Unexpected temnospondyl diversity in the early Carnian Grabfeld Formation (Germany) and the palaeogeography of metoposaurids

Article *in* Fossil Record · December 2024

DOI: 10.3897/fr.27.121996

Raphael Moreno
State Museum of Natural History Stuttgart

Fossil Record 27 (3) 2024, 381–400 | DOI 10.3897/fr.27.121996

Unexpected temnospondyl diversity in the early Carnian Grabfeld Formation (Germany) and the palaeogeography of metoposaurids

Raphael Moreno[1,2], Sanjukta Chakravorti[1,2], Samuel L. A. Cooper[1,2], Rainer R. Schoch[1,2]

1 *Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany*
2 *Fachgebiet Paläontologie, Institute für Biologie, Universität Hohenheim, 70599 Stuttgart, Germany*

https://zoobank.org/00E2F554-551C-47A1-976A-1D9CDE52885B

Corresponding author: Raphael Moreno (raphael.moreno@smns-bw.de)

Academic editor: Florian Witzmann ♦ **Received** 29 February 2024 ♦ **Accepted** 24 June 2024 ♦ **Published** 30 December 2024

Abstract

The Middle–Late Triassic Grabfeld Formation formed in a generally arid, hostile setting with frequent evaporation under alternating sabkha and playa conditions. Here we report evidence of four temnospondyl taxa from the upper part of the sequence (‘Bunte Estherienschichten’), including (1) *Metoposaurus* sp., (2) a capitosaur, (3) *Gerrothorax* sp. and (4) *Plagiosternum* sp. This early Carnian assemblage provides the stratigraphically oldest evidence of metoposaurids and the last report of plagiosternines in the Central European Basin. The stratigraphic age of these strata and the occurrence of Metoposauridae therein sheds new light on the palaeogeographic distribution of the group and their occurrence before the Carnian Pluvial Event.

Key Words

Euryhaline, Gipskeuper, Late Triassic, *Metoposaurus*, Middle Keuper, Temnospondyli

Introduction

The Triassic Keuper sequence of the Central European Basin (CEB) is particularly noteworthy for preserving a variety of distinct, large-bodied temnospondyl amphibians (Schoch 2021). During the Triassic (251–201 Ma), temnospondyls were relatively abundant and display high levels of morphological disparity and taxonomic diversity (Schoch and Milner 2000, 2014). Temnospondyls achieved a near global distribution across the slowly rifting Pangaean supercontinent, and hence today preserve rich fossil assemblages on all continents (Schoch 2000). The diverse temnospondyl assemblage of the German Keuper (see Schoch 2021 for an overview) is comprised of capitosaurs (*Mastodonsaurus*, *Tatrasuchus*, *Capitosaurus*, *Cyclotosaurus*), plagiosaurs (*Plagiosaurus*, *Plagiosuchus*, *Gerrothorax*, *Plagiosternum*, *Megalophthalma*), trematosaurs (*Trematolestes*, *Hyperokynodon*) and metoposaurs (*Callistomordax*, *Metoposaurus*). The occurrence of often multiple taxa in these German fossil localities (Schoch and Moreno 2024) indicate stable habitation conditions, which allowed for niche partitioning among the different groups. While the large capitosaurs likely occupied the role of apex predators in these aquatic realms, the streamlined trematosaurs and related metoposaurs pursued active hunting strategies (Fortuny et al. 2017a; Kalita et al. 2022). With their flat bodies and hypothesised tolerance for changing environmental conditions (Sanchez and Schoch 2013), plagiosaurs are regarded as generalists, feeding at the bottom of lakes and fluvial systems. The stratigraphic range of capitosaurs extends from the Induan to the Rhaetian (Schoch and Milner 2000; Konietzko-Meier et al. 2019). Plagiosaurs occur from the Ladinian to the Rhaetian (Schoch and Milner 2014).

The Late Triassic family Metoposauridae Watson 1919 (Table 1) combine a near-global distribution with a relatively short stratigraphic range (Lucas 2020). Therefore, they have been considered by some authors to be a key tetrapod group for terrestrial biostratigraphic correlation (Lucas 2020). Metoposaurids were two-to-four-meter long stereospondyl temnospondyls characterised by short limbs and flat skulls with anteriorly placed orbits and needle-like teeth (Sulej 2007). Based on previously published records, the Metoposauridae of Central and Western Europe (Fig. 1A) have a brief stratigraphic range from the late Carnian to late Norian, with the oldest described CEB materials originating from the Stuttgart Formation (231 Ma; Zeh et al. 2021) in southern Germany (Sulej 2002, 2007). Outside the CEB, metoposaurids are described from the Carnian of Morocco (Jalil 1999), Madagascar (Fortuny et al. 2019) and India (Chakravorti and Sengupta 2019). Furthermore, metoposaurids occur in North America where they occupy their longest stratigraphic range from the middle Carnian to the Rhaetian (Hunt 1993). However, no records of Metoposauridae have yet been definitely identified from the base of the earliest Carnian.

Here, we review the diversity of temnospondyl remains from the Grabfeld Formation, a late Ladinian–early Carnian rock sequence of southern Germany. This formation is characterized by evaporites and mudstone-dominated sabkha and playa deposits with few fossiliferous horizons. Even temnospondyls, the most abundant tetrapod group in the German Triassic, are notoriously rare in the Grabfeld Formation and their taxonomy had long remained elusive. All specimens reviewed herein fall within the upper part of the sequence, the 'Bunte Estherienschichten' (Fig. 1). So far, the only described occurrence is an isolated temnospondyl clavicle tentatively assigned to *Metoposaurus* sp. by Wild (1974). However, this record has either been overlooked or rejected by subsequent review studies (Schoch and Wild 1999; Schoch 2021) as it has not been cited, and consequently the stratigraphic range of metoposaurids was figured to start in the basal part of the Stuttgart Formation (late Carnian; Schoch 2021). The objective of the present study is to examine the available body of evidence on temnospondyls from the Grabfeld Formation with particular emphasis on metoposaurids and their revised palaeobiogeographic and stratigraphic distributions.

Geological setting

Southern Germany is famous for its unique geological landscape. Among the most prominent natural regions of the South German Scarplands are the Keuper escarpments with its outcrops of Middle and Late Triassic epicontinental strata (Fig. 1).

The strata between the brackish lacustrine sediments of the Erfurt Formation (Lower Keuper) and the fluvial dominated sandstones of the Stuttgart Formation (Schilfsandstein) have historically received varying nomenclature in different regions of southern Germany (Nitsch et al. 2005). In the latter half of the 20th century the Keuper strata had been investigated more intensively (Gwinner 1980) and the general comprehension of regional correlation of these strata began to be better understood. Often confusing regional terminology was unified (see Nitsch et al. 2005 for a summary on the topic) and the term Grabfeld Formation was coined by the Deutsche Stratigraphische Kommission to define the succession (DSK 2005; Nitsch et al. 2005).

The Grabfeld Formation consists mostly of grey and occasionally coloured clays that are separated by numerous thin dolomitic banks (Nitsch 1996; Etzold and Schweizer 2005; Freudenberger 2005). Stratigraphic correlation of the formation is based mostly on these dolomitic banks that allow for basin wide correlation (Nitsch 1996). The Grabfeld Formation is wedged in by the underlying Ladinian Erfurt Formation, which encompasses a carbonate siliciclastic succession deposited in a deltaic environmental setting that is influenced by lagoonal and transgressive sequences (Mujal and Schoch 2020). The overlying Stuttgart Formation of the Middle Keuper was deposited in a similar palaeoenvironmental setting that was dominated by fluvial systems (Stollhofen et al. 2008).

The Grabfeld Formation encompasses alternating sabkha and playa deposits that formed during a transition towards a more arid climate (Nitsch et al. 2005). The sedimentary succession represents small-cycle deposits of brackish to saline ephemeral lakes.

Table 1. Spatial and temporal ranges of the family Metoposauridae.

Name	Age range	Region	Reference
Metoposaurus diagnosticus	middle Carnian	Europe	Milner and Schoch 2004
Metoposaurus krasiejowensis	late Carnian − middle/late Norian	Europe	Sulej 2007
Metoposaurus algarvensis	middle Carnian − middle/late Norian	Europe	Witzmann and Gassner 2008; Brusatte et al. 2015
Almasaurus habazzi	middle Carnian	Morocco	Jalil 1999
Dutuitosaurus ouazzoui	middle Carnian	Morocco	Jalil 1999
Arganasaurus lyazidi	middle Carnian − late Carnian	Morocco	Jalil 1999
Arganasaurus azerouali	middle Carnian − late Carnian	Morocco	Jalil 1999
"*Metoposaurus hoffmani*" *	middle Carnian − late Carnian	Madagascar	Fortuny et al. 2019
Panthasaurus maleriensis	middle Carnian − late Carnian	India	Chakravorti and Sengupta 2019
Anaschisma browni	middle Carnian − late Norian	North America	Hunt 1993
Buettnererpeton bakeri	middle Carnian − late Carnian	North America	Gee and Kufner 2022
Apachesaurus gregorii	late Carnian − Rhaetian	North America	Hunt 1993
Metoposauridae indet.	middle Carnian − Rhaetian	North America	Baird 1986; Spielmann and Lucas 2012; Heckert and Lucas 2015
Metoposauridae indet.	late Norian	Zimbabwe	Barrett et al. 2020

* this species was recently identified a *nomen dubium* by Fortuny et al. (2019).

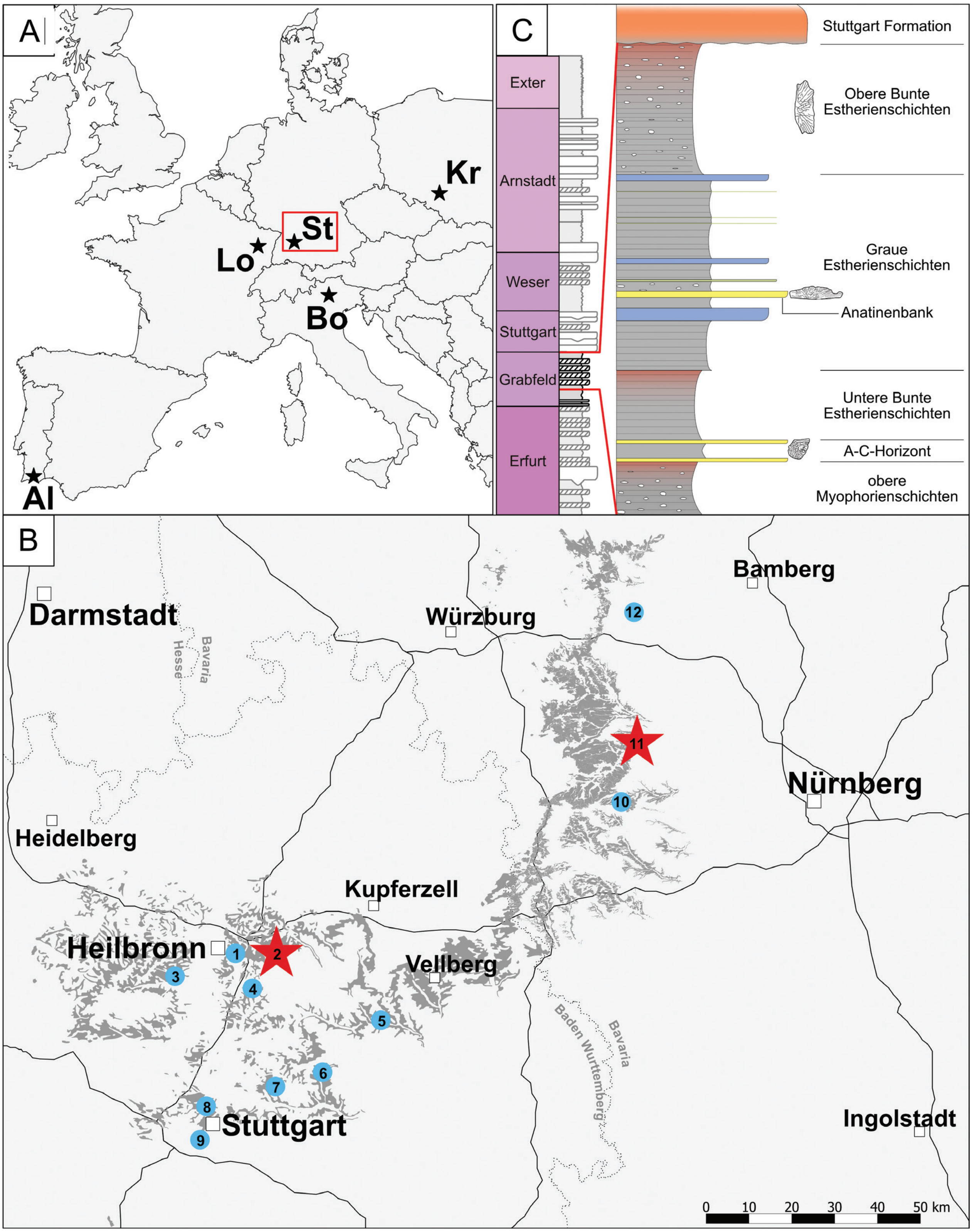

Figure 1. A. Distribution of *Metoposaurus* in Europe; **B.** *Metoposaurus*-bearing fossil localities in southern Germany. Blue circles indicate localities within the Stuttgart Formation, while red stars indicate localities with Grabfeld Formation occurrence; **C.** Stratigraphic log of the Grabfeld Formation following (Emmert et al. 1974; Nitsch et al. 2005), stratigraphic column modified from (Schoch and Moreno 2024). Lo – Lorraine, Saint-Nicolas-de-Port quarry, St – Stuttgart, Baden-Württemberg, Bo – Bolzano, Raibl beds, Kr – Krasiejów, Al – Algarve, Portugal. (1) Jägerhaus quarry Heilbronn, (2) Affaltrach, (3) Stockheim (Brackenheim), (4) Rote Wand Helfenberg, (5) Fichtenberg-Michelbächle, (6) Geißgurgelbach, (7) Winnenden Hannweiler, (8) Stuttgart Feuerbacher Heide, (9) Stuttgart Sonnenberg, (10) Markt Obernzenn–Ipsheim (Kaubenheim) area, (11) Neustadt an der Aisch, (12) Ebrach. **A–C**-Horizont – Acrodus-Corbula-Horizont.

These cyclothems are ideally tripartite and consist of a claystone–dolomite horizon (ephemeral and ingression phase), followed by an evaporitic sulphate horizon (playa phase) and an unstratified claystone–nodular sulphate horizon (palaeosol phase; Aigner and Bachmann 1992; Nitsch et al. 2005).

Thürach (1888) first divided the Grabfeld Formation into lower, middle and upper sections, a system which is still followed today. These sections of the Grabfeld Formation encompass an evaporitic-siliciclastic intercalation. In the middle Grabfeld Formation, repeated marine ingressions form thin dolomitic beds. However, a marine influence for these beds is still debated for the higher parts of the succession starting from the 'Acrodus-Corbula Horizont' (Fig. 2) (Linck 1972; Aigner and Bachmann 1992; Nitsch 1996; Nitsch et al. 2005).

Towards the southeast of the basin, the facies of the Grabfeld Formation interlocks with the marginal facies of the Vindelician Highlands. This marginal facies is represented by the Benk Formation and consists of fluvial sandstones (DSK 2005; Nitsch et al. 2005).

The cyclitic nature of the Grabfeld Formation is represented not only by fine layered mudstones and thin dolomitic layers but also by the fossil contents. Conchostracs, bivalves and rare fish remains are indicative of rapid changes in salinity from brackish to hypersaline and limnic milieus (Nitsch et al. 2005). Marine ingressions in the southern parts of the basin allowed for entry of euryhaline Tethyan taxa to invade the CEB as is documented by the presence of various sauropterygians (*Nothosaurus*, *Simosaurus*, *Psephosaurus*) in the upper Grabfeld Formation (Rieppel and Wild 1994; Nitsch et al. 2005; Schoch 2021).

While *Psephosaurus suevicus* is only known from fragmentary carapace fragments (Rieppel 2000), *Simosaurus gaillardoti* and *Nothosaurus edingerae* are each known from cranial and postcranial material (Rieppel 1994; Rieppel and Wild 1994). Until now, only few temnospondyl remains have been reported. *Capitosaurus arenaceus* Münster 1836 was the historically first mentioned temnospondyl from the marginal facies of the Grabfeld Formation, the Benker Sandstone, near Bayreuth in eastern Bavaria. Broili (1915) described the bones to be of white colour, embedded in a yellow-whiteish matrix of fine-grained sandstone. The first mention of temnospondyl remains from the basin facies of the Grabfeld Formation of Bavaria come from Emmert et al. (1974) and Wild (1974) subsequently (Fig. 1B). Schoch and Witzmann (2011) as well as Schoch and Milner (2014) mention the presence of a single osteoderm of the plagiosaurid *Gerrothorax* from the 'Anatinenbank' of Kaubenheim, Bavaria. We have located this specimen (SMNS 97109) in the collection of the State Museum of Natural History Stuttgart (SMNS). Additionally, new material has recently been recognised in the palaeontological collection of the SMNS, including fragmentary pectoral girdle elements, vertebra and a phalange, which are reported herein (Table 2). These materials originated from different localities in Baden-Württemberg and Bavaria, Germany (Fig. 1B).

Materials and methods

Metoposauridae

Three metoposaurid temnospondyl bones are described from various stratigraphic and geographic horizons of the Grabfeld Formation of southern Germany (Table 2).

A fragmentary angular, SMNS 97058, was found in 1935 by a student, G. Buck, near Affaltrach in northern Baden-Württemberg (Fig. 2A) (Linck 1972). The specimen was gifted to O. Linck and found its way to the collection of the SMNS as part of a donation in later years. This fossil was found in the 'Anatinenbank' of the 'Graue Estherienschichten' (Fig. 1C). The same horizon has yielded a mineralized phalange and a presumable caudal vertebra of indeterminate temnospondyls from Stockheim (Brackenheim), west of Heilbronn. Together with SMNS 97058, these specimens were added to the palaeontological collection as part of a donation by O. Linck.

Table 2. Examined temnospondyl material from the Grabfeld Formation of southern Germany.

Specimen	Systematic palaeontology	Material	Horizon	Locality	Reference
SMNS 97058	*Metoposaurus* sp.	isolated angular	Anatinenbank	Affaltrach, Baden-Württemberg	this study
SMNS 55899	*Metoposaurus* sp.	fragmentary clavicle	Acrodus-Corbula Horizont	Altheim, Bavaria	Wild 1974
SMNS 59770	*Metoposaurus* sp.	fragmentary interclavicle	Obere Bunte Estherienschichten	Neustadt an der Aisch, Bavaria	this study
SMNS 97109	*Gerrothorax* sp.	isolated dermal bone	Acrodus-Corbula Horizont	Kaubenheim, Bavaria	Schoch and Witzmann 2011; this study
SMNS 59771	*Plagiosternum* sp.	fragmentary interclavicle	Obere Bunte Estherienschichten	Neustadt an der Aisch, Bavaria	this study
SMNS 97123	Capitosauroidea indet.	isolated intercentrum	Grabfeld Formation	Westheim, Bavaria	this study
SMNS 97125	Temnospondyli indet.	isolated intercentrum	Anatinenbank	Stockheim, Baden-Württemberg	this study
SMNS 97124	Temnospondyli indet.	isolated phalange	Anatinenbank	Stockheim, Baden-Württemberg	this study

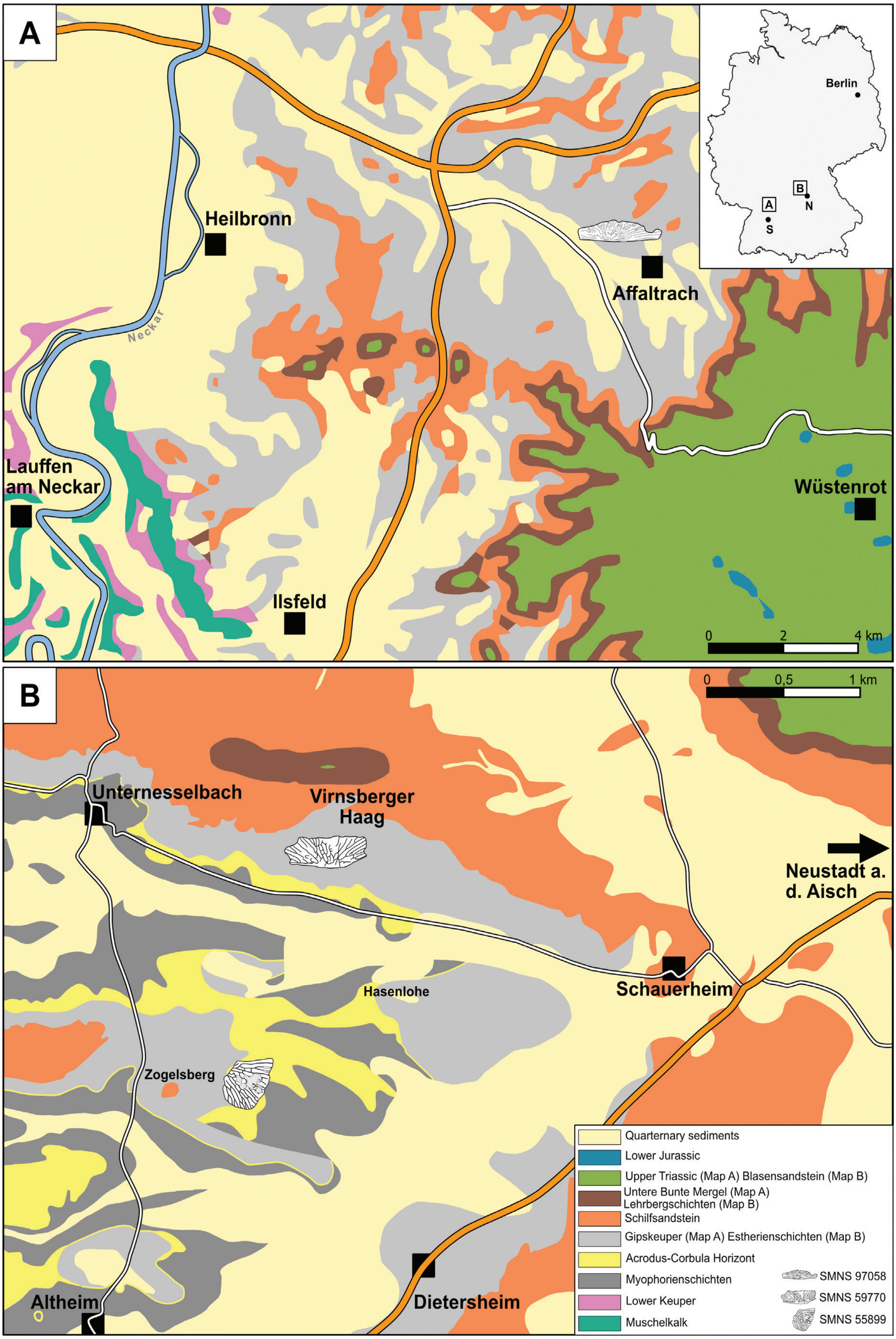

Figure 2. Geological map (redrawn from Bundesanstalt für Geowissenschaften und Rohstoffe) of the study areas. **A.** Heilbronn; **B.** Neustadt an der Aisch.

The rubblestone (*Lesestein*) specimen, SMNS 55899, described by Wild (1974) was identified as deriving from the 'Acrodus-Corbula Horizont' at the base of the 'Untere Bunte Estherienschichten' (Fig. 1B; 2B). Based on its dermal sculpture, it is identified as a partial clavicle of a metoposaurid (Wild 1974). Wild produced a mould to aid in his description of the specimen, although this could not be relocated in the SMNS. We therefore produced a new cast of the missing bone using a green latex silicone mould.

Another partial fragment, SMNS 59770, was collected in the vicinity of Neustadt an der Aisch (Fig. 1B) only a few kilometres from the collection horizon of SMNS 55899 (Fig. 2B). This specimen was collected from a field approximately 15 m north of the road connecting the municipalities of Unternesselbach and Schauerheim. This proposed fragmentary interclavicle of a metoposaurid is stratigraphically derived from the 'Obere Bunte Estherienschichten'.

Capitosauroidea

A gently deformed isolated vertebra of an indeterminate capitosauroid was recovered from an unspecified layer within the Grabfeld Formation south of Westheim between Illesheim and Marktbergel southwest of Neustadt an der Aisch.

Plagiosauridae

SMNS 59771, an interclavicle fragment of a plagiosternine from the 'Obere Bunte Estherienschichten' of the same locality as SMNS 59770 consistent with finds of *Plagiosternum granulosum* from the Heldenmühle quarry at Crailsheim (Fig. 1B).

SMNS 97109, a dermal bone fragment of a plagiosaurine, consistent with *Gerrothorax pulcherrimus* from the 'Acrodus-Corbula Horizont' (basal part of 'Untere Bunte Estherienschichten', upper Grabfeld Formation) Kaubenheim, Bavaria. This specimen has wrongly been attributed to have originated from the 'Anatinenbank' by Schoch and Witzmann (2011) and Schoch and Milner (2014).

Institutional abbrevations: **SMNS**, Staatliches Museum für Naturkunde Stuttgart.

Results

Description

Temnospondyli Zittel, 1888
Stereospondyli Fraas, 1889
Metoposauridae Watson, 1919

***Metoposaurus* Lydekker, 1890**

Type species. *Metopias diagnosticus* (= *Metoposaurus diagnosticus*) (Meyer, 1842).

***Metoposaurus* sp.**
Fig. 3A–G

Angular (SMNS 97058)

Material. SMNS 97058, isolated angular preserved in original matrix, exposed in external lateral view (Fig. 3A).

Locality. An unspecified outcrop in the vicinity of Affaltrach, northern Baden-Württemberg (Fig. 1B).

Horizon. 'Anatinenbank', 'Graue Estherienschichten', Middle Grabfeld Formation, Middle Keuper, early Carnian, lowermost Upper Triassic (Fig. 1C).

Description. The angular (SMNS 97058) measures approximately 82 mm in anteroventral length and a maximum depth of 20 mm in height (Fig. 3A). The bone is asymmetrically elliptical with a somewhat flat ventral margin and a widely concave dorsal margin in lateral view (Fig. 3A). The bone is relatively short with a longitudinal length accounting for more than four times the bone height. The specimen is fairly well preserved albeit for the posterodorsal margin and a small section at the anteroventral side which are damaged. A small anterodorsal sulcus associated with a disarticulated suture boundary with the dentary is present. The external surface is strongly ornamented with a distinct sculpture which radiates outwards from the posteroventral margin. The posteroventral sculpture is composed of sinuously folded ridges and grooves forming a weakly polygonal texture. Radiating dorsal, dorsoanterior, and anteriorly, the sculpture forms few very well-developed elongate ridges which for the most part are straight, somewhat narrow, and neatly arranged forming a 'striated' appearance. Distal bifurcation of the ridges is rare but confined to only the distal extremities of the bone. This ornamentation pattern is consistent with *Metoposaurus* spp. (Sulej 2007). The ventral margin is noticeably thicker where it is developed into a weak ventral keel. The ornamented sculpture does not extend onto the ventral surface of the angular as observed in some capitosauroids including *Mastodonsaurus* (Schoch 1999).

Remarks. The shape of the bone and ornamentation pattern in SMNS 97058 are consistent with the angular in *Metoposaurus diagnosticus* from the overlaying Stuttgart Formation, as well as with *Metoposaurus krasiejowensis* from the Norian of Poland (Sulej 2007). The pattern and placement of the sculpture, notably in the presence of radiating ridges, is vastly different than the heavily reticulated, polygonal pattern of the angular of *Mastodonsaurus* (Rinehart and Lucas 2013). The isolated nature of the bone indicates that this individual was either in a late stage of decay when it was buried, or possibly represents an osteological immature individual which had not fully fused the angular to the other bones in the lower jaw.

Clavicle (SMNS 55899)

Material. SMNS 55899, incomplete clavicle preserved mostly as an external mould (Fig. 3B, C).

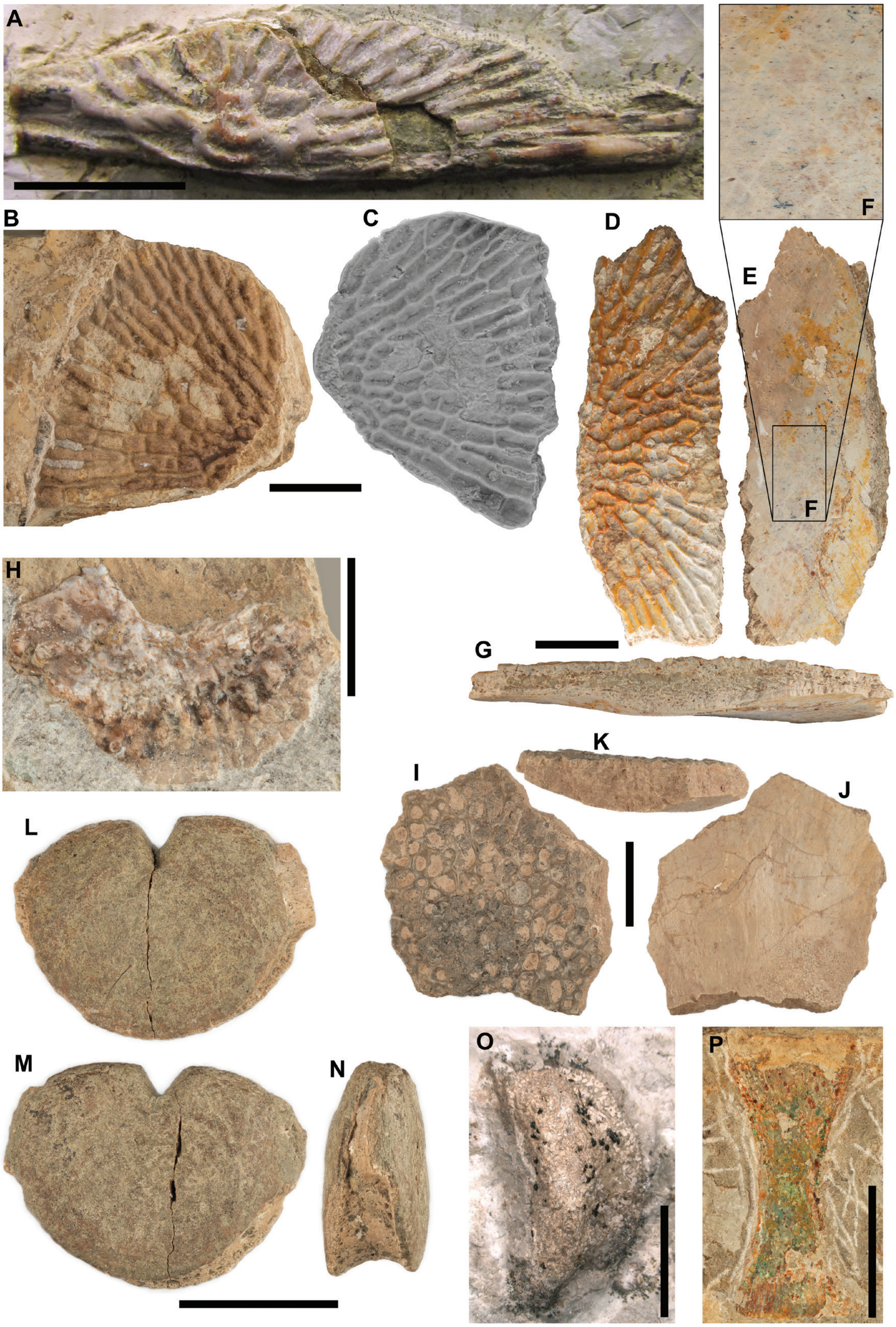

Figure 3. Fragmentary temnospondyl specimens collected from the Grabfeld Formation of southern Germany. **A.** SMNS 97058, a fragmentary angular of *Metoposaurus* sp. **B–C**, SMNS 55899, a fragmentary clavicle of *Metoposaurus* sp.; **B.** Natural mould; **C.** Silicone mould; **D–G.** SMNS 59770, a fragmentary interclavicle of *Metoposaurus* sp. in **D.** Ventral; **E.** Dorsal; **F.** Lateral view; **G.** Close-up of vascular foramina; **H.** SMNS 97109, a fragmentary dermal bone of *Gerrothorax* sp. **I–K**, SMNS 59771, a fragmentary interclavicle of *Plagiosternum* sp. in **I.** Dorsal; **J.** Lateral; **K.** Ventral view. **L–N**, SMNS 97123, an isolated capitosauroid vertebra in **L.** Anterior; **M.** Posterior, **N.** Lateral view; **O.** SMNS 97125, an isolated temnospondyl caudal vertebra in ventral view; **P.** SMNS 97124, an isolated temnospondyl phalange. Scale bars: 20 mm (**A–G, L–N, P**); 50 mm (**O**); 10 mm (**H, I–K**).

Locality. Near Altheim at the base of the Zogelsberg in the district of Neustadt an der Aisch, Middle Franconia, Bavaria (Fig. 1B, 2B).

Horizon. Collected loose from rubblestone (*Lesestein*) derived from the 'Acrodus-Corbula Horizont' at the base of the 'Untere Bunte Estherienschichten', Upper Grabfeld Formation, Middle Keuper, lowermost Upper Triassic.

Description. Marginal section of a large metoposaurid clavicle preserved mostly as an external mould (Fig. 3B) in a nodular dolostone measuring at its extremities 148 mm by 76 mm by 45 mm. The mould of the original bone, which preserves impressions of the original ventral (external) bone surface measures approximately 80 mm by 55 mm. Almost all of the original bone is absent except for a few bone splinters which are embedded around the margin of the void. An indeterminate rectangular bone is additionally preserved in cross section on the reverse margin of the matrix although the identity of the bone cannot be determined. Details of the original ornamentation are described based on a silicon mould (Fig. 3C) produced for this study.

Sculpture comprises a margin concentration of small and shallow polygonal pits arranged in a honey comb-like structure. Distally, these shallow sloped ridges radiate into mostly straight lines which proximally bifurcate in a clear 'Y' shape pattern. The area occupied by the honey comb-like polygonal pits is very narrow compared to the preserved region (and missing regions) occupied by the elongate bifurcating ridges. Collectively, all of the ridges are shallow and smooth, therefore unlike the much deeper and more deeply excavated ridges in the sculpture of Capitosauroidea (Wild 1974).

Remarks. According to Wild (1974), the area of bone represented as an external mould in SMNS 55899 derives from the posterolateral margin, likely close to the ascending process of the clavicle. The ornamentation sculpture including the small polygonal pits which are confined to a small area of the bone surface, is diagnostic of *Metoposaurus* spp. (Sulej 2002). The ornamentation of *Cyclotosaurus* distinctly differs from *Metoposaurus* by having relatively large and rhomboidal polygons (Antczak and Bodzioch 2018). The morphology of SMNS 55899 most closely matches the clavicle of *Metoposaurus diagnosticus* from the Carnian of Germany based on materials examined in the SMNS (SMNS 81981 and SMNS 81983).

Interclavicle (SMNS 59770)

Material. SMNS 59770, large isolated interclavicle fragment, likely from the posteromedial region (Fig. 3D–G).

Locality. Field exposure approximately 15 m north of the road connecting the municipalities of Unternesselbach and Schauerheim, Middle Franconia, Bavaria (Fig. 1B).

Horizon. 'Obere Bunte Estherienschichten', Upper Grabfeld Formation, Middle Keuper, lowermost Upper Triassic.

Description. A large rectangular fragment of a metoposaurid interclavicle measuring approximately 107 mm by 38 mm. The bone is broken on all sides, meaning that the precise placement of this fragment and the original size of the interclavicle cannot be reliably estimated. The bone is topographically flat and dense in cross section with a notable bulge towards the midpoint with a maximum thickness of approximately 13 mm and a minimum thickness on the lateral margins of approximately 7 mm. The ventral (external) surface (Fig. 3D) is strongly sculptured with a mosaic of shallow radiating ridges which towards the inferred midpoint of the bone, interconnect forming a regionalised polygonal network. Laterally, these polygonal ridges radiate forming thin, evenly spaced shallow ridges which do not laterally intersect one another, although proximally some display a single 'Y' shaped bifurcation. The polygonal pits formed by this medial interconnection of the ridges are fairly small and shallow throughout, with their extent appearing to be constricted to a brief regionalised area of the external sculpture. Topographically, all ridges are shallow and smooth; therefore, they distinctly differentiate from the much taller and steeper ridges and grooves in the interclavicles of capitosauroids. The dorsal (internal) surface (Fig. 3E) is smooth and irregularly concave with numerous fine vascular foramina (Fig. 3F) orientated downslope of the medial bulge (Fig. 3G). The bone is scarred with delicate cross-cutting diagenetic fractures which are responsible for the splintered margins around the edges of the bone.

Remarks. As stated above, the presence of shallow ridges and grooves, small medially localised polygonal sculpture, and thin radiating ridges strongly supports referral of SMNS 59770 to Metoposauridae rather than to Capitosauroidea. In capitosauroids, the polygonal pits are much deeper and wider with taller and steeper radiating ridges. A similar criterion had previously been used to refer SMNS 55899 (redescribed herein) to *Metoposaurus* sp. by Wild (1974). The polygonal area is tightly confined to a small area of the bone, which combined with the small size of the polygonal pits, is a character shared between *Metoposaurus krasiejowensis* from Poland and *Metoposaurus diagnosticus* from the CEB, with this character considered by many authors to be highly diagnostic of the genus *Metoposaurus* (Hunt 1993; Long and Murry 1995; Sulej 2002). The ornamentation and sculpture patterns are near enough identical in both SMNS 59770 and SMNS 55899, which despite representing different bones in the pectoral girdle, supports the hypothesis that both elements likely belong to a single metoposaurid taxon. An absence of pustules or tubercles additionally rules out either of these specimens belonging to Plagiosauridae, which are otherwise also present in the Grabfeld Formation (SMNS 59771 – this paper). The presence of a medial bulge (Fig. 3G) on the dorsal surface is consistent to that observed on the interclavicles of other metoposaurs observed in the SMNS collection. Although we have clearly demonstrated SMNS 59770 and SMNS 55899 as belonging to Metoposauridae rather than Captiosauroidea or Plagiosauridae, it is not possible to identify which species of metoposaur these fragments belong to due to their incompleteness. However, based on our current understanding of Metoposauridae palaeobiogeography, the only genus present in Europe is *Metoposaurus*: *M. diagnosticus* (Meyer 1842) (Germany), *M. krasiejowensis* (Sulej 2002) (Poland), and *M. algarvensis* (Brusatte et al. 2015) (Portugal), with the former species (*M. diagnosticus*) found in the overlaying Stuttgart Formation (Milner and Schoch 2004). We therefore tentatively refer these specimens based on the geographic location as *Metoposaurus* sp.

Plagiosauridae Abel, 1919
Plagiosaurinae Shishkin, 1986

***Gerrothorax* Nilsson, 1934**

Type species. *Gerrothorax pulcherrimus* (Fraas, 1913).

***Gerrothorax* sp.**
Fig. 3H

Dermal bone (SMNS 97109)

Referred material. SMNS 97109, an isolated dermal bone (Fig. 3H).

Locality. An unspecific outcrop near Kaubenheim, Middle Franconia, Bavaria.

Horizon. Derived from the 'Acrodus-Corbula Horizont' at the base of the 'Untere Bunte Estherienschichten', Upper Grabfeld Formation, Middle Keuper, lowermost Upper Triassic.

Description. A small fragmentary dermal bone, most closely resembling the osteoderms of *Gerrothorax*. It is embedded in a light brown dolomitic matrix (Fig. 3H). The element is damaged and measures approximately 24 mm in length and 11 mm in width. The sculpturing of the bone shows the characteristic pustular ornamentation, although most of the pustules are broken and only seen in transverse section. One margin is flat without pustules, but covered by faint ridges connecting to the pustules of the ornamented part. This resembles the marginal overlapping zone of osteoderms in *Gerrothorax*, although some transport might have worn off part of the surface in SMNS 97109.

Plagiosterninae Shishkin, 1986
***Plagiosternum* Fraas, 1896**

Type species. *Plagiosternum granulosum* (Fraas, 1889).

***Plagiosternum* sp.**
Fig. 3I–K

Plagiosternine interclavicle (SMNS 59771)

Referred material. SMNS 59771, a partial fragmentary interclavicle (Fig. 3I–K).

Locality. Field exposure approximately 15 m north of the road connecting the municipalities of Unternesselbach and Schauerheim, Middle Franconia, Bavaria (Fig. 1B).

Horizon. 'Obere Bunte Estherienschichten', Upper Grabfeld Formation, Middle Keuper, early Carnian, lowermost Upper Triassic.

Description. The specimen is a fragmentary interclavicle measuring approximately 47 mm in length and 41 mm in width, attributed to Plagiosterninae. The ventral surface (Fig. 3I) of the fragment features irregular small polygonal reticulated ornamentation with pustular structures present on nodular points. The ridges of the ornamentation are of medium height. The dorsal surface (Fig. 3J) shows a radiating pattern originating from the thickest part of the fragment. In lateral view (Fig. 3K), the height of the fragment increases towards the centre, from 5 mm to a maximum of 10 mm. The cross section is reminiscent of the medial region of the interclavicle based on *Plagiosternum* materials housed at the SMNS.

Remarks. The ornamentation of SMNS 59771 differs from that of other Plagiosauridae like *Plagiosuchus* or *Gerrothorax*, in which it primarily consists of pustules. The ornamentation further differs from the ones found in other Stereospondyli by having an overall weaker polygonal structure than Capitosauroidea, Trematosauridae and Metoposauridae. Additionally, vascular openings within the pits are not visible. Given the indistinguishable difference to comparative materials of *Plagiosternum granulosum* (SMNS 11825 and SMNS 11826; Fraas, 1889), we tentatively assign this fragmentary interclavicle to *Plagiosternum* sp.

Temnospondyli Zittel, 1888
Stereospondyli Fraas, 1889

Capitosauroidea indet.
Fig. 3L–N

Vertebra (SMNS 97123)

Referred material. SMNS 97123, a single gently deformed intercentrum (Fig. 3L–N).

Locality. An unspecified outcrop south of Westheim, Illesheim, Middle Franconia, Bavaria, (Fig. 1B).

Horizon. From an unspecified horizon within the Gipskeuper (Grabfeld Formation).

Description. The intercentrum (Fig. 3L, M) measures a width of 34 mm, height of 29 mm and anteroposterior length of 13 mm. The dorsal surface of the intercentrum is open and shows a very small "V" shaped *chorda incisure*. The pleurocentral facets are well established on the anterior side and are positioned laterally to the *chorda incisure*. Anterior and posterior surfaces of the intercentrum are very slightly concave. Paired parapophyses are found high in the lateral flank, inclined posteriorly but are broken. The flanks are highly concave as is the *tuber articularis* (Fig. 3N).

Remarks. Based on the size, morphology and position of the parapophysis and the absence of a haemal arch, we attribute the intercentrum to the posterior trunk region. It is most consistent with intercentra of early-branching capitosauroids (Schoch and Milner 2000). The intercentrum differs substantially from *Metoposaurus krasiejowensis* (Sulej 2007) by its rounder shape and higher placement of the parapophysis within the lateral flank. In conclusion, the intercentrum is more consistent with that of capitosauroids in its near circular transverse shape, the position and morphology of the parapophysis, and the more pronounced facets for the pleurocentra (Warren and Snell 1991; Schoch 1999).

Temnospondyli Zittel, 1888

Temnospondyli indet.
Fig. 3O, P

Caudal vertebra (SMNS 97125)

Referred material. SMNS 97125, a single intercentrum partially still embedded in matrix (Fig. 3O).

Locality. An unspecified outcrop in the vicinity of Stockheim (Brackenheim), northern Baden-Württemberg (Fig. 1B).

Horizon. 'Anatinenbank', 'Graue Estherienschichten', Middle Grabfeld Formation, Middle Keuper, early Carnian, lowermost Upper Triassic.

Description. The intercentrum is partially embedded in a light-grey, beige dolostone (Fig. 3O). The visible parts measure 11 mm in length and 4 mm in width. A very slight concavity is noticeable on the presumed ventral surface of the specimen.

Remarks. The small size of SMNS 97125 suggest that this intercentrum can tentatively be attributed to a vertebra of the caudal series. The concavity found on the presumed ventral surface point to this structure being the latera of the intercentrum, suggesting the dorsal part of the specimen to be covered by the matrix. Due to the size of the vertebra, it cannot be ruled out that it potentially belongs to a juvenile individual. In the absence of any diagnostic features, we refer this specimen to Temnospondyli indet.

Phalange (SMNS 97124)

Referred material. SMNS 97124, a single isolated phalange embedded in matrix (Fig. 3P).

Locality. An unspecified outcrop in the vicinity of Stockheim (Brackenheim), northern Baden-Württemberg (Fig. 1B).

Horizon. 'Anatinenbank', 'Graue Estherienschichten', Middle Grabfeld Formation, Middle Keuper, early Carnian, lowermost Upper Triassic.

Description. The specimen is an isolated phalange embedded in a light-grey, beige dolostone and is covered in a greenish mineral phase (Fig, 3P). It measures approximately 39 mm in length. The phalange has an hourglass-shape with either the dorsal or ventral side exposed. The width varies from 9 mm in the midshaft to 17 mm in the epiphyseal region. The epiphyseal regions show slight concavity on the exposed surface, whereas the bone is flat in the midshaft.

Remarks. The morphology of this phalange is indistinguishable from other stereospondyl phalanges. In comparison to the phalanges of *Nothosaurus* (Klein et al. 2022), which also occurs in the Grabfeld Formation, the hourglass-shape of the phalange is more pronounced than the constricted shaft in *Nothosaurus*. No phalanges are known from *Simosaurus* or *Psephosaurus*, the only other sauropterygians from the Grabfeld Formation of Germany (Rieppel 1994; Rieppel and Wild 1994). The present phalange resembles those of *Metoposaurus krasiejowensis* (Konietzko-Meier et al. 2020) more than those of *Nothosaurus*. We therefore attribute SMNS 97124 to Temnospondyli indet.

Discussion

Geological age correlation and constraints

To date, the Late Triassic timescale still lacks substantially detailed numerical ages for most of its stages (Lucas 2018). Given that the Late Triassic is a crucial period for the evolution and extinction of various tetrapod groups, accurately correlating geological and biotical events is vital for our understanding of these key events (Lucas 2018). In the Central European Basin (CEB), the Ladinian–Carnian boundary is indicated by the presence of the index fossil *Myophoria kefersteini okeni*, found in the 'Bleiglanzbank' in the middle of the Grabfeld Formation (Urlichs and Tichy 2000). The base of the Cordevolian (early Carnian) substage is found in the 'Estherienschichten' within the upper parts of the Grabfeld Formation and is indicated by the presence of the spinicaudatan *Laxitextella multireticulata* (Zhang et al. 2020). The 'Anatinenbank' (Fig. 1C) is extremely rich in *Laxitextella taxitexta* which is used biostratigraphically as an index for the upper Cordevolian substage (Kozur and Weems 2010; Gale et al. 2023). The Cordevolian age of the upper Grabfeld Formation is further supported by palynological evidence (Zhang et al. 2020). Another line of evidence is supported based on Milankovitch cyclicity of the fossil-bearing horizons of the Grabfeld Formation, which place the base of the Carnian at around ~237 Ma (Stollhofen et al. 2008). As the Carnian–Norian boundary has no clear Global Stratotype Section and Point (GSSP) (see Ogg 2012 as well as Lucas 2018 and references therein for in depth discussion), we are following recent results of Kohút et al. (2018) supporting the "short Norian" hypothesis. In order to contextualise the biostratigraphic and palaeobiogeographic significance of the new *Metoposaurus* materials from the Grabfeld Formation, it is necessary to evaluate the currently known global distributions of this family and the precise ages of their depositional environments.

Recent radiometric zircon dating of the Schilfsandstein (Zeh et al. 2021) indicate a delayed onset of ~3 Ma of the Carnian Pluvial Event (CPE; Dal Corso et al. 2020) in the Schilfsandstein compared to the NW Tethys region.

Following Zeh et al. (2021), the CPE begins in the Julian 2 (234 Ma) in the NW Tethys basin and in the Tuvalian 2 (231 Ma) in the Schilfsandstein of the CEB respectively and lasts until the Carnian–Norian boundary (221 Ma), indicating a probable 13 Ma duration for the CPE (Fig. 4; Zeh et al. 2021). Reliable zircon dating is an essential tool to help more precisely date occurrence points for temnospondyls in terrestrial environments. Biostratigraphically, precise dating of the temnospondyl-bearing localities of Poland are still highly debated. Szulc et al. (2015) summarized the ongoing discussions regarding the placement of the Krasiejów and Lisowice bone bearing horizon. Szulc et al. (2015) argued for a placement of the Krasiejów beds into the Norian, roughly equivalent to the lower parts of the Germanic Arnstadt Formation, while other authors suggest a Carnian age based on phytosaur occurrence (Dzik and Sulej 2007; Butler et al. 2014; Lucas 2020). In the Lisowice bone-bearing horizons, multiple lines of evidence (radiometric zircon dating (Kowal-Linka et al. 2019) as well as palynological evidence (Fijałkowska-Mader et al. 2015)) support the proposed middle–late Norian age of these bone-bearing beds. A similar co-occurrence of phytosaurs with *Metoposaurus algarvensis* in the AB2 unit of the Grés de Silves Formation of the Algarve of southern Portugal suggest a late Carnian–early Norian age of this stratum (Mateus et al. 2014; Brusatte et al. 2015).

In Morocco, the metoposaurids (*Almasaurus*, *Arganasaurus*, *Dutuitosaurus*) of the Argana basin are confined to the Irohalène (T5) member of the Timezgadiouine Formation (Jalil 1999; Buffa et al. 2019). Based on the co-occurrences of *Brachychirotherium*, *Atreipus*–*Grallator* and *Eubrontes* in the ichno-assemblages recovered from the Timezgadiouine Formation (Lagnaoui et al. 2012; Zouheir et al. 2018), the T5 member can be assigned to the early Carnian (Otischalkian) *Brachychirotherium* biozone (Klein and Lucas 2010). The base of the Otischalkian is indicated by the occurrence of parasuchids (Martz and Parker 2017) so therefore the *Brachychirotherium* biozone and hence the T5 member, are potentially of similar late Carnian age as the base of the Popo Agie Formation of Wyoming (Lovelace et al. 2023). Given these inconsistencies we assume an early–late Carnian age for the T5 member of the Timezgadiouine Formation.

The occurrence of osteoderms assigned to the phytosaur *Parasuchus* (Sharma and Kumar 2015) in the Tiki Formation of India indicates the placement of this strata into the late Carnian Otischalkian land vertebrate faunachron (LVF; Lucas 1998) in lack of radiometric dating alternatives. Furthermore, additional phytosaur material, as described and discussed by Datta et al. (2021), allow for a more detailed and global correlation of the Indian Tiki and Maleri formations. Datta et al. (2021) conclude that based on the presence of the widely used index taxa *Hyperodapedon* and *Parasuchus* in the Tiki Formation and lower Maleri Formation, these formations are considered to be late Carnian–early Norian in age. The use of these index taxa allows for additional correlation of these formations with other metoposaurid-bearing strata. Based on the occurrence of *Hyperodapedon* and *Parasuchus* the lower Maleri and Tiki formations can be correlated to the Isalo II of Madagascar (Fortuny et al. 2019), the Wolfville Formation of Nova Scotia (Sues et al. 2021), the Popo Agie Formation of Wyoming (Lovelace et al. 2023), the Camp Springs conglomerate of the Dockum Group of Texas, and the Timezgadiouine Formation of Morocco. Following Lovelace et al. (2023) and Martz and Parker (2017), the Camp Springs conglomerate contains the oldest known record of basal parasuchids, providing the base of the Otischalkian LVF (Lucas 1998). The lower Ischigualasto Formation of Argentina was successfully radioisotopically dated to 231 Ma (Martínez et al. 2012). The presence of *Hyperodapedon* in the lower Ischigualasto Formation and the radiometric dating of the purple-ochre transition of the Popo Agie Formation conclude similar ages for the other correlated strata, which places them presumably contemporaneous with the Germanic Schilfsandstein in the early Tuvalian 2 substage. The upper Maleri Formation is suggested to be Norian in age based on the disappearance of *Hyperodapedon*, *Parasuchus* and the metoposaurid *Panthasaurus* and the occurrences of more derived phytosaurs (Datta et al. 2021).

In North America, metoposaurids occur in the Late Triassic continental strata of the Chinle Group, Dockum Group and Chugwater Group of the western USA as well as the Chatham Group in the eastern part of the country (Hunt 1993). Lovelace et al. (2023) integrated the Popo Agie Formation of the Chugwater Group of Wyoming with the biostratigraphic correlations of the Chinle Group and Dockum Group (Martz and Parker 2017). On the basis of phytosaur biostratigraphy and laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS), the Popo Agie Formation can be placed in the Otischalkian. Additional radiometric dating suggests a maximum depositional age of the purple-ochre transition of the Popo Agie Formation of Wyoming of 230 ± 5 Ma (Lovelace et al. 2023). The following Adamanian begins at ~222 Ma with the occurrence of leptosuchomorph phytosaurs (Martz and Parker 2017; Lovelace et al. 2023).

Recent reports of indeterminate metoposaurid material from the Tashinga Formation of Zimbabwe (Barrett et al. 2020) also provided first radiometric ages for this formation, placing its depositional age around 209 Ma (late Norian). This presumable occurrence of a metoposaurid in the late Norian of southern Africa exceeds the last known record of the group in India by more than 10–15 Ma and demonstrates survivorship of Metoposauridae at high-latitudes in both Gondwana and Laurasia during the later stages of the Late Triassic.

The confirmed presence of *Metoposaurus* in the early Carnian Grabfeld Formation of southwestern Germany therefore has significant implications for the palaeogeographic distribution history (Fig. 4) of the group.

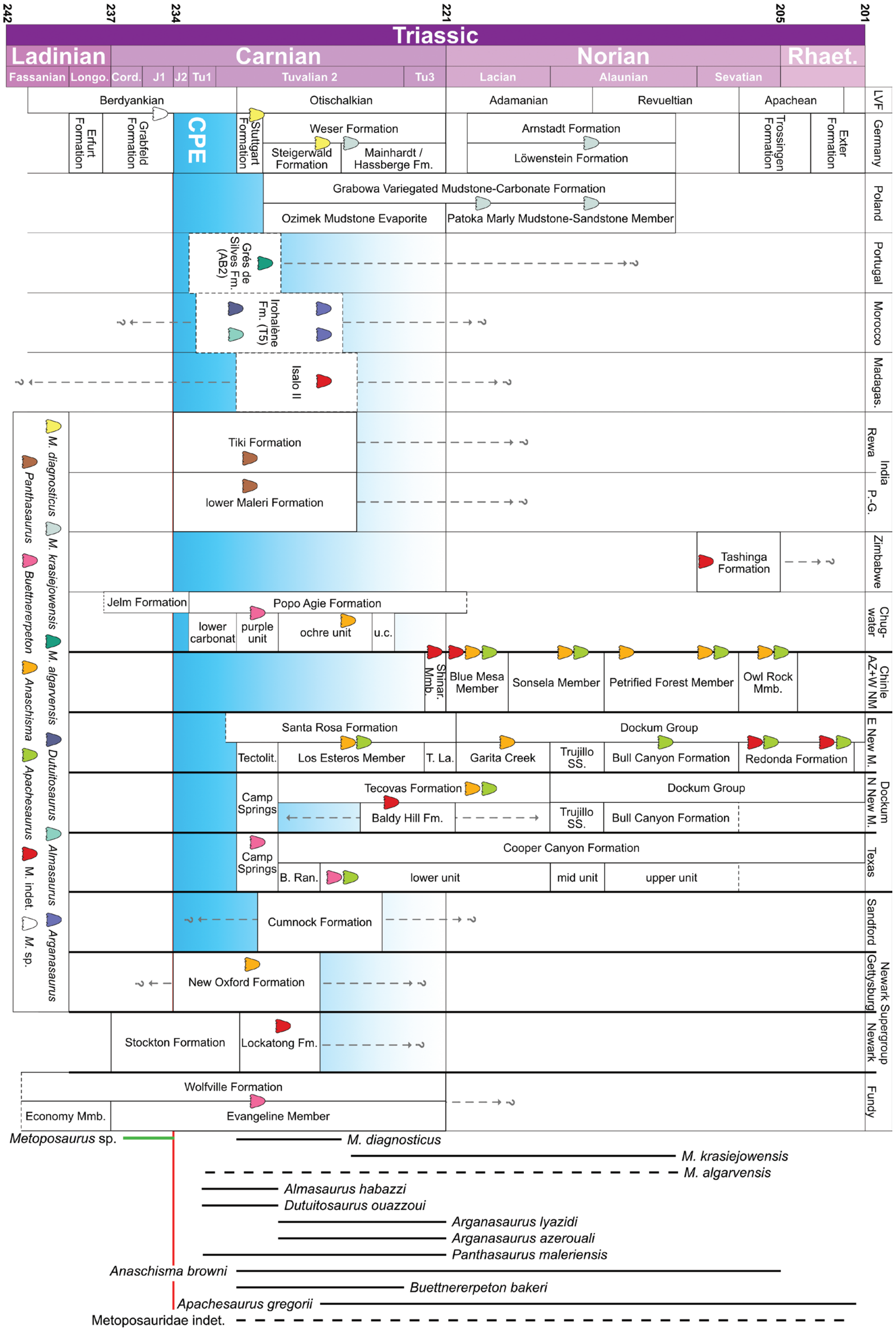

Figure 4. Stratigraphic correlation of the German Middle and Late Triassic *Metoposaurus*-bearing formations with other metoposaurid-bearing formations around the world. Correlations are based on (DSK 2005; Szulc et al. 2015; Martz and Parker 2017; Zouheir et al. 2018; Buffa et al. 2019; Datta et al. 2021; Sues et al. 2021; Zeh et al. 2021; Lovelace et al. 2023). Abbrevations: Rhaet. – Rhaetian, Longo. – Longobardian, Cord. – Cordevolian, J – Julian, Tu – Tuvalian, LVF – Land Vertebrate Faunachron, CPE – Carnian Pluvial Event, Madagas. – Madagascar, P.-G. – Pranhita-Godavari, AZ – Arizona, NM – New Mexico, TX – Texas, u.c. – upper carbonate, Shinar. – Shinarump, Mmb. – Member, Tectolit. – Tectolito, T. La. – Tres Lagunas, SS. – Sandstone, B. Ran. – Boren Ranch, Fm. – Formation.

The new *Metoposaurus* sp. materials represent the oldest known records of Metoposauridae, thereby pushing back their first occurrence in the fossil record of the CEB from the late Carnian to the early Carnian: an extension of approximately 5 million years.

Global palaeoenvironmental distribution of metoposaurids

The diversity of temnospondyls in the Grabfeld Formation is unexpectedly high given the hostile palaeoenviromental conditions. These new occurrence points therefore have novel implications for the current understanding of metoposaurid distribution and their ecosystem occupation throughout the Triassic. In Europe, three species of metoposaurids are formally recognised: (1) *Metoposaurus diagnosticus* (Meyer 1842), (2) *Metoposaurus krasiejowensis* (Sulej 2002) and (3) *Metoposaurus algarvensis* (Brusatte et al. 2015) (Table 2).

The oldest global occurrence of *Metoposaurus* sp. is from the early Carnian Grabfeld Formation (Gipskeuper) (Fig. 4; this paper), with this genus surviving throughout most of the Late Triassic within the CEB. Traditionally, *M. diagnosticus* has been recognised in the late Carnian fluvial and floodplain facies of the Stuttgart Formation (Schilfsandstein; Meyer 1842), and the lacustrine Lehrbergschichten (lower Steigerwald Formation; Seegis 1997). *M. krasiejowensis* occurs in sandstones of the Kieselsandstein or Blasensandstein (Hassberge Formation; Seegis 1997; Milner and Schoch 2004), as well as the Arnstadt Formation (Stubensandstein; Milner and Schoch 2004). The sandstones of the Kieselsandstein and Stubensandstein are clearly distinguishable by grainsize and cementation and derive from a terminal alluvial fan in the case of the Kieselsandstein, while the Stubensandstein originated from an extensive river system (Milner and Schoch 2004). Outside of the Germanic Basin, *M. krasiejowensis* is best known from the late Carnian–early Norian freshwater ephemeral marly clays of the Patoka Member of the Grabowa Formation of Poland (Bodzioch and Kowal-Linka 2012; Szulc et al. 2015; Jewuła et al. 2019). Additionally, *M. algarvensis* is recognised from the fluvial or deltaic mudstones of the AB2 beds of the Grés de Silves Formation in southern Portugal (Witzmann and Gassner 2008; Brusatte et al. 2015). Furthermore, the Raibl Schichten of the Heiligenkreuz yielded the *nomen dubium* "*M.*" *santaecrucis*, which exhibits strong morphological similarities to *M. diagnosticus* (Koken 1913). This occurrence is notable, because the specimen was found within a non-marine bed within an otherwise marine sequence (Hunt 1993).

In northern Africa the Irohalène Member (T5) of the Timezgadiouine Formation of Morocco have yielded a diverse assemblage of metoposaurids: (1) *Dutuitosaurus ouazzoui*, (2) *Almasaurus habazzi*, (3) *Arganasaurus lyazidi* and (4) *Arganasaurus azerouali* (Buffa et al. 2019). Within T5, *Dutuitosaurus ouazzoui* and *Almasaurus habazzi* occur in the lower parts of the member while *Arganasaurus lyazidi* and *Arganasaurus azerouali* co-occur in the upper parts of the formation (Jalil 1999). Hofmann et al. (2000) describe the T5 lithology as cyclically stacked sandstones with interbedded mudstones that are interpreted to have been deposited in a meandering river and floodplain system. However, Zouheir et al. (2018) describe the upper parts of the member as dry playa red beds indicating a drying-upwards trend during a transition from semiarid to arid climates.

In India the sole representative of Metoposauridae, *Panthasaurus maleriensis*, occurs in the fluvial sandstones and mudstones of the Tiki Formation and lower Maleri Formation (Chakravorti and Sengupta 2019).

Similarly, "*M. hoffmani*" of Isalo II in Madagascar, recently reappraised to Metoposauridae indet. by Fortuny et al. (2019), occurs in the fluvial sandstones and conglomerates as the only representative of the group in this region.

The metoposaurids of North America are similar across the different basins of the continent, only varying in their co-occurrence with each other. Following recent revisions of the group by Gee and Parker (2018); Gee et al. (2019); Gee and Jasinski (2021); Kufner and Gee (2021) and Gee and Kufner (2022) currently three species of metoposaurids are considered valid in North America: (1) *Anaschisma browni*, (2) *Buettnererpeton bakeri* and (3) *Apachesaurus gregorii* (Fig. 4). *Anaschisma browni* occurs in the ochre unit of the Popo Agie Formation (Kufner and Gee 2021) of Wyoming, the Bluewater Creek Formation (Heckert 1997), the Blue Mesa Member (Long and Murry 1995), Sonsela Member (Spielmann et al. 2007), Petrified Forest (Long and Murry 1995) and Owl Rock Member (Spielmann et al. 2007) of the Chinle Group in Arizona and eastern New Mexico as well as the Santa Rosa Formation (Heckert and Lucas 2015), Tecovas Formation (Hunt 1993) and Garita Creek Formation (Hunt 1993) of western New Mexico and Texas. Futhermore, *Anaschisma* is found in the New Oxford Member of the Gettysburg basin in Pennsylvania (Hunt 1993), not only extending the geographic range of the taxon tremendously but also establishing a stratigraphic range from the late Carnian–late Norian. *Apachesaurus gregorii* shows a similar stratigraphic range as *Anaschisma browni* occurring in the Bluewater Creek Formation (Heckert 2004), the Blue Mesa Member (Hunt 1993), Sonsela Member (Gee and Parker 2018), upper Petrified Forest Member (Gee and Parker 2018) and Owl Rock Member (Spielmann et al. 2007) of the Chinle Group in Arizona and eastern New Mexico as well as the Santa Rosa Formation (Hunt 1993), Tecovas Formation (Hunt 1993), Bull Canyon Formation (Hunt 1993) and Redonda Formation (Spielmann and Lucas 2012) of western New Mexico and Texas. In the Cooper Canyon Formation *Apachesaurus* was recovered from the lower unit (Hunt 1993). Currently, *Apachesaurus* has not been recovered from eastern North America, limiting its palaeobiogeographic range. *Buettnererpeton bakeri* has the shortest stratigraphic range of the North American metoposaurids as it only occurs in the purple unit of the Popo Agie Formation (Kufner and Gee 2021) and the contemporaneous Camp Springs conglomerate (Kufner and Gee 2021) of the Chinle Group. In eastern North America, *Buettnererpeton* is recovered from the Evangeline Member of the Wolfville Formation, Nova Scotia (Hunt 1993). *Buettnererpeton* shares a similar sized lateral geographic range with *Anaschisma*.

Additionally, indeterminate material of metoposaurids has been recovered from the early Carnian Lockatong Formation of the Newark basin (Baird 1986), the early Carnian Baldy Hill Formation of the Dockum Group (Heckert and Lucas 2015), the late Carnian Cumnock Formation of Sanford basin (Heckert et al. 2012), the early Norian Shinarumpa (Dubiel and Hasiotis 2011) and Bluewater Creek Formation of the Chinle Group (Heckert 1997), the late Norian Redonda Formation (Spielmann and Lucas 2012) as well as the late Norian Tashinga Formation of Zimbabwe (Barrett et al. 2020). The lithology of these strata is comprised of predominantly coarse-grained sandstones, siltstones and mudstones originating from a diverse fluvial system with interbedded floodplains and lacustrine environments (Colbert and Olsen 2001; Heckert 2004; Spielmann and Lucas 2012; Heckert and Lucas 2015; Barrett et al. 2020).

Palaeogeographic implications

Based on the correlations of metoposaurid-bearing strata (Fig. 4) and the herein reported new material from the Grabfeld Formation of southern Germany, a biogeographic distribution scenario can be assumed for the dispersal of metoposaurids across Pangea during the Late Triassic. As the material of the Grabfeld Formation is confidently placed in the early Carnian Cordevolian and Julian 1 substages, they precede the CPE and all other global occurrences of Metoposauridae at current knowledge. This suggests that the first appearance of Metoposauridae in the fossil record occurs in the CEB around the Ladinian–Carnian boundary and is further supported by the occurrence of *Callistomordax kugleri* (Schoch 2008), the sister taxon to Metoposauridae, from the Erfurt Formation of Germany. As a result of the still debated stratigraphic positions of other metoposaurid-bearing horizons of Europe the following scenario for metoposaurid distribution is proposed:

1. An initial radiation of Metoposauridae occurred with the onset of the CPE at the Julian–Tuvalian boundary in the Central European basin. From there, a first dispersal event via aquatic pathways potentially connected southern European Metoposauridae with northern Africa and eventually with India and Madagascar. The geographic distance between the Indian and other metoposaurid-bearing localities suggest emerging endemism of the group in this region due to diverging climatic conditions.
2. A second wave of radiation and dispersal started from Europe or northern Africa and connected these regions with North America. The early late Carnian occurrence of *Buettnererpton* and *Anaschisma* in different basins of the Newark Supergroup and Wyoming (Gee et al. 2019; Gee and Kufner 2022) suggest widespread aquatic pathways the group could have dispersed through.
3. The occurrence of indeterminate metoposaurid material from Zimbabwe (Barrett et al. 2020) suggest a potential third dispersal event occurring in the late Carnian–late Norian emerging from India and/or Madagascar. As Zimbabwe and these regions are found in similarly high palaeolatitudes this origin hypothesis is suggested.

The last known Metoposauridae in Europe vanish in the middle–late Norian, while the family flourishes in North America up to the Rhaetian and potentially up to the Triassic–Jurassic boundary (Fig. 4). Climatic studies of the Triassic (Sellwood and Valdes 2006; Dunne et al. 2021) have shown that the climate zones of Pangea were divided into different climatic belts and tetrapod diversity was linked to latitudinal biodiversity gradients. While Europe and North America were situated at similar palaeolatitudes in Late Triassic Pangea, potential climatic differences might not have been the trigger for the early disappearance of Metoposauridae from Europe as different groups of temnospondyls still persisted throughout the Rhaetian in this region. Palaeohistological studies of metoposaurids from Poland and India found a milder climate in these regions, compared to the climatic conditions present in Morocco (Teschner et al. 2023). Rather than climatic differences, Milner and Schoch (2004) have shown that in the case of European Metoposauridae, changes of source water and transported sediment might have an implicit impact on existing faunal components.

Physiological implications

The physiological tolerances of temnospondyls have long been debated (Laurin and Soler-Gijón 2010). While some families have been recovered from vastly different terrestrial aquatic palaeoenvironmental settings, others seem to be more restricted in their osmotic tolerance. For example, mastodonsaurids in the Middle and Late Triassic of Germany are found in freshwater fluvial, lacustrine and deltaic environments as well as in coastal or nearshore deposits (Schoch 2015). The same can be said for Plagiosauridae (*Plagiosaurus*, *Plagiosternum*, *Gerrothorax*), which are found in the same ecological range (Hagdorn and Reif 1988; Schoch and Seegis 2016) as the aforementioned capitosaurs. On the other hand, most authors concluded for Metoposauridae to have been inhabiting freshwater fluvial and lacustrine environments exclusively (Hunt 1993).

Marine affinities have been proposed for different groups of temnospondyls (DeFauw 1989). The association of temnospondyl remains with ammonoids and bivalves from the marine and nearshore deposits of the Early Triassic of Svalbard and Greenland (Scheyer et al. 2014; Kear et al. 2015) demonstrate the adaptability of the group for a wide range of potential habitats. Dutuit (1983) suggested marine migration for Metoposauridae based on the co-occurrence with phytosaurs in the Moroccan Argana Basin. The presented arguments were rejected by subsequent studies (Buffetaut and Martin 1984; Hunt 1993) showing the availability of inland connections between metoposaurid-bearing localities and the clear absence of the group from marine strata. Other studies (Laurin and Soler-Gijón 2001, 2010) report clear evidence of Palaeozoic stegocephalians from marine or saline environments, or argue specifically for the case of euryhalinity in Metoposauride (DeFauw 1989; Milner 1990) based on morphological features the group exhibits.

Until now, there has not been solid evidence for marine affinities of Metoposauridae, while Early Triassic Trematosauridae (*Aphaneramma*; Lindemann 1991; Fortuny et al. 2017b) and Plagiosauridae like *Gerrothorax* or *Plagiosternum* (Hagdorn and Reif 1988; Schoch 2021) have clearly been recovered from marine strata. While there is still no direct evidence for marine affinities of Metoposauridae, the occurrence of *Nothosaurus* and several euryhaline invertebrates (Linck 1972; Rieppel and Wild 1994) in the 'Anatinenbank' of the Grabfeld Formation indicates clear marine influence in this layer. The fragmentary nature of the recovered specimens might indicate an allochthonous origin. Based on the preservation of the bones (clean fractures, minimal abrasion), the temnospondyl remains have likely not been transported over a long distance and might even potentially be autochthonous. Comparisons with the autochthonous *Nothosaurus* material (Rieppel and Wild 1994) from the same layer demonstrate a ubiquitous condition of preservation with the temnospondyl remains. Had these materials been transported over a long distance or been reworked from foreign strata, one would expect the bones to be more severely abraded and rounded. Regardless, the occurrence of temnospondyls in the marine influenced 'Anatinenbank' opens discussion on the possibility for the osmotic tolerances of the group. The palaeoenvironment of the 'Anatinenbank', and Grabfeld Formation as a whole, is clearly different from the 'typical' palaeoenvironmental setting of other metoposaurid-bearing horizons. Further exceptions to the usual interpretation of freshwater fluvial and lacustrine habitats are known from elsewhere in Germany and Morocco: The Lehrbergschichten (Weser Formation) and Kieselsandstein (Hassberge Formation) represent playa lakes (Seegis 1997; Milner and Schoch 2004) or a terminal alluvial fan interfingering into a playa (Kern and Aigner 1997) respectively. Contrastingly, the upper parts of the T5 member of the Timezgadiouine Formation are debated to either represent a meandering river and floodplain environment (Hofmann et al. 2000) or a dry playa red bed (Zouheir et al. 2018). Seegis (1997) specifically interpreted the salinity content of the different Lehrberg lakes to vary from freshwater to euhaline (0–40‰ salinity), which falls in line with the interpretations of the salinity content for the 'Anatinenbank', which is referred to be «equivalent to regular sea water» (Linck 1972). Due to the cyclicity of the Grabfeld Formation, the metoposaurid material described herein were recovered from different phases within the cyclothems. The last stage, the palaeosol phase, is the least fossiliferous and interpreted as to have never been marine (Nitsch et al. 2005). The fossil occurrences of this phase are restricted to conchostracs and occasional fish remains. Additionally, this phase has yielded *Metoposaurus* sp. (SMNS 59770) and is interpreted to have the most restricted freshwater inflows and most terrestrial influence (Nitsch et al. 2005). Therefore, the presence of Metoposauridae in the early and late stages of the Grabfeld Formation cyclothems argue for a wider ecological niche of the group than previously recognised (*sensu* Hunt 1993). The occurrence of the plagiosaurids *Gerrothorax* and *Plagiosternum* in these brackish claystone-dolostones fits in line with their presumed tolerance for changing or generally higher salinity (Sanchez and Schoch 2013) as well as their occurrence in other marine-influenced depositional environments (Tverdokhlebov et al. 2003; Kear et al. 2015; Schoch 2021). Recent comparative studies on the histology of *Metoposaurus* and *Cyclotosaurus* from Poland have revealed potential differences in the mode of life and ecological niche partitioning between those taxa (Kalita et al. 2022; Teschner et al. 2023). This observation is congruent with the predominant occurrence of *Metoposaurus* in local lacustrine environments of the Stuttgart Formation, while *Cyclotosaurus* dominates the respective channel facies (Schoch and Moreno 2024). Furthermore, the scarcity of the described metoposaurid materials, as well as the small size of the *Metoposaurus* skull (SMNS 56633; Seegis 1997) combined with their higher frequency in the Lehrbergschichten, might support the indication of intraspecific variability due to environmental factors in *Metoposaurus* (Sulej 2007).

Conclusion

In the early Carnian Grabfeld Formation of southern Germany, temnospondyls have hitherto been considered to be extremely rare, in low diversity and based on largely undiagnostic material. In this study, we have presented evidence of geographically and stratigraphically widespread occurrence of this group in the upper parts of the Grabfeld Formation. Although fragmentary in nature, the presence of diagnostic temnospondyl remains across the cyclothems is indicative of their presence in this harsh environment. The 'Estherienschichten' formed under lacustrine conditions, with the dolomitic Corbula and Acrodus units at their base representing a limnic or lagoonal facies with siliciclastic content that connects to the marginal Benk Formation of northeastern Bavaria (Etzold and Schweizer 2005), where the historically oldest temnospondyl find, *Capitosaurus arenaceus*, was recovered (Münster 1836). This cyclotosaurid represents the only temnospondyl from this siliciclastic channel facies. The capitosauroid intercentrum reported here (SMNS 97123) adds to this picture and documents the presence of this group also in the basin facies. Surprisingly, the temnospondyl diversity was still higher in the Grabfeld Formation than in the marginal facies, as shown by the distinctive dermal bones here referred to *Plagiosternum* and *Gerrothorax*. Whereas *Plagiosternum* is known from shallow marine, coastal and lagoonal environments of the late Ladinian Meissner and Erfurt Formations (Schoch 2015), *Gerrothorax* has been characterized as a tolerant pioneer taxon that coped with a wide range of environmental conditions (Schoch and Witzmann 2011; Sanchez and Schoch 2013). Thus, these observations are consistent with the occurrence of metoposaurids and suggest the persistence of salinity-tolerant temnospondyl taxa in the Grabfeld Formation. Furthermore, the Gipskeuper *Metoposaurus* marks the earliest record of the Metoposauridae. The identification of *Gerrothorax* in the Grabfeld Formation bridges a gap between the occurrences in the Lower Keuper and overlaying Schilfsandstein in their long stratigraphic range from the Ladinian to the Rhaetian (Schoch 2021; Schoch and Moreno 2024). Likewise, the recognition of *Plagiosternum* provides new evidence of their occurrence outside of the Ladinian and thereby extending their stratigraphic range into the Late Triassic.

Although the marine influence of the 'Anatinenbank' and other dolomitic beds in the upper Grabfeld Formation is still debated (Linck 1972; Nitsch 1996), the presence of sauropterygians like *Nothosaurus* (Rieppel and Wild 1994) is clearly indicative of euryhaline and at least temporal marine conditions in the basin. While invertebrates of the formation are well studied (Linck 1972), the knowledge of vertebrates is still lacking. The supposed rarity of temnospondyls might be consequential of insufficient sampling efforts in the Grabfeld Formation, or represents general inhospitable conditions for large groups of vertebrates. Although only fragmentary, the occurrence of temnospondyls in this environment and stratigraphically wide range within the upper Grabfeld Formation demonstrates them to be a regular faunal component of this ecosystem. Palaeoenvironmental comparisons with the upper T5 member of the Timezgadiouine Formation of Morocco potentially solidify a euryhaline physiology of Metoposauridae, and while marine affinities are not directly concluded from the investigations herein, it is evident, that theories of euryhalinity in Metoposauridae and temnospondyls in general should not be dismissed.

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.

Author contributions

Raphael Moreno: Conceptualization (lead); Methodology (equal); Investigation (lead); Writing – original draft preparation (lead); Writing – review and editing (lead); Visualization (lead). Sanjukta Chakravorti: Methodology (equal); Investigation (supporting); Writing – original draft preparation (supporting); Writing – review and editing (supporting). Samuel L. A. Cooper: Methodology (equal); Investigation (supporting); Writing – original draft preparation (supporting); Writing – review and editing (supporting). Rainer Schoch: Resources (lead); Writing – review and editing (supporting); Supervision (lead).

Acknowledgments

We thank Isabell Rosin for preparation of the silicone mould used on SMNS 55899 and preparation of SMNS 97109, as well as G. Buck, A. Jansen and O. Linck for collection and donation of the specimens to the SMNS. RM was supported through a grade scholarship from the State Graduate Sponsorship Program by the Ministry of Science and Art of Baden-Württemberg. We thank the editor Florian Witzmann as well as Dorota Konietzko-Meier and an anonymous reviewer for their suggestions and comments which helped improving this manuscript.

References

Abel O (1919) Die Stämme der Wirbeltiere. Walter de Gruyter and Company, Berlin und Leipzig, 914 pp. https://doi.org/10.5962/bhl.title.2114

Aigner T, Bachmann GH (1992) Sequence-stratigraphic framework of the German Triassic. Sedimentary Geology 80: 115–135. https://doi.org/10.1016/0037-0738(92)90035-P

Antczak M, Bodzioch A (2018) Ornamentation of dermal bones of *Metoposaurus krasiejowensis* and its ecological implications. PeerJ 6: e5267. https://doi.org/10.7717/peerj.5267

Baird D (1986) Some Upper Triassic reptiles, footprints, and an amphibian from New Jersey. The Mosasaur 3: 125–153.

Barrett PM, Sciscio L, Viglietti PA, Broderick TJ, Suarez CA, Sharman GR, Jones AS, Munyikwa D, Edwards SF, Chapelle KEJ, Dollman KN, Zondo M, Choiniere JN (2020) The age of the Tashinga Formation (Karoo Supergroup) in the Mid-Zambezi Basin, Zimbabwe and the first phytosaur from mainland sub-Saharan Africa. Gondwana Research 81: 445–460. https://doi.org/10.1016/j.gr.2019.12.008

Bodzioch A, Kowal-Linka M (2012) Unraveling the origin of the Late Triassic multitaxic bone accumulation at Krasiejów (S Poland) by diagenetic analysis. Palaeogeography, Palaeoclimatology, Palaeoecology 346–347: 25–36. https://doi.org/10.1016/j.palaeo.2012.05.015

Broili F (1915) Über *Capitosaurus arenaceus* Münster. Centralblatt für Geologie und Paläontologie, 569–575.

Brusatte SL, Butler RJ, Mateus O, Steyer J-S (2015) A new species of *Metoposaurus* from the Late Triassic of Portugal and comments on the systematics and biogeography of metoposaurid temnospondyls. Journal of Vertebrate Paleontology 35: e912988. https://doi.org/10.1080/02724634.2014.912988

Buffa V, Jalil N, Steyer J-S (2019) Redescription of *Arganasaurus* (*Metoposaurus*) *azerouali* (Dutuit) comb. nov. from the Upper Triassic of the Argana Basin (Morocco), and the first phylogenetic analysis of the Metoposauridae (Amphibia, Temnospondyli). Papers in Palaeontology 5: 699–717. https://doi.org/10.1002/spp2.1259

Buffetaut E, Martin M (1984) Continental vertebrate distribution, faunal zonation and climate in the Late Triassic. In: Reif W-E, Westphal F (Eds) Third Symposium on Mesozoic Terrestrial Ecosystems, Short Papers. ATTEMPTO, Tübingen, 25–29.

Butler RJ, Rauhut OWM, Stocker MR, Bronowicz R (2014) Redescription of the phytosaurs *Paleorhinus* (‘*Francosuchus*’) *angustifrons* and *Ebrachosuchus neukami* from Germany, with implications for Late Triassic biochronology: Redescription of two phytosaurs from Germany. Zoological Journal of the Linnean Society 170: 155–208. https://doi.org/10.1111/zoj.12094

Chakravorti S, Sengupta DP (2019) Taxonomy, morphometry and morphospace of cranial bones of *Panthasaurus* gen. nov. *maleriensis* from the Late Triassic of India. Journal of Iberian Geology 45: 317–340. https://doi.org/10.1007/s41513-018-0083-1

Colbert EH, Olsen PE (2001) A new and unusual aquatic reptile from the Lockatong Formation of New Jersey (Late Triassic, Newark Supergroup). American Museum Novitates 3334: 1–24. https://doi.org/10.1206/0003-0082(2001)334%3C0001:ANAUAR%3E2.0.CO;2

Dal Corso J, Bernardi M, Sun Y, Song H, Seyfullah LJ, Preto N, Gianolla P, Ruffell A, Kustatscher E, Roghi G, Merico A, Hohn S, Schmidt AR, Marzoli A, Newton RJ, Wignall PB, Benton MJ (2020) Extinction and dawn of the modern world in the Carnian (Late Triassic). Science Advances 6: eaba0099. https://doi.org/10.1126/sciadv.aba0099

Datta D, Ray S, Bandyopadhyay S (2021) Cranial morphology of a new phytosaur (Diapsida, Archosauria) from the Upper Triassic of India: implications for phytosaur phylogeny and biostratigraphy. Papers in Palaeontology 7: 675–708. https://doi.org/10.1002/spp2.1292

DeFauw SL (1989) Temnospondyl amphibians: A new perspective on the last phases in the evolution of the Labyrinthodontia. Michigan Academician 21: 7–32.

DSK (Deutsche Stratigraphische Kommission) (2005) 253 Stratigraphie von Deutschland IV: Keuper. Schweizerbart Science Publishers, Stuttgart, Germany, 296 pp. http://www.schweizerbart.de//publications/detail/isbn/9783510613762/CFS_Courier_Forschungsinstitut_Senckenbe.

Dubiel RF, Hasiotis ST (2011) Deposystems, paleosols, and climatic variability in a continental system: The Upper Triassic Chinle Formation, Colorado Plateau, U.S.A. In: From river to rock record: The preservation of fluvial sediments and their subsequent interpretation. SEPM Society for Sedimentary Geology, 393–421. https://doi.org/10.2110/sepmsp.097.393

Dunne EM, Farnsworth A, Greene SE, Lunt DJ, Butler RJ (2021) Climatic drivers of latitudinal variation in Late Triassic tetrapod diversity. . Palaeontology 64: 101–117. https://doi.org/10.1111/pala.12514

Dutuit J-M (1983) Homogénéité et répartition des métoposauridés et phytosauridés sont-elles en relation avec les espaces marins du Trias supérieur? Comptes Rendus de l’Academie des Sciences. Séries III, Sciences de la Vie 296: 833–836.

Dzik J, Sulej T (2007) A review of the early late Triassic Krasiejów biota from Silesia. Palaeontologia Polonica 64: 1–27.

Emmert U, Bader K, Frank H, Heller F, Jerz H, Prashnowsky AA, Salger M, Schnitzer WA (1974) Geologische Karte von Bayern 1:25000 Erläuterungen zum Blatt Nr. 6429 Neustadt a. d. Aisch. Bayrisches Geologisches Landesamt, München, 143 pp.

Etzold A, Schweizer V (2005) Der Keuper in Baden-Württemberg. In: DSK (Deutsche Stratigraphische Kommission) (Ed.) Stratigraphie von Deutschland IV: Keuper. Schweizerbart Science Publishers, Stuttgart, 214–258.

Fijałkowska-Mader A, Heunisch C, Szulc J (2015) Palynostratigraphy and palynofacies of the Upper Silesian Keuper (southern Poland). Annales Societatis Geologorum Poloniae 85: 637–661. https://doi.org/10.14241/asgp.2015.025

Fortuny J, Marcé-Nogué J, Konietzko-Meier D (2017a) Feeding biomechanics of Late Triassic metoposaurids (Amphibia: Temnospondyli): a 3D finite element analysis approach. Journal of Anatomy 230: 752–765. https://doi.org/10.1111/joa.12605

Fortuny J, Arbez T, Mujal E, Steyer J-S (2019) Reappraisal of ‘*Metoposaurus hoffmani*’ Dutuit, 1978, and description of new temnospondyl specimens from the Middle–Late Triassic of Madagascar (Morondava Basin). Journal of Vertebrate Paleontology 39: e1576701. https://doi.org/10.1080/02724634.2019.1576701

Fortuny J, Gastou S, Escuillié F, Ranivoharimanana L, Steyer J-S (2017b) A new extreme longirostrine temnospondyl from the Triassic of Madagascar: phylogenetic and palaeobiogeographical implications for trematosaurids. Journal of Systematic Palaeontology 16: 675–688. https://doi.org/10.1080/14772019.2017.1335805

Fraas E (1889) Die Labyrinthodonten der schwäbischen Trias. Palaeontographica (1846–1933): 1–158.

Fraas E (1896) Die Schwäbischen Trias-Saurier nach dem Material der Kgl. Naturalien-Sammlung in Stuttgart zusammengestellt. Schweizbart, Stuttgart, 18 pp.

Fraas E (1913) Neue Labyrinthodonten aus der schwäbischen Trias. Palaeontographica (1846–1933) 60: 275–294.

Freudenberger W (2005) Der Keuper in Franken und Oberpfalz (Bayern). In: DSK (Deutsche Stratigraphische Kommission) (Ed.) Stratigraphie von Deutschland IV: Keuper. Schweizerbart Science Publishers, Stuttgart, 203–213.

Gale A, Keupp H, Schweigert G, Sell J (2023) A new phosphatic cirripede from the Carnian (Upper Triassic) of Bavaria, Germany. Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen 309: 19–29. https://doi.org/10.1127/njgpa/2023/1145

Gee BM, Parker WG (2018) A large-bodied metoposaurid from the Revueltian (late Norian) of Petrified Forest National Park (Arizona, USA). Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen 287: 61–73. https://doi.org/10.1127/njgpa/2018/0706

Gee BM, Jasinski SE (2021) Description of the metoposaurid *Anaschisma browni* from the New Oxford Formation of Pennsylvania. Journal of Paleontology 95: 1061–1078. https://doi.org/10.1017/jpa.2021.30

Gee BM, Kufner AM (2022) Revision of the Late Triassic metoposaurid “*Metoposaurus*” *bakeri* (Amphibia: Temnospondyli) from Texas, USA and a phylogenetic analysis of the Metoposauridae. PeerJ 10: e14065. https://doi.org/10.7717/peerj.14065

Gee BM, Parker WG, Marsh AD (2019) Redescription of *Anaschisma* (Temnospondyli: Metoposauridae) from the Late Triassic of Wyoming and the phylogeny of the Metoposauridae. Journal of Systematic Palaeontology 18: 233–258. https://doi.org/10.1080/14772019.2019.1602855

Gwinner MP (1980) Eine einheitliche Gliederung des Keupers (Germanische Trias) in Süddeutschland. Neues Jahrbuch für Geologie und Paläontologie - Monatshefte 4: 229–234. https://doi.org/10.1127/njgpm/1980/1980/229

Hagdorn H, Reif W-E (1988) “Die Knochenbreccie von Crailsheim” und weitere Mitteltrias-Bonebeds in Nordost-Württemberg - Alte und neue Deutungen. In: Hagdorn H (Ed.) Neue Forschungen zur Erdgeschichte von Crailsheim: zur Erinnerung an Hofrat Richard Blezinger. Goldschneck-Verlag, 116–143.

Heckert AB (1997) The tetrapod fauna of the Upper Triassic lower Chinle Group (Adamanian: latest Carnian) of the Zuni Mountains, west-central New Mexico. In: Lucas SG, Estep JW, Williams TE, Morgan GS (Eds) New Mexico’s Fossil Record 1. New Mexico Museum of Natural History and Science Bulletin., 29–40.

Heckert AB (2004) Late Triassic microvertebrates from the lower Chinle Group (Otischalkian-Adamanian: Carnian), southwestern U.S.A. In: Heckert AB (Ed.) Late Triassic Microvertebrates. New Mexico Museum of Natural History and Science Bulletin., 1–170.

Heckert AB, Lucas SG (2015) Triassic vertebrate paleontology in New Mexico. In: Lucas SG, Sullivan RM (Eds) Fossil Vertebrates in New Mexico. New Mexico Museum of Natural History and Science Bulletin, 77–96. https://core.ac.uk/reader/345083970 [December 11, 2023]

Heckert AB, Mitchell JS, Schneider VP, Olsen PE (2012) Diverse new microvertebrate assemblage from the Upper Triassic Cumnock Formation, Sanford Subbasin, North Carolina, USA. Journal of Paleontology 86: 368–390. https://doi.org/10.1666/11-098.1

Hofmann A, Tourani A, Gaupp R (2000) Cyclicity of Triassic to Lower Jurassic continental red beds of the Argana Valley, Morocco: implications for palaeoclimate and basin evolution. Palaeogeography, Palaeoclimatology, Palaeoecology 161: 229–266. https://doi.org/10.1016/S0031-0182(00)00125-5

Hunt AP (1993) Revision of the Metoposauridae (Amphibia: Temnospondyli) and description of a new genus from western North America. Museum of Northern Arizona Bulletin 59: 67–97.

Jalil N-E (1999) Continental Permian and Triassic vertebrate localities from Algeria and Morocco and their stratigraphical correlations. Journal of African Earth Sciences 29: 219–226. https://doi.org/10.1016/S0899-5362(99)00091-3

Jewuła K, Matysik M, Paszkowski M, Szulc J (2019) The late Triassic development of playa, gilgai floodplain, and fluvial environments from Upper Silesia, southern Poland. Sedimentary Geology 379: 25–45. https://doi.org/10.1016/j.sedgeo.2018.11.005

Kalita S, Teschner EM, Sander PM, Konietzko-Meier D (2022) To be or not to be heavier: The role of dermal bones in the buoyancy of the Late Triassic temnospondyl amphibian *Metoposaurus krasiejowensis*. Journal of Anatomy 241: 1459–1476. https://doi.org/10.1111/joa.13755

Kear BP, Poropat SF, Bazzi M (2015) Late Triassic capitosaurian remains from Svalbard and the palaeobiogeographical context of Scandinavian Arctic temnospondyls. In: Kear BP, Lindgren J, Hurum JH, Milàn J, Vajda V (Eds) Mesozoic Biotas of Scandinavia and its Arctic Territories. Geological Society, London, Special Publications. The Geological Society of London, 113–126. https://www.lyellcollection.org/doi/10.1144/SP434.11 [November 8, 2023]

Kern A, Aigner T (1997) Faziesmodell für den Kieselsandstein (Keuper, Obere Trias) von SW-Deutschland: eine terminale alluviale Ebene. Neues Jahrbuch für Geologie und Paläontologie - Monatshefte 1997: 267–285. https://doi.org/10.1127/njgpm/1997/1997/267

Klein H, Lucas SG (2010) Tetrapod footprints - their use in biostratigraphy and biochronology of the Triassic. Geological Society, London, Special Publications 334: 419–446. https://doi.org/10.1144/SP334.14

Klein N, Eggmaier S, Hagdorn H (2022) The redescription of the holotype of *Nothosaurus mirabilis* (Diapsida, Eosauropterygia)—a historical skeleton from the Muschelkalk (Middle Triassic, Anisian) near Bayreuth (southern Germany). PeerJ 10: e13818. https://doi.org/10.7717/peerj.13818

Kohút M, Hofmann M, Havrila M, Linnemann U, Havrila J (2018) Tracking an upper limit of the “Carnian Crisis” and/or Carnian stage in the Western Carpathians (Slovakia). International Journal of Earth Sciences 107: 321–335. https://doi.org/10.1007/s00531-017-1491-8

Koken E (1913) Beitrage zur Kenntnis der Schichten von Heiligenkreuz (Abteital, Sudtirol). Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt 16: 1–43.

Konietzko-Meier D, Teschner EM, Bodzioch A, Sander PM (2020) Pentadactyl manus of the *Metoposaurus krasiejowensis* from the Late Triassic of Poland, the first record of pentadactyly among Temnospondyli. Journal of Anatomy 237: 1151–1161. https://doi.org/10.1111/joa.13276

Kowal-Linka M, Krzemińska E, Czupyt Z (2019) The youngest detrital zircons from the Upper Triassic Lipie Śląskie (Lisowice) continental deposits (Poland): Implications for the maximum depositional age of the Lisowice bone-bearing horizon. Palaeogeography, Palaeoclimatology, Palaeoecology 514: 487–501. https://doi.org/10.1016/j.palaeo.2018.11.012

Kozur HW, Weems RE (2010) The biostratigraphic importance of conchostracans in the continental Triassic of the northern hemisphere. In: Lucas SG (Ed.) The Triassic Timescale. Geological Society, London, Special Publications. The Geological Society of London, 315–417. https://www.lyellcollection.org/doi/10.1144/SP334.13 [April 17, 2023]

Kufner AM, Gee BM (2021) Reevaluation of the holotypes of *Koskinonodon princeps* Branson and Mehl, 1929, and *Borborophagus wyomingensis* Branson and Mehl, 1929 (Temnospondyli, Metoposauridae). Journal of Vertebrate Paleontology 41: e1922067. https://doi.org/10.1080/02724634.2021.1922067

Lagnaoui A, Klein H, Voigt S, Hminna A, Saber H, Schneider JW, Werneburg R (2012) Late Triassic Tetrapod-Dominated Ichnoassemblages from the Argana Basin (Western High Atlas, Morocco). Ichnos 19: 238–253. https://doi.org/10.1080/10420940.2012.718014

Laurin M, Soler-Gijón R (2001) The oldest stegocephalian from the Iberian Peninsula: evidence that temnospondyls were euryhaline. Comptes Rendus de l’Académie des Sciences - Series III - Sciences de la Vie 324: 495–501. https://doi.org/10.1016/S0764-4469(01)01318-X

Laurin M, Soler-Gijón R (2010) Osmotic tolerance and habitat of early stegocephalians: indirect evidence from parsimony, taphonomy, palaeobiogeography, physiology and morphology. In: Vecoli M, Clément G, Meyer-Berthaud B (Eds) The terrestrialization process: modelling complex interactions at the biosphere–geosphere interface. Geological Society, London, Special Publications. The

Geological Society of London, 151–179. https://doi.org/10.1144/SP339.13 [May 4, 2022]

Linck O (1972) Die marine Fauna des süddeutschen Oberen Gipskeupers, insbesondere der sogenannten Anatinenbank (Trias, Kam, Mittl. Keuper, km1) und deren Bedeutung — Evertebraten I. Jahreshefte des Geologischen Landesamtes Baden-Württemberg 14: 145–253.

Lindemann FJ (1991) Temnospondyls and the Lower Triassic palaeogeography of Spitsbergen. In: Fifth Symposium on Mesozoic Terrestrial Ecosystems and Biota, extended abstracts. Contr. Palaeont. Mus. Univ. Oslo, 72.

Long RA, Murry PA (1995) Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. New Mexico Museum of Natural History and Science Bulletin 4: 254.

Lovelace DM, Fitch AJ, Schwartz D, Schmitz M (2023) Concurrence of Late Triassic lithostratigraphic, radioisotopic, and biostratigraphic data support a Carnian age for the Popo Agie Formation (Chugwater Group), Wyoming, USA. Geological Society of America Bulletin: 20. https://doi.org/10.1130/B36807.1

Lucas SG (1998) Global Triassic tetrapod biostratigraphy and biochronology. Palaeogeography, Palaeoclimatology, Palaeoecology 143: 347–384. https://doi.org/10.1016/S0031-0182(98)00117-5

Lucas SG (2018) The Late Triassic Timescale. In: Tanner LH (Ed.) The Late Triassic World: Earth in a Time of Transition. Topics in Geobiology. Springer International Publishing, 26 pp.

Lucas SG (2020) Biochronology of Late Triassic Metoposauridae (Amphibia, Temnospondyli) and the Carnian pluvial episode. Annales Societatis Geologorum Poloniae 90: 409–418. https://doi.org/10.14241/asgp.2020.29

Lydekker R (1890) Part IV Catalogue of the fossil Reptilia and Amphibia in the British Museum of Natural History. British Museum of Natural History, London, 295 pp.

Martínez RN, Apaldetti C, Alcober OA, Colombi CE, Sereno PC, Fernandez E, Malnis PS, Correa GA, Abelin D (2012) Vertebrate succession in the Ischigualasto Formation. Journal of Vertebrate Paleontology 32: 10–30. https://doi.org/10.1080/02724634.2013.818546

Martz JW, Parker WG (2017) Revised formulation of the Late Triassic land vertebrate "faunachrons" of Western North America. In: Ziegler KE, Parker WG (Eds) Terrestrial Depositional Systems. Elsevier, 39–125. https://doi.org/10.1016/B978-0-12-803243-5.00002-9

Mateus O, Butler RJ, Brusatte SL, Whiteside JH, Steyer J-S (2014) The first phytosaur (Diapsida, Archosauriformes) from the Late Triassic of the Iberian Peninsula. Journal of Vertebrate Paleontology 34: 970–975. https://doi.org/10.1080/02724634.2014.840310

Meyer H von (1842) Letter on Mesozoic amphibians and reptiles. Neues Jahrbuch für Mineralogie, Geographie, Geologie, Paläontologie, 301–304.

Milner A (1990) The radiations of temnospondyl amphibians. In: Taylor PD, Larwood GP (Eds) Major Evolutionary Radiations. Systematics Association Special Volume. Clarendon Press, Oxford, 321–350. https://doi.org/10.1093/oso/9780198577188.003.0015

Milner AR, Schoch RR (2004) The latest metoposaurid amphibians from Europe. Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen 232: 231–252. https://doi.org/10.1127/njgpa/232/2004/231

Mujal E, Schoch RR (2020) Middle Triassic (Ladinian) amphibian tracks from the Lower Keuper succession of southern Germany: Implications for temnospondyl locomotion and track preservation. Palaeogeography, Palaeoclimatology, Palaeoecology 543: 109625. https://doi.org/10.1016/j.palaeo.2020.109625

Münster G (1836) Communications addressed to Professor Bronn. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, 580–581.

Nilsson T (1934) Vorläufige Mitteilung über einen Stegocephalenfund aus dem Rhät Schonens. Geologiska Föreningeni Stockholm Förhandlingar 56: 428–442. https://doi.org/10.1080/11035893409444893

Nitsch E (1996) Fazies, Diagenese und Stratigraphie der Grabfeld-Gruppe Süddeutschlands (Keuper, Trias). Universität Köln.

Nitsch E, Beutler G, Hauschke N, Etzold A, Laaß M (2005) Feinstratigraphische Korrelation der Grabfeld-Formation (Keuper, Trias) zwischen Hochrhein und Ostsee. Hallesches Jahrbuch für Geowissenschaften Beiheft 19: 135–150.

Ogg JG (2012) Triassic, Chapter 25. In: Gradstein FM, Ogg JG, Schmitz MD, Ogg GM (Eds) The geologic time scale 2012. Vol. 1. Elsevier, 681–730.

Rieppel O (1994) Osteology of *Simosaurus gaillardoti* and the relationships of stem-group Sauropterygia. Fieldiana Geology, New Series 28: 1–85. https://doi.org/10.5962/bhl.title.3399

Rieppel O (2000) Sauropterygia I. Verlag Dr. Friedrich Pfeil, München, 134 pp. https://pfeil-verlag.de/en/publications/handbuch-der-palaeoherpetologie-encyclopedia-of-paleoherpetology-part-12a-sauropterygia-i-placodontia-pachypleurosauria-nothosauria-pistosauria/

Rieppel O, Wild R (1994) *Nothosaurus edingerae* Schultze, 1970: Diagnosis of the species and comments on its stratigraphical occurrence. Stuttgarter Beiträge zur Naturkunde Serie B 204: 13.

Rinehart LF, Lucas SG (2013) The functional morphology of dermal bone ornamentation in temnospondyl Amphibians. In: Tanner LH, Spielmann JA, Lucas SG (Eds) The Triassic System: New Developments in Stratigraphy and Paleontology. New Mexico Museum of Natural History and Science Bulletin. Albuquerque.

Sanchez S, Schoch RR (2013) Bone histology reveals a high environmental and metabolic plasticity as a successful evolutionary strategy in a long-lived homeostatic Triassic temnospondyl. Evolutionary Biology 40: 627–647. https://doi.org/10.1007/s11692-013-9238-3

Scheyer TM, Romano C, Jenks J, Bucher H (2014) Early Triassic marine biotic recovery: The predators' perspective. PLOS ONE 9: e88987. https://doi.org/10.1371/journal.pone.0088987

Schoch RR (1999) Comparative osteology of *Mastodonsaurus giganteus* (Jaeger, 1828) from the Middle Triassic (Lettenkeuper: Longobardian) of Germany (Baden-Württemberg, Bayern, Thüringen). Stuttgarter Beiträge zur Naturkunde Serie B: 175.

Schoch RR (2000) Biogeography of stereospondyl amphibians. Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen 215: 201–231. https://doi.org/10.1127/njgpa/215/2000/201

Schoch RR (2008) A new stereospondyl from the German Middle Triassic, and the origin of the Metoposauridae. Zoological Journal of the Linnean Society 152: 79–113. https://doi.org/10.1111/j.1096-3642.2007.00363.x

Schoch RR (2015) Amphibien und Chroniosuchier des Lettenkeupers. In: Hagdorn H, Schoch RR, Schweigert G (Eds) Der Lettenkeuper - Ein Fenster in die Zeit vor den Dinosauriern, 203–230.

Schoch RR (2021) Amphibien und Reptilien der Germanischen Trias. In: Hauschke N, Franz M, Bachmann GH (Eds) Trias: Aufbruch in das Erdmittelalter Band 1. Verlag Dr. Friedrich Pfeil, München, 324–340.

Schoch RR, Wild R (1999) Die Wirbeltier-Fauna im Keuper von Süddeutschland. In: Hauschke N, Wilde V (Eds) Trias: eine ganz andere Welt, Mitteleuropa im frühen Erdmittelalter, 395–408.

Schoch RR, Milner AR (2000) Stereospondyli: Stem-Stereospondyli, Rhinesuchidae, Rhytidostea, Trematosauroidea, Capitosauroidea. Verlag Dr. Friedrich Pfeil, München, 203 pp.

Schoch RR, Witzmann F (2011) Cranial morphology of the plagiosaurid *Gerrothorax pulcherrimus* as an extreme example of evolutionary stasis. Lethaia 45: 371–385. https://doi.org/10.1111/j.1502-3931.2011.00290.x

Schoch RR, Milner AR (2014) Temnospondyli I. Verlag Dr. Friedrich Pfeil, 150 pp.

Schoch RR, Seegis D (2016) A Middle Triassic palaeontological gold mine: The vertebrate deposits of Vellberg (Germany). Palaeogeography, Palaeoclimatology, Palaeoecology 459: 249–267. https://doi.org/10.1016/j.palaeo.2016.07.002

Schoch RR, Moreno R (2024) Synopsis on the temnospondyls from the German Triassic. Palaeodiversity 17: 9–48. https://doi.org/10.18476/pale.v17.a2

Seegis D (1997) Die Lehrbergschichten im Mittleren Keuper von Süddeutschland: Stratigraphie, Petrographie, Paläontologie, Genese. 1. Aufl. Hennecke, Remshalden, 382 pp.

Sellwood BW, Valdes PJ (2006) Mesozoic climates: General circulation models and the rock record. Sedimentary Geology 190: 269–287. https://doi.org/10.1016/j.sedgeo.2006.05.013

Sharma KM, Kumar J (2015) Phytosaurian osteoderms from the Late Triassic Tiki Formation (Shahdol District, Madhya Pradesh), India.

Shishkin MA (1986) New data on plagiosaurs from the Triassic of the USSR. Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Geologicheskii 61: 97–102. [in Russian]

Spielmann JA, Lucas SG (2012) Tetrapod fauna of the Upper Triassic Redonda Formation, east-central New Mexico: The Characteristic Assemblage of the Apachean Land-vertebrate Faunachron. Albuquerque, 128 pp.

Spielmann JA, Lucas SG, Heckert AB (2007) Tetrapod fauna of the Upper Triassic (Revueltian) Owl Rock Formation, Chinle Group, Arizona. In: Lucas SG, Spielmann JA (Eds), The Global Triassic. New Mexico Museum of Natural History and Science Bulletin, 371–383.

Stollhofen H, Bachmann GH, Barnasch J, Bayer U, Beutler G, Franz M, Kästner M, Legler B, Mutterlose J, Radies D (2008) Upper Rotliegend to Early Cretaceous basin development. In: Littke R, Bayer U, Gajewski D (Eds) Dynamics of complex intracontinental basins: the Central European Basin System. Springer, Berlin, 181–211.

Sues H-D, Olsen PE, Fedak TJ, Schoch RR (2021) Diverse assemblage of Middle Triassic continental tetrapods from the Newark Supergroup of Nova Scotia (Canada). Journal of Vertebrate Paleontology 41: e2023168. https://doi.org/10.1080/02724634.2021.2023168

Sulej T (2002) Species discrimination of the Late Triassic temnospondyl amphibian *Metoposaurus diagnosticus*. Acta Palaeontologica Polonica 47: 535–546.

Sulej T (2007) Osteology, variability, and evolution of *Metoposaurus*, a temnospondyl from the Late Triassic of Poland. Palaeontologia Polonica 64: 29–139.

Szulc J, Racki G, Jewuła K, Środoń J (2015) How many Upper Triassic bone-bearing levels are there in Upper Silesia (southern Poland)? A critical overview of stratigraphy and facies. Annales Societatis Geologorum Poloniae 85: 587–626. https://doi.org/10.14241/asgp.2015.037

Teschner E, Garbay L, Janecki P, Konietzko-Meier D (2023) Palaeohistology helps reveal taxonomic variability in exceptionally large temnospondyl humeri from the Late Triassic Krasiejów deposit (SW Poland). Acta Palaeontologica Polonica 68: 63–74. https://doi.org/10.4202/app.01027.2022

Thürach H (1888) Übersicht über die Gliederung des Keupers im nördlichen Franken im Vergleich zu den benachbarten Gegenden. Geognostisches Jahresheft 1: 75–162.

Tverdokhlebov VP, Tverdokhlebova GI, Surkov MV, Benton MJ (2003) Tetrapod localities from the Triassic of the SE of European Russia. Earth-Science Reviews 60: 1–66. https://doi.org/10.1016/S0012-8252(02)00076-4

Urlichs M, Tichy G (2000) Correlation of the Bleiglanzbank (Gipskeuper, Grabfeld Formation) of Germany with Upper Ladinia beds of the Dolomites (Italy). Zentralblatt für Geologie und Paläontologie, Teil 1 9/10: 997–1007.

Warren AA, Snell N (1991) The postcranial skeleton of Mesozoic temnospondyl amphibians: a review. Alcheringa: An Australasian Journal of Palaeontology 15: 43–64. https://doi.org/10.1080/03115519108619009

Watson DMS (1919) The structure, evolution and origin of the Amphibia — The Orders Rhachitomi and Stereospondyli. Philosophical Transactions of the Royal Society of London, Series B 209(360–371): 1–73. https://doi.org/10.1098/rstb.1920.0001

Wild R (1974) Ein Labyrinthodonten-Rest (Amphibia) aus den Estherienschichten (Mittlerer Keuper) von Mittelfranken. Geol. Bl. NO-Bayern 24: 48–55.

Witzmann F, Gassner T (2008) Metoposaurid and mastodonsaurid stereospondyls from the Triassic – Jurassic boundary of Portugal. Alcheringa: An Australasian Journal of Palaeontology 32: 37–51. https://doi.org/10.1080/03115510701757316

Zeh A, Franz M, Obst K (2021) Zircon of Triassic Age in the Stuttgart Formation (Schilfsandstein)—Witness of Tephra Fallout in the Central European Basin and New Constraints on the Mid-Carnian Episode. Frontiers in Earth Science 9: 778820. https://doi.org/10.3389/feart.2021.778820

Zhang Y, Ogg JG, Franz M, Bachmann GH, Szurlies M, Röhling H-G, Li M, Rolf C, Obst K (2020) Carnian (Late Triassic) magnetostratigraphy from the Germanic Basin allowing global correlation of the Mid-Carnian Episode. Earth and Planetary Science Letters 541: 116275. https://doi.org/10.1016/j.epsl.2020.116275

Zittel KA (1888) Handbuch der Paläeontologie. Abteilung 1. Paläozoologie Band III. Vertebrata (Pisces, Amphibia, Reptilia, Aves). Oldenbourg, München, 900 pp.

Zouheir T, Hminna A, Klein H, Lagnaoui A, Saber H, Schneider JW (2018) Unusual archosaur trackway and associated tetrapod ichnofauna from Irohalene member (Timezgadiouine formation, late Triassic, Carnian) of the Argana Basin, Western High Atlas, Morocco. Historical Biology 32: 589–601. https://doi.org/10.1080/08912963.2018.1513506