

A phytosaur osteoderm from a late middle Rhaetian bone bed of Bonenburg (North Rhine-Westphalia, Germany): Implications for phytosaur extinction

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Academic editor: Florian Witzmann ♦ Received 23 October 2023 ♦ Accepted 21 February 2024 ♦ Published 13 March 2024

Abstract

Although there are problematic earliest Jurassic records, phytosaurs are thought to have become extinct during the Rhaetian. A newly-discovered left paramedian phytosaur osteoderm from a clay pit in Bonenburg, Kreis Höxter, North Rhine-Westphalia, Germany, is the youngest, well-dated phytosaur record. This osteoderm was found in a bone bed (Bone Bed 2) in the Contorta Beds of the Rhaetian Exter Formation. Palynology constrains the age of Bone Bed 2 to the late middle Rhaetian (ca. 203.5 million years ago). The Bonenburg osteoderm cannot be assigned to any named species. It most closely resembles some osteoderms from the Rhaetian of Halberstadt in Central Germany. Phytosaurs survived in Europe to at least the late middle Rhaetian, probably falling victim to the end-Triassic extinction event about two million years later.

Key Words

End-Triassic extinction event, Exter Formation, Germany, osteoderm, Phytosauria, Rhaetian

Introduction

Phytosaurs are a distinctive clade of predominantly Late Triassic basal archosauriforms with clear adaptations to a semi-aquatic lifestyle (Stocker and Butler 2013). Most phytosaur remains are from fluvial deposits. However, phytosaur habitats occasionally extended into the marine realm as evidenced by phytosaur finds in marine sediments from the Alps (Renesto and Paganoni 1998; Gozzi and Renesto 2003; Renesto 2008; Butler et al. 2019). From the Carnian onwards, phytosaurs were already widespread, being found in many Norian localities of the Triassic Northern Hemisphere (Brusatte et al. 2013; Lucas 2018; Brownstein et al. 2023). However, there are many fewer phytosaur finds from the Triassic Southern Hemisphere (Brusatte et al. 2013; Barrett et al. 2020; Datta and Roy 2023). Phytosaur systematics relies heavily on the well-ossified skulls (Jones and Butler

2018) which are commonly found in isolation. In addition to skulls and skeletons, the phytosaur fossil record consists of their characteristic osteoderms, the subject of the current contribution.

Classical rock units for phytosaur discoveries are the Middle and Upper Keuper sediments of the Germanic Basin. The Keuper can be subdivided into the Lower Keuper (also Lettenkeuper; roughly late Ladinian to Carnian in age), the Middle Keuper (presumed to cover the Norian) and the Upper Keuper (Rhaetian). After the continental conditions of the Middle Keuper, the Upper Keuper is mainly marine-deltaic (Barth et al. 2018), recording the initial marine incursions into the Germanic Basin, followed by its complete inundation in the Early Jurassic. In central and northern Germany, the deposits of the Upper Keuper, traditionally also called *Rhät* as a lithostratigraphic term, are assigned to the Exter Formation (Barth et al. 2018).

The locality of Bonenburg and its lithostratigraphy

The Bonenburg clay pit (Fig. 1) is a relatively new fossil locality that was put on the map by the unique discovery of a Triassic plesiosaur skeleton (Sander et al. 2016; Wintrich et al. 2017). However, most fossils from Bonenburg come from several bone beds (condensation horizons rich in teeth, fish scales and bones) (Sander et al. 2016).

The stratigraphy of the Bonenburg clay pit (Fig. 1B) presents one of the best examples for the epicontinental Triassic-Jurassic boundary in Europe (Sander et al. 2016; Schobben et al. 2019; Gravendyck et al. 2020), with a continuous section from the Norian to the Sinemurian (Fig. 1B). However, most of the section in the pit pertains to the Rhaetian Exter Formation. The base of the Exter Formation starts out with about 2 m of Postera Beds. No fossils are found in this unit. Next come > 11 m of the Contorta Beds (Sander et al. 2016; Gravendyck et al. 2020). These consist of dark clay- and siltstones and, within them, at least four bone beds are intercalated (Sander et al. 2016; Gravendyck et al. 2020) (Fig. 1B). On top of the Contorta Beds, there are about 16.5 m of the Triletes Beds of the Exter Formation, overlain by marine carbonates and mudstones of Hettangian age, pertaining to the Pylonotenton Formation.

Biostratigraphic dating of Bone Bed 2

The three best defined bone beds in the Contorta Beds (Fig. 1B) are located 0 m, 7 m and 9 m above the base of the Contorta Beds. Bone Bed 1 is about 1 cm thick, containing mainly small fish and shark teeth (Sander et al. 2016). Bone Bed 2, the source of the osteoderm described in this study, is divided into two parts: the lower Bone Bed 2a and the upper Bone Bed 2b, separated by 8 cm of claystone (Sander et al. 2016). Bone Bed 2 is the most important overall due to its faunal contents. Bone Bed 3 hosts larger bones and is less continuous than Bone Bed 2. The material from Bone Bed 3 is often heavily abraded and encased in phosphate concretions.

Bone Bed 2 contains a vertebrate fauna of Rhaetian age (Sander et al. 2016; Wintrich et al. 2017) and, together with the entire section, has been precisely dated, based on palynomorphs (Fig. 1B). Dense sampling and good palynomorph preservation allowed the subdivision of the palynozones of the North German Basin (Barth et al. 2018) into subzones in the Bonenburg section (Gravendyck et al. 2020). Thus, Bone Bed 2 is situated in the upper half of the RLb subzone of Gravendyck et al. (2020). Subzone RLb is the middle subzone of the *Rhaetipollis-Limbosporites* palynozone (Fig. 1B). The high location of Bone Bed 2 in this subzone indicates that the bone bed is late middle Rhaetian in age (Fig. 1B).

By age interpolation based on the Triassic chronostratigraphic chart of Ogg et al. (2020), Bone Bed 2 is about 203.5 million years old, two million years before the end of the Triassic 201.4 million years ago. This palynologically determined age is consistent with the occurrence

of the conchostracan *Euestheria brodieana* (Kozur and Weems 2010) right below Bone Bed 2 (Schobben et al. 2019), which, according to Ogg et al. (2020, fig. 25.5), occurs in the middle and late Rhaetian.

Bone Bed 2 faunal contents

The Contorta Beds containing the bone beds are of marine origin (Sander et al. 2016). As the Contorta Beds are a transgressive unit of marine-deltaic deposits (Barth et al. 2018), the bone beds, including Bone Bed 2, were sourced from a very wide range of habitats, from open marine to terrestrial (Sander et al. 2016). In Bone Bed 2, teeth, scales and skull fragments of Chondrichthyes and of Actinopterygii, as well as tooth plates of Dipnoi (Sander et al. 2016) represent fully aquatic, mainly marine habitats. Vertebrae and other remains belonging to ichthyosaurs and plesiosaurs are common (Sander et al. 2016) and represent open marine habitats. Semi-aquatic and terrestrial habitats are represented by a high diversity of tetrapods. Postcranial bones of the putative choristoderan *Pachystropheus* are common and remains of Temnospondyli are moderately common (Sander et al. 2016; Konietzko-Meier et al. 2019). Much rarer finds belong to Cynodontia, Rhynchocephalia, Phytosauria, Pterosauria and Dinosauria (Sander et al. 2016; pers. obs. PMS).

Phytosaur osteoderms

From sufficiently articulated skeletons, it is known that phytosaurs had a paramedian row of osteoderms running down the neck (on either side of the sagittal plane, thus two rows) and two dorsal paramedian rows of osteoderms (thus four rows altogether), extending from the trunk to at least the base of the tail (Stocker and Butler 2013). In addition, phytosaurs had a gular shield of osteoderms, protecting the neck region ventrally (Huene 1922; Stocker and Butler 2013). All types of osteoderms appear to have been partially overlapping (Huene 1922). However, because the osteoderms are not connected to the skeleton in phytosaurs, they are often found in isolation (e.g., Huene (1922)). Isolated osteoderms can be assigned to either the paramedian or gular series and to one side of the body, based on patterns of asymmetry. Further information on phytosaur osteoderm morphology is found in Suppl. material 1.

Extinction - the last phytosaurs

Phytosaurs most likely became extinct some time before or at the Triassic-Jurassic boundary. How far phytosaurs ultimately survived into the Rhaetian or even the Jurassic is still a subject of debate. In their review paper on phytosaurs, Stocker and Butler (2013) somewhat apodictically note that 'At present, the confirmed fossil record of the group extends from late Carnian – latest Rhaetian'. Another view is that very few phytosaurs managed to survive into the Rhaetian in the first place (Lucas 2018). This, amongst other things,

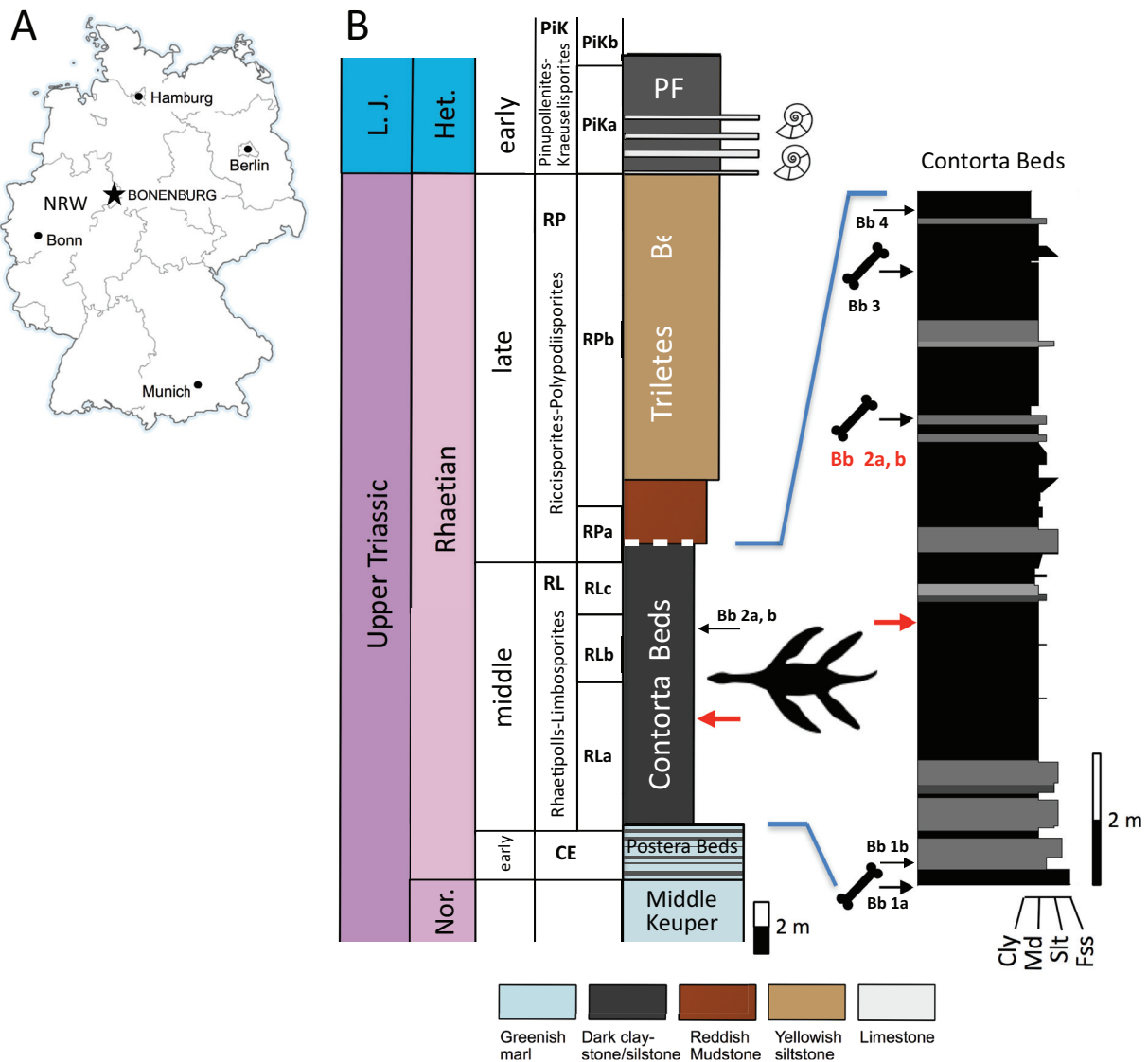


Figure 1. Locality and stratigraphy of Bonenburg clay pit #3 of Lücking Brick Company. **A.** Location of the clay pit in the eastern part of the State of North Rhine-Westphalia, Germany; **B.** Simplified stratigraphy of the Norian to Hettangian section exposed at the Bonenburg clay pit, with a special emphasis on the location of the four bone beds and the plesiosaur skeleton in the section. The main part of the section is made up by the Exter Formation which is subdivided into the Postera Beds, Contorta Beds and Triletes Beds, in ascending order. The thick dashed line on top of the Contorta Beds indicates truncation by a low-angle fault. Note that the reddish mudstones above the dashed white line also belong to the Triletes Beds. Colours of the rock types in the main stratigraphic column approximate colours in fresh outcrop. General abbreviations: Bb, bone bed; Cly, claystone; Fss, fine-grained sandstone; Het., Hettangian; L. J., Lower Jurassic; Md, mudstone; Nor., Norian; PF, Pisonotenton Formation; Slt, siltstone. Abbreviations of palynozones: CE, *Classopollis-Enzonalasporites* palynozone; RL, *Rhaetipollis-Limbosporites* palynozone; RP, *Riccisporites-Polypodisporites* palynozone; PiK, *Pinuspollenites-Kraeuselisporites* palynozone. Subzones are labelled alphabetically. Modified from Wintrich et al. (2017), palynostratigraphy is from Gravendyck et al. (2020).

led Lucas to conclude for terrestrial tetrapods that ‘There is no compelling evidence of tetrapod mass extinctions at either the Carnian-Norian or the Triassic-Jurassic boundaries’. These diverging statements invite a review of the contender for the ‘last phytosaur’ status and, more generally, of the European record of latest Triassic and earliest Jurassic (if any) phytosaurs (Table 1).

***Machaeroprosozus* from the Wingate Sandstone of Utah**

The phytosaur genus *Machaeroprosozus* (*Redondasaurus*) is known from the Late Triassic of the western

United States (Hunt and Lucas 1993; Lucas 2018; Brownstein 2023). It was first described from the Redonda Formation, the uppermost unit of the Dockum Group (Hunt and Lucas 1993). One specimen of *Machaeroprosozus* (UMNH VP22354), in particular, was noted to be the ‘last phytosaur’ (Lucas et al. 1997) because it was discovered within the Wingate Sandstone of Lisbon Valley, southern Utah (Morales and Ash 1993). The Wingate Sandstone consists of fine-grained eolian sandstones (Martz et al. 2014) and overlies the Church Rock Member, which is the uppermost member of the Chinle Formation (Morales and Ash 1993). It was

Table 1. The global record of post-Norian (Rhaetian and Jurassic) phytosaurs, organised by age, youngest occurrences at the top.

Taxon	Collection, Spec. #	Locality	Age	Formation	Material	Remarks	Key references
Phytosauria indet.	?	Hettange-Grande	Hettangian	Bonebed in <i>Angulata</i> Zone	Teeth	May be reworked, may not be phytosaur	Huene and Maubeuge 1954; Buffetaut 1993
? Phytosauria indet.	Various	Southern Germany	Norian to Hettangian	Rhaeto-Liassic Bonebed	Teeth	Teeth named ' <i>Termatosaurus albertii</i> ,' may be sauropterygian.	Maisch and Kapitzke 2010
"cf. <i>Mystriosuchus</i> "	SMNS	St. Audries Bay, Watchet, UK	Rhaetian to Hettangian	Pre- <i>planorbis</i> Beds, Blue Lias	Rostrum fragment	May be thalattosuchian, not phytosaur	Maisch and Kapitzke 2010
<i>Machaeroprotopus</i> sp.	UMNH VP22354	Lisbon Valley, Utah, USA	Rhaetian (not latest)	Big Indian Rock beds, Wingate Sandstone	Partial skull impression	–	Martz et al. 2014
Phytosauria indet.	WMNM P98442	Bonenburg, Germany	late middle Rhaetian	Upper part of Contorta Beds, middle Exter Formation	Isolated osteoderm	–	This study
<i>Mystriosuchus</i> sp.	NMB, many	Niederschönthal (today Schönthal, part of Füllinsdorf) near Basel, Switzerland	early to middle Rhaetian	Lower bonebed, Belchen Member of Klettgau Formation	Isolated cranial and postcranial bones, teeth, osteoderms	Huene (1911a, b) called material <i>Mystriosuchus ruetimeyeri</i> , in Huene (1922) paradigm of <i>Angistorhinops ruetimeyeri</i>	Huene 1911a, b, 1922; Meyer and Wetzel 2021
<i>Mystriosuchus</i> sp.	MfN MB.R. 2747	Steinlah near Salzgitter, Germany	early Rhaetian	Lower part of Exter Formation	Partial skeleton incl. osteoderms	<i>Angistorhinops ruetimeyeri</i> of Huene. Represents the only substantial Rhaetian phytosaur material from Europe (Jones and Butler 2018)	Schlönbach 1860; Huene 1922; Jones and Butler 2018; Butler et al. 2019; R. Irmis pers. comm.
Phytosauria indet.	MfN MB.R. 4224, 4372.1	Halberstadt, Germany	early Rhaetian	Exter Formation?	Isolated osteoderms	Sculpture similar to Bonenburg osteoderm WMNM P98442	Huene 1922
Phytosauria	MfN, many	Halberstadt, Germany	early Rhaetian	Exter Formation?	Isolated cranial and postcranial bones, teeth, four osteoderms	Contains both "small phytosaur" and <i>Angistorhinops ruetimeyeri</i> of Huene. Some may pertain to <i>Mystriosuchus</i> sp. nov.	Huene 1922
Phytosauria indet.	Various	UK	early Rhaetian	Rhaetic bone bed	Teeth	–	Storrs 1994; Stocker and Butler 2013; Whiteside and Duffin 2021; Cawthorne et al. 2024
<i>Jupijkam paleofluvialis</i>	Yale Peabody Museum YPM VPPU 7920	Nova Scotia, Canada	late Norian to early Rhaetian	Whitewater Mbr. of Blomidon Fm.	Antorbital skull, single osteoderm	Illustration and description of osteoderm uninformative	Brownstein 2023
Phytosauria indet.	PIMUZ uncat.	Hallau, Switzerland	late Norian to early Rhaetian	Klettgau Formation	Teeth	–	Peyer 1944; Sander 1999; Whiteside et al. 2017
Phytosauria indet.	Institut royal des Sciences naturelles de Belgique uncat.	Saint-Nicolas-de-Port, France	late Norian to early Rhaetian	Grès Infraliasiques Formation	Teeth	–	Cuny 1995; Godefroit and Cuny 1997
Phytosauria indet.	Natural History Museum of Zimbabwe	Zimbabwe	late Norian to early Rhaetian	Tashinga Formation	Mandibular fragments, osteoderms, teeth	Osteoderms surface collected and poorly preserved	Barrett et al. 2020
<i>Mystriosuchinae</i> indet.	Indian Statistical Institute ISIR276	India	late Norian to Rhaetian	lower Dharmaran Formation	Partial skull	No details given on morphology and age	Datta and Ray 2023
Phytosauria indet.	PIMUZ uncat.	Grisons, Switzerland	late Norian to Rhaetian	Kössen Formation	Dorsal and caudal vertebrae, ilium	–	Furrer 1993, 2023, PMS pers. obs.

previously believed that the Wingate Sandstone was completely Jurassic in age, but later studies suggest that the Wingate encompasses the Triassic-Jurassic boundary, although its exact location within the lower part of the Wingate is not known (Martz et al. 2014). This circumstance makes it difficult to determine the exact age of the 'last phytosaur' find or any other fossil from the basal Big Indian Rock beds of the Wingate. Martz et al. (2014, p.436) conclude that the Big Indian Rock beds are 'probably Rhaetian (though not latest Rhaetian)' in age. Thus, this 'last phytosaur' is no younger than late (but not latest) Rhaetian in age and not Jurassic.

cf. *Mystriosuchus* from the Blue Lias of England

Another contender for the 'last phytosaur' is a rostral fragment assigned to cf. *Mystriosuchus* (SMNS 55194). This fragment was discovered at St. Audries Bay near Watchet in Somerset, England, in 1986 (Maisch and Kapitzke 2010). It was described as being most comparable to *Mystriosuchus* in morphology (Maisch and Kapitzke 2010). However, because of the incompleteness of the specimen, the possibility cannot be excluded that the fragment derives from another longirostrine taxon of marine reptile, such as a thalattosuchian crocodylomorph (Maisch and Kapitzke 2010). Arguing against this assignment until recently was

that thalattosuchians were not known from the Hettangian. However, a new Hettangian-Sinemurian teleosaurid (Benani et al. 2023) and an early Pliensbachian stem thalattosuchian (Wilberg et al. 2023) have changed this situation. In fact, Wilberg et al. (2023) provide strong evidence for a Rhaetian or even Norian origin of *Thalattosuchia*, and the rostral fragment from St. Audries Bay thus could pertain to this clade.

The rostral fragment was discovered in-situ within the so-called *Pre-planorbis* Beds, below the first occurrence of *Psiloceras planorbis* (Maisch and Kapitzke 2010). The *Pre-planorbis* Beds are located in the basal part of the Blue Lias Formation (Maisch and Kapitzke 2010). The age estimation was based on dating using ammonites of the genus *Neophyllites* (Maisch and Kapitzke 2010), which seems to indicate the rocks containing the find to be Hettangian in age (Lindström et al. 2017). In other studies, the Triassic/Jurassic boundary was placed within the *Pre-planorbis* Beds (Martin et al. 2015). The debate on the age of the rocks at St. Audries Bay is still ongoing and, thus, is the debate on the age of this potential phytosaur specimen. In fact, in the most recent study (Weedon et al. 2019), the presence of the phytosaur specimen in the beds in question has been used to argue for their Triassic age.

Aim of the study

The aim of our study is to present clear evidence for the survival of phytosaurs into the late middle Rhaetian, at least in Central Europe, within a million or two years of the end of the Triassic. The evidence is the presence of an unequivocal phytosaur osteoderm found in Bonenburg, Germany. This find would appear to represent the youngest known phytosaur remains, based on clear stratigraphic and morphologic evidence (Table 1).

Institutional abbreviations

GPIT, Paläontologische Sammlungen der Universität Tübingen, Tübingen, Germany; **MCSNB**, Museo Civico di Scienze Naturali di Bergamo, Bergamo, Italy; **MfN**, Museum für Naturkunde, Berlin, Germany; **NMB**, Naturhistorisches Museum Basel, Basel, Switzerland; **PIMUZ**, Paläontologisches Institut und Museum der Universität Zürich, Zurich, Switzerland; **UNMH**, Utah Museum of Natural History, Salt Lake City, USA; **SMNS**, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; **WMNM**, LWL-Museum für Naturkunde, Münster, Germany.

Materials and methods

Materials

The Bonenburg osteoderm WMNM P98442 was found during the annual excavation campaign of the University of Bonn in collaboration with the WMNM at the

Bonenburg clay pit in Bone Bed 2 in 2017. As is typical for the fossils from Bone Bed 2, the osteoderm was found on its own, without any other non-osteodermal bones or similar osteoderms around it.

Methods

We took size measurements of the osteoderm using dial callipers and documented the morphology of the bone with photographs and interpretive drawings. For comparison, we studied the other published Rhaetian phytosaur material from Europe, in particular MfN MB.R. 2747 from Steinlah, and the Niederschönthal and Halberstadt material (Table 2). In addition, we compared WMNM P98442 to phytosaur osteoderms from the German Middle Keuper at the SMNS and GPIT by personal observation, as well as in the relevant literature. Since the classical genera *Mystriosuchus* and *Nicrosaurus* are the two best known phytosaur genera of the German Keuper (Hungerbühler and Hunt 2000; Hungerbühler 2002; Jones and Butler 2018) and for which osteoderms are well known, we also included those in our research. These two genera are known from the Löwenstein Formation of southern Germany and are middle and late Norian in age (Hungerbühler and Hunt 2000; Hungerbühler 2002; Jones and Butler 2018). Specifically, they are from the middle Stubensandstein, a subunit of the Löwenstein Formation. For understanding the temporal significance of the specimen, it was necessary to compile the stratigraphic range of Rhaetian phytosaurs on a global scale (Table 1).

Results

Systematic paleontology

Archosauriformes Gauthier, Kluge & Rowe, 1988 **Phytosauria Jaeger, 1828**

Phytosauria indet.

Material. One single, slightly damaged left paramedian osteoderm, WMNM P98442.

Locality and horizon. Clay pit #3 of Lücking Brick Company, 1 km north of the village of Bonenburg, City of Warburg, North Rhine-Westphalia, Germany (Fig. 1A). The specimen derives from Bone Bed 2 in the dark marine mudstones of the Contorta Beds of the Exter Formation, 7 m in the section above the base of the Contorta Beds and 17.5 m below the Triassic-Jurassic boundary exposed in the pit (Fig. 1B).

Morphological description. The external side of the Bonenburg osteoderm WMNM P98442 is extensively sculptured, whereas the internal, or visceral, side is smooth (Fig. 2). The external side is dominated by a rounded ridge or keel, indicating the orientation of the osteoderm relative to the body long axis (Fig. 2A, B). This anteroposterior ridge is offset medially as can be

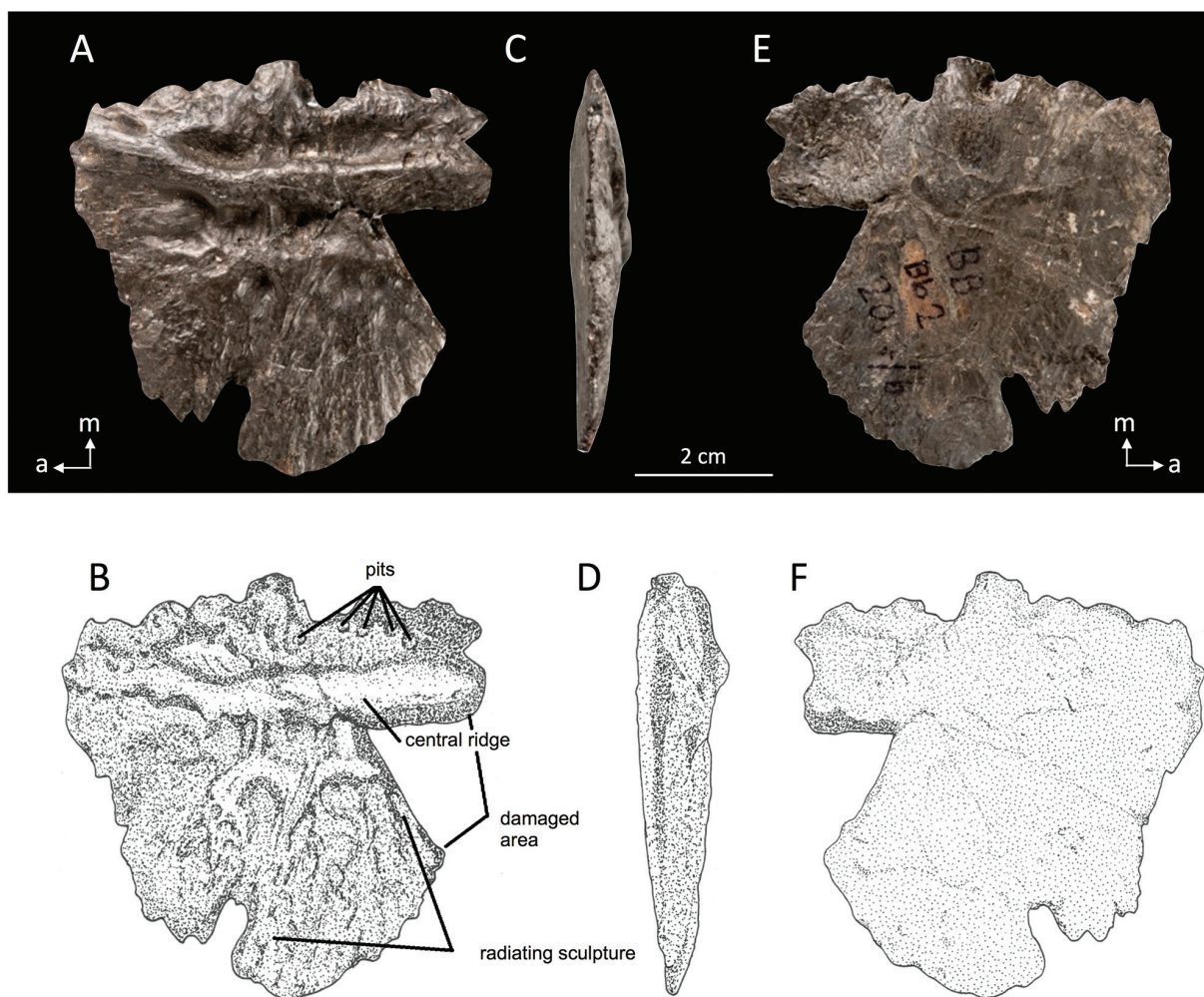


Figure 2. Left paramedian phytosaur osteoderm WMNM P98442 from the late middle Rhaetian Bone Bed 2 of the Contorta Beds of the Exter Formation of Bonenburg, North Rhine-Westphalia, Germany. **A, B.** Photograph and drawing of external view showing the typical phytosaur radiating sculpture and the central longitudinal ridge of a paramedian osteoderm. Note that the anterior part (left) is less sculptured and that the ridge does not extend to the anterior edge; **C, D.** Photograph and drawing of anterior view. Note the thinness of the edge which was underlapping the preceding osteoderm; **E, F.** Photograph and drawing of internal view, showing the flat and smooth surface. Abbreviations: a, anterior; m, medial.

seen on articulated phytosaur specimens, providing the medial direction. One end of the ridge extends to the margin of the osteoderm, whereas the other does not. The latter asymmetry indicates anterior because the ridge does not reach the anterior osteoderm margin in phytosaur osteoderms. Together with the asymmetry of the location of the ridge, the location of the anterior margin indicates that the osteoderm is from the left side of the body. The thickness of the osteoderm decreases in anterior and lateral directions (Fig. 2C, D). The osteoderm shows two distinct indentations, one on the lateral and one on the posterior margin (Fig. 2). The latter resulted from damage sustained during discovery. The bone shows no signs of abrasion.

In mediolateral direction, the osteoderm is 62 mm wide and in anteroposterior direction, it is 64 mm long. It shows a maximum thickness of about 13 mm at its centre. Except for the thick ridge, the external sculpture on the osteoderm is of relatively low relief (Fig. 2A, B). Towards lateral, there are some indistinct pits, but there

are no sharp crests or grooves. Only the region medial to the main ridge shows a deep sulcus.

The lateral part of the external surface of the osteoderm, that is not sculptured, shows a radial, fan-like structure on the surface of the bone (Fig. 2A, B). This structure originates in the centre of the bone, right below the middle of the anteroposterior ridge. The fan structure also affects the silhouette of the lateral part of the bone. The internal surface of the osteoderm is completely flat and shows no sculpturing. There are multiple small hole-like structures on the medial part of the external surface of the bone (Fig. 2E, F).

The general morphology of the Bonenburg osteoderm (Fig. 2) fits the description of phytosaur osteoderms in the literature (Huene 1922; Gozzi and Renesto 2003; Scheyer et al. 2014) (Fig. 3). A more detailed investigation of the osteoderms of the Lombardian *Mystriosuchus* specimen MCSNB 10087 (Gozzi and Renesto 2003) and other articulated and osteoderm-bearing phytosaur skeletons might help to further constrain the anatomical position of the Bonenburg osteoderm.

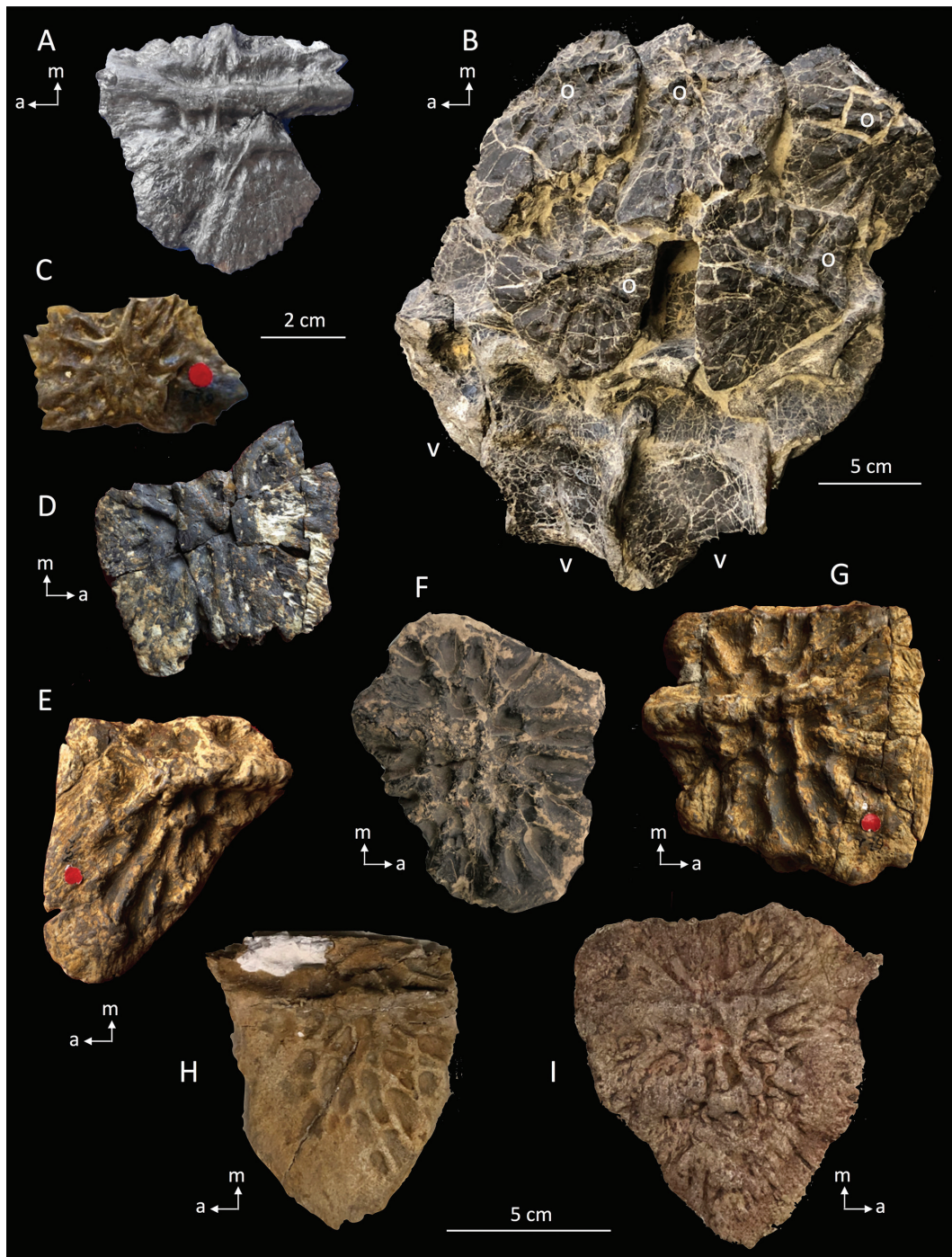


Figure 3. Comparison of selected Rhaetian and Norian phytosaur osteoderms in external view. **A.** WMNM P98442, left paramedian osteoderm from the Rhaetian Bone Bed 2, Exter Formation, Bonenburg, Germany. Note the resemblance of sculpture to C and D; **B.** MfN MB.R. 2747, five articulated paramedian osteoderms of the left side in association with anterior dorsal vertebrae of *Myrstriosuchus* sp. (Butler et al. 2019), Exter Formation, Steinlah near Salzgitter, Germany. Note the resemblance of sculpture to F; **C.** Isolated gular osteoderm MfN MB.R. 4224 from the Rhaetian of Halberstadt (Germany) figured by Huene (1922, fig. 112) and assigned to '*Angistorhinops ruetimeyeri*' by him. Note the resemblance of sculpture to A and D; **D.** Isolated left paramedian osteoderm MfN MB.R. 4372.1 from the Rhaetian of Halberstadt, Germany. Note the resemblance of sculpture to A and C; **E.** Isolated left paramedian caudal osteoderm MfN MB.R. 4374.1 from the Rhaetian of Halberstadt (Germany) figured by Huene (1922, fig. 87) and assigned by him to a small indeterminate phytosaur; **F.** Right paramedian osteoderm NHMB N. B. 14 of '*Angistorhinops ruetimeyeri*' from the Rhaetian bone bed of Niederschönthal (northern Switzerland) figured by Huene (1911b, Pl. VIII, fig. 2). Note the resemblance of sculpture to B; **G.** Right paramedian osteoderm MfN MB.R. 4219 from the Rhaetian of Halberstadt (Germany) figured by Huene (1922, fig. 113) and assigned to '*Angistorhinops ruetimeyeri*' by him; **H.** Left paramedian osteoderm SMNS uncatalogued of *Myrstriosuchus* sp. from the middle Norian Stubensandstein of Aixheim, southwestern Germany; **I.** Right paramedian osteoderm SMNS 4063/7 of *Nicrosaurus kapffi* from the middle Norian Stubensandstein of Heslach near Stuttgart, south-western Germany. Abbreviations: a, anterior; m, medial; o, osteoderm; v, vertebra.

Table 2. Rhaetian phytosaur osteoderms from Europe personally examined in this study, organised by age, youngest occurrences at the top.

Taxon	Collection, Spec. #	Locality	Age	Formation	Osteoderm Material	Other Material	Remarks	Key references
Phytosauria indet.	WMNM P98442	Bonenburg, Germany	late middle Rhaetian	upper Contorta Beds, middle Exter Formation	Isolated osteoderm	–	–	This study
<i>Mystriosuchus</i> sp.	NMB N. B. 14, N. B. 15, N. B. 31, N. B. 644, N. B. uncat. excavation Strübin 1901	Niederschönthal (today Schönthal, part of Füllinsdorf) near Basel, Switzerland	early to middle Rhaetian	lower bonebed, Belchen Member of Klettgau Formation	Isolated osteoderms	Isolated cranial and postcranial bones, teeth	Huene (1911a, b) called material <i>Mystriosuchus ruetimeyeri</i> , in Huene (1922), hypodigm of <i>Angistorhinops ruetimeyeri</i>	Huene 1911a, b, 1922; Meyer and Wetzel 2021
<i>Mystriosuchus</i> sp.	MB.R. 2747	Steinlah near Salzgitter, Germany	early Rhaetian	lower Exter Formation	Osteoderms with ant. dorsal column	Partial skeleton	<i>Angistorhinops ruetimeyeri</i> of Huene. Represents the only substantial Rhaetian phytosaur material from Europe (Jones and Butler 2018)	Schlönbach 1860; Huene 1922; Jones and Butler 2018; Butler et al. 2019; R. Irmis pers. comm.
Phytosauria indet.	MfN MB.R. 4224, 4372.1	Halberstadt, Germany	early Rhaetian	Exter Formation?	Isolated osteoderms	–	Sculpture similar to Bonenburg osteoderm WMNM P98442	Huene 1922
Phytosauria indet.	MfN MB.R. 4219, 4369.1, 4371.1, 4373.1, 4374.1, 4375.1, 4376.1, 4377.1, 4383.1-2, 4391.1-5	Halberstadt, Germany	early Rhaetian	Exter Formation?	Isolated osteoderms	Isolated cranial and postcranial bones, teeth	Contains both “small phytosaur” and <i>Angistorhinops ruetimeyeri</i> of Huene. Some may pertain to <i>Mystriosuchus</i> sp. nov.	Huene 1922

Discussion

Comparisons with skeletally associated phytosaur osteoderms from Europe

Rhaetian MfN MB.R. 2747, *Mystriosuchus* sp.

The only skeleton close in age to the Bonenburg find bearing osteoderms is specimen MfN MB.R. 2747, assigned to *Mystriosuchus* sp., from Steinlah near Salzgitter, northern Germany (Tables 1, 2). See also the review of European Rhaetian phytosaurs in Suppl. material 1.

The osteoderms of MfN MB.R. 2747 (Fig. 3B) are from the dorsal region, with representation from all four paramedian rows, as already noted by von Huene (1922). The preservation of the bone of MfN MB.R. 2747 with its black colour and heavy diagenetic cracking makes discerning sculpture somewhat difficult (Fig. 3B). Compared to the Bonenburg osteoderm (Fig. 3A), the osteoderms of MfN MB.R. 2747 are much larger and thicker and have a much coarser sculpture than WMNM P98442 (Fig. 3B). They are clearly not from the same phytosaur taxon.

Middle Keuper (Norian) phytosaurs from Germany

There is only one Middle Keuper phytosaur skeleton, SMNS 10260, with associated osteoderms. SMNS 10260 is the anterior half of a skeleton of *Mystriosuchus planirostris*, currently on display at the SMNS. However, note that the complete skull SMNS 13007 was used to replace the partial skull of SMNS 10260 in the display. Osteoderms are still attached to the throat region of the SMNS 10260. Numerous isolated *Mystriosuchus planirostris* osteoderms are also preserved in the SMNS collections (Fig. 3H). None of these osteoderms resembles the Bonenburg osteoderm (Fig. 3A) because their sculpture mainly consists of elongate, radially arranged pits separated by thin ridges and a regularly crenelated margin (Huene 1922, fig. 1; pers. obs. PMS).

A potential second case of association consists of a skull and a single osteoderm from the Stubensandstein of Pfaffenhofen, Baden-Württemberg, both bearing the accession number SMNS 12593. The skull is the holotype of *Nicrosaurus meyeri*. However, Hungerbühler (1998: 146) notes that there are no postcrania with *N. meyeri*, contradicting the label accompanying the osteoderm. The sediment attached to the osteoderm vs. the skull in SMNS 12593 suggests that they came from two different horizons (Rainer Schoch, pers. comm. 2023). Interestingly, though, the sculpture of dermal skull bones of SMNS 12593 and that of the osteoderm match. Similarly, the dermal skull bone sculpture and osteoderm sculpture (Fig. 3I) match in fossils labelled as *Nicrosaurus kapffi* in the SMNS collections. None of the Middle Keuper osteoderms (Fig. 3H, I) resembles the Bonenburg osteoderms (Fig. 3A) in shape and sculpture.

Alpine Norian phytosaurs

Records from the Alps are also older than the Bonenburg specimen. Important phytosaur material with associated osteoderms comes from the marine successions of the southern Alps, specifically from the middle Norian Zorzino Limestone (Renesto and Paganoni 1998; Gozzi and Renesto 2003) near Bergamo, northern Italy. The articulated skeleton MCSNB 10087, assigned to the Middle Keuper species *Mystriosuchus planirostris* (Gozzi and Renesto 2003; but see Butler et al. (2019, p. 205)), preserves at least 19 paramedian osteoderms in two regions close to their original location. Gozzi and Renesto (2003) describe two types of osteoderms which differ in shape and sculpturing. The first type is from the medial paramedian rows of the trunk and is oval. The sculpture on its external surface radiates out from the ridge at the centre of the bone. There is no great mediolateral asymmetry (Gozzi and Renesto 2003, fig. 15A; pers. obs. PMS). The second type of osteoderm has a sub-pentagonal to triangular outline and forms the lateral paramedian

row which continues on to the proximal region of the tail, whereas the medial row is restricted to the trunk (Gozzi and Renesto 2003). The sculpturing of these osteoderms is concentrated on the medial part, close to the medially placed anteroposterior ridge (Gozzi and Renesto 2003, fig. 15B; pers. obs. PMS). The asymmetry of this second type of osteoderm is thus similar to WMNM P98442 (Fig. 2A, B). However, the sculpture of the osteoderms of MCSNB 10087 agrees with that of the same species from the Middle Keuper (Fig. 3H), as exemplified by SMNS 10260 and not with the Bonenburg osteoderm (Fig. 3A).

A mass accumulation of *Mystriosuchus steinbergeri* Butler et al. 2019 from the middle Norian marine Dachsteinkalk of the Austrian Alps also includes an osteoderm associated with one of the skulls (Butler et al. 2019). This osteoderm is roughly triangular and shows little sculpture on its outer surface (Butler et al. 2019, figs 15E, F). The bone is roughly of the same size as the Bonenburg osteoderm, but does not offer a good match in terms of sculpture. However, it also appears to be poorly preserved.

Comparison with isolated Upper Keuper (Rhaetian) osteoderms

Osteoderms from Niederschönthal, Switzerland

The osteoderms from the Rhaetian bone bed collection from Niederschönthal at the NMB (Table 2) are large to very large and their sculpture (Fig. 3F) does not match with the Bonenburg osteoderm (Fig. 3A). Instead, the size and sculpture of the Niederschönthal osteoderms is rather similar to those of the Steinlah phytosaur MfN MB.R. 2747. Although assignment to the same taxon is hampered by the insufficient understanding of phytosaur osteoderm morphology, the hypothesis of von Huene (1922) of taxonomic identity MfN MB.R. 2747 and the Niederschönthal osteoderms appears plausible from the perspective of osteoderm morphology, but the Bonenburg specimen clearly represents a different taxon.

Osteoderms from Halberstadt, Central Germany

Huene (1922) assigned skeletal (non-osteoderm) phytosaur material from Halberstadt to a large phytosaur (*A. ruetimeyeri*) and to a small, unnamed taxon (Table 2). In addition, he assigned some isolated osteoderms from the locality to either of these taxa, however, without providing arguments for his assignment beyond size and general resemblance (or lack thereof) to the Steinlah phytosaur MfN MB.R. 2747.

We concur with Huene (1922) that the robust sculpture of most Halberstadt osteoderms is similar to the large osteoderms associated with MfN MB.R. 2747 and the large isolated osteoderms from Niederschönthal. Huene (1922) explicitly included two osteoderms, MfN MB.R. 4373.1 and MfN MB.R. 4374.1 (Fig. 3E), with the smaller unnamed phytosaur. However, the Bonenburg osteoderm

(Fig. 3A) also differs in sculpture and size from those two Halberstadt ones.

On the other hand, one small osteoderm (MfN MB.R. 4224, Fig. 3C) from Halberstadt resembles the Bonenburg one (Fig. 3A) despite being a gular osteoderm and not a paramedian one. The two osteoderms share a similar sculpture and a characteristic frayed margin with bone spicules extending into the former soft skin. Von Huene had already described this feature as ‘*Rand gezackt*’ (jagged edge). Another Halberstadt osteoderm, MfN MB.R. 4372.1, also shows this feature and a similar sculpture (Fig. 3D).

To sum it up, the Bonenburg osteoderm offers a poor match with any named European phytosaur taxon and differs clearly from most other Rhaetian European osteoderms (Fig. 3). Morphological diversity of Rhaetian osteoderms, thus, is consistent with the existence of at least two, if not three, phytosaur taxa during this time period in Europe.

Comparison with non-European Rhaetian osteoderms

Osteoderm of *Jupijkam*

There are two reports of probably Rhaetian phytosaur osteoderms from outside Europe. One is a single paramedian osteoderm which is part of the hypodigm of the newly-described mystriosuchine phytosaur *Jupijkam paleofluvialis* (Brownstein 2023) from Nova Scotia, Canada. The fossil is from the upper part of the Whitewater Member of the Blomidon Formation, making it most likely early Rhaetian in age (Brownstein 2023, fig. 1). However, the external sculpture of this osteoderm appears relatively featureless and the illustration (Brownstein 2023, fig. 6) does not allow for a meaningful comparison with the European osteoderms.

Paleogeographically, the find is closest in paleolatitude to the Moroccan osteoderms, well south of the European Keuper phytosaur occurrences and far south of the Lithuanian and Greenland occurrences (Brusatte et al. 2013). This fact makes the statement of Brownstein (2013) that *Jupijkam* represents the northernmost occurrence of Phytosauria puzzling.

Indeterminate osteoderms from Zimbabwe

Barrett et al. (2020) describe various remains of taxonomically indeterminate phytosaurs from the Tashinga Formation of Zimbabwe. The upper part of this formation is late Norian to early Rhaetian in age, based in part on a radiometric date of 209.4 ± 4.5 Ma from a horizon 7.5 m below a phytosaur-bearing horizon (Barrett et al. 2020, fig. 9). The surface-collected phytosaur remains include seven isolated osteoderm fragments (Barrett et al. 2020). The preservation of these osteoderms, as illustrated by Barrett et al. (2020, fig. 9), is insufficient for a meaningful comparison with the European osteoderms (Fig. 3).

The Bonenburg osteoderm and phytosaur extinction

Possible reworking

The importance of the Bonenburg osteoderm for the debate on phytosaur extinction hinges on the assumption that the specimen is not reworked from older beds. This is a natural concern in bone beds which certainly are time-averaged. The possibility of reworking has been raised for another specimen from Bone Bed 2 of Bonenburg before (Konietzko-Meier et al. 2019), the humerus of cf. *Cyclotosaurus*, a large temnospondyl amphibian. As in the case of this humerus, the Bonenburg osteoderm is well preserved and not abraded (Fig. 2) and does not differ in appearance from the other bones in the deposit. Although we currently cannot exclude the possibility of reworking, there is no positive evidence for this process, either.

Rarity of phytosaur remains in Bonenburg

The rarity of phytosaur remains (the single osteoderm) compared to other vertebrates (Sander et al. 2016; see above) in the Bonenburg bone bed is noteworthy. In particular, the complete lack of phytosaur teeth at Bonenburg is striking, given that teeth are abundant in other Rhaetian European bone beds (Table 1). Taken at face value, the rarity could be interpreted as indicating a decline of phytosaurs by the late middle Rhaetian. However, phytosaurs are not the only faunal element of extreme rarity at Bonenburg and an environmental explanation is equally likely (Suppl. material 1).

Conclusions

During the 2017 excavation campaign in the Rhaetian bone beds at the Bonenburg clay pit in North Rhine-Westphalia, Germany, a phytosaur osteoderm was found. The host unit of the bone beds are the fine-grained dark clastics of the Contorta Beds of the Exter Formation. The bone bed from which the osteoderm derives, Bone Bed 2, is dated palynologically with high precision (Gravendyck et al. 2020) as late middle Rhaetian.

The osteoderm from Bonenburg is most definitely phytosaurian in origin and pertains to the dorsal paramedian osteoderm rows. However, the osteoderm currently cannot be assigned to a named taxon. This possibly could be rectified by further comparative morphological research, including quantitative approaches and machine-learning, on phytosaur osteoderms aimed at refining the current descriptive terminology, especially of the outer sculpture or ornamentation.

The Bonenburg find indicates the survival of phytosaurs into the late middle Rhaetian, at most two million years before the end of the Triassic. The osteoderm currently is the youngest well-dated evidence for

phytosaurs and, thus, currently lays claim to being ‘the last phytosaur’. Of the other two contenders to this ‘title’, one is not precisely dated and the other may not be a phytosaur. However, that phytosaurs were still thriving a few million years before the end of the Triassic is also suggested by the large body size of the Steinlah phytosaur *Mystriosuchus* sp. (Jones and Butler 2018) and the improved dating of the Rhaetian phytosaur finds from Switzerland (Meyer and Wetzel 2021) and northern Germany. It thus appears likely that phytosaurs fell victim to the end-Triassic extinction event, inconsistent with the view of Lucas (2018) of their gradual extinction in the Late Triassic.

Acknowledgements

This paper arose from the Bachelor’s thesis of the second author who also executed the drawings in Fig. 2. Despite the small, single fossil this study is based on, so many people contributed to its completion, for which we are very grateful. Tanja Wintrich (University of Bonn, Germany) led the 2017 excavation campaign during which the osteoderm specimen was recovered and we thank her and all the students who participated in the excavation. Citizen scientist Michael Mertens (Schwaney, Germany) supported us as always with locating the bone beds and providing geological information. Olaf Dülfer (University of Bonn, Germany) is thanked for support in the preparation lab and Achim Schwermann (WMNM) is thanked for curatorial support. Rainer Schoch (SMNS) provided access to phytosaur material kept at the SMNS, as did Walter Etter at NHMB and Daniela Schwarz and Oliver Hampe at the MfN. Oliver Hampe also provided a photograph of MfN MB.R. 4224. We thank Dorota Konietzko-Meier and Andrea Prino (University of Bonn, Germany) for discussion on temnospondyl dermal bone. Rainer Schoch was knowledgeable in all questions regarding phytosaurs. The specimen photographs of the Bonenburg osteoderm were taken by Georg Oleschinski (University of Bonn, Germany). We thank Jelle Heijne (University of Bonn, Germany) for photographs of the phytosaur osteoderm collection at GPIT and Alessandro Lania (University of Bonn, Germany) for taking photographs of the osteoderms of the *Mystriosuchus* skeleton MCSNB 10087. These photos clarified the contradiction between the text and the caption of figure 15 in Gozzi and Renesto (2003). Generous funding for the annual Bonenburg excavation campaigns was provided by the Heritage Development Program of the state of NRW through the administrative support of Achim Schwermann (WMNM). This work would not have been possible without the unfaltering and generous support of the owner and operator of the Bonenburg clay pit, August Lücking Ziegelwerke GmbH and Co KG, and especially its CEO, Joachim Thater. We thank Mike Benton (University of Bristol) and an anonymous reviewer for the very helpful reviews of earlier versions of this work.

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Supplementary material 1

Description of phytosaur osteoderm morphology and discussion of phytosaur rarity at Bonenburg

Authors: P. Martin Sander, Paul W. Wellnitz

Data type: docx

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