The Nothosaurs of the Southern German Lettenkeuper (Triassic, Late Ladinian)

Dissertation

der Mathematisch-Naturwissenschaftlichen Fakultät

der Eberhard Karls Universität Tübingen

zur Erlangung des Grades eines

Doktors der Naturwissenschaften

(Dr. rer. nat.)

vorgelegt von

Dipl.- Geol. Juliane Katharina Mittag geb. Hinz

aus Reutlingen

Tübingen

2020

Gedruckt mit Genehmigung der Mathematisch-Naturwissenschaftlichen Fakultät der Eberhard Karls Universität Tübingen.

Tag der mündlichen Qualifikation:	24.11.2020
Stellvertretender Dekan:	Prof. Dr. József Fortágh
1. Berichterstatter:	Prof. Dr. James Nebelsick
2. Berichterstatter:	PD Dr. Ingmar Werneburg

Ich erkläre hiermit, dass ich die zur Promotion eingereichte Arbeit mit dem Titel: The Nothosaurs of the Southern German Lettenkeuper (Triassic, Late Ladinian) selbständig verfasst, nur die angegebenen Quellen und Hilfsmittel benutzt und wörtlich oder inhaltlich übernommene Stellen (alternativ: Zitate) als solche gekennzeichnet habe. Ich erkläre, dass die Richtlinien zur Sicherung guter wissenschaftlicher Praxis der Universität Tübingen (Beschluss des Senats vom 25.5.2000) beachtet wurden. Ich versichere an Eides statt, dass diese Angaben wahr sind und dass ich nichts verschwiegen habe. Mir ist bekannt, dass die falsche Abgabe einer Versicherung an Eides statt mit Freiheitsstrafe bis zu drei Jahren oder mit Geldstrafe bestraft wird.

"If I have seen further, it is by standing upon the shoulders of giants"

Isaac Newton, 1675

I dedicate this work to Prof. Dr. Hans-Ulrich Pfretzschner, who was always there for me. He was my supervisor, my mentor, and he will always be my inspiration for scientific curiosity, pursuit of knowledge, and beyond.

Table of contents

1. Summary

1.1. Zusammenfassung

Die zu den heute ausgestorbenen Sauroptergygiern gehörende Ordnung der Nothosaurier bildete zusammen mit den Ichthyosauriern die Spitze der Nahrungskette triassischer mariner Ökosysteme. Mit Ausnahme zweier in Nordamerika gefundener Sauropterygier beschränkte sich die Verbreitung der Sauropterygier und der dazu gehörigen Ordnung der Nothosaurier im Speziellen auf den Tethysrand und das Germanische Becken, das während der Trias einen der Hauptlebensräume der Nothosaurier darstellte. Bisher wurde angenommen, dass die hauptsächliche Verbreitung von Nothosauriern im voll marinen Muschelkalk erfolgte und die Diversität dieser Tiergruppe im Lettenkeuper mit der zunehmenden Verlandung des Germanischen Beckens von Norden her nach und nach geringer wurde. Im Rahmen dieser Arbeit werden neue Nothosaurierfunde aus dem Lettenkeuper des Germanischen Beckens vorgestellt, die ein neues Licht auf die Diversität und zeitliche Verteilung der Nothosaurier in Süddeutschland werfen.

Bei eigenen Grabungen im Lettenkeuper von Vellberg-Eschenau bei Schwäbisch Hall wurde im Jahr 2017 ein vollständig erhaltener Schädel einer neuen Nothosaurierart entdeckt. Im Zuge einer ausführlichen Publikation wurde der Fund als *Nothosaurus cristatus* neu beschrieben, gezeichnet und in einer eigenen phylogenetischen Analyse in den Stammbaum der Nothosaurier eingegliedert. Dieser Fund ist von großer Relevanz, da er zeigen konnte, dass die Diversität von Nothosauriern im Lettenkeuper größer ist als bisher angenommen wurde. Im Zuge einer zweiten Publikation wurde ein Hinterhaupt eines Nothosauriers beschrieben, der im Rahmen einer Notgrabung im Lettenkeuper von Kupferzell im Jahr 1977 ergraben und fälschlicherweise als landlebender Archosaurier *Batrachotomus kupferzellensis* bereits im Jahr 1999 beschrieben wurde. Die im Rahmen der Arbeit angefertigte Publikation beinhaltet Zeichnungen des Hinterhaupts und erläutert die Stratigraphie der Fundstelle Kupferzell. Des Weiteren beschreibt sie den Schädelfund als *Nothosaurus giganteus* und bestimmt diesen anhand von Vergleichen mit anderen Nothosauriern. Dieser Fund konnte erneut aufzeigen, dass große Nothosaurier im schon stark verlandenden Germanischen Becken zur Zeit des Lettenkeupers existierten und dass der marine Einfluss im heutigen Süddeutschland während dieser Zeit größer war als bisher angenommen.

1.2. Summary in English

The order of Nothosauria belongs to the superorder of Sauropterygia, a group of extinct marine reptiles. Nothosaurs formed, together with ichthyosaurs, the top of the food chain of Triassic marine ecosystems. Except for two sauropterygian species from North America, the distribution of sauropterygians in general and nothosaurs in special was limited to the coastlines of the Tethys sea and the Germanic Basin, which formed one of the main habitats of nothosaurs. Until now, it was assumed that the main diversification of nothosaurs in the Germanic Basin took place during the fully marine Muschelkalk (Anisian) and that the diversity of this group decreased during the Lettenkeuper (Ladinian) due a regressive trend leading to sea-level lowstands and a subsequent drying up of the Germanic Basin beginning in the northern part of the basin. In this work, new nothosaur finds from the from the Lettenkeuper are presented. They shed a new light on the diversity and temporal distribution of nothosaurs in southern Germany.

During own excavations in the Lettenkeuper sediments of Vellberg-Eschenau close to Schwäbisch Hall in 2017, a completely preserved skull of a new *Nothosaurus* species was discovered. In a detailed publication, the new find was described as *Nothosaurus cristatus*. Detailed drawings as well as an own phylogenetic analysis were made and *N. cristatus* was embedded in the existing phylogenetic tree of nothosaurs. This find is of great relevance because it shows that the diversity of *Nothosaurus* species during the Lettenkeuper was higher than previously expected. In a second publication, the occiput of a *Nothosaurus* skull was described. It was recovered during a salvage excavation in the Lettenkeuper of Kupferzell in 1977 and erroneously described as skull part of the archosaurian reptile *Batrachotomus kupferzellensis* in 1999. This publication contains the re-description of the occiput as *Nothosaurus giganteus* based on comparisons with other nothosaurs, detailed comments about the stratigraphy of the find location, and drawings of the found skull elements. This find underlines that large nothosaurs still existed in the already strongly regressionally affected Germanic Basin during the time of the Lettenkeuper and that the marine influence in present-day southern Germany was bigger than previously expected.

2. List of publications

Already published:

Juliane K. Hinz, Andreas T. Matzke, and Hans-Ulrich Pfretzschner. "A new nothosaur (Sauropterygia) from the Ladinian of Vellberg-Eschenau, southern Germany." Journal of Vertebrate Paleontology 39.2 (2019): e1585364.

Juliane K. Hinz, Andreas T. Matzke, Felix J. Augustin and Hans-Ulrich Pfretzschner. "A *Nothosaurus* (Sauropterygia) skull from Kupferzell (late Ladinian, SW-Germany)." Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen 297/1 (2020): 101-111.

3. Own contribution

"A new nothosaur (Sauropterygia) from the Ladinian of Vellberg-Eschenau, southern Germany."

- Leading the excavation resulting in the find of *Nothosaurus cristatus*.
- Supervision of the preparation of the find.
- Examination and discovery that the find represents a new species.
- Detailed drawings of the find.
- First author and main writer of the publication.
- Data generation for the phylogenetic matrix.
- Analysis and interpretation of the results and the phylogenetic matrix.
- Correspondence with the handling editor of the journal.
- Review and resubmission of the manuscript.

"A *Nothosaurus* (Sauropterygia) skull from Kupferzell (Triassic, late Ladinian; SW Germany)"

- Examination and discovery that the find represents no *Batrachotomus kupferzellensis* but a *Nothosaurus giganteus* instead.
- Detailed drawings of the find.
- First author and main writer of the publication.
- Analysis and interpretation of the results including comparison with several other nothosaurs skulls and the definition of own ratios for a better understanding of skull proportions.
- Correspondence with the handling editor of the journal.
- Review and resubmission of the manuscript.

4. Introduction

In the end of the Paleozoic era, the first reptiles conquered marine habitats. *Mesosaurus tenuidens* GERVAIS, 1965 and *Stereosternum tumidum* COPE, 1885, both parareptiles of crocodile-like appearance, evolved during the Early Permian (CARROLL 1982, HUENE 1941, MOTANI 2009, OELOFSEN & ARAÚJO 1987). During the Late Permian, eosuchian reptiles of the families of Tangasauridae HAUGHTON, 1924 and Claudiosauridae CARROLL, 1981 adapted towards an aquatic lifestyle (CURRIE 1981). At the end of the Permian, the Permo-Triassic mass extinction event killed an estimated 48,6% (BENTON 1995) to 49% (SEPKOSKI 1996) of all marine families, including marine reptiles. During the following Mesozoic, at least twelve different groups of marine reptiles evolved (CARROLL 1982), from which the four most species-rich groups were the Ichthyopterygia OWEN, 1840, the Sauropterygia OWEN, 1860, the Mosasauridae GERVAIS, 1852, and the Chelonioidea BAUR, 1893 (MOTANI 2009). From these four major groups, the Ichthyopterygia and Sauropterygia evolved at the beginning of the Mesozoic during the Early Triassic while the Chelonioidea and the Mosasauridae first occurred during the Lower and Upper Cretaceous, respectively (Fig. 1).

The superorder of Sauropterygia, which includes around 100 species (MOTANI 2009), splits into the Eosauropterygia TSCHANZ, 1989 and the Placodontiformes NEENAN et al., 2013. The Eosauropterygia are divided into the Pistosauroidea BAUR, 1887–1890, the Pachypleurosauria NOPCSA, 1928, and the Nothosauroidea BAUR, 1889, from which the genus of *Nothosaurus* MÜNSTER, 1834 is within the focus of this study. From all Eusauropterygia, only species belonging Plesiosauria BLAINVILLE et al., 1835, an order included in the Pistosauroidea, survived the end-Triassic mass extinction event (Fig. 1). Finds of Early Triassic eosauropterygians are rare and limited to the Upper Lower Triassic Olenekian stage. A potential cause could be lethally hot ocean surface temperatures and a greenhouse climate during the Indusium, the earliest stage of the Lower Triassic (SUN et al. 2012). This harsh climate may have impeded an earlier evolution and radiation of marine reptiles.

During the Olenekian (Fig. 2), the basal *Majiashanosaurus discocoracoidis* JIANG et al., 2014, the nothosauroid *Hanosaurus hupehensis* YOUNG, 1972, and probably the

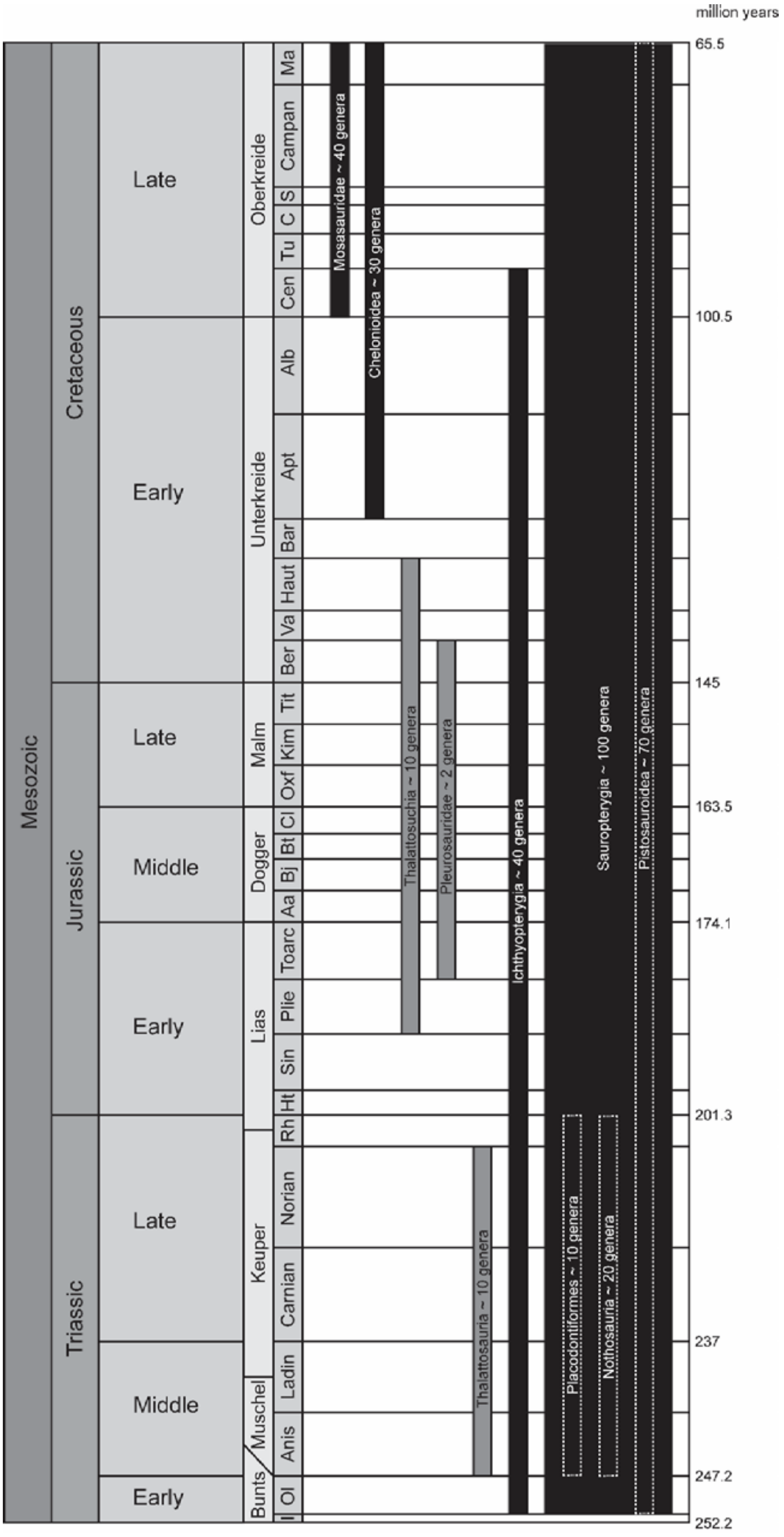


Figure 1: Geologic timescale of the Mesozoic with additional information about the occurrence of groups of marine reptiles. The groups highlighted in black are the most species-rich groups mentioned in chapter 4, the groups highlighted in dark grey are not so species-rich and remain without further mention. The dashed lines mark suborders within the order of Sauropterygia, which are mentioned in chapter 4. Modified after Motani (2009).

pistosaurid *Kwangsisaurus orientalis* Young, 1959 appeared in the eastern region of the Tethyan Sea in the area of the modern People’s Republic of China. At the same time, the pistosaurids *Cymatosaurus erikae* Maisch, 2014 and *Cymatosaurus erytheus*, Huene, 1944, and the pachypleurosaurian *Dactylosaurus gracilis* Gürich, 1884 populated the Germanic Basin through the East Carpathian and Silesian-Moravian gates in the area of modern Poland (Kowal-Linka & Bodzioch 2017). Simultaneously, the pistosaurid *Tanaisosaurus kalandadzei* Sennikov, 2001 appeared the at Tethyan coast of modern day European Russia. While the evolution and radiation of all taxa listed above was restricted to the coasts of the Tethyan Sea and the Germanic Basin, *Corosaurus alcovensis* Case, 1936, a pistosaurid, was found in todays North America at the former coast of the Panthalassic Ocean. This is remarkable because only one more Triassic pistosaurid, the Middle Triassic *Augustasaurus hagdorni* Sander et al., 1997, is known from outside the Tethyan province. It still remains unclear how these taxa made their way to the Panthalassic Ocean.

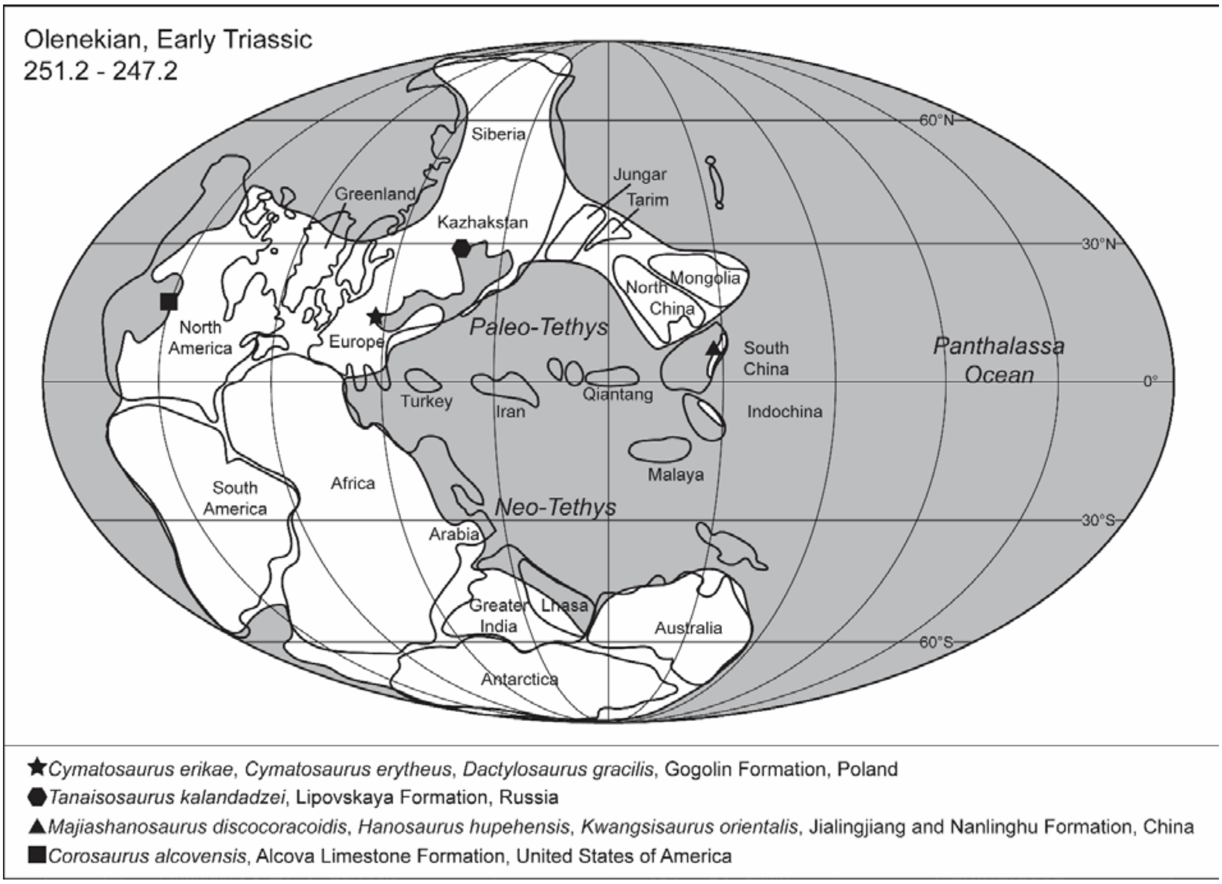


Figure 2: Paleomap of the Olenekian, Lower Triassic. The symbols point out find locations of early sauropterygians. Modified after Sun et al. (2015)

An Early Triassic sea passage between the eastern part of the Panthalassic Ocean and the western region of the Tethyan province did not exist (DORÉ 1991, RICOU 1995, ZIEGLER 1988) and therefore, the sauropterygians of the Germanic Basin and western margin of the Tethyan Sea can be excluded as potential ancestors of the Panthalassic pistosaurs (RIEPPEL 1998). Some authors suggest a faunal and floral exchange between the eastern Tethyan Sea and the western Panthalassic Ocean (GRANDE 1994, ROSS & ROSS 1981) and DORÉ (1992) proposes a connection between the Tethyan Sea and the Boreal Sea in the north during periods of marine transgression in the Lower Triassic. A precise reconstruction of the migration path of Panthalassic sauropterygians will have to await better material although newer finds like the primitive Russian *Tanaisosaurus kalandadzei* point towards the boreal pathway.

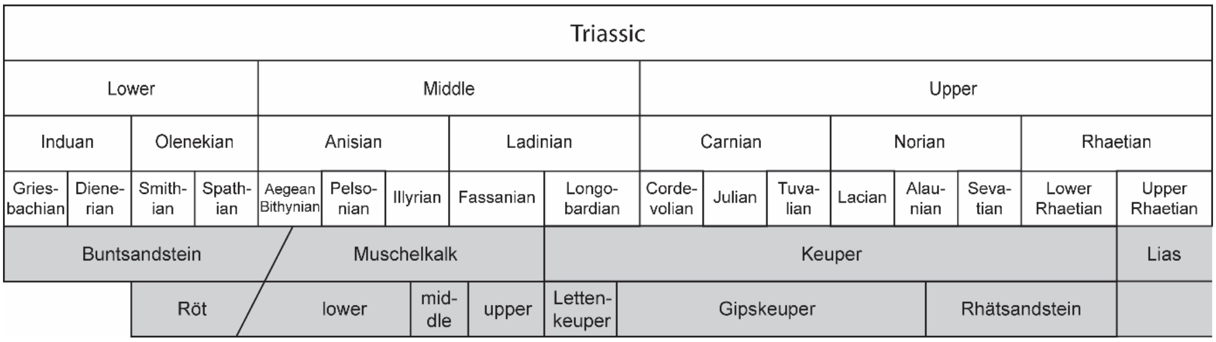
During the Lower Middle Triassic (Anisian), sauropterygians greatly diversified (MOTANI 2009) and occupied a broad variation of marine dietary niches, ranging from durophagous hard-shell feeders (Placodontiformes) to coastal hunters (Nothosauria), and open water hunters (Pistosauroidea). The opening of the Burgundy Gate created a connection between the Germanic Basin and the western and southwestern Tethyan provinces (RIEPPEL et al. 1997). Through this gate, sauropterygians inhabited the regions of modern Italy (E.G. PEYER 1939, RENESTO 2010), Spain (SANZ 1983), and Israel (E.G. HAAS 1979, RIEPPEL et al. 1997).

This study focuses on the *Nothosaurus* species from the uppermost Middle Triassic (Ladinian) sediments of the Germanic Basin. Due to the strongly continental influence, the German Triassic cannot be directly correlated with the open marine Tethyan Triassic (KOZUR & BACHMANN 2005) and is therefore listed as parastratigraphical supergroup with three divisions, each with three subdivisions in lower, middle, and upper parts. The tri-fold German Triassic was introduced by VON ALBERTI (1834) for the sequence of Buntsandstein, Muschelkalk, and Keuper (SCHRÖDER 1982) (Fig. 3).

The sediments of the German Triassic were deposited in a cratonic basin with its center in northern Germany (AIGNER & BACHMANN 1992). Regressive marine tendencies of the uppermost Permian (TUCKER 1991) continued into the Buntsandstein and led to terrestrial sedimentation of evaporites and sandstones. The Upper Buntsandstein is characterized by fluvial deposits, transgressional surfaces (HINZE 1967), and playa deposits with frequent marine ingressions in its uppermost part. The rising sea level played a major role in the radiation of sauropterygians, which first occurred in the Germanic Basin during the uppermost Upper Buntsandstein (HUENE 1944, MAISCH 2014).

At the beginning of the Muschelkalk, a transgressive tendency led to predominantly marine sediments with some regression-driven evaporite events during the Middle Muschelkalk. The fully marine conditions of the Lower Muschelkalk led to a radiation of the Placodontiformes, Pachypleurosauria, and, of biggest importance for this study, nothosaurs (RIEPPEL 1999). A hiatus in sauropterygian fossil finds occurs during the Middle Muschelkalk where a salinity crisis led to hostile environments for all of the shore-bound reptiles mentioned above (HAGDORN 1991). In the Upper Muschelkalk, a transgression from the south resulted in the deposition of vast carbonate platforms in the alpine region. A few sauropterygians bridged the Middle Muschelkalk gap (HAGDORN 1991, RIEPPEL 1999), including the genera *Placodus* AGASSIZ, 1834 (RIEPPEL 1995), *Cyamodus* VON MEYER, 1847 (GÜRICH 1884, KUHN-SCHNYDER 1960), and the species *Nothosaurus marchicus* KOKEN, 1893 (RIEPPEL & WILD 1996). New sauropterygian genera and taxa like *Nothosaurus giganteus* MÜNSTER, 1834 and *Simosaurus gaillardoti* VON MEYER, 1842 appeared during the Upper Muschelkalk. Then, a regressive trend took over and continued into the following Lettenkeuper.

During the Upper Lettenkeuper and Lower Gipskeuper, the resulting sea-level lowstands led to an erosion of the underlying sediments caused by river channels of a fluvial drainage system (BEUTLER & SCHUBERT 1987, WURSTER 1964). A following transgression during the Gipskeuper induced the sedimentation of dolomites followed by regression-based evaporite layers and playa as well as mudflat deposits.



<table>
<tr><td colspan="17">Triassic</td></tr>
<tr><td colspan="4">Lower</td><td colspan="5">Middle</td><td colspan="8">Upper</td></tr>
<tr><td colspan="2">Induan</td><td colspan="2">Olenekian</td><td colspan="3">Anisian</td><td colspan="2">Ladinian</td><td colspan="3">Carnian</td><td colspan="3">Norian</td><td colspan="2">Rhaetian</td></tr>
<tr><td>Gries-bachian</td><td>Diene-rian</td><td>Smith-ian</td><td>Spath-ian</td><td>Aegean Bithynian</td><td>Pelso-nian</td><td>Illyrian</td><td>Fassanian</td><td>Longo-bardian</td><td>Corde-volian</td><td>Julian</td><td>Tuva-lian</td><td>Lacian</td><td>Alau-nian</td><td>Seva-tian</td><td>Lower Rhaetian</td><td>Upper Rhaetian</td></tr>
<tr><td colspan="4">Buntsandstein</td><td colspan="4">Muschelkalk</td><td colspan="8">Keuper</td><td>Lias</td></tr>
<tr><td colspan="2"></td><td colspan="2">Röt</td><td colspan="2">lower</td><td>mid-dle</td><td>upper</td><td>Letten-keuper</td><td colspan="4">Gipskeuper</td><td colspan="3">Rhätsandstein</td><td></td></tr>
</table>

Figure 3: Nomenclature and parallelization of the Tethyan Triassic (white) including stages and substages and the tri-fold German Triassic (grey) including lithostratigraphic units. The sizes of the boxes do not represent the lengths of each stage. Modified after HINZ et al. (2019).

Sauropterygian remains in general and *Nothosaurus* remains from the Lower Keuper in particular are rare and only four diagnostic species including two valid Keuper-only species are identified yet. The first is *Nothosaurus edingerae* SCHULTZE, 1970, which is known from the Gipskeuper only and is represented by two skulls (RIEPPEL & WILD 1994, SCHULTZE 1970). The second is the newly discovered *Nothosaurus cristatus* HINZ et al., 2019 only known from the Lettenkeuper. Also present in the Lower Keuper are *Nothosaurus chelydrops* FRAAS, 1896, which was synonymized with *Nothosaurus giganteus* (RIEPPEL & WILD 1996), and *Nothosaurus mirabilis* MÜNSTER, 1834, which all evolved during the Upper Muschelkalk. This is interesting because there still exists a species rich *Nothosaurus* fauna in the Lower Keuper even though the drying up of the Germanic Basin is almost completed during this time. The following Schilfsandstein deeply eroded into the Gipskeuper sediments by forming a river channel system cutting into the underlying sediments (WURSTER 1964). Thin layers of shales were deposited between the river channels. A transgression led to local deposition of marine carbonates and shales including marine faunal elements (DITTRICH 1989, DUCHROW 1984). The sediments of Kieselsandstein, Stubensandstein, Knollenmergel, and Rhaet predominantly consist of fluvial and deltaic sediments of purely continental origin. Interbedding gypsum layers indicate smaller flooding events (AIGNER & BACHMANN 1992).

5. Aim of this study

The Middle Triassic deposits of southern Germany have been well-studied for over 150 years (VON JÄGER 1828, VON MEYER 1832, VON MEYER 1847-1855) and important localities containing Muschelkalk and Lower Keuper fossils are known (HAGDORN et al. 2015). From all southern German Lower Keuper localities only Vellberg-Eschenau and Kupferzell provide larger amounts of *Nothosaurus* material from the Lower Keuper, while in a third location, Affaltrach, only two skulls of *Nothosaurus edingerae* were found. In a fourth location, Hoheneck, two partially preserved skulls and two lower jaw fragments of *Nothosaurus chelydrops*, now a junior synonym of *Nothosaurus giganteus*, were found (RIEPPEL & WILD 1996).

The lagerstätten of Vellberg-Eschenau and Kupferzell, both from the Lettenkeuper, which are in the focus of this study, are world famous for their richness in fossils from terrestrial and lacustrine paleoenvironments (HAGDORN et al. 2015, SCHOCH & SEEGIS

2016, URLICHS 1982, WILD 1980) including well-preserved macrofossils of vertebrates such as fishes, amphibians, terrestrial, and aquatic reptiles. While remains of terrestrial fauna are vastly occurring, bone elements of aquatic reptiles are comparatively rare, often undescribed or only mentioned for the sake of completeness (HAGDORN et al. 2015, HAGDORN et al. 2015, SCHOCH 2002, SCHOCH 2015)

The first publication described herein introduces a newly discovered *Nothosaurus* species represented by a completely preserved skull which was discovered by the authors during an excavation in Vellberg-Eschenau in 2017. This find is of great importance due to the fact that it marks the first find of a nothosaur exclusively (HINZ et al. 2019) from the Lettenkeuper as well as the first discovery of a new *Nothosaurus* species from the Germanic Basin of southern Germany since the discovery of the Muschelkalk-only species *Nothosaurus jagisteus* RIEPPEL, 2001.

The second publication focuses on the description of a *Nothosaurus* occiput from Kupferzell and includes a revision of the specimen SMNS 80261 which was described as highly deformed *Batrachotomus kupferzellensis* occiput by GOWER (1999) and is reassigned to the taxon *Nothosaurus* now. This find represents the only *N. giganteus* from the Lettenkeuper not belonging to former *N. chelydrops* and shows a set of skull features resembling more closely the classical Muschelkalk morphotype of *N. giganteus* (HINZ et al. 2020).

This study focuses on the description of *Nothosaurus* material from the Lettenkeuper of Vellberg-Eschenau and Kupferzell to shed light on the diversity of this remarkable group of extinct marine reptiles in the challenging and changing environment of the drying up Germanic Basin.

The following text is based on the publications from HINZ ET AL. (2019) and HINZ ET AL. (2020). Short phrases, figure explanations, or sequences of a few words are sometimes identical due to the technical language used in paleontology in general and descriptive anatomy in particular.

6. A potential geographical origin of the Sauropterygia

6.1. Existing theories

The geographical origin of sauropterygians is still a subject of discussion (see Chapter 5). During the early Triassic Olenekian, sauropterygian taxa emerged at different locations along the northern coast of the Tethyan Sea (see Fig. 2). Finds of *Cymatosaurus erikae*, *Cymatosaurus erytheus*, and *Dactylosaurus gracilis* were made in modern day eastern Europe. At the same time, *Majiashanosaurus discocoracoidis*, *Hanosaurus hupehensis*, and probably *Kwangsisaurus orientalis* appeared in the eastern region of the Tethyan Sea in the area of the modern People's Republic of China. Simultaneously, the pistosaurid *Tanaisosaurus kalandadzei* appeared in modern day European Russia.

Due to the fact that all of this finds occur at the same time, different theories about the origin of sauropterygia are discussed (e.g., KLEIN 2010, STORRS 1991). For a long time, the two major ideas about the origin and radiation of the sauropterygians were:

(1) "Out of Europe" – Sauropterygia had their origin in the Germanic Basin in modern day Europe and migrated towards Asia along the northern coast of the Tethyan Sea or via island hopping along the equator.

(2) "Out of Asia" – the first sauropterygians occurred in Asia and migrated towards modern day Europe along the northern coast of the Tethyan Sea or via island hopping along the equator.

Island hopping along the equator was excluded from the theories due to very hot climates and resulting ocean temperatures of over 40°C at the equator during the Indusium (SUN et al. 2012) and early Olenekian. During this time, the ocean on the height of the equator was a hostile environment for vertebrates. During the late Olenekian, the ocean temperatures slightly decreased to a point where vertebrate life was possible above 30° northern and below 30° southern latitude. Because of that, a migration of sauropterygians along the coasts of islands along the equator (Fig. 2) can be dismissed as potential traveling route. Therefore, the only possible migratory route of sauropterygians is along the northern shores of the Tetyhan Sea.

A problem concerning both theories, "Out of Europe" as well as "Out of Asia", is the enormous traveling distance between the eastern and western region of the Tethyan province, which can’t explain the almost simultaneous appearance of sauropterygians in Asia and Europe and the simultaneous appearance of *Corosaurus alcovensis* in todays North America at the former coast of the Panthalassic Ocean.

6.2. “Out of Russia”

The find of the very early and primitive pistosaurid *Tanaisosaurus kalandadzei* in European Russia in 2001 (SENNIKOV 2001) brought up a new possible theory of the migration of Sauropterygia, “Out of Russia”, which points out that the origin of sauropterygians may lie in the central Tetyhan province, in a shallow basin in the region of nowadays Don Basin, Russia. From there, sauropterygians may have migrated westwards and eastwards along the shores of the Tethyan Sea until they reached the Germanic Basin and the eastern Tethyan province in the area of modern day China.

6.3. Materials and methods

For further testing the hypothesis of “Out of Russia”, a database containing all European, Asian, and Russian Sauropterygia was created with the goal of plotting the finds on a paleoglobe to visualize the spatial distrubution of sauropterygians through time. The novel database created for this purpose contains 938 sauropterygian finds from the orders of Pachypleurosauria and Nothosauroidea including their find location, geographic coordinates, and catalogue number.

For the creation of the paleoglobe, the freeware GPlates (MÜLLER ET AL. 2018), originally created for analyzing movements of tectonic plates through time, was used. For GPlates, a free set of paleo maps named PALEOMAP PaleoAtlas created by SCOTESE (2016) was used to visualize the paleogeography. PALEOMAP PaleoAtlas contains 91 maps from the Neoproterozoic to the Phanerozoic and allows scrolling forwards and backwards in time when loaded as time dependent files into GPlates.

In a next step it was attempted to plot the geographical coordinates from finds listed in the sauropterygian database on a new time dependent layer of the paleoglobe in order to allow moving the coordinates back and forth in time together with the paleomaps. For this purpose, a software called PaleoData Plotter SCOTESE (2016) was delivered with the PALEOMAP PaleoAtlas. This software can convert geographical coordinates given as table in the *.csv (comma separated values) format into the legacy PLATES data format, which can be imported into GPlates. It was written exclusively for Mac OS X and only an unstable version with limited functionality and a number of bugs was available, which was unable to properly convert the database of the sauropterygian finds.

In order to create a readable *.dat file in the PLATES database format, example *.dat files delivered with the PaleoData Plotter served as reference for reimplementing the conversion algorithm as a Python 3 script. Since Python interpreters are available for most modern operating systems, e.g., Microsoft Windows, this newly developed script can be used to transform any given *.csv file containing the necessary key variables for each given data point into a *.dat file readable in GPlates. Those necessary key variables are (1) URN: a unique identification number; (2) Label: a meaningful name; (3) PlateID: tectonic plate ID specified by the U.T. Institute for Geophysics, Austin, Texas, USA; (4) Latitude; (5) Longitude; (6) SymbolOrNumber: in which shape the data point should be drawn, e.g., “circle”, “square”, or “diamond”; (7) Size; (8) Azimuth.

The URN is a unique identification number, whereas the label should be a meaningful description of the data point. The PlateID can be chosen from a predefined list available at the website of the U.T. Institute for Geophysics, Austin, Texas, USA, but a standard value of 101 works as well. SymbolOrNumber and Size define in what shape and size the data point is drawn on the paleoglobe.

The Python script is easily extendable and it is planned to make it publicly available as an online tool for researchers to effortlessly transform find databases into a GPlates compatible file format.

6.4. Results, discussion, and conclusions

After importing the sauropterygian database in GPlates, the data showed a rapid increase of sauropterygians in the late Olenekian (see Fig. 4) and early Anisian (see Fig. 5), which populated the Germanic Basin from the east through the East Carpathian and Silesian-Moravian gates in the area of nowadays Poland (KOWAL-LINKA & BODZIOCH 2017). This fits well to the “Out of Russia” theory, because the shallow basin in which *Tanaisosaurus kalandadzei* dwelled was connected to the eastern gates leading into the Germanic Basin. Furthermore, the “Out of Russia” theory is supported by the find of the Olenekian *Corosaurus alcovensis* outside the Tethyan province in the Panthalassic Ocean. This find indicates that sauropterygians were able to migrate from the Tethyan Sea to the Panthalassic Ocean during the earliest time of sauropterygian evolution. DORÉ (1992) assumes a connection between the Tethyan Sea and the northern Boreal Ocean, which was directly linked to the Panthalassic Ocean. A northwards migration of one group of Sauropterygia from the basin in which *Tanaisosaurus kalandadzei* lived could therefore have been possible.

In contrast to “Out of Russia”, “Out of Europe” is not supported by the data, which show a migration of Sauropterygia into the Germanic Basin from the east and not out of the basin (see Figs. 4 and 5). The data support for “Out of Asia” is weak. Only three finds of Sauropterygia are known from the Olenekian of China, from which one, *Kwangsisaurus orientalis*, is of uncertain age and may also be from the Anisian (YOUNG, 1965). The two Chinese sauropterygians, which are definitely from the Olenekian, were found in central China (*Hanosaurus hupehensis*, Hubei Province) and eastern China (*Majiashanosaurus discocoracoidis,* Anhui Province*)*. No direct evidence for a migration direction can be derived from these two isolated finds, although later Chinese sauropterygians from the Anisian are mainly found in modern southern China and not as far north as their Olenekian ancestors (JIANG et al. 2005, LI & LIU 2020, LIU et al. 2014, LIU et al. 2011). Furthermore, the geographical distance between the eastern Tethyan province, the Germanic Basin, and the Panthalassic Ocean in the region of the modern central United States of America speak against an Asian origin on Sauropterygia.

The paleomaps provided by SCOTESE (2016) were made for displaying large-scale paleogeography and especially the positions of shallow marine areas remain unresolved. Therefore, the maps lack several basins including the Germanic Basin. This leads to some sauropterygian finds being seemingly located on dry land instead of coastal regions on the paleomap

It is therefore concluded that the “Out of Russia” hypothesis should be strongly taken into consideration as possible origin and starting point for the migration of sauropterygians. Hopefully, more, better, and clearly dateable finds of sauropterygian remains along the northern coasts of the Tethyan Ocean will help answering this question in the future.

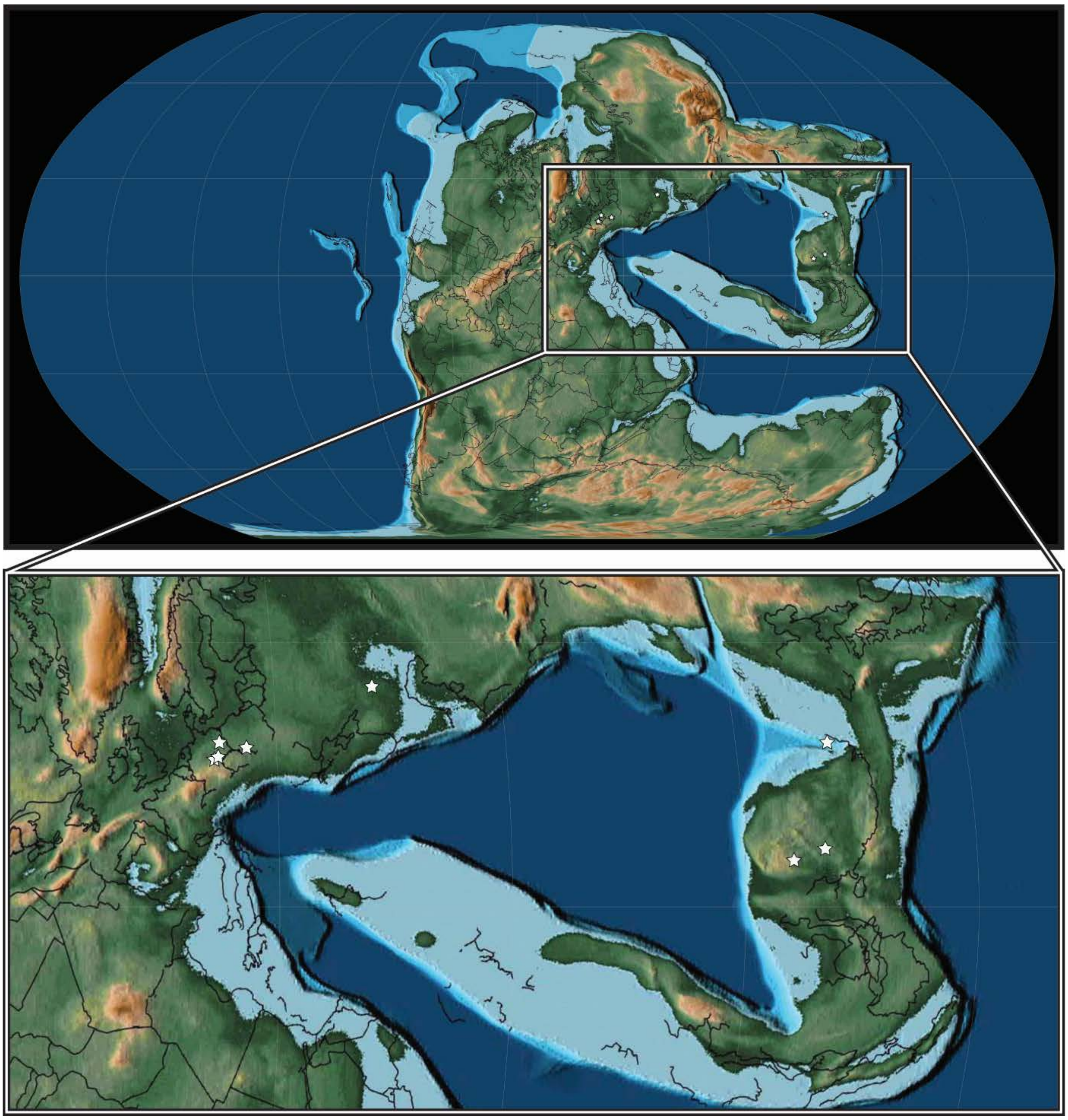


Figure 4: World map and enlarged detail map showing the paleogeography during the Olenekian (250 Ma). The black lines on the maps represent present-day borders. The maps were generated in GPlates 2.1. Stars mark the locations of sauropterygian finds from the database described in Chapter 6. In this map, each star represents one find location of sauropterygian remains. The finds in modern day Europe are all located at the eastern margin of the Germanic Basin, which is unfortunately not visualized in the map. Especially shallow marine areas are hard to incorporate into paleomaps and the displacement of shorelines and the missing basins are caused by the low resolution of the large-scale maps lacking precise information about regional geology and paleogeography, as discussed in Chapter 6.4.

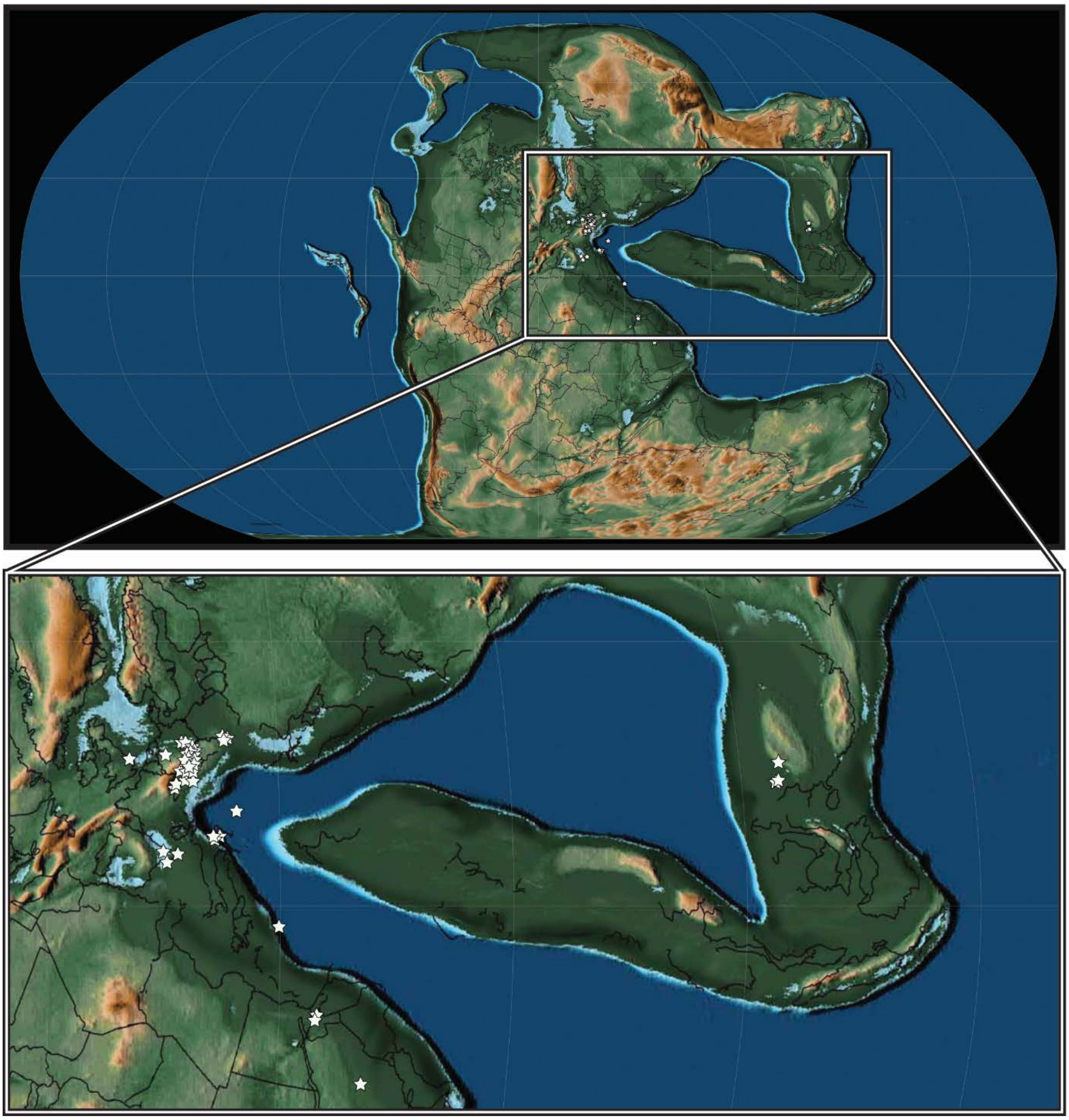


Figure 5: World map and enlarged detail map showing the paleogeography during the early Anisian (247 Ma). The black lines on the maps represent present-day borders. The maps were generated in GPlates 2.1. Stars mark the locations of sauropterygian finds from the database described in Chapter 6. In this map, each star represents one find location of sauropterygian remains. The find locations show that the sauropterygians in modern day Europe migrated westwards and southwards in the Germanic Basin, which is unfortunately not visualized in the map. After the opening of the Burgundy Gate, the sauropterygians inhabited the western coasts of the Tethyan Sea and migrated southwards until they crossed the equator and reached modern day Arabia. Especially shallow marine areas are hard to incorporate into paleomaps and the displacement of shorelines and the missing basins are caused by the low resolution of the large-scale maps lacking precise information about regional geology and paleogeography, as discussed in Chapter 6.4.

7. A new nothosaur (Sauropterygia) from the Ladinian of Vellberg-Eschenau, southern Germany

7.1. The history of Vellberg-Eschenau

In the region of Vellberg-Eschenau, Muschelkalk was and still is actively mined in quarries. Two quarries, Obersontheim-Ummenhofen and Schumann quarry, are still active. The work described herein refers to the Schumann quarry, in which amateur paleontologists, who focused on the Keuper sediments lying atop the Muschelkalk, began searching for fossils during the 1980s. Since 2000, regular scientific excavations are carried out by the SMNS. Additionally, the GPIT led two excavations in the Schumann quarry in the years 1998 and 2017 (Fig. 6). The continuous excavations, together with the helpful work of amateur paleontologists, led to the discovery of over 1000 fossils each year (SCHOCH & SEEGIS 2016) including several new reptile taxa (SCHOCH 1997, SCHOCH 2011, SCHOCH 2011, SCHOCH & SUES 2014, SCHOCH & SUES 2015). The continuity of excavations in the Schumann quarry allowed detailed stratigraphical analyses and provided information about rapidly occurring local changes in stratigraphy.

Figure 6: Panoramic view of Schumann quarry. The massive grey banks are Muschelkalk layers, the yellowish and dark grey sediments lying atop are Keuper sediments. The arrow marks the excavation site of 2017.

7.2. Stratigraphy

In the Schumann quarry sediments of the Muschelkalk and Keuper crop out. While the Muschelkalk is actively mined (e.g., for road building purposes), the overlying Keuper sediments are treated as overburden and are stripped off for Muschelkalk mining. In the following, the fossil-rich part of the Keuper sequence is described. Therefore, the description and nomenclature developed by SCHOCH (2002) is used.

The Keuper sediments of Vellberg-Eschenau belong to the Upper Lettenkeuper, Erfurt Formation (HAGDORN et al. 2015, SCHOCH 2002). The fossil-rich layers of the Upper Lettenkeuper sequence of Vellberg-Eschenau start with the Untere Graue Mergel, which can be subdivided into a series of well distinguishable strata (Fig. 7). Layer E1 has a thickness of 10-15 cm and consists of a sequence of brown siltstones, which fine up into dark mudstones. Locally, coal can be present in the mudstone. Besides shells of bivalves and gastropods, E1 contains rare remains of mastodonsaurs, plagiosaurs, and the stereospondyl *Callistomordax kugleri* SCHOCH, 2008. The following layer E2 is 1-3 cm thin and formed by unstratified mudstones of green color. Dolomitic concretions with diameters of a few millimeters are common. Sometimes a base layer of coaly clasts may be present (SCHOCH & SEEGIS 2016). The surfaces of the clasts are occasionally covered with shrinkage cracks, which are filled with green matrix. The layer contains fossil remains of algae, ostracods, fish scales, capitosaurs, and bystrowianid reptilomorphs. The top of E2 is undulated and formed by a dolomitic coquina named E3 or by E4, a layer formed by green siltstones. E3 sometimes forms a local facies within the siltstones of E4 and grows into the underlying layer E2 (see Fig. 7) by replacing the mudstones. The coquina contains remains of bivalves and ostracods. Thin bonebeds may occur at the top of E3. The siltstones of E4 are laminated and the color varies from green in the bottom part (E4a) over grey in the middle (E4b) to brown in the top part of the layer (E4c). Locally, yellow laminae, dry cracks (E4b), or thin layers of green claystone can be present. In the Schumann quarry, the thickness of E3 and E4 ranges between 15 cm and 40 cm. At the base of E4, bivalves, ostracods, and brachiopods are preserved in great numbers. Furthermore, remains of nothosaurs, plagiosaurs, and actinopterygians are common. Atop lies E5, a brown marly siltstone layer which forms no sharp boundary with E4. The sediments

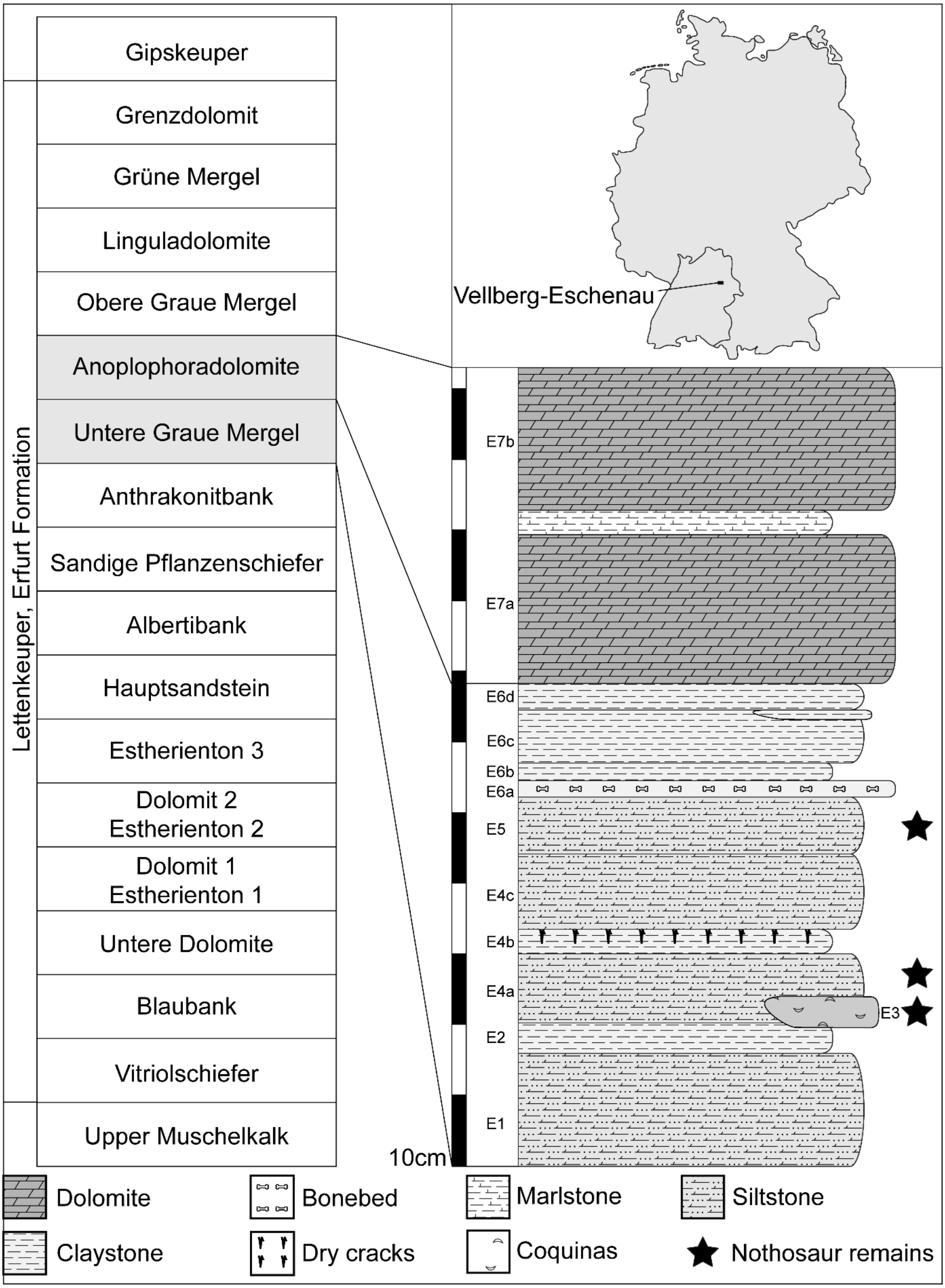


Figure 7: The location and stratigraphy of the find location Vellberg-Eschenau. The Untere Graue Mergel and Anoplophoradolomite are highlighted in grey because only these horizons contain fossils. Modified after S*CHOCH* *(2016)*

of E5 are rich in quartz silt and show a horizonal bedding. Fine embedded carbonate grains lead to an overall powdery texture of the sediments. The lower part of the layer contains large amounts of invertebrate fossils including ostracods and bivalve shell fragments, whereas the upper part of E5 comprises more vertebrate fossils. Here, remains of actinopterygians, dipnoi, capitosaurs, mastodonsaurs, plagiosaurs, stereospondyls, trematosaurs, archosaurs, and nothosaurs occur. The following layer E6a is a relatively thin bonebed with a maximum thickness of 1-2 cm. A barely consolidated clay matrix contains large amounts of fish scales and teeth, mainly from actinopterygians, as well as worn bone fragments, from mastodonsaurs and archosaurs. Atop lies the very thin and poorly stratified green claystone layer E6b, in which bivalve clusters, plant fragments, and isolated bone remains of actinopterygians, dipnoi, capitosaurs and mastodonsaurs were found. The following layer E6c is 10-15 cm thick and forms, together with E6d, the most fossil rich stratum at Vellberg-Eschenau. The base of E6c consists of remarkably dark grey claystones which may contain pyrite crystals or yellowish dolomite clasts, whereas the color gradates to light brown in the upper part of the stratum. The lower part of E6c comprises ostracods, conchostracans, gastropods, and well-preserved complete or almost complete skeletons of tetrapods, as well as fossil remains of actinopterygians and dipnoi. The upper part of E6c contains large amounts of isolated crushed bones, mostly from actinopterygians. Tetrapod finds are rare. The atop lying layer E6d has a thickness of only a few centimeters and consists of laminated mudstones with a high carbonate content. Skulls of mastodonsaurs and remains of *Batrachotomus kupferzellensis* GOWER, 1999 are abundant. The following starum E7 belongs to the Anoplophoradolomit and forms a 70-90 cm thick dolomite layer, which is separated into E7a and E7b by a grey marlstone layer of 3 cm thickness. The lower dolomite layer, E7a, contains well-preserved fossil remains of plagiosaurs, mastodonsaurs, and archosaurs. In contrast to that, E7b contains no fossils at all.

7.3. Paleoecology

The rapidly horizontally and vertically changing thicknesses of the sediment layers in Vellberg-Eschenau point towards a diverse swampy environment, in which brackish lagoons (E4), shallow lakes (E5), and deeper lakes with a potentially stagnating bottom zone (E6c) existed. The lagoon was inhabited by actinopterygians like *Saurichthys* AGASSIZ, 1834 and *Acrodus* AGASSIZ, 1838, a cartilaginous fish. *Nothosaurus* and

Plagiosternum granulosum FRAAS, 1889 roamed the lagoon as predators feeding on fish. The shallow lakes were also inhabited by a fish fauna formed by *Saurichthys* and other actinopterygians, whereas all known predators were of amphibian origin. Smaller amphibians like *Plagiosuchus pustuliferus* FRAAS, 1913, *Callistomordax kugleri* and *Trematolestes hagdorni* SCHOCH, 2006 were hunting in the lake for fish. The apex predator was *Mastodonsaurus giganteus* VON JÄGER, 1828, which presumably fed on the amphibians listed above. In the deep lakes, *Saurichthys*, other actinopterygians, and young dipnoi were a potential prey for *Callistomordax kugleri* and diapsid reptiles. The apex predator of these lakes was *Mastdonsaurus giganteus*, too. The swampy land surrounding the lakes was inhabited by the carnivorous archosaurian *Batrachotomus kupferzellensis*. The remarkable co-occurrence of marine and terrestrial taxa in the sediment layers of Vellberg-Eschenau can be explained by the presence of alternating shore and lake habitats caused by rises and falls of the sea level. Sea level lowstands led to more terrestrial sedimentation and remains of taxa like *Batrachotomus kupferzellensis* were deposited, whereas for example *Nothosaurus* inhabited the Vellberg-Eschenau lagoons during sea level highstands.

7.4. Materials and methods after HINZ ET AL. (2019)

Systematic paleontology:

Order EOSAUROPTERYGIA RIEPPEL, 1994
Suborder EUSAUROPTERYGIA TSCHANZ, 1989
Infraorder NOTHOSAUROIDEA BAUR, 1889 (in VON ZITTEL et al. 1889)
Superfamily NOTHOSAURIA BAUR, 1889 (in VON ZITTEL et al. 1889)
Family NOTHOSAURIDAE BAUR, 1889 (in VON ZITTEL et al. 1889)
Genus *NOTHOSAURUS* MÜNSTER, 1834
Nothosaurus cristatus, sp. nov.

Holotype: an almost complete skull catalogued as GPIT/RE/09800

Type locality: Schumann quarry, about 3 km southeast of Vellberg-Eschenau, Baden-Württemberg, Germany

Distribution: Middle Triassic (Ladinian), lower part of the Lower Keuper, Erfurt Formation, Lettenkeuper, Layer E5 of the Untere Graue Mergel. GPS coordinates: 49°04′26.9N and 9°54′15.6E (WGS84).

Diagnosis: A medium-sized *Nothosaurus* with a condylobasal length of 38.3 cm. Postorbital excluded from the orbit, jugal large and almost in contact with the orbit, pronounced sagittal crest on the parietal anterior to the parietal foramen, ectopterygoid with a long posterior reaching extension flanking the pterygoid.

Etymology: Named after the sharp sagittal crest which is unique among the genus *Nothosaurus*.

7.5. Description

The holotype skull described herein is dorsoventrally flattened. The overall shape of the ventral and dorsal skull surfaces is unaffected and therefore it was possible to take measurements of the skull (Tab. 1). The right side of the skull is slightly better preserved, except for the occiput. There, the left side of the skull is better preserved. The following description is a shortened version of the published description found in HINZ et al. (2019).

***N. cristatus* GPIT/RE/09800**	**in mm**
Condylobasal skull length	383,0
Distance from tip of premaxilla to naris left	87,3
Distance from tip of premaxilla to naris right	87,7
Maximum width of snout at premaxilla	44,7
Minimum width of snout at premaxilla	38,5
Naris width left	13,1
Naris width right	13,9
Naris length left	24,0
Naris length right	22,8
Smallest distance between nares	13,0
Orbit width left	26,5
Orbit width right	27,3
Orbit length left	35,4
Orbit length right	37,3
Smallest distance between both orbits	23,3
Distance between naris and orbit left	21,7
Distance between naris and orbit right	23,0
Distance between orbit and upper temporal fenestra left	39,0
Distance between orbit and upper temporal fenestra right	43,1
Maximum length of upper temporal fenestra left	135,9
Maximum length of upper temporal fenestra right	128,8
Width of upper temporal fenestra at anterior tip of parietal foramen left	49,5
Width of upper temporal fenestra at anterior tip of parietal foramen right	52,8
Width of parietal foramen	15,7
Length of parietal foramen	13,0
Maximum occipital skull width	162,3

Table 1:Measuring distances of the holotype skull of N. cristatus (GPIT/RE/09800), all measurements in mm.

The premaxilla is long, slender, and only weakly constricted. It holds alveoli for five premaxillary fangs. From these fangs, four are preserved on the left side and three on the right side. The maxilla forms the lateral rims of the external nares and orbits. In its anterior part, a remarkable sharp medial extension of the maxilla cuts between the nasal and the relatively small prefrontal and almost establishes a contact with the anteromedial rim of the orbit. Posteriorly, the maxilla excludes the jugal and the postorbital from the orbit. Each maxilla holds, from front to back, three small maxillary teeth, two enlarged maxillary fangs, and 21 maxillary teeth reaching as far back as the anterior rim of the upper temporal fenestra. In dorsal as well as in ventral view of the skull, rows of neurovascular foramina are visible in the snout region. An anterior reaching process of nasals form the medial margin of the external nares, which are of elongated oval shape. The nasals show remarkably straight sutures with the neighbouring maxillas. Posteriorly, the nasal closely approaches the orbit without establishing a direct contact (Fig. 8). The frontal is strongly sculpted and forms three anteromedial processes which contact the nasals. It widens posteriorly to the orbit and narrows again halfway between the orbit and the upper temporal fenestra forming an overall leaf shape. The orbits are shaped like an elongated oval and are slightly oblique with their long axis oriented in anteromedial-posterolateral direction. Anteriorly the fused parietals form two large processes intruding between the frontal and the postfrontal on each side of the skull. The anterior margin of the upper temporal fenestra is constricted. On the intertemporal skull roof, the parietal forms a strongly developed sagittal crest, which is triangular in cross-section. The crest splits directly in front of the large sub-rounded parietal foramen, encloses the foramen itself, and continues in a shallower but more sharp-edged form posterior to the foramen. A well-developed transverse occipital crest marks the transition between the occipital skull surface and the skull roof. The postfrontal has an overall elongated triangular shape and establishes a remarkably pointed contact with the maxilla. It does not contact the upper temporal fenestra. The jugals are long and taper posteriorly. The left jugal is preserved in situ, the right jugal is disarticulated and can be found on the ventral side of the skull. The jugals come close to the orbit but no direct contact is established. The postorbital

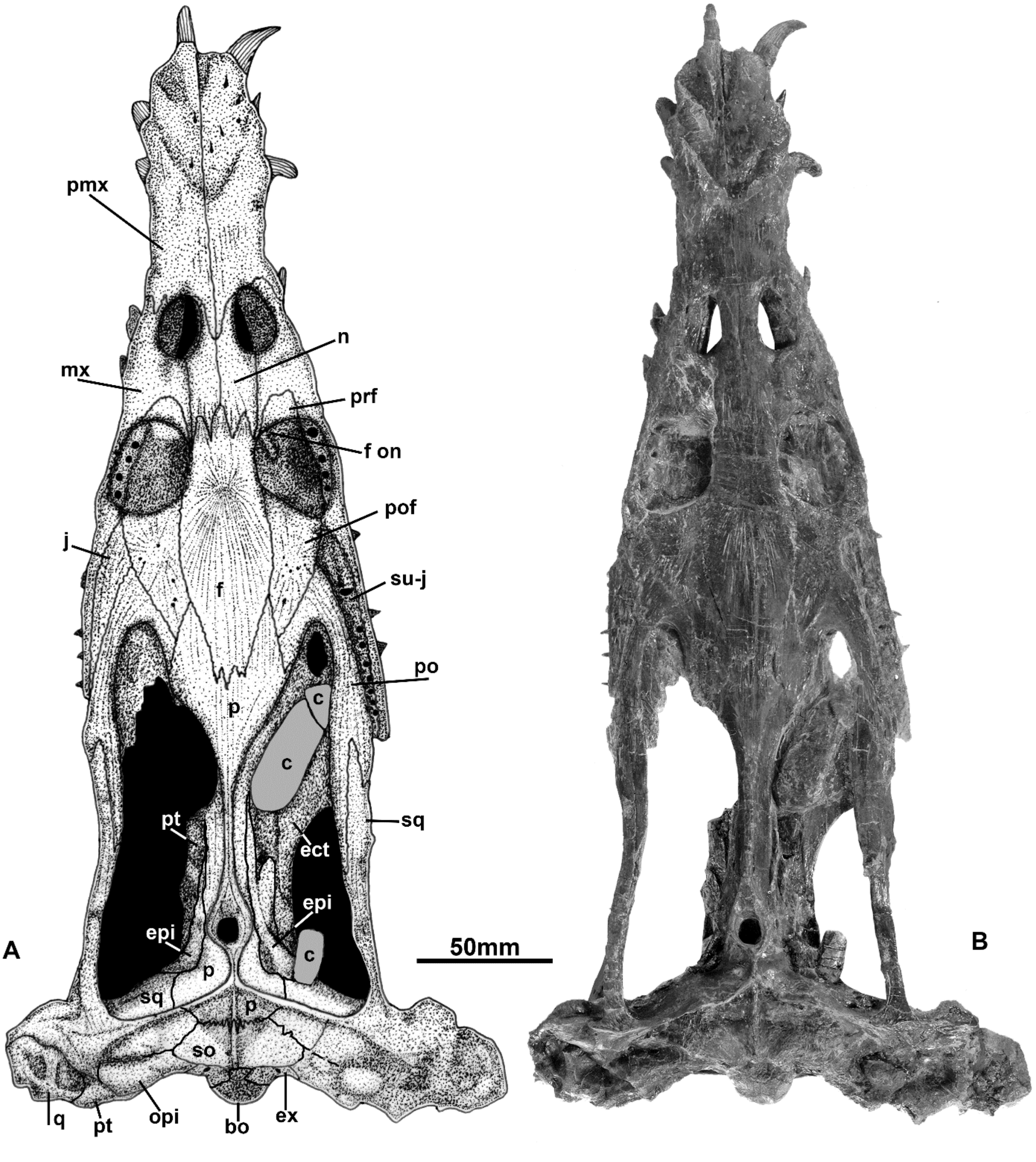


Figure 8: Nothosaurus cristatus*, sp. nov., GPIT/RE/09800, from the Lower Keuper of Germany. Drawing (A) and photograph (B) of the skull in dorsal view. Abbreviations: bo, basioccipital; c, coprolite; ect, ectopterygoid; epi, epipterygoid; ex, exoccipital; f, frontal; f on, orbitonasal foramen; j, jugal; mx, maxilla; n, nasal; opi, opisthotic; p, parietal; pmx, premaxilla, po, postorbital; pof, postfrontal; prf, prefrontal; pt, pterygoid; q, quadrate; so, supraoccipital; sq, squamosal; su-j, sutural facet for the jugal. Modified after Hinz et al. (2019).*

is completely excluded from the orbit, which is unique among nothosaurs. The postfrontal forms an anterior reaching triangular tip which contacts the postfrontal medially and the jugal laterally. Both squamosals are fully preserved and both zygomatic arches are therefore intact, which is rare among nothosaur finds. A long

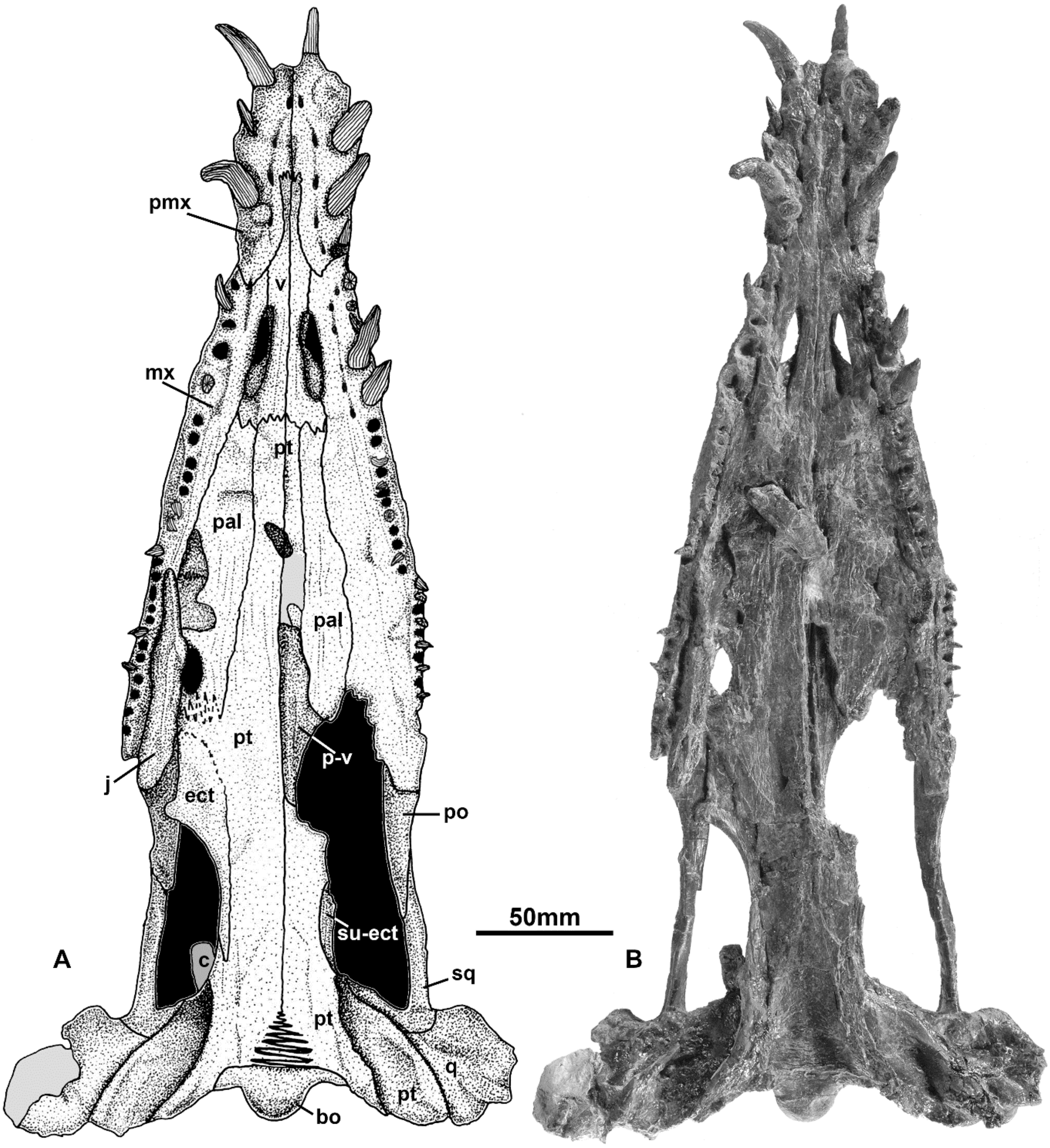


Figure 9: Nothosaurus cristatus, *sp. nov., GPIT/RE/09800, from the Lower Keuper of Germany. Drawing (A) and photograph (B) of the skull in ventral view. Abbreviations: bo, basioccipital; c, coprolite; ect, ectopterygoid; j, jugal; mx, maxilla; pal, palatine; pmx, premaxilla; po, postorbital; pt, pterygoid; p-v, parietal in ventral view; q, quadrate; sq, squamosal; su-ect, sutural facet for ectopterygoid; v, vomer. Modified after* HINZ ET AL *(2019).*

anteriorly directed process of the squamosal forms over half of the zygomatic arch, and posteriorly, the squamosal forms a bony plate, which creates the posterior margin of the upper temporal fenestra. A quadratojugal is not present.

On the ventral side of the skull (Fig. 9), the vomer divides the paired premaxillas halfway by a long anterior process with a strongly serrated suture. Only the right palatine is fully preserved. It is slender, long, and tapers towards the anterior end. It has no contact with the ectopterygoid. The pterygoids form the posteromedial margin of the subtemporal fenestra and are characterized by a strongly serrated median suture in the posteriormost 25 mm. The ridge-like ramus quadratus emerges in a 40-degree angle from a bony plate formed by the pterygoid. The right ectopterygoid is fully preserved. A strongly developed knob-like transversal process is located at the lateral margin of the ectopterygoid. Unique among nothosaurs, a slender posterior process of the ectopterygoid flanks the pterygoids, reaching as far back as two thirds of the length of the subtemporal fenestra (Fig. 9). This may be associated with the shape and massiveness of the sagittal crest by stabilizing the intertemporal skull against torsion during biting.

On the occiput (Fig. 8), both quadrates are preserved but the one on the right side is damaged due to diagenetic compression. The cranioquadrate passage is visible. The articular condyles are also visible and oriented in an angle of 30 degrees. The epipterygoids are very large, which is also possibly related to the strongly developed sagittal crest. In lateral view, the epipterygoid has an overall X-shaped appearance. The upper anterior ramus is massive, the lower anterior ramus is somewhat shorter and less pronounced in its shape. The upper posterior ramus is well developed, dorsoventrally flattened, and tapers off at the posterior margin of the upper temporal fenestra. The lower posterior ramus is weaker developed and runs parallel to the upper posterior ramus. The supraoccipital forms the major part of the occipital skull table and shows a sagittal ridge. In the rather small exoccipitals, both jugular foramens are visible. The knob-like occipital condyle is formed by the basioccipital. No prootics are visible. The left opisthotic is cylindrical and well preserved. The shape and position of the opisthotic causes an interlocking of the bones engaged in the occipital skull table.

7.6. Comparison

The skull of the newly discovered *Nothosaurus* species described herein was compared with all other valid nothosaurs from which well-preserved skulls are known. These were: (i) *Nothosaurus mirabilis* MÜNSTER, 1834, (ii) *Nothosaurus giganteus* MÜNSTER, 1834, (iii) *Nothosaurus marchicus* KOKEN, 1893, (iv) *Nothosaurus haasi* RIEPPEL et al., 1997, (v) *Nothosaurus tchernovi* HAAS, 1979, (vi) *Nothosaurus edingerae* SCHULTZE, 1970, (vii) *Nothosaurus yangjuanensis* JIANG et al., 2006, and

(viii) *Nothosaurus jagisteus* RIEPPEL, 2001. Furthermore, the lariosaurs (ix) *Lariosaurus juvenilis* EDINGER, 1921, (x) *Lariosaurus xingyiensis* LI & LIU, 2002, (xi) *Lariosaurus winkelhorsti* KLEIN & ALBERS, 2009, and (xii) *Lariosaurus youngi* LI & RIEPPEL, 2004 as well as the pistosaurs (xiii) *Wangosaurus brevirostris* MA et al., 2015, (xiv) *Augustasaurus hagdorni* SANDER et al., 1997, (xv) *Pistosaurus longaevus* VON MEYER, 1839, and (xvi) *Yunguisaurus liae* CHENG et al., 2006, were used for the comparison, too. Based on phylogenetic analyses, LIN et al. (2017) reassigned the previously existing taxa *Nothosaurus juvenilis*, *Nothosaurus winkelhorsti*, and *Nothosaurus young*i to the genus *Lariosaurus*. Due to this fact and the close relationship between nothosaurs and lariosaurs, the lariosaurs listed above were included in this comparison. The pistosaurs were added because they show either sagittal crests or interesting morphologies on their hyoids/ectopterygoids.

7.6.1. General shape of the skull

Nothosaurus species show a wide range of skull sizes ranging from a condylobasal length of 12.9 cm in *N. edingerae* (SMNS 59072) to an estimated over 70 cm in *N. giganteus* (SMNS 57074). With a condylobasal length of 38.3 cm, *N. cristatus* lies well within this range. All nothosaurs, including *N. cristatus*, show have a constricted premaxillary rostrum, which can be found anterior to the external nares. The specific manifestation of the constriction varies from none in *N. edingerae* (SCHULTZE 1970) to very pronounced in *N. yangjuanensis* (JIANG et al. 2006). Additionally, two rostral shapes can be found in nothosaurs: long rostrums with almost parallel lateral margins and typically very weak constrictions (*N. mirabilis*, *N. jagisteus*, *N. tchernovi*, see RIEPPEL & WILD (1996), RIEPPEL et al. (1997), and RIEPPEL (2001)) as well as spoon-shaped rostrums with a rounded to sub-rounded premaxilla and pronounced constrictions *(N. giganteus*, *N. marchicus*, *N. yangjuanensis*, see RIEPPEL & WILD (1996) and JIANG et al. (2006)) (HINZ ET AL. 2019). *N. haasi* is an exception: It shows a long and slender rostrum, which is, in contrast to the rostrums of the other long-snouted species listed above, nonparallel edged (RIEPPEL et al. 1997). The rostrum in *N. cristatus* is long, slender, shows parallel margins, and is very weakly constricted. It closely resembles the long-snouted species *N. mirabilis*, *N. jagisteus*, and *N. tchernovi*.

7.6.2. Tooth counts

In nothosaurs in general, the premaxilla holds four or five large anterograde fangs. The premaxilla of *Nothosaurus cristatus* has alveoli for five fangs, which is similar to all *N. jagisteus*, *N. marchicus*, *N. tchernovi*, *N. haasi*, and *N. mirabilis*. Therefore, *N. cristatus* is clearly distinguishable from *N. yangjuanensis*, *N. giganteus*, and *L. winkelhorsti*, which have only four fangs and one small premaxillary tooth. *L. youngi* probably also has four fangs (JI et al. 2014), but this is still a subject of discussion. Due to the state of preservation in *N. edingerae* and *L. juvenilis*, their tooth counts remain unclear.

7.6.3. The orbitonasal region

In *N. cristatus* as well as in all other nothosaurs species except *N. youngi* and *N. haasi*, the nasals form the inner (medial) margins of the nares. The nasals separate the premaxilla from the frontal in all nothosaurs and lariosaurs with the exception of *N. haasi*, one *N. mirabilis* skull (SMNS 13155, published in RIEPPEL & WILD (1996)), and one *N. giganteus* skull (SMNS 57047, also published in RIEPPEL & WILD (1996)). In these skulls, the nasals are separated by a contact established between the premaxilla and the frontal, which both form long and slender processes contacting each other and dividing the nasals along the midline suture. In *N. cristatus*, the lateral suture between the nasal and maxilla is parallel to the midline suture. *N. cristatus* shares this feature with *N. mirabilis* and *N. tchernovi*. In *L. juvenilis*, the suture is parallel in its anterior part but tapers towards the midline suture in the posterior part. In all other lariosaur and nothosaurs species, the nasals are either triangular or leaf-shaped and do not resemble the almost rectangular shape of the nasals seen in *N. cristatus* (Fig. 8).

The prefontals are half-moon shaped in *N. cristatus*. This prefrontal shape can also be found in some skulls of *N. mirabilis* (SMNS 13155 and SMF R-641, both published in published in RIEPPEL & WILD (1996)). Some nothosaurs and lariosaurs have large prefrontals (*N. yangjuanensis*, *N. marchicus*, and *L. juvenilis*), the rest has no prefrontals at all. Altogether, the shape and occurrence of prefrontals seems to be highly variable in nothosaurs.

7.6.4. The postorbital bridge

The length of the postorbital bridge strongly varies in nothosaurs. To further quantify this variation, the ratio of the maximum length of the postorbital bridge to the maximum orbitonasal length was calculated (PO-ratio). In *N. cristatus*, the postorbital bridge has a length of 40 mm and is therefore almost twice as long as the orbitonasal bridge (21 mm). This leads to a PO-ratio of 1.9, which is a remarkably high value (HINZ ET AL. 2019). Comparable values can only be found in one *N. giganteus* skull (PO-ratio 2.4 found in SMNS 7162) and one *N. mirabilis* skull (PO-ratio of 1.5 in SMNS 56286). All other nothosaurs show significantly lower PO-ratios of around 1, e.g. 0.83 in *N. mirabilis* (SMNS 57047), 0.94 in *N. tchernovi* (HUJ-Pal. 3665, published in RIEPPEL & WILD (1996)), and 1.0 in *N. giganteus* (SMF R-475, published in RIEPPEL & WILD (1996)). PO-ratios significantly below 1 can be found for example in *N. edingerae* (0.42 in SMNS 59072) and *N. haasi* (0.5 in HUJ-Pal. 2550, published in RIEPPEL & WILD (1996)).

The postfrontal of *N. cristatus* is large and unconstricted. Only *N. mirabilis*, *N. jagisteus*, and some *N. marchicus* share this feature. All other nothosaurs and lariosaurs show a prominent lateral constriction of the postfrontal, which may vary in its position on the lateral margin of the postfrontal. In *N.cristatus*, the postorbital is completely excluded from the orbit. This is unique among all other known nothosaurs and can therefore be treated as autapomorphy.

7.6.5. The sagittal crest and the location of the parietal foramen

The parietal of *N. cristatus* forms a sharp sagittal crest anterior and posterior to the parietal foramen, while all other nothosaurs known until today have a flat and table-like parietal skull table anterior to the parietal foramen. So far, a sagittal crest posterior to the parietal foramen is only known from *N. edingerae* and now from *N. cristatus* (HINZ ET AL. 2019). In pistosaurs, sagittal crests are more common (e.g., in *Augustasaurus hagdorni*, *Pistosaurus longaevus*, and *Yunguisaurus liae*), but unlike in nothosaurs, the parietal foramen is located close to the anterior end of the upper temporal fenestra. Therefore, the sagittal crest is always located posterior to the parietal foramen (HINZ ET AL. 2019). In contrast to the pistosaurs mentioned above, *Wangosaurus brevirostris*, discovered in 2015 and described by MA et al. (2015), has a posteriorly lying parietal foramen and a sagittal crest anterior and posterior to the parietal foramen, silimar to the state preserved in *N. cristatus*.

7.6.6. The vomer

In *N. cristatus*, an elongated and slim anteromedial process formed by the vomer divides half of the palatal part of the premaxillas. The process ends in a strongly serrated suture between the third and fourth premaxillary fang. A similar process can be found in all *N. mirabilis*, and *N. haasi*. This shape of the vomer is bound to long-snouted nothosaurs. This can unfortunately not be verified for all known *N. jagisteus* and the holotype of *N. tchernovi*, in which the articulated lower jaw overlies the area of interest. Nothosaurs with rather round or spoon-shaped snouts like *N. giganteus*, *N. edingerae*, *N. marchicus*, and *N. yangjuanensis* have rather short vomers which lack the slender anterior reaching process.

7.6.7. The ectopterygoid and hyoid

An autapomorphy in *N. cristatus* is a far posteriorly extending process of the ectopterygoid which flanks the pterygoid in the intertemporal skull region. The complete ectopterygoid is only preserved on the right side of the skull, while it is broken off on the left side of the skull. There, a remarkably large facet for the ectopterygoid can be found on the pterygoid. In *L. xingyiensis*, *L. youngi*, and *Yunguisaurus liae*, hyoids, which are not sutured to the pterygoids, are preserved at a similar location and orientation. Although this might roughly look like the same shape, it has nothing to do with the state preserved in *N. cristatus*, which is therefore, in this regard, unique among all known nothosaurs, lariosaurs and pistosaurs.

7.7. Phylogeny

A phylogenetic analysis of *N. cristatus* was performed in order to assess its phylogenetic relationship to other nothosaurs. For this, PAUP 4.0 b10 (SWOFFORD 2002) and, for further verification, PAUP version 4.0 a164 (SWOFFORD 2018) were used. Both versions of PAUP generated identical results. The phylogenetic analysis was based on the character data matrix originally published by LIU et al. (2014) and later updated by LIN et al. (2017), who updated the characters 2, 32, and 67, and applied changes to the original codings. The changes of LIN et al. (2017) mainly affected *L. youngi* and *L. xingyiensis* due to the fact that *L. xingyiensis* was within the scope of their work and new results, which came up during their research, led to necessary changes in the matrix. A re-evaluation of all stated characters in the matrices of LIU et al. (2014) and LIN et al. (2017) led to the correction of some incorrectly coded characters and the identification of two pairs of correlated characters (see chapter 13.2). Furthermore, *N. zhangi* LIU et al., 2014 was excluded from the matrix because only 12 of 74 characters can be coded. The changes resulted in a data matrix containing 23 taxa and 72 characters (see chapter 14). Using PAUP, a heuristic search was performed (ADDSEQ = RANDOM, NREPS = 1000, HOLD = 100) (HINZ ET AL. 2019). All characters were treated as equally weighted and unordered. Furthermore, all characters were parsimony-informative. This resulted in a single parsimonous tree (Fig. 10) with a retention index (RI) of 0.53, a consistency index (CI) of 0.389, and a tree length of 216. As also suggested by its osteology, *N. cristatus lies* within the group of long-snouted nothosaur taxa, which form a monophyletic clade, in which *N. jagisteus* is a sister taxon to (*N. cristatus* (*N. tchernovi*, *N. mirabilis*)). An attempt to add *Wangosaurus brevirostris* to this phylogenetic analysis was made in order to clarify its position within the phylogenetic tree. This led to a tree without resolution and therefore marked *Wangosaurus* as a rogue taxon within the studied nothosaurs and lariosaurs.

Despite the fact that earlier works suggest a monophyly of the genera *Nothosaurus* and *Lariosaurus* (E.G. CHENG et al. 2012, JIANG et al. 2014, LIU et al. 2011, MA et al. 2015, RIEPPEL & WILD 1996, SATO et al. 2010, SATO et al. 2014, SATO et al. 2013, WU et al. 2011), this is not supported by the phylogeny performed herein. This could be an artifact of the combination of two phylogenies on species level originally created by RIEPPEL et al. (1997) and RIEPPEL (2001), which separately studied *Lariosaurus* and *Nothosaurus* and which were mixed together for the creation of the matrix published by LIU et al. (2014). In this new matrix, LIU et al. (2014) also removed outgroups and derived taxa like *Pistosaurus* and *Cymatosaurus*. The monophyly of *Lariosaurus* and *Nothosaurus* will therefore remain a point of further discussion.

7.8. Discussion and conclusions

The newly discovered *N. cristatus* shows all autapomorphies described for the genus *Nothosaurus* published in RIEPPEL (2000). Additionally, *N. cristatus* shows a set of derived characters within the genus *Nothosaurus*, such as an almost parallel-edged long and slender rostrum, slender longitudinal oval external nares, a maxillary tooth row extending far posteriorly, and a parietal foramen located far posterior on the parietal skull table. These characteristics closely link *N. cristatus* to *N. mirabilis*, *N.*

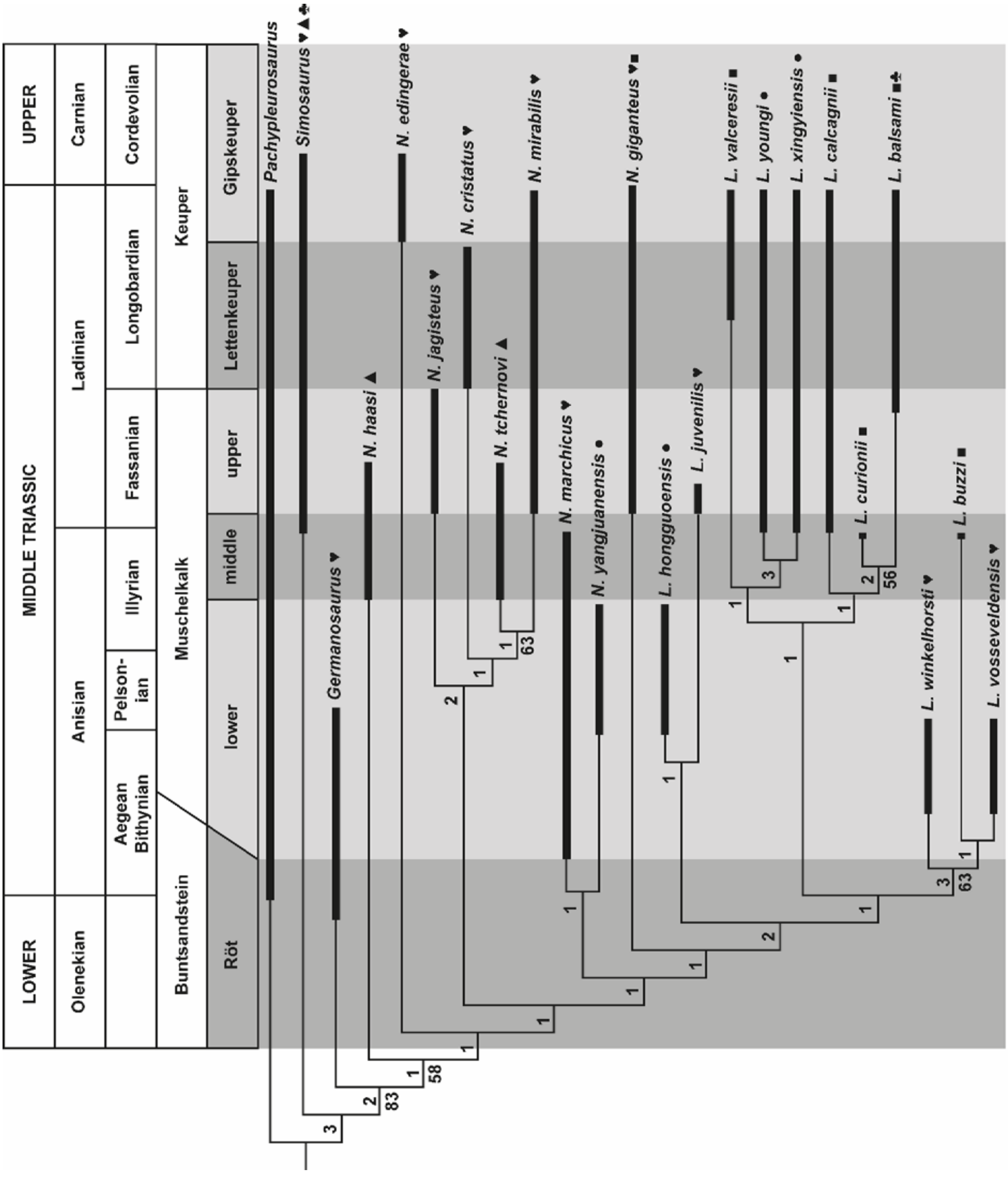


Figure 10: Strict consensus tree indicating the phylogenetic relationship of Nothosaurus cristatus, sp. nov., with other nothosaurids and lariosaurids. See text for tree statistics. Abbreviations: ♥, Germanic Basin; ▲, Middle East, Israel; ■, Monte San Giorgio; ♣, France, Spain; ●, East Asia, China. Modified after HINZ ET AL. (2019).

tchernovi, and *N. jagisteus*. What differs *N. cristatus* from the aforementioned other nothosaurs, is a set of three autapomorphies:

1. The postorbital is completely excluded from the orbit. Instead of the postorbital, the maxilla and the postfrontal meet behind the orbit and form the posterior margin of the orbit.
2. A pronounced sagittal crest anterior and posterior to the parietal foramen is formed by the parietal.
3. The ectopterygoid forms a far posterior reaching extension flanking the pterygoid.

The phylogenetic analysis pointed out that *N. cristatus* is a sister taxon of *N. mirabilis* and *N. tchernovi*, and that these three taxa form a clade together with *N. jagisteus*. The most conspicuous feature of *N. cristatus* is the strongly developed sagittal crest. Except *N. cristatus*, only *N. edingerae* shows a sagittal crest posterior to the parietal foramen but none anterior to the foramen. Interestingly, a sagittal crest is more common in pistosaurs but, in contrast to nothosaurs, their parietal foramen lies far anterior. In *Augustasaurus hagdorni*, the parietal foramen lies close to the suture between the frontal and the parietal. In *Yunguisaurus liae*, the foramen is located even farther anterior. Its anterior half is formed by the frontal and its posterior half by the parietal. In *Augustasaurus* as well as in *Yunguisaurus*, the sagittal crest lies posterior to the parietal foramen. Unlike other pistosaurs, *Wangosaurus brevirostris*, discovered by MA et al. (2015) in China, has a far posterior lying parietal foramen, which is located close to the posterior end of the parietal skull table. Interestingly, *Wangosaurus* has pronounced sagittal crests anterior as well as posterior to the parietal foramen, which makes its parietal skull table morphologically similar to *N. cristatus*. In contrast to the similarities mentioned before, the occipital skull region of *Wangosaurus* differs from the one found in any other pistosaurs and *N. cristatus but* resembles more closely the occiputs of other nothosaurs like *N. yangjuanensis*, *N. marchicus*, and *N. giganteus*. Further examinations are needed to clarify the affinity of *Wangosaurus* and to check if it really is a pistosaur or more closely related to the nothosaurs. All nothosaurs have a closed palate, in contrast to pistosaurs, which have a posteriorly open palate. Unfortunately, only the dorsal side of the skull of *Wangosaurus* is prepared and therefore it cannot be verified if *Wangosaurus* is truly a pistosaurid or probably a closer relative of nothosaurs. A re-examination of the type specimen, including the preparation of the ventral side of the skull and an improvised character scoring for a phylogenetic analysis, are inevitable.

From what is known until now, *N. cristatus* and *N. edingerae* remain the only nothosaurs exlusively known from the Keuper of the Germanic Basin and the only crested nothosaurs. More articulated specimens or new finds of cranial material will hopefully improve our knowledge of Keuper nothosaurs in the future.

8. A *Nothosaurus* (Sauropterygia) skull from Kupferzell (Triassic, late Ladinian; SW Germany)

8.1. The history of Kupferzell

During the construction of a new section of the Autobahn A6 (highway 6) between Heilbronn and Nuremberg in 1977, close to the junction Kupferzell, an amateur paleontologist named Georg Wegele discovered several well-preserved vertebrae while prospecting a weathered cut at the embankment alongside the newly built roadbed. The finds were presented to paleontologists at the Natural History Museum of Stuttgart (SMNS) who identified the remains as *Mastodonsaurus giganteus* VON JÄGER, 1828. A rescue excavation was launched and within two months, over 30000 fossils were recovered (MUNDLOS & WEGELE 1978, SCHOCH 2006). Due to the time pressure, neither find drawings, nor sedimentological analyses or high-resolution stratigraphy were made (HAGDORN et al. 2015).

8.2. Stratigraphy

The Kupferzell lagerstätte belongs to the Upper Lettenkeuper, Erfurt Formation (BRUNNER 1977, HAGDORN et al. 2015, HINZ et al. 2020, URLICHS 1982). The Upper Lettenkeuper sequence of Kupferzell starts with the Anthrakonitbank, a massive dolomite layer of 0.4 to 0.6 m thickness, which is topped by a fine-layered rippled limestone. In the Kupferzell region, the Anthrakonitbank contains a bonebed consisting of fish remains, coprolites, plagiosaur and mastodonsaur remains, and rare finds of nothosaurs (URLICHS 1982). The following lower part of Untere Graue Mergel consists of green to grey marlstones with a top layer of dark yellow to olive green color. In the upper third, a dark clay horizon containing a bank of clay-rich coal as well as plant remains occurs. Atop lies a siltstone layer containing red hematite concretions. Channels of around 0.2 m depth and 3 to 5 m width running in N-S direction are deepened into the surface of the siltstone. The channels worked as traps for vertebrate remains (HAGDORN et al. 2015, WILD 1980). The following green marlstones contain plagiosaur remains as well as rare mastodonsaur and thecodont finds. A layer of brownish marlstones with mastodonsaur and plagiosaur bones lies atop the green layer. Between these vertebrate rich layers, dry cracks filled with sediments of the upper brownish layer occur (WILD 1987). The upper half of the upper layer bears carbonate nodules containing nothosaur remains (SCHOCH 1999, URLICHS 1982) (Fig.

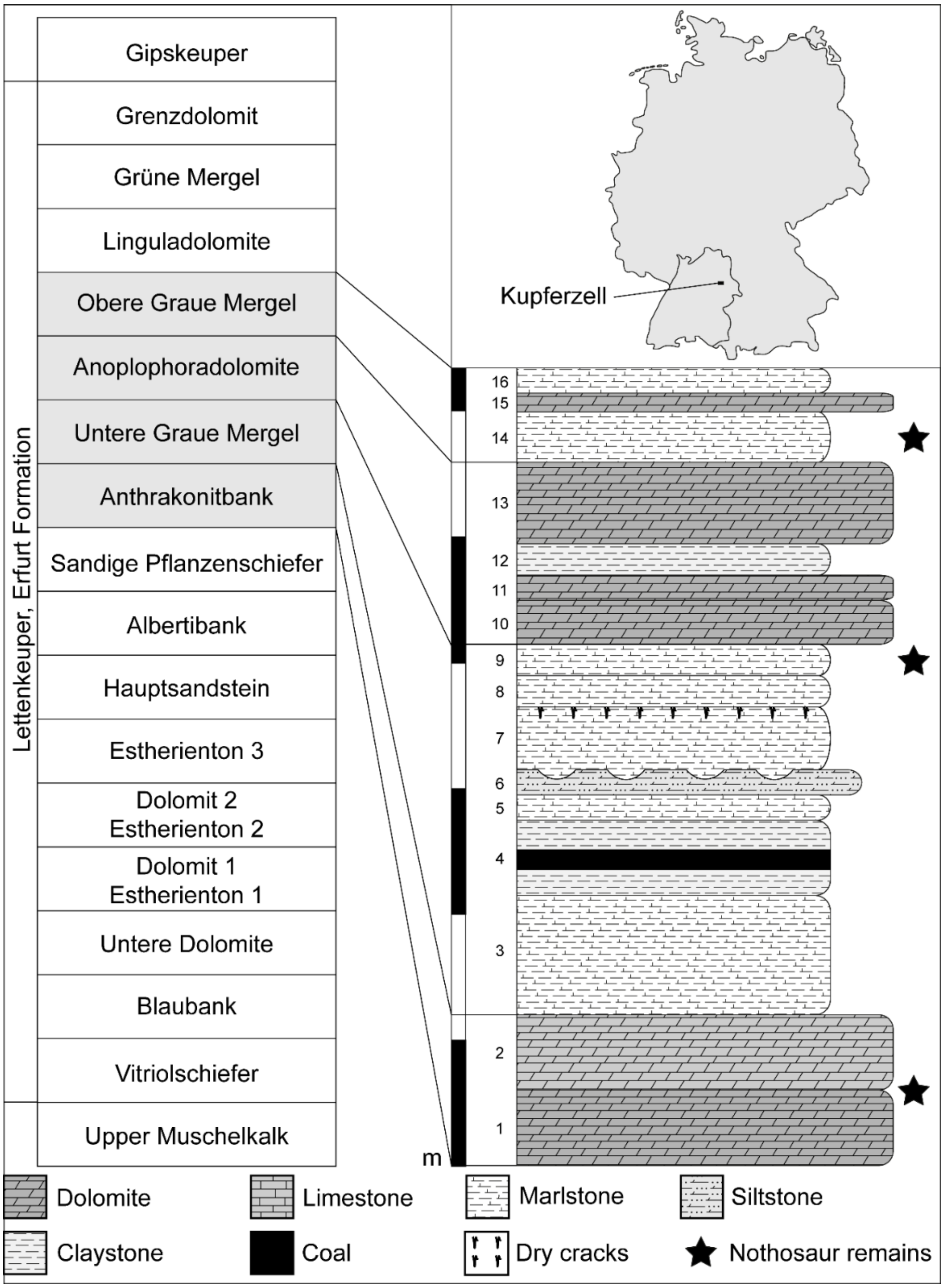


Figure 11: Stratigraphy and location of the Kupferzell site with a short description of all layers after URLICHS (1982) and HAGDORN et al. (2015). The Anthrakonitbank consists of a massive dolomite layer (1) which is followed by a limestone (2). The base of the following Untere Graue Mergel sequence is formed by a green to grey marlstone (3) which is topped by a coal-rich claystone (4). Atop lies a grey marlstone layer (5), which is followed by a brown siltstone (6) containing red hematite concretions and erosion channels in its uppermost part. The following green marlstones (7) with dry cracks are topped by a yellow dolomitic marlstone (8) and an ochre brown marlstone (9), which represents the uppermost part of the Untere Graue Mergel. The following Anoplophoradolomit sequence yields massive dolomite layers (10, 11), between which lies an only a few centimeters thin clay and marlstone layer separating the two massive dolomite banks. Atop lies a claystone layer (12), followed by a heavily eroded dolomite layer (13). The Obere Graue Mergel consist of light violet to grey marlstones (14, 16) with an interbedded dolomite layer (15). Modified after HINZ ET AL. (2020).

11). Besides the vertebrate remains, one specimen of the bivalve *Unionites brevis* VON SCHAUROTH, 1857, remains of charophyte algae, and ostracods were found within the sediments (URLICHS 1982). Atop the Untere Graue Mergel lies the Anoplophoradolomit, which consists of interbedding layers of dolomite, marlstones, and claystones. One specimen of *Unionites brevis* was recovered from the Anoplophoradolomit at the excavation site of Kupferzell. The following relatively thin Obere Graue Mergel consist of light grey to light violet marlstones. A bonebed within this layer contains nothosaur vertebrae as well as rare finds of mastodonsaurs, thecodonts, and plagiosaurs. In earlier stratigraphic approaches, the Obere Graue Mergel weren't treated as separate layers but were counted as one layer together with the Anoplophoradolomit and the Linguladolomit. This resulted in a confusion of the Untere and Obere Graue Mergel in earlier works (HAGDORN 1980, WILD 1987). See Fig. 11.

8.3. Paleoecology

The Lettenkeuper ecosystem of the Kupferzell region is construed as landscape formed by shallow and deep lakes housing amphibians like *Gerrothorax pulcherrimus* FRAAS 1913, *Kupferzellia wildi* SCHOCH, 1997, *Mastodonsaurus giganteus*, and *Plagiosuchus pustuliferus*. A hinterland consisting of swamps and marshes, from which the agile predatory reptile *Batrachotomus kupferzellensis* (GOWER 1999) is preserved, surrounded the lakes. River floods and storms concentrated the fossil remains in channels, leading to an extremely high density of bones and bone fragments at Kupferzell (HAGDORN et al. 2015, HINZ et al. 2020). The abundance of river channels transporting and accumulating vertebrate remains is also supported by the rapidly horizontally decreasing number of finds at the find location as well as by the enormous amount of isolated bones found at the locality. Besides the terrestrial deposits, the sedimentation of dolomites and the occurrence of scarce nothosaur remains (URLICHS 1982) indicate frequent marine intercalations during the Lettenkeuper.

Besides isolated bones, complete skulls, and rare semi-articulated and disarticulated skeletons of *Mastodonsaurus*, *Gerrothorax*, and *Batrachotomus kupferzellensis*, an occiput and postcranial material of one nothosaur were found during the excavation (HAGDORN et al. 2015) in Kupferzell. WILD (1980) estimated that 70% of all fossil remains belong to *Gerrothorax*, and 20% to *Mastodonsaurus*. Although this might be biased because preferably larger remains like skulls and scapulae were preparated, it still shows that other vertebrate genera are not very abundant in the Kupferzell Lagerstätte. A second counting of the prepared and the unprepared vertebrate fossils substantiated the estimation and showed a ratio of 3:1 (*Gerrothorax*:*Mastodonsaurus*) (HAGDORN et al. 2015). The rarity of nothosaur finds from Kupferzell is underlined by the fact that from 30000 fossils recovered during the rescue excavation, only 69 isolated postcranial bones, bone fragments, and one occiput belong to nothosaurs (pers.obs.).

8.4. Materials and methods after (HINZ ET AL. 2020)

Referred material: a crushed occiput catalogued as SMNS 80261

Remark: GOWER (1999, 2002) , and GOWER & SCHOCH (2009) referred to this specimen to *Batrachotomus kupferzellensis*

Diagnosis: A combination of characteristic cranial features including a crested supraoccipital, a large condyle, a large opisthotic, a closed posteriormost palate, and a far posterior lying parietal foramen represents bone topology typical for nothosaurs.

As a result of the preservation, diagnostic features of the viscerocranium remain uncertain.

Systematic paleontology:

Order EOSAUROPTERYGIA RIEPPEL, 1994
Suborder EUSAUROPTERYGIA TSCHANZ, 1989
Infraorder NOTHOSAUROIDEA BAUR, 1889 (in VON ZITTEL et al. 1889)
Superfamily NOTHOSAURIA BAUR, 1889 (in VON ZITTEL et al. 1889)
Family NOTHOSAURIDAE BAUR, 1889 (in VON ZITTEL et al. 1889)
Genus *NOTHOSAURUS* MÜNSTER, 1834
Nothosaurus giganteus MÜNSTER, 1834

8.5. Description and comparison

The occiput described in this work is strongly dorsoventrally compressed, underwent taphonomic distortion and only the skull posterior to the parietal foramen is preserved (see Figs 12 and 13).

The maximum skull width of SMNS 80261 is 18.8 cm. Unfortunately, the condylobasal skull length is not preserved and had to be estimated for size comparison with other nothosaurs skulls. Two skulls of similar proportions were used for this estimation: *Nothosaurus cristatus*, catalogued under GPIT/RE/09800, published by HINZ et al. (2019), has a maximum skull width of 16.23 cm and a condylobasal length of 38.3 cm, and *Nothosaurus mirabilis* catalogued under SMNS 56286, which has a maximum skull width of 21 cm and a condylobasal length of 43.4 cm. This led to an estimated condylobasal skull length of approximately 40 cm in SMNS 80261. To further quantify the skull proportions of the Kupferzell skull and other nothosaurs, a new parameter, the PFPS-ratio was introduced. For this, the length of the skull table posterior to the parietal foramen and the maximum skull width were put into ratio. The skull described herein (SMNS 80261) has a PFPS-ratio of 0.09.

The following description is a shortened version of the published description found in HINZ et al. (2020).

The Kupferzell skull has fused parietals enclosing an oval parietal foramen with a length-to-width ratio of 2.2. Sagittal crests anterior and posterior to the parietal foramen are absent in the intertemporal skull region, but a small crest is visible on the parietal portion of the occipital skull table (Fig. 12). The anterior parts of the squamosals are missing. The preserved posterior parts of the squamosals are remarkably bulky in their appearance and bend inwards. Only the posterior margin of the upper temporal fenestra is preserved. The margin is anteromedially-posterolaterally bevelled in an acute angle of 40 degrees. The pterygoids show a nothosaur-typical strongly serrated suture in the posteriormost 4.4 cm (Fig. 13). In contrast to the missing quadratojugals, the quadrates are preserved on both sides of the skull. On the occipital skull table, the remarkably large supraoccipital displays a sagittal ridge. Together with the

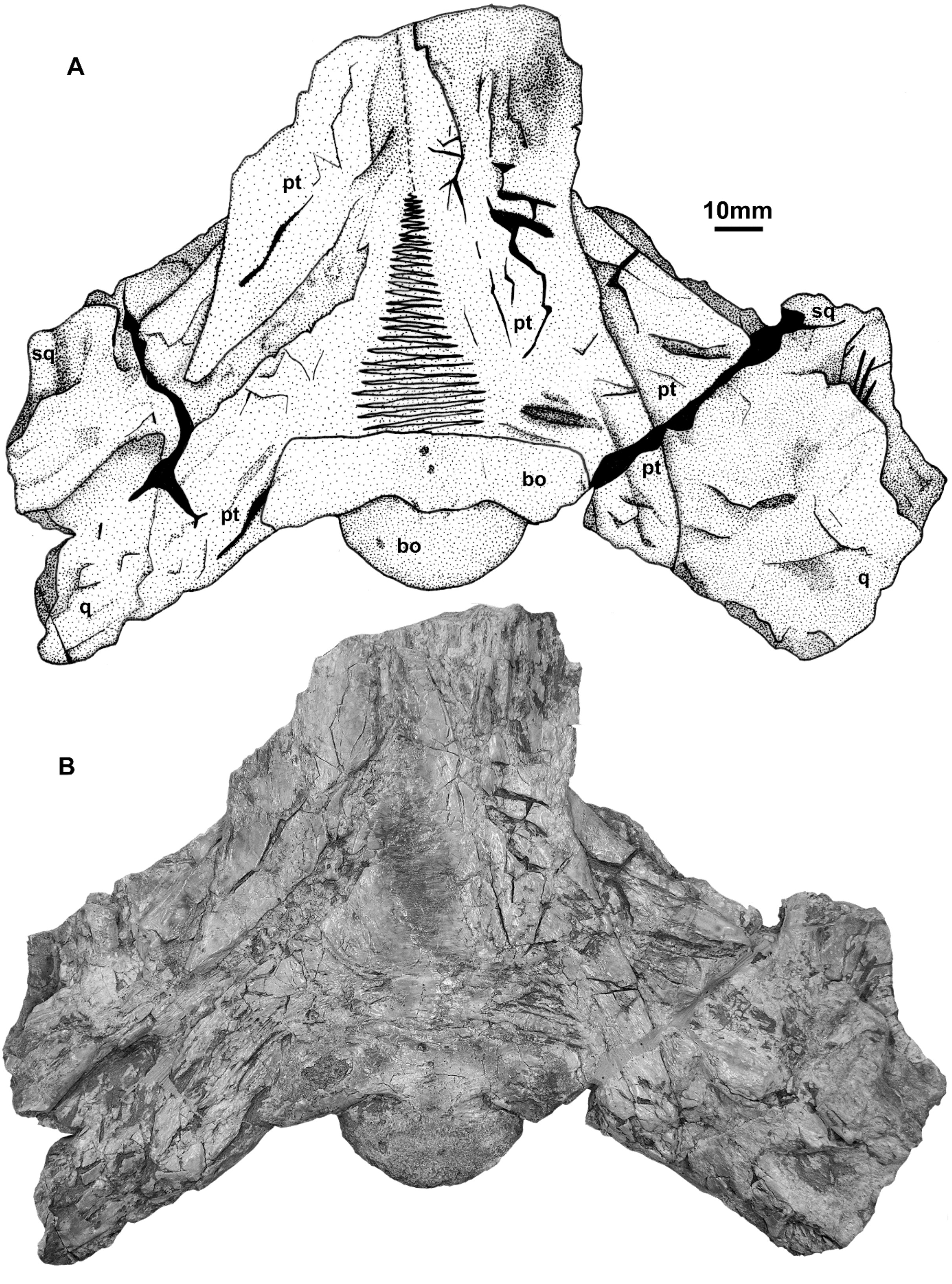


Figure 12: The skull of Nothosaurus giganteus *SMNS 80261 from the Lettenkeuper (Erfurt Formation, Late Ladinian). Skull in dorsal view. A: drawing, B: photograph, Abbreviations: bo = basioccipital, ex = exoccipital, fju = jugular foramen, opi = opisthotic, p = parietal, q = quadrate, so = supraoccipital, soc = supraoccipital crest, sq = squamosal. Modified after HINZ ET AL. (2020), so = supraoccipital, soc = supraoccipital crest, sq = squamosal. Modified after HINZ ET AL. (2020).*

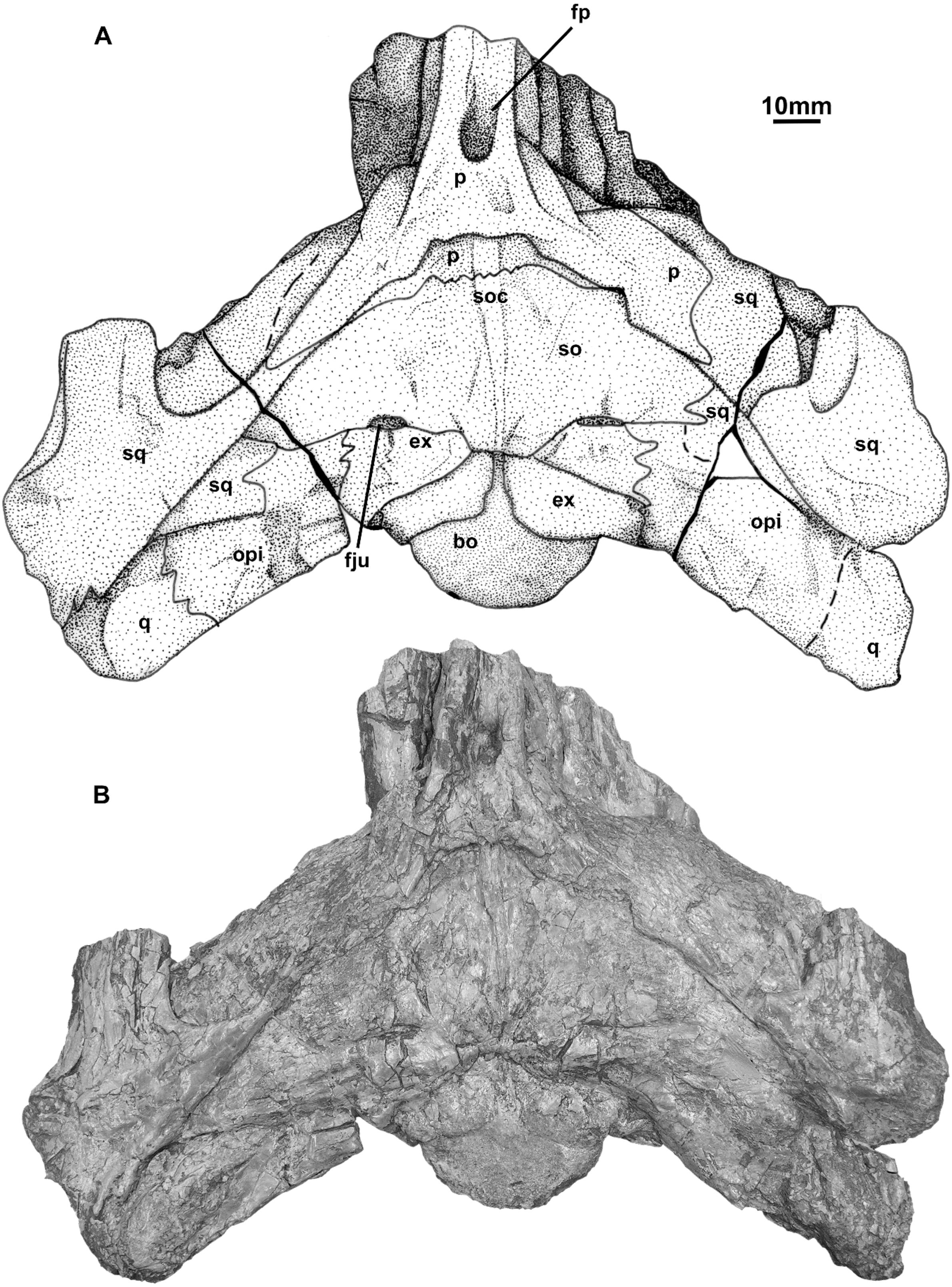


Figure 13: The Kupferzell skull of Nothosaurus giganteus *SMNS 80261 from the Lettenkeuper (Erfurt Formation, Late Ladinian). Skull in ventral view. A: drawing, B: photograph, Abbreviations: bo = basioccipital, pt = pterygoid, q = quadrate, sq = squamosal. Modified after Hinz et al. (2020).*

supraoccipital, the exoccipitals embed the jugular foramens and form the dorsal and lateral margin of the foramen magnum. The ventral rim of the foramen magnum is shaped by the basioccipital, which also forms the strongly flattened condyle (Figs. 12-13). The large opisthotics are preserved on both sides of the skull. They contact the quadrates, the squamosals, the supraoccipital, and the exoccipitals by forming strongly serrated sutures. This causes a massive interlocking of the bones involved in the occipital skull region.

For species identification, SMNS 80261 was compared to occiputs of other nothosaurs from the Germanic Basin. Only nothosaurs from the Upper Muschelkalk (Lower Ladinian) and Keuper (Middle to Upper Ladinian) were used for this comparison: *N. jagisteus* RIEPPEL, 2001 is only known from the Upper Muschelkalk, *N. giganteus* MÜNSTER, 1834, and *N. mirabilis*, MÜNSTER 1834, are known from the Upper Muschelkalk and Keuper, and *N. cristatus*, HINZ et al., 2019 and *N. edingerae* SCHULTZE, 1970, are known exclusively from the Keuper. *N. marchicus* KOKEN, 1893 was omitted since it is restricted to the Anisian (see Fig. 10).

8.5.1. Comparison with *Nothosaurus edingerae*

Two skulls of *N. edingerae* are known from the Gipskeuper sediments of Affaltrach, southern Germany. The holotype SMF R-4035, first published by EDINGER (1922), and SMNS 59072, published by SCHULTZE (1970). Both skulls have lengths of around 13 to 14 cm and are therefore remarkably small (Tab. 2) compared to the Kupferzell skull with its estimated length of approximately 40 cm. For the comparison of the maximum skull widths, only the left half of the holotype was used due to the fact that in SMNS 59072 both quadratic regions as well as both jaw joints are missing. The measured 3.4 cm of the well-preserved left half was doubled and resulted in an estimated maximum skull width of 6.8 cm. This value is also significantly smaller than the maximum width of 18.8 cm measured in SMNS 80261 (Fig. 14). Both *N. edingerae* skulls have an oval parietal foramen with a length-to-width ratio of 2:1. The same ratio can also be seen in the Kupferzell skull. The Kupferzell skull lacks sharp ridges flanking the parietal foramen laterally and a prominent sagittal crest posterior to the parietal foramen, which can be seen in *N. edingerae*. The PFPS-ratios of *N. edingerae* and SMNS 80261 differ only slightly (Tab 2). A sagittal ridge on the occipital skull table is only visible in the Kupferzell skull but not in *N. edingerae*. Considering the remarkable differences in size

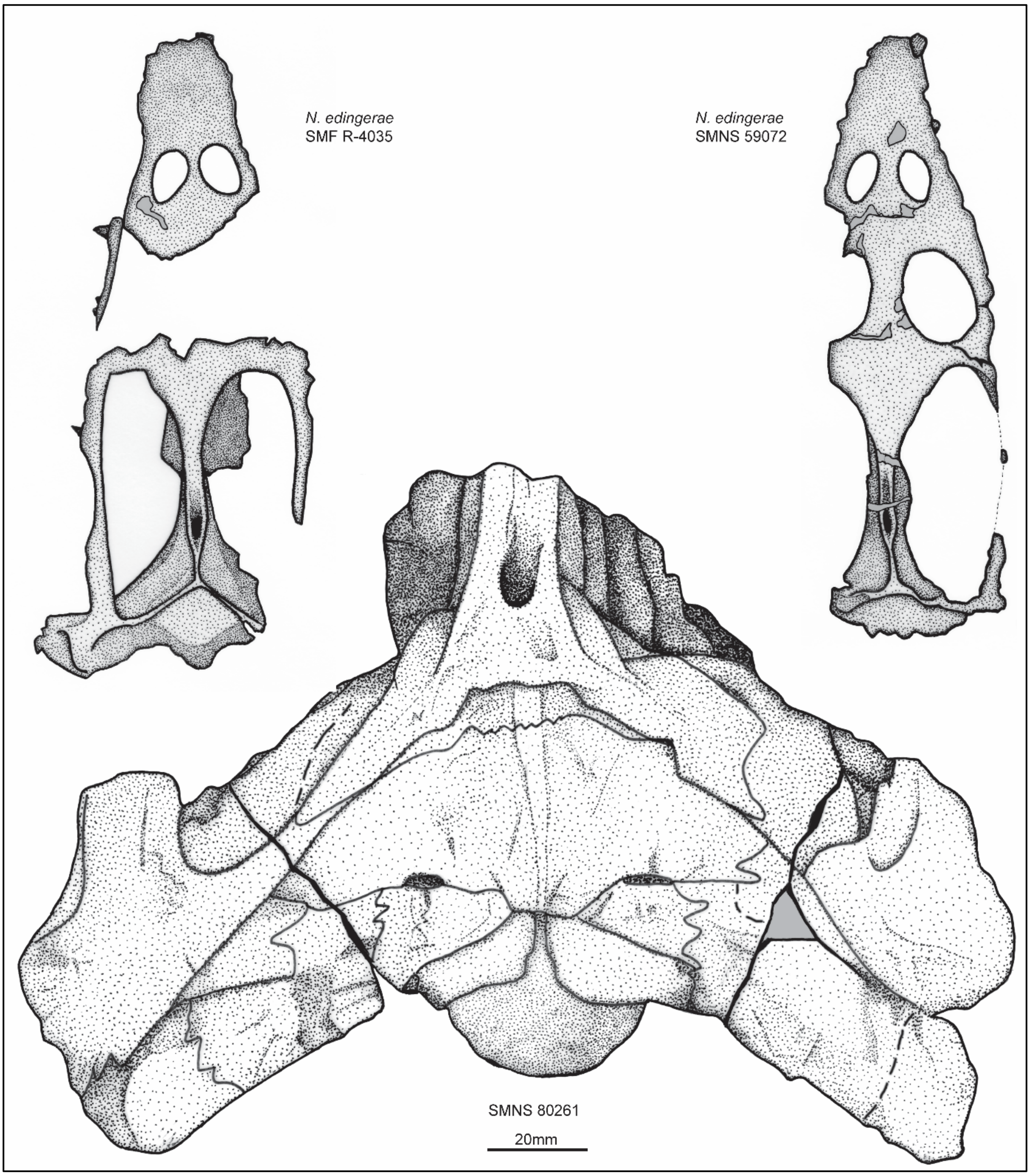


Figure 14: Comparison of SMNS 80261 and N. edingerae*. All skulls are brought to the same size ratio. The drawing of SMNS 80261 is modified after* H*INZ ET AL. (2020).*

and the absence a sagittal crest posterior to the parietal foramen, SMNS 80261 clearly differs from all known *N. edingerae* skulls.

all length measurements in cm	Catalogue number	Skull length	Maximum skull width	Parietal foramen ratio and shape	PFPS-ratio	Sagittal crest
***N. edingerae* Holotype**	SMF R-4035	14	6.8	oval 2:1	0.13	posterior to PF
N. edingerae	SMNS 59072	12.9	-	oval 2:1	-	posterior to PF
Kupferzell skull	SMNS 80261	40*	18.8	oval 2:1	0.09	none

Table 2: Measurements taken for the comparison of SMNS 80261 with N. edingerae.

8.5.2. Comparison with *Nothosaurus jagisteus*

The *N. jagisteus* skull used for this comparison is the holotype of this species and was published by RIEPPEL (2001). The condylobasal skull length of this specimen is 18.3 cm and the maximum skull width is 8.7 cm. In these proportions, *N. jagisteus* is remarkably smaller than the Kupferzell skull with its estimated length of 40 cm and a maximum width of 18.8 cm (Tab. 3). The oval shape as well as the length-to-width ratio of 2:1 in the parietal foramen are identical in both compared species. In contrast to the flat and widening post-foraminal parietal skull table of the Kupferzell skull, the skull of *N. jagisteus* shows a remarkable constriction of the parietal skull table posterior to the parietal foramen (Fig. 15). SMNS 80261 has a PFPS-ratio of 0.09 and *N. jagisteus* has a PFPS-ratio of 0.18. This remarkable difference, together with the differences in size and width, led to an exclusion of *N. jagisteus* as potential candidate for SMNS 80261.

all length measurements in cm	Catalogue number	Skull length	Maximum skull width	Parietal foramen ratio and shape	PFPS-ratio	Sagittal crest
***N. jagisteus* Holotype**	SMNS 56618	18.3	8.7	oval 2:1	0.18	none
Kupferzell skull	SMNS 80261	40*	18.8	oval 2:1	0.09	none

Table 3: Measurements taken for the comparison of SMNS 80261 with N. jagisteus

8.5.3. Comparison with *Nothosaurus cristatus*

For the comparison with *N. cristatus*, the holotype skull catalogued under GPIT/RE/09800 and described by HINZ et al. (2019) was used. The condylobasal skull

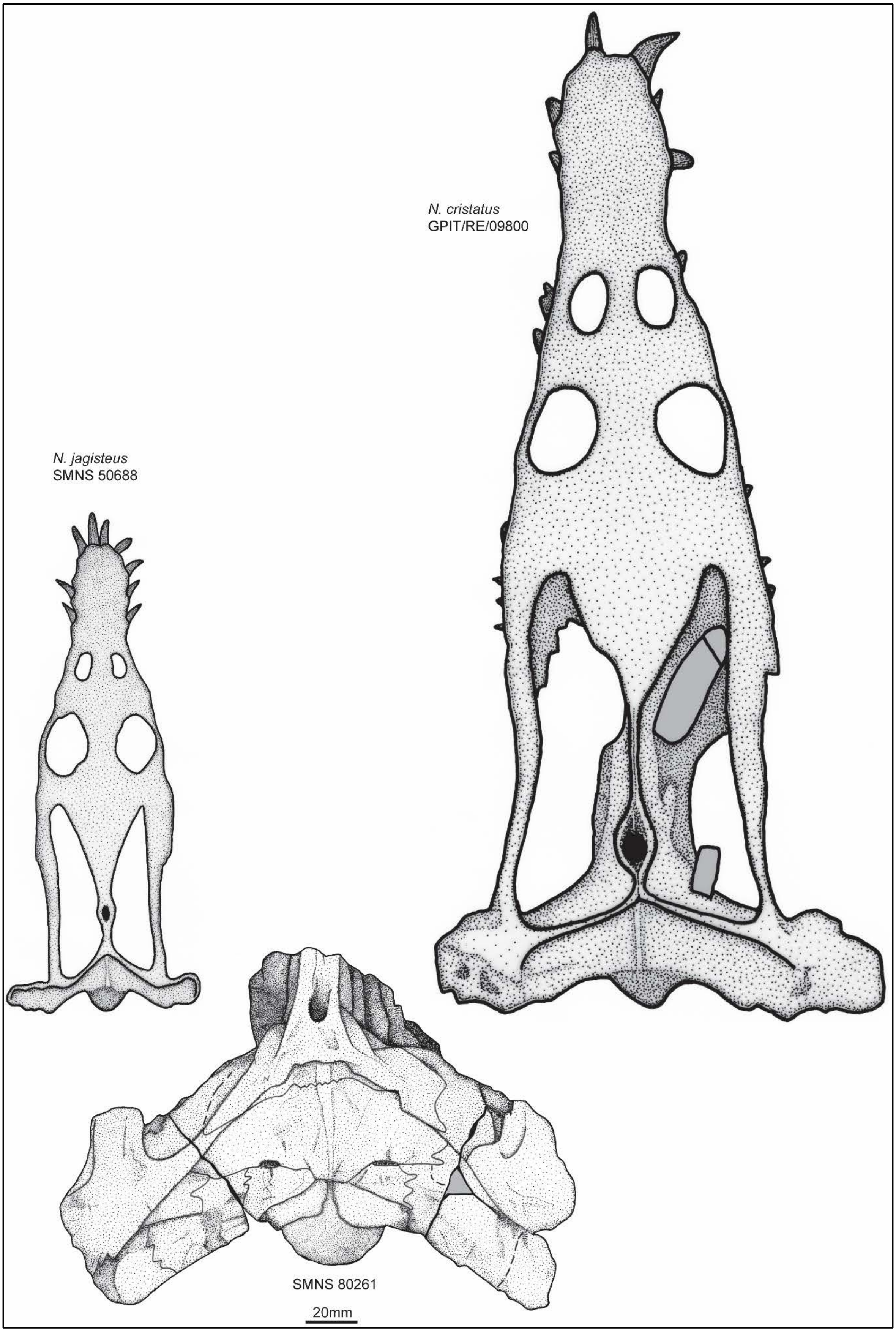


Figure 15: Comparison of SMNS 80261, N. jagisteus*, and* N. cristatus*. All skulls are brought to the same size ratio. Drawings redrawn after HINZ ET AL. (2019), HINZ ET AL. (2020), and RIEPPEL (2001).*

length is similar *in N. cristatus* (38.3 cm) and SMNS 80261 (40 cm). This similarity is also reflected in the maximum skull width, which is 16.2 cm in *N. cristatus* and 18.8 cm in the Kupferzell skull. Both skulls show remarkable differences in the shape of the parietal foramen. The parietal foramen in *N. cristatus* is sub-rounded with a length-to-width ratio if 1.22:1, whereas the foramen in the Kupferzell skull is oval with a ratio of 2:1. In clear contrast to the flat parietal skull table of the Kupferzell skull, a long and sharp sagittal crest is located anterior to the parietal foramen in *N. cristatus*. In the latter, the sagittal crest splits right in front of the parietal foramen, forming sharp ridges enclosing the foramen itself, and continues in a shallower and less pronounced form posterior to the parietal foramen (Fig. 15). These characteristics are also not present in SMNS 80261 (Tab. 4). With a value of 0.09, the PFPS-ratio of *N. cristatus* is similar to the PFPS-ratio of 0.08 found in the Kupferzell skull. In *N. cristatus* as well as in SMNS 80261, a small crest on the parietal and supraoccipital is visible on the occipital skull surface. Overall, the appearance of *N. cristatus* is slenderer than the bulky appearance of the Kupferzell skull. Together with the remarkable differences regarding the sagittal crest, *N. cristatus* can be excluded as reference for SMNS 80261.

all length measurements in cm	**Catalogue number**	**Skull length**	**Maximum skull width**	**Parietal foramen ratio and shape**	**PFPS-ratio**	**Sagittal crest**
N. cristatus **Holotype**	GPIT/RE/ 09800	38.3	16.2	sub-rounded 1.22:1	0.08	anterior and posterior to pf
Kupferzell skull	SMNS 80261	40*	18.8	oval 2:1	0.09	none

Table 4: Measurements taken for the comparison of SMNS 80261 with N. cristatus*.*

8.5.4. Comparison with *Nothosaurus mirabilis*

For the comparison of the Kupferzell skull with *Nothosaurus mirabilis*, four different skulls of *N. mirabilis* were used. Since the holotype of *N. mirabilis* is a partial postcranial skeleton described by von Meyer (1847-1855), an uncatalogued paratype skull, housed at the Urwelt-Museum Bayreuth and also described by von Meyer (1847-1855) was used for this comparison. Additionally, the skulls catalogued as BMNH R-42829 and SMF R-641, both described in Rieppel & Wild (1996), and SMNS 56286 (pers. obs.) were used for the comparison. With its estimated condylobasal length of 40 cm, the Kupferzell skull lies well within the length range of N. mirabilis, which spans from

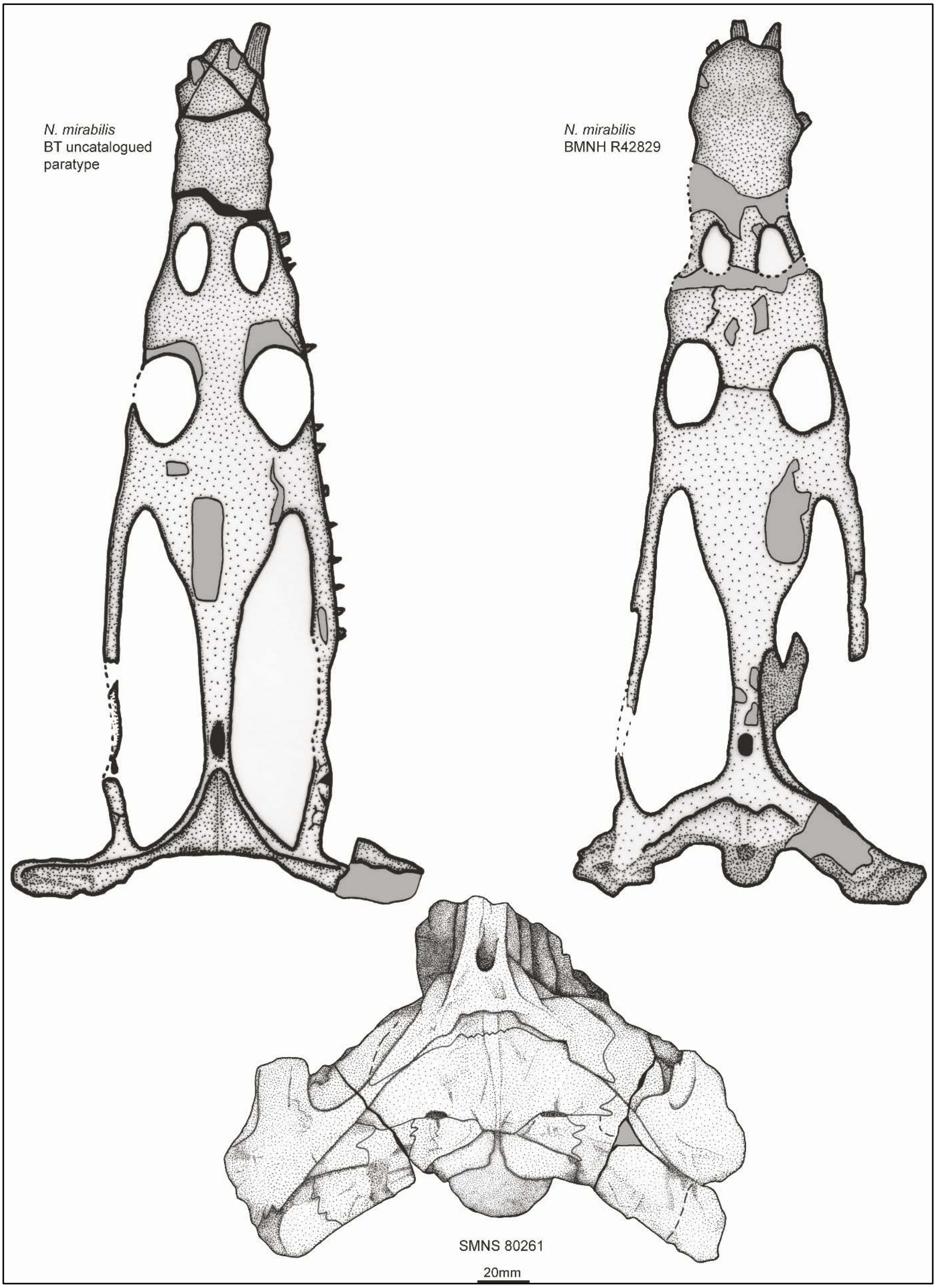


Figure 16: Comparison of SMNS 80261 and N. mirabilis*. All skulls are brought to the same size ratio. Drawings redrawn after* H*INZ ET AL. (2020) and* R*IEPPEL (2001).*

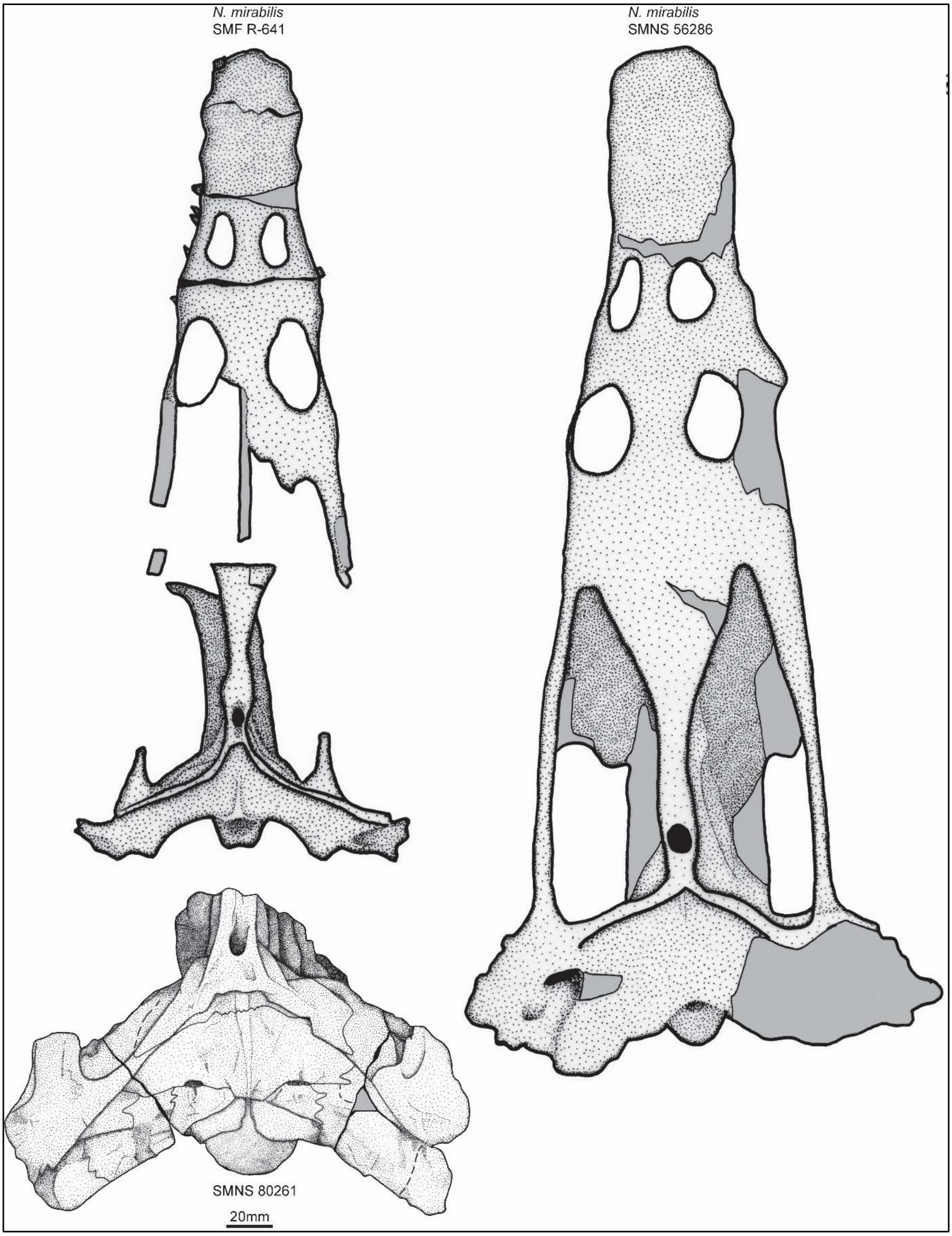


Figure 17: Comparison of SMNS 80261 and N. mirabilis*. All skulls are brought to the same size ratio. Drawings redrawn after Hinz et al. (2020) and Rieppel (2001).*

31.3 cm in the uncatalogued paratype to 43.3 cm in SMNS 56286. This also applies for the maximum skull width, which is 18.8 cm in the Kupferzell skull and varies between 13.4 cm in SMF R-641 and 21cm in SMNS 56286 in *N. mirabilis*. In SMNS

56286, only one half of the posterior end of the skull is preserved. Only this half was measured and the result was doubled for this comparison of maximum skull widths. The shape of the parietal foramens of *N. mirabilis* is oval in the uncatalogued paratype, SMF R-641, and BMNH R-42829, whereas the parietal foramen is sub-rounded in SMNS 56286 (Tab. 5). The Kupferzell skull has an oval parietal foramen and therefore lies well within the group of oval-foraminal *N. mirabilis* specimen. However, *Nothosaurus mirabilis* shows a large amount of intraspecific variation. This is strongly reflected in the shape and overall appearance of the parietal skull table posterior to the parietal foramen. The post-foraminal skull table is relatively short and noticeably constricted in SMNS 56286 (PFPS-ratio 0.07) and SMF R-641(PFPS-ratio 0.05), broad and elongated in BMNH R-42829 (PFPS-ratio 0.16), and very short with a parietal foramen lying close to the posterior margin of the parietal skull table in the uncatalogued paratype (PFPS-ratio 0.03). The post-foraminal parietal skull table of the Kupferzell skull (PFPS-ratio 0.09) is longer than in most *N. mirabilis*, except for BMNH R-42829, which has a remarkably long parietal skull table and a very small parietal foramen. The biggest difference of SMNS 80261 compared to all *N. mirabilis* specimens can be found in the zygomatic arches. The zygomatic arches are broad and bulky, and bent inwards in the Kupferzell skull, whereas they are slender and bent outwards in BMNH R-42829 and the uncatalogued paratype, and slender and straight in SMNS 56286 and SMF R-641 (Figs. 16-17). Even though *N. mirabilis* shows a wide variation in sizes and SMNS 80261 lies well within this size ranges, the rather slender

all length measurements in cm	**Catalogue number**	**Skull length**	**Maximum skull width**	**Parietal foramen ratio and shape**	**PFPS-ratio**	**Sagittal crest**
N. mirabilis	BT uncat paratype	31.1	14.4	oval 2.08	0.03	none
N. mirabilis	SMNS 56286	43.4	21	sub-rounded 1.2:1	0.7	none
N. mirabilis	SMF R-641	34.4	13.4	oval 1.81:1	0.05	none
N. mirabilis	BMNH R-42829	32.7	13.6	oval 2:1	0.16	none
Kupferzell skull	SMNS 80261	40*	18.8	oval 2:1	0.09	none

Table 5: Measurements taken for the comparison of SMNS 80261 with N. mirabilis*.*

and gracile shape of *N. mirabilis* skulls, which is also expressed in the shape of the zygomatic arches, clearly exclude *N. mirabilis* as reference species for the Kupferzell skull.

8.5.5. Comparison with *Nothosaurus giganteus*

Four skulls of *Nothosaurus giganteus* were used for the comparison with the Kupferzell skull: the partially preserved skull SMNS 57047 described in RIEPPEL & WILD (1996) and the former holotypes of *Paranothosaurus amsleri* PEYER, 1939 catalogued under PIMUZ T 4829, *Nothosaurus baruthicus* GEISSLER, 1895 catalogued as SMF R-475, and *Nothosaurus chelydrops* FRAAS, 1896 catalogued under SMNS 7162, all now synonymized with *N. giganteus*. The condylobasal skull lengths of N. giganteus vary between 46.6 cm in SMF R-475 to 56 cm in SMNS 7162. In this length comparison, the gigantic skull SMNS 57047 is not represented due to its missing snout. The Kupferzell skull, with its estimated length of 40 cm, lies slightly below the lengths of the *N. giganteus* skulls used for this comparison. This also applies for the maximum skull widths, spanning from 25.6 cm in SMF R-475 to 56 cm in SMNS 57047, being comparably larger than the 18.8 cm measured in SMNS 80261 (Tab. 6). A strong variation can also be found in the shape of the parietal foramen in *N. giganteus*. It is oval in SMNS 57047 and SMF R-475, triangular in PIMUZ T 4829, and sub-rounded in SMNS 7162 (Figs. 18-19). The parietal skull table posterior to the parietal foramen also shows a remarkable amount of variation in the compared *N. giganteus* skulls. The parietal foramen lies in a long distance to the posterior end of the parietal skull table in in SMNS 7162 (PFPS-ratio 0.23), in intermediate distance in SMF R-475 (PFPS-ratio 0.06) and PIMUZ T 4829 (PFPS-ratio 0.015), and very close to the posterior margin in SMNS 57047 (PFPS-ratio 0.009). The Kupferzell skull has a PFPS-ratio of 0.09 and lies well within this range. RIEPPEL & WILD (1996) pointed out that a strong intraspecific variation can be seen in *N. giganteus*. This fits well with the wide varieties of sizes, lengths, and shapes of the parietal foramens in *N. giganteus* described above. In all *N. giganteus* skulls as well as in the Kupferzell skull, a small crest is present on the parietal and supraoccipital on the occipital skull table. Major similarities between *N. giganteus* and the Kupferzell skull can be seen in the zygomatic arches. SMNS 80261 and all *N. giganteus* have bulky and inwards bending zygomatic arches, which cannot be found among other *Nothosaurus* species considered in this comparison. Based on the size

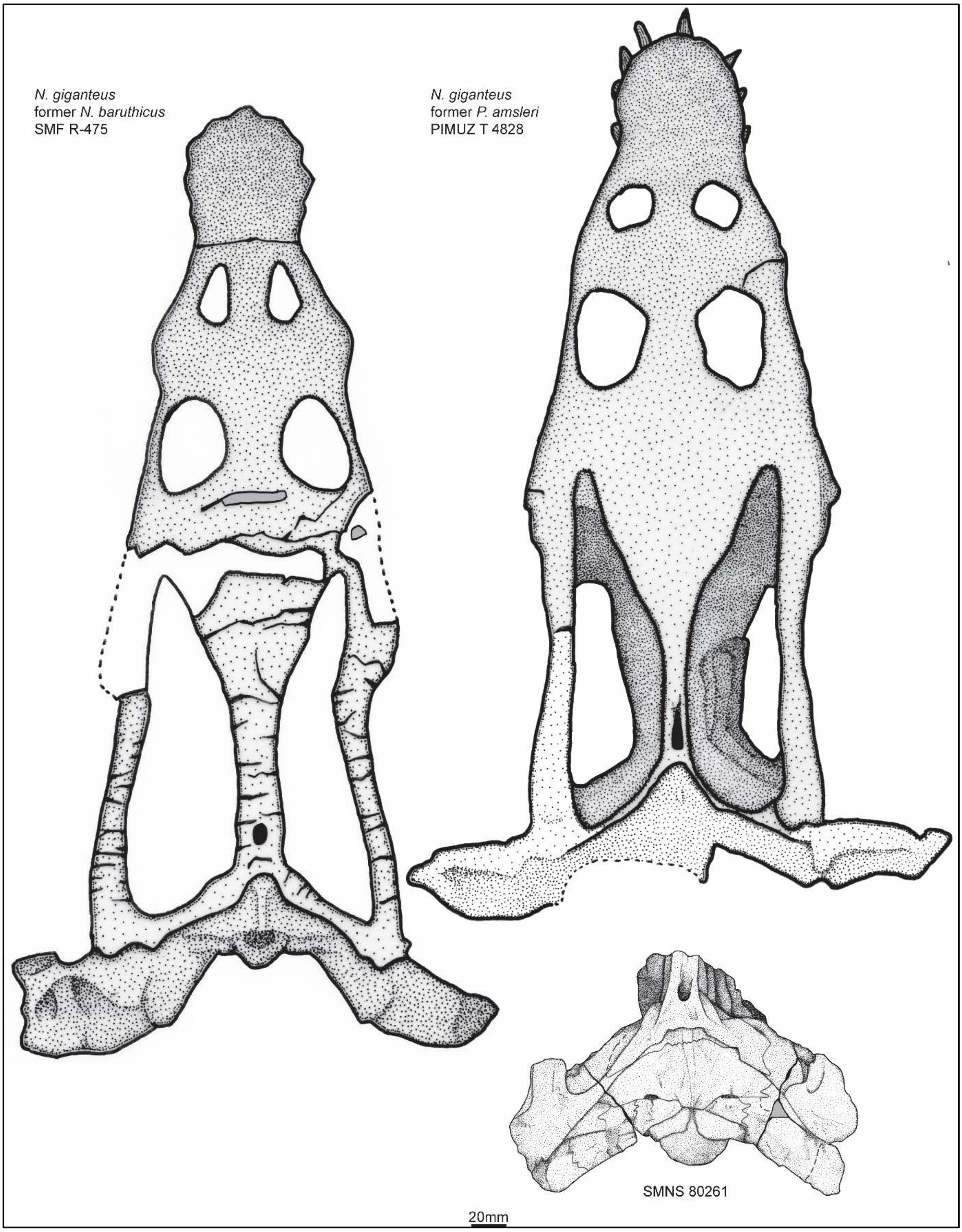


Figure 18: Comparison of SMNS 80261 and N. giganteus*. All skulls are brought to the same size ratio. Drawings redrawn after* H*INZ ET AL. (2020) and* R*IEPPEL (2001).*

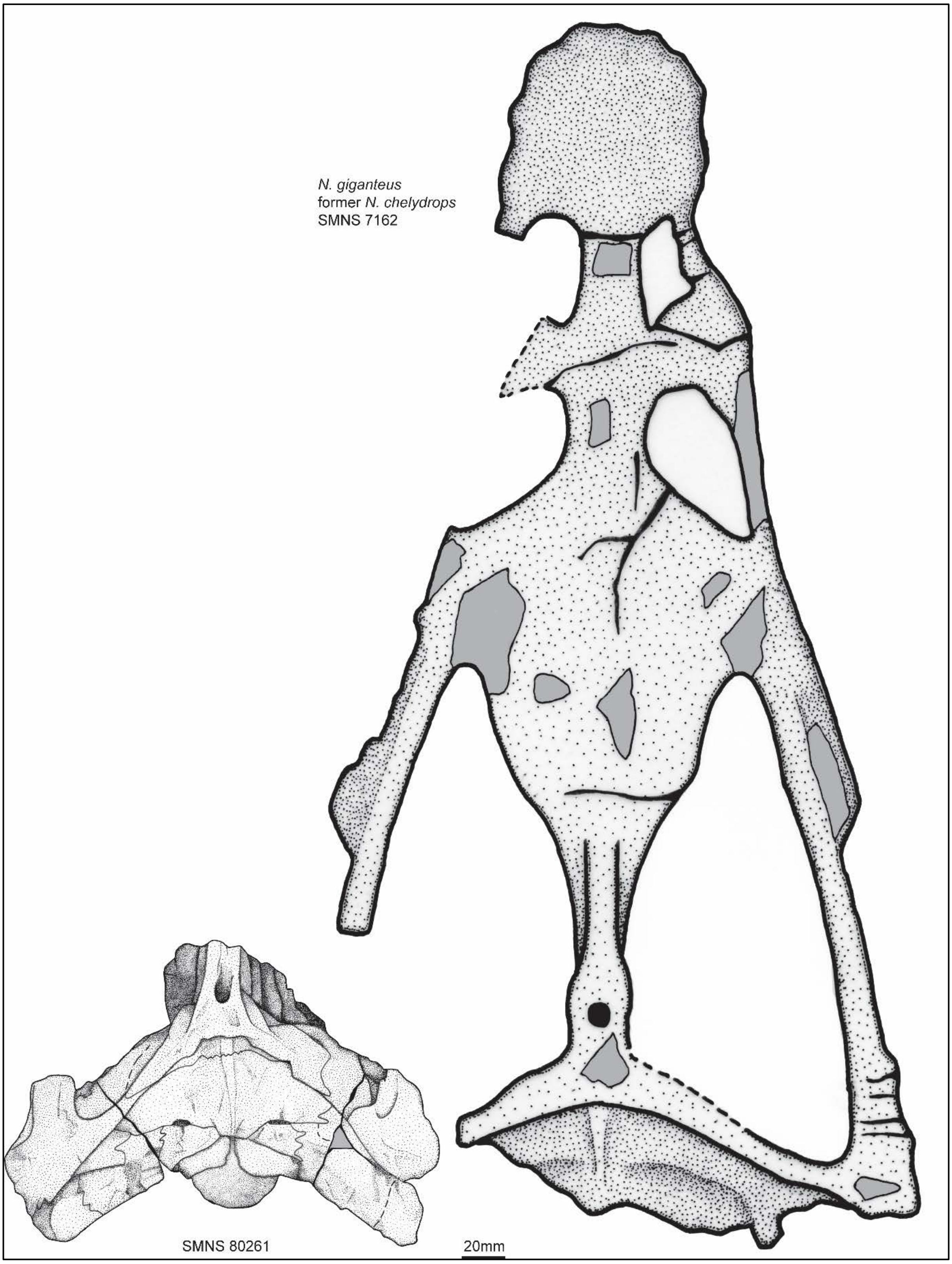


Figure 19: Comparison of SMNS 80261 and N. giganteus*. All skulls are brought to the same size ratio. Drawings redrawn after* HINZ ET AL. *(2020) and* RIEPPEL *(2001).*

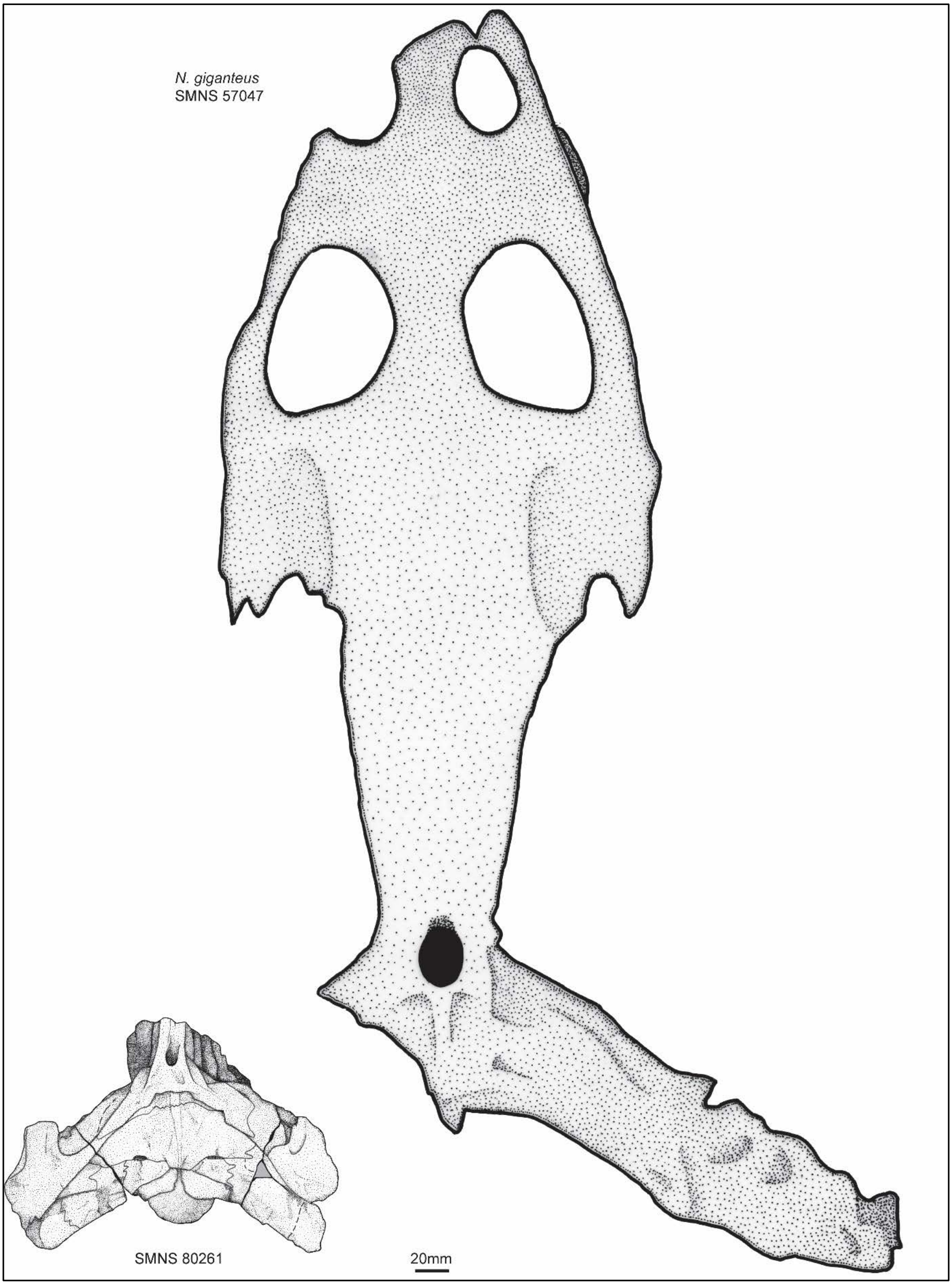


Figure 20: Comparison of SMNS 80261 and N. giganteus*. All skulls are brought to the same size ratio. Drawings redrawn after* H*INZ ET AL. (2020) and* R*IEPPEL (2001).*

and the bulkiness of the zygomatic arches, we assign the Kupferzell skull to *N. giganteus*.

all length measurements in cm	**Catalogue number**	**Skull length**	**Maximum skull width**	**Parietal foramen ratio and shape**	**PFPS-ratio**	**Sagittal crest**
N. giganteus	SMNS 57047	-	56	oval 1.59:1	0.015	none
N. giganteus (chelydrops)	SMNS 7162	56	29.7	sub-rounded 1.12:1	0.23	none
N. giganteus (P. amsleri)	PIMUZ T 4829	47.5	27.8	triangular 3.8:1	0.015	none
N. giganteus (baruthicus)	SMF R-475	46.6	25.6	oval 1.67:1	0.06	none
Kupferzell skull	SMNS 80261	40	18.8	oval 2:1	0.09	none

Table 6: Measurements taken for the comparison of SMNS 80261 with N. giganteus*.*

8.6. Discussion and conclusion

The skulls of *Nothosaurus* are known for their heterochronous and heterogeneous development. Even regarding diagnostic features, they show a large degree of variability (RIEPPEL 2000, RIEPPEL & WILD 1996, VOETEN et al. 2018). This can especially be seen in species like *N. giganteus* and *N. mirabilis*, from which a large quantity of cranial material is known.

RIEPPEL & WILD (1996) synonymized seven species with *N. giganteus*: (i) *Nothosaurus andriani* VON MEYER, 1839; (ii) *Nothosaurus angustifrons* VON MEYER & PLIENINGER, 1844; (iii) *Nothosaurus aduncidens* VON MEYER, 1847-1855; (iv) *?Opeosaurus suevicus* VON MEYER, 1847-1855; (v) *Nothosaurus baruthicus* GEISSLER, 1895; (vi) *Nothosaurus chelydrops* FRAAS, 1896; and (vii) *Paranothosaurus amsleri* PEYER, 1939.

The only referred *N. giganteus* cranial material from the Lower Keuper consists of two large skulls catalogued as SMNS 7162 and SMNS 80205, and two mandibular fragments (SMNS 7214b and SMNS 10506), all from Hoheneck, southern Germany. The material was originally described as *N. chelydrops* by FRAAS (1896) and is now a junior synonym of *N. giganteus* by the definition of RIEPPEL & WILD (1996). The authors themselves stated in their publication that *N. chelydrops* shows an exclusive set of features like a triangular-shaped skull and a unique shape of the anterior constriction of the upper temporal fenestra. A third remarkable feature, oblique orbits, may also be caused by diagenetic distortion (RIEPPEL 2000). As stated by RIEPPEL & WILD (1996), the question about the validity of *N. chelydrops* as an own species has to await better and more complete material.

The unique features of former *N. chelydrops* are not preserved in SMNS 80261. Major differences between the Kupferzell skull and the holotype skull of *N. chelydrops* catalogued under SMNS 7162 can be found in the angulation of the occipital crest (40° in SMNS 80261 and 25° in SMNS 7162) and the PFPS-ratio (0.09 in SMNS 80261 and 0.23 in SMNS 7162). In the Kupferzell skull, the parietal table posterior to the parietal foramen widens whereas it is straight in former *N. chelydrops*. The Kupferzell skull resembles more closely the Muschelkalk morphotype of *N. giganteus*, which can be seen in SMF R-475 and SMNS 51927, both described in RIEPPEL & WILD (1996). Therefore, SMNS 80261 is the first cranial material of *N. giganteus* with Muschelkalk affinities from the Lower Keuper.

So far, four nothosaur species are known from the Lettenkeuper (*N. giganteus*, *N. mirabilis*, *N. cristatus*, and *N. edingerae*) and three are known from the Upper Muschelkalk (*N. giganteus*, *N. mirabilis*, and *N. jagisteus*). Only *N. giganteus* and *N. mirabilis* occur in both lithostratigraphical units. Except for *N. edingerae*, all Lower Keuper nothosaurs show large skull sizes ranging from 38.3 cm in *N. cristatus* to 56 cm in *N. giganteus* (SMNS 7162, former *N. chelydrops*). This indicates that the Lower Keuper, which is generally treated as more terrestrial, provided habitats suitable for large predatory marine reptiles. This is of great importance because the Lower Keuper of southern Germany is so far described as heterogenic landscape formed by small and large lakes, swampy lowlands, and brackish lagoons (SCHOCH 2014). The presence of *N. giganteus* and other big nothosaurs such as *N. cristatus* and *N. mirabilis* in this ecosystem points towards more frequent transgressional events in the Lower Keuper, especially in the Untere Graue Mergel, than judged by the lithological data alone. The well-preserved specimens, like the Kupferzell postcranial material catalogued as SMNS 80266 from the Untere Graue Mergel of Kupferzell, and the holotype skull of *N. cristatus* (GPIT/RE/09800) from the Untere Graue Mergel of Vellberg-Eschenau, in which even small and fragile features as well as surface textures are preserved, show no signs of far allochthonous transportation and washing up on the beaches of the lagoons like stated by KLEIN et al. (2015) for small nothosaurs of the Lower Muschelkalk of Winterswijk, Netherlands. Therefore, it can be concluded that the area of todays Kupferzell and Vellberg-Eschenau provided a suitable habitat for large nothosaurs.

Further finds will certainly help to validate these conclusions and quantify the marine influence of the deposits of the Lower Keuper, especially of the Untere Graue Mergel. The results of this study underline the importance of the Kupferzell fossil site and the Lettenkeuper to provide new insights into the paleoecology and paleoenvironment of the Late Triassic of the Germanic Basin.

9. Acknowledgments

I would like to thank my supervisor Prof. Dr. Hans-Ulrich Pfretzschner, who unfortunately died before he was able to correct my work. He accompanied me from my studies and my diploma to this thesis. His scientific curiosity and broad and detailed knowledge in so many scientific fields kindled my passion for science and helped me even through harsh times. I would also like to thank Prof. Dr. James Nebelsick for being the first corrector of this work after Prof. Dr. Pfretzschners death. I would also like to express my gratitude to PD Dr. Ingmar Werneburg, who, at short notice, became the second corrector of this work and helped me in many ways to achieve this thesis. My gratitude also goes to my workgroup members and friends Dr. Andreas Matzke, who supervised me, and MSc Felix Augustin who also supported me during this thesis and the publications listed herein. Henrik Stöhr is thanked for the preparation of *N. cristatus*.

All of this work wouldn’t have been possible without access to the collections of the SMNS, which was granted by Dr. Erin Maxwell and Dr. Rainer Schoch, and the Muschelkalkmuseum Ingelfingen, which is led by Dr. h.c. Hans Hagdorn, who shared his knowledge about Kupferzell and nothosaurs with me. Furthermore, I would like to gratefully thank the Schumann family from Vellberg-Eschenau who welcomed us during our excavation in their quarry.

Special thanks go to the excavation team of Vellberg-Eschenau 2017. G. Wild, A. Sattler, M. Schubert, T. Gabler, D. Schulz, and S. Ring did an excellent fieldwork and made the excavation a really great time.

I also express my deepest gratitude to my husband and my mother, who supported me in all situations during the last years. Their help, open ear, support, no matter if emotional or IT-ical, their comments on my manuscript, and the knowledge that they are always there for me, were and still are the backbone of my work. Thank you so much!

10. List of abbreviations

Aa – Aalenian

Alb – Albian

Anis – Anisian

Apt – Aptian

Bar – Barremian

Ber – Berriasian

Bj – Bajocian

Bt – Bathonian

BT – Urweltmuseum Bayreuth

Bunts – Buntsandstein

C – Coniacian

Campan – Campanian

Cen – Cenoman

Cl – Callovian

FMNH – Field Museum of Natural History, Chicago

GPIT – Geologisch-Paläontologisches Institut Tübingen

Haut – Hauterivian

Ht – Hettangium

HUJ-Pal. – The Hebrew University, Jerusalem, Paleontological Institute

I – Induan

IVPP – Institute for Vertebrate Paleontology and Paleoanthropology, Beijing

Kim – Kimmeridgian

Ladin – Ladinian

Ma – Maastrichtian

Muschel – Muschelkalk

Ol – Olenekian

Oxf – Oxfordian

P. amsleri – *Paranothosaurus amsleri*

PF - parietal foramen

PFPS-ratio – Length of the parietal skull table posterior to the parietal foramen divided by the maximum occipital skull width

PIMUZ – Paläontologisches Institut und Museum Zürich

Plie – Pliensbachian

PO-ratio – Length of the postorbital bridge divided by the length of the orbitonasal bridge

Rh – Rhaetian

S – Santonian

Sin – Sinemurian

SMF – Senckenbergmuseum Frankfurt

SMNS – Staatliches Museum für Naturkunde Stuttgart

Tit – Tithonian

Toarc – Toarcian

Tu – Turonian

Va – Valangian

11. List of figures and tables

12. References

AGASSIZ, L. (1834): Abgerissene Bemerkungen über fossile Fische. – Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, 1834: 379-390.

AGASSIZ, L. (1838): Recherches sur les poissons fossiles, vol. 3. In: 73-140 pp; Neuchâtel (Petitpierre).

AIGNER, T. AND BACHMANN, G. H. (1992): Sequence-stratigraphic framework of the German Triassic. – Sedimentary Geology, 80: 115-135.

BAUR, G. (1887–1890): Pistosauridae. – Handbuch der Palaeontologie, 3: 498-499.

BAUR, G. (1889): ART. XXXIII.--*Palaeohatteria* Credner, and the Proganosauria. – American Journal of Science (1880-1910), 37: 310.

BAUR, G. (1893): Notes on the classification of the Cryptodira. – American Naturalist, 27: e674.

BENTON, M. J. (1995): Diversification and extinction in the history of life. – Science, 268: 52-58.

BEUTLER, G. AND SCHUBERT, J. (1987): Fazielle Entwicklung des Mittleren Lettenkeupers im Thüringer Becken. – Z Geol Wiss, 15: 475-484.

BLAINVILLE, H.-M. D., PRÊTRE, J. G. AND FRANKE (1835): Description de quelques espèces de reptiles de la Californie: précédée de l'analyse d'un système général d'erpétologie et d'amphibiologie. pp; (Imprimerie et fonderie de Fain, rue Racine, no 4).

BRUNNER, H. (1977): Zur Stratigraphie und Sedimentpetrographie des Unteren Keupers (Lettenkeuper, Trias) im nördlichen Baden-Württemberg. – Jahresberichte und Mitteilungen des Oberrheinischen Geologischen Vereins, 169-193.

CARROLL, R. L. (1982): Vertebrate paleontology and evolution. 698 pp; New York (W.H. Freeman and Company).

CHENG, L., CHEN, X., ZENG, X. AND CAI, Y. (2012): A new eosauropterygian (Diapsida: Sauropterygia) from the Middle Triassic of Luoping, Yunnan Province. – Journal of Earth Science, 23: 33-40.

CHENG, Y.-N., SATO, T., WU, X.-C. AND LI, C. (2006): First complete pistosauroid from the Triassic of China. – Journal of Vertebrate Paleontology, 26: 501-504.

COPE, E. D. (1885): A contribution to the vertebrate paleontology of Brazil. – Proceedings of the American Philosophical Society, 23: 1-21.

CURRIE, P. J. (1981): Osteology and relationships of aquatic eosuchians from the Upper Permian of Africa and Madagascar. – PhD: 526.

DITTRICH, D. (1989): Beckenanalyse der oberen Trias der Trier-Luxemburger Bucht. pp; (Serv. Geol. Luxembourg).

DORÉ, A. (1991): The structural foundation and evolution of Mesozoic seaways between Europe and the Arctic. – Palaeogeography, Palaeoclimatology, Palaeoecology, 87: 441-492.

DORÉ, A. (1992): Synoptic palaeogeography of the northeast Atlantic seaway: Late Permian to Cretaceous. – Geological Society, London, Special Publications, 62: 421-446.

DUCHROW, H. (1984): Der Keuper im Osnabrücker Bergland: mit einer Revision der nordwestdeutschen Keuper-Gliederung. pp; (Naturwiss. Museum).

EDINGER, T. (1921): Über *Nothosaurus*. – 74.

EDINGER, T. (1922): Über *Nothosaurus*. III. Ein Schädelfund im Keuper. – Senckenbergiana, 4: 37-42.

FRAAS, E. (1889): Die Labyrinthodonten der Schwäbischen Trias. – Palaeontographica, 36: 1-158.

FRAAS, E. (1896): Die schwäbischen Trias-Saurier nach dem Material der Kgl. Naturalien-Sammlung in Stuttgart zusammengestellt. 18 pp; (E. Schweizerbart'sche Verlagshandlung).

FRAAS, E. (1913): Neue Labyrinthodonten aus der schwäbischen Trias. – Palaeontographica (1846-1933), 275-294.

GERVAIS, P. (1852): Zoologie et paléontologie françaises (animaux vertébrés): ou nouvelles recherches sur les animaux vivants et fossiles de la France. 154 pp; (Arthus Bertrand).

GERVAIS, P. (1865): Description du *Mesosaurus tenuidens*: Reptile fossile de l'Afrique australe. In: Académie des Sciences et Lettres de Montpellier, Mémoires de la Section des Sciences, Tome Sixième. 169-175 pp; Montpellier (Boehm et Fils).

GOWER, D. J. (1999): The cranial and mandibular osteology of a new rauisuchian archosaur from the Middle Triassic of southern Germany. – Stuttgarter Beiträge zur Naturkunde B, 280: 1-49.

GOWER, D. J. (2002): Braincase evolution in suchian archosaurs (Reptilia: Diapsida): evidence from the rauisuchian *Batrachotomus kupferzellensis*. – Zoological Journal of the Linnean Society, 136: 49-76.

GOWER, D. J. AND SCHOCH, R. R. (2009): Postcranial anatomy of the rauisuchian archosaur Batrachotomus kupferzellensis. – Journal of Vertebrate Paleontology, 29: 103-122.

GRANDE, L. (1994): Studies of paleoenvironments and historical biogeography in the Fossil Butte and Laney Members of the Green River Formation. – Rocky Mountain Geology, 30: 15-32.

GÜRICH, G. (1884): Üer einige Saurier des oberschlesischen Muschelkalkes. – Zeitschrift der deutschen geologischen Gesellschaft, 125-144.

HAAS, G. (1979): Ein Nothosaurier-Schädel aus dem Muschelkalk des Wadi Ramon (Negev, Israel). – Annalen des Naturhistorischen Museums in Wien, 83: 119-125.

HAGDORN, H. (1980): Saurierreste aus dem Lettenkeuper im Landkreis Schwäbisch Hall (I). – Der Haalquell, 32: 21-23.

HAGDORN, H. (1991): Muschelkalk: a field guide. 80 pp; (Goldschneck-Verlag Weidert).

HAGDORN, H., HEUNISCH, C. AND SCHOCH, R. (2015): Biostratigraphie und Alter des Lettenkeupers. – Der Lettenkeuper—ein Fenster in die Zeit vor den Dinosauriern, 41-47.

HAGDORN, H., KELBER, K.-P. AND SCHOCH, R. (2015): 15. Fossile Lebensgemeinschaften im Lettenkeuper. – Paleodiversity, 359-385.

HAGDORN, H., SCHOCH, R., SEEGIS, D. AND WERNEBURG, R. (2015): 14. Wirbeltierlagerstätten im Lettenkeuper. – Palaeodiversity, 325-358.

HAUGHTON, S. H. (1924): On reptilian remains from the Karroo beds of East Africa. – Quarterly Journal of the Geological Society, 80: 1-11.

HINZ, J. K., MATZKE, A. T., AUGUSTIN, F. J. AND PFRETZSCHNER, H.-U. (2020): A *Nothosaurus* (Sauropterygia) skull from Kupferzell (Triassic, late Ladinian; SW Germany). – Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen, 297/1: 101-111.

HINZ, J. K., MATZKE, A. T. AND PFRETZSCHNER, H.-U. (2019): A new nothosaur (Sauropterygia) from the Ladinian of Vellberg-Eschenau, southern Germany. – Journal of Vertebrate Paleontology, e1585364.

HINZE, C. (1967): Der Obere Buntsandstein (Röt) im südniedersächsischen Bergland. – Geologisches Jahrbuch, 84: 637-716.

HUENE, E. V. (1944): *Cymatosaurus* und seine Beziehungen zu anderen Sauropterygiern. – Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Monatshefte, Abteilung B, 1944: 192-222.

HUENE, F. V. (1941): Osteologie und systematische Stellung von *Mesosaurus*. – Palaeontographica Abteilung A, 45-58.

JI, C., JIANG, D.-Y., RIEPPEL, O., MOTANI, R., TINTORI, A. AND SUN, Z.-Y. (2014): A new specimen of Nothosaurus youngi from the Middle Triassic of Guizhou, China. – Journal of Vertebrate Paleontology, 34: 465-470.

JIANG, D.-Y., MOTANI, R., TINTORI, A., RIEPPEL, O., CHEN, G.-B., HUANG, J.-D., ZHANG, R., SUN, Z.-Y. AND JI, C. (2014): The Early Triassic eosauropterygian *Majiashanosaurus discocoracoidis*, gen. et sp. nov. (Reptilia, Sauropterygia), from Chaohu, Anhui Province, People's Republic of China. – Journal of Vertebrate Paleontology, 34: 1044-1052.

JIANG, D., MAISCH, M., HAO, W., SUN, Y. AND SUN, Z. (2006): Nothosaurus yangjuanensis n. sp.(Reptilia, Sauropterygia, Notho-sauridae) from the middle Anisian (Middle Triassic) of Guizhou. – Neues Jahrbuch für Geologie und Paläontologie Monatshefte, 2006: 257-76.

KLEIN, N. AND ALBERS, P. C. (2009): A new species of the sauropsid reptile Nothosaurus from the Lower Muschelkalk of the western Germanic Basin, Winterswijk, The Netherlands. – Acta Palaeontologica Polonica, 54: 589-598.

KLEIN, N., VOETEN, D. F., LANKAMP, J., BLEEKER, R., SICHELSCHMIDT, O. J., LIEBRAND, M., NIEWEG, D. C. AND SANDER, P. M. (2015): Postcranial material of *Nothosaurus marchicus* from the Lower Muschelkalk (Anisian) of Winterswijk, The Netherlands, with remarks on swimming styles and taphonomy. – Paläontologische Zeitschrift, 89: 961-981.

KOKEN, E. (1893): Beiträge zur Kenntnis der Gattung *Nothosaurus*. – Zeitschrift der Deutschen Geologischen Gesellschaft, 45: 337-377.

KOWAL-LINKA, M. AND BODZIOCH, A. (2017): Genesis of the Lower Triassic bonebeds from Gogolin (S Poland): The impact of microbial mats on trapping of vertebrate remains. – Palaeogeography, Palaeoclimatology, Palaeoecology, 466: 38-58.

KOZUR, H. W. AND BACHMANN, G. H. (2005): Correlation of the Germanic Triassic with the international scale. – Albertiana, 32: 21-35.

KUHN-SCHNYDER, E. (1960): Über Placodontier. – Paläontologische Zeitschrift, 34: 91-102.

LI, J. AND LIU, J. (2002): A new species of Lariosaurus (Sauropterygia: Nothosauridae) from Triassic of Guizhou, southwest China. – Vertebrata Pal Asiatica, 40: 114-126.

LI, J. AND RIEPPEL, O. (2004): A new nothosaur from Middle Triassic of Guizhou, China. – Vertebrata PalAsiatica, 42: 1-12.

LI, Q. AND LIU, J. (2020): An Early Triassic sauropterygian and associated fauna from South China provide insights into Triassic ecosystem health. – Communications biology, 3: 1-11.

LIN, W.-B., JIANG, D.-Y., RIEPPEL, O., MOTANI, R., JI, C., TINTORI, A., SUN, Z.-Y. AND ZHOU, M. (2017): A New Specimen of Lariosaurus xingyiensis (Reptilia, Sauropterygia) from the Ladinian (Middle Triassic) Zhuganpo Member, Falang Formation, Guizhou, China. – Journal of Vertebrate Paleontology, 37: e1278703.

LIU, J., HU, S.-X., RIEPPEL, O., JIANG, D.-Y., BENTON, M. J., KELLEY, N. P., AITCHISON, J. C., ZHOU, C.-Y., WEN, W. AND HUANG, J.-Y. (2014): A gigantic nothosaur (Reptilia:

Sauropterygia) from the Middle Triassic of SW China and its implication for the Triassic biotic recovery. – Scientific reports, 4: 7142.

LIU, J., RIEPPEL, O., JIANG, D.-Y., AITCHISON, J. C., MOTANI, R., ZHANG, Q.-Y., ZHOU, C.-Y. AND SUN, Y.-Y. (2011): A new pachypleurosaur (Reptilia: Sauropterygia) from the lower Middle Triassic of southwestern China and the phylogenetic relationships of Chinese pachypleurosaurs. – Journal of Vertebrate Paleontology, 31: 292-302.

MA, L.-T., JIANG, D.-Y., RIEPPEL, O., MOTANI, R. AND TINTORI, A. (2015): A new pistosauroid (Reptilia, Sauropterygia) from the late Ladinian Xingyi marine reptile level, southwestern China. – Journal of Vertebrate Paleontology, 35: e881832.

MAISCH, M. W. (2014): A well preserved skull of *Cymatosaurus* (Reptilia: Sauropterygia) from the uppermost Buntsandstein (Middle Triassic) of Germany. – Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen, 272: 213-224.

MOTANI, R. (2009): The evolution of marine reptiles. – Evolution: Education and Outreach, 2: 224-235.

MUNDLOS, R. AND WEGELE, J. (1978): Die Kupferzeller Sauriergrabung 14. März bis 3. Juni 1977. Ein Report. – Aufschluß, 29: 13-19.

MÜLLER, R. D., CANNON, J., QIN, X., WATSON, R. J., GURNIS, M., WILLIAMS, S., PFAFFELMOSER, T., SETON, M., RUSSELL, S. H. AND ZAHIROVIC, S. (2018): GPlates: building a virtual Earth through deep time. – Geochemistry, Geophysics, Geosystems, 19: 2243-2261.

MÜNSTER, G. Z. (1834): Vorläufige Nachricht über einige neue Reptilien im Muschelkalke von Baiern. – Neues Jahrbuch für die Mineralogie, Geognosie, Geologie und Petrefactenkunde, 1834: 521-527.

NEENAN, J. M., KLEIN, N. AND SCHEYER, T. M. (2013): European origin of placodont marine reptiles and the evolution of crushing dentition in Placodontia. – Nature Communications, 4: 1-8.

NOPCSA, F. V. (1928): The genera of reptiles. – Palaeobiologica, 1: 163-188.

OELOFSEN, B. AND ARAÚJO, D. (1987): *Mesosaurus tenuidens* and *Stereosternum tumidum* from the Permian Gondwana of both southern Africa and South America. – South African Journal of Science, 83: 370-372.

OWEN, R. (1840): Report on British fossil reptiles, part 1. – Report of the British Association for the Advancement of Science, 1839: 43-126.

OWEN, R. (1860): Palaeontology, or a systematic summary of extinct animals and their geological relations. pp; (Adam and Charlos Black).

PEYER, B. (1939): Die Triasfauna der Tessiner Kalkalpen XIV *Paranothosaurus amsleri*. – Abhandlungen der Schweizerischen Palaeontologischen Gesellschaft Serie Zoologie, 65: 1-87.

RENESTO, S. (2010): A new specimen of *Nothosaurus* from the latest Anisian (Middle Triassic) Besano formation (Grenzbitumenzone) of Italy. – Rivista Italiana di Paleontologia e Stratigrafia (Research In Paleontology and Stratigraphy), 116:

RICOU, L.-E. (1995): The plate tectonic history of the past Tethys Ocean. In: The Tethys Ocean. 3-70 pp; Berlin (Springer).

RIEPPEL, O. (1995): The genus *Placodus*: systematics, morphology, paleobiogeography, and paleobiology. 58 pp; (Field Museum of Natural History).

RIEPPEL, O. (1998): *Corosaurus alcovensis* Case and the phylogenetic interrelationships of Triassic stem-group Sauropterygia. – Zoological Journal of the Linnean Society, 124: 1-41.

RIEPPEL, O. (1999): Phylogeny and paleobiogeography of Triassic Sauropterygia: problems solved and unresolved. – Palaeogeography, Palaeoclimatology, Palaeoecology, 153: 1-15.

RIEPPEL, O. (2000): Handbuch Der Paläoherpetologie - Sauropterygia I: Placodontia, Pachypleurosauria, Nothosauroidea, Pistosauroidea. pp; München (Pfeil Verlag).

RIEPPEL, O. (2001): A new species of *Nothosaurus* (Reptilia: Sauropterygia) from the upper Muschelkalk (lower Ladinian) of southwestern Germany. – Palaeontographica Abteilung A, 263: 137-161.

RIEPPEL, O., MAZIN, J.-M. AND TCHERNOV, E. (1997): Speciation along rifting continental margins: a new nothosaur from the Negev (Israel). – Comptes Rendus de l'Académie des Sciences-Series IIA-Earth and Planetary Science, 325: 991-997.

RIEPPEL, O. AND WILD, R. (1994): *Nothosaurus edingerae* Schultze, 1970: Diagnosis of the Species and Comments on its Stratigraphical Occurrence. – Stuttgarter Beiträge für Naturkunde Serie B, 204: 1-13.

RIEPPEL, O. AND WILD, R. (1996): A Revision of the Genus *Nothosaurus* (Reptilia: Sauropterygia) from the Germanic Triassic with Comments on the Status of *Conchiosaurus clavatus*. – Fieldiana Geology, 34: 1-82.

ROSS, C. AND ROSS, J. (1981): Late Paleozoic faunas around the Paleopacific margin. – Evolution Today, 425-40.

SANDER, P. M., RIEPPEL, O. C. AND BUCHER, H. (1997): A new pistosaurid (Reptilia: Sauropterygia) from the Middle Triassic of Nevada and its implications for the origin of the plesiosaurs. – Journal of Vertebrate Paleontology, 17: 526-533.

SANZ, J. (1983): Los Notosaurios (Reptilia, Sauropterygia) españoles. – Estudios Geológicos (Madrid), 39: 193-215.

SATO, T., CHENG, Y.-N., WU, X.-C. AND LI, C. (2010): Osteology of *Yunguisaurus* (Reptilia; Sauropterygia), a Triassic pistosauroid from China. – Paleontological research, 14: 179-195.

SATO, T., CHENG, Y.-N., WU, X.-C. AND SHAN, H.-Y. (2014): *Diandongosaurus acutidentatus* Shang, Wu & Li, 2011 (Diapsida: Sauropterygia) and the relationships of Chinese eosauropterygians. – Geological Magazine, 151: 121-133.

SATO, T., ZHAO, L. J., WU, X. C. AND LI, C. (2013): A new specimen of the Triassic pistosauroid *Yunguisaurus*, with implications for the origin of Plesiosauria (Reptilia, Sauropterygia). – Palaeontology, 57: 55-76.

SCHOCH, R. (2006): Kupferzell: Saurier aus den Keupersümpfen. – Stuttgarter Beiträge zur Naturkunde Serie C, 1-79.

SCHOCH, R. R. (1997): A new capitosaur amphibian from the Upper Lettenkeuper (Triassic: Ladinian) of Kupferzell (southern Germany). – Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen, 239-272.

SCHOCH, R. R. (1999): Comparative Osteology of *Mastodonsaurus giganteus* (Jaeger, 1828) from the Middle Triassic (Lettenkeuper: Longobardian) of Germany (Baden-

Württemberg, Bayern, Thüringen); with 4 Plates. – Stuttgarter Beiträge zur Naturkunde B, 278: 1-175.

SCHOCH, R. R. (2002): Stratigraphie und Taphonomie wirbeltierreicher Schichten im Unterkeuper (Mitteltrias) von Vellberg (SW-Deutschland). 30 pp; Stuttgart (Staatliches Museum für Naturkunde).

SCHOCH, R. R. (2006): A complete trematosaurid amphibian from the Middle Triassic of Germany. – Journal of Vertebrate Paleontology, 26: 29-43.

SCHOCH, R. R. (2008): A new stereospondyl from the German Middle Triassic, and the origin of the Metoposauridae. – Zoological Journal of the Linnean Society, 152: 79-113.

SCHOCH, R. R. (2011): New archosauriform remains from the German Lower Keuper. – Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen, 260: 87-100.

SCHOCH, R. R. (2011): A procolophonid-like tetrapod from the German Middle Triassic. – Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen, 259: 251-255.

SCHOCH, R. R. (2014): Amphibian evolution: the life of early land vertebrates. pp; Chichester (John Wiley & Sons).

SCHOCH, R. R. (2015): 10. Reptilien des Lettenkeupers. – Paleodiversity, 231-264.

SCHOCH, R. R. AND SEEGIS, D. (2016): A Middle Triassic palaeontological gold mine: the vertebrate deposits of Vellberg (Germany). – Palaeogeography, Palaeoclimatology, Palaeoecology, 459: 249-267.

SCHOCH, R. R. AND SUES, H.-D. (2014): A new archosauriform reptile from the Middle Triassic (Ladinian) of Germany. – Journal of Systematic Palaeontology, 12: 113-131.

SCHOCH, R. R. AND SUES, H.-D. (2015): A Middle Triassic stem-turtle and the evolution of the turtle body plan. – Nature, 523: 584-587.

SCHRÖDER, B. (1982): Entwicklung des Sedimentbeckens und Stratigraphie der klassischen Germanischen Trias. – Geologische Rundschau, 71: 783-794.

SCHULTZE, H. (1970): Über *Nothosaurus*. Neubeschreibung eines Schädels aus dem Keuper. – Senckenbergiana lethaea, 51: 211-237.

SCOTESE, C. (2016): PALEOMAP PaleoAtlas for GPlates and the PaleoData Plotter Program, PALEOMAP Project. – Geological Society of America Abstracts with Programs, 48:

SENNIKOV, A. (2001): Discovery of a Primitive Sauropterygian from the Lower Triassic of the Donskaya Luka (Don Basin) and the Range of Triassic Marine Reptiles in Russia. – Palaeontological Journal, 35: 301-309.

SEPKOSKI, J. J. (1996): Patterns of Phanerozoic extinction: a perspective from global data bases. In: Global events and event stratigraphy in the Phanerozoic. 35-51 pp; (Springer).

STORRS, G. W. (1991): Anatomy and relationships of *Corosaurus alcovensis* (Diapsida: Sauropterygia) and the Triassic Alcova Limestone of Wyoming. – Journal of Vertebrate Paleontology, 17: 526-533.

SUN, Y., JOACHIMSKI, M. M., WIGNALL, P. B., YAN, C., CHEN, Y., JIANG, H., WANG, L. AND LAI, X. (2012): Lethally hot temperatures during the Early Triassic greenhouse. – Science, 338: 366-370.

SWOFFORD, D. (2002): PAUP* version 4.0 b10. – Sinauer, Sunderland, MA,

SWOFFORD, D. (2018): PAUP* version 4.0 a164. – Sinauer, Sunderland, MA,

TSCHANZ, K. (1989): *Lariosaurus buzzii* n. sp. from the Middle Triassic of Monte San Giorgio (Switzerland) with comments on the classification of nothosaurs. – Palaeontographica Abteilung A, 153-179.

TUCKER, M. E. (1991): Sequence stratigraphy of carbonate-evaporite basins: models and application to the Upper Permian (Zechstein) of northeast England and adjoining North Sea. – Journal of the Geological Society, 148: 1019-1036.

URLICHS, M. (1982): Zur Stratigraphie und Fossilführung des Lettenkeupers (Ob. Trias) bei Schwäbisch Hall (Baden-Württemberg). – Jahresberichte und Mitteilungen des Oberrheinischen Geologischen Vereins, 213-224.

VOETEN, D. F., REICH, T., ARAUJO, R. AND SCHEYER, T. M. (2018): Synchrotron microtomography of a *Nothosaurus marchicus* skull informs on nothosaurian physiology and neurosensory adaptations in early Sauropterygia. – PloS one, 13:

VON ALBERTI, F. (1834): Beitrag zu einer Monographie des bunten Sandsteins, Muschelkalks und Keupers: und die Verbindung dieser Gebilde zu einer Formation. pp; (JG Cotta'schen Buchhandlung).

VON JÄGER, G. F. (1828): Über die fossile reptilien: welche in Würtemberg aufgefunden worden sind. 48 pp; (JB Metzler).

VON MEYER, H. (1832): Palaeologica zur Geschichte der Erde und ihrer Geschöpfe. pp; (S. Schmerber).

VON MEYER, H. (1839): Mittheilungen an Professor Bronn gerichtet. – Neues Jahrb. Miner. Geog. Geol. Petrefaktenkunde, 559-560.

VON MEYER, H. (1842): *Simosaurus*, die Stumpfschnauze, ein Saurier aus dem Muschelkalke von Luneville. – Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, 1842: 184-197.

VON MEYER, H. (1847): Die Placodonten, eine Familie von Sauriern der Trias. pp; (Fischer).

VON MEYER, H. (1847-1855): Zur Fauna der Vorwelt: Die Saurier des Muschelkalkes mit Rücksicht auf die Saurier aus buntem Sandstein und Keuper. 167 pp; Frankfurt am Main (Heinrich Keller).

VON SCHAUROTH, C. (1857): Die Schalthierreste der Lettenkohlenformation des Grossherzogthums Coburg. – Zeitschrift der Deutschen Geologischen Gesellschaft, 9: 85-148.

VON ZITTEL, K. A. (1889): Handbuch der Paläontologie. 1. Paläozoologie: 3. Vertebrata: Pisces, Amphibia, Reptilia, Aves. 900 pp; Munich and Leipzig (Oldenbourg).

WILD, R. (1980): The fossil deposits of Kupferzell, southwest Germany. – Mesozoic Vertebrate Life, 1: 15-18.

WILD, R. (1987): Massengrab für Saurier. – Kosmos, 74: 790-797.

WU, X.-C., CHENG, Y.-N., LI, C., ZHAO, L.-J. AND SATO, T. (2011): New information on *Wumengosaurus delicatomandibularis* Jiang et al., 2008 (Diapsida: Sauropterygia), with a revision of the osteology and phylogeny of the taxon. – Journal of Vertebrate Paleontology, 31: 70-83.

WURSTER, P. (1964): Geologie des Schilfsandsteins. pp; (Geologisches Staatsinstitut in Hamburg).

YOUNG, C. (1959): On a new Nothosauria from the Lower Triassic beds of Kwangsi. – Vertebrata PalAsiatica, 3: 73-78.

YOUNG, C. (1965): On the new nothosaurs from Hupeh and Kweichou, China. – Vertebrata PalAsiatica, 9: 315-356.

YOUNG, C. (1972): A marine lizard from Nanchang, Hupeh Province. – Memoirs of the Institute of Vertebrate Paleontology and Paleoanthropology A, 9: 17-27.

ZIEGLER, P. A. (1988): Evolution of the Arctic-North Atlantic and the Western Tethys: A visual presentation of a series of Paleogeographic-Paleotectonic maps. – AAPG memoir, 43: 164-196.

13. Appendix 1 – Published manuscript " A new nothosaur (Sauropterygia) from the Ladinian of Vellberg-Eschenau, southern Germany”

A NEW NOTHOSAUR (SAUROPTERYGIA) FROM THE LADINIAN OF VELLBERG-ESCHENAU,

SOUTHERN GERMANY

JULIANE K. HINZ,*, ANDREAS T. MATZKE, and HANS-ULRICH PFRETZSCHNER

Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Keplerstraße 17, 72074 Tübingen, Germany, juliane.hinz@uni-tuebingen.de; matzke@uni-tuebingen.de; hans-ulrich.pfretzschner@uni-tuebingen.de

ABSTRACT—A new species of Nothosaurus from the Lower Keuper (Lettenkeuper, Ladinian, Erfurt Formation) of Vellberg-Eschenau, southern Germany, is described on the basis of a nearly complete skull that is only missing the lower jaw. Together with Nothosaurus edingerae, it is the only valid Nothosaurus species exclusively known from the Lower Keuper (Ladinian) of the Germanic Basin. Nothosaurus cristatus, sp. nov., differs from all other nothosaurs by exhibiting a postorbital that is excluded from the orbital margin by the postfrontal, the maxilla, and the jugal. The postfrontal and the maxilla form the posterior orbital margin exclusively. The parietal forms a pronounced and sharp crest anterior to the parietal foramen, which is unique among Nothosaurus. The ectopterygoid bears a long posterior process. A phylogenetic analysis of Nothosaurus cristatus, based on LIU ET AL. (2014, Scientific Reports 4:7142, doi: 10.1038/srep07142) with modified characters after LIN ET AL. (2017, Journal of Vertebrate Paleontology, doi: 10.1080/02724634.2017.1278703), yielded a nearly unchanged topology that supported the monophyly of (N. jagisteus (N. cristatus (N. mirabilis + N. tchernovi))).

http://zoobank.org/urn:lsid:zoobank.org:pub:9AABA62F-251A-4936-8145-4DBB5458D48B

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

Citation for this article: Hinz, J. K., A. T. Matzke, and H.-U. Pfretzschner. 2019. A new nothosaur (Sauropterygia) from the

Ladinian of Vellberg-Eschenau, southern Germany. Journal of Vertebrate Paleontology. DOI: 10.1080/02724634.2019.1585364.

INTRODUCTION

The Sauropterygia are an extinct, diverse group of Mesozoic reptiles. Throughout the Triassic, sauropterygians played a major role in marine biota, and together with ichthyosaurs they were the top predators of the time. Sauropterygians are found in Triassic marine sediments around the world, especially in China (LI & RIEPPEL, 2004; JIANG ET AL., 2005, 2006; LIN ET AL., 2017; LIU ET AL., 2014) and Europe (SANDER, 1989; RIEPPEL & WILD, 1996; RIEPPEL, 2000; DIEDRICH, 2009). In North America, nothosaurs are rare, with only two known species: *Corosaurus alcovensis* (e.g., RIEPPEL, 1998) and *Augustasaurus hagdorni* (e.g., RIEPPEL et al., 2002). Sediments of the Germanic Basin are famous for their rich sauropterygian fauna (RIEPPEL, 2000), extending from the Lower Muschelkalk to the lower part of the Keuper (Gipskeuper, Grabfeld Formation, upper Ladinian–lower Carnian). Remains of nothosaurs in particular are quite common in marine deposits of the Muschelkalk, including N. giganteus, *N. mirabilis*, *N. jagisteus*, and *N. marchicus*. *Nothosaurus* remains from the Lower Keuper are rare: only a few diagnostic specimens and one valid species are hitherto known, and skulls are even scarcer. So far, the only known species from the Gipskeuper is *N. edingerae*, which is represented by two skulls (SCHULTZE, 1970; RIEPPEL, 1994). Another skull from the Lower Keuper is *N. chelydrops*, which was synonymized with N. giganteus (RIEPPEL & WILD, 1996). Another small, as yet undescribed skull (SMNS 91361) from the Lower Keuper of Vellberg-Eschenau (Lettenkeuper, Erfurt Formation) can be assigned to *N. mirabilis* (and is also assigned to *N. jagisteus* by SCHOCH, 2015). In this paper, we report a new species of the sauropterygian genus *Nothosaurus* from the Lower Keuper of Vellberg-Eschenau, southern Germany (Fig. 1).

Institutional Abbreviations—GPIT, Geologisches Paläontologisches Institut Tübingen, Tübingen, Germany; **SMF**, Senckenberg Museum, Frankfurt am Main, Germany; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany.

STRATIGRAPHY

The Lower Keuper (Lettenkeuper, Erfurt Formation) in southern Germany is a mixture of terrestrial and marine successions with an alternating series of claystones, siltstones, dolomites, and marlstones. The Lettenkeuper overlies the marine Muschelkalk and has a thickness of about 20–25 m. According to SCHOCH (2002) and SCHOCH & SEEGIS (2016), the fossiliferous layers at the Eschenau Quarry are just below the *Anoplophora*-dolomite layer in the upper part of the Lettenkeuper, cataloged E1 to E7 (Fig. 1). The new *Nothosaurus* specimen described herein is from layer E5. This layer consists of a chocolate-brown to beige-colored marlstone that is only a few centimeters thick. However, the total thickness of E5 is almost similar to the height of the compressed skull; therefore, no further subdivision of the layer in which the new *Nothosaurus* specimen was found can be made.

MATERIALS AND METHODS

The skull was found in August 2017 by an excavation team from the University of Tübingen at the Eschenau Quarry. The specimen was recovered from the field by using a plaster jacket and was later prepared mechanically.

SYSTEMATIC PALEONTOLOGY

Order EOSAUROPTERYGIA RIEPPEL, 1994
Suborder EUSAUROPTERYGIA TSCHANZ, 1989
Infraorder NOTHOSAUROIDEA BAUR, 1889 (in ZITTEL, 1887–1890)
Superfamily NOTHOSAURIA BAUR, 1889 (in ZITTEL, 1887–1890)
Family NOTHOSAURIDAE BAUR, 1889 (in ZITTEL, 1887–1890)
Genus *NOTHOSAURUS* MÜNSTER, 1834
NOTHOSAURUS CRISTATUS, sp. nov.
(Figs. 1–7)

Holotype—GPIT/RE/09800, almost complete skull, lacking mandible.

Type Locality—Eschenau Quarry (after SCHOCH & SEEGIS,2016), located about 3 km southeast of Vellberg-Eschenau in Baden-Württemberg, Germany (Fig. 1).

Distribution—Lower part of the Lower Keuper, Lettenkeuper, Erfurt Formation, Untere Graue Mergel, just below the Anoplophora-dolomite layer, Middle Triassic (Ladinian), Layer E5 (Schoch & Seegis, 2016; Fig. 1), Global Positioning System (GPS) coordinates 49°04′26.9N and 9°54′15.6E.

Diagnosis—Medium-sized *Nothosaurus* with a skull length of at least 383 mm; postfrontal and maxilla meet behind the orbit, forming its posterior margin; postorbital excluded from the orbit; jugal long, slender, and almost reaching the orbital margin; parietals fused and forming a pronounced, sharp ridge along the midline anterior to the large parietal foramen; ectopterygoid large with long, slender posterior extension. Etymology—After the pronounced sagittal crest that is unique among *Nothosaurus*.

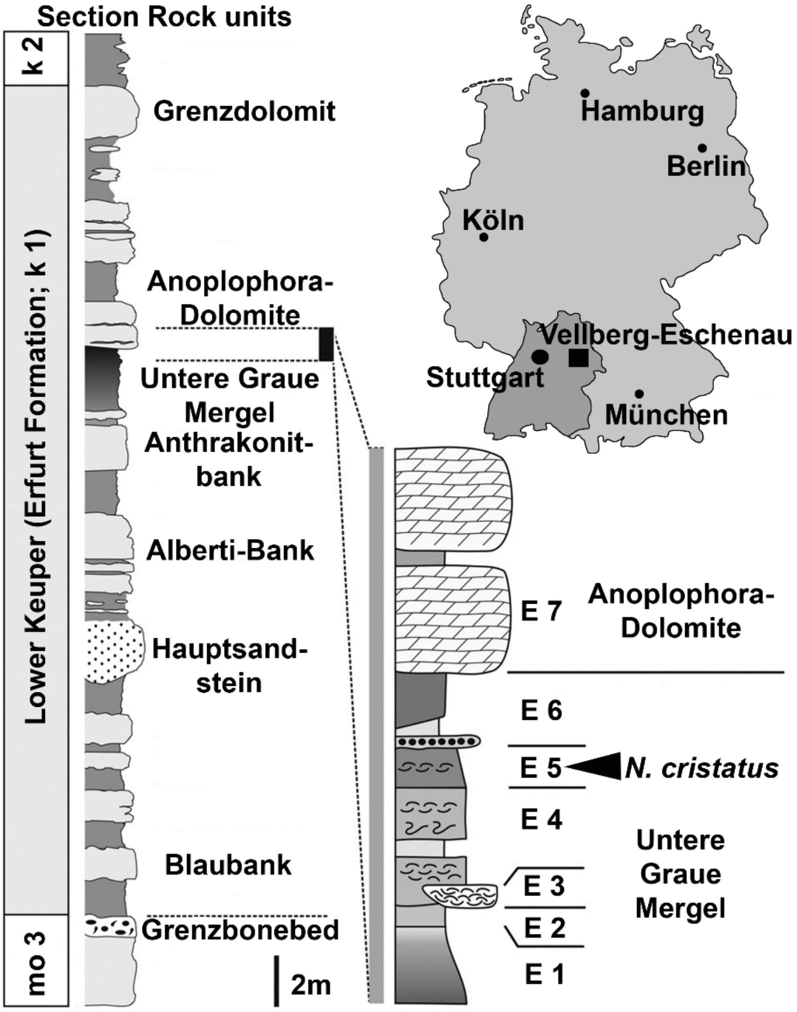


FIGURE 1. Map and stratigraphic chart of Vellberg-Eschenau, southern Germany. Stratigraphic columns modified after Schoch & Seegis (2016). The layer that produced GPIT/RE/09800 (E5) is marked with an arrowhead. For further details

about the stratigraphy of the Germanic Basin, see Figure 9. Abbreviations: k1, Lettenkeuper; k2, Gipskeuper; mo 3, Upper Muschelkalk.

DESCRIPTION

The skull is dorsoventrally compressed, and the posterior part with the occiput and braincase is flattened. The general dorsal and ventral shape of the skull is unaffected by the compression, and skull measurements can be taken (see Appendix S1 in Supplemental Data 1). In general, the right side of the skull is better preserved than the left side, except for the occiput, where the left side shows a better state of preservation.

Skull Roof

Premaxilla—The elongate and slender premaxilla shows almost parallel lateral edges and a weak constriction of the snout (Fig. 2). It is paired with a straight median suture. A tapered posteromedial process reaches back along the midline and separates the nasals for more than halfway between the external nares. The contact between the premaxilla and the maxilla lies in the anterolateral corner of the external naris and is characterized by a sinusoidal suture. Each premaxilla holds alveoli for five fangs. Three fangs are preserved on the right side and four on the left side. Replacement teeth are in the third alveolus on the right side and the fifth on the left side. In ventral view (Fig. 3), the posterior half of the paired premaxillae is divided by long and slender anterior processes of the vomers. Laterally, the premaxilla contacts the maxilla with an almost straight suture by forming a posteriorly oriented process.

Maxilla—Dorsally, the maxilla is a long and slender bone forming most of the lateral margins of the skull (Fig. 2). It builds the largest part of the margins of the external nares and orbit. Anteriorly, it contacts the premaxilla and reaches its maximum width between the nares and the orbits. There, it is sutured with the nasal medially and the prefrontal posteriorly. An acute medial extension of the premaxilla enters between the nasal and the prefrontal, almost reaching the orbital margin. Posteriorly, the maxilla builds the entire lateral orbital margin and establishes a pointed contact with the postfrontal at the posterolateral edge of the orbit, excluding the jugal and the postorbital from the orbit. There, the maxilla and the jugal run together posteriorly, showing a straight suture before ending approximately at the same height as the anterior end of the squamosal. Unfortunately, the posterior-most end of the maxilla is not well preserved on either side. Therefore, it remains unclear whether the maxilla established a short contact with the postorbital.

On its palatal side (Fig. 3), each maxilla exhibits an identical tooth count of three small maxillary teeth, followed by two large maxillary fangs, and a row of 21 maxillary teeth. Anteriorly, the maxilla contacts the premaxilla, and medially it meets the vomer in a straight suture, passing along and forming the outer margin of the internal naris. Extending far posteriorly, it contacts the palatine in a straight suture. A maxillary-ectopterygoid contact is not visible due to the poor preservation in this area on both sides.

Neurovascular Foramina—In dorsal view, a row of regularly spaced neurovascular foramina is located in the anterior region of the snout where it spans from the premaxilla to the anterior region of the maxilla. The ventrally located foramina lie parallel and medially to the tooth row. The ventral foramina are considerably larger than the ones on the dorsal side of the skull.

Nasal—The nasals bear anteriorly directed processes, which enclose the complete median margins of the nares (Fig. 2), where they also contact the premaxillae medially. The premaxilla and the nasal form a posteromedially directed suture, and the premaxillae separate the nasals for about 20 mm. Close to the level of the posterior margin of the naris, the nasals meet each other and form a median suture that is slightly shorter than 50% of the whole nasal length. The nasal contacts the maxilla laterally, the frontal posteriorly, and closely approaches the orbit, but without contact.

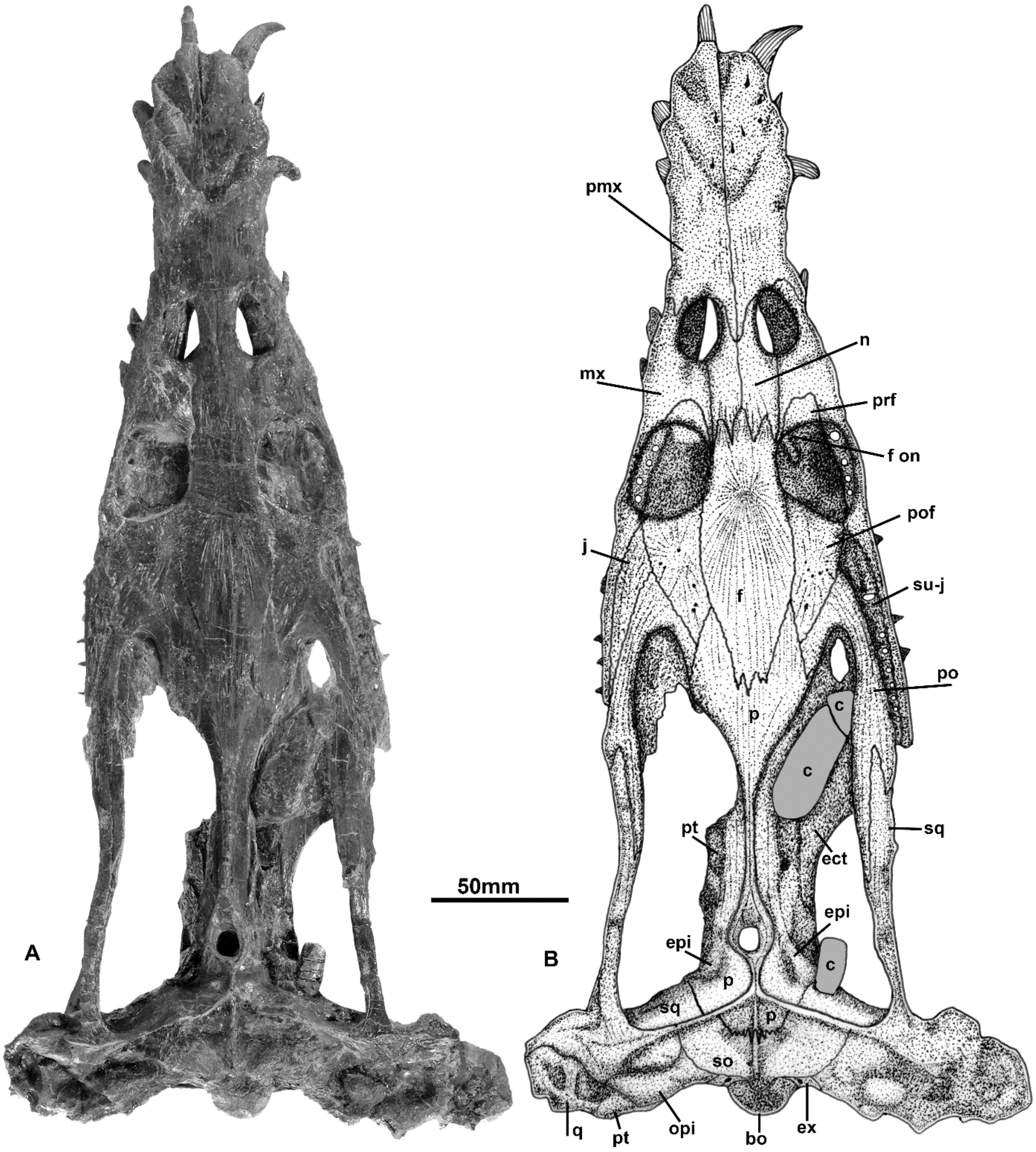


FIGURE 2. *Nothosaurus cristatus*, sp. nov., GPIT/RE/09800, from the Lower Keuper of Germany. A, photograph and B, drawing of the skull in dorsal view. Abbreviations: bo, basioccipital; c, coprolite; ect, ectopterygoid; epi, epipterygoid; ex, exoccipital; f, frontal; f on, orbitonasal foramen; j, jugal; mx, maxilla; n, nasal; opi, opisthotic; p, parietal; pmx, premaxilla, po, postorbital; pof, postfrontal; prf, prefrontal; pt, pterygoid; q, quadrate; so, supraoccipital; sq, squamosal; su-j, sutural facet for the jugal.

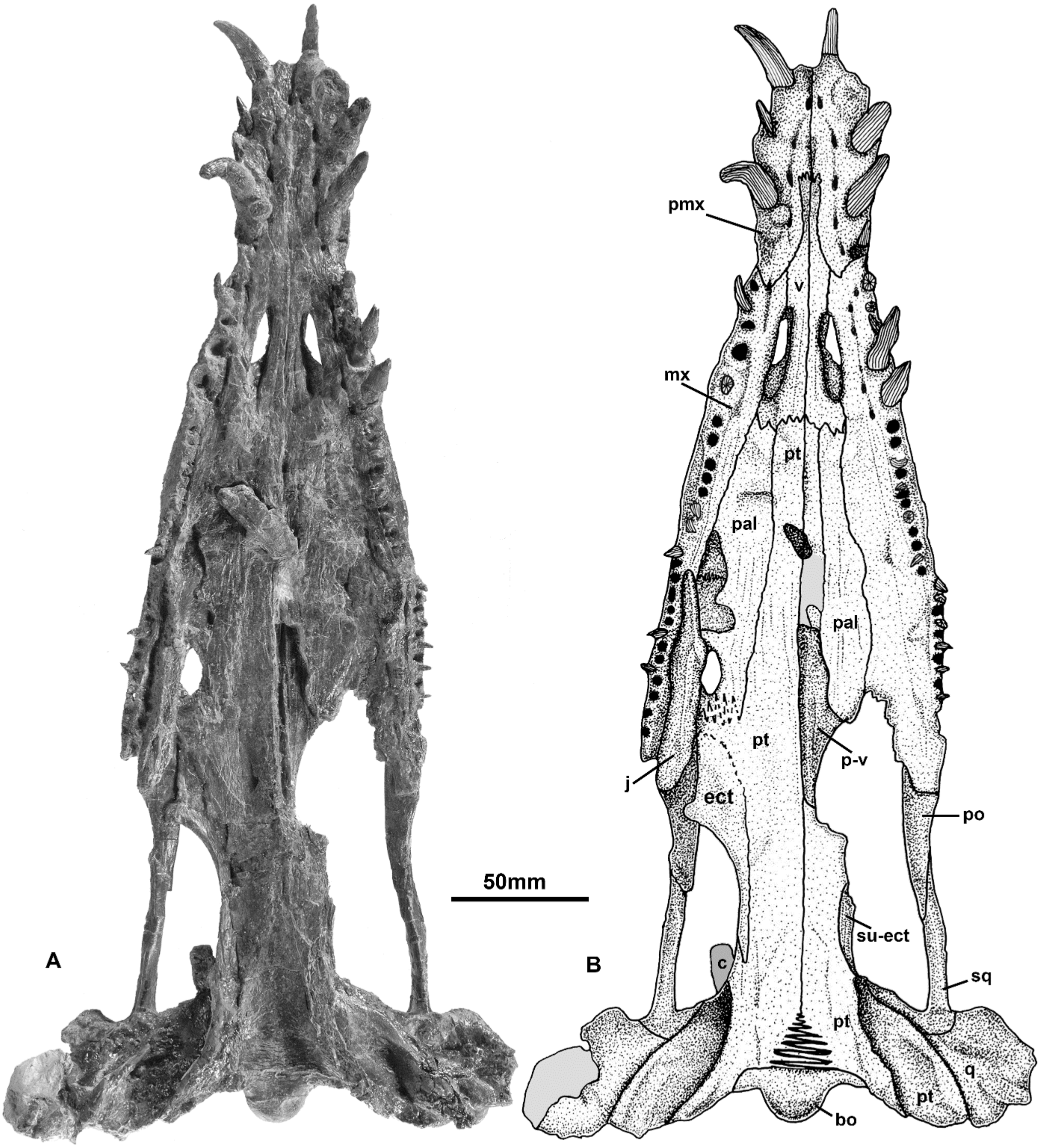


FIGURE 3. *Nothosaurus cristatus*, sp. nov., GPIT/RE/09800, from the Lower Keuper of Germany. A, photograph and B, drawing of the skull in ventral view. Abbreviations: bo, basioccipital; c, coprolite; ect, ectopterygoid; j, jugal; mx, maxilla; pal, palatine; pmx, premaxilla; po, postorbital; pt, pterygoid; p-v, parietal in ventral view; q, quadrate; sq, squamosal; su-ect, sutural facet for ectopterygoid; v, vomer.

Frontal—The frontal is fused, sculptured, and forms the inner margins of the orbit and the interorbital bar. Anteriorly, it meets the prefrontal and the nasal. It approaches the maxilla without contact. Three short anteromedial processes of the frontal characterize the suture between the frontal and the nasals, from which the medial one separates the nasals along the medial suture for a few millimeters. Posterior to the orbit, the frontal first broadens up to 33 mm and then forms a long, slightly convex suture with the postfrontal. It narrows again approximately halfway between the orbit and the upper temporal fenestra. The tapering of the frontal gradually increases after the contact with the parietal.

Parietal—The parietals are fused and contribute to the dorsal as well as to the occipital region of the skull. Anteriorly, the parietal contacts the frontal with a strongly serrated suture (Figs. 2–4). Here, the parietal reaches its greatest width of 40 mm. A large triangular anterior process intrudes between the frontal and the postfrontal on each side. A contact with the postorbital is exposed anterolaterally. The parietal converges strongly posterior to the contact with the postorbital and forms almost the entire medial margin of the upper temporal fenestra, except for the anterior-most part, which is formed by the postorbital. About 35 mm posterior to its maximum width, the parietal starts to form a strongly developed sagittal crest of 40 mm length anterior to the parietal foramen (Figs. 2, 5, 6). The crest, formed by the parietal, is triangular in cross-section, with a width of 12– 14 mm at its base and a width of 2–4 mm at the top. Right in front of the parietal foramen, the sagittal crest splits and encloses an almost circular parietal foramen, which is 13 mm long and 11 mm wide. Anteriorly, on the inner rim of the parietal foramen, a vertical ridge runs down into the foramen. The foramen lies close to the posterior margin of the intertemporal skull roof. Posterior to the parietal foramen, the parietal forms a weaker crest, which is 8 mm long and shallower but sharper in its form. Below the parietal foramen, the parietal contacts the epipterygoid. A transverse occipital crest marks the border between the intertemporal skull roof and the occipital surface of the parietal. It constitutes less than half of the posterior margin of the upper temporal fenestra and contacts the squamosal laterally (Fig. 6) in an almost straight suture. On the occipital surface, the parietal carries a distinct median ridge (Figs. 2, 5, 8). Posteriorly, it contacts the supraoccipital and laterally, the squamosal. Ventrally, the left pterygoid is partially broken off and the parietal is visible in this area (Fig. 3). A comparison with the situation on the dorsal side of the skull shows that the frontal overlaps the parietal. In ventral view, the parietal clearly underlies the frontal and extends further anteriorly than on the dorsal side of the skull.

Squamosal—In contrast to the preservation in many other *Nothosaurus* specimens, both squamosals are completely preserved in *N. cristatus* and thus both zygomatic arches are intact (Fig. 2). Anteriorly, the squamosal forms a very long process, spanning over half of the upper temporal fenestra. Together with the postorbital, it forms the zygomatic arch. Posteriorly, the squamosal expands into a bony plate forming the main portion of the posterior margin of the upper temporal fenestra. A distinct mediolaterally running ridge marks the transition between the zygomatic arch and the posterior end of the upper temporal fenestra toward the occipital surface of the skull. Posteriorly, the occipital portion of the squamosal forms a triangular bulge with the quadrate situated laterally and the opisthotic medially. The squamosal ontacts the supraoccipital medially.

Prefrontal—The prefrontal is a relatively small bone that forms the anteromedial margin of the orbit. Medially, it forms a small bulge alongside the contact with the suture of the nasals and establishes a short sutural contact with the frontal, excluding the nasal and the maxilla from the orbit. It flattens laterally and shows a distinct and moderately serrated suture with the maxilla. The prefrontal extends anteriorly over almost half of the orbitonasal bridge.

Postfrontal—The postfrontal is sculptured and forms the posterior margin of the orbit together with the maxilla (Figs. 2, 4). The postfrontal and the maxilla only have a pointed contact and are separated posteriorly by an interjacent jugal. At its medial side, the postfrontal establishes contact with the frontal anteriorly and the parietal posteriorly. It has an elongated triangular shape and no contact with the upper temporal fenestra. Jugal—The jugal is long, with a wider anterior part and a tapering posterior end. Only the left jugal is preserved in articulation (Figs. 2, 4A, C), whereas the right one is detached from the skull roof, exposing the sutural facet (Figs. 2, 4B, D). The right jugal is not missing but can be found attached to the palatal side of the skull (Fig. 3). The jugal meets the maxilla laterally and together they run posteriorly, where they both end at the

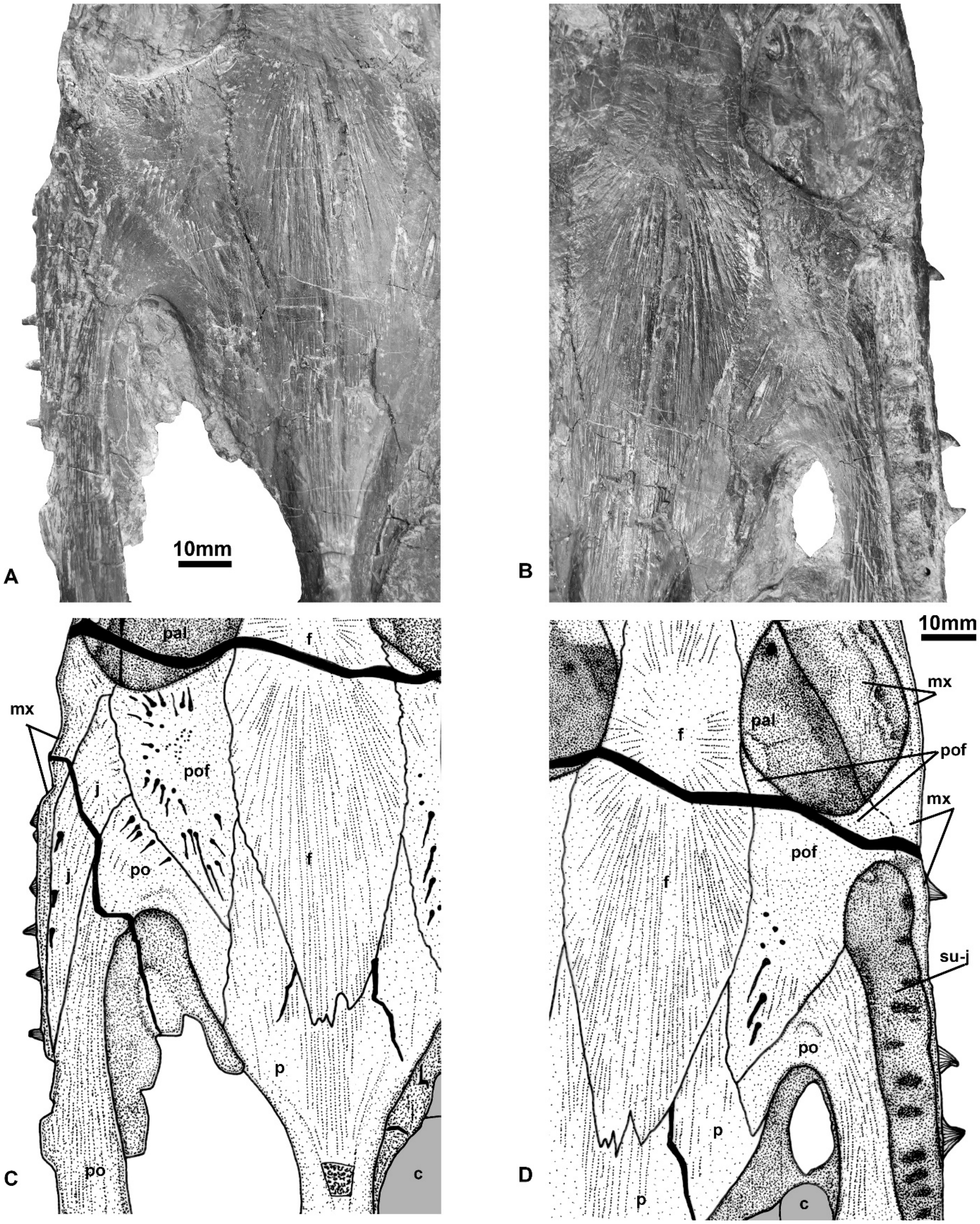


FIGURE 4. *Nothosaurus cristatus*, sp. nov., GPIT/RE/09800, from the Lower Keuper of Germany. A, photograph and C, drawing of the left postorbital skull roof. B, photograph and D, drawing of the right postorbital skull roof. Abbreviations: c, coprolite; f, frontal; j, jugal; mx, maxilla; p, parietal; pal, palatine; po, postorbital; pof, postfrontal; su-j, sutural facet for jugal.

same level. The jugal contacts the postfrontal and the postorbital medially. It comes close to the margin of the orbit, in which it definitely does not participate. The jugal remains clearly separated from the squamosal.

Postorbital—Remarkably, the postorbital is completely excluded from the orbit in *N. cristatus* (Figs. 2, 4). The triangular anterior tip of the postorbital is constrained by the jugal laterally and the postfrontal medially. The postorbital forms the entire anterior margin of the upper temporal fenestra, beginning close to the level where the contact between the postorbital and the parietal is exposed posteromedially. The anterior part of the zygomatic arch is formed by the postorbital. Posterior to the end of the maxilla and the jugal, the postorbital widens to a small bulge forming the base of the zygomatic arch (Fig. 6).

Quadratojugal—Due to poor preservation in the posterolateral region of the skull, no remains of the quadratojugal are identifiable.

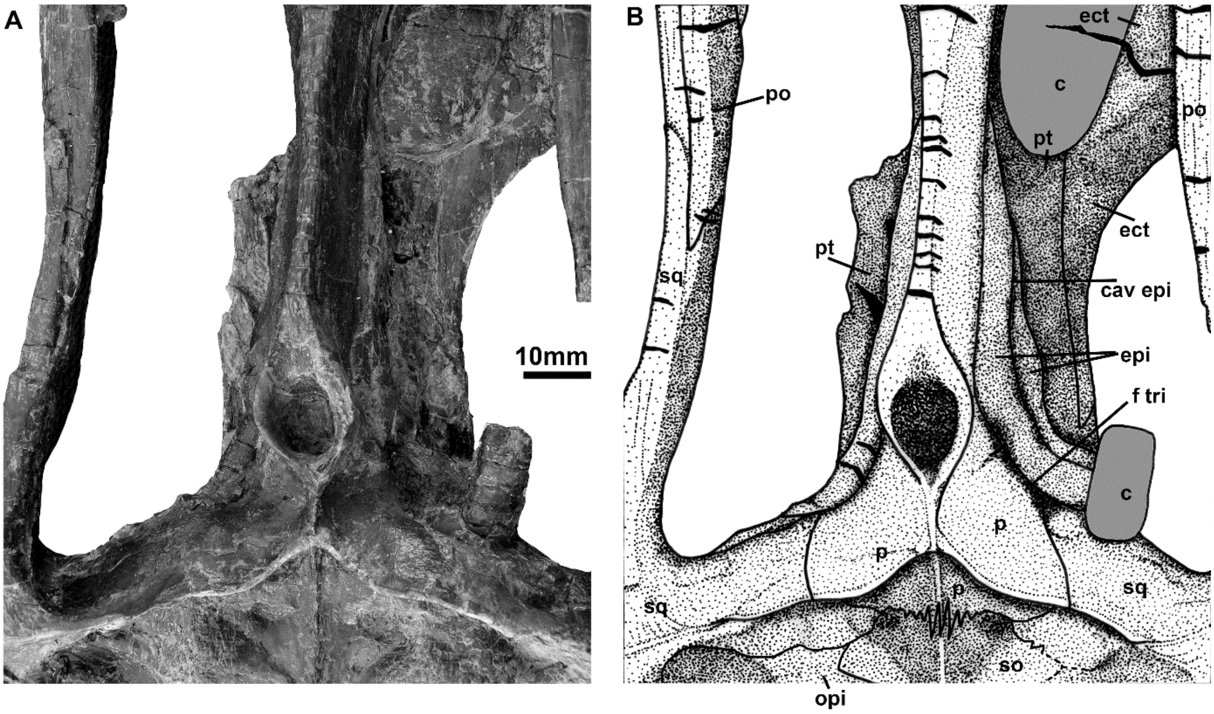


FIGURE 5. *Nothosaurus cristatus*, sp. nov., GPIT/RE/09800, from the Lower Keuper of Germany. A, photograph and B, drawing of the posterior skull roof with the parietal crista and parietal foramen. Abbreviations: c, coprolite; cav epi, anterior opening of the cavum epiptericum; ect, ectopterygoid; epi, epipterygoid; f tri, trigeminal foramen; opi, opisthotic; p, parietal; po, postorbital; pt, pterygoid; so, supraoccipital; sq, squamosal.

Skull Openings

Naris—The external naris is of elongated oval shape, 23 mm long and 13.5 mm wide (Fig. 2). The naris is bordered by the premaxilla, the maxilla, and the nasal, of which the contribution of the maxilla is slightly larger than that of the nasal. A small foramen is located at the anterolateral margin of the left naris. A distinct bulge marks the transition between the lateral margin of the external naris and the nasal floor. Medially, the opening of the internal naris is visible.

Orbit—Both orbits are dorsoventrally compressed but completely preserved. The anterior margin is formed by the prefrontal medially and the maxilla laterally. It is convex overall and shows a small posteriorly pointing dent at its middle, which is actually the squashed part of the ventral extension of the prefrontal that forms part of the anterior internal orbital cavity. There, the orbitonasal foramen is visible in the right orbit. The frontal forms the entire straight medial margin of the orbit. The lateral margin, which is formed by the maxilla, is almost straight, whereas the posterior margin, formed by the postfrontal and the maxilla, is evenly convex. This leads to an elongate oval shape of the orbit, with a slightly anteromedial–posterolateral orientation of the long axis. With a length of 36 mm and a width of 27 mm on both sides, the orbits are relatively small.

Upper Temporal Fenestra—The upper temporal fenestra has a length of 132 mm and a maximum width of 51 mm. The anterior margin is constricted and formed entirely by the postorbital. The inner margin widens after the constriction and continues almost parallel from that point onward, when the characteristic sagittal crest rises from the parietal. The outer margin, built by the postorbital and the squamosal, is almost straight. The posterior margin of the upper temporal fenestra is anteromedially–posterolaterally beveled and involves the parietal and the squamosal. A dominant ridge for the neck and jaw abduction muscle attachment marks the transition to the occipital skull roof.

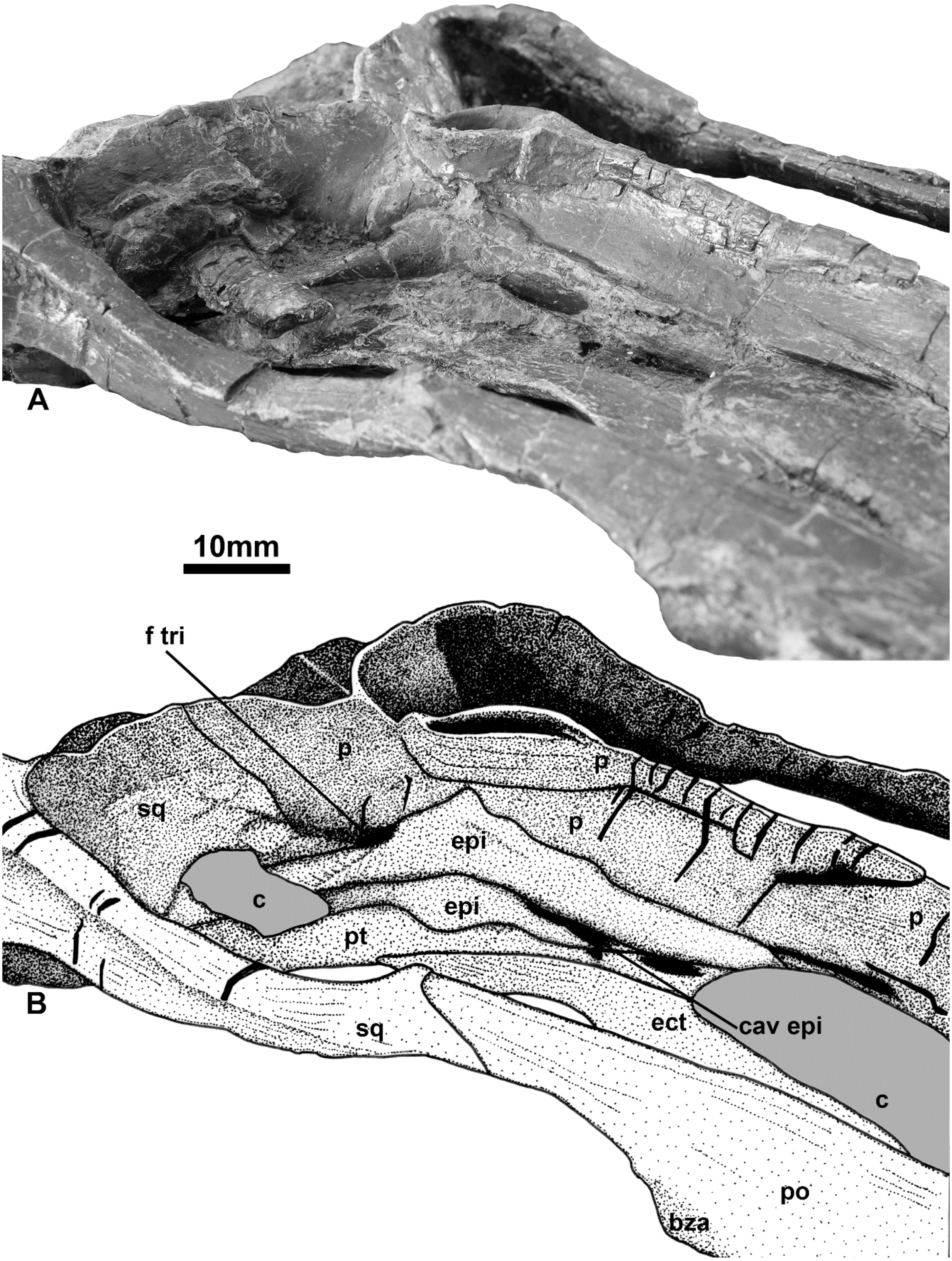


FIGURE 6. *Nothosaurus cristatus*, sp. nov., GPIT/RE/09800, from the Lower Keuper of Germany. A, photograph and B, drawing of the right posterior part of the skull in anterolateral view with the parietal crista, the parietal foramen, and the epipterygoid. Abbreviations: bza, base of the zygomatic arch; c, coprolite; cav epi, anterior opening

of the cavum epiptericum; ect, ectopterygoid; epi, epipterygoid; f tri, trigeminal foramen; p, parietal; po, postorbital; pt, pterygoid; sq, squamosal.

Palatal Elements

Vomer—Both elements are preserved and meet with each other along a straight median suture (Fig. 3). A large and slightly constricted anteromedial process reaches far between the premaxillae, splitting them almost halfway. The anterior tip of the vomeropremaxillary suture is strongly serrated, as are the posterior sutures with the palatine and the pterygoid. Laterally, the vomer contacts the maxilla and together they form the internal narial opening, which is an elongated oval.

Palatine—Both palatines are preserved, but only the right one is complete (Fig. 3). It is long, slender, and tapers slightly toward its anterior end. The palatine is excluded from the internal naris by the vomer, with which it forms a serrated vomeropalatinal suture. The palatine contacts the maxilla laterally and the pterygoid medially. Posteriorly, the palatine-pterygoid suture is difficult to identify due to the displaced jugal. It seems that there is no contact with the ectopterygoid (see Ectopterygoid, below).

Pterygoid—The right pterygoid is complete, but only the posterior half of the left pterygoid is preserved (Fig. 3). The median suture between the pterygoids is straight, except for the posterior-most 25 mm, where it is strongly serrated. The pterygoid contacts the vomer anteriorly and the palatine laterally. Posteriorly, and only visible on the right side, the pterygoid meets the ectopterygoid. The pterygoid forms the posteromedial margin of the fenestra subtemporalis where it forms a sharp ridge, which continues further posteriorly until it reaches the posterior end of the skull. Laterally, the ridge-like ramus quadratus extends at an angle of ca. 40° from a bony plate that forms the ventral part of the posterior margin of the subtemporal fenestra. This slightly biconvex ridge marks the contact between the pterygoid-squamosal anteriorly and the quadrate posteriorly.

Ectopterygoid—Only the right ectopterygoid is preserved (Figs. 3, 7). The entire anterior region of the ectopterygoid is problematic to interpret due to inadequate preservation. The displaced and overlying jugal and a dorsally attached coprolite embossing the thin bone surface affect the whole region. Therefore, it remains unclear whether there is an ectopterygoid-palatine contact anteriorly or, as we interpret it, the palatine is separated from the ectopterygoid by a small lateral extension of the pterygoid. In any case, the anterior ectopterygoid suture is difficult to identify and definitely—at least in part—co-ossified with the adjacent bones. Generally, in *Nothosaurus*, the ectopterygoid contacts the pterygoid medially and posteriorly and the maxilla anterolaterally. However, no direct contact between the maxilla and the ectopterygoid is observable on either side. A well-developed, knob-like processus transversus marks the lateral margin of the ectopterygoid. On the right side, where the ectopterygoid is still in situ, the processus transversus is far posterior to the posterior end of the maxilla. Further posteriorly, the suture runs parallel to the median suture of the pterygoid before it ends at about two-thirds of the length of the fenestra subtemporalis. This posterior process (Fig. 7) is remarkable in its shape and position, and even though the left ectopterygoid is missing, an articular facet of this process is preserved. The unique shape of the ectopterygoid in this specimen correlates with the well-developed sagittal crest in order to stabilize the intertemporal skull region against torsion exerted on this skull region during unilateral biting.

Occipital Elements

The whole occipital region is heavily compressed and has been crushed during fossilization. Most of the sutures, except for the parietal, are difficult to identify.

Quadrate—Both quadrates (Figs. 2, 3, 8) are preserved, but the right one is rather damaged due to the diagenetic compression. Dorsally, the quadrate meets the squamosal anteriorly and the opisthotic medially. In occipital view, the cranioquadrate passage can be seen. It is divided by a bony bar emerging laterally to the triangular bulge of the squamosal. In lateral view, the quadrate is visible as a rather thin bony plate, ascending at an angle of ca. 30° from posterior to anterior, oriented in the parasagittal plane along the long axis of the skull. The articular condyles are well developed and also oriented at an angle of 30°. Ventrally, the quadrate contacts the squamosal and the pterygoid medially. A deep cavity is located anterior to the condyles, marking the transition between the squamosal and the quadrate.

Epipterygoid—The epipterygoids are strongly dorsoventrally compressed and remarkably large (Figs. 2, 5, 6). This is related to the massive sagittal crest and the bending forces, high loads, and reaction forces applied to this area of the temporal region of the skull. The ectopterygoid spans between the parietal dorsally and the pterygoid ventrally and forms the lateral wall of the cavum epiptericum. The epipterygoid is characterized by two anterior and two posterior processes, which creates an ‘X’-shaped lateral appearance of the bone. The relatively massive triangular upper anterior ramus of the epipterygoid is 45 mm long. It narrows anteriorly and tapers off at approximately half of the length of the temporal fenestra. The lower anterior process (30 mm) is somewhat shorter and reaches only two-thirds of the length of the upper anterior ramus. The recess for the trigeminal nerve exit (Figs. 5, 6) is located at the posteromedial margin of the temporal fenestra. The maximum height of the epipterygoid lies directly below the anterior margin of the parietal foramen. From there, the lower posterior ramus of the epipterygoid branches off. It is dorsoventrally flattened, extends posterolaterally, and shows a distinct suture to the dorsal surface of the pterygoid at its base. The posterior end of the right epipterygoid is covered by a coprolite.

Supraoccipital—The supraoccipital shows a distinct sagittal ridge and forms the medial part of the occipital skull roof (Figs. 2, 5, 8). Anteriorly, it contacts the parietal via a strongly serrated suture. Laterally, it is triangular in shape and contacts the squamosal anteriorly and the opisthotic posteriorly. Ventrally, it forms the dorsal margin of the compressed foramen magnum and contacts the crushed exoccipitals laterally.

Exoccipital—The rather small exoccipitals are crushed on both sides (Figs. 2, 8). They contact the supraoccipital dorsally, the opisthotic laterally, and the basioccipital ventrally. Despite the heavy crushing, both jugular foramina are visible. The exoccipitals form the lateral margins of the foramen magnum.

Basioccipital—The basioccipital (Figs. 2, 8) alone forms the knob-like occipital condyle. Two lateral flanges emerging from the main portion of the basioccipital contact the opisthotic, the exoccipital, and the pterygoid ventrally. Dorsoventral flattening of the occipital region complicates the elucidation of the exact sutures.

Prootic—Due to the dorsoventral compression, no sign of the prootic can be found.

Opisthotic—The opisthotic contacts the squamosal anteriorly, the supraoccipital medially, the exoccipital posteromedially, the quadrate posterolaterally, and the pterygoid ventrally (Figs. 2, 5, 8). All sutures are rather straight, but the overall curvature of the sutures results in a strong interlocking of the bones involved in the occipital region of the skull. The left opisthotic is somewhat better preserved and shows a cylindrical shape, with its long axis oriented approximately 30° in the anteromedial–posterolateral direction, and a thickened lateral edge.

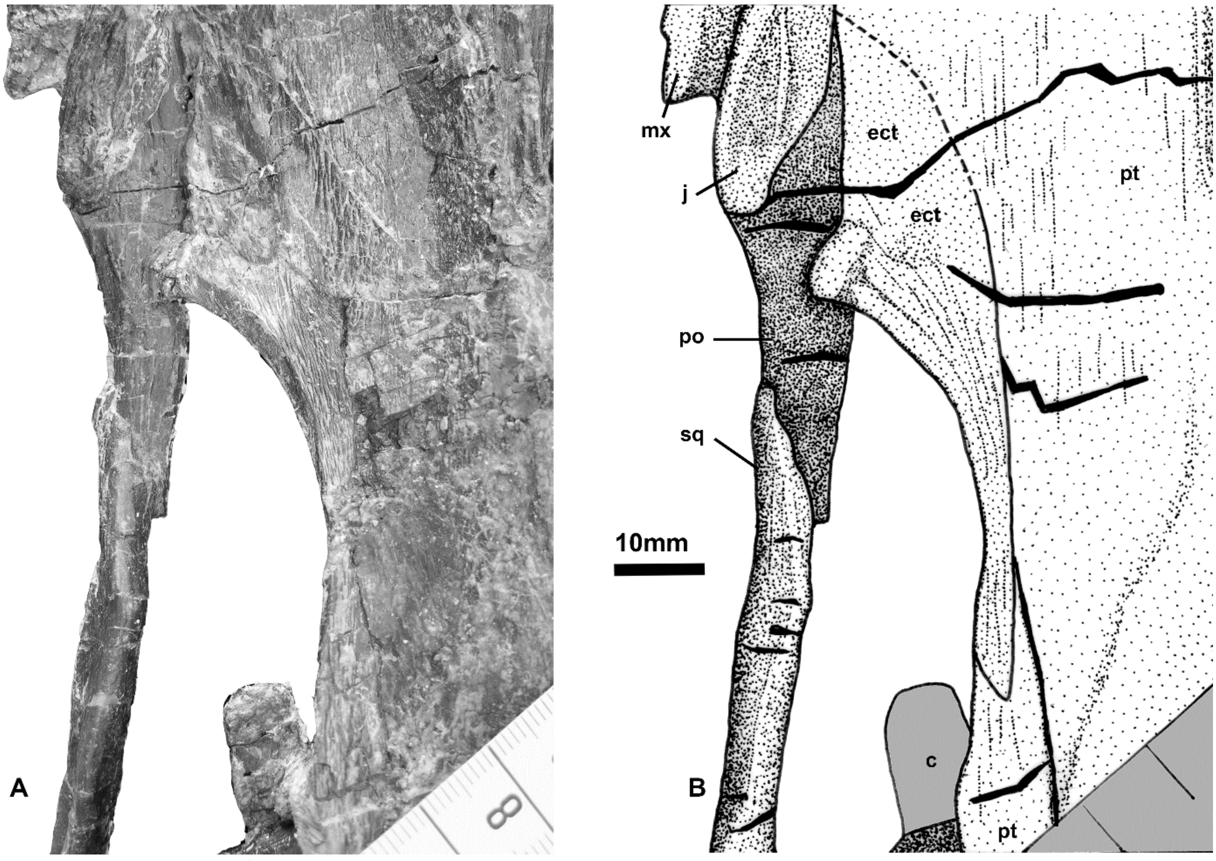


FIGURE 7. *Nothosaurus cristatus*, sp. nov., GPIT/RE/09800, from the Lower Keuper of Germany. A, photograph and B, drawing of the ventral part of skull with the ectopterygoid. Abbreviations: c, coprolite; ect, ectopterygoid; j, jugal; mx, maxilla; po, postorbital; pt, pterygoid; sq, squamosal.

COMPARISON

The new nothosaurid species *Nothosaurus cristatus*, sp. nov., described here is compared with all valid nothosaurs with well-known skulls, including *N. mirabilis*, *N. giganteus*, *N. marchicus*, *N. haasi*, *N. tchernovi*, *N. edingerae*, *N. yangjuanensis*, and *N. jagisteus* (Münster, 1834; Koken, 1893; Schultze, 1970; Haas, 1979; Rieppel et al., 1997; Rieppel, 2001; Jiang et al., 2006). It is also compared with species of *Lariosaurus*, including *L. juvenilis*, *L. xingyiensis*, *L. winkelhorsti*, and *L. youngi* (Edinger, 1921; Li & Liu, 2002; Li & Rieppel, 2004; Klein & Albers, 2009), as well as with the pistosaurs *Wangosaurus brevirostris*, *Augustasaurus hagdorni*, *Pistosaurus longaevus*, and *Yunguisaurus liae* (von Meyer, 1839; Sander et al., 1997; Cheng et al., 2006; Ma et al., 2015), because they show interesting details on the ectopterygoid/hyoid or the sagittal crest. Recently, Lin et al. (2017) reassigned ‘*N.*’ *juvenilis*, ‘*N.*’ *youngi*, and ‘*N.*’ *winkelhorsti* to *Lariosaurus* based on the results of their phylogenetic analysis. Here, we decided to include these three species in the general *Nothosaurus* comparison.

General Shape of the Skull

Because skull lengths of *Nothosaurus* species range from very small (13 cm in *N. edingerae*) to very large (over 70 cm in *N. giganteus*), the specimen described here with its condylobasal length of 38.3 cm lies well within the size range of nothosaurs. All species of *Nothosaurus* show a constriction of the premaxillary rostrum located in front of the external nares. The degree of constriction may vary from weak or none in *N. edingerae* (e.g., RIEPPEL & WILD, 1996) to very pronounced in *N. yangjuanensis* (Jiang et al., 2006). Two main shape types of the premaxillary rostra can be distinguished in nothosaurs: elongated rostra with almost parallel lateral margins of the premaxilla and a weak constriction, and spoon-shaped rostra with a rounded or subrounded premaxilla and a more pronounced constriction (*N. giganteus*, *N. marchicus*, *N. yangjuanensis*). In the case of *N. cristatus*, the rostrum is elongated, parallel-edged, and the constriction is weakly developed. It therefore resembles the rostrum shape type of *N. mirabilis*, *N. jagisteus*, and *N. tchernovi*. A long and slender rostrum is also developed in *N. haasi*, but contrary to the species listed above, *N. haasi* shows a more pronounced constriction and nonparallel edges of the premaxillary rostrum.

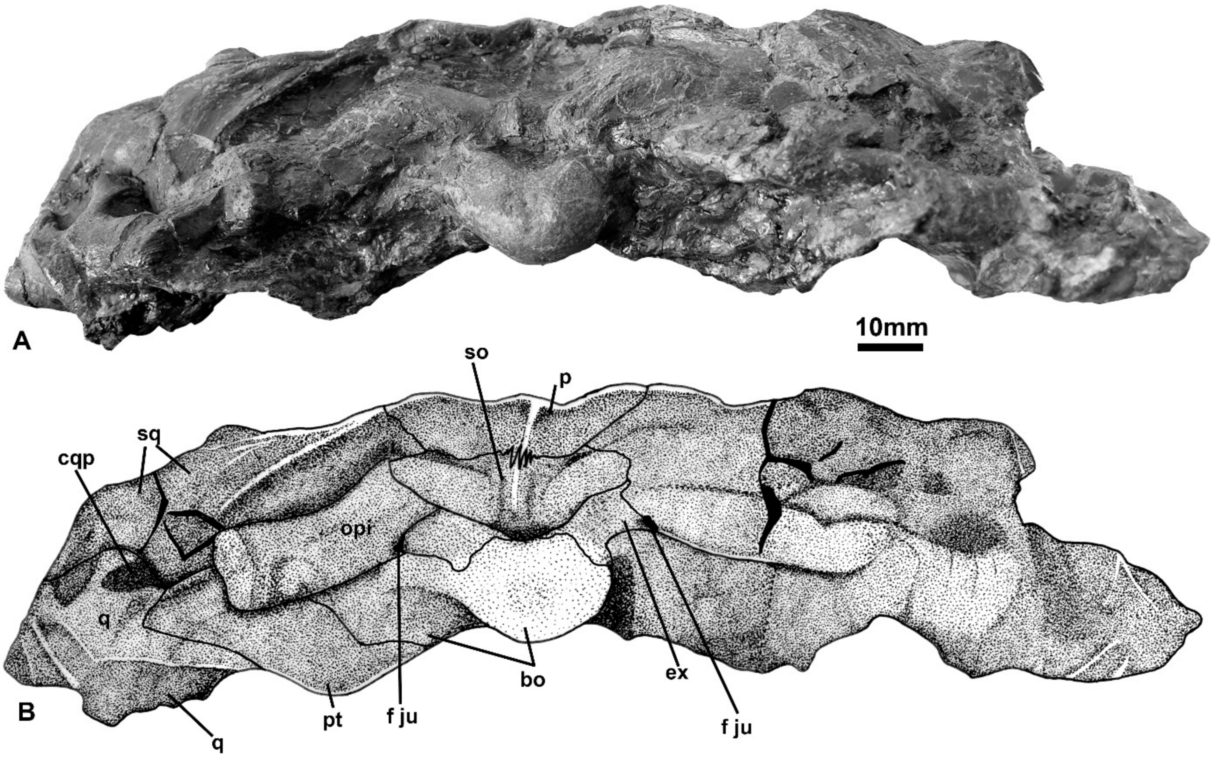


FIGURE 8. *Nothosaurus cristatus*, sp. nov., GPIT/RE/09800, from the Lower Keuper of Germany. A, photograph and B, drawing of the skull in posterior view. Abbreviations: bo, basioccipital; cqp, cranio quadrate passage; ex, exoccipital; f ju, jugular foramen; opi, opisthotic; p, parietal; pt, pterygoid; q, quadrate; so, supraoccipital; sq, squamosal.

Tooth Positions and Counts

The premaxilla in nothosaurs carries between four and five large anterograde fangs. *Nothosaurus cristatus* exhibits five alveoli for large fangs and shares this character with *N. marchicus*, *N. jagisteus*, *N. tchernovi*, *N. haasi*, and *N. mirabilis*. *Nothosaurus cristatus* can therefore be distinguished from nothosaur species having only four large fangs and one small premaxillary tooth, including *N. giganteus*, *N. yangjuanensis*, *L. winkelhorsti*, and probably *L. youngi*, which seems to share this character (Ji et al., 2014). Due to incomplete preservation, the tooth counts of *L. juvenilis* and *N. edingerae* remain unclear.

Orbitonasal Region

In *N. cristatus*, this region is characterized by paired nasals that cover the complete medial margins of the external nares. This condition can be found in all nothosaur species, except *N. haasi* and *L. youngi*. Nasals that are sutured with each other are characteristic of all nothosaur species except for *N. haasi*, SMNS 57047 (*N. giganteus*; RIEPPEL & WILD, 1996:fig. 12), and SMNS 13155 (*N. mirabilis*; RIEPPEL & WILD, 1996:fig. 60a). There, the nasals are separated along their midline by a premaxilla-frontal contact caused by two long and slender processes; therefore, it seems that this condition is variable. In *N. cristatus*, the midline suture and the suture between the nasal and the maxilla are parallel to each other along the orbitonasal bridge. This is also seen in *N. tchernovi*, *N. mirabilis*, and to some extent in *L. juvenilis*. In the latter species, this character is restricted to the anterior part of the nasal whereas the posterior part of the nasal tapers toward the midline suture. All other nothosaur species show rather triangular- or leaf-shaped nasals not resembling the rectangular shape found in *N. cristatus*.

The half-moon–shaped prefrontal of *N. cristatus* resembles the prefrontal described in some (SMNS 13155: RIEPPEL & WILD, 1996:fig. 60a; SMF R-641: RIEPPEL & WILD, 1996:fig. 59a), but not all, *N. mirabilis* skulls (RIEPPEL & WILD, 1996). Larger prefrontals also occur in *L. juvenilis*, *N. yangjuanensis*, and to some extent in *N. marchicus*, although the size of the prefrontal seems to be variable.

Postorbital Bridge

In GPIT/RE/09800, the postorbital bridge is 40 mm long, which is almost twice as long as the orbitonasal bridge (21 mm). This results in a postorbital length ratio of 1.9. A similar length ratio is only reached by some N. mirabilis specimens (values ranging from 0.83 in specimen SMNS 59074, up to over 1.5 in SMNS 56286) and *N. giganteus* (values over 2, e.g., in SMNS 7162). Smaller values can be found in *N. edingerae* (0.42) or *N. haasi* (0.5). *Nothosaurus cristatus* features a quite large and unconstricted postfrontal, which also occurs in *N. mirabilis*, *L. juvenilis*, some *N. marchicus* specimens, and to some extent in *N. jagisteus*. All other species show a lateral constriction of the postfrontal. Contrary to the state in all other described *Nothosaurus* species, the postorbital of *N. cristatus* is completely excluded from the orbit. This autapomorphy makes the skull described herein unique among known *Nothosaurus* skulls.

Sagittal Crest Formed by the Parietal and Location of the Parietal Foramen

Another autapomorphy of *N. cristatus* is the prominent, sharp sagittal crest formed by the parietal bones anterior to the parietal foramen. In all previously known nothosaurs, the parietals anterior to the parietal foramen form a flat, table-like skull roof. In all nothosaurs, the parietal foramen is located close to the posterior end of the parietal skull roof. A sagittal crest located behind the parietal foramen is so far only known from *N. edingerae* and now from *N. cristatus*, where the crest is shorter. Sagittal crests are also known from pistosaurids such as *Pistosaurus*, *Augustasaurus*, and *Yunguisaurus*. Unlike in nothosaurs, the parietal foramen of pistosaurids is located close to the anterior end of the upper temporal fenestra. Therefore, the prominent and sharp sagittal crest forms behind the parietal foramen. The recently described *Wangosaurus* (MA ET AL., 2015) differs from other pistosaurids in showing a posteriorly located parietal foramen and an anterior sagittal crest, similar to *N. cristatus* (see below).

Vomer

A long and slender anteromedial process, which divides the palatal portion of the premaxilla halfway, characterizes the vomer of *N. cristatus*. It ends between the third and the fourth premaxillary fang. This is also seen in *N. mirabilis* and *N. haasi*. This vomer shape seems to be restricted to long-snouted nothosaurs. Unfortunately, it is impossible to test this for *N. jagisteus* and *N. tchernovi* because the skulls of the holotypes are preserved with articulated lower jaws, which cover the part of the vomer in question. All short- and round-snouted nothosaurs, such as *N. giganteus*, *N. marchicus*, *N. edingerae*, and *N. yangjuanensis*, seem to have rather short vomers that do not reach far anteriorly.

Ectopterygoid and Hyoid

The ectopterygoid of *N. cristatus* is strongly developed and shows an autapomorphic posteriorly extending process flanking the pterygoid in the intertemporal region (Figs. 3, 7). Although lacking the left ectopterygoid, a large facet for the posteriorly extending process of the ectopterygoid is well exposed on the pterygoid (Fig. 3; see above). In *L. youngi*, *L. xingyiensis*, and *Yunguisaurus liae* (e.g., SATO ET AL., 2010), the hyoids are preserved and exposed at a similar location and orientation, but they are definitely not sutured to the pterygoids.

PHYLOGENETIC ANALYSIS

In order to assess the phylogenetic relationships of *N. cristatus*, a phylogenetic analysis was carried out. We used both PAUP* version 4.0b10 (SWOFFORD, 2000) as well as PAUP* version 4.0a164 (SWOFFORD, 2018) for Windows with identical results. The present analysis is based on the data matrix of LIU ET AL. (2014), which was later slightly updated by LIN ET AL. (2017), particularly for *L. youngi* and *L. xingyiensis*. We agree with the changes made by LIN ET AL. (2017) for characters 2, 32, and 67, and their coding changes. We also revised some incorrectly coded characters as well as identified two pairs of correlated characters (see Appendix S2 in Supplemental Data 1). *Nothosaurus zhangi* was excluded from the analysis because in this taxon only 12 of the original 74 characters can be coded, and *L. vosseveldensis* (e.g., KLEIN ET AL., 2016) was readded. These changes resulted in a new data matrix with 23 taxa and 72 characters (Supplemental Data 2). A heuristic search (ADDSEQ = RANDOM, NREPS = 1000, HOLD = 100) was performed. All characters were treated as unordered and were given equal weight, and the characters were all parsimony-informative. This leads to a single most parsimonious trees (Fig. 9) with a tree length of 216, a consistency index (CI) of 0.389, and a retention index (RI) of 0.53, results similar to those of LIU ET AL. (2014). The new taxon *N. cristatus*, as already suggested by its osteology, is closely related to other long-snouted species of *Nothosaurus*, and these taxa form a monophylum. *Nothosaurus jagisteus* is the sister taxon of this group, which includes (*N. cristatus* (*N. mirabilis*, *N. tchernovi*)).

We also attempted to include *Wangosaurus* (MA ET AL., 2015) in this cladistic analysis, although 38 characters had to be coded with question marks due to the short and preliminary description of this important species. However, it turned out that *Wangosaurus* is a rogue taxon and the results show no resolution.

As pointed out by LIN ET AL. (2017), this cladistic analysis does not support the monophyly of *Lariosaurus* and *Nothosaurus* despite the fact that all published phylogenies of the Sauropterygia assume monophyly of these genera (e.g., RIEPPEL & WILD, 1996), SATO ET AL. (2010, 2013, 2014), LIU ET AL. (2011), WU ET AL. (2011), CHENG ET AL. (2012), JIANG ET AL. (2014), and MA ET AL. (2015). The nonmonophyly of *Nothosaurus* and *Lariosaurus* in our analysis might be an artifact of combining two species-level matrices (from Rieppel, 1997, 2001) of these two closely related genera, as well as the removal of most of the outgroup and derived taxa such as *Cymatosaurus* and *Pistosaurus*. The monophyly of *Nothosaurus* and *Lariosaurus* remains an open question. The results of the bootstrap (1,000 replications) of the data matrix (Supplemental Data 2) presented here as well as the Bremer support (decay index) are included in Figure 9.

However, bootstrap values and Bremer support were low in the current analysis.

DISCUSSION AND CONCLUSIONS

Nothosaurus cristatus is a new nothosaurid from the middle Ladinian of southern Germany. It shares all autapomorphies of the genus *Nothosaurus* (RIEPPEL, 2000). *Nothosaurus cristatus* shows a suite of relatively derived characters within *Nothosaurus*, such as a long and slender rostrum with parallel lateral edges, a long and slender external narial opening, a long posterior extension of the maxillary tooth row, and a parietal foramen located far posteriorly. Osteologically, *N. cristatus* is therefore more similar to *N. mirabilis*, *N. tchernovi*, and *N. jagisteus*. It differs from all known *Nothosaurus* species by the following autapomorphies: (1) postfrontal and maxilla meet behind the orbit forming the posterior orbital margin, and, as a result, the postorbital is excluded from the orbit; (2) parietals form a pronounced, sharp crest along the midline, which is situated anteriorly and posteriorly to the large parietal foramen; and (3) ectopterygoid is large, with a long, slender posterior extension. The strict consensus tree of the cladistic analysis indicates that *N. cristatus* is the sister taxon of *N. mirabilis* and *N. tchernovi* and forms a clade with *N. jagisteus*. As pointed out

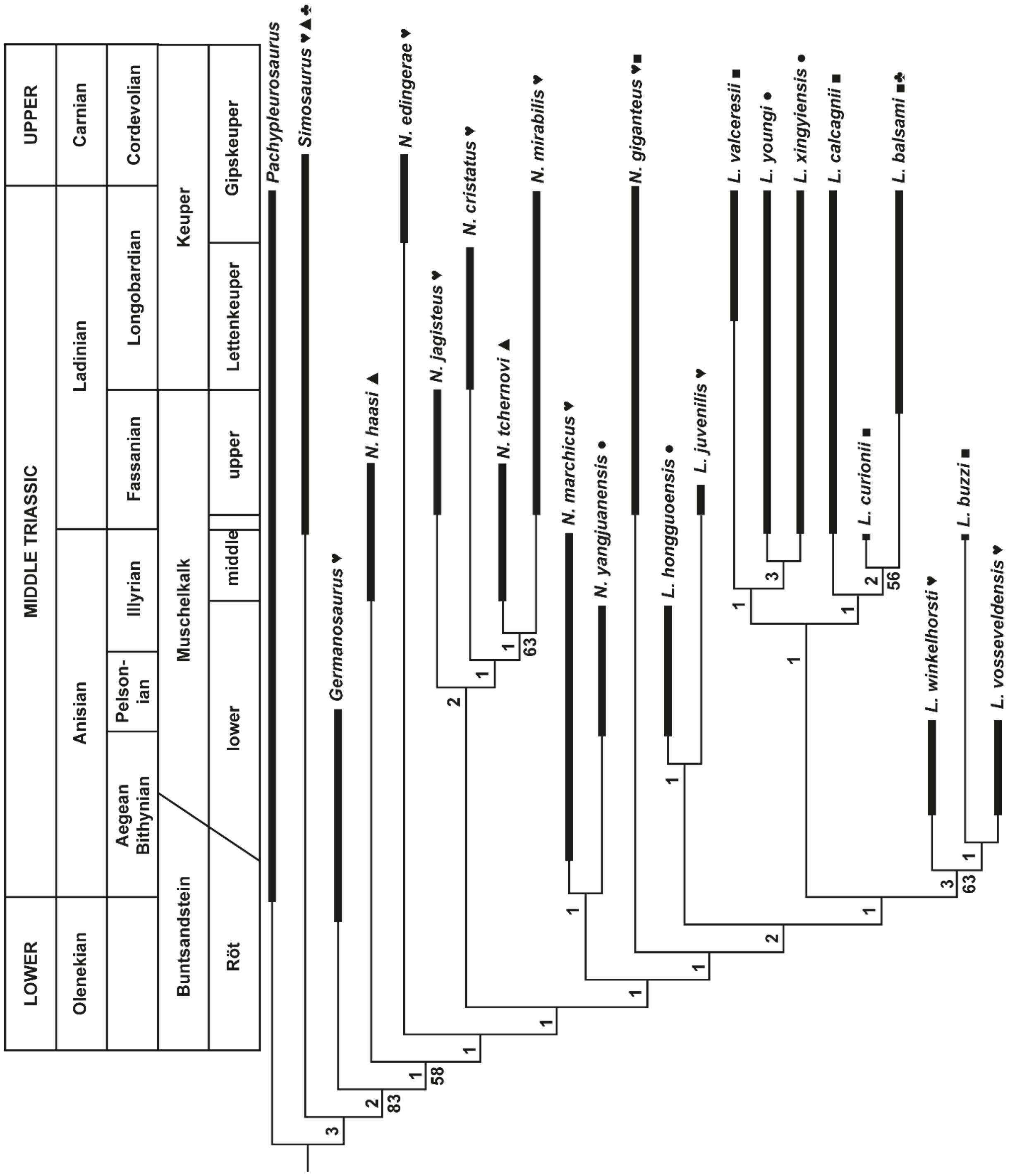


FIGURE 9. Strict consensus tree indicating the phylogenetic relationship of *Nothosaurus cristatus*, sp. nov., with other nothosaurids and lariosaurids. See text for tree statistics. Abbreviations: ♥, Germanic Basin; ▲, Middle East, Israel; ■, Monte San Giorgio; ♣, France, Spain; ●, East Asia, China.

above, the sagittal crest of *N. cristatus* is unique within the genus *Nothosaurus*. In pistosaurids, the presence of a sagittal crest is common. In *Augustasaurus*, the parietal foramen is located anteriorly, close to the frontal-parietal suture. In *Pistosaurus*, it is located just posterior to the frontal-parietal suture. In *Yunguisaurus*, the parietal foramen is further anteriorly, and the parietal foramen is formed by the parietal and the frontal. The sagittal crest in the aforementioned pistosaurs is formed by the parietal posterior to the parietal foramen. Recently, MA ET AL. (2015) described a new and quite unusual pistosaurid, *Wangosaurus brevirostris*, from China. In *Wangosaurus*, the parietal foramen is close to the posterior end of the dorsal skull roof; thus, the sagittal crest is expressed anteriorly. In fact, the whole region is morphologically similar to *N. cristatus*. Only the part of the skull anterior to the temporal fenestra is different in *Wangosaurus* and more similar to that region in *N. giganteus*, *N. yangjuanensis*, and *N. marchicus* than that in the pistosaurids mentioned above. Unfortunately, information on the ventral side of *Wangosaurus* is currently unavailable, and it remains unclear whether *Wangosaurus* possesses a posteriorly open palate similar to that in *Augustasaurus*, *Pistosaurus*, and *Yunguisaurus* or a *Nothosaurus*-like closed palate. *Wangosaurus* shows an occipital skull table similar to *Nothosaurus*, which is a condition not found in other pistosaurids. To clarify the affinities of *Wangosaurus* to either pistosaurids or *Nothosaurus*, the type specimen should be restudied to improve character scoring for phylogenetic analysis.

Together with *N. edingerae*, the new nothosaur described herein is the only valid species exclusively known from the Keuper of the Germanic Basin. Hopefully, new finds of more articulated specimens will improve our knowledge about nothosaurids from the Lower Keuper.

ACKNOWLEDGMENTS

We sincerely thank the Schumann family who granted access to their quarry in Vellberg-Eschenau. The excavation team from the University of Tübingen, G. Wild, A. Sattler, M. Schubert, T. Gabler, D. Schulz, and S. Ring, is thanked for their excellent field work. We would also like to thank M. Maisch (Albstadt) for helpful discussions about sauropterygians and the new specimen. H. Stöhr (Tübingen) did the exquisite preparation, and the photographs (Figs. 2, 3) were taken by W.

Gerber (Tübingen). We also thank R. Schoch (Stuttgart) for granting access to the sauropterygian collection of the Staatliches Museum für Naturkunde Stuttgart. F. Mittag (Tübingen) and G. A. Cordero (Tübingen) are thanked for proofreading, and S. Reiss (Cologne) is thanked for helpful comments.

REFERENCES

CHENG, L., CHEN, X., ZENG, X. AND CAI, Y. (2012): A new eosauropterygian (Diapsida: Sauropterygia) from the Middle Triassic of Luoping, Yunnan Province. – Journal of Earth Science, 23: 33-40.

CHENG, Y.-N., SATO, T., WU, X.-C. AND LI, C. (2006): First complete pistosauroid from the Triassic of China. – Journal of Vertebrate Paleontology, 26: 501-504.

DIEDRICH, C. G. (2009): Palaeogeographic evolution of the marine Middle Triassic marine Germanic Basin changements–with emphasis on the carbonate tidal flat and shallow marine habitats of reptiles in Central Pangaea. – Global and Planetary Change, 65: 27-55.

EDINGER, T. (1921): Über *Nothosaurus*. II. Zur Gaumenfrage. –

HAAS, G. (1979): Ein Nothosaurier-Schädel aus dem Muschelkalk des Wadi Ramon (Negev, Israel). – Annalen des Naturhistorischen Museums in Wien, 83: 119-125.

JI, C., JIANG, D.-Y., RIEPPEL, O., MOTANI, R., TINTORI, A. AND SUN, Z.-Y. (2014): A new specimen of *Nothosaurus youngi* from the Middle Triassic of Guizhou, China. – Journal of Vertebrate Paleontology, 34: 465-470.

JIANG, D.-Y., MAISCH, M. W., HAO, W.-C., PFRETZSCHNER, H., SUN, Y.-L. AND SUN, Z.-Y. (2005): *Nothosaurus* sp.(Reptilia, Sauiopterygia, Nothosauridae) from the Anisian (Middle Triassic) of Guizhou, southwestern China. – Neues Jahrbuch für Geologie und Paläontologie Monatshefte, 9: 565.

JIANG, D.-Y., MOTANI, R., TINTORI, A., RIEPPEL, O., CHEN, G.-B., HUANG, J.-D., ZHANG, R., SUN, Z.-Y. AND JI, C. (2014): The Early Triassic eosauropterygian *Majiashanosaurus discocoracoidis*, gen. et sp. nov. (Reptilia, Sauropterygia), from Chaohu, Anhui Province, People's Republic of China. – Journal of Vertebrate Paleontology, 34: 1044-1052.

JIANG, D., MAISCH, M., HAO, W., SUN, Y. AND SUN, Z. (2006): *Nothosaurus yangjuanensis* n. sp.(Reptilia, Sauropterygia, Notho-sauridae) from the middle Anisian (Middle Triassic) of Guizhou. – Neues Jahrbuch für Geologie und Paläontologie Monatshefte, 2006: 257-76.

KLEIN, N. AND ALBERS, P. C. (2009): A new species of the sauropsid reptile *Nothosaurus* from the Lower Muschelkalk of the western Germanic Basin, Winterswijk, The Netherlands. – Acta Palaeontologica Polonica, 54: 589-598.

KLEIN, N., VOETEN, D. F., HAARHUIS, A. AND BLEEKER, R. (2016): The earliest record of the genus *Lariosaurus* from the early middle Anisian (Middle Triassic) of the Germanic Basin. – Journal of Vertebrate Paleontology, 36: e1163712.

KOKEN, E. (1893): Beiträge zur Kenntnis der Gattung *Nothosaurus*. – Zeitschrift der Deutschen Geologischen Gesellschaft, 45: 337-377.

LI, J. AND LIU, J. (2002): A new species of *Lariosaurus* (Sauropterygia: Nothosauridae) from Triassic of Guizhou, southwest China. – Vertebrata Pal Asiatica, 40: 114-126.

LI, J. AND RIEPPEL, O. (2004): A new nothosaur from Middle Triassic of Guizhou, China. – Vertebrata PalAsiatica, 42: 1-12.

LIN, W.-B., JIANG, D.-Y., RIEPPEL, O., MOTANI, R., JI, C., TINTORI, A., SUN, Z.-Y. AND ZHOU, M. (2017): A New Specimen of *Lariosaurus xingyiensis* (Reptilia, Sauropterygia) from the Ladinian (Middle Triassic) Zhuganpo Member, Falang Formation, Guizhou, China. – Journal of Vertebrate Paleontology, 37: e1278703.

LIU, J., HU, S.-X., RIEPPEL, O., JIANG, D.-Y., BENTON, M. J., KELLEY, N. P., AITCHISON, J. C., ZHOU, C.-Y., WEN, W. AND HUANG, J.-Y. (2014): A gigantic nothosaur (Reptilia: Sauropterygia) from the Middle Triassic of SW China and its implication for the Triassic biotic recovery. – Scientific reports, 4: 7142.

LIU, J., RIEPPEL, O., JIANG, D.-Y., AITCHISON, J. C., MOTANI, R., ZHANG, Q.-Y., ZHOU, C.-Y. AND SUN, Y.-Y. (2011): A new pachypleurosaur (Reptilia: Sauropterygia) from the lower Middle Triassic of southwestern China and the phylogenetic relationships of Chinese pachypleurosaurs. – Journal of Vertebrate Paleontology, 31: 292-302.

MA, L.-T., JIANG, D.-Y., RIEPPEL, O., MOTANI, R. AND TINTORI, A. (2015): A new pistosauroid (Reptilia, Sauropterygia) from the late Ladinian Xingyi marine reptile level, southwestern China. – Journal of Vertebrate Paleontology, 35: e881832.

MÜLLER, R. D., CANNON, J., QIN, X., WATSON, R. J., GURNIS, M., WILLIAMS, S., PFAFFELMOSER, T., SETON, M., RUSSELL, S. H. AND ZAHIROVIC, S. (2018): GPlates: building a virtual Earth through deep time. – Geochemistry, Geophysics, Geosystems, 19: 2243-2261.

MÜNSTER, G. Z. (1834): Vorläufige Nachricht über einige neue Reptilien im Muschelkalke von Baiern. – Neues Jahrbuch für die Mineralogie, Geognosie, Geologie und Petrefactenkunde, 1834: 521-527.

RIEPPEL, O. (1994): Osteology of *Simosaurus gaillardoti* and the relationships of stem-group Sauropterygia. –

RIEPPEL, O. (1998): *Corosaurus alcovensis* Case and the phylogenetic interrelationships of Triassic stem-group Sauropterygia. – Zoological Journal of the Linnean Society, 124: 1-41.

RIEPPEL, O. (2000): Handbuch Der Paläoherpetologie - Sauropterygia I: Placodontia, Pachypleurosauria, Nothosauroidea, Pistosauroidea. pp; München (Pfeil Verlag).

RIEPPEL, O. (2001): A new species of *Nothosaurus* (Reptilia: Sauropterygia) from the upper Muschelkalk (lower Ladinian) of southwestern Germany. – Palaeontographica Abteilung A, 263: 137-161.

RIEPPEL, O., MAZIN, J.-M. AND TCHERNOV, E. (1997): Speciation along rifting continental margins: a new nothosaur from the Negev (Israel). – Comptes Rendus de l'Académie des Sciences-Series IIA-Earth and Planetary Science, 325: 991-997.

RIEPPEL, O., SANDER, P. M. AND STORRS, G. W. (2002): The skull of the pistosaur *Augustasaurus* from the Middle Triassic of northwestern Nevada. – Journal of Vertebrate Paleontology, 22: 577-592.

RIEPPEL, O. AND WILD, R. (1996): A Revision of the Genus *Nothosaurus* (Reptilia: Sauropterygia) from the Germanic Triassic with Comments on the Status of *Conchiosaurus clavatus*. – Fieldiana Geology, 34: 1-82.

SANDER, P. M. (1989): The pachypleurosaurids (Reptilia: Nothosauria) from the Middle Triassic of Monte San Giorgio (Switzerland) with the description of a new species. – Phil. Trans. R. Soc. Lond. B, 325: 561-666.

SANDER, P. M., RIEPPEL, O. C. AND BUCHER, H. (1997): A new pistosaurid (Reptilia: Sauropterygia) from the Middle Triassic of Nevada and its implications for the origin of the plesiosaurs. – Journal of Vertebrate Paleontology, 17: 526-533.

SATO, T., CHENG, Y.-N., WU, X.-C. AND LI, C. (2010): Osteology of *Yunguisaurus* (Reptilia; Sauropterygia), a Triassic pistosauroid from China. – Paleontological research, 14: 179-195.

SATO, T., CHENG, Y.-N., WU, X.-C. AND SHAN, H.-Y. (2014): *Diandongosaurus acutidentatus* Shang, Wu & Li, 2011 (Diapsida: Sauropterygia) and the relationships of Chinese eosauropterygians. – Geological Magazine, 151: 121-133.

SATO, T., ZHAO, L. J., WU, X. C. AND LI, C. (2013): A new specimen of the Triassic pistosauroid *Yunguisaurus*, with implications for the origin of Plesiosauria (Reptilia, Sauropterygia). – Palaeontology, 57: 55-76.

SCHOCH, R. R. (2002): Stratigraphie und Taphonomie wirbeltierreicher Schichten im Unterkeuper (Mitteltrias) von Vellberg (SW-Deutschland). 30 pp; Stuttgart (Staatliches Museum für Naturkunde).

SCHOCH, R. R. (2015): 10. Reptilien des Lettenkeupers. – Paleodiversity, 231-264.

SCHOCH, R. R. AND SEEGIS, D. (2016): A Middle Triassic palaeontological gold mine: the vertebrate deposits of Vellberg (Germany). – Palaeogeography, Palaeoclimatology, Palaeoecology, 459: 249-267.

SCHULTZE, H. (1970): Über *Nothosaurus*. Neubeschreibung eines Schädels aus dem Keuper. – Senckenbergiana lethaea, 51: 211-237.

SCOTESE, C. (2016): PALEOMAP PaleoAtlas for GPlates and the PaleoData Plotter Program, PALEOMAP Project. – Geological Society of America Abstracts with Programs, 48:

SHANG, Q. (2006): A new species of *Nothosaurus* from the early Middle Triassic of Guizhou, China. – Vertebrata PalAsiatica, 44: 238-249.

SWOFFORD, D. (2002): PAUP* version 4.0 b10. – Sinauer, Sunderland, MA,

SWOFFORD, D. (2018): PAUP* version 4.0 a164. – Sinauer, Sunderland, MA,

TSCHANZ, K. (1989): *Lariosaurus buzzii* n. sp. from the Middle Triassic of Monte San Giorgio (Switzerland) with comments on the classification of nothosaurs. – Palaeontographica Abteilung A, 153-179.

VON MEYER, H. (1839): Mitteilung an Prof. Bronn. – Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, 1839: 559-560.

VON ZITTEL, K. A. (1889): Handbuch der Paläontologie. 1. Paläozoologie: 3. Vertebrata: Pisces, Amphibia, Reptilia, Aves. 900 pp; Munich and Leipzig (Oldenbourg).

WU, X.-C., CHENG, Y.-N., LI, C., ZHAO, L.-J. AND SATO, T. (2011): New information on *Wumengosaurus delicatomandibularis* Jiang et al., 2008 (Diapsida: Sauropterygia), with a revision of the osteology and phylogeny of the taxon. – Journal of Vertebrate Paleontology, 31: 70-83.

14. Appendix 2 Supplement of the published manuscript " A new nothosaur (Sauropterygia) from the Ladinian of Vellberg-Eschenau, southern Germany”

Supplemental Data 1

Journal of Vertebrate Paleontology

A new nothosaur (Sauropterygia) from the Ladinian of Vellberg-Eschenau, southern Germany

JULIANE K. HINZ,* ANDREAS T. MATZKE, and HANS-ULRICH PFRETZSCHNER

Institut und Museum für Geologie und Paläontologie der Universität Tübingen,
Keplerstraße 17, 72074 Tübingen, Germany

14.1. Supplement 1. Measurements (in mm) of *N. cristatus* n. sp.

Skull total length	383.0
Distance from tip of premaxilla to naris left	87.3
Distance from tip of premaxilla to naris right	87.7
Maximal width of snout at premaxilla	44.7
Minimal width of snout at premaxilla	38.5
Naris width left	13.1
Naris width right	13.9
Naris length left	24.0
Naris length right	22.8

Smallest distance between nares	13.0
Orbit width left	26.5
Orbit width right	27.3
Orbit length left	35.4
Orbit length right	37.3
Smallest distance between both orbits	23.3
Distance between naris and orbit left	21.7
Distance between naris and orbit right	23.0
Distance between orbit and upper temporal fenestra left	39.0
Distance between orbit and upper temporal fenestra right	43.1
Maximal length of upper temporal fenestra left	135.9
Maximal length of upper temporal fenestra right	128.8
Width of upper temporal fenestra at anterior tip of parietal foramen left	49.5
Width of upper temporal fenestra at anterior tip of parietal foramen right	52.8
Width of parietal foramen	15.7
Length of parietal foramen	13.0
Maximal width of skull at level of occiput	162.3

14.2. Supplement 2. Changes of the character codings with explanations.

For the preparation of our manuscript we investigated original material of the following sauropterygians: *Simosaurus*, *Nothosaurus edingerae*, *N*. *marchicus*, *N*. *mirabilis*, *N*. *giganteus*, *N*. *jagisteus*, *Cymatosaurus erikae* and *C*. *gracilis*, as well as *Henodus* and *Placodus*. With our personal observations and the complete literature, we started to test the data matrix published by Liu et al. 2014 and the updated version by Lin et al. 2017.

Summary

In total we changed 52 character states. Additionally, the characters 26 and 27 turned out to be connected and therefore character 26 was excluded. Characters 44 and 45 are connected as well, but in this case we slightly changed the character description. With these changes implemented into the data matrix, it turned out that character 33 was parsimony uninformative and it was therefore excluded as well. This leads to a modified order of the characters starting with 27 that is now→26, 28→27, 29→28, 30→29, 31→30, 32→31, 34→32 and from character 34 all following character numbers are minus two until 74 that is now→72.

Nothosaurus zhangi was excluded from this analysis because from the 74 possible characters of the data matrix provided by Liu et al. 2014, 65 (88%) are unknown. *L*. *vosseveldensis* (for data codings see Klein et al. 2016) was included as Taxon 22, as well as *N*. *cristatus* as Taxon 23. Therefore, the new data matrix consists of 23 taxa and 72 characters.

Changes of original data matrix published by Liu et al. 2014, with the exception of the taxa *N*. *youngi* and *L*. *xingyiensis* that were already corrected by Lin et al. 2017.

The original order and the original character numbers of Liu et al. 2014 and Lin et al. 2017 are still used in the list below.

1. The use of unknown character state (?) versus variable character state (0/1)

Liu et al. 2014 always coded variable characters with a question mark. This is highly unusual. It was later corrected by Lin et al. 2017 for *N. youngi* and *L. xingyiensis*. The following codings were changed from a question mark to variable.

Character 8: 0/1) for *N. giganteus* (at least in SMNS 57047 no maxilla foramen present Rieppel & Wild 1996 p. 16)

Character 10: (0/1) for *N. mirabilis* (Rieppel & Wild 1996)

(0/1) for Pachypleurosauria (premaxilla-frontal contact in *Keichosaurus* versus a nasal-nasal contact in *Dactylosaurus*/*Anarosaurus*/*Serpianosaurus* and in *Neusticosaurus* it is variable)

Character 11: (0/1) for *N. marchicus* (Rieppel & Wild 1996)

Character 13: (0/1) for Pachypleurosauria (nasals large in *Dactylosaurus*/ *Anarosaurus*/ *Neusticosaurus*/ *Serpianosaurus* versus small nasals in *Keichosaurus*)

Character 14: (0/1) for Pachypleurosauria (nasal-prefrontal contact in *Neusticosaurus*/ *Keichosaurus*/ *Serpianosaurus*; variable in *Neusticosaurus* (Sander 1989) *Dactylosaurus* (Rieppel & Lin 1995: Fig.16, p. 15) and no contact in *Anarosaurus*)

(0/1) for *Simosaurus* variable after Chaves et al. 2018 p. 312

Character 17 (0/1) for *Simosaurus* variable after Chaves et al. 2018 p. 321

Character 19 (0/1) for *N. mirabilis* after Rieppel & Wild 1996 (Fig. 58 versus Fig. 59)

(0/1) for *N. giganteus* (Rieppel & Wild 1996)

Character 27 (0/1) for *N*. *marchicus* (RIEPPEL & WILD 1996)

Character 28 (0/1) for *N*. *marchicus* (RIEPPEL & WILD 1996)

Character 33: (0/1) for Pachypleurosauria (mandibular articulation at level with condyle (0) in *Neusticosaurus*/ *Serpianosaurus*/ *Keichosaurus* and distinctly behind (1) in *Dactylosaurus*/ *Anarosaurus*)

Character 46: (0/1) for *L*. *buzzi* (TSCHANZ 1989 p. 159: maxilla with 3 or 4 teeth in front of fangs)

2. **Character 29**: quadratojugal present (0) absent (1). Liu et al. 2014 coded many taxa despite the fact that the character states were never mentioned in the publication. Some publications mention that the 'quadratojugal can not be verified' and therefore it must be coded with a question mark. If the quadratojugal is not even mentioned in the publications, we assume that it must be coded with a question mark as well.

(0) for *N*. *mirabilis* quadratojugal present after RIEPPEL & WILD 1996 p. 68-69

(?) for *N*. *juvenilis* quadratojugal not mentioned by RIEPPEL 1994

(?) for *N*. *tchernovi* quadratojugal not mentioned by RIEPPEL ET AL. 1999.

(?) for *N*. *jagisteus* quadratojugal cannot be verified; see RIEPPEL 2001: p 144

(?) for *L*. *hongguoensis*. LIN ET AL 2017 changed the original coding by LIU ET AL. 2014

(0) to absent (1), however, after Jiang et al. 2006: 'There is no evidence for a quadratojugal'

(?) for *L*. *buzzi* quadratojugal is not mentioned by TSCHANZ 1989

(?) for *L*. *calgagnii* quadratojugal not mentioned in HÄNNI 2004

(?) for *L*. *curionii* quadratojugal not mentioned in RIEPPEL 1998, 2000

(?) for *L. valceresii* quadratojugal not mentioned in Tintori & Renesto 1990)

3. Other changed character codings

Pachypleurosauria (*Keichosaurus*, *Anarosaurus*, *Daytylosaurus*, *Neusticosaurus*, *Serpianosaurus*, *Dianopachysaurus*) (Peyer 1931, Mazin 1985, Sues & Carroll 1985, Sander 1989, Rieppel 1989, Tschanz 1989, Rieppel & Lin 1995, Lin & Rieppel 1998, Holmes et al. 2008, Liu et al. 2011)

7 (0) all pachypleurosaurids have paired premaxillas

32 (1) supraoccipital crest reduced because it is small in all pachypleurosaurids, but never absent

N. winkelhorsti (see Klein & Albers 2009)

28 (?) absent. No constriction described or figured

30 (0) pterygoid. ‘A prominent flange…’ p. 594

N. yangjuanensis

12 (1) was coded correctly by Jiang et al. 2006 char 7

23 (1) jugal-squamosal contact present Jiang et al. 2006: Fig.2, p. 265

N. marchicus

19 (1) skull table posterior to parietal foramen constricted Rieppel & Wild 1996

N. mirabilis

22 (1) always excluded except for SMNS 56838, but this specimen fragmentary and undiagnostic, after Rieppel & Wild p.66

N. juvenilis

23 (?) at the original skull the area in question is missing see Rieppel 1994

N. giganteus

10 (1) for *N. giganteus* (Rieppel & Wild 1996)

N. edingerae (see Rieppel & Wild 1994)

5 (0) no constriction see p.4

9 (0) nasals paired

28 (0) no anterior constriction of upper temporal fenestra

L. hongguoensis **(**see Jiang et al. 2006)

8 (?) maxillary foramen not mentioned in original description. It was originally coded by Liu et al. 2014 with (0) and later changed by Lin et al. 2017 to (1)

9 (0) nasals paired

12 (0) nasals shorter than wide

22 (0) jugal entering orbita

30 (?) transverse flanges unknown

L. buzzi (see Tschanz 1989)

19 (1) constriction posterior to parietal foramen present

L. calcagnii

20 (?) prefrontal small see Hänni 2004, Peyer 1931

22 (1) HÄNNI 2004 p.23

32 (2) HÄNNI 2004 p.24: ‘strong sagittal crest’

L. curionii (RIEPPEL 1989 and 2000)

11 (0) n not entirely forming lateral margin of naris

12 (?) length of nasal including the posterior part of nasal unknown

18 (1)

28 (0) no constriction

30 (?) no palate described

32 (?) not described

L. valceresii (TINTORI & RENESTO 1990)

23 (?) jugal unknown

30 (?) palate unknown

L. vosseveldensis (KLEIN ET AL. 2016)

15 (0) In our opinion, the parietal foramen of *L. vosseveldensis* is located in the center, and therefore much more similar to *L. winkelhorsti* or *L. buzzi* than to all other species of *Lariosaurus* or *Nothosaurus* and therefore recoded to (0).

4. connected characters

Characters 26 & 27

Character (26): Postfrontal

(0) entering upper temporal fossa

(1) excluded

Character (27): Postorbital forming entire anterior margin of upper temporal fenestra

(0) absent

(1) present

If the postfrontal is reaching the upper temporal fenestra, it is obvious that the postorbital is never forming the entire anterior margin. Therefore, the coding for the two characters are identical in LIU ET AL. (2014) except for *N*. *edingerae* (0) in 26 and (1) in 27, because the postfrontal of this taxon is very small, slender and forming only a small part of the upper temporal fenestra and therefore the postorbital in *N*. *edingerae* is larger, but only slightly. The codings for *N*. *youngi* provided by Liu are (1) and (1), later corrected by LIN ET AL. 2017 to (0/1) and (1). Due to the fact that both characters are connected, the character (26) is removed from the analysis.

Character 44 & 45

Character (44): Premaxillary teeth

(0) more than 5
(1) 5

Character (45): Premaxillary fangs

(0) absent
(1) present but less than 5
(2) 5 or more

These two characters are connected as well. For example, the *Nothosaurus* species *marchicus*, *jagisteus*, *tchernovi*, *haasi* and *mirabilis* all have 5 premaxillary fangs and therefore also exactly 5 premaxillary teeth; leading to the similar character status that is coded for two different characters.

Therefore, the character definition of character the original (44) now (42) is changed to: premaxillary fangs absent (0) and fangs present (1) and original character (45) now (43) is changed to: premaxillary fangs less than 5 (0) and 5 or more (1); (no fangs (-)).

New data for original character 44, now 42:

0011111111 1111111111 111

New data for original character 45, now 43:

--?0011?01 111?1???11 101

5. Data codings for *N. cristatus*:

2201110100 1101110211 0101011?11 2????????? ?1111????? ?????????? ?????????? ??

ADDITIONAL LITERATURE CITED

CHAVES, C. D. M., ORTEGA, F. AND PÉREZ-GARCÍA, A. (2018): Cranial variability of the European Middle Triassic sauropterygian *Simosaurus gaillardoti*. – Acta Palaentologica Polonica, 63: 315-326.

HÄNNI, K. (2004): Die Gattung *Ceresiosaurus*. (vdf Hochschulverlag AG).

HOLMES, R., CHENG, Y.-N. AND WU, X.-C. (2008): New information on the skull of *Keichousaurus hui* (Reptilia: Sauropterygia) with comments on sauropterygian interrelationships. – Journal of Vertebrate Paleontology, 28: 76-84.

LIN, K. AND RIEPPEL, O. (1998): Functional morphology and ontogeny of *Keichousaurus hui* (Reptilia, Sauropterygia).

MAZIN, J. M. (1985): A specimen of *Lariosaurus balsami* Curioni 1847, from the eastern Pyrenees (France). – Palaeontographica Abteilung A, 159-169.

PEYER, B. (1931): *Ceresiosaurus calcagnii* nov. gen. nov. spec. – Abhandlungen der Schweizerischen Palaontologischen Gesellschaft, 62: 1-87.

RIEPPEL, O. (1998): The status of the sauropterygia reptile genera Ceresiosaurus, Lariosaurus, and Silvestrosaurus from the Middle Triassic of Europe. – Fieldiana (Geology), ns, 38: 1-46.

RIEPPEL, O. AND LIN, K. (1995): Pachypleurosaurs (Reptilia: Sauropterygia) from the Lower Muschelkalk, and a review of the Pachypleurosauroidea. (Field Museum of Natural History).

SUES, H.-D. AND CARROLL, R. L. (1985): The pachypleurosaurid *Dactylosaurus schroederi* (Diapsida: Sauropterygia). – Canadian Journal of Earth Sciences, 22: 1602-1608.

TINTORI, A. AND RENESTO, S. (1990): A new *Lariosaurus* from the Kalkschieferzone (Uppermost Ladinian) of Valceresio (Varese, N. Italy). – Bollettino della Società Paleontologica Italiana, 29: 309-319.

15. Appendix 3 – Codings for the phylogeny described in chapter 13

Pachypleurosauria	**000000?000010?00000000000000000010?100000000000?00001000011100000100000?00100**
Simosaurus	221000000001001?1011000001100001001000100121010-100000101110001120100001010 0
Germanosaurus	2111101001011110011101111000??0?????????????1???0???????????????0??????????
N. winkelhorsti	11?110111001010000010111011111120??????????1100???????????????????????????
N. yangjuanensis	22011001000000101211010111110?1120?????1021?112001001100101010021111010001
N. marchicus	22011001001001 10?2?1011?1???11110101??1????12200?1001????1010020?00??101?1
N. mirabilis'	22011101001101 1012?10??001111111011111 1???212?11?1???011100100?0?????1????
N. juvenilis	11?011010011001001010101000 01?110???????????1?010???????????????01???011???
N. giganteus	22011001001101101101 01??0?11101101?11?10212111000102110100011 0211?10010??1
N. zhangi	?????????????????????????????????101100??1?????0??0??????????????????????
N. tchernovi	22011100001100101 2111--00?11111?011?????2?21211111???????00110????????????
N. haasi	02001100010111101 2111--1000011120??????????12011?????????11110?????????01?
N. youngi	2{1 2}00100100{0 1}10011020101010{0 1}11101{1 2}00{0 1}{0 1}{0 1}11111112{0 1}000111{0 1}00{0 1}{0 2}{0 1}000021112110{0 1}001
N. jagisteus	22011101001101101211010101101011011111 1?21112110??0?10111001100 0000??11???
N. edingerae	2200?000??100?111211???10011?11?????????????1?0?0??????????????????????????
L. hongguoensis	11001001?01??1100101010101101011010001 1100?0200?????0??0?010?0210021?01102
L. buzzii	0100101110010100 0101???1000011120100 1?11??11??00010?0100?0001111?0??10110?
L. calcagnii	0101000?000?001012100?000000111?00101?1???2????0110201010110102100 31111101
L. curionii	1100000?01110?10?211???001111110000?1?1?2?20?000011??0110110100111????????
L. balsami	1100100?010?0?10021?00100??0?11200001?1?2???????001?1001101101??1103110110?
L. valceresii	11?1100?000000101210??00000011100???1?1?1??02??001010????1000021112110?102
L. xingyiensis	{1 2}1001001001{0 1}00100210110101111 01201{0 1}010111121200011120100 01{0 1}000211{0 1}211??01?
N. cristatus	220111010011011102110101011 1?1120??????????1211???????????????????????????

16. Appendix 4 – A *Nothosaurus* (Sauropterygia) skull from Kupferzell (Triassic, late Ladinian; SW Germany)

A *Nothosaurus* (Sauropterygia) skull from Kupferzell (Triassic, late Ladinian; SW Germany)

Juliane K. Hinz, Andreas T. Matzke, Felix J. Augustin, and Hans-Ulrich Pfretzschner

With 3 figures

Abstract: Although the Triassic fossil Lagerstaette Kupferzell (Lettenkeuper, Erfurt Formation) is well known for the abundance of well-preserved vertebrate fossils, sauropterygian remains are still unpublished. Here, we describe an only partially preserved *Nothosaurus* skull from Kupferzell and refer it to *Nothosaurus giganteus*. The skull described herein is the second occurrence of *N. giganteus* from the Lower Keuper of the Germanic Basin and the first skull aside from the material from the Hoheneck Kalk which was originally referred to *N. chelydrops* and is now treated as a junior synonym of *N. giganteus*. The presence of such large predatory marine reptiles indicates a stronger marine influence in the Lettenkeuper than currently thought.

Key words: Sauropterygia, *Nothosaurus giganteus*, Lettenkeuper, Ladinian, Triassic, Kupferzell, Germanic Basin.

INTRODUCTION

In 1977, the amateur paleontologist Georg Wegele discovered well-preserved bones from the Lettenkeuper (Erfurt Formation, Ladinian, Lower Keuper) at the construction site of a new section of the motorway A6 between Nuremberg and Heilbronn, close to the junction Kupferzell. Due to the abundance of fossil finds and the exceptional preservation, the importance of the locality was immediately recognized, and a salvage excavation was launched. Over 30,000 fossils were recovered within two months (MUNDLOS & WEGELE 1978; SCHOCH 2006). The shortage of time allowed neither the production of find drawings, nor high-resolution stratigraphy or sedimentological analyses (HAGDORN et al. 2015a). Today, the fossil Lagerstaette Kupferzell is world famous for its richness in vertebrate fossils including fishes, amphibians, and reptiles (for an overview, see HAGDORN et al. 2015c).

Among the 30,000 fossils, only very few remains belong to nothosaurs, the only marine vertebrates recovered so far from Kupferzell. Sauropterygian remains in general, and those of *Nothosaurus* in particular, are rare in the Lower Keuper and only a few diagnostic specimens have hitherto been identified. So far, only two species are exclusively known from the Lower Keuper: *Nothosaurus cristatus* represented by an exceptionally preserved skull from the Lettenkeuper of Vellberg-Eschenau (HINZ ET AL. 2019) and *Nothosaurus edingerae*, which is represented by two skulls from the Gipskeuper [= Grabfeld Formation in modern lithstratigraphy] (EDINGER 1921; RIEPPEL & WILD 1994; SCHULTZE 1970). Additionally, two species occur in the Lower Keuper as well as in the Upper Muschelkalk: *Nothosaurus mirabilis* and *Nothosaurus giganteus* (RIEPPEL & WILD 1996). Of particular interest here is that the presence of *N. giganteus* in the Lower Keuper is based so far on the referral of *N. chelydrops* (FRAAS 1896) to *N. giganteus* by RIEPPEL & WILD (1996). Herein we provide a detailed description of the *Nothosaurus* skull material from Kupferzell (SMNS 80261), which was originally described as a highly deformed *Batrachotomus* occiput by GOWER (1999).

Institutional abbreviations: BT, Urwelt-Museum Bayreuth; GPIT, Geologisch-Paläontologisches Institut Tübingen; PIMUZ, Paläontologisches Institut und Museum Zürich, SMF, Senckenbergmuseum Frankfurt; SMNS, Staatliches Museum für Naturkunde Stuttgart

GEOLOGICAL SETTING

The Kupferzell fossil Konzentratlagerstaette geologically belongs to the Erfurt Formation and lies within the Upper Lettenkeuper (e.g., BRUNNER 1977; URLICHS 1982; HAGDORN ET AL. 2015a; HAGDORN ET AL. 2015b; HAGDORN ET AL. 2015c). The Lettenkeuper (Lower Keuper, Erfurt Formation) in southern Germany is a mixture of terrestrial and marine successions with an alternating series of claystones, siltstones, dolomites, and marlstones and has a thickness of about 20–25 m. At the excavation site, sediments from the Anthrakonitbank up to the Obere Graue Mergel were exposed (Fig. 1). Between Kupferzell and Herdtlingshagen, the first horizon with recorded *Nothosaurus* remains is the Anthrakonitbank, which includes a bonebed containing the remains of fishes, plagiosaurs, and mastodonsaurs as well as coprolites (URLICHS 1982) between the basal dolomite and the following limestone layer. The next distinct sedimentary unit is the Untere Graue Mergel consisting of green to grey marlstones.

Carbonate nodules in the uppermost marlstone layer containing nothosaur postcranial material mark the second *Nothosaurus*-bearing horizon (SCHOCH 1999; URLICHS 1982). The following Anoplophoradolomit is devoid of fossils and consists of layers of dolomite, interbedded with marlstones and claystones. Above the Anoplophoradolomit follows a relatively thin layer, the Obere Graue Mergel, comprising light grey to light violet marlstones. A bonebed at the base of this layer contains nothosaur vertebrae as well as rare material of plagiosaurs, mastodonsaurs, and thecodonts. In earlier stratigraphic descriptions, the Obere Graue Mergel was not treated as a separate layer but included in a bed also containing the Anoplophoradolomit and the Linguladolomit. This led to the confusion of the Untere and Obere Graue Mergel (HAGDORN 1980; WILD 1987). The last stratigraphic layer exposed at the Kupferzell excavation site is the Obere Graue Mergel, resting on top of the Anoplophoradolomit, constituting the third horizon that contains nothosaur vertebrae.

The Lettenkeuper environment of the Kupferzell region has been interpreted as a mosaic of shallow and deep lakes surrounded by a possibly swampy hinterland. This landscape was inhabited by small and large amphibians, such as *Kupferzellia* (SCHOCH 1997), *Plagiosuchus* (FRAAS 1913), *Gerrothorax* (FRAAS 1913) and *Mastodonsaurus* (v. Jäger 1828), as well as by the large carnivorous rauisuchian *Batrachotomus* (GOWER 1999). Storm events and river floods concentrated the fossil remains in channels, leading to an extremely high density of bones and bone fragments at Kupferzell (HAGDORN et al. 2015). In addition to these terrestrial deposits, marine intercalations repeatedly occurred throughout the Lettenkeuper. In Kupferzell, these marine episodes are evinced by the presence of dolomites and the sparse nothosaur remains (URLICHS 1982), including cranial (see below) as well as postcranial material (pers. obs).

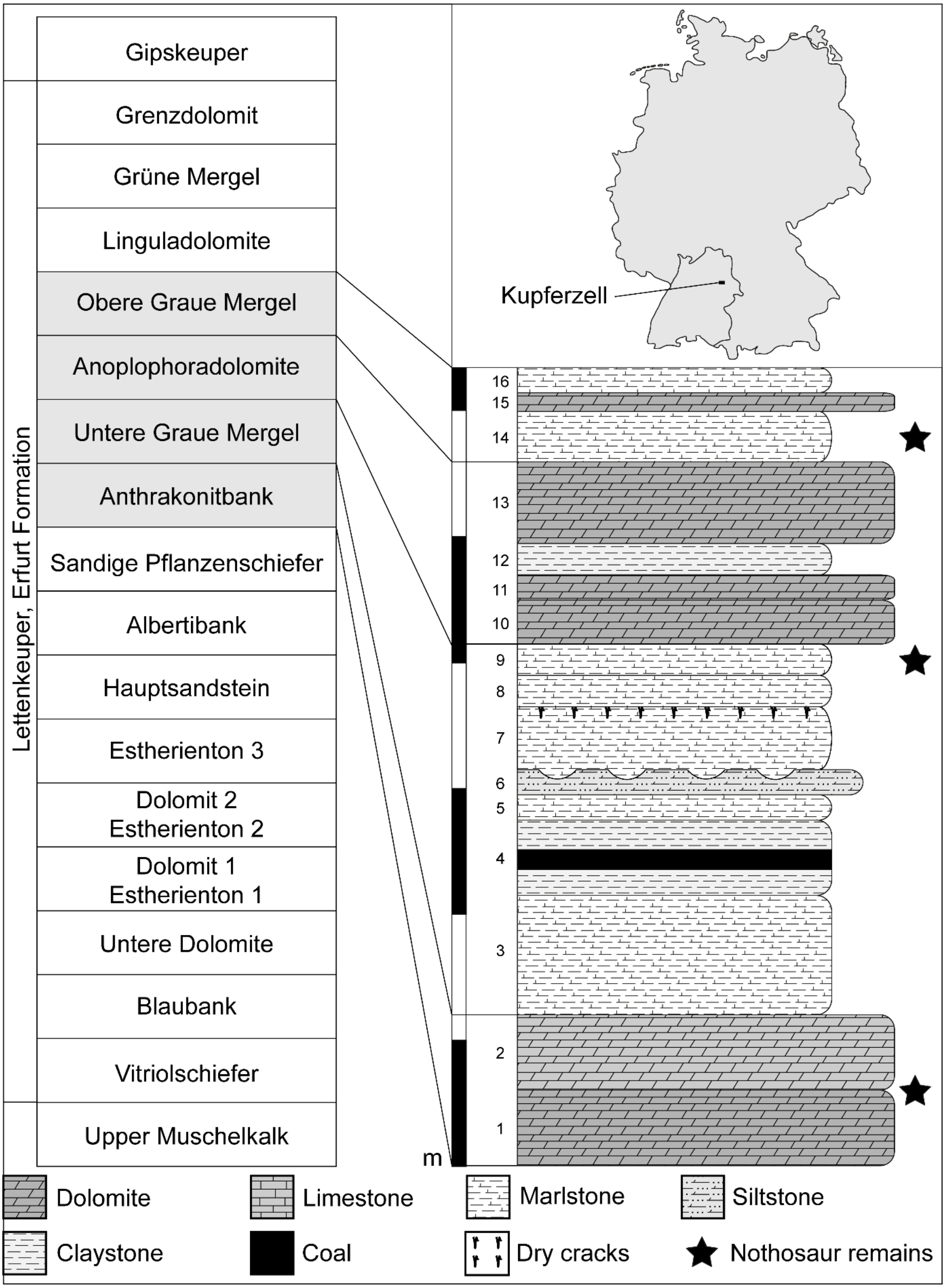


Fig. 1. Stratigraphy and location of the Kupferzell site with a short description of all layers after Urlichs (1982) and Hagdorn et al. (2015). The Anthrakonitbank consists of a massive dolomite layer (1) which is followed by a limestone (2). The base of the following Untere Graue Mergel sequence is formed by a green to grey marlstone (4)

which is topped by a coal-rich claystone (5). Atop lies a grey marlstone layer (5), which is followed by a brown siltstone (6) containing red hematite concretions and erosion channels in its uppermost part. The following green marlstones (7) with dry cracks are topped by a yellow dolomitic marlstone (8) and an ochre brown marlstone (8), which represents the uppermost part of the Untere Graue Mergel. The following Anoplophoradolomit sequence yields massive dolomite layers (10, 11), between which lies an only a few centimeters thin clay and marlstone layer separating the two massive dolomite banks. Atop lies a claystone layer (12), followed by a heavily eroded dolomite layer (13). The Obere Graue Mergel consist of light violet to grey marlstones (14, 16) with an interbedded dolomite layer (15).

SYSTEMATIC PALEONTOLOGY

Order EOSAUROPTERYGIA RIEPPEL, 1994
Suborder EUSAUROPTERYGIA TSCHANZ, 1989
Infraorder NOTHOSAUROIDEA BAUR, 1889 (in ZITTEL, 1887–1890)
Superfamily NOTHOSAURIA BAUR, 1889 (in ZITTEL, 1887–1890)
Family NOTHOSAURIDAE BAUR, 1889 (in ZITTEL, 1887–1890)
Genus *NOTHOSAURUS* MÜNSTER, 1834
NOTHOSAURUS GIGANTEUS MÜNSTER, 1834 Figs. 2, 3

Referred material: SMNS 80261, a heavily crushed occiput.

Remark: This specimen was initially referred to *Batrachotomus kupferzellensis* by GOWER (1999, 2002) and GOWER & SCHOCH (2009)

The cranial remains can be referred to the genus *Nothosaurus* through a diagnostic combination of characteristic features for this genus including the nothosaur-typical topology of bones within the occipital skull surface like a crested supraoccipital, a remarkably large opisthotic, a large condyle as well as the presence of a far posterior lying parietal foramen, and a closed posteriormost palate.

Due to the state of preservation, diagnostic features of the facial skull and the snout remain unclear.

DESCRIPTION

The occiput described herein is heavily crushed and strongly dorsoventrally compressed. Only the cranium posterior to the parietal foramen is preserved. The preserved skull parts comprise the posterior end of the intertemporal skull region including the parietal foramen, the posterior ends of the zygomatic arch, the posterior end of the pterygoids, and the almost complete occiput. The maximum width of the occipital skull region is 18.8 cm. Following the proportions of similarly sized nothosaur skulls, this results in an estimated total condlyobasal length of approximately 40 cm. For the estimation, the skulls of *N. cristatus* (GPIT/ RE/09800, maximum width 16.23 cm, condylobasal length 38.3 cm, HINZ ET AL. 2019) and *N. mirabilis* (SMNS 56286, maximum width 21 cm, condylobasal length 43.4 cm, pers. obs.) were used. The parietal skull table length posterior to the parietal foramen in SMNS 80261 measures 1.67 cm. To further quantify the differences between skull proportions of different nothosaur skulls, we introduce a new parameter, which is calculated as a ratio of post-foraminal skull table length to the maximum skull width (henceforth called PFPS-ratio); in SMNS 80261, this ratio is 0.09.

Parietal (Fig. 2): The parietals are fused into a single parietal element and contribute to the dorsal and marginally to the anteriormost occipital region of the skull. Posteriorly, the parietal contacts the fused supraoccipital and, laterally, the squamosals. It includes an oval parietal foramen with a length of 1.3 cm and a width of 0.6 cm, resulting in a length-to-width ratio of 2.2. Anteriorly, on the inner rim of the parietal foramen, a vertical groove descends into the foramen. The parietals do not support a crest anterior or posterior to the parietal foramen. A shallow ridge on the parietal is, however, preserved in the occipital portion of the skull.

Squamosal (Fig. 2): The anterior parts of the squamosals are broken off. Therefore, only the posterior end of the squamosal forming the zygomatic arch, parts of the posterior of the upper temporal fenestra, and a small portion taking part in the occipital skull region are preserved. In the occipital region, the squamosal forms a triangular process, which contacts the quadrate posterolaterally, the opisthotic posteromedially, and the supraoccipital anteromedially.

Upper Temporal Fenestra (Fig. 2): The shape of posterior margin of the upper temporal fenestra is best preserved on the left side of the skull. It is anteromedially-

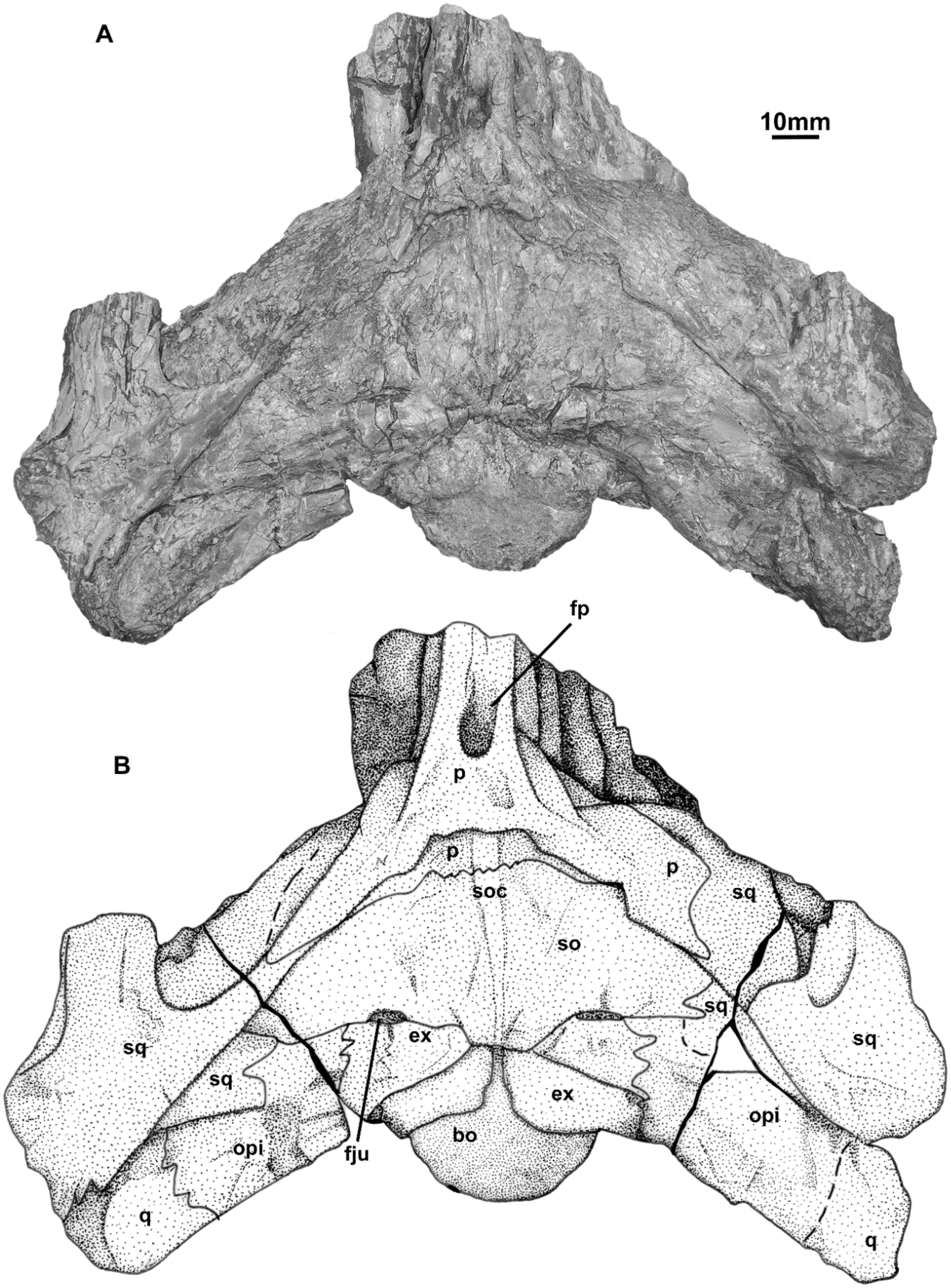


Fig. 2. The Kupferzell skull of *Nothosaurus giganteus* SMNS 80261 from the Lettenkeuper (Erfurt Formation, Late Ladinian). Skull in dorsal view. **A** – Photograph, **B** – drawing, Abbreviations: bo = basioccipital, ex = exoccipital, fju = jugular foramen, opi = opisthotic, p = parietal, q = quadrate, so = supraoccipital, soc = supraoccipital crest, sq = squamosal.

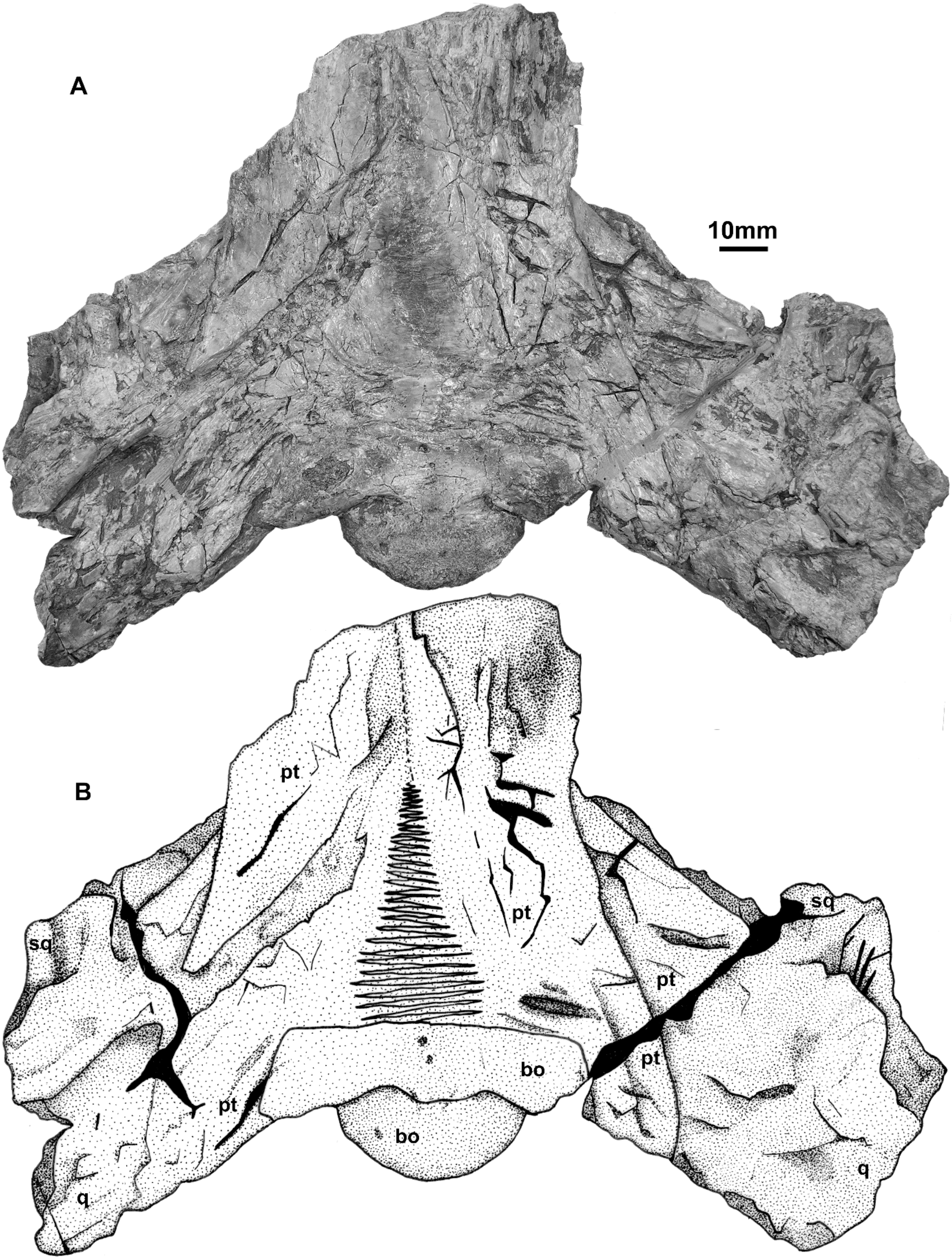


Fig. 3. The Kupferzell skull of *Nothosaurus giganteus* SMNS 80261 from the Lettenkeuper (Erfurt Formation, Late Ladinian). Skull in ventral view. **A**: photograph, **B**: drawing, Abbreviations: bo = basioccipital, pt = pterygoid, q = quadrate, sq = squamosal.

posterolaterally beveled in an acute angle of 40 degrees and involves the parietal and squamosal.

Pterygoid (Fig. 3): The posterior ends of both pterygoids are preserved. A crack, associated with the taphonomic distortion of the skull, bisects the posterior portion of the right pterygoid. The preserved part of the median suture between both pterygoids is straight, except for the posteriormost 4.4 cm, where a strong serration, which is typical in nothosaurs, can be seen. The pterygoid forms the posteromedial margin of the subtemporal fenestra where it forms a sharp ridge, which continues towards the posterior end of the skull in a convex curve. Laterally, in an angle of approximately 40 degrees, the ridge-like ramus quadratus extends from a bony plate, which forms the ventral part of the posterior margin of the subtemporal fenestra.

Quadrate (Figs. 2, 3): Both quadrates are partially preserved, but the right one is damaged as a result of diagenetic compression. On the left side, the dorsal portion of the quadrate meets the squamosal dorsally and the opisthotic medially. Although the exact positions of the sutures remain unclear, the ventral portion of the quadrate contacts the squamosal anteriorly and the pterygoid medially.

Quadratojugal: A quadratojugal cannot be identified on either side.

Supraoccipital (Fig. 2): The supraoccipital bears a distinct sagittal ridge and forms a major part of the occipital skull roof. Anteriorly, it contacts the parietal through a slightly serrated suture. Laterally, a wing-like process of the supraoccipital contacts the squamosal posteriorly and laterally, and the opisthotic and exoccipital posteroventrally. It also forms the dorsal margin of the compressed foramen magnum.

Exoccipital (Fig. 2): The exoccipitals contact the supraoccipital dorsally, the opisthotic laterally, and the basioccipital ventrally. Except for the serrated opisthotic-exoccipital suture, all other sutures are straight. Both jugular foramina are visible. The left jugular foramen lies completely embedded between the supraoccipital and the exoccipital, whereas the right one has a pointed contact with the squamosal. The exoccipitals compose the lateral margins of the foramen magnum.

Basioccipital (Figs. 2, 3): The basioccipital forms the ventral margin of the foramen magnum and the knob-like occipital condyle, which is completely flattened and dorsoventrally only 0.7 cm thick. In dorsal view, the basioccipital contacts the exoccipital anteriorly. The ventral part of the exoccipital forms two lateral flanges emerging from the main portion of exoccipital, which contact the pterygoid anteriorly and laterally.

Opisthotic (Fig. 2): The opisthotic contacts the squamosal anterolaterally, the supraoccipital anteromedially, the exoccipital medially, the quadrate posterolaterally, and the pterygoid ventrally. All sutures are slightly serrated, except for the anterior contact with the supraoccipital. The left opisthotic is somewhat better preserved and shows an almost 90-degree angle within the opisthotic-squamosal suture, which causes a strong interlocking of the bones involved in the occipital region of the skull.

COMPARISONS

Due to the state of preservation, especially the lack of the facial skull region, most of the diagnostic features of the Kupferzell skull remain unclear. To identify the preserved part of the Kupferzell skull, we compared the occipital skull region of SMNS 80261 only to other occiputs of nothosaurs known from Upper Muschelkalk (Lower Ladinian) and Keuper (Middle to Upper Ladinian) deposits of the Germanic Basin: (i) *N. jagisteus* RIEPPEL, 2001, (ii) *N. giganteus* MÜNSTER, 1834, and (iii) *N. mirabilis* MÜNSTER, 1834, all occurring in the Keuper and the Upper Muschelkalk as well as (iv) *N. cristatus* HINZ ET AL., 2019 and (v) *N. edingerae* SCHULTZE, 1970, which are known exclusively from the Keuper. *N. marchicus* KOKEN, 1893 was excluded since it is restricted to the Anisian.

Comparison with *N. edingerae*

There are two known skulls of *N. edingerae* (the holotype SMF R-4035 first published by EDINGER 1921 and later described by SCHULTZE 1970 and SMNS 59072 described by RIEPPEL & WILD 1994), both from the Gipskeuper [= Grabfeld Formation]. Both skulls are comparatively small with overall skull lengths of approximately 14 cm in the holotype and 12.9 cm in SMNS 59072. Both are remarkably smaller than the Kupferzell skull, which has an estimated skull length of 40 cm. SMF R-4035 lacks the posterior part of the right zygomatic arch, the right quadratic region and the right joint, whereas SMNS 59072 lacks the left zygomatic arch, the right and left quadratic region and both jaw joints. Due to this fact, only the completely preserved left half of SMF R-4035 was measured for this comparison. The measured width of 3.4 cm leads to an estimated total maximum skull width of 6.8 cm.

This is significantly smaller than the measured 18.8 cm maximum width of SMNS 80261. *N. edingerae* and SMNS 80261 both show an elongated oval parietal foramen with a length-to-width ratio of 2:1. In contrast to SMNS 80261, the skull of *N. edingerae* shows sharp ridges flanking the foramen laterally. The Kupferzell occiput also lacks a prominent sagittal crest posterior to the parietal foramen, which is present in both *N. edingerae* skulls. The holotype of *N. edingerae* shows a PFPS-ratio of 0.13 whereas the Kupferzell skull has a PFPS-ratio of 0.09. On the parietal and occipital skull table, a noticeable ridge is present in SMNS 80261 but absent in *N. edingerae*. Therefore, SMNS 80261 clearly differs from *N. edingerae*.

Comparison with *N. jagisteus*

The holotype cranium of *N. jagisteus* (SMNS 56618, described by RIEPPEL 2001) has a total length of18.3 cm whereas the Kupferzell skull is here proposed to have been approximately twice as large. The maximum width of the occipital region of *N. jagisteus* is with 8.7 cm much smaller than SMNS 80261 (18.8 cm). The parietal foramen in *N. jagisteus* is oval and has a length-to-width ratio of 2:1, similar to SMNS 80261. In *N. jagisteus*, a ridge runs along the lateral margins of the parietal skull table, beginning anterior to the parietal foramen, reaching back to the contact with the occipital skull surface. SMNS 80261 shows similar ridges flanking the parietal foramen, but it completely differs in the region posterior to the foramen. Here, *N. jagisteus* shows a prominent constriction of the parietal posterior to the parietal foramen, whereas the region is unconstricted and widens in SMNS 80261. *N. jagisteus*, has a PFPS-ratio of 0.18 and SMNS 80261 a ratio of 0.09. Due to the differences in size, the missing constriction posterior to the parietal foramen and the markedly different PFPS-ratio, *N. jagisteus* can also be excluded as potential candidate species for SMNS 80261.

Comparison with *N. cristatus*

For this comparison, the holotype skull of *N. cristatus* (GPIT/RE/09800, described by HINZ ET AL. 2019) is used. The maximum skull width of *N. cristatus* (16.2 cm) is almost similar to SMNS 80261 (18.8 cm). The distance between the posterior end of the condyle and the anterior margin of the parietal foramen is shorter in *N. cristatus* (6.75 cm) than in SMNS 80261 (11.5 cm). In SMNS 80261, the parietal foramen is oval with a length-to-width ratio of 2:1 whereas the foramen in *N. cristatus* is sub-rounded with a ratio of 1.22:1. In contrast to the wide and flat parietal skull table of SMNS 80261, a long, sharp sagittal crest is located anterior to the parietal foramen in *N. cristatus*. With a value of 0.08, the PFPS-ratio of *N. cristatus* is similar to that of 0.09 measured in the Kupferzell skull. In *N. cristatus*, the crest splits right in front of the parietal foramen, surrounds the parietal foramen, and continues in a lower and less pronounced form posteriorly. In contrast to *N. cristatus*, the parietal table in the Kupferzell skull is flat, wide, and shows no crest anterior or posterior to the parietal foramen.

Additionally, the region posterior to the parietal foramen is wider in SMNS 80261 than in *N. cristatus*. In both, *N. cristatus* and SMNS 80261, a small crest on the parietal and supraoccipital on the occipital skull table is exposed, but the occipital crest is remarkably sharper and less obtusely angled in *N. cristatus* (15 degrees) than in SMNS 80261 (40 degrees). Overall, *N. cristatus* is more gracile in appearance than SMNS 80261. Therefore, the Kupferzell skull is clearly not conspecific with *N. cristatus*.

Comparison with *N. mirabilis*

The holotype specimen of *N. mirabilis* is a partial postcranial skeleton (v. MEYER 1855), but the uncatalogued paratype, housed at the Urwelt-Museum in Bayreuth (BT) and described in the same publication, is used for the comparison. Furthermore, the *N. mirabilis* skulls catalogued as SMNS 56286 as well as the skulls BMNH R-42829 and SMF R-641 described in RIEPPEL & WILD (1996), are used for the comparison with SMNS 80261. The Kupferzell skull has a maximum width of 18.8 cm and lies well within the size spectrum of the studied *N. mirabilis* skulls that range from 13.6 cm in BMNH R-42829 to 21 cm in SMNS 56286. The length-to-width ratios of the oval parietal foramina in all *N. mirabilis* specimens range from 1.81:1 in SMF R-641 to SMNS 56286 and 2.08:1 in

the paratype. SMNS 80261 shows a ratio of 2:1, which is similar to *N. mirabilis*. The Kupferzell skull shows prominent lateral ridges flanking the parietal foramen, which are absent in all *N. mirabilis*. A wide intraspecific variation is found in the post-foraminal parietal skull table of *N. mirabilis*. SMF R-641 (PFPS 0.05) and SMNS 56286 (PFPS 0.07) show distinct constrictions and a relatively short post-foraminal skull table, whereas in BMNH R-42828 (PFPS 0.16), the region is broad and elongated. In the paratype, the parietal foramen is located close to the posterior end of the parietal skull table (PFPS 0.03). With a PFPS-ratio of 0.09, the part of the parietal skull table posterior to the parietal foramen of SMNS 80261 is longer than in most *N. mirabilis*, except for BMNH R-42829, which shows a remarkably small parietal foramen and an exceptionally long post-foraminal parietal skull table.

The striking difference between all observed *N. mirabilis* specimens and SMNS 80261 is the massive posterior portion of the zygomatic arch. All *N. mirabilis* have gracile posterior ends of the zygomatic arches, contrary to SMNS 80261, in which the arches are thick and bulky in their overall appearance. Furthermore, the preserved parts of the zygomatic arches bend inwards in SMNS 80261, but in the considered *N. mirabilis* skulls they are either straight (SMNS 56286 and SMF R-641) or bend outwards (BMNH R-42829 and the paratype). Therefore, the Kupferzell skull with its overall bulky appearance and the width and curvature of the posterior end of the zygomatic arches is notably different from all considered *N. mirabilis* specimens.

Comparison with *N. giganteus*

For the comparison with *N. giganteus*, the partially preserved skull SMNS 57047 described in RIEPPEL & WILD (1996) as well as the former holotypes of *N. chelydrops* (FRAAS, 1896) SMNS 7162, *Paranothosaurus amsleri* (PEYER, 1939) PIMUZ T 4829, and *N. baruthicus* (GEISSLER, 1895) SMF-R 475, now all synonymized with *N. giganteus*, are used. *N. giganteus* shows a wide range of maximum occipital skull widths, ranging from 56 cm in SMNS 57047to 25.6 cm in SMF R-475. With 18.8 cm, the Kupferzell skull lies below this this range. The shape of the parietal foramen also strongly varies from almost round with a ratio of 1:1.2 in SMNS 7162 to sub-rounded in SMNS 57047 (1:1.59), oval in SMF-R 475 (1:1.67), and almost triangular in PIMUZ T 4829 (1:3.8). The parietal foramen lies close to the posterior margin of the broad parietal skull table in SMNS 57047 (PFPS 0.009), at intermediate distances in SMF-R 475 (PFPS 0.06) and PIMUZ T 4829 (PFPS 0.015), whereas a longer parietal skull table can be found in SMNS 7162 (PFPS 0.23). As pointed out by RIEPPEL & WILD (1996), *N. giganteus* shows a strong intraspecific variation, which is also reflected in the wide range of PFPS-ratios. With a PFPS-ratio of 0.09, the Kupferzell skull lies within this this range. The parietal skull tables posterior to the parietal foramen are broad and unconstricted in SMNS 7162, SMF-R 475, and SMNS 57047, and widen posteriorly in PIMUZ T 4829 and SMNS 80261. A small crest on the parietal and supraoccipital is exposed on the occipital skull table of all *N. giganteus* skulls and the Kupferzell skull. The angulation of the occipital crest in *N. giganteus* varies from 25 degrees in SMNS 7162 to 40 degrees in PIMUZ T 4829, which is agrees with the 40-degree angle observed in SMNS 80261. Major similarities between the Kupferzell skull and *N. giganteus* can be found in the posterior part of the zygomatic arch. SMNS 80261 and all *N. giganteus* skulls show broad and inwardly curved zygomatic arches. This characteristic feature was not found among the other *Nothosaurus* species considered in this comparison. Based on the bulkiness and size of the Kupferzell skull in general and its massive zygomatic arches in particular, we assign SMNS 80261 to *Nothosaurus giganteus*.

DISCUSSION AND CONCLUSION

It is known that *Nothosaurus* crania develop heterogenerously and heterochronously and show a large degree of variability regarding even diagnostic features (RIEPPEL 2000; RIEPPEL & WILD 1996; VOETEN ET AL. 2018). This is particularly true for *Nothosaurus* species from which lots of cranial material is known, like *N. giganteus* and *N. mirabilis*. RIEPPEL & WILD (1996) synonymized seven species with *N. giganteus*, including *N. chelydrops* Fraas, 1896, the only referred skull material from the Lower Keuper.

So far, two large skulls (SMNS 7162 and SMNS 80205) and two mandibular fragments (SMNS 7214b and SMNS 10506), all from the Lower Keuper of Hoheneck, represent the only cranial material referable to *N. giganteus* following the definition of RIEPPEL & WILD (1996). They also mentioned several unique features of *N. chelydrops*, such as an unusual triangular outline of the skull, the shape of the anterior constriction of the upper temporal fenestra, and oblique orbits. The shape of the orbits might be a result of diagenetic distortion (RIEPPEL 2000). As stated by RIEPPEL & WILD (1996), the question concerning the validity of *N. chelydrops* as an own species instead of a junior synonym of *N. giganteus* has to await better material. The features of former *N. chelydrops* outlined above and described by RIEPPEL & WILD (1996) are not preserved in SMNS 80261. Major differences in the preserved parts of the Kupferzell skull and former *N. chelydrops* can be found in the PFPS-ratio (0.09 in SMNS 80261 and 0.23 in SMNS 7162) and in the angulation of the occipital crest (40° in SMNS 80261 and 25° in SMNS 7162). In difference to the straight parietal skull table posterior to the parietal foramen in former *N. chelydrops*, the post-foraminal parietal skull table widens in SMNS 80261. In these respects, SMNS 80261 resembles more closely the

Muschelkalk morphotype of *N. giganteus* as for example seen in SMF-R 475 and SMNS 51972 (both figured and described in RIEPPEL & WILD 1996). Therefore, SMNS 80261 is the first *N. giganteus* with Muschelkalk morphotype affinities from the Lower Keuper.

The sauropterygian fauna of the more terrestrial Lettenkeuper is remarkably diverse and clearly distinct from the fully marine Upper Muschelkalk fauna. Whereas four species of nothosaurs are known from the Lettenkeuper (N. *mirabilis*, *N. edingerae*, *N. giganteus*, *N. cristatus*), there are only three from the Upper Muschelkalk (*N. jagisteus*, *N. mirabilis*, *N. giganteus*). Of these, only *N. mirabilis* and *N. giganteus* occur in both lithostratigraphic units. *N. jagisteus* is restricted to the Upper Muschelkalk and *N. cristatus* and *N. edingerae* have only been found in Lower Keuper sediments. Due to the fact that three of the known Lower Keuper nothosaurs have large skull sizes ranging from 38.3 cm in GPIT/RE/09800 (*N. cristatus*) to 52 cm in SMNS 7162 (former *N. chelydrops*), it can be assumed that the Lower Keuper provided suitable habitats for large predatory marine reptiles. This is interesting because so far the Lettenkeuper is described as a heterogenic landscape composed of swampy lowlands, small and large lakes, and brackish lagoons (SCHOCH 2014). We thus conclude, from the data provided herein, that the marine transgressional events in the Lower Keuper, especially in the layer of the Untere Graue Mergel, were more extensive than judged by the lithological data alone.

Further discoveries will certainly help to corroborate these findings and quantify the marine influence on the Lower Keuper deposits in southern Germany. The results presented herein highlight the importance of the Lettenkeuper in general and the Kupferzell fossil site in particular, to provide further novel and significant insights into the paleontology and environmental conditions of the early Late Triassic of the Germanic Basin.

ACKNOWLEDGEMENTS

We would like to thank Erin Maxwell and Rainer Schoch from the SMNS for access to the collection. The two reviewers, Dennis Voeten, Uppsala, and Rainer Schoch, SMNS, are thanked for their helpful comments and suggestions that improved our manuscript significantly. We express our gratitude to Günter Schweigert from the SMNS, for handling the manuscript as editor. Dieter Seegis, SMNS, is thanked for inspiring discussions about Kupferzell. Thanks also go to Hans Hagdorn, Ingelfingen, for access to his museum and fruitful discussions about the find locality.

REFERENCES

BRUNNER, H. (1977): Zur Stratigraphie und Sedimentpetrographie des Unteren Keupers (Lettenkeuper, Trias) im nördlichen Baden-Württemberg. – Jahresberichte und Mitteilungen des Oberrheinischen Geologischen Vereins, 169-193.

EDINGER, T. (1922): Über *Nothosaurus*. III. Ein Schädelfund im Keuper. – Senckenbergiana, 4: 37-42.

FRAAS, E. (1896): Die schwäbischen Trias-Saurier nach dem Material der Kgl. Naturalien-Sammlung in Stuttgart zusammengestellt. 18 pp; (E. Schweizerbart'sche Verlagshandlung).

FRAAS, E. (1913): Neue Labyrinthodonten aus der schwäbischen Trias. – Palaeontographica (1846-1933), 275-294.

GEISSLER, G. (1895): Ueber neue Saurier-Funde aus dem Muschelkalk von Bayreuth. – Zeitschrift der deutschen geologischen Gesellschaft, 331-355.

GOWER, D. J. (1999): The cranial and mandibular osteology of a new rauisuchian archosaur from the Middle Triassic of southern Germany. – Stuttgarter Beiträge zur Naturkunde B, 280: 1-49.

GOWER, D. J. (2002): Braincase evolution in suchian archosaurs (Reptilia: Diapsida): evidence from the rauisuchian *Batrachotomus kupferzellensis*. – Zoological Journal of the Linnean Society, 136: 49-76.

HAGDORN, H. (1980): Saurierreste aus dem Lettenkeuper im Landkreis Schwäbisch Hall (I). – Der Haalquell, 32: 21-23.

HAGDORN, H., HEUNISCH, C. AND SCHOCH, R. (2015): Biostratigraphie und Alter des Lettenkeupers. – Der Lettenkeuper—ein Fenster in die Zeit vor den Dinosauriern, 41-47.

HAGDORN, H., KELBER, K.-P. AND SCHOCH, R. (2015): 15. Fossile Lebensgemeinschaften im Lettenkeuper. – Paleodiversity, 359-385.

HAGDORN, H., SCHOCH, R., SEEGIS, D. AND WERNEBURG, R. (2015): 14. Wirbeltierlagerstätten im Lettenkeuper. – Palaeodiversity, 325-358.

HINZ, J. K., MATZKE, A. T. AND PFRETZSCHNER, H.-U. (2019): A new nothosaur (Sauropterygia) from the Ladinian of Vellberg-Eschenau, southern Germany. – Journal of Vertebrate Paleontology, e1585364.

KOKEN, E. (1893): Beiträge zur Kenntnis der Gattung *Nothosaurus*. – Zeitschrift der Deutschen Geologischen Gesellschaft, 45: 337-377.

MUNDLOS, R. AND WEGELE, J. (1978): Die Kupferzeller Sauriergrabung 14. März bis 3. Juni 1977. Ein Report. – Aufschluß, 29: 13-19.

MÜNSTER, G. Z. (1834): Vorläufige Nachricht über einige neue Reptilien im Muschelkalke von Baiern. – Neues Jahrbuch für die Mineralogie, Geognosie, Geologie und Petrefactenkunde, 1834: 521-527.

PEYER, B. (1939): Die Triasfauna der Tessiner Kalkalpen XIV *Paranothosaurus amsleri*. – Abhandlungen der Schweizerischen Palaeontologischen Gesellschaft Serie Zoologie, 65: 1-87.

RIEPPEL, O. (2000): Handbuch Der Paläoherpetologie - Sauropterygia I: Placodontia, Pachypleurosauria, Nothosauroidea, Pistosauroidea. pp; München (Pfeil Verlag).

RIEPPEL, O. (2001): A new species of *Nothosaurus* (Reptilia: Sauropterygia) from the upper Muschelkalk (lower Ladinian) of southwestern Germany. – Palaeontographica Abteilung A, 263: 137-161.

RIEPPEL, O. AND WILD, R. (1994): *Nothosaurus edingerae* Schultze, 1970: Diagnosis of the Species and Comments on its Stratigraphical Occurrence. – Stuttgarter Beiträge für Naturkunde Serie B, 204: 1-13.

RIEPPEL, O. AND WILD, R. (1996): A Revision of the Genus *Nothosaurus* (Reptilia: Sauropterygia) from the Germanic Triassic with Comments on the Status of *Conchiosaurus clavatus*. – Fieldiana Geology, 34: 1-82.

SCHOCH, R. (2006): Kupferzell: Saurier aus den Keupersümpfen. – Stuttgarter Beiträge zur Naturkunde Serie C, 1-79.

SCHOCH, R. R. (1997): A new capitosaur amphibian from the Upper Lettenkeuper (Triassic: Ladinian) of Kupferzell (southern Germany). – Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen, 239-272.

SCHOCH, R. R. (1999): Comparative Osteology of *Mastodonsaurus giganteus* (Jaeger, 1828) from the Middle Triassic (Lettenkeuper: Longobardian) of Germany (Baden-Württemberg, Bayern, Thüringen); with 4 Plates. – Stuttgarter Beiträge zur Naturkunde B, 278: 1-175.

SCHOCH, R. R. (2014): Amphibian evolution: the life of early land vertebrates. Chichester (John Wiley & Sons).

SCHULTZE, H. (1970): Über *Nothosaurus*. Neubeschreibung eines Schädels aus dem Keuper. – Senckenbergiana lethaea, 51: 211-237.

URLICHS, M. (1982): Zur Stratigraphie und Fossilführung des Lettenkeupers (Ob. Trias) bei Schwäbisch Hall (Baden-Württemberg). – Jahresberichte und Mitteilungen des Oberrheinischen Geologischen Vereins, 213-224.

VOETEN, D. F., REICH, T., ARAUJO, R. AND SCHEYER, T. M. (2018): Synchrotron microtomography of a *Nothosaurus marchicus* skull informs on nothosaurian physiology and neurosensory adaptations in early Sauropterygia. – PloS one, 13:

VON JÄGER, G. F. (1828): Über die fossile reptilien: welche in Würtemberg aufgefunden worden sind. 48 pp; (JB Metzler).

VON MEYER, H. (1855): Zur Fauna der Vorwelt: Die Saurier des Muschelkalkes mit Rücksicht auf die Saurier aus buntem Sandstein und Keuper. 167 pp; Frankfurt am Main (Heinrich Keller).

WILD, R. (1987): Massengrab für Saurier. – Kosmos, 74: 790-797.