



# A large temnospondyl humerus from the Rhaetian (Late Triassic) of Bonenburg (Westphalia, Germany) and its implications for temnospondyl extinction

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## Abstract

Temnospondyls are a group of basal tetrapods that existed from the Early Carboniferous to the Early Cretaceous. They were characteristic members of Permian and Triassic continental faunas around the globe. Only one clade, the Brachyopoidea (Brachyopidae and Chigutisauridae), is found as relics in the Jurassic of eastern Asia and the Cretaceous of Australia. The other Late Triassic clades, such as Plagiosauridae, Metoposauridae, and Cyclotosauridae, are generally believed to have gone extinct gradually before the end of the Triassic and putative Rhaetian records are stratigraphically poorly constrained. Temnospondyl humeri all show a similar morphological pattern, being stout, short, with widened ends, and with a typical torsion between the proximal and distal heads. Based on these characters, a humerus found in a Rhaetic-type bonebed in unequivocally Rhaetian sediments (marine Exter Formation) in a clay pit at Bonenburg (eastern Westphalia, Germany) was identified as pertaining to the temnospondyl cf. *Cyclotosaurus* sp. The humeral midshaft histology also supports temnospondyl affinities and serves to exclude plesiosaurs and ichthyosaurs from consideration. This find is the geologically youngest record of a non-brachyopoid temnospondyl, indicating that cyclotosaurids survived well into the Rhaetian, likely falling victim to the end-Triassic extinction.

**Keywords** Temnospondyli · *Cyclotosaurus* · Paleohistology · Rhaetic bonebed · Formación Exter

## Resumen

Los Temnospóndilos son un grupo de tetrápodos basales que existieron des del Carbonífero Inicial hasta el Cretácico Inicial. Ellos fueron miembros característicos de las faunas continentales del Pérmico y el Triásico de todo el globo. Tan solo un clado, Brachyopoidea (Brachyopidae y Chigutisauridae), se encuentran como relictos en el Jurásico de Asia oriental y del Cretácico de Australia. Los otros clados del Triásico Superior, como Plagiosauridae, Metoposauridae, y Cyclotosauridae, generalmente se cree que se extinguieron gradualmente antes del final del Triásico y los putativos registros en el Raetiense están estratigráficamente pobremente constreñidos.

Los húmeros de Temnospóndilos muestran en todos los casos un patrón morfológico similar, siendo robustos, cortos, con un final ancho, y con una torsión típica entre las cabezas proximales y distales. En base a estos caracteres, un humero encontrado en un *Rhaetic-type bonebed* en sedimentos inequívocamente Raetienses (Formación marina Exter) en un pozo de barro en Bonenburg (Este de Westphalia, Alemania), fueron identificados como pertenecientes al temnospóndilo cf. *Cyclotosaurus* sp. El corte histológico en el eje intermedio del humero también apoya la afinidad con temnospóndilos y sirve para excluir plesiosaurios y ictiosaurios. Este hallazgo es el registro geológico más joven de un temnospóndilo no-braquiopodo, indicando que los cyclotosauridos sobrevivieron hasta bien entrado el Raetiense, posiblemente siendo víctimas de la extinción de finales del Triásico.

**Palabras clave** Temnospondyli · *Cyclotosaurus* · Paleohistología · Rhaetic bonebed · Formación Exter

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## 1 Introduction

Temnospondyls are a large and diverse group of basal amphibian-grade tetrapods. The first finds of temnospondyls date back to the 1820s, when Jaeger described a giant tooth and a piece of the occiput and erected two genera—*Salamandroides* (Jäger 1824) and *Mastodonsaurus* (Jäger 1828). Currently, about 200 genera and 300 species of temnospondyls are known (Schoch 2013). Fossil remains of temnospondyls are found worldwide and document a high taxic and ecological diversity for this group. The largest temnospondyls had a length of up to 6 m (Schoch and Milner 2000), whereas the smallest were only few centimeters long (Boy 1972). Temnospondyls were found in sediments originating from stream, lake and swamp environments (Schoch and Milner 2000; Pawley and Warren 2005). Unequivocally marine forms were reported only from the Early Triassic (Schoch 2014) of the Scandinavian Arctic (Spitsbergen) and Greenland (Schoch and Milner 2000; Kear et al. 2016).

Temnospondyli were first reported from the Early Carboniferous, and they flourished worldwide during the Carboniferous, Permian, and Triassic periods. The only groups present in the Late Triassic are members of the clade Stereospondyli, represented by Brachyopoidea (Brachiopidae and Chigutisauridae), Plagiosauridae, Trematosauroida (including Metoposauridae), and Capitosauroida (Schoch 2013). It is thought, that the majority of temnospondyls had disappeared well before the end-Triassic extinction event (Milner 1993; Lucas and Tanner 2004; Lucas 2017). Finds of non-brachyopids from the Late Triassic are limited mostly to the Carnian and Norian (Schoch and Milner 2000; Schoch 2013; and references therein; but see Lucas 2017, and below). Rhaetian records of temnospondyls are rare and even if present, very often their age is questionable. The main problem with the previous putative records of Rhaetian non-brachyopoid temnospondyls is their origin from continental redbed sequences, in particular of the North American interior, that lack both well-resolved global biostratigraphic correlations and radioisotopic dating.

### 1.1 Youngest records of temnospondyl clades

The only post-Triassic records of temnospondyls pertain to brachyopoids. Brachyopoidea survived in Asia, east of the Turgai Strait, at least until the Late Jurassic (e.g. Shishkin 1991; Maisch and Matzke 2005; Averianov et al. 2008); in Africa (Steyer and Damiani 2005), and in Australia until the Early Cretaceous (Warren 1977; Warren and Hutchinson 1983; Milner 1990; Warren et al. 1991, 1997; Vickers-Rich 1996; Warren and Marsicano 1998, 2000; Schoch 2013). Records of brachyopoids from the Late Triassic are known

from Argentina and India (Marsicano 1993, 1999; Sengupta 1995) while the clade appears to be absent from Europe.

The stratigraphically best constrained record of Rhaetian temnospondyls is the plagiosaurid *Gerrothorax pulcherrimus* that has been described from the Swedish Late Triassic Höganäs Formation of the Bjuv coal mine near Helsingborg (Scania Province) (Fraas 1913; Nilsson 1934, 1946). Based on palynology and plant biostratigraphy, the Triassic-Jurassic boundary has been located in the Helsingborg area at the top of the middle to late Rhaetian Bjuv Member (e.g., Nilsson 1934; Vajda and Wigforss-Lange 2009). However, marine index fossils are lacking in the Höganäs Formation that would corroborate the proposed position of the Triassic-Jurassic boundary in Scania.

Remains of *Gerrothorax pulcherrimus* (Jenkins et al. 2008; Clemmensen et al. 2016; Marzola et al. 2018) and cyclotosaurids (Sulej et al. 2014; Marzola et al. 2017, 2018) have been collected in the Fleming Fjord Formation of East Greenland, previously dated as early Rhaetian. The latest age estimations would place the beds between the mid-Norian to the late Norian (Clemmensen et al. 1998; Andrews et al. 2014). Milàn et al. (2012) briefly noted the presence of non-brachyopoid temnospondyl fragments from the early Rhaetian Kap Stewart Formation (age after Wotzlaw et al. 2014). Based on tusk size, these remains belong to a capitosaurid, although the material is very fragmentary and non-diagnostic (Milàn et al. 2012).

A temnospondyl record of possible Rhaetian age is the small metoposaurid *Apachesaurus* from the continental redbed Redonda Formation of New Mexico (Hunt 1993) that was dated as Norian at the time of the description of the taxon. The fauna from the Redonda Formation (Chinle Group) was the basis for the Apachean land vertebrate faunochron (LVF) of Lucas (2010), which extends from the late Norian to the end of the Triassic (Lucas 2010, 2017). The youngest occurrences of *Apachesaurus* from the top member of the Redonda (Spielmann and Lucas 2012) conceivably could be as young as late Rhaetian based on chonchostracan stratigraphy (Spielmann and Lucas 2012). However, a Triassic-Jurassic boundary cannot be recognized with certainty in the Redonda Formation, and magnetostratigraphic dating of the entire Chinle sediments has been fraught with uncertainties (Lucas and Spielmann 2013).

Putative post-Norian temnospondyl material was described from a bonebed of the Algarve region, Portugal, by Witzmann and Gassner (2008) who assigned a latest Triassic or Early Jurassic age to the bonebed. However, a basal phytosaur described by Mateus et al. (2014) and a new species of *Metoposaurus* (Brusatte et al. 2015) from these beds support a chronostratigraphic age for this material around the Carnian-Norian boundary. Dzik et al. (2008) reported temnospondyl remains (cyclotosaurids and plagiosaurids)

from the Polish Late Triassic locality of Lisowice (Lipie Śląskie clay pit). Paleobotanical data indicated an early Rhaetian age for this fauna (Dzik et al. 2008; Niedźwiedzki and Sulej 2008), but the latest integrated geological study summarized in Szulc et al. (2015) indicates a Norian age, instead.

Plagiosaurid and capitosaurid remains are also known from the Saint-Nicolas-de-Port locality in France, which originally was dated as Rhaetian. However, the vertebrate fauna corresponds to the top of the Middle Keuper of Germany and thus should be placed close to the boundary between the middle Norian and the late Norian (Buffetaut and Wouters 1986).

In the older literature, there are also reports of temnospondyls from the classical Rhaetic bonebeds of SW England, such as Aust Cliff (Storrs 1994). However, this material, consisting of tooth-bearing bones and isolated teeth, was reassigned to a large holostean-grade fish related to *Birgeria* for which Storrs (1994) erected the genus *Severnichthys*.

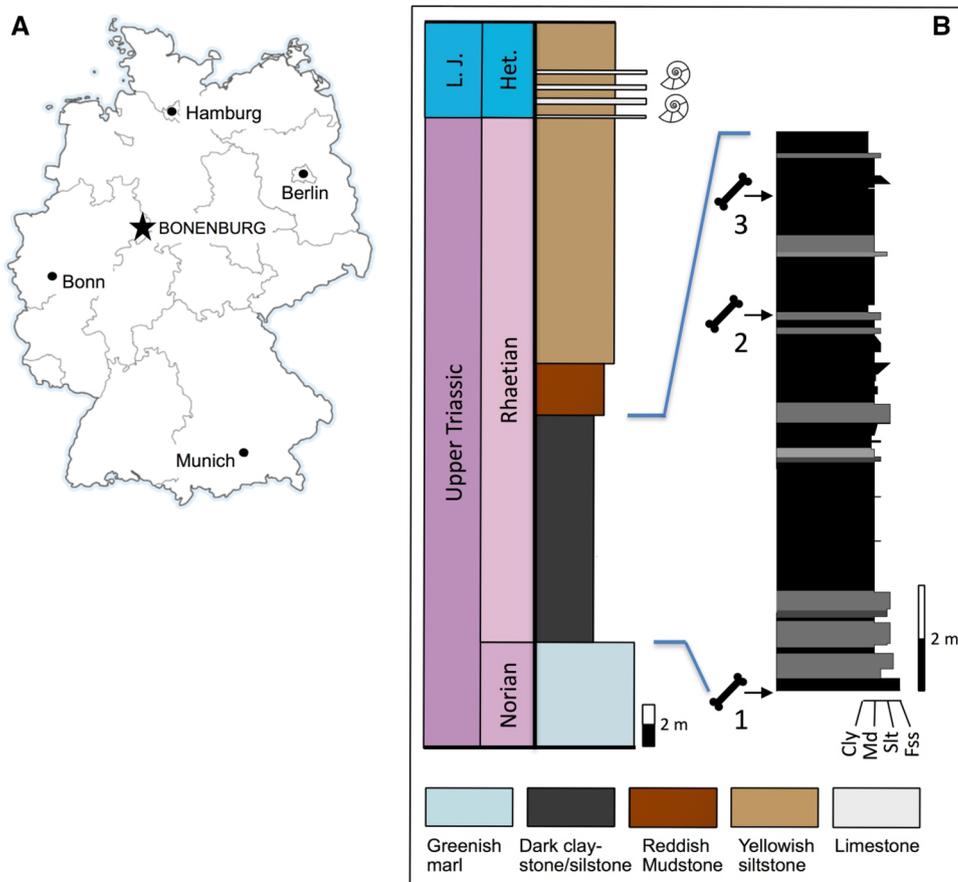
This brief review shows that there are no unequivocal records of non-brachiopoid temnospondyls of Rhaetian age because of the inherent difficulties of dating continental, and in particular redbed, sequences, the source of most temnospondyl remains. We here describe the first unequivocal

Rhaetian non-brachiopoid temnospondyl fossil, a humerus collected from a Rhaetic-type bonebed in a clay pit (clay pit #III of the Ziegelwerke Lücking) near Bonenburg, City of Warburg, in eastern Westphalia, Germany. The Bonenburg pit offers excellent exposures and marine biostratigraphic control, suggesting that the specimen is late Rhaetian and thus the youngest unequivocal non-brachiopoid temnospondyl amphibian record known to date. To augment the morphological description of the humerus, paleohistology was used as an additional tool for distinguishing the find from amniotes known from this bonebed at this locality and to corroborate its temnospondyl affinities.

## 1.2 Geological Setting of the Bonenburg Clay Pit

The pit is divided into two geological blocks separated by a fault, with four geological stages being represented (Norian through Sinemurian). Lying to the northeast of the fault, there are middle Sinemurian dark ammonite-bearing shales, while to the southwest of the fault, there is a section comprising the upper Norian (Steinmergelkeuper), thick Rhaetian sediments, a conformable and excellently exposed Triassic/Jurassic boundary, and the lowermost Hettangian (Sander et al. 2016), again bearing ammonites. The lower

**Fig. 1** Locality and horizon of cf. *Cyclotosaurus* sp. humerus LWL-MFN P 64371. **a** Location of Bonenburg clay pit in eastern North Rhine-Westphalia, Germany. **b** Measured section of the Norian to Hettangian deposits with the three superimposed bonebeds (indicated by bone symbol and number) in the Exter Formation. Horizons of lowermost Jurassic ammonites indicated by silhouettes. Colors of the rock types in the main stratigraphic column approximate colors in fresh outcrop. Abbreviations: Cly, claystone; Fss, fine-grained sandstone; Hett., Hettangian; L. J., Lower Jurassic; Md, mudstone; Slt, siltstone. Modified from Wintrich et al. (2017)



**Table 1** Faunal list of bonebed 2 from the Rhaetian Exter Formation of clay pit in Bonenburg, City of Warburg, Westphalia, Germany. The material is accessioned to the collections of LWL-MFN, Münster, Germany (Sander et al. 2016; Wintrich et al. 2017)

Taxon	Material	Clade	Frequency
<i>Hybodus cloacinus</i>	Teeth	Chondrichthyes	Very common
<i>Lissodus minimus</i>	Teeth	Chondrichthyes	Very common
<i>Rhomphaiodon minor</i>	Teeth	Chondrichthyes	Very common
<i>Nemacanthus monilifer</i>	Fin spines	Chondrichthyes	Very common
Hybodontiformes indet.	Fin spines	Chondrichthyes	Very common
<i>Saurichthys</i> sp.	Teeth	Actinopterygii	Common
<i>Sargodon tomicus</i>	Teeth	Actinopterygii	Common
<i>Ceratodus latissimus</i>	Teeth	Dipnoi	Moderately common
cf. <i>Cyclotosaurus</i>	Humerus	Temnospondyli	Unique
Temnospondyli indet.	Jaw and girdle fragments	Temnospondyli	Rare
cf. <i>Shonisaurus</i>	Vertebrae	Ichthyosauria	Moderately common
Plesiosauria sp. A	Vertebrae	Plesiosauria	Moderately common
Plesiosauria sp. B	Vertebrae	Plesiosauria	Moderately common
Plesiosauria sp. C	Vertebrae	Plesiosauria	Moderately common
<i>Pachystropeus rhaeticus</i>	Vertebrae, limb bones	Choristodera/Thalattosauria	Very common
<i>Lepagia gaumensis</i>	Tooth	Cynodontia	Unique

part of the Rhaetian consists of about 10 m thick dark marine clays and siltstones of the Exter Formation. The Exter Formation is followed by 16.5 m of maroon, grey, yellowish mudstones, and siltstones. The dark shales of the Exter Formation contain three Rhaetic-type bonebeds (Fig. 1). The middle one is divided into a lower bonebed (bonebed 2a) and an upper bonebed (bonebed 2b) that are separated by 8 cm of dark mudstone.

The Bonenburg bonebed fauna consists of Chondrichthyes, Osteichthyes, and tetrapods (Table 1; see also Sander et al. 2016, Wintrich et al. 2017). Chondrichthyes and Osteichthyes are represented mainly by teeth and scales, forming the matrix of the bonebed, but also by fin spines and skull bones (Sander et al. 2016, Wintrich et al. 2017). Both plesiosaurs and ichthyosaurs were recognized mostly in the form of isolated vertebrae and teeth from bonebeds 2 and 3. Moreover, a single non-mammalian synapsid tooth (Schwermann 2016) and abundant isolated bones of the putative oldest choristodere *Pachystropeus rhaeticus* are known from bonebed 2 (Sander et al. 2016, Wintrich et al. 2017). In addition to the bonebed material, the Bonenburg clay pit produced an articulated skeleton of a plesiosaur (Sander et al. 2016, Wintrich et al. 2017), which was discovered by private collector Michael Mertens about 3 m below bonebed 2 in 2013.

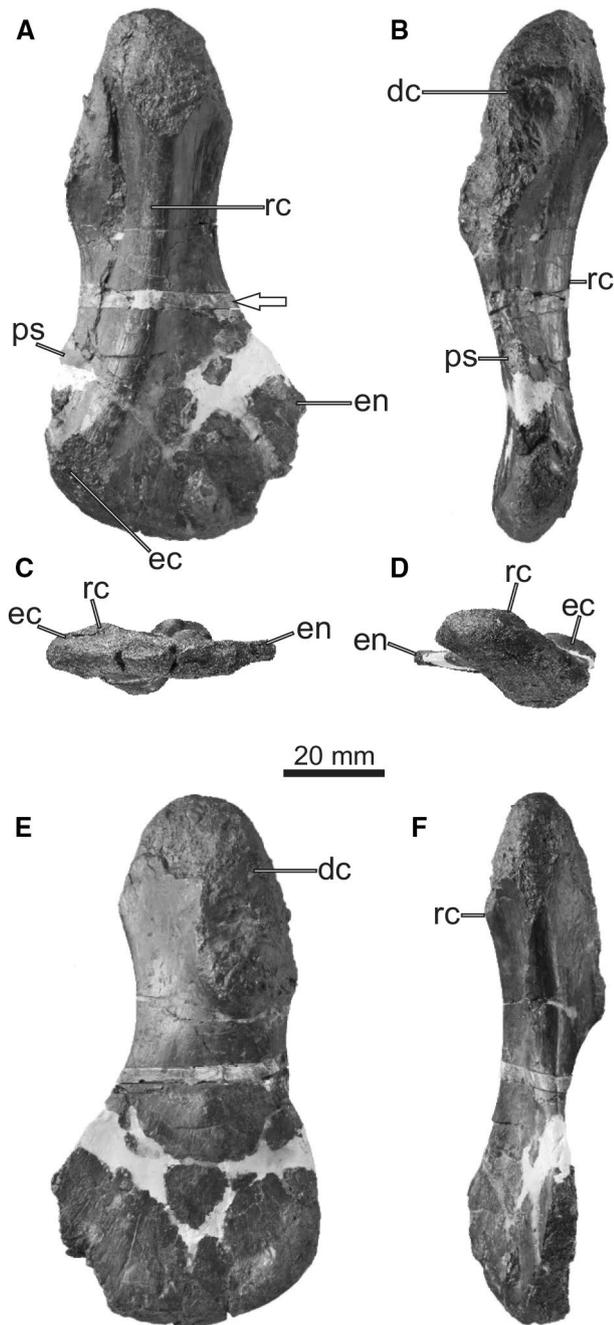
## 2 Material

The specimen on which this study is based is a left humerus of a temnospondyl. The humerus was found in bonebed 2 (although it is not known whether it derives from bonebed

2a or 2b) in the clay pit #III of the Ziegelwerke Lücking, 1 km N of the village of Bonenburg (Sander et al. 2016, Wintrich et al. 2017). The discovery was made by Michael Mertens in 2014. The original specimen (Fig. 2) is in the collections of the LWL Museum für Naturkunde, Münster, Germany, accessioned under the collections number LWL-MFN P 64371. A plaster cast is accessioned to the collections of the Goldfuß Museum (Steinmann Institute, University of Bonn) under the collections number STIPB A 168.

## 3 Methods

After the mechanical preparation, two thin sections of the humerus were done approximately at midshaft. Because of the strong dark diagenetic coloration of the bone, especially in the outermost part, it was necessary to grind one of the two sections down to below standard thickness of 50 µm to allow observation in polarized light and to reveal histological details in the darkest parts. After sectioning, the bone was reconstructed from molds taken before section by filling the gap with plaster molds taken before sectioning. The thin sections were done in the paleohistological laboratory of the Division of Paleontology of the Steinmann Institute, University of Bonn, Germany, following the procedure described by Lamm (2013), although with one deviation: instead of silicon-carbide paper for grinding of the thin sections, a slush of silicon-carbide grinding powder was used with grit sizes of 400 and 600. Additionally, the sections were polished with a grit size of 800, and protected finally with a cover slip.



**Fig. 2** Cf. *Cyclotosaurus* sp. humerus LWL-MFN P 64371 in **a** dorsal, **b** anterior, **c** distal, **d** proximal, **e** ventral, and **f** posterior views. Abbreviations: dc, deltopectoral crest; ec, ectepicondyle; en, entepicondyle; ps, supinator process; rc, radial crest. The arrow marks the plane of histological sectioning

## 4 Results

### 4.1 Systematic paleontology

Temnospondyli Zittel, 1887–1890

Stereospondyli Zittel, 1887–1890

Capitosauroida Säve-Söderbergh, 1935

Cyclotosauridae Shishkin, 1964

*Cyclotosaurus* Fraas, 1889

cf. *Cyclotosaurus* sp.

### 4.2 Morphological description

The humerus is 167 mm long. At its narrowest point, in the middle of the shaft, it is 50 mm wide, whereas it has a maximum width of 87 mm at the distal end (Fig. 2). The torsion angle between the proximal and distal ends is about  $34^\circ$ . The shaft is dorsoventrally flattened and short (Fig. 2). In dorsal view, the radial crest (after Sulej, 2007) is centered along the dorsal side of the shaft and extends from its proximal posterior margin to the distal anterior margin in a slight curve (Fig. 2a). The proximal end is slim and of about the same width as the shaft. The articular surface is convex with a tight curvature that tapers to a narrow termination.

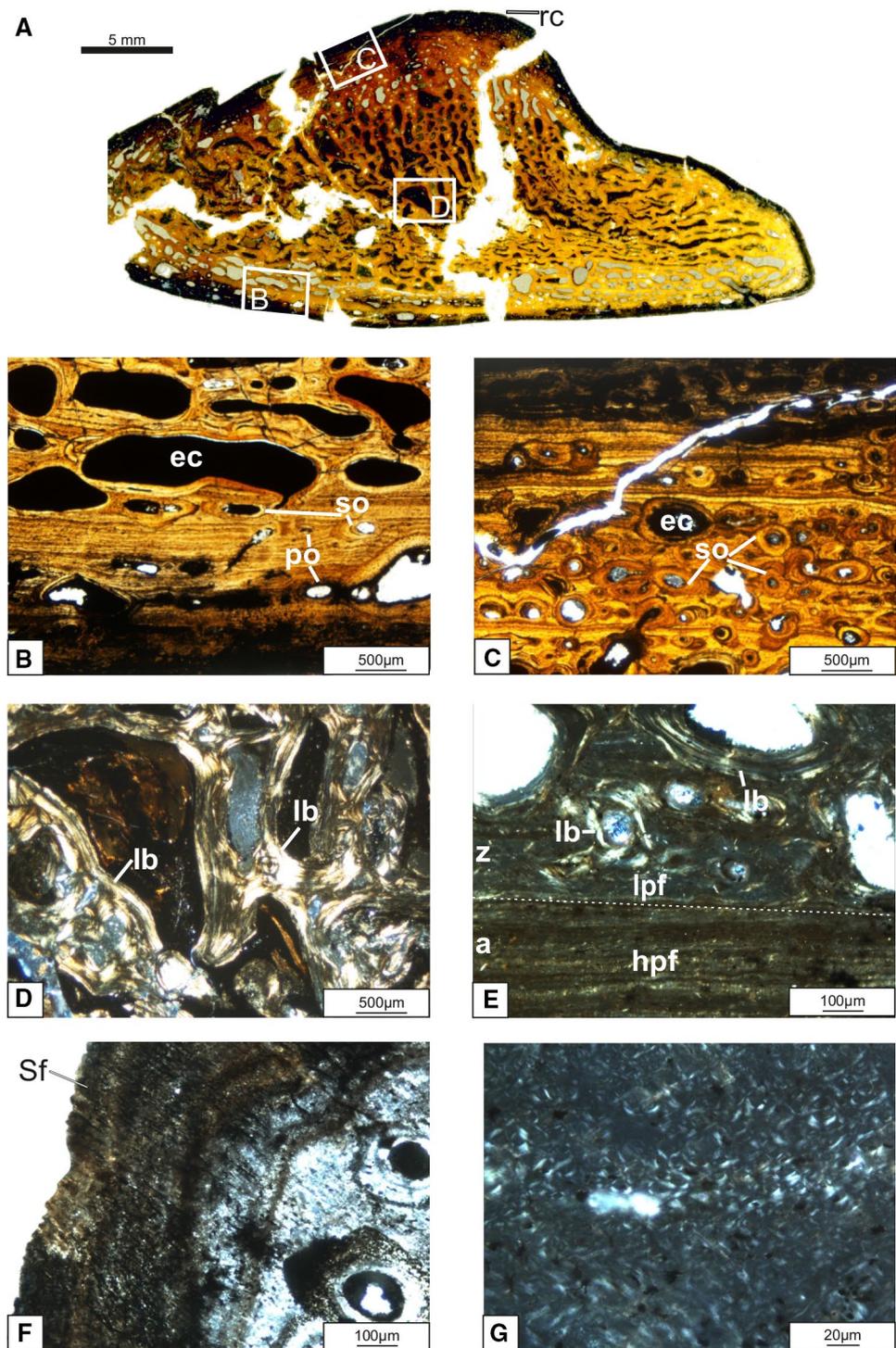
In addition, the entire articular surface of the proximal end is unfinished bone (Fig. 2a, d). This suggests that cartilage was covering the articular surface during the lifetime of the animal.

The deltopectoral crest (Fig. 2b, e) forms the anterior edge of the humerus head and extends almost to the mid-shaft. The distal margin of the humerus extends in a semi-circular end and is wider compared to the rest of the bone (Fig. 2a, e); it shows a posteriorly widened, thin entepicondyle and a thicker ectepicondyle (Fig. 2a, c). The ventral side of the shaft is relatively smooth and flat (Fig. 2e). The anterior margin of the humerus is more or less straight except for the middle of the shaft, where there is a smooth and rounded margin. The supinator process is not recognizable (Fig. 2a, e). The posterior margin of the shaft is longer than the anterior margin and forms an even curve from proximal to distal (Fig. 2a, e).

### 4.3 Histological description

The histological cross section done approximately in the middle of the shaft is triangular, reflecting the transversal morphology of the shaft, with the top of the triangle representing the radial crest (Fig. 3a). The entire bone section is highly spongy (Fig. 3a). A precise transition zone between medullary region and cortex or perimedullary region is difficult to define. The inner part of the bone is somewhat crushed, and thus it is difficult to determine

**Fig. 3** Histology of the mid-shaft of cf. *Cyclotosaurus* sp. humerus LWL-MFN P 64371. **a** Microanatomy of the midshaft, image in correct anatomical position with dorsal to the top. Areas in boxes are enlarged in subsequent figure parts as labelled. **b** Close-up of cortex on ventral side; image in normal light. **c** Close-up of cortex on dorsal side with accumulation of secondary osteons; image in normal light. **d** Close-up of central part of section with secondary trabeculae; image in cross-polarized light. **e** Lamellar-zonal bone tissue showing highly organized parallel-fibered bone in an annulus and less organized parallel-fibered bone in a zone; image in cross-polarized light. **f** Sharpey's fibers visible in the periosteal bone next to the posterior edge. **g** Fibrous structure of deep cortex. Images f and g in cross-polarized light are taken from the thinner of the two sections. Abbreviations: a, annulus; ec, erosion cavity; hpf, highly organized parallel-fibered bone; lb, lamellar bone; lpf, less organized parallel-fibered bone; po, primary osteon; rc, radial crest; Sf, Sharpey's fibers; so, secondary osteon; z, zone



if an empty medullary region was present. Over most of the section, irregular bone trabeculae are visible, with large intertrabecular cavities orientated dorsoventrally (Fig. 3a). Posteriorly, the trabecular bone nearly reaches the surface, and trabeculae orientation is anteroposteriorly (Fig. 3a). Only in the outermost part, a thin compact layer is visible,

mostly consisting of lamellar-zonal bone with various orientations of the vascular canals. On the ventral side, the vascular canals differ in size, but a dominant longitudinal pattern is visible, forming rows oriented parallel to the bone surface (Fig. 3b). On the anterior and dorsal sides, the vascular canals located close to the bone surface are smaller and

longitudinally arranged (Fig. 3c). The different organization of vascularization results in two microanatomical patterns, the first in the deeper part of section with irregular trabeculae and the second with a layered organization of the trabeculae.

Notably, even the trabeculae in the deep parts of the section retain some primary bone in the interstitial areas between the secondary bone. Only a very small area in the central section seems to be exclusively of secondary origin (Fig. 3d). The amount of primary bone increases towards the periphery, with the cortex consisting mostly of parallel-fibered bone, although the degree of crystallite organization varies (Fig. 3e). In the cortex, primary bone in the areas of the annuli is very highly organized, showing an almost lamellar structure, whereas it is less organized in the zones (Fig. 3e). Secondary lamellar bone (Fig. 3d, e) is found around the erosion cavities inside the section and also fills most of the space between the cavities.

Remodeling activity appears to follow the primary vascularity. Dorsally, especially in the area of the radial crest, the remodeling process is very intensive, resulting in a large amount of secondary osteons (Fig. 3c). On the ventral side, erosion exceeds deposition, resulting in the secondary erosion cavities oriented perpendicularly to the bone surface (Fig. 3b). Also, the increasing size of the erosion cavities in the inner part of the bone is clearly visible (Fig. 3a). However, it is not possible to estimate the size of the largest cavities, because many of the trabeculae have been destroyed by crushing. Small secondary osteons are also present between the erosion cavities.

Short Sharpey's fibers are visible below the bone surface (Fig. 3f), and in some areas in the innermost part of the bone, some thick fibers are present (Fig. 3g). Osteocyte lacunae are preserved in high numbers in every part of the thin section. They vary in shape from lenticular to isometric.

## 5 Discussion

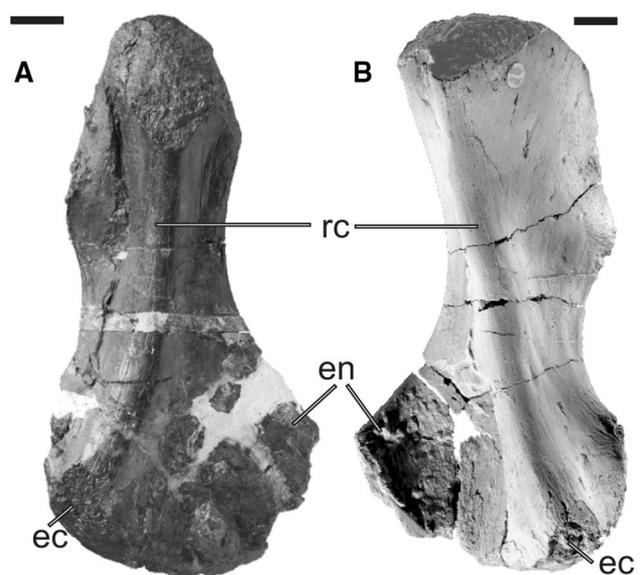
### 5.1 Morphological comparison with ichthyosaur and plesiosaur humeri

Since ichthyosaur and plesiosaur humeri bear a superficial resemblance to the bone described in this paper, they need to be included in the discussion. The humeri of ichthyosaurs and plesiosaurs are both simplified morphologically compared to those of terrestrial tetrapods, but they differ from the present specimen in important ways. The Bonenburg humerus is too elongated to pertain to an ichthyosaur, presenting a distinctive shaft. Such a shaft is primarily seen in Jurassic ichthyosaurs, while many Triassic ones are dorsoventrally flattened or even disc-like. The bone also has

a continuous dorsal crest, which is lacking in ichthyosaurs (cf. McGowan and Motani 1999). The lack of a continuous dorsal crest applies to plesiosaurs as well, which also lack the torsion between the proximal and distal ends. Humeri of plesiosaurs have a straight shaft, with an oval cross section at midshaft (Romer 1956; O'Keefe 2004). Furthermore, the proximal end of the plesiosaur humerus is thickened and has an oval articular surface, while its distal end is distinctly widened and flattened.

### 5.2 Morphological comparison with other Late Triassic Temnospondyli

As already noted, the Stereospondyli, including the Brachiopteroidea (Brachiopidae and Chigutisauridae), Plagiosauridae, Trematosauroida (represented by Metoposauridae), and Capitosauroida (represents by Cyclotosauridae) are the only temnospondyl groups known from the Late Triassic (Schoch 2013). Plagiosauridae is a long-lived taxon, appearing first in the Middle Triassic and surviving until the end of Norian (Jenkins et al. 2008). The Late Triassic plagiosaurids are *Plagiosaurus depressus* and *Gerrothorax pulcherrimus* (Jaekel 1914; Fraas 1913; Nilsson 1939, 1946; Hellrung 2003; Jenkins et al. 2008). The only known humerus of *Plagiosaurus* belongs to *P. depressus* and was described by Nilsson in 1939. It shows significant torsion, with the proximal and distal ends being at a right angle; a much greater torsion angle than in LWL-MFN P 64371. The *Plagiosaurus* humerus lacks a clearly visible deltopectoral crest



**Fig. 4** The comparison of humeri of **a** cf. *Cyclotosaurus* sp. (LWL-MFN P 64371) and **b** *Cyclotosaurus intermedius* (ZPAL Ab III 887-3) in dorsal view. Abbreviations: ec, ectepicondyle; en, entepicondyle; rc, radial crest. Scale bars equal 1 cm

on the proximal part of the ventral side, but it has a strongly pronounced *latissimus dorsi* process (Nilsson 1939). The humeri of *Gerrothorax* are known for Middle and Late Triassic species and are very similar to that of *P. depressus* (Hellrung 2003; Jenkins et al. 2008). The proximal and distal ends of *Gerrothorax* humeri are at a right angle to each other. The ends are roughened, indicating cartilage presence, and are relatively poorly ossified (Warren and Snell 1991). The ectepicondyle and entepicondyle are weakly expressed (Hellrung 2003). The length of the humerus of *G. pustuloglomeratus* is about 37 mm (Hellrung 2003). Humeri of *G. pulcherrimus* are up to 45 mm long (Jenkins et al. 2008). This means that LWL-MFN P 64371 is significantly longer than the humeri of the different *Gerrothorax* species.

Among trematosaurids, the metoposaur humerus has been described and well characterized in many studies (Fraas 1889; Case 1931, 1932; Sawin 1945; Olsen 1951; Chowdhury 1965; Dutuit 1976; Sengupta 2002; Barycka 2007; Sulej 2007). In all metoposaur taxa, the humerus shows the same general morphology: the shaft is very short, while the distal end is distinctly widened, with a pronounced ectepicondyle and a well-defined supinator process. The humeral shaft is noticeable curved, with the shorter and more strongly curved margin being the anterior one (Fraas 1889; Case 1931, 1932; Sawin 1945; Dutuit 1976; Sengupta 2002; Barycka 2007; Sulej 2007). The humerus of *Metoposaurus krasiejowensis* is known from numerous different-sized specimens that represent a growth series. The smallest of these has a length of 56 mm, whereas the largest measures 107.5 mm (Barycka 2007; Teschner et al. 2018). Among other metoposaurids known humerus length of *Koskinonodon perfectus* ranges from 72 mm to 139 mm (Olsen 1951). The humeri of metoposaurids show always strong torsion between the proximal and distal heads (Olsen 1951; Barycka 2007). However the most distinctive differences between the metoposaurids humeri and the Bonenburg bone are the widening of the distal end and the presence of a supinator process in the metoposaurids.

The humerus is known for only one *Cyclotosaurus* species, *C. intermedius* from the Late Triassic of Poland (Sulej and Majer 2005), and only from a single specimen (Fig. 4). This humerus (ZPAL Ab III 887-3) is about 130 mm long, with the proximal head almost as broad as the shaft; the distal end is rounded and slightly wider. The proximal and distal articular surfaces are flat. The deltopectoral ridge present at the anterior border of the proximal head extends to the midshaft. The distal end is rounded with a thin entepicondyle, a strongly pronounced ectepicondyle, and a weakly differentiated supinator process (Sulej and Majer 2005). On the dorsal side, the radial crest is well visible along the whole length of the bone. The torsion angle of the shaft is about 70°. The morphology of ZPAL Ab III 887-3 is close to specimen LWL-MFN P 64371, with the exception of two characters: (i) the Polish specimen

has a greater angle of torsion than the Bonenburg specimen; (ii) the shape of the proximal and distal articular surfaces are strongly convex in LWL-MFN P 64371, as opposed to ZPAL Ab III 887-3 in which they are almost flat (Fig. 4).

The different humerus torsion observed in *Cyclotosaurus intermedius* and in cf. *Cyclotosaurus* sp. from Bonenburg might potentially reflect the different loading on the forelimb connected with different modes of life and environmental conditions. A lower degree of twist in forelimb bones indicates that rotational movements were more limited than in bones with greater torsion (Gregory 1949; Rackoff 1980). The low degree of twist in forelimb bone of cf. *Cyclotosaurus* sp. compared to *Cyclotosaurus intermedius* would suggest a fully aquatic mode for the former. However, the large sample available for *Koskinonodon perfectus* and *Metoposaurus krasiejowensis* show that humeral torsion may vary considerably within different populations and individuals of the same taxon (Olsen 1951; Barycka 2007). The reasons for such high variability remain an open question. Bone torsion would appear to be strongly linked to the function of the forelimb and thus should be constant within a taxon, or at least be related to changes in function and loading caused by ontogenetic stage and sexual dimorphism. Such a large scatter of the proximo-distal angle in metoposaurids species may thus indicate of low selective pressures on the forelimb performance (Barycka 2007) which results in high intraspecific variability of this character. Since postcranial remains of *Cyclotosaurus* are very rare, we cannot exclude the possibility that variability in torsion is also great in this taxon as a result of low biomechanical loading on the forelimbs. Alternatively, the variability in the torsion of cyclotosaurid humeri could result from differences in the degree of diagenetic crushing of the bone trabeculae. Evidence for crushing is found in the collapsed trabeculae seen in the central region of the thin section, but it is difficult to evaluate how much this affects bone shape.

The difference in articular surface morphology could be related to ontogeny. The *Cyclotosaurus* humerus described by Sulej and Majer (2005) is about 40 mm shorter than the Bonenburg specimen and has less well developed articular surfaces; these differences suggests that the Krasiejów specimen pertains to a considerably younger individual. A gradual change of shape of articular surfaces during ontogeny toward more convex surfaces was also observed for *Koskinonodon perfectus* (Olsen 1951). Finally the different shapes of the bone ends, as well as the different torsion of the shaft, may be species-specific and vary between species of *Cyclotosaurus*.

The final taxon of temnospondyls that the Bonenburg humerus can be compared with is the brachyopoids. The postcrania of brachyopoids are very scantily represented, but humeri are known for a few taxa. A partial humerus is known for Late Triassic *Compsoceros* from Brasil

(Dias-de-Silva et al. 2012) and a complete one from India (Sengupta 1995). Apart from these Late Triassic specimens, the Permian *Bothriceps major* (Woodward 1909, Warren et al. 2011), the Early Triassic *Batrachosuchus* (Cherini 1977), the Middle Triassic *Pelorocephalus* (Bonaparte 1978) and *Vigilius* (Welles and Estes 1969), the post-Triassic taxa *Siderops kehli* (Warren and Hutchinsosn 1983) and *Gobiops desertus* (Shishkin 1991) have preserved humeri. All of the above mentioned taxa have typical stereospondyl humeri, including a well-developed supinator processes and being much more slender than the Bonenburg humerus. In *Gobiops*, the humerus differs from other brachyopoids in that the degree of torsion between the distal and proximal ends is reduced (Shishkin 1991).

### 5.3 Histology as a tool to support taxonomical diagnosis

#### 5.3.1 Histological comparison with ichthyosaur and plesiosaur bones

The bone microanatomy of the Bonenburg humerus shares a cancellous interior and a thin cortex at midshaft with some ichthyosaurs (Houssaye et al. 2014), leading to a superficial resemblance with this clade. However, the arrangement and the size of the trabeculae and vascular spaces of the cancellous bone differ in the two taxa. In particular, the Bonenburg humerus has larger vascular cavities than in ichthyosaurs. These cavities show a layered, circumferential arrangement in the outer region of the section, unlike in ichthyosaurs that have a more equidimensional network of trabeculae (Lopuchowycz and Massare 2002; Houssaye et al. 2014). At the histological level, ichthyosaurs differ distinctively from the Bonenburg humerus in that their primary trabeculae are at least partially formed by woven-fibered bone matrix, entirely missing in LWL-MFN P 64371.

Plesiosaur humeral and femoral bone microanatomy and histology (Wintrich et al. 2017) is very different from that of LWL-MFN P 64371. Plesiosaurs lack cancellous bone at midshaft but preserve a continuous cortical growth record from the fetal bone tissue onward, consisting of radial fibrolamellar bone (Wintrich et al. 2017). Plesiosaurs show distinctive growth marks consisting of an abrupt directional change of the radial canals (Wintrich et al. 2017), while those in the Bonenburg bone are annuli and LAGs. Mature plesiosaur propodials show dense Haversian bone (Krahl et al. 2013; Wintrich et al. 2017).

#### 5.3.2 Histological comparison with long bones of Temnospondyli

Despite differences in phylogenetic position and geologic age, temnospondyl long bone histology is distinctive from

marine reptile histology (e.g., de Ricqlès 1975; Damiani 2000; Steyer et al. 2004; Ray et al. 2009; Mukherjee et al. 2010; Sanchez et al. 2010a, b, c; Konietzko-Meier and Sander 2013; Konietzko-Meier and Klein 2013; Konietzko-Meier and Schmitt 2013; Sanchez and Schoch 2013; Konietzko-Meier et al. 2016; Teschner et al. 2018). The most common bone matrix type in temnospondyls is parallel-fibered bone with a distinctive organization of collagen fibers. Notably, in almost every temnospondyl sample the single fibers of the matrix are recognizably as separate strings in cross-polarized light, giving the parallel-fibered matrix a ‘rough’ appearance. In some areas, the periosteal cortex may even resemble metaplastic bone. Lamellar bone tissue is present in temnospondyls, but mostly as a secondary deposit in erosion cavities or as infilling in primary and secondary osteons. In cross-polarized light, this lamellar bone does not show as ordered a structure as in Amniota (see Georgiadis et al. 2016 for comparison). As a result, the borders between the bone matrix and the primary and secondary lamellar bone are not as sharp as in Amniota (e.g., Klein and Sander 2008a, b).

In temnospondyls, the remodeling process always follows the vascular pattern of the primary tissue, unlike in Amniota, where remodelling activity appears to have little regard for primary vascularity. While secondary enlargement and infill of vascular spaces due to remodeling activity is taking place, the primary pattern is mostly preserved, even in the highly remodeled perimedullary region. Temnospondyls are notable for the almost exclusive lack of radial canals, the dominant orientation of vascular canals being longitudinal, and plexiform (Konietzko-Meier et al. 2016). Finally, a unique character of temnospondyl long bones is the high amount of Sharpey’s fibers in the cortex (Konietzko-Meier et al. 2016). In conclusion, specimen LWL-MFN P 64371 from Bonenburg shows many of the distinctive histological features of temnospondyl long bones.

### 5.4 Paleocological setting of the specimen

The sediments of bonebed 2 (Fig. 1) that yielded humerus LWL-MFN P 64371 were deposited in a shallow marine environment with normal salinity (Sander et al. 2016), with the bonebed representing a concentration deposit from which all the fine-grained sediment was winnowed. This is also indicated by the major component of the bonebed (teeth of marine sharks and bony fish) as well as by the sedimentology and invertebrate fossils such as ophiuroids (Sander et al. 2016). The highly spongy microanatomy of the cf. *Cyclotossaurus* humerus (Fig. 3) indicates an aquatic mode of life, consistent with its occurrence in these marine deposits. However, the Bonenburg bonebed 2 is highly time-averaged and produces samples representing a wide range of habitats (Sander et al. 2016), as is typical for Rhaetic-type bonebeds

in general (Storrs 1994, Mears et al. 2016). Continental, and even terrestrial, input into the bonebed is documented by a single non-mammalian synapsid tooth (Schwermann 2016), whereas river habitats are represented by common lungfish teeth (Sander et al. 2016). On other hand, the Bonenburg bonebed 2 contains choristoderes, ichthyosaurs and plesiosaurs, representing open-water marine to coastal marine elements (Sander et al. 2016; Wintrich et al. 2017). Especially, the high abundance and good preservation of *Pachystropheus* would indeed suggest a shallow marine habitat. However, the environmental signal of the most abundant tetrapod bones in the bonebed, choristodere *Pachystropheus rhaeticus* (Sander et al. 2016), is not clear a priori because later choristoderes were freshwater inhabitants. Thus, the marine depositional environment of the bonebed cannot be taken as evidence that the last non-brachyopid temnospondyls were marine. We propose that the cf. *Cyclotosaurus* humerus was transported out to sea from a freshwater habitat. This is consistent with the notion that marine temnospondyls only existed in the Early Triassic, whereas temnospondyls in general are reliable indicators of freshwater conditions (Schoch and Milner 2000; Pyenson et al. 2014; Sulej et al. 2014; Clemmensen et al. 2016).

### 5.5 Implications for cyclotosaurid evolution

*Cyclotosaurus* is the best documented and most species-rich cyclotosaur genus. Based only on the finds diagnostic to species, the genus ranges from the middle Carnian to the late Norian (Schoch 2008; Marzola et al. 2017, 2018). Different species of *Cyclotosaurus* have been reported from Germany (Fraas 1913; Kuhn 1932, 1939, 1942), Poland (Sulej and Majer 2005), Greenland (Jenkins et al. 1994; Marzola et al. 2017, 2018), Spitsbergen (Kear et al. 2016), and Thailand (Ingavat and Janvier 1981).

Among European species, the stratigraphically oldest undisputed representative of *Cyclotosaurus* is *C. robustus* from the middle Carnian Schilfsandstein beds (= Stuttgart Formation) of southwestern Germany (Meyer and Plieninger 1844; Quenstedt 1850; Schoch and Milner 2000; Schoch 2008). Of similar stratigraphic age is *Cyclotosaurus buechneri* also from the Stuttgart Formation (Witzmann et al. 2016). The stratigraphically next youngest species is the late Carnian species *C. ebrachensis* (Kuhn 1932) from Franconia (northern Bavaria). *C. intermedius* from Krasiejów (Opole region, Poland) was originally described also as a late Carnian species (Sulej and Majer 2005). However, the latest dating suggests that the sediments at Krasiejów are younger, i.e., middle Norian in age (Szulc et al. 2015). Thus *C. intermedius* is stratigraphically correlated with the middle Norian species *C. mordax* and *C. posthumus* (Fraas 1913), both from southern Germany. The youngest known

European cyclotosaurs is the late Norian *C. hemprichi* from Halberstadt in central Germany (Kuhn 1939, 1942; but see Lucas 2017 and below). *Cyclotosaurus* species outside of Europe are known from Thailand, Spitzbergen, and Greenland. The source units are the Norian Huai Hin Lat Formation near Chulabhorn Dam in northeastern Thailand, the De Geerdalen Formation of Spitsbergen (middle–late Carnian in age), and the Norian Fleming Fjord Formation (Ingavat and Janvier, 1981; Jenkins et al. 1994; Kear et al. 2016; Marzola et al. 2017, 2018), respectively. The bone described here thus is the youngest record of the *Cyclotosaurus* known so far.

### 5.6 Implications for Temnospondyli evolution and the end-Triassic extinction event

Traditionally, it was assumed that temnospondyls existed up to Triassic–Jurassic boundary and fell victim to the large extinction event at the end of the Triassic (Colbert 1958). This assumption was later questioned by Milner (1993) and Lucas and Tanner (2004) who posited that the majority of temnospondyls, with the exception of Brachyopoidea, had gone extinct far ahead of the end-Triassic extinction event because of the lack of unequivocally Rhaetian records of the group. The latest review by Lucas (2017, p. 376) states “The record of almasaurids ends in the Otischalkian, and that of mastodontosaurids [capitosaurids in this paper] and trematosaurids [metoposaurids in this paper] ends in the Adamanian. Capitosaurid records are no younger than Revueltian, and metoposaurids and plagiosaurids have records that end in the Apachean”. Assuming that the correlation of the Apachean with the late Norian and the entire Rhaetian is correct, the only Rhaetian non-brachiopid temnospondyls would be metoposaurids and plagiosaurids.

The cf. *Cyclotosaurus* sp. humerus from bonebed 2 at Bonenburg now strongly suggests the survival of at least one more group of non-brachyopid temnospondyls, the capitosaurids, to the late Rhaetian. The previous youngest record of this clade predates the late Norian (Lucas 2017). The Rhaetian occurrence of metoposaurids and plagiosaurids remains unconfirmed but appear likely. Survival of at least capitosaurids would also imply that non-brachiopid temnospondyls were affected by the end-Triassic extinction event and did not go extinct gradually before (contra Milner 1993; Lucas and Tanner 2004; Lucas 2017). However, it cannot be excluded that non-brachyopid temnospondyl diversity and abundance had already decreased gradually during the Norian and that there were only a few populations left in the Rhaetian. In order to be able to decide between these alternatives, more discoveries from chronostratigraphically well constrained Rhaetian localities are needed.

## 6 Conclusions

The large left temnospondyl humerus described here was found in an unequivocally Rhaetian bonebed in the Exter Formation of Bonenburg (Westphalia, Germany). Based on the histological features, mostly the organization of the vascularity and coarse character of the collagen fibres, as well as the structure of the perimedullary region, the bone can be confidently assigned to temnospondyls. At the morphological level, most of the temnospondyl humeri known from the Late Triassic can be excluded from comparison with the Bonenburg specimen simply based on the facts that they are much smaller with less ossified articulation surfaces. This applies especially to plagiosaurids. Metoposaurids have a very characteristically wide distal end and well developed supinator process, both of which are lacking in the specimen described here. Compared to brachyopoids, the Bonenburg bone is more robust and lacks a well developed supinator process which is always present in brachyopoids. Thereby, we assign the Bonenburg humerus to a cyclotosaurid as cf. *Cyclotosaurus* sp. The specimen from Bonenburg is the first unequivocal non-brachyopoid temnospondyl record from the Rhaetian stage because records from the Apachean LVF cannot be shown with certainty to pertain to this stage and the age of the Bjuv Member of the Höganäs Formation of Scania is not constrained by marine index fossils. However, more fossil evidence from the Late Triassic is needed to understand temnospondyl evolution and extinction during this critical time period in the history of life.

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