PalZ (2025) 99:319–337
https://doi.org/10.1007/s12542-025-00729-w

RESEARCH PAPER

The morphology and evolutionary history of the temnospondyl genus *Cyclotosaurus* with a focus on material from Germany

Rainer R. Schoch[1,2] · Florian Witzmann[3] · Ingmar Werneburg[4] · Ralf Werneburg[5] · Eudald Mujal[1] · Raphael Moreno[1]

Received: 4 October 2024 / Accepted: 23 March 2025 / Published online: 12 June 2025

Abstract

The capitosauroid genus *Cyclotosaurus* was first recognized in the Carnian Stuttgart Formation of Feuerbacher Heide at Stuttgart in the nineteenth century. A revision of the type material and the other German samples from stratigraphically younger Carnian and Norian deposits reveal numerous differences between these. Cladistic analysis of the German species plus the taxa from Poland and Greenland concurs roughly with stratigraphy, albeit with two main post-*C. robustus* lineages that date back to the Stuttgart Formation: (1) a slender-skulled clade formed by *C. buechneri* and *C. ebrachensis* and (2) a broad-skulled clade formed by *C. posthumus, C. naraserluki, C. intermedius* and *C. hemprichi*. *Cyclotosaurus* was the single apex predator in Carnian and Norian fluviatile environments.

Keywords Capitosauria · Phylogeny · Stereospondyli · Temnospondyli · Triassic

Introduction

During Triassic time, many freshwater environments were dwelled by large temnospondyl predators, the stereospondyls. These caiman- to gharial-like taxa reached sizes between two and five metres and are mostly known by their massive skulls, robust pectoral girdles and vertebrae (Damiani & Steyer, 2005; Schoch & Milner, 2000; Warren, 2000). The life cycles of these predominantly aquatic forms were remarkably distinct from those of modern amphibians, with even small juveniles closely resembling adults (Fröbisch et al., 2010; Schoch & Witzmann, 2024). In Germany, stereospondyls were most diverse during the late Ladinian, when up to eight distinct taxa inhabited a range of habitats that are preserved in the Lower Keuper or Erfurt Formation (Schoch, 2015). This abundance of stereospondyls contrasts the absence of these and other tetrapods in many rocks of the subsequently deposited Grabfeld Formation (Gipskeuper; Moreno et al., 2024). However, by the late Carnian, large-scale rivers and delta systems again harboured a diverse suite of stereospondyls (Schoch & Moreno, 2024). During the Tuvalian (early late Carnian), the Central European Basin was subject to increased siliciclastic input that formed abundant fluvial deposits (Beutler et al., 1999; Franz & Barnasch, 2021). These fine-grained sandstones are locally rich in plant fossils (Jaeger, 1827; Kelber & Hansch, 1995), which earned them their regional stratigraphic name Schilfsandstein ("reed sandstone").

These rocks also yielded a range of tetrapods among which the temnospondyls rank as most abundant: the trematosauroids *Metoposaurus diagnosticus* and *Hyperokynodon keuperinus* (Meyer, 1842; Schoch, 2024), the plagiosaurid *Gerrothorax* sp. (SMNS 17032, Hellrung, 2003; Schoch & Witzmann, 2012), and the most common but long neglected capitosauroid *Cyclotosaurus robustus* (Fraas, 1889; Meyer & Plieninger, 1844; Quenstedt, 1850) which forms the subject of the present study.

Handling Editor: Hans-Dieter Sues.

✉ Rainer R. Schoch
rainer.schoch@smns-bw.de

1 Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany

2 Institut für Biologie, Fachgebiet Paläontologie, Universität Hohenheim, 70599 Stuttgart, Germany

3 Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstraße 43, 10115 Berlin, Germany

4 Fachbereich Geowisenschaften, Universität Tübingen, 72017 Tübingen, Germany

5 Naturhistorisches Museum Schloss Bertholdsburg, 98553 Schleusingen, Germany

Cyclotosaurus robustus was one of the first temnospondyls to be discovered in Germany, after Jaeger's (1828) report on *Mastodonsaurus giganteus* from the "Lettenkohle" (Erfurt Formation) and Münster's (1836) description of *Capitosaurus arenaceus* from the Benker Sandstein (Grabfeld Formation) had been published. The first remains of *C. robustus* were found in a large sandstone quarry within the Feuerbacher Heide, then an open grassland area on the Killesberg hill north of the Stuttgart city centre. It was originally described as *Capitosaurus robustus*, figured by Meyer and Plieninger (1844) and in more detail by Quenstedt (1850) who emphasized the closed otic fenestrae (squamosal embayment) and on their basis argued for an amphibian nature of temnospondyls.

Cyclotosaurus was later also reported from higher levels within the Middle Keuper of Germany: *C. posthumus* and *C. mordax* from Pfaffenhofen in northern Württemberg (Fraas, 1913), *C. ebrachensis* from Ebrach in northern Bavaria (Kuhn, 1932), *C. hemprichi* from Halberstadt in Saxony-Anhalt (Kuhn, 1939, 1942) and *C. buechneri* from Bielefeld in Lower Saxony (Witzmann et al., 2016) (Fig. 1). At Krasiejów, southeastern Poland, the new species *C. intermedius* was added by Sulej and Majer (2005) and some elements described as *Cyclotosaurus* sp. from Wożniki (Sulej et al., 2011), and further specimens were reported from the Norian of east-central Greenland (*C. naraserluki*: Marzola et al. 2017), from Svalbard (Kear et al., 2015; Wiman, 1914), from Poland (Dzik et al., 2008) and Thailand (Ingavat & Janvier, 1981). Isolated bones from the Rhaetian bonebed of Bonenburg in Northrhine Westphalia have also been referred to *Cyclotosaurus* (Konietzko et al., 2019).

The objective of the present study is to (1) reexamine the existing material of *Cyclotosaurus* in Germany, (2) trace the morphological variation within and between samples, (3) analyse the phylogenetic relationship of all *Cyclotosaurus* species and (4) discuss the evidence on the evolutionary history of the genus across the Carnian–Norian Keuper sequence.

Geological setting and collecting history

The northern Württemberg region in Germany is famous for its abundance of buildings constructed from the local Schilfsandstein or Stuttgart Formation. As mapped by Wurster (1968), the municipal area of Stuttgart comprises several kilometre-wide, interconnected units of channel sandstones that fall within that formation. At the Killesberg hill, these pale brown to greenish-grey sandstones were quarried along several slopes, one of which was located within the Feuerbacher Heide, then a vast heath covering several square kilometres. There, tall red cliffs (Rote Wand, Steigerwald member of Weser Formation) formed the overburden of the quarried Schilfsandstein. The steep slopes resulted from extensive quarrying from the early 1500 s well over 400

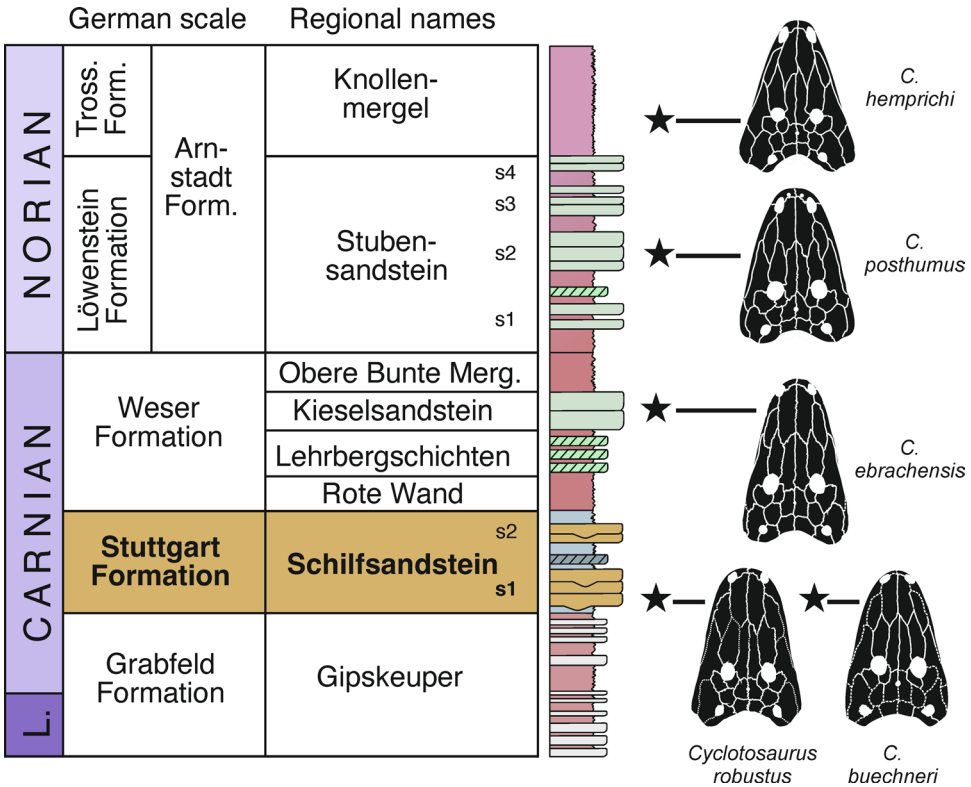

Fig. 1 Stratigraphic range of the genus *Cyclotosaurus* Fraas, 1889 in the German Triassic

years, so that in the late nineteenth century a valley had been formed. In 1850, some 100 people worked in the main site known as Kochenhof quarry. In a picture by Christian Septimus von Martens dated 1845, this man-made valley is figured, and the impressive size of the quarry in relation to the depicted workers suggests that the sandstone sequence was some 20 m thick.

The Kochenhof quarry was abandoned in 1904 and subsequently filled with debris, and today it forms part of a recreation area (Höhenpark Killesberg). The fossiliferous sandstones of the Kochenhof quarry vary between pale brown and grey, locally containing dark brown stains. The colour of the fossil bones ranges from black (most common) over dark blue and brown to pale purple. These colour differences, as well as the variable lithology and content of mud clasts, suggest that the bones might stem from different horizons, which also correlates with the variation in sediment coloration. Some blocks preserve plant remains and small unidentified bone fragments in oblique embedding.

The Stuttgart Formation yielded remains of *Cyclotosaurus* also in other regions. Fragmentary material was collected in coarse sandstone beds at the clay pit Klapproth of Mittelhausen near Erfurt in Thuringia. The material comprises a portion of the cheek with an otic fenestra consistent with that of *Cyclotosaurus*, and similar to the Feuerbacher Heide locality, *Metoposaurus* is also present in Mittelhausen (Werneburg, 1990). More recently, a single well-preserved skull was reported as an additional species, *C. buechneri*, from the Schilfsandstein of Bielefeld (Witzmann et al., 2016).

The single specimen from the Weser Formation (Blasensandstein), a complete skull, was reported by Kuhn (1932) from the sandstone quarry at Ebrach, between Bamberg and Würzburg in Upper Franconia. The skull of *Cyclotosaurus ebrachensis* was found in a massive white, quarzitic sandstone at the base of the Blasensandstein just above the Plattensandstein (bed 5 of Kuhn, 1932).

More numerous are the finds from the mid-Norian Löwenstein Formation, which all fall within the Middle Stubensandstein (sc2) of northern Württemberg. The "White quarry" at Pfaffenhofen near Güglingen in the Stromberg region yielded two beautifully preserved partial skulls for which two separate species, *C. posthumus* and *C. mordax*, were erected (Fraas, 1913). They were both found in a massive channel sandstone at the base of the quarried section (Berckhemer, 1938; Hungerbühler, 1998). In the 1980 s, rocks of the Middle Stubensandstein yielded a range of well-preserved specimens from a small sandstone quarry at Magstadt in the Stuttgart region, which are reported and described here for the first time.

The whereabouts of the impressive skull material of *Cyclotosaurus hemprichi* from the Baerecke-Limpricht clay pit of Halberstadt, Saxony Anhalt, are currently unknown. It was embedded in grey mudstones and the preservation was exquisite, as Kuhn's (1942) figures show.

Material and methods

Material. The studied material encompasses predominantly remains of the skull and pectoral girdle from three different horizons in the Upper Triassic: the Stuttgart, Weser and Löwenstein formations (see holotypes and referred material listed in the systematic section).

Phylogenetic analysis. The dataset was analysed using TNT 1.6 (Goloboff & Morales, 2023) Tree searches under equal character weighting were performed using a Traditional Search with 1000 Wagner trees replications, random addition sequence, and TBR branch swapping holding 10 trees per replicate. Values of Bremer and Bootstrap support (GC = groups recovered versus groups contradicted) were calculated, the latter through a Traditional search with 1000 iterations. The analysis was run in the ACCTRAN mode, and all characters were treated as unordered.

Abbreviatios

Anatomical. A, angular, apo, anterior palatal opening, crf, crista falciformis, cro, crista obliqua, cv, columna verticalis, ec, ectopterygoid, eo, exoccipital, f, frontal, fm, foramen magnum, f-vo, fodina vomeralis, ico, intercoronoid, ipv, interpterygoid vacuity, ju, jugal, la, lacrimal, m, maxilla, n, nasal, na, naris, p, parietal, pf, postfrontal, ph, processus hamatus, pl, palatine, pm, premaxilla, po, postorbital, pop, paroccipital process, pp, postparietal, pq, paraquadrate foramen, prf, prefrontal, ps, parasphenoid, psp, postsplenial, pt, pterygoid, q, quadrate, qj, quadratojugal, sp, splenial, sq, squamosal, st, supratemporal, stw, subtemporal window, ta, tabular, tar, torus arcuatus, vo, vomer.

Institutional. BSM, Bayerische Staatssammlung für Paläontologie, Munich, Germany. GPIT, Geologisch-Paläontologisches Institut, Tübingen, Germany. HMH, Heimatmuseum Halberstadt, Germany. MB, Museum für Naturkunde Berlin, Germany. Namu, Naturkundemuseum Bielefeld, Germany. NMK, Naturhistorisches Museum, Kassel, Germany. NHMS, Naturhistorisches Museum, Schleusingen, Germany. SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany. UMO-BSP-BT, Urwelt-Museum Oberfranken, Bayreuth, Germany.

Systematic palaeontology

Temnospondyli Zittel, 1888
Stereospondyli Zittel, 1888
Capitosauroidea (Säve-Söderbergh, 1935)
Cyclotosauridae Shishkin, 1964
Cyclotosaurinae (Shishkin, 1964)

Genus ***Cyclotosaurus*** Fraas, 1889

Hercynosaurus Jaekel, 1914
Hemprichisaurus Kuhn, 1939

Diagnosis. Autapomorphies: (1) broad-parabolic skull with postorbital portion 0.3–0.34 times the preorbital one; (2) choana very broad, ranging from oval to circular; (3) anterior palatal vacuity heart-shaped. A more variable feature is that the tip of the premaxilla may be perforated by symphyseal tusks (shared with *Mastodonsaurus*).

Type species. *Cyclotosaurus robustus* (Meyer & Plieninger, 1844).

Cyclotosaurus robustus (Meyer & Plieninger, 1844).
Figures 2, 4a, b, 5a, 6a

Capitosaurus robustus Meyer & Plieninger, 1844
Mastodonsaurus robustus Quenstedt, 1850
Mastodonsaurus cyclotis Quenstedt, 1850

Holotype. GPIT PV 30086, a partial skull roof and complete palate on two blocks (61 cm skull length, Fig. 2d, e).

Type locality. Feuerbacher Heide (Kochenhof quarry, Killesberg), Stuttgart, Baden-Württemberg, Germany (Fig. 1).

Type horizon and age. Massive light brown or greenish-grey sandstone unit within the Schilfsandstein facies, lower Stuttgart Formation (Carnian: early Tuvalian, see Zeh et al., 2021), Late Triassic (Fig. 1).

Comment. In the holotype of *C. robustus*, the palate is exposed in dorsal view (Fig. 2e). There, the basicranial region, cultriform process, both pterygoids and the left jaw margin up to the posterior margin of the choana are well preserved. Comparisons with the figure in Quenstedt (1850: Pl. 1, Fig. 1) reveal that the premaxilla and marginal skull roof have been lost.

Referred specimens. Feuerbacher Heide (Schilfsandstein, lower Stuttgart Formation). MB.Am.483 (cast of anterior palate). GPIT-PV 44620–44849 (numerous bone fragments of the dermal shoulder girdle and skull). SMNS 833 (right palatine and choana, originally referred to *Mastodonsaurus keuperinus* by Fraas, 1889). SMNS 4139 (right part of skull, 54 cm). SMNS 4935 (partial skull roof, ca. 42 cm, figured by Meyer & Plieninger, 1844, pl. IX, fig. 1). SMNS 5775 (best-preserved skull, 50 cm). SMNS 7414 (posterolateral margin of skull). SMNS 91417 (interclavicle). SMNS 91484 (partial interclavicle). SMNS 91492 (partial interclavicle). Stuttgart-Bopser (Schilfsandstein). SMNS 97116 (partial interclavicle). SMNS 97136 (three intercentra). Stuttgart, Steinbruch near Waldorfschule (Schilfsandstein). SMNS 91493 (interclavicle). Wendelsheim. GPIT uncatalogued: Posterolateral portion of skull roof, ventral view. Klapproth clay pit, Mittelhausen near Erfurt. MB.Am.1493 (fragment of skull roof and mandible, skull length ca. 16 cm). MB.Am.1494 (fragment of cheek).

Diagnosis. Autapomorphies: (1) Postorbital skull table foreshortened, with parietal only 1.3 times longer than wide and supratemporal as long as wide, (2) choana with irregular oval outline.

Cyclotosaurus buechneri Witzmann et al., 2016
Figures 3g, 5b

Holotype. Namu ES/k 36,053, nearly complete skull in dorsal view (29.5 cm).

Type locality. Bielefeld, district Sieker, North Rhine-Westphalia, Germany.

Type horizon and age. Stuttgart Formation, late Carnian (Tuvalian), Late Triassic.

Diagnosis. Autapomorphies: (1) orbits medially placed with short interorbital distance; (2) region lateral to orbitae only as wide or 10% wider than width of orbitae; (3) postorbital skull region slender; (4) preorbital projection of jugal shorter than half the length of snout.

Cyclotosaurus ebrachensis Kuhn, 1932
Figures 3f, 4c, 5c, 6b

Holotype. BSM 1931X1, a complete skull prepared from both sides (35 cm).

Type locality. Sandstone quarry at Ebrach, Upper Franconia, Bavaria, Germany.

Type horizon and age. Sandstone bed 5, lower part of Blasensandstein, Hassberge Formation (Middle Keuper, Norian), Late Triassic (Kuhn, 1932).

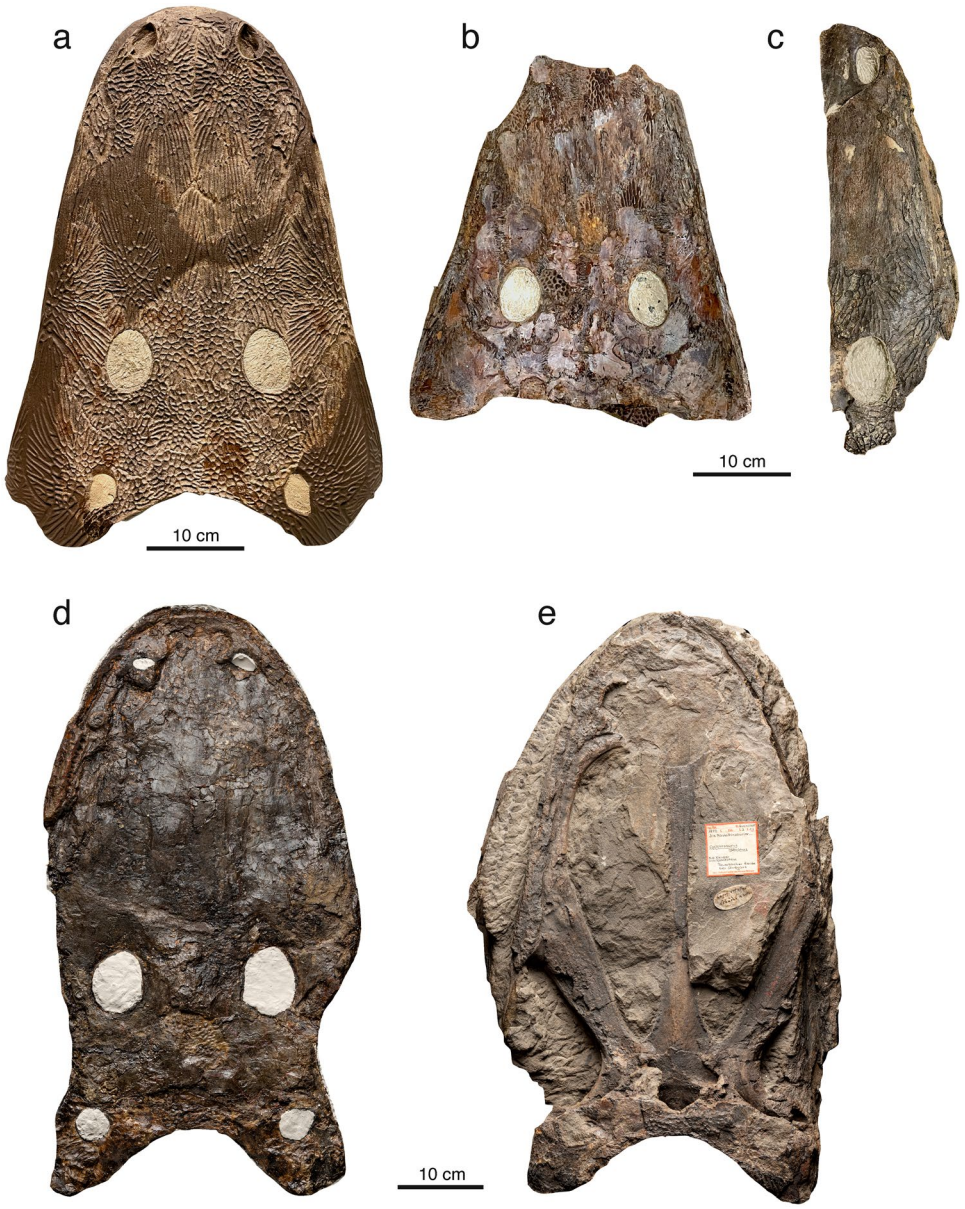

Fig. 2 *Cyclotosaurus robustus* (Meyer & Plieninger, 1844). **a** SMNS 5775, skull in dorsal view; **b** SMNS 4935, skull roof in ventral view; **c** SMNS 4139, anterior-right part of skull in dorsal view; **d, e** GPIT 30086, (holotype of *C. robustus*) (**d** ventral view of skull roof, **e** dorsal view of palate)

Diagnosis. Autapomorphies: (1) Dermal ornament fine, (2) skull slender (skull width at mid-orbit level: skull length = 0.62), especially jugal narrower than in other species, (3) anterior palatal vacuity without anterior constriction, (4) pineal foramen tiny.

Cyclotosaurus posthumus Fraas, 1913
Figures 3a–d, 4c–f, 5e, 6c

Cyclotosaurus mordax Fraas, 1913

Holotype. SMNS 12988, a large portion of a skull (52.5 cm).

Type locality. White (Burrer's) quarry near Pfaffenhofen, Stromberg region, Baden-Württemberg, Germany.

Type horizon and age. Basal, massive light grey to white sandstone unit within Middle Stubensandstein, Löwenstein Formation (Middle Keuper, Norian), Late Triassic.

Referred material. The two main samples include the historic material from Pfaffenhofen (Fraas, 1913), and new material collected in the 1970 s at Magstadt. SMNS 12195 (interclavicle). SMNS 13014 (anterior part of skull, ca. 46 cm total length, holotype of *C. mordax* Fraas, 1913). SMNS 18417 (partial interclavicle). SMNS 59769 (partial jaw with teeth). SMNS 91543 (left quadratojugal). Magstadt, sandstone quarry "Äußere Winterhalde" (Middle Stubensandstein). SMNS 50006 (interclavicle). SMNS 50009 (preorbital region, skull length ca. 48 cm). SMNS 50059

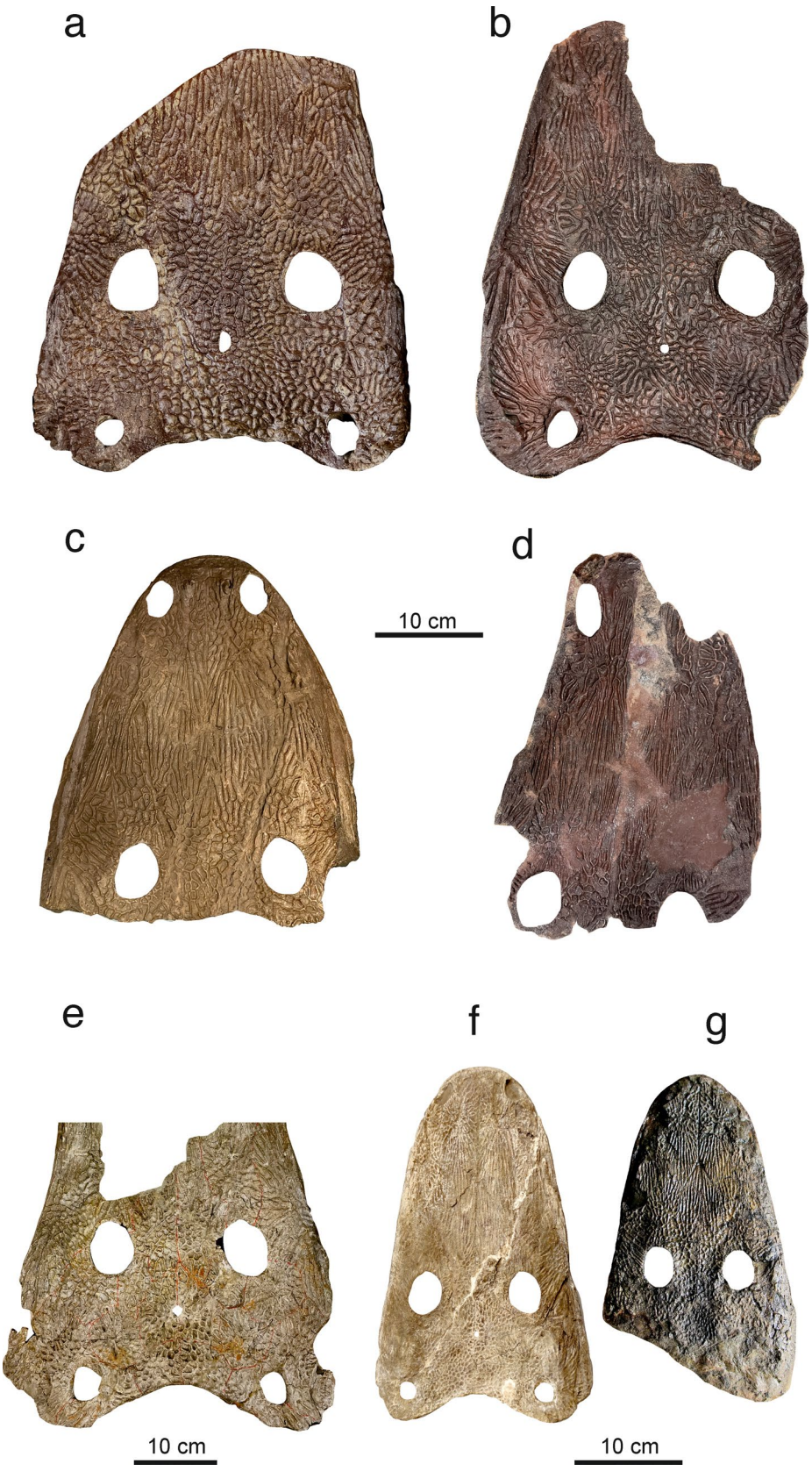

Fig. 3 **a–e** *Cyclotosaurus posthumus* (Fraas, 1913). **a** SMNS 51426; **b** SMNS 50063; **c** SMNS 13014 (holotype of *C. mordax*); **d** SMNS 50009; **e** SMNS 12988 (holotype of *C. posthumus*); **f** *Cyclotosaurus ebrachensis* (Kuhn, 1932), BSM 1931 X1 (holotype). **g** *Cyclotosaurus buechneri* Witzmann et al., 2016, Namu ES/k 36,053 (holotype)

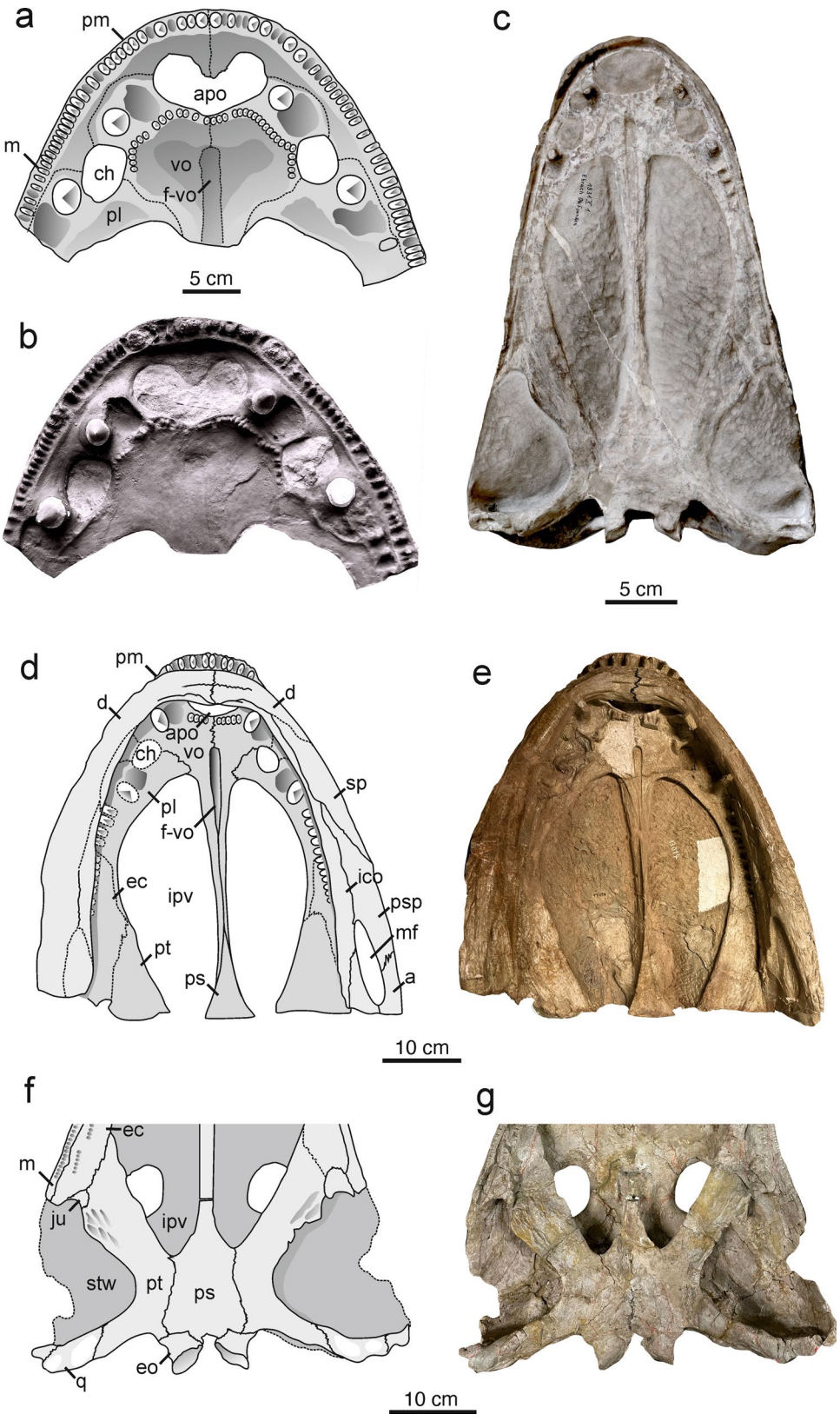

Fig. 4 Palate of *Cyclotosaurus*. **a, b** *C. robustus*, anterior part of palate in ventral view (MB.Am.483, cast, location of original fossil unkown); **c** *C. ebrachensis*, BSM 1931X1; **d, e** *C. posthumus* (holotype of *C. mordax*), SMNS 13014; **f, g** *C. posthumus* (SMNS 12988), posterior part of palate in ventral view

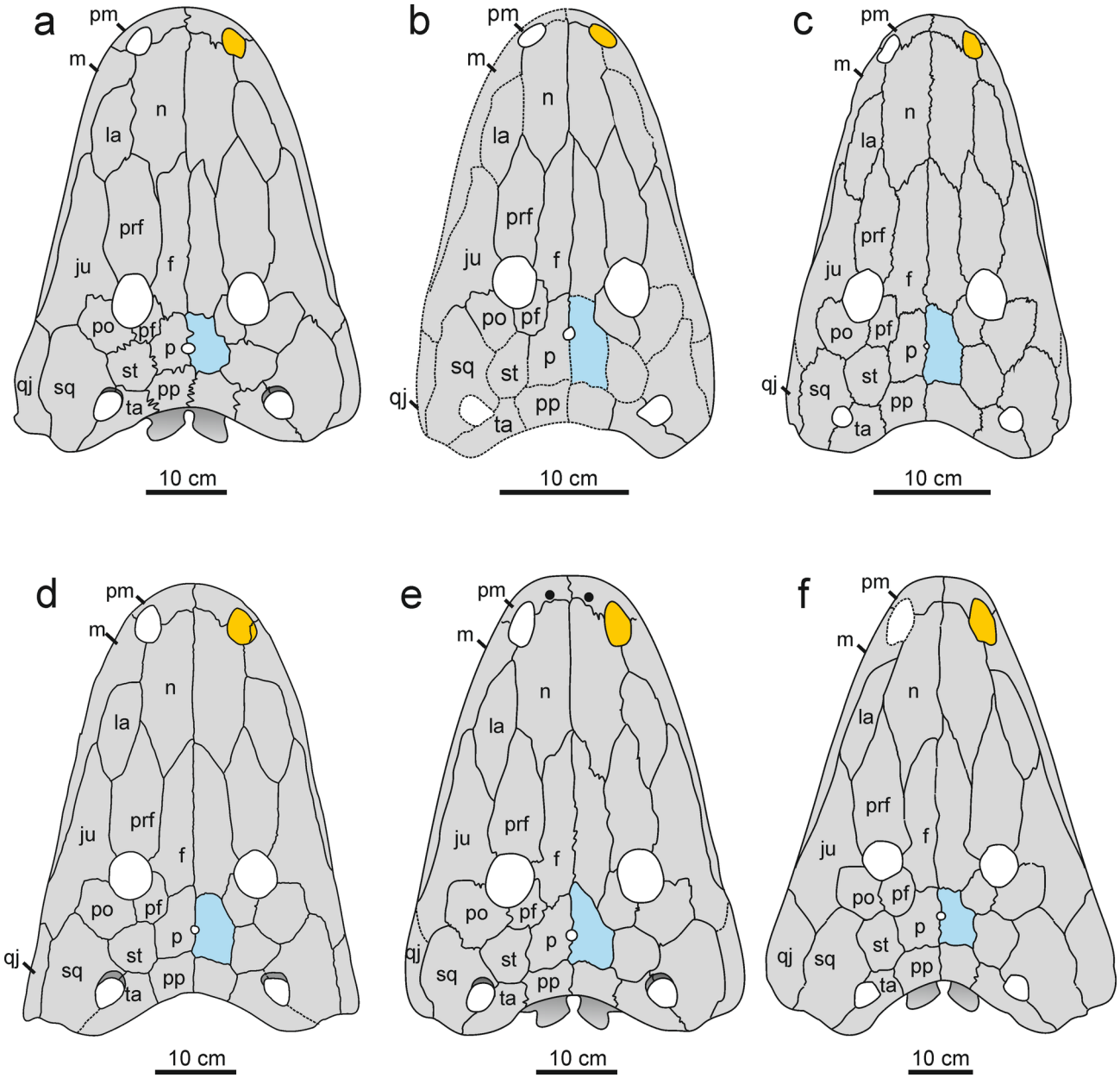

Fig. 5 **a** *Cyclotosaurus robustus* (SMNS 5775); **b** *C. buechneri* (after Witzmann et al., 2016); **c** *C. ebrachensis* (BSM 1931 X1); **d** *C. intermedius* (after Sulej and Majer 2005); **e** *C. posthumus* (SMNS 13014, 50,063); **f** *C. hemprichi* (after Kuhn, 1942). Parietal highlighted in blue, naris in yellow

(left preorbital skull, skull length ca. 50 cm). SMNS 50063 (partial skull, ca. 46 cm). SMNS 51102 (partial skull, 41.5 cm). SMNS 51426 (partial large skull, ca. 46 cm). SMNS 51436 (interclavicle fragment).

Diagnosis. Autapomorphies: (1) interorbital distance wide (IOW:SL = 0.22), (2) naris only slightly shorter than orbit, (3) internarial distance smaller than in type species, (4) ornament coarse (i.e., larger polygons), (5) choana shorter than in type species, (sub)circular.

Comment. We consider *C. mordax* a junior synonym of *C. posthumus* (named a few pages before *C. mordax*) because its characteristic features are also found in specimens of the Magstadt sample and the two type specimens fall onto a continuous morphological range (see description).

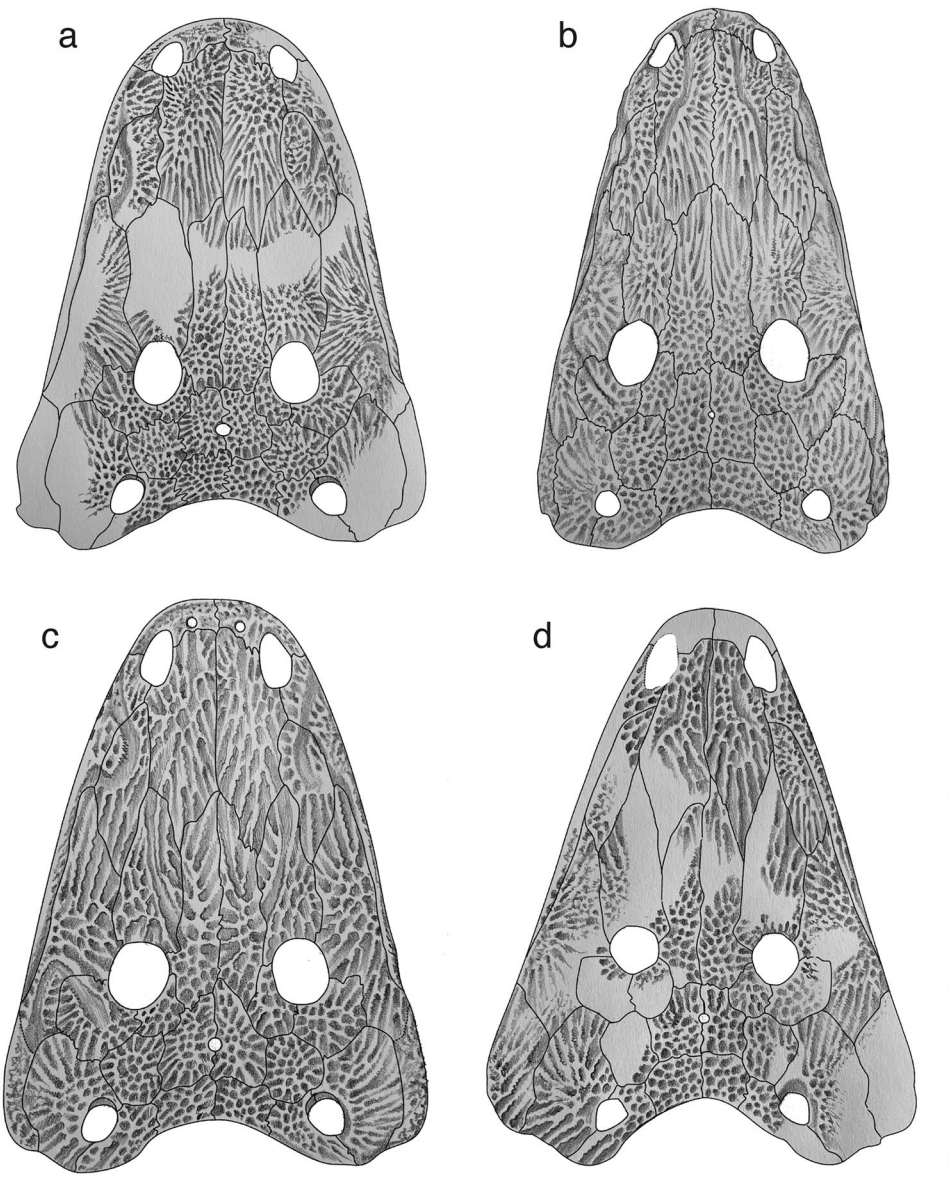

Fig. 6 Skull roof and dermal ornament in different species of *Cyclotosaurus*. **a** *C. robustus* (SMNS 5775); **b** *C. ebrachensis* (BSM 1931 X1). **c** *C. posthumus* (SMNS 13014, 50,063). **d** *C. hemprichi* (after Kuhn, 1942). See scales in Fig. 5

Cyclotosaurus hemprichi Kuhn, 1942
Figures 5f, 6d

Hercynisaurus carinidens Jaekel, 1914
Hemprichisaurus keuperinus Kuhn, 1939
Metoposaurus ultimus Kuhn, 1939

Holotype. HMH, a complete large skull with mandible (62.5 cm), location currently unknown. The mandible was figured by Kuhn (1939) and the skull by Kuhn (1942).

Type locality. Former Baerecke-Limpricht clay quarry, Halberstadt, Saxony-Anhalt, Germany.

Type horizon and age. Basal, massive light grey to white sandstone unit within Middle Stubensandstein, Löwenstein Formation (Middle Keuper, Norian), Late Triassic.

Referred material. MB.Am.505 (isolated large fang), 507a (isolated large fang, original to Jaekel, 1914, fig. 31), 507b (isolated tooth), 547a, b (two disk-like intercentra), 568 (three disk-like intercentra), 570 (fragments of six ribs, original to Jaekel, 1914, fig. 33a-f), 572 (two teeth), 573 (dorsally open intercentrum of the tail, original to Jaekel, 1914, fig. 32: 2a-c), 577 (disk-like intercentrum, original to Jaekel, 1914, fig. 32: 1a-c), 1547 (large part of a left lower jaw ramus). MB.Am.507, 573, 570, and 577 constitute the type material of *Hercynosaurus carinidens* Jaekel, 1914. Material probably belonging to *C. hemprichi*: MB.Am.564

(12 jaw fragments), 567 (fragment of parietal bone), 576 (four fragments of palatal bones).

Diagnosis. Autapomorphies: (1) Quadratojugal wide and lateral margin of skull tapering, (2) naris elongate oval and slightly longer than orbit, (3) orbit small and round, less than 10% skull length.

Cyclotosaurus intermedius Sulej and Majer, 2005.
Figure 5d

Holotype. ZPAL Ab III 1173, complete skull with both hemimandibles attached (52 cm).

Type locality. Krasiejów, Opole, Silesia, Poland.

Type horizon and age. Drawno Beds, Grabowa Formation, early Norian, Late Triassic.

Referred material. From the lower horizon: ZPAL Ab III 680 (hemimandible), 887/3 (humerus), 887/2 (scapulocoracoid), 887/1 (interclavicle). From the upper horizon: 471/25 (lacrimal); 471/20 (jugal); 471/16 (palatine), 471/8, 471/19, 471/31, 471/45 (pterygoids), 471/113, 472/28 (hemimandibles), 397 (clavicle), 471/51 (cleithrum), 367 (interclavicle) (Sulej and Majer, 2005).

Diagnosis. Autapomorphies: (1) projection of the quadrate behind the posterior margin of the skull roof, (2) presence of a shagreen of denticles on the vomer, palatine and anterior pterygoid.

Description

In this section we focus on newly recognized features of the type species and the differences to other German taxa referred to *Cyclotosaurus* Fraas, 1889. A general overview on the morphology of the different species is provided in Figs. 5 and 6.

General proportions. The proportions of the skull table and interorbital region differ between the type species and stratigraphically younger samples, with *C. hemprichi* forming an extreme end point regarding the small size of the orbits and the tapering skull margins (Fig. 5f). In all other species, the skull has a parabolic outline with the width of the snout (at posterior level of nares) measuring around 0.5 times the width at the anterior margin of the orbits. Instead, the reported concave lateral margin of the skull in the type specimen of *C. posthumus* results from distortion.

The skull morphology is largely consistent with the cyclotosaurid *Tatrasuchus* in most proportions and differs from the incompletely known *Capitosaurus* by the parabolic outline of the preorbital region (Schoch & Moreno, 2024). The width of the skull differs between the studied species of *Cyclotosaurus*, with *C. buechneri* and *C. ebrachensis* having distinctly narrower skulls than other species.

Ontogeny and size disparity. The two slender skulls of *C. buechneri* and *C. ebrachensis* are substantially smaller than those of all other taxa. This suggests that the relative width of the skull—specifically the jugal—may have been subject to developmental change. However, in the two large samples (*C. robustus*, *C. posthumus*), ontogenetic or individual variation is recognized in several features, but not in the relative width of the jugal. Admittedly, small specimens are only known in *C. robustus* (Mittelhausen sample), but in these fragments the width of the skull cannot be ascertained. The skull may therefore have become relatively broader in adults, but the outgroup comparison (*Tatrasuchus*, *Xenotosuchus*) does not support that (Damiani, 2008).

Ontogenetic change is recognized in the following features. In *C. robustus*, the occipital margin becomes more strongly concave in larger adults, as exemplified by the type specimen figured by Quenstedt (1850) as compared with SMNS 5775. In *C. posthumus*, the width of the squamosal-tabular bridge and its posterior margin vary with size, in smaller specimens being relatively narrower with a stepped margin. Variation in the size and arrangement of teeth has not been recognized in the studied samples.

Ornament. The dermal sculpturing varies both within and between the samples, with *C. posthumus* having the coarsest and *C. ebrachensis* the finest (Fig. 6). By "coarse" we refer to the size of the polygons as defined by the ridges, which are larger and fewer in number in *C. posthumus* compared with *C. ebrachensis*. *C. robustus* and *C. posthumus* are similar in the size of the polygons, but differ in the height of the ridges, which is generally greater in the samples from the Löwenstein Formation compared with those of the Stuttgart and Weser Formations. A third feature is the thickness of the ridges: in *C. robustus*, the ridges are not only the lowest but also much thinner than in other samples. In addition, ornamentation differs also in the nature of the ridges and their arrangement between samples. For instance, in *C. robustus*, the jugal is covered by elongate ridges, whereas in *C. posthumus* this region houses mostly radially arranged polygons. All samples share elongate radial ridges on the prefrontal, lacrimal and nasal.

Lateral line. The lateral line sulci are faintly developed in *C. robustus* and most deeply imprinted and continuous in *C. posthumus*. In *C. robustus*, sulci are only present on the maxilla, lacrimal, postorbital and jugal, whereas they are entirely absent on the frontal, supratemporal and postfrontal. In the

type specimen of *C. mordax*, the groove on the premaxilla, the lacrimal flexure and the supraorbital sulcus on the prefontal are especially wide and deeply impressed. By contrast, the holotype of *C. posthumus* and the sample from Magstadt has only poorly defined lateral line sulci except for the lateral flexure and jugal regions. The most continuous lateral lines are present on *C. ebrachensis* and *C. intermedius*, where the prefrontal and supratemporal also bear well-defined sulci.

Preorbital region. In *Cyclotosaurus*, the length of the preorbital region relative to skull length ranges between 0.59 and 0.67. It is proportionally shorter in the Carnian samples, especially *C. buechneri* and *C. ebrachensis*, and longest in *C. hemprichi*. In the sample from the Löwenstein Formation, the length of the preorbital region varies broadly, with the short-snouted type specimen of *C. mordax* and the long-snouted holotype of *C. posthumus* forming end points on a continuum. On a gross scale, the relative length of the preorbital region is consistent with many other capitosauroids (*Tatrasuchus*: 0.6, *Eocyclotosaurus*: 0.66, *Parotosuchus*: 0.64–0.69, *Stanocephalosaurus*: 0.73, *Paracyclotosaurus*: 0.65).

The frontal, prefrontal and nasal are of similar length, whereas the lacrimal is throughout shorter and narrower. In *C. robustus*, *C. buechneri* and *C. ebrachensis*, the premaxilla is slightly shorter than in the Norian taxa. In the Carnian samples, the bone is usually not penetrated by symphyseal tusks. Small premaxillary tusk openings are present in the type specimens of *C. mordax* and *C. naraserluki*, whereas they are absent in *C. ebrachensis*, *C. intermedius* and apparently were also in *C. hemprichi*.

In *Cyclotosaurus*, the naris is distinctly smaller than the orbit and located in a terminal position in the Carnian taxa, whereas the Norian taxa have a larger naris (as long as the orbit in *C. hemprichi*) and the tip of the premaxilla is anteriorly extended. In *C. robustus*, the naris has a well-rounded medial margin but its lateral margin tapers anteriorly. In contrast, the naris of *C. posthumus* has a more symmetrical oval outline. In all *Cyclotosaurus* species, the naris is generally longer than in *Tatrasuchus*.

Interorbital region. In all *Cyclotosaurus* species, the orbit is relatively small compared with other stereospondyls, ranging between 0.09 and 0.125 times the skull length. The orbit has an elongate oval outline in *C. robustus*, but is more rounded in the Norian taxa. The studied samples differ markedly in the width of the interorbital region as well as the infratemporal (jugal) width. In post-Schilfsandstein *Cyclotosaurus*, the orbits are placed more laterally, which is most clearly expressed in *C. ebrachensis* and *C. posthumus* (interorbital distance: skull length = 0.2). Conversely, the two taxa from the Stuttgart Formation (*C. robustus*, *C. buechneri*) have interorbital distances ranging between 0.166 and 0.188 times skull length. With the lateral placement of the orbits, the width of the jugal decreases relative to that of the interorbital distance. The contribution of the frontal to the orbit margin varies both in and between the samples. Even in *C. robustus* (SMNS 5775), the postfrontal reaches further anterior on the right side than on the left, and in *C. posthumus*, a contact between prefrontal and postfrontal is established on one side (SMNS 50063) (Kamphausen, 1994). In *C. hemprichi*, the prefrontal and postfrontal appear to have been widely separate (Kuhn, 1942).

Postorbital skull table. In *Cyclotosaurus*, the parietal and supratemporal are foreshortened with respect to other capitosauroids (e.g., *Tatrasuchus*). This is most pronounced in *C. robustus* in which the supratemporal is as wide as long, and the parietal is shorter than in all other taxa. In contrast, *C. buechneri* and *C. ebrachensis* have a relatively long parietal. The pineal foramen of *Cyclotosaurus* is smaller than in many other capitosauroids, but especially tiny in *C. ebrachensis* and *C. hemprichi*.

The occipital margin of the skull table is well concave, with the distance between the posteriormost points of the postparietal and tabular equaling the length of the postparietal. In *C. robustus*, medium-sized and large adults differ in that the latter have a more strongly concave occipital margin. In *C. posthumus*, the occipital margin varies more broadly with some specimens having much less concave margins (SMNS 50063, 51,102). The posterolateral tabular wing differs between the samples, from very broad and short in *C. ebrachensis* to slender and elongated in *C. hemprichi* (Fig. 5).

Cheek region. The most characteristic feature is the posteriorly closed otic fenestra, the morphology of which is quite consistent in the different *Cyclotosaurus* species. Unlike in *Tatrasuchus*, it is always firmly sutured, and the region differs from that of heylerosaurines in the elongated rather than round shape of the fenestra. The lateral excursion of the postorbital is always large but varies in outline especially in the Magstadt sample of *C. posthumus*. The two slender-headed taxa, *C. buechneri* and *C. ebrachensis*, have a markedly narrower squamosal and postorbital and the cheek does not make a lateral excursion. In both taxa, the quadratojugal is extremely slender and posteriorly tapers in the latter taxa where it does not reach the occipital margin of the cheek (Fig. 5b, c). In contrast, *C. hemprichi* has a much wider cheek with a quadratojugal twice as wide as that of other species.

Anterior palate. This region is consistent with that of *Parotosuchus* and early branching capitosauroids in many features, especially the large unpaired medial anterior opening (Fig. 4a, b; Schoch, 2008, 2018). This fenestra is

heart-shaped in *C. robustus* and is anteriorly constricted by a wide posterior premaxillary process (SMNS 5775, MB.Am.483). In the Norian specimens from Germany, this region is not well exposed. In *C. intermedius*, the opening is larger, with a much narrower tooth-bearing arcade of the premaxilla. In both *C. intermedius* and *C. naraserluki*, the anterior palatal opening has a gently rounded posterior margin and the posterior process of the premaxilla is slenderer. The choana forms a relatively short, broad oval opening in *C. robustus* (SMNS 833, 5775, MB.Am.483) and in *C. posthumus* and *C. naraserluki* it is round, whereas it is more elongate in *C. intermedius* and *C. hemprichi.*

Dentition. The maxillary teeth increase slightly in size in the region lateral to the choana up to the anterior level of the vomerine tusks; up to there, the bases of the maxillary teeth are transversely extended and very closely set. Further anteriorly, the premaxillary teeth are oval to round and larger, especially along the blunt anterior margin. There is space for 12–14 teeth on the premaxilla (*C. robustus*) and about 120 on the maxilla (*C. intermedius*).

The tusks of the vomer and palatine are closely placed and their bases are obliquely oval, with the palatine tusks being gently larger than those of the vomer (*C. robustus*) or equally sized (*C. intermedius*). The vomerine tooth row is continuous in *C. robustus* but interrupted by a wider gap in *C. intermedius* and *C. ebrachensis* and a narrower gap in *C. posthumus* (holotype of *C. mordax*). The vomerine tusks of *C. hemprichi* (MB.Am.507a, b) have a well-developed carina on the tip.

Kuhn (1932) first mentioned a shagreen of teeth in the palate of *C. ebrachensis*, which was later also reported on the vomer and palatine of *C. intermedius* (Sulej and Majer, 2005). In *C. robustus* (SMNS 5775), small teeth and irregular elevations are also present on the vomer, located between the choana and the countersunk fodina vomeralis.

Palatine and ectopterygoid. The palatine teeth posterior to the tusks are only very gently larger than the adjacent maxillary teeth in *C. robustus* (SMNS 833). The teeth of the palatine-ectopterygoid tooth row become continuously smaller posteriorly, their number of the ectopterygoid ones remaining unknown because of damage. In *C. posthumus*, at least 24 ectopterygoid teeth are present as contrasted by more than 40 in *C. intermedius* (Sulej and Majer, 2005).

Pterygoid. In all *Cyclotosaurus* species, the palatine ramus of the pterygoid is almost twice as wide at its anterolateral margin than where it merges with the basipterygoid and quadrate rami. The base of the cultriform process widens posteriorly and the interpterygoid vacuity has a symmetrical outline with a pointed posterior end. The proportions are similar in the holotype of *C. posthumus*, but there the posterior end is rounded. In ventral view, the whole lateral half of the palatine ramus is ornamented with reticulate ridges (Fig. 4e). The epipterygoid attachment is preserved as gently concave rounded structure on the dorsal side of the basipterygoid ramus in the type specimen of *C. posthumus*, covering about half the length of that ramus on the left side. On the right side, the basis of the epipterygoid is faintly preserved. The insula jugalis or ventral exposure of the jugal is well exposed as a triangular structure between the pterygoid and maxilla.

Parasphenoid. The cultriform process bears a tall ventral crest (*C. posthumus*) that merges posteriorly into the lateral margins of the deltoid basal plate, much like in *Eocyclotosaurus* (Schoch, 2000b). The pterygoid-parasphenoid suture is gently curved, giving a concave lateral margin of the basal plate. As in most late-branching capitosauroids, the pterygoid contacts the exoccipital by a distinct posteromedial process. Throughout the studied taxa, the ventral surface of the basal plate is entirely smooth and contains a sagittally oval depression.

Occiput. The occiput is well-preserved in the holotypes of *C. robustus* and *C. posthumus*, as well as one Magstadt specimen (SMNS 51102). In SMNS 12988 (*C. posthumus*), it is preserved in great detail (Fig. 7f), but this skull is more heavily affected by crushing. The most conspicuous differences to *C. intermedius* are that the occipital condyles are relatively far separated and the lateral portion of the quadratojugal is more extended. Furthermore, the paroccipital process has a stepped, L-shaped ventral margin and the posttemporal fenestra is taller than in both *C. intermedius* and the specimen from Thailand (Ingavat & Janvier, 1981). In the small specimen of *C. posthumus* (SMNS 51102), the crista obliqua forms a ridge, whereas in SMNS 12988, it appears as a tall sheet of bone, with its medial and lateral portions likely broken off. The stapes is not preserved in any specimen.

Mandible. The lower jaw is partially preserved in SMNS 51102 (*C. posthumus*) in which the labial side is exposed from the symphysis up to the hamate process; the postglenoid region is not preserved. The hamate process is somewhat taller than in *C. intermedius*, whereas the surangular is lower and the torus arcuatus forms a more restricted dorsal bulge. In the symphysis, sockets for a pair of large tusks and several dentary teeth are present, but no accessory teeth posterior to the tusks.

Pectoral girdle. The interclavicle is known from a range of specimens from the Stuttgart Formation (Feuerbacher Heide, Stuttgart-Bopser) and the Löwenstein Formation (Pfaffenhofen, Magstadt). The interclavicle is relatively

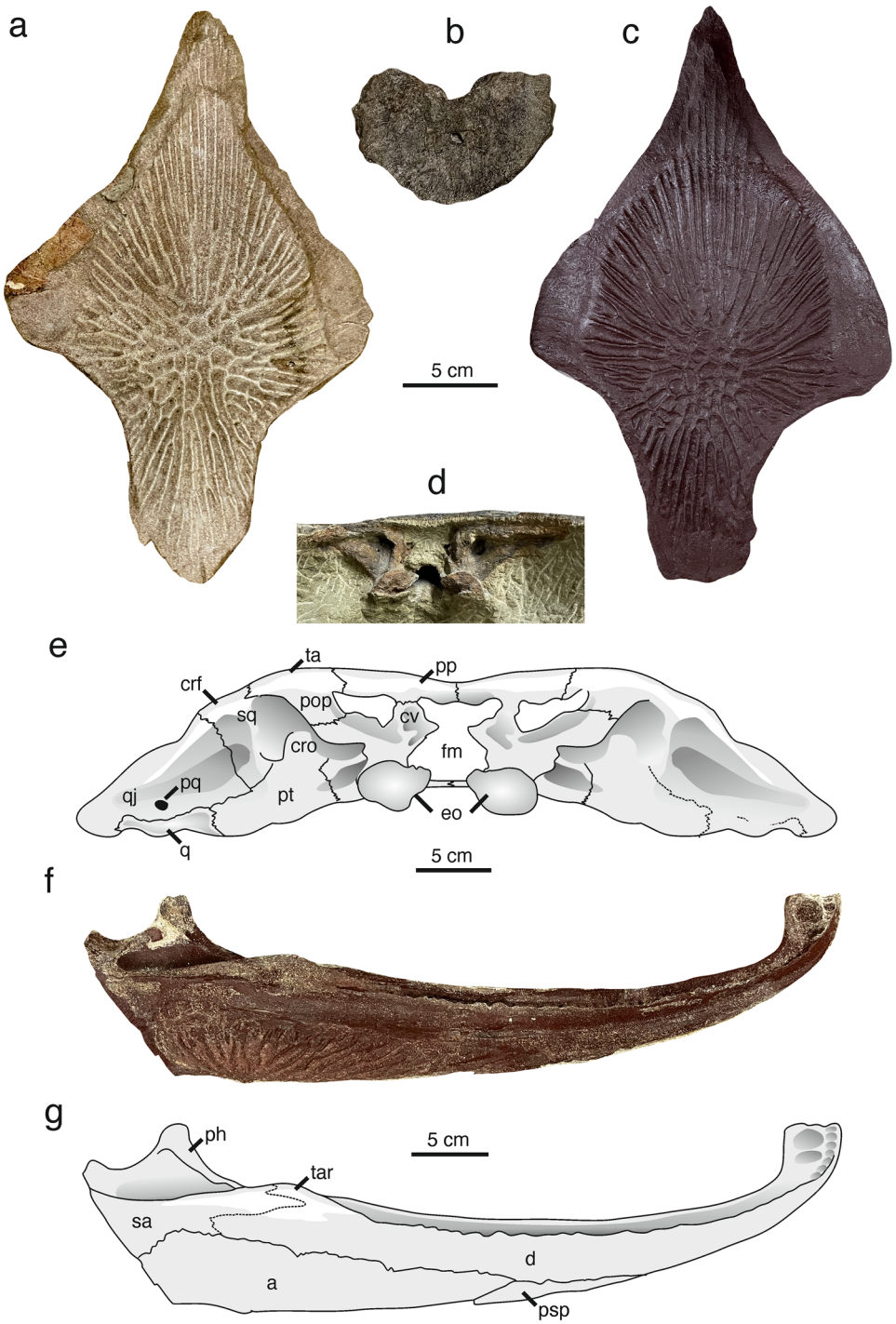

Fig. 7 Occiput, mandible and postcranium of *Cyclotosaurus*. **a, c** *C. posthumus*, interclavicle in ventral view (**a** SMNS 12195; **c** SMNS 50723); **b** *C. robustus*, intercentrum (SMNS 97136); **d,** *C. robustus*, partially exposed occiput in posterior view (GPIT PV 30086). **e** *C. posthumus*, occiput in posterior view (SMNS 12988); **f, g** *C. posthumus*, partial mandible in lateral view (SMNS 51102)

broad (width: length = 0.65) with the anterior and posterior portion of equal length. The outline is similar to that of *Mastodonsaurus cappelensis* (Schoch et al., 2023) and much wider than in *M. giganteus* (Schoch et al., 2024). The anterior end is pointed and slenderer than the posterior one, and it lacks the anteriorly extended "spoon" of *M. giganteus*. In *C. intermedius*, the posterior portion is slightly wider and the anterior part anteriorly not pointed. Consistent with the skull, the ornament is coarser in interclavicles of *C. posthumus* as compared to those of *C. robustus*. The clavicle is mostly present with fragments from Feuerbacher Heide.

Axial skeleton. Three intercentra from the type locality and horizon of *C. robustus* (SMNS 97136) are consistent with

capitosauroids. They are wedge-shaped and low, transversely twice as wide as tall, with a large rounded notochordal incisure on the dorsal margin. The parapophysis is pronounced. These intercentra are lower and dorsally more open than those of *Mastodonsaurus cappelenesis* (Schoch et al., 2023) and *Eryosuchus garjainovi* (Ochev, 1966). In contrast, the presacral intercentra of *C. hemprichi* first described by Jaekel (1914) form large, massive discs. They are amphicoelous with their anterior and posterior faces about equally concave and bear a small, dorsally located notochordal opening (MB.Am.568, 577). An intercentrum of the anterior tail region is dorsally open (MB.Am.573).

Discussion

Phylogenetic relationships

State of the art. The intrarelationships of capitosauroids were studied by Schoch (2000a, 2008, 2018), Damiani (2001), Steyer (2003), Maganuco (2009), Fortuny et al. (2011), Witzmann et al. (2016), and Marzola et al. (2017).

Our new phylogenetic analysis is based on a slightly extended data set to that of Marzola et al. (2017). We merged the terminal taxa *Cyclotosaurus posthumus* and *C. mordax* after we recognized that the extended sample from the coeval Magstadt locality includes specimens that are morphologically intermediate between the two types from Pfaffenhofen. We therefore kept the recoded data set of *C. posthumus* as a single OTU from the Löwenstein Formation in the matrix.

New characters. Four additional characters were added to the data set of Marzola et al. (2017).

(70) Quadratojugal. (0) Contributing to occipital margin of cheek, or (1) posteriorly tapering, ending well anterior to occipital margin of squamosal. (71) Parietal. (0) Square-shaped or less than twice as long as wide, or (1) at least twice as long as wide. (72) Length of naris. (0) Naris 50–55% orbit length, or (1) 60–100% orbit length. (73) Intercentrum. (0) Dorsally open, or (1) stereospondylous, forming closed disc.

Results. A single MPT was found requiring 112 steps. As the analysis focused on in-group relationships within the genus *Cyclotosaurus*, early diverging capitosauroids were not included (Fig. 8). The outgroup was *Rhineceps nyasaensis*, and the basalmost taxon of the ingroup is *Eryosuchus garjainovi*. The late diverging capitosauroids fall into two clades: one containing *Procyclotosaurus*, *Paracyclotosaurus*, the heylerosaurines and mastodonsaurids, and a second one encompassing the genera *Tatrasuchus* and *Cyclotosaurus* (Fig. 8).

Within the genus *Cyclotosaurus*, the following topology was obtained. (1) *Cyclotosaurus robustus* nests at the base of the *Cyclotosaurus* clade. (2) *C. buechneri* and *C. ebrachensis* are found to be sister taxa diverging before the Norian species. (3) The Norian clade falls into two subgroups, (a) *C. posthumus* and *C. naraserluki* and (b) *C. intermedius* and *C. hemprichi*. This tree departs from the previous topologies in a range of features, but it is consistent in that *C. robustus* forms the basalmost taxon and *C. buechneri* is an early diverging taxon nesting above *C. robustus*.

Evolutionary history of *Cyclotosaurus*

The single specimen of "*Cyclotosaurus*" *papilio* from the Upper Muschelkalk (Wepfer, 1923), which was destroyed during World War II, has more affinities with the genus *Eocyclotosaurus* and related taxa in the preserved margin of the skull and the tiny size of the orbits (Schoch & Moreno, 2024). The only other taxa with closed squamosal embayment are *Tatrasuchus kulczyckii* (Maryánska & Shishkin, 1996) and *T. wildi* (Schoch, 1997), but these have been found by recent analyses to nest below *Cyclotosaurus* (Marzola et al., 2017; Schoch, 2008; Schoch et al., 2023) (Fig. 8).

The incomplete skull of *Capitosaurus arenaceus* Münster, 1836 was reported by that author as having closed otic fenestrae. Meyer and Plieninger (1844) already mentioned that the posterior margin of the holotype skull was poorly preserved and that the closed fenestrae were only preserved as imprints. It remains unclear whether this resulted from damage after the first description, or the skull was indeed found in that poorly preserved state. In its present state, the specimen lacks the posterior margin and the otic region (Schoch, 2008). At any rate, *Capitosaurus* is consistent in most features with *Cyclotosaurus*, but the anteriorly narrowing preorbital region and the distinctly larger naris distinguish it clearly from *C. robustus*.

Thus, the stratigraphically oldest, diagnostic finds of the genus *Cyclotosaurus* are from the thick channel sandstones of the lower Stuttgart Formation (Schilfsandstein). The existence of two separate species in this time slice, *C. robustus* and *C. buechneri*, is not surprising when the distance between their occurrences is considered. The disarticulated sample from Mittelhausen in Thuringia is consistent with *C. robustus* in the shape of the postorbital skull and cheek, and stems from much smaller, juvenile specimens compared with the hypodigm.

More surprising is the finding that *C. buechneri* and *C. ebrachensis* form a clade, which is not only supported by the two characters included in the present analysis, but also their sharing of a uniquely slender preorbital region and a low ratio of the preorbital skull length relative to that of the whole skull (< 0.6). As the shared features are not entirely consistent with the small size of the two type specimens,

the two species are indeed be closely related. This suggests that during the late Carnian, at least two separate clades persisted, one ending up in *C. ebrachensis* and a second one in *C. posthumus* and related species.

The Norian species of *Cyclotosaurus* share a larger naris, a coarser dermal ornament, more laterally placed orbits, a narrower jugal, and dorsally extended "stereospondylous" intercentra. The Pfaffenhofen and Magstadt samples of *C. posthumus* exemplify considerable variation in the position of the orbit and the length of the preorbital region. The laterally extended cheek of *C. hemprichi* indicates a more voluminous adductor musculature and in concert with the small size of the orbit these may be simple size-related characters in this largest taxon.

Cyclotosaurus was present in the Norian of Greenland, Germany, Poland and Thailand. *Cyclotosaurus naraserluki* cannot be constrained any further than Norian. Corroy (1928) referred fragmentary capitosauroid bones from Ruaux in Lorraine (France) to *Cyclotosaurus*, all of which are indeterminate. Milner et al. (1996) tentatively referred fragmentary material from the Steinmergelkeuper (Norian) of Medernach (Luxembourg) to *Cyclotosaurus*. Witzmann and Gassner (2008) assigned large, amphicoelous intercentral discs from the Upper Triassic of the Algarve, Portugal to *Mastodonsaurus*- or *Cyclotosaurus hemprichi*-like capitosaurs. Recently, Konietzko-Meier et al. (2019) reported a humerus from the Rhaetian locality at Bonenburg as *Cyclotosaurus* sp., and hitherto undescribed small dermal bone fragments from the Rhaetian bonebed of the Stuttgart region are also consistent with skulls and clavicles of this genus; in all these cases, a referral to a particular species is impossible, but demonstrates the presence of capitosauroids well into Rhaetian time (Mujal et al., 2025).

Palaeoecology and habitats

Most stereospondyls were predominantly or fully aquatic throughout their lifespan (Schoch & Witzmann, 2011), which suggests that their abundance in stream and lake deposits indicates a relative proximity of their habitats. The palaeoenvironmental setting in which *Cyclotosaurus robustus* existed has recently become somewhat better understood (Mujal et al., 2025). According, fine- to medium-grained siliciclastic sediments filled the entire Central European Basin, with rhythmically changing facies patterns that were deposited in numerous single channels that are arranged in larger belts. Their geometry resembles that of chanthe Mississippi delta, with sandstone units formed in meandering channels and mudstone sequences forming intercalated lagoonal deposits (Wurster, 1968). The facies architecture of the Schilfsandstein shares features with the modern Ganga System of India (Shukla et al., 2010). The fluvial environments of the Lower Stuttgart Formation encompassed channel belts and floodplains that formed in a more humid but still seasonal climate compared with the Grabfeld and Weser formations (Franz & Barnasch, 2021; Franz et al., 2021). The modern Ganga plain is exposed to a similar mix of seasonal humid monsoonal and drought conditions (Shukla et al., 2010).

In the channel deposits of the Stuttgart Formation, S-SW-directed palaeocurrents transported sand grains and mica that originated in the Norwegian Caledonides. While most authors now accept a primarily fluvial origin of the sandstones, a limited marine influence cannot be ruled out (Franz & Barnasch, 2021) and therefore the setting may best be described as an extensive estuary (Shukla et al., 2010). This is in line with the palaeobotanical and palynological analyses of Franz et al. (2021), who found that the preserved macroplant sample at Feuerbacher Heide includes nearly 60% sphenophytes, 15% cycadophytes, 20% pteridophytes and pteridospermaphytes, 5% coniferophytes and a few lycophytes. Translated into macroplant eco-groups, the locality is dominated by river plants (60%) with substantial input from wet and dry lowland dwellers and a small but noticeable component of coastal inhabitants. The rivers probably collected remains of lowland plants during phases of flooding and transported them over some distance. The good preservation and abundance of sphenophytes (*Equisetites arenaceus*) at Feuerbacher Heide indicate that the riverbanks and floodplains were densely vegetated. The presence of plant species of the coastal eco-group suggests the relative neighbourhood of brackish water bodies or lagoons.

At Feuerbacher Heide, *Cyclotosaurus robustus* is more abundant and present with larger specimens than *Metoposaurus diagnosticus*. This suggests that the locality was closer to the habitat of *C. robustus* than that of *M. diagnosticus*. Because *C. robustus* is throughout larger than *M. diagnosticus* at this site, and its occurrence is restricted to channel deposits, *C. robustus* probably formed an apex predator in these late Carnian river systems. However, these fluviatile environments housed more than one large predator, probably as a result of habitat differentiation. For instance, the Jägerhaus quarry at Heilbronn yielded the two fragmentary specimens of *Hyperokynodon keuperinus* (Schoch, 2024) but did not produce any specimens of *Cyclotosaurus*. In turn, this large trematosaurid is absent in all the Schilfsandstein localities of the Stuttgart region. This suggests that the two large predators dwelled different environments or regions. Following Gehrmann and Aigner (2002), the Jägerhaus quarry encompasses a sequence of tidally influenced channel deposits. *Cyclotosaurus* and *Hyperokynodon* may thus have had different salinity tolerances, whereas *Metoposaurus* and *Gerrothorax* are both known for their occurrence in a wider range of palaeoenvironments, which suggests a higher plasticity in these two latter taxa (Moreno et al., 2024; Sanchez

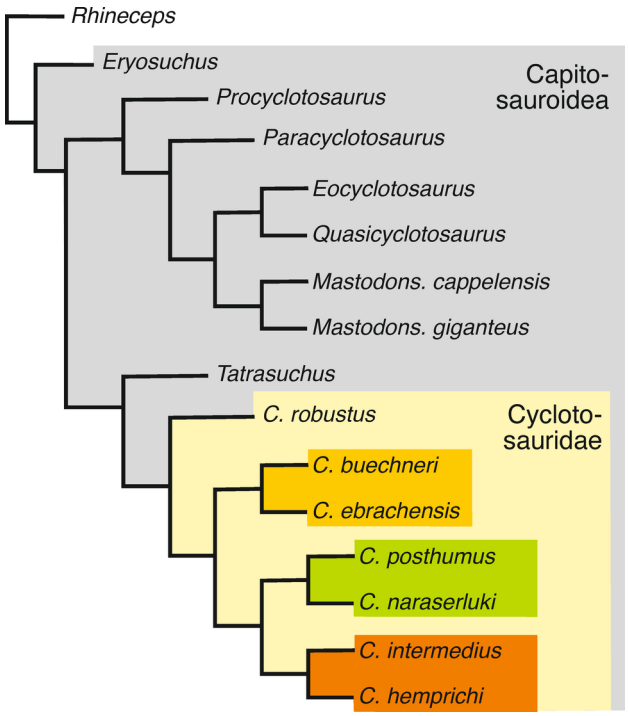

Fig. 8 Phylogeny of late-diverging capitosauroids with emphasis on the genus *Cyclotosaurus*

& Schoch, 2013; Schoch & Witzmann, 2012; Witzmann & Soler-Gijón, 2010).

The absence of *Cyclotosaurus* in early Carnian playa deposits of the Central European Basin might be explained by its preference of stream environments (Mujal et al., 2025). The single skull of *Capitosaurus arenaceus*, a potential early diverging *Cyclotosaurus* relative, was found in the marginal channel facies known as Benk Formation (a lateral siliciclastic variant of the Grabfeld Formation or Gipskeuper). In the extensive streams of the late Ladinian, *Mastodonsaurus giganteus* was the abundant apex predator, accompanied by the much smaller *Tatrasuchus wildi* in lakes and coastal environments of lagoons (Schoch & Moreno, 2024; Schoch et al., 2022, 2024).

During the latest Carnian and throughout the Norian, the river systems in the Central European Basin were predominantly aligned East and Southeast, with palaeocurrents indicating source areas in the Vindelician Highlands and Bohemian Mass (Beutler et al., 1999). The fluvial channels of the Weser and Löwenstein Formations were smaller and more locally restricted than those of the Stuttgart Formation (Beutler et al., 1999). *Cyclotosaurus ebrachensis* was collected in fine-grained sandstones that were probably deposited in the marginal areas of braided rivers (Frings, 1982). This locality also yielded a skull of *Metoposaurus diagnosticus* and one skull each of the phytosaurs *Ebrachosuchus neukami* and *Parasuchus angustifrons* (Kuhn, 1932, 1936). As in the much younger Pfaffenhofen locality, these taxa are associated with *Gerrothorax pulcherrimus* and an aetosaur (Berckhemer, 1938; Kuhn, 1936).

The deposits of Krasiejów and Woźniki (Patoka Member, Grabowa Formation) were recently suggested to have a younger age than formerly believed. Based on lithostratigraphy, Szulc et al. (2015) dated them into the earliest Norian which contradicts biostratigraphic data for Krasiejów and Woźniki (Sulej et al., 2018, 2021). At Krasiejów, lacustrine beds rich in bivalves, bony fishes and *Metoposaurus krasiejowensis* are intercalated within a fluvial sequence (Dzik and Sulej, 2007). *C. intermedius* is much rarer than *Metoposaurus* and co-occurs with the phytosaur *Paleorhinus* cf. *arenaceus*.

At Pfaffenhofen, the material of *C. posthumus* was found in the same horizons as the gracile gharial-like phytosaur *Mystriosuchus planirostris* (Hungerbühler, 1998). These massive white sandstones were deposited in small channels that formed episodically in a rather arid setting (Junghans et al., 1997). In other places, such small channels also yielded fully shelled stem-turtles and aetosaurs (Joyce et al., 2013; Schoch & Desojo, 2016) and occur in 1–10 km wide belts that were associated with short-lived ponds and small lakes (Brenner, 1973). Breccias evidence seasonal flooding events after heavy rainfall (Etzold & Schweizer, 2005). *Cyclotosaurus hemprichi* was found in the Norian Knollenmergel. Its palaeoenvironment was interpreted as freshwater-dominated, with shallow swamps that were possibly situated in a marine delta (Jaekel, 1914).

The Carnian–Norian occurrences of *Cyclotosaurus* were evidently bound to river channels and overlapped with those of gracile gharial-like phytosaurs (*Ebrachosuchus*, *Parasuchus*, *Paleorhinus*, *Mystriosuchus*). *Cyclotosaurus* did not overlap with the larger and heavier *Nicrosaurus kapfi*, which dwelled different environments (Kimmig & Arp, 2010).

The co-occurrences of *Cyclotosaurus* with both metoposaurs and phytosaurs in riverine systems suggests rich ecosystems that allowed for support of multiple predator species. This niche partitioning has recently also been proposed based on the basis of skull and jaw shape, separating the gharial-like phytosaurs as fish specialists from the crocodile-like *Cyclotosaurus* as generalists and the facultative preying metoposaurs (Rinehart et al., 2023).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12542-025-00729-w.

Acknowledgements We thank Fabian Mohl, Anita Roth-Nebelsick and Günter Schweigert for helpful advice and discussions and Oliver Rauhut for providing photographs of BSM 1931X1. Finally, we are grateful to Jean-Sébastien Steyer and Tomas Sulej for their thoughtful reviews.

Funding Open Access funding enabled and organized by Projekt DEAL.

Data availability The data associated with this article are provided in the Supplementary file.

Declarations

Conflict of interest The authors declare that they have no competing interests.

References

Berckhemer, F. (1938). Wirbeltierfunde aus dem Stubensandstein des Strombergs. *Aus der Heimat, 55*, 188–198.

Beutler, G., Hauschke, N., & Nitsch, E. (1999). Faziesentwicklung des Keupers im Germanischen Becken. In N. Hauschke & V. Wilde (Eds.), *Trias. Eine ganz andere Welt* (pp. 129–174). Pfeil.

Brenner, K. (1973). Stratigraphie und Paläogeographie des Oberen Mittelkeupers in Südwest-Deutschland. *Arbeiten Aus Dem Institut Für Geologie und Paläontologie der Universität Stuttgart Neue Folge, 68*, 101–222.

Corroy, G. (1928). Les vertébrés du Trias de Lorraine et le Trias Lorrain. *Annales De Paléontologie, 17*, 81–136.

Damiani, R. J. (2001). A systematic revision and phylogenetic analysis of Triassic mastodonsauroids (Temnospondyli, Stereospondyli). *Zoological Journal of the Linnean Society London, 133*, 379–482.

Damiani, R. J. (2008). A giant skull of the temnospondyl *Xenotosuchus africanus* from the Middle Triassic of South Africa and its ontogenetic implications. *Acta Palaeontologica Polonica, 53*, 75–84.

Damiani, R. J., & Steyer, J. S. (2005). A giant brachyopoid temnospondyl from the Upper Triassic or Lower Jurassic of Lesotho. *Bulletin De La Société Geologique De France, 176*, 243–248.

Dzik, J., & Sulej, T. (2007). A review of the early Late Triassic Krasiejów biota from Silesia, Poland. *Palaeontologia Polonica, 64*, 3–27.

Dzik, J., Sulej, T., & Niedźwiedzki, G. (2008). A dicynodont−theropod association in the latest Triassic of Poland. *Acta Palaeontologica Polonica, 53*, 733–738.

Etzold, A., & Schweizer, V. (2005). Der Keuper in Baden-Württemberg. In *Stratigraphie von Deutschland IV. Keuper*, ed. *Deutsche Stratigraphische Kommission, Courier Forschungsinstitut Senckenberg, 253*, 215–258.

Fortuny, J., Galobart, A., & de Santisteban, C. (2011). A new capitosaur from the Middle Triassic of Spain and the relationships within the Capitosauria. *Acta Palaeontologica Polonica, 56*, 553–566.

Fraas, E. (1889). Die Labyrinthodonten der Schwäbischen Trias. *Palaeontographica, 36*, 1–158.

Fraas, E. (1913). Neue Labyrinthodonten aus der schwäbischen Trias. *Palaeontographica, 60*, 275–294.

Franz, M., & Barnasch, J. (2021). Der Keuper im zentralen Germanischen Becken. In N. Hauschke & V. Wilde (Eds.), *Trias. Eine ganz andere Welt* (pp. 83–108). Pfeil.

Franz, M., Kustatscher, E., Heunisch, C., Niegel, S., & Röhling, H. G. (2021). The Schilfsandstein and its flora; arguments for a humid mid-Carnian episode? *Journal of the Geological Society, 176*, 133–148.

Frings, U. (1982). Sedimentologische Untersuchungen im oberen Blasensandstein in Nürnberg. *Geologische Blätter Für Nordost-Bayern und Angrenzende Gebiete, 32*, 13–34.

Fröbisch, N. B., Olori, J., Schoch, R. R., & Witzmann, F. (2010). Amphibian development in the fossil record. *Seminars in Cell and Developmental Biology, 21*, 424–431.

Gehrmann, O., & Aigner, T. (2002). The Schilfsandstein (Upper Triassic) near Heilbronn (SW-Germany): Evidence for tidal influence. *Neues Jahrbuch Für Geologie und Paläontologie Abhandlungen, 223*, 377–403.

Goloboff, P. A., & Morales, M. E. (2023). TNT version 1.6, with a graphical interface for MacOS and Linux, including new routines in parallel. *Cladistics, 39*, 144–153.

Hellrung, H. (2003). *Gerrothorax pustuloglomeratus*, ein Temnospondyle (Amphibia) mit knöcherner Branchialkammer aus dem Unteren Keuper von Kupferzell (Süddeutschland). *Stuttgarter Beiträge Zur Naturkunde B, 330*, 1–130.

Hungerbühler, A. (1998). Taphonomy of the prosauropod dinosaur *Sellosaurus*, and its implications for carnivore faunas and feeding habits in the Late Triassic. *Palaeogeography, Palaeoclimatology, Palaeoecology, 143*, 1–29.

Ingavat, R., & Janvier, P. (1981). *Cyclotosaurus* cf. *posthumus* Fraas (Capitosauridae, Stereospondyli) from the Huai Hin Lat Formation (Upper Triassic), northeastern Thailand, with a note on capitosaurid biogeography. *Geobios, 14*, 711–725.

Jaeger, G. F. (1827). *Über die Pflanzenversteinerungen welche in dem Bausandstein von Stuttgart vorkommen*. Metzler.

Jaeger, G. F. (1828). *Über die fossile Reptilien welche in Württemberg aufgefunden worden sind*. Metzler.

Jaekel, O. (1914). Über die Wirbeltierfunde der oberen Trias von Halberstadt. *Paläontologische Zeitschrift, 1*, 155–215.

Joyce, W., Schoch, R. R., & Lyson, T. (2013). The girdles of the oldest fossil turtle, *Proterochersis robusta*, and the age of the turtle crown. *BMC Evolutionary Biology, 13*, 266.

Junghans, W. D., Aigner, T., & Ricken, W. (1997). Fluviatile Architektur des Mittleren Stubensandsteins am südwestlichen Schönbuch (Trias, Baden-Württemberg). *Neues Jahrbuch Für Geologie und Paläontologie Abhandlungen, 204*, 285–320.

Kamphausen, D. (1994). Eine Schädelasymmetrie bei *Cyclotosaurus* Fraas (Amphibia, Stegocephalia) aus dem Stubensandstein (Trias) von Württemberg (SW-Deutschland). *Stuttgarter Beiträge Zur Naturkunde, Serie B, 210*, 1–12.

Kear, B. P., Poropat, S. F., & Bazzi, M. (2015). Late Triassic capitosaurian remains from Svalbard and the palaeobiogeographical context of Scandinavian Arctic temnospondyls. In B. P. Kear, J. Lindgren, J. H. Hurum, J. Milàn, & V. Vajda (Eds.), *Mesozoic biotas of Scandinavia and its arctic territories* (Vol. 434, pp. 113–126). Geological Society of London Special Publication.

Kelber, K. P., & Hansch, W. (1995). Keuperpflanzen. Die Enträtselung einer über 200 Millionen Jahre alten Flora. *Museo, 11*, 1–157.

Kimmig, J., & Arp, G. (2010). Phytosaur remains from the Norian Arnstadt Formation (Leine Valley, Germany), with reference to European phytosaur habitats. *Palaeodiversity, 3*, 215–224.

Konietzko-Meier, D., Werner, J. D., Wintrich, T., & Sander, P. M. (2019). A large temnospondyl humerus from the Rhaetian (Late Triassic) of Bonenburg (Westphalia, Germany) and its implications for temnospondyl extinction. *Journal of Iberian Geology, 45*, 287–300.

Kuhn, O. (1932). Labyrinthodonten und Parasuchier aus dem mittleren Keuper von Ebrach in Oberfranken. *Neues Jahrbuch Für Mineralogie, Geologie und Paläontologie B, Beilageband, 69*, 94–143.

Kuhn, O. (1936). Weitere Parasuchier und Labyrinthodonten aus dem Blasensandstein des mittleren Keuper von Ebrach. *Palaeontographica A, 83*, 61–98.

Kuhn, O. (1939). Beiträge zur Keuperfauna von Halberstadt. *Paläontologische Zeitschrift, 21*, 258–286.

Kuhn, O. (1942). Über *Cyclotosaurus hemprichi* Kuhn und einige weitere Tetrapodenreste aus dem Keuper von Halberstadt. *Beiträge Zur Geologie Von Thüringen, 6*, 181–197.

Maganuco, S., Steyer, J. S., Pasini, G., Boulay, M., Lorrain, S., Bénéteau, A., & Auditore, M. (2009). An exquisite specimen of *Edingerella madagascariensis* (Temnospondyli) from the Lower Triassic of NW Madagascar; cranial anatomy, phylogeny, and restorations. *Memorie della Società Italiana di Scienze Naturale e Del Museo Civico di Storia Naturale di Milano, 36*, 1–72.

Maryánska, T., & Shishkin, M. A. (1996). New cyclotosaurid (Amphibia: Temnospondyli) from the Middle Triassic of Poland and some problems of interrelationships of capitosauroids. *Prace Muzeum Ziemi, 43*, 53–83.

Marzola, M., Mateus, O., Shubin, N. H., & Clemmensen, L. B. (2017). Cyclotosaurus naraserluki, sp. nov., a new Late Triassic cyclotosaurid (Amphibia, Temnospondyli) from the Fleming Fjord Formation of the Jameson Land Basin (East Greenland). *Journal of Vertebrate Paleontology, 73*, e1303501.

Meyer, H. V. (1842). Labyrinthodonten−Genera. *Neues Jahrbuch Für Mineralogie, Geographie, Geologie, Paläontologie, 1842*, 301–304.

Meyer, H. V., & Plieninger, T. (1844). *Beiträge zur Paläontologie Württemberg's, enthaltend die fossilen Wirbeltierreste aus den Triasgebilden mit besonderer Rücksicht auf die Labyrinthodonten des Keupers*. Schweizerbart.

Milner, A. R., Duffin, C., & Delsate, D. (1996). Plagiosaurid and capitosaurid amphibian material from the Late Triassic of Medernach, Grand-Duchy of Luxembourg: Preliminary note: Jurassic-Triassic vertebrates. *Bulletin De La Société Belge De Géologie, 104*, 43–53.

Moreno, R., Chakravorti, S., Cooper, S. L. A., & Schoch, R. R. (2024). *Unexpected temnospondyl diversity in the early Carnian Grabfeld Formation and the palaeogeography of metoposaurids*. Fossil Record.

Mujal, E., Sues, H. D., Moreno, R., Schaeffer, J., Sobral, G., Chakravorti, S., Spiekman, S. N. F., and Schoch, R. R. 2025. Triassic terrestrial tetrapod faunas of the Central European Basin, their stratigraphical distribution, and their palaeoenvironments. *Earth-Science Reviews*.

Münster, G. G. (1836). Briefliche Mittheilungen. *Neues Jahrbuch Für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, 1836*, 580–583.

Ochev, V. I. (1966). *Systematics and phylogeny of capitosauroid labyrinthodonts* (p. 184). Saratov (Saratov State University Press).

Quenstedt, F. A. (1850). *Die Mastodonsaurier aus dem grünen Keupersandstein Württemberg's sind Batrachier*. Tübingen: Laupp and Siebeck.

Rinehart, L. F., Lucas, S. G., Hunt, A. P., & Heckert, A. B. 2023. Skull and jaw shape as indicators of trophic guild association in temnospondyl amphibians and other aquatic predators. In: S. G. Lucas, G. S. Morgan, A. P. Hunt, & A. J. Lichtig (eds.). Fossil Record 9, 94, 585–609.

Sanchez, S., & Schoch, R. R. (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.

Säve-Söderbergh, G. (1935). On the dermal bones of the head in labyrinthodont stegocephalians and primitive reptilia with special reference to Eotriassic stegocephalians from East Greenland. *Meddelelser Om Grønland, 98*, 1–211.

Schoch R. R. 2015. Amphibien und Chroniosuchier des Lettenkeupers. In: Hagdorn, H., R.R. Schoch, and G. Schweigert (Eds) *Der Lettenkeuper—ein Fenster in die Zeit vor den Dinosauriern. Palaeodiversity* Sonderband 11: 203–230

Schoch, R. R. (1997). A new capitosaurid amphibian from the Upper Lettenkeuper (Ladinian) of Kupferzell (Southwestern Germany). *Neues Jahrbuch Für Geologie und Paläontologie, Abhandlungen, 203*, 239–272.

Schoch, R. R. (2000a). The origin and intrarelationships of capitosaurid amphibians. *Palaeontology, 43*, 705–727.

Schoch, R. R. (2000b). The status and osteology of two new cyclotosaurid amphibians from the Upper Moenkopi Formation of Arizona (Amphibia: Temnospondyli; Middle Triassic). *Neues Jahrbuch Für Geologie und Paläontologie Abhandlungen, 216*, 387–411.

Schoch, R. R. (2008). The Capitosauria (Amphibia): Characters, phylogeny, and stratigraphy. *Palaeodiversity, 1*, 189–226.

Schoch, R. R. (2018). The temnospondyl *Parotosuchus nasutus* (v. Meyer, 1858) from the Early Triassic Middle Buntsandstein of Germany. *Palaeodiversity, 11*, 107–126.

Schoch, R. R. (2024). Cranial morphology and phylogenetic relationships of the Late Triassic temnospondyl *Hyperokynodon keuperinus*. *Neues Jahrbuch Für Geologie und Paläontologie Abhandlungen, 310*, 147–160.

Schoch, R. R., & Desojo, J. B. (2016). Cranial anatomy of the large aetosaur Paratypothorax andressorum Long & Ballew, 1985, from the Upper Triassic of Germany and its bearing on aetosaur phylogeny. *Neues Jahrbuch Für Geologie und Paläontologie Abhandlungen, 279*, 73–95.

Schoch, R. R., & Milner, A. R. (2000). Stereospondyli. In P. Wellnhofer (Ed.), *Handbuch der Paläoherpetologie, 3B*. Pfeil.

Schoch, R. R., Milner, A. R., Witzmann, F., & Mujal, E. (2023). A revision of *Mastodonsaurus* from the Anisian of Germany, and the evolutionary history of mastodonsaurid temnospondyls. *Neues Jahrbuch Für Geologie und Paläontologie Abhandlungen, 309*, 123–140.

Schoch, R. R., & Moreno, R. (2024). Synopsis on the temnospondyls from the German Triassic. *Palaeodiversity, 17*, 9–48.

Schoch, R. R., Seegis, D., & Mujal, E. (2022). The Middle Triassic vertebrate deposits of Kupferzell (Germany): Palaeoenvironmental evolution of complex ecosystems. *Palaeogeography, Palaeoclimatology, Palaeoecology, 603*, 111181.

Schoch, R. R., & Witzmann, F. (2011). Bystrow's Paradox: Gills, fossils, and the fish-to-tetrapod transition. *Acta Zoologica, 92*, 251–265.

Schoch, R. R., & Witzmann, F. (2012). Cranial morphology of the plagiosaurid *Gerrothorax pulcherrimus* as an extreme example of evolutionary stasis. *Lethaia, 45*, 371–385.

Schoch, R. R., & Witzmann, F. (2024). The evolution of larvae in temnospondyls and the stepwise origin of metamorphosis. *Biological Reviews, 99*, 1613–1637.

Schoch, R. R., Witzmann, F., Moreno, R., Werneburg, R., & Mujal, E. (2024). Growing giants: Ontogeny and life history of the temnospondyl *Mastodonsaurus giganteus* (Stereospondyli) from the Middle Triassic of Germany. *Fossil Record, 27*, 401–422.

Shishkin, M. A. (1964). Podotryad stereospondyli. In Y. A. Orlov (Ed.), *Osnovy Paleontologij* (pp. 83–122). Moscow: Nauka.

Shukla, U. K., Bachmann, G. H., & Singh, I. B. (2010). Facies architecture of the Stuttgart Formation (Schilfsandstein, Upper Triassic), central Germany, and its comparison with modern Ganga System, India. *Palaeogeography, Palaeoclimatology, Palaeoecology, 297*, 110–128.

Steyer, J. S. (2003). A revision of the Early Triassic "capitosaurs" (Stegocephali, Stereospondyli) from Madagascar, with remarks on their comparative ontogeny. *Journal of Vertebrate Paleontology, 23*, 544–555.

Sulej, T., Bronowicz, R., Talanda, M., & Niedźwiedzki, G. (2011). A new dicynodont-archosaur assemblage from the Late Triassic (Carnian) of Poland. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh, 101*, 261–269.

Sulej, T., Kowalski, J., Bodzioch, A., & Hara, E. (2021). Eucynodont teeth from the Late Triassic of Krasiejów, Southern Poland. *Historical Biology, 33*, 3633–3640.

Sulej, T., & Majer, D. (2005). The temnospondyl amphibian *Cyclotosaurus* from the Upper Triassic of Poland. *Palaeontology, 48*, 157–170.

Sulej, T., Niedźwiedzki, G., Tałanda, M., Dróżdż, D., & Hara, E. (2018). A new early Late Triassic non-mammaliaform eucynodont from Poland. *Historical Biology, 32*, 80–92.

Szulc, J., Racki, G., Jewula, K., & Srodon, 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.

Warren, A. A. (2000). Secondary aquatic temnospondyls of the Upper Permian and Mesozoic: The stereospondyls. In R. L. Carroll & H. Heatwole (Eds.), *Amphibian Biology Paleontology: The evolutionary history of amphibians* (Vol. 4, pp. 1123–1149). Chipping Norton: Surrey Beattey.

Wepfer, E. (1923). *Cyclotosaurus papilio* n. sp. aus der Grenzregion Muschelkalk-Lettenkohle des nördlichen Baden, ein Beitrag zur Kenntnis des Stegocephalen-Hinterhauptes. *Mitteilungen der Badischen geologischen Landesanstalt, 9*, 367–390.

Werneburg, R. (1990). Metoposaurier (Amphibia) aus dem Unteren Keuper (Obertrias) von Thüringen. *Veröffentlichungen des Naturhistorischen Museums Schleusingen, 5*, 31–38.

Wiman, C. (1914). Über die Stegocephalen aus der Trias Spitzbergens. *Bulletin of the Geological Institute University of Upsala, 13*, 1–34.

Witzmann, F., & Gassner, T. (2008). Metoposaurid and mastodonsaurid stereospondyls from the Triassic-Jurassic boundary of Portugal. *Alcheringa, 32*, 37–51.

Witzmann, F., Sachs, S., & Nyhuis, C. J. (2016). A new species of *Cyclotosaurus* (Stereospondyli, Capitosauria) from the Late Triassic of Bielefeld, NW Germany, and the intrarelationships of the genus. *Fossil Record, 19*, 83–100.

Witzmann, F., & Soler-Gijón, R. (2010). The bone histology of osteoderms in temnospondyl amphibians and in the chroniosuchian *Bystrowiella*. *Acta Zoologica, 91*, 96–114.

Wurster, P. (1968). Paläogeographie der deutschen Trias und die paläogegographische Orientierung der Lettenkohle in Südwestdeutschland. *Ecologae Geologicae Helvetiae, 61*, 157–166.

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.