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# A new species of *Cyclotosaurus* (Stereospondyli, Capitosauria) from the Late Triassic of Bielefeld, NW Germany, and the intrarelationships of the genus

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**Abstract.** A nearly complete dermal skull roof of a capitosaur stereospondyl with closed otic fenestrae from the middle Carnian Stuttgart Formation (Late Triassic) of Bielefeld-Sieker (NW Germany) is described. The specimen is assigned to the genus *Cyclotosaurus* based on the limited contribution of the frontal to the orbital margin via narrow lateral processes. A new species, *Cyclotosaurus buechneri* sp. nov., is erected based upon the following unique combination of characters: (1) the interorbital distance is short so that the orbitae are medially placed (shared with *C. robustus*); (2) the region lateral to the orbitae is only slightly broader than the orbitae (shared with *C. posthumus*, *C. ebrachensis*, *C. intermedius*, and *C. mordax*); (3) the postorbital region is slender (shared with *C. ebrachensis*); (4) the preorbital projection of the jugal is shorter than half the length of the snout (shared with *C. mordax*, *C. ebrachensis*, *C. intermedius*, *C. posthumus*, and *C. hemprichi*). A phylogenetic analysis of seven *Cyclotosaurus species*, including *C. buechneri*, and eight further capitosaur taxa with the Rhinesuchidae as an outgroup finds a monophyletic *Cyclotosaurus*. In accordance with its stratigraphic occurrence, *C. buechneri* nests at its base but is more derived than *C. robustus*. Among the more derived *Cyclotosaurus* species, *C. ebrachensis* and *C. intermedius*, as well as *C. posthumus* and *C. hemprichi*, form sister groups, respectively. However, the phylogenetic position of *C. mordax* with respect to both groups remains unresolved. In the phylogenetic analysis presented here, *Cyclotosaurus* is the sister group of the Heylerosaurinae (*Eocyclotosaurus* + *Quasicyclotosaurus*). *Cyclotosaurus buechneri* represents the only unequivocal evidence of *Cyclotosaurus* (and of a cyclotosaur in general) in northern Germany.

## 1 Introduction

The largest amphibians in earth's history can be found among the capitosaur stereospondyls, a group of temnospondyls that reached body lengths of more than 5 m with large skulls and heavily ossified postcranial skeletons. Throughout the Triassic period, these superficially crocodile-like aquatic predators dominated the limnic and fluviatile ecosystems but sometimes also occurred in lagoonal and coastal marine strata (Schoch and Milner, 2000; Damiani, 2001; Steyer, 2003; Schoch, 2008, 2014; Maganuco et al., 2009; Fortuny et al., 2011, 2012; Sidor et al., 2014; Kear et al., 2015; ; Marcé-Nogué et al., 2015). A cranial feature, present in some capitosaurs, is the posteriorly closed squamosal embayments (or "otic notches"), called the otic fenestrae. Capitosaurs bearing this character are often informally called "cyclotosaurs", literally meaning "round-ear lizards", although recent phylogenetic analyses suggest that this character may not be an indicator of a closer phylogenetic relationship (Damiani, 2001; Schoch, 2008; Fortuny et al., 2011; Sidor et al., 2014). In Triassic strata of Germany, cyclotosaurs with closed otic
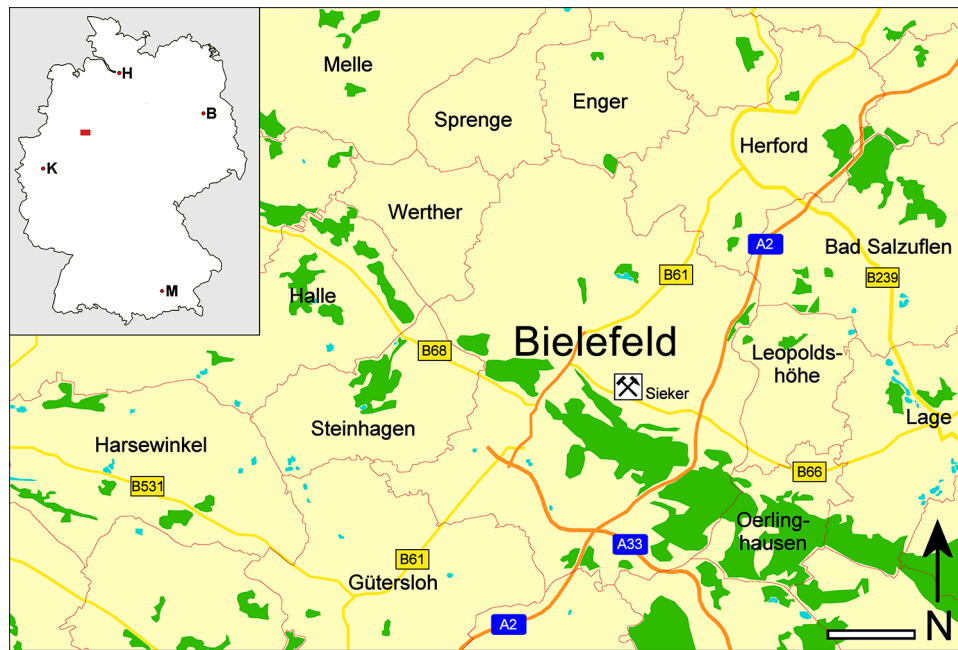
**Figure 1.** Geographical setting of the fossil locality of Bielefeld-Sieker. Abbreviations: B, Berlin; H, Hamburg; K, Köln (Cologne); M, München (Munich). The scale bar is equal to 5 km.

fenestrae are represented by an isolated find of *Eocyclotosaurus lehmani* (*E. woschmidti*) from the Upper Buntsandstein (Anisian) of Baden-Württemberg (Ortlam, 1970) as well as different species of the genus *Cyclotosaurus,* known from the middle Carnian (?upper Ladinian) to the late Norian (Schoch and Milner, 2000). *Cyclotosaurus* is the best documented and most species-rich cyclotosaur genus. Its first remains were found more than 150 years ago in the southern German state of Württemberg. Furthermore, *Cyclotosaurus* is among the earliest temnospondyl genera ever described (Meyer and Plieninger, 1844; Quenstedt, 1850). Different species of *Cyclotosaurus* were later reported from Germany (Fraas, 1913; Kuhn, 1932, 1939, 1942), Poland (Sulej and Majer, 2005), Greenland (Jenkins et al., 1994; Sulej et al., 2014), Spitsbergen (Kear et al., 2015), and Thailand (Ingavat and Janvier, 1981). In Germany, *Cyclotosaurus* specimens are thus far known from the southern states of Baden-Württemberg and Bavaria, and an isolated finding was reported from central Germany (Saxony-Anhalt) (Jaekel, 1914; Kuhn, 1939, 1942). Remains of cyclotosaurs were almost unknown from northern Germany, with the exception of some dermal bones ("armor plates") from Keuperian sandstone layers (referrable to the Late Triassic Stuttgart Formation; Duchrow, 1984) north of the city of Melle (approximately 20 km north of Bielefeld, Fig. 1), briefly mentioned by Römer (1857, p. 682). These rare finds were later mentioned by von der Marck (1892) and Dienemann (1928, 1939). Römer (1857) assigned these specimens to "*Mastodonsaurus robustus*" (*Cyclotosaurus robustus*) based on similarities to findings of "*Mastodonsaurus robustus*" from the Stuttgart

Formation (Schilfsandstein) of Württemberg described by Quenstedt (1850). Unfortunately, the specimens from Melle were illustrated by neither Römer (1857) nor by von der Marck (1892) and Dienemann (1928, 1939) and it can thus not be stated whether they belonged to the skull or the dermal pectoral girdle. They were part of the *Oberbergrat* Jugler collection and are believed to be lost.

More than 40 years ago the skull of a cyclotosaur was discovered by Dr. Martin Büchner, then director of the Museum of Natural History in Bielefeld, during an excursion of the natural history society of Bielefeld (Naturwissenschaftlicher Verein für Bielefeld und Umgebung) in the Pape quarry in the Teutoburg Forest, which at that time served as a landfill for excavated soil. The sandstones that contained the skull originated from a construction site for a new bank building in Bielefeld-Sieker (Fig. 1). The find was brought to the Staatliches Museum für Naturkunde in Stuttgart, Germany, where it was prepared. It became part of the collection of the Museum of Natural History in Bielefeld and was assigned to *Cyclotosaurus robustus*. The skull became renowned locally in Bielefeld and surrounding areas through several media articles. A cast of the "ancient amphibian from Bielefeld" (*Bielefelder Urlurch*) is on display in a glass showcase mounted in the floor of an underground station in Bielefeld. In spite of this, the skull has never been described scientifically, with only brief mention in the scientific literature. In the *Handbook of Paleoherpetology*, Schoch and Milner (2000, p. 154) mentioned that *C. robustus* had been found in Bielefeld in addition to southern Germany, but they did not explicitly refer to the skull under study and neither de-

**Figure 2.** *Cyclotosaurus buechneri* sp. nov. from the middle Carnian Stuttgart Formation (Late Triassic) of Bielefeld, NW Germany, holotype and only specimen (Namu ES/k 36053).

scribed nor illustrated it. Büchner (2008a, b) mentioned and illustrated the skull and referred it to as *Cyclotosaurus robustus*. In this study, we provide a description of the specimen and a phylogenetic analysis of the genus *Cyclotosaurus* based largely on the data matrix of Damiani (2001) and Schoch (2008). Our analysis includes the Bielefeld skull and – for the first time – all valid species of *Cyclotosaurus*. Because of the unique combination of characters present in the Bielefeld specimen, we erect a new species, *Cyclotosaurus buechneri* sp. nov.

## 2 Material

The specimen described herein is an almost complete skull roof in dorsal view. It shows a well-preserved dermal sculpture and is embedded in sandstone with the palate and occiput obscured (Fig. 2). The mandible and postcranial remains are unknown. The sutures between the skull roofing elements can be traced on the dorsal side of the skull, whereas, in the posterolateral part, the sutures of the ventral surface of the skull roof are preserved as imprints on the surface of the steinkern, i.e., consolidated sediment matrix that remained as a cast of the inner surface of the dermal skull roof after the

original bones were lost. The specimen is housed in the collection of the Museum of Natural History in Bielefeld, Germany (inventory number Namu[1] ES/k 36053), and has so far been tentatively designated *Cyclotosaurus robustus*.

For comparison, we studied the following *Cyclotosaurus* specimens housed in the Staatliches Museum für Naturkunde Stuttgart, Germany: *C. robustus* (SMNS[2] 4139, 4935, 5775), *C. mordax* (SMNS 13014, 50059, 50063, 51102, 51426, 55112), and *C. posthumus* (SMNS 12988).

## 3 Locality and geological setting

The stereospondyl skull described in this study was found in September 1975 within the sandstone of the former excavation pit for a bank building in Bielefeld-Sieker (N 0′31.32″52° E 34′1.68″8°), North Rhine-Westphalia, northwestern Germany (Fig. 1). An approximately 10 m thick succession of clay-rich sandstone and intercalated argillaceous marlstone of the Carnian (Late Triassic) Stuttgart Formation (Büchner, 1975; Mestwerdt and Burre, 1981) was temporarily exposed at this locality. The sandstone is especially rich in fragments of *Equisetites arenaceus*. These plant fossils are a characteristic feature of the sandstone facies of the Stuttgart Formation in general and are the reason for its name "Schilfsandstein" (literally "sandstone with reed") within the classical literature (e.g., Jaeger, 1827). In some cases, the overall bright-grey sandstone shows spots of intense green coloration in this locality and, in contrast to the marlstone, it contains only minor amounts of pyrite.

Associated sediments of the Stuttgart Formation are interpreted as predominantly fluviatile and lacustrine (Nitsch, 2005). Thick accumulations of sandstones are regarded as channel fills, which might apply for the former outcrop in Bielefeld-Sieker as well. In addition to the occurrence in Germany, a similar, time-equivalent facies is present in Poland ("piaskowiec trzcinowy") and northern France ("grès à roseaux") (Nitsch, 2008).

## 4 Systematic paleontology

This published work and the nomenclatural acts it contains have been registered in Zoobank: http://zoobank.org/References/076EFB19-198E-4A0C-B399-A99643EF5A11.

### Temnospondyli von Zittel, 1887–1890

### Stereospondyli von Zittel, 1887–1890

Capitosauroidea Säve-Söderbergh, 1935, emend. Schoch and Milner, 2000

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[1]Namu, Naturkunde-Museum Bielefeld, Germany.

[2]SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany.

### *Cyclotosaurus* Fraas, 1889

*Hercynosaurus* Jaekel, 1914
*Hemprichisaurus* Kuhn, 1939
Type species: *Cyclotosaurus robustus* (Meyer and Plieninger, 1844)

Diagnosis (emended after Schoch and Milner, 2000): (1) Frontals with broad descending processes that connect with the roof of the broad sphenethmoid; (2) short choana of round to ovate outline; (3) vomerine plate short; (4) broad triangular area at the base of the cultriform process merging continuously into the cultriform crest; (5) basal plate of parasphenoid delta shaped with elongated basicranial suture (shared with Mastodonsauridae); (6) squamosal embayment closed to otic fenestra (shared with *Eocyclotosaurus*, *Quasicyclotosaurus*, *Kupferzellia* (*Tatrasuchus*), and *Procyclotosaurus*); (7) pterygoid–exoccipital contact by means of posterior process of pterygoid (shared with *Eocyclotosaurus* and *Quasicyclotosaurus*); (8) frontal contribution to orbital margin limited or obliterated (obliteration shared with *Eocyclotosaurus* and *Quasicyclotosaurus*); (9) quadrate ramus of pterygoid laterally aligned and abbreviated (Schoch, 2008; shared with Mastodonsauridae).

### *Cyclotosaurus buechneri* sp. nov.

Figures 2, 3

LSID urn:lsid:zoobank.org:act:BEA3C090-24EC-4E39-BE5D-74898812C1A0. Date of registration: 20 March 2016.
2000 *Cyclotosaurus robustus*. – Schoch and Milner, p. 154.
2008a *Cyclotosaurus robustus*. – Büchner, p. 134, fig.
2008b *Cyclotosaurus robustus*. – Büchner, fig. 8.
2013 *Amphibienschädel* (amphibian skull). – Büchner, fig. 3.03–6.

Derivation of name: In honor of Dr. Martin Büchner, former director of the Museum of Natural History in Bielefeld. Martin Büchner discovered the holotype and only known specimen in 1975, and has a life-long record of outstanding contributions to the museum's geological collection and the popularization of geosciences in the region.

Holotype and only specimen: Namu ES/k 36053, an almost complete cranium in dorsal view, embedded in sandstone with the palate and occiput obscured.

Type locality and horizon: Bielefeld, district Sieker, North Rhine-Westphalia, northwestern Germany; Stuttgart Formation, middle Carnian, Late Triassic.

Diagnosis: A species within *Cyclotosaurus* with the
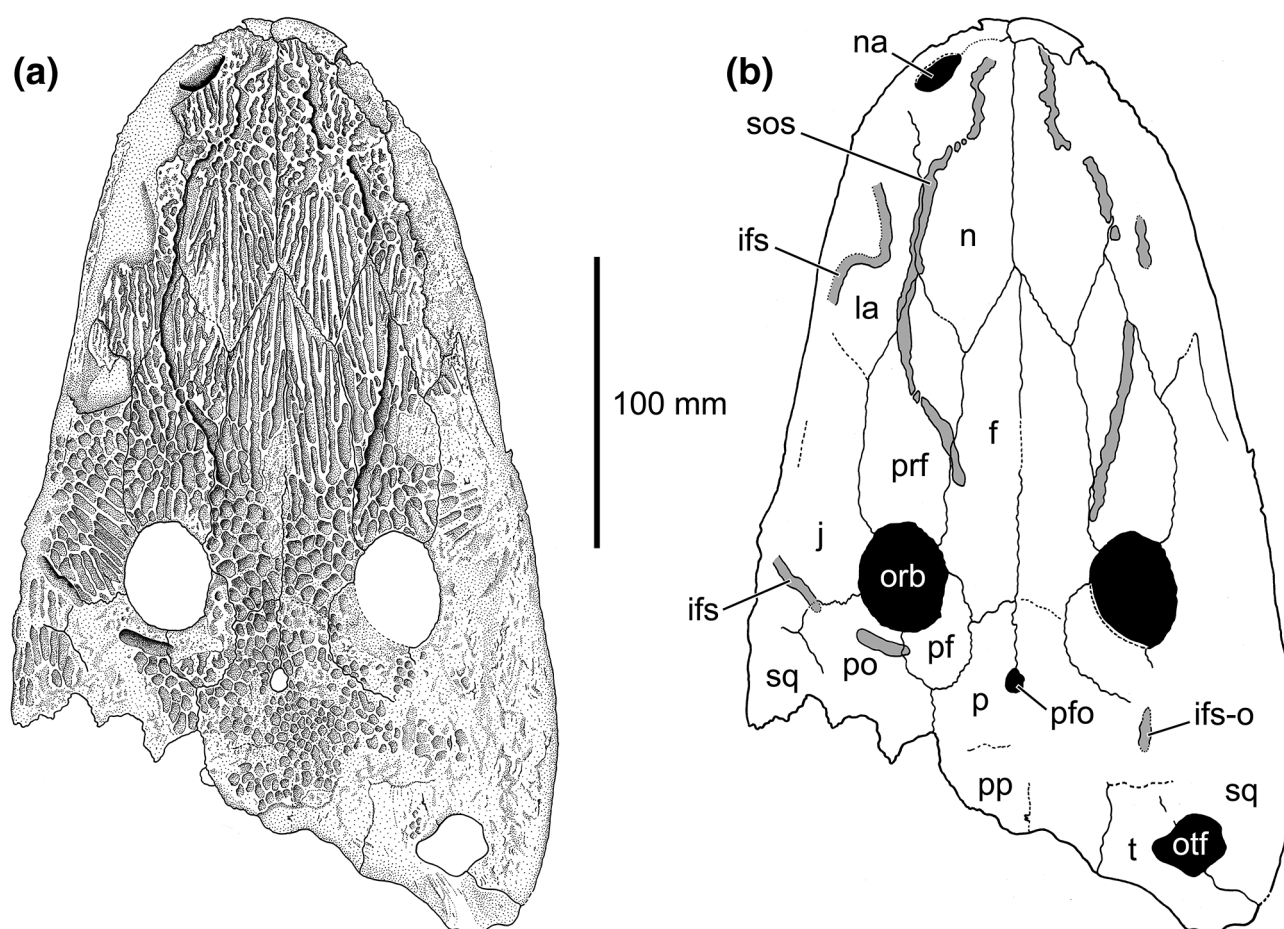
**Figure 3.** *Cyclotosaurus buechneri* sp. nov. from the middle Carnian Stuttgart Formation (Late Triassic) of Bielefeld, NW Germany, holotype and only specimen (Namu ES/k 36053). Drawings of the specimen with **(a)** dermal sculpture and **(b)** dermal sculpture omitted and lateral line sulci highlighted. Abbreviations: f, frontal; ifs, infraorbital sulcus; ifs-o, otic part of infraorbital sulcus; j, jugal; la, lacrimal; n, nasal; na, naris; otf, otic fenestra; p, parietal; pf, postfrontal; pfo, parietal foramen; po, postorbital; pp, postparietal; prf, prefrontal; sos, supraorbital sulcus; sq, squamosal; t, tabular.

following unique combination of characters: (1) orbitae medially placed with short interorbital distance (shared with *C. robustus*); (2) region lateral to orbitae only slightly wider than width of orbitae (shared with *C. posthumus*, *C. ebrachensis*, *C. intermedius*, and *C. mordax*); (3) postorbital skull region slender (shared with *C. ebrachensis*); (4) preorbital projection of jugal shorter than half the length of snout (shared with *C. mordax*, *C. ebrachensis*, *C. intermedius*, *C. posthumus*, and *C. hemprichi*, but dissimilar to *C. robustus*).

## 5 Description

### 5.1 Shape and proportions of the skull

The skull has a parabolic outline with the lateral margins being straight to slightly convex rather than concave (Figs. 2, 3). Measured from the tips of the premaxillae to the preserved posterior end of the postparietals, the skull is 280 mm

long. A sagittal line from the premaxillary tip to the level of the posterior end of the postotic bar measures 308 mm. The preorbital part of the skull (the "snout") is elongate and measures 175 mm in the midline. The posterior border of the skull table (formed by postparietals and tabulars) was apparently distinctly concave but its exact outline is not preserved.

### 5.2 Teeth

Marginal teeth of the labyrinthodont type are exposed in labial view in the region of the left premaxilla–maxilla boundary. They are barely visible because of a thick layer of lacquer coat that was applied to the skull during preparation. Other teeth are not exposed.

### 5.3 Openings of the skull roof

The large external nares are placed at the anterolateral margin of the snout and open anterolaterally. They are ovate in out-

line, with their longitudinal axis being oriented anteromedially. The maximum length / width ratio of the well-preserved left naris measures 21 to 9.9 mm. The nares are bordered anteriorly by the premaxilla and medially and posteromedially by the nasal. The maxilla forms the posterolateral boundary of the naris, but its anterior expansion lateral to the naris remains unclear. The orbitae are located in the posterior third of the skull roof. They are ovate in outline and their longitudinal axis is oriented anteroposteriorly. The maximum length/width ratio of the left orbit measures 38/27 mm, and that of the right orbit is 36/27 mm. The skull roof is dorsally concave between the orbitae. This concavity extends anteriorly along the median suture of the frontals. Here, two anteriorly running, shallow, broad ridges are formed, which extend from the anteromedial orbital margin. The interorbital concavity likewise extends posteriorly along the medial part of the postorbital skull table. The orbitae are framed by the prefrontal anteriorly, the frontal anteromedially, the postfrontal medially and posteromedially, the postorbital posterolaterally, and the jugal laterally. The parietal foramen (pineal opening) is located on the interparietal suture and well posterior to the orbital margin. Posteriorly the postotic bar of the tabular closes the squamosal embayment (or "otic notch") so that an otic fenestra is formed on each side. Posterolaterally, a squamosal–tabular contact is established. The preserved otic fenestra has an irregularly rounded outline with a maximum anteroposterior extension of 24 mm and maximum mediolateral extension of 27 mm.

## 5.4　Dermal sculpture

The dermal sculpture (or ornament) consists of furrows and polygons that are rather regular in outline, which is a common condition in many stereospondyls (Witzmann et al., 2010). Polygons are visible on the anterior half of nasal and lacrimal, the posterior two thirds of the prefrontal, the posterior third of the frontal, the ossification center of the jugal, and – where preserved – on the parietal, postparietal, postfrontal, postorbital, and supratemporal. Ridges and furrows, representing "zones of intensive growth" (Bystrow, 1935), are present on the anteriormost part and the posterior half of the nasal, the posterior half of the lacrimal, the anterior third of the prefrontal, the anterior two thirds of the frontal, the posterior, and posteromedial part of the jugal and – where preserved – on the squamosal. The sculpture is almost completely eroded on the premaxilla, the maxilla, and the tabular. The sizes of polygons differ; those on the postorbital skull table are distinctly smaller than those on the frontal, prefrontal, and jugal.

## 5.5　Lateral line sulci

In some regions of the skull roof, the lateral line sulci are deeply impressed and well visible, whereas in others they are largely or completely obscured by the "normal" dermal sculpture. The lateral line sulci are most prominent on the medial part of the snout: the supraorbital sulcus extends posterolaterally from the ossification center of the nasal along the nasal–lacrimal and prefrontal–lacrimal boundary and then curves medially to the ossification center of the prefrontal. From here it extends towards the frontal, where it cannot be traced any longer. A Z-shaped flexure of the infraorbital sulcus is visible on the left lacrimal. In the posteromedial region of the jugal, a short portion of the suborbital part of the infraorbital sulcus is preserved that runs posteromedially towards the postorbital, where it is visible directly posterior to the orbit. Poor preservation of the bone surface precludes recognition of further parts of the lateral line system. A short, elongate, anteroposteriorly depression on the right side of the postorbital skull table might represent the preserved portion of the otic part of the infraorbital sulcus.

## 5.6　Particular bones of the dermal skull roof

The premaxilla is an anteroposteriorly short bone that forms the prenarial region and is shorter than the naris. Posteriorly the premaxilla contacts the nasal with a concave suture and constitutes the anterior (and probably anterolateral) border of the external naris. Its posterolateral extension is unknown. There is no trace of a septomaxilla.

The nasal is an elongate element that is comparatively shorter but wider than the frontal. The nasal reaches its maximum width on the level of the anterior tip of the lacrimal. Its triangular posterior projection nests between the prefrontal and frontal. Anterolaterally, it forms the medial and posteromedial margin of the naris.

The frontal participates in the formation of the anteromedial part of the orbital margin, but only via a narrow lateral process. Each frontal forms an anteromedially aligned suture with the nasal, so that the conjoint anterior portions of both frontals form an anteriorly directed wedge that nests between the nasals. The frontal reaches its maximum width between the orbitae, where it forms the lateral process with which it participates in the orbital margin.

The parietal is an anteroposterior short element that is wider than long. Its maximum transverse expansion is slightly larger than that of the frontal. The anterior border to the frontal is visible in the left parietal and is anteromedially inclined. The anterolateral margin of the parietal is distinctly concave to accommodate the postfrontal. Laterally, the parietal forms a straight border with the supratemporal. The posterior suture with the postparietal cannot be traced with certainty and is therefore stippled in Fig. 3. The parietal foramen is located slightly anterior to the midlength of the parietals. The interparietal suture in front of the foramen is well visible and only slightly meandering. In contrast, the suture is completely concealed by dermal sculpture posterior to the foramen.

The lacrimal is an anteroposteriorly elongate and transversally narrow element that does not participate in the orbital

margin. Posteriorly a pointed, seemingly triangular portion is formed that nests between the prefrontal and jugal. Here, a slightly laterally convex lacrimal–nasal suture is visible. The anterior portion of the lacrimal is poorly preserved but appears to be pointed. The prefrontal forms the anterior orbital margin. The length of this bone accounts for almost the half of the preorbital skull length. It is a slender element whose lateral and medial margins are roughly parallel to each other but converge anteriorly to form a tip that wedges in between nasal and lacrimal.

The prefrontal terminates anteriorly at the level of the anterior tip of the frontals. The postfrontal forms a convex medial border with the frontal and parietal, and a convex lateral border with the postorbital and supratemporal. It forms part of the posterior and – via an anterior process – posteromedial margin of the orbit. A contact to the prefrontal as in some specimens of *Cyclotosaurus mordax* (Schoch and Milner, 2000; Schoch, 2008) is not established.

The postorbital is placed in the posterolateral portion of the skull roof. Its exact outline is unclear since the rear part of the specimen is not sufficiently preserved. The postorbital forms the posterolateral border of the orbit and, via a pronounced projection, large parts of the cranial portion lateral to the orbit. The named projection forms a suture with the jugal, which runs first nearly transversally and then turns abruptly in a posterolateral direction, forming a blunt wedge between jugal and squamosal. The posterior and posteromedial border of the postorbital cannot be traced because of the poor preservation.

A broad medial extension of the jugal forms most of the lateral orbital margin. The jugal is graded posteromedially to accommodate the aforementioned lateral projection of the postorbital. Its acute anterior margin reaches at least slightly farther anteriorly than the level of the posterior tip of the nasal and wedges in between the lacrimal and maxilla. The posterior extension of the bone is not clear, and also its lateral border with the maxilla is mostly not visible. However, the width of the jugal lateral to the orbit is virtually identical to the maximum orbital width.

The borders of the postparietal are mostly not visible, only on the left side of the skull, and an anterior suture to the parietal and a part of the medial suture between the postparietals are indicated. The posterior part of the postparietals is preserved as an imprint of the internal bone surface on top of the steinkern. It shows the posterior part of the internal sutures between the postparietals as well as the anteroposteriorly aligned suture of the right postparietal with the tabular.

Most of the sutures of the tabular with its surrounding elements are not or only poorly preserved (and thus questionable) on the dorsal bone surface, or they are visible as imprints on the steinkern. The tabular horn is laterally directed and forms a suture with the squamosal at the posterolateral side of the skull. Thus, the squamosal embayment is completely closed posteriorly by a robust postotic bar and a true

postotic fenestra is formed that is encircled by the tabular posteromedially and by the squamosal anterolaterally.

The squamosal, supratemporal, quadratojugal, and maxilla are too poorly preserved to provide proper descriptions of their outlines and morphologies.

## 6 Phylogenetic analysis

To test the phylogenetic affinities of the Bielefeld specimen, we ran a phylogenetic analysis using the data set of capitosaur relationships from Schoch (2008), which is a modified and supplemented version of the data set from Damiani (2001). Because our first aim was to determine the phylogenetic position of the Bielefeld skull and the intrarelationships of the genus *Cyclotosaurus*, we reduced the number of taxa to a total of 16 (see below). Three new characters were added, which resulted in a total of 69 characters (38 of which being parsimony informative): #67, margins of skull lateral to otic fenestra/otic notch: laterally convex (0) or laterally straight (1); #68, interorbital width: interorbital width to width of orbitae smaller than 1.8 (0) or equal to or larger than 1.8 (1); #69, posteromedial margin of tabular: concave (0) or straight to convex (1). Character 32 of Schoch (2008) was reformulated for the present analysis as follows: #32, denticle field: present on parasphenoid and/or pterygoid (0) or absent (1). *Cyclotosaurus robustus* was taken as representative of the genus in the analysis of Schoch (2008), and this taxon was recoded for the present study based on Quenstedt (1850), Schoch and Milner (2000) and personal observations (SMNS 4139, 4935, 5775). Apart from *C. robustus* and the Bielefeld specimen, the following species of *Cyclotosaurus* were included for the first time in a phylogenetic analysis and scored based on data from the literature and personal observations: *C. mordax* (Fraas, 1913; SMNS 13014, 50059, 50063, 51102, 51426, 55112), *C. posthumus* (Fraas, 1913; SMNS 12988), *C. intermedius* (Sulej and Majer, 2005), *C. ebrachensis* (Kuhn, 1932), and *C. hemprichi* (Kuhn, 1939, 1942). Further members of the ingroup are *Eryosuchus garjainovi* (new characters coded after Schoch and Milner, 2000), *Kupferzellia (Tatrasuchus) wildi* (Schoch, 1997), *Procyclotosaurus stantonensis* (Schoch and Milner, 2000), *Paracyclotosaurus crookshanki* (Mukherjee and Sengupta, 1998), *Mastodonsaurus giganteus*, *M. cappelensis* (Schoch and Milner, 2000), *Eocyclotosaurus wellesi*, and *Quasicyclotosaurus campi* (Schoch, 2000a). The Rhinesuchidae (Schoch and Milner, 2000) served as an outgroup. For the character list and data matrix, see Appendices A and B.

The analysis was performed with PAUP*4.0 (Swofford, 2003) using branch-and-bound search settings (multistate taxa interpreted as polymorphism) with all characters unordered except for characters 10 and 11, which were ordered. Three most parsimonious trees were recovered (tree length, TL = 114; consistency index, CI = 0.6754, CI excluding uninformative characters = 0.5978; homoplasy index, HI = 0.4035, HI excluding uninformative charac-
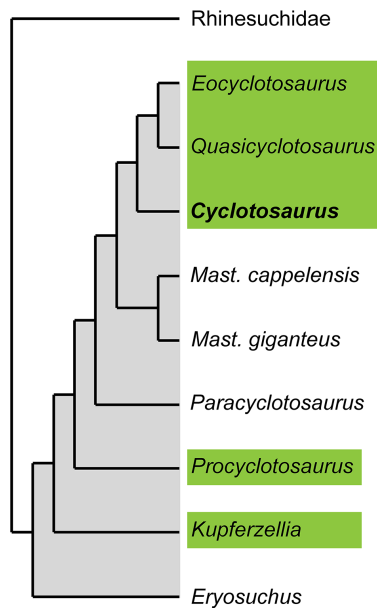
**Figure 4.** Phylogenetic position of the genus *Cyclotosaurus* within the capitosaur taxa chosen for the present PAUP analysis (the intrarelationships of the genus are shown in Fig. 5). The strict consensus of the three most parsimonious trees is shown with "cyclotosaurs" (i.e., forms with squamosal embayment closed to an otic fenestra) highlighted in green. Capitosauroids sensu Schoch (2008) are highlighted in grey. Abbreviation: *Mast.*, *Mastodonsaurus*.

ters = 0.4022; retention index, RI = 0.6783; and rescaled consistency index, RC = 0.4581). The strict consensus of the three trees is shown in Fig. 4, and the intrarelationships of the genus *Cyclotosaurus* (based on the consensus tree) are shown in Fig. 5. In all trees *Cyclotosaurus* (corresponding to Cyclotosaurinae of Schoch and Milner, 2000) is shown to be monophyletic, with *C. ebrachensis* and *C. intermedius* as well as *C. posthumus* and *C. hemprichi* forming sister taxa, respectively. However, the relationship of these two groups with *C. mordax* is not resolved. Likewise, the Bielefeld specimen clusters as a sister to this clade in all trees, and *C. robustus* always forms the basalmost species (Fig. 5). *Cyclotosaurus* is supported by the following synapomorphies: #7 (state 0), lateral lines weakly impressed; #16 (0), vomerine plate short; #20 (1), anterior palatal vacuity medially subdivided by anterior process; #21 (0), pterygoid–parasphenoid suture as long as basal plate is wide; #24 (2), cultriform process slender with deep ventral crest; #25 (0), ectopterygoid excluded from lateral margin of interpterygoid vacuity; #48 (1), quadrate ramus of pterygoid laterally aligned and abbreviated; #66 (1), snout width wide parabolic. The post-*C. robustus* clade containing the Bielefeld specimen as its basalmost member is supported by one synapomorphy: #13 (0), preorbital projection of jugal shorter than half the length of the snout. The remaining grouping of *Cyclotosaurus* is supported by #44 (1), labial wall of adductor chamber dorsally convex; #68 (1), in-

terorbital width to width of orbitae equal to or larger than 1.8. The sister-group relationship of *C. ebrachensis* and *C. intermedius* is supported by three synapomorphies: #32 (0), denticle fields on the palate; #67 (1), the laterally straight margin of the skull lateral to the otic fenestra; #69 (1), the straight to convex posteromedial margin of the tabular. The grouping of *C. posthumus* and *C. hemprichi* is supported by two synapomorphies: #1 (1), the tapering preorbital region; #66 (0), the elongate, parabolic snout width.

The sister group of *Cyclotosaurus* is a clade formed by *Eocyclotosaurus* + *Quasicyclotosaurus* (Heylerosaurinae sensu Schoch and Milner, 2000). This grouping of (*Cyclotosaurus* + (*Eocylotosaurus* + *Quasicyclotosaurus*)) is supported by #49 (1), palatine ramus of pterygoid ornamented; #54 (2), otic fenestra sutured to encircle an otic fenestra; #65 (1), posterior process of pterygoid present, contacting exoccipital. The sister taxon of this grouping is *Mastodonsaurus* (*M. giganteus* + *M. cappelensis*). Successive sister groups of the clade formed by (*Mastodonsaurus* + (*Cyclotosaurus* + *Heylerosaurinae*)) (from derived to more basal) are *Paracyclotosaurus crookshanki*, *Procyclotosaurus*, *Kupferzellia* (*Tatrasuchus*), and *Eryosuchus*.

## 7 Discussion

### 7.1 Generic assignment

The most striking feature of the Bielefeld skull is the presence of a rounded otic fenestra – i.e., the squamosal embayment is completely closed posteriorly by a postotic bar formed by tabular and squamosal. In stereospondyls, the presence of otic fenestrae is called the "cyclotosaur condition" and is characteristic of a group informally called cyclotosaurs (Schoch, 2008). Fortuny et al. (2012) showed on the basis of finite-element analysis (FEA) that the otic fenestra in stereospondyls is an adaptation for the distribution of stress and deformation during skull raising. The known taxa with otic fenestrae are *Procyclotosaurus* from the Ladinian of England (Schoch and Milner, 2000); *Cyclotosaurus* from the Carnian and Norian of Germany, Poland, Greenland, and Thailand (Fraas, 1913; Kuhn, 1932, 1942; Schoch and Milner, 2000; Sulej and Majer, 2005; Schoch et al., 2008); *Kupferzellia* (otic fenestra closed in adults) from the upper Ladinian of southern Germany (Schoch, 1997); *Eocyclotosaurus* from the Anisian of France, Germany, England, and North America (Heyler, 1969; Ortlam, 1970; Schoch, 2000a; Schoch and Milner, 2000); and *Quasicyclotosaurus* from the Anisian of North America (Schoch, 2000a, 2008).

However, in contrast to earlier discussions (Welles and Cosgriff, 1965), it appears that this "cyclotosaur condition" evolved at least two times independently (Shishkin, 1980; Damiani, 2001; Schoch, 2008; Fortuny et al., 2011, 2012; Sidor et al., 2014).
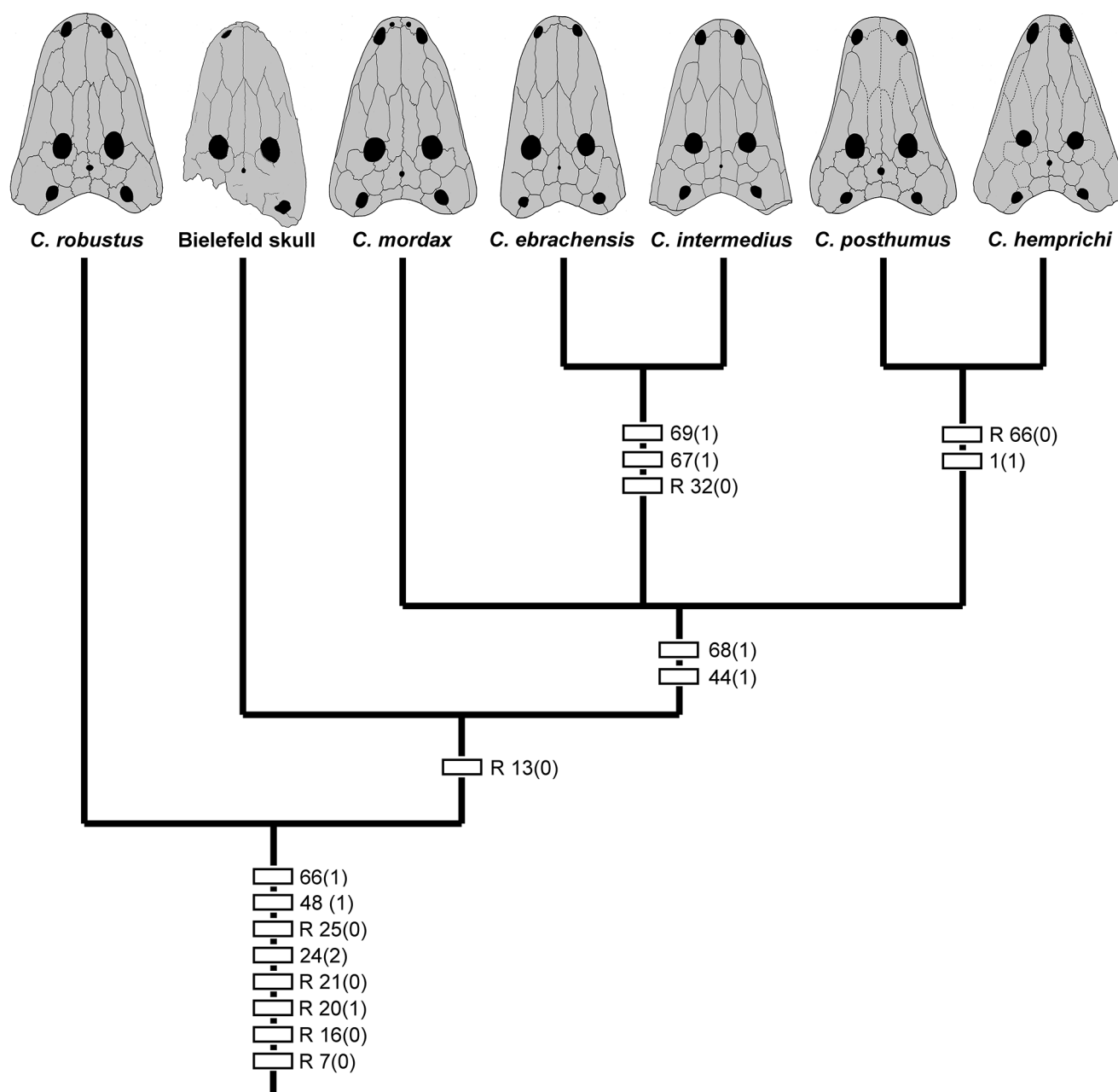
**Figure 5.** Intrarelationships of the different species of *Cyclotosaurus* as found in the strict consensus tree of the present PAUP analysis. Supporting characters (white rectangles) are mapped on nodes. The numbers refer to the characters listed in the Appendix and their state is given in brackets. R: reversal. Skulls redrawn after Kuhn (1932), Sulej and Majer (2005), Schoch and Milner (2000), and Schoch (2008).

According to Schoch (2008), there are two main phylogenetic hypotheses about cyclotosaur relationships: the monophyly scenario (or Pancyclotosauria hypothesis) and the convergence scenario (Eocyclotosauria and Paracyclotosauria hypothesis). In the monophyly scenario, *Cyclotosaurus*, *Eocyclotosaurus*, and *Quasicyclotosaurus* are closely related and the otic fenestrae therefore evolved once in their stem group (Schoch and Milner, 2000; Schoch, 2000b) and a sec-

ond time in *Kupferzellia* and *Procyclotosaurus*. In the convergence scenario, *Cyclotosaurus* is more closely related to *Procyclotosaurus* and *Kupferzellia* (within a clade called Eucyclotosauria) than to *Eocyclotosaurus* and *Quasicyclotosaurus* (within a clade called Paracyclotosauria). Thus, in this scenario, the otic fenestra must have evolved once within the Eucyclotosauria and a second time within the Paracyclotosauria (Schoch, 2008).

The phylogenetic analysis of Schoch (2008) supported the convergence scenario, and it was further supported by the phylogenetic analyses of Fortuny et al. (2011) and Sidor et al. (2014), according to which *Eocyclotosaurus* and *Quasicyclotosaurus* (on the one hand) and *Cyclotosaurus* (on the other hand) were not closely related. In contrast, the phylogenetic analysis presented herein supports the monophyly hypothesis with *Cyclotosaurus* being the sister group of the Heylerosaurinae (*Eocyclotosaurus* + *Quasicyclotosaurus*). If this grouping is correct (it is admittedly based on a rather small number of taxa), it implies that the otic fenestrae evolved only once in its stem-group. However, in this scenario the otic fenestrae also evolved more than once in capitosaurs: it may have evolved a second time in *Kupferzellia (Tatrasuchus)* and a third time in *Procyclotosaurus* (both of which are not closely related to *Cyclotosaurus* in the present analysis, in contrast to Schoch, 2008, where they form the Eucyclotosauria, and to Fortuny et al., 2011, where *Kupferzellia (Tatrasuchus)* is the sister taxon of *Cyclotosaurus*, and *Procyclotosaurus* is the sister taxon of the Heylerosaurinae). Alternatively, the otic fenestrae may have evolved in post-*Eryosuchus* capitosaurs with a reversal in post-*Procyclotosaurus* forms according to the present analysis (Fig. 4).

To which existing groups of capitosaurs with closed otic fenestra can the Bielefeld skull be attributed to? An assignment to *Procyclotosaurus* can be ruled out because this taxon has a triangular skull with broad cheeks and a slender, tapering snout (Schoch and Milner, 2000) that differs considerably from the parabolic outline of the Bielefeld specimen. *Eocyclotosaurus* and *Quasicyclotosaurus* can be excluded because of their more slender snouts with concave lateral margins and the sutured prefrontal–postfrontal contact medial to the orbitae (Schoch, 2000a, 2008). *Kupferzellia (Tatrasuchus)* has a much broader postorbital skull and a proportionally shorter snout, which is more tapering anteriorly (Schoch, 1997; Schoch and Milner, 2000). Instead, a diagnostic feature that unites the Bielefeld skull with *Cyclotosaurs* is the limited contribution of the frontal to the orbital margin via narrow lateral processes (Schoch and Milner, 2000). This assignment is supported by the present analysis in which the Bielefeld specimen constantly nests within a monophyletic *Cyclotosaurus* clade.

## 7.2 Species assignment

In the complete absence of palatal characters, it is more difficult to assign the Bielefeld specimen to a particular species of *Cyclotosaurus*. The stratigraphically oldest undisputed representative of *Cyclotosaurus* is *C. robustus* from the Schilfsandstein (middle Carnian) of southwestern Germany (Meyer and Plieninger, 1844; Quenstedt, 1850; Schoch and Milner, 2000; Schoch, 2008). Its autapomorphic characters are the much widened parabolic skull whose lateral margins are convex, plus the short interorbital width. The late Carnian

taxa *C. intermedius* from the Opole region of Poland (Sulej and Majer, 2005) and *C. ebrachensis* (Kuhn, 1932) from Franconia (northern Bavaria) are the stratigraphically next youngest species. Schoch (2008, p. 214) pointed to the similarity between both species, "which apparently hardly differ at all". However, *C. intermedius* differs from all other known *Cyclotosaurus* species in the projection of the quadrate posterior to the hind margin of the skull roof (Sulej and Majer, 2005). Both species possess denticles on the palate (Kuhn, 1932; Sulej and Majer, 2005), but *C. ebrachensis* is characterized by the unique combination of an undivided, ovate anterior palatal vacuity and circular choanae (Kuhn, 1932). These taxa are stratigraphically followed by the middle Norian species *C. mordax* and *C. posthumus* (Fraas, 1913), both from southern Germany, and the late Norian *C. hemprichi* from Halberstadt in central Germany (Kuhn, 1939, 1942). *C. mordax* is unique among *Cyclotosaurus* in bearing two apertures in the anteriormost part of the snout which accommodated the fangs of the lower jaw (Fraas, 1913). *C. posthumus* and *C. hemprichi* are similar in the outline of the skull since both have anteriorly tapering snouts. However, the margins of the snout are laterally concave in *C. posthumus* rather than straight as in *C. hemprichi*, and the orbitae are proportionally much larger and ovate in contrast to the relatively small, round orbitae in *C. hemprichi* (Fraas, 1913; Kuhn, 1942; Schoch and Milner, 2000). The diagnostic characters listed above for each of the six *Cyclotosaurus* species suggest that these species are valid.

However, some additional specimens may belong to *Cyclotosaurus* but their taxonomic state is unclear. A partial skull from the upper Ladinian (upper Muschelkalk) of southern Germany described as *Cyclotosaurus papilio* by Wepfer (1923) might represent the oldest *Cyclotosaurus* specimen known; however, according to Schoch (2008), it shows no diagnostic features that warrant an assignment to that genus. Ingavat and Janvier (1981) described the posterior part of a skull from the Norian of Thailand, which they assigned to *Cyclotosaurus* cf. *posthumus*. Postcranial remains, mainly intercentra that resemble those of *C. hemprichi* from Halberstadt, have been reported from the Norian of Luxemburg (Milner et al., 1996) and the ?Carnian–Norian of Portugal (Witzmann and Gassner, 2008). A late Norian temnospondyl specimen from Jameson Land in Greenland was assigned to *Cyclotosaurus* cf. *posthumus* by Jenkins et al. (1994). Kear et al. (2015) tentatively referred the holotype of *Capitosaurus polaris* (Wiman, 1914) from the middle to late Carnian lower De Geerdalen Formation of Spitsbergen, Svalbard, to *Cyclotosaurus* sp.

Our comparison of the Bielefeld specimen focused on the six valid *Cyclotosaurus* species listed before. Apart from their later geological appearance (which in itself does not justify an exclusion), *C. hemprichi* differs from the Bielefeld specimen in its tapering, triangular snout and the small, circular orbitae, and *C. posthumus* differs by its laterally concave margins of the snout. *C. mordax* shows a marked differ-

ence in the presence of the two apertures in the anteriormost part of the snout, which are clearly absent in the Bielefeld specimen. The two species *C. intermedius* and *C. ebrachensis* have a straight skull margin lateral to the otic fenestrae (Kuhn, 1932; Sulej and Majer, 2005), in contrast to the convex margin present in the Bielefeld specimen and all other known species of *Cyclotosaurus*. The remaining species, *C. robustus*, is similar to the Bielefeld specimen in the position of the orbitae, which are located more medially in contrast to the more lateral position in all other *Cyclotosaurus* species. Also, its stratigraphic age (middle Carnian Schilfsandstein, Stuttgart Formation) might be an argument in favor of a close relationship of the Bielefeld specimen and *C. robustus*. However, there are marked differences in proportions between the Bielefeld skull and *C. robustus*. First, the region lateral to the orbitae is much more slender in the Bielefeld specimen (with a ratio of width lateral to the orbit to orbital width of 1.1) than in all known specimens of *C. robustus* (ratio of 1.6–1.7). Second, the posterior skull region is more slender in the Bielefeld skull (ratio of maximum skull width to skull length of 0.65) than in *C. robustus* (ratio of 0.79–0.85). The Bielefeld skull is indeed more slender than those of all other species of *Cyclotosaurus* (ratio of 0.81 in *C. mordax*; 0.84 in *C. posthumus*; 0.82 in *C. intermedius*; 0.87 in *C. hemprichi*), paralleled only by *C. ebrachensis* with a ratio of 0.70.

With a skull length of ca. 280 mm the Bielefeld skull attains about 75 % the size of the smallest known complete skull of *C. robustus*, which has a length of ca. 365 mm (Schoch and Milner, 2000, fig. 101), and thus one could argue that the different proportions of the Bielefeld skull might represent a juvenile character of *C. robustus*. However, there are no indications of proportional widening of the skull and of the region lateral to the orbits in the known size range of 365–560 mm skull length in *C. robustus* (Quenstedt 1850; Schoch and Milner 2000; personal observations). Furthermore, the skull proportions of small juveniles closely resemble those of large adults in another derived capitosaur stereospondyl, *Mastodonsaurus giganteus* (Schoch, 2014), which is closely related to *Cyclotosaurus* according to the analyses of Fortuny et al. (2011), Sidor et al. (2014), and the present study (but see Schoch, 2008). Therefore, the proportions of the Bielefeld skull are not regarded as juvenile here, and this is supported by the "adult" dermal sculpture of pits and ridges (sensu Bystrow 1935; see also Witzmann et al. 2010) that does not differ in its distribution on the dermal skull roof from that in *C. robustus*.

In conclusion, although there is no autapomorphic character present on the visible side of the Bielefeld specimen, the description and comparisons above reveal a unique combination of characters. This combination includes the short preorbital extent of the jugal, the narrow region lateral to the orbit, the narrow postorbital skull, and the medial position of the orbitae. For this reason, it is justifiable to erect a new species, *Cyclotosaurus buechneri* sp. nov., for this specimen.

The phylogenetic analysis suggests that *C. buechneri* sp. nov. is a basal member of the genus, which is in accordance with its stratigraphic age. It is more derived than *C. robustus* in the presence of a short jugal, but more plesiomorphic than all other *Cyclotosaurus* species (except for *C. robustus*) by the small interorbital width. Since the specimens from Melle have neither been described nor illustrated and their taxonomical referral is thus questionable, *Cyclotosaurus buechneri* sp. nov. is the only undoubted evidence of *Cyclotosaurus* (and of a cyclotosaur in general) from the northern part of Germany.

## Appendix A: List of characters

1. Preorbital region. Parabolic (0) or tapering (1). From Damiani (2001, #1, reformulated by Schoch, 2008).

2. Posterolateral skull corners (quadrates). Posterior to distal end of tabular horns (0) or anterior (1). From Damiani (2001, #2).

3. Otic notch. Deeply incised into posterior skull margin (0) or reduced to an embayment (1). From Damiani (2001, #3).

4. Tabular horns. Directed posteriorly (0) or laterally (1). From Damiani (2001, #4).

5. Orbital margins. Flush with plane of skull roof (0), well elevated above plane of skull roof (1), or emplaced on high sockets protruding even level of posterior skull table (2). From Damiani (2001, #5, reformulated and recoded by Schoch, 2008).

6. Postorbital–prepineal growth zone. Absent (0) or present (1). From Damiani (2001, #6).

7. Lateral line sulci. Weakly impressed, discontinuous (0) or continuous, well impressed (1). From Damiani (2001, #7).

8. Lacrimal flexure of infraorbital canal. Absent (0), stepped (1), or Z-shaped (2). From Damiani (2001, #8).

9. Occipital sensory canal. Absent (0) or present (1). From Damiani (2001, #9).

10. Supraorbital sensory canal. Traversing nasal (0), nasal and lacrimal (1), or only lacrimal (2). From Damiani (2001, #10, reformulated and newly coded by Schoch, 2008). Character states ordered (because they form a sequence of geometric states).

11. Frontal. Excluded from orbit (0), entering medial margin of orbit in a narrow strip (1), or forming most of the medial margin of orbit (2). From Damiani (2001, #11, recoded by Schoch, 2008). Character states ordered, because they form a morphological sequence of states.

12. Supratemporal. Entering dorsal margin of otic notch (0) or excluded from dorsal margin of otic notch (1). From Damiani (2001, #12).

13. Preorbital projection of jugal. Shorter than half the length of snout (0) or as long or longer (1). From Damiani (2001, #13, reformulated by Schoch, 2008).

14. Postorbital. Laterally not wider than orbit (0) or with lateral wing projecting well beyond orbit (1). From Damiani (2001, #14, recoded by Schoch, 2008).

15. Naris. Oval (0) or narrow and elongated (1). From Damiani (2001, #15).

16. Vomerine plate. Short and as wide as long (0) or narrow and longer than wide (1). From Damiani (2001, #16, reformulated by Schoch, 2008).

17. Occipital condyles. Anterior to quadrate condyles (0) or level with or posterior to these (1). From Damiani (2001, #17).

18. Choanal outline. Oval-shaped (0), narrow and slit-like (1), or circular (2). From Damiani (2001, #18). This character is here coded unordered, since no morphological transformation series is apparent.

19. Transvomerine tooth row. Transverse (0) or V-shaped (1). From Damiani (2001, #19).

20. Anterior palatal vacuity. Unpaired (0), medially subdivided by anterior process (1), or completely subdivided (2). From Damiani (2001, #20, recoded by Schoch, 2008).

21. Pterygoid–parasphenoid suture. As long as basal plate is wide (0) or substantially longer than basal plate is wide (1). From Damiani (2001, #21, reformulated by Schoch, 2008).

22. Posterolateral process of vomer. Absent (0) or present (1). From Damiani (2001, #22).

23. Cultriform process extension between vomers. Extends beyond anterior margin of interpterygoid vacuities (0) or underplated by vomers (1). From Damiani (2001, #23).

24. Cultriform process. Ventrally flat (0), flat with central ventral ridge (1), or slender with deep ventral crest ("knife-edged") (2). From Damiani (2001, #24, reformulated by Schoch, 2008). This character is here coded unordered, since no morphological transformation series apparent.

25. Ectopterygoid exposure. Excluded from the lateral margin of interpterygoid vacuities (0) or entering margin, wedged between palatine and pterygoid (1). From Damiani (2001, #25, reformulated by Schoch, 2008).

26. Crista muscularis, extension. Behind posterior border of parasphenoid-pterygoid suture (0) or level with that border (1). From Damiani (2001, #26).

27. Crista muscularis, midline. Discontinuous (0) or confluent in midline (1). From Damiani (2001, #27).

28. Parasphenoid pockets. Facing posterodorsally, located along the posterior rim of the plate (0), or ventrally, entirely located on the flat surface (1). From Damiani (2001, #28).

29. Exoccipital–pterygoid suture. Absent (0) or present (1). From Damiani (2001, #29).

30. Marginal teeth. Circular or moderately oval (0) or anteroposteriorly compressed and closely set (1). From Damiani (2001, #30).

31. Ectopterygoid tusks. Present (0) or absent (1). From Damiani (2001, #31).

32. Denticle field. Present on parasphenoid and/or pterygoid (0) or absent (1). From Damiani (2001, #32). Reformulated for the present study.

33. Quadratojugal. Excluded from quadrate trochlea (0) or forming lateral portion of it (1). From Damiani (2001, #33).

34. Cheek region, posterior view. Rounded (0) or straight, box-like (1). From Damiani (2001, #34).

35. Posttemporal fenestra. Narrow and slit-like (0) or triangular (1). From Damiani (2001, #36).

36. Tabular horn. Short, supported only by paroccipital process (0), or posteriorly extended, supported by two ventral ridges (1). Damiani (2001, #36, reformulated by Schoch, 2008).

37. Crista obliqua of pterygoid. Absent (0) or present (1). From Damiani (2001, #37).

38. Crista muscularis of parasphenoid. Visible in occipital view (0) or not visible (1). From Damiani (2001, #38).

39. Basioccipital. Present (0) or absent (1). From Damiani (2001, #39).

40. Crista falciformis. Absent (0) or present (1). From Damiani (2001, #40).

41. Postglenoid area. Short boss (0); distinct process (1); or extended, longer than glenoid facet (2). From Damiani (2001, #41, reformulated and recoded by Schoch, 2008).

42. Hamate process of prearticular. Absent or rudimentary, forming at best an anterior margin of the glenoid facet (0); present, raised well above glenoid and as high as quadrate trochlea (1); or substantially higher than quadrate trochlea (2). From Damiani (2001, #42).

43. Posterior Meckelian fenestra. Small and round (0) or elongated, reaching one-quarter to one-third of mandible length (1). From Damiani (2001, #43, reformulated by Schoch, 2008).

44. Labial wall of adductor chamber. Dorsally horizontal (0) or dorsally convex (1). From Damiani (2001, #44).

45. Coronoid series. With tooth patch (0) or single row of teeth (1). From Damiani (2001, #45).

46. Prearticular. Sutures with splenial anteriorly (0) or separated from it by dentary or coronoid 2 (1). From Damiani (2001, #46, reformulated by Schoch, 2008).

47. Glenoid facet. Above level of dorsal surface of dentary (0) or below (1). From Damiani (2001, #47).

48. Quadrate ramus of pterygoid. Parasagittally aligned (0) or laterally aligned and abbreviated (1). From Schoch (2008, #48).

49. Palatine ramus of pterygoid. Ventrally smooth (0) or ornamented (1). From Schoch (2008, #49).

50. Basal plate of parasphenoid. Short anterior to entrance foramina of carotid (0) or much elongated anteriorly (1). From Schoch (2008, #50).

51. Cultriform process. Merges continuously from basal plate (1) or forming a deltoid base (1). From Schoch (2000a).

52. Vomerine tusks. Posterior to anterior palatal vacuity (0) or lateral to it (1). From Schoch (2008, #48).

53. Postparietals and tabular length. Shorter than parietals (0) or as long or longer (1). From Schoch (2008, # 53).

54. Otic fenestra. Tabular and squamosal separated by otic notch posteriorly (0), separated by narrow slit (1), or sutured to encircle an otic fenestra (2). From Schoch (2008, #54; Damiani 2001: #4–2).

55. Orbit anteriorly extended. Oval or round (0) or anteriorly extended, indented into prefrontal (1). From Schoch (2008, #55).

56. Tip of snout. Pre-narial portion shorter than naris (0) or as long or longer (1). From Schoch (2008, #56).

57. Snout penetrated by tusks. Tip of snout completely ossified (0) or bearing paired openings anterior to naris to accommodate large symphyseal tusks (1). From Schoch (2008, #57).

58. Postorbital and prefrontal. Widely separated (0); nearing one another by thin projections (1); or sutured, excluding jugal from orbit margin (2). From Schoch (2008, #58).

59. Interpterygoid vacuities. Equally wide anteriorly and posteriorly (0) or tapered posteriorly (1). From Morales and Shishkin (2002, #10).

60. Tip of tabular. Equally wide throughout (0) or anterodistally broadened (1). From Schoch (2008, #60, based on Damiani, 2001, who listed the derived character state as a synapomorphy of *Eryosuchus garjainovi* and "*Stanocephalosaurus*" *pronus*).

61. Posterior margin of anterior palatal depression. Concave (0) or straight (1). From Schoch (2008, #61).

62. Posterior boss of quadrate ("hyoid tubercle" of Morales and Shishkin 2002). Occipital face of quadrate with prominent posterior boss (0) or smooth (1). From Schoch (2008, #62).

63. Tabular, posterior. Wider than long (0) or posteriorly extended, as long as wide (1). From Schoch (2008, #63).

64. Epipterygoid. Short, tetrahedral (0) or anteriorly expanded with process paralleling sphenethmoid (1). From Schoch (2008, #64, based on Schoch, 2000c).

65. Posterior process of pterygoid. Absent (0) or present, contacting exoccipital (1). From Schoch (2008, #65).

66. Snout width. Elongate parabolic (0), wide parabolic (1), or anteriorly expanded (2). From Schoch (2008, #66).

67. Margins of skull lateral to otic fenestra/otic notch: laterally convex (0) or laterally straight (1). New character.

68. Interorbital width: interorbital width to width of orbits smaller than 1.8 (0) or equal to or larger than 1.8 (1). New character.

69. Posteromedial margin of tabular: concave (0) or straight to convex (1). New character.

## Appendix B:  Character–taxon matrix

Abbreviations: *C*, *Cyclotosaurus*; *M.*, *Mastodonsaurus*; *Pc.*, *Paracyclotosaurus*.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Eocyclotosaurus* | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Eryosuchus* | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0, 1 | 2 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Kupferzellia* | 0 | 1 | 0 | 1 | ? | 0 | 0 | 2 | 0 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 0 |
| *M. cappelensis* | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 2 | 2 | 1 | 0 | 0 | 0 | 1 | 1 |
| *M. giganteus* | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 2 | 2 | 1 | 0 | 0 | 0 | 1 | 1 |
| *Pc. crookshanki* | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 2 | 1 | 1 | 1 | 0 | 1 | 1 |
| *Procyclotosaurus* | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 1 | 1 | 1 | 0 | 1 | 1 |
| *Quasicyclotosaurus* | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 |
| Rhinesuchidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *C. robustus* | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0, 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 |
| *C. ebrachensis* | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| *C. intermedius* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| *C. mordax* | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0, 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| *C. posthumus* | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | ? | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| *C. hemprichi* | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | ? | ? | 1 | 0 | ? | 0 | 0 | 1 |
| Bielefeld skull | 0 | ? | 0 | 1 | 0 | 0 | 0 | 2 | ? | 1 | 1 | 1 | 0 | 1 | 0 | ? | ? |

| | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Eocyclotosaurus* | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Eryosuchus* | 0 | 0 | 0, 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| *Kupferzellia* | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| *M. cappelensis* | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *M. giganteus* | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Pc. crookshanki* | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Procyclotosaurus* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | ? | 1 | 1 | 1 | 1 | 0 |
| *Quasicyclotosaurus* | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| Rhinesuchidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *C. robustus* | 2 | 0 | 0, 1 | 0 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *C. ebrachensis* | 2 | 0 | 0 | 0 | 1 | 0 | ? | ? | ? | ? | ? | ? | ? | 1 | 0 | 1 | 0 |
| *C. intermedius* | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 |
| *C. mordax* | 0 | 0 | ? | 0 | 1 | 0 | 2 | ? | 1 | 1 | 1 | ? | 1 | 1 | 1 | 1 | 0 |
| *C. posthumus* | 2 | ? | ? | 0 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *C. hemprichi* | 0 | 0 | 1 | 0 | ? | 0 | 2 | ? | ? | ? | ? | 1 | ? | 1 | 1 | ? | 0 |
| Bielefeld skull | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |

| | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Eocyclotosaurus* | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | ? | ? | ? | ? | 0 | 1 | 1 | 1 |
| *Eryosuchus* | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Kupferzellia* | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 |
| *M. cappelensis* | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |
| *M. giganteus* | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |
| *Pc. crookshanki* | 1 | 1 | 1 | 1 | 1 | 1 | ? | ? | 0 | 0 | ? | 1 | 0 | 0 | 0 | 1 | 1 |
| *Procyclotosaurus* | 1 | 1 | 1 | 1 | 1 | 1 | ? | ? | ? | ? | ? | ? | ? | 0 | ? | 1 | 1 |
| *Quasicyclotosaurus* | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | ? | ? | ? | 0 | 1 | 1 | 1 |
| Rhinesuchidae | 0 | 0 | 0 | 0 | 0 | 0, 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *C. robustus* | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | ? | ? | ? | ? | 1 | 1 | 1 | 1 |
| *C. ebrachensis* | 1 | 1 | ? | 1 | 1 | 1 | ? | ? | ? | ? | ? | ? | ? | 1 | 1 | 1 | 1 |
| *C. intermedius* | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | ? | 0 | 0 | 1 | 1 | 1 | 1 |
| *C. mordax* | ? | 1 | ? | ? | 1 | 1 | ? | 2 | 1 | 1 | ? | ? | 0 | 1 | 1 | 1 | 1 |
| *C. posthumus* | 1 | 1 | ? | 1 | 1 | 1 | ? | ? | ? | ? | ? | ? | ? | 1 | 1 | 1 | 1 |
| *C. hemprichi* | 1 | 1 | 1 | 1 | 1 | 1 | ? | ? | 1 | ? | ? | ? | ? | 1 | 1 | 1 | 1 |
| Bielefeld skull | ? | 1 | ? | ? | ? | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |

| | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Eocyclotosaurus* | 0 | 1 | 2 | 0 | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0, 1 | 1 |
| *Eryosuchus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Kupferzellia* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *M. cappelensis* | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *M. giganteus* | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Pc. crookshanki* | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | ? | 0 | 0 | 0 | 1 | 0 |
| *Procyclotosaurus* | 0 | 1 | 1 | 0 | 0 | 0 | 1, 2 | 1 | 1 | 1 | 1 | 0 | ? | ? | 0 | 0 | 0 | 0 |
| *Quasicyclotosaurus* | 0 | 1 | 2 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 0 | ? | 1 | 0 | 0 | 0 | 1 |
| Rhinesuchidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0, 1 | 0 |
| *C. robustus* | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *C. ebrachensis* | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | ? | ? | 1 | 1 | 1 | 1 |
| *C. intermedius* | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | ? | 1 | 1 | 1 | 1 | 1 |
| *C. mordax* | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | ? | 0 | ? | ? | 1 | 0 | 1 | 0, 1 |
| *C. posthumus* | ? | 0 | 2 | 0 | ? | ? | 0 | 1 | 1 | ? | ? | 0 | ? | 1 | 0 | 0 | 1 | 0 |
| *C. hemprichi* | 0 | 0 | 2 | 0 | 0 | 0 | ? | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| Bielefeld skull | ? | ? | 2 | 0 | 0 | 0 | 0 | ? | 1 | ? | ? | 0 | ? | ? | 1 | 0 | 0 | 0 |

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