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Late middle Rhaetian vertebrates from Exter Formation bone beds of Bonenburg (Westphalia, Germany): Implications for the end-Triassic extinction event

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Abstract. There is a long history of collecting and studying Rhaetian marine condensation horizons rich in vertebrate remains, termed "bone beds", in Central and Western Europe. However, most outcrops are small and ephemeral. The recently discovered Rhaetian bone beds at the village of Warburg-Bonenburg (Westphalia, Germany) have been systematically excavated since 2015, producing a wealth of primarily marine fossils, both in terms of number of specimens and taxonomic diversity. In addition, the richest bone bed (Bone Bed 2) has been dated with high precision to the late middle Rhaetian (ca. 203 million years) based on palynostratigraphy. We here review the finds from the locality and their implications for our understanding of Rhaetian marine and terrestrial vertebrate faunas and the end-Triassic extinction event (ETEE), updating our 2016 report. In general, the Bonenburg fauna is similar to many other Rhaetian bone beds. Selachian diversity is high and rare new elements are represented. Among osteoichthyans, the birgeriid *Severnichthys* and, in particular, mawsoniid coelacanth fossils are important elements. Many of the latter were previously assigned to the enigmatic reptile *Pachystropheus*. Although the presence of temnospondyl remains in European Rhaetian bone beds has been questioned, such remains are common in Bonenburg. They pertain to at least two taxa of capitosauroids, including cf. *Cyclotosaurus*, and to plagiosaurids, including *Plagiosaurus*. Ichthyosaur remains are common as well, the most distinctive of which are large but very short shastasaurid vertebral centra and fragments of cortical bone of the giant shastasaurid cf. *Ichthyotitan*. Vertebrae and long bones of bona fide and presumed plesiosaurians are the most abundant remains of large-bodied vertebrates. At least three taxa are represented in Bonenburg based on vertebral morphology, body size and ontogenetic stage, as indicated by bone histology and neurocentral suture fusion. The most common reptilian remains, however, are vertebrae and long bones of *Pachystropheus rhaeticus* E. v. Huene 1935, which is interpreted either as the geologically oldest choristodere or as the youngest surviving thalattosaur. Humeri are up to 16 cm long. Continental input is represented by rare sphenodontid and non-mammalian synapsid remains, a phytosaur osteoderm,

a pterosaur ungual and a sauropodomorph dinosaur ungual resembling *Plateosaurus*. The Bonenburg fauna is important because of the unequivocally last global occurrence of certain taxa (i.e., non-brachyopoid temnospondyls and phytosaurs) and the unequivocally Triassic occurrence of others (i.e., plesiosaurians). The Bonenburg records of non-brachyopid temnospondyls, giant shastasaurid ichthyosaurs, *Pachystropheus* and phytosaurs suggest a severe vertebrate mass extinction at the end of the Triassic as opposed to gradual extinction during the Late Triassic. A strong reduction in plesiosaurian body size is similarly suggestive of a mass extinction.

Key words: Bone Bed, Rhaetian, Westphalia, Ichthyosauria, Plesiosauria, end-Triassic extinction event

Kurzfassung. Als Bonebed bezeichenete rhätische marine Kondensationshorizonte, die reich an Wirbeltierresten sind, werden in Mittel- und Westeuropa seit langem besammelt und untersucht. Die meisten Aufschlüsse sind jedoch klein und kurzlebig. Die kürzlich entdeckten Bonebeds bei Bonenburg (Westfalen, Deutschland) wurden seit 2015 systematisch ausgegraben und lieferten eine Fülle von hauptsächlich marinen Fossilien, sowohl was die Anzahl der Exemplare als auch die taxonomische Vielfalt betrifft. Darüber hinaus konnte das wichtigste Bonebed (Bonebed 2) anhand von Palynomorphen mit hoher Genauigkeit in das späte Mittelrhätium (ca. 203 Millionen Jahre) datiert werden. Wir besprechen hier die Funde von der Fundstelle und ihre Bedeutung für unser Verständnis der rhätischen marinen und terrestrischen Wirbeltierfaunen und des endtriassischen Aussterbeereignisses und aktualisieren unseren Bericht von 2016. Im Allgemeinen ähnelt die Bonenburger Fauna vielen anderen rhätischen Bonebeds. Die Vielfalt der Selachier ist hoch, aber es sind seltene neue Elemente vertreten. Unter den Osteoichthyern sind der Birgeriide *Severnichthys* und insbesondere die mawsoniiden Quastenflosser wichtige Elemente. Viele Funde der letzteren wurden bisher dem rätselhaften Reptil *Pachystropheus* zugeordnet. Obwohl das Vorhandensein von Temnospondylen-Resten in den rhätischen Bonebeds in Frage gestellt wurde, sind solche Reste in Bonenburg häufig. Sie gehören zu mindestens zwei Taxa von Capitosauroiden, darunter *Cyclotosaurus*, und zu Plagiosauriden, darunter *Plagiosaurus*. Überreste von Ichthyosauriern sind ebenfalls häufig zu finden: vor allem große, aber sehr kurze Shastasaurier-Wirbelzentren und Fragmente von Kortikalknochen des riesigen Shastasauriers cf. *Ichthyotitan*. Wirbel und Langknochen von Plesiosauriern sind die häufigsten Überreste großer Wirbeltiere, und neben *Rhaeticosaurus* sind mindestens zwei weitere Taxa vertreten. Sie unterscheiden sich in der Wirbelmorphologie, der Körpergröße und dem ontogenetischen Stadiums, das durch Knochenhistologie und dem Grad der Verwachsung der Neurozentralsutur angezeigt wird. Die häufigsten Reptilienreste sind jedoch Wirbel und Langknochen des erwähnten *Pachystropheus rhaeticus* E. v. Huene 1935, der alternativ als der geologisch älteste Choristodere oder als geologisch jüngster Thalattosaurier interpretiert wird. Die Humeri sind bis zu 16 cm lang. Der kontinentale Eintrag in die Bonebeds besteht aus seltene Sphenodontiden- und Synapsidenresten, einem Phytosaurier-Osteoderm, einem Pterosaurier-Unguale und dem Unguale eines sauropodomorphen Dinosauriers ähnlich *Plateosaurus*. Die Bonenburger Fauna ist von großer Bedeutung, da einige Taxa (z. B. die nicht-brachiopoiden Temnospondylen und das Phytosaurier-Osteoderm) die geologisch jüngsten Belege für diese Gruppen sind während andere (Plesiosaurier) die geologisch ältesten Belege darstellen. Die Bonenburger Funde von Temnospondylen, sehr großen shastasauriden Ichthyosauriern, *Pachystropheus* und Phytosaurier deuten auf ein schweres Massenaussterben am Ende der Trias hin. Eine starke Verringerung der Körpergröße der Plesiosaurier deutet ebenfalls auf ein Massenaussterben hin.

Schlüsselwörter: Bonebed, Rhaetium, Westfalen, Ichthyosauria, Plesiosauria, end-triassisches Aussterbeereignis

Introduction

The bone beds of the Rhaetian epicontinental Triassic are among the historically most important localities in Triassic vertebrate palaeontology, both in the UK (e.g., Aust Cliff and other southwestern UK localities; Storrs 1994; Slater et al. 2016; Cross et al. 2018) and in continental Europe (e.g., Olgahain near Tübingen, Hallau in Switzerland, Saint-Nicolas-de-Port in France and Habay-la-Vieille in Belgium; Peyer 1956, Clemens 1980; Cuny 1995; Godefroit 1999; Godefroit & Cuny 1997; Godefroit & Knoll 2003; Whiteside et al. 2017). The continental European bone beds (not to be confused with the bone beds of American usage; Martill 1999) have been important for their remains of early mammaliaforms (Peyer 1956; Clemens 1980; Clemens

& Martin 2014; Debuysschere et al. 2015; Debuysschere 2017; Whiteside & Duffin 2021). The bone beds offer a rare glimpse into terrestrial faunas in Europe in the last 5 to 10 million years of the Triassic (Storrs 1994; Cuny 1995; Godefroit 1999; Godefroit & Cuny 1997; Godefroit & Knoll 2003; Sander et al. 2016; Wintrich et al. 2017a; Cross et al. 2018; Moreau et al. 2021; Numberger-Thuy et al. 2025). Bone beds in the European sense of condensation horizons enriched in vertebrate remains are a typical feature of several stratigraphic units in the European epicontinental Triassic ("Germanic Facies"). The term "bone bed" refers to often dense, geographically widespread accumulations of frequently poorly preserved, isolated bones and teeth of primarily marine vertebrates, with some terrestrial input. Sedimentologically, bone beds are pronounced condensation horizons, surfaces of non-deposition with the only input being vertebrate remains. Such surfaces may also be subject to erosion; and winnowing of the silt and clay particles may result in the concentration of the coarser vertebrate fragments. Poor preservation of the bones is related to both mechanical abrasion and long exposure on the seafloor (Storrs 1994; Martill 1999).

Bone beds in the European epicontinental Triassic occur both in the Muschelkalk facies of the Middle Triassic and as part of the latest Triassic transgression of the Rhaetian sea. Like the Muschelkalk sea, this sea flooded the Central European Basin and the regions in France and Poland connecting it to the Tethys. The age of the classical Rhaetian bone beds is often difficult to constrain because they lack invertebrate index fossils and because of their condensed nature. In recent decades, palynostratigraphy has improved this situation in continental Europe by being able to date the rock units hosting the bone beds (e.g., Meyer & Wetzel 2021; Gravendyck et al. 2020).

The marine to marginal marine bone beds of the epicontinental Rhaetian are of importance because of their bearing on the end-Triassic extinction event (ETEE). This most elusive of the Big Five mass extinction events, the reality of which has been doubted on occasion (e.g., Lucas 2018), has recently received renewed interest in connection with the search for an extinction mechanism linked to large igneous provinces (LIPs; Wignall 2001). In the case of the ETEE, the presumed "culprit producing massive environmental perturbations", is the Central Atlantic Magmatic Province (CAMP, Whiteside et al. 2007, 2010; Ruhl et al. 2020; Oliveira et al. 2023) related to the initial break-up of Pangea with the opening of the North Atlantic. The classical Late Triassic sections of the Alps, deposited in the western Tethys, provide the standard stratigraphic framework for

Figure 1: Location of the Bonenburg clay pit #3 of Lücking brick company in the eastern part of the state of North Rhine-Westphalia (NRW), Germany. Background: View of pit looking northwest during the 2017 excavation campaign.

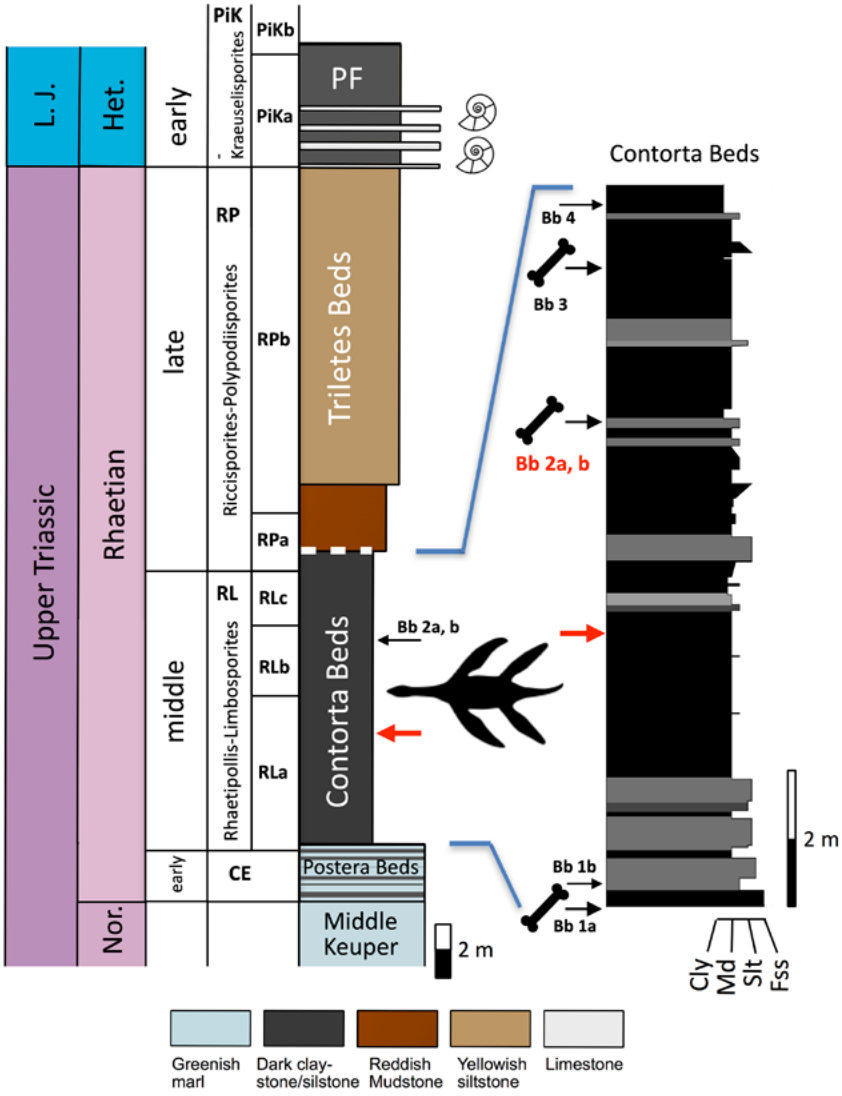


Figure 2: Simplified stratigraphy of the Norian to Hettangian section exposed at the Bonenburg clay pit #3 of Lücking brick company, North Rhine-Westphalia, Germany, with a special emphasis on the location of the four bone beds and the holotype skeleton of the oldest plesiosaur *Rhaeticosaurus* in the section. The main part of the section is made up of the Exter Formation, which is subdivided into the Postera Beds, Contorta Beds, and Triletes Beds. The thick white 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. The colours of the rock types in the main stratigraphic column approximate colours in the fresh outcrop. General abbreviations: Bb, bone bed; Cly, claystone; Fss, fine-grained sandstone; Het., Hettangian; L. J., Lower Jurassic; Md, mudstone; Nor., Norian; PF, Psilonotenton Formation; Slt, siltstone. Abbreviations of palynozones: CE, Classopollis-Enzonalasporites palynozone; RL, Rhaetipollis-Limbosporites palynozone; RP, Ricciisporites-Polypodiisporites palynozone; PiK, Pinuspollenites-Kraeuselisporites palynozone. Subzones are labelled alphabetically. Modified from Wintrich et al. (2017a), palynostratigraphy is from Gravendyck et al. (2020).

the Triassic-Jurassic transition. For example, the GSSP (Global Boundary Stratotype Section and Point) for the base of the Jurassic Period is located at Kuhjoch in the Northern Calcareous Alps of Austria (Hillebrandt et al. 2013; Schobben et al. 2019). Aside from biostratigraphy, the boundary sections also provide an important chemostratigraphic framework through geochemical proxies for the characterization of the ETEE. A negative excursion of the ∂C13 curve in the last 100,000 years of the Triassic, reflecting environmental perturbations through a collapse of plant productivity, is observed across sections in Europe (review in Ogg et al. 2020; Schobben et al. 2019; Lindström et al. 2017). However, these late Norian to Early Jurassic Tethyan marine deposits have a scarce vertebrate record that is difficult to correlate in any detail with the Late Triassic chronostratigraphy (e.g., Furrer 1993, 2023, Sander et al. 2022). The Triassic-Jurassic transition is also recorded in many continental sections across North America, South America, Southeast Asia, China, southern Africa, and eastern Central Europe, but all of these sections are difficult to correlate with the marine record and lack reliable radiometric dates (Ogg et al. 2020, Lucas 2018). Consequently, the position of the Triassic-Jurassic boundary in these sections remains uncertain, obscuring the temporal patterns of land vertebrate evolution. In fact, numerous units in South America, southern Africa, and China classically considered to be Late Triassic are now considered to be Early Jurassic in age. The European Rhaetian bone beds, combined with the Hettangian marine lagerstätten, primarily of the UK, provide a crucial link between these two contrasting situations in the vertebrate, particularly tetrapod, fossil record: well-dated but vertebrate fossil-poor marine formations juxtaposed with poorly dated but vertebrate fossil-rich terrestrial formations (e.g., Tanner 2004; Weedon et al. 2018).

Probably the most exciting European Rhaetian bone bed locality to be discovered in recent years is that of Bonenburg in central Germany (Fig. 1) (Sander et al. 2016; Wintrich et al. 2017a; Gravendyck et al. 2020). This locality in Kreis Höxter, eastern North Rhine-Westphalia (NRW), is in an active clay pit opened in 2007. The outcrop uniquely combines extensive exposure of at least four stacked bone beds with high-precision palynostratigraphic age control (Fig. 2; Gravendyck et al. 2020). Bone Bed 2 is the richest of these bone beds.

The locality was "put on the map" (Fig. 1) by the discovery of the oldest known plesiosaur skeleton, and the only one from the Triassic. However, this skeleton does not come from any of the bone beds but from the shales below Bone Bed 2 (Wintrich et al. 2017a).

The purpose of this contribution is to provide an update to the preliminary description of the locality and its fauna (Sander et al. 2016), incorporating numerous important additions to the vertebrate record made through regular excavation campaigns by the University of Bonn and the LWL-Museum für Naturkunde (collections acronym WMNM) in Münster since 2015 (Table 1). The high productivity of the Bonenburg bone beds is not due to exceptional fossil richness (Fig. 3, 4), but rather because of their extensive and continued exposure in an active clay pit, allowing us to follow the mining progress to recover fossils. In contrast to other sites, we are not dependent on gradual weathering of natural outcrops, as at Aust Cliff and some other southwestern UK localities, nor are we limited by the short access window typical of construction sites.

The Bonenburg pit #3 is very close to the brick factory of the Lücking company (about 1.2 km), but it is not the primary source of its raw materials. Due to this proximity, mining a subordinate volume of raw material remains economical, and only requires roughly two short (two-week) mining campaigns per year. This relatively slow extraction rate allows scientific excavations to keep pace with mining while also maintaining fresh outcrop faces. Currently, the palaeontological collecting activities are conducted within the framework of the Denkmalschutzgesetz NRW (cultural heritage protection legislation), which considers each fossil as a potential object of "portable palaeontological cultural heritage" (*bewegliches Bodendenkmal*) based on its scientific value. This definition, naturally, applies to only a few invertebrate fossils, but it covers all larger vertebrate fossils from the bone beds, some of the microscopic specimens, and unique discoveries such as the plesiosaur skeleton (Wintrich et al. 2017a). Since 2013, the law has been amended to stipulate that all objects of portable palaeontological cultural heritage are owned by the state of North Rhine-Westphalia (Denkmalschutzgesetz NRW §18 *Schatzregal*). In return, the state is obligated to manage these resources and to fund their scientific study. This has led to a successful cooperation at Bonenburg between the LWL-Museum für Naturkunde and the University of Bonn. The LWL-Museum für Naturkunde is responsible for palaeontological cultural heritage protection in northeastern NRW (the Westphalia-Lippe region) and thus oversees the legal aspects of palaeontological excavations, while the University of Bonn contributes expertise on marine vertebrates. In addition, the museum is the repository for all specimens and samples emanating from our work at Bonenburg.

Research highlights from Bonenburg since the report by Sander et al. (2016) include, first, the detailed palynological study of the Bonenburg section (Gravendyck 2021; Gravendyck et al. 2022, 2023), which established a palynostratigraphic framework with implications for understanding the ETEE (Schobben et al. 2019; Gravendyck et al. 2020). Second, from a

Table 1: Excavation campaigns and their scientific leaders in the bone beds of the Contorta Beds of the Rhaetian Exter Formation of Lücking clay pit #3, Bonenburg, Westphalia, Germany, from 2015 to 2024.

Year	Leadership	Dates
2015	Prof. Martin Sander, Dr. Achim Schwermann	May 22 – May 30
2016	Tanja Wintrich, Dr. Achim H. Schwermann	Aug. 22 – Sep. 2
2017	Tanja Wintrich, Dr. Rico Schellhorn	Sep. 13 – Sep. 25
2018	Tanja Wintrich, Thorsten Plogschties	July 24 – Aug. 3
2019	Dr. Tanja Wintrich, Thorsten Plogschties	July 13 – July 26
2021	Dr. Achim Schwermann, Jelle Heijne	Oct. 4 – Oct. 15
2022	Jelle Heijne, Dr. Achim Schwermann	Sep. 12 – Sep. 24
2023	Jelle Heijne, Dr. Achim Schwermann	Sep. 11 – Sep. 23
2024	Jelle Heijne, Dr. Achim Schwermann	Sep. 16 – Sep. 27

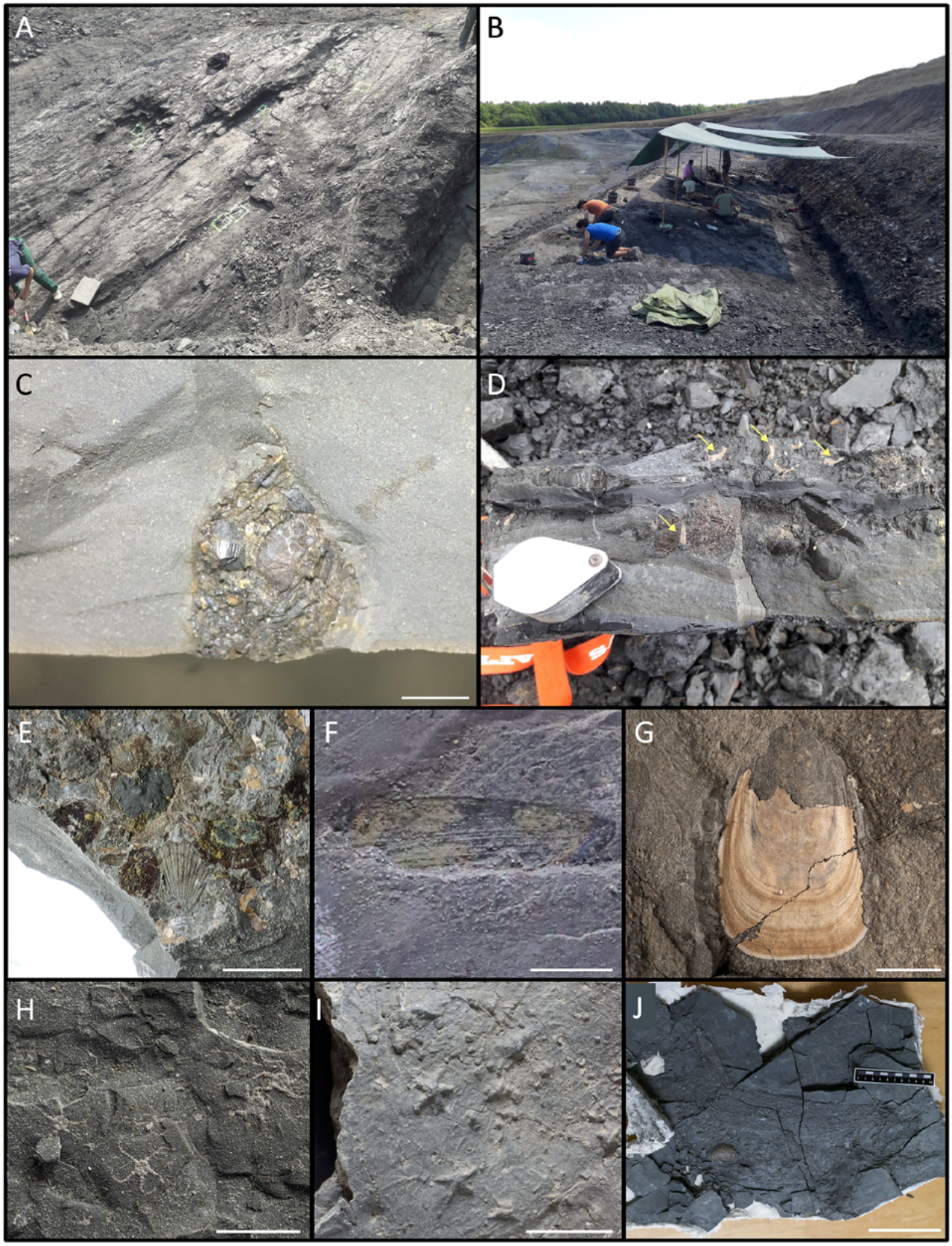


Figure 3: Outcrop situation, fossil occurrence and invertebrate fossils. **A** Excavation surface of Bone Bed 2 affected by numerous small parallel faults. **B** View of excavation surface of Bone Bed 2 in July 2018. View to the south, note the dip of the surface to the west, where it disappears under thick younger deposits of Rhaetian and Hettangian age. **C** Hand specimen (WMNM P117513) of sediment directly below Bone Bed 2 with an invertebrate burrow dug from the base of the bone bed into the underlying sediment. After burrow abandonment, the open burrow became filled in by the initial sedimentation of the bone bed. **D** Hand specimen of Bone Bed 3. ▶

vertebrate palaeontological perspective, there has been a substantial increase in the amount of vertebrate fossils recovered from the Bonenburg bone beds (Figs. 4-12), obtained in nine excavation campaigns to date (Table 1). The quantity of material now likely rivals what has been collected in other major localities over the past two centuries. As with any fossil site, increasing the number of specimens recovered (Fig. 5) also increases the likelihood of discovering rare elements. In Bonenburg, these rare discoveries (Table 2) include a type of hybodont cephalic spine (Fig. 6A-C) and archosaur fossils, in particular one dinosaur claw and one pterosaur claw (Fig. 12F-J) (Hack 2022; Hack et al. 2026), and a single phytosaur osteoderm (Fig. 12E) (Wellnitz 2022; Sander & Wellnitz 2024). A second class of finds are moderately common but previously unrecognized fossil groups (Fig. 5), such as the basisphenoid bones of mawsoniid coelacanths (Hartung et al. 2021) and, in particular, the rich record of temnospondyl amphibians (Prino 2023; Prino et al. 2024). This clade is commonly believed to be absent from Rhaetian bone beds, at least in the UK (Storrs 1994). Fig. 5 provides an overview of the vertebrate fauna from Bonenburg and relative frequencies of occurrence.

A different line of research has focused on the bone histology of numerous Bonenburg taxa (Fig. 13). These studies have supported morphological interpretations of temnospondyls (Prino et al. 2024) and plesiosaurs (Wintrich et al. 2017a) but also allowed detection of the presence of giant shastasaurid ichthyosaurs in the bone bed fauna (Perillo 2022, Perillo & Sander 2024). Finally, the affinities of the most common yet most enigmatic reptile from Bonenburg, *Pachystropheus rhaeticus*, may be clarified by future histological investigations.

Excavation campaigns and techniques 2016 to today

As noted, the purpose of this contribution is to report on the progress of fossil recovery and research since the initial bone bed excavation campaign at Bonenburg in 2015, which followed several years of fossil recovery by local citizen scientist and collector Michael Mertens (Sander et al. 2016). Annual excavation campaigns (Fig. 3A, B), with a Covid-related gap in 2020, have since yielded hundreds of relevant fossils from Bone Bed 2 each season (Fig. 5). The focus of collecting has been on larger bones that stand out against the matrix of small fish teeth and scales. These larger bones occur at densities of fewer than 10 items per square metre, with approximately one well-preserved specimen per square metre (Fig. 3, 4). The excavated area of Bone Bed 2 has varied from season to season, ranging between 50 and 200 m^2 (e.g., Fig. 3A, B). In a minor operation, a total of 10 m^2 was excavated from Bone Bed 3.

Over the years, the annual excavation campaigns were led by various researchers from the two collaborating institutions (Table 1). Participation has ranged from 3 to 15 students, primarily MSc students from the University of Bonn, along with BSc students who participated for credit in the "Field Methods in Paleontology" module (B45). The project has also benefitted from the involvement of citizen scientists with an interest in the Triassic. While most fossil specimens are still undergoing curation, preparation and study (Fig. 4), numerous MSc and BSc theses have been completed based on the Bonenburg material (Table 3). Also, several studies have been published in international peer-reviewed journals (Schwermann 2016; Wintrich et al. 2017a; Konietzko-Meier et al. 2019; Gravendyck et al. 2020, Hartung et al. 2021; Perillo & Sander 2024; Prino et al. 2024; Sander & Wellnitz 2024; Hack et al. 2026).

The fossil recovery techniques established in 2015 and described by Sander et al. (2016) are still used with only minor modifications (Fig. 3, 4). A crucial improvement involves the extensive application of the stabilizer acryloid to preserve specimens. After careful removal from the bone bed, the specimens need to air-dry for an hour or two, depending on the weather, until the surface is dry but before desiccation cracks develop in the surrounding mudstone matrix. At this stage, the fossil is coated several times with a fairly viscous preparation of acryloid (in consistency similar to soft honey), with curing intervals between applications. If the specimen retains too much water content, the acryloid will turn a milky

Note the dominance of larger components over mm-sized teeth and scales. The most common fossils are coprolites. The matrix of the bone bed is rich in pinkish phosphate. **E** Shell hash layer with different kinds of bivalves, Lingula (light beige) and spinicaudatan conchostracan remains (brown) (WMNM P119262). **F** Elytron (beetle wing) of an indeterminate beetle in very fine-grained sediment (WMNM P119263). **G** Shell of the inarticulate brachiopod Lingula showing colour banding (WMNM P117512). **H** Articulated small ophiuroid (WMNM P121668). **I** Ophiuroid resting trace from a horizon about 1 m above Bone Bed 2 (WMNM P119261). **J** Articulated fish skeleton from a horizon below Bone Bed 2 (WMNM uncat.). Scale bars represent: 2 mm (C); 5 mm (F); 1 cm (E, G, H, I); 10 cm (J).

Table 2: Vertebrate fauna of the Contorta Beds of the Rhaetian Exter Formation of Lücking clay pit #3, Bonenburg, Westphalia, Germany. Current to May, 2025. For taxa not mentioned in the text, see Sander et al. (2016).

Euselachii				
Taxon	**Material**	**Clade**	**Frequency**	**References**
"*Hybodus*" *cloacinus*	Teeth	Hybodontiformes	Very common	Sander et al. 2016, synonymized with "*H.*" *cuspidatus* by Vida et al. 2025
Hybodontiformes indet. A, probably pertaining to "*H.*" *cloacinus*	Large fin spines and cephalic spines	Hybodontiformes	Fin spines very common, cephalic spines rare	Sander et al. 2016
Lissodus minimus	Teeth	Hybodontiformes	Common	Sander et al. 2016
Hybodontiformes indet. B, very likely pertaining to *Lissodus minimus*	Small fin spines	Hybodontiformes	Moderately common	Sander et al. 2016
Hybodontiformes indet. C,	Cephalic spine new form	Hybodontiformes	Unique	This study
Neoselachii				
Nemacanthus (*Rhomphaiodon*) *monilifer* (*minor*)	Teeth	Synechodontiformes	Very common	Sander et al. 2016; Vida et al. 2025
Nemacanthus monilifer, probably pertaining to *R. minor* or vice versa	Fin spines (only)	Synechodontiformes	Very common	Sander et al. 2016
Grozonodon candaui	Teeth	Synechodontiformes	Moderately common	This study
Synechodus rhaeticus	Teeth	Synechodontiformes	Rare	This study
Parascylloides turnerae	Teeth	probably Synechodontiformes	Common	This study
Pseudocetorhinus pickfordi	Teeth	probably Synechodontiformes	Rare	This study
Osteichthyes				
Saurichthys sp.	Teeth	Actinopterygii	Common	Sander et al. 2016
Sargodon tomicus	Jaw fragments, teeth	Actinopterygii	Common	Sander et al. 2016
Gyrolepis albertii	Teeth	Actinopterygii	Common	Sander et al. 2016
cf. *Lepidotes* sp.	Teeth	Actinopterygii	Common	Sander et al. 2016
Severnichthys acuminatus	Jaw fragments, teeth	Actinopterygii	Common	Sander et al. 2016
Ceratodus latissimus	Teeth, skull bones	Dipnoi	Moderately common	Sander et al. 2016
Ptychoceratodus serratus	Teeth	Dipnoi	Rare	This study

Taxon	Material	Clade	Frequency	References
Mawsoniidae indet. sp. 1	Basisphenoids	Actinistia	Common	Hartung et al. 2021
Mawsoniidae indet. sp. 2	Basisphenoids	Actinistia	Common	Hartung et al. 2021
Mawsoniidae indet.	Principal coronoids, angulars, etc.	Actinistia	Common	This study
Temnospondyli				
cf. *Cyclotosaurus* sp.	Pterygoid, humerus, 2 femora	Temnospondyli	Moderately common	Konietzko-Meier et al. 2019; Garbay MSc 2021; Prino et al. 2024
Capitosauroidea indet. morphotype 1	Clavicle, angular	Temnospondyli	Moderately common	Prino et al. 2024
Capitosauroidea indet. morphotype 2	Interclavicle, dermal bone indet.	Temnospondyli	Moderately common	Prino et al. 2024
Capitosauroidea indet.	Dentary, femora	Temnospondyli	Moderately common	Prino et al. 2024
Capitosauroidea indet.	Teeth with carinae	Temnospondyli	Rare	This study
Plagiosaurinae indet.	Parietal, interclavicle, dermal bone indet.	Temnospondyli	Moderately common	Prino et al. 2024
Ichthyosauria				
cf. *Ichthyotitan*	Cortical bone fragments, vertebrae, ribs	Ichthyosauria	Moderately common	Sander et al. 2016; Witkowski BSc 2017; Lamsfuß BSc 2022; Perillo & Sander 2024
Shastasauridae indet. morphotype 1	Short vertebral centra	Ichthyosauria	Common	Sander et al. 2016; Witkowski BSc 2017; Lamsfuß BSc 2022
Shastasauridae indet. morphotype 2	Large neural arch, large ribs	Ichthyosauria	Moderately common	Sander et al. 2016; Witkowski BSc 2017; Lamsfuß BSc 2022
Ichthyosauria indet.	Teeth, vertebrae, ribs, long bones	Ichthyosauria	Moderately common	Sander et al. 2016; Witkowski BSc 2017; Lamsfuß BSc 2022
Plesiosauria				
Rhaeticosaurus mertensi	Skeleton	Plesiosauria	Unique	Wintrich et al. 2017a
cf. *Rhaeticosaurus*	Vertebrae, propodial, ulna	Plesiosauria	Moderately common	Neuhof MSc 2019; this study
Indet. plesiosaur morphotype 1	Large vertebrae, large propodial	plesiosaurians	Moderately common	Sander et al. 2016; Neuhof MSc 2019; this study
Indet. plesiosaur morphotype 2	Small vertebrae	plesiosaurians	Moderately common	Sander et al. 2016

Lepidosauromorpha				
Taxon	**Material**	**Clade**	**Frequency**	**References**
cf. *Diphyodontosaurus*	Jaw fragment	Sphenodonta	Unique	Sander et al. 2016
Archosauromorpha				
Pachystropheus rhaeticus	Vertebrae, limb bones	Choristodera/ Thalattosauria	Very common	Sander et al. 2016; Wild BSc 2018
Phytosauria indet.	Osteoderm	Phytosauria	Unique	Sander & Wellnitz 2024
Non-sauropod Sauropodomorpha indet.	Thumb claw (or ungual digit II)	Dinosauria	Unique	Hack et al. 2026
Pterosauria indet.	Claw	Pterosauria	Unique	Hack et al. 2026
Synapsida				
Lepagia gaumensis	Tooth	Synapsida	Unique	Schwermann 2016

white as drying continues. If applied correctly, the acryloid will seal off the fossil and its surrounding matrix, preventing both cracking and pyrite decay. Fossils treated in this way appear to be stable, some since 2016. The acryloid coating is sometimes too thick to allow detailed examination of the specimen, and the shiny surface of the treated specimens also makes examination difficult. However, excess acryloid is easily removed by using an acetone-soaked cotton pad or rag, resulting in a matte finish after repeated applications.

Our screen-washing campaign, aimed at the recovery of early mammal teeth, was described in detail by Sander et al. (2016). However, the screen-washing concentrate contained so few terrestrial amniote remains (only two identifiable specimens were recovered, Sander et al. 2016, Schwermann 2016), that screen washing was discontinued in 2018 in favour of collecting macroscopically.

In addition to the collecting efforts by the University of Bonn and the WMNM, the holdings of fossils at the WMNM from the Contorta Beds of Bonenburg were significantly increased by the acquisition of Michael Mertens' private collection through the Heritage Development Program of the state of NRW.

Geology, stratigraphy and invertebrate record of the Bonenburg clay pit

The Central European Basin and its stratigraphy

In Europe, the Rhaetian stage is represented by the Alpine Rhaetian, deposited in the western Tethys sea, and the epicontinental Rhaetian deposits. The latter resulted from the Rhaetian transgression onto the European continent, which marked the end of the continental sedimentation of the Middle Keuper in Central Europe. Although sediments from the Rhaetian transgression are widespread across Europe, their distribution is patchy (Barth et al. 2018). This reflects the fact that the sea level rise was insufficient to flood many of the pre-existing topographic highs, producing a rather complex palaeogeography (Barth et al. 2018). One prominent palaeogeographic feature was the Central European Basin (CEB), which extended from Poland in the east to the east coast of the British Isles in the west. The basin's sediments have been well characterized in the subsurface and crop out sporadically from the southern margin of

Figure 4: Mode of vertebrate fossil occurrence. **A** Largest mass accumulation of fossils recovered so far from Bone Bed 2 consisting of bones, fin spines and coprolites trapped by a log on the seafloor. **B** Shastasaurid vertebral centrum emerging from Bone Bed 2a. The immediately overlying Bone Bed 2b is visible in the lower half of the image. **C** Plesiosaur vertebral centrum still embedded in Bone Bed 2a. Note that the centrum extends below and above the layer of scales and teeth into the claystone hosting the bone bed. **D** Hybodont fin spine after recovery from the bone bed. **E** Assortment of plesiosaur and ichthyosaur vertebral centra and large indeterminate bone shaft from 2017 excavation. **F** Large and anteroposteriorly short shastasaurid ichthyosaur vertebral centrum (Shastasauridae indet. morphotype 1).

Table 3: Student theses on vertebrate fossils from the Contorta Beds of the Rhaetian Exter Formation of Lücking clay pit #3, Bonenburg, Westphalia, Germany.

Vida, T. 2024. A taxonomic and paleoecological review of the Rhaetian chondrichthyan fauna of Bonenburg (NRW) Germany. – M.Sc. Thesis, Rheinische Friedrich-Wilhelms-Universität Bonn, Bonn, Germany.

Prino, A. 2023. The temnospondyl fossils from the Rhaetian (Late Triassic) of Bonenburg (North Rhine-Westphalia) and their implications for Temnospondyli extinction. – M.Sc. Thesis, Rheinische Friedrich-Wilhelms-Universität Bonn, Bonn, Germany.

Wellnitz, P. 2022. Phytosaur osteoderms from the Rhaetian bonebed of Bonenburg, Westphalia, Germany – Implications for End-Triassic Extinction. – B.Sc. Thesis, Rheinische Friedrich-Wilhelms-Universität Bonn, Bonn, Germany.

Perillo, M. 2022. Giant shadows in the Late Triassic sea: Histological analysis on putative and genuine giant ichthyosaurs bone fragments. – M.Sc. Thesis, Rheinische Friedrich-Wilhelms-Universität Bonn, Bonn, Germany.

Lamsfuß, T. 2022. Description and taxonomic assignment of ichthyosaur and other marine reptile fossil material from the Rhaetian (Late Triassic) of Bonenburg, Germany, and study of amphicoely as a novel tool for identification of ichthyosaur vertebrae. – B.Sc. Thesis, Ruhr-Universität Bochum, Bochum, Germany.

Hack, J. 2022. Beschreibung und Einordnung von zwei terminalen Phalangen von basalen Sauropodomorphen und Theropoden aus dem Rhät (späte Trias) der Grube Bonenburg (Kreis Höxter, NRW) und ihre Bedeutung für das Massenaussterben an der Trias/Jura-Grenze. – B.Sc. Thesis, Rheinische Friedrich-Wilhelms-Universität Bonn, Bonn, Germany.

Garbay, L. 2021. A rare stereospondyl femur from the Rhaetian of Bonenburg (Germany) and the implication why long bones are not a valid size-proxy for Stereospondyli. – M.Sc. Thesis, Rheinische Friedrich-Wilhelms-Universität Bonn, Bonn, Germany.

Neuhof, M. 2019. Study on the origin of plesiosaurs, based on two unequal propodials from the Bonenburg locality, Germany. – M.Sc. Thesis, Rheinische Friedrich-Wilhelms-Universität Bonn, Bonn, Germany.

Wild, A.-L. 2018. Osteological description of *Pachystropheus* vertebrae from Bonenburg. – B.Sc. Thesis, Rheinische Friedrich-Wilhelms-Universität Bonn, Bonn, Germany.

Witkowski, J. 2017. Beschreibung der *Shonisaurus*-Wirbel aus dem Rhät-Bonebed (Obertrias) von Bonenburg, Kreis Höxter, Nordrhein-Westfalen (Deutschland). – B.Sc. Thesis, Rheinische Friedrich-Wilhelms-Universität Bonn, Bonn, Germany.

Werner, J.D. 2016. Description of a temnospondyl humerus from the Rhaetian (Late Triassic) of Bonenburg, (Westphalia, Germany) and its implications for temnospondyl extinction. – B.Sc. Thesis, Rheinische Friedrich-Wilhelms-Universität Bonn, Bonn, Germany.

the German Northern Plains southward to the London-Brabant, Rhenish, and Bohemian massifs.

One such surface occurrence is a small tectonic block on the western margin of the Hessian Depression descending from the Eggegebirge hills in the west. Parts of this block are well exposed in the Bonenburg clay pit. The small scale of the block is illustrated by the history of discovery of the Rhaetian deposits. Exploratory drilling before excavation of the clay pit began had suggested it would yield black Sinemurian mudstones (as in a neighbouring pit), but upon the onset of mining, the black shales encountered in the boreholes turned out to be the lithologically similar deposits of the Exter Formation. The current clay pit exposes both, a Late Triassic to earliest Jurassic section, and the Sinemurian Arietenton and Obtususton formations, offset by a large normal fault. The Late Triassic to earliest Jurassic section northwest of the fault includes the Norian-age Arnstadt Formation, the Rhaetian-age Exter Formation, and the Hettangian Psilonotenton Formation (Fig. 2). Southeast of the fault, there are only Sinemurian rocks (see Sander et al. 2016). Both the Exter Formation and the Sinemurian units are mined.

In addition to the main fault, numerous low-angle faults traverse the pit, as a result of the stair-step tectonics at the eastern flank of the Eggegebirge hills. In the southwestern Triassic part of the pit, the beds dip approximately 35° to the west. Due to the terrain rising towards the Eggegebirge, the fossiliferous Contorta Beds of the Exter Formation will be encountered at increasing depth as mining continues.

Stratigraphic section of the Bonenburg clay pit

In the stratigraphic framework of the "Germanic Facies" of the Triassic, the Rhaetian as a lithostratigraphic term is equivalent to the Upper Keuper. In the CEB, the Upper Keuper is represented by a single formation, the Exter Formation, which consists of three members (Will 1969; Beutler et al. 2005; Barth et al. 2018; Gravendyck et al. 2020). From oldest to youngest, these are the Postera Beds, the Contorta Beds and the Triletes Beds. In the Bonenburg clay pit, this entire sequence is well developed and completely exposed, underlain by the upper Middle Keuper (Arnstadt Formation) and overlain by the Hettangian (Fig. 2), Sinemurian and lower Pliensbachian. The base of the Arnstadt Formation is not exposed, only about the top ten metres are visible, depending on mining progress. The Arnstadt deposits consist of grey-green marls with purple patches typical of the terrestrial and playa sediments of the formation. They lack discernible bedding but exhibit the blocky appearance indicative of pedogenic overprint.

Exter Formation. The Postera Beds in Bonenburg (Fig. 2) are only about 2 m thick and consist of greenish-grey sand and siltstone with ripple bedding, intercalated with some finer grained, dark grey-green mudstones. To date, no fossils other than palynomorphs have been recovered from the Postera Beds (Schobben et al. 2019). Neither the eponymous bivalve *Unionites postera* nor any other macrofossils have been found in these sediments. Even microfossils are rare, and palynomorphs are available only from a few productive samples, while most are barren. The few productive samples display the key taxa of the Classopollis-Enzonalasporites zone, which is also suitable for correlation of the Postera Beds with contemporaneous sections across the CEB (Schobben et al. 2019; Gravendyck et al. 2020).

The Contorta Beds, on the other hand, are at least 11 m thick (Fig. 2), and possibly much more. The exact thickness is difficult to assess because the top of the beds is discordantly sheared off by a low-angle fault. Thus, in the NW corner of the pit, there are at least 15 m of Contorta Beds. Lithologically, the Contorta Beds are a series of black shales with a variable silt and fine sand content. The member is named after the European and Tethyan index fossil for the Rhaetian Stage, the bivalve *Rhaetavicula contorta* (Ogg et al. 2020). Whereas some beds in the member are pure claystone devoid of even any silt component, others are fine, ripple-bedded sandstone. For a detailed lithological log, see Sander et al. (2016) and Gravendyck et al. (2020). Palynofacies analysis reveals that the Contora Beds are bounded by marine ingressions at the base and top, corresponding to the first and second maximum flooding of the Rhaetian sea, respectively (Barth et al. 2018; Gravendyck et al. 2020).

At least four bone beds (designated bone beds 1 through 4) are present in this section (Fig. 2). However, due to their thinness and the patchy distribution of larger bones, the bone beds are difficult to detect in outcrop. Bone Bed 1 occurs at the base of the Exter Formation and is characterized by a uniformly small grain size of the fossils. Only small fish scales and shark teeth a few millimetres in size have been observed to date. Approximately 50 cm above this basal bone bed, termed Bone Bed 1a, another bone bed has been observed in a sandy matrix containing larger components, including abundant coalified wood. This bone bed is termed Bone Bed 1b (Fig. 2) and has not yet been excavated in detail. It is possible that some of the fossils from the early days of collecting originate from Bone Bed 1b based on their lithological similarities, especially in terms of their induration by pyrite. Bone Beds 1a and 1b are both rich in pyrite and seem to be discontinuous at the outcrop scale.

Bone Bed 2, located approximately 8.1 m above the base of the Contorta Beds (Fig. 2), has been the primary focus of annual excavation campaigns since 2015 (Table 1). At this stratigraphic level, two bone bed horizons are present, separated by 8 cm of dark grey claystone: the lower horizon Bone Bed 2a and the upper horizon Bone Bed 2b. Both are typically around 10 mm thick and consist of a dense accumulation of fish scales, fish teeth and shark teeth. Larger individual bones are embedded in this layer of scales and teeth (Fig. 4C). In addition, several spectacular accumulations of larger fossils have been discovered, often clustered around a large baffle such as a fossilized log (Fig. 4A). Large coprolites are an important component of these concentrations (Fig. 4A), while smaller coprolites are found throughout the regular scale-and-teeth accumulations. On average, one larger bone, distinct in size from the normal bone bed components, was found per square metre of excavation. Bone Bed 2b appears to have more larger components than Bone Bed 2a, though overall preservation is better in this lower horizon. Interestingly, Bone Bed 2a fills invertebrate burrows that extend downward from its basal surface (Fig. 3C), a feature also reported from the British Rhaetian (Korneisel et al. 2015). These burrows, which are up to 2 cm across and reach up to 6 cm down into the sediment, created localized areas of exceptionally good preservation because scales and teeth were rapidly deposited into the open burrows, removing them from currents on the seafloor.

Larger fossils, most commonly hybodont fin spines (Fig. 4D) and plesiosaur (Fig. 4C) and ichthyosaur vertebrae (Fig. 4B), are generally preserved lying flat in Bone Bed 2 (Fig. 4B, C), unless incorporated into larger accumulations. Ichthyosaur vertebrae, in particular, were strongly affected by corrosion (Fig. 4E, F) due to chemical or physical processes on the seafloor, as has been observed in other Rhaetian localities (e.g., Fischer et al. 2014; Sander et al. 2020), destroying morphological information (see below). The strong abrasive action of the hydraulically agitated fine fraction of the bone bed on larger bones is strikingly documented by a large plesiosaurian cervical vertebra (WMNM P64631). The postzygapophyses of this specimen were truncated by abrasion (Fig. 10H) where they extended above the sediment surface. The rest of the vertebra, which came to rest with the anterior articular surface facing downwards, is well preserved (Fig. 10H, I).

In light of discussions on bone bed genesis (Martill 1999), we recorded the long axis orientation of all

elongate fossils. A weak preferred orientation of long bones and wood was observed in Bone Bed 2a only; orientation in Bone Bed 2b is even less pronounced. Since elongate fossils are rare among the larger material, the dataset remains small and lacks statistical significance. The few localized larger accumulations of bones and coprolites (Fig. 4A) against baffles can provide further support for the presence of currents on the seafloor, however.

An interesting pattern is emerging regarding the interplay of fossil recovery and regional tectonics: large fossils are preferentially found near faults (Fig. 3A). The most likely explanation for this peculiar pattern is that fossils represent inhomogeneities within the sediment, causing the mudstones of the Contorta Beds to fracture along these inhomogeneities rather than deform through ductile processes.

Bone Bed 3 is located 2 m above Bone Bed 2, which in the southern part of the pit is within the top 50 cm of the Contorta Beds (Fig. 2). Bone Bed 3 has yielded, on average, the largest but also the most poorly preserved fossils and notably lacks the fine fraction of scales and teeth. Bone Bed 3 also contains large coprolites and, in some places, the bone bed is heavily indurated by a matrix of pinkish-gray amorphous phosphate rock (Fig. 3D). This bone bed appears discontinuous and has not been exposed for more than a couple of square metres during any one excavation campaign. Poor preservation limits its scientific potential as key morphological features, especially in the abundant plesiosaurian vertebrae, are not preserved, and many bones are abraded beyond recognition. In addition to abrasion, severe fracturing of the bones from Bone Bed 3 influences their morphology in unpredictable ways.

Bone Bed 4 was observed only in the NW corner of the pit where the Contorta Beds are thicker. Bone Bed 4 is located 80 cm above Bone Bed 3. It is thinner than Bone Bed 3, similarly discontinuous and distinctive in its high amount of pyrite. Otherwise, Bone Bed 4 resembles Bone Bed 3, containing coprolites as well as small and large bones.

Articulated fish skeletons (Fig. 3J) are found in the pure claystones occurring in the 30 cm interval below Bone Bed 2 as well as in the other most fine-grained parts of the Contorta Beds which occur below Bone Bed 2, i.e., from about 3 to 6 m above the base of the member. The plesiosaur skeleton, holotype of *Rhaeticosaurus mertensi* Wintrich et al. 2017, was recovered from these very fine-grained deposits, at a level 4.6 m above the base of the Contorta Beds. These lower, clay-rich layers have also yielded articulated small ophiuroids of up to 15 mm in diameter (Fig. 3H) and are similar to those described from the Contorta Beds of Winterswijk (NL) by Thuy et al. (2012). Additional finds from these clay layers include beetle elytra (Fig. 3F) and the inarticulate brachiopod *Lingula*, which often preserves the original distinctive colour banding (Fig. 3G). These brachiopods are sometimes concentrated in shell horizons (Fig. 3E). Occasionally, isolated bones are found in the Contorta Beds as well, such as the fragmentary rib of a large ichthyosaur (WMNM P98701), with a diameter of 40 mm and a preserved length of 50 cm. WMNM P98701 came from a level several decimetres below Bone Bed 2. This part of the section represents the lowest energy level, with little to no water movement near the seabed. Only clay particles settled from suspension onto what was likely a dysoxic to anoxic seafloor.

Approximately 60 cm above Bone Bed 2, in a fine-grained sandstone bed, resting traces of the echinoderm *Asteriacites* are frequently encountered (Fig. 3I). These trace fossils may have been produced either by ophiuroids or asteroids (Meyer & Wetzel 2021). An asteroid origin would be particularly significant because asteroids require normal marine salinity, whereas ophiuroids can tolerate reduced salinity. However, the exact species of these trace fossils, either *A. lumbricalis* or *A. stelliformis* (Meyer & Wetzel 2021), needs to be ascertained first, as only *A. stelliformis* is exclusively associated with asteroids. In other very fine-grained horizons, directly below Bone Bed 2 and between Bone Bed 2 and Bone Bed 3, abundant remains of spinicaudatan (conchostracan) crustaceans have been recovered (Fig. 3E; Fig. 2 in Schobben et al. 2019). Conchostracan crustaceans are extremely rare in marine deposits (Hethke et al. 2019), making their abundant occurrence in Bonenburg striking. However, palynofacies analysis of the interval between bone beds 2 and 3 reveals an increased abundance of the chlorophycean alga *Botryococcus*, which is commonly interpreted as an indication of brackish conditions (Tyson 1995). This suggests at least some freshwater influx during this interval, as further supported by the coinciding temporary disappearance of acritarchs, which indicate fully marine conditions (see figs. 3, 4 in Gravendyck et al. 2020).

The Triletes Beds, also known as "Event Beds", overlie the Contorta Beds with a sharp contact. The basal 3 m of the Triletes Beds consist of poorly bedded, dark red mudstones with thin, medium-grey horizons. Above this unit, there is about 1 m of medium-grey mudstone, which transitions abruptly to a roughly 11-m thick interval of thinly bedded yellow mudstones. Rare

teepee structures occur within the yellow mudstones, suggesting mud cracking and thus episodes of subaerial exposure. Collectively, the Triletes Beds record a progressive shallowing of the sea and deposition on a muddy shoreline or tidal flat which is consistent with previous interpretations as a deltaic environment (Will 1969; Barth et al. 2018) and palynofacies analysis of the Bonenburg material (Gravendyck et al. 2020).

The Triletes Beds are devoid of macrofossils of any kind and represent the marine extinction interval in Bonenburg (Schobben et al. 2019; Gravendyck et al. 2020). In contrast, plant microfossils are abundant and exceptionally wellpreserved compared to other CEB sections (see figs. 6-9 and detailed comparison in Gravendyck et al. 2020). The palynofloral assemblage characterizes the source vegetation as shrubby-herbaceous, with a canopy dominated by seed ferns and an understory of ferns, clubmosses and bryophytes. The consistent occurrences of reworked spores in the Triletes Beds suggest significant terrestrial erosion, a pattern also documented in nearby successions in Schandelah (Lower Saxony) and Winterswijk (van de Schootbrugge et al. 2020; Bos et al. 2024). The uppermost Rhaetian appears to be missing based on an abrupt change in palynofloral diversity that cannot be attributed to floral turnover alone (Gravendyck et al. 2020).

Psilonotenton Formation. At the top of the Exter Formation, there is a well-exposed Triassic-Jurassic boundary, marked by a distinctive, 5–8 cm thick oyster shell layer weathering chocolate-brown. This horizon belongs to the Psilonotenton Formation. The lowermost ammonite zone of the epicontinental (boreal) Jurassic, the Planorbis Zone (Ogg et al. 2020), is well represented by its index fossils *Psiloceras planorbis*, a smooth-ribbed, moderately evolute ammonite. Although the oyster shell bed has not been extensively sampled, it has yielded various isolated ichthyosaur bones, including a humerus assignable to Neoichthyosauria. The section continues into the Sinemurian, reaching the base of the stage at the western margin of the outcrop.

Palynostratgraphy of the Bonenburg section and biostratigraphic implications

From a vertebrate palaeontological perspective, the chronostratigraphic and environmental insights provided by palynology are of great value. For the epicontinential Rhaetian sections in Europe, palynology provides an important stratigraphic framework (e.g., Barth et al. 2018; Schneebeli-Hermann et al. 2018; Gravendyck et al. 2020) and enables reliable correlations with the Tethyan Rhaetian and Hettangian (Lindström et al. 2017; Schneebeli-Hermann et al. 2018, Schobben et al. 2019; Ogg et al. 2020). When combined with carbon isotope stratigraphy, palynological data also serves to constrain the Triassic-Jurassic boundary across Europe (Lindström et al. 2017; Barth et al. 2018; Schobben et al. 2019).

Outcrop samples face the drawback of a potential degradation of palynomorphs by oxidation through weathering. However, because of its great thickness and fresh exposure, the Bonenburg section is well suited for palynological research. This contrasts with the general situation in the CEB, where most palynological work has been conducted on subsurface material recovered from boreholes (see fig. 1 in Barth et al. 2018 and fig. 2 in Bos et al. 2024 for section overviews). The recent detailed study at Bonenburg (Schobben et al. 2019; Gravendyck et al. 2020) provides an excellent palynostratigraphic framework for other Triassic-Jurassic boundary sections (Fig. 2); this framework integrates well with previous studies and was further corroborated by a similar core-based study from the Rhaetian succession at Winterswijk (Bos et al. 2024). The Winterswijk section ends in an erosional surface in the Triletes Beds, directly overlain by Oligocene sediments, however. Thus, Jurassic rocks are not preserved at Winterswijk.

In the Bonenburg section, a well-preserved and informative palynological record begins at the base of the Contorta Beds and extends to the top of the outcrop, i.e., near the base of the Sinemurian (Gravendyck et al. 2020, Fig. 2), thereby capturing a detailed record of the Rhaetian palynozones of the CEB (Barth et al. 2018; Schobben et al. 2019; Schneebeli-Hermann et al. 2020). The Postera Beds at the base of the section were mostly barren, but two productive samples allow assigning this part of the section to the lower Rhaetian Classopollis-Enzonalasporites pollen zone.

The Contorta Beds yield a palynoflora indicative of the Rhaetipollis-Limbosporites zone, which is recognizable throughout Europe (Lindström et al. 2017; Barth et al. 2018, supplementary figure in Gravendyck et al. 2020). The Rhaetipollis-Limbosporites zone can be divided into three subzones (RLa to RLac). Importantly, the Contorta Beds in Bonenburg revealed changing abundances of aberrant palynomorphs and pollen tetrads, which were later studied in great detail in other sections, especially in the nearby localities of Schandelah, Winterswijk and Rødby (all CEB), as well as Stenlille (Danish Basin) (Lindström et al. 2019; Bos et al. 2024a, 2024b). The occurrence of such aberrant

palynomorphs hints at the environmental stressors preceding the extinction interval, and the timing of peak occurrences provides a stratigraphic event that can be correlated across nearby sections together with the chemostratigraphic record (Bos et al. 2024a). The Triletes Beds are entirely within the Ricciisporites-Polypodiisporites zone. Finally, the Pinuspollenites-Kraeuselisporites zone at the top of the section represents the lower part of the Hettangian. As noted, the very base of the Psilonotenton Formation is likely missing at Bonenburg due to the absence of the lowermost ammonite index taxon, *Psiloceras tilmani*. An abrupt change in the palynoflora further corroborates a hiatus at the very top of the Rhaetian and the base of the Hettangian (Fig. 2).

According to this palynostratigraphic framework, the base of the Contorta Beds coincides with the beginning of middle Rhaetian. The late Rhaetian begins near the top of the Contorta Beds, right above Bone Bed 3. Bone Bed 1 formed during the first maximum flooding of the Rhaetian sea, within the middle Rhaetian pollen subzone RLa, while Bone Bed 3 slightly predates the second maximum flooding near the top of pollen subzone RLc. The horizon of the type specimen of the plesiosaur *Rhaeticosaurus mertensi* is correlated with the upper part of RLa and coincides with palynologically inferred signs of ecological disturbance, based on changes in diversity indices, the carbon isotope record, and a temporary increase in malformed pollen and spores (figs. 11, 12 in Gravendyck et al. 2020). This disturbance pattern seems to be at least regional in scale, because similar signals have been observed in both the palynological and chemostratigraphic records in Winterswijk (Bos et al. 2024a). Likewise, Bone Bed 2 is associated with an interval of even higher levels of disturbance indicators (Gravendyck et al. 2020), also present in Winterswijk (Bos et al. 2024a).

Bone Bed 2 is located in the upper part of pollen subzone RLb and is thus late middle Rhaetian in age (Fig. 2). In the absence of volcanic ash deposits, assigning a precise numeric age for Bone Bed 2 is challenging. However, interpolation based on the Triassic time scale of Ogg et al. (2020) provides a reasonable estimate. The base of the Rhaetian Stage is dated at 205.74 Ma and the end of the Triassic Period at 201.36 Ma (Ogg et al. 2020), suggesting an approximate age of 203.5 to 204 Ma for Bone Bed 2. Reference to Barth et al. (2018, fig. 2) would suggest a slightly younger age for Bone Bed 2 of about 203 Ma. Accordingly, the organisms preserved in Bone Bed 2 would have lived at most 2.4 Ma, but possibly as little as 1.4 Ma before the end of the Triassic. The holotype of *Rhaeticosaurus mertensi*, the oldest known plesiosaur, would have lived 500,000 to 1 million years earlier.

While the Contorta Beds of the Exter Formation have long been correlated with the middle Rhaetian in the CEB, Bonenburg is unique in combining high-resolution palynological dating with systematic vertebrate fossil collecting in a single section (Fig. 2). The precise bio- and chemostratigraphic framework distinguishes the Bonenburg vertebrate fauna from virtually all other faunas from epicontinental Rhaetian bone beds across Europe. These are typically dated by lithostratigraphic correlation, often with low precision, because of the patchy distribution of epicontinental Rhaetian deposits and the condensed nature of most Rhaetian sections. Even extensive vertebrate-bearing units from the late Norian to early Jurassic in the Alps, such as the Kössen Formation of eastern Switzerland (Furrer 1993; Sander et al. 2022) and Austria, are dated with a lower precision than the Bonenburg section because they lack ammonoids, conodonts, and palynomorphs. Any vertebrate taxon recorded at Bonenburg thus has important implications for reconstructing extinction patterns during the final 5 million years of the Triassic.

Using chemostratigraphy, Schobben et al. (2019) were able to correlate the Bonenburg section with the GSSP for the base of the Jurassic at Kuhjoch, Austria. The Contorta Beds correlate with the Pre-event Beds, and the lower three quarters of the Triletes Beds correlate with the Schattwald Beds (Event Beds) at Kuhjoch. However, all known epicontinental Triassic-Jurassic boundary sections appear to exhibit a hiatus in the latest Rhaetian to earliest Jurassic (Lindström et al. 2017; Schobben et al. 2019), i.e., in the transition from the Triletes Beds to the Psilonotenton Formation. For vertebrate palaeontology, this gap is less consequential, as vertebrate fossils in the CEB are generally restricted to the Contorta Beds, including Bonenburg. Thus, this hiatus does not affect the study of vertebrates in this context.

Vertebrate fauna of the Bonenburg clay pit

Chondrichthyes

Due to the abundance of fossils at Bonenburg, there are more and better specimens of common Rhaetian chondrichthyan remains than elsewhere (Sander et al. 2016), accounting for 26% of the specimens recovered during the 2015-2024 excavations (Fig. 5) and also by

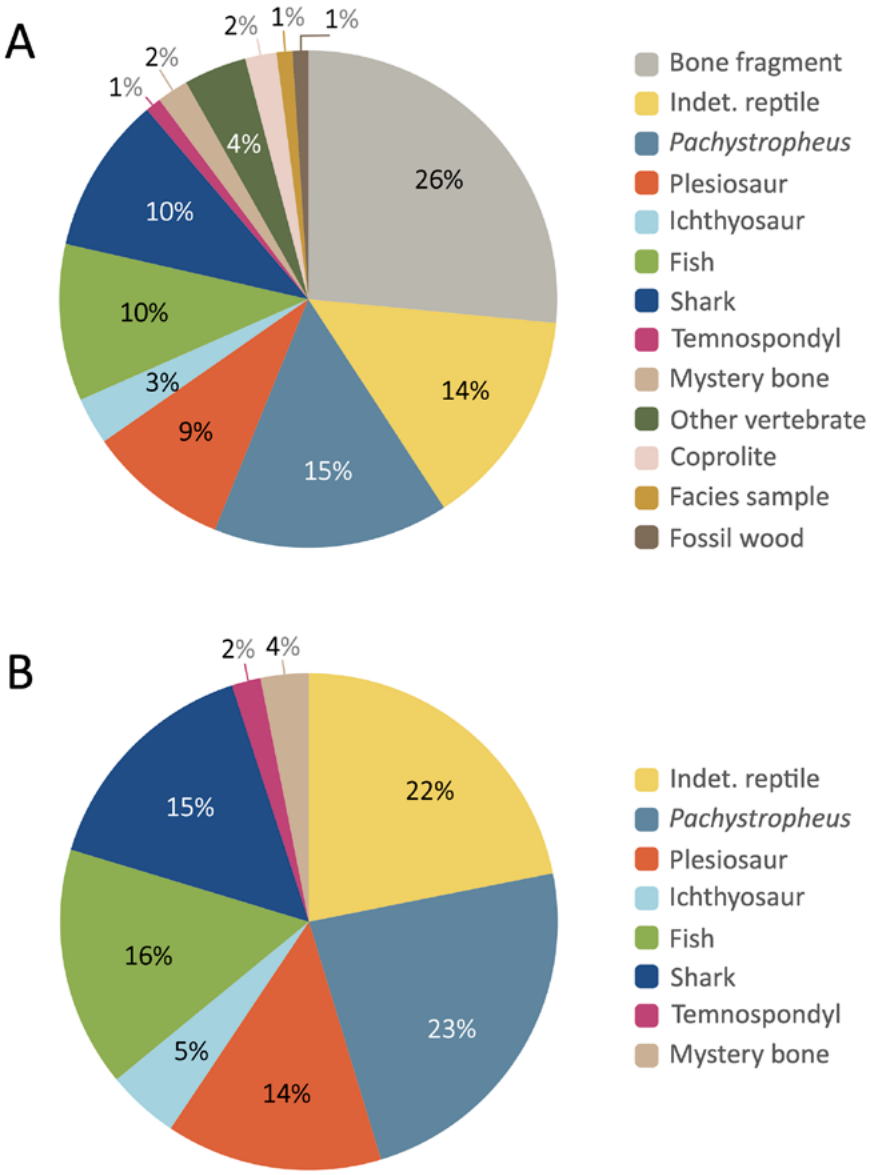


Figure 5: Composition of the finds from the bone beds at Bonenburg in the collections of WMNM. **A** All specimens. **B** Vertebrate fossils.

the 2015 and 2016 screen-washing campaigns. These efforts yielded hundreds of chondrichthyan remains larger than about 10 mm, mainly fin spines, although many incomplete spine specimens were not collected. The chondrichthyan fauna was reviewed and figured in some detail by Sander et al. (2016) and also dealt with by Vida (2024) and Vida et al. (2025).

The most distinctive chondrichthyan fossils are large hybodont fin spines (Fig. 3D), sometimes reaching 20 cm in length and in a state of great completeness unknown from other European Rhaetian localities. These fin spines presumably represent the same shark as the large-toothed taxon "*Hybodus*" *cloacinus* (Fig. 6E). Note that the species "*H.*" *cloacinus* was synonymized with "*H.*" *cuspidatus* by Vida et al. (2025), but we feel that this synonymy cannot be established at this time without further work. Also note that we put the genus name in quotes because the taxon may pertain to the genus *Polyacrodus* instead of to *Hybodus*. The other clearly hybodont tooth fossils from Bonenburg pertain to *Lissodus minimus*, which like "*H.*" *cloacinus* are also very abundant, as in other Rhaetian deposits. Commonly encountered small fin spines presumably derive from the same shark as the *Lissodus minimus* teeth.

Of particular interest are finds of hybodont cephalic spines. In extant sharks, these cephalic spines are paired, and there are one or two pairs (e.g., Cappetta 2012, Fig. 37) placed symmetrically on the posterodorsal part of the head. The more common type of cephalic spine from Bonenburg has two lateral root lobes (Fig. 6C; see also Moreau et al. 2021, called a "dorsal" spine by these authors). A new type of cephalic spine

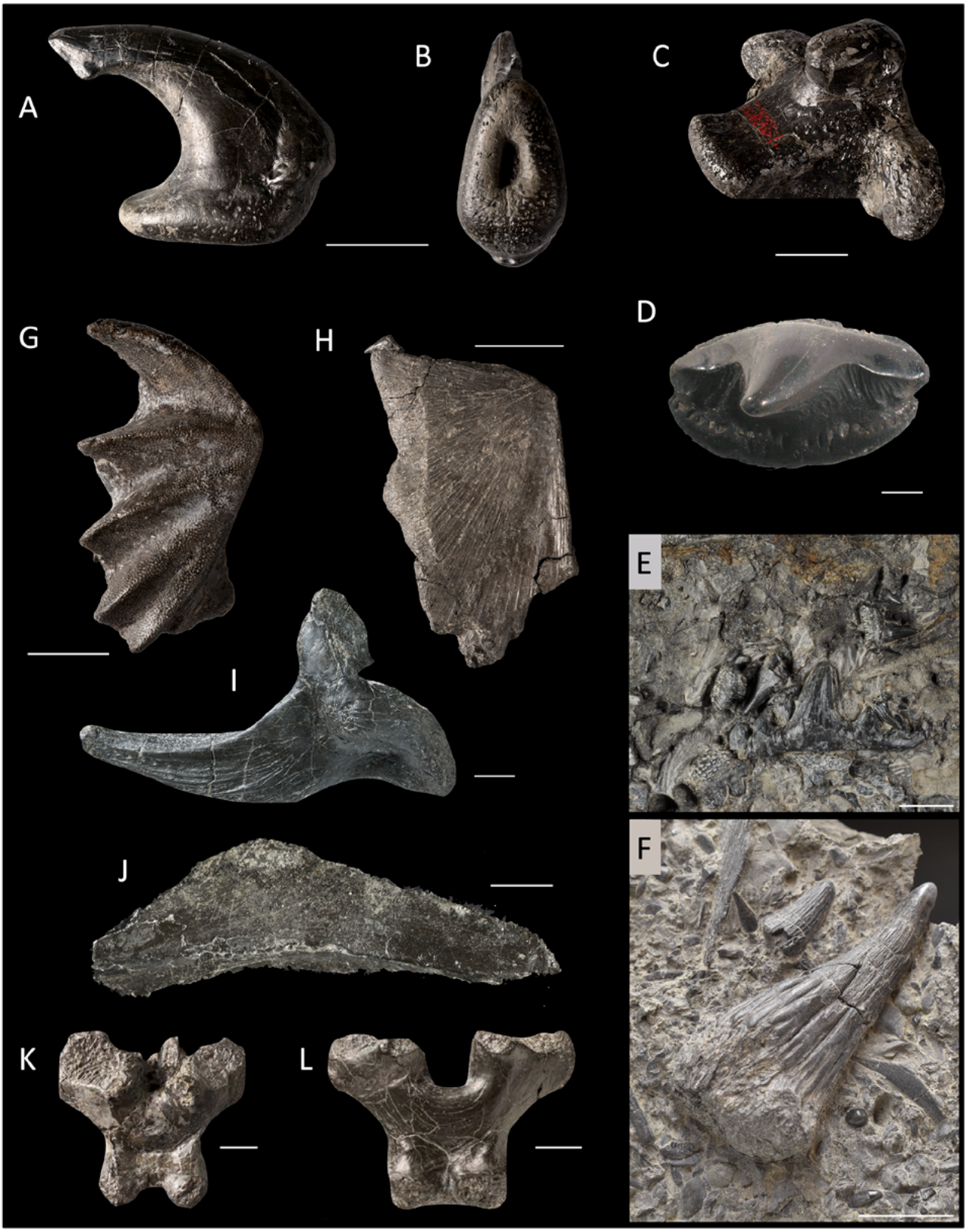


Figure 6: Chondrichthyans and sarcopterygians. **A**, **B** New type of hybodont cephalic spine (WMNM P97665) in (**A**) lateral view and (**B**) basal view. **C** Hybodont cephalic spine (WMNM P97688), presumably pertaining to "*Hybodus*" *cloacinus*. **D** Shark tooth *Grozonodon candaui* (WMNM P64343). **E** Shark tooth "*Hybodus*" *cloacinus* (WMNM P119279). **F** *Severnichthys* tooth (WMNM uncat.). **G** Small, possibly juvenile dipnoan cf. *Ptychodus serratus* tooth (WMNM P117514). **H** Dipnoan ?*Ceratodus* skull bone (WMNM P117515). **I** Mawsoniid coelacanth principal coronoid (WMNM P64369). **J** Mawsoniid coelacanth angular in lateral view (WMNM P118416). **K** Basisphenoid of mawsoniid coelacanth sp. 1 in dorsal view (WMNM P81018). **L** Basisphenoid of mawsoniid coelacanth sp. 2 (WMNM P81017) in ventral view. Scale bars represent: 1 mm (D); 5 mm (E, G); 1 cm (A-C, F, I-L); 2 cm (H).

(Fig. 6A, B), known from a single specimen (WMNM P97665), lacks the lateral root lobes completely and uniquely has a large basal foramen sunken into an olive-shaped root. This type of cephalic spine, not yet associated with any teeth, is also known from the Rhaetian of the Swiss locality of Niederschönthal (RK personal observation) and the Lower Keuper of southern Germany (Böttcher 2015, fig. 8.10) from one specimen each. Note that this Bonenburg cephalic spine specimen was figured by Vida et al. (2025, fig. 5g) as "*H.*" *cuspidatus/cloacinus* and not distinguished from the cephalic spine with the lateral lobes.

The remaining chondrichthyan fossils from Bonenburg pertain to Neoselachii. This includes the second very common tooth type at Bonenburg, the synechodontiform *Rhomphaiodon minor* (Sander et al. 2016). Very likely, these teeth derive from the same shark as the fin spine type *Nemacanthus monilifer* (Cuny & Risnes 2005). However, as in the case of "*H.*" *cloacinus*, fossils showing the unequivocal association of teeth and fin spines are required to establish the synonymy (contra Vida et al. 2025). Other neoselachian shark remains consist of further synechodontiform teeth, namely the moderately common *Grozonodon candaui* (Fig. 6D) and the rare *Synechodus rhaeticus* (Sander et al. 2016, fig. 17j). Neoselachian teeth that either also pertain to Synechodontiformes or are of uncertain affinities (Vida et al. 2025) are the common *Parascylloides turnerae* (Vida et al. 2025, fig. 9b) and the rare *Pseudocetorhinus pickfordi* (Sander et al. 2016, fig. 17H) (Table 2).

Considering the precise biostratigraphic dating of the Bonenburg section, it is of particular interest to compare the stratigraphic occurrence of the vertebrate fossils with previous records. Biostratigraphically, the Bonenburg chondrichthyan fauna is typically Rhaetian, with no taxa extending into the Jurassic, with the possible exception of "*H.*" *cloacinus* (Duffin 1993). Typical Rhaetian chondrichthyans are *Rhomphaidon minor*, *Lissodus minimus*, and *Parascylloides turnerae*, all of which may be considered index fossils. Note that *Parascylloides turnerae* was initially thought to be a symphyseal tooth of *Rhomphaidon* (Thies et al. 2014). *Nemacanthus* fin spines are also typical Rhaetian elements, as is "*H.*" *cloacinus*. The abundance of basal neoselachians is typical for Rhaetian faunas of Europe.

Fin and cephalic spines of sharks always represent an individual that has died, whereas teeth are continuously shed by living sharks. Fin spines are unusually well preserved at Bonenburg, in contrast to other Rhaetian bone bed localities, indicating limited postmortem transport of the remains. This suggests that the respective chondrichthyans were common in the environment. The great abundance of certain chondrichthyan teeth taxa at Bonenburg, e.g., "*H.*" *cloacinus*, *Lissodus minimus*, and *Rhomphaiodon minor*, may allow reconstruction of the dentition of these taxa in the future.

Actinopterygii

The Bonenburg bone beds contain the typical "assortment" of isolated actinopterygian teeth and scales known from many other Rhaetian bone beds across Europe (Storrs 1994; Fischer et al. 2014; Allard et al. 2015; Nordén et al. 2015; Korneisel et al. 2015; Mears et al. 2016; Slater et al. 2016; Cross et al. 2018; Cavicchini et al. 2018; Moreau et al. 2021; Evans et al. 2024). Representative material was described in Sander et al. (2016) and is listed in Table 2. It consists not only of dental material but also of jaw fragments bearing teeth. The actinopterygians are less informative regarding biostratigraphy because many, at least at the genus level, have extensive pre- and post-Rhaetian ranges. The only typically middle Norian to Rhaetian element is the semionotid *Sargodon tomicus*, which is found in many Rhaetian bone beds around Europe but nowhere else (Paleobiology Database 2025). *Sargodon* teeth and jaw fragments are common in Bone Bed 2, especially the characteristic incisifiorm teeth. The large birgeriid *Severnichthys* is also represented by good specimens (Fig. 6F) that are distinct from temnospondyl amphibians (see discussion below). *Severnichthys* was also reported by Evans et al. (2024) based on small teeth with a distinct enamel cap from UK localities, but no justification is given for this assignment.

In addition to the bone bed material, articulated actinopterygian skeletons occasionally occur in the dark claystones (Fig. 3J) of the Exter Formation hosting the bone beds. Such fossils were found below and above Bone Bed 2 during its excavation. The largest skeleton is ca. 40 cm in length, but the affinity of these fish fossils has not been studied yet. Clearly, the abundant actinopterygian remains from Bonenburg require further study.

Non-tetrapod Sarcopterygii: Actinistia

Coelacanthidae have been reported from the European Rhaetian from the UK bone beds (Allard et al. 2015; Moreau et al. 2021; Quinn et al. 2025) and from the Peygros Quarry in southern France (Deesri et al. 2018). In Bonenburg, relatively common peculiar V-shaped bones (Fig. 6K-L) with a wide range of sizes were

initially identified as braincase elements of a small reptile, likely *Pachystropheus*. However, these bones are actually basisphenoids of mawsoniid coelacanths. Two specimens, WMNM P81018 (Fig. 6K) and WMNM P81017 (Fig. 6L), collected in 2016 and 2018 from Bone Bed 2, respectively, were studied in detail by Hartung et al. (2021). The two specimens show distinctive differences in morphology and represent two different morphotypes (Fig. 6K-L), but neither can be assigned to a known species.

There are abundant other bones of coelacanths, in particular at least 40 angulars (Fig. 6J) and a smaller number of quadrates. Also, coelacanths are represented by several mawsoniid principal coronoids (Fig. 6I) (Quinn et al. 2024, 2025), which we erroneously identified as ectopterygoids of *Pachystropheus* (Sander et al. 2016, fig. 20G), following Storrs (1996). All three kinds of coelacanth bones vary greatly in size, indicating quite some variation in body size among the Bonenburg coelacanths. In addition, it is not clear if all these remains only pertain to mawsoniid coelacanth or if other taxa might be represented as well (see Quinn et al. 2025).

The large number of basisphenoid specimens from Bonenburg and their good preservation suggest that these mawsoniids indeed belong to the marine fauna and were not washed in from freshwater habitats. The Mawsonidae are the sister clade of the living coelacanths. They first appear in freshwater in the continental Triassic of North America, and the last surviving mawsoniids from the Late Cretaceous were also freshwater denizens (Hartung et al. 2021). The Bonenburg finds now indicate that mawsoniids had an intervening marine phase in their evolution (Hartung et al. 2021), as already suggested by the French find (Deesri et al. 2018). Given the extensive stratigraphic range of mawsoniid coelacanths, the finds from Bonenburg are of little stratigraphic value.

Non-tetrapod Sarcopterygii: Dipnoi

Among the Dipnoi, there are characteristic large and often heavily worn *Ceratodus latissimus* tooth plates, known from numerous Rhaetian bone beds, including Aust Cliff, where the main bone bed has sometimes been called the "*Ceratodus* Beds" (Storrs 1994). Finds from the UK were discussed by Storrs (1994) and most recently by Moreau et al. (2021). The Swiss locality of Niederschönthal (Meyer et al. 2025), today Schöntal, part of the municipality of Frenkendorf near Basel, has also yielded large *Ceratodus* tooth plates (Huene 1911), as has Saint-Nicolas-de-Port in France (Godefroit 1997). In Bonenburg, such finds come from bone beds 2 and 3 (Sander et al. 2016). Strikingly, some of the very large tooth plates are still attached to heavily corroded jaw bones. There is also a bone of the skull roof of a large lungfish (Fig. 6H), likely pertaining to *Ceratodus* (possibly an anterior mediolateral bone). As already noted in 2016, there are also smaller lungfish teeth (Fig. 6G) from Bonenburg with sharp ridges, possibly pertaining to *Ptychoceratodus serratus* (Skrzycki 2015; Pawlak et al. 2020), as well as scales of this genus. However, the Bonenburg lungfish still await detailed study. In terms of habitat preference, Triassic dipnoans are freshwater to marginal marine (Pawlak et al. 2020).

Temnospondyli

Although Storrs (1994) concluded that all temnospondyl records from the British Rhaetian are erroneous and instead represent remains of *Severnichthys*, a view reiterated by Evans et al. (2024), a different picture is emerging from the Bonenburg bone beds 2 and 3 (Konietzko-Meier et al. 2019; Prino et al. 2024). Temnospondyl remains (Table 4) are not only moderately common (accounting for 2% of all finds until 2025; Fig. 5), but they are also remarkably diverse. Both cranial bones and elements of the appendicular skeleton (i.e., girdle and limb bones) are present, but remains of the postcranial axial skeleton have not been identified with certainty. Only the strange flattened vertebral centra with poorly ossified surfaces and large apophyses, discussed with the ichthyosaurs below, may possibly represent temnospondyl amphibians instead, requiring further histological study. Taking a parsimonious approach, we posit that there are at least two taxa of large-bodied temnospondyls pertaining to Capitosauroidea represented by Bonenburg finds: cf. *Cyclotosaurus* sp. and one or two other taxa of large-bodied capitosauroids assigned to Capitosauroidea indet. (Prino et al. 2024). Note, however, that in the meantime more temnospondyl material has been recovered than reported by Prino et al. (2024).

Cf. *Cyclotosaurus* sp. is represented by a large, well-preserved left humerus (WMNM P64371; Fig. 7F, G) that is 167 mm long (Konietzko-Meier et al. 2019). We also assign the ornamented part of a pterygoid (WMNM P97556) to this taxon (Prino et al. 2024). In addition, a large and slender left femur (WMNM P97790; Fig. 7H) also possibly pertains to this taxon. The preserved length of this femur is 274 mm, but since the proximal and distal ends are not well preserved, it must have originally been somewhat longer. Because of its

Table 4: Temnospondyl remains (excluding teeth) from Lücking clay pit #3, Bonenburg, Westphalia, Germany. "MM" in the column "Year" indicates that the specimen was collected by Michael Mertens.

WMNM Spec. #	Year	Bone Bed	Anatomy	Histology	Taxon	Reference
P97556	–	–	Left pterygoid fragment	–	cf. *Cyclotosaurus* sp.	Prino et al. 2024
P64371	MM 2014	2	Left humerus	yes	cf. *Cyclotosaurus* sp.	Konietzko-Meier et al. 2019
P97790	MM 2019	2a	Left femur	yes	Capitosauria indet.	Garbay MSc 2021; Prino et al. 2024
P97553	–	2a	Proximal right femur	yes	cf. *Cyclotosaurus* sp.	Prino et al. 2024
P97557	2018	2a	Right angular in matrix	–	Capitosauroidea indet. morphotype 1 (fine ornamentation)	Prino et al. 2024
P97791	2018	2a	Left clavicle fragment	yes	Capitosauroidea indet. morphotype 1 (fine ornamentation)	Prino et al. 2024
P98583	–	2a	Interclavicle fragment	yes	Capitosauroidea indet. morphotype 2 (robust ornamentation)	Prino et al. 2024
P97555	MM	3	Dermal bone fragment	–	Capitosauroidea indet. morphotype 2 (robust ornamentation)	Prino et al. 2024
P97559	MM	2b	Right dentary	–	Capitosauroidea indet.	Prino et al. 2024
P97470	2017	2b	Right parietal	–	Plagiosaurinae	Prino et al. 2024
P97554	2015	2a	Interclavicle fragment	–	Plagiosaurinae	Prino et al. 2024

slender morphology, one might consider this bone to be of amniote origin, but the histology is clearly temnospondyl (Prino et al. 2024). However, because of its large size, the large femur could potentially represent a brachyopid instead (see below). The morphology of the proximal half of a small right femur (P97553) resembles the much larger WMNM P97790 and possibly also pertains to cf. *Cyclotosaurus* sp. based on histology. Morphologically, the two femora show more similarities to the capitosauroid *Paracyclotosaurus* than to *Mastodonsaurus* (Prino et al. 2024).

Among the large ornamented dermal bones from Bonenburg, two morphotypes can be distinguished, one showing fine ornamentation (morphotype 1) and one showing robust ornamentation (morphotype 2) (Prino et al. 2024). Both morphotypes are assigned to Capitosauroidea indet., but one of them may well pertain to cf. *Cyclotosaurus* sp. If not, then there are three different Capitosauroidea represented in the Bonenburg fauna.

Ornamentation morphotype 1 is represented by a partial left clavicle (WMNM P97991) and an angular (WMNM 97557; Fig. 7D). The clavicle preserves its massive lateral part that carries fine ornamentation and differs in histology and ornamentation from the fragmentary interclavicle WMNM P98583. The well-preserved posterior part of the angular also shows this ornamentation (Prino et al. 2024).

Ornamentation morphotype 2 is represented by the fragment of an interclavicle (WMNM P98583) (Fig. 7E), more specifically a portion of the left lateral wing (Schoch 1999) and by an indeterminate dermal bone fragment with coarse ornamentation (WMNM P97555). The ornamentation of these specimens is more robust, and the spaces between the ridges are larger than in morphotype 1. The ornamentation actually resembles that of the Early to Middle Triassic capitosauroid *Mastodonsaurus*. Histologically, the interclavicle also differs from the one other capitosaur dermal bone sectioned for

histology, the partial clavicle WMNM P97991 (Prino et al. 2024).

However, the coarseness of the ornamentation of morphotype 2 is reminiscent of brachyopoids as well. This group of peculiar, large-bodied temnospondyls is the only one to survive the ETEE and is known from the Middle Jurassic of Asia (Averianov et al. 2008) and Early Cretaceous of Australia (Warren et al. 1997), representing the last-surviving temnospondyls (Schoch 2013). However, brachyopoids are not known from Europe but only from the neighbouring continents (Prino et al. 2024; So & Mann 2024), all of which were still amalgamated into Pangea during the Late Triassic. This pattern argues against WMNM P98583 and WMNM P97555 representing brachyopoids.

A large-bodied temnospondyl is also represented by a fragmentary right dentary (WMNM P97559; Fig. 7A, B) that, while pertaining to Capitosauroidea, cannot be assigned to *Cyclotosaurus* or other Cyclotosauridae because the dentary has distinctive, transversely widened tooth pits (Fig. 7B). The isolated teeth described below may belong to this taxon. The dentary actually resembles that of the Early and Middle Triassic *Mastodonsaurus* more than that of *Cyclotosaurus* but lacks sufficiently preserved dermal ornamentation.

Probable remains of a large temnospondyl also include teeth with labyrinthine infolding in their dentine (e.g., WMNM P97475; Fig. 7C), a lenticular crown cross section, nearly smooth or finely striated enamel, and unserrated cutting edges (carinae). One of the teeth has a completely smooth enamel surface and others show fine longitudinal lines. The carinae are distinctly set off from the labial and lingual surfaces of the teeth and have a rounded, smooth cross section without denticles or pseudodenticles. The smoothness of these teeth may have been enhanced by preburial abrasion on the seafloor, however. Notably, the teeth show little labiolingual asymmetry in lingual curvature and in the placement of the carinae (slightly more lingual, i.e., greater convexity of the labial surface). Carinate teeth are common in temnospondyls (Schoch & Milner 2014; Riccetto et al. 2025), but at least those described by Riccetto et al. (2025) do not match the Bonenburg ones in having recurving, asymmetrical crowns and carinae only near the crown apex.

Whereas labyrinthine infolding might suggest affinities with *Severnichthys*, the laterally flattened crown with carinae is not known for actinopterygians. The size and shape of the Bonenburg ?temnospondyl teeth are entirely different from those assigned to *Severnichthys*, most recently by Evans et al. (2024), and as represented at Bonenburg by partial jaws (e.g., Sander et al. 2016, fig 18A) and large isolated teeth (Fig. 6F).

As an alternative to temnospondyls, these teeth might pertain to ichthyosaurs since there are bona fide ichthyosaur teeth among the Bonenburg fossils (see below). There are several differences, however. For one, most ichthyosaur teeth are not carinate. In addition, laterally flattened teeth with carinae are only known for two Triassic taxa of giant ichthyosaurs, much larger than the Bonenburg teeth, the Anisian *Thalattoarchon* (Fröbisch et al. 2013) and the Norian *Himalayasaurus* (Motani et al. 1999). The crown shape is different from the Bonenburg teeth in both of these taxa, however. The teeth of the giant Carnian ichthyosaur *Shonisaurus* have carinae, but the crown shows little labiolingual compression (Kelley et al. 2022). Among Jurassic taxa, only *Temnodontosaurus* spp. teeth have carinae (Bennion et al. 2024). Ichthyosaur teeth also have labyrinthine infolding, but the infolding usually influences the morphology of the crown base, which is not seen in the four Bonenburg teeth. We thus provisionally assign the Bonenburg tooth crowns to temnospondyls. However, it is important to note that tooth morphology of temnospondyls remains insufficiently studied (Bystrow 1938; Schultze 1969; Warren & Davey 1992; Riccetto et al. 2025). Future systematic study based on a wider sample and including the morphology and histology of teeth as well as positional variation is necessary to solve the problem of the taxonomic affinities of the Bonenburg teeth.

Smaller temnospondyls are represented in Bonenburg by plagiosaurine plagiosaurs (Plagiosaurinae contains only the genera *Gerrothorax* and *Plagiosaurus*). The cranial material consists of a right parietal with the pineal foramen and orbital margins preserved (WMNM P97470; Fig. 7I). However, since the parietal does not participate in the margin of the orbit in *Gerrothorax*, the bone cannot belong to this taxon. Instead, the Bonenburg parietal might belong to *Plagiosaurus depressus*, as described from the Norian or Rhaetian of Halberstadt in central Germany or to a new taxon closely related to *P. depressus* (Prino et al. 2024). The postcranial material includes an interclavicle fragment (WMNM P97554; Fig. 7J), with the typical plagiosaurine ornamentation of pustules arranged in radial ridges or scattered randomly, and an osteoderm (WMNM P117512), not figured in Prino et al. 2024). These postcranial fossils also resemble *Gerrothorax pulcherrimus*, to which other Rhaetian material from Skåne, Sweden, was historically assigned

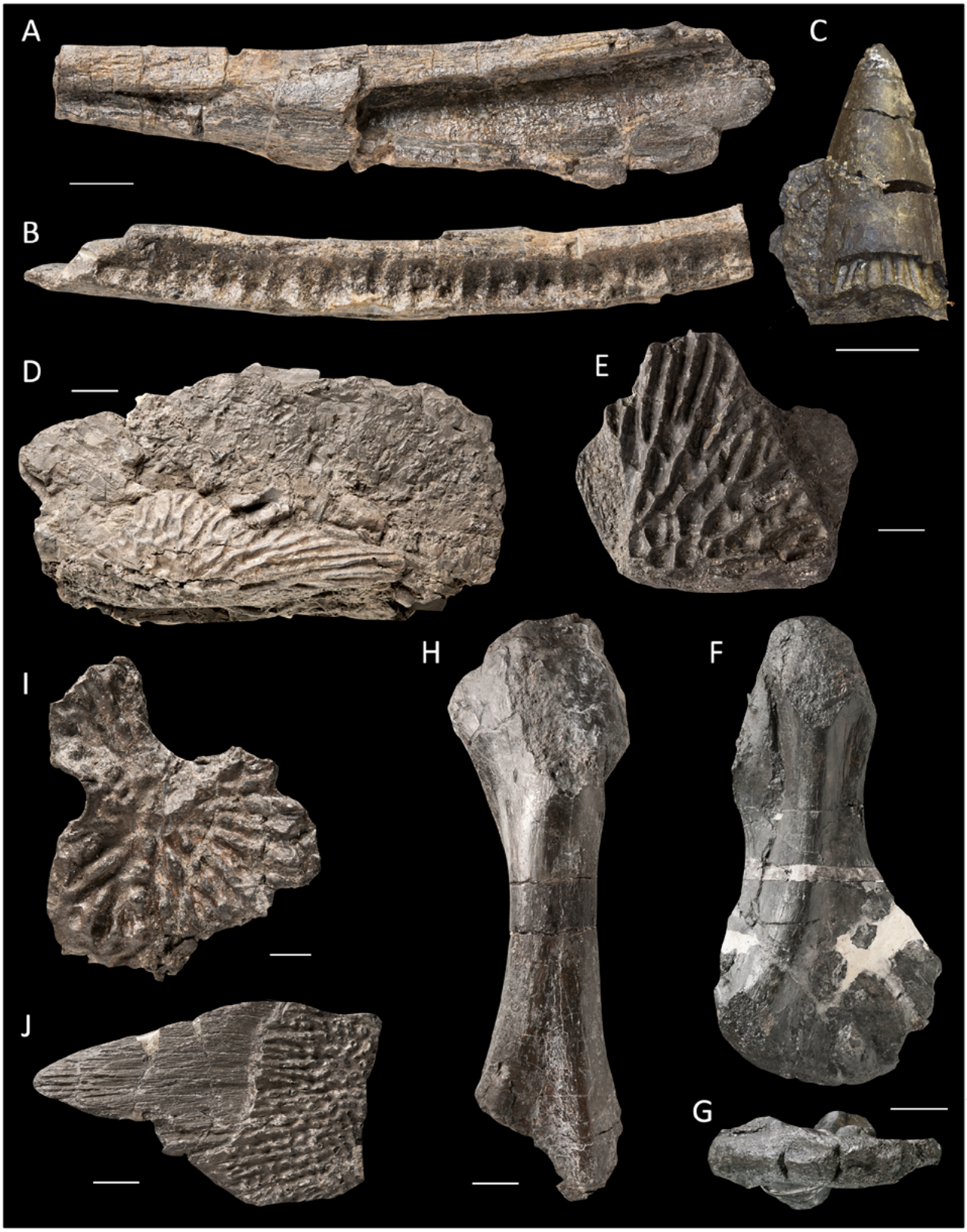


Figure 7: Temnospondyli. **A**, **B** Capitosauria indet. fragmentary right dentary (WMNM P97559) in (A) medial and (B) dorsal view. **C** ?Temnospondyl tooth (WMNM P97472). **D** Right angular (WMNM P97557) of Capitosauria indet. ornamentation morphotype 1. **E** Interclavicle fragment (WMNM P98583) of Capitosauria indet. ornamentation morphotype 2. **F** Left humerus of cf. *Cyclotosaurus* (WMNM P64371) in dorsal view. **G** Same in distal view. **H** Femur of Capitosauria indet. (WMNM P97790) in dorsal view. **I** Plagiosaurinae parietal (WMNM P97470). **J** Plagiosaurinae interclavicular fragment (WMNM P97554). Scale bars represent: 5 mm (C, I); 1 cm (J); 2 cm (A, B, D, E, F-H).

(Nilsson 1952), but also stratigraphically poorly constrained Norian or Rhaetian plagiosaurine material from Halberstadt (Jaekel 1914; Kuhn 1939). We thus cannot exclude the possibility that both genera of plagiosaurines are represented at Bonenburg.

The European latest Triassic record of temnospondyls has received little attention (Prino et al. 2024). This is possibly due to Storrs' notion (1994), see also Evans et al. (2024), that temnospondyls are absent from the UK Rhaetian, and to the difficulty of dating many putatively Rhaetian bone beds (e.g., Saint-Nicolas-de-Port, Niederschönthal) and other localities (e.g., Halberstadt). However, a similar picture to that from Bonenburg emerges from other localities such as Niederschönthal, where von Huene (1911) recorded two specimens of temnospondyl dermal bone. A recent re-examination of the collection at NHB by PMS confirmed this, one of the specimens being the remains of a large cyclotosaur interclavicle (see also Meyer et al. 2025, fig. 5C). In addition, there is also *Gerrothorax* at Niederschönthal (pers. obs. PMS in the NHB collections).

In conclusion, from the biostratigraphical and ecological perspective, the Temnospondyli are one of the most interesting taxa from Bonenburg. Not only are they diverse and fairly common but can also be identified to a relatively low taxonomic level despite their fragmentary nature, as typical for bone bed fossils. As already noted by Konietzko-Meier et al. (2019) and above, Bonenburg provides the last definitive record (last appearance date, LAD) of cyclotosaurs. In addition, as shown by Prino et al. (2024) and this review, the locality also provides the LAD of non-brachiopoid plagiosaurs and indicates the possible presence of brachyopoids in Europe. Finally, some of the Bonenburg temnospondyls were notably large-bodied as demonstrated, e.g., by the femur P97790 and the clavicle WMNM P97791. The Bonenburg record thus suggests Triassic temnospondyls were still thriving in the late middle Rhaetian (Konietzko-Meier et al. 2019; Prino et al. 2024), which is inconsistent with the notion of their gradual extinction, as espoused most recently by Lucas (2018), and their putative absence from the UK Rhaetian.

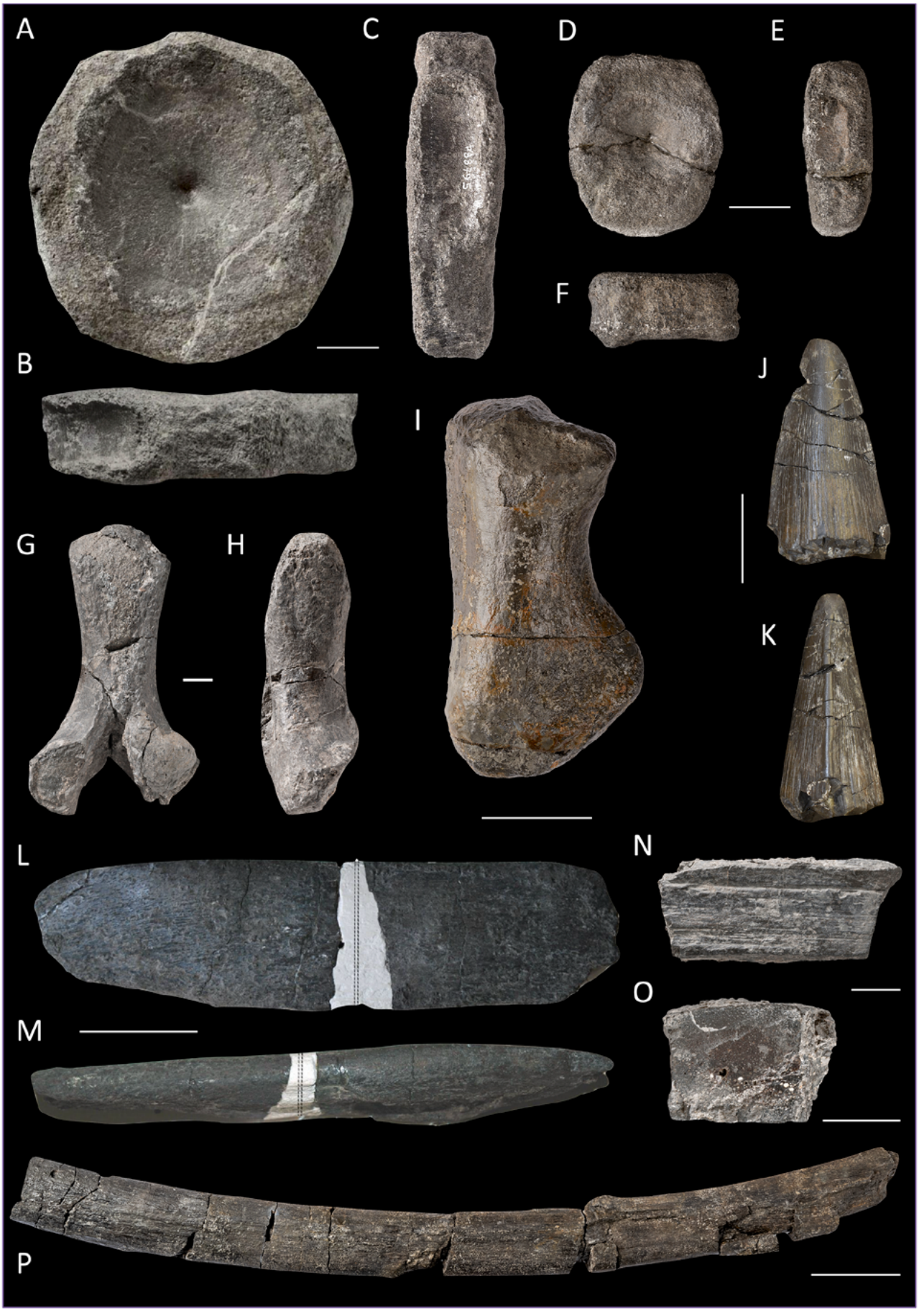
Ichthyosauria

Compared to some other Central European Rhaetian bone beds (e.g., Niederschönthal and Halberstadt), ichthyosaur remains are common at Bonenburg, in particular in Bone Bed 2 (Fig. 4B, E, F). The remains consist of teeth, vertebral centra, neural arches, ribs, girdle bones, and limb bones (Fig. 8). Ichthyosaurs are also common in some UK bone beds (fide Storrs 1994; Mears et al. 2016; Lomax et al. 2018, 2024) and in the French Rhaetian (Fischer et al. 2014). The only material from Bonenburg probably representing a named species, *Ichthyotitan severnensis* Lomax et al. 2024, is cortical bone fragments provisionally assigned to this species based on size and bone histology (Perillo & Sander 2024).

At least two, but probably three, taxa are represented in the Bonenburg ichthyosaur material that currently cannot be assigned to species. These taxa can be distinguished by differences in the size and shape of the bones, in particular the centra and neural arches. Although it is likely that some of this material represents postcranial material of *I. severnensis*, this is difficult to establish.

Cf. *Ichthyotitan*. In addition to the sheer size of the cortical fragments (Fig. 8L, M), the presence of this taxon at Bonenburg is suggested by bone histological evidence. Peculiar bone segments from Aust Cliff and other Westbury Formation sites, long interpreted as the shafts of large dinosaur femora (Galton 2005; Redelstorff et al. 2014), were recently hypothesized to represent fragments of jaw bones, specifically surangulars, of a giant ichthyosaur (Lomax et al. 2018). Based on some of these jaw bones, Lomax et al. (2024) recently described *Ichthyotitan severnensis* as a new taxon. The dinosaurian nature of the English finds had already been questioned by Redelstorff et al. (2014), who did not consider an ichthyosaurian affinity, however. In Bonenburg, only fragments of such large bones with a thick cortex were found (Fig. 8L, M) (Perillo & Heijne 2023; Perillo & Sander 2024), and small, cubic centimetre-sized ones are common (Fig. 8N, O) (Sander et al 2016; Perillo & Sander 2024). Testing the

Figure 8: Ichthyosauria. **A**-**C** Large disk-shaped dorsal vertebral centrum (WMNM P88795) of Shastasauridae indet. morphotype 1 in (**A**) anterior view, (**B**) dorsal view and (**C**) ?left lateral view. **D**, **E** Short and tall caudal vertebral centrum (WMNM P88768) of Shastasauridae indet. morphotype 1 in (**D**) anterior view, (**E**) ?left lateral view, and (**F**) dorsal view. **G** Shastasauridae indet. morphotype 2 neural arch (WMNM P88754) in posterior view. **H** Same in left lateral view. **I** Shastasauridae indet. humerus (WMNM P117120) in ?dorsal view. **J** Presumable ichthyosaur tooth WMNM 97475 in labiolingual view and **K** in mesial or distal view. Note the distinct but unserrated carinae and the great labiolingual and mesiodistal symmetry of the tooth. **L** Large fragment of cortical bone (WMNM P88133) of cf. *Ichthyotitan* in external view. **M** Same in side view. Area reconstructed in plaster indicates location of thin section in Fig. 13D, E. **N** Small blocky fragment of cortical bone (WMNM P88130) of cf. *Ichthyotitan* in external view. **O** Same in cross section. Note the dominantly longitudinal vascular canal orientation, as also seen in thin section in Fig. 13D, E. **P** Incomplete rib of Shastasauridae indet. morphotype 2. Scale bars represent: 1 cm (J, K, N, O); 2 cm (A-H); 5 cm (I, L, M, P).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hypothesis that the bone shafts are ichthyosaurian in affinity, we recently conducted a comparative histological study (Perillo & Sander 2024). Sampling jaw bones of the largest ichthyosaur skeleton known, the holotype of *Shonisaurus sikanniensis* Nicholls & Manabe 2004 from the middle Norian of Canada (Nicholls & Manabe 2004), we found the same peculiar histology already observed by Redelstorff et al. (2014). We observed a new feature, intrinsic fibre tissue (Fig. 13D, E), which is shared by all sampled putative skull bones, including the UK material (Redelstorff et al. 2014; Perillo & Sander 2024; Lomax et al. 2024), a putative French giant ichthyosaur jaw (Fischer et al. 2014; Perillo & Sander 2024) and cortical fragments from Bonenburg (Fig. 8L-O). We thus follow the proposal of Lomax et al. (2018, 2024) that the giant "mystery bone" pieces are also the remains of giant ichthyosaurs, consistent with a short report by von Huene (1912), who also described a giant ichthyosaur jaw section from Aust Cliff. This paper has not been cited in the recent literature, however, probably because the specimen is lost.

Axial skeletal material: Shastasauridae indet. morphotype 1. Very short vertebral centra (38 centra are inventoried at the WMNM) of various sizes are assigned to this taxon. The centra all are strikingly short and appear to form a size cluster (Fig. 4B, E, F, 8A-F). These large centra have a diameter between about 90 and 130 mm and show a dorsoventral height-to-length ratio of over 3.0 and as much 5.0. Since the centra are typically found lying flat on the bedding plane (Fig. 4B), the shortness was exaggerated by compaction and abrasion. The original anteroposterior length is measured best along the floor of the neural canal (Fig. 8B), which seems to have the least cancellous bone and thus experienced the least compaction. Because of long exposure on the seafloor, the upper side of the centra is commonly heavily corroded (Fig. 4E, F, 8A), destroying all morphological features and accentuating the periosteal vs. the endochondral territories of the internal trabecular architecture (Fig. 4E). This kind of erosion is also seen in late Norian to Rhaetian centra from the Kössen Formation of the Swiss Alps (Sander et al. 2022). Strangely, no neural arch has been collected from Bonenburg that would fit with these short centra.

Two similarly short (HL ratio >5) vertebral centra like those from Bonenburg were described by Fischer et al. (2014, fig S3) from the Rhaetian of Cuers (southern France) as part of the "Cuers ichthyosaur". The centra are 115 mm and 119 mm wide, less than the largest Bonenburg specimens. Storrs (1994) also figured a large and very short centrum (diameter 200 mm) from the Westbury Formation in the UK.

In general, short and large vertebral centra similar to the ones from Bonenburg are found in the shastasaurid ichthyosaurs *Shonisaurus* and *Shastasaurus*, especially in *Shonisaurus popularis* from the Carnian of Nevada, USA (see Sander et al. 2022; Kelley et al. 2022). However, the shortness of some of the European Rhaetian bone bed centra exceeds that of all other ichthyosaurs and appears diagnostic. Currently, we feel that the evidence is insufficient for erecting a new taxon based on the Bonenburg, French, and UK vertebral material and assign the short vertebral centra in open nomenclature to Shastasauridae indet. morphotype 1 instead.

The case of the "Cuers ichthyosaur" is interesting in that the short centra mentioned above form part of an individual that includes jaw elements provisionally referred to *Ichthyotitan severnensis* by Lomax at al. (2024). However, the type and referred material of *Ichthyotitan* and the jaw of the "Cuers ichthyosaur" must originate from much larger ichthyosaurs than even the largest centra from Bonenburg (Lomax et al. 2024) and from the "Cuers ichthyosaur". Thus, we are left with conflicting evidence as to the identity of the short vertebral centra, which may represent a distinct taxon or may pertain to very small, i.e., juvenile, individuals of *Ichthyotitan*. However, the centra show no evidence of pertaining to juveniles.

A peculiar kind of very short vertebral centra (Fig. 4E, lower left) are probably also heavily abraded ichthyosaurian centra but could pertain to very large temnospondyls. However, histological observations on WMNM P88794 disagree with a temnospondyl affinity because the trabeculae of secondary bone tissue of these vertebrae are irregular, unlike those of temnospondyls (Fig. 13A-C). In contrast to the unequivocal ichthyosaur centra, which are circular in anteroposterior outline (Fig. 4B, E, F, 8A) (except for the caudals, Fig. 8D), these centra have more of a pentagonal outline (Fig. 4E). The strange vertebral morphology might also have resulted from differential abrasion on the seafloor caused by the internal histological structure. The denser endochondral bone underlying the neural canal and the rib articular facet (see Houssaye et al. 2018) thus became inverted as ridges.

Axial skeletal material: Shastasauridae indet. morphotype 2. Neural arches (e.g., WMNM P88754, Fig. 8G) and especially two fragmentary ribs indicate the presence of ichthyosaurs larger than Shastasauridae indet. morphotype 1 and are here assigned to

Shastasauridae indet. morphotype 2. The neural arch WMNM P88754 is 106 mm tall, measured along its longest axis, and the articular facet to the centrum is 38 mm long. This arch is thus too large to fit on the shortest vertebrae. The separation of centrum and arch is not indicative of a juvenile status because the centrum and the arch do not fuse in ichthyosaurs (McGowan & Motani 2003). Of the two fragmentary ribs, one (WMNM P88791) is 142.2 mm long, but the anteroposterior width is 50.3 mm and the mediolateral width is 31.8 mm. The other rib (WMNM P98701; Fig. 8P) is not from a bone bed but was discovered some metres below Bone Bed 2A. It is over 500 mm long, and the maximum diameter is 41 mm. Both of these fragmentary ribs are thus in the size range of the largest ichthyosaur ribs described in the literature, such as the ribs from the Kössen Formation associated with a vertebra 262 mm wide and 237 mm high (Sander et al. 2022). The shafts of the ribs of this find are about 40 mm in maximum diameter. The midshaft rib diameter of the 21-m holotype skeleton of *S. sikanniensis* is 50 mm (as measured in fig. 9 of Nicholls & Manabe, 2004). Similar-sized ribs have also been described from the French Rhaetian (Fischer et al 2014), in particular from Autun. Of course, rib diameter is a poor size proxy, but it is clear that giant ichthyosaurs with shastasaurid affinity abounded in the Tethys and Panthalassan Rhaetian, as already noted by Fischer et al. (2014), Sander et al. (2022), McGaughey et al. (2023), and Lomax et al. (2024). Based on their larger size, Shastasauridae indet. morphotype 2 fossils are more likely to pertain to *Ichthyotitan severnensis* than the short vertebral centra of Shastasauridae indet. morphotype 1.

Axial skeletal material: Ichthyosauria indet. Ichthyosauria indet. is represented by a size cluster of vertebral centra from around 30 to 60 mm in height, most of which are clearly not caudals. These rather nondescript ichthyosaur centra cannot be assigned to any particular taxon and are not discussed further.

Appendicular bones. There is a fragment of large flat bone (WMNM P88786) which may represent a humerus or an element of the shoulder girdle such as the scapula, coracoid, or clavicle. The heavily damaged and incomplete bone appears stout and robust, measuring 136 mm across and 161 mm along the curved surface. A smaller but complete limb bone is WMNM P88755, likely a humerus (Fig. 8I). The specimen is 170 mm long and dorsoventrally it measures up to 50 mm at its largest extent. The bone is angled anteriorly, while its posterior edge appears straight in dorsoventral view. The proximal end is 80 mm wide anteroposteriorly and 50 mm high dorsoventrally. It is split into two triangular surfaces, the posterior of which is shorter. This complex morphology is consistent with a humerus, but we do not rule out identification as a femur.

Isolated teeth. The teeth (e.g., WMNM P97475; Fig. 8J, K) are slightly striated, especially around the base of the crown and bear carinae mesially and distally with the presumed mesial carina being more prominent. Notably, the teeth are labiolingually symmetrical with only a slight labiolingual curvature at best. The labyrinthine infolding of the dentine is typical for ichthyosaurs, but this trait is shared with Temnospondyli (see above). Also, the teeth show longitudinal wrinkles on the enamel surface, typical for ichthyosaurs but lacking in temnospondyls. The Late Triassic *Shonisaurus* (Kelley et al. 2022) and the Early Jurassic *Temnodontosaurus* (Bennion et al. 2023) show carinate, striated teeth of a larger size than the Bonenburg teeth described here. Importantly, however, neither the *Shonisaurus* teeth nor any of the *Temnodontosaurus* tooth morphotypes described by Bennion et al. (2023) are laterally flattened and labiolingually symmetrical. The bilaterally nearly symmetrical, carinate and wrinkled teeth from Bonenburg thus represent a different morphotype, also compared to the other Triassic bicarinate ichthyosaur teeth, i.e., those of *Thalattoarchon* (Fröbisch et al. 2013) and *Himalayasaurus* (Motani et al. 1999).

Sphenodonta

In the microfauna, obtained by screen washing in 2015 and 2016, only two diagnostic tetrapod specimens were recovered from the concentrate. One is a sphenodont jaw fragment (WMNM P64372), assignable to cf. *Diphyodontosaurus* sp. (Sander et al. 2016). The other is a non-mammaliaform cynodont tooth discussed below (Schwermann 2016). Both specimens are heavily abraded.

Among the vertebral material initially identified as *Pachystropheus* in the field, there are also a few vertebrae that clearly cannot be assigned to this taxon. These are five isolated centra (WMNM P98480; WMNM Bb 2017/86; WMNM P98482; WMNM P98557; WMNM P98558) (Fig. 12A-D). With a height of approximately 6 mm and a width of approximately 10 mm, they are much flatter and broader than *Pachystropheus* centra and possibly pertain to Sphenodonta.

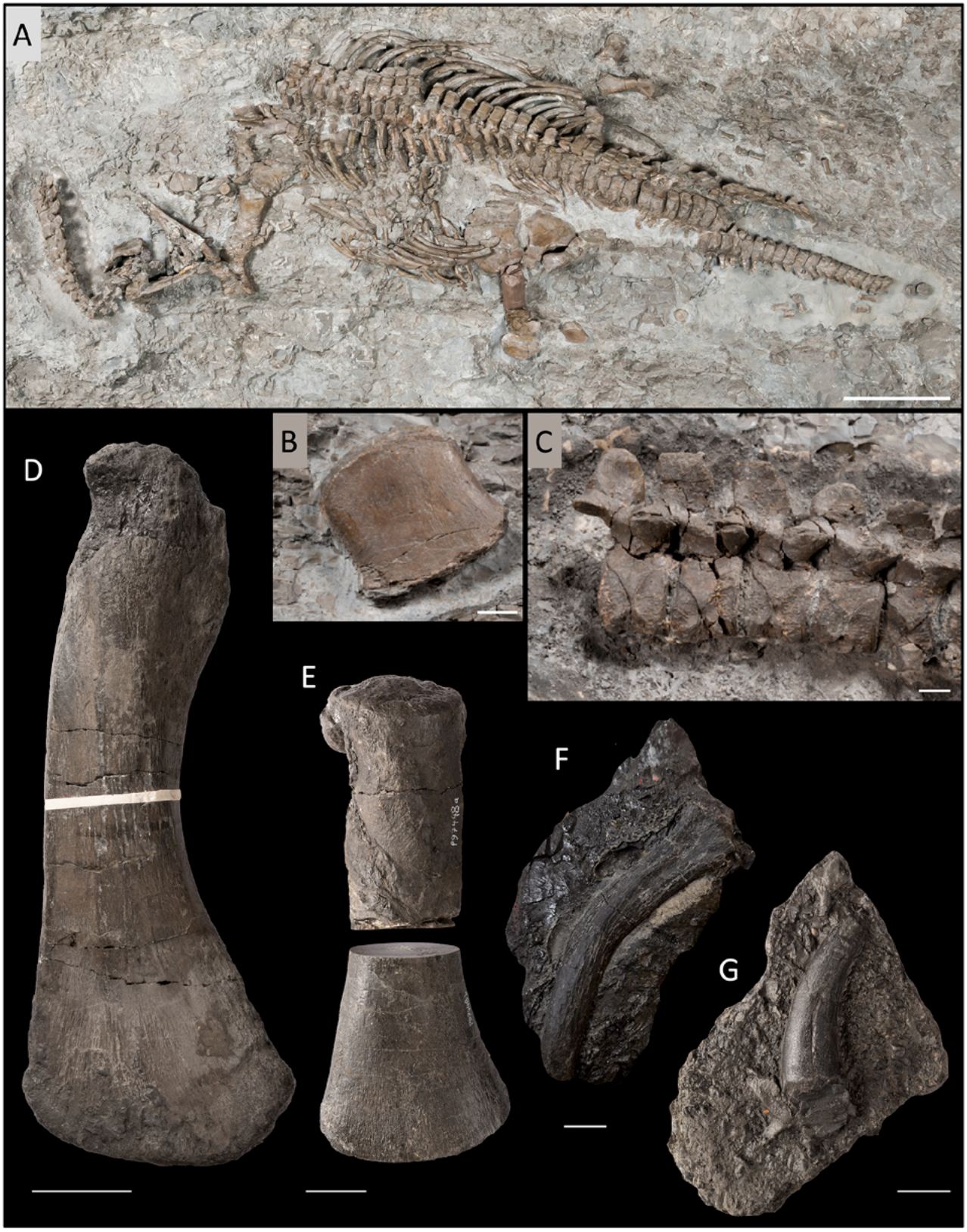

Figure 9: Plesiosauria. **A** Holotype skeleton of *Rhaeticosaurus mertensi* Wintrich et al. 2017 (WMNM P64047). **B** Tibia of same. **C** Anterior cervical column in right lateral view of same. **D** Indet. plesiosaur morphotype 2, large propodial (WMNM P117120) in ?dorsal view. Area reconstructed in plaster indicates location of thin section in Fig. 13I. **E** cf. *Rhaeticosaurus* propodial (WMNM P97448) in ?dorsal view. Gap in the shaft indicates location of thin section in Fig. 13H. **F** Indet. plesiosaur morphotype 2 proximal part of large dorsal rib (WMNM P2024/161). **G** Plesiosauria indet. tooth (WMNM P98411). Scale bars represent: 1 cm (B, C, G); 2 cm (E, F); 5 cm (D); 20 cm (A).

Plesiosaurs

Until the discovery of the skeleton of *Rhaeticosaurus mertensi* (Wintrich et al. 2017a), there was no unequivocal evidence for the existence of Triassic Plesiosauria, although historically many isolated vertebrae from Rhaetian bone beds had been assigned to Plesiosauria (e.g., Huene 1902, 1911). Although these isolated finds from the European Rhaetian bone beds probably pertain to Plesiosauria or stem plesiosaurs, this cannot be proven following the definition of Plesiosauria in Wintrich et al. (2017a). We cannot rule out the possibility that these isolated finds represent intermediate forms between the Middle Triassic *Augustasaurus* or the Carnian *Bobosaurus* and the unequivocal plesiosaurian *Rhaeticosaurus* (Wintrich et al. 2017a). Because of the near-complete lack of a Norian eosauropterygian record (a time span of >20 million years), we have no idea what these intermediate forms looked like, although they certainly existed. We are thus cautious in this review and note that the only unequivocal plesiosaurian material from Bonenburg is the holotype of *Rhaeticosaurus mertensi* and certain isolated bones from the bone beds assigned to this species. We hence use the more informal term "plesiosaurs" to denote possible stem plesiosaurians.

In the UK, there is a rich and diverse record of entire skeletons of small-bodied Plesiosauria from the Hettangian (Benson et al. 2012). Based on this record, these authors suggested a Late Triassic origin for Plesiosauria because of the lack of sufficient evolutionary time for so many different lineages to have evolved after the ETEE during the earliest Jurassic (Benson et al. 2012). The holotype skeleton of *Rhaeticosaurus* (Fig. 9A-C) was found in the middle part of the Contorta Beds, in very fine-grained dark mudstones about 3 m below Bone Bed 2. *Rhaeticosaurus* is also small-bodied, like most of the Hettangian plesiosaurs from the UK. Histology and the well-visible neurocentral sutures indicate that the holotype of *Rhaeticosaurus* is a juvenile that had reached close to final size (Wintrich et al. 2017a).

The plesiosaurs from the Bonenburg bone beds, on the other hand, have not been studied in any detail, and only a few have been previously figured (Sander et al. 2016). Isolated plesiosaur bones, pertaining to at least three but possibly more taxa based on size and morphology, are the second most abundant reptile remains (second after *Pachystropheus*) from Bone Bed 2 (see Figs. 4C, 4E, 5, 9, 10) and probably the most common elements in Bone Bed 3. Whereas it is reasonable to assume that some of the plesiosaur fossils represent *Rhaeticosaurus*, others record the presence of a different taxon of small plesiosaur and of a much larger plesiosaur (Fig. 9, 10).

Not surprisingly, vertebrae are most abundant among the plesiosaur remains in the bone beds (Fig. 4C, E, 10), deriving from different body regions (Fig. 10). Determining position along the vertebral column is the first step in any diversity assessment because the positional morphology is uniform across plesiosaurians. Size is assessed as adult size, this means that a larger vertebra with an open neurocentral suture (resulting in separation of centrum and arch) cannot be the same taxon as a smaller one in the same position along the column with the neural arch attached (Fig. 10).

Rhaeticosaurus is represented in Bone Bed 2 by a propodial, either humerus or femur, with a total length of 173 mm. The propodial is relatively little expanded distally with an evenly curved distal edge (Fig. 9E). Bone histology (Fig. 13H) is identical to that of the holotype (Wintrich et al. 2017a). For comparison, the length of the holotype humerus is 183 mm, and that of the holotype femur is 185 mm, but these values are exaggerated by normal microfaults (Fig. 9A; Wintrich et al. 2017a). There also is a small ulna (WMNM P151129) fitting in size, shape, and gracility with the radius of the *Rhaeticosaurus* holotype.

Another small-bodied plesiosaur taxon, indet. plesiosaur morphotype 1, is indicated by cervical vertebrae with a straight-sided V-shaped neurocentral suture (Fig. 10G), as opposed to the ventrally concave suture in *Rhaeticosaurus*. These vertebrae (Fig. 10E) have the zygapophyseal articular surfaces medially inclined, as in all plesiosaurs. This is a feature only known from plesiosaurs, as opposed to *Bobosaurus* and all more basal sauropterygians that have horizontal facets (Wintrich et al. 2017a).

A medium- to large-sized plesiosaur taxon, here listed as indet. plesiosaur morphotype 2, is represented by numerous finds, including vertebrae with an articular surface of up to 90 mm in diameter (Fig. 10K), ribs with a shaft diameter of up to 25 mm, a large and massive but fragmentary coracoid (WMNM P88785) and a large propodial 335 mm in length (WMNM P117120, Fig. 9D). The propodial looks very different from those of *Rhaeticosaurus* in that its anterior margin is convex in the proximal and shaft regions. The distal end is dorsoventrally flattened and expanded in typical plesiosaur fashion. The bone is relatively long and slender compared to the propodials of most Middle Jurassic and later plesiosaurs but resembles the humerus of the probably earliest Jurassic rhomaleosaurid *Lindwurmia* (Vincent & Storrs 2019) in its slenderness and curved

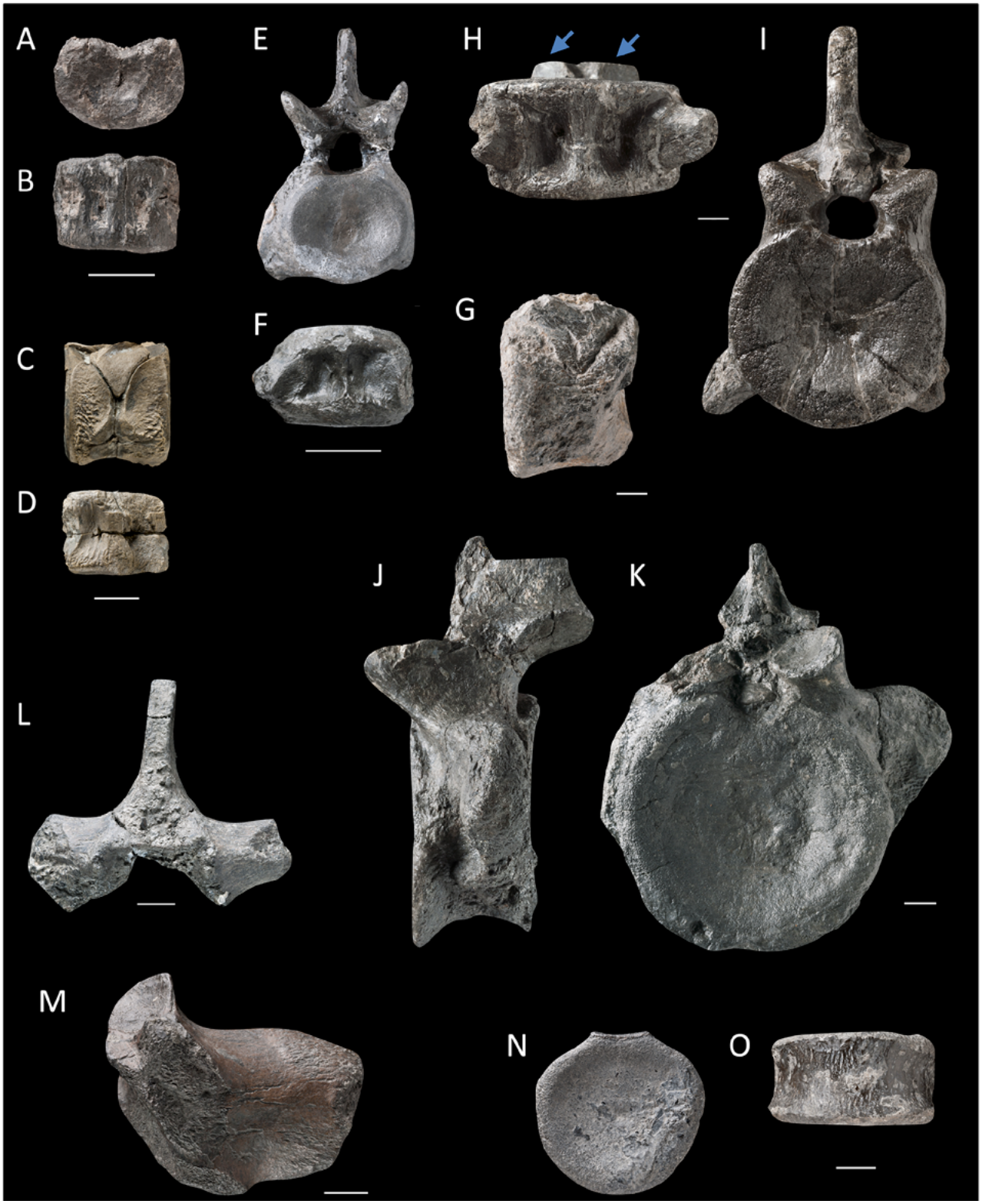

Figure 10: Plesiosaurian vertebrae. **A, B** Indet. plesiosaur morphotype 1 (WMNM P64360). Juvenile anterior cervical centrum in dorsal view (**A**) and ventral view (**B**). **C, D** Isolated cervical vertebra, part of holotype of *Rhaeticosaurus mertensi* Wintrich et al. 2017 (WMNM 64047) in lateral view (**C**) and ventral view (**D**). **E, F** Indet. plesiosaur morphotype 1 (WMNM P64376). Adult anterior cervical vertebra in anterior view (**E**) and ventral view (**F**). **G** Indet. plesiosaur morphotype 1 (WMNM uncat.). Adult cervical vertebra in lateral view. **H, I** Indet. plesiosaur morphotype 2 (WMNM P97476), adult posterior cervical vertebra in ventral view (**H**) and anterior view (**I**). Blue arrows in H indicate postzygapophyses truncated by abrasion; the centrum is positioned as it was located in the bone bed. **J, K** Indet. plesiosaur morphotype 2 (WMNM P64361). Adult pectoral vertebra in left lateral view (**J**) and anterior view (**K**). **L** Indet. plesiosaur morphotype 2 (WMNM P98039). Juvenile dorsal neural arch in anterior view. **M** Indet. plesiosaur morphotype 2 (WMNM P97505). Fragment of adult dorsal neural arch in posterior view. **N, O** Indet. plesiosaur morphotype 2 (WMNM P P97487). Juvenile/fetal dorsal vertebral centrum in left anterior view (**N**) and ventral view (**O**). Scale bars represent: 1 cm (C, D, G-O); 2 cm (A, B, E, F).

shaft. WMNM P117120 is also of similar size to the left humerus of *Lindwurmia* (297 mm as measured from fig. 5 of Vincent & Storrs (2019). The plesiosaurian nature of propodial bone WMNM P117120 is not only indicated by its morphology (Fig. 9D) but also by its histology because it shows the autapomorphic plesiosaurian radial fibrolamellar bone (Fig. 13I; Sander & Wintrich 2021).

Indet. plesiosaur morphotypes 1 and 2 as well as *Rhaeticosaurus* have a distinctive pair of ventral pits in their cervicals. At the bottom of these pits are the intervertebral artery foramina (Fig. 10B, D, F, H). Note that the intervertebral artery foramina were previously known as "subcentral foramina" (Wintrich et al. 2017b). The pits or sunken areas on the ventral side of the cervicals (Fig. 10B, D, F, H) may be of systematic value, as they have not been described for Jurassic plesiosaurs with the exception of *Lindwurmia* (Vincent & Storrs 2019) and the rhomaleosaurid *Meyerasaurus* (Smith & Vincent 2010). The pits appear less pronounced in *Rhaeticosaurus* (Fig. 10D) than in some indet. plesiosaur morphotype 1 (Fig. 10F) and morphotype 2 (Fig. 10H) vertebral centra. We cannot entirely rule out the possibility that indet. plesiosaur morphotype 1 are the posterior cervicals of *Rhaeticosaurus* because the holotype lacks the posterior neck region. Under this hypothesis, the concave-sided "V" of the anterior cervicals of *Rhaeticosaurus* would change to a straight-sided "V" in the posterior direction along the column.

A quantitative analysis of body size evolution in plesiosaurs across the Triassic-Jurassic boundary would be of particular interest, following the approach of Benson et al. (2012). This analysis would involve propodial length and vertebral centrum diameter. Currently, both measures suggest that the large Rhaetian plesiosaur from Bonenburg, indet. plesiosaur morphotype 2, is in the size range of large early Jurassic plesiosaurs such as large rhomalaeosaurids (Benson et al. 2012), *Lindwurmia* (Vincent & Storrs 2019), and the Pliensbachian *Westphaliasaurus* (Schwermann & Sander 2011). Thus, indet. plesiosaur morphotype 2 from Bonenburg indicates that large-bodied plesiosaurs already existed in the Triassic.

Plesiosaurs are common at the UK Rhaetian bone bed localities as well (Storrs 1994; Mears et al. 2016), particularly at Aust Cliff, and in continental bone bed localities such as Niederschönthal in Switzerland (Meyer et al. 2025), where Huene (1902) was impressed by the size of the vertebrae, including one that measures 87 mm horizontally across the articular surface (M.B. 2, verified by PMS on Jan. 20, 2023). Some of the UK cervical vertebrae also show deep pits on the ventral side (e.g., Storrs 1994, fig. 7M). Storrs also documented the large size of the specimen in this figure, an "idealized cervical", as being 75 mm long but did not comment on its size. Storrs (1994) saw no evidence that more than one taxon of plesiosaur is present in the Rhaetian, a view that has obviously been superseded by more recent work (Benson et al. 2012, Wintrich et al. 2017a, this review). However, Storrs' (1994) notion that the Rhaetian bone bed plesiosaurs cannot be diagnosed to species is still largely true.

Choristodera or Thalattosauria

The most common reptile fossils to be found in Bone Bed 2 are the remains of the putative earliest choristodere *Pachystropheus rhaeticus* (Fig. 11), originally described from Rhaetian rocks of the UK (E. von Huene 1935, Storrs et al. 1996; Williams et al. 2022; Quinn et al. 2024). Although generally considered to be the earliest choristodere, *Pachystropheus* has alternatively been assigned to Thalattosauria based on its morphological similarity to *Endennasaurus* (Williams et al. 2022; Cawthorne et al. 2024, Quinn et al. 2024), e.g., the shape of the ilium. Phylogenetic character analysis (Quinn et al. 2024) supported this hypothesis. Although conclusive evidence is lacking for either hypothesis of affinity because of the disarticulated and fragmentary nature of all the material, *Pachystropheus* is important from the perspective of the ETEE. New data on thalattosaur bone histology (Klein et al. 2023) will hopefully help test these competing hypotheses.

All regions of the skeleton of this relatively small reptile are represented, probably with the exception of the skull (see Quinn et al. 2024). Here, as with the plesiosaurs, further research is needed. In fact, the *Pachystropheus* ectopterygoid figured by Storrs et al. (1996), to which a Bonenburg specimen shows great similarity (Fig. 6I), was interpreted as a coelacanth jaw bone (primary coronoid) by Quinn et al. (2024, 2025).

Several dozen *Pachystropheus* vertebrae of different positions in the column and ontogenetic stages have been found (Wild 2018). *Pachystropheus* vertebral centra are elongated and laterally compressed, characteristics that remain constant throughout the vertebral column (Fig. 11E-K). The centra are at least 1.3 times as long as high. They are platycoelous or sometimes slightly amphicoelous (Fig. 11F, I). Most vertebrae have a visible neurocentral suture except for the sacrals. The centrum and the neural arch are mostly disarticulated, and merely the centra are preserved. This may be caused by their robustness compared to the arches and by the

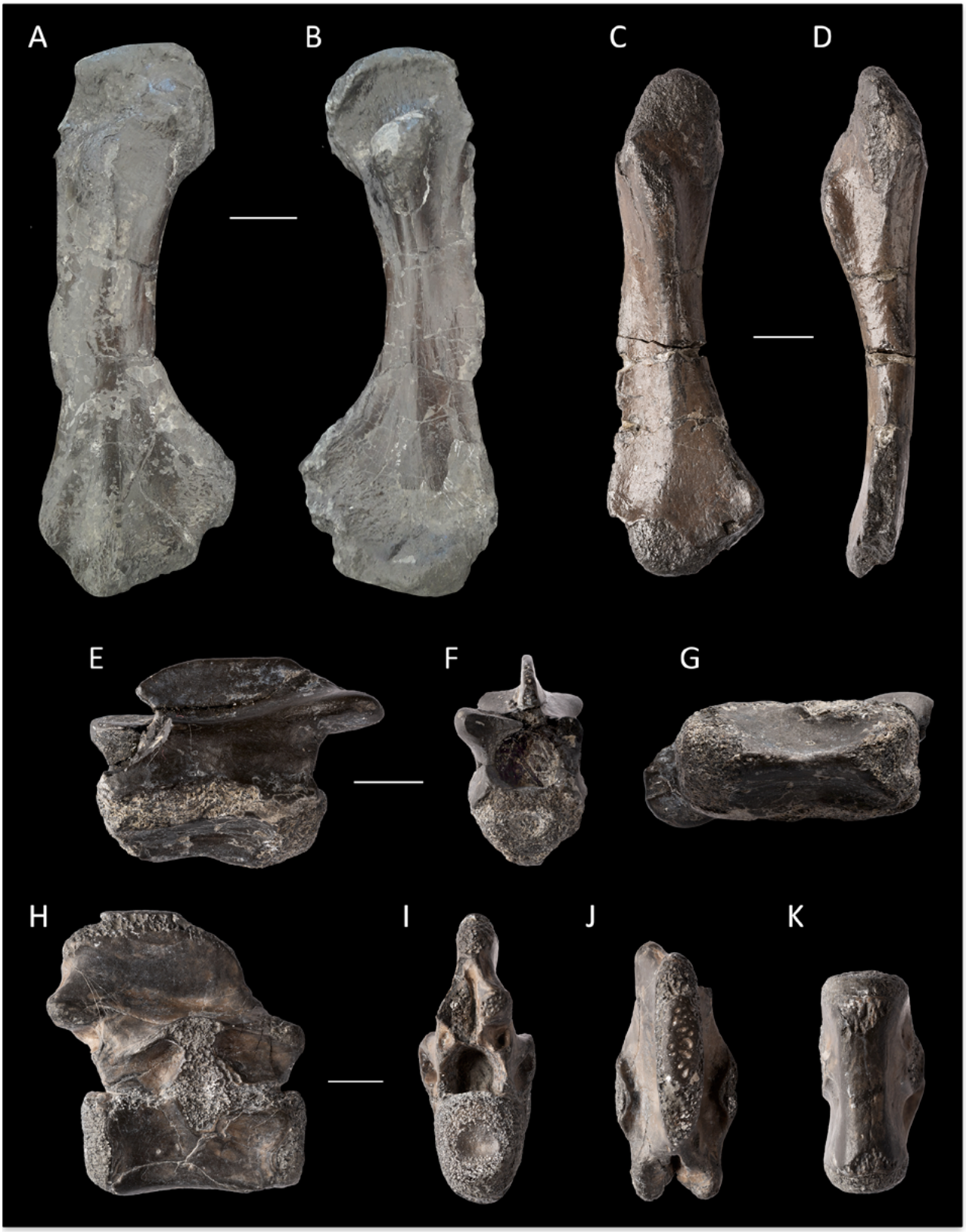

Figure 11: *Pachystropheus rhaeticus* E. v. Huene 1935. **A**, **B** Very large right humerus (WMNM P98447) in dorsal view (**A**) and ventral view (**B**). **C**, **D** ?Juvenile humerus (WMNM P64365) in ventral view (**C**) and posterior view (**D**). **E**-**G** Adult cervical vertebra (WMNM P98551) in left view (**E**), anterior view (**F**) and ventral view (**G**). **H**-**K** Adult dorsal vertebra (WMNM P98549) in right lateral view (**H**), posterior view (**I**), dorsal view (**J**) and ventral view (**K**). Scale bars represent: 5 mm (E-K); 1 cm (C, D); 2 cm (A, B).

unfused neurocentral suture, presumably indicating a juvenile condition. The top of the neural spine in some specimens shows distinct vertical grooves, also present in the British material (E. von Huene 1935; Storrs et al. 1996). Many presacral vertebral centra show small lateral fossae that are positioned right under, or next to, the rib articular facet (Fig. 11H). The centra vary greatly in size. The largest centrum in the dorsal region is 28 mm long and the smallest only 9 mm. Covering the entire column, the smallest one is a caudal centrum with a length of 6 mm (Wild 2018).

There are also some limb bones, especially humeri (Fig. 11A-D), which are most easily recognized among the long bones. The humeri are elongate and slender with an expanded distal end and a distinct deltopectoral crest (Fig. 11B-D). Humeral morphology is most similar to terrestrial amniotes, although some morphological simplification is apparent, either indicating juveniles (Fig. 11C, D) or incipient aquatic adaptation. The latter can reasonably be assumed given the abundance of the finds compared to unquestionably terrestrial reptiles such as dinosaurs (see below). Notably, the humeri vary greatly in size and appear to form an ontogenetic series, as also seen in the British material.

Among the most distinctive long bones from Bonenburg is a right humerus (WMNM P98447) (Fig. 11A, B) 161 mm in length, which is at the uppermost end of the *Pachystropheus* humeral size spectrum and probably pertains to this taxon. The bone has expanded proximal and distal ends, which appear to have been flattened by sediment compaction, and a slender and dorsoventrally flattened shaft (Fig. 11A, B). The anterior margin of the bone is nearly straight. The head has an evenly rounded articular surface in dorsoventral view. In ventral view, there is a distinctive deltopectoral crest ending proximally in a knob. The crest is located closer to the posterior margin of the bone than to the anterior one, which is an unusual feature. The distal end is divided, from preaxial to postaxial, into a supinator process, the large ectepicondyle, and the entepicondyle (Fig. 11A, B). There is an entepicondylar notch but no foramen. Likewise, there is no ectepicondylar foramen. In the ventral view, there is no distinct capitulum, but this may still be covered by matrix. A fragment of a similar humerus about two thirds the size of WMNM P98447 is figured in Storrs et al. (1996, fig. 10).

Phytosauria

Phytosauria are a common and diverse clade of primarily Late Triassic semiaquatic archosaurs recorded from continental and, rarely, marine deposits around the world (Jones & Butler 2018; Butler et al. 2019). Phytosaurs had the lifestyle later adopted by eusuchian crocodiles, and there are remarkable convergences in the morphology of the two clades. This includes ossifications of the skin, i.e., osteoderms (Fig. 12E). In phytosaurs, osteoderms were found in the gular region and in a generally double row of paramedian osteoderms along the vertebral column (Huene 1922; Hungerbühler 1998; Stocker & Butler 2013) back to the base of the tail. Since these osteoderms are not co-ossified with the rest of the skeleton, they are often found in isolation, and it may be difficult to associate a particular osteoderm morphology with a particular phytosaur taxon. However, since characteristics of osteoderm sculpture are also seen on the dermal bones of the skull, some association is possible, all the more because phytosaur systematics relies heavily on skulls.

The Rhaetian phytosaur record is not well understood because of the problem of dating of the continental deposits in the Western Interior of the United States and the marginal marine late Norian and Rhaetian deposits, particularly of the "bone bed" type (see above) of Europe. There is only one diagnosable species of Rhaetian phytosaur from Europe, based on a partial skeleton including osteoderms from near Salzgitter, northern Germany (Huene 1922). It is assigned to a new, as yet unnamed, species of *Mystriosuchus* (Jones & Butler 2018; Butler et al. 2019), representing a phytosaur of unusually large size. Remains of similarly large phytosaurs, including isolated osteoderms showing the same morphology as those of *Mystriosuchus* n. sp., are known from the Rhaetian localities of Halberstadt and Niederschönthal (Sander & Wellnitz 2024). This material as well as the *Mystriosuchus* specimen from Salzgitter, were used by Huene (1922) as the hypodigm of his taxon "*Angistorhinops ruetimeyeri*". Finally, phytosaur teeth, which are conspicuously missing in Bonenburg, are common in other putative Rhaetian bone beds such as Niederschönthal (Huene 1922; Meyer et al. 2025), Hallau (Peyer 1943), Halberstadt (Huene 1922), and Saint-Nicolas-de-Port (Cuny 1995; Goidefroit & Cuny 1997)

Bone Bed 2 at Bonenburg has yielded a single, relatively small phytosaur osteoderm (Fig. 12E; WMNM P98442), discovered during the 2017 excavation. The asymmetry of this osteoderm suggests that it is from one of the left paramedian rows. Whereas its morphology and sculpture are typically phytosaurian, the sculpture of WMNM P98442 is different from the osteoderm of *Mystriosuchus* n. sp. discussed above (Sander & Wellnitz 2024). In fact, among the isolated

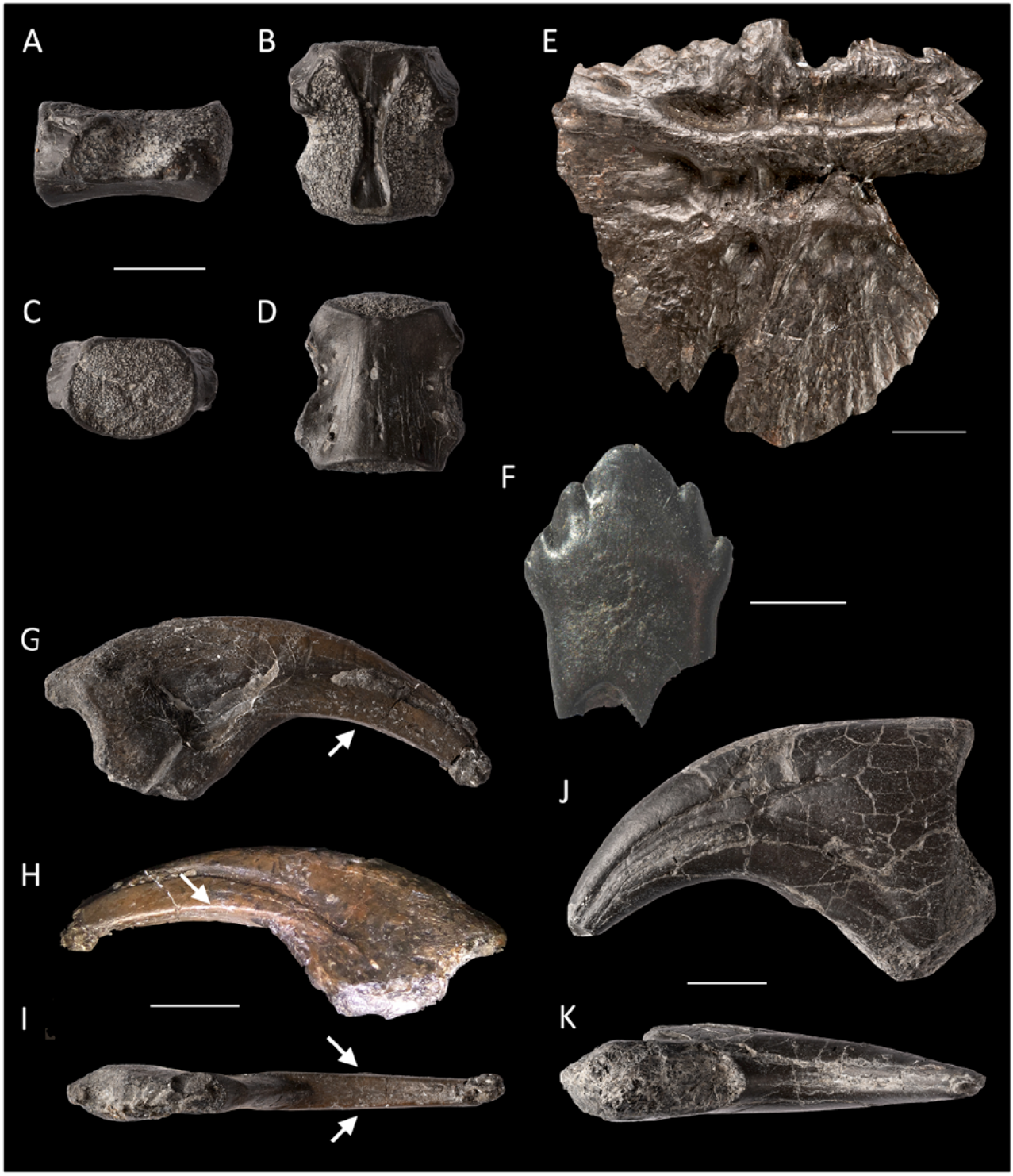

Figure 12: Other rare amniotes: Sphenodonta, Phytosauria, Pterosauria, Dinosauria, Synapsida. **A**-**D** Probable sphenodont vertebral centrum (WMNM P98480) in (**A**) left lateral, (**B**) dorsal, (**C**) anterior, and (**D**) ventral view. **E** Phytosauria indet. osteoderm (WMNM P98442) in external view. **F** Synapsid *Lepagia gaumensis* (WMNM P64198). **G**-**I** Pterosauria indet. manual ungual (WMNM P91002) in lateral/medial view (**G**), oblique lateral/medial view (**H**), and palmar view (**I**). Note the sharp edges (arrows) on the distal part of the palmar side, best visible in (**H**). **J**, **K** cf. *Plateosaurus* sp. ungual (WMNM P91001) in lateral/medial view (**J**) and palmar view (**K**). Scale bars represent: 1 mm (F); 5 mm (A-D, G-I); 1 cm (E, J, K).

osteoderms from Norian to Rhaetian European localities reviewed by Sander & Wellnitz (2024), there is only one match, a small osteoderm from Halberstadt.

The phytosaur osteoderm from Bonenburg is important because the late middle Rhaetian age of Bone Bed 2 makes it the youngest stratigraphically well-constrained phytosaur record worldwide (Sander & Wellnitz 2024). There are two potentially younger contenders for the "last phytosaur", but both are inconclusive. The record from New Mexico (Martz et al. 2014) is a partial skull and thus can be confidently assigned to Phytosauria. It is the stratigraphically highest phytosaur specimen from the Chinle Group, but the age of the horizon cannot be constrained beyond Rhaetian or possibly Hettangian. The second contender is a segment of very slender rostrum from the Blue Lias of southwest England which was identified by Maisch & Kapitzke (2010) as close to the well-known *Mystriosuchus* of Norian and Rhaetian age. However, the age of the discovery horizon of the rostrum segment is contentious, being either Rhaetian or earliest Hettangian in age (Sander & Wellnitz 2024). The other problem associated with the specimen is that its identification as a phytosaur is not beyond doubt, given the morphological similarity to thalattosuchian crocodylomorph rostra. According to the latest research, thalattosuchians have ghost lineages extending into at least the Rhaetian and appear in the fossil record in the Hettangian or Sinemurian (Benani et al. 2023; Wilberg et al. 2023).

Pterosauria

The global record of Pterosauria begins in the middle Norian marine deposits of the Italian Alps with several valid species known from partial or complete skeletons. Late Norian to early Rhaetian pterosaurs have been described from the Kössen Formation of the Swiss Alps as *Caviramus* (Fröbisch & Fröbisch 2006) and *Raeticodactylus* (Stecher 2008), although the two species may be synonymous. It thus is not entirely surprising that pterosaur remains should be discovered in the Bonenburg bone beds, given the large number of fossils from the locality. However, the general fragility of pterosaur bones means that most pterosaur remains are from laminated still-water sediments and do not appear suited to preservation in a condensed high-energy deposit. It thus came as somewhat of a surprise that an ungual claw (WMNM P91002), discovered in Bone Bed 2b in 2017 (Fig. 12G-I) and initially identified as that of a small theropod, is actually better assigned to a pterosaur. The gracility and strong curvature of the ungual suggest that it is from the manus and not the pes (Hack et al. 2026).

The ungual is laterally flattened and strongly curved (Fig. 12G-I). It also is bilaterally highly symmetrical, so it cannot be assigned to the left or the right side of the body. The ungual is relatively large, with a dorsopalmar height of 11.1 mm and a length measured orthogonally to the height of 16.3 mm. The distinctive feature of this ungual, so far not recorded in the literature for either theropods or pterosaurs, is found on its palmar side (Fig. 12H, I), which is divided into two parts (Hack et al. 2026). The proximal part, originating from the flexor tubercle, is mediolaterally very narrow and uniformly convex. The distal part of the palmar side is completely flat and bears sharp edges medially and laterally, extending onto the medial and lateral sides of the ungual (Fig. 12G, H).

A referral to Pterosauria thus appears most likely, although a possible theropod affinity cannot be ruled out (Hack et al. 2026). A theropod affinity of WMNM P91002 is less likely because the theropod claws in question are less gracile and less curved. It is also less likely on the basis of a morphometric discriminant analysis that yielded support for a pterosaurian affinity (Hack et al. 2026). An argument against the identification as a pterosaur might be the relatively large size of the ungual, which is larger than any described specimens from the Triassic or Early Jurassic (although only slightly larger than the largest unguals referred to *Dimorphodon macronyx*, see Sangster 2021). It is only by the Middle Jurassic that pterosaurs clearly larger than the Bonenburg specimen are documented, e.g., the recently described *Dearc sgiathanach* (Jagielska et al. 2022).

Dinosauria: Sauropodomorpha

Another manual ungual claw discovered in Bone Bed 2b in 2017 (Fig. 12J, K; WMNM P91001) pertains quite obviously to an early-branching sauropodomorph, probably a plateosaurid or early-branching massopodan (Hack et al. 2026). The robust ungual has the typical deep shape seen in the first and second manual unguals of *Plateosaurus trossingensis* (Fig. 12J, K). The body side of origin could not be determined because of the strong bilateral symmetry of this bone. The dorsopalmar height of the ungual at its proximal end is 36.6 mm. The length measured orthogonally to the height is 59.5 mm. The mediolateral width measured at the widest point, immediately distal to the extensor tubercle, is 13.8 mm. Based on the curvature and depth, the ungual is likely a second one

because of the stronger curvature and greater height of the first manual ungual of *Plateosaurus* (Huene 1926; Mallison 2010; Schaeffer 2024). The size of the individual can be reasonably well constrained in comparison with the Tübingen skeleton (GPIT 2) of *Plateosaurus trossingensis* digitized by Mallison (2010). This skeleton is 5.57 m long, which is somewhat below average for the species (see Sander 1992; Klein & Sander 2007; Dupuis et al. 2025). In GPIT 2, the first ungual measures 63 mm along the curvature and the second 47 mm, bracketing the Bonenburg ungual's length along the curvature of 62.4 mm. However, considering that the tip of the Bonenburg ungual is probably missing (Fig. 12J, K), it may have even been slightly larger than the first ungual of GPIT 2 (Hack et al. 2026).

Assignment to a particular genus or species does not appear possible for the Bonenburg ungual. Rhaetian sauropodomorphs from Europe include the small and early-branching *Thecodontosaurus* (Whiteside & Marshall 2008) and *Pantydraco* (Galton et al. 2007) and the far larger sauropodiform *Camelotia* (Galton 1985), all from England. The only manual ungual associated with the type material of the latest Norian sauropodiform *Schleitheimia schutzi* from Schaffhausen, Switzerland (PIMUZ AIII 546, though not described in Rauhut et al. 2020, see Hack et al. 2026) differs notably from WMNM P91001 and earlier-branching Sauropodomorpha in its reduced curvature and overall proportions.

Cynodontia

The only synapsid specimen from Bonenburg, the tooth of a non-mammaliaform cynodont (WMNM P64198, Fig. 12F), was assigned by Schwermann (2016) to *Lepagia gaumensis*. It was recovered by screen washing in 2015.

"Missing" faunal elements

The large number of specimens from several excavation campaigns has resulted in the recovery of some extremely rare or unique records of particular clades (e.g., Phytosauria, Pterosauria), rendering the absence of certain other clades conspicuous. Based on their occurrence in other Rhaetian bone beds and other European Rhaetian fossil localities, it would be reasonable to expect the following clades: Holocephali, Placodontia, non-sauropodomorph Dinosauria, and Mammaliaformes (in systematic order). In the Bonenburg bone beds, the almost complete lack of teeth of terrestrial tetrapods is noteworthy. There are no mammalian teeth, no dinosaur teeth (not even those of theropods) and no phytosaur teeth. Discussing these elements is of interest for three reasons: first, it raises awareness about what some unidentified finds in the collections and some future finds might be; second, rare and absent taxa may help in constraining habitat sampling and the depositional environment of the bone bed (see below); and third, the absence of taxa may have implications for their extinction at the global level.

Two "glaring omissions" are worth discussing in more detail: myriacanthid holocephalans and placodonts. Holocephali, specifically myriacanthid tooth plates and fin spines, are known from the European Rhaetian at Aust Cliff (Storrs, 1994) and from the Kössen Formation of the Swiss Alps (Duffin & Furrer 1981). Their preservation potential is similar to that of the abundant selachian remains from Bonenburg, but no holocephalan remains have been found so far, despite the great hardness of their tooth plates. Thus, their absence remains puzzling.

From both epicontinental bone bed localities and from Alpine deposits, it is known that cyamodontid placodonts thrived in the Rhaetian. Specifically, *Psephoderma alpinum* is known from teeth in the British Rhaetian in the Marston Road Quarry (see Nordén et al. 2015). This publication also provides a review of Norian and Rhaetian European placodonts, with reports of teeth and the characteristic osteoderms coming, for example, from southern German and Swiss epicontinental localities, such as Niederschönthal (Huene 1911), but also from the Kössen Formation (Neenan & Scheyer 2014). All of these deposits and the Marston Road Quarry are characterized by proximity to a palaeocoast and are clearly more shallow-water deposits than at Bonenburg. So, possibly, the lack of placodonts is caused by the lack of suitable habitat. However, given that some faunal elements, such as the temnospondyl amphibians, indicate more distant habitats than the coast, the absence of placodonts is even more puzzling. Alternatively, placodonts may already have been extinct by the late middle Rhaetian. We may entertain this hypothesis because none of the Rhaetian occurrences of placodonts from UK bone beds as recorded by Nordén et al. (2015) are, with any certainty, as young as Bonenburg. In general, they are considered early Rhaetian in age (Cawthorne et al. 2024). Although the placodont remains from the UK and Swiss bone beds could potentially have been reworked from older deposits, they do not differ in appearance from the other fossils from these bone beds.

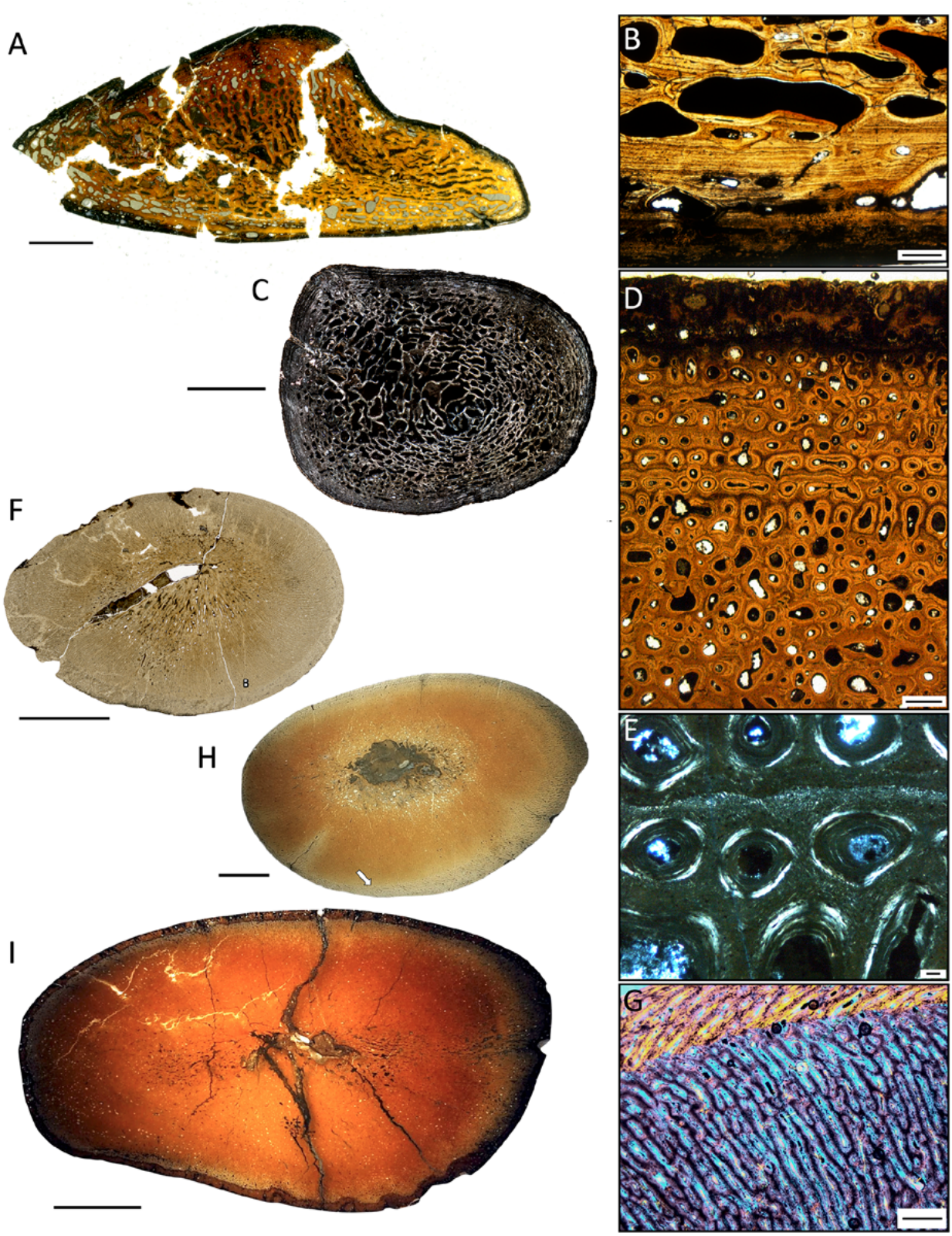

Figure 13: Bone histology and microanatomy of Bonenburg Rhaetian tetrapod fossils, in phylogenetic order. **A** cf. *Cyclotosaurus* humerus (WMNM P64371) midshaft cross section. **B** Close-up of cortex. **C** Capitosauria indet. femur (WMNM P97790) midshaft cross section. **D** cf. *Ichthyotitan* cortical fragment (WMNM P88133). Overview of cortical histology. **E** Close-up of the same in cross-polarized light. **F** *Rhaeticosaurus mertensi* Wintrich et al. 2017 (WMNM P64047) femur midshaft cross section. **G** Close-up of (**F**) in cross-polarized light and lambda filter. **H** cf. *Rhaeticosaurus* propodial (WMNM P97448) midshaft cross section. **I** Indet. plesiosaur morphotype 2 propodial (WMNM P117120) midshaft cross section. Scale bars represent: 10 µm (E); 500 µm (B, D, G); 5 mm (A, H); 10 mm (C, F, I).

Habitat representation of the fauna

After the taxonomic review of the Bonenburg vertebrate fauna, we turn to a review of its environmental information content. As discussed above, the Contorta Beds at Bonenburg are clearly marine and were deposited under anoxic conditions. However, as indicated by the autochthonous invertebrate fauna, there may have been changing salinities, excluding stenohaline pelagic invertebrates such as echinoderms (except for the euryhaline ophiuroids) and cephalopods. The plesiosaur skeleton 3 m below Bone Bed 2 also suggests fully marine conditions since Plesiosauria were generally marine, and the high degree of articulation excludes long postmortem transport. However, while dominated by marine fossils numerically, the bone beds also contain numerous allochthonous faunal elements, thus sampling a very wide range of habitats and environments.

Pelagic

Ichthyosaurs in general are pelagic animals that did not depend on benthic invertebrates as prey. Instead, they hunted nekton such as fish and in particular coleoid cephalopods in the water column (e.g., Sander et al. 2021). The latter prey group has not been discovered in the Contorta Beds despite the high preservation potential of the keratinous arm hooklets of Triassic cephalopods (e.g., Landon et al. 2017; Cross et al. 2018). Such hooklets are also frequently found in Triassic ichthyosaur stomachs (e.g., Sander 1989). In addition, the giant size indicated by some of the ichthyosaur fossils, and even the large size indicated by the short, disk-shaped vertebral centra, are inconsistent with the marginal marine inner-shelf setting of Bonenburg, as would be the case for modern cetaceans. In fact, the relative abundance of giant ichthyosaur remains across the European epicontinental Rhaetian (UK, France, Bonenburg) may suggest that at least at times the habitat was more pelagic and the sea level was higher than suggested by the patchy distribution, thinness, and condensed nature of the epicontinental Rhaetian deposits. The condensation horizons represented by the bone beds may have resulted as much from sediment starvation as from winnowing by high-energy processes in the deeper parts of the Rhaetian sea. Accordingly, there is a lack of ichthyosaur remains in the bone beds closer to the palaeocoast such as the southern German and Swiss localities like Niederschönthal.

Open marine

The most obvious open-marine faunal elements in the bone beds are the plesiosaurs and some of the hybodont sharks (*"Hybodus" cloacinus*), as well as the synechodontiform chondrichthyans (*Rhomphaiodon minor*, *Synechodus rhaeticus*). A refined habitat analysis of chondrichthyans and osteichthyan fish still awaits the taxonomic study of these fossils. The overwhelming dominance of sharks and osteichthyan remains together with the dominance of plesiosaur and ichthyosaur remains among the larger bones are in line with a fully marine environment sampled by the bone beds. Plesiosaurs are generally considered open-marine animals, although perhaps closer inshore than ichthyosaurs (Motani 2009); it is only during the Cretaceous that there were some apparent freshwater plesiosaurs (Sato et al. 2005). The marine preference of the Bonenburg plesiosaurs is also supported by the fact that the stem-line pistosaurs such as *Pistosaurus*, *Augustasaurus* and *Bobosaurus* come from more open-water deposits than other Triassic sauropterygians (Sander et al. 1997; Krahl et al. 2013; Wintrich et al. 2017a).

The abundance of the mawsoniid coelacanths (Hartung et al. 2021) suggests that they were fully marine, as discussed above. Possibly, the same applies to the enigmatic *Pachystropheus* based on its status as the most abundant reptile taxon in Bone Bed 2. However, this habitat preference is inconsistent with the hypothesized affinity with Choristodera, all of which come from freshwater habitats. A thalattosaurian affinity of *Pachystropheus* would definitely be more in line with its abundance in Bone Bed 2. Quinn et al. (2024) argue in favour of a shallower marine habitat and possibly terrestrial abilities for *Pachystropheus*.

Coastal, brackish

The subset of the Bonenburg fish fauna that inhabited shorelines and estuaries includes some hybodont sharks (*Lissodus minimus*), actinopterygians and possibly the ceratodontid lungfishes, which also inhabited freshwater (Storrs 1994; Pawlak et al. 2020). Similarly, the plagiosaurine plagiosaurs are thought to have been able to tolerate brackish water (Schoch et al. 2022). At least some phytosaurs also pertain to the "coastal, brackish" group (Gozzi & Renesto 2009, Butler et al. 2019). However, the rarity of phytosaurs

(and especially their teeth!) at Bonenburg compared to more coastal localities such as Niederschönthal, Halberstadt and Hallau (Huene 1911, 1922, Peyer 1943) indicates that preferred phytosaur habitats must have been located further away.

Freshwater

The diverse and relatively abundant capitosauroid temnospondyls are the most obvious input into the bone beds from freshwater habitats (Prino et al. 2024). This is because none of the clades of temnospondyls, including the living ones, tolerate saltwater with the exception of the trematosaurs and to a lesser extent, plagiosaurs (Schoch & Milner 2000, 2014). However, the relative abundance of temnospondyls compared to phytosaurs at Bonenburg is puzzling from the environmental perspective because in many faunas of the continental Triassic, both groups are abundantly represented and often co-occur. The lungfishes are also typical elements pertaining to these continental freshwater faunas (Pawlak et al. 2020).

Terrestrial

Terrestrial input in the Bonenburg bone beds was clearly limited, and the terrestrial elements such as the sauropodomorph claw, the sphenodont jaw fragment and vertebrae, and the cynodont tooth were probably only discovered due to the high number of fossils in general. Thus, the rarity of dinosaurs, both as bones and also as teeth in Bonenburg, is noteworthy when compared with the English and other continental European bone beds. The limited terrestrial input is also indicated by the lack of theropod teeth and the extreme rarity of tetrapod remains in the screen-washing concentrate. Many other Rhaetian bone beds, on the other hand, are important sources for "early mammals" (mammaliaform synapsids), as discussed above.

The habitat preference of the pterosaur, represented in Bonenburg by a single claw (Hack et al. 2026), is difficult to constrain. The Triassic pterosaur record is almost exclusively from marine rocks (e.g., Wild 1984; Dalla Vecchia 2003, 2009a, b, 2021; Fröbisch & Fröbisch 2006; Stecher 2008), but there is a clear preservational bias because the fragility of pterosaur bones means that they would preserve best in marine still-water sediments. It is often assumed that the clade foraged over water bodies, but pterosaurs must have required access to terrestrial habitats for resting and reproduction, and there were likely species that lived in terrestrial habitats as well.

Implications of the Bonenburg fauna for the end-Triassic Extinction Event

Given the relatively late and well-constrained age of the vertebrates from the Contorta Beds at Bonenburg, within two million years of the end of the Triassic, the fauna has implications for the nature of the ETEE. Specifically, the fauna is the youngest well-dated and diverse tetrapod fauna from the European Rhaetian, postdating the extensively researched faunas of the basal bone bed in the Westbury Formation of the southwestern UK, most of which are dated as early Rhaetian (e.g., Cawthorne et al. 2024; Evans et al. 2024) or have mainly produced non-tetrapod vertebrates (e.g., Quinn et al. 2024).

From the extinction perspective, the chondrichthyans from Bonenburg are interesting because they suggest the extinction of many species within this time interval, but there is no extinction at higher taxonomic levels (Cappetta 2012). The only possible survivor at the species level may be *"Hybodus" cloacinus* which was also potentially reported from the Lower Jurassic of the UK (Duffin 1993). However, further research is needed into the Bonenburg chondrichthyan fauna, primarily by comparisons with other faunas. Nonetheless, it must be kept in mind that few other Late Triassic chondrichthyan faunas are as securely dated as Bonenburg. The sarcopterygians, on the other hand, do not appear to be informative regarding extinction.

Among the most relevant Bonenburg records regarding the ETEE are obviously the temnospondyls. Their abundance and diversity this close to the Triassic-Jurassic boundary are inconsistent with a gradual decline and disappearance as espoused by Lucas (2018). Instead, they are suggestive of a mass extinction event at the end of the Triassic (Prino et al. 2024). Similarly, the Bonenburg records of giant shastasaurid ichthyosaurs fit the pattern of a sudden extinction at the end of the Triassic, after giant shastasaurids were ubiquitous and dominant in the Rhaetian. This was already suggested by Fischer et al. (2014), while Sander et al. (2022) established that ichthyosaurs were particularly hard hit by the ETEE, with a loss of all giant forms and a severe bottleneck that only let the Neoichthyosauria pass through. McGaughey et al. (2023) and Lomax et al. (2024) similarly noted that giant shastasaurid ichthyosaurs existed in the Tethys and Panthalassa until the late Rhaetian. The Bonenburg fauna also reveals that it was not a case of just one large shastasaurid

ichthyosaur taxon surviving into the late middle Rhaetian, but two or even three species (cf. *Ichthyotitan*, Shastasauridae indet. morphotype 1, and Shastasauridae indet. morphotype 2).

The ETEE implications of the enigmatic *Pachystropheus* depend on its affinities to thalattosaurs vs. choristoderans. As a thalattosaur, *Pachystropheus* would be the last record of this clade (see also Quinn et al. 2024) since the last unquestionable thalattosaur record comes from the late Norian to early Rhaetian Kössen Formation of Austria (Müller 2007). As a choristodere, the rich *Pachystropheus* record from Bonenburg would indicate that the clade was not affected by the ETEE, similar to the situation for neoichthyosaurian ichthyosaurs. Obviously, the implications of *Pachystropheus* for the ETEE add urgency to elucidating the affinities of this taxon.

The Bonenburg record of plesiosaurs, particularly the *Rhaeticosaurus* holotype skeleton (Wintrich et al. 2017a), has clarified that many plesiosaur lineages crossed the boundary into the Jurassic, as already hypothesized by Benson et al. (2012). However, this does not necessarily mean that plesiosaurs were unaffected by the environmental perturbation causing the extinctions. Plesiosaurs must have been around for some time in the Norian, without leaving a record. No later than the Rhaetian, they had evolved body sizes much larger than the earliest Jurassic forms. Bonenburg is not unique in having yielded the bones of large plesiosaurs, as noted above, but a more detailed size evolution analysis using propodial and dorsal centrum dimensions is clearly called for to better understand this pattern and a possible body size decrease across the Triassic-Jurassic boundary.

The last clade from Bonenburg to be discussed in the context of the ETEE are the phytosaurs. The Bonenburg record is the last unequivocal one of the clade (Sander & Wellnitz 2024). However, as with the temnospondyls, long neglected evidence from other Rhaetian localities also indicates that phytosaurs were thriving in the European Rhaetian and then went extinct (Sander & Wellnitz 2024).

Certain faunal elements from Bonenburg are not informative regarding the extinctions or are ambivalent because of their rarity and low diversity (i.e., dinosaurs, pterosaurs, sphenodonts and synapsids). The possible exception among these rare elements is the sauropodomorph claw, which is the youngest well-constrained record of a non-sauropod sauropodomorph from Europe (Hack et al. 2026). However, the lack of non-sauropod sauropodomorphs in the European Lower Jurassic is presumably due to extensive flooding by the Early Jurassic epicontinental sea that obliterated all terrestrial habitats. We also know that non-sauropod sauropodomorphs thrived on most other continents until the end of the Early Jurassic (Sander & Lallensack 2018). A similar case, where an absence of evidence is not necessarily evidence of absence, are the placodonts, which are conspicuously missing from the Bonenburg fauna. However, the group may have been extinct by late middle Rhaetian times, consistent with a more gradual extinction pattern, or it may be absent for ecological reasons.

In conclusion, this analysis of the Bonenburg fauna, augmented by other Rhaetian vertebrate occurrences around Europe, gives mixed signals regarding the nature of the ETEE in the marine realm. The terrestrial realm is too poorly represented at Bonenburg and in other Rhaetian bone beds to reach any conclusions concerning the ETEE. Among the two dominant marine elements in the Bonenburg fauna, the contrast between the disappearance of the giant ichthyosaurs and the persistence of the plesiosaurs is puzzling. However, this review also indicates that there is not a single vertebrate group from Bonenburg for which we can rule out the possibility that the ETEE influenced their evolution.

Taphonomy and possible reworking

The origin of the Rhaetian bone beds across Europe has intrigued geologists for two centuries (Sykes 1977; Storrs 1994; Cross et al. 2018 and historical references therein), but a comprehensive discussion of their genesis is beyond the scope of this review. What does need to be considered in the context of the LAD of taxa is the time-averaging, specifically, reworking of pre-fossilized bones. As noted by Konietzko-Meier et al. (2019) in their analysis of the cf. *Cyclotosaurus* sp. humerus, there is no evidence for reworking in the Bonenburg bone beds, such as different kinds of preservation. We cannot, however, exclude reworking in the case of heavily abraded bones lacking all morphology. In contrast, reworking appears unlikely for fragile bones such as those of *Pachystropheus* or larger fish skull elements and the unusually complete chondrichthyan fin spines, whose excellent preservation would not be possible if reworking had occurred. In the absence of detailed sedimentological and petrographic analyses of the fossils in thin sections, we assume that time averaging is limited to 10ka to 100ka, at most.

This time frame thus does not affect our conclusions in regard to ichthyosaur, temnospondyl and phytosaur extinction.

Future perspectives and directions

At the most fundamental level, future research at Bonenburg will focus on continued excavation, primarily of Bone Bed 2, necessitated by its continuing destruction by mining. Continued excavation is essential not only to preserve fossil material but also to capitalize on the scientific potential of this unique site. As the number of recovered specimens increases, particularly of underrepresented taxa, new insights into morphology, taxonomic composition, and patterns of abundance and absence will emerge. This effort also includes re-examination of unidentified material currently subsumed under generic labels such as "reptile bone" in the WMNM collections.

Based on our review of the vertebrate fauna, future research will prioritize the completion of the morphological work on both the tetrapod and the chondrichthyan taxa from the bone beds, as well as on the articulated actinopterygian fishes. In parallel, detailed studies of the invertebrate fauna of the Contorta Beds are expected to yield significant results. Further geochemical studies of the Rhaetian section at Bonenburg and across the Triassic-Jurassic boundary will be undertaken. An additional focus will be placed on the lowermost Hettangian transgressive horizon, the chocolate-brown weathering oyster shell hash, as a potential source of marine reptile bones which may be diagnostic to genus.

Finally, long-term management of the Bonenburg clay pit as a natural heritage site will become increasingly important. Strategies for preserving the exceptional stratigraphic section from the upper Middle Keuper through the Exter Formation and into the Hettangian must be developed to ensure preservation and continued access for future research once mining ceases.

Conclusions

The scientific significance and future research potential of clay pit #3 of the August Lücking company at Bonenburg (Kreis Höxter, North Rhine-Westphalia, Germany) can be attributed to the following key aspects:

1. Exceptional stratigraphic control
Palynostratigraphy of the Exter Formation has established Bonenburg as the site of the most accurately dated Rhaetian bone beds currently known. The main bone bed, Bone Bed 2, is dated to the upper part of the middle Rhaetian Rhaetipollis-Limbosporites palynomorph assemblage zone.

2. High fossil yield and rare discoveries
The abundant material generated by the annual scientific excavation campaigns at Bonenburg has led to the discovery of very rare fossils, such as selachian cephalic spines and pterosaur claws.

3. Identifications of coelacanth remains
Coelacanth remains have now been recognized in the Exter Formation bone beds. They were previously misidentified and inventoried as Reptilia indet., suggesting they may be more abundant than previously thought.

4. Diverse temnospondyl assemblage
The Bonenburg bone bed fauna displays a remarkably high diversity of temnospondyl amphibians, including at least three to four species-level taxa (two to three capitosaurs and at least one plagiosaurine plagiosaur), marking the LAD of their respective clades.

5. Ichthyosaur dominance and extinction
Abundant remains of two taxa of large and giant shastasaurid ichthyosaurs underscore the notion of the ETEE having a catastrophic effect on this clade.

6. Exceptional plesiosaur record
Bonenburg has produced the most extensive record of Triassic plesiosaurs to date, including the only known Triassic plesiosaur skeleton, the holotype of *Rhaeticosaurus mertensi* Wintrich et al. 2017, as well as at least two other taxa. Interestingly, this clade appears to have been little affected by the ETEE, aside from a reduction in body size.

7. Youngest phytosaur record
Bone Bed 2 has produced the youngest unequivocal phytosaur record, documenting that this clade of archosaurs survived until at least the late middle Rhaetian before falling victim to the ETEE.

8. Epicontinental Rhaetian pterosaur record
Bone Bed 2 also has produced the probable first record of a pterosaur from an epicontinental Rhaetian bone bed. The find greatly expands the upper size limit of Triassic pterosaurs.

9. Notable absences

Certain taxa common in other Rhaetian bone beds are conspicuously absent from Bonenburg. The absence of holocephalan tooth plates could result from sampling bias or an environmental signal, whereas the lack of placodont remains may be a result of extinction.

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