of localities known at the time.

Temnospondyli

Cyclotosaurus ebrachensis. This taxon is based on a single well-preserved skull from Ebrach (Kuhn, 1933; Schoch and Moreno, 2024; Schoch et al., 2025).

Metoposaurus diagnosticus (Fig. 6C). Several finds from the

Lehrbergschichten and one each from the Kieselsandstein and Blasensandstein make this temnospondyl the most commonly recovered tetrapod from the Weser Formation (Milner and Schoch, 2004).

Gerrothorax pulcherrimus. Fragmentary but diagnostic remains from the Stuttgart area document the presence of this plagiosaurid in the Lehrbergschichten (Hellrung, 2003), and Kuhn (1933) reported an interclavicle (as *G. franconicus*) from Ebrach.

Synapsida: Cynodontia

Lucas et al. (2001) reported a (now apparently lost) jaw fragment with a postcanine tooth of a mammal-like cynodont from Geissgurgelbach in the Welzheim Forest in Württemberg.

Reptilia: Lepidosauromorpha

Polysphenodon muelleri. A skull with an associated series of vertebrae and the left fore- and hindlimb of this rhynchocephalian was found in a drill core from the Steinmergelkeuper sequence at Fallersleben near Hannover (Jaekel, 1911; Fraser and Benton, 1989).

Reptilia: Archosauromorpha

Ebrachosaurus singularis. This aetosaurian taxon was based on a specimen comprising a set of osteoderms and an ilium lost during WWII (Kuhn, 1936).

Parasuchus (formerly '*Francosuchus*') *angustifrons*. An excellently preserved skull of this phytosaur was found at Ebrach (Butler et al., 2014; Kammerer et al., 2016).

Ebrachosuchus neukami. A form with a greatly elongated snout represents a second phytosaur taxon from Ebrach (Butler et al., 2014).

Reptilia indet.

Brenner (1973) reported unidentified reptilian teeth from a bonebed on top of the lower Kieselsandstein in Württemberg.

Tetrapod tracks. There is a substantial record of tetrapod tracks from the Blasensandstein of northern Bavaria, the Ansbacher Sandstein (Lehrbergschichten level) (both equivalent to the Steigerwald Formation, which is also present in the Stuttgart region and is coeval with the base of the Weser Formation in southern Germany), and the Kieselsandstein in northern Württemberg (Hassberge Formation, which is laterally equivalent to the Weser Formation and overlies the Steigerwald Formation in southern Germany). The ichnoassemblages from the upper Carnian Steigerwald Formation in northern Bavaria are most similar, almost equivalent to those from the Stuttgart Formation and additionally include "*Chirotherium*" *wondrai*, *Atreipus-Grallator* (*Atreipus metzneri*) (Haubold and Klein, 2002; Klein, 2021, 2025). The ichnofaunas from the Hassberge Formation in northern Bavaria and the Stuttgart region include the type material of *Brachychirotherium hassfurtense* and *B. thuringiacum* as well as the ichnotaxa *Apatopus lineatus*, *Atreipus-Grallator*, *Grallator cursorius* (Fig. 6D), *Atreipus* isp., *Evazoum* isp. (Fig. 6D), *Brachychirotherium* isp., *Rhynchosauroides* isp. (Fig. 6D), and *Procolophonichnium lockleyi* (Haubold and Klein, 2002; Haderer, 2012, 2015, 2017; Klein et al., 2015; Klein and Lucas, 2013, 2015, 2021, 2025, and references therein). *Grallator* is better documented from the Hassberge and Löwenstein formations (Haubold and Klein, 2002).

Palaeoenvironments. The deposition started with the sedimentation of red mudstones (Rote Wand) in widespread hypersaline settings (Beutler et al., 1999; Bachmann et al., 2021). The strata of the somewhat younger Lehrbergschichten formed in a succession of larger and more permanent water bodies. These offered improved ecological conditions, especially during deposition of the third Lehrbergbank, which has yielded a low-diversity invertebrate and fish fauna (Seegis, 1997). In this lacustrine ecosystem, *Metoposaurus diagnosticus* was the apex predator, accompanied by the euryhaline *Gerrothorax pulcherrimus* (Seegis, 1997). As in the small lacustrine deposit of the Stuttgart Formation in the Limpurger Berge, the temnospondyls were small-sized, possibly a plastic response to the relatively poor environmental conditions. The Lehrberg lakes were subject to repeated evaporation (Seegis, 1997; Beutler et al., 1999),



(caption on next page)

Fig. 6. Selected Triassic tetrapod fossils from the CEB in the Staatliches Museum für Naturkunde Stuttgart (SMNS) collections III. Specimens from the: Carnian, Stuttgart Formation (A, B), Weser Fm. (C) and Hassberge Fm. (D); Norian, Lower Arnstadt Fm. (E–J) and Trossingen Fm. (K, L). A. *Cyclotosaurus robustus* (SMNS 5775). B. *Chelonipus torquatus*, convex hyporelief (SMNS 19107, holotype of *Chel. "plieningeri"*). C. *Metoposaurus diagnosticus* (SMNS 56633). D. *Evazoum* isp. (*Eva*), *Grallator cursorius* (*Gra*), and *Rhynchosauroides* isp. (*Rhy*), convex hyporelief (SMNS 81826). E. *Nicosaurus kapffi* (SMNS 4379). F. *Aetosaurus ferratus* (SMNS 5770, holotype). G. *Paratypothorax andressorum* (SMNS 19003). H. *Saltoposuchus connectens* (SMNS 12352a). I. *Procompsognathus triassicus* (SMNS 12591, holotype). J. cf. *Isochirotherium* isp., convex hyporelief (SMNS 56605). K. *Isochirotherium* isp., convex hyporelief (SMNS 97139). L. *Proganochelys quenstedtii* (cast of SMNS 16980). M. *Plateosaurus* sp. (SMNS 58958).

which must have resulted in fluctuating salinity levels.

The streams formed braided or meandering rivers with narrow channels (Beutler et al., 1999). As in the channel facies of the Stuttgart Formation, *Cyclotosaurus robustus* was a stream-dwelling aquatic predator, but, during the late Carnian, it co-existed with phytosaurs, arguably the stratigraphically oldest known in the CEB (but see discussions on "*Zanclodon*" *arenaceus* and *Mesorhinosuchus fraasi*). The sparse remains of the putative aetosaur, *Ebrachosaurus singularis*, were also preserved in a channel deposit, much like the Norian aetosaur occurrences. Terrestrial tetrapods were apparently restricted to the shores of the water bodies. Skeletal remains of dinosaurs or dinosauriforms have not yet been found in the upper Carnian strata of the CEB, but their tracks attributable to these groups are common (Haderer, 2012, 2015, 2017). Their body fossils would most likely be preserved in floodplain deposits that have not been identified to date.

3.22. Grabowa Formation (Middle Keuper Subgroup)

In Śląsk (former Upper Silesia), Poland, the strata of the Grabowa Formation formed on a vast floodplain under a pronounced seasonality, containing alternating palaeosol horizons, lacustrine mudstones, and high-energy fluvial conglomerates (Jewuła et al., 2019). The large clay pit at Krasiejów (Opole Voivodeship) was discovered in 1974, when the Strzelce cement plant extensively exposed mudstones. Dzik and Sulej (2007) dated the Krasiejów sequence as Carnian based on the presence of the phytosaur *Parasuchus*. Palynological analysis by Fijałkowska-Mader et al. (2015) placed Krasiejów in the *Classopolis meyeriana* Zone, which is middle Norian in age. However, Qvarnström et al. (2024) noted that ongoing research on bromalites from the Krasiejów section has recovered palynomorphs that are widely known from Carnian-age deposits in the CEB. The pit exposes the the *Ozimek* Member and the Patoka Member of the Grabowa Formation, with mudstones and siltstones with grainstone lenses (Fijałkowska-Mader et al., 2015; Qvarnström et al., 2024). The tetrapod assemblage from the Woźniki clay pit closely resembles that from Krasiejów in its composition (Qvarnström et al., 2024). As in the Trossingen Formation (see section 3.26), Vertisol formation resulted in a large-scale homogenization of the sediments (Szulc, 2005).

Tetrapod body fossils Temnospondyli

Cyclotosaurus intermedius. A complete skull and various cranial and postcranial remains document the presence of this large-sized capitosaur at Krasiejów (Sulej and Majer, 2005).

Metoposaurus krasiejowensis. This temnospondyl is represented by the bulk of the skeletal remains of temnospondyls at Krasiejów. Sulej (2007) published a major monograph on its anatomy. He proposed a subspecies *M. diagnosticus krasiejowensis* for the reception of the material (Sulej, 2002), which Brusatte et al. (2015) subsequently elevated to the species level, *M. krasiejowensis*.

Synapsida: Dicynodontia

Woźnikella triradiata. Szczygielski and Sulej (2023) described this medium-sized kannemeyeriiform dicynodont based on cranial and postcranial remains, possibly representing a single individual, from Woźniki.

Synapsida: Cynodontia

Polonodon woznikiensis. A single non-mammaliaform cynodont tooth from the Woźniki clay pit was reported by Sulej et al. (2020). Kowalski et al. (2019) referred additional isolated cynodont teeth from Krasiejów to the same taxon.

Reptilia: Testudinata

Proterochersis cf. *P. porebensis*. Czepiński et al. (2021) reported several fragments of the carapace, plastron, and postcranial bones of this fully shelled stem-turtle from Kocury.

Reptilia: Lepidosauromorpha

Rhynchocephalia. Kowalski et al. (2019) described jaw fragments of a variety of rhynchocephalians from Krasiejów, which they tentatively identified as cf. *Diphydontosaurus*, cf. *Planocephalosaurus*, and cf. *Clevosaurus*.

Reptilia: Archosauromorpha

Ozimek volans. This remarkable, small-sized archosauromorph, with an elongate neck and very long and gracile limb bones, was described based on several articulated specimens from Krasiejów (Dzik and Sulej, 2016). The structure of its cervical vertebrae and scapula indicates tanystropheid affinities (Pritchard and Sues, 2019; Spiekman et al., 2021a).

Tanystropheidae indet. Dzik and Sulej (2007) illustrated a small cervical vertebra from Krasiejów that is probably referable to a tanystropheid.

Archosauromorpha indet. Recurved teeth with longitudinal striations and non-serrated carinae were documented by Czepiński et al. (2021).

Parasuchus sp. Well-preserved material of this early-diverging phytosaur was excavated at Krasiejów (Dzik and Sulej, 2007). Specific identification must await a detailed study of these specimens.

Kowalski et al. (2019) reported isolated teeth of the possible pseudosuchian cf. *Protecovasaurus* and the aetosaur cf. *Revueltosaurus* from Krasiejów.

Stagonolepis olenkae. Sulej (2010) described several disarticulated specimens of this aetosaur, which he considered closely related to *Stagonolepis robertsoni* from the Lossiemouth Sandstone Formation of Scotland.

Kocurypelta silvestris. This paratypothoracine aetosaur was named by Czepiński et al. (2021) based on a left maxilla and osteoderms from Kocury.

Polonosuchus silesiacus. Based on cranial bones, vertebrae, and osteoderms (Sulej, 2005), this up to 6 m long rauisuchid loricatan is closely related to the poorly known German *Teratosaurus suevicus* and the North American *Postosuchus* spp. (Brusatte et al., 2009).

Archosauria indet. Vertebral remains and a skull bone have been referred to archosaurs, but their fragmentary nature precludes a confident taxonomic identification (Czepiński et al., 2021).

Silesaurus opolensis. This taxon represents a distinct clade of non-dinosaurian dinosauriforms, Silesauridae, which since has also been identified from the United States, Brazil, Morocco, and Tanzania (Dzik, 2003; Nesbitt et al., 2017). It is documented by an extensive suite of skeletal remains from Krasiejów. Coprolites attributed to *Silesaurus* contain many beetle elytra (Qvarnström et al., 2019, 2024). Many phylogenetic analyses (e.g., Nesbitt et al., 2010) found Silesauridae as the sister-taxon to Dinosauria. Recently, Norman et al. (2022), however,

presented an alternative hypothesis that Silesauridae represents a paraphyletic assemblage of stem-ornithischians and proposed a new ornithischian clade Parapredentata, which they defined as the least inclusive clade that includes *Iguanodon bernissartensis* and *Silesaurus opolensis*.

Velocipes guerichi. This theropod taxon is based on a partial fibula from Kocury (Huene, 1932b; Skawiński et al., 2017).

Tetrapod tracks. A few footprints have been reported from different horizons within the Grabowa Formation (Pieńkoski et al., 2014), and particularly from Woźniki (Sulej et al., 2011b), where dinosauro-morph tracks are the most common tetrapod footprints (Qvarnström et al., 2024). Altogether, the tracks reported were identified as cf. *Grallator* isp., *Brachychirotherium* isp., cf. *Apatopus* isp., *Chirotheriidae* indet., cf. *Pseudotetrasauropus* isp., a 'lacertoid-like' track (possibly *Rhynchosaur-oidea*), indeterminate tracks supposedly produced by large synapsids (possibly dicynodonts), and swimming traces. Tracks are preserved in sandstone and likely limestone beds within floodplain deposits (Pieńkoski et al., 2014).

Palaeoenvironment. The Krasiejów deposit formed in a freshwater lake that was under fluvial influence. The different frequencies of tetrapod remains in the lacustrine marlstones and cross-laminated channel mudstones suggest habitat partitioning, with *Metoposaurus diagnosticus* and *Parasuchus* sp. dwelling in the lake and *Cyclotosaurus intermedius* inhabiting either the river or lake shores (Dzik and Sulej, 2007). Both temnospondyls were large-bodied, indicating better living conditions than in the impoverished lakes of the Lehrbergschichten in southern Germany. The lacustrine biota encompasses characean algae, molluscs, crustaceans, actinopterygians and dipnoans. The river introduced carcasses of terrestrial reptiles, which shed light on the community further inland. In this habitat, the rauisuchid loricatan *Polonosuchus silesiacus* probably preyed on the omnivorous or herbivorous *Stagonolepis olenkae* and the possibly omnivorous *Silesaurus opolensis*.

The recently rediscovered Kocury locality near Dobrodzień northeast of Opole exposes claystones and mudstones that possibly belong to the Patoka Member of the Grabowa Formation (Czepiński et al., 2021). It long ago yielded the proximal portion of a theropod fibula described by F. Huene (1932b) as *Velocipes guerichi* (Skawiński et al., 2017). Recent excavations at Kocury recovered shells and other postcranial remains of the stem-turtle *Proterochersis* cf. *P. porebensis*, osteoderms and bones of the aetosaur *Kocurypelta silvestris*, archosauromorph teeth, skeletal remains of indeterminate archosaurs, and dipnoan remains (Czepiński et al., 2021; Qvarnström et al., 2024).

3.23. Lisowice Beds and Woźniki Limestone Member (Middle Keuper Subgroup)

Both the Lisowice Beds and Woźniki Limestone Member are part of the Grabowa Formation (Jewuła et al., 2019) but considering the different lithologies (carbonate rather than siliciclastic) and faunas compared to other sites exposing the formation, these units are listed in a separate section. In Śląsk, grey mudstones and sandstones exposed in the Lipie Śląskie clay pit near Lubliniec have yielded numerous skeletal remains of tetrapods. The bones are either embedded in limestone concretions or covered with calcareous and pyritic crusts. The fossil assemblage includes dipnoans, a hybodont shark, and palaeonisciform fishes (Dzik et al., 2008) as well as various tetrapod taxa. Dzik et al. (2008) dated the Lipie Śląskie occurrence as Rhaetian, but detrital zircon dating indicates that the Lisowice Beds have a maximum depositional age of late Norian (Kowal-Linka et al., 2019). Furthermore, the dominance of conifer pollen, especially *Classopollis meyeriana*, supports a middle-late Norian date (Fijałkowska-Mader et al., 2015). The Lipie Śląskie occurrence is stratigraphically younger than the Krasiejów deposits.

Tetrapod body fossils. The Lipie Śląskie clay-pit preserves skeletal

remains of a diverse tetrapod assemblage.

Temnospondyli

A large cyclotosaur is documented by cranial and postcranial remains. Based on the size of the mandible it attained an estimated skull length of 75 cm (Sulej and Niedźwiedzki, 2010).

Plagiosauridae. Represented by several elements including osteoderms (Sulej and Niedźwiedzki, 2010).

Synapsida: Dicynodontia

Lisowicia bojani. This giant kannemeyeriiform dicynodont is known from the remains of a large, partial skeleton (Sulej and Niedźwiedzki, 2019; Sulej et al., 2024). The humerus and femur are 49 cm and 56 cm long, respectively.

Synapsida: Cynodontia

Polonodon sp. This non-mammalian cynodont is represented by bi- and multicuspid postcanine teeth (Sulej et al., 2020).

Synapsida: Cynodontia: Mammaliaformes

Hallautherium sp. This morganucodontan mammaliaform is documented by a lower molariform tooth (Świło et al., 2014).

Reptilia: Archosauromorpha

Smok wawelski. This 5–6 m long pseudosuchian (Niedźwiedzki et al., 2012) was originally identified as a dinosaur (Dzik et al., 2008) but published anatomical details suggest affinities with Paracrocodylomorpha. It is known from a partial skeleton including a well-preserved braincase with distinctive features from Lisowice. Additional teeth and postcranial bones were subsequently recovered from a locality at Marciszów near Zawiercie (Niedźwiedzki and Budziszewska-Karwowska, 2018).

Coelophysoidea indet. A coelophysoid theropod is documented by cervical vertebrae and footprints in an intercalated sandstone (Dzik et al., 2008).

Pterosauria indet. A pterosaur is known from wing-finger phalanges (Kowal-Linka et al., 2019).

Tetrapod tracks. The Zawiercie locality, corresponding to the Woźniki Limestone in the Kraków-Częstochowa Upland of southern Poland, preserves sparse footprints of archosaurs and probably dicynodonts (Sadlok and Wawrzyniak, 2013). According to these authors, some footprints might be attributable to dinosaurs, but the poor preservation of the specimens precludes confident identification. The purported dicynodont tracks are large, in line with the presence of the giant dicynodont in the same stratigraphic horizon.

3.24. Patoka Member of Grabowa Formation (former Zbąszynek Beds) (Middle Keuper Subgroup)

The Poręba clay pit in the Kraków-Częstochowa Upland (Jura Krakowsko-Częstochowska) in southern Poland exposes a section of yellow carbonate conglomerates and grey fluvial mudstones, which are interbedded with horizontally stratified sandstones (Sulej et al., 2012). The tetrapod remains accumulated in bone breccias. The sequence, formerly known as Zbąszynek Beds, is in Subzone IVb of the *Corollina meyeriana* Zone, which is middle or late Norian in age (Niedźwiedzki et al., 2014) and now referred to the Patoka Member of the Grabowa Formation (Qvarnström et al., 2024). These rocks constitute fluvial strata with alternating mudstones, conglomerates, and sandstones. The depositional setting is generally interpreted as a semi-arid alluvial plain/lacustrine environment, differing from other localities included in the same geological unit (see section 3.22).

Tetrapod body fossils. Sulej et al. (2012) and Niedźwiedzki et al. (2014) provided a summary of the tetrapod assemblage from this unit. Although some taxa have been studied in more detail, others have yet to

be described. We report all taxa for which information is available.

Temnospondyli

Temnospondyli indet. Isolated teeth and a shaft of a large bone possibly belong to large temnospondyls (Niedźwiedzki et al., 2014).

Reptilia: Pan-Testudines

Proterochersis porebensis. This fully shelled stem-turtle is known from complete carapaces and postcranial bones (Szczygielski and Sulej, 2016). Its skeletal remains represent over 80 % of the recovered tetrapod bones (Qvarnström et al., 2024).

Reptilia: Archosauromorpha

Aetosauria indet. An armour spine, a dorsal vertebra, and multiple fragments of osteoderms were recovered during several excavations (Sulej et al., 2012).

Silesauridae indet. This group of dinosauriforms is represented by the proximal end of a femur (Niedźwiedzki et al., 2014).

Herrerasauridae indet. Niedźwiedzki et al. (2014) based this identification of an incomplete scapulocoracoid, the proximal portion of a femur, and the proximal end of a fibula.

Theropoda indet. An articulated pelvis and the distal portion of a tibia a theropod suggest possible coelophysoid affinities (Sulej et al., 2012; Niedźwiedzki et al., 2014).

Tetrapod tracks. A few track occurrences have been reported from Skarszyn, a locality exposing strata formerly correlated to the Patoka Member (former Zbąszynek Beds; Gierliński, 2009). Footprints were preserved at the base of coarse-grained clastic deposits and were assigned to the dinosaurian ichnotaxa *Evazoum* isp. and *Pseudotetrasauropus* isp.

3.25. Lower Arnstadt and Löwenstein Formation (Middle Keuper Subgroup)

The Norian Arnstadt Formation (classically known as Steinmergel-keuper) includes many different playa deposits formed under arid conditions in the central part of the CEB (Franz and Barnasch, 2021). The Arnstadt and Löwenstein formations begin in the zone of the spinicaudatan *Euestheria buravasi* (Bachmann et al., 2021). In southern Germany, the Löwenstein Formation (corresponding to proximal facies, laterally equivalent to the lower portion of the Arnstadt Formation northwards; Hauschke et al., 2021) contains up to four sandstone units (classically known as Stubensandstein S1–S4), which derived from sediment sources in the neighbouring Bohemian Massif. In this region, on the margin of the CEB, the succession is intercalated with mudstone sequences and is referred to as the Löwenstein Formation (Etzold and Schweizer, 2005; Hauschke et al., 2021). The upper part of the Löwenstein Formation, corresponding to the Trossingen Formation in southern Germany and Klettgau Formation in Switzerland, is discussed separately below.

The channel deposits alternate with red mudstones (floodplain) and carbonates (lake deposits), with abundant pedogenic horizons and locally thin coal seams. Most of the water bodies were small ponds. Larger lakes probably had hypersaline conditions, but some were inhabited by bivalves, semionotids, and dipnoans. The stream deposits include those from complex, condensed channels arranged in up to 10 km wide belts along with abundant sheet flood and crevasse splay deposits (Brenner, 1973; Junghans et al., 1997).

Classical tetrapod localities of the Stubensandstein in southern Germany are situated in S1 at Kaltental and Heselach in the Stuttgart area, S2 at Aixheim-Neuhaus and Burrer's quarry at Pfaffenhofen in the Stromberg region, and S3 at Untere Mühle near Trossingen in the Baar region (Berckhemer, 1938; Brenner, 1973; Hungerbühler, 1998).

Tetrapod body fossils. Tetrapod body fossils are much more common than in the Weser Formation (Brenner, 1973; see section 3.21), with the taxonomic diversity and abundance in the lower Stubensandstein (S1) being higher than those in the Weser Formation and peaking in the

middle Stubensandstein (S2). In the upper Stubensandstein (S3, S4), fossils become much less common (Brenner, 1973). The tetrapods include the biostratigraphically significant taxa *Aetosaurus* and *Myrstriosuchus*, which are also found in northern Italy in strata from the *Mesohimavatites columbianus* ammonoid zone, which dates from the late Alauian (Bachmann et al., 2021).

Temnospondyli

Cyclotosaurus posthumus. Two skulls from Pfaffenhofen (E. Fraas, 1889) and five additional specimens from Magstadt near Stuttgart document the presence of this large aquatic capitosauroid in fluvial sandstones (E. Fraas, 1913a; Schoch and Moreno, 2024; Schoch et al., 2025).

Metoposaurus diagnosticus. A single specimen in the Natural History Museum (London), labelled only as coming from "Stuttgart", was reported by Milner and Schoch (2004). The very different bone colour and matrix composition rule out its origin from the Stuttgart Formation (e.g., at Feuerbacher Heide) but are consistent with finds from the Middle Stubensandstein (S2) of the southwestern Stuttgart area.

Gerrothorax pulcherrimus. A large skull and associated postcranial remains were found in a light grey sandstone at Pfaffenhofen (E. Fraas, 1913a; Hellrung, 2003; Schoch and Witzmann, 2011).

Reptilia: Testudinata

Proterochersis robusta. A total of 20 steinkern specimens of this fully shelled stem-turtle were found at Stuttgart (Rohracker) and Rudersberg, Lorch and Murrhardt in the Swabian Forest region (E. Fraas, 1913b; Joyce et al., 2013). Its shell is dome-shaped. Karl and Tichy (2000) placed several specimens from Murrhardt in Württemberg in a new taxon, *Murrhardtia staeschei*, but Szczygielski and Sulej (2016) synonymised it with *P. robusta*.

Proganochelys quenstedtii. First reported from a single steinkern from the S3 of Neuhausen/Aich near Tübingen (Baur, 1887), this large-bodied, more flat-shelled stem-turtle became better known from finds in the upper Norian Trossingen and Klettgau formations (see below). A large, complete specimen from Aixheim-Neuhaus forms the stratigraphically oldest known record of this taxon (Gaffney, 1990).

Keuperotesta limendorsa. Szczygielski and Sulej (2016) recognised a third stem-turtle based on a specimen from Rudersberg.

Reptilia: Archosauromorpha

Nicrosaurus kapffi (Fig. 6E). Several large skulls of *Nicrosaurus kapffi*, a robustly built, deep-snouted phytosaur, were found in quarries (S1) at Heselach and Kaltental near Stuttgart (Meyer, 1861; Hungerbühler, 2000). *Nicrosaurus meyeri* is a more gracile second species co-occurring at Heselach, formerly known as *Belodon plieningeri* (Hungerbühler and Hunt, 2000). However, the two taxa possibly represent males and females of the same species. Heller (1954) named *Coburgosuchus goeckeli* based on a partial cranium from the upper Burgsandstein (which is the regional equivalent of the Löwenstein Formation) of Coburg (Bavaria). Although it closely resembles, and has usually been synonymised with, *Nicrosaurus*, Spielmann and Lucas (2012) noted differences in cranial structure and retained it as a distinct taxon.

Myrstriosuchus planirostris. This slender-snouted phytosaur was found in light yellow sandstones (S2) at Aixheim and in the massive white sandstones of Pfaffenhofen (S2) (Hungerbühler, 2002), as well as in the Arnstadt Formation at the vicinity of Göttingen, Lower Saxony (Kimmig and Arp, 2010). The more heavily built *M. westphali* is known from the Untere Mühle quarry (S3) at Trossingen (Hungerbühler and Hunt, 2000). Again, the two taxa possibly represent a single, sexually dimorphic species.

Aetosaurus ferratus (Fig. 6F). Skeletal remains of this small aetosaur were found in a quarry at Kaltental near Stuttgart (S1) and remains of somewhat larger individuals have been recovered from Pfaffenhofen (S2) (Fraas, 1877; Schoch, 2007). Teschner et al. (2023) recently reinterpreted the famous assemblage of 24 articulated skeletons from

Kaltental (E. Fraas, 1896) as a nursery of juvenile individuals.

Paratypothorax andressorum (Fig. 6G). An almost complete set of large dorsal osteoderms of this aetosaur was first reported from Heslach (Meyer, 1861; Long and Ballew, 1985) and traditionally assigned to phytosaurs. A second, complete specimen including the skull and much of the skeleton including the dorsal dermal armour was excavated near Murrhardt in 1945, and Schoch and Desojo (2016) described its skull. *Paratypothorax andressorum* (or a closely related species) has also been reported the Chinle Formation of the American Southwest, in Algeria, and in Greenland (Long and Ballew, 1985; Lucas et al., 2006).

Teratosaurus suevicus. Initially identified as dinosaur (F. Huene, 1907–1908), a maxilla and a tentatively referred ilium from the Heslach quarry (S1) were subsequently identified as belonging to a *Postosuchus*-like rauisuchid (Meyer, 1861; Benton, 1986; Brusatte et al., 2009).

Apatosuchus orbitoangulatus. A partial skull from Pfaffenhofen (S2) was first described as a dinosaur (*Halticosaurus orbitoangulatus*; F. Huene, 1932b) but later reidentified as a small-bodied loricatan pseudosuchian (Sues and Schoch, 2013).

Saltoposuchus connectens (Fig. 6H). This small-bodied, long-limbed saltoposuchid crocodylomorph is known from partially articulated cranial and postcranial remains from Pfaffenhofen (S2) (Huene, 1921; Spiekman, 2023).

Efraasia minor. This up to 6.5 m long sauropodomorph dinosaur is known from five specimens (plus three tentative specimens) from Pfaffenhofen (S2) and Ochsenbach (S1) (F. Huene, 1932b; Galton, 1973, 2001; Yates, 2003).

Plateosaurus gracilis. A second sauropodomorph, 4.5–6 m long and formerly referred to as *Sellosaurus*, was found at Heslach (S1), Aixheim-Neuhaus (S2), and Untere Mühle near Trossingen (S3) (F. Huene, 1932b; Yates, 2003; Hungerbühler, 1998).

Dolichosuchus cristatus is known only from an isolated tibia of a theropod dinosaur from Kaltental (S1) (von Huene, 1932a, 1932b), which closely resembles the corresponding element of *Liliensternus liliensterni* from the Trossingen Formation of Thuringia (Rauhut and Hungerbühler, 2000).

Procompsognathus triassicus (Fig. 6I). This taxon is based on the partial postcranial skeleton of a probably juvenile coelophysid theropod from Pfaffenhofen (S2) (Huene, 1921; Sereno and Wild, 1992; Rauhut and Hungerbühler, 2000).

Halticosaurus longotarsus. Poorly preserved, possibly chimeric postcranial remains from Pfaffenhofen may include bones of an indeterminate coelophysoid theropod (F. Huene, 1907, Huene, 1932b; Rauhut and Hungerbühler, 2000).

Tetrapod tracks. In Württemberg, the Löwenstein Formation yielded the ‘lacertoid’ ichnotaxon *Rhynchosauroides*, the probably sauropodomorph ichnotaxon *Evazoum*, the tridactyl (dinosauriform and/or theropod) ichnotaxa *Grallator* and *Atreipus*, and the pseudosuchian ichnotaxon *Brachychirotherium* (Haderer, 2012, 2015; Klein, 2021; Haderer and Schwarzkopf, 2023). The same ichnoassemblage is known from northern Bavaria (Klein and Lucas, 2021). Wagensommer et al. (2022) reported relatively small crocodylomorph and dinosaurian footprints from Rosenberg NE of Stuttgart. Haderer (1991) described a manus-pes set with a slender pes print and identified it as cf. *Isochirotherium* from the Löwenstein Formation (lower Stubensandstein) of Stromberg, northern Württemberg (Fig. 6J). If this identification is correct, this represents the stratigraphically youngest occurrence of this ichnogenus (Klein and Lucas, 2021). Interestingly, a new fossil track recently recovered from the Stubensandstein in the Backnang region (NE Stuttgart), is probably also referable to *Isochirotherium*. It is a natural cast (preserved in convex hyporelief) of a large (28 cm long) left pes track, with digit III the longest, digit II subequal, digits I and IV much shorter, and digit V with a large basal pad and the distal phalangeal portion curved outwards (Fig. 6K). A smaller partial chirotheriid track is overprinting digit III. This large track is definitively a different morphotype than that described by Haderer (1991). Therefore, it is possible that two different ichnospecies of *Isochirotherium* occurred in the Late Triassic.

Palaeoenvironments. The lower Arnstadt Formation (stratigraphically equivalent to the Löwenstein Formation or Stubensandstein) strata were laid down on a large alluvial plain with successive pulses of fluvial sediment input, especially from the Bohemian Massif (Beutler et al., 1999). The distal parts of the alluvial fans probably offered excellent conditions for the formation of diverse aquatic ecosystems, as indicated by the presence of bivalves and osteichthyans (Brenner, 1973). In contrast to the Erfurt and Stuttgart formations, lakes were restricted to certain regions and formed local ponds populated by semionotids and dipnoans. Burrer’s quarry at Pfaffenhofen is the only locality that preserves different depositional environments in a single section. At this locality, temnospondyls, phytosaurs, and aetosaurs are restricted to channel sandstones (Berckheimer, 1938). The stem-turtle *Proterochersis robusta* is also found in massive channel sandstones (Joyce et al., 2013). In contrast, the dinosaurs *Efraasia minor*, *Halticosaurus longotarsus*, and *Procompsognathus triassicus*, the crocodylomorph *Saltoposuchus connectens*, and loricatan *Apatosuchus orbitoangulatus* were found in mudstones deposited on the floodplain. Klein and Lucas (2021) hypothesised that *Atreipus*, which combines a tridactyl pes imprint with a much smaller manus imprint, was possibly produced by a *Silesaurus*-like reptile. If substantiated this would extend the presence of this group in the CEB outside present-day Poland.

The fluvial channels were home to the temnospondyls *Cyclotosaurus intermedius* and *Gerrhoxorax pulcherrimus*. The absence of larger lakes correlates with the rarity of *Metoposaurus diagnosticus*, but a single skull of this species from the Stuttgart region documents its continued presence in the basin (Milner and Schoch, 2004). The streams were home to phytosaurs, whose abundance documents widespread similar conditions. However, the non-overlap of the two different phytosaur genera might suggest that they occupied different environments. Correspondingly, *Cyclotosaurus* has not been found together with the large-bodied *Nicrosaurus kapfki* but co-occurs with the long-snouted piscivore *Mystriosuchus planirostris* at Pfaffenhofen. *Aetosaurs ferratus* and/or *Paratypothorax andressorum* are found in channel sandstones at Heslach, Kaltental, Murrhardt, and Pfaffenhofen (Schoch and Desojo, 2016). Serrated teeth from carnivorous archosaurs, including phytosaurs, associated with a skeleton of *Plateosaurus gracilis* indicate scavenging (Hungerbühler, 1998).

3.26. Trossingen and Klettgau formations (Middle Keuper Subgroup)

The Trossingen Formation (locally named Knollenmergel or Feuerletten) forms a regional unit, laterally equivalent to the upper part of the Arnstadt Formation and is mostly late Norian (Sevatian) in age (Etzold and Schweizer, 2005; Bachmann et al., 2021). The typical purple or brown mudstone facies with pedogenic carbonate nodules that dominates both the Knollenmergel and the upper part of the Stubensandstein sequence makes the distinction between the Löwenstein Formation (upper Stubensandstein, S3 and S4) and Trossingen Formation (Knollenmergel proper) difficult in places. The famous *Plateosaurus* localities in the Knollenmergel facies may therefore differ in age. The Klettgau Formation of northern Switzerland forms a marginal, condensed sequence spanning the late Norian. The Rhaetian part of the sequence is probably absent in the Frick region (Jordan et al., 2016).

Classical tetrapod localities in the Knollenmergel facies are the Obere Mühle at Trossingen (Seemann, 1933; Schoch and Seegis, 2014), the former Baerecke-Limpricht clay pit at Halberstadt (Jaekel, 1914; Kuhn, 1939), and the former Gruhalde clay quarry at Frick in northern Switzerland (Jordan et al., 2016). Benton and Wild (in Benton, 1994) provided a detailed inventory of the other German occurrences from the Upper Triassic.

Despite having similar tetrapod assemblages, the lithological differences between the localities of the Trossingen and Klettgau formations are rather substantial. The section at Obere Mühle in Trossingen encompasses monotonous purple mudstone yielding sauropodomorph

remains within a 12 m thick succession (Schoch and Seegis, 2014). Four different excavation periods at this site between 1912 and 2024 have unearthed a total of 108 skeletons of various degrees of completeness to date. At Halberstadt, a complex alternation of pale sandstones and grey mudstones yielded sauropodomorph remains in a 6 m thick mudstone sequence. Phytosaurs and capitosaurids occur mostly but not exclusively in sandstones. The stem-turtles and plagiosaurids have longer stratigraphic ranges (Kuhn, 1939). At Frick, mostly grey silty mudstones alternate with thin local channel sandstones and dolostones, with sauropodomorph remains occurring in up to six distinct horizons (Jordan et al., 2016). The turtle remains are from a different locality and from a horizon that can be correlated with the middle dinosaur beds at Frick (Scheyer et al., 2022). A recent discovery of an early-diverging averostran theropod was made in the upper part of the section (Zahner and Brinkmann, 2019).

Tetrapod body fossils. The Trossingen and Klettgau formations together build a very rich and diverse faunal assemblage.

Temnospondyli

Cyclotosaurus hemprichi. An excellently preserved skull and various postcranial elements of this species were found in the Halberstadt clay pit (Kuhn, 1939, 1942; Schoch and Moreno, 2024).

Plagiosaurus depressus. A partial skull and postcranial remains of this plagiosaurine were found at Halberstadt (Jaekel, 1914; Witzmann and Schoch, 2024).

Synapsida: Cynodontia

Thomasia antiqua. Hahn (1973) reported a molariform tooth of this haramiyid mammaliaform associated with a skeleton of *Plateosaurus* from Halberstadt.

Reptilia: Testudinata

Proganochelys quenstedtii (Fig. 6L). This fully shelled stem-turtle is known from a skeleton from Halberstadt (Jaekel, 1914), three specimens from Obere Mühle at Trossingen (Gaffney, 1990), and a disarticulated skeleton from Frick (Scheyer et al., 2022).

Reptilia: Lepidosauromorpha

Elachistosuchus huenei. This small-bodied reptile, probably less than 20 cm long, was found together with a skeleton of *Plateosaurus* in the Halberstadt clay pit (Janensch, 1949; Sobral et al., 2015). Initially classified as a pseudosuchian, a recent phylogenetic analysis recovered it as a lepidosauromorph (Ezcurra and Sues, 2022).

Parvosaurus harudensis. Freisem et al. (2024) found a skull of this early-diverging spheodontian inside one of the blocks forming part of the holotype of *Elachistosuchus huenei* through μ CT scanning.

Rhynchocephalia indet. Jaw elements with characteristic rhynchocephalian dentitions occur at Frick (Sander, 1992).

Reptilia: Archosauromorpha

Myriosuchus sp. Disarticulated cranial postcranial remains assigned to this phytosaur were reported by Jaekel (1914), F. Huene (1922), and Kuhn (1939) from one mudstone and two sandstone horizon(s) at Halberstadt.

Aetosauria. Matzke and Maisch (2011) reported isolated aetosaurian cranial bones and osteoderms from the Obere Mühle locality at Trossingen. Aetosaur osteoderms have also been found at Frick (Sander, 1992).

Plateosaurus trossingensis (Fig. 6M). This best-known European sauropodomorph dinosaur was originally described by Meyer (1837) as *P. engelhardti* from Heroldsburg near Nuremberg. This taxon is the most common large tetrapod in the Trossingen Formation (Schaeffer, 2024), with at least 105 partial and complete skeletons from Obere Mühle at Trossingen (F. Huene, 1926, 1932b; Seemann, 1933; Galton, 2001; Yates, 2003) and many additional finds from Degerloch (F. Huene,

1907–1908), Halberstadt (*P. longiceps*, Jaekel, 1914), Frick (Sander, 1992), Ellingen (Moser, 2003), and many other localities. *Plateosaurus trossingensis* attained body sizes between 4.5 and 9 m length. Based on the rich Trossingen and Frick material, bone histological analyses have revealed that individual life histories were influenced by environmental factors and that individuals of the same inferred age could differ in body size (N. Klein and Sander, 2007; see also Nau et al., 2020). Similarly, pathologies identified on the tails of several individuals shed light on the palaeobiology and lifestyle of *Plateosaurus*, including potential interactions with their habitats and/or conspecifics and predators (Schaeffer et al., 2024). The taxonomic diversity of sauropodomorphs in these deposits remains contentious (Yates, 2003; Lallensack et al., 2021). For instance, Regalado Fernández and Werneburg (2022) recently designated a partial postcranial skeleton from Obere Mühle at Trossingen, collected by F. Huene in 1922 and identified by him as *Plateosaurus*, as the holotype of a new taxon of massopodan sauropodomorph, *Tuebingosaurus maierfritzorum*.

Ruehleia bedheimensis. A partial skeleton lacking the skull of this 5 m long *Plateosaurus*-like sauropodomorph was found at Großer Gleichberg near Römhild in Thuringia (Galton, 2001); four additional specimens have also been attributed to this taxon. Galton distinguished *Ruehleia bedheimensis* from *Plateosaurus* spp. by various features of the pelvic girdle and the presence of three rather than two carpals.

Pterospodylus trielbae. This taxon is represented by a small dorsal vertebra from Halberstadt, which probably belonged to a coelophysoid (Rauhut and Hungerbühler, 2000).

Liliensternus liliensterni. At least two incomplete, up to 4 m long subadult skeletons of this coelophysoid theropod were recovered from the Römhild locality in Thuringia (F. Huene, 1934). Kirmse et al. (2024) reported cranial and postcranial remains of several presumably adult individuals from the Trossingen Formation of Ellingen that represent a 7–9 m long stem-averostran closely related to or referable to *Liliensternus*.

Notatesseraeraptor frickensis. The uppermost part of the mudstones in the Frick clay pit yielded a partial skeleton with an excellently preserved skull of this early-diverging averostran theropod (Zahner and Brinkmann, 2019).

Palaeoenvironments. The Trossingen Formation (Knollenmergel) facies formed on a vast alluvial plain under semi-arid climatic conditions, which were triggered by monsoonal influence (Etzold and Schweizer, 2005). The plain would periodically dry out, leading to the formation of characteristic carbonate nodules and abundant slickensides in the dominant Vertisols. Occasional heavy precipitation produced conglomerates in some places, but monotonous mudstone sequences dominate by far, suggesting the presence of vast clayey plains with at least locally dense vegetation. The latter is documented by abundant root traces in individual layers at Trossingen (Schoch and Seegis, 2014). The locally rich finds indicate relatively diverse ecosystems, and the larger body size and abundance of the herbivorous sauropodomorphs compared to the Löwenstein Formation indicates more abundant vegetation than in earlier Norian palaeoenvironments. At Halberstadt, fluvial channels were populated by phytosaurs and temnospondyls, much as in the Löwenstein Formation. Apparently both the Knollenmergel and Stubensandstein facies persisted through most of the time interval represented by the Arnstadt Formation, which is consistent with the close similarities between their respective tetrapod assemblages.

3.27. Tomanová Formation

The outcrops of this geological unit in the Tatra Mountains on the border between Poland and Slovakia have yielded tetrapod footprints (Niedźwiedzki, 2011). The Tomanová Formation mainly consists of fluvial deposits of late Norian–Rhaetian age based on its macroflora (Niedźwiedzki, 2011 and references therein). Tetrapod tracks, which were mostly produced by dinosaurs, include the following ichnotaxa: cf.

Moyenisauropus isp., cf. *Grallator* isp., *Anchisauripus* isp., cf. *Kayentapus* isp., cf. *Eubrontes* isp., other indeterminate tridactyl tracks correlated to theropods, and indeterminate oval to round tracks possibly made by sauropodomorphs (Niedzwiedzki, 2011).

3.28. Exter Formation (Upper Keuper Subgroup)

A clay pit at Warburg-Bonenburg (North Rhine-Westphalia) exposes a continuous section ranging from the upper Norian to the Hettangian (Wintrich et al., 2017; Prino et al., 2024). It has yielded numerous specimens of fishes and tetrapods in an unusually thick succession of Rhaetian strata (Prino et al., 2024). The upper Norian horizon has not yet produced any vertebrate fossils. The Rhaetian section is divided into (in ascending order) the Postera Beds (with the unionid bivalve “*Unionites*” *posterus*), the Contorta Beds (with the bivalve *Rhaetavicula contorta*), and the Triletes Beds (with the megaspore *Triletes*) (Gravendyck et al., 2020). It is topped by the Hettangian Psilonotenton. Four bonebeds in the Contorta Beds have yielded skeletal remains of a diverse assemblage of freshwater and terrestrial tetrapods (Sander et al., 2016). Of these, Bonebed 2 can be dated as late middle Rhaetian based on its position in the middle subzone of the *Rhaetipollis-Limbosporites* Zone of the CEB (Gravendyck et al., 2020; Prino et al., 2024) estimated that this bonebed predates the end of the Triassic by 1.5 to 2 million years. A partial skeleton of a latest Triassic plesiosaur (*Rhaeticosaurus mertensi*) was discovered between Bonebeds 1b and 2a (Wintrich et al., 2017).

Tetrapod body fossils *Temnospondyli*

Capitosauroida indet. Konietzko-Meier et al. (2019) described a large temnospondyl humerus that they tentatively referred to *Cyclotosaurus*. Prino et al. (2024) described additional cranial and postcranial bones, which indicate the presence of at least two different taxa.

Plagiosaurinae indet. Prino et al. (2024) described a parietal and an incomplete interclavicle referable to this clade.

Synapsida: Cynodontia

Lepagia gaumensis. A single postcanine tooth from Bonenburg is indistinguishable from the teeth of this cynodont taxon from the Rhaetian of Gaume, Belgium (Schwermann, 2015).

Reptilia: Lepidosauromorpha

Diphydontosaurus avonis. A jaw fragment closely resembles jaws of this rhynchocephalian taxon from the Upper Triassic of southwestern England (Schwermann et al., 2017).

Reptilia

Pachystropheus rhaeticus. This aquatic reptile, originally interpreted as a choristoderan but more likely a thalattosaur (Quinn et al., 2024), is the most common tetrapod in the Rhaetian sequence of the Bonenburg clay pit (Sander et al., 2016).

Reptilia: Archosauromorpha

Phytosauria. This clade is documented by an isolated dorsal osteoderm resembling those found at Halberstadt (Sander and Wellnitz, 2024).

3.29. Rhaetian Bonebeds (Upper Keuper Subgroup)

At the end of the Triassic Period, the Rhaetian Transgression inundated southwestern and central England, the CEB, and France (Fischer et al., 2012). This event was possibly related to the initial breakup of Pangaea. The fluvial and lacustrine strata of the Exter Formation indicate increased precipitation during this interval (Paul, 2021b).

The widespread Rhaetian bonebeds are concentrates of countless bones, scales, and teeth of both marine and terrestrial vertebrates,

mollusc shells, phosphatised coprolites, and phosphatic nodules. In the CEB, these condensation horizons and their faunal content have been documented in North Rhine-Westphalia, Württemberg, and Canton Schaffhausen (Switzerland) (Fischer et al., 2012). Suan et al. (2012) proposed a scenario in which the phosphatic components of the bonebeds (including the vertebrate remains) became heavily phosphatised in current-dominated shallow-water marine settings and later were reworked and introduced into the basin by storms. Although the skeletal remains are disassociated, fragmentary, and abraded, they provide an informative record of tetrapod diversity near or at the Triassic–Jurassic transition.

Tetrapod body fossils *Temnospondyli*

Capitosauroida indet. Fragments of dermal bones with ornamentation closely resembling those of *Cyclotosaurus* were found in the Stuttgart region (Schoch and Moreno, 2024; Schoch et al., 2025).

Plagiosaurinae indet. Isolated dermal armour elements of *Gerrothorax*-like plagiosaurids, identified by their tubercular ornament, have been reported from the Rhaetian bonebed at Esslingen in Württemberg (Schoch and Witzmann, 2011).

Synapsida: Cynodontia

Tricuspes tuebingensis. Isolated tricuspid tooth crowns of this enigmatic cynodont from Bebenhausen near Tübingen were described by E. Huene (1933), Clemens (1980), and Clemens and Martin (2014). This taxon is also known from Hallau-Bratelen.

Oligokyphus spp. Teeth and tooth fragments of this tritylodontid cynodont from the Bebenhausen assemblage were named *Oligokyphus triserialis*, *O. biserialis*, ‘*Stathmodon*’, *Mucrotherium cingulatum*, and *Uniserium enigmaticum* (Hennig, 1922; E. Huene, 1933; Kühne, 1950). Kühne (1950) demonstrated that *Mucrotherium* and *Uniserium* are based on fragmentary postcanine teeth of *Oligokyphus*, which had a wide geographic distribution (Fedak et al., 2015).

Indeterminate non-mammalian cynodonts and haramiyid mammaliforms. Dorka and Heinrich (2006) described isolated teeth from a Rhaetian bonebed near Friedland (Lower Saxony), documenting an occurrence of this facies at a site close to the centre of the CEB.

Synapsida: Cynodontia: Mammaliaformes

Thomasia antiqua. Plieninger (1847b) first described molariform teeth of this haramiyid mammaliaform from a Rhaetian bonebed probably near Degerloch, which today is part of the city of Stuttgart (Hahn, 1973; Clemens and Martin, 2014). Teeth referable to this taxon are also known from the Rhaetian bonebed at Hallau-Bratelen in Canton Schaffhausen (Switzerland) (Peyer, 1956; Clemens, 1980) and coeval strata in western Europe including southwestern England. The upper molariforms of *Thomasia* were long placed in a separate genus *Haramiya* (Clemens and Martin, 2014).

Morganucodonta. Clemens (1980) named three new taxa of early-diverging mammaliaforms based on isolated teeth from the Hallau-Bratelen bonebed in Canton Schaffhausen (Switzerland) – the morganucodontids *Morganucodon peyeri* and *Helvetiodon schutzi* and the morganucodontan *Hallautherium schalchi*.

Eoraetia siegerti. Dietrich (1937) described an isolated ulna of a derived non-mammaliaform cynodont or mammaliaform from the Rhaetian beds of Halberstadt.

Reptilia: Lepidosauromorpha

Deltadectes elvetica is an early-diverging rhynchocephalian based on jaw fragments from Hallau-Bratelen (Whiteside et al., 2017). In addition to this taxon, these authors reported from this locality a fragment of a maxilla that they identified as cf. *Diphydontosaurus* sp. and a fragment of a dentary that they referred to *Paleollanosaurus*, a sphenodontian otherwise known only from the upper Carnian Tecovas Formation of Texas.

Reptilia

Pachystropheus rhaeticus. Isolated dorsal vertebrae of this possibly thalattosaurian reptile were found in the Stuttgart region (E. Huene, 1935) and are indistinguishable from specimens from the Rhaetian of southwestern England (Storrs et al., 1996; Quinn et al., 2024).

Reptilia: Archosauromorpha

Angistorhinopsis ruetimeyeri. F. Huene (1911) described cranial and postcranial remains of a large-bodied phytosaur from the upper Norian or lower Rhaetian of Niederschönthal in Canton Basel-Landschaft (Switzerland) and named it *Mystriosuchus ruetimeyeri*. Later F. Huene (1922) described teeth, cranial and postcranial bones from the Rhaetian of Halberstadt as well as a partial skull and numerous elements of a skeleton from the Rhaetian bonebed of Steinlah near Salzgitter (Lower Saxony). He proposed a new genus *Angistorhinopsis* for the reception of “*Mystriosuchus ruetimeyeri*”. Witzmann et al. (2014) considered the German fossils currently indeterminate because the Swiss material appears to be non-diagnostic.

Schleithemia schutzi. This taxon is based on postcranial remains of a non-sauropod sauropodiform dinosaur from Canton Schaffhausen (Switzerland) (Rauhut et al., 2020). Referred material from the Hallau-Bratelen bonebed was probably reworked from the underlying uppermost part of the uppermost Norian Klettgau Formation (former Knollenmergel).

Gresslyosaurus ingens is another possible non-sauropod sauropodiform and was described from the upper Norian or lower Rhaetian of Niederschönthal in Canton Basel-Landschaft (Switzerland) (Rütimeyer, 1856; F. Huene, Huene, 1907, 1932b). It has long been synonymised with *Plateosaurus* (e.g., Galton, 2001), but Moser (2003) and Rauhut et al. (2020) observed major differences in the structure of the sacral vertebrae between the two taxa.

4. Tetrapod diversity, palaeoenvironments and habitat preferences

This overview of all currently known occurrences of terrestrial tetrapods in the CEB shows that the osteological and ichnological records provide complementary pictures, albeit with some notable differences between them (Fig. 7; Tables S1, S2). The most conspicuous feature is that both records appear to be proportionally inverse in terms of (ichno-) taxonomic diversity in each stratigraphic unit: when skeletal remains are abundant, tracks are rare or absent, and vice versa. Such a difference exists not only in the absolute number of taxa and ichnotaxa, but also in the number of major clades represented by them. This is especially striking in the case of temnospondyls, which have a rich osteological record but a poor ichnological one (Figs. 2, 3).

We would like to stress that the fossil record is here analysed in terms of taxonomic diversity (i.e., presence/absence of species and ichnospecies, not the absolute numbers of specimens or minimum numbers of individuals). This is important because certain tetrapod groups (e.g., temnospondyls) and ichnotaxa (e.g., *Rhynchosauroides* and chirotheriids), when present in a particular locality or unit, are usually abundant. Therefore, even without considering the absolute numbers of individuals or specimens in each locality or unit, this contrast between both types of fossil record is readily noticeable (Fig. 7). Furthermore, such a quantitative approach in terms of absolute abundance could unnecessarily skew results because of additional preservational and/or taphonomic biases: small footprints could be overrepresented because a single individual might leave multiple tracks in a limited area (see discussion in Mujal et al., 2018; De Jaime-Soguero et al., 2021). At the same time, skeletons of small-bodied tetrapods (and juvenile individuals of larger ones) are commonly underrepresented because the preservation potential of small and delicate elements is low as they are more easily weathered (and eventually destroyed) during sedimentation (Behrensmeyer, 1978). In general, these examples, mainly related to

size, already show a dichotomy between the preservation of body and trace fossils. Most of the differences in the occurrences of the skeletal remains and the tracks might in fact reflect preservational biases, with specific environments more likely to preserve either one or the other type of fossils (Behrensmeyer and Hook, 1992); this point is further discussed in connection with the palaeoenvironmental settings in section 5.2. At the same time, such bias is also influenced by the habitat preferences of the given groups (Fig. 8). This is especially evident in the case of temnospondyls, a diverse clade with predominantly aquatic modes of life, that rarely produced footprints. Conceivably, their tracks were often obliterated in the aquatic settings they occupied (Mujal and Schoch, 2020). Altogether, this results in a low likelihood for the preservation of temnospondyl tracks in the fossil record (Mujal and Schoch, 2020; De Jaime-Soguero et al., 2021; Klein and Lucas, 2021). Somewhat comparable to temnospondyls in this respect are procolophonids, which do not have a definitive ichnological record. However, in this case it could be due to potentially overlooking or misinterpreting some track morphotypes. For instance, *Rhynchosauroides* is an ichnogenus with a ‘lacertoid-like’ morphology that could have been produced by a variety of reptilian trackmakers including procolophonids (Klein and Niedźwiedzki, 2012; Mujal et al., 2018; De Jaime-Soguero et al., 2021; Klein and Lucas, 2021; Riccetto et al., 2025).

It is noteworthy that the ichnological record predates the osteological record for the first appearances of some taxonomic groups in the CEB (Fig. 7). This is especially the case for non-archosaur archosauromorphs and avemetatarsalians, where the first occurrences of tracks attributed to those groups are stratigraphically older than those of their skeletal remains. An interesting case is that of the Early Triassic ichnogenus *Protochirotherium*, which has been ascribed to medium- to large-sized archosauriform trackmakers (Klein et al., 2013; Klein and Lucas, 2021), for which coeval skeletal remains are unknown from the CEB (although they are well-known from coeval strata in European Russia; Shishkin et al., 2023). Similarly, purported synapsid tracks are relatively abundant and diverse from Lower and lower Middle Triassic formations (especially the ichnogenes *Procolophonichnium*, *Dicynodontipus*, and *Capitosauroides*) but they do not have any known skeletal counterparts. Pseudosuchians have a rich and diverse track record in the Anisian of the CEB but almost no skeletal remains. The oldest known definitive osteological record of synapsids is a molariform tooth of a traversodontid cynodont from the upper Ladinian Erfurt Formation of Germany (Hopson and Sues, 2006), but there is no matching ichnological record. In turn, the osteological record of synapsids from the Upper Triassic is more extensive, whereas footprints attributed to the group are almost entirely unknown from strata from this time interval (only represented by *Procolophonichnium lockleyi* from the Carnian Hassberge Formation; Klein et al., 2015). Some large indeterminate tracks possibly made by dicynodonts have been reported from the Norian of Poland (Sulej et al., 2011b; Sadlok and Wawrzyniak, 2013; Pieńkowski et al., 2014).

Another major feature apparent by comparing the osteological and ichnological records is a marked dichotomy between the Lower–lower Middle Triassic and the upper Middle–Upper Triassic units. In the lower units (roughly coinciding with the Buntsandstein and Muschelkalk subgroups), tracks predominate whereas body fossils are dominant in the upper units (roughly coinciding with the Keuper facies deposits). This difference is especially marked between the middle–upper Anisian and upper Ladinian strata, with the former being rich in tracks and the latter in skeletal remains (Fig. 7). This most likely reflects the type of the predominant palaeoenvironmental settings during these time intervals (Fig. 8).

A broad overview of the palaeoenvironments dominating in each geological unit of the CEB (Tables S3, S4; see also Hauschke et al., 2021) reported in this study shows that: (1) the Early Triassic was characterized by relatively inland and low-energy alluvial settings (alluvial plains); (2) during the Middle Triassic there was a progressive trend to coastal environments throughout the Anisian, coinciding with the

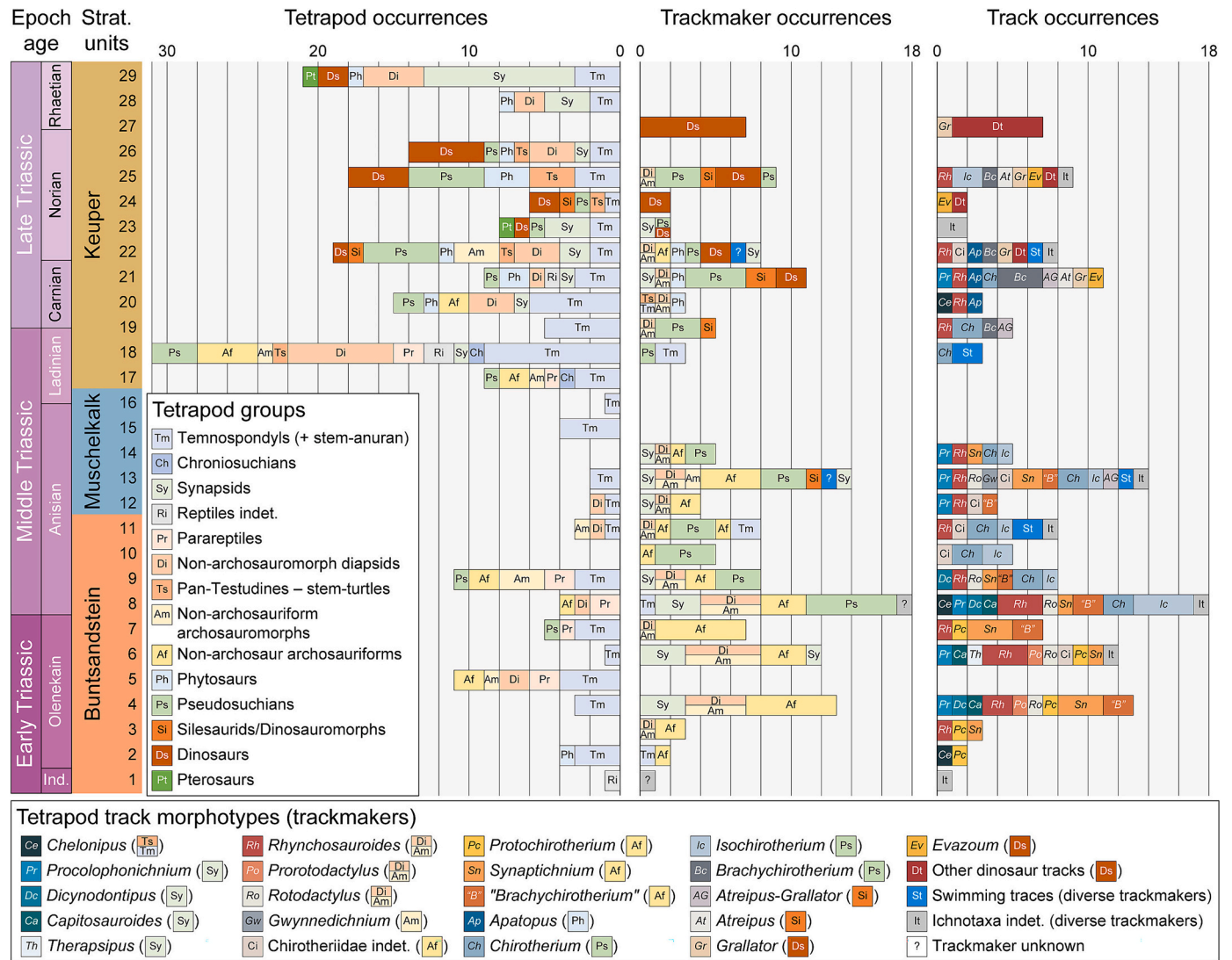


Fig. 7. Diversity of Triassic terrestrial tetrapod fauna and ichnofauna in the Central European Basin. Tetrapod occurrences (based on Table S1) account for skeletal remains identified at species level, when possible (otherwise the lowest taxonomic rank available is used). Track occurrences (based on Table S2) account for tetrapod footprints, classified at ichnogenus level in the graph, although the number of ichnospecies is also considered; indeterminate track morphotypes are also included. Trackmaker occurrences account for the corresponding producers based on the track occurrences; note that, in some cases, the producers of swimming traces and indeterminate ichnotaxa are also identified (see text for discussion). Numbers 1 to 29 in the stratigraphic units (Strat. units) correspond to those listed in the text (sections 3.1 to 3.29), in the same order. The length of the epochs and ages is not temporally scaled, since some units may have the same age, and otherwise would be overlapped (see also Figs. 2, 3).

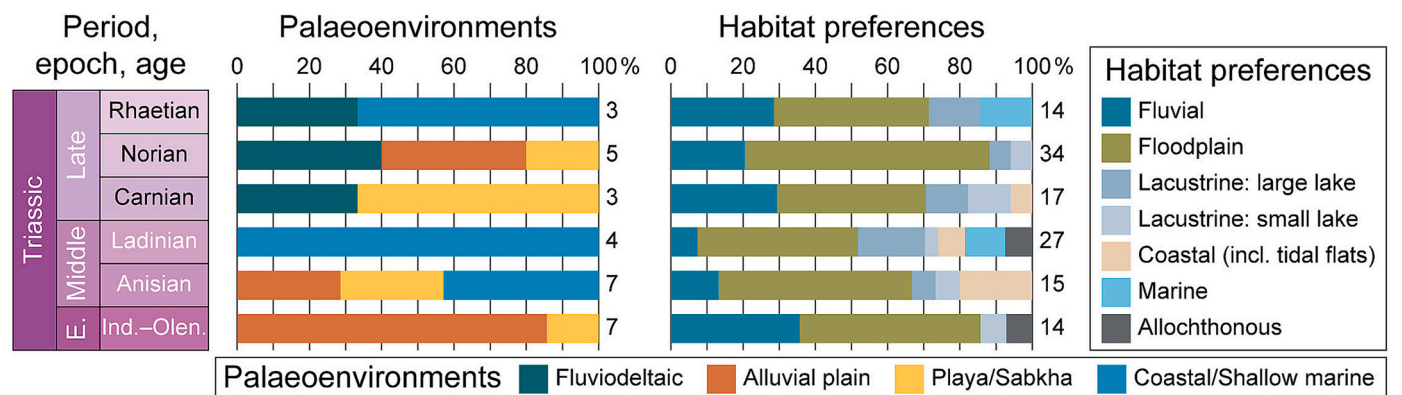


Fig. 8. Distribution of major palaeoenvironments (or depositional settings of the studied units, primarily based on Hauschke et al., 2021) and habitat preferences of tetrapods (based on ecological interpretations of the skeletal remains) in each Triassic age. Numbers on the right of each bar correspond to the total occurrences (in the case of habitat preferences, this is based on the presence/absence of each tetrapod group in each habitat).

marine transgressions from the Tethys (e.g., Franz et al., 2013), which led to the establishment of coastal and shallow-water marine environments in the Ladinian; (3) the Late Triassic started with relatively arid conditions (documented by playa and sabkha settings dominating early in the Carnian) followed by an extended episode of increased precipitation (Carnian Humid Episode) and a change toward deltaic and fluvial settings in the Norian, ending with another marine transgression in the Rhaetian (Fig. 8).

The habitat preferences inferred for the tetrapods of the CEB (based on their skeletal record; see section 2 and Table S5) show changes throughout the Triassic, likely mirroring the respective palaeoenvironmental settings (Fig. 8). In general, faunas inhabiting floodplains are dominant, being proportionally more abundant in the Anisian and Norian. Faunas from fluvial settings show a marked decrease from the Early to the Middle Triassic, whereas faunas more likely to inhabit lacustrine, coastal and marine settings become more abundant and diverse (the two latter reflecting the Tethys transgression represented by the Muschelkalk Group). A notable increase in the proportion of faunas from fluvial habitats is inferred for the Late Triassic but never reaching the same extent as that found for the Early Triassic. Faunas in lacustrine habitats can be traced throughout the entire Triassic, but those considered tied to large lakes appear first in the Anisian. Tetrapods for which marine habitat preferences have been inferred are only present when coastal and shallow-water marine habitats dominated. It should be noted that this work focuses on terrestrial (including freshwater) tetrapods, and thus assessments of habitat preferences are only concerned with those groups.

5. Discussion

5.1. Tetrapod groups

5.1.1. Temnospondyls

Temnospondyls were the most widespread and common tetrapods in many Triassic deposits of the CEB. In Germany, four distinct phases of temnospondyl diversification can be distinguished: (1) an Olenekian “*Parotosuchus* fauna” with similarities to assemblages from the Cis-Urals of Russia and from the Torrey Member of the Moenkopi Formation in Utah, and even South Africa (Lucas and Schoch, 2002); (2) an early Anisian “*Eocyclotosaurus* fauna” with strong resemblance to assemblages from the ‘Keuper’ in England and the Holbrook/Anton Chico Member of the Moenkopi Formation in Arizona/New Mexico; (3) a late Ladinian “*Mastodonsaurus* fauna” similar to the Polish and Cis-Uralian tetrapod communities and (4) a late Carnian to late Norian “*Cyclotosaurus* fauna” with close resemblance to the assemblages from the Fleming Fjord Group in East Greenland (Clemmensen et al., 2020), but less so to the tetrapod assemblage from Krasiejów (Poland) and even less so to roughly coeval assemblages in Morocco and North America. These four different temnospondyl faunas clearly show biogeographic changes through time, resembling assemblages from other regions in each time interval. Hypothetically, these changes in the similarities between the German temnospondyl faunas and those from elsewhere could be related to transgression/regression phases of the Tethys (see also Moreno et al., 2024b). From the Induan to the Olenekian, sea levels rose, creating a barrier between the CEB and eastern basins, before subsequently dropping again in the Anisian (Haq, 2018). Starting in the Fassanian substage of the Ladinian, sea levels rose steadily to the Tuvanian substage of the Carnian, dropping again in the early Norian. During the late Norian, sea levels remained largely unchanged but dropped again toward the Triassic–Jurassic transition (Haq, 2018).

The “*Parotosuchus* fauna” represents a low-diversity tetrapod community that existed in seasonally fluctuating environments with temnospondyl apex predators (*Parotosuchus* spp., *Odenwaldia heidelbergensis*, *Meyerosuchus fuerstenbergensis*). These conditions prevailed throughout the Olenekian, and similar patterns are observed in the lower Olenekian of Utah (*Parotosuchus*; Lucas and Schoch, 2002) and the Olenekian of the

southern Urals (*Parotosuchus orenburgensis* and *P. orientalis*). The “*Parotosuchus* fauna” is known from the Volpriehausen and Solling formations in the CEB. Only at one locality in the Solling Formation (Bernburg) did the habitat support two large-bodied temnospondyls, *Parotosuchus nasutus* and *Trematosaurus brauni*, which differ greatly in cranial structure, reflecting different modes of feeding (Fortuny et al., 2011). The slender-snouted *Trematosaurus* was presumably a euryhaline fish-eater that co-existed with the crocodile-like apex predator *Parotosuchus* in an estuarine deltaic setting. The apparently terrestrially adapted *Scelerothorax hyselonotus* from the Volpriehausen Formation of Queck near Fulda is probably an endemic form (Schoch et al., 2007).

The “*Eocyclotosaurus* fauna” of the Röt Formation represents a separate assemblage formed by the immigration into the CEB of more derived capitosauroids such as *Mastodonsaurus cappelenensis* and heylerosaurine cyclotosaurids. Both clades also occur in southern England (Paton, 1974; Milner et al., 1990; Schoch et al., 2023), but western North America has only yielded heylerosaurines to date (Schoch and Milner, 2000). In the American Southwest, the “*Eocyclotosaurus* fauna” either formed part of a more diverse temnospondyl community in larger lakes (*Eocyclotosaurus wellsi*, *Quasicyclotosaurus campi*, *Vigilius wellsi*) or was restricted to a single aquatic predator in smaller streams (*Eocyclotosaurus appetolatus*; Rinehart et al., 2015). In the CEB, *Mastodonsaurus* spp. was probably the apex predator in lakes throughout its stratigraphic range, although it has occasionally also been found in channel deposits of Anisian and Ladinian age (Schoch, 1999; Schoch et al., 2023).

The Ladinian “*Mastodonsaurus* fauna” is the most diverse temnospondyl assemblage in the CEB. It is best known from the Erfurt Formation of Germany, but similar assemblages occurred in southern Poland (Miedary Beds) and the Cis-Urals of Russia (Bukobay Gorizont). These temnospondyls thrived in large lakes, where *Mastodonsaurus giganteus* was the dominant predator and usually accompanied by *Plagiosuchus pustuliferus* or *Gerrothorax pulcherrimus* (Schoch and Seegis, 2016; Schoch et al., 2022, 2024). In more diverse ecosystems, *Tatrasuchus wildi*, *Trematolestes hagdorni*, or *Callistomordax kugleri* were present in addition to the aforementioned taxa. Lagoonal environments were inhabited by *Plagiosternum granulosum*, whereas the only known specimen of its close relative *Megalophthalma ockeri* was recovered from deposits of a large fluvial channel (Schoch et al., 2014).

The “*Cyclotosaurus* fauna” spans by far the longest time interval, but it shows a reduction in taxic diversity from the Carnian to the Norian. This might reflect the appearance of phytosaurs, which likely occupied similar or even the same ecological niches as temnospondyls (Rinehart et al., 2023). With four very divergent taxa during the late Carnian (*Cyclotosaurus* spp., *Gerrothorax pulcherrimus*, *Hyperokynodon keuperinus*, and *Metoposaurus diagnosticus*), temnospondyls continued to be dominant aquatic predators in the large deltaic setting of the Stuttgart Formation. This changed with the reduction in size of rivers and lakes in the CEB. *Cyclotosaurus* shared habitats with phytosaurs, and *Metoposaurus diagnosticus* was largely confined to lakes. *Gerrothorax pulcherrimus* was a pioneer taxon with unusual ecomorphological plasticity (Schoch and Witzmann, 2011; Sanchez and Schoch, 2013). By the late Norian and Rhaetian, only *Cyclotosaurus* spp. and plagiosaurines appear to have been present, which is consistent with the absence of evidence for the presence of larger lakes in the Arnstadt and Exter formations. The records of plagiosaurine and capitosauroid temnospondyls from the Rhaetian Exter Formation at Bonenburg are the stratigraphically youngest records of these groups in the CEB; only brachyopoids (which are unknown from the CEB) survived the ETME (Prino et al., 2024).

5.1.2. Chroniosuchians

A single chroniosuchian, the bystrowianid *Bystrowiella schumanni*, from the upper Ladinian Erfurt Formation highlights palaeobiogeographical ties with the Middle Triassic tetrapod assemblages from the Cis-Urals (Shishkin et al., 2023), mirroring the overall similarity of “*Mastodonsaurus* fauna” to that of the Bukobay Gorizont in the Cis-Urals.

The palaeobiology of these stem-amniotes remains poorly understood, and *Bystrowiella* probably represents an allochthonous faunal element in the lacustrine deposits of the Erfurt Formation because most of its skeletal remains are isolated osteoderms and vertebrae that were probably transported or reworked (Witzmann et al., 2008; Hagdorn et al., 2015).

5.1.3. Synapsida

In contrast with their rich and diverse fossil record in the Cis-Urals and especially in Gondwana, dicynodonts had long remained unknown in the CEB until Lucas and Wild (1995) tentatively assigned a humerus from the upper Ladinian Erfurt Formation to the kannemeyeriiform *Dinodontosaurus*, which is otherwise known only from Argentina and Brazil. Subsequently, however, Maisch et al. (2009) re-identified this specimen as a temnospondyl humerus. Finally, a partial mandible of a kannemeyeriiform dicynodont was reported from the Stuttgart Formation of Obernzenn, Bavaria (Schoch, 2012) and later referred to the medium-sized stahleckeriid kannemeyeriiform *Woznikella triradiata* (Szczygielski and Sulej, 2023). The giant stahleckeriid kannemeyeriiform *Lisowicia bojani* from the upper Norian of Lisowice, is the largest known dicynodont and established the persistence of this clade, at least in the northern part of the CEB (in present-day Poland), into the latest Triassic (Sulej and Niedźwiedzki, 2019; Sulej et al., 2024). Several taxa of kannemeyeriiform dicynodonts have been reported from the Middle Triassic of Cis-Urals (Shishkin et al., 2023), but the highly fragmentary nature of the known specimens makes it difficult to assess the actual diversity of these synapsids. *Lisowicia bojani* possibly occupied an ecological role comparable to that of the sauropodomorphs in the German and Swiss localities, in the southern part of the CEB, and it is noteworthy that there are no known records of Triassic sauropodomorphs from the northern part of the CEB except possibly for some poorly preserved tracks tentatively attributed to sauropodomorphs (Niedźwiedzki, 2011).

The presence of cynodonts including mammaliaforms in the CEB has long been known (Plieninger, 1847b), but the fossil record remains limited to isolated teeth (E. Huene, 1935; Hahn, 1973; Hahn et al., 1984). The stratigraphically earliest record in the CEB is a lower post-canine tooth of the traversodontid cynodont *Nanogomphodon wildi* from the upper Ladinian Erfurt Formation of Baden-Württemberg (Hopson and Sues, 2006). The oldest known mammaliaforms from the CEB are late Norian in age and comprise haramiyids and morganucodontans. Cynodonts were likely more diverse than the isolated teeth would suggest, but the lack of cranial remains renders an assessment of their diversity difficult if not impossible. Despite intensive search efforts, the rich samples of small tetrapod bones and teeth from Kupferzell and Vellberg have yet to yield a single cynodont tooth or bone.

In contrast to the skeletal record, tracks of potential synapsid trackmakers are known from Lower and Middle Triassic formations, occasionally being relatively abundant (e.g., *Procolophonichnium*). Synapsid ichnotaxa are virtually absent in upper Middle and Upper Triassic strata except for a few mostly indeterminate tracks (Figs. 3, 7; see also section 4).

5.1.4. Procolophonoidea

Procolophonoids are known from Anisian and Ladinian aged horizons in the CEB. Martinelli et al. (2016) referred isolated humeri from the upper Ladinian Erfurt Formation to Owenettidae, but all other specimens can be assigned to Procolophonidae. There are still no records of Late Triassic procolophonoids from the CEB, unlike in North America and in southwestern England (e.g., Meade et al., 2024). The reasons behind the sparse record of Middle Triassic and absence of fossils of Late Triassic procolophonoids, respectively, remain uncertain. Potential hypotheses are (1) that they were in ecological competition with other groups of comparably adapted tetrapods (e.g., synapsids, lepidosauromorphs, and possibly some archosauromorphs), and/or (2) that there is a taphonomic bias against remains attributable to this group.

Considering the records of other tetrapod taxa of comparable body size, the latter hypothesis appears less plausible. Noteworthy, procolophonids were still diverse in the Late Triassic (e.g., Butler et al., 2024; Meade et al., 2024; Zanchett Dalle Laste et al., 2024).

5.1.5. Diapsida incertae sedis

In addition to the readily identified major diapsid clades, two morphologically distinctive taxa have so far defied phylogenetic assessment. *Quasicolognathus eothern* from the Erfurt Formation of Vellberg is closely related to the Norian-age *Colognathus obscurus* from the United States (Sues et al., 2022b). Both belong to a group of highly specialized but still poorly known reptiles with uncertain higher-level relationships. Similarly, the affinities of *Stauromatodon mohli* remain unresolved.

5.1.6. Drepanosauromorpha

The recent identification of a drepanosauromorph from the Grès à Voltzia (Spiekman et al., in review) adds considerably to the known diversity of Anisian-age Triassic tetrapods from the CEB. Drepanosauromorphs were previously known only from Upper Triassic strata in northern Italy, southwestern England, and the United States, but their presence in the Middle Triassic had been predicted by the phylogenetic hypothesis of Pritchard et al. (2021) that found them as the sister-taxon to the late Permian (Lopingian) Weigeltisauridae.

5.1.7. Lepidosauromorpha

The diversity of lepidosaurs and their stem-taxa was recently substantially increased by the discovery of new taxa in the upper Middle and Upper Triassic of the CEB. Relatively complete or at least diagnostic finds led to the recognition of several new taxa from the Erfurt Formation. In this time interval, rhynchocephalians are more readily identified because of their distinctive dentition. However, their taxonomic diversity was apparently low and, to date, is confined to a single taxon, *Wirtembergia hauboldae* (Sues and Schoch, 2024). Various rhynchocephalian taxa have been identified from Carnian to Rhaetian formations in the CEB. Most recently, Freisem et al. (2024) described a new sphe-nodontian, *Parvosaurus harudensis*, based on a skull from the Arnstadt Formation of Halberstadt.

Among stem-lepidosaurs, Schoch and Sues (2018a) identified *Fraxinisauro rozynekae* from the Erfurt Formation of Vellberg, which is most closely related to the Middle Jurassic *Marmoretta oxoniensis* from England and Scotland (Ford et al., 2021). Sobral et al. (2020) described the stem-lepidosaur *Vellbergia bartholomaei*, from the same horizon and locality, which Ford et al. (2021) recovered as most closely related to Rhynchocephalia in their phylogenetic analysis. In addition, there are four undescribed taxa of lepidosauromorphs from the same locality (Schoch, 2015b; Sobral and Schoch, in review).

The Early Triassic taxa *Sophineta cracoviensis* and *Pamelina polonica* from Czatkowice are possibly stem-lepidosaurs. The former has been recovered in a polytomy with Rhynchocephalia and Squamata (Ford et al., 2021), while the latter is a kuehneosaurid, a group with possible lepidosauromorph affinities (Evans, 2009), although such relationships have been contested (Pritchard et al., 2021). To date, no indisputable stem-squamates have been identified from the Triassic of the CEB. Recently, the enigmatic diapsid reptile *Elachistosuchus huenei* from the Arnstadt Formation of Halberstadt was found to be more closely related to lepidosauromorphs than to other diapsid groups (Ezcurra and Sues, 2022).

5.1.8. Pachystropheus and relatives

Numerous skeletal remains of a small-bodied aquatic reptile from the Erfurt Formation of Vellberg closely resemble those of *Pachystropheus rhaeticus*, which was long considered an early choristoderan and is known from Rhaetian bonebeds in Baden-Württemberg (E. Huene, 1935) and North Rhine-Westphalia (Sander et al., 2016) in Germany and in southwestern England (Storrs et al., 1996; Quinn et al., 2024).

However, the choristoderan affinities of *Pachystropeus* have recently been questioned and it is more likely that this taxon represents a thallosaur (Quinn et al., 2024).

5.1.9. Pan-Testudines – stem-turtles

Stem-turtles representing three major evolutionary stages of Pan-Testudines have now been identified in the upper Ladinian and in the middle and upper Norian of the CEB. The late Ladinian *Pappochelys rosinae* is the earliest known undisputed stem-turtle but it has no fully formed shell. The shell-bearing Norian testudinans *Proterochersis* spp. and *Keuperotesta limendorsa* have highly domed carapaces with a full complement of bony elements (Szczygielski and Sulej, 2016). The more crownward stem-turtle *Proganochelys quenstedtii* has a broader and more flattened carapace (Gaffney, 1990). Karl (2005) named a shell fragment of what he interpreted as a stem-turtle from the Upper Muschelkalk (lower Ladinian) of northern Bavaria *Priscochelys hegnabrunnensis*. Subsequently, however, Scheyer (2008) reidentified this fossil as a fragment of a placodont carapace.

5.1.10. Non-archosauriform archosauromorphs

The most common archosauromorph clade in the CEB is Tanysauria, as represented by Trachelosauridae and Tanystropheidae (Fraser and Rieppel, 2006; Spiekman and Scheyer, 2019; Spiekman et al., 2024a). It ranges from the lower Anisian to the Norian. *Tanystropheus* spp. for the most part lived in shallow-water marine settings and is therefore not included in our analysis, but the tanystropheid *Macrocnemus bassanii* had predominantly terrestrial habits (Rieppel, 1989). The mode of life of *Amotaurus rotfeldensis* remains unclear, but its presence in the sandstones of Rotfelden suggest that it was not restricted to marine settings (Fraser and Rieppel, 2006). In contrast, *Trachelosaurus fischeri* possibly had marine habits based on its similarities to *Dinocephalosaurus orientalis* from SW China (Spiekman et al., 2024a, 2024b). The presence of additional tanysaurians is indicated by highly fragmentary remains of “*Tanystropheus antiquus*” (Skawiński et al., 2017; Spiekman and Scheyer, 2019). In addition, isolated jaw remains tentatively referred to *Lamprosauroides goepperti* from the Lower Muschelkalk of Krapkowice and Gogolin (Poland) and Winterswijk (the Netherlands) possibly represent a *Dinocephalosaurus*-like tanysaurian (Spiekman and Klein, 2021; Spiekman et al., 2024b).

The virtual absence of rhynchosaurs in the CEB is surprising because rhynchosaurs are well-documented from the Middle and Upper Triassic of the British Isles (Benton, 1990). *Eifelosaurus triadicus* from the Anisian of the Eifel region of Rhineland-Palatinate is an early-diverging rhynchosaurid (Sues et al., 2022a). Furthermore, a cluster of three juvenile rhynchosaurs has been recovered from the Upper Buntsandstein of Rotfelden in the Black Forest region (Sues and Schoch, 2023a). There are still no known records of rhynchosaurs from any stratigraphically younger formation in the CEB.

The recent discovery of the trilophosaurid *Rutiotomodon tythos* in the upper Ladinian Erfurt Formation has established the presence of this archosauromorph clade in the CEB (Sues and Schoch, 2023b). This taxon is of palaeoecological interest because it is one of only two known probably herbivorous tetrapods from the Erfurt Formation.

5.1.11. Non-archosaurian archosauriforms

Archosauriform reptiles were unexpectedly diverse in the CEB during the late Ladinian. The extensively armoured doswelliid *Jaxtasuchus salomoni* from the Erfurt Formation of Vellberg is most closely related to *Doswellia kaltenbachii* from the upper Carnian Falling Creek Formation of Virginia (Schoch and Sues, 2014). *Polymorphodon adorfii* from the same horizon and locality (Sues et al., 2020) was found closely related to doswelliids in a recent phylogenetic analysis by Ezcurra and Sues (2022). As a third archosauriform from the same horizon and locality is represented by a still undescribed taxon with distinctive osteoderms. The earliest known eucrocopodan archosauriform from the CEB is *Marcianosuchus angustifrons* from the upper Buntsandstein of Rotfelden,

which closely resembles *Euparkeria capensis* in various features (Sues et al., 2024).

5.1.12. Pseudosuchia

The oldest taxon representing this group in the CEB is the poposauroid *Ctenosauriscus koeneni*, from the lower Solling Formation (Butler et al., 2011), of late Olenekian age. In the Röt Formation only indeterminate remains of a tall-spined poposauroid are known. This relatively scarce record is complemented by a wealth of tracks, especially those attributed to the ichnogenera *Chirotherium* and *Isochirotherium*, indicating that pseudosuchians were already apex predators in the Early Triassic terrestrial tetrapod communities. These ichnotaxa are also known from the marginal deposits of the Muschelkalk facies, indicating that pseudosuchians were still present in the basin until they diversified again during the Ladinian following the regression of the Muschelkalk Sea.

At least two loricatan pseudosuchians, including the top predator, up to 5 m long *Batrachotomus kupferzellensis*, are known from the Erfurt Formation of Vellberg (Gower, 1999; Gower and Schoch, 2009; Schoch, 2015b; Mujal et al., 2022). *Dyoplax arenaceus*, known only from an indistinct natural mould of the skeleton from the Stuttgart Formation, has been interpreted as an erpetosuchid pseudosuchian (Maisch et al., 2013). Five pseudosuchian taxa are currently known from the upper Norian Löwenstein Formation: two aetosaurs (*Aetosaurus ferratus* and *Paratypothorax andressorum*), two loricatans (*Apatosuchus orbitoangulatus* and *Teratosaurus suevicus*), and an early crocodylomorph (*Saltoposuchus connectens*). The Krasiejów and Lisowice localities yielded two large-bodied pseudosuchians, the rauisuchid *Polonosuchus silesiacus* and the loricatan *Smok wawelski*, respectively; both attained total body lengths of at least 5 m and were apex predators in their respective communities.

5.1.13. Phytosauria

Aside from the problematical *Mesorhinosuchus fraasi* from the Olenekian Middle Buntsandstein Subgroup and “*Zanclodon*” *arenaceus* from the Carnian Stuttgart Formation, phytosaurs are known in the CEB from the Carnian to the Rhaetian. The early-diverging *Parasuchus* in the CEB is present in the Carnian Blasensandstein at Ebrach (Bavaria; ‘*Franco-suchus*’) and Grabowa Formation at Krasiejów (Poland), and the long-snouted *Ebrachosuchus* co-occurs at Ebrach (Butler et al., 2014). Lep-tosuchomorph phytosaurs are represented by the long-snouted, gharial-like *Myrstriosuchus* and by *Nicrosaurus* from the Norian Löwenstein Formation of Baden-Württemberg. The stratigraphically youngest phytosaurs in the CEB are represented by mostly fragmentary remains of uncertain taxonomic identity from Rhaetian strata in Germany and northern Switzerland.

5.1.14. Non-dinosaurian avemetatarsalians

Although skeletal remains of non-dinosaurian avemetatarsalians are still unknown from Germany, their presence in at least two horizons in southern Poland (Grabowa Formation and Lisowice Beds) establishes that these reptiles were present in the CEB. *Silesaurus opolensis* (Dzik, 2003) and at least one other small-bodied dinosauro-morph (Niedźwiedzki et al., 2014) are known from Poland. This contrasts with the common occurrence of various ichnotaxa (certain ichnospecies of *Chirotherium*, *Rotodactylus*, *Prorotodactylus*) that have been interpreted as produced by early avemetatarsalians (e.g., Brusatte et al., 2011). In the case of *Rotodactylus* and *Prorotodactylus*, however, other trackmakers are more likely (Padian, 2013; Fichter and Kunz, 2013; Mujal et al., 2017; Klein and Lucas, 2021). The presence of tracks assigned to the *Atreipus-Grallator* type from the Lower Muschelkalk of Germany is intriguing (Klein and Lucas, 2018). They would represent a less ambiguous occurrence of avemetatarsalians in the CEB already during the early Middle Triassic.

5.1.15. Dinosauria

The abundance of sauropodomorphs is a typical feature of the upper Norian strata in the CEB, with the Knollenmergel facies of the Arnstadt Formation having yielded scores of skeletons and skeletal remains of *Plateosaurus* spp. and closely related taxa at currently 46 localities in Germany and northern Switzerland (F. Huene, Huene, 1907-1908, 1926, 1932b; Galton, 2001; Moser, 2003; Yates, 2003; Lallensack et al., 2021; Regalado Fernández and Werneburg, 2022; Regalado Fernández et al., 2023; Schaeffer, 2024). The stratigraphically oldest known sauropodomorphs in the CEB are *Plateosaurus gracilis* and *Efraasia minor* from S1 and S2 of the Löwenstein Formation. It is noteworthy that the Polish localities suggest the absence of sauropodomorphs in the northern region of the CEB until the Norian. At least in the Lisowice Beds, the presence of a giant dicynodont suggests a possible regional differentiation among megaherbivores, perhaps influenced by climatic and/or floral differences between the Polish and German sites. It was not until the latest Triassic (Rhaetian) that sauropodomorphs might have appeared in the northern region of the CEB, as the ichnological record suggests (Qvarnström et al., 2024).

Theropods are much more widespread palaeogeographically, but much less numerous, than sauropodomorphs and appear to predominantly or exclusively comprise coelophysoids (Rauhut and Hungerbühler, 2000). *Procompsognathus triassicus* is based on the partial postcranial skeleton of a juvenile coelophysid (Spiekman et al., 2021b). *Liliensternus liliensterni* is a Norian theropod that might either represent a non-coelophysid coelophysoid or a stem-averostran (Marsh and Rowe, 2020; Spiekman et al., 2021b). Zahner and Brinkmann (2019) recovered *Notatesseraeraptor frickensis* as an early-diverging averostran theropod, but their analysis is problematical because they omitted *Liliensternus liliensterni* from their phylogenetic analysis. A recent discovery of theropod remains from the Trossingen Formation of Ellingen (Bavaria) has established the presence of a large-bodied stem-averostran closely related (if not referable) to *Liliensternus liliensterni* with an estimated total length of 7–9 m (Kirmse et al., 2024).

The purported occurrence of a herrerasaurid in the Patoka Member (former Zbąszynek Beds) of the Grabowa Formation (Niedźwiedzki et al., 2014) is of considerable potential interest because Herrerasauridae is a clade of early-diverging dinosaurs otherwise known only from upper Carnian to lower Norian of Argentina and Brazil. However, this identification requires confirmation from additional, more complete material.

The ichnological record indicates the presence of theropod dinosaurs in almost all Upper Triassic localities that preserve tetrapod tracks. The diversity of morphotypes of tridactyl tracks indicates a considerable variety of theropods, yet to be mirrored by the record of body fossils for this group. In contrast, sauropodomorph footprints are surprisingly much less common. Such differences in the presence of the different kinds of dinosaurian remains in the fossil record possibly reflects their preservation potential in different depositional settings. The theropod record in the CEB shows a predominance of relatively small-sized animals with less robust skeletons, which are less likely to be preserved than those of the larger and more robust sauropodomorphs.

Except for the possibility that silesaurids are stem-ornithischians (Norman et al., 2022), there are as yet no definitive records of ornithischians from the Upper Triassic of the CEB.

5.2. Evolution of tetrapod faunas and their palaeoenvironments

The palaeoenvironmental distribution of terrestrial tetrapods based on both the skeletal and track records from the CEB in the Lower, Middle, and Upper Triassic documents how faunas evolved and were replaced throughout the period (Figs. 9–11). These changes may stem from two main processes: (1) the evolution of tetrapod groups on a global level throughout the Triassic, and (2) the palaeoenvironmental changes in the CEB and the corresponding changes of the local faunas (i. e., the transition from alluvial-plain settings to a marine transgression

and finally to fluviodeltaic settings). The latter process may influence the applicability of the concept of 'Land Vertebrate Faunachrons' (LVFs) (Lucas, 1998; for discussion see Rayfield et al., 2005, 2009 and Butler, 2013). Lucas (1998 et seq.) has proposed a global correlation scheme for Triassic continental strata in different regions based on tetrapods shared between them. Although the LVFs for the Upper Triassic are now well-defined and in general use for the diverse tetrapod assemblages from the southwestern and western United States (Martz and Parker, 2017), a comparable zonation in the CEB remains problematic (e.g., see discussion for *Mastodonsaurus* in Rayfield et al., 2009 and Schoch et al., 2023). Some of the taxa reportedly shared between the two regions (e.g., *Aetosaurus*, *Metoposaurus*) are not definitively documented from North America whereas others (e.g., *Parasuchus* ["*Paleorhinus*"]) require taxonomic revision before their stratigraphic utility can be assessed (Butler, 2013; Kammerer et al., 2016). Furthermore, as discussed in this work, the incomplete fossil record possibly obscures similarities as well as differences between tetrapod faunas when comparing various successions, which in turn might be composed of a variety of strata representing different depositional settings. Consequently, our analysis is focused on the potential environmental constraints on the distribution of tetrapod body fossils and tracks within the CEB throughout the Triassic (Figs. 9–11).

By correlating tetrapod (ichno)faunas with their palaeoenvironmental settings, coupled with inferences concerning habitat preferences for each taxon, we can explore potential preservational/taphonomic biases (e.g., Behrensmeyer and Hook, 1992) that could affect reconstructions of these ecosystems. At the same time, it is important to stress that the fossiliferous units herein reported have differences in both spatial and temporal extent. However, since we consider tetrapod occurrences only in terms of presence/absence rather than absolute numbers (see section 2), our analysis and interpretations of the palaeoenvironmental distribution are not influenced by differences between stratigraphic units. This non-biased result is evident from the tetrapod habitat preferences in each stage (Fig. 8), because the proportions of each inferred habitat remain relatively stable despite the differences in the total number of different taxa in each stage. Instead, as indicated in section 4, the changes in habitat preferences are well correlated with the palaeoenvironmental settings recorded from each stage.

Generally, the Lower Triassic formations have yielded very few skeletal remains of tetrapods, which has traditionally been attributed to harsh, arid environmental conditions in the northern arid belt of Pangaea in the immediate aftermath of the EPME (Romano et al., 2020; see also Lucas, 2017 for discussion). Nevertheless, this tetrapod diversity is notably higher when the track record is taken into consideration. In fact, occurrences of tetrapod tracks in Lower Triassic alluvial plain deposits are surprisingly common and diverse, with a predominance of footprints attributed to diapsid, specifically archosauriform reptiles (Fig. 9). The presence of tracks purportedly produced by synapsids is also remarkable in view of the current absence of any skeletal record for this group from the Lower Triassic in the CEB. Bernardi et al. (2018) observed a similar mismatch between the records of body fossils and tracks of tetrapods on a global scale. Considering the fossil record of the CEB, this mismatch most likely reflects a preservational bias. All in all, this points to a higher diversity when both skeletal and track records are considered, providing a more complete picture of these ecosystems.

The Middle Triassic strata record a much greater tetrapod diversity than that of the Lower Triassic ones (Table S1), although the most common taxonomic groups (temnospondyls and non-archosaur archosauriforms) largely remain the same (Figs. 2, 7, 10). The most obvious difference is in the ichnological record, with the Middle Triassic yielding a large number of diverse pseudosuchian tracks, which are not known from Lower Triassic strata. The general increase in diversity of tetrapods in the Middle Triassic can be explained by the continued recovery following the EPME as well as the onset of more humid conditions, which allowed ecosystems to flourish and tetrapods to diversify.

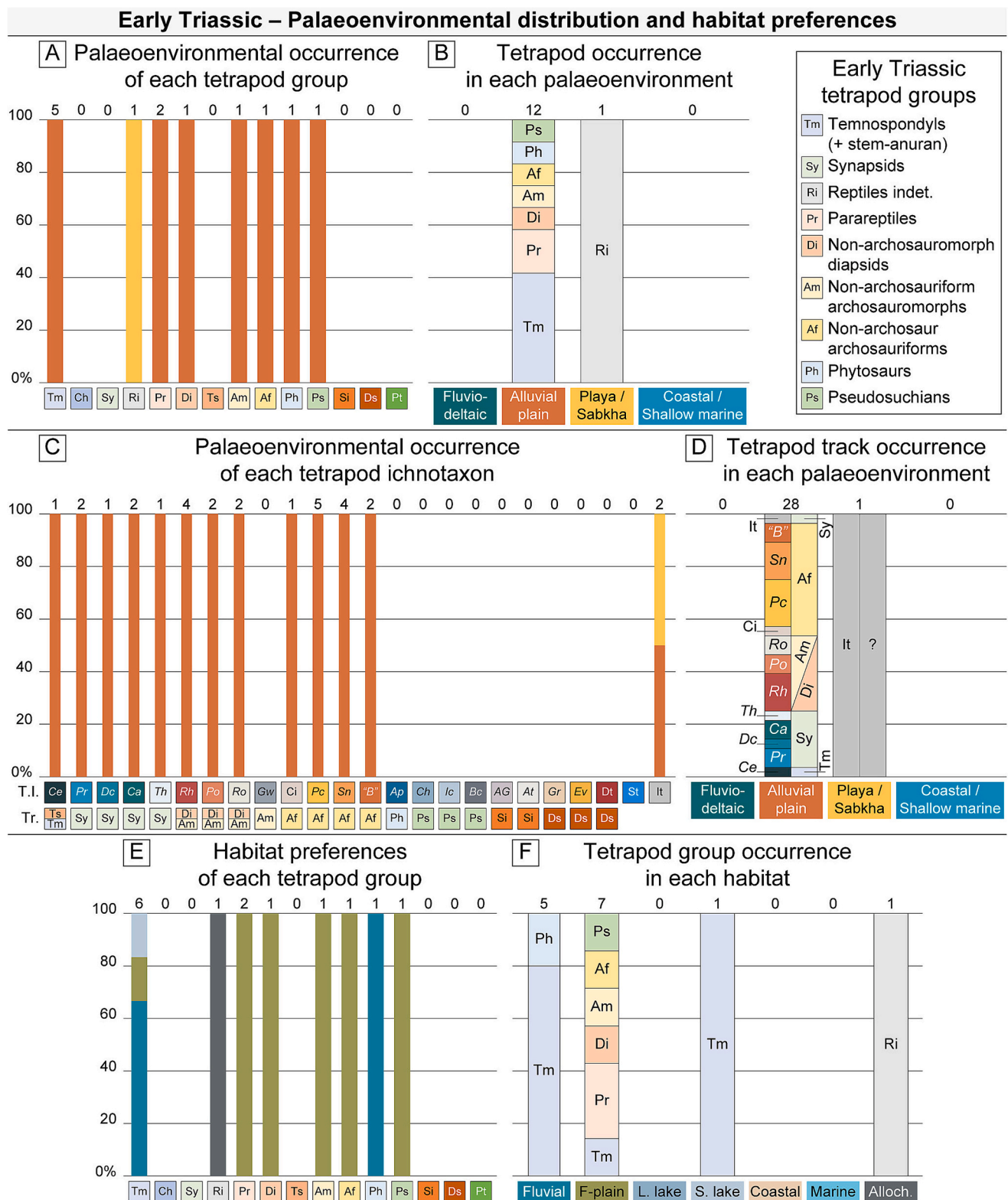


Fig. 9. Occurrence of Early Triassic tetrapods on each palaeoenvironmental setting and their habitat preferences. A. Percentage of occurrences of each tetrapod group (based on the skeletal record, Table S3) within the defined palaeoenvironments. B. Tetrapod group (based on Table S3) relative proportions (percentages) in each palaeoenvironment; the graph indicates the percentage that each tetrapod group represents in each setting. C. Same graph as A but based on the tetrapod track record (Table S4); T.L., tetrapod ichnotaxa (see legend in Fig. 7); Tr., trackmakers. D. Same graph as B but based on Table S4; corresponding trackmakers (when identifiable) are shown on the right side of the bar. E. Percentage of occurrences of each tetrapod group (based on the skeletal record, Table S5) in the defined habitats. F. Tetrapod group (based on Table S5) relative proportions in each habitat. Colours of the bars in graphs A and C correspond to palaeoenvironments in graphs B and D, respectively; colours of the bars in graph E correspond to habitats in graph F. Above each bar, the number of total occurrences for each tetrapod group (A, E), tetrapod ichnotaxon (C), palaeoenvironment (B, D) and habitat (F) is indicated.

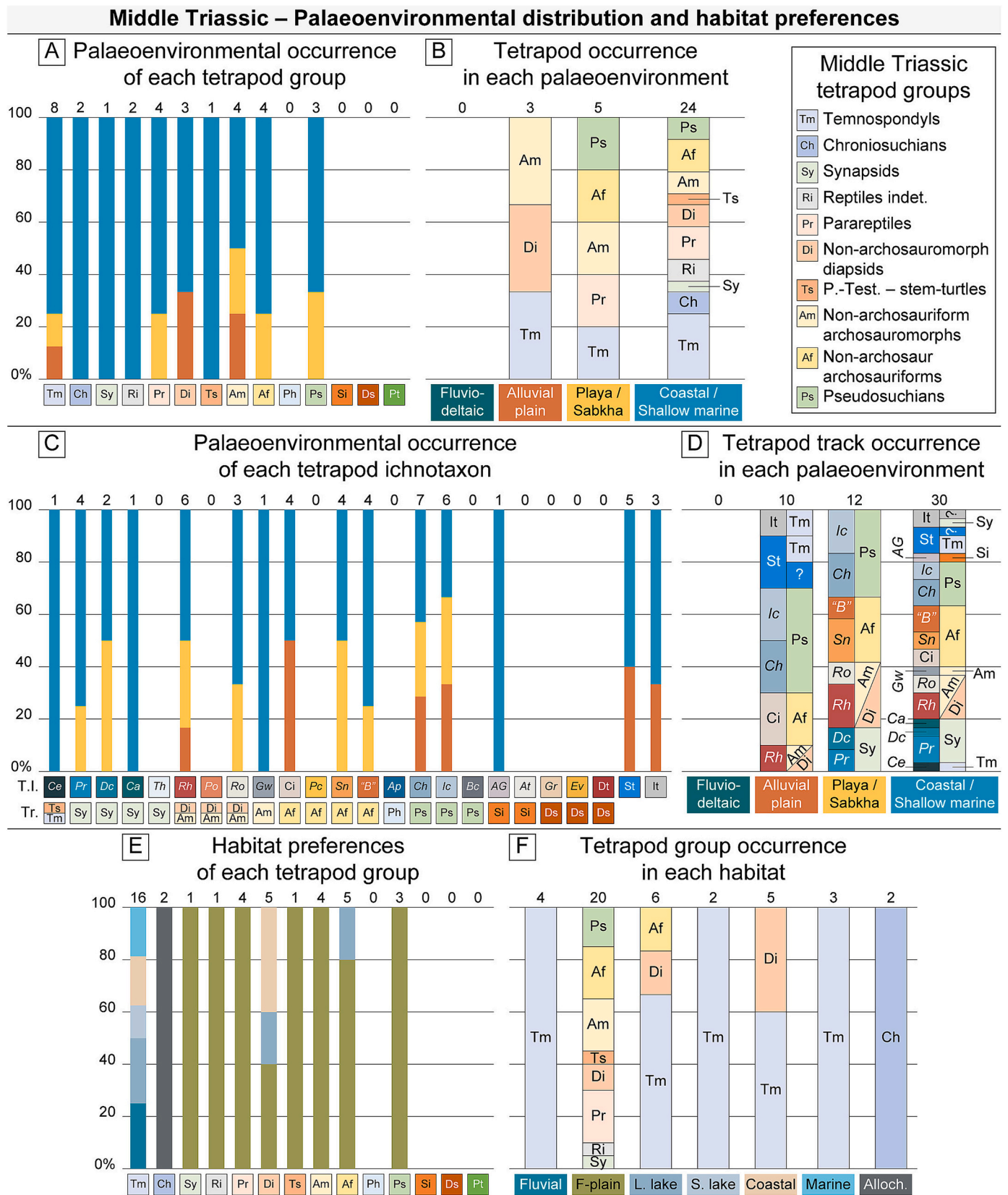


Fig. 10. Occurrence of Middle Triassic tetrapods on each palaeoenvironmental setting and their habitat preferences. Graphs A–F are as those in Fig. 9.

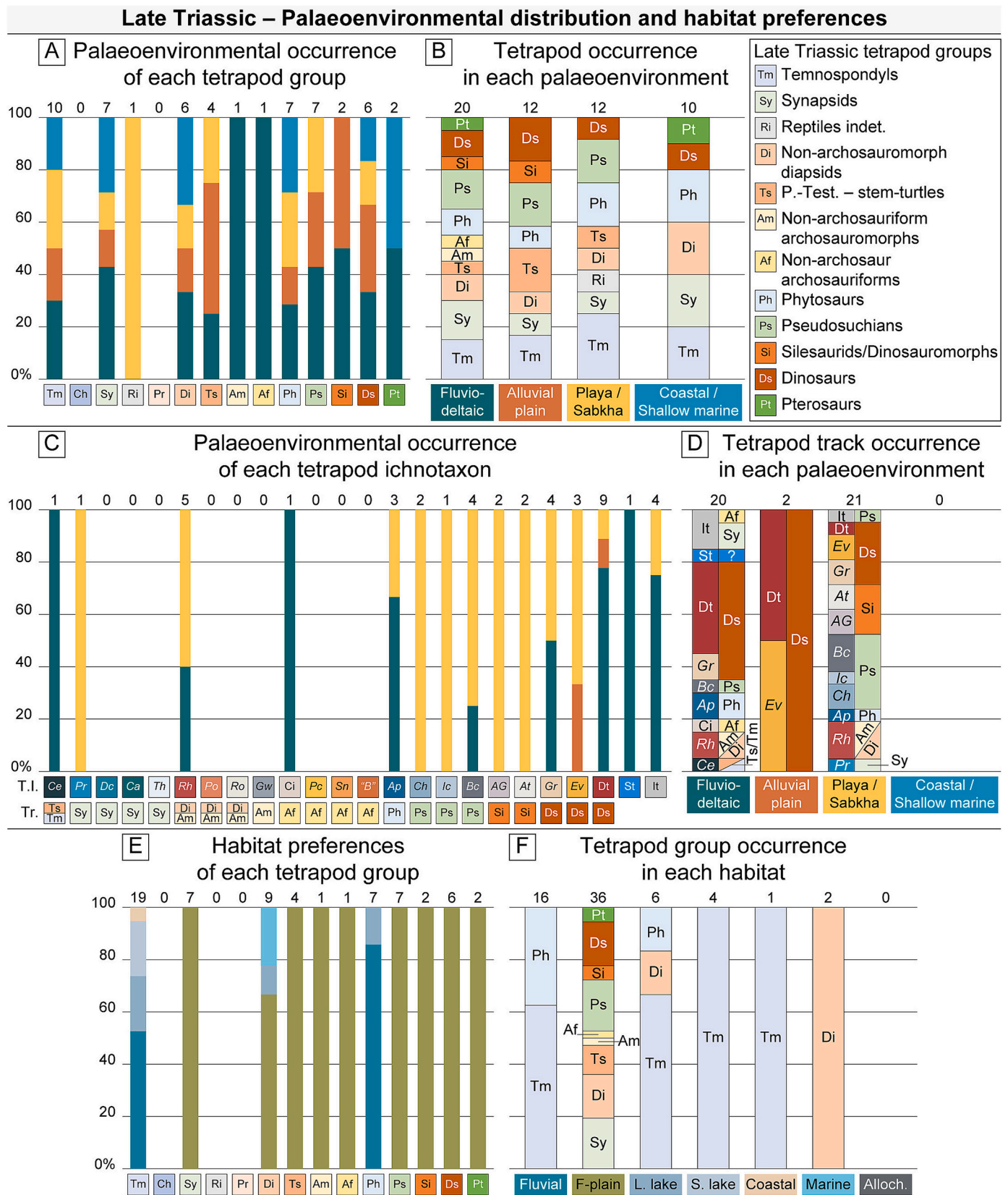


Fig. 11. Occurrence of Late Triassic tetrapods on each palaeoenvironmental setting and their habitat preferences. Graphs A–F are as those in Fig. 9.

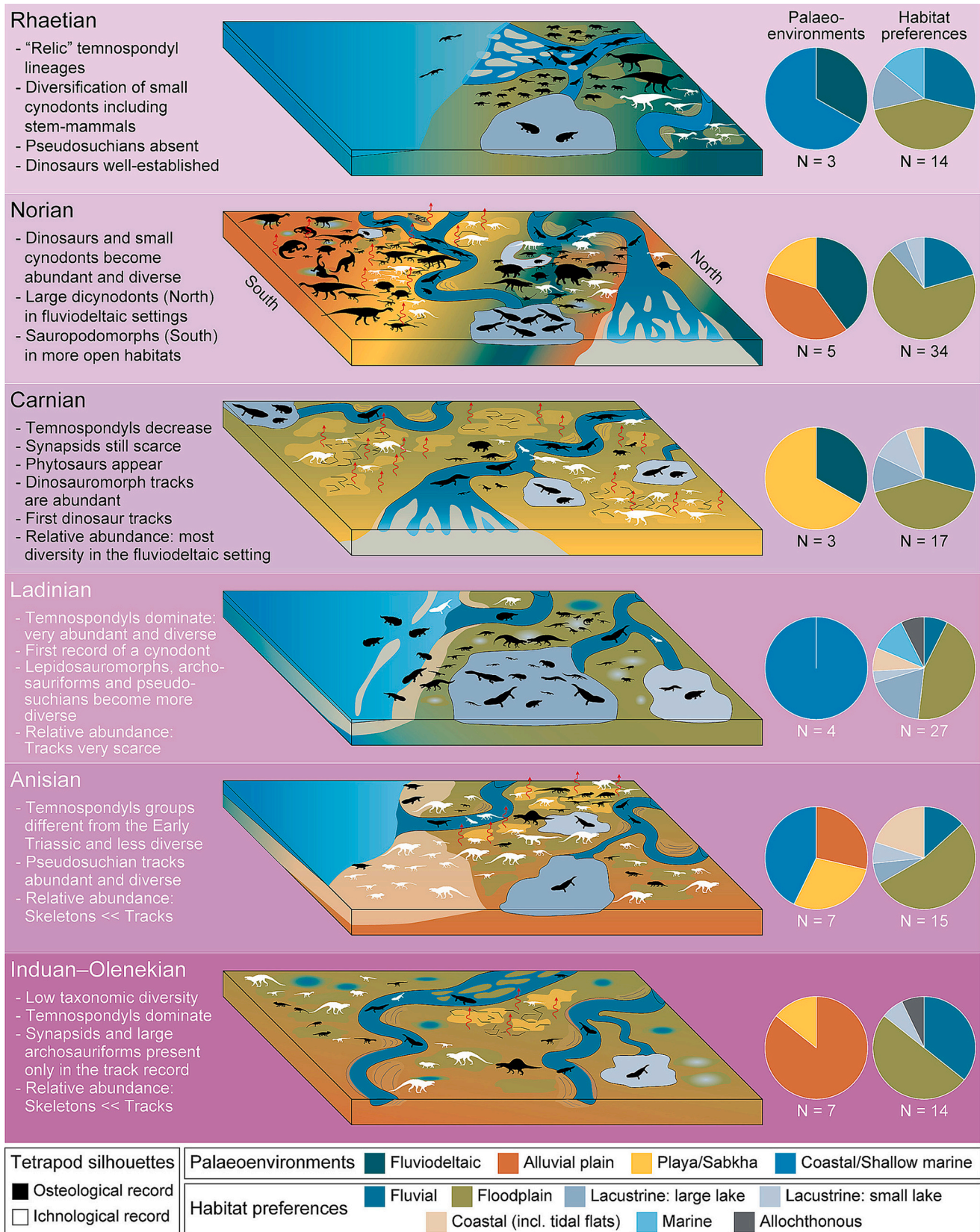


Fig. 12. Palaeoenvironmental reconstructions of Triassic terrestrial tetrapod ecosystems in the CEB. Reconstructions summarise the main features of the tetrapod record in each stage, according to their palaeoenvironmental distribution (based on depositional setting of each unit; see Tables S1–S4) and habitat preferences (based on palaeoecological interpretations of skeletal taxa; see Table S5). Silhouettes and environments (by EM) are not to scale. Plants, invertebrates, fishes and marine tetrapods (groups not included in this study; see section 2) are not represented.

Indeed, the coastal to shallow-water marine settings are much more fossiliferous than the more inland and drier settings represented by the Lower and Middle Buntsandstein subgroups (Figs. 7, 9, 10). Overall, temnospondyls are the most abundant and diverse group, probably related to the presence of more suitable habitats linked to aquatic environments.

The ichnological record of the Middle Triassic shows a great abundance of tracks attributable to small reptiles, especially the ichnogenera *Rhynchosauroides* and *Rotodactylus* (which were already present in the Lower Triassic), and to medium- and large-sized archosauriforms, especially pseudosuchians (which are represented mainly by chirotheriid tracks). These groups are not only the most abundant but are also the most widespread in the different palaeoenvironments (Fig. 10). In the marginal facies of the Muschelkalk in the CEB, tracks attributed to dinosauromorphs (*Atreipus-Grallator*) have been recorded, but their skeletal counterparts are so far known only from the Norian of Poland (Figs. 2, 3).

The fossil record of Upper Triassic deposits presents notable differences with respect to those for the Lower and Middle Triassic (Figs. 2, 3, 7, 11). At this time, the CEB was located at about 30° to 35° N palaeolatitude as Pangaea drifted northward. The skeletal record shows the appearance of various new tetrapod groups, such as phytosaurs and dinosaurs, as well as stem-turtles with fully developed shells and a variety of generally small-sized and often mammal-like synapsids. Pseudosuchians were also more diverse in the Late Triassic, especially in the early Norian, but they were rapidly replaced by dinosaurs in the late Norian (Fig. 2; Qvarnström et al., 2024). The track record also shows a shift toward tetrapods characteristic for the Late Triassic (Fig. 3), especially dinosaurs. Interestingly, pseudosuchian tracks also show a shift from the Early–Middle Triassic to the Late Triassic, when they became less abundant and diverse (unlike their skeletal record). Both skeletal and track records show that non-archosaurian archosauromorphs became much scarcer in the Late Triassic (Figs. 7, 11). Possibly, these taxa were replaced by other diapsid reptiles, including lepidosauromorphs and pseudosuchians as well as synapsids. The same is true for procolophonids, which are absent from the Upper Triassic of the CEB although they are well-documented from the Upper Triassic of southwestern England (e.g., Butler et al., 2024; Meade et al., 2024).

The palaeoenvironmental distribution of Late Triassic footprints appears more restricted than that of body fossils, which can again be linked to taphonomic biases: more energetic depositional environments imply coarser lithologies, precluding the preservation of footprints, especially those left by small animals (see discussion in Marchetti et al., 2019b; Mujal et al., 2020; De Jaime-Soguero et al., 2021).

A comparison of the palaeoenvironmental distribution and habitat preferences for certain groups of tetrapods in the CEB throughout the Triassic also shows interesting patterns (Fig. 12). Temnospondyls are by far the most widely distributed group in terms of habitat preferences (Figs. 9–11), which in part might explain their rich skeletal record (Schoch and Moreno, 2024) as well as the relatively high ecological diversity in this clade. Favourable environmental conditions, with more humid settings, throughout the period and especially during the Middle Triassic also played a role (Moreno et al., 2024b). It is worth noting that the appearance and wide distribution of phytosaurs in the Late Triassic, a group that has been interpreted to occupy comparable or identical ecological niches as temnospondyls, do not appear to affect the distribution and diversity of the latter. This suggests that the drop in temnospondyl diversity at the end of the Triassic, with the extinction of most of their lineages (Schoch and Milner, 2000), is related to other causes.

Another relevant comparison is between sauropodomorph dinosaurs and large dicynodont synapsids, which apparently did not co-exist. This might follow a palaeogeographic pattern (Fig. 12), considering that Poland occupied a more northerly palaeoposition than southern Germany during the Triassic (Fig. 1), and climatic differences might have played a role in their geographical distribution. Alternatively, the two megaherbivores occupied different habitats. As dicynodonts are known

from stream deposits (Stuttgart Formation, Lisowice Beds), they possibly preferred gallery forests along the periphery of larger rivers. Conversely, large sauropodomorphs exemplified by *Plateosaurus trossingensis* inhabited vast playa plains where they probably subsisted on bushy vegetation, especially gymnosperms.

Overall, the distribution of tetrapod taxa and ichnotaxa within the CEB can be linked to the presence of suitable environmental conditions and, consequently, available habitats (Fig. 12). This suggests that correlations of Triassic tetrapod assemblages at a global scale should also take palaeoenvironments into consideration. In general, the rich skeletal and ichnological records from the Triassic of the CEB provides an important reference for understanding Triassic tetrapod assemblages in other regions of the world.

6. Conclusions

Several general conclusions concerning the evolution of terrestrial (including freshwater) tetrapods in the Triassic of the CEB can be drawn from the present analysis:

- (1) The strata from the beginning of the Triassic are almost devoid of tetrapod fossils in the CEB, which contrasts strongly with much more fossiliferous coeval continental deposits in South Africa, Russia, and China, and certain marginal marine units in Madagascar and Svalbard, and the Panchet Formation of West Bengal, India (Schoch and Milner, 2014). This presumably reflects their formation in the low-latitude arid belt with possibly hyperarid climatic conditions in the aftermath of the EPME. In regions outside the CEB, temnospondyls attained considerable diversity with a dominance of euryhaline trematosaurids and rhytidosteids during this time interval. Conceivably, aridity or seasonally unstable conditions in streams and lakes forced these taxa to invade lagoons or shallow-water marine environments in some regions, in which trematosauroids were particularly successful.
- (2) In Central Europe, late Early and Middle Triassic tetrapod assemblages vary considerably in terms of taxonomic diversity, overall showing the recovery of tetrapod communities following the EPME. Whereas temnospondyls were present from the early Olenekian, they diversified at the beginning of the Anisian (Röt Formation, three taxa) and attained their greatest diversity during the late Ladinian (Erfurt Formation, nine taxa), probably as a response to increasing availability of freshwater environments and tolerance of fluctuating salinity in at least some forms (Moreno et al., 2024a). Similar conditions prevailed in the Southern Urals during deposition of the Bukobay Gorizont (five taxa) (Shishkin et al., 2023). Among amniotes, only procolophonoids are found in both Olenekian and Anisian deposits in Germany, in each instance with two taxa, and persisted into the late Ladinian.
- (3) The ichnofaunas tell a rather different story. Especially in the Olenekian, the poor body fossil record for tetrapods from the German Volpriehausen and Hardeggen formations (currently confined to temnospondyls) and the current absence of skeletal remains from the Detfurth Formation sharply contrast with the abundance and diversity of tetrapod tracks in these formations (only amniotes, with at least seven ichnotaxa; Fichter and Kunz, 2015), mainly tracks of small-sized tracks of reptiles and (most likely) synapsids. In contrast to the Lower Triassic formations in Germany, those in Poland have yielded a more diverse and extensive skeletal record, possibly because of the nature of the deposits (cave fills at Czatkowice).
- (4) The presence of tracks of larger tetrapods (*Protochirotherium*) in the Olenekian suggests that large-sized archosauriforms may have been present, but no skeletal remains of such reptiles have been recovered to date from known horizons in the CEB (Klein,

2021). By contrast, large-bodied archosauriforms are well known from roughly coeval strata in the Orenburg and Bashkortostan regions of Russia (Shishkin et al., 2023), in New Mexico, USA (Nesbitt et al., 2006) and in South Africa (Gower et al., 2014). Undisputed dicynodont tracks are still unknown from the Lower Triassic of the CEB, which is in contrast with the almost global distribution of lystrosaurids in the earliest Triassic.

- (5) The fossil record of the lower Anisian Röt Formation and the correlative Grès à Voltzia in eastern France has recently been found to be more diverse than previously assumed for the CEB. Rhynchosaurs, a eucrocopodan archosauriform, and a drepanosauromorph reptile have now been documented from strata in the Black Forest region of Germany and Alsace and Lorraine in France, respectively. For this time interval, the body fossil record (with currently three temnospondyl and seven amniote taxa) approaches the diversity of the rich tetrapod track record although the latter is still more extensive than the former. In particular, the track record indicates the presence (and a relatively high diversity) of medium- and large-sized non-archosaurian archosauriforms and pseudosuchians.
- (6) The differences between Middle and Late Triassic tetrapod assemblages are still evident, but not as pronounced as traditionally assumed. Whereas there was an almost total replacement of temnospondyl taxa (except for the long-ranging *Gerrothorax*), the composition of terrestrial amniote assemblages appears to have changed more gradually from the Anisian to the Norian. Firstly, the Erfurt Formation has yielded a considerable diversity of reptilian taxa that were previously unknown from the Ladinian or not represented in the CEB. They currently include several taxa of lepidosauromorphs, a colognathid, a trilophosaurid archosauromorph, a shell-less stem-turtle, procolophonoids, two taxa of non-archosaurian archosauriforms and two of pseudosuchian archosaurs. Secondly, a newly discovered assemblage from the upper Carnian Stuttgart Formation includes small diapsids comparable to those of the Ladinian and increases the otherwise impoverished tetrapod record of this unit in the CEB.
- (7) Diverse microvertebrate assemblages have been documented from the Lower and Upper Triassic in Poland in recent years. The identification of similar depositional environments elsewhere in the CEB would undoubtedly lead to the discovery of many additional small-sized tetrapods.
- (8) Skeletal and track records of tetrapods provide different yet complementary pictures throughout the Triassic. Lower and Middle Triassic deposits are richer (both in terms of abundance and diversity) in tracks than in skeletal remains whereas Upper Triassic ones present the opposite pattern. These differences predominantly reflected palaeoenvironmental and taphonomic biases, with different lithologies more likely to preserve one or the other type of fossils.
- (9) This review of terrestrial faunas and ichnofaunas highlights the significance of Triassic continental strata in the CEB as an important record for studying the evolution of tetrapods and their adaptations to different palaeoenvironments.

CRediT authorship contribution statement

Eudald Mujal: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Hans-Dieter Sues:** Conceptualization, Data curation, Formal analysis, Investigation, Project administration, Supervision, Validation, Writing – original draft, Writing – review & editing. **Raphael Moreno:** Investigation, Validation, Writing – review & editing. **Joep Schaeffer:** Investigation, Validation, Writing – review & editing. **Gabriela Sobral:** Investigation, Validation, Writing – review & editing. **Sanjukta Chakravorti:** Investigation, Validation, Writing – review & editing. **Stephan**

N.F. Spiekman: Investigation, Validation, Writing – review & editing. **Rainer R. Schoch:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Project administration, Supervision, Validation, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank Hans Hagdorn, Edgar Nitsch, Dieter Seegis, and Florian Witzmann for many fruitful discussions. We gratefully acknowledge helpful reviews from P. John Hancox, Mike Benton, an anonymous reviewer, and the editor Christopher Fielding, for also handling the manuscript. This study was supported by DFG grant SCHO-791/7-1.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.earscirev.2025.105085>.

Data availability

Data are provided in supplementary material.

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